

A revision of *Acrenhydrosoma* (Copepoda, Harpacticoida) with the establishment of *Dyacrenhydrosoma* gen. nov. and *Paracrenhydrosoma* gen. nov. and descriptions of two new species.

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Abstract: *Acrenhydrosoma perplexa* is redescribed from cotype and other material. It possesses only two setae on the antennal exopod, a mandibular palp with three setae, and a maxillulary coxal endite partially fused to a basis which bears only three setae. The P1 endopod-2 has two armature elements and the P5 baseopod, in both sexes, has an outer seta borne on a submarginal peduncle. The male P5 exopod bears only two setae. The posterior margin of the preanal somite has a dorsal, dentate, pseudoperculum overlaying the operculum which is situated near the anterior margin of the anal somite.

A new species, with a urosome structure similar to *Acrenhydrosoma* is described from mangrove forests in S.E. Asia and is placed in *Dyacrenhydrosoma* gen. nov. as *D. breviseta* sp. nov.. It can be distinguished from *Acrenhydrosoma* by the absence of a seta on the abexopodal margin of the antennal allobasis, a maxillulary coxal endite (represented by 1 seta) completely fused to the basis which bears only two setae, reduced armature of the maxilla, short terminal setae without penicillate tips on P1 exopod-3, only two setae on P2-P4 endopod-2, a female P5 baseopod with only one inner spine and an exopod with only 2 setae.

Material from northern Norway, attributed to *Acrenhydrosoma perplexa* by T. Scott (1903) is described and placed in *Paracrenhydrosoma* gen. nov. as *P. normani* sp. nov. It is very similar to *Acrenhydrosoma maccalli* but can be distinguished from it by features on the P5. *A. maccalli* and *A. karlingi* are moved to *Paracrenhydrosoma* which can be distinguished from *Acrenhydrosoma* by the absence of a pseudoperculum on the preanal somite, and also by an operculum situated in the posterior half of the anal somite, a broader, emarginate rostrum, a mandibular palp with four setae, a maxillulary coxal endite (bearing two setae) completely separate from a basis bearing six setae, a P1 endopod-2 with three setae and a female P5 exopod with two setae.

Résumé: Révision de *Acrenhydrosoma* (Copepoda, Harpacticoida) avec établissement de *Dyacrenhydrosoma* gen. nov. et *Paracrenhydrosoma* gen. nov. et description de deux nouvelles espèces.

Acrenhydrosoma perplexa est redécrite à partir d'un cotype et d'autres spécimens. L'espèce possède seulement deux soies sur l'exopodite antennaire, un palpe mandibulaire avec trois soies, et un endite coxal maxillulaire partiellement fusionné au basis, qui porte seulement trois soies. L'armature de l'endopodite-2 des P1 est constituée de deux éléments, et le baséopodite de P5 présente, chez les deux sexes, une soie externe insérée sur un pédoncule. L'exopodite P5 mâle porte seulement deux soies. Le bord postérieur du somite préanal présente un pseudopercule dorsal dentelé au-dessus de l'opercule qui est situé près du bord antérieur du somite anal.

Une nouvelle espèce, avec une structure de l'urosome semblable à celle d'*Acrenhydrosoma*, est décrite des mangroves de l'Asie du sud-est et est classée dans le genre *Dyacrenhydrosoma* gen. nov., sous le nom de *D. breviseta* sp. nov.. Elle peut être distinguée de *Acrenhydrosoma* par l'absence de soie sur le bord abexopodal de l'allobasis antennaire, un endite coxal maxillulaire (représenté par une soie) complètement fusionné au basis, qui porte seulement deux soies, une armature réduite de la maxille, de courtes soies distales sans terminaisons barbelées sur l'exopodite-3 des P1, seulement deux soies sur l'endopodite-2 des P2-P4, un baséoendopodite P5 femelle avec seulement une épine interne et un exopodite avec seulement deux soies.

Le matériel du nord de la Norvège, attribué à *A. perplexa* par T. Scott (1903), est décrit et placé dans le genre *Paracrenhydrosoma* gen. nov. sous le nom de *P. normani* sp. nov.. Il est très proche de *Acrenhydrosoma maccalli* mais peut s'en distinguer par des caractères des P5. *A. maccalli* et *A. karlingi* sont également placées dans *Paracrenhydrosoma*, qui peut être distingué de *Acrenhydrosoma* par l'absence d'un pseudopercule sur le somite préanal ainsi que par un opercule situé sur la moitié postérieure du somite anal, un rostre plus large à extrémité aplatie, un palpe mandibulaire avec quatre soies, un endite coxal maxillulaire portant deux soies et complètement séparé du basis qui porte six soies, un endopodite-2 des P1 avec trois soies, et un exopodite P5 femelle avec deux soies.

Keywords: Harpacticoida, Cletodidae, *Acrenhydrosoma*, *Dyacrenhydrosoma* gen. nov., *Paracrenhydrosoma* gen. nov., mangrove forest, Malaysia.

Introduction

The genus *Acrenhydrosoma* Lang, was established by Lang (1944) to accommodate *Cletodes perplexa* T. Scott, 1899. Lang (1936) had previously transferred this species from *Cletodes* to *Enhydrosoma* Boeck, as *E. perplexum* (T. Scott), on the basis of the structure of the antennal exopod, the size of the maxilla and maxilliped, the setation of the P3 and P4 exp-3 and the form of the setae on the P5 baseoendopod. Lang (1944) removed the species from *Enhydrosoma* to a new genus primarily because of the peculiar structure of the P5 in both sexes and the presence of three setae on the antennal exopod reported by both Scott (1899) and Sars (1920). However, close inspection of the descriptions by these latter two authors reveals that there are sufficient discrepancies between them, and possible errors in both, to cast doubt on the exact characteristics of this species and the generic diagnosis of Lang (1944). Since then, two further species from the west coast of America have been added to the genus by Lang (1965) and Schizas & Shirley (1994), as *A. karlingi* Lang, 1965 and *A. maccalli* Schizas & Shirley, 1994.

During a recent study of the diversity of benthic copepods in mangrove forests of tidal estuaries in Malaysia and Thailand, (Gee & Somerfield, 1997; Somerfield et al. 1998) three species belonging to the family Cletodidae were found at all the sample sites. The cletodid fauna was dominated by one species of *Enhydrosoma*, tentatively identified as *E. longifurcatum* Sars, 1904. A new species described by Gee (1998) as *Limnocletodes mucronatus* Gee, 1998 was common and a new *Acrenhydrosoma*-like species rare at all the sample sites. In this paper, I describe the new species from Malaysia, and redescribe *A. perplexa* from cotype, and other material deposited in the Natural History

Museum, London. It was found that some of this material did not belong to *A. perplexa* but is very similar to specimens of *A. maccalli*. I conclude that the species from Malaysia and the west coast of America should be placed in new genera.

Methods

Habitat. The sample sites, at which the new species was found, are described in detail in Gee & Somerfield (1997). Briefly, most of the material was obtained from the Merbok mangrove forest, surrounding the Sungai Merbok estuary in Kedah Province, north-west Peninsular Malaysia (5° 40' N, 100° 60' E). The average salinity was around 20-25‰, and samples of sediment which was over 80% silt/clay (taken by scraping the surface few mm) and decaying leaves (picked individually) were taken primarily under *Rhizophora apiculata* Bl. trees between high water neap and high water spring tides. A few leaf and mud samples were also collected by Dr. Chittima Aryuthaka from under *R. apiculata* trees in the middle and upper reaches of the Klong Nao, in the Ranong mangrove forest of Muang District, Thailand, 650 km southwest of Bangkok at 9° 50' N, 98° 35' E.

Systematic procedures. Animals were fixed in 10%, and preserved in 4%, formalin. Before dissection the habitus was drawn and body length measurements made from whole specimens temporarily mounted in lactophenol. Specimens were dissected in lactophenol, the parts individually mounted in lactophenol under coverslips subsequently sealed with nail varnish. All drawings were prepared using a camera lucida on a Nikon Optiphot 20 differential interference contrast microscope. The terminology of the body and appendages morphology

follows that of Huys & Boxshall (1991).

Abbreviations used in the text and figures are P1-P6 for thoracopods 1-6; exp(enp)-1(-2-3) to denote the proximal (middle, distal) segment of a ramus; and ae for aesthetasc. Body length was measured from the base of the rostrum to the median posterior border of the anal somite.

All type material has been deposited in the Natural History Museum, London.

On the figures, all the scales are in millimeters.

Systematics

Family CLETODIDAE T. Scott, 1904 (sensu Por, 1986)

Genus *Acrenhydrosoma* Lang, 1944

Diagnosis.

Cletodidae. Body semi-cylindrical, tapering posteriorly, with pronounced segmentation and sensillum-bearing socles on posterior border of all somites except preanal. Genital double somite of female with ventral sub-cuticular rib. Mid-dorsal posterior border of preanal somite with strongly developed, dentate pseudopericulum overlaying semi-circular anal operculum situated near anterior margin of anal somite. Caudal rami cylindrical, nine times longer than maximum width; seta I, II & VII arising in proximal third of ramus, seta III at mid-ramus. Rostrum fused to cephalothorax, narrowly rounded anteriorly. Antennule 5-segmented in female with aesthetasc on third and distal segments; 7-segmented, sub-chirocer in male with aesthetascs on distinctly swollen fifth segment and on distal segment; both sexes with well developed pinnate setae on most segments and a tube seta issuing from an integumental invagination on segment-2. Antenna with a plumose seta on abexopodal margin of allobasis; exopod 1-segmented with two setae; endopod armed with two large pinnate spines and a small seta on lateral margin and three spine and two geniculate setae on distal margin. Mandibular coxa slender, palp 1-segmented with three setae. Maxillulary coxal endite bearing one seta and partially fused to a basis without rami and bearing three setae. Maxilla with two syncoxal endites each with three armature elements; allobasal endite with large spine and two setae; endopod represented by two setae not fused at base. Maxilliped sub-chelate; syncoxa with one seta, unarmed basis oval, endopod represented by a flexible claw and one accessory seta. Swimming legs with 3-segmented exopods and 2-segmented endopods; setae on distal margin of P1 exp-3 and enp-2 with penicillate tips; setal formula as follows:

	Exopod	Endopod
P1	0:0:022	0:011
P2	0:0:022	0:020
P3	0:0:122	0:021
P4	0:0:122	0:021

Male P3 enp-2 with outer spine fused to segment. P5 with endopodal lobe of baseoendopod extended into long, dentate, mucroniform process with two spines on inner margin in female and one in male. Peduncle, bearing baseoendopodal outer seta, articulates with anterior face of baseoendopod medial to exopod; baseoendopod with two tube pores, one on small peduncle on anterior face and one at site of proximal inner spine. Exopod more or less fused to baseoendopod, with three armature elements in female and two in male. Female genital field with common genital slit connecting gonopores covered by vestigial P6s each bearing two setae; copulatory pore large opening at ventral sub-cuticular rib. Male P6 barely distinguishable from somite but asymmetrical without armature elements.

Type species. *A. perplexa* (T. Scott, 1899) designated by Lang (1944) by monotypy.

Acrenhydrosoma perplexa (T. Scott, 1899)

(Figs 1-4)

Material examined. 2 females (1 dissected onto 3 slides) and 2 males (antennules and antennae of one dissected onto 1 slide) labelled co-types, collected by T. Scott from Moray Firth, Scotland, 1898 - NHM Reg. No. 1956.9.25.16: From the Norman Collection at NHM 1 female and 2 males labelled co-types from Moray Firth, 1898; 1 male labelled Plymouth, Devon, 1903; 1 male labelled Salcombe, Devon, 1876 - NHM Reg. No. 1911.11.8.45103-09: 1 female from Scilly Isles U.K. collected by London sub-aqua Club, identified by J.B.J. Wells, NHM Reg. No. 1967.10.31.79.

Redescription of female.

Body (Fig.1) length 0.544 - 0.563 mm (mean = 0.554 mm, n = 3), semi-cylindrical, tapering posteriorly from posterior border of cephalothorax, without clear distinction between prosome and urosome; body surface with minute tubercles. Cephalothorax rounded anteriorly, with pattern of subcuticular ribs, sensilla and tube pores as in Fig. 1A-B; posterior border smooth with six small sensillum-bearing socles. Free prosomites and urosomite-1 (P5-bearing) with subcuticular ribs in anterior dorsal region and five tube pores distributed as in Fig. 1; posterior border smooth with eight sensillum-bearing socles (four on urosomite-1). Urosomites 2-4 with two pairs of tube-pores; posterior border smooth dorsally and laterally but with row of small spinules ventrally, with six sensillum-bearing socles. Urosomites 2-3 fused to form genital double somite, line of fusion indicated by presence of socles dorsally and laterally and by ventral subcuticular rib. Preanal somite (Fig. 2A) without sensilla but with two pairs of tube pores; mid-dorsal posterior border with strongly dentate pseudopericulum overlaying anal operculum situated near anterior margin of anal somite. Operculum semi-circular, with fine setules and a pair of long sensillum-bearing socles. Caudal rami (Fig. 1C) cylindrical, elongate, nine times longer than maximum

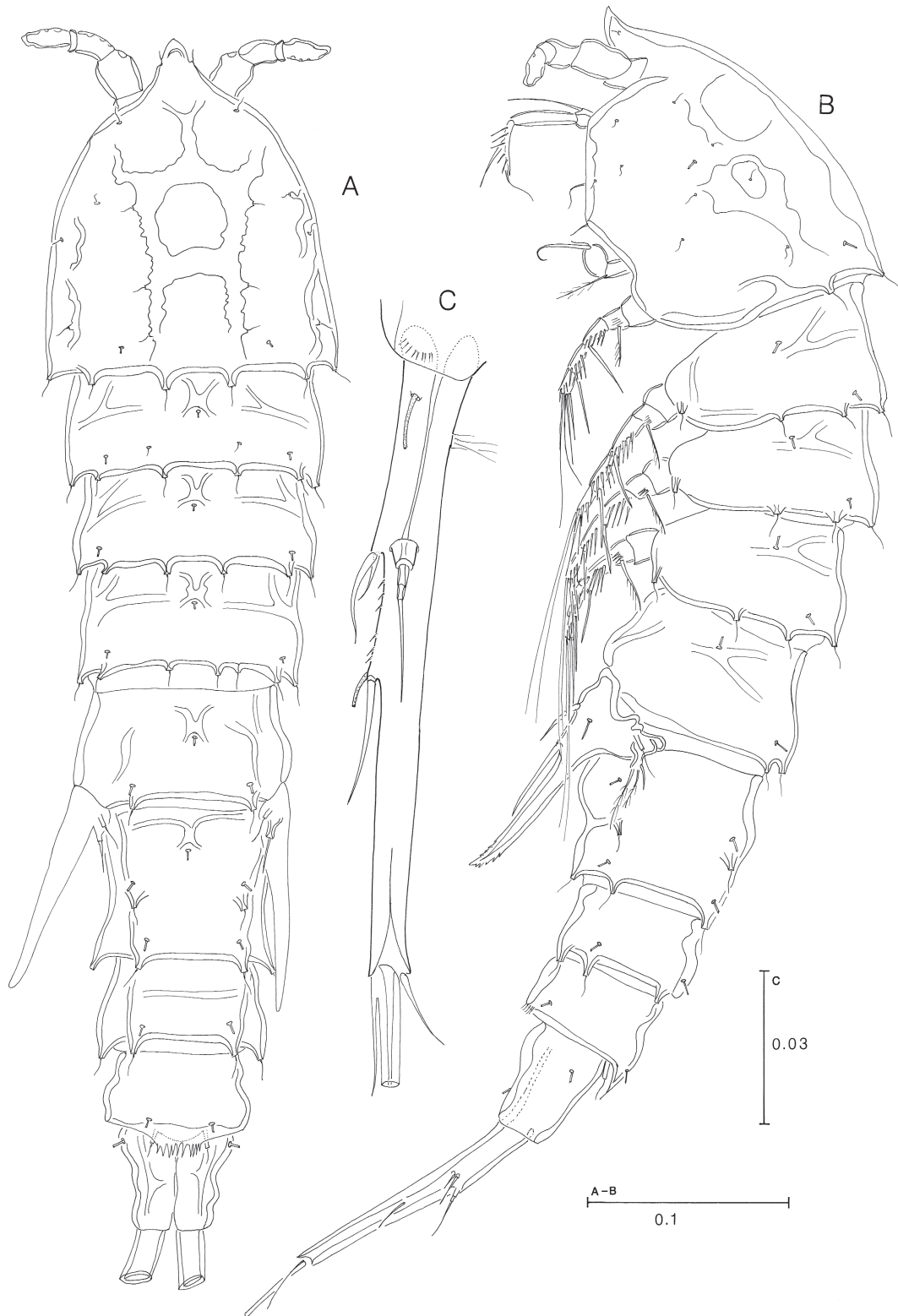


Figure 1. *Acrenhydrosoma perplexa*. Female: (A) habitus, dorsal view, (B) habitus, lateral view, (C) caudal ramus, dorsal view. Scales in mm.

Figure 1. *Acrenhydrosoma perplexa*. Femelle : (A) habitus, vue dorsale, (B) habitus, vue latérale, (C) rame caudale, vue dorsale. Echelles en mm.

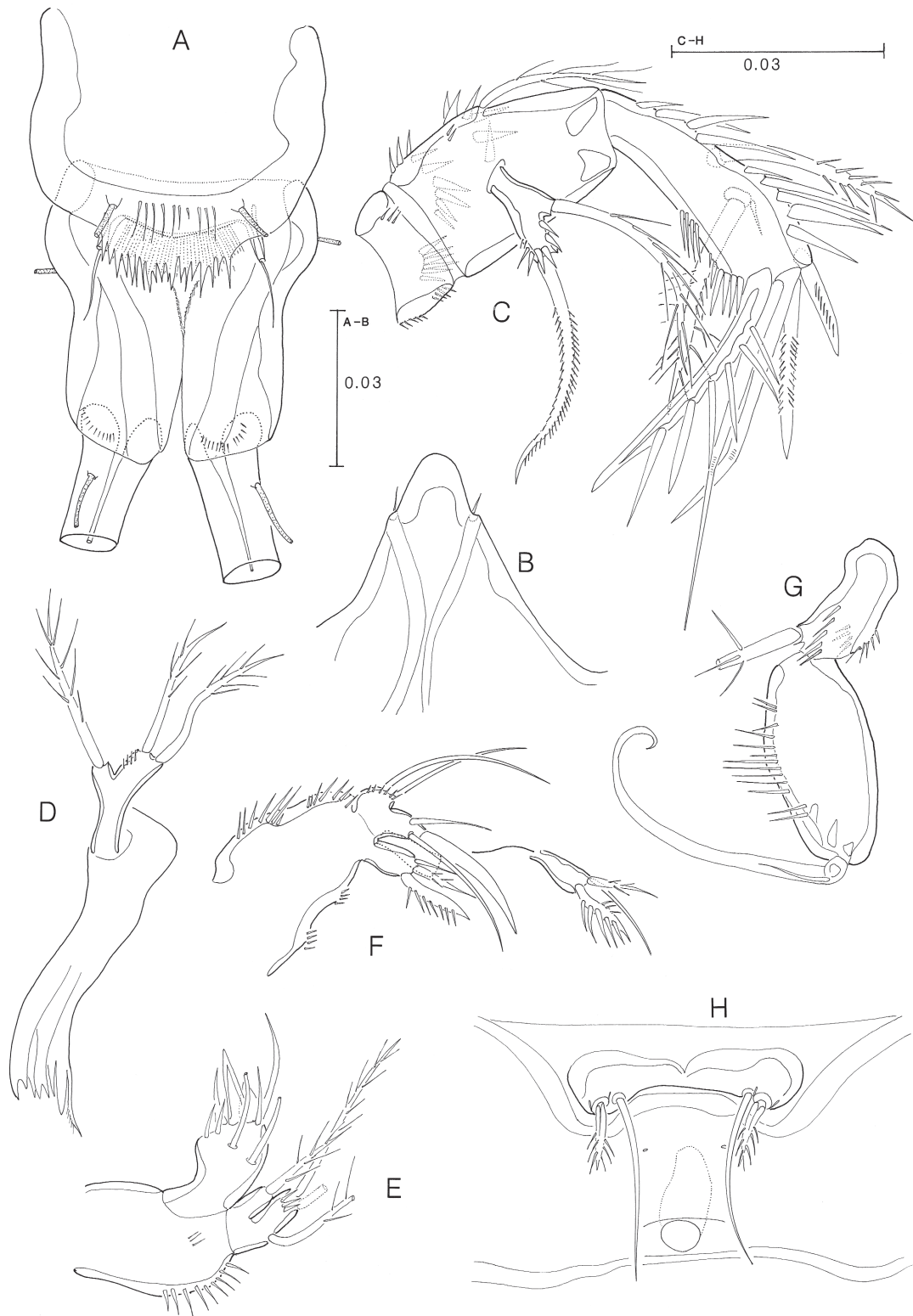


Figure 2. *Acrenhydrosoma perplexa*. Female: (A) preanal and anal somite, dorsal view, (B) rostrum, (C) antenna, (D) mandible, (E) maxillule, (F) maxilla, (G) maxilliped, (H) genital field. Scales in mm.

Figure 2. *Acrenhydrosoma perplexa*. Femelle : (A) somite anal et préanal, vue dorsale, (B) rostre, (C) antenne, (D) mandibule, (E) maxillule, (F) maxille, (G) maxillipède, (H) région génitale. Echelles en mm.



Figure 3. *Acrenhydrosoma perplexa*. Female: (A) P1, (B) P3. Male: (C) P3 endopod. Scale in mm.

Figure 3. *Acrenhydrosoma perplexa*. Femelle : (A) P1, (B) P3. Mâle : (C) endopodite de P3. Echelle en mm.

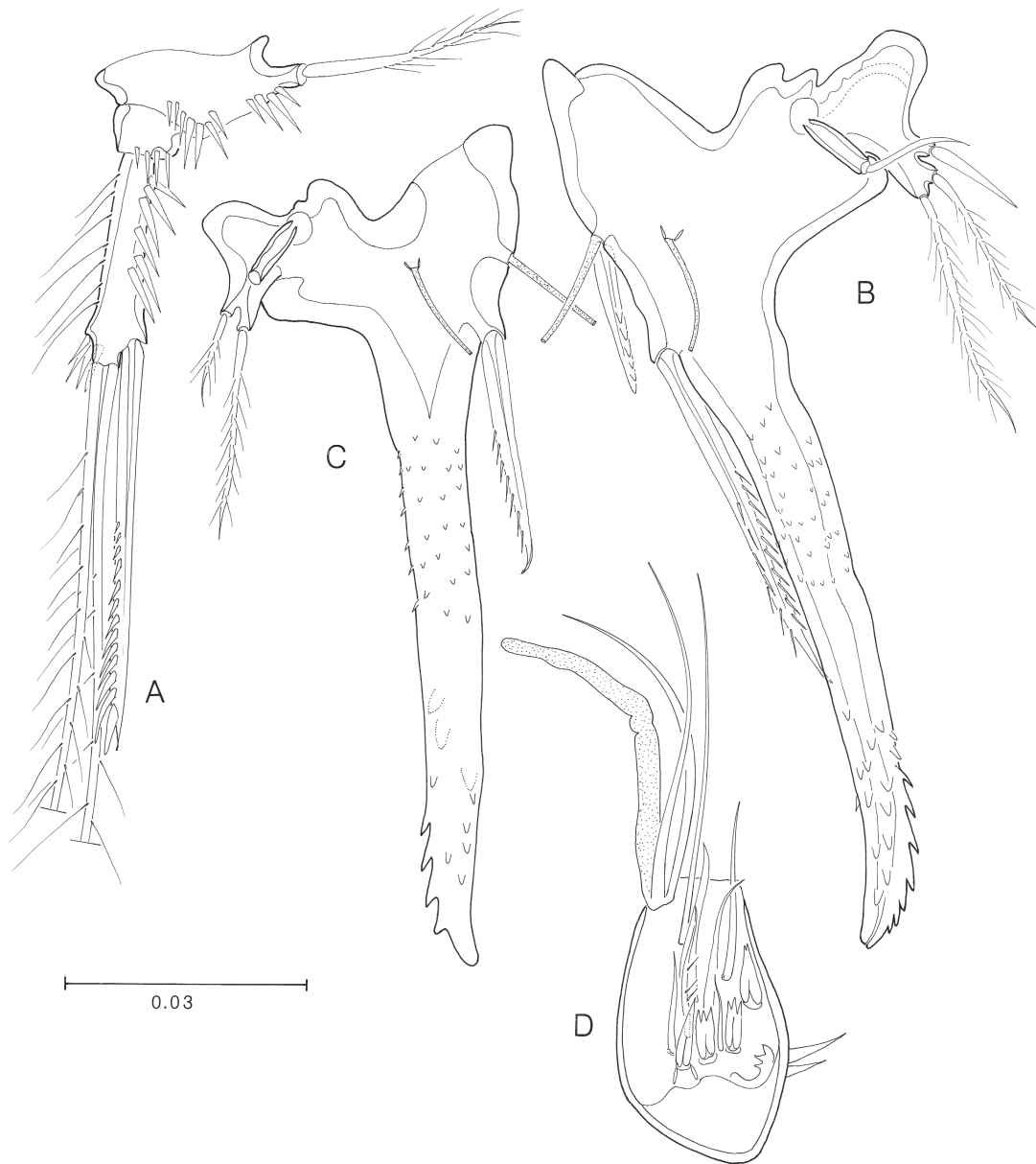


Figure 4. *Acrenhydrosoma perplexa*. Female: (A) P4 endopod, (B) P5. Male: (C) P5, (D) antennular segment 5, anterior view. Scale in mm.

Figure 4. *Acrenhydrosoma perplexa*. Femelle : (A) endopodite de P4, (B) P5. Mâle : (C) P5, (D) article antennulaire 5, vue antérieure. Echelle en mm.

width, tube pores on proximal dorsal surface and associated with seta III, row of minute spinules on ventral distal margin; lateral setae I and II and dorsal seta VII arising at 32% of ramus length, lateral seta III at 53% of ramus length; distal margin bearing slender seta IV fused at base to minutely pinnate, well-developed seta V, seta VI small.

Rostrum (Fig. 2B) well developed, fused to cephalothorax, recurved (Fig. 1B), narrowly rounded anteriorly, with a pair of lateral sensilla.

Antennule short, stout, 5-segmented (as in Fig. 6A) with one to four strongly pinnate setae on all segments except segment 4; segment 1 with three rows of spinules; segment 2 with a tube seta set in integumental invagination, segment 3 with aesthetasc fused at base to one seta, segment 4 small, segment 5 with distal trithek of one large pinnate seta, a smooth seta and a small aesthetasc. Setal formula as follows 1-[1], 2-[7], 3-[7 + ae)], 4-[1], 5-[11 + ae)].

Antenna (Fig. 2C). Coxa well-developed, with four short rows of spinules. Allobasis, with partial suture line on dorsal surface in region of exopod, with two groups of spinules and one plumose seta on abexopodal margin. Exopod 1-segmented with row of spinules on distal margin; bearing two large setae, distal seta with small closely set pinnules, lateral seta with fewer long pinnules. Free endopod segment with two rows of strong spinules on outer margin, and smaller spinule rows on distal and inner distal margin; lateral armature of two large pinnate spines and a small naked seta; distal armature of two minutely pinnate spines, one large spinulose spine and two geniculate setae.

Mandible (Fig. 2D). Coxa slender, elongate; gnathobase with fine, pointed, bicuspid and tricuspid teeth and small pinnate seta at inner distal corner. Palp 1-segmented with small row of spinules and three pinnate setae.

Maxillule (Fig. 2E). Praecoxa with small row of surface spinules and a larger row of marginal spinules; arthrite of praecoxa with two anterior surface tube setae and, on distal margin, three sharply pointed spines and four setae. Coxal endite distinct but partially fused to basis, with one pinnate seta. Basis and rami completely fused into 1-segmented palp with a row of spinules near distal margin; armed with two setae on distal margin and one on lateral margin.

Maxilla (Fig. 2F). Syncoxa with four rows of spinules and two endites, each bearing a pectinate spine, a pinnate seta and a naked seta. Allobasal endite with one large spine and two naked setae; endopod represented by two setae not fused at base.

Maxilliped (Fig. 2G) well-developed, subchelate. Syncoxa with two rows of spinules and one large pinnate seta. Basis oval, with row of spinules on palmar margin. Endopod represented by a flexible claw with one accessory seta.

P1 (Fig. 3A). Praecoxa narrow with row of small spinules. Coxa with three rows of setules on anterior surface. Basis with row of spinules at base of inner and outer pinnate setae, on distal margin at base of endopod and medially on anterior face. Exopod 3-segmented, each segment with row of strong spinules on outer and distal margin and row of long setules on inner margin; exp-3 with two outer spines and two equally long, bipinnate, terminal setae with penicillate tips. Endopod 2-segmented, enp-1 small with spinule row on outer and distal margin; enp-2 three times longer than enp-1; enp-2 with row of spinules on outer and distal margins and row of setules on inner margin; armed with one distal pinnate seta with penicillate tip and an outer pinnate spine.

P2-P4 (Figs 3B, 4A). Protopods as for P1 except basis without inner seta and inner row of spinules much smaller. Exopods 3-segmented, ornamented as for P1 except for prominent hyaline frills present at segment articulations; P3 and P4 exp-3 with distal inner seta. Endopods 2-segmented;

enp-1 small; enp-2 ornamented as for P1; P3-P4 enp-2 with a large (very large on P4) pinnate outer spine. Setal formula of swimming legs as in generic diagnosis.

P5 (Fig. 4B). Basal portion of baseoendopod tapering towards outer margin; cylindrical peduncle, bearing basal outer seta, articulating on anterior face (not on outer margin); tube pores medially on anterior surface and at base of proximal inner spine; endopodal lobe extended into very long, cylindrical, mucroniform process with minutely bifid tip; ornamented with large denticles distally and small denticles medially; inner margin armed with two strong, bipinnate spines. Exopod small, at least partially fused to baseoendopod outside of basal peduncle, bearing three elements, a naked spine and two pinnate setae, outer seta slightly shorter than inner seta.

Genital field (Fig. 2H). Vestigial P6s, each bearing a pinnate spine and a long naked seta, forming small flaps over gonopores which open into a common genital slit. Copulatory pore large, opening at ventral subcuticular rib marking line of fusion of urosomites 2-3, with simple copulatory duct leading to oval seminal receptacle. Two small pores present between gonopores and copulatory pore but no tubes discerned.

Redescription of male.

As in female except for urosome, antennules, P3 endopod and P5.

Body slightly smaller than female, 0.527-0.539 mm (mean 0.533 mm, $n = 3$). Genital somite separate; vestigial P6 forming a small asymmetrical plate fused to somite and without armature.

Antennule 7-segmented, short, stout, sub-chirocer with principal articulation between segments 5 and 6. Segmentation and armature (except for segment 5) as shown in Fig. 6C-D. Segment 1 with three rows of spinules and a pinnate seta. Segment 2 almost square with four pinnate setae and a tube seta. Segment 3 small, triangular, without pinnate setae. Segment 4 extremely narrow. Segment 5 markedly swollen with row of spinules on dorsal surface, anterior margin with three-/four? terminally dentate spines and one pinnate seta, other setae naked, also bearing a large aesthetasc fused at base to one seta (Fig. 4D). Segment 6 small rectangular and segment 7 hook-shaped with distal trithek of two naked setae and an aesthetasc. Setal formula as follows 1-[1], 2-[9], 3-[8], 4-[2], 5-[13/14 + ae], 6-[2], 7-[9 + ae].

P3 endopod (Fig. 3C). 2-segmented, as in female except that outer spine fused to segment, without ornamentation but recurved at tip.

P5 (Fig. 4C). As in female except that baseoendopod with only one spine on inner margin (proximal spine absent) and exopod with only two armature elements (outer naked spine absent).

Remarks

Descriptions of *Acrenhydrosoma perplexa* have been given previously by Scott (1899), when he first discovered the species in the Moray Firth (Scotland) and Sars (1920) based on material from Hvalør outside Oslofjord. Although it is almost certain that they were both describing the same species there are discrepancies between the descriptions which have caused some confusion as to the exact characteristics of this species. Sars (1920) shows a plumose seta on the abexopodal margin of the antennal allobasis which Scott (1899) does not mention. This was obviously an oversight on the part of the latter author as all the specimens I have examined from the type locality possess this seta. On the other hand both Scott (1899) (Plate XI, fig.14) and Sars (1920) (Plate LIII) show the antennal exopod with three armature elements, one terminal and one lateral large pinnate seta and a small naked element proximal to the lateral seta. Scott described this as “a small hair” but Sars describes it as a seta. However, in all the specimens I have examined from the type locality and south-west England I cannot find any evidence for a naked element proximal to the lateral seta and the only ornamentation on the exopod segment is a row of small spinules near the distal margin. Within the Cletodidae, three elements are found on the antennal exopod of the adult only in *Triathrix* Gee & Burgess, the closely related *Sphingothrix* Fiers, and in *Limnocletodes* Borutsky. In the former two genera a small naked element is present closely adjacent to the pinnate seta on the distal margin of the exopod and therefore, would not be homologous to the naked seta illustrated by Scott and Sars for *A. perplexa*. I can only conclude, therefore, that these authors were mistaken, or that in some specimens there is one (or more) setules sometimes present as additional ornamentation near the base of the antennal exopod.

Scott (1899) (Plate XI. Fig. 18) figures the P4 enp-2 with four armature elements (i.e. he clearly shows an inner seta on this limb) whereas Sars (1920) illustrates it with only three elements (Plate LIII) as is shown here in Fig. 4A. In none of the specimens I have examined is there an inner seta on P4 enp-2.

In addition, there are mistakes in the published descriptions of the P5 of both sexes of *A. perplexa*. Both Scott (1899) and Sars (1920) describe and/or figure the P5 as having no peduncle bearing an outer baseoendopodal seta but such a peduncle and seta is present in all the specimens I have examined. However, it is not found on the outer margin but articulates with the anterior face of the baseoendopod, medial to the exopod. In addition both Scott and Sars state that the male P5 is the same as in the female and Scott (1899, Plate 11 fig. 20) illustrates the male P5 with three elements on the exopod. However, in all the males that I have examined the P5 exopod only bears two setae, the

naked outer spine found in the female is absent in the male. Similarly, all the male specimens have only one spine on the inner margin of the baseoendopod, the proximal spine, present in the female, is absent in the male.

The postoral head appendages of *A. perplexa* have not previously been described although Sars (1920) figures them (showing about eight setae on the maxillulary basis) but merely states that they “are normal”. However, Gee (1994) showed that there is considerable variation in the structure of the mandible, maxillule and maxilla in Cletodidae which could be of considerable phylogenetic significance. In addition, neither Scott (1899) nor Sars (1920) noted the peculiar dorsal structure of the preanal somite with a semi-hyaline, strongly dentate, pseudoperculum (usually only present in those families which lack a true operculum), or the position of the operculum near the anterior margin of the anal somite. As far as I am aware, both these characters are unique within the Cletodidae (except for the new species from Malaysia).

A. perplexa appears to be a rare species inhabiting fine, or muddy, sand sediments in shallow, inshore waters. In addition to the records in Lang (1948) (but excluding that of T. Scott, 1903) it has been recorded from Loch Creran in Scotland (Olafsson, pers. comm.), off the Northumberland coast (personal record), the Isles of Scilly in south-west England (Wells, 1970) and in Douarnenez Bay, Finistère, France (Bodin, 1984).

Genus *Dyacrenhydrosoma* gen. nov.

Diagnosis.

Cletodidae. Similar to *Acrenhydrosoma* except in the following characters: Antennal allobasis without seta on abexopodal margin. Maxillulary coxal endite completely fused to basis but represented by one seta, palp with only two additional setae. Maxillary proximal and distal syncoxal endites with 2:1 armature elements respectively, allobasal endite without setae (but with fused terminal claw). P1 exp-3 setae on distal margin without penicillate tips, unequal in length, outer distal seta very short, only equal in length to distal outer spine. P3-P4 enp-2 with only two elements (outer spine absent). P5 baseoendopod with only one inner spine in both sexes, exopod with two setae. Male with sexual dimorphism only in the urosome and antennule.

Type and only species: *Dyacrenhydrosoma breviseta* sp.nov..

Etymology. The prefix *Dy* is the Greek for two, referring to the reduced setation of P3 and P4 enp-2; the retention of *Acrenhydrosoma* indicates that the structure of the P5 is very similar to that genus.

Gender. Feminine.

Dyacrenhydrosoma breviseta sp. nov.
(Figs 5 - 8)

Material examined. Holotype: an adult female dissected onto 3 slides, NHM Reg. No. 1999.660 collected from the Merbok mangrove forest. Paratypes 1 female and 1 male, each dissected onto 3 slides, 2 females and 2 males preserved in spirit, from the Merbok mangrove forest, NHM Reg. No. 1999.661-666; 1 spirit preserved female from the Ranong mangrove forest, NHM Reg. No. 1999.667.

Description of female.

Body (Fig. 5) length 0.331 - 0.453 mm (mean = 0.397 mm, n = 5). Structure and ornamentation similar to *A. perplexa* except for fewer socles on posterior border of cephalothorax and free prosomites but median dorsal socles more strongly developed; anal somite with dentate dorsal cuticular ridges as in Fig. 8D; ventral posterior border of urosomites without spinule row. Exact distribution of tube pores not ascertained due to dirt on specimens. Caudal rami (Figs 5, 7A, 8D-E) cylindrical, elongate, 11 times longer (measured on ventral outer margin) than maximum width (at point of insertion of seta II); with two tube pores, one proximal and one associated with seta III; row of minute spinules on ventral distal margin; lateral setae I and II arising at 24%, triarticulate dorsal seta VII at 34% and lateral seta III at 63% of ramus length.

Rostrum (Fig. 6A) well developed, fused to cephalothorax, recurved ventrally (Fig. 5B), rounded anteriorly with pair of lateral sensilla and patch of fine setules on ventral surface.

Antennule (Fig. 6A) as in *A. perplexa*. Setal formula 1-[1], 2-[7], 3-[7 + ae], 4-[1], 5-[11+ae].

Antenna (Fig. 7B). Coxa without spinule rows. Allobasis with two groups of setules, but no seta, on abexopodal margin. Exopod bearing two setae shorter and stouter than in *A. perplexa*. Endopodal lateral spines naked; large seta on distal margin minutely pinnate rather than strongly spinulose as in *A. perplexa*.

Mandible (Fig. 8A), very small. Coxa slender, elongate; gnathobase with fine, pointed, bicuspid and tricuspid teeth and small seta at inner distal corner. Palp 1-segmented with three small pinnate setae.

Maxillule (Fig. 8B) very small. Praecoxa with small row of spinules; arthritis of praecoxa with one seta on anterior surface and, on distal margin, six sharply pointed spines and one seta. Coxa, basis and rami completely fused into 1-segmented palp with a row of spinules and only three setae; proximal seta representing coxal endite, two setae on distal margin basal in origin; rami completely unrepresented.

Maxilla (Fig. 7E) minute. Syncoxa with three rows of spinules and two endites; proximal endite with two elements, one a pinnate spine; distal endite with one pinnate seta. Allobasal endite with recurved spine but no setae; endopod represented by two setae not fused at base.

Maxilliped (Fig. 8C) as in *A. perplexa* except that endopodal claw with a stout proximal portion and a long slender, flexible distal portion; without accessory seta.

P1 (Fig. 7C). Praecoxa small, triangular. Coxa with two rows of setules on anterior surface and a row of long setules on outer margin. Basis with a central pore; row of spinules at base of inner and outer pinnate seta and on distal margin at base of endopod. Exopod as in *A. perplexa* except that terminal setae on exp-3 without penicillate tips, outer distal seta very short, only as long as distal outer spine. Endopod as in *A. perplexa* except that enp-1 very small and articulating with posterior face of basis; enp-2 nearly five times longer than enp-1; enp-2 with setules rather than spinules on outer margin.

P2-P4 (Figs 7D, 8F). Protopods as for P1 except coxa without setules on outer margin and basis without inner seta. Rami as for *A. perplexa* except that enp-2 with setules rather than spinules on outer margin and on P3 and P4 without outer spine. Setal formula of swimming legs as follows:

	Exopod	Endopod
P1	0:0:022	0:011
P2	0:0:022	0:020
P3	0:0:122	0:020
P4	0:0:122	0:020

P5 (Fig. 8G). General structure as in *A. perplexa* except that: On baseoendopod, tubes associated with pores not discerned; mucroniform extension of endopodal lobe longer and more slender and spinular ornamentation much finer; surface distinctly covered with fine hairs, inner margin with only one spine (proximal spine of *A. perplexa* absent). Exopod bearing only two pinnate setae, outer slightly shorter than inner.

Genital field (Fig. 6B). As in *A. perplexa* except that armature of vestigial P6s reduced to two minute spines and copulatory pore minute, opening at ventral subcuticular rib marking line of fusion of urosomites-2-3. Shape of seminal receptacles, and presence of tube pores between gonopores and copulatory pore, not discernible.

Description of male.

As in female except for urosome and antennules.

Body slightly smaller than female, 0.338-0.397 mm (mean 0.363 mm, n = 3). Genital somite separate; vestigial P6 forming a small asymmetrical plate fused to somite and without armature (Fig. 6E). Ventral posterior border of urosomites-2-5 with median row of spinules (Fig. 6E).

Antennule (Fig. 6C-D) 7-segmented as in *A. perplexa*.
Etymology. The specific name *breviseta* refers to the short outer distal seta on P1 exp-3.

Genus *Paracrenhydrosoma* gen. nov.

Diagnosis. Cletodidae. Similar to *Acrenhydrosoma* except in the following characters: Genital double somite with

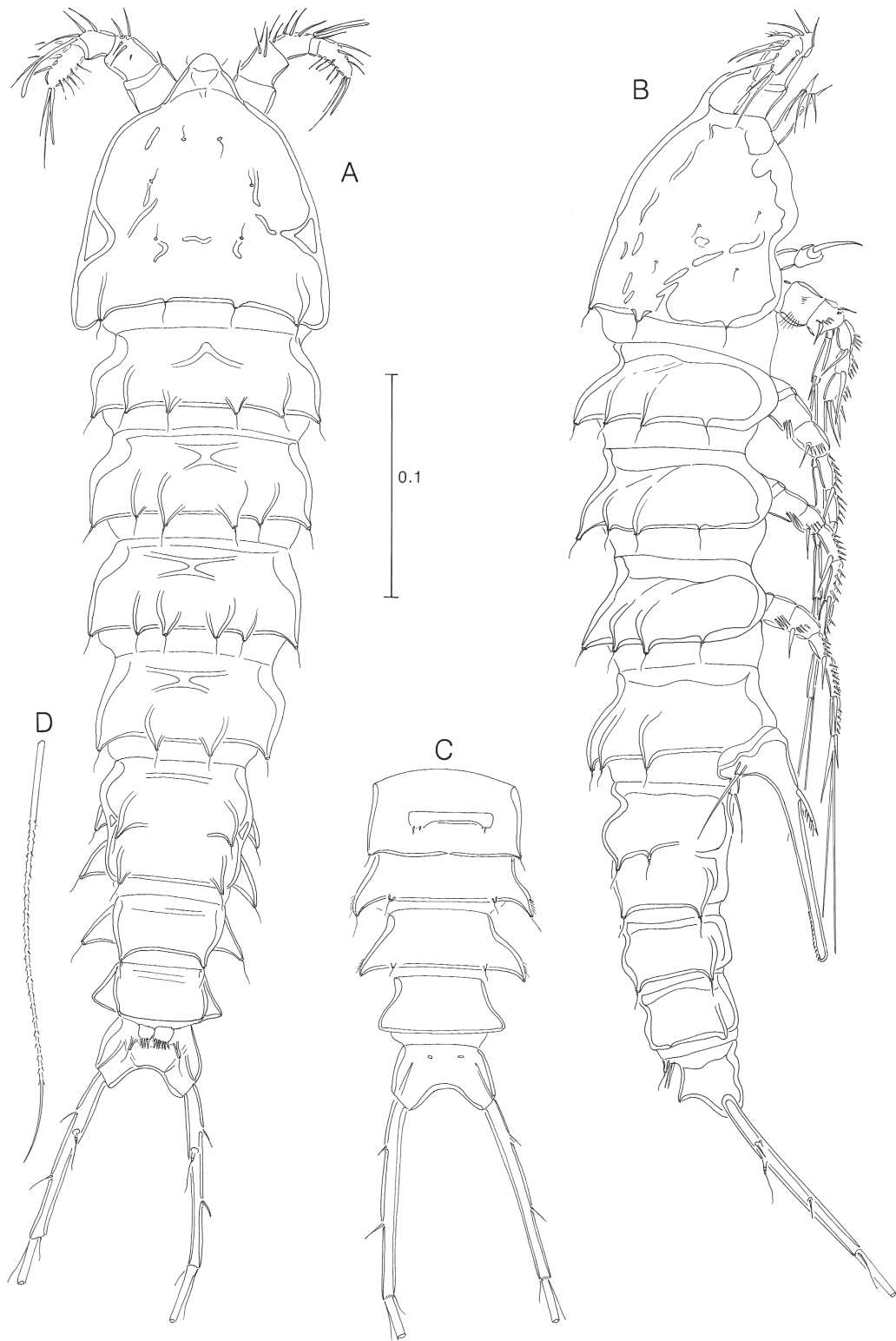


Figure 5. *Dyacrenhydrosoma breviseta*. Female: (A) habitus, dorsal view, (B) habitus, lateral view, (C) urosome (excluding P5-bearing somite), ventral view, (D) caudal ramus seta V. Scale in mm.

Figure 5. *Dyacrenhydrosoma breviseta*. Femelle : (A) habitus, vue dorsale, (B) habitus, vue latérale, (C) urosome (sauf le somite portant P5), vue ventrale, (D) soie V de la rame caudale. Echelle en mm.

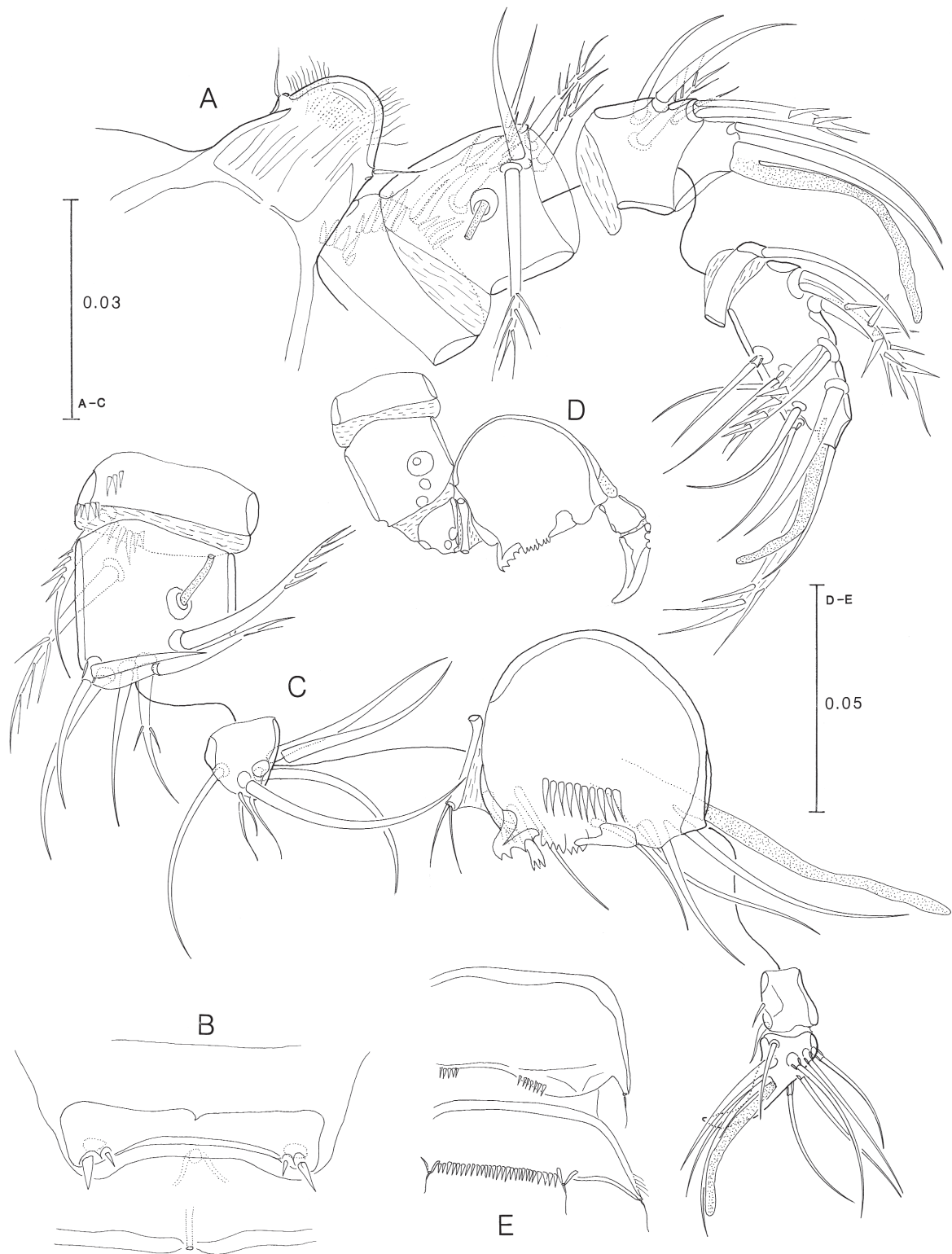


Figure 6. *Dyacrenhydrosoma breviseta*. Female: (A) rostrum and antennule, (B) genital field. Male: (C) antennule disarticulated, (D) antennule, armature omitted, (E) urosomites 2 and 3, ventral view. Scales in mm.

Figure 6. *Dyacrenhydrosoma breviseta*. Femelle : (A) rostre et antennule, (B) région génitale. Mâle : (C) antennule désarticulée, (D) antennule, armature omise, (E) urosomites 2 et 3, vue ventrale. Echelles en mm.

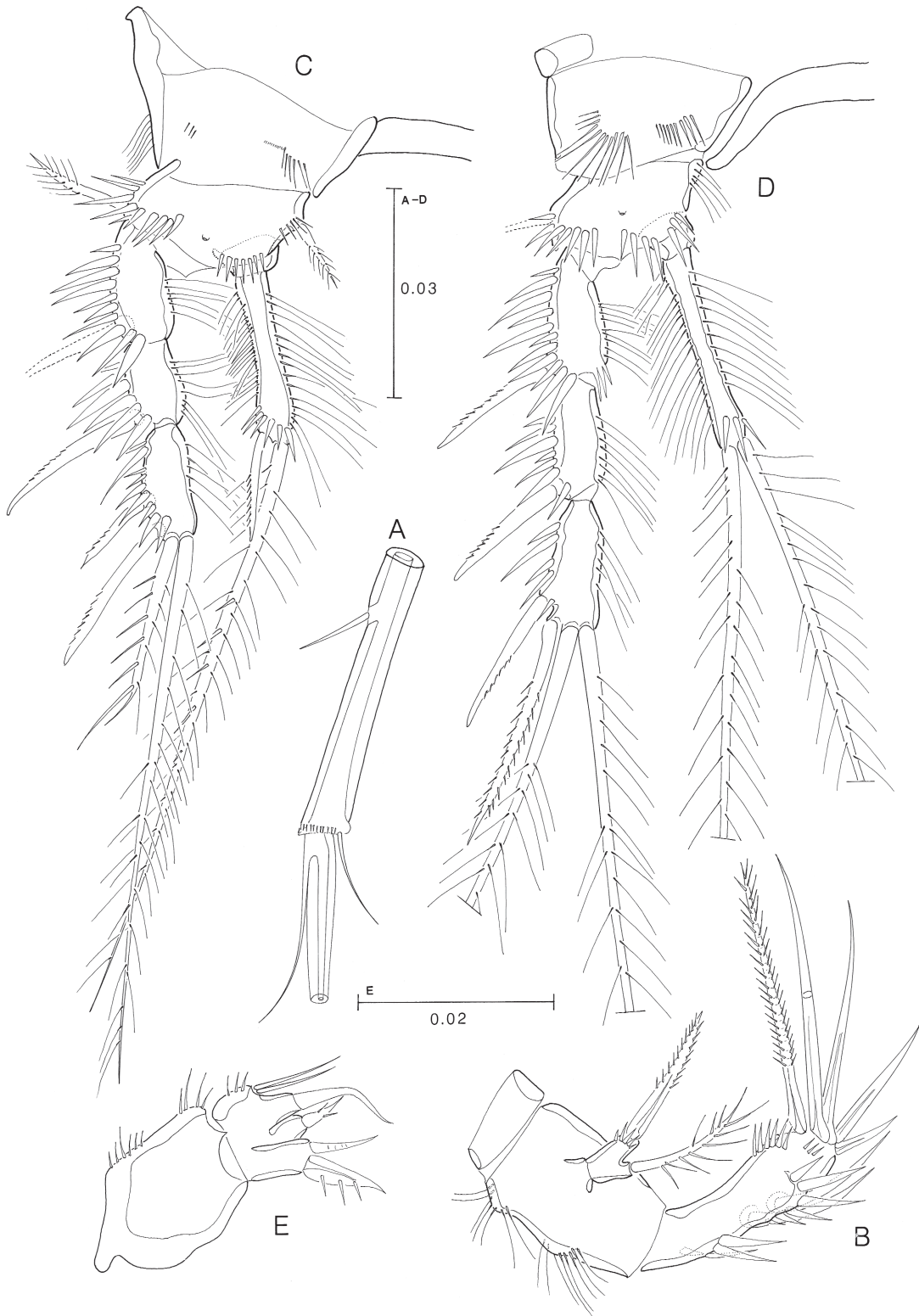


Figure 7. *Dyacrenhydrosoma breviseta*. Female: (A) distal portion of caudal ramus, ventral view, (B) antenna, (C) P1, (D) P2, (E) maxilla. Scales in mm.

Figure 7. *Dyacrenhydrosoma breviseta*. Femelle : (A) rame caudale partie distale, vue ventrale, (B) antenne, (C) P1, (D) P2, (E) maxille. Echelles en mm.

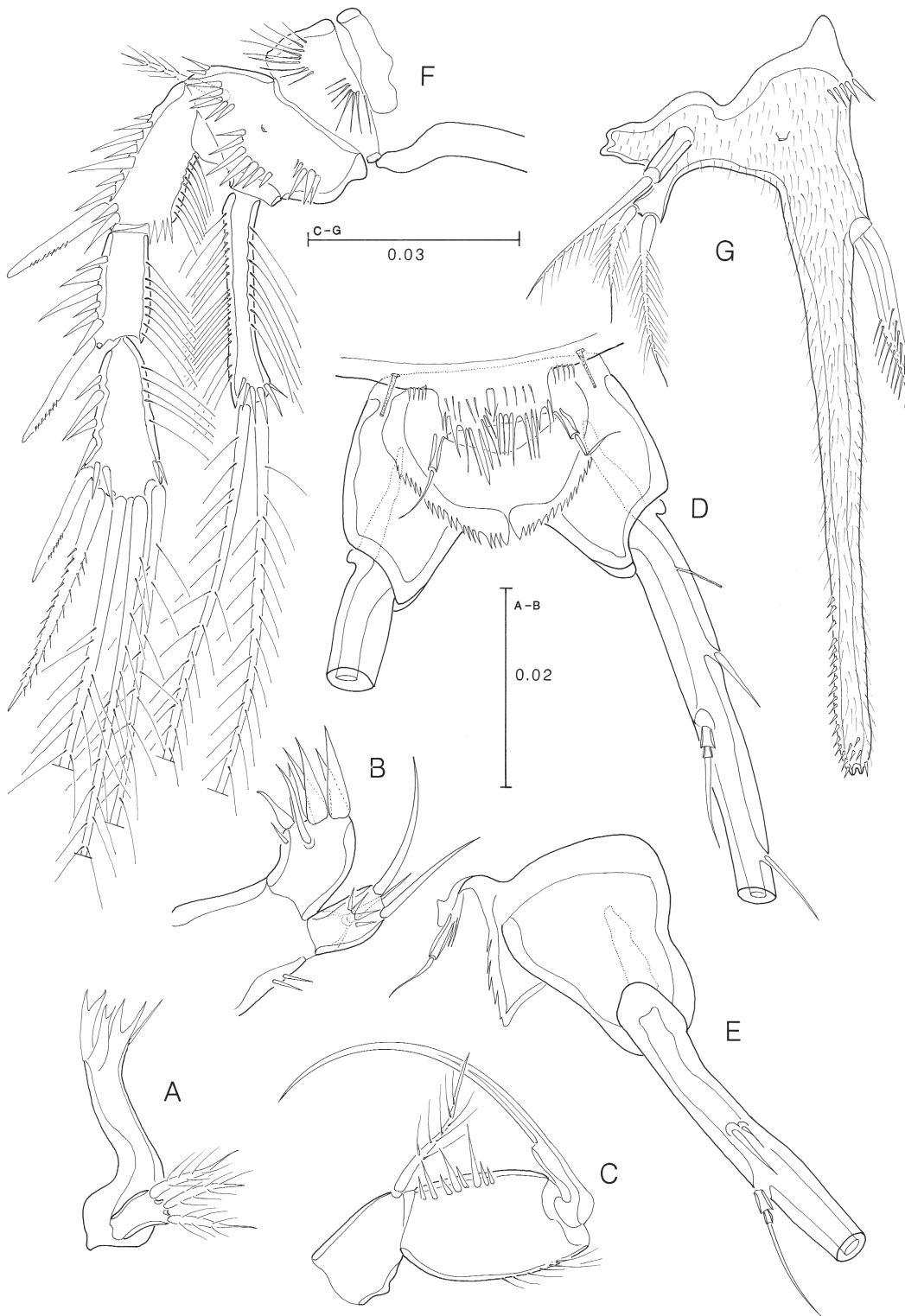


Figure 8. *Dyacrenhydrosoma breviseta*. Female: (A) mandible, (B) maxillule, (C) maxilliped, (D) preanal somite posterior border and anal somite, dorsal view, (E) anal somite and anterior portion of caudal ramus, lateral view, (F) P3, (G) P5. Scales in mm.

Figure 8. *Dyacrenhydrosoma breviseta*. Femelle : (A) mandibule, (B) maxillule, (C) maxillipède, (D) bord postérieur du somite préanal et somite anal, vue dorsale ; (E) somite anal et partie antérieure de la rame caudale, vue latérale, (F) P3, (G) P5. Echelles en mm.

continuous median subcuticular rib marking line of fusion. Preanal somite without dentate pseudoperculum. Anal operculum in distal half of anal somite. Caudal rami with two extra tube pores distal to seta III. Rostrum with broadly rounded, slightly emarginate distal margin. Mandibular palp usually with four setae (three setae reported for *P. karlingi*). Maxillary coxal endite separate from basis and bearing two setae, basis with six setae (two exopodal, one endopodal and two basal?). P1 enp-2 with three armature elements. Female P5 exopod with two setae.

Type species. By designation, *Acrenhydrosoma maccalli* Schizas & Shirley, 1994 = *Paracrenhydrosoma maccalli* (Schizas & Shirley, 1994) comb. nov..

Other species. *Acrenhydrosoma karlingi* Lang, 1965 = *Paracrenhydrosoma karlingi* (Lang, 1965) comb. nov., *P. normani* sp. nov..

Etymology. The prefix is from the Greek *para* meaning near, and the retention of *Acrenhydrosoma* indicates that the structure of the P5 is very similar to that genus.

Gender. Feminine.

During examination of the specimens of *A. perplexa* deposited in the Natural History Museum, London, it was apparent that the two specimens (one of each sex) collected by A. M. Norman from the extreme north coast of Norway and identified by T. Scott (1903) as *A. perplexa*, did not belong to that species. The following description of the Norwegian material is confined to those features which differ from *A. perplexa*.

Paracrenhydrosoma normani sp. nov.
(Figs 9-11A)

Synonym: *Acrenhydrosoma perplexa* (T. Scott, 1899) sensu T. Scott (1903).

Material examined. Holotype: adult female spirit preserved (1 antennule mounted on 1 slide), collected by A.M. Norman in 1890 from 3-9 m in Bög Fjord, East Finmark, northern Norway, NHM Reg. No. 1911.11.8.45110. Paratype: 1 male (1 antennule mounted on same slide as female), spirit preserved, from same collection as holotype, NHM Reg. No. 1911.11.8.45111.

Description of female.

Body (Fig. 9) length 0.664 mm. Dorsal posterior border of free prosomites and dorsal and lateral border of urosomites with minute spinule row, approximately two more sensillum-bearing socles than *A. perplexa*. Line of fusion on genital double-somite marked by continuous sub-cuticular rib. Preanal somite (Fig. 10A) without dorsal dentate pseudoperculum but with dorsal spinule row between two tube pores. Anal operculum situated in posterior half of somite, semicircular with dorsal row of spinules and ventral hairs, opercular sensillum-bearing socles very short. Caudal rami cylindrical, tapering posteriorly, eight times longer than width at insertion point of seta II with two lateral tube

pores distal to seta III (in addition to tube pores proximal to seta III and seta II). All lateral setae more strongly developed than in *A. perplexa*; setae I & II insert at 37%, seta VII at 50% and seta III at 59% of ramus length. Ramus with generous scattering of fine setules.

Genital field (Fig. 10B). Vestigial P6 with a well developed pinnate seta and a naked seta. Anterior margin of genital slit with row of spinules. Copulatory pore larger than in *A. perplexa*.

Antennule and antenna as in *A. perplexa* except that the subdistal spines on the antennal endopod are only minutely pinnate.

Rostrum (Fig. 9A), prominent, fused to cephalothorax, with broadly flattened semi-hyaline anterior margin slightly concave medially; and a pair of well developed sensilla.

Mandible (Fig. 10C). Palp 1-segmented with four plumose setae, three on distal margin (one on basal endite?, two representing endopod?) and one arising from proximal anterior face of palp (exopodal?).

Maxillule (Fig. 10D). Exact armature of praecoxal arthrite could not be determined in whole specimen. Coxal endite not fused to basis, bearing two setae (one pinnate). Basis with six setae, three on or near distal margin and three proximally on lateral margin.

Maxilla and maxilliped as in *A. perplexa*.

P1 (Fig. 10E). Basis with clearly distinguished tube pore at base of outer seta on one side but not discernible on other side; inner basal spine more strongly pinnate than *A. perplexa*. Enp-2 only twice as long as enp-1, enp-2 bearing three armature elements (an inner distal seta, a terminal seta with penicillate tip, and an outer spine).

P2-P4. Structure and setal formula as in *A. perplexa*.

P5 (Fig. 10F) Baseopod with small row of spinules at base of proximal inner spine and row of minute spinules just distal to distal spine articulation; tube pore at base of distal spine in addition to those on anterior face and at base of proximal spine; distal spine about equal in length to proximal spine. Exopod with a tube pore on anterior face, and two pinnate setae on distal margin.

Description of male.

As in female except for urosome, antennule, P3 endopod and P5.

Body length 0.527 mm, genital somite and urosomite-3 not fused.

Antennule as in *A. perplexa* except that anterior surface of segment 5 with naked setae in place of three terminally dentate spines (see Fig. 4D); pinnate seta much more strongly developed.

P3 (Fig. 11A) enp-2 with outer spine fused to segment, recurved, with a few pectinate pinnules.

P5 as in female except proximal inner seta on baseopod absent.

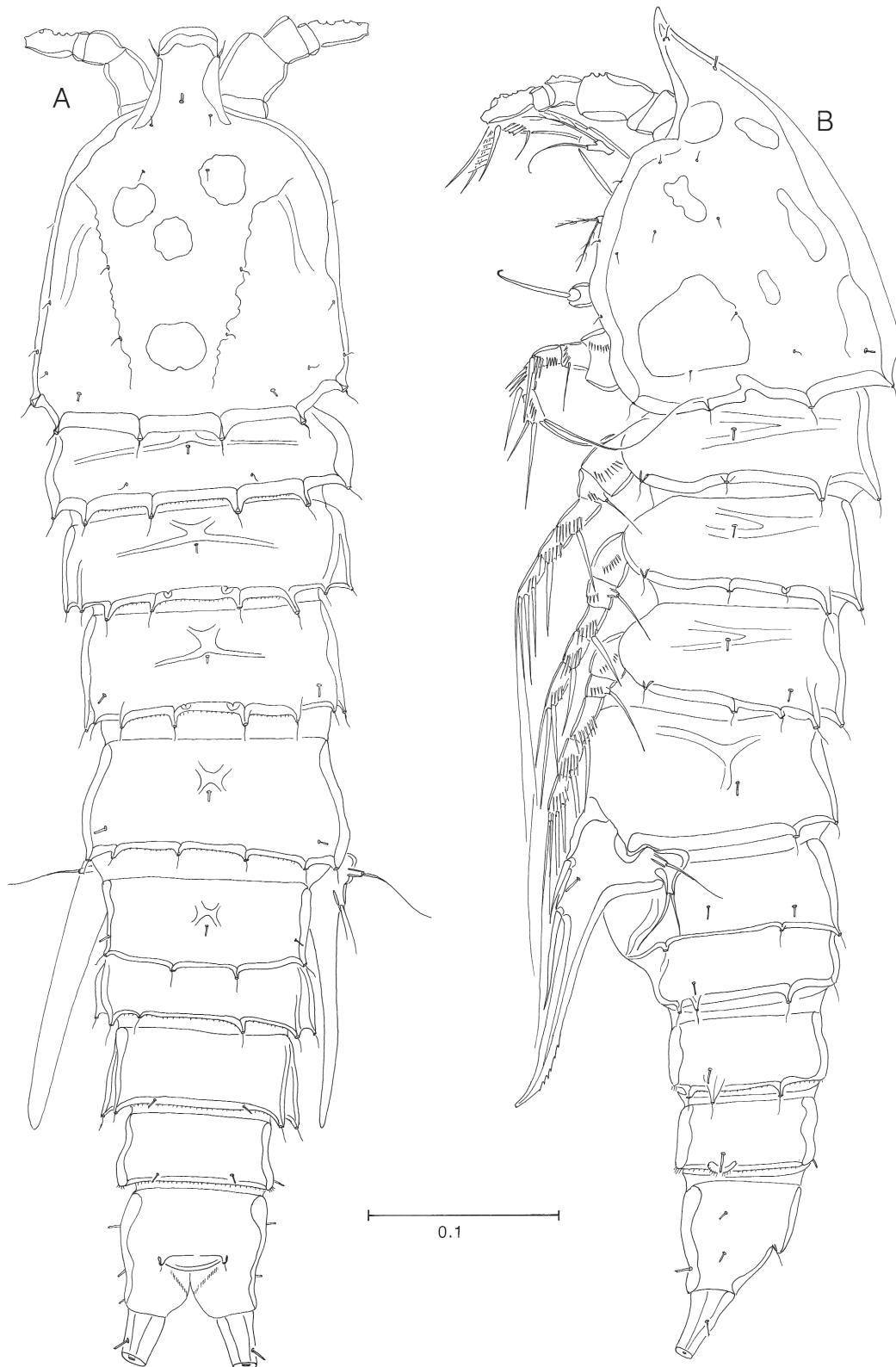


Figure 9. *Paracrenhydrosoma normani*. Female habitus: (A) dorsal view, (B) lateral view. Scale in mm.

Figure 9. *Paracrenhydrosoma normani*. Femelle : (A) habitus vue dorsale, (B) vue latérale. Echelle en mm.



Figure 10. *Paracrenhydrosoma normani*. Female: (A) posterior border of preanal somite, anal somite and caudal ramus, dorsal view, (B) genital field, (C) mandible, (D) maxillule, (E) P1, (F) P5. Scales in mm.

Figure 10. *Paracrenhydrosoma normani*. Femelle : (A) bord postérieur du somite préanal, somite anal et rame caudale, vue dorsale, (B) région génitale, (C) mandibule, (D) maxillule, (E) P1, (F) P5. Echelles en mm.

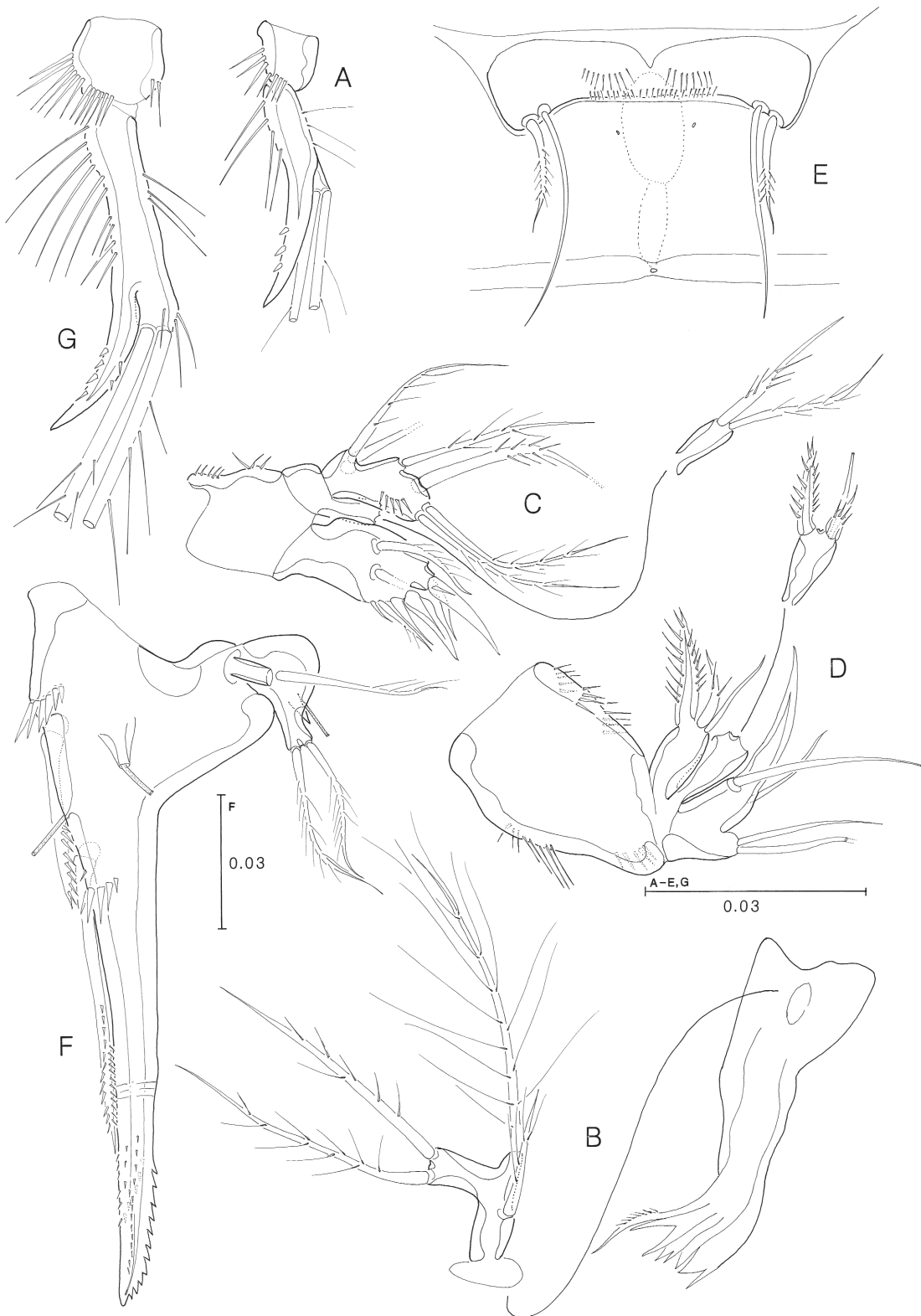


Figure 11. *Paracrenhydrosoma normani*. Male: (A) P3 endopod. *Paracrenhydrosoma maccalli*. Female: (B) mandible, (C) maxillule, (D) maxilla, (E) genital field, (F) P5. Male: (G) P3 endopod. Scales in mm.

Figure 11. *Paracrenhydrosoma normani*. Mâle : (A) endopodite de P3. *Paracrenhydrosoma maccalli*. Femelle : (B), mandibule, (C) maxillule, (D) maxille, (E) région génitale, (F) P5. Mâle : (G) endopodite de P3. Echelles en mm.

Etymology. The species name is in honour of Rev. A.M. Norman who originally collected the specimens in the summer of 1890.

Paracrenhydrosoma maccalli (Schizas & Shirley, 1994)
(Fig. 11B-G)

Synonym. *Acrenhydrosoma maccalli* Schizas & Shirley, 1994.

Material examined. 3 females (one dissected onto 3 slides) and 4 males (1 dissected onto 4 slides) collected by N. Schizas from an intertidal mudflat in Auke Bay, Alaska (58°22'N 134°40'W) NHM Reg. No.1999.668-674.

This species has been described in an excellent paper by Schizas and Shirley (1994) and the first author kindly provided me with the above material from the type locality in Alaska with which to compare the specimens of T. Scott (1903) from Northern Norway. The following are some supplementary observations or corrections to the original description.

Female.

Body. Preanal somite without dorsal dentate pseudo-perculum but with row of setules between a pair of dorsal tube pores; anal operculum in distal half of anal somite.

Caudal rami cylindrical, tapering posteriorly, about 9.5 times longer than width at insertion point of seta II, with two lateral tube pores distal to seta III (in addition to tube pores proximal to seta III and seta II). All lateral setae more strongly developed than in *A. perplexa*; setae I & II insert at 40%, seta VII at 47% and seta III at 61% of ramus length. Rami with generous scattering of fine setules.

Genital field (Fig. 11E). Anterior margin of genital slit with a row of spinules and two additional medial groups of spinules. Copulatory pore minute.

Mandible (Fig. 11B). Coxa moderately slender, gnathobase with three or four bicuspid teeth and one pinnate seta at the inner distal margin. Palp 1-segmented with four setae arranged as in *P. normani*.

Maxillule (Fig. 11C). Armature of distal margin of praecoxal arthrite consists of three spines two pinnate setae and a small naked seta. Coxal endite completely separate from basis, bearing two pinnate setae. Basis and rami completely fused bearing six pinnate setae, two proximally and two distally on outer margin and two on distal margin.

Maxilla (Fig. 11D). Proximal and distal syncoxal endites each with three elements (two pinnate spines and a naked seta) on distal margin. Allobasal endite with a fused claw and two setae. Endopod represented by two setae not fused at base.

P5 (Fig. 11F). Baseoendopod with a tube pore on median conical process on anterior face, a tube pore on inner margin near base of distal spine and a row of strong spinules at base of both inner spines. Distal spine over twice as long as

proximal spine. Exopod with surface tube pore and lateral chitinous projection, two setae on distal margin.

Male.

Antennule indistinctly 7-segmented. As in *A. perplexa* except that anterior margin of swollen fifth segment bears four pinnate setae in place of terminally dentate spines.

P3 (Fig. 11G) enp-2 with outer spine fused to segment, recurved, with pectinate pinnules on outer and inner margin.

P5. Proximal spine on inner margin of baseoendopod absent, distal spine much shorter than in female. Chitinous projection on exopod not apparent.

Remarks.

The Norwegian specimens are extremely similar to those from Alaska in general body facies and in the structure of the head appendages, mouthparts and swimming legs. The length/width ratio of the caudal rami is slightly smaller in the Norwegian specimens and there are fewer spinule rows on the anterior margin of the genital field. However, they can be distinguished most clearly from the Alaskan specimens in the details of the structure of P5. In both sexes, the P5 of the Norwegian specimens lack the conical process supporting the median tube pore on the baseoendopod and the distinctive concentric rings on the mucroniform process. In addition, the spinule row at the base of the distal inner spine of the baseoendopod is composed of minute spinules only visible under a x100 oil immersion objective in the Norwegian material whereas in the Alaskan material it is composed of large spinules, clearly visible under a x40 objective. Further, in the females, the distal inner spine of the baseoendopod is much shorter in the Norwegian material (about as long as the proximal spine) compared to the Alaskan material (twice as long as the proximal spine) and the chitinous projection on the exopod of the latter cannot be discerned in the former. It is on the basis of these differences, reinforced by the wide geographic separation of the two sets of specimens, that I have assigned the Norwegian material to a new species.

Discussion

The species dealt with in this paper (and including *P. karlingi*, specimens of which I have not examined) can be distinguished from other genera of Cletodidae by the peculiar structure of the P5, in which the endopodal lobe is elongated into a mucroniform process and the exopod is situated outside the outer basal peduncle and appears to articulate with or be partially fused to the posterior face. Another distinctive feature of these species is the structure of the female genital field in which the vestigial P6s bear two armature elements and the gonopores are joined by a common genital slit with spinule rows on the anterior

margin in some species. As far as I am aware, the only other cletodid with a similar genital field is *Enhydrosoma curticauda* Boeck (see Gee, 1994). This species also has a distinctive P5 in both sexes in which the endopodal lobe of the baseopod is unusually attenuated, bearing a strong spine at its tip in the female (in addition to two spines on the inner margin) and the exopod articulates with the posterior face of the baseopod. It can be postulated that the P5 in the species under consideration here, could easily be derived from that of *E. curticauda* by the fusion of the distal spine with the elongate endopodal lobe and the outward displacement of a posterior-face articulating exopod. These features would suggest that *Acrenhydrosoma* is most closely related to *E. curticauda*. Gee (1998) has suggested that the development of the endopodal lobe into a mucroniform process in *Limnocletodes mucronatus* Gee, 1998 by a similar process of elongation of the lobe and fusion with a terminal seta is a case of parallel evolution rather than implying any close relationship with *Acrenhydrosoma*. In all *Limnocletodes* species the P5 exopod articulates with the border of the baseopod medial to the outer peduncle.

Of the *Acrenhydrosoma*-like species discussed here, the species assigned to *Paracrenhydrosoma* are most similar to *E. curticauda* in the structure of the preanal and anal somite (normal posterior border on former and operculum in posterior half of latter), the mandible (palp with four setae), the maxillule (completely separate coxal endite with two setae, basis with six setae) and the P1 endopod (with three armature elements). It is the development of a dentate pseudoperculum on the preanal somite and the position of the operculum in the anterior half of the anal somite which serve as synapomorphies for *A. perplexa* and *D. breviseta* and justifies placing them in a separate genus from *P. maccalli*, *P. karlingi* and *P. normani*. Other apomorphies include the loss of a seta (exopodal?) on the mandible, loss of a seta and at least partial fusion of the maxillary coxal endite, loss of at least three setae on the maxillary basis, and the loss of the inner seta on P1 enp-2.

D. breviseta has been placed in a separate genus to *A. perplexa* on the basis of the following characters: loss of a seta on the abexopodal margin of the antenna; the complete fusion of the maxillary coxal endite with the basis and the loss of the endopodal seta; the reduced armature of the syncoxal and allobasal endites of the maxilla; the loss of the accessory seta on the maxillipedal endopod; the structure of the setae on P1 where both the exopodal and endopodal setae are without penicillate tips and the outer seta on the distal margin of exp-3 is very short, only as long as the distal outer spine; the loss of the outer spine on P3 and P4 enp-2; and the loss of the proximal inner seta on the female P5 baseopod.

The lack of sexual dimorphism on the P3 endopod in the male of *D. breviseta* may be assumed, at first sight, to be a

direct consequence of the absence of the outer spine on P3 enp-2 in the female. Huys (1990) has shown that within the superfamily Laophontoidea, a sexually dimorphic apophysis on P3 endopod is never present in the male if the corresponding outer element is absent in the female. However, within the Cletodidae, a sexually dimorphic apophysis on P3 endopod is often present in the male when the outer element is absent in the female (e.g. in the genera *Kollerua* Gee, where the sexually dimorphic male P3 endopod is 2-segmented; and some species of *Cletodes* Brady, where the sexually dimorphic male P3 endopod is 3-segmented) leading to the hypothesis that the male apophysis in the Cletodidae must be at least partially segmental in origin. It is suggested that the absence of sexual dimorphism in *Dyacrenehydrosoma*, along with the reduced setae on P1 exp-3 and possibly some of the reductions and fusions seen in the mouthparts, are neotenic characters. Further evidence for a tendency towards neotenic development in this group has recently come to light with the discovery of another closely related genus from China (also with reduced setae on P1 exp-3 and no sexual dimorphism) in which the P2-P4 exopods are 2-segmented as a result of the failure of the proximal two segments to separate (a phenomenon also found in the genus *Enhydrosomella* Monard).

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