BULLETIN DE L'INSTITUT ROYAL DES SCIENCES NATURELLES DE BELGIQUE, BIOLOGIE, 65: 151-236, 1995
BULLETIN VAN HET KONINKLIJK BELGISCH INSTITUUT VOOR NATUURWETENSCHAPPEN, BIOLOGIE, 65: 151-236, 1995

New Tetragonicipitidae (Copepoda, Harpacticoida) from the Yucatecan continental shelf (Mexico), including a revision of the genus *Diagoniceps* Willey*

by Frank FIERS

Abstract

Representatives of the family Tetragonicipitidae encountered in samples from marine and lagoonal localities on the Yucatecan continental shelf are described. *Ph. yucatanensis* n. sp. is added to the *furciger* species-group of the genus *Phyllopodopsyllus*. Resulting from the discovery of four new species which, at first sight, show close resemblance with the species known in the genus *Diagoniceps* WILLEY, a review of the genus is presented. Initially, the type-species of the genus *Diagoniceps*, *D. laevis* WILLEY, is redescribed in detail based on material from the Bahamas and specimens reported previously from Bermuda, type-region. Three out of the six previously described *Diagoniceps* species, i.e. *D. bocki* LANG, *D. menaiensis* GEDDES and *Diagoniceps* spec. BODIN are re-examined and redescribed. After comparison and discussion of the taxonomically important characteristics the following conclusions are presented:
(1) *Diagoniceps laevis* WILLEY and *D. mexicana* n. sp., are retained in the genus;
(2) *D. bocki* LANG, *D. kunzi* MARINOV, and *Diagoniceps* spec., the latter considered here as a distinct species, named *A. bodini* n. sp., are assigned to the genus *Aigondiceps* n. gen., with *D. bocki* designated as type-species;
(3) *D. menaiensis* GEDDES and *D. trifidus* YEATMAN are assigned to the genus *Nidiagoceps* n. gen., with the former designated as type-species;
(4) *Diagoniceps monodi* CHAPPUIS & KUNZ is considered as *species inquirenda*.
(5) the specimens reported from Bermuda by COULL and identified as *D. laevis*, represent an unknown species, *O. elegantissima* n. sp. which with *O. xamaneki* n. sp. and *O. clarkae* n. sp. constitutes the genus *Odaginiceps* n. gen. (*O. clarkae* n. sp. is proposed as type-species). In addition, the genus *Godianiceps* n. gen. is erected for *G. maya* n. sp. found in the famous Nichupté Lagoon near Cancun. Finally, an updated key to the currently recognised genera of the family Tetragonicipitidae is compiled.
Key-words: Harpacticoida, Tetragonicipitidae, *Phyllopodopsyllus*, *Diagoniceps*, taxonomy.

Résumé

Les représentants de la famille Tetragonicipitidae rencontrés dans les échantillons provenant des localités marines et lagunaires de la plate-forme continentale du Yucatan ont été décrits. *Ph. yucatanensis* n. sp. est ajoutée au groupe *furciger* du genre *Phyllopodopsyllus*. Résultant de la découverte de quatre nouvelles espèces qui, au premier abord, montrent une étroite ressemblance avec les espèces connues dans le genre *Diagoniceps* WILLEY, une révision du genre est présentée. Initialement, l'espèce type du genre *Diagoniceps*, *D. laevis* WILLEY, fût redécrite en détails sur base du matériel venant des Bahamas et de specimens rapportés précédemment des Bermudes, région type. Trois des six espèces décrites et attribuées au genre *Diagoniceps*: i.e. *D. bocki* LANG, *D. menaiensis* GEDDES and *Diagoniceps* spec. BODIN, ont été réexaminées et redécrites. Après une comparaison et une discussion au sujet des caractéristiques taxonomiques importantes, les conclusions suivantes ont été tirées:
(1) *Diagoniceps laevis* WILLEY and *D. mexicana* n. sp. sont conservées dans le genre;
(2) *D. bocki* LANG, *D. kunzi* MARINOV et *Diagoniceps* spec. (considérée ici comme une espèce distincte et nommée *A. bodini* n. sp.) sont assignées au genre *Aigondiceps* n. gen., dont *D. bocki* est désignée comme espèce type;
(3) *D. menaiensis* GEDDES and *D. trifidus* YEATMAN sont assignées au genre *Nidiagoniceps* n. gen., le premier étant désigné comme l'espèce type;
(4) *Diagoniceps monodi* CHAPPUIS & KUNZ est considérée comme *species inquirenda*;
(5) Les spécimens rapportés des Bermudes par COULL et identifiés comme *D. laevis* représentent une espèce inconnue, *O. elegantissima* n. sp. qui avec *O. xamaneki* n. sp. et *O. clarkae* n. sp. constituent le genre *Odagoniceps* n. gen. (*O. clarkae* est représenté comme l'espèce type). En plus, le genre *Godianiceps* n. gen. est défini pour l'espèce *G. maya* n. sp. trouvée dans le fameux lagon Nichupté proche de Cancun. Finalement, la mise à jour d'une clé de détermination concernant les différents genres connus actuellement dans la famille Tetragonicipitidae est établie.
Mots-clefs: Harpacticoida, Tetragonicipitidae, *Phyllopodopsyllus*, *Diagoniceps*, taxonomie.

* A result from the Xaman-Ek oceanographic campaigns on the Yucatán shelf.

Introduction

So far eight genera are currently recognized within the world-wide distributed harpacticoid family Tetragonicipitidae LANG, 1944 (originally spelled as Tetragonicepsidae, see WELLS, 1967; BODIN, 1988). Initially the genera *Tetragoniceps* BRADY, 1880, *Pteropsyllus* T. SCOTT, 1906, *Diagoniceps* WILLEY, 1930, *Phyllopodopsyllus* T. SCOTT, 1906, and *Paraphyllopodopsyllus* LANG, 1944 were unified in the family. LANG (1944, 1948) however, omitted the genus *Laophontella* THOMPSON & A. SCOTT, 1903 which he ascribed, although with severe reservations, to the Laophontoidea. But, when POR (1964a) defined the tetragonicipitid genus *Willeyella* to accommodate *W. horrida* POR (1964a) and the previously described *Phyllopodopsyllus armatus* WILLEY, 1935 LANG (1965) reconsidered his previous opinion and removed *Laophontella* to the present family. The striking resemblance of the genera *Willeyella* and *Laophontella* impelled LANG (1965) to synonymize *Willeyella* with the latter.

Within a rather short period after appearance of LANG's 1948 monograph, the validity of the genus *Paraphyllopodopsyllus* LANG, 1944 became questionable as several species assigned to *Phyllopodopsyllus* and *Paraphyllopodopsyllus* were found to display intermediary characteristics between both genera. LANG (1965) consequently withdrew *Paraphyllopodopsyllus*. His view has currently been followed by subsequent authors (COULL, 1973; KUNZ, 1984; BODIN, 1988). However, where LANG (1944, 1948) defined the genus *Paraphyllopodopsyllus* mainly on the ramal complement of the natatorial legs and the shape of the antennule (without a hook shaped process on segment II), several, not to mention most, characteristics of these species were (and still are) only superficially known or were omitted in the original descriptions. Most inquiring is that KUNZ's 1984 phylogenetic analyses of the genus *Phyllopodopsyllus* resulted in the definition of a species-group more or less unifying the same species previously assembled in the genus *Paraphyllopodopsyllus*. Thus there seems to be a sufficient number of arguments indicating that this genus could be re-established. Unfortunately, as our knowledge about the taxonomic value of most features is quite inadequate, a redefinition of *Paraphyllopodopsyllus* can only be a result from a detailed revision of the genus *Phyllopodopsyllus*.

The original description of *Protogoniceps hebraeus* POR, 1964a is inaccurate and shows several discrepancies between text and illustrations (LANG, 1965). The generic diagnosis has been corrected by COULL (1973), but the generic affinities to the other tetragonicipitid genera remain unclear. Its place as a taxon which branched off early from a common ancestor with the *Phyllopodopsyllus* - *Laophontella* - *Oniscopsis* group as proposed by KUNZ (1984) is without doubt disputable.

The genus *Oniscopsis* CHAPPUIS, 1954 with its compact body shape and reduced appendages, has long be considered as a paramesochrid (LANG, 1965; COULL, 1973) although CHAPPUIS (1954) offered sufficient arguments in the original description to attribute the genus *Oniscopsis* to the Tetragonicipitidae. Only recently, BECKER & KUNZ (1981) re-inforced CHAPPUIS' 1954 designation and allocated *Oniscopsis* to the present family.

The genus *Fearia* COULL, 1971, principally defined on the median position of the process on the first antennular segment, was synonymized with *Tetragoniceps* by KUNZ (1984) because of the inter-specific variability of the antennular protuberance in the genus *Tetragoniceps*, ranging from a median to distal position along the posterior directed margin of the segment. Again, as the genus *Tetragoniceps* seems to be a polyphyletic grouping (indications are: shape, chaetotaxy, and fusion degree of the fifth legs in both sexes) the arguments used to unify both genera seem to be inappropriate. But considering the deplorable taxonomical insight of the groupings within the family Tetragonicipitidae, it is preferable to maintain KUNZ's decision for the moment.

Finally, the peculiar genus *Pyrocletodes* COULL, 1973 comprising the species *P. desuramus* COULL, 1973 and *P. coulli* DINET, 1976 has been subject of discussion to which family it has to be referred. POR (1986) boldly pinned the allocation of the genus *Pyrocletodes* to the Tetragonicipitidae on DINET (1976) although the latter only stated that the genus could not be referred properly to a particular family. It is apparent that the genus *Pyrocletodes* cannot be maintained in the family Tetragonicipitidae as the morphology of the buccal and pedigerous appendages is fundamentally different.

It is obvious that we are still a long way from a sound phylogenetic interpretation of the several evolution lines within the Tetragonicipitidae. The present generic diagnoses are primarily based on place and shape of antennular processes, and on the shape and degree of ramal fusion of the female fifth legs. But as many aspects such as sexual dimorphic characteristics of natatorial legs and fifth legs, were often overlooked or misinterpreted, important indications of character states and character state changes remain undetected. In my opinion, the currently employed generic diagnostic characteristics represent only a crude indication of the major evolutionary trends within the family but are not a reflection of the complex phylogenetic history of this group.

A revision of the genus *Phyllopodopsyllus* is beyond the scope of the present study, but with the discovery of four new species closely related with those actually constituting the genus *Diagoniceps*, a revision of the genus is presented herein. In this respect, three previously known species, *D. laevis* WILLEY, 1930, *D. bocki* LANG, 1948, and *D. menaiensis* GEDDES, 1968 are redescribed. This resulted in the redefinition of the genus and the erection of four other tetragonicipitid genera. Unfortunately, material of the most arresting *Diagoniceps monodi* described by CHAPPUIS & KUNZ, 1955 from Dakar (Senegal) could not be obtained to re-study. As the original description of this species is particularly short, and certainly not detailed enough for the purposes of the present study, the species is considered as *species inquirenda*.

Material and Methods

Sediment samples recovered during oceanographic campaigns on the continental shelf of the Yucatán peninsula and during an investigation on benthic organisms in Nichupté Lagoon (Cancun) were fixed with a 4% formaldehyde solution. Materials from a blue hole in the Bahamas containing *D. laevis*, were collected by SCUBA-divers, and treated as the other samples. The animals were separated from the sediments either by flotation in a sugar solution or by centrifugation in a ludox gradient. The sorted animals were replaced in 75% denatured ethylalcohol for long-term storage.
Dissected parts of specimens are mounted in glycerine and stored with sealed cover glasses. Observations were made with 100x oil immersion lens on a Leitz Diaplan lightmicroscope equipped with phase contrast. Drawings were made with a camera lucida. Specimens used for S.E.M. observations were critical point dryed, and examined with a Philips 515 S.E.M.
Specimens used for re-examination and redescription were borrowed from the United States Natural History Museum (*D. laevis* WILLEY), the "Naturhistoriska Riksmuseet", Stockholm (*D. bocki* LANG), the Israel National collections of Natural History, Jerusalem (*D. bocki* LANG) and the "Université de Bretagne Occidentale", Brest (*D. menaiensis* GEDDES and *Diagoniceps* spec. BODIN). Types of the newly described species are deposited in the collections of the United States Natural History Museum (labeled USNM no.), the "Naturhistoriska Riksmuseet" (labeled SMNH no.), the Royal Belgian Institute of Natural Sciences (labeled COP no.), and the "Université de Bretagne Occidentale" (personal collection of Ph. Bodin).

Taxonomical account

Genus **Phyllopodopsyllus** T. SCOTT, 1906

Phyllopodopsyllus yucatanensis n. sp.
Fig. 1 - 5

TYPE-MATERIAL

Holotype female dissected on 7 slides, labeled COP 3959A-H; allotype male dissected on 4 slides, labeled COP 3960 A-D; 1 paratype female dissected on a single slide, COP 3961; paratypes: 15 ♀♀, 11 ♂♂, and 8 copepodids ethanol-preserved, labeled COP 3962-3970.

TYPE-LOCALITY

Central West Atlantic: Northern region of the Yucatán continental shelf, México (22°45' N - 87°54.7' W), at a depth of 57.5 m.

ETYMOLOGY

The specific name *yucatanensis* refers to the Yucatán continental shelf, type-region of the species.

DESCRIPTION

HOLOTYPE FEMALE

Habitus (Fig. 1a, b): typical fusiform body-shape, with moderately long expanded caudal rami; length: 640 μm; genital double-somite slightly longer than wide, with both somites entirely fused; fusion line marked laterally and ventrally by rigid internal sclerotized ridge; postero-ventral margin of second abdominal somite elevated, forming a barrier between cavity formed by foliaceous fifth legs and exterior; anal somite with spinulose crescentic anal operculum.
Quadrate rostrum, with single pair of sensillae, separated from cephalothorax with a discreet suture.
Caudal rami (Fig. 1d, 2a) with massive expanded inner lateral margin, about 2.5 times as long as wide, without a dorsal carina; two lateral setae implanted in proximal third, and one arising from distal third; dorsal seta inserted near the inner distal corner of ramus; median terminal setae, half as long as entire body-length, with an irregular globulous basal part, being as long as 3/4 of total length of supporting ramus; outer terminal seta confluent with median one, former longer than globulous part of latter; inner terminal seta half as long as globulous part of median seta.
Integument of all somites and caudal rami densely furnished with minute pits, except for ventral surface of urosomal somites, being smooth; identical integumental pattern present on dorsal surfaces of antennular segments and on anterior surfaces of P1-P5; surface pits not drawn in accompanying illustrations; hyaline fringe of all somites straight, except for lateral parts of second abdominal somite, and ventral margin of penultimate somite; ventral posterior margins of anal somite ornamented with minute spinules.
Antennule (Fig. 2d) 8-segmented with on second segment a large unguiform posteriorly directed unguiform process and a sharp, slightly curved, anterior directed process; first segment about four times as long as wide, with strongly sclerotized margins, and a short transversal blunt process in proximal fourth of ventral surface; segments (Roman numerals) with following armament (Arabic numerals): I(1)-II(9)-III(6)-IV(4+aest)-V(1)-VI(3)-VII(4)-VIII(7+aest).
Buccal appendages as in *Ph. furciger* SARS *sensu* MIELKE (1989), except for the armed distal elements of maxillular arthrite.
P1 (Fig. 3a). Coxa ornamented with anterior and posterior transversal row of spinules; basis with setulose outer and spinulose inner element; exopodite three-segmented; endopodite two-segmented; proximal segment of the latter reaching beyond exopodite, and armamented with

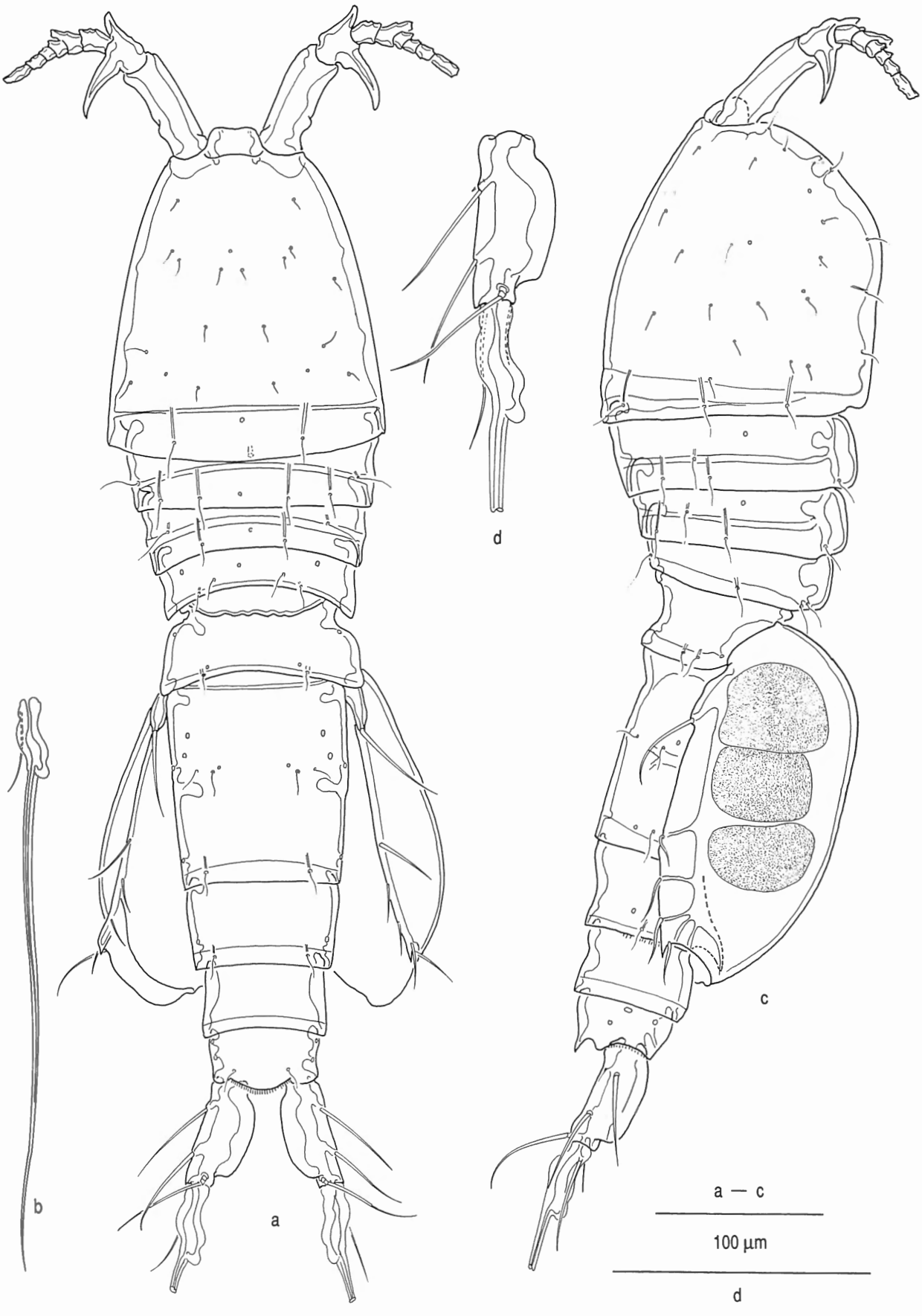

Fig. 1. – *Phyllopodopsyllus yucatanensis* n. sp.: a, female habitus, dorsal; b, left median caudal setae; c, female habitus, lateral; d, left caudal ramus, dorsal (a-d, holotype female; pitted nature of integument not drawn).

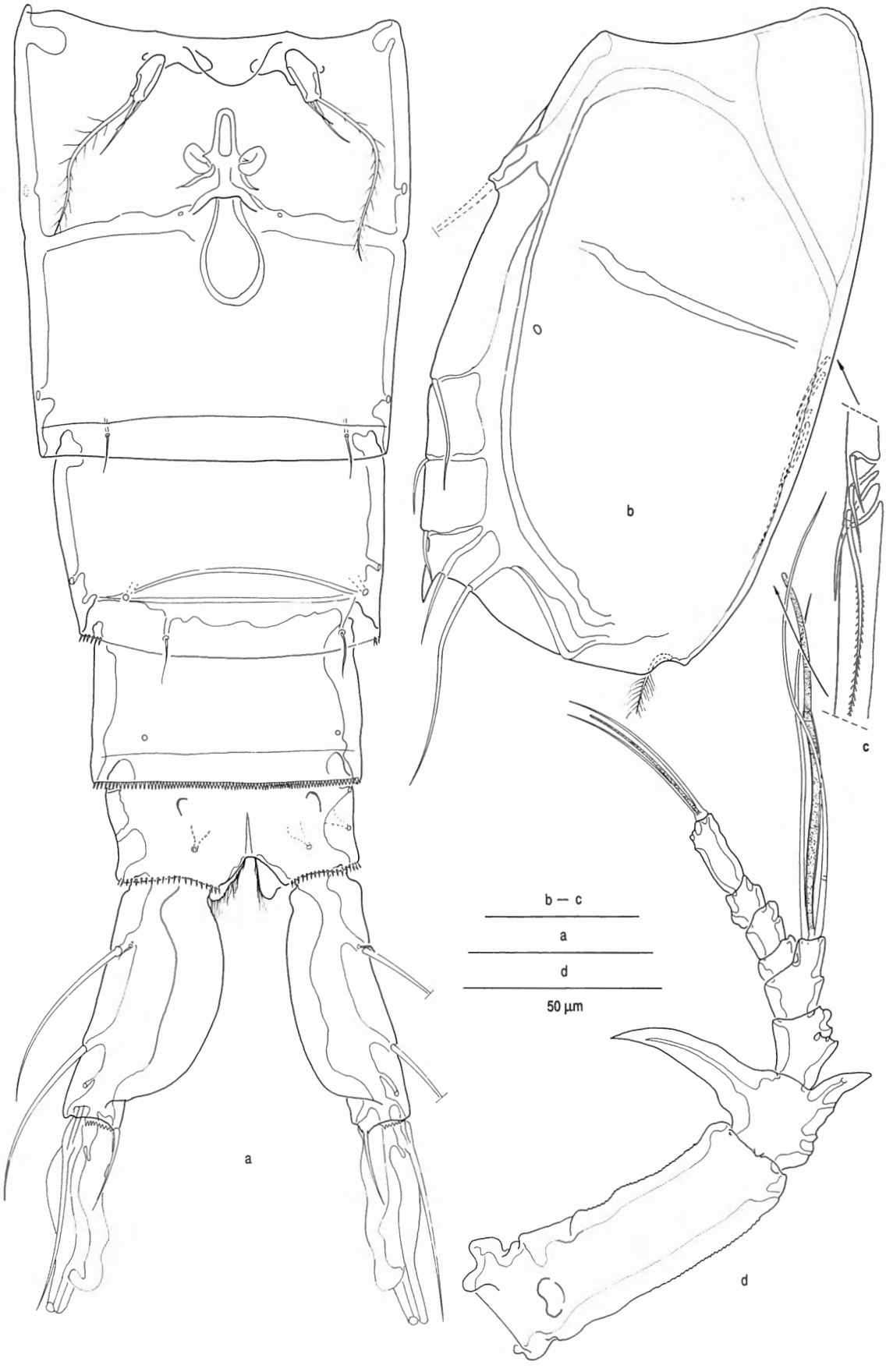

Fig. 2. – *Phyllopodopsyllus yucatanensis* n. sp.: a, female abdomen, ventral; b, right female P5, external (anterior) view; c, part of medial margin, internal (posterior) view; d; antennule, ventral (a-d, holotype female; pitted nature in b-d not illustrated).

Fig. 3. – *Phyllopodopsyllus yucatanensis* n. sp.: a, P1, posterior; b, P2, anterior; c, P3, posterior; pair of P5, anterior (a-c, holotype female; d, allotype male).

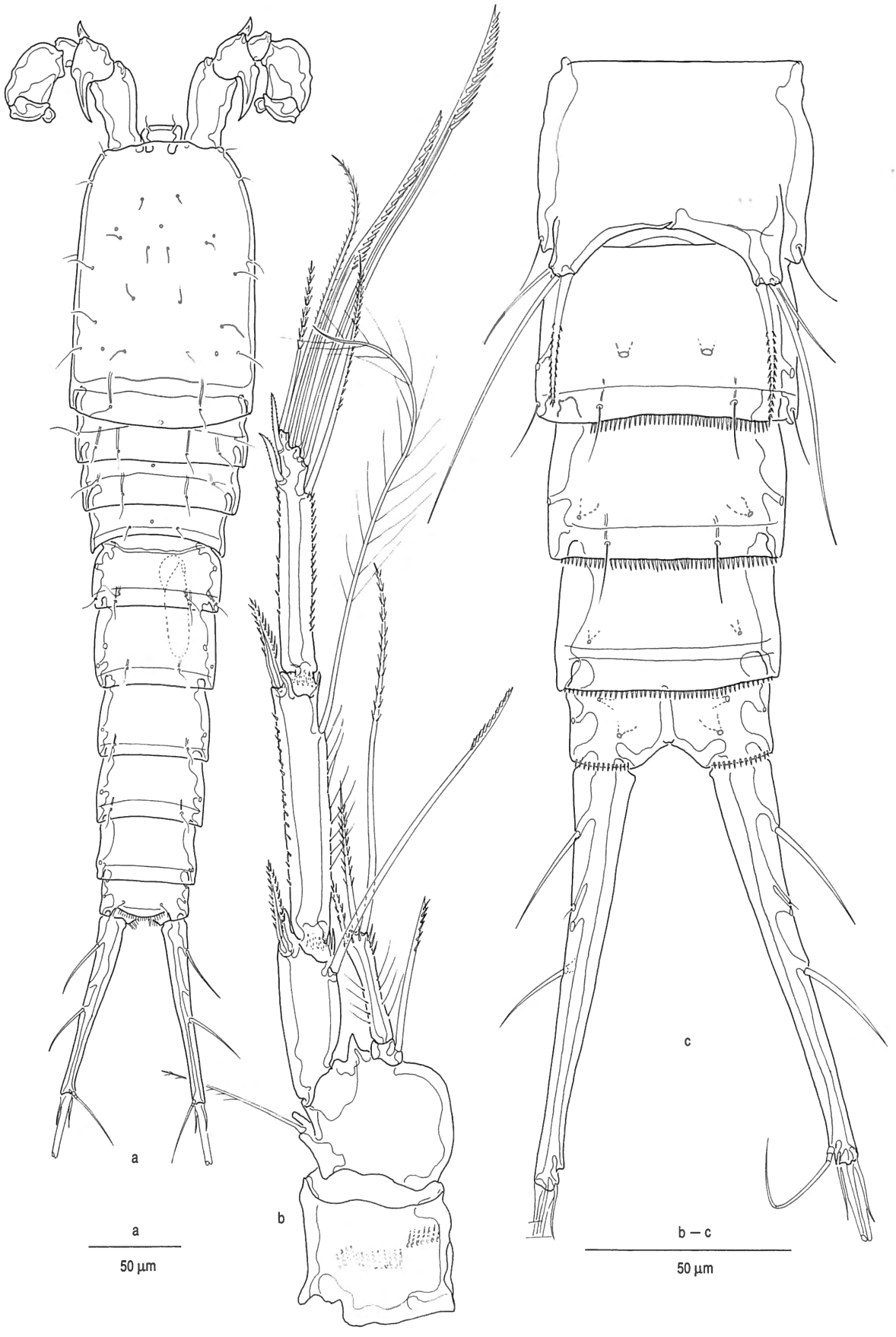

Fig. 4. – *Phyllopodopsyllus yucatanensis* n. sp.: a, male habitus, dorsal; b, female P4, posterior; c, male abdomen, ventral (a-c, allotype male; pitted nature of integument not illustrated in a-c).

a short and robust pectinate seta, implanted in distal fourth of inner margin.
P2 (Fig. 3b) - P3 (Fig. 3c). Coxae ornamented with a transversal row of slender spinules on frontal surface; bases with a distinct sharp extension between both rami and on the inner distal corner; exopodites three-segmented, endopodites two-segmented; endopodite P2 reaching to distal end of second exopodal segment, of P3 just beyond middle of second exopodal segment; distal outer corners of first and second exopodal segments sharply extended; inner seta on first P2 and P3 exopodal segments and on first endopodal segment of P2 pectinate; outer distal seta on second endopodal segments short with blunt tip, ornamented with some long setules; chaetotaxy in Table I.
P4 (Fig. 4b) with two transversal rows of spinules on frontal surface of coxa, and basis with a single median sharp extension and a crescentic inner margin; endopodite two-segmented, just reaching to distal margin of proximal exopodal segment; proximal endopodal segment with an inner pectinate seta, slightly longer that second endopodal segment; three-segmented exopodite armamented with pectinate setae on first and third segments; distal outer corner of first exopodal segment sharply extended, of second and third segments blunt; chaetotaxy in Table I.
P5 (Fig. 2b, c) typically foliaceous with a sharp tooth on distal outer corner; outer margin with 4, distal margin with 3, and inner margin with 4 setae.
P6 vestiges longer than wide, having three setae: median and inner one short and smooth, outer one three times as long as inner ones and plumose (Fig. 2a); genital field present in distal half of first anterior genital somite, having a short ductus connecting the wide genital pore and the small paired seminal receptacula; P5 cavity containing 6 (holotype) or 4 eggs (some paratypes).

ALLOTYPE MALE

Habitus (Fig. 4a): fusiform body-shape, with a parallel sided urosome, and characterized by its long, nearly cylindrical, caudal rami; length: 520 μm.
Caudal rami 8 times as long as wide, smoothly tapering posteriorly, with lateral setae in proximal half, and dorsal seta inserted closely to the inner distal corner of ramus; median terminal setae with normal appearance; outer terminal seta confluent with median one, and only slightly longer than inner one.
Integument of somites as in female; ventral surfaces of urosomal somites smooth, but posterior fringe incised forming a row of distinct sharp teeth (Fig. 4c).
Antennule (Fig. 5d) 6-segmented, sub-chirocer; first and second segments as in female; fourth segment ovate, strongly sclerotized, bearing principal aesthetasc; fifth and sixth segments small.
P2-P4 (Fig. 5a-c) with general aspects as in the female, but coxae more densely ornamented with transversal rows; endopodite P2 typically dimorphic, with inner terminal seta as long as supporting segment; endopodite P3 complemented with three terminal elements on second segment (inner one small), and a minute sharp processus on the outer distal corner; inner seta on proximal P4 endopodal segment very slender, smooth, and only reaching to distal margin of second segment; the latter with a large terminal spine and a small curved sub-distal outer element; P4 exopodite armed with a S-shaped processus on distal outer corner of median segment, and bearing only two inner pectinate setae on third segment.
P5 (Fig. 3d) with confluent baseoendopodites, bearing a very long outer seta, and two apical spines and a inner sub-distal slender seta on the endopodal lobe; exopodite long ovate, reaching far beyond distal end of baseoendopodite, and having a sharp extension on outer distal corner; setal armament: two outer smooth setae, a distal seta and spine, and a single inner spine.
P6 vestiges prominent, each bearing an inner spine, and a median and outer smooth seta (Fig. 4c); left P6 more strongly sclerotized that right one.

Variability: observed only in body-lengths, ranging from 636 to 652 μm, and number of eggs in brood pouch.

DISCUSSION

So far, more than 50 different species and sub-species are attributed to the genus *Phyllopodopsyllus* T. SCOTT, 1906 (KUNZ, 1984; BODIN, 1988; MIELKE, 1989; KUNZ, 1995). KUNZ (1984) distinguished 9 different species-groups within the genus, based on the combination of shape and number of antennular segments and the setal complements of the legs. Although the naturalness of these group definitions is debatable, the group division of the genus is a most practical identification tool.
The presence of an 8-segmented antennule with a large unguiform process on the second segment, and a setal

Table I: Chaetotaxy of *Phyllopodopsyllus yucatanensis* n. sp.

	P1	P2	P3	P4♀	P4♂
EXO	0-0-022	1-0-122	1-0-222	1-1-322	1-1-222
END	1-020	0-021	1-021	1-021	1-011

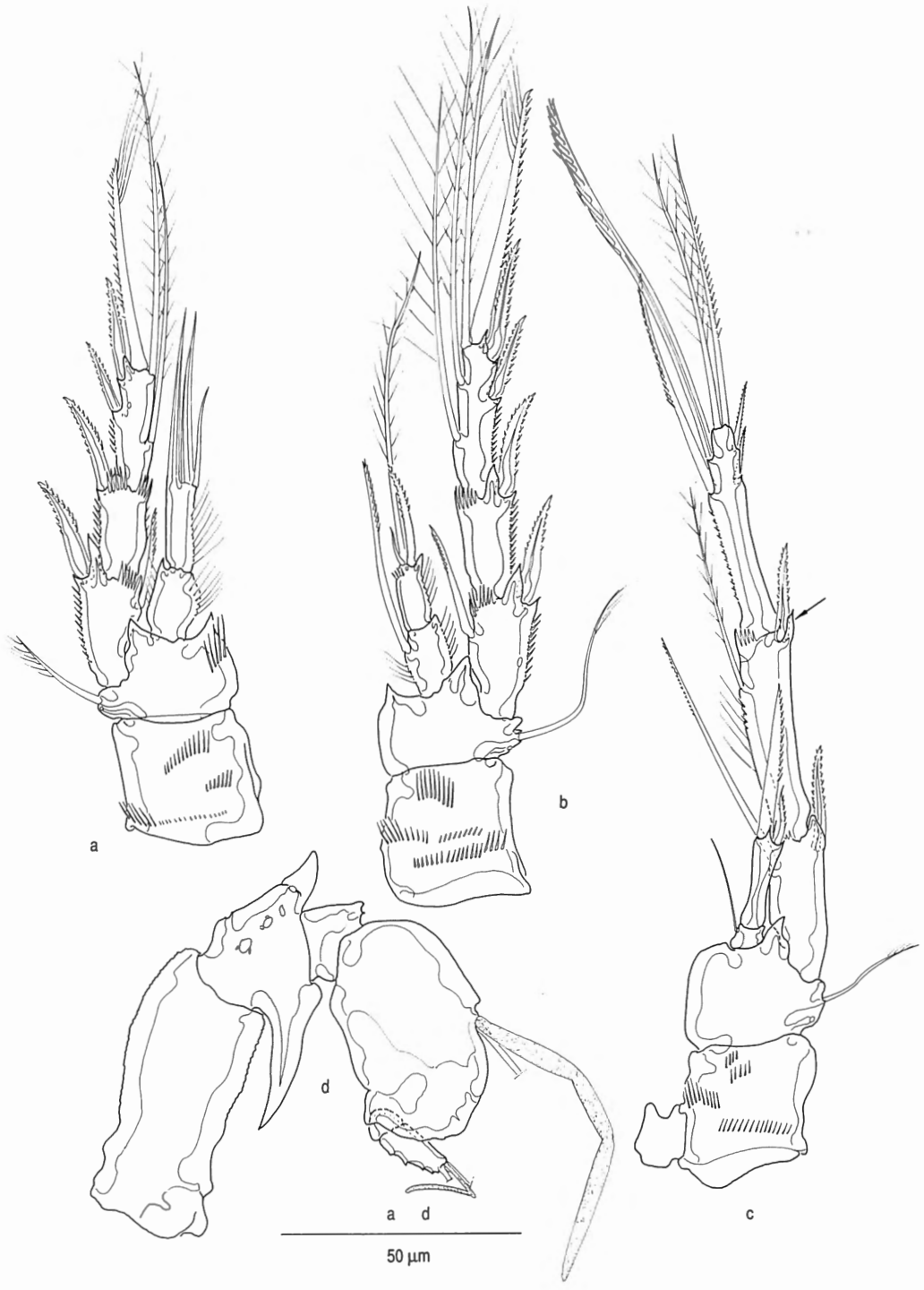

Fig. 5. – *Phyllopodopsyllus yucatanensis* n. sp.: a, P2; b, P3; c, P4, d, contour of antennule (a-d, allotype male; a-c, anterior; d, ventral).

complement of respectively 5 and 6 elements on the P2 and P3 exopodites, in combination with a two-segmented P4 endopodite, commission *Phyllopodopsyllus yucatanensis* n. sp. to the *furciger* species-group. Within the group, *Ph. yucatanensis* n. sp. is most closely related to *Ph. parafurciger parafurciger* GEDDES, 1968a and *Ph. parafurciger carolinensis* COULL, 1971. The three congeners differ from the other group members because of the presence of a peculiar additional sharp process on the anterior distal corner of the second antennular segment (a feature also found in other species-groups viz. *Ph. bahamensis* GEDDES, 1968a; *Ph. geddesi* KUNZ, 1984, among others).

The here described species is distinguished from its closest relatives by the much more expanded female caudal rami (note that left ramus is illustrated in a tilted position in

Fig. 2a) having a much longer outer distal seta on the rami (nearly as long as the ramus), and the considerably longer inner distal seta on the second endopodal segment of the female P4. The males of *Ph. yucatanensis* n. sp. are separable from their congeners by the long inner pectinate seta on the first endopodal segment of the P3 (reaching far beyond distal segment), by the very short and slender inner seta on the proximal segment of the P4 endopodite, and the short, curved outer sub-distal element on the second P4 endopodal segment.

Males of *Ph. parafurciger* are known to display only two terminal elements on the male P3 endopodite, whereas in most other tetragonicipitid species and in *Ph. yucatanensis* n. sp. the segment bears an additional short and smooth inner seta. The small seta is hardly visible as it can be hidden beyond the accompanying larger setae (especially when the leg is observed posteriorly), and it seems highly possible that this additional seta also is present in *Ph. parafurciger*. Neither GEDDES (1968a) nor COULL (1971) mentioned a reduced chaetotaxy in the male P4 exopodite (1-1-322 in female, 1-1-222 in male) in their descriptions of *Ph. parafurciger* and *Ph. p. carolinensis*. However, the absence of an inner seta on the third segment of the P4 exopodite is a common feature in the genus *Phyllopodopsyllus* and other tetragonicipitid genera. Even the related *Ph. furciger* SARS, 1907 displays this particular sexual dimorphism (see MIELKE, 1989). It seems highly possible that the male P4 complement in *Ph. parafurciger* and *Ph. p. carolinensis* is comparable with the here described species and possess only two inner setae on the last segment. But, KUNZ (1995: Fig. 1C and D) described the number of elements on the P4 exopodites in both sexes of specimens from Tanzania, identified as *Ph. furciger*, as identical with 2 inner, 2 distal and 2 outer elements. The closely related *Ph. furciger* is currently treated in the literature as a very variable species (see KUNZ, 1995). The several references to this species demonstrate considerable differences in length/width ratio of the P1 endopodite (Galapagos specimens, in MIELKE, 1989), chaetotaxy of the P4 exopodite (see examples in KUNZ, 1984 and 1995), and the shape of the female caudal rami. KUNZ (1995: p. 84) related these differences to the hypothesis that *Ph. furciger* "has a tendency to develop locally different populations". In my opinion, the present knowledge on morphological variability and species specificity of many features is too insufficient to lend weight on such hypotheses. A detailed re-analysis of reported material of *Ph. furciger* and its congeners will certainly lead to the description of many different species actually considered as conspecific with *Ph. furciger*.

Genus **Diagoniceps** WILLEY, 1930

Diagoniceps laevis WILLEY, 1930
Fig. 6 - 11, Plate I

MATERIAL

(1) Bahamas, Long Island. Land locked, 80 m diameter and 20 m deep, blue hole, about 1.75 km from coast line, 4.5 km north east from Millerton Settlement (coord. 23°31'30" N - 75°14'07" W). Sample at -12 m: sandy bottom; t°: 28.5°C; SO_4: 1.7 g/l; Cl: 20.0 g/l; Ca: 1.3 g/l. Sample at - 15 m: mixed sand and silt; t°: 28.0°C; SO_4: 1.8 g/l; Cl: 19.7 g/l; Ca: 1.35 g/l. Leg. P. Lagrou, 5 August 1985. From sample at - 15 m: 4 ♀ ♀ dissected (COP 3934, 3935, 3937 and 3939), 2 ♂ ♂ dissected (COP 3936, 3938) and 5 ♀ ♀ and 4 ♂ ♂, ethanol-preserved, COP 3924; from sample at - 12m: 2 ♀ ♀, 7 ♂ ♂ and 1 copepodid, ethanol-preserved, COP 3933.
(2) Bermuda, Lovers Lake: 3 ♀ ♀ (topotypic), partially dissected and mounted on a single slide, USNM 171272, and one undissected ♂, mounted on a single slide, USNM 171272, Leg. H.C. Yeatman, 2 August 1955 (Yeatman, 1980).

REDESCRIPTION
(based on materials from the Bahamas)

FEMALE

Body slender with nearly parallel lateral margins, only slightly tapering in second half of urosome (Fig. 6a, b); length, including rostrum and caudal rami, 660 to 685 μm; cephalothorax short, about 1/4 of body length and about as high as wide; genital double- somite entirely fused, showing a broad sclerotized internal band; anal somite with a convex anal operculum, furnished with minute spinules along the margin.

Integument of somites smooth; hyaline fringes of prosomal and ventral fringe of genital double somite smooth, of urosomal somites finely incised; ventral side of anal somite with minute spinules above articulation with caudal rami; integumental sensillae along posterior margins and on surfaces of prosomal somites equal in length.

Caudal rami (Fig. 7d) nearly 3 times as long as wide (2.90-3.05) with a distinct blunt protuberance in second half of inner margin; proximal half of inner margin strongly folded (Plate Ic); in lateral view, proximal half distinctly wider than distal half (Fig. 7e); bi-articulate dorsal seta arising in posterior half, near inner margin; two lateral setae implanted in proximal third and one close to distal edge; outer terminal seta minute, reduced to a blunt curved element; median terminal seta, 220 μm long, with irregularly shaped bulbous proximal part and slender smooth distal part; medial terminal seta reaching just beyond bulbous part of median terminal one; integument of rami smooth.

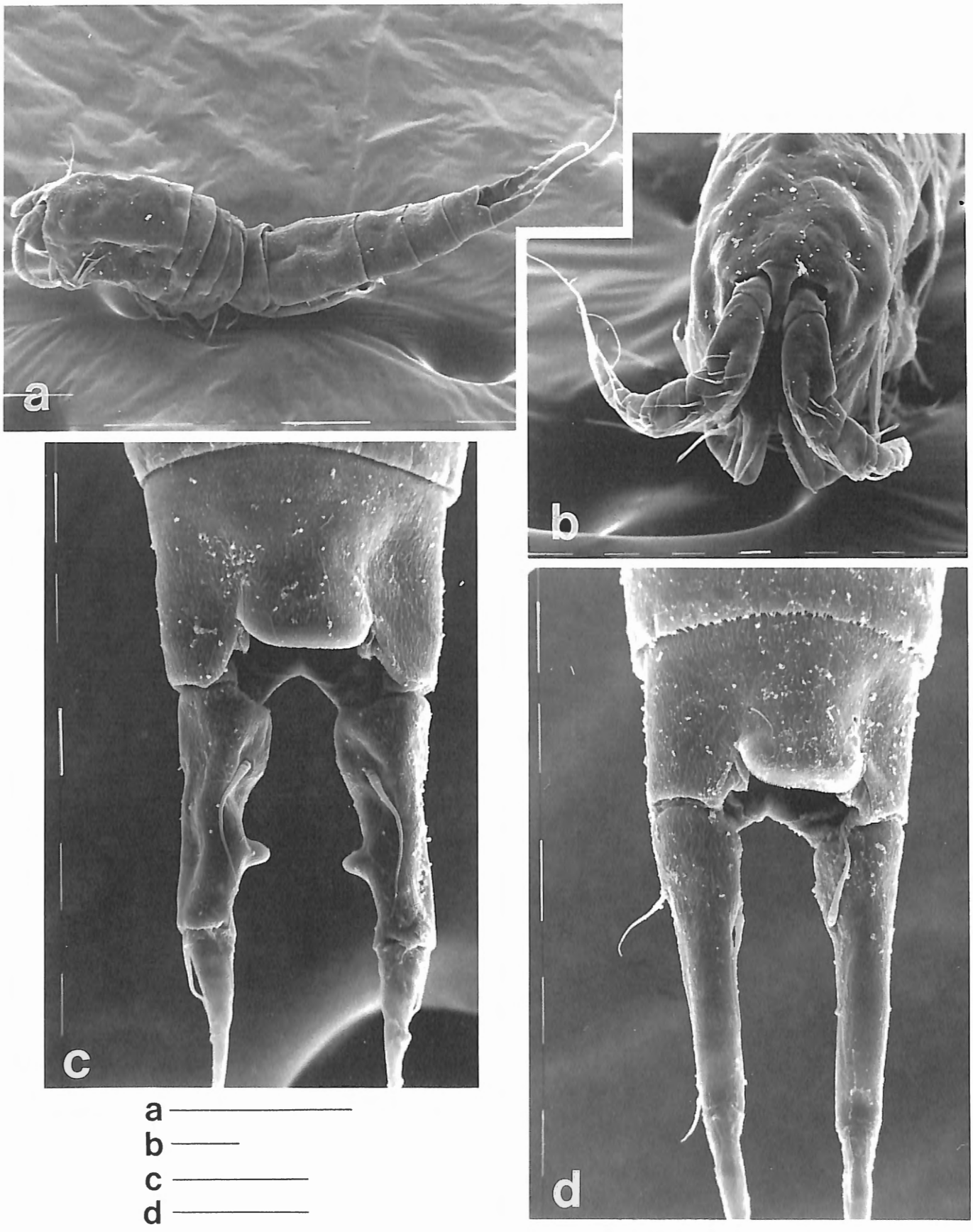

Plate I. – *Diagoniceps laevis* WILLEY, 1930: a, female habitus; b, frontal view of female head; c, female anal somite and caudal rami, dorsal view; d, male anal somite and caudal rami (specimens from the Bahamas; scale a = 200 μm; scales b-d = 20 μm).

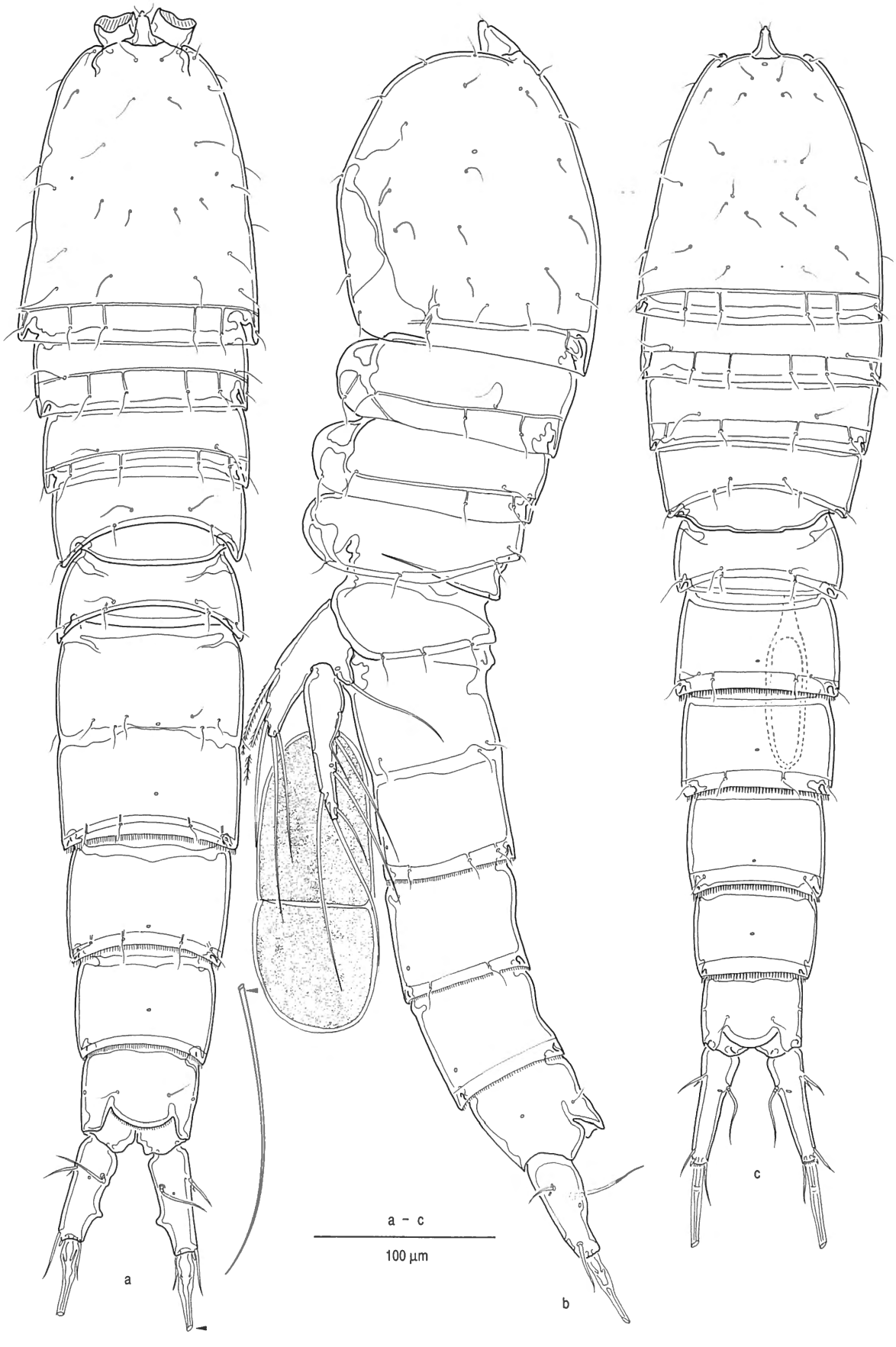

Fig. 6. – *Diagoniceps laevis* Willey, 1930: a, female habitus, dorsal; b, habitus of ovigerous female, lateral; c, male habitus, dorsal (a-b, COP 3934; c, COP 3936).

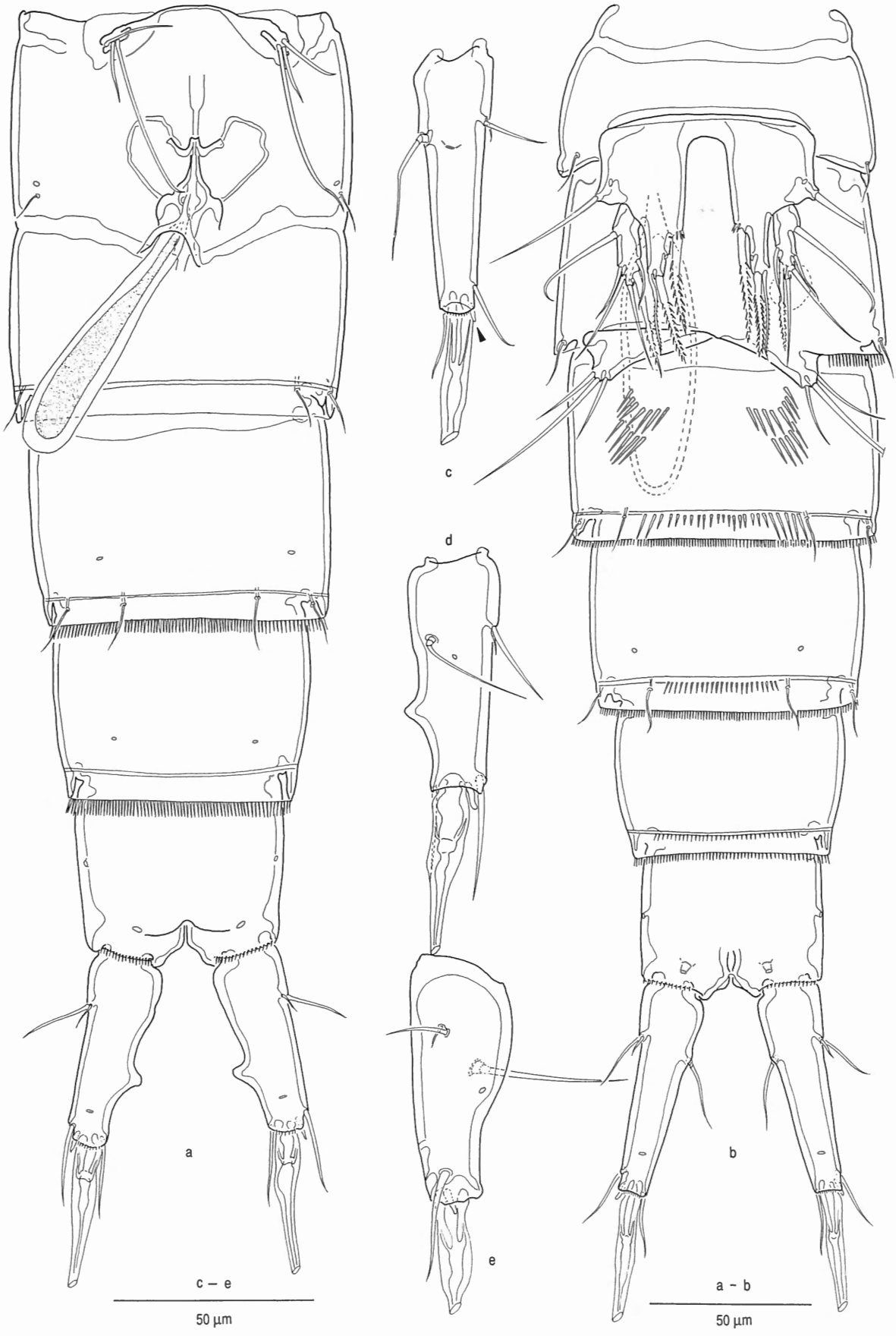

Fig. 7. – *Diagoniceps laevis* Willey, 1930: a, female abdomen, ventral; b, male abdomen and fifth pedigerous somite, ventral; c, male caudal ramus, dorsal; d, female caudal ramus, dorsal; e, female caudal ramus, lateral (a, d-e, COP 3934-3935; b-c, COP 3936).

Rostrum with short basal part, and lean apex, bended ventrally between basal segments of antennulae (Plate Ib); separated from cephalothorax by a descreet suture; recurved position of rostrum giving impression that apex reaches just to distal margin of first antennule segment (Fig. 6a); integument smooth except for single pair of sensillae.

Antennule (Fig. 8a) 9-segmented with second segment up to 2.5 times as long as first one; proportional lengths of segments (L/W): 0.68-1.68-0.77-0.65-0.66-1.00-0.88-0.88-3.00, and setal armament (Arabic numerals): I(1)-II(9)-II(7)-IV(4+aest)-V(2)-VI(4)-VII(2)-VIII(2)-IX(7+aest); seta on segment I plumose; all other setae smooth; aesthetasc on segment IV rather wide at base, and reaching far beyond segment IX; integument of all segments smooth, except for a short row of slender spinules on frontal margin of segment I.

Antenna (Fig. 8b) with basis, bearing a single segmented exopodite and a two-segmented endopodite; abexopodal margin of basis furnished with long and rigid spinules; exopodal segment with a sub-distal and two terminal spinulose setae; ornamented with minute spines near distal margin; first endopodal segment with a long spinulose abexopodal seta; second endopodal segment with two spines and two slender setae in distal third of abexopodal margin (Fig. 8c), and 7 terminal elements; exopodal and abexopodal margins of second endopodal segment ornamented with spinules, and distal margin having a rather long and wide hyaline tube.

Gnathobasis of mandible (Fig. 8g) with multi-dentate teeth and a single lateral seta; pars molaris prominent, surface smooth; coxa-basis large, bearing three spinulose setae on inner margin, and furnished with a row of long slender spinules; exopodal segment slender, half as long as endopodite, and armamented with a proximal seta and two apical setae; endopodite with two median setae on inner margin and 7 apical setae (2 outer apical ones fused near implantation).

Labrum (Fig. 8h) broad, with ornamented apex, and set with a short row of slender spinules on both sides of median hairy field; paragnath (Fig. 9c) is a simple semi-ovate lobe, ornamented apically with spinules.

Maxillule (Fig. 8i) with six pinnate spines and two surface setae on arthrite; coxal extension with 4 distal setae, and basal extension armamented with two smooth setae, one plumose seta and one pinnate element; endopodite and exopodite distinct, bearing 3 and 2 setae respectively.

Maxilla (Fig. 8j) with three endites on syncoxa, each with three elements; claw of basis armed in distal half, accompanied with three setae: two smooth ones and one ornamented with strong spinules; endopodite two-segmented, armamented with a spinulose seta on proximal and distal segment, and with 3 smooth setae on distal margin of distal segment; integument smooth, except for few spinules on proximal endite.

Basis of maxilliped (Fig. 8k) cylindrical, up to 4 times as long as wide, ornamented with a sub-distal short row of slender spinules, and armed with two setulose setae; palm nearly cylindrical, with a median and sub-distal seta on inner margin, and a proximal row of spinules; claw furnished with minute spinules, decreasing in length towards tip, and accompanied with two slender setae.

P1 (Fig. 9a) with three-segmented exopodite and two-segmented endopodite; coxa and basis sparsely ornamented with long and slender spinules; outer seta of basis spinulose; medial one curved and armed along both sides of stem; first endopodal segment reaching just beyond exopodite (about 6 times as long as wide), bearing a serrate inner seta in distal fourth; second endopodal segment (4 times as long as wide) with a short medial and two geniculate terminal setae; coupler narrow.

P2-P4 (Figs. 9b, c; Fig. 10c) with three-segmented exopodites and two-segmented endopodites; coxae and bases sparsely ornamented; basis of P2 with a large strong medial spinule, the other legs without; P2 and P3 endopodites reaching just to or slightly beyond middle of median exopodal segment; bearing on proximal segments a short and smooth (P2) or a long pectinate seta (P3); distal setae of second segments long and plumose; outer distal edges of first and second exopodal segments produced in a rather large and strong conical edge; P4 with typically prolonged exopodite, nearly 4 times as long as endopodite, bearing 3 rigid pectinate setae on inner margin of distal segment; outer distal edge of median exopodal segment rounded, not produced in a sharp process; endopodite reaching beyond first exopodal segment, bearing a pectinate seta on inner margin of proximal and distal segments; inner distal seta twice as long as outer one, reaching to distal end of third exopodal segment; couplers of P2-P4 rather wide, with a concave distal margin, and smooth surfaces; setal formula of legs listed in Table I.

P5 (Fig. 10a) with slender, long ovate exopodite, twice as long as endopodal lobe of leg, and bearing 6 smooth setae: 4 lateral ones, 1 apical one, and 1 sub-distal inner one; proximal outer exopodal seta often orientated along the margin (and as such difficult to observe); baseoendopodite with short outer conus bearing a smooth seta; endopodal lobe armamented with two spines and a plumose seta along inner side, and two (inner plumose, outermost smooth) apical ones; integument of both rami smooth, except for some fragil hairs along the inner margin of the endopodal lobe.

P6 (Fig. 7a) slightly protruded, bearing three elements: a very long inner seta (reaching to fusion line of first abdominal somite), and median and outer setae equally short; genital complex situated in second half of last thoracic somite, with deep crescentic genital pore on the fusion line; pore canal narrow and short, leading to paired anteriorly expanded receptacula; single median egg-sac containing 4-5 eggs, reaching to distal end of second abdominal somite.

MALE

Length, including rostrum and caudal rami, ranging from 621 to 654 μm (USNM 171272: 635 μm); prosome more

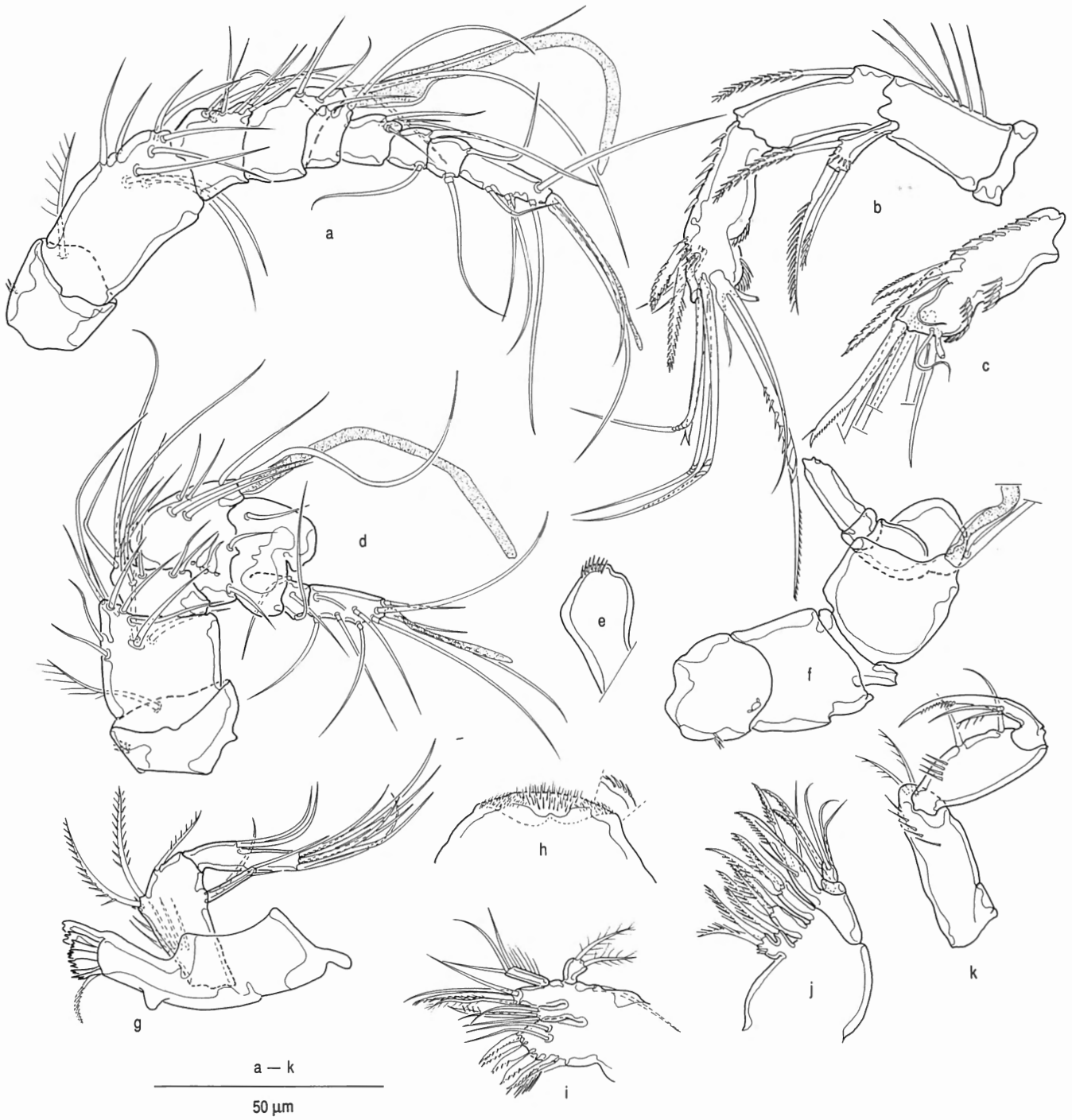

Fig. 8. – *Diagoniceps laevis* Willey, 1930: a, female antennule; b, antenna, outer view; c, ultimate segment of antenna, inner view; d, male antennule; e, paragnath; f, contour of male antennule; g, mandible; h, labrum; i, maxillule; j, maxilla; k, maxilliped (a-c, e, g-i, k, COP 3934; d, e, j, COP 3936).

tapering and urosomal part more slender than in female. Integument of prosomal and dorsum of urosomal somites as in the female; ventral surface of first abdominal somite ornamented with 2 mediolateral crescentic spinule rows on both sides, and a transversal row of slender spinules parallel to the posterior margin; second and third abdominal somites with smooth ventral surfaces, except for a row of spinules parallel with posterior margin (Fig. 7b).

Caudal rami (Fig. 7c) tapering posteriorly, without protuberance along inner margin, and with same armament as in female, except for the less bulbous distal part of median terminal seta; L/W-ratio ranging from 3.78 (USNM 171272) to 4.00.

Antennule (Figs. 8d, f) sub-chirocer, 8-segmented, with second segment 2.5 times as long as first one (in illustration second segment seems shorter, which results from inclined position); segments VI-VIII strongly sclerotized,

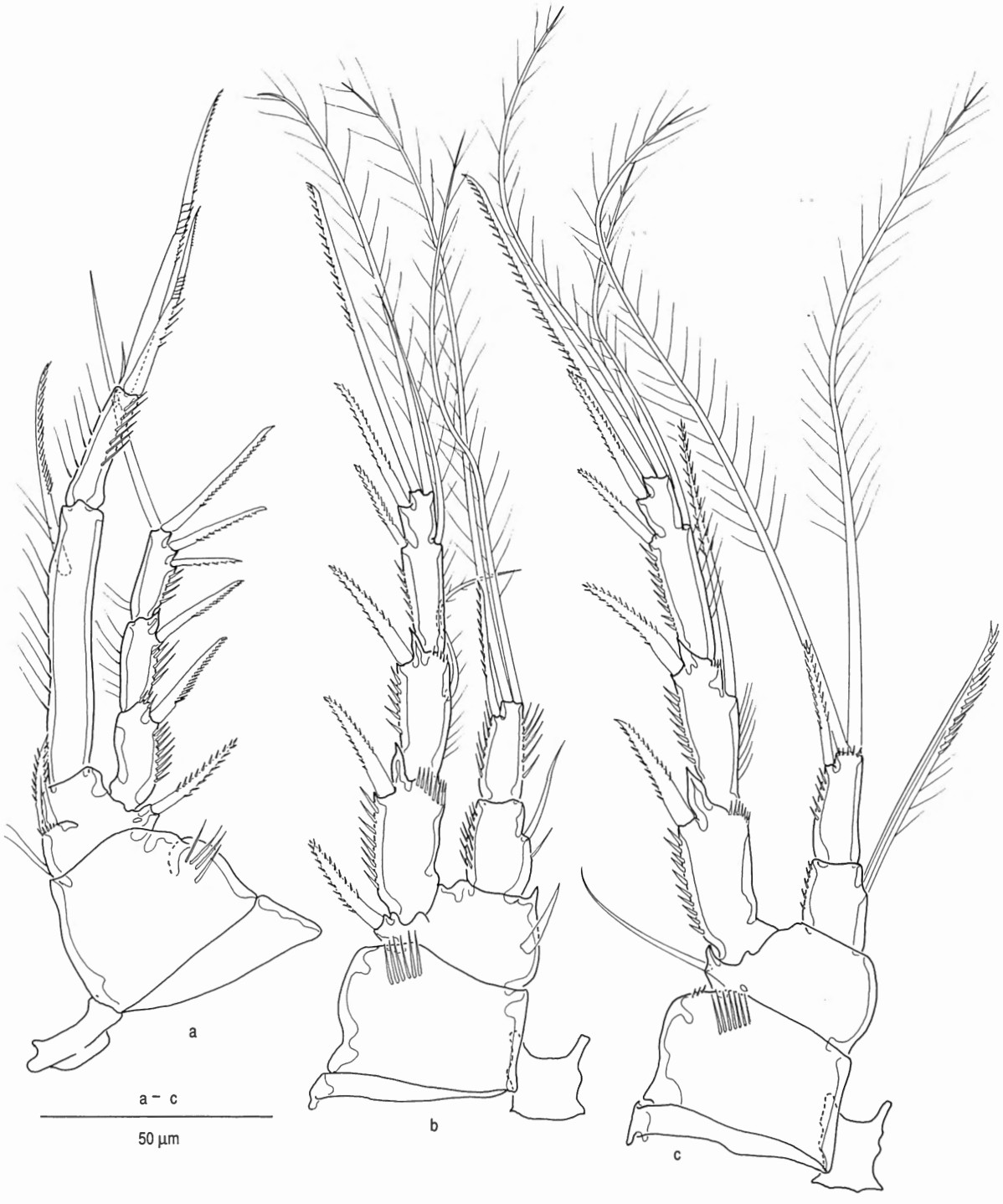

Fig. 9. – *Diagoniceps laevis* Willey, 1930: a, P1; b, P2; c, P3 (a-c, of female COP 3935, illustrated anteriorly).

forming sub-chirocer apparatus; setal armament (Arabic numerals): I(1)-II(11)-III(8)-IV(10+aest)-V(1)-VI(1)-VII(2)-VIII(9+aest); 2 setae on palm of segment IV short, flame-shaped; integument of all segments smooth, except for spinules on segment I.

P2 (Figs. 11b, c) with exopodite as in female; endopodite two-segmented with short inner smooth seta on proximal segment; inner distal element on second endopodal segment short; median and outer distal elements sinusoid, thickened in proximal and median third, very slender in distal third, without any ornamentation.

Outer distal edge of first exopodal segment of P3 (Fig. 11a) produced in a long outwards bended blunt (specimens from the Bahamas, Fig. 11f) or sharp (Bermuda specimen) attenuation (Fig. 12d), reaching beyond middle of second exopodal segment; exopodal segments two and three as in the female; inner pectinate seta of proximal endopodal segment somewhat more rigid than

in female, 2 (Fig. 11e) to 2.5 (Fig. 11a) times as long as second endopodal segment; second endopodal segment shorter than in female (L/W-ratio: 2 in male; 2.6 in female), having a blunt outer sub-distal processus and distinctly shorter spinules along outer margin; outer sub-distal spine slightly modified: somewhat thickened proximally and armed along the outer side of the stem only; distal setae as in female.
P4 rami and segments with proportional lengths as in female; third exopodal segment without distalmost inner pectinate seta (Fig. 10d); outer distal edge of second exopodal segment produced into a short sharp process (Fig. 10e); inner median seta of second endopodal segment short and smooth (Fig. 11g), just reaching beyond distal edge of segment; outer distal seta as long as inner one, only reaching to distal margin of second exopodal segment.
P5 (Fig. 10b) with baseoendopodites of opposite legs fused; exopodal segment short, just reaching beyond distal margin of endopodal lobe, bearing 6 elements: 3 outer smooth setae, one distal smooth seta, a sub-distal spinulose seta, and an inner proximal smooth seta; outer cone of baseoendopodite not produced; endopodal lobe with a distal seta and spine, and an inner spine, arising in second third of inner margin.
Right P6 (Fig. 6b) triangular but not differentiated from somite; left P6, slightly larger than right one and articulating with somite; both bearing three slender setae: a short outer and median, and, a long (twice as long as the other) medial one.

Variability. - A female specimen (COP 3939) was found possessing 2 inner smooth setae on the proximal endopodal segment of P2 (Fig. 11h), and a male specimen (COP 3936) shows a distinct subdistal articulation fissure (resembling an implantation of a seta) on the inner margin of the third P4 exopodal segment. The suspected pectinate seta might be detached during manipulation of the animal but was not found on the slides.

DISCUSSION

Although the type-series of this species seem to be lost, the here described specimens, recovered from sediments in a blue hole in the Bahamas, resemble the original description and illustrations of *D. laevis* in most aspects. Noticeable differences are the setal ornamentation of the female P5 exopodite and the shape of the modified endopodite male P2.
Neither WILLEY (1930) nor YEATMAN (1980) noticed the proximalmost outer seta on the female P5 exopodite. In both descriptions the female P5 was considered as bearing 5 instead of 6 exopodal setae. Indeed, in the several specimens at hand, and in YEATMAN's topotypic specimens, this seta is often found lying right on the outer margin of the segment, and is as such hardly visible.
The only reference of male dimorphism in the legs comes from WILLEY (1930) whereas YEATMAN (1980) provided an illustration of the male habitus. It should be noted that WILLEY's figure of the male P3 (1930: Fig. 40) was erroneously labeled as male P4 by LANG (1948 Fig. 361:1). The legs of the Bahamian male specimens agree nearly entirely with these described in the original description. The sole arresting differences noted are the length of the inner terminal seta of the P2 endopodite and the number of elements on the third exopodal segment of the P4. Although some variability of the male setal complement of the P4 may be found (see above), it is highly possible that WILLEY overlooked the reduced chaetotaxy of the male P4 exopodite.
The male P2 endopodite figured by WILLEY (1930: Fig. 23) shows a very long inner terminal seta which differs noticeably from the minute seta found in the Bahamian specimens (see Fig. 12c) and in the male specimen studied by YEATMAN (1980, see Fig. 12b herein). However, when this appendage is closely observed, it appears that this small seta is often found pasted to the inner edge of the long median element. In those cases, the exact length of the inner seta can only be guessed as its tip harmonizes with the stem of the accompanying element. Thus it seems evident that the long inner seta figured in the original description represents in fact the thickened smoothly curved outer margin of the median element.
YEATMAN's material from Bermuda shows some minor differences in the shape of the outer processus on the male P3 exopodite. Male specimens from the Bahamas show invariably a posteriorly recurved distal outer processus, while the male from Bermuda possesses a flattened sharp processus. Presence of spinules on the posterior surface of the second exopodal segment was not detected in the Bermuda specimen because of the anterior-posterior orientation of this appendage on the slide.
Finally, it turned out that the specimens identified as *D. laevis* from Castel Harbour (Bermuda) reported by COULL (1970) and COULL & HERMAN (1970), represent an unknown species. Based on the USNM-stored material of this collection, this species is described below as *O. elegantissima* n. sp. and assigned to the here defined new genus *Odaginiceps*.

REVIEW OF THE TAXONOMIC CHARACTERISTICS

Since WILLEY (1930) defined the genus *Diagoniceps* for *D. laevis*, only five species (*D. bocki* LANG, 1948; *D. monodi* CHAPPUIS & KUNZ, 1955; *D. menaiensis* GEDDES, 1968; *D. kunzi* MARINOV, 1973; *D. trifidus* YEATMAN, 1980) and a single un-named male specimen recovered from the French Atlantic coast (BODIN, 1979) have been added.
When GEDDES (1968) appointed *D. menaiensis* as the fourth *Diagoniceps* species, the presence of a three-segmented P1 endopodite created serious doubts on the monophyletic nature of this assemblage. Aware of this problematic situation, GEDDES (1968) preferred to enlarge the original generic diagnosis to accommodate his specimens rather than erecting a new monotypic genus

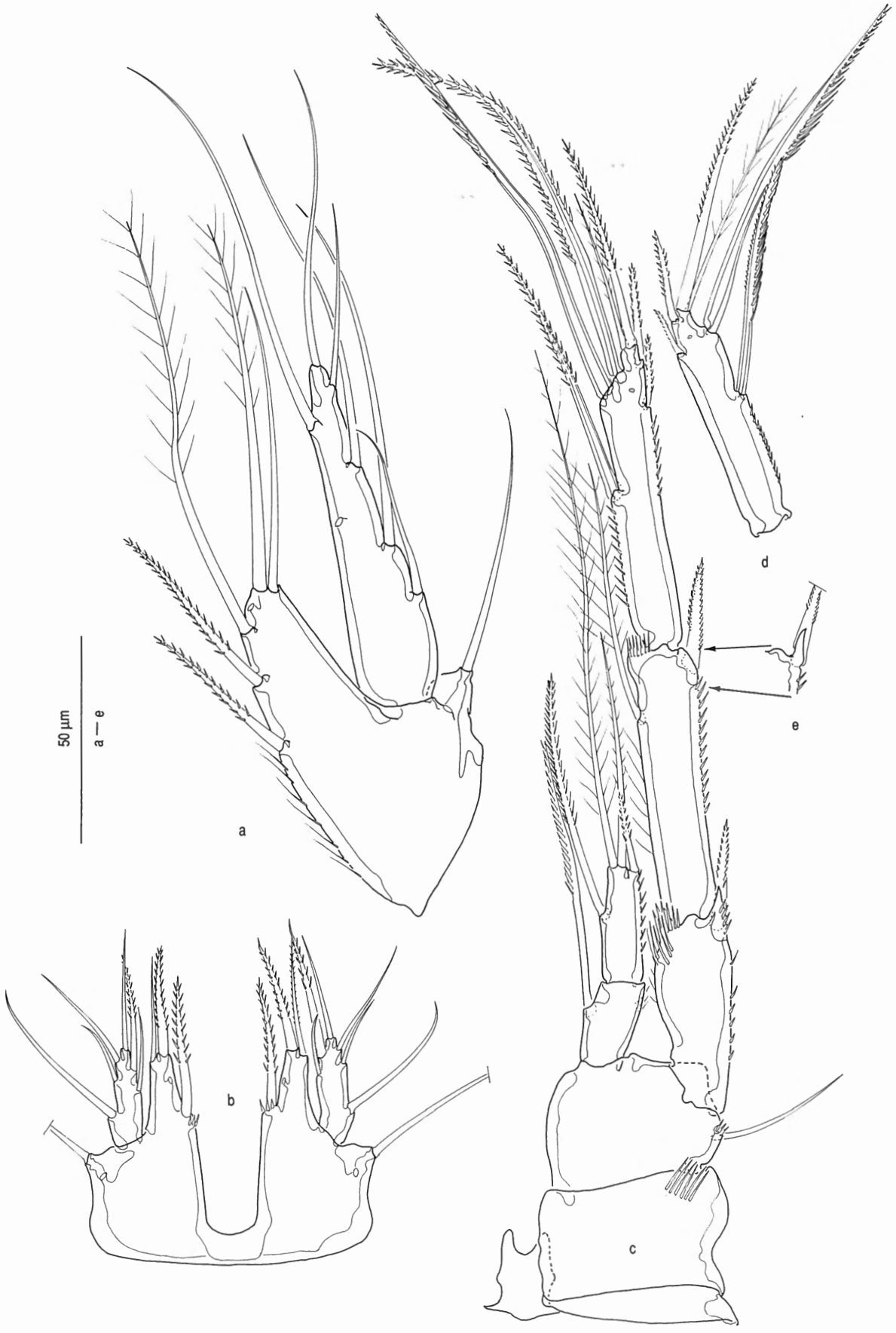

Fig. 10. – *Diagoniceps laevis* Willey, 1930: a, female leg 5; b, male leg 5; c, female leg 4, anterior; d, distal exopodal segment leg 4 of male; e, outer distal edge of male second exopodal segment, (a, c, COP 3934; b, e, COP 3936; d, USNM 171272).

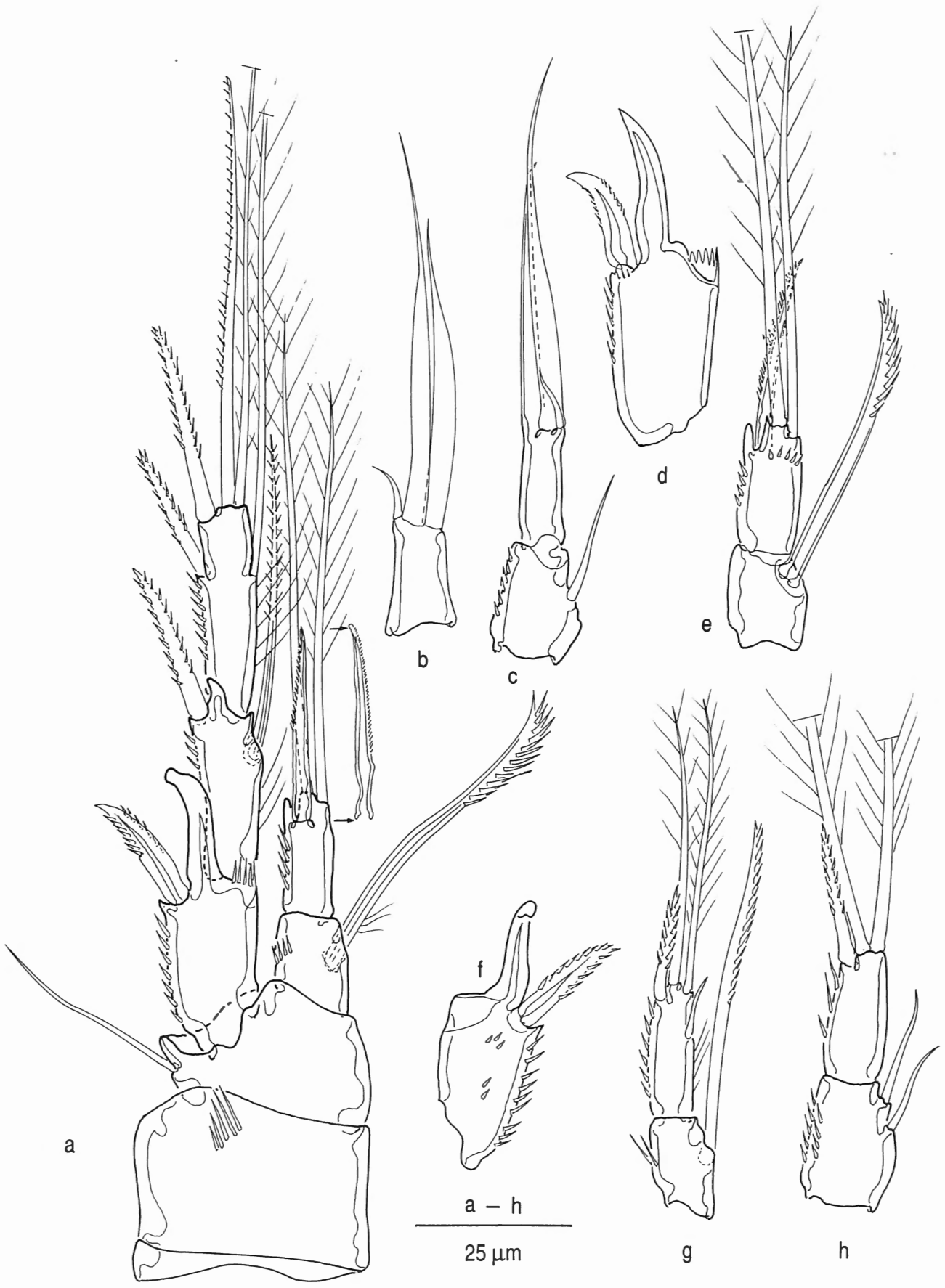

Fig. 11. – *Diagoniceps laevis* Willey, 1930: a, male leg 3, anterior; b, distal endopodal segment leg 2 of male, more or less laterally orientated; c, endopodite of male leg 2; d, first exopodal segment of male leg 3; e, endopodite of male leg 3; f, first exopodal segment of male leg 3; h, anomalous leg 2 endopodite of female (a, c, e-g, COP 3934; b, d, USNM 171272).

for *D. menaiensis*. Whereas BODIN (1979: p. 342) stated correctly that *D. menaiensis* should be allocated to an other genus, YEATMAN (1980) re-inforced GEDDES (1968) opinion after redescribing *D. laevis* and adding a second species to the genus characterized by a three-segmented endopodite in the first leg. He justified the generic assignation of *D. trifidus* and *D. menaiensis* because of the comparable setal complement on the terminal exopodal segments of the natatorial legs of both species and that of *D. laevis*.

With the discovery of several species in benthic samples recovered from the Yucatecan continental shelf and a species from Bermuda, the previously held discussion on the monophyletic nature of the genus *Diagoniceps* takes an interesting turn. In the following paragraphs, and based on the redescription of the type-species of the genus, the characteristics thought to be relevant for a phylogenetic analysis, are reviewed.

1. *Habitus.*

D. laevis is characterized by a graciously slender fusiform body devoid of particular integumental structures. Only at high magnification, a rather irregular pattern of minute spinules becomes visible (see Plate I: c and d).

Except for the work of YEATMAN (1980) who figured the habitus of the female of *D. trifidus* and the male of *D. laevis*, not a single description of the other species was accompanied with an illustration of the habitus. The body-shape was described to be cylindrical for *D. trifidus* and *D. laevis* (YEATMAN, 1980), lean in *D. monodi* ("élancé", CHAPPUIS & KUNZ, 1955), and with "abdomen somewhat more slender than thorax" (LANG, 1948: p. 895) for *D. bocki*, but is absolutely unknown for *D. menaiensis* and *D. kunzi*.

Consequently, no exact information on the shape, and most important, on the degree of fusion of the female genital somites is available. Only from *D. monodi* and *D. bocki* (see POR, 1964) we have an impression of the ventral surface of the genital double somite as they are the sole species from which the female genital field has been described.

As demonstrated above, the two original components of the genital double-somite in *D. laevis* are entirely fused. The former fusion line between both somites is in this species indicated by a rigidly sclerotized internal ridge, rather wide laterally and ventrally, but very fine in the dorso-median region. But, more important, there is no trace of a former fringe present on the lateral and dorsal external surfaces of the genital complex.

Based on the rudimentary figure of the genital complex provided by CHAPPUIS & KUNZ (1955: Fig. 16), we can assume that *D. monodi* has a female genital double-somite similar with that of *D. laevis*. The same could be concluded for *D. bocki* from the illustrations of the urosome in POR (1964: Fig. 56), but re-examination of the type-series of this species revealed a distinct external unornamented transversal ridge on the genital complex.

In contrast, the illustration of the habitus of *D. trifidus* in YEATMAN (1980: Fig. 1) leads to suspect that this species has a dorso-median transversal fringe, representing the remnant of the ancestral division of both somites. In addition, examination of *D. menaiensis* demonstrated that a comparable remnant is present. Unfortunately, most of the dorsum of the genital double somite of the specimen is not visible in the preparation at hand, so that the range of the fringe has to be confirmed.

Three species (*O. clarkae* n. sp., *O. elegantissima* n. sp., *O. xamaneki* n. sp.) from the Central West Atlantic, hereafter named the *clarkae* group, possess distinctly more angular body somites, ornamented along the posterior margins with a sinuate fringe, with in addition, a sinuate dorsal transversal remnant of the ancestral posterior margin of the sixth thoracic somite. Although a transversal ridge is present on the female genital complex in *D. bocki* (and presumably also in *D. kunzi* and the female of *Diagoniceps* spec.), the angular aspect of the somites with ornamented posterior ridges of the animals of the *clarkae* group seem to be important features differentiating this group from the other species actually unified in *Diagoniceps*.

Among the other tetragonicipitid genera, vestiges of the ancestral fringe on the genital double somite are only found in *Oniscopsis* CHAPPUIS, 1954 (see KITAZIMA, 1983 and MIELKE, 1989) and *Laophontella* THOMPSON & A. SCOTT, 1903 (pers. obs.). The presence of such vestiges is unknown for *Protogoniceps* POR, 1967. HUYS & BOXSHALL, 1991 claimed to have found a tetragonicipitid species still possessing separated genital somites in the female, but most unfortunately, the description has not been provided yet so that we are unaware of any other features of the body.

Integumental ornamentations on somites are described for *D. monodi* which has urosomal somites ornamented with minute setules on the surface, but with smooth posterior margins (CHAPPUIS & KUNZ, 1955) and for *D. bocki* which is furnished with long and slender spinules along the posteroventral margins of the urosomal somites and has an irregular pattern of short rigid protuberances on the dorsum of the urosome (see POR, 1964).

Although always present, integumental structures are hardly visible. Large and/or distinct surface structures are rare and are known so far for *Diagoniceps* spec. BODIN, 1977 only. Re-examination of the type-series of *D. bocki* revealed only the presence of minute, hardly visible, integumental structures, but distinct protuberances on the penultimate and ultimate somites as mentioned by POR (1964) for this species were not found.

2. *Rostrum.*

The rostrum of *D. laevis* is discreetly separated from the cephalothorax with a fine delicate suture. This situation is probably present in all other known species. Personal observations on representatives of the genera *Oniscopsis*, *Laophontella* and *Phyllopodopsyllus* revealed an identical individualization of the rostrum.

Observed in dorsal view, the rostrum in *D. laevis* is a short triangular element, not reaching beyond the distal edge of the first antennular segment. SEM observations clearly showed that the rostrum is a wedge shaped structure fitting between the antennular basal segments (see Pl. Ib). Re-examination of *D. bocki* and *Diagoniceps* spec. revealed a similar rostrum, whereas the rostrum in *D. menaiensis* has a distinctly wider proximal part which covers partially both basal antennular segments. A comparable rostrum is probably present in *D. monodi* as, in contrast with the description as "small and triangular" (CHAPPUIS & KUNZ, 1955), the accompanying illustration leads one to suppose that the rostrum in this species is a forwards directed plate, more resembling the rostum found in *D. menaiensis* than the one of *D. laevis*.
The large and broad rostrum in the *clarkae* species-group differs significantly from the small triangular rostrum in *D. laevis*, *D. bocki* and *Diagoniceps* spec. In the *clarkae* group the rostrum is a large laminar forwards directed broad structure, covering to some extent the dorsal surface of the first antennular segment.

3. *Caudal rami*

The basic shape of the female caudal rami seems to be roughly cylindrical, only slightly tapering towards the posterior margin. The only exceptions known so far are found in *D. menaiensis*, and the here described *Odaginiceps xamaneki* n. sp., both possessing short ovate rami, and *D. laevis*, having a rounded protuberance in the posterior half of the inner margin. Striking modifications of the basic morphology of the caudal rami as found in the other tetragonicipitid genera seem not to be present. The caudal rami of the males can be quite different from the rami of the females. In *D. laevis* of which females have an inner processus, males have normal tapering rami without peculiar structures. In *D. menaiensis* the male caudal rami are distinctly longer than in females, and are in fact more similar to these of the females of *D. trifidus*. In contrast, males of *D. bocki* have distinctly shorter rami than in the female. It seems quite possible that the (unknown) female of *Diagoniceps* spec. will be found to have considerably longer rami than the male, or that the (unknown) male of *D. kunzi* possesses nearly quadrate rami comparable with those known for the males of *D. bocki* and *Diagoniceps* spec.
The setal complement of the rami consists of 7 setae: a bi-articulate dorsal seta, three lateral and three terminal ones. Only the here described *Godianiceps maya* n. sp. forms an exception to this rule, as female and male rami are complemented with only 6 setae, lacking one of the proximal lateral setae.
In female specimens, the median terminal seta has a globulous or lobed aspect near the base, while males possess an unmodified median terminal seta. Modification of the setal base is a genuine aspect for Tetragonicipitidae where unmodified median terminal setae seem to be an exception.
The distalmost lateral seta arises from a position close to the distal outer corner of the lateral margin in *D. laevis*, and the species of the *clarkae* species-group, but has a more ventrally situated articulation in *D. menaiensis*, *D. bocki*, *Diagoniceps* spec., and *Godianiceps maya* n. sp. The outer terminal seta in *D. laevis* is strongly reduced in length, and is confluent with the median seta. A similar arrangement is found in *D. bocki*, and *Godianiceps maya* n. sp. A longer, but still confluent outer terminal seta, is present in *D. menaiensis*, *D. mexicana* n. sp., and probably in *D. trifidus*. It is highly probable that the outer distal element on the caudal rami as illustrated for *D. monodi* and *D. kunzi* is in fact the distal lateral seta, and that the outer terminal seta is very small and confluent with the median one as in *D. laevis*.
But, the caudal rami of the three species representing the *clarkae* species-group bear a long outer terminal seta with a more or less swollen base, and is not fused near its implantation with the median one.
The caudal armament of *D. monodi* appears to be quite different from that of the other species. Dorsal seta and (most probably both) proximal lateral seta(e) arise in the distal half of the ramus. From the illustrations Fig. 13 and 15 provided by CHAPPUIS & KUNZ, it seems that the distal outer element has a rather ventral position, and more important, seems to be modified into a robust appendage equal to the length of the expanded basal basal part of the median terminal seta. The absence of outer and inner terminal setae has to be re-confirmed, but, if present, it seems apparent that both are minute and hidden by the corpulent lateral and median setae.
The position, shape and fusion rate of the terminal setae in the other tetragonicipitid genera is far from adequately known. Relying on the excellent illustrations provided by MIELKE (1989) it seems that the median and outer setae are fused in *Tetragoniceps galapagoensis* and *Phyllopodopsyllus* (several species), but free in *Pteropsyllus trisetosus* and in the females of *Oniscopsis robertsoni*. The nature of the terminal setae of those species may be representative for their genus, but examination of the illustrations from other species (as an example *Tetragoniceps scotti* SARS, 1911) indicates that we can expect several kinds of modifications and fusion rates. Future re-examination of the caudal setae may reveal the phylogenetic significance of these modifications.

4. *Antennulae.*

So far, the main diagnostic characteristics used to distinguish *Diagoniceps* from the genera *Phyllopodopsyllus* and *Protogoniceps* have been the short first antennular segment and the absence of a sharp process (hook) on the second segment. However, with the allocation of the genus *Oniscopsis* CHAPPUIS, 1954 from the Paramesochridae to the present family (BECKER & KUNZ, 1981), even these aspects became inadequate to feature as key characteristics.
The female antennula of all *Diagoniceps* species is basically 9-segmented, although *D. bocki* shows a tendency to

reduce the number as segments VII and VIII are fused in some specimens. The setal armament of the several species (unified in their final genera) is given in Table II, and compared with the antennular complement in the other tetragonicipitid genera. It appears that the setal armament is mainly the same in all *Diagoniceps* related species, including the species unified in the *clarkae* group. The sole exceptions observed are an additional seta on segment III in *D. menaiensis* and one seta less on segment V in *D. bocki* but with an additional seta (5) on the aesthetasc bearing segment IV of the latter.

Phyllopodopsyllus shows the most interspecifically variable setal armament on segments III to VI, a supplementary argument of the polyphyletic nature of this genus. *Pteropsyllus* has a 7- or 8-segmented antennule but the total number of setae on segment VII or VII+VIII equals with the number found in the other genera. The terminal aesthetasc seems to be lost in this genus (see MIELKE, 1989 for *P. trisetosus*). The antennula of *Oniscopsis*, unique within the family because of the fused segments III and IV, seems to display slight interspecific differences in the number of setae on segments II and III. *O. robinsoni* CHAPPUIS & DELAMARE DEBOUTTEVILLE, 1956 bears 8 and 11 setae on segments II and III (MIELKE, 1989; pers. obs.) but has a 10 and 12 complement on these segments in *O. inabai* KITAZIMA, 1983.

Like *Oniscopsis*, *Laophontella* is characterized by a reduced number of antennular segments, but instead of a fusion between median and terminal segments, the smaller number of segments results from the fusion of first four segments (I+II+III+IV) and the segments VII+VIII (a feature which is rarely found in harpacticoids). Although the conglomerate nature of the first segment, the number of setae (20+Aest) is the same as in those antennulae with separated segments having a complement of I(1)-II(9)-III(6)-IV(4+Aest) as found in the genera *Pteropsyllus*, some *Phyllopodopsyllus* species, and *Oniscopsis*.

Among the here described *Diagoniceps* related species, ornamentation of the antennular armament is of generic importance. Except for the plumose seta on the first segment, antennular setae are smooth in *D. laevis*, *D. bocki*, *D. menaiensis* and *Diagoniceps* spec. while several setae have a pinnate ornamentation in the species of the *clarkae* group. The presence of ornamented setae seems unique within the family. Unfortunately, we are unaware of such features for *D. monodi* and *Protogoniceps hebraeus*.

The proportional lengths of the two first antennular segments appear to be important taxonomical characteristics. The second antennular segment in *D. laevis* has a prolonged shape, being almost 2.5 times as long as the first one. An identical situation is found in *D. bocki* and *Diagoniceps* spec., and has been illustrated for *D. kunzi*, but was not described in detail for *D. monodi*. In contrast, the antennulae in *D. menaiensis*, *D. trifidus*, and the species of the *clarkae* group have a second segment which is only slightly longer than the basal one. Moreover, whereas the second antennular segment in *D. laevis* and congeners is a unmodified cylindrical element, the *clarkae* group (and in some lesser degree *D. menaiensis*) shows a rigidly sclerotized extension along the posteriorly directed margin of the segment.

The median expanded region of the male antennule of *D. laevis* is basically similar in all other species, and in the other tetragonicipitid genera. The palm of the antennulae, formed by the segments IV, V and VI, shows a distinct suture on the ventral surface (indicating two segments) but shows no trace of an articulation on the dorsally directed surface.

The inner surface of the palm is complemented with a number of short swollen setae in *D. laevis*, *D. bocki*, *Diagoniceps* spec., *D. mexicana* n. sp., *Godianiceps maya* n. sp. and the species of the *clarkae* group. In *D. menaiensis* three of these setae have a globulous aspect, but in addition, antennular segment VI possesses a large unguiform element. Such modification is undoubtedly of

Table II: Female antennular armament in Tetragonicipitidae (see Table III for species unified in new genera).

	Seg I	Seg II	Seg III	Seg IV	Seg V	Seg VI	Seg VII	Seg VIII	Seg IX
Diagoniceps	1	9	7	4+Aest	2	4	2	2	7+Aest
Aigondiceps n. gen.	1	9	7	5+Aest	1	4	2	2	7+Aest
Nidiagoceps n. gen.	1	9	8	4+Aest	2	4	2	2	7+Aest
Odaginiceps n. gen.	1	9	7	4+Aest	2	4	2	2	7+Aest
Godianiceps n. gen.	1	9	7	4+Aest	2	4	2	2	7+Aest
Phyllopodopsyllus[1-2]	1	9	6,7,8	3,4+Aest	1,2	3,4		4[3]	7+Aest
Oniscopsis[1-2]	1	8-10	11-12+Aest		2	3	2	2	7+Aest
Tetragoniceps[1]	1	7	7	4+Aest	2	4		4	7+Aest
Pteropsyllus[1]	1	9	6	4+Aest	2	3		11	
Laophontella (pers. obs.)			20 + Aest		2	3		4	7+Aest

[1]: after MIELKE, 1989, and the herein described *Ph. yucatanensis*; and [2]: KITAZIMA, 1981; KITAZIMA, 1983; [3]: species with separated segments VII and VIII bear 2 setae on each segment.

significant phylogenetic importance, and it is presumed that a comparable and homologous structure will be found in the, as yet, unknown male of the closely related *D. trifidus*.

5. *Buccal appendages*

The basic plan of the antenna is identical in all species: a basis with a one-segmented exopodite, bearing three pinnate elements, and a two-segmented exopodite complemented with 11 elements on its ultimate segment. The abexopodal margin of the basis never bears an element, but the abexopodal edge of the first endopodal segment is in the majority of the species equipped with a long plumose seta. So far, the only known species without an abexopodal seta is *D. menaiensis*. The antenna of the closely related *D. trifidus* is described with a rather short (not reaching beyond the distal margin of the supporting segment) abexopodal seta. The absence of an abexopodal seta on the first endopodal segment in *D. kunzi* has to be confirmed.

Except for some minor differences (ornamentation, number of teeth), the mandible has a nearly similar structure in all Tetragonicipitidae: a large well developed gnathobasis, bearing a long distally widening coxa-basis with clearly defined exopodal and endopodal rami. Only the exopodal ramus displays a noteworthy inter-specific variability.

D. laevis has a short (only half as long as endopodite) one-segmented mandibular exopodite, with a proximal, a sub-distal and an apical seta. A similar exopodite is found in *D. mexicana* n. sp., bearing four terminal setae, *D. menaiensis* having three (not four) lateral and three apical elements, *D. monodi* with two lateral and three terminal setae, and *Godianiceps maya* n. sp. which is complemented with two proximal, one sub-distal, and two terminal setae.

A two-segmented mandibular exopodite has been reported for *D. trifidus* and *D. bocki* (in POR, 1964). But re-examination of *D. bocki* revealed that the mandibular exopodite is three-segmented, with from proximal to distal segment, 1, 2, and 4 setae respectively. As such the exopodite of *D. bocki* is similar with the mandibular ramus of the species constituting the *clarkae* group, except that the latter possess only three setae on the terminal segment. Unfortunately, the mandible of *Diagoniceps* spec. was not found on the slide.

The maxillulae are similar in all species studied here, although the number of setae and spines, and the ornamentation on the surface of the constituting segments may differ. The presence or absence of an epipodal seta may turn out to be of generic importance in the family, but as the description of this buccal appendage has often been omitted, confirmation is needed before the phylogenetic importance can be inferred.

In all species, except for *Godianiceps maya* n. sp. which bears a one-segmented endopodal ramus, the maxilla is characterized by three to four endites and a two-segmented endopodite. In the species of the *clarkae* group and in *Godianiceps maya* n. sp., the proximal endite is a simple cylindrical appendage complemented with three pinnate spines whereas in the other species, inclusive *D. monodi*, the proximal endite is a bifid structure bearing a single element on the distal ramus and two (*D. laevis*, *D. mexicana* n. sp., and *D. monodi*?) or three (the other species) elements on the proximal part. Only *D. menaiensis* possesses a maxilla equipped with 4 distinct endites. The bifid aspect of the proximal endite in the descriptions of the maxilla in GEDDES (1968) and BODIN (1979) is a result of the appositional location of both endites. The separation of both endites is obvious when observed with phase contrast.

Among the other tetragonicipitid genera a two-segmented maxillar endopodite seems common. So far, only *Oniscopsis inabai* KITAZIMA, 1983 is known to possess a three-segmented endopodite. Bifid proximal maxillar endites are described for *Tetragoniceps*, *Laophontella*, and for at least two *Phyllopodopsyllus* species (*Ph. opistoceratus* GEDDES, 1968; *Ph. parafurciger* GEDDES, 1968), although maxillae with four endites seems to be common in *Phyllopodopsyllus* (*Ph. simplex* KITAZIMA, 1981; *Ph. punctatus* KITAZIMA, 1981; *Ph. setouchiensis* KITAZIMA, 1981; *Ph. thiebaudi santacruzensis* MIELKE, 1989; *Ph. galapagoensis* MIELKE, 1989; *Ph. kunzi* MIELKE, 1989, and for *Ph. angolensis* and *Ph. furciger* in MIELKE, 1989) and in the three species of *Oniscopsis* (pers. obs.; KITAZIMA, 1983; MIELKE, 1989). In all these species the distal cylindrical endite (forming the proximal part of a bifid endite) is distinctly separated from the proximal one.

The prehensile maxilliped is basically the same in all species, but differs among them in the setal number on the several segments. A full complement is found in *D. menaiensis*: 3 elements on basis, 2 on inner margin of palm, and 3 setae accompanying the claw. In *D. trifidus* the third element on the basis and claw are probably overlooked in the original description. The species of the *clarkae* group possess a comparable complement of the maxillipedal elements, but have only two setae on the claw. *D. laevis* and *D. mexicana* n. sp. bear two elements on the basis, palm and claw, whereas *D. bocki* and *Diagoniceps* spec. possess a full complement on basis and claw, but have only one (the distalmost) left on the palm. It seems highly probable that the third seta of the basis has been overlooked in the description of *D. kunzi*. The most advanced maxillipeds are found in *Godianiceps maya* n. sp. as they possess only two elements on the basis and none on either the palm or the claw. Finally, the complete absence of setae on the three maxillipedal segments in *D. monodi* needs confirmation.

6. *First leg.*

Segmentation and chaetotaxy of the P1 endopodite is undoubtedly of phylogenetic importance (BODIN, 1979). *D. laevis* has a two-segmented P1 endopodite, complemented with three elements on the distal edge of the distal segment. Both outer elements on the distal segment have a pectinate aspect, while the inner one is a short

slender seta. A similar situation is found in *D. mexicana* n. sp., and the three species forming the *clarkae* group. A two-segmented P1 endopodite with only two terminal elements is present in the *D. bocki* (pers. obs.), *Diagoniceps* spec. and *Godianiceps maya* n. sp., and probably in *D. kunzi* as this species resembles *D. bocki* closely. CHAPPUIS & KUNZ (1955) mentioned only two setae on the distal segment of the P1 endopodite of *D. monodi*. But, as the inner one is easily overlooked, their statement has to be confirmed in the future.

Although the general appearance of the P1 endopodite of *D. menaiensis* and *D. trifidus* resembles the P1 endopodite of the other species, it differs significantly as it has three segments instead of two. This, in combination with other features viz. the genital- double somite, shape of the rostrum, shape of antennular segments, the particularly modified male antennule, and the nature of the inner elements on the male P5 exopodite, indicate that both species represent a distinct evolutionary branch among the *Diagoniceps*-like species. So far, the sole tetragonicipitid genus defined with a three-segmented P1 endopodite is *Pteropsyllus*. However, it is apparent that the latter is not directly related with *D. menaiensis* and *D. trifidus*, but has more in common with the genus *Phyllopodopsyllus* (viz. prolonged first antennular segment, and the foliaceous exopodite of female P5). Note that the segmentation of the P1 endopodite in *Protogoniceps*, originally described as three-segmented (POR, 1964), has been corrected as two-segmented by COULL (1973) on the basis of the original figures.

Thus the presence of a three-segmented endopodite in *D. menaiensis* and *D. trifidus* is unique among the *Diagoniceps* related species. Taking in consideration the above mentioned characteristics, which are assumed to represent plesiomorphic character states, it seems appropriate (and in accordance with the remarks of BODIN, 1979) that *D. menaiensis* and *D. trifidus* are representatives of a group which branched off early in the tetragonicipitid evolutionairy history.

7. *Natatorial legs.*

All species considered herein possess three-segmented exopodites and two-segmented endopodites. Within the family, modifications of this basic plan are known only in genera *Oniscopsis* (two-segmented P1 exopodite, one-segmented P4 endopodite), and *Laophontella* (reduction of segment dimensions).

In an effort to argue about the generic designation of *D. trifidus*, YEATMAN (1980) labored with the setal armament of exopodites and endopodites of *D. laevis*, *D. menaiensis*, and *D. trifidus* but could not come to a general conclusion.

In Table III, the chaetotaxies of the several *Diagoniceps* related species are listed. Without going in detail too far and discussing the several complements observed for each

Table III: Chaetotaxy of P2-P5 (^{1}: the seta is strongly reduced; setal armament: - means unknown).

Genus	P2		P3		P4				P5 (exo/bas)	
Species	exo	end	exo	end	exo ♀	end ♀	exo ♂	end ♂	♀	♂
Diagoniceps Willey										
laevis Willey	0-1-122	1-021	0-1-122	1-021	0-1-322	1-121	0-1-222	1-121	6/5	6/3
mexicana n. sp.	0-1-122	1-021	0-1-122	1-021	0-1-322	1-121	0-1-222	1-121	6/5	6/3
Aigondiceps n. gen.										
bocki Lang	1-1-123	1-121	1-1-223	1-121	1-1-323	1-121	1-1-223	1-121	6/5	4/3
kunzi Marinov	1-1-123	1-121	1-1-223	1-121	1^1-1-323	1-121	–	–	6/5	–
bodini n. sp.	1-1-123	1-121	1-1-223	1-121	–	–	1-1-223	1-121	–	6/3
Nidiagoceps n. gen.										
menaiensis Geddes	1-0-023	1-021	1-0-023	1-021	1-1-323	1-021	1-1-323	1-121	6/5	6/3
trifidus Yeatman	1-0-022	1-021	1-1-022	1-121	1-1-322	1-121	–	–	6/5	–
Odaginiceps n. gen.										
clarkae n. sp.	0-0-023	0-021	0-0-023	0-021	0-0-222	1-020	0-0-222	1-020	6/5	6/3
elegantissima n. sp.	0-0-022	0-021	0-0-022	0-021	0-0-222	1-020	–	–	6/5	–
xamaneki n. sp.	0-0-023	0-021	0-0-023	1-021	0-1-322	1-021	0-1^1-222	1-021	6/5	6/3
Godianiceps n. gen.										
maya n. sp.	1-1-122	1-021	1-1-222	1-021	1-1-322	1-121	1-1-222	1-121	5/5	4/3
? *Diagoniceps monodi*	1-1-122	1-021	1-1-222	1-121	1-1-322	1-121	1-1-322	1-121	6/5	5/3

known and herein described species, the following generalities are concluded: (1) *D. bocki*, *Diagoniceps* spec. (=*D. bodini* n. sp.) and *D. kunzi* possess the most complete chaetotaxies; (2) the chaetotaxies within the species-groups considered are variable (but species-specific); (3) those species with a 322 complement on the ultimate segment of the female P4 exopodite have a complement in the male P4 of 222; and (4) the endopodal chaetotaxy of the P4 endopodite is equal in males and females, except for *D. menaiensis* showing an additional seta on inner edge of the distal endopodal segment of the male P4.

Of generic importance is the presence and shape of the inner elements on the proximal P2 endopodal segments. In *D. laevis* and its closest congener *D. mexicana* n. sp. the P2 inner element is a rather short smooth unmodified seta, whereas in *D. bocki*, *Diagoniceps* spec., and *D. menaiensis* the inner seta is a moderately long pectinate robust appendage. A similar pectinate seta is present in *Godianiceps maya* n. sp. Unfortunately, an exact description of this appendage has not been provided for the species *D. kunzi*, *D. trifidus* and *D. monodi*, but we assume here that this element is pectinate as in their congeners. An inner element is absent in both sexes of the species assigned to the *clarkae* group.

Sexual dimorphic features on the endopodites of the legs are identical in the here considered *Diagoniceps* related species and in all tetragonicipitids: P2 endopodite with two long smooth elements rather swollen over 3/4 of the length of their stem and accompanied with a short slender unarmed inner seta; P3 endopodite with the sub-distal outer spine more or less different in appearance than its female homologue; and the P4 endopodite often with more rigidly shaped and shorter elements than in the female. Only *Pterinopsyllus* has a strongly modified proximal segment in the P4 endopodite, and some species of *Phyllopodopsyllus* possess less elements on the distal P4 endopodal segment (ex.: *Ph. yucatanensis* n. sp., *Ph. paramossimani* LANG, 1934).

In addition, the distal edge of the second endopodal P3 segment shows in most of the species one or two small but distinctly extended processes. In the males of *D. laevis* the inner margin is equipped with a distinct processus near the implantation of the sub-distal outer spine, whereas in its closest congener, *D. mexicana* n. sp., this margin shows a small triangular extension on the same place. Males of *D. bocki* have the inner distal corner extended into a triangular process, but lack a modification on the outer margin. Such structure is also present in the male P3 of its closest congener, *Diagoniceps* spec. which in addition shows also a triangular anterior processus in the middle of the distal edge. In *D. menaiensis* and in the two known males of the *clarkae* group, three triangular processes are present on the male P3: one on the inner margin, one in the middle of the distal edge, and one on the inner distal corner.

No similar modifications on the distal edge in the male P3 of *Godianiceps maya* n. sp. has been observed, and we are unaware of the presence of any similar structures in the male P3 of *D. monodi*.

P3 modifications in the males in the other tetragonicipitid genera seem restricted to transformations of the outer subdistal spine and the lengths of the terminal setae. The only example known to me of an additional processus along the outer margin of the second segment has been described by KITAZIMA (1981) for *Ph. punctatus*.

Sexual dimorphism in the exopodites of the legs is far less documented. Sexual modifications of the exopodal rami (spine lengths, segment dimensions) are most explicitly displayed in the P4 of the species attributed to the genera *Oniscopsis* and *Laophontella*. Most species having a 322 or 333 complement on the terminal female P4 exopodite, bear a 222 or 223 armament in the male. Unfortunately, the P4 chaetotaxy differences seem often to be overlooked, and will have to be confirmed in many cases.

Presence or absence of a processus on the outer distal corner of the median exopodal segment of the P4 emerges to be of phylogenetic importance. Whereas the female of *D. laevis* lacks an outer attenuation, the median segment of the male P4 exopodite displays a rather long sharp, slightly curved extension on its distal outer corner. A comparable structure is found in the males of *D. bocki*, *Diagoniceps* spec. and the species of the *clarkae* group. But whereas males of *D. laevis* possess a sharp extension in the P4, in those species having in the female P4 an attenuated outer distal corner, males possess a sinuate blunt outer processus on the median segment. The median P4 segment in *D. menaiensis* and *Godianiceps maya* n. sp. (both species having a rounded outer distal corner in the female P4) display no sexual modifications on the outer corner.

The statement of CHAPPUIS & KUNZ (1955) that no sexual dimorphism is present in *D. monodi* has to confirmed. It is obvious that presence or absence of sexual dimorphic features in the male P4 exopodite have not been accurately observed in the descriptions of the other tetragonicipitid species. However, relying on the illustrations of Tetragonicipitidae from the Galapagos Islands provided by MIELKE (1989), it becomes clear that similar modifications of the median exopodal segment of the P4 are common within the family. *Tetragoniceps galapagoensis* MIELKE, 1989, having a rounded distal outer corner in its female P4, has a distinct sharp processus in the P4 of the male, similar to that described for *D. laevis*. On the other hand, in *Pteropsyllus trisetosus* MIELKE, 1989 the median P4 segment is identical in both sexes, and resembles as such *D. menaiensis* and *Godianiceps maya* n. sp. Unfortunately, whether this is also true for the other species attributed to these genera is not known.

Within the genus *Phyllopodopsyllus*, at least two forms of sexual dimorphic modifications occur on the median P4 exopodal segment. Females of *Ph. furciger* (sensu MIELKE, 1989) and *Ph. thiebaudi santacruzensis* MIELKE, 1989 have a sharp attenuation of the outer corner, but males of these species lack the attenuation entirely, showing instead a rounded outer distal corner. In contrast, the P4 median segment in *Ph. angolensis* KUNZ, 1984 (see MIELKE, 1989) and *Ph. galapagoensis* MIELKE, 1989 is identical in both sexes.

Based on these examples it is assumed here that the sexual dimorphic transformations of the median exopodal segment of the P4 may turn out to be of primordial importance in a revision of the genus *Phyllopodopsyllus* as such structures and modifications may lie at the base to test the monophyletic nature of the groups presently defined within this genus.

Finally, *D. laevis* is unique among the other species in that the proximal P3 exopodal segment in the male shows a large bended process on the outer distal corner. The closely related *D. mexicana* n. sp. does not show any trace of modifications on the segment in question, although the female of this species has a similar sharp extension of the distal corner as in the females of *D. laevis*.

8. *Fifth legs.*

The basic morphology of the female P5 in the known *Diagoniceps* species is identical with the fifth leg present in *D. laevis*: exopodite not fused with the baseoendopodite, neither ramus expanded to form a brood pouch, and complemented with five baseoendopodal and six exopodal elements. The exopodal segment has a gracious long ovate appearance in most of the species. Only *D. bocki*, *D. monodi*, and *D. kunzi* show a slightly more angular P5 exopodite.

Among the other tetragonicipitid genera, a *D. laevis* P5 type is found only in the genus *Protogoniceps* and in some species of the genus *Tetragoniceps*. The presence of several types of P5 in the latter will certainly turn out to be a strong argument in the discussion on the polyphyletic nature of the genus *Tetragoniceps*.

The female P5 of *Godianiceps maya* n. sp. differs fundamentally from the *D. laevis* P5 type as the exopodite has a more rounded shape (not elongated), bearing only five elements.

The fifth legs in the four known *Diagoniceps* males are similar in appearance: a short endopodal lobe with three spines, and an ovate exopodite with two inner, one apical, and three outer elements. Only *D. bocki*, *D. monodi* and the here described *Godianiceps maya* n. gen., n. sp. are exceptions as the male P5 possesses four (*D. bocki* and *G. maya*) or five elements (*D. monodi*).

Form and ornamentation of the elements on the male P5 exopodite are certainly of phylogenetic importance. The exopodite in *D. laevis* and *D. mexicana* n. sp. is complemented with only a single pinnate spine, arising from sub-distal position along the inner margin of the segment. The apicalmost seta, the three outer lateral setae, and the proximal inner seta all are un-ornamented slender setae. In contrast, in all other known species of which the males are known, and those species referred to as the *clarkae* group, the P5 possesses at least two pinnate elements, even when the complement is reduced as in *D. bocki* and the herein described *Godianiceps maya* n. sp.

In the two known males of the *clarkae* group the sub-distal inner exopodal spine is rather slender but distinctly ornamented with short spinules along both sides of the stem. More explicitly is the robust shape of the proximal inner one furnished with long spinules on either side (*O. clarkae*) or along the inner margin (*O. xamaneki*). A comparable morphology of the exopodal appendages is found in *D. menaiensis*, but whereas the apicalmost element is a smooth seta in the *clarkae* group, *D. menaiensis* (and probably *D. trifidus*) bears a long bi-pinnate and anttenuated distalmost seta and a considerably shorter, less ornamented proximal inner spine.

In *D. bocki* and *Diagoniceps* spec, apicalmost and subdistal inner elements are bi-pinnate spines, and whereas *Diagoniceps* spec. still possess a slender, unornamented proximal inner seta, *D. bocki* has lost this element. At first sight, a situation as in *D. bocki* is present in *Godianiceps maya* n. sp. possessing only four elements of the exopodite. However, as the distalmost pinnate spine has sub-apical position, it is assumed here that the inner elements in this species are homologous with the two inner spines found in *D. menaiensis* and the *clarkae* group.

The male P5 exopodite of *D. monodi* has been described possessing 5 appendages: two smooth outer setae, and an apical and two inner spiniform elements. Unfortunately, an illustration was not provided. No other species is known so far having a complement on the P5 exopodite which fits with this description. Only the male P5 of *D. menaiensis* shows some resemblance as it bears three pinnate elements. However, it seems clear that the P5 in *D. monodi* distinctly differs from that of *D. menaiensis* as the latter bears relatively short inner spines and has an apical spine with a slender appearance.

9. *Conclusions.*

It is apparent that the three species referred to in the preceeding paragraphs as the *clarkae* species-group are not to be assigned to the genus *Diagoniceps* or any other presently known tetragonicipitid genus. These three species are unified within the genus *Odaginiceps* n. gen. The two species *D. menaiensis* and *D. trifidus*, both characterized by their three-segmented endopodite in P1, are removed from *Diagoniceps* and unified in the genus *Nidiagoceps* n. gen. *D. bocki*, *D. kunzi*, and *Diagoniceps* spec. (considered here as a undescribed species, named *A. bodini* n. sp.) are assembled in the genus *Aigondiceps* n. gen. *D. monodi* cannot be properly assigned neither to *Diagoniceps* nor to one of the other genera, as the description of this species is far from sufficiently detailed to provide indications of to which group it could be referred. From the previously described species, only *D. laevis* remains in the genus *Diagoniceps*, but is joined with a second species, *D. mexicana* n. sp., described in the following pages.

Based on the here presented review of the salient features of the *Diagoniceps* related species and the Tetragonicipitidae in general, it would be interesting to analyse the phylogenetic relationships between the different taxa. However, as has been stressed in the introduction of this paper, and in the several paragraphs of the previous section, our knowledge of the character states and character state changes in the other genera actually unified within

the family Tetragonicipitidae is still too sketchy. As such, it is perhaps wiser to postpone such analysis until more information becomes available.

Genus **Diagoniceps** WILLEY, 1930 amended

SYNONYMY

Diagoniceps, gen. nov. - WILLEY, 1930: p. 94-95; LANG, 1944: p. 27; NICHOLLS, 1944: p. 492; LANG, 1948: p. 894; LANG, 1965: p. 386; COULL, 1973: p. 14; KUNZ, 1984: p. 34-35; BODIN, 1988: p. 145.

AMENDED DIAGNOSIS

Tetragonicipitidae with a slender fusiform, nearly cylindrical, body; without external remnants of fusion line between genital somites; somites without marked integumental structures; rostrum very narrow, strongly bended ventrally, and fitting between basal antennular segments; caudal rami cylindrical, dimorphic in type-species; outer terminal seta short to extremely small, confluent with median terminal seta.

Antennulae 9-segmented with short, square first segment, and long (up to 3 times as long as wide) second segment; principal aesthetasc on segment IV; integument of antennular segments smooth, except for short row of slender spinules on segment I.

Antenna with basis, bearing a well developed one-segmented exopodite with three pinnate setae, one abexopodal seta on first endopodal segment and 11 elements on second segment; exopodite and endopodite of mandible distinct, one-segmented, former half as long as latter; maxillule with single slender and plumose epipodal seta, and distinct one-segmented exopodite and endopodite; maxilla with three endites, each having three pinnate spines; maxillar claw accompanied with a robust pinnate seta, and endopodite two-segmented bearing 3 smooth and 2 pinnate setae; basis, palm and claw of maxilliped armamented with 2, 2 and 2 setae respectively.

P1-P4 exopodites three-segmented, endopodites two-segmented; endopodite P1 complemented on distal segment with 3 elements; proximal endopodal segments P2-P4 with inner seta: short and smooth in P2, long and pectinate in P3 and P4; proximal exopodal segments without inner armament, and distal exopodal segments with single inner seta in P2 and P3, with 3 pectinate setae in P4; aspect of P4 exopodite prolonged; exopodite P5 articulating, long ovate, with 6 smooth setae; endopodal lobe of baseoendopodite with two pinnate setae and one setulose seta on inner margin, and one setulose and one smooth seta on distal edge; P6 vestiges with three smooth elements.

Male: setae on caudal rami as in female, except for less bulbous basis of median terminal seta; aspect of rami more slender, lacking inner process or spinulose ornamentation; antennule sub-chirocer, 8-segmented, but with palm only subdivided on ventral side; segment IV with principal aesthetasc and two flame-shaped setae; dimorphism typical tetragonicipitid in P2 and P3, with in addition a long sharp extended outer process on first exopodal segment of P3, and inner seta of second endopodal segment P4 reduced; second exopodal segment P4 extended into a small sharp process, and third exopodal segment with two inner pectinate setae; P5 exopodite complemented with 6 elements, inner proximal one short and smooth; P6 vestiges armed with three elements.

TYPE-SPECIES

Diagoniceps laevis WILLEY, 1930, by original designation.

OTHER SPECIES

Diagoniceps mexicana n. sp., described below.

Diagoniceps laevis WILLEY, 1930

SYNONYMY

Diagoniceps laevis, sp. n. - WILLEY, 1930: p. 98-99, Fig. 28-37, 39-45, Pl.V: Fig. 38.

Diagoniceps laevis WILLEY, 1930 - LANG, 1948: p. 895, Fig. 361(1); CHAPPUIS & KUNZ, 1955: p. 1023; POR, 1964: p. 250; GEDDES, 1968: p. 443; COULL, 1973: p. 14; MARINOV, 1973: p. 321; WELLS, 1976: p. 133; YEATMAN, 1980: p. 123-125, Fig. 14-22; WELLS, 1981: p. 7; KUNZ, 1984: p. 34; WELLS, 1985: p. 9, 10; BODIN, 1988: p. 145. Non *Diagoniceps laevis* WILLEY: COULL, 1970: Table 8; COULL & HERMAN, 1970: Table 1 (= *Odaginiceps elegantissima* n. sp.).

TYPE-LOCALITY

Bermuda, Mangrove Lake. Salinity: 30.7‰. Leg. A. WILLEY, 17 August 1928 (WILLEY, 1930).

REDESCRIPTION

See above.

Diagoniceps mexicana n. sp.
Fig. 12 - 15

TYPE-MATERIAL

Holotype: female, dissected on 6 slides, labeled COP 3974 A-F; allotype: male dissected on 6 slides, labeled COP 3973 A-F; paratypes: one female dissected on a single

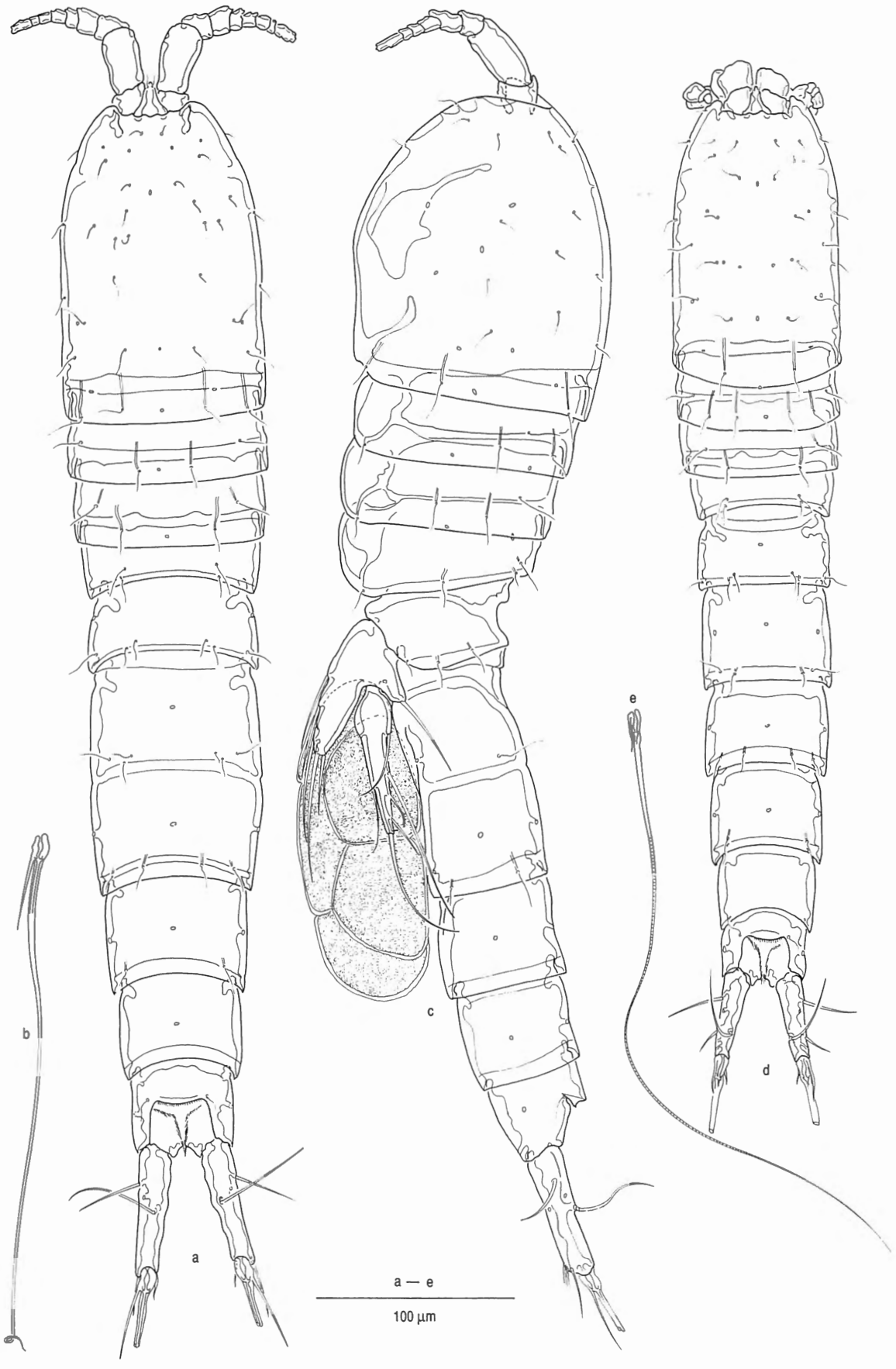

Fig. 12. – *Diagoniceps mexicana* n. sp.: a, female habitus, dorsal; b, left median caudal setae; c, female habitus, lateral; d, male habitus, dorsal; e, left median caudal setae (a-c, holotype female; d-e, allotype male).

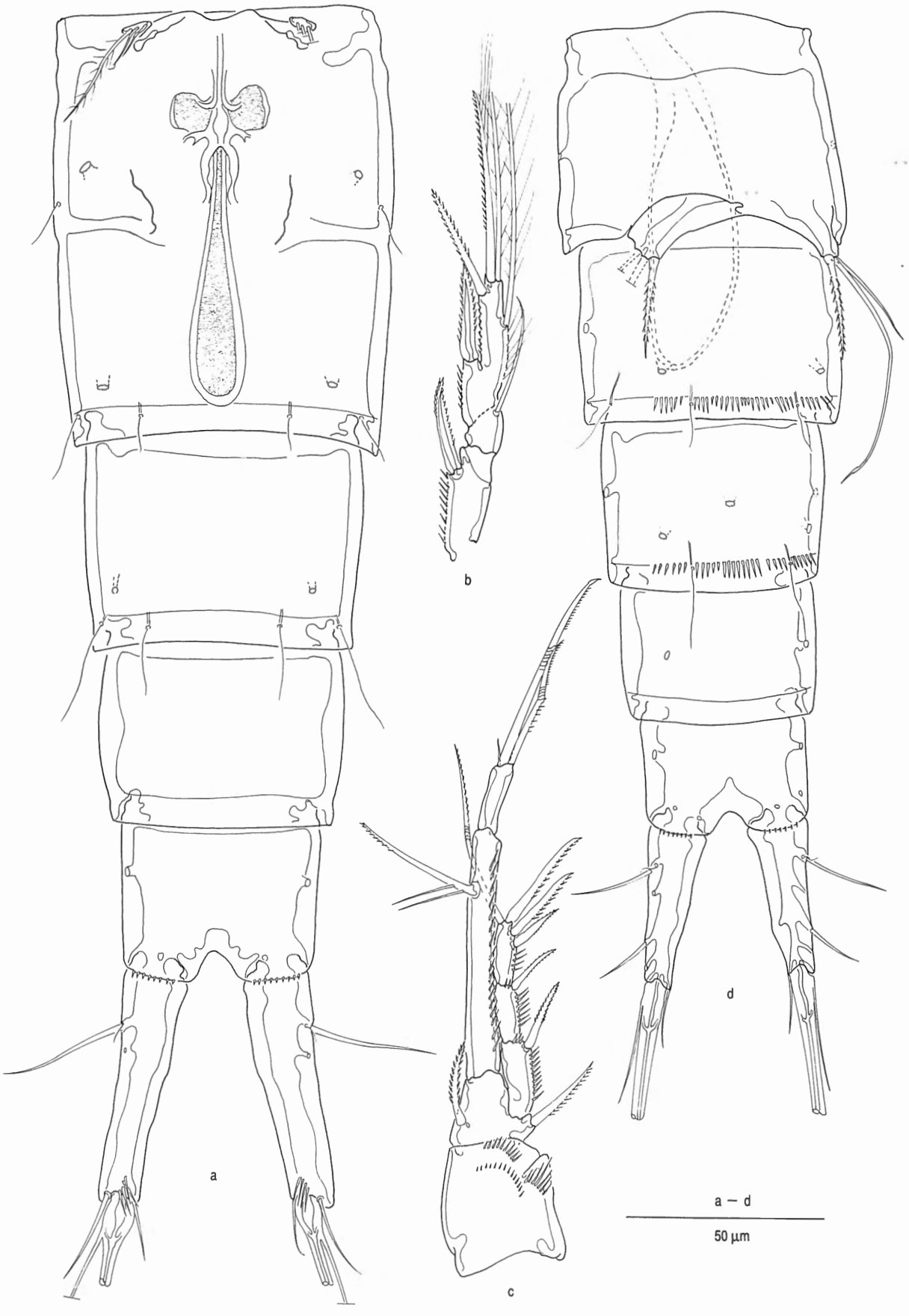

Fig. 13. – *Diagoniceps mexicana* n. sp.: a, female abdomen, ventral; b, anomalous P2 exopodite; c, P1, anterior; d, male abdomen, ventral (a-c, holotype female; d, allotype male).

slide, labeled COP 3974, and 2 ♀♀ and 1 ♂ preserved in alcohol, labeled COP 3975.

TYPE-LOCALITY

Western Central Atlantic, México: northern region of Yucatán continental shelf (22° 45' N - 87° 54.7' W) at a depth of 57.4 m. Leg. CINVESTAV, July 1990.

ETYMOLOGY

The specific name refers to the type-region of the species.

DESCRIPTION

FEMALE

Body (Fig. 12a, b) slender, fusiform, nearly cylindrical, with slowly tapering thoracic region and posterior part of urosome; length: 600 μm; rostrum (Fig. 12a, c) as in *D. laevis*; integument of somites as in *D. laevis*, but with lateral surfaces of cephalothorax partially ornamented with minute pits (not illustrated).
Caudal rami (Fig. 13a) cylindrical, 4 times as long as wide, with a slightly sinuate inner margin, a short rounded extension of distal outer corner, and a cluster of spinules on ventral surface near distal edge; two lateral setae in proximal fourth, biarticulate dorsal seta arising near middle, and third lateral seta implanted close to distal corner; principal apical setae (Fig. 12b) fused, with outer one nearly half as long as ramus, and inner one almost as long as half the body length (270 μm), with short globulous proximal part, and smooth stem; inner apical seta short, just reaching beyond bulbous part of inner principal one.
Antennule (Fig. 14a) nine-segmented, with segment II twice as long as segment I; segmental complement as in *D. laevis*.
Antenna and buccal appendages as in *D. laevis*, except for palp of mandible and maxilliped; mandibular palp (Fig. 14c) ornamented with two clusters of spinules on coxa-basis, endopodite slightly longer than coxa-basis, and exopodite 1 proximal, 1 sub-distal and 4 distal setae.
Maxilliped (Fig. 14d) somewhat more slender than in *D. laevis*, ornamented as in the latter, but with an unarmed geniculated endopodal claw.
P1 (Fig. 13c) with ornamented coxa and smooth basis; outer and innner element of latter pinnate; first endopodal segment reaching far beyond exopodite, with inner pectinate seta implanted in distal fourth; third exopodal segment with two outer spines, one outer distal one and one inner distal geniculated seta.
P2-P4 (Fig. 15a-c) as in type-species, except for following structures: presence of a sharp process on outer distal corner of median P4 exopodal segment, coxae ornamented with two or three transversal rows of spinules, and basis of P2 without large spine near inner margin.
P5 (Fig. 14f) as in type-species, but inner sub-distal and inner apical seta pinnate, and outer distal seta considerably shorter.
P6 vestiges minute, bearing three setae: outer one plumose, median and inner one smooth (Fig. 13a); genital pore field narrow, long ovate; gonoduct short connecting two medium sized receptacula; single egg-sac with 7 eggs.

MALE

Habitus (Fig. 12 d) as in female, except for separated last thoracic and first abdominal somites; length: 495 μm; rostrum as in female; caudal rami as in female, except for absence of bristle row on distal end of ventral surface, and the normal shape of median terminal seta.First and second abdominal somites ornamented with a transversal row of slender spinules along posteroventral margin (Fig. 13d); ventral surface of abdominal somites smooth.
Antennule (Fig. 14b) sub-chirocer, 8-segmented, with segment II more than twice as long as segment I; segmentation between segment 4 and 5 undivided on ventral surface; armament as in *D. laevis*.
Sexual dimorphism in P2 as in type-species (Fig. 15e); subdistal outer spine of endopodite P3 slightly swollen, pinnate along outer margin of stem, and accompanied with a minute sharp outer processus (Fig. 15f); first exopodal segment P3 as in female; inner seta on second endopodal segment P4 short, barbed along one side; last exopodal segment P4 with only two inner elements.
P5 (Fig. 14e) with one-segmented right exopodite, and two-segmented left exopodite; all exopodal elements smooth except inner sub-distal pinnate seta.
P6 bearing one inner spine, a median and an outer smooth seta; median one more than twice as long as inner and outer elements (Fig. 13d).

VARIABILITY

The female holotype bears an anomalous exopodite P2, illustrated in Fig. 13b.

DISCUSSION

Diagoniceps mexicana n. sp. resembles *D. laevis* in many aspects. Both species share a slender smooth body without an external transversal crest on the genital double-somite, possesses a lean, ventrally directed rostrum, a prolonged second segment of the antennule, and have a similar setal armament on the natatorial legs. *D. mexicana* n. sp. is easily distinguishable from its congener because of the nearly cylindrical caudal rami, without an inner protuberance in the female, the longer second antennular segment, and the long endopodite in the P1. Furthermore, the male of *D. mexicana* n. sp. lacks the long outer process on the first P3 exopodal segment and has only a minute outer protuberance on the outer distal edge of the second endopodal segment on the P3.

Fig. 14. – *Diagoniceps mexicana* n. sp.: a, female antennule, ventral; b, male antennule, ventral; c, mandibular palp; d, maxilliped; e, male P5, posterior; f, female P5, anterior (a, c, d, f, holotype female; b, e, allotype male).

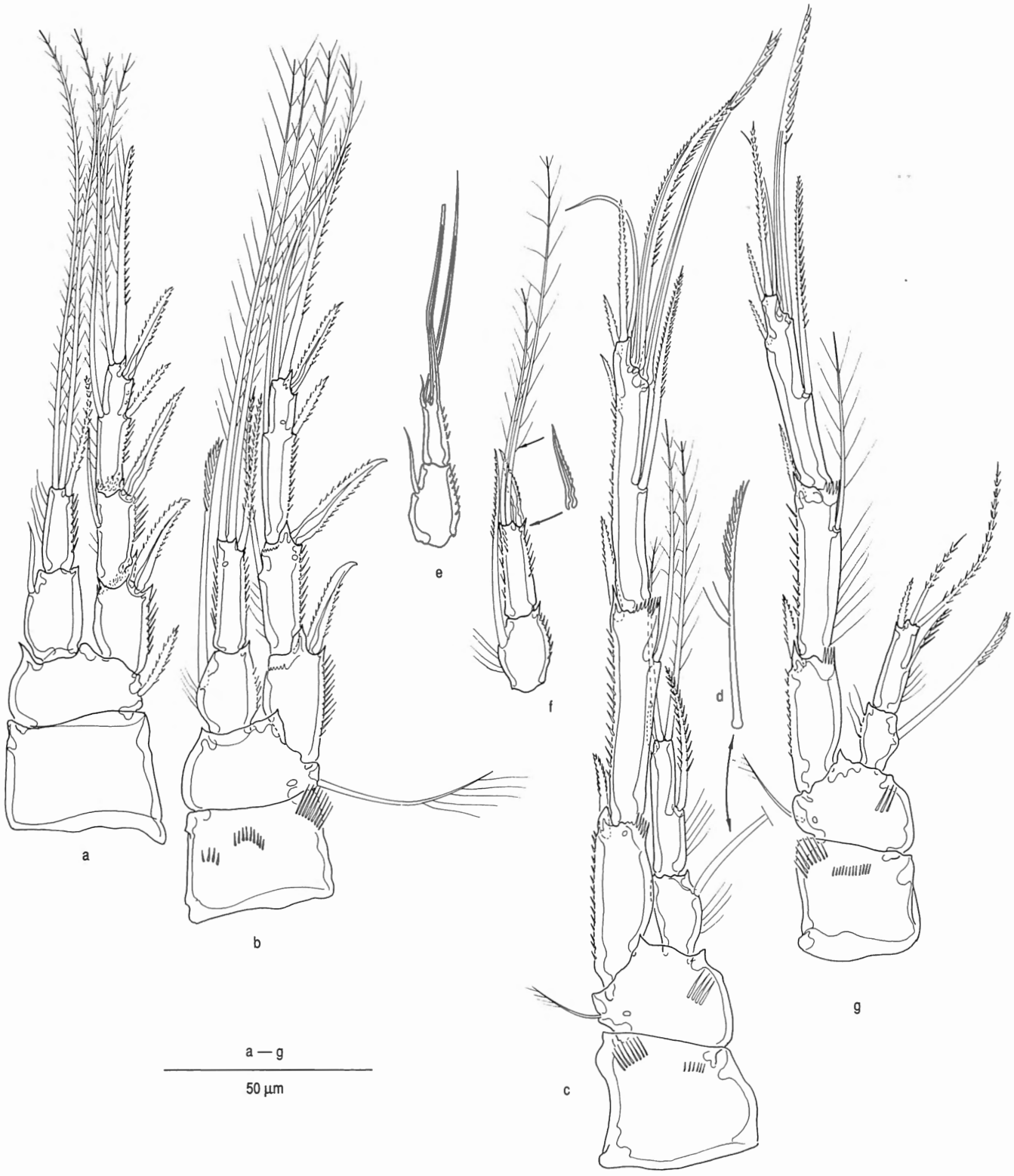

Fig. 15. – *Diagoniceps mexicana* n. sp.: a, P2, posterior; b, P3, anterior; c, left P4, anterior; d, inner pectinate seta of right first endopodal segment of P4; e, endopodite P2; f, endopodite P3; g, P4, anterior (a-d, holotype female; e-g, allotype male).

Genus **Aigondiceps** n. gen.

SYNONYMY

Diagoniceps auctorum, part.

DIAGNOSIS

Tetragonicipitidae with fusiform compressed body, having fused genital double-somite furnished with a distinct median transversal fringe; surface of cephalothorax and pedigerous somites ornamented, urosomal somites furnished with rows of spinules along posterior margins; rostrum minute, strongly bended ventrally; caudal rami cylindrical, considerably longer than wide in female, short, nearly quadrate in male, and bearing 7 elements; distal lateral seta with ventral position; outer terminal seta minute, confluent with median one.

Antennule 9-segmented, tendency to fuse segments VII and VIII; segment II distinctly longer than segment I; principal aesthetasc on segment IV; segment I with row of slender spinules; seta on segment I plumose, all other setae on segments II-IX smooth.

Antenna with basis, bearing a well-developed one-segmented exopodite with two pinnate terminal elements and a slender pinnate lateral one; one abexopodal seta on first endopodal segment, and 11 elements on second endopodal segment; mandible with three-segmented exopodite, and one-segmented endopodite; endopodite longer than exopodite; maxillule with bulbous epipodal plumose seta, and one-segmented exopodite and endopodite; maxilla with three endites of which proximal is bifid; maxillar claw accompanied with one armed and two smooth setae; endopodite two-segmented; maxilliped with three setae on basis, one on inner margin of palm, and claw with single additional seta.

P1-P4 exopodites three-segmented, endopodites two-segmented; second endopodal segment P1 bearing three terminal elements; proximal endopodal segments with inner setae: strongly pectinate in P2, plumose in P3, and finely pectinate in P4; proximal exopodal segments in P2-P4 with inner element, and distal exopodal segments in P2 with one plumose, in P3 with two plumose, and in P4 with three pectinate inner setae; aspect of P4 exopodite prolonged; P5 exopodite ovate, with broad base, bearing 6 setae (4 smooth ones, 2 spinulose ones); baseoendopodite with 5 spinulose elements on endopodal lobe.

Male having same body-shape as female except for separated genital somites; caudal rami much shorter than in female, bearing same complement; antennule subchirocer indistinctly 9-segmented, with short bulbous setae on inner side of palm, and principal aesthetasc on segment IV; sexual dimorphism typically tetragonicipitid in P2 and P3; proximal endopodal segment of P3 with 1 or 2 triangular extensions on distal edge; median exopodal segment of P4 with outer distal corner protruded into sinuate blunt process; P5 exopodite quadrate to short ovate, bearing 4 to 6 elements: 2-3 outer smooth ones, 0-1 smooth proximal inner seta, and apical and inner sub-distal pinnate; P6 vestiges with three elements.

TYPE-SPECIES

Diagoniceps bocki LANG, 1948, here designated.

ETYMOLOGY

The generic name is an anagram of *Diagoniceps*, gender neutral.

OTHER SPECIES

Diagoniceps kunzi MARINOV, 1973 and *Diagoniceps bodini* n. sp. (= *Diagoniceps* spec. BODIN, 1979).

Aigondiceps bocki (LANG, 1948) comb. nov.
Figs. 16 - 21

SYNONYMY

Diagoniceps bocki n. sp.- LANG, 1948: p. 895, Fig. 361(2).
Diagoniceps bocki LANG, 1948 - CHAPPUIS & KUNZ, 1955: p. 1023; POR, 1964: p. 249-251, Fig. 46-70, Pl. 135 (neotypes); GEDDES, 1968: p. 443; COULL, 1973: p. 14 (key); MARINOV, 1973: p. 321; WELLS, 1976: p. 133; BODIN, 1979: p. 345-347 (key); WELLS, 1985: p. 9; BODIN, 1988: p. 145.

TYPE-MATERIAL

Syntype female, dissected, mounted on 7 slides, and labeled SMNH 4673 (A-G). Syntype male, dissected on 5 slides, labeled SMNH 4672 (A-E), and 11 ♀♀, 2 ♂♂ (1 damaged), and 3 CV copepodites preserved in alcohol, labeled SMHH 2262. Material deposited in the collections of the "Naturhistoriska Riksmuseet", Stockholm.

TYPE-LOCALITY

Sweden, Gullmarfjord, at -34 m on silty bottom. Coll. et det. K. Lang, 3 April 1937 (Gullmarsfjord in *Gazetteer of Sweden*, n° 72, 1963, Gullmarn city: coord. 58° 20' N - 11° 33' E).

ADDITIONAL MATERIAL

(1) 4 slightly damaged females, labeled as syntypes, from Gullmarfjord (- 60 m, silty sediments, 6 July 1936. Coll. et det. K. LANG), labeled SMNH 2270.

(2) 1 female and 1 male, dissected, from Skagerrak, labeled COP 38 (without further specifications), deposited in the collections of the Israel National Collections of Natural History (Hebrew University). Det. D. POR.

REDESCRIPTION

FEMALE

Habitus (Fig. 16a, b) fusiform, slightly compressed, with strongly tapering pedigerous somites, distinctly constricted behind pedigerous somites, and with parallel sided urosome; length: 758 μm (dissected specimen; 737-763 μm in ethanol preserved specimens); largest width (±200 μm) in posterior fourth of cephalothorax; length of cephalothorax about 1/3 of whole body length.

Integument of cephalothorax densely pitted (not shown in illustrations), and of other somites furnished with hardly visible minute spinules; posterolateral margins of fifth pedigerous somite, second genital and second urosomal somite spinulose; third urosomal somite furnished with long spinules along entire posteroventral margin (Fig. 19a); posterior margins of all somites minutely sinuate.

Rostrum small, triangular, not reaching beyond basal antennular segment; anal operculum crescentic with a sinuate dorsal ridge.

Caudal rami (Fig. 16c) more or less cylindrical, about 2.75 times as long as wide, with a rounded outer extended corner, and a tuft of long setules near the inner distal corner; two lateral setae and one bi-articulate dorsal seta implanted in distal fourth; third lateral seta arising from ventral surface, implanted closely to distal margin; principal terminal seta with bulbous proximal part, confluent with minute outer terminal seta (indicated by arrow in Fig. 16c); inner terminal seta minute, as long as outer one.

Antennule (Fig. 17b) 8-segmented in leptotype, 9-segmented in most paraleptotype females, with a plumose seta on segment I, and smooth setae on segments II-IX; second segment longer than first one; setal armament of paralectotypes: I(1)-II(9)-III(7)-IV(5+aesth)-V(1)-VI(4)-VII(2)-VIII(2)-IX(7+aesth); of lectotype with fused VII and VIII: 4 setae; integument of segments smooth, except for a row of slender spinules along anterior directed surface of segment I.

Antenna (Fig. 17a) with abexopodal margin of basis ornamented with long spinules; exopodite with two terminal pinnate spines and one lateral, long and slender, pinnate seta; first endopodal segment bearing a plumose abexopodal seta; second endopodal segment having 11 elements.

Labrum (Fig. 17e) wide, furnished with short spinules on both edges; apex slightly crescentic, hyaline, and smooth.

Mandible (Fig. 17d) with strong gnathobasis, and a long densely ornamented coxa-basis, bearing three setae (2 plumose, 1 smooth); biting edge set with 4 dentate teeth and 4 spinules; accessorial seta broken; exopodite three-segmented, with 1, 2 and 4 smooth setae, respectively; endopodite one-segmented, almost twice as long as exopodite and having 2 lateral and 6 distal setae.

Distal edge of maxillular arthrite armed with 7 long pinnate spines, a plumose seta, and two smooth setae on surface (Fig. 17h); coxal and basal extension with 4 and 6 distal elements, respectively; epipodal seta globulous at base, plumose all around the stem; exopodite and endopodite distinct, bearing 3 and 4 setae respectively, and furnished with setules along outer margin.

Maxilla (Fig. 17c) having three endites; proximal one bifid, with 3 and 1 spines on proximal and distal extension, respectively; median and distal endites each with three ornamented elements; claw unarmed, accompanied with 2 plumose setae and one strong element ornamented with two strong spinules; endopodite two-segmented, bearing 2 and 5 setae respectively.

Maxilliped (Fig. 17f, g) with cylindrical basis, bearing three inner distal elements, and ornamented with 3 crescentic rows of long spinules; palm nearly cylindrical, having a single median smooth seta, and a row of minute spinules along anterior margin of segment; claw slightly longer than supporting segment, smooth, bearing a single additional pinnate seta; basis and palm detached in lectotype.

P1 (Fig. 18a) with densely ornamented protopodal segments; first endopodal segment with ornamented anterior surface and inner margin, reaching just beyond the exopodite; inner pectinate seta of first endopodal segment heavily armed with long spinules along inner margin of stem, and very wide and robust; second endopodal segment 4 times as long as wide, bearing 2 elements: an inner plumose seta, and an outer pinnate spine; three-segmented exopodite with outer distal spine ornamented with widely spaced long and slender spinules along outer margin.

P2-P3 (Fig. 18b, c): anterior surfaces of protopodal segments densely ornamented with transversal rows of spinules; posterior surface of coxae with a single transversal row; basis of P2 with outer spine, of P3 with smooth seta; inner distal corner and median margin of P2 and P3 bases forming sharp extension; intercoxal plate U-shaped, ornamented with spinules on lateral extensions; first endopodal segment of P2 with inner robust pectinate seta; of P3 with an inner unmodified plumose element; chaetotaxy in Table III.

P4 (Fig. 19b) with ornamentation of protopodal segments and intercoxal plate as in P3; endopodite distinctly shorter than first exopodal segment, bearing a pectinate seta on proximal segment and 4 pinnate elements on second segment; both distal endopodal setae attenuated; first and second exopodal segments with minute sharp extension of distal outer corner; inner setae of third exopodal segment robust, and bi-pinnate.

P5 (Fig. 21a) characterized by a small ovate exopodite, bearing six setae, and a endopodal lobe with five pinnate elements; posterior and anterior surface of rami smooth; inner margin of baseoendopodite and exopodite furnished with long fragile hairs; outer margins of baseoendopodite and exopodite with spinules; row of long spinules in front of articulation between exopodite and baseoendopodite.

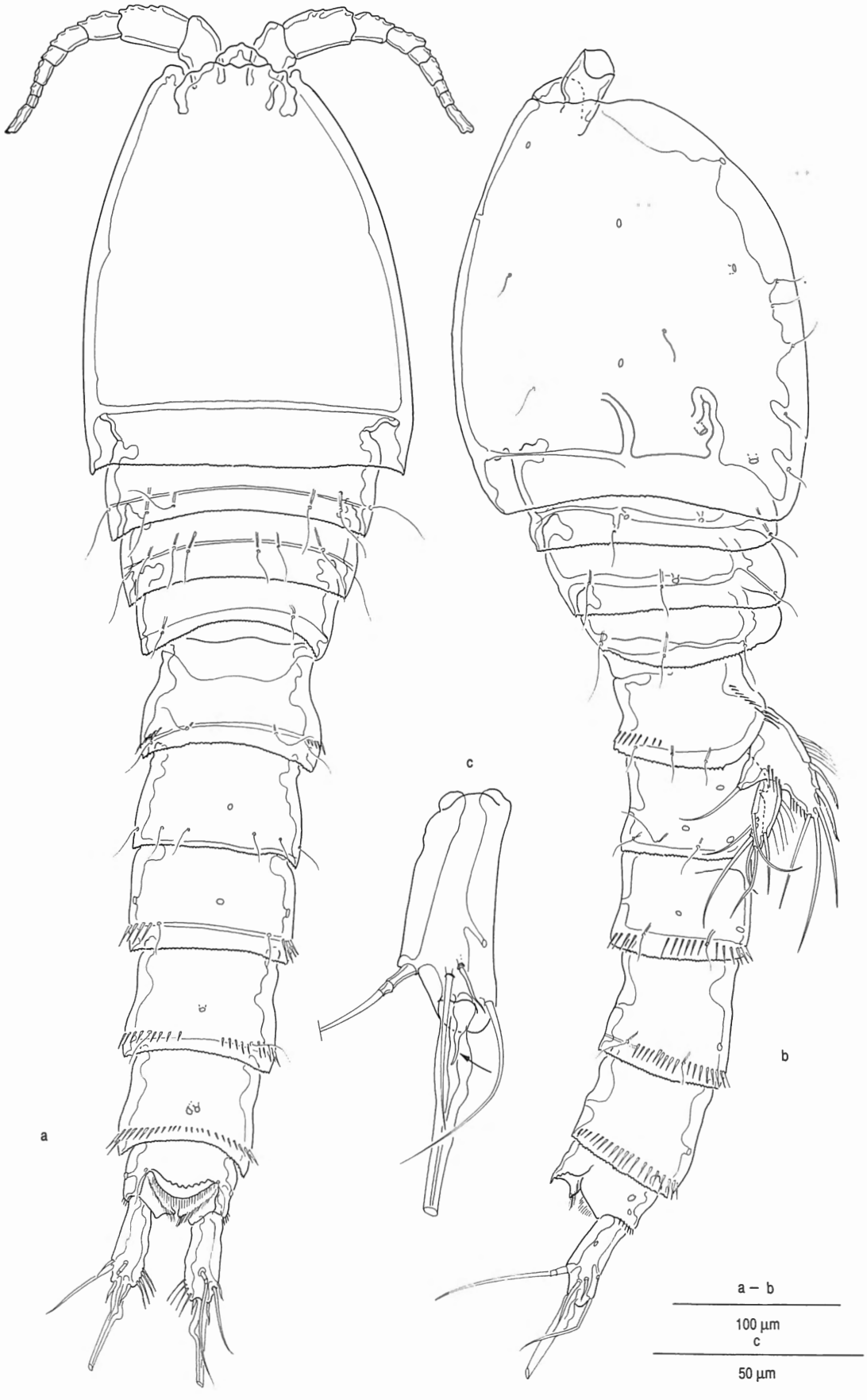

Fig. 16. – *Aigondiceps bocki* (LANG, 1948): a, female habitus, dorsal; b, female habitus, lateral; c, right caudal ramus, lateral (a-c, lectotype female).

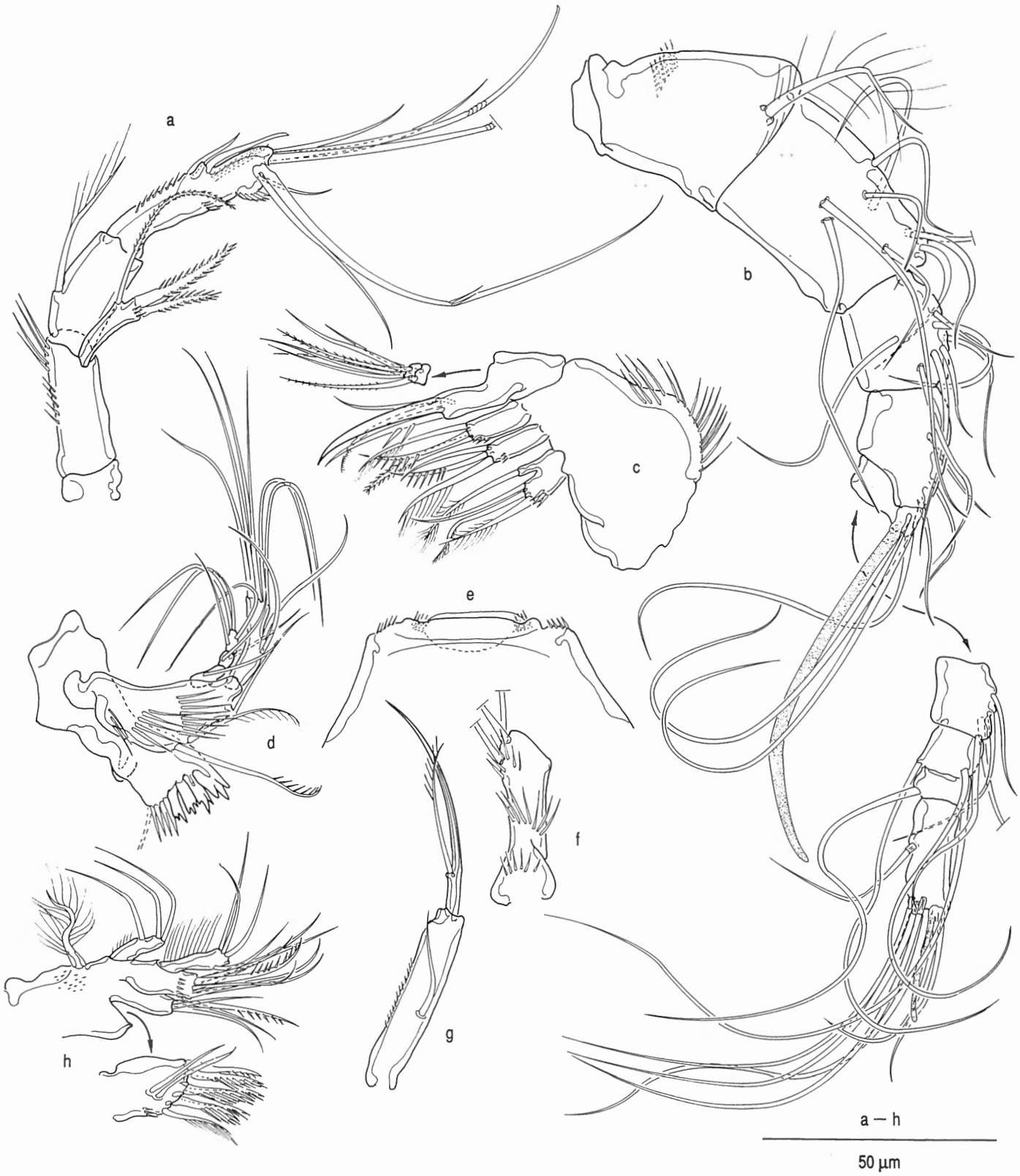

Fig. 17. – *Aigondiceps bocki* (LANG, 1948): a, antenna; b, antennule; c, maxilla; d, mandible; e, labrum; f, basis of maxilliped; g, endopodite of maxilliped; h, maxillule (a-f, lectotype female; g-h, paralectotype male).

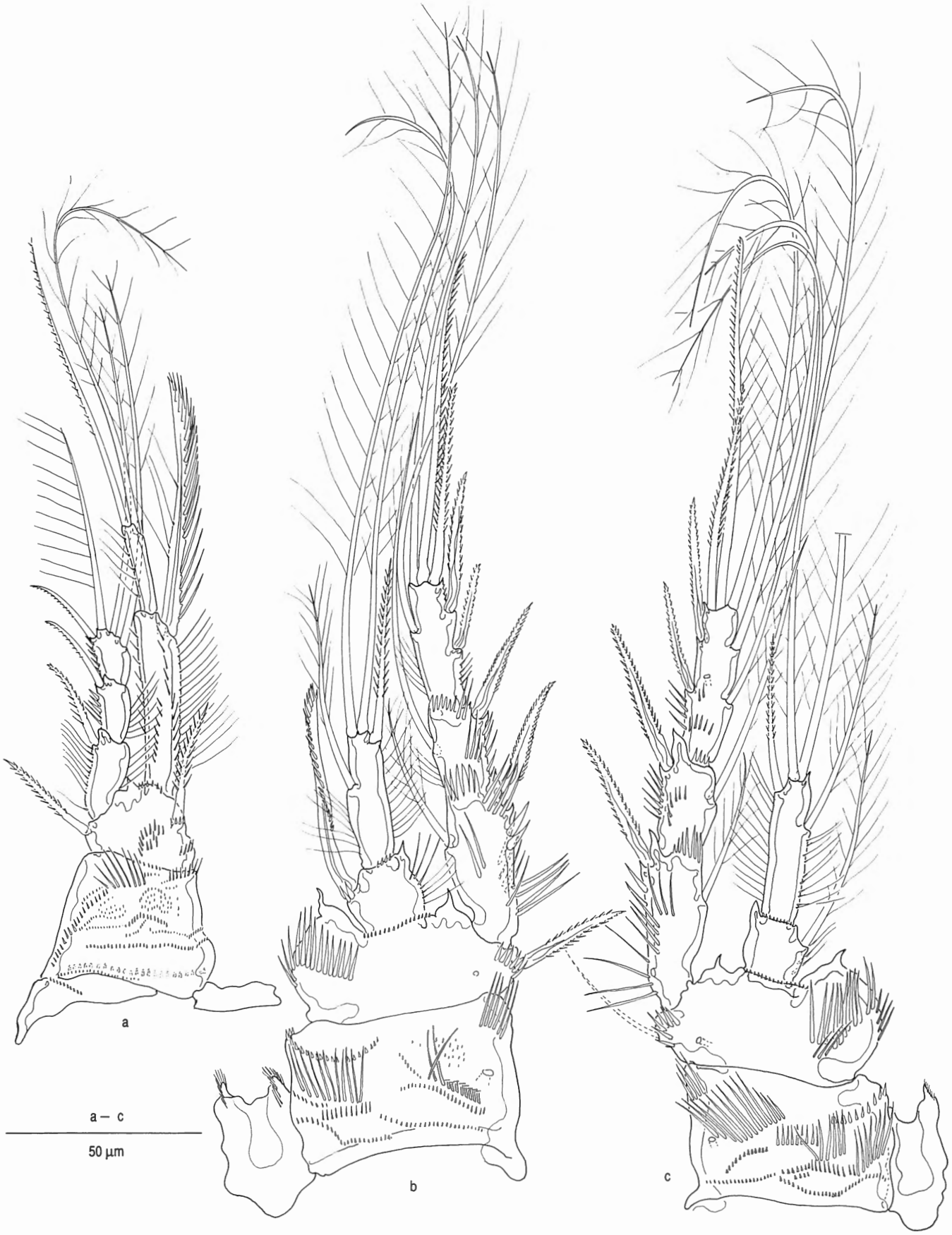

Fig. 18. – *Aigondiceps bocki* (LANG, 1948): a, P1; b, P2; c, P3 (a-c, anterior, a, paraleptotype male, b-c, leptotype female).

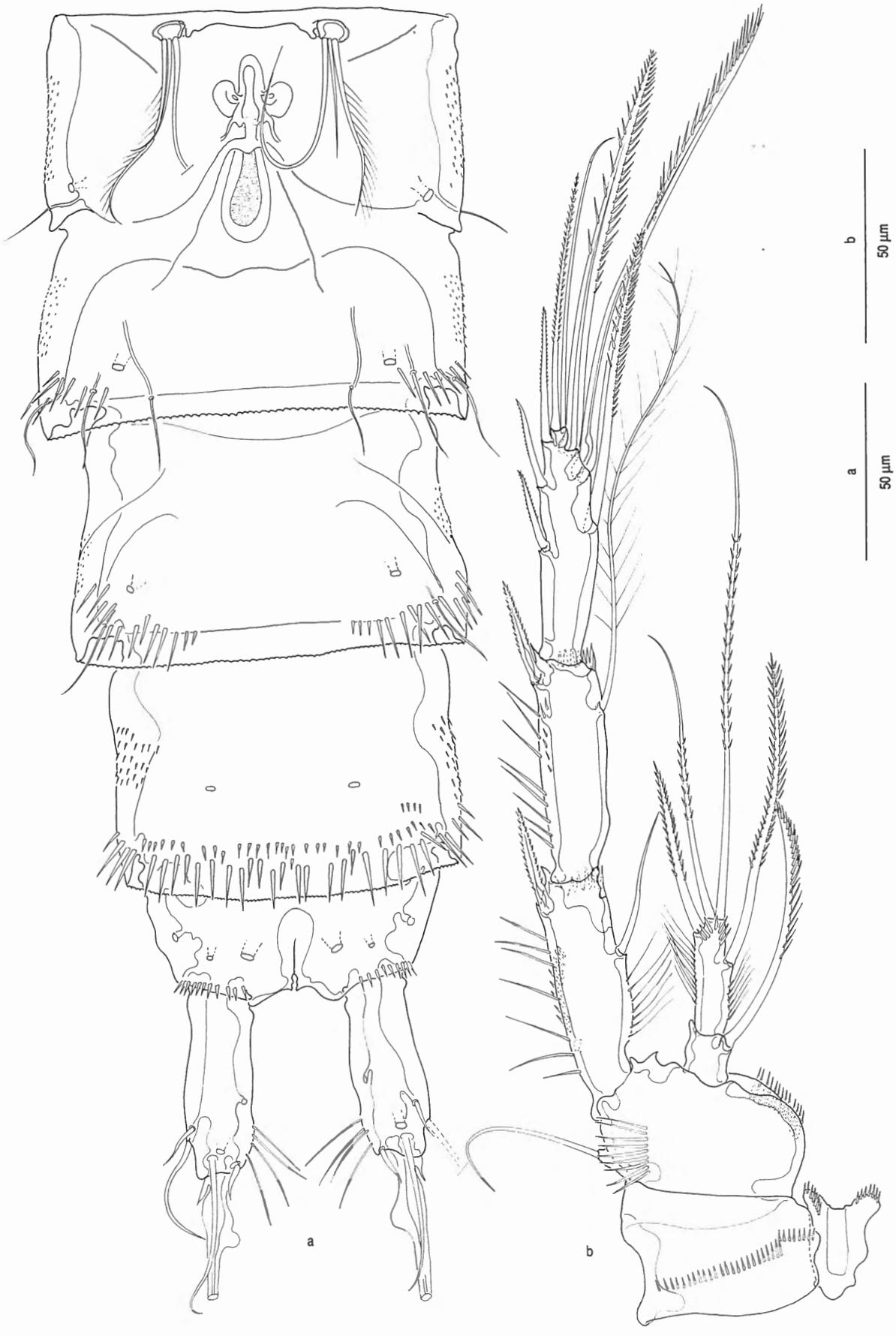

Fig. 19. – *Aigondiceps bocki* (LANG, 1948): a, female abdomen, ventral; b, P4, posterior (a-b, lectotype female).

P6 vestiges short, bearing a long outer plumose seta, a short smooth median and a long smooth inner element (Fig. 19a); internal transversal band very wide on ventral surface, with deep pore orifice; receptacula small; egg-sacs not present.

MALE

Habitus (Fig. 20a) as in the female, except for the nearly quadrate caudal rami; length: 500 μm (500 - 517 μm, n=3); integumental structures as in the female, except for the continuous posteroventral rows of spinules of urosomal somites (Fig. 20c).
Caudal rami only slightly longer than wide, with convex inner margin, and strongly sclerotized integument; two lateral setae implanted close to distal outer corner; third seta implanted ventrally, and bi-articulate dorsal seta articulating close to inner margin.
Antennule (Fig. 20b) 9-segmented, although articulation between segment IV and V not complete; sub-chirocer, with aesthetasc on segment IV and segment IX; second segment 2.5 times as long as wide; setae on palm short but not particularly modified.
Mouthparts, P1 and protopodal segments of P2-P4 as in female.
P2 exopodite with sharp extension on outer distal corner of second segment (Fig. 21e); endopodite with robust pectinate seta on proximal segment and armamented with typically modified distal elements; P3 exopodite as in female; P3 endopodite with a spinulose inner seta on proximal segment; second P3 endopodal segment having modified bi-dentate outer spine, two terminal plumose setae and a single inner smooth seta, and large sharp process on inner distal corner.
P4 (Fig. 21b) resembling female P4 closely, except for outer distal corner of second exopodal segment, bearing a blunt S-shaped structure, and the presence of only two inner pectinate setae on third segment.
P5 (Fig. 21c) with short exopodite, bearing two outer smooth setae, and an apical and inner sub-distal pinnate element; endopodal lobe of baseoendopodite rather short, bearing three spines; inner and outer margins of rami smooth; anterior row of spinules
near articulation between exopodite and baseoendopodite present.
Right P6 vestige not differentiated from somite; each bearing a spine and two smooth setae.

Variability: Some female specimens possess an 8-segmented antennule. In these cases, segments VII and VIII are fused but a more or less distinct suture indicating the previous articulation between both segments is visible. The fusion of the segments does not affect the number of setae.

DISCUSSION

The original description of this species is very insufficient and rather inaccurate, and consists of three sketchy illustrations and a description covering not quite five lines. LANG (1948: p. 895) reported that most of the specimens were lost before they could be observed, but two vials with indication "syntypes" are stored in the collections of the "Naturhistoriska Riksmuseet" (Stockholm). Both vials contain several specimens of *D. bocki*. The labels indicate that the specimens are from Gullmarfjord and were collected and identified by LANG. More curiously, vial SMNH 2262, collected 6 Juli 1937 at -34 m, contains 12 ♀♀, 3 ♂♂, and 3 juveniles, whereas vial SMNH 2270, collected 3 April 1936 at - 60 m holds 4 ♀♀.
LANG (1948) reported that from his original collection (26 ♀♀ and 13 ♂♂ from Gullmarfjord and 2 ♀♀ from Mseskär) only 2 ♀♀ were saved and available for description. Fortunately, he accurately listed the presence of specimens in the several samples he collected and provided information on number of specimens, presence of egg sacs and spermatophores, sampling dates and station depths. Among those samples, two are of major interest herein: one non-ovigerous female found in the sample collected at - 34 m on 3 April, and 3 non-ovigerous females and 3 adult males in the sample from - 60 m collected on 6 July.
As the collection present in the "Naturhistoriska Riksmuseet" consists of 22 specimens in two vials only, it is my opinion that the regrettable accident leading to the presumed loss of the collection is a result from the fact that LANG thoughtlessly put the specimens collected at different dates and different depths together. As he has always been known as a very conscientious researcher, it seems highly probably that all specimens in the vials are from Gullmarfjord and that those from Mseskär were lost as this vial is not included in the SMNH catalogue.
When POR (1964) provided a redescription of this species, based on material found in samples from localities ranging from 72 to 150 m depth in the Skagerrak, he designated his specimens as neotypes, and deposited them in the Hebrew University under number COP 38. But the "neotypes" designation cannot be considered as valid as it does not meet the strict requirements of Art. 75 of the ICZN (P.K. TUBBS, *in litt.*).
At first glance, the specimens described by POR (1964) agree in most aspects with the type-specimens studied herein. However, the description of the Skagerrak specimens differs from these from Gullmarfjord in the more distinct integumental structures on the anal somite; the chaetotaxy of the buccal appendages and P4 endopodite; and the sexual dimorphism of endopodite P2. The integumental structures on the surface of the urosomites in the Gullmarfjord specimens are difficult to see. Only those ornaments on the lateral margins of the anal somite are somewhat larger and more easily observable. Moreover, only the pre-anal somite in these species is furnished along its entire posterior margin with slender spinules, whereas the preceeding urosomites possess only

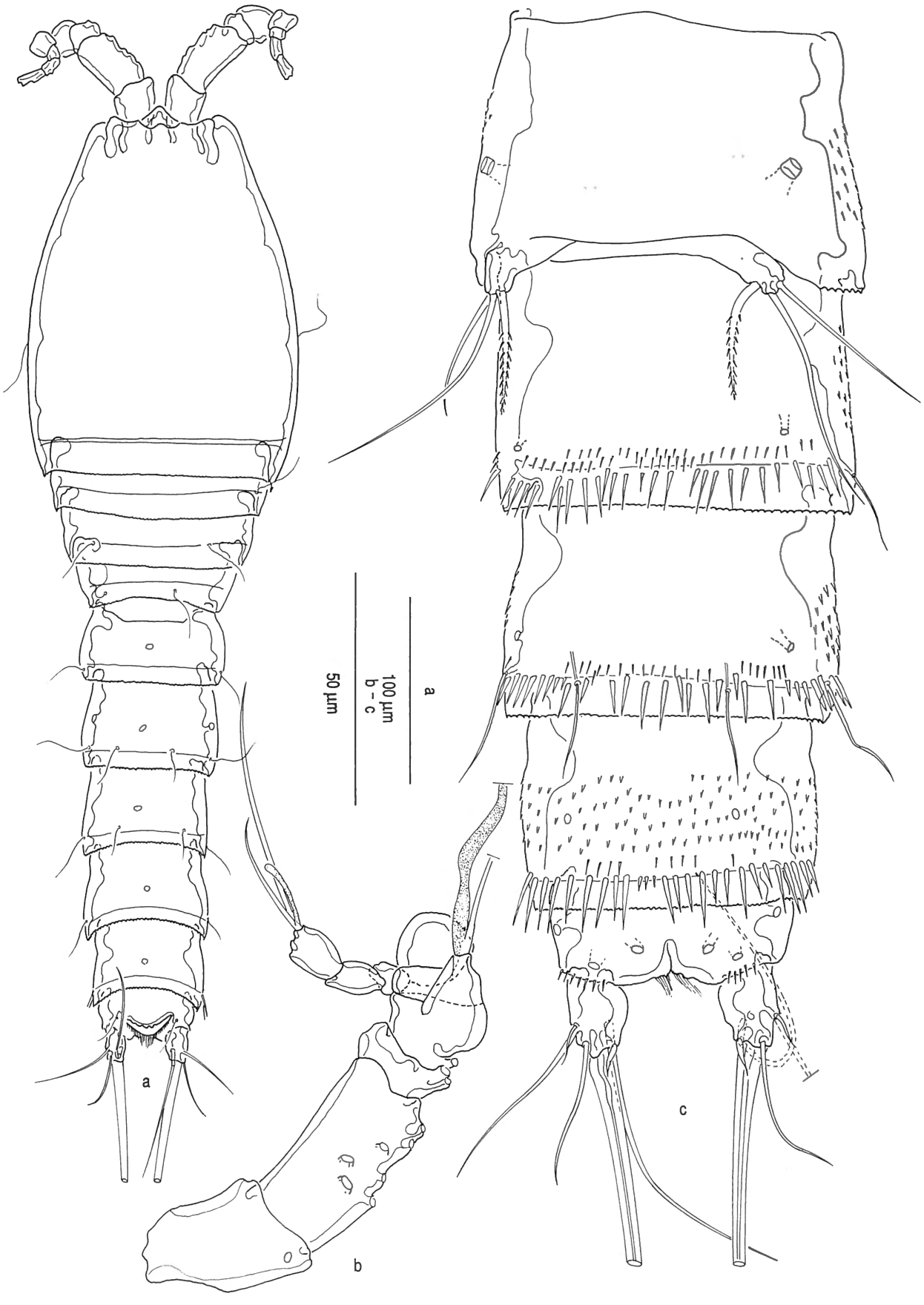

Fig. 20. – *Aigondiceps bocki* (LANG, 1948): a, male habitus, dorsal; b, contour of antennule, ventral; c, male abdomen, ventral (a-c: paraleptotype male).

Fig. 21. – *Aigondiceps bocki* (LANG, 1948): a, female P5, posterior; b, male P4, anterior; c, male P5, posterior; d, male endopodite P3, anterior; e, male P2, anterior (a, leptotype female; c-e, paraleptotype male).

a few spinules on the dorso- lateral and ventro-lateral corners. In contrast, the specimens described from Skagerrak have a distinct pattern of transversal spinules on the dorsal surface of the anal somite, and are ornamented with spinules over the entire posteroventral margins of the first and second abdominal somite.
The setal complement of the buccal appendages described for the Skagerrak specimens is incorrect. Re-examination of the mouthparts (except for the maxilliped which is not detectable on the slides) revealed no differences between the Gullmarfjord and Skagerrak specimens.
More arresting is POR's illustration of the male P2 endopodite (POR, 1964: Fig. 67) showing a long ornamented sub-distal outer element, accompanied with two long, but slender terminal setae. It is apparent that the illustration is not that of the P3 endopodite, as the inner element of the documented proximal segment is pectinate as in the female P2 (compare illustrations 68(P3), 66(P2♀) in POR, 1964, and Fig. 21e(P2♂) and 18b(P2♀), herein). But, re-examination clearly showed that the sexual modifications of the P2 (and additionally of the P3) in the male from Skagerrak are identical with those of the Gullmarfjord males.
POR (1964: p. 250) reported on the variability of the endopodite P4 chaetotaxy, and listed the setal formula of this appendage as 1.21(2)1. The setal formula of the right P4 endopodite of the female specimen from Skagerrak is 1.121, while its left endopodite is complemented with an additional distal setae, resulting in a setal complement of 1.131. An comparable situation was observed on the left P3 exopodite of the same specimen where an additional outer spine arises on the outer margin.
The proportional lengths of the segments of P1 and P4 are somewhat erroneously in the illustrations given by POR (1964: Fig. 65 and 69 respectively). From the figures, it appears that the endopodite in the Skagerrak specimens just reaches beyond the distal edge of the first exopodal segment. However, meassurements of the P4 rami of the Skagerrak specimens revealed that the endopodite does not reach quite to the implantation of the inner seta on the first exopodal segment, and thus is identical with the length of this appendage encountered in the Gullmarfjord specimens. Comparable differences are noted in the P1, where the first segment of the exopodite in the Skagerrak specimens is distinctly longer than the first exopodal segment of the P1 in the specimens from Gullmarfjord, and were the sub-distal outer spine on the terminal exopodal segment is significantly longer in Skagerrak specimens than in the Gullmarfjord animals. However, these differences were not found re-examining the Skagerrak specimens.
Although the more accentuated integumental ornamentation of the specimens from Skagerrak, it seems clear that the latter are conspecific with *Aigondiceps bocki* described from Gullmarfjord.
Among the type-specimens, a single female specimen is furnished with large stalked organisms in the same way as reported by POR (1964). Whereas POR (1964: p. 251) speculated on the possibility that these structures represented special eggs, or fungal fructifications, he rejected, on advice of his colleagues, the possibility that they represented stages of stalked ciliates.
Close examination of these structures revealed clearly that they are representatives of suctorians from the order Endogenida COLLIN, 1912, resembling *Tokophrya* (Ciliophora, see LYNN & SMALL, 1989). Similar epizoid specimens were found on the herein described *Odaginiceps elegantissima* n. sp. The latter is complemented with several stades of the stalked suctorians of the order Exogenida COLLIN, 1912 which are living in a transparent lorica.
Epizoid organisms occur frequently on benthic and planktonic copepods (GUILCHER, 1950; HERMAN & MIHURSKI, 1964; HERMAN *et al.*, 1971; HOCKIN, 1984; pers. obs.) but presence of such organisms and location on the copepod body are generally not mentioned.
GUILCHER (1950) described short stalked suctorians (*Ophryodendron faurei* and *Acineta bocqueti*) found on the head of the phytal copepods *Psamathe* (=*Scuttelidium*) *longicauda* (Tisbidae), *Porcellidium fimbriatium* (= *P. viride*) and *P. tenuicauda* (Porcellidiidae). In contrast, infestations on planktonic copepods (*Tisbe* spec. see GUILCHER, 1950; *Acartia tonsa* HERMAN & MIHURSKI, 1964; often on freshwater zooplankters, pers. obs.) constist of long stalked suctorians placed all over the body and appendages.
The striking similarity of the position on the genital somites of suctorians on specimens of *Aigondiceps bocki* found by POR (1964) in the Skagerrak and those from Gullmarfjord collected by LANG (1948) may be an indication that for those epizoids a particular location on the body is more advantageous than others.

Aigondiceps bodini n. sp.
Figs. 22 - 23

SYNONYMY

Diagoniceps spec. - BODIN, 1979: p. 342-346, Fig. 17.

TYPE-MATERIAL

Holotype male, dissected on a single slide, deposited in the collections of Ph. Bodin, Université de Bretagne Occidentale (Brest).

TYPE-LOCALITY

French Atlantic coast: intertidal zone of "Plage du Martrais, île de Ré" (near La Rochelle). Leg. Ph. Bodin, 27 September 1965 (n°: LXXV).

ETYMOLOGY

The species is dedicated to Philippe Bodin (Brest) in appreciation of his outstanding contributions in the fields of harpacticoid taxonomy and ecology.

DESCRIPTION

FEMALE

Unknown.

HOLOTYPE MALE

Note: the description is based on the sole specimen known so far. The description is kept to a minimum and deals mainly with the features contrasting *A. bodini* from its two congeners.

Sides of urosomal somites furnished with dense pattern of minute blunt spinules; posterodorsal margin of urosomal somites minutely sinuate; posteroventral margin of urosomal somites set with long slender spinules, arranged in discrete groups (Fig. 22b).

Anal operculum distinctly convex, furnished with slender spinules, lacking a dorsal transversal ridge.

Caudal rami (Fig. 22a) nearly twice as long as wide, slowly tapering distally; two lateral setae implanted in middle of outer margin; third lateral seta arising from ventral surface, close to outer distal corner; bi-articulate dorsal seta implanted in distal half; outer terminal seta slightly globulous at basis, 2.5 times as long as caudal ramus; median terminal seta with slightly bulbous basal part; inner terminal seta only half as long as supporting ramus.

Rostrum (Fig. 22c) small, triangular, not reaching beyond distal end of first antennular segment.

Antennule 9-segmented although articulation between segments IV and V not complete; second antennular segment twice as long as first one.

Antenna (Fig. 22d) devoid of integumental stuctures on basis and first endopodal segments; exopodite with three pinnate elements, and furnished with a short row of spinules; first endopodal segment with an abexopodal seta; second endopodal segment bearing 11 elements and a long hyaline tubular pore (indicated by arrow in Fig. 22e).

Mandible and maxillule not found; maxille as in *A. bocki* with two-segmented endopodite bearing two setae on proximal segment and 5 setae on second one; maxilliped as in *A. bocki*, but having two accessorial setae on claw, and has a less densely ornamented basis.

P1 (Fig. 23a) with crescentic rows of spinules on coxa; outer element of basis flagellated, and inner element bi-pinnate; first endopodal segment reaching beyond exopodite, bearing a slender pectinate inner spine, slightly swollen near base; second endopodal segment with two geniculate distal setae; distal and sub-distal outer spines on third exopodal segment ornamented with long widely spaced spinules along outer margin of stem.

P2 exopodite with sharply extended outer distal corners on first and second segments; inner seta of proximal endopodal segment heavily pectinate, inner seta on second endopodal segment plumose, and terminal elements of second segment typically modified (Fig. 23b); protopodal segments without marked anterior integumental structures; posterior surfaces un-ornamented (legs are posterio-anterior orientated on slide).

P3 exopodite as in P2; inner seta of proximal and distal endopodal segments pectinate, although less robust than in P2; distal edge of distal segment with two sharp processes (indicated by arrows in Fig. 23c); terminal endopodal elements plumose, outer spine rather slender but strongly pinnate along outer margin of stem.

P4 exopodite with a sharp sinuate process on distal outer corner of second exopodal segment (Fig. 23d); proximal endopodal segment with pectinate inner seta; second endopodal segment complemented with bi-pinnate inner setae, two plumose terminal elements, and short outer spine (Fig. 23e).

P5 (Fig. 22d) with short endopodal lobe, and tapering exopodite; former with three spines, the latter with three outer smooth seta, an apical and sub-distal spine and a inner proximal smooth seta; integument of rami smooth, except for some spinules along inner margin of baseoendopodite and outer margin on exopodite.

P6 (right) differentiated from somite, bearing inner spine and two outer smooth setae.

DISCUSSION

It is apparent that the male of *A. bodini* n. sp. cannot be confused with the male *A. bocki* as they show considerable differences in P1 morphology and the chaetotaxy of the P5 with four exopodal elements in the former, six in the latter.

The differences between the present species and *A. kunzi* are, however, less evident. It seems regular in *Aigondiceps* n. gen. that males have considerably shorter caudal rami than females. As such we can only rely on differences in the morphology of the natatorial legs to discriminate *A. bodini* n. sp. from *A. kunzi*. Both species have a similar chaetotaxy, but *A. kunzi* is known to have a knot-like inner seta on the first exopodal segment of the P4. Although it may turn out that the male of *A. kunzi* possesses a normal seta, both species may be separated on the basis of the form of this seta.

More outspoken, however, seems to be length ratio of the P1 rami. In *A. kunzi* the first endopodal segment reaches far beyond the distal edge of the exopodite, whereas the inner pectinate seta is implanted distinctly higher that the exopodite. In contrast, the first endopodal segment of the P1 in *A. bodini* n. sp. is only somewhat larger than the exopodal ramus, while the inner pectinate seta arises from a position slightly below the distal edge of the exopodite.

If the absence of an abexopodal seta on the first endopodal segment of the antenna in *A. kunzi* constitutes a reality cannot be said. This seta is easily detached

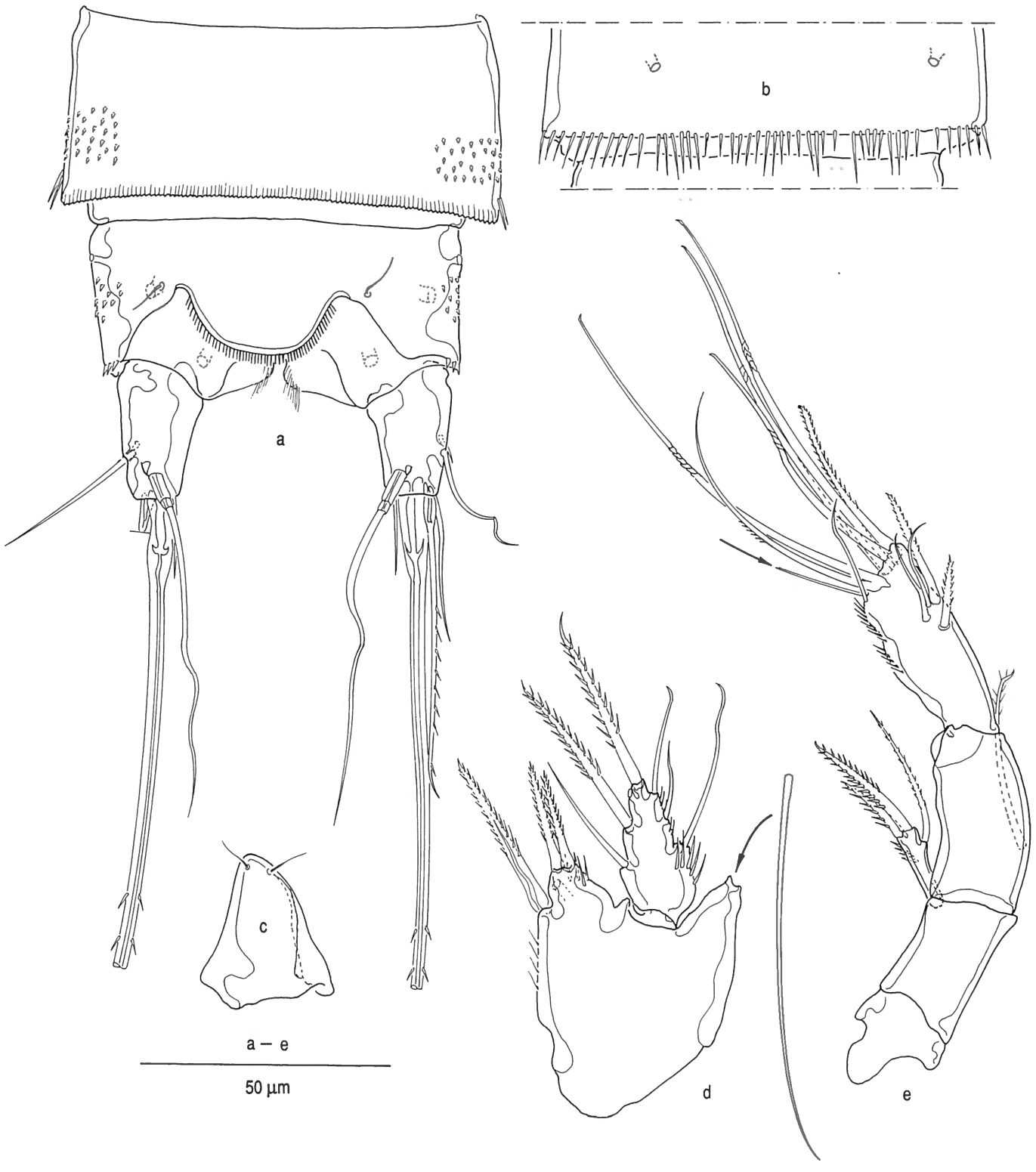

Fig. 22. – *Aigondiceps bodini* n. sp.: a, ultimate urosomal somites, dorsal; b, postero-ventral margin of penultimate somite; c, rostrum, dorsal; d, P5; e, antenna, arrow indicating long hyaline tube pore (a-e drawn after male specimen from La Rochelle (France), BODIN collection, Brest).

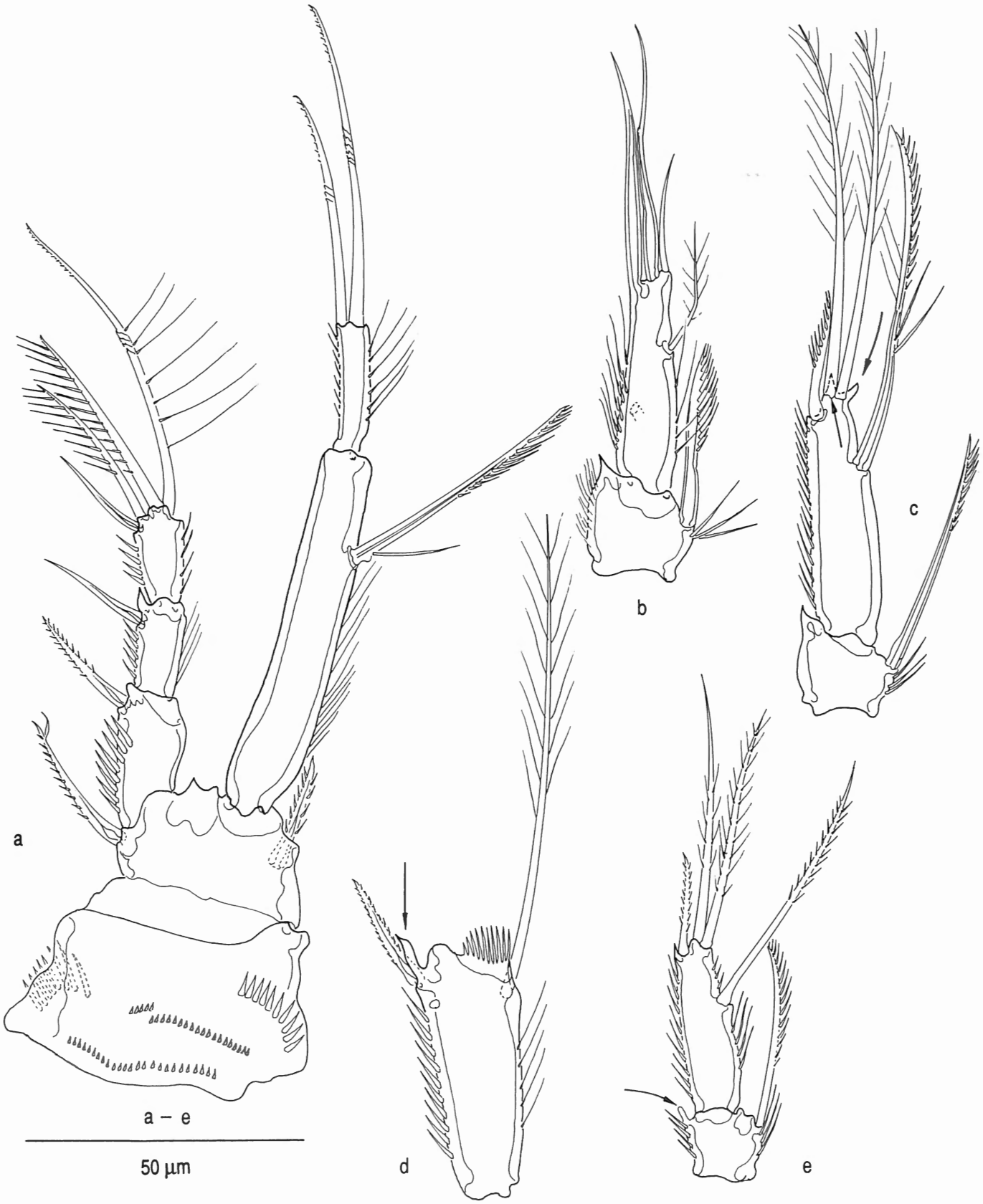

Fig. 23. – *Aigondiceps bodini* n. sp.: a, P1, posterior; b, P2 endopodite, posterior; c, P3 endopodite, posterior; d, median exopodal segment P4, anterior; e, P4 endopodite, anterior (a-e drawn after male specimen from La Rochelle (France), BODIN collection, Brest).

during dissection or can be orientated so that the stem coincides with the abexopodal margin of the segment which makes this element hardly visible.
The absence of an inner element on the P1 basis of *A. kunzi* is probably an error, and has to be confirmed after re-examination of the type-series.

Aigondiceps kunzi (MARINOV, 1973) comb. nov.

SYNONYMY

Diagoniceps kunzi n. sp.- MARINOV, 1973: p. 321-323, Fig. 10.
Diagoniceps kunzi MARINOV, 1973. - BODIN, 1979: p. 347 (key); KUNZ, 1984: p. 34-35; WELLS, 1985: p. 9; BODIN, 1988: p. 145.

TYPE-MATERIAL

A single female specimen, probably present in the collection of the author, Varna (Bulgaria).

TYPE-LOCALITY

West coast of Black Sea: Stomopolo Bay (Bulgaria) at a depth of 20 m in silty sand (MARINOV, 1973).

DIFFERENTIAL DIAGNOSIS

FEMALE

Length: 950 μm, with long (L/W-ratio: 1/5.81) nearly cylindrical caudal rami ornamented with long spinules in median half of inner margin; lateral and dorsal caudal setae arising in distal half of rami; antennule 9-segmented, typical for genus; maxilliped typical, but with two (?) setae on basis, and 1 (?) on claw; endopodite P1 nearly twice as long as exopodite, with inner pectinate seta arising from a position far above distal margin of exopodite; chaetotaxy of legs as in type-species, but inner seta on proximal segment of P4 exopodite minute, bulbous; P5 as in type-species.

MALE

Unknown.

DISCUSSION

Although the description of *Aigondiceps kunzi* comb. nov. is very incomplete, the P5 morphology, the prolonged aspect of the second segment of the antennule, and the setal armament of the legs, clearly show that this species has close affinities with the type-species of the genus, *A. bocki*. *A. kunzi* differs from the latter and from *A. bodini* n. sp. in the following aspects: the very long P1 endopodite, the longer caudal rami, and the globulous aspect of the inner proximal seta on the P4 exopodite.

Genus **Nidiagoceps** n. gen.

SYNONYMY

Diagoniceps auctorum, partim.

DIAGNOSIS

Tetragonicipitidae with fusiform depressed body, possessing fused genital somites furnished with a distinct median transversal fringe; integumental ornamentation unknown for cephalothorax and pedigerous somites; urosomal somites with hardly visible rows of spinules, and minutely sinuate hyaline fringe; rostrum short, protruded anteriorly, covering partially basal antennular segment; caudal rami variable from ovate to conical, bearing 7 elements; outer terminal seta rather long, confluent with median one.
Antennule 9-segmented, bearing principal aesthetasc on segment IV; segment II as long as segment I with slightly crescentic and strongly sclerotized inner margin; segment I with row of slender spinules; antenna with basis, bearing well developed exopodite complemented with three pinnate elements; first endopodal segment with or without abexopodal seta; second endopodal segment with 11 elements; mandible having one-segmented endopodite and exopodite, the latter half as long as the former; maxillule bearing a long and slender epipodal plumose seta; 4 endites on maxilla, proximal two opposed; claw with additional pinnate element and two smooth accompanying setae; endopodite indistinctly two-segmented; maxilliped bearing 3 setae on basis, 2 on inner side of palm, and two on basal part of smooth claw.
P1 with three-segmented rami; second endopodal segment without inner element; third endopodal segment with 3 terminal appendages; inner elements of proximal endopodal segments pectinate in all legs; proximal exopodal segments of P2-P4 with an inner seta, and distal exopodal segments in P2 and P3 without inner setae, in P4 with 3 long and pectinate inner elements; P5 exopodite short to long ovate, bearing an inner sub-distal and outer median pinnate setae, and an apical and 3 outer smooth setae; baseoendopodite with 5 pinnate elements.
Male habitus unknown, caudal rami conical (in type-species), with outer terminal seta not fused with median one; rostrum somewhat shorter than in female, but distinctly protruded anteriorly; antennule sub-chirocer, 9-segmented, having a large unguiform structure on inner margin of palm; dimorphic modifications of endopodites typically tetragonicipitid; endopodite P4 sometimes with one inner element more than in female; distal outer

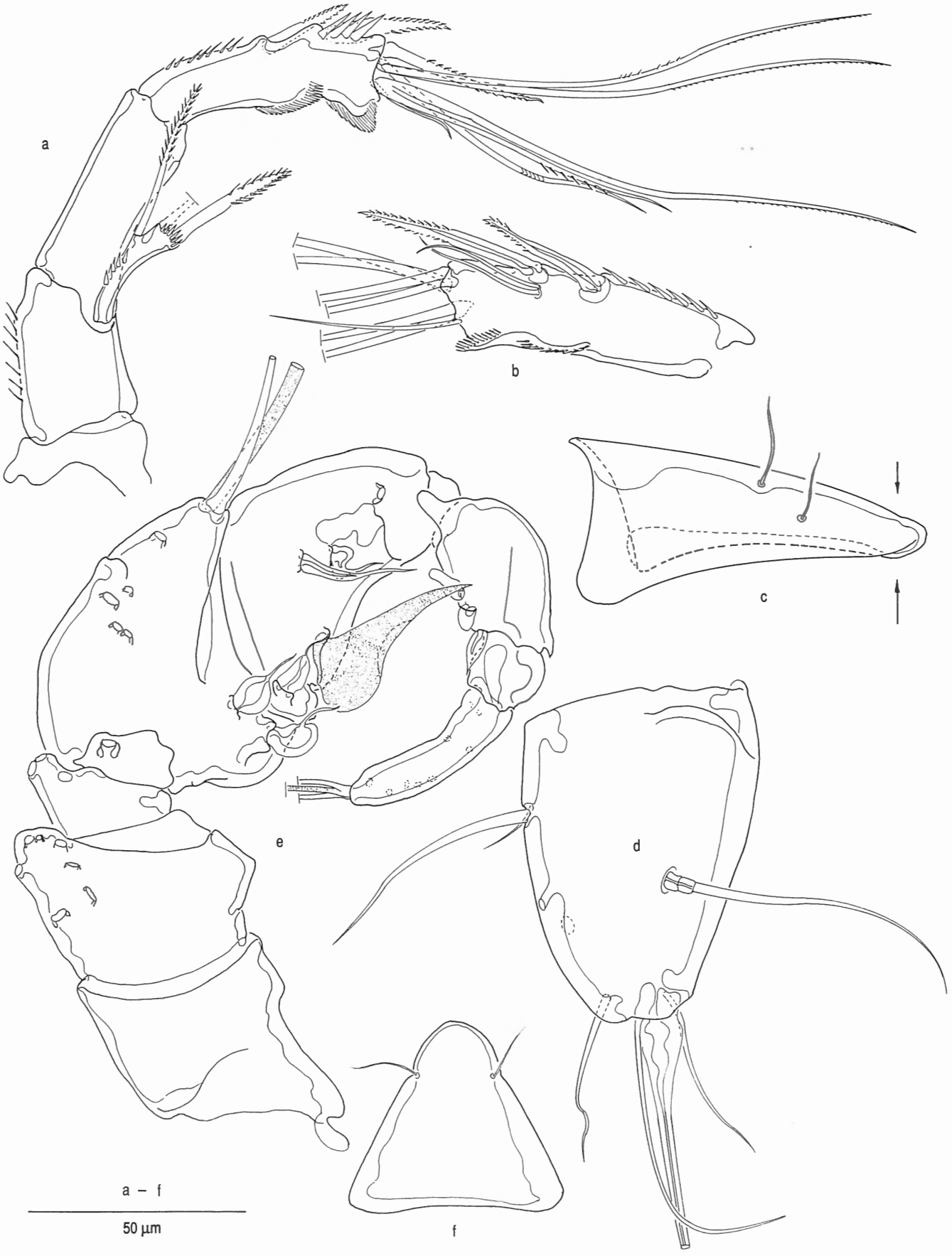

Fig. 24. – *Nidiagoceps menaiensis* (GEDDES, 1968): a, antenna exopodal side; b, antennal endopodite, abexopodal view; c, female rostrum (folded, arrows indicating distal edge of first antennular segment; d, female caudal ramus, dorsal; e; male antennula, ventral; f, male rostrum, dorsal (a-f drawn after specimens from La Rochelle (France), BODIN collection, Brest).

Fig. 25. – *Nidiagoceps menaiensis* (GEDDES, 1968): a, P1, anterior; b, maxilliped; c, maxilla; d, maxillule; e, female P4 endopodite (a-e drawn after specimens from La Rochelle (France), BODIN collection, Brest).

Fig. 25. – *Nidiagoceps menaiensis* (GEDDES, 1968): a, P1, anterior; b, maxilliped; c, maxilla; d, maxillule; e, female P4 endopodite (a-e drawn after specimens from La Rochelle (France), BODIN collection, Brest).

sub-distal smooth seta; claw smooth, accompanied with three setae: two pinnate ones and one smooth element.
P1 (Fig. 25a) with three-segmented rami; coxa with some short rows of long spinules; basis ornamented with spinules near implantation of medial spine; outer spine of basis flagellated; distal setae of third exopodal segment geniculate; first endopodal segment as long as exopodite, bearing a pectinate inner sub-distal element; second endopodal segment short; third endopodal segment 3 times as long as median one, bearing a slender smooth inner distal seta, and two straight pectinate spines.
Coxa of P2 (Fig. 26a) and P3 ornamented with rows of long and short spinules; bases of both legs with triangular process on medial corner and between articulation of rami; cluster of long spinules on medial margin; outer element on P2 basis spiniform and flagellated, but unmodified and smooth in P3; three-segmented exopodites, two-segmented endopodites; exopodal segments with sharply extended outer corners; inner appendage of proximal exopodal segments pinnate, of proximal endopodal segments pectinate; outer distal spines on distal endopodal segments long, only pinnate along upper outer part of stem (Fig. 26c).
P4 exopodite with triangular process on distal outer corner of proximal segment, but with rounded distal outer corner in median segment; inner elements on proximal and median segments bi-pinnate, of terminal segment pectinate; endopodite reaching just beyond distal edge of first exopodal segment, bearing pectinate element on inner margin of proximal segment; chaetotaxy in Table III.
P5 (Fig. 27c) bearing long ovate, strongly tapering, exopodite, complemented with 6 elements; endopodal lobe of baseoendopodite not quite reaching middle of exopodite, bearing 5 minutely pinnate setae/spines; surface of both rami smooth, except for some minute spinules along inner edge of baseoendopodite.
P6 vestiges represented as small socles, bearing three long smooth setae; genital complex not well distinguishable on slide, but contour clearly tetragonicipitid shaped; no egg-sac observed.

MALE

Habitus unknown (resembling female?), but clearly with a more slender urosome; length 0.86 mm (GEDDES, 1968), 0.80 mm (BODIN, 1979); integument ornamented as in female, and lacking spinules along postero-ventral margins of ultimate urosomal somites.
Rostrum (Fig. 24f) somewhat shorter than in female, as long as segment I of antennule, with rounded apex between pair of sensillae.
Caudal rami (Fig. 27a) conical, distinctly longer than in female; dorsal surface not observed; two lateral setae in proximal third of margin, distal lateral seta arising some distance from outer distal corner; bi-articulate dorsal seta implanted close to middle of inner margin; outer terminal seta not confluent with median one, and as long as ramus; median terminal seta not expanded; inner terminal seta short, about 1/3 of length of ramus.
Antennule (Fig. 24e) large, with robust appearance, 9-segmented; posteriorly directed margin of segment II somewhat protruded, distinctly stronger sclerotized than other segments; palm of chirocer part with suture on ventral surface, but without dorsal one; aesthetasc bearing segment with two globulous setae, and succeeding segment with two bulbous setae, one long conical seta, and a large articulating unguiform process; finger of subchirocer apparatus composed of three strongly sclerotized segments, bearing three bulbous setae on first segment, none on second, and 11+Aest on ultimate segment.
Buccal appendages, P1, and exopodites of P2 and P3 as in the female.
Endopodite P2 (Fig. 26b) with shorter distal segment than in female, bearing an inner short smooth seta, and two long modified elements on distal edge; distal edge and inner sub-distal corner of P3 endopodite ornamented with triangular processes (Fig. 26d); outer distal spine, considerably shorter than in female, somewhat expanded and rigid, armed with long spinules in median part of outward directed margin of stem.
P4 exopodite (Fig. 27d) as in the female with rounded outer distal corner of median segment, and bearing three pectinate spines on inner margin of terminal segment; proportional lengths of segments, and shape of setae and spines as in female, but with an additional inner plumose seta on second segment.
Baseoendopodite P5 bearing three robust and pinnate spines on endopodal lobe; the latter not reaching to the middle of exopodite (Fig. 26e); exopodite long ovate, not tapering distally, furnished with 3 smooth outer setae, one pinnate apical long element, and two pinnate short spines along inner margin; left P5 (Fig. 26e) with a short suture in proximal third of inner margin; right P5 exopodite (Fig. 26f) with a distinct suture in same region, but over entire width of segment; posterior surface of left P5 exopodite without suture.
Right P6 vestige distinct from supporting somite, bearing an inner spine, a median and outer smooth seta; left P6 vestige not observed.

DISCUSSION

Although the original description of *D. menaiensis* is less detailed than the description given by BODIN (1979), it is obvious that the specimens from La Rochelle are conspecific with the Menai Bridge specimens (type-locality). Re-examination of the specimens from La Rochelle revealed, besides some additions of ornaments on the buccal appendages, that the maxilla in *D. menaiensis* has 4 endites instead of 3, and that the male P2 possesses three terminal elements on the second endopodal segment.

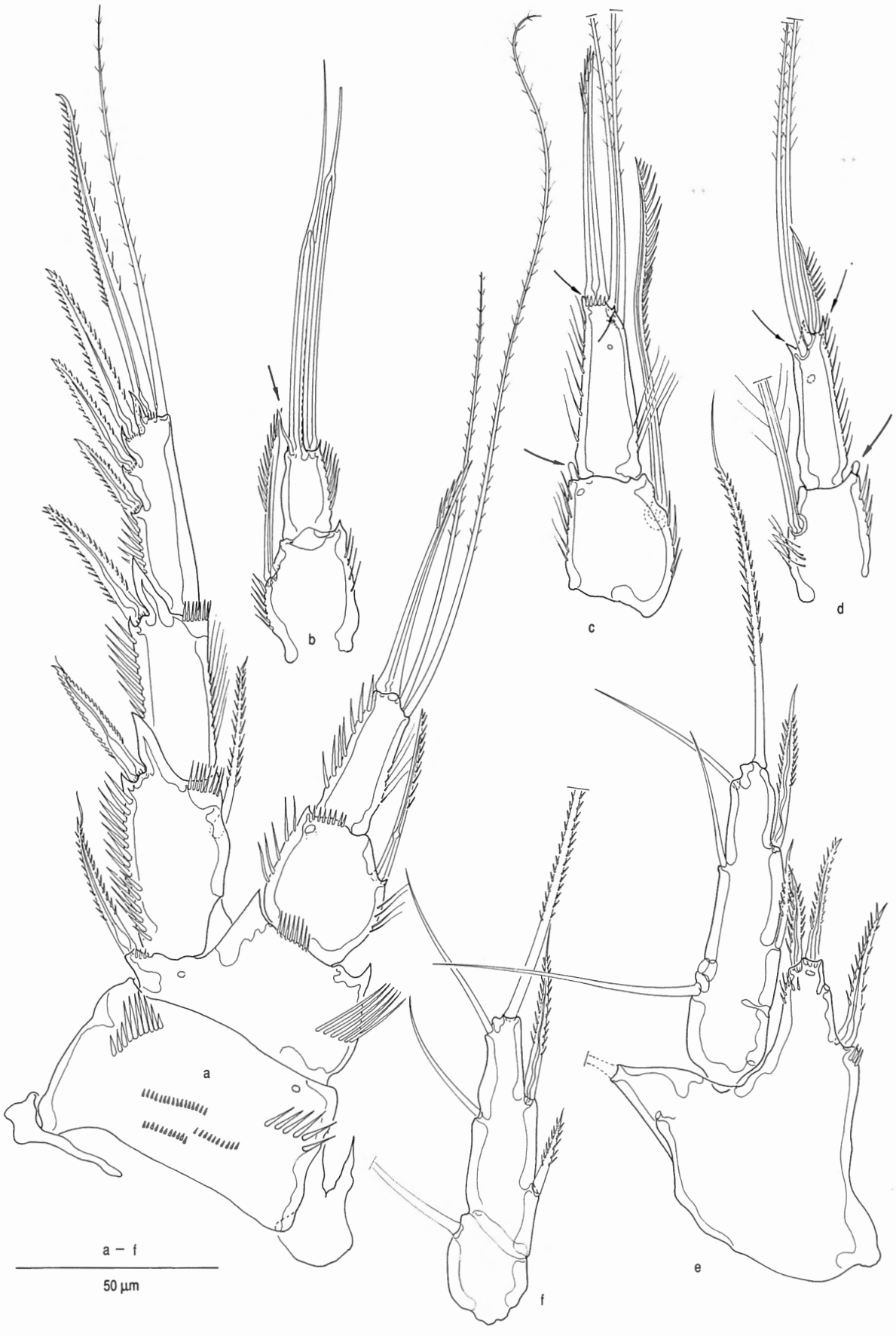

Fig. 26. – *Nidiagoceps menaiensis* (GEDDES, 1968): a, female P2, anterior; b, endopodite male P2, posterior; c, female P3 endopodite, anterior; d, male endopodite P3, posterior; e, male left P5, anterior; f, exopodite of male right P5, posterior (a-f drawn after specimens from La Rochelle (France), BODIN collection, Brest).

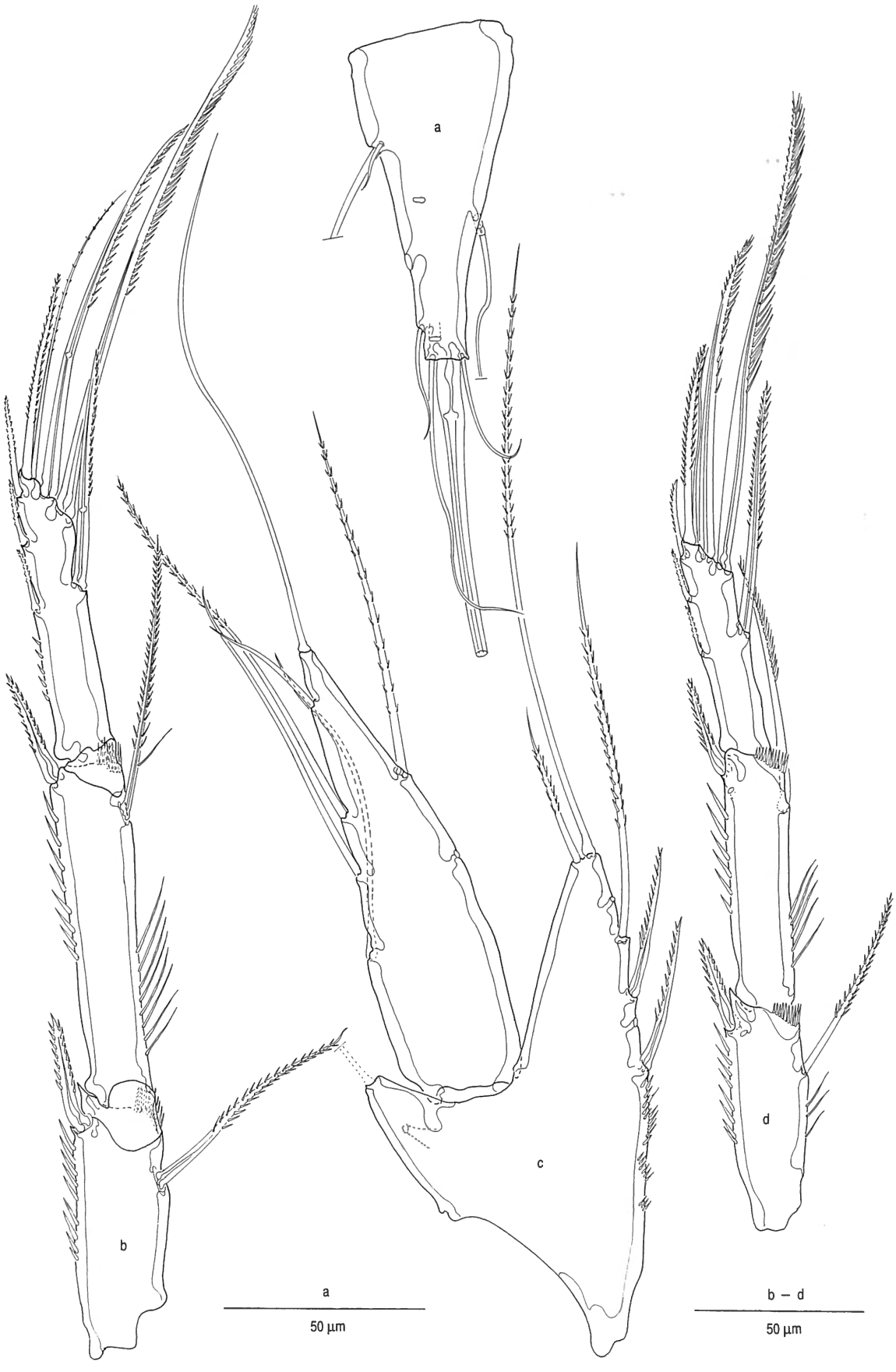

Fig. 27. – *Nidiagoceps menaiensis* (GEDDES, 1968): a, male caudal ramus, ventral; b, female exopodite P4, posterior; c, female P5, posterior; d, male exopodite P4, anterior (a-d drawn after specimens from La Rochelle (France), BODIN collection, Brest).

Nidiagoceps trifidus (YEATMAN, 1980) comb. nov.

SYNONYMY

Diagoniceps trifidus n. sp. - YEATMAN, 1980: p. 121-123, Figs. 1-13.
Diagoniceps trifidus YEATMAN, 1980. - WELLS, 1981: p. 7; KUNZ, 1984: p. 34; WELLS, 1985: p. 9; BODIN, 1988: p. 145.

TYPE-MATERIAL

Five females deposited in the USNM registered under catalogue numbers 171270 (holotype) and 171271 (paratypes).

TYPE-LOCALITY

Between Metro Sewer outfall and entrance of Lake Washington Ship Canal, Seattle (Washington State, U.S.A.).

DIFFERENTIAL DIAGNOSIS

FEMALE

Length ranging from 750 to 780 μm, with cylindrical caudal rami tapering distally, and about twice as long as wide; lateral caudal rami and dorsal seta arising from distal half of ramus; cephalic appendages as in type-species (?); terminal exopodal segments of P2-P4 with two outer spines; second endopodal segments of P3 and P4 with four elements; P5 with short ovate exopodite (twice as long as wide); chaetotaxy of P2-P5 in Table III.

MALE

Unknown.

DISCUSSION

The present species is closely related with *Nidiagoceps menaiensis* but differs mainly from the type-species in the chaetotaxy of the second endopodal segments and terminal exopodal segments of the legs, and the long, almost cylindrical appearance of the female caudal rami.
In *N. menaiensis* it has been mentioned that the endopodite P4 of the male bears an additional inner seta, having no homologue in the female. In a forthcoming paper, FIERS (in press) argues that male dimorphic structures and complements often can be referred to the ancestral characterstates of the appendages. The male of *N. menaiensis* with its additional inner seta on the P4 endopodite represents an other example, besides the Donsiellinae and Cletodidae.

Genus **Odaginiceps** n. gen.

DIAGNOSIS

Tetragonicipitidae with fusiform depressed body; with dorsal and lateral remnants of transversal fringe on genital double somite; posterior margins of somites minutely to deeply incised; and surfaces often ornamented with spinules; rostrum large and wide, reaching beyond first antennular segment, distinctly separated from cephalothorax, not bended ventrally; caudal rami of variable form, from cylindrical to short slightly globulous, ornamented with long bristles; outer terminal seta long, not fused with median one, slightly to strongly bulbous at base.
Antennule 9-segmented without prolonged second segment, having a distinctly strongly sclerotized posterior margin; principal aesthetasc on segment IV; first segment ornamented with row of broad spinules; antenna with basis, bearing well developed exopodite complemented with three pinnate setae; first endopodal segment with an abexopodal seta; second endopodal segment with 11 elements; short one-segmented endopodite and three-segmented exopodite on mandibular palp, respectively with 8 and 6 setae; maxillule with thickened epipodal seta, and one-segmented exopodite and endopodite, both with three setae; maxilla bearing three endites, each with three elements, claw accompanied with robust armed seta, and endopodite two-segmented; basis of maxilliped with 2 to 3 setae, palm with 2 and claw with 2 setae; maxillipedal integument densely ornamented.
P1 with two-segmented endopodite, bearing three terminal elements on second segment; P2-P4 with three-segmented exopodites and two-segmented endopodites; exopodal segments of P2 and P3 without inner armament; proximal segment endopodite without inner seta; P5 with long ovate exopodite, distinct from baseoendopodite, bearing 6 setae.
Male: habitus resembling female body-shape, shorter; caudal rami as in female, more slender in one species; antennule sub-chirocer, 9-segmented, without largely expanded segments, rigid and short smooth setae on inner surface of palm; dimorphism of P2 endopodite typical; outer sub-distal spine of P3 endopodite swollen at base, pinnate along outer margin of stem; endopodite P4 as in female, at the most with shorter setae/spines; exopodites as in female, except for curved hook-shaped process on distal outer corner of median segment of P4 and reduced number of inner pectinate setae on terminal segment when female possesses three inner setae; six elements on P5 exopodite with inner proximal one spiniform with long armature; baseoendopodite with three endopodal spines; P6 with typical complement of three elements.

TYPE-SPECIES

Odaginiceps clarkae n. sp., here designated.

ETYMOLOGY

The generic name is an anagram of *Diagoniceps*, gender feminine.

OTHER SPECIES

Odaginiceps elegantissima n. sp. and *Odaginiceps xamaneki* n. sp., both described below.

Odaginiceps clarkae n. sp.
Figs. 28 - 32

TYPE-MATERIAL

Holotype female dissected and mounted on 8 slides, labeled COP 3955 A-H; allotype male dissected and mounted on 8 slides, labeled COP 3956 A-H; paratype male, dissected and mounted on 4 slides (COP 3957 A-D), and 4 ♀♀, 5 ♂♂, and 1 ♀CV, ethanol preserved, labeled COP 3958.

TYPE-LOCALITY

West Central Atlantic: Quintana Roo State, Nichupté Lagoon (Cancun, Mexico). Sample MEX 93-104: sandy bottom with *Thalassia testudinum* bed (21°06'36" N - 86°46'19" W) at - 2.27 m with a salinity of 31.85‰. Leg. G. de la Cruz, 27 March 1993.

ETYMOLOGY

The species is named in honour of Janice Clark, Collection Manager at the Division of Crustacea of the U.S. National Museum of Natural History, in appreciation of her continuous efforts to provide requested specimens and information.

DESCRIPTION

HOLOTYPE FEMALE

Habitus (Fig. 28a, b) fusiform depressed, post-cephalic somites tapering posteriorly; slightly constricted behind pedigerous somites; length: 823 μm, with largest width near posterior margin of cephalothorax.
Integument of cephalothorax smooth, of all other somites ornamented with irregular pattern of hardly visible spinules; posterior margin of cephalothorax and pedigerous somites minutely sinuate; of fifth leg bearing somite and genital somites minutely sinuate in dorsomedian region, but more deeply incised along lateral edges; abdominal somites with deeply incised posterior edge; ventral corners of second genital and abdominal somites furnished with some slender spinules; ventral surface of second abdominal somite with a transversal row of short and very slender spinules in anterior region (Fig. 29a).
Rostrum far reaching beyond distal margin of first antennular segment; tapering anteriad; apex slightly bifid; single pair of sensillae; ventral surface with pore orifice, in distal third.
Caudal rami of cylindrical type, tapering in posterior direction, with in lateral view, a distinct inclination in median third; 3.5 times as long as wide; inner margin, and proximal part of outer edge ornamented with long slender spinules; proximal lateral setae arising from middle of outer margin; dorsal bi-articulate seta, implanted in median third, near inner edge; distal lateral seta short; outer terminal seta with only slightly swollen base, as long as supporting caudal ramus, not fused with median one; median terminal seta with swollen sinuate base (Fig. 28c, d); inner terminal seta, as long as distal lateral one.
Note: as the buccal appendages resemble those of the other species in the genus they are illustrated in detail for *O. elegantissima*. The description here deals with the differences observed.
Antennula (Fig. 31b) 9-segmented, without prolonged second segment; integument smooth except for a row of coarse spinules on the anteriorly directed surface of segment I; posteriorly directed margin of second segment somewhat accentuated, and more strongly sclerotized than in other segments; setal complement and setal ornamentation as in *O. elegantissima*; antennule somewhat more robust in appearance than in *O. elegantissima*.
Antenna, mandible and maxilla similar with these of *O. elegantissima*.
Maxillule (Fig. 31e) with same armament as in *O. elegantissima*; prae-coxal part with three parallel rows of slender spinules; coxal and basal extensions each ornamented with a horse-shoe shaped row of spinules.
Maxilliped (Fig. 31 c: illustrated in posterior view); with short spinules along inner margin of basis, and long spinules on anterior surface of palm; outer proximal edge furnished with very long and slender spinules.
P1 coxa (Fig. 29b) ornamented with several rows of long spinules on both sides (Fig. 29c); outer margin of coxa protruded, strongly sclerotized; basis spinulose on inner margin, bearing a flagellated inner pinnate and a long finely armed outer spine; median distal part of basis strongly crescentic, smooth; first endopodal segment shorter than exopodite, heavily armed along inner and outer margins, and bearing a sub-distal inner pectinate seta; second endopodal segment as long as 2/3 of first segment, complemented with strong spinules along outer margin, fine hairy elements along inner edge; three distal elements: an outer spine, a median geniculate seta and a minute inner element.
P2-P3 coxae and bases as in P1 (Fig. 30a, b); three-segmented exopodites and two-segmented endopodites; hyaline fringes on inner distal corners of exopodite segments 1 and 2, and on endopodite segment 1, coarse and large; first and third exopodal segments furnished

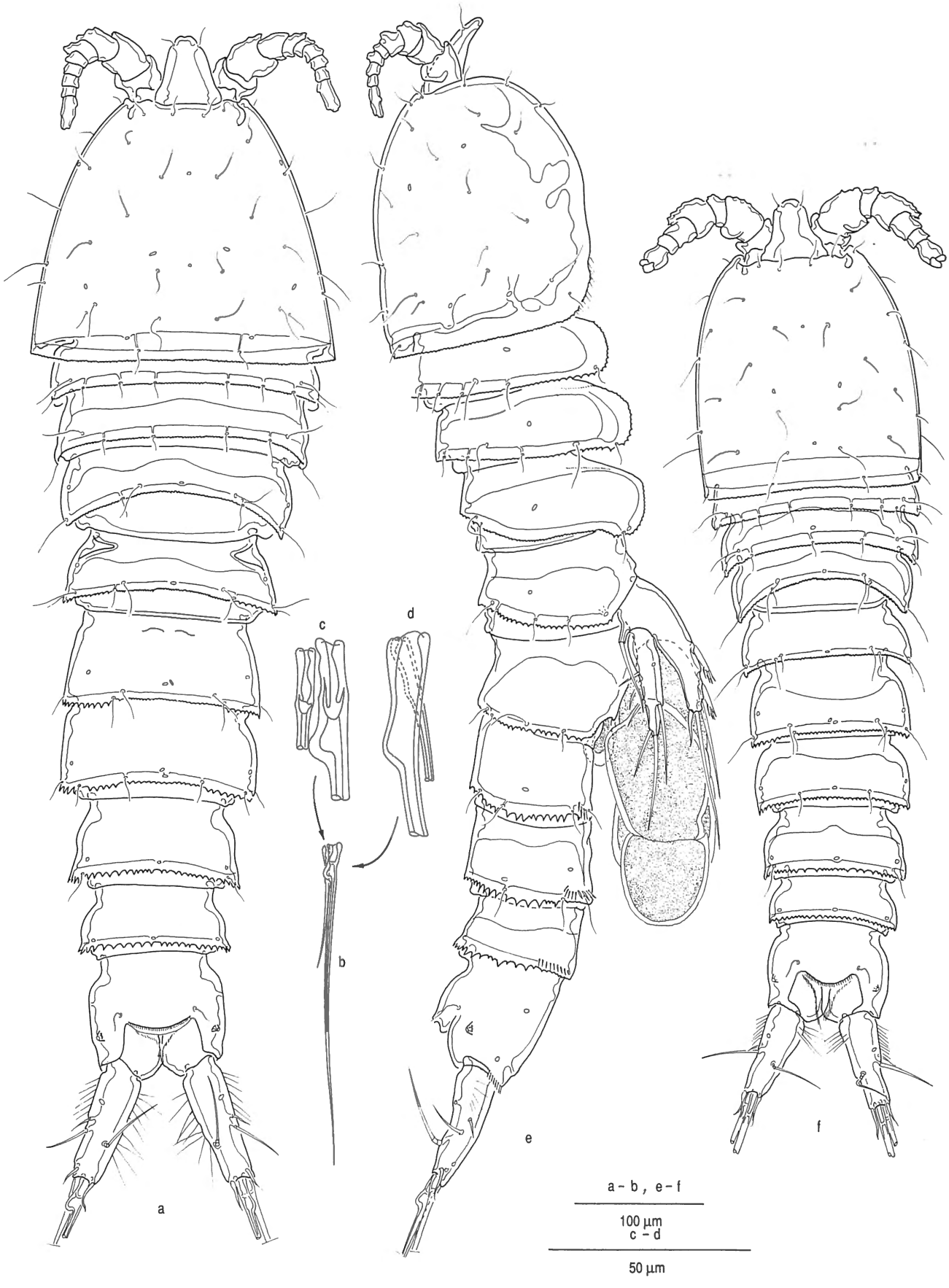

Fig. 28. – *Odagniceps clarkae* n. gen, n. sp.: a, female habitus, dorsal; b, median caudal setae (left ramus); c, proximal part of median caudal setae, dorsal; d, proximal part of median caudal setae, lateral; e, female habitus, lateral; f, male habitus, dorsal (a-e, holotype female; f, allotype male).

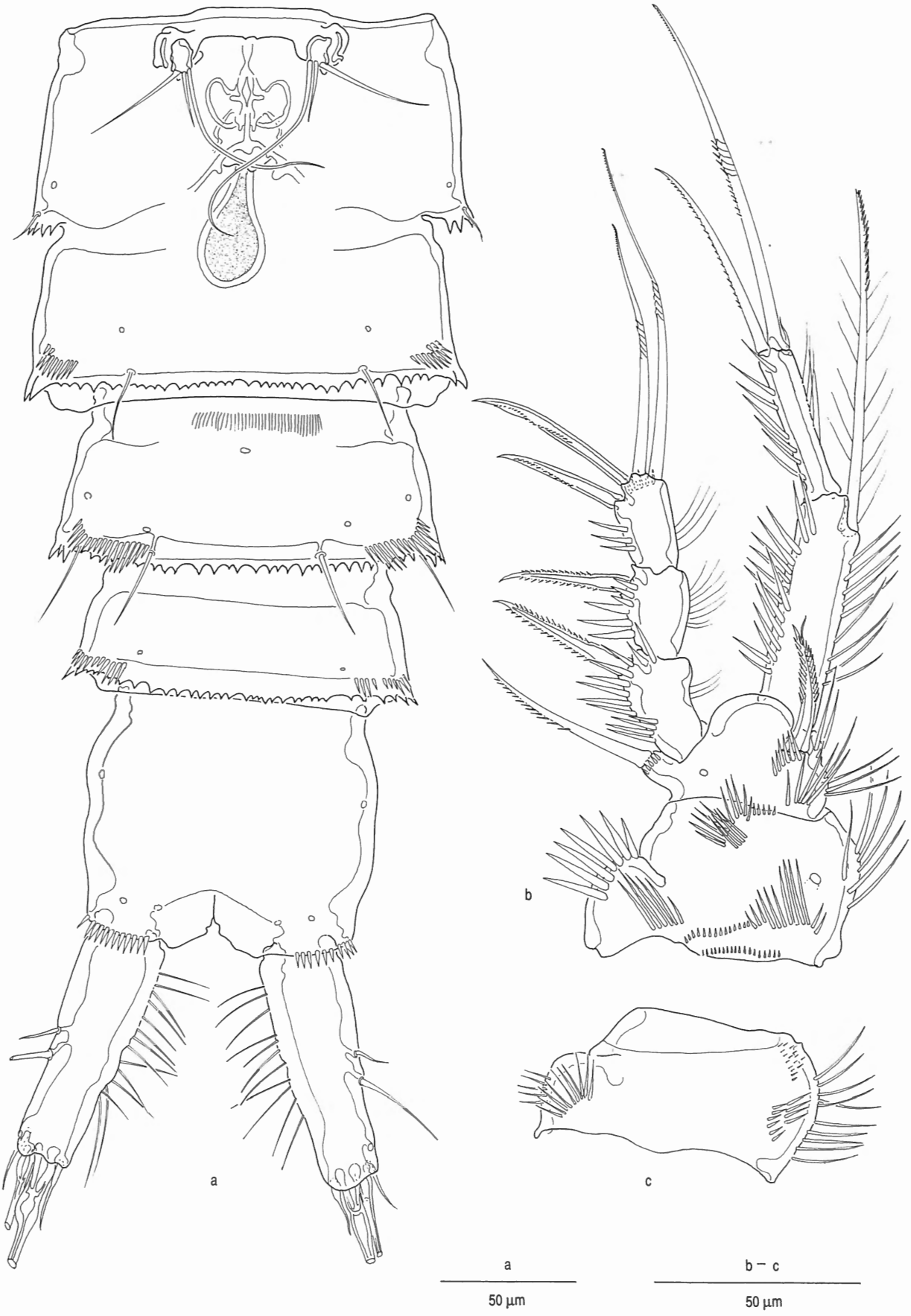

Fig. 29. – *Odaginiceps clarkae* n. gen., n. sp.: a, abdomen, ventral; b, P1, anterior; c, P1 coxa, posterior (a-c, holotype female).

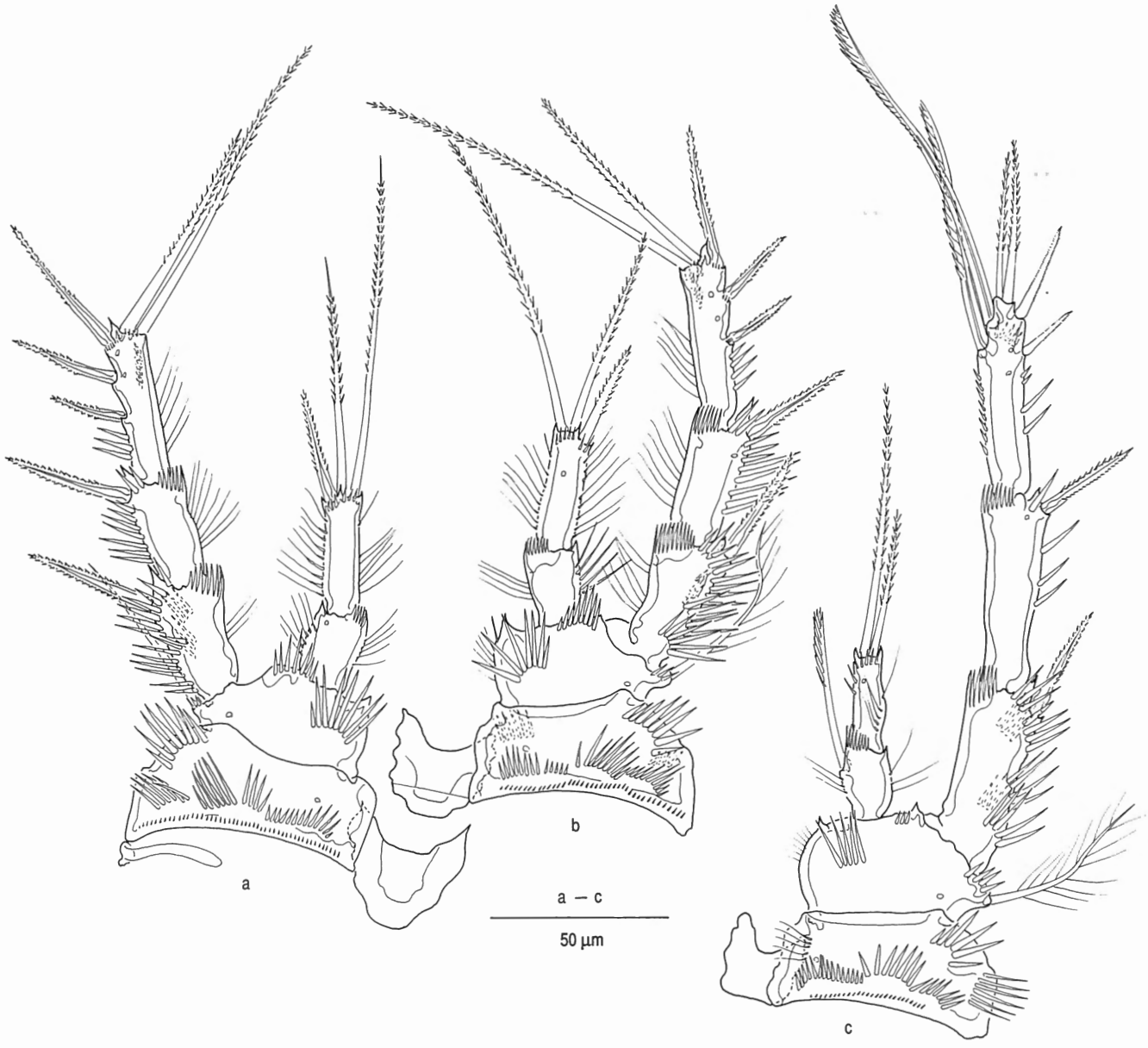

Fig. 30. – *Odaginiceps clarkae* n. gen., n. sp.: a, P2; b, P3; c, P4 (a-c, holotype female, all illustrated anteriorly).

with coarse spines along the outer margins and on the posterior surfaces; distal elements on third exopodal segments and second endopodal ones, pinnate; chaetotaxy in Table III.

P4 rami ornamented as in preceding legs; endopodite reaching just beyond distal margin of first exopodal segment; inner setae on third exopodal segment, and first endopodal one, pectinate; chaetotaxy in Table III.

P5 (Fig. 31a) with distinct exopodite, reaching beyond endopodal lobe of baseoendopodite; 5 baseoendopodal elements and 6 exopodal ones; outer setae on exopodite globulous at base; margins of rami ornamented with slender spinules.

P6 (Fig. 29a) somewhat longer than wide, bearing three smooth setae, inner one longest, median shortest; genital pore sinuate, connected with short slender duct to receptacula; single egg sac with 5 eggs.

ALLOTYPE MALE

Habitus (Fig. 28f) resembling closely habitus of female, except for separated genital somites and length (708 µm); dorsal and lateral ornamentation of somites as in female; posteroventral margins of abdominal somites set with long and slender spinules over entire length (Fig. 32a).

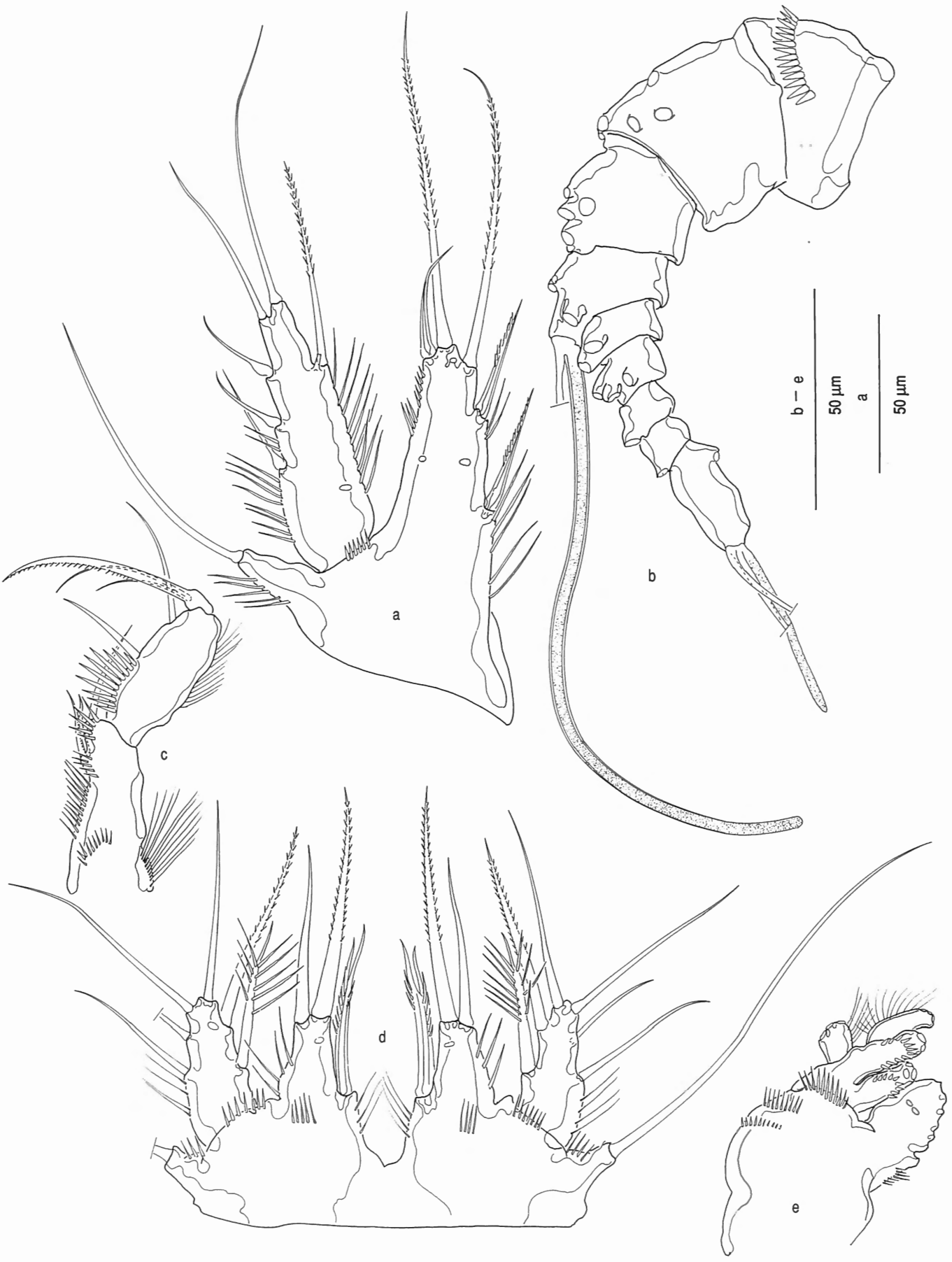

Fig. 31. – *Odaginiceps clarkae* n. gen., n. sp.: a, P5; b, antennule; c, maxilliped, anterior; d, P5; e, contour of maxillule showing integumental ornamentation (a-c, e, holotype female; d, allotype male).

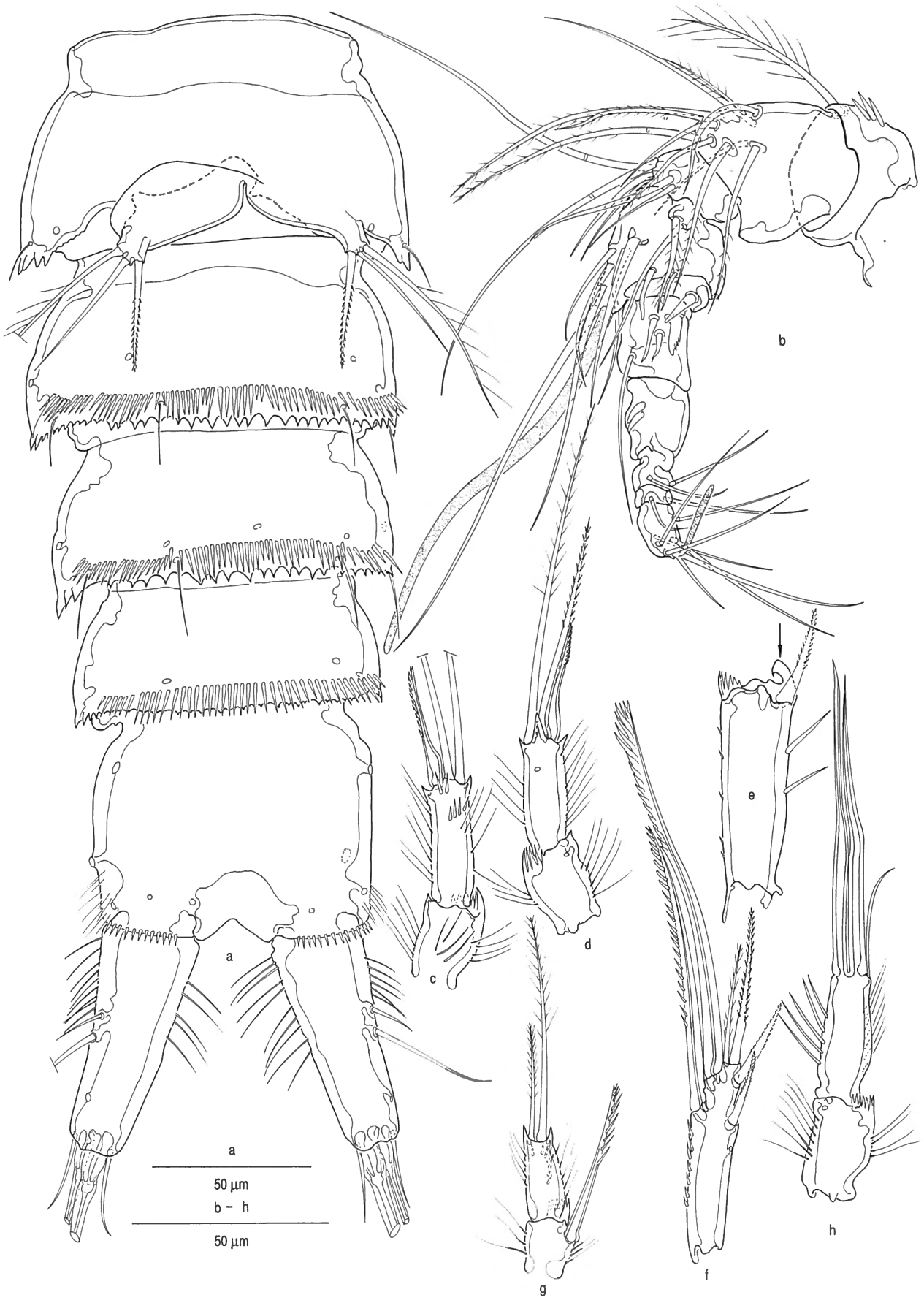

Fig. 32. – *Odaginiceps clarkae* n. gen., n. sp.: a, abdomen, ventral; b, antennule, ventral; c, endopodite P3, posterior; d, endopodite P3, anterior; e, second exopodal segment P4, posterior; f, third exopodal segment P4, posterior; g, endopodite P4, anterior; h, endopodite P2, anterior (a, c, g, paratype male COP 3957; b, d, e, f, h, allotype male).

Antennule (Fig. 32b) 9-segmented with first and second segment as in female; segments IV-VII strongly sclerotized but not strongly expanded; inner surface of palm bearing 6 (1, 1, 3, 2 respectively) short and thick setae, of which one (segm. VI) is sinuate; principal aesthetasc on segment IV, additional one on segment IX.
P1 and exopodites of P2 and P3 as in female; terminal elements of P2 endopodite typically modified, inner seta as long as supporting segment (Fig. 32h); second segment of endopodite P3 with a moderately large triangular terminal extension; inner seta plumose, outer one pinnate; outer sub-distal spine globulous at base, armed along outer margin of stem (Fig. 32c, d); P4 second exopodal segment with a curved and blunt extension on outer distal corner; third exopodal segment and endopodite P4 as in female, except for the plumose aspect of terminal elements on endopodite (Fig. 32g).
P5 (Fig. 31d) typical with endopodal lobe and short ovate exopodite; inner element of baseoendopodite armed with long spinules, inner distal element pinnate, and outer one smooth; exopodite with 6 elements: outer and distal ones smooth and slender, sub-distal inner one short pinnate, and proximal inner one with long fragile spinules.
Right P6 vestige distinct, left one fused with somite (Fig. 32a), both with two setae and one spine.

Odaginiceps elegantissima n. sp.
Figs. 33 - 37

SYNONYMY

Diagoniceps laevis WILLEY, 1930 - COULL, 1970: Table 8; COULL & HERMAN, 1970: Table 1.

TYPE-MATERIAL

One ovigerous female (holotype) dissected and mounted on 10 slides, USNM 125615 (slides A-J), prosome of an adult female (lacking several segments of appendages) and 1 copepodid CIV, ethanol-preserved, USNM 126866.

TYPE-LOCALITY

Bermuda, Castel Harbour, station at -16 m, in sandy-silt sediments (see COULL, 1970 for more details).

ETYMOLOGY

The specific name *elegantissima* alludes to the elegant way the holotype female is ornamented with suctorian epizoids.

DESCRIPTION

HOLOTYPE FEMALE

Habitus (Fig. 33a, b) fusiform, slightly depressed, having a rather elongated impression in dorsal view; length, including rostrum and caudal rami, 974 μm, with largest width in anterior part of body.
Posterior margin of cephalothorax, and pedigerous somites II and III minutely sinuate; margins of pedigerous somite IV and V minutely sinuate dorsomedian, and furnished with distinctly more deeply incised fringe laterally; genital double somite with distinct transversal dorsal sinuate fringe; posterior fringe of urosomal somites more deeply incised dorsally than ventrally; ventral surfaces of genital somites and second abdominal somite ornamented with spinules near lateral corners, with in addition a cluster of long slender spinules in proximal half of second abdominal somite; anal operculum with a transversal spinulose dorsal ridge, and concave smooth posterior edge.
Caudal rami (Fig. 33d) with slightly crescentic lateral margins, furnished with long slender spinules along inner margin; proximal lateral setae and bi-articalate dorsal seta implanted in distal half; proximal lateral seta arising from distalmost outer corner; outer terminal seta thickened at base, as long as caudal ramus; median terminal seta with swollen basal part, and inner terminal one short, not reaching beyond swollen part of median one.
Antennule (Fig. 35b) 9-segmented with smooth integument, except for row of spinules on segment I; setal armament as follows: I(1)-II(9)-III(7)-IV(4+aesth)-V(2)-VI(4)-VII(2)-VIII(2)-IX(7+aesth); seta on segment I plumose; one plumose and one pinnate seta on segment II, and two and one pinnate setae on segment III and V, respectively; posteriorly directed margin of segment II slightly protruded, strongly sclerotized.
Antennule (Fig. 35d) with long spinules on abexopodal margin of basis; and spinulose seta on first endopodal segment; abexopodal spines on second endopodal segment fagellated; exopodite ornamented with two rows of minute spinules (Fig. 35c).
Biting edge of gnathobasis (Fig. 36b) formed by simple strong distal teeth, a three-dentate tooth and a bipinnate seta on corners; teeth flanked with a row of small spinules; mandibular palp (Fig. 36a) with short endopodal segment, and three-segmented exopodite, armamented with two median and 6 terminal setae on endopodite, and 1, 3, 2 setae on exopodal segments; coxa-basis with three distal plumose setae, and surface ornamented with long spinules.
Maxillular arthrite (Fig. 36c) with 10 armed distal spines, and two surface setae; epipodal seta with thickened basal part, plumose; coxal extension bearing 5 finely pinnate setae, and basal extension having 8 terminal mainly smooth setae; endopodite and exopodite each with three (smooth, plumose, respectively) setae; prae-coxal surface furnished with field of minute spinules and rami ornamented with setules along margins.

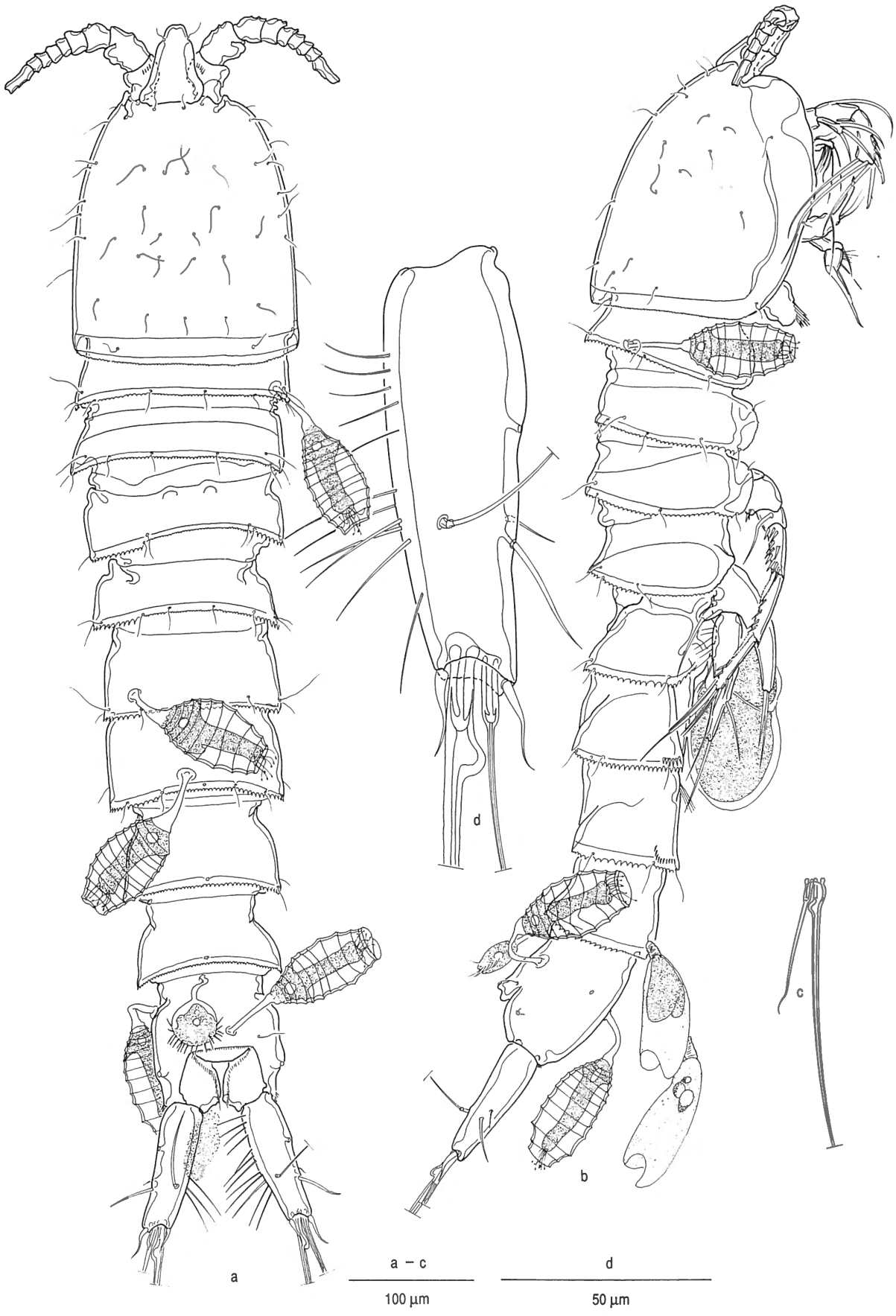

Fig. 33. – *Odaginiceps elegantissima* n. gen., n. sp.: a, female habitus, dorsal; b, female habitus, lateral; c, median caudal setae, left pair; d, right caudal ramus, dorsal (a-d, holotype female).

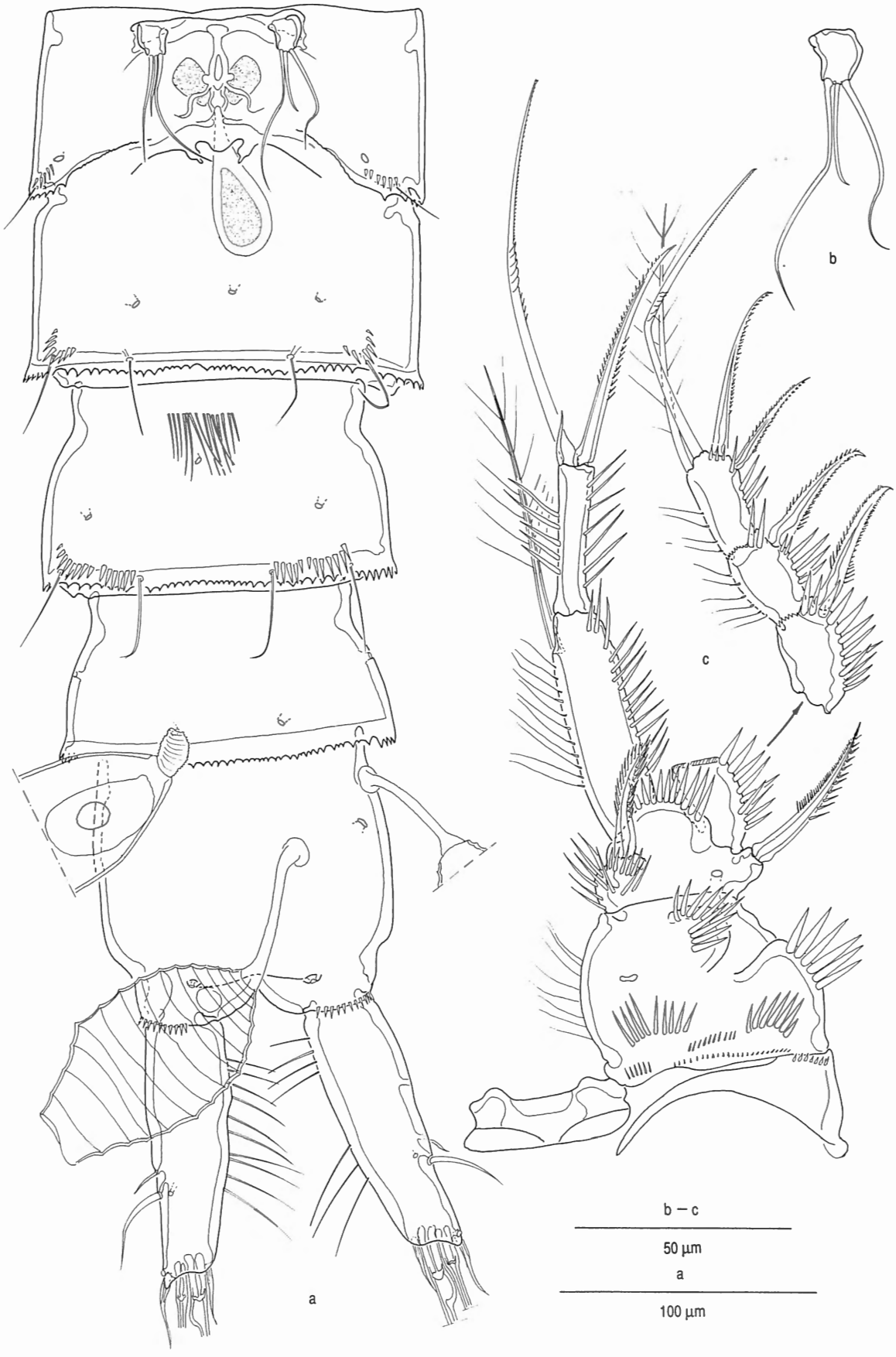

Fig. 34. – *Odaginiceps elegantissima* n. gen., n. sp.: a, abdomen, ventral; b, left P6; c, P1, frontal (a-c, holotype female).

Fig. 35. – *Odaginiceps elegantissima* n. gen., n. sp.: a, rostrum, ventral; b, antennule, dorsal; c, exopodal segment of antenna, outer side; d, antenna; e, endopodal segment of antenna, exopodal side; f, paragnath; g, labrum (a-f, holotype female).

Fig. 36. – *Odaginiceps elegantissima* n. gen., n. sp.: a, mandibular palp; b, mandibular gnathobasis; c, maxillule; d, maxilla (endites detached); e, maxilliped; f, P5 (a-f, holotype female).

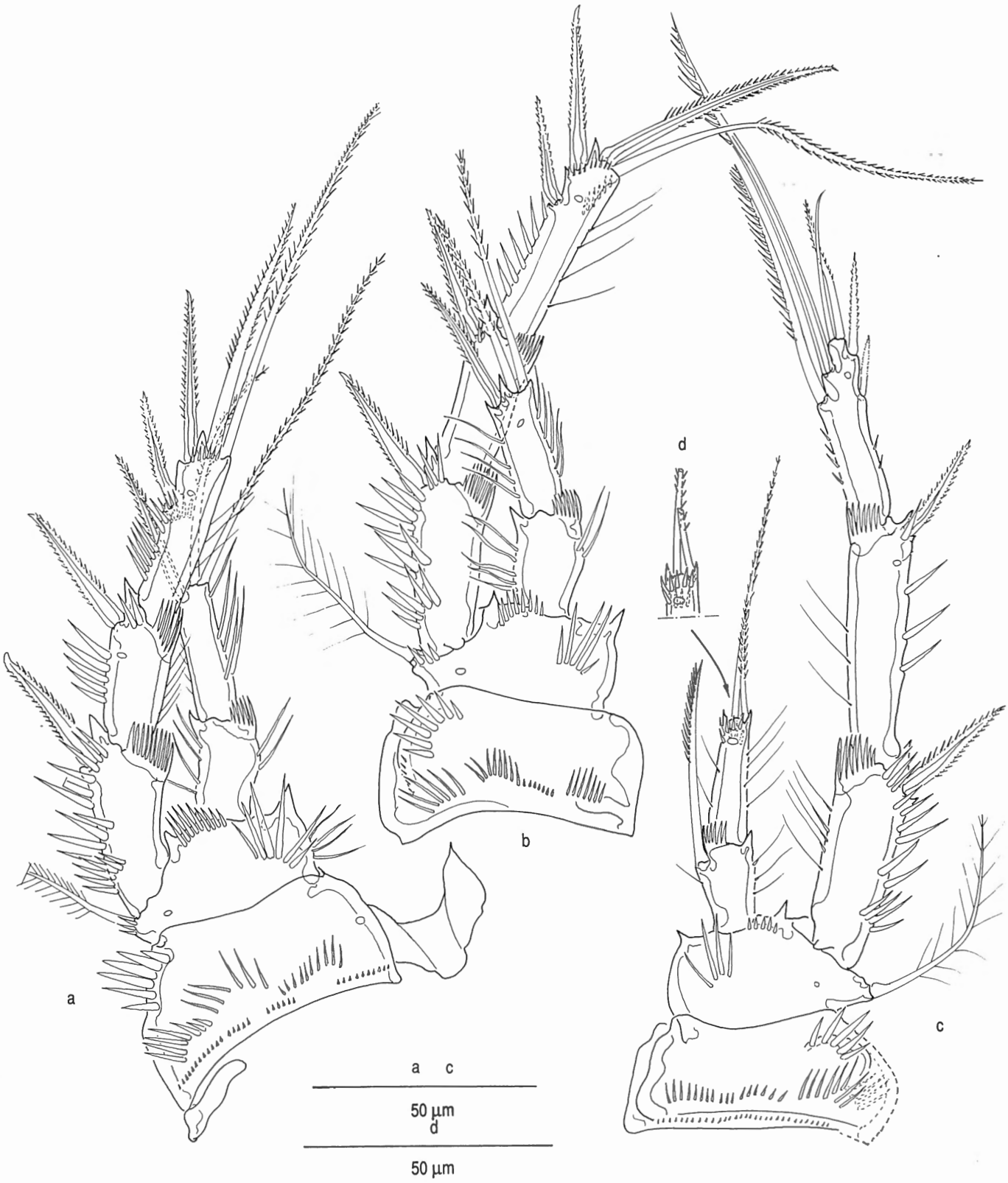

Fig. 37. – *Odaginiceps elegantissima* n. gen., n. sp.: a, P2; b, P2; c, P3; d, distal end of second endopodal segment P4, somewhat enlarged, (a-d, holotype female, illustrated anterior).

Three endites on maxillar syncoxa each equipped with three elements (Fig. 36d); claw of basis armed in distal half, accompanied with two smooth setae and one rigid and pinnate seta; endopodite two-segmented with on proximal segment a large rigid and partially pinnate seta and one smooth seta, and on distal segment two setae, confluent at base; surface of syncoxa with inner field of minute spinules, and two irregular rows of spinules near outer margin; basis inner extension ornamented with a row of spinules.
Maxilliped (Fig. 36e, illustrated in anterior view) having relatively short basis, furnished with long spinules along inner margin, and bearing three setae; proximal outer corner of basis broken during dissection; endopodal segment with two setae, and ornamented with two spinule rows along inner margin and slender hair-like setules along outer margin; claw pinnate and accompanied with two setae.
P1 (Fig. 34c) heavily ornamented on anterior surface of protopodal components and along margins of each ramal segment; first endopodal segment not quite reaching distal margin of third exopodal segment; inner seta on first endopodal segment rigid and plumose, implanted subdistally; second endopodal segment rather long, with outer terminal element spiniform; third exopodal segment with two outer spines, an outer distal geniculate seta and an inner plumose seta.
P2-P4 (Fig. 37a-c) with heavily ornamented coxae and bases; inner distal corner of each leg produced into sharp process; P4 exopodite with typical prolonged appearance; terminal elements on exopodites and endopodites pinnate, except for inner distal smooth seta and pectinate nature of inner elements on third exopodal segment of P4; chaetotaxy of legs in Table III.P5 (Fig. 36f) resembling closely fifth leg of type-species, except for the more elongated exopodite; the plumose aspect of inner subdistal seta on baseoendopodite, and the less bulbous proximal parts of outer elements on exopodite.
P6 vestiges (Fig. 34a, b) well developed, with three slender setae of which median is the shortest; genital pore orifice with bilobed margin, strongly sclerotized; holotype carried 4 eggs compacted together.

MALE

Unknown.

DISCUSSION

O. elegantissima n. sp. resembles *O. clarkae* n. sp. in many aspects and can be easily confused examining the habitus only. However, the presence of only two outer spines on the ultimate exopodal segments of P2 and P3 distinguish the present species clearly from the latter. Other differences are the shorter ornaments on the maxillipeds, the spinulose field on the coxa of the maxillule, the long and well defined median row of spinules on the ventral surface of the second abdominal somite, and the distinctly longer P5 exopodite with normal outer setae.

Odaginiceps xamaneki n. sp.
Figs. 38 - 42

TYPE-MATERIAL

Holotype female dissected on 7 slides, labeled COP 3976 A-G; allotype male, dissected on 6 slides, and labeled COP 3977 A-F; paratypes: 3 ♂♂ preserved in alcohol, labeled COP 3978.

TYPE-LOCALITY

West Central Atlantic, western region of Yucatán continental shelf (20° 13,1' N - 91° 51,34' W) at a depth of 40.9 m. Leg. CINVESTAV, Mérida (Mexico), July 1990.

ETYMOLOGY

The specific name *xamaneki* is a conjunction of Xaman Ek (pronounced *shamanek*), the Mayan goddess of the Polar Star, and is the name used to denote the marine research campaigns on the Yucatán Shelf.

DESCRIPTION

HOLOTYPE FEMALE

Habitus (Fig. 38a, b) as in its congeners, but somewhat more depressed, and with short caudal rami; length 671 μm; posterior margins of somites sinuate; ventral surface of second abdominal somite with central group of moderately long slender spinules; posteroventral margin of second abdominal somite furnished with long spinules on both sides, but with smooth median part, of third abdominal somite entirely ornamented with spinules (some broken off, but fracture plane indicated in Fig. 39a); posteroventral margin of anal somite with long spinules, posterolateral margin with minute spinules.
Rostrum (Fig. 40 b) as in the other species of the genus, but with a rounded apex between pair of sensillae.
Caudal rami (Fig. 38c) with straight outer margin, and strongly convex inner edge; only slightly longer than wide; inner margin furnished with long slender spinules; biarticulate dorsal seta with central position; proximal lateral setae arising from median position along outer margin, while distal lateral seta is implanted on distal outer corner; outer terminal seta not fused with median one, as long as anal somite; median terminal seta broken; inner terminal seta short, only as long as 1/3 of caudal ramus.

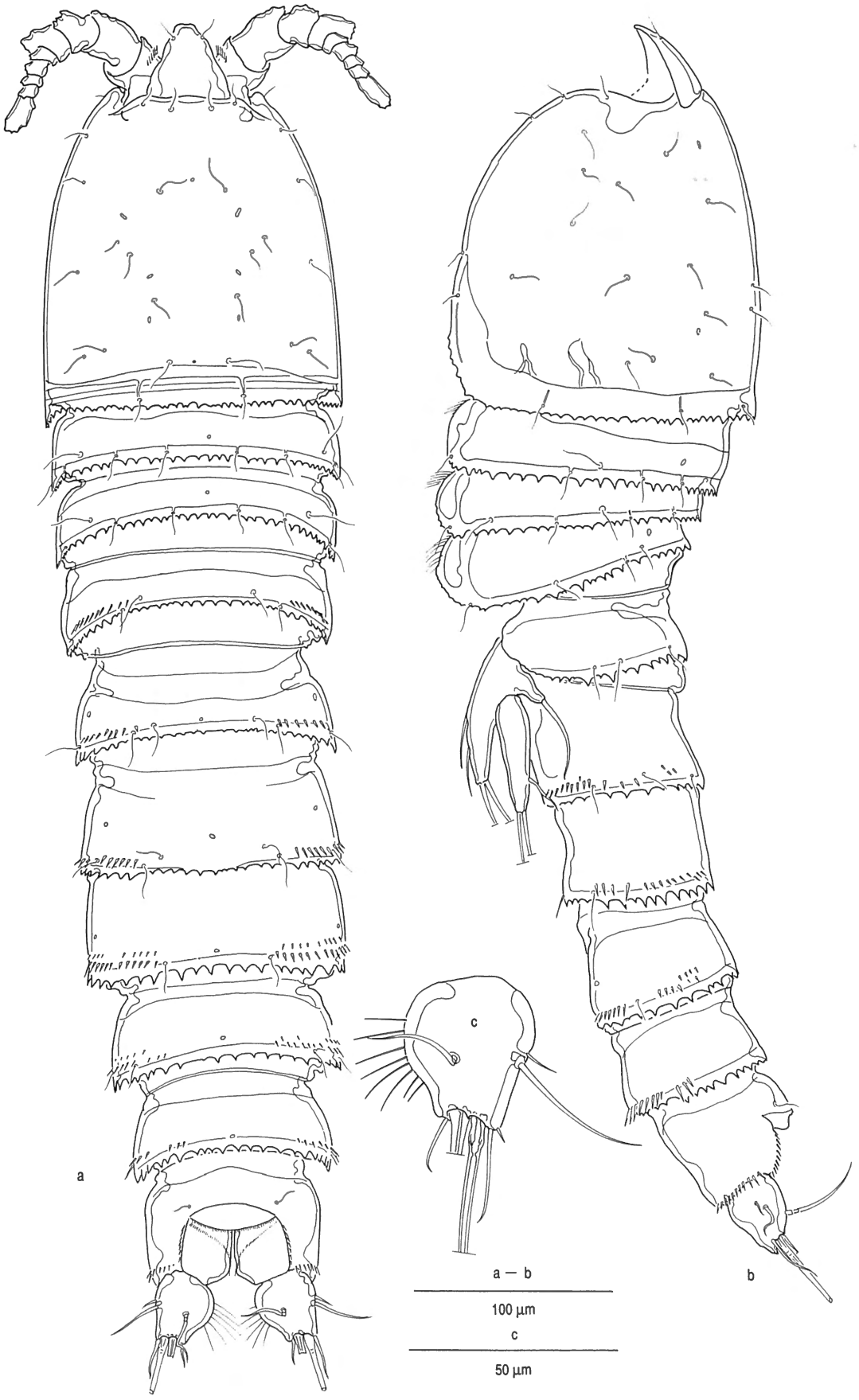

Fig. 38. – *Odaginiceps xamaneki* n. gen., n. sp.: a, female habitus, dorsal; b, female habitus, lateral; c, caudal ramus, dorsal (a-c, holotype female; fine integumental ornamentation not drawn).

Fig. 39. – *Odaginiceps xamaneki* n. gen., n. sp.: a, female abdomen, ventral; b, P1, frontal; c, P5, posterior (a-c, holotype female).

Antennule (Fig. 40a) 9-segmented (broken in holotype) with same complement as in the other species, and with a strongly sclerotized protuberance along posterior directedly margin of second segment.
Buccal appendages as in type-species. P1 (Fig. 39b) as in *O. clarkae*, except for the presence of more slender setules along inner and outer margins of endopodite.
P2-P3 (Fig. 40d, e) resembling legs of *O. clarkae* in general, but differ from the latter in the following aspects: less spinules on protopodal elements; presence of inner pectinate seta on proximal segment of P3; inner terminal seta on endopodites plumose, outer one short and smooth; outer endopodal spine implanted on same height as terminal elements, and considerably longer than supporting segment; chaetotaxy of the legs in Table III.
P4 (Fig. 41e) differs from P4 of *O. clarkae* in chaetotaxy (see Table III), less dense ornamentation on protopodal segments, and the much longer pectinate seta on proximal segment of endopodite; inner seta on median exopodal segment and outer terminal seta on endopodite short and smooth.
P5 (Fig. 39c) with long ovate exopodite, almost twice as long as endopodal lobe; chaetotaxy, shape of elements, and ornamentation as in *O. clarkae*.
P6 vestiges (Fig. 39a) indistinctly separated from supporting somite; outer seta plumose, median and inner one smooth; genital pore covered by a crescentic plate, with short copulatory duct, leading to two small receptacula; no egg-sac observed.

ALLOTYPE MALE

Habitus (Fig. 42 a) more tapering than in female; length 484 μm (484 - 451 in paratypes); ornamentation of somites as in female except for entire complement of posteroventral margins of abdominal somites (Fig. 42c)
Caudal rami (Fig. 42c) less globulous than in female, without ornaments on inner edge; outer and median terminal setae, not fused, slightly modified near base.
Antennule (Fig. 40c) nine-segmented, with principal aesthetasc on segment IV, and additional one on segment IX; armament as in *O. clarkae*; row of spinules along anteriorly directed edge of segment I shorter than in female.
Buccal appendages and P1 as in female.
P2 (Fig. 41c) without modifications on exopodite, and endopodite with typical terminal elements; inner terminal seta nearly as long as supporting segment; P3 exopodite as in female; second P3 endopodal segment with long plumose terminal setae; outer spine swollen in proximal part, ornamented along both margins of the stem, and blunt; distal edge of second segment with a sharp median and outer sub-distal extension (Fig. 41d); median exopodal segment of P4 with a long blunt sinuate process on outer distal corner, and a strongly reduced inner seta, implanted on posterior surface and not reaching beyond margin of segment; terminal exopodal segment of P4 with one inner pectinate seta less than in female; P4 endopodite bearing distinctly shorter pectinate inner element than in female; terminal setae of second endopodal segment long and plumose; outer sub-distal seta as in female.
P5 (Fig. 41a) anterior surface of baseoendopodite ornamented with two transversal rows of long spinules; endopodal lobe of baseoendopodite reaching slightly beyond middle of exopodite, bearing two terminal spiniform elements, and an inner spine implanted just below the middle of inner edge; exopodite rather rectangular, having three outer and one apical smooth setae; inner sub-distal element pinnate, and proximal inner spine ornamented with long and slender spinules along inner margin of stem.
Right P6 vestige differentiated from somite, left one not (Fig. 42c); each with an inner spine, a smooth median and a plumose outer seta.

DISCUSSION

O. xamaneki n. sp. differs significantly from the other two species of the genus *Odaginiceps* n. gen. in the distinctly shorter and more expanded caudal rami, the complementary presence of an inner pectinate element on the proximal endopodal segments of P3 and 4, and in the chaetotaxy of the P4 exopodite, bearing an additional inner element on the median segment and three pectinate elements instead of only two as in both other species. These arresting differences, in addition with the striking short aspect of the outer terminal seta on the second endopodal segments in P2-P4, are sufficient to consider the definition of a separate (but closely related) genus for *O. xamaneki* n. sp.
Despite these differences, however, it is thought that it is more realistic to keep this species unified with the two other in a single genus, until the specific and generic importance of the character changes within the family are better understood.

Genus **Godianiceps** n. gen.

DIAGNOSIS

Tetragonicipitidae with fusiform compressed body, and cephalothorax posteriorly extended, covering largely second pedigerous somite; without external remnants of fusion line between genital somites; surface of all somites smooth; rostum minute, bended between basal antennular segments; caudal rami cylindrical, with 6 elements, and outer terminal seta confluent with median one.
Antennulae 9-segmented, with second segment as long as first one; seta on segment I plumose, setae on other segments smooth; principal aesthetasc implanted on segment IV; antenna with basis bearing well-defined exopodite equipped with three elements, an abexopodal

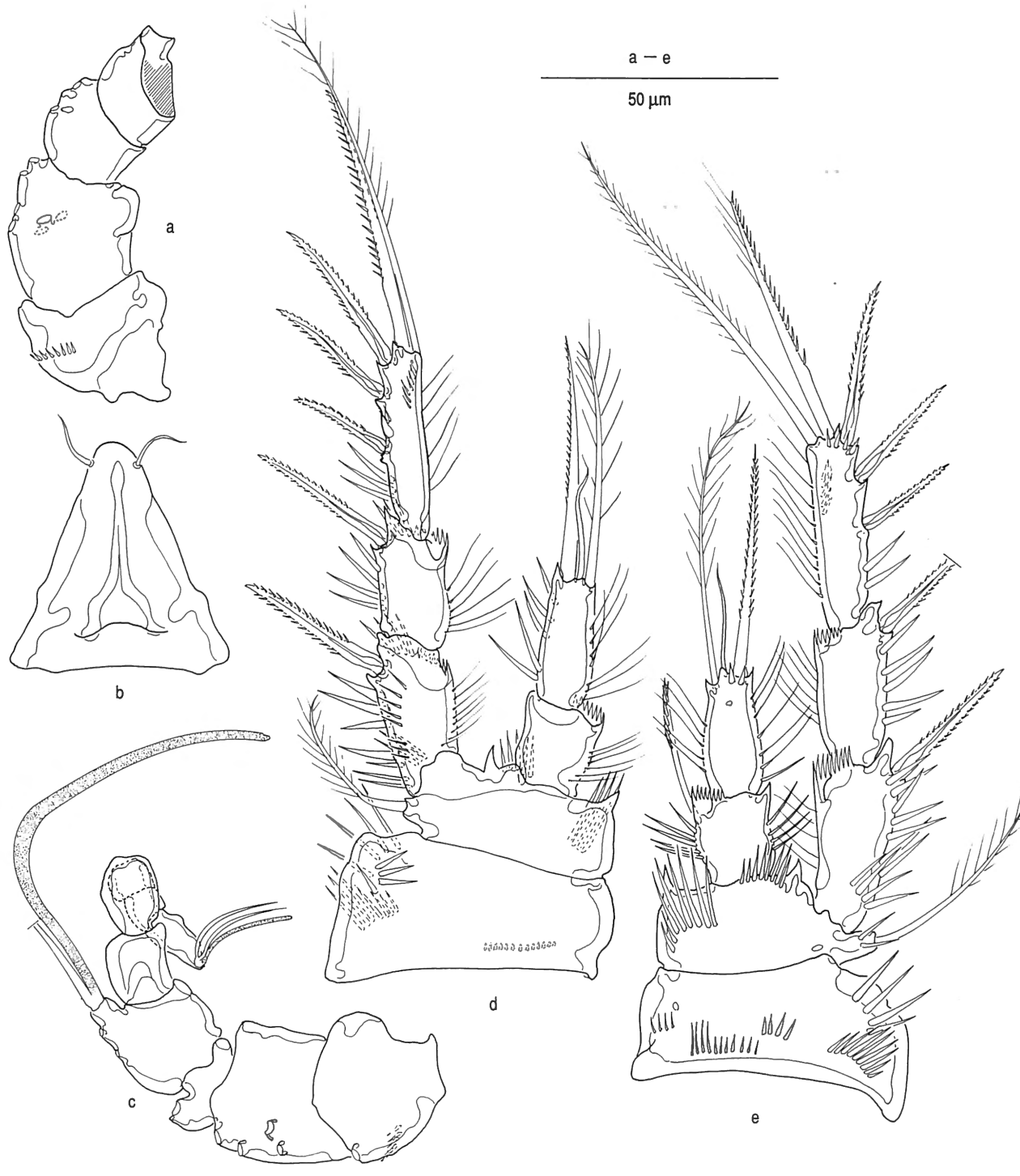

Fig. 40. – *Odaginiceps xamaneki* n. gen., n. sp.: a, contour of segments I-IV of female antennule, dorsal; b, rostrum, ventral; c, contour of male antennule, ventral; d, P2; e, P3 (a, d-e, holotype female; b-c, allotype male).

seta on first endopodal segment, and second endopodal segment complemented with 9 elements; exopodite and endopodite of mandible, one-segmented, equal in length, and having 9 and 5 setae respectively; maxillule with single, slender plumose epipodal seta, and distinct exopodite and endopodite; maxilla with three cylindrical endites; claw accompanied with two smooth setae and one pinnate element; endopodite one-segmented; maxilliped with two setae on basis, but without elements on palm or claw.

P1-P4 exopodites three-segmented, endopodites two-segmented; distal segment of P1 endopodite with two long pinnate spines; proximal endopodal segments of P2-P4 with inner pectinate spine; endopodite P4 shorter than half first exopodal segment; outer distal corners of P4 exopodal segments not extended; chaetotaxy of

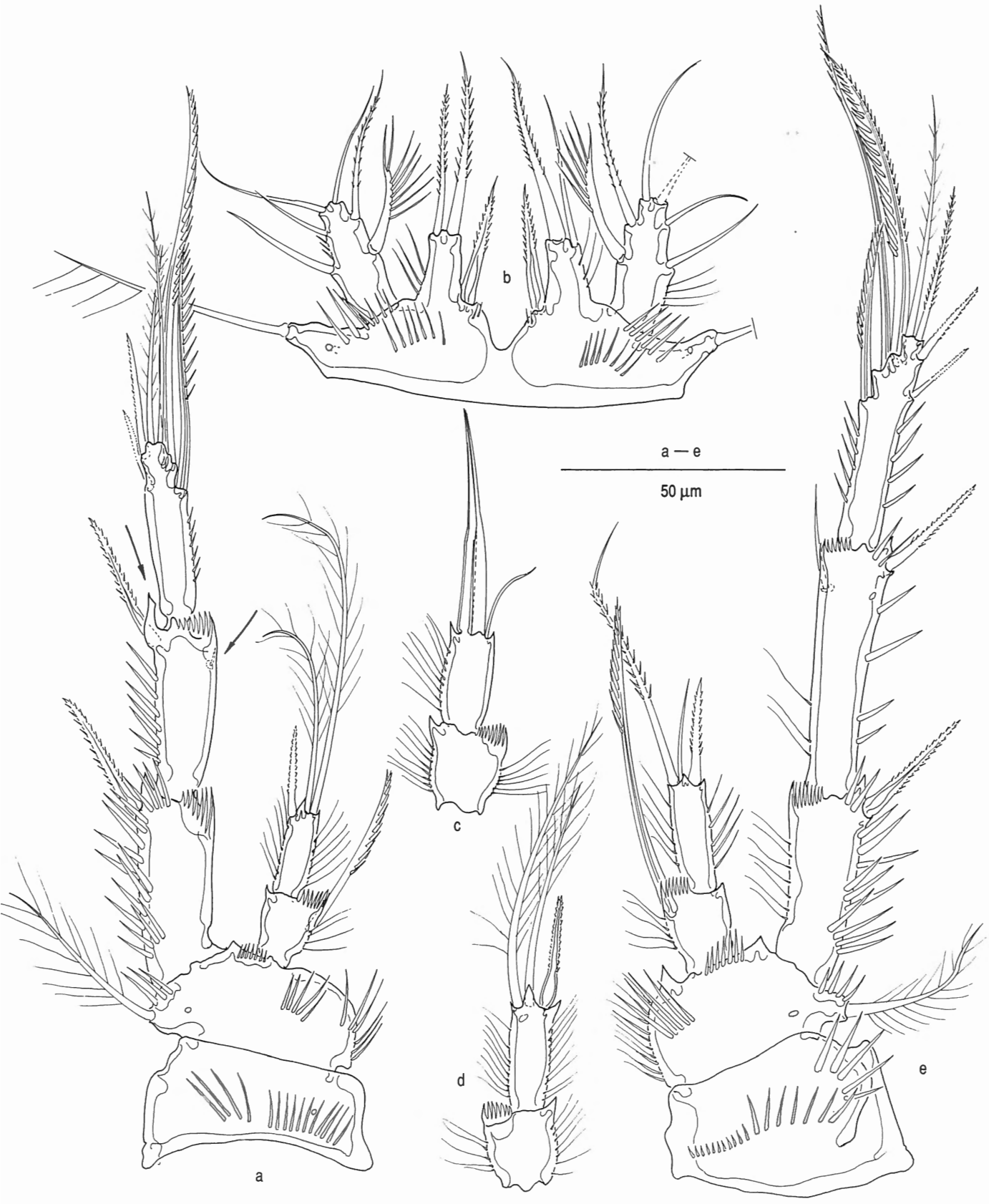

Fig. 41. – *Odaginiceps xamaneki* n. gen., n. sp.: a, P4; b, P5; c, endopodite P2; d, endopodite P3; e, P4 (a-d, allotype male; e, holotype female; a-e, anterior view).

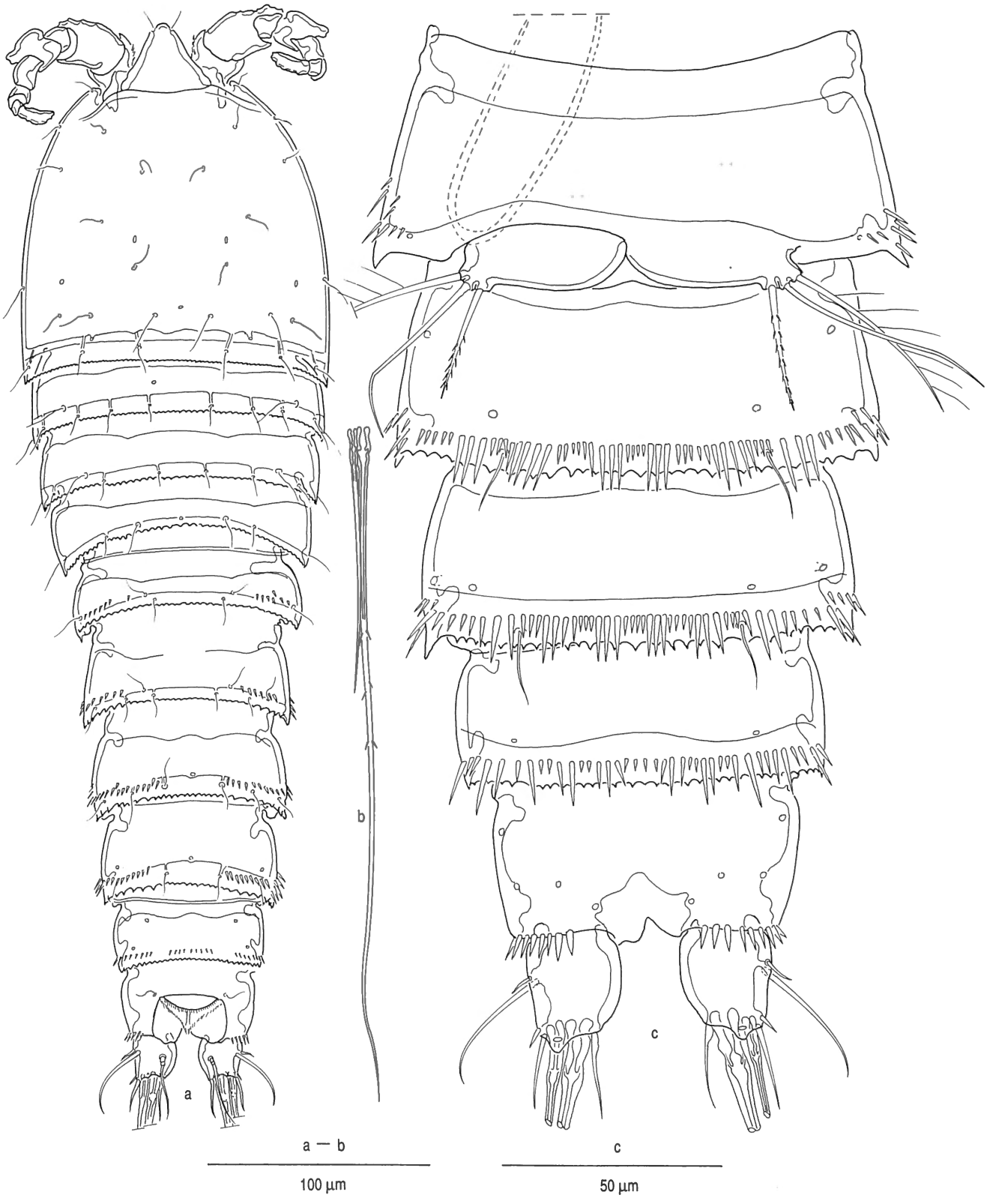

Fig. 42. – *Odaginiceps xamaneki* n. gen., n. sp.: a, male habitus, dorsal; b, median caudal setae, left pair; c, male abdomen, ventral (a-c, allotype male; fine integumental ornamentation in a, b not drawn).

exopodites and endopodites in Table III; P5 exopodite only 1.5 times as long as wide, rounded appearance, bearing five elements; endopodal lobe of P5 with 5 spines; P6 vestiges with two plumose setae.
Male habitus as in female, except for individualized genital somites; ventral surface of urosomal somites furnished with transversal rows of spinules; caudal setae as in female, except for unmodified aspect of terminal median one; antennule 9-segmented with segment IV bearing principal aesthetasc and three short rigid setae; sexual dimorphism of P2 and P3 endopodites typically tetragonicipitid, without modifications on distal edge of P3; exopodite P4 as in female, except for presence of only two inner pectinate elements on third segment; P5 endopodal lobe with three robust spines; P5 exopodite small, bearing one outer and one terminal smooth seta, and two inner robust pinnate spines; P6 vestiges equipped with a single robust spine.

TYPE-SPECIES

Godianiceps maya, here designated, by monotypy.

ETYMOLOGY

The generic name *Godianiceps* is an anagram of the generic name *Diagoniceps*, gender neutral.

Godianiceps maya n. sp.
Figs. 43 - 49

TYPE-MATERIAL

Holotype female dissected on three slides, labeled COP 3927 A-C; allotype male dissected on two slides, labeled COP 3931 A-B; paratypes: 4 ♀♀, 21 ♂♂, and 5 juveniles ethanol preserved, labeled COP 3926; 4 ♀♀ dissected (COP 3928, 3929, 3933, 3934) and 1 ♂ (COP 3932).

TYPE-LOCALITY

West Central Atlantic, Quintana Roo State, Nichupté Lagoon (Cancun, Mexico). Sample MEX 93-103: Sandy bottom, *Thalassia testudinum* bed (21°07'01" N - 86°46'33" W) at - 2.95 m with a salinity of 32.35‰. Leg. G. de la Cruz, 27 March 1993.

DESCRIPTION

HOLOTYPE FEMALE

Habitus fusiform compressed and compact, with large cephalic region constituting almost half the entire body length, and overlapping nearly entire second pedigerous somite (Fig. 43a, b); length: 605 μm, with largest width (240 μm) about halfway the cephalothorax (length range: 605 - 617 μm, in paratypes); thoracic region strongly tapering towards fifth somite, with distinctly posteriorly produced rounded pleurotergites; urosomal somites far less tapering; genital double somite as long as wide, with a wide intern sclerotized lateral band, becoming bifurcated ventrally, enveloping the genital pore (Fig. 44b); anal somite longer than penultimate somite with a triangular, smooth anal operculum.
Integument of cephalothorax, thoracic and urosomal somites smooth, except for the finely serrate posterior margins of urosomal somites and a longitudinal row of minute spinules parallel with dorsal margin of anal sinus; all somites with rigidly sclerotized integument.
Caudal rami (Fig. 43b) cylindrical, more than twice as long as wide, with a rounded outer distal edge, and bearing only 6 setae; biarticulate dorsal and proximal lateral seta arising in distal half; distal lateral seta implanted at the basis of rounded extension; outer and median terminal setae confluent at base; the former very diminutive; the latter as long as the thoracic and urosomal somites combined; medial distal seta minute. Integument of the rami smooth.
Rostrum small and triangular; apex not reaching beyond first antennular segment, fused with the cephalothorax; integument smooth except for pair of subapical sensillae.
Antennule (Fig. 45b, c) 9-segmented with segment II as long as segment I; L/W ratios of each segment: 1.14-1.10-1.10-1 (without aesthetasc socle) -0.75-1.65-1-1-2.80, and armature (Arabic numerals) on each segment (roman numerals): I(1)-II(9)-III(7)-IV(4+aest)-V(2)-VI(4)-VII(2)-VIII(2)-IX(7+aest); seta on segment I plumose, all other setae on following segments smooth; integument of all segments smooth.
Antennule (Fig. 46a) with smooth segments, except for two transversal spinule rows on the second endopodal segment and a single row on the exopodite; abexopodal margin of first endopodal segment with plumose seta; second endopodal segment with 9 elements: 2 lateral setae, 5 geniculate terminal elements and 2 smooth setae; no setae present on inner surface of second segment; exopodite well defined, one-segmented, bearing two apical pinnate spines and a smooth lateral seta.
Mandible (Fig. 46c) with robust gnatobasis, having 4 multi-dentate, and 2 bi-dentate distal teeth; accessorial seta long, bi-pinnate; coxa-basis large, with curved aspect, and furnished with two rows of long spinules along inner margin, and complemented with three smooth setae; exopodite and endopodite one-segmented, equal in length; exopodite with two proximal setae, one minute sub-distal seta, and two distal setae; endopodite having two median

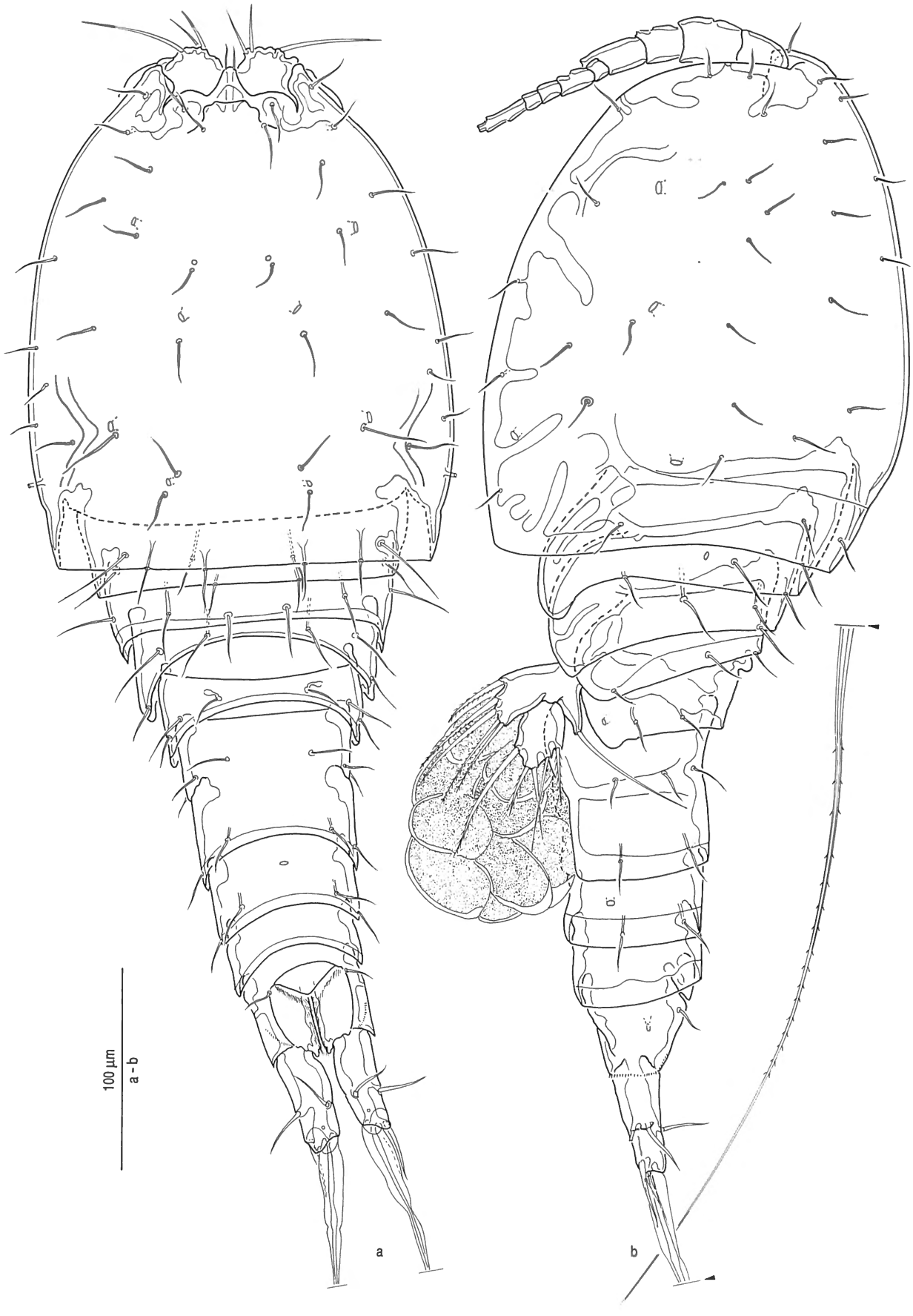

Fig. 43. – *Godianiceps maya* n. gen., n. sp.: a, female habitus, dorsal; b, habitus of ovigerous female, lateral (a-b, holotype female).

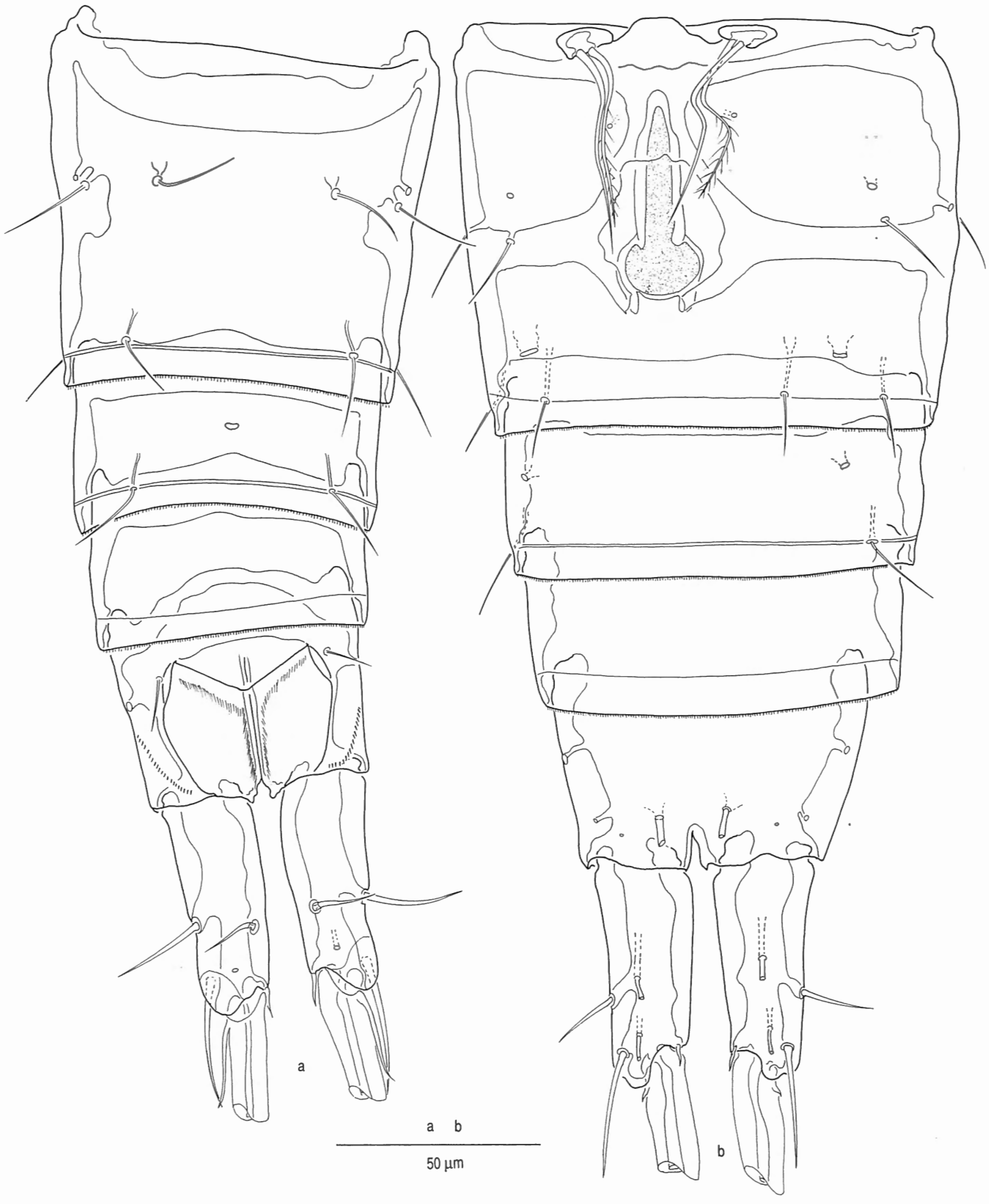

Fig. 44. – *Godianiceps maya* n. gen., n. sp.: a, female abdomen, dorsal; b, female abdomen, ventral, slightly flattened (a, allotype male; b, holotype female).

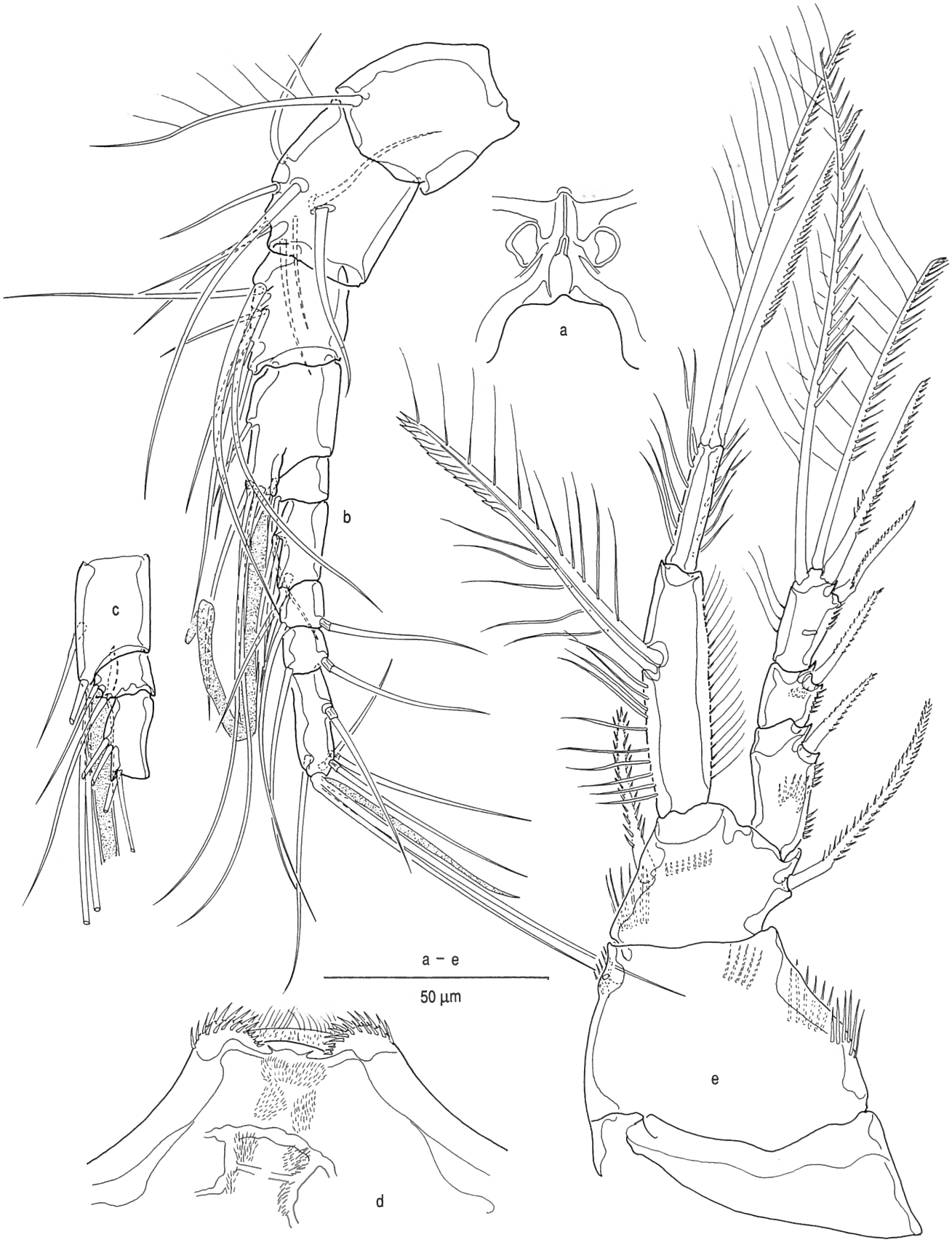

Fig. 45. – *Godianiceps maya* n. gen., n. sp.: a, female genital field; b, female antennule, ventral; c, segments IV-VI of female antennule, dorsal; d, labrum; e, P 1, posterior (a, paratype female COP 3929; b-e, holotype female).

setae, one sub-distal seta, and three distal double setae; all elements smooth.
Maxillule (Fig. 46f) with typical tetragonicipitid appearance; arthrite complemented with 2 surface setae, 8 armed distal spines, and 2 setae on dorsal corner; coxal extension (Fig. 46g), and basal extension each with 5 pinnate setae; epipodal seta long, unmodified and plumose; exopodite and endopodite distinct, bearing 3 and 4 smooth setae respectively.
Maxillule (Fig. 46b) having smooth surface, except for few minute spinules along outer margin; three cylindrical endites, each bearing three long and pinnate spines; basis with armed claw, accompanied with two slender setae; endopodite one-segmented, having 5 setae: 2 geniculate, 3 smooth and unmodified.
Maxilliped (Fig. 46d) with long cylindrical basis, furnished with two short rows of spinules on posterior surface, three horse-shoe shaped rows of spinules on anterior surface, and bordered along the inner margin with slender spinules; two distal pinnate long setae on inner distal corner; palm with minute spinules along inner and outer margin, without setae; claw slender, without accompanying setae, and pinnate in distal fourth.
P1 (Fig. 45e) with high coxa and basis, both ornamented with rows of slender spinules on frontal surface; inner and outer armament of basis spiniform; exopodite three-segmented, endopodite two-segmented with proximal segment as long as entire exopodite; second endopodal segment 4 times as long as wide, bearing two apical spiniform elements; inner seta of first endopodal segment pectinate distally, and ornamented with long setules along other parts of stem; inner and outer margins of both endopodal segments densely furnished with long spinules.
P2-P3 (Fig. 47a-b) with smooth posterior surfaces, and ornamented anterior surfaces of protopodal elements; basis of P2 with spinules on inner edge, of P3 with hairy like ornamentation; inner corner and median distal region of bases not protruded into a sharp extension; outer margins of exopodal segments ornamented with minute spinules; inner setae on proximal endopodal segments pectinate, terminal setae on second segments plumose, and outer sub-distal spine longer than supporting segment; inner and outer margins of endopodal segments furnished with long hair-like spinules; chaetotaxy in Table III.
P4 (Fig. 47c) devoid of integumental structures on protopodal segments; endopodite, only half as long as first exopodal segment, bearing a pectinate seta on minute proximal segment, and bi-pinnate spines on second segment; not prolonged exopodal aspect; third exopodal segment with three robust and pectinate inner setae; chaetotaxy in Table III.
P5 (Fig. 48c) rather short, not reaching towards end of sixth thoracic somite, bearing five spinulose setae on baseoendopodite, and two spinulose and three smooth setae on exopodite; exopodal segment short, at the most 1.5 times as long as wide; integument of both rami smooth, except for the spinulose inner margin of the endopodal lobe.
P6 (Fig. 44b) formed by two small socles, bearing two long pinnate setae. Genital field situated in anterior half of sixth thoracic somite, having a short duct and two small recetabula. Single median egg-sac with more than ten small eggs. P5 clasping only apical third of single egg-sac; the latter reaching to middle of second abdominal somite.

ALLOTYPE MALE

Habitus and length as in the female, only contrasting from the latter in the slightly more slender, and differently ornamented, abdominal somites (Fig. 48a); P6 bearing somite with an irregular pattern of spinules on ventral surface; other abdominal somites with smooth ventral surface, except for a transversal row of spinules parallel to posterior margin.
Antennule (Fig. 49c, d) 9-segmented with first two segments as in female; segments IV and V completely separated, bearing respectively on inner side of palm 3 and 1 short flame-shaped setae; segment 6 with two short modified setae; principal aesthetasc on segment IV, additional one on ultimate segment.
Buccal appendages, P1 and exopodites P2-P3 as in female; endopodite P2 (Fig. 49f) with typically modified terminal elements; inner seta slightly longer than supporting segment; endopodite P3 (Fig. 49a) bearing an inner pinnate terminal seta and an outer plumose seta, both half as long as female terminal elements; outer sub-distal spine modified, with bulbous base, smooth stem, and bifid apex; endopodite P4 (Fig. 49b) as in female, except for considerably shorter terminal setae on second segment; exopodite as in female, but with only two inner pectinate setae on inner margin of third segment (Fig. 49e).
P5 (Fig. 48b) without protruded endopodal lobe, and small nearly quadrate exopodite; endopodal regio with three pinnate spines, the inner one twice as long as both apical ones; exopodite with four elements: two inner pinnate spines, and an apical and outer smooth seta; surface of baseoendopodite with some spinules arranged in transversal rows.
Both P6 vestiges distinct from supporting somite (Fig. 48a); left one somewhat larger than right one, but each bearing a single robust smooth element; surface and distal margin of both vestiges ornamented with some minute spinules.

Species inquirenda

Diagoniceps monodi CHAPPUIS & KUNZ, 1955

SYNONYMY

Diagoniceps monodi n. sp. - CHAPPUIS & KUNZ, 1955: p. 1020-1023, Fig.1-16.
Diagoniceps monodi CHAPPUIS & KUNZ, 1955 - LANG, 1965: p. 386; GEDDES, 1969: p. 443; MARINOV, 1973: 321; WELLS, 1976: p. 133 (key); BODIN, 1979: p. 347 (key); KUNZ, 1984: p. 34-35; BODIN, 1988: p. 145.

Fig. 46. – *Godianiceps maya* n. gen., n. sp.: a, antenna; b, maxilla; c, mandible; d, maxilliped; e, syncoxa of maxilliped; f, maxillule; g, coxal endite of maxillule (a-b, paratype female COP 3929; c, f, holotype female; d-e, paratype female COP 3927).

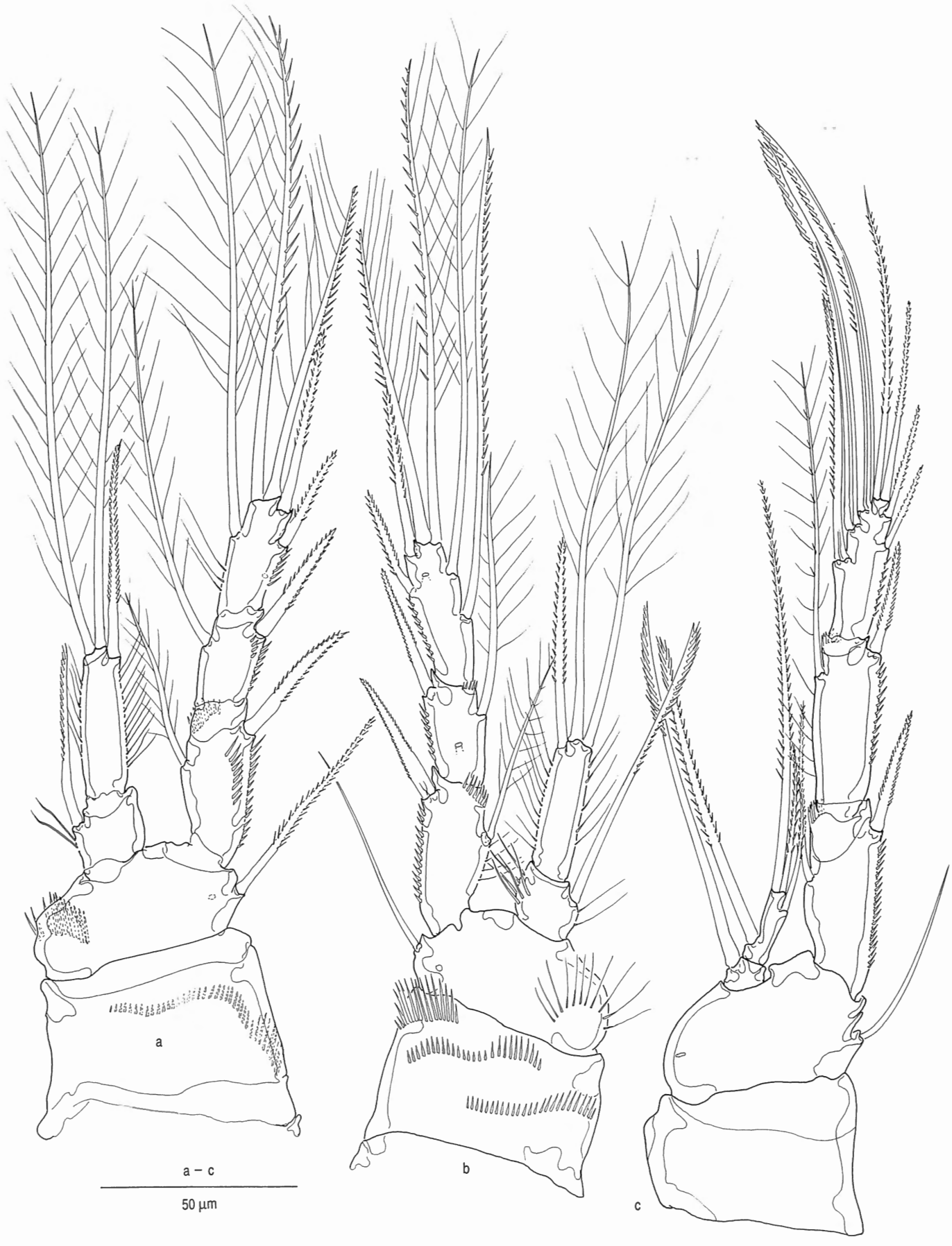

Fig. 47. – *Godianiceps maya* n. gen., n. sp.: a, P2, posterior; b, P3, anterior; c, P4, posterior (a-c, holotype female).

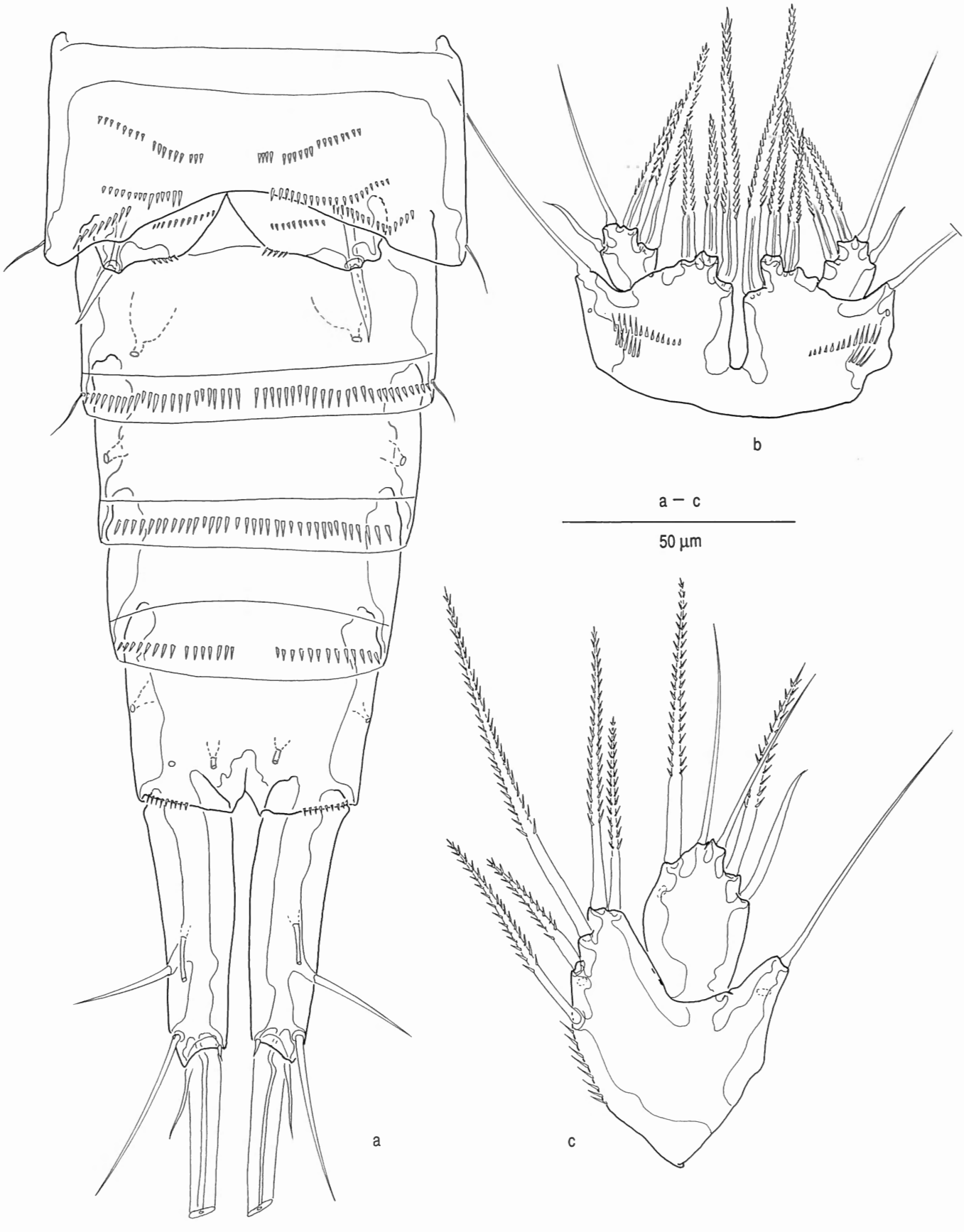

Fig. 48. – *Godianiceps maya* n. gen., n. sp.: a, male abdomen, ventral; b, male P5; c, female P5 (a-b, paratype male COP 3931; c, paratype female COP 3929).

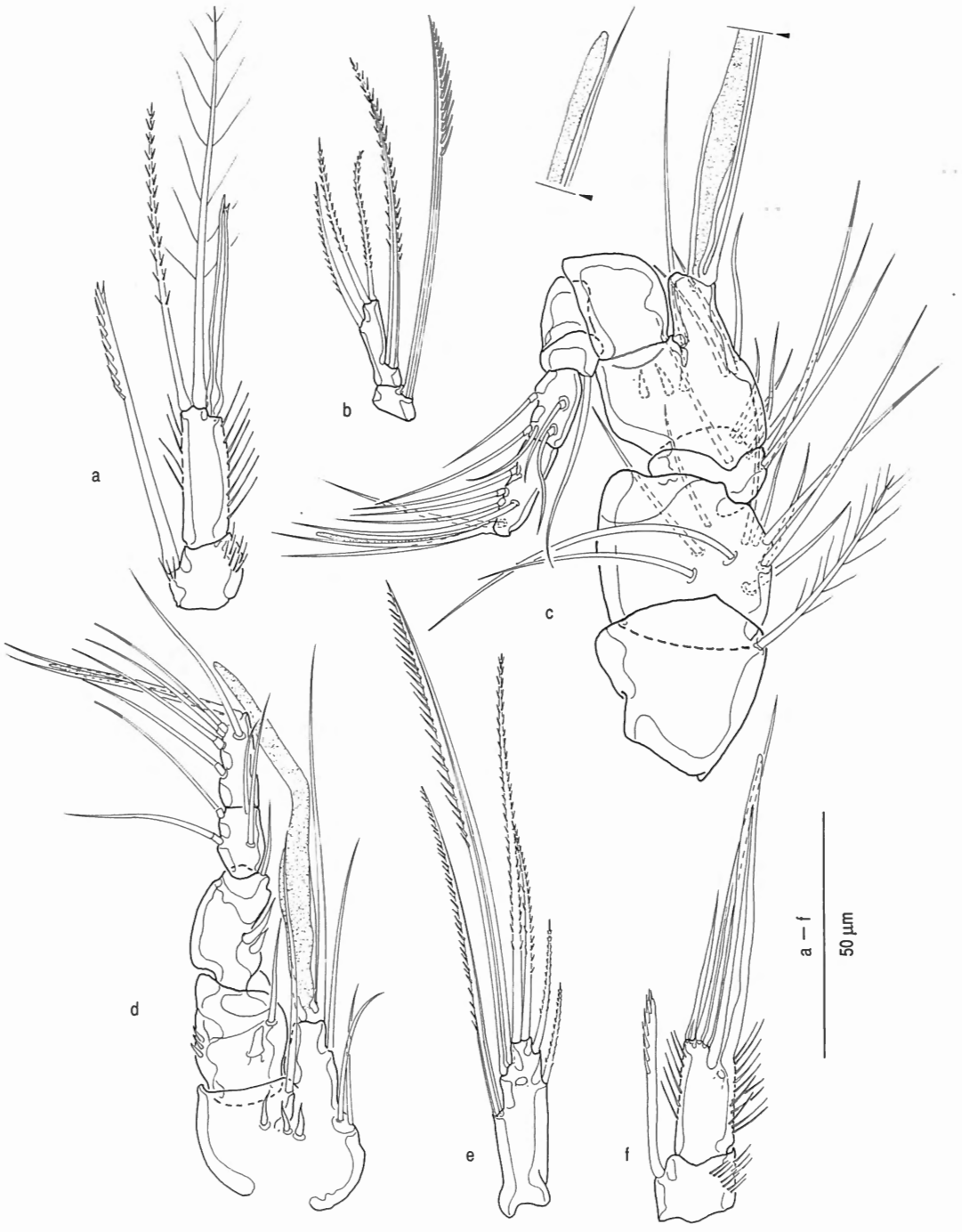

Fig. 49. – *Godianiceps maya* n. gen., n. sp.: a, endopodite P3; b, endopodite P4; c, antennule, ventral; d, segments IV-VIII of male antennule, dorsal; e, third exopodal segment P 4; f, endopodite of male P2 (a, f, paratype male; d-e, allotype male).

TYPE-LOCALITY

East Central Atlantic: Senegal, near Dakar, sub-littoral sands (CHAPPUIS & KUNZ, 1955).

TYPE-MATERIAL

Unknown.

DIFFERENTIAL DIAGNOSIS

FEMALE

Large (1.1 mm) but slender Tetragonicipitidae, with anterior body-part longer than urosome; rostrum triangular, forwards directed; caudal rami nearly cylindrical, slightly expanded proximally, and divergent; caudal setae implanted in proximal half of ramus; distal

lateral seta robust, half as long as supporting ramus; median terminal seta with globulous proximal part; outer and inner terminal setae absent (?); antennule 9-segmented; proportional lengths and complement unknown; antenna with basis, bearing exopodite with two terminal slender elements and a lateral plumose seta; mandible with one-segmented exopodite and endopodite, bearing 6 (?) and 5 (?) setae, respectively; maxillule with slender plumose epipodal seta; maxilla with bifid proximal endite, cylindrical median and distal one; claw accompanied with (?) 4 setae; endopodite (?) one-segmented complemented with (?) 4 setae; inner margin of maxillipedal palm furnished with spinules; neither basis nor palm or claw with additional setae.
P1 without inner element on basis (?), endopodite two-segmented bearing two geniculate terminal appendages, and three-segmented exopodite; P2-P4 with three-segmented exopodites and two-segmented endopodites; proximal endopodal segments with pectinate element on inner margin; chaetotaxy in Table III; P5 resembling closely P5 of *D. bocki*, and bearing 6 exopodal and 5 endopodal setae/spines; surface densely furnished with spinules; P6 vestiges minute or absent, represented by three slender setae.

MALE

Somewhat shorter than female; antennule unknown; no sexually dimorphic modifications observed in P2-P4(?); endopodal lobe of P5 with three pinnate spines; exopodite ovate, bearing 5 elements: two outer smooth setae, a large robust apical pinnate spine, and a smooth seta and a pinnate spine on the inner margin; P6 with three elements: an inner spine, and a median and outer seta.

DISCUSSION

Diagoniceps monodi is in many ways a remarkable species. In the section dealing with the taxonomical characteristics of the *Diagoniceps* related species and the tetragonicipitid genera in general, the unique features of the appendages of this species have frequently been mentioned.
Without doubt, the most arresting feature of this species is the absence of sexual dimorphic transformations of the endopodites in P2 and P3. Absence of sexual modifications in the endopodites could at once be considered as a character state requiring the definition of a separate genus for this species, as all Tetragonicipitidae have distinct sexual modifications in the legs. However, CHAPPUIS & KUNZ (1955: p. 1022, translated from French) stated: ".... we didn't find noticeable differences between both sexes. Notably those mentioned by WILLEY (*for D. laevis*) on P2 and P4 were not observed".
The illustration of the male P2 endopodite of *D. laevis* provided by WILLEY (1930: Fig. 39) is a robust drawing of the setal modifications which could lead to the assumption that a large apophysis arises from the outer distal corner of the segment. In addition, in the comments on the original description of *D. laevis* given above, it has been noted that the length of the inner distal element has been erroneously illustrated. It seems obvious that the transparent elements known in the P2 endopodite of *D. laevis* and in all tetragonicipitid species so far, were overlooked or misinterpreted by CHAPPUIS & KUNZ (1955) in their description of *D. monodi*.
The absence of dimorphism in the P4 endopodite has to be confirmed. Several examples are known in the Tetragonicipitidae were the endopodite P4 appendages are identical with these of the female, but form and presence of additional processes on the P4 exopodite, and lengths and ornamentations of the setae on the endopodite, are quite often different in the males.
D. monodi shares with *Godianiceps maya* n. sp. a comparable setal complement of the natatorial legs (see Table III), but differs distinctly from the latter by the presence of an additional seta on the inner margins of the distal endopodal segments in P2 and P3. Other differences between these species are the body-shape (lean in *D. monodi*, fusiform compressed in *G. maya*), the shape of the rostrum (large, prominent in the former, minute and bended ventrally in the latter), and the female P5 (6 exopodal elements in *D. monodi*, only 5 in *G. maya*).
Two indications of *D. monodi* suggest affinities with the genus *Aigondiceps* n. gen. (including *D. bocki*, *D. kunzi*, and *D. bodini* n. sp.). The general shape of the female P5 exopodite of *D. monodi* resembles closely this ramus in *A. bocki*, as both species have an exopodite with rather parallel sided lateral margins, and very short outer smooth setae. Secondly, it appears from the illustration of caudal rami of *D. monodi* that the distal lateral seta (in this species modified) originates from a ventral position near the corner of the ramus. So far, a comparable position of the distal lateral element is only known (and thought herein to be characteristic) for the species unified in the genus *Aigondiceps* n. gen.
However, it is obvious that based on the concise original description, *D. monodi* cannot be assigned to neither genus defined here, nor to any other genus of the family presently known.

Key to the tetragonicipitid genera

LANG (1965) amended his 1948 key by deleting the genus *Paraphyllopodopsyllus* LANG, 1944 (considered as congeneric with *Phyllopodopsyllus* T. SCOTT, 1906) and adding the genus *Laophontella* THOMPSON & A. SCOTT, 1903. The most recent key to the genera of the family has been compiled by COULL (1973). COULL (1973) did not include the genus *Oniscopsis* CHAPPUIS, 1954 because of LANG's (1965) assumptions that the genus was a paramesochrid taxon instead of a member of the family Tetragonicipitidae. COULL (1973) updated the generic diagnoses, and provided most valuable information on the genus *Protogoniceps* POR, 1964a after consulting the original drawings made by the author.

KUNZ (1984) synonymized *Fearia* COULL, 1971 with *Tetragoniceps* BRADY, 1880, but included in his analyses the genera *Oniscopsis* CHAPPUIS, 1954 and *Laophontella* THOMPSON & A. SCOTT, 1903. The phylogenetic analysis of the tetragonicipitid genera of KUNZ (1984) undoubtedly has to be amended and corrected in the future. The tables unifying the main characteristics of each species, and the definitions of species-groups within the large genus *Phyllopodopsyllus* are most useful for identification purposes of the several genera and species.
It is obvious that several genera of the family have to be scrutinized. This will probably result in the re-establishment of the genera *Paraphyllopodopsyllus* LANG, 1944 and *Fearia* COULL, 1971, but certainly will result in the definition of new genera.
Based on the results of the present study, an updated key to the genera of the Tetragonicipitidae is presented here. The key basically refers to the female morphology, but can equally serve to identify males when couplet 1 is omitted and entries are done through couplets 2 and 5. The genus *Pyrocletodes* COULL, 1973 is not included as this genus is not considered as a tetragonicipitid taxon, and the genera *Paraphyllopodopsyllus* and *Fearia* are omitted.

1 - Female P5 large and foliaceous, forming brood-pouch; endopodal lobe of P5 distinct or confluent with exopodite: **2**

- Female P5 not foliaceous, exopodite fused with or separated from baseoendopodite: **5**

2 - 3-segmented P1 endopodite; antenna with minute exopodite, bearing a single seta; endopodal lobe of female P5 distinct; rostrum large and prominent: **Pteropsyllus**

- 2-segmented P1 endopodite; antenna with a well defined one-segmented exopodite, bearing 2-3 elements; endopodal lobe of female P5 confluent with exopodite; rostrum small: **3**

3 - Antennule 8- or 9-segmented, with principal aesthetasc implanted on segment IV; first antennular segment up to 3 times as long as second one, without process on posteriorly directed margin: **Phyllopodopsyllus**

- These characteristics not combined: **4**

4 - Antennule 8-segmented with principal aesthetasc on segment III; P1 exopodite 2-segmented; endopodite P4 one-segmented: **Oniscopsis**

- Antennule 5-segmented with principal aesthetasc arising from a large distal pedestal on segment I; P1 exopodite 3-segmented; endopodite P4 minute, two-segmented: **Laophontella**

5 - First segment of antennule at least 2.5 times as long as second segment: **6**

- First segment of antennule equal or distinctly shorter than second one: **7**

6 - First segment of antennule with a processus on posteriorly directed margin; second antennular segment without processus; rostrum minute: **Tetragoniceps**

- First segment of antennule without processus on posteriorly directed margin; second antennular segment with large unguiform processus; rostrum large and prominent: **Protogoniceps**

7 - P1 exopodite three-segmented; rostrum triangular, reaching just beyond first antennal segment; inner element on proximal endopodal segments of P2-P4 pectinate: **Nidiagoceps**

- P1 exopodite two-segmented; other characteristics not combined: **8**

8 - Rostrum large, reaching far beyond first antennular segment; proximal segments of exopodites P2-P4, and P2 endopodite, without inner elements: **Odaginiceps**

- Rostrum minute, not reaching beyond first antennular segment; proximal exopodal segments P2-P4 with or without inner element; proximal endopodal segments P2-P4 with inner element: **9**

9 - Terminal exopodal segments P2-P4 with 3 outer spines; distal endopodal segments P2 and P3 with 4 setae/spines, in all: **Aigondiceps**

- Terminal exopodal segments P2-P4 with 2 outer spines; distal endopodal segments P2 and P3 with 3 setae/spines, in all: **10**

10 - Body cylindrical; distal segment of P1 endopodite with two long and one minute setae; exopodite P5 long ovate, with 6 setae: **Diagoniceps**

- Body fusiform compressed; distal segment of P1 endopodite with two long elements only; exopodite P5 short, with 5 setae: **Godianiceps**

Acknowledgements

I am most indebted to my colleagues Philippe BODIN (Université de Bretagne Occidentale, Brest), Janet REID and Janice CLARK (Smithsonian Institution, Washington) Karin SINDEMARK (Naturhistoriska Riksmuseet, Stockholm), and F.D. POR (Hebrew University, Jerusalem) for the loan of the specimens deposited in their collections. Patrik LAGROU, my diving instructor and one of the most active and spirited persons I know, is greatly acknowledged for the samples from a blue hole in the Bahamas. Gustavo de la CRUZ and his collaborators of Marine Ecology Section of the "Departemento de Recursos del Mar" (CINVESTAV-IPN, Mérida) collected and offered me those most arresting samples from Nichupté Lagoon. Marc BERGMANS, is greatly acknowledged for his valuable information on the existence of the literature dealing with infested copepods. Special thanks go to Miss Véronique GHENNE and M. Julien CILLIS (K.B.I.N., Brussels) for their technical assistance in treating the samples and the S.E.M. observations. Research and possibilities to organize the Xaman Ek oceanographic cruises resulted from the financial support offered by the European Community (CI1-bc-*-CT91-0890 HSMU) and Mexican National Science Foundation, CONACyT (211085-5-1284N).

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Frank FIERS
Royal Belgian Institute of Natural Sciences
Department of Invertebrates
Vautierstraat 29
B-1040 Brussels, Belgium

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