STYRACOTHORACIDAE (COPEPODA: HARPACTICOIDA), A NEW FAMILY FROM THE PHILIPPINE DEEP SEA

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ABSTRACT

A new family is proposed to accommodate *Styracothorax gladiator,* new genus, new species, collected from 2,050-m depth in the Philippine Sea. The Styracothoracidae is placed in the Cervinioidea on account of the fused rostrum, the setation of the antennary endopod, the reduction of the maxillulary exopod, and the uniramous fifth legs in at least the female. A suite of synapomorphies, including the subchelate maxilliped, suggests a sister-group relationship with the cave-dwelling Rotundiclipeidae. The primitive features of the Styracothoracidae and the phylogenetic relationships of the cervinioid families are discussed.

The present work arises from a study of the bathyal and mainly abyssal harpacticoids collected during the second leg of the French ESTASE Expedition in 1984. Copepods were collected on board the RV *Jean Charcot* during its cruise off the Philippine west coast from Manila to Surabaya in Indonesia.

The harpacticoid copepod fauna of Philippine deep waters has received relatively little attention, despite the fact that extensive surveys have been carried out in the Philippine Trench during the Danish *Galathea* Expedition and the various cruises of the Russian research vessel *Vityaz* (Belyaev, 1972). Virtually all our knowledge of Philippine deep-sea harpacticoids is contained in Itô's excellent papers (1982, 1983) on Cerviniidae, Thalestridae, and Ameiridae from an abyssal locality southeast of Mindanao. The description by Itô of highly distinctive harpacticoid taxa such as *Tonpostratiotes tenuipedalis, Abyssameira reducta,* and *Parameiropsis magnus,* gives an indication that this area might reveal other unsuspected discoveries. The only other deep-water harpacticoid described from the Philippine Sea is *Pontostratiotes horrida* (Cerviniidae) from 4,300 meters depth in the northeastern sector near the Bonin Islands (Izu-Bonin Trench) (Brotskaya, 1959), but this locality is quite remote from the Philippine waters proper.

This paper reports on the first deep-water harpacticoid to be described from off the west coast of the Philippines. The single female collected represents the type of a new family and was found to be infested by an as yet unknown developmental stage of tan-tulocarid that is described in a separate account (Huys *et al.,* 1993).

MATERIALS AND METHODS

The holotype female was dissected in lactic acid and the dissected parts were placed in lactophenol mounting medium. Preparations were sealed with glyceel (Gurr®, BDH Chemicals Ltd., Poole, England).

All drawings have been prepared using a camera lucida on a Leitz Diaplan interference microscope. The descriptive terminology is adopted from Huys and Boxshall (1991).

DESCRIPTIONS

Styracothoracidae, new family

Diagnosis. —Body slightly depressed, prosome distinctly wider than urosome. First pedigerous somite fused to cephalosome. Cephalothorax distinctly deflexed, with 1 pair of anterior and 2 pairs of posterior, backwardly directed hornlike projections. Second to fourth pedigerous somites with pairs of dorsal and lateral processes. Posterior margin of body somites spinular both dorsally and laterally; cuticle profusely ornate with tubercles, ridges, denticles, and spinules, particularly dorsally and dorsolaterally. Rostrum fused to cephalic shield, prominent, anteriorly directed. Female genital double-somite without internal chitinous rib ventrally; original segmentation marked by dorsal and lateral ornamentation and by lateral constriction. Anal operculum vestigial; anal somite concealed beneath spinous posterior rim of penultimate somite. Caudal rami short, with 7 setae. Sexual dimorphism unknown.

Antennule slender, with large posterior spinous processes on segment 2 and smaller ones on segments 1–4; 7-segmented in fe-

male, with aesthetascs on segments 4 and 7; setae bare (except segment 1). Antenna with discrete basis and bisetose, unisegmented exopod; endopod with 1 seta on proximal segment and 3 lateral plus 7 apical setae on distal segment. Labrum undivided, with fine spinules. Mandible with biramous palp; basis unarmed; endopod 1-segmented with 2+7 setae; exopod 2-segmented with setal formula [4–2]. Paragnaths well developed, ornamented lobes with broad teeth distally. Maxillule with both rami defined at base; exopod with 2 setae; endopod with 6 setae; basal endites discrete; no epipodite. Maxillary syncoxa with 3 endites, praecoxal endite bilobate; endopod indistinctly segmented, with geniculate setae. Maxilliped with syncoxa bearing 2 setae; basis asetose; endopod unisegmented with 3 small spines and 1 long claw.

P1 with well-developed 3-segmented protopod; basis with extremely long inner seta; rami 2-segmented; endopod not prehensile. P2–P4 with 3-segmented rami.

Female fifth pair of legs not fused medially but with distinct intercoxal sclerite; uniramous; extremely elongated; with 5 setae each.

Female gonopores fused to form transverse genital slit covered on both sides by vestigial P6 bearing 3 setae; median copulatory pore minute; seminal receptacle bilobate.

Male unknown.

Marine, free-living.

Type Genus.—*Styracothorax,* new genus.

Styracothorax, new genus

Diagnosis.—As for family.

Type Species.—*Styracothorax gladiator,* new species.

Etymology.—The generic name is derived from the Greek *styrax,* genitive *styrakos,* meaning the spike at the lower end of the shaft of a spear, and *thorax,* meaning breastplate or chest, and alludes to the posteriorly directed, hornlike projections on the cephalothorax and free thoracic somites.

Gender.—Masculine.

Styracothorax gladiator,
new species

Material Examined.—One female collected during ESTASE II expedition (14 Novem-

ber–8 December 1984) to the Philippine deep waters on board the RV *Jean Charcot* (organized by the CNRS; coordinators L. D. Labeyrie and B. Metivier); station CP02 (14°05.40'N, 120°02.46'E), taken on 14 November 1984 at a depth of 2,050 m northwest of Manila; collected with dredge-net and sorted in CENTOB, Brest (coordinator M. Segonzac). Dissected on 13 slides and deposited in The Natural History Museum, London, under reg. no. 1992.1066.

Description of Female (Figs. 1A, 2A–D, 3A–F, 4A–E, 5A–C, 6A, B, 7A–D).—Total body length 610 μm from tip of rostrum to posterior margin of caudal rami (measured around dorsal curvature in lateral aspect; Fig. 1A). Prosome distinctly wider than urosome (Fig. 2A). Entire body covered with minute denticles dorsally and laterally (Figs. 1A, 2A). Cephalothorax large, measuring one-third of total body length; distinctly deflexed relative to main body axis; with 2 pairs of lateral, backwardly directed, hornlike processes (Fig. 1A); hind margin with another pair of similar but longer processes dorsolaterally and 2 small protuberances middorsally (Fig. 2A); P1-bearing somite incorporated. Epimeral areas of cephalothorax not particularly produced ventrally, all appendages clearly exposed in lateral aspect (Fig. 1A). Rostrum prominent (Figs. 1A, 7A), anteriorly directed; fused with dorsal cephalic shield; lateral margins spinulose; with 2 pairs of sensilla and 1 pair of raised pores. First 3 thoracic somites each with 1 pair of dorsolateral and 1 pair of ventrolateral hornlike processes; dorsolateral ones decreasing in length in anteroposterior direction; tergites with dorsal swelling between dorsolateral processes (Fig. 1A). Posterior and lateral margins of cephalothorax and prosomites with conspicuous tricuspidate processes (Figs. 1A, 2A). These margins with longer spinous processes in all urosomites except anal somite (Fig. 7B). P5-bearing somite with middorsal tuft of long setules (Figs. 2A, 7B). Last thoracic and first abdominal somites completely fused and forming bilaterally constricted genital double-somite (Figs. 4A, 7B); original segmentation also marked by dorsal and lateral ornamentation consisting of spinous processes, sensilla, and raised pores. Ventral surface of genital double-somite and following somites largely without surface ornamenta-
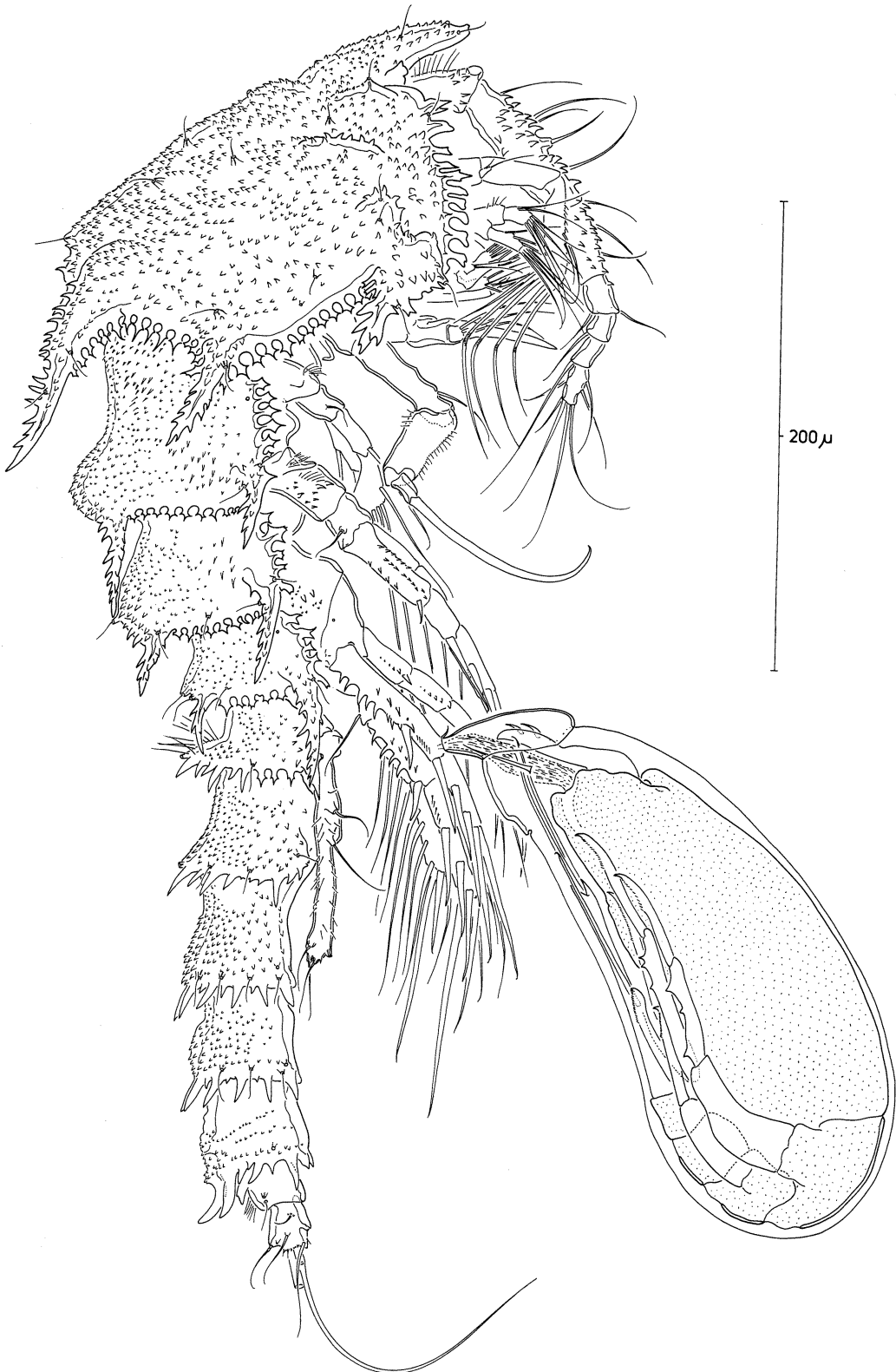
Fig. 1. *Styracothorax gladiator,* new genus, new species. Habitus, female, lateral view showing attached sexual female stage of *Itoitantulus misophricola* Huys, Ohtsuka, and Boxshall (Tantulocarida).
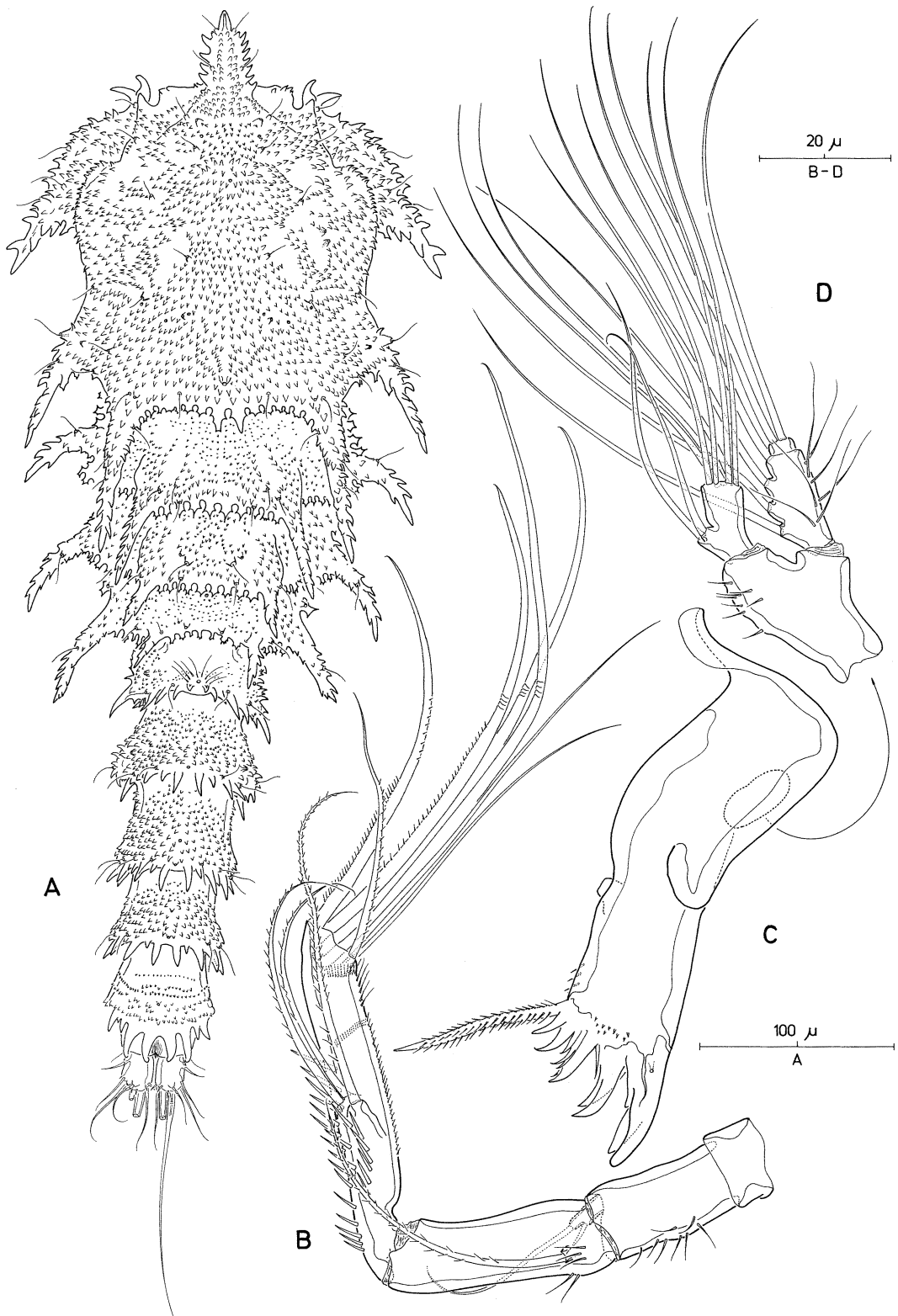
Fig. 2. *Styracothorax gladiator*, new genus, new species. A, habitus, female, dorsal view; B, antenna; C, mandibular gnathobase; D, mandibular palp (pinnate ornamentation of all exopodal and endopodal setae omitted).
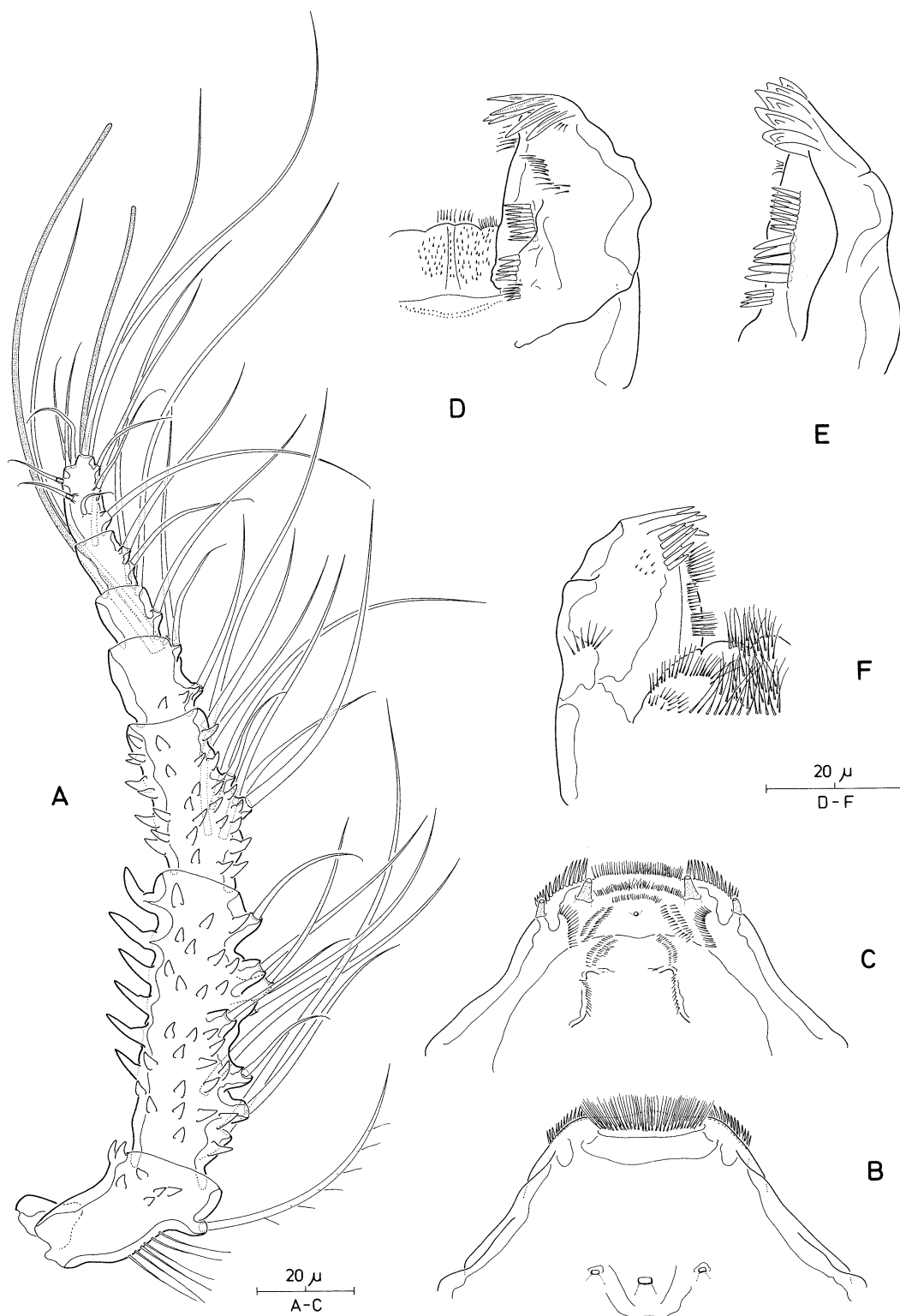
Fig. 3. *Styracothorax gladiator,* new genus, new species. A, antennule; B, labrum, anterior view; C, labrum, posterior view; D, right paragnath, anterior view; E, right paragnath, lateral view; F, right paragnath, posterior view.

tion except for posterior margin (Fig. 4A). Dorsal spinous processes of penultimate somite distinctly bent and covering most of anal somite (Fig. 7B, D). Anal somite small, with spinules around ventral rear margin; dorsal operculum absent. Caudal rami short, 1.4 times longer than wide; with 3 large pores and 7 bare setae (Fig. 7B, D): seta I well developed, VII arising from dorsal process and tri-articulated at base.

Antennule 7-segmented (Fig. 3A), with 6 large spinous processes along the posterior margin of segment 2 and smaller ones on dorsal surface of segments 1–4. Segment 1 with long setules along anterior margin; segment 2 longest. All setae bare except for segment 1; setal formula: [1, 9, 8, 4+ae, 2, 4, 11+ae].

Antenna (Fig. 2B) with coxa not ornamented. Basis without setae but with fine spinules along anterior margin. Exopod small, 1-segmented, with 1 short lateral and 1 long apical seta. Endopod 2-segmented; proximal endopod segment with 1 lateral seta; distal compound segment with 3 setae laterally and 7 setae (3 geniculate) around distal margin.

Labrum (Fig. 3B, C) well-developed muscular lobe; ventral margin ornamented with long median setules and short lateral spinules; anterior face with 3 pores (Fig. 3B); posterior face with symmetrical pattern of tiny spinular rows, 2 pairs of tube pores laterally, and 1 simple pore medially (Fig. 3C).

Mandible with long gnathobase (Fig. 2C) bearing long teeth along distal margin and multipinnate seta at dorsal corner. Palp biramous (Fig. 2D), with relatively short rami; basis without armature; endopod 1-segmented, setal formula [2+7]; exopod 2-segmented, compound proximal segment with long setules and 4 lateral setae, distal segment with 2 apical setae. All setae of both rami pinnate (ornamentation omitted in Fig. 2D).

Paragnaths (Fig. 3D–F) well-developed chitinized lobes; distal margin with series of flattened, overlapping teeth; anterior face concave, with 3 rows of anteriorly directed spinules; posterior face with tiny spinular rows; area between paragnaths with long setules posteriorly and minute denticles anteriorly.

Maxillule (Fig. 4D, E) with well-developed praecoxal arthrite with 9 spines and 1 tube seta at distal margin and 2 geniculate tube setae arising from anterior surface. Coxa with 5 setae and 1 geniculate spine; epipodite absent. Basis (Fig. 4E) with 2 endites: proximal endite with 1 geniculate and 3 simple setae, distal endite with 3 setae. Exopod small bisetose segment. Endopod defined at base, 1-segmented with 6 setae.

Maxilla (Fig. 4B, C) with 3 long endites on syncoxa: proximal endite bilobate, derived from fusion of praecoxal endites, each lobe bearing 3 setae; coxal endites with 3 setae each. Basis (Fig. 4B) fused to at least proximal segments of incompletely subdivided endopod to form allobasis; basal armature consisting of fused claw and 3 discrete setae, endopodal armature of 6 simple and 5 geniculate setae.

Maxilliped (Fig. 5A) subchelate, slender and elongate. Syncoxa long, with setular rows and 2 pinnate setae. Basis without armature but with spinules along inner and outer margins. Endopod 1-segmented, rectangular; ornamented with very long, curved claw and 3 small spines; claw with proximal half of inner margin serrate.

P1 (Fig. 5B) with well-developed 3-segmented protopod; precoxa and coxa with long spinules; basis with long setules and extremely long seta at inner margin, and short seta at outer margin. Exopod 2-segmented, outer spines extremely long and seta-like; proximal segment without inner seta; distal segment with 6 setae in total. Endopod not prehensile, 2-segmented, shorter than exopod; proximal segment with 1 inner seta; distal segment with 3 setae.

P2–P4 (Figs. 5C, 6A, B) with unornamented intercoxal sclerites. Coxae with setules and curved spinous processes at outer margin. Bases transversely elongated; with seta at outer corner and long setules at inner margin. Proximal segment of exopods with curved spinous processes; outer spine of exp–1 P2 and inner seta of exp–2 P4 strongly reduced in size. Endopods shorter than exopods; outer distal corner of proximal and middle segments with toothlike process. Spine and seta formula as follows:

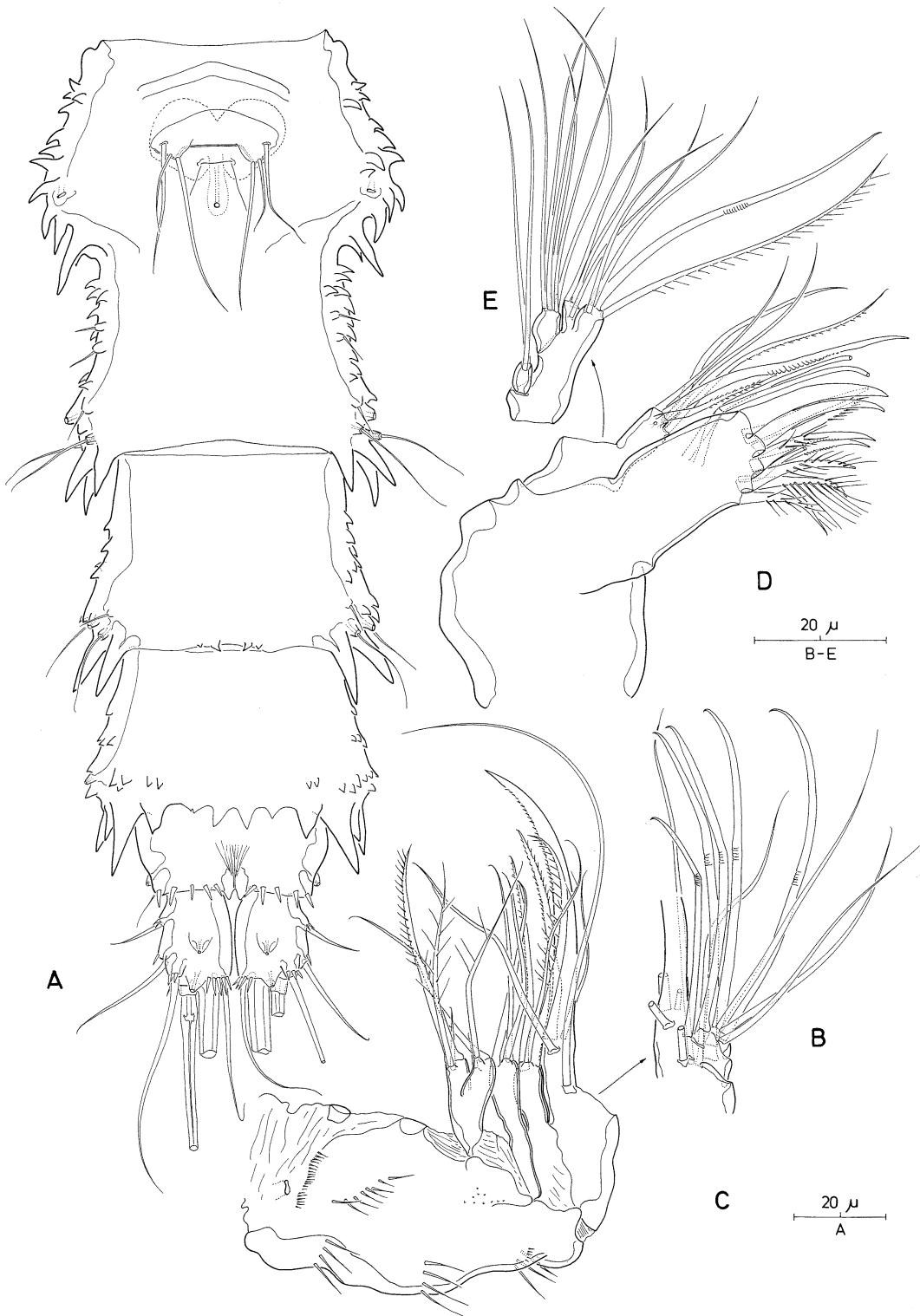|	coxa	basis	exopod segment			endopod segment		
			1	2	3	1	2	3
P1	0–0	1–1	1–0;	2,3,1		0–1;	1,1,1	
P2	0–0	1–0	I–1;	I–1;	III,I,3	0–1;	0–2;	I,2,2
P3	0–0	1–0	I–1;	I–1;	III,I,4	0–1;	0–1;	0,2,2
P4	0–0	1–0	I–0;	I–1;	III,I,4	0–1;	0–1;	0,2,2

Fig. 4. *Styracothorax gladiator,* new genus, new species. A, urosome (excluding P5–bearing somite), ventral view; B, maxilla, endopod and proximal portion of allobasis; C, maxilla (endopod omitted), posterior view; D, maxillule (basis and rami omitted); E, maxillule, basis and rami.
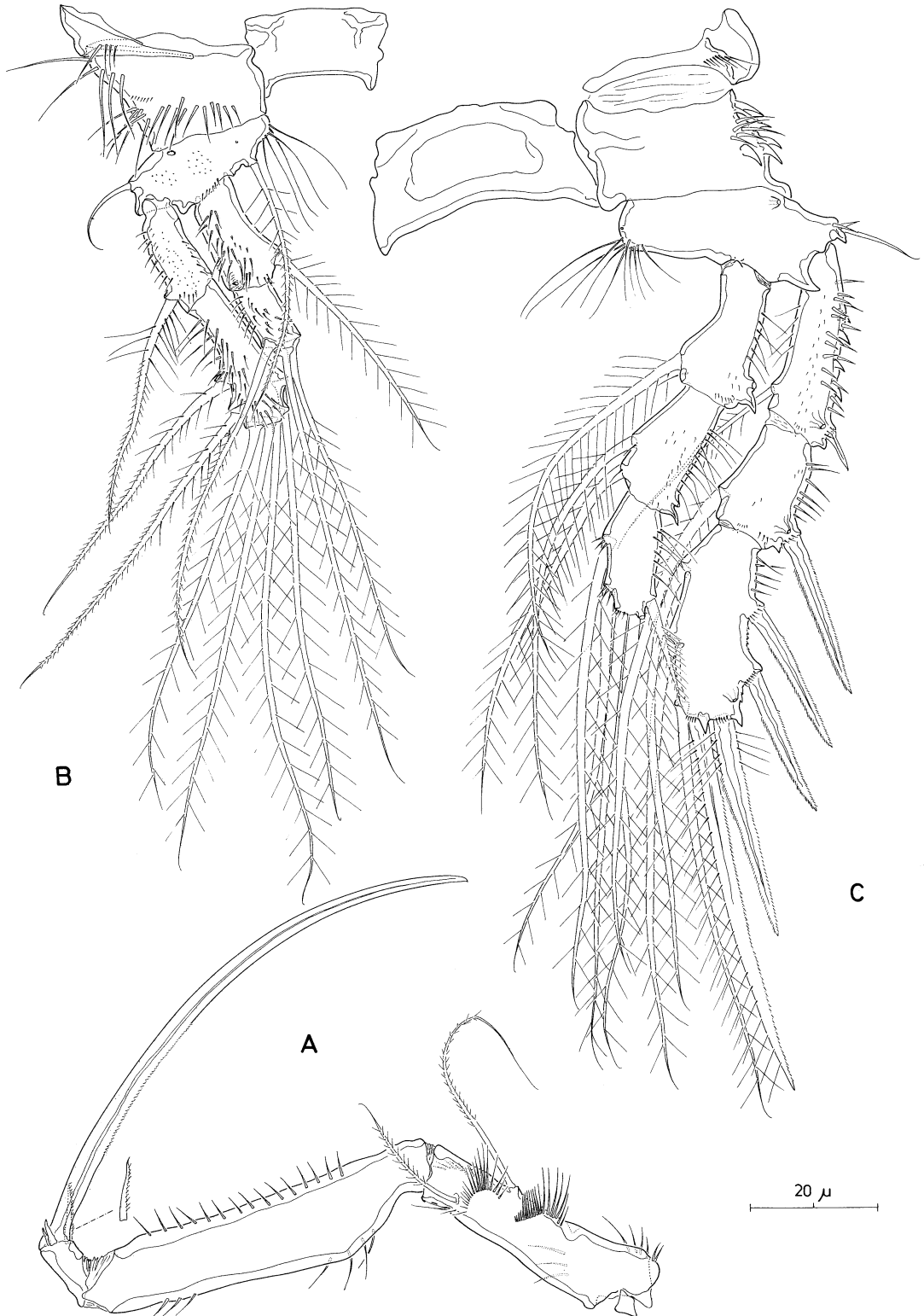
Fig. 5. *Styracothorax gladiator,* new genus, new species. A, maxilliped; B, P1, anterior view; C, P2, anterior view.
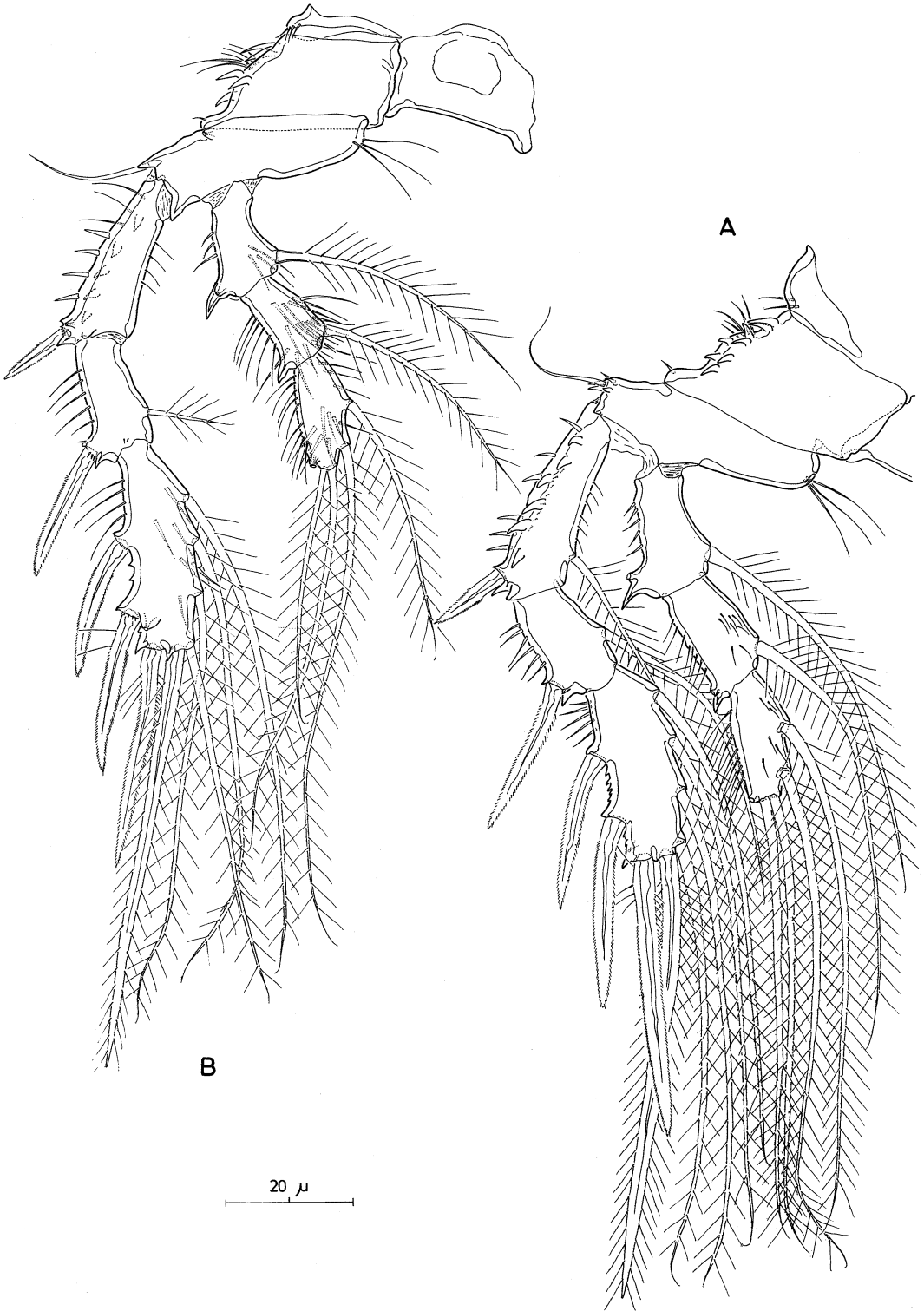
Fig. 6. *Styracothorax gladiator,* new genus, new species. A, P3, posterior view; B, P4, anterior view.
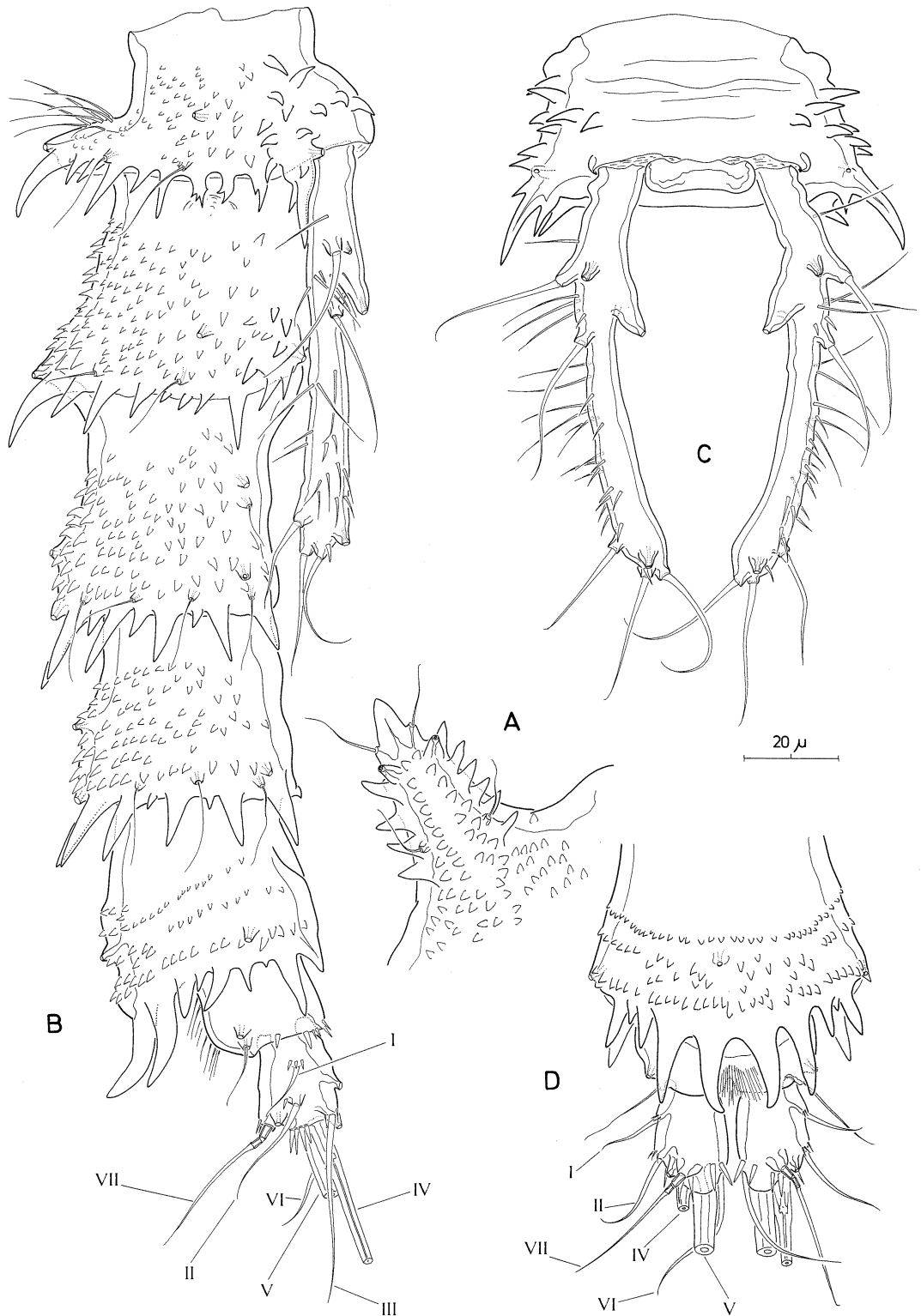
Fig. 7. *Styracothorax gladiator,* new genus, new species. A, rostrum, dorsal view; B, urosome, lateral view; C, P5–bearing somite and fifth pair of legs, ventral view; D, caudal rami, anal somite, and posterior half of penultimate somite, dorsal view.

P5 (Fig. 7B, C) uniramous, 1-segmented; very elongated, about 8 times as long as wide, slightly bent inward; outer margin furnished with numerous long setules, 5 bare setae, and 2 raised pores; inner margin with conical process (bearing pore) at about one-third distance from base. Fifth pair of legs connected by flattened intercoxal sclerite.

Female gonopores fused to form transverse genital slit covered on both sides by vestigial P6 bearing 3 slender setae (Fig. 4A); copulatory pore minute, located in shallow midventral depression; seminal receptacles fused to bilobate reservoir positioned at level of genital slit.

Male. — Unknown.

Etymology. — The species name is derived from the Latin *gladiator,* meaning "one who handles the sword," and alludes to the elaborate ornamentation of the body and appendages.

DISCUSSION

The most conspicuous feature of *S. gladiator* is perhaps the elaborate ornamentation of the body, in particular the presence of long backwardly directed, hornlike processes on the dorsal and lateral sides of the cephalothorax and the thoracic somites. Similar structures are typically found in various deep-water harpacticoids, such as the Ancorabolidae (e.g., *Ancorabolus* Norman, *Echinopsyllus* Sars, *Ceratonotus* Sars, *Dorsiceratus* Drzycimski). However, the paired arrangement of these thoracic processes is particularly reminiscent of most Cerviniidae (e.g., Por, 1969; Dinet, 1978).

Comparison of setation patterns with the hypothetical ancestral harpacticoid defined by Huys and Boxshall (1991) shows that *S. gladiator* retains a suite of primitive features on the mouthparts and the thoracopods. For example, the ancestral endopodal and basal setation of the maxilla (Huys and Boxshall, 1991: table 6, fig. 3.10.1) conforming to a formula [4, 3, 2, 2, 4] essentially remained unchanged in *S. gladiator.* Since the pattern is obscured by incomplete segmental boundaries, it is impossible to allocate all armature elements to their respective segments. However, the full complement of 14 setae plus claw is retained. Another plesiomorphic character is exhibited by the mandible, retaining the maximum number of 6

setae on the exopod. The setation formula [4, 2] indicates that the 2-segmented condition of this ramus arose as a result of fusion of the three proximal segments. The maxillule shows some modifications in the setation plan of the endopod and exopod, but the protopod has undergone fewer modifications, as illustrated by the possession of two discrete endites on the basis, the retention of the maximum of six setae on the coxal endite, and a high number of armature elements on the praecoxal arthrite. Finally, the spine and seta formula on the distal exopod segment of thoracopods 2–4 (III,I,3 in leg 2, III,I,4 in legs 3 and 4) is the most primitive recorded among harpacticoids.

Speculations about the possible relationships of *S. gladiator* are hampered by the lack of information on the male, but the general facies of the body, the mouthparts, and the uniramous fifth legs suggest a certain affinity with the families of the Cervinioidea. According to Huys (1988a) this superfamily currently accommodates the Cerviniidae, Aegisthidae, and Rotundiclipeidae. Each of these families has successfully exploited its own habitat. The Cerviniidae is an essentially deep-water taxon known from bathyal and abyssal sediments, though a few genera are recorded from the continental shelf (Sars, 1903; Montagna, 1979). The Rotundiclipeidae are cavernicolous and thus far known only from a single anchialine cave-dwelling genus in the Canary Islands (Huys, 1988a) and another as yet undescribed genus from Roadside Cave in Bermuda (Huys and Iliffe, in preparation). The Aegisthidae are found exclusively in the mesopelagic and upper bathypelagic zones of the world oceans (Boxshall, 1979).

Huys (1988a) did not formally present a diagnosis of the Cervinioidea, but defined the taxon on the basis of four synapomorphies: (i) antennule 8-segmented in the female, 10-segmented and with 4 aesthetascs in the male, (ii) rostrum fused to cephalothorax, (iii) reduced maxillulary exopod, and (iv) loss of the P5 endopod. Except for (i), this combination of characters can be regarded as diagnostic for *S. gladiator* as well, and to this suite might be added, (v) the reduction in setation (3 setae) on the lateral margin of the second antennary endopod segment.

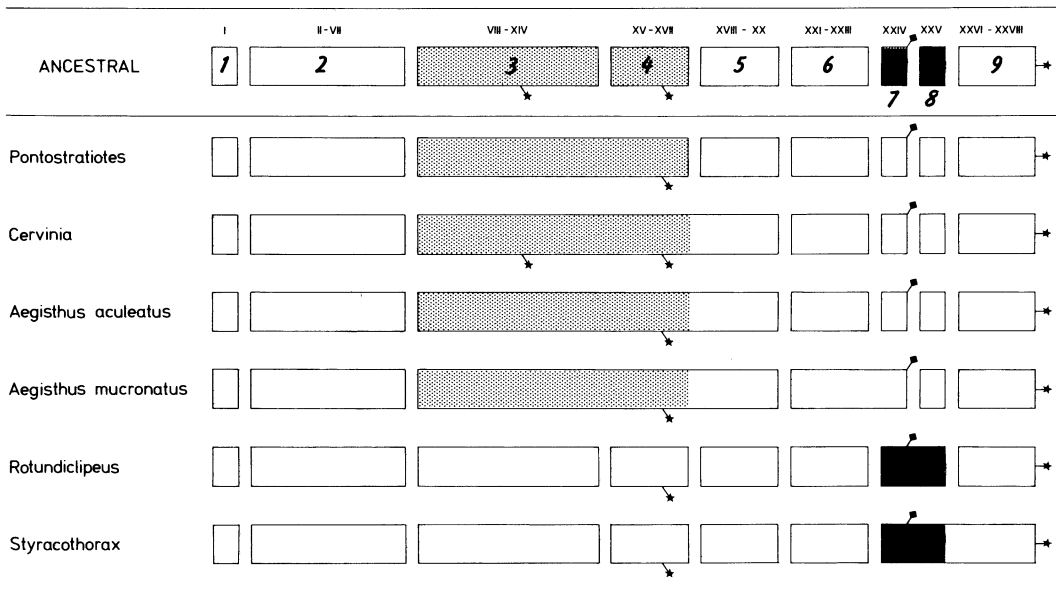For two reasons the antennulary charac-

Fig. 8. Schematic comparison of segmental homologies in the female antennules of representatives of Cervinioidea, showing the positions of the aesthetascs derived from ancestral segments XI, XVI and XXVIII (asterisks), and of the posterior seta derived from segment XXIV (diamond). Roman numerals refer to ancestral segments, Arabic numerals denote actual segments.

ter defined in (i) can no longer be regarded as supporting evidence for the monophyly of the Cervinioidea. First, reexamination of the 8-segmented antennules in Cerviniidae and Rotundiclipeidae revealed that the respective segmental fusion patterns are not homologous. The large aesthetasc derived from ancestral segment XVI and found on segment 4 in the majority of the harpacticoid families, is located on segment 3 in all Cerviniidae. This is interpreted as evidence that the third segment is a compound segment derived by fusion of the homologues of segments 3 and 4 in the Rotundiclipeidae. Similarly, using the posterior seta of ancestral segment XXIV (Huys and Boxshall, 1991) as a reference point, shows the seventh segment in Rotundiclipeidae to be homologous to segments 7 and 8 combined, of the Cerviniidae. Maintaining the Rotundiclipeidae in the Cervinioidea on the basis of the other synapomorphies (ii)–(v) means that the ancestral condition of the antennule was 9-segmented and that the 8-segmented antennule has evolved twice through two nonhomologous fusion events. Fusion of segments 3 and 4 is found in Cerviniidae and Aegisthidae (Fig. 8), further reinforcing their sister-group relationship already hint-

ed at by Lang (1948) and subsequently corroborated in a cladogram by Huys (1988a). Fusion of segments 7 and 8 in the Rotundiclipeidae is shared with the Styracothoracidae (Fig. 8).

A second problem relates to the shared possession of 4 aesthetascs on the male antennule in Cerviniidae, Rotundiclipeidae, and Aegisthidae. This distribution pattern of sensory elements is unique among the Harpacticoida and was therefore considered apomorphic by Huys (1988a) on the assumption that the supernumerary aesthetascs were novel structures. Using Calanus finmarchicus (Gunnerus) as the reference for comparison, Huys and Boxshall (1991) charted the distribution of antennulary aesthetascs in the different copepod orders and concluded that despite an overall trend of reduction certain "key segments" are very conservative throughout the Podoplea. Comparative analysis shows that the cerviniid aesthetascs are derived from such ancestral key segments, notably VII, XI, XVI and XXVIII, and hence their presence is of limited significance in assessing phylogenetic relationships in the Harpacticoida.

The hypothetical phylogenetic relationships of the cervinioid families are depicted
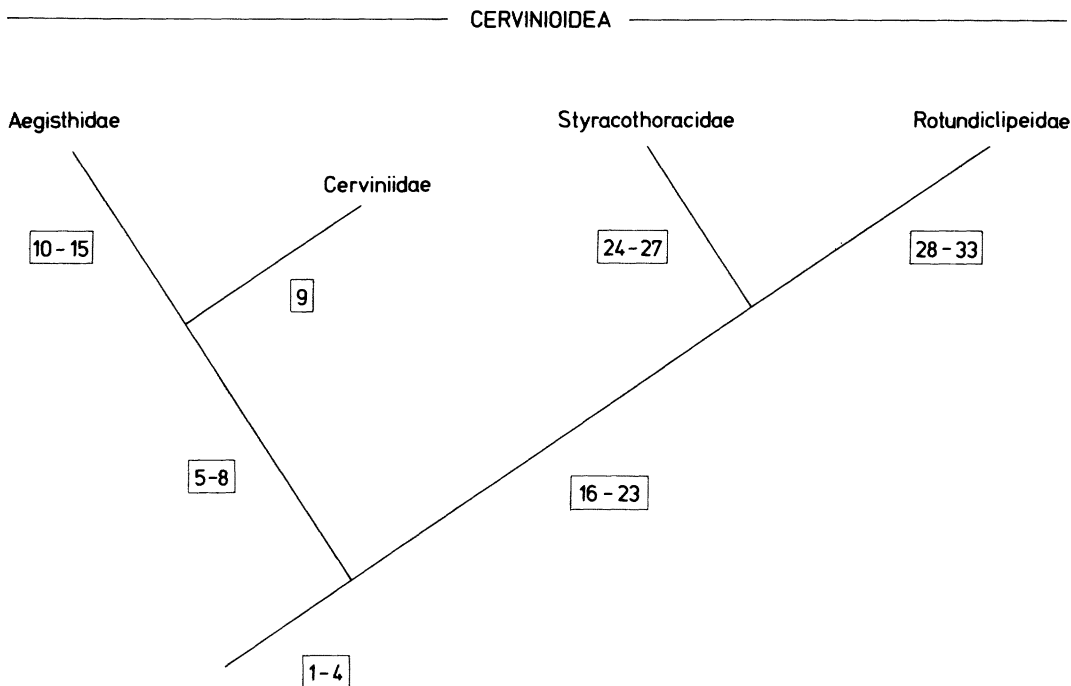
CERVINIOIDEA

Fig. 9. Cladogram depicting relationships between the four families of the Cervinioidea. Numerals refer to apomorphic character states given in Table 1.

in Fig. 9, using the apomorphic character states compiled in Table 1. *Styracothorax gladiator* is considered to be the sister group of the stygobiont Rotundiclipeidae on account of a suite of fusion and reduction processes in the antennules to the first leg (Table 1). However, comparison of their respective autapomorphies reveals that *Styracothorax* should be placed in a distinct family. The establishment of a new family on the base of a single female might appear premature, but is regarded here as the best alternative to letting it float around in *incertae sedis* land. There is no convincing morphological evidence to satisfactorily assign *S. gladiator* to any of the existent families without dramatically expanding their respective diagnostic boundaries.

A character of particular interest shared by the Rotundiclipeidae and Styracothoracidae is the subchelate maxilliped. The maxilliped of their direct outgroup, the Cerviniidae, in many respects conforms to the ancestral harpacticoid design, though having fewer armature elements than in the Polyarthra. This might be regarded as evidence that the "prehensile" or raptorial type of maxilliped arose convergently in the Har-

pacticoida, since it represents the most common type outside the Cervinioidea. Another unusual character is the 2-segmented nonprehensile condition of both rami on leg 1. This segmentation pattern was thus far found only in the planktonic *Euterpina acutifrons* (Dana). Comparison with the earliest copepodid stages known in the Cerviniidae (see Itô, 1983) suggests that this condition evolved through a heterochronic event, and that the same mechanism might be applied to explain the segmentation of the mandibular exopod.

The position of the Cerviniidae is the weakest link in the phylogenetic scheme, since it is supported by one autapomorphy only. This large disproportion in number of evolutionary novelties is a well-known problem in any cladistic analysis where a primitive taxon shares a sister-group relationship with an extremely specialized taxon such as the Aegisthidae. Failure to detect a sufficient number of apomorphies for a particular clade is often also indicative of its potential paraphyletic status. This raises the possibility of the Aegisthidae constituting a highly advanced lineage within the Cerviniidae. However, the condition of the

Table 1. Synapomorphic character states applied to generate cladogram in Fig. 9; plesiomorphic alternatives listed in parentheses.

1. Rostrum fused to dorsal cephalic shield (free).
2. Antenna with 3 setae on lateral margin of second endopod segment (5).
3. Maxillulary exopod reduced to small trisetose lobe (well-developed discrete segment with at least 4 setae).
4. P5 uniramous in both sexes; exopod and baseoendopod completely fused with no trace of endopodal lobe left (biramous with endopod bearing armature).
5. Antennule 8-segmented in ♀; segments 3 and 4 fused; aesthetasc [XVI] on third segment (9-segmented; aesthetasc on segment 4).
6. Maxillulary endopod incorporated into basis (free).
7. P6 ♀ an elongated, rectangular process (small operculum).
8. Caudal rami elongated (not elongated).
9. Pleurotergite of first pedigerous somite [P1] largely concealed under dorsal cephalic shield or incompletely incorporated into cephalosome (size equal to following pleurotergites).
10. Antennule 7-segmented in ♀; segment 5 fused to compound segment [3–4] (free).
11. Antenna with allobasis and 2-segmented exopod (basis and 4-segmented exopod).
12. Gross sexual dimorphism in mandible, maxillule, maxilla and maxilliped (no sexual dimorphism).
13. Mandibular palp vestigial (biramous with 4-segmented exopod and 1-segmented endopod).
14. Maxilliped 2-segmented, representing single protopodal segment and 1-segmented endopod (4-segmented, representing syncoxa, basis and 2-segmented endopod).
15. Caudal rami extremely elongated, at least twice as long as whole body, with 3 setae (not extremely elongated, with 7 well-developed setae).
16. Antennule 8-segmented in ♀, segment 7 (XXIV) fused to segment 8 (XXV) (free).
17. Loss of armature on mandibular basis (armature consisting of 4 setae).
18. Loss of coxal epipodite on maxillule (epipodite represented by 2 setae).
19. Fusion of praecoxal endites on maxilla (free, widely separated).
20. Maxilliped subchelate, endopod 1-segmented, loss basal endite and extreme reduction of syncoxal endites (maxilliped "stenopodial" not subchelate, endopod 2-segmented, basal endite represented by 2 setae, syncoxal endites represented by 2, 3, and 2 setae, respectively).
21. Loss of inner seta on proximal exopod segment of P1 (present).
22. Fusion (failure to separate) of middle and distal exopodal and endopodal segments of P1 (rami 3-segmented).
23. Genital and first abdominal somites completely fused to form genital double-somite in female (free).
24. First pedigerous somite completely incorporated into cephalosome (discrete).
25. Cephalothorax and thoracic somites profusely ornamented with backwardly directed horny processes (no such ornamentation).

Table 1. Continued.

26. Antennule 7-segmented in ♀, compound segments XXIV–XXV and XXVI–XXVIII fused (free).
27. Antennary exopod 1-segmented (4-segmented).
28. Antenna with allobasis (basis and first endopodal segment free).
29. Mandible with styletlike gnathobase and uniramous palp representing elongate basis and 1-segmented endopod (gnathobase unmodified; palp uniramous).
30. Loss of precoxal endite of maxilla (present).
31. P1 with 1-segmented rami (2-segmented).
32. Endopods of P2–P4 2-segmented (3-segmented).
33. Fifth legs in both sexes reduced to 2 spines arising from somite (exopod and basis forming large segment).

first pedigerous somite in the Aegisthidae prevents such a demotion (character 9). The lack of cladistic evidence in support of the cerviniid branch is interpreted here as merely artificial and temporary, since the identification of additional synapomorphies will be largely dependent on the discovery of new taxa in the Cervinioidea. The lack of a "missing link" between the Aegisthidae and the Cerviniidae makes it impossible for certain characters to be scored accurately. For example, the design of the mandibular exopod in the Cerviniidae (proximal segment elongated, distal 3 segments vestigial or incorporated) is unusual, but its phylogenetic significance cannot be assessed since the entire palp is rudimentary or entirely lost in the Aegisthidae (see Huys, 1988b). It is, therefore, impossible to identify whether the gross reduction in the Aegisthidae was preceded in time by such an exopodal transformation. Confirmation of the opposite event by the discovery of a "missing link" would further strengthen the monophyletic status of the Cerviniidae.

The root cause of the difficulties in delineating the boundaries in evolutionary terms of a supposedly well-known family such as the Cerviniidae might be found in our fragmentary knowledge on biodiversity of deep-sea harpacticoids. For example, the first representative of the Cerviniidae was described as early as 1878 by G. Stewardson Brady, but nearly 80% of all species have been discovered in the last three decades. The total number of species stands now at 70. However, Dinet's (1978) report of 12 species of *Pontostratiotes* occurring in the

Bay of Biscay only indicates the gross underestimation of this figure. It is clear that the exploration of the abyssal ooze is still in its infancy and the total neglect of the hadal community is certainly one explanation for the extensive gaps in our knowledge on copepod evolution. Copepods have been reported from 9,995–10,002 m in the Kermadec Trench (Belyaev, 1972), yet only four harpacticoids (Brotskaya, 1963; Becker, 1974, 1979) were described from depths greater than 6,000 m, the upper limit of the hadal zone.

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