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NEW TANTULOCARID, *STYGOTANTULUS STOCKI*, PARASITIC ON HARPACTICOID COPEPODS, WITH AN ANALYSIS OF THE PHYLOGENETIC RELATIONSHIPS WITHIN THE MAXILLOPODA

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ABSTRACT

A new genus of Tantulocarida, *Stygotantulus,* is described based on material from an anchialine pool on Lanzarote, Canary Islands. It is the most primitive tantulocarid known and is ectoparasitic on representatives of at least two families of harpacticoid copepods. It is distinguished by the presence of 7 abdominal somites in the tantulus larva. The musculature of the penis on trunk somite 7 of the male suggests that it is derived by modification of the seventh thoracopods. The importance of trunk somite numbers in maxillopodan systematics is reexamined and an attempt is made to apply the concept of homology to the developmental processes determining somite numbers. The classification of the Crustacea, including the Tantulocarida, proposed by Starobogatov (1986), is criticized and the validity of the developmental-functional concept of the prototagma, as used by Starobogatov, is refuted. A new scheme of phylogenetic relationships among seven major maxillopodan groups is presented.

Tantulocarids are small, ectoparasitic crustaceans found only on crustacean hosts. They have an unusual and highly abbreviated life cycle (Boxshall and Lincoln, 1987). Saclike adult females release infective tantulus larvae which attach directly to a new host. Once attached, the female tantulus forms a trunk sac behind the cephalon and sloughs the larval trunk. The male tantulus forms a trunk sac at the posterior end of the thorax within which a unique kind of metamorphic reorganization takes place. The presumed adult male differentiates inside the sac while being supplied with nutrients via an internal tissue connection to the larval cephalon. Tantulocarids exhibit no cephalic limbs at any stage of their life cycle, but their basic tagmosis and male gonopore location was interpreted by Boxshall and Lincoln (1987) as evidence that their affinities lie with the Thecostraca (sensu Grygier, 1985, 1987).

In the present account we report on a new tantulocarid collected by Prof. Jan Stock from an anchialine lava pool on Lanzarote in the Canary Islands. In the pool it is parasitic on harpacticoid copepods from at least two distinct families. In the last decade studies of the crustacean fauna of anchialine habitats in the Canary Islands and elsewhere have revealed a range of distinctive forms, such as the Remipedia (Garcia-Valdecasas, 1984). The new tantulocarid is also distinctive, representing the most primitive type yet found. The characters exhibited prompted us to reexamine the phylogenetic relationships of the Tantulocarida within the Maxillopoda, and to comment upon the new classification of the Crustacea, including the Tantulocarida, proposed by Starobogatov (1986).

Subclass Tantulocarida
Boxshall and Lincoln, 1983
Family Basipodellidae
Boxshall and Lincoln, 1983
Stygotantulus, new genus

Diagnosis.—Tantulus larva comprising cephalon, 6 pedigerous thoracic somites, and 7-segmented abdomen. Cephalon covered with dorsal shield ornamented with longitudinal and transverse lamellae. Oral disc located anteriorly on ventral surface. Cephalic stylet barbed. Free thoracic somites 1–6 each with well-developed tergite and bearing pair of thoracopods. Thoracopods 1–5 biramous, comprising unsegmented protopod bearing well-developed endite, and 1- (leg 1) or 2-segmented (legs 2–5) rami. Thoracopod 6 lacking endite. Caudal rami distinct, armed with 1 short and 2 long setae. Adult male in trunk sac located posterior to tergite of sixth thoracic somite. Male cephalothorax incorporating first and second thoracic somites. Thoracopods 1–5 biramous with 1-segmented rami. Thoracopod 6 uniramous, 2-segmented. Abdomen 2-segmented, first somite elongate, bearing recurved median penis ventrally. Second abdominal somite with discrete caudal rami carrying 3 apical setae.

Type-species.—*Stygotantulus stocki,* new genus, new species.

Etymology.—The generic name was derived from the Greek *styx, stygo,* meaning the lower world, and *tantulus* which forms part of the name Tantulocarida. The species is named for Prof. Jan Stock who collected the copepod hosts.

Remarks.—The new genus can be distinguished from all other genera by the 7-segmented abdomen of its tantulus larva. It also differs from all known genera in the complexity of the cephalic stylet. The basally directed, dorsal barb on the stylet is unique to *Stygotantulus.* On the basis of the 7-segmented abdomen, the well-developed thoracopodal endites and rami in the tantulus, and the location of the trunk sac containing the male behind the sixth thoracic tergite, the new genus is placed in the family Basipodellidae. We recognize that the family is based primarily on plesiomorphic characters, and, as such, may be paraphyletic. It appears to be most closely related to *Basipodella* Becker which has a 6-segmented abdomen in the tantulus stage (Boxshall and Lincoln, 1983) and is also known from harpacticoid hosts (Becker, 1975; Boxshall, 1983).

Stygotantulus stocki, new species

Tantulus Larva

Body comprising cephalon, 6 pedigerous thoracic somites, and 7-segmented abdomen (Fig. 1A, B). Total body length 94 μm from tip of rostrum to end of caudal rami. Cephalon about 1.5 times longer than wide (43 × 29 μm), covered with entire dorsal shield ornamented with fine longitudinal and transverse lamellae (precise pattern difficult to ascertain under light microscope). Shield with 2 pairs of pores located dorsolaterally near posterior margin and pair of fine setules anterolaterally. Oral disc about 9 μm in diameter, located anteriorly on ventral surface. Cephalic stylet 27 μm long; with flared proximal opening (Fig. 3C), fine basally directed dorsal barb (Fig. 1B), and slight ventral swelling located proximal to finely pointed tip. Tip protruding through central pore of oral disc in 1 specimen (Fig. 1B). Median striated organ in head appearing to be muscular and associated with stylet. Quadrilobate glandular structure visible through integument, lobes having homogeneous contents and leading dorsally towards common median duct anteriorly directed (this not traceable further than shown in Fig. 1).

Tergites of 6 free thoracic somites distinct, ornamented with very fine lamellae (Fig. 3B). Thoracopod 1 (Fig. 2A) with unsegmented protopod bearing medial endite proximally and few spinules along lateral margin. Endite armature visible only as spine under light microscope. Endopod 1-segmented, bearing single short seta from distal protrusion. Exopod 1-segmented, bearing 2 naked setae on distal margin, inner longer than outer. Thoracopods 2–5 biramous with undivided protopod bearing medial endite proximally and both rami distally in slight concavity (Fig. 2B). Endite armature visible as spinous element and blunt process under light microscope. Endopod apparently 2-segmented; first segment comprising swollen base and constricted distal part, armed with 2 naked setae laterally; second segment short, bearing opposable spine and toothed spatulate element apically. Exopod 2-segmented; first segment short, unarmed; second segment bearing 1 short and 3 long naked setae. Thoracopod 6 with simple protopod lacking endite, bearing 2 tiny spinules midway along medial margin (Fig. 2C, arrowheads) and 2 apical setae. One seta located on broad base, possibly representing segment of ramus, other seta originating more anteromedially from surface of protopod. Short spinule located near base of posterior seta.

Abdomen length 19 μm, greatest width 11 μm. First abdominal somite with rounded posterolateral angles; second to seventh somites tapering anteriorly and slightly wider than preceding somite. Second abdominal somite narrowing ventrally and lacking dorsal ornamentation; third to seventh ornamented with fine longitudinal lamellae dorsally (Fig. 1A). Caudal rami wider than long, bearing 1 short and 2 long naked setae apically.

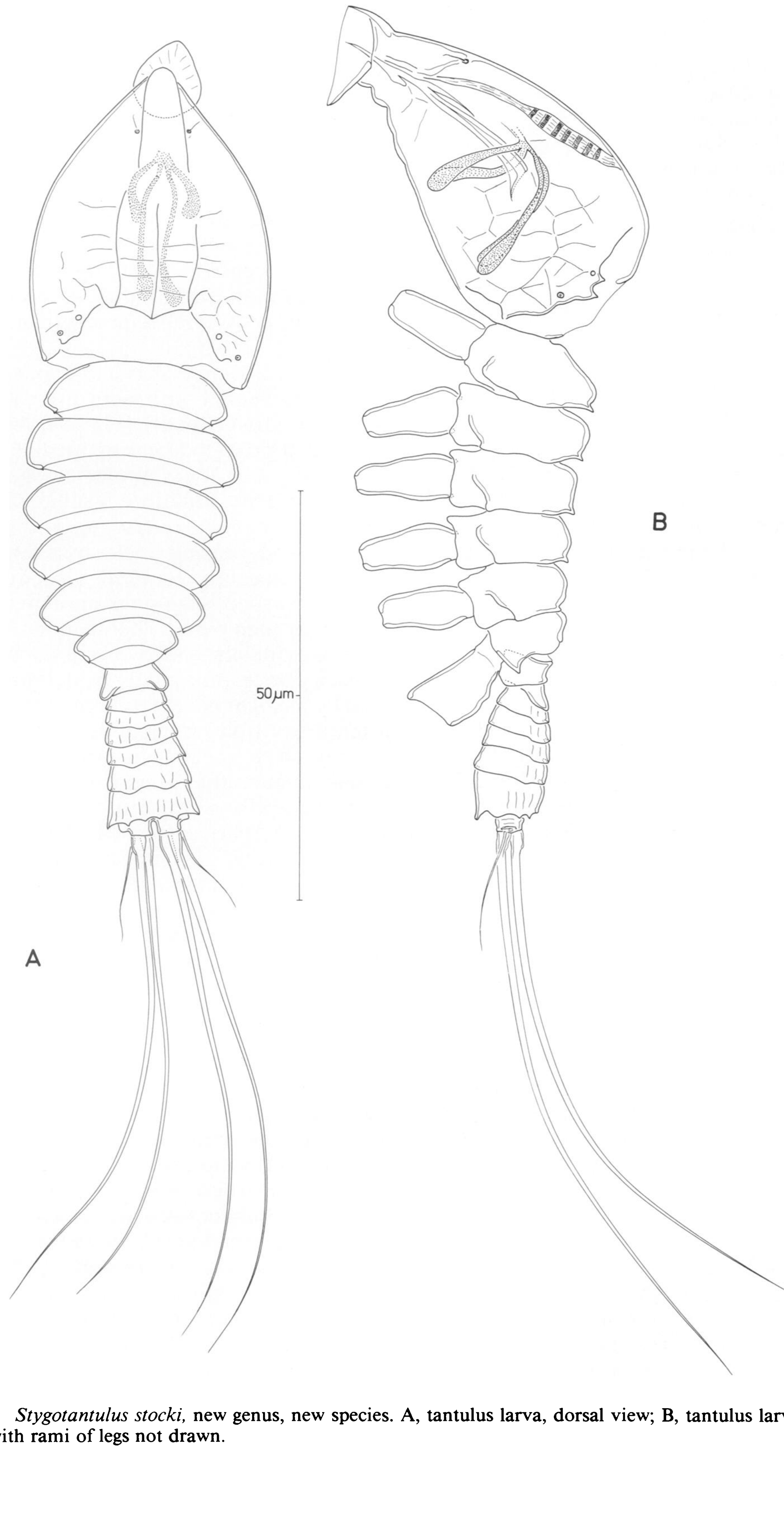

Fig. 1. *Stygotantulus stocki,* new genus, new species. A, tantulus larva, dorsal view; B, tantulus larva, lateral view with rami of legs not drawn.

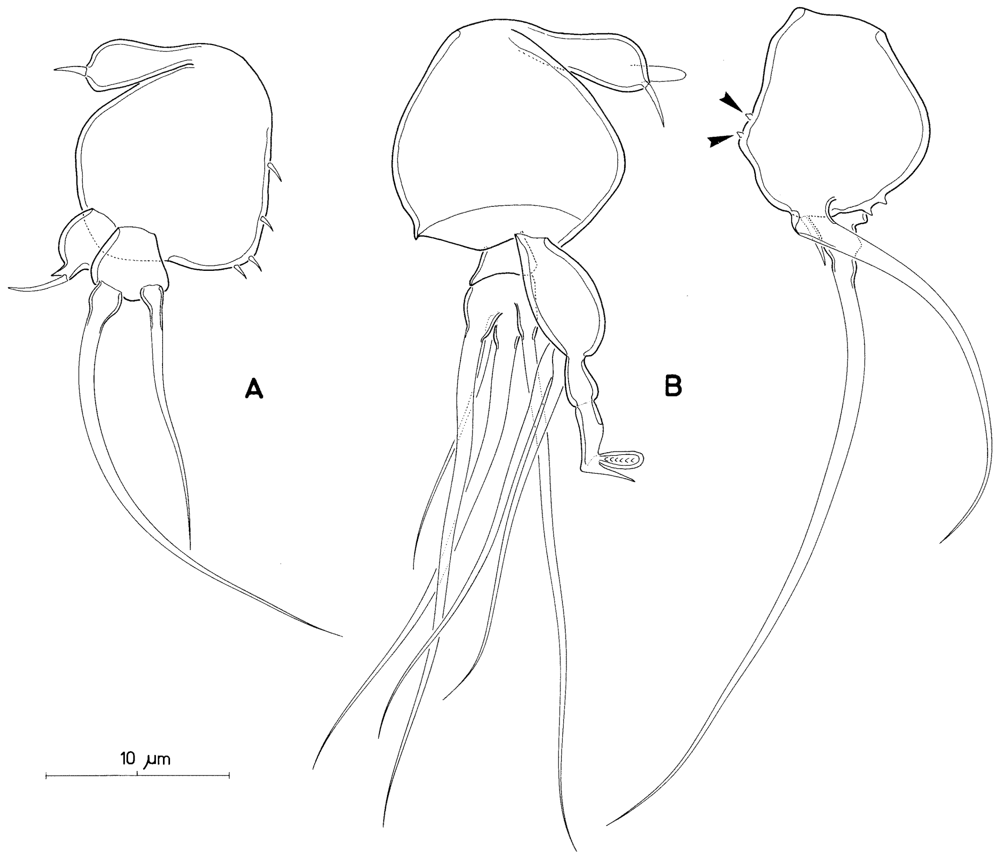

Fig. 2. *Stygotantulus stocki,* new genus, new species, tantulus larva. A, thoracopod 1, anterior; B, thoracopod 2, anterior; C, thoracopod 6, anterior.

Adult Male

Male developing within trunk sac formed immediately posterior to sixth thoracic tergite of preceding tantulus stage (Fig. 3A). All 6 tergites (Fig. 3B) separated from each other and from posterior margin of cephalic shield by expansion of trunk sac. Male attached to larval head by tissue connection (Fig. 3A) referred to as umbilical cord by Boxshall and Lincoln (1987). Abdomen of preceding tantulus deflected ventrally by growth of sac.

Total body length about 400 μm; comprising large cephalothorax incorporating first and second thoracic somites, 4 free pedigerous somites, and 2-segmented abdomen (Fig. 4A). Cephalothorax damaged during removal from sac but 4 pairs of aesthetascs present anteriorly, 1 of these bifid (Fig. 4B). Rostrum small, anteriorly directed. Free thoracic somites decreasing in size posteriorly, each with well-developed tergite ornamented with fine longitudinal lamellae. First abdominal somite elongate (34 × 19 μm), with concave sides; second just wider than long (22 × 23 μm), with convex sides and marked anal slit (Fig. 4C). Both somites ornamented with fine longitudinal lamellae. Penis situated medially at extreme posterior end of first abdominal somite; comprising swollen basal part and curved, tapering distal part with opening at tip (Fig. 4D). Extrinsic muscle originating on ventral surface of somite anterior to penis base and inserting proximally on posterior wall of penis. No other internal organs associated with penis visible. Caudal rami about 2.8 times longer than wide (17 × 6 μm), bearing 1 short outer seta and 2 long distal setae.

Thoracopods 1 and 2 carried posteriorly on cephalothorax. Thoracopods 1–4 similar, each with protopod comprising broad muscular proximal segment and incom-

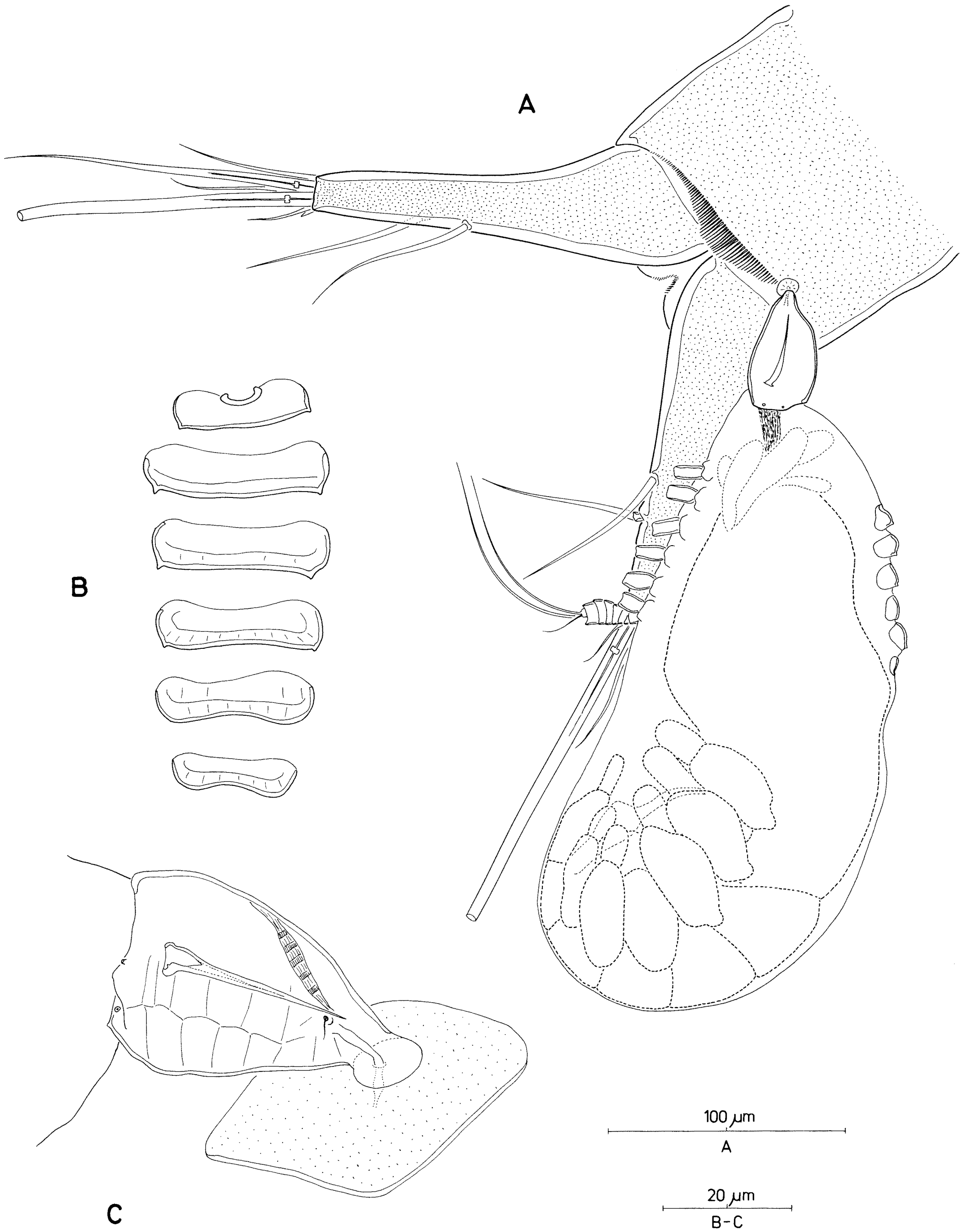

Fig. 3. *Stygotantulus stocki,* new genus, new species. A, adult male contained within trunk sac of preceding tantulus larva, attached to anal somite of host; B, disarticulated thoracic tergites from trunk sac, dorsal view; C, attached head of tantulus, lateral view showing ventral surface of stylet.

pletely fused distal segment, separated by suture line posteriorly but not anteriorly (Fig. 5A). Armed with pair of brush setae, about 27 μm long, located proximally on medial margin. Both rami 1-segmented, exopod longer than endopod. Endopod subrectangular, bearing, around distal margin, short naked seta and 4 long, articulated setae na-

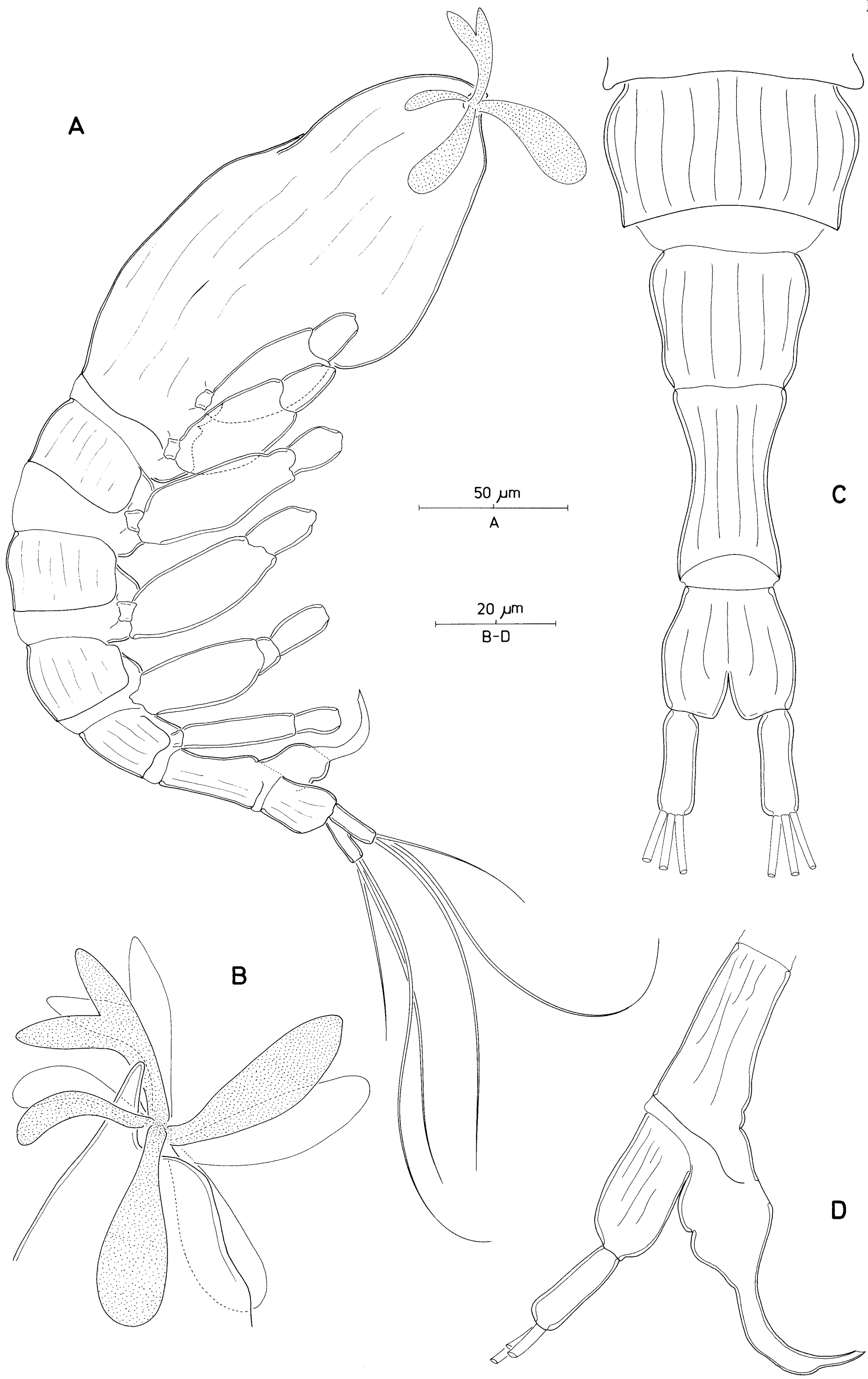

Fig. 4. *Stygotantulus stocki,* new genus, new species. A, adult male, lateral view with limb setae not drawn; B, tip of cephalothorax showing rostrum and aesthetascs, lateral; C, fifth and sixth thoracic somites and abdomen, dorsal; D, abdomen, lateral view showing median penis.

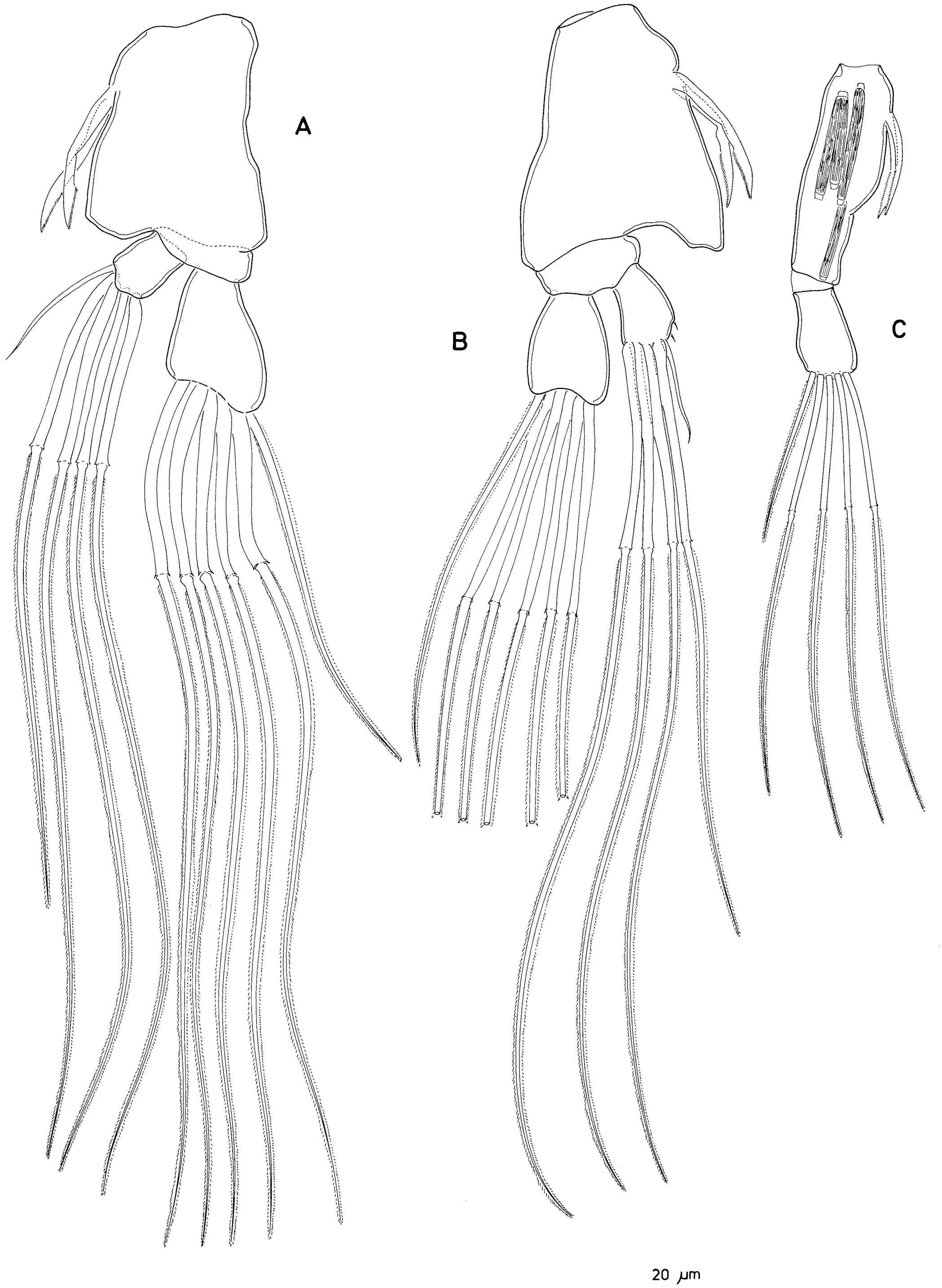

Fig. 5. *Stygotantulus stocki,* new genus, new species, adult male. A, first thoracopod, anterior; B, fifth thoracopod, anterior; C, sixth thoracopod, anterior view showing muscles visible through integument.

ked proximally and bilaterally serrate distally. Exopod expanded distally; armed with 5 articulated and distally serrate setae, and short outer serrate seta. Thoracopod 5 (Fig. 5B) similar except for complete separation of large proximal (syncoxa) and small distal (basis) protopodal segments. Tiny spinules present on medial margin of endopod. Thoracopod 6 (Fig. 5C) uniramous, comprising single protopod segment bearing 2 brush setae and 1-segmented exopod. Protopod with indentation about midway along medial margin, at level of insertion of some intrinsic thoracopodal muscles. Exopod armed as other exopods except only 4 articulated setae present.

Material Examined.—Holotype tantulus larva, 1 paratype developing male within expanding trunk sac of preceding tantulus. Holotype attached to aesthetasc on antennule of damaged, and unidentifiable, harpacticoid belonging to tisbiform group of families. Paratype attached ventrally to anal somite (Fig. 3A) of copepodid IV stage of an undescribed new genus of canuellid harpacticoid. Stored in collections of Zoölogisch Museum, Amsterdam, Registration Nos. ZMA Co 102.810a (holotype) and Co 102.810b (paratype, on 2 slides).

Type Locality.—Amsterdam Expedition to the Canary Islands, Station 85/53, anchialine lava pool situated 50–100 m from sea near Playa de Montana Bermeja, Lanzarote (UTM Coordinates FT61415 × 320395). Pool separated from sea by ridge of lava and pumice; tidal activity perceptible in pool via subterranean connections with sea. Salinity of water in pool about 27.9‰. Sample taken on 14 May 1985 by Karaman-Chappuis method.

Phylogenetic Affinities of the Tantulocarida

Homology of the Tantulocaridan Penis

Although tantulocarids lack any recognizable cephalic appendages at any stage of the life cycle, Boxshall and Lincoln (1987) suggested that their affinities lie with the Thecostraca (sensu Grygier, 1985, 1987) because they shared the possession of 6 pairs of thoracopods and a median penis on the seventh trunk somite of the male. This latter character is regarded as particularly robust, since it is a compound character involving the location of the gonopores on the correct somite and the evolution of a median penis. The penis in the new genus has at least 1 extrinsic muscle and in a new species of *Microdajus* (Boxshall *et al.*, in press) several intrinsic muscles are present. The tantulocaridan penis appears, therefore, to represent a modification of the seventh pair of thoracopods and can be considered homologous with the penis of thecostracans, which is derived by medial fusion of the seventh thoracopods (Grygier, 1987). Its possession is a synapomorphy of the Tantulocarida-Thecostraca grouping. The paired penes of ostracods probably also represent modified thoracopods, and the studies of Schulz (1976) have indicated that they originate in close proximity to the seventh postcephalic somite. Schulz (1976) assigned the penes of *Cytherella* to the sixth trunk somite, but Grygier (1984) pointed out that their strongest skeletal support was derived from the seventh and eighth somites.

Numbers of Trunk Somites

The relationship of the Tantulocarida-Thecostraca grouping to other maxillopodans is problematic, because the Tantulocarida are now known to possess up to 13 trunk somites (in *S. stocki*) rather than the total of 11 which has previously been regarded as diagnostic of the Maxillopoda (Dahl, 1956; Newman *et al.*, 1969; Newman, 1983; Grygier, 1983). The reinterpretation of the abdomen of *Basipodella harpacticola* Becker as 12-segmented (Boxshall and Lincoln, 1983) and the discovery of the fossil Skaracarida (Müller and Walossek, 1985) had already raised questions concerning the ancestral segmentation pattern of the Maxillopoda. These latter authors suggested that 12 trunk somites (including the telson) may be the ancestral state for the Maxillopoda.

The concept of homology is central to the cladistic method, enabling characters to be defined and compared. As currently applied to crustacean body segmentation, homology is a crude numerical-positional concept and little importance is attached to developmental criteria. For example, the possession of 11 postcephalic trunk somites has been regarded as the main apomorphy linking the Copepoda, Mystacocarida, Thecostraca

(=Cirripedia/Ascothoracida/Facetotecta), and Ostracoda within the Maxillopoda, yet the developmental processes by which somite numbers are attained are very heterogeneous. Copepods primitively undergo 11 molts from first nauplius to adult (Boxshall *et al.,* 1984). The last molt is definitive. The evolution of determinate growth in copepods is the result of two processes: the limitation of numbers of trunk somites by the sudden cessation of molting, and the precocious attainment of sexual maturity (progenesis). The correlation of these separate processes can be interpreted as evidence of a progenetic origin of the Copepoda as a whole (Boxshall, 1983). Assuming an ancestral ontogeny of six naupliar stages (as in cirripedes (Moyse, 1987)) and two cyprids (as in ascothoracids (Grygier and Fratt, 1984)), thecostracans primitively undergo eight molts between first nauplius and the attainment of adult body segmentation. In contrast to copepods, however, the last molt is not definitive, since cirripedes continue to molt periodically throughout adult life (Darwin, 1851). Thus, there is no evidence that the evolution of a short trunk in thecostracans is developmentally correlated with the early onset of sexual maturity. Conversely there is evidence that in ascothoracids there is at least one discrete postlarval stage between the attainment of adult body segmentation and the onset of sexual maturity (Grygier, 1984). It is probable that the selective pressures leading to the evolution of a short, 11-somite trunk in thecostracans were different from those affecting copepods, and may have involved shortening of the body to enable it to be completely enclosed within a protective carapace (Boxshall, 1983). The 11 trunk somites of copepods and thecostracans are homologous in a strict positional sense, but developmentally they are the end products of nonhomologous processes. This interpretation is reinforced by the convergence in trunk somite number indicated in Fig. 6. Ferrari (1988) has analyzed in detail the developmental patterns in numbers of ramal segments in the swimming legs of copepods. He noted numerous similar cases of developmental convergence in which the same adult segmentation patterns were produced by nonhomologous developmental processes.

Compound Eyes

The distribution of compound eyes, presumed present in the ancestral crustacean stock (Hessler and Newman, 1975), in the maxillopodan groups provides additional evidence of developmental heterogeneity. The loss of compound eyes in copepods (and in mystacocarids also) may be due to the simultaneous cessation of molting and precocious onset of sexual maturity occurring at a stage of development prior to the full development of compound eyes. This would explain the loss of a major sense organ as a secondary consequence of a more advantageous evolutionary change in basic body form. Compound eyes are retained in the thecostracan groups (and in branchiurans and ostracods also). Again this can be interpreted as evidence that the shortening of the body in thecostracans was not brought about by a paedomorphic event homologous with that occurring in the copepod lineage.

The compound eyes of cirripede cyprid larvae (Thecostraca), branchiurans, and ostracods vary in numbers of crystalline cone cells and retinular cells, and in the configuration of the rhabdom, but they all share the presence of bipartite pigment cells surrounding the cone (Hallberg and Elofsson, 1983). The anatomy of the compound eye of ascothoracid larvae is not known in great detail, but it appears to be closest to that found in cirripede cyprids (Hallberg *et al.,* 1985).

Classification of Starobogatov (1986)

The new classification of the Crustacea proposed by Starobogatov (1986) (English translation, by Grygier, published in 1988) little resembles that summarized by Bowman and Abele (1982) or Schram (1986). The methodology employed by Starobogatov (1986) relies heavily on a refinement of the concept of primary heteronomy as proposed initially by Ivanov (1944) and later developed by Melnikov (1971). The underlying principle of primary heteronomy holds that metamerism exhibited by the ancestral stock of the Articulata (including annelids and arthropods) arises during embryological development as a result of the activity of 2 separate organizing centers, one larval (primary) and the other postlarval (second-

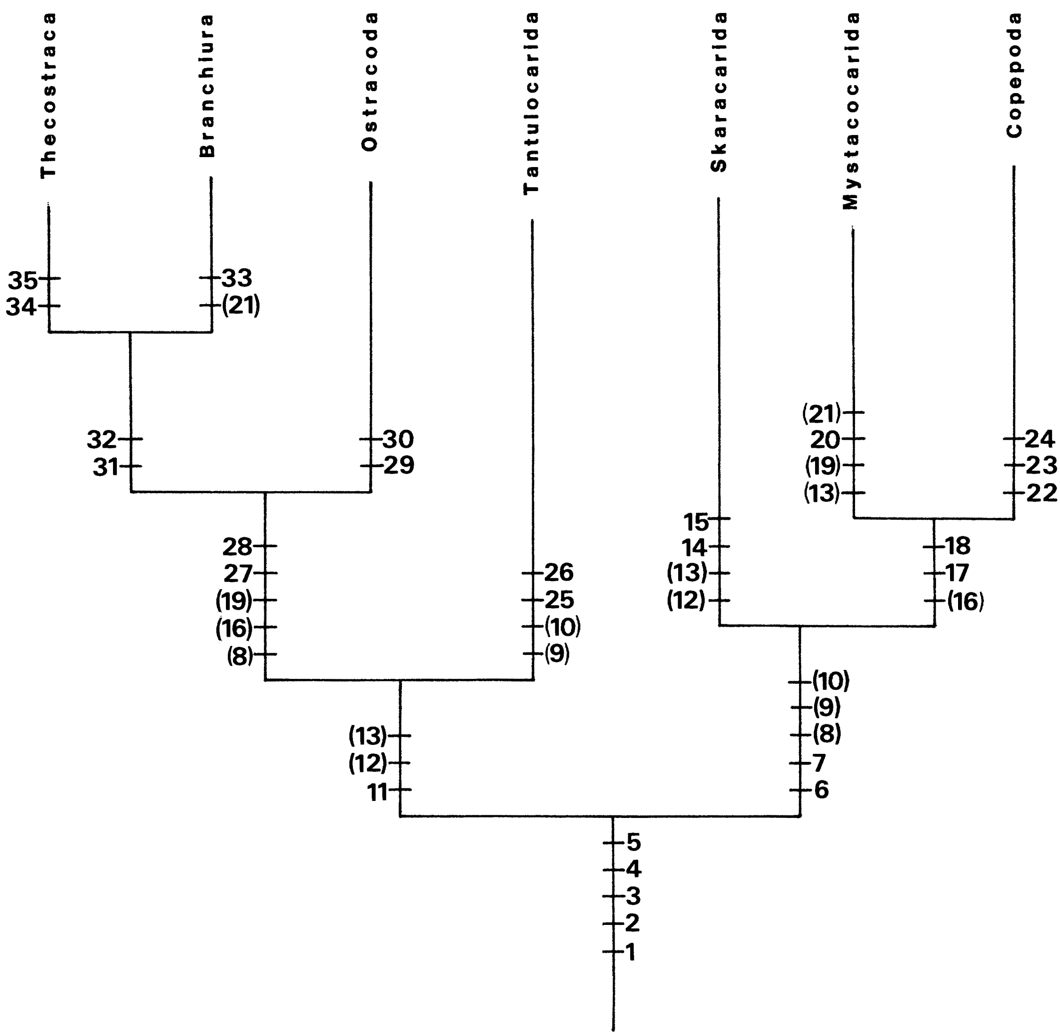

Fig. 6. Phylogenetic relationships of the seven major maxillopodan taxa (Thecostraca, Branchiura, Ostracoda, Tantulocarida, Skaracarida, Mystacocarida, and Copepoda). Numbered apomorphies refer to the characters listed in Table 1, parentheses indicate convergence.

ary). Each center follows its own rules of growth, with the former laying down somites gradually from anterior to posterior, the latter in the opposite direction. Manton (1949) found no such distinction in the development of the Onychophora and concluded that such heteronomy was secondary in the articulates. This conclusion was supported by Anderson (1959). Heteronomy appears to be associated with the evolution of specialized larvae which function early (Manton, 1949).

The primary heteronomy of the Crustacea is not in question. The studies by Manton on *Hemimysis* (1928) and *Nebalia* (1934), and by Anderson on *Limnadia* (1967) and *Tetraclita* (1969) provide clear evidence of two such organizing centers. The anterior center corresponds to the functional nauplius and is expressed by the virtually simultaneous formation of the naupliar somites. The postnaupliar somites proliferate from the anterior end of the telson, which is the posterior center. Starobogatov's (1986) interpretation of development is different. The concept of primary heteronomy is the starting point, but, by the use of "indirect data," Starobogatov arrives at a combined developmental-functional concept, the *prototagma*. Anterior and posterior prototagmata together comprise the larval segments, and are separated by a third prototagma comprised of postlarval segments derived from a growth zone. The classification of the Crustacea produced by Starobogatov (1986) is based on the relationship between these prototagmata and adult tagmosis and segmentation patterns, type of carapace, and degree of heteronomy of the trunk appendages.

The Tantulocarida are placed by Starobogatov (1986) in the Class Ascothoracioides. This group is diagnosed by the composition of the middle and posterior prototagmata; the middle prototagma consists of three somites and the posterior of five to eight including the anal segment. The class includes the Ascothoracida, Mystacocarida, and Copepoda as well as the Tantulocarida. The last three taxa are placed in the subclass Cyclopiones, diagnosed by "carapace not flexed along dorsomedial line, but in all known forms to some extent reduced, first antennae used for floating or swimming." The Tantulocarida (as the superorder Basipodelliformii) are then placed in the infraclass Calanioini together with the gymnoplean copepods. The Calanioini is diagnosed by the location of the major body articulation behind the sixth trunk somite.

This classification scarcely deserves serious consideration. It is based on an extremely small number of characters compared to a modern cladistic classification of the same and related taxa (see Grygier, 1983, 1987, for example). Functional analysis is not used as a method of understanding and delimiting characters, but function itself is used as a character. Virtually no attempt is made to assess the homology of structures or to assess the plesiomorphic-apomorphic polarity of character states. Rather than list other deficiencies in methodology it seems most instructive to examine the "indirect method" of identifying prototagma which is central to Starobogatov's system. The indirect method uses deviations in the sequence of somite formation of definitive somites and appendages (Starobogatov, 1988, in letter to Grygier). The identification of the prototagma boundaries in the Ascothoracioides is based on the appearance of thoracopod 3 before thoracopod 2 in the development of *Derocheilocaris*. The copepods, ascothoracids, and tantulocarids are presumably placed in this class by analogy, since they do not show this character. Reference to the original data on the development of *Derocheilocaris* (see Delamare-Deboutteville, 1954; Hessler and Sanders, 1966) clearly shows that there is no deviation in the orderly sequence of somite separation from the telson. Somites are progressively budded off the anterior end of the telson in the typical crustacean anamorphic manner. The only deviation is in the rate of development of the appendages, thoracopod 3 becoming functional before thoracopod 2 in *D. typicus* Pennak and Zinn and *D. remanei* Delamare-Deboutteville and Chappuis. In *D. katesae* Noodt, however, it is thoracopod 4 that appears before thoracopods 2 and 3 (McLachlan, 1977). The indirect method of determining boundaries between prototagmata is clearly unreliable when species within a single genus can show differences in "prototagmosis." We interpret this heterochrony as evidence of morphogenetic plasticity within the genus in response to particular functional needs. Similar functional heterochrony is seen in other crustaceans. For example, in the decapod *Palaemon serratus* (Pennant), pereiopod 5 becomes functional before pereiopod 4 (see Fincham, 1983), but both belong to the same prototagma in Starobogatov's system. It is apparent to us that developmental criteria are very important in assessing homology of body somites (as discussed above), but we find no evidence that the eventual role of an appendage in the adult has any effect on the pattern of proliferation of the postcephalic somites. Any heterochrony in the sequence of appendage development can readily be attributed to the functional specialization of the larvae concerned. We thus conclude that the basic concept of the prototagma as a developmental-functional entity is invalid.

Phylogenetic Relationships of Tantulocarida

Grygier's (1987) recent study of maxillopodan phylogeny was completed before the new information on the tantulocaridan penis and trunk segmentation was available. The primary aim of that study was to assess the systematic position of the Facetotecta in relationship to other thecostracans. Our aim is to determine the position of the Tan-

Table 1. Character set for analysis of relationships among maxillopodan taxa.

Character	Plesiomorphic state	Apomorphic state
1. Antennule	biramous	uniramous
2. Trunk limbs	15 pairs	7 pairs
3. Trunk somites including telson	16	13 maximum
4. Male gonopores	trunk somite 8	trunk somite 7
5. Tapetal cells of nauplius eye	absent	present
6. Trunk somites including telson	13	12 maximum
7. First trunk limb	unmodified	modified as maxilliped
8. Endite on thoracopods 2–6	present	absent
9. Carapace	present	absent
10. Compound eyes	present	absent
11. Male trunk limb 7	unmodified	modified as penis
12. Female trunk limb 7	present	absent
13. Trunk limb exopod	3-segmented	1 or 2-segmented
14. Trunk limbs 2–6	present	absent
15. Caudal rami	1-segmented	3-segmented
16. Trunk somites	12 or 13	11
17. Antennary exopod in adult	14 segments	9 segments maximum
18. Mandibular exopod in adult	13 segments	7 segments maximum
19. Antennule segments	9 or more	8 or less
20. Trunk limbs 2–5	biramous	buds
21. Gonopores (male)	on trunk somite 7	on trunk somite 5
22. Intercoxal sclerites on thoracopods 2–6	absent	present (as couplers)
23. First trunk somite	free	fused to cephalon
24. Maxilliped	biramous	uniramous
25. Cephalic appendages	present	absent
26. Oral disc	absent	present
27. Antennary exopod in adult	14 segments	2 segments
28. Bipartite pigment cells in compound eye	absent	present
29. Naupliar carapace	absent	present
30. Trunk limbs 3–6	present	lost
31. Lateral gut caeca in carapace	absent	present
32. Antennulary attachment device	absent	present
33. Poison spine	absent	present
34. Postmaxillulary limb buds in nauplius	present	absent
35. Frontal filaments	not associated with compound eye	associated with compound eye

tulocarida and we present a phylogeny (Fig. 6) incorporating all the major taxa previously attributed to the Maxillopoda. The Malacostraca was used as the out-group in accordance with the scheme of maxillopodan origins proposed by Newman (1983). The phylogenetic scheme was generated by hand and the characters used are given in Table 1. The plesiomorphic states for characters 1–5, 9–12, and 15 are based on the out-group. Those for characters 6–8, 13 and 14, and 16–35 are determined by in-group analysis, in which it is assumed that evolution has proceeded largely by oligomerization (Boxshall *et al.,* 1984; Hessler and Newman, 1975). Transition series of 3 or more states of any given character (for example, characters 3, 6, and 16 in Table 1) are treated in discrete steps rather than as multistate characters.

This analysis relies on relatively few characters and many of these are unsatisfactory, since they cannot be scored for all taxa. This is due in part to the great diversity exhibited by maxillopodans. For example, some have no cephalic appendages but a full complement of trunk limbs, while others have all the cephalic limbs but only a single pair of trunk limbs. The only limb common to every maxillopodan is the first postcephalic trunk limb. Also, it is difficult to find characters that are equally applicable to both fossil and recent taxa. However, despite its preliminary nature and the considerable convergence evident within the group, this analysis indicates that there are two main lineages within the Maxillopoda: the lineage leading to the Copepoda (comprising Copepoda, Mystacocarida, and Skaracarida) and that leading to the Thecostraca (comprising Thecostraca, Branchiura, Ostracoda, and Tantulocarida). The former is best characterized by the modification of the first trunk limb as a maxilliped, the latter by the modification of the male seventh trunk limb as a penis (presumed to have been lost secondarily in the Branchiura). The Tantulocarida share the loss of the compound eyes and carapace with the copepod lineage, but are placed at the base of the thecostracan lineage on the presence of the penis, the loss of the female seventh trunk limb, and the 2-segmented state of the thoracopodal exopods. The cladogram presented by Grygier (1987) contains fewer taxa, but the Thecostraca, Branchiura, and Copepoda are in the same relative positions as in Fig. 6.

Relationships between maxillopodan taxa were also analyzed in Schram (1986), a work completed prior to the publication of new data on the Skaracarida (Müller and Walossek, 1985), Tantulocarida (Boxshall and Lincoln, 1987), and Facetotecta (Grygier, 1987). Schram's cladogram (1986, fig. 43-6) divides the Maxillopoda into an unresolved trichotomy. The Tantulocarida form one branch. The second branch groups the thecostracan taxa together and places the Copepoda as the sister group of the Thecostraca on the possession of 4 or more naupliar stages, a character state that we interpret as plesiomorphic. The third branch comprises the Branchiura, Mystacocarida, and Ostracoda. These are linked by the reappearance of the mandibular palp and the possession of less than six thoracic somites. We interpret the possession of the mandibular palp as plesiomorphic to the Maxillopoda on the basis of in-group analysis. The presence in the ostracod *Cytherella* of paired penes, derived from the thoracopods of trunk somite 6, 7, or 8 (see above), indicates that a thorax of less than six somites cannot be used as an apomorphy of this lineage. Schram shows the Branchiura and Mystacocarida as sister groups but specifies no synapomorphy. The differences between Fig. 6 and the cladogram of Schram (1986) can be attributed to differing interpretation of homology, polarity of character states, and new data unavailable to Schram.

We have reservations about the position of the Skaracarida in Fig. 6. This group exhibits many basic features that differ from the recent maxillopodan taxa. For example, the caudal rami are 3-segmented. This is treated in Table 1 as an apomorphic character state for the Skaracarida, because the out-group, the Malacostraca, and the majority of other maxillopodans have 1-segmented caudal rami. However, it is possible that it is a plesiomorphy, since evolution within the Crustacea is presumed to proceed typically by oligomerization (Hessler and Newman, 1975; Boxshall *et al.*, 1984). Some cirripedes have multisegmented caudal appendages on the abdominal rudiment (Newman *et al.*, 1969), but this may be the result of secondary annulation, as found in the thoracopodal cirri. We have regarded the ascothoracidan 1-segmented condition as the plesiomorphic state of the Thecostraca. Other characters of skaracarids are difficult to interpret because of their general "palaeozoic" appearance. The antennae, for example, appear to have 14 exopodal segments but these may not be true segments, separated proximally and distally by joints containing arthrodial membrane. In *Skara annulata* Müller and Walossek there are more "joints" on the posterior side of the antennary exopod than on the anterior side (Müller and Walossek, 1985). This suggests that these "joints" on skaracarid limbs may not be homologous with the segments of recent maxillopodans. There are similar differences in the subdivision of the protopods of the postmandibular limbs which make the identification of homologies with recent maxillopodans extremely difficult. Despite these problems we consider that it is more informative to bring such fossil taxa into an exploratory analysis of this sort rather than to ignore them.

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ANNOUNCEMENT

The following application has been received by the International Commission on Zoological Nomenclature and has been published in the Bulletin of Zoological Nomenclature, volume 45, part 3 (23 September 1988). Comment or advice on this application is invited for publication in the Bulletin and should be sent to the Executive Secretary, ICZN, % British Museum (Natural History), Cromwell Road, London SW7 5BD, United Kingdom.

Case 2622. *Pleuromma princeps* Scott, 1894 (currently *Gaussia princeps*; Crustacea, Copepoda): proposed conservation of the specific name.