



## TWO NEW FAMILIES OF COPEPODS (COPEPODA: SIPHONOSTOMATOIDA) PARASITIC ON ECHINODERMS

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### A B S T R A C T

The description of *Dichelina phormosomae* is supplemented by study of new material from a deep-water echinoid collected in the North Atlantic, and the homology of some mouthparts is reinterpreted. The phylogenetic relationships between *Dichelina* and other echinoderm-inhabiting siphonostomatoids are analysed. Based on inferences from the phylogenetic analysis, two new families of siphonostomatoid copepods parasitic on echinoderms are established, the Dichelinidae and the Codobidae. The hitherto unplaced genus *Stephopontius* is formally assigned to the family Nanaspidae.

Eleven families of copepods are known to occur exclusively on echinoderm hosts. These are, within the order Siphonostomatoida, the Brychiopontiidae, Calverocheidae, Cancerillidae, Micropontiidae, Nanaspidae, and Stellicomitidae, in the order Poecilostomatoida, the Pionodesmatidae, Synapticolidae, and Synaptiphilidae, and in the order Cyclopoida, the Chordeumiidae and Cucumariocolidae. Representatives of several other families in these three orders (e.g., Asterocheridae, Pseudanthessiidae, and Ascidicolidae Enterognathinae respectively) utilize echinoderms as hosts, but not exclusively.

There are, however, two existing siphonostomatoid genera found on echinoderm hosts that are not placed in any of the currently recognized families. These are *Dichelina* Stephensen, 1933, and *Codoba* Heegaard, 1951. The uncertainty surrounding the classification and relationships of these two genera is not a result of lack of information, because adequate descriptions are available of both genera (Stephensen, 1933; Stock, 1968a; Boxshall, 1988). The aims of the present paper are to provide supplementary descriptive notes on *Dichelina*, based on study of new material from the deep Northeastern Atlantic, and to examine the phylogenetic relationships of *Dichelina* and *Codoba*, using the methods of phylogenetic systematics. In addition, Humes and Cressey (1959), when establishing the family Nanaspidae (as Nanaspidae), noted similarities in tagmosis between the

genus *Stephopontius* Thompson and Scott, 1903, and their new genus, *Nanaspis* Humes and Cressey, 1959. Earlier, Sewell (1949) had tentatively attributed *Stephopontius* to the family Cancerillidae. This genus is also included in the analysis in order to determine its affinities. The type and only species of *Stephopontius* was collected from washings of marine invertebrates; the actual host is unknown but is presumed here to be a holothurian echinoderm.

### MATERIALS AND METHODS

Adult females of *Dichelina phormosomae* Stephensen, 1933, were collected from the intestine of the echinoid *Phormosoma placenta* Wyville Thompson at various localities around the Porcupine Seabight in the Northeastern Atlantic (Table 1). Specimens for scanning electron microscopy were washed in distilled water, dehydrated through graded acetone, and critical point dried. They were attached to stubs, sputter coated with gold-palladium, and examined in a Hitachi S–800 Field Emission Microscope.

The phylogenetic analysis was performed using PAUP 3.1.1. All characters were treated as IRREVERSIBLE UP even though this commonly generates longer, less parsimonious trees, and a BRANCH AND BOUND search was carried out to find the shortest tree. The use of IRREVERSIBLE UP characters is based on the findings of Huys and Boxshall (1991), who showed oligomerization to be the predominant evolutionary trend in the Copepoda. The taxa included in the analysis, in addition to *Dichelina* and *Codoba*, are all specialist echinoderm-inhabiting families of siphonostomatoids. Their inclusion is based partly on the assumption that the nearest relatives of these two genera are likely to be found among taxa utilizing the same host phylum and partly on the basis of *a priori* recognition of similarities, such as the loss

Table 1. Locality data for *Dichelina phormosomae* found in intestine of *Phormosoma placenta*.

Station number	Locality	Number of females	Date	Gear	Depth (m)
97791	49°N 12°W	1	24.04.1978	BN 1.5–30	1,404–1,398
50522	49°N 11°W	1	08.06.1979	OTSB–14	1,000–965
101098	49°N 12°W	4	07.09.1979	BN 1.5–30	1,120–1,130
50903	51°N 13°W	1	07.11.1980	OTSB–14	1,265–1,250
50904	51°N 13°W	3	08.11.1980	OTSB–14	1,035–1,020
51007	51°N 13°W	1	02.05.1981	OTSB–14	1,020–1,030
51305	51°N 13°W	2	18.02.1982	OTSB–14	1,005–965
51308	51°N 13°W	1	19.02.1982	OTSB–14	1,205–1,230

of the inner seta from the basis of the first swimming leg (lost in all echinoderm-inhabiting siphonostomatoid families, except the Brychiopontiidae (see Humes, 1974)). The Brychiopontiidae was selected as out-group because it shares the greatest number of plesiomorphies with the Asterocheridae, a basal family within the order (Huys and Boxshall, 1991). Where possible, two taxa were included from each of the currently recognised families. This was not possible for the Calverocheridae because a relatively complete description was available for only a single taxon. Two of the genera (*Nanaspis* and *Allantogynus* Changeux, 1958) currently allocated to the Nanaspidae were included plus the hitherto unplaced *Stephontius*, which resembles members of that family according to Humes and Cressey (1959). The Cancerillidae is represented by four genera in the matrix because of the relative heterogeneity of this family: i.e., the extreme plesiomorphy of *Parartotrogus* T. and A. Scott, 1893, relative to the other included genera.

## RESULTS

### Supplementary Description of *Dichelina phormosomae*

Mean body length of adult female 3.27 mm, ranging from 2.86 mm to 3.68 mm (based on 12 specimens). Antennule (Fig. 1A, a) indistinctly 6-segmented: setal formula 6, 5, 8, 1, 1 + ae, 8. Rostrum (Fig. 1A, r) weakly developed, subrectangular. Antenna (Fig. 1A, an; Fig. 2C) uniramous, with no vestige of exopod; indistinctly 4-segmented. Second segment ornamented with raised patch of spinules; third segment ornamented with curved, ridge-like, longitudinal row of tiny spinules; distal segment slightly curved, ornamented with 4 comb-like transverse rows of spinules on convex surface and armed with 2 equal apical claws (Fig. 2D). Mandibular palp an elongate lobe bearing large seta subapically and tiny seta apically (Fig. 1A, mn; 1C). Oral cone short, tips of labrum and labium rounded, with slit-like distal opening (Fig. 1A, oc). Maxillule unilobate, lacking outer lobe (palp); elongate inner lobe (Fig. 1A, ml) located immediately lateral to labial part of oral cone (Fig. 1B). Maxilla sub-

chelate (Fig. 1A, mx), comprising robust unarmed syncoxa and distal curved claw formed by basis: tip of claw hooked, with subapical pore opening on flank of claw; claw opposing rounded swelling proximally on syncoxa. Maxilliped indistinctly 3-segmented (Fig. 2A), comprising unarmed syncoxa, long basis ornamented with 4 more-or-less longitudinally orientated spinulate ridges and slightly curved endopodal subchela. Subchela ornamented with about 6 or 7 conspicuous comb-like spinule rows, orientated transversely; subdistal row and preceding row incomplete, around convex surface only; distal row encircling small, claw-like setal element (Fig. 2B).

Swimming legs highly reduced. Leg 1 positioned near posterolateral corners of ventral cephalothoracic surface; comprising single lobe bearing 3 naked setae around apex and ornamented with longitudinal rows of fine spinules. Legs 2, 3, and 4 each represented by pair of isolated setae located ventrolaterally on pedigerous somites (Fig. 1D). Leg 5 apparently absent.

*Remarks.*—The new Atlantic material, from *Phormosoma placenta*, is tentatively identified as *Dichelina phormosomae* which was originally described from *Phormosoma bur-sarium* Agassiz and *P. verticillatum* Mortensen in the Philippines (Stephensen, 1933). Subsequent to the original record, Stephensen (1935: 223) tentatively identified as *D. phormosomae* material collected from *Paraphormosoma alternans* (De Meyere) from the Celebes Sea, off Borneo. The Atlantic specimens are slightly smaller than the types (mean female body length 3.27 mm compared with 3.8 mm) but, despite a number of fine-scale differences, all the essential features of the appendages and the gross body morphology in the Atlantic material are closely similar to those described by Stephensen. The

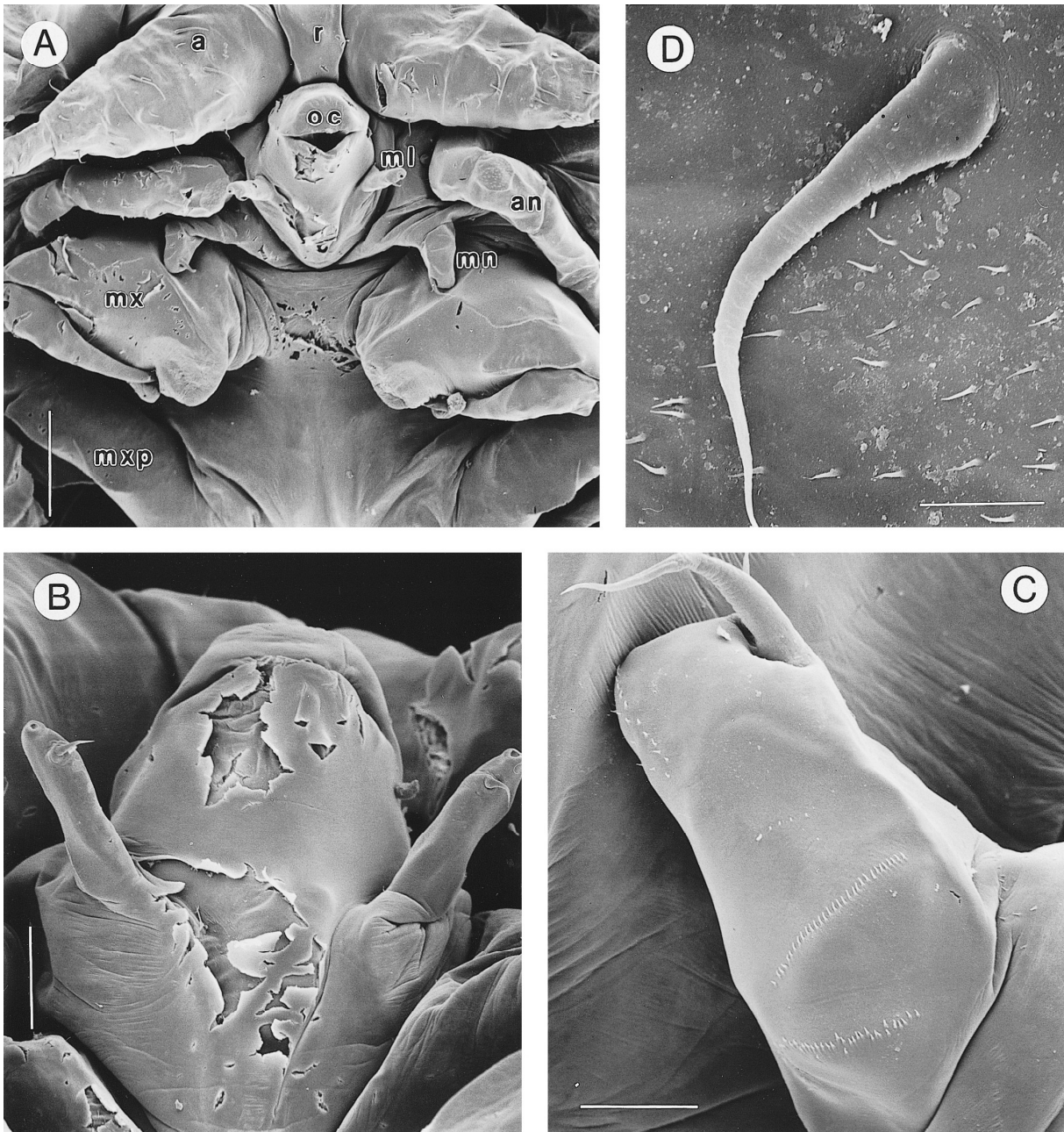


Fig. 1. *Dichelina phormosomae* ♀. A, Oral region, ventral; B, Oral cone and maxillule, posterior; C, Mandibular palp, anterior; D, Seta representing leg 3, ventral. Abbreviations a = antennule, an = antenna, ml = maxillule, mn = mandibular palp, mx = maxilla, mxp = maxilliped, oc = oral cone, r = rostrum. Scale bars A = 150  $\mu$ m; B = 50  $\mu$ m; C = 20  $\mu$ m; D = 10  $\mu$ m.

differences identified here mainly concern the fine setation of the antennule, the spinular ornamentation of some other appendages, and the presence of setal vestiges of the second and third swimming legs. Such apparent differences are readily explicable by differences in observation techniques between Stephensen in 1933 and the present account. We regard their significance, therefore, as insufficient to justify the establishment of a new species, despite the enormous distance be-

tween the type locality in the Indo-Pacific and the Northeastern Atlantic. The discovery of males from the Atlantic may allow this identification to be verified.

Stephensen (1933) found it difficult to identify the postoral mouthparts with any certainty. The lobe identified as the ?mandible by Stephensen (1933) and as the mandibular palp by Stock (1968a) is here reinterpreted. It bears only two setae in *D. phormosomae* but three setae in *D. seticauda* (Stock, 1968a:

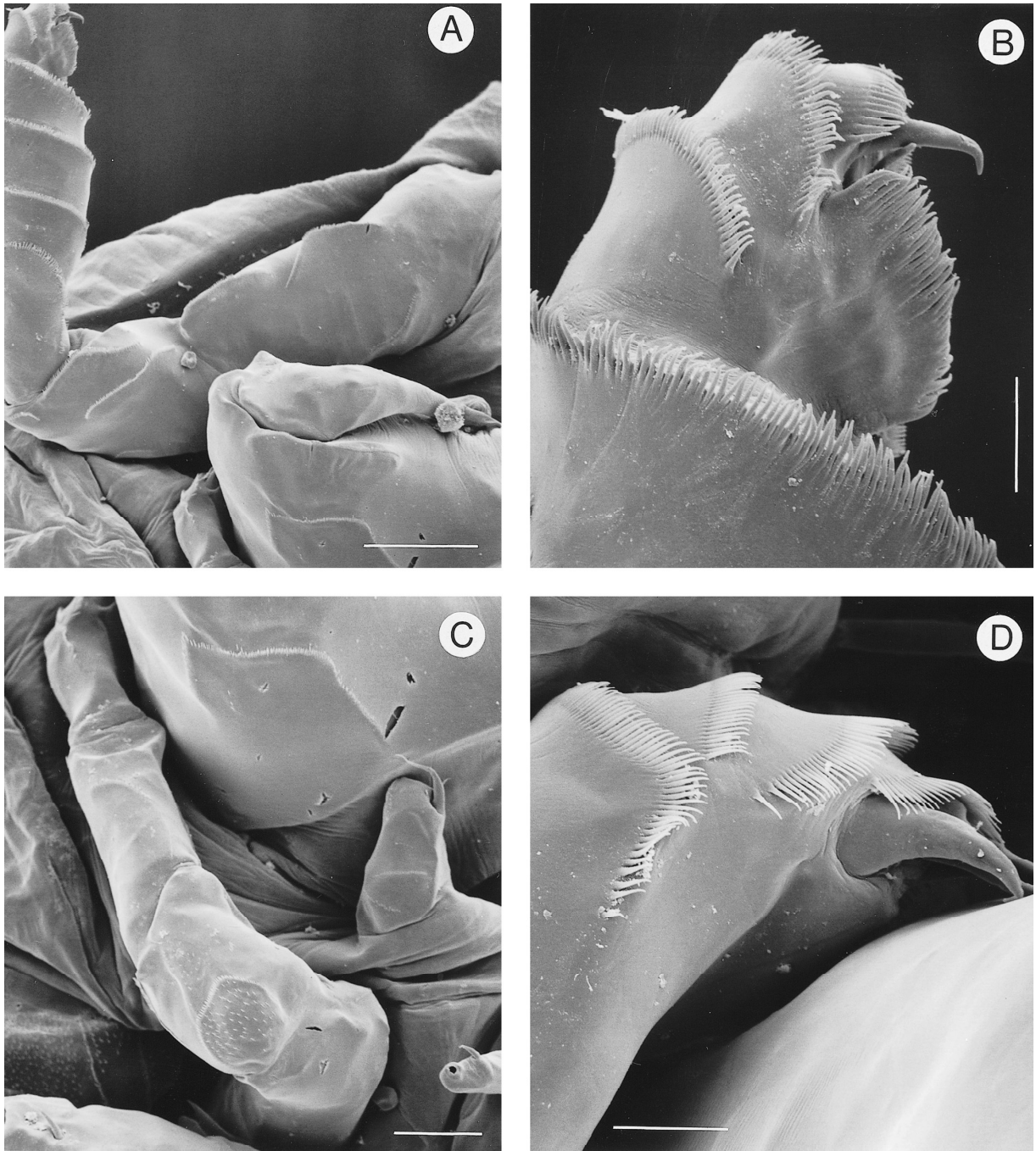


Fig. 2. *Dichelina phormosomae* ♀. A, Maxilliped, anterior; B, Detail of maxilliped tip, showing ornamentation and distal claw-like element; C, Antenna, ventral; D, Tip of antenna showing ornamentation and distal elements. Scale bars A = 100  $\mu$ m; B = 10  $\mu$ m; C = 50  $\mu$ m; D = 15  $\mu$ m.

Fig. 8). The presence of three setae on the lobe is strong evidence that it does not represent the mandibular palp because a maximum of two setae is present on this palp in the whole of the Siphonostomatoidea (Huys and Boxshall, 1991). The position of this lobe, posterolateral to the labium (posterior lip of oral cone), also suggests that it is maxillary in origin rather than mandibular. The bisetose lobe referred to as the maxillule by

both Stephensen (1933) and Stock (1968a) is here reinterpreted as the mandibular palp. It is located some distance lateral to the oral cone, as is the isolated seta representing the mandibular palp in stelicomitids and nanaspids. Given the similarity to these other two families, the alternative interpretation, that the mandible is entirely lost and that, uniquely, inner and outer lobes of the maxillule are widely separated, is considered unlikely.

Table 2. Characters, character states, and matrix scores used in PAUP analysis.

Character number	Plesiomorphic/apomorphic	States
1. Articulation between prosomites 1 and 2	expressed/not expressed	0/1
2. Articulation between prosomites 2 and 3	expressed/not expressed	0/1
3. Articulation between prosomites 3 and 4	expressed/not expressed	0/1
4. Prosome-urosoma articulation	expressed/not expressed	0/1
5. Articulation between fifth pedigerous and genital double-somites	expressed/not expressed	0/1
6. Articulation between genital double and abdominal somite 2	expressed/not expressed	0/1
7. Articulation between abdominal somites 2 & 3	expressed/not expressed	0/1
8. Chitinous ribs on dorsal cephalothoracic shield	absent/present	0/1
9. Fourth pedigerous somite	normal/strongly reduced	0/1
10. Female antennule segmentation	10 to 20-segmented/ less than 10 segmented	0/ 1
11. Male antennule	geniculate/non-geniculate	0/1
12. Male antennule	not swollen/subchirocerate	0/1
13. Antennary exopod	1-segmented/1 seta/absent	0/1/2
14. Antennary endopodal claw	straight or slightly curved/ short & strongly recurved	0/ 1
15. Mandibular palp	1-segmented with 2 setae/ 1 seta on cephalic surface/ absent	0/ 1/ 2
16. Mandibular palp	adjacent to oral cone/ antero-laterally displaced	0/ 1
17. Maxillule	bilobate/unilobate	0/1
18. Maxilla	not subchelate/subchelate	0/1
19. Maxilliped endopod	3-segmented/ 2-segmented (I, II-III)/ 1-segmented (I-III)	0/ 1/ 2
20. Leg 1 intercoxal sclerite	present/absent	0/1
21. Leg 1 location	across midline/lateral	0/1
22. Inner seta on basis of leg 1	present/absent	0/1
23. Endopod of leg 1	3-segmented/ 2-segmented/ 1-segmented/ incorporated into basis	0/ 1/ 2/ 3
24. Exopod of leg 1	3-segmented/ 2-segmented/ 1-segmented	0/ 1/ 2
25. Terminal setation on leg 1 endopod	2/1/0 setae	0/1/2
26. Inner seta on exopod segment 1 of leg 1	present/absent	0/1
27. Female leg 5, outer & distal setal elements	3/2/absent	0/1/2
28. Male leg 5, outer & distal setal elements	3/2/1/absent	0/1/2/3
29. Male leg 5, inner hyaline elements	2/1/0/absent	0/1/2/3

## PHYLOGENETIC ANALYSIS

### Characters

The characters used in this analysis are listed in Table 2. They are mostly self explanatory, relating to the expression of particular articulations between body somites or to segmentation and setal features of the appendages. Additional notes on some characters are presented below.

Character 8 is the presence of chitinous ribs on the dorsal cephalothoracic shield and is shared only by *Dichelina* species and the Stellicomitidae. The reduction of the fourth

pedigerous somite (Ch. 9) is exhibited by the genera comprising the Cancerillidae. There is no evidence that this character is also shared with genera such as *Dichelina*, in which the pedigerous somites are incompletely fused to form a trunk, because the trunk often retains indications of its original segmentation, as in *D. phormosomae*. The condition of the antennary claw is difficult to score because, in several taxa, e.g., Calverocheridae or Brychiopontiidae, it exhibits unique (autapomorphic) states, which are uninformative. This character as used here refers only to the presence of a particular kind of short and highly

Table 3. Character matrix used for PAUP analysis. Characters and states as listed in Table 2. Species used in matrix as follows, with data sources: *Codoba discoveryi* from Boxshall (1988), *Allantogynus delamarei* from Changeux (1958), *Nanaspis mixta* from Humes (1975), *Micropontius ovooides* from Gooding (1957), *Brychiopontius falcatus* from Humes (1974), *Stellicomes tumidulus* and *Onychopygus impavidus* from Humes and Cressey (1959), *Parophiopsyllus ligatus* from Humes and Hendler (1972), *Parartotrogus arcticus* and *Cancerilla tubulata* from Sars (1915), *Stephopontius typicus* from Sewell (1949), *Dichelina phormosomae* from Stephensen (1933) and present account, *Dichelina seticauda* from Stock (1968a), *Calverocheres globosus* from Stock (1968b), and *Ophiopsyllus reductus* and *Micropontius glaber* from Stock, Humes, and Gooding (1963).

Taxa	Characters																													
Siphonostomatoida	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	
1. <i>Brychiopontius</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	2	
2. <i>Codoba</i>	0	0	0	0	0	0	0	0	0	0	?	?	2	0	2	0	0	0	2	1	0	1	1	1	0	1	0	?	?	
3. <i>Nanaspis</i>	0	1	1	0	0	0	1	0	0	1	0	1	2	0	1	1	0	1	1	1	1	1	2	2	1	1	1	1	1	
4. <i>Allantogynus</i>	0	1	1	0	0	1	1	0	0	1	?	?	2	0	1	1	0	1	1	1	1	1	2	2	0	1	2	?	?	
5. <i>Stephopontius</i>	0	0	1	0	1	1	1	0	0	1	0	1	2	0	1	1	0	1	1	1	?	1	2	2	1	1	2	?	?	
6. <i>Stellicomes</i>	1	1	1	1	1	1	1	1	0	1	1	0	1	0	1	1	0	0	1	1	0	1	2	2	1	1	0	0	2	
7. <i>Onychopygus</i>	1	1	1	1	1	1	1	1	0	1	1	0	2	0	1	1	0	1	1	1	0	1	2	2	0	1	0	0	2	
8. <i>Micropontius glaber</i>	0	0	0	0	1	1	1	0	0	0	0	2	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	2
9. <i>Micropontius ovooides</i>	0	0	0	0	1	1	1	0	0	0	0	2	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	2
10. <i>Dichelina phormosomae</i>	0	0	0	0	1	1	1	0	1	0	1	2	0	0	0	1	1	2	1	1	3	2	2	2	1	2	3	3	3	
11. <i>Dichelina seticauda</i>	0	1	1	1	1	1	1	0	1	?	?	2	0	0	0	1	1	2	1	1	1	3	2	1	1	2	?	?	?	
12. <i>Calverocheres</i>	0	0	0	0	0	0	1	0	0	0	?	?	0	0	2	0	1	0	1	0	0	1	1	0	0	0	0	?	?	
13. <i>Cancerilla</i>	0	0	0	0	0	0	1	0	1	1	1	0	1	1	2	0	1	1	1	0	0	1	2	2	0	1	1	0	0	
14. <i>Parartotrogus</i>	0	0	0	0	0	0	0	0	1	1	0	0	0	1	2	0	0	0	1	0	0	1	1	1	0	1	0	0	0	
15. <i>Ophiopsyllus</i>	0	0	0	0	1	0	1	0	1	1	1	0	1	1	2	0	0	1	2	0	0	1	2	2	0	1	0	2	2	
16. <i>Parophiopsyllus</i>	0	0	1	0	1	0	1	0	1	1	1	0	2	1	2	0	0	1	2	0	0	1	2	2	0	1	2	2	2	

recurved claw. Taxa lacking such a claw on the antenna are scored as a zero in the matrix (Table 3). The mandibular palp (Ch. 15) becomes reduced to a single seta (state 1) or is lost (state 2). The seta, when present, is isolated and located on the ventral cephalic surface some distance lateral to the oral cone (Ch. 16).

The reduction of the bilobate maxillule to a unilobate condition (Ch. 17) takes place by loss of the outer lobe in *Cancerilla* Dalyell, 1851, as indicated by the reduction series within the family Cancerillidae. The single lobe retained in the Calverocheridae and *Dichelina* is here identified as the inner lobe, partly on positional evidence.

Leg 1 provides several characters (Ch. 20–26) including the loss of the intercoxal sclerite and the lateral migration of the legs to the posterolateral angles of the cephalothorax. Characters relating to legs 2 to 4 are not utilized in this analysis. Even within robustly defined families, such as the Cancerillidae, there is a sequential loss of segments, rami, or entire limbs in the more posterior legs. Within the family Stellicomitidae there is reduction in leg segmentation; within the Nanaspidae there is reduction in limb segmentation and loss of rami, and even the two

species of *Dichelina* show different leg states with vestigial legs 3 and 4 retained in *D. phormosomae* but not in *D. seticauda*. These independent reductions/losses of characters relating to legs 2 to 4 within families and genera indicate a high level of homoplasy between families. Including such characters, with their high levels of homoplasy, would significantly reduce the quality of this small matrix, so characters relating to the posterior swimming legs were omitted.

Simple setal counts are used for some characters (Ch. 25, 27, 28). Such counts can only be used on the assumption that, for any given character, setae are lost in the same sequence in all taxa exhibiting one or more losses.

#### Phylogenetic Relationships

Two trees were generated by the PAUP 3.1.1 analysis. Both have a length of 99, and a consistency index of 0.414, but differ in f values (tree one = 1,384 and tree two = 1,192). The only difference in topology of the two trees is the relative position of the out-group, the Brychiopontiidae. Tree two is adopted as the working hypothesis here, because it has the lowest f value (Fig. 3) and it places the Brychiopontiidae as the sister-group to the in-group. The in-group is defined

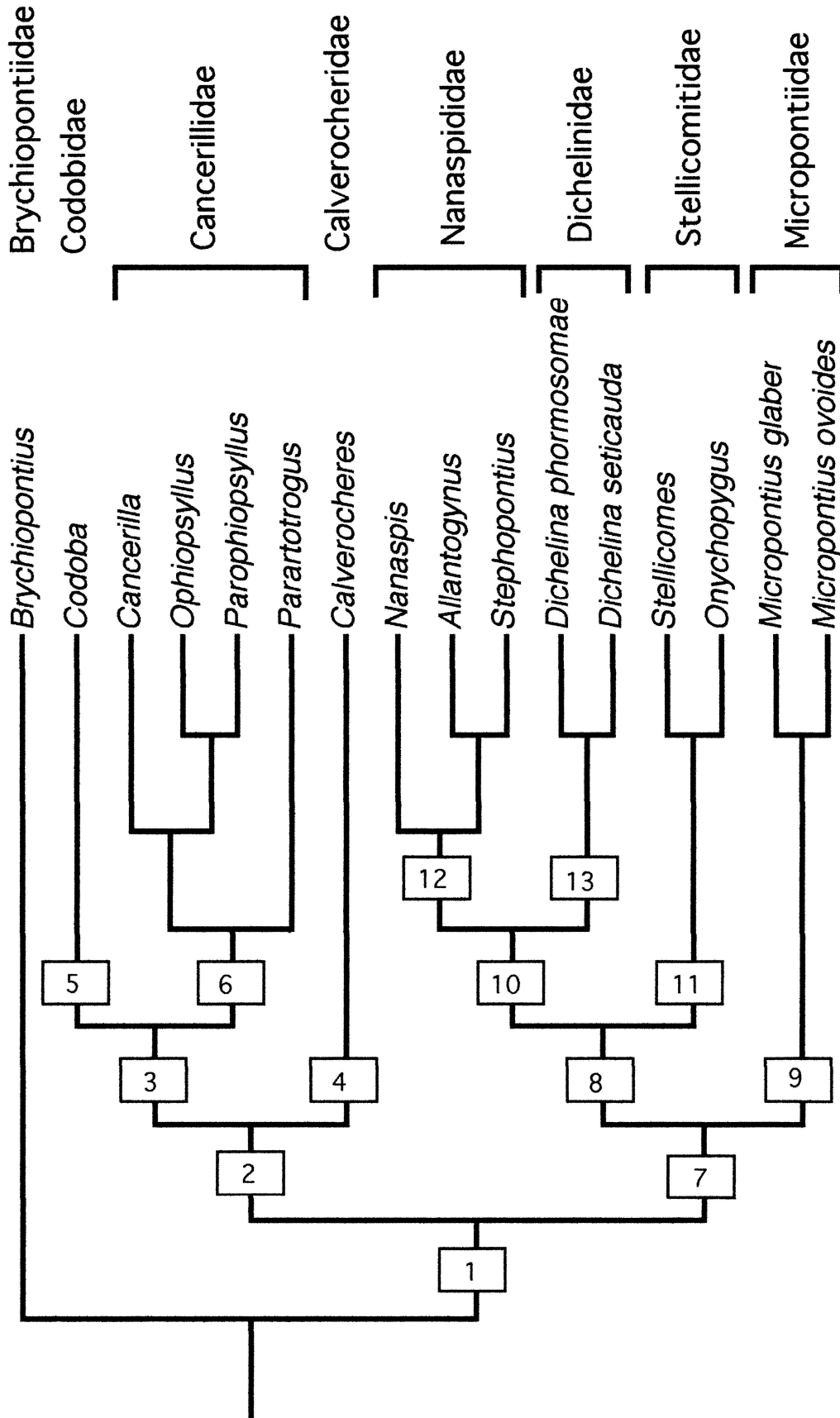


Fig. 3. Cladogram generated by PAUP 3.1.1 analysis of the character matrix presented in Table 3. Apomorphies defining numbered branches as follows: box 1 = Character Nos. 19 (state 0 > 1), ch 22 (0 > 1); 2 = ch 15 (0 > 2), 23 (0 > 1); 3 = ch 24 (0 > 1), 26 (0 > 1); 4 = ch 7 (0 > 1), 17 (0 > 1); 5 = ch 13 (0 > 2), 19 (1 > 2), 20 (0 > 1); 6 = ch 9 (0 > 1), 10 (0 > 1), 14 (0 > 1); 7 = ch 7 (0 > 1), 13 (0 > 1), 26 (0 > 1), 29 (0 > 1); 8 = ch 10 (0 > 1), 20 (0 > 1), 23 (0 > 2), 24 (0 > 2); 9 = ch 5 (0 > 1), 6 (0 > 1), 13 (1 > 2), 29 (1 > 2); 10 = ch 12 (0 > 1), 13 (1 > 2), 18 (0 > 1), 21 (0 > 1), 27 (0 > 1), 28 (0 > 1); 11 = ch 1 (0 > 1), 2 (0 > 1), 3 (0 > 1), 4 (0 > 1), 5 (0 > 1), 6 (0 > 1), 8 (0 > 1), 11 (0 > 1), 15 (0 > 1), 16 (0 > 1), 29 (1 > 2); 12 = ch 3 (0 > 1), 15 (0 > 1), 16 (0 > 1); 13 = ch 6 (0 > 1), 8 (0 > 1), 17 (0 > 1), 19 (1 > 2), 23 (2 > 3), 25 (0 > 1), 27 (1 > 2).



by the absence of the inner seta from the basis of leg 1 and by failure of separation of the distal two segments (II and III) of the maxillipedal endopod. Two main clades are apparent in Fig. 3. The first of these comprises the Calverocheridae, *Codoba*, and the four included genera of the family Cancerillidae and is characterised by loss of the mandibular palp and by the 2-segmented state of leg 1 endopod.

The Calverocheridae is the first to diverge from this lineage, characterised by the unilobate state of the maxillule and by reduction in abdominal segmentation. *Codoba* and the Cancerillidae are united by the 2-segmented state of the exopod of leg 1 and by the loss of the inner seta from the first exopodal segment of the same leg. *Codoba* exhibits a highly derived antenna (reduced to a small lobe), a 1-segmented maxillipedal claw, and lacks an intercoxal sclerite between the first swimming legs. The Cancerillidae retains the plesiomorphic state in all three of these characters but is robustly defined by synapomorphies, including the reduction of the fourth pedigerous somite, the recurved antennary claw, and the reduced segmentation of the female antennule. *Codoba* differs significantly from the cancerillid genera and cannot be included in the family Cancerillidae because it lacks the diagnostic synapomorphies listed above. It is here recognised as the type of a distinct, monotypic family.

The second major clade consists of three current families, the Micropontiidae, Stellicomitidae, and Nanaspidae including *Stephopontius*, plus the hitherto unplaced genus *Dichelina*. The entire clade is characterised by four synapomorphies: the articulation between ancestral abdominal somites 2 and 3 is not expressed; the antennary exopod is reduced to a single seta at most; the inner seta is lost from the first exopodal segment of leg 1; and the male fifth leg retains, at most, a single hyaline element on the inner margin of the free exopodal segment. The Micropontiidae is the first group to diverge within this clade. It is characterised by reduced abdominal segmentation, by the loss of the vestigial exopodal seta from the antenna, and by the loss of the last hyaline element from the inner margin of the free exopodal segment of the fifth leg. The main lineage is defined here by the derived states of four characters: the reduced antennular segmentation, the

loss of the intercoxal sclerite of leg 1, and the 1-segmented conditions of both rami of leg 1.

The next split within the second clade is the separation of the genera of the Stellicomitidae from the branch comprising the Nanaspidae (including *Stephopontius*) and *Dichelina*. The Stellicomitidae is characterised by a large number of synapomorphies, especially the huge reduction in expression of body segmentation (characters 1 to 6 are all derived in this lineage), the reduction of the mandibular palp to a single hirsute seta located lateral and somewhat anterior to the oral cone, and the loss of the geniculation in the male antennule. Synapomorphic character states linking *Dichelina* species with the Nanaspidae (incorporating *Stephopontius*) include the subchirocerate/chirocerate nature of the male antennule, the loss of the seta representing the antennary exopod, the subchelate form of the maxilla, the lateral displacement of leg 1 to the posterolateral angles of the cephalothorax, and the reductions in the fifth legs of both sexes.

*Nanaspis*, *Allantogynus*, and *Stephopontius* are united on the basis of the following synapomorphies: the reduction of the mandibular palp to a single hirsute seta located lateral and somewhat anterior to the oral cone and the failure of expression of the articulation between pedigerous somites 3 and 4. In the original description of *Stephopontius*, the appendage identified by Thompson and Scott (1903: pl. 20, fig. 24) as the mandible is undoubtedly the maxillule. The isolated, hirsute seta (pl. 20, fig. 25) is homologous with the similar seta (representing the mandibular palp) located just lateral to the base of the maxillule in other nanaspidid genera. The presence of this mandibular seta, the body tagmosis and the structure of the maxillule are some of the diagnostic synapomorphies of the Nanaspidae, and *Stephopontius* is here transferred to the Nanaspidae (cf. Fig. 3).

The sister group of the Nanaspidae is the terminal clade comprising the two *Dichelina* species. This clade is characterised by the following synapomorphic states: the unilobate maxillule, the 1-segmented maxillipedal claw, the incorporation of the endopod into the basis in leg 1 with only a single terminal seta retained, and loss of the inner seta from the first exopodal segment of leg 1. On the basis of the phylogenetic analysis, *Dichelina* can-

not be included in the family Nanaspididae, since it lacks many of the diagnostic synapomorphies of that family, and the genus is here recognised as the type of a distinct monogeneric family.

#### DIAGNOSES OF NEW FAMILIES

##### Family **Dichelinidae**, fam. nov.

Podoplea, Siphonostomatoida. Body transformed, cylindrical; comprising cephalothorax, incorporating first pedigerous somite, and trunk consisting of weakly defined second to fifth pedigerous somites and a posterior region bearing paired genital apertures. Cephalothorax with X-shaped pattern of chitinous ribs marking dorsal surface. Posterior region partly subdivided in male. Genital apertures ventrolateral in female, ventral in male. Caudal rami incorporated into posterior margin of trunk.

Rostrum small, poorly defined. Antennule indistinctly 6-segmented in female, aesthetasc on segment 5; segmental homologies indeterminate. Male antennule 4-segmented; subchirocerate, with geniculation between segments 3 and 4. Antenna 4-segmented; comprising separate coxa, basis, and 2-segmented endopod; apical segment armed with 3 setae; exopod absent. Oral cone short, well developed, with labrum and labium fused, with slit-like opening at tip. Mandibular stylet absent; palp lobate, located ventrolaterally between bases of antennae and maxillae, armed with 2 setae. Maxillule unilobed, located adjacent to midline, posterior to oral cone, armed with 3 setae. Maxilla subchelate, comprising robust syncoxa and distal claw representing basis. Maxilliped 3-segmented, comprising slender syncoxa and basis plus distal claw representing fused endopodal segments. Claw ornamented with rows of fine spinules.

First legs widely separated, each located laterally near posterior margin of cephalothorax; intercoxal sclerite absent; each leg a 2-segmented remnant; first segment formed by protopod and armed with inner seta representing endopod, second segment (exopod) bearing 3 setae. Legs 2 to 4 each reduced to single seta located along ventrolateral surface of postcephalic trunk, or with legs 3 and 4 absent. Fifth leg absent. Leg 6 represented by unarmed genital opercula in both sexes. Egg sacs paired, multiseriate.

*Type-genus.*—*Dichelina* Stephensen, 1933.

*Remarks.*—*Dichelina* cannot be accommodated in any of the existing families of siphonostomatoids and, by inference from the topology of Fig. 3, is here treated as the type of a new family which belongs in a monophyletic group together with the existing families Nanaspididae, Stellicomitidae, and Micropontiidae. *Dichelina* possesses chitinous markings on the dorsal cephalothoracic shield as in the Stellicomitidae, but it retains geniculate antennules in the male which are also found in the Micropontiidae and Nanaspididae but not the Stellicomitidae. The new family can also be distinguished from the other families by the extreme reduction of its posterior swimming legs and by the unique form of the maxillule.

##### Family **Codobidae**, fam. nov.

Podoplea, Siphonostomatoida. Body slightly transformed cyclopiform, with slightly swollen prosome. Prosome comprising cephalothorax, incorporating first pedigerous somite, and 3 free pedigerous somites, each with pair of posterolaterally directed epimeral processes. Urosome short, 5-segmented; with genital and first abdominal somites fused to form genital double-somite in female. Genital apertures paired, lateral in female. Caudal rami with 6 setae in total.

Rostrum anteriorly directed. Antennule 20-segmented in female; segmental homologies: segments 1 (I) to 8 (VIII) free, segment 9 (IX–XII) presumably compound, segments 10 (XIII) to 19 (XXII) free, apical segment (XXIII–XXVIII) compound. Antenna vestigial; represented by unarmed lobe. Oral cone well developed. Mandible reduced to stylet without teeth; palp absent. Maxillule bilobed: inner lobe (endite) with 1 seta; outer lobe (palp) with 2 setae. Maxilla comprising unarmed syncoxa and recurved distal claw. Maxilliped 3-segmented, comprising unarmed syncoxa, basis, and distal unsegmented subchela incorporating endopod; basis with single seta; endopod with 2 proximal setae plus 2 spiniform apical elements, not claw-like.

Swimming legs 1 to 4 biramous, with single protopodal segment; rami medially directed; intercoxal sclerites absent. Inner seta on basis of leg 1 absent; inner coxal seta absent in all legs. Segmentation of rami indis-

tinct, setal armature reduced. Fifth leg absent. Leg 6 represented by unarmed opercular plate closing genital aperture on each side. Egg sacs lacking; eggs loose inside capsule enclosing adult female (Heegaard, 1951). Male unknown.

*Type-genus.*—*Codoba* Heegaard, 1951.

*Remarks.*—Boxshall (1988) redescribed *Codoba* from the type material of *C. discoveryi* Heegaard, 1951, but was unable to assign it to any of the existing siphonostomatoid families. *Codoba* exhibits a number of highly derived characters including the autapomorphic vestigial condition of the antenna, the separation and reduction of swimming legs 1 to 4, and the loss of the fifth legs. However, the presence of a plesiomorphic, 20-segmented antennule suggests that this genus diverged early from the main siphonostomatoid lineage. *Codoba* is here treated as the type of a new family. On the basis of the phylogenetic analysis (Fig. 3) the Codobidae belongs in a monophyletic group with the Calverocheridae and Cancerillidae.

#### HOST-PARASITE RELATIONSHIPS

Siphonostomatoids occur as parasites or associates of all extant classes of echinoderms. Of the families considered in this account, members of the Brychiopontiidae and Nanaspidae occur exclusively on sea cucumbers (Holothuria). The members of the Stellicomitidae occur on sea stars (Asterozoa), and those of the Cancerillidae and Codobidae occur on brittle stars (Ophiurozoa). The sea urchins (Echinozoa) act as hosts to three families, the Calverocheridae, Dichelinidae, and Micropontiidae.

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