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***Pholenota spatulifera* Vervoort (Copepoda: Harpacticoida):  
aberrant laophontid or specialized diosaccid?†**

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*Pholenota spatulifera* Vervoort 1964, being originally placed as *incertae sedis* in the Laophontidae, is redescribed and refigured on the basis of the holotype female. It is suggested that the species cannot be assigned to any of the families of the Laophontoidea T. Scott, nor to the family Normanellidae Lang. The structure of the mouthparts, the swimming legs and of the genital complex unequivocally reveal instead that *P. spatulifera* should be allocated to the Diosaccidae. Despite the specialized morphology of the P1 it is provisionally concluded that the genus *Pholenota* Vervoort 1964 is most closely related to *Amphiascus* G. O. Sars 1905, particularly to the *minutus*-complex, suggesting a polyphyletic origin of the latter genus.

KEYWORDS: *Pholenota spatulifera* Vervoort 1964, Harpacticoida, Diosaccidae, Laophontidae, taxonomy, *Amphiascus* G. O. Sars.

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**Introduction**

In 1964 Vervoort proposed the new genus *Pholenota* to accommodate a single female collected during a faunistic survey of the Ifaluk Atoll, Caroline Islands, and obtained as a result of the Coral Atoll Project of the Pacific Science Board. The taxonomic position of the new species, *P. spatulifera* is problematic, because its morphology combines features drawn both from the Laophontidae T. Scott (*sensu lato*) and from the Diosaccidae G. O. Sars. Despite the presence of three-segmented endopods on P2 to P4, the genus was referred, however very provisionally, to the Laophontidae (Vervoort, 1964). The aberrant structures, not the least the presence of spatulate setae on the swimming legs, were interpreted as possible specializations in relation to the habitat, being crevices in porolithon heads just inside the *Heterocentrotus* zone of the seaward reef margin. The primitive nature of the mouthparts, however, excludes a close affinity with the Laophontidae, even in its broadest sense (*sensu* Lang, 1948). Lang (1965) also failed to reveal the genuine relationships of *P. spatulifera*.

The present author's attention was particularly drawn by Vervoort's illustration of 3 setae on the basis of the maxilliped. With regard to this character alone it would be justifiable to place the species in a separate family, since this is a very primitive

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character retained from the ancestral copepodan stock. Within the Harpacticoida the maximum number of 3 setae is reported only in some Canuellidae such as *Sunaristes* Hesse (e.g. Humes and Ho, 1969), *Brianola* Monard (e.g. Hamond, 1973 a) and *Ifanella* Vervoort (Vervoort, 1964), but re-examination of this material proved these records to be erroneous. In order to settle its relationships a redescription of *P. spatulifera* is presented on the basis of the holotype. The present paper forms part of a series (Huys, 1988 a, in press a-b; Huys and Willems, 1989) contributing to a redefinition of the taxonomy of the superfamily Laophontoidea T. Scott (Huys, in press c).

### Material and methods

*Material examined.* HOLOTYPE female deposited in National Museum of Natural History (Smithsonian Institution), Washington, D.C. under no. NMNH 00109761; collected by F. M. Bayer in Caroline Islands (North Pacific Ocean), Ifaluk Atoll, Sta. 638: from crevices in porolithon heads just inside *Heterocentrotus* zone on seaward margin, middle of Falarik (17 October 1953); associated copepod fauna, see Vervoort (1964: 6); stained in weakly alkaline solution of Chlorazol Black E; dissected and mounted in 'Berleze' fluid on 7 slides.

All drawings have been prepared using a camera lucida on a Leitz Dialux 20 interference microscope. The terminology is adopted from Lang (1948, 1965) except for (1) the terms *pars incisiva*, *pars molaris* and *lacinia mobilis*, which are omitted in the description of the mandibular gnathobase (Mielke, 1984), (2) the segmental composition of the mandible and maxilliped which are followed according to Boxshall (1985: 341-345). The setae of the caudal rami are named and numbered as proposed by Huys (1988 b). Abbreviations used in the text and figures are: A1, antennula; A2, antenna; P1-P6, first to sixth thoracopods; exp., exopod; enp., endopod; exp (enp)-1(-2, -3), to denote the proximal (middle, distal) segment of a ramus.

### Taxonomy

#### HARPACTICOIDA

#### Family DIOSACCIDAE G. O. Sars 1906

#### Genus *Pholenota* Vervoort 1964

*Diagnosis (amended).* Diosaccidae. Body cylindrical, with distinct separation between prosome and urosome. Rostrum large and long, defined at the base. Epimeral plates of thoracic somites 2 to 4 moderately developed, rounded. Genital and first abdominal somites fused to form a genital double-somite; fusion line marked dorsally and laterally by internal chitinous rib. Anal operculum weakly developed. Pseudoperculum absent. Caudal rami slightly longer than broad, with 7 setae (seta 1 well developed).

Antennule 8-segmented, slender; with pinnate setae on segments I-II and aesthetascs on segments IV and VIII. Antenna with basis; exopod 3-segmented, segments with 1, 1 and 3 setae; proximal endopod segment with abexopodal spine. Labrum simple, setulose. Mandible with biramous palp; basis with 3 inner setae; endopod unisegmented; exopod bi-segmented. Maxillula with fused protopodal segments; precoxal arthrite well developed; epipodite absent; basis with 2 endites; exopod with 2, endopod with 4 setae. Paragnaths separate, setulose. Maxillary syncoxa with 3 endites, middle endite with 2 setae; basis produced into claw-like endite; endopod 2-segmented. Maxilliped with 4 setae on syncoxa; basis bisetose; endopod unisegmented, with 1 claw and 3 setae.

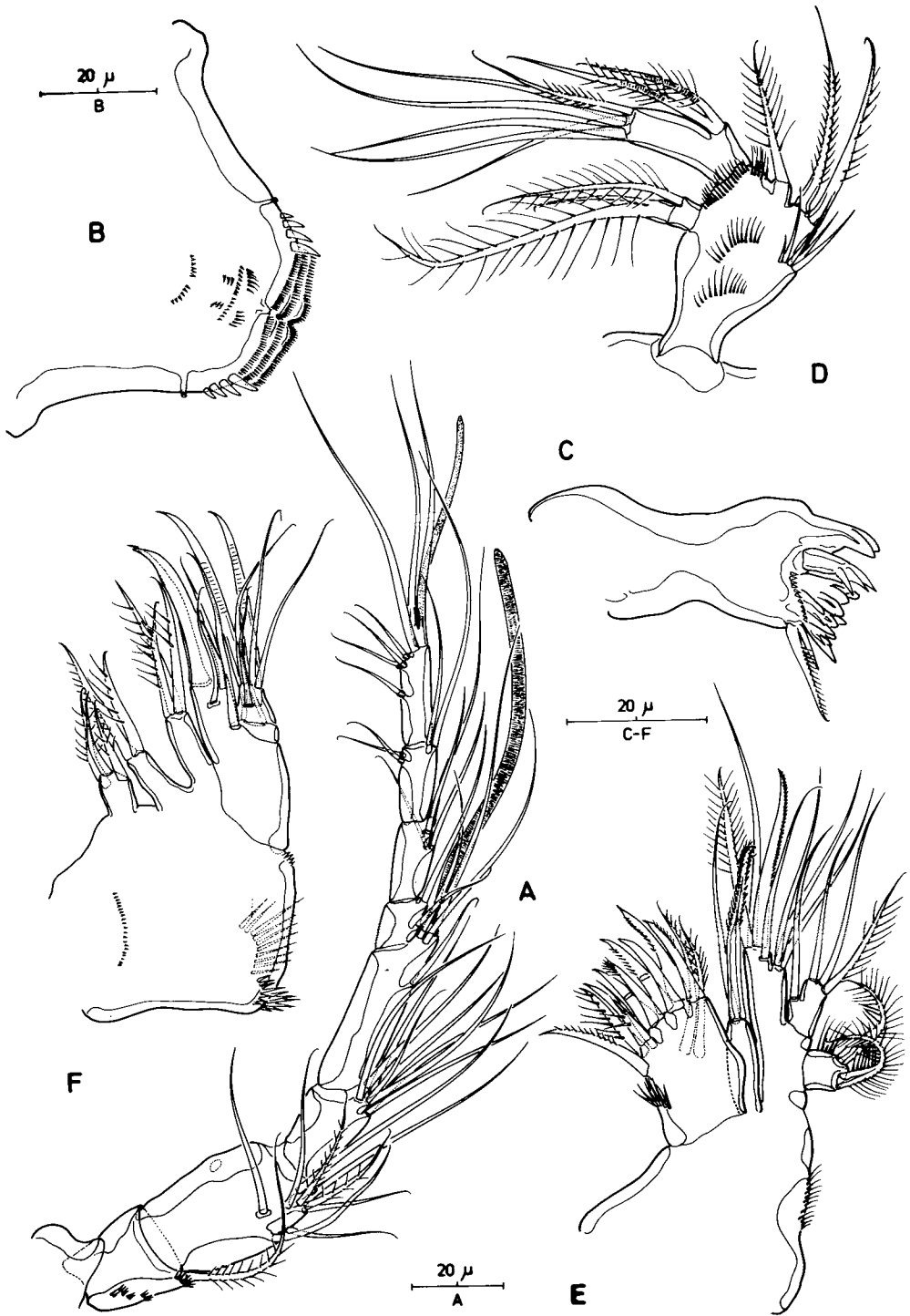


FIG. 1. *Pholenota spatulifera* Vervoort 1964 (female) (a) Antennule. (b) Labrum, anterior view. (c) Mandible, gnathobase. (d) Mandible, palp. (e) Maxillula. (f) Maxilla.

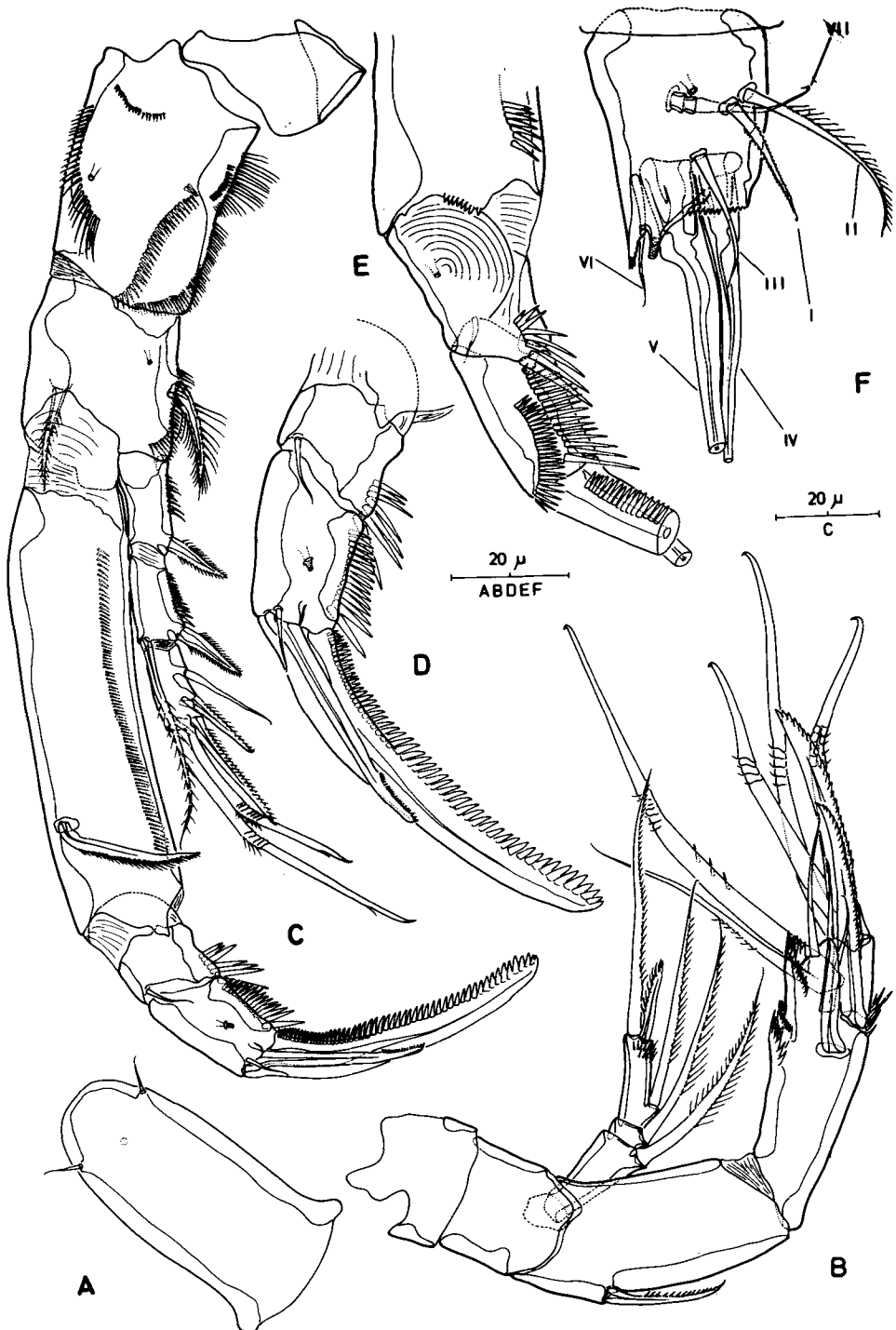


FIG. 2. *Pholenota spatulifera* Vervoort 1964 (female) (a) Rostrum. (b) Antenna. (c) Leg 1, posterior view. (d) Leg 1, posterior view of enp-1 and enp-2. (e) Same, anterior view. (f) Caudal ramus, lateroventral view.

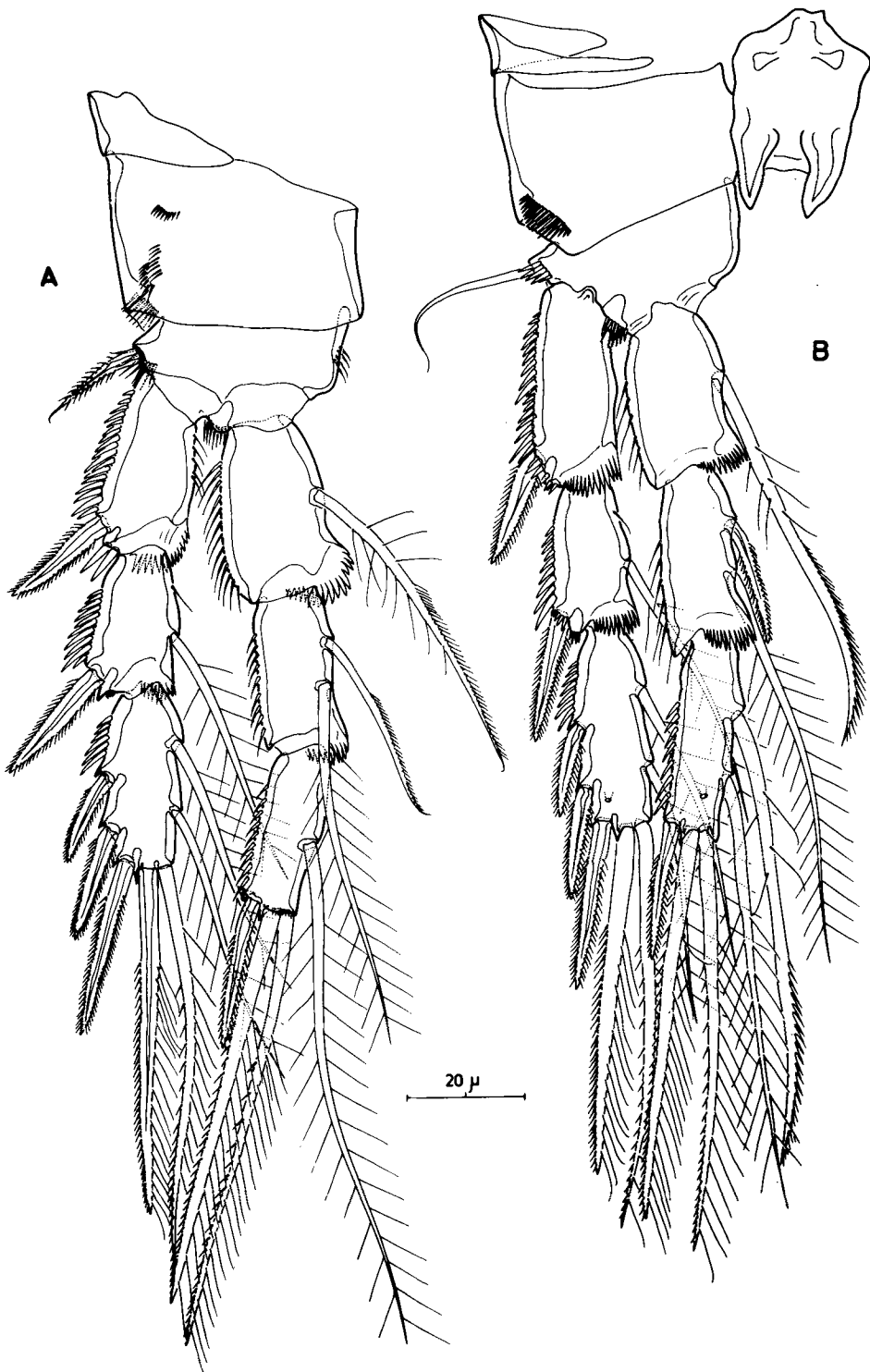


Fig. 3. *Pholenota spatulifera* Vervoort 1964 (female) (a) P2, posterior view. (b) P3, anterior view.

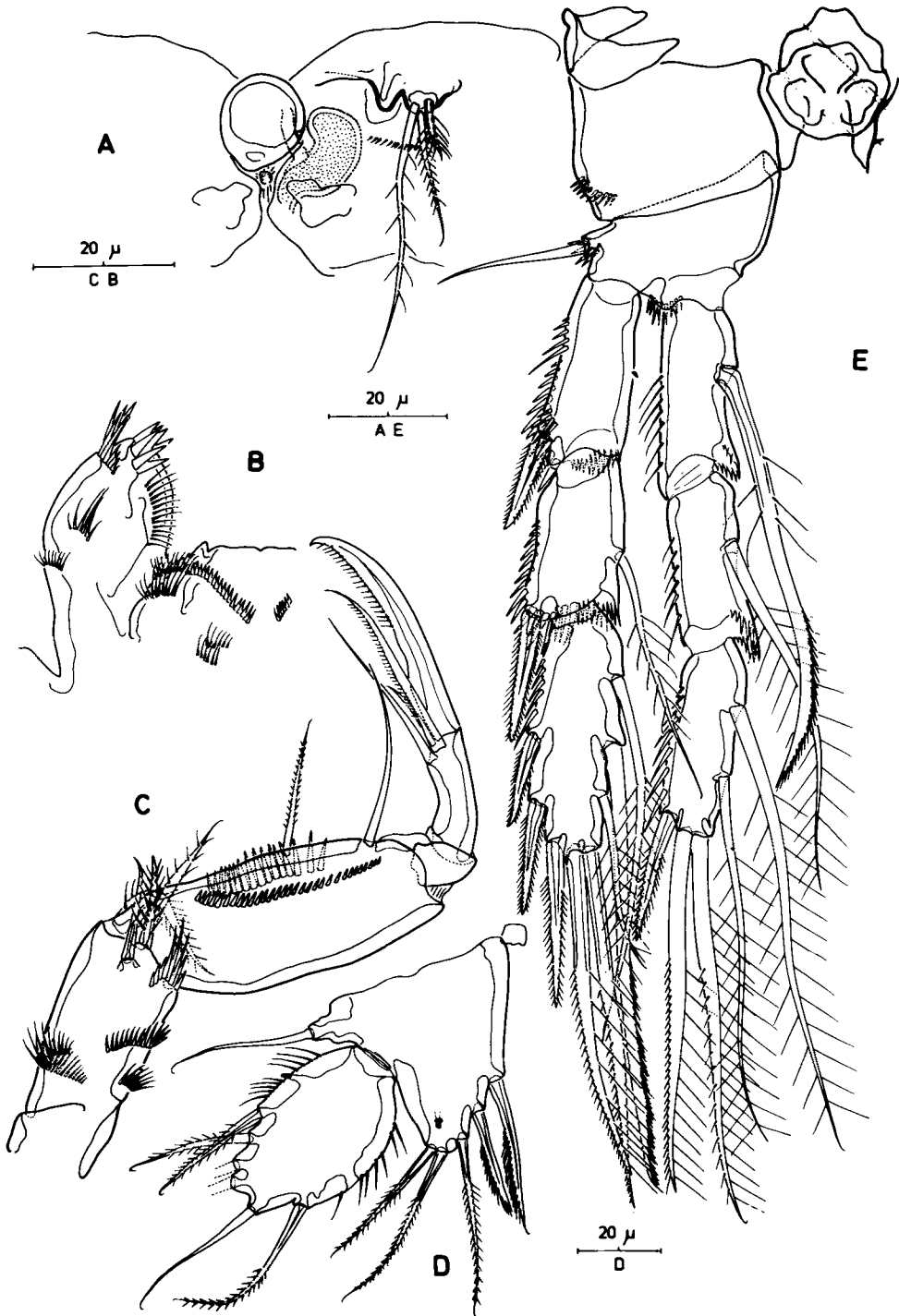


FIG. 4. *Pholenota spatulifera* Vervoort 1964 (female) (a) Left half of genital complex. (b) Left paragnath, anterior view. (c) Maxilliped. (d) P5, anterior view. (e) P4, posterior view.

P1 to P4 with 3-segmented protopods and rami. Leg 1 prehensile; coxa and basis distally produced; exopod with inner seta on middle segment and 5 elements on distal segment; enp-1 elongated, robust, with subdistal inner seta; enp-2 with 1 setule; enp-3 with 1 setule, 1 small and 1 large pectinate claw. Exp-1 P2–P4 without inner seta. Fifth pair of legs not fused; rami separate; exopod with 6 setae; endopodal lobe with 5 setae. Genital complex with separate gonopores covered by vestigial P6 bearing 3 setae; seminal receptacles paired; copulatory pore small, covered by large epicopulatory bulb.

Male unknown.

*Type and only species. Pholenota spatulifera* Vervoort 1964 (by monotypy).

### ***Pholenota spatulifera* Vervoort 1964**

*Redescription* Based on dissected holotype.

*Female* (Figs 1–4).

Total body-length 480  $\mu\text{m}$ , measured from the anterior tip of the cephalothorax to the posterior margin of the caudal rami (Vervoort, 1964). Hind margin of abdominal somites with spinules.

Rostrum (Fig. (a)) large, recurved and rounded anteriorly; defined at base; with 2 lateral sensillae.

Antennule (Fig. 1 (a)) slender, 8-segmented; borne on a small sclerotized pedestal; segment I with several tiny spinules; segment IV longest. Setal ornamentation: I-[1 pinnate]; II-[7 + 2 pinnate]; III-8, IV-[3 + (1 + 1 aesthetasc)]; V-2, VI-4, VII-4, VIII-[5 + (2 + 1 aesthetasc)].

Antenna (Fig. 2 (b)). Coxa unornamented. Basis and proximal endopod segment separate. Exopod 3-segmented; middle segment small; segments with 1 seta, 1 seta, and 2 setae plus 1 spiniform seta. Endopod 2-segmented; segment 1 with abexopodal spine; segment II with 2 curved spines and 2 basally fused setae on abexopodal face, with 1 spine, geniculate setae and 2 simple setae around anterior margin.

Labrum (Fig. 1 (b)) well developed; anterior margin with 2 secretory pores and coarse spinules laterally, and with fine spinular rows medially.

Mandible (Figs 1 (c), (d)) with strong gnathobase bearing several multicuspidate teeth and 1 pinnate seta. Palp biramous; basis large, with 3 inner setae and several spinular rows. Exopod small, first segment with 1 seta, second segment fused with 2 apical setae. Endopod unisegmented; with 2 (basally fused) lateral and 6 apical setae.

Paragnaths (Fig. 4 (b)) well developed bilobate processes; outer lobe large, with coarse spinules apically and fine spinules along both lateral margins.

Maxillule (Fig. 1 (e)) without boundaries between protopodal segments. Precoxal arthrite strong, with 2 setae on anterior surface, and 10 spines/setae around the distal margin. Epipodite absent. Coxal endite with 1 seta and 1 bipinnate spine. Basal endites closely set; proximal endite with 3 setae, distal endite with 2 setae, 1 claw and 1 bipinnate spiniform seta. Endopod with 1 lateral and 3 apical setae. Exopod bisetose, setae plumose and stout.

Maxilla (Fig. 1 (f)). Syncoxa with 2 spinular rows along the outer margin and 3 subcylindrical endites at the inner margin; proximal and distal endites with 3 spines, middle endite with 2 spines. Basis produced into claw-like endite bearing 3 setae and 1 claw. Endopod bi-segmented; segment I with 1 geniculate claw; segment II with 4 setae and 1 geniculate claw.



Maxilliped (Fig. 4(c)) with long syncoxa bearing 4 spinular rows and 4 bipinnate setae. Basis large, posterior and anterior surface with 1 seta and 1 spinular row each. Endopod unisegmented, but some arthrodistal sclerites are discernible at the base; with 2 setae, 1 small and 1 strong pinnate claw.

P1 to P4 with well developed precoxae and 3-segmented rami.

P1 (Figs 2(c), (d), (e)) with distally produced coxa and basis; coxa with several spinular rows; basis with outer spine, and inner seta standing on anterior surface. Exp-1 with outer pinnate spine; exp-2 with outer pinnate spine and inner plumose seta; exp-3 with 1 bare seta and 2 pinnate spines along outer margin and 2 geniculate setae distally. Endopod large, prehensile; articulation with basis surrounded with flexible membrane; enp-1 much longer than exopod, with inner seta near subdistal corner; enp-2 with pivot-joint proximally and inner setule; enp-3 with coarse spinules and bearing 3 elements: 1 setule, 1 distally pectinate claw and 1 robust claw, provided with stout spinules along the inner margin.

P2 to P4 (3(a), (b), 4(e)) without inner seta on exp-1. Intercoxal sclerite with 2 distal processes (Fig. 3(b)). Basis with outer bipinnate spine (P2) or smooth seta (P3–P4). Spine- and seta formulae as follows:

	Exopod	Endopod
P2	0.1.223	1.2.121
P3	0.1.223	1.2.221
P4	0.1.323	1.1.221

Fifth pair of legs (Fig. 4(d)) not fused medially; vestige of intercoxal sclerite discernible. Rami separate. Baseoendopod with smooth outer setae on small protuberance; endopodal lobe moderately produced, with 3 bipinnate setae and 2 uniserrate spines. Exopod oval, slightly damaged in the present material but the scars indicate that the armature consists of 6 setae.

Genital double-somite resulting from fusion of genital and first abdominal somites; original segmentation marked by internal chitinous rib both laterally and dorsally, and by slight swelling on either lateral side. Genital complex (Fig. 4(a)) with small copulatory pore located in median depression and partly covered anteriorly by large epicopulatory bulb (interpreted as 'heavily encased egg' in the original description). Seminal receptacles paired but small. Genital pores separate, covered by vestigial P6 armed with 3 pinnate elements increasing in length adaxially.

Caudal ramus (Fig. 2(f)) slightly longer than wide, with 7 setae; seta I well developed, bipinnate; setae IV and V longest, with irregularly swollen base; dorsal seta (VII) tri-articulated at base; a tube-pore is discernible at the inner distal corner.

*Male.* Unknown.

## Discussion

The present redescription provides a plethora of evidence for the removal of the genus *Pholenota* from the superfamily Laophontoidea in general and from the Laophontidae in particular where it is currently placed as *incertae sedis*. The condition exhibited in the cephalosomic appendages of *P. spatulifera* is generally more primitive in terms of segmentation and setation than in the Laophontoidea. The antennary basis is completely separate and bears a 3-segmented exopod in *P. spatulifera* whereas in the

Laophontidae and related families the basis is always fused with the proximal endopod segment to form an allobasis and the exopod is at most unisegmented and quadrisetose. The mandibular palp also shows a richer setation on the basis (at most 2 setae in Laophontoidea; compare *Esola bulligera* (Farran)), the exopod (maximum 1 seta) and the endopod (at most 4 setae; compare *Laophontopsis borealis* Huys and Willems). The well developed, trisetose, precoxal endite found on the maxillary syncoxa of *Pholenota* is always vestigial in the Laophontoidea. The maxilliped differs in all aspects from the laophontoidean condition. The syncoxa bears 4 setae instead of at most 2 (for example some Laophontidae; *Infrapedia coralliophila* (Fiers)), the basis is bisetose whereas in the Laophontoidea the basis lacks setae, and the endopod is provided with 4 armature elements of which 3 are well developed. The latter segment usually shows a claw and at most 2 vestigial elements in the Laophontoidea.

The prehensile P1 is only superficially reminiscent of the Laophontidae. Similarities are, however, found in the distally produced coxa and basis, and in the migration of the inner seta to the anterior surface of the basis. None of the Laophontidae (and Laophontoidea) however, have a 3-segmented endopod, an inner seta on the middle exopod segment and 5 armature elements on the distal exopod segment. *P. spatulifera* differs also in the presence of 3 armature elements on the distal endopod segment, whereas 2 elements are a diagnostic feature for the superfamily Laophontoidea. The other legs also differ considerably from the laophontoidean design, in possessing 3-segmented endopods (instead of at most 2-segmented ones) and in having 3 inner setae (instead of 2) on the distal exopod segment of P4. The presence of an epicopulatory bulb in the female genital complex has never been demonstrated for any of the Laophontidae nor for that matter any of its relatives. All these differentiating characters make a direct relationship with the superfamily Laophontoidea very unlikely. The discovery of the male might provide further differences in the sexual dimorphism of endopod P3 and in the setation and arrangement of the sixth pair of legs since these characters are diagnostic apomorphies for the Laophontoidea as a whole (Huys, in press c).

The reason why Vervoort (1964) nevertheless provisionally allocated *P. spatulifera* to the Laophontidae might be searched for in the broad familial diagnosis of the Laophontidae presented by Lang (1948) in his monograph. Lang's idea of dividing the family into three subfamilies was tenable at that time, but the subsequent discovery of transitional genera such as *Pholenota* and *Apolethon* Wells led some authors to suggest that '...it is best to consider the family a heterogeneous assemblage of genera with certain common features which serve to distinguish them from other harpacticoid families' (Wells, 1967). The recent removal of the Donsiellinae to the Thalestridae (Hicks, 1988) and the upgrading to family status of the Normanellinae (Huys and Willems, 1989) has narrowed extensively the definition of the Laophontidae. However, for various reasons it is impossible to allocate *Pholenota* either to the Donsiellinae or to the Normanellidae without grossly expanding the respective diagnoses. Conversely, despite the absence of the male, there are many more characteristics pointing to a diosaccid affinity, an alternative idea already expressed by Vervoort (1964).

The shape of the rostrum, the 8-segmented antennule, the antenna with 3-segmented exopod and 1 seta on the proximal endopod segment, the design of the mandible, the bisetose exopod on the maxillula, the 3-2-3 setation of the endites on the maxillary syncoxa and the setation of the maxilliped leave no doubt that *P. spatulifera* is a genuine diosaccid. This is corroborated by the structure of the female genital complex with separate gonopores and the small copulatory pore partly concealed underneath a large epicopulatory bulb. The presence of 3 inner setae on the distal

exopod segment of P4 is a primitive character, but very common amongst Diosaccidae. The structure of leg 1 is not found in any of the other genera of the family, however it can easily be derived from the type found in for instance *Amphiascus* G. O. Sars through elongation of the coxa and basis, and through extensive development of enp-1 and of the distal claw. The exopodal setation on the first leg in *P. spatulifera* is the most primitive found in the Diosaccidae: exp-2 with inner seta, exp-3 with 5 setae/spines. As to the relationships the discussion is therefore restricted to the general showing the same configuration: *Robertsonia* Brady, *Amphiascus*, *Amphiascopsis* Gurney, *Dactylopodamphiascopsis* Lang, *Amonardia* Lang, *Pseudamphiascopsis* Lang, *Metamphiascopsis* Lang, *Paramphiascopsis* Lang, *Bulbamphiascus* Lang, *Typhlamphiascus* Lang, *Rhyncholagena* Lang, *Pararobertsonia* Lang and *Cladorostrata* Shen and Tai.

Except for *Cladorostrata*, all other genera also have the same endopodal segmentation and setation, i.e. 3-segmented with 1, 1 and 3 armature elements, respectively. Species of *Cladorostrata* can be readily distinguished from *P. spatulifera* by the presence of a bifid, anteriorly directed plate underneath the rostrum and arising from the anterior face of the labrum (Shen and Tai, 1963). Other differences include the short antennules, the unisegmented antennary exopod and the modified maxilliped.

Both *Robertsonia* and *Pararobertsonia* differ from *Pholenota* in the presence of numerous pinnate spines and setae on virtually all antennular segments. Representatives of *Robertsonia* are unique within the Diosaccidae in having the proximal aesthetasc located on the third segment instead of the fourth (compare for example Hamond, 1973 b). They can also be differentiated from *P. spatulifera* by the antennary allobasis and the loss of the seta on exp-2 of this limb. These features are also found in *Pararobertsonia*, but this genus shows a remarkable sexual dimorphism on the mandibular endopod.

The genus *Rhyncholagena* differs primarily in the presence of the 'bottle-shaped' rostrum and in the conspicuous surface ornamentation of most of the body somites. The monotypic *Dactylopodamphiascopsis* is readily identifiable by the very elongate exopod of the P1 and the foliaceous rami of the P5.

*Bulbamphiascus* and *Typhlamphiascus* are reminiscent of *Pholenota* in the presence of only 5 setae/spines (4 in *T. unisetosus* Lang) on the distal endopod segment of P3, but both genera have a different seta formula on the antennary exopod and possess an inner seta on the proximal exopod segment of P2 to P4. A detailed discussion of the respective relationships of *Amphiascopsis*, *Metamphiascopsis* and *Amonardia* requires knowledge of the male morphology (Lang, 1965: 226), however, these genera are easily distinguishable from *Pholenota* on the basis of the middle exopod segment of leg 1 which is distinctly elongated.

Comparison of the remaining genera reveals that *Pholenota* might have closest affinities with the genus *Amphiascus*, particularly with the *minutus*-group. Lang (1948) established four species complexes (*minutus*-, *varians*-, *amblyops*-) on the basis of setation patterns on the antennary exopod and the swimming legs. The value of this system has frequently been criticized during revisory work or when new species were added (Wells, 1968; Hicks, 1989). Lang (1965) recognised the gross difficulties in adequately defining specific boundaries within the *minutus*-group, however, it can nonetheless be said that this species complex displays characters not found in any of the other groups nor in any of the closely related genera. They have for instance two inner setae on the middle exopod segment of P2 and P3. This formula is also found in *P. spatulifera* and the close resemblance is found in nearly every detail of the cephalosomic

appendages (compare setation antennary exopod; maxillipedal syncoxa with 4 setae; exopodal armature of mandibular palp). The armature of exp-3 of P1, consisting of a naked seta, 2 bipinnate spines and 2 geniculate setae in *P. spatulifera*, is shared with for example *Amphiascus tenuiremis* (Brady and Robertson) (compare Lang's description (1965) of *A. minutus* (Claus) sp. 1).

The transfer of *P. spatulifera* to the Diosaccidae is well grounded. The genus can be considered as being a specialized member of the *Amphiascus*-related group of genera. If the hypotheses of a close relationship with the *A. minutus*-group can be substantiated with further evidence, the current taxonomic concept of the genus *Amphiascus* would no longer be tenable. The polyphyletic nature of the genus is also indicated in other species complexes. For instance, the male of *A. undosus* Lang, currently belonging to the *pacificus*-group, has the outer distal corner of exp-2 P2 produced into a curved hook-like structure; this character is also found in some species of *Paramphiascopsis* (Hicks, 1986).

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