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First record of *Phyllognathopus bassoti* Rouch, 1972 from India, with remarks on the family Phyllognathopodidae Gurney, 1932 (Crustacea, Copepoda, Harpacticoida)

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Phyllognathopus bassoti Rouch, 1972, originally described from Long Island, Papua New Guinea, and later reported from the Philippines, is found for the first time in India. This subterranean species is redescribed and its ecology and zoogeography are discussed. Also, the systematics of the family Phyllognathopodidae is discussed and a key to genera and species is given. As a result of the taxonomic analysis, three species are here synonymized: *Phyllognathopus insularis* Chappuis, 1940 and P. *camptoides* Bozic, 1965 with *P. chappuisi* Delachaux, 1924; and *P. volcanicus* Barclay, 1969 with *P. viguieri* (Maupas, 1892). It has been observed that odonate nymphs prey on adults and copepodids of *P. bassoti*, an interaction not known until now.

Keywords: copepods, harpacticoids, taxonomy, groundwater, family key.

Introduction

Phyllognathopodidae Gurney, 1932 represent an early, relatively unsuccessful, attempt to colonize freshwater (Huys & Boxshall 1991). It is a primitive family (Lang 1948, Borutzky 1952, Dussart 1967) and, as such, important for understanding the phylogeny and evolution of harpacticoid copepods. Unfortunately its systematics is confused (Lehman & Reid 1992, Bruno & Cottarelli 1999). Until now, only three genera have been described: *Phyllognathopus* Mrazek, 1893 (syn. *Viguierella* Perrier, 1893), *Allophyllognathopus* Kiefer, 1967 and *Parbatocamptus* Dumont & Maas, 1988. Both *Allophyllognathopus* and *Parbatocamptus* are known from a single male (Kiefer 1967, Dumont & Maas 1988), which alone can lead to systematic confusion.

However, the main cause of the confusion in the family Phyllognathopodidae is the incredible variability, wide distribution and eurotopicity of the type species of *Phyllognathopus*, *P. viguieri* (Maupas, 1892). Although great variability is well known in some freshwater harpacticoid copepods (see Ishida 1994, Karanovic 1999), it is not often combined with the other two factors, at least not as much as in cyclopoid copepods. Perhaps the best illustration of the remarkable eurotopicity of this species is given by Yeatman (1983), who found it in Fiji, Tonga and Western Samoa in «tree holes, taro leaf axils, old auto tires, tin cups, plastic containers, bamboo, old boats and ground pools». The wide distribution of *P. viguieri* (possibly cosmopolitan, although not reported from Australia) is probably due, *inter alia*, to human activities, as suggested by its occurrence in botanical gardens and greenhouses. Even Lowndes (1931) stated that he had obtained specimens from pineapples bought from food stores, by adding water to the leaf axils and examining this water after a few weeks. Because of its great variability, often in the same population in a microhabitat, Lang (1948) synonymized all previously known forms, varieties, subspecies and species with *P. viguieri*. In contrast, Bozic (1966) showed that the hybridization did not take place between one species from Africa

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(*Phyllognathopus camptoides* Bozic, 1965), and one French population of *P. viguieri*, which he assigned as *Phyllognathopus coecus* nom. nov. He claimed to recognize different species in the *P. viguieri*-complex, but provided neither a key for their identification nor a taxonomically correct list. A species list was provided by Dussart & Defaye (1990), who mistakenly included two species described by Por (1964) in the genus *Phyllopodopsyllus* T. Scott, 1906 (family Tetragonicipitidae Lang, 1944), adding to the confusion.

Bozic's (1966) hybridization experiments encouraged other copepodologists to examine material of Phyllognathopodidae carefully and to consider the possibility of more than one species in the genus *Phyllognathopus*. Thus, Rouch (1972) described *P. bassoti* from the interstitial of Lake Wisdom on Long Island, Papua New Guinea. Bruno & Cottarelli (1999) found the same species in the Philippines, providing data about its variability and ecology. During an investigation of the copepod fauna from groundwaters of the Indian subcontinent, we have found *P. bassoti* for the third time. Because of differences with the original description by Rouch (1972) and the redescription by Bruno & Cottarelli (1990), as well as the zoogeographical importance of this finding, we redecribe it once again. In addition to a detailed redescription of *P. bassoti* and comments on its distribution and ecology, we provide an overview of the systematics in the family Phyllognathopodidae.

Material and methods

We sampled a domestic freshwater bore-well (Kandukur) and an overhead water reservoir, filled from a similar well (Guntur). The material was preserved by 10% formaldehyde, and later separated with a dissecting microscope and moved to 70% ethanol. Specimens were dissected in Faure's medium, prepared following the procedure of Stock & Vaupel Klein (1996). Dissected appendages were covered with a coverslip. For the urosome or the whole animal, two human hairs were mounted between the slide and coverslip, so the parts could not be compressed. By moving the coverslip carefully by hand, the whole animal or a particular appendage could be positioned, making possible the observation of morphological details. During the examination water slowly evaporated, and appendages or whole animals eventually remained in completely dry Faure's medium. All drawings were prepared using a drawing attachment on a Leica-DMLS brighfield compound microscope, with C-PLAN achromatic objectives. Specimens, which were not drawn, were examined in a mixture of equal parts of distilled water and glycerol. Morphological terminology follows Huys & Boxshall (1991), except for the swimming legs armature formula, where a simplified version is used. The material is deposited in the Western Australian Museum, Perth (prefix WAM), and in the Natural History Museum, London (prefix NHM).

Results

Family Phyllognathopodidae Gurney, 1932

Genus *Phyllognathopus* Mrazek, 1893

Phyllognathopus bassoti ROUCH, 1972

Figures 1-25

Material Examined

India, Andhra Pradesh, town of Kandukur (about 15 km inland from the Bay of Bengal), domestic freshwater bore-well, 20 November 1998, leg. Y. Ranga Reddy, 15°15'N 79°47'E: 1 male + 2 females (each specimen dissected on 1 slide; females: WAM C28610 & C28611, male WAM C28612).

India, Andhra Pradesh, town of Guntur, Brindavan Gardens, domestic water reservoir, 7 January 1999, leg. Y. Ranga Reddy, 16°18'N 80°29'E: 6 males and 4 females (2 males, WAM C28613 & C28614, and 2 females, WAM C28615 & C28616, dissected on 1 slide each; others in alcohol, WAM C28617) + 10 males and 11 females, all in alcohol, in the NMH, London.

India, Andhra Pradesh, town of Guntur, Brindavan Gardens, domestic water reservoir, 25 June 1999, leg. Y. Ranga Reddy, 16°18'N 80°29'E: 13 males and 15 females, all in alcohol, in junior author's private collection, Nagarjunanagar.

India, Andhra Pradesh, town of Guntur, Brindavan Gardens, domestic water reservoir, 16 April 2000, leg. Y. Ranga Reddy, 16°18'N 80°29'E: 8 males and 10 females, all in alcohol, in the junior author private collection.

Redescription

Female. Preserved specimens colourless; nauplius eye not visible. Habitus (Figs 1 & 2) cylindrical and slender, without demarcation between prosome and urosome; prosome/urosome ratio 0.86; greatest width at first urosomal (fifth pedigerous) somite, but hard to locate. Body length/width ratio about 4.7; cephalothorax just slightly wider than genital double-somite. All free pedigerous somites (first one not fused with cephalothorax), without expansions laterally or dorsally.

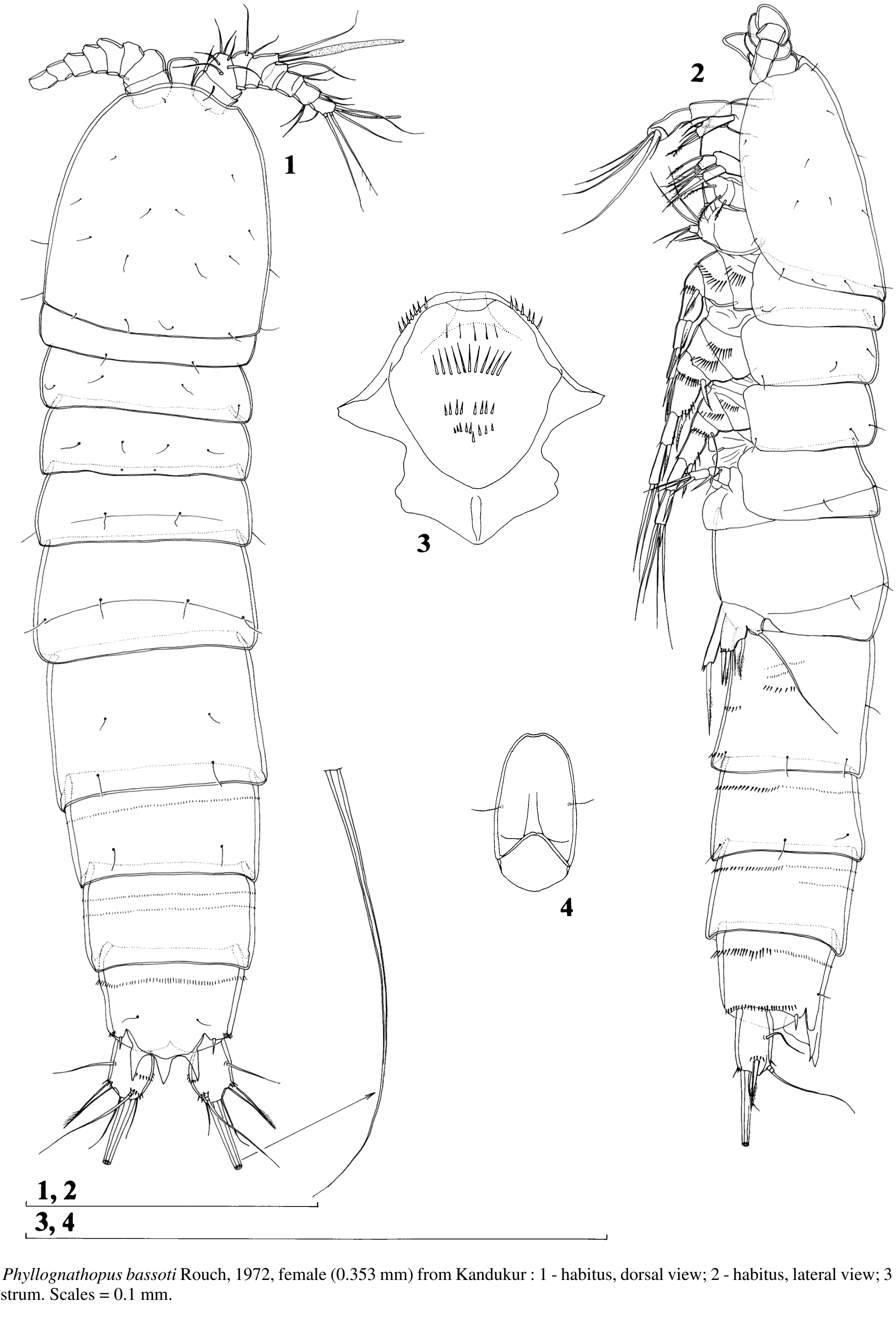

Fig. 1-4 *Phyllognathopus bassoti* Rouch, 1972, female (0.353 mm) from Kandukur : 1 - habitus, dorsal view; 2 - habitus, lateral view; 3 - labrum; 4 - rostrum. Scales = 0.1 mm.

Integument not strongly chitinized, smooth and without integumental windows. Rostrum (Fig. 4) well developed, unornamented, linguiform, reaching middle of second antennular segment, with slightly concave anterior tip, about 1.9 times as long as wide and demarcated at base. Cephalothorax about 1.2 times as long as wide; represents 24% of total body length. Surface of dorsal shield covering cephalothorax ornameted with few large sensillae, as well as tergites of pedigerous somites. Hyaline fringes of all somites narrow and smooth. Genital double-somite (Fig. 5) about 0.8 times as long as wide (ventral view), without any trace of subdivision, ornamented with 2 dorsal sensillae at middle and 6 posterior sensillae (2 dorsal, 2 ventral and 2 lateral), as well as with several short rows of small spinules (2 at midlength, ventrally; 1 near posterior margin, also ventrally; and 3 on each side at anterior part, ventrolaterally) . Single small copulatory pore situated just beyond midlength of double-somite; copulatory duct long and narrow, «T»-shaped, with small and ovoid seminal receptacle on each side (Fig. 5); genital apertures not visible nor any trace of sixth legs. Third urosomal somite ornamented with row of spinules at anterior part (which shortly interrupted ventrally and also dorsal spinules much smaller than ventral ones), as well as with 6 large posterior sensillae (2 dorsal, 2 ventral, and 2 lateral). Preanal somite with similar row of spinules and with additional one dorsally (both at anterior part), but without any sensillae. Anal somite (Figs 5 & 7) ornamented with row of spinules anteriorly (similar to preceding 2 somites), with pair of large dorsal sensillae, and also with short row of spinules on posterior margin (2 next to anal operculum strongest). Anal operculum (Fig. 7) convex, slightly reaching beyond posterior margin of anal somite, representing 62% of somite's width and terminating in 3 strong spine-like processes, which reach beyond middle of caudal rami. Anal sinus smooth.

Caudal rami (Figs 1, 2, 5 & 7) relatively short, cylindrical, divergent, with space between them about 1 ramus wide, about 1.5 times as long as greatest width (ventral view), and armed with 6 armature elements (2 lateral, 1 dorsal and 3 apical). Ornamentation of several small rows of minute spinules (at base of distal lateral and dorsal seta, at middle near inner margin dorsally, and near posterior margin ventrally). Dorsal seta relatively long, inserted close to inner posterior corner at about 5/6 of ramus length, about twice as long as caudal ramus, biarticulate at base and smooth. Proximal lateral seta thin and smooth, inserted at midlength of ramus slightly dorsolaterally, about as long as ramus. Distal lateral seta about as long as proximal one, spiniform and unipinnate at distal end. Inner apical seta very small, smooth, about half as long as ramus (ventral view). Middle apical seta strongest, without breaking plane, smooth, and 0.4 times as long as body. Outer apical seta also without breaking plane and smooth, about 1.6 times as long as outer apical one.

Antennula (Fig. 6) 8-segmented, with single spinule on first segment, approximately reaching middle of cephalothorax, with broad aesthetasc on fourth segment (reaching beyond tip of appendage for length of last 2 segments), and more slender apical aesthetasc on eighth segment, fused basally to apical seta; setal formula: 1.8.2.2.1.2.4.6. All setae smooth and without breaking planes. Only 2 setae on second, 1 on third and 3 subapical setae on eighth segment articulating on basal part. Length ratio of antennular segments, from proximal end, 1 : 0.7 : 0.6 : 0.7 : 0.5 : 0.7 : 0.6 : 0.9.

Antenna (Fig. 8) short, composed of coxa, basis, 2-segmented endopod and 1-segmented exopod. Coxa very short, unornamented. Basis rectangular, about 0.7 times as long as wide, unarmed and ornamented with long spinules on distal inner corner. First endopodal segment subrectangular, about 1.5 times as long as wide, unarmed and unornamented. Second endopodal segment about 2.5 times as long as wide, ornamented with few large spinules along anterior surface and with row of large spinules along posterior surface and subdistally; lateral armature consisting of 2 unipinnate spines flaking small and smooth seta; apical armature consisting of 1 slender seta, 1 spine and 4 geniculate setae. Exopod banana-shaped, reaching beyond middle of second endopodal segment, about 3.8 times as long as wide, unornamented, armed with 3 lateral unipinnate and 2 apical bipinnate short setae; all setae of almost similar length.

Labrum (Fig. 3) large compared to cephalothorax, with trapezoidal free part, rigidly sclerotized, with short and almost straight cutting edge, ornamented with 4 parallel rows of spinules on ventral (anterior) surface and with 2 rows of spinules distally, 1 on each side of cutting edge . Gustatory papillae not visible on dorsal (posterior) surfce.

Mandibula (Figs 9 & 10) with broad cutting edge on elongated coxa, with 2 coarse teeth ventrally, 1 smooth seta dorsally, and several smaller teeth in between. Palp composed of basis, 1-segmented endopod and 1-segmented exopod. Basis large, about 1.8 times as long as wide, unarmed, ornamented with single spinule on ventral surface. Endopod about twice as long as wide, much smaller than basis, armed with 1 lateral unipinnate seta and 3 apical smooth ones. Exopod about same size as endopod, 2.8 times as long as wide, armed with 2 apical bipinnate setae; outer seta about 1.4 times as long as inner one.

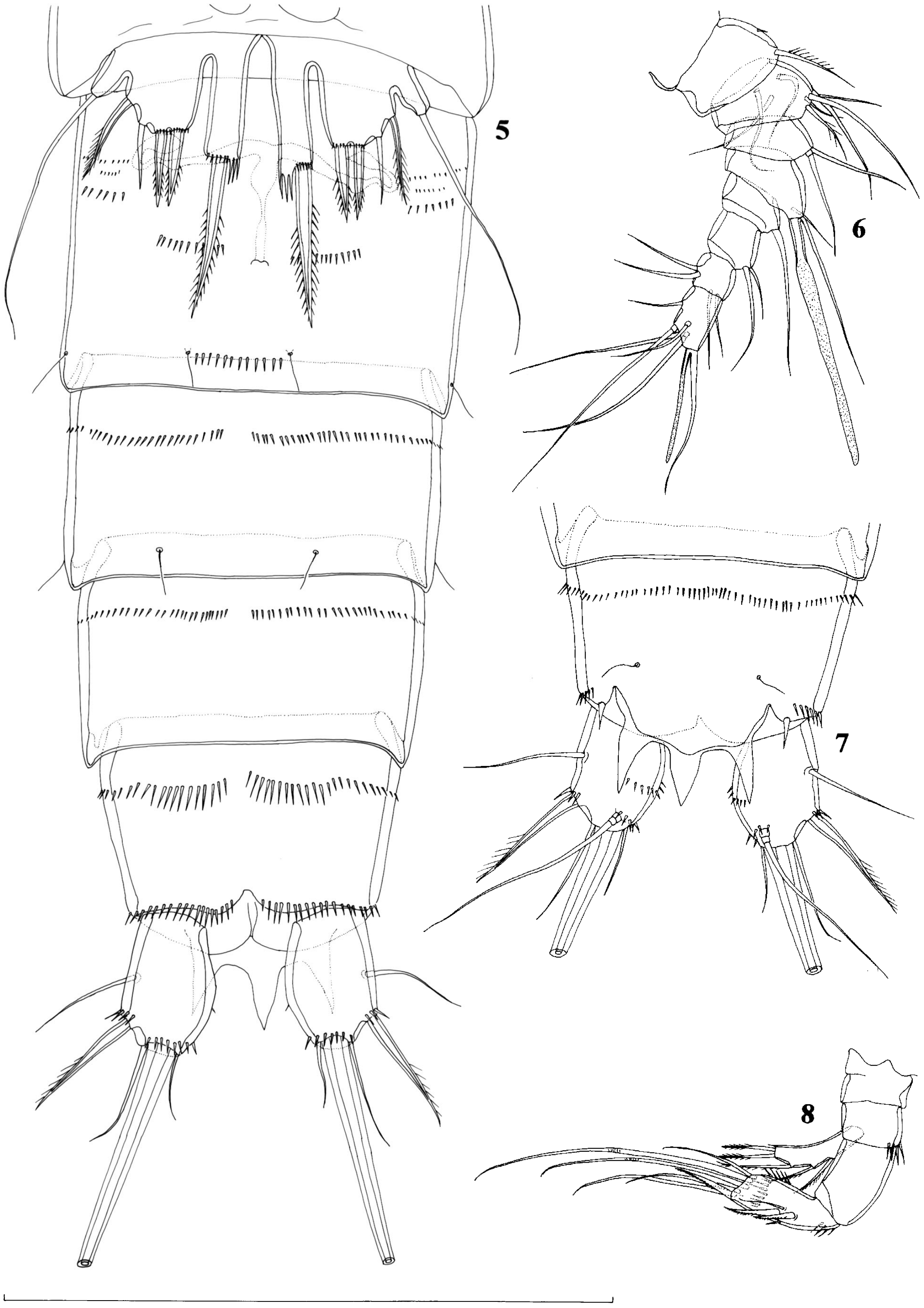

Fig. 5-8 *Phyllognathopus bassoti* Rouch, 1972, female (0.353 mm) from Kandukur : 5 - urosome, ventral view; 6 - antennula; 7 - anal somite and caudal rami, dorsal view; 8 - antenna. Scale = 0.1 mm.

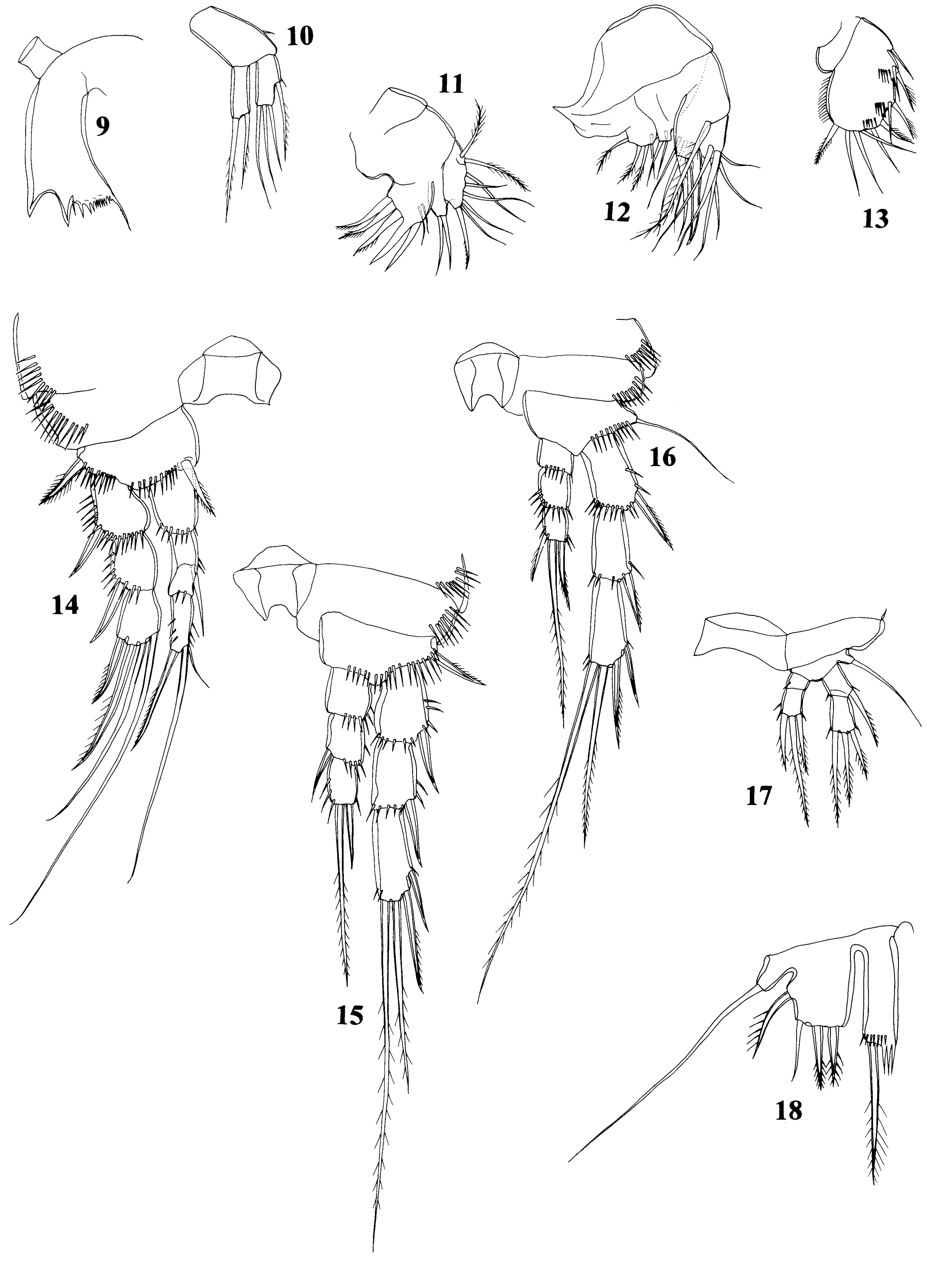

Fig. 9-18. *Phyllognathopus bassoti* Rouch, 1972; 9-17 female (0.353 mm) from Kandukur; 18, female (0.362 mm) from Guntur : 9 - coxa of mandibula; 10 - mandibular palp; 11 - maxillula; 12 - maxilla; 13 - maxilliped; 14 - first swimming leg; 15 - second swimming leg; 16 - third swimming leg; 17 - fourth swimming leg; 18 - fifth leg. Scale = 0.1 mm.

Maxillula (Fig. 11) with large praecoxa, arthrite of which rectangular, short, unornamented, and armed with 2 slender anterior surface seta and 5 apical strong elements (2 smooth and straight, 3 unipinnate and curved at distal end). Coxal endite armed with 2 smooth elements of about same length. Basis slightly shorter than coxal endite, armed with 3 apical elements (1 unipinnate and strong, 2 smooth and slender) and 5 lateral elements (3 smooth and 2 bipinnate); all armature elements on basis of similar length. Endopod and exopod reduced.

Maxilla (Fig. 12) with 2 endites on syncoxa; proximal one armed with 4 setae, distal with 2. Basis partly fused basally with syncoxa, drawn out into strong claw, with smooth and strong seta at base (of about same length as claw) and additional 3 slender and smooth setae situated more basally and 1 long bipinnate seta at base of endopod. Endopod represented by single but relatively large segment, armed with 6 smooth setae.

Maxilliped (Fig. 13) with unarmed, unornamented and short coxa. Basis and single endopodal segment fused forming allobasis, which elliptical, about 1.7 times as long as wide, ornamented with row of hairs along outer margin and with 3 short and parallel transverse rows of spinules near inner margin. Single smooth seta present on ex basal inner distal corner. Endopodal armature consists of 5 inner and 5 apical setae (outermost one relatively stout and spiniform); 3 inner setae unipinnate, outermost seta bipinnate; all other setae on maxilliped smooth.

First, second and third swimming legs with 3-segmented endopods and exopods (Figs 14, 15 & 16), fourth swimming leg with 2-segmented endopod and exopod (Fig. 17). Swimming legs armature formula as follows (legend: inner/outer spine or seta; inner/terminal/outer):

	Exopod			Endopod		
Segments	1	2	3	1	2	3
First leg	0/1	0/1	0/2/2	0/0	1/0	1/1/1
Second leg	0/1	0/1	0/2/2	0/0	1/0	0/2/0
Third leg	0/1	0/1	0/2/2	0/0	0/0	1/2/0
Fourth leg	0/1	0/2/1	-	0/0	1/2/0	-

Intercoxal sclerites of all swimming legs with concave distal margin, without any surface ornamentation. Praecoxa and coxa of first, second and third leg ornamented with arched row of large spinules near outer margin and unarmed; praecoxa and coxa of fourth leg both unarmed and unornamented. Basis ornamented with row of long spinules along posterior margin (except on fourth leg, which unornamented), armed with outer pinnate spine on first and second swimming legs, and with outer smooth long seta on third and fourth legs; basis of first leg with additional spine on inner distal corner, reaching 6/7 of first endopodal segment. Exopods and endopods of all swimming legs ornamented with spinules along outer and posterior margins (ornamentation again considerably reduced on fourth leg). Exopod and endopod of about same length on first and fourth leg, endopod of second leg as long as first 2 exopodal segments, while endopod of third swimming leg only reaching middle of second exopodal segment. All endopodal segments on 1 leg of similar size, as well as exopodal ones.

Fifth leg (Figs 5 & 18) with all segments fused to single cuticular plate, but with strongly produced endopodal end exopodal lobes, as well as with well developed basal setophore. Endopodal lobe cylindrical, slender, about 2.7 times as long as wide, with distal margin produced and serrated at inner part, ornamented with transverse row of spinules along distal margin and armed with single, strong and bipinnate, apical seta, which somewhat longer than than lobe itself. Exopodal lobe squarish, shorter than endopodal one, unornamented and armed with 4 armature elements of about same lenth; outer element spiniform and unipinnate, subapical one slender and smooth, while 2 apical elements spiniform and bipinnate distally. Basal setophore with very long, slender and smooth, outer basal seta, which about 1.8 times as long as seta on endopodal lobe.

Sixth legs absent.

Male. Habitus, colour, ornamentation of prosomal somites, rostrum, dorsal ornamentation of urosomal somites, anal operculum and caudal rami (Fig. 19) similar to female. Genital somite free, without spinules (except those on sixth leg), as well as succeeding somite. Fourth urosomal somite with characteristic ventral row of large spinules (Fig. 19). Preanal and anal somites without spinules ventrally on anterior part; anal somite with row of spinules along posterior margin ventrally and dorsally. Single spermatophore (Fig. 21) visible inside genital somite and positioned longitudinally.

Antennula (Fig. 20) not strongly geniculate, also 8-segmented, but seventh and eighth segments partly fused. Armature similar to female, except for 1 seta less on sixth segment and 2 setae more on third and fourth segments.

Antenna, labrum, mandibula, maxillula, maxilla, maxilliped and swimming legs similar to female.

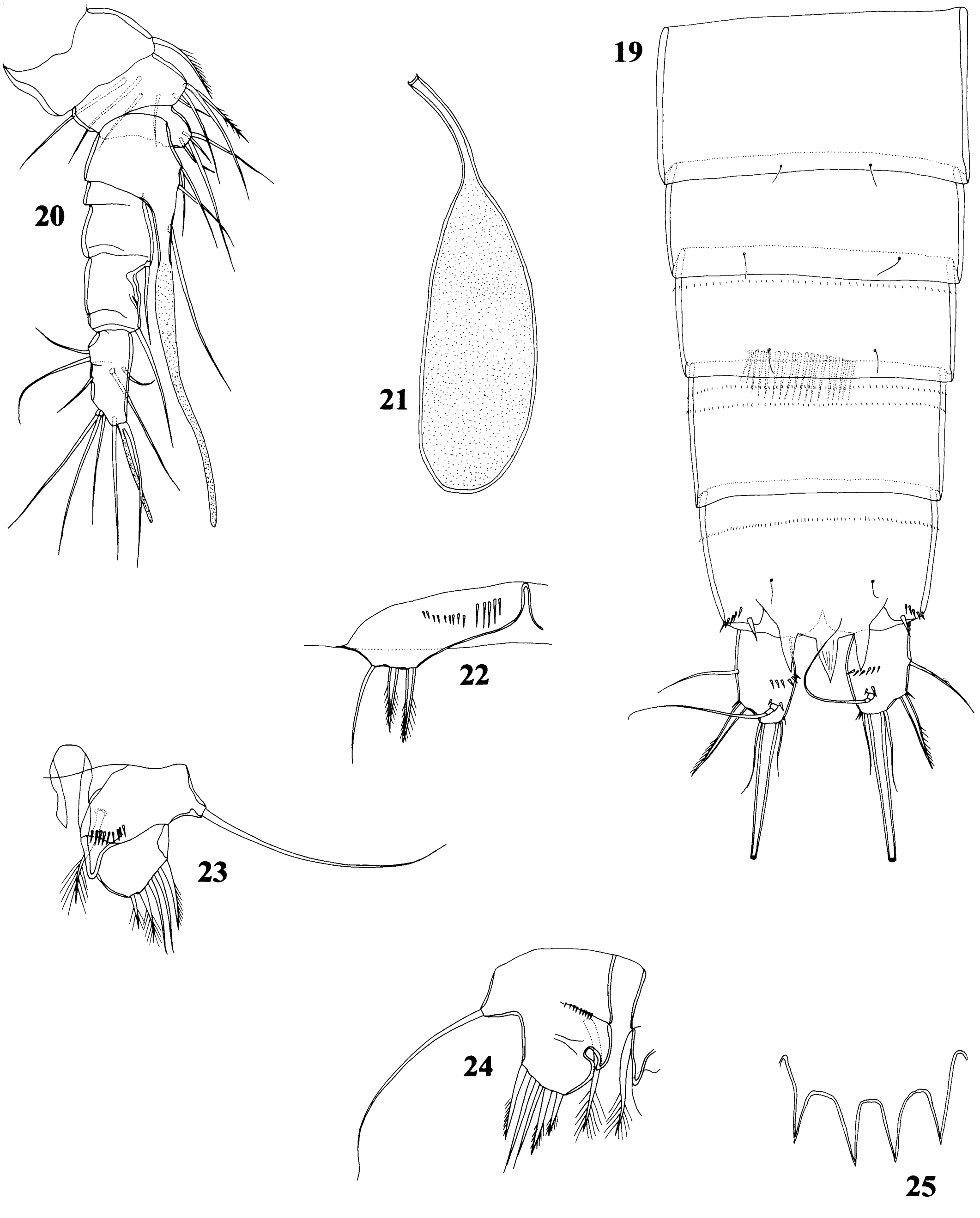

Fig. 19-25 *Phyllognathopus bassoti* Rouch, 1972; 19-22 & 24, male (0.3 mm) from Kandukur. 23, male (0.362 mm) from Guntur; 25, male (0.381 mm) from Guntur: 19 - abdomen, dorsal view; 20 - antennula; 21 - spermatophore; 22 - sixth leg; 23 - fifth leg; 24 - fifth leg; 25 - anal operculum. Scales 0.1 mm.

Fifth leg (Figs 23 & 24) with endopodal lobe reduced and characteristically modified, exopod partly fused to large basis. Exopod similar to female, but less quadrate and with additional smooth seta subapically. Endopodal lobe rigidly sclerotized, produced distally like spiniform process, not reaching middle of exopod, with its single seta located on posterior surface and proximally. Basis ornamented with transverse row of spinules on anterior surface, at base of endopodal lobe.

Sixth leg (Fig. 22) distinct, broad and short, simple cuticular plate, ornamented with transverse row of spinules and armed with 3 elements: innermost bipinnate spine, middle similar, but somewhat shorter, spine and outermost smooth seta, which about 1.5 times as long as middle spine and 1.3 times as long as innermost spine.

Variability

Body lengths from 0.342 mm to 0.423 mm (0.377 mm average; n=6) in females, and from 0.3 mm to 0.385 mm (0.362 mm average; n=7) in males. Number of spiniform processes on anal operculum usually 3, but 1 male has 4 processes instead (Fig. 25). Fifth leg in male with different shape of fusion (Figs 23 & 24), while same leg in female shows constant shape (Figs 5 &18), but with or wothout row of small spinules on distal margin of exopod. Additionally, the junior author observed specimens with 5 spiniform processes on anal operculum, serrated middle process in some of those animals with 3 processes on anal operculum, 3-segmented endopod of maxilla, as well as somewhat longer rostrum, up to 2.6 times as long as wide. No other form of variability observed.

Discussion

Phyllognathopus bassoti was originally described by Rouch (1972) from the interstitial of Lake Wisdom on Long Island, Papua New Guinea. This small island is an old volcano, in which a freshwater lake is situated (surface area c. 100 square kilometers). Two minute islands appeared in Lake Wisdom in March 1968, as a result of a volcanic eruption, and the type material of this species was collected from the interstitial of one them, 20 months after their formation. That is why Rouch (1972) did not consider an active migration as probable, but rather speculated about alternative dispersal mechanisms. The subsequent discovery of this species in two wells (one of them freshwater; the other one «slightly brackish») on Bantayan Island of the Philippines (Bruno & Cottarelli 1999), further strengthens the case against active dispersal in this species.

Bruno & Cottarelli (1999) found significant variability in the population from the Philippines, the most important characters being: 1-segmented endopod of the fourth swimming leg in one male and four spines (instead of three) on the anal operculum of the same specimen. The main difference between their material and the original description is the exopod of the male fifth leg, which bears six instead of five setae. Also, they seem to have misinterpreted one of the cuticular spines on the female's fifth leg endopodal lobe as a tiny seta, which they emphasized as another significant difference. However, we consider they have correctly interpreted, unlike Rouch (1972), the true morphology of the fifth leg endopodal lobe in male. We also found the number of spines on the anal operculum (Figs 19 & 25), as well as the shape of the fifth leg in male (Figs 23 & 24), to be variable in the Indian population. The number of spines on the exopod of the fifth leg in male is often a variable feature in harpacticoid copepods (often the left and right leg have differences on the same animal), and the shape of this appendages is variable, especially in Phyllognathopodidae, so we do not recognize the populations from Long Island, the Philippines and India as different.

It seems that the main habitat of *P. bassoti* is the freshwater interstitial, which makes the understanding of its dispersal difficult, but one should never exclude the possibility of the presence of this species in surface habitats, at least as eggs or nauplii. This would help to explain the distribution of some other subterranean species (for example *Speocyclops demetiensis* (Scourfield, 1932) on the Azores, reported by Petkovski (1984) and Defaye & Dussart (1991)), but unfortunately this is hard to prove. If experiments on drying and recovering parts of the subterranean freshwater communities succeed, they would certainly change our present perception of their complex zoogeography. Also, as Reid (2001) rightly observed, «further pursuit of imaginative collecting and ecologically oriented studies on copepods living at the natural extremes permissible to these basically aquatic forms are bound to provide additional insights on many aspects of their fundamental biology». *Phyllognathopus bassoti* has been found consistently and in fairly good numbers, mainly as adults (females outnumbering males) along with its late copepodids, on several occasions in a domestic reservoir, fed from a bore-well, at Guntur (see Material and methods). It is the sole copepod, co-occuring with oligochaetes, chironomid larvae, odonate nymphs and mites in the algal mass that accumulates at the bottom of the reservoir. Algal scrapings from the inner walls yielded *P. bassoti*, suggesting the tendency of the species to crawl or climb out of water, as observed in other copepod species (see Reid 2001). What is remarkable is the persistence of this species in the above reservoir, notwithstanding periodic treatmans with bleaching powder. While *P. bassoti* is a typical stygobite at Kandukur, it is probably a stygophile at Guntur. A fortuitous examination of the gut contents of the odonate nymphs (by the junior author), in the Guntur samples, revealed the presence of easily recognizable adult (as well as some juvenile) carcasses of *P. bassoti*, suggesting an active preying on this copepod species. Such an interaction between odonates and harpacticoid copepods (H.J. Dumont, pers. comm. to the junior author) is not yet known.

Two critical publications for understanding the systematics of the family Phyllognathopodidae are those by Lang (1948) and Bozic (1966), and, although opposite in their results, they have theoretically correct basic ideas. Lang (1948) asserted correctly that a form could not be accepted as distinct if it fits within the range of variability of a previously known one (at least not on the morphological evidence alone), but unfortunately he synonymized all previously known forms, varieties, subspecies and species with *Phyllognathopus viguieri* (Maupas, 1892), though some were outside its range of variability. Bozic (1966) correctly assumed that two populations which are not able to breed are likely to be separate species, but he accepted almost all different morphological forms (synonymized by Lang) as good species, despite conducting hybridization experiment only on two, not even close, forms. Lang's opinion was followed by Chappuis (1955), Kiefer (1960a, 1960b, 1960c, 1968, 1978), Jakobi (1970) and Yeatman (1983), while Bozic's results greatly influenced Barclay (1969), Rouch (1972), Dussart & Defaye (1990), Defaye & Heymer (1996) and Bruno & Cottarelli (1999). Other copepodologists have stayed confused, or tried to either find some compromise or avoid discussion on this theme: Borutzky (1952), Dussart (1967), Damian-Georgescu (1970), Van De Velde (1974), Watkins & Belk (1975), Shen *et al.* (1979), Dussart (1984), Dumont & Maas (1988), Lehman & Reid (1992), and Ishida & Kikuchi (2000). We consider the Phyllognathopodidae to contain three valid genera, but, because of the variability of every population, in which a significant number of specimens have been examined, we can accept as valid species only those forms with significant morphological differences. These are all included in the following key to genera and species of the family Phyllognathopodidae Gurney, 1932:

1\. Exopod of fifth leg in male 2-segmented ....
...............................*Parbatocamptus jochenmartensi*
....Dumont & Maas, 1988
\- Same ramus 1-segmented 2
2\. Endopod of third swimming leg in male with 3 .... strap-like armature elements ....
..........*Allophyllognathopus brasiliensis* Kiefer, 1967
\- Same ramus without strap-like armature elements 3
3\. Distalmost endopodal segment of fourth swimming leg with 2 setae ....
..........*Phyllognathopus paracamptoides* Bozic, 1968
\- Same segment with 3 setae 4
4\. Endopodal lobe of fifth leg in female
....with only 1 seta
......................*Phyllognathopus bassoti* Rouch, 1972
\- Same lobe in female with 2 setae 5
5\. Exopod of fourth swimming leg 3-segmented ......
................*Phyllognathopus viguieri* (Maupas, 1892)
\- Same ramus 2-segmented..
..........*Phyllognathopus chappuisi* (Delachaux, 1924)

Parbatocamptus jochenmartensi was reported with the second and third swimming legs endopods 2-segmented (Dumont & Maas 1988), subsequently repeated by Lehman & Reid (1992). However, from the drawings of this species it is clear that figure «11a» represents the second leg (its basis bears a strong outer spine) and not the fourth one, so this species has 2-segmented endopods of the third and fourth legs, which are almost identical. We consider the interpretation of the second and fourth swimming legs by Dumont & Maas (1988) as a *lapsus calami*.

The transformed armature elements on the endopod of the third leg in male of *Allophyllognathopus brasiliensis* Kiefer, 1967, from our point of view, shed new light on the «Salakform» of Menzel (1926). He described this form from Java as *Viguierella sp.* and Chappuis (1928) named it *Viguierella coeca menzeli*. It was reported from Guam by Watkins & Belk (1975) as *Phyllognathopus viguieri menzeli*, but was never properly redescribed. This form has the transformed apical spine on the third endopodal segment of the third swimming leg in male, and, although that could be accepted as an atavistic feature of *Phyllognathopus viguieri*, it may be an undiscovered Phyllognathopodid genus. However, this form is worth detailed morphological studies and special care should be given to its mouth parts.

Dussart (1984) reported two females from the interstitial of New Caledonia as *Phyllognathopus sp*. They probably belong to the species described by Bozic (1968) from damp mosses of Reunion, *Phyllognathopus paracamptoides*. Specimens from New Caledonia have 1-segmented exopod of the fourth swimming leg, but their armature is the same as in *P. paracamptoides* and Bozic (1968) figured that exopod as partly fused. However, Dussart's specimens have 2-segmented endopod of the fourth leg, while those described by Bozic (1968) have 1-segmented one, but again they have the same armature (only 2 setae apically, which is unusual in *Phyllognathopus*). They also share a short third exopodal segment of the first swimming leg, similar caudal rami and anal operculum. Since the males in both populations are not described yet (Bozic found one juvenile male only) we need to wait to make a decision about their taxonomic status.

Phyllognathopus chappuisi was described by Delachaux (1924) from Surinam with later additions by Chappuis (1940). Two other species are its junior synonyms, although they have been listed by Dussart & Defaye (1990) as valid species: *P. insularis* Chappuis, 1940 from Marion Island, Indian Ocean (Chappuis 1940), and *P. camptoides* Bozic, 1965 from Gabon (Bozic 1965, 1966) and the Democratic Republic of Congo (ex Zaire) (Defaye & Heymer 1996). Chappuis (1940) tried to distinguish *P. insularis* from *P. chappuisi* by the shape of the male fifth leg, but this is a variable character in the family Phyllognathopodidae. Bozic (1965) admitted that he had relied on Lang's (1948) figures while describing *P. camptoides* and was unaware of Chappuis's (1940) paper (which Lang did not mention in his monograph). Subsequently Bozic (1966) described the male of *P. camptoides* and mentioned also *P. chappuisi* and *P. insularis*, but failed to distinguish his *P. camptoides* from latter two species. Defaye & Heymer (1996) described two males and three females from Lake Kivu as *Phyllognathopus cf. camptoides* Bozic, 1965 and we consider that they found enough variability to synonymize these three species: exopod of the fifth leg in female with four setae (as in *P. insularis*); exopod of the fifth leg in male with 5 setae (as in *P. chappuisi*); different armature formula of the second swimming leg in male and female.

Phyllognathopus viguieri (Maupas, 1892) is the only species with 3-segmented exopod of the fourth swimming leg and it is probably most primitive, because it shares this important character with the other genera of the family Phylloghanthopodidae. As we pointed out in the introduction, this species is incredibly variable and hence the attempts to distinguish some other species on the basis of the male fifth leg alone (*P. coecus* (Maupas, 1892)) or the shape of caudal rami (*P. paludosus* (Mrazek, 1893)) were correctly dismissed by Lang (1948). Dimorphism and even polymorphism in caudal rami shape is well known in harpacticoid copepods and *P. viguieri* is certainly not the most extreme example of this phenomenon (see Schminke 1991). We also think that the relative length of one seta on the fifth leg exopod in female is not enough to distinguish alone any species from *P. viguieri*, so we are synonymizing here *Phyllognathopus volcanicus* Barclay, 1969 with the former. This species was found in New Zealand (Barclay, 1969) sympatrically with «typical» *P. viguieri* and we consider them two morphs (see also Kiefer 1960b, Yeatman 1983).

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