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Some remarks on the taxonomic status of *Paraschizopera* Wells, 1981 (Copepoda: Harpacticoida)

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Abstract

The monotypic genus *Paraschizopera* Wells, 1981 (*ex* Diosaccidae) is transferred to the Tetragonicipitidae on the basis of segmentation of antennary exopod and P2-P4 endopods, setation of P1 and overall similarity in mouthpart structure. *Paraschizopera* is the most primitive genus of the family and closely related to *Diagoniceps* Willey, 1930 which is redefined to encompass only the *laevis*-group. The *menaiensis*-group is allocated to *Paraschizopera* which includes now *P. beckeri* Wells (type-species), *P. menaiensis* (Geddes) and *P. trifida* (Yeatman). The new name *D. brevicauda* is proposed for *Diagoniceps* sp. *sensu* Bodin (1979). Keys are provided to the species of *Paraschizopera* and *Diagoniceps*, and to the genera of the Tetragonicipitidae.

Introduction

In 1979 Becker & Schriever described a juvenile harpacticoid taken at 920 m depth in the Peru Trench for which they proposed the name *Paraschizopera* sp. This new generic name was first used by Becker (1972) in his Ph. D. dissertation when he described and illustrated a copepodid V stage under the name '*Paraschizopera* Diosaccidae gen. et sp. nov.'. Becker & Schriever (1979) hesitated in formally validating the new generic name on the wrong assumption that the International Code of Zoological Nomenclature does not permit names to be based on juvenile stages. Probably for the same reason they declined to give a trivial name. According to Article 17(2) (ICZN, 3rd edn.) the International Code of Zoological Nomenclature does not exclude names proposed for one stage in the life history. However, since the generic name *Paraschizopera* was published in the absence of an associated nominal species name, the principle of Binominal Nomenclature (Art. 5a) was not consistently applied. Consequently, *Paraschizopera* does not satisfy the criterion of availability for generic names published after 1930 since its publication was not accompanied by the fixation of a type species (Art. 13(b)).

In order to maintain stability in the nomenclature, Wells (1981) formally proposed Becker & Schriever's immature specimen as the holotype of a new species *Paraschizopera beckeri* Wells, 1981, which in itself constitutes the type species (by monotypy) of the new genus *Paraschizopera* Wells, 1981. *Paraschizopera* Becker & Schriever, 1979 is an unavailable name which cannot enter into the synonymy of *Paraschizopera* Wells, 1981.

Relationships

Becker & Schriever (1979) placed *Paraschizopera* in the Diosaccidae but did not present any supporting evidence for this. In the discussion on relationships they identified a 'Verwandtschaftsgruppe' comprising *Paraschizopera*, *Schizopera* Sars and *Schizoperoides* Por, the latter probably being the closest relative of the new genus. Becker & Schriever claimed this relationship on the basis of the trisetose, one-segmented antennary exopod, the presence of only 2 outer spines on the distal exopod segment of P1-P4 and the tendency towards reduction in the number of endopodal segments of P2-P4. Conversely, they postulated that both genera could not possible have been derived

from one another because *Schizoperoides* retains the 3-segmented condition in the endopod of P2-P3 and *Paraschizopera* displays the plesiomorphic character states (Becker, 1972) for the mandibular exopod (2-segmented) and the proximal exopod segment of P2-P4 (inner seta present). Recently, Mielke (1992) also considered *Paraschizopera* in his phylogenetic scheme on the relationships of *Schizopera*, *Eoschizopera* Wells & Rao and *Schizoperopsis* Apostolov but excluded *Schizoperoides* from his analysis. Based on the presence of 2 outer spines on the distal exopod segment of P2-P4, Mielke regarded *Paraschizopera* as the hypothetical outgroup of the '*Schizopera* complex' in which both *Eoschizopera* and *Schizoperopsis* represent paraphyletic groupings. Surprisingly, only the former was formally relegated to a junior subjective synonym of *Schizopera*.

Neither phylogenetic scenario is convincing. In both, it is the reduced number of exopodal spines on P2-P4 that represents the only key character, however its usefulness is limited since it is known to have arisen convergently in the Diosaccidae (Mielke, 1992). An alternative scenario is that *Paraschizopera* is not a diosaccid. Becker & Schriever (1979) stressed the atypical diosaccid characters such as the 2-segmented condition of the P2-P4 endopods, a character found only in *Pseudostenhelia* Wells, *Onychostenhelia* Itô and some species of *Pseudomesochra* T. Scott. The presence of 2-segmented P2-P4 endopods (occasionally reduced to a 1-segmented condition in e.g. *Oniscopsis* Chappuis) is a diagnostic family characteristic for the Tetragonicipitidae. Similarly, the caudal ramus of *Paraschizopera* has a very distinctive shape, and within the Diosaccidae is only remotely reminiscent of the condition in some species of *Schizopera* and *Schizoperoides* (Becker & Schriever, 1979). Caudal rami are sexually dimorphic in the majority of the Tetragonicipitidae with the female condition frequently resembling the shape in *Paraschizopera*. The 1-segmented antennary exopod is another unusual diosaccid character, however, this condition and the precise arrangement of the 3 exopodal setae (1 lateral, 1 subapical, 1 apical) is found in the majority of the Tetragonicipitidae (in some species the exopod can be further reduced to a bisetose or unisetose knob). The mouthparts of *Paraschizopera* agree in all aspects with a typical tetragonicipitid. Finally, the setation pattern of the 3-segmented P1 exopod, lacking inner setae on proximal and middle segments and 4 setae present on the distal segment is a standard feature for the Tetragonicipitidae, the only exception being *Oniscopsis* where the exopod became secondarily 2-segmented.

The unmodified fifth leg (as opposed to the foliaceous P5 of e.g. *Phyllopodopsyllus* T. Scott) relates *Paraschizopera* to *Tetragoniceps* Brady and *Diagoniceps* Willey. Conversely, the 3-segmented P1 endopod of *P. beckeri* links it to the genera *Pteropsyllus* T. Scott and some species of *Diagoniceps*. The only two tetragonicipitids that exhibit the combination of these two characters are *Diagoniceps menaiensis* Geddes and *D. trifida* Yeatman. *D. menaiensis* has remained an enigma since its description (Geddes, 1968). Its inclusion in the genus has been questioned by several workers (Geddes, 1968; Coull, 1973; Bodin, 1979) mainly because of the 3-segmented P1 endopod. The discovery of *D. trifida* led Yeatman (1980) to conclude that both species could not be justifiably separated from the genus *Diagoniceps*. Yeatman (1980) however, overlooked Marinov's (1974) description of *D. kunzi* Marinov, and for some obscure reason did not include *D. monodi* Chappuis & Kunz or *D. bocki* Lang in his discussion. Kunz (1984) made an overall comparison including all species and established two groups within *Diagoniceps*. The *laevis*-group contains all species with a 2-segmented P1 endopod: the type-species *D. laevis* Willey, *D. bocki*, *D. monodi* and *D. kunzi*. The *menaiensis*-group includes *D. menaiensis* and *D. trifida*, and is defined by the 3-segmented P1 endopod and the absence of the inner seta on P2 exp-2. Despite being based on a subadult, it is clear that *P. beckeri* belongs to the *menaiensis*-group. Becker & Schriever (1979) and Wells (1981) identified the immature specimen as a copepodid V female but comparison of the fifth leg setation pattern with Bodin's (1979) redescription of *D. menaiensis* suggests that it is a CV male.

The *menaiensis*-group shows also a number of other distinctive characters such as the sexual dimorphism in the rostrum, the absence of inner setae on the middle exopod segment of P2 and the presence of a modified, swollen spine anterior to the geniculation in the male antennule. On the basis of this suite of characters the *menaiensis*-group is formally synonymized with the genus *Paraschizopera*. It is unfortunate that the type-species is based on a copepodid only, particularly when detailed descriptions are available for both sexes of *P. menaiensis* (Geddes, 1968; Bodin, 1979). Bodin (1979) listed some differences between his specimens and Geddes' types but considered these as insufficient to warrant the establishment of a new species. Whereas most of these discrepancies can be attributed to deficiencies in the original description, one major differ-

ence illustrated by Bodin but not included in the discussion is the different shape and setation of the female P2 endopod. In the females of Anglesey (Fig. 1A) the distal endopod segment is distinctly longer than the proximal and bears 1 spine and 2 long setae. In Bodin's illustration this segment is slightly shorter than the proximal and possesses two juxtaposed smooth setae apically. This is exactly the condition as found in the Anglesey males (Fig. 1B), except that the minute inner seta (arrowed in Fig. 1B) was overlooked, and therefore Bodin must have unintentionally illustrated a male specimen. Bodin also illustrated an extra seta on the distal segment of the male P4 endopod. Re-examination of the types of *P. menaiensis* (BNMH reg. nos. 1967.8.1.1-2) failed to discern this seta. Instead, a secretory pore was found in an almost identical position (Fig. 1D), suggesting that the additional seta in the French specimens might well be a tubular extension of the pore. Inspection of the type material also revealed that the male P5 exopod is 2-segmented (Fig. 1E). It is interesting to note that this segment boundary has also been reported in some males of *Tetragoniceps* (Por, 1965), and in combination with the 3-segmented P1 endopod and the unmodified P5 reinforces the very primitive position of *Paraschizopera*.

P. menaiensis and *P. trifida* can be easily differentiated by the different swimming leg setal formula and caudal ramus shape. The only substantial difference between *P. beckeri* and *P. trifida* is the presence of an extra seta on P4 exp-3 in the latter, however, it is possible that this seta is only added at the final moult. Clearly, we have to await the discovery of adult specimens before we can assess the status of the type-species. *P. trifida* was also described from the American Pacific seaboard (Yeatman, 1980) but from a much shallower locality than *P. beckeri*.

Paraschizopera Wells, 1981

Diagnosis. Tetragonicipitidae. Rostrum sexually dimorphic. Antennule 9-segmented in ♀; segment 1 shorter than segment 2; proximal segments without spinous processes; haplocer in ♂ with 3 segments distal to geniculation and modified swollen spine on segment 6. Antennary exopod with 3 discrete setae. Mandibular exopod well developed, elongate, usually 2-segmented. Maxillule without epipodite. P1 with with 3-segmented exopod and endopod. P2-P3 exp-3 without inner setae. P2 exp-2 without inner seta. Swimming leg sexual dimorphism in P2 endopod (enp-2 reduced in size, with outer spine missing and distal setae modified) and P3 endopod (outer spine modified). P5 not modified in ♀.
Gender. Feminine. Caudal rami sexually dimorphic.

Type-species. P. beckeri Wells, 1981 (by monotypy).
Other species. P. maenaiensis (Geddes, 1968), *P. trifida* (Yeatman, 1980).

Key to the species of *Paraschizopera* Wells, 1981

1. P2-P3 exp-3 with 5 setae/spines; P3 exp-2 without inner setae ..... *menaiensis* Geddes, 1986.
   P2-P3 exp-3 wiht 4 setae/spines; P3 exp-2 with inner seta ..... 2.
2. P4 exp-3 with 6 setae/spines .... *beckeri* Wells, 1981.
   P4 exp-3 with 7 setae/spines ..... *trifida* Yeatman, 1980.

The removal of the *menaiensis*-group to *Paraschizopera* requires a redefinition of *Diagoniceps* which is restricted herein to the *laevis*-group only.

Diagoniceps Willey, 1930

Diagnosis. Tetragonicipitidae. Rostrum not sexually dimorphic. Antennule 9-segmented in ♀; segment 1 shorter than segment 2; proximal segments without spinous processes; haplocer in ♂ with 4 segments distal to geniculation, without modified swollen spine on segment 6. Antennary exopod with 3 discrete setae. Mandibular exopod well developed, elongate, usually 2-segmented. P1 with 3-segmented exopod and 2-segmented endopod. P2-P3 exp-3 with 1–2 inner setae. P2 exp-2 with inner seta. Swimming leg sexual dimorphism in P2 endopod (outer spine of enp-2 modified) and occasionally P4 endopod (inner seta of enp-2 lost). P5 not modified in ♀. Caudal rami sexually dimorphic.

Type-species, D. laevis Willey, 1930 (by monotypy).

Bodin's (1979) excellent description of *Diagoniceps* sp. based on two males from La Rochelle, leaves no doubt that he was dealing with a distinct species. Despite the unique setal formula in the exopods of P2-P4 and the very short caudal rami, Bodin refrained

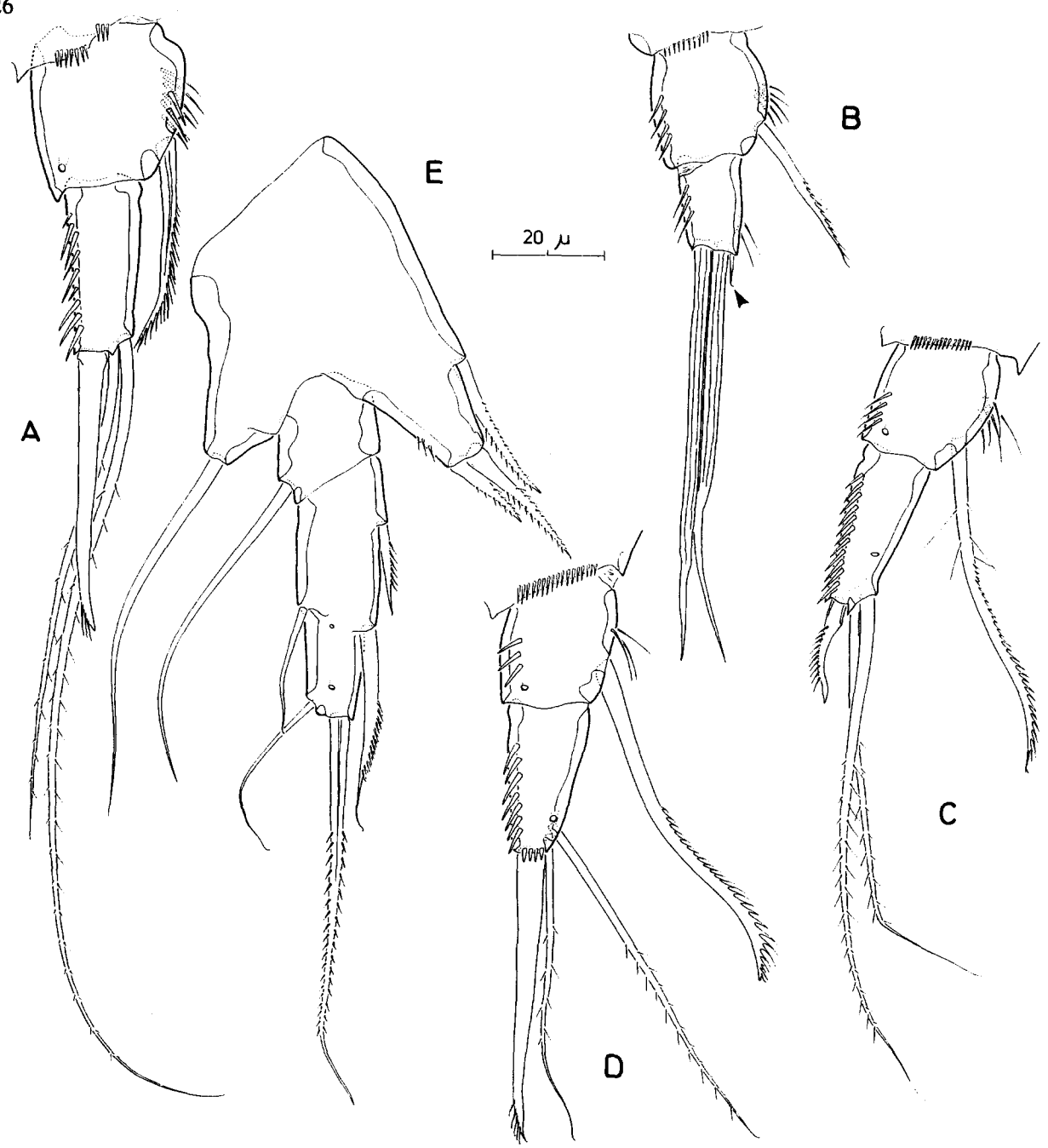

Fig. 1. *Paraschizopera menaiensis* (Geddes, 1968). A, P2 endopod ♀; B, P2 endopod ♂ (minute seta arrowed); C, P3 endopod ♂; D, P4 endopod ♂; E, P5 ♂.

from establishing a new species chiefly because of the lack of information on the female. At present, only the males of *D. laevis* and *D. bocki* are described, however, it is known that sexual dimorphism does not occur in the exopods of the thoracopods. Therefore, the La Rochelle specimens can be easily separated from all other *Diagoniceps* species and the very short caudal ramus provides an additional discriminating character. On the basis of these differences Bodin's material is regarded here as representing a new species *D. brevicauda* sp. n.

The five species contained in the genus *Diagoniceps* can be identified by the key below. It has to remarked that Marinov's (1974) setal formula of the P3 exopod in *D. bocki* contradicts Por's (1964) description.

Key to the species of *Diagoniceps* Willey, 1930

1. P2-P3 exp-3 with 6 and 7 setae/spines, respectively;
   P2 enp-2 with 4 setae/spines ..... 2.
   P2-P3 exp-3 with 5 and 5–6 setae/spines, respectively;
   P2 enp-2 with 3 setae/spines ..... 4.
2. P4 exp-3 with 8 setae/spines ..... 3.
   P4 exp-3 with 7 setae/spines *brevicauda* sp.n.
3. Caudal ramus twice as long as anal somite ..... *kunzi* Marinov, 1974.
   Caudal ramus about as long as anal somite ..... *bocki* Lang, 1948.
4. P2-P4 exp-1 without inner seta ..... *laevis* Willey, 1930.
   P2-P4 exp-1 with inner seta ..... *monodi* Chappuis & Kunz, 1955.

Key to the genera of Tetragonicipitidae

Since Coull's (1973) key to the genera of the Tetragonicipitidae, the genus *Oniscopsis* Chappuis has been re-allocated to the family (Becker & Kunz, 1981) after having been previously transferred to the Parameosochridae (Lang, 1965) and the genus *Fearia* Coull has been relegated to a junior subjective synonym of *Tetragoniceps* Brady (Kunz, 1984). Por's (1986) statement that *Pyrocletodes* Dinet is a tetragonicipitid is considered a slip of the pen. Since Coull's (1973) revision of the family 36 species and subspecies have been described, invalidating some of the characters used in his key. A new key to genera is proposed below incorporating these changes and the present redefinition of *Diagoniceps*.

1. P1 exopod 2-segmented ..... *Oniscopsis* Chappuis, 1955.
   P1 exopod 3-segmented ..... 2.
2. Cephalothorax with paire processes backwardly directed, spinous ..... *Laophontella* Thompson & A. Scott, 1903.
   Cephalothorax without paired backwardly directed, spinous processes ..... 3.
3. P1 endopod 2-segmented ..... 5.
   P1 endopod 3-segmented ..... 4.
4. First antenulary segment longest; P5 exopod ♀ foliaceous; P2-P4 exp-1 without inner seta ..... *Pteropsyllus* T. Scott, 1906.
   First antennulary segment not distinctly elongate; P5 exopod ♀ not modified; P2-P4 exp-1 with inner seta ..... *Paraschizopera* Wells, 1981.
5. First antennulary segment with dentiform projection . *Tetragoniceps* Brady, 1878.
   First antennulary segment without dentiform projection ..... 6.
6. P2-P3 exp-2 with inner seta ..... *Diagoniceps* Willey, 1930.
   P2-P3 exp-2 without inner seta ..... 7.
7. P2-P4 exp-1 with inner seta; P5 ♀ a large foliaceous plate ..... *Phyllopodopsyllus* T. Scott, 1906.
   P2-P4 exp-1 without inner seta; P5 ♀ not modified, with separate exopod and baseoendopod ..... *Protogoniceps* Por, 1964.

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