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The relationship of the genus *Schizopera* Sars within the family Diosaccidae (Copepoda: Harpacticoida)

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A review of *Schizopera* Sars indicates that four species are so much more primitive in the antenna and leg setation that they should be removed to a new genus, *Eoschizopera*, which can be considered as a direct and immediate ancestor of *Schizopera*. A further, new, species is described in this new genus. The relationships within this branch of the family Diosaccidae are discussed and the scheme of family evolution proposed by Lang is modified to include *Eoschizopera* and other genera not considered by him (*Goffinella*, *Protopsammotopa*, *Psammotopa*, *Actopsyllus*, *Balucopsylla*, *Schizoperoides*). *Actopsyllus hartmannorum* Kunz is removed to a further new genus—*Helmutkunzia*.

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INTRODUCTION

Lang (1965a) has pointed out that the curious modified hyaline spine on the inner edge of the third segment of the male P.3 exopod is a feature unique to *Schizopera* Sars as this genus is presently defined. He is so convinced of this that when it is not mentioned in the description of a species assigned to the genus on the sum of other characters he presumes that it has been overlooked. Although no author has stated specifically that it is absent, several have declared that with the exception of the P.2 endopod the P.2–P.4 is identical in both sexes. However, we have been able to confirm that this spine in fact is present in species for which it had not been noted in the original description, viz., *S. borutzkyi* Monchenko, 1967, *S. taricheana* Por, 1968a, *S. lacus-amari* Por & Marcus, 1972, *S. carolinensis* and *S. anomala* Coull, 1971, *S. gligici* Petkovski, 1957 (information on this species coming from Professor Neikova's male specimen (Mikhailova-Neikova, 1966)) and *S. neglecta* Akatova, 1935 (the specimen of Monchenko, 1967). In addition Kunz (1974) reports its presence in *S. brusinae* Petkovski, 1954. For *S. chaetosa* Petkovski, 1954 and *S. noodti* Rouch, 1962 the original material is lost and we have been unable to obtain information on the status of subsequently discovered specimens.

Although this investigation does not cover all species in which this point is in doubt the success that we have had in revealing the presence of the spine in all the species which now have been examined in detail is probably sufficient to confirm Lang's view on the universality of this character in *Schizopera* species.

The genus is characterised also by a more or less cylindrical body-shape, a reduced leg setation in which there are always only two outer setae or spines on the third exopod segment of P.2–P.4, and a uniform type of female genital field. None of these characters is unique to the genus but they serve to relate it to a group of genera within the family (Lang, 1948: 763 *et seq.*) and they led Lang (1948, 1965a) to consider *Schizopera* to have a monophyletic origin.

A further character of the genus considered important by Lang (1948) is the antenna with an allobasis and a two-segmented exopod, but since then five species have been described in which this appendage differs from this condition.

Of these five exceptional species *S. anomala*, which has an allobasis but only a one-segmented exopod, can be regarded as a minor departure from the *Schizopera* plan. As with *S. arenicola* Chappuis & Serban, 1953, *S. gauldi* Chappuis & Rouch, 1960 and *S. varnensis* Apostolov, 1967 which have the P.4 endopod reduced to two segments, and the several species with only two segments in the endopod of P.1, such modifications can be recognized as representing advanced evolutionary trends within the genus.

Such a simple model cannot be proposed to explain the more primitive antenna in *S. crassipinata* Chappuis, 1954, *S. indica* Rao & Ganapati, 1969 and *S. syltensis* Mielke, 1973, where a definite basis is present, and *S. gligici* in which the basis is perhaps present but ill-defined. Furthermore, *S. syltensis* is even more primitive in that the antennal exopod is three-segmented, and in *S. crassipinata* and *S. indica* the setation of P.2–P.4 is more primitive than in all other *Schizopera* species except *S. marlieri* Rouch & Chappuis, 1960 (the authors do not say whether this species has a basis or an allobasis and Dr Rouch has confirmed that the original material is no longer extant). In Table 1 we set

out the total number of setae on the distal segment of both rami of P.2–P.4 in the female for all species assigned to *Schizopera* at the present time for which this information is available in the literature. From this, if we exclude the four species with the primitive antenna and *S. marlieri* in which the state of this appendage is in doubt, we can conclude that the primitive formula is 4.4.4. for both rami, with most species showing a reduction in the endopods to 4.4.3. or less. Thus there seem to be some reasonable grounds for considering the species *crassipinata*, *indica*, *syltensis*, *gligici* and *marlieri* as doubtful members of the genus *Schizopera*.

We propose, therefore, to separate *S. crassipinata*, *S. gligici*, *S. indica* and *S. syltensis* from *Schizopera* and to place them in a new genus, *Eoschizopera*, whose diagnosis is given below; its systematic position is considered later.

Table 1. Some characteristics of *Schizopera* species and related genera. (Author and date are not cited when a description can be found in Lang, 1948)

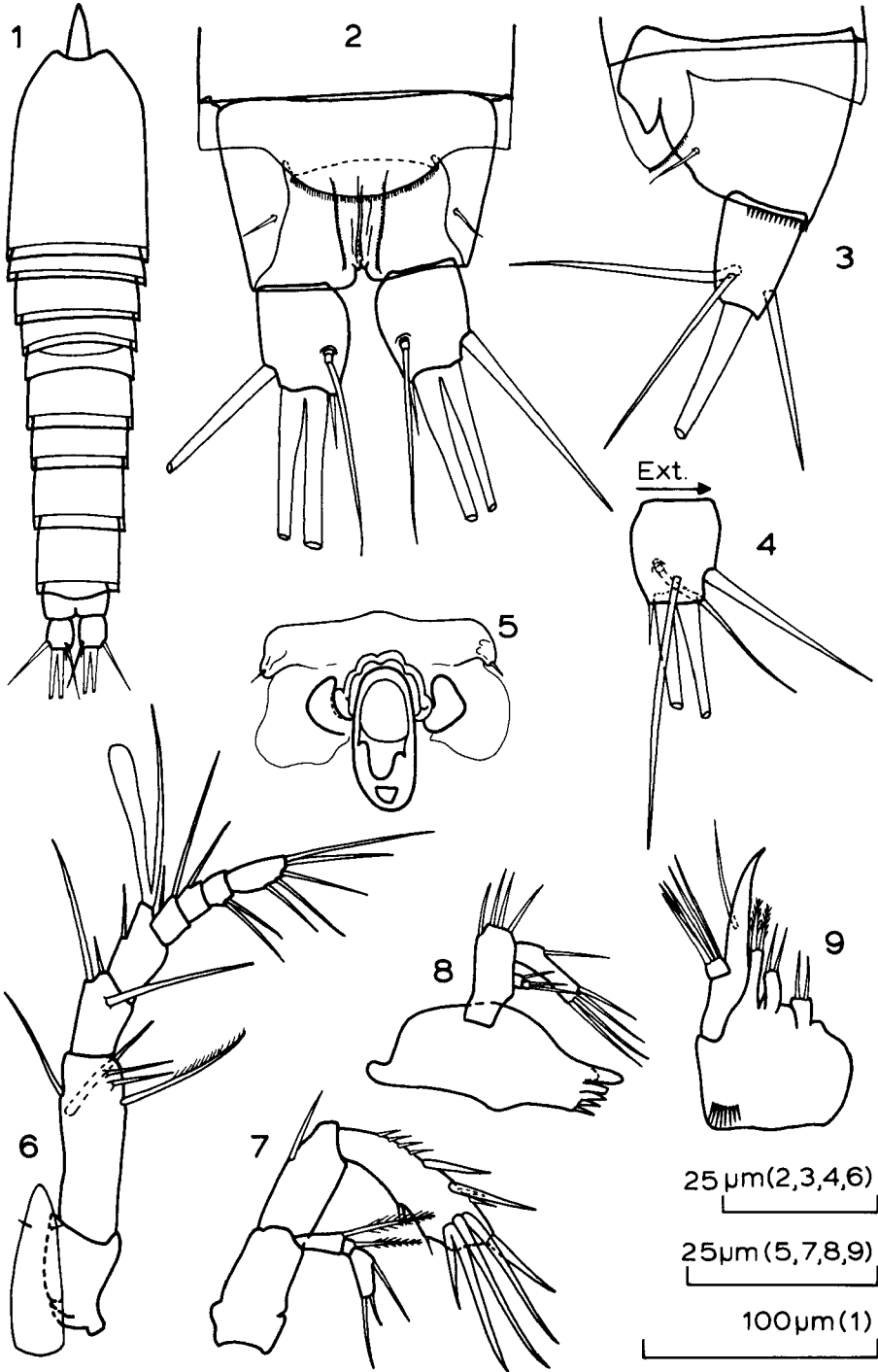
Total no. of setae and/or spines on:		Antenna	No. of segs. in antenna exopod	species
P.2-P.4 Exp. distal seg.	P.2-P.4 Enp. distal seg.			
4.4.4.	4.4.4.	Allobasis	2	<i>S. carolinensis</i> Coull, 1971
4.4.4.	4.4.4.	Allobasis	1	<i>S. anomala</i> Coull, 1971
4.4.4.	4.4.3.	Allobasis	2	list (i)
4.4.4.	4.3-4.3	Allobasis	2	<i>S. neglecta</i>
4.4.4.	4.3.3.	Allobasis	2	list (ii)
4.4.4.	4.3.2. or 4.	Allobasis	2	<i>S. variseta</i> Bozic, 1964
4.4.4.	4.3.2.	Allobasis	2	list (iii)
4.4.4.	3.4.3.	Allobasis	2	<i>S. monardi</i> Petkovski, 1955
				<i>S. lacus-amari</i> Por & Marcus, 1972
4.4.4.	3.3.3.	Allobasis	2	<i>S. borutzkyi</i> Monchenko, 1967
4.4.4.	2.3.3.	Allobasis	2	<i>S. pontica</i> Chappuis & Serban, 1953
4.4.4.	3.3.2.	Allobasis	2	<i>S. arenicola</i> Chappuis & Serban, 1953
4.4.4.	3.2.2.	Allobasis	2	<i>S. kunzi</i> Apostolov, 1967
				<i>S. varnensis</i> Apostolov, 1967
3.3.3.	2.2.3.	Allobasis	2	<i>S. gauldi</i> Chappuis & Rouch, 1960
5.5.4.	4.2.4.	Basis	2	<i>S. crassipinata</i> Chappuis, 1954
4.4.5.	5.5.4.	Basis	2	<i>S. indica</i> Rao & Ganapati, 1969
4.5.5.	4.4.3.	?	2	<i>S. marlieri</i> Rouch & Chappuis, 1960
4.4.5.	4.4.3.	indistinct basis	2	<i>S. gligici</i> Petkovski, 1957
4.4.5.	4.4.3.	Basis	3	<i>S. syltensis</i> Mielke, 1973
4.4.5.	3.3.2.	Basis	3	<i>Eoschizopera reducta</i> n. sp.
4.4.6.	4.5.4.	Basis	3	<i>Actopsyllus longipes</i> Wells, 1967
4.4.5.	3.4.3.	Basis	3	<i>A. hartmannorum</i> Kunz, 1971
4.4.5.	4.4.3.	Basis	2	<i>Balucopsylla similis</i> Rao, 1972
4.4.4.	4.4.4.	Allobasis	1	<i>Protopsammotopa</i> Geddes, 1968
4.4.4.	3.4.4.	Allobasis	1	list (iv)
3.3.3.	3.4.4.	Allobasis	1	<i>Psammotopa chappuisi</i> Noodt, 1955
4.3.4.	5.4.4.	Allobasis	1	<i>Goffinella stylifer</i>
4.4.4.	4.3.3.	Allobasis	1	<i>Schizoperoides expeditionis</i> Por, 1968b

(i) *Schizopera paradoxa*, *inopinata*, *validor*, *consimilis*, *compacta*, *rotundipes*, *hiatiana*, *triacantha*, *brusinae* Petkovski, 1954, *chaetosa* Petkovski, 1954, *pratensis* Noodt, 1958, *vicina* Herbst, 1960, *knabeni* Lang, 1965a, *baltica* Lang, 1965b, *taricheana* Por, 1968a.

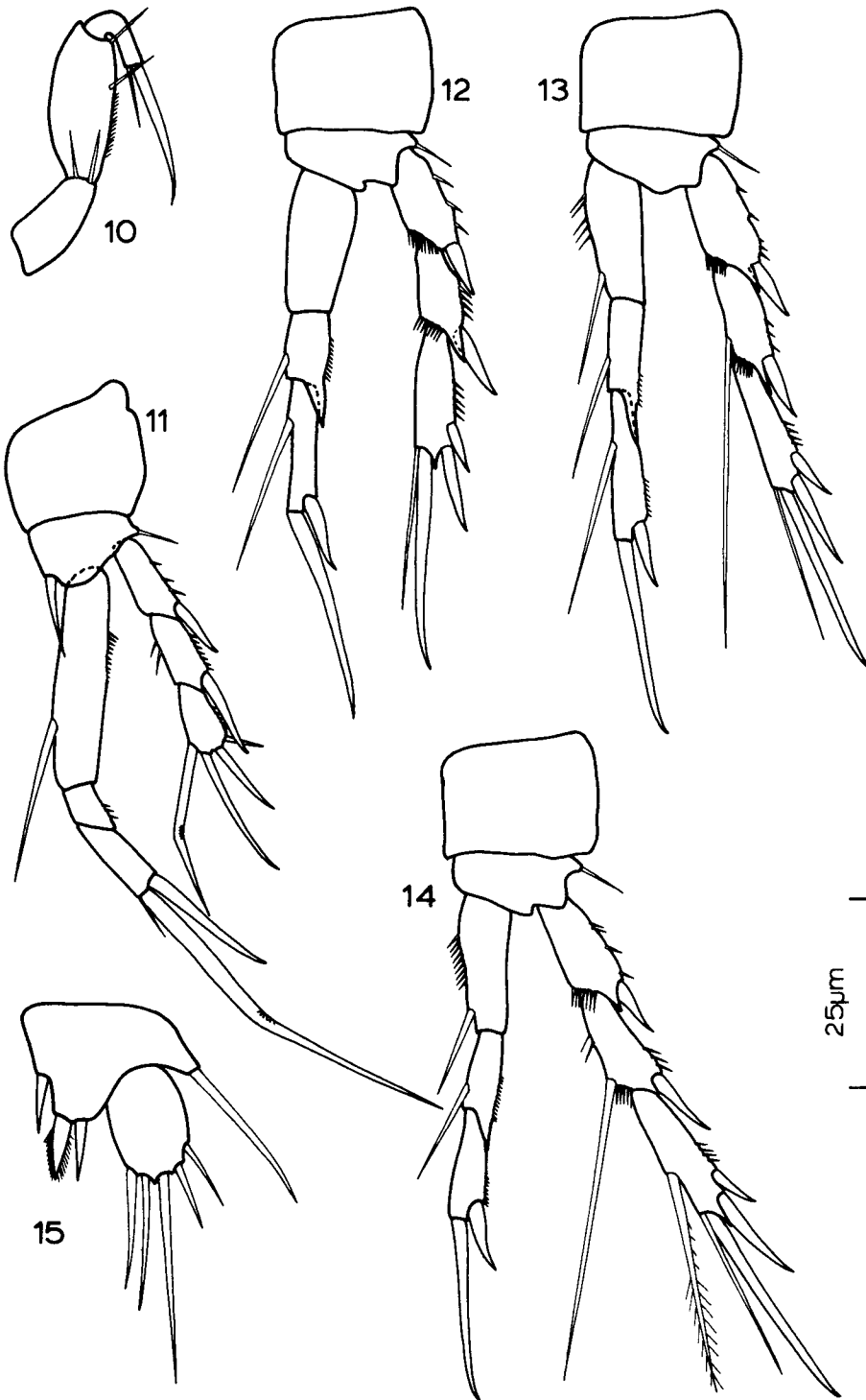
(ii) *Schizopera longicauda*, *ornata* Noodt & Purasjoki, 1953, *bozici* Lang, 1965a.

(iii) *Schizopera stephanidesi*, *langi* Petkovski, 1954, *minuta* Noodt, 1955, *nana* Noodt, 1955, *noodti* Rouch, 1962, *californica* Lang, 1965a.

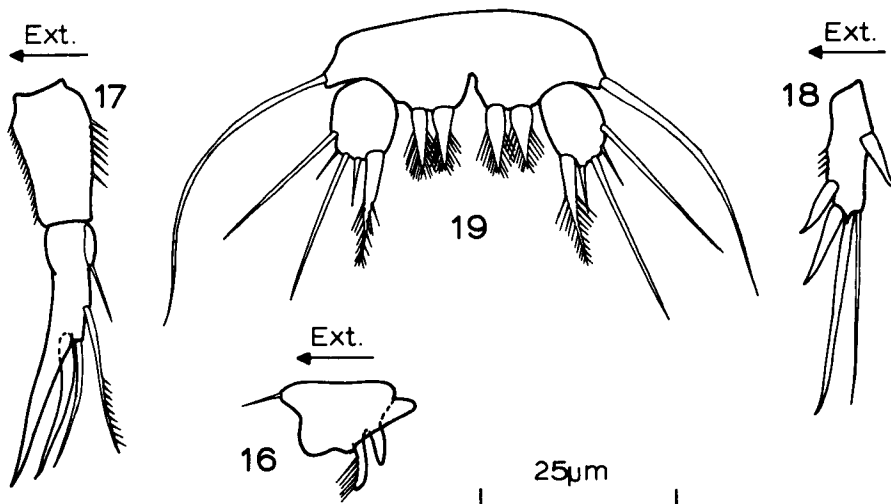
(iv) *Psammotopa vulgaris* Pennak, 1942, *phyllosetosa* (Noodt, 1952), *polyphylla* Noodt, 1955.



Figures 1 to 9 *Eoschizopera reducta* gen. et sp. nov., 1, ♂ dorsal; 2-3, ♀ anal operculum, last segment and caudal rami, dorsal and lateral; 4, ♀ left caudal ramus, ventral; 5, ♀ genital field; 6, ♀ rostrum and antennule; 7, ♀ antenna; 8, ♀ mandible; 9, ♀ maxilla.



Figures 10 to 15. *Eoschizopera reducta* gen. et sp. nov., ♀. 10, Maxilliped; 11 to 15, P.1–P.5.



Figures 16 to 19. *Eoschizopera reducta* gen. et sp. nov., ♂. 16, Basis of P.1; 17, endopod of P.2; 18, third segment of exopod of P.3; 19, P.5.

DIAGNOSIS OF *EOSCHIZOPERA* GEN. NOV.

Body cylindrical, unadorned except for some sensillae. Female antennule eight-segmented, elongate. Antenna with basis and a two- or three-segmented exopod. P.1 with three-segmented exopod and a two- or three-segmented endopod. Endopod prehensile. Distal segment of exopod with four setae. Rami of P.2–P.4 three-segmented. Distal segment of exopod with two outer setae. Exopod of P.5 distinct. Basis of male P.1 with modified inner edge. Endopod of male P.2 two-segmented, the second segment with a strong claw or unguiform process. Distal segment of male exopod of P.3 with a thickened hyaline spine on the inner edge.

Selection of a type-species is difficult as there is much variation in the setation of P.2–P.4 but we propose *Schizopera syltensis* Mielke, 1973, as this has the most primitive antenna.

We consider the primitive setation of the distal segment of the rami of P.2–P.4 to have been 5.5.5., but acknowledge that this is a guess and that no present species has this extreme condition.

To this genus we would add *Schizopera marlieri* as *incertae sedis* until the condition of the antenna is known for certain.

The new species whose description follows belongs to this genus also, as is shown by its primitive antenna, P.2–P.4 exopod setation and the spine on the male P.3 exopod. Its principal departure from the other species is the quite advanced setation of P.2–P.4 endopod, which characteristic is referred to in the trivial name.

DESCRIPTION OF *EOSCHIZOPERA REDUCTA* SP. NOV.

This description is based on five females and two males collected by G. C. Rao on 29 March 1969 in coarse and medium sands with fine shell gravel and

little detritus, 10-30 cm below the surface between the low and mid-tide levels of the intertidal zone of Seaward Bay, Sound Island, North Andaman, India ($12^{\circ} 58' 06''$ N, $92^{\circ} 59' 17''$ E). The sand is siliceous and angular, with a median diameter varying between 350 and 700 μ m. Sea temperature $28-30^{\circ}$ C, salinity $33-34^{\circ}$ /oo. The male holotype and paratypes of both sexes have been deposited with the Zoological Survey of India, Calcutta. *Holotype*. Regd. no. C 1367/2. *Paratypes*. Regd. nos. C 1368/2 and C 1369/2.

Female

Length 330 μ m. Body cylindrical, about six times as long as broad. Rostrum defined at the base, elongate, pointed, with a pair of sensillae. Anal operculum not well defined. Posterior edge of the penultimate segment forms a pseudoperculum. Genital suture represented by a dorso-lateral patch of chitin only. Genital field as in Fig. 5.

Somitic ornamentation. All somites bare except for a few sensillae at the posterior edge of all segments except the last two. All segments except the first and last abdominal ones with a deep plain hyaline frill, that of the penultimate segment forming a shallow pseudoperculum which is minutely dissected. Last segment with fine spinules ventral and lateral (Figs 2 and 3).

Caudal ramus (Figs 2 to 4) slightly longer than broad. Apically with two well developed principal setae and a small inner seta. One seta on the outer edge near to the distal corner. One dorsal articulated seta and one ventral seta.

Antennule (Fig. 6) elongate, eight-segmented. Second segment the longest, the last four segments small. An aesthete on the fourth segment.

Antenna (Fig. 7) basis without a seta. First endopod segment with one inner seta. Second segment with two strong spines on the inner edge. Exopod of three-segments, the first two with one seta at the inner distal corner, the third segment with one inner and two terminal setae. Second segment small but clearly defined.

Mandible palp (Fig. 8) well developed. Basis with four setae. Endopod of one segment with one inner and four terminal setae. Exopod of two-segments, the first with one seta, the second with two setae.

Maxillule. An adequate preparation of this appendage was not obtained.

Maxilla (Fig. 9) short and broad. Syncoxa with a short spinule row near the outer distal corner and with three endites. Basis with one seta and an unguiform projection. Endopod of one segment with five setae.

Maxilliped (Fig. 10) well developed and prehensile. Basis with two setae at the inner distal corner. Inner edge of the first endopod segment with short spinules on the basal half, a seta about halfway along, and a seta at the distal corner. Second segment well developed, with a seta and a claw terminally.

P.1 (Fig. 11). Coxa bare. Basis short; with a weak outer seta and a strong inner spine. Rami three-segmented. Exopod about as long as the first endopod segment. Outer edge of all segments spinulose. Inner edge of second segment with two thin setules. Last segment with one geniculate seta and three spines. Second segment without an inner seta. First endopod segment with a long seta about two-thirds of the way along the inner edge and outer edge with some minute spinules; about twice as long as the last two segments together. Second

segment with a few spinules on the outer edge; without an inner seta. Third segment with a weak seta, a long geniculate seta and a claw-like spine.

P.2–P.4 (Figs 12 to 14). Coxa bare. Basis short; with a weak outer seta. Rami three-segmented, endopods slightly longer than the exopods. Outer edge of all exopod segments spinulose and with all outer spines stout. Last segment terminally with a long thin seta and a claw-like spine. Inner distal corner of first two segments with a fringe of spinules. First endopod segment elongate and broad. Outer distal corner of second segment an unguiform projection. Outer edge of second segment of *P.2* and second and third segments of *P.3* and *P.4* spinulose. Last segment with an outer spine and terminally with a long claw-like spine.

Setal formula

	Exopod			Endopod		
<i>P.2</i>	0.	0.	0.2.2.	0.	1.	1.1.1.
<i>P.3</i>	0.	1.	0.2.2.	1.	1.	1.1.1.
<i>P.4</i>	0.	1.	1.2.2.	1.	1.	0.1.1.

P.5 (Fig. 15) very small. Rami distinct. Inner expansion of basendopod not reaching to halfway along the exopod; with three spines, the middle one plumose. Exopod oval, with five setae.

Male

Length as female. Differs from the female in the following characters.

Abdomen. First two segments distinct. Posterior edge of first segment with a hyaline frill and sensillae.

Antennule haplocerate.

P.1. Inner edge of basis strongly chitinized. Inner spine curved and plumose (Fig. 16).

P.2 Endopod two-segmented. First segment with spinules on the inner edge and short hairs on the outer edge. Second segment as Fig. 17.

P.3 with a hyaline spine on the inner edge of the third exopod segment (Fig. 18).

P.5 (Fig. 19). Basendopods of both sides confluent but with a deep cleft between them. Inner expansion with two massive plumose spines. Exopod almost circular, with four setae and a massive plumose spine. Outer seta of basendopod extremely long.

P.6 of each side a separate plate with two setae.

SYSTEMATIC RELATIONSHIPS

Eoschizopera and *Schizopera* sensu stricto

In 1948 Lang proposed a scheme of evolutionary pathways within the Diosaccidae that has not been challenged seriously and which we believe is capable of adaptation to the knowledge now available (Fig. 20). Since then several new genera of diosaccids have been described. Most of these make either no major modifications necessary, or are not related to the section of the family with which we are concerned at the moment. However, the final

resolution of the taxonomic position of *Goffinella* Wilson, *Psammotopa* Pennak and *Protopsammotopa* Geddes which are "close to *Schizopera* Sars, 1905, with which they share a reduced limb armature" (Geddes, 1968) and the description of *Actopsyllus* Wells, 1967, *Balucopsylla* Rao, 1972, *Schizoperoides* Por, 1968b and *Eoschizopera* makes a review of Lang's (1948) scheme urgent.

Lang's primary division in this section of the family is based on the antenna. *Rhyncholagena* Lang, *Robertgurneya* Lang and *Typhlamphiascus* Lang retain the primitive basis while *Amphiascus* Sars, *Bulbamphiascus* Lang, *Amphiascoides* Nicholls (= *Amphiascella* Lang), *Paramphiascella* Lang, *Haloschizopera* Lang and *Schizopera* have progressed to the advanced allobasis. If we accept this primary division as valid then it is obvious that *Eoschizopera* (with a basis) cannot be closely related to the *Schizopera*-group; indeed, it must belong to the sister group and be related to *Robertgurneya*-*Typhlamphiascus* in which there is a tendency to reduced leg setation and, in *Robertgurneya*, to the assumption of an allobasis in the antenna.

This arrangement could be satisfactory only if the male P.3 exopod of *Eoschizopera* did not have a modified spine. We agree with Lang (1965a) that this is a fundamental characteristic of *Schizopera* which is unlikely to have evolved more than once. Thus there must be a close relationship between *Schizopera* and *Eoschizopera*.

Nevertheless it can be argued that Lang is correct in proposing that two lines sprang from the ancestral stock. One developed an antennal allobasis early on and led to the *Amphiascus*-*Bulbamphiascus*-*Haloschizopera*-*Amphiascoides*-*Paramphiascella* group of recent genera. In this line leg setation and the antennal exopod have remained in a relatively primitive state. In the sister group (all other genera considered in this paper) the assumption of an allobasis was delayed. Before it arose the group split further into the *Eoschizopera*-group and the *Rhyncholagena*-group. Within both reduction in other characters has occurred independently, but has progressed much further in the former.

Related genera

Actopsyllus, *Balucopsylla*, *Protopsammotopa*, *Psammotopa*, *Goffinella* and *Schizoperoides* share with *Eoschizopera* and *Schizopera* a reduced leg setation, with at most two outer setae on the distal segment of P.2-P.4 (Table 1). As far as is known none of them display the modified spine in the male P.3 exopod. That all belong to this section of the family is demonstrated by the genital field.

Actopsyllus

The two species of this genus require separate treatment. *A. longipes* Wells, 1967 has a basis and a three-segmented exopod to the antenna. It can be separated from the *Eoschizopera*-group on the endopod of male P.2, which bears a seta on the first segment and generally resembles the condition in *Typhlamphiascus* and *Robertgurneya*. Also, the distal segment of P.4 exopod has two inner setae, a condition never found in *Eoschizopera*-*Schizopera*.

A. hartmannorum Kunz, 1971 does not belong to this genus. Its only similarity with *A. longipes* is the combination of two outer setae on the distal segment of the exopod of P.2-P.4 and the antenna, with a basis and a three-

segmented exopod. The leg setation is reduced to a condition not inconsistent with *Eoschizopera*. It resembles *E. reducta* in the antenna, except that the second segment is bare. In all these characters it is close to *Balucopsylla*. However, it is readily distinguished from all four genera in the male P.2 endopod which, although modified, is not equipped with a strong claw. Of the genera we are considering *A. hartmannorum* may be a link between *Eoschizopera* and *Balucopsylla*.

We propose the creation of a new genus which we name *Helmutkunzia* in honour of Dr Helmut Kunz, whose diagnosis is the description of *Actopsyllus hartmannorum*, its sole and type-species.

Balucopsylla

As mentioned above *Balucopsylla* seems to be a further step in a sequence *Eoschizopera*–*Helmutkunzia* (Fig. 20), in which there is evidence of some reduction in antennal exopod and, particularly, sexual dimorphism—there being no differences between the sexes in the P.2 in *Balucopsylla*. This last is sufficient for maintaining generic distinction.

Protopsammotopa and *Psammotopa*

In *Protopsammotopa* the antenna has an incompletely fused allobasis and a male P.2 endopod very similar to *Eoschizopera*–*Schizopera*. In *Psammotopa* the allobasis is complete and the male P.2 is like that of the female. The leg setation is reduced beyond that of *Protopsammotopa*. Both genera have a one-segmented antennal exopod.

The evidence suggests an origin in or near *Eoschizopera* but distinct from *Helmutkunzia*.

Goffinella

This monotypic genus presents some problems. The antenna is advanced—with a complete allobasis and a one-segmented exopod. As in *Psammotopa* there is a total lack of sexual dimorphism in P.2 but the setation is more primitive, with five setae on the distal endopod segment of P.2, of which three are apical. It also has some flattened setae on P.4, which is a characteristic of *Psammotopa*. We can only wonder whether Wilson's (1932) figure of P.2 is accurate. It is possible even that this is an anomalous feature of the specimen drawn. Wilson does not describe the P.2 in the text.

A recent attempt (Wells, in press) to clear up these apparent anomalies was frustrated by the fact that the material lodged in the U.S. National Museum as *G. styliifer* proved to be that of a new species of *Protopsammotopa* (*P. wilsoni*). It appears that all the original material of *G. styliifer* is lost and the genus must remain enigmatic.

Schizoperoides

This monotypic genus, known from a single female only, defies any attempt at assessing its relationships. According to Por (1968b) "the relationship to *Schizopera* is obvious from the reduced armature of the exopod [of P.5]". Since the P.5 has the rami fused, the antennal exopod is curiously modified, the mandible lacks an exopod, the body is "covered with hair" and the rostrum is short and broad, it presents so many features different from *Schizopera* and

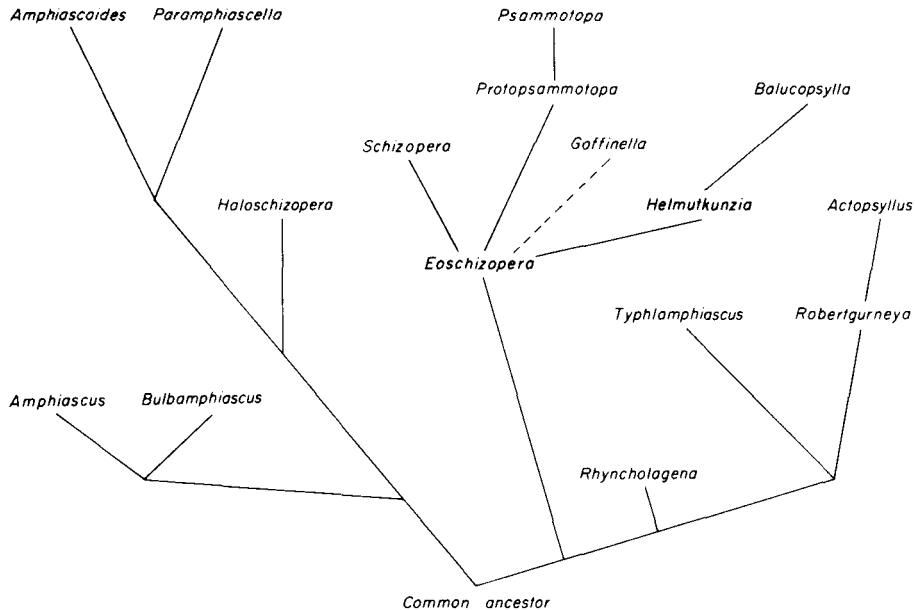


Figure 20. Possible evolutionary relationships in part of the family Diosaccidae (modified after Lang, 1948).

its allies that it can only be related to this branch of the family by the genital field being "of the *Amphiacella* [sic] and *Schizopera* type".

We summarize the possible relationships of these genera in Fig. 20.

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