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THE DISTRIBUTION OF THE DIPLOCHETA AND THE "LOST" CONTINENT PACIFICA (DIPLOPODA)

by

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ABSTRACT

After a brief review of the classification and distribution of the orders of the Diplocheta: Julida, "Cambalida" and Spirostreptida, the interrelationship of these groups is discussed mainly on account of the structure of the gnathochilarium and male gonopods. The conclusions are related to the distributional patterns of the groups, and a hypothesis is developed with regard to the possible dispersal of the diplochetan orders and families. It is suggested that the dispersal started in the southern hemisphere and that the northern Diplocheta reached the Holarctic by way of a pacific route, involving the former existence of a "lost" continent Pacifica.

INTRODUCTION

The examination of a number of cambaloid millipedes collected during a trip through eastern Australia and Tasmania (Jeekel, 1981) and of other Australian material of the same group at hand, triggered a series of thoughts which eventually involved the taxonomy, phylogeny and distributional history of the entire superorder Diplocheta. Admittedly, these viewpoints are not based on a thorough taxonomical study of the Diplocheta; they even consist partly of a number of generalizations and hypothetical assumptions, and on that account they may be regarded as highly controversial. Nevertheless it seems worth while to put on record these points of view, in order that they may serve as a working hypothesis or at least evoke a discussion on one of the major challenges of diplopodology: the explanation of the present-day distribution of Diplopoda.

In this paper I will briefly discuss the classificatory status of the cambaloid millipedes and the current internal classification of the group. After giving a rough sketch of the known distribution of the Diplocheta, I will try to evaluate two character complexes which have played a major role in the characterization of the high-level taxa in the superorder: the gnathochilarium and the gonopods. The conclusions drawn with regard to the possible phylogeny of the superorder lead to a hypothesis trying to explain its distribution.

THE CLASSIFICATION OF THE JULIFORM DIPLOPODS

For an evaluation of the taxonomic position of the cambaloid millipedes we have to take into consideration the classification of the juliform Diplopoda in general. This group, united as Juliformia by Attems (1926) or as Opisthospermophora by Verhoeff (1926-1932), is traditionally divided into three large and diversified equivalent taxa currently designated as the orders Spirobolida, Julida and Spirostreptida. The position of the relatively minor, but rather heterogeneous group of cambaloid millipedes in recent literature has been that of a fourth separate order, or as a group subordinate to either the Spirostreptida or the Julida.

The interrelationship of the three main orders was judged differently by various authors. Laying emphasis on the configuration of the gnathochilarium, Verhoeff (1926-1932: 1610, 1675) united his Spiroboloidea, Spirostreptidea and Cambaloidea as Chorizognatha, opposed to the Symphyognatha consisting of the Julida only. In his recent cladistic study on the Julida, Enghoff (1981) tends to support this view.

Other authors, however, advocated the isolation of the Spirobolida (Cook, 1895; Hoffman, 1980) from the Spirostreptida and Julida, combining the latter in the superorder Diplocheta. In this point of view less weight is accorded to the gnathochilarial structure, but support is found in a set of other characters, including the structure of the gonopods. Although in my opinion these characters do not fully justify a separation on such a high taxonomic level, I share the opinion of Hoffman.

The position of the cambaloids has been that of a taxon equivalent to the other three groups (Verhoeff, 1926-1932; Brölemann, 1935; Chamberlin & Hoffman, 1958, Mauriès, 1983), or subordinated to the Julida (Mauriès, 1971) or to the Spirostreptida (Attems, 1926; Hoffman, 1980).

There seems to be no reason to question the monophyly of the Juliformia as a whole, or that of the Spirobolida, Julida and Spirostreptida; strong doubts must be expressed regarding the monophyly of the cambaloid millipedes, a group often regarded as "primitive" or "ancestral".

In the context of the present paper and only for reasons of convenience I adhere to a separate ordinal status of the cambaloids, referring to the group henceforth as "Cambalida" (adjective: "cambalidan").

INTERNAL CLASSIFICATION OF THE "CAMBALIDA"

Throughout this century great confusion has reigned regarding the classification of the "Cambalida". The two principal authors of the past generation who had a general opinion on the problem, Attems and Verhoeff, not only advocated entirely different views, but in the course of time also changed their opinion repeatedly.

It would lead us too far to discuss the history of "cambalidan" classification. Rather I would like to confine myself to the ideas put forward by Hoffman (1980) and Mauriès (1983). Following these authors, but applying some minor simplifications, the following classificatory outline may serve the present purpose:

Fam. Cambalidae (with the genera enumerated by Hoffman, with the addition of the genus *Zinagon* Chamberlin in accordance with Mauriès);
Fam. Cambalopsidae (in accordance with the concept of Hoffman, but with the inclusion of the Pericambalidae proposed by Mauriès);
Fam. Iulomorphidae (the genera enumerated by Hoffman, excluding *Zinagon*);
Fam. Pseudonannolenidae (the genera enumerated under this family by Hoffman, as well as those referred by him to the Physiostreptidae and Choctellidae, two groups kept separate by Mauriès as well).

The available evidence does not seem to justify a status of the Physiostreptidae and Choctellidae coordinate to that of the other families. To do justice to the morphological discontinuities they might be treated as subfamilies, next to a similar status for *Pseudonannolene* and for *Epinannolene* and allies.

Hoffman and Mauriès differ in opinion with regard to the mutual relationship of their families. Hoffman combined the families Cambalidae, Cambalopsidae and Iulomorphidae in a suborder, coordinate to a suborder combining the Pseudonannolenidae, Physiostreptidae, Choctellidae and Pericambalidae, and a similar taxon embracing the spirostreptidans in the traditional sense. Mauriès brought Cambalidae and Cambalopsidae together, opposing a combination of the Iulomorphidae, Pseudonannolenidae, Physiostreptidae and Choctellidae.

With regard to the Cambalopsidae and the Cambalidae monophyly can hardly be questioned. However, the internal coherence of the Iulomorphidae and the Pseudonannolenidae is not fully warranted, in particular because of insufficient knowledge of the morphology of all pertaining genera.

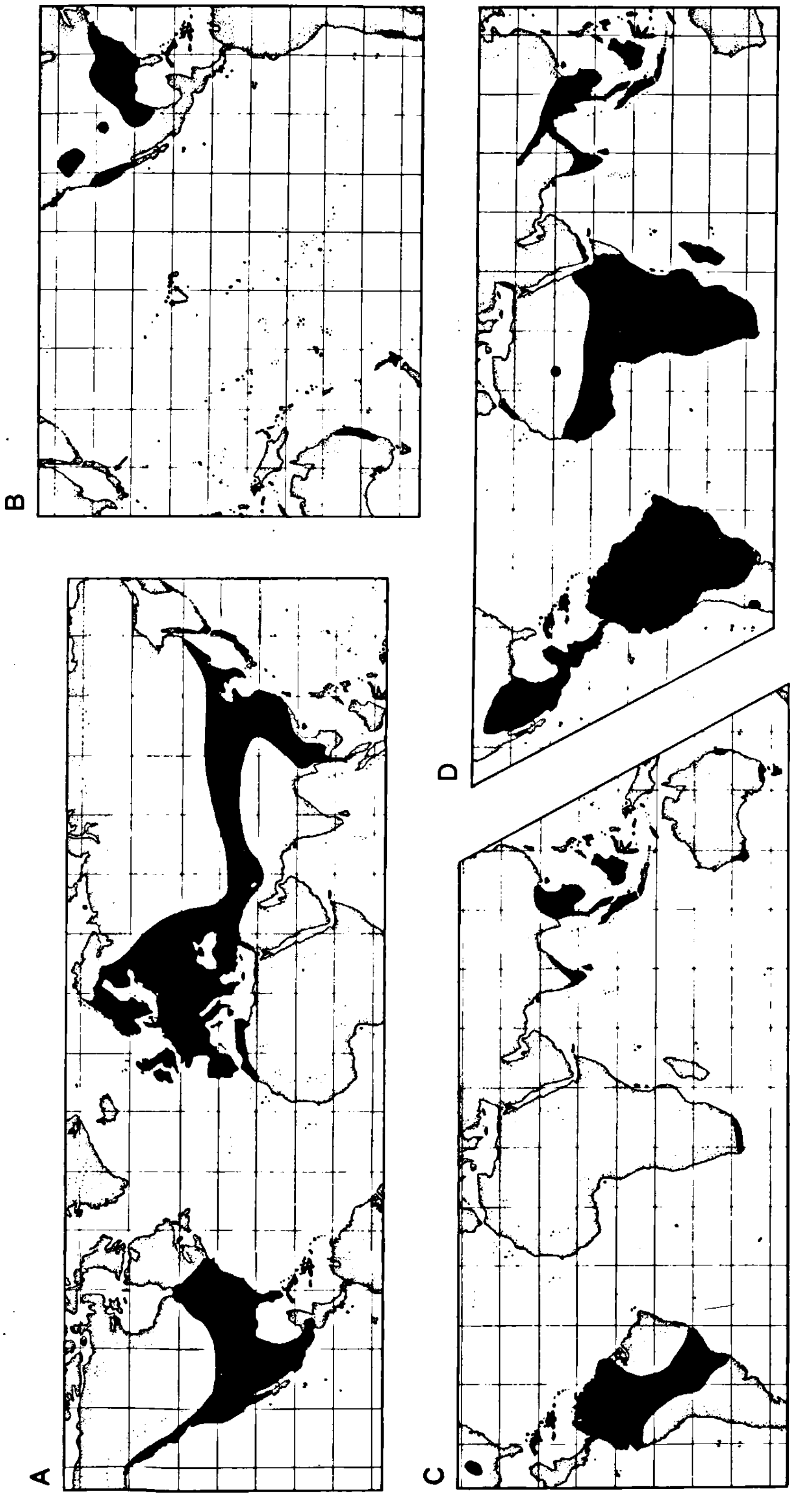


Fig. 1. Approximate distributional ranges of diplochetan groups. A, Julida; B, Cambalidae (the recent record of a cambalid from Iran (Mauriès, 1983) not shown); C, Iulomorphidae (Australia, Africa), Cambalopsidae (Southeast Asia), Pseudonannolenidae (America); D, Spirostreptida.

DISTRIBUTION OF THE DIPLOCHETA

Julida

This large and very diverse order is distributed throughout the temperate and subtropical zones of the northern hemisphere (fig. 1A). Penetrations into the tropical part of the world have occurred only on a minor scale, and concern the occurrence of representatives in Central America and in Southeast Asia. In the latter area Julida have been recorded from Burma, and were found in the northern part of the Malayan peninsula (Jeekel, unpubl.). Otherwise the southern limit of the distribution conforms to that of the Palearctic and Nearctic regions.

Spirostreptida

This order occurs throughout the Neotropical, Afrotropical and Oriental regions (fig. 1D), the pattern being largely Gondwanic. It is likewise a large and very diverse group. Just as the Julida it is completely absent in the Australian region. Penetrations towards the north have occurred through Central America to the southeastern U.S.A., in the Caribbean area, and north of the Sahara, but these concern relatively few species closely related to taxa widespread in South America or Africa.

"Cambalida"

This relatively small but diversified group occupies a strongly fragmented area. Its main diversity is found in the southern hemisphere.

Of particular interest is the distributional area of the family Cambalidae (fig. 1B). Members of this group are known to occur with moderate diversity in eastern Australia (Jeekel, unpubl.), with slight diversity in New Zealand and Chile. On the northern hemisphere Cambalidae occur in North America, with diversity focussing in the western U.S.A., they are relatively richly represented on the Hawaiian islands (but apparently not on Hawaii itself), and have a single species in Japan (never recorded again since its description by Attems in 1909). Mauriès (1983) described a species referred to the North-American genus *Nannolene* Bollman from Chiraz, Iran, an amazingly isolated occurrence not indicated on map 1B.

The remaining three families are mainly southern in distribution (fig. 1C). The Cambalopsidae occur in the Oriental region with a moderate degree of diversity. The Iulomorphidae appear to occupy all ecologically suitable areas of Australia and Tasmania, with considerable diversity. They occur, with less diversity, also in a zone paralleling the south-east of South Africa. The Pseudonannolenidae focus in South America, where *Pseudonannolene* Silvestri and allies are confined mainly to Brazil and adjacent areas, *Epinannolene* Brölemann and related genera occur in the Venezuelan-Colombian area and the Caribbean, *Physiostreptus* Silvestri occurs in Ecuador, whereas *Choctella* Chamberlin has been found only in a relatively small area in the southern U.S.A.

The range of the Spirobolida includes all suitable parts of the tropical and subtropical regions of the world, excluding only the central and western parts of the Palearctic region.

THE TAXONOMIC POSITION OF THE "CAMBALIDA"

Since various authors in recent years have stressed the relationship of the "Cambalida" with either the Julida or the Spirostreptida, or held the opinion that the group should have a status coordinate to these two orders, it is necessary to analyse the position of the four "cambalidan" families. For briefness sake I will confine myself here to a discussion of two character complexes which played an important role in the diagnoses of the groups: the gnathochilarium and the gonopods.

Gnathochilarium

In each of the three large orders of the Juliformia, the Spirobolida, Spirostreptida and Julida, the configuration of the sclerites of the

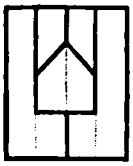
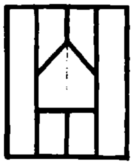
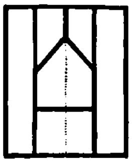
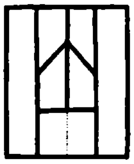
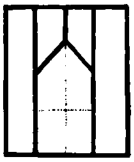
	JULIDA	CAMBALIDAE	IULOMORPHIDAE	PSEUDONANNOLENIDAE	CAMBALOPSIDAE	SPIROSTREPTIDA
	All groups, excl. Parajulidae ♂					
	Parajulidae ♂					
		Cambala Nannolene Dimerogonus	Iulomorpha	Epinannolene Choctella Typhlonannolene	Glyphiulus Hypocambala	
				Pseudonannolene	Pericambala	
		Leiodere		Physiostreptus Holopodostreptus Cambalomma	Trachyjulus	All groups

Fig. 2. Diagram representing the various types of gnathochilarium in the Diplocheta (oral margin above). Thin lines: hypothetical basic structure; fat lines: actually present sutures. Only a selection of generic names of the four "cambalidan" families is given.

gnathochilarium shows a marked stability and is typical, except for some minor deviations. In the "Cambalida", on the other hand, the configuration varies considerably with respect to the presence or absence of sutures, and at least three patterns may be distinguished (for illustrations of juliform gnathochilaria see Attems, 1926: figs. 243, 248, 254, 260, and Enghoff, 1981: fig. 3).

The various types of gnathochilaria in the Diplocheta are illustrated in fig. 2. In this diagram the hypothetical ancestral configuration is taken as basic pattern: three pairs of medial sclerites (from oral to aboral: lamellae linguales, promental and mental sclerites), laterally accompanied by a pair of large sclerites, the stipites.

In the Julida, the promental sclerites are united in a single median promental sclerite; the mental sclerites are laterally coalesced with the aboral part of the stipites, but their median suture is present. According to Enghoff (1981) this so-called symphyognathous gnathochilarium is one of the principal autapomorphies of the order.

However, there is an exception to this configuration: the males in the family Parajulidae have the mental sclerites separated from the stipites, a unique configuration in the Diplocheta.

The gnathochilarium of the Spirostreptida is characterized mainly by the fact that the promental and mental sclerites are united in a single median piece, the duplomentum.

One of the three types of gnathochilarium in the "Cambalida" is essentially the same as that of the Spirostreptida. Similarity is greatest between the Spirostreptida and *Physiostreptus* (Pseudonannolenidae); in other "cambalidan" genera the duplomentum is more triangular, instead of pentagonal. The other two types are characterized by the presence of a suture separating promentum and mentum, and differ from each other by the presence or absence of a median suture separating the two promental sclerites.

It is important to note that the gnathochilarium in the order Spirobolida suggests that of the Spirostreptida, but the duplomentum is generally broadly triangular, extending orally to separate medially the two lamellae linguales. Such an oral extension of the duplomentum (or of the promentum) is found also in most "Cambalida" (except *Physiostreptus* and *Iulomorpha* Porat (see Schubart, 1966: fig. 91) and part of the Julida (see Enghoff, 1981: 304)).

Gonopods

In the Juliformia both pairs of legs of the 7th somite of the male are involved in forming the copulatory apparatus. However, the development of each of the two pairs varies between a condition where both pairs are well developed to a condition in which the posterior gonopods are reduced, vestigial or completely absent.

In the order Julida both pairs are generally well developed, but in certain families (e.g. the Nemasomatidae) the posterior gonopods are relatively small, although evidently functional. In principle the anterior gonopods consist of a coxite and a telopodite, but the latter may be reduced or absent, in particular in the more typical Julida. Generally the julidan anterior gonopod is provided with a flagellum arising from the basis of the coxite, but otherwise its structure is simple. The flagellum, which in some unrelated julidan taxa may be reduced or even absent, is normally passing through a sheath-like structure of the posterior gonopod.

Typically, the posterior gonopods of the Julida are highly complicated structures, and it seems obvious that these are mainly involved in the transfer of sperm. On the other hand the anterior gonopods seem to function as a protective shield for the more delicate posterior gonopods, and perhaps also as a clasping organ during copulation. Generally speaking the typical Julida (e.g. the family Julidae) might be characterized as opisthospermophorous. In those groups in which the posterior gonopods are small and have a relatively simple structure, such as found in the Nemasomatidae, Zosteractinidae, etc., the anterior gonopods may also have some function in the transfer of sperm, and one might call them amphispermophorous.

Within the "Cambalida" the whole functional range from opisthospermophory to proterospermophory is found. In the Cambalopsidae the anterior gonopods have a relatively simple structure, are two-jointed and have no flagellum. As in the Julida their function seems to be that of a clasper, although some function in the transfer of sperm cannot be excluded. The posterior gonopods are rather small, but complicated and delicate, and seem to have the main function in sperm transfer. The cambalopsid gonopods may therefore be characterized as opisthospermophorous, with a certain tendency towards amphispermophory.

Following Mauriès (1971), Hoffman (1980) pointed out that the Cambalidae show a great resemblance to the julidan family Nemasomatidae, except for the different configuration of the gnathochilaria. At least with regard to the cambalid genus *Dimerogonus* Attems, and other as yet undescribed Australian representatives of the family, I share this point of view. The copulatory apparatus in this genus consists of rather simple, two-jointed anterior gonopods bearing a flagellum, and small, but evidently functional posterior gonopods (fig. 3; compare with Schubart, 1934: figs. 293-294). Other Cambalidae, e.g. *Nannolene* Bollman and *Cambala* Gray (Mauriès, 1983) have more com-

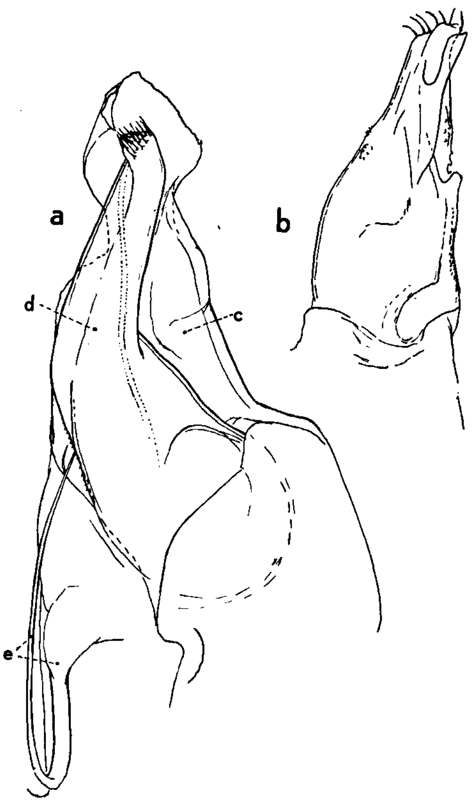


Fig. 3. Gonopods of *Dimerogonus orophilus* Attems from South Australia: a, left anterior gonopod, aboral aspect; b, left posterior gonopod, oral aspect; c, coxite; d, telopodite; e, flagellum.

plicated anterior gonopods suggesting considerable involvement in sperm transfer. On this account I tend to regard the Cambalidae as amphispermophorous.

In the telopodite of the anterior gonopods of *Dimerogonus* I could establish the presence of a fine internal channel, ending at the apex of the telopodite, and probably belonging to a prostatic gland. I do not know if such a gland exists in the Julida or in other cambalid genera.

In the Iulomorphidae the anterior gonopods seem to be basically similar to those of the Cambalidae, and this holds especially for the gonopods in certain Australian genera like *Amastigogonus* Brölemann and *Victoriocambala* Verhoeff. In these genera (fig. 4) the telopodite of the anterior gonopods contains a channel, which I regard homologous to the channel in *Dimerogonus*. However, in both these genera the channel ends apically in a small free process, the pseudoflagellum. At the same time, however, the coxal basis of the gonopods in *Victoriocambala* has a vestige of a true 'julidan-cambalid' flagellum. In all iulomorphids the posterior gonopods are weakly developed, and seem to have hardly any function in the transfer of sperm.

In an other Australian iulomorphid genus, *Atelomastix* Attems (fig. 5), the anterior gonopods are more complicated, the telopodite being terminally split into three processes, one of which the pseudoflagellum. In the South African genus *Iulomorpha* Porat (see Schubart, 1966) the telopodite of the anterior gonopods is distally split into two (or three) lobes or processes, one of which contains the end of the prostatic channel but it is rather broad instead

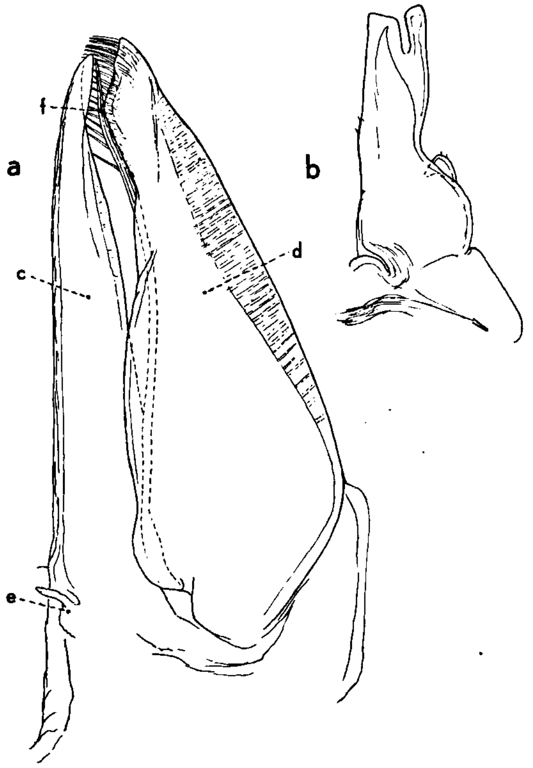


Fig. 4. Gonopods of *Victoriocambala* spec. from Victoria: a, left anterior gonopod, aboral aspect; b, right posterior gonopod, oral aspect; c, coxite; d, telopodite; e, flagellum; f, pseudoflagellum.

of acuminate. Altogether the Iulomorphidae may be characterized as amphispermophorous, with a strong tendency towards proterospermophory.

Proterospermophory is obvious in the Pseudonannolenidae and Spirostreptida simply because in these groups the posterior gonopods are completely lacking, their suppression being indicated by slight vestiges. In the Pseudonannolenidae the anterior gonopods seem to have essentially the same structure as in the Iulomorphidae, although perhaps a little less complicated. In *Choctella* the telopodite is of a simple type, and it appears to lack a pseudoflagellum (see Hoffman, 1965). It is not known whether or not a prostatic channel is present, although it seems likely that this is the case. Whereas in *Choctella* and most other "Cambalida" the coxite ends distally in a process about equalling the length of the telopodite, such a coxal process appears to be missing in *Pseudonannolene*, *Epinannolene* and *Physiostreptus*. In these and allied genera the apex of the anterior gonopods is formed by the telopodite which is divided in two or three smaller lobes or processes, one of which contains the prostatic channel. In *Epinannolene* the channel-bearing process is attenuate and finely tapering, in the other genera it is broader and shorter (see Carl, 1914; Mauriès, 1969, 1981 (*Epinannolene*); Brölemann, 1929 (*Pseudonannolene*); Carl, 1913 (*Physiostreptus*)).

I think it was Hoffman (1972) who first alluded to the homology of the channel in the telopodite of the anterior gonopod of the Iulomorphidae and the channel in the so-called telopodite of the spirostreptidan gonopod. When one accepts the view that Spirostreptida, Pseudonannolenidae and Iulomorphidae are related groups, the suggested homology is the only logical conclusion. This means in turn that the so-called telopodite of the spirostreptidan gonopod is in fact the homolog of the pseudoflagellum in the Iulomorphidae. Actually, the true telopodite of the spirostreptidan gonopod is the greater part of what is usually called the coxite plus the pseudoflagellum, the true coxite being a small part of the base of the gonopod which is as yet difficult to define exactly. Comparison of the anterior gonopod of *Atelomastix* (fig. 5) and the gonopod of an arbitrarily chosen spirostreptid, *Plusioporus* Silvestri (fig. 6), illustrates this point. It is obvious that if the supposed homologies will prove to be correct the current terminology of the spirostreptidan gonopod is wrong and should be revised to accommodate both Spirostreptida and "Cambalida".

Within the Juliformia, the Spirobolida seem to have the most typical opisthospermophorous copulatory apparatus: the two-jointed anterior gonopods appear to have only a supporting and even enveloping function with regard to the delicate and often quite complicated posterior gonopods.

CONCLUSIONS

Overlooking the differences in gnathochilarial structure, especially with regard to the presence or absence of sutures, I think the existing variability can be explained only by assuming that the structure was not yet genetically stabilized in the phase of initial radiation of the Juliformia. Stabilization probably occurred independently during subsequent phases, e.g. prior to the start of the radiation of the Spirostreptida. Even symphyognathy in the Julida was not yet fully fixed at the onset of the radiation of the order, as is shown by the sexual dimorphy in the gnathochilarium of the Parajulidae. Evidently the main characteristic of the julidan gnathochilarium is the persistence of the median suture separating the mento-stipites. I must conclude therefore, that the sutures of the gnathochilarium are of little value in establishing the interrelationship of the present-day higher juliform taxa.

Perhaps of greater significance is the extension in oral direction of the promentum or duplomentum. Considering the distribution of this character throughout the Juliformia, I suppose that the condition in which the promentum or duplomentum separates the lamellae linguales completely is the ancestral one, which persisted in the Spirobolida, most

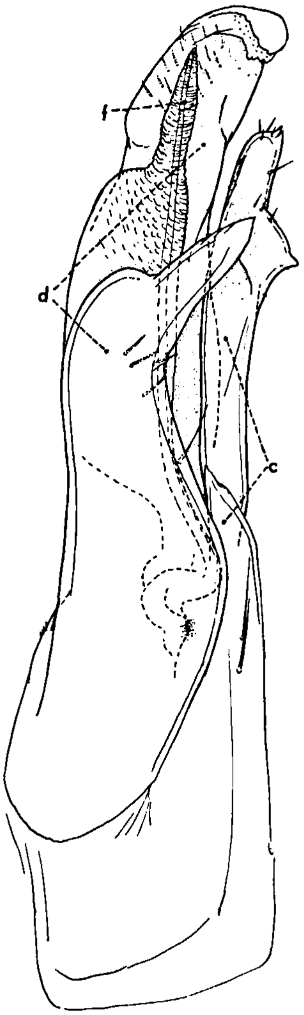


Fig. 5. Right anterior gonopod of *Atelomastix* spec. from South Australia, aboral aspect: c, coxite; d, telopodite; f, pseudoflagellum.

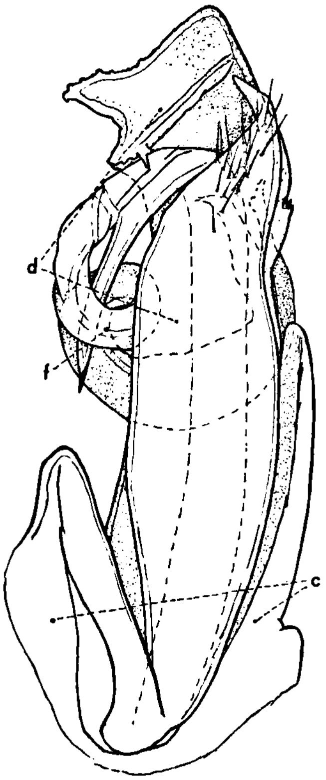


Fig. 6. Left (anterior) gonopod of *Plusioporus oyapokanus* (Attems) from Surinam, oral aspect: c, coxite; d, telopodite; f, pseudoflagellum.

"Cambalida" and part of the Julida. The retraction of the mental sclerites in the Spirostreptida, certain "Cambalida" (*Physiostreptus*, *Iulomorpha*) and certain Julida (the family Julidae) is the derived condition which occurred independently, and may have limited value.

Because of its complicated structure the copulatory apparatus of the male will give us more useful indications towards the interrelationship of the diplochetan taxa than the structure of the gnathochilarium. Overlooking the morphology of the gonopods in the various diplochetan taxa, it seems evident that the Iulomorphidae are particularly important. The genus *Atelomastix* has anterior gonopods which tend strongly towards the spirostreptidan gonopods. The relationship of this genus to the Spirostreptida is also indicated by the structure of the first pair of legs of the male, which is purely spirostreptidan. One might see *Atelomastix* as a primitive member of the Spirostreptida, if it were not for the presence of functional posterior gonopods and a different gnathochilarium. The Spirostreptida might also be seen as Iulomorphidae in which the coxa of the anterior gonopods is reduced and the telopodite is hypertrophied.

The Pseudonannolenidae seem also related to the Iulomorphidae, but besides the loss of the posterior gonopods, they show a different tendency of development in the anterior gonopods, in which the coxite is proportionally more strongly developed as against an obvious simplification of the telopodite.

The iulomorphid genus *Victoriocambala* tends strongly towards the Cambalidae and Julida, on account of the presence of a vestigial flagellum. Although provided with a pseudoflagellum, the anterior gonopods in this genus show a great similarity to certain representatives of the Cambalidae and Julida.

Altogether I regard the Iulomorphidae as intermediate between the Julida and Cambalidae on the one side and Spirostreptida and Pseudonannolenidae on the other. This might mean that the ancestors of these groups had anterior gonopods with a flagellum and a pseudoflagellum, and that amphispermophory belonged to the groundplan of the Diplocheta.

Lacking a flagellum and a pseudoflagellum, and with the telopodite of the anterior gonopods being relatively small and simple, the Cambalopsidae are difficult to associate with the above-mentioned groups. Mauriès (1983) brought this family together with the Cambalidae in a suborder Cambalidea, but this leaves out the many important differences between the two groups. For the present I prefer to regard the Cambalopsidae as a group which branched off from the diplochetan stem at an early stage of its radiation.

A similar process, but during an earlier phase of evolution may account for the separate position of the Spirobolida.

Summarizing the previous discussion the suggested interrelationship of the juliform taxa is illustrated in a diagram (fig. 7).

DISTRIBUTIONAL HISTORY

Perhaps one of the most interesting points evolving from the previous discussion is that the functional change of the copulatory apparatus from opisthospermophory, via amphispermophory to proterospermophory in the Julida, "Cambalida" (minus Cambalopsidae) and Spirostreptida has a particular geographical pattern, ranging from the Holarctic (opisth., amph.: Julida, Cambalidae), southward along both sides of the Pacific (amph.: Cambalidae) to Australia (amph., amph.-prot.: Iulomorphidae) and westwards (amph.-prot., prot.: Iulomorphidae, Spirostreptida) towards America (prot.: Pseudonannolenidae, Spirostreptida). Since all of these groups except the Julida and part of the Cambalidae occur in the southern hemisphere it seems likely that the initial radiation of the Diplocheta took place there. Ancestors of the iulomorphid type evolved towards the Iulomorphidae of today in the southeastern part of the southern continent and the Pseudonannolenidae in the west, leading to a fragmentary distributional pattern and taxonomically rather isolated taxa probably due to considerable extinction. On the other hand the Spirostreptida succeeded to occupy most of Gondwana, except Australia, and persisted there as a successful group.

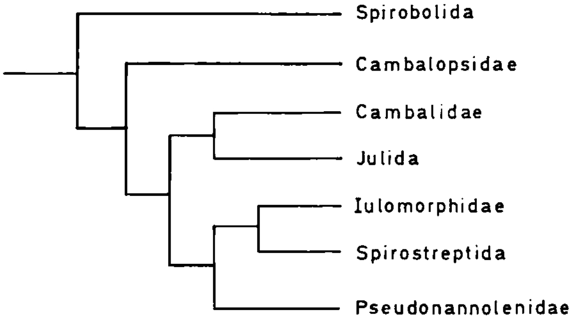


Fig. 7. Supposed interrelationship of the juliform taxa.

Neither Iulomorphidae, Pseudonannolenidae or Spirostreptida managed to penetrate the northern continent(s) except in relatively recent times. Only the genus *Choctella* may indicate a certain penetration of the northern continent at an early time, possibly via an early connection between the Brazilian shield and the eastern half of North America.

Considering the present-day distribution it seems quite likely that the connection between the southern and northern taxa of the Diplocheta is to be found in the Pacific region. It is assumed that the Cambalidae and Julida, just as the Iulomorphidae, Spirostreptida and Pseudonannolenidae, descended from an

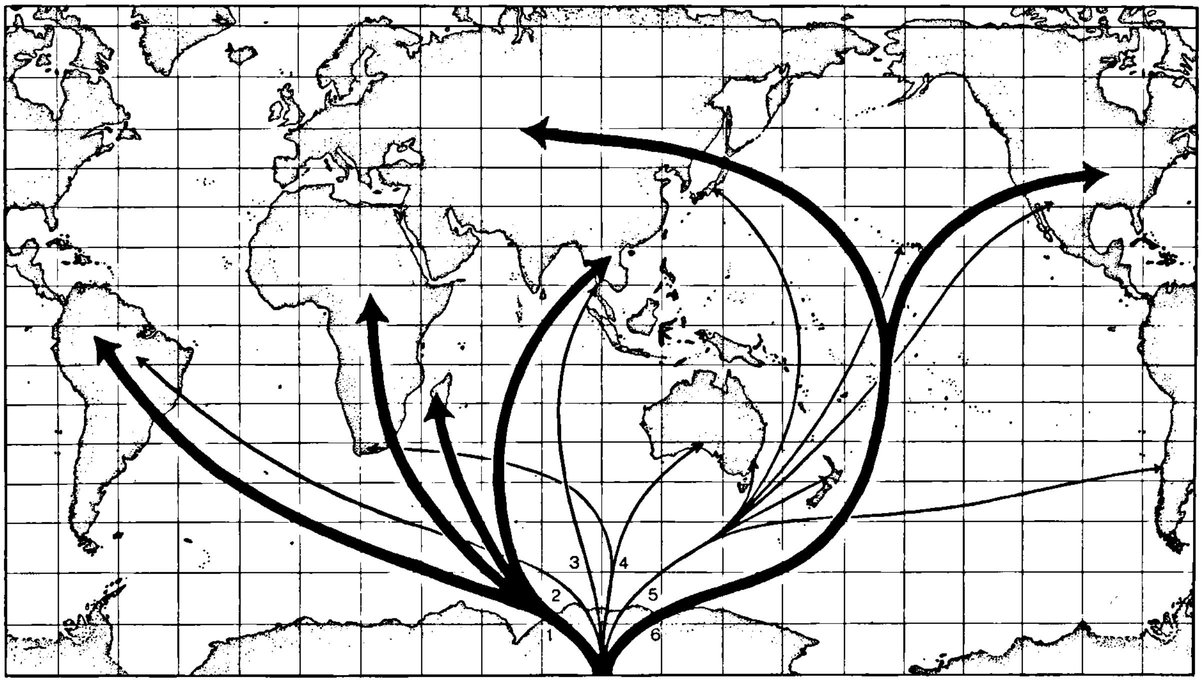


Fig. 8. Diagrammatic representation of the dispersal of the diplochetan groups, assuming a southern origin. 1, Spirostreptida; 2, Pseudonannolenidae; 3, Cambalopsidae; 4, Iulomorphidae; 5, Cambalidae; 6, Julida. The fat arrows indicate the dominant taxa of the southern (Spirostreptida) and northern (Julida) hemispheres. The amphi-Pacific distribution of the Cambalidae is explained by assuming a dispersal route from eastern Gondwana northward. The Holarctic range of the Julida is supposed to be the result of dispersal northward similar to that of the Cambalidae, with extinction in the southern hemisphere and radiation and dispersal westward towards Europe and eastward to North America.

ancestor of the iulomorphid type in the eastern part of the southern continent. They migrated northward in the Pacific area where both groups penetrated the Holarctic region and dispersed westward in the Palearctic and eastward in North America. This hypothesis is illustrated in fig. 8. Obviously, the Julida were most successful in occupying the Holarctic region; the Cambalidae suffered from a considerable amount of extinction leading to their current fragmented distributional pattern.

PALEOGEOGRAPHY

Considering the Gondwanic distributional patterns of the Spirostreptida, Iulomorphidae, Pseudonannolenidae and Cambalopsidae, it seems likely that the initial phase of evolution of the Diplocheta occurred during the early Mesozoic or late Paleozoic. The distribution of the Diplocheta in the southern hemisphere must therefore be explained along the lines of the division of the southern continent, Gondwana, into the southern continents of today, but will not be discussed here. The only point I want to make concerns southeastern Asia. Contrary to the more general opinion among geologists, the evidence of diplopod distribution points towards a close contact between India, Farther India and the Sunda area prior to the collision of India and Central Asia. With regard to diplochetan distribution the occurrence of the Spirostreptida and Cambalopsidae in Southeast Asia again supports this evidence. It is therefore that I see the present composition of Southeast Asia as the result of the collision of a number of smaller continental blocks of which India was the most recent addition (see e.g. Ridd, 1971; Crawford, 1974; McElhinny et al., 1981; Archbold et al., 1982; Audley-Charles, 1983, for the geological opinion).

It seems quite unlikely that the current distribution of the Cambalidae, taking into account their taxonomical relationship with the Julida and the Iulomorphidae, can be explained by assuming a migration northward (or southward) along both sides of the Pacific. It seems rather unlikely that ever a continuous land bridge existed which would have enabled such a dispersal. Rather I tend to explain this distributional pattern by following the ideas of certain geologists with regard to the former existence of a continental block, originally lying east and northeast of Australia which subsequently split, the fragments drifting towards South America, North America and East Asia (see e.g. Nur & Ben-Avraham, 1977; Audley-Charles, 1983). Especially the Lost Pacifica concept of the first authors is very attractive considering the current distribution of the Cambalidae. The occurrence of the Cambalidae on the Hawaiian islands has always been regarded as a rare, if not unique, case of passive transoceanic dispersal over a long distance. I regard it much more plausible to explain it by assuming a drift of the continental basis of this island range away from one of the northern continental blocks.

It is likewise possible that the explanation of the distribution of the Cambalidae should be sought along the lines of the Pacifica concept of Melville (1981). Unfortunately, I am not competent to give an opinion on the geological foundation of the various Pacifica concepts.

EPILOGUE

The distributional pattern as illustrated here for the Diplocheta seems to be unique in Diplopoda. However, a pattern as shown by the Cambalidae and Julida together is more or less paralleled by at least one group: the order Craspedosomatida (= Chordeumatida). Here too we are dealing with a taxon combining a Holarctic distribution with an amphi-Pacific range extending southward to include Australia and Tasmania, New Zealand and Chile. Unfortunately the internal classification of this order has not yet been worked out satisfactorily, and does not yet provide a basis even for a preliminary evaluation.

Outside the Diplopoda perhaps the order Lithobiida of the Chilopoda may ultimately provide a comparable distributional pattern.

At any rate, the eventual consequence of the forelying hypothesis may be the exciting idea that at least one, and possibly more of the higher diplopod taxa dominant in the northern hemisphere found their origin in the southern part of the world and reached the Holarctic by way of a Pacific route of dispersal.

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