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The evolution of segmentation of centipede trunk and appendages

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Abstract

The segmentation of centipedes is interpreted in the light of a biphasic model of segmentation (holomeric plus meromeric). The mid-body anomaly (e.g. in the alternating short and long terga, or in the sequence of segments with and without spiracles) is regarded as due to an early patterning of the embryo, occurring before the onset of meromeric segmentation and affecting a level within the fourth eosegment of the trunk. Comparisons with the Diplopoda suggest that genital structures such as millipede gonopods did probably develop originally at this spot, whose position remained marked even after the transition from a putatively progoneate to the current opisthogoneate condition of centipedes, perhaps following gene duplication and divergence of expression patterns of the paralogues. A new lower limit for the number of leg-bearing segments [27, in a male specimen of *Schendylops oligopus* (Pereira, Minelli & Barbieri,1995)] is established for Geophilomorpha. Coevolutionary trends involving the segmentation of the trunk, the segmentation of the appendages (especially the antennae), the postembryonic developmental schedule and the presence or absence of regeneration ability supports a recent view of the appendages as evolutionarily divergent duplicates of the main body axis.

Key words: Serial homology – centipedes – Chilopoda – Geophilomorpha – meromeric segmentation – holomeric segmentation – paramorphic axes – regeneration

Introduction

The origin and evolution of arthropod segmentation have become hot topics of research, following the recent burst of discoveries in the field of developmental genetics. Most experimental work has been carried on arthropods with highly derived body segmentation and tagmosis, like *Drosophila* and other insects. However, a growing body of data is now being produced for other arthropod taxa as well, including branchiopod anostracans (*Artemia*), possessing a higher number of segments and a possibly primitive tagmosis. However, data for the myriapod groups are extremely limited. This is unfortunate, for two reasons at least. First, in most traditional views of the evolution of arthropod segmentation the multisegmented condition of myriapods and the modest degree of tagmatization of their body are regarded as primitive within the phylum: primitive, at least, in respect to the insect condition (e.g. Dohle 1988). Second, recent investigations in molecular phylogeny (e.g. Friedrich and Tautz 1995; Boore et al. 1995, 1998) and comparative neurology (Whitington et al. 1991) have apparently shaken the traditional belief in close affinities of insects and myriapods, the first being perhaps phylogenetically closer to crustaceans (or to some crustacean groups at least) than to the latter (or to some myriapod groups at least). The possible revised phylogenies emerging from this molecular evidence may suggest new scenarios for the evolution of segmentation within arthropods (Dohle 1997).

In spite of the virtual absence of data on the developmental genetics of myriapods (but see Grenier et al. 1997; Smith 1998), we believe that a careful re-examination of the current evidence and of a few hitherto unpublished data may suggest a new interpretation of the origin and evolution of segmentation in the myriapod groups. In this paper we will discuss segmentation in one major myriapod clade, the centipedes (Chilopoda). The potential interest of Chilopoda as a model group for the study of segmentation has been repeatedly stressed in recent years, e.g. by Minelli and Bortoletto (1988), Minelli and Fusco (1997), Fusco and Minelli (2000) and Arthur (1999).

We will build here on the conceptual framework developed by one of us in two recent papers (Minelli 2000a; b). The first of these papers develops a biphasic model of segmentation, introducing the concepts of holomeric and meromeric segmentation. These are two levels, or two temporal layers, of segmentation. Holomeric segmentation corresponds to an earlier phase involving the whole body axis or the whole axis of an appendage. Products of holomeric segmentation are ‘primary segments’ or eosegments (a term first introduced by Minelli and Bortoletto 1988). The subsequent phase of meromeric segmentation that often (but not necessarily) develops within one or more eosegment(s) is possibly just a kind of extended compartmentalization *sensu* Garcia-Bellido et al. (1973). Current evidence suggests that this process follows two rules. First, when more than two segmental units are formed within an eosegment, these units arise from a stereotyped pattern of subdivisions, where only the first and the last unit (those in contact to the anterior or posterior boundary of the eosegment) are allowed to divide. Second, when several contiguous eosegments undergo meromeric segmentation, the genealogy of segmental units thus generated is the same in all of them, but for a possible truncation of the genealogical tree in one or a few terminal eosegments, at the anterior (proximal in the appendage) or the posterior (distal in the appendage) end of the array. According to Minelli (2000a), processes of meromeric segmentation give rise to vertebrate rhombomeres, the annulation of leeches, the subdivision of the distal part of the insect antenna in flagellomeres, and also the segmentation of the trunk in centipedes. The leg-bearing section of a centipede body has been interpreted by the same author as comprising eight eosegments, which undergo meromeric segmentation under stereotyped patterns of subdivision, different in the different centipede groups. In this paper we will add new data and discuss this interpretation of segmentation in a phylogenetic perspective. We believe we will be able at last to settle the old dispute between two opposite interpretations of the evolution of myriapod segmentation, i.e. Verhoeff's principle of elongation (*Elongationsprinzip*, e.g. Verhoeff 1928) and Brölemann's principle of abbreviated development (*tachygenèse*, e.g. Brölemann 1921, 1932) (see also Minelli 1992).

The other paper (Minelli 2000b) suggests that appendages such as legs, antennae, etc. may be regarded as kinds of duplicates (paramorphs) of the main body axis, specifically characterized by the lack of an endodermal component. Qualifying the appendages as paralogues of the main body axis means that the evolution of the appendages is not independent from the evolution of the trunk, in so far as their growth and patterning continue to depend on a largely common set of genes. In Minelli (2000b) reference to centipedes was limited to mentioning that the correspondence between trunk and appendages extends, in this group, to the developmental modus. In the anamorphic centipedes (Scutigeromorpha, Lithobiomorpha and Craterostigmomorpha) the number of body segments increases postembryonically (but during the early stage(s) only: hemianamorphosis) and this behaviour has an equivalent in the postembryonic increase in the number of segments of the antennae and the posterior legs (again, early stages only, and posterior legs only). On the contrary, in the epimorphic centipedes (Scolopendromorpha and Geophilomorpha) the number of body segments does not increase postembryonically and all legs are present at hatching. In most Scolopendromorpha there is either no postembryonic increase in the number of antennomeres or it is very limited, although in a few it is considerably greater than in some Lithobiomorpha. There is no postembryonic increase in the number of antennomeres in the Geophilomorpha.

Materials and methods

Segment counts

The following discussion of segment number in centipedes is mainly based on our previous work and other literature data (summaries in Minelli and Bortoletto 1988; Minelli 1993; Berto et al. 1997), but also on our ongoing taxonomic and morphological studies of world-wide geophilomorphs.

Phylogeny

As to the relationships of the main centipede clades, we will follow centipede phylogeny as outlined by Shinohara (1970) and Dohle (1985) on the basis of mainly morphological characters. This is also supported by Giribet et al.'s (1999) analysis of molecular data (see also Edgecombe et al. (1999) and Shultz and Regier (1997) for alternative molecular phylogenies of the Chilopoda). For the internal phylogeny of Scolopendromorpha, we have consulted Schileyko and Pavlinov (1997), but we had some problems accepting the character polarity given to characters no. 1, 2, 3, 4, 9, 10 in their matrix. Accordingly, these have been re-coded as in legend of Figure 5. In our re-analysis we left out Schileyko & Pavlinov's character no. 2 (number of leg-bearing segments), as we intended not to bias the analysis with a preconceived polarity to be given to the alternative states with 21 versus 23 pairs of legs. We agree with Schileyko and Pavlinov (1997) that the order Scolopendromorpha needs complete revision of its classification using both new characters and new methods of analysis and regard our phylogeny as provisional.

Results

The segmentation of the trunk

Number of segments

The conventional description of the centipede body identifies two tagmata, the head and the trunk.

The segmental composition of the head is currently interpreted in the same terms as the insect head. Centipede head appendages have been also identified and named correspondingly: antennae, mandibles, maxillae I (= insect maxillae), maxillae II (in insects, fused into a labium). This topic requires a revisitation in the light of the new insights in arthropod phylogeny, with increasing evidence suggesting a closer relationship between insects and crustaceans (or, at least, some crustacean groups) than between insects and the myriapod groups. Nevertheless, a larger clade Mandibulata comprising all these arthropods, to the exclusion of Chelicerata, could still hold. If so, the chances that the segmental composition of the centipede head has been grossly misunderstood would be very limited. On the other hand, the traditional views as to the segmental composition of the insect head have been also repeatedly questioned, in recent years, especially from the viewpoint of the expression patterns of genes involved in early embryonic patterning of the main body axis. However, the very detailed analysis performed by Rogers and Kaufman (1996, 1997) on the structure of the head as revealed by engrailed protein patterns in insects belonging to different orders (Diptera, Siphonaptera, Orthoptera, Hemiptera) seems to finally settle the question in favour of recognizing six head segments, two pre-oral and four postoral. Accordingly, until direct evidence of gene expression in the centipede head becomes available, we can still reasonably count six segments here too. Minelli and Bortoletto (1988) adopted this same figure when developing the 'octonary model' of centipede segmentation discussed below.

The first postcephalic segment of centipedes is conventionally described as the first (modified) trunk segment, or maxillipedal segment, whose appendages are the poison-claws.

The following leg-bearing segments are distinctly heteronomous in Lithobiomorpha and in Craterostigmomorpha; in Scolopendromorpha the heteronomy is apparent in the anterior segments, less so or not at all in the more posterior ones; and Geophilomorpha are nearly homonomous. In this paper we will not analyse the differentiation and patterning of trunk segments (see Minelli 1992; Minelli and Fusco 1995, 1997; Turcato et al. 1995; Berto et al. 1997; Fusco 1999; Fusco and Minelli 2000). The following discussion deals instead with the number (this section) and the origin (below) of the segments.

It has long been known that all adult centipedes have an odd number of leg-bearing segments. This number is 15 in Scutigeromorpha, Lithobiomorpha and Craterostigmomorpha; 21 or 23 in Scolopendromorpha; 27–191 in Geophilomorpha (but see Kettle et al. 1999, 2000 for a homeotic mutant male of *Strigamia maritima* (Leach, 1817) with 48 pairs of legs!).

Up to the present, the lowest number of leg-bearing segments recorded in a geophilomorph centipede was indeed 29 (Minelli and Bortoletto 1988). This number is known to occur in three geophilid and one schendylid species, i.e. in both sexes of *Dinogeophilus oligopodus* Pereira, 1984 and in the males of *Geophilus persephones* Foddai & Minelli, 1999 (female unknown), *Geophilus richardi* Brölemann, 1904 (most males of this species, however, have 31 leg-bearing segments and females have 33) and *Schendylops oligopus* (Pereira, Minelli & Barbieri, 1995) (31 in the females).

We record here for the first time the occurrence of a still lower number of leg-bearing segments, i.e. 27, in a male specimen of *Schendylops oligopus* (Fig. 1): this is thus the lowest number of leg-bearing segments ever recorded in a geophilomorph. In addition to the two males forming the original type material (Pereira et al. 1995), we have now seen 29 males and 35 females of this species, plus 13 juveniles of uncertain sex. All males but one have 29 pairs of legs and all females have 31, in accordance with the usual sexual dimorphism of schendylid geophilomorphs. The exceptional male with 27 pairs of legs has been collected by M.O. de A. Ribeiro in Brazil, Distrito Agropecuario Rio Suframa (J) (03°34′S, 60°60′W) (Brazil) on 7 November 1990 (coll. A. Minelli, Padova) together with five males and five females that had the ordinary numbers of segments.

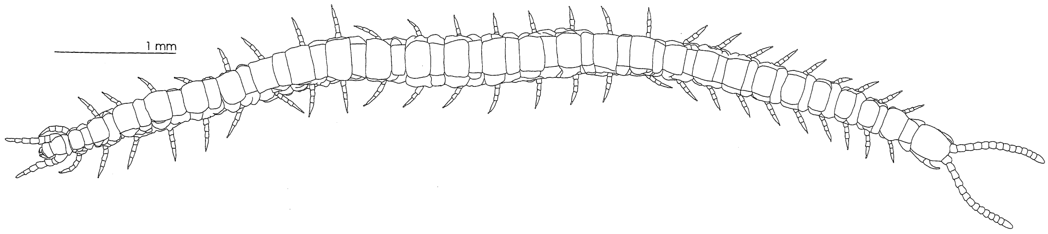

Fig. 1. Habitus of the geophilomorph specimen with the lowest known number (27) of leg-bearing segments. It is a male *Schendylops oligopus* Pereira, Minelli & Barbieri, 1995 from Brazil, Distrito Agropecuario Rio Suframa (J) (03°34′ S, 60°60′ W) (coll. A. Minelli, Padova)

With this new finding, the hiatus between Scolopendromorpha (21 or 23 pairs of legs) and Geophilomorpha (an odd number of leg-bearing segments in the range 27–191) is further reduced. We have strong reasons to believe, however, that the geophilomorph species with a very low number of leg-bearing segments do not represent transitional steps in a morphocline from scolopendromorph-level to geophilomorph-level segmentation, but individual (and parallel) instances of secondary reduction in segment number (see below).

Development of segments

All centipedes with 15 leg-bearing segments in the adult condition, i.e. Scutigeromorpha, Lithobiomorpha and Craterostigmomorpha, develop hemianamorphically. That is, the juvenile hatching from the egg is a larva showing a number of segments and appendages lower than the adult one. The final complement of body segments and appendages is progressively reached through some larval moults (anamorphic phase of the postembryonic development). Reproductive maturity, however, requires further postlarval moults without associated changes in segmentation (epimorphic phase of the postembryonic development).

According to the evidence available to date (detailed postembryonic developmental schedules are known for just a sample of centipede species; see Andersson 1976, 1978, 1980, 1982a, b, 1983, 1984a, b; also Verhoeff (1902–25) and Lewis (1981) for summaries of older evidence), the first larval stage of Scutigeromorpha possesses only four pairs of fully developed legs, whereas the first larval stage of Lithobiomorpha is more advanced, already possessing seven pairs (but sometimes six or eight; Andersson 1979) of fully developed legs. The Craterostigmomorpha begin their postembryonic development in a still more advanced condition, the first free stage already possessing 12 of the 15 pairs of legs present in the adult. Finally, all body segments develop in the epimorphic Chilopoda (Scolopendromorpha and Geophilomorpha) during the embryonic life and the postembryonic development of their appendages is limited (with the exception of a few species such as *Otostigmus longicornis* (Tömösváry, 1885)) to a very small increase in the number of antennal segments in some Scolopendromorpha. The apparently counterintuitive result thus obtained (but see below) is that centipedes with the lowest final number of segments require anamorphosis, whereas those with higher and sometimes very high numbers of segments achieve their full complement of segments during embryonic life or, at most, before beginning active postembryonic life (see Chalande (1905) for some old evidence of the addition of a few subterminal segments in geophilomorphs after hatching).

Regeneration of segments

One could expect some power of regeneration of trunk segments in the arthropods with anamorphic development, but no data support this expectation. In our view, this fact suggests that the posterior growth zone of anamorphic (or hemianamorphic) myriapods is not a conventional unpatterned blastema, but an organized region where *at least* the holomeric segmentation has been already, and definitively, completed.

Origin of segments

Minelli and Bortoletto (1988) proposed a biphasic model of centipede segmentation whereby the segment complement of the whole body (head and terminal segments included) would result from one or more runs of binary subdivision of a small, but not necessarily fixed, number of primary segments ('eosegments'). This model has been critically revised by Minelli (2000a), by suggesting that:

(a) secondary segmentation does not extend over the whole body length, but is limited to the leg-bearing part of the trunk;

(b) the number of eosegments affected by meromeric segmentation is the same (eight) in all centipedes; and

(c) the secondary subdivision of the eosegments follows the rules of the meromeric segmentation: (1) merosegments are formed from a stereotyped pattern of subdivisions, where only the merosegments in contact to the anterior and posterior boundary of the eosegment are allowed to divide; (2) contiguous eosegments undergoing meromeric segmentation generate merosegments according to identical lineage patterns apart from possible lineage truncation in one or a few terminal eosegments. These rules probably derive from some basic properties of metazoan cell biology (cell adhesion, cell sorting).

Thus, a two-merous meromeric segmentation of eight trunk eosegments would give rise to 16 segmental units corresponding to the forcipular segment plus the 15 leg-bearing segments of Scutigeromorpha, Lithobiomorpha and Craterostigmomorpha. A uniform three-merous meromeric segmentation of eight trunk eosegments would give rise, instead, to 24 segmental units: an attractive interpretation for the Scolopendromorpha with 23 leg-bearing segments (but see below). Further degrees of meromeric segmentation (with 4–24 units per eosegment) would generate the higher numbers of segments present in the Geophilomorpha. For instance, a stereotyped four-merous meromeric segmentation of eight trunk eosegments could produce the forcipular segment plus 31 leg-bearing segments, whereas a stereotyped 24-merous meromeric segmentation would produce the forcipular segment plus 191 leg-bearing segments (the highest number recorded thus far, in *Gonibregmatus plurimipes* Chamberlin, 1920).

Comparison with other instances of meromeric segmentation (in particular, with the meromeric annulation of (eo)segments in leeches) suggests that the degree of meromeric segmentation might be incomplete at the two ends (anterior and posterior) of the segmental array. It has been pointed out already (Minelli 2000a) that some reduction in the degree of meromeric segmentation of the last eosegment(s), comparable indeed to that observed in the annulation of leeches, could explain the sexual dimorphism in the number of segments exhibited by all Geophilomorpha excluding the Mecistocephalidae. We will see below that a lower degree of meromeric segmentation of the first trunk eosegment(s) could also explain how the first step beyond the 15 leg-bearing-segments condition was obtained, with the 21 leg-bearing segments of putatively basal (see later) Scolopendromorpha. This interpretation will be deferred to a later section, however, as it requires an adequate discussion of the 'mid-body segmental anomaly.'

The segmentation of the appendages

Number of antennal segments

In strict numerical terms, the antennal segments of the five traditional centipede orders seem to follow a trend opposite to that of the body segments. In the Scutigeromorpha the number of antennal segments is very high (up to 400+) and variable individually. The number of antennomeres becomes lower and more stable in Lithobiomorpha. In this group, the range is 17 to approximately 100, with highest numbers being quite probably a secondary (and adaptive) modification of specialized cave species such as *Lithobius lorioli* Demange, 1962 (99–101 antennomeres), *L. pedisulcus* Serra, 1977 (108–109), *L. drescoi* Demange, 1958 (100–103), *L. sbordonii* Matic, 1967 (111) and *L. matulici* Verhoeff, 1899 (106–110) (Eason 1992; Negrea and Minelli 1994). The number of antennomeres is generally variable, even within those species where this number is very low (around 20). In the remaining groups the number of antennomeres is fixed or nearly fixed. It is 17–18 in the only known species of Craterostigmomorpha and 14 in all Geophilomorpha. In several genera of Scolopendromorpha, the number of antennomeres is 17 and generally invariant within the species, but numbers higher than 17 as well as intraspecific variability are known, for instance, for several *Scolopendra* species, e.g. 19; 17–18; 18–23; and even 21–31 (*S. viridis* Say, 1821). Numbers lower than 17 have been given for *Tidops simus* Chamberlin, 1915 (13) and *Kartops guianae* Archey, 1923 (11) which Lewis (2000) suggested were probably the result of damage. These species are apparently known only from single specimens and are worth revisiting.

This increasing reduction and stabilization of the number of antennomeres can be interpreted as an instance of increasing paedomorphosis (progenesis). Curiously, this trend runs parallel to an opposite increasing peramorphosis (retardation) of the meromeric segmentation of the trunk.

Development of antennal segments

The number of antennomeres increases postembryonically in Scutigeromorpha and Lithobiomorpha. We are not sure, in this respect, about Craterostigmomorpha, where the final number of 17–18 antennomeres, however, is present since the beginning of postembryonic life. In some Scolopendromorpha with more than 17 antennomeres there is convincing evidence of a small postembryonic increase in the number of antennomeres. In *Scolopendra amazonica* Bücherl 1946 (possibly, a taxon not specifically distinct from *S. morsitans* Linnaeus 1758) Lewis (1968) demonstrated that bigger (adult) specimens have a slightly higher number of antennomeres than the smaller (juvenile) ones; moreover, whereas the 16 proximal antennomeres in specimens with 17 antennomeres are all of more or less equal size, the penultimate and antepenultimate ones in specimens with 18 antennomeres are small, obviously having been formed by recent subdivision of the former penultimate one. In Geophilomorpha all 14 antennomeres are already present since the beginning of postembryonic life.

The peculiar structure of the antenna in Scutigeromorpha presents great difficulties in tracing detailed homologies, at the level of single antennomeres, with the corresponding appendages of the other centipedes. But comparisons are possible, and interesting, between Lithobiomorpha, where there is a postembryonic increase in the number of antennomeres, and the groups where this number is not subject to postembryonic increase. These comparisons have been first proposed by Lewis (2000), who noticed that Lithobiomorpha, as described by Scheffel (1969) and Andersson (1979), pass through a larval stage (LII) with 14 antennomeres (the same number as in Geophilomorpha) and 17 (as in the majority of Scolopendromorpha). We believe that these numerical identities are not due to pure chance.

Regeneration of centipede appendages

Regeneration of appendages (legs and antennae) is well documented in Scutigeromorpha and Lithobiomorpha, whereas there is only limited evidence of regeneration of the last pair of legs and antennae in Scolopendromorpha and no reliable example of regeneration of legs or antennae in Geophilomorpha. We have no data about the possible occurrence of regeneration in Craterostigmomorpha.

Leg regeneration in Scutigeromorpha was studied by Verhoeff (1902–25) and Cameron (1926). The process is well characterized by what Verhoeff (1902–25) described as 'plötzliche Regeneration', i.e. sudden regeneration. That means, that the regenerating appendage is already equipped with all its parts as soon as it appears. This event occurs either after the first moult following amputation, or a moult later, apparently depending on the timing of the amputation within the intermoult.

The course of regeneration is somewhat different in Lithobiomorpha, where Newport (1844) first described the phenomenon. As for the leg, Verhoeff (1902–25) noted that the newly regenerating telopodite consists of praefemur, femur, tibia and a one-article tarsus and completely lacks setae, epidermal glands, muscles and tendons. After another moult, the appendage is not simply longer, now attaining about half the length of a normal leg, but also possesses the trochanter, the second tarsal article, the claw and its tendon; the musculature is also developing, although still gracile; many sensory setae and epidermal glands have appeared too. Still lacking, however, are the spines, only the (originally) stronger ones being now present as small anlagen. At a still further stage, the appendage appears complete, although still smaller than a normal one. The regeneration of the lithobiomorph antenna also takes place in a stepwise fashion. Following amputation distal to the second antennomere of the left antenna of a mature female of *Lithobius forficatus* (Linnaeus, 1758), Verhoeff (1902–25) obtained a first nine-segment regenerate that grew after one more moult to a 32-segment regenerate. Scheffel (1989) obtained, in *L. forficatus*, a modal value of six antennomeres in the first regenerating antenna. This figure matches quite well the number of antennomeres in the first (LO) larvae, which are seven in *L. forficatus*

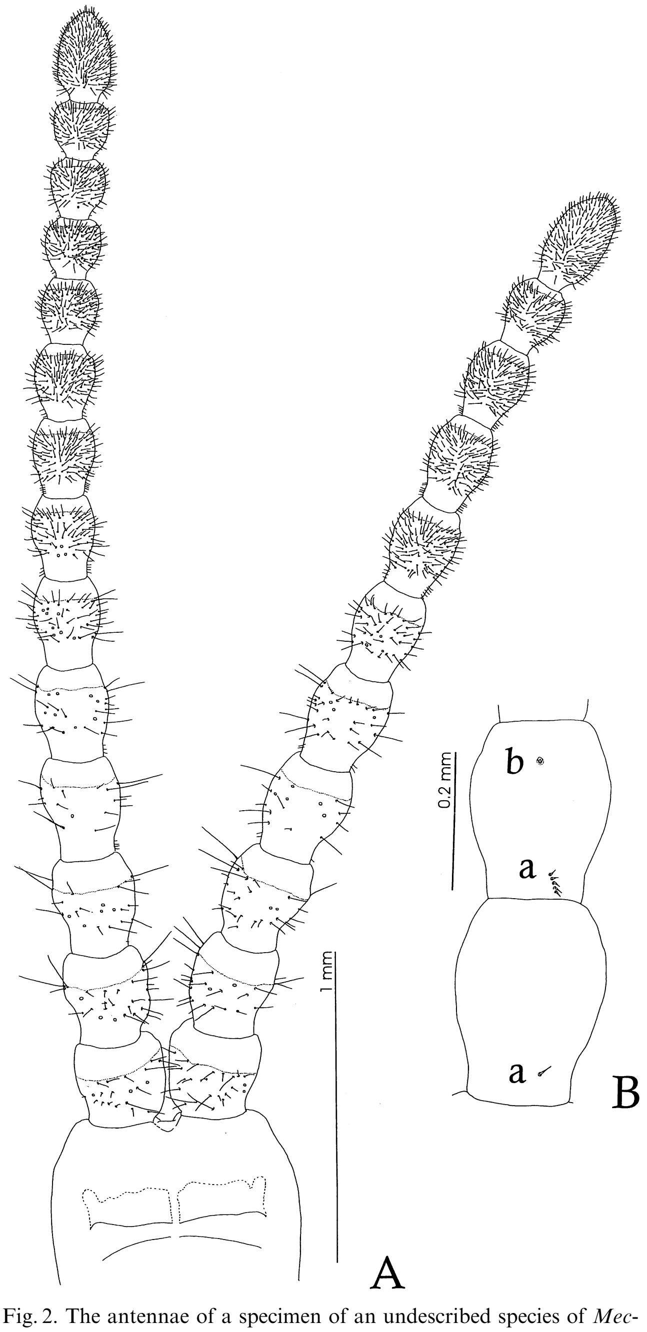

Fig. 2. The antennae of a specimen of an undescribed species of *Mecistocephalus* from Tahiti, leg. P. Lehtinen. A, ventral view of the antennae (the left is defective); B, dorsal view of antennomeres VI-VII of the right (normal) antenna, to show the positions of the sensilla microtrichoidea (a) and coeloconica (b) considered in Table 2

(Andersson 1979) and *L. validus* Meinert, 1872 (= *L. punctulatus* C.L. Koch, 1847) (Kos 1997). Less easy to interpret, from a numerical point of view, are the results published by Weise (1991) on the regeneration of antennae removed from third stage larvae of *L. forficatus*. In this case, the regenerates observed 7 ± 1 days after amputation presented five to 12 articles.

Verhoeff (1940) described also a putative case of regeneration affecting a forcipular telopodite in a *Lithobius* specimen he identified as *L. latro sellanus* Verhoeff, 1937. The evidence in favour of regeneration is not compelling, the case being based on the conditions of a specimen as found in nature, but we do not see any serious reasons for rejecting it.

As for the Scolopendromorpha, Newport (1844) was the first to provide circumstantial evidence of regeneration. Specimens with terminal legs of reduced size and with a subnormal armature of spines, suggesting regeneration, are not rare, e.g. in *Scolopendra* spp. and *Cryptops* spp. Species of this latter genus, as those of *Asanada*, *Alipes* and, perhaps, *Rhysida*, readily shed the anal legs. No data are available, on the other hand, as to the possible regeneration of trunk legs. As to the antennae, Lewis (1968) identified as regenerated a sizeable percentage of the antennae in a Nigerian population of *Sc. amazonica*, the criterion being that an antenna with a few proximal 'normal' antennomeres followed by a variable number of very small (= short) ones should be confidently regarded as the product of regeneration.

As for the Geophilomorpha, we do not know any reliable instance of regeneration of either the antennae or the legs and are inclined to think that no such regeneration actually occurs in this group. To be sure, geophilomorph specimens with an antenna shorter than normal, with n < 14 antennomeres are sometimes found (Fig. 2). It may be tempting to regard these 'defective' appendages as due to regeneration after total or partial ablation of the original appendage during a previous developmental stage, but all circumstantial evidence we are aware of points in a different direction. In these defective antennae, the arrangement of selected markers (sensilla) allows the identification of the individual segmental components, thus suggesting simple repair of a distally damaged antenna, with reshaping of the last surviving antennomere, following one or more moults, without fully excluding, in some instances at least, the outcome of developmental defects, i.e. nondisjunction (*not* fusion!) of two or more conventional antennomeres. This interpretation was given by Minelli (2000a) to the eight defective legs of the holotype of *Geophilus persephones* Foddai & Minelli, 1999.

Verhoeff (1940) claimed regeneration for a forcipular telopodite in a specimen of *Schizotaenia* (*Eurytion*) *dudichii* Verhoeff, 1940, but this example is not convincing. Verhoeff's illustration shows a nearly normal trochanteropraefemur followed by a nearly normal tarsungulum. The lack of the tibial segment may be explained as in the case of *G. persephones*.

Origin of antennal segments

The postembryonic increase in the number of antennomeres as illustrated by Scheffel (1969) and Andersson (1979) for the first larval stages (LO to LII) of several lithobiomorph species is a clear example of meromeric segmentation which follows the two rules defined and illustrated by Minelli (2000a) (see above). Segments 1, 2, 4 and 6 of the typical seven-antennomere appendage of the first larval stage of most lithobiomorph species behave like trunk eosegments ready to undergo stereotyped meromeric segmentation. The course of this process is the same for 'eo-antennomeres' 2, 4 and 6, but abridged for the most proximal 'eo-antennomere' 1. For example, during the further development to a 14-antennomere appendage as found in the LII stage, each of the 'eo-antennomeres' 2, 4 and 6 gives rise to three units, whereas the meromeric segmentation of 'eo-antennomere' 1 is only two-merous.

We believe, however, that the seven-segmented antenna in L0 lithobiomorph larvae (but L0 of *Lamyctinus coeculus* (Brölemann, 1889) has eight antennomeres and L0 of *Esastigmatobius* has 10; see Andersson 1979) already possesses a

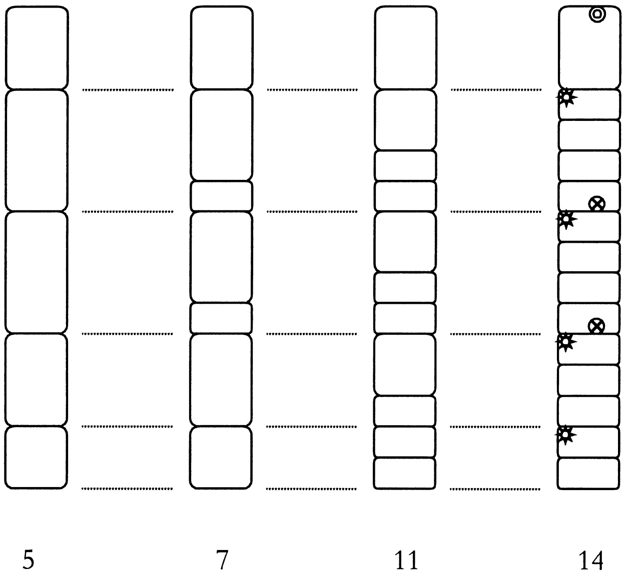

Fig. 3. Hypothetical pattern of meromeric segmentation during the embryonic development of the antenna in Geophilomorpha. No more than five eosegments (first antenna from left) are involved. Symbols on the complete (normal) 14-antennomere antenna mark the dorsal (clusters of) specialized sensilla usually present on selected antennomers (see text)

first degree of meromeric segmentation, the basic holomeric pattern of the appendage only including five primary units (Fig. 3). Quite probably, the low and more or less strictly fixed number of antennomeres found in Craterostigmomorpha, Scolopendromorpha and Geophilomorpha is the result of heterochronic (progenetic) arrest of a meromeric segmentation perfectly comparable to that of Lithobiomorpha (cf. Lewis 2000).

Two characteristic distribution patterns of antennal sensilla support the model in Figure 3.

On the antennae of most Geophilomorpha there are (a) a cluster of dorsal specialized sensilla (sometimes reduced to just one sensillum, as in some Geophilidae) close to the ectolateral corner on the antennomeres II, V, IX and XIII and (b) a single dorsal sensillum microtrichoideum close to the proximal border of antennomeres VI and X. We believe that the ectolateral sensilla mark the distal end of the set of merosegments derived from each of eosegments 1–4, whereas the proximal sensillum microtrichoideum mark the proximal end of eosegments 3 and 4. This analysis suggests five eosegments giving rise to antennomeres I-II, III-V, VI-IX, X-XIII, and XIV, respectively. Interestingly, exactly the same distribution of specialized sensilla has been described for a larva II *Lithobius microps* Meinert, 1868 which has 14 antennomeres (Lewis 2000).

Geophilomorph antennae with less than 14 antennomeres are not so rare. The best evidence we can offer for the value as segmental markers of the patterns of antennal sensilla is provided by a series of defective antennae in a population of *Schendylops pampeanus* (Pereira and Coscarón 1975–76) from Argentina: Bosques, Florencio Varela. Two of these specimens were illustrated by Pereira and Coscarón (1975–76) and one more by Pereira (1999), but the sample (161♀♀ 130♂♂ 85 juv.) contained no less than 13 defective specimens (Table 1). The number of antennomeres in these defective antennae ranges between five and 13 (no specimen with 11 antennomeres was found, probably just by chance). Despite their conspicuous defects, all antennae have the usual ectolateral sensilla on antennomeres II, V, IX and XIII, whenever enough antennomeres are present; therefore, in antennae with five, nine or 13 antennomeres, ectolateral sensilla are present on the terminal antennomere too; that never happens in a normal geophilomorph antenna. But the last antennomere, irrespective of the total antennomere number, is *always* provided with the usual set of external and internal claviform and apical specialized sensilla, as present on antennomere XIV of all normal geophilomorph antennae.

We found similar patterns in other defective antennae, e.g. in the 11-antennomere left antenna of *Mecistocephalus* sp. in Figure 2. In this specimen, for antennomeres I to X, kind, number and distribution of both dorsal and ventral sensilla in the defective antenna agree quite closely with those in the normal antenna. The matching is particularly good for the dorsal sensilla microtrichoidea (Table 2), where the single proximal sensillum on antennomeres VI and X allows comparing the two antennae up to antennomere X included. Again, in a female *Orphnaeus brevilabiatus* (Newport, 1845) (Oryidae) from Tonkin (MNHN Paris) both dorsal and ventral pattern of sensilla on antennomeres II, V, IX and XIII are the same in the normal and the defective antenna, but for the presence of the terminal sensilla (normally on antennomere XIV) on the XIII (terminal) antennomere of the defective antenna.

A reasonable explanation for these patterns seems to be repair after loss of one or more terminal antennomeres, involving a repatterning of sensilla in what becomes the terminal article, but without any regeneration (formation of new antennomeres following the damage).

Lewis (2000) pointed out that scolopendromorphs that showed a postembryonic increase in antennomere number could regenerate antennomeres after loss, but in *Cryptops* spp. where the antennomere number is fixed at 17 the missing antennomeres cannot be regenerated. In *Cryptops* spp. with a reduced number of antennomeres some are elongated, as in some specimens of *S. pampeanus*, e.g. the specimen with five antennomeres.

Our examples of *S. pampeanus*, *Mecistocephalus* sp. and *O. brevilabiatus* with a reduced number of antennomeres can also be interpreted as a response to antennomere loss. The distribution of markers (specialized sensilla) on the antennomeres is consistent with loss of one or more distal antennomeres. Repair after damage would seem to be a simpler explanation for these defective antennae although a developmental abnormality is always a possibility.

The alternating behaviour (dividing versus not dividing) of the seven elements in the antenna of L0 lithobiomorph larvae suggests that these seven units may derive from a previous run of meromeric division of a basic four- or five-segmented condition. We favour the five-segment interpretation (Fig. 3), according to which only two units display the full meromeric segmentation in giving rise to a 14-antennomere appendage, because this corresponds to the complete sensillar marking of Geophilomorpha that we have just discussed.

Discussion

Correlation between trunk and appendages and between segmentation and developmental schedules

Recent evidence from molecular developmental genetics casts doubts on the traditionally assumed independence of patterning of the trunk along its different 'Cartesian' body axes (Held 1995; Munn and Steward 1995; Newman 1996). In addition,

Table 1. Segmental composition (antennomere I through XIV) and distribution of sensilla on left (l) and right (r) antennae of 13 specimens (A to M) of *Schendylops pampeanus* Pereira and Coscarón from Argentina: Buenos Aires: Florencio Barela, Bosques, with at least one defective antenna each. In two antennae (? in the table) one or more distal antennomeres are missing. All terminal articles end with the usual complex of apical and lateral (claviform) sensilla (*). The specialized sensilla on antennomere II, V, IX and XIII are marked by +. When the terminal article in a defective antenna is either V, IX or XIII, both * and + occur together on it (the + sensilla, however, displaced to a less lateral position)

Specimen	A		B		C		D		E		F		G		H		I		J		K		L		M	
Sex	♀		♀		♂		♀		♀		♀		♂		♂		♂		♀		♂		♂		♀	
Side	l	r	l	r	l	r	l	r	l	r	l	r	l	r	l	r	l	r	l	r	l	r	l	r	l	r
Antennomeres	14	10	7	14	10	9	12	12	10	12	6	8	8	14	13	8	12	8	6	?	13	7	?	8	5	14
XIV	*			*										*												*
XIII	+			+										+	* +						* +					+
XII							*	*		*							*									
XI																										
X		*			*				*																	
IX	+	+		+	+	* +	+	+	+	+				+	+		+			+	+					+
VIII												*	*			*		*						*		
VII			*																			*				
VI											*								*							
V	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	* +	+
IV																										
III																										
II	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

Table 2. Number of dorsal sensilla microtrichoidea (a) and coeloconica (b) on the antennae of the *Mecistocephalus* sp. specimen of Fig. 2A; position of *a* and *b* as in Fig. 2B

	Defective antenna (11 antennomeres)		Normal antenna (14 antennomeres)	
	a	b	a	b
XIII			2	–
XII			2	–
XI			3	–
X	1	1	1	1
IX	4	2	3	2
VIII	4	1	3	1
VII	5	1	5	1
VI	1	–	1	–
V	5	–	5	–
IV	6	–	5	–
III	5	–	6	–
II	5	–	5	–

comparative morphological evidence suggests deep-rooted correlation (or, at least, parallelism) in the ways these axes become patterned during embryonic or postembryonic development (Minelli 1996, 1997, 2000b). Arthropods, in particular, provide extensive evidence for a still more pervasive network of correlations involving, besides the antero-posterior and dorso-ventral patterning of the main body axis, also the proximo-distal (PD) axis of the appendages and the 'temporal axis' of ontogenetic development (Minelli 1996).

Although a comprehensive and in-depth analysis of these patterns lies outside the scope of the present paper, we summarize here briefly (Table 3) the comparative evidence concerning body and appendage segmentation in centipedes and the correlation between segmentation and developmental schedules in the same group.

Hemianamorphic development correlates with a postembryonic increase in the number of antennomeres and with the ability to regenerate antennae and legs; it correlates, also, with high to very high (and generally variable) number of antennomeres but also, perhaps counterintuitively, with lower (and invariant) number of trunk segments. Epimorphic development correlates with the opposite features, i.e. lack of postembryonic increase in the number of antennomeres, reduced or lacking ability to regenerate antennae and legs, low (and generally fixed) number of antennomeres and higher to very high number of trunk segments. We will offer below an interpretation of these correlations. This will require, however, a prior discussion of some morphological and developmental peculiarities of centipede organization.

The mid-body anomaly and the origin of the opisthogoneate condition

The ventral aspect of an average lithobiomorph or scolopendromorph is approximately homonomous, but the dorsal and lateral aspects are more or less distinctly marked by an alternation of segments with long tergum dorsally and spiracles laterally and segments with short tergum dorsally and no spiracle laterally. This basic pattern, however, is 'disturbed' by what seems to be the lack of a short-tergum segment, or a segment without spiracles. The leg-bearing segments with spiracles are, thus, the following: (1), 3, 5, 8, 10, 12, 14 in Lithobiomorpha (but on 3 and 10 only in *Catanopsobius*); 3, 5 (7), 8, 10, 12, 14, 16, 18, 20 (22) in Scolopendromorpha. Spiracles on segment 1 are only present in a few representatives of the Lithobiomorpha, as are those on segment 7 in Scolopendromorpha. In scolopendromorphs with 21 leg-bearing segments the last pair of spiracles open on segment 20, in those with 23 leg-bearing segments, on segment 22. In the following we will refer to the break in the regular alternation of short versus long terga, or segments with versus segments without spiracles, as to the mid-body anomaly of Lithobiomorpha and Scolopendromorpha. Topographically equivalent 'anomalies' are also known in the other centipede groups.

The peculiar morphology of the dorsal side of the Scutigeromorpha and the unique nature and arrangement of their

Table 3. Postembryonic behaviour of trunk and appendage segmentation in the major centipede clades

	Trunk: postembryonic increase in the number of segments	Antennae: postembryonic increase in the number of antennomeres	Antennae: regeneration	Legs: regeneration	Number of leg-bearing segments	Number of antennomeres
Scutigeromorpha	yes (first stages only: hemianamorphosis)	yes	yes?	yes	15	up to 400+
Lithobiomorpha	yes (first stages only: hemianamorphosis)	yes	yes	yes (first stages only?? posterior legs only??)	15	17–100+
Craterostigmomorpha	yes (first stage only: hemianamorphosis)	no?	no?	?	15	17–18
Scolopendromorpha	no (epimorphosis)	yes	yes	last legs only?	21, 23	11(?) to 34; mainly 17–21
Geophilomorpha	no (epimorphosis)	no	no	no	27–191 (odd values only)	14

respiratory openings forbid a direct comparison with Lithobiomorpha, Craterostigmomorpha and Scolopendromorpha. The segmental ‘anomaly’, however, is clearly visible in this group too, in the long tergal plate covering three leg-bearing segments (6–8), rather than two, as the ‘normal’ terga. The segmental ‘anomaly’ concealed under the gross homonomy of Geophilomorpha will be described later.

The segmental ‘anomaly’ has been carefully investigated by Demange (1963, 1967, 1969), who studied in great detail the musculature of this region, not only in centipedes, but also in helminthomorph millipedes, which have a similar segmental ‘anomaly’ at the trunk site where their male gonopods are developed.

According to Demange, some factor acting very early in development inhibits the production of a short-tergum segment (or, at least, of its spiracles and appendages), also causing some troubles in the neighbouring segments.

In our opinion, Demange’s interpretation is basically correct. In particular, we agree with him in pointing to a very early determination of the segmental ‘anomaly.’ However, rather than stating the problem in the traditional terms of segment number, or long- versus short-tergum segments, we prefer to develop here an analysis of this feature in terms of holomeric and meromeric segmentation.

In the centipedes with 15 leg-bearing segments, i.e. Scutigeromorpha, Lithobiomorpha and Craterostigmomorpha (Fig. 4), the segmental ‘anomaly’ affects the derivatives of eosegment 4 which span, in our interpretation, leg-bearing segments 6 and 7. We do not see the need to assume the repression, or the disappearance, of a whole segmental unit, however. From these basic assumptions, let us develop our argument in respect to the Geophilomorpha and the Scolopendromorpha.

In most Geophilomorpha, the mid-body anomaly is much less conspicuous than in the other centipedes and sometimes (e.g. Mecistocephalidae) hardly visible at all. In this clade, the series of spiracles is continuous and the terga are usually uniform along the whole trunk. Nevertheless, different kinds of mid-body anomaly are widespread in this clade too. What is peculiar to geophilomorphs is that the mid-body anomaly is less clearly localized than in other centipedes and generally extends over several segments. The phenomenon has been very aptly described by Eason (1964; pp. 35–36) in the following terms: ‘Characteristic of the Geophilomorpha is a change in the structure of the trunk which occurs before the mid-point of the body at about the junction of the anterior two-fifths with the posterior three-fifths; this change may be striking and abrupt as in *Nesoporogaster* [..], spread over several segments as in *Geophilus* and related genera [..], or absent altogether as in *Strigamia*. At this point, which will be called the ‘transition’, the body becomes broader, reaching its maximum breadth a few segments further back, and each segment becomes longer so that the legs become more widely spaced; at the same time the legs themselves become more slender, the arrangement of the pleurites alters and they become less well chitinized, the sterna lose much of their reticulation, and changes in the arrangement of the sternal pores frequently take place; it is also around this point that the characteristic sternal fossae of the Himantariidae are found and the carpophagus fossae of *Geophilus* terminate’. Particularly instructive is the behaviour of the segments provided with sternal fossae in several species of the family Himantariidae. These depressions, whose size, shape and precise location on the sternum vary according to the species, occur on a short range of contiguous segments. In *Stig-*

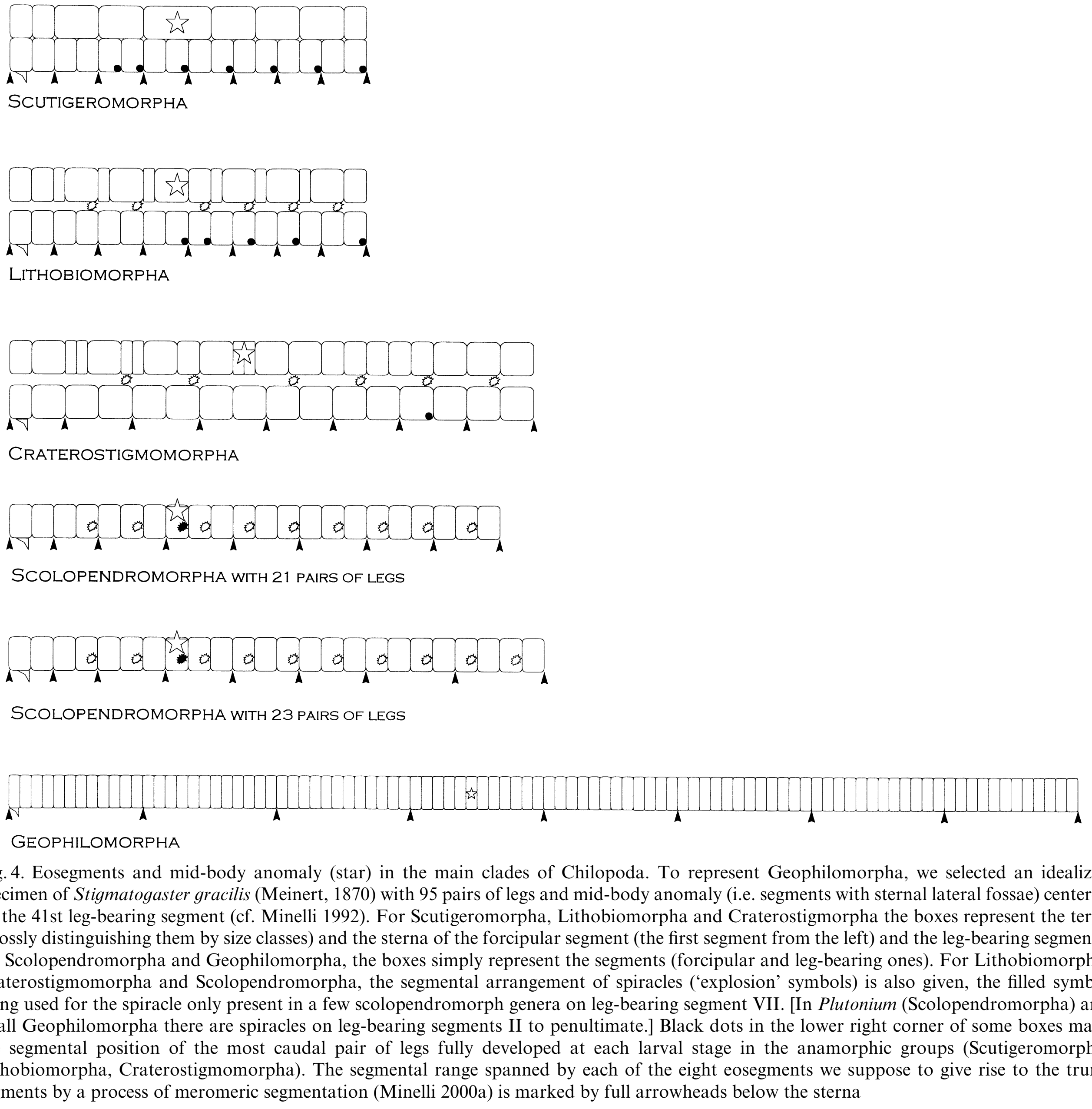

Fig. 4. Eosegments and mid-body anomaly (star) in the main clades of Chilopoda. To represent Geophilomorpha, we selected an idealized specimen of *Stigmatogaster gracilis* (Meinert, 1870) with 95 pairs of legs and mid-body anomaly (i.e. segments with sternal lateral fossae) centered on the 41st leg-bearing segment (cf. Minelli 1992). For Scutigeromorpha, Lithobiomorpha and Craterostigmorpha the boxes represent the terga (grossly distinguishing them by size classes) and the sterna of the forcipular segment (the first segment from the left) and the leg-bearing segments; for Scolopendromorpha and Geophilomorpha, the boxes simply represent the segments (forcipular and leg-bearing ones). For Lithobiomorpha, Craterostigmomorpha and Scolopendromorpha, the segmental arrangement of spiracles ('explosion' symbols) is also given, the filled symbol being used for the spiracle only present in a few scolopendromorph genera on leg-bearing segment VII. [In *Plutonium* (Scolopendromorpha) and in all Geophilomorpha there are spiracles on leg-bearing segments II to penultimate.] Black dots in the lower right corner of some boxes mark the segmental position of the most caudal pair of legs fully developed at each larval stage in the anamorphic groups (Scutigeromorpha, Lithobiomorpha, Craterostigmomorpha). The segmental range spanned by each of the eight eosegments we suppose to give rise to the trunk segments by a process of meromeric segmentation (Minelli 2000a) is marked by full arrowheads below the sterna

matogaster gracilis (Meinert, 1870), Minelli (1992) demonstrated that in the juveniles the range of segments with sternal fossae is very short, but it expands with age, both in anterior and in posterior directions. Extrapolating backwards in development, this sternal marking seems to 'pour out' from a morphogenetic spot placed at about 0.43 of relative trunk segment position. If we assume that the leg-bearing portion of the trunk derives from a regular meromeric segmentation of eight eosegments, the virtual origin of the sternal marking falls right in the middle of the segment range of the derivatives of eosegment 4 (assuming uniform meromeric segmentation, this range spans between 0.375 and 0.50 of relative segment position) (Fig. 4). This result is in good agreement with the interpretation we have derived for the three main clades of centipedes with 15 leg-bearing segments.

A more intriguing question is, whether the anomaly occurs in the domain of eosegment 4 in Scolopendromorpha too, as we would expect from a consideration of the phylogenetic position of this clade.

The *absolute* segmental position of the anomaly (which virtually disappears in *Plutonium*, where a full series of spiracles occurs on leg-bearing segments II to XX included) is the same in the Scolopendromorpha with 21 leg-bearing segments as in those with 23. This circumstance suggests that (a) the two groups of scolopendromorphs do not differ as to the segmental composition of the anterior part of the trunk, anomaly included, hence (b) they will probably differ in the degree of meromeric segmentation of one or more eosegments in the *posterior* part of the trunk.

Simple arithmetic could suggest (Minelli 2000a) that a transition from 15 to 23 leg-bearing segments would be quite easy. It would require, in fact, that each of eight eosegments uniformly split into three units, rather than two. One of the segmental derivatives would become the forcipular segment, the other 23 [23 = (3 × 8)–1, as were 15 = (2 × 8)–1 in the former instance] developing into leg-bearing segments. However, a difficulty in respect to accepting 23 leg-bearing segments, rather than 21, as the plesiomorphic condition within Scolopendromorpha comes from the current understanding of the internal phylogeny of this centipede group. Schileyko and Pavlinov (1997) have recently published a cladistic analysis involving all genera. Their results suggest that 21 leg-bearing segments are the plesiomorphic state in Scolopendromorpha. As we had difficulties in accepting the polarity they attributed to a few characters in their matrix, we have re-run the analysis on a revised matrix, and also on a further matrix excluding the character '# of leg-bearing segments' (details on the analysis in Materials and Methods and in the legend to Fig. 5). Our strict consensus cladogram (Fig. 5) is very poorly resolved. In principle, it does not rule out the hypothesis that the presence of 23 pairs of legs in *Scolopendropsis* may be plesiomorphic within Scolopendromorpha. One evolutionary step would have thus produced the 21 pair condition of most remaining genera. Reversal to 23 pairs may have occurred just once, at the base of a clade comprising *Newportia*, *Tidops*, *Dinocryptops*, *Ectonocryptops*, *Scolopocryptops*, *Kethops*, *Thalkethops* and *Kartops*.

In animals with prevailing three-merous meromeric segmentation, the eighth segmental unit of the trunk, where the mid-body anomaly occurs, would be a derivative of eosegment 4 provided that one of the eosegments 1–3 is not affected by meromeric segmentation. Alternatively, two of these three eosegments would have to undergo two-merous rather than three-merous meromeric segmentation. As a uniform two-merous meromeric segmentation of the eight eosegments corresponding to the leg-bearing trunk (inclusive of the forcipular segment) seems to satisfactorily account for the ancestral condition from which the Scolopendromorpha evolved, the second alternative seems to be more likely. From this premise, a revised interpretation of the body segmentation of Scolopendromorpha with 21 leg-bearing segments can be developed (Fig. 4).

In this context it might be interesting to cite some embryological evidence from Heymons's (1901) monograph on the development of *Scolopendra*. In this centipede, the segmentation of the germ band does not begin at (or, better, close to) the cephalic end, as in many other arthropods, but at the level of what Anderson (1973) interprets as the 11th to 13th segments of the trunk (forcipular segment included) (cf. Figure 12 of Heymons (1901), reproduced here as Figure 6a). In our interpretation (Fig. 3) these three segments are the merosegments of one eosegment, the fifth one, i.e. the first eosegment following the one involved in the mid-body anomaly. Furthermore, in a more advanced developmental stage also illustrated by Heymons (1901) (his Figure 8, reproduced here as Figure 6b) a major step in the degree of differentiation of segments is observed between the future leg-bearing segments 7 and 8, that is, at the level of the future mid-body anomaly, whose position is thus apparently marked even before the germ band is completely differentiated.

Summing up, in all centipedes the mid-body anomaly seems to affect the segmental derivatives of the meromeric segmentation of eosegment 4. There are some interesting implications of this result. First, it is fully compatible with Minelli's (2000a) biphasic model of segmentation. Second, it suggests that the embryonic patterning expressed by the mid-body anomaly is determined *before* the onset of meromeric segmentation and concomitantly with (or immediately after) the process of holomeric segmentation. Third, the variety of features developing at the mid-body anomaly, especially in Geophilomorpha, provides a clear instance of the uncoupling of positional homology from special homology (Minelli and Schram 1994).

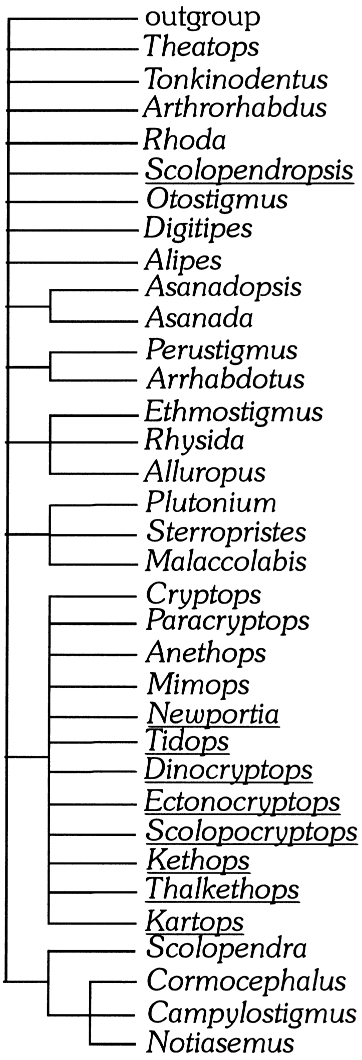

Fig. 5. A revisitation of Schileyko and Pavlinov's (1997) phylogeny of Scolopendromorpha. Character no. 2 of the original matrix has been deleted. The following characters have been re-coded (character no. as in the original matrix): no. 1 – anisosegmentation (alternation of macro- and microsegments) present (0) versus absent (1); no. 3 – spiracles on macrosegments the seventh body segment excluded (0) versus on macrosegments the seventh included (1) versus on all segments (2); no. 4 – spiracles open with atrium (0) versus without atrium or covered by a flap (1); no. 9 – terminal legs similar to locomotory legs (0) versus modified (1); no. 10 – armature of terminal legs absent (0) versus present (prefemoral spines or a tibio-tarsal 'saw') (1). The revised matrix (16 characters for 35 taxa) has been analysed by HENNIG86 (Farris 1988). We applied the commands 'mh*' and 'bb*' to find the shortest cladograms. We obtained 2654 (overflow) trees, 65 steps long with c.i. 29 and r.i. 69. Then we calculated the strict consensus obtaining the cladogram 66 steps long, with c.i. 28 and r.i. 68, reproduced in this figure. Underlined genera with 23 pairs of legs, the remaining ones with 21

In addition, this feature invites enquiring whether other arthropods exhibit a comparable patterning of the main body axis, perhaps 'disguised' under very different morphologies. A preliminary analysis of millipede body segmentation (Minelli

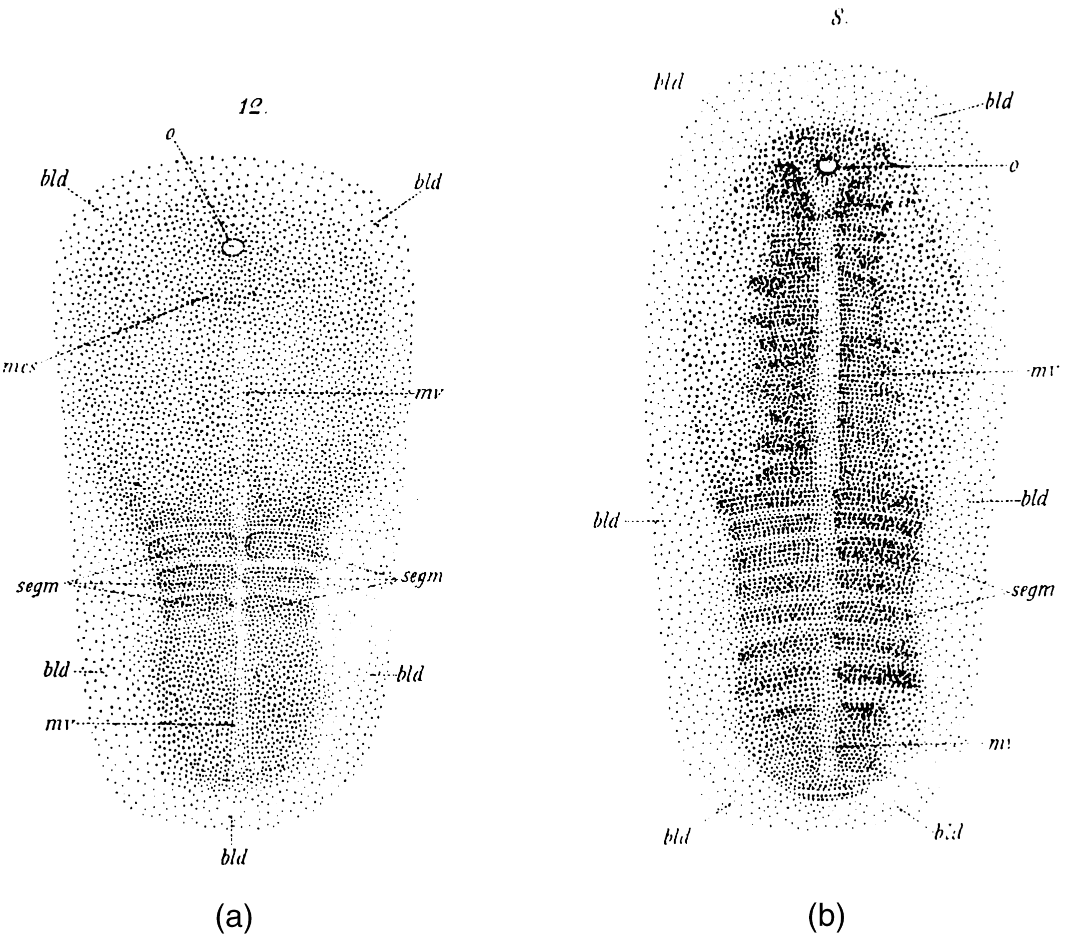

Fig. 6. Two stages of germ band differentiation in *Scolopendra cingulata* Latreille, 1829 (after Heymons 1901). (a), germ band with the first three somites; (b), a later stage with most somites differentiated: the three segments bracketed under the label '*segm.*' on the right are the same as those in (a), i.e. trunk segments 11th to 13th (forcipular segment included)

and Hoffman, in prep.) suggests that this is the case in Diplopoda too. In Polydesmida at least, it seems to be easy to demonstrate that the gonopod-developing 'ring' derives from meromeric segmentation of trunk eosegment 4.

The problem remains, however, of deriving the Scolopendromorpha with 23 pairs of legs from those with 21 pairs of legs. If the degree of meromeric segmentation in the anterior part of the trunk is the same in the two groups (see above), then we must assume that the difference affects the last eosegments, possibly with eosegments 7 and 8 undergoing four-merous (rather than three-merous) meromeric segmentation (Fig. 4). The latter degree of meromeric segmentation would approach the lowest degree of meromeric segmentation found in Geophilomorpha. At this point, however, our speculations must cease for lack of evidence. At present, it would be no less speculative to articulate detailed models of meromeric segmentation corresponding to the individual numbers of leg-bearing segments exhibited by Geophilomorpha in their inter- and intraspecific variation. It is quite possible that the very conspicuous variation observed in many species is genetically controlled, at least in part.

Some speculations, however, may be developed as to the possible primitive significance of the mid-body anomaly and to the cause(s) of its increasing fading out, culminating with the apparent lack of any mid-body patterning in the scolopendromorph genus *Plutonium* and in some Geophilomorpha. Comparisons with other arthropods and especially with helminthomorph millipedes suggest that the 'hot spot' falling within eosegment 4 was probably associated with sexual differentiation. Centipedes, however, are opisthogoneate myriapods and there may be a selective advantage to them in having the sexual appendages (gonopods) close to the posteriorly located genital opening. That is, their gonopods, if any, are placed at the posterior end of the body. One may wonder whether this event occurred following a duplication of an *AbdB*-class gene originally expressed at (or, better, starting with) a trunk level within eosegment 4, with retention of the original site of expression by one of the paralogous genes and displacement of the other paralogue's expression to the posterior end of the body. If so, a similar but possibly independent event might have occurred in insects. Some insects have indeed a 'hot spot' of morphological differentiation on the II abdominal sternum, i.e. in the position possibly homologous to eosegment 4 of myriapods (thus, in terms of holomeric segmentation). A suggestion in this sense was made by Minelli and Schram (1994), who pointed to a possible positional homology between the secondary penis of male dragonflies and the gonopods of millipedes. On the other hand, insects are opisthogoneate, as centipedes are, but insect genital openings are posterior to abdominal segment 7 or 8 or 9 (with few exceptions), whereas those of

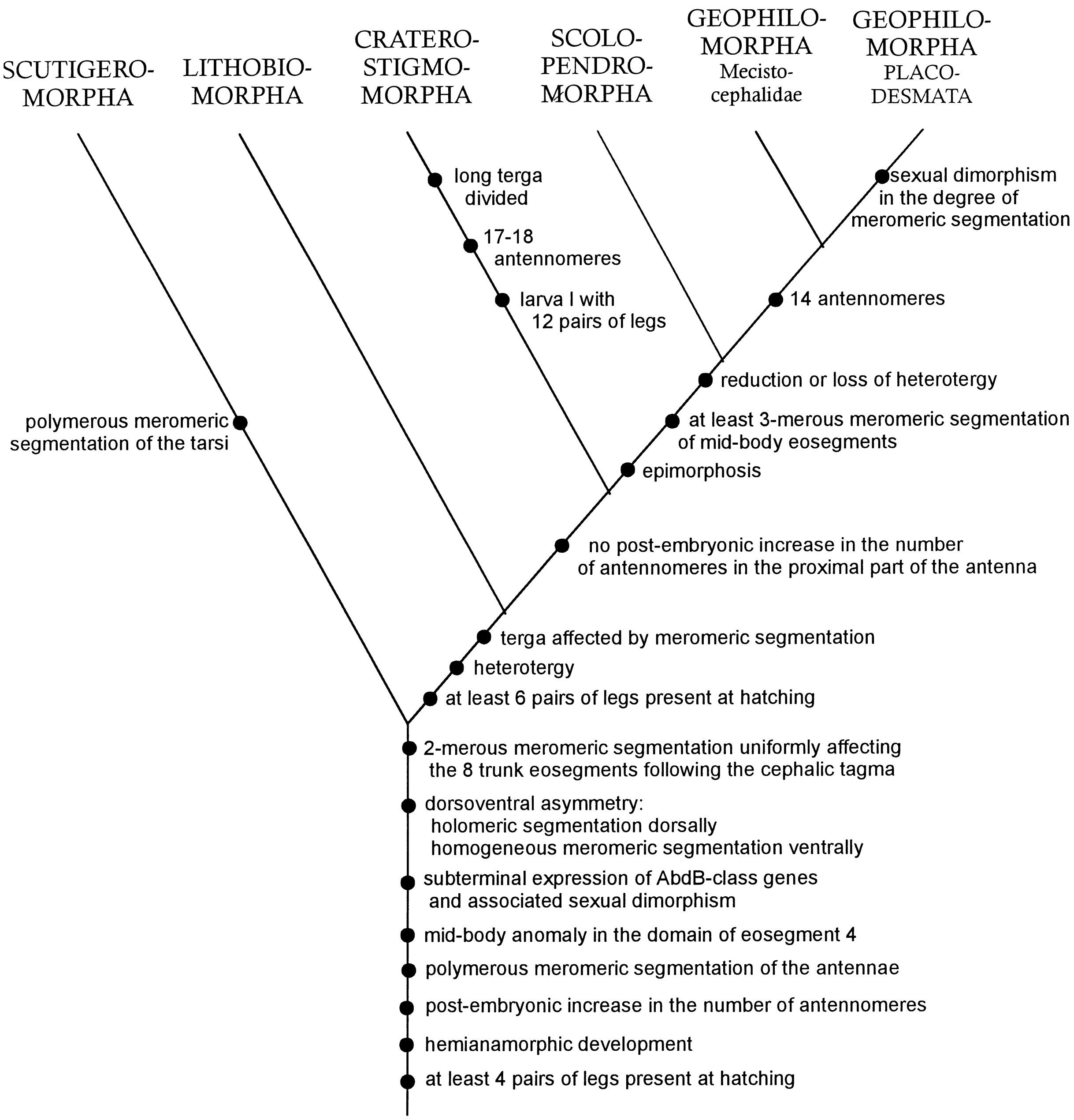

Fig. 7. Main features of the segmentation of trunk and appendages plotted onto centipede phylogeny

centipedes are apparently placed at the very end of the body. This generally overlooked topographical difference may perhaps suggest an independent origin of the opisthogoneate condition in the two clades.

An evolutionary perspective

If we plot the results above onto a centipede phylogeny we obtain a scenario such as in Figure 7. The following evolutionary trends are worth discussion.

Heterochrony in segmentation processes

In the evolution of centipede segmentation the three following trends can be recognized: (i) increasing reduction of the anamorphic phase of postembryonic development; (ii) increasing degree of meromeric segmentation of the trunk; and (iii) increasing integration of (reduction of time interval between) holomeric and meromeric segmentation, so that the products of the latter acquire the full organization of trunk segments.

In our opinion, these three trends are strictly associated and express a consistent heterochronic trend of meromeric segmentation. It is quite possible that in all centipedes the holomeric segmentation is completed in an early embryonic phase, but the timing of meromeric segmentation is possibly not the same in all centipedes, being perhaps earlier in the epimorphic and later in the anamorphic forms.

It is quite possible, however, that meromeric segmentation is completed during the embryonic life in all centipedes, that is, also in those developing by hemianamorphosis.

In fact, only in Scutigeromorpha does the number of segments with full-developed appendages in each larval stage following the first coincide with the number of segmental units obtained by meromeric segmentation of a growing number of eosegments (5, 7, 9, 11, 13, 15 leg-bearing segments, corresponding, in our interpretation, to 3, 4, 5, 6, 7 and 8 complete eosegments, respectively) (Fig. 4). This correspondence is already lost in Lithobiomorpha, where the first larval stage exhibits a more advanced segmentation [with (6–)7(–8) full-formed leg-bearing segments] than its equivalent in Scutigeromorpha (four segments only). These two facts (the decoupling of meromeric segmentation and anamorphic development and the more advanced segmentation stage at hatching) suggest that meromeric segmentation is somewhat anticipated in Lithobiomorpha in respect to its course in Scutigeromorpha. The Craterostigmomorpha exhibits a further step in the same direction, where the anamorphic phase is reduced to one stage only; the animal hatching with 12 (of 15) completely formed segments. Finally, in the Epimorpha (Scolopendromorpha and Geophilomorpha) the meromeric segmentation is anticipated to such a degree as to be completely accomplished well in advance of hatching. The strict temporal proximity of holomeric and meromeric segmentation is probably a major prerequisite for the approximately uniform segmental patterning evolved by the Scolopendromorpha and, to a more advanced degree, by the Geophilomorpha.

Sexual dimorphism

The evolutionary trend in segmentation that we have sketched in the last section is largely paralleled by a corresponding trend in the reduction of the sexual dimorphism of the posterior terminal appendages (gonopods). As for the male sex, the Scutigeromorpha possess two pairs of gonopods, whereas the Lithobiomorpha only possess one pair (often inconspicuous), but gonopods are at most vestigial in Craterostigmomorpha (Dohle 1990) and virtually lost in Scolopendromorpha: for instance, *Scolopendra morsitans* has a pair of narrowly conical genital appendages but these are absent in *Scolopendra valida* Lucas, 1840 (Demange and Richard 1969). As for the females, both Scutigeromorpha and Lithobiomorpha possess conspicuous gonopods, but these appendages appear to be lost in the Craterostigmomorpha and Scolopendromorpha. An adaptive explanation may be suggested of these conspicuous differences in the development of the terminal appendages in the female sex. In scutigeromorphs and lithobiomorphs the gonopods are of use in egg deposition, but comparable appendages would be useless, as such, to the other centipedes, which have developed parental care, with the mother remaining curled round her eggs for the whole time required for the embryos to develop. Rudimentary gonopods are present, however, in Geophilomorpha, in both sexes. Therefore, we must suppose that these appendages were still present, albeit possibly much reduced, at the root of the epimorphic clade. By consequence, a further reduction of the gonopods did probably evolve, in parallel, in the Craterostigmomorpha and in the Scolopendromorpha.

But this is not the whole story. In Lithobiomorpha and in Geophilomorpha, the sexual dimorphism is not limited to the gonopods but also affects, to a greater or lesser degree, the last pair of locomotory legs (also the penultimate pair in some male *Lithobius*), as it does in many Scolopendromorpha. Examples in the latter clade include specializations of the end legs in *Scolopendra morsitans* and the genera *Alipes*, *Digitipes* and *Otostigmus* (*Parotostigmus*) and a few *Cryptops* species; modified penultimate legs occur in *Cryptops* whereas in *Otostigmus* (*Otostigmus*) sexual dimorphism is seen in the terga of posterior segments and possibly the shape of sternum XXI; the male of *Otostigmus* (*P.*) *caudatus* Brölemann, 1902 has a long process on tergum XXI. These specializations, as is usual for sexual traits developing in the posterior subterminal region of the body, are probably under the control of some *AbdB*-class gene (Kondo et al. 1997; Kagoshima et al. 1999; Damen and Tautz 1999; Kettle et al. 1999, 2000; Minelli 2000a). In a previous paragraph we have suggested a possible evolutionary interpretation of this 'sexualization' of the posterior appendages, following gene duplication, divergence and new expression pattern of one of the paralogues.

Macro-evolutionary trends

Increasing elongation seems thus to dominate the evolution of epimorphic centipedes, despite the secondary occurrence, within the subclade with the highest degree of meromeric segmentation and subsequent assimilation of its segmental products (Geophilomorpha), of several lines undergoing secondary shortening of the body.

However, this does not mean that Verhoeff's *Elongationsprinzip* wins over Brölemann's *tachygenèse*, because our interpretation of segmentation leads to recasting the whole question in completely new terms. In terms of holomeric segmentation, there is probably no change at all within Chilopoda, all of them developing the same complement of eosegments. The evolution concerns instead the degree of meromeric segmentation. Here, the main trend is one of elongation, from a two-merous to a mainly three-merous segmentation and from the latter level to those, more advanced, of the Geophilomorpha. Within the latter group, however, the degree of meromeric segmentation may follow either course – of further increase or, to the contrary, of secondary reduction of the number of segmental units per eosegment. A detailed analysis of these trends must await a full resolution of geophilomorph phylogeny. However, our current understanding of cladistic relationships within the group (Foddai 1998; Foddai and Minelli 2000) already allows the identification of some highly polymerous (i.e. polypodous) phyletic lines, such as those of Himantariidae, Dignathodontidae, Eriphantidae, Oryidae, Gonibregmatidae and Eucratonychidae. Opposite trends towards oligomerization culminate (within the Geophilidae and the Schendylidae) with the species with 27 or 29 leg-bearing segments mentioned above.

The present analysis confirms a macroevolutionary trend already observed in centipedes from a different perspective (morphological complexity of the trunk: Berto et al. 1997; Fusco and Minelli 2000), that is, that the so-called Williston's rule (a macroevolutionary trend towards less numerous and more specialized elements in a series; cf. Saunders and Ho 1984) does not apply here. In other terms, we have good reasons for discounting the popular notion that the body architecture of centipedes, and of the worm-like geophilomorphs in particular, represents a primitive step in the evolution of arthropod segmentation. On the contrary, this group experienced an idiosyncratic evolution of meromeric segmentation, probably paralleled, but with different 'rules', by the other major group of myriapodous arthropods, the helminthomorph millipedes.

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Zusammenfassung

Die Evolution der Segmentierung des Rumpfs und der Anhänge bei den Chilopoden

Die Segmentierung der Chilopoden wird im Sinne des biphasischen (holomerischen und meromerischen) Segmentierungmodells von Minelli (2000a) interpretiert. Die Mittelrumpfanomalie, die man in der sonst regelmäßigen Alternierung von Kurz-und Langterga oder von stigmentragenden und stigmenlosen Segmenten beobachtet, wird als eine ontogenetisch sehr frühe Störung des embryonalen Patternings betrachtet, die vor dem Beginn der meromerischen Segmentierung im Gebiete des vierten Eosegmentes stattfindet. Ein Vergleich mit den Diplopoden zeigt, daß wahrscheinlich mit Tausendfüßlergonopoden vergleichbare Genitalstrukturen an der gleichen Stelle ursprünglich entwickelt waren; die Stelle blieb jedoch "markiert" nachdem die Chilopoden von einem progoneaten zu einem opisthogoneaten Stande evolviert waren, vielleicht als Konsequenz einer Genduplikation und einer Divergenz des Expressionsmusters der paralogen Gene. Eine neue Untergrenze für die Segmentenzahl in den Geophilomorpha [27 beintragende Segmente, im Männchen von *Schendylops oligopus* (Pereira, Minelli & Barbieri, 1995)] wurde bestimmt. Koevolutionäre Trends in der Rumpfsegmentierung, der Segmentierung der Anhänge (der Antennen insbesondere), dem nachembryonialen Entwicklungsmodus und der Neigung zur Regeneration stimmen mit Minelli's (2000b) Konzept der Anhänge als duplizierte und entwicklungsgeschichtlich divergente Kopien (Paramorphe) des Körperhauptaxis überein.

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