Ber. nat.-med. Verein Innsbruck	Suppl. 10	S. 37 — 46	Innsbruck, April 1992

8th International Congress of Myriapodology, Innsbruck, Austria, July 15 - 20, 1990

Towards a New Comparative Morphology of Myriapods

by

Alessandro MINELLI
Dipartimento di Biologia, via Trieste 75, I-35121 Padova, Italy

Abstract: For a new approach to myriapod morphology the following points are suggested: (a) the adoption of a biological concept of homology, broad enough to accommodate "conventional" homology s.s., serial homology, and structural comparisons within the ontogeny of a single individual; (b) identification of postembryonic stages, possibly along the lines of GRANDJEANs stase concept; (c) an appraisal of heterochrony; (d) identification of the repetitive pattern occurring at the infrasegmental, segmental and suprasegmental level; (e) a developmentally meaningful identification of segmental positions along the body axis. Alternative developmental scenarios are constrasted in order to show their possible bearing on the homologization of serial structures.

1. Introduction:

In an age marked by the extraordinary developments in molecular biology, there is often the danger of underestimating the importance of morphology: by this term, I do not mean the simple description of anatomical structures, but also their comparative and historical interpretation, in the sense of SNODGRASS (1951) and CHAUDONNERET (1988). At the same time, we must be aware of the fact, that the science of form also needs permanent refinement and updating, as happens to other more dynamic fields within biology. This necessary progress of morphology must proceed both as a revision of its conceptual foundations and as unceasing empirical enquiry. In the following, I shall briefly develop this point of view, in respect to the study of myriapods. But let me begin with a hint to some major problems of our science.

In addition to the more general difficulties currently encountered in classic morphology, inclusive of descriptive embryology, i.e. scarcity of active workers and even scarcer academic interest and financial support by research funding agencies, the morphology of myriapod groups is hindered by two further problems. First, the long debated issue of holophyly (monophyly s.str.) of Myriapoda, which is currently advocated by a minority of workers (e.g. BOUDREAUX 1979) and strongly rejected by others (e.g. DOHLE 1980, 1988; MINELLI 1983). Even the informal term "myriapods" colloquially used for this probably paraphyletic assemblage does not help to ask (and to answer) meaningful questions in comparative morphology.

Second, the study of myriapods has started too often from an insect-centered perspective. There is a common additional assumption, which however has been never investigated thoroughly, that myriapods are — collectively — the primitive counterpart of insects, i.e. a living collection of plesiomorphic traits, a few derived characters excepted, like the poison claws of centipedes, and the gnathochilarium of millipedes and pauropods.

2. Recent Advances:

However, in spite of these traditional shortcomings, the study of myriapod groups has recently witnessed substantial progress. This development can be followed in the Proceedings of the International Congresses of Myriapodology. First, a valuable body of new descriptive evidence has been gathered.

New, partly unexpected body plans have been described in newly discovered Palaeozoic fossils. The best documented form is probably *Devonobius delta* SHEAR & BONAMO, the prototype of the new centipede order Devonobiomorpha, from Devonian rocks of the United States (SHEAR & BONAMO 1988), but still older and less conventional forms are also known from Upper Silurian beds of the United Kingdom (SELDEN & JERAM 1992). These Silurian myriapods belong to the oldest known land arthropod fauna, but it is also possible that some suggestions as to the origin and evolution of "myriapods" will be obtained by a thorough study of the marine fossil *Cambropodus gracilis* ROBISON, a recently described Cambrian form, loosly referred by ROBISON (1990) to the "uniramian arthropods".

Another wealth of information has been gathered by a careful study of living forms. I only mention the recent re-evaluation of *Craterostigmus* by DOHLE (1990) and detailed investigations with the aid of transmission electron microscopy of many structures, including the so-called coxal and anal "glands" of centipedes (ROSENBERG 1982, 1983a, 1983b, 1984, 1985, 1990; ROSENBERG & SEIFERT 1977, ROSENBERG & BAJORAT 1984, LITTLEWOOD 1983, LITTLEWOOD & BLOWER 1987), the eyes (PAULUS 1979, 1986; SPIES 1981), the sternal glands of geophilomorph centipedes (TURCATO & MINELLI 1990, HOPKIN & ANGER 1992) and others more. These studies are of more than purely descriptive importance. Indeed, they have led to a completely new view of the nature and function of the coxal and anal organs of centipedes and to a new understanding of the homology relationships of the visual organs of different groups of tracheate arthropods. Moreover, we begin to gain a new sense of the phylogenetic importance of previously lesser known structures, such as the sense organs (HAUPT 1979) and the sternal glands of geophilomorphs (MINELLI & TURCATO in prep.).

In contrast to such progress in the morphology of adult stages, we have progressed but little with the study of embryonic development, since DOHLEs (1964) monograph on *Glomeris* and KNOLLs (1974) and DOHLEs (1970) papers on *Scutigera*. More effort has been devoted to describing the post-embryonic stages of several species, but in this field, too, I believe that very few recent papers have really improved our understanding of the origin and development of the body plan of the different myriapod groups. A few fundamental ideas were put forward in the late sixties and in the seventies, especially by DEMANGE (1967, 1969, 1974), DOHLE (1974) and BLOWER (1978), but they have never been re-examined, in spite of the challenge that some of them presented for certain conventional views of arthropod development. In particular, I refer to DOHLEs (1974) important (and puzzling) contention that, in diplopods, "there is always one "false" sternite included in a ring". Furthermore, BLOWERs (1978) analysis of millipede anamorphosis suggested, along similar lines, that one pair of legs "is suppressed in all stadia of juloids and in all stadia of polydesmoids except the second, but the extra pair persists in all stadia of nematophorans except the second, where they are suppressed." Only the comparative morphology of the so-called "thoracic" segments of diplopods has been briefly revised by KRAUS (1990).

However, I am convinced that we are at the beginning of a new understanding of the morphology and morphogenesis of our animals, depending upon our ability to extend to the myriapod groups the extraordinary progress witnessed in the last ten years in the molecular genetics of development, especially in *Drosophila.* As I have stressed elsewhere (MINELLI & BORTOLETTO 1988), this approach can help us to understand, *inter alia*, the different patterns of "diplosegmentation" and other regularities of the body plan of myriapods, at the infrasegmental as well as at the segmental and suprasegmental level. Worth mentioning is finally ENGHOFFs (1990) recent effort to apply the rigorous principles of cladistics to the identification of the external morphology of the "groundplan" of chilognathan millipedes.

3. Homology Concepts:

An important debate has recently developed on the concept (or concepts) of homology. I need not stress here the importance of this notion for comparative morphology. I shall limit myself to a couple of ideas from the recent literature that I regard as especially useful for us, and develop them to obtain a conceptual framework, as open and flexible as possible. For further aspects, I refer to AX (1989), BOCK (1977, 1989), DOHLE (1989), GOODWIN (1984), GOODWIN & TRAINOR (1983), MINELLI & PERUFFO (1991), OSCHE (1973, 1982), PATTERSON (1982), RIEDL (1978), RIEPPEL (1988), ROTH (1984), SHUBIN & ALBERCH (1986), VAN VALEN (1982), WAGNER (1989) and to the extensive literature cited therein.

WAGNER (1989) has recently contrasted two kinds of homology concepts, i.e. historical and biological. Historical concepts of homology defined homology relationships by reference to the common ancestry of the structures under comparison, whereas biological concepts proceed from the identification of common biological processes underlying the structures being compared.

I do not intend to look for the right homology concept. Obviously, we should refer to a historical concept of homology whenever we try to identify synapomorphies in an effort to reconstruct phylogenetic relationships, but I believe that in other contexts a biological concept of homology can be far more meaningful. More in detail, I agree with VAN VALENs (1982) concept of homology as a relationship founded on a common informational background shared by the structures under comparison (see also MINELLI 1992, MINELLI & PERUFFO 1991). This notion seems to me wide enough to apply to all of the different comparisons we can establish between and within our animals. At the same time, it seems to be useful, especially in the study of myriapods, to distinguish several aspects, or components, of homology relationships (Fig. 1):

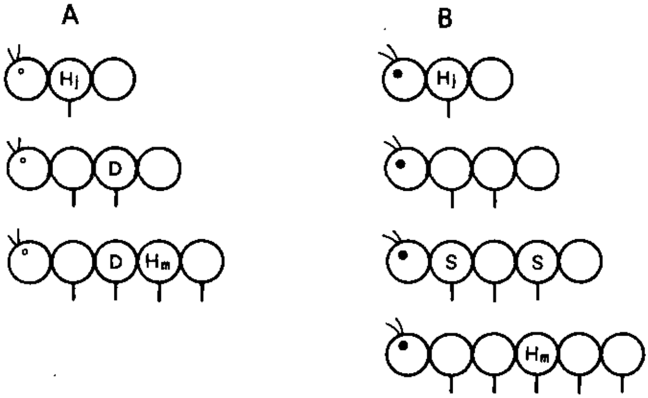

Fig. 1: Different kinds of homology statements can be involved in the comparative morphology of myriapods. The schematic drawings refer to two idealized anamorphic species, A and B. We can distinguish: "conventional" homology involving comparisons of structures in two different species, either at a juvenile (Hj) or adult (Hm) stage; serial homology (S), involving intra-individual comparisons; and comparisons of structures of the same individual or of individuals of the same species and sex in different developmental stages.

A) "Conventional" homology, as applied in a comparison of individual features of two different animals, A and B. Perhaps we could further distinguish the homologies identified when comparing immature stages, from those identified when comparing adult specimens, or the homologies identified between individuals belonging to different species from the homologies identified between individuals of the same species, possibly differing in sex, or representing different morphs within a polymorphic species.

B) Serial homology, or homonomy; and

C) Comparison of selected body structures across developmental time.

All possible homology statements are a more or less complicated product of A · B · C. Identifying and separating the three factors cannot but help reducing the complexity of our analysis.

Another aspect of homology relationships is worth stressing here, i.e. the relativity of all homology relationships. Relativity of homology relationships means, that the homology between two features cannot simply be stated as an all-or-nothing alternative. Instead, the two features under comparison can be said to be homologous to the extent to which they share a common informational background; which is obviously the same for identical features (cfr. VAN VALEN 1982, ROTH 1984, MINELLI & PERUFFO 1991).

4. Identifying Developmental Stages:

The preliminary requirement for a meaningful approach to the identification of homologies, as outlined in the previous section, is obviously an unambiguous identification of developmental stages. This is a far from easy task, however, even in the apparently simplest case of the epimorphic centipedes. We know very little about the possible occurrence of intraspecific variability in the number of moults preceding maturity in these animals, but we do about (a) interspecific differences in the number of moults preceding maturity, and (b) the occurrence of a variable number of mature-to-mature moults (LEWIS 1961, 1981; MINELLI 1985). It is probable, at least for some geophilomorph species, that the actual number of moults undergone before maturity is larger than the number of post-embryonic stages conventionally recognized (as Adolescens I, etc.) on the basis of chaetotaxy or the number of coxal organs. All these facets of the post-embryonic development of epimorphic centipedes can be briefly summarized by saying that the developmental value of the different moults may be quite diverse, both within the ontogeny of a particular individual and in comparisons between different species. Accordingly, homologizing stages on the simple basis of their numerical order does not seem to be justified. It is true that hatching and achieving maturity for the first time both offer reasonably comparable landmarks in an ontogeny, but this does not seem to be enough. A somewhat similar point about moults has been stressed by DEMANGE (1974), when discussing the development of diplopods.

In this context, it is probably worth the effort of a re-analysis of the developmental schedules of myriapods according to the "stase vs. stage" model first propounded by the acarologist GRANDJEAN (1938) and subsequently developed by the same author (GRANDJEAN 1951, 1957, 1970) and other acarologists, until ANDRÉ (1986, 1987, 1988, 1989; also ANDRÉ & JOCQUÉ 1987) finally attempted to apply it to other arthropod groups.

The concept of stase can be best defined by GRANDJEANs (1951: 271) own words: " J'appelle *stase,* chez un Arthropode, une période de la vie comprise entre deux mues, à condition que ces mues apportent aux caractéres des changements de nature discontinue et que leur nombre, pour tout un phylum, soit constant ou dérive, par réduction, d'un nombre primitif constant. Je désigne également par stase l'animal lui-même au cours de cette période."

In GRANDJEANs concept, therefore, two stases are separated by a moult, but not all moults separate stases. Stases are phases of development, but some moults have no ostensible developmental effects, they simply produce, within the same stase, a replica of the animal, of the same size or larger.

In a sense, GRANDJEANs terminology simply rationalizes two more or less widespread notions: first, that moults do not always have the same developmental value; second, that the number of post-embryonic stages, *per se,* is not always of phylogenetic importance. The stase concept, however, may allow more meaningful and straightforward comparisons of developmental stages. I cannot enter here into details which will be developed elsewhere (MINELLI, in prep.), but — to return to the previous example — it seems to be worth investigating to what extent the classic "stages" recognized in the post-embryonic development of geophilomorphs can be equated to stases, and how far they are actually comparable across the whole group.

Problems with comparisons of developmental stages are perhaps even larger in hemianamorphic and anamorphic myriapods, not to mention those exhibiting further developmental complications, like periodomorphosis. Again, these problems will be dealt with in detail elsewhere.

5. Heterochrony:

Remaining at the level of the relationships between morphology and developmental biology, I shall say a few words on heterochrony. This concept has recently gained a rather wide interest, as documented, for instance by the works of ALBERCH (1985), GOULD (1977), McNAMARA (1987) and RAFF & WRAY (1989). In a sense, however, this concept is anything but new in myriapodology. Quite long ago, VERHOEFF (1928, 1928/32) advocated an "Elongationsprinzip" and BROLEMANN (1921, 1930, 1932) contrasted it with his "principe de tachygenèse": both concepts clearly presupposed a general uncoupling of sexual maturation and somatic development. In a more general sense, transition from one developmental mode to another (including epimorphosis, hemianamorphosis and anamorphosis), as has occurred several times within the tracheate arthropods, is also an expression of heterochrony.

At a lower, perhaps more conventional level of complexity, heterochrony can be observed in the widespread retention of juvenile traits in adult myriapods. Common examples include geophilomorphs of small adult size, without sternal pores, with less differentiated last legs and less numerous coxal organs; or lithobiomorphs, also of small adult size, with a reduced number of antennal joints, ocelli, coxal organs, spines etc.

These heteromorphic patterns are not always simple (the correlations between the different characters and their evolutionary transitions should always be studied case by case), but a few regularities are easily observed. For instance, the reduction and even the absence of sternal pores very common in paedomorphic geophilomorphs certainly did evolve independently many times. Failure to perceive this homoplasy has led to the establishment of some artificial "genera" like *Brachygeophilus* and *Brachyschendyla.* In their current concept, they are both "waste baskets" for numerous paedomorphic geophilids resp. schendylids of very different origins.

6. Identifying Segmental Positions:

In discussing the origin and the nature of the concept of serial homology, BOCK (1989: 343) says that this concept "did not survive well the transmutation of the theoretical foundation of homology from typological idealism to evolutionary theory. Clearly one could not homologize members of these repeated series as individual homologues. No sense existed in attempting to homologize the 37th vertebra in one species of a snake with the 37th vertebra of a second species." I believe that BOCK is right only in so far as there is no way of homologizing positions along the body axis. Perhaps this problem has no general solution or, at least, none for snakes, but it seems to have one for myriapods, or at least for some of them. This does not mean, however, that the best candidate for *homology relationship with the 37th segment of a given specimen is necessarily the 37th segment of* another specimen. Let me explain this concept by a concrete example.

In many species of himantariid geophilomorphs, some sternites are "marked" by special features, like the lateral grooves of *Stigmatogaster gracilis* (MEINERT), or the horseshoe grooves of *Bothriogaster signata* (KESSLER). These "marked" sternites occur in an uninterrupted series extending over a number of segments, increasing at each moult. In addition to this developmental change, there is some individual variation – at comparable developmental stages – in the ordinal number of the first and the last "marked" segment. This variation is commonly expressed in the taxonomic literature by giving the range of the possible position for both the first and the last "marked" segment. ATTEMS (1929), for instance, gives the positions 34 - 39 and 49 - 54, respectively, for the fore and hind ends of the "marked" region in *Stigmatogaster gracilis,* and the positions 30 - 41 and 42 - 52 for the corresponding extremes in *Bothriogaster s. signata.*

It is reasonable to suppose that ATTEMS did not consider homology relationships and the same can be generally supposed for the other authors who have adopted the same kind of description. However, this lack of sensitivity leads to inaccurate descriptions, with consequences that probably also bear on taxonomy, not merely on general, or theoretical, morphology.

In fact, himantariids (including the species mentioned above) exhibit a substantial (sometimes enormous) intraspecific variation in the number of body segments. Accordingly, one could expect a relationship between the ordinal number of the first and last "marked" segment and the total number of body segments. I have verified the existence of such a relationship for *Stigmatogaster gracilis* (Fig. 2), but similar relationships are likely to occur generally within the family.

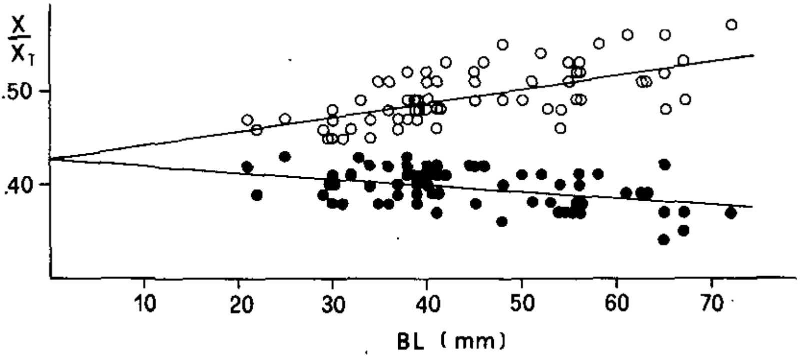

Fig. 2: *Stigmatogaster gracilis* (MEINERT): Linear regression of the relative segmental positions of the fore and hind ends (black dots and open circles respectively) of the series of sternites "marked" with lateral grooves vs. body length (BL), as observed in 66 Italian specimens. Relative segmental positions (X/X_T) are calculated by dividing by the total number of leg-bearing segments (X_T) the actual segmental positions X where the fore- or hind-end of the marked sternite series occur. For both regressions, $p < 0.001$.

Accordingly, it seems to be reasonable to assume that the two extremities of the "marked" sternal region of *Stigmatogaster* identify — at least for a given body length or, better, for a given developmental stage — two reasonably homologizable points. They occur at different positions in different individuals, but these positions are strictly dependent on the total number of segments. Therefore, what is invariant is the relative segmental position of the two points, not the absolute one. It is easy to interpret this circumstance as dependent on the fact that the definitive segment number is established before the first sternites are marked. This precedence of the establishment of segments over the time of differentiation of a given structure involving one or more segments clearly shows that, in species with variable segment number, we should always refer to relative, instead of absolute, segmental positions. This seems to be necessary, for instance, when describing the range of sternites with *carpophagus*-structure occurring in many geophilid species.

A further aspect of developmental biology bearing on the possible homologization of segmental positions of different individuals, both within a species and between species, would be the relative segment-autonomy of the development of the structure we are considering, as opposed to a possible synorganization involving interactions between segments. Unfortunately, our current knowledge of myriapod developmental biology is all too scanty to implement this theoretical view with actual examples.

7. Homeosis vs. Phylogenetic Change:

A better knowledge of development is also necessary, before we can justifiably ask whether antennae, for instance, or mouthparts, can actually be regarded as modified legs, or not. Of course, I do not want to raise doubt about the serial homology between these structures; we do not need the example of extraordinary homoeotic mutants like *Drosophila's* Antennapedia, to be convinced that antennae and legs occupy corresponding positions in different body segments. The problem at issue is another. Are we sure that the antennae were ever something like legs, in the same sense as we consider millipede gonopods directly replace normal walking legs, in ontogeny as well as in phylogeny?

A better insight into this kind of problem can be obtained by contrasting the two developmental scenarios of Fig. 3. In A, the development of the appendages precedes the differentiation of tagmata; in B, the reverse happens. Within the first scenario, the peculiar appendages finally developing in the head region can be defined as modified legs, but this is not true in the other case, where tagmal differentiation precedes the development of appendages. In this case, the appendages of the head region are still serially homologous with those of the trunk, but we cannot reasonably say that *they have ever been true legs. Homoeotic mutations like Antennapedia change the kind of append*ages by changing the identity of the segment, i. e. disturbing tagmosis (cf. the scenario of Fig. 3 B). In this sense, these mutants cannot be regarded as a proof that "today's antenna is yesterday's leg."

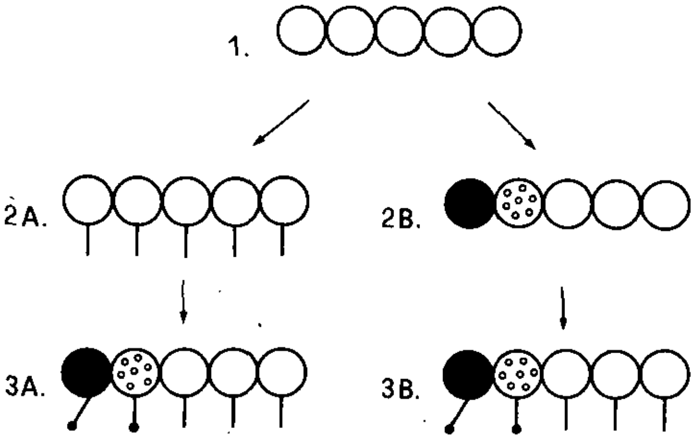

Fig. 3: Two possible, contrasting scenarios (A, B) for the development of different kinds of serially homologous appendages. In the sequence on the left (A) the primary segmental pattern (1) is first interpreted (2A) to give a secondary pattern, with the establishment of serially homologous appendages of a uniform type, then (3 A) tagmosis appears, involving changes both in the primary segmental pattern (segmental identities become specified) and in the derived pattern of serially homologous appendages ("cephalic" appendages in contrast to ordinary walking legs). In the sequence on the right (B), the primary segmental pattern (1) is first modulated by tagmosis (2B), then the newly regionalized segmental pattern is interpreted, giving rise to serially homologous segmental appendages which have already been diverse since their origin.

Once more, I think that we must be very cautious, in view of our poor knowledge of development. However, with the help of the new conceptual and experimental tools at our disposal, we can now hope to place the comparative morphology of our animals on a sounder basis.

8. Acknowledgements:

This work has been partly supported by grant n. 89.02692.04 of the Italian C.N.R. and by grants from the Italian Ministero della Publica Istruzione.

9. Literature:

ALBERCH, P. (1985): Problems with the interpretation of developmental sequences. — Syst. Zool. **34:** 46 - 58.

ANDRÉ, H.M. (1986): The stases in Collembola: a case study. — In: DALLAI, R. (ed.), 2nd int. Seminar Apterygota. University of Siena: 301 - 305.

— (1987): The concept of stase in Collembola. — In: STRIGANOVA, R.B. (ed.), Soil fauna and soil fertility. Nauka, Moscow: 606 - 610.

— (1988): Age-dependent evolution: from theory to practice. — In: HUMPHRIES, C.J. (ed.), Ontogeny and systematics. Columbia University Press, New York: 137 - 187.

— (1989): The concept of stase. — In: ANDRÉ, H.M. & J.-Cl. LIONS (eds.), L'ontogenèse et le concept de stase chez les Arthropodes. Agar Publishers, Wavre: 3 - 16.

ANDRÉ, H.M. & R. JOCQUÉ (1987): The definition of stase in spiders and other arachnids. — In: BAERTS, L., R. JOCQUÉ & J.P. MAELFAIT (eds.), 9ème Colloque européen d'Arachnologie. Mém. Soc. r. BelgeEnt. **33:** 1 - 14.

ATTEMS, C. (1929): Geophilomorpha. — Das Tierreich **52:** 24 + 1 - 388. W. de Gruyter, Berlin-Leipzig.

AX, P. (1989): Homologie in der Biologie — ein Relationsbegriff im Vergleich von Arten. — Zool. Beitr. N.F. **32:** 487 - 496.

BLOWER, J.G. (1978): Anamorphosis in the Nematophora. — Abh. Verh. naturwiss. Ver. Hamburg N.F. **21/22:** 97 - 103.

BOCK, W.J. (1977): Foundation and methods of evolutionary classification. — In: HECHT, M.K., P.C. GOODY & B.M. HECHT (eds.), Major patterns in vertebrate evolution. — Plenum Press, New York: 851 - 895.

— (1989): The homology concept: its philosophical foundation and practical methodology. — Zool. Beitr. N.F. **32:** 327 - 353.

BOUDREAUX, H.B. (1979): Arthropod phylogeny with special reference to insects. — Wiley, New York: VIII + 320.

BROLEMANN, H.W. (1921): Principe de contraction contre principe d'élongation. — Bull. Soc. Hist. nat. Toulouse **49:** 340 - 359.

— (1930): Eléments d'une faune des Myriapodes de France. Chilopodes. — Faune de France (Paris: Lechevalier) **25:** 10 + 1 - 405.

— (1932): La contraction tachygenétique des Polydesmiens (Myriapodes) et leurs affinités naturelles. — Bull. Soc. zool. France **57:** 387 - 396.

CHAUDONNERET, J. (1988): Qu'est ce que la morphologie? — Int. J. Insect Morphol. Embryol. **17:** 409 - 417.

DEMANGE, J.-M. (1967): Recherches sur la segmentation du tronc des Chilopodes et des Diplopodes Chilognathes (Myriapodes). — Mém. Mus. natn. Hist. nat. Paris A **44:** 1 - 188.

— (1969): La réduction métamerique chez Chilopodes et les Diplopodes Chilognathes (Myriapodes). — Bull. Mus. nat. Hist. nat. Paris (2) **40:** 532 - 538.

— (1974): Réflexions sur le développement de quelques Diplopodes. — Symp. zool. Soc. London **32:** 273 - 287.

DOHLE, W. (1964): Die Embryonalentwicklung von *Glomeris marginata* (VILLERS) im Vergleich zur Entwicklung anderer Diplopoden. — Zool. Jb. Anat. **81:** 241 - 310.

— (1970): Über die Eiablage und Entwicklung von *Scutigera coleoptrata* (Chilopoda). — Bull. Mus. natn. Hist. nat. Paris (2) 4 (1969), Suppl. **2:** 53 - 57.

— (1974): The segemntation of the germ band of Diplopoda compared with other classes of arthropods. — Symp. zool. Soc. London **32:** 143 - 161.

— (1980): Sind die Myriapoden eine monophyletische Gruppe? Eine Diskussion der Verwandtschaftsbeziehungen der Antennaten. — Abh. naturwiss. Ver. Hamburg, N.F. **23:** 45 - 104.

— (1988): Myriapoda and the ancestry of insects. The Charles H. Brookes Memorial Lecture. — The Manchester Polytechnic in coll. with the British Myriapod Group: 28 pp.

— (1989): Zur Frage der Homologie ontogenetischer Muster. — Zool. Beitr., N.F. **32:** 355 - 389.

— (1990): Some observations on morphology and affinities of *Craterostigmus tasmanianus* (Chilopoda). — In: MINELLI, A. (ed.), Proc. 7th int. Congr. Myriapodology (Brill, Leiden): 69 - 79.

ENGHOFF, H. (1990): Phylogeny of chilognathan millipedes (external morphology). — In: MINELLI, A. (ed.), Proc. 7th int. Congr. Myriapodology (Brill, Leiden): 69 - 79.

GOODWIN, B.C. (1984): Changing from an evolutionary to a generative paradigm in biology. — In: POLLARD, J.W. (ed.), Evolutionary theory: Paths into the future. — John Wiley & Sons, Chichester.....: 99 - 120.

GOODWIN, B.C. & L. TRAINOR (1983): The ontogeny and phylogeny of the pentadactyl limb. — In: GOODWIN, B., N. HOLDER & C. WYLIE (eds.), Development and evolution. — Cambridge University Press, Cambridge: 75 - 98.

GOULD, S.J. (1977): Ontogeny and phylogeny. — Belknap Press, Harvard, Cambridge, 14 + 501 pp.

GRANDJEAN, F. (1938): Sur l'ontogénie des acariens. – C.R. Acad. Sci. Paris **206 D:** 146 - 150.

— (1951): Les relations chronologiques entre ontogenèse et phylogenèse d'après les petits caractéres discontinus des Acariens. — Bull. biol. France Belg. **85:** 269 - 292.

— (1957): L'evolution selon l'âge. – Archs. Sci. Genève **10:** 477 - 526.

— (1970): Stases. Actinopiline. Rappel de ma classification des Acariens en trois groupes majeurs. Terminologie en soma. — Acarologia **11:** 796 - 827.

HAUPT, J. (1979): Phylogenetic aspects of recent studies on myriapod sense organs. — In: CAMATINI, M. (ed.), Myriapod Biology. — Academic Press, London: 391 - 406.

HOPKIN, S.P. & H.S. ANGER (1992): On the structure and function of the glue-secreting glands of *Henia vesuviana* (NEWPORT, 1845) (Chilopoda: Geophilomorpha). — Ber. naturw.-med. Ver. Innsbruck, Suppl. **10:** 71 - 79.

KNOLL, H. J. (1974): Untersuchungen zur Entwicklungsgeschichte von *Scutigera coleoptrata* L. (Chilopoda). — Zool. Jb. Anat. **92:** 47 - 132.

KRAUS, O. (1990): On the so-called thoracic segments in Diplopoda. — In: MINELLI, A. (ed.), Proc. 7th int. Congr. Myriapodology (Brill, Leiden): 63 - 68.

LEWIS, J.G.E. (1961): The life history and ecology of the littoral centipede *Strigamia* (= *Scolioplanes*) *maritima* (LEACH). — Proc. zool. Soc. London **137:** 221 - 247.

— (1981): The biology of centipedes. — Cambridge Univ. Press, Cambridge ... Sydney: 476 pp.

LITTLEWOOD, P.M.H. (1983): Fine structure and function of the coxal glands of Lithobiomorph centipedes: *Lithobius forficatus* and *L. crassipes* (Chilopoda, Lithobiidae). — J. Morphol. **177:** 157 - 179.

LITTLEWOOD, P.M.H. & J.G. BLOWER (1987):The chemosensory behavior of *Lithobius forficatus*. 1. Evidence for a pheromone released by the coxal organs (Myriapoda: Chilopoda). — J. Zool. London **211:** 65 - 82.

McNAMARA, K.J. (1986): A guide to the nomenclature of heterochrony. – J. Paleont. **60:** 4 - 13.

MATSUDA, R. (1987): Animal evolution in changing environments with special reference to abnormal metamorphosis. — Wiley, New York: 17 + 355 pp.

MINELLI, A. (1983): Considerazioni sulla filogenesi e la sistematica dei Miriapodi. — Atti 13 Congr. naz. ital. Entomologia, Sestriere-Torino 1983: 551 - 560.

— (1985): Post-embryonic development and the phylogeny of geophilomorph centipedes (Chilopoda). — Bijdr. Dierk. **55:** 143 - 148.

— (1992): Biological systematics: The state of the art. — Chapman & Hall, London, in press.

— (in prep.): Post-embryonic developmental schedules of some myriapod groups.

MINELLI, A. & S. BORTOLETTO (1988): Myriapod metamerism and arthropod segmentation. — Biol. J. Linn. Soc. **33:** 323 - 343.

MINELLI, A. & B. PERUFFO (1991): Developmental pathways, homology and homonomy in metameric animals. — J. Evolut. Biol. **4:** 429 - 445.

MINELLI, A. & A. TURCATO, A. (in prep.): The sternal pore areas of geophilomorph centipedes.

OSCHE, G. (1973): Das Homologisieren als grundlegende Methode der Phylogenetik. — Aufs. Red. senckenberg. naturf. Ges. **24:** 155 - 165.

— (1982): Rekapitulationsentwicklung und ihre Bedeutung für die Phylogenetik — Wann gilt die "Biogenetische Grundregel"? — Verh. naturwiss. Ver. Hamburg N.F. **25:** 5 - 31.

PATTERSON, C. (1982): Morphological characters and homology. – In: JOYSEY, K.A. & A.D. FRIDAY (eds.), Problems of phylogenetic reconstruction. — Systematics Association Spec. Vol. 21 (Acad. Press, London): 21 - 74.

PAULUS, H.F. (1979): Eye structure and the monophyly of the Arthropoda. — In: GUPTA, A.P. (ed.), Arthropod phylogeny. — Van Nostrand Reinhold Co., New York: 299 - 383.

— (1986): Evolutionswege zum Larvalauge der Insekten — ein Modell für die Entstehung und die Ableitung der ozellären Lateralaugen der Myriapoda von Fazettenaugen. — Zool. Jb. Syst. **113:** 353 - 371.

RAFF, R.A. & G.A. WRAY (1989): Heterochrony: Developmental mechanisms and evolutionary results. — J. evol. Biol. **2:** 409 - 434.

RIEDL, R. (1978): Order in living organisms: a systems analysis of evolution. — Wiley, New York: 313 pp.

RIEPPEL, O.C. (1988): Fundamentals of comparative biology. — Birkhäuser .. Berlin: 202 pp.

ROBISON, R.A. (1990): Earliest-known uniramous arthropod. — Nature **343:** 163 - 164.

ROSENBERG, J. (1982): Coxal organs in Geophilomorpha (Chilopoda). Organization and fine structure of the transporting epithelium. — Zoomorphology **100:** 107 - 120.

— (1983 a): Coxal organs of *Lithobius forficatus* (Myriapoda, Chilopoda). Fine-structural investigation with special reference to the transport epithelium. — Cell Tiss. Res. **230:** 421 - 430.

— (1983 b): Coxal organs in Scolopendromorpha (Chilopoda): Topography, organization, fine structure and signification in centipedes. — Zool. Jb. Anat. **110:** 383 - 393.

— (1984): Ultrastructure of the anal organs in the larval stages of *Lithobius forficatus* L. (Chilopoda: Lithobiomorpha). — Int. J. Insect Morphol. Embryol. **13:** 29 - 35.

— (1985): Untersuchungen zur feinstrukturellen Organisation und Funktion der Coxalorgane bei Chilopoda. — Bijdr. Dierkunde **55:** 181 - 189.

— (1990): Untersuchungen zur funktionellen Morphologie der Analorgane von Geophilidae (Geophilomorpha). — In: MINELLI, A. (ed.), Proc. 7th int. Congress Myriapodology (Brill, Leiden): 115 - 123.

ROSENBERG, J. & K.H. BAJORAT (1984): Einfluß der Coxalorgane von *Lithobius forficatus* L. (Chilopoda) auf die Sorption von Wasserdampf. — Zool. Jb. Physiol. **88:** 247 - 344.

ROSENBERG, J. & G. SEIFERT (1977): The coxal glands of Geophilomorpha (Chilopoda): Organs of osmoregulation. — Cell Tiss. Res. **182:** 247 - 251.

ROTH, L.M. (1984): On homology. — Biol. J. Linn. Soc. **22:** 13 - 29.

SELDEN, P.A. & A.J. JERAM (1992): Myriapods and arachnids from the Upper Silurian Ludlow Bone Bed, UK: the earliest land animals. — Ber. naturw.-med. Ver. Innsbruck, Suppl. **10:** 33.

SHEAR, W.A. & P.M. BONAMO (1988): Devonobiomorpha, a new order of Centipedes (Chilopoda) from the middle Devonian of Gilboa, New York State, USA, and the phylogeny of Centipede orders. — Amer. Mus. Novit. **2927:** 1 - 30.

SHUBIN, N.H. & P. ALBERCH (1986): A morphogenetic approach to the origin and basic organization of the tetrapod limb. — Evol. Biol. **20:** 319 - 387.

SNODGRASS, R.E. (1951): Anatomy and morphology. — J. New York entomol. Soc. **59:** 71 - 73.

SPIES, T. (1981): Structure and phylogenetic interpretation of diplopod eyes (Diplopoda). — Zoomorphology **98:** 241 - 260.

TURCATO, A. & A. MINELLI (1990): Fine structure of the ventral glands of *Pleurogeophilus mediterraneus* (MEINERT) (Chilopoda Geophilomorpha). — In: MINELLI, A. (ed.), Proc. 7th int. Congress Myriapodology (Brill, Leiden): 165 - 173.

VAN VALEN, L. (1982): Homology and causes. — J. Morphol. **173:** 305 - 312.

VERHOEFF, K.W. (1928): Durch Zucht erhaltene Formen des *Polydesmus complanatus, illyricus* VERH. und ihre Bedeutung, sowie Beurteilung der Elongation. (110. D.-A.). — Z. Morph. Ökol. Tiere **12:** 684 - 705.

— (1928/32): Klasse Diplopoda. — In: Dr. H.G. Bronn's Klassen und Ordnungen des Tier-Reichs, **5** (II): 12 + 2084 pp., Taf. 1 - 11. Akad. Verlagsges., Leipzig.

WAGNER, G.P. (1989): The biological homology concept. — Ann. Rev. Ecol. Syst. **20:** 551 - 569.

Zeitschrift/Journal: Berichte des naturwissenschaftlichen-medizinischen Verein Innsbruck

Jahr/Year: 1992

Band/Volume: S10

Autor(en)/Author(s): Minelli Alessandro

Artikel/Article: Towards a New Comparative Morphology of Myriapods. 37-46