

## Morphology is still an indispensable discipline in zoology: facts and gaps from Chilopoda

Carsten H. G. Müller<sup>1\*</sup> & Jörg Rosenberg<sup>2</sup>

<sup>1</sup>*Ernst-Moritz-Arndt-Universität Greifswald, Zoologisches Institut und Museum, Abteilung Cytologie und Evolutionsbiologie, Johann-Sebastian-Bach-Str. 11–12, 17487 Greifswald; e-mail: camueller2@freenet.de*

<sup>2</sup>*Universität Duisburg-Essen, Universitätsklinikum Essen, Zentrales Tierlaboratorium, Hufelandstr. 55, 45122 Essen, Germany; e-mail: sommerhaus-rosenberg@ruhr-universitaet-bochum.de*

\*Corresponding author

### Abstract

The importance of morphology as a descent discipline of biosciences has been questioned several times in recent years, especially by molecular geneticists. The criticism ranged between an assumed already comprehensive knowledge on animals body plans resulting in no longer need for morphological research and claims that morphological data do not contribute properly to the phylogenetic reconstructions on all systematic levels or to evolutionary research based on the modern synthesis. However, at least the first assumption of an overall knowledge on animal's outer and inner morphology at present state seems to be unjustified with respect to what is known about Myriapoda. The present paper underlines the necessity and legitimacy to carry out morphological studies in the still widely neglected subgroups of Myriapoda and among them especially in the Chilopoda. Many interesting morphological data on Chilopoda could be gained in recent years, as for instance from epidermal glands and eyes. Gaps of knowledge on the external and internal morphology of centipedes hamper the ability to compare morphological data among the five known chilopod subgroups, to conduct character conceptualisations, to draw scenarios of evolutionary transformations of certain organ systems and/or to use morphological data for reconstructing strongly disputed euarthropod interrelationships. Fundamental gaps in our knowledge on body organisation in Chilopoda are visible on various quality levels. On the one hand, new or improved techniques in analysing or visualising structures (e.g., cLSM,  $\mu$ -CT, PC-based 3D-reconstruction) have practically not yet been applied on any centipede. On the other hand, some organs or organ systems, such as the alimentary canal, salivary glands, reproductive systems or cuticular sense organs, are poorly understood or totally unknown with regard to their fine-structural organisation, either concerning all or only some chilopod taxa. In addition, the body organisation of hardly available taxa like Craterostigmomorpha must be widely considered a blank spot on the map of Chilopodology, even on histological level. Fine structural data in chilopods are also limited to adults, developmental studies are generally low in number, technically outdated and do not cover the full systematic range. Examples are given for both current areas of high research activity and also for morphological character complexes yet neglected but indeed worth primary exploration or re-investigations.

**Keywords:** evolutionary morphology, new research techniques, literature, light microscopy, electron microscopy

### Questioning and reviving of comparative and evolutionary morphology

Morphology as a scientific discipline that concentrates on the outer form and anatomy of living organisms in its widest sense may be traced back more than 200 years ago to scientific descriptions of the famous German writer and philosopher Johann Wolfgang von Goethe (1749–1832) (see review by Scholtz 2009, in press). The long-reaching historical background of morphological research implies a wealth of morphological characters described since then. However, the quality of these data varies strongly with the methods used for the studies or the descriptive and interpretive skills of the morphologist.

In contrast to functional morphology, the relevance of which is seemingly unquestioned by bioscientists, the comparative or evolutionary morphology has become more and more marginalised in the past 40 years (cf. Richter 2007). The upcoming of neurophysiology, molecular genetics (in population ecology and systematics) and, more recently, also of evolutionary developmental biology led to at least three major waves of replacement of evolutionary and systematic morphologists. This replacement is reflected in expiring of research facilities or academic chairs at universities with a main focus on morphology, cutting off financial resources and the subsequent loss of adequate personnel that is able to carry out morphological and/or taxonomical studies properly. The decimation of morphology has been legitimated by arguments that appear at best as a result of misunderstandings and misinterpretations of what the methodology of evolutionary/systematic morphology wants to achieve. In many other cases, decline of morphological studies on adult organisms seems to be the result of pure ignorance. Richter (2007) lists three of those misleading arguments that have been used to dismiss morphology:

First, it is claimed that among the animal kingdom all important structures and organ systems appear to be known. Therefore, no innovation could be expected from descriptive morphology. Richter (2007) contradicts to that assertion by putting forward limits of typological thinking and the impossibility to predict anatomical patterns of hitherto uninvestigated taxa by interpolation from currently discussed ground patterns.

Second, it is claimed that for phylogenetic reconstructions morphological characters may be abandoned with ease (Hillis & Wiens 2000, Scotland et al. 2003). Richter (2007) and Sudhaus (2007) object to that by depicting evolutionary transformations as well as the determination of plesiomorphies and apomorphies to require the consideration of morphological data for phylogenetic analyses.

Third, it is assumed that using of morphological data does not contribute to the understanding and further refining of the theory of evolution in general and of the ‘modern synthesis’ in particular (Ghiselin 2006). Richter (2007) refutes Ghiselin’s (2006) criticism by referring to restrictions inherent in the concept of the ‘modern synthesis’. According to Richter (2007), unilateral consideration of speciation processes and changes among populations is unwarranted and overcome by appearance of evolutionary developmental biology, a discipline that at least served for a renaissance of morphology discernible in early ontogenesis (see Love 2006 for review).

In the past ten years, methods in morphological research have improved enormously due to advanced technical capacities. This concerns both the application of non-invasive morphological scanning methods as for instance micro-computer-tomography ( $\mu$ CT), a technique that has been transferred and adapted from clinical diagnostics (see theoretical

reviews of Wirkner & Richter 2004, Betz et al. 2007 and Friedrich & Beutel 2008; read for example Friedrich et al. 2009 for practical application in arthropod systematics) or confocal laser scanning microscopy (cLSM) if based on vibratome sections (e.g. Harzsch & Hansson 2008) or wholemounts of at least semitransparent organisms (e.g. Chaetognatha: Harzsch & Müller 2007, Harzsch et al. 2009). Neurons individually identifiable by (immunohistochemical) markers have been used increasingly for improving our understanding of phylogenetic relationships among Euarthropoda (see neurophylogeny concept of Harzsch 2006). Furthermore, cell proliferation patterns and morphogenesis of tissues/organs can now be demonstrated by using confocal 4D microscopy, which actually is a 3D imaging along a certain timespan (theoretical review by Schnabel et al. 1997, practical applications done by e.g. Hejnal et al. 2006, Wolff & Scholtz 2006). Technical instrumentaria have also evolved further on the field of invasive morphology, even if classical histological methods are concerned. Nowadays, it is possible to reconstruct complex organ systems with the aid of softwares like AMIRA or IMARIS that enable the researcher not only to autoalign histological section series but also provide him with a valuable tool to visualise a given organ system investigated much more realistically and comprehensively as it could be done with a conventional semischematic drawing. Even though simplified reconstructions, as for instance given by black-white illustrations, (semi-)schematic drawings are still thought to be necessary for morphological descriptions. Wirkner & Richter (2009) underline the innovative and superior approach of PC-based 3D reconstruction for all fields of morphological research. The main advantage for the morphologist or reader of papers based on morphology literature is the gain of a third dimension, which is not necessarily provided by a drawing, even if it comes from in a cutaway perspective. PC-based 3D reconstructions are even imaginable on the ultrastructural level based on the examination of serial ultrathin sections. However, this approach is still highly time-consuming and in a developmental stage.

All these methodological inventions and refinements enable the morphologist to accelerate, more effectively describe and eventually homologise complex structures. According to Wirkner & Richter (2009), a four-level methodology is favoured to bring forward evolutionary morphology into the 21st century. It comprises 1) the description of certain characters (cell types, tissues, organs, organ systems), 2) the character conceptualisation including the definition of primary homologous characters, 3) a subsequent phylogenetic analysis preferably based on cladistic methods, and 4) drawing of an evolutionary scenario that gives rise to the evolutionary transformation of certain characters after having been mapped on the most parsimonious tree. Wirkner & Richter (2009) convincingly demonstrate the validity of their model on the basis of an analysis of the highly complex circulatory system in peracarid crustaceans.

### **Conflicts in euarthropod phylogeny and status of Myriapoda in 'modern' evolutionary morphology**

In the previous chapter it could be shown that the mission 'morphology' in Euarthropoda is far from being accomplished. New characters are about to be investigated by the aid of elaborated invasive morphological methods, accompanied by approved or newly developed non-invasive morphological methods. Even on the arguably basic level of descriptive histology (LM) and ultrastructure (EM), numerous gaps of knowledge may be listed, especially when concerning the Euarthropoda. However, these gaps of knowledge vary with

the taxon addressed. The 'attractiveness' of a certain taxon certainly depends on its diversity and availability in the environment around a potential researcher, the behaviour of the tissue while being fixed, the taxonomic status and practical manageability, the reasonable expectation to gather funding money and of course the size of the community of researchers, in this case of the myriapodologists. This may explain why the subgroups of Myriapoda, the Pauropoda, Symphyla, Diplopoda, and in particular the Chilopoda, the scope of this review, are still widely underrepresented in arthropod literature. This seems astonishing and hard to accept as in each phylogenetic hypothesis dealing with euarthropod interrelationships the Myriapoda came out as a key sister group, whose evolution was always hard to explain for respective protagonists under whatever phylogenetic conditions. The traditional view according to which Myriapoda, treated either as a monophyletic group (Tracheata/Atelocerata-hypothesis: e.g. Hennig 1969, Ax 1999, Bäcker et al. 2008) or paraphyletic restgroup (e.g. Labiophora-hypothesis by Kraus & Kraus 1994 or Kraus 2001), are assumed to have evolved or reduced the same features in adaptation towards living on land just as insects. However, homology of presumably synapomorphic characters, such as tracheae, Mapighian tubules, palp-less mandibles, postantennal organs, indirect transfer or spermatophores and the loss of 2nd pair of antennae, are strongly divergent in detail, have been lost in several lineages or are based on insufficient comparative morphological data (see Richter & Wirkner 2004). In addition, Tracheata were never confirmed in a molecular analysis (Edgecombe 2009 in press). In the light of the currently favoured Tetraconata-hypothesis (monophyletic or paraphyletic Crustacea + Hexapoda: e.g. Dohle 2001, Richter 2002, Giribet et al. 2005, Harzsch 2006, Dunn et al. 2008, Ertas et al. 2009), all aforementioned characters would consequently have to be interpreted as a result of convergent evolution in the lineages of Myriapoda and Hexapoda. This implies that former tracheate features have to be treated as additional apomorphies for insects and myriapods (see Edgecombe 2004). The Myriochelata/Paradoxopoda concept requires the highest degree of convergence in 'tracheate' characters. Support for a sister group relationship of Myriapoda and Chelicerata is almost exclusively molecular (e.g. Friedrich & Tautz 1995, Pisani et al. 2004, Mallatt et al. 2004, Dunn et al. 2008). Morphological support does only seem to exist with regard to early neurogenesis (e.g. Stollewerk & Chipman 2006, Mayer & Whittington 2009), data from adults are so far non-existent. The monophyly of the Myriapoda is likewise controversial and strongly depends on their gross phylogenetic affiliation (see above). In all concepts so far presented, Myriapoda are considered to be either monophyletic or paraphyletic (see Shear & Edgecombe 2009 in press for review). This controversy is often caused by wealth of upcoming molecular analyses, where morphological data remain disregarded.

Either way, as molecular signals are quite stable in favour of the Myriochelata/Paradoxopoda concept, progress in the conflict of those phylogenetic concepts may only be made if further morphological data (embryos, juvenile stages, adults) are explored or more information are obtained from already known character complexes by advanced study methods. Thereby, considerable gaps of knowledge have to be filled, especially in a key taxon like Myriapoda.

Our knowledge on the biology, comparative and functional morphology (including both histology and ultrastructure) of Myriapoda in general and of Chilopoda in particular is in many aspects preliminary (see Rosenberg & Müller 2009). In past times, research was mainly done by light microscopy (LM), earliest works date back till the beginning of the 19th century.

Up to 77 records are counted. Well known researchers from this period are e. g. Tömösváry, Balbiani, Prenant, Saint Rémy, Kowalevsky, Heymons, and Duboscq. Myriapods often were the inspiration for outstanding findings, the fundamentals of which even our current knowledge relies on. For instance, it was Grenacher (1880), who first identified the microvillar system within the retinula cells of the compound eyes of *Scutigera* as a light guiding system and named this complex as rhabdom. Or one could name Plateau (1878), who for the first time detected a chitinous membrane within the midgut of *Cryptops*, where it encloses the food. Later on, this membrane was named 'peritrophic membrane' ('membrane péritrophique') by Balbiani (1890), a term that is still used today. The first description of nephrocytes in Arthropoda was given by Plateau (1878) in *Lithobius*.

From the beginning of the 20th century up to now, there has been an increase in morphological research, again based in particular on light microscopy. Up to 205 records are counted; they are likewise based on light microscopy. Additionally, starting from the middle of the last century electron microscopy found entry into and rapid acceptance in morphological research (transmission and scanning electron microscopy – TEM, SEM). Round about 160 records using electron microscopical methods are counted with respect to Chilopoda. With the invention and aid of this technique, it became possible to examine cellular structures and/or organs particularly with regard to its possible function (functional morphology). In recent years, an increase in activity of morphological research is noticeable. Many initiatives have led to morphological studies using elaborated or established methods; most of them followed a comparative approach. These studies are focused on exploring morphogenesis or, among adults, the histology (LM), outer ultrastructure (SEM), and/or internal ultrastructure (TEM) of various Chilopoda. In this context, the circulatory systems (Wirkner & Pass 2000, 2002), respiratory-tracheal systems (Hilken 1997, 1998), eyes (e.g. Müller 2008), coxal and anal organs (e.g. Rosenberg 1985, Rosenberg et al. 2006), nephrocytes (e.g. Seifert & Rosenberg 1974), cuticular sensilla (Ernst 2000, Ernst et al. 2002, 2006, 2009, Ernst & Rosenberg 2003, Keil 1975, 1976), solitary and compound epidermal glands (e.g. Müller et al. 2003, Hilken et al. 2005, Rosenberg & Hilken 2006, Antoniazzi et al. 2009, Müller et al. 2009), nervous system (e.g. Strausfeld 1998, 2005, Harzsch 2004, Sombke et al. 2009), neurogenesis (e.g. Stollewerk & Chipman 2006), mouth and gut structures (e.g. Koch & Edgecombe 2006, 2008, Koch et al. 2009, Hilken & Rosenberg 2009), as well as the genital system (e.g. Prunesco & Prunesco 1999, 2000) are good examples for current research topics. However, some organs/organ systems of Chilopoda, as for instance the alimentary canal, the salivary glands, and perivascular/pericardial cells are still completely unknown. Here, one could speak of a fundamental gap, meaning that white landmarks are still detectable in the anatomy atlas of Chilopods. But these fundamental gaps do not only occur with regard to certain organs/organ systems. On the contrary, some taxa like hemicopid Lithobiomorpha are quite poorly studied as their main diversity range lies outside Europe, where at least in classic times the majority of anatomists were housed. This is also true for the two species of Craterostigmomorpha from New Zealand and Tasmania. In particular today, such craterostigmomorph material, freshly fixed and suitable for fine-structural examinations, is hard to obtain. However, this problem of material recruitment needs to be overcome. Our scan on chilopod literature revealed that there are still enormous gaps in our knowledge of Craterostigmomorpha. Today, only their general outer morphology (see for instance Dohle 1990) eyes (Müller & Meyer-Rochow 2006), anal organs (Borucki & Rosenberg 1997, Rosenberg et al. 2006), epidermal glands (e.g. Müller et al. 2009), cuticular

sensilla (Ernst et al. 2002, 2006, Edgecombe & Giribet 2004), neurosecretory organs (Gabe 1956), female genital system (Prunesco 1965, Prunesco et al. 1996), male genital system including sperm structures (Carcupino et al. 1996) as well as, on histological level alone, the Malpighian tubules (Prunesco & Prunesco 1996), tracheal system (Manton 1965, Prunesco 1965, Hilken 1997, 1998) and circulatory system (Wirkner & Pass 2000, 2002) received some attention. The quality of anatomical knowledge is even weaker in Henicopidae. In summary, fundamental gaps are found where studies were only based on the examination of a single species, excluding comparative morphological aspects. Whenever morphological data are missed in each of the five chilopod subgroups (higher ranked taxa), we speak of a fundamental gap of knowledge. Likewise, methodological heterogeneity turns out to be problematic. A third aspect falling in the category of fundamental gaps of knowledge is conservative visualisation of structures or character models. With the exception of the work of the comparative histological work of Fanenbruck (2009) on the cephalic musculature of selected myriapod taxa and the most recent studies of Sombke and co-workers (2009) on the brain anatomy and olfaction systems, 3D reconstructions or non-invasive approaches like  $\mu$ -CT have not been tried for illustrating chilopod morphology. Unfortunately, myriapodologists still lag behind standards successfully established in many papers dealing with chelicerates, crustaceans and hexapods (e.g. Wirkner & Prendini 2007, Wirkner & Richter 2009, Hünefeld 2007).

As a second category of deficiency we define cases in which there is indeed a clear demand for an improved understanding of characters, but in the aim to correct or complete previous data or to broaden a given taxon sampling. This filling of partial gaps of knowledge applies to all reinvestigations using the same but perhaps improved method (e.g. avoiding of fixation artefacts, see Rosenberg's and co-workers' (2006) re-investigation of the anal organ of *Craterostigma tasmanianus*), adding of study species within a subgroup for which basic morphological data already exist (lower-ranked taxa). Old literature, although often being a true source of inspiration, might be insufficient in quality in character description and contains an outdated or ambiguous terminology. Filling partial gaps of knowledge seems to be advisable whenever a character set needs to be rounded up for clarity or substantial corrections to current knowledge may be expected. In our opinion, the of course necessary TEM-investigation of cellular architecture of antennal sensilla in non-geophilomorph/lithobiomorph centipedes would only fill a partial gap of knowledge as long as SEM-comparisons of sensilla show same typology. Then, structures already described from *Lithobius* and *Geophilus* (see Keil 1975, 1976, e.g. Ernst 2000) are most likely re-visited in other taxa. However, peculiar, structurally diverging sensilla, such as the antennal collared sensilla with bulbous bases in *Craterostigma tasmanianus* (see Ernst et al. 2006), may provide a more comprehensive impression of type diversity. In contrast, TEM-examinations of many peristomatic sensilla, as shown by SEM for instance by Koch & Edgecombe (2006, 2008) for Scutigleromorpha and Lithobiomorpha, are more demanded. Outer sensillar morphology does barely fit the classification of Ernst (1976–2000) and the location on the body is also new, all in all making this a more fundamental gap of knowledge.

The third category, minor gaps of knowledge is rarely applicable in Chilopoda (e.g. the arrangement of body musculature in *Lithobius forficatus*, thoroughly and beautifully shown by Rilling in 1960, 1968). Even today basic descriptive morphology is needed to discover the comparative histological and fine structural architecture of various organ systems among the

five subgroups of Chilopoda. Since the introduction of micromorphological techniques (transmission and scanning electron microscopy – TEM, SEM,  $\mu$ -CT), we achieve a deeper knowledge on biology of Chilopoda and on functional correlations.

In the following, a survey on morphological investigations by LM and SEM/TEM on various organs and organ systems from the 19th century up to now is provided. This inventory part of the paper is located on the CD-Rom attached to this volume (Rosenberg & Müller 2009).

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