

Department of Zoology, Field Museum of Natural History, Chicago, IL, USA

Larval chaetotaxy of Coleoptera (Insecta) as a tool for evolutionary research and systematics: less confusion, more clarity

A. Y. SOLODOVNIKOV

Abstract

Chaetotaxy of beetle larvae is a significant source of characters for descriptive and phylogenetic aspects of systematics of this largest group of animals of comparable age. Survey of the mostly modern systematic literature employing larval chaetotaxy in Coleoptera reveals, however, that contrary to some general claims for the utility of this character set, use of larval chaetotaxy is rather limited. This is mostly because researchers find working with larval chaetotaxy difficult and time consuming. Factors that make exploration of chaetotaxy so cumbersome are methodologically analysed here and divided into two categories: intrinsic and operational. It is revealed that the most dangerous of them are operational, which arise from the multiplication of inconsistencies coming from different levels of comparative morphological research. As a result, ill-defined assessments of larval chaetotaxy may bring more confusion than clarity to the systematics of beetles, especially to its phylogenetic component which is intuitively avoided by researchers who refuse to use chaetotaxy. This paper attempts to scrutinize the sources of these inconsistencies undermining studies of larval chaetotaxy in hope of eliminating them from present and future systematic studies of Coleoptera. Some methodological issues raised here are also applicable to adult Coleoptera, to other insects and invertebrates, or to the proper ways of exploring the comparative morphology of living organisms, underlying evolutionary and systematic research.

Key words: Coleoptera – systematics – larvae – chaetotaxy – comparative morphology – homology – consistency – phylogeny – descriptions

Introduction

The insect order Coleoptera, with over 350 000 described species is the largest group of animals of comparable age (Beutel and Leschen 2005), and its diversity has challenged biological systematics for over 200 years. Historically, morphology of adults strongly prevailed as a ground for the beetle systematics (Lawrence et al. 1995). But, starting with the early past century, the investigation of larval morphology, alone or in combination with the morphology of adults, led to the most significant phylogenetic hypotheses for beetles as a whole (e.g. Crowson 1955; Lawrence and Newton 1982; Lawrence et al. 1995) and for various beetle subgroups (to mention just a few: Lawrence 1974, 1994; Beutel 1995; Marvaldi 1997; Beutel and Haas 1998; Thayer 2000; Bologna and Pinto 2001; Di Giulio et al. 2003; Grebennikov and Scholtz 2004; Balke et al. 2005; Grebennikov and Maddison 2005; Solodovnikov and Newton 2005). Now there are molecular data, which are rapidly becoming influential for beetle systematics (Caterino et al. 2000; Vogler 2005), the most robust results though coming when molecular data are analysed together with adult and larval morphology (e.g. Caterino and Vogler 2002; Balke et al. 2005). Such evolutionary research, requiring simultaneous analysis of massive and diverse character sets, significantly raises standards for the quality, consistency and compatibility of the data. With rare exceptions (e.g. Beutel and Haas 1998; Gorb and Beutel 2000; Makarov 2002) and in line with the general unfortunate trend in modern phylogenetics (Poe and Wiens 2000), morphological characters, especially larval, are neglected methodologically. Of them, the system of characters known as 'larval chaetotaxy' needs methodological research most urgently.

To make the study of larval chaetotaxy a clearer and more successful endeavour, naturally, the factors making it so cumbersome must be understood and, to the extent possible, reduced or eliminated. It is impossible to eliminate intrinsic difficulties, that is, the facts that structures of chaetotaxy are minute and display complex general and serial variability

within and across taxa of various ranks. But the truth is that, among factors most strongly hindering investigation of chaetotaxy, many appear to be the opposite: operational in nature. Namely, these are methodological flaws and inconsistencies of the modes of observation, interpretation and recording (description) of the organs of chaetotaxy; inconsistencies in the process of comparison of the already described (published) data on chaetotaxy with newly observed structures; or inconsistencies in generalizing the chaetotaxic characters for phylogenetic or other kinds of analyses. Elimination, or at least reduction, of problems of this sort is doable. This study critically analyses the pool of related literature and targets a few main conceptual flaws infesting current investigations of larval chaetotaxy of beetles. The ideas presented here were first developed based on detailed examination of the subject for Staphylinidae, one of the largest beetle families and the area of my practical taxonomic work including study of some larvae (Solodovnikov and Newton 2005; Solodovnikov 2005, 2006). However, when the problems detected in this group were assessed with a much broader pool of literature for Coleoptera (many but not all are cited below in this paper), Insecta [e.g. Hoffman and Brushwein 1992 (Neuroptera); Hardy 1973; Kitching 1984 (Lepidoptera); Williams 1985 (Trichoptera); Belkin 1950; Ward 1976 (Diptera)], or other invertebrates [e.g. Szeptycki 1979 (Collembola); Griffiths et al. 1990 (Acari); Watling 1989; Garm 2004 (Crustacea); Samnailiev and Dimitrov 1980 (Trematoda); Kostadinova 1997 (Digenea)], it became clear that issues raised here are relevant for the study of larval chaetotaxy in very wide array of other invertebrates too.

Larval chaetotaxy of Coleoptera: general summary

Definition

The term 'chaetotaxy' is derived from Greek words 'chaitē' = long hair; and 'taxis' = arrangement (Gordh and Head-

rick 2001). But in the literature on beetle larvae which considers chaetotaxy in sufficient detail (e.g. Thomas 1957; Ashe and Watrous 1984; Bousquet and Goulet 1984; Wheeler 1990; Lawrence 1991; Kovarik and Passoa 1993; Makarov 1996, 2002; Kilian 1998), 'chaetotaxy' usually is understood more broadly and delimited loosely, also including a number of other structures observed on the surface of the cuticle (microtrichia, granules, asperities, setiferous tubercles, bristles, scales, spines of the cuticle, gland openings, etc.), as very schematically shown here in Fig. 1. For instance, Ashe and Watrous (1984) defined larval chaetotaxy as 'a variety of cuticular structures that may be important in taxonomic analysis'. But sometimes chaetotaxy is understood more narrowly, as a system of setae only, whereas the system of pore-like sensilla of the larval cuticle is called 'porotaxy' (e.g. Alarie 1997). A more precise definition of chaetotaxy as 'all cuticular structures associated with primary external receptors, i.e. sensilla' was suggested by Makarov (1996) for the larvae of Carabidae, similarly to acarology chaetotaxy called there 'chaetome'. For the purposes of this paper, I refer to 'chaetotaxy' in its broadest sense, i.e. including setae and all other structures of the larval cuticle, sensory and non-sensory.

Relevance for systematics, and state of knowledge

As a functionally important part of the exoskeleton, chaetotaxy of beetle larvae is morphologically diverse and contains evolutionary information. It has been used for diagnostic purposes (numerous larval descriptions, diagnoses, keys, etc.), and it was repeatedly called as a source of characters useful for phylogenetic reconstruction (e.g. Ashe and Watrous 1984; Bousquet and Goulet 1984; Wheeler 1990; Arndt 1993; Kovarik and Passoa 1993; Makarov 1996, 2002; Kilian 1998; Thayer 2000; Tomkovich and Chaika 2001; Alarie and Bilton 2005; Grebennikov and Maddison 2005). However, despite such claim, most of special studies employing larvae in phylogenetic considerations have not included chaetotaxy, or included it on a very limited basis, and only a small fraction employed larval chaetotaxy broadly (e.g. Alarie 1997; Kilian 1998; Alarie and Balke 1999; Thayer 2000; Alarie and Bilton 2005; Grebennikov and Maddison 2005; Makarov and Bokhovko 2005). The reasons for not using chaetotaxy in phylogenetic analysis, based on published or personally communicated complaints of colleagues (e.g. Thomas 1957; Ashe and Watrous 1984; Bousquet and Goulet 1984; Wheeler 1990; Kovarik and Passoa 1993; Makarov 1996, 2002; Kilian 1998; Solodovnikov and Newton 2005), are mostly the difficulties of doing so, in particular of establishing homology among structures across a broad and diverse taxon sample. For instance, Makarov (1992, 1996, 2002) had to apply a rather elaborate method (sigillotaxy) for inferring homologies of chaetotaxic structures, namely assessing various sensilla with respect to their areas of muscle attachment to the exoskeleton.

With all these problems, however, beetle systematics still tries to employ this set of characters, mostly because there are not many other characters available in larvae. This practicality as a major driving force of studying chaetotaxy is partly responsible for the phenomenon that chaetotaxic features of beetle larvae are mostly known as characters (certain seta present or absent, certain seta simple or frayed, certain 'pore' or 'sensillum' located here or there, etc.), but not as organs or their systems (what kind of receptor is a particular seta,

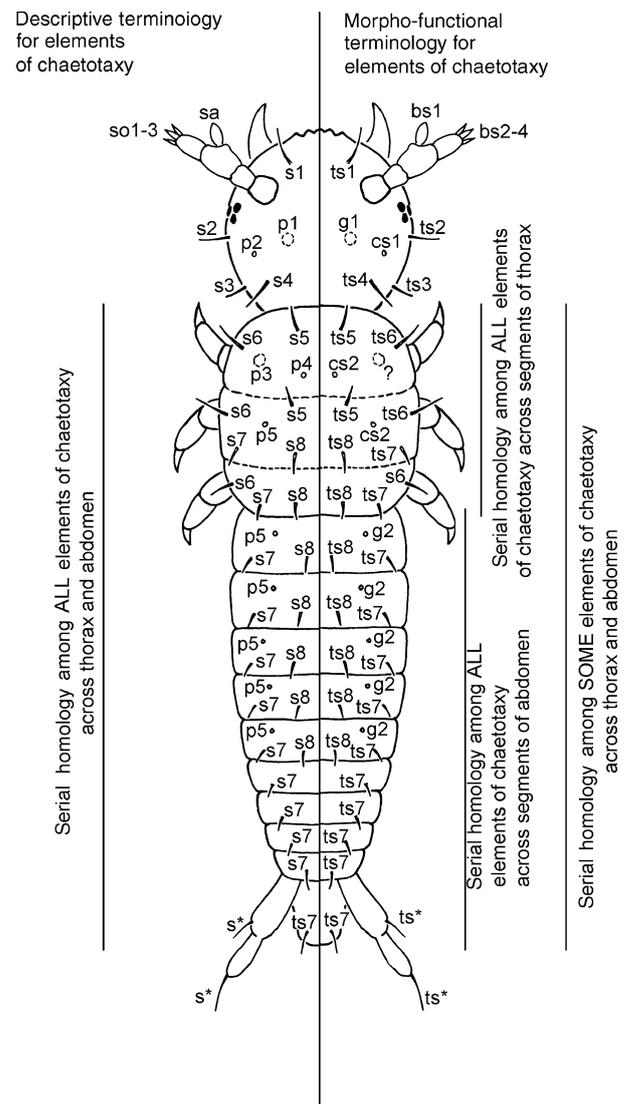


Fig. 1. Hypothetical simplified beetle larva with the elements of chaetotaxy (*sensu lato*, i.e. including sensory and non-sensory organs) viewed at the descriptive (left side) and morpho-functional (right side) levels mapped as follows: bs1–4, various basiconic sensilla; cs1,2, various campaniform sensilla; g1,2, various glands (gland openings); p1–5, various 'pores'; s1–8, various setae; sa, sensory appendage; so1–3, various solenidia; ?, organ of unclear nature; *, structure of unclear serial homology. Note, that with the closer morpho-functional examination, sensory appendage (sa) and solenidia (so) appear to be various basiconic sensilla (bs), all setae (s) proved to be trichoid sensilla (ts), pores (p) appear to be either glands (g), or campaniform sensilla (cs), or, as p3, an organ of unknown nature requiring additional even more detailed study for its proper understanding and naming. Moreover, hypotheses about homology of chaetotaxic structures (here only serial homology is considered) may be changed when knowledge is raised from descriptive to higher, morpho-functional level (compare serial homologies on left and right sides of the diagram)

solenidion or 'pore', etc.). Numerical phylogenetic methods, especially hungry for large numbers of characters (which is not always good, as opposed to control of the quality of characters – e.g. see Makarov 2002; Rieppel and Kearney 2002) recently stimulated this practical, character-gaining trend further. When compared with the chaetotaxy of some species or groups of beetles, or other invertebrates where these features have been more carefully explored morphologically and

biologically (e.g. Snodgrass 1926; Slifer 1970; Scott and Zacharuk 1971; McIver 1975, 1982; Zacharuk 1980; Griffiths et al. 1990; Zacharuk and Shields 1991; Chaika and Tomkovich 1997; Keil 1997a,b; Tomkovich and Chaika 2001; Sinitsina and Chaika 2003; Garm 2004; Triseleva and Safonkin 2005), the level of knowledge of larval chaetotaxy of most Coleoptera appears rather superficial, mainly descriptive. So, although the current mostly descriptive knowledge of chaetotaxy is satisfactory for the diagnostic purposes of alpha-taxonomy, its applicability for phylogenetic reconstructions is limited and requires more detailed investigation of these structures.

Systems of chaetotaxy

Since larval chaetotaxy of beetles is a complex of structures demonstrating some patterns in their distribution, similar to the analogous systems for other arthropods (e.g. Belkin 1950; Ward 1976; Szeptycki 1979; Kitching 1984; Williams 1985; Watling 1989; Griffiths et al. 1990; Hoffman and Brushwein 1992), there have been repeated attempts to develop systems of designations for various chaetotaxic features in beetle larvae (e.g. Thomas 1957; Ashe and Watrous 1984; Bousquet and Goulet 1984; Kovarik and Passoa 1993; May 1994). All these systems are based on comparative examination of a certain sample of taxa for evaluating stable versus variable elements of chaetotaxy, finding homologous structures among them, and providing those with a system of designations. Because of the great diversity of beetle larvae, and difference in approaches of researchers, chaetotaxy systems for various beetle groups vary in details. For instance, Bousquet and Goulet (1984) based their system on primary setae (setae of the first larval instar), whereas other authors (Ashe and Watrous 1984; Kovarik and Passoa 1993) considered setae of the later larval instars too. Ashe and Watrous (1984) and Kovarik and Passoa (1993) established serial homologies between thoracic and abdominal elements of chaetotaxy, but Bousquet and Goulet (1984) did not. Methods for establishing serial homology vary among Ashe and Watrous (1984), Kovarik and Passoa (1993), and others. At the same time, due to basic similarity of all beetle larvae and exchange of ideas among researchers, these systems have much in common including major conventions on naming and labelling of setae, pores, etc. Superficially, they look as the hypothetical scheme in Fig. 1. More important, that despite the special differences among various chaetotaxic systems for beetle larvae, all of them agree in the fundamental principle of comparative biology: they are truly informative and meaningful only when they are homology based, i.e. when only homologous structures receive the same designation across the whole set of analysed taxa. Under this condition, special chaetotaxic systems is a necessary instrument for building up the comparative morphological knowledge. No attempt has been made to provide a system of chaetotaxy beyond the limits of particular beetle families or superfamilies, and it is not even clear whether such an inclusive chaetotaxic system, applicable to taxonomically remote larvae from different habitats, is at all possible (Makarov 1996).

Factors hindering study of chaetotaxy

Critical analysis of the literature reveals several factors responsible for the numerous difficulties associated with the study of larval chaetotaxy. Here they are ranked in the order from intrinsic (1–3: factors related to the properties of

chaetotaxy itself), to operational factors (4, 5: factors related to the methods of investigation of chaetotaxy). One issue (factor 4 here), is in fact intermediate between intrinsic and operational, it is an interference of the complexity of chaetotaxic structures with the pitfalls of the method of comparative morphology. All these factors are considered below in detail.

Poorly developed technology of larval taxonomy

Since larvae are in general more poorly known than adults, the technology of larval taxonomy is also significantly less developed (Newton 1990; Lawrence 1991). Larvae have less sclerotized exoskeleton than adults and in many cases need special preparation for morphological study. Difficulties with identification of larvae that should be matched with their respective adults do not allow using all larval specimens accumulated in collections, and thus restrict research to reliably identified material only, which is less abundant than that for adults.

Chaetotaxic structures at the edge of light microscopy, expenses of detailed study

Some of the elements of larval chaetotaxy are at the limit of resolution of the light microscopy used by most practicing beetle systematists. This may create fuzzy observations or artefacts. For instance, if a small seta is broken off, it is sometimes difficult to distinguish its small setal socket from a 'pore' (which may be a different kind of sensillum) under the light microscope. Special, more detailed studies of the form (and possible function) of elements of chaetotaxy using more powerful techniques like scanning or transmission electron microscopy (e.g. Bologna and Di Giulio 2002; Sinitsina and Chaika 2003), laser scanning microscopy, or histological study and elements of an experimental approach (e.g. Corbière 1968, 1969; Corbière-Tichané 1969, 1970, 1971; Corbière-Tichané and Bermond 1971; Zacharuk et al. 1977) are limited.

Complicated variation

As with all other features of the animal organism, chaetotaxy is subject to variability. Interspecific variability studied at various taxonomic ranks, is the main focus of the taxonomic and phylogenetic studies. Similar to all other organisms, the pattern of the interspecific variability in the beetle larvae is blurred by the intraspecific variability. Moreover, since larval morphology changes during ontogeny (from one instar to another: variation *in time*), and chaetotaxic structures are subject to serial variation among metameric segments of the larval body (serial variation *in space*), the entire pattern of variability that comparative morphological investigation of chaetotaxy must deal with is more complex than that for adults.

Difficulties of the observation of chaetotaxy multiplied by pitfalls of the methodology of comparative morphological research

Comparative morphological investigation of chaetotaxy, in general, starts with the rather superficial descriptions of shape of various organs and proceeds towards more and more detailed knowledge of their external and internal structures, and then towards their assessment as morpho-functional complexes (the latter *sensu* Schwenk 2001). Various levels of

morphological knowledge are reflected in different terminology employed for the same structures. For instance, such elements of larval chaetotaxy as 'seta', 'solenidion', 'sensory appendage' and 'pore' represent a descriptive level of knowledge that differentiates structures only based on their shape, without insight into the nature of the organs they designate. But 'trichoid sensillum' (seta), various 'basiconic sensilla' (sensory appendage and solenidia), 'campaniform sensillum' or 'gland' (often observed as 'pore') can be the names for the same structures understood at a deeper morpho-functional level (Fig. 1).

To enhance a consistent and biologically meaningful growth of morphological knowledge, establishing and testing homologies among observed structures within and across taxa is critical (Rieppel 1988). The better structures are known, the more keys one has for the proper assessment of their homology (using *a priori* criteria of homology *sensu* Lauder 1986, 1994). Thus, at the initial, mostly descriptive stage hypotheses of homology are more tentative than at the later, more advanced morpho-functional stage. Similarly, descriptive terminology signals not only the more superficial level of morphological knowledge but also the more tentative homology assessments, whereas justifiably applied morpho-functional terminology assures a deeper level of structural knowledge and more sound homology assessments. Naturally, each level of definitions should be consistent with the quality of the underlying data. For instance, if one observes only 'a poorly sclerotized spot on the cuticle', this can be conventionally called a 'pore' (or something else), but it is premature to call it a 'campaniform sensillum' only on the basis of such superficial observation. To prove that a particular 'pore' is a 'campaniform sensillum', one should detect certain external cuticular structures, sense cell, etc. (e.g. Snodgrass 1926; McIver 1975).

In reality, things are more complicated because any observation is theory-laden (Rieppel and Kearney 2002), whereas the theory comes from the existing broader knowledge based on earlier or related observations. Thus, with sufficient comparative data, observing 'a poorly sclerotized spot on the surface of the cuticle' in a taxon A, and applying the broader knowledge that in a related and better studied taxon B a similar looking structure in the same position was shown to be a 'campaniform sensillum', one can consider these structures homologous in taxa A and B. Moreover, one can call this structure a 'campaniform sensillum' in taxon A, too. Such a deduction is a hypothesis that can be tested by more detailed observations of this structure in taxon A (gaining more *a priori* criteria of homology *sensu* Lauder 1986, 1994), or by broader phylogenetic analysis including taxa A and B, which may confirm or not the homology of 'campaniform sensilla' in both taxa (based on the *a posteriori* criteria of homology *sensu* Lauder 1986, 1994). If the hypothesis is correct, *a priori* naming the observed structure 'campaniform sensillum' is not harmful, whereas if it is incorrect, application of the morpho-functional term to the taxon A in this case can be misleading. In practice, the chance for such mistakes may be significant, since there are many similar looking, but in fact, different structures among chaetotaxy, making homology assessment based on *a priori* criteria difficult (for reasons see Makarov 1996).

Both descriptive and morpho-functional terminology are used in the literature on Coleoptera, the former prevailing. As regards morpho-functional terms, it can be said for sure that in many cases their application comes, as shown above, from assumptions only, i.e. their use is not supported by adequate

morphological observations. For example, there is one rather conspicuous pore-like structure on the prothoracic tergite of some staphylinid larvae of the tribe Staphylinini (tentatively, I consider this structure homologous across Staphylinini, based on such classical criteria of homology as resemblance of position, resemblance of special quality, and transitions through intermediate forms) that has been given different names (all morpho-functional terms) in some modern descriptions where chaetotaxy was studied and illustrated in sufficient detail: 'gland' (Kranebitter and Schatz 2002), 'campaniform sensilla' [sic] (Schmidt 1994), and 'coeloconic sensillum' (Stanic 2004). At the same time, I am unaware of any morphological work that has investigated that structure in detail sufficient for assigning it a morpho-functional term. Future special morphological investigation may prove whether any of these interpretations is correct. The problem is that morpho-functional nomenclature implies a certain level of biological content. Thus, for example, if the data about that structure are extracted for a larger phylogenetic analysis straight from the literature now, the validity of phylogenetic inference can be undermined by incorrect hypotheses of homology.

In addition to the concealed sources of misinterpretations another layer of informational 'noise' is added when authors, not appreciating the issues discussed above, apply descriptive and morpho-functional terms inconsistently. For instance, in Ashe and Watrous (1984) the chaetotaxic elements of the larvae of Aleocharinae (setae, styli, solenidia, campaniform sensilla, glands, etc.) were defined in a strictly descriptive way. These descriptive definitions are consistent with the current state of knowledge about the respective structures. But whereas their terms 'seta', 'stylus', 'solenidion (solenidium)' are truly just descriptive terms, their use of the term 'campaniform sensillum' for a 'circular, thin spot on the surface of the cuticle' is a case of inconsistency, since that term has a more precise morpho-functional meaning. Another example of an incorrect use of terminology is very abundant. Very often, in the descriptive literature on beetle larvae, 'setae' are contradistinguished to 'sensilla' so, that these two terms become mutually exclusive (e.g. Marvaldi 2005, as the most recent available example). Although the research community usually recognizes what is meant in each particular case, terminologically such contradistinction is simply incorrect since it mixes various hierarchical levels of the same nomenclature (a seta is a particular kind of sensillum). Issues discussed in this section are also illustrated in the Fig. 1.

Lack of methodological consistency and violation of the homology principle in application of systems of chaetotaxy

Since the major principle of existing chaetotaxic systems is homology, their successful application is possible only on condition that this fundamental rule of comparative biology is strictly obeyed. In practice, unfortunately, this is not always the case. Consider, for example, applications of the Ashe and Watrous (1984) system. Like other chaetotaxic systems for coleopteran larvae, this is an explicitly homology-based system. The authors examined its applicability within the staphylinid subfamily Aleocharinae only, where it was subsequently used (Ashe 1986; Ahn 1996, 1997; Thayer et al. 2004). Ashe and Watrous' system also has been applied to some non-aleocharine groups of Staphylinidae: subfamilies Proteininae, Pselaphinae, Neophoninae, Omaliinae, Glypholomatinae and Microsilphinae (Thayer 2000), Oxyporinae (Goodrich

and Hanley 1995), Paederinae (Frانيا 1987), Staphylininae (Chani Posse 2006), and even outside Staphylinidae, to the beetle family Hydraenidae (Delgado and Soler 1997). Consistent application of the system of Ashe and Watrous within and outside Aleocharinae means that only homologous structures would be named similarly, i.e. for instance, setae 'A1' on the protergite of *Atheta coriaria* (Ashe and Watrous 1984), *Eustilicus* (Frانيا 1987), *Oxyporus stygicus* (Goodrich and Hanley 1995) and *Limnebius cordobanus* (Delgado and Soler 1997) would be homologous. If taxa outside those analysed by Ashe and Watrous have structures for which homologues within the system are found only tentatively, these structures should be designated as such; if particular structures are not found, their names should not be used.

Among the existing applications of Ashe and Watrous (1984), approaches of different authors are different. In Ashe (1986); Thayer (2000); Thayer et al. (2004) and Chani Posse (2006), this principle of homology is explicitly stated and strictly followed: setae and 'pores' to which the homologous elements within Ashe and Watrous' system were not found or were recognized tentatively are marked by, respectively (*) or (?) there. The approach in Frانيا (1987), in general, is as in the above listed papers, i.e. an attempt was made to find homologies of chaetotaxic structures between *A. coriaria* and the examined genera of Paederinae, but this is explained less straightforwardly and some is left for inference by the reader. Delgado and Soler (1997) explicitly departed from the homology-based application of the Ashe and Watrous system, as indicated by their statement: 'The notation and designation of setae and rows also follow the Ashe-Watrous system... However, we made no attempt to homologize setae between Hydraenidae and Staphylinidae. Thus, the same setal code does not necessarily mean a direct homology' (p. 39). Application of the Ashe-Watrous system in Ahn (1996, 1997) and Goodrich and Hanley (1995) is not explained. Ahn (1996, 1997) mentioned, in general, that he followed Ashe and Watrous' system, whereas the only explanation that one can find in the methods section of Goodrich and Hanley (1995, p. 214) is: 'a system similar to that of Ashe and Watrous (1984) was used for interpretation of the setae of the head'. In these cases, and especially for *O. stygicus* in Goodrich and Hanley (1995), a species belonging to the subfamily Oxyporinae, which is rather remote from Aleocharinae, it is not clear whether the homology principle was strictly followed.

This demonstrated inconsistency in approaches leads to ambiguity, which lowers the value of all these generally very informative and careful contributions, because they leave to the user much additional research for proper evaluation of the data. In the case of Delgado and Soler (1997), once the principle of homology was explicitly abandoned, the situation is less ambiguous, but one should clearly understand that this is not really Ashe and Watrous' system any more, but a different system, that misleadingly employs Ashe and Watrous' terminology and some conventions. This should be very clearly kept in mind in case of large-scale phylogenetic research in Coleoptera, which may require extraction of data from the literature. If, in such a project, the statement of non-homology in Delgado and Soler (1997) is overlooked and the respective chaetotaxic structures are misinterpreted as homologous based on the designations and illustrations only, one cannot imagine worse damage to the analysis. The listing of similar examples from the coleopterological literature could be continued, but

these from Staphylinidae are enough to clearly make the point.

Conclusions

Larval chaetotaxy of Coleoptera is a complex system of organs, mostly sensory or closely associated with the senses ('chaetome' *sensu* Makarov 1996) (Fig. 1). Some non-sensory organs on the surface of the cuticle (e.g. gland openings) are sometimes also considered under a loose practical (descriptive) definition of chaetotaxy. Mostly, chaetotaxy is examined as a source of diagnostic characters in a purely descriptive way, and only seldom (e.g. Makarov 1996, 2002) is viewed as a system of organs. Such pattern is also true for the application of chaetotaxy to phylogenetic aspects of systematics. This is unfortunate, since an efficient use of chaetotaxy for phylogeny reconstruction requires its understanding at a higher morpho-functional level (Fig. 1, right half).

With rare exceptions, the morpho-functional complexity of larval chaetotaxy is not appreciated enough within the community of beetle systematists. Thus, use of descriptive and morpho-functional terms, inconsistently with the underlying knowledge of the respective structures, is common. A further layer of inconsistencies is added when comparisons and generalizations on the larval chaetotaxy, as on any other system of organs, are not homology-based. These multiple sources of confusion in the study of chaetotaxy have led to the situation where scattered descriptive literature on this subject is hardly compatible not only across large groups of beetles, but even within particular beetle families and subfamilies. Such informational 'noise' undermines usage of published data on chaetotaxy for diagnostics and even more so for phylogenetic reconstructions. Moreover, it hinders new research on chaetotaxy, which inevitably relies on some existing background. From a very general perspective, it seems that chaetotaxy is a set of characters, that are not inherently better, nor worse than other characters for inferring phylogeny, and apparently its utility is limited to a certain taxonomic level determined by the tempo of its evolution, the latter is likely to be group-specific.

Recommendations

The larvae being studied should be well preserved and identified to the best of available knowledge (genus, species, instar, to the extent possible). In addition to deduction-based and rearing-based matching of larvae with the respective adults, new techniques for the DNA-based association of larvae with adults have now become available (e.g. Miller et al. 2005; Caterino and Tishechkin 2006). If larvae of more than one instar are available, differences among instars must be detected (e.g. Kranebitter and Schatz 2002; Staniec 2004). Making comparisons among various species, one must make sure that larvae of the same instar are compared. If the species compared differ in the number of larval instars in their development, the problem of determining homology of their characters including chaetotaxy even among the 'same' instar becomes more complex (Minelli 2003; Minelli et al. 2006), and comparisons should be done with the respective caution. In Coleoptera, where great majority of species having three larval instars, but with few exceptions with two, or, instead, more than three larval instars, such situation is rare but possible.

The elements of chaetotaxy to be described (or analysed) should be clearly defined, well observed (understood) organs

separated from less clear structures. If respective data is available, various organs among observed structures can be defined, and, based on clarity of the observation and comparison, either descriptive or morpho-functional terminology consistently applied. If the nature and function of organs are unknown, the observed morphological structures should be clearly defined and named with descriptive terms. A combination of morpho-functional and descriptive terms may need to be used for different organs whose natures are respectively more or less certain. On encountering a new structure, an attempt to place it in the context of existing terminology is expected. All unclear, ambiguous structures, ambiguous or unclear homologies should be clearly marked as such (by *, ?, etc.) (e.g. Thayer 2000; Caterino and Tishechkin 2006). Given the underlying complexity of larval chaetotaxy, it is much better to express more concerns and doubts rather than assign some structures to the wrong class, hindering future investigations. When describing (or illustrating) chaetotaxy, using the accepted conventions is preferred. But if some structures do not fall into the categories provided by existing conventions, an other suitable designation system can be invented or adopted for explicitly justified reasons. Searching for homologous elements between larva(e) under study and a particular existing 'system of chaetotaxy', there is no need to stick to the latter if there are too many ambiguities. Each existing system is likely to be limited in scope and applicability. Often, new internally consistent designations, or simply good detailed descriptions and illustrations of chaetotaxy even without any special designations (e.g. Schmidt 1994; Staniec 2004) will work better than the problematic application of some predominant system. However, if some system is applied, it should be done based on the principle of homology.

If data on chaetotaxy are extracted from scattered literature for a larger phylogenetic analysis, given the tremendous potential for ambiguities and misinterpretations at the descriptive stage, all published descriptions of chaetotaxy and their further applications have to be critically assessed.

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Zusammenfassung

Larvale Chaetotaxie von Käfern (Insecta) als Werkzeug für Evolutionsforschung und Systematik: weniger Verwirrung, mehr Klarheit

Die larvale Chaetotaxie von Käfern stellt wichtige Merkmale für deskriptive und phylogenetische Aspekte der Systematik dieser größten Tiergruppe zur Verfügung. Die Auswertung überwiegend moderner systematischer Schriften, in denen larvale Chaetotaxie bei Käfern angewendet wird, hat jedoch ergeben, dass, entgegen der allgemeinen Behauptung der Nützlichkeit dieses Merkmalskomplexes, dessen tatsächliche Anwendung recht begrenzt bleibt. Dies rührt hauptsächlich daher, dass larvale Chaetotaxie als schwierig und zeitraubend angesehen wird. Die Faktoren, welche chaetotaxonomische Untersuchungen erschweren, werden hier methodologisch analysiert und in zwei Gruppen unterteilt: intrinsische Faktoren und operationale Faktoren. Es wird aufgezeigt, dass die operationalen Faktoren die größten Gefahren mit sich bringen, bedingt durch die Multiplikation widersprüchlicher Befunde von verschiedenen Ebenen vergleichend-morphologischer Forschung. Als Resultat können fehlgeleitete Bewertungen larvaler Chaetotaxie mehr zur Verwirrung als zur Aufklärung der Käfersystematik beitragen. Dies trifft insbesondere auf die phylogenetische Komponente der Systematik zu, die von Forschern, welche die Verwendung der Chaetotaxie ablehnen, intuitiv gemieden wird. Die vorliegende Arbeit versucht, die Quellen der widersprüchlichen Befunde zu ergründen, welche den Wert von Untersuchungen zur larvalen Chaetotaxie untergraben, sodass sie in aktuellen und zukünftigen systematisch-coleopterologischen Untersuchungen vermieden werden können. Einige der hier erörterten methodologischen Gesichtspunkte sind auch anwendbar auf adulte Käfer, andere Insekten und Wirbellose oder allgemein auf die korrekte Vorgehensweise bei der Erforschung der vergleichenden Morphologie lebender Organismen, die der Systematik und Evolutionsforschung zugrunde liegen.

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Author address: A. Yu. Solodovnikov (for correspondence), Department of Zoology, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605–2496, USA.
E-mail: asolodovnikov@fieldmuseum.org