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Autor(en): **Kolibá, Jií**

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An approach to the higher taxa based on transformation series: A theory and examples from Cleroidea (Insecta: Coleoptera)

by Jiří Kolibáč

Abstract. The absence of inclusive synapomorphies is a frequent phenomenon in nature, as demonstrated through examples of the families Cleridae and Thanerocleridae (Coleoptera). All character states in organisms are the products of phyletic transformation. Therefore, taxa should be defined on the basis of ordered and polarized sequences of character states present in subgroups and not on the basis of inclusive synapomorphies. An explanation is given of a higher taxa concept based on transformation series (TSC = transformation series concept). According to this concept, higher sister taxa are independent transformation paths of a certain character; in other words, these taxa are considered to be identical with various transformation series of one and the same character. Neither recent nor observed fossil taxa can be considered actual ancestors. Actual ancestors are not recognizable and may only be conceived as hypothetical constructions. Since the observed primitive taxa are distant in time from the actual ancestors, they also differ in their character states to a greater or smaller extent. A way of classifying primitive taxa is explained, as is the term “quasiancestor”: this is an observed (recent or fossil) taxon that appears to look like the ancestor of other observed taxa. Quasiancestral taxa do not form paraphyletic groups in classification because they are not actual ancestors.

Keywords. phylogenetic taxonomy – multistate characters – transformation series – Cleroidea

Firm points do not and cannot exist in reality for the very reason that everything changes and evolves. And yet “firm” things do exist: namely, the directions of the changes, the trajectories of evolution, the tendencies and derivations of these changes. These things are recognisable and are of long-term validity. B. Slavík

...it is absurd to adore isolated products of an uninterrupted series of transformations, as if they were eternal and real. Life is not a thing or a state of some thing but an uninterrupted movement or change. S. Radhakrishnan

Introduction

Establishing the rank of higher taxa is a perennial problem in phylogenetic taxonomy. In phylogenetic taxonomy, a group of species whose common ancestor exhibited unique apomorphy can be denoted as a higher taxon. In practical taxonomy, higher taxa share a common apomorphy or a sequence of apomorphic states of multistate characters (AX 1984, FOREY *et al.* 1992; see Fig. 1). One of the basic principles of formal classification is that sister taxa should occupy equivalent ranks (HENNIG 1950). This basic and logical postulate causes considerable inconvenience in practice. First of all, in fully resolved pectinate cladograms the number of dichotomous divisions often exceeds that of the systematic categories acknowledged by the International Code of Zoological Nomenclature. Several authors have addressed this problem, for example by introducing a number of prefixes to the existing categories (FARRIS 1976); other authors have suggested using a number rank system (HENNIG 1969, GRIFFITHS 1974, LØVTRUP 1977) or sequencing (NELSON 1972, 1973). Whatever the case, at present, taxa of the same rank are classified more or less disproportionately.

In this paper a different way of defining higher taxa is proposed, which should contribute to more equivalent ranks in classifications and, above all, to greater naturalness of taxa. The concept proposed here has its origin in my study of beetles of the superfamily Cleroidea and, therefore, the examples given below also arise from my own observations on this superfamily. This paper is concerned with only the higher taxa, that is, those of the rank of genus and higher.

The following terms have been used in the text:

C h a r a c t e r = body part(s) or organ(s); **m u l t i s t a t e c h a r a c t e r** = character whose states form a transformation series; **t r a n s f o r m a t i o n s e r i e s** = sequence of character states of a particular multistate character, invariably ordered and polarized. In the text to follow, the term "transformation series" corresponds to such terms as lineage, phyletic line and higher taxon. **T r a n s f o r m a t i o n s e r i e s c o n c e p t (T S C)** = concept of higher taxa based on transformation series.

A c t u a l t r a n s f o r m a t i o n = an event that actually took place in the past in actual taxa and is hypothetical from the present point of view. Similarly, an actual ancestor, a taxon and a character state are also real but hypothetical events. **O b s e r v e d t r a n s f o r m a t i o n** = an event that can be observed in recent or fossil records (i.e. recorded and studied) taxa. An observed transformation is a more or less altered reflection of an actual transformation. Similarly, an observed ancestor, taxon and character state are also more or less altered reflections of their actual counterparts. Thus, reality is hypothetical and the observed phenomenon is a mere reflection of reality.

R i c h t a x o n = a taxon comprising a large number of subgroups or members; **p o o r t a x o n** = a taxon comprising a small number of subgroups or members. An extreme case of a poor taxon is a monotypic taxon.

According to the classical cladistic method, the higher taxa are defined and determined on the basis of apomorphies (e.g. AX 1984). From this basic principle derives the use of multistate characters, the states of which form the transformation series. (In entomological taxonomic literature, with which I am in constant contact, one can only rarely encounter a higher taxon that would be defined exclusively by a multistate character.) In richer groups, a character rarely occurs in an absolutely identical state in all subgroups. Each of the subgroups has its own phylogeny and, because it is a higher taxon, the subgroups cannot be in a direct ancestor-to-descendant relationship. Furthermore, species and even individual organisms are subject to constant changes, right down to the level of information noise in DNA replication (see literature on the quasispecies, e.g. NOWAK 1992). In the phenotype, this internal instability is sometime

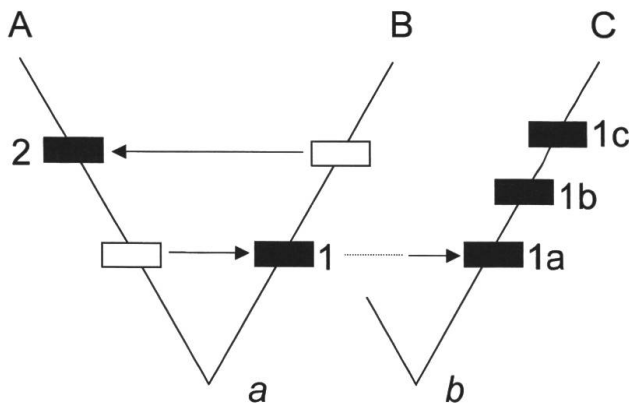


Fig. 1. Classical way of differentiation of two higher taxa A, B based on synapomorphies 1, 2 (Fig. 1a). C is distinguished from A by the apomorphies 1a, 1b, 1c of the multistate character 1 (Fig. 1b). Empty rectangle = plesiomorphy, solid rectangle = apomorphy.

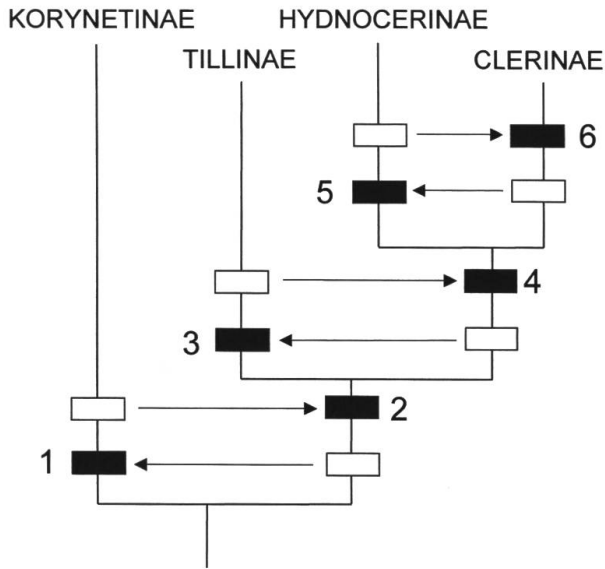


Fig. 2. The traditional way of differentiation of the Cleridae subfamilies based on “inclusive” synapomorphies. 1 = the fourth tarsomeres reduced; 2 = prothorax with lateral edge; 3 = front coxal cavities closed; 4 = the first tarsomeres reduced and covered from above by second tarsomeres; 5 = antennae short; 6 = pronotum with two tubercles and longitudinal furrow in middle.

generally denoted as fluctuation variability. Thus, synapomorphy of a genus is an abstraction of the essential traits of the character states of its species; the synapomorphy of a tribe is an abstraction of the generic states, and so on.

It is possible for two taxa to have identical character states if the characters are molecular sequence data. However, inclusive synapomorphies (derived states shared by all subtaxa of a taxon) in the form of a single identical state, found in the phenotypes of several taxa, rarely exist. Obviously, all groups show more or less stabilized character states that are common to the members of a given group to a considerable extent. However, these states may not be apomorphic within a higher group, although they can also be plesiomorphic. In higher taxa, many transformations may occur that can be preserved even in the recent subtaxa, bearing testimony to evolutionary changes and indirectly indicating phyletic lines (indirectly because the actual ancestors are not and cannot be known, see below).

A study of the family Cleridae supports the above considerations. For example, the subfamily Clerinae comprises about 100 genera and 1,600 species distributed all over the world, and it is the richest subfamily within the Cleridae. In proportion to these figures, the genera in this subfamily show morphological as well as ecological variability. Due to that, no unique apomorphy has yet been found that would be really shared by all or at least a majority of members of the Clerinae, and that would separate this subfamily from its supposed sister group, the Hydnocerinae (in spite of this fact, the Clerinae is a monophyletic group; see KOLIBÁČ 1997a). Fig. 2 shows the traditional way of distinguishing subfamilies of Cleridae by their synapomorphies. My studies (KOLIBÁČ 1987, 1989a,b) have revealed that none of the five of six apomorphies shown in Fig. 2 are shared by all genera in the subfamily in question (see also (Figs 3–8)). The coxal cavities in *Falsotillus* Pic and the related genera (Tillinae) are partly open (cf. character 3 in Fig. 2). The two subfamilies, Hydnocerinae and Clerinae, comprise genera (e.g. Hydnocerinae: *Callimerus* Gorham, or Clerinae: *Eleale* Newman) that show an ancestral

or derived (i.e. secondarily prolonged) state of the first tarsomere (character 4). The antennae of *Lemidia* Spinola, as well as those of certain species of the genus *Callimerus* Gorham, are equally long or even relatively longer than in some Clerinae (e.g. *Trichodes* Herbst, *Dieropsis* Gahan, etc.; character 5). The pronota of some Clerinae from different phyletic lines do not show typical clerine structure due to secondary reduction (*Apopemopsis* Schenkling, *Colyphus* Spinola, *Placopterus* Wolcott), or the pronotum is in a primitive state (*Dozocolletus* Chevrolat and related South African genera; character 6). Besides, some Hydnocerinae (*Lemidia*) and Korynetinae (*Pylus* Newman) also show the clerine structure of pronotum. Similarly, states of multistate characters are the “synapomorphies” in the korynetine branch of the subfamilies of Cleridae (Korynetinae including former Tarsosteninae, Enopliinae, Epiphloeinae), such as the vanishing lateral edge on the prothorax (character 2), the tegmen in dorsal or ventral position, etc. The only true synapomorphy in the Cleridae is the reduction of the fourth tarsomere (character 1), a character which I have observed in virtually all representatives of the korynetine branch examined (93% of genera studied). Even here, however, a certain variability was observed in the size of the tarsomere relative to the remaining ones (see KOLIBÁČ 1989a).

The situation in the family Cleridae indicates that all synapomorphies described by earlier authors are in fact multistate characters that form transformation series. Furthermore, the Cleridae show several distinct transformation series, which are shown in Figs 3 to 8. These include the transformation series of the lateral edge, pronotum, tarsi, antennae, tegmina, and wings. Examinations of the Cleridae have revealed no more than mere records of the changes occurring during phylogeny. The sequences of such changes are termed here the transformation series and are considered, in the sense of materialistic science, to be phenomena objectively occurring in nature. The origin of these sequences is not connected here with any of the models of character evolution (morphocline, Fitch minimum mutation model, character evolution, punctuated equilibrium, etc.), and it is not the purpose of this paper to attempt an explanation of how the transformation occurred in evolutionary time. Any of the known synapomorphies can be considered to be a certain character state of the multistate character forming the transformation series, in which only one state has been known so far.

It is a generally known fact that living organisms preserve certain characters in their ancestral ¹⁾ character state. Polarized character states can serve to compile transformation series (for particulars on transformation series analysis, their determination, determining the order and polarizing, see e.g. LIPSCOMB 1992, MABEE 1989, MICKEVICH 1982,

¹⁾ I am aware of the fact that the recent higher taxa cannot be considered the ancestors of other recent higher taxa. At most, they may be recent descendants of actual ancestors. As far as any actual ancestors did exist we can only consider them as hypothetical constructions or series of plesiomorphic characters deduced (e.g. through outgroup analysis) from the characters of recent or fossil organisms. Fossils often contain more plesiomorphic states than do recent taxa, and thus they can indicate the directions and modes of character transformations and the ensuing information. However, they cannot be considered to be actual ancestors. In the text to follow, actual ancestors are considered hypothetical constructions. Recorded and studied primitive taxa are termed “observed ancestors”.

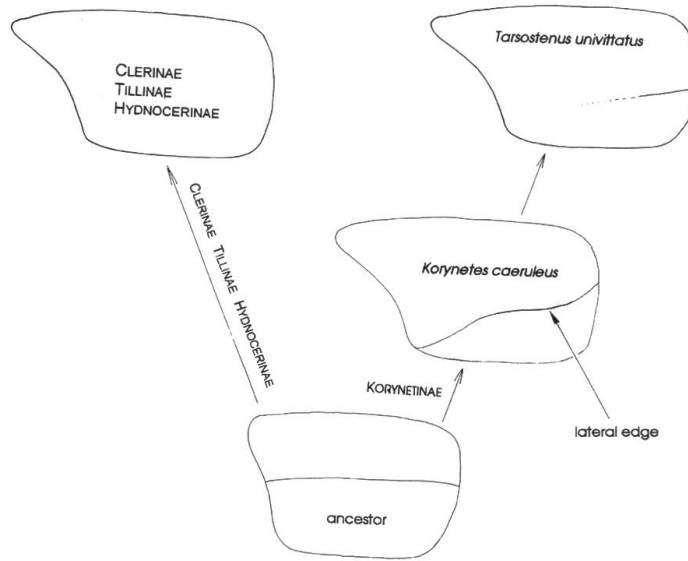


Fig. 3. The course of the prothoracal lateral edge reduction. The lateral edge is perfectly lacking in members of Tillinae, Clerinae, Hydnocerinae. Fluent reduction of the lateral edge is also observable in some genera of Korynetinae. The character states were figured according to concrete species (as indicated) which are representatives of larger groups. (According to KOLIBÁČ 1997a; modified.)

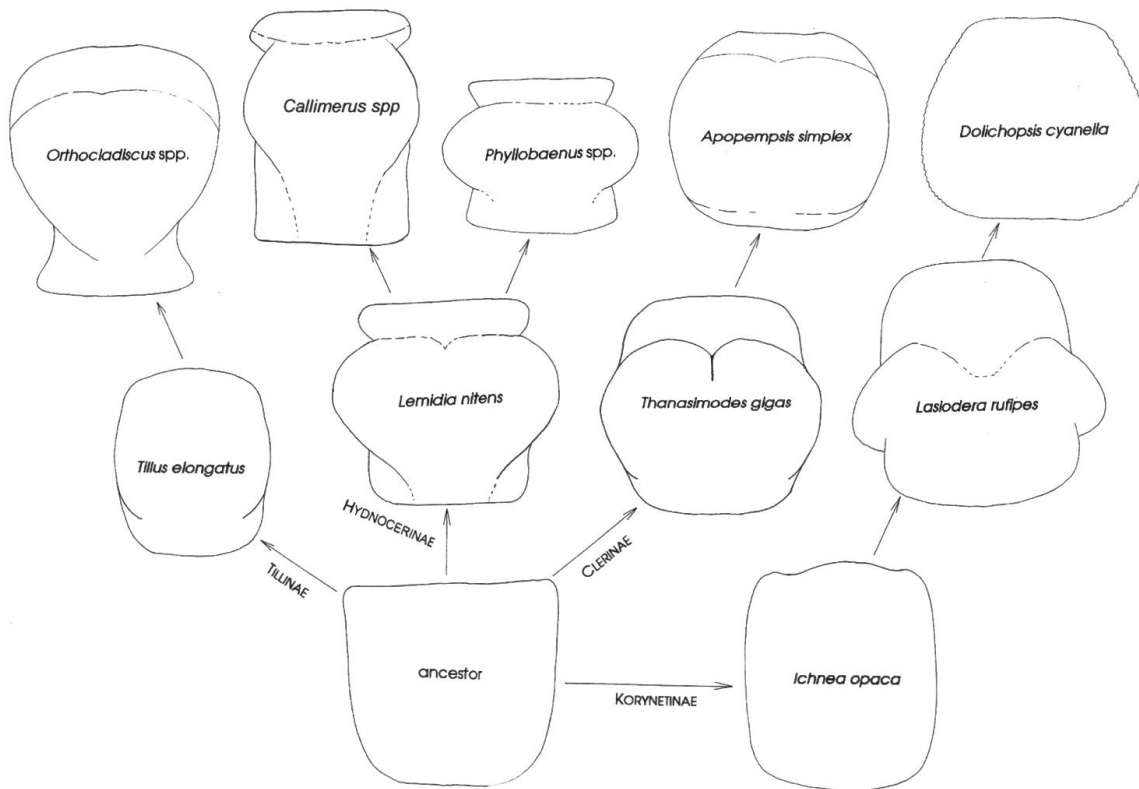


Fig. 4. Transformation series of pronotal shape and its structures in the Cleridae subfamilies. The character states were figured according to concrete species (as indicated) which are representatives of larger groups. (According to KOLIBÁČ 1997a; modified.)

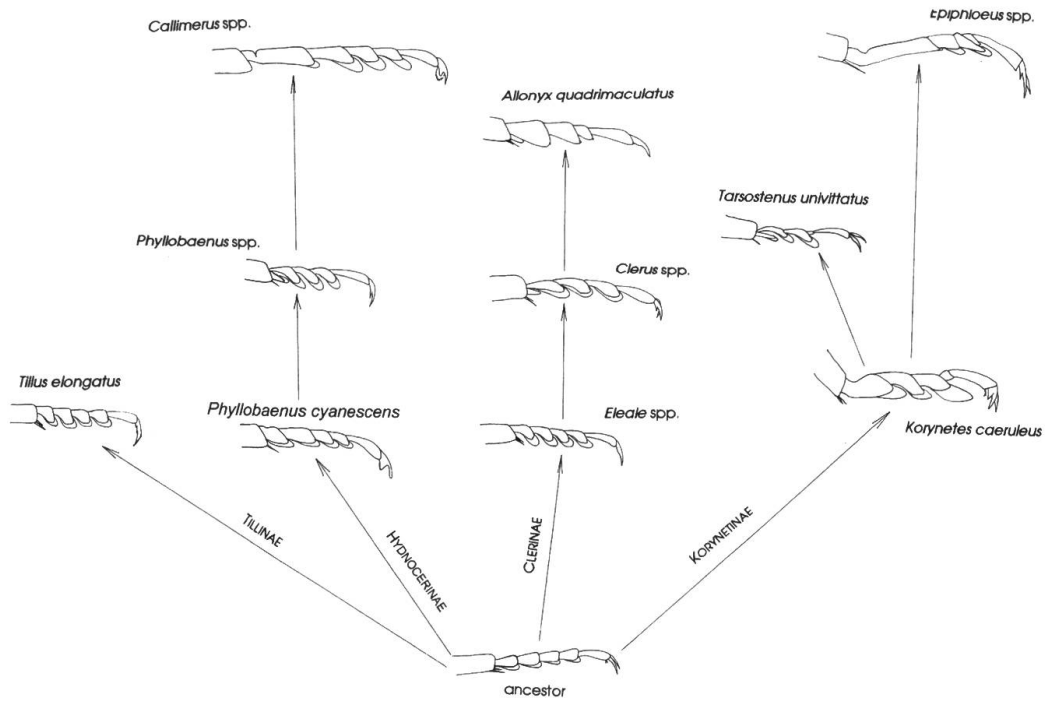


Fig. 5. Transformation series of hind tarsi in the Cleridae subfamilies. The character states were figured according to concrete species (as indicated) which are representatives of larger groups. (According to KOLIBÁČ 1997a; modified.)

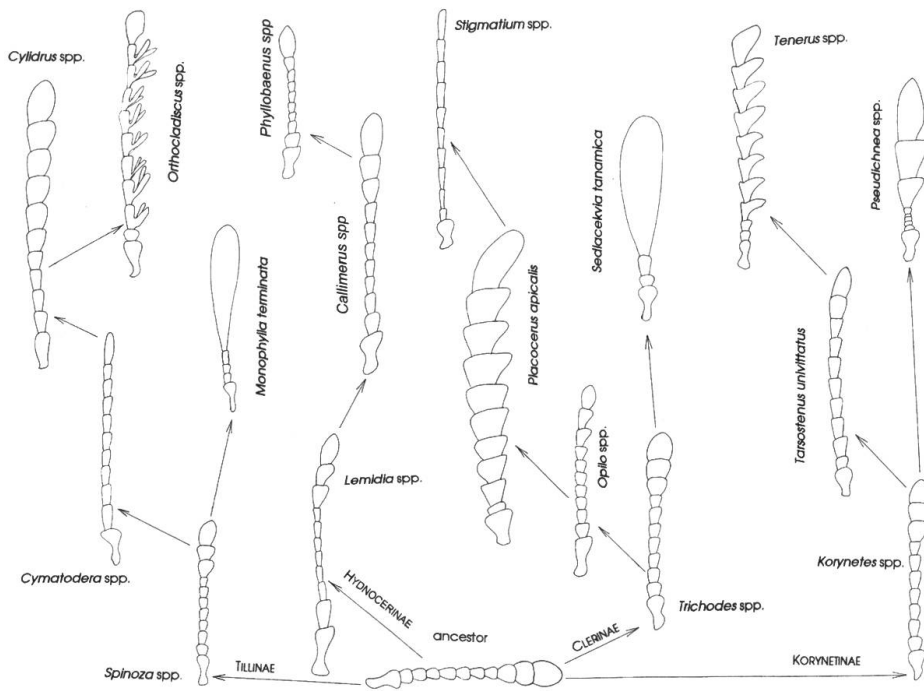


Fig. 6. Transformation series of antennae in the Cleridae subfamilies. The character states were figured according to concrete species (as indicated) which are representatives of larger groups. (According to KOLIBÁČ 1997a; modified.)

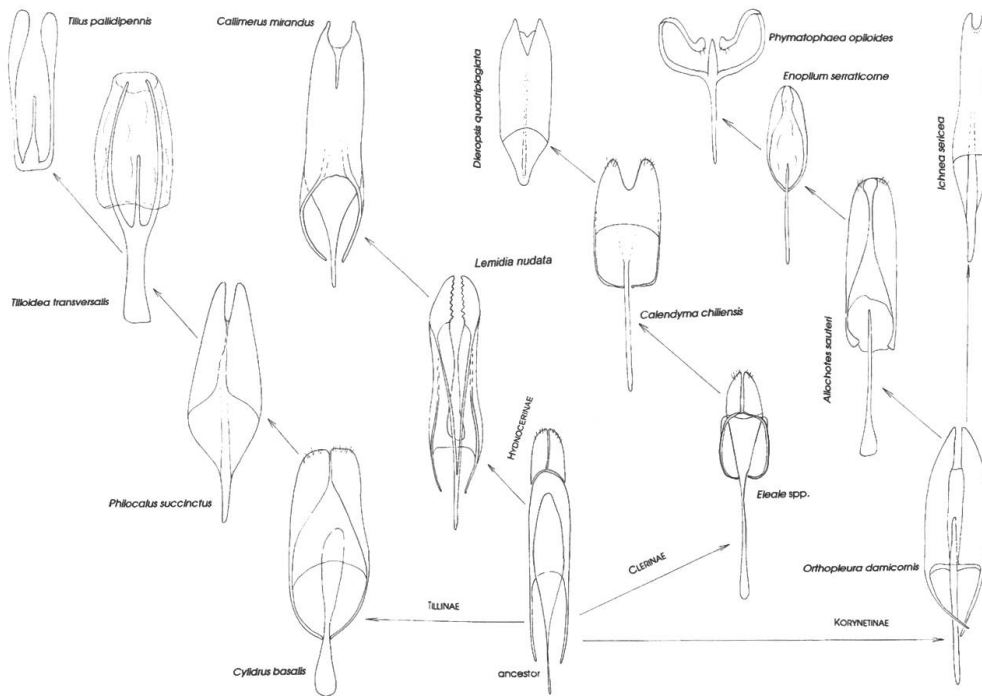


Fig. 7. Transformation series of tegmina in the Cleridae subfamilies. Tegmina of Tillinae, Hydnocerinae, Clerinae dorsally, these of Korynetinae ventrally. Ancestral tegmen is probably situated dorsally. The character states were figured according to concrete species (as indicated) which are representatives of larger groups. (According to KOLIBÁČ 1997a; modified.)

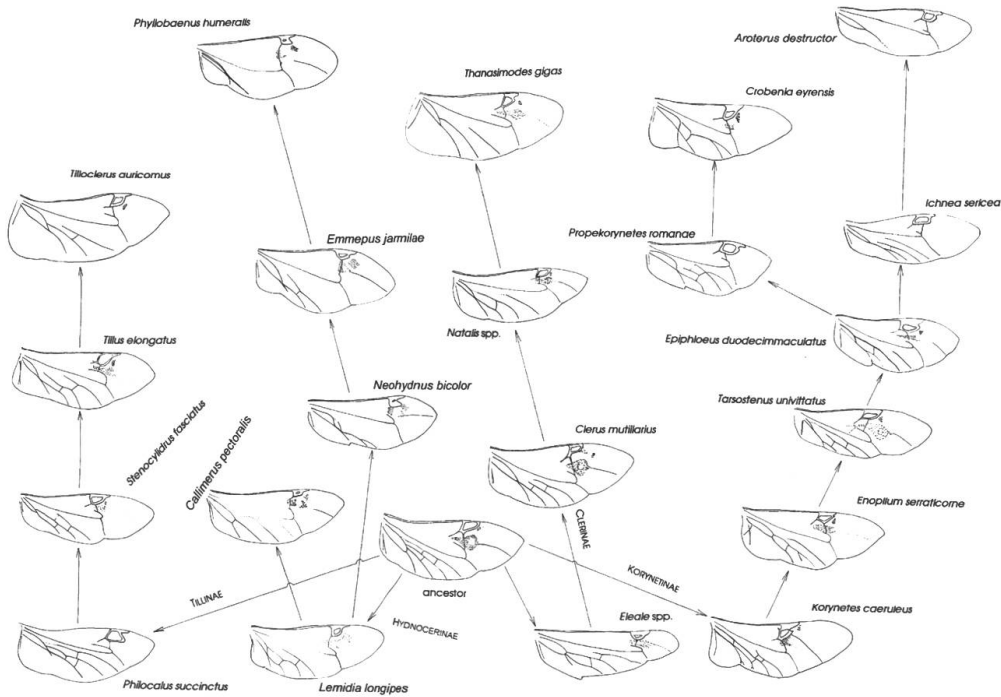


Fig. 8. Transformation series of wings in the Cleridae subfamilies. The character states were figured according to concrete species (as indicated) which are representatives of larger groups. (According to KOLIBÁČ 1997a; modified.)

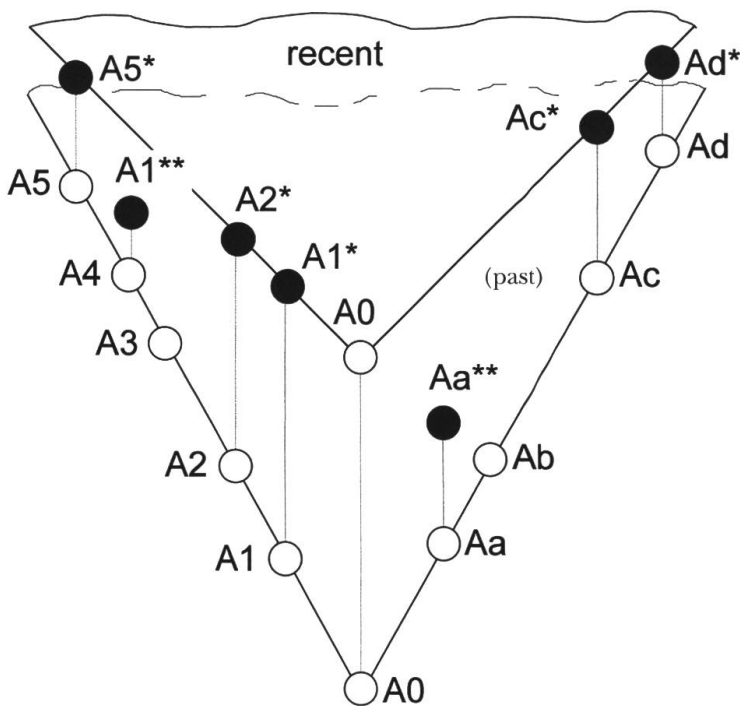


Fig. 9. Scheme showing phylogeny of higher taxa. Solid circles = observed taxa. A0 is the ancestral state of character A from which arise two independent transformation series (or two higher taxa), A1–A5 and Aa–Ad. Subtaxa comprising recent representatives show character states (marked with an asterisk *) more or less altered against those of their actual ancestors (= empty circles). Similarly, also known fossils (A1**, Aa**) are altered against their ancestors (marked with two asterisks **). Therefore, transformation series compiled from both recent and fossil taxa are a mere reflection of the actual transformation processes having taken place in the past. Therefore, even the ancestral character status is merely hypothetical (empty circle); the actual state is not and cannot be known. Transformation

series derived from the observed taxa are hypotheses of their phylogeny. To what extent these hypothesis approach reality cannot be ascertained. Such a hypothesis can only be rendered precise or proved false by successively adding further character states to the transformation series or by adding the transformation series of other characters.

MICKEVICH & WELLER 1990). There are several different ways to optimise a transformation series on a tree. Transformation series analysis (TSA) by MICKEVICH (1982) is often considered the best method (HAUSER & PRESCH 1991). However, a taxonomist sometimes has to choose among several equally scanty but different transformations. His choice would not be arbitrary but based on all procurable biological data, so that the chosen branching is a hypothesis about a character transformation. The transformation series of any multistate character forms sequences that should correspond to the transformation of the character in time. Therefore, these sequences can be considered to be indirect records of the phylogeny of the taxa showing the given character states. They are indirect, because the taxa examined are not in a direct ancestor-descendent relationship; only the sequences of character states indicate the pertinence of the taxa to a common phyletic line (Fig. 9). The observed transformation series are a reflection of actual transformations having taken place in the past. These indirect witnesses of character transformations are in fact the only possible documents of phylogeny obtainable. Their existence in nature is an objective phenomenon from the scientific point of view. Therefore, I suggest that the transformation series be identified with higher taxa; in other words, *the term "higher taxon" be the name of the transformation series of one or several multistate characters.* Classical phylogenetic

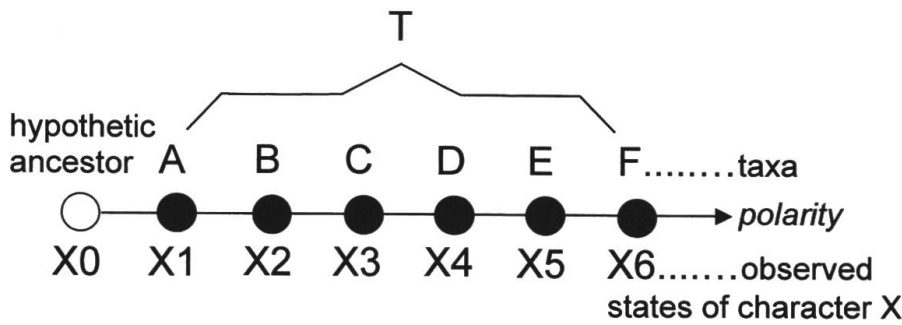


Fig. 10. The principle of the concept of higher taxa based on transformation series. The transformation series composed of states of the character X forms the higher taxon T. The states X1 to X6

occur in the subtaxa A to F. The transformation series is derived from the hypothetical state X0, which is deduced from an outgroup analysis or as a common ancestor of T and its sister group.

taxonomy, based on synapomorphies, can hypothesize on the relationships between taxa on the basis of the system (FOREY *et al.* 1992, MICKEVICH & WELLER 1990). In contrast, higher taxa based on transformation series (and thus also the transformation series as such) are themselves hypotheses of phylogeny.

Concept of higher taxa classification

The taxa are treated hereafter as the transformation series of the observed characters (cf. Fig. 9). According to the concept proposed here, the higher taxon can be visualised as a sequence of the character states of a particular character (or several characters) found in concrete subtaxa. Fig. 10 shows a generalized example of the transformation series of multistate character X, with states X0 to X6, being the higher taxon comprising subtaxa A to F. Practical examples of transformation series and the classification based on them are shown in the subsequent text.

In cladistic taxonomy, higher taxa are usually defined on the basis of the derived states of different characters (Fig. 1). If the higher taxa were to be based on transformation series (or even in common taxonomy), the problem of paraphyly would arise (Fig. 11). All subtaxa (b1–b4) of taxon **b** share the character state A3. Since taxon **b** derives from the actually existing taxon **a** (although the subtaxon a3 may be hypothetical), taxon **a** is paraphyletic – it does not comprise all lineages derived from that taxon.

Should taxa **a**, **b** be monophyletic, all subtaxa in taxon **b** would show character A in its ancestral state A0. Taxa **a**, **b** would be differentiated from a hypothetical ancestor showing character states A0, B0, as in Fig. 12. However, as mentioned above, it is practically impossible that any character could occur in all members of a rich taxon in a single (ancestral) state. Therefore, the example shown in Fig. 12 (similar to the classical scheme in Fig. 1) would actually be like that in Fig. 13. The sequences of character states A1–A5 and Ai–Aiv (or B1–B4 and Bi–Bv) form independent transformation paths of characters A and B and, hence, different transformation series of the two characters. The taxa formed by the two transformation series are monophyletic. Two independent transformation series of one character – either A or B – would be sufficient to separate

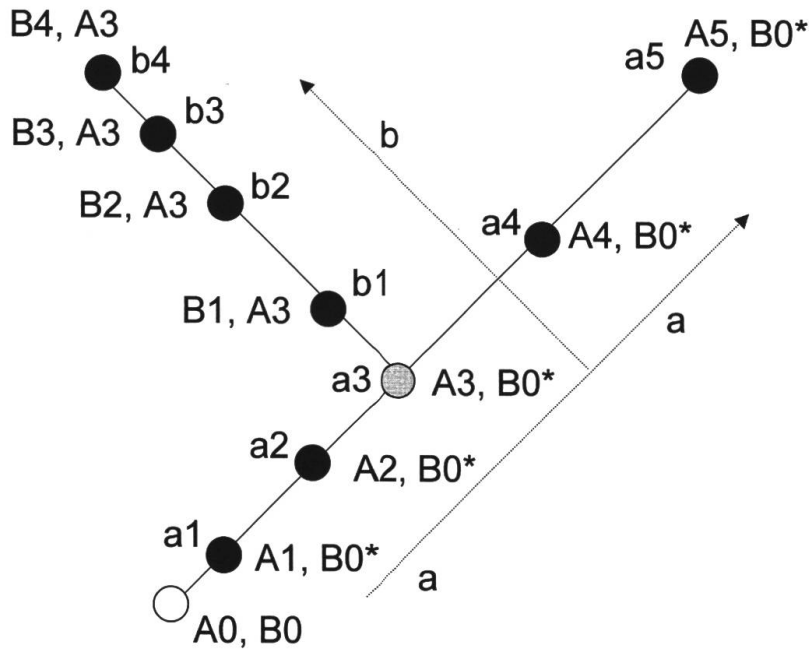


Fig. 11. The taxon **a** is composed of the subtaxa a1 to a5 and based on transformation series of the character A (the states A1–A5). All subtaxa of **a** share the primitive state B0*. The taxon **b** is composed of the subtaxa b1 to b4 and based on transformation series of B (B1–B4). **b** is derived from **a** and from the real state A3, which is shared by all subtaxa of **b**. The state A3 and the subtaxon a3 can actually be occurring in **a** (grey circle). That is why the taxon **a** is paraphyletic.

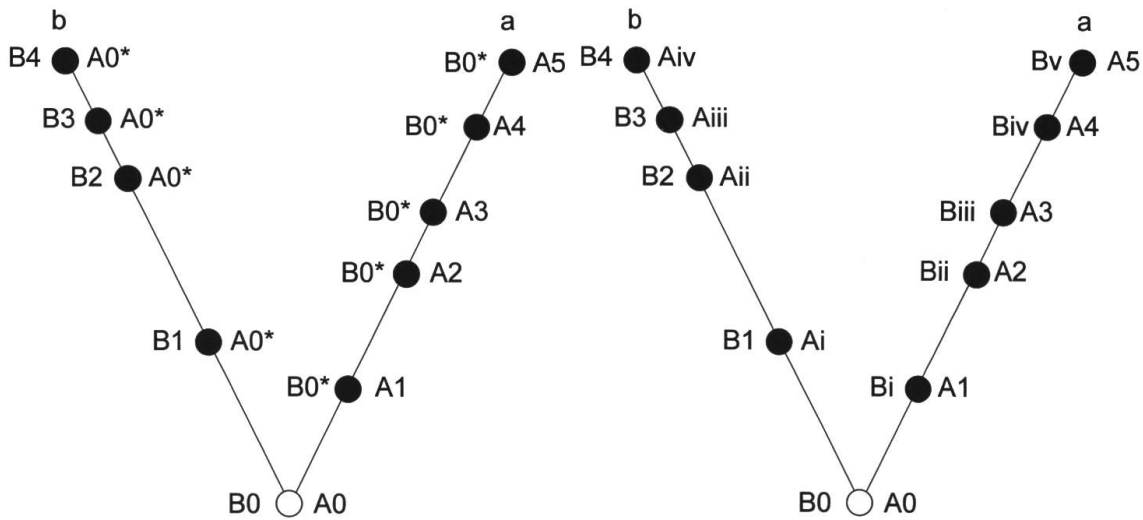


Fig. 12. The taxa **a**, **b** (see Fig. 11) are monophyletic because transformation series of the characters A, B are derived from a common hypothetical ancestor (empty circle). Asterisks in A0* and B0* mean that the character states are nearly equal to the ancestral states A0 and B0. The scheme is closely comparable to the classical “cladistic” method in Fig. 1.

Fig. 13. It is not too probable in nature that the same primitive states, such as A0* or B0*, be shared by all subtaxa of the taxa **a**, **b** as shown in Fig. 12. The character A is probably also transformed within subtaxa of the taxon **b**. A sequence of states (Ai–Aiv) of A forms a transformation series. Similarly, the character B in **a** forms a transformation series which is composed of the states Bi–Bv.

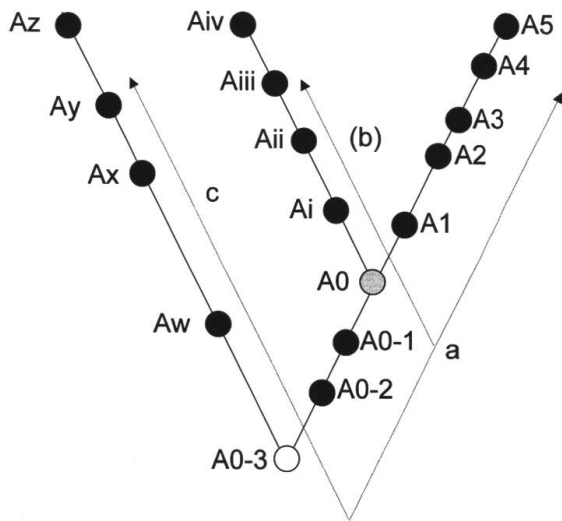


Fig. 14. The sister taxa **a**, **c** have the same rank and are based on transformation series of the character A. **b** is a part of the taxon **a**. See text for details.

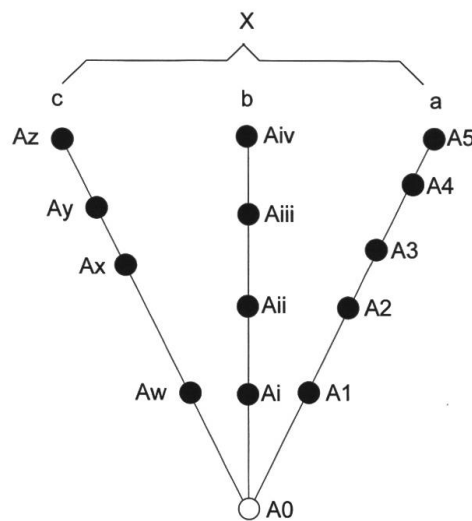


Fig. 15. Principle of TSC. The taxa **a**, **b**, **c** have the same rank because they are derived from a single hypothetical ancestor (or a hypothetical ancestral character state). **a**, **b**, **c** are independent modes of the character A transformation (**a** = A1–A5, **b** = Ai–Aiv, **c** = Aw–Az). Let us consider **a**, **b**, **c** to be tribes in a subfamily X; if any other transformation series is not derived from A0, then **a**, **b**, **c** are *all* tribes of X. See text for details.

them. If a taxon is defined as the transformation series of a particular character, then it follows from the preceding paragraph that *sister taxa are the independent evolutionary transformations of at least one character*. The higher taxa defined in this way are certainly monophyletic and occupy the same taxonomic rank. Should some taxa be discovered later showing more primitive character states (e.g. A0–1, A0–2 in Fig. 14) than the hypothetical A0 in Fig. 13, then taxon **b** would become a mere part of taxon **a**. A sister taxon to **a** could only be another independent sequence of character states, e.g. Aw–Az, which would form a transformation series, or higher taxon, denoted as **c** in Fig. 14. Hence, it follows that *monophyletic higher taxa of the same rank, based on transformation series, must be independent transformations (phyletic lineages) of a particular character, which are derived from a single hypothetical ancestral state and comprise all derived groups*. Should the higher taxa meet all conditions of monophyly and equal rank, the principle of dichotomy need not, and even cannot, be strictly applied in their classification (cf. KOLIBÁČ 1997b). Sister taxa can, but need not, form pairs. In other words, *all subtaxa of equal rank, contained in a particular systematic unit (higher taxon), for example all subfamilies of a family, must be derived from a single hypothetical ancestor, and they are formed along independent paths of transformation of a single or several multistate characters*. This is fundamental to the transformation series concept of higher taxa (TSC). In a cladogram, all taxa of equal rank invariably

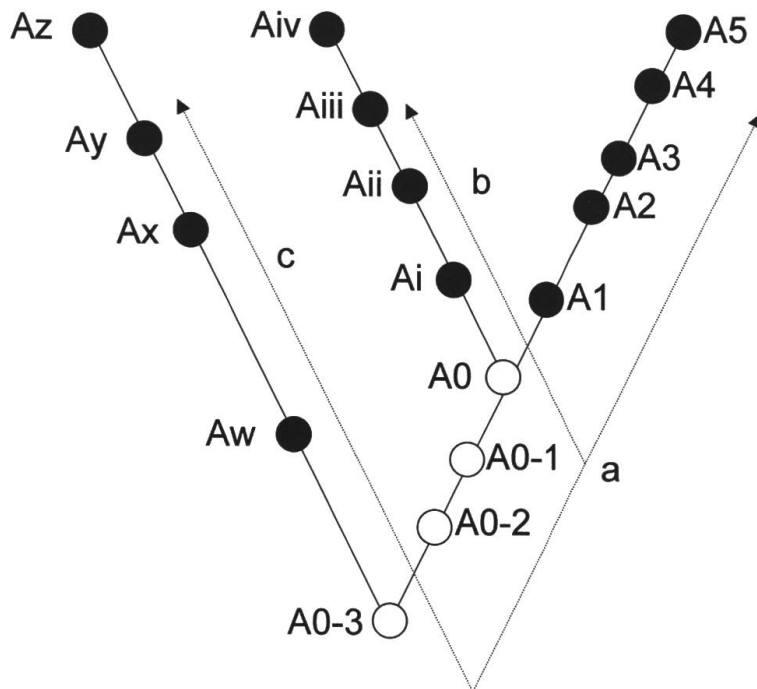


Fig. 16. In practice, if A0-1 and A0-2 are hypothetical states, the taxon **c** is not paraphyletic and the taxa **a**, **b**, **c** have the same rank. Compare with Fig. 14, also for explanation of abbreviations.

form a bush (Figs 15, 20). For example, taxa **a**, **b** and **c** in Fig. 15 are monophyletic and occupy equal ranks because they are independent transformation series of the multistate character A, which are derived from the hypothetical ancestral state A0. In practice, the most primitive states in lineages – here Aw, Ai, A1 – are often almost identical and resemble the hypothetical state A0 (see some primitive character states in Figs 3–8). This, of course, is evidence showing that the taxa – here **a**, **b** and **c** – are actually derived from a common ancestral character state. At the same time, it becomes obvious that not all transformation series can find their place in classification: there was certainly more branching during phylogeny than the systematic categories employed at present.

The requirement that equal rank taxa be derived from a single ancestral state is unusual and hardly acceptable to many taxonomists. The problem arises from replacing the pectinate cladogram by a scheme in which names of subtaxa, the sequences of which directly form the higher taxon, are used to denote character states (Fig. 10). (Using the names of subtaxa to denote character states is formal and can naturally be replaced by numerical or symbolic denominations.) Certainly, evolution corresponds with dichotomy rather than polytomy, e.g. in Figs 15, 20 or 21. The concept of a single ancestor, shared by all higher taxa of equal rank (Fig. 15), is based on the following consideration: If all subtaxa (fossil or recent) denoted as A0-1, A0-2 in Fig. 14 and bearing a record of the sequence of a multistate character were known, then taxa **a**, **b** would have to form a single higher taxon, being the sister taxon to **c**. However, if the subtaxa (or character states) A0-1, A0-2 were merely hypothetical, then the higher taxa **a**, **b**, **c** can exist, occupying the same taxonomic rank (Fig. 16). (In cladistic practice, the taxa **a**, **b**, **c** would probably form a bush.) In taxonomy, this is probably the most frequent

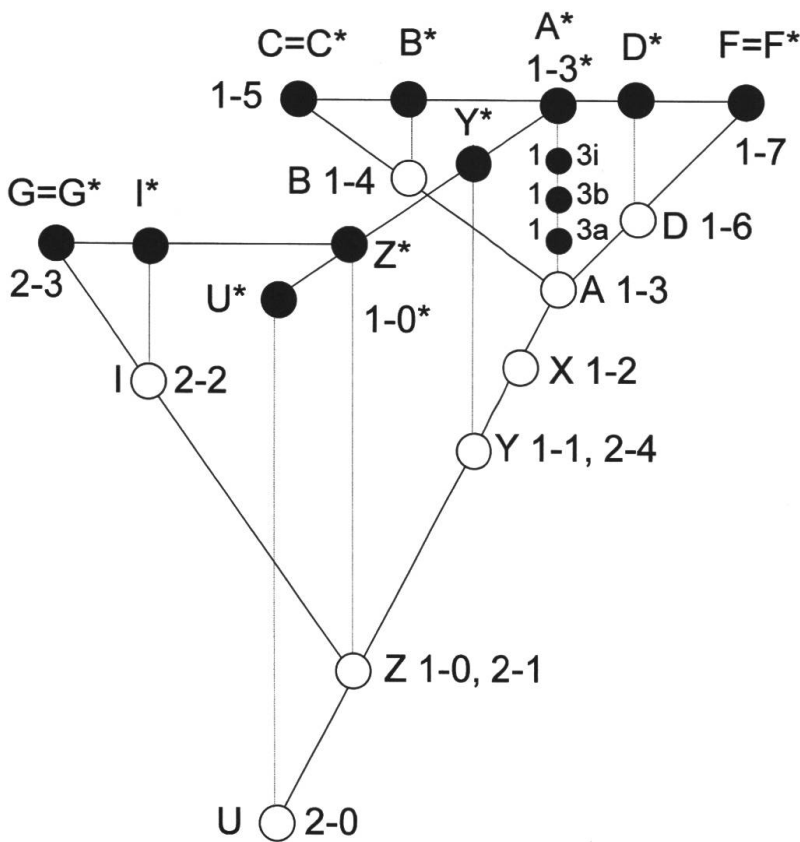


Fig. 17. Model phylogeny of several lineages. Empty circles marked with capital letters without asterisk (U, Z, A, etc.) mean actual ancestors which are not known. Solid circles marked with letters with an asterisk mean recent observed taxa derived from those ancestors. Lineages from Y to C and F are distinguished on the basis of transformation series of the character 1 (the states 1-1, 1-2, etc.). The states 1-3a to 1-3i are intermediate states in phyletic transformation between A and A*. They are observable in some recorded fossils. If A* (or, better, AA*) is considered a genus, all taxa between A and A* should be classified within it. The taxon A itself is an exception because it is unknowable. The genus AA* could be written as the interval (A;A*>. All taxa derived from Y (like A,

B, F, etc.) form the tribe T which is based on transformation series starting with the character state 2-4. (Other states of the character 2 are not figured.) Another transformation series starts from 2-2 in I and ends in 2-3 in G. Empty circle = actual or hypothetical taxon. Solid circle = observed recent or fossil taxon. See text for details.

case in practical classification. The system constructed in this way is exemplified by the classification of a part of the families of Cleroidea in MAJER (1994). However, if a subtaxon were discovered bearing the character state corresponding to A0-1 or A0-2, then this would result in the case shown in Fig. 14. That is to say, subtaxon A0-1 (A0-2) could not be included in the existing taxa **b** or **a**.

A model phylogeny of several lineages is shown in Fig. 17. The course of the phylogeny is congruent with a transformation of the characters 1 and 2. The character states of the actual ancestral taxa (e.g. 1-3 in A or 1-0 in Z) as well as the other taxa of the lineages are reflected into recent (observed) taxa in more or less changed states (1-3* in A* and 1-0* in Z*). For example, the taxon A is the actual ancestor from which the lineages BC and DF have been derived. The character states 1-4 (in the taxon B) and 1-6 (in D) are derived from the ancestral state 1-3 (in A). Let us assume that actual transformation events can be deduced from states of character 1 (in the recent taxa) which are marked with an asterisk in Fig. 17. It has been mentioned above (Fig. 9) that an observed state (e.g. 1-3*) differs from an ancestral one. The state 1-3 had been transformed several times (1-3a, 1-3b, ..., 1-3i) before it came to the observed state 1-3*

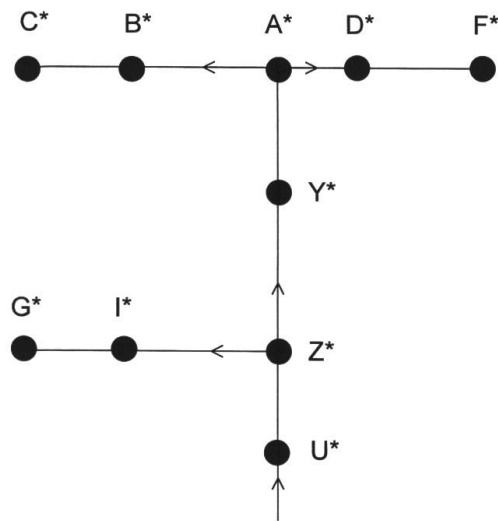


Fig. 18. A schema of transformation series from Fig. 17 in a fashion that may be deduced in common taxonomy. The taxon A^* (or the taxon Y^*A^*) seems to be paraphyletic if C^*B^* and D^*F^* had the same rank as Y^*A^* . Similarly, Z^* (or U^*Z^*) would be mentioned as a paraphyletic ancestor if it did not include I^*G^* and $Y^*A^*C^*F^*$. Figs 17 and 19 show that the observed taxa Z^* and A^* are not paraphyletic in reality because they are derived from (or unequal to) the actual ancestors Z and A .

in the recent taxon A^* (a process known as phyletic transformation). (A character state in a recent higher taxon is considered an abstraction of the essential states of its members. It is impossible to ascertain how much the states 1–3 and 1–3* differ from one another because the exact form of state 1–3 cannot be known. Character states of the ancestors (e.g. $A-A^*$) are more distant from each other in time than those of the descendants (e.g. $B-B^*$). We can therefore suppose that character states of the actual ancestors (e.g. 1–3 in A) and those of the observed ancestors (1–3* in A^*) are more different in their structures than the equivalent character states in descendants (e.g. 1–4 in B and 1–4* in B^*). The character states of the youngest (the “most recent”) taxa in a lineage can look nearly the same as the states of their ancestors (e.g. $C = C^*$). However, this consideration does not have to be universally valid.

The transformation series shown in Fig. 18 is derived from Fig. 17 and it is composed only of the observed taxa and their character states. Taxon A^* appears to be an ancestor of the descendent lineages B^*C^* and D^*F^* in the transformation series (Fig. 18). However, it has been explained in the preceding text (namely Fig. 17) that A^* is not an actual ancestor of the lineages mentioned. Therefore, let us term A^* a *quasiancestor*. Furthermore, any recorded fossil with the character states 1–3a to 1–3i cannot be considered the actual ancestor. Thus, how should the taxa A^* or Y^* be classified? They cannot be classified within any of the descendent lineages because of a paraphyly. Fig. 19 shows a simplified view of Fig. 17; higher taxa are marked with the dotted (grey) areas in the figure: for example the area of the quadrangle UZZ^*U^* (excepting the abscissa UZ where hypothetical ancestors are situated) can be considered a tribe. It has been mentioned above that the quasiancestor A^* is not a direct ancestor of the lineages B^*C^* and D^*F^* but it is a descendent of the actual ancestor A . Since the lineages B^*C^* , D^*F^* and the quasiancestor A^* are derived from the unique ancestor A , these taxa form a higher taxon of the same rank (e.g. the subtribes). Then all taxa between A and Z

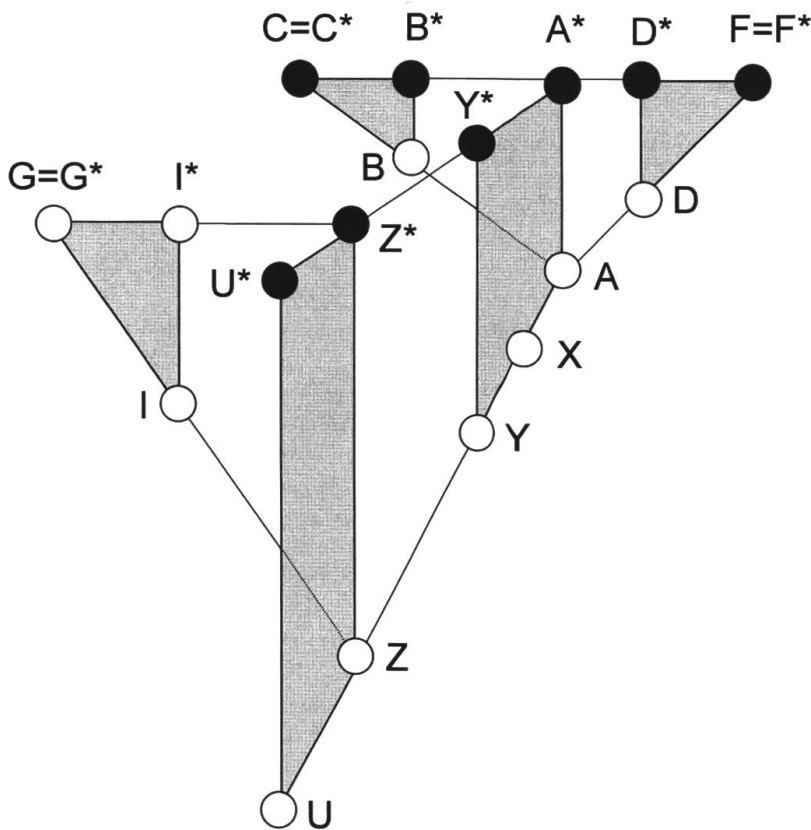


Fig. 19. A classification consequent to Fig. 17. The taxa IGI*, T (= YFC), and UZZ*U* are tribes. The latter is a quasiancestral tribe. The taxa BCB*, DFD*, and YAA*Y* are subtribes. The latter is a quasiancestral subtribe. The dotted areas indicate that all chronotaxa (or fossils) among ancestors and recent taxa are included in the above-mentioned higher taxa. The taxa are represented by areas, except for the abscissas representing actual ancestors. For example, the quadrangle UZZ*U* represents a tribe which, however, does not comprise the abscissa UZ on which lie the hypothetical actual ancestors. These ancestors are in fact paraphyletic but are only seemingly contained in the higher taxa, since they can

never be found or discerned. That is why actual ancestors are factually excluded from the classification and system.

(excluding Z itself, i.e. taxa starting with Y) can be added to the taxon A* because they are also defined on the basis of character 1 transformation (Fig. 17). The transformation series Y*A* is derived from ancestor A in the opposite polarity than the other transformation series and it appears ostensibly to be a paraphyletic group (see Fig. 18 and preceding text). Since Y*A* is derived from the quasiancestor A* and seems to be an ostensible ancestor of B*C and D*F*, let us name the taxon Y*A* a *quasiancestral group* or a *quasiancestral taxon*. If the tribe T is established for the transformation series starting with the state 1-1, then T will be composed of three subtribes: BCB*, DFD* and the quasiancestral subtribe YAA*Y*.

DE QUEIROZ & GAUTHIER (1992: 455) believe that not all taxa should be included in higher taxa (the problem of “mandatory categories”). Their belief is based on their hypothesis that ancestral taxa (or stem species) are paraphyletic. Obviously, it is sometimes impossible to determine to which higher taxon a particular (mostly fossil) lower taxon should belong. Such a taxon may be classified as a taxon *incertae sedis*. However, this problem is theoretically resolved by the concept of a quasiancestral taxon. Suppose a fossil beetle is found which can be classified in the family Cleridae. This family came into existence somewhere in the early Mesozoic and the four extant subfamilies in the late Jurassic at the latest. Suppose further that our fossil dates back to

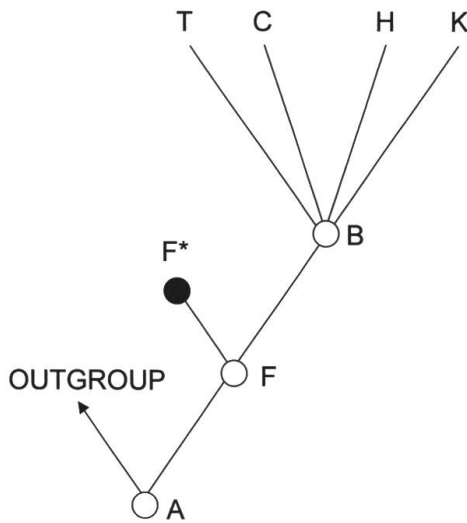


Fig. 20. A model of the phylogeny of Cleridae in the event that fossil F^* is found, which antedates the differentiation of subfamilies in Cleridae. A = actual ancestor of the family Cleridae, B = actual ancestor of subfamilies of Cleridae, F = actual ancestor of the fossil F^* , T = Tillinae, C = Clerinae, H = Hydnocerinae, K = Korynetinae.

the early Jurassic, i.e. to the time at which the extant subfamilies were not yet differentiated (Fig. 20). However, our fossil F^* is not identical with ancestor F which lies directly on the line connecting the ancestor of Cleridae (A) with the ancestor B of the subfamilies of this family (according to the current state of knowledge, the subfamilies of Cleridae show polytomic division; see KOLIBÁČ 1997a). F^* is more or less changed in relation to F. Therefore, one may create a fifth, quasiancestral subfamily which would comprise both extinct and incidental extant taxa between A and B. This subfamily does not comprise the actual ancestors of the subfamilies of Cleridae but merely their descendants, and thus it is not paraphyletic. It can be visualized again as the area of the quadrangle FBB^*F^* , excluding the abscissa FB. F^* and B^* would be the observed descendants of the actual ancestors F and B (B^* is not figured in Fig. 20).

A classification of the subfamily Hydnocerinae could be a concrete example of such classification (KOLIBÁČ 1998). The tribe Lemidiini is

more primitive than two other tribes, the character states of which are mostly derived from Lemidiini. This makes Lemidiini a quasiancestor of the both remaining tribes: Hydnocerini Spinola and Callimerini. (In the above-cited paper, Lemidiini is based mostly on unique autapomorphies.) In phylogenetic taxonomy, the Lemidiini cannot be classified as an independent negatively defined higher taxon (e.g. a tribe) without an apomorphy. Genera of Lemidiini should be added to one of the remaining descendent tribes. However, there is no evidence in the Lemidiini indicating with which of the descendent groups it is more related; moreover the group is distinctively morphologically and geographically determined (by plesiotypies, i.e. negatively, of course). It follows from the quasiancestral taxon concept that Lemidiini is not the actual ancestor and so it can be classified as an independent higher taxon with the same rank as both of the advanced groups. Transformation series derived from the quasiancestor Z^* (Fig. 18) are higher taxa of the same rank (it may be, for example, a transformation series of character 2; Fig. 17). Since a group derived from the character state 1-1 (in the taxon Y) was marked as the tribe T, all taxa derived from Z^* (or sister groups of the tribe T), i.e. U^*Z^* , I^*G^* , and T, respectively, also have tribal rank (Fig. 18). The tribe U^*Z^* is a quasiancestral taxon. The higher taxa established above are derived from their actual ancestors and they include all transition stages. For example, all fossil taxa derived from ancestor D belong to the recent genus D^* , which is classified within the subtribe D^*F^* (Fig. 19). The subtribe D^*F^* can be illustrated by an area as shown in Fig. 19. Thus, this

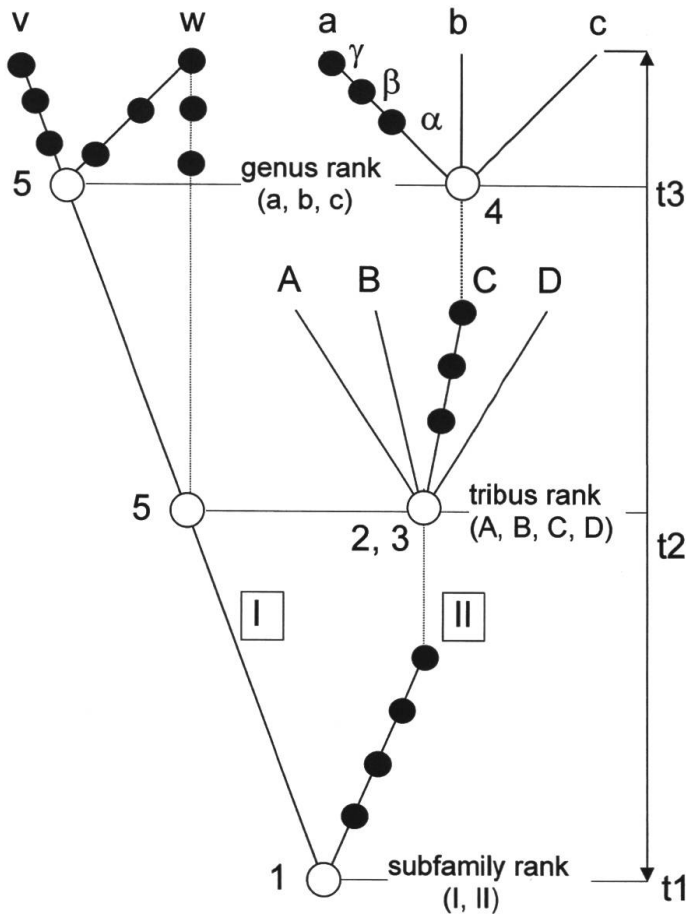


Fig. 21. A schema of the higher taxa classification based on transformation series. 1, 2, 3, 4, 5 are multistate characters. Taxa of the same rank are based on transformation series of pertinent characters. The rank of taxa is determined by the time when character transformations started. The subfamilies I, II are based on two independent transformations of the character 1. They started at the time t1. A, B, C, D are independent transformations (starting at t2) of the characters 2, 3 and they form tribes in the subfamily II. a, b, c, d are based on transformations (starting at t3) of the character 4 and form genera of the tribe C and α, β, γ are species of the genus a. Then v and w are based on transformations of character 5 and form genera in the subfamily I, but they can also form monotypic tribes. It depends on start of the transformation process: whether it started in t1 or t2 (the dotted line).

subtribe should be marked DFD*, similarly the subtribes YAY*A*, BCB*, and the tribes IGI*, UZZ*U*, as well.

The classification by transformation series corresponds, to a considerable extent, with the original opinion of HENNIG (1950) that taxa of equal taxonomic ranks should have originated in approximately the same period of time. Fig. 21 shows a schematic classification of the higher taxa according to independent transformation series of one and the same character. The taxa v, w in subfamily I can be classified as genera or monotypic tribes, depending on the time at which the two taxa were separated by the transformation of character 5. If transformations of character 5 started at the time of the tribe's origin (marked with the dotted line in Fig. 21) than v, w would be at tribal rank; if it started at the time of genera origin, then v, w would be of genus rank.

Although the preceding examples have been based on just one character, this does not mean that the higher taxa could not be based on a larger number of multistate characters and thus on several independent transformation series. Such a system is more substantiated. Principally, however, independent transformation paths of a single

character are quite sufficient. If, however, only one multistate character were known in sister higher taxa, then it could be difficult to classify primitive subtaxa in each lineage (e.g. Aw, Ai, A1 in Fig. 15 – such states may be very similar). In the Cleridae, such is the case of, e.g., the genera *Eleale* Newman and *Epiclines* Chevrolat, which lack any distinct derived character state permitting their classification in any of the existing subfamilies. Therefore, it is of advantage if each higher taxon can be defined by more than one multistate character.

BRYANT (1989) suggests hypothetico-deductive testing of taxa by means of additional synapomorphies. It has been explained above that real synapomorphies hardly exist. Characters and their states form inter-nested sets of increasingly modified versions of other characters. What is character at one level on the tree is a character state at a higher level and a modification or variation of a character state at an even higher level (cf. Fig. 21). Thus, all characters can be seen as modifications of other characters. One might envision a great chain of characters (or synapomorphies, or homologies) stretching from those of complete generality on to those true for only a single species (PLATNICK 1979). According to MICKEVICH & WELLER (1990), a character is a set of nested synapomorphies of character states.

However, for example, no inclusive synapomorphy has been found for the subfamily Clerinae. While there is a common synapomorphy in the subfamily Korynetinae (shortened fourth tarsomere), this does not mean that any species showing fourth tarsomere in the primitive, non-shortened state could not belong to Korynetinae. It could merely be the beginning of a lineage as, e.g., in the subtaxon Aw in higher taxon **c** in Fig. 15.²⁾ Of course, higher taxa based on transformation series can be suitably tested by adding further transformation series of another multistate character. For the purpose of such testing it is better (but not essential) that the transformation of the additional multistate character occur even in sister higher taxa. Besides the testing, the additional transformation series may help in deciding whether a particular subtaxon (especially a primitive one) actually belongs to the given higher taxon. For example, in Fig. 15 the higher taxa **a**, **b**, **c** are defined by independent transformations of character A, but subtaxa with the character states Aw, Ai, A1 are similar to their ancestor (the state A0). Therefore the subtaxa are also similar to each other. That is why a classification of such primitive subtaxa can be difficult. However, if subtaxa of the taxon **c** show derived states of a character other than A, than it would be possible to decide that, for example, the subtaxon showing the state Aw actually belongs to taxon **c**, not **b** or **a** (Fig. 15). In other words, *independent transformations of (at least) one character in different lineages define all higher taxa of the same rank, whereas derived character states of characters that are unique in a particular lineage (higher taxon) help in determining the pertinence of a subtaxon to a higher taxon.* These unique characters in a derived state are what in cladistics are termed the synapomorphies, but in the concept proposed here

²⁾ This principle can be demonstrated through the simplified example of Mammalia. Let us use here a model definition of recent mammals as hairy animals with red blood cells lacking nuclei. Yet their ancestor with the reptiles was not hairy and its red blood cells may have possessed nuclei. Therefore, the lineages leading from that ancestor to mammals probably acquired both apomorphies gradually, and they should be included with the mammals (i.e. Synapsida, syn. *Theromorpha*).

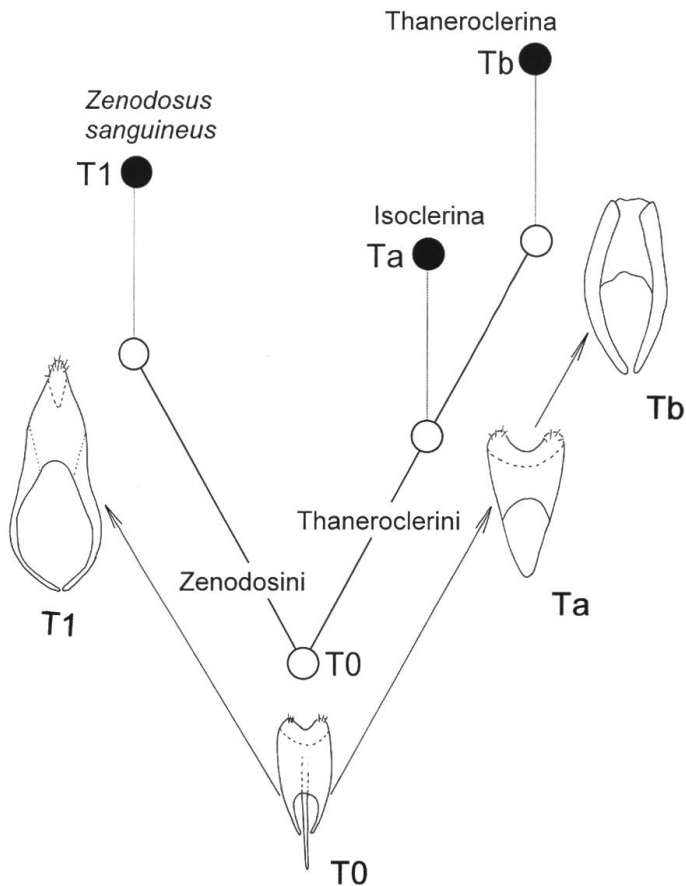


Fig. 22. A classification of the tribes Zenodosini and Thaneroclerini based on transformation series of the tegmen. T0 = hypothetical ancestral state, T1 = tegmen of *Zenodosus sanguineus* Say, Ta = generalized tegmen of the subtribe Isoclerina, Tb = generalized tegmen of the subtribe Thaneroclerina. See text for details.

they need not (and cannot) be perfectly unistate and, for this reason, they cannot be shared by all subtaxa. Moreover, higher taxa as units cannot be defined on the basis of such unique characters.

Classification of higher taxa in practice

According to the concept of higher taxa explained above, it is easiest to define rich lineages containing numerous character states of each multistate character. It is more difficult to classify monotypic taxa (lineages) or, for example, genera poor in species or showing uniform characters. Such difficult definition can be demonstrated using a simplified example from the family Thanerocleridae (for particulars, see KOLIBÁČ 1992). The monotypic tribe Zenodosini shows a highly derived character state of the tegmen (T1 in Fig. 22). Subtaxa in the sister tribe Thaneroclerini show a different mode of transformation of the tegmen (Ta, Tb in Fig. 22). (The hypothetical ancestral state T0 apparently resembles that in the more advanced members of the family Trogositidae. Ta is the state found in primitive representatives of the subtribe Isoclerina.) Although the tribe Zenodosini is monotypic, it forms an independent transformation series of tegmen

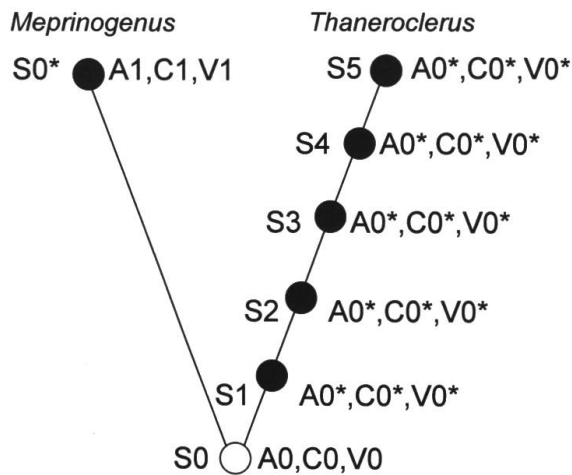


Fig. 23. A classification of the genera *Meprinogenus* and *Thaneroclerus*. The character states closely related to those of an ancestor are marked by an asterisk. A = antennal club, C = colour, S = body size; S1 to S5 are states of the growing body size in the *Thaneroclerus* species: *T. termitincola*, *T. quasitardatus*, *T. buquet*, *T. aino*, *T. impressus*. V = wing venation. See text for details.

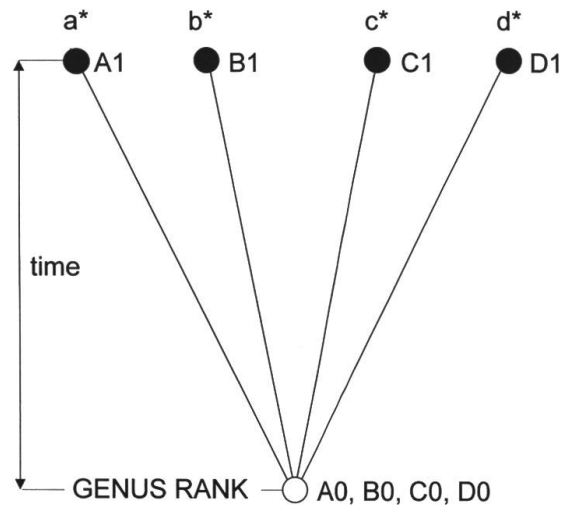


Fig. 24. An example of four monotypic genera classification. The genera **a***, **b***, **c***, **d*** are marked by an asterisk – they are metataxa. The genera are based on rather a poor data set: the autapomorphies A1, B1, C1, and D1.

and can thus be classified without any problem. The classification of the genera *Meprinogenus* Kolibáč and *Thaneroclerus* Lefebvre from the subtribe *Thaneroclerina* is more complicated. The five species of the genus *Thaneroclerus* show great mutual similarity, differing only in size and minute differences in the structure of their copulatory organs. The species can be arranged to form a transformation series of body dimensions. *Meprinogenus indicus* (Corporaal), the only species of *Meprinogenus*, is distinctly derived from *Thaneroclerus* (against this genus, its antennae, coloration and wing are in the apomorphic state). So far, no multistate character has been found in the two genera that would form two independent transformation series. Therefore, the classification scheme of the two sister genera resembles Fig. 12. Against *Meprinogenus*, the genus *Thaneroclerus* shows derived antennal club, body coloration and wing venation (A, C, V in Fig. 23). In *Thaneroclerus*, body size forms dimensions (like *Meprinogenus*) and shows characters A, C, V in a state similar to that in all *Thaneroclerus* spp.

The classification of very poor or monotypic higher taxa can actually be based on synapomorphies (see Fig. 1). An extreme situation is shown in Fig. 24. Four monotypic genera **a**, **b**, **c**, **d** are classified on the basis of autapomorphies of species. Such classification is possible if there is a reason to believe that the species are the last remains of extinct lineages that separated from a common ancestor at the time when the genera originated. However, the classification modes mentioned above (Figs 23, 24) are only a temporary solution, as it is impossible to determine with certainty on the basis of mere synapomorphies and on the absence of transformation series of a shared character,

whether or not the classified taxa actually stem from a common ancestor. In the classification of the family Thanerocleridae (KOLIBÁČ 1992), I have employed the term “metataxon” to denote such uncertain higher taxa, and I have marked them with an asterisk (e.g. *Meprinogenus** Kolibáč). Thus, the term metataxon, used in this way, is slightly different from the concept of DONOGHUE (1985) or KLUGE (1989).

In contrast, more “bushes” can be found in rich and strongly diversified higher taxa, exceeding the number of systematic categories contained in the International Code of Zoological Nomenclature. This means that each lineage need not have its own name, or that one can use such names as “division”, “cohort”, etc. However, this does not refute the fact that a system consisting of higher taxa, classified on the basis of the transformation series concept, is more internally consistent than that of classical taxonomy.

Discussion

In a series of papers, DE QUEIROZ & GAUTHIER (1990, 1992, 1994) have attempted to harmonize biological taxonomy with evolutionary theory, and they have suggested that certain fundamental changes be made in the concepts and principles of the present system of biological nomenclature (the problem of mandatory categories has already been mentioned above). These authors associate names of taxa with crown clades, using node-based definitions. Crown clades are clades stemming from the immediate common ancestor of sister groups with extant representatives (*l.c.* 1992: 468). Thus, natural phylogenetic units are divided into two parts, each of which bears its own name: the crown clades, comprising extant groups (e.g. Mammalia), and stem-based clades, comprising extinct groups as well as the crown clade (e.g. Synapsida). The existence of each taxon depends upon that of the sister group, with which condition hardly any classification can comply. Therefore, for example the group Rhipidistia-Choanata (*l.c.* 1992: 474) did not exist until the discovery of *Latimeria chalumnae*, their extant sister group (Actinistia-Latimeria). Should the species *L. chalumnae* be exterminated by man, then even the quoted sister group would vanish from the system and would become part of Crossopterygii-Sarcopterygii. Thought to an absurd conclusion, science has no method to prove the non-existence of a phenomenon and therefore there is no definitive proof that *L. chalumnae* has actually been exterminated to the last fish. Therefore, the moment may soon come at which one will be unable to say whether the taxon Rhipidistia-Choanata is or is not extant, which taxon does not comprise *Latimeria* at all. Similarly, with the extinction of *Sphenodon punctatum* the important taxon Lacertilia-Squamata would vanish (or become uncertain) (*l.c.* 1992: 474). Therefore, the node definition is at variance with the postulated system stability and the denomination and existence of an entity would depend upon the existence of another one.

In this inheres the major difference between the higher taxa concept based on transformation series (TSC) and the de Queiroz and Gauthier concept or other contingent concepts. In the terminology of DE QUEIROZ & GAUTHIER (1990, 1992, 1994), higher taxa formed according to the TSC are most similar to stem-based higher taxa. The TSC forms dynamic higher taxa that comprise extinct and extant subgroups and involve a change or

transformation of a clade from the ancestor to its most derived recent descendants. In this, the TSC resembles WILEY'S (1978, 1981) evolution species concept: "An evolutionary species is a single lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate." In my opinion, it becomes apparent that both species and higher taxa are equally dynamic in substance and they can be defined by describing the course of character changes in a lineage. Higher taxa formed according to the TSC are natural phylogenetic entities, which are self-defining. Their existence as such does not depend upon sister groups, only their ranking – the name of the category – may be arbitrary (when Linnaean categories are used). In the TSC, sister taxa are invariably of the same ranks. The node-based system is rather adapted to practical classification. (According to DE QUEIROZ & GAUTHIER 1992: 472 – "*Taxonomies are practical reference systems that permit communication and facilitate access to the literature.*") In my opinion, their statement is at variance with the often-emphasized postulate of the authors that a system be phylogenetic and evolutionary. I believe that a biological system should be a scientific hypothesis rather than a practical identification tool.

The apomorphy-based definition is the third method of forming higher taxa (according to DE QUEIROZ & GAUTHIER 1992). This is the most frequent method used in entomology. The higher taxa are defined on the basis of common character states. This concept mostly involves static higher taxa into which character transformation, having occurred during phylogeny, cannot be projected. Primitive groups (both fossil and recent) lacking marked apomorphies can hardly be classified in recent taxa and hence they are often classified separately as paraphyletic taxa. The recent taxa do not comprise these ancestral groups and, therefore, they themselves are not monophyletic.

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Address of author:

Dr. Jiří Kolibáč
Moravian Museum
Department of Entomology
Hviezdoslavova 29a
627 00 Brno
CZECH REPUBLIC
e-mail: ento.kol@volny.cz

