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THE CANALIZED EVOLUTIONARY POTENTIAL: INCONSISTENCIES IN PHYLOGENETIC REASONING

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Abstract.—Holomorphological similarities can be based on synapomorphies, symplesiomorphies, convergences, diffuse parallelisms through parallel selection, and underlying synapomorphies (i.e., close parallelism as a result of inherited factors within a monophyletic group causing incomplete synapomorphy). Two sets of minimum criteria for asserting synapomorphies are given; one does not allow for outside parallelism and secondary reductions, reversals or change, while the other allows for reductions in apomorphic part taxa (subgroups) and outside parallelism in groups which cannot be sister groups. A theoretical scheme of argumentation (cladogram) secured through synapomorphies satisfying the strictest criteria is drawn. Three modifications of synapomorphies satisfying the second set of criteria are discussed and exemplified. The remaining six hypothetical trends can be explained as underlying synapomorphies, as diffuse parallel selections (including convergence) or as secondary reductions (and reversals). Hypothetical phylogenetic trees with the distribution of character alternatives for each taxon including hypothetical ancestors are given for each alternate explanation, discussed and exemplified from chironomid morphology. When the monophyly of every taxon is established, underlying synapomorphy may assert monophyly for the collective taxon. As the underlying synapomorphy consists in the capacity to develop synapomorphy, loss of this capacity can be regarded, under certain circumstances, as a new synapomorphy. There appears to be analogy between species genetics (pleiotropy, polygenes, suppressive genes) and supraspecific phylogenetics. The canalized evolutionary potential exemplified through underlying synapomorphies corresponds to the potential information classes of Wiley and Brooks (1982). [Evolutionary potential; underlying synapomorphy; parallel selection; secondary reduction; Chironomidae.]

All adherents of phylogenetic systematics agree that degrees of relationships are reflected by nested patterns of synapomorphous similarity, that monophyletic groups are defined by shared derived characters (synapomorphies), and that the method of character analysis has to be based on outgroup comparison combined with ontogenetic evidence when applicable. Nevertheless, the methods of reasoning of researchers in this field are often so different that they reach opposite conclusions regarding what is the plesiomorphous and what the apomorphous character or trend alternative, and which are the generally more plesiomorphic or generally more apomorphic taxa.

Some systematists (e.g., Platnick *in* Brundin, 1981:145) claim that a taxon cannot be more apomorphic or plesiomorphic than others except in being positionally farther or closer to the base of a cladogram. However, I along with Brundin (1981:154) perceive the anagenetic pro-

gression as "an expression of life's incessant work with the two alternatives, conservatism and change, as realized by species cleavage via the rule of deviation" and as distinguished by means of investigation of the adjusted evolution index (Sæther, 1970:37-42, 1971:359, 1976:15-22, 1979b:310). As a rule, estimates of the relative plesiomorphy/apomorphy of a group coincide with its positional plesiomorphy/apomorphy (Sæther, 1970:fig. 38, 1971:fig. 10, 1976:fig. 3, 1979b:fig. 4).

There is not even agreement about what constitutes the minimum criteria for asserting that a character is synapomorphous. Furthermore, most cladists do not seem to appreciate the need for a definition. Some authors, among them Hennig (1966:120-121), Schlee (1971, 1975:319), Eldredge and Cracraft (1980:74), and Wiley (1981:121), regard convergence and parallelism as nearly inseparable features as far as their usefulness or hindrance to phylogenetic systematics is concerned. Yet

Hennig, for instance, used parallelisms (in the form of underlying synapomorphies; see below) as if they were true synapomorphies. It is not uncommon to encounter expressions such as "at least some of the species of the group have" such and such an apomorphic character alternative in order to invoke synapomorphy, while *all* members of a group have to share the derived feature if it shall be considered an objective synapomorphy. Otherwise it is parallelism or a subjective synapomorphy with secondary reduction or change.

SOME DEFINITIONS

As stated in Sæther (1979b:305) holomorphological similarities can be based on: (1) synapomorphies; (2) symplesiomorphies; (3) convergence (i.e., parallel selection influencing analogous structures); (4) diffuse parallelism as a result of *parallel selection* influencing homologous structures; or (5) underlying synapomorphies (i.e., close parallelism as a result of common inherited genetic factors causing incomplete synapomorphy; Sæther, 1977:29, 1979b). All of these similarities except convergence satisfy nearly all the different definitions of homology including that of Eldredge and Cracraft (1980:36), who conceptualized homology simply as synapomorphy (including symplesiomorphy) at some hierarchical level. Yet only synapomorphies and underlying synapomorphies can show or indicate a genealogical relationship between two groups or taxa.

Schlee (1971:23, 1975:319) gave two minimum criteria for asserting synapomorphy and thus demonstrating monophyly: (a) There should be a principal deviation present within the whole group, but not in the same formation in any taxon outside the group. (b) The homologous character alternative should be present not just in the sister group, but also uniformly in distantly related groups, to show that this character alternative is plesiomorphous, thus implying that alternative (a) is derived.

Characters fulfilling these criteria are sometimes called "true" synapomorphies.

(They are, however, better called objective synapomorphies.) The consequence of these criteria is that there is no room even for secondary reductions or change. In their practical work, neither Schlee or Hennig nor anybody else has strictly followed these criteria (for a further discussion, see Sæther, 1979b:306). In accordance with the repeated practical applications, I (Sæther, 1979b:306) proposed that the first minimum criterion be corrected to: (a) There should be a principal deviation present within the whole group or clearly secondarily reduced in apomorphic taxa. The deviation should not be present in the same formation in any taxon outside the group which could be regarded as a possible sister group.

I use plesiomorphous and apomorphic for character states of trends, and plesiomorphic and apomorphic for groups and taxa. The meaning of *-ous* is "abounding in, full of," while *-ic* is an adjective ending denoting mostly. A character alternative can be fully apomorphic or fully plesiomorphous, while a taxon always has to possess both plesiomorphous and apomorphic characters and, thus, only is relatively plesiomorphic or relatively apomorphic. (The exception is an onliving ancestral species which is entirely plesiomorphous relative to its descendants.)

▷ THEORETICAL SCHEME OF ARGUMENTATION

Figure 1 shows a theoretical scheme of argumentation (cladogram). In this diagram, *A*, *B*, and *C* are taxa above the species level, *X* their presumed sister group and "All other" the remaining groups of the same categorical level within the next higher inclusive level. *A*, *B* and *C* can for instance signify subfamilies of a family with *X* as their sister group (subfamilies, family or families) and "All other" as all other families within the order (or suborder).

Trends 1 to 10.—Seven (1-7) synapomorphies and autapomorphies, fulfilling the criteria of Schlee (1971), establish the monophyletic groups. Trends 8-10 fulfill the criteria given by Sæther (1979b), and

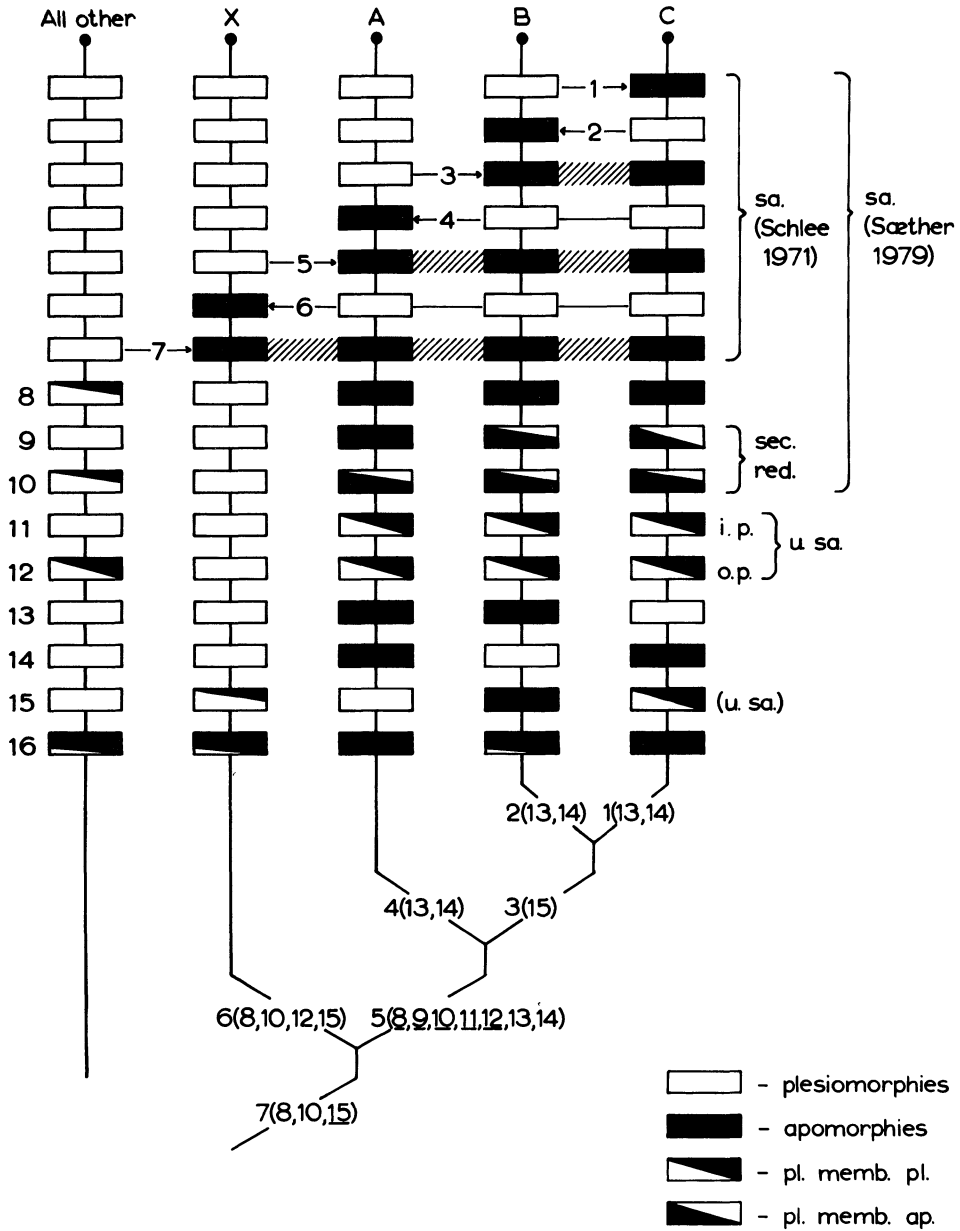


FIG. 1. Theoretical scheme of argumentation (cladogram) illustrating the relationships of taxa A, B, C and their sister group X by means of seven types of synapomorphies (sa.) satisfying the criteria of Schlee (1971). "All other" refers to the remaining groups of the same categorical level within next higher inclusive level. Three types of trends (8-10) satisfying the criteria of Sæther (1979b) include outside parallelism (8, 10) in distant groups and secondary reductions (sec.red.) in apomorphic taxa. Trends of types 11-16 can be explained as underlying synapomorphies (u.sa.) with inside (i.p.) and outside (o.p.) parallelism, as diffuse parallel selection or as secondary reductions or reversals. Underlined numbers in parentheses signify direction of trend evidence according to Sæther (1979b), non-underlined numbers alternate direction of evidence. Additional abbreviations: pl. memb. pl. = plesiomorphic members have the plesiomorphic character alternative; pl. memb. ap. = plesiomorphic members have the apomorphic character alternative.

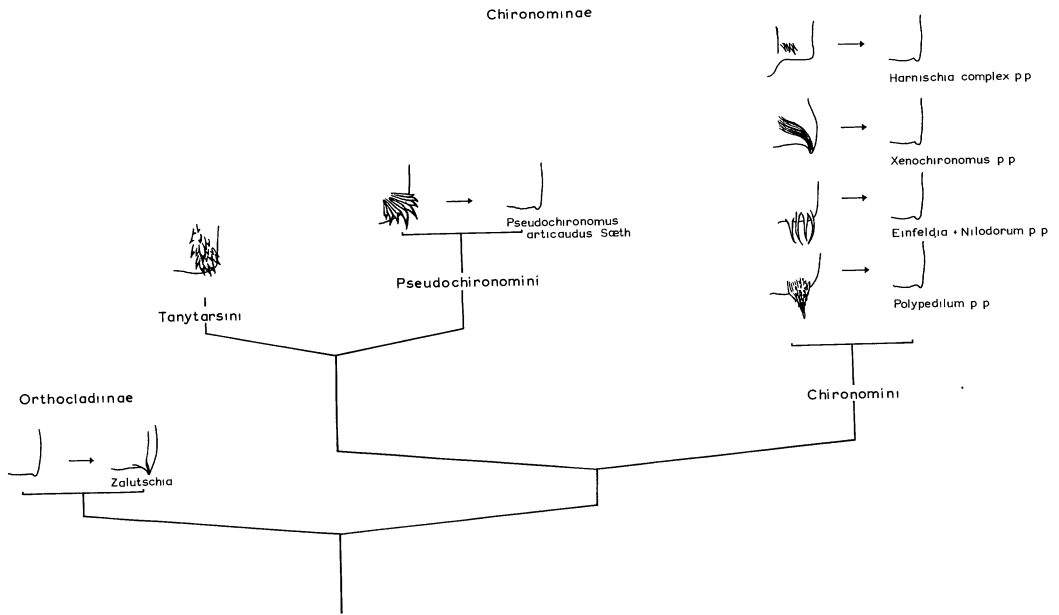


FIG. 2. Cladogram and development of caudolateral spur of abdominal segment VIII of pupae in Chironominae and Orthoclaadiinae. The spur of *Zalutschia* Lip. is developed by convergence. The spurs in Chironominae are secondarily reduced in apomorphic taxa (from Sæther, 1979c).

all support trend 5 asserting the monophyly of $A+B+C$. Trends 8 and 10 show outside parallelisms, while 9 and 10 demonstrate secondary reductions (reversals or changes) in apomorphic member taxa. The plesiomorphic members of "All others" have the plesiomorphic character alternative, while the outside parallelisms take place in apomorphic members. Inside $A+B+C$ the plesiomorphic members have the apomorphic character alternative, while the secondary reductions take place in the apomorphic members. An example of a synapomorphy with outside convergence and inside secondary reductions is given in Figure 2 showing the development of a caudolateral spur in the subfamily Chironominae. A similar spur occurs in the genus *Zalutschia* Lipina of the subfamily Orthoclaadiinae. Here, however, the spur is a result of a strengthening of the mesal paratergite margin, an independently evolved structure or convergence, while in the Chironominae it is developed as a restructuring of a seta or at least a

surface ornamentation (Sæther, 1979c:173). The reductions within Chironominae are secondary reductions, but may be an underlying synapomorphy for the *Harnischia* complex plus *Xenochironomus* which form a monophyletic unit.

There are several reasons why the argumentation cannot stop with trends of types 1-10, but that all kinds of character distributions have to be analyzed and an attempt made to explain them. Synapomorphies always are probabilistic. They can never be unequivocally proven, only falsified, and conflicting evidence is often present. Evidence fulfilling the strictest criteria for synapomorphy, but pointing in different directions, is discussed in Sæther (1970, 1976, 1979a, 1979b:307, 1979c). Holometabolous insects in particular show apparent incongruence between larval, pupal and imaginal characters and even between male and female features. Different apparent monophyletic groups can and have been "established" based on different stages. At one time the chironomid

subfamily Orthoclaadiinae contained about 15 genera based on imagines and about 55 genera based on immatures. Synapomorphies cannot be distinguished from parallelisms when the taxa maintaining the plesiomorphic character alternative are undescribed or extinct, and dichotomy in old groups can in fact be due to secondary dichotomy resulting from extinction (Andersson, 1977:16; Sæther, 1979c:178; Brundin, 1981:99). Phylogenetic studies based just on one semaphoront easily can lead to erroneous results. In addition, if the semaphoronts studied consist of extinct fossils, this problem is exacerbated, and the necessity of studying all possible available trends (whether apparent synapomorphies or apparently caused by parallelism) is increased.

Trends 11 and 12.—It is not of major importance for phylogenetic considerations to distinguish between convergence and parallelism or between parallelism and synapomorphy. A greater matter of concern is the separating of similarities that are not caused by inherited factors (homoplasy) from those that are (i.e., convergence plus diffuse parallelism as a result of parallel selection from synapomorphies plus underlying synapomorphies). The underlying synapomorphies are expressions of the canalized evolutionary potential of a monophyletic group (Brundin, 1972:111, 1976:140, 1981:97; Sæther, 1979b:306; see below). In underlying synapomorphy, the apomorphic character alternative is not present in the whole group, not necessarily even in the most plesiomorphic taxa of the group. Otherwise, assertion of underlying synapomorphies should fulfill all the criteria for assertion of synapomorphies. When the monophyly of different groups has been established by objective synapomorphies, an underlying synapomorphy may assert monophyly for a collective taxon. If the trends 1, 2 and 4 in Figure 1 are established, trends 11 and 12 assert monophyly for group $A+B+C$. Trend 11 is termed a unique inside parallelism by Brundin (1976:140) and used repeatedly by Brundin (1966).

In the female genitalia of the Chironomidae, there are three such unique inside-parallelisms: (a) the division of gonapophysis VIII into two principal lobes (Fig. 3); (b) the development of an apodeme lobe; and (c) the division of tergite IX into two setigerous protrusions. Each of these occur in one or several taxa of each subfamily of the semifamily Chironominae, but not outside the semifamily in chironomids or in other dipterans (Sæther, 1977:31, 1979a, 1979b, 1979c; Brundin and Sæther, 1978). These underlying synapomorphies were used for establishing the monophyly of the semifamily Chironominae. Later the objective synapomorphy, loss of tracheal connection, shown in Figure 7 was found.

The apomorphic character alternatives usually do *not* appear in the more plesiomorphic taxa. If they did the character distribution could often be interpreted as secondary reduction of the types shown in trends 9 and 10. However, the character distribution illustrated in trend 11 can be interpreted also in other ways.

There are three main alternatives for all of trends 11–16 (Fig. 4): underlying synapomorphy (u.s.a.); parallel selection or convergence (p.s.); and secondary reduction, reversal or change (as additional apomorphies; s.r.).

For trend 11 (u.s.a.), the "synapomorphy" for $A+B+C$ with their hypothetical ancestor II consists of the capacity or tendency to develop the apomorphic character alternative, a . Within $A+B+C$, the plesiomorphic character alternative is $p(a)$, that is plesiomorphic p with the potential information value of (a). Loss of either p or (a) can be regarded as an apomorphy within $A+B+C$; that is the plesiomorphic character alternative $p(a)$ with the apomorphic alternatives a or p (as a reversal).

The second explanation—parallel selection (p.s.)—assumes that the apomorphies of A , B and C are not strictly serially homologous, but three independent apomorphies developed through parallel selection or convergence. This is often a likely explanation for simple, reductionistic

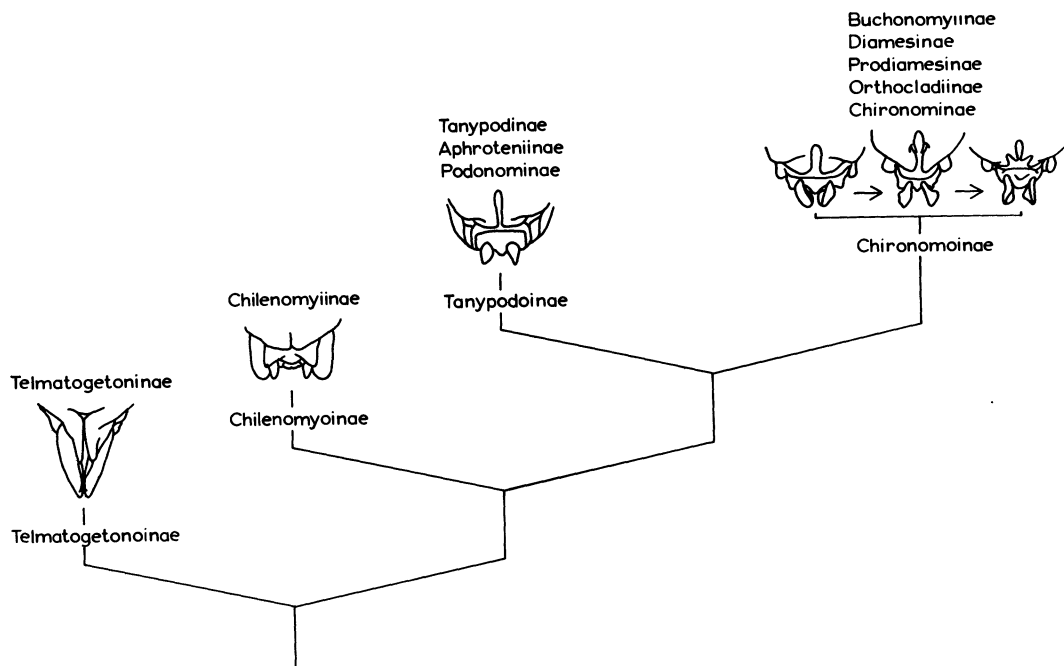


FIG. 3. Cladogram and formation of gonapophysis VIII in semifamilies of Chironomidae. (The term semi-family with the ending *-inae* is necessary to introduce for chironomids if the family is to remain undivided, the subfamilies are to be kept, and the classification is to accurately reflect the hypotheses of genealogical descent by phyletic sequencing and subordination [Wiley, 1981:205-232]).

trends such as loss of setae, reductions in numbers of flagellomeres, or for changes caused by adaptations to a particular mating or feeding behavior.

The third explanation (s.r.) assumes that *a* is a true synapomorphy for *A+B+C* including the hypothetical ancestors II and III, but that the apparent plesiomorphic character alternatives in *A*, *B* and *C* are secondary independent reductions and reversals back to a state confusingly resembling of the plesiomorphic character alternative. In *A*, *B* and *C* the plesiomorphic character alternative thus equals three separate autapomorphies—*a*₁, *a*₂ and *a*₃.

There has been a tendency for entomologists including myself to emphasize parallel selection (see for instance Brundin, 1966; Sæther, 1970, 1977; Lehmann, 1972). However, vertebrate paleontologists have emphasized secondary reduction. This apparently is a result of the different em-

phasis put on estimation of the relative anagenetic levels (see discussion between Platnick and Brundin *in* Brundin, 1981). In order to evaluate all possible explanations for different morphoclines or trends, it is necessary to secure a satisfactory perspective by estimation of the assumed basic design, a ground plan of the archetype or theoretical progenitor. A comparison of the ground plan of the group in question with the different member taxa gives an idea about different anagenetic levels. The anagenetic component consists of synapomorphies, convergences and all kinds of parallelisms (i.e., the plesiomorphic character state has to be known before these components can be evaluated). However, without a preceding cladistic analysis, or at least an investigation into the relative age of homologous character states in a transformation series, the rates and degrees of divergence cannot be properly weighted.

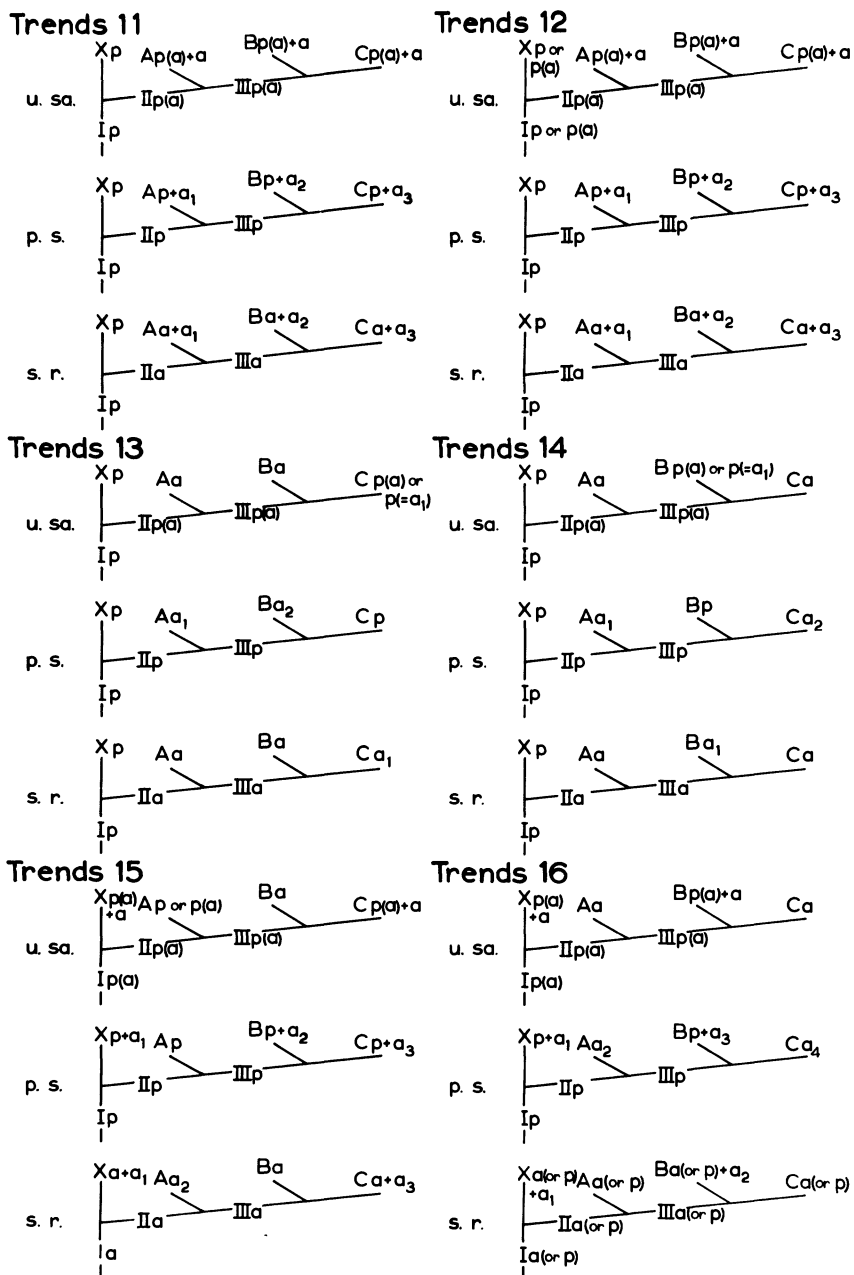


FIG. 4. The three main alternative explanations—underlying synapomorphy (u.s.a.), parallel selection or convergence (p.s.), and secondary reduction, reversal or change (s.r.)—for trends 11–16 shown in Figure 1. Symbols and abbreviations: I–III = hypothetical ancestors; p = plesiomorphous character alternative; a = apomorphous character alternative; $p(a)$ = plesiomorphous with the underlying capacity of developing the apomorphous character alternative present; a_1, a_2, a_3 = autapomorphies through parallel selection or secondary reduction; $p(=a_1)$ = loss of underlying capacity resulting in secondary plesiomorphy.

A method for evaluating anagenetic trends was introduced by Illies (1960) and improved by Sæther (1970; for discussions of adjusted evolution index see Sæther, 1970, 1976, 1979b). This emphasis on anagenetic trends has, however, obscured the primary importance of cladogenetic trends in the analysis of synapomorphic schemes of argumentation. Lehmann (1972) for instance does not discuss which group may constitute the sister group of *Eukiefferiella* Thienemann, but bases his trends on general anagenetic analyses by previous authors (particularly Brundin, 1956, 1966). Sæther (1970, 1971, 1975, 1976) does regard some character states as plesiomorphous because they are anagenetically plesiomorphous. They could, however, be cladistically synapomorphic for certain groups under certain circumstances (see trend 16 below). What the entomologists often tend to forget is that a synapomorphy, for instance trend 5 for group $A+B+C$, is a symplesiomorphy for the inclusive groups, A , B and C taken separately. Vertebrate paleontologists among others, however, emphasize this point to the exclusion of anything other than the study of the pattern in sister groups. They will thus have a tendency to prefer explanations of secondary reduction, reversals or changes.

The difference between trends 11 and 12 is that in 12 some distantly related groups show an outside parallelism. There is thus the possibility that X and the hypothetical ancestor I in an underlying synapomorphy (u.s.a.) may possess the character alternative $p(a)$. This alternative then will not be a synapomorphy for $A+B+C$.

Trends of the type shown in 11 and 12 are very unlikely to be anything other than underlying synapomorphies if they are of a comparatively complex structure, since the apomorphic character alternative does not occur in the plesiomorphic part of the taxa. This makes most underlying synapomorphies operationally recognizable and separable from secondary reductions as illustrated in trends 9 and 10.

However, distributions of the type in trends 9 and 10 may hide underlying synapomorphies. But these will not be operationally separable from secondary reductions.

Trends 13 and 14.—Whether trends 13 and 14 should be regarded as results of underlying synapomorphies (u.s.a.), parallel selections (p.s.) or secondary reductions (s.r. in Fig. 4) depends on the composition of A , B and C . If A and B have numerous taxa and C is monotypic, trend 13 most likely shows a secondary reduction (i.e., the apparent plesiomorphous character state in C in reality is an autapomorphy, a_1). If A and B are monotypic and C has numerous taxa, it is more likely that the apparent identical apomorphies of A and B are separate autapomorphies, a_1 and a_2 . The number of inclusive taxa in A , B and C is irrelevant for underlying synapomorphies. Trends 13 and 14 can always show underlying synapomorphies, but the likelihood increases in proportion with the complexity of both the apomorphic and the plesiomorphous character alternative. While underlying synapomorphies are the most parsimonious solution for the other trends 11–16, for 13 and 14 parallel selections and secondary reductions are equally parsimonious.

An example of character distribution of this type is shown in Figure 5. The genera *Paracricotopus* Thienemann et Harnisch, *Rheocricotopus* Thienemann et Harnisch, *Doncricotopus* Sæther and *Nanocladius* Kieffer form a monophyletic group with *Psectrocladius* Kieffer as their plesiomorphic sister group (Sæther, 1980b:131, 1981a:224). The labral seta $S I$ (seta anteriores) of the larva is simple in *Nanocladius*, *Doncricotopus* and *Paracricotopus* (one species of the last, however, has indication of an apical bifurcation), while *Rheocricotopus* has bifid $S I$ and *Psectrocladius* palmate $S I$. The $S I$ is of great taxonomic value in larval Orthoclaadiinae where very few genera have simple $S I$. Since the simple $S I$ is not common among orthoclad larvae, it may be an underlying synapomorphy for *Paracricotopus* + *Rheocricotopus* + *Doncricotopus* +

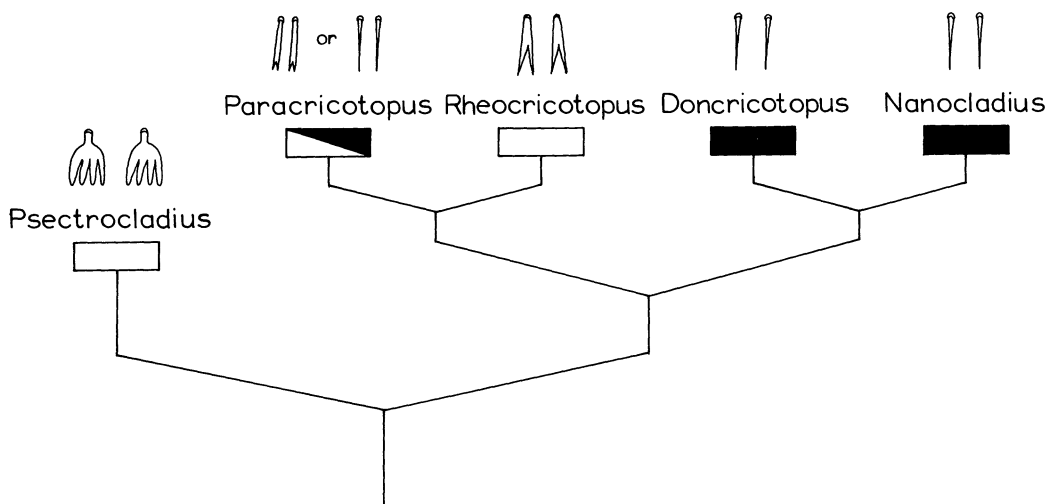


FIG. 5. Cladogram and formation of *S I* (seta anteriores) in the larval labrum of the *Psectrocladius* group.

Nanocladius. However, the trend consists in a simple reduction and can also be regarded as a possible parallel selection.

One interesting consequence of regarding trends 13 and 14 as underlying synapomorphies is that the plesiomorphous condition in *C* for trend 13 and in *B* for trend 14 under certain circumstances can be regarded as an apomorphy, since the synapomorphy for $A+B+C$ is $p(a)$ (plesiomorphous with the latent possibility of developing the apomorphous character alternative) and not p . A loss of the tendency or ability to develop the apomorphous character alternative thus can be regarded as a new apomorphy, particularly if the taxon contains many subtaxa. An example of this is shown in Figure 6. An underlying synapomorphy for the semifamily Chironominae is the tendency for division of tergite IX into two setigerous protrusions. In the Chironominae, however, this tendency is present only in two genera, *Lauterborniella* Bause and some specimens of *Omisus* Townes (Sæther, 1977: 131, 1963, 1979a:fig. 9, 1980a:118). It appears that the tendency for division is lost in the tribes Tanytarsini and Pseudochironomini and almost lost in most Chironomini.

Trend 15.—This trend is essentially a combination of trends of types 11 and 12 and of types 13 and 14. However, since the apomorphous character alternative is present only in the more apomorphic members of taxa *X* and *C*, underlying synapomorphy is the most likely explanation at least if the trend is based on a reasonably complex character. If a more detailed analysis within *X* and *C* shows a complex distribution of the apomorphous character alternative, the chances of underlying synapomorphy being the correct explanation will increase due to increased parsimony as compared to other explanations.

Figure 7 shows the distribution of the tracheal connection to the pupal thoracic respiratory organ in two semifamilies of chironomids. In Tanypodoinae there is a direct tracheal connection to the respiratory organ via the pharate adult spiracle. This is the plesiomorphous condition. The connection is lost in the semifamily Chironominae, but has re-evolved as an indirect connection via the pharate adult integument in the subfamily Prodiamesinae, and the tribes Pseudochironomini and Chironomini of the subfamily Chironominae (Coffman, 1979; Murray and Ashe, 1981:66). The loss of the tracheal connec-

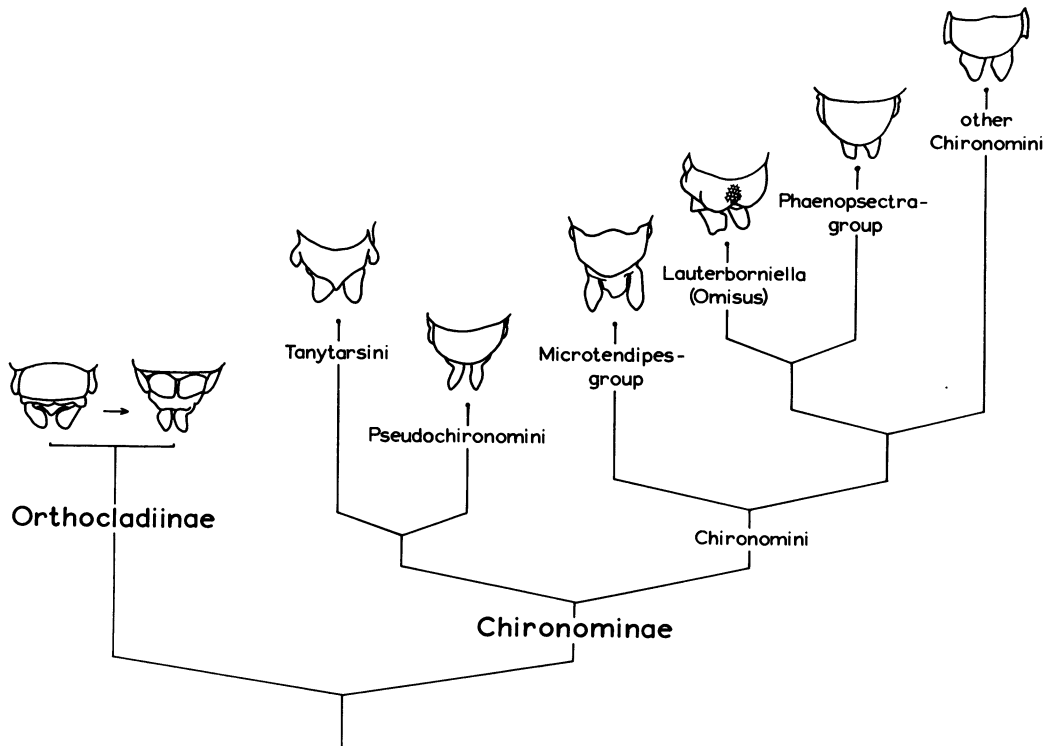


FIG. 6. Cladogram and formation of tergite IX and gonocoxite IX in Orthoclaadiinae and tribes and groups of Chironominae (adapted from Sæther, 1977:figs. 1 and 9).

tion is a synapomorphy for the Chironominae. The secondary indirect connection can be an underlying synapomorphy for Prodiamesinae + Orthoclaadiinae + Chironominae, it may have been acquired independently three times, or independently and secondarily reduced twice. However, if the Chironominae was examined as a unit, without division into tribes, it would appear as if the indirect tracheal connection needed to have been independently acquired only twice, once in the Prodiamesinae and once in the Chironominae. There also is the possibility that Prodiamesinae, not the Orthoclaadiinae, is the sister group of Chironominae (Sæther, 1976:13), and that Pseudochironomini is not the sister group of Tanytarsini but of the Chironomini (Sæther, 1977:138). In no case, however, can the secondarily acquired indirect tracheal connection be regarded as a true synapomorphy.

Trend 16.—Trends of type 16 constitute difficult types of possible underlying synapomorphies, where the plesiomorphic character alternatives occur in a few very plesiomorphic members of different groups. Characters of this type found in the chironomids are for instance three details of the male genitalia: (1) a complex aedeagus (or male intromittent organ resulting from the combination of gonapophyses IX and surrounding phalli); (2) a double male gonostylus (distal part of principal, outer genital claspers); and (3) the absence of a megaseta (spine, "Griffel") at the apex of the gonostylus. The apomorphic character alternatives of these are: (1) reduced, not complex aedeagus; (2) a single gonostylus; and (3) presence of an apical megaseta.

A complex aedeagus is present in the presumed sister group of the Chironomidae, the Ceratopogonidae, and also in

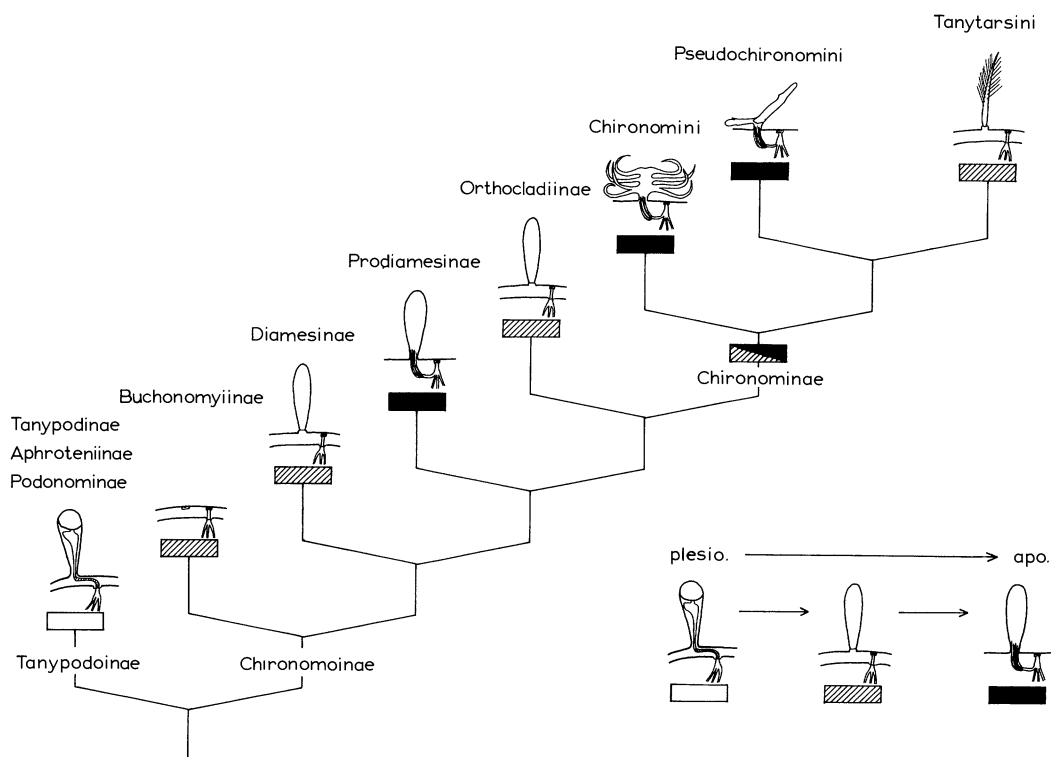


FIG. 7. Cladogram and the distribution of the tracheal connection to the pupal thoracic respiratory organ in the semifamilies Tanypodinae and Chironominae.

Simuliidae and Thaumaleidae (Brundin and Sæther, 1978:273; Wood and Borkent, 1982:203). Among the Chironomidae, a complex aedeagus is present only in some plesiomorphic taxa of different subfamilies: Telmatogetoninae; some Podonomininae; *Ablabesmyia* Johannsen of the Tanypodinae; *Buchonomyia* Fittkau of the Buchonomyiinae; *Protanypus* Kieffer of the Diamesinae; to some extent *Prodiamesa* Kieffer of the Prodiamesinae; and *Pseudochironomus* Malloch of the Chironominae (Fittkau, 1962:68; Hirvenoja, 1973:23-29; Sæther, 1977:49; Brundin and Sæther, 1978:273). It appears very unlikely that a complex aedeagus should have appeared independently several times in different plesiomorphic groups. It is also unlikely that the reduction of a complex aedeagus to a similar form in nearly all chironomids should be independently arrived at by parallel selections.

The underlying synapomorphy here is the tendency or capacity to reduce the aedeagus (note that Fittkau [1962:71] regards the trend as going in the opposite direction). The Telmatogetoninae, the most plesiomorphic subfamily, however, may not possess this capacity since all members of the presumed sister group of the chironomids, the ceratopogonids, have a complex aedeagus. The Chilenomyiinae, a new subfamily recently described by Brundin (1983), has a reduced aedeagus and the capacity for reduction thus is present in all other chironomids if it is not secondarily lost. Since the plesiomorphic character alternative for all chironomids except Telmatogetoninae is a complex aedeagus with the capacity for reduction, $p(a)$, a complex aedeagus without the capacity for reduction, p , can be regarded as a new apomorphy. However, in order to make this a likely proposition,

it is necessary that the group in question consists of many taxa with none or little change in the aedeagus. Buchonomyiinae consists of just two described species while the other groups consist of single genera.

Double gonostyli with each part articulating separately with the gonocoxite are among the chironomids found only in *Buchonomyia* and possibly in the orthoclad *Propsilocerus* Kieffer. The Prodiamesinae *Prodiamesa* Kieffer, as well as the orthoclads *Diplocladius* Kieffer, *Stictocladus* Edwards, *Plhudsonia* Sæther, *Austrobrillia* Freeman, *Eurycnemus* v.d. Wulp, *Brillia* Kieffer, *Euryhopsis* Oliver, *Xylotopus* Oliver, *Tokunagayusurika* Sasa and *Diplosmittia* Sæther have gonostyli divided to a common base; Podonominae have double gonostyli showing different grades of fusion. (Two additional undescribed orthoclad species, however, belonging to *Cricotopus* v.d. Wulp and *Orthocladus* v.d. Wulp, respectively, also have divided gonostyli.) *Plhudsonia* and to some extent *Diplocladius* and *Stictocladus* have one part of the divided gonostylus articulated to a common base (Sæther, 1982:467), while all the others have gonostyli merely forked to base (Sæther, 1981b:30; overlooked by Wood and Borkent, 1982:205). A number of other chironomids have what can be considered partial division. Gonostyli similar to those of *Buchonomyia* are, however, found in the Tipulomorpha (Brundin, 1966:80) and in *Parasimulium* Malloch of the Simuliidae (Wood and Borkent, 1982).

Brundin (1966:80) and Brundin and Sæther (1978:273) regarded the gonostylus of the nematocerous Diptera in their basic design as being double and articulating separately with the gonocoxite. Schlee (1975:323) considered double gonostyli as convergences or parallel selections, while Wood and Borkent (1982:205) did not want to concur or disagree with any of these views. Presuming that the double gonostyli really is the basic design at least for the Chironomoidea, the tendency to fusion of the two parts can be regarded as an underlying synapomorphy. The plesiomorphous character alternative is $p(a)$.

The loss of the tendency to fusion with

the retention of a similar form of division could be present in a plesiomorphic group of the Orthocladiinae, namely *Diplocladius*, *Stictocladus*, *Plhudsonia*, *Austrobrillia*, *Eurycnemus*, *Brillia*, *Euryhopsis*, *Xylotopus*, *Tokunagayusurika* and *Propsilocerus*. This group of genera have been very difficult to place, except for being at the base of the orthoclads, since they are said to possess only basically plesiomorphous characters. Since all these genera have similar gonostyli, they may have lost the tendency to fusion $p(a)$ retaining the character alternative p which, in this case, can be regarded as a new synapomorphy ($p = a_1$). *Diplosmittia*, the remaining described orthoclad with divided gonostyli, is positionally high in the hierarchy of the orthoclads (Sæther, 1977:fig. 36, 1981b:30). There is thus the clear possibility that the division here is secondarily acquired through parallel selection or secondary change. However, as several other orthoclads show a tendency for division by having larger or smaller outer heels, the underlying synapomorphy could conceivably have been retained throughout the orthoclad hierarchy. The above-mentioned undescribed species of *Cricotopus* and *Orthocladus* with double gonostyli could be regarded as giving evidence for such a retention.

An apical megaseta of the gonostylus appears to be present in some members of all Culicomorpha families. Nevertheless, both Sæther (1977:84) and Brundin and Sæther (1978:273) regarded the absence of an apical megaseta to be the plesiomorphous design within chironomids, primarily since more plesiomorphic members lack a megaseta while the more apomorphic members either have a megaseta or the absence obviously is the result of secondary reductions. (In the Chironominae, for instance, the gonostylus cannot be folded in and there is no use for a megaseta.) The tendency to develop a megaseta is regarded as an underlying synapomorphy. However, again Schlee (1975:320) regarded the trend as going in the opposite direction. Among the orthoclads, most of the same genera that have double gonostyli (excluding *Diplosmittia*, but in-

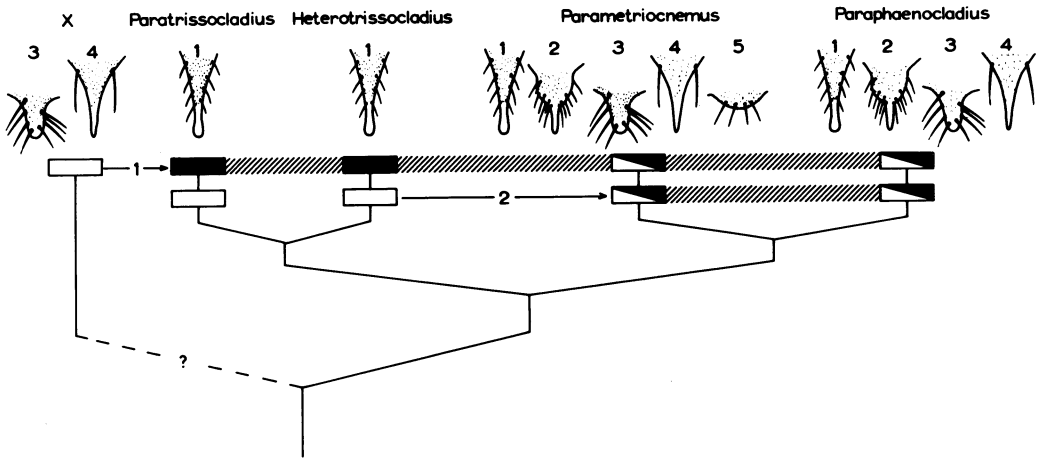


FIG. 8. Cladogram and formation of the male anal point in the *Heterotrissocladius* group.

cluding a couple more) also lack megasetae. Again, the lack could be regarded as the loss of the tendency to develop megasetae and could be used as a defining feature, a new synapomorphy.

Trends with more than one apomorphic character alternative.—There appears to be a good analogy between genetics on the species level and phylogenetics on the supraspecific level. Underlying synapomorphies behave analogous to depressed recessive alleles in the heterozygous condition or genes whose expression is blocked by suppressor genes. The recessive alleles can change to dominance or the suppressor genes can disappear in different offspring in the same way as the underlying tendency becomes apparent. As with pleiotropy, where one gene affects several characters, the same tendency may govern different trends. The different trends thus cannot be regarded as independent.

The tendency in chironomids to copulate on the ground instead of swarming causes changes in antennae, palps, wings, legs and genitalia, and these changes cannot be seen as independent trends.

Like for polygenes, which jointly control one and the same character, several trends may control one and the same feature. The orthoclad genera *Paratrissocladius*

Zavrel, *Heterotrissocladius* Spärck, *Parametriocnemus* Goetghebuer and *Paraphaenocladus* Thienemann form a monophyletic group (Sæther, 1975:57–62). Their sister group may be *Psilometriocnemus* Sæther (Sæther, 1969:106, 1982:480) or the *Cardiocladius* group (Sæther and Halvorsen, 1981:282). For the most part, the male genitalia (or hypopygia) of these genera are very similar. Several species cannot be identified to genus using the hypopygium only. One type of male anal point is common and unique: an anal point tapering to a broad, rounded, microtrichia-free apex with very weak lateral seta basally and medially (1 in Fig. 8). This type, with small modifications, is the only one present in *Paratrissocladius* and *Heterotrissocladius*. In *Parametriocnemus* and *Paraphaenocladus*, however, other types also occur. One (2 in Fig. 8) is essentially a modification of the first with a median swelling and is unique to *Parametriocnemus* and *Paraphaenocladus*. However, the type found in *Psilometriocnemus* (3 in Fig. 8) and one resembling the one present in *Tvetenia* Kieffer of the *Cardiocladius* group (4 in Fig. 8) both are present in both genera. An as yet undescribed species of *Parametriocnemus* does not have a proper anal point at all, but the base of the point is present (5 in Fig. 8). The anal point of this group thus shows at least two

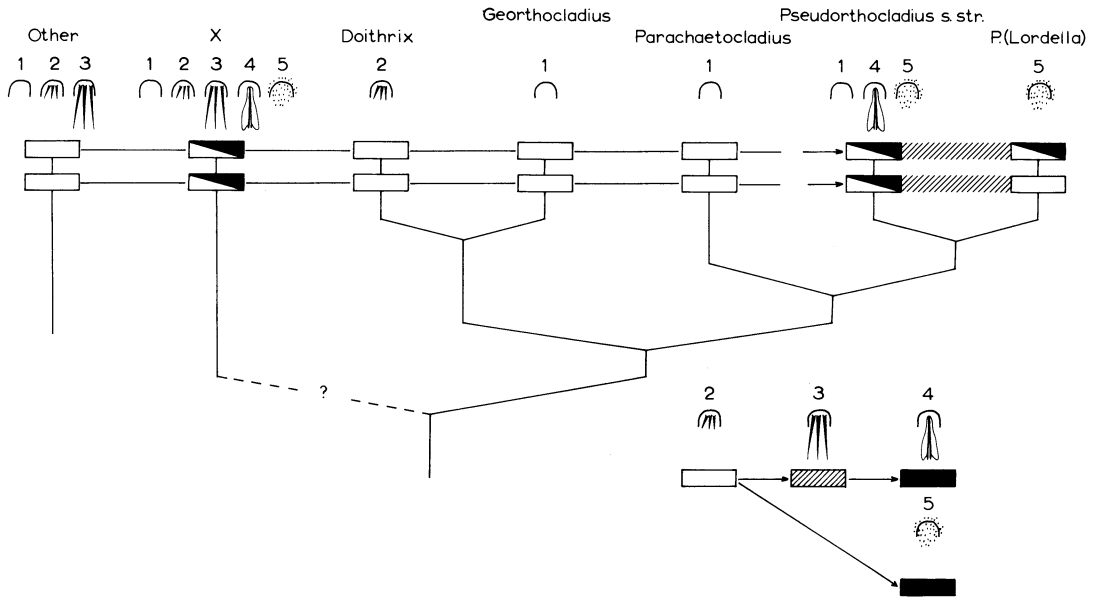


FIG. 9. Cladogram and formation of the male virga in the *Pseudorthocladus* group.

underlying synapomorphies with a common plesiomorphous character alternative (3 or 4).

The virga of the chironomids consists of a terminal group of spines sometimes attached to the distal end of the endophallus. It has not been well examined in all groups and subfamilies. However, in the orthoclads there are at least five principal types: (1) virga absent; (2) virga consisting of a small cluster of about 2 to 6 short, weak spines; (3) these spines moderately long and thin; (4) spines very long with equally long, transparent, lateral lamellae; and (5) very short spines scattered over a large field. (In addition some types such as in *Eukiefferiella sivertseni* Aagaard [1979] may be unique autapomorphies.) Among these types either (1) or (2) is the plesiomorphous condition within the Orthoclaadiinae. The genera *Doithrix* Sæther and Sublette, *Georthocladus* Strenzke, *Parachaetocladus* Wülker and *Pseudorthocladus* Goetghebuer form a distinct, well-founded monophyletic unit (Sæther and Sublette, 1983). The distribution of the different types of virga is as illustrated in Figure 9. It is not clear which genus or genera

constitute the sister group of these four genera. However, the groups which could be sister groups are the only ones where types 4 and/or 5 occur. There thus are at least two underlying synapomorphies with a common plesiomorphous character alternative. Type 3 may be seen as a step in the trend between 2 and 4. Type 1 probably is best regarded as secondary reductions from type 2 (or other types), but could conceivably represent yet another underlying synapomorphy.

THE CANALIZED EVOLUTIONARY POTENTIAL

As stated by Brundin (1972:111, 1976:140), parallelisms (or underlying synapomorphies) are expressions of the canalized evolutionary potential of a monophyletic group. The term underlying synapomorphy was adapted from Tuomikoski (1967:141) who stated that "parallel apomorphies may sometimes be used as evidence of monophyly and are then better comparable to synapomorphies than to convergent similarities. More precisely, in these cases, the underlying synapomor-

phy is the agreement in capacity to develop parallel similarity."

Although this underlying potential is little used consciously in phylogenetic reasoning and directly discredited by many authors, it has been applied more or less subconsciously by several authors (including Hennig in many of his papers). Other writers, such as Gauld and Mound (1982), recognized the tendency of and the difficulties with reversals and parallelisms, but failed to see that these do not have to be homoplasious.

Wiley (1981:121) stated that both parallelisms and convergence are nonhomologies although by his definition on the same page parallelisms as underlying synapomorphies are homologies, the common character consisting in the common capacity. Since Wiley defined character to correspond with what other authors are calling character state, condition, or alternative, he avoided including also parallelism through parallel selection in homology. If characters are defined as including different character states, diffuse parallelisms through parallel selection will be included in definitions of homoplasy, but not in nonhomology.

Wiley never considered underlying synapomorphies. Nevertheless, on the population level and concerning problems connected with speciation, it seems to me that Wiley (1981:98-104) and Wiley and Brooks (1982) concurred with the idea of underlying synapomorphy even if the implication for phylogenetic reasoning is not understood.

Wiley and Brooks (1982:4) characterized the different sorts of information associated with living organisms in four classes: (1) canalized stored information; (2) canalized potential information; (3) noncanalized stored information; and (4) noncanalized potential information. The second class "may consist of alternate ontogenetic pathways or alternate behavioral characters not expressed in the individual because it is blocked by the expression of other information or has not received the right signal for expression." Class 4 "includes recessive alleles in the heterozy-

gous condition coding for structural gene products." These potential information classes appear to be descriptions of underlying synapomorphy.

Wiley and Brooks (1982:19) further suggested that the information expressed in descendant species is constrained by the ancestors of that species. Species are the victims of the historical burden they inherit. Wiley and Brooks (1982) stated: "The degree to which polymorphic characters across species indicate phylogenetic patterns is a direct measure of the degree to which canalized potential information may be constrained by canalized stored information." Again they seem to be referring to underlying synapomorphies.

Why then this apparent common neglect of the canalized evolutionary potential in phylogenetic reasoning? The reasons may be many. One argument may concern losing the ability for falsification. Underlying synapomorphies are more difficult to falsify than true synapomorphies. More importantly, when two synapomorphies are in conflict, one of them does not necessarily falsify the other if it is regarded as an underlying synapomorphy. However, the same problem exists if one admits that parallelisms and secondary reductions or reversals exist. Furthermore, as mentioned above, synapomorphies can never be proven not to be secondary due to the possibility of the taxa maintaining the plesiomorphous character alternative being undescribed or extinct.

Another explanation is that the conflicting evidence is less obvious and insurmountable when only one stage, instar, or ontogenetic level is studied. That is one reason why ontogenetic evidence is regarded as a powerful phylogenetic tool by vertebrate phylogeneticists. Holometabolous insects, in particular, show apparent incongruence between larval, pupal and imaginal characters as well as between male and female features. In chironomids, purportedly different monophyletic groups have been "established" on the base of different stages or sexes (Sæther, 1979b:308). The different stages belong to different "grades." In most cases there is

apparently conflicting evidence between stages. All kinds of holomorphological similarities whatever their base need to be discussed, and as many trends with as many steps as possible analyzed.

The high amount of conflicting evidence in chironomids is to a large extent caused by the entering of drastically new adaptive zones in many phyletic lines, but often just by one stage. The larvae normally are aquatic but different lines have become fully terrestrial, marine, parasitic, or symbiotic, or they live in hot springs, hyperhaline waters, phytotelmata, etc. Also in their normal aquatic habitats they occupy the full range of biotopes from the arctic and alpine glacier brooks to tropical ponds, from pristine ultra-oligotrophic lakes to cesspools. They inhabit all aquatic habitats and all biogeographic areas of the world. There are stenotopic as well as eurytopic species. They also are easy to collect and all stages are known from most of the genera. The chironomids furthermore are a very old group with most of the recent genera in existence already at the transition between the Jurassic and Cretaceous epochs or soon thereafter. The chironomids thus are uniquely suited to be phylogenetic test animals for hierarchical and biogeographical reconstructions. Hopefully, when equally well-known groups have been better studied phylogenetically, phylogeneticists will no longer remain oblivious to the reality and consequences of the canalized evolutionary potential.

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