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ON PHENETIC AND CLADISTIC RELATIONS AMONG GENERA OF FAMILY CAPILLARIIDAE

V. BARUŠ and J. LIBOSVÁRSKÝ

Institute of Vertebrate Zoology, Czechoslovak Academy of Sciences, Brno

Abstract. Phenetic and cladistic relationships among seventeen genera of capillariids were studied by the methods of numerical taxonomy. The additive binary coding of characters was adopted and similarity coefficients were computed by means of the simple matching and Jaccard's formula. The resulting matrices of similarity coefficients were treated by the single linkage cluster analysis. Phenetic analysis of nine mostly morphological characters revealed the existence of four major groupings. The analysis based on all criteria produced a greater number of groupings. The highest phenetic similarity was shown by genera *Echinocoleus* and *Baruscapillaria*, the genus *Pseudocapillaroides* was linked with the other clusters most freely. Cladistic analysis resulted in six and nine groupings. After our appraisal, the analysis based on nine characters produced a large group of primitive, rather heterogeneous genera. Analysis based on all criteria studied suggested that genera parasitizing in poikilothermal vertebrates formed the most advanced groups. Our analyses revealed that the family Capillariidae was well differentiated and, at the level of genera, had a complex division. In our concept, the genera *Capillaria*, *Pseudocapillaria*, *Pseudocapillaroides* and possibly also *Calodium* were primitive and heterogeneous. Genera *Capillaria* and *Eucoleus* might be regarded as ancestors of the other capillariids. All other genera might be held due to adaptations to parasitism in different groups of vertebrates and in their different organs and tissues as derived (evolutionary younger).

In the matter of the internal classification of the family Capillariidae Neveu-Lemaire, 1936, there are in principle two antagonistic trends. The first concept, formulated largely by Dujardin (1845) and accepted by other authors later on, acknowledged the existence of one or several genera (no more than five) within this family. For example, Travassos (1915) held as valid merely the genus *Capillaria* Zeder, 1800, (with two subgenera), similarly Yorke and Maplestone (1926) held as valid only the genera *Capillaria*, *Hepaticola* Hall, 1916, and *Eucoleus* Dujardin, 1845. The same approach to the structure of the family Capillariidae was shown also by Sprehn (1932). This rather narrow view on the internal classification of this family was expressed, e.g., also by Baylis (1931), Neveu-Lemaire (1936), Bain and Wertheim (1981) etc. López-Neyra (1947) presented altogether five genera within this family. Skryabin et al. (1957), after having conducted a historical analysis of this family, included also five valid genera in their monograph using another combination than López-Neyra (1947). In our opinion, the classification of the family Capillariidae into one or few genera does not respect the contemporary complex situation in this numerous group of nematodes (the number of hitherto described species having reached almost 300).

In contrast to the first concept, several authors described and established new genera in an attempt to view the morphological and biological variability of the family in a more objective way and to pursue to differentiate among the particular groups of species. Hence, Freitas and Lent (1935) described genus *Capillostrongyloides* and Skarbilovich (1946) established genus *Skrjabinocapillaria*. Also López-Neyra (1947), after having revised this family, set up two new genera, *Aonchotheca* and *Echinocoleus*. It was, however, only **Freitas** (1959) and several authors later on, who expressed their concerns for this problem and called attention to pursue the issue.

The revisional study by **Moravec** (1982) presents, beyond doubt, a new impetus to solve the problem. This author stipulated altogether 19 genera of capillariids described up to now. The asset of his pioneer work is the new concept of the internal structure of this family, including 16 valid genera. **Moravec** and **Cosgrove** (1982) added another new genus *Pseudocapillaroides*. **Moravec** (1982) newly defined also the diagnoses of genera and the main differential characters in the key, a deed which makes it possible to appraise the interrelations of genera within this family. Undoubtedly, the right and detailed formulation of the diagnosis of the type genus (*Capillaria*), following the interpretation by **Moravec** (1981) and **Baruš** et al. (1981), contributed to this new concept.

Should this new approach be commonly adopted, we regard it as useful to estimate the interrelation of the generic taxa from different points of view. Our effort to contribute to this issue has also been motivated by the fact that the schema of the hypothetic evolution of the genera of the family Capillariidae offered by **Moravec** (1982) was based merely on the morphology of the posterior body end in males (pseudobursa) and on the form of spicular sheath of recent taxa. In the present paper, we adopted the evolutionary hypothesis (with little variation) formulated by **Maggenti** (1981) for adenophorean parasites, with a special emphasis laid on the terrestrial origin of the nematode parasitism. Estimating the interrelations among the genera of capillariids, we used stuctural (morphological) characters and ecological features which possessed an evident generic value, viz. **Moravec** (1982), and **Lomakin** and **Trofimenko** (1982).

To classify a set of taxa by use of several combined criteria in combination two distributional techniques were adopted in the present paper: the phenetic (numerical) and the cladistic (sometimes also called phylogenetic) one. The phenetic analysis gives pair-wise similarities based on all phenotypic characters available (overall similarity), whereas the cladistic analysis gives pairwise similarities based on characters showing derived patristic similarities (synapomorphies) (**Sneath** and **Sokal** 1973, **McAllister** and **Coad** 1978, **Harper** 1979, **McNeil** 1979, 1982). Though presented here in a very simplified way and not including the views of evolutionists, these two approaches to taxa classification contemporarily represent the two major taxonomical schools which energetically dispute and oppose each other (see the pages of the journal Systematic Zoology). Yet we feel with **Farris** (1979) that "... little has been settled, and probably very little could even be settled ...", unless "... it is recognized that the various positions are not quite so mutually exclusive as they are usually taken to be."

Adopting the two approaches we are inclined not to diverge from the well known and elaborate fields of numerical taxonomy. We wish to learn by trial and error more about phenetic affinities and to contribute to the matter of phylogenetic arrangement of taxa. Our goal is to bring more objectivity into the relations among genera of capillariids from both the aspects.

ANALYSIS OF DATA

Altogether seventeen genera of nematodes of the family Capillariidae were considered in this study (after **Moravec** 1982; **Moravec** and **Cosgrove** 1982): (1) *Schulmanela* Ivashkin, 1964, (2) *Paracapillaria* Mendonça, 1963, (3) *Capillostrongyloides* Freitas et Lent, 1935, (4) *Pseudocapillaria* Freitas, 1959, (5) *Freitascapillaria* Moravec, 1982, (6) *Baruscapillaria* Moravec, 1982, (7) *Liniscus* Dujardin, 1845, (8) *Pearsonema* Freitas et Mendonça, 1960, (9) *Echinocoleus* López—Neyra, 1947,

Table 1. List of characters employed with some further information

Character	Character tree	No. of states	Primitive state	Advanced state[1]
1. Vulvar appendages	linear	3	absent	present
2. Spicule	linear	3	present, well sclerotized	absent
3. Lateral praebursal wings	linear	2	absent	present
4. Spicular sheath	linear	2	with spines	without spines
5. Ova	branching	3	non-segmented, oviparous	ovoviviparous possible segmentation in the host
6. Ova	linear	2	free	enclosed in capsules
7. Development of pseudobursa	branching	4	pseudobursa not developed or markedly reduced, posterior body end lateraly dilated, two lateral papillae	pseudobursa not developed, post. body end narrowed with small papillae pseudobursa developed, with long, protracted papillae
8. Dorsal support of pseudobursa	linear	3	absent	present
9. Main groups of hosts	linear	3	stenothermal vertebrates	poikilothermal vertebrates
10. Biotop of a definitive host	linear	3	land	water
11. Localization in the definitive host	branching	6	mouth cavity, esophagus, stomach, intestine	liver, spleen skin
12. Classes of definitive hosts	branching	6	mammals, birds, reptiles, amphibians, fish	fish mammals, birds
13. Presumption of circulation of larval steps in a definitive host	linear	3	endogenous development without circulation of larvae	endogenous development with circulation of larvae

[1] Two advanced ends are given in the branching character trees.

(10) *Capillaria* Zeder, 1800, (11) *Eucoleus* Dujardin, 1845, (12) *Pterothominx* Freitas, 1959, (13) *Aonchotheca* López—Neyra, 1947, (14) *Calodium* Dujardin, 1845, (15) *Gessyella* Freitas, 1959, (16) *Skrjabinocapillaria* Skarbilovich, 1946 and (17) *Pseudocapillaroides* Moravec et Cosgrove, 1982. Subgenera presented by Moravec (1982) were not included in our analysis.

In this set of taxa 13 different characters were analysed (Table 1). Of them 3 had two states, 7 three states, 1 four states and 2 six states. A two-states character is usually determined by the presence or absence of a certain feature. Three or more states, besides the two marginal states, i.e., presence and absence, offer one or more intermediate states. In such a way, through the multistate characters some variability can be evidenced. This is a great advantage since many characters cannot be explicitly described in a straightforward manner, by two states only. Another asset of a multistate charater is that it can be used in both linear and branching character trees. In order to gain a phylogenetic measure a primitive and an advanced (derived) state was given in each character examined. This procedure, though generally well founded, may be tributary to different ways of thinking.

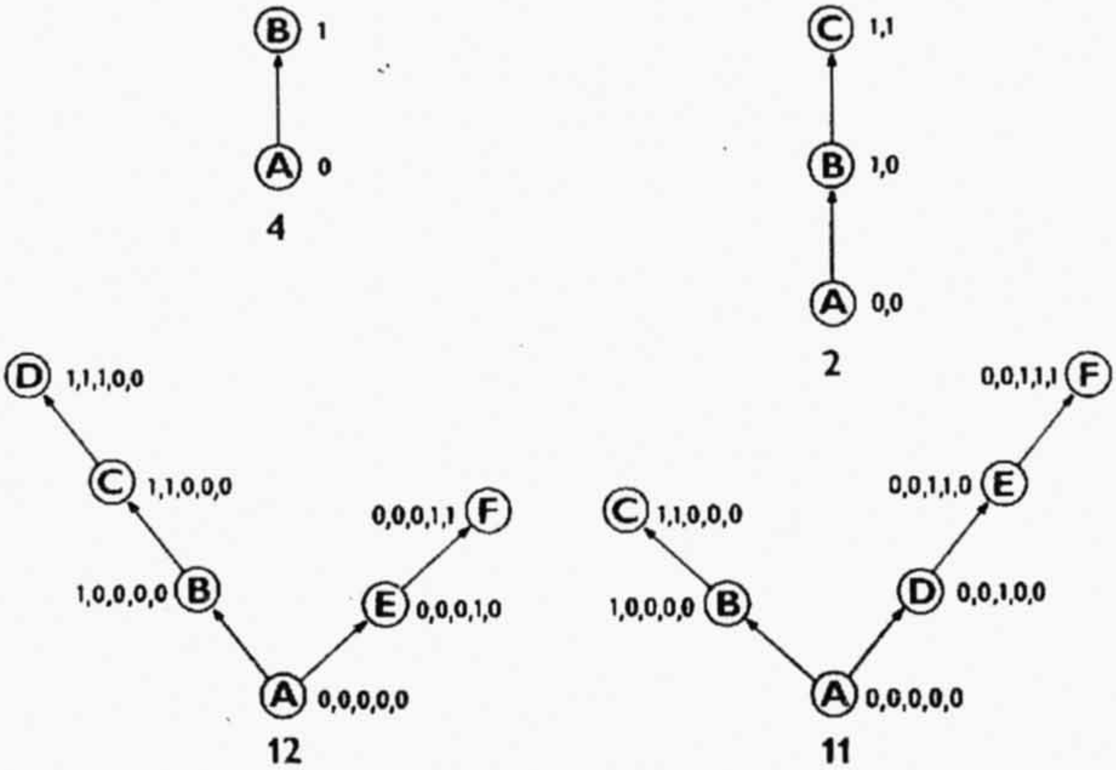

Fig. 1. Examples of additive coding of four types of character trees. Numbers below the character trees relate to the particular characters. 4, Spicular sheath with spines = A, without spines = B. 2, Spicule present and well sclerotized = A, present and slightly sclerotized = B, absent = C. 12, Classes of definitive hosts: mammals or birds or reptiles or amphibians or fish = A, reptiles or amphibians or fish = B, amphibians or fish = C, fish = D, mammals or birds or amphibians = E, mammals or birds = F. 11, Localization in the definitive hosts: mouth cavity or esophagus or stomach or intestine = A, intestine or liver = B, liver or spleen = C, respiratory organs or intestine = D, urinary bladder or kidneys = E, skin = F.

The character states were coded by additive binary coding. The primitive states were coded by zeros, the advanced (derived) by ones. The multistate characters were coded by a combination of both these digits. Unknown and inapplicable states were coded by minus 1 and skipped in the calculations. The number of digits in each character was one less than in the states. Coded primary data are given in Table 2. Examples of coding different types of character trees are shown in Fig. 1. Let us take as an example the spicule (character No. 2). If the spicule was present and well sclerotized, it was hold for a primitive state (the coding was 0,0). If the spicule was absent, the situation was taken as an advanced state (the coding was 1,1). If the spicule was present but only slightly sclerotized, it was held for an intermediate state and coded as 1,0.

A possible disadvantage of the additive coding inheres in a danger that a certain character or a character set may be more emphazised than the others. This can easily happen if two or more taxa presented by multistate characters share more primitive or advanced states. In such a way the weight of this character may be exaggerated. Despite this inconvenience we did not use a non-ad-

Table 2. Coded primary data set. Characters and character states (0 or 1) of 17 genera of **Capillariidae**. Phenetic and cladistic groupings of these taxa are pictured in Figs. 2 and 3

Taxa	Characters																														
	1		2		3	4	5		6	7			8		9		10		11					12					13	
1	1	0	0	0	0	0	1	0	0	0	1	1	1	0	1	1	1	1	1	1	0	0	0	1	0	0	0	0	1	0
2	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0
4	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
5	1	0	0	0	1	0	0	0	0	0	1	1	1	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0
7	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	1	0	0	1	1	0	1	1
8	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	1	1
9	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0
10	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
11	1	0	1	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0
12	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
13	1	0	1	0	1	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
14	1	0	1	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	0
15	1	1	0	0	1	1	0	0	1	0	1	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	−1	−1
16	1	1	1	1	1	1	0	0	0	0	1	1	−1	−1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
17	0	0	0	0	0	1	0	1	0	1	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1

ditive coding, for with many characters employed the additive coding appears simple and adequate (Sneath and Sokal 1973).

As a measure of phenetic relationships among the taxa we chose the simple matching coefficient. Though it is one of the oldest and simplest coefficients, Baroni—Urbani and Buser (1976), after having re-examined several other coefficients, recommended it to general use. The formula to compute this coefficient is $\Sigma (a + d)/\Sigma (a + b + c + d)$. For any pair of states "a" symbolizes advanced features shared by both taxa (1,1); "d" denotes primitive features shared by both taxa (0,0); "b" represents a feature with the joint score of 1,0; "c" indicates a feature with a joint score of 0,1. The sum of "a" and "d" gives the number of matches, the sum of "b" and "c" the number of mismatches.

In addition to the simple matching coefficient we used the Jaccard's (cladistic) coefficient, which has the formula $\Sigma (a)/\Sigma (b + c + a)$. This coefficient belongs to the class of techniques which neglect the primitive conjoint states both in the nominator and denominator. In other words, only the advanced shared states and mismatches are measured by this coefficient.

In case a character was not given in either one or both compared taxa, it was left out in both the numerator and denominator. In either of the techniques the coefficients fluctuate between 0 and 1. Low similarities are close to zero, high similarities to one.

As a next step each of the coefficients was arranged into similarity matrices and treated by the single linkage clustering method (also called the nearest neighbour method), which is one of the traditional hierarchic clustering techniques. Within the similarity matrix coefficients, which exceed the current similarity level, are searched. A new group is linked with the current cluster, if there is at least one element higher than the given similarity level; for details see Davies (1971), Clifford and Stephenson (1975), Libosvárský (1981) etc. The steps of similarity levels were set to equal 0.05 of the similarity scale.

During the first trial all characters were treated, the primary matrix comprising 17 taxa and 40 digits (= 13 characters) (Table 2). During the second trial, mainly morphological criteria (characters 1 to 9 inclusive) were put in, the primary matrix comprising 17 taxa and 16 digits (= 9 characters). Each matrix was subjected to phenetic and cladistic procedure. The results, two phenograms and two cladograms, are depicted in Figs. 2 and 3.

To handle the primary data the institute's minicomputer Wang 2 200 was used. J. L. has written the computer programme in BASIC to calculate the Jaccard's a coefficient. The simple matching coefficients and the single linkage cluster were calculated by use of the programmes translated from Davies (1971).

RESULTS

1. Phenetic relationships. The cluster analysis of the phenetic relationships (Fig. 2, above) of the similarity matrix of the morphological characters (1 to 9) shows that the group of genera *Baruscapillaria*, *Pearsonema* and *Echinocoleus* makes a separate cluster at the highest level of similarity (= 0.937). Three other groups are visible on the left side of the diagram. Genera *Capillaria* and *Pseudocapillaria* fuse with the preceding group, genera *Paracapillaria* and *Capillostrongyloides* make an independent cluster and genera *Liniscus*, *Aonchotheca* and *Pseudocapillaroides* are linked together at a low similarity level to join all other groups mentioned. The remaining seven genera stay more or less independent of each other and cluster with the previous groups at the lowest similarity level (= 0.737).

The treatment of the whole set of characters (Fig. 2, below) shows the highest phenetic similarity (= 0.966 of the similarity scale) between the genera *Baruscapillaria* and *Echinocoleus*. There was only one character in which the two taxa differed, i. e., the absence (in *Baruscapillaria*) vs. presence (in *Echinocoleus*) of spines of the spicular sheath. The second pair of very similar genera was formed by *Pseudocapillaria* and *Capillaria*. Of the two differing features, one was again the presence (in *Capillaria*) and the other the absence (in *Pseudocapillaria*) of spines of the spicular sheath.

At a lower similarity level (= 0.816) four further genera (*Paracapillaria*, *Pterothominx*, *Aonchotheca* and *Skrjabinocapillaria*) fused together and clustered with the four previous taxa. This genera had in common the non-segmented free ova, endogenous development of larvae without circulation in the host and parasitism in the

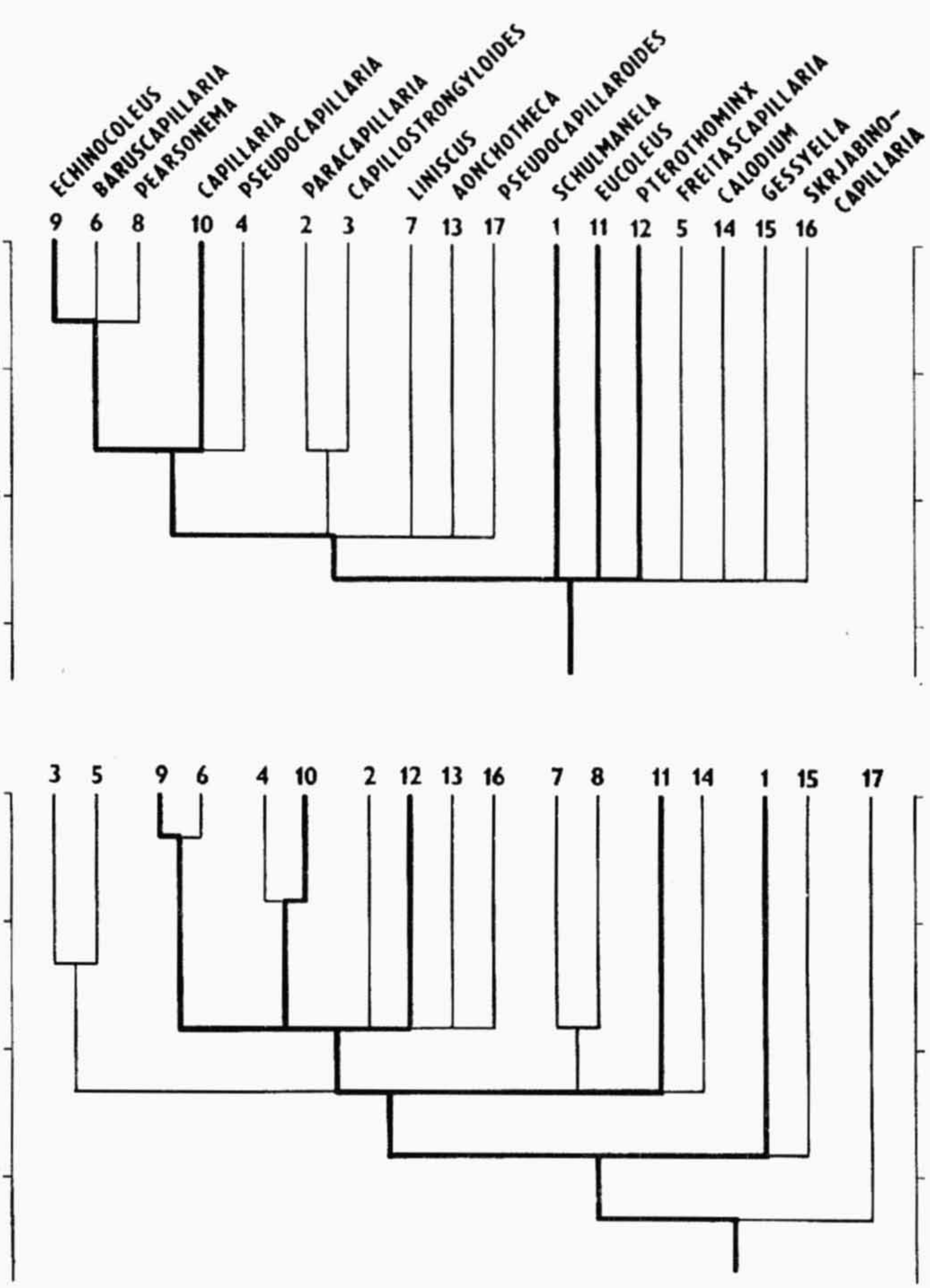

Fig. 2. Phenograms showing phenetic relations among genera of capillariids. Above, phenogram based on morphological criteria including the main groups of hosts (characters 1 to 9). Below, phenogram based on all criteria studied (characters 1 to 13). Similarity matrices were computed by means of the simple matching coefficient. Clustering was carried out by the single linkage clustering method. Numbers above the phenograms are code numbers of genera. The lines connecting taxa having spicular sheaths with spines are bold faced. The similarity scale is shown as the abscissa.

digestive tract. Four genera, *Liniscus* and *Pearsonema*, *Capillostrongyloides* and *Freitascapillaria*, the two and two clustering separately, join the previous cluster at the similarity level of 0.766.

In the lower section of the phenogram still five genera can be found. The genera *Calodium* and *Eucoleus* stand close to the others. The remaining three genera *Schulmanela*, *Gessyela* and *Pseudocapillaroides* are rather independent. They differ from the other genera considered by a greatest number of character states.

As it can be seen that the two phenetic analyses gave different results, the authors would rather prefer the simpler analysis which results from the treatment of mainly morphological characters (Fig. 2, above). In the whole set of characters (Fig. 2, below) the relationships between the taxa were probably exceedingly influenced by non-morphologic characters.

2. Cladistic relationships. Taking the cladistic distribution of genera, based mainly on morphological characters, first the following evolutionary hypothesis may be developed (Fig. 3, above).

The genera *Capillaria* and *Eucoleus* represent the most primitive taxa. Both possess spicular sheath with spines and pseudobursa has not developed yet. Two other characters split off: vulvar appendages are either absent (in *Eucoleus*) or possibly also present (in *Capillaria*), stenothermal vertebrates being definitive hosts of *Eucoleus*, stenothermal and poikilothermal vertebrates of *Capillaria*. The 2nd group comprising genera *Pseudocapillaria*, *Calodium* and *Pseudocapillaroides* is characterized by spicular sheath without spines. Many other characters, however, show different states: vulvar appendages were mostly absent but could also be present, spicule present or absent, praebursal wings absent or present, type of reproduction oviparous or ovoviviparous and as hosts either steno- or poikilothermal vertebrates are invaded. Also the 3rd group involving genera *Freitascapillaria*, *Schulmanela*, *Liniscus* and *Pterothominx* shows many loose characters: vulvar appendages either present or absent, spicule present or absent, praebursal wings present or absent, spicular sheath with spines or without spines and pseudobursa either developed or not developed. Both steno- and poikilothermal hosts are invaded.

The 4th group enclosing genera *Paracapillaria* and *Capillostrongyloides* is characterized by homogenous, mostly advanced character states: spicular sheath without spines, developed pseudobursa and the definitive hosts are poikilothermal vertebrates. The 5th group, composed of two genera standing very close to each other (*Pearsonema* and *Baruscapillaria*) joined by *Echinocoleus* at a lower level of cladistic similarity, has two advanced characters in common: developed pseudobursa and parasiting in birds and mammals. The last (6th) group comprising genera *Aonchotheca*, *Skrjabinocapillaria* and *Gessyella* is rather compact with many characters in advanced stage: spicular sheath is without spines, praebursal wings present, vulvar appendages present and developed praebursa. The mismatch relates to the host, both steno- and poikilothermal animals are invaded. In addition, in *Gessyella* the ova are enclosed in capsules.

The cladistic distribution of genera based on all diagnostic characters shows a somewhat different picture (Fig. 3, below). The 1st group containing *Capillaria* and *Pseudocapillaria* possesses no common derived characters. Most of the characters are of primitive nature. Both genera are parasitic in the digestive tract of different classes of vertebrates. The spicular sheath is with spines in *Capillaria*, without spines in *Pseudocapillaria*. The 2nd group enclosing genera *Pseudocapillaroides* and *Eucoleus* is primitive as well. Stemming from the same origin the genera differ in their hosts, mammals and birds in *Eucoleus* and poikilothermal animals in *Pseudocapillaroides*. The 3rd group enrolling genera *Baruscapillaria* and *Echinocoleus* possesses a developed pseudobursa, most other characters being mostly primitive.

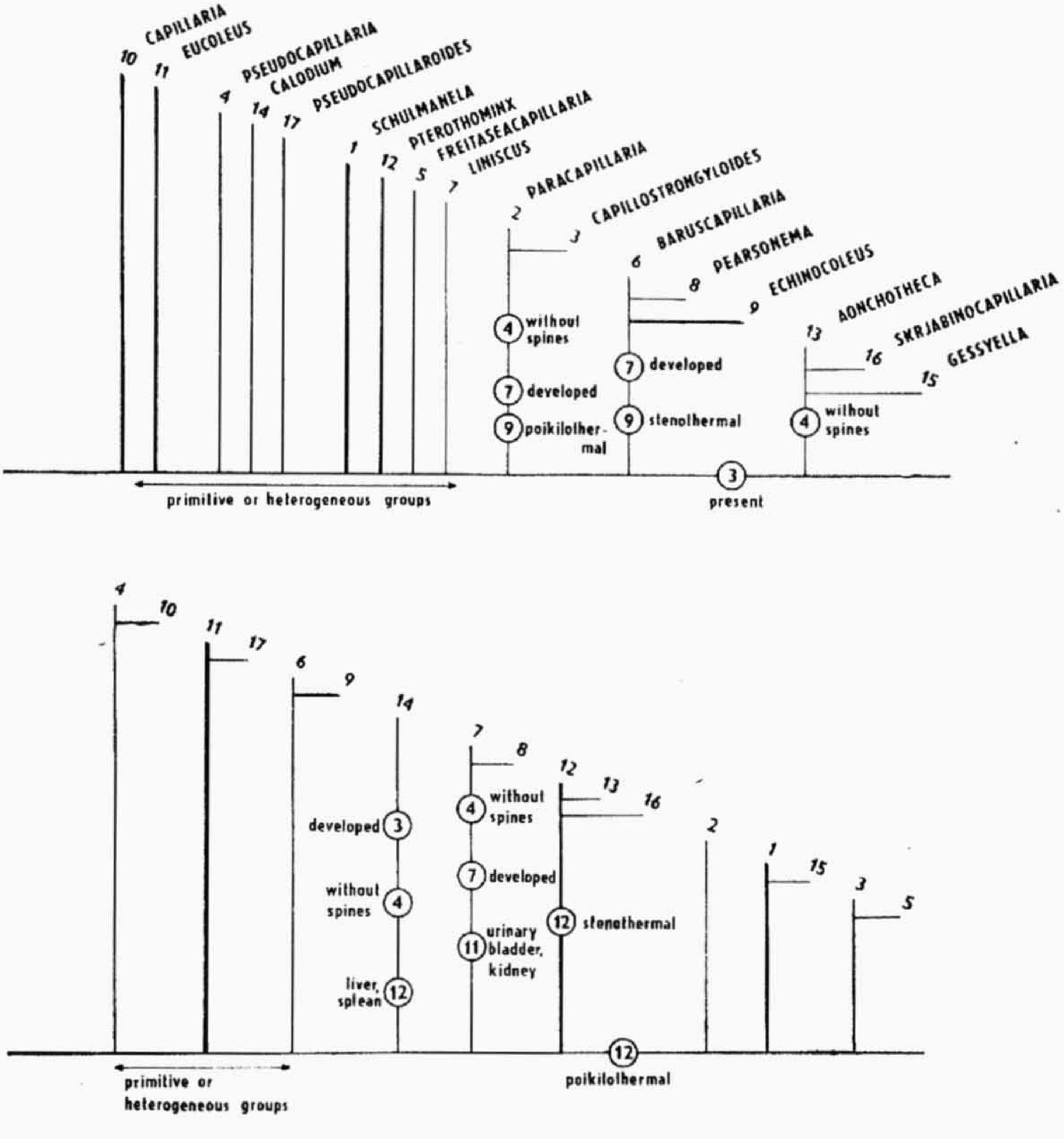

Fig. 3. Cladograms indicating systematic relationships among genera of capillariids. Above, cladogram based on morphological criteria including the main groups of hosts (characters 1 to 9). Below, cladogram based on all criteria studied (characters 1 to 13). Similarity matrices computed by means of Jaccard's (cladistic) coefficients were treated by the single linkage clustering method. Numbers above the cladograms are code numbers of genera. Numbers in the cladograms relate to the particular characters: 3, lateral praebursal wings; 4, spicular sheath; 7, development of pseudobursa; 9, main groups of hosts; 11, localization in the definitive hosts; 12, classes of definitive hosts. The lines connecting taxa having spicular sheaths with spines are bold faced.

Genus *Calodium* appears to be a unique, specialized genus with developed praebursal wings, spicular sheath without spines and produces ova which are segmented in the host. Liver and spleen are invaded. The 5th group formed by *Liniscus* and *Pearsonema* is specialized too, the adults are parasitic in urinary bladder and kidneys.

The 6th large group breaks into parasites of terrestrial (*Pterothominx*, *Aonchotheca* and *Skrjabinocapillaria*) and aquatic (*Schulmanela, Capillostrongyloides, Freitascapillaria, Gessyella* and *Paracapillaria*) animals. The former group has a developed preabursa with wings whereas other characters are either heterogeneous or primitive (e.g., the differing character is the praebursal support, all genera are parasitic in digestive tract only). The latter group formed by *Schulmanela* and *Gessyella* (with *Paracapillaria* as the most primitive form) together with *Capillostrongyloides* and *Freitascapillaria* is rather heterogeneous. The similarity goes largely on the account of the many states relating to the environment (character 9 and 10), the location in the host (character 12) and the host itself (character 11).

According to the present authors' view, the indicated evolutionary groups are inferior to the preceding arrangement, since much stress was given to the non-morphologic characters.

From the comparison of phenetic and cladistic analyses based on the morphological characters (characters 1 to 9) it is evident that the status of two intimely related groups of genera, i. e., *Echinocoleus, Baruscapillaria* and *Pearsonema, Paracapillaria* and *Capillostrongyloides*, remained unchaged. Besides, one new group consisting of phenetically closely related genera *Capillaria* and *Pseudocapillaria*, was established as freely communicating with a number of other genera. The creation of this group contrasts with the results of cladistic analysis, for both genera in question were positioned into the most heterogeneous clusters at the bottom of the cladogram. Undoubtedly, the shift of the genera goes on the account of the shared, primitive characters.

In comparing the arrangements of genera resulting from phenetic and cladistic analyses of the whole set of characters, it is apparent that even more clusters located at the high similarity levels remained more or less unchained. Only genera showing loosed affinities obtained different distributional patterns.

DISCUSSION

In our opinion, when estimating the interrelations of genera of the family Capillariidae, it is necessary to proceed from broad connections, i.e., from similarities among the families of the order Trichocephalida (Capillariidae, Trichocephalidae, Trichinellidae, Trichosomoididae and Cystopsidae). The arrangement of this order into the class Adenophorea is evident. According to Maggenti (1981), the adaptation of this and other orders of nematodes to parasitism in vertebrates is of terrestrial origin. The same author deduced that trichocephalids appear to be most closely related to the soil-inhabiting dorylaimids. The hypothesis on the terrestrial origin of adaptations to parasitism in order Trichocephalida is supported also by the fact that this order nowadays reached its maximum expansion in land vertebrates. It is a case of the specialized families Trichocephalidae and Capillariidae (with numerous species parasiting in land vertebrates) and families Trichinellidae and Trichosomoididae (with low number of species).

In all trichocephalid nematodes apparent similarity or even a total congruence can be traced in the following characters: morphology of the head end (topography of cephalic papillae), presence of stylet (also in adults) presence of bacillary bands, and form of eggs. In our opinion, this may also be regarded as one of the important proofs of their joint origin from a hypothetic primitive group of nematodes (Prototrichocephalata). Among the recent families of this order, the capillariids and trichocephalids may be appraized as most closely related. By their morphological and biological features, as well as by a considerable number of recent species (if compared with the families Trichinellidae, Trichosomoididae and Cystopsidae) the trichocephalids and capillariids represent a dynamic, developing branch (derived from one common evolutionary line), i.e., the hypothetical group Prototrichocephalata. While the family Trichocephalidae, being morphologically and biologically markedly homogenous and stabilized, may be considered on the basis of parasite-host relations as a family strictly specialized and adapted to parasitism in the digestive tract of mammals, the family Capillariidae is morphologically and biologically heterogenous, apparently, this being the result of the adaptation to and specialization on parasitism in tissues and organs of various hosts (poikilo- and stenothermal vertebrates). Assuming that the relation between the both families is very close, we undertook the analysis of similarities among the genera of capillariids. In our analysis, those characters were viewed as primitive which were common both in capillariids and trichocephalids. The same characters are evident, to a various extent, also in the other families of the order Trichocephalida. Among the morphological characters, it is, e.g., the presence of spicule, the presence of spines on the spicular sheath, the absence of vulvar appendages and lateral pseudobursal wings, non-segmented ova, and especially the simple morphology of pseudobursa. From the comparison of the formation of the posterior body end of males in the families Trichocephalidae, Trichinellidae and Capillariidae it follows, that the simple shape, i.e., the posterior end rounded or with two more or less developed lateral papillae without a cuticular pseudobursa, is evidently common (and, in our opinion, also primitive). In tune with **Moravec** (1982) and other authors, we consider the morphology of the posterior body end in males (pseudobursa) as very important in the systematics of the family Capillariidae. In our opinion, however, this character possesses also an extraordinary weight in the appraisal of similarities and evolutionary relations among the genera in question. In accordance with the hypothesis presented by **Maggenti** (1981) (relating to the terrestrial origin of parasitism of nematodes in vertebrates), we take the terrestrial origin of the definitive host (stenothermal vertebrates) as a primitive character.

The analysis and the evolutionary interpretation of life cycles of nematodes of the family Capillariidae appear to be very complex. In this family (and also in the other Trichocephalida) we meet with three types of evolutionary cycles: heteroxenous, simple direct and complex direct. Contrary to **Maggenti** (1981), we viewed the simple direct type of life cycle as original (primitive) and the heteroxenous one (with an intermediate host or a parathenic host) as derived or evolutionary younger within a single line. The reason for this deviation follows from the comparison of the evolutionary cycles of nematodes of the family Trichocephalidae, which are explicitly of simple direct type. On the basis of similar analogy, we conclude on the originality of localization of capillariids in the organism of the definitive hosts. In our opinion, the parasitism of capillariids in the digestive tract of the definitive hosts is original, parasitism in the other organs and tissues is derived (evolutionary younger).

Backed by this working hypothesis on the evolutionary succession of selected morphologic and biological characters, we carried out the analyses of phenotypic and cladistic similarities among the recent genera of the family Capillariidae. We are well aware that these analyses are to some extent biased, as, due to the additive coding, the separate characters had not the same weight. On the other hand, we are convinced that our analyses of similarities tend to present objective approaches to the issue, especially when four different variants are offered.

The results may be interpreted as follows. The family Capillariidae has a very complex division at the level of genera. The concept of classification or differentiation into a greater number of genera, presented in a synthetic way by **Moravec** (1982), is, according to our results, realistic and competent. It is possible to assume, that the number of genera will be further increased in relation to the knowledge gained. Moreover, we suppose that the relation and similarity shown among the genera of capillariids will bring about a constitution of categories higher than genus. The authors who in an attempt to simplify the situation do not respect the systematic importance of marked morphological characters for differentiation of genera (e.g., **Butterworth** and **Beverly-Burton** 1980, etc.) disguise the morphologic and evolutionary relations and structures, the critical analysis of which is of a great value to make it possible to proceed further towards precision and improvement in the system of nematodes in general.

The complexity of interrelations of genera of capillariids is expressed by appraisal of their phenetic similarities (Fig. 2). Despite some differences resulting from the methods adopted it is possible to clearly document in both variants the similarity between apparently primitive genera *Capillaria* and *Pseudocapillaria* on one side and between evolutionary higher situated genera *Echinocoleus* and *Baruscapillaria* (possibly also *Pearsonema*) on the other side. In the former case, the genera parasite in various groups of vertebrates (poikilothermal and stenothermal), in the latter case the genera (species) parasite only in stenothermal vertebrates. Even though the morphological affinity of genera mentioned above is evident, their validity is without any doubt. All other genera of capillariids are then more or less different one from another. In the second phenogram, which includes all characters treated, the interesting parasite-host relationships are shown especially at the intermediate level of similarity. There are three couples which show similarity and apparently also kinship: *Capillostrongyloides* and *Freitascapillaria*, *Liniscus* and *Pearsonema*, *Eucoleus* and *Calodium*. It remains, however, a fact, that the mutual relations of generic categories in the family studied are not free from obscurity.

The cladistic analysis, in our opinion, resulted in a more lucid picture (Fig. 3). In congruence with our reasoning, concerning the ways of evolution of the separate characters, genera *Capillaria*, *Eucoleus*, *Pseudocapillaria*, *Pseudocapillaroides* and possibly also *Calodium* univocally represent themselves as primitive and heterogeneous categories. Genera *Capillaria* and *Eucoleus* are regarded as ancestors of the other capillariids. All other genera are held in the course of adaptation to parasitism in different groups of vertebrates and in their different organs and tissues as derived (evolutionary younger). The analyses based on all criteria strengthened the dependence of genera (and species) upon two main groups of hosts — poikilothermal or stenothermal vertebrates. From these analyses it is possible to infer a narrow relationship between the couples of genera *Aonchotheca* and *Skrjabinocapillaria*, *Schulmanela* and *Gessyella*. The synonymity of these generic categories is very probable (**Moravec** 1982).

О ФЕНЕТИЧЕСКИХ И КЛАДИСТИЧЕСКИХ ВЗАИМООТНОШЕНИЯХ СРЕДИ РОДОВ СЕМЕЙСТВА *CAPILLARIIDAE*

В. Баруш и Й. Либосварски

Резюме. При помощи методов нумерической таксономии изучали фенетические и кладистические взаимоотношения среди 17 родов семейства Capillariidae. Применяли аддитивное бинарное кодирование и при помощи спаривания и формулы Жакара вычисляли коэффициенты сходства. Матрицы коэффициентов сходства подвергали групповому анализу. При фенетическом анализе девяти, большей частью морфологических признаков обнаружено, что эти роды разделяются в 4 главные группы. Однако при

помощи анализа, основанного на всех критериях, выявлено большее количество групп. Самое большое фенетическое сходство обнаружено у родов *Echinocoleus* и *Baruscapillaria*, тогда как род *Pseudocapillaroides* больше всех отличается от других родов. При помощи кладистического анализа было обнаружено 6 и 9 групп. При анализе на основе 9 признаков выявлена большая группа примитивных, довольно гетерогенных родов. При анализе на основе всех критерий обнаружено, что роды, паразитирующие у пойкилотермных позвоночных, образуют самые продвинутые группы. Было также обнаружено, что семейство *Capillariidae* хорошо дифференцировано и что его разделение на уровне родов комплексно. По мнению авторов роды *Capillaria*, *Pseudocapillaria*, *Pseudocapillaroides* и, возможно, также *Calodium* примитивны и гетерогенны. Роды *Capillaria* и *Eucoleus* можно считать предками других капилярий. Все другие роды (эволюционно моложе) адаптировались к паразитированию в разных группах позвоночных и их разных органах и тканях.

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V. B., Ústav pro výzkum obratlovců ČSAV,
Květná 8, 603 65 Brno, ČSSR

FOLIA PARASITOLOGICA (PRAHA) 31: 240, 1984.

T. K. Kabilov: Geľminty pozvonochnykh zhivotnykh Uzbekistana, razvivayushchiyesya s uchastiyem nasekomykh. (Helminths of vertebrates in Uzbekistan developing with participation of insects). *Publ. House Fan, Tashkent 1983, 128 pp., 65 Figs., 13 Tables. Price 1.20 R.*

It is common knowledge that many helminths, including some causative agents of serious diseases, complete their development in various insect species. Our information on their interrelationships is still insufficient and the solution of these problems is therefore very topical. The author of this book paid attention to those problems as regards the territory of Uzbekistan. As basic material he used his collections made between 1969—1980, when he examined 81 210 insect specimens belonging to 278 species of 10 orders. Helminths were found in 183 insect species, out of which 92 species were proved to harbour them for the first time. A total of 103 taxa of larval forms from 46 genera and 23 families (3 Trematoda, 21 Cestoda, 6 Acanthocephala and 73 Nematoda) was found, out of which 57 were identified down to the rank of species. Thirty four forms are described for the first time. With different species their insect hosts, the prevalence and intensity of host infection, data about localities are given and occasionally hosts of adult stages are mentioned. Descriptions and figures presented only with first finds in the territory of the USSR or with finds in a new host. Most numerous helminths were found in the families Tenebrionidae (69), Scarabaeidae (14) and Carabidae (11).

The following text covers an ecologic analysis of the fauna of larval forms of helminths depending on different landscape zones, the peculiarities of biocenotic relationships between the helminths developing in insects and the definitive hosts, and also discussed is the role of insects in the maintenance of natural focality of some helminthiases. At the end of the volume there is a survey of literature used. In this part a considerable number of misspellings have been overlooked by the proofreader in references of foreign authors. There are other numerous inaccuracies in the Latin names of different taxa in the text and primarily in Tables. It is to be regretted that there is no subject index.

The publication contains many new data on the interrelationships between helminths and their insect intermediate hosts. The materials presented are valuable for studies intended in other geographic regions.

Dr. V. Černý, C.Sc.