

**Cladistic Analysis of Neanuridae(Collembola)
Using Character Weighted and Character Unweighted Approaches**

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흑무늬톡토기과의 형질평가 및 형질非평가方法에
依한 CLADISM 分析

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적 요

흑무늬 톡토기과의 6 개 아과들에서 20 개 형질복합을 추출하여 형질평가방법과 Wagner algorithm 의 형질 비평가방법을 사용하여 계통수를 작성, 비교하였다. 전자의 방법을 위해 진화적 형질순서와 극성을 결정하고 고등급의 파생공유 형질을 토대로한 단계통군과 자매군을 확인하여 계통분화를 추적하였다.

이 두가지 방법에 의한 계통수에서 분지 방식은 매우 다르게 나타났으나 나열순서는 유사했고, 단지 마지막의 2 개 아과가 후자에서는 반대로 나타났다.

그 원인은 후자의 방법으로는 파생형질수가 많은 분류군에서의 형질상태가 Wagner algorithm 에서 누적 효과를 일으킨 때문인 것으로 생각되며 아울러 1, 10 및 20 번 등 형질의 적응이동(adaptive shift)상 나타낼 중요한 의의를 적절히 평가, 반영할 수 없는 데 있는 것으로 추정된다.

Key words: Collembola, Neanuridae, phylogeny, cladistics.

INTRODUCTION

There have been a number of works dealing with phylogeny of neanurid Collembola, but some of them are restricted to categories of the rank as low as the subfamily (Cassagnau, 1983; Deharveng, 1983) or genus (Deharveng, 1982), while those of the family level, Neanuridae, are simply depicted as branching of the subtaxa as part of a phylogenetic tree of the order Collembola (Yosii, 1961; Salmon, 1964; Cassagnau, 1971; Uchida, 1971; Massoud, 1976).

In view of its ever-growing significance of the recently developed new methodologies in taxonomy and the importance of adaptive shifts and the underlying mechanisms for origi-

nating higher categories (Bock, 1965), an attempt to construct a phylogenetic tree of subfamilies of the neanurid Collembola using cladistics (Henning, 1966; Wiley, 1981) would be worth making and perhaps even an urgent task. Although the theory and practice still remain a matter of much controversy, it is becoming more adopted and justified from an evolutionary perspective which it provides and this is a relatively objective means ensuring systematization of taxa, based mainly on determinations of character transformation, monophyly, sister-group relationship and cladogram preparation (Ashlock, 1974; Kavanaugh, 1978).

MATERIAL

Six subfamilies of the family Neanuridae have been examined. Five of the taxa come from the monograph of Massoud (1967) and the remaining one from Lee's recent study (Lee, 1983). It is to be noted that one of the former five subfamilies, Odontellinae, has been recently raised to a new family, separate from Neanuridae, based on differences in a few anatomical features formerly overlooked (Deharveng, 1981). I employed here, nevertheless, the Massoud's scheme of classification hoping to examine and analyze the involved characters and monophylies on a trial basis of cladistics.

Another family, Hypogastruridae, in addition, was taken as an out-group or a hypothetical ancestor for character comparison and for computing branching sequences. This group is certainly regarded more "primitive" than and closest to the present Neanuridae by being in the same lineage or sharing a common ancestor (Cassagnau, 1971; Uchida, 1971; Massoud, 1976; Deharveng, 1981).

The taxa analyzed thus are as follows:

Family Neanuridae

Subfamily Odontellinae Massoud, 1967

Subfamily Brachystomellinae Stach, 1949 sensu Massoud, 1967

Subfamily Frieseinae Massoud, 1967

Subfamily Pseudachorutinae Stach, 1949 sensu Massoud, 1967

Subfamily Neanurinae Yosii, 1961

Subfamily Caputanurinae Lee, 1983

Family Hypogastruridae (as out-group)

METHODS AND RESULTS

1. Character weighted approach

The prime objective of phylogenetic inference is the recognition of monophyly and parallelism through character analysis. It is, therefore, critical to determine whether a character in question is primitive (=ancestral=plesiomorphy) or derived (=advanced=apomorphy). For this purpose the criteria proposed by a few workers were employed (Kluge & Farris, 1969; Schaeffer *et al.*, 1972; Kluge, 1976; Hecht, 1976) which may reveal a trend

in character states, that is a transformation series or a morphocline, enabling thus to determine the direction of change, the polarity (Hecht, 1976), (Tab. 1).

Table 1. Character states of morphocline series
0 : Plesiomorphy, 1, 2, 3, : Apomorphy, 1', 2', 3', : of different polarity

No.	Character	W.T.		Character States
1	Habitus	IV	cylindrical	(0), robust(1), flat (2), extremely flat(3)
2	Apic. lobe	II	trilobed	(0), unilobed (1), absent(2)
3	III.A.O.	II	uniform	(0), variable (1),
4	P.A.O.	I	tuberculated	(0), absent (1),
5	Eyes	II	8+8 or >	(0), 5+5 or > (1), 3+3 or >(2)
6	Mouthparts	V	chewing	(0), Md. red. or lost (1'), modif'd. for sucking ² (2'), specializ'd. for sucking(3')
7	Maxillary palp	IV	present	(0), absent (1)
8	Saliv. gland	V	normal	(0), enlarged (1)
9	V ₁ , V ₂ (Vertex)	IV	present	(0), absent (1)
10	Hd-Th.I.	V	distinct	(0), fused (1)
11	S.s.(Th. II - III)	II	in Th. II & Th. III	(0), only in Th. II (1)
12	Tubercle	II	absent	(0), developed (1)
13	Paratergite	II	absent	(0), developed (1)
14	Claw	II	complete	(0), only Ung. (1)
15	Tenant hair	I	present	(0), often pres. (1), absent(2)
16	Ventral tube setae	II	4+4 or <	(0), 4+4 or > (1)
17	Furcal complex.	IV	developed	(0), reduced (1), absent(2) with 7+7 setae
18	Abd. VI	VI	entire	(0), bilobed (1)
19	Anal spine	I	present	(0), absent (1)
20	Polar Migtn.	V	absent	(0), if present, cryptopygy (1), if present, cryptophthalmy too(2)

The next step was assigning weight to each character following the system of Hecht and Edwards (Hecht, 1976; Hecht & Edwards, 1976). One of the five weighting types was assigned to each character depending on the information content, which then, could be put in increasing order of the content as follows: (I) loss character states, (II) simplification by reduction or fusion, (III) whose degree of development is related to ontogenetic or allometric processes, (IV) functionally integrated character complexes and (V) unique and innovative character complexes (Tab. 2).

Since the characters in lower weight categories tend to be subject to parallelism only the last two of them, types IV and V, were mainly utilized because their information contents are considered to play vital roles in occupying a new adaptive zone, originating thus a taxon of a higher category. It is to be emphasized also that functional character complexes have not been taken apart into smaller components as normally practised in phenetic taxonomy,

to avoid undue weighting.

Unfortunately, as far as Collembola is concerned, the actual knowledge concerning anatomy, development, life histories and various aspects of biochemistry is severely limited, which restricts, naturally, the number of character complexes available. Twenty character complexes, nevertheless, were extracted and the results of their examination as well as weighting type determination are as follows:

Table 2. Distribution of states and weighting of characters

Character	1	2	3	4	5	6	7	8	9	10
Weight	N	II	II	I	II	V	N	V	N	V
(Char. Abb.)	HA	AL	3A	PA	EY	MP	ML	SG	VV	HT
Hypogastruridae	0	0 ₍₁₎	0	0 ₍₁₎	0 _(1,2)	0	0	0	0 ₍₁₎	0
Odontellinae	1 ₍₁₎	1 ₍₂₎	0	0	1	1	0	0	1	0
Brachystomellinae	1	0 ₍₁₎	0	0 ₍₁₎	0 _(1,2)	1	1	0	1	0
Frieseinae	0 ₍₁₎	0 ₍₁₎	1	1	0 _(1,2)	2	1	0	1	0
Pseudachorutinae	2 ₍₁₎	0 ₍₁₎	1	0 ₍₁₎	0 _(1,2)	2 ₍₃₎	1	0 ₍₁₎	1	0
Neanurinae	2 ₍₁₎	0 _(1,2)	0	1 ₍₀₎	2 ₍₁₎	3 ₍₂₎	1	1	1	0
Caputanurinae	3	0	0	0	2	3	1	0	1	1

Character	11	12	13	14	15	16	17	18	19	20
Weight	II	II	II	II	I	II	N	N	I	V
(Char. Abb.)	SS	TB	PT	CL	TH	VT	FU	A6	AS	PM
Hypogastruridae	1	0	0	0	0	0 ₍₁₎	0 ₍₁₎	0	0	0
Odontellinae	0	0	0	1 ₍₀₎	1	1	1 ₍₀₎	0	0 ₍₁₎	0
Brachystomellinae	1	0	0	1	1	1	1 ₍₀₎	0	1	0
Frieseinae	1	0	0	1	1	1	1	0	0 ₍₁₎	0
Pseudachorutinae	1	0 ₍₁₎	1 ₍₀₎	1	2	1	1 ₍₀₎	0	1	0
Neanurinae	1	1 ₍₀₎	0	1	2	1	2	1 ₍₀₎	1	1
Caputanurinae	1	0	0	1	2	1	2	0	1	2

*For abbreviations see Table 1 and the text.

1) Habitus

The general body shape displays cylindrical in ancestral forms as in Hypogastruridae which is the out-group in this study. But in neanurid subfamilies it ranges from robust to finely elongated to flat forms, all considered apomorphies as compared to cylindrical plesiomorphy, and the morphocline ending with extremely dorso-ventrally flat body shape in Caputanurinae is recognized. Since the flat body form characterizes, in general, parasitic animals meeting adaptive requirements of new ecological niches, this character was assigned type N taking into account its role presumably played in invading new adaptive zones.

2) Apical lobe

Minute lobal projections on the apex of antennae vary in number from three to one, to total absence. This reductional trend, with variability in number even within a subfamily as well as throughout the neanurid subtaxa renders the character of type II. According to the ultrastructural study of the unusual "eversible sac of the antennal tip" of *Hypogastrura socialis* it was known to have a neurosecretory glandular function (Altner & Thies, 1973). Unfortunately no similar investigation was ever undertaken with any neanurid species. It is to be noted, however, that in a remotely related Collembola species, *Allacma fusca*, a Symphypleone, proprioceptive as well as chemosensitive role were suggested for the "multifunctional sensory complex" of the antennal tip (Altner & Thies, 1978). No homologies, however, would be considered among those organs of the cited groups with respect to that of apical lobes in neanurid species until thorough comparative ultrastructural studies are carried out.

3) Third antennal segment organ (III. A.O.)

Little is known of the function of the organ except by a recent study reporting that the outer pegs ("guard setae") of this organ are the points of attachment of bipolar sensory cells running to intrinsic muscles of the third and fourth antennal segments. The cells are apparently mechanoreceptors, though presumed chemoreceptor cells are also associated with all 4 pegs (Altner & Thies, 1984). However the study is concerned with *Allacma fusca*, a Symphypleone, which is only distantly related with the Neanuridae, and the homology between them, therefore, remains still obscure. Even in Onychiuridae which is considered one of the families closest to Neanuridae and whose third antennal organ is certainly most differentiated among Collembola the value of its taxonomical character is questioned by the variability recently verified with the number of the sense clubs ("sense organ") (Chi, 1985). In Neanuridae in question, however, the structure of the organ is quite simple and the uniformity prevails among most subfamilies except for Frieseinae and Pseudachorutinae. Its obvious absence, however, in *Gulgastrura* sp., constitutes an exception not only for Hypogastruridae to which the *Gulgastrura* was originally assigned but also throughout the Collembola order. For its poor informations content available and the variability as well as the loss case it is assigned type II.

4) Postantennal organ (P. A.O.)

This organ consists of vesicles, the number and shape being variable in different taxa. It is totally absent in Frieseinae, partially in Brachystomellinae and mostly in Neanurinae. One of the best developed organs can be seen in *Morulina* of Neanurinae in which it looks like a morula whence the generic name derived. Regarded as irregular and loss character it is weighted type I. Its functional morphology has seldom been studied. Some examples, however, can be referred to concerning that of *Anurida maritima*, a neanurid species, which was known to be an olfactory organ (Dallai, 1971), while that of an onychiurid species was suggested to be a sensory organ assuming the roles of both chemoreception and hygroreception (Karuhize, 1971).

5) Eyes

The number of ocelli, normally 8 in the out-group, Hypogastruridae, is equally observed in the neanurid family, but they may be reduced or absent and even variable within a subfamily depending on the taxa and the general tendency of reduction is recognized. This reduction or absence of the ocelli is frequently found in cave-dwelling and deep soil forms and even in parasitic ones in other insect orders. Since reduction or loss data do not necessarily offer any reliable base of affinity it is assigned the weighting type II.

6) Mouthparts

This is one of the characters most modified in Neanuridae among Collembola. The mandible with molar plate, certainly a plesiomorphy as in Hypogastruridae, directs its change in Neanuridae toward a variety of forms, tending to be reduced or even lost in Odontellinae and Brachystomellinae and even to simpler tridentate or bidentate forms. The maxillae, on the other hand, display a variety of forms, often species-specific, and its reduction culminated by styliform in most Neanurinae as well as in Caputanurinae. The mouthparts, on the whole, seem to have undergone their modifications in three ways, one toward reduction or complete loss of the mandible, another of unknown specific function but still with many complicated structures, and the third toward extreme reduction for specializing in sucking food habits as obviously seen in Neanurinae, Caputanurinae and partially in Pseudachorutinae, hence apparently displaying, on the whole, three polarities(6¹, 6², 6³). As already noted earlier a functional character complex like mouthparts should not be dealt with by its anatomical details but as a whole unit(Kim & Ludwig, 1978). Since mouthparts evolutions should have been critical in shifting adaptive zone and occupying a new ecological niche the change must have been that of a unit as integrated components of food processing apparatus. This, therefore, is to be seen type V.

7) Maxillary palp

This sensory organ has been treated as a character independent from other mouthparts for mastication and piercing food material. It was considered critical in separating Odontellinae possessing the organ, from all the remaining subfamilies of Neanuridae lacking in it, which led to the creation of a new family, Odontellidae(Deharveng, 1981). Considered as important autapomorphy among Neanurinae it is assigned type IV.

8) Salivary glands

With the recent discovery of giant chromosomes from the salivary gland of a neanurid species (Prabhoo, 1961), after Diptera in animal kingdom in chronistic order, this gland drew special attention in conjunction with its ecological niche occupation by the taxa with their distinctive food habits. This inference is based on data suggesting that the enlargement of the gland and the polytene development are associated with the active secretory function of the gland for extra-oral digestion. It is accompanied by the reduction of mouthparts, often in stylet form of maxillae, which is certainly to help pierce food substrate and suck up partially digested fluid. The enlargement of the gland has so far been demo-

nstrated mainly from Neanurinae (Cassagnau, 1966), always those with reduced mouthparts (Cassagnau, 1968; Cassagnau *et al.*, 1979; Lee, 1980). In view of the role played by the gland in the adaptive shift of the animal, the character is assigned the type V.

9) Head chaetotaxy

The absence of the setae, V_1 and V_2 in the head vertex characterizes Neanuridae against Hypogastruridae, the out-group in the present study, in which the two setae occur mostly (Cassagnau, 1974). Since chaetotaxy is considered one of the most important characters reflecting phylogenetic relationships, it is to be valued as type IV.

10) Head and prothorax

In neanurid family the prothorax is well differentiated with its own chaetotaxical pattern even though the tergite is less developed than meso-, and metathoraxes. Curiously, in Capitanurinae however, we see head and prothorax not so distinguishable as in other neanurid groups. My interpretation was that it is due to the fusion of the two segments first, with subsequent reunion of the segments, but accompanied by shifting the demarcation between the head and thorax in an inextraordinary way, as can be recognized in the light of general chaetotaxies typical to head and prothorax respectively (Lee, 1983). Since this unusual "reshuffling" is entirely exceptional throughout the Collembola it is considered certainly associated with an occupation of a special niche, along with a drastic divergence in both morphology and functional physiology which, however, remains to be known. In this sense of the unique modification weighting type V was assigned.

11) Sensory setae in the thorax

Sensory setae(s.s.) in lateral tergites are observed in Th. II in Hypogastruridae and all of neanurid subfamilies except Odontellinae in which they occur not only in the second but also in the third thoracic segment. Since the evolutionary status of the chaetotaxy is still obscure it is assigned type II.

12) Tubercles

Tubercles occur in Neanurinae and only exceptionally in Pseudachorutinae, with some variation in the extent of development according to taxa in the Neanuridae. They may be regarded as derived state, namely, apomorphy as well as autapomorphy of Neanuridae. Since the character, however, shows the tendency of reduction and much variation in varying taxa and part of the body it is weighted type II.

13) Paratergites

They are found only in Pseudachorutinae, hence, an autapomorphy of the subfamily even though they show different extents of development in varying taxa, even to absence. It is assigned type II.

14) Claws

The complete form with unguis and unguiculus as can be seen in Hypogastruridae is

observed only in certain groups of Odontellinae among neanurid subfamilies. In all the remaining members of Neanuridae the unguiculus is completely absent, which is, therefore, an apomorphy. Since the claw, moreover, was known to be subject to easy modification by environmental factors as demonstrated with cave Collembola (Christiansen, 1961) it is assigned type II.

15) **Tenant hair**

As an accessory organ helping locomotion by claws tenant hair is assigned type I as a character, subject to easy change of shape and loss by environmental factors (Christiansen, 1961).

16) **Ventral tube chaetotaxy**

This character shows reduction in number of setae from 8 to 4 on each side to complete absence and is assigned type II. Concerning the functions of the ventral tube, the maximal water absorption in a slightly acidic condition (pH. 5~6) was explained (Jaeger & Eisenbeis, 1984) while the groove running along the median of the ventral tube was discovered to play a conductive role for excretion of metabolic wastes (Verhoef *et al.*, 1983). No relevant information, however, is available from any neanurid member.

17) **Furcal complex**

The chaetotaxy of dens showing 7+7 is considered a plesiomorphy and their reduced one to complete absence is observed in different subfamilies of Neanuridae. The reductional trend is accompanied by regressions of both furca and retinacle, comprising the furcal complex. Considering that jumping organ is the most effective locomotory apparatus in Collembola as among apterygote hexapods and thus associated closely with ecological niches involved it is assigned type IV.

18) **Abdominal segment VI**

After Cassagnau, concerning the evolution of the abdominal end in Neanuridae, the ancestral stage assumes "non bilobé et sans tubercules", followed by "bilobation nette" and then comes the reunion of the two tubercles connected by transversal reticulations (Cassagnau, 1980). Of the subfamilies of Neanuridae, however, we take only two states, that is, entire and bilobed forms. In view of the capability of this character differentiating taxa it is assigned type IV.

19) **Anal spines**

It is one of the characters that is highly variable and subject to environmental influences and is assigned type I.

20) **Polar migration**

The migration of the abdominal end toward the ventral side is known to be ubiquitous under the name of "cryptopygy" and was regarded as a result of posterior migration of

body segments (Cassagnau, 1974). With finding not only the posterior migration but also migration to the anterior side in Caputanurinae the terms "cryptophthalmy" and "bipolar migration" were coined representing the extraordinary states of the orientation, which certainly suggests a most advanced stage of the body plan of Neanuridae (Lee, 1983). These characters as a whole are considered to reveal extreme divergences of the animal although they are still of unknown significance. Thus, we assign type V to this bipolar migration.

The result of the analysis made so far is as shown in Tables 1 and 2.

Of the 20 character complexes examined we find 11 are weighting types I and II, 5 in type IV and 4 in type V. No characters of type III were available certainly due to the absence of knowledge required for the assignment, namely, ontogenetic processes of the characters (Table 3). Five characters (8, 10, 12, 13, 18) are plesiomorphies throughout all the subfamilies excluding Neanurinae, Caputanurinae or Pseudachorutinae respectively depending on the character. Remarkable is the single character in the state of 11⁰ exclusively shown by Odontellinae as plesiomorphy among entire neanurid subfamilies and even the out-group, Hypogastruridae. Six synapomorphies (6, 9, 14, 15, 16, 17) are noticed for all the neanurid subfamilies, half of which (6, 15, 17) are showing morphocline series, and one synapomorphy (1) is identified for five subfamilies of Neanuridae excepting Frieseinae while the character state (7¹) representing the absence of maxillary palp, of weighting type IV, is a synapomorphy of neanurid subfamilies excluding, however, Odontellinae. Another character (19) is seen to be synapomorphy with respect to four of the subfamilies of Neanuridae, that is except Odontellinae and Frieseinae. In addition, Frieseinae and Neanurinae are shown to share a synapomorphy (4) while character 5 comprises a synapomorphy of Odontellinae, Neanurinae and Caputanurinae but in a morphocline series. Furthermore, Neanurinae and Caputanurinae share a synapomorphy in a morphocline series (20). In this connection we see now that there are 10 autapomorphies as apomorphy (1, 2, 5, 8, 10, 12, 13, 18, 20¹, 20²) including those of a morphocline as in character 20.

Table 3. Exclusive synapomorphy and autapomorphy

Taxa set	Characters	No. of Synapomorphy, M, V.
Od-Br-Fr-Ps-Ne-Ca	6, 9	2
Br-Fr-Ps-Ne-Ca	7	1
Od-Br-Fr-Ps	17	1
Od-Br	1, 6	2
Fr-Ps	6	1
Ps-Ne	1	1
Ne-Ca	6, 17	2
Taxa	Characters	No. of Autapomorphy, I - V
Od	2(II), 5(II), 11(II)	3
Ps	13(II)	1
Ne	8(V), 12(II), 18(N), 20 ¹ (V)	4
Cc	1(N), 10(V), 20 ² (V)	3

To infer phylogenetic affinities, sister groups were determined first by their synapomorphic character states. Use was made, however, only of the characters of weighting types IV and V for cladogram construction for their presumed critical roles in adaptive shifts as mentioned earlier (Fig. 1).

First, we confirm that the synapomorphies for all the neanurid subfamilies against the out-group, Hypogastruridae, are characters 6 and 9, concerned with modified mouthparts (6^{1-3}) and absence of the setae V_1 and V_2 (9^1) respectively, thus demonstrating the monophyletic nature of the family Neanuridae. The next character state suggesting monophyly by containing largest number of subtaxa is character 7 which combines together only 5 neanurid subfamilies separating Odontellinae. Then comes character 17, putting together Brachystomellinae, Fieseinae and Pseudachorutinae on the one hand (17^1) and Neanurinae and Caputanurinae on the other (17^2). Now the mouthparts type divide the former three, giving rise to a sister-groups of Fieseinae-Pseudachorutinae (6^2), and an isolated one, Brachystomellinae (6^1). Still in the remaining branch leading to Neanurinae and Caputanurinae is the group with "specialized for sucking" mouthparts, thus embodying the two subfamilies encoded type 6^3 . The phylogenetic scheme based on those data of characters of IV and V weighting types finally offers a cladogram as represented in Fig. 1.

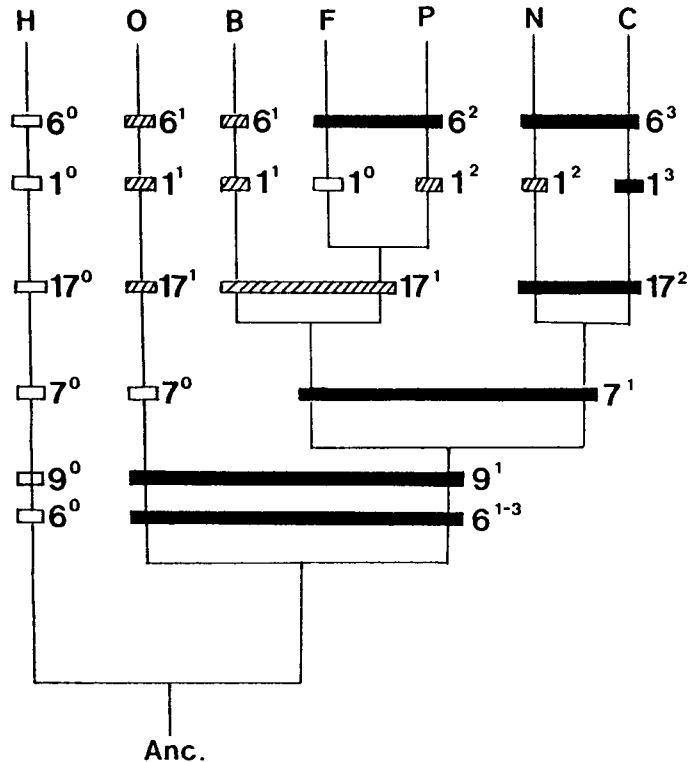


Fig. 1. Cladogram of the character weighted method

Black bar: synapomorphy, Hollow bar: plesiomorphy, Hatched bar: character states representing apomorphy or synapomorphy but presumably involved with parallelism or mosaic evolution depending on characters. Only characters of weighting types IV and V are indicated.

2. Character unweighted approach

Kluge and Farris suggested an algorithm for computing Wagner trees, which is based on applying the parsimony criterion to derive an estimated tree of minimum evolutionary steps (Kluge & Farris, 1969; Wiley, 1981). First we determine, in a binary fashion, whether a character state in each transformation series is plesiomorphy, describing with discrete data (0=plesiomorphy, 1=apomorphy). This is performed by specifying the character conditions in the out-group certainly considered ancestral to the taxon in question. On application of this procedure to the present taxa we first obtained a character matrix as featured in Table 4 which is based on Table 2. Conversions of the figures from Table 2 were made by assigning 0 for 0 and 1st stages and 1 for 2nd and 3rd stages of the transformation series when the morphocline goes up to 2 or 3, respectively.

For computing Wagner trees then we began with determining the difference between a taxon and a hypothetical ancestor, Hypogastruridae, which is taken as the out-group and the following formula was used.

$$D(\text{Txn}, \text{Anc.}) = \sum_i |X(\text{Txn}, i) - X(\text{Anc}, i)| \dots (1)$$

Where : Txn=a taxon

i=the *i*th character of the taxon

The length of a line between a taxon and its ancestor is termed the "interval of the taxon" which is defined in no other way than by the equation (1) above and can be expressed also as below:

$$\text{Int}(\text{Txn}) = D[\text{Txn}, \text{Anc}(\text{Txn})]$$

Now we get the intervals of the taxa of each subfamily as follows:

$$D(\text{Od}, \text{H})=4, D(\text{B}, \text{H})=5, D(\text{F}, \text{H})=7, D(\text{P}, \text{H})=9, D(\text{N}, \text{H})=14, D(\text{C}, \text{H})=12$$

Where : Od=Odontellinae, B=Brachystomellinae, F=Frieseinae, P=Pseudachorutinae,

Table 4. Character matrix

Char. No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Taxon																				
Hypo.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Odon.	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Brach.	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	1	0	0	1	0
Fries.	0	0	1	1	0	1	1	0	1	0	1	0	0	1	0	1	0	0	0	0
Pseud.	1	0	1	0	0	1	1	0	1	0	1	0	0	1	1	1	0	0	1	0
Nean.	1	0	0	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	0
Capu.	1	0	0	0	1	1	1	0	1	1	1	0	0	1	1	1	1	0	1	1
"Ancestors"																				
X	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0
Y	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	1	0	0	0	0
Z	0	0	1	0	0	1	1	0	1	0	1	0	0	1	0	1	0	0	0	0
Q	1	0	1	0	0	1	1	0	1	0	1	0	0	1	1	1	0	0	1	0
R	1	0	0	0	1	1	1	0	1	0	1	0	0	1	1	1	1	0	1	0

N=Neanurinae, C=Capitanurinae, H=Hypogastruridae (out-group)

Because the Taxon Od. shows the least distance from taxon H, that is, 4, we connect Od to H to form the interval, Int(Od), as shown in Fig. 2a.

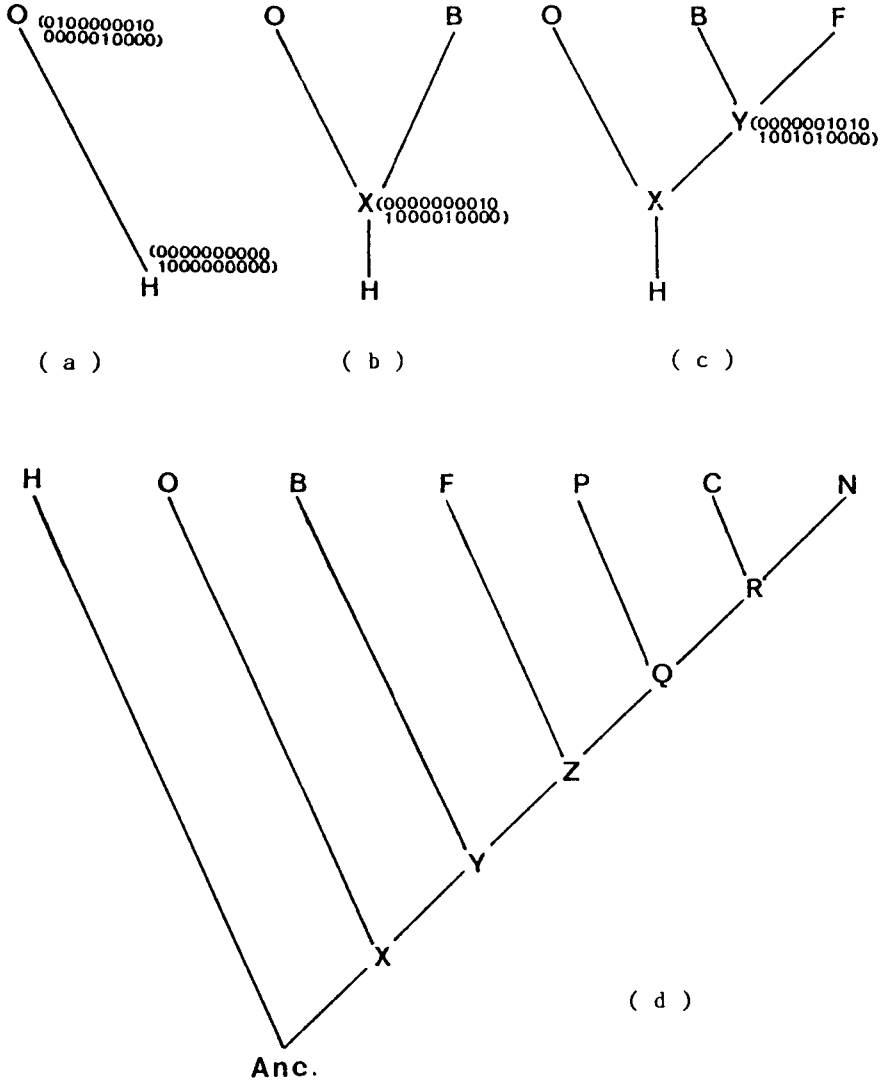


Fig. 2. Cladogram by Wagner algorithm of the character unweighted method.

Since the next short distance from taxon H is Int(B)=5 of Brachystomellinae we compute the character matrix of a new common ancestor of Od and B by taking the median of each transformation series of Od, H and B as below.

Taxon		Character Matrix																	
H	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Od	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
B	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	1	0	0	1
X (Med.)	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0

and it gives the next development of the cladogram like Fig. 2b.

Again, since the next short distance from taxon H was $\text{Int}(F)=7$ we take Frieseinae(F) and the distances between F and each of the remaining taxa are computed, excluding, however, the out-group, Hypogastruridae, using the following formula,

$$D(\text{Nxt Txx}, \text{Int Txn}) = \frac{D(\text{Nxt Txn}, \text{Txn}) + D[\text{Nxt Txn}, \text{Anc}(\text{Txn})] - D[\text{Txn}, \text{Anc}(\text{Txn})]}{2}$$

which gives the following results.

$$D[F, \text{Int}(\text{Od})] = \frac{7+5-2}{2} = 5, \quad D[F, \text{Int}(\text{B})] = \frac{4+5-3}{2} = 3, \quad D[F, \text{Int}(\text{X})] = \frac{5+7-2}{2} = 5$$

We find this time that the least difference is that of Brachystomellinae, 3, and, therefore, F is connected to $\text{Int}(\text{B})$. We need, however, then the character matrix of the hypothetical common ancestor "y" and get it by taking median from each transformation series of B, F and X, which, at length, gives rise to the series shown in the lower part of the Table 4, designated Y. This gives a new cladogram as in Fig. 2, c.

Next we repeat the process by taking P which showed earlier the next short distance, i.e., $\text{Int}(\text{P})=9$.

Finally we complete the cladogram covering the whole taxa in consideration, as shown in Fig. 2d.

DISCUSSIONS

The cladogram obtained by the character weighted method (Fig. 1) reveals that the branchings began with different states of mouthparts and those of chaetotaxy in the vertex (V_1 , V_2), and then a sensory organ in the mouth (maxillary palp), separating thus Hypogastruridae from Neanuridae, and Odontellinae from the remainder of neanurid subfamilies respectively. The maxillary palp in the state of plesiomorph (7^0) shared by both the out-group (Hypogastruridae) and Odontellinae of Neanuridae seems to suggest a close relationship of the two taxa, isolating thus the latter from all the remaining neanurid subfamilies. This viewpoint was so stressed by Deharveng that this character, with a few other characteristic features, led him to separate Odontellinae and create a new family, Odontellidae, postulating its origin arisen prior to hypogastrurid-neanurid lineage development (Deharveng, 1981). According to Massoud, however, Neanuridae is characterized by modified mouthparts with only a few exceptions (Massoud, 1967) and in addition to the absence of the state, V_1 and V_2 , in the vertex (Cassagnau, 1974), the modified mouthparts are very likely to justify the monophyly including Odontellinae as opposed to all other Collembola groups.

By contrast to this, different states of body shape (1) are found interposed among varying lineages and sister-groups, apparently suggesting parallelisms, as is certainly the case with Hypogastruridae and Frieseinae, or as part of mosaic evolutions prevailing among characters of weighting types I-III as will be referred to later.

Now we find that the mouthparts are decisive in developing two sister-groups of different polarity ($6^2, 6^3$) meanwhile Odontellinae and Brachystomellinae of different lineage are represented by the same character state, 6^1 , which may suggest another case of parallelism. The reason for the same character state assignment, however, for the latter two subfamilies, contrary to Deharveng's idea of separation (Deharveng, 1981) was that the two taxa are considered to be in the same trend of mandible reduction because some Odontellinae species are provided with a mandible only on one side. That is, they are unpaired and consequently, to a greater extent, consistent with Brachystomellinae in which mandibles are entirely lost on both sides. An over-all impression, therefore, is that the mouthparts underwent changes with three polarities: $6^1, 6^2$, and 6^3 .

When we see the directions of character trends of all weighting types we find that in Neanurinae and Caputanurinae the character trends of $1(1^2, 1^3)$, $10(10^0, 10^1)$, and $20(20^1, 20^2)$ are opposite to those of $4(4^1, 4^0)$, $8(8^1, 8^0)$, $12(12^1, 12^0)$ and $18(18^1, 18^0)$. A similar case is found between Brachystomellinae and Frieseinae by characters with $4(4^0, 4^1)$, $(6^1, 6^2)$ versus $1(1^1, 1^0)$, $19(19^1, 19^0)$ and this kind of contradicting trends are observed, more or less, in almost all combinations of any two taxa. These confusing situations are apparently due to mosaic evolutions. Between Neanurinae and Caputanurinae, in this connection, it is certainly the latter that is more evolved or specialized in the light of the unusual automorphic states in characters like 1, 10, and 20 among others. As regards the Neanurinae Fjellberg's recent study of dorsal chaetotaxy stating that the seta m_5 in Th. II - III are present in all Neanurinae while p_1 in Abd. I - IV is absent universally in the subfamily (Fjellberg, 1984) may serve additional supporting evidences of the monophyly of the taxon.

By using the Wagner algorithm for the character unweighted approach, on the other hand, we were able to obtain character matrices of hypothetical ancestors in all stages of cladogenesis, that is, in each branching point. The final cladograms (Fig. 2) depict the branching sequence of each taxon in such a way corresponding to an increasing order of intervals between respective taxa and the out-group, Hypogastruridae, obtained earlier in the computing process.

As compared to the cladogram from the character weighted method (Fig. 1) we see that the branching pattern of the character unweighted one (Fig. 2d) is not even comparable. A prominent similarity, however, is recognized in the order of taxa arrangement, except in the last two subfamilies, Neanurinae and Caputanurinae, which are reversed. This contradictory sequence is considered to have arisen from the accumulation of evolved states, coded "1", in Neanurinae against Caputanurinae, like 4, 8, 12, and 18, which is double in number that of the latter subfamily and reflected to the cladogram through the algorithmic computation. Meanwhile, it may also have come from undue character weighting by the second

method, not taking into account the meaning of extraordinarily specialized states of character, 1³, 10¹, and 20², which are exclusive autapomorphies of Caputanurinae not only among the neanurid family but also throughout Collembola order.

In spite of this partial difference, one thing to be emphasized is that Odontellinae is revealed to be closest to the out-group, Hypogastruridae, in both cladograms, leaving all other remaining neanurid subfamilies to the second branch of neanurid lineages, that is, as a sister-group of Odontellinae. This data may serve, in a way therefore, a partial base justifying the idea of independent lineage of Odontellinae as conceived by Deharveng (1981) although the rank of category to be assigned is a matter of opinion and remains to be elucidated by further works.

SUMMARY

An attempt was made to try cladistic analysis for six subfamilies of neanurid Collembola using a character weighted method by Schaeffer, Edwards and Hecht, and a character unweighted method using Wagner algorithm devised by Kluge and Farris. The former method involving determinations of transformation series, polarity, monophyly and sister-group, based on synapomorphies of higher weighting types has led to a cladogram in general agreement in taxa sequence with that of classical taxonomy, although the branching pattern produced was quite different and even uncomparable. As the first application of cladistics for Neanuridae this study also enabled the uncovering of various character states, "shuffled", presumably due to parallelism and mosaic evolution.

The cladogram was not comparable, however, with the results from a character unweighted approach in branching pattern, but the taxa arrangements were very similar, the only difference being in the sequence of the last two subfamilies, Neanurinae and Caputanurinae, which are reversed in the cladogram by the second method. This is supposed to have arisen either from the accumulation of characters in evolved state, coded "1", in Neanurinae against Caputanurinae, in the course of algorithmic computation, or from undue weighting of characters like Nos. 1, 10 and 20 which apparently, reflect great specializations and divergences undergone by Caputanurinae in the course of their invading new adaptive zone.

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