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WHAT MAKES THE FORMICINI THE FORMICINI?

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Summary:

The methods of modern systematics, especially pattern cladistics are discussed. Special emphases is placed on (1) the separation of pattern and process, (2) homology, and (3) the parsimony concept.

The tribe Formicini is given as an example. The synapomorphies of the tribe and the internal phylogeny are presented. The two major clades show different and opposing patterns of variation. *Cataglyphis* genus group is variable in male genitalia but shows rather uniform social organization; whereas *Formica* genus group shows uniform male genitalia and diverse social organization.

Key words: Systematics, Cladistics, Phylogeny, Formicini.

Résumé: Qu'est-ce qui fait que les Formicini sont les Formicini ?

Les méthodes de la systématique sont discutées, spécialement celle de la 'cladistique transformée'. Il est traité de façon plus approfondie (1) de la séparation des caractères et des processus, (2) de l'homologie, et (3) du critère de parcimonie.

La tribu des Formicini est donnée comme exemple. Les synapomorphies et la phylogénie de la tribu sont présentées. Les deux branches majeures montrent des modèles de variation différents et même opposés. Le groupe du genre *Cataglyphis* montre une grande variation des genitalia mâles, mais une organisation sociale uniforme; tandis que la groupe du genre *Formica* montre des genitalia mâles uniformes et une organisation sociale diversifiée.

Mots clés: Systématique, Cladistique, Phylogénie, Formicini.

"What makes ...?" has two different meanings. Firstly it can refer to the attributes which define a thing - how it is constituted. Secondly it can refer to the developmental process which leads to the construction of a thing - how it is produced. In systematics this division is represented by the distinction between pattern and process. In biology it is represented by the distinction between form and function or comparative and general biology (Nelson, 1970). In philosophical terms, it is the distinction between being and becoming. Neither 'way of seeing'

(Rieppel, 1988) is supreme, but there can be no function without form: A function is a change of structures i.e. a relation of two or more different structures has to be recognized or assumed before a change can directly be observed or inferred respectively.

Thus, to understand life, the first step is a description of structures or forms, independently of processes such as how they became into existence. This is of special importance in the study of bio-diversity in which the underlying processes (e.g. evolution) cannot be observed directly. Thus phylogeny can only be inferred from a system based on observable facts: i.e. such a system, for example a cladogram, can subsequently be explained by process theories i.e. evolution.

This thinking has led recently to an often misunderstood divorce in phylogenetic systematics between the old, now widely accepted 'Hennigian school' with the presumption of evolution and the 'pattern' or 'transformed Cladists' accepting evolution only as the most parsimonious explanation of the obtained cladogram, based on homologies and parsimony (see Beatty, 1982, Patterson, 1982a; Nelson, 1989a). Nevertheless, the exclusive use of special characters (homologies or synapomorphies) and parsimony led to major advances in systematics (e.g. Königsmann, 1978; Kristensen, 1981; Carpenter, 1982).

'Formicini' is the name of a tribe within the ant subfamily Formicinae ants. A tribe is a monophyletic group ranked below the subfamily level. There are no rules per se, how large a tribe has to be, some might include close to 2000 species as in the Camponotini, other may be monotypic, such as the Santschiellini. In the Code of Zoological Nomenclature, it is recommended that the suffix -ini be added to the name of a tribe and that a nominal taxon has to be fixed, which is also the name bearing type of its nominotypical taxon.

The actual chosen level in the hierarchy is due to the historical treatment of the group, but all the tribes should be monophyletic groups at an equivalent level within a cladogram throughout at least the respective family (in this example the Formicidae). All those requirements are arbitrary but the criterion of monophyly based on a rigorous procedure of discovery.

What is cladistics and what a monophyletic group? Cladistics is one of a number of competing approaches within systematics, including evolutionary systematics, phenetics and numerical taxonomy (Tab.1). All aim to provide the necessary reference system within biology, and to reflect to some extent the assumed phylogeny. The advantage of cladistics, especially pattern cladistics is, that it is not an authoritarian system: it is a procedure of discovery (Nelson, 1989b), which is logically consistent and independent of the case under study. It is based on the most parsimonious arrangements of homologies, resulting in a cladogram, and it is independent of process theories or explanations. Phylogeny

can be inferred by the so obtained cladogram or hierarchy of more or less inclusive monophyletic groups diagnosed by synapomorphies, and finally evolutionary theory can be used to explain the phylogenetic tree (see Janvier, 1984).

Tab.1. The relationships between pattern cladistics, phylogenetic systematics, phenetics and evolutionary systematics.

	Parsimony criterion	Homologies (Synapomorphies)	independence of process theory
Pattern Cladistics	+	+	+
Phylogenetic Systematics	+	+	-
Numerical Taxonomy, Phenetics	+	-	-
Evolutionary Systematics	-	-	-

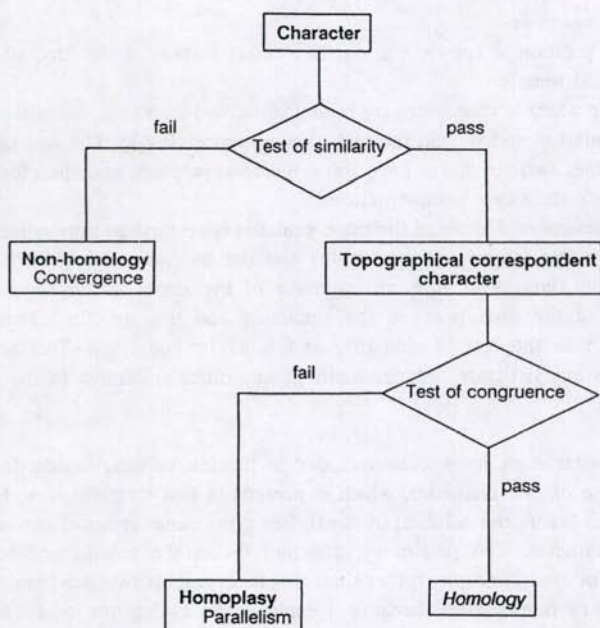


Fig. 1. The test of homology (after Patterson, 1982 and Rieppel, 1988, modified.).

A synapomorphy or homology is a relation expressed as one character which is as a homologue part of the respective related two organisms. Characters are defined parts of an organism. Their definition has to be done in the context of the whole organism. A character 'double row of bristles' as the character, only makes sense, if its position is known, e.g. on the ventral surface of the hind tibiae of the workers and females.

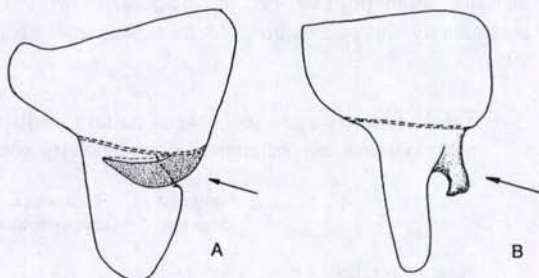


Fig. 2. Test of similarity: Two non-homologies (Convergences). Arrow indicating the median lobe: A: *Proformica*; B: *Cataglyphis* (for further explanation see text).

To decide whether characters are homologous, two tests must be passed, first the test of similarity and second the test of congruence (Fig.1). The test of similarity tests whether two structures have the same relative place and therefore whether they include the same basic structures.

In two genera of Formicini the male genitalia have median appendices between the outer valve (stipes and squamula) and the median valve (volsella) (Fig.2). Whereas in *Cataglyphis* it is an appendix of the stipes in *Proformica* it is an appendix of the area between the squamula and the volsella. Therefore, this character fails the test of similarity and is a non-homology. This test can be applied to any structure independently of any other structures in the respective organisms.

Different characters have to be included in the test of congruence. In the most simple case of one character, which is present in two terminal taxa, the test of congruence favors the solution of A+B, being the same group diagnosed by this special character. The parsimony criterium favors the solution of one special character or synapomorphy rather than that it represents two independent special characters or homoplasies, because it explains the cladogram in one and not in two steps (Fig.3).

A third test, the test of conjunction, may be added. This criterion tests whether two supposed homologues occur in the same organism: if wings and front limbs are considered as homologues then they should never be present in the same organisms, as they are in angels (= Homonymy) (Patterson, 1982b).

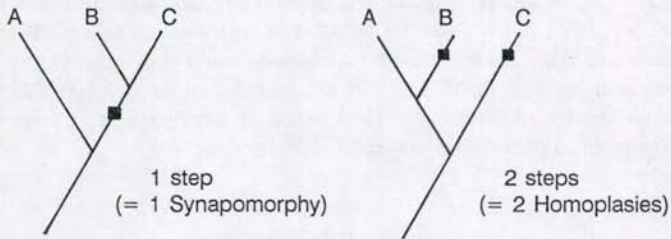


Fig. 3. Congruence. The same Character interpreted as synapomorphy or homoplasy.

Which characters can be included in this procedure? Almost any morphological characters are usable. Morphological characters sometimes show the tendency to be homoplasies, although they look overall similar, if they are not finely enough resolved. This case will be discovered by the test of congruence. For other characters, such as behavioral or molecular, it must be shown that the test of homology is applicable. In the case of molecular characters the test of parsimony is not congruence, as in morphological characters, but similarity (Patterson, 1988). There is no similar test for behavioral characters.

How many groups must be included in the test? As relationship are assumed to be universal and relative, a third group has to be included to work out the degree of relatedness (i.e. 'C is more related to A than to B').

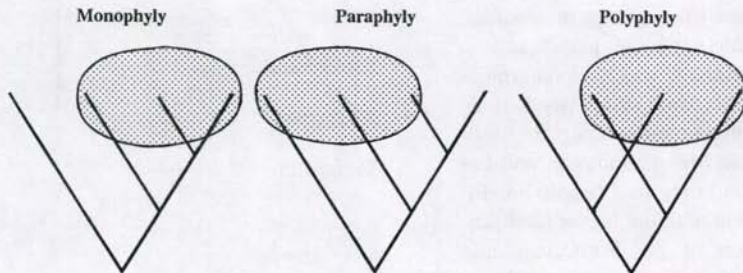


Fig. 4. The concepts of monophyly, paraphyly and polyphyly.

One of the important, even crucial outcomes of cladistics is the discovery of paraphyletic groups (Fig.4), groups (X) which include another group (A X) and therefore a sister group relation between (A) and (X \ A), the later is not diagnosable by synapomorphies and is therefore excluded from the cladogram (Nelson, 1989), but it might be included as a stemgroup in a phylogenetic tree (Janvier, 1984). To recognize homologies demands that we recognize the things being compared as organisms - with the homologues as their parts. Beyond that, the recognition of homologies (and hence of monophyletic groups) is directly comparable to discovering new species (Patterson, 1982b).

The tribe Formicini

The tribe Formicini is a monophyletic group in the subfamily Formicinae, including the seven genera *Formica*, *Polyergus*, *Rossomyrmex*, *Proformica*, *Alloformica*, *Cataglyphis* and an undescribed genus (Fig. 5.; Agosti, 1989; Agosti, in prep.). *Formica* and *Polyergus* have a holarctic distribution, all the remaining are palae-arctic. *Formica* includes approximately 150 species and *Cataglyphis* about 60 spp., the remaining genera have only a few species included. *Polyergus* and *Rossomyrmex* are obligate slavemakers on *Formica* spp. and *Proformica* spp. respectively. Wherever they occur they are among the dominant ant species in the particular ant communities.

The tribe Formicini is diagnosed by the following synapomorphies (Fig.4): A double row of bristles on the ventral side of the hind tibiae; a slit shaped propodeal spiraculum; the placement of the spiraculum close to the metanotum; and a double folded sagitta. Although the synapomorphies have been established using different outgroups (Camponotini, Melophorini p.p. and Lasini) they must remain provisional until the higher classification of the Formicinae and with it the polarity and the

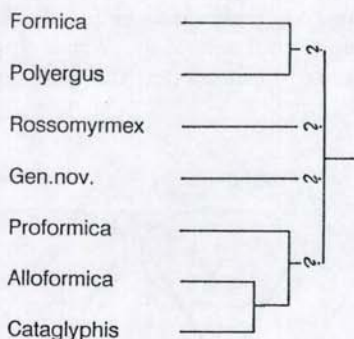


Fig. 5. The phylogeny of Formicinae (Agosti, 1989)

distribution of the characters are resolved.

Within the tribe, two main groups can be diagnosed: *Formica* genus group with *Formica* and *Polyergus* diagnosed by a cranial appendix of the subgenital plate, and the *Cataglyphis* genus group with *Cataglyphis*, *Proformica* and *Alloformica* with a caudally three lobed subgenital plate and a separation between the ergot and the dorsal end of the serrated face of the sagitta. No homologies of *Rossomyrmex* and the new genus with any other group have yet been established.

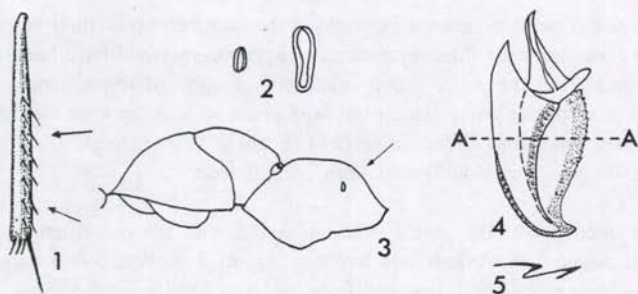


Fig. 6. The synapomorphies of Formicini: 1: double row of bristles on hind tibia; 2: slit shaped propodeal spiraculum; 3: position of the propodeal spiraculum; 4: double folded sagitta, A---A position of cross section; 5: cross section of sagitta.

An interesting phenomenon within the two large genera, *Formica* and *Cataglyphis*, can be observed: Whereas in *Formica* with over 150 spp. only very limited variation in the size of male genitalia occurs, those of *Cataglyphis* vary tremendously (Emery, 1906; Agosti, in prep.). Therefore it is easy to find homologies which allow to infer the phylogeny of this genus and consequently to define species groups. The question arises, why such variation occurs in one genus, whereas in the other large genus, *Formica*, there is hardly any morphological variation, but variation in social behavior, such as slave making or living in supercolonies.

Not all characters vary regularly, providing therefore are homologies at every level. Analysis of the variation of the subgenital plate provides for some groups (such as *Formica* + *Polyergus*, *Proformica* or the *C.bicolor*-group s.str.) synapomorphies or diagnostic characters, whereas for other groups (*Cataglyphis* and the *bicolor*-group s.lat.) they represent the plesiomorphic condition and therefore do not diagnose relationship.

The new genus includes two North African species, formerly placed in *Proformica* (Espadaler & Cagniant, 1987), and does not belong to any of the known genus-groups within Formicini and even Formicinae. Nevertheless it can be diagnosed by three of the four synapomorphies for the tribe. Any supposed relationship with *Proformica* is negated by the fact that of the four species analyzed so far do not have significant variation in their genitalia, although all those species have an allopatric distribution.

The social parasitic genera *Polyergus* is the sister group of their respective host genus *Formica* or for *Rossomyrmex* no synapomorphy could have been established to demonstrate the sister group relation; but none of those genera is a sister group of a species group within the host genus as it is the case for *Strongylognathus*, *Anergates* and *Teleutomyrmex* with their sister group, the *Tetramorium caespitum*-group, making *Tetramorium* paraphyletic.

The discovery of the gaster reflexion system and the construction of the first gastral segment in workers and females (Agosti & Bolton, 1990) suggests that a sister group relationship between Formicini and Lasiini is unlikely.

The claim of systematics to provide a reference system for biology is in this case still far from being fulfilled. Further studies will concentrate on the phylogeny of the whole subfamily Formicinae, which almost certainly represents a monophyletic group. Already preliminary results show that the general trend from an asepalous to a long sepalous proventriculus might have occurred several times (Eisner, 1956; Agosti, research in progress): for example, the anatomy of the proventriculi of *Camponotus* and *Formica* is different (Eisner, 1956).

Another, more urgent problem, is the question of species-groups and species within the particular genera. Whereas species-groups are a problem of systematics the description of species is the task of taxonomy. Unfortunately, the problem is not so clear-cut and there is a lot of confusion at this level, which has led to different solutions (compare the species concepts in e.g. Francoeur, 1973 and Agosti, 1989). This needs revisionary studies of the genera. To get closer to a solution of this question in groups with very few morphological characters as in *Formica*, one might include other techniques and characters, such as hydrocarbons of the cuticula, mandibular or other gland compounds or DNA-fingerprinting.

This might need new tests of homology, as Patterson (1988) has shown for molecular data, and raises the question whether there is a procedure for discovering species based on characters, analogous to cladistics.

References

- AGOSTI, D., 1989. Versuch einer phylogenetischen Wertung der Merkmale der Formicini (Hymenoptera, Formicidae), Revision der *Formica exsecta*-gruppe und Liste der Formicidae Europas. *Diss ETH*. No.8774.
- AGOSTI, D. & BOLTON, B., 1990. New Characters to separate *Formica* L. and *Lasius* Fabr.. *Entom.Gazette* (in press).
- BEATTY, J., 1982. Classes and Cladists. *Syst.Zool.* **31**: 25-34.
- CARPENTER, J.M., 1982. The phylogenetic Relationship and natural Classification of the Vespoidea (Hymenoptera). *Syst.Ent.* **7**: 11-38.
- EISNER, T., 1957. A comparative morphological Study of the Proventriculus of ants (Hymenoptera: Formicidae). *Bull.Mus.comp.Zool.Harv.* **116**: 439-490 + 25pls.
- EMERY, C., 1906. Rassegna critica delle specie paleartiche del genere *Myrmecocystus*. *Memorie R.Accad.Sic.Ist.Cl.Sci.fis.Bologna* (6), **V. 3**: 47-61.
- ESPADALER, X. & CAGNIANT, H., 1987. Contribution à la connaissance des fourmis marocaines. Description du mâle de *Proformica theryi* Santschi, 1936 (Hymenoptera, Formicidae) *Nouv.Revue Ent.(N.S.)* **4**: 133-138.
- FRANCOEUR, A., 1973. Révision taxonomique des espèces néarctique du group *fusca*, genre *Formica* (Formicidae, Hymenoptera). *Mem.Soc.Ent. Québec* **3**: 316pp.
- JANVIER, PH., 1984. Cladistics: Theory, Purpose, and evolutionary Implications. In POLLARD, J.W. (ed.), *Evolutionary Theory: Path into the Future*. pp. 39-75. John Wiley & Sons, Chichester, N.Y.
- KÖNIGSMANN, E., 1978. Das phylogenetische System der Hymenoptera. Teil 4: Aculeata (Unterordnung Apocrita). *Dtsch.Ent.Z.N.F.* **25**: 365-435.
- KRISTENSEN, N.P., 1981. Phylogeny of Insect Orders. *Ann.Rev.Entomol.* **26**: 135-157.
- NELSON, G., 1970. Outline of a Theory of Comparative Biology. *Syst.Zool.* **19**: 373-384.
- NELSON, G., 1989a. Species and Taxa: Systematics and Evolution. In OTTE & ENDLER, J.A. (eds.), *Speciation and its Consequences*. Sinauer Associates, Inc. Sunderland, Mass., pp. 60-81.
- NELSON, G., 1989b. Cladistics and evolutionary Models. *Cladistics* **5**: 275-289.
- PATTERSON, C., 1982a. Classes and Cladists or Individuals and Evolution. *Syst.Zool.* **31**: 284-286.
- PATTERSON, C., 1982b. Morphological Characters and Homology. In Joysey, K.A. & Friday, A.E. (eds.), *Problems of Phylogenetic Reconstruction*, pp. 21-74. London and New York: Academic Press.
- PATTERSON, C., 1988. Homology in Classical and Molecular Biology. *Mol.Biol.Evol.* **5**: 603-625.
- RIEPEL, O.C., 1988. *Fundamentals of Comparative Biology*. Birkhäuser Verlag, Basel, Boston. 202pp.