ALTERNATIVE MODELS OF CLASSIFICATION OF PARASITIC PSOCODEA: PHTHIRAPTERA

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With 3 figures

SOLBRIG (1966) writes in the introduction of his book entitled "Evolution and systematics": "... Understanding the world of organisms that surround us requires the ordering of the multitude of forms into some sort of rational system. Consequently, systematics is as old as man's guest for knowledge, and the effort to classify and understand the variability of animals and plants has led to the development of all the other branches of biology."

The goal of systematic investigations is groupings of species, i.e. their classification, which should correspond to real natural system. It is generally accepted that affinity of numerous characters indicates the relationships of organisms which they possess. On the other hand, if less characters of one species correspond to the other then both species are less related. This assumption hides a danger, that among chosen characters, some of them proving common genealogical stock of group species, are in fact convergent. Therefore, systematics is based on new methods in order to obtain possible credible results which are useful for proper interpretation. The application of different scientific methods, very often without elimination of subjectiveness in interpretation of data, resulted in divergent results. Even system of insects was in last years rebuilt and improved. One of the most interesting interpretations is HENNIG's (1969) system, graphically presented by LYAL (1985) (fig. 1). Among the pterygous insects the Neoptera is the group which is characterized mostly by the composition of wings along the body. It is opposite to Paleoptera (the May flies, Dragon flies and related fossil forms) which wings are placed on the side. On the other hand, the type of metamorphosis is a criterion of the division of the Neoptera into Holometabola (comprising about 88 % of all known species) and Polynoeoptera (= Paurometabola), defined also as Hemimetabola, i.e. the insects with so-called not full metamorphosis, in which all nymphal stages are similar to imagines. HENNIG thinks that the nearest phylogenetic line of Psocodea or sister-group, is the superorder Condylognatha comprising the orders Thysanoptera (thrips) and Hemiptera (bugs); whereas external group, lateral phylogenetic branch are Zoraptera (about 20 species living in termites' nests).

In the formulation of this idea two sister-groups, i.e. Psocoptera (= Copeognatha) and Pthiraptera, as the orders, would belong to the superorder Psocodea (= Pscooidae or Corrodentia).

Psocoptera (book lice, barklice) comprises about 1600 species distributed throughout the world; their body length ranges from 0.5 to 5.0 mm. They occurred already in the Permian like the Permospodica. Among present-living Psocoptera some species, e.g. Liposcelis divinatorius, have completely reduced wings (GÜNTHER 1974), and they have been found the most close the chewing lice. They are free-living insects (feed on fungi, fragments of plant and animal origin), though sometimes they inhibit bird or mammals' nests. However, all the species (about 5000) included, by many authors in Pthiraptera, are parasites. They are obligatory ectoparasites of birds and mammals. They all are secondarily wingless and feed on skin debris, dermal products, feathers, furs, sebaceous exudates or blood of their hosts.

The classification of Pthiraptera was presented in different ways. The controversy exists over various criteria of phylogenetic relationship and taxonomic rankings of four subordinate groups: Anoplura, Rhynchophthirina, Ischnocera and Amblycera. Anoplura (= Siphunculata) comprises about 500 species feeding exclusively on mammals' blood. Like all Pthiraptera they are dorsoventrally flattened. They are distinguished by a small head narrower than the thorax. The head in the Anoplura is prognathous, i.e. the mouth is moved anteriorly, and the clypeus forms the acute angle with the main body axis. Antennae are filiform in both sexes, most often five-segmented. The mouthparts are piercing-sucking. The compound eyes (oculi compositae) are reduced to single ommatidia or completely absent. The thorax with obliterated segmentation. Thick, strong legs are type-sticky adhesive, and the tarsi are terminated with single flexible claw, opposed to the prominent appendix of tibia; strongly attaching to hair. Abdominal segmentation is not evident, and the number of 9 segments may be determined by consecutive tergal plates.

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Fig. 1. Phylogeny and classification of the Nepomorpha according to EVOL (1998).

Fig. 2. Controversial systems of parasitic Psocodea according to a) BOUDREAU (1979), b) KIM & LUDWIG (1982), c) LVAL (1985).
The monophyly of Phthiraptera is not questioned. However, mutual relations between subordinated four groups: Anoplura (ANO), Rhynchophthiriphila (RHY), Ichneumonida (ISC) and Amblycera (AMB). Namely, BOUDREAU (1979) applying cladistic procedures of monophyly of taxa gives the names to all the groups. Instead of Phthiraptera he improves subchord Phthiraptera1 with the following synopsomorphies: dorsoventrally flattened body, complete reduction of wings, ocelli, highly reduced compound eyes and maxillae, the presence of one pair thoracic and usually six pairs abdominal spiracles. In this formulation Phthiraptera comprises two orders: Mallophaga, restricted to Amblycera, with developed maxillary palpi, and Anoplura without maxillary palpi. The last taxon is divided by BOUDREAU into two suborders (sister-groups) Ichneumonida and Lipoptenida with also two infrarorders: Rhyhophthiriphila and Siphunculata (fig. 2).

LYAL (1985) also accepts monophyly of groups, but he refuses the names improved by BOUDREAU. He also negates KIM'S and LUDWIG'S (1982) point of view presented the „Mallophaga” as monophyletic. He states, at the same time, that opinions of the authors, mentioned above, may rather cause further confusion of the system than its clarification. Thus, according to LYAL (1985) Anoplura and Rhynchophthiriphila would form, within Phthiraptera, monophyletic group, as a sister-group for Ichneumonida. In turn, Amblycera is a sister-group of all taxa (ANO + RHY + ISC). Certainly, superior taxa — Psocodea and Phthiraptera, according to LYAL, are also sister-groups (fig. 3).

1 The name was created on the base term of Phthiraptera. BOUDREAU (1999) uses, probably unintended emendation „Phthiraptera", and LLYAL (1985) referring to BOUDREAU - „Phthiraptera".

LYAL proves the monophyly of the Phthiraptera by 25 features. Comparing Lipsodeae and Phthiraptera characters, he accepts them as sister-groups, and the Psocodea, as a whole, as parphyletic with respect to the Phthiraptera. This is an alternative hypothesis in relation to KIM'S and LUDWIG'S (1982) concept, according to which Psocodea (Psocodea with Pernoposca + Phthiraptera) is a monophyletic group. In their opinion taxa RHY + ISC is a sister-group of the Amblycera, and RHY + ISC + AMB, forming the order of Mallophaga to Anoplura; consequently the Psocodea would be a sister-group of those four taxa together. In the authors' opinion, Anoplura is neither related to the Ichneumonida, to the Rhynchoptiririphila, but many similarities result from parallel evolution. This idea, as well as EMMERSON'S (1982) view that the order Mallophaga comprises three suborders: Amblycera, Ichneumonida and Rhychoptiririphila seems to be valid, despite different views of some cladists.

Uniformity of most opinions concerns the community of ancestors of Phthiraptera, i.e. Prothoririphila. It is supposed that there were nidiocoles inhabiting, during a whole life, the nests of birds and mammals, feeding or different organic matter or microorganisms, o.g. fungi occurring there. Gradual adaptation to new habitat (birds' feathers, mammal's hair and body surface) caused considerable modifications of head, thorax, legs, sense organs structures, as well as affected reproduction. The Phthiraptera reaches the highest obligate type of parasitism, being highly specific against hosts.

The beginning of parasitism of nidiocoles Psocodea, therefore the origin of Phthiraptera is differently placed in time. The lack of fossil materials makes the investigators put the hypotheses based on present relations in parasitic-host relations, also in respect to zoographical. The knowledge of phylogeny and the evolution of present hosts is advantageous. It assumes that mammal nests and hair were available for Protophthiriphila from the mid and late Triassic, and birds’ feathers (Archaeopteryx) from the mid Jurassic. KIM & LUDWIG (1982) state, that Phthiraptera could originate already in Upper Carboniferous, i.e. about 300 million years ago. Systematic discrepancy and exploitation of respective host groups followed on doubtlessly later. So, for example TRAUHL (1991) considers that Anoplura were associated with rodents in the Palaeocene (about 60 million years ago).

After this short review of the latest attempt to classify Phthiraptera, it is worth to think over what kind of progress they contribute to the improvement of the system which has been already modified and transformed. First of all, the results obtained by scientists (90 years) should be reviewed from the point of view of applied methods. For a long time cladistic methods have dominated in animal systematics, though not necessarily in the form such as that of HEINIGG's (1966). Formation of genealogical tree of sister groups, according to which pleiomorphic and apomorphic characters is fundamentally convergent with traditional methods of constructing the phylogenetic tree using the conception of the concept of specialized species (or characters). That is why, EICHLER (1991) considered that two groups (which presently we would call „sister-groups”) Psocodea and Phthiraptera, according to the Rhynchoptiririphila, this dichotomy is not preserved in the classification of lower systematic units either by EICHLER (1941) or CLAY (1974). Those authors divide the order Phthiraptera into three suborders: Rhycoptiririphila, Mallophaga and Anoplura. However, later EICHLER (1985) accepted, in general, KÖNIGSMANN's (1960) view, according to which, there are on the same evolutionary surface Amblycera, Anoplura, Ichneumonida and Rhychoptiririphila, as the suborders of the Phthiraptera. HAAB (1980) stays in opposition to KIM'S and LUDWIG'S (1978) view which anyway were more recently reported by the same authors in 1982. HAAB, states that in phylogenetic process the reduction of structures is not less important guide than the acquisition of new characters.

However, every possible relation between the groups in linear expression is not clear. There have been attempts to solve this problem by the cladistic methods depending on characters’ choice and decision which of them are pleiomorphic or apomorphic. This may lead to different final results. Here is the point of the controversy in the cladists’ idea, e.g. KIM & LUDWIG (1982) as well as LLYAL (1985). The cladists employ comparatively not a great number of characters, so their selection depends on many existing characters that should be regarded as particularly important. Because of it, the choice of characters is always loaded with subjectivism, in the case when within the same species (consequently in comprehensive units) both ancient (pleiomorphic) and later acquired characters (apomorphic) often occur. For example, in the biting lice from the genus Senuchopteryx asymmetric and complicated in outline clypea’s sclerization should be treated as specified apomorphic character. On the other hand, properly developed two-segmented labial pulpi (ZLOTORZYCKA 1984) should be recognized as ancient characters (pleiomorphic). Then correct cladogram is based on the foundation (more difficult to prove), that the set of groups considered is monophyletic. Giving opinions in this manner „ex cathedra”, it is partly risky. In case of the parasites in which adaptive abilities, e.g. to specific feathers type, the temperature of host body, etc. do
not facilitate the scientific workers' decisions; which similarities should be recognized as homologous and which not. That's the reason why the cladists want to limit themselves to the study of characters (in their opinion) if possible unquestionable, giving evidence of the common genesis of considered the species or their groups. Therefore, only not numerous characters are useful for them.

In the presence of all the difficulties, and insufficient or the lack of knowledge about (fossil) ancestors of present living organisms, cladistic methods most certainly solving systematic problems in an elegant way, are not accepted by all authors. EICHLER (1978) says that cladistics, as a method, may be useful in the systematics, but on condition that the results obtained in this way will be verified by the evolutionary method. The author means traditional morphological studies. However, we know that morphologist's interpretation depends on his/her approach to the problem. And here logical mistakes in.

In our opinion, one is not allowed to verify either a posteriori, or a priori the results obtained by "bei-
ter" (more objective) methods using the methods leading to "worse" (more subjective) results. Contrary, a better method can test the credibility of the results obtained with a worse method. Later, EICHLER stresses that calling cladistic analyses as "objective in the cladistic systematics" in misunderstanding because the cladograms reflect only genealogical relationships. That critique however, does not explain why evolutionary methods without paleontological data, could be better. Another systematic school, opposite to HENNIG's phylodynamics, is phenetic analysis, improved by SNEATH & SOKAL (1973). This method leads to obtaining of the phenograms visually similar to the cladograms, thus preserving the dichotomy of divi-
sion into species groups. The fundamental difference is here computer ordering of possible numerous characters equally weighing the advocates of that method insisted on drawing simple conclusions, treating the results obtained as status quo of determined segment of organic world. Equal weighing of all the characters is necessary for organic world. Thus, like units are not objectively selected, the mean of allocation, makes the results objective to a high degree. We will not con-
centrate on that method, because the classification of the Phylidiacea was elaborated in this way. Up to now, phenetic methods have served partial elaborations of the group, namely to study systematic relationships within the genus Strigophlaeus (Ricinidae) (LONC 1990). In the latter paper, the author proved that having the same data matrix it is possible to obtain, using different procedures, not wholly congruent phenograms or dendrograms. What one can to do, is to evaluate the efficiency of the different methods, so that the cladist can get to a better way of thinking.

EICHLER, W. (1978): Kritische Einwände gegen die Hen-


Buchbesprechung

COMBES, C. (Hrsg.; 1988): L'adaptation [Die Anpassung]. – Paris (Verl. „Pour la Science“); geb.; 216 S., reichlich illustriert. – Wo heutzutage sogar z.T. die Anpassung überhaupt in Frage gestellt wird, da macht es direkter Spaß, ein solches vorzüglich farbgebildetes Sammelwerk von solide untermauerten Beiträgen der verschiedensten Anpassungsbeispielen in die Hand zu nehmen. Das sehr ausführliche Vorwort des als Schistosomenforscher renommierten Herausgebers läßt z.T. philosophische Züge erkennen. Anschließend werden behandelt: Fische der Antarktis (Kälteanpassung); die Brachiopoden; die Weddellrobben (Tauchtiefe); Schmetterlinge als Ingenieure; Thermoregulation überwinternder Schmetterlinge; Vogelzug; Mechanismus der Fischschwärme; Tonverständigung der Grillen; Erkennung bei Kaulquappen; Partnerwahl bei Laubenvögeln; Geruchserkennung der Mäuse; Beutefinden beim Sandskorpion; Infrarotempfang bei Schlangen; Tonorientierung der Eulen; Chemische Waffen der Nasutitermiten; Fluchtsystem der Schaben; Tarnung bei Krabben; Mimetik der Sexualsignale von Leuchtkäfern; das Favorisationsprinzip des Parasitismus (von COMBES selbst ausführlich diskutiert); die Biochemie der Malariaresistenz (Drepanozytose und Thalassämie); Schistosomen; Sacculina; Parasitimus und Genetik im Reich der Insekten (Parasitoide). Der parasitologische Teil umfaßt etwa 16% des Umfangs. Als Parasitologe hätte ich persönlich mir vielleicht auch noch die Hirnwurmgeschichte gewünscht – aber es sind genügend andere beeindruckende parasitologische Beispiele enthalten. S. 214 ein Druckfehler: Frans statt Franz HUBER; sonst ist der Bildband in jeder Hinsicht prächtig ausgestattet.

Wd. EICHLER (Berlin).