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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 posses. 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 Polyneoptera (= 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 Phthiraptera, as the orders, would belong to the superorder Psocodea (= Psocoidea 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 Permopsocida. Among present-living Psocoptera some species, e.g. Liposcelus 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 Phthiraptera, 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 Phthiraptera was presented in differend 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 Phthiraptera 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.

Rhynchophthirina was created only on the base of

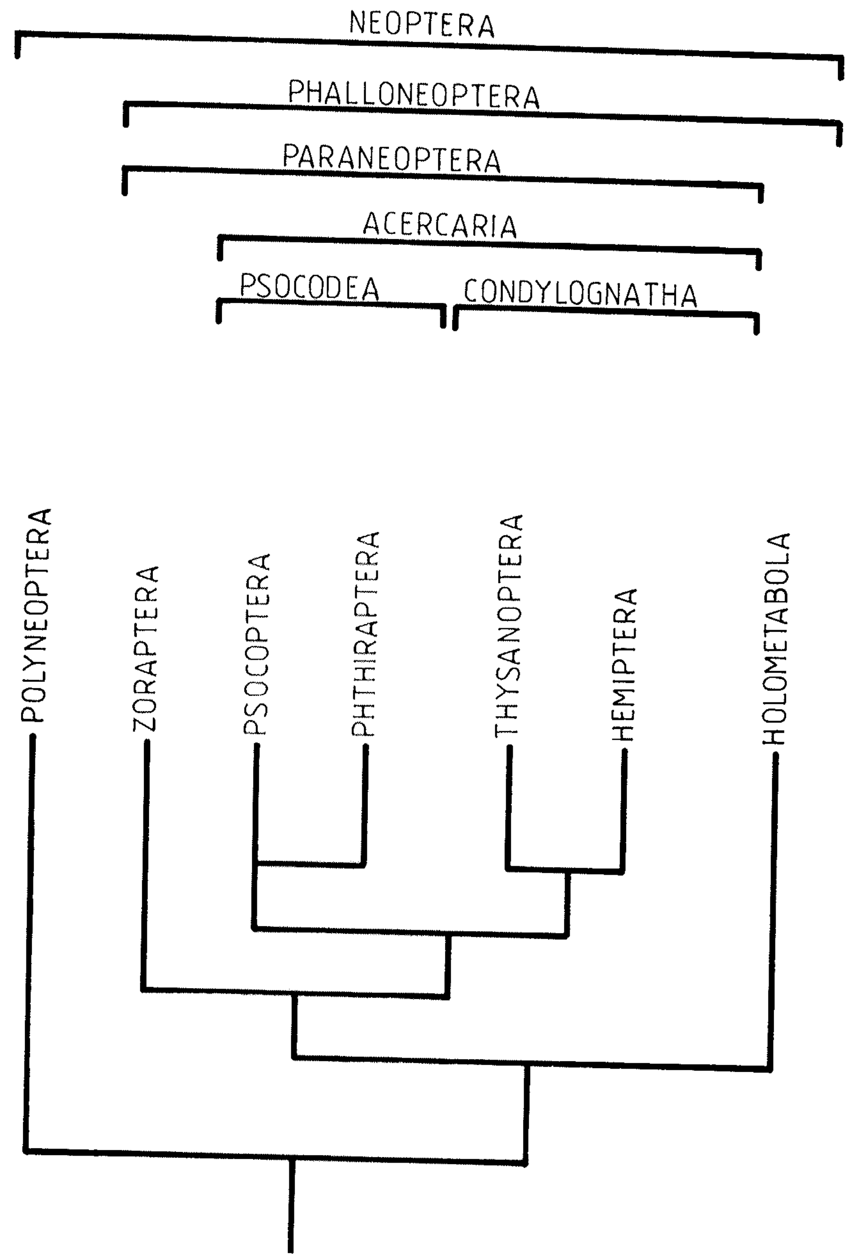

Fig. 1. Phylogeny and classification of the Neoptera according to LYAL (1985).

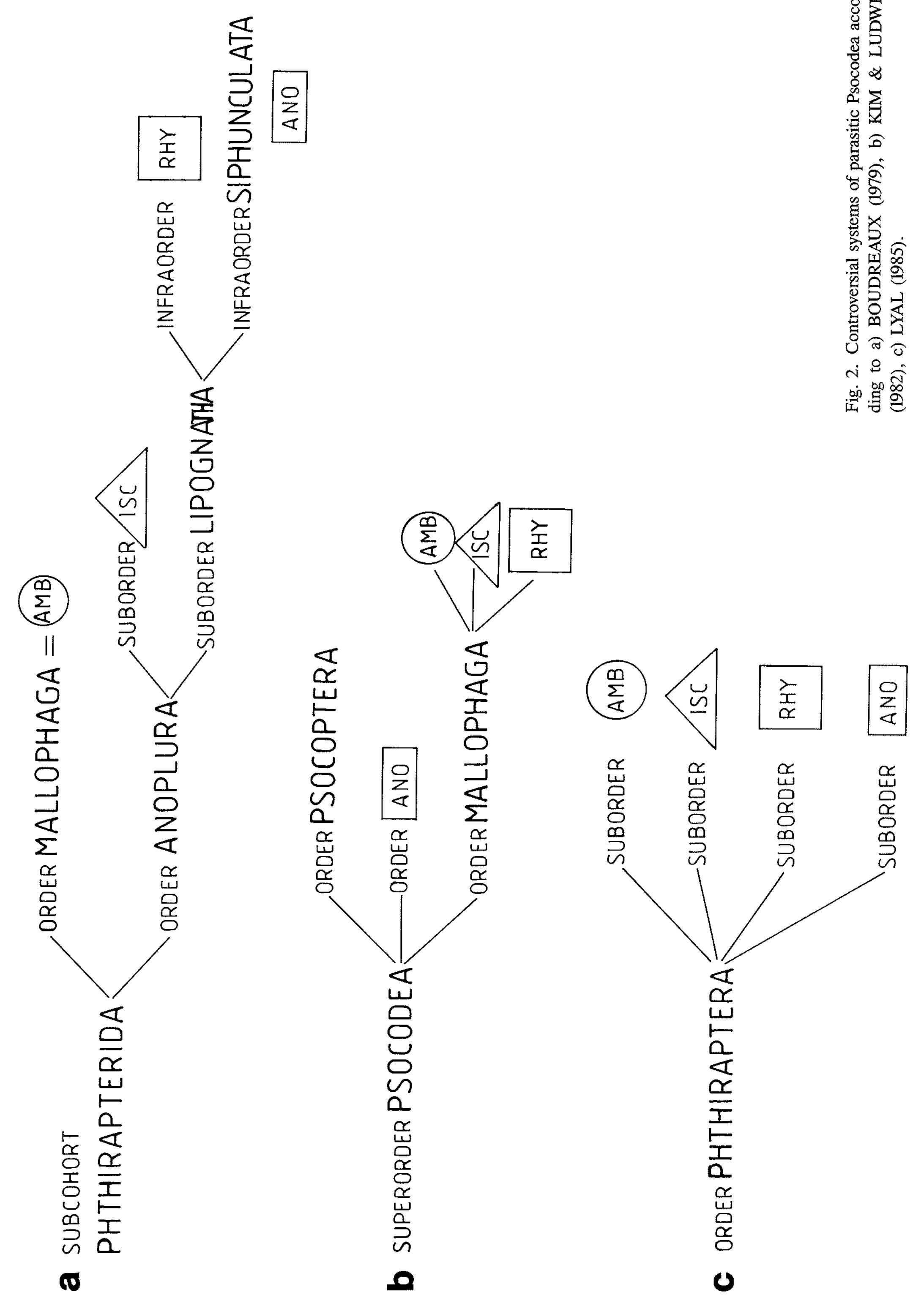

Fig. 2. Controversial systems of parasitic Psocodea according to a) BOUDREAUX (1979), b) KIM & LUDWIG (1982), c) LYAL (1985).

a single specimen of *Haematomyzus elephantis* PIAGET, a parasite of the African (*Loxodonta africana*) and Asiatic Elephant (*Elephas maximus*). Later, CLAY (1963) described *Haematomyzus hopkinsi* from the Ward Hog (*Phacochoerus aethiopicus*, Suidae) in Kenya and Uganda, and more recently EMERSON & PRICE (1988) – *H. porci* from the Bush Pig (*Phacochoerus porcus*) in Ethiopia. Similarly, like in the Anoplura, the head is prognathic, but the clypeus forms long rostrum terminated with small comb-shaped mandibles. They are pointed laterally outside. At the base of rostrum filiform five-segmented antennae arise.

However, the Mallophaga (Ischnocera + Amblycera) is characterized by the head wider than thorax and orthognathy type, i.e. the mouth is displaced onto ventral side. The type of mouthpart is chewing. In the Ischnocera, the mandible are strong, and they have primitive structure; the maxillary palpi were completely reduced. The antennae, usually 5-, rarely 3- or 4-segmented, arise from lateral margins of head. They are either equal, filiform in both sexes or the first three segments have heteromorphic structure in the males. The mesothorax and metathorax form compact pterothorax. In the Amblycera, the mandible are weaker or differently modified. Besides, there are four-segmented maxillary palpi present. The antennae 4- or 5-segmented, capitate, equal in both sexes, at least partly located in antennal fossae. The thorax consists of three segments, always on the dorsal side, separated from each other.

The monophyly of Phthiraptera is not questioned: However, mutual relations between subordinated four groups: Anoplura (ANO), Rhynchophthirina (RHY), Ischnocera (ISC) and Amblycera (AMB). Namely, BOUDREAUX (1979), applying cladistic postulate of monophyly of taxa gives the names to all the groups. Instead of Phthiraptera he improves subcohort Phthirapterida[1] with the following synapomorphies: 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 Phthirapterida comprises two orders: Mallophaga, restricted to Amblycera, with developed maxillary palpi, and Anoplura without maxillary palpi. The last taxon is divided by BOUDREAUX into two suborders (= sister-groups) Ischnocera and Lipognatha with also two infraorders: Rhynchophthirina and Siphunculata (fig. 2).

LYAL (1985) also accepts monophyly of groups, but he refuses the names improved by BOUDREAUX. He also negates KIM's and LUDWIG's (1982) point of view presenting the „Mallophaga" taxon 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, accordings to LYAL (1985) Anoplura and Rhynchophthirina would form, within Phthiraptera, monophyletic group, as a sister-group for Ischnocera. 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. BOUDREAUX (1979) uses, probably unintended emendation „Phthriapterida", and LYAL (1985) refering to BOUDREAUX – „Phthiriapterida".

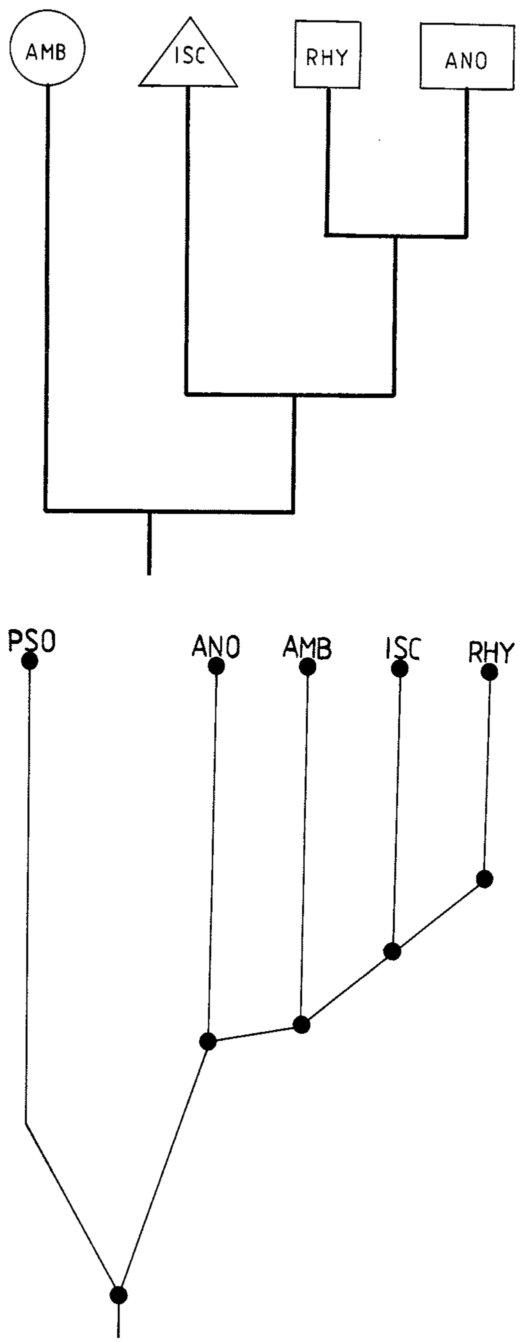

Fig. 3. Cladograms of a) Phthiraptera according to LYAL (1985), b) Psocodea according to KIM & LUDWIG (1982).

LYAL proves the monophyly of the Phthiraptera by 23 features. Comparing Liposcelidae and Phthiraptera characters, he accepts them as sister-groups, and the Psocoptera, as a whole, as paraphyletic with respect to the Phthiraptera. This is an alternative hypothesis in relation to KIM's and LUDWIG's (1982) conception according to which Psocodea (Psocoptera with Permopsocida + 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 Psocoptera would be a sister-group of those four taxa together. In the authors' opinion, Anoplura is neither related to the Ischnocera, nor to the Rhynchophthirina, but many similarities result from parallel evolution. This idea, as well as EMERSON's (1982) view that the order Mallophaga comprises three suborders: Amblycera, Ischnocera and Rhynchophthirina seems to be valid, despite different views of some cladists.

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

The beginning of parasitism of nidicolous Psocoptera, 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 parasite-host relationships, also in respect to zoogeographic. The knowledge of phylogenesis and the evolution of present hosts is advantageous. It assumes that mammal nests and hair were available for Protophthiraptera from the mid and late Triassic, ande birds' feathers (*Archaeopteryx*) from the mid Jurassic. KIM & LUDWIG (1982) state, that Phthiraptera could originate already in Upper Carboniferous, i.e. about 300 mln years ago. Systematic divergency and exploitation of respective host groups followed undoubtedly later. So, for example TRAUB (1980) considers that Anoplura were associated with rodents in the Palaeocene (about 60 mln years ago).

After this short review of the latest attempts 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 for many years should be revised from the point of view of applied methods. For a long time cladistic methods have dominated in animal systematics, though not necessecarily in the form such as that of HENNIG's (1966). Formation of genealogical tree of sister-groups of organisms based on plesiomorphic and apomorphic characters is fundamentally convergent with traditional methods of constructing the phylogenetic tree using the conceptions of primitive species (or characters) and specialized species (or characters). That is why, EICHLER (1941) considered that two groups (which presently we would call „sister-groups") Psocoptera and Phthiraptera come from Psocoidea. 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: Rhynchophthirina, Mallophaga and Anoplura. However, later EICHLER (1963) accepted, in general, KÖNIGSMANN's (1960) view, according to which, there are on the same evolutionary surface Amblycera, Anoplura, Ischnocera and Rhynchophthirina, as the suborders of the Phthiraptera. HAUB (1980) stays in opposition to KIM's and LUDWIG's (1978) view which anyway were more precisely reported by the same authors in 1982. HAUB, states that in phylogenetic process the reduction of structures is not less important guide than the acquirement 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 plesiomorphic 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 LYAL (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 bis subjectivism, in the case when within the same species (consequently in comprehensive units) both ancient (plesiomorphic) and later acquired characters (apomorphic) often occur. For example, in the biting lice from the genus *Struthiolipeurus* asymmetric and complicated in outline clypeus' sclerotization should be treated as specilized apomorphic character. On the other hand, proper developed two-segmented labial palpi (ZŁOTORZYCKA 1984) should be recognized as ancient characters (plesiomorphic). Then correct cladogram is based on the foundation (more difficult to prove), that the set of groups considered is monophyletic. Giving opinions in this matter „ex cathedra", is, particularly, risky. In case of the parasites in which adaptative 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 do 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 common (fossil) ancestors of present living organisms, cladistic methods, though 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 mistake is. In our opinion, one is not allowed to verify either a posteriori, or a priori the results obtained by „better“ (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 „phylogenetic systematics“ is misunderstanding, because the cladograms reflect only genealogical relationships. That critigue however, does not explain why evolutionary methods without palaeontological help, could be better.

Another systematic school, opposite to HENNIG's phylosophy, 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 division into species groups. The fundamental difference is here computer ordering of possible numerous characters equally weighting. The advocates of that method renounce drawing simple conclusions, treating the results obtained as status quo of determined segment of organic world. Equal weighting of all the characters is necessary for transformation data. Though their unit values are not objectively selected, the mean of allocation, makes the results objective to a high degree. We will not concentrate on that method, because the classification of the Phthiraptera was not elaborated in this way. Up to now, phenetic methods have served partial elaborations of the group, namely to study systematic relationships within the genus *Strigiphilus* (Philopteridae) (LONC 1989) and *Ricinus* (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 wholy congruent phenograms or dendrograms. What one can to then. Does one choose „the best solution“, i.e. the results most congruent with the earlier results of cladistic analysis, or those based on traditional morpho-evolutionary studies? But, the problem of logical mistake, mentioned above, returns again. That's why, we should look at the problem from another point of view. If we conceive, e.g. phylogenetic tree of animal groups or only the relations between species groups not as the effect of linear events, projected in one plane, but in many spaces, in mathematical sense, we could see that multidimension in various phenetic variants. Then, the discussion is useless. It is only possible to estimate which plane in the best way (for authors of course) show the similarity and differences within the species groups examined.

Thus, there is not the classification system fully objective and perfect, and perhaps it can't be, but multidimension of the relationships between organisms cause that natural system of animals is in the same way as unimaginable for us, as the construction in n-dimensional space.

Summary

Three systems of Phthiraptera, according to BOUDREAUX, KIM and LUDWIG as well as LYAL, based on cladistic rules were discussed. It has been denoted that cladistic methods can lead to positive taxonomic settlements when the division into plesiomorphic and apomorphic characters is correct. However, that is charged by the subjectiveness from many reasons. The most objective results in taxonomy can be obtained by using phenetic (numerical) analysis of all equally weighted characters. It comes to conclusion that credibility one of many classification conceptions of the same group, e. g. Phthiraptera may be regularly conducted when systems charged by subjectiveness will be compared with classification based on data elaborated in more objective way.

Zusammenfassung

Alternative Klassifikationsmodelle bei den parasitischen Psocodea (Phthiraptera). Nach modernen Klassifikationsmethoden werden auf der Basis des Hennigschen Systems der höheren Insektengruppen (Pterygota) drei kladistische Gliederungen der Tierläuse (Phthiraptera) diskutiert.

BOUDREAUX führt, nach strengkladistischen Prinzipien über monophyletische Abstammung, den Terminus Phthirapterida als Subkohort mit zwei Ordnungen ein: Mallophaga mit palpi maxillares (nach anderen Authoren = Amblycera) und Anoplura ohne palpi maxillares. Weiterhin untergliedert er die Anoplura in zwei Unterordnungen: Ischnocera und Lipognatha. Die Lipognatha umfassen die Infraordnungen Rhynchophthirina und Siphunculata. LYAL ist derselben Meinung wie BOUDREAUX, daß alle diese Gruppen monophyletisch sind, doch akzeptiert er keine

neuen Termini. Er verneint auch KIMs und LUDWIGs Ansicht, daß Ischnocera + Rhynchophthirina eine monophyletische Gruppe bilden. Nach LYAL sind innerhalb der Ordnung Phthiraptera Anoplura und Rhynchophthirina monophyletisch, während die Ischnocera ihre Schwestergruppe bildet. In seinem System sind die Amblycera die Schwestergruppe der Anoplura + Rhynchophthirina + Ischnocera. Damit gibt LYAL eine alternative Hypothese zur Konzeption von KIM und LUDWIG, daß die Psocodea, umfassend Psocoptera mit Permopsocida + Phthiraptera, eine monophyletische Gruppe bilden. Nach ihrer Auffassung bilden die Rhynchophthirina + Ischnocera die Schwestergruppe der Amblycera und Amblycera + Ischnocera + Rhynchophthirina die Ordnung Mallophaga. Diese wäre die Schwestergruppe der Anoplura. Auch EMERSON teilt diese Ansicht, wenn er die Unterordnungen Amblycera, Ischnocera und Rhynchophthirina in der Ordnung Mallophaga zusammenfaßt.

Bei der kritischen Diskussion der vorgestellten Konzeptionen, auch in bezug auf die älteren Klassifikationssysteme, möchten wir darauf hinweisen, daß der Erfolg der kladistischen Analyse von der Entscheidung abhängig ist, welche Merkmale der zu erforschenden Gruppe plesiomorph und welche apomorph sein sollen. Aus verschiedenen Gründen können solche Entscheidungen subjektiv sein, obwohl die Kladisten die Merkmale, welche zur Konstruktion des Kladogramms nützlich sind, sehr vorsichtig wählen. Ferner ist bemerkenswert, daß die traditionelle morphologische Klassifikation nicht weniger subjektiv ist als die kladistische. Verhältnismäßig objektive Ergebnisse soll die phänetische (numerische) Analyse bringen, die auf mehreren Merkmalen basiert. Diese Methode betrachtet alle Merkmale gleichwertig und erlaubt verschiedene Prozeduren. Auch mit derselben Merkmalsmenge bekommen wir im Resultat ungleiche Phänogramme. Unserer Meinung nach zeugt dies nicht für die Schwäche der numerischen Taxonomie, sondern für die vielseitigen Abhängigkeiten zwischen den Organismen, so daß unser Tiersystem mit einer Konstruktion im n-dimensionalen Raum zu vergleichen ist, welche von jeder Seite anders aussieht.

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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 direkt Spaß, ein solches vorzüglich farbbebildertes 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 Nasuti-Termiten; 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).