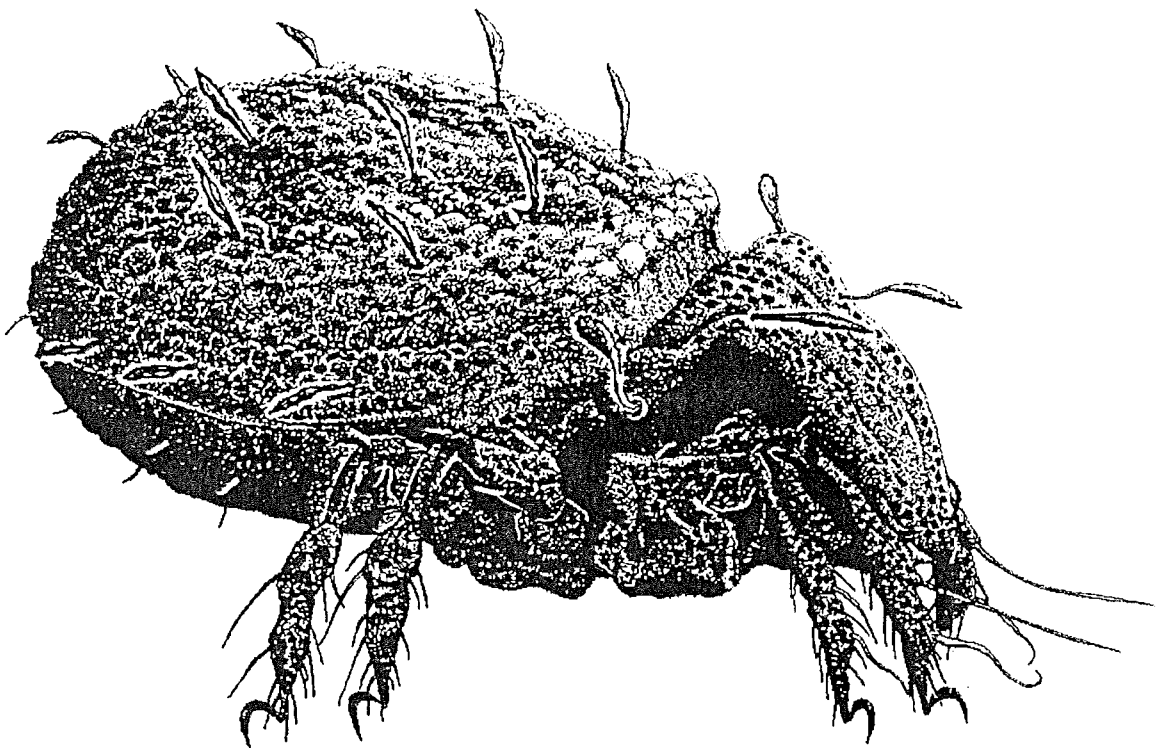


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PHYLOGENY AND HOST-PARASITE RELATIONSHIPS OF THE MITE FAMILY
HARPIRHYNCHIDAE (ACARI, PROSTIGMATA)

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ФИЛОГЕНИЯ И ПАРАЗИТО-ХОЗЯИННЫЕ СВЯЗИ КЛЕЩЕЙ СЕМЕЙСТВА
HARPIRHYNCHIDAE (ACARI, PROSTIGMATA)

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Key words: Harpirhynchinae, Harpypalpinae, Ophioptinae, phylogeny, host-parasite relationships

Ключевые слова: Harpirhynchinae, Harpypalpinae, Ophioptinae, филогения, паразито-хозяйинные связи

ABSTRACT

The Reconstruction of phylogeny of the mite family Harpirhynchidae, the permanent parasites of birds, was made by the cladistic method with the software PAUP 3.0s. The cladistic analysis included the closely related family Ophioptidae, permanent parasites of the Colubridae and Elapidae snakes. Representatives of all 14 genera have been examined. The predatory mite family Cheyletidae was used as the outgroup. The analysis was based on 84 morphological characters.

Single obtained cladogram includes two general clusters. One of them comprises the subfamily Harpypalpinae and the family Ophioptidae, the second cluster is represented by the subfamily Harpirhynchinae.

The node uniting the taxa Harpirhynchinae, Harpypalpinae and Ophioptidae is marked by 9 synapomorphies. Some of these apomorphies also occur in other parasitic mite families of the Cheyletoidea, however the structure of the palps in these 3 taxa is unique, and proves the monophyly of this group. Therefore we include the Ophioptidae into the family Harpirhynchidae as a subfamily.

The cluster of the subfamily Harpirhynchinae includes 6 generic groups: 3 groups are represented by 1 genus each (*Harpirhynchus*, *Harpyrhynchoides* and *Perharpyrhynchus*), 2 groups include each a pair of genera — *Metharpyrhynchus* and *Neharpyrhynchus*, *Anharpyrhynchus* and *Trichorhynchiella*, and one group includes 3 genera *Ralliharpyrhynchus*, *Harpyrhynchiella*, and *Cypsharpyrhynchus*.

Based on the obtained cladogram two hypotheses of harpirhynchid mite evolution are discussed. The most probable hypothesis it suggests, that ancestors of the Harpirhynchidae had become parasites on some ancestor of birds and coevolved with these hosts. The ancestor of Ophioptinae probably migrated from birds onto the snakes.

РЕЗЮМЕ

Реконструкция филогении клещей семейства Harpirhynchidae, постоянных паразитов

птиц, была проведена кладистическим методом с использованием компьютерной программы PAUP 3.0s. В кладистический анализ были включены представители близкородственного семейства Ophioptidae, представленного постоянными паразитами змей семейств Colubridae и Elapidae. Были исследованы представители всех 14 родов. В качестве внешней группы были использованы хищные клещи семейства Cheyletidae. Анализ был основан на 84 внешне-морфологических признаках.

Единственное полученное древо состоит из двух основных кластеров. Один из них включает подсемейства Harpypalpinae и семейство Ophioptidae, второй — подсемейство Harpirhynchinae.

Ветвь, объединяющая представителей Harpirhynchinae, Harpypalpinae и Ophioptidae, маркирована 9 синапоморфиями. Некоторые из этих апоморфий встречаются у других паразитических клещей надсемейства Cheyletoidea, однако строение пальп у этих 3 таксонов клещей уникально и доказывает монофилию данной группы. Поэтому, мы включаем Ophioptidae в состав семейства Harpirhynchidae в ранге подсемейства.

Кластер подсемейства Harpirhynchinae включает 6 родовых групп: 3 группы представлены каждая одним родом (*Harpirhynchus*, *Harpyrhynchoides* and *Perharpyrhynchus*), 3 другие группы включают каждая по два рода — *Metharpyrhynchus* и *Neharpyrhynchus*, *Anharpyrhynchus* и *Trichorhynchiella*, *Harpyrhynchiella* и *Cypsharpyrhynchus*.

Основываясь на полученной кладограмме, обсуждаются две гипотезы эволюции Harpirhynchidae. Согласно наиболее вероятной гипотезе, предок Harpirhynchidae перешел к паразитизму еще на общем предке птиц и коэволюционировал с этими хозяевами. Предок современных Ophioptinae, вероятно, перешел с птиц на змей.

INTRODUCTION

The family Harpirhynchidae was proposed by Dubinin [1957] within the superfamily Cheyletoidea. According to the concept of this author the family consists of two subfamilies: Harpirhynchinae Dubinin (2 genera) and Ophioptinae Southcott (1 genus). The first subfamily includes permanent skin parasites of different bird taxa (Aves), while the second subfamily comprises skin parasites of snakes (Colubridae and Elapidae). It is worthy of note that the subfamily Ophioptinae was originally established as a taxon of the family rank [Southcott, 1956].

Baker and coauthors [1958] restored the family rank for the Ophioptidae. On the contrary, Lawrence [1959] considered that the genera of the Ophioptidae and also the Psorergatidae, parasites of mammals, should be included into the Harpirhynchidae. Moreover, this author did not recognize any subdivision of the Harpirhynchidae. Volgin [1969] included the genus *Psorergates* (Psorergatidae) into the family Harpirhynchidae, but recognized Ophioptidae as a separate family.

At the present time many acarologists have recognized the taxa Harpirhynchidae, Ophioptidae and Psorergatidae as separate families [Kethley, 1970, 1990; Krantz, 1978; Giessen, 1990].

Fain [1972, 1976] described a number of new species and established 6 new genera in the Harpirhynchidae. The family was subdivided into two subfamilies: Harpirhynchinae with 3 tribes, Harpirhynchini, Metharpyrhynchini and Perharpyrhynchini, and Harpypalpinae with a single genus [Fain, 1972].

Moss and Wojcik [1978] made an attempt to propose a new classification of the family based on numerical methods. They confirmed the separate position of the family Harpypalpinae, but rejected the subdivision of the Harpirhynchinae into three tribes, proposed by Fain [1972] and even its subdivision into several genera. They recognized the single genus *Harpirhynchus* within the latter subfamily, which was divided into several species groups.

Lombert and Moss [1983] described one more genus, *Harpypalpoidea* within the Harpypalpinae. Their study of external morphology of the Harpypalpinae, specifically immatures, had revealed a certain similarity of this family with the Ophioptidae. However, these authors did not propose any idea concerning possible phylogenetic relationships between the Harpirhynchinae, Harpypalpinae and Ophioptidae.

Recently, Fain [1994, 1995] carried out a revision of the Harpirhynchinae and proposed improved diagnoses for this subfamily and Harpypalpinae [Fain et al., 1999]. These publications also contained descriptions of three new genera created within the Harpirhynchinae. It is worthy of note, that most of these new genera corresponds to the «species groups» recognized earlier by Moss and Wojcik [1978].

At the present time the family Harpirhynchidae, *sensu* Fain, includes 12 genera and 55 species [Fain, 1995; Fain et al., 1999]. However the suprageneric structure of the family still remains unclear and relationships between subfamilies of harpirhynchid and ophioptid mites have not been studied, despite the interesting data obtained by Lombert and Moss [1983]. An absence of phylogenetic hypothesis for the Harpirhynchidae also makes an obstacle for the analysis of their host-parasite relationships.

The present paper proposes, for the first time, a phylogenetic hypothesis for the family Harpirhynchidae and its relationships with the family Ophioptidae by the cladistics method. The obtained data serve as a basis for the analysis of mite distributions among host taxa.

MATERIAL AND METHODS

Material. The representatives of each genera of the families Harpirhynchidae (11 genera) and Ophioptidae (2 genera) have been examined. Most of specimens examined are deposited in the Institut royal des Sciences naturelles de Belgique (Bruxelles, Belgium) and in the Musee royal de l'Afrique centrale (Tervuren, Belgium).

Full collection data on materials examined were given in the paragraphs «Materials» in the papers of Fain [1964, 1994, 1995; Fain et al., 1999].

Methods. The study of phylogenetic relationships between Harpirhynchidae and Ophioptidae was based on a cladistic method. Recent taxonomic studies of these families [Fain, 1964, 1994, 1995; Fain et al., 1999] have shown, that all their genera could be considered with a high degree probability as the monophyletic taxa. Therefore the genera were treated in the analysis as the operational taxonomic units (OTU). The Cheyletidae have been chosen as an outgroup.

The software PAUP 3.0s was used for the phylogenetic reconstruction. The character optimization was made by DELTRAN algorithm (Delayed transformation). The basic data matrix (Table 1) includes all characters, which could be considered as informative characters in descriptions of taxa of the generic rank. All characters obtained equal weight. Any autapomorphic characters were not included because they are not informative for the cladogram pattern.

The reconstruction of phylogeny included two steps. At first step we used 84 characters, with all characters being unordered. At the second phase the doubtful characters and those displayed themselves as homoplasies at the first step of analysis were omitted.

Chaetotaxy follows that of Fain [Fain et al., 1999] (Fig. 1). This nomenclature is based on a topology of setae and have been successfully used for many groups of prostigmatid mites [Fain, 1970, 1973, 1979; Fain et al., 1997; Bochkov, 1997].

Table 1. Data matrix
Таблица 1. Матрица данных

Taxa	Characters											
	1	2	3	4	5	6	7	8	9	10	11	12
	1	1	1	1	1	1	1	1	1	1	1	1
	2	2	2	2	2	2	2	2	2	2	2	2
	3	3	3	3	3	3	3	3	3	3	3	3
	4	4	4	4	4	4	4	4	4	4	4	4
	5	5	5	5	5	5	5	5	5	5	5	5
	6	6	6	6	6	6	6	6	6	6	6	6
	7	7	7	7	7	7	7	7	7	7	7	7
	8	8	8	8	8	8	8	8	8	8	8	8
	9	9	9	9	9	9	9	9	9	9	9	9
	10	10	10	10	10	10	10	10	10	10	10	10
	11	11	11	11	11	11	11	11	11	11	11	11
	12	12	12	12	12	12	12	12	12	12	12	12
<i>Cheyletidae</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Harpirhynchus</i>	0	1	1	1	0	0	1	1	0	0	0	0
<i>Harpyrhynchoides</i>	0	1	1	1	0	0	1	1	0	0	0	0
<i>Perharpyrhynchus</i>	0	1	1	1	0	0	1	1	0	0	0	0
<i>Neharpyrhynchus</i>	0	1	1	1	0	0	1	1	0	0	0	0
<i>Metharpyrhynchus</i>	0	1	1	1	0	0	1	1	0	0	0	0
<i>Ralliharpirhynchus</i>	0	1	1	1	0	0	1	1	0	0	0	0
<i>Harpyrhynchiella</i>	0	1	1	1	0	0	1	1	0	0	0	0
<i>Cypsharpirhynchus</i>	0	1	1	1	0	0	1	1	0	0	0	0
<i>Anharpirhynchus</i>	0	1	1	1	0	0	1	1	0	0	0	0
<i>Trichorhynchiella</i>	0	1	1	1	0	0	1	1	0	0	0	0
<i>Harpypalpus</i>	0	1	1	1	0	0	1	1	0	0	0	0
<i>Harpypalpoides</i>	0	1	1	1	0	0	1	1	0	0	0	0
<i>Ophiptes</i>	1	0	1	1	1	0	0	2	1	1	1	0
<i>Afrophiotes</i>	1	0	1	1	1	0	0	2	1	1	1	0

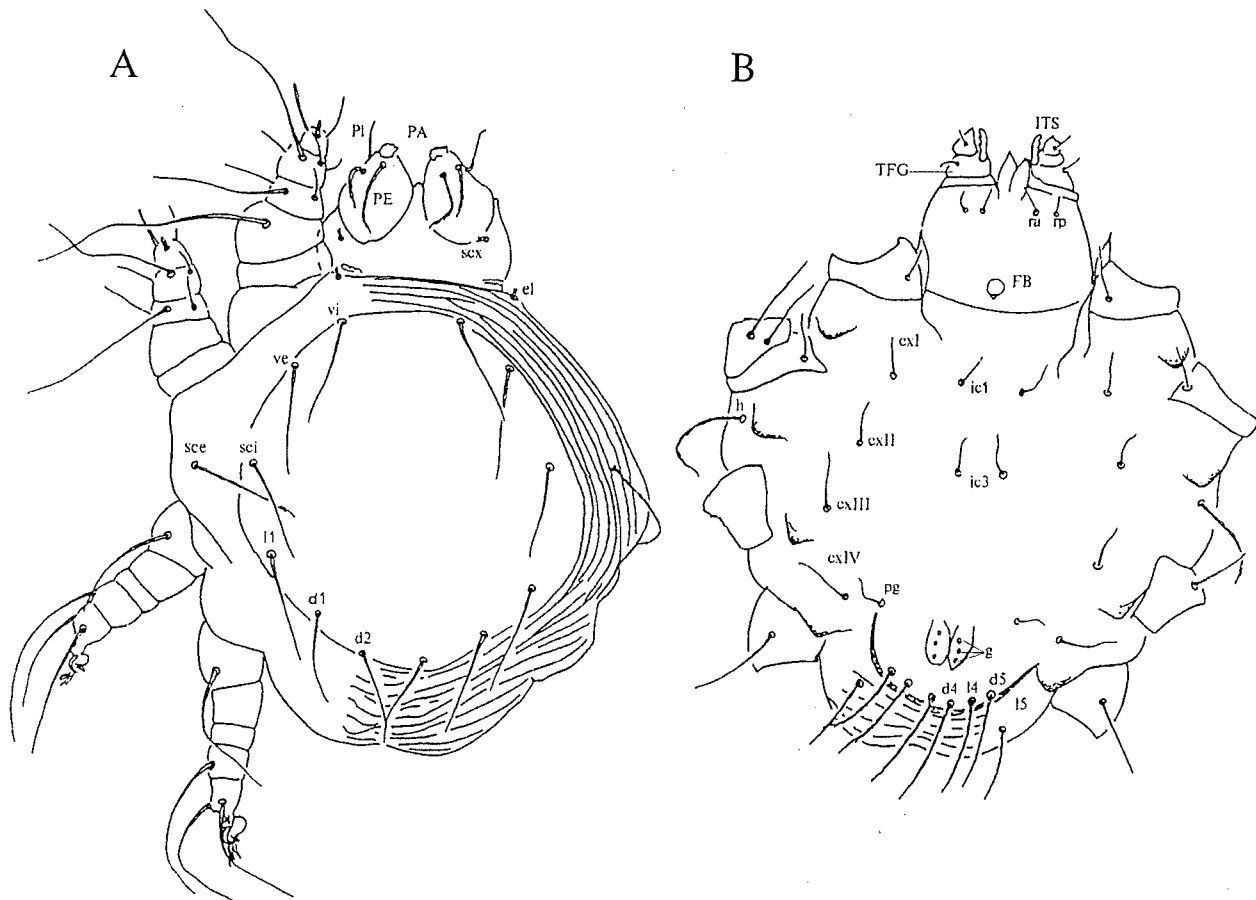


Fig. 1. A hypothetical species of the family Harpirhynchidae, female. A — dorsal view; B — ventral view.
 Рис. 1. Схема строения клеща семейства Harpirhynchidae, самка. А — дорсально; В — вентрально.

SYSTEMATICS NOTES ON TAXA USED IN THE CLADISTIC ANALYSIS

The careful study of materials used for the analysis has led us to make some preliminary changes in taxonomic status of some species and genera of Harpirhynchidae.

1. Within the genus *Harpirhynchus*, Fain et al., [1999] established the subgenus *Pseudoharpirhynchus* that comprised two species: *H.(P.)agapornis* Fain, 1972 (type species) and *H.cylindripalpus* (Fritsch, 1954). The latter species was conventionally included into this subgenus. It was originally described by Fritsch [1954] based on females only from *Fringilla coelebs* (Passeriformes: Fringillidae) from Germany. Later, Fain [1995] collected females from *Passerina cirilis* (Passeriformes: Emberizidae) died in the Antwerpen Zoo, and identified them also as *H.cylindripalpus*.

Until both males and females of *H.cylindripalpus* are recollected from the type host we will consider this taxon as *incertae sedis*. In the present study we exclude this species from the analysis.

The type species of the subgenus *Pseudoharpirhynchus*, *H.agapornis*, differs from the representatives of the nominative subgenus by the chaetotaxy of idiosoma and legs III–IV, idiosomal shape, and modified palpal setae. All listed features are also characteristic of the representatives of the genus

Harpyrhynchoides. An additional study of *H.agapornis* has shown, that it is similar by named characters to the genus *Harpyrhynchoides*. *H.agapornis* differs from other species of this genus only by the position of the genital opening in males, which is situated in the central part of the hysterosoma dorsum. In the *Harpyrhynchoides* this opening is situated in the posterior third part of the hysterosoma. However such character as a relative position of the genital opening is widely variable character. For example, among the related family Cheyletidae the position of male genital opening is highly variable within a genus [Volgin, 1969]. The variability is observed well in different species of the genus *Neochelyletilla*, the parasites of birds, for example in *N.smallowoodae* Baker, 1949 and *N.megaphallos* [Lawrence, 1959]. In the first species the male genital opening is disposed in the posterior one third, in the second species it is situated in the anterior one third. Based on features mentioned above we propose including *H.agapornis* into the genus *Harpyrhynchoides*, and consider the subgenus *Pseudoharpirhynchus* as a junior synonym of this genus.

2. Two species, *Harpirhynchus longipilus* Banks, 1905 and *H.brevis* Ewing, 1911 were described incompletely. Therefore we consider them as taxa *incertae sedis* within the Harpirhynchinae [Fain, 1995].

CHARACTER ANALYSIS

Characters of the adult: gnathosoma
(characters 1–20)

1. Peritremes. The peritremes are present in most predaceous mites of the subcohort Raphignathae, including the family Cheyletidae. They are also present in mites of the family Harpirhynchidae. The peritremes are probably secondarily absent in mites of the family Ophioptidae.

Peritremes present — 0; peritremes absent — 1.

2. Segments of peritremes. The peritremes are segmented along all their length in the Cheyletidae, while in the Harpirhynchidae they are segmented only in their lateral parts. The comparison of the segmentation state with that in distant outgroups (Syringophilidae etc.) suggests that the first state of this character is ancestral.

Peritremes segmented along all length — 0; peritremes segmented in lateral ends only — 1.

3. Hypostome. In the Cheyletidae the hypostome and stylophore are fused. They form a strong beak. This is probably the ancestral state inherited from the archaic ancestor. The hypostome is secondary free in the Harpirhynchidae, Ophioptidae, Demodicidae, and Psorergatidae.

Hypostome and stylophore fused — 0; hypostome free — 1.

4. Sclerotization of pharyngeal bulb (FB) (Fig. 1B). FB is slightly sclerotized in the Cheyletidae and Syringophilidae. In the Harpirhynchidae, Ophioptidae and in most parasitic mites of the superfamily Cheyletoidea, in which the gnathosoma is not reduced, FB is strongly sclerotized.

FB weakly sclerotized — 0; FB strongly sclerotized — 1.

5. Number of free segments in a palp (Fig. 1). The ancestral number of free segments in a palp is five, as it is observed in most Cheyletidae. Only three free palpal segments in the Harpirhynchidae and Ophioptidae (the trochanter-femur-genu — (TFG), tibia and tarsus).

5 free palpal segments — 0; 3 free palpal segments — 1.

6. Structures of palpal tarsus. There are 4 well developed setae and 1 solenidion on the palpal tarsus in the Cheyletidae. In the Harpirhynchidae the palpal tarsus bears only one seta, but the traces of other structures are recognizable. In the Ophioptidae the palpal tarsus has one seta only.

Palpal tarsus with several sensorial structures or their traces — 0; palpal tarsus with one seta only, without traces of any sensorial structures — 1.

7. Shape of TFG in a palp. The TFG in a palp is more or less elongated in the Harpirhynchidae; the shape of this segment is nearly triangular with slightly elongated apex in the Ophioptidae.

TFG more or less elongated — 0; TFG almost triangular with slightly elongated apex — 1.

8. Modified setae in a palp (Fig. 1). Most predaceous Cheyletidae the femur and genu of palp

have only hair-like nonmodified setae. In the Harpirhynchidae and Ophioptidae the TFG of palp has modified setae. There are usually 3 modified setae PA, PI, PE in TFG.

Femur and genu of palp without modified setae — 0; modified setae in TFS present — 1.

9. Setae PE. In the Cheyletidae, Ophioptidae, Harpyalpinae and in most Harpirhynchinae the seta PE is present. In the genera *Harpyrhynchiella* and *Cypsharpirhynchus* this seta is absent.

Setae PE present — 0; setae PE absent — 1.

10. Position of seta PE. The modified setae are situated in one place on the apex of the palp in the Harpirhynchidae. In the Ophioptidae as well as in mites of the family Psorergatidae the seta PE is situated behind the setae PA and PI at the level of the middle part of palps. Probably it is the ancestral condition of this character.

Seta PE situated in the middle part of palps, behind of setae PA, PI — 0; setae PA, PI, PE situated closely to one another in apex of palp — 1.

11. Shape of seta PI. The seta PI is serrate, hair-like in the Harpyalpinae and in the genus *Trichorhynchiella* (Harpirhynchinae). It is probably the ancestral state because this seta is similar in shape with those in femur and genu of palpa in the Cheyletidae. This seta is wide comb-like in other genera of the Harpirhynchinae, while within the genus *Metharpyrhynchus* it varies from comb-like (as in *M. jynx* Fain, 1972) to finger-like (as in *M. mossi* Fain, 1995). As far the comb-like form of seta PI is a feature of the most genera of the Harpirhynchinae, and the finger-like form apparently developed within *Metharpyrhynchus*, we provide this genus with a code corresponding to the comb-like state only. In the Ophioptidae the seta PI is finger-like.

Seta PI serrate, hair-like — 0; seta PI wide, comb-like — 1; seta PI finger-like — 2.

12. Shape of inner seta in palpal tibia (ITS) (Fig. 1B). In most Cheyletidae the seta ITS is hair-like. This seta is finger-like with two apices curved upside in the Harpirhynchinae and harpoon-like with three or two teeth curved down in the Harpyalpinae and Ophioptidae.

ITS hair-like — 0; ITS finger-like — 1; ITS harpoon-like — 2.

13. Number of teeth in a harpoon-like seta IST. In the Harpyalpinae, the number of teeth on the IST is 3, in the Ophioptidae, this number is 2.

ITS with two teeth — 0; ITS with three teeth — 1.

14. Setae pts. In the Cheyletidae and in most Harpirhynchinae, the seta pts is present. In two genera of the Harpirhynchinae (*Harpyrhynchiella* and *Cypsharpirhynchus*), in all Ophioptidae and Harpyalpinae this seta is absent.

Setae pts present — 0; setae pts absent — 1.

15. Setae scx. In the Cheyletidae and Harpirhynchidae the seta scx present. It is always absent in the Ophioptidae.

Setae *scx* present — 0; setae *scx* absent — 1.

16. Shape of seta *scx*. The seta *scx* has one apex in the Cheyletidae and absent in Ophioptidae. In all Harpirhynchidae this seta possesses two apices.

Seta *scx* having one apex — 0; seta *scx* having two apices — 1.

17. Dorsal setae of rostrum (*rd*). In the Cheyletidae and closely related outgroup taxa, Raphignathidae, Syringophilidae and etc, the setae *rd* present. In the Ophioptidae and Harpirhynchidae these setae absent.

Setae *rd* present — 0; setae *rd* absent — 1.

18. Setae *rp* (Fig. 1B). In the Cheyletidae, Ophioptidae, Harpypalpinae, and most Harpirhynchinae the setae *rp* present. In the genera *Harpyrhynchiella* and *Cypsharpirhynchus* these setae absent.

Setae *rp* present — 0; setae *rp* absent — 1.

19. Relative positions of setae *ra* and *rp* (Fig. 1B). In the Cheyletidae, Syringophilidae, Myobiidae and Harpirhynchinae the setae *rp* are situated behind the level of setae *ra*. In the Harpypalpinae and Ophioptidae these setae are situated at the same transversal line as the setae *ra*.

Setae *rp* located distinctly posteriad to setae *ra* — 0; seta *rp* and *ra* located on the same transversal line — 1.

20. Position of seta *rp*. In the Cheyletidae and Harpirhynchidae the seta *rp* is situated ventrally. In the Ophioptidae this seta is situated laterally.

Seta *rp* situated ventrally — 0; seta *rp* situated laterally — 1.

Legs (characters 21–42)

21. Legs I–II in female. In the Cheyletidae, Ophioptidae, Harpypalpinae and in some genera of the Harpirhynchinae the legs I–II of female are well developed. In several genera of the Harpirhynchinae (*Neharpyrhynchus*, *Metharpyrhynchus*, *Anharpyrhynchus*, *Trichorhynchiella*, *Ralliharpirhynchus*, *Cypsharpirhynchus*, *Harpyrhynchiella*) the legs I–II of female are reduced in this or that way (smaller in size, some segments fused). In the *Perharpyrhynchus*, both sexes have four free segments in legs I–II (the genu and tibia are fused as in immature instars of the Harpirhynchinae), but these legs are normal in size. It is worthy of note, that in this genus the legs I–II are normally developed, but the legs IV are completely absent, setae *sci*, *h* and *ic3* are also absent (the latter two setae are absent in larvae of the Harpirhynchinae). We believe that in the *Perharpyrhynchus* we observe the manifestation of some larval features in adult mites, but not a reduction of these structures. Therefore, the structure of legs I–II in *Perharpyrhynchus* is treated as a plesiomorphic state.

Legs I–II of female completely developed — 0; legs I–II of female reduced in one way or another — 1.

22. Shape of legs III–IV. In the Cheyletidae, Ophioptidae and Harpypalpinae the legs III–IV are normally developed. In the Harpirhynchinae these legs are reduced up to two or one segments.

Legs III–IV normally developed — 0; legs III–IV reduced to two or one segments — 1.

23. Segments of legs III–IV in female. As it was said above, in the Cheyletidae, Ophioptidae and Harpypalpinae the legs III–IV in the female consist of five free segments. While in the Harpirhynchinae the segments of these legs are reduced. In most Harpirhynchinae the legs III–IV consist of one or two well developed segments bearing long whip-like setae. In females of *Ralliharpirhynchus*, *Cypsharpirhynchus* and *Harpyrhynchiella*, these legs are almost completely reduced and have no whip-like setae.

Legs III–IV in female consist of one or two segments — 0; legs III–IV in female almost completely reduced — 1.

24. Pretarsus of legs I–II in female. In the Cheyletidae, Ophioptidae and Harpypalpinae the pretarsus of legs I–II in female is well developed. It is also present in females of certain genera of the Harpirhynchinae, but in genera *Neharpyrhynchus*, *Metharpyrhynchus*, *Anharpyrhynchus*, *Trichorhynchiella*, *Harpyrhynchiella* the pretarsus of legs I–II fused with tarsal apex and in the genera *Cypsharpirhynchus*, *Ralliharpirhynchus* the pretarsus of legs I–II is completely absent.

Pretarsus of legs I–II present in female, but not fused with tarsus — 0; pretarsus and tarsus of legs I–II fused in female — 1; pretarsus of legs I–II absent in female — 2.

25. Protrusion of ambulacrum. In the Cheyletidae and Harpirhynchinae, when the ambulacrum is present, it has no protrusion. In the Harpypalpinae and Ophioptidae the ambulacrum of all legs with the well developed cup-like protrusion.

Ambulacrum without protrusion — 0; ambulacrum of all legs with cup-like protrusion — 1.

26. Tarsal claws. In the Cheyletidae and Harpirhynchidae the tarsal claws are present. In the Harpirhynchinae they are present only on legs I–II, except females of the genera *Cypsharpirhynchus*, *Ralliharpirhynchus* and several species of the *Metharpyrhynchus*. In both sexes of the Ophioptidae the tarsal claws are absent.

Tarsi in male or female, or in both sexes with claws — 0; claws on all legs absent in both sexes — 1.

27. Shape of empodium. In the Cheyletidae and Harpirhynchidae the empodium has one basic stem. In the Ophioptidae the empodium has four basic stems.

Empodium with one basic stem — 0; empodium with four basic stems — 1.

28. Coxal sclerotization. In predaceous forms of the Cheyletidae, as in all predaceous Raphignathae, the coxae are well sclerotized. In the Harpirhynchidae and Ophioptidae, as in most parasitic Cheyletoidea, the coxae are weakly sclerotized, except areas along the epimeres and epimerites.

Coxae well sclerotized — 0; coxae sclerotized along epimeres and epimerites only — 1.

29. Shape and sclerotization of the epimeres.

In most predaceous forms of Cheyletidae the coxal fields are not reduced. In certain genera of the Harpirhynchidae, the epimeres are present, but weakly developed and not enclosed into a sclerotized ring. In the Ophioptidae, the well developed epimeral structures are present, but it is not clear if these structures are primitive or not.

Epimeres well developed — 0; epimeres weakly developed or absent — 1.

30. Protrusions of coxae. In the predaceous Cheyletidae, Harpirhynchidae and Ophioptidae the coxae have no any protrusions. In the Harpypalpinae all coxae with slight membranous protrusions.

Coxae without protrusions — 0, coxae with protrusions — 1.

31. Number of setae in tarsus I. In the Cheyletidae and Ophioptidae the tarsus I bears 10 setae including the solenidion omega. In most Harpirhynchinae the tarsus I carries 9 setae. Only in females of the *Ralliharpirhynchus* and *Harpyrhynchiella* the number of setae of the tarsus I is reduced, but males of these genera have 9 setae on the leg I. In both sexes of Harpypalpinae the tarsus I bears 8 setae.

Tarsus I bears 10 setae, including solenidion — 0; tarsi I bears 9 setae — 1; tarsi I bears 8 setae — 2.

32. Number of setae on tarsi III–V. In the Cheyletidae the tarsi III–IV have 7 setae, in the Ophioptidae these tarsi bears 8 setae, and in the Harpypalpinae these segments carry only 6 setae. In the Harpirhynchinae the tarsi III–IV are fused with other leg segments. Therefore, the initial number of these setae on tarsi III–IV in Harpirhynchinae is unclear. This characters is coded only for the Ophioptidae and Harpypalpinae.

Tarsi III–IV with 7–8 setae — 0; tarsi III–IV with 6 setae — 1.

33. Number of setae on tibiae III–IV. As it was said earlier, the number of setae on leg segments III–IV was coded only for the Ophioptidae and Harpypalpinae. Tibiae III–IV bear 3–4 setae in the Cheyletidae, 3 setae in the Harpypalpinae, and only 2 setae in the Ophioptidae.

Tibiae III–IV with 4–3 setae — 0; tibiae III–IV with 2 setae — 1.

34. Form of inner tibial seta on legs. In the most of predaceous Cheyletidae and in all Harpirhynchidae the inner tibial seta is hair-like in shape. In the Ophioptidae this seta is finger-like.

Inner tibial seta legs hair-like — 0; inner tibial seta finger-like — 1.

35. Setal number on apical segment of legs IV in harpirhynchine females. In most harpirhynchine females, the apical segment of legs IV bears 9 setae or less. However, in females of *Trichorhynchiella* this segment carries 10 setae, and in females of the *Anharpyrhynchus* it bears more than 20 setae. We believe that in two latter cases the number on apical setae of legs IV is multiplied and therefore this character state is an apomorphy.

Apical segment of legs IV in female with 9 setae or less — 0; apical segment of leg IV in female with 10 or more setae — 1.

36. Solenidion of tibia I. In the Cheyletidae and other distant outgroup, the solenidium gamma is present. This structure is absent in the Ophioptidae and Harpirhynchidae.

Solenidion of tibia I present — 0; solenidion of tibia I absent — 1.

37. Solenidion of genu I. In the Cheyletidae and in more distant outgroups, the solenidium sigma is present. In the Ophioptidae and Harpirhynchidae this solenidion is absent.

Solenidion sigma present — 0; solenidion sigma absent — 1.

38. Setae of femur IV. In most Cheyletidae and in all Harpypalpinae the femur IV bears one or two setae; these segments are fused in Harpirhynchinae and these segments have no any setae in Ophioptidae.

Femur IV with 1–2 setae — 0; femur IV without seta — 1.

39. Seta of coxa I. In the Cheyletidae, Ophioptidae, Harpypalpinae and in most genera Harpirhynchinae the coxae I bears a seta. In the genera *Harpyrhynchiella*, *Cypsharpirhynchus* and *Trichorhynchiella* the coxae I have no setae.

Seta on coxa I present — 0; seta on coxa I absent — 1.

40. Setae on coxae II–III. In the Cheyletidae, Ophioptidae, Harpypalpinae and in some genera of Harpirhynchinae the coxae II–III bear setae. In the genera *Harpirhynchus*, *Harpyrhynchoides*, *Perharpyrhynchus*, *Neharpyrhynchus*, *Metharpyrhynchus*, *Ralliharpirhynchus*, *Harpyrhynchiella*, *Cypsharpirhynchus*, *Anharpyrhynchus* and *Trichorhynchiella* these coxae have no any setae.

Setae on coxae II–III present — 0; setae on coxae II–III absent — 1.

41. Seta on coxa IV. In the Cheyletidae and Harpypalpinae the seta on coxa IV is present, while in the Harpirhynchinae and Ophioptidae this seta is absent.

Seta on coxa IV present — 0; seta on coxa IV absent — 1.

Idiosoma (characters 42–73)

42. Position of gnathosoma and legs I in females. In most Cheyletidae and Harpirhynchinae, in all Ophioptidae and Harpypalpinae the gnathosoma are positioned terminally and the legs I are situated ventrally. Only in the females of two genera, *Anharpyrhynchus* and *Trichorhynchiella*, the gnathosoma and the legs I are situated dorsally.

Gnathosoma and legs I in female situated terminally and ventrally, respectively — 0; gnathosoma and legs I in female situated dorsally — 1.

43. Lateral propodosomal lobes in female. In the females of the Cheyletidae, Ophioptidae, Harpypalpinae and in most Harpirhynchinae the propodosoma has no lobes. Only in females of two genera, *Harpyrhynchiella* and *Cypsharpirhynchus*, a pair of lateral lobes is present.

Propodosoma without lateral lobes — 0; propodosoma with pair of lateral lobes — 1.

44. Lateral opisthosomal lobes in female. In females of the Cheyletidae, Ophioptidae, Harpypalpinae and in most Harpirhynchinae the opisthosoma has no lobes. In females of two genera, *Anharpyrhynchus* and *Trichorhynchiella*, it carries a pair of lateral lobes.

Opisthosoma without lateral lobes — 0; opisthosoma with lateral lobes — 1.

45-46. Shape of idiosoma in females. In females of most Cheyletidae, in all Ophioptidae and Harpypalpinae and in some genera of the Harpirhynchinae the idiosoma is rhomb-like, circular or subcircular. In females of the genera *Neharpyrhynchus* and *Metharpyrhynchus* the idiosoma is greatly elongated, sacciform (in the genus *Harpirhynchus* it is slightly sacciform). In females of the genera *Anharpyrhynchus*, *Trichorhynchiella*, *Harpirhynchiella*, *Cypsharpirhynchus* and *Ralliharpirhynchus* the idiosoma is wider than longer. The modification of idiosoma in female is an apomorphic character, but it is obviously displayed in two separate ways and therefore it should be coded as two the different characters: 45 and 46.

45. Idiosoma circular or subcircular — 0; idiosoma elongated or sacciform — 1.

46. Idiosoma circular or subcircular — 0; idiosoma wider than longer — 1.

47. Cuticular pattern on idiosoma. In the predaceous Cheyletoidea, in all Harpirhynchidae the idiosoma is striated transversally or partly longitudinally. In the Ophioptidae the surface of idiosoma has no striation, but the idiosoma is covered with many small tubercules.

Idiosoma striated — 0; idiosoma without striation, covered with many small tubercules — 1.

48. Scales or verrucosities on idiosoma in female. In the predaceous forms of the Cheyletidae as well as in all Harpypalpinae and Ophioptidae, except *Ophioptes congoensis* Fain, 1962, the cuticle surface is not covered with scales or verrucosities. In the Harpirhynchinae there are certain areas with scales or verrucosities on idiosomal surface of the genera *Anharpyrhynchus*, *Trichorhynchiella*, *Harpirhynchiella* and *Cypsharpirhynchus*. Within the genus *Harpirhynchoides* there are also similar structures, but they are apparently secondary in origin.

Scales or verrucosities on cuticle absent — 0; scales and verrucosities on cuticle present — 1.

49. Propodosomal shield in female. In most predaceous forms of Cheyletidae, in all Harpypalpinae and in a number of genera in the Harpirhynchinae, the propodosomal shield is present. It is completely absent in all Ophioptidae and in the genera *Anharpyrhynchus*, *Trichorhynchiella*, *Harpirhynchiella*, and *Cypsharpirhynchus* (Harpirhynchinae). In females of the latter genus, there are only rudiments of this shield.

Propodosomal shield present — 0; propodosomal shield absent or represented by there rudiments only — 1.

50. Hysterosomal shield. In the Cheyletidae, the hysterosomal shield is present, but it is absent in all other parasitic families of the Cheyletoidea, including the Ophioptidae and Harpirhynchidae.

Hysterosomal shield present — 0; hysterosomal shield absent — 1.

51. Position of male genital aperture (MGA). In predaceous forms of the Cheyletidae the MGA is situated terminally. It is positioned dorsally in different parasitic forms of this family. In all Harpypalpinae and in some genera of the Harpirhynchinae (*Harpirhynchoides*, *Perharpirhynchus*, *Ralliharpirhynchus*) the MGA is situated dorsally, namely in the posterior part of idiosoma. In all Ophioptidae and in males of the genus *Neharpyrhynchus*, in the genus *Harpirhynchus* it is situated dorsally in the middle part of idiosoma. In the genera *Metharpyrhynchus*, *Anharpyrhynchus*, *Cypsharpirhynchus* and *Harpirhynchiella* the MGA is situated at the base of the gnathosoma.

MGA situated terminally or in a posterior part of idiosoma — 0; MGA situated at base of gnathosoma — 1.

52. Vulva. In the Cheyletidae, Ophioptidae and Harpypalpinae the vulva is simple, slit-like, without additional structures except genital setae. The anterior end of vulva in Harpirhynchinae has a pocket-like structure.

Vulva without a pocket-like structure — 0; vulva with a pocket-like structure anteriorly — 1.

53. Sclerotized structures near the vulva. In Cheyletidae and Harpirhynchinae, there are no sclerotized structures near the vulva. It is surrounded by the sclerotized ring, crescent, or lies on a small plate in the Ophioptidae and Harpypalpinae.

Vulva free — 0; vulva surrounded by a sclerotized ring, crescent, or lies on a small plate — 1.

54. Length of vulvar slit. In the Cheyletidae and especially in the Ophioptidae and Harpypalpinae the vulvar aperture is slit-like and short. In the Harpirhynchinae it is relatively long, but only in two genera, *Anharpyrhynchus* and *Trichorhynchiella*, it is extremely long and the anterior end of the vulvar slit extends to the level of legs II, while the posterior end reaches the terminus.

Vulvar slit about one third of idiosomal length or less — 0; vulvar slit about a half of idiosoma — 1.

55. Ventral sclerotized crescent of opisthosoma (SC) in males. In males of the Cheyletidae, Ophioptidae and Harpirhynchinae the opisthosomal venter has no SC, while in the Harpypalpinae SC is present.

Opisthosomal venter of male without SC — 0; opisthosomal venter of male with SC — 1.

56. Length of setae *el*. In the Cheyletidae the setae *el* are always absent. In Harpirhynchidae these setae are present, but represented by microchaeta. In the Ophioptidae these setae are well developed, and they are slightly shorter than other idiosomal setae. We believe that the well developed setae *el* are the ancestral character state.

Setae *el* well developed — 0; setae *el* are represented by microchaetae — 1.

57. Shape of setae *el*. In the Harpirhynchinae and in most Ophioptidae the seta *el* has a single apex. In the Harpypalpinae this seta has two apices.

Seta *el* with a single apex — 0; seta *el* with two apices — 1.

58. Position of setae *sci* in relation to setae *vi*, *ve* in females. In most Cheyletidae females, in all Ophioptidae and Harpirhynchinae the setae *sci* are adjacent to the setae *vi*, *ve*. In females of the Harpypalpinae, the setae *sci* are situated posterior to setae *vi*, *ve*, behind the level of leg II bases.

Setae *sci* of female is adjacent to setae *vi* and *ve* — 0; setae *sci* of female situated posterior to setae *vi* and *ve* — 1.

59. Position of setae *vi*, *ve* in females. In the families Cheyletidae, Ophioptidae, Harpypalpinae, and in most Harpirhynchinae the setae *vi*, *ve* are situated dorsally. In two genera of the Harpirhynchinae (*Metharpyrhynchus* and *Neharpyrhynchus*), these setae are situated ventrally, together with setae *sci*.

Setae *vi*, *ve* situated dorsally — 0; setae *vi*, *ve* situated ventrally — 1.

60. Form of setae *vi*, *ve* in males. In the primitive Cheyletidae the setae *vi*, *ve* are commonly hair-like in shape; in the Ophioptidae and Harpirhynchinae these setae are hair-like. In the Harpypalpinae the setae *vi* and *ve* are small and resemble a spear tip in shape.

Setae *vi*, *ve* hair-like — 0; setae *vi*, *ve* small, resembling a spear tip — 1.

61. Setae *sce*, *h* in females. In the Cheyletidae, Harpypalpinae and usually in the Harpirhynchinae the setae *sce*, *h* are well developed. In some genera of the Harpirhynchinae (*Metharpyrhynchus* and *Neharpyrhynchus*) these setae are very short or completely absent, as in *Harpyrhynchiella*.

Setae *sce*, *h* well developed in female — 0; setae *sce*, *h* of female short or absent — 1.

62. Setae of *d* and *l* series. In the Cheyletidae, Ophioptidae and Harpypalpinae, the setae of the *d* and *l* series are present, in the Harpirhynchinae these setae are absent, except the setae *l5*.

Setae of series *d* and *l* present — 0; setae of series *d* and *l* absent — 1.

63. Position of setae *d1*, *l1*. In most Cheyletidae and in all Harpypalpinae the setae *d1*, *l1* are situated posterior to propodosomal setae (*vi*, *ve*, *sci*, *sce*). In the Harpirhynchinae these setae are absent. In the Ophioptidae the setae *d1*, *l1* located more closely to propodosomal setae.

Setae *d1*, *l1* remote from propodosomal setae — 0; setae *d1*, *l1* close to propodosomal setae — 1.

64. Position of setae *l5* in female. In the Cheyletidae the setae *l5* are situated dorsally or terminally. In the Harpirhynchinae these setae are disposed dorsally, while in the Harpypalpinae and Ophioptidae they are situated ventrally.

Setae *l5* situated dorsally or terminally — 0; setae *l5* situated ventrally — 1.

65. Setae *d3*, *l3*. In the Cheyletidae and Ophioptidae the setae *d3* and *l3* are present, while in the Harpirhynchinae all setae of *d* and *l* series are absent. In the Harpypalpinae the setae *d3*, *l3* are absent.

Setae *d3*, *l3* present — 0; setae *d3*, *l3* absent — 1.

66. Setae *ic1* in female. In the Cheyletidae, Ophioptidae, Harpypalpinae and in most Harpirhynchinae the seta *ic1* is present. In the genera *Metharpyrhynchus*, *Harpyrhynchiella* and *Cypsharpirhynchus* this seta is absent.

Setae *ic1* present — 0; setae *ic1* absent — 1.

67. Seta *ic3*. In the Cheyletidae, Ophioptidae and Harpypalpinae and in most Harpirhynchinae the setae *ic3* are present. In the genera *Harpirhynchus*, *Metharpyrhynchus*, *Harpyrhynchiella* and *Cypsharpirhynchus* these setae are absent in both sexes; in the *Trichorhynchiella* these setae are absent in female (male is unknown for this genus). In the genus *Perharpyrhynchus* the setae *ic3* are also absent, but we consider that it is the result of pedomorphosis in this genus (as it was already discussed for the character 21). Therefore we consider this character in the genus *Perharpyrhynchus* as a plesiomorphic condition.

Setae *ic3* present — 0; setae *ic3* absent — 1.

68. Setae *ic4*. In the Cheyletidae and Ophioptidae the setae *ic4* are present, while in the Harpirhynchidae *ic4* are absent.

Setae *ic4* present — 0; setae *ic4* absent — 1.

69. Form of setae *ic3*. In the Cheyletidae and Harpirhynchidae, the setae *ic3* are hair-like, and in the Ophioptidae this setae are thick, finger-like.

Setae *ic3* hair-like — 0; setae *ic3* thick finger-like — 1.

70. Setae *pg* in females. In the Cheyletidae, Harpypalpinae and many genera of Harpirhynchinae the setae *pg* are present. In several genera of Harpirhynchinae (*Harpirhynchus*, *Neharpyrhynchus*, *Metharpyrhynchus*, *Ralliharpirhynchus*) and in the Ophioptidae these setae are absent.

Setae *pg* present — 0; setae *pg* absent — 1.

71. Setae *g* in female. In females of the Cheyletidae, Ophioptidae and Harpypalpinae the setae *g* are present. In the Harpirhynchinae the setae *g* are absent.

Setae *g* present — 0; setae *g* absent — 1.

72. Form of setae *g* in female. In females of the Cheyletidae the setae *g* are hair-like, whilst in the Harpirhynchinae they are absent. In the Harpypalpinae and Ophioptidae the setae *g* are represented by microchaetae with bases being sunk into the cuticle.

Setae *g* hair-like — 0; setae *g* as microchaetae with sunk bases — 1.

73. Number of setae *g* in male (probably, together with anal setae). In male of the Cheyletidae five pairs of genito-anal setae are present, comparing to only four pairs of setae in the Ophioptidae (males are known only for the genus *Ophioptes*). In the Harpirhynchidae only two or three pairs of setae *g* present.

Setae *g* 5–4 pairs — 0; setae *g* 3–2 pairs — 1.

Immature instars (characters 74–84)

74. Legs. In immature instars of the Cheyletidae and Harpirhynchinae all legs are present. In the Ophioptidae and Harpypalpinae the legs are completely absent in all immature instars.

Legs present — 0; legs completely absent — 1.

75. Peritremes. In immature instars of the Cheyletidae and Harpirhynchinae the peritremes are present. In the Ophioptidae and Harpypalpinae the peritremes are absent.

Peritremes present — 0; peritremes absent — 1.

76. Propodosomal shield. In immature instars of the Cheyletidae and Harpirhynchinae the propodosomal shield is present, and only in the Ophioptidae and Harpypalpinae the propodosomal shield is absent.

Propodosomal shield present — 0; propodosomal shield absent — 1.

77. Anus. In immature instars of the Cheyletidae and Harpirhynchinae the anus is opened, while in the Ophioptidae and Harpypalpinae there are no any remnants of the anus on a cuticle surface.

Anus present — 0; anus absent — 1.

78. Setae PE and *pts* in teleonymph. In the teleonymph of the Cheyletidae and Harpirhynchinae the setae PE and *pts* are present. In the Ophioptidae and Harpypalpinae these setae are absent.

Setae PE, *pts* of teleonymph present — 0; setae PE, *pts* of teleonymph absent — 1.

79. Form of setae PA. In immature instars of the Harpirhynchinae the setae PA are narrow, comb-like, in the Ophioptidae and Harpypalpinae these setae are wide, comb-like.

Seta PA narrow, comb-like — 0; seta PA wide, comb-like — 1.

80. Form of setae ITS. In the Cheyletidae the setae ITS are hair-like in immature instars. In Harpirhynchinae and Harpypalpinae this seta is same as in adults (character 12). In Ophioptidae the setae ITS are wide, comb-like, with numerous anterior teeth.

Setae ITS hair-like — 0; setae ITS finger-like — 1; setae ITS harpoon-like — 2; setae ITS wide comb-like — 3.

81. Seta *rp* in teleonymph. In the Cheyletidae and Harpirhynchinae the seta *rp* is present. In the Ophioptidae it is absent.

Seta *rp* present — 0; seta *rp* absent — 1.

82. Setae *vi*, *ve*. In immature instars of the Cheyletidae and Harpirhynchinae the setae *vi*, *ve* are present. In the Ophioptidae and Harpypalpinae the setae *vi*, *ve* are absent.

Setae *vi*, *ve* present — 0; setae *vi*, *ve* absent — 1.

83. Position of setae *sce*. In immature instars of the Cheyletidae and Harpirhynchinae the setae *sce* are situated dorsally. In the Ophioptidae and Harpypalpinae they are disposed ventrally.

Setae *sce* situated dorsally — 0; setae *sce* situated ventrally — 1.

84. Position of setae *d1*, *d2*. In immature instars of the Cheyletidae and Harpypalpinae the setae *d1*, *d2* are situated dorsally. In Ophioptidae the setae *d1*, *d2* are situated ventrally. In Harpirhynchinae these setae are absent.

Setae *d1*, *d2* situated dorsally — 0; setae *d1*, *d2* situated ventrally — 1.

RESULTS AND DISCUSSION

The first step in the cladistic analysis, the developing of the preliminary cladogram, was based on 84 characters (Table 1); all characters were not ordered. The single tree has been obtained with the following general indices: length 113 steps, consistency index (CI) 0.798, homoplasy index (HI) 0.204 (Fig. 2).

Two general clusters are well recognized within this tree. The first cluster includes all representatives of the subfamily Harpirhynchinae, the second incorporates the subfamily Harpypalpinae and the family Ophioptidae. The monophyly of the branch Harpirhynchidae — Ophioptidae within the Cheyletoidea is supported quite well, because it is based on 11 clear synapomorphies. Five of them are represented by reductions of respective structures and therefore their homoplasy could not be completely excluded: setae *rd* absent (character 17), solenidion on tibia I and genu I absent (36, 37), coxae weakly sclerotized, except areas along epimeres and epimerites (28), hysterosomal shield absent (50). Six other synapomorphies are clearly evolved character states: free hypostome (3), strongly sclerotized pharyngeal bulb (4), junction of palpal trochanter, femur and genu (5), three comb- or finger-like modified setae in palps (8), the presence of inner modified setae in palpal tibia (12), shape of seta ITS (80).

Despite some of these character states occur in other parasitic families of the Cheyletoidea, the palpal structure in the families Harpirhynchidae — Ophioptidae is unique (characters 5, 6, 12). The most intriguing thing in the cladogram obtained is the relegation of the Harpypalpinae and Ophioptidae in the second general cluster. The uniting of these two groups in this cluster is supported by 15 synapomorphies. Derived state of seven characters are reductions of certain structures: setae *pts* absent (character 14), legs of immature instars completely absent (74), peritremes in immature instars absent (75), propodosomal shield in immature instars absent (76), anus in immature instars absent (77), setae PE, *pts* in teleonymph absent (78), setae *vi*, *ve* in immature instars absent (82). 8 other states are obviously evolved modifications of morphological structures: harpoon-like inner setae of palpal tibia (12), seta *rp* situated at the same transversal line as *ra* (19), ambulacrum in all legs with a cup-like protrusion (25), the vulva is surrounded by sclerotized ring, crescent, or situated on a small plate (53), setae *15* situated ventrally (64), setae *g* in female are represented by microchaetae (72), seta

Phylogeny of the Harpirhynchid mite

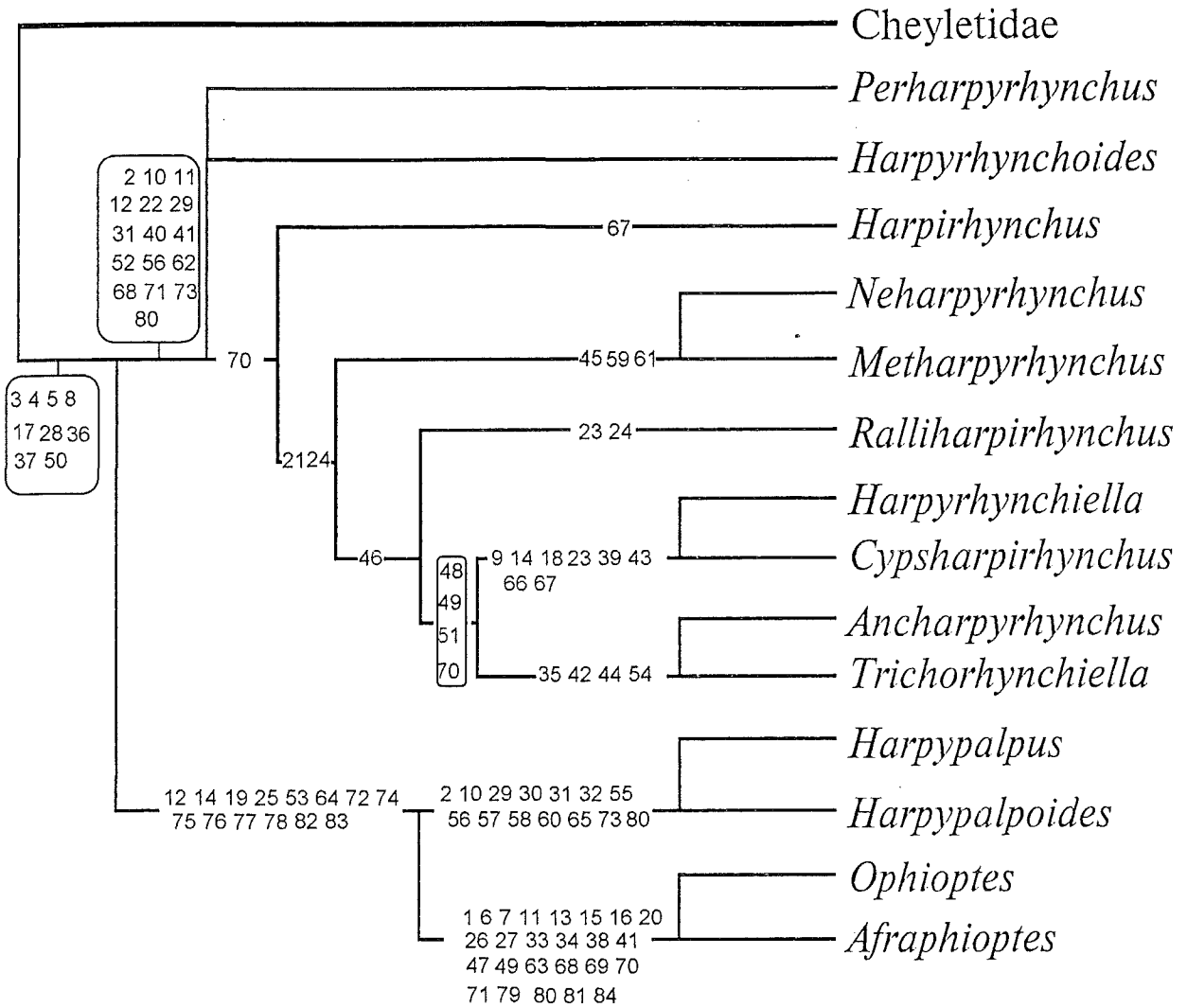


Fig. 2. Cladogram of the Harpirhynchidae based on all characters. PAUP 3.0s (DELTRAN): tree 1, length 122 steps, CI = 0.804, HI = 0.196.
 Рис. 2. Кладограмма Harpirhynchidae, основанная на всех признаках. PAUP 3.0s (DELTRAN): 1 дерево, длина 122 шага, CI = 0.804, HI = 0.196.

PA wide comb-like (79), setae *sce* in immature instars situated ventrally (83).

Moss and Lombert [1983] admitted the possibility of the independent loss of legs in immature instars of Harpypalpinae and Ophioptidae. If we accept this suggestion, it is also possible to suggest that the transition of dorsal hysterosomal setae to the ventral side of the body, and the reduction of peritremes and reduction of anus depend upon the reduction of legs i.e., these characters correlate with the reduction of legs. However there is a number of characters, which unite the Harpypalpinae and Ophioptidae, but do not obviously correlate with the reduction of legs. Naturally, some of these characters could appear convergently, but it is difficult to suggest a convergent origin of all these different characters.

At the same time, only five characters, which are present in Ophioptidae in a plesiomorphic state, are represented in Harpirhynchinae and Harpypalpinae by apomorphic states.

The character 2 (peritremes being segmented only in lateral ends) in Harpirhynchinae and Harpypalpinae is more primitive state in relation to Ophioptidae, in which the peritremes are completely reduced. For other evolved character states — 10 (setae PA, PI, PE situated together on the apex of a palp), 16 (shape of seta *sca*), 29 (epimeres weakly developed or absent), 73 (2–3 pairs of setae *g* in male) — there is a high probability of their independent origin. Besides, the polarity of the character 10 is doubtful. It is possible that the separated position of setae PE from setae PI, PA is not a plesiomorphy but rather an apomorphy of Harpirhynchinae and Harpypalpinae.

Based on these conclusions we have included the Ophioptidae into the family Harpirhynchidae as a taxon of a subfamilial rank in the consequent discussion. The monophylies of the subfamilies Harpirhynchinae, Harpypalpinae, and Ophioptinae are strongly supported by 17, 16, and 24 synapomorphies, respectively.

As for relationships between genera of the subfamily Harpirhynchinae, three generic groups are well recognized in the cluster of this subfamily. The group *Neharpyrhynchus*-*Metharpyrhynchus* is marked by three synapomorphies: idiosoma elongated, sac-ciform (character 45), setae *vi*, *ve* in female situated ventrally (59), setae *sce*, *h* in female short or absent (61). The group *Harpyrhynchiella*-*Cypsharpyrhynchus* is supported by 8 synapomorphies: setae PE absent (character 9), setae *pts* absent (14), setae *rp* absent (18), legs III-IV in female without whip-like setae (23), setae on coxa I absent (39), propodosoma in female with lateral lobes (43), setae *ic1* absent (66), setae *ic3* absent (67). The group *Anharpyrhynchus*-*Trichorhynchiella* is marked by four synapomorphies: apical segment of leg IV in female with 10 or more setae (character 35), gnathosoma and legs I in female situated dorsally (42), opisthosoma in female with lateral lobes (44), length of vulvar slit is two times shorter than idiosoma (54). All these characters, except the characters 45, are quite reliable at this taxonomic level.

However certain intermedial nodes in this part of cladogram are supported by a lesser number of synapomorphies or some synapomorphies that seem to be doubtful. All harpirhynchine genera, except two plesions (*Perharpyrhynchus* and *Harpyrhynchoides*) are joined into one cluster by a single synapomorphy 70 (setae *pg* in females absent). This derived character state could be developed independently. Moreover, according to the obtained cladogram this character undergoes a reversion, namely in the node joining the genera *Anharpyrhynchus*, *Trichorhynchiella*, *Harpyrhynchiella*, *Cypsharpyrhynchus* that is quite doubtful in cases of seta reductions.

The node joining the genera *Neharpyrhynchus* - *Trichorhynchiella* is marked by two synapomorphies: legs I, II in female reduced (character 21) and pretarsus and tarsus of legs I, II fused in female (24). These character states are observed in mites living inside cysts. They apparently developed independently resulting from a very special life manner of mites and perhaps have no high taxonomic weight. Similar conclusion could be made for the characters 45, 46 (shape of female idiosoma).

More complicated problem is a phylogenetic value of synapomorphies in the node *Harpyrhynchiella* - *Trichorhynchiella*: scales and verrucosities in female cuticle (character 48), propodosomal shield in female is rudimentary or absent (49), male genital aperture situated dorsally near basis of gnathosoma (51). The character 48 varies within some genera, for example in the *Harpyrhynchoides*. The position of male genital aperture (51) as it discussed above in the paragraph «Materials» is also a character of low taxonomic value.

Therefore the cluster carrying the genera *Anharpyrhynchus*, *Trichorhynchiella*, *Harpyrhynchiella*, *Cypsharpyrhynchus* is probably heterogeneous. It

apparently unites different harpirhynchine mites adapted for living in cysts. These mites are characterized by the wide idiosoma, reductions of shields and idiosomal setae, and male genital aperture moved forwards. The latter character state often occurs in different groups of parasitic Prostigmata. We consider that this generic group is a morphological type, but not a true phylogenetic line.

Based on the discussion above we suggested that characters 21, 24, 45, 46, 48, 49, 51, 67, 70 marking some doubtful nodes, could be excluded at the second step of the phylogenetic analysis. Besides, we have excluded the characters 11 (shape of seta *PI*) and 67 (setae *ic3* absent), which when displayed manifests a homoplasy (Fig. 2).

At the second step of the analysis all the rest characters were considered as ordered characters. Single tree was obtained with the following general indices: length 92, CI 0.848, HI 0.152 (Fig. 3). This tree demonstrates more polytomies than the previous one does (Fig. 2), however according to our opinion it better represents the phylogenetic relationships within the Harpirhynchidae at the recent state of knowledge.

The structure of the consensus cladogram (Fig. 3) does not allow to recognize all generic groups which could completely correspond to the tribes proposed by Fain [1972]. The genera *Metharpyrhynchus* and *Neharpyrhynchus* could comprise the tribe Metharpyrhynchini, and the genus *Perharpyrhynchus* could represent the tribe Perharpyrhynchini. However, the acceptance of this taxonomic resolution logically demands erecting of all other generic groups to a tribe level. In this case the subfamily Harpirhynchinae would consist tribes, three of which would a single genus.

We believe that subsequent studies in the Harpirhynchidae and discoveries of new genera would confirm the pertinency of these tribes. At the present stage of investigation we suggest to recognize 6 generic groups within the subfamily Harpirhynchinae: *Harpirhynchus* group (1 genus), *Harpyrhynchoides* group (1 genus), *Perharpyrhynchus* group (1 genus, =Perharpyrhynchini), *Metharpyrhynchus* group (*Metharpyrhynchus* and *Neharpyrhynchus*, partly = Metharpyrhynchini), *Anharpyrhynchus* group (*Anharpyrhynchus* and *Trichorhynchiella*), *Harpyrhynchiella* group (*Ralliharpyrhynchus*, *Harpyrhynchiella* and *Cypsharpyrhynchus*).

It is also necessary to note that the taxonomical interpretation of the obtained cladogram has a significant similarity to the numerical classification proposed by Moss and Wojcik [1978]. Species groups recognized by these authors correspond to certain genera described by Fain [1972, 1995] and some generic groups recognized in the present study. Thus the «*agapornis*» group corresponds to *Harpyrhynchoides*, «*porphyrio*» group — to *Ralliharpyrhynchus*, «*jacana*» group — to *Perharpyrhynchus*, «*monstrosus*» group — to *Anharpyrhynchus*, «*squamiferus*» group — to *Neharpyrhynchus*, «*nidu-*

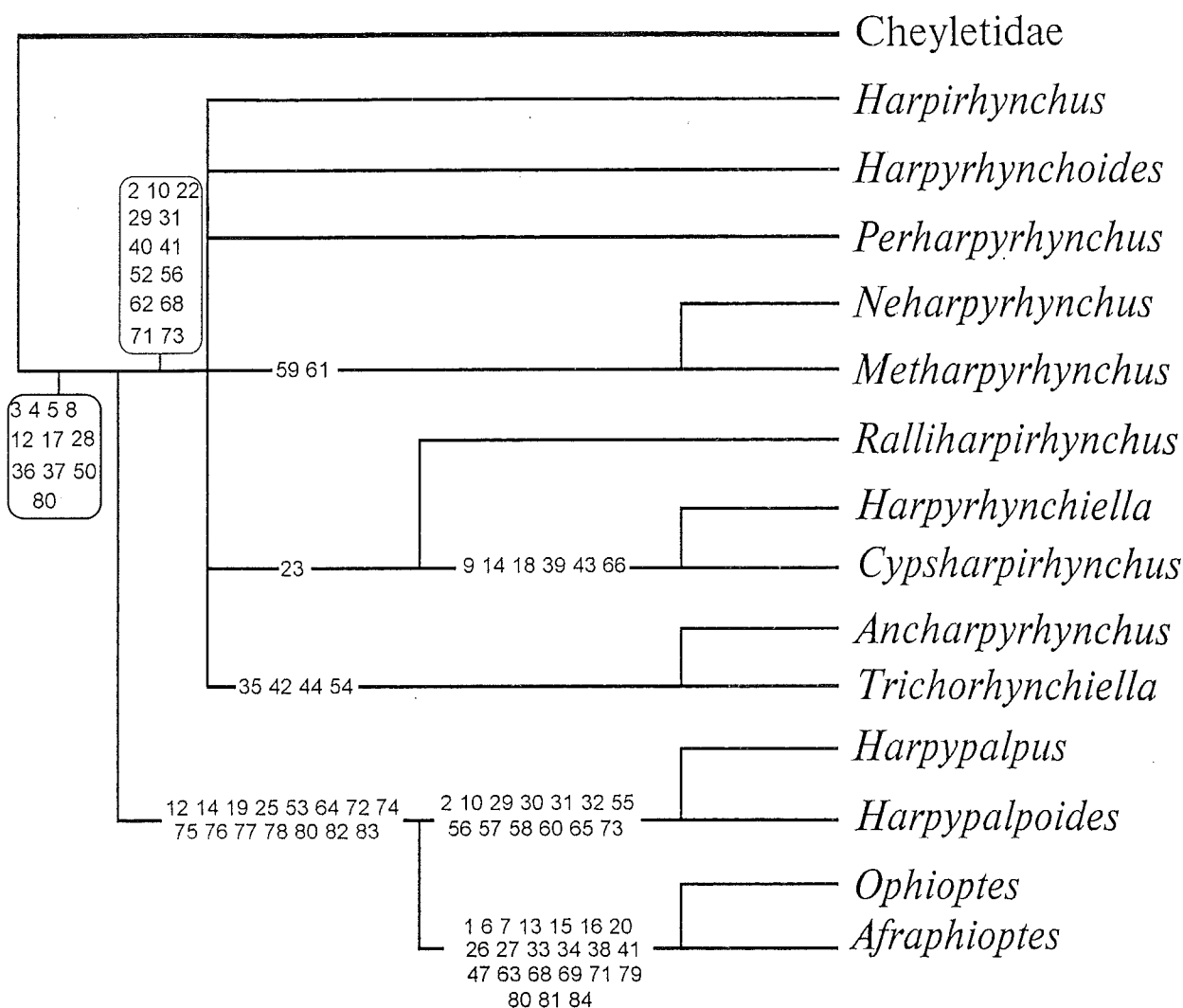


Fig. 3. Cladogram of the Harpirhynchidae, characters 11, 21, 24, 45, 46, 48, 49, 51, 67, 70 excluded. PAUP 3.0s (DELTRAN): tree 1, length 91 steps, CI = 0.857, HI = 0.143
 Рис. 3. Кладогамма Harpirhynchidae, признаки 11, 21, 24, 45, 46, 48, 49, 51, 67, 70 исключены. PAUP 3.0s (DELTRAN): 1 дерево, длина 91 шаг, CI = 0.857, HI = 0.143.

lans» group — to *Harpirhynchus*, «reductus» group — to *Harpyrhynchiella* and *Cypsharpirhynchus*.

HOST-PARASITE RELATIONSHIPS OF THE FAMILY HARPIRHYNCHIDAE

According to our analysis three subfamilies can be recognized within the family Harpirhynchidae. The subfamily Harpirhynchinae includes parasites dwelling on a skin surface, in feather follicles, and sometimes producing cysts; these mites occur on birds of different orders [Moss, 1979; Fain, 1994a, 1995]. The Harpypalpinae includes parasitic mites forming cysts in a skin layer which associated exclusively with passeriform birds (Aves: Passeriformes) [Moss, 1979; Lombert, Moss, 1983]. Mites of the subfamily Ophioptinae occur under scales of two «higher» snake families, Colubridae and Elapidae [Southcott, 1956; Fain, 1964; Beron, 1974; Lizaso, 1981].

Mites of all subfamilies obtain a unique complex of synapomorphies in the gnathosoma structure, that have been developed in the result of

parasite mode of life. Therefore it seems rather doubtful to suppose that each subfamily had an independent origin from the predatory cheyletoid-like ancestors, as it was suggested by Moss [1979] in relation to the subfamilies Harpirhynchinae and Harpypalpinae. As far as this author considered the Harpirhynchidae as a monophyletic taxon, he probably accepted a concept of a wide monophyly. In our opinion similar characters in three subfamilies of the Harpirhynchidae could not originate independently. Apparently these features have been inherited from a common cheyletoid-like ancestor, which developed a parasitic mode of life.

Within the family, the subfamilies Harpypalpinae and Ophioptinae are the sister groups in relation to the Harpirhynchinae. Numerous synapomorphies uniting these two taxa also prove that two first subfamilies had a common ancestor. As it can be drawn out of the phylogenetic hypothesis (Fig. 3), such features as the absence of legs, peritremes and anus, the development of unique similarities in the idiosomal chaetotaxy pattern in immature instars,

as well as the development of some apomorphies in adults, have been developed in a common ancestor of mites of these subfamilies.

If we admit the independent reduction of legs in immature instars in the Harpypalpinae and Ophioptinae as it was suggested [Lombert, Moss, 1983], it is difficult to imagine an independent origin of all other synapomorphies, even if some of them are partly correlated.

At present only two hypotheses could be proposed to explain the origin and evolution of the host parasite-relationship within the Harpirhynchidae.

According to a first hypothesis, some cheyletoid-like predatory ancestor had started its ectoparasite mode of life on a common ancestor of birds and reptiles. On these ancestors the harpirhynchid mites have splitted into two main phyletic branches. One branch had lead to the Harpirhynchinae, the other branch had given rise to the origin of the ancestor of the harpypalpine and ophioptine mites. The mites of both branches have evolved in 2 parallel lines represented in the present time on birds by the mite subfamilies Harpirhynchinae and Harpypalpinae, respectively. On the reptiles only mites of the second branch have survived. Nowadays they are represented by the Ophioptinae. Representatives of the harpirhynchine branch had apparently been extinct yet on ancestors of reptiles. The possible reason for this extinction is probably the peculiarities of the moulting process in reptiles. These animals loose entire external dermal layer or large pieces of it [Landmann, 1984]. Slowly moving harpirhynchine mites probably could not survive in such conditions.

This hypothesis has two restrictions. It cannot explain clearly why the Harpypalpinae are present on Passeriformes only and are absent from all other bird orders, and also why the Ophioptinae are associated only with higher snakes of the families Colubridae and Elapidae and are absent from other snake families and the lizards. It could be expected however that the representatives of the latter subfamily occur on some other snakes and lizards.

According to a second hypothesis, the mites of the family Harpirhynchidae were formed only on a common ancestor of birds, which probably had appeared in the upper Jura [Kurochkin, 1993]. Later origin of this mite group already on certain bird orders and subsequent migrations onto other bird orders seems quite doubtful. Recent Harpirhynchidae are widely distributed on birds of different orders (Table 2).

As it was mentioned above, the Harpypalpinae are associated exclusively with the Passeriformes. In the frames of the second hypothesis it is possible to suggest that ancestors of the Harpypalpinae-Ophioptinae branch were originally associated with the bird phylum that gave the origin to Passeriformes. Adult mites of the Harpypalpinae are more similar to the ancestral forms than the representatives of the Harpirhynchinae. It is expressed not only in the

structure of legs, but in the idiosomal chaetotaxy, as well. Moss [1979] stressed that in general the adult mites of the subfamily Harpypalpinae are more primitive by their morphological features. It looks like a paradox that the mites of more primitive subfamily are associated with the highly evolved hosts. On the contrary, the immature instars of the Harpypalpinae are highly derived in their morphology, because they have lost legs and are characterized by a quite specialized idiosomal chaetotaxy. Apparently in this case we have here two principally different pathways in the morphological evolution of mites of these subfamilies [Lombert, Moss, 1983]. In the Harpirhynchinae the progressive characters are represented in adults, whilst in the Harpypalpinae and Ophioptinae they are developed in immatures.

Relationships of Passeriformes with the higher Neornithes are not clear [Kurochkin, 1993]. It is possible that this order represents some earlier separated branch. Certain parasitological data support the hypothesis of the early origin of Passeriformes. Thus, the rather archaic representatives of the families Rhinonyssidae (Mesostigmata) and Ereyneidae (Prostigmata) are associated with Passeriformes [Moss, 1979]. The feather mite family Proctophylloidae (Astigmata) restricted to the passerines is one of most evolved feather mite families but is also characterized by certain archaic features [Mironov, 1998]. If one admits the hypothesis of earlier origin of Passeriformes the separate phylogenetic position of the Harpypalpinae could be easily explained by their coevolution with the passerines.

The next key point of a second hypothesis is an idea of the secondary migration of mites belonging to the Harpypalpinae — Ophioptinae branch from birds onto the snakes. The possibility of this host shift was originally proposed by J. Kethley [after: Lombert, Moss, 1983]. Certain snakes feed on nestlings and adult birds. Most of these preys are small passerine birds. Recent subfamily Ophioptinae is associated exclusively with Colubridae and Elapidae [Fain, 1964]. These two snake families are closely related and represent a group of higher snakes [Rieppel, 1988]. So, it is possible to suggest, that the ancestor of the Ophioptinae migrated from some ancestral passerines onto the common ancestor of these families of snakes.

It was found out that mites of subfamily Ophioptinae are situated on the skin surface, or make only little caves under scales, but never produce any subcutaneous capsules in the skin (observations made during the of present study). It is possible to suggest that this is the ancestral mode of location of the harpirhynchid mites and it was typical for the ancestors of the family.

On the contrary, the representatives of the Harpypalpinae form cysts in a skin of recent passerines [Moss, 1979; Lombert, Moss, 1983]. Therefore the Harpypalpinae obtain more derived

Phylogeny of the Harpirhynchid mite

Table 2. Distribution on the bird taxa of the harpirhynchin and harpyalpin genera
Таблица 2. Птицы — хозяева клещей подсемейств Harpirhynchinae и Harpyalpininae

Mite genus	Host family	Host order
<i>Harpirhynchus</i>	Fringillidae, Icteridae, Corvidae, Alaudidae, Sylviidae	Passeriformes
<i>Neharpyrhynchus</i>	Ploceidae, Fringillidae, Muscicapidae, Certhiidae, Paridae, Emberizidae, Troglodytidae, Sturnidae, Aegithalidae	Passeriformes
	Trochilidae	Apodiformes
<i>Metharpyrhynchus</i>	Sylviidae, Ploceidae, Estrildidae	Passeriformes
	Picidae	Piciformes
<i>Perharpyrhynchus</i>	Jacaniidae, Recurvirostridae	Charadriiformes
<i>Ralliharpirhynchus</i>	Rallidae	Gruiformes
<i>Harpyrhynchiella</i>	Apodidae	Apodiformes
<i>Cypsharpirhynchus</i>	Apodidae	Apodiformes
<i>Anharpyrhynchus</i>	Corvidae, Meliphagidae	Passeriformes
<i>Trichorhynchiella</i>	Estrildidae	Passeriformes
<i>Harpyrhynchoides</i>	Phasianidae	Galliformes
	Scolopacidae	Charadriiformes
	Columbidae	Columbiformes
	Accipitridae	Falconiformes
	Ciconiidae, Ardeidae	Ciconiiformes
	Psittacidae	Psittaciformes
	Tytonidae, Strigidae	Strigiformes
	Anatidae	Anseriformes
	Alaudidae, Emberizidae, Muscicapidae, Fringillidae, Corvidae	Passeriformes
	Picidae	Piciformes
	Cuculidae	Cuculiformes
	Coliidae	Coliiformes
<i>Harpyalpus</i>	Ploceidae, Troglodytidae, Paridae, Corvidae, Eurylamiidae, Turdidae, Fringillidae, Emberizidae	Passeriformes
<i>Harpyalpoides</i>	Sturnidae, Hirundinidae, Emberizidae	Passeriformes

characters in idiosomal and leg chaetotaxy comparing to the Ophioptinae. Thus, in the Ophioptinae the tarsus I bears 10 setae, setae *el* are well developed, setae *d3*, *l3* are always present, and genital shield of male bears 4 pairs of setae; in the Harpyalpinae tarsus I with 8 setae only, setae *el* are weakly developed, setae *d3*, *l3* are absent, and genital shield of male with 3 pairs of setae.

Based on the facts listed above, we suggest that a second hypothesis is more reliable, because it needs less assumptions. Surely, this hypothesis leaves some problems unsolved. For example, if the ancestors of Harpyalpinae-Ophioptinae could successfully migrate onto such far related hosts as the snakes, why they could not migrate onto different birds of prey (Falconiformes, Strigiformes). It also could not explain, why the harpyalpine mites had begun to produce intracutaneous cysts, while the ophioptin mites did not develop this feature.

Host Associations of the Harpirhynchinae

Among 27 recent orders of birds [Howard, Moore, 1991] the mites of the family Harpirhynchidae are recorded from the representatives of 16 bird orders [Moss, 1979]. However the latter author used for the analysis a certain number of undescribed species deposited in his collection. Since that time none of these species was described. Therefore we use in the present work only the data on host-parasite associations based on really described representatives of the subfamily.

All recent orders of birds could be grouped into three groups [Kurochkin, 1993]. The Palaeornithes includes Struthioniformes, Ralliformes, Tinamiformes, Casuariiformes and Apterygiformes. The Harpirhynchinae are not known from these orders. The second group, Paraneornithes, includes only the Galliformes and Anseriformes. As it is shown in table 2, only the genus *Harpyrhynchoides* is associated with both orders. The third group, Neornithes, comprises 20 orders, among them the harpirhynchine mites are recorded from birds of 12 orders [Fritsch, 1954; Moss, 1979; Fain, 1994a, 1995].

The mites of the most archaic genus *Harpyrhynchoides* can be found on the representatives of all 12 orders. They are known both from such a derived order as Passeriformes and the archaic orders Galliformes and Anseriformes. A wide distribution of this genus among the host orders is probably a result of its early origin, as it is shown in the cladogram (Fig. 3). Perhaps the ancestor of this archaic genus had appeared even on a common ancestor of Paraneornithes and Neornithes.

The genus *Harpyrhynchoides* includes 30 species. Fain [1994] separated them into two groups, A and B, based on one character only (one or two free segments in a leg III in females). This genus splitting up is useful only for the species identification but cannot be supported by our results of analysis of the genus structure.

According to Moss [1979], the number of harpirhynchine mite species really existing in the world could exceed 2.5 thousands. Therefore our analysis of the genus structure and associations of its members with bird taxa could be considered as a preliminary one. An attempt to recognize certain species groups was based on 11 characters (Table 3). In general these characters have a mosaic distribution and do not correlate with one another. However the most primitive species, with relatively full set of leg and body chaetotaxy are clearly restricted to the Galliformes (Table 3). Despite their general primitive chaetotaxy, these species bear only 2 setae on genua I–II whilst other species of the genus have 3–4 setae.

Mites associated with Galliformes represent the «*coturnix*» species group. Most evolved species of the genus are associated mainly with Passeriformes. They comprise the «*zumpti*» species group. Most morphological characters of this group are obviously represented by derived states (Table 3). The only exception in this group both in chaetotaxy and host associations is *H.anatum* Fain, 1976 known from Anseriformes; females of this species has not setae *pg*.

The group associated with the Psittaciformes is heterogeneous in their morphological features and apparently includes several groups. However, the morphological similarity between species associated with parrots from certain geographical region, Africa, Asia or South America is manifested. The group restricted to pigeons and doves (the family Columbiformes) is also heterogeneous. Mites from other orders of birds are represented by 1–2 species only.

The genera *Neharpyrhynchus* and *Metharpyrhynchus* are distributed on two bird's orders. The common host order for both these genera is the Passeriformes. Besides, this host group, *Neharpyrhynchus* occurs on the hummingbirds (Apodiformes: Trochilidae), and *Metharpyrhynchus* — on the woodpeckers (Piciformes: Picidae).

Other 7 genera are represented by a few species and each genus is restricted to a certain bird order (Table 2). Three of them (*Harpirhynchus*, *Anharpyrhynchus* and *Trichorhynchiella*) are the specific parasites of the Passeriformes. Two genera (*Cypsharpirhynchus*, *Harphyrhynchiella*) are restricted to the swifts (Apodiformes: Apodidae). Both genera living on swifts and the genera *Anharpyrhynchus*, *Trichorhynchiella* living on passerines are the most evolved genera by their morphological features.

Host associations of the subfamily Harpyalpinae

Representatives of both genera of the Harpyalpinae are distributed on 10 families of Passeriformes (Table 2) [Fritsch, 1954; Moss, 1979; Lombert, Moss, 1983; Fain et al., in press]. All these species are associated with the higher passerines of the suborder Oscines. Probably the biodiversity of

Phylogeny of the Harpirhynchid mite

Table 3. Characters, host orders and geographical distribution of mites of the genus *Harpyrhynchoides*
Таблица 3. Признаки, отряд хозяев и распространение клещей рода *Harpyrhynchoides*

Mite species	Characters*											Host order	Region
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI		
<i>coturnix</i>	0	1	0	0	0	2	1	0	0	0	0	Galliformes	Africa
<i>numidae</i>	0	?	?	0	0	2	1	?	?	0	0	Galliformes	Africa
<i>alectori</i>	0	1	0	0	0	2	1	0	0	0	0	Galliformes	Europe
<i>capellae</i>	0	0	1	0	0	1	1	0	0	0	0	Charadriiformes	Europe
<i>metropeliae</i>	0	0	0	0	1	1	1	1	1	0	0	Columbiformes	S.America
<i>capitatus</i>	0	1	0	?	?	1	1	1	?	?	0	Columbiformes	S.America
<i>modestus</i>	1	0	2	0	1	1	1	1	1	1	1	Columbiformes	S.America
<i>coxatus</i>	1	0	0	0	1	1	1	1	1	1	0	Columbiformes	S.America
<i>oenae</i>	0	1	2	0	1	1	1	1	1	1	0	Columbiformes	Africa
<i>columbae</i>	0	1	0	0	1	1	0	1	1	1	1	Columbiformes	Europe
<i>tracheatus</i>	0	?	?	0	1	1	?	?	1	1	0	Falconiformes	Europe
<i>leptoptilus</i>	0	1	0	0	1	1	1	1	1	1	0	Ciconiiformes	Africa
<i>herodius</i>	0	0	2	0	1	0	0	1	1	0	0	Ciconiiformes	Europe, N.America
<i>kakatoe</i>	0	?	0	0	1	0	1	1	1	1	1	Psittaciformes	Australia
<i>rosellacinus</i>	1	0	0	0	1	1	1	1	1	1	0	Psittaciformes	Australia
<i>amazonae</i>	1	1	2	0	1	1	1	1	1	1	0	Psittaciformes	S.America
<i>lawrence</i>	1	0	2	0	1	1	1	1	1	1	0	Psittaciformes	S.America
<i>psittaci</i>	1	?	?	0	0	1	1	?	0	1	0	Psittaciformes	Africa
<i>agapornis</i>	1	1	2	0	1	1	1	0	0	1	0	Psittaciformes	Africa
<i>psittaculae</i>	0	1	2	0	1	1	1	1	1	1	1	Psittaciformes	Asia
<i>squamosus</i>	0	0	2	0	1	1	1	1	1	1	1	Psittaciformes	Asia
<i>tyto</i>	0	0	0	0	1	1	1	1	1	1	1	Strigiformes	Europe
<i>asio</i>	?	0	2	?	?	1	1	1	1	1	1	Strigiformes	Europe
<i>anatum</i>	1	?	?	1	1	1	1	?	0	1	0	Anseriformes	Europe, Africa, Asia
<i>zumpti</i>	1	0	2	1	0	1	1	1	1	1	0	Passeriformes	Africa, S.America
<i>rubeculinus</i>	1	?	?	1	0	1	1	?	1	1	0	Passeriformes	Europe
<i>parazumpti</i>	1	?	?	1	0	1	1	?	1	1	0	Passeriformes	Europe
<i>kirgizorum</i>	1	0	2	1	0	1	1	1	1	1	0	Passeriformes	Asia
<i>pectinifer</i>	1	?	0	0	1	1	1	1	1	1	0	Piciformes	Africa
<i>vercammeni</i>	1	?	?	?	0	1	1	?	1	1	0	Cuculiformes	Africa
<i>cristagalli</i>	1	?	?	0	0	1	1	0	1	1	0	Coliiformes	Africa

*List of characters: I. in female, legs IV with 2 segments - 0, with 1 segment - 1; II. in male, setae *vi* serrate - 0, smooth - 1; III. in male, distance *g3-g3* longer than *g2-g2* or *g1-g1* - 0, *g1-g1* longer than *g3-g3* or *g2-g2* - 1, position of setae *g* another - 2; IV. in female, setae *pg* present - 0, absent - 1; V. in female, setae *l5* longer than 40 μ m - 0, shorter - 1; VI. genus I-II with 4 setae - 0, with 3 setae - 1, with 2 setae - 2; VII. femur I-II with 3 setae - 0, with 2 setae - 1; VIII. in male, preapical segment of leg III with 2 setae - 0, with 1 seta - 1; IX. in female, preapical segment of leg III with 2 setae - 0, with 1 seta - 1; X. in female, preapical segment of leg IV with seta - 0, without seta - 1; XI. scale on cuticle of idiosoma absent - 0, present - 1.

these genera that have become known quite recently is still not well recovered for making a clear analysis on their host-associations within Passeriformes.

Host Associations of the Subfamily Ophioptinae

At present the subfamily includes 16 species belonging to two genera *Ophioptes* (14 species) and *Afrophioptes* (2 species) [Fain, 1964, 1965; Beron, 1974; Lizaso, 1981]. All of them are associated with snakes of the families Colubridae and Elapidae. The list encompassing most of recently described species and their host associations was published by Fain [1964]. Since this publication 4 new species have been described: i.e. *O.machadoi* Fain, 1965 ex *Dispholidus typus* (Colubridae) from Angola; *O.beshkovi* Beron, 1974 ex *Coluber najadun* (Colubridae) from Bulgaria; *O.longipilis* Lizaso, 1981, and *O.brevipilis* Lizaso, 1981 from many snake species of the genera *Oxyrhopus*, *Chironius*, *Philodrias*, *Mastigodrias*, *Leimadophis*, and *Lygophis* (Colubridae) from Brasil.

Within the genus *Ophioptes* Fain [1964] the «*parkeri*» species group was recognized. It included 3 species which were characterized by the presence of setae on femur III. We suppose, that 9 other species could be referred to as the «*schoutedeni*» species group. Two species described by Lizaso [1981] should be considered as *insertae sedis* within the *Ophioptes*, because their diagnoses are incomplete.

Recently known genera and species groups of the Ophioptinae are clearly associated with certain geographical groups of the hosts, whilst their association with certain taxa of snakes are not observed. Perhaps it is caused by the poor state of knowledge of the real biodiversity of the Ophioptinae.

Species of the «*parkeri*» group (*Ophioptes*) are distributed on different Colubridae in South America and Cuba. Species of the «*schoutedeni*» group occur on different continents (Africa, Eurasia, North and South America) and parasitize both Colubridae and Elapidae. The genus *Afrophioptes* is restricted to the African Colubridae.

Host specificity of the Harpirhynchidae

The range of host specificity in species of the Harpirhynchidae is still a question. Based on the analysis of publications and of our own data it is possible to conclude that such well examined species as *Neharpyrhynchus plumaris* Fritsch, 1954, *Anharpyrhynchus monstrosus* Fritsch, 1954, *Harpyrhalpus longipes* Fritsch, 1954, *Ophioptes parkeri* Sambon, 1928, are commonly associated with a certain host family or closely related families [Fritsch, 1954; Fain, 1964, 1995; Moss, 1979]. It is possible that some species of the Harpirhynchinae are restricted to certain genus or even species. This is observed, for example, in harpirhynchine species living on Galliformes or in *Harpyrhynchoides rubeculinus* [Cerny et Sixl, 1971] from *Erithacus rubec-*

ula (Passeriformes: Turdidae) [Cerny, Sixl, 1971; Fain et. al., in press].

It can be concluded, that harpyrhynchid species are oligoxenous parasites in general. Their host specificity is not as high as in Demodicidae [Nutting, 1985], Psorergatidae [Giessen, 1990], and Myobiidae [Fain, 1994b; Bochkov, 1997]. However, even this rate of specificity is suitable enough to recognize traces of coevolutionary relationships, based on general correlations of the phylogenetic hypothesis [Kim, 1985].

As it is shown in the discussion, certain coincidence of the phylogenetic hypothesis for the Harpirhynchidae with the recent macrophylogenetic concept for the birds displays traces of their coevolutionary relationships. Concluding, we could only suppose that further studies of the harpirhynchid mite biodiversity, and host associations of this taxon would give numerous new data to propose more clear and detailed pattern of coevolution and discover possible host shift events during the evolution of this family.

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