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Phylogeny and system of the Cheyletidae (Acari: Prostigmata) with special reference to their host-parasite associations

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Summary

The reconstruction of the phylogeny of the mite family Cheyletidae (Acari: Prostigmata) was effectuated by a cladistic method with the software PAUP 3.1. Representatives of most of the cheyletid genera have been examined. The predator mites of the family Stigmaeidae were used as outgroup. The analysis was based on 91 morphological characters. The obtained strict consensus tree has included 13 principal clusters and numerous ungrouped genera. Among these ungrouped genera, two genera, *Bak* and *Caudacheles* may be recognized as separate groups, since they possess some autapomorphic characters, which clearly separate these mites from the other cheyletids. All the established groups have been considered as tribes and the ungrouped genera have been included in the paraphyletic tribe "Cheyletini". Thus, the family Cheyletidae includes now 15 tribes: Acaropsellini (= Acaropseini) VOLGIN, 1969, Bakini VOLGIN, 1969, Cheletogenini VOLGIN, 1969, Cheletosomatini VOLGIN, 1969, Chelonotini VOLGIN, 1969, Cheyletiini VOLGIN, 1969, Cheyletiellini VOLGIN, 1969, "Cheyletini" LEACH, 1814, Cheletomorphini **trib. nov.**, Criokerontini SMILEY, 1977, Metacheyletiini FAIN, 1980, Niheliini SMILEY, 1977, Ornithocheyletiini VOLGIN, 1969, Teinocheylini FAIN, 1974 and one unnamed tribe including the genera *Caudacheles* and *Alliea*.

A new hypothesis on the phylogenetic evolution of the Cheyletidae and an analysis of their host-parasite associations are proposed. Parasitism of birds by feather mites and of mammals by skin and pilicolous mites probably started in the nests of their vertebrate hosts (FAIN, 1979f). In the particular case of cheyletid mites the parasitism was probably initiated by predacious mites living in the nests. This transfer of predation to parasitism probably happened repeatedly and at different periods of time. Parasitic associations between cheyletids and vertebrates are more common than the associations between these mites and the invertebrates. In the invertebrates these associations are generally restricted to a phoresy.

Key words: Cheyletidae, evolution, systems, mites, parasites

Résumé

Les auteurs proposent une reconstruction phylogénétique de la famille Cheyletidae (Acari: Prostigmata) au moyen d'une méthode cladistique utilisant le programme PAUP 3.1. Des représentants de la plupart des genres connus de cette famille ont été examinés. Les acariens prédateurs de la famille Stigmaeidae ont été choisis comme groupe témoin (outgroup). L'analyse cladistique fut basée sur 91 caractères morphologiques. Elle a montré l'existence de 13 groupes principaux et de nombreux genres non groupés. Parmi ces derniers il y a 2 genres, *Bak* et *Caudacheles* qui doivent etre considérés comme des groupes distincts a cause de leurs caractères autapomorphiques qui les séparent nettement de tous les autres genres de Cheyletidae. Tous les groupes retenus sont élévés au rang de tribu et les genres non groupés ont été réunis dans une tribu paraphylétique "Cheyletini". Après ce remaniement la famille Cheyletidae compte actuellement les 15 tribus suivantes: Acaropsellini (= Acaropseini) VOLGIN, 1969, Bakini VOLGIN, 1969, Cheletogenini VOLGIN, 1969, Cheletosomatini VOLGIN, 1969, Chelonotini VOLGIN, 1969, Cheyletiini VOLGIN, 1969, Cheyletiellini VOLGIN, 1961, "Cheyletini" LEACH, 1814, Cheletomorphini **trib. nov.**, Criokerontini SMILEY, 1977, Metacheyletiini FAIN, 1980, Niheliini SMILEY, 1977, Ornithocheyletiini VOLGIN, 1969, Teinocheylini FAIN, 1974, et une tribu innominée formée des genres *Caudacheles* et *Alliea*. Une nouvelle hypothèse sur l'évolution phylogénétique des Cheyletidae et une analyse de leurs associations hote-parasite sont proposées. Comme pour d'autres groupes d'acariens parasites (p. e. les Astigmates plumicoles des oiseaux et les pilicoles des mammifères (FAIN, 1979f), le parasitisme par les Cheyletidae a très probablement pris naissance dans les nids de leurs hotes, oiseaux ou mammifères. L'association parasitaire entre cheyletidés et vertébrés est plus fréquente que celle entre cheyletidés et invertébrés. Dans le cas des invertébrés l'association relève généralement de la simple phorésie.

Mots-cle: Cheyletidae, evolution, systematique, acariens, parasites

Introduction

The family Cheyletidae LEACH, 1815 (Acari: Prostigmata) is a basic taxon of the superfamily Cheyletoidea. According to the classification of Acari proposed by KETHLEY (1982), the family Cheyletidae belongs to the superfamily Cheyletoidea, subcohort Raphignathae, cohort Eleutherengona, suborder Prostigmata. The position of this family within the superfamily Cheyletoidea and its relations with other cheyletoid families has been discussed by BOCHKOV (1999, 2001 in press).

Cheyletid mites have a world wide distribution and they occur on all the continents. The mites of the family Cheyletidae occupy a great variety of habitats. Some of them are free -living predators inhabiting on plants, soil and plant debris, other groups are nidicolous predators living in nests of birds and mammals and insect colonies. A small group of cheyletids are dwelling into the feather quills of birds. Investigation on cheyletid mites is very interesting because it could help us to understand the origin and the mechanism of evolution in parasitism (BEKLEMISHEV, 1970).

Some representatives of this family are also quite important for the agricultural economy and the health of man and domestic animals. Many predaceous Cheyletidae feed on microarthropods causing damage to agricultural plants and grain supply (VOLGIN, 1969). Other mites are parasites of domestic animals (rabbits, cats, dogs etc)

Table 1. List of genera used in cladistic analysis

* – genera studied with literature data
** – number of known species according to GERSON *et al.* (1999), with alterations.

Genus	number of known species **	number of studied species
Acaropsella VOLGIN, 1962	10	2
Acaropsellina SUMMERS, 1976	12	2
Apodicheles FAIN, 1979	2	2
Bak YUNKER, 1961	11	3
Bakericheyla VOLGIN, 1966	6	6
Bothrocheyla VOLGIN, 1964	3	1
* *Camincheyletus* SMILEY et WHITAKER, 1981	1	-
Caudacheles GERSON, 1968	3	1
Chelacaropsis BAKER, 1949	6	4
Chelacheles BAKER, 1958	10	3
Cheletacarus VOLGIN, 1961	5	1
Cheletogenes OUDEMANS, 1905	12	1
Cheletoides OUDEMANS, 1904	2	1
Cheletomimus OUDEMANS, 1904	14	1
Cheletomorpha OUDEMANS, 1904	7	2
Cheletonella WOMERSLEY, 1941	5	1
**Cheletophanes* OUDEMANS, 1904	2	-
Cheletophyes OUDEMANS, 1904	14	4
Cheletopsis OUDEMANS, 1904	9	5
Cheletosoma OUDEMANS, 1904	1	1
Chelonotus BERLESE, 1893	1	1
Cheyletia HALLER, 1884	5	2
Cheyletiella CANESTRINI, 1886	7	4
Cheyletus LATREILLE, 1796	70	27
* *Chiapacheylus* DE LEON, 1962	3	-
Criokeron VOLGIN, 1966	2	2
Cunliffella VOLGIN, 1969	7	4
Dubininiola VOLGIN, 1969	3	1
Eucheyletia BAKER, 1949	16	9
Eucheyletiella VOLGIN, 1969	7	6
Eutogenes BAKER, 1949	14	1
Galagocheles FAIN, 1979	1	1
Grallacheles DE LEON, 1962	2	1
Hemicheyletia VOLGIN, 1969	41	4
Hoffmannita PELAEZ, 1962	3	2
Hylopecheyla FAIN, 1972	2	2
Hypopicheyla VOLGIN, 1969	2	2
Ker MUMA, 1964	6	2
Lepidocheyla VOLGIN, 1963	2	2
Metacheletoides FAIN, 1972	4	4
Metacheyletia FAIN, 1972	2	1
Mexecheles DE LEON, 1962	8	3
Microcheyla VOLGIN, 1966	4	2
Muricheyla FAIN, 1972	1	1
Neoacaropsis VOLGIN, 1962	2	1
Neochelacheles SMILEY et WILLIAMS,1972	1	1
Neocheyletiella BAKER, 1949	13	7
Neoeucheyla RADFORD, 1950	6	2
Nihelia DOMROW et BAKER, 1960	3	2
Nodele MUMA, 1964	6	2
Ornithocheyletia VOLGIN, 1964	26	17
* *Oudemansicheyla* VOLGIN, 1969	2	-
Paracaropsis VOLGIN, 1969	1	1
Paracheyletia VOLGIN, 1955	4	2
Paracheyletiella KUZNETZOV, 1977	1	1
Pavlovskicheyla VOLGIN, 1965	3	2
Promuricheyla FAIN, 1979	1	1
Prosocheyla VOLGIN, 1969	6	2
Samsinakia VOLGIN, 1965	6	4
Smileycheles FAIN, 1979	1	1
Teinocheylus FAIN, 1974	2	2
Thewkachela IDE et KETHLEY, 1977		
* *Tutacheyla* CORPUZ-RAROS, 1972	2	-
Zachvatkiniola VOLGIN, 1969	1	1

and sometimes provoke dermatitis in persons dealing with infected pets (BRONSWIJK and KREEK, 1976; FAIN *et al.*, 1982).

Because of their harmful role these mites have been actively studied during these last decades. About 72 genera and more than 400 species have been described in this family of mites (GERSON *et al.*, 1999; FAIN and BOCHKOV, 2001, in press;). However, in spite of this great activity in the research of new taxa and biotopes, some important problems, such as the phylogenetical relationships between the taxa had been neglected until now except for the monograph of VOLGIN (1969).

The suprageneric taxonomic system of Cheyletidae proposed by VOLGIN (1969) also needs a revision. Recently, FAIN *et al.* (1997) and GERSON *et.al.* (1999) have re-investigated the generic composition of cheyletid subfamilies represented by parasites, but the relationships between such subfamilies as well as between them and cheyletid taxa of predators were not investigated.

The aim of this study is to elaborate new hypotheses concerning the phylogenetic relationships within the family Cheyletidae by mean of a cladistic analysis. Cladograms constitute the basis for a comprehensive revision of the taxonomic system and the elaboration of an evolutionary scenario in this family of mites. The better knowledge acquired by these studies will enable us to propose new and more credible hypotheses concerning the origin and the host-parasite association of these mites.

This paper comprises the following chapters: materials and methods (i); historical account of the cheyletid taxonomy (ii); analysis of characters (iii); cladistic analysis (iv); taxonomic system of the Cheyletidae and diagnoses of suprageneric taxa (v); evolution of the Cheyletidae and analysis of their host-parasite associations (vi).

MATERIAL AND METHODS

Material

For this study we have re-examined the collections of Cheyletidae deposited in the three following institutions: Institut royal des Sciences naturelles de Belgique (Bruxelles, Belgium), Zoological Institute of the Russian Academy of Sciences (St. Petersburg, Russia) and Musée royal de l'Afrique Centrale (Tervuren, Belgium). The species deposited in these institutions represent 57 genera of Cheyletidae. Besides, the type material of four more genera has been borrowed from other Museums and examined: i.e. the genera *Alliea* and *Thewkachela* both studied by A.F., the genus *Paracheyletiella* examined by A.B and the genus *Cheletosoma* examined by both authors.

Among the 72 genera recently recognized in the Cheyletidae (FAIN and BOCHKOV, 2001 in press), two genera, *Alliea* and *Thryonomycheyla,* have been excluded from our analysis, because they are based only on males (for both genera) or on an incomplete female (*Alliea*).

The representatives of 11 genera were missing in the collections that we have studied. In this group five genera, i.e. *Camincheyletus, Chiapacheylus*, *Cheletophanes, Oudemansicheyla* and *Tutacheyla*, had been adequately described and thus were included in our analysis. Certain morphological details of the genera *Anthribicheyla, Atarsacheylus, Columbicheyla, Eucheletopsis, Laeliocheyletia* and *Sciurocheyla,* necessary for our study were not explicitly mentioned in the original descriptions and therefore we have not retained these genera in our study. Nevertheless, remarks and suggestions concerning the taxonomic position in a new system of the Cheyletidae of all the genera not retained in the analysis are given in the discussion part.

The list of genera (64) used in the cladistic analysis is given in Table 1.

Methods

The study of the phylogenetic relationships existing between cheyletid genera was based on a cladistic method. The software PAUP 3.1 (SWOFFORD, 1993) was used for the phylogenetic reconstruction. MacClade 3.02 (MADDISON and MADDISON, 1992) was used for the analysis of character distribution. The basic data matrix (Table 2) includes 91 characters and 64 ingroup taxa used in analysis. We were restricted to using heuristic methods of tree computation because other search algorithms permit no more than 20 taxa. For this reason, we also could not calculate the bootstrap values. The search used the tree-bisection-reconnection (TBR) branch-swapping algorithm, kept all minimal trees (MULPARS option). The outgroup comparison was used for estimating ancestral states of characters. The family Stigmaeidae have been chosen as an outgroup. If some character was represented within a genus by several states, only the plesiomorphic state was used for coding, because other state had apparently arisen independently within such genus. All characters were weighted equally and most of them were coded binary. The character optimization was made by DELTRAN algorithm (Delayed transformation) because homoplasies for mites, according our opinion, are more common than reversions. The reconstruction of phylogenetic relationships included two steps. In the first step we used 91 characters. In the second phase the doubtful characters (homoplasies) with consistency index less than 0.5 were omitted.

The chaetotaxy of the idiosoma follows that of FAIN (1979c). This nomenclature is based on a topology of setae and has been successfully used in studies of many groups of prostigmatic mites (FAIN, 1970, 1973; FAIN *et al.*, 1997; BOCHKOV, 1997; BOCHKOV and MIRONOV, 1998a; BOCHKOV *et al.*, 1999). The chaetotaxy of the legs follows that of GRANDJEAN (1944).

HISTORICAL ACCOUNT TO THE CHEYLETID TAXONOMY

A comprehensive account of the history of the cheyletid mites, have been given in the monographs of VOLGIN

Table 2. Data matrix

	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901 1111111111222222222233333333334444444445555555556666666666777777777888888888899
OUTGROUP **Stigmaeidae**	00000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000
Acaropsella	00000000000000000100000000010000000000010000000000000000000000000000000000000000111111111
Acaropsellina	00000000000000000100000000010000000000010000000000000000000000000000000000000000111111111
Apodicheles	10000000000010000000000000000000000100000000000000010000000101111101111110000000011111111
Bak	00000000000000000000000000000000000100000002000000000001000000001000000100000000011111111
Bakericheyla	10000000000010000000000000000000000100000000000000010000000100000000011100000000011111111
Bothrocheyla	00000000000000000000111000010111111001000100000000000000000000000000010100001000111111111
Camincheyletus	00000000000000000100000000000000000101000000000000000000000000000000010010000000111111111
Caudacheles	00000001000000000001000000000000000100001000000000000000000000000000010100100011111111
Chelacaropsis	00000000000000000100000000010000000000010000000000000000000000000000000000000000111111111
Chelacheles	00000000000000000100000000010000000000000010000000001000000000000000000000000111111111
Cheletacarus	00000000000000000000000000010000000001000000000010000000000000000000000000000111111111
Cheletogenes	00000000000000000000010000010100000000100000000100000000000000000000010200000011111111111
Cheletoides	00000000000000000100000000010000001000001000000000000000000000000010000001001111111111
Cheletomimus	00000000000000000000000000010000000000000000000000000000000000000000000000010111111111
Cheletomorpha	00000000000000000000000000010000000100000000001000000000000000000001001010000011111111
Cheletonella	00000000000000000000000000000000010000000000000000000000000000000001001000000011111111
Cheletophanes	00000000000000000000000000010000000010000000001000000000000000000001000001011111111
Cheletophyes	00000000000000000000000000000000000000000000000000000000000000000001000000001111111
Cheletopsis	00000000000000000001000000001000000100000010000000000000000000000001000000010011111111
Cheletosoma	00000001000000000001000000010000001000000100000000000000000000000001000000010011111111
Chelonotus	00000000010000000000100000010000001000000000100000001000000000000000010010000000111111111
Cheyletia	00000000000000000000011100000111110011001000000000000000000000000001010000100011111111
Cheyletiella	10000000000010100000000000000000000100000000010000000000100000000000011010000000111111111
Cheyletus	00000000000000000000000000000000000101000000000000000000000000000000010010000000111111111
Chiapacheylus	00000000100000000000011000001111010000011000000000000000000000000000010100001000111111111
Criokeron	00100010000000010000000000000000000100000000000000000000000010000000001000001000011111111
Cunliffella	00000000000000000000011110001011111001000100000000000000000000000000010100001000111111111
Dubininiola	00000000000000000000011000000111010000011000000000000000000000000000010100001000111111111
Eucheyletia	00000000000000000000000000000000000101000000000000000000000000000000010010000000111111111
Eucheyletiella	10000000000010100000000000000000000100000000010000000000100000000000011010000000111111111
Eutogenes	00000001000000000000000000000000000100001000000010000000000000010000001000000011111111111
Galagocheles	01010000000101001000000000000000000100010000000000000000000010000000001000001000111111111
Grallacheles	00000000000000000000011000000111010000010000000000000000000000000000010100001000111111111
Hemicheyletia	00000000000000000000000000010000000000000000000000000000000000000000000000010111111111
Hoffmannita	00000000000000000000011000001111010010001000000000000000000000000000010100001000111111111
Hylopecheyla	00000000000000000000000000000000000100000000000000000000000000000000010010000000111111111
Hypopicheyla	00000000000000000000011000001111010011001000100000000000000000000000010100001000111111111
Ker	00000001000000000000000000000000000100000000000000000000000000000000010010000000111111111
Lepidocheyla	00000000000000000000000000000100010000001000000000000000000000000000010100000000111111111
Metacheletoides	00000000000000000010000000010000001000001000000000000000000000000000010000000100111111111
Metacheyletia	10000000000000000000000000010000000100000000001000000000000000010100110001000000000111111111
Mexecheles	00000000000000000000000000000100000001000000000001000000000000000000010010100001111111111
Microcheyla	00000000000000000000011010000111100010001000000000000000000000000000010100001000111111111
Muricheyla	00001000011000000000100000000000001000000000000000100000000000000000010010000000111111111
Neoacaropsis	00000000000000001000000001000000000000000000000000000000000000000000000000000111111111
Neochelacheles	00000000000000000010000000100000000000000010000000001000000000000000000000000111111111
Neocheyletiella	10000000000010000000000000000000000100000000000000010000001111100011111000000000111111111
Neoeucheyla	00000000000000000000011110001011111001000100000000000000000000000000010100001000111111111
Nihelia	01010000000101001000000000000000000100010000000000000000000010000000001000001000111111111
Nodele	00000000000000000000000000000100000000000000000000000100000000000000000010010000000111111111
Ornithocheyletia	10000000000010000000000000000000000100000000000000010000001000101000001001000000011111111
Oudemansicheyla	00000000000000000000011000000111110000011000000000000000000000000000010100001000111111111
Paracaropsis	00000000000000000100000000010000000000010000000000000000000000000000000000000111111111
Paracheyletia	00000000000000000000000000000000000000100000000000000000000000000000000000000111111111
Paracheyletiella	00000000000000000000000000000000000000100000000000000000000000000000?000000000111111111
Pavlovskicheyla	00000001000000000000000000000000000000100000000000000000000000000000010010000000111111111
Promuricheyla	00001000011000000000000000000000000100000000000000010000000000000000010010000000111111111
Prosocheyla	00000000000000000000000000000000000000100000010000000000000000000000010000000111111111111
Samsinakia	00000000000000000000000000000011101001100100010000000000000000000000010100001000111111111
Smileycheles	01010100000100001000000000000000000101010000000000000000000100000000010000010000111111111
Teinocheylus	10000000000010001000000000000000000110000000100000000000010101000000000100000000011111111
Thewkachela	00000000010000000000100010000000001000000000000000010000000000000000010010000000111111111
Tutacheyla	00000000000000000000000000000100000000000000000000000000000000000000000000000010111111111
Zachvatkiniola	00000000000000000000000000000000000100000000000000000000000000000000010010000000111111111

(1969), SUMMER and PRICE (1970), FAIN *et al.* (1997) and GERSON *et al.* (1999).

Modern taxonomic studies on the Cheyletidae are relatively recent and they began really with the monograph of VOLGIN (1969). This author published a general taxonomic review of the Cheyletidae, he proposed a detailed system for this family and established a numerous of new taxa of suprageneric rank, tribes and subfamilies.

VOLGIN (1969) divided the Cheyletidae into two subfamilies: The Cheyletinae, including only predaceous genera, and the Cheyletiellinae, grouping all the genera associated with birds and mammals.

Composition of the Cheyletinae:

The representatives of the Cheyletinae have a well-developed gnathosoma, comb-like setae on palpal tarsi, teeth on palpal claw, narrow tarsi on legs I, and in the male a ventral position of the genital orifice. This subfamily was divided into eight tribes. The largest of these tribes Cheyletini included 16 genera (we given below the genera which are valid at present time). This tribe is characterised by only plesiomorphic characters. Within this tribe VOLGIN recognised four groups of genera that he considered as forming natural or monophyletic entities: The first group included four genera: *Cheyletus, Eucheyletia, Cheletonella* and *Zachvatkiniola* (i). Morphologically these mites are characterized by the absence of eyes, biologically they are associated with nests of mammals and birds. The second group included the genera *Nodele, Cheletophanes, Cheletacarus, Paracheyletia, Mexecheles* and *Cheletomorpha*; these mites have long legs I and they are living on trees (ii). The third group was represented by only two genera, *Hemicheyletia* and *Cheletomimus*; these mites have short legs and are also living on trees (iii). The fourth group comprised the genera *Ker* and *Pavlovskicheyla*; these mites are lacking teeth on the palpal claw (iv). Two other genera, *Cheletophyes* and *Lepidocheyla* could not be assignated to a defined group.

The tribe Allieini included only one genus *Alliea. Alliea laruei* YUNKER, 1960, the type species is represented by an incomplete female (lacking the gnathosoma). The male has no comb-like setae, no teeth on the palpal claw and the solenidion ω*1* (leg I) has moved towards the apex of tarsus I and far from the fan-like guard seta.

The tribe Cheyletiini was characterized by a number of apomorphic characters, such as the shape of the setae on legs, idiosoma and palps. This tribe included 10 genera, eight of them were arranged into two groups: The first group included the genera *Cheyletia, Hypopicheyla* and *Samsinakia.* These mites bear aberrant flattened setae on the dorsal shields and they are associated with insects (i). The second group comprised two genera, *Neoeucheyla* and *Bothrocheyla.* The mites of these genera bear a cloud-like seta on the ventral surface of the palpal tarsus (ii). The four other genera, *Chiapacheylus, Grallacheles, Myrmicocheyla* and *Oudemansicheyla* remained ungrouped.

The tribe Cheletogenini (*Cheletogenes, Eutogenes* and *Prosocheyla*) was characterised by the reduction of the pretarsus on legs I.

The tribe Bakini (*Bak* and *Chelacheles*) included mites with abnormally elongated body. However, by the other characters these genera are quite different from each other (see analysis of characters).

The tribe Acaropseini consisted of five genera: *Acaropsella, Acaropsellina, Neocaropsis, Paracaropsis* and *Chelacaropsis.* These mites bear only one well-developed comb-like seta on palpal tarsi. Other characters, such as leg and palpal chaetotaxy are similar in all these genera.

The tribe Chelonotini included only one genus *Chelonotus* associated with tropical squirrels. The mites of this genus have numerous autapomorphic characters.

The tribe Cheletosomatini included four genera, *Cheletosoma, Cheletoides, Cheletopsis* and *Eucheletopsis*, and was characterised by ultralong setae on the body, only one comb-like seta on palpal tarsi and other apomorphic characters. The mites of all these genera are predaceous inhabiting in bird's quills

Composition of the Cheyletiellinae:

The representatives of the subfamily Cheyletiellinae (sensu VOLGIN) as a rule have no comb-like setae on palpal tarsi and no teeth on palpal claws, but their tarsi are short and thick. In males, the genital orifice is situated dorsally. This subfamily, created by VOLGIN (1961) was based mainly on characters, which are in relation with their parasitic life.This subfamily was therefore an artificial taxon.

The subfamily Cheyletiellinae was divided into two tribes: The Cheyletiellini with four genera, *Cheyletiella, Eucheyletiella, Nihelia* and *Criokeron*, associated with mammals and the Ornithocheyletiini with three genera, *Bakericheyla, Neocheyletiella* and *Ornithocheyletia*, associated with birds. It should be noted, that the first tribe was obviously artificial, actually it included mostly genera with very few characters in common, except for their parasitic habitat. On the contrary, the last tribe is a natural group, because its genera have numerous synapomorphies (see analysis of characters).

The monograph of SUMMERS and PRICE (1970) was published almost simultaneously with that of VOLGIN (1969). The suprageneric system of VOLGIN was not accepted and only few new species and one new genus *Laeliocheyletia* were added, when several genera were synonymised.

SMILEY (1970) rised the subfamily Cheyletiellinae to the family rank. Later, this author (SMILEY, 1977) proposed for two tribes of VOLGIN (1969), Cheyletiellini, Ornithocheyletiini, and the tribe Teinocheylini, created by FAIN (1974), the subfamily rank within the family Cheyletiellidae. He also created two new subfamilies each represented by a single genus: i.e. Criokerontinae for the genus *Criokeron* and Niheliinae for the genus *Nihelia*. After these modifications proposed by SMILEY (1977), the family Cheyletiellidae included five subfamilies.

FAIN (1979a) described several new parasitic genera with intermediate characters between the families Cheyletidae and Cheyletiellidae and proposed to restrict the family Cheyletiellidae to the genera *Cheyletiella* and *Eucheyletiella*, they differed from the other cheyletid-like mites by the absence of claws on all the legs. This author also elevated the tribe Chelonotini to the subfamily rank. Moreover, FAIN (1980) described a new cheyletid subfamily Metacheyletiinae, for the genus *Metacheyletia* found in the quills of parrots.

Recently, an extensive review of the family Cheyletidae has been carried out by FAIN *et al.* (1997) and GERSON *et al.* (1999). These authors has provided new definitions, keys and figures of all recently known cheyletid genera and subfamilies. The paper of GERSON *et al.* (1999) also included a list of all the known cheyletid species and gave the references of all the papers published after the monograph of VOLGIN (1969). Moreover, the family Cheyletiellidae was included in the family Cheyletidae as a subfamily; the subfamily Ornithocheyletiinae was divided into three tribes: Ornithocheyletiini (genera *Ornithocheyletia* and *Bakericheyla*), Apodichelini (genus *Apodicheles*) and Neocheyletiellini (genus *Neocheyletiella*). It was mainly based on differences in the leg chaetotaxy in these genera (FAIN *et al*, 1997). The genera *Muricheyla, Promuricheyla* and *Thewkachela* were conventionally removed from the subfamily Chelonotinae and placed in the subfamily Cheyletinae, because the synapomorphies in these genera were neglected by these authors (GERSON *et al.*, 1999).

A brief revision of the generic composition of the family Cheyletidae and a reappraisal study of certain genera was carried out by FAIN and BOCHKOV (2001, in press). According to these authors, the family Cheyletidae includes at present 72 valid genera and two genera of *incertae sedis*.

At present, there are two very important problems in the cheyletid taxonomy. The first is the generic composition of some tribes and subfamilies, for example Cheyletini, which is obviously artificial and characterised only by plesiomorphic characters (i). The relationships between the suprageneric groups is another problem which needs a special phylogenetic study (ii). An attempt to resolving these problems is given in this paper.

CHARACTERS USED IN THE CLADISTIC ANALYSIS

In this study we have used mainly, or exclusively, the morphological characters of the females, because in certain genera the males and immatures are still unknown. It appears, however, that in most of the cases these characters are similar in both sexes and can, therefore, be used at the generic level.

The following characters have not been retained in your study because they present a disordered distribution i.e. number and shape of teeth on palpal claws, shape of the peritremes, presence or absence of hysterosomal shield, presence or absence of idiosomal setae (*d1-d5, l1-l5*), gnathosomal and idiosomal ornamentation, chaetotaxy of some leg segments (tibia I and femora III-IV), position of the solenidions of tibia and tarsi III-IV.

Finally, we have also excluded from our analysis the characters which are directly related with a parasitic mode of life such as position of solenidion *ω1* and of guard seta (*ft'*) on tarsal apex, reduction in size of setae of palpal tarsus, disappearance of comb-like setae in all instars and short tarsi of all legs. These characters have originated independently as adaptations to parasitism and they are not restricted to the family Cheyletidae but are also observed in other families of mites such as the Syringophilidae, Harpirhynchidae and other parasitic families of Cheyletoidea.

The eyes are regularly absent in the parasitic species but may also be lacking in some predaceous genera. We have, thus, retained them in our analysis.

Gnathosoma (Characters 1-35)

*- autapomorphic character

1. LENGTH OF GNATHOSOMA (Fig. 1A, 1B). The gnathosoma is well developed in most predaceous genera and in the representatives of the outgroup (Stigmaeidae). Its length, including palps, is usually more than 30% of the idiosomal length. It should be noted that the gnathosoma is also well developed in the predaceous tribe *Bakini*, which has an unusually long body, and in the parasitic subfamilies Chelonotinae, Criokerontinae and Niheliinae. The other parasitic genera have relatively small gnathosoma.

APOMORPHY: Length of gnathosoma, including palps, less than 30% of the body length.

2. APEX OF GNATHOSOMA. In most cheyletid species the gnathosomal apex bears a few short median protuberances. In other species these protuberances are completely lacking. In the subfamily Niheliinae the apex bears a number of well developed median protuberances (Fig. 1C-E).

APOMORPHY: Median protuberances of gnathosomal apex are numerous and well developed.

3*. PROTRUSIONS OF GNATHOSOMAL BASE. In most cheyletid genera the gnathosomal base has not any protrusions. In the genus *Criokeron* the gnathosomal base has a pair of powerful ventral protrusions.

APOMORPHY: Gnathosoma with one pair of strong ventral protrusions.

4-5. PROTRUSIONS OF PALP. In most cheyletid mites and in the outgroup the palps are devoid of protrusions and teeth.

4. In the subfamily Niheliinae the femur and genu of the palps are completely fused and this segment (femur-genu) bears a lateral protrusion (Fig. 4B).

APOMORPHY: Palps well developed, with femur and genu fused, genu with lateral protrusion.

5. In the genera *Muricheyla* and *Promuricheyla* the palpal tarsus bears a small tooth on the inner side (Fig. 3E, F)

APOMORPHY: Palpal tarsus with small tooth on inner side.

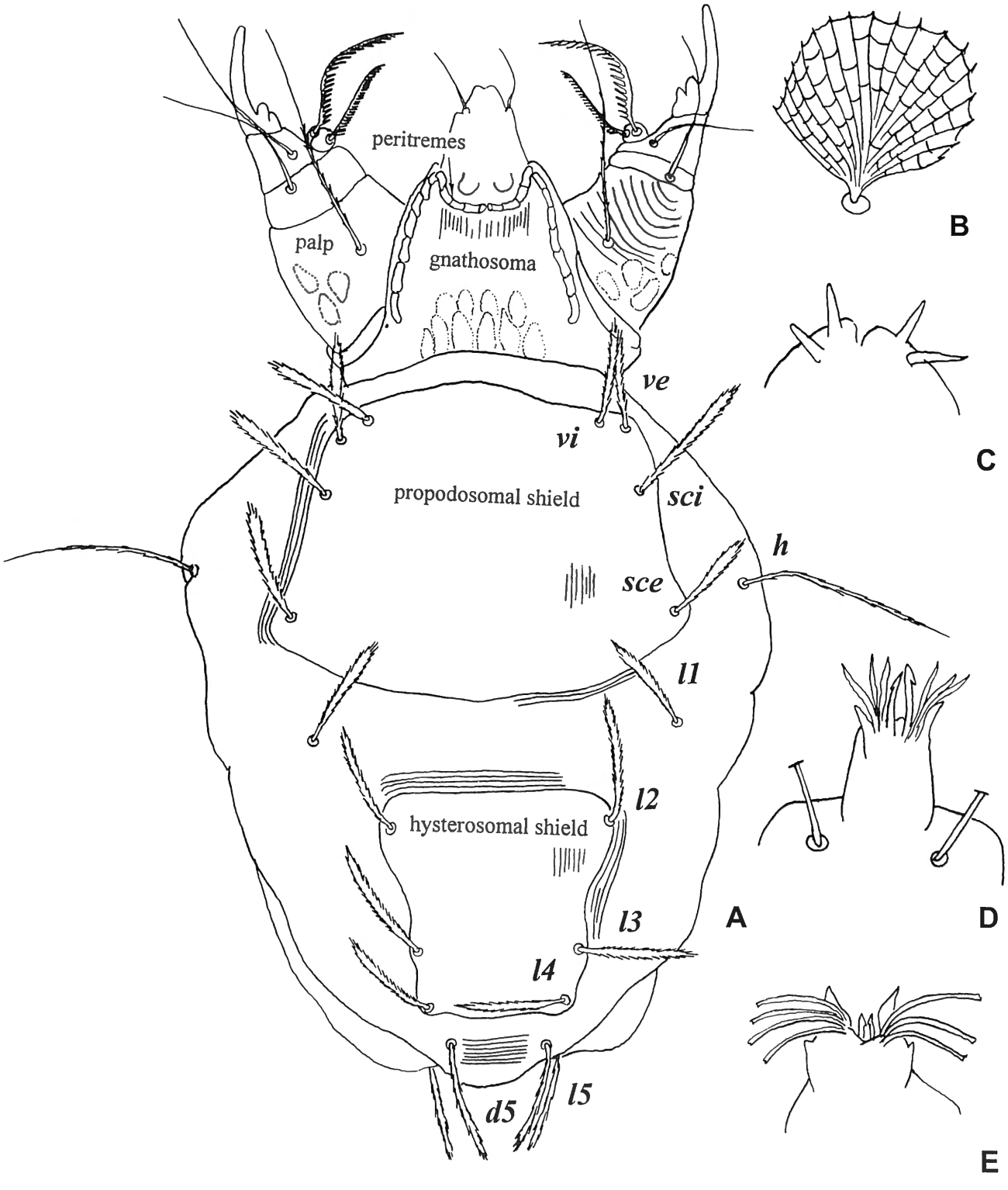

Fig. 1 — A-E (details of females). - *Cheyletus malaccensis* in dorsal view (A). *Neoeucheyla bulgarica*, fan-like seta (B). Hypostomal apex in ventral view : *Metacheletoides numidae* (C), *Galagocheles lemuricola* (D) and *Nihelia cynictis* (E).

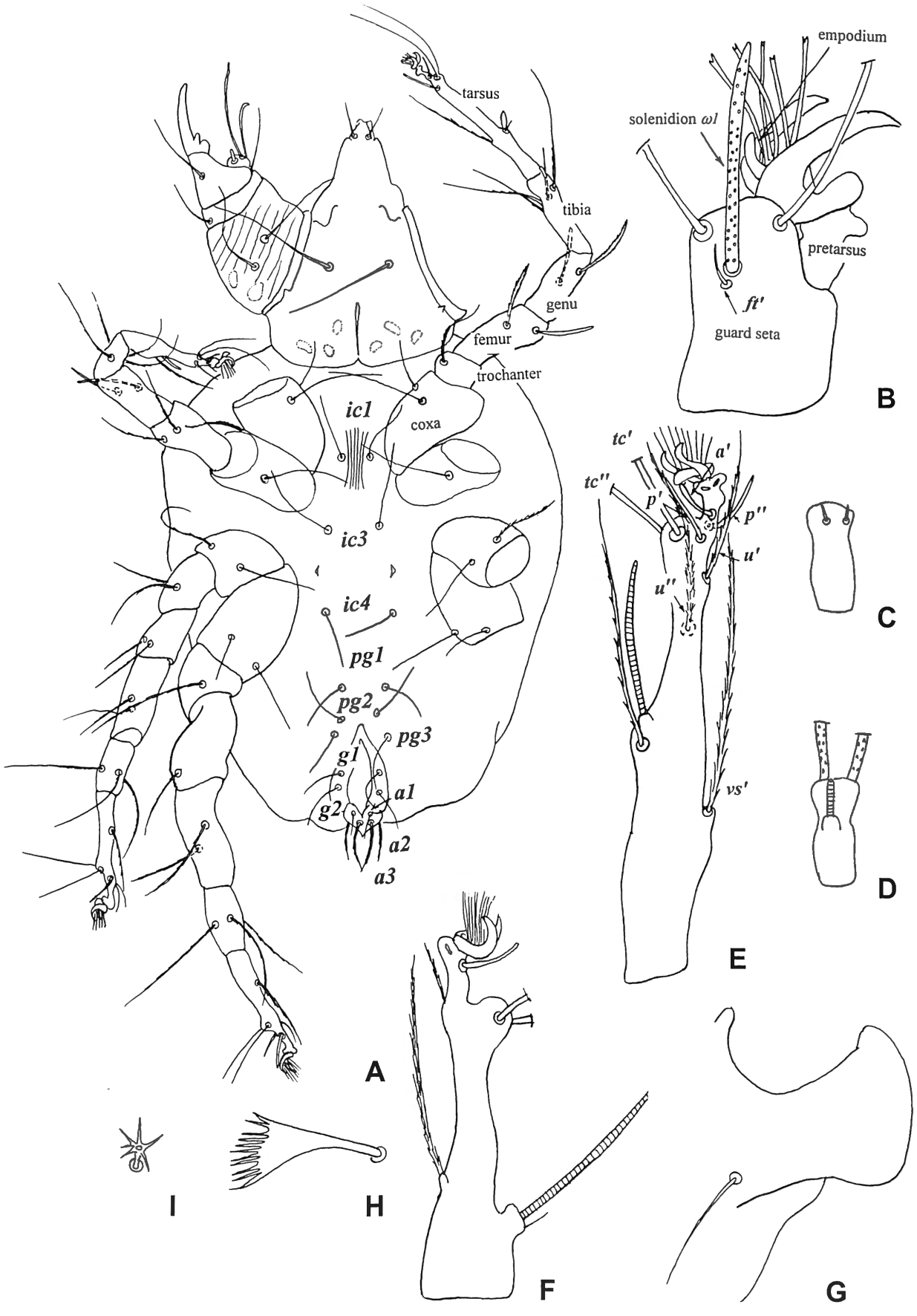

Fig. 2 — A-I (details of females). - *Cheyletus malaccensis*, in ventral view (A). *Neocheyletiella microrhyncha*, tarsus I in lateral view (B). *Cheletogenes ornatus*, tasus I in ventral view (C) and in dorsal view (D). Tarsus I in lateral view : *Cheletonella vespertilionis* (E) and *Hemicheyletia bregetovae* (F). *Chelonotus selenorhynchus*, lobe of coxa II (G). *Metacheletoides numidae*, seta *p'* of leg.III (H). *Criokeron thailandicus*, solenidion of genu I.

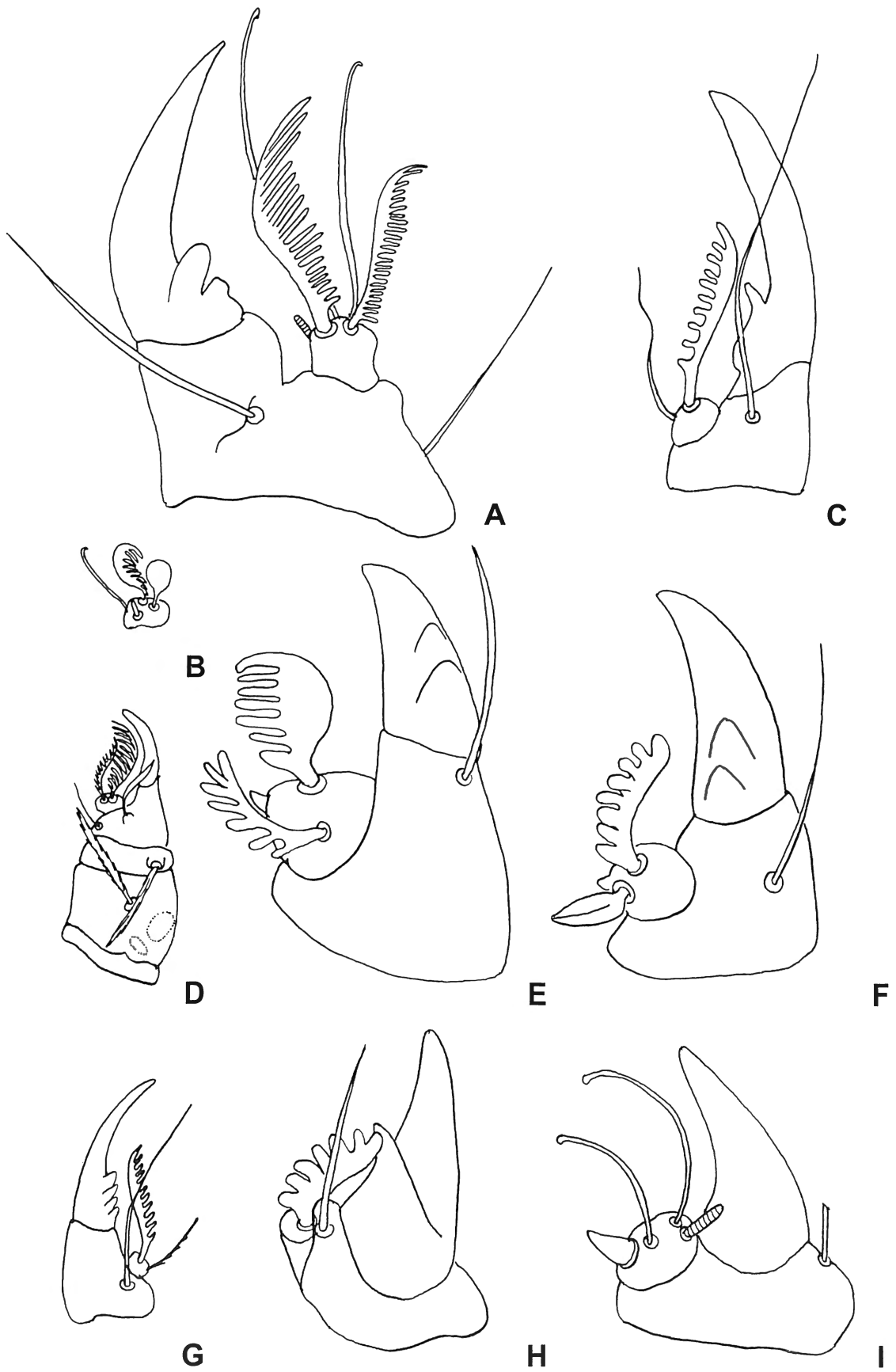

Fig. 3 — A-I (details of females). - *Cheyletus baloghi*, tibia and tarsus of palp in dorsal view (A). *Neoeucheyla tuberculicoxa*, palpal tarsus in dorsal view (B). *Cheletopsis norneri*, tibia and tarsus of palp in dorsal view (C). *Pavlovskicheyla semenovi*, palp in dorsal view (D). Tibia and tarsus of palp in dorsal view : of *Promuricheyla lukoschusi* (E), of *Muricheyla sicista* (F) and of *Chelacaropsis moorei* (G). *Chelonotus selenorhynchus,* tibia and tarsus of palp in dorsal view (H) and ventral view (I).

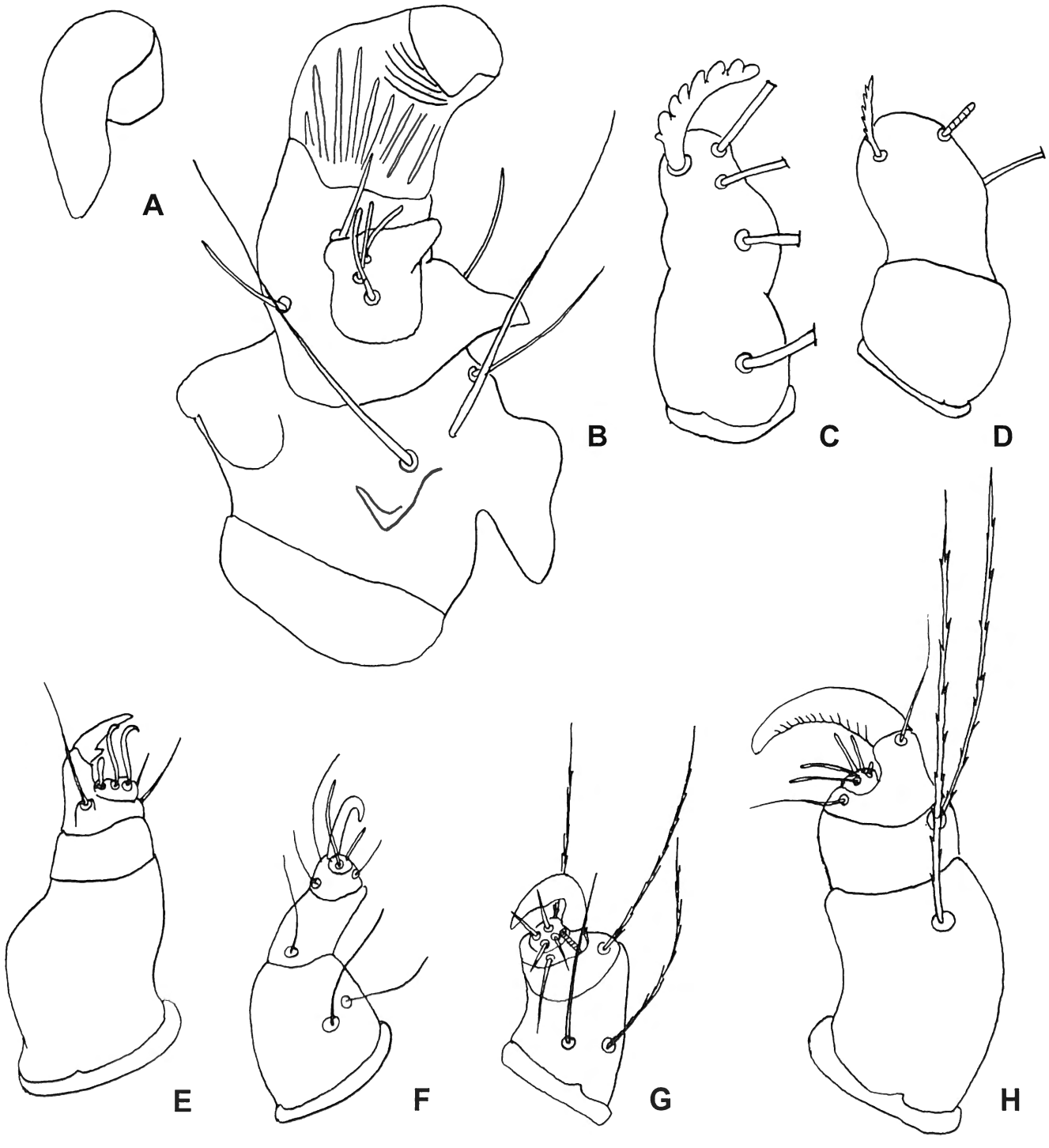

Fig. 4 — A-H (details of females). - *Nihelia cynictis*, claw of palp (A). Palp (B-H) : of *Galagocheles lemuricola* (B), in ventral view (B), of *Criokeron thailandicus*, in dorsal view (C) and ventral view (D), of *Metacheyletia obesa*, in ventral view (E), of *Ornithocheyletia canadensis*, in ventral view (G), of *Teinocheylus longissimus*, in ventral view (F) and of *Eucheyletiella ochotonae*, in dorsal view (H).

6*. PALPAL TARSI (Fig. 4B-H). In most cheyletid mites the palpal tarsi are small but well visible. In the genus *Smileycheles* the palpal tarsi are almost completely reduced.

APOMORPHY: Palpal tarsus almost completely reduced.

7*. SEGMENTATION OF PALPS. In most cheyletid mites and in the outgroup the palp consists of five free segments: narrow trochanter, well developed femur, genu, tibia with claw, and small, greatly reduced tarsus. In the genus *Criokeron* the palps are weakly developed and all the palpal segments are fused (Fig. 4D, C).

APOMORPHY: Palps weakly developed, with segments completely fused.

8-16. CLAW OF PALP. In most of the predaceous cheyletid genera the palpal claws are slightly curved medially and have teeth on their inner margin. In some species of the outgroup these teeth are also present and the claw is curved laterally as well (Fig. 3A, C; G).

8. In the genera *Caudacheles*, *Cheletosoma, Eutogenes, Ker* and *Pavlovskicheyla* the claws are smooth and curved laterally (Fig. 3D).

APOMORPHY: Claw laterally curved without teeth.

9*. In genus *Chiapachelylus* the claws have a structure being typical for other predaceous genera, but its teeth are replaced by a median ridge.

APOMORPHY: Claw laterally curved without teeth, but with a median ridge.

10. In some species of the parasitic subfamily Chelonotinae the palpal claw is very strong and large and bears basally one or two teeth (Fig. 3E, F, H, I).

APOMORPHY: Claw unusually strong and large, with one or two teeth, curved laterally.

11. In genera *Muricheyla* and *Promuricheyla* the claw teeth are situated almost dorsally (Fig. 3E, F).

APOMORPHY: Claw teeth situated almost dorsally.

12. In parasitic subfamily Niheliinae the palpal claws are flat and curved ventrally (Fig. 4A).

APOMORPHY: Claw curved ventrally, flat and strong.

13. The claws of three parasitic subfamilies Cheyletiellinae, Ornithocheyletiinae and Teinocheylinae are curved ventro-laterally and without teeth (Fig. 4E-H).

APOMORPHY: Claw strongly curved ventro-laterally, without teeth.

14. In two genera *Galagocheles* and *Nihelia* the inner side of palpal claws is covered with thick ridges (Fig. 4B).

APOMORPHY: Inner side of claw covered with thick ridges.

15. In the subfamily Cheyletiellinae the palpal claws are deeply striated on their inner side.

APOMORPHY: Claw with deeply striations on their inner part.

16*. In the genus *Criokeron* the claws are absent.

APOMORPHY: Claw absent.

17. CHAETOTAXY OF PALPAL TARSUS. In most predaceous species the palpal tarsus bears two dorsal comb-like setae (outer and inner ones), two ventral well developed thickened setae and one solenidion (Fig. 3A). The palpal tarsus is greatly reduced in parasitic mites of the subfamilies Niheliinae and Teinocheylinae. Therefore, some or all setae are absent, as in the genus *Smileycheles*. In other parasitic genera at least three setae of palpal tarsus are present.

APOMORPHY: Palpal tarsus with less than three setae.

18-22. SHAPE OF DORSAL SETAE OF PALPAL TARSUS. In most predaceous cheyletid mites the dorsal setae of the palpal tarsus are comb-like and well developed.

18. In the tribe Acaropsellini and the genera *Caminch-eyletus* and *Chelacheles* the outer dorsal seta is well developed, with numerous tines, while the inner dorsal seta is weakly developed, with very short tines (Fig. 3G).

APOMORPHY: Outer dorsal seta of palpal tarsus comb-like, with well developed tines, inner seta with very short tines.

19. In the genera *Cheletoides* and *Metacheyletoides* the outer dorsal seta is well developed, but without or with small tines, while the inner dorsal seta is smooth.

APOMORPHY: Outer dorsal seta of palpal tarsus nude or with very short tines, well developed, inner seta smooth.

20. In the genera *Caudacheles, Cheletopsis, Cheletoso-ma, Criokeron* and *Neochelacheles* the outer dorsal seta is comb-like, the inner dorsal seta is smooth (Fig. 3C).

APOMORPHY: Outer dorsal seta of palpal tarsus comb-like, inner dorsal seta smooth.

21. In the genera *Chelonotus, Muricheyla* and *Thewka-chela* the outer dorsal seta is comb-like, the inner dorsal seta is modified into a short and strong thorn (Fig. 3F, I).

APOMORPHY: Inner dorsal seta of palpal tarsus thorn-like.

22. In the genera *Bothrocheyla, Cunliffella* and *Neoeu-cheyla* the inner ventral seta is cloud-like (Fig. 3B).

APOMORPHY: Inner ventral seta of palpal tarsus cloud-like.

23-24. SHAPE OF SETAE OF PALPAL TIBIA. The palpal tibia in all cheyletid mites and in the outgroup bears three setae having dorsal, ventral and lateral positions respectively. In most cheyletid mites all these setae may be hair-like or thickened.

23. In the tribe Cheyletiini, excluding *Samsinakia*, and in genus *Cheletogenes* the dorsal seta of the palpal tibia is fan-like (Fig. 1B).

APOMORPHY: Dorsal seta of palpal tibia fan-like.

24. In the tribe Cheyletiini, excluding *Samsinakia*, the ventral seta of palpal tibia is fan-like.

APOMORPHY: Ventral seta of palpal tibia fan-like.

25-30. NUMBER AND POSITION OF SETAE OF PALPAL FEMUR-GENU. The presence of three setae on palpal femur (one seta dorsal and two setae ventral), and two setae on palpal genu (one seta dorsal and one seta ventral) is an ancestral state, because this number of setae is found in many cheyletid species and in representatives of the outgroup.

25. In the genera *Cheyletia, Cunliffella, Neoeucheyla* and *Thewkachela* one genual seta of palp is reduced.

APOMORPHY: One genual seta of palp reduced.

26*. In the genus *Microcheyla* both genual setae of palp are reduced.

APOMORPHY: Both genual setae of palp reduced.

27*. In the genus *Metacheyletia* only one dorsal seta is present on the palpal femur, all other setae of palpal femur-genu are absent.

APOMORPHY: All setae of palpal femur-genu reduced, except dorsal seta of palpal femur.

28. In females of the tribe Acaropsellini and genus *Chelacheles* and *Neochelacheles* the ventral genual seta of palp is situated on the base of the palpal genu and the palpal femur. In males of these genera this seta is situated on the palpal genu.

APOMORPHY: Ventral genual seta placed on the base of palpal genu.

29. The ventral genual seta is moved towards the palpal femur in the genera *Bothrocheyla, Cheletacarus, Cheletogenes, Cheletomimus, Chelonotus, Cunliffella, Hemicheyletia, Lepidocheyla, Neoeucheyla, Nodele, Tutacheyla* and tribe Cheletosomatini.

APOMORPHY: Ventral genual seta moved towards the palpal femur.

30. In the genera *Cheletomorpha, Cheletophanes, Chiapacheylus, Hoffmannita, Hypopicheyla* and *Mexecheles* both genual setae of palp are moved to the femur.

APOMORPHY: Both genual setae moved towards the femur.

31-35. SHAPE OF THE SETAE OF PALPAL FEMUR-GENU. In most cheyletid genera and in outgroup the setae of palpal femur-genu are hair-like or thickened.

31. In the tribe Cheyletiini, excluding the genus *Samsinakia*, and in the genus *Cheletogenes* the dorsal setae of the palpal genu are fan-like.

APOMORPHY: Dorsal seta of palpal genu fan-like.

32. In the tribe Cheyletiini, excluding the genus *Samsinakia,* the ventral setae of the palpal genu are fan-like.

APOMORPHY: Ventral seta of palpal genu fan-like.

33. In tribe Cheyletiini and in the genus *Lepidocheyla* the outer ventral seta on the palpal femur is fan-like.

APOMORPHY: Outer ventral seta of femur fan-like.

34. In the genera *Bothrocheyla, Cheyletia, Cunliffella, Microcheyla, Neoeucheyla* and *Oudemansicheyla* the inner ventral seta of the palpal femur is fan-like.

APOMORPHY: Inner ventral seta of palpal femur fan-like.

35. In the genera *Bothrocheyla, Cheyletia, Cunliffella, Microcheyla, Neoeucheyla* and *Oudemansicheyla* all setae of the palpal femur-genu are fan-like.

APOMORPHY: All setae of femur-genu fan-like.

Idiosoma (Characters 36-47)

36. EYES. The presence of eyes is undoubtedly a plesiomorphic state. In the genus *Hoffmannita* the eyes are absent, but their vestiges are clearly recognised. The eyes are absent in all parasitic and in some predaceous cheyletids i.e. tribe Cheletosomatini and the genera *Bak, Cameincheyletus, Caudacheles, Cheletonella, Cheyletus, Eucheyletia, Eutogenes, Hylopecheyla* and *Zachvatkiniola.*

APOMORPHY: Eyes absent.

37*. POSITION OF SETAE. In most cheyletid and stigmaeiid genera the idiosomal nipple-like protrusions for setae are absent. In the genus *Teinocheyus* setae *vi* are situated on niple-like protrusions.

APOMORPHY: Setae *vi* situated on nipple-like protrusion.

38-41. ADDITIONAL NEOTRICHIAL SETAE. The neotrichial setae are present in many predaceous and few parasitic cheyletid genera. The presence of these setae is considered as an apomorphy, because in some primitive cheyletid mites and in Stigmaeidae these setae are always absent.

38. The median neotrichial setae are cloud-like or have another aberrant shape, they differ in shape from the lateral setae in the genera *Bothrocheyla, Camincheyletus, Cheletomorpha, Cheyletia, Cheyletus, Cunliffella, Eucheyletia, Hoffmannita, Hypopicheyla, Mexecheles, Neoeucheyla, Paracheyletia, Prosocheyla* and *Samsinakia.*

APOMORPHY: Neotrichial setae of abnormal shape.

39. In the genera *Cheyletia, Hypopicheyla* and *Samsinakia* the neotrichial setae form a continuous layer of squamate setae on the dorsal surface of idiosoma.

APOMORPHY: Neotrichial setae squamate-like, large, forming continuous layer.

40. In the tribe Acaropsellini, subfamily Niheliini, Criokerontinae and the genera *Cheletogenes, Cheletophanes, Cheletophyes, Ker, Lepidocheyla, Pavlovskicheyla* and *Paracheyletiella* the median neotrichial setae are represented by 6 pairs (or fewer) of setae similar in shape to the lateral ones.

APOMORPHY: There are 6 pairs (or fewer) median setae similar to the lateral setae.

41. There are 10 pairs (or fewer) median neotrichial setae similar to lateral setae, in the genera *Caudacheles, Chiapacheylus, Dubininiola, Eutogenes* and *Oudemansicheyla.*

APOMORPHY: Median neotrichial setae represented by not fewer than 10 pairs, similar in shape to the lateral setae.

42. SHAPE OF ANAL SETAE *a3*. In most cheyletid mites the anal setae *a3* are hair -like.

In the tribe Cheyletiini and the genera *Eucheyletia, Prosocheyla* and *Zachvatkiniola* these setae are fan-like (apomorphic state).

APOMORPHY: Setae *a3* fan-like.

43. LENGTH OF IDIOSOMAL SETAE. In most cheyletid mites the body setae, except *l5* in some parasitic genera, are shorter than half the length of the idiosoma. In tribe Cheletosomatini these setae exceed one half the length of idiosoma (ultralong setae).

APOMORPHY: Some body setae more than half the idiosomal length (ultralong setae).

44-47. SHAPE OF BODY. The shape of idiosoma in most cheyletoid and stigmaeid mites is rhombus-like or ovoid.

44. In the genera *Bak, Chelacheles* and *Neochelacheles* the body is elongate and there is a distinct reduction of the opisthosoma, more marked in genus *Bak* than in the other two genera *Chelacheles* and *Neochelacheles.*

APOMORPHY: Body elongated, opisthosoma partly reduced (1), strongly reduced (2).

45*. In the genus *Teinocheylus* with the elongate vermiform body the opisthosoma is well developed.

APOMORPHY: Body vermiform, opisthosoma well developed.

46. In the genera *Chelonotus*, *Hypopicheyla* and *Samsinakia* more than half of the length of gnathosoma is covered with the rounded anterior extension of the body.

APOMORPHY: More than half of length of gnathosoma covered with anterior extension of body.

47. In the subfamily Cheyletiellinae the body has shoulder-like lateral protrusions.

APOMORPHY: Shoulder-like lateral protrusions of idiosoma present.

Legs (Characters 48-82)

48-51. LENGTH OF LEGS. The cheyletoid mites usually have four pair of legs, consisting of five free segments - trochanter, femur, genu, tibia and tarsus (Fig. 2A). The latter segment includes the tarsus and the pretarsus (Fig. 2E). The pretarsus in most predaceous mites is well developed and bears two claws and an empodium with numerous tines.

48*. In the genus *Metacheyletia* the legs IV are vestigal.

APOMORPHY: Legs IV reduced.

49. In tribe Cheletogenini the pretarsus I is completely reduced (Fig. 2C, D).

APOMORPHY: Pretarsus I reduced.

50. The lengths of legs in most of the cheyletid mites reach about 60 or 70% the length of the idiosoma. In the genera *Cheletomorpha* and *Mexecheles* the legs I are longer than the idiosoma.

APOMORPHY: Legs I longer than idiosoma.

51. In three genera *Cheletacarus, Nodele* and *Cheletophanes* the legs I reach 80 or 90% of the length of the idiosoma.

APOMORPHY: Legs I about 80 to 90% the length of idiosoma.

52. APICAL TARSAL KNOB. In most cheyletid and stigmaeiid mites the tarsi are without a knob covering the pretarsus and claws. In the parasitic subfamily Ornithocheyletiinae the tarsus bears dorsally, in its apical part, a well developed knob almost completely covering the pretarsus and claws (Fig. 2B).

APOMORPHY: Tarsus with well developed knob almost completely covering pretarsus and claws in its apical part.

53-54. PROTRUSIONS OF LEGS. Usually, the leg segments in the cheyletid mites are lacking protrusions.

53. In two parasitic genera, *Muricheyla* and *Promuricheyla* the protrusions are present on the tarsi III-IV.

APOMORPHY: Tarsi III-IV with protrusions.

54. The genera *Chelonotus* and *Thewkachela* have lobes on coxae II (Fig. 2G).

APOMORPHY: Coxae II with lobes

55-57. POSITION OF THE LEGS. In most genera of the Cheyletidae the coxae I are close to the coxae II and the coxae III close to the coxae IV respectively, the distance between the coxae II and the coxae III is equal or less than half of the body width.

55. In the genera *Chelacheles* and *Neochelacheles* the distance between coxae II and III is equal or longer than half of the body width.

APOMORPHY: Distances between coxae II and III more than half of the body width.

56*. In the genus *Bak* the distance between coxae II and III is longer than the body width.

APOMORPHY: Distances between coxae II and coxae III exceed the body width.

57*. In the genera *Neocheyletiella* and *Teinocheylus* the coxae III are removed from coxae IV. However, in the former genus, the distance between these pairs of coxae is not so large as in *Teinocheylus* and it is more the result of a significant reduction of the coxae. Therefore, the state of this character for *Neocheyletiella* is coded as a plesiomorphic one.

APOMORPHY: Coxae III removed from coxae IV.

58-60. CLAWS OF LEGS.

58. In most of the cheyletoid mites the claws are present on tarsi of all legs. In the subfamily Cheyletiellinae the claws are absent on tarsi of all legs.

APOMORPHY: Claws absent on all legs.

59*. In the genus *Teinocheylus* the claws are absent only on tarsi of the legs III-IV.

APOMORPHY: Claws absent on tarsus of legs IV.

60. In the subfamily Ornithocheyletiinae all tarsal claws are larger than in other cheyletid genera (Fig. 2B).

APOMORPHY: Tarsal claws well developed, large.

61. EMPODIUM OF LEG TARSI. The tarsal empodium in the predaceous forms bears numerous tines, however, in the subfamilies Niheliinae, Teinocheylinae, Criokerontinae the empodium bears only a few teeth (5-7) or the teeth of empodium are fused each other as in the genus *Neocheyletiella*.

APOMORPHY: Empodium with less than 8 tines.

62-64. CHAETOTAXY OF LEG COXAE. In most cheyletid mites the formula of the coxal setae is 2-1-2-2.

62*. In the genus *Metacheyletia* the setae on coxa III are absent.

APOMORPHY: Setae on coxa III absent.

63. In the genera *Apodicheles, Neocheyletiella* and *Ornithocheyletia* the coxa IV bears only one seta.

APOMORPHY: Coxa IV with one seta.

64. In the genera *Neocheyletiella* and *Apodicheles* the coxa III bears one seta.

APOMORPHY: Coxa III with one seta.

65-67. CHAETOTAXY OF LEG TROCHANTERS. In most of the cheyletid mites the formula of the trochanteral setae is 1-1-2-1.

65. In the genera *Apodicheles, Bak* and *Eutogenes* the trochanter III bears one seta.

APOMORPHY: Trochanters III with one seta.

66. In the genera *Apodicheles* and *Ornithocheyletia* the setae on trochanter IV are absent.

APOMORPHY: Trochanter IV without setae.

67*. In the genus *Metacheyletia* the setae on all trochanters (I-III) are absent.

APOMORPHY: Trochanters of all legs without setae.

68-69. CHAETOTAXY OF LEG GENUA. In most cheyletid mites the formula of genual setae is 2-2-2-2.

68. In the genera *Apodicheles*, *Metacheyletia* and *Neocheyletiella* the genu III bears one seta.

APOMORPHY: Genu III with one seta.

69. Two genera *Apodicheles* and *Neocheyletiella* have no setae on genu IV.

APOMORPHY: 69. Genu IV without setae.

70-71. CHAETOTAXY OF LEG TIBIAE. In most cheyletid mites the formula of the tibial setae is 4 or 5-4-4-4.

70. In the genera *Apodicheles, Bakericheyla* and *Neocheyletiella* the tibiae III bear three seta.

APOMORPHY: Tibia II with three setae.

71. In the genera *Apodicheles, Bakericheyla* and *Neucheyletiella* the tibiae IV bear three seta.

APOMORPHY: Tibia IV with three setae.

72. SOLENIDION OF TIBIA II. The tibia II bears a solenidion in the tribe Acaropsellini and the genera *Caudacheles, Chelacheles, Cheletacarus, Cheletophanes, Cheletomimus, Hemicheyletia, Neochelacheles, Paracheyletia* and *Tutacheyla*. The presence of this solenidion is undoubtedly a plesiomorphic state.

APOMORPHY: Solenidion of tibia II absent.

73. SOLENIDION OF TIBIA I. This solenidion present in most cheyletid mites. In the genera *Apodicheles, Cheyletiella* and *Eucheyletiella* the solenidion of tibia I is absent.

APOMORPHY: Solenidion of tibia I absent.

74-75. SHAPE OF OUTHER SETA OF COXAE III. In most cheyletid mites this seta is hair-like and nude.

74. The outer seta on coxae III is fan-like in the tribe Cheyletiini and in the genera *Caudacheles* and *Lepidocheyla.* In the genus *Cheletogenes* this seta is also fan-like, but more narrow and, therefore, this character state has been coded for the genus as a separate apomorphic state.

APOMORPHY: Outer seta on coxae III fan-like (1) or very narrow fan-like (2).

75. The outer seta on coxae III is serrate in the genera: *Caminchеyletus, Cheletomorpha, Cheletonella, Chelonotus, Cheletophanes, Cheyletiella, Cheyletus, Eucheyletia, Eucheyletiella, Hylopecheyla, Ker, Mexecheles, Muricheyla, Nodele, Ornithocheyletia, Pavlovskicheyla, Promuricheyla, Thewkachela* and *Zachvatkiniola.*

APOMORPHY: Outer seta on coxae III serrate.

76-77. POSITION OF SOLENIDION ω*1* AND SETA V1. In most predaceous genera the solenidion ω*1* is situated on the basal half of the tarsus, near the guard seta (*ft'*) and at the same level as the unpaired ventral setae v1.

76*. In the genus *Caudacheles* the solenidion ω*1* is situated near the tarsal apex and is removed far from the guard seta, the latter is situated at the same level as seta v1.

APOMORPHY: Solenidion ω*1* situated near tarsal apex and removed from guard and v1 setae.

77. In two genera *Cheletomorpha* and *Mexecheles* the seta v1 is situated anterior to solenidion ω*1* and guard seta.

APOMORPHY: Seta v1 situated anterior to solenidion ω*1* and guard seta.

78. SHAPE OF SOLENIDION σ. In most cheyletid and stigmaeiid mites the solenidion σ of the genu I is rod-like or globular. In the subfamilies Criokerontinae and Niheliinae the solenidion σ of the genu I is modified into stellate seta (Fig. 2I).

APOMORPHY: Solenidion σ of genu I modified into stellate seta.

79. SHAPE OF GUARD SETA (*ft'*). In most cheyletid mites the guard seta on the tarsus I is hair-like. In the tribe Cheyletiini and in the genera *Caudacheles* and *Lepidocheyla* this seta is fan-like.

APOMORPHY: The guard seta (*ft'*) fan-like.

80. SHAPE OF SETAE *P'* AND *P''*. In most cheyletid mites the setae *p'* and *p''* are hair-like with or without barbs. In the tribe Cheletosomatini these setae are plume-like (Fig. 2H). In the genus *Ornithocheyletia* these setae are similar in shape with ones of the former genera, but are more deeply dissected. In the genus *Neocheyletiella* setae *p'* and *p''* are feather-like.

APOMORPHY: Setae *p'* and *p''* plume-like.

81. NIPPLE-LIKE PROTRUSION OF TARSUS I. In most cheyletid and stigmaeiid genera the tarsi I are lacking a nipple-like protrusion. In the genera *Cheletogenes, Cheletomimus, Cheletophanes, Eutogenes, Hemicheyletia* and *Tutacheyla* solenidion ω*1* is situated on small nipple-like protrusion (Fig. 2F).

APOMORPHY: Solenidion ω*1* situated on small nipple-like protrusion.

82. LENGTH OF APICAL SETAE OF TARSUS I. In most of the cheyletid mites the setae *tc'* and *tc''* of tarsi I are not longer than this segment and other setae not longer than the half of this segment (Fig. 2E). In the tribe Cheletogenini several apical setae of tarsi I are abnormally long; in *Cheletogenes* these are setae *tc'* and *tc''*, in the genera *Eutogenes* and *Prosocheyla,* some pretarsal setae are ultralong.

APOMORPHY: Setae of tarsal apex ultralong.

Characters for outgroup comparison (Characters 83-91)

The following apomorphic characters, which strongly support the monophyly of the Cheyletidae, were used for outgroup comparison only. The Cheyletidae are characterized by the following characters: stylophore present (absent in Stigmaeidae) (character **83**); absence of solenidia on genu III in both sexes and on tibiae and tarsi of legs III-IV in females (present in Stigmaeidae) (character **84**); situation of peritremes on rostral shield (on gnathosomal base in Stigmaeidae) (character **85**); palpal tarsus with only five setae, including solenidion (with numerous setae in Stigmaeidae) (character **86**); only one seta on coxa II (2 setae in Stigmaeidae) (character **87**); 2 setae on femur III-IV (6-3 setae in Stigmaeidae) (character **88**); 2 setae on genua I-II, excluding solenidion (5-4 in Stigmaeidae) (character **89**); 4 setae on tibiae II-IV, excluding solenidion, (5 in Stigmaeidae) (character **90**); 8-10 setae on tarsi I, excluding solenidion, (13 setae in Stigmaeidae) (character **91**).

CLADISTIC ANALYSIS

The first step in a cladistic analysis, is to develop a preliminary cladogram. This cladogram is based on 91 characters (Table 2) with all the characters not ordered.

Table 3. Consistency index of characters used in cladistic analysis

(N - number of character, CI - consistency index)

N	CI	N	CI	N	CI	N	CI	N	CI	N	CI	N	CI	N	CI	N	CI	N	CI
1	1	11	1	21	05	31	0.5	41	0.3	51	0.3	61	0.3	71	1	81	0.3	91	1
2	1	12	1	22	1	32	0.5	42	0.5	52	1	62	0.5	72	0.5	82	1		
3	1	13	1	23	0.5	33	1	43	1	53	1	63	1	73	0.5	83	1		
4	1	14	1	24	1	34	0.5	44	1	54	1	64	0.3	74	0.7	84	1		
5	1	15	1	25	0.3	35	0.5	45	1	55	1	65	0.3	75	0.3	85	1		
6	1	16	1	26	1	36	0.3	46	0.3	56	1	66	0.5	76	1	86	1		
7	1	17	0.5	27	1	37	1	47	1	57	1	67	1	77	1	87	1		
8	0.5	18	0.3	28	1	38	0.2	48	1	58	1	68	0.5	78	1	88	1		
9	1	19	1	29	0.1	39	0.3	49	1	59	1	69	1	79	0.5	89	1		
10	1	20	0.3	30	0.3	40	0.2	50	1	60	1	70	1	80	1	90	1		

The analysis of the first 1000 trees computing by heurisitic algorithm has shown that the character 72 (absence of solenidion on tibia II) is reversed in most cheyletid mites. As far there is a quite low probability of reversion of this structure, we have used the **Inrevers. Up** option for this character.

Subsequent search with this assumptions, and by means of the same algorithm, have found more than 1000 trees. However, the most short tree and all general clasters were obtained for the first 100 trees. The strict consensus tree (parameters: tree length = 137, consistency index CI = 0. 67, retention index RI = 0. 86, rescaled index RC = 0. 58) is given in Fig. 5 and the consistence indexes for all characters - in Table 3.

The strict consensus tree allows to establish the clusters as follows. I. The group including the genera *Cheletomimus*, *Hemicheyletia* and *Tutacheyla* is supported by the non-unique character 82 (solenidion ω*1* situated on small nipple-like protrusion).

II. The group including the genera *Cheletomorpha* and *Mexecheles* is supported by two characters - 50 (legs I longer than idiosoma) and 77(seta v1 situated anterior of solenidion ω*1* and guard seta).

III. The group including the genera *Ker* and *Pavlovskicheyla* is supported by one non-unique character 8 (claw laterally curved, without teeth).

IV. The group corresponding to the tribe Acaropseini, sensu VOLGIN, is supported by the character 28 (ventral genual seta of palpal genu placed on base of genu). It includes also the genera *Chelacheles* and *Neochelacheles* as a separate subgroup The latter subgroup is supported by two characters 44 (body elongated, opisthosoma partly reduced) and 55 (distance between coxae II and III more than half of the body width).

V. The group corresponding to the tribe Cheyletiini, sensu VOLGIN, is supported by the character 31 (dorsal seta of palpal tibia fan-like.) and the character 32 (ventral seta of palpal tibia fan-like). This group includes two subgroups: the subgroup *Neoeucheyla* supported by the character 22 (inner ventral seta of palpal tarsus cloud-like), and the subgroup *Oudemansicheyla* supported by the character 41 (median neotrichial setae represented by 10 pairs or more, similar in shape to lateral setae). The latter character has very low consistency index (CI = 0.333).

VI. The group corresponding to the tribe Cheletogenini, sensu VOLGIN, is supported by the character 49 (pretarsus I reduced) and the character 82 (setae of tarsal apex ultralong).

VII. The group including the genera *Cheletacarus* and *Cheletophanes*, is supported by the character 51 (length of legs I consist 0.8-0.9 of idiosomal length). This character has low consistency index (CI = 0.333).

VIII. The group corresponding to the tribe Cheletosomatini, sensu Volgin, is strongly supported by two characters: character 43 (some setae of body abnormally long) and character 80 (setae *p'* and *p''* of legs II-IV plume-like). This group is divided into two subgroups: the *Cheletoides-Metacheletoides* subgroup, supported by the character 19 (outer dorsal seta of palpal tarsus nude or with very short tines, inner seta smooth) and the *Cheletopsis-Cheletosoma* subgroup, supported by the character 20 (outer dorsal seta of palp tarsus comb-like, inner seta smooth) which has low consistency index (CI = 0. 333).

IX. The group corresponding to the subfamily Chelonotini, sensu FAIN *et al.* (1997), is supported by the characters 10 (claw unusually strong and large, with one or two teeth, curved laterally) and 21 (inner dorsal seta of palpal tarsus thorn-like). The latter character is reversed in the genus *Promuricheyla.* This group is divided in two subgroups: the *Chelonotus-Thewkachela* subgroup, supported by the character 54 (coxae II with lobes) and the *Muricheyla-Promuricheyla* subgroup, supported by the char-

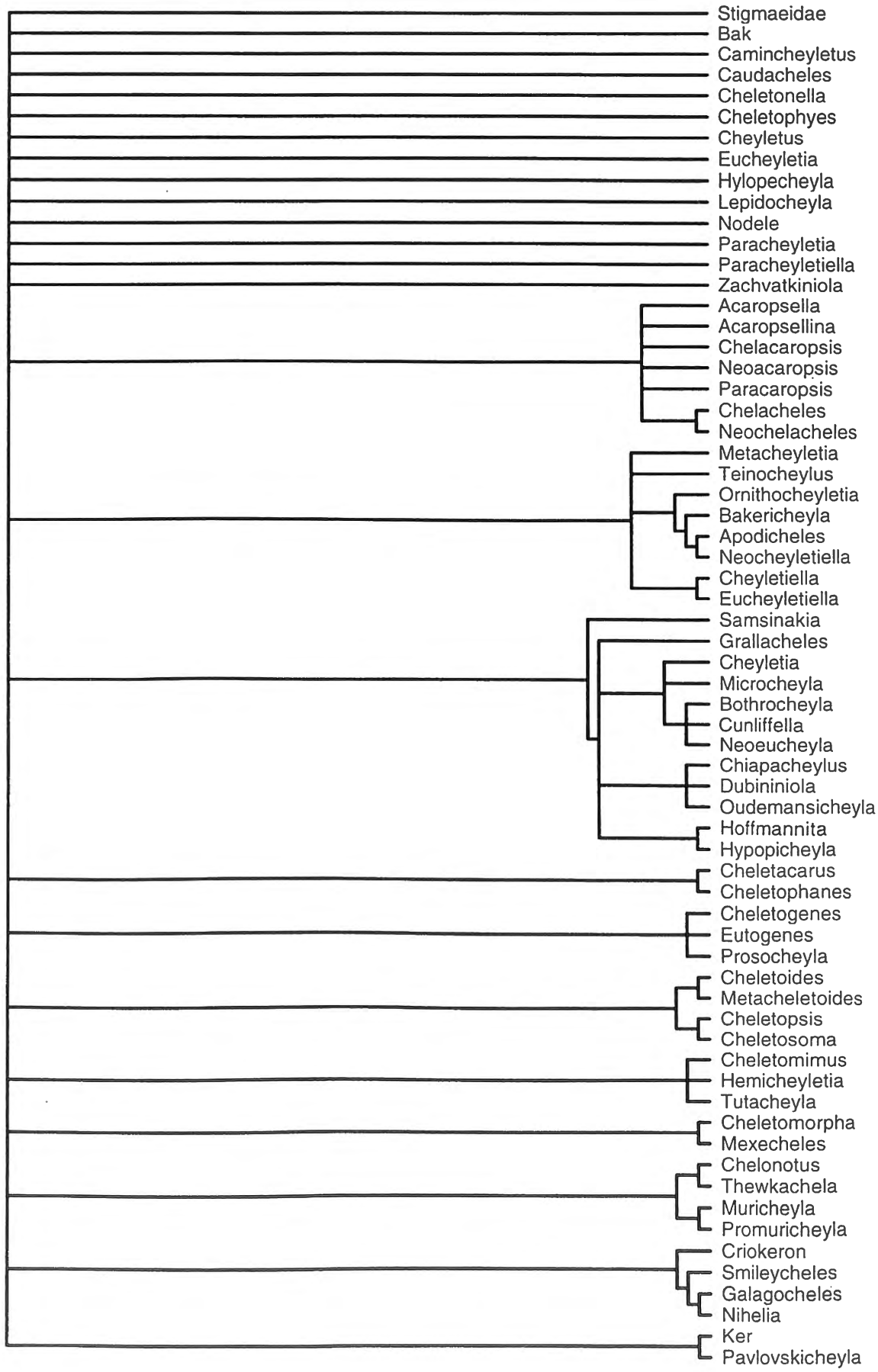

Fig. 5 — Strict consensus cladogram of Cheyletidae for first 100 tress (tree length = 137, CI = 0. 67, RI = 0. 86, RC = 0. 58), heuristic algorithm (PAUP 03.1).

acter 11 (teeth of palpal claw situated dorsally) and the character 53 (tarsi III-IV with protrusions).

X. The group including the subfamilies Criokerontinae and Niheliinae, sensu FAIN *et al.* (1997), supported by the character 61 (empodium with less than 8 teeth.) and the character 78 (solenidion σ of genu I modified into a stellate seta) and it consists of two subgroups. The Niheliinae subgroup is supported by three following characters: character 2 (gnathosomal apex with numerous and well developed protuberances), character 4 (palpal femur and genu fused, with lateral protrusion) and character 12 (palpal claw curved ventrally, flat and strong). The Criokerontinae subgroup (one genus) is supported by three autapomorphic character states: character 3 (gnathosoma with one pair of very developed ventral protrusions), character 7 (palps weakly developed with completely fused segments) and character 16 (palpal claw absent).

XI. The group including other parasitic subfamilies Cheyletiellinae, Metacheyletiinae, Ornithocheyletiinae and Teinocheylinae, sensu FAIN *et al.* (1997), is supported by character 1 (length of gnathosoma less than 1/3 of body length) and, except Metacheyletiinae, by the character 13 (palpal claw strongly curved ventro-laterally, without teeth). This group consists of four subgroups. The Cheyletiellinae subgroup is supported by two characters 15 (palpal claw with notches on its inner part) and 47 (shoulder-like protrusions of idiosoma present laterally). The Metacheyletiinae subgroup (one genus) is supported by three autapomorphic characters: character 27 (all setae of femur-genu reduced, excluding dorsal seta of femur), character 48 (legs IV reduced) and character 67 (trochanters of all legs without setae). The Ornithocheyletiinae subgroup is supported by character 52 (tarsus with well developed knob) and character 60 (tarsal claws very developed, large). The structure of this subgroup has not any clusters corresponding to tribes created by FAIN *et al.* (1997) for the subfamily Ornithocheyletiinae. Teinocheylinae subgroup (one genus) is supported by four autopomorphic characters: character 37 (setae *vi* situated on protrusions), character 45 (body vorm-like, opisthosoma well developed), character 57 (coxae III moved from coxae IV) and character 59 (claws absent on tarsus of legs III-IV).

Other genera, most of which belonging to the tribe Cheyletini, sensu VOLGIN, are remained ungrouped. Within these genera, two genera i.e. *Bak*, belonging to the tribe Bakini, sensu of VOLGIN, and *Caudacheles,* a quite peculiar genus described by GERSON (1968), have important autopomorphic characters. The former genus is characterized by the characters 44 (body elongated, opisthosoma strong reduced) and 76 (distance between coxae II and coxae III more than body width). The latter genus is supported by character 76 (solenidion ω*1* far moved aside from guard and v1 setae).

In the second step of the analysis, all characters with CI less than 0.5, such as 8, 20, 25, 29, 30, 36, 38, 39, 40; 41, 46, 51, 61, 64, 65, 75 and 81, were excluded. The 27 trees have been obtained using heuristic algorithm. The strict consensus tree has the following parameters: tree length 89, CI = 0. 854, RI = 0.936 and RC = 0.8 (Fig. 6). This consensus tree is topologically quite similar to one obtained at the first step, only three groups (*Hemicheyletia, Cheletacarus, Pavlovskicheyla*) and two subgroups (*Cheletopsis* and *Oudemansicheyla*) are not recognisable in this cladogram.

Thus, we may conclude, that most of the generic groups and subgroups established at the second step of analysis are well substantiated and supported by characters which carry a phylogenetic weight and are quite reliable at this taxonomic level. An exception is observed in the group XI, which is supported by character 1, and the node uniting the Cheyletiellinae, Ornithocheyletiinae and Teinocheyletinae subgroups. This node is supported by character 13 (palpal claw strongly curved ventro-laterally, without teeth). These two characters are undoubtedly adaptations to the parasitic mode of life and have arisen independently in these highly specialised parasitic mites. However, these characters were used in analysis, because they characterise some morphologic tendencies towards parasitism (parasitism on skin surface) within the cheyletids, while other parasitic cheyletid mites (Chelonotinae, Criokerontinae and Niheliinae) produce well-distinguished parasitic adaptations used for attaching to the skin and the hair of mammals.

TAXONOMIC SYSTEM OF THE CHEYLETIDAE

Discussion

According to the data obtained by the cladistic analysis, the family Cheyletidae includes 12 principal generic groups corresponding to a certain extent to the subfamilies and tribes of the previous authors, i.e. Acaropsellini, Cheletogenini, *Cheletomorpha-Mexecheles*, Cheletosomatini, Chelonotinae, Cheyletiellini, Cheyletiini, Criokerontinae, Metacheyletiinae, Niheliinae, Ornithocheyletinae and Teinocheyletinae and also numerous ungrouped genera (Fig. 6). Within the ungrouped genera, two, i.e. *Bak* and *Caudacheles*, are treated as separate generic groups. The representatives of these genera possess many unique autapomorphic character states, which strongly separate these mites from the other cheyletids.

We propose to consider all the recognised suprageneric groups as tribes and to include the ungrouped genera into an artificial (paraphyletic) tribe "Cheyletini". It is quite probable, that almost all the tribes have arisen independently from a common cheyletid stock. The tribes Criokerontini and Niheliini seem to be closely related to each other, because their representatives have a common unique character, i.e. stellate solenidion on the genu I.

Thus, the family Cheyletidae includes 15 tribes, i.e. Acaropsellini, Bakini, Cheletogenini, Cheletosomatini, Chelonotini, Cheyletiini, Cheyletiellini, "Cheyletini", Cheletomorphini **trib. nov.**, Criokerontini, Metacheyletiini, Niheliini, Ornithocheyletiini, Teinocheylini and one unnamed tribe including the genus *Caudacheles*.

The tribes Cheyletiellini, Metacheyletiini, Ornithocheyletiini and Teinocheylini represent a common stalk in the obtained cladogram. Nevertheless, the characters

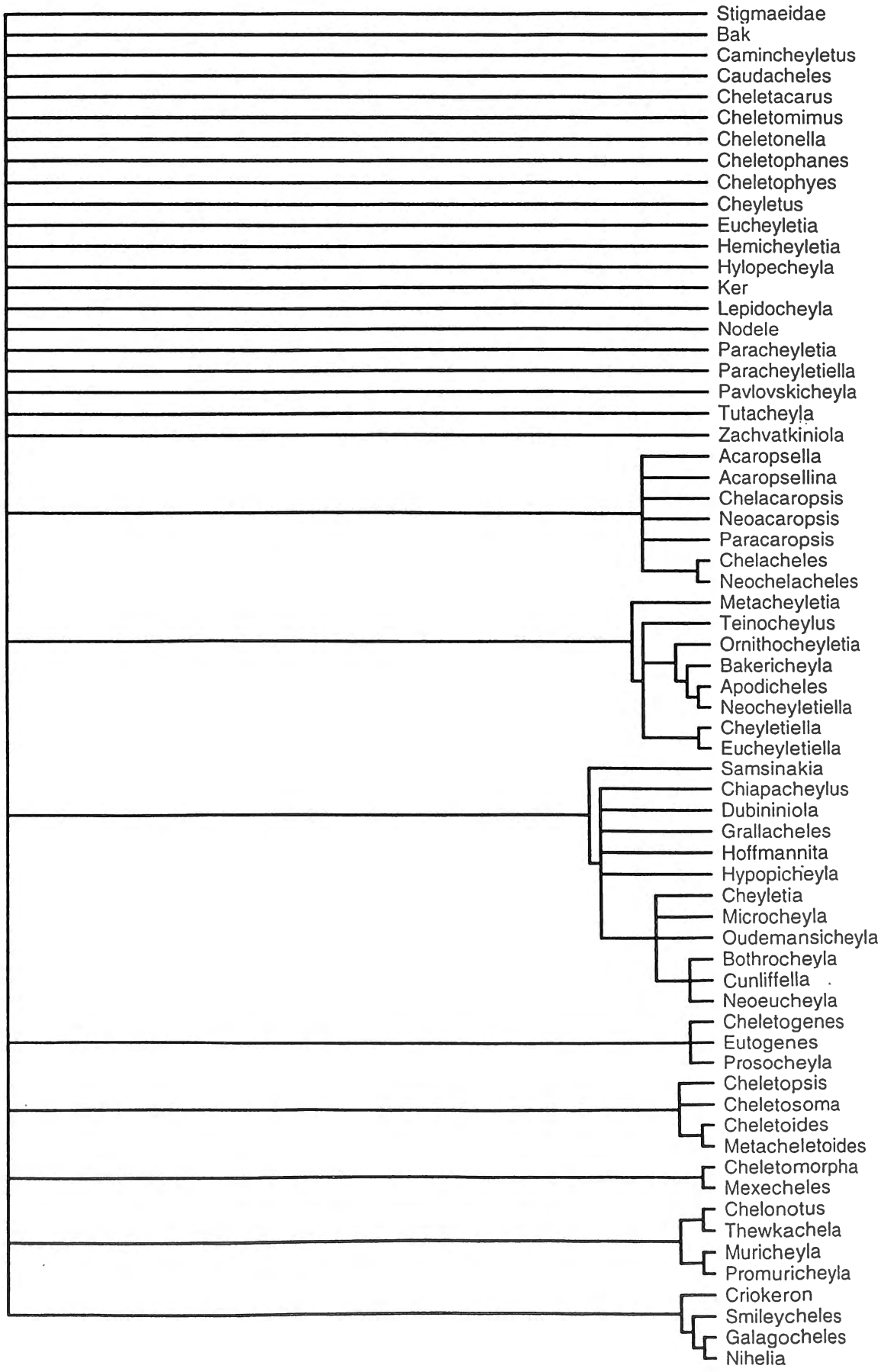

Fig. 6 — Strict consensus cladogram of Cheyletidae for 27 trees (tree length 89, CI = 0. 854, RI = 0.936, RC = 0.8), heuristic algorithm (PAUP 03. 1).

uniting these tribes (small gnathosoma, palpal claws curved laterally, short and nude setae on palpal tarsus, absence of comb-like setae in all instars) have probably appeared independently in the ancestor of these respective tribes as a result of their parasitic mode of life. The listed characters are obviously adaptative and cannot prove the affinities of these tribes.

We give here a list of the generic group that we have recognized by cladistic analysis in the first step, and also some additional groups that we have discerned within some tribes.

Within the tribe "Cheyletini" we recognise five generic groups: *Cheyletus* group (*Camincheyletus, Cheyletus, Eucheyletia* and *Zachvatkiniola*) including the genera without eyes and with serrate seta on coxae III (i); *Hylopecheyla* group (only one genus) including the parasitic mites with short tarsi and some other characters associated with parasitic mode of life (ii); the *Hemicheyletia* group (*Cheletomimus, Hemicheyletia* and *Tutacheyla*) including the genera with relatively short legs, the palpal femur with four setae and very short guard seta of tarsi I (iii); the artificial "*Cheletacarus*" group (*Cheletacarus, Cheletophanes, Nodele, Paracheyletia* and *Paracheyletiella*) including the genera with legs I not exceeding the length of idiosoma (iv); and the *Pavlovskicheyla* group (*Pavlovskicheyla* and *Ker*) including the mites without teeth on palpal claw (v).

The *Chelacheles* generic group (*Chelacheles* and *Neochelacheles*) is well recognizable within the tribe Acaropsellini. Actually the members of this group are characterised by their very long body and the great distance between coxae II and III exceeding the half of the idiosomal width.

Three generic groups are recognised within the tribe Cheyletiini: the *Neoeucheyla* group (*Bothrocheyla, Cunliffella* and *Neoeucheyla*) including the genera with a cloud-like seta on palpal tarsus (i); the *Oudemansicheyla* group (*Chiapacheylus, Dubininiola* and *Oudemansicheyla*) including the genera with numerous neotrichial setae on idiosoma, which are similar in shape with other idiosomal setae (ii); the *Hypopicheyla* group (*Hypopicheyla* and *Samsinakia*) including the mites with numerous flattened polygonal setae and gnathosoma being partly or almost completely covered with idiosoma (iii).

In appears from this discussion that most of the suprageneric groups created by the previous authors have been substantially revised and their composition modified.

Position of genera not included in the analysis

As we have noted above, eight cheyletid genera could not be returned in our cladistic analysis, for different reasons. We propose, however, to include provisionally these genera in any of the tribes that we have established.

The genus *Alliea* is the most closely related to *Caudacheles*. In the representatives of these genera, the guard seta is fan-like and the solenidion on tarsus I is almost apical. Some gnathosomal characters of the males of *Alliea*, for example the toothless palpal claw, are also present in the females of *Caudacheles*. Therefore we may expect that the discovery of the female of *Alliea* will confirm this narrow relationship and confirms the validity of the tribe Allieini proposed by VOLGIN (1969).

The genus *Anthribicheyla* possesses all characters of the tribe Cheyletini: two comb-like setae, the hair-like shape of the guard seta of tarsi I, the primitive aspect of the palpal chaetotaxy etc...

The genus *Atarsacheylus* belongs to the *Chelacheles* group (tribe Acaropsellini) because it has an elongated body shape, arch-like peritremes and a palpal chaetotaxy similar to these generic group.

The genus *Columbicheyla* possesses the main principal characters of the tribe Cheyletiini i.e. fan-like setae on the palpal tibia and fan-like guard seta on tarsus I.

Type species of the genus *Eucheletopsis*, *E. major* TROUESSART, 1893 was redescribed and depicted by OUDEMANS (1906). In the figures of this author the solenidion $\omega 1$ and the guard seta had been omitted, probably overlooked by OUDEMANS. We think, therefore that this genus should be included in the tribe Cheletosomatini.

The genus *Laeliocheyletia,* could belong to the *Hemicheyletia* group (tribe Cheyletini) because it has a small guard seta on tarsi I and 4 setae on palpal genu, as in genera of these group.

The genus *Sciurocheyla* belongs to the tribe Niheliini. It is represented by a single species, unadequately described, *S.* squamosa DOMROW et BAKER, 1963. Unfortunately, this species was not available for our study. From the original figures, this species resembles very much a mite of the genus *Smileycheles,* also represented by a single species, *S. camerounensis* FAIN, 1979. Only a new study of *Sciurocheyla squamosa* will allow to precise the status of these genera.

The position of the genus *Thryonomycheyla* remains unclear because females of this genus are unknown.

Diagnoses of suprageneric taxa based on female characters

I. Tribe "Cheyletini" LEACH, 1815

Type genus: *Cheyletus* LATRELLE, 1796

DEFINITION: Gnathosoma well developed, about 30%, or more, length of idiosoma, without protrusions. Gnathosomal apex with short median protuberances. Palpal tarsi with 2 dorsal comb-like setae and 2 ventral well-developed sickle-like setae. Palpal slender, claws slightly curved medially, with or without teeth. All setae of palpal tibia hair-like or lanceolate. Palpal femur and palpal genu not fused, without protrusions, bearing altogether 5 setae. Idiosoma ovoid or rombus-like. Eyes present or absent. Shoulder-like projections of idiosoma absent. All idiosomal setae not exceeding half of idiosomal length. Neotrichial setae present or absent. Length of all legs not exceeding the idiosomal length. Legs IV normally developed. Tarsi slender, with knobs not covering pretarsus or

without knobs. Guard seta of tarsus I hair-like, variable in length, solenidion ω*1* situated in basal half of tarsus I. Tibia I with solenidion. Tibia II with or without solenidion. Genu I with a rod-like solenidion. Seta v1 of tarsus I situated almost at same level as solenidion ω*1* and guard seta. Pretarsus and claws present on all legs. Apical setae of tarsus I normally long. Tarsal setae *p'* and *p''* II-IV hair-like. Coxae III with 2 setae. Trochanters I-IV with 1 seta. Distance between coxae II and III less than half of idiosomal width. MALE. Palpal tarsus with 2 comb-like and 2 sickle-like setae.

INCLUDED GENERA: *Anthribicheyla, Camincheyletus, Cheletacarus, Cheletonella, Cheletomimus, Cheletophanes, Cheletophyes, Eucheyletia, Hemicheyletia, Hylopecheyla, Ker, Laeliocheyla, Lepidocheyla, Nodele, Paracheyletiella, Paracheyletia, Pavlovskicheyla, Tutacheyla* and *Zachvatkiniola.*

II. Tribe Cheletomorphini trib. nov.
Type genus: *Cheletomorpha* OUDEMANS, 1904

DEFINITION: Gnathosoma well developed, about 30%, or more, length of idiosoma, without protrusions. Gnathosomal apex with short median protuberances. Palpal tarsi with 2 dorsal comb-like setae and 2 well developed sickle-like ventral setae. Palpal claws slender, slightly curved medially, with teeth. All setae of palpal tibia hair-like. Palpal femur with 5 setae, not fused with palpal genu, without protrusions. Idiosoma ovoid. Eyes present. Shoulder-like projections of idiosoma absent. All idiosomal setae not exceeding half of idiosomal length. Neotrichial setae present. Length of all legs I exceeding idiosomal length. Legs IV normally developed. All tarsi slender, tarsi I very long, without knobs covering pretarsus. Guard seta of tarsus I hair-like well developed, solenidion ω*1* situated in basal half of tarsus I. Tibia I with solenidion. Tibia II without solenidion. Genu I with rod-like solenidion. Seta v1 of tarsus I situated more apical than solenidion ω*1* and guard seta. Pretarsus and claws present on all legs. Apical setae of tarsus I normally long. Tarsal setae *p'* and *p''* II-IV hair-like. Coxae III with 2 setae. Trochanters I-IV with 1 seta. Distance between coxae II and III less than half of idiosomal width. MALE. Palpal tarsus with 2 comb-like and 2 sickle-like setae.

INCLUDED GENERA: *Mexecheles.*

III. Tribe Acaropsellini VOLGIN, 1969
Type genus: *Acaropsellina* SUMMERS, 1976

DEFINITION: Gnathosoma well developed, about 30%, or more, length of idiosoma, without protrusions. Gnathosomal apex with short median protuberances or without them. Palpal tarsi with 1 well developed comb-like seta, 1 slightly barbed dorsal seta and 2 well developed sickle-like ventral setae. Palpal claws slightly curved medially, with teeth, not thickened. All setae of palpal tibia hair-like. Palpal femur with 3 setae, palpal genu with 2 setae, not fused with femur, without protrusions, ventral seta of palpal genu situated at base of the segment. Idiosoma ovoid. Eyes present. Shoulder-like projections of idiosoma absent. All idiosomal setae not exceeding half of idiosomal length. Neotrichial setae present or absent. Length of all legs not exceeding idiosomal length. Legs IV normally developed. Tarsi slender, with knobs not extending to pretarsus. Guard seta of tarsus I short, solenidion ω*1* situated in basal half of tarsus I. Solenidions on tibia I-II present. Genu I with rod-like solenidion. Seta v1 of tarsus I situated at same level as solenidion ω*1* and guard seta. Pretarsus and claws present on all legs. Apical seta of tarsus I normally long. Tarsal setae *p'* and *p''* hair-like. Coxae III with 2 setae. Trochanters I-IV with 1 seta. Distance between coxae II and III less than half of idiosomal width. MALE. Palpal tarsus with 1 shortly barbed seta, 1 short nude seta and 2 sickle-like setae.

INCLUDED GENERA: *Acaropsella, Atarsacheylus, Chelacaropsis, Chelacheles, Neoacaropsis, Neochelacheles* and *Paracaropsis.*

IV. Tribe Bakini VOLGIN, 1969
Type genus: *Bak* YUNKER, 1961

DEFINITION: Gnathosoma well developed, without protrusions. Gnathosomal apex with short median protuberances. Palpal tarsi with 2 dorsal comb-like setae and 2 well developed sickle-like ventral setae. Palpal claws slightly curved medially, with teeth, not thickened. All setae of palpal tibia hair-like. Palpal femur with 3 setae, palpal genu with 2 setae, not fused with femur, without protrusions. Idiosoma vermiform. Eyes absent. Shoulder-like projections of idiosoma absent. All idiosomal setae not exceeding half of idiosomal length. Neotrichial setae absent. Length of all legs not exceeding idiosomal length. Legs IV normally developed. Tarsi slender without knobs covering pretarsus. Guard seta of tarsus I hair-like well developed, solenidion ω*1* situated in basal half of tarsus I. Tibia I with solenidion. Tibia II without solenidion. Genu I with rod-like solenidion. Seta v1 of tarsus I situated at same level as solenidion ω*1* and guard seta. Pretarsus and claws present on all legs. Apical seta of tarsus I normaly long. Tarsal setae *p'* and *p''* II-IV hair-like. Coxae III with 2 setae. Trochanters I-IV with 1 seta. Distance between coxae II and III exceeding idiosomal width. MALE. Palpal tarsus with 2 comb-like and 2 sickle-like setae.

INCLUDED GENERA: type genus only.

V. Tribe Cheyletiini VOLGIN, 1969
Type genus: *Cheyletia* HALLER, 1884

DEFINITION: Gnathosoma well developed, about 30%, or more, length of idiosoma, without protrusions. Gnatho-

somal apex with short median protuberances. Palpal tarsi with 2 dorsal comb-like setae and 2 well developed sickle-like ventral setae (in *Neoeucheyla* group the inner ventral setae are cloud-like). Palpal claws slightly curved medially, with teeth, not thickened. Dorsal and ventral setae of palpal tibia fan-like. Palpal femur and palpal genu not fused, without protrusions, bearing altogether 5-3 setae (most of these setae fan-like). Idiosoma oval. Eyes present (strongly reduced in *Hoffmannita*). Shoulder-like projections of idiosoma absent. All idiosomal setae not exceeding half of idiosomal length. Neotrichial setae present. Length of all legs not exceeding idiosomal length. Legs IV normally developed. Tarsi slender without knobs covering pretarsus. Guard seta of tarsus I fan-like, solenidion ω*1* situated in basal half of tarsus I. Tibia I with solenidion. Tibia II without solenidion. Genu I with rod-like solenidion. Seta v1 of tarsus I situated at same level as solenidion ω*1* and guard seta. Pretarsus and claws present on all legs. Apical seta of tarsus I normally long. Tarsal setae *p'* and *p''* II-IV hair-like. Coxae III with 2 setae. Trochanters I-IV with 1 seta. Distance between coxae II and III less than half of the idiosomal width. MALE. Palpal tarsus with 2 comb-like and 2 sickle-like setae.

INCLUDED GENERA: *Bothrocheyla, Chiapacheylus, Columbicheyla, Cunliffella, Dubininiola, Grallacheles, Hoffmannita, Hypopicheyla, Microcheyla, Neoeucheyla, Oudemansicheyla* and *Samsinakia.*

VI. Tribe Cheletogenini VOLGIN, 1969
Type genus *Cheletogenes* OUDEMANS, 1905

DEFINITION: Gnathosoma well developed, about 30%, or more, length of idiosoma, without protrusions. Gnathosomal apex with short median protuberances. Palpal tarsi with 2 dorsal comb-like setae and 2 well developed sickle-like ventral setae. Palpal claws slightly curved medially, with teeth, not thickened. All setae of palpal tibia hair-like (ventral seta fan-like in *Cheletogenes*). Palpal femur and palpal genu not fused, without protrusions, bear altogether 5 setae. Idiosoma ovate or rombus-like. Eyes present or absent. Shoulder-like projections of idiosoma absent. All idiosomal setae not exceeding half of idiosomal length. Neotrichial setae present. Length of all legs not exceeding idiosomal length. Legs IV normally developed. Tarsi slender without knobs covering pretarsus. Guard seta of tarsus I hair-like, short, solenidion ω*1* situated in basal half of tarsus I on nipple-like protrusion. Tibia I with solenidion. Tibia II without solenidion. Genu I with rod-like solenidion. Seta v1 of tarsus I situated at same level as solenidion ω*1* and guard seta. Pretarsus and claws absent on legs I. Apical setae of tarsus I abnormally long. Tarsal setae *p'* and *p''* II-IV hair-like. Coxae III with 2 setae. Trochanters I-IV with 1 seta. Distance between coxae II and III less than half of the idiosomal width. MALE. Palpal tarsus with 2 comb-like and 2 sickle-like setae.

INCLUDED GENERA: *Eutogenes* and *Prosocheyla.*

VII. Tribe Cheletosomatini VOLGIN, 1969
Type genus: *Cheletosoma* OUDEMANS, 1965

DEFINITION: Gnathosoma well developed, about 30%, or more, length of idiosoma, without protrusions. Gnathosomal apex with short median protuberances. Both dorsal setae of palpal tarsus without teeth, both ventral setae well developed, sickle-like. Palpal claws slightly curved medially, with teeth, not thickened. All setae of palpal tibia hair-like. Palpal femur with 4 setae, palpal genu with one seta, not fused with femur, without protrusions. Idiosoma ovate. Eyes absent. Shoulder-like projections of idiosoma absent. Some idiosomal setae longer than half of idiosomal length. Neotrichial setae absent. Length of all legs not exceeding idiosomal length. Legs IV normally developed. Tarsi slender without knobs covering pretarsus. Guard seta of tarsus I hair-like, variable length, solenidion ω*1* situated in anterior half of tarsus I. Tibia I with solenidion. Tibia II without solenidion. Genu I with rod-like solenidion. Seta v1 of tarsus I situated behind level of solenidion ω*1* and guard seta. Pretarsus and claws present on all legs. Apical setae of tarsus I normally long. Tarsal setae *p'* and *p''* II-IV plume-like. Coxae III with 2 setae. Trochanters I-IV with 1 seta. Coxae II and III separated by less than half of the idiosomal width. MALE. Palpal tarsus with 1 comb-like seta and 3 nude setae or all 4 tarsal setae are nude.

INCLUDED GENERA: *Cheletoides, Cheletopsis, Eucheletopsis* and *Metacheletoides.*

VIII. Tribe Chelonotini VOLGIN, 1969
Type genus *Chelonotus* BERLESE, 1893

DEFINITION: Gnathosoma well developed, about 30%, or more, length of idiosoma, with small protrusions or without ones. Gnathosomal apex with short median protuberances. Palpal tarsi with 1 dorsal comb-like seta, 1 dorsal torn-like seta (comb-like in *Promuricheyla*) and 2 well developed sickle-like ventral setae. Palpal claws unusually strong and large, with one or two teeth situated dorsally, curved laterally. All setae of palpal tibia hair-like. Palpal femur and palpal genu not fused, without protrusions, bear altogether 5 setae. Idiosoma ovate. Eyes absent. Shoulder-like projections of idiosoma absent. All idiosomal setae not exceeding half of idiosomal length. Neotrichial setae absent. Length of all legs not exceeding idiosomal length. Legs IV normally developed. Tarsi slender without knobs covered pretarsus. Guard seta of tarsus I hair-like, variable length, solenidion ω*1* situated in basal half of tarsus I. Tibia I with solenidion. Tibia II without solenidion. Genu I with rod-like solenidion. Seta v1 of tarsus I situated at same level as solenidion ω*1* and guard seta. Pretarsus and claws present on all legs. Apical seta of tarsus I normally long. Tarsal setae *p'* and *p''* II-IV

hair-like. Coxae III with 2 setae. Trochanters I-IV with one seta. Distance between coxae II and III less than half of the idiosomal width. MALE. Unknown.

INCLUDED GENERA: *Muricheyla, Promuricheyla* and *Thewkachela.*

IX. Tribe Niheliini SMILEY, 1977
Type genus: *Nihelia* DOMROW et BAKER, 1960

DEFINITION: Gnathosoma well developed, about 30%, or more, length of idiosoma, without or with protrusions. Gnathosomal apex with long and numerous median protuberances. Palpal tarsi strongly reduced, without comb-like setae. Palpal claws hypertrophied, curved ventrally, flat and strong, without teeth. All setae of palpal tibia hair-like. Palpal femur and palpal genu fused, with lateral protrusion, bear altogether 5 setae. Idiosoma rombus-like. Eyes absent. All idiosomal setae not exceeding half of idiosomal length. Neotrichial setae present. Length of all legs not exceeding idiosomal length. Legs IV normally developed. Tarsi thickened without knobs covering pretarsus. Guard seta of tarsus I hair-like, solenidion ω*1* situated in apical half of tarsus I. Tibia I with solenidion. Tibia II with solenidion or absent. Solenidion on genu I stellate. Seta v1 of tarsus I situated at same level as solenidion ω*1* and guard seta. Pretarsus and claws present on all legs. Apical seta of tarsus I normally long. Tarsal setae *p'* and *p''* II-IV hair-like. Coxae III with 2 setae. Trochanters I-IV with 1 seta. Distance between coxae II and III less than half of idiosomal width. MALE. Palpal tarsus with 4 well developed setae. Palpal claw not modified. Palps of usual structure.

INCLUDED GENERA: *Galagocheles, Sciurocheyla* and *Smileycheles.*

X. Tribe Criokerontini SMILEY, 1977
Type genus *Criokeron* VOLGIN, 1966

DEFINITION: Gnathosoma well developed, about 30%, or more, length of idiosoma, with pair of large lateral hook-like processes. Gnathosomal apex with short median protuberances. Palps strongly reduced without claw, palpal tarsus fused with palpal tibia, with 1 comb-like setae and 2 well developed sickle-like setae. Palpal femur fused with genu, without protrusions. Idiosoma ovate. Eyes absent. Shoulder-like projections of idiosoma absent. All idiosomal setae not exceeding half of idiosomal length. Neotrichial setae absent. Length of all legs not exceeding idiosomal length. Legs IV normally developed. Tarsi thickened without knobs covering pretarsus. Guard seta of tarsus I hair-like, solenidion ω*1* situated at midlevel of tarsus I. Tibia I with solenidion. Tibia II without solenidion. Solenidion on genu I stellate. Seta v1 of tarsus I situated at same level as solenidion ω*1* and guard seta. Pretarsus and claws present on all legs. Apical seta of tarsus I normally long. Tarsal setae *p'* and *p''* II-IV hair-like. Coxae III with 2 setae. Trochanters I-IV with 1 seta. Distance between coxae II and III less than half of the idiosomal width. MALE. Palpal tarsus with 1 comb-like, 1 barbed and 2 sickle-like setae. Palpal claw present, palps of usual structure.

INCLUDED GENERA: type genus only.

XI. Tribe Cheyletiellini VOLGIN, 1969
Type genus: *Cheyletiella* CANESTRINI, 1886

DEFINITION: Gnathosoma less than 30% of idiosomal length, without protrusions. Gnathosomal apex with short median protuberances. Palpal tarsi with 4 short nude setae and solenidion. Palpal claws with fine ventral striations curved ventro laterally, without teeth, not thickened. All setae of palpal tibia hair-like. Palpal femur with 3 setae, palpal genu with 2 setae, not fused with femur, without protrusions. Idiosoma rhombus-like. Eyes absent. Shoulder-like projections of idiosoma present. All idiosomal setae, except *l5*, not exceeding half of idiosomal length. Neotrichial setae absent. Length of all legs not more than idiosomal length. Legs IV normally developed. Tarsi thickened without knobs covering pretarsus. Guard seta of tarsus I hair-like, solenidion ω*1* situated in apical half of tarsus I. Solenidions on tibia I-II absent. Genu I with rod-like solenidion. Seta v1 of tarsus I situated behind solenidion ω*1* and guard seta level. Pretarsus present on all legs, all tarsal claws absent. Apical seta of tarsus I normally long. Tarsal setae *p'* and *p''* II-IV hair-like. Coxae III with 2 setae. Trochanters I-IV with one seta. Distance between coxae II and III less than half of the idiosomal width. MALE. Palpal tarsus with 2 short and nude setae and 2 flag-like setae.

INCLUDED GENERA: *Eucheyletiella.*

XII. Tribe Ornithocheyletiini VOLGIN, 1969
Type genus: *Ornithocheyletia* VOLGIN, 1964

DEFINITION: Gnathosoma less than 30% of idiosomal length, without protrusions. Gnathosomal apex with short median protuberances. Palpal tarsi with 4-3 short nude setae. Palpal claws curved ventro laterally, without teeth, not thickened. All setae of palpal tibia hair-like. Palpal femur with 3 setae, palpal genu with 2 setae not fused with femur, without protrusions or with small protrusions (*Apodicheles*). Idiosoma ovate. Eyes absent. Shoulder-like projections of idiosoma absent. All idiosomal setae, excluding *l5*, not exceeding half of idiosomal length. Neotrichial setae absent. Length of all legs not exceeding idiosomal length. Legs IV normally developed. Tarsi thickened with knobs covering pretarsus. Guard seta of tarsus I hair-like, solenidion ω*1* situated in apical half of tarsus I. Tibia I with solenidion. Tibia II without solenidion. Genu I with rod-like solenidion or globular. Seta v1

of tarsus I situated at same level as solenidion ω*1* and guard seta. Pretarsus and well developed claws present on all legs. Apical seta of tarsus I normally long. Tarsal setae *p'* and *p'* hair-like, but sometimes deeply dissected (*Ornithocheyletia)* or feather-like (*Neocheyletiella*). Coxae III with 2-1 setae. Trochanters III-IV with or without seta. Distance between coxae II and III less than half of the idiosomal width. MALE. Palpal tarsus with 4-3 short nude setae.

INCLUDED GENERA: *Apodicheles, Bakericheyla* and *Neocheyletiella*

XIII. Teinocheylini FAIN, 1974
Type genus: *Teinocheylus* FAIN, 1974

DEFINITION: Gnathosoma less than 30% of idiosomal length, without protrusions. Gnathosomal apex with short median protuberances. Palpal tarsi with 2 very short nude setae. Palpal claws curved ventro laterally, without teeth, not thickened. All setae of palpal tibia hair-like. Palpal femur with 3 setae, palpal genu with 2 setae, not fused with femur, without protrusions. Idiosoma vermiform. Eyes absent. Shoulder-like projections of idiosoma absent. All idiosomal setae not exceeding half of idiosomal length. Neotrichial setae present. Length of all legs not exceeding idiosomal length. Legs IV normally developed. Tarsi thickened without knobs covering pretarsus. Guard seta of tarsus I hair-like, solenidion ω*1* situated in apical half of tarsus I. Tibia I with solenidion. Tibia II without solenidion. Genu I with rod-like solenidion. Seta v1 of tarsus I situated at same level as solenidion ω*1* and guard seta. Pretarsus present on all legs, claws absent on legs IV. Apical seta of tarsus I not normally long. Tarsal setae *p'* and *p''* II-IV hair-like. Coxae III with 2 setae. Trochanters I-IV with 1 seta. Distance between coxae II and III less than half of the idiosomal width. MALE. Palpal tarsus with 2 short nude setae.

INCLUDED GENERA: type genus only.

XIV. Tribe Metacheyletiini FAIN, 1980
Type genus: *Metacheyletia* FAIN, 1972

DEFINITION: Gnathosoma less than 1/3 of idiosomal length, without protrusions. Gnathosomal apex with short median protuberances. Palpal tarsi with 4 short and nude setae. Palpal claws slightly curved medially, with one tooth, not thickened. All setae of palpal tibia hair-like. Palpal femur and palpal tarsus each with one seta, genu not fused with femur, without protrusions. Idiosoma ovate. Eyes absent. Shoulder-like projections of idiosoma absent. All idiosomal setae not exceeding half of idiosomal length. Neotrichial setae absent. Length of all legs not exceeding idiosomal length. Legs IV completely reduced. Tarsi thickened without knobs covering pretarsus. Guard seta of tarsus I hair-like, solenidion ω*1* situated in apical half of tarsus I. Tibia I with solenidion. Tibia II without solenidion. Genu I with rod-like solenidion. Seta v1 of tarsus I situated at same level as solenidion ω*1* and guard seta. Pretarsus and claws present on all legs. Apical seta of tarsus I normally long. Tarsal setae *p'* and *p''* II-IV hair-like. Coxae II-III and trochanters all legs without setae. Distance between coxae II and III subequal to half of idiosomal width. MALE. Palpal tarsus with 4 short nude setae.

INCLUDED GENERA: type genus only.

XV. Unnamed tribe including genus *Caudacheles*

DEFINITION: Gnathosoma well developed, about 30% length of idiosoma, without protrusions. Gnathosomal apex with short median protuberances. Palpal tarsi with 1 dorsal comb-like setae, 1 dorsal short nude seta and 2 well developed sickle-like ventral setae. Palpal claws slightly curved medially, without teeth, not thickened. All setae of palpal tibia hair-like. Palpal femur with 3 setae; palpal genu with 2 setae, not fused femur, without protrusions, bear altogether 5 setae. Idiosoma ovate. Eyes absent. Shoulder-like projections of idiosoma absent. All idiosomal setae not exceeding half of idiosomal length. Neotrichial setae present. Length of all legs not exceeding idiosomal length. Legs IV normally developed. Tarsi slender without knobs covering pretarsus. Guard seta of tarsus I fan-like, solenidion ω*1* situated in apical half of tarsus I. Solenidion on tibia I-II present. Genu I with rod-like solenidion. Seta v1 of tarsus I situated at same level with guard seta and behind solenidion ω*1*. Pretarsus and claws present on all legs. Apical seta of tarsus I normally long. Tarsal setae *p'* and *p''* II-IV hair-like. Coxae III with 2 setae. Trochanters I-IV with one seta. Distance between coxae II and III less than half of idiosomal width. MALE. Unknown.

INCLUDED GENERA: only genus *Caudacheles*.

EVOLUTION OF THE CHEYLETIDAE AND ANALYSIS OF THEIR HOST-PARASITE ASSOCIATIONS

A phylogenetic hypothesis of the cheyletoid mites (Cheyletoidea) was proposed by BOCHKOV (1999, 2001 in press). According to this hypothesis, the family Myobiidae was excluded from this superfamily and the taxonomic status of the subfamily Epimyodicinae (Cloacaridae) has been risen to the family rank. In a separate publication (BOCHKOV *et al.*, 1999) the family Ophioptidae had been included into the family Harpirhynchidae as a subfamily. Monophyly of all cheyletoid families, (Cheyletidae, Syringophilidae, Harpirhynchidae, Psorergatidae, Demodicidae, Cloacaridae and Epimyodicidae), as well as of the cheyletoids as a whole, is well supported by numerous apomorphies (BOCHKOV, 2001, in press).

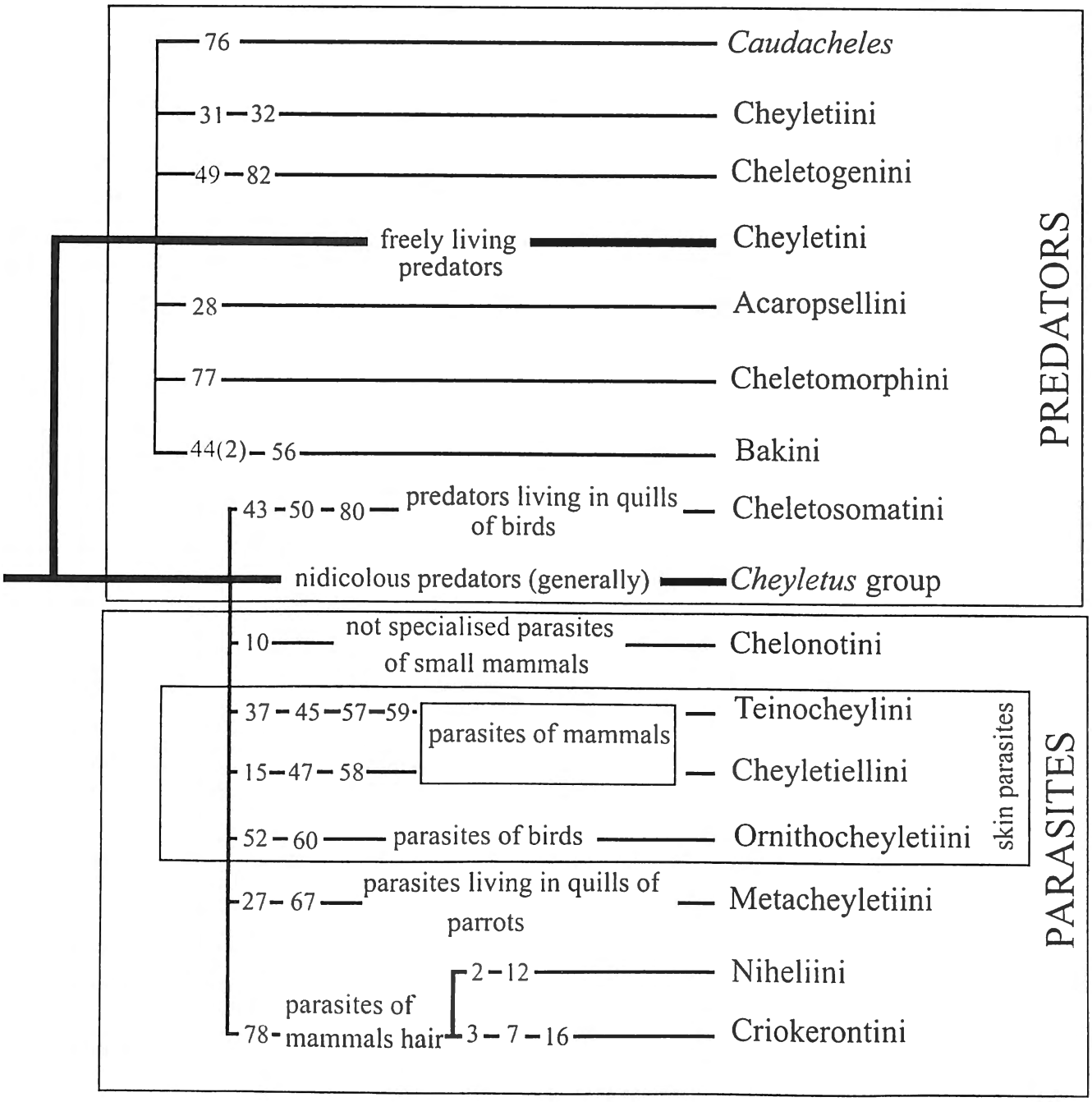

Fig. 7 — Phylogenetic system of Cheyletidae.

According to our phylogenetic hypothesis (BOCHKOV, 1999; BOCHKOV, 2001, in press) the family Cheyletidae is a sister group of the family Syringophilidae (mites parasitizing quills of birds). It should be noted that only the family Cheyletidae includes both predators and parasites, all the other families of Cheyletoidea are represented by specialized parasitic mites.

The common ancestor of the superfamily Cheyletoidea was probably a predator, feeding on microarthropods. The phylogeny and recent distribution of the cheyletoid mites on host taxa suggest that the common ancestor of the parasitic families of the Cheyletoidea (after splitting the lineage of Cheyletidae and Syringophilidae) had become a parasite on the common ancestor of the amniotic vertebrates, diapsids and sinapsids (BOCHKOV, 1999). Therefore, the evolutionary tracks of the Cheyletidae and the other parasitic cheyletoid mites dispersed not later than the beginning of the Carboniferous period, since a divergence of the diapsids and sinapsids from a common stock of the amniotic vertebrates is usually dated from the beginning of this period (CARROLL, 1992).

Thus, the cheyletid mites were primarily free-living predators. The recent representatives of this family show different types of specialised predation.

The phylogram shown in Fig. 7 is derived from the strict consensus tree obtained at the second step of ana-

lysis. The single difference between this phylogram and the cladogram consists in the structure of the tribe "Cheyletini". This tribe was separated artificially into two phylogenetic branches - the *Cheyletus* group, represented by nidicolous predators, and the other "Cheyletini", represented mainly by freely-living predators.

Tribe "Cheyletini"

The paraphyletic tribe "Cheyletini" includes the most archaic mites of the family. These mites probably, are the closest to the ancestor of the Cheyletidae. This tribe contains numerous ungrouped genera and several generic groups.

The members of the *Cheyletus* group commonly occur in nests of vertebrates, and also, secondarily in soil and in grain supplies. The species of the genus *Cheyletus* live in the nests of birds and mammals, in soil, litter, granaries, house dust, etc. The genera *Eucheyletia, Zachvatkiniola* and *Cameincheyletus* are associated with nests of mammals and grain supplies. This group is generally represented by mites devoid of eyes. In our opinion, the ancestor of this group was also the ancestor for the cheyletid associated with mammals and birds. The *Cheyletus*-like archaic predatory cheyletids have numerous preadaptations to the parasitic mode of life i.e. well developed chelicerae, stylophore etc (Akimov and Gorgol, 1990).

It is quite possible that the mites living in nests of some mammals or birds have independently changed predation to parasitism. Such transition to parasitism via nest predation is rather common for arthropods (Beklemishev, 1970; Fain, 1979f).

For example, the parasitic species of the genus *Hylopecheyla* (*Hylopecheyla* group), associated with South Asian squirrels (Rodentia: Sciuridae) and tupaids (Scandentia) (Fain and Nadchatram, 1980), are closely related to the *Cheyletus* group and possess almost "predaceous" morphology.

The mites of the other groups of the tribe "Cheyletini" and some ungrouped genera are predators living on plants.

The representatives of the *Hemicheyletia* group (the mites with relatively short legs) for the most part live on trees.

The mites of the *Pavlovskicheyla* group are dwellers on plant debris and dung. One species of this group, *Pavlovskicheyla platydemae* Thewke et Enns, 1975, is a parasite located under elytra of the beetle *Platydema ruficorne* (Tenebrionidae) (Thewke and Enns, 1975). Also, the members of the ungrouped genus *Cheletophyes* are associated with the carpenter bees (Xylocopinae) in South-East Asia (Fain *et al.*, 1980).

Tribe Cheletomorphini

The representatives of the tribe *Cheletomorphini* are mites with unusually long legs I, generally living on trees, but can occur in other habitats. Probably, the legs I allow them to detect the approach of their prey. It is interesting to note, that phoresy of *Cheletomorpha lepidopterorum* (Shaw, 1794) on butterflies is quite frequent (Van Eyndhoven, 1964).

The members of the tribe Cheletogenini are specialised predators, for the most part living on trees and bushes. The claws and pretarsus of legs I are completely absent in these mites, but the apical setae of the anterior legs are abnormally long.

Unnamed tribe including *Caudacheles* and *Alliei*

A few peculiar species of the unnamed tribe including *Caudacheles* and *Alliei* were found on plants, in grains and on a rat (Muridae: *Rattus*) (Yunker, 1960; Gerson, 1968).

Tribe Bakini

This tribe includes highly specialised species frequently occuring in with bee hive debris (Gerson *et al,* 1999).

Tribe Acaropsellini

The mites of the tribe Acaropsellini are associated with stored products, plants and soil, or sometimes occur in nests of rodents and birds. Representatives of the genera *Neochelacheles* (*N. messersmithi* Smiley et Williams, 1972) and *Paracaropsis* (*P. travisi* Baker, 1949) were found on insects (Smiley and Wiliams, 1972; Klimov, 1998).

Tribe Cheyletiellini

Most representatives of the tribe Cheyletiellini live on plants or in plant debris. Some species of this tribe i.e. *Bothrocheyla* spp. or *Dubininiola* spp. , may be found, occasionally in the nests of vertebrates.

The females of the genera *Samsinakia*, *Hypopicheyla* and *Cheyletia* are deeply specialized to phoresy on bugs of the genus *Aradus* (Aradidae) or beetles of the family Tenebrionidae (Volgin, 1969; Bochkov and Mironov, 1998b). In these genera the dorsum of the body is covered with flat polygonal setae; in two former genera, the gnathosoma is situated almost ventrally. These mites, are probably dwellers in some peculiar habitats, which are regularly visited by aradids or tenebrionids.

The cheyletids associated with birds are represented by three independent phyletic lines or tribes: predaceous mites living in quills (Cheletosomatini) (i); parasitic mites living in quills of parrots (Metacheyletiini) (ii) and parasitic mites living on bird skin (Ornithocheyletiini) (iii).

Tribe Cheletosomatini

All mites of the tribe Cheletosomatini live in quills of birds and prey on mites of the families Syringophilidae, Syringobiidae and other mites inhabiting quills. These

mites are highly specialised predators and they have developed certain specific adaptations for the life inside quills. Nevertheless, they resemble very much the nidicolous predators of the *Cheyletus* group. It is possible that these two groups (*Cheyletus* group and Cheletosomatini) derived from a common ancestor, probably a nidicolous predator living in the nest of birds.

The mites of the genus *Cheletopsis* are associated with birds of the order Charadriiformes (VOLGIN, 1969; MIRONOV *et al.*, 1991; KIVGANOV and BOCHKOV, 1994) (Table 4).

All known species of the genus *Cheletoides* are associated with gallinaceous birds (Galliformes). The first species, *C. uncinatus* HELLER, 1880 was collected from the quills of *Pavo cristatus*, the second, *C. chirunduensis* FAIN, 1979 was found in the quills of *Numida meleagris* (FAIN, 1979e).

The single species of the genus *Eucheletopsis*, *E. major* (OUDEMANS, 1904) was found in the quills of a swallow of the genus *Hemiprogne* (Passeriformes) (OUDEMANS, 1906).

The genus *Metacheletoides* includes four species, two of them live in the quills of *Numida meleagris* and the two others were found in the quills of *Crinifer* sp. (Cuculiiformes) (FAIN, 1979e). It should be noted that the species associated with birds from the genus *Crinifer* is clearly distinguished from the species described from the guineafowl by the presence of a bifurcate seta *ft'* on the legs I.

Thus, the representatives of the tribe Cheletosomatini are mainly associated with birds of the orders Galliformes and Charadriiformes, while one genus *Eucheletopsis,* is known from the order Passeriformes. The relationships of the Passeriformes with the other terrestrial higher Neornithes are not clear (KUROCHKIN, 1993). It is possible that this order represents some earlier separated branch. According to other acarological data, the representatives of the families Rhinonyssidae, Ereynetidae, Harpirhynchidae (Harpypalpinae) and Proctophyllodidae occurring on passerines are characterised by certain archaic features (Fain , 1969; MOSS, 1979; MIRONOV, 1998; BOCHKOV *et al.*, 1999).The discovery on passerines, of cheletosomatin mites, which are mainly associated with ancient orders of birds supports the hypothesis that this order of birds originated earlier than it was believed until now.

TRIBE ORNITHOCHEYLETIINI

Mites of the tribe Ornithocheyletiini are highly specialised skin parasites of birds. There are two types of food specialisation within this tribe. The mites of the genus *Bakericheyla* are blood-sucking, while the mites of the genus *Ornithocheyletia* are lymph-sucking (AKIMOV and GORGOL, 1990). The food specialisation of the two other genera, *Apodicheles* and *Neocheyletiella*, is unknown.

The members of this tribe show interesting adaptations for safe attachment to skin of birds. For example, mites of the genera *Ornithocheyletia* and *Bakericheyla* spin a web and live under this cobweb in a mode quite similar to the spider mites of the family Tetranychidae (VOLGIN, 1969; AKIMOV and GORGOL, 1990).

The mites of the genus *Neocheyletiella* are associated with two orders of hosts, Passeriformes and Columbiformes. They are also monoxenous or oligoxenous parasites. (Table 5).

The mites of the genus *Bakericheyla* are associated with birds belonging to three orders: Apodiformes, Cor-

Table 4. Distribution of species of the genus *Cheletopsis* on the host taxa from the order Charadriiformes.

Mite species	Host species	Host family	Locality
C. impavida	*Tringa totanus*	Scolopacidae	France
''	*Calidris minutus*	Scolopacidae	Kazakhstan
''	*Calidris temmincki*	Scolopacidae	Kirghizia
''	*Calidris ruficollis*	Scolopacidae	Russia (Siberia)
C. anax	*Tringa totanus*	Scolopacidae	France
C. basilica	*Tringa totanus*	Scolopacidae	France
C. animosa	*Tringa totanus*	Scolopacidae	France
C. magnanima	*Tringa flavipes*	Scolopacidae	Chili
C. mariae	*Actitis hypoleucos*	Scolopacidae	Kirghizia
C. charadrii	*Charadrius dubius*	Scolopacidae	Kirghizia
C. daberti	*Tringa glareola*	Scolopacidae	Ukraine
''	*Calidris temminckii*	Scolopacidae	Poland
C. norneri	*Sterna hirundo*	Laridae	Europe, Kazakhstan, Kirghizia
''	*Gelochelidon nilotica*	Laridae	Europe, Kazakhstan

Table 5. Distribution of the species of the genus *Neocheyletiella* on the host taxa.

Mite species	Host species	Host family	Host order	Locality
N. avicola	*Ara sp.*	Psittacidae	Psittaciformes	Antwerp Zoo
"	*Agapornis fisheri*	Psittacidae	Psittaciformes	Antwerp Zoo
"	*Erythrura prasina*	Psittacidae	Psittaciformes	Antwerp Zoo
N. pittae	*Pitta moluccensis megarhyncha*	Pittidae	Passeriformes	Antwerp Zoo
N. media	*Leiothrix lutea*	Timaliidae	Passeriformes	China, Nepal
N. siva	*Minla cyanouroptera*	Timaliidae	Passeriformes	Antwerp Zoo
N. microrhyncha	*Hirundo rustica*	Hirundinidae	Passeriformes	Europe, Canada
"	*Delichon urbica*	Hirundinidae	Passeriformes	Russia
"	*Riparia riparia*	Hirundinidae	Passeriformes	Russia
"	*Petrochelidon pyrrhonota*	Hirundinidae	Passeriformes	Russia
"	*Cecropis abyssinicus*	Hirundinidae	Passeriformes	Rwanda
"	*Psalidoprocne albiceps*	Hirundinidae	Passeriformes	Rwanda
N. rohweri	*Sitta pygmaea*	Sittidae	Passeriformes	USA
N. smallwoodae	*Leucosticte australis*	Fringillidae	Passeriformes	Australia
N. artami	*Artamus cyanopterus*	Artamidae	Passeriformes	Australia
N. amandavae	*Amandava amandava*	Estrildidae	Passeriformes	Antwerp Zoo
N. megaphallos	*Estrilda erythronotos*	Estrildidae	Passeriformes	Africa

aciiformes and Passeriformes (Table 6). Apparently, the species of this genus do not have a high host specificity at the species level. Actually, the most common species of this genus, *Bakericheyla chanayi* (BERLESE et TROUESSART, 1889), has been found on different orders of birds (AKIMOV and GORGOL, 1990 and present paper).

The mites of the genus *Ornithocheyletia* are associated with birds of five different orders: Columbiformes, Galliformes, Passeriformes, Piciformes and Psittaciformes (Table 7). Their species are mainly monoxenous, rarely oligoxenous parasites. However, at the present time, it is difficult to recognise defined species groups restricted to a certain bird order.

The mites of the genus *Apodicheles* are restricted to the swifts, Apodidae (Apodiformes) (FAIN, 1979b).

Thus, the ornithocheyletin mites parasitize birds of six

Table 6. Destribution of the species of the genus *Bakericheyla* on the host taxa.

Mite species	Host species	Host family	Host order	Locality
B. chanayi chanayi	Different species from the orders Passeriformes and Coraciiformes			Cosmopolitan
B. chanayi latior	*Paroaria gularis*	Emberizidae	Passeriformes	Antwerp Zoo
B. faini	*Cossypha dichrura*	Turdidae	Passeriformes	Africa
B. subquadrata	*Merops pusillus*	Meropidae	Coraciiformes	Africa
B. transvaalica	*Merops pusillus*	Meropidae	Coraciiformes	Africa
"	*Merops bullockoides*	Meropidae	Coraciiformes	Africa
"	*Merops nubicoides*	Meropidae	Coraciiformes	Africa
"	*Merops persica*	Meropidae	Coraciiformes	Africa
"	*Merops apiaster*	Meropidae	Coraciiformes	Africa
B. benoiti	*Merops bullockoides*	Meropidae	Coraciiformes	Africa
B. africana	*Cypsiurus parvus*	Apodidae	Apodiformes	Africa

Table 7. Distribution of the species of the genus *Ornithocheyletia* on the host taxa.

Mite species	Host species	Host family	Host order	Locality
O. francolini	*Francolinus natalensis*	Phasianidae	Galliformes	South Africa
O. canadensis	*Picus viridis*	Picidae	Piciformes	Canada
O. lukoschusi	*Hirundo rustica*	Hirundinidae	Passeriformes	The Netherlands
O. mironovi	*Riparia riparia*	Hirundinidae	Passeriformes	Kirghizia
O. dubinini	*Sturnus vulgaris*	Sturnidae	Passeriformes	Russia, Moldavia
O. barri	*Sturnus vulgaris*	Sturnidae	Passeriformes	USA
O. lamprocolius	*Lamprocolius chloropterus*	Sturnidae	Passeriformes	Central Africa
O. eulabes	*Gracula religiosa*	Sturnidae	Passeriformes	Antwerp Zoo
O. pinguis	*Turdus merula*	Turdidae	Passeriformes	Italy
O. aitkeni	*Turdus fumigatus*	Turdidae	Passeriformes	Brasil
O. garrulax	*Garrulax leucolophus*	Timaliidae	Passeriformes	Antwerp Zoo
O. leiothrix	*Leiothrix lutea*	Timaliidae	Passeriformes	Antwerp Zoo
O. lepidus	*Garrulax leucolophus*	Timaliidae	Passeriformes	Antwerp Zoo
O. granatina	*Uraeginthus ianthinogaster*	Estrildidae	Passeriformes	Antwerp Zoo
O. phylloscopi	*Phylloscopus trochilus*	Sylviidae	Passeriformes	Russia, Ukraine
O. lichmerae	*Lichmera indistincta*	Meliphagidae	Passeriformes	Australia
,,	*Grallina cyanoleuca*	Grallinidae	Passeriformes	Australia
O. lonchurae	*Lonchura castaneothorax*	Estrildidae	Passeriformes	Australia
O. hallae hallae	*Columba livia*	Columbidae	Columbiformes	Cosmopolitan
O. hallae similis	*Chalcophas indica*	Columbidae	Columbiformes	Antwerp Zoo
O. geopeliae	*Geopelia striata*	Columbidae	Columbiformes	Antwerp Zoo
O. lawrenceae	*Psittacula sp.*	Psittacidae	Psittaciformes	USA
O. psittaculae	*Psittacula krameri*	Psittacidae	Psittaciformes	Antwerp Zoo
O. psittaci psittaci	*Psittacus erithacus*	Psittacidae	Psittaciformes	Antwerp Zoo
O. psittaci poicephali	*Poicephalus senegalus*	Psittacidae	Psittaciformes	Western Africa
O. smileyi	*Myopsitta monachus*	Psittacidae	Psittaciformes	Antwerp Zoo
O. argentinensis	*Nandays nanday*	Psittacidae	Psittaciformes	Antwerp Zoo
,,	*Forpus passerinus*	Psittacidae	Psittaciformes	Antwerp Zoo

orders belonging to two different phyletic lines, Paraneornithes and Neornithes. Perhaps the common ancestor of this tribe had already appeared even on a common ancestor of these groups of the Aves.

TRIBE METACHEYLETIINI

The tribe Metacheyletiini includes only two species of the genus *Metacheyletia*. These mites live in quills of parrots (FAIN, 1980; ATYEO *et. al.*, 1984). There are some disagreements among opinions concerning their mode of life. ATYEO *et al.* (1984) believed that they are predators, since the cheliceral stylets in these mites are too short to penetrate the quill wall. On the contrary, we consider these mites as highly specialised parasites and we are basing this opinion on other morphological characters, i.e.: short tarsi of the legs I-III, reduction of legs IV, short and nude setae of palpal tarsus and the relatively small size of gnathosoma. It is possible that these mites, as observed in the immature instars of the Syringophilidae, use the orifices in quill walls which were made by other mites.

Other parasitic tribes are associated with small eutherial mammals. There are three directions of specialisation in the cheyletid parasites of the mammals: the parasites specialised to live on the skin, those attached on the hairs,

Table 8. Distribution of the species of the genus *Cheyletiella* on the host taxa.

Mite species	Host species	Host family	Host order	Locality
C. parasitivorax	*Oryctolagus cuniculus*	Leporidae	Lagomorpha	Cosmopolitan
C. strandmanni	*Lepus sp.*	Leporidae	Lagomorpha	Taiwan
C. furmani	*Sylvilagus palustris*	Leporidae	Lagomorpha	USA
C. dengi	*Oryctolagus cuniculus*	Leporidae	Lagomorpha	China
C. romerolagi	*Romerolagus diazi*	Leporidae	Lagomorpha	Mexico
C. katangae	*Lepus whytei*	Leporidae	Lagomorpha	Zaire
C. yasguri	*Canis familiaris*	Canidae	Carnivora	Cosmopolitan
C. blakei	*Felis catus*	Felidae	Carnivora	Cosmopolitan

and the non-specialised parasites. The representatives of each evolutionary line display peculiar morphotypes.

PARASITES SPECIALISED TO LIVE ON SKIN

These mites are represented by two unrelated tribes, Cheyletiellini and Teinocheylini. They lack claws either on all the legs (Cheyletiellini) or only on the fourth pair of legs (Teinocheylini), they have no palpal comb-like setae, and no protrusions on the body or on the legs. The gnathosoma of these mites is small and the palpal claws are curved ventro-laterally.

TRIBE CHEYLETIELLINI

The tribe Cheyletiellini is represented by parasites of the lagomorphs (Lagomorpha). The mites of the genus *Cheyletiella* parasitise different hosts of the family Leporidae (Table 8). Two species of this genus live on the predaceous mammals of the order Carnivora, namely on dogs (Canidae) and cats (Felidae). One undescribed species was found on the silver fox (SMILEY, 1977). We think that the parasitism of the genus *Cheyletiella* on carnivorous mammals is a secondary phenomenon. Some representatives of this genus migrated from the leporids onto their predators, the canids and the felids. Itching dermatitis in man caused by *Cheyletiella yasguri* SMILEY, 1970 has been frequently reported in Europe. The mites, however, were never found on the skin of man and the itch was produced by the contact with an infected dog (contact dermatitis) (FAIN *et al.*, 1982).

The representatives of the genus *Eucheyletiella* are associated with picas (Lagomorpha: Ochotonidae). Most species of this genus are monoxenous parasites (BOCHOV and MIRONOV, 1999) (Table 9).

TRIBE TEINOCHEYLINI

The tribe Teinocheylini includes only two species of the genus *Teinocheylus*, which parasitise rodents of the family Ctenodactylidae (FAIN *et al.*, 1982). These mites are highly specialised parasites clearly different from other cheyletid mites. Their hosts, the ctenodactylid rodents represent the oldest group among the recent rodents (HARTENBERGE, 1985).

PARASITES ASSOCIATED WITH HAIR OR SKIN

This evolutionary line includes two closely related tribes of the Cheyletidae, the Criokerontini and the Niheliini. In these mite groups, both palps and idiosoma (Niheliini) or only gnathosoma (Criokerontini) are well developed and

Table 9. Destribution of the species of the genus *Eucheyletiella* on the host species from the genus Ochotona (Lagomorpha: Ochotonidae).

Mite species	Host species	Locality
E. ochotonae	*Ochotona macrotis*	Kirghizia
E. faini	*O. rufescens*	Iran, Turkmenia
E. takahasii	*O. hyperborea*	Japon
E. johnstoni	*O. princeps*	USA
E. pusillinus	*O. pusilla*	Russia
E. pallasius	*O. pallasi*	Russia
E. daurica	*O. daurica*	Russia

bear retrorse hooks for attaching to the hair or the skin of their hosts. These attaching organs are, however, always less developed in these mites than in the true pilicolous mites (listrophoroids and myobiids) and some resemble more closely the ventral retrorse projections observed in some primitive psoroptid mites such as in the genus *Gaudalges* living on lemurs (FAIN, 1963). The presence of a stellate solenidion on genu I in these tribes suggests that they are closely related to each other.

TRIBE CRIOKERONTINI

The tribe Criokerontini includes two species. These mites are parasites of *Tupaia glis* (Scandentia: Tupaidae) (FAIN *et al.*, 1997).

TRIBE NIHELIINI

The tribe Niheliini includes four genera parasitizing primates, carnivores and rodents (FAIN, 1979).

Two species of the genus *Nihelia* are associated with small mongooses of the genera *Herpestes* and *Cynictis* (Carnivora: Viverridae).

The single species of the genus *Galagocheles* was found on a lory of the genus *Galago* (Primates: Lorisidae).

The species of the monotypic genera *Sciurocheyla* and *Smileycheles* were found on rodents of the genera *Menetes* sp. (Sciuridae) and *Zenkerella insignis* (Anomaluridae), respectively.

It is possible that the common ancestor of these mites inhabited the nests of different tropical mammals.

NON-SPECIALISED PARASITES

This evolutionary line includes two not allied groups i.e. the genus *Hylopecheyla* (see - ''Cheyletini'') and the tribe Chelonotini.

TRIBE CHELONOTINI

The tribe Chelonotini includes three species which are associated with Oriental squirrels (Sciuridae) and one species from *Sicista subtilis* (Sminthidae) (FAIN *et al.* 1997). These mites keep some typical characters of cheyletid predators: the palpal comb-like seta, the slim tarsi of the legs etc... . However, they possess also some specialised characters, such as protrusions on tarsi and coxae of the legs, strong palpal claws etc... It is quite enigmatic that males and immature instars of these mites are unknown. The absence of these instars on the hosts suggest that they live in the nests of these rodents.

The single species of the genus *Chelonotus* (*C. selenirhynchus* BERLESE, 1893) is associated with several species of the genus *Callosciurus* (DOMROW, 1964).

The mites of the monotypic genus *Promuricheyla* (*P. lukoschusi* FAIN, 1972) were found on *Nannosciurus surrutilus*.

The mites of the genus *Thewkachela* (*T. ratufi* IDE et KETHLEY, 1977) were found on two species of the genus *Ratufa* (IDE and KETHLEY, 1977).

The mites of the monotypical genus *Muricheyla* (*M. sicista* FAIN, 1972) are parasitic on *Sicista subtilis* from the Caucasus (FAIN, 1979a).

GENUS *INCERTAE SEDIS*

The single species of the genus *Thryonomycheyla* (*T. congolensis* FAIN, 1972) was found from the rodent *Thryonomys swinderianus* (Rodentia: Thryonomyidae) from Zaire (FAIN, 1979a). The relationships of this genus with the other cheyletid groups are not clear. This species was described by only a single male specimen (FAIN, 1979a). The male and teleonymph of a second undescribed species of this genus have been studied recently by us. This teleonymph has a deeply specialised aspect: a very small gnathosoma, palps with fused segments without claw, while the male resembles the representatives of the tribe Chelonotini.

HOST SPECIFICITY IN THE CHEYLETIDAE AND THE MYOBIIDAE

Only small mammals have been found parasitized by Cheyletidae and Myobiidae. Mites of the second group are more specialised than those of the first one. The structures of the Myobiidae are greatly modified by the parasitic mode of life. It is worthy of note that both families of mites never occur on the same order of mammals, except in the Rodentia, but when that happens in this order of mammals, then the two families of mites, as a rule, parasitize different families of rodents. Actually, the Cheyletidae are associated in most part with rodents of the suborder Sciuromorpha. The Myobiidae are not present in this suborder but they parasitize a large number of rodents of the suborder Myomorpha. There are only three exceptions to this rule. The first is that of a cheyletid species, *Muricheyla sicista*, which was found on *Sicista subtilis* (Myomorpha: Sminthidae). The myobiids are not represented in the rodents of the family Sminthidae. A second exception is the presence of cheyletid mites on a rodent of the genus *Zenkerella* (Myomorpha: Anomaluridae). Myobiids are also present in this family but in another genus, *Idiurus* (FAIN, 1975, 1979). The last exception is the occurrence of cheyletids and myobids on *Ctenodactylus gundii* (Myomorpha: Ctenodactylidae) (FAIN and LUKOSCHUS, 1977; FAIN *et al.*, 1982).

Myobiids and cheyletids living on mammals have similar mode of life and they feed on lymph and living cells. We think that the cheyletid mites associated with mammals form a more recent parasitic group than the Myobiidae, and that they had an opportunity to occupy the host taxa which were free from myobiid parasites.

CONCLUSIONS

It is suggested from this review that the parasitic Cheyletidae were primarily free living predators, frequently asso-

ciated with nests of vertebrates. These mites, being predators, have numerous preadaptations to the parasitic mode of life and they possess high ecological plasticity. Therefore it was quite easy for these mites to adapt to parasitism on the vertebrates. Furthermore, during their long contact with the hosts in these nests they acquired new characters which have prepared them to a parasitic mode of life.

According to our phylogenetical hypothesis, the parasitism on vertebrates has arisen independently in several phylogenetic lines of the cheyletids associated with nests of vertebrates. Such transition from nest predation to true parasitism probably occured repeatedly and at different times. The cheyletid mites are more widely represented on birds than on mammals. Possibly, it is in relation with a more early origin of parasitism in the cheyletids associated with bird nests than in the cheyletids associated with mammal nests. An independent origin of the parasitism in many different cheyletid phyletic lines, arisen significantly later than the origin of such a parasitic group as myobiid mites, is probably main reason which could explain the recent mosaic distribution of the Cheyletidae among the mammalian taxa.

The associations of cheyletid mites with invertebrates are less frequent than their associations with vertebrates. They do not present a main line in the cheyletid evolution. The associations with invertebrates are, as a rule, restricted to phoresy, while true parasitism was only observed occasionaly.

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