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In memory of the great Russian acarologist V.I. Volgin

NEW OBSERVATIONS ON PHYLOGENY OF CHEYLETOID MITES (ACARI: PROSTIGMATA: CHEYLETOIDEA)

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ABSTRACT

The mite superfamily Cheyletoidea (Acari: Prostigmata) includes 5 families: Cheyletidae, Syringophilidae, Harpirhynchidae (including Ophioptinae), Psorergatidae, and Demodicidae. A new hypothesis of cheyletoid phylogeny was carried out with maximum parsimony approach. *Raphignathus collegiatus* (Raphignathidae) and *Storchia robusta* (Stigmaeidae) were selected as outgroups. Cheyletoid ingroup species are represented by *Eucheyletia asiatica* and *Cheyletiella parasitivorax* (Cheyletidae), *Syringophilus bipectinatus* and *Picobia sturni* (Syringophilidae), *Harpyrhynchoides columbae*, *Harpypalpus holopus* and *Ophioptes parkeri* (Harpirhynchidae), *Psorobia foinae* (Psorergatidae), and *Demodex folliculorum* (Demodicidae). These species exhibit most characters observed in cheyletoid mites. Their character states were selected on the basis of strong *a priori* evidence of their being stable or ancestral in respective families or subfamilies. In total, 11 terminal taxa and 127 characters (11 autapomorphies) were included in the analysis. All characters were unordered and unweighted. The exact search option (Branch and Bound) was used. Supports for branches were estimated by Bremer support indices (BS). A single tree revealing the superfamily Cheyletoidea as a monophyletic group (BS 8) splitting onto 2 main lineages was obtained. Lineage I (BS 1): Cheyletidae (BS 2) – Syringophilidae (BS 2); lineage II (BS 15): Harpirhynchidae (BS 3) (Psorergatidae-Demodicidae) (BS 23). The reciprocal exchange of outgroup positions showed the same result. The topology of obtained cladogram corresponds to the phylogenetic hypothesis proposed earlier (Bochkov 2002) with exception for the branch bearing the families Epimyodicidae and Cloacaridae, because they were recently excluded from the superfamily (Bochkov and OConnor 2008).

Key words: Cheyletoidea, cladistic analysis, mites, parasites, phylogeny, Prostigmata

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РЕЗЮМЕ

Надсем. Cheyletoidea (Acari: Prostigmata) включает 5 семейств: Cheyletidae, Syringophilidae, Harpirhynchidae (включая Ophioptinae), Psorergatidae и Demodicidae. Предложена новая гипотеза филогении хейлетоидей, разработанная с позиций парсимониальной кладистики. В качестве внешних групп были выбраны *Raphignathus collegiatus* (Raphignathidae) и *Storchia robusta* (Stigmaeidae). Хейлетоидеи представлены в анализе видами *Eucheyletia asiatica* и *Cheyletiella parasitivorax* (Cheyletidae), *Syringophilus bipectinatus* и *Picobia sturni* (Syringophilidae), *Harpyrhynchoides columbae*, *Harpypalpus holopus* и *Ophioptes parkeri* (Harpirhynchidae), *Psorobia foinae* (Psorergatidae) и *Demodex folliculorum* (Demodicidae). Данные виды демонстрируют большинство признаков, присущих хейлетоидным клещам. Определенные состояния этих признаков характеризуют соответствующие семейства или подсемейства хейлетоидов или являются анцестральными в пределах данных таксонов, чему есть серьезные *a priori* свидетельства. Всего в анализ было включено 11 терминальных таксонов и 127 признаков (11 автопоморфий). Признаки не ордированы и не взвешены. В виду небольшого числа включенных в анализ таксонов была использована точная поисковая стратегия (Branch and Bound). Поддержка ветвей оценивалась с помощью индекса Бремера (ИБ). Было получено одно древо, которое поддерживает монофилию надсемейства (ИБ 8) и представлено 2 основными эволюционными линиями. Линия I (ИБ 1): Cheyletidae (ИБ 2) – Syringophilidae (ИБ 2); линия II (БП ИБ): Harpirhynchidae (ИБ 3) (Psorergatidae-Demodicidae) (ИБ 23). Взаимное изменение позиции внешних групп дало тот же результат. Полученная кладограмма соответствует филогенетической гипотезе предложенной Бочковым (Bochkov 2002), с учетом того, что семейства Epimyodicidae и Cloacaridae были недавно исключены из состава хейлетоидей (Bochkov and OConnor 2008).

INTRODUCTION

The mite superfamily Cheyletoidea Dubinin, 1954 (Acari: Prostigmata) was established almost simultaneously by Dubinin (1954) and Cunliffe (1955). The phylogeny of this superfamily has undergone significant modifications [see Bochkov (2002) for the historical account of cheyletoid systematics and most important references]. According to the "classical" variant, this superfamily included eight families (Krantz 1978). The free-living forms are represented only in the family Cheyletidae, which also includes permanent parasites of birds and mammals, whereas the other seven families comprise exclusively permanent parasites of vertebrates: Syringophilidae (bird parasites living in quills), Harpirhynchidae (bird ecto- and intraskin parasites), Ophioptidae (snake ectoparasites), Cloacaridae (turtle and mammalian endoparasites), Myobiidae (mammalian ectoparasites), Demodicidae and Psorergatidae (mammalian's intraskin parasites). Bochkov et al. (1999) lowered the rank of the family Ophioptidae to the subfamily of Harpirhynchidae. The cladistic analysis of the Cheyletoidea was performed by Bochkov (2002) for the first time; in the results of this analysis, the family Myobiidae was moved to the separate superfamily Myobioidea, as it was formerly proposed by Volgin (1969), and the subfamily Epimyodicinae (Cloacaridae) was elevated to the familial status. The relationships among cheyletoid families hypothesized by Bochkov (2002) are depicted in Fig. 1. Later on, Bochkov et al. (2008), using different eleutherengone outgroups, clearly showed that myobiids are not closely related to "higher" Raphignathae (Cheyletoidea and Raphignathoidea). Finally, Bochkov and OConnor (2008) demonstrated that the sister families Cloacaridae and Epimyodicidae are also not cheyletoids. The chelicerae of these mites are actually unfused that precludes their inclusion in the Cheyletoidea where they were previously placed. The superfamily Cloacaroidea, *incertae sedis* within the infraorder Eleutherengona, was established for these two families. Thus, the supefamily Cheyletoidea currently includes the five following families: Cheyletidae, Syringophilidae, Harpirhynchidae, Psorergatidae, and Demodicidae.

The putative phylogenetic hypothesis proposed by Bochkov (2002) was based on 61 external morphological characters. Many of these characters were used to characterize such families as Myobiidae, Cloacaridae, and Epimyodicidae, therefore the set of characters being applicable to the five cheyletoid families mentioned above is actually much lesser in number. The seta characters play "a key role" in the phylogenetic reconstruction of eleutherengones (Bochkov et al. 2008). In the parasitic cheyletoids, however, the homologies of the leg and partly the idiosomal setae with other prostigmatic mites are still not established. Therefore, a rich set of the potentially phylogenetic informative characters was omitted in my previous study.

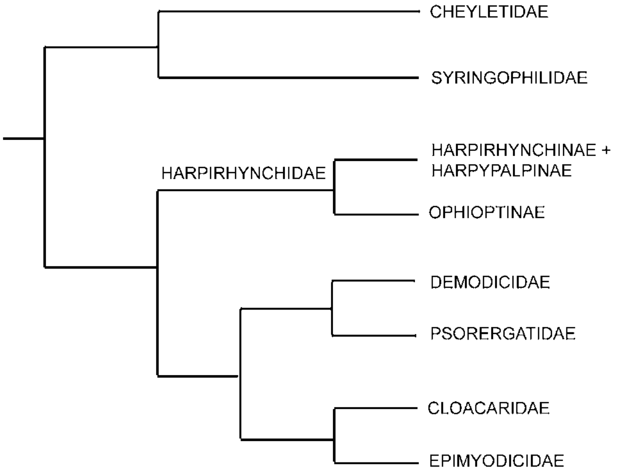

Fig. 1. Phylogeny of Cheyletoidea proposed by Bochkov (2002).

In this paper I undertake a new cladistic analysis of the superfamily Cheyletoidea. This analysis is based on the examination of species from most recognized cheyletoid genera (Table 1). Almost all external morphological characters (127 characters) potentially important for phylogenetic reconstructions of cheyletoids were used. The homologies of most setae and other external structures with other eleutherengones were established (Tables 2–9).

MATERIAL AND METHODS

Most specimens studied are housed in the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia; l'Institut royal des Sciences naturelles de Belgique, Brussels, Belgium (IRSNB); le Musée royal de l'Afrique Centrale, Tervuren, Belgium (MRAC); the Museum of Zoology, University of Michigan, Ann Arbor, USA (UMICH).

Table 1. Material examined.

Family/Subfamily	Number of taxa examined		Number of recognized taxa	
	Species	Genera	Species	Genera
Cheyletidae	340	70	380	72
Syringophilidae	98	27	167	36
Harpirhynchinae	52	9	57	10
Harpypalpinae	10	2	10	2
Ophioptinae	4	2	17	2
Demodicidae	10	4	86	7
Psorergatidae	15	3	70	3

Table 2. Setation of gnathosoma in cheyletoid mites and outgroups.

Family/Subfamily	Species	Setae
Raphignathidae	*Raphignathus collegiatus* Atyeo et al., 1961	*elc. p, m, n, ao1, ao2*
Stigmaeidae	*Storchia robusta* (Berlese, 1885)	*elc. p, m, n, ao1, ao2*
Cheyletini	*Eucheyletia asiatica* Volgin, 1955	*elc. p, n, ao1, ao2*
Cheyletiellini	*Cheyletiella parasitivorax* (Mégnin, 1878)	*elc. p, n, ao1, ao2*
Syringophilinae	*Syringophilus bipectinatus* Heller, 1880	*elc. p, n, ao1, ao2*
Picobiinae	*Picobia sturni* Skoracki et al., 2004	*elc. p, n, ao1, ao2*
Harpirhynchinae	*Harpyrhynchoides columbae* Fain, 1972	*elc. p, m, n*
Harpypalpinae	*Harpypalpus holopus* (Berlese et Trouessart, 1889)	*elc. p, m, n*
Ophioptinae	*Ophioptes parkeri* Sambon, 1928	*m, n*
Psorergatidae	*Psorobia foinae* Fain et Lukoschus, 1968	*elc. p, n*
Demodicidae	*Demodex folliculorum* (Simon, 1842)	*elc. p, n*

The gnathosomal setation (Table 2) follows Grandjean (1947). Names of palpal setae (Table 3) follow Grandjean (1946). The idiosomal setation (Table 4) follows Grandjean (1939) as adapted for Prostigmata by Kethley (1990) with a single exception. In my opinion, setae *4c sensu* Kethley (setae of coxae IV) are actually aggenital setae as suggested by Grandjean (1944) for Stigmaeidae. The leg setation (Tables 5–9) follows Grandjean (1944) as applied to Raphignathidae by Atyeo (1963).

Selection of taxa. Among five families of cheyletoid mites, the families Demodicidae and Psorergatidae are not separated into subfamilies; the uniform external morphology of their representatives does not allow suspecting their polyphyletic origin (Nutting 1985; Giessen 1990). The family Harpirhynchidae is subdivided into the three subfamilies Harpirhynchinae, Harpypalpinae, and Ophioptinae. The monophyly of this family as well as each of its three subfamilies was shown by Bochkov et al. (1999) and Bochkov (2002). Nevertheless, I include all of them in this analysis to be consistent with our previous results. The family Syringophilidae is relatively morphologically monotonous (Bochkov et al. 2004). Despite the rather high morphological similarity of syringophilid supraspecific taxa, they have been reasonably well arranged into the two natural groups or subfamilies, Syringophilinae and Picobiinae (Johnston and Kethley 1973; Fain et al. 2000). Since the monophyly of Syringophilidae have never been formally testified, I include both these subfamilies in the analysis. Monophyly of the family Cheyletidae, including 13 tribes, was demonstrated by Bochkov and Fain (2001). For this reason I include in the analysis only two tribes, the less specialized tribe Cheyletini represented by free-living species, and the highly specialized para-

Table 3. Setation of palps in cheyletoid mites and outgropus.

Species	Femur	Genu	Tibia	Tarsus
Raphignathus collegiatus	*d, v’,v”*	*d, l”*	*d, lT, l’*	*ba, bp, lp, va, acm, sul, ul’, ul”*, ω
Storchia robusta	*d, v’,v”*	*d, l”*	*d, lT, l’*	*ba, bp, lp, va, acm, sul, ul’, ul”*, ω
Eucheyletia asiatica	d, v’,v”	d, l”	d, lT, l’	*acm, sul, ul’, ul”*, ω
Cheyletiella parasitivora	*d, v’,v”*	*d, l”*	*d, lT, l’*	*acm, sul, ul’, ul”*, ω
Syringophilus bipectinatus	*d, v’,v”*	*d, l”*	*d, lT, l’*	*acm, sul, ul’, ul”*, ω
Picobia sturni	*d, v’,v”*	*d, l”*	*d, lT, l’*	*acm, sul, ul’, ul”*, ω
Harpyrhynchoides columbae	*d, v*	*d, l”*	*d, lT*	1 seta
Harpypalpus holopus	*D*	*d, l”*	*d, lT*	1 seta
Ophioptes parkeri	*D*	*d, l”*	*d, lT*	1 seta
Psorobia foinae	*d, v*	*d, l”*	*lT*	3 setae
Demodex folliculorum	*V*	*d, l”*	–	3–4 setae

sitic tribe Cheyletiellini. Inclusion of the other 11 tribes would not change the relationship pattern between the cheyletoid families, because the differences between the cheyletid tribes mostly concern specialized characters, which are inapplicable for the other families of Cheyletoidea (Bochkov and Fain 2001).

I agree with Yeates (1995) and Prendini (2001) that it is preferable to use real species in a cladistic analysis rather than supraspecific taxa. For this reason, the set of characters used in our data matrix is based on the real species selected after the comparative investigations of the majority of cheyletoid species known to date. These species exhibit most of the characters observed in cheyletoid mites. Their character states were selected on the basis of strong *a priori* evidence of their being stable or ancestral in the respective families or subfamilies. *Raphignathus collegiatus* Atyeo et al., 1961 (Raphignathidae) and *Storchia robusta* (Berlese, 1885) (Stigmaeidae) were selected as outgroups. Cheyletoid ingroup species are given in Table 2. Since the character states of the selected species are applicable, as a rule, to a whole subfamily or family under the analysis, I use below these supraspecfic names instead the name of respective species.

Cladistic analysis. In total, 11 terminal taxa and 127 characters (11 autapomorphies) were included in the analysis (Table 10). The autapomophies were included in the analysis for future phylogenetic speculations and diagnostic purposes. Preparing and editing of the data matrix were done using NEXUS Data Editor 0.5.0 (Page 2001). The state of each character in outgroups was designated as “0”, ingroup states as “1, 2 ...”, and inapplicable characters as “–”. The reconstruction of phylogenetic relationships was performed with PAUP 4.0b.10 for IBM (Swofford 2001). All characters were unordered and unweighted. The exact search option (Branch and Bound) was used due to the small number of taxa. Support for branches was estimated by Bremer support indices calculated with the program Autodecay (Eriksson 1998). Analysis of character distributions, drawing, and editing of the trees was conducted using WINCLADA (Nixon 1999). The received cladogram is depicted in Fig. 2.

ANALYSIS OF CHARACTERS

Gnathosoma (Fig. 3; Tables 2 and 3). In all cheyletoid mites, the chelicerae are fused to each other in the common structure, the stylophore. The stylophore is completely or partially (if the hypostome is free) fused with the subcapitulum. In Cheyletidae and Syringophilidae, the hypostome is fused with the stylophore, forming the attenuate rostrum bearing from two to four pairs of the apical hyaline protuberances (lips); whereas in the other cheyletoids, the hypostome is free, membranous, bilobate, devoid of lips, and the rostrum is short. In Syringophilidae, the subcapitulum is deeply submerged into the idiosoma and its posterior margin is visible as the widely rounded internal apodeme. The stigmae are present in most cheyletoids and situated close to each other on the rostral part of the stylophore (Cheyletidae and Syringophilidae), at the basal part of the subcapitulum (Ophioptinae) or immediately behind of

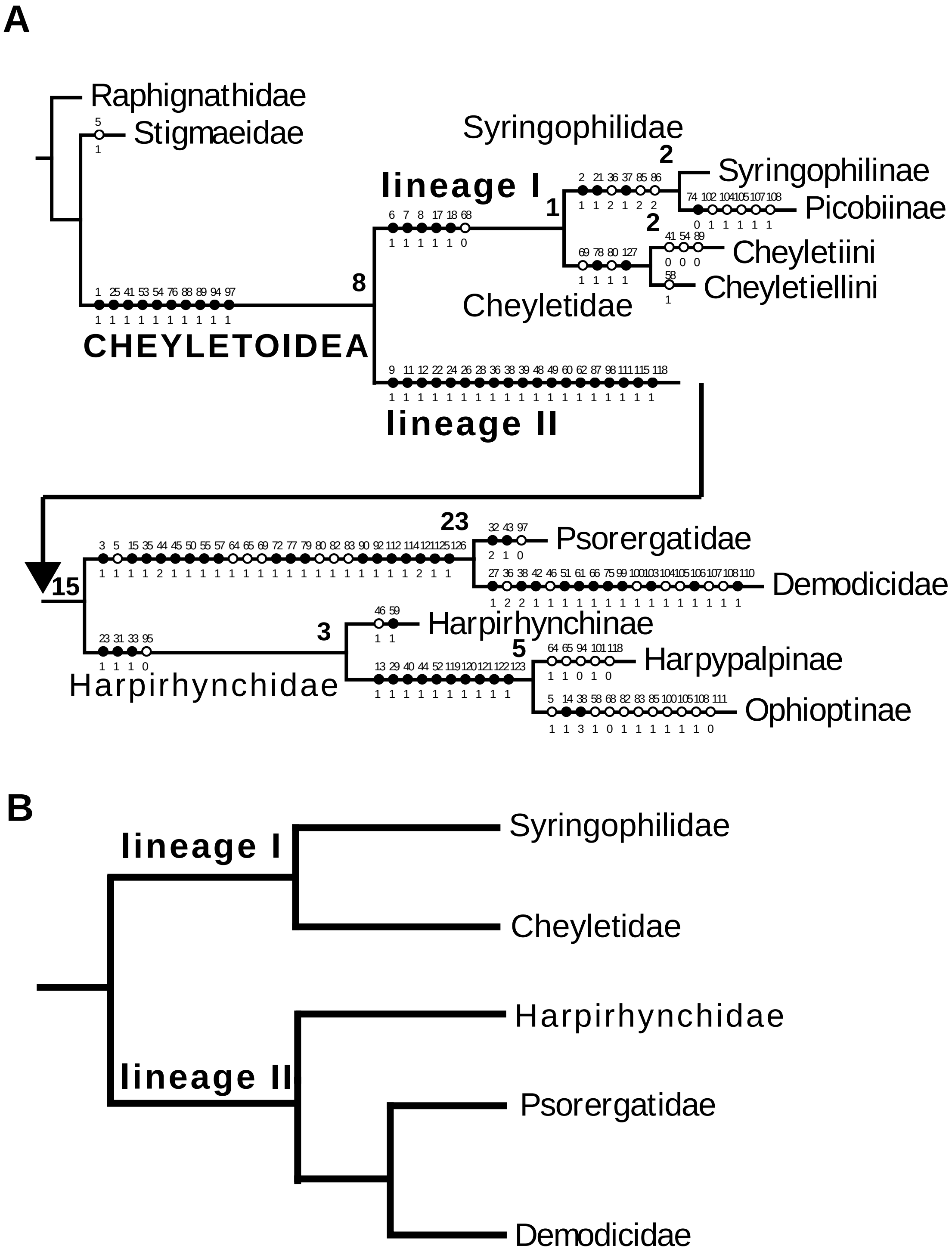

Fig. 2. Phylogeny of Cheyletoidea: A – A single most parsimonious tree (tree length 197, CI $_{\text{excluding uninformative characters}}$ 0.7, RI 0.8) found under the unordered and unweighted data set; character numbers are indicated above branches where unambiguous, their state changes below branches; non homoplasious state changes are in black, homoplasious state changes are in white; bold numbers above branches are Bremer indices; B – The phylogenetic relationships of the cheyletoid families.

the subcapitulum, laterally (Harpirhynchinae and Harpypalpinae). In Demodicidae and Psorergatidae, the stigmae and peritremes are secondarily absent. In Cheyletidae and Syringophilidae, the peritremes are removed at the rostral part of the stylophore; they are arch-like or M-shaped initially and completely completely segmented. In Harpirhynchinae and Harpypalpinae, the peritremes are linear, situated immediately behind the subcapitulum, and only their distal ends are segmented; in Ophioptinae, the peritremes are absent. In most cheyletoids, excluding Cheyletidae and Syringophilidae, the pharyngeal bulb is strongly scleroitized. In the higher raphignathoids, the full set of the subcapitular setae includes *m, n, ao1, ao2,* and *elc.p* (Table 2). In Cheyletidae and Syringophilidae, setae *m* are absent, whereas in all other cheyletoids, setae *ao1* and *ao2* are absent; in ophioptines, setae *elc.p* are absent; in demodicids and psorergatids, these setae have modified shape; in Harpirhynchidae, setae *m* and *n* are situated at the same level. Cheyletoids retain the typically raptorial palps. These palps consist of the five articulated segments and the thumb-claw complex. In syringophilids, the palps are linear, the palpal femur is fused with the palpal genu, the palpal tarsus is fused with the palpal tibia, and the tibial claw is absent. In other cheyletoids, the palpal trochanter, femur, and tarsus are fused into single segment, the palpal tibia and tarsus are displaced to the ventral side of the palpal trochanter-femur-genu, and the tibial claw is lost. In Harpirhynchidae, the palpal tarsus is not fused with tibia and small membranous; in demodicids and psorergatids, the palpal tarsus is completely fused with the palpal tibia. In cheyletoid mites, the full set of the palpal setae includes three setae on femur (*d, v’, v*”), two setae on genu (*d, l*”), three setae on tibia (*d, l’, l’*), and four setae + solenidion on tarsus (*acm, sul, ul’, ul*” + ω). These setae are secondarily absent in the different cheyletoid families or subfamilies (Table 3). In cheyletoids, excluding Cheyletidae and Syringophilidae, eupathidia of the palpal tarsus and seta *v’F* of the palpal femur are absent; in Harpypalpinae and Ophiotinae, seta *v”F* of the palpal femur is absent; finally, in Demodicidae, seta *dF* of the palpal femur is absent. In Harpirhynchidae, setae *dF, dG*, and *l”G* are grouped together in the apical part of the palpal trochanter-femur-genu, thickened and barbed; seta *l’T* of the palpal tibia is modified in the shape, stout, with the bifurcate apex (Harpirhynchinae) or harpoon-like (Harpypalpinae and Ophioptinae). In the Demodicidae and Psorergatidae, setae of the palpal tibia-tarsus are small, spoor-like or claw-like.

1. Chelicerae: free (0), fused to each other and with subcapitulum (1).

2. Basal part of gnathosoma: not submerged (0), deeply submerged into idiosoma (1).

3. Stigmae: present (0), absent (1).

4. Position of stigmae: situated closely to each other (0); widely separated, if peritremes present, they situated on distal ends of peritremes (1).

5. Peritremes: present (0); absent (1).

6. Situation of peritremes: in basal part of subcaputulum (0); on rostral part of stylophore (1).

7. Segmentation of peritremes: not segmented or sigmeted in distal parts (0); completely segmented (1).

8. Shape of peritremes: linnear (0); arch-like or M-shaped (1).

9. Pharyngeal bulb: indistinct (0); strongly sclerotized (1).

10. Ventral setae of subcapitulum *m*: present (0); absent (1).

11. Setae *ao1*: present (0); absent (1).

12. Setae *ao2*: present (0); absent (1).

13. Situation of setae *m*: above level of setae *n* (0); at same level with setae *n* (1).

14. Setae *elc.p*: present (0); absent (1);

15. Setae *elc.p*: not modified in shape (0); modified in shape (1).

16. Rostrum: short (0); attenuate (1).

17. Hypostomal apex: free (0); fused with stylophore (1).

18. Hypostomal lips: absent (0); present (1).

19. Tibial claw of palp: present (0); absent (1);

20. Palpal thumb claw complex: present (0); absent (1);

21. Palpal segments: with 5 segments (0); with 3 segments, tibia and tarsus; femur and genu fused (1); with 3 segments, trochanter, femur and genu fused (2); with 2 segments, trochanter, femur and genu fused and tibia and tarsus fused (3).

22. Situation of tibia-tarsus: in terminal position (0); displaced to ventral side of trochanter-femur-genu (1).

23. Shape of palpal tarsus: normally developed or fused with tibia (0); small membranous bearing single lateral seta (1).

24. Solenidion of palpal tarsus: prsent (0); absent (1).

25. Eupathidia *ba, bp, lp, va* of palpal tarsus: present (0); absent (1).

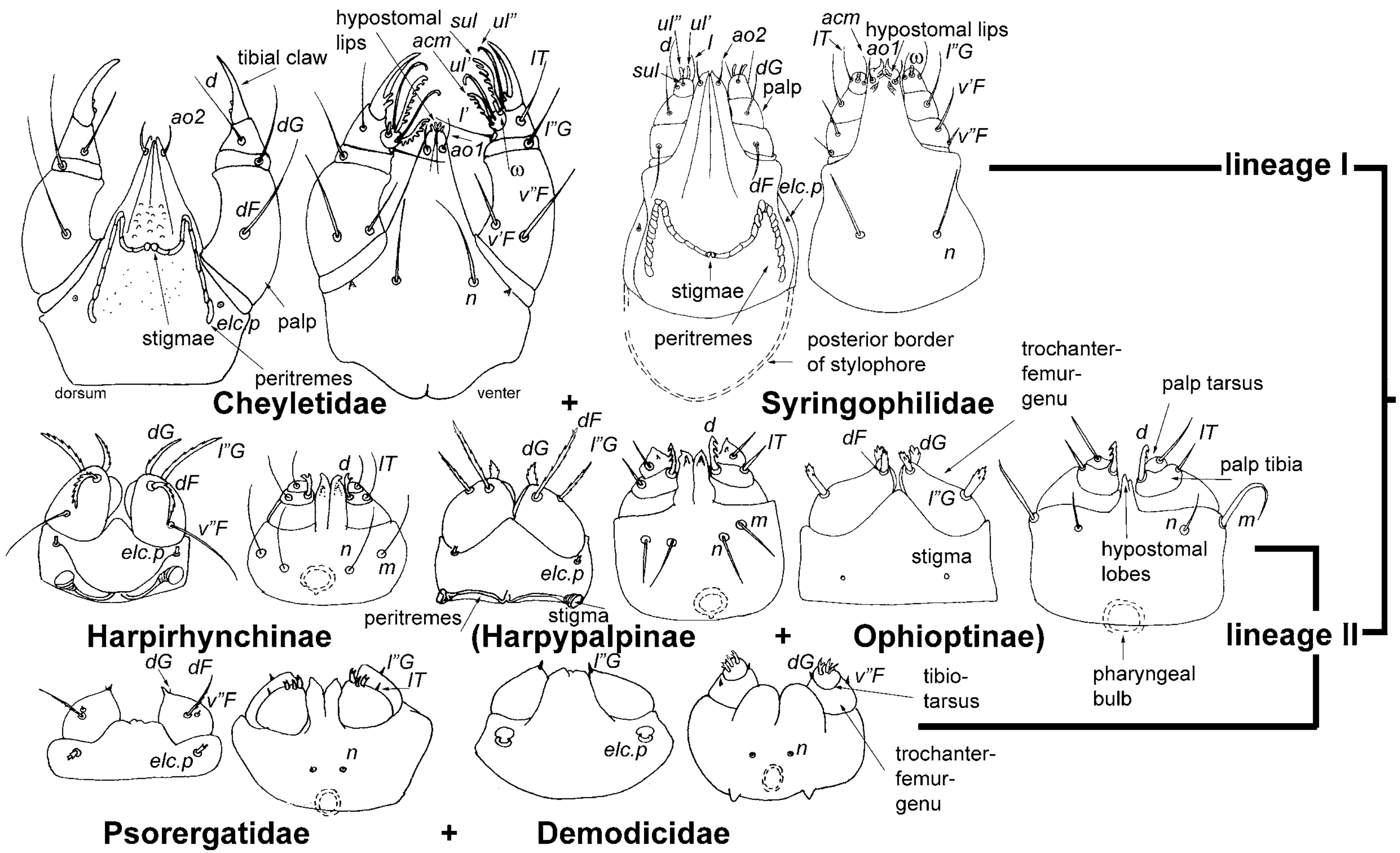

Fig. 3. The gnathosomal structure of Cheyletoidea.

26. Eupathidia *acm, sul, ul', ul*" of palpal tarsus: present (0); absent (1).

27. Setae *dF* of palpal femur: present (0); absent (1).

28. Setae *v'F* of palpal femur: present (0); absent (1).

29. Setae *v"F* of palpal femur: present (0); absent (1).

30. Palpal setae *dG, l"G* (if present), and *v"F* (if present): filiform (0); strongly thickened, with distinct barbs (1); spur-like (2).

31. Setae *dG* and *l"G* of palpal genu: far situated from each other, in usual position (0); grouped together with in apical part of segment (1).

32. Situation of setae *v"F* of palpal femur: lateroventrally (0); at apex of femur-genu (1); in middle part of femur-genu close to *dF* (2).

33. Shape of Seta *l'T* of palpal tibia: filiform (0); strongly thickened (1).

34. Modified seta *l'Ti* of palpal tibia: with bifurcate apex (0); harpoon-like (1).

35. Setae of palpal tibia-tarsus (other than *l'T*): filiform (0); claw-like (1).

Idiosoma (Fig. 4; Table 4). In raphignathoid mites, the idiosoma is rhomboid-like in outline and the opisthosoma initially is moderately developed; however, in Harpirhynchidae and Psorergatidae, it is strongly reduced, and, on the contrary, in Syringophilidae and Demodicidae, it is secondarily elongated. In raphignathoid mites, the leg coxae are usually grouped together but in Syringophilidae, coxae III and IV are situated far from coxae I and II. The dorsal shields of cheyletoids undergo a tendency to fuse. In cheyletids and syringophilids, both the propodonotal and hysteronotal shields are initially present; in some of them, however, the hysteronotal shield is transversally subdivided secondarily into the large hysteronotal and small pygidial shields, or in some cheyletids, the hysteronotal shield is paired. In Harpirhynchinae, Harpypalpinae, and Psorergatidae, remnants of the hysteronotal shield are fused with the propodonotal shield forming the large prodorsal shield. In Ophioptinae, the dorsal shields are secondarily lost, and in Demodicidae only the propodonotal shield is present. In raphignathoid mites, the female genital and anal orifices are situated close to each other but not completely fused. This situation remains in cheyletids and syringophilids, whereas in other cheyletoids, the genital and anal orifices are completely fused. In Harpypalpinae and Ophioptinae, the sclerotized structures, an unpaired crest, ring or ovoid plate are present near this orifice. In psorergatids, an unpaired (in males) or paired (in females) genital lobe is situated ventrally. Among cheyletoid males, the male genital orifice is situated terminally in free-living cheyletids, in parasitic cheyletids and in all other cheyletoids it is situated dorsally. In demodicids, so called "opisthosomal organ", a deep cuticular invagination situated on the opisthosoma ventrally, is present behind the anal-genital orifice. The full idiosomal setation of cheyletoids includes four pairs of the propodonotal setae (*vi, ve, si,* and *se*) and subcoxal setae *scx*; two-three pairs of setae per segment C, D, E, F, and H; aggenital setae (*ag*), pseudoanal setae (*ps*), and genital setae (*g*) (Table 4). This full set of setae is present in most Cheyletidae and Syringophilidae. In some cheyletids, especially in free-living forms, the neotrichial setae are often observable, sometimes forming the plastrone. In syringophilids, this phenomenon is much rarer (*Torotrogla* and *Trypetoptila*) and concerns only the setae of the aggenital series. In psorergatids, the propodonotal setae are reduced in number and in Demodicidae, almost all idiosomal setae, excluding the alveoli of *c2*, are disappeared. In Harpirhynchinae and Psorergatidae, many of the hysteronotal setae are lost. In Harpypalpinae and Ophioptinae, the opisthosomal setae are displaced on the ventral idiosomal surface. In immatures of Harpypalpinae and Ophioptinae, setae *scx* are absent, these setae are absent in all stages of Psorergatidae and Demodicidae; in Harpirhynchidae, Psorergatidae, and Demodicidae, the aggenital setae are absent in both sexes. In parasitic cheyletoids such as Harpirhynchidae and Psorergatidae, the genital and pseudoanal setae are strongly reduced in number and sometimes it is very difficult to establish their homologies. For this reason, I use for these setae the common name "setae of the anal-genital complex". In Harpypalpinae and Ophioptinae, setae of the anal-genital complex are modified and sunk into the idiosomal cuticle; in females of Psorergatidae, these setae are absent and represented in males by a single pair. The cupules are absent in all parasitic cheyletoids, including parasitic cheyletids, whereas in free-living Cheyletidae, three pairs of cupules (*im, ip, ih*) are present.

36. Opisthosoma: moderately developed (0); strongly reduced (1); elongated (2).

37. Coxae I–II and III–IV: grouped together (0); widely separated (1).

38. Dorsal shields: propodonotal and hysternotal shields present (0); remnants of hysteronotal shield fused with propodonotal shield (1); only propodonotal shield present (2); dorsal shields absent (3).

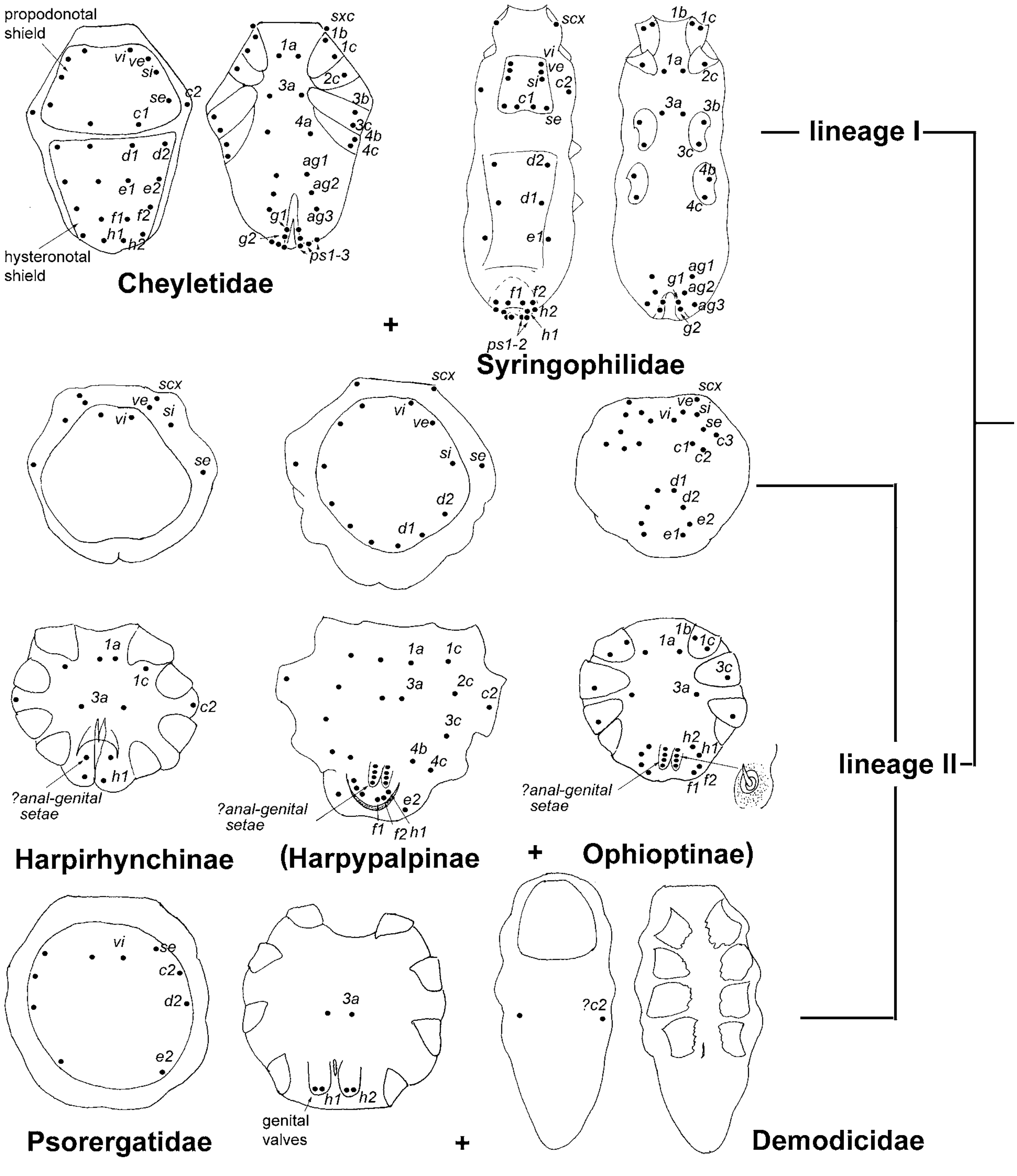

Fig. 4. The idiosomal structure of Cheyletoidea.

Table 4. Setation of idiosoma in cheyletoid females and outgroups.

Species	Setae
Raphignathus collegiatus	*scx, vi, ve, sci, sce, c1, c2, d1, e1, f1, h1, h2, ps1–3, ag1–2* (2), *g1–3* (0)
Storchia robusta	*vi, ve, sci, sce, c1, c2, d1, d2, e1, e2, f1, f2, h1, h2, ps1–3, ag1–4*(4), *g1–2*(0)
Eucheyletia asiatica	*scx, vi, ve, sci, sce, c1, c2, d1, d2, e1, e2, f1, f2, h1, h2, ps1–3, ag1–3* (2), *g1–2* (2)
Cheyletiella parasitivora	*scx, vi, ve, sci, sce, c1, c2, d1, d2, e1, e2, f1, f2, h1, h2, ps1–3, ag1–3* (2), *g1–2* (0)
Syringophilus bipectinatus	*scx, vi, ve, sci, sce, c1, c2, d1, d2, e1, f1, f2, h1, h2, ps1–2, ag1–3* (3), *g1–2* (2)
Picobia sturni	*scx, vi, ve, sci, sce, c1, c2, d1, d2, e1, f1, f2, h1, h2, ps1–2, ag1–3* (3), *g1–2* (2)
Harpyrhynchoides columbae	*scx, vi, ve, sci, sce, c2, h1, g1* (3)
Harpypalpus holopus	*scx, vi, ve, sci, sce, c1, c2, d1, d2, e2, f1, f2, h1, ps1–3* (2), *g1* (0)
Ophioptes parkeri	*scx, vi, ve, sci, sce, c1, c2, c3, d1, d2, e1, e2, f1, f2, h1, h2, ps1–3* (3), *g1* (1)
Psorobia foinae	*vi, sce, c2, d2, e2, h1, h2 (–), –(g)*
Demodex folliculorum	*?c2*

() – number of setae in male.

39. Genital and anal orifices in females: separated (0); fused (1).

40. Sclerotized structures (ring, crests, plates) near vulva: absent (0); present (1).

41. Situation of male genital orifice: ventrally or terminally (0); dorsally (1).

42. Opisthosomal organ: absent (0); present (1).

43. Genital lobes: absent (0); present (1).

44. Setae *scx*: present in all stages (0); absent only in immatures (1); absent in all stages (2).

45. Propodonotal setae: present (0); strongly reduced in number (*vi* and *se* could be present) (1).

46. Hysteronotal setae: present (0); strongly reduced in number (setae of segments D, E and F) or completely absent (1).

47. Situation of setae of segments E and F: dorsally (0); ventrally (1).

48. Aggenital setae in females: present (0); absent (1).

49. Aggenital setae in males: present (0); absent (1).

50. Setae of anal-genital complex in females: present (0); absent (1).

51. Setae of anal-genital complex in males: present (0); absent (1).

52. Genital setae: filiform, not sunck into idiosomal cuticle (0); spur-like, sunck into idiosomal cuticle (1).

53. Cupules *ia*: present (0); absent (1).

54. Cupules *im, ip,* and *ih*: present (0); absent (1).

Legs (Fig. 5; Tables 5–9). In most cheyletoids, the legs have the full number of segments; however, in Harpirhynchines, most segments of legs III and IV are fused. The cheyletoid pretarsus initially bears a pair of claws and the fleshy empodium with the tenet hairs. In Psorergatidae and Demodicidae, the empodium is strongly reduced in size, membranous and devoid of the tenet hairs. The ambulacral membrane forms the cup–like structure in Ophioptinae and has the attenuate protrusion in Harpypalpinae, Psorergatidae, and Demodicidae. In Ophioptinae and Cheyletiellini, the tarsal claws are absent. In Demodicidae and Psorergatidae, the condylophores and basal piece, structures well developed in the other cheyletoids, are strongly reduced. Sets of the leg setae are given in Tables 5–9 and in Fig. 5. Cheyletidae and Syringophilidae possess the maximal set of setae, and mites of the subfamily Picobiinae even remain an unpaired seta *it*" on tarsi I. It should be noted that in the frame of these two families, different leg setae are secondarily lost; however, the absence of these setae plays a role only for elucidation of the intrafamilial relationships. In Psorergatidae, the leg setation is strongly reduced in number, and in Demodicidae, the leg setae, excluding tarsal solenidia, are lost.

55. Shape of empodium: distinctly developed, with tenet hairs (0); strongly reduced, membranous, without tenet hairs (1).

56. Ambulacrum of legs: without protrusions (0); with cap-like protrusion (1); with attenuate protrusion (2).

57. Condylophores and basilar piece: distinctly developed (0); strongly reduced or absent (1).

58. Leg tarsal claws: present (0); absent (1).

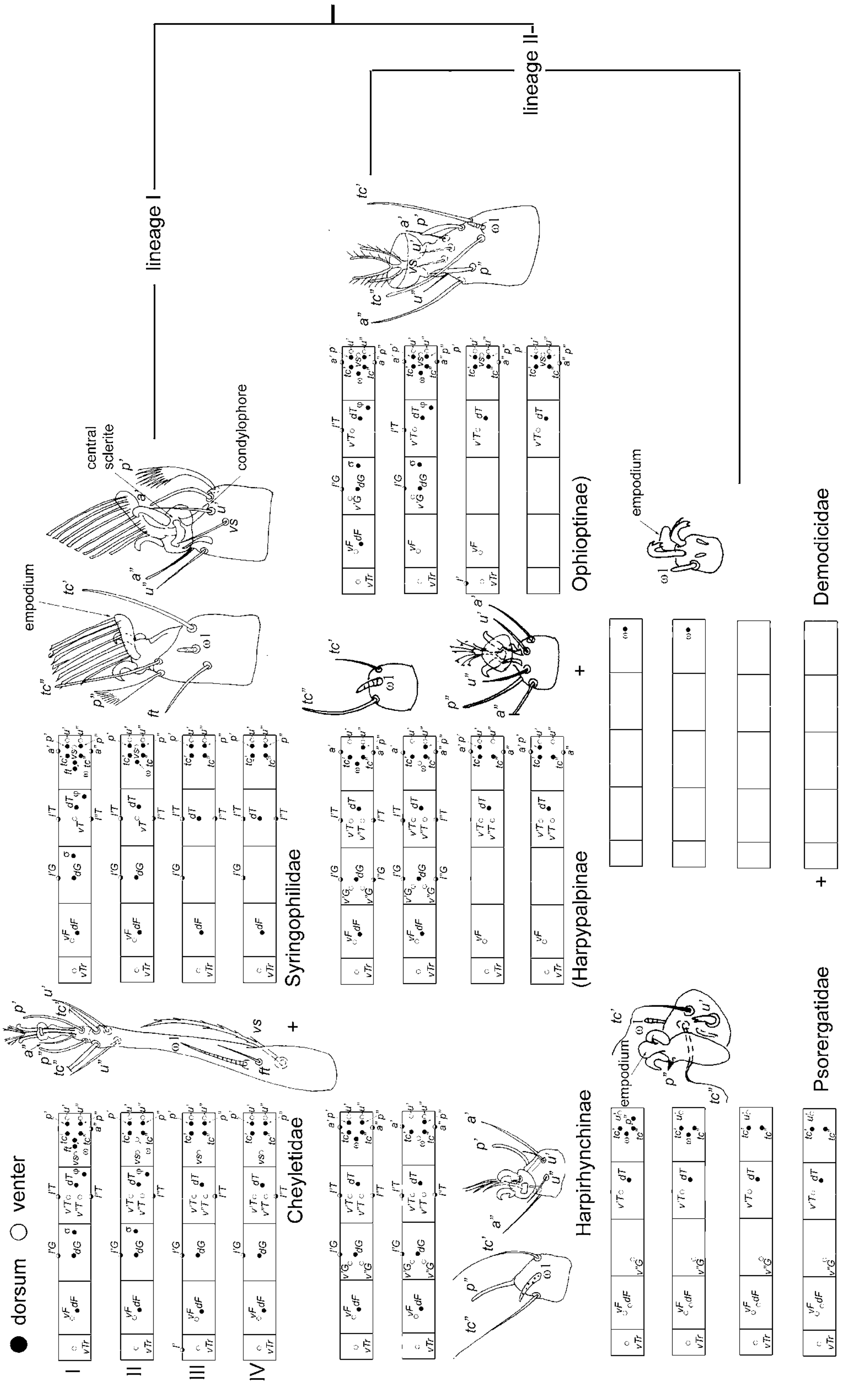

Fig. 5. The leg structure of Cheyletoidea.

Table 5. Setation of leg tarsi in cheyletoid mites and outgroups.

Species	Tarsus I	Tarsus II	Tarsus III	Tarsus IV
Raphignathus collegiatus	*(ft),(tc),(p), (a),(u), (pl), vs, (ve), (bl),(vb),* 2ω	*(tc), p', (a),(u), pl', vs, (ve), (bl),(vb),* ω	*(tc), (a),(u), vs, (ve), (bl),(vb),* ω	*(tc), (a),(u), vs, (ve), (bl), (vb),* ω
Storchia robusta	*(ft),(tc),(p), (a),(u), (pl), vs,* ω,ω(M)	*(tc), p', (a),(u), pl', vs,* ω,ω (M)	*(tc), (a),(u), pl', vs,* ω,ω (M)	*(tc), (a),(u), pl', vs,* ω, ω (M)
Eucheyletia asiatica	*ft,(tc), (p), a", (u), vs,* ω	*(tc), (p),(u), vs,* ω	*(tc), (p),(u), vs,* ω (M)	*(tc), (p),(u), vs,* ω (M)
Cheyletiella parasitivora	*ft,(tc), (p), a", (u), vs,* ω	*(tc), (p),(u), vs,* ω	*(tc), (p),(u), vs*	*(tc), (p),(u), vs*
Syringophilus bipectinatus	*ft, (tc),(p),* ω *(a),(u), vs*	*(tc),(p),(u), vs,* ω	*(tc),(p),(u)*	*(tc),(p),(u)*
Picobia sturni	*ft, (tc),(p), it",* ω *(a),(u), vs*	*(tc),(p),(u), vs,* ω	*(tc),(p),(u)*	*(tc),(p),(u)*
Harpyrhynchoides columbae	*(tc),(p), (a),(u),* ω	*(tc), p",(a),(u),* ω	–	–
Harpypalpus holopus	*(tc), p", (a),(u),* ω	*(tc), p", (a), (u),* ω	*(tc), (a),(u)*	*(tc), (a),(u)*
Ophioptes parkeri	*(tc), (p), (a), (u), vs,* ω	*(tc), (p), (a), (u), vs,* ω	*(tc), (p), a", (u), vs*	*(tc), (p), a", (u), vs*
Psorobia foinae	*(tc), ?p",?u',* ω	*(tc),?u',* ω	*(tc),?u'*	*(tc),?u'*
Demodex folliculorum	ω	ω	–	–

() – pair of setae; (M) – solenidion of male.

Table 6. Setation of leg tibiae in cheyletoid mites and outgroups.

Species	Tibia I	Tibia II	Tibia III	Tibia IV
Raphignathus collegiatus	*d,(l),(v),* 2φ	*d, (l), (v),* φ	*d, (l),(v),* φ	*d, l', (v),* φ
Storchia robusta	*d,(l), (v),* 2φ	*d, (l),(v),* φ	*d, (l),(v),*φ	*d, (l),(v),* φ
Eucheyletia asiatica	*d, (l), (v),* φ	*d, l", (v)*	*d, l", (v)+* φ (M)	*d, l", (v)*
Cheyletiella parasitivora	*d, (l), (v)*	*d, l", (v)*	*d, l", (v)*	*d, l", (v)*
Syringophilus bipectinatus	*d, (l), v,* φ	*d, (l), v*	*d, (l)*	*d, (l)*
Picobia sturni	*d, (l), v,*φ	*d, (l), v*	*d, (l)*	*d, (l)*
Harpyrhynchoides columbae	*d, (l), (v)*	*d, (l), (v)*	–	–
Harpypalpus holopus	*d, (l), (v)*	*d, (l), (v)*	*d, (v)*	*d, (v)*
Ophioptes parkeri	*d, l', v'*	*d, l', v'*	*d, v'*	*d, v'*
Psorobia foinae	*d, v'*	*d, v'*	*d, v'*	*d, v'*
Demodex folliculorum	–	–	–	–

() – pair of setae.

Table 7. Setation of leg genua in cheyletoid mites and outgroups.

Species	Genu I	Genu II	Genu III	Genu IV
Raphignathus collegiatus	*d, (l),(v),* σ	*d, (l),(v),* σ	*d, l’,(v)*	*d, l’, (v)*
Storchia robusta	*d,(l), v,* σ	*d,(l), v*	*d, v*	*d, v*
Eucheyletia asiatica	*d, l’,* σ	*d, l’*	*d, l’*	*d, l’*
Cheyletiella parasitivora	*d, l’,* σ	*d, l’*	*d, l’*	*d, l’*
Syringophilus bipectinatus	*d, l’,* σ	*d, l’*	*l’*	*l’*
Picobia sturni	*d, l’,* σ	*d, l’*	*l’*	*l’*
Harpyrhynchoides columbae	*d, l’, (v)*	*d, l’, (v)*	–	–
Harpypalpus holopus	*d, (l),(v)*	*d, (l),(v)*	–	–
Ophioptes parkeri	*d, l’, v’*	*d, l’, v’*	–	–
Psorobia foinae	*v”*	*v”*	*v”*	*v”*
Demodex folliculorum	–	–	–	–

() – pair of setae.

Table 8. Setation of leg femora in cheyletoid mites and outgroups.

Species	Femur I	Femur II	Femur III	Femur IV
Raphignathus collegiatus	*d, (l),(v), bv*	*d,(l), (v), bv”*	*d, l’, v*	*d, l’, v*
Storchia robusta	*d,(l), bv*	*d,(l), bv*	*d, l’, v*	*d, v*
Eucheyletia asiatica	*d, v*	*d, v*	*d, v*	*d, v*
Cheyletiella parasitivora	*d, v*	*d, v*	*d, v*	*d, v*
Syringophilus bipectinatus	*d, v*	*d, v*	*d*	*d*
Picobia sturni	*d, v*	*d, v*	–	–
Harpyrhynchoides columbae	*d, v*	*d, v*	–	–
Harpypalpus holopus	*d, v*	*d, v*	*v*	*v*
Ophioptes parkeri	*d, v*	*V*	*v*	–
Psorobia foinae	*d, v*	*d, v*	*d, v*	*d, v*
Demodex folliculorum	–	–	–	–

() – pair of setae.

59. Most segments of legs III–IV: articulated (0); fused (1).

60. Seta *ft*I: present (0); absent (1).

61. Setae *tc*I-IV: present (0); absent (1).

62. Seta *vs*I: present (0); absent (1).

63. Seta *vs*III–IV: present (0); absent (1).

64. Seta *p*’I: present (0); absent (1).

65. Seta *p*’II: present (0); absent (1).

66. Seta *p*”I: present (0); absent (1).

67. Seta *p*”II: present (0); absent (1).

68. Setae *p*III–IV: present (0); absent (1).

69. Seta *a*’I: present (0); absent (1).

70. Setae *a*II: present (0); absent (1).

71. Seta *a*’III–IV: present (0); absent (1).

72. Seta *a*”I: present (0); absent (1).

73. Seta *a*”III–IV: present (0); absent (1).

74. Seta *it*”I: present (0); absent (1).

75. Seta *u*’I–IV: present (0); absent (1).

76. Setae *pl*I: present (0); absent (1).

77. Seta *u*”I–IV: present (0); absent (1).

78. Situation of solenidion ω1II: dorsally (0); ventrally (1).

79. Seta *l’* of tibia I: present (0); absent (1).

80. Seta *l’* of tibia II: present (0); absent (1).

81. Seta *l’* of tibiae III–IV: present (0); absent (1).

82. Seta *l”* of tibia I: present (0); absent (1).

83. Seta *l”* of tibia II: present (0); absent (1).

84. Seta *l”* of tibiae III–IV: present (0); absent (1).

Table 9. Setation of leg trochanters and coxae in cheyletoid mites and outgroups.

Species	Trochanter/ coxa I	Trochanter/ coxa II	Trochanter/ coxa III	Trochanter/ coxa IV
Raphignathus collegiatus	*v/1a, 1b, 1c*	*v/2b, 2c*	*l, v/3a, 3b, 3c*	*v/4a, 4c*
Storchia robusta	*v/1a, 1b, 1c*	*v/2b, 2c*	*v/3a, 3b, 3c*	*v/4a, 4b, 4c*
Eucheyletia asiatica	*v/1a, 1b, 1c*	*v/2c*	*l, v/3a,3b,3c*	*v/4a, 4b, 4c*
Cheyletiella parasitivora	*v/1a, 1b, 1c*	*v/2c*	*l, v/3a,3b,3c*	*v/4a, 4b, 4c*
Syringophilus bipectinatus	*v/1a, 1b, 1c*	*v/2c*	*v/3a, 3b, 3c*	*v/4b, 4c*
Picobia sturni	*v/1a, 1b, 1c*	*v/2c*	*–/3a, 3b, 3c*	*–/4b, 4c*
Harpyrhynchoides columbae	*v/1a, 1c*	*v/–*	*–/3a*	*–/–*
Harpypalpus holopus	*v/1a, 1c*	*v/2c*	*v/3a, 3c*	*v/4c*
Ophioptes parkeri	*v/1a, 1b, 1c*	*v/2c*	*l, v/3a, 3c*	*–/–*
Psorobia foinae	*v/1a*	*v/–*	*v/–*	*v/–*
Demodex folliculorum	*–/–*	*–/–*	*–/–*	*–/–*

85. Setae *v* of tibiae I–II: paired (0); unpaired (1); absent (2).
86. Setae *v* of tibiae III–IV: paired (0); unpaired (1); absent (2).
87. Solenidion φI: present (0); absent (1).
88. Solenidion φρI: present (0); absent (1).
89. Solenidion φII: present (0); absent (1).
90. Seta *d* of genua I–II: present (0); absent (1).
91. Seta *d* of genua III–IV: present (0); absent (1).
92. Seta *l'* of genua I–II: present (0); absent (1).
93. Seta *l'* of genua III–IV: present (0); absent (1).
94. Seta *l"* of genua I–II: present (0); absent (1).
95. Seta *v'* of genua I–II: present (0); absent (1).
96. Seta *v"* of genua I–II: present (0); absent (1).
97. Seta(e) *v* of genua III–IV: present (0); absent (1).
98. Solenidion σI: present (0); absent (1).
99. Seta *d* of femur I: present (0); absent (1).
100. Seta *d* of femur II: present (0); absent (1).
101. Situation of seta *d* of femur I–II: dorsally (0); ventrally, near *v* (1).
102. Seta *d* of femora III–IV: present (0); absent (1).
103. Seta *v* of femora I–II: present (0); absent (1).
104. Seta *v* of femur III: present (0); absent (1).
105. Seta *v* of femur IV: present (0); absent (1).
106. Seta *v* of trochanters I–II: present (0); absent (1).
107. Seta *v* of trochanter III: present (0); absent (1).
108. Seta *v* of trochanter IV: present (0); absent (1).
109. Seta *l'* of trochanter III: present (0); absent (1).
110. Setae *1a*: present (0); absent (1).
111. Setae *1b*: present (0); absent (1).
112. Setae *1c*: present (0); absent (1).
113. Setae *2c*: present (0); absent (1).
114. Setae *3a*: present (0); absent (1).
115. Setae *3b*: present (0); absent (1).
116. Setae *4a*: present (0); absent (1).
117. Setae *4b*: present (0); absent (1).
118. Setae *4c*: present (0); absent (1).

Immature instars (Fig. 6). In Cheyletidae, Syringophilidae, and Harpirhynchinae, the external morphology of immature instars does not strongly differ from those of adults, excluding the fused femur and genu of legs I and II in immature Harpirhynchinae. Immature instars of the other cheyletoids are dissimilar with adults. In Harpypalpinae and Ophioptinae, all immature instars are apode, without the anal orifice, the genu palpal seta *l"G* is absent, and seta *dG* is comb-like, the propodonotal setae are strongly reduced in number and the hysteronotal setae are situated ventro-terminally or ventrally. In immature Psorergatidae, the legs are two-segmented, the idiosomal and leg setae are absent. In immature Demodicidae, the legs are one segmented, setation of the legs and idiosoma is absent. In immature instars of the both last families, the tarsal claws are modified into small plates with two-three apices. The full life-cycle is not well known only for Ophioptidae. In all other mites, larva, two nymphal stages (protonymph and tritonymph), and adults (female and male) are present. In Cheyletidae, males moult directly from protonymphs.

119. Seta *l"G* of immature instars: present (0); absent (1).
120. Seta *dG* of immature instars: filiform (0); comb-like (1).

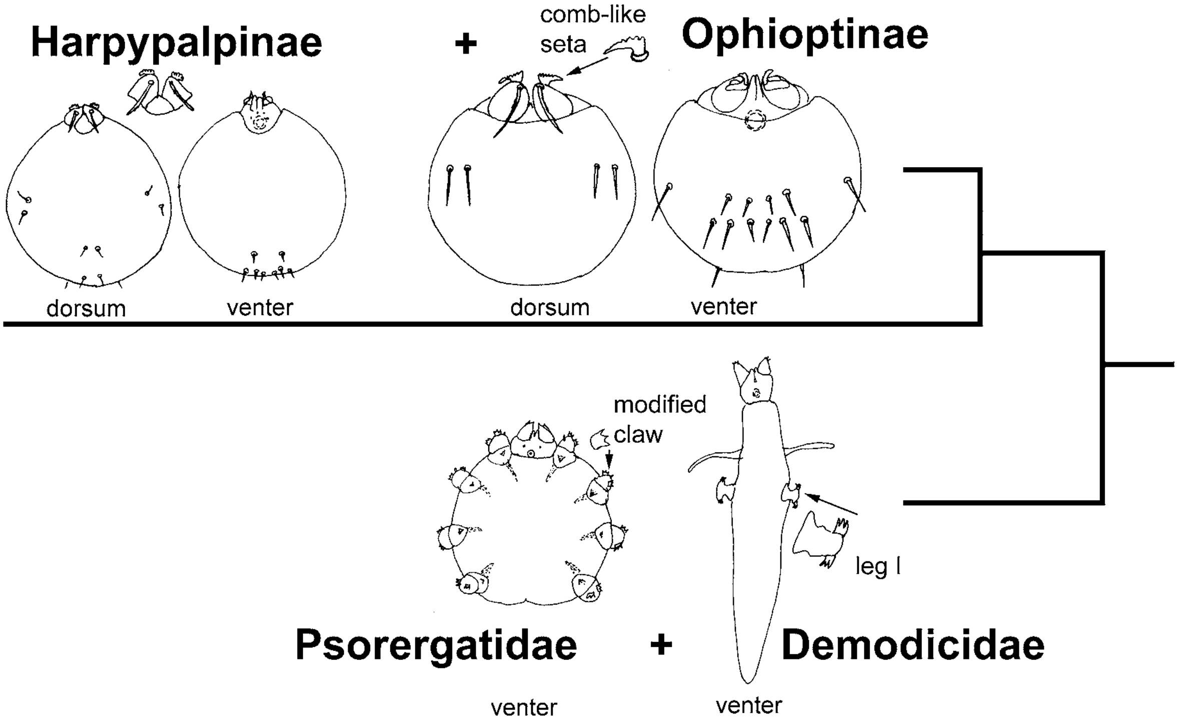

Fig. 6. The structure of immature instars of Cheyletoidea (lineage II).

121. Propodonotal setae of immature instars: present (0); mostly absent (1); all setae absent (2).

122. Hysterosomal setation in immature instars: not displaced ventrally (0); displaced ventrally (1).

123. Anal orifice in immatures: present (0); absent (1).

124. Articulated leg segments in immature instars: five (0); four (1); two (2); one (3); apode (4).

125. Tarsal claws of immature instars: not modified (0); modified into small plates with 2–3 apices (1).

126. Leg setae (excluding solenidion ω*1* in immatures): present (0); absent (1).

127. Male moulting: from tritonymph (0); from protonymph (1).

RESULTS

A single tree (tree length 197, CI $_{\text{excluding uninformative characters}}$ 0.7, RI 0.8) was obtained (Fig. 2). A tree obtained after the successive weighting (Farris 1969) (tree length 114.43, CI $_{\text{excluding uninformative characters}}$ 0.9, RI 0.9) was identical in topology to it. The reciprocal exchange of the positions of outgroups (Raphignathidae and Stigmaeidae) revealed the same result. The topology of obtained cladogram corresponds to that of the phylogenetical hypothesis proposed earlier (Bochkov 2002; Fig. 1) with exception for the lineage of the families Epimyodicidae and Cloacaridae, which were recently excluded from the superfamily (Bochkov and OConnor 2008).

The monophyly of Cheyletoidea (Bremer support index [BS] 8) is well supported by five unambiguous synapomorphies: stylophore fused with subcapitulum (1); absence of eupatidia *ba, bp, lp,* and *va* of palpal tarsus (25); absence of setae *pl*I (76), solenidion φρI (88), and cupules *ia* (53).

Two more synapomorphies – absence of seta *l″* of genua I–II (94 – reversed in Harpirhynchinae) and seta(e) *v* of genua III and IV (97 – reversed in Psorergatidae) are not so solid and have exclusions within these families.

Three other synapomorphies are false and would be homoplasies if more free-living cheyletids were included in the analysis. The first of them, the dorsal position of the male genital orifice (41) has

Table 10. Data matrix.

Taxa	Characters						
	1	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
Raphignathidae	0000000000	00000-0000	0000000000	000-000000	0000000000	0000000000	0000001100
Stigmaeidae	00001---00	00000-0001	0000000000	000-000000	0000000000	0000000000	0000001100
Cheyletini	1000011101	00-0011101	0000100000	000-000000	0000000000	0010000000	0000000011
Cheyletiellini	1000011101	00-0011101	0000100000	000-000000	1000000000	0011000100	0000000011
Syringophilinae	1100011101	00-001111-	1000100000	000-021000	1000000000	0011000000	0010000001
Picobiinae	1100011101	00-001111-	1000100000	000-021000	1000000000	0011000000	0010000001
Harpirhynchinae	1001000010	110000001-	2111110101	1110010110	100001-110	0011000011	01-0000-00
Harpypalpinae	1001000010	111000001-	2111110111	1111010111	1001001110	0111020001	0111100100
Ophioptinae	10011---10	1111-0001-	2111110111	1011010311	1001001110	0111010101	0100000000
Psorergatidae	101-1---11	11-010001-	3101110102	020-110110	1012100111	0011121001	0111101111
Demodicidae	101-1---11	11-010001-	3101111102	000-120210	110211-111	1-11121001	1111111111

Taxa	Characters					
			1	1111111111	111111111	1111111
	7777777778	8888888889	9999999990	0000000001	111111112	2222222
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567
Raphignathidae	0001000000	0001000000	0000000000	0000000000	0000001000	0000000
Stigmaeidae	0001000000	0000000000	0000101000	0000000000	0000000000	0000000
Cheyletini	1011010101	1000000100	0001111000	0000000000	0000000000	0000001
Cheyletiellini	1011010101	1000000110	0001111000	0000000000	0000000000	0000001
Syringophilinae	1011010000	0000220110	1001111000	0000000010	0000010000	0000000
Picobiinae	1010010000	0000220110	1001111000	0101101110	0000010000	0000000
Harpirhynchinae	-0-1010000	-00-0-1110	-0-10--100	0-0--0---0	1010111100	0001000
Harpypalpinae	0001010000	1001001110	1010001100	1100000010	1000111011	1114–00
Ophioptinae	0001010000	1111111110	1011011101	0100100100	0000111111	1114–00
Psorergatidae	1111011011	1111111111	1111100100	1000000010	1111111100	2-02110
Demodicidae	1111111011	1111221111	1111111111	-111111111	1111111100	2-03110

clearly independent origin at least in Cheyletidae, Syringophilidae, and in the common ancestor of Harpirhynchidae (Psorergatidae-Demodicidae). In all tribes of free-living cheyletids this orifice is in the terminal position. The second false synapomorphy is the absence of cupules *im, ip*, and *ih* (54). As in the case of the character 41, these cupules are present in all free-living cheyletids and were independently lost in parasitic Cheyletidae, Syringophilidae, and in the common ancestor of Harpirhynchidae (Psorergatidae–Demodicidae). The third false synapomorphy is the absence of solenidion φII (89). In our cladogram, this character undergoes reversion in Cheyletini, a single unit among cheyletoids in our data set retaining this character. Its absence in Cheyletiellini, actually, is not typical for cheyletids, because mites of most cheyletid tribes, both free-living and parasitic, retain this solenidion.

In the obtained tree, two phylogenetic lineages are clearly recognizable (Fig. 2). Lineage I (BS 1) includes families Cheyletidae and Syringophilidae and is supported by five unique synapomorphies: peritremes situated on rostral part of stylophore (6), distinctly segmented (7), arch-like or M-shaped (8); hypostomal apex fused with stylophore (17); hypostomal lips present (18). The relatively low BS of this lineage can be explained by many homoplastic characters (loss of setae) which originated in parallel in Syringophilidae and in mites of lineage II. In Syringophilidae, these characters arose as a consequence of their parasitism in quills. The most important synapomorphies of Cheyletidae (BS 2) are the ventral situation of solenidion on tarsi II and male moulting from protonymph (127). Yet, in these mites setae *a*'I are absent (69). These setae are also absent in Demodicidae, but demodicids lost all tactile leg setae. The synapomorphies of syringophilids (BS 2) are gnathosoma deeply submerged into idiosoma (2); free segmented linear palps (21); widely separated coxae I–II and III–IV (37). Setae *4a* are independently lost in Syringophilidae and in the branch Harpirhynchidae (Psorergatidae–Demodicidae).

Lineage II (BS 15) is represented by three families Harpirhynchidae (Psorergatidae–Demodicidae). It is supported by 18 synapomorphies: presence of strongly sclerotized pharyngeal bulb (9); absence of setae *ao1* and *ao2* (11 and 12); palpal tibia-tarsus dislocated to ventral side of trochanter-femur-genu (24); absence of eupathidia on palpal tarsus (28); absence of hysteronotal shield (38); completely fused genital and anal orifices in females (39); absence of aggenital setae in females and males (48 and 49); absence of setae *ft*, *vs*I, solenidion φI, σI, coxal setae *1b* (reversed in Ophioptinae), *3b*, and *4c* (reversed in Harpypalpinae) (60, 62, 87, 98, 111, 115, 118). The high BS of this lineage is explained by disappearance of many idiosomal and leg setae.

The monophyly of Harpirhynchidae (BS 3) is supported by three unique synapomorphies: strongly reduced, membranous tarsus (23); seta *l"G* grouped together with *dG* in apical part of palpal throchanter-femur-genu (31); modified setae *l'T* of palpal tibia (33). The relationships among the harpirhynchid subfamilies Harpirhynchinae (Harpypalpinae–Ophioptinae) corresponds to those in the phylogenetic hypothesis proposed earlier (Bochkov et.al. 1999). The sister relationships between Harpypalpinae and Ophioptinae (BS 5) is supported by 11 unique synapomorphies: subcapitular setae *m* and *n* situated at same level (13); setae *v'F* of palpal femur absent (29); female vulva edged by sclerotized structures (40); setae *scx* absent in immature instars (44); genital setae spur-like, surrounded into idiosomal cuticle (52); in immature instars – seta *l"G* of palpal genu absent (119), seta *dG* of palpal femur comb-like (120), most prodorsal setae absent (121), hysterosomal setae dislocated on ventral side of idiosoma (122), anal orifice absent (123). Finally, immature instars of these two subfamilies are apode, but this character (124) is not unambiguous being coded as polymorphic.

The monophyly of the Psorergatidae–Demodicidae branch (BS 23) is supported by 18 unique synapomorphies; most of them, however, are represented by reductions: stigmae absent (3); setae *elc. p.* modified (15); setae of palpal tibia-tarsus short, spur-like (35); setae *scx* absent (44); propodonotal setae strongly reduced in number (45); setae of anal-genital complex in female absent (50); empodium strongly reduced, membranous (55); condylophores and basal piece strongly reduced or absent (57); absence of setae *a"*I, *u"*I–IV, *l'* of tibia I, *d* and *l'*of genua I–II, *1c, 3a* (72, 77, 79, 90, 92, 112, 114); in immature instars, – idiosomal setation absent (121), tarsal claws modified into small plates with 2–3 apices (125), tactile leg setae absent (126).

The monophyly of Demodicidae is supported by ten unambiguous synapomorphies: setae *dF* of palpal femur absent (27); presence of opishosomal organ (42); setae of anal-genital complex in male absent (51). Other synapomorphies (61, 66, 75, 99, 103, 106, 110) concerning the absence of different leg setae, are formal due to the total absence of the tactile setae in demodicids.

The monophyly of Psorergatidae is supported by two unambiguous synapomorphies: setae *v"F* situated in the middle part of palpal trochanter-femur-genu close to *dF* (32) and presence of genital lobes (43).

DISCUSSION

The ancestor of lineage I undoubtedly was a predator preying on other arthropods. Most apomorphic modifications of these mites concern the gnathosomal structures and, probably, serve for more effective preying. At the same time, in these mites, the idiosoma and legs are relatively archaic and weakly modified like those in the other predator Raphignathae. Syringophilids, probably, originated from a common ancestor with Cheyletidae. These mites developed some adaptations to the parasitic mode of life in feather quills: the stylophore surrounded into the idiosoma or the elongate body; they lost some structures, which are unnecessary for permanent parasites: the thumb-claw complex, cupules, and the strong sclerotization of the dorsal shields. In these mites, some idiosomal setae (*4a* and *ps3*) undergo a reduction in parallel to parasitic cheyletoids of lineage II. The external morphology of syringophilids perfectly corresponds to the dermoglyphid morphoecotype established by Mironov (1987) for quill-living feather mites. In these mites, the idiosoma is egg-shaped or teretial, weakly sclerotized; the legs are short and thickened; the idiosomal setae form around the mite a hemispherical sensitive zone. In Cheyletidae, parasitism on birds and mammals originated independently in several phylogenetic lineages (tribes) (Bochkov and Fain 2001; Bochkov 2004). All cheyletids are permanent ectoparasites, excluding mites of the tribe Chelonotini. In this tribe, females only are ectoparasites in ears of East Asian squirrels, whereas immature instars and males are nest predators (Bochkov et al. 2008). Cheyletids belong to the skin mite morphoecotype established by Bochkov (2007). In these mites, the idiosoma is strongly flattened dorso-ventrally, weakly sclerotized, and sometimes bears different ventral apophyses; the legs are normally developed.

Lineage II is represented by exclusively permanent parasites of vertebrates, which can be characterized by the unique palpal structure. All three families of this lineage demonstrate a tendency towards intracutaneous parasitism (part of Harpirhynchidae) or obligate intracutaneous parasitism (Demodicidae and Psorergatidae) (Moss 1979; Nutting 1985; Giesen 1990). The remaining Harpirhynchidae are relatively slow-moving ectoparasites, which are very often embedded in the host epidermis. For this reason, in the evolution of this mite lineage the reduction tendencies prevail. In Harpirhynchinae, the hysterosomal setae are strongly reduced in number. In Psorergatidae, this tendency towards the setal reduction is much clearer than in harpirhynchids. In these mites, many setae represented in harpirhynchids are absent. Whereas in demodicids, almost the all idiosomal setae and all leg setae, excluding the tarsal solenidion, are absent. All these mites belong to the intradermal morphoecotype (Bochkov 2007). Their idiosoma is weakly sclerotized, rounded outline or vermiform; the idiosomal and leg setation is strongly reduced in number; the legs are shortened.

It is presumed from the wide distribution of these mites on birds (Harpirhynchidae) and mammals (Psorergatidae–Demodicidae) that the common ancestor of this branch could have occurred on the common ancestor of birds and mammals (Bochkov 2002); however, switching during an early phase of host evolution can not be excluded (Bochkov et al. 2008). A possible reason for the absence of cheyletoids on recent reptiles (excluding snakes) coul probably be explained by peculiarities of their molting. Squamata lose the entire external dermal layer or large pieces of it during the molt (Landmann 1986); moreover, they have a multilayered keratinized epithelium, and skin glands are absent. The high probability of loss of mites during reptile molting seems to have prevented original establishment of cheyletoid parasites on these hosts. These mites are probably absent also on crocodilians because of their aquatic mode of life. In birds, the skin has undergone significant evolutionary changes comparable to what is seen in the integument of mammals. This perhaps allowed some cheyletoid mites of the family Harpirhynchidae to transfer to intradermal parasitism in capsules similar to those induced by species of Psorergatidae (Literak et al. 2005).

The indirect argument of the long time parasitic relationships between vertebrates and cheyletoids is a record of mite eggs on the dinosaur's feathers from the Lower Cretaceous period (northeast Brazil) (Martill and Davis 1998). Authors believed that these eggs were laid by feather mites (Astigmata: Psoroptidia). These rounded shape eggs, however, are more similar with those of Cheyletoidea, than with strongly elongated eggs of feather mites.

The position of the subfamily Ophioptinae associated with snakes of the superfamily Colubroidea in the core of the bird parasites can be explained by the switching of its ancestor from passerine birds (Kethley in Lombert and Moss 1983; Bochkov et al. 1999; Bochkov 2002; Bochkov et al. 2008). Certain snakes feed on nestlings and adult birds, and most of these preys are small-sized passerine birds, which are common hosts of harpypalpins. This hypothesis is strongly supported by data about the host associations of ophioptines, which are limited in their distribution to hosts of the two closely related families Colubridae and Elapidae (Fain 1964).

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