

Phylogeny of quill mites of the family Syringophilidae (Acari: Prostigmata) based on their external morphology

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Abstract. External morphological characters were used to reconstruct a phylogeny of the mite family Syringophilidae (Acariformes: Cheyletoidea), which are permanent parasites inhabiting the quills of bird feathers. A total of 53 syringophilid genera and 79 characters were included in the data matrix; maximum parsimony (MP) and Bayesian analyses (BA) were performed to determine their phylogenetic relationships. The consensus of unweighted MP trees was weakly resolved. Only four generic groups were recognized: *Aulonastus* + *Krantziaulonastus* (i) and (*Creagonycha* + *Kethleyana*) + (*Megasyringophilus* + *Selenonycha*) (ii) – both with low Bremer support (BS 1); the subfamily Picobiinae – *Picobia*, *Calamincola*, *Columbiphilus* (*Neopicobia* + *Rafapicobia*) (BS 12) (iii) and *Psittaciphilus* generic group – (*Meitingsunes* + *Psittaciphilus*) (*Peristerophila* + (*Neoperisterophila* + (*Castosyringophilus* + *Terratosyringophilus*))) (BS 2) (iv). BA revealed a consensus tree with a topology similar to MP. The two main groups recognized by MP, the subfamily Picobiinae and *Psittaciphilus*, both received the highest support of 1; while two other groups recognized by MP – *Aulonastus* + *Krantziaulonastus* and (*Creagonycha* + *Kethleyana*) + (*Megasyringophilus* + *Selenonycha*) received relatively low support of 0.73–74 and 0.76–77, respectively. The consensus of re-weighted MP trees was almost fully resolved but, the majority of the generic groups, excluding the Picobiinae and *Psittaciphilus* were supported by just a few non-unique synapomorphies with a high probability of homoplastic origin. The most intriguing result is the paraphyly of the Syringophilinae in respect to picobiines. The pattern of the re-weighted tree demonstrates only patches of parallel evolution at the level of syringophilid genera and bird orders. Perhaps horizontal shifts on phylogenetically distant hosts and colonization of quill (calamus) types other than primaries and secondaries were also important in the evolution of the syringophilids.

INTRODUCTION

Mites of the family Syringophilidae (Acariformes: Cheyletoidea) are permanent, highly specialized parasites of birds living inside the quill (calamus) of feathers. They feed on the tissue fluids of the host by piercing the quill wall with their styletiform movable cheliceral digits. All representatives of the family have a distinctly elongated idiosoma with weakly sclerotized cuticle and relatively short legs. In these mites, reproduction and development take place inside the quills. The syringophilids infect newly developing quills via a natural opening in the quill wall – the umbilical plug “superior umbilicus”. Only young fertilized females disperse, while males reproduce locally and then die (Kethley, 1971).

According to the system proposed by Mironov & Bochkov (2009), this family belongs to the superfamily Cheyletoidea (suborder Trombidiformes, infraorder Prostigmata, parvorder Eleutherengona). Within the superfamily Cheyletoidea, Syringophilidae is the sister group to the Cheyletidae. The sister-group relationships between these two families have solid morphological support (Bochkov et al., 2008; Bochkov, 2008, 2009), which is confirmed by molecular analyses (Dabert et al., 2010; Zhao et al., 2012).

Syringophilids are mono- or oligoxenous parasites; most of them are associated with a single host species or species of one genus; more rarely they occur on hosts belonging to various families or even orders. The syringophilid genera are mostly restricted to a particular order or family of hosts (Kethley, 1970; Bochkov et al., 2004; Skoracki, 2011). To date, the Syringophilidae includes more than 270 species grouped in 53 genera. These mites were recorded from more than 373 species of birds belonging to 77 families and 21 orders of the total of 226 families and 34 orders of extant birds (Clements et al., 2011). Apparently the number of species described represents only a small fraction of the actual syringophilid biodiversity, because their expected number is estimated as 5000 species based on their host specificity and number of potential hosts (Johnston & Kethley, 1973). Although several species of syringophilids belonging to different genera can parasitize one host individual, records of syringophilids belonging to different species in one quill are rarer (Casto, 1976; Głowska, unpubl. data).

Strict host specificity of syringophilids could potentially reveal the phenomenon of parallel evolution, which is often observable in acariform mites that are permanent parasites (Fain, 1994). This makes coevolutionary studies

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between syringophilids and their avian hosts especially interesting, since data on such host-parasite associations are often used to validate the phylogeny of their hosts (Klassen, 1992; Whiteman & Parker, 2005; Hypsa, 2006; Bochkov et al., 2011). There are, however, two main problems, which seriously hamper the development of co-evolutionary reconstructions for syringophilids. (i) This family is very monotonous morphologically (Johnston & Kethley, 1973; Bochkov et al., 2004), having only a limited set of the external morphological structures. These are represented mostly by setae, which are significantly fewer in number compared to those of mites of the sister family Cheyletidae. A combination of features such as the presence/absence of particular setae, and sometimes their locations, are the main generic characteristics (Skoracki, 2011). These features have a high probability of being of homoplastic origin and are, therefore, not especially reliable for phylogenetic analyses. (ii) Material useful for molecular phylogenetic analyses is absent for many syringophilid taxa and it would require a lot of time of meticulous collecting in order to obtain this material. During recent years, however, there has been some progress in this direction (Glowska et al., 2012).

The present work is an attempt to construct the phylogeny of this family based on external morphology using modern phylogenetic methods (maximum parsimony and Bayesian analysis). Despite the assumption that most species of syringophilids remain to be described we can state that at least 70% of their extant genera are known to date based on the distribution of these mites and, therefore, such work is justified. As a relatively small number of characters have been found since the paper of Johnston & Kethley (1973), we understand the flaws of this morphological approach, but hope that such an analysis will be helpful as an external test for future molecular-based studies, and as a rationale for the molecular systematics of this group by providing diagnostic synapomorphies (Mooi & Gill, 2010).

Historical review

The family Syringophilidae was erected by Lavoipierre (1953) for the monotypic genus *Syringophilus* Heller, 1880, which was previously included in the family Myobiidae (Ewing, 1938; Baker, 1949). Unaware of this work, Dubinin (1957) established a family with the same name for two former myobiid genera, *Syringophilus* Heller, 1880 and *Picobia* Haller, 1878.

Only a few more papers were published on syringophilids (Oudemans, 1906; Fritsch, 1958; Lawrence, 1959; Clark, 1964) before the revision of this family carried out by Kethley (1970), who re-examined all 23 species previously described in the Syringophilidae, provided descriptions of 11 new species and established 14 new genera.

Later on, Johnston & Kethley (1973) proposed a variant of the original syringophilid system based on the results of a phenetic analysis. This analysis confirmed all of the previous syringophilid genera established by Kethley (1970) and divided the family into two unequal subfamilies, Syringophilinae Lavoipierre, 1953 with 15 genera and monogeneric Picobiinae Johnston & Kethley, 1973.

Syringophilines were characterized by rounded palpal tibiotarsus, multiserrate proral setae (*p*), absence of physogastry in females and well developed setae on the body and legs in the immature stages. The picobiines have truncate palpal tibiotarsi, rod-like proral setae, presence of physogastry in females and very small setae in the immature stages. The established subfamilies also differ ecologically. Syringophilines mainly occupy quills of the primary, secondary, tertiary, covert and tail feathers, whereas all picobiines at that time were recorded only from body feathers.

The third syringophilid subfamily – Lobatinae was created by Casto (1977) for the monotypic genus *Cuculiphilus* Casto, 1977 (now *Calamincola*) found in the primaries and greater primary coverts of *Crotophaga sulcirostris* Swainson (Cuculidae). These mites are characterized by some distinctive female features like presence of opisthosomal lobes, U-shaped peritremes, propodonal shield divided into lateral and medial fragments and dentate movable cheliceral digits. In addition, this subfamily has the main characteristics of the subfamily Picobiinae, e.g. the truncated palpal tibiotarsus, unequal tarsal claws, rod-like proral setae, absence of leg setae *l'RI–II* and *dFIII–IV*, and tendency to physogastry. For these reasons the genus *Calamincola* was included in the subfamily Picobiinae (Fain et al., 2000).

A few taxonomic works on syringophilids were published between 1970 and 1990 (Kethley, 1973; Casto, 1977, 1979, 1980a, b; Philips & Norton, 1978; Liu, 1988). However, the number of systematic studies on syringophilids greatly increased at the end of 1990's (Chirov & Kravtsova, 1995; Kivganov & Sharafat, 1995; Bochkov & Mironov, 1998, 1999; Skoracki, 1999; Skoracki & Dabert, 1999a, b, 2000; Skoracki et al., 2000; Fain et al., 2000). Since the beginning of XXI century the diversity of syringophilids was studied mainly by A.V. Bochkov and M. Skoracki (with collaborators).

In addition, there has been only one phylogenetic study on syringophilids since the paper by Johnston & Kethley (1973) that of the genus *Picobia* by Skoracki et al. (2004). The need for phylogenies based both on morphological and molecular data is obvious. Such analyses can be used to group the numerous syringophilid genera described to date and provide a solid basis for the analysis of the co-evolutionary relationships between these parasitic mites and their bird hosts.

MATERIAL AND METHODS

Material

This study is based on the examination of most of the species of the syringophilids, which are housed in five main collections (a total of 275 species from 53 genera out of the 278 species and 53 genera currently described): Department of Animal Morphology, Adam Mickiewicz University, Poznan, Poland (AMU), Royal Belgian Institute of Natural Sciences, Brussels, Belgium (ISNB); Royal Museum for Central Africa, Tervuren, Belgium (MRAC); Museum of Zoology, University of Michigan, Ann Arbor, USA (UMMZ); Zoological Institute, Russian Academy of Sciences, Saint-Petersburg, Russia (ZISP).

Representatives of the genera *Procellariysyringophilus* Kethley, 1970 (1 species) and *Trypetoptila* Kethley, 1970 (1 species) were not available for this study and characters of these mites were obtained from the original descriptions (Kethley, 1970).

Host systematics follows Clements et al. (2011).

Syringophilid external morphology

A detailed discussion of the morphological characters used in the present study is provided by Skoracki (2011). A character list is given in Appendix 1. The gnathosomal setation follows Grandjean (1946), while the idiosomal setation follows Grandjean (1939) as adapted for Prostigmata by Kethley (1990), and the system of nomenclature for leg chaetotaxy follows that proposed by Grandjean (1944). The application of these chaetotaxic schemes to the Syringophilidae was recently described by Bochkov et al. (2008) and Skoracki (2011).

Taxa selection

The external morphology of the representatives of each syringophilid genus is very similar. The species are distinguished, with a few exceptions, by the shape of the hypostomal protuberances, number of lines on the proral setae, number of peritremal segments, setal ornamentation, position of setae *dI* and quantitative characters such as lengths of setae, stylophore, etc. Therefore, syringophilid genera are not subdivided into subgenera, but there is no reason to doubt their monophyly (Skoracki, 2011). It allows us to prepare the syringophilid phylogenetic reconstruction at the generic level. We agree, however, with Yeates (1995) and Prendini (2001) that it is preferable to include real species in a cladistic analysis rather than supra-species taxa. In our analyses each genus is represented by a single species (Table 1).

Previously the monophyly of the family Syringophilidae was repeatedly tested with numerous outgroups and always received high support (Bochkov, 2002, 2008; Bochkov et al., 2008). For this reason, only two outgroups – a free living predator *Cheyletus eruditus* (Schränk, 1781) and quill-inhabiting predator *Metacheleteoides numidae* Fain, 1972, both belonging to the sister family Cheyletidae, were used in the analyses.

Cladistic analysis

Only qualitative characters, such as the presence/absence of a structure or the form of certain morphological features were used in this analysis. Characters having multiple states were treated as unordered and not modified into binary characters. All characters were unordered and initially unweighted. In total, 55 species and 79 characters were included in the data matrix (Table 1). Preparing and editing the data matrix were done using NEXUS Data Editor 0.5.0 (Page, 2001). Analysis of character distributions, drawing and editing of the trees were performed in TreeView 1.5.2 (Page, 1988) and WINCLADA (Nixon, 1999).

Maximum parsimony analysis

The construction of the phylogenetic relationships was performed with PRAP2 (Muller, 2004) implemented in PAUP 4.0b.10 for IBM (Swofford, 2001). The parsimony ratchet analysis was used because of the relatively large number of taxa (1000 iterations with other options by default). Results of the PRAP ratcheted initial analysis were checked using NONA implemented in WINCLADA (Nixon, 1999): three independent ratcheted analyses with 100,000 iterations each and other options by default. Support for each branch was estimated using Bremer indices calculated with PRAP.

Bayesian analysis

The software MrBayes version 3.2 (Ronquist et al., 2011) was used and the standard discrete (morphological) model applied (Lewis, 2001). Three independent simultaneous runs with four

chains each (three hot and one cold) were used with 15 million generations and sampling frequency of 100. The analysis was considered as finished when the standard deviation of split frequencies dropped below 0.005. Three independent analyses were conducted to check that the output data were similar and that the optimal topology was found.

RESULTS

Unweighted parsimony analysis

The initial analysis yielded 945 equally maximally parsimonious trees (tree length 218, CI for phylogenetically informative characters – 0.37, RI – 0.69, and RC – 0.27). The consensus tree is very weakly resolved (Fig. 1). Three independent analyses of our data using NONA yielded 5694–6120 shortest trees whose consensus trees had the same topology as the consensus obtained with PAUP.

As mentioned above, the syringophilid monophyly was strongly supported using many outgroups and below we list only the main characters supporting the monophyly of this family (Bremer index [BI] 17): the gnathosoma deeply submerged into the idiosoma (character 1); four segmented linear palps (character 5); widely separated coxae I–II and III–IV (character 45), absence of setae *4a* (character 57) and absence of various leg setae, which are present in the sister family Cheyletidae.

In the consensus, only four generic groups are recognizable; two of them, *Aulonastus* + *Krantziaulonastus* and (*Creagonycha* + *Kethleyana*) + (*Megasyringophilus* + *Selenonycha*), have very low Bremer supports (1).

Two other groups received higher Bremer supports. The first of them (BI 12) unites genera of the subfamily Picobiinae – *Picobia*, *Calamincola*, *Columbiphilus* + (*Neopicobia* + *Rafapicobia*). In the majority consensus tree (50%, not shown), this group is placed in the core of the family. The most notable synapomorphies characteristic of picobiines are the truncate palpal apex (character 7), eupathidium *sul* represented by microseta (character 14), reduced setae on palpal tarsus, body and legs of the immature stages (characters 16 and 31), capability to physogastry (character 41) and legs I and II thicker than legs III and IV (character 43).

The second *Psittaciphilus*-group (BI 2) includes genera mostly associated with psittaciform and columbiform birds: (*Meitingsunes* + *Psittaciphilus*) + (*Peristerophila* (*Neoperisterophila* + (*Castosyringophilus* + *Terratosyringophilus*))). This group is characterized by distinctive but not unique synapomorphies, such as absence of setae *vi* (character 17), leg I thicker than legs II–IV (character 43), absence of seta *vsII* (character 60), multiserrate proral setae (character 64) and absence of *dFIV* (character 75).

The monophyly of the clade *Peristerophila* + (*Neoperisterophila* + (*Castosyringophilus* + *Terratosyringophilus*)) (BI 2) was previously hypothesized by Bochkov et al. (2004) mostly based on the following synapomorphies: presence of sausage-like hypostomal lips (character 10), legs I and II sub-equal in length (character 43) and parallel apodemes I (character 47).

TABLE 1. Character matrix.

Taxa	Characters
<i>Cheyletus eruditus</i> (Schrank, 1781)	1 1111111112 222222223 333333334 444444445 555555556 666666667 777777777
<i>Metacheletoideus numidae</i> Fain, 1972	1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890
<i>Apodisyringiana haszprunari</i> Skoracki, 2005	000000000 000000000 000000000 000000000 000000000 000000000 000000000
<i>Apodisyringophilus collocatus</i> Skoracki & O'Connor, 2010	000000000 000000000 0001000000 0-00000000 000000000 000000000 0010000000
<i>Ascetomyia porzanae</i> (Bochkov & Galloway, 2004)	1100110000 0000000010 0101000001 0000000110 0-00100020 1000011001 1110000111
<i>Aulobia sylviae</i> Bochkov & Mironov, 1998	1100110000 0000000110 0101000001 0000001110 0-01111-00 1000011001 1110000111
<i>Aulonastus prunellae</i> Bochkov & Mironov, 1999	1100110100 0010000100 1101000001 0101-0-110 0-001110000 1000011000 1110000010
<i>Betasyringophiloides motacillae</i> (Bochkov & Mironov, 1998)	1100110000 0000001-00 0101000001 0000001110 0-00111-10 1000011000 1110000010
<i>Blaszakia tauracos</i> Skoracki & Sikora, 2008	1100110000 0000000100 0101000000 0000001110 0-10111-10 1000011001 1110000110
<i>Bochkovia phalaropi</i> Skoracki & O'Connor, 2010	1110110000 0010000100 0101000000 0000001110 0-10110110 1000011000 1110000010
<i>Bubophilus asiobius</i> Skoracki & Bochkov, 2002	1100110000 0010000100 0101000001 0000001110 0-00110110 1000011000 1110000010
<i>Calamincola lobatus</i> (Casto, 1977)	1100111000 1011070100 1111001000 7301-1-011 1020110110 001011000 110-000010
<i>Casosyringophilus claravis</i> Skoracki & Glowska, 2008	1100110101 0000001-00 1101000001 0001-0-110 0-11111-00 1000011001 1111000010
<i>Charadriophilus lyudmilae</i> Bochkov & Chistyakov, 2001	1110110000 0000000000 0111000000 0000001110 0-00110110 1000011000 1110000010
<i>Chenophila kanduli</i> Bochkov, 1998	1100110100 0010000100 0101000000 0000001110 0-10110110 1000011000 1110000010
<i>Ciconichtenophilus phoeniconaias</i> Skoracki & O'Connor, 2010	1101110000 0000000100 0101000000 0000001110 0-10110110 1000011001 1110000010
<i>Colinophilus wilsoni</i> Kethley, 1973	1110110000 0010000010 0101000000 0000001110 0-10110110 1000011000 1110000010
<i>Columbiphilus polonica</i> (Skoracki et al., 2001)	1100111100 0001010100 0101001000 1201-1-010 1120110110 0000111000 110-000010
<i>Corvitorotoglus alpha</i> Skoracki & Bochkov, 2010	1110110100 0010000100 1101000011 0000001110 0-00110000 1000011000 1110000010
<i>Creogomcha totani</i> (Oudemans, 1904)	1110110000 0010000100 1101000001 0001-0-110 0-00100020 1100001000 1110000010
<i>Crotophagisyringophilus io</i> Skoracki, 2008	1110110100 0010000100 1101000001 0101-0-110 0-00110100 1000011000 1110000010
<i>Cuctilisyringophilus chirovi</i> (Bochkov & Mironov, 1998)	1111110000 0010000100 1101000001 0000001110 0-00110110 100101001 1110110010
<i>Fritschisyringophilus lonchurae</i> Bochkov et al., 2004	1100110101 0010000100 0101000001 0000000110 0-10111-10 1000011000 1110110010
<i>Galliphilopsis lophurus</i> Skoracki & Sikora, 2004	1110110000 0000001-00 0101000001 0000001110 0-00110110 1000011000 1110110110
<i>Kalamotrypes cracidus</i> Skoracki & Sikora, 2011	1101110000 0000000100 0101000000 0000001110 0-10110110 1000011000 1110000010
<i>Kethleyana gebochelidoni</i> Kivganov, 1995	1110110100 0010000100 1101000101 0001-0-110 0-00100020 1100001000 1110000010
<i>Megasyringophilus aquilus</i> Skoracki et al., 2010	1100110000 0000001-00 0101000001 0001-0-110 0-00111-10 1000011000 1110000010
<i>Meitingsunes columbicus</i> Skoracki, 2011	1111110000 0010000100 010100100 0000001110 0-10110110 1000011000 1110000010
<i>Mironovia coturnae</i> Bochkov et al., 2004	1110110000 0000001-00 0101000000 0000001110 0-10110110 1000011000 1110000010
<i>Neaulobia mironovi</i> Bochkov & Perez, 2002	1110110000 0000000100 0101000001 0000001110 0-00111-10 1000011000 1110110010
<i>Neaulonastus bisetatus</i> (Fritsch, 1958)	1100110000 0000001-00 0101000000 0000001110 0-00111-10 1000011000 1110110010
<i>Neosyringophilopsis troglodytis</i> (Fritsch, 1958)	1110110100 0010000100 0101000001 0100100010 0-00110110 1000011000 1110000010
<i>Neoperisterophila regiusi</i> Skoracki, 2005	1100110101 0000001-01 0101000001 0-01-0-110 0-11111-00 1000011001 1111000010
<i>Neopicobia modularis</i> (Skoracki & Magowski, 2001)	1100111000 0101110100 0101011000 1301-0-010 1220110110 0000011000 110-001010
<i>Nigarobia helleri</i> (Oudemans, 1904)	1100110000 0000000100 0111000001 0000001110 0-00111-10 1001011001 1110000010
<i>Paranigarobia calidridis</i> (Bochkov & Mironov, 1998)	1100110000 0010000100 0101000000 0000001110 0-00110110 1001011011 1110000010
<i>Peristerophila columbae</i> (Hirst, 1920)	1100110101 00100001-00 0101000001 0000001110 0-11111-00 1000011001 1111000010
<i>Phalarophilus fulcarius</i> Skoracki et al., 2011	1100110000 0000000100 0101000000 0000001110 0-00111-10 1000011001 1110000010
<i>Philoxanthomea clarki</i> Kivganov, 1995	1110110100 0010000100 1101000101 0000001110 0-00100000 0000011000 1110000010
<i>Pleisyringophilus kratos</i> Skoracki & O'Connor, 2010	1100110000 0001110000 0101001000 1201-0-110 1020111-11 0101011000 110-000010
<i>Picobia heert</i> Haller, 1878	1110110100 0001000000 0101001000 0000000110 0-10110100 1000011001 1110000010
<i>Psittaciophilus amazonae</i> Fain et al., 2000	1110110000 0000001-10 0101000001 0010000110 0-10110110 1000011001 1111000010
<i>Pteroclidisyringophilus re</i> Skoracki & O'Connor, 2010	1110110000 0000000100 0101000001 0000001110 0-10110110 1000011000 1110000010
<i>Rafapiobia zinnitra</i> Skoracki, 2011	1100111000 0101110100 0101001000 1301-0-010 1220110110 0000011000 110-001010
<i>Selenonychia charadriiformicus</i> Skoracki, 2011	1100110100 0010000100 1111000001 0000001110 0-00100020 1200001000 1110000010
<i>Sibbarokris langei</i> Bochkov & Mironov, 1999	1101110010 0010100100 0101000000 0000001110 0-10110120 1000011001 1110000010
<i>Syringophiloides minor</i> (Berlese, 1887)	1100110000 0000000100 0101000000 0000001110 0-10111-10 1000011001 1110000110
<i>Syringophilopsis fringillae</i> (Fritsch, 1958)	1100110100 0010000100 0101000001 0000100110 0-00110100 1000011000 1110000010
<i>Syringophilus bipunctatus</i> Heller, 1880	1100110000 1010000100 0101000000 0000001110 0-00110100 1000011000 1110000010
<i>Terratosyringophilus georgionus</i> Skoracki & Glowska, 2008	1100110101 00100001-00 1101000001 0001-0-110 0-11111-00 1000011000 1110000010
<i>Tinamiphilopsis arconte</i> Skoracki et al., 2012	1111110000 0010000100 0101000000 0000001110 0-00110110 1000011000 1110000010
<i>Toratorgla menulae</i> Skoracki et al., 2000	1110110100 0010000100 1101000011 0000100110 0-00100020 1000011000 1110000010
<i>Trypetoptila casmerodia</i> Kethley, 1970	1101110100 0010000100 0101000011 0001-0-010 0-00110000 1000011000 0110000010

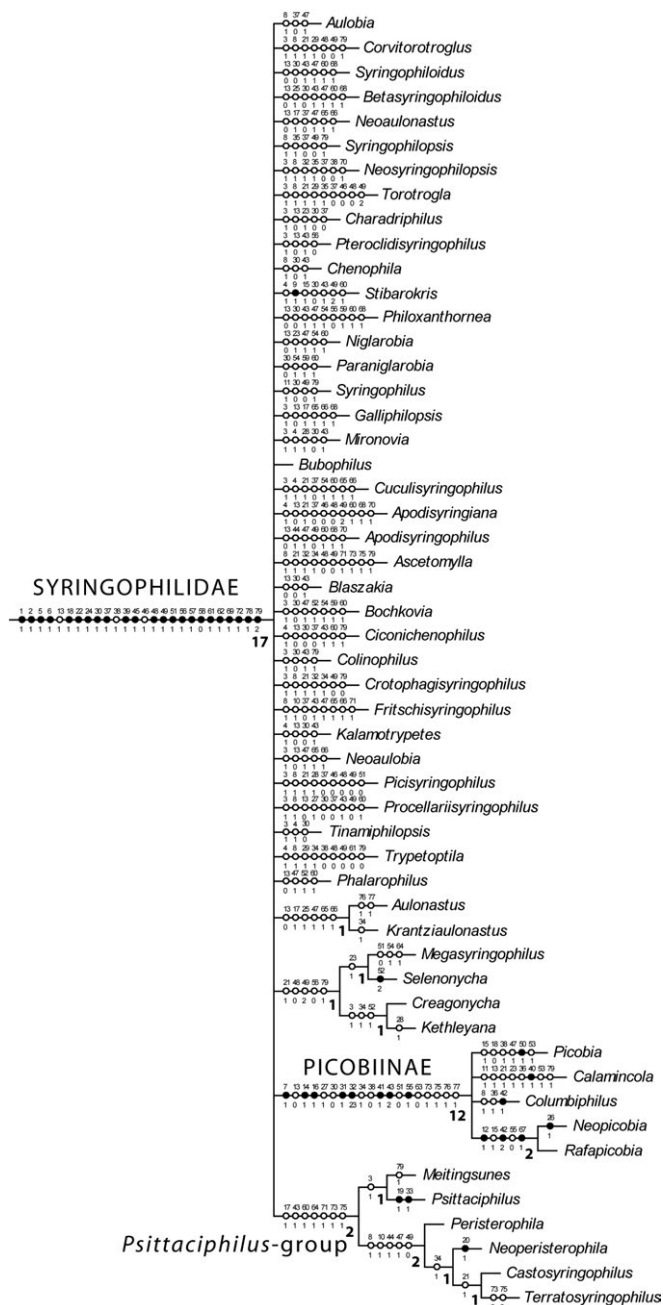


Fig. 1. Strict consensus of 945 equally maximum parsimonious trees found for unordered and unweighted data set using PRAP2 implemented in PAUP 4.0b.10 for IBM: ratcheted analysis (1000 iterations with other options by default); tree length 218, CI for phylogenetically informative characters 0.37, RI 0.69, and RC 0.27. Circles unambiguous synapomorphies; black circles unique synapomorphies; white circles homoplasies. Numbers above circles characters; numbers below circles or squares character states; bold numbers at nodes Bremer indices. Outgroups are not shown.

Bayesian analysis

The Bayesian analysis (BA) revealed a consensus tree with a topology similar to the unweighted parsimony analysis (MP) (Fig. 2). The family is considered monophyletic with 100% support. In comparison with MP, the BA consensus tree comprises four additional generic

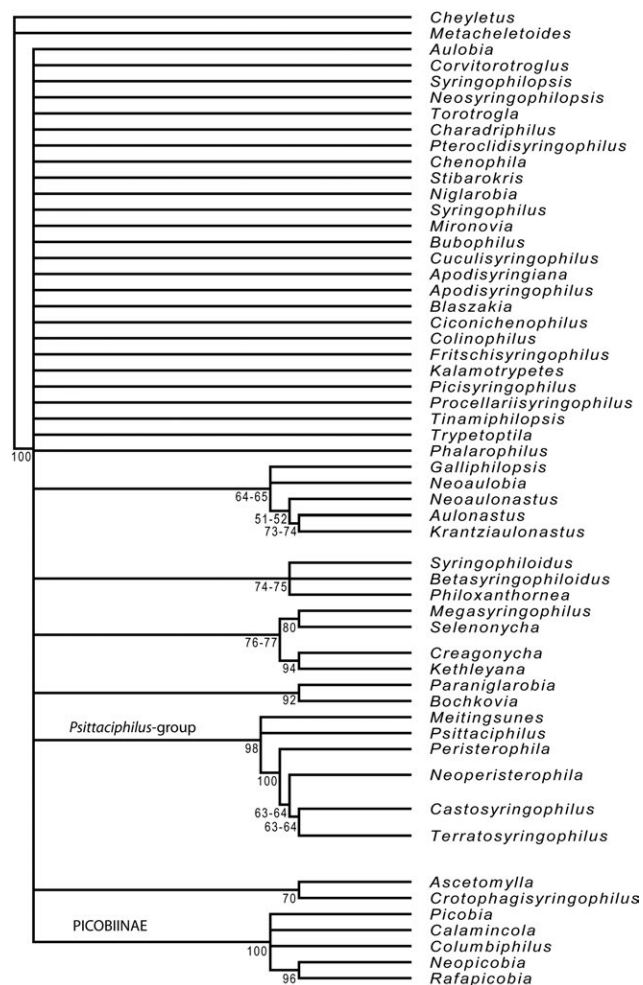


Fig. 2. Consensus tree obtained using Bayesian analysis, MrBayes version 3.2 (standard discrete model). Numbers below branches posterior probabilities.

groups. Among them, two nodes uniting *Paraniglarobia* + *Bochkovia* and *Syringophiloidus*, *Betasyringophiloidus*, *Philoxanthorhea* have posterior probabilities of 0.92 and 0.74–0.75, respectively. The third group *Ascetomylla* + *Crotophagisyringophilus* has 0.70 support and the group uniting the genera *Galliphilopsis*, *Neoaulobia* + (*Neoaulonastus* + (*Aulonastus* + *Krantziaulonastus*)) has only 0.64–0.65 support. Two main groups recognized by the MP analysis, the subfamily Picobiinae and the *Psittaciphilus*-group have the highest support – 1. The other two groups that received low Bremer support (BS1) in the MP analysis are *Aulonastus* + *Krantziaulonastus* and (*Creagonycha* + *Kethleyana*) + (*Megasyringophilus* + *Selenonycha*) are also not strongly supported by BA, 0.73–74 and 0.76–77, respectively.

Weighted parsimony analysis

The unweighted analysis demonstrated a high rate of homoplasy (HI 0.63) and relationships among many syringophiline genera remained unresolved in the consensus tree (Fig. 1). For this reason we checked our data for the presence of the secondary phylogenetic signal, as suggested by Trueman (1998), and applied successive weighting (Farris, 1969) to our data based on the RC indi-

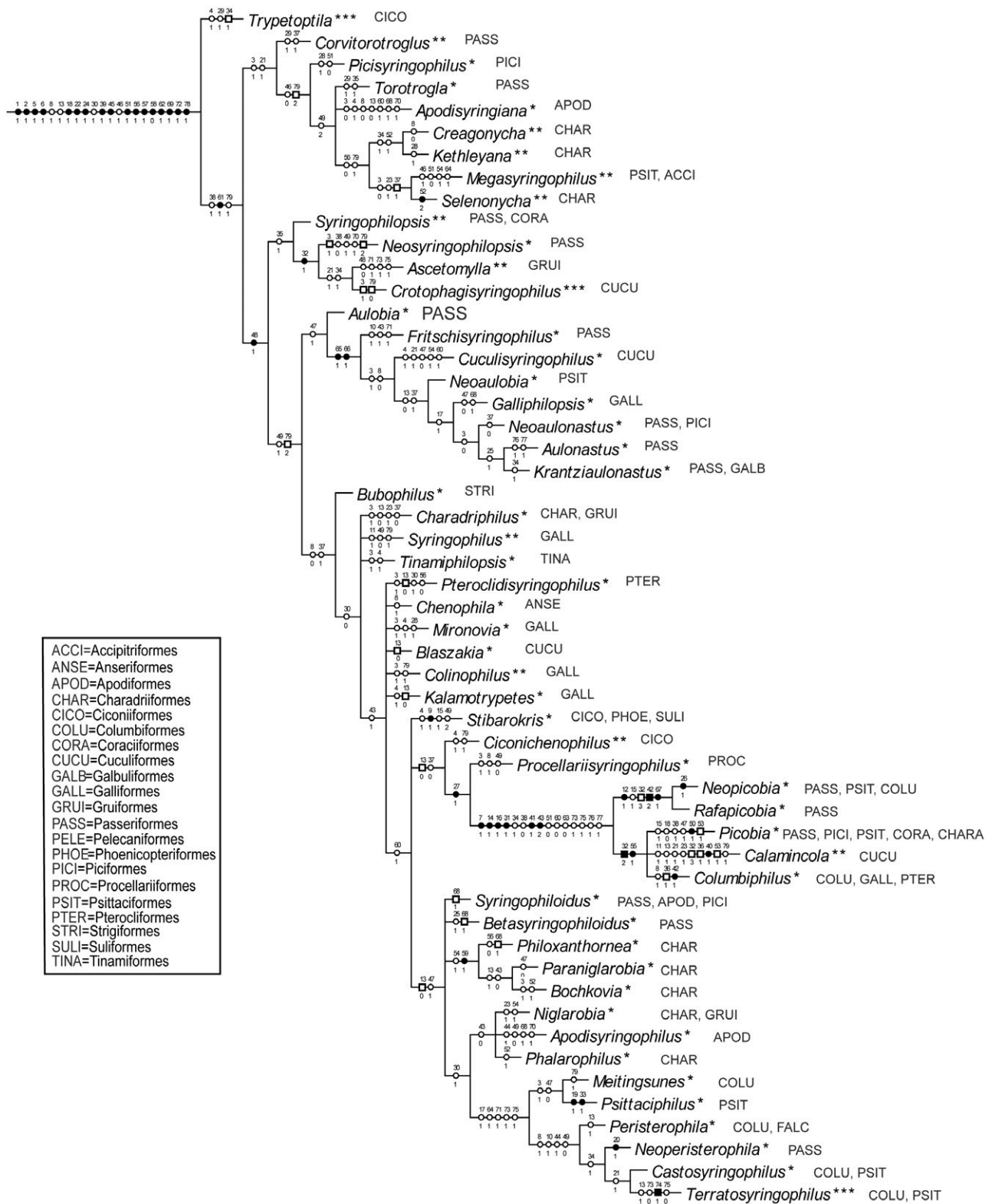


Fig. 3. Strict consensus of 111 most parsimonious trees found after successive weighting according to RC using PAUP 4. 0b. 10: tree length 66.43, CI excluding parsimony uninformative characters, 0.7, RI 0.83, and RC 0.63. Circles unambiguous synapomorphies; squares synapomorphies under DELTRAN transformation; black circles or squares unique synapomorphies; white circles or squares homoplasies. Numbers above circles or squares characters; numbers below circles or squares character states; * small sized genera, ** medium sized genera, *** large sized genera. Outgroups are not shown.

ces. Tree length became stabilized after four successive re-weightings and 111 most parsimonious trees (length – 66.43, CI excluding parsimony uninformative characters

– 0.7, RI – 0.83, and RC – 0.63) were finally obtained. The strict consensus of these trees is provided in Fig. 3.

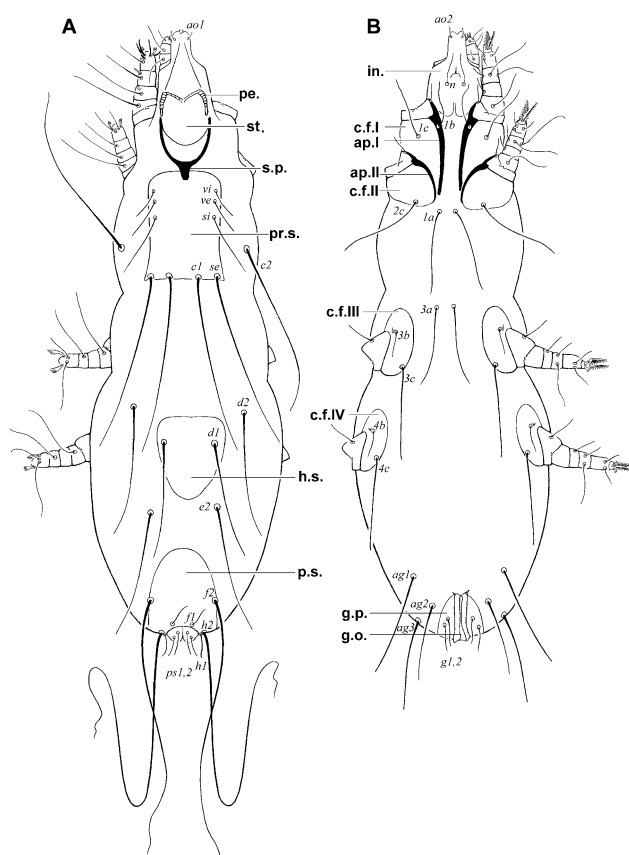


Fig. 4. Syringophilid mite (Syringophilidae), general scheme of female. A – dorsal view; B – ventral view. Abbreviations: ap. – apodeme; c.f. – coxal field; g.o. – genito-anal opening; g.p. – genital plate; h.s. – hysteronotal shield; in. – infracapitulum; pe. – peritremes; p.s. – pygidial shield; pr.s. – propodonal shield; st. – stylophore; s.p. – stylophore protuberance.

In our data matrix, 28 characters (22%) are represented by the presence/absence of particular setae. In acariform mites, a reversion of such a character state is a relatively rare event (see discussion in Mironov et al., 2005). Therefore, we used DELTRAN (slow or delayed) transformation for character pathways favouring parallelisms over reversions. Non-unambiguous characters appearing only after DELTRAN transformation are indicated on the re-weighted consensus tree (Fig. 3).

The picobiines and genera from psittaciform-columbiform birds are placed in the core of the tree and the subfamily Syringophilinae is paraphyletic in respect to these groups. This re-weighted consensus is considerably more resolved than the consensus of the unweighted trees but the majority of its generic groups, excluding the two mentioned above, are supported by a few non-unique synapomorphies, which are highly likely to be of homoplastic origin. As a result, most clades of this consensus are not reliable or diagnosed by the morphological markers. Such generic groups appear occasionally often as a result of analysis based on a scarce data matrix where characters are highly likely to be of homoplastic origin (for example, different reductions). On the other hand, in our case most of the generic groups that appeared after the re-weighted analysis could be characterized by such characters as

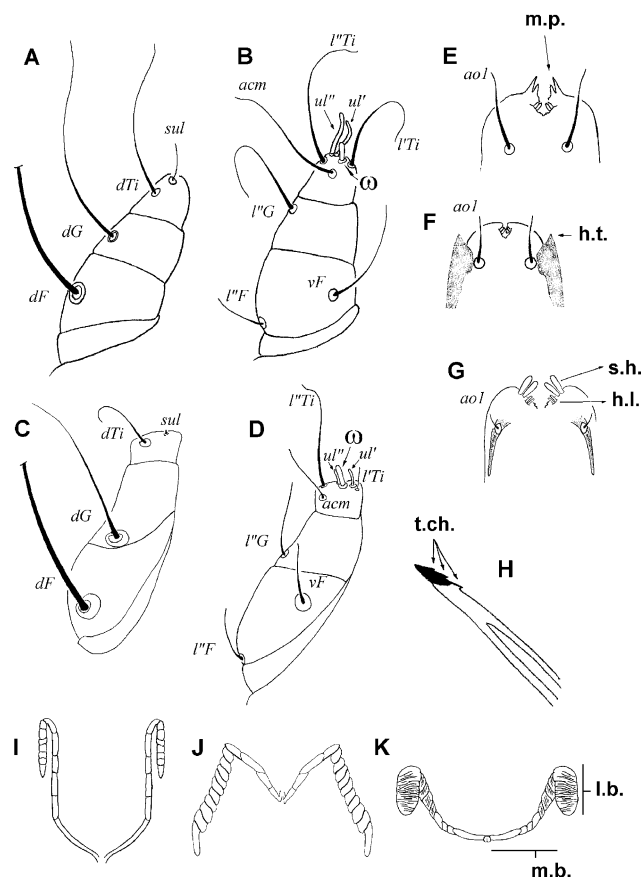


Fig. 5. Details of syringophilid morphology. A, B – palps of Syringophilinae in dorsal and ventral view; C, D – palps of Picobiinae in dorsal and ventral view; E–G – hypostomal apex; H – distal tip of movable cheliceral digit; I–K – peritremes. Abbreviations: m.p. – medial protuberances; h.t. – hypostomal teeth; s.h. – sausage-like hypostomal structures; h.l. – hypostomal lips; t.ch. – teeth of movable cheliceral digit; l.b. – lateral branch of peritremes; m.b. – medial branch of peritremes.

body size (character 79), especially in small sized genera (see Fig. 3). It should be taken into consideration that in the analyses based on the data matrix with the limited set of characters, a particular character can dramatically affect the tree pattern, sometimes uniting phylogenetically distant taxa. For this reason we excluded character 79 (body size) from our data and repeated these analyses. The consensus of re-weighted trees based on this reduced matrix (not shown) had almost the same pattern as the consensus based on the initial matrix. It could be concluded that character 79 does not seriously affect the pattern of the tree but could serve as the distinct morphological character for some generic groups. Thus, at least some of the clades obtained using the re-weighted analysis could represent natural groups, which are just weakly supported by the morphological data. A similar situation is present in the phenetic dendrogram produced by Johnston & Kethley (1973). In that dendrogram, the main generic groups are characterized by body size. At the same time, this character did not determine the pattern of the dendrogram. It should be mentioned, however, that the pattern of the consensus parsimonious tree obtained in

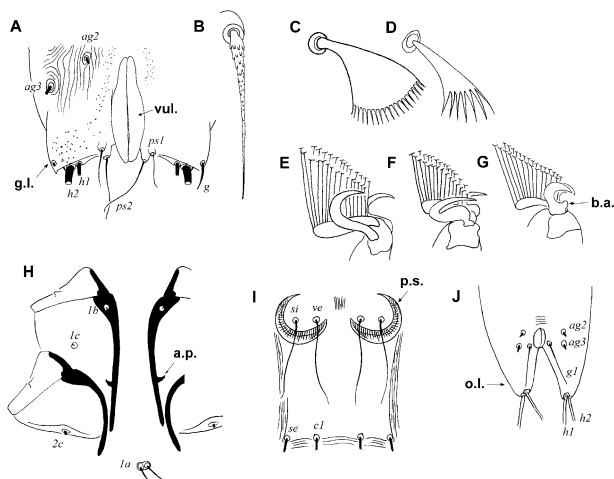


Fig. 6. Details of syringophilid morphology. A – posterior part of opisthosoma in ventral view; B – ornamentation of propodotal setae; C, D – proral setae; E–G – empodium and claws; H – coxal fields and apodemes of legs I and II; I – propodotal shield; J – opisthosoma in ventral view. Abbreviations: vul. – vulva; g.l. – genital lobes; b.a. – basal angle of claw; a.p. – apodeme protuberance; p.s. – pocket-like structures; o.l. – opisthosomal lobes.

this study is absolutely non-congruent with the dendrogram in Johnston & Kethley (1973).

DISCUSSION

It is hypothesized that the cheyletid-like ancestor of syringophilids evolved from micro-predators in the nests (in wide sense) of birds or even theropod dinosaurs, to become parasites in bird quills (Bochkov, 2008, 2009). Originally, the syringophilid ancestors were probably predators on other mites inhabiting wing vanes. Such ecological switches occurred several times in the cheyletids, the closest relatives of syringophilids. The bird nest fauna associated with nidicolous cheyletids is very rich and includes representatives of various genera and tribes (Volgin, 1969). Representatives of two tribes transferred from bird nests into feather quills. Most species of the tribe Cheletosomatini are obligate predators dwelling in wing-quills but mites of one cheletosomatine genus, *Picocheyletus* became parasites in the quills of birds of the family Capitonidae (Piciformes) (Bochkov & O'Connor, 2003). Finally, mites of the genus *Metacheyletia*, the only genus in the tribe Metacheyletiini, are probably also parasites rather than predators in quills of parrots and African passerines (Bochkov & Skoracki, 2011).

Based on the “molecular clock” hypothesis the cheyletids and syringophilids diverged from one another approximately 180–185 million years ago in the Early Jurassic (Dabert et al., 2010). There is no consensus among ornithologists, whether the famous *Archaeopteryx* is a bird (O'Connor & Zhou, 2012; Turner et al., 2012) or not (Mayr et al., 2005; Xu et al., 2011). However, even if *Archaeopteryx* is the earliest bird derivative, it is known only from the Late Jurassic and thus, syringophilids were, probably, already associated with the ancestors of birds –

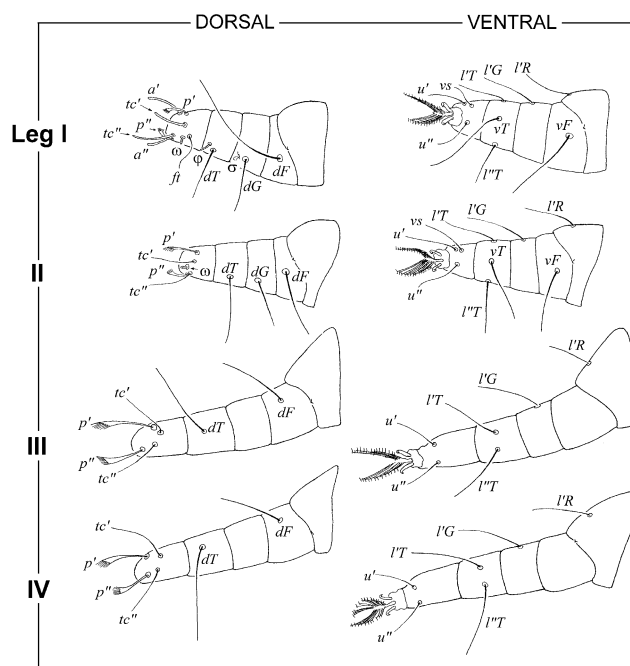


Fig. 7. General scheme of legs I–IV.

theropod dinosaurs, many of which had feathers (Mayr et al., 2005; Xu et al. 2010).

All extant birds (Neornithes) are placed in one of two infraclasses: Palaeognathae (ratites and tinamous) and Neognathae with two cohorts, Galloanserae (landfowl and waterfowl) and Neoaves (other neognaths) (Dyke & Van Tuinen, 2004; Livezey & Zusi, 2007; Mayr, 2008). To date, syringophilids are recorded living on 21 of 34 orders of neognathous and palaeognathous (Tinamiformes) birds (Skoracki, 2011; Skoracki et al., 2012b). These mites are absent on birds of the orders: Caprimulgiformes, Cariamiformes, Coliiformes, Eurypygiformes, Gaviiformes, Falconiformes, Mesitornithiformes, Otidiformes, Phaethoniformes, Podicipediformes, Sphenisciformes, Struthioniformes, and Trogoniformes. Their absence on penguins (Sphenisciformes) is perhaps explainable in terms of the modifications of the feathers of these hosts. Their absence, however, on birds of the other orders is not adequately explored (or not explored at all) and there is a high probability that they are also infected by syringophilids.

Syringophilids are highly host specific. According to recently obtained data (Skoracki et al., 2012b), 70.5% of syringophilid species are monoxenous, 28.4% are associated with hosts of one genus or one family and only 1.1% parasitize birds belonging to distantly related families or orders. The host-parallel evolution of syringophilid species within a particular genus is unknown because of the quite limited number of special molecular coevolutionary studies (Glowska, 2011).

At the generic level the host specificity of syringophilids is less strict but still significant. Thirty nine syringophilid genera (74%) parasitize birds of one order and only 14 genera (26%) are associated with birds of two or even five orders (Fig. 3). Among them, the genera *Peris-*

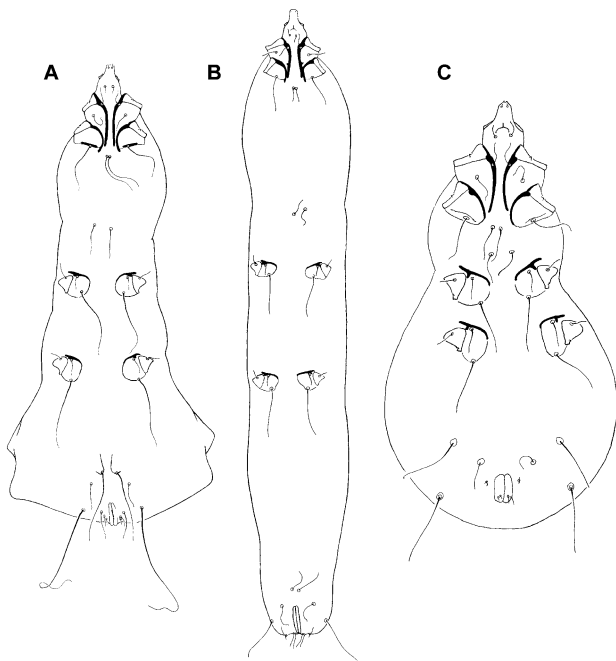


Fig. 8. Types of physogastric female idiosoma. A – bell-shaped; B – vermiform; C – bulb-shaped.

terophila and *Megasyringophilus* provide a typical example of mite transmission from prey species, columbiform or psittaciform birds, to predators of the order Accipitriformes (Fig. 3). Some of these 14 genera, however, are simultaneously associated with birds of the orders Piciformes and Passeriformes or Columbiformes and Psittaciformes. The sister relationships between these host orders are supported by many analyses (Sibley et al., 1988; Johansson & Ericson, 2003; Fain & Houde, 2004; Livezey & Zusi, 2007). Thus, the host associations of such syringophilid genera are explainable in terms of parasitism of their representatives on the common ancestor of these orders. It should be mentioned, however, that some ornithologists consider Passeriformes and Psittaciformes to be sister orders (Ericson et al., 2006; Hackett et al., 2008; Wang et al., 2012) and, thus, these host associations can be also a result of host switches.

The strong incongruence between the phylogenetic pattern of our syringophilid tree (Fig. 3) and the main alternative bird phylogenies (Livezey & Zusi, 2007; Mayr, 2008; Hackett et al., 2008) is clear.

In the syringophilid tree, mites on the earliest derivate branches are associated with birds of the advanced clade Neoaves, whereas genera associated with the earliest derivate clades of extant birds, Tinamiformes (Palaeognathae) and Galloanserae (Anseriformes and Galliformes), are mosaically distributed in the core of the tree. As mentioned above, syringophilids were probably associated with the first birds or even with bird-like dinosaurs. This contradiction between presumable syringophilid parasitism of the common bird ancestor and the phylogenetic pattern obtained could be explained by the multiple switches from hosts of the Neoaves clade to palaeognathous and galloanserae birds, and subsequent co-

speciation. Thus, the hypothesis of Skoracki & Sikora (2004) and Skoracki et al. (2012a) that the initial association of the genus *Tinamiphilopsis* was with Tinamiformes contradicts the currently observed pattern. Following the pattern of the current tree, birds of these ancient host lineages underwent sorting events, lost their ancestral syringophilids or become extinct due to competition with new invaders. The relationships of most syringophilid genera do not agree with the modern views on phylogenetic links between the orders of Neoaves (Ericson et al., 2006; Livezey & Zusi, 2007; Mayr, 2008; Hackett et al., 2008). This incongruence could also be explained by horizontal switches of syringophilid to phylogenetically distant hosts. Kethley & Johnston (1975) consider host switches as the main mode of evolution in this family and even proposed a new term – resource tracking. According to their hypothesis, host distribution of syringophilid species is determined by thickness of the quill wall and ability of mites to pierce it. In the phenogram presented by Johnston & Kethley (1973), as in our tree, groups syringophiline genera based on body size and as in our analysis, the body sizes, although associated with other characters, were not the principal characteristics separating these groups.

In the evolution of syringophilids horizontal transfers between phylogenetically distant hosts were, probably, very important and determined the pattern of the phylogenetic relationships among most of the syringophilid genera. It is likely that host shifts are the main mode of evolution for some parasitic groups, despite the fact that their representatives are strictly host specific (Page, 2003). As a result these parasites demonstrate the partial or total absence of a congruent pattern with their hosts (Dabert et al., 2001; Johnson et al., 2002; Klimov et al., 2007).

In our tree, however, two other evolutionary aspects are also retraced. The first is the distribution of these mites on various types of quills. The wing-feathers, i.e. primaries and secondaries are probably the ancestral type of syringophilid habitat. In comparison, predatory mites of the family Cheyletidae inhabiting quills are associated exclusively with wing-feathers (Bochkov et al., 2002). The majority of the representatives of this family, including the earliest derivate genera, are associated with the vanes of these feathers. In cases of high levels of infection, a few mites may, however, colonize quills of other feathers (greater, lesser and median coverts, scapulars, tail feathers), including even body coverts. Mites of the subfamily Picobiinae mostly dwell in the body covert feathers but probably originally dwelt in wing quills, because representatives of the archaic genus *Calamincola* occupy these microhabitats (Casto, 1977). The picobiines are considerably more morphologically specialized than syringophilines and possess some advanced features like heterosomy, which, probably, allows them to occupy successfully small quills of the body coverts. Thus, picobiines avoided competition with other syringophilids and formed an evolutionary line parallel to the syringo-

philines. Unfortunately, the biodiversity of this group is still poorly studied.

Another evolutionary aspect – the host-parasite parallel evolution is very weakly represented in our phylogenetic tree. Some closely related syringophilid genera, for example, *Creagonycha* + *Kethleyana*, *Neoaulonastus* (*Aulonastus* + *Krantziaulonastus*), *Philoxanthorhea* (*Paraniglarobia* + *Bochkovia*), etc. parasitize hosts belonging to the same order or closely related orders (Fig. 3). The most notable example is the *Psittaciphilus* group, which includes genera mainly associated with psittaciform and columbiform birds (Fig. 3), which some researchers (Sibley et al., 1988; Livezey & Zusi, 2007) suggest as phylogenetically very closely related. Even in the present case, however, there are some cases that violate this “harmonious picture”. Mites of the genus *Neoperisterophila* belonging to this group are associated with passerines and some *Peristerophila* species with Accipitriformes.

In conclusion, we should stress again the weakness of the morphological approach for constructing the phylogeny of syringophilids due to the scanty set of characters available for phylogenetic analysis, along with a high probability of their parallel origin, because apomorphic conditions of many of these characters are represented by reductions. Such “poor” external morphology is probably the response of these mites to relatively stable and uniform conditions in feather quills (Bochkov et al., 2004). We avoid, therefore, making any taxonomic decisions until our data can be compared with a molecular based phylogenetic hypothesis.

CONCLUSION

1. The subfamily Picobiinae is a monophyletic group. 2. The subfamily Syringophilinae is paraphyletic in respect to Picobiinae. 3. The genera associated with psittaciform and columbiform birds (*Castosyringophilus*, *Meting-sunes*, *Peristerophila*, *Psittaciphilus*, and *Terratosyringophilus*) form a monophyletic group. 4. The reconstructed phylogeny of Syringophilidae at the generic level is incongruent with all modern bird phylogenies and allows recognizing only some patches of the parallel evolution with hosts; it suggests that host shifts [resource tracking according to Kethley & Johnston (1975)] and colonization of quill types other than primaries and secondaries played the most important role in the evolution of this mite group.

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APPENDIX 1. Characters used in the analyses (see Figs 4–8).

- Basal part of gnathosoma: not submerged (0), deeply submerged into idiosoma (1). (Fig. 4B).
- Stylophore apodeme: indistinct (0), distinctly developed (1). (Fig. 4A).
- Posterior part of stylophore: rounded (0), strongly constricted (1). (Fig. 4A).
- Projection on posterior end of stylophore: absent (0), present (1). (Fig. 4A).
- Palpal tibia and tarsus: separated (0), fused (1). (Figs 6A–D).
- Claw-like seta on palps: present (0), absent (1). (Figs 6A, C).
- Palpal apex: rounded (0), truncate (1). (Figs 6A, C).
- Projections on hypostomal apex: absent (0), present (1). (Fig. 6E).
- Hypostomal lateral teeth: absent (0), present (1). (Fig. 6F).
- Hypostomal lips: normally developed (0), large sausage-like (1). (Fig. 6G).
- Shape of peritremes: M-shaped (0), U-shaped (1). (Figs 6I–K).
- Distinct borders between chambers in lateral branches of peritremes: present (0), absent (1). (Figs 6J, K).
- Distal tip of movable cheliceral digit: edentate (0), dentate (1). (Fig. 6H).
- Eupathidium *sul* of palpal tarsus: well developed (0), reduced to microseta (1). (Figs 6A, C).
- Adoral setae *ao1* and *ao2*: well developed (0), reduced (not reaching hypostomal apex) (1). (Figs 6E, G).
- Setae on palp tarsus in immature stages: well developed (0), reduced to small spinose structures (1).
- Setae *vi*: present (0), absent (1). (Fig. 4A).
- Position of setae *vi* and *ve*: at same transverse level (0), *vi* anterior to *ve* (1). (Fig. 4A).

19. Position of setae *ve* and *si*: *ve* anterior to *si* (0), at same transverse level (1). (Figs 4A, 5I)
20. Position of setae *cl* and *c2*: *c2* anterior to *cl* (0), at same transverse level (1). (Fig. 4A).
21. Position of setae *cl* and *se*: at same transverse level (0), *se* anterior to *cl* (1). (Fig. 4A).
22. Setae *el*: present (0), absent (1). (Fig. 4A).
23. Position of setae *fl* and *f2*: *fl* close to *f2* (0), *fl* far from *f2* (1). (Fig. 4A).
24. Setae *ps3*: present (0), absent (1). (Fig. 4A).
25. Setae *ps2*: present (0), absent (1). (Fig. 4A).
26. Setae *gl*: present (0), absent (1). (Fig. 4B, 5A).
27. Setae *g2*: present (0), absent (1). (Fig. 4B).
28. Setae *ag3*: present (0), absent (1). (Fig. 4B).
29. Neotrichious aggenital setae: present (0), absent (1). (Fig. 4B).
30. Ornamentation of dorsal setae: absent (0), present (1). (Fig. 5B)
31. Setae on body and legs in immature stages: well developed (0), reduced to small spinose structures (1).
32. Propodonal shield: entire (0), divided into 2 wide fragments (1), divided into 2 narrow fragments (2), shirt-like (3). (Fig. 4A).
33. Pocket-like prodorsal structures: absent (0), present (1). (Fig. 5I).
34. Hysteronotal shield: present (0), absent (1). (Fig. 4A).
35. Shape of hysteronotal shield: entire (0), divided (1). (Fig. 4A).
36. Pygidial shield: present (0), absent (1). (Fig. 4A).
37. Fusion of hysteronotal and pygidial shields: present (0), absent (1). (Fig. 4A).
38. Genital plate: absent (0), present (1). (Fig. 4B).
39. Opisthosoma: moderately developed (0), elongated (1). (Fig. 4A).
40. Opisthosomal lobes: absent (0), present (1). (Fig. 5J).
41. Physogastric females: absent (0), present (1). (Figs 4A, 8A–C).
42. Shape of idiosoma in physogastric females: worm-shaped (0), campanuliform (1), bulb-shaped (2). (Figs 8A–C).
43. Leg thickness: subequal in thickness (0), legs I thicker than legs II–IV (1), legs I–II thicker than legs III–IV (2). (Fig. 4A).
44. Length of legs I and II: legs I longer than II (0), subequal in length (1). (Fig. 4A).
45. Location of coxal fields I–II and III–IV: grouped together (0), widely separated (1). (Fig. 4B).
46. Apodemes I and II: similar in shape (0), different in shape (1). (Figs 4B, 5H).
47. Shape of apodemes I: divergent (0), parallel (1). (Figs 4B, 5H).
48. Degree of apodeme I divergence: strongly divergent (0), slightly divergent (1). (Figs 4B, 5H).
49. Fusion of apodemes I and II: present (0), absent (1), indistinct (2). (Figs 4B, 5H).
50. Thorn-like protuberances of apodemes I: absent (0), present (1). (Fig. 5H).
51. Apodemes III and IV: absent (0), present (1). (Fig. 4B).
52. Shape of claws: moderately curved (0), strongly curved (1), broadly open (2). (Figs 5E–G).
53. Size of antaxial and paraxial members of tarsal pairs of claws: equal (0), unequal (1). (Figs 5E–G).
54. Basal angle of tarsal claws: absent (0), present (1). (Figs 5E–G).
55. Coalescence of setae *la*–*la*: absent (0), present (1). (Fig. 5H).
56. Position of setae *3a* and *3b*: at same transverse level (0), setae *3a* anterior to *3b* (1). (Fig. 4B).
57. Setae *4a*: present (0), absent (1). (Fig. 4B).
58. Setae *a'* of tarsus I: present (0), absent (1). (Fig. 7).
59. Setae *vs* of tarsus I: present (0), absent (1). (Fig. 7).
60. Setae *vs* of tarsus II: present (0), absent (1). (Fig. 7).
61. Setae *vs* of tarsus III: present (0), absent (1). (Fig. 7).
62. Setae *vs* of tarsus IV: present (0), absent (1). (Fig. 7).
63. Setae *p'* and *p''* of tarsi I–IV: rod-like (0), fan-like (1). (Fig. 7).
64. Shape of setae *p'* and *p''* on tarsi I–IV: with 4–15 long tines (0), multiserrate with about 20–30 short tines (1). (Figs 5C, D)
65. Setae *dT* of tibia III: present (0), absent (1). (Fig. 7).
66. Setae *dT* of tibia IV: present (0), absent (1). (Fig. 7).
67. Solenidion *phi* of tibia I: present (0), absent (1). (Fig. 7).
68. Setae *dG* of genu II: present (0), absent (1). (Fig. 7).
69. Setae *dG* of genu IV: present (0), absent (1). (Fig. 7).
70. Setae *l'G* of genu IV: present (0), absent (1). (Fig. 7).
71. Setae *dF* of femur II: present (0), absent (1). (Fig. 7).
72. Setae *vF* on femur III: present (0), absent (1). (Fig. 7).
73. Setae *dF* on femur III: present (0), absent (1). (Fig. 7).
74. Position of setae *dF* of femur III: dorsal (0), ventral (1). (Fig. 7).
75. Setae *dF* of femur IV: present (0), absent (1). (Fig. 7).
76. Setae *l'R* of trochanter I: present (0), absent (1). (Fig. 7).
77. Setae *l'R* of trochanter II: present (0), absent (1). (Fig. 7).
78. Setae *v* of trochanter III: present (0), absent (1). (Fig. 7).
79. Body size: small: 400–893 µm (0), medium 894–1387 µm (1), large 1388–1881 µm (2).