

Phylogeny of the feather mite family Ptiloxenidae GAUD, 1982 (Acari: Pterolichoidea)

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Abstract: A morphological analysis of all species of feather mite family Ptiloxenidae was carried out. The phylogenetic analysis was performed on 64 characters using *Cheylabis latus* (Cheylabididae) and *Grenieria simplex* (Syringobiidae) as outgroups. It generated a single most parsimonious tree of 168 steps and CI = 0.821. Ptiloxenidae consists of two clusters; the first creates genera *Ptiloxenus*, *Ptiloxenoides* and *Schizurolichus*, the second one only the genus *Sokoloviana*. Existence of the genus *Schizurolichus* is not supported and it should be synonymised with *Ptiloxenus*. Comparison of the tree obtained with the phylogeny reconstruction of birds (SIBLEY & AHLQUIST 1990) suggests a general cospeciationary tracking of bird speciation by mites as a main evolutionary factor of Ptiloxenidae. On the other hand, the host-parasite relationships between lapwings (*Vanellus*, Charadriidae) and their *Sokoloviana* species seem to be better correlated with the geographical region than with the speciation course of hosts.

Introduction

Feather mites are highly specialised and permanent ectoparasites or parasites living exclusively on/in feathers or skin of birds. They are the most frequent part of the parasitofauna of birds which consists of about 2,000 described species belonging to over 440 genera and 33 families (GAUD & ATYEO 1996). Besides the taxonomic and morphologic studies, recently more interest is focused on the reconstructing of the feather mites phylogeny course and on comparing the results with the host phylogenetic (MOSS et al. 1977; MIRONOV 1991; DABERT & EHRNSBERGER 1995; MIRONOV & DABERT in prep.)

In the present paper, we made a detailed morphological analysis of the mites of the family Ptiloxenidae (Fig. 1). We reconstructed the phylogenetic relationships between all species of the family (cladistic analysis) and compared this hypothesis with the phylogeny and geographical distribution of the hosts. We tested some avian phylogenetic hypotheses using the phylogeny reconstructions of their ptiloxenid mites.

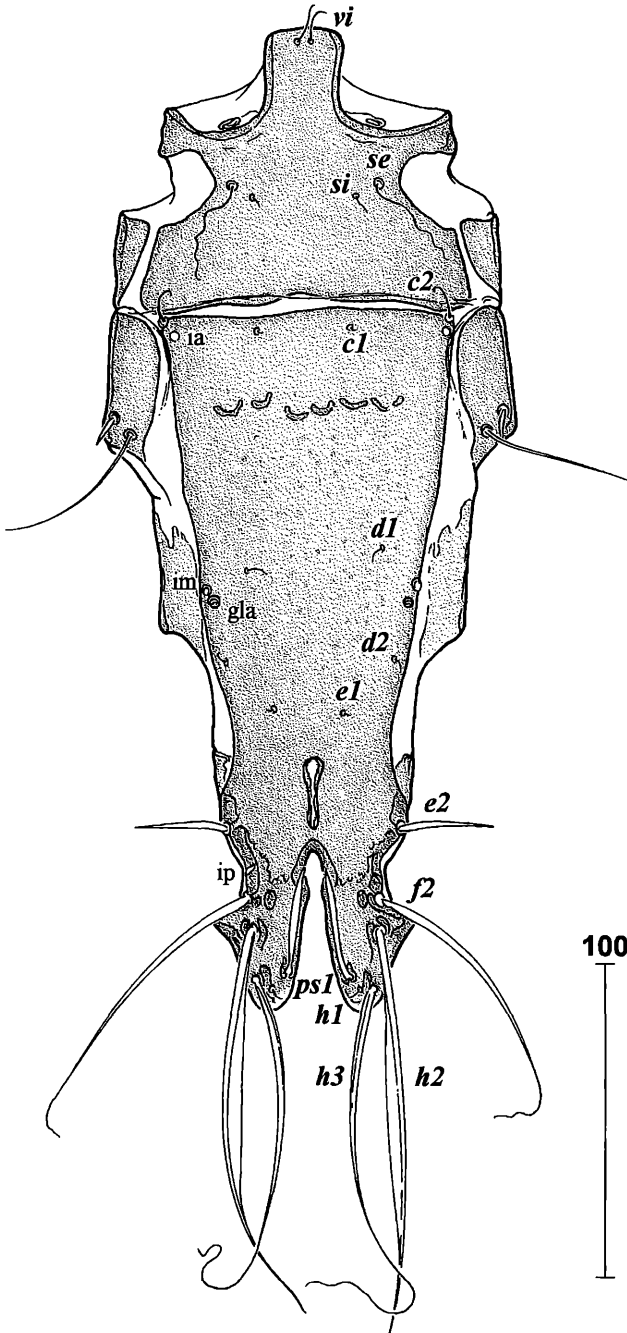


Fig. 1a: *Sokoloviana cornuta* DABERT & EHRNSBERGER, 1996, a member of the family Ptiloxenidae GAUD, 1982 (from DABERT & EHRNSBERGER 1996). Dorsal views of the male. Designations of the setae follow GRIFFITHS et al. 1990.

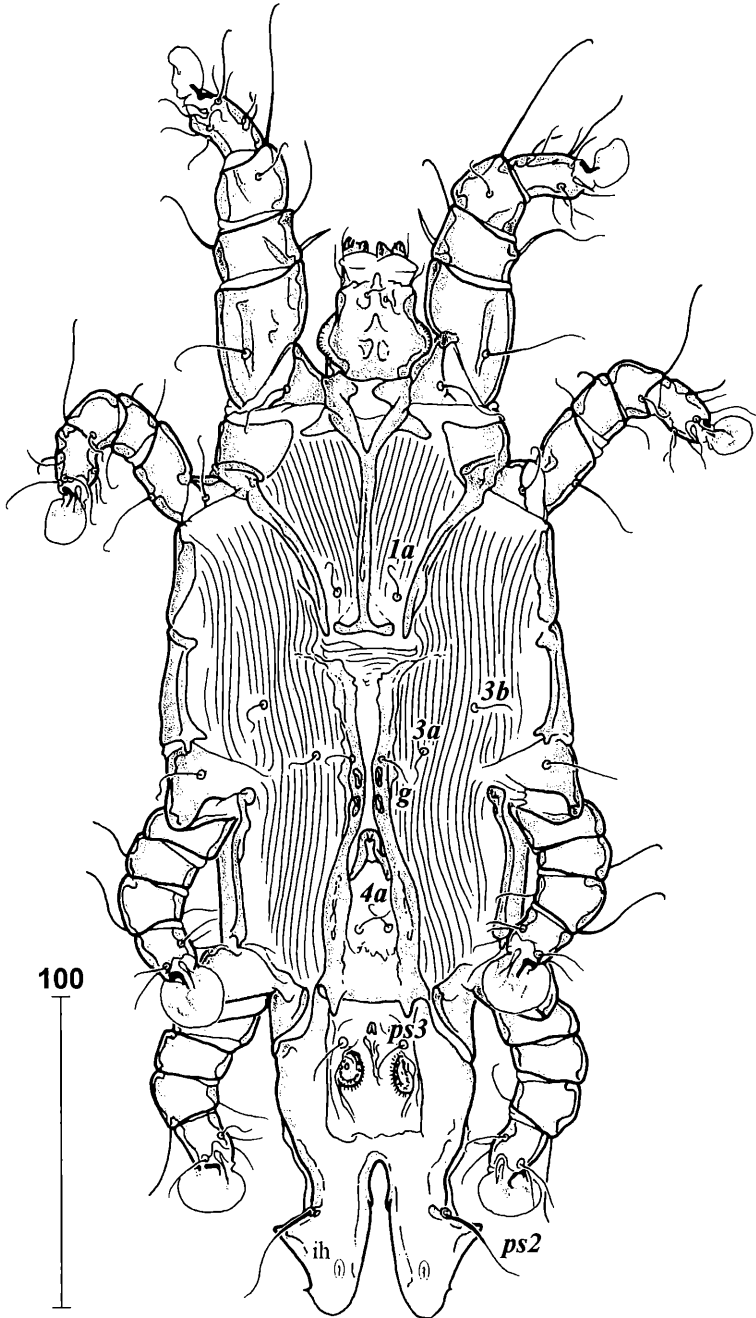


Fig. 1b: *Sokoloviana cornuta* DABERT & EHRNSBERGER, 1996, a member of the family Ptiloxenidae GAUD, 1982 (from DABERT & EHRNSBERGER 1996). Ventral views of the male. Designations of the setae follow GRIFFITHS et al. 1990.

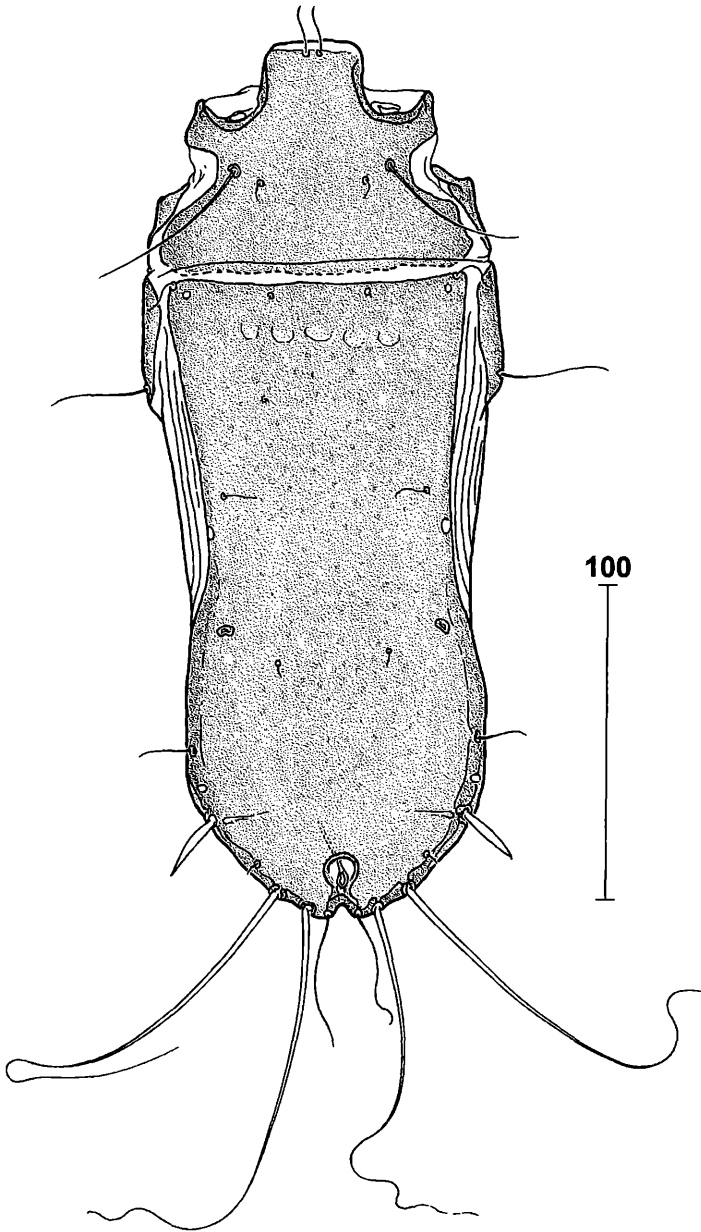


Fig. 1c: *Sokoloviana cornuta* DABERT & EHRNSBERGER, 1996, a member of the family Ptiloxenidae GAUD, 1982 (from DABERT & EHRNSBERGER 1996). Dorsal views of the female. Designations of the setae follow GRIFFITHS et al. 1990.

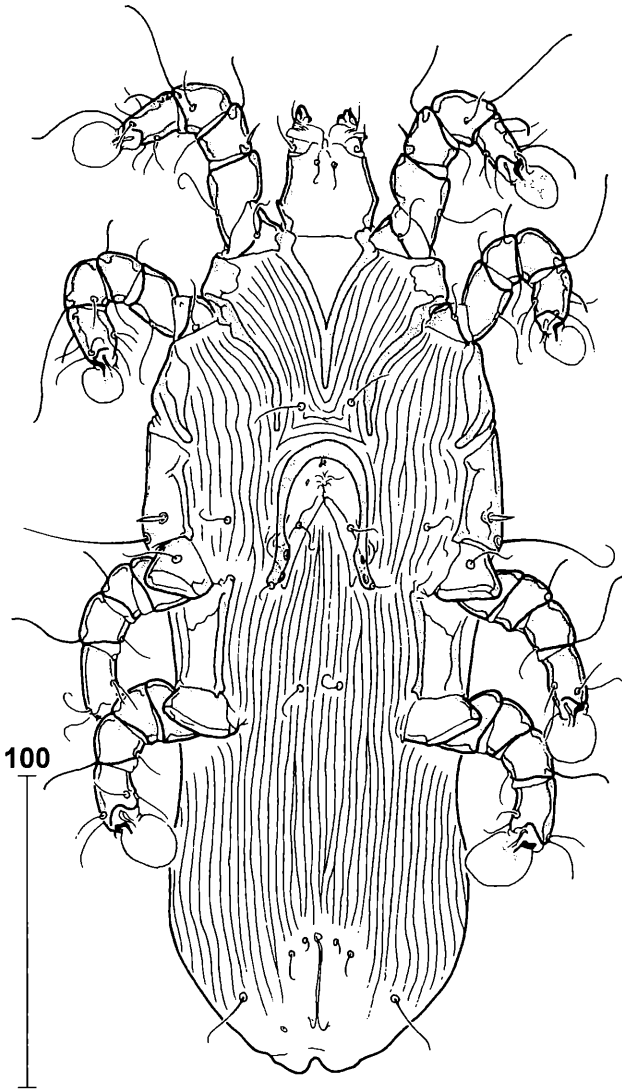


Fig. 1d: *Sokoloviana cornuta* DABERT & EHRNSBERGER, 1996, a member of the family Ptiloxenidae GAUD, 1982 (from DABERT & EHRNSBERGER 1996. Ventral views of the female. Designations of the setae follow GRIFFITHS et al. 1990.

The feather mite family Ptiloxenidae was established by GAUD (1982) for four genera: *Ptiloxenus* HULL, 1934, *Ptiloxenoides* GAUD, 1982, *Sokoloviana* DUBININ, 1951 and *Schizurolichus* CERNÝ, 1969. He defined this family by the elongated body shape, strong sclerotised dorsal shields, Y-shaped sternum, complete body and leg chaetotaxy (in females also setae ad present), setae si set posteriorly to se. GAUD & ATYEO (1996) have added to this characteristic: coxal fields without shield, setae c3 blade-like, well developed epigyna of females, large adanal discs with multidentate corollas in males, opisthosomal lobes in males. They pointed out the resemblance or even the close relationship with the quills inhabiting mites of the family Syringobiidae. Both families possess similar general body shape, dorsal sclerotisation, chaetotaxy, situation of scapular setae and form of ambulacrum.

Material and methods

Cladistic analysis was conducted by software PAUP 3.0 (SWOFFORD 1991), using branch-and-bound algorithm. Plesiomorph states are designated as “0”. Characters coded as having multiple states should be interpreted as polymorph. All binary characters were treated as ordered, multistate as unordered. An equal weight one was given to all characters. DELTRAN optimization method was used (parallelisms more possible than reversals). The constraints option of PAUP was used for testing the alternative topology hypotheses against the most parsimonious tree. The bootstrap analysis was performed for testing the robustness of obtained phylogeny reconstruction. The tree was rooted using outgroups method with outgroups treated as being paraphyletic.

All known species of the Ptiloxenidae and two outgroups were analysed (Tab. 1). *Grenieria simplex* was chosen as the representative of the family Syringobiidae which is probably a sister group for the Ptiloxenidae. The second very distinct outgroup was *Cheylabis latus* (Cheylabidae). We were far from recognising this mite as the real ancestral form. It resembles, even if seemingly, the very archaic pterolichoid morphotype. On the other hand, it possesses some highly specialised structures, e. g. form of genital system. We decided to use it in the outgroup analysis in order to avoid construction of a hypothetical ancestor. Moreover, this undoubtedly distant taxon was required in aiding the character polarisation establishing by syringobiid outgroup. Syringobiidae – although being a very close outgroup to Ptiloxenidae – are highly modified due to a shifting to completely different microhabitats. Living in the quills forced some adaptations which may be secondarily reductive and can be falsely recognised as plesiomorphic.

Mite species	Host species	Sample source
Outgroups:		
<i>Cheylabis latus</i> Cheylabidiidae	<i>Eianus caeruleus</i>	Uganda (UGA)
<i>Grenieria simplex</i> Syringobiidae	<i>Chlidonias nigra</i> <i>Sterna hirundo</i> <i>Sterna repressa</i> <i>Sterna forsteri</i> <i>Sterna albifrons</i>	Poland (UAM), Michigan, USA (UMMZ) E USA (BMOC) Egypt (UMMZ) Mexico (NU) South Africa (UAM)
Ingroup: Ptiloxenidae		
<i>Ptiloxenoides phoenicopteri</i>	<i>Phoeniconaias minor</i> <i>Phoenicopterus ruber</i> <i>Pelecanus occidentalis urinator</i> (NEW HOST)	Kenya (UGA) Italy, Egypt, Galapagos Islands (UGA) Galapagos Islands (UGA)
<i>Ptiloxenus colymbi</i>	<i>Tachybaptus ruficollis</i>	Germany (UAM), Africa (NU)
<i>Ptiloxenus major</i>	<i>Podiceps cristatus</i> <i>Rollandia rolland</i> (NEW HOST) <i>Podiceps occipitalis</i> (NEW HOST)	Germany (UAM) Paraguay (NU) Argentina (NU)
<i>Schizurolichus elegans</i>	<i>Podiceps dominicus</i>	Cuba, Venezuela, Paraguay (NU)
<i>Sokoloviana cornuta</i>	<i>Cladorhynchus leucocephalus</i>	Australia (UMMZ)
<i>Sokoloviana ibidorhynchae</i>	<i>Ibidorhyncha strutersi</i>	China (UGA, AMNH, UAM)
<i>Sokoloviana chilensis</i>	<i>Vanellus chilensis</i>	Argentina, Paraguay (UMMZ) Colombia (NU, USNM)
<i>Sokoloviana vanelli</i>	<i>Vanellus indicus atronuchalis</i> <i>Vanellus miles miles</i> <i>Vanellus miles novaehollandiae</i> (= <i>V. lobatus</i>) <i>Vanellus duvaucelli</i> <i>Vanellus tricolor</i> <i>Vanellus cinereus</i>	Vietnam (USNM, NU, AMNH) Australia (UGA, USNM) Australia (UGA, USNM) India, Malaysia (NU, USNM) Java (NU, USNM) China, Japan (NU, USNM)
<i>Sokoloviana allocerca</i>	<i>Vanellus crassirostris leucoptera</i> <i>Vanellus senegallus</i>	Sudan (NU, USNM) Sudan (NU, USNM)
<i>Sokoloviana gracilis</i>	<i>Himantopus himantopus</i> <i>Himantopus ceylonensis</i> <i>Himantopus leucocephalus</i> <i>Himantopus melanurus</i> <i>Himantopus meridionalis</i> <i>Himantopus mexicanus</i> <i>Himantopus novaehollandiae</i>	Egypt (UMMZ) Ceylon (NU, USNM) Celebes (NU, USNM) Argentina (NU, USNM) Mozambique (NU, USNM) Florida, USA (NU, USNM) New Zealand (UMMZ)
<i>Sokoloviana kucheruki</i>	<i>Charadrius vociferus</i>	Nebraska, USA (NU) Haiti, Puerto Rico (NU, USNM)
<i>Sokoloviana leptosoma</i>	<i>Vanellus albiceps</i>	Mozambique (UMMZ)
<i>Sokoloviana mariae</i>	<i>Recurvirostra avosetta</i> <i>Recurvirostra novaehollandiae</i> <i>Recurvirostra americana</i> <i>Recurvirostra andina</i>	Western Siberia, Russia (ZISP) SW Africa (NU, USNM) NW Australia (UGA, AMNH) Mexico (NU, USNM) no data (UGA, AMNH)
<i>Sokoloviana pavlovskiyi</i>	<i>Charadrius semipalmatus</i>	no material examined
<i>Sokoloviana rehbergi</i>	<i>Haematopus ostralegus</i> <i>Haematopus bachmani</i> <i>Haematopus leucopodus</i> <i>Haematopus moquini</i>	Germany (UAM) Alaska, USA (BMOC) Falkland Islands (USNM) SW Africa (NU, SAIMR)
<i>Sokoloviana tropica</i>	<i>Haematopus ater</i> <i>Haematopus palliatus</i>	Falkland Islands (ZISP) Peru (NU, USNM) Texas, USA (NU)
<i>Sokoloviana zumpti</i>	<i>Vanellus coronatus</i>	Africa (NU, USNM)

Tab. 1 Mite material data analysed in the present study. Abbreviations used see text. We have failed to obtain the material of *Sokoloviana pavlovskiyi*; literature data were used.

The bird phylogeny reconstruction made by SIBLEY & AHLQUIST (1990) was used to prove a comparison to the mites phylogeny scheme. This widely criticised work (e. g. KRAJEWSKI 1991; O'HARA 1991; RAIKOW 1991; LANYON 1992) is probably not a perfect estimation, especially on the low taxonomic levels, but it is the only comprehensive bird phylogeny reconstruction. Using it simultaneously with other more detailed phylogenies published (e. g. CHU 1995 for Charadriiformes) it should be quite reliable for supraspecific levels (see BLEIWEISS et al. 1995). We used the data of BOCK (1958) for discussing the distribution of the ptiloxenid mites on lapwings.

All microscopic observations were undertaken by light microscope Olympus BHS with Nomarsky interference contrast. The chaetotaxy nomenclature follows GRIFFITHS et al. (1990).

Abbreviations used: AMNH – American Museum of Natural History, New York, USA; BMOG – collection of B. M. OCONNOR, University of Michigan, Ann Arbor, USA; NU – University of Nebraska, USA; SAIMR – South African Institute for Medical Research, Johannesburg, South Africa; UAM – Adam Mickiewicz University, Poznan, Poland; UMMZ – Museum of Zoology, University of Michigan, Ann Arbor, USA; USNM – US National Museum of Natural History, Washington, USA; UGA – University of Georgia, Athens, USA; ZISP – Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.

Results

Character argumentation

A character argumentation of morphological analysis of the mite family Ptiloxenidae is briefly presented below. We used 64 morphological characters of imaginal stages (datamatrix in Appendix). We were unable to analyse potentially informative characters of immature stages due to absence of larvae and nymphs in the majority of available study material. Most of the characters described here were figured in DABERT & EHRNSBERGER (1996).

General body morphology

1. Sexual dimorphism

A pronounced sexual dimorphism is very often in feather mites in comparison to free-living Astigmata although in some not highly specialised forms the external differences between sexes are poorly expressed. Sexual dimorphism is very distinct in Ptiloxenidae in comparison to both outgroups. It is

most probably a secondary simplification in the case of *Grenieria simplex*; most Syringobiidae males differ strongly from females.

Character states: 0 – poorly expressed, 1 – very distinct.

2. Male polymorphism

The only polymorphic males are present in the genus *Schizurolichus*. Homomorphic males possess symmetrical opisthosomal lobes and setae e2 as macrochaetae. In heteromorphic males one of the lobes is wider than the second one and has reduced interlobar membrane. Also setae e2 are lanceolate.

Character states: 0 – absent, 1 – present.

3. Shape of sternum of males

Fusion of epimeres I into V- or Y-shaped sternum is often interpreted as adaptive reinforcement of the body due to living in the difficult conditions of vane surface. Indeed, the most modified vane inhabitants possess fused sternum. The presence of a sternum in the quill inhabiting outgroup Syringobiidae – among many other characteristics – points out the primarily external way of living of these mites. Ptiloxenidae being typical vane mites own a well-developed sternum. Especially mites of the genus *Sokoloviana* have a strong sternum with a long fused part.

Character states: 0 – epimeres I free, 1 – Y-shaped with short terminal part, 2 – Y-shaped with long terminal part.

4. Additional shields of sternum

The strong Sclerotisation of coxal fields, especially in advanced species, is common in the outgroup Syringobiidae. Additional shields on the propodosoma ventrum are rather poorly developed in Ptiloxenidae. Nevertheless, small shields varying in shapes well define some species groups in the genus *Sokoloviana*.

Character states: 0 – absent, 1 – shield between branches, 2 – terminal shield, 3 – shield between branches and terminal shield, 4 – external shields, 5 – external and terminal shields.

5. Bases of anterior epimeres

Hardly sclerotised and thickened bases of propodosomal epimeres are present in some pterolichoid and freyanoid mites. Probably this feature originated independently several times and could be treated as apomorphy (*Cheylabis latus*).

Character states: 0 – normal, 1 – very thick.

6. Sclerotisation of pronotum

Pronotum is uniformly shaped among Ptiloxenidae; it is completely covered by a big pronotal shield. In the outgroup Syringobiidae the pronotal shield has a well defined antero-medial part and is often variously sculptured (*Grenieria*).

Character states: 0 – poorly sclerotised, 1 – totally covered by uniform shield, 2 – totally covered by shield with sculptured antero-medial part.

7. Sclerotisation of male hysteronotum

Ptiloxenidae being advanced vane inhabitants always possess a well-developed, uniformly shaped hysteronotal shield. The shield has a narrow pygidial crevice in the genus *Ptiloxenus*. Dorsal sclerotisation may be variously reduced in the outgroup Syringobiidae.

Character states: 0 – some poorly developed shields, 1 – medial hysteronotal shield present, 2 – hysteronotum sclerotised with pygidial crevice, 3 – whole hysteronotum sclerotised.

8. Sculpture of hysteronotal shield in males

Hysteronotum in Ptiloxenidae is rather poorly sculptured. It is usually uniformly dotted or covered by a very fine net-like pattern (all *Sokoloviana* species from Charadriidae). Other sculpture is rare.

Character states: 0 – dotted, 1 – many small rounded lacunas, 2 – fine net-like pattern, 3 – striated.

9. Anterior hysteronotal apodemes in males

Anterior hysteronotal apodemes occur in some feather mites, especially in males. We suppose that these endocuticular processes serve as attachments for intertergal muscles (see EVANS 1992). In several species of Ptiloxenidae, these structures own a shape of several highly sclerotised transversal sclerites at the anterior margin of hysteronotal shield. There is a row of rounded lacunas in this place in *Sokoloviana rehbergi*.

Character states: 0 – absent, 1 – several pairs, 2 – one pair, 3 – clear lacunas.

10. Sclerotisation of opisthonotum in females

Strongly sclerotised opisthonotum is present in some pterolichoid mites. The strong sclerotisation of the dorsal opisthosoma is also present in Ptiloxenidae.

Character states: 0 – none, 1 – covered by shield with strongly sclerotised posterior half and lateral borders, 2 – covered by shield with strongly sclerotised lateral borders only.

11. Opisthoventral sclerites in males

Opisthoventral sclerites are formed by lateral margins of hysteronotal shield bent on the ventral opisthosoma. They are big in well-sclerotised mites and minute or absent in weakly sclerotised ones. Both *Grenieria* (and other Syringobiidae) and Ptiloxenidae possess well-developed opisthoventral sclerites. The triangle hooks on the medial margins of opisthoventral sclerites are an autapomorphy of *Ptiloxenoides phoenicopteri*.

Character states: 0 – small, 1 – big, 2 – big with medial hooks.

12. Supranal concavity in males

Supranal concavity is a weakly sclerotised, and often surrounded by a cuticular wall, small area lying anteriorly to terminal cleft. It originated probably by partial fusion of medial edges of opisthosomal lobes. All males of the family Ptiloxenidae possess a supranal concavity. In the genera *Ptiloxenus*, *Ptiloxenoides* and *Schizurolichus* this structure is more reduced than in *Sokoloviana* and often replaced by a small longitudinal sclerite. It is variously shaped and may well define species groups.

Character states: 0 – absent, 1 – narrow slit separated from terminal cleft, 2 – narrow slit fused with terminal cleft, 3 – reduced (remnant sclerite), 4 – elongated oval fused with cleft by narrow sclerite, 5 – small, rounded separated from terminal cleft.

13. Opisthosomal lobes in males

Opisthosomal lobes are very common in males of various feather mites families. They primarily serve as structures improving the fixing ability to tritonymphs and females during precopulatory guarding and copulation. Males' lobes, similarly as in females, can improve the aerodynamic properties of mite. The form of the lobes well characterises the genera or species groups among Ptiloxenidae. The absence of the lobes in *Grenieria* and many other Syringobiidae should probably be interpreted as a reversion due the shifting into the quills.

Character states: 0 – absent, 1 – short, triangle, 2 – long, parallel-sided, 3 – long, bent, 4 – short, tongue-like.

14. Translobar sclerites in males

Transverse sclerotised bands on opisthosomal lobes of males are a common synapomorphy for the whole family. The complete sclerotisation of the ventral side of the lobes in *Sokoloviana cornuta* is an autapomorphy.

Character states: 0 – absent, 1 – present, 2 – whole ventrum of lobes sclerotised.

15. Cribrum

Cribrum is a variously shaped, perforated cuticular structure lying on the dorsal surface of each male's opisthosomal lobes and mainly surrounded by thickened margins. The function of the cribrum is unknown. It is best developed in the genus *Sokoloviana* and can be ellipsoid, round, or slit-like. *Ptiloxenus major* and *Schizurolichus elegans* possess similar structures which are probably homologous to those of *Sokoloviana*. These structures are poorly developed and convex in *Schizurolichus* and *Ptiloxenus* (vs. concave in *Sokoloviana*).

Character states: 0 – absent, 1 – small, rounded, 2 – slit-shaped, 3 – big, elongated, 4 – big, ovoid, 5 – remnant.

16. Lateral horn on lobes in males

A very big triangle lateral horn on opisthosomal lobes is present in *Sokoloviana cornuta*. In *Ptiloxenus colymbi* there is a very small lateral spine at the base of setae h2.

Character states: 0 – absent, 1 – very small at the base of h2, 2 – very big, triangle.

17. Medial thorns on lobes in males

Medial thorns on opisthosomal lobes are the autapomorphy of *Ptiloxenoides phoenicopteri*.

Character states: 0 – absent, 1 – present.

18. Lateral membranes of lobes in males

Some males of the family Ptiloxenidae own variously shaped lateral membranes on lobes. It is difficult to show a specific pattern in presence and shape of these structure among particular taxa. Generally, *Sokoloviana* possesses better developed lateral membranes than *Ptiloxenus*, *Ptiloxenoides* and *Schizurolichus*.

Character states: 0 – absent, 1 – narrow as enlargement of postlobar membrane, 2 – rectangle, two-partial, 3 – narrow, rounded, 4 – narrow, doubled, rounded, 5 – acute terminally, two-partial.

19. Interlobar membranes in males

Interlobar membranes are present in the genera *Ptiloxenus* and *Schizurolichus* only.

Character states: 0 – absent, 1 – from base of terminal cleft to setae ps1, 2 – along whole lobes.

20. Postlobar membranes of males

It seems that small postlobar membranes with asymmetrically extended internal margins are the common synapomorphy of the whole family Ptiloxenidae. This general shape is modified in a few cases, mainly as autapomorphies.

Character states: 0 – absent, 1 – tongue-shaped with internal extension, 2 – big, lamelliform, 3 – tongue-shaped with external tooth, 4 – tongue shaped, symmetrical.

21. Opisthosomal lobes in females

Presence of opisthosomal lobes in females is rarer than in males. These structures are generally better developed in ptiloxenid mites inhabiting grebes (Podicipediformes) and flamingoes (Phoenicopteriformes). In *Sokoloviana*, there exists a shallower or deeper terminal cleft on the opisthosoma terminus. Distinct “lobes“ present in species inhabiting lapwings (Vanellinae) are in reality membranes being a different character (see No. 23).

Character states: 0 – absent, 1 – small with shallow terminal cleft, 2 – long with big terminal cleft.

22. Lateral and interlobar membranes in females

These structures are present in females having distinct opisthosomal lobes: *Ptiloxenus colymbi* and *Schizurolichus elegans*.

Character states: 0 – absent, 1 – present.

23. Terminal membranes in females

Membranous outgrowths of female opisthosoma are present in some ptiloxenid mites. Females of the genera *Ptiloxenus* and *Schizurolichus* own rounded terminal (postlobar) membranes. All females of the genus *Sokoloviana* inhabiting lapwings have distinct membranes with a small terminal tooth.

Character states: 0 – absent, 1 – rounded, 2 – with terminal tooth.

24. Paired ventral shields on opisthosoma terminus in females

Some females of the genus *Sokoloviana* possess on the terminal opisthosoma a pair of small shields on the sides of the terminal cleft.

Character states: 0 – absent, 1 – present.

25. Margins of legs segments

Changes of these character states are often connected with changes of character No. 5. Highly thickened dorsal and ventral margins of podomeres are apomorphic (*Cheylabis latus*).

Character states: 0 – normal, 1 – very wide.

26. Tibiotarsal torsion of legs IV in males

The common synapomorphy of the genera *Ptiloxenus* and *Schizurolichus* is the 90 degree counterclockwise tibiotarsal torsion on legs IV in males.

Character states: 0 – absent, 1 – present.

27. Tarsal apophyses in males

Ptiloxenidae have poorly developed leg apophyses. A great variety of apophyses, especially on posterior legs, is present in the closely related family Syringobiidae. In Ptiloxenidae, only males of the genera *Ptiloxenus* and *Schizurolichus* possess distinct apical hooks on tarsi IV.

Character states: 0 – absent, 1 – all legs with apico-ventral tarsal apophyses, 2 – legs IV with dorsal tarsal apophyse.

28. Ambulacrum

Ambulacrum (pretarsus) is one of the most distinctive features in feather mites. Very often it has a form of a variously shaped membranous disc with some specifically formed sclerites. Mites of the outgroup *Cheylabis latus* have a big and rounded central sclerite. Central sclerite is hexagonal with big anterior rounded appendix (remnant of claw) in the outgroup *Grenieria* (and other Syringobiidae) and the family Ptiloxenidae.

Character states: 0 – central sclerite round, 1 – central sclerite hexagonal with anterior big “claw“ part.

Genito-anal region

29. Aedeagus

Aedeagus is poorly or very poorly developed in mites analysed here. The shortest aedeagus has *Cheylabis latus* – a cuticular ring with diameter bigger than the length. The second outgroup *Grenieria* possesses a relatively well-developed aedeagus which is as long as the phalobases. Ptiloxenidae have very short, needle-like aedeagus.

Character states: 0 – shorter than wide, 1 – longer than wide, 2 – three or four times longer than wide, 3 – as long as phalobases.

30. Situation of genital organ in males

Male genital organ is set primarily between bases of posterior legs. In some astigmatid mites, especially in feather mites, this structure can be shifted anteriorly (e. g. Thoracosathesidae) or posteriorly (e. g. Gabuciniidae). We consider the terminal shifting of the aedeagus in *Cheylabis latus* as an apomorphy.

Character states: 0 – between bases of legs, 1 – terminally.

31. Epiandrum

Presence of half-moon-shaped sclerite connected with genital organ of males is a synapomorphy of the genus *Grenieria*.

Character states: 0 – absent, 1 – present.

32. Paragenital sclerites in males

Paragenital sclerites on sides of genital organ are probably a synapomorphy of Ptiloxenidae and the outgroup *Grenieria* (whole Syringobiidae). In both families, these structures can be very variously modified and their shape is the most polymorphic character analysed here. Generally the simplest, free sclerites have *Sokoloviana* species from lapwings and to the genera *Ptiloxenus* and *Schizurolichus*. The most complex big and fused paragenital sclerites occur in *gracilis* species group.

Character states: 0 – absent, 1 – free, short, 2 – free, elongated posteriorly, fused with opisthoventral sclerites, 3 – free, elongated anteriorly, 4 – fused posteriorly, highly elongated, 5 – fused anteriorly and posteriorly, highly elongated, 6 – short, fused posteriorly, 7 – free with medial extensions posteriorly.

33. Supranal concavity in females

Although named as in males the supranal concavity of females has probably different origin. It is always connected with the terminal end of the inseminatory canal. Supranal concavity is frequent in feather mites including the whole family Ptiloxenidae. Usually, it is separated from the terminal cleft although sometimes it can be incorporated into the cleft.

Character states: 0 – absent, 1 – circular, incorporated into terminal cleft, 2 – circular, separated from terminal cleft.

34. Genital opening in females

Dorsal situation of genital opening is probably plesiomorphic in feather mites. All females of Ptiloxenidae own dorso-terminal genital openings (with the exception of *Ptiloxenus major* – a probable reversy).

Character states: 0 – dorsal, 1 – terminal.

35. Inseminatory canal in females

Membranous and short inseminatory canal is a plesiomorph state. In many feather mites (including Ptiloxenidae) this duct is well-sclerotised and easily visible after maceration. Spermduct is heavily sclerotised and unusually long in the outgroup *Cheylabis latus* (autapomorphy).

Character states: 0 – short, membranous, 1 – short, sclerotised, 2 – very long, sclerotised.

36. Intraspermathecal tube in females

The inseminatory canal can enter the interior of receptaculum seminis. This part (intraspermathecal tube) may distinctly differ in shape from the remaining part of inseminatory canal. Neither Ptiloxenidae nor the outgroup *Grenieria* (whole Syringobiidae) possess the intraspermathecal tube. In *Cheylabis latus*, this structure is very well-developed as a long, trumpeted-shaped structure with thick walls.

Character states: 0 – absent, 1 – big, trumpet-shaped.

37. Ductus conjunctivus

The short efferent parts of paired oviducts coming from the receptaculum seminis are often specifically shaped and strongly sclerotised. *Cheylabis latus* has a modified, big and mace-like ductus conjunctivus. These structures are long and tubular in *Grenieria simplex*. Somewhat similar are ductus conjunctivi in all Ptiloxenidae but considerably shorter.

Character states: 0 – absent, 1 – mace-like, 2 – long, tubular, 3 – short, cylindrical or trumpet-like.

38. Epigynum

Epigynum or pregenital sclerite is very common in feather mites. Its absence or weak development is considered rather as secondary reduction (*Grenieria simplex*). Females of the family Ptiloxenidae possess a well-developed, horse-shoe-shaped epigynum. Branches of epigynum are reduced in *Ptiloxenus colymbi* and *Schizurolichus elegans* (remnants are visible).

Character states: 0 – flat, 1 – horse-shoe-shaped, 2 – reduced to small spot, 3 – semicircular.

39. Shape of paragynal sclerites in females

Shape of the paragynal sclerites well define all three mite groups investigated. Simple, inverted V-shaped sclerites are possessed by the outgroup *Cheylabis latus* (plesiomorphy). In the outgroup *Grenieria simplex* sclerites are parallel-sided. All mites of the family Ptiloxenidae own inverted V-shaped sclerites with elongated, bent forwards latero-terminal corners.

Character states: 0 – simple, inverted V, 1 – with bent latero-terminal corners, inverted V, 2 – parallel.

40. Anus

We consider the ventro-terminally situated anal slit as plesiomorphic in feather mites. Many feather mites, including the outgroup *Grenieria simplex* and the ingroup Ptiloxenidae, have the anus shifted far on the ventral opisthosoma.

Character states: 0 – terminal, 1 – ventral.

41. Adanal sclerites in males

The presence of small adanal sclerites at the bases of setae ps3 is common in *Ptiloxenus*, *Ptiloxenoides* and *Schizurolichus* and rare in *Sokoloviana*.

Character states: 0 – absent, 1 – present.

42. Adanal discs

Adanal discs flanking anal slit are common in both, psoroptid and acaridid mites, and originate from one pair of ad setae. This absence can be reduction. We suppose that the absence of discs in the outgroup *Cheylabis latus* is an apomorphy. But the remnant ring structures with central dot could also be interpreted as plesiomorphic unmodified areolae of setae ad.

Character states: 0 – present, 1 – absent.

43. Corolla

The symmetrical, rounded and polydentate corolla of *Grenieria simplex* and most of the Ptiloxenidae is interpreted as plesiomorph. The presence of a distinct terminal sclerite on the terminal margin of the corolla is undoubtedly a common synapomorphy of the genera *Ptiloxenus*, *Ptiloxenoides* and *Schizurolichus*.

Character states: 0 – symmetrical, dentate, 1 – with terminal sclerite.

44. Membrane of adanal discs

Smooth membranes surrounding adanal discs are plesiomorphic to radiated ones. In the genera *Ptiloxenus*, *Ptiloxenoides* and *Schizurolichus*, these membranes are asymmetrically enlarged posteriorly. It is apparently connected with the asymmetry of the corollas (see No. 43).

Character states: 0 – smooth, 1 – symmetrical, radiated, 2 – asymmetrical, posteriorly radiated.

Chaetotaxy and poroidotaxy

45. Cheliceral seta

Chelicerae of Astigmata only possess a single seta which is primarily spine-like and set near the origin of fixed digit. Such a character state is present in *Cheylabis latus*. Cheliceral seta is shifted ventro-posteriorly and modified into flattened structure in the second outgroup and in Ptiloxenidae.

Character states: 0 – in anterior part of chelicera, simple, 1 – in ventro-medial part, flattened.

46. Palpal solenidion

The single apical solenidion is very short in almost all feather mites. Comparing this character state with free-living astigmatic mites, we suppose that the long solenidion of *Cheylabis latus* is its autapomorphy.

Character states: 0 – short, 1 – long.

47. Shape of setae c3

Short and blade-like setae c3 are common in many feather mites inhabiting the vane surface and originated independently in various lineages. It is an adaptation to living between barbs of feathers functioning as a spreader to a more favourable fixation of the mite onto a highly aerated area. Hair-like setae occurring in the *Grenieria simplex* are probably a secondary reversion connected with the shifting of the syringobiid mites from vane to the quills.

Character states: 0 – hair-like, 1 – blade-like.

48. Setae e2 in males

Setae e2 are well developed as big, basely thickened setae in ptiloxenid mites inhabiting non-charadriiform hosts. In the genus *Sokoloviana*, only *S. cornuta* possesses these setae lanceolate; remaining species own setae e2 minute and hair-like.

Character states: 0 – hair-like, 1 – lanceolate, 2 – macrochaetae.

49. Setae f2 in females

Lanceolate setae f2 are characteristic for ptiloxenid females, similarly as in many pterolichoid families living on vane surface. Setae f2 shaped as macrochaetae are the autapomorphy of *Schizurolichus elegans*. Hair-like f2 in *Grenieria simplex* are probably reversals; many other syringobiids have these setae lanceolate as remnants of primary external way of living.

Character states: 0 – hair-like, 1 – lanceolate, 2 – macrochaetae.

50. Setae f2 in males

Modifications of setae f2 in males and females are often incongruent and should be analysed separately. These setae are variously shaped in males of Ptiloxenidae but always more or less dilated.

Character states: 0 – hair-like, 1 – lanceolate, 2 – lanceolate with distal hair-like part, 3 – macrochaetae, 4 – fish-bone-like.

51. Setae h2 in males

Variouly shaped membranes especially on terminal setae are common in feather mites inhabiting vane surface. Hair-like setae are either plesiomorphic or a reversal due to shifting into the quill (Syringobiidae). Setae h2 may bear

membranes but are not as polymorphic and usually weaker developed than in h3 (No. 52).

Character states: 0 – hair-like, 1 – hair-like, basely dilated, 2 – with medial membrane, 3 – with lateral membranes.

52. Setae h3 in males

Membranous extensions on setae h3 well define some species groups of Ptiloxenidae. Leaf-like setae with longitudinal veins are characteristic for mites from all non-charadriiform hosts, i. e., Podicipediformes and Phoenicopteriformes. Triangle membranes are common among all *Sokoloviana* species inhabiting lapwings subfamily Vanellinae. And finally, narrow setae with dentate margins have *Sokoloviana* species from oystercatchers (Haematopodidae) and the ibisbill (Ibidorhynchidae).

Character states: 0 – hair-like, 1 – lateral triangle membranes, 2 – leaf-like, striated, 3 – lateral semicircle membranes with dentate margin, 4 – narrow, margins dentate.

53. Shape of setae ps1 in males

Terminal setae ps1 are usually short and hair-like. In many vane inhabitants including Ptiloxenidae these setae are thickened and needle-like or lanceolate.

Character states: 0 – hair-like, 1 – needle-like, 2 – lanceolate.

54. Situation of setae ps1 in males

All *Sokoloviana* males have setae ps1 situated near the lobe terminus at the $\frac{1}{3}$ - $\frac{1}{4}$ of the lobe length. In other Ptiloxenidae, these setae are set close to the base of the terminal cleft or on the lobe tip.

Character states: 0 – terminally, 1 – $\frac{1}{3}$ from the lobe base, 2 – on the base of lobe, 3 – at lobe terminus, 4 – $\frac{1}{4}$ - $\frac{1}{3}$ from lobe terminus.

55. Setae ps2 and ps3 in females

Setae ps2 are usually set posterolaterally to setae ps3. The reverse situation is a synapomorphy of the genus *Grenieria simplex*.

Character states: 0 – ps2 posterolateral to ps3, 1 – ps2 anterolateral to ps3.

56. Central setae in males

Primarily genital setae are set posteriorly to coxal setae 3a. The shifting of setae g to more anterior position is a common synapomorphy of *Ptiloxenus*, *Ptiloxenoides* and *Schizurolichus*. It is also present in two *Sokoloviana* species from the *gracilis* group.

Character states: 0 – g posteriorly to 3a, 1 – g on the level or anteriorly to 3a.

57. Setae g on epigynum

Genital setae g are set together with genital acetabules on the elongated branches of the epigynum in three *Sokoloviana* species of the *gracilis* group. It is probably a synapomorphy of these mites.

Character states: 0 – no, 1 – yes.

58. Setae of segment AD in females

The maximal number of setae of the segment AD is two pairs (Cheylabidiidae) in feather mites. One pair is present in Syringobiidae, Ascouracaridae, Kiwilichidae and Ptiloxenidae. Mites from remaining families have no ad setae.

Character states: 0 – 2 pairs, 1 – 1 pairs.

59. Opisthonotal glands

These glands are typical for Astigmata and are also present in almost all feather mites (i. e. reduced in some *Ascouracaridae*). Sometimes they are especially strongly sclerotised and visible as dark structures on the sides of opisthosoma. Opisthonotal glands with highly sclerotised striated walls are characteristic for some Ptiloxenidae, especially for *Sokoloviana*.

Character states: 0 – weakly sclerotised, 1 – strongly sclerotised.

60. Cupules ih in males

The maximal number of idiosomal cupules is four in Astigmata. In feather mites these structures are often reduced. Anterior cupules ia are the most stable, terminal ih are rarely present. The full set of cupules is present in some Ptiloxenidae (*Ptiloxenus*, *Ptiloxenoides*, *Schizurolichus*) and is a plesiomorphic condition. In *Sokoloviana* cupules ih, if present, have a form of ovoid and convex organs with longitudinal slit.

Character states: 0 – not modified elliptical slits, 1 – convex oval with a longitudinal slit, 2 – ih reduced.

61. Setae cG on genu I and II

Setae cG on anterior legs are primarily hair-like. These setae are hair-like on genua II and lanceolate on genua I in all Ptiloxenidae (synapomorphy). In the outgroup *Grenieria simplex* setae cG II are also hair-like and cG I are thick, bifurcate apically. Other members of the family Syringobiidae possess both of these setae, modified in quite a number of variations.

Character states: 0 – both hair-like, 1 – cG I lanceolate, cG II hair-like, 2 – cG I thick, bifurcate apically, cG II hair-like.

62. Solenidion sigma 2

The loss of solenidion sigma 2 on the genu I is an autapomorphy of *Cheylabis latus*.

Character states: 0 – present, 1 – absent.

63. Setae d and e on tarsi IV in males

The shortening of setae d and loss of setae e on tarsi IV of males is probably a common synapomorphy of Ptiloxenidae and syringobiid mites (all tarsal setae are hair-like and complete in the genus *Plutarchusia*). The elongated, stiletto-like seta d is characteristic for all *Sokoloviana* species inhabiting the plovers family Charadriidae. The presence of the spine-like seta e in *Ptiloxenoides phoenicopteri* is probably a reversion.

Character states: 0 – hair-like, 1 – spine-like, 2 – d spine-like and long, e absent, 3 – d spine-like and short, e absent.

64. Shape of proral and unguinal setae on tarsi

All mites investigated here own well-developed flattened proral setae. After comparison with many other pterolichoid mites we suppose that flattened bifurcate proral setae on all legs are plesiomorphic. It seems that the common synapomorphy for Ptiloxenidae is the simplification of proral setae on tarsi I. The slender form of these setae differ from the big leaf-like proral setae in the outgroup *Cheylabis latus*. In the second outgroup *Grenieria simplex* all setae are trifid. The shape of these setae in *Ptiloxenoides phoenicopteri* are its own autapomorphy.

Character states: 0 – all bifurcated, 1 – on tarsi I simple, on II-IV bifurcated, 2 – all tripled, 3 – on tarsi I bifurcated, on II-IV tripled.

Cladistic analysis of Ptiloxenidae

We obtained a single most parsimonious tree (Fig. 2) of 168 steps and CI = 0.821 (excluding uninformative characters 0.782, RC = 0.668). This value exceeds by far the expected CI for 19 taxa: 0.559 (SANDERSON & DONOGHUE 1989) and points out the good fit of the data to the tree topology. The bootstrap analysis performed on 100 replications brought to a very similar tree topology (Fig. 3). The only difference was cancelling of the trichotomy of *Sokoloviana chilensis*-*S. vanelli*-(*S. allocerca*, *S. leptosoma*). However, the bootstrap support was extremely weak here (2 %). Generally, the Ptiloxenidae cluster is very stable (100 %) in our analysis and defined by following synapomorphies: distinct sexual dimorphism; pronotum completely covered by a shield; hysteronotum covered by a big shield in males; hardly sclerotised opisthonotum in females; presence of transobar sclerites on well developed

opisthosomal lobes in males; postlobar membranes with internal extensions in males; presence of terminal cleft between mainly small opisthosomal lobes in females; very short aedeagus; circular supranal concavity in females; genital opening terminal; inseminatory canal short and well-sclerotised; short cylindrical or trumpet-like ductus conjunctivi in females; well developed epigynum in females; paragnal sclerites with bent latero-terminal corners in females; setae c3 blade-like; setae f2 lanceolate in males and females; setae ps1 lanceolate; proral and unguinal setae simple on tarsi I and bifurcated on tarsi II-IV.

The family Ptiloxenidae was divided into two main clusters (Fig. 2). The first cluster (I) included the genera *Ptiloxenus*, *Schizurolichus* and *Ptiloxenoides*, the second one (II) formed the genus *Sokoloviana*. Cluster I was very stable; the bootstrap values exceeded 80 % for the root and all internal branches. Analysis of this cluster showed the incompatibility of the traditional classification of the family with the tree topology. The cladistic analysis strongly supported the hypothesis that *Schizurolichus elegans* is not a separate genus but only a highly modified species of the genus *Ptiloxenus*. *Schizurolichus elegans* and *Ptiloxenus colymbi* are closely related by having several synapomorphies (especially big opisthosomal lobes in females and reduction of branches of epigynum). *Ptiloxenus major* is a sister group for this clade. Alternative hypotheses were less parsimonious: *Schizurolichus* is a sister group of the monophyletic *Ptiloxenus* (one tree, 171 steps, CI = 0.807), *Schizurolichus* is a sister group of the cluster *Ptiloxenus* – *Ptiloxenoides* (one tree, 175 steps, CI = 0.789) and *Schizurolichus* is a sister group of the cluster *Ptiloxenus* – *Ptiloxenoides* – *Sokoloviana* (one tree, 180 steps, CI = 0.767). We degrade the genus *Schizurolichus* to a synonym of the genus *Ptiloxenus*.

Cluster II consisted of the single genus *Sokoloviana*. The cluster was worse supported than the first one (43 %) and less internally balanced. The worse supported internal clades A, a2 and B (Fig. 3) were at about 60% - 80% probability of correctness (HILLIS & BULL 1993). Clades a1, b1 and b2 were over 95 % of correctness. All the species of this genus were grouped into two clusters (Fig. 2). Generally, the first cluster (A) contained more diversiform species than the second one (B). The cluster A (44 %) was defined by the following synapomorphies: supranal concavity as a narrow slit separated from terminal cleft in males; setae f2 lanceolate in males and setae h2 with medial membrane. The mites from the second cluster B were characterised by a fine net-like pattern of the hysteronotum; rounded, narrow lateral membranes on the lobes in males and long, spine-like setae d on tarsi IV in males. Each of both clusters was also divided into two distinct branches.

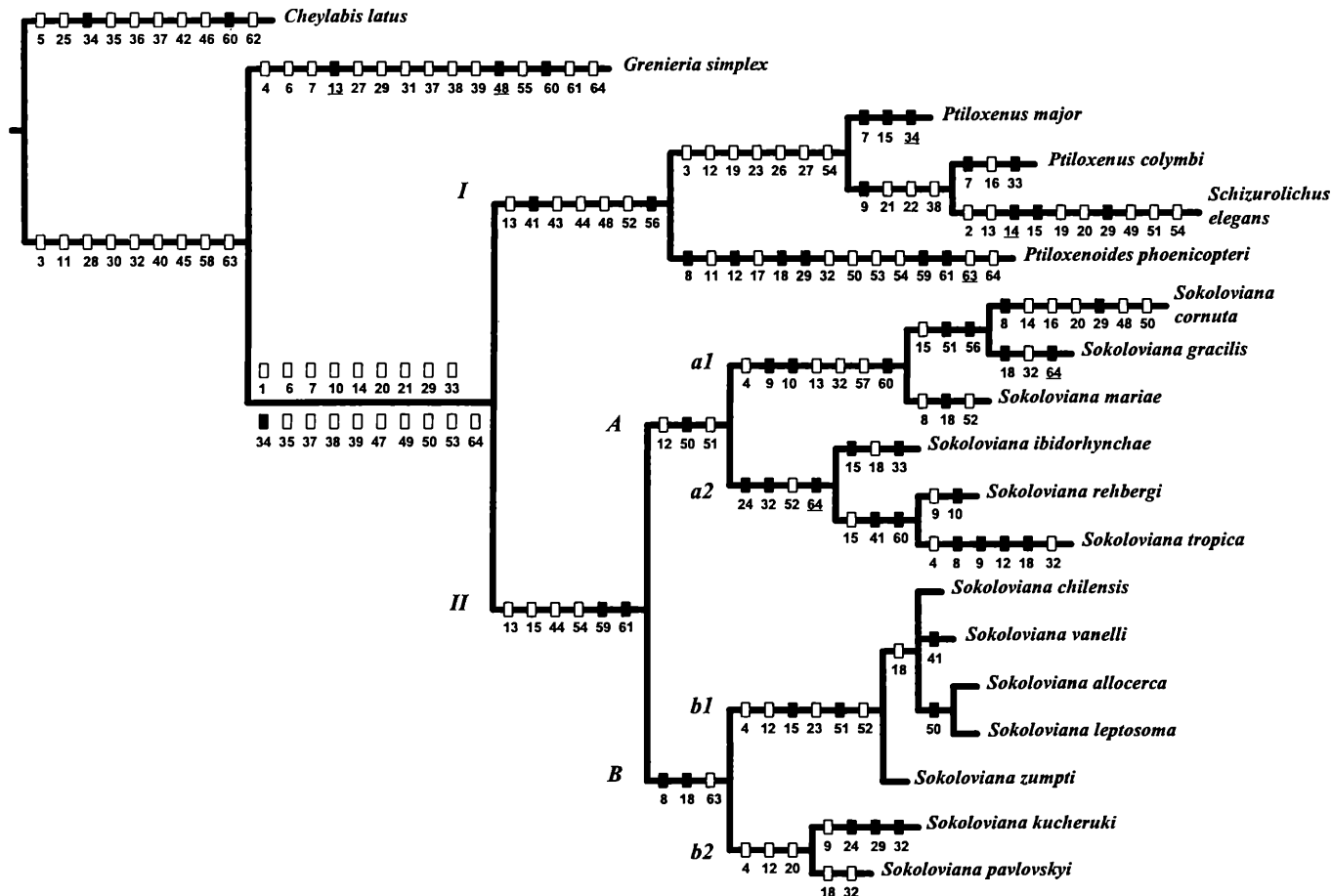


Fig. 2: Phylogram of the family Ptiloxenidae obtained from branch- and bound method carried on 64 morphological characters. Hollow boxes designate out- and synapomorphies, filled boxes homoplasies, underlying numbers reversals. I, II, A, B, a1, a2, b1, b2 – designations of clades discussed in text.

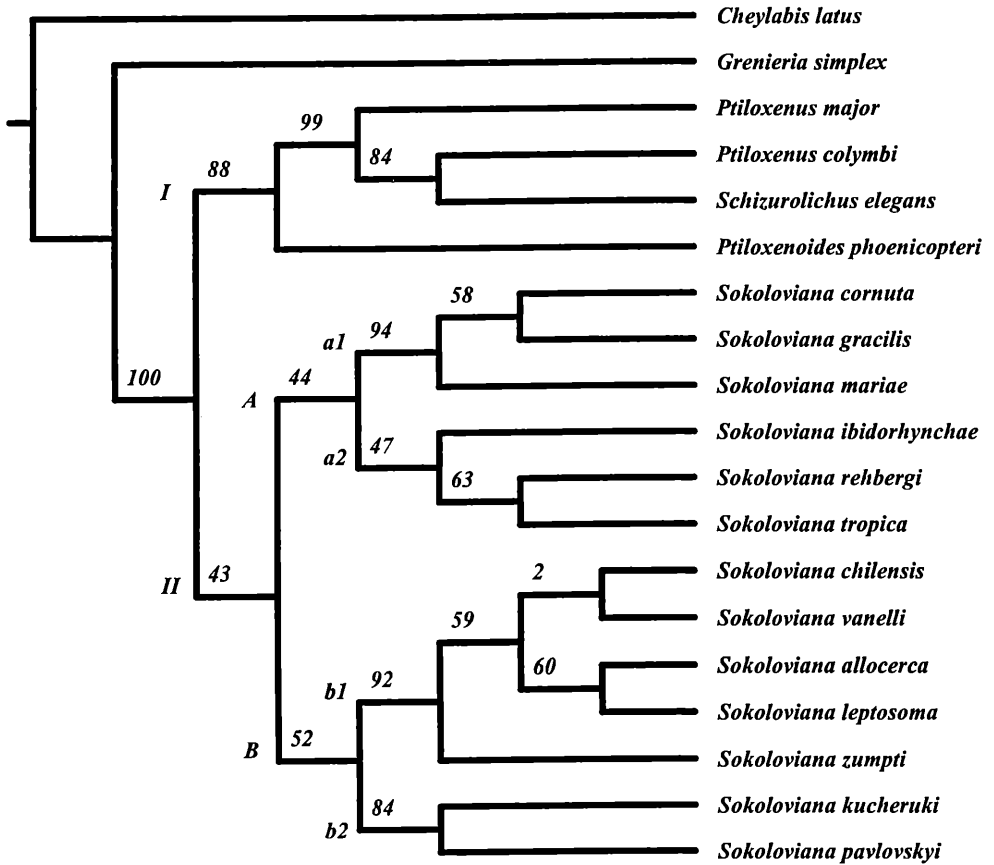


Fig. 3: Bootstrap 50% majority-rule consensus tree of the family Ptiloxenidae. The numbers are the bootstrap supports for particular clades. Designations of clades as in Fig. 2.

Cluster a1 (94 %) included well-defined and highly modified species. The characteristic synapomorphies were: sternum with terminal shield and shield between branches in males; several pairs of anterior hysteronotal apodemes; opisthosoma sclerotised along margins in females; shortened, tongue-like opisthosomal lobes in males; highly elongated paragenital sclerites with broad junction posteriorly; setae g set on epigynum; cupules ih convex oval, with longitudinal slit in males. The second cluster a2 (47 %) was defined by a pair of ventral shields on opisthosoma terminus in females; paragenital sclerites with medial extensions posteriorly; setae h3 with narrow, dentated margins in males and all proral setae bifurcated. Both clusters of the clade B (52 %) contained less diversiform species than those of cluster A. Particular species of cluster b1 (92 %) are very uniformly shaped and there was a very weak support for the branching inside this clade. However, the whole cluster was well-defined by the following common apomorphies: a triangle shield be-

tween the branches of sternum in males; elongated, oval supranal concavity fused with the terminal cleft by a narrow sclerite in males; big, ovoid cribrum; membranous opisthosomal extensions with terminal tooth in females; setae h2 basely dilated in males; setae h3 with lateral triangle membranes. The sister cluster b2 (84 %) was characterised by the following synapomorphies: external shields on sternum in males; rounded supranal concavity separated from terminal cleft in males and tongue-shaped, symmetrical postlobar membranes in males.

Discussion

Mites of the family Ptiloxenidae are inhabiting water-birds which are traditionally classified in four orders. Particular ptiloxenid genera are restricted to particular bird orders: *Ptiloxenus* (including *Schizurolichus*) with Podicipediformes, *Ptiloxenoides* with Phoenicopteriformes and Pelecaniformes, *Sokoloviana* with Charadriiformes. On the early derived Charadriiformes (SIBLEY & AHLQUIST 1990) ptiloxenid mites are very diversiform and rich in species, sometimes monoxenous (*Sokoloviana*). On evolutionary younger hosts, only few species live (*Ptiloxenus* on Podicipidae), or even one species of mite only (*Ptiloxenoides phoenicopterii*) inhabits several birds from two orders (Pelecaniformes and Phoenicopteriformes). A remarkable evolutionary event is the absence of ptiloxenid mites on the charadriiform suborders Scolopaci, Lari and Alci and some families of Charadrii: Burhinidae, Dromadidae, Glareolidae, Pluvianellidae, Thinocoridae and Chionididae. We suppose that it could be interpreted rather as an partial extinction than as shifting from one host group to another. It is interesting to compare this host range with an analogous one of syringobiid mites (Tab. 2). These two feather mites families are probably most closely related and shared a common ancestor. Simplifying, one can say that Syringobiidae are ptiloxenid-like mites which have shifted into the quills. Although both mite groups inhabit different microhabitats and exploit different food sources they clearly avoid one another. The only known examples of co-occurrences of both mite families are two species of the plovers genus *Charadrius*.

Comparison of the phylogeny reconstruction of birds (SIBLEY & AHLQUIST 1990) with the phylogenetic tree of the Ptiloxenidae showed a close resemblance of both trees topologies (Fig. 4). The co-speciatory tracking of birds speciation by mites was well expressed on the level of hosts families and sub-families. The only ambiguous situation was the relationship between *Sokoloviana ibidorhynchae* and *Ibidorhyncha strutersi* (Ibidorhynchidae).

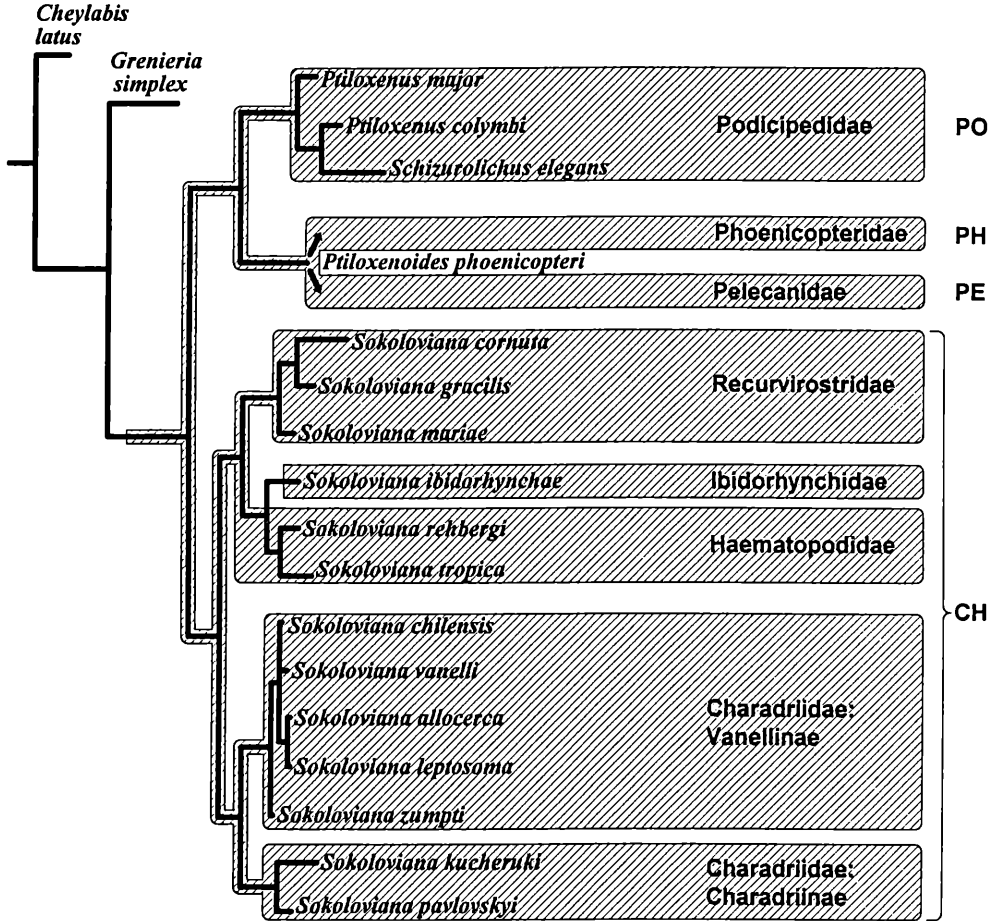


Fig. 4: Comparison of the phylogram of mites (Ptiloxenidae) with the tree of its hosts (data after SIBLEY & AHLQUIST 1990). PO – Podicipediformes, PH – Phoenicopteriformes, PE – Pelecaniformes, CH – Charadriiformes.

The problem depends on the uncertainty of the ibisbill's position in the wader phylogram. It was excluded from the most comprehensive work of SIBLEY & AHLQUIST (1990). This species also caused serious problems in the phylogenetic reanalyses of STRAUCH's osteological data (1978) conducted by CHU (1995). Only the removing of ibisbill from the datamatrix enabled an obtaining of a reasonable number of trees.

CHU concluded that *Ibidorhyncha* is probably connected with cluster of the *Recurvirostridae* (CHU 1995, Fig. 5, 7) or should be treated as a separate monophyllum in the polytomous cluster including *Recurvirostridae*, *Haematopodidae* and *Charadriidae* (ibid, Fig. 6). Also other papers do not answer this question (JEHL 1968; JOHNSGARD 1981). *Ibidorhyncha* was placed with *Recurvirostridae*, with *Haematopodidae*, with *Charadriidae* as a separate sub-family or in a separate monotypic family without clear connection with other families of *Charadriodea*.

The analysis of the phylogenetic tree of *Ptiloxenidae* showed the close relationship of *Sokoloviana ibidorhynchae* from ibisbill to *Sokoloviana* species inhabiting oystercatchers (*Haematopodidae*). Joining this species into the clusters of *Sokoloviana* inhabiting *Recurvirostridae* or *Charadriidae* was less parsimonious: 171 steps, CI = 0.807 and 170 steps, CI = 0.812, respectively. Because of generally parallel phylogeny course of the *Ptiloxenidae* and their hosts we suppose that our observations could to some extent be helpful in solving problems with the proper classification of ibisbill. It is worth mentioning that another feather mite genus *Bychovskiata* (*Avenzoariidae*) also inhabiting these hosts shows an identical pattern of phyletic relationships as *Sokoloviana* (MIRONOV & DABERT, in prep.).

Quite similar is the uncertainty of the systematic position of the *Cladorhynchus leucoptera*. This highly distinctive recurvirostrid bird is often considered as being most closely related to the avocets genus *Recurvirostra* (i. e. STRAUCH 1978; JOHNSGARD 1981; CHU 1994, 1995). After SIBLEY & AHLQUIST (1990), genera *Cladorhynchus*, *Himantopus* and *Recurvirostra* build a trichotomous clade. And, finally, CHRISTIAN et al. (1992) postulate close relationships between *Recurvirostra* and *Himantopus* with *Cladorhynchus* as a sister group for this monophyllum.

The analysis of the phylogenetic relationships of *Sokoloviana* mites inhabiting these three bird genera gave no support for any of the above hypotheses. The highly distinctive *S. cornuta* from *Cladorhynchus leucoptera* is most closely related to the *S. gracilis* from numerous *Himantopus* species. The alternative hypotheses which could support one of the avian phylogenetic relationships were only slightly less parsimonious: monophyly of *S. cornuta* and *S. mariae* (from *Recurvirostra*) – 160 steps, CI = 0.825, monophyly of

S. gracilis and *S. mariae* – 159 steps, CI = 0.830. Now it would be too risky to falsify the bird phylogeny by the mite's one or to suggest the mite shifting between hosts (although this is relatively possible due to common feeding associations with the *Recurvirostra novaehollandiae* and *Himantopus himantopus*, see HAYMAN et al. 1991).

The analysis of host/parasite relationships on the genus and species level is difficult because of the detailed results of phylogenetic studies on birds. Quite frequently, there also exist some reciprocally excluding hypotheses about the course of bird speciation. Such an example is the comparison of the phylogenetic relationships of lapwings (Vanellinae) with the speciation reconstruction of *Sokoloviana* species living on these birds. The Vanellinae are a well-defined plover group which consists of one genus *Vanellus* with about 24 species (HAYMAN et al. 1991). Resolving the problem of the relationships within the lapwings is difficult because of very variable and clearly adaptive external characteristics and simultaneously too uniform internal anatomy (BOCK 1958). It resulted in obtaining highly polytomous branching which did not properly answer the phylogenetic questions (e. g. CHU 1995, Fig. 5). Also the analyses carried out on a reduced number of species yielded various results depending on character types used, e. g. osteological data (STRAUCH 1978; CHU 1995) versus DNA-DNA hybridisation (SIBLEY & AHLQUIST 1990).

The comparison of bird-parasite relationships was difficult in this case not only due to vagueness in host phylogeny reconstruction. We are not sure if the obtained branching out of *Sokoloviana* living on Vanellinae is proper. This clade was partly polytomous and very weakly defined by only three (two informative) characters for five taxa analysed.

Analysing the geographical distribution of both hosts and feather mites (Fig. 5) was, however, more interesting. According to the hypothesis proposed by BOCK (1958), lapwings have originated in Africa and the non-African species have spread out from there. He showed the possible routes of dispersal to other continents which explained the close phyletic relationships between some geographically distant species and their relatives in Africa. The distribution of the *Sokoloviana* mites from lapwings seems to be better correlated with the geographical region than with the speciation course of hosts. Three species: *S. allocerca*, *S. leptosoma* and *S. zumpti* are restricted to Africa. *Sokoloviana chilensis* is restricted to South America only. The last *S. vanelli* lives in Far East and in Australia. The diversification of *Sokoloviana* also took place in Africa where new species originated in three distant places: northwards *leptosoma*, centrally *allocerca* and southwards *zumpti*. The absence of *Sokoloviana* on several lapwings is also very interesting.

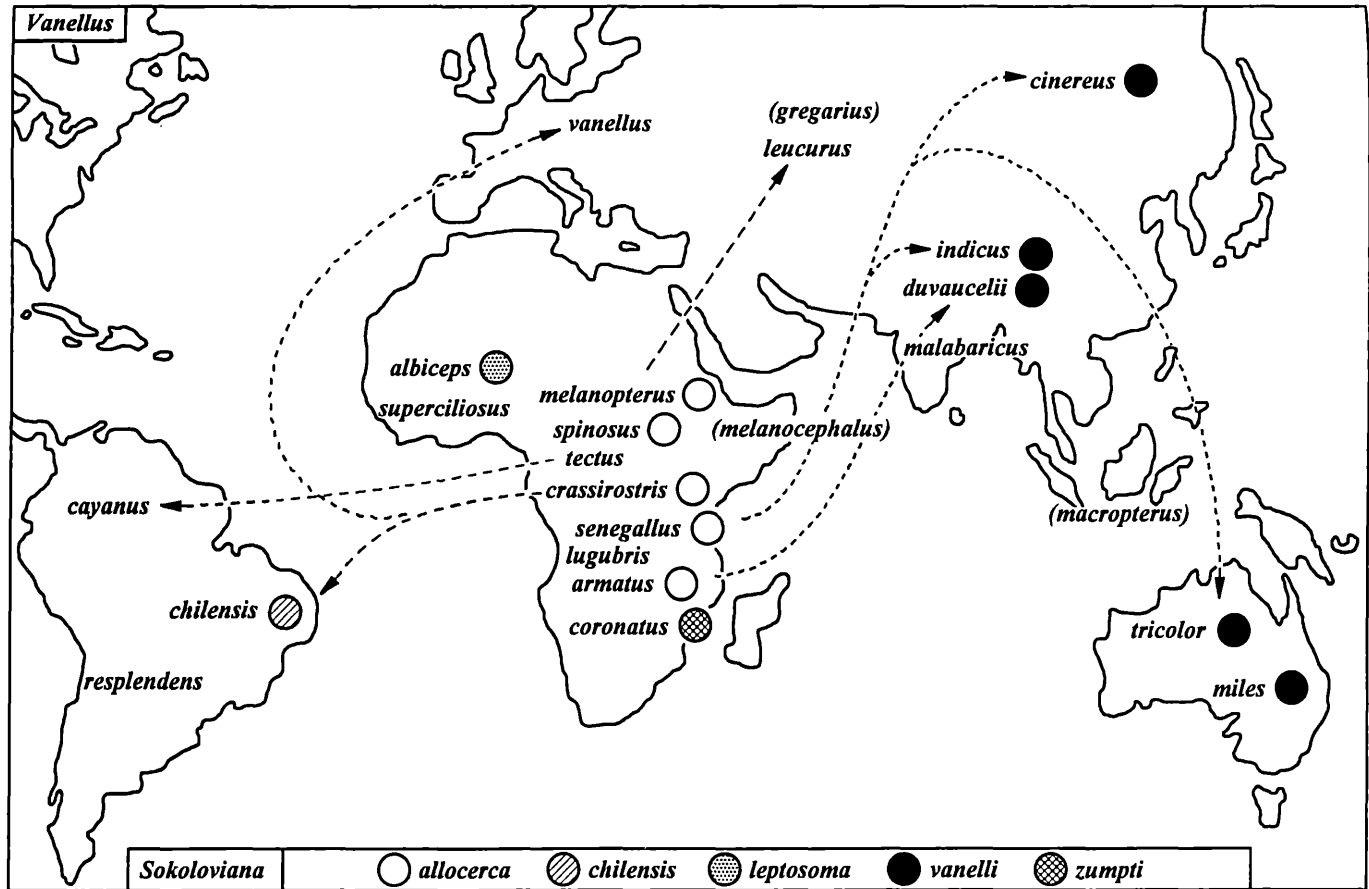


Fig. 5: Geographical distribution of the *Sokoloviana* species group inhabiting lapwings (Vanellinae) compared with the ranges of its hosts (based on the present study and literature data). Bird distribution and possible dispersal routes (dashed line) after BOCK (1958), modified. Circles designate *Sokoloviana* species, names designate the species of the host genus *Vanellus*. Not investigated host species are designated by parentheses.

Charadriiformes	Ptiloxenidae feather vanes	Syringobiidae feather quills	Pterolichidae Magimeliinae feather vanes	Pterolichidae Pterolichinae feather vanes	Freyanidae Burhinacariinae feather vanes	Avenzoariidae Avenzoariinae feather vanes	Alloptidae Alloptinae feather vanes
Chadrii Dromadidae Chionidae Pluvianellidae Thinocoridae Burhinidae Haematopodidae Ibidorhynchidae Recurvirostridae Glareolidae Charadriidae	- - - - - <i>Sokoloviana</i> <i>Sokoloviana</i> <i>Sokoloviana</i> - <i>Sokoloviana</i>	- - - - - - - - <i>Leptosyringobia</i> <i>Longipedia</i> <i>Phyllochaeta</i>	- - - - - - - - <i>Xiphiurus</i> <i>Magimelia</i> <i>Montchadskiana</i> <i>Triphyllochaeta</i> <i>Xiphiurus</i>	- - - - - - - - -	- - - - - <i>Burhinacarus</i> <i>Cernyella</i> - - <i>Freyanomorpha</i> <i>Freyanomorpha</i>	<i>Zachvatkinia</i> ? - - <i>Attagivora</i> - <i>Bychovskia</i> <i>Bychovskia</i> <i>Bychovskia</i> - <i>Bychovskia</i> <i>Ovöfreyana</i>	<i>Alloptes</i> <i>Alloptes</i> - - - <i>Alloptes</i> - <i>Alloptes</i> <i>Homeobrephosceles</i> <i>Brephosceles</i>
Scolopaci Jacanidae Rostratulidae Scolopacidae	- - - -	- - <i>Eurysyringobia</i> <i>Limosilichus</i> <i>Megasyringobia</i> <i>Phyllochaeta</i> <i>Plutarchusia</i> <i>Sammonica</i> <i>Sikyonemus</i> <i>Syringobia</i>	- - <i>Montchadskiana</i> <i>Pilochaeta</i>	<i>Grallolichus</i> - -	- - -	- <i>Rostratobia</i> <i>Avenzoaria Bregetovia</i> <i>Capelloptes</i> <i>Pomeranzevia</i> <i>Pseudavenzoaria</i> <i>Rafalskiata</i> <i>Bychovskia</i>	- - <i>Alloptes</i> <i>Dichobrephosceles</i>
Lari Laridae Stercorariidae Rynchopiidae	- - - -	<i>Grenieria</i> <i>Plutarchusia</i> <i>Thecarthra</i> <i>Thecarthra</i>	- - -	- - -	- - -	<i>Laronyssus</i> <i>Zachvatkinia</i> <i>Zachvatkinia</i> <i>Hemifreyana</i>	<i>Alloptes</i> <i>Alloptes</i> <i>Alloptes</i>
Alci Alcidae	-	-	-	-	-	-	<i>Alloptes</i>

Tab. 2 Host-parasite associations of six feather mite families inhabiting flight feathers of charadriiform birds.

Putting aside some clear gaps in material examined, two absences are evident: first in North America and second in Europe and Western and Central Asia. The explanation of the first absence is trivial: there are no lapwings in North America. The absence of *Sokoloviana* on Eurasian lapwings is unclear.

It seems that the African ancestors of these birds were already infected by *Sokoloviana* before they conquered new continents (see the dispersal routes figured on Fig. 5). The hypothesis of the competition with another feather mite is difficult to prove. Mites of the pterolichid subfamilies Magimeliinae (*Triphyllochaeta*, *Magimelia*, *Montchadskiana*) and, in limited degree, of the avenzoariid subfamily Avenzoariinae (*Bychovskiata*, *Ovofreyana*) and the alloptid subfamily Alloptinae (*Brephosceles*) are the potential competitors (Tab. 2). They inhabit the same part of vanes and show similar morphological adaptations. However, they coexist with *Sokoloviana* in a stable equilibrium on many lapwing species. Also the climate is probably not the key factor explaining the absence of *Sokoloviana* on Eurasian lapwings. There are some *Sokoloviana* species (although from different species groups) which inhabit birds even on subboreal part of host's range e. g. *S. gracilis*, *S. mariae* or *S. rehbergi*.

These and other problems concerning the geographical distribution of *Sokoloviana* must remain unsolved until more complete data is gathered.

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	0000000011111111122222222233333333334444444 4	4555555555566666
	12345678901234567890123456789012345678901234567 8	9012345678901234
<i>Cheylabis latus</i>	0000100000000000000000001000000012110000??010 0	0000000000020100
<i>Grenieria simplex</i>	0025021000100000000000000113111000022210100100 0	0000001001022032
<i>Ptiloxenus major</i>	10100120011311500011101001211101201031111112101 2	1102210101000031
<i>Ptiloxenus colymbi</i>	10100120111311010011211001211101111033111112101 2	1102210101000031
<i>Ptiloxenoides phoenicopteri</i>	10200132012211001101100000012106211031111112101 2	1402120101101013
<i>Schizurolichus elegans</i>	11100130111330500022211001212101211033111112101 (12)	2132230101000031
<i>Sokoloviana cornuta</i>	10230131121142120003100000012104211031110101101 1	1310240111111031
<i>Sokoloviana ibidorhynchae</i>	10200130011121400201100100011107111031110101101 0	1?24240001121030
<i>Sokoloviana chilensis</i>	10210132011421400401102000011101211031110101101 0	1111240001121021
<i>Sokoloviana vanelli</i>	10210132011421400401102000011101211031111101101 0	1111240001121021
<i>Sokoloviana allocerca</i>	10210132011421400401102000011101211031110101101 0	1211240001121021
<i>Sokoloviana gracilis</i>	10230130121141100101100000011105211031110101101 0	1210240111111030
<i>Sokoloviana kucheruki</i>	10240132211521200304100100012107211031110101101 0	1100240001121021
<i>Sokoloviana leptosoma</i>	10210132011421400401102000011101211031110101101 0	1211240001121021
<i>Sokoloviana mariae</i>	10230133121141200101100000011104211031110101101 0	1223240011111031
<i>Sokoloviana pavlovskyi</i>	10240132??1521?00504100?0001?1032????1110101101 0	11002400011?10??
<i>Sokoloviana rehbergi</i>	10200130321121300001100100011107211031111101101 0	1224240001111030
<i>Sokoloviana tropica</i>	10220131111221300301100100011102211031111101101 0	1224240001111030
<i>Sokoloviana zumpti</i>	10210132011421400301102000011101211031110101101 0	1111240001121021

Appendix - datamatrix for the family Ptiloxenidae

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Biosystematics and Ecology](#)

Jahr/Year: 1998

Band/Volume: [14](#)

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