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PHYLOGENY OF FEATHER MITES OF THE SUBFAMILY PTERODECTINAE (ACARIFORMES: PROCTOPHYLLODIDAE) AND THEIR HOST ASSOCIATIONS WITH PASSERINES (PASSERIFORMES)

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ABSTRACT

A phylogenetic hypothesis of the feather mite subfamily Pterodectinae Park et Atyeo, 1971 (Astigmata: Proctophyllodidae), currently including 165 species in 19 genera, was constructed by means of the maximum parsimony approach. It is shown that the proctophyllodid mites characterized by the epigynum fused to epimerites in females and by the absence of terminal membranous extensions of the opisthosoma in males that were arranged by previous authors into two subfamilies, Pterodectinae and Rhamphocaulinae, constitute a common phylogenetic branch within Proctophyllodidae. It is proposed to threat this whole branch as the subfamily Pterodectinae. The subfamily Pterodectinae in the new sense consists of two branches, which are treated as the tribes Pterodectini trib. nov. and Rhamphocaulini Park et Atyeo, 1971 stat. nov. The generic contents of these tribes are rearranged comparing to those in Pterodectinae and Rhamphocaulinae of previous authors.

A preliminary hypothesis about the origin and dispersion of Pterodectinae on passerine hosts is proposed. It is suggested that this subfamily originated on the ancestors of Passeriformes. The origin and subsequent diversification of two major phylogenetic branches (Pterodectini and Rhamphocaulini) was related with two main taxonomic grouping of avian hosts, passerines and hummingbirds (Apodiformes: Trochilidae), respectively; although on the latter hosts they are of secondary origin. The phylogeny, host associations and geographic distribution of pterodectines predominately associated with passerines generally correspond to the phylogeny and historical biogeography of the order Passeriformes. The current distribution of pterodectines among passerines was realized by cospeciation with their hosts, and also by numerous cases of switching to new host taxa, mainly within Passeriformes, but also to bird of other orders.

Nanopterodectes nom. nov. is proposed for the pterodectine genus *Nanodectes* Mironov in Mironov et al. 2008b (Acariformes: Proctophyllodidae), which was preoccupied (Rentz 1985; Orthoptera: Tettigoniidae); the sole species of this genus gets a new name *Nanopterodectes formicivorae* (Mironov, 2008) comb. nov.

Key words: Proctophyllodidae, Pterodectinae, phylogeny, systematics, host associations, Passeriformes

ФИЛОГЕНИЯ ПЕРЬЕВЫХ КЛЕЩЕЙ ПОДСЕМЕЙСТВА PTERODECTINAE (ACARIFORMES: PROCTOPHYLLODIDAE) И ИХ ПАРАЗИТО-ХОЗЯИННЫЕ СВЯЗИ С ВОРОБЬИНЫМИ (PASSERIFORMES)

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РЕЗЮМЕ

Для перьевых клещей подсемейства Pterodectinae Park et Atyeo, 1971 (Astigmata: Proctophyllodidae), включающего в настоящее время 165 видов и 19 родов, методом максимальной парсимонии впервые построена филогенетическая гипотеза. Установлено, что проктофиллодиды, характеризуемые слиянием эпигиния с эпимеритами у самок и утратой терминальных мембранозных образований у самцов и распределяемые

предшествующими авторами по двум отдельным подсемействам, Pterodectinae и Rhamphocaulinae, образуют единую ветвь в рамках семейства Proctophyllodidae. Предложено рассматривать всю эту ветвь в качестве подсемейства Pterodectinae. Подсемейство Pterodectinae, принятое в настоящей работе, представлено двумя ветвями, которые предложено рассматривать в качестве триб Pterodectini trib. nov. и Rhamphocaulini Park et Atyeo, 1971 stat. nov. Родовой состав триб существенно ревизован по сравнению с таковым у Pterodectinae и Rhamphocaulinae в понимании предшествующих авторов.

Разработана предварительная гипотеза о происхождении и путях распространения клещей подсемейства Pterodectinae по воробьиным. Предполагается, что это подсемейство возникло на предках отряда Passeriformes. Формирование и последующее распространение двух основных филогенетических ветвей (трибы Pterodectini и Rhamphocaulini) были связаны соответственно с двумя крупными таксономическими группами птиц, воробьиными (Passeriformes) и колибри (Apodiformes: Trochilidae), хотя вторая группировка хозяев и является для птеродектин вторичной. Филогенетические отношения, распределение по таксонам хозяев и географическое распространение представителей семейства Pterodectinae, связанных преимущественно с воробьиными, в общих чертах совпадает с филогенией и исторической зоогеографией этого отряда. Современное распространение птеродектин на воробьиных является как результатом их коспециации с хозяевами, так и многочисленных горизонтальных переходов на новых хозяев, главным образом в пределах отряда Passeriformes, а в редких случаях и на птиц других отрядов.

Новое название *Nanopterodectes* nom. nov. предложено для рода *Nanodectes* Mironov in Mironov et al. 2008b (Acariformes: Proctophyllodidae), которое оказалось преоккупированным (Rentz 1985; Orthoptera: Tettigoniidae); единственный вид этого рода птеродектин получает новое название *Nanopterodectes formicivorae* (Mironov, 2008) comb. nov.

INTRODUCTION

The family Proctophyllodidae Trouessart et Megnin, 1884 (Astigmata: Analgoidea) is the most species-rich family of feather mites and includes about 400 species arranged in 40 genera and three subfamilies (Gaud and Atyeo 1996; Hernandes et al. 2007). The subfamily Pterodectinae Park et Atyeo, 1971, which is in the main focus of the present study, to date has included 165 species in 19 genera (Park and Atyeo 1971a; Gaud and Atyeo 1996; Mironov and Fain 2003; Mironov 2008; Mironov et al. 2008b; Valim and Hernandes 2008, 2009). In the plumage of avian hosts, pterodectines inhabit large feathers with well developed vanes, such as the primary and secondary flight feathers and the tail feathers, where they are located in narrow corridors formed by barbs on the ventral side of vanes. Pterodectines are highly adapted to these microhabitats and usually have a strongly elongated and slightly flattened body, with extensive dorsal shields and with most dorsal setae significantly reduced in size. Representatives of the subfamily Pterodectinae are mostly distributed on passerines (Passeriformes) and hummingbirds (Apodiformes: Trochilidae), several species are associated with Piciformes and Coraciiformes, and a few species

have been recorded from Gruiformes, Musophagiformes and Caprimulgiformes. The host association of one pterodectine species with a few gruiform hosts is apparently natural although of secondary origin, while the records of a pterodectine species on hosts from the two latter orders are quite questionable and could be accidental contaminations. In geographic aspect, the subfamily Pterodectinae is distributed worldwide, but the majority of pterodectines is apparently associated with hosts from tropical regions of the World.

In the latter half of the previous century, biodiversity of pterodectines has been most extensively explored in Africa (Gaud 1952, 1953, 1957, 1964, 1979; Till 1954, 1957; Gaud and Mouchet 1957; Gaud and Till 1961; Mironov and Kopij 1996a, 1996b, 1997; Mironov and Fain 2003; Mironov and Wauthy 2009). In the New World, most taxa have been described from South America (Berla 1958, 1959a – 1959c, 1960; Park and Atyeo, 1973a, 1973b, 1974a, 1974b, 1975; Černý 1974; OConnor et al. 2005; Hernandes and Valim 2005, 2006; Mironov et al. 2008b; Valim and Hernandes 2006, 2008, 2009). To a much lesser extent the fauna of these mites was studied in other areas of the Old World (Sugimoto 1941; Gaud and Petitot 1948, Gaud 1962, 1968; Atyeo and Gaud

1977; Mironov 1996, 2006, 2008; Kuroki et al. 2006; Mironov et al. 2008a; Mironov and Proctor 2009). A detailed generic revision of Pterodectinae was carried out by Park and Atyeo (1971a); and a revised key to genera was given by Gaud and Atyeo (1996). Identification keys to species were given mainly for the genera associated with hummingbirds (Park and Atyeo 1973a, 1973b, 1974a, 1974b, 1975), and only for a few genera associated with other birds taxa (Gaud 1979; Mironov 1996, 2006; Hernandes and Valim 2006). Recent publications with redescriptions of old pterodectine species (Mironov 2006; Valim and Hernandes 2006, 2008) are very helpful in this situation.

The subfamily Pterodectinae was established by Park and Atyeo (1971a) in the course of series of systematic revisions of proctophyllodid mites, which these authors carried out in the beginning of 1970s. In this generic revision of the Pterodectinae, Park and Atyeo gave uniform diagnoses for all 12 genera they recognized within this subfamily (including 8 newly established genera). The authors presented two main diagnostic features differentiating Pterodectinae from Proctophyllodinae: the fusion of the epigynum with epimerites IIIa into an entire sclerotized structure having a form of the Mauritanian arch in females, and the absence of terminal lamellae or other membranous structures on the opisthosoma of males. Respectively, the subfamily Proctophyllodinae was determined by having a free epigynum in females and a pair of terminal lamellae or at least narrow membranous extensions on the posterior margin of opisthosoma in males. Park and Atyeo (1971a) arranged pterodectine genera known in that time into two generic groups based on details of setation of legs I, II. The *Pterodectes* group was characterized by having ventral setae *wa* of tarsi I, II moved to apical part of these segments and by relatively short solenidion *σ1* of genu I. Representatives of the *Trochilodectes* group were determined by having ventral setae *wa* at midlevel position, together with two other ventral setae *ra* and *la*, and by solenidion *σ1* of genu I longer than corresponding solenidion *ω3* of tarsus I. These generic groups also clearly differ from each other by their host associations: the *Trochilodectes* group (4 genera) is restricted to hummingbirds, while mites of the *Pterodectes* group (8 genera) are known from various non-trochilid hosts. In subsequent years, six more genera were described in the context of the *Pterodectes* group (Mironov 1996, Mironov et

al. 2008a, Mironov and Wauthy 2009; Valim and Hernandez 2008, 2009). Finally, it was proposed to move four genera from the *Pterodectes* group to a new generic group *Proterothrix* (Mironov et al. 2008b), because representatives of the latter group clearly differed from remaining genera of the *Pterodectes* group and from the *Trochilodectes* group by having antero-mesal position of pseudanal setae *ps3* in relation to anal suckers in males.

In discussing the current state of suprageneric classification of Pterodectinae it is necessary to point out that Park and Atyeo (1971b, 1972a) almost simultaneously with establishing of the subfamily Pterodectinae created two more proctophyllodid subfamilies, Rhamphocaulinae Park et Atyeo, 1971 and Allodectinae Park et Atyeo, 1972, all representatives of which were restricted to hummingbirds. The rationale for establishing these subfamilies is quite unclear, because by most diagnostic features these taxa coincide with the subfamily Pterodectinae, including such characteristics as the epigynum fused with epimerites in females and absence of membranous structures on opisthosoma in males. The only morphological character differing both subfamilies from pterodectines was the extensive sclerotization of coxal fields I-IV, a feature which is rather variable even within some genera of feather mites. In turn, these subfamilies differed from each other only by the presence (in Rhamphocaulinae) and absence (in Allodectinae) of apical claw-like extension on tarsi I-IV (Park and Atyeo 1971b, 1972a, 1972b). Only much later, in the review of supraspecific feather mite taxa of the World, the subfamily Allodectinae was synonymized with Rhamphocaulinae without any comments (Gaud and Atyeo 1996). In addition, the new content of rhamphocaulines proposed in that monograph was expanded by the genus *Sclerodectes* Park et Atyeo, 1973, which was originally placed within the Pterodectinae and referred to the *Trochilodectes* group (Park and Atyeo 1973a). It is only possible to suggest that in establishing Allodectinae and Rhamphocaulinae the authors were impressed by the very unusual location of these mites, in the quills of flight feathers rather than on the surface of vanes, and did not take into account a number of similarities in leg chaetome of these two subfamilies and pterodectines of the *Trochilodectes* group. It is also surprising that the fact that *Trochilodectes* generic group (Pterodectinae) and the subfamily Rhamphocaulinae are associated with the same and very particular host group (hum-

mingbirds) also did not awake any suggestion about their possible close relationships.

Thus, the 19 genera of Pterodectinae are currently arranged in three generic groups, however phylogenetic relationships between these groups and within them have never been analyzed to confirm or restructure the recent classification. Moreover, the recent generic content (4 genera) of the subfamily Rhamphocaulinae (Gaud and Atyeo 1996) and even its substantiation as a natural taxon of subfamilial rank seems to be quite doubtful. Based on these problems in the system of Proctophyllodidae, the main goal of the present study is the analysis of phylogenetic relationships between genera of the subfamilies Pterodectinae and also its relationships with the subfamily Rhamphocaulinae. The secondarily goal is a general overview of geographical distribution and host associations of the subfamily Pterodectinae with the goal of making a preliminary hypothesis on their origin and pathways of dispersal among passerine hosts. Analyses of phylogenetic relationships of most species-rich pterodectine genera, such as *Montesauria* Oudemans, 1905, *Pterodectes* Robin, 1877, and *Proterothrix* Gaud, 1968, are suggested as subsequent steps in the phylogenetic study of Proctophyllodidae.

MATERIAL AND METHODS

Material

In total, representatives of almost all genera (21 of 23 genera) of the subfamilies Pterodectinae and Rhamphocaulinae and nearly 60% of recently known 184 species of these subfamilies have been examined.

Depositories of specimens represented in the data matrix are given in Table 1 by the following abbreviations: MNHN – the Muséum national d'Histoire naturelle (Paris, France), MRAC – the Musée royal de l'Afrique central (Tervuren, Belgium), ZIN – the Zoological Institute of the Russian Academy of Sciences (Saint Petersburg, Russia).

General morphological terms including leg and idiosoma chaetotaxy follow Gaud and Atyeo (1996); morphological terms concerning specifically proctophyllodid mites are those of Park and Atyeo (1971a) and subsequent taxonomic works on this group of mites (Mironov and Fain 2003; Mironov 2006, 2008; Valim and Hernandes 2008). General schemes of external morphological features of pterodectine mites used in the analysis are given in Figs. 1–3.

Scientific names of avian hosts follow "The Howard and Moore Complete Checklist" (Dickinson 2003); and passerine phylogeny follows recent concepts based on molecular studies (Ericson et al. 2002; Barker et al. 2004).

Phylogenetic analysis

Although the main goal of the study was to examine relationships at the generic level, all operational taxonomic units (OTUs) were represented by real species in the cladistic analysis. Pterodectine genera incorporating a relatively low number of species and not posing questions with regard to their monophyly were represented by one species per genus. In the cases of the species rich-genera *Montesauria* and *Pterodectes*, each species-group recognized within them was represented by one species. Specimens representing the genera *Cotingodectes* Valim et Hernandes, 2008 and *Berladectes* Valim et Hernandes, 2009 were not available for study; morphological data for them were taken from recent taxonomic publications (Valim and Hernandes 2008, 2009) (Abbreviation VH in Table 1). To avoid excessive polytomies, representatives of the two monotypic species-groups, *listroprocta* (*Montesauria*) and *megacaula* (*Proterothrix*), were not included, because they differed from the *emberizae* and *wolffi* groups of corresponding genera only by autoapomorphic features. *Trouessartia crucifera* Gaud, 1957 (Trouessartiidae) representing the closest analgoidean family (Dabert and Mironov 1999) was used as a distant outgroup. *Proctophyllodes vitzthumi* Fritsch, 1961 (Proctophyllodidae: Proctophyllodinae) and one species from each genus of the subfamily Rhamphocaulinae represented close outgroups and potential ingroups.

Qualitative morphological characters implying the presence/absence of a certain structure or certain form of morphological structure were used in the cladistic analysis (Table 2). A few autoapomorphic characters were also included in the analysis, because they are important for diagnoses, helpful for understanding evolutionary tendencies, and useful for future phylogenetic research at lower taxonomic levels. Because in the present analysis single pterodectine species are used to represent supraspecific taxa (genera or species groups), characters states appearing as autoapomorphies in terminal lineages actually represent true synapomorphies for species-groups and genera. Characters implying the presence/absence of
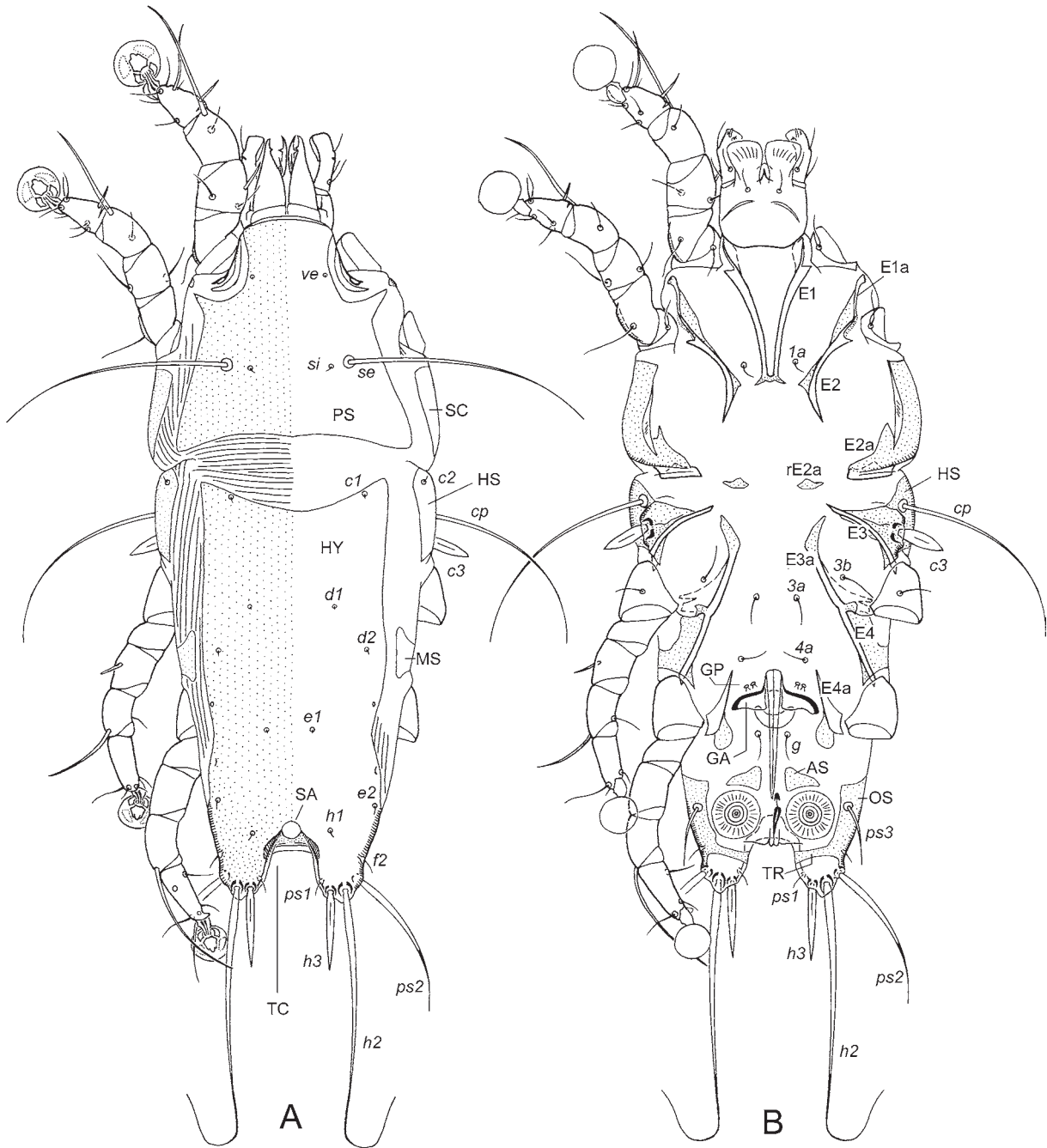
Fig. 1. Generalized morphology of a pterodectine male.
Abbreviations: AS – anal shields, E1–E4a – epimerites I-IVa, respectively, GA – genital arch, GP – genital papillae, HS – humeral shields, HY – hysteronotal shield, MS – metapodosomal sclerite, OS – opisthoventral shields, PS – prodorsal shield, rE2a – rudimentary sclerite of epimerites IIa, SA – supranal concavity, SC – scapular shields, TC – terminal cleft, TR – translobar apodeme. Names of setae after: Gaud and Atyeo (1996).
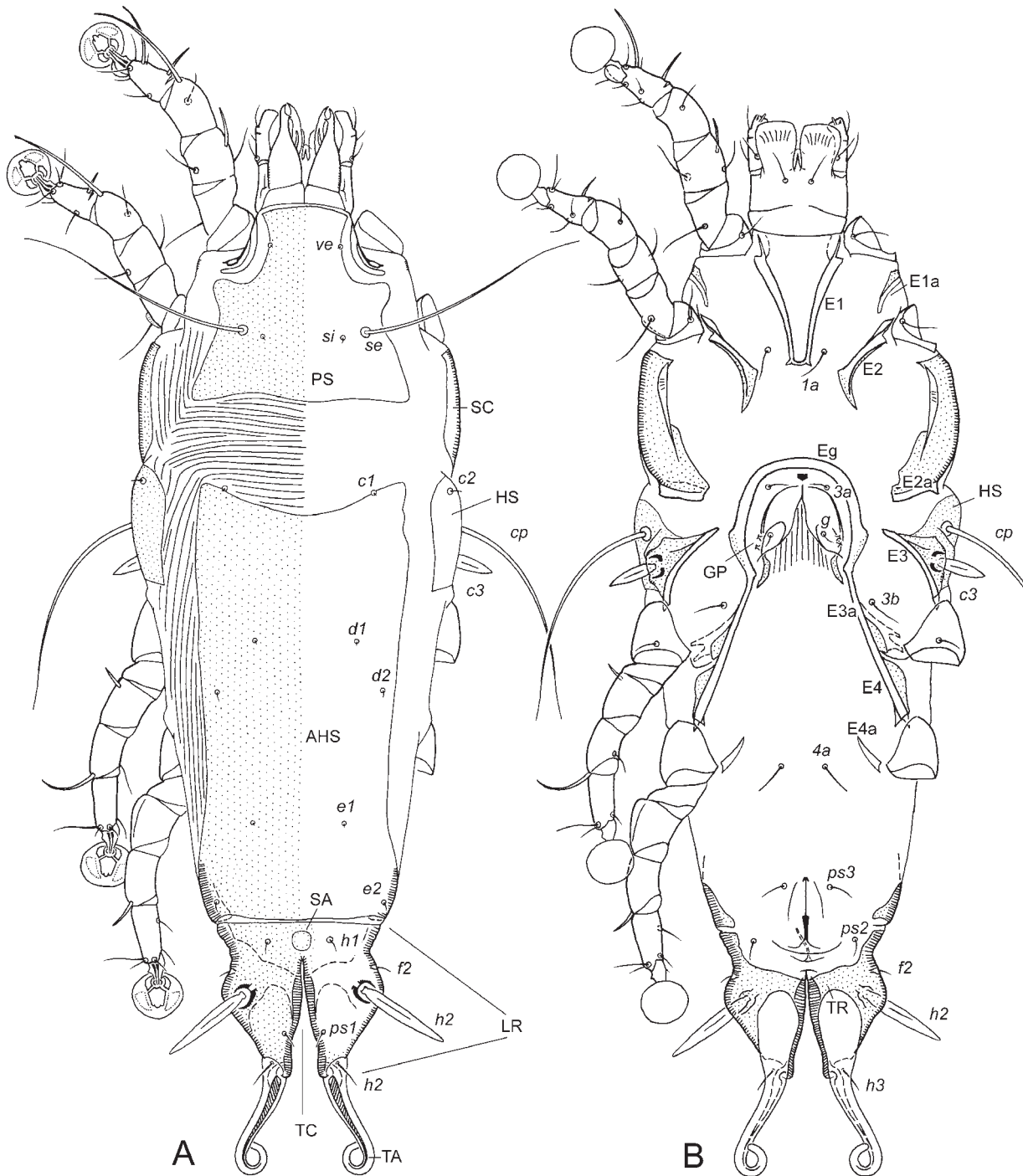
Fig. 2. Generalized morphology of a pterodectine female.
Abbreviations: AHS – anterior hysteronotal shield, E1–E4a – epimerites I-IVa, respectively, EG – epigynum, GP – genital papillae, HS – humeral shields, LR – lobar region, PS – prodorsal shield, SA – supranal concavity, SC – scapular shields, TA – terminal appendages, TC – terminal cleft, TR – translobar apodeme. Names of setae after: Gaud and Atyeo (1996).
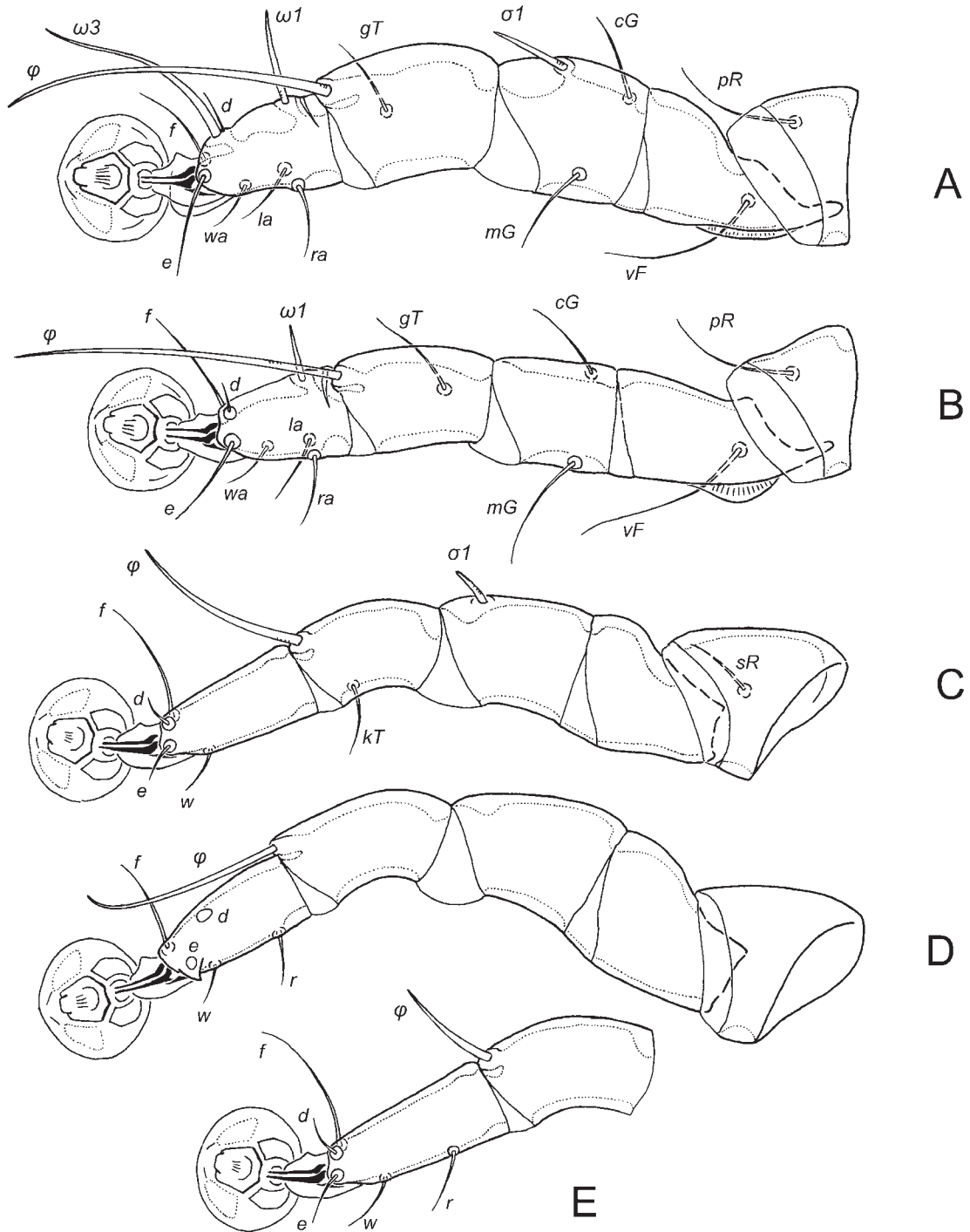
Fig. 3. Scheme of leg chaetome in pterodectines: A-D – legs I-IV of male, respectively; E – tibia and tarsus IV of female. Names of setae after Gaud and Atyeo (1996).

Table 1. Feather mite species used in phylogenetic analysis, their host associations, and source of material.

Mite species	Host species	Host family	Source
Trouessartia crucifera Gaud, 1957	*Hirundo rustica* Linnaeus, 1758	Hirundinidae	ZIN
Proctophyllodes vitzthumi Fritsch, 1961	*Sitta europaea* Linnaeus, 1758	Sittidae	ZIN
Alaudicola bilobata (Robin, 1877)	*Alauda arvensis* Linnaeus, 1758	Alaudidae	ZIN
Anisodicus megadiscus (Gaud et Mouchet, 1957)	*Deleornis fraseri cameroonensis* (Bannerman, 1921)	Nectariniidae	ZIN
Dolichodectes edwardsi (Trouessart, 1885)	*Acrocephalus arundinaceus* (Linnaeus, 1758)	Sylviidae	ZIN
D. myrmecocichlae (Mironov et Fain, 2003)	*Myrmecocichla nigra* (Viellot, 1818)	Turdidae	ZIN
Montesauria cylindrica (Robin, 1877)	*Pica pica* (Linnaeus, 1758)	Corvidae	MRAC
M. dolichodectina (Mironov et Fain, 2003)	*Acrocephalus rufescens* (Sharpe et Bouvier, 1876)	Sylviidae	ZIN
M. emberizae Mironov et Kopij, 1997	*Emberiza tahapisi* Smith, 1836	Emberizidae	ZIN
M. heterocaula (Gaud et Mouchet, 1957)	*Nigrita canicapilla* (Strikland, 1841)	Estrildidae	MRAC
M. jesionowskii Mironov et Kopij, 1997	*Apalis thoracica* (Shaw, 1811)	Cisticolidae	ZIN
M. merulae (Gaud, 1957)	*Turdus merula* (Linnaeus, 1758)	Turdidae	MRAC
M. papillo (Gaud et Petitot, 1948)	*Ploceus hypoxanthus* (Sparrman, 1788)	Ploceidae	ZIN
M. acridothera Mironov, 2006	*Acridotheres tristis* (Linnaeus, 1766)	Sturnidae	ZIN
Pedanodectes blaszaki Mironov, 2008	*Cynniris cupreus* (Shaw, 1812)	Nectariniidae	ZIN
P. marginarus Mironov et Kopij, 1997	*Camaroptera brachyura* (Vieillot, 1820)	Cisticolidae	ZIN
Berladectes neotropicus (Hernandes et Valim, 2006)	*Elaenia chiriquensis* Lawrece, 1865	Tyrannidae	VH
Cotingodectes interifolius (Trouessart, 1899)	*Rupicola peruviana* (Latham, 1790)	Cotingidae	VH
Metapterodectes furnarius Mironov, 2008	*Furnarius rufus* (Gmelin, 1788)	Furnariidae	ZIN
Pterodectes crassus Trouessart, 1885	*Cyanocorax chrysops* (Vieillot, 1818)	Corvidae	VH
Pt. ralliculae Atyeo et Gaud, 1977	*Rallina forbesi* (Sharpe, 1887)	Rallidae	ZIN
Pt. rutilus (Robin, 1877)	*Hirundo rustica* Linnaeus, 1758	Hirundinidae	ZIN
Pt. paroariae Mironov, 2008	*Paroaria capitata* (Orbigney et Lafresnaye, 1837)	Emberizidae	ZIN
Tyrannidectes berlai Mironov, 2008	*Myiarchus tyrannulus* (Muller, 1776)	Tyrannidae	ZIN
Afroproterothrix marginata Mironov et Wauthy, 2009	*Oriolus brachyrhynchus* Swainson, 1837	Oriolidae	ZIN
Megalodectes major (Trouessart, 1885)	*Menura novaehollandiae* Latham, 1802	Menuridae	MNHN
Nanopterodectes formicivorae (Mironov, 2008)	*Formicivora rufa* (Wied-Neuwied, 1831)	Thamnophilidae	ZIN
Neodectes hymenostomus (Gaud, 1968)	*Myzomela cardinalis* (Gmelin, 1788)	Meliphagidae	ZIN
Proterothrix wolffi (Gaud, 1962)	*Gerygone flavolateralis* (Gray, 1859)	Acanthizidae	ZIN
Allodectes amaziliae Park et Atyeo, 1972	*Amazilia fimbriata* (Gmelin, 1788)	Trochilidae	ZIN
Rhamphocaulus sinuatus Park et Atyeo, 1971	*Phaethornis longirostris* (DeLattre, 1843)	Trochilidae	ZIN
Schizodectes hiterminalis Park et Atyeo, 1972	*Phaethornis superciliosus* (Linnaeus, 1766)	Trochilidae	ZIN
Sclerodectes gracillimus (Trouessart, 1886)	*Heliothryx a. aurita* (Gmelin, 1788)	Trochilidae	ZIN
Syntomodectes topazae Park et Atyeo, 1973	*Topaza pella* (Linnaeus, 1758)	Trochilidae	ZIN
Toxerodectes gladifer (Trouessart, 1899)	*Eulampis jugularis* (Linnaeus, 1766)	Trochilidae	ZIN
Trochilodectes rhamphodonis Park et Atyeo, 1974	*Ramphodon naevius* (Dumont, 1818)	Trochilidae	ZIN
Xynonodectes sp.	*Anthracothorax viridis* (Audebert et Vieillot, 1801)	Trochilidae	ZIN

Table 2. Characters used in the phylogenetic analysis.

No.	Characters and coding
1	Prodorsal shield: entire (0), split into anterior and posterior parts (1), with pair of deep incisions on posterior margin (2).
2	Coxal fields I: not sclerotized (0), extensively sclerotized (1).
3	Coxal fields II: not sclerotized (0), extensively sclerotized (1).
4	Coxal fields III: not sclerotized (0), extensively sclerotized (1).
5	Coxal fields IV: not sclerotized (0), extensively sclerotized (1).
6	Vertical seta(e) *vi*: present (0), absent (1).
7	Position of idiosomal setae *c2*: laterally, on humeral shield or on soft tegument (0), on hysteronotal shield (1).
8	Form of idiosomal setae *c3*: straight, lanceolate or spiculiform, (0), curved, sabre-shaped (1).
9	Idiosomal setae *c1*: present (0), absent (1).
10	Idiosomal setae *d1*: present (0), absent (1).
11	Idiosomal setae *d2*: present (0), absent (1).
12	Idiosomal setae *e1*: present (0), absent (1).
13	Idiosomal setae *f2* in male: present (0), absent (1).
14	Idiosomal setae *f2* in female: present (0), absent (1).
15	Idiosomal setae *ps1* in male: present (0), absent (1).
16	Idiosomal setae *ps1* in female: present (0), absent (1).
17	Metapodosomal sclerites in male: absent (0), present (1).
18	Form of coxal fields II in male: open (0), closed (1).
19	Opisthosomal lobes in male, form and size: present, moderately elongated, not longer than width (0), absent, opisthosoma parallel-sided, truncated (1), absent, opisthosoma narrowed and rounded terminally (2), present, elongated, attenuate apically (3), present, elongated, each dissected into two lobules (4), present, elongated, rounded apically (5).
20	Length of opisthosoma and position of anal suckers in male: short, suckers at posterior margin (0), elongated, suckers at posterior margin (1), elongated, suckers closer to level of trochanters IV (2), elongated, suckers at midlevel of opisthosoma (3).
21	Terminal cleft size in male, form and size: absent or small, shallowly concave (0), large, angular or semiovate (1), large with additional incisions on inner margins of lobes (2), long and narrow (3).
22	Sclerotized subtegumental extension in anterior end of terminal cleft in male: absent (0), present (1).
23	Opisthoventral shields in male: absent (0), present (1).
24	Translobar apodemes in male: absent (0), present, crossing lobes (1), present, crossing opisthosoma anterior to terminal cleft (2).
25	Ventral sclerotization of lobes in males: absent or present near on distal margin (0), in distal half (1), all surface of lobes (2), wide band along margin of rounded opisthosoma (3).
26	Terminal lamellae in males: absent (0), pair of lamellae or short membranous extensions (1).
27	Genital arch in males, position of its base: at level of trochanters IV (0), between trochanters III and IV (1), posterior to trochanters IV (2), at level of trochanters III (3).
28	Sclerotized extension on posterior margin of genital arch: absent (0), present (1).

Table 2. *Continued.*

No.	Characters and coding
29	Wing-like lateral extensions of genital arch: absent (0), present (1).
30	Epimerites IV in male: absent or poorly developed (0), present, thick, not encircling genital arch (1), present, encircling genital arch, with long posterior extensions (2)
31	Fusion of epimerites IV with genital arch: absent (0), present (1).
32	Genital shield in male: absent (0), present, paired (1), present, unpaired (2).
33	Position of anterior pair of genital papillae in male: anterior to arch (0), posterior to arch (1).
34	Position of posterior pair of genital papillae in male: anterior to arch (0), posterior to arch (1).
35	Position of setae $h1$ in male: anterior to base of opisthosomal lobes, distant from lateral margins (0), in postero-lateral part of lobes near setae $ps2$ (1)
36	Size of setae $h2$ in male: large, macrosetae or lanceolate (0), minute, setiform (1).
37	Tooth-like extension on opisthosomal lobes near base of setae $h2$ in male: absent (0), present (1).
38	Position of setae $ps1$ in male: dorsal (0), ventral (1).
39	Position of setae $ps1$ in relation to $h3$ in males: approximately at same level or posterior (0), moved far anterior (1), moved laterally from inner margin of cleft (2).
40	Position of setae $ps2$ in male: anterior to level of setae $h2$ (0), slightly posterior or at level of setae $h2$ (1).
41	Distance between seta $ps3$ in males: closer to each other than anal suckers (0), much wider than distance between suckers (1).
42	Position of $ps3$ in relation to level of anal suckers in males: anterior (0), at level of sackers or posterior (1), far anterior to level of suckers (1).
43	Terminal appendages in females: absent (0), present (1).
44	Lobar region in female: separated (0), not separated (1).
45	Epigynum and epimerites IIIa: free (0), fused (1).
46	Form of setae $ps2$ in female: setiform (0), disc-like (1).
47	Form of setae $ps3$ in female: setiform (0), disc-like (1).
48	Ventral seta s of tarsus I: present (0), absent (1).
49	Ventral seta s of tarsus II: present (0), absent (1).
50	Position of ventral seta wa on tarsus I: approximately at midlevel, together with setae ra, la (0), in anterior part of segment (1).
51	Position of ventral seta wa on tarsus II: approximately at midlevel, together with setae ra, la (0), in anterior part of segment (1).
52	Length of solenidion $\sigma1$ on genu I: longer than segment (0), shorter than or subequal to segment (1).
53	Solenidion $\sigma1$ of genu II: present (0), absent (1).
54	Solenidion $\sigma1$ of genu III: present (0), absent (1).
55	Length of solenidion $\sigma1$ on genu III: shorter than segment (0), equal to or longer than segment (1).
56	Setae sR of trochanters III: present (0), absent (1).

Table 2. *Continued.*

No.	Characters and coding
57	Position of solenidion σ*1* on genu III in male: apical or at midlevel (0), basal (1).
58	Ventral crest on genu IV in male: absent (0), present, distal (1), present, ventral (2).
59	Ventral crest on tarsus IV in male: absent (0), present (1).
60	Ratio of solenidia φ of tibiae III and IV in female: subequal (0), solenidion of tibia IV much shorter (1).
61	Length of solenidion φ of tibia IV in female: longer than segment (0), shorter than segment (1).
62	Size of setae *h3* in female: macrochaetae, subequal to setae *h2* (0), small, setiform (1).
63	Length of setae *d, f* of tarsus III: subequal (0), seta *d* nearly twice shorter than *f* (1).
64	Length of setae *d, f* of tarsus IV: subequal (0), seta *d* nearly twice shorter than *f* (1).
65	Legs I in female: normal, slightly larger than or subequal to legs II (0), hypertrophied, much longer and thicker than legs II, genu and tibia strongly modified (1).

idiosomal setae belonging to the "terminal complex", situated on the posterior margin of opisthosoma, were considered as separate characters for males and females, because the loss of these setae may be inconsistent in different sexes of analgoidean feather mites, for instance Alloptidae Gaud, 1957.

In total, 37 OTUs and 65 characters, 7 of which represented autapomorphies in the ingroup (Pterodectinae + Rhamphocaulinae), were included in the maximum parsimony-based cladistic analysis (Table 3). Constructing of the data matrix was done using NEXUS Data Editor 0.5.0 (Page 2001). All characters were treated as unordered; characters having multiple states (three or more) were not modified into binary characters and were treated as polymorphic. Reconstruction of phylogenetic relationships was performed with PAUP 4.0 beta version for Windows 95/NT (Swofford 1998). The branch and bound algorithm was used for the maximum parsimony analysis. For *a posteriori* optimization of character states and tracing of character changes in lineages, the DELTRAN option (delayed transformation), which favours parallelism over reversal, was applied. Bremer indices used for estimating support for branches were calculated by means of Autodecay (Eriksson 1998). Trees were drawn using Winclada, version 1.0 (Nixon 1999).

RESULTS

The branch-and-bound search produced five shortest trees having length 128 steps and standard indices as follows: CI=0.61, RI=0.79, RC=0.52 (uninformative characters excluded). Strict consensus of these trees is shown in Fig. 4. The differences between these trees lay only in the position of the genus *Alaudicola* in relation to the *Montesauria* complex, in the position of the genus *Tyrannidectes* in relation to other genera of the *Pterodectes* complex and in the position of *Montesauria emberizae* in relation to the genus *Pedanodectes*.

The analysis shows that all proctophyllodid genera referred to Pterodectinae and Ramphocaulinae form a common branch, which is a sister clade to the subfamily Proctophyllodinae. The "Pterodectinae – Ramphocaulinae" branch is characterized by the fusion of the epigynum with epimerites IIIa in females (character 45) and the absence of membranous structures on opisthosomal lobes in males (26). However the obtained result does not support the traditional suggested relationships between Pterodectinae and Ramphocaulinae (Park and Atyeo 1971a, 1971b; Gaud and Atyeo 1996)[1]. All four genera referred to the Ramphocaulinae constitute a terminal cluster

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[1]It is interesting to note here that similar pattern of branching (all hummingbird-associated pterodectine genera and ramphocauline genera constitute a common branch versus the branch of remaining pterodectine genera) was inferred based on the analysis of molecular sequences of the nuclear amino acids gene HSP70 (P.B. Klimov, University of Michigan, USA, personal communication).

Table 3. Data matrix of character states for Pterodectinae and outgroup taxa. Character states are scored as 0 to 5, inapplicable states as "–".

Taxa	Character states						
	1 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890	5555555556 1234567890	66666 12345
Trouessartia crucifera	0000000010	0000000000	1000000000	0000000000	0001000000	0000000000	00000
Proctophyllodes vitzthumi	0000010000	0000000010	0000000000	0000000000	0010000110	0010000000	01000
Alaudicola bilobata	1000010000	0000000000	0011010000	0011000000	1110100111	1110010001	11000
Anisodiscus megadiscus	0000010001	0111110001	0010011000	0011000000	1210100111	1111-0-001	11110
Dolichodectes edwardsi	0000010000	0000001132	0012010002	0211000010	1110100111	1110000201	11110
Dolichodectes myrmecocichlae	0000010000	0000001132	0012010002	0111000010	1110100111	1110000001	11110
Montesauria cylindrica	0000010000	0011000000	0110010000	0011100000	1110100111	1110000001	11110
Montesauria dolichodectina	0000010000	0000001000	0010010000	0111000000	1110100111	1110000001	11110
Montesauria emberizae	0000011000	0000000000	0010010000	0011000000	1110100111	1110000001	11110
Montesauria heterocaula	0110010000	0000000000	0010010000	0011000000	1110100111	1110000001	11110
Montesauria jesionowskii	0000010000	0011000000	0010010000	0011000020	1110100111	1110000001	11110
Montesauria merulae	0000010000	0011000000	0010010000	0011001020	1110100111	1110000111	11110
Montesauria papillo	0000010000	0000000000	0010010010	0011000000	1110100111	1110000001	11110
Montesauria acridothera	0000010000	0011000000	0110010000	0011100000	1110100111	1110000001	11111
Pedanodectes blaszaki	0000011011	0100000010	0010010100	1011000000	1110100111	1110001001	11110
Pedanodectes marginatus	0000011011	0100000010	0010010000	1011000000	1110100111	1110001001	11110
Berladectes neotropicus	0000010000	0000000053	3010010002	0200000000	1110100111	1110000001	11110
Cotingodectes interifolius	0000010000	0000000043	2010210002	0000000000	1110100111	1110000001	11110
Metapterodectes furnarius	0000010000	0000000000	0010010000	0000000000	1110111111	1111-1-001	11110
Pterodectes crassus	2000010000	0000000000	0010010000	0000000000	1110111111	1110010001	11110
Pterodectes ralliculae	0000010000	0011000052	1010210000	0011000020	1110100111	1110000111	11110
Pterodectes rutilus	0000011000	0000000000	0010010000	0000000000	1110100111	1110000001	11110
Pterodectes paroariae	0000010000	0000000000	0010110000	0000000000	1110100111	1110000001	11110
Tyrannidectes berlai	0000010000	0000000000	0010010000	0000000000	1110100111	1110010001	11110
Afroproterothrix marginata	0000010010	1011000000	0000010000	0000000000	0011100111	1110001001	11000
Megalodectes major	0000010000	0000000000	0010012000	0000000000	0010100111	1110000000	11000
Nanopterodectes formicivorae	0000010001	1011000000	0000010000	0000000000	0010100110	0110001001	11000
Neodectes hymenostomus	0000010000	0000000000	0000010001	0011000000	0010100111	1110001001	11110
Proterothrix wolffi	0000010000	0000000000	0000010001	0000000000	0010100111	1110001001	11110
Allodectes amaziliae	0111110100	0000001020	0010313000	0000010100	1110100110	0010100000	01110
Rhamphocaulus sinuatus	0111110100	0000001020	0010313000	0000010100	1010100110	0010100000	01110
Schizodectes hiterminalis	0111110000	0000001000	1010010000	0000000000	1110100110	0010100000	01110
Sclerodectes gracillimus	0111110000	0000000000	1010010000	0000000001	1011100110	0010100000	01110
Syntomodectes topazae	0000010000	0000000000	0010010000	0000000001	1111100110	0010100000	01110
Toxerodectes gladifer	0000010000	0000000000	1000010000	0000000001	1111100110	0010100000	01110
Trochilodectes rhamphodonis	0000010000	0000001000	0010010000	0000000000	1010100110	0010100000	01110
Xynonodectes sp.	0000010000	0000000000	0000010000	0000000000	1110100110	0010100000	01110

inside one of pterodectine branches, but do not form a sister branch of the whole subfamily Pterodectinae sensu Park and Atyeo. The monophyletic trunk "Pterodectinae – Ramphocaulinae" splits into two major branches, which are considered here in taxonomic sense as the tribes Ptreodectini (branch I) and Rhamphocaulini (branch II), respectively (Fig. 4). Branch I bears 15 genera of the subfamily Pterodectinae which are mostly associated with passerines. This branch is characterized by moving of seta *wa* on tarsi I, II to the apical part of these segments (50, 51), shortened solenidion σ*1* on genu I in both sexes (52), and shortened solenidion φ of tibia IV in females (61). Branch II includes four genera previously included in the Pterodectinae (*Trochilodectes* group sensu Park and Atyeo 1971) and all four genera previously included in the Ramphocaulinae (sensu Gaud and Atyeo 1996), with the latter forming a terminal cluster in this branch (*Allodectes, Rhamphocaulus, Schizodectes*, and *Sclerodectes*). Branch II is characterized by moving of pseudanal setae *ps3* to lateral margins of opisthosoma in male (41) and elongated solenidion σ*1* III in both sexes (56), and shortened apico-dorsal setae *d* of tarsi III, IV in females (63, 64). Derived genera of this branch referred by Gaud and Atyeo (1996) to Rhamphocaulinae are characterized
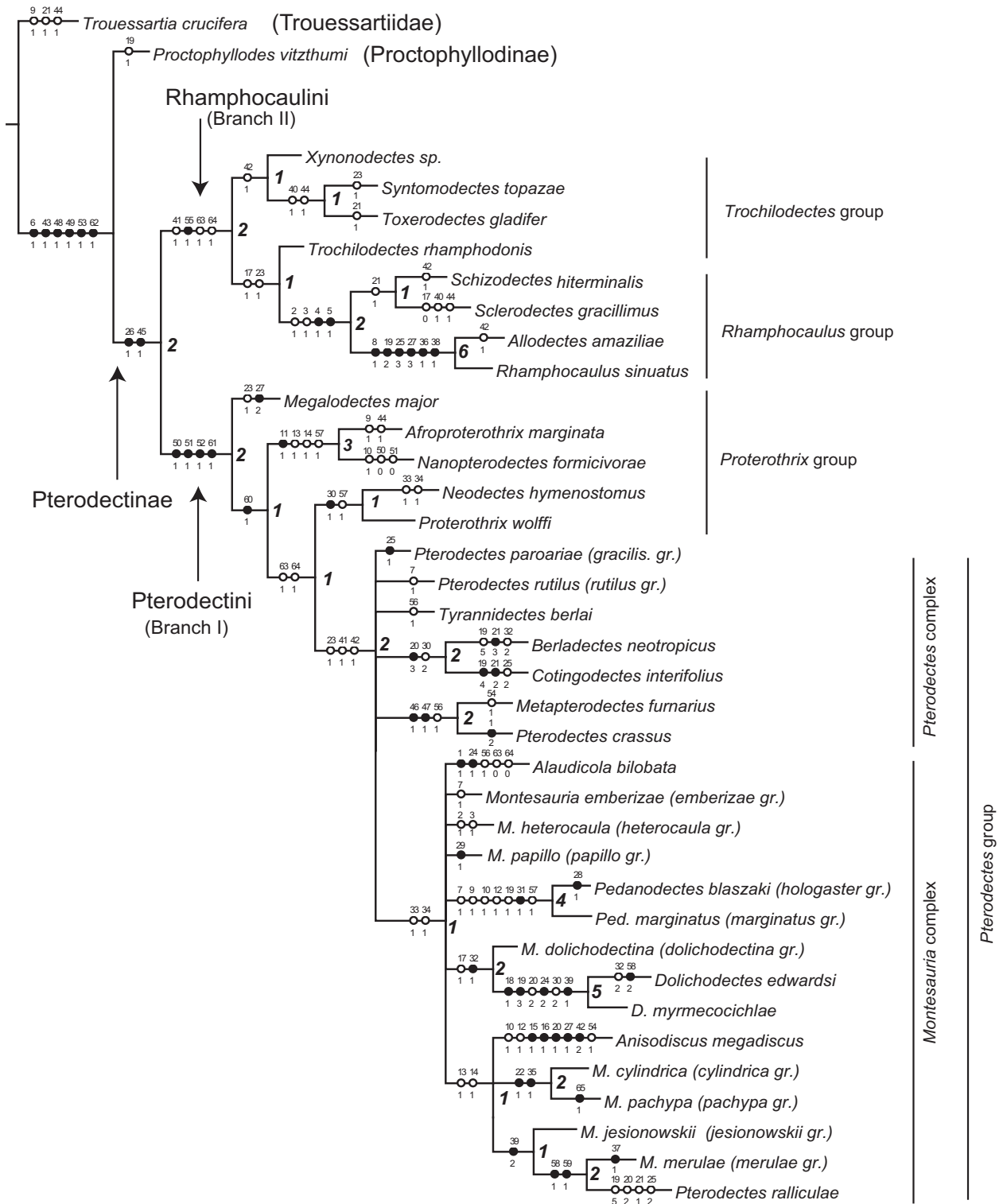
Fig. 4. Phylogeny of Pterodectinae. Strict consensus of five most parsimonious trees. DELTRAN character optimisation. Numbers above circles (black – unique apomorphy, white – homoplasy) refer to characters; numbers under circles refer to a character state achieved in the respective node. Numbers in bold Italics near nodes are values of Bremer index.

only by extensive sclerotization of coxal fields I–IV (2–5).

In the basal part of branch I, there are three clusters apparently representing early derivative lineages: the sole genus *Megalodectes,* the genera *Afroproterothrix* + *Nanopterodectes,* and *Neodectes* + *Proterothrix*. All these genera retain the antero-mesal position of setae *ps3* in males that is obviously a plesiomorphic state, because this position of these setae is typical for proctophyllodines and for most other mites of the superfamily Analgoidea. Although this set of five genera is paraphyletic, it may be referred as the *Proterothrix* generic group to stress the morphological primitiveness of these taxa in relation to other genera of the branch I. The other ten genera of the branch I (*Pterodectes* generic group in present sense), are characterized by the following apomorphies in males: opisthoventral shields are well developed (23), setae *ps3* are moved and apart from each other closer to lateral margins of opisthosoma, and backward, to the level of anal suckers or posterior to it (41, 42).

The upper part of branch I bears an unresolved node uniting a large cluster of the *Montesauria* complex, and five small clades. Representatives of these small clades with unresolved relationships may be referred to as the *Pterodectes* complex. The more derived *Montesauria* complex is clearly characterized by moving of genital papillae in males backward, to the level of genital arch base or even posterior to it (33, 34). It is interesting to note that the same character state was developed independently in the genus *Neodectes* belonging to the *Proterothrix* group. There are no synapomorphies that unite mites of the *Pterodectes* complex into a sister branch to the *Montesauria* complex, possibly because the former branch had split into several separate lineages too quickly. Within the *Pterodectes* complex, the clade bearing the genus *Metapterodectes* and *Pterodectes crassus* is characterized by modification of two pairs of pseudanal setae *ps2* and *ps3* into sucker-like structures in females (46, 57). The clade *Berladectes* + *Cotingodectes* is characterized by an elongated opisthosoma with anal discs situated in its distal part (20.3) and by the development of posterior extension in epimerites IV in males (30.2). Thus, according to the result of analysis, the genus *Pterodectes* in the current concept, even after recent removing of some species into separate genera (Mironov et al. 2008b; Valim and Hernandes 2009), appears to be a paraphyletic taxon not supported by any apomorphy.

Relationships between seven lineages constituting the *Montesauria* complex (Fig. 4) are not completely resolved. Three of these lineages lead to obviously derived genera and others represent three species groups of the genus *Montesauria*. This shows that the genus *Montesauria* in the traditional concept (Park and Atyeo 1971a; Mironov 2006, 2008) also appears paraphyletic. One of these clusters unites five species groups of *Montesauria* (*cylindrica, pachypa, merulae, jesionowskii), Pterodectes ralliculae,* and the genus *Anisodiscus* and is characterized by the loss of opisthosomal setae *f2* in both sexes (13, 14). Within this cluster, the genus *Anisodiscus* is the most divergent taxon having a large number of apomorphies: the strongly elongated opisthosoma with anal discs retained near its posterior margin (20.1), and the loss of three pairs of idiosomal setae *d1, e1, ps1* and solenidion *σ1* on trochanters III (10, 12, 15, 16, 54), setae *ps3* moved posterior to anal suckers in males (42). The second cluster bears the genus *Dolichodectes* and the *dolichodectina* species group of *Montesauria* and is marked by the development of the metapodosomal sclerites (17) and paired genital shield (32.1). *Dolichodectes* is characterized by the following apomorphies in males: closed coxal fields II (18), strongly elongated opisthosomal lobes with attenuate apices (19.3), elongated opisthosoma with anal discs situated closer to trochanters IV than to lobar apices (20.2), translobar apodemes crossing opisthosoma (24.2), epimerites IVa encircling genital arch (30.1) and setae *ps1* moved strongly anterior to the level of macrosetae *h3* (39.1). The third cluster of derived taxa represents the genus *Pedanodectes* and is marked by the following features: in both sexes, median idiosomal setae *c1, d1* and *e1* are absent (9, 10, 12), in males, the opisthosoma is truncated (19.1), epimerites IV are connected with the genital arch (31), and solenidion *σ1* of trochanters III is in the most base of segment (57). The genus *Alaudicola* is marked by the following features: in both sexes, prodorsal shield split into anterior and posterior parts (1), setae *sR* on trochanters III are absent (56), in males, translobar apodemes cross opisthosomal lobes (24.1), in females, setae *d* and *f* of tarsi III and IV are subequal length (63, 64). The two latter characters appear here as reversals, because in all other representatives of the *Montesauria* and *Pterodectes* complexes, tarsal setae *d* III, IV are much shorter than corresponding setae *f*. It is interesting to note that *Pterodectes ralliculae* Atyeo et Gaud, 1977, provision-

ally placed by its authors in the genus *Pterodectes*, appears in the cladogram as a sister lineage to the *Montesauria merulae* species group, and its position within the cluster containing several species groups of *Montesauria* is clearly supported by a number of apomorphies. The placement of this species in the genus *Pterodectes* was an obvious mistake of its authors.

Branch II splits into two clusters. One of them bears three genera (*Syntomodectes, Toxerodectes,* and *Xynonodectes*) belonging to the *Trochilodectes* generic group sensu Park and Atyeo (1971); this lineage is characterized by moving of setae *ps3* lateral or postero-lateral in relation to anal suckers (41). The second cluster is marked by the presence of metapodosomal sclerites and opisthoventral shields in males (17, 23). The apical part of this cluster bears four genera (*Allodectes, Rhamphocaulus, Schizodectes,* and *Sclerodectes*) and is characterized only by the extensive sclerotization of coxal fields I–IV (2–5). These genera constituted the subfamily Rhamphocaulinae in the concept of Gaud and Atyeo (1996). The lineage of *Allodectes* + *Rhamphocaulus* is marked by following apomorphies: in both sexes, subhumeral setae *c3* curved and relatively elongated (8); in males, the opisthosoma is attenuated and rounded posteriorly (19.2) posterior end of opisthosoma with wide ventral sclerotization (25.3), genital arch moved to the level of trochanters III (27), strongly shortened setae *h2* (36), and moving of setae *ps1* to ventral side of opisthosoma in males (38). These two genera are the most morphologically derived genera in the branch II. In contrast to the lineage of *Allodectes* + *Rhamphocaulus,* mites of the genera *Schizodectes* and *Sclerodectes* are characterized by having a large terminal cleft separating well developed opisthosomal lobes (20.1).

DISCUSSION

Phylogeny and systematics

In the result of cladistic analysis it was found that phylogenetic relationships between the proctophyllodid genera characterized by having the epigynum fused with epimerites in females and by lacking any membranous extensions on the opisthosoma in males constitute a common phylogenetic branch in the family Proctophyllodidae. However, phylogenetic relationships between genera of these proctophyllodids do not correspond to the current taxonomic arrangement of them into subfamilies and generic groups (Park and Atyeo 1971a; Gaud and Atyeo 1996). Based on the results of analysis, the most reasonable taxonomic reformation of the current system is to unite all these proctophyllodid mites into the subfamily Pterodectinae. In turn, the two major branches (I, II) bearing pterodectines in the present sense (Fig. 4) deserve to be treated as the tribes Pterodectini trib. n. and Rhamphocaulini stat. n. (Table 4). Thus, Rhamphocaulinae, the taxon of familial grouping retains; its rank is decreased, while its generic content is expanded by the inclusion of four genera, formerly referred to the *Trochilodectes* group of the subfamily Pterodectinae sensu Park and Atyeo (1971a).

The tribe Pterodectini is determined by having setae *wa* of tarsi I, II moved to apical part of the segment, solenidion σ*1* of genu I shorter than or subequal to this segment, and solenidion σ*1* of genu III significantly shorter than this segment. The genus *Nanopterodectes* represents an exception regarding the former character, because tarsal setae *wa* in this genus are not noticeably moved to the apical part of the tarsi I, II. This character state could be probably explained by shortening of leg segments in representatives of this genus and generally smaller body size of these mites regarding to most other pterodectines. The tribe Rhamphocaulini is characterized by the following set of characters: ventral setae *wa* on tarsi I, II are situated at the midlevel of these segments (near bases of corresponding setae *la* and *ra*), solenidion σ*1* of genu I is definitely longer than this segment, and solenidion σ*1* of genu III is subequal or longer than segment.

Within the tribe Pterodectini, it is currently expedient to recognized two generic groups, *Proterothrix* and *Pterodectes*. Although the first group is paraphyletic and unites early derivative Pterodectini, its genera clearly differ from the representatives of the monophyletic *Pterodectes* group by retaining a very distinct plesiomorphic feature, the antero-mesal position of pseudanal setae *ps3* in relation to anal suckers. In turn, two generic complexes can be recognized within the *Pterodectes* group. The *Montesauria* complex is monophyletic and includes pterodectines characterized by moving of genital papillae to base of genital apparatus in male. Relationsips between lineages of *Pterodectes* complex are not completely

Table 4. Host associations and distribution of genera and species-groups of the subfamily Pterodectinae.

Tribe	Mite taxa (generic group, genus, species group)	Species (n)	Host families and number of recorded mite species	Range
	Group *Pterodectes*			
	Alaudicola Mironov, 1996	4	Passeriformes: Alaudidae – 3, Muscicapidae – 1	Eurasia, Africa
	Anisodiscus Park et Atyeo, 1971	5	Passeriformes: Cisticolidae – 1, Nectariniidae – 4	Africa
	Dolichodectes Park et Atyeo, 1971	6	Passeriformes: Monarchidae – 1, Muscicapidae –2, Platisteiridae – 1, Sylviidae – 1, Turdidae – 1	Eurasia, Africa
	Montesauria Oudemans, 1905	51		
	cylindrica gr.	6	Passeriformes: Corvidae – 2, Sturnidae – 3, Viduidae – 1	Eurasia, Africa
	dolichodectina gr.	3	Passeriformes: Pycnonotidae – 1, Sylviidae – 2	Africa
	emberizae gr.	4	Passeriformes: Emberizidae –3, Viduidae –1	Africa
	heterocaula gr.	7	Passeriformes: Estrildidae – 7,	Africa
	jesionowskii gr.	1	Passeriformes: Cysticolidae – 1	Africa
	listroprocta gr.	1	Passeriformes: Picathartidae –1	Africa
Pterodectini	*merulae* gr.	9	Passeriformes: Dicruridae – 1, Laniidae – 1, Muscicapidae – 1, Pycnonotidae – 2, Turdidae – 3; Piciformes: Lybiidae – 1	Eurasia, Africa
	pachypa gr.	5	Passeriformes: Sturnidae – 5	Eurasia, Africa
	papillo gr.	14	Passeriformes: Ploceidae – 10, Passeridae – 1, Cysticolidae –3	Eurasia, Africa
	M. reticulifera (Trouessart et Neumann, 1888)**	1	Passeriformes: Alaudidae – 1	North America
	Pedanodectes Park et Atyeo, 1971	6		
	hologaster gr.	3	Passeriformes: Nectariniidae – 3,	Africa
	marginatus gr.	3	Passeriformes: Cysticolidae –1, Laniidae –1, Platysteiridae – 1	Africa
	Berladectes Valim et Hernandes, 2009	1	Passeriformes: Tyrannidae – 1	South America
	Cotingodectes Valim et Hernandes, 2009	2	Passeriformes: Cotingidae – 2	South America
	Metapterodectes Mironov, 2008	3	Passeriformes: Emberizidae – 1, Furnariidae –2	South America
	Pterodectes Robin, 1877	26		
	gracilis gr.	19	Passeriformes: Emberizidae – 4, Icteridae – 3, Turdidae – 4, Parulidae – 2, Thraupidae – 3, Troglodytidae – 1, Tyrannidae –2	New World
	rutilus gr.	1	Passeriformes: Hirundinidae – 1	Old World, North America
	P. crassus (Trouessart, 1885)*	1	Passeriformes: Corvidae – 1	South America
	P. ralliculae Atyeo et Gaud, 1977*	1	Gruiformes: Rallidae – 1	Indo-Malaya: New Guinea

Table 4. *Continued.*

Tribe	Mite taxa (generic group, genus, species group)	Species (n)	Host families and number of recorded mite species	Range
	P. intermedius (Trouessart, 1885)**	1	Passeriformes: Eurylaimidae – 1	Indo-Malaya: Malacca
	P. phylloproctus Trouessart, 1885**	1	Caprimulgiformes: Podagridae –1 (?)	Indo-Malaya: New Guinea
	P. trouessarti Berlese, 1898**	1	Passeriformes: Laniidae –1 (?)	Europe
	P. trulla Trouessart, 1885**	1	Musophagiformes: Musophagidae – 1 (?)	Africa: Gabon
	Tyrannidectes Mironov, 2008	2	Passeriformes: Tyrannidae – 2	South America
	Group *Proterothrix*			
	Afroproterothrix Mironov et Wauthy, 2009	1	Passeriformes: Oriolidae – 1	Africa
	Megalodectes Park et Atyeo, 1971	1	Passeriformes: Menuridae –1	Australia
	Nanopterodectes Mironov nom. nov.	1	Passeriformes: Thamnophilidae – 1	South America
	Neodectes Park et Atyeo, 1971	3	Passeriformes: Meliphagidae – 3	Australia
	Proterothrix Gaud, 1968	22		
	megacaula gr.	1	Passeriformes: Muscicapidae – 1	South East Asia
	schizothyra gr.	4	Coraciiformes: Alcedinidae – 4	Africa, Madagascar
	wolffi gr.	17	Passeriformes: Acanthizidae – 1, Dicruridae – 1, Eurylamiidae – 2, Monarchidae – 4, Paradisaeidae – 5, Paradoxornithidae –3, Rhipiduridae – 1	Indo-Malaya, Australia
	Group *Rhamphocaulus*			
	Allodectes Park et Atyeo, 1972	12	Apodiformes: Trochilidae – 12	South America
	Rhamphocaulus Park et Atyeo, 1971	3	Apodiformes: Trochilidae – 3	South America
	Schizodectes Park et Atyeo, 1973	2	Apodiformes: Trochilidae – 2	South America
	Sclerodectes Park et Atyeo, 1973	2	Apodiformes: Trochilidae – 2	South America
	Group *Trochilodectes*			
	Syntomodectes Park et Atyeo, 1971	2	Apodiformes: Trochilidae – 2	South America
	Toxerodectes Park et Atyeo, 1971	15	Apodiformes: Trochilidae – 15	South America
	Trochilodectes Park et Atyeo, 1971	10	Apodiformes: Trochilidae – 10	South America
	Xynonodectes Park et Atyeo, 1971	4	Apodiformes: Trochilidae – 4	South America

Notes. *– species does not belong to corresponding genus according to the present study, ** – species inquerenda in corresponded genus, (?) – questionable host association.

resolved and its monophyly is questionable, but in relation to the *Montesauria* complex they may be evaluated as a grouping retained plesiomorphic position of genital papillae.

The genera formerly referred to the *Trochilodectes* group (Park and Atyeo 1971a) also represent a para-

phyletic grouping in the tribe Rhamphocaulini and can be characterized by the absence of sclerotization in all coxal fields. Four derived genera of this tribe formerly constituting the subfamily Rhamphocaulinae (*Allodectes, Rhamphocaulus, Schizodectes* and *Sclerodectes*) are characterized by extensively sclero-

tized coxal fields and may be provisionally referred to as the *Rhamphocaulus* group.

Host associations and diversification on passerine hosts

All known data on host associations of pterodectines (in sense of the present study) with avian order and families are summarized in Table 4. For species-rich genera containing several distinct species groups, these data are given separately for each particular group. For uncertain species (species inquerenda) and for species whose placement in corresponding genus appeared questionable or incorrect in the course of the present cladistic analysis, the data of host associations are also given separately.

Based on the analysis of general host associations of pterodectine genera and species-groups (Table 4), the pattern of their phylogenetic relationships (Fig. 4), and a current concept of the phylogeny and of historical biogeography of passerines (Ericson et al. 2002; Barker et al. 2004), a provisional hypothesis describing the evolution and diversification of Pterodectinae on Passeriformes may be generally outlined. As mentioned previously, pterodectines are currently distributed throughout the World on birds from 34 families of Passeriformes. These mites are also very diverse on apodiforms, but they are restricted only to one family, the hummingbirds (Apodiformes: Trochilidae). Particular species from this family (for instance representatives of the genera *Campylopterus* Swainson, 1827 and *Amazilia* Lesson, 1843) can simultaneously bear up to four species belonging to different genera (Park and Atyeo 1975; personal field observations in 2008). Reliable host associations of pterodectines with birds from orders other than passeriforms and apodiforms are exceptional cases; an in these cases all such species belong to derived pterodectine genera mostly distributed on recent passerines (*Montesauria, Proterothrix,* and *Pterodectes*). This gives evidence that these exceptional associations are apparently of a secondarily origin, and the orders Piciformes, Coraciiformes, Gruiformes and others do not have now any primary pterodectine fauna.

Based on these data on host distribution among bird orders, it is most reasonable to conclude that the subfamily Pterodectinae originated on the ancestor of passeriforms as a result of splitting of the ancestral proctophyllodid lineage into pterodectines and proctophyllodines. That splitting could be possibly have been caused by the specialization of ancestral proctophyllodids to different groups of flight feathers or even different zones within the vanes. Thus, adults and tritonymphs of many pterodectine species are mostly located in distal part of vanes and in zones definitely distant from rachis, even in fast flying birds like swallows, and apparently represent proctophyllodids that are more resistant to the difficult conditions on flight feather (vibration, strong air stream, instant changes of temperature) than mites of subfamily Proctophyllodinae. Mites of the latter subfamily may occupy various zones of vane, but usually they sit much closer to the rachis than to the free margin of the vane. This difference in location on the vane is particularly noticeable and in the case of cohabitation of species from these subfamilies on the same bird individual (for instance on hosts from the families Alaudidae, Sylviidae, Turdidae; personal observation on alive captured birds).

An alternative suggestion that pterodectines could have originated on the common ancestor of passerines and closely related non-passeriform orders (Piciformes, Coraciiformes, Apodiformes) needs too many additional hypotheses and therefore is quite improbable. Thus, it would be necessary to admit that primary pterodectines went completely extinct on all coraciiforms and piciforms, and also on swifts (Apodiformes: Apodidae). Additional evidence for the origin of Pterodectinae on passeriforms is the recent distribution of its sister subfamily Proctophyllodinae. This subfamily is also predominantly distributed on Passeriformes and only erratically occurs on several non-passeriform orders (see data in: Atyeo and Braasch 1966); as in pterodectines, there is no specific proctophyllodine genera restricted to bird orders other than passerines.

A great diversity of pterodectines on Trochilidae could be the most serious objection to the primary origin of this subfamily in the frame of Passeriformes. However this diversity could have the following explanation. Pterodectine genera restricted to trochilids constitute a monophyletic group, but are quite different from each other in size, in form of the body and even in biology, much more than pterodectine genera living on passerines. At the same time these quite different species occur on one host species occupying different microhabitats in flight feathers. It seems most probable that primitive pterodectines similar to *Trochilodectes* transferred from some New World suboscines to the ancestor of trochilids and

experienced a burst of speciation because they either did not face any competitors like the pterolichoid mites (Eustathiidae) that are now very diverse on the sister family Apodidae, or were able to replace them and specialize to different niches in the flight plumage. The most notable achievement of this speciation was the adaptation in the most derived genera (*Rhamphocaulus* group) to live inside quills rather on vanes of flight feathers.

Thus, the most reasonable conclusion is that pterodectines arose on the passeriform ancestors that originated in Gondwana and then further dispersed around the World by different routes (Ericson et al. 2002; Barker et. al. 2004). Pterodectines dispersed along with passerines, and the origin of generic groups was caused by the splitting of the main major branches of passerines (cospeciations process), although colonizing new host taxa by horizontal transfer probably took place many times during the evolution of this subfamily of mites. Early derivative lineages of pterodectines (*Proterothrix* group) were formed on suboscines that migrated to South America and on the infraorder Corvida (oscines) that originated in Australia and then dispersed to Indonesia, South East Asia and finally to Africa. *Nanopterodectes* is the only representative of this generic group on New World suboscines in South America. The genus *Megalodectes* arose on lyrebirds (Menuroidea: Menuridae) and *Neodectes* was formed on honeyeaters (Meliphagoidea: Meliphagidae) in Australia. The genus *Proterothrix* is currently distributed on various families of birds including coraciiforms in the Old World, but the greatest number of its species occurs on representatives of Corvoidea. Therefore, *Proterothrix* was probably formed on the ancestors of corvoideans in Australia and Indo-Malayan region, but further its representatives dispersed to South East Asia and Africa and occupied some hosts from the infraorder Passerida (Muscicapidae, Paradoxornithidae) and also kingfishers (Coraciiformes: Alcedinidae). Two species referred to *Proterothrix* were recorded from Eurylaimidae (Trouessart 1885; Canestrini and Kramer 1899; Park and Atyeo 1971a), which belongs to the Old World suboscines; unfortunately these specimens were unavailable for re-examination to judge whether they are really close to *Proterothrix* species associated with Corvoidea or if they instead represent an independent lineage of the *Proterothrix* group related in their origin with the Old World suboscines.

The *Pterodectes* group was formed on the Passerida, which split from the early corvoideans in Indonesia and then dispersed throughout the Old World and invaded to the New World via Bering land bridge and reached South America that took place in the period between 15 Mya and 5 Mya (Ericson et al. 2001; Barker et al. 2004). The *Montesauria* complex is mainly associated with representatives of Passerida which diversified in the Old World, and therefore this complex may be referred to as the "derived pterodectines of the Old World". Two highly advanced genera of this complex, *Pedanodectes* and *Anisodiscus*, were formed in Africa and restricted to a few host families, while representatives of the paraphyletic genus *Montesauria* have dispersed among birds of many different passerine families. It is obvious that a number of transfers from one host species to another took place in the course of evolution and dispersion of the genus *Montesauria* and related genera in the Old World, because mite species from the same species group may occur on hosts from different superfamilies and infraorders of oscines and even on birds from other orders. For instance, the *merulae* group unites species which are mostly associated with birds from the closely related families Turdidae, Muscicapidae, and Pycnonotidae (Passerida: Muscicapoidea), but also includes a few species recorded on particular hosts from Dicruridae (Corvida: Corvoidea) and Lybiidae (Piciformes).

The *Pterodectes* complex was apparently formed on those representatives of Passerida that invaded North America. *Pterodectes rutilus* is the only representative of this complex which is distributed almost worldwide due to its association with the cosmopolitan host *Hirundo rustica* Linnaeus, 1758 and some related swallow species (Hirundinidae). On the descendants of the Passerida that invaded North America, the families Icteridae, Cardinalidae, Thraupidae, and Parulidae, mites of the *Pterodectes* complex successfully dispersed in both North and South America. In the course of dispersing in the New World, mites of the *Pterodectes* complex apparently colonized various groups of New World subosicnes. Only suggestion of many cases of horizontal transfer could explain the occurrence of representatives from the genera *Pterodectes* and *Tyrannidectes* on birds belonging to phylogenetically distant groups of passerines, oscines and suboscines, in Central and South Americas. Thus, species of the *gracilis* species group of the genus *Pterodectes* occur on birds of the families

Thraupidae, Emberizidae (Passerida: Passeroidea) and Tyrannidae (the New World suboscines).

This preliminary hypothesis of origin and diversification of Pterodectinae may be summarized in following conclusions. The origin and evolution of two major phylogenetic branches of Pterodectinae are related to two main lineages of avian hosts, passerines and hummingbirds; however, on the latter host group they are secondarily in origin. The phylogeny, recently known host associations and geographic distribution of Pterodectinae associated with passerines generally corresponds to the phylogeny and historical biogeography of the order Passeriformes. Diversification of the tribe Pterodectini, representatives of which are mainly distributed among passerines, was realized by cospeciation with hosts and also by numerous cases of colonization of new host taxa, mainly belonging to Passeriformes but occasionally to other bird orders.

Subsequent detailed elaboration of the proposed hypothesis needs additional extensive investigations of pterodectine biodiversity on passerines, especially suboscines and birds representing archaic lineages of Corvida.

Taxonomic correction

Nanopterodectes Mironov nom. nov. is proposed in the present paper as a substitution name for the feather mite genus *Nanodectes* Mironov in Mironov et al. (2008b), which is preoccupied (Rentz 1985; Orthoptera: Tettigoniidae). The sole species of this genus gets a new name: *Nanopterodectes formicivorae* (Mironov, 2008) comb. nov.

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