

# Nakridletia ord.n.

– enigmatic insect parasites support sociality and endothermy of pterosaurs

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Orders are gross formal ranks of insects. All ~350.000 named species of beetles belong to the single order Coleoptera; moths, skippers and butterflies form the order Lepidoptera. All solitary, social and parasitic wasps, with bees and ants are housed within Hymenoptera. Altogether, insects are placed within 42 orders (Rasnitsyn & Quicke 2002), of which 31 are living (Klass et al. 2002). Parasitic fleas and lice (Siphonaptera, Phthiraptera), predatory ice-crawlers and gladiators (Grylloblattodea, Mantophasmatodea) are all wingless as well as about 5% of insect species (Whiting et al. 2003).

Parasitism and/or wingless require a general morphological reorganisation and thus the absence of insect orders parasitising extinct sauria was surprising. Now we designate a new insect order, Nakridletia, for excellently preserved *Strashila incredibilis* Rasnitsyn, 1992 (Strashilidae), *Parazila saurica* Vršanský et Ren, gen. et sp.n. and *Vosila sinensis* Vršanský et Ren, gen. et sp.n. (Vosilidae) - giant pterosaur parasites from the Upper Jurassic of Siberia (Rasnitsyn 1992) and the Middle Jurassic of China (Ren et al. 2002, Rasnitsyn & Zhang 2004, Chen et al. 2004, Liu et al 2004, Gao & Ren 2006) respectively. The latter also represents the oldest direct evidence for ectoparasitism.

Pediculid lice-like adaptations, characteristic for infestation of stenothermous, restricted to endotherm social hominoids (Ferris 1951), indicate endothermy and perhaps also the sociality of pterosaurs.

**Key words:** fossil insects, new order, ectoparasites, pterosaur parasites, Jurassic, Mecopteroidea

## Introduction

A major portion of the diverse range of insects, as well as herbivores, parasitoids or vertebrate ectoparasites, have parasitic feeding strategies (Sukhdeo and Bansemir 1996, Labandeira 2002). Insect ectoparasites in particular are associated with harming the host, despite the fact that host-parasite relations are often phylogenetically significant and positive to both of them, with entire ecosystems often regulated by parasites. No flea species (Siphonaptera), parasitic helminth (Platyhelminthes), parasitic nematode (Nematoda), mite, or tick (Acari) with the exception of only one of the 5.000 extant louse species (Phthiraptera) is listed as threatened by the IUCN, despite impassioned pleas for parasite conservation beginning more than a decade ago (Whiteman & Parker 2005) (endangered status was proposed for the louse parasitising the endangered iberian lynx, *Lynx pardinus* (Perez & Palma 2001)).

In addition to the close relationship with most of animal species, insect ectoparasites are found to significantly influence human history, with louse identified from mummies (Ewing 1924, Horne 1979, El Najjar et Mulinski 1983, Rick et al. 2002), prehistoric coprolites (Fry 1977, Reinhard & Largent 1989), historic deposits (Kenward 1999) and storerooms (Mumcuoglu et al. 2003), as well as pre-pottery sites (Zias & Mumcuoglu 1991). They were reported to have significantly

influenced war (Peacock 1916), can change behaviour and cause psychological trauma or neurosis (Held & Bernstein 1989; Boll-Klatt, Beurich & Schmeling-Kludas 2003).

The harm, often associated with infections and multiple infestations, is also known in humans (e.g., Sasaki et al. 2006). Louse-borne infectious diseases affected nearly one-third of Napoleon's soldiers returning from Russia (buried in Vilnius), which might have been a major factor in the French retreat from Russia (Raoult et al. 2006). Other transferred vectors include those of *Rickettsia prowazekii*, the aetiological agent of louse-borne epidemic typhus (LBET) (Robinson et al. 2003) or Trench fever (*Bartonella quintana*) (Sasaki et al. 2006). Plague killed one third of the European population in the 14<sup>th</sup> century.

Bee-eaters are infested by three species of chewing lice (*Meropoeus meropis*, *Meromenopon meropis* and *Brueelia apiastri*) of which *M. meropis* infests 94% of all adults (Darolova et al. 1998).

There are thirty five distinct lineages, with multiple *Acinetobacter* and *Staphylococcus* species, represented by eight widely divergent groups of Bacteria, associated with ectoparasitic chewing lice of North American pocket gophers (Reed et Hafner 2002).

The harm of lice-related (*Bovicola bovis*) damage is known on cattle (light spot, which is reversed only after 13 weeks (Coles et al. 2003)), and the chewing lice *Damalinea* was reported to cause widespread hair-loss syndrome in black-tailed deer of the Pacific northwest in western Oregon and Washington (Bildfell et al. 2004).

Ectoparasites are also common in water mammals such as otters (Kim & Emerson 1974, Kim 1975), or marine seals - after infection with viruses (e.g., alphaviruses), the lice on southern elephant seals (*Mirounga leonina*) remain infected for life - nearly all have neutralizing antibodies against the virus, even no virus-associated pathology (Linn et al. 2001).

Diverse fleas (14 species of 5 families) are common north of the Arctic Circle in Norway (Hastriter et al. 2004).

Fossil insect ectoparasites are scarce because of their potential for preservation.

#### Systematic palaeoentomology

Class Insecta Linné, 1758

Superorder Papilionidea Laicharting, 1781 (=Mecopteroidea auct.)

Order Nakridletia, ord.n.

Proposed type for the case of typification: *Strashila incredibilis* Rasnitsyn, 1992. [Figs. 2,4]

**Composition:** *Strashila* Rasnitsyn, 1992 (Strashilidae Rasnitsyn, 1992); *Vosila* Vršanský et Ren, gen.n. and *Parazila* Vršanský et Ren, gen.n. (Vosilidae Vršanský et Ren, fam.n.)

**Stratigraphic and geographic range:** ?Bathonian Middle Jurassic – ?Tithonian Upper Jurassic. Asia.

**Differential diagnosis.** The present order may be housed within Holometabola based on the structure of terminalia with aedeagus and articulated volsellae with gonostyli. The sucking beak is characteristic for the Mecopteroidea. The dorsoventrally flattened, wingless order Nakridletia differs from all Mecopteroidea (and also from all other ordina) in having gill-like abdominal appendages. Head is large, with large eyes. Meso and metanotum is unique (similar to that of lice) in being extremely short, male terminalia permanently protruded.

General habitus similar to some lice (non-homometabolans), but except for the terminalia, the difference is the long hind leg nipper with processus present apically (dorsal in lice).

**Description.** Head large with large eyes. Pronotum concealing head, without paranotalia. Meso and metanota almost reduced, wings entirely reduced. Abdominal segment margins apparent at least laterally. Male terminalia protruded. Legs with 5-segmented tarsi, 1<sup>st</sup> segment with apical spur. Hindlegs extremely enlarged, femur strong, tibia long, strong with apical processus forming nipper with 1<sup>st</sup> tarsal segment.

**Remarks.** Rasnitsyn (1992) noticed a beak in *Strashilla* which is undetectable now, as a cause of partial damage to the specimen by application of alcohol.

Laterally distant coxae are uncharacteristic for the Holometabola and Polyneoptera, but characteristic of parasites and/or embryonised (in heteroptera diverge secondarily).

**Derivation of name:** nakridletia is after *nakridle* (Slavic for on wings). A proposed English vernacular name is *Paraglida* or *paragliders* after paragliding or wing-over flight.

Vosilidae Vršanský et Ren, fam.n.

**Type species.** *Vosila sinensis* sp.n. Daohugou, Inner Mongolia, China. Middle Jurassic.

**Composition.** Besides the type species, *Parazila saurica* sp.n. Daohugou, Inner Mongolia, China. Middle Jurassic.

**Differential diagnosis.** Differs from the Strashilidae in possessing gill-like abdominal appendages and more massive hind femora.

**Description.** Cuticle of head, nota and legs strong. Head hypognathous, large, with large eyes. Antennae moniliform. Wings reduced. Tarsi 5-segmented, the 2<sup>nd</sup> segment articulated subapically, pretarsus very long. Hindlegs extremely enlarged and widened femur and tibia, latter with apical process forming nippers with the basitarsus- aperture rounded. Body lacking sclerotisation, with subequal terga and gill-like appendages. Male terminalia large, external.

**Remarks.** For comparison with *Strashila* see the differential diagnosis of Vosila.

*Vosila* Vršanský et Ren, gen.n.

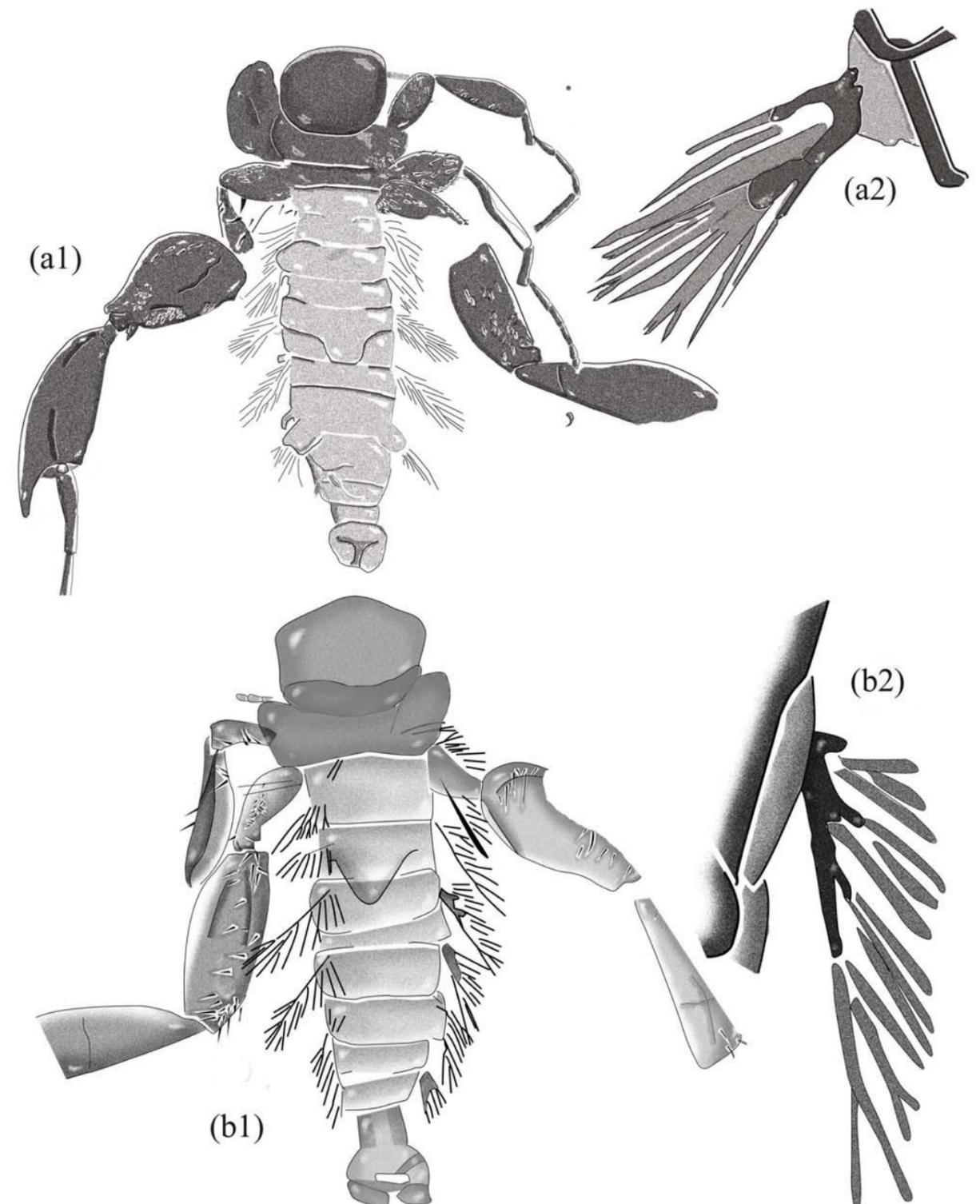
**Type species:** *Vosila sinensis* Vršanský et Ren, sp.n.. Daohugou, China. Middle Jurassic.

**Differential diagnosis.** Differing from *Strashila* in having more robust pronotum and meso and metanotum, all femora more massive, hindleg nipper aperture round, and pretarsi very long. The ratio of legs is very different from *Strashila*: Forelegs femur, tibia, tarsus 0,8mm; 1,2mm; 2,4mm; compared with 0,7mm:1,6mm:2,5mm (1: 1,5: 0,63: 0,5: 0,38: 0,38: 1,13 vs. 1: 2,5: 0,7: 0,6: 0,6: 0,6: 0,8: 0,5); midlegs 1,1mm: 1,3mm: 1,8mm compared with 1,0mm:1,6mm, 2,8mm (1: 1,18: 0,45: 0,36: 0,18: 0,27: 0,82 vs. 1: 1,7: 0,6: 0,5: 0,4: 0,4: 0,7: 0,4); hindleg 1,8mm: 2,8mm: ? compared with 3,2mm:3,4mm:3,0mm (1: 1,6: 0,6: 0,33... vs. 1: 1,1: 0,35: 0,15: 0,07: 0,07: 0,17: 0,12). Generally, *Vosila* has fewer chaeta. Unlike *Strashila*, the abdominal appendages with large gill-like structures, but without lateral abdominal prolongations.

**Description.** Dorsoventrally flattened insect with strong cuticle (except for abdomen). Head hypognathous, large, perhaps triangular, with distinct large eyes. Antennae moniliform. Pronotum slightly transversal, wings reduced. Legs coxae short, tarsi 5-segmented, the 2<sup>nd</sup> segment articulated subapically, pretarsus very long. Hindlegs extremely enlarged and widened femur and tibia, latter with apical process forming nippers with the basitarsus- aperture rounded. Body lacking sclerotisation, with subequal terga and gill-like appendages. Male terminalia large, external.

**Composition:** type species only.

**Derivation of name:** a jigsaw: *vosila* means that which is transferred, *voš* [:wash:] means louse and *vōs* [:was:] is also Latin for you, *sila* means power and *šila* means sewed.



**Figure 1.** Supposed pterosaur parasites of the order Nakridletia ord.n. (Vosilidae): *Vosila sinensis* Vršanský et Ren, gen. et sp.n. Middle Jurassic, Daohugou, Inner Mongolia, China. Holotype CNU-PARA-001. a1) general habitus; a2) gill-like appendages. Abdomen 5mm long. b) *Parazila saurica* Vršanský et Ren, gen. et sp.n. Holotype CNU-NN-PARA-002 b1) general habitus b2) gill-like apperndages. Overall body length 5.7mm.

*Vosila sinensis* Vršanský et Ren, sp.n. [Figs. 1a, 3a]

**Holotype.** CNU-PARA-001. A complete specimen. Daohugou, Inner Mongolia, China. ?Bathonian Middle Jurassic.

**Description.** Head covered by slightly transversal, quadrate pronotum (1.1/1.2mm). Meso and metanotum extremely narrow. Abdomen almost lacking sclerotisation, about 5mm long and 1mm wide when unfed. Abdominal appendages consisting of three distinct parts (Fig. 1b3). The basalmost articulation is weakly sclerotised, narrow, with proximal part with an aperture. The central hardly sclerotised part consists of three lobes, two proximal parts closely associated. To the central part, plain, gill-like appendages are articulated. Three to the distal lobe, eight to the central lobe, and a sigle to the proximal lobe. All gill-like appendages cover over 2mm<sup>2</sup>.

Terminalia protruded from body, about 0.5mm long.

Foreleg femur robust, with numerous long sensilla, tibia only with 5 sensilla. Basitarsus with terminal claw and row of very small sensillar pits. Segment 2 attached subapically. Measurements 0.8mm; 1.2mm; 0.5mm; 0.4mm; 0.3mm; 0.3mm; 0.9mm. Midleg femur robust, with numerous spurs, tibia with two longitudinal ridges. Measurements (Femur, tibia, basitarsus, tarsi) 1.1mm; 1.3mm; 0.5mm; 0.4mm; 0.2mm; 0.3mm; 0.9mm. Hindlegs asymmetrical. Right coxa very long (1.3mm), femur not very robust with numerous sensilla (1.8mm), tibia very long (2.8mm). Left femur extremely robust with two longitudinal ridges and numerous sensilla. Tibia with apical process, very long, with two longitudinal ridges. Measurements 1.8mm; 2.8mm; 1.1mm; 0.6mm (data of terminal tarsal segments missing). Nipper aperture formed by the apical process and basitarsus round and wide.

**Character of preservation:** 1 complete specimen.

**Derivation of name:** after China.

*Parazila* Vršanský et Ren, gen.n.

**Type species.** *P. saurica* sp.n. (by monotypy and present designation).

**Differential diagnosis.** Nota wider than body, hind border of third and/or fourth abdominal segment (probably sternum) strongly arcuate, mid femora more than half hind femora width, gill-like abdominal appendages pectinate backward (unlike in *Vosila* with pectination on both sides).

**Description.** Pronotum pentangular, slightly narrowed posteriorly, widest anteriorly, with posterior median elongation. Mesonotum nearly reduced, extremely short and narrow. Metanotum distinct, wider than pronotum. Mid femur robust (length/width 1:4). Hind trochanter comparatively long, subconical, femora and tibiae extremely robust. Abdomen narrow, tapering backward, with seven pairs of gill-like appendages, basalmost as long as abdomen wide, following gradually shorter. Fourth segment with obscure sclerotised arcuate structure. Last visible abdominal segment narrow, subcylindrical. Male terminalia about as wide as penultimate visible segment, about twice as wide as ultimate one, transversal, with base (fused gonocoxae) width some 2.5 times length, with wide orifice between forceps bases. Forceps long and very thick.

**Species included.** Type only.

**Remarks.** The large pentangular pronotum is perhaps an apomorphy. Obscure triangular sternal elongation of the body is a shared apomorphy with *Strashila*, as in *Vosila* it is quadrate in outline, but in *Strashila* it occurs in the second segment. Strengthened mid femora is a shared apomorphy (possibly synapomorphy) with *Strashila*. Gill-like appendages are synapomorphic with *Vosila* (more primitive state with gill-like appendages nearly missing in *Strashila*), but the pectinate shape and polarization of veins on one side are more primitive than palm-like in *Vosila*. Reduced mesonotum is a shared apomorphy (perhaps a homoplasy with *Strashila*).

Hind legs are preserved in opposite direction to each other, which may indicate they may have been used in both positions: nipper posteriorly as in original description (Rasnitsyn 1992) as well as anteriorly as indicated by Grimaldi (2005).

The known species of *Parazila* is smaller than *Vosila*. Pronotum is of comparable length, but wider in *Parazila* (length/ width ratio 0.86: 0.92). As in *Vosila*, hindlegs are deeply asymmetrical. According to the reverse asymmetry in both genera, it is possible that *Vosila* is preserved in reverse (negative) position (impossible to approve). So the right femur of *Parazila* is very robust (length width ratio 2.16), of comparable habitus and length than left one in *Vosila*. Tibia is much longer in *Vosila* (2.8mm: 1.7mm)

**Derivation of name:** modified after *parasitus* (Latin for parasite). Gender feminine.

*Parazila saurica* Vršanský et Ren, sp.n. [Figs. 1b, 3b]

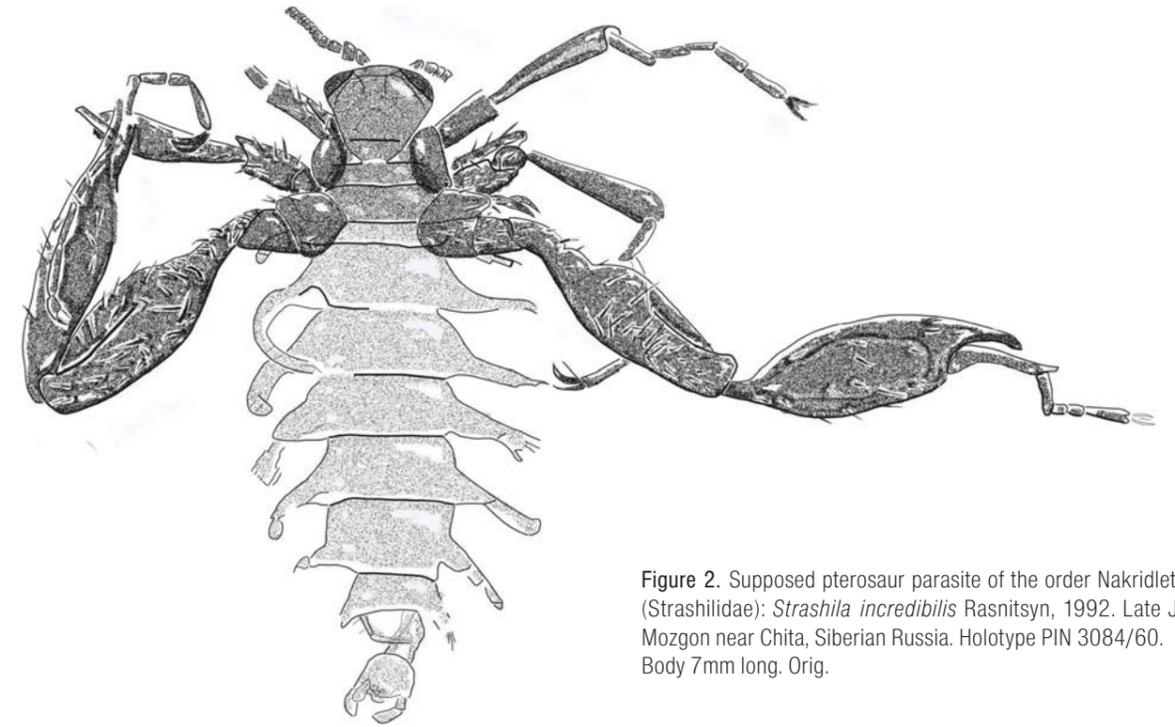
**Holotype.** CNU-NN-PARA-002, nearly complete male with head invisible (apparently hidden under enlarged pronotum), fore legs, most of antennae and part of mid and hind legs lost. Middle Jurassic Jiulongshan Formation. Daohugou, Inner Mongolia, China. Deposited in the Capital Normal University, Beijing, China.

**Description.** Overall body length 5.7mm. Pronotum transversal, with median elongation (length/width 1.17/1.42mm). Mesonotum nearly reduced (0.32/1.28mm), metanotum massive (0.35/1.84mm). Abdomen wide at most 1.13mm. Mid coxa distinct (0.64/0.28mm), femur massive (1.42/0.35mm). Hind legs asymmetrical (see genus remarks). Right trochanter elongate (0.71/0.35mm), femur 1.77/0.82mm, tibia 0.73/0.46mm. Left leg with apparently longer trochanter (0.92/0.35mm), less robust femur (1.70/0.74mm) and more robust tibia (?/0.67mm). Lateral abdominal appendages decreasing in length posteriorly, complete length of the best preserved fourth one is 1.24mm, the seventh one 0.57mm. The fourth appendage consists of five triples of outgrowths attached to distinct more massive base. Terminalia length/ width 0.53/0.71mm, forceps longer than half width of terminalia, about twice as long as wide, curved inward and rounded apically.

**Remarks.** All legs are characterized by distinct ridges occurring also in both *Vosila sinensis* and *Strashila incredibilis*: these might be either real life time structures or a postmortem deformation of less rigid cuticular areas.

**Derivation of name:** after saurus (Latin for reptile).

**Character of preservation:** one nearly complete specimen.



**Figure 2.** Supposed pterosaur parasite of the order Nakridletia ord.n. (Strashilidae): *Strashila incredibilis* Rasnitsyn, 1992. Late Jurassic, Mozgon near Chita, Siberian Russia. Holotype PIN 3084/60. Body 7mm long. Orig.

## Discussion

Terrestrial ecosystems prior to parasitoid and parasite diversifications were simpler in food web structures (Labandeira 2002) with the rather rapid appearance of major parasitoid taxa during the Middle Jurassic – Early Cretaceous. The transition to parasitoidism was accomplished by modifications in the reproductive biology of numerous holometabolous lineages (Godfray 1994).

An important development in early parasitoids was a shift in larval food sources, from less nutritious plant tissues to more proteinaceous animal tissues which were often supplied by the adult (Malyshev 1968). Nevertheless, the hematophagy more likely originated from inquiline associations in vertebrate nests by a shift from nest detritivory of epidermis, feces, sebum, and other exudates to blood feeding (Balashov 1999) – this hypothesis is most relevant to the origin of ectoparasitism in Phthiraptera, since many members of the closely related Psocoptera are nest associates of the vertebrate host (Waage 1979) as well as in Strashilidae – with the present species representing the oldest record of any ectoparasite.

Except for *Strashila*, the oldest possible flea *Saurophythrus longipes* Ponomarenko, 1976 comes from the Early Cretaceous of the Transbaikalian Siberia (Ponomarenko 1976, 1988), and the flea *Tarwinia australis* Jell et Duncan, 1986 from the Early Cretaceous of Australia (Riek 1970).

The 44myr old bird (ancestor to modern Anseriformes (swans, geese and ducks) or Charadriiformes (shorebirds)) louse *Megamenopon rasnitsyni* (Insecta: Phthiraptera: Amblycera: Menoponidae) from the crater of the Eckfeld maar in Germany has feather remnants in the

foregut, indicating an early origin for lice, perhaps inherited from early-feathered theropod dinosaurs (Wappler et al. 2004).

Voigt (1952) described and illustrated eggs of sucking lice (Phthiraptera: Anoplura) attached to mammal hair imbedded in Baltic amber, as well as a Miocene *Lutzomyia* swarm was preserved with strands of mammalian hair (Peñalver & Grimaldi 2005).

Another pterosaur parasite, *Saurodectes vrsanskyi* Rasnitsyn et Zherikhin, 1999 was excluded from Anoplura (Dagleish et al. 2006) and perhaps also deserves its own order. The same author excluded fossil mites from Anoplura (Kumar 2004, Kumar and Kumar 1999, 2001).

Before the phylogenetic relation of the new order is analysed, immense **homoplasies (convergences) with lice are explained**. The independently achieved characteristics of the Strashilidae and the Pediculidae lice parasitising humans are 1) Nipper on hindlegs formed by apical tibial process, basitarsus and its terminal spur (2); 3) Leg asymmetry resulting in lateral movements – possibly related to their heterozygosity; 4) Abdominal stigma-joined process, with attached gill-like filaments (*Pthirus pubis* segments 1-5 closely crowded - stigmata of segments 3-5 apparently lying in one lateral processes); 5) Notum reduced to large extant; 6) protruded male terminalia. 7) Dorsoventally flattened head and probably 8) reduced labial palps (large palp would be visible in the specimen).

Differences might be restricted to compound eyes and antennae which are reduced (3-5 antennal segments) in lice.

Nevertheless, nipper (1)+2): is paradoxically formed at the dorsal part of the tibia in the new order and gill-like filaments (4)) are wide, unlike sensilla-based in lice. The relation of both taxa might be definitely excluded based on the presence of the primitive, 5-segmented tarsi of all legs, a characteristic lost in the Pennsylvanian (Mississippian) Psocoptera. The close relation of the psocopteran family Liposcelididae and lice is well documented, excluding the possibility of the Strashilidae belonging to lice. Liposcelididae are the sister taxon to the louse suborder Amblycera, making parasitic lice (Phthiraptera) a polyphyletic order - parasitism independently arose twice within Psocodea, once in the common ancestor of Amblycera and once in the common ancestor of all other parasitic lice (Johnson et al. 2004). The most primitive stem group represented by *Cretoscelis burynitica* of the family Liposcelididae was reported from the mid-Cretaceous (~100 Myr) of Myanmar, with lice diversification time estimated at 145myr, and with an indication that the hosts of lice would have been early mammals, early birds and possibly other feathered theropod dinosaurs, and/or haired pterosaurs (Grimaldi & Engel 2006).

In particular, the apomorphic presence of articulations between the basal plate, mesomere and ventral plate (= sclerite on the permanently everted endophallus) is observed consistently throughout the psocid families Pachytroctidae and Liposcelididae and the louse suborder Amblycera, providing support for a clade composed of these three groups, although possible homoplasy was detected in some Ischnocera (Yoshizawa & Johnson 2006) – supporting the polyphyly of lice. Alternatively, parasitism may have evolved once and been subsequently lost in the Liposcelididae (Murrell and Baker 2005). The close relationship between Phthiraptera and Liposcelididae, and the elevated substitution rate of mtDNA appears to originate in the common ancestor of Phthiraptera and Liposcelididae, and directly corresponds to an increased G+C content (Yoshizawa & Johnson 2003). Thus, the relation of lice and Strashilidae may be definitively excluded.

The *phylogenetic relations of the Strashilidae* are within holometabolans. Based on the structure of male terminalia, with characteristic aedeagus, the presence of a sucking beak, and articulated volsellae with gonostyli, Strashilidae can be placed within Mecopteroidea (Rasnitsyn 1992). Their unique morphology and a separate ordinal rank can be finally concluded only after excluding the eventual placement within basal fleas. All things being the equal, all living fleas are laterally compressed and this character is considered as plesiomorphical within fleas (Grimaldi 2005), and Mecoptera paraphyletic in respect to fleas as a sister group to Boreidae are supported by molecular evidence based on 18S rDNA (Whiting 2002).

Byers (1996) indicates fleas have more in common with nematocerosus Diptera than with Mecoptera, and the sperm structure of Boreidae and Siphonaptera differs significantly (Dallai et al. 2003), but the Mecoptera + Siphonaptera form a relatively well-supported monophyletic group. However, the placement of *Nannochorista* as a sister group to the fleas is not supported by a more extensive molecular and morphological analysis (Whiting 2002), which argues for a sister group relationship with Boreidae. The monophyly of Siphonaptera and Ceratophylloidea (Leptopsyllidae+ Ceratophyllidae+ Ischnopsyllidae) is well supported. However, phylogenetic relationships among fleas are poorly known (Lewis & Lewis 1985).

In contrast, Strashilidae are flattened dorsoventrally, and possess a wide pronotum, which excludes the possibility of presenting stem fleas - their ordinal rank is thus entirely natural.

Another argument against the relation of the Strashilidae and Siphonaptera is that the parasitism of fleas to flying vertebrates is a phylogenetical novelty. Peculiarities of the host-parasite relationships in the family Ischnopsyllidae consist of their connection with relatively young bat families Vespertilionidae and Molossidae. Ischnopsyllidae originated during the Paleocene or, more likely, during the terminal Eocene- Oligocene in south-eastern Asia – from here on the tribes Chriopteropsyllini and Ischnopsyllini spread over in Afrotropical, Indo-Malayan and Golarctic regions, the tribe Porribiini in Australia, while the tribe Sternopsyllini in the Neotropical region. Ancestors of the tribe Sternopsyllini reached South America via Australia and Antarctica. Fleas of the tribe Nycteridopsyllini penetrated into North America from Asia later via the Beringian bridge (Medvedev 1990).

The terminalia of Strashilidae are characteristic of holometabola and related to the Mecopteroidea, but with primitive volsellae, which allows the attribution of the Strashilidae as a sister group to the Mecoptera, and possibly Mecopteroidea. Terminalia of the Protomecoptera are unknown.

The analyses of *coevolutionary relationships* between host and parasite phylogenies, is made extremely difficult by the complex interplay of cospeciation, host switching, sorting (extinction), duplication (intra-host speciation) and inertia (lack of parasite speciation) events, all of which may produce incongruence between host and parasite phylogenies (Paterson et Banks 2001)

The evolutionary history of mammal-flea associations has been shown to involve mainly association by colonization with frequent host switching, rather than association by descent (Traub, 1980; Krasnov & Shenbrot, 2002; Lu & Wu, 2003).

Page et al. (1998) pointed out that the cytochrome b is evolving two to three times more rapidly in lice than in birds, and louse cytochrome b is highly divergent compared to that of most other insects.

Investigations into the coevolutionary history of seabirds (orders Procellariiformes and Sphenisciformes) and their lice (order Phthiraptera) and examination of the codivergent nodes revealed that seabirds and lice have cospeciated synchronously and that lice have evolved at around 5.5 times the rate of seabirds. (Paterson et al 2000).

Hafner & Nadler (1988) find a high degree of concordance in the branching patterns of the trees, which suggests that there is a history of cospeciation in this host–parasite assemblage. In several cases where the branching patterns were identical in the host and parasite phylogenies, the branch lengths were also very similar, suggesting that the speciation of these hosts and ectoparasites was roughly contemporaneous and causally related.

The occurrence of numerous parasites in a single pterosaur host is questionable. In living hosts, some threshold of defence against parasites in the host species is present, which limits the host's ability to cope with multiple parasite species (e.g. because of presumably costly defence systems - Schmid-Hempel & Egert 2003) but instead maintains their pressure (expressed as a number of parasite species) at a 'tolerable' level (Combes 2001).

Very little can be extracted about either principal (currently the one used by the majority of individuals in the parasite population) and/or the

original (the one in which the parasite first evolved) *host of the Strashilidae*. Attributing Strashilidae as pterosaur parasites is based on the presence of strong claws on all extremities, long strong hindlegs with distinct nippers (*chela*), adapted for membrane phoresy such as in living bat insect ectoparasites (c.f., long legs of the Streblidae flies); and an unsclerotised body apparently serving as a blood reservoir (Rasnitsyn 1992). These adaptations are even more apparent in the present genus *Vosila*, where sclerite margins are unsclerotised in the center – a homologue to that of living lice, and the nipper is plesiomorphically adapted for phoresy on hairs with a circular diameter (compared with pinsette-like in *Strasila* adapted for advaced, plain, hairs).

A blood feeding adaptation excludes the possibility of hair and/or feather feeding, but cannibalism in pre-imaginal stages remains obscure. In fleas, the larvae (except for *Uropsylla tasmanica*) are not parasitic and feed on organic matter found in the nest of the host, but third-instar larvae readily cannibalise naked pupae, however a complete cocoon structure can protect pupa from cannibalism (Lawrence & Foil, 2002). Interspecific cannibalism during periods of food shortage might be complicated by intraspecific cannibalism. A strong female bias caused by their larger size during periods of lowest food availability allows them to cannibalise males under conditions of food shortage (Krasnov et al. 2005a).

Rich and diverse sensillar apparatus suggest a high variety of cues in searching for hosts. Living fleas determine vibrations, increased concentration of CO<sub>2</sub>, increased temperature, light (Benton & Lee 1965, Cox et al. 1999, Humphries 1968) as well as host odour (Crum et al. 1974 and Vaughan & Mead-Briggs 1970).

The aquatic habits which may be excluded by analogy with living water mammal ectoparasites. E.g., *Antarctophthirus ogmorhini* from the Weddell seal *Leptonychotes weddellii* are: (1) the cuticle of the ventral and lateral surfaces is 1:3 thinner than that of the dorsal surface, (2) the body has numerous stiff spines which are covered by a thick layer of the seal's sebum that closely surrounds the body of the louse, (3) the whole body is covered by a close layer of leaf-like scales which are apparently able to trap air bubbles and thus to provide a small zone of air close to the surface of the cuticle (Mehlhorn et al 2002). However, the function of gill-like appendages remains obscure.

In the future, the presence of ectoparasites may be investigated indirectly by studying the presumable hosts. By analogy, feral pigeons (*Columba livia*) with impaired preening, owing to slight bill deformities, have higher louse loads (Phthiraptera: Insecta: Ischnocera) than pigeons with normal bills. High louse loads reduce the survival of pigeons, suggesting that lice select for efficient preening and against bill deformities. In a reciprocal experiment, preening with a normal bill selects for a small body size in lice, which may facilitate their escape from preening (Clayton et al. 1999).

Most individuals of the parasite occur on a few host individuals, while most host individuals have only a few, if any, parasites (Anderson & May 1978). Possible traits for preservation of the present specimens are disarticulation from the host during preening near or directly in the water or, although never found associated, from a dead vertebrate. The hosts' diving behaviour can effectively influence ectoparasite (lice) communities (Felso & Rozsa 2006). The present specimens apparently fossilised completely without blood. Both specimens perhaps originated from an exhausted animal which soon died in the water.

Generally, females survive longer than males at all air temperatures, except for the highest temperature when the survival time of both sexes was similarly low; males of both species survived for less time than females at all RHs (Krasnov et al. 2002a). The preserved specimens also perhaps represent at least once fed individuals, because newly emerged fleas survived for a significantly longer time.

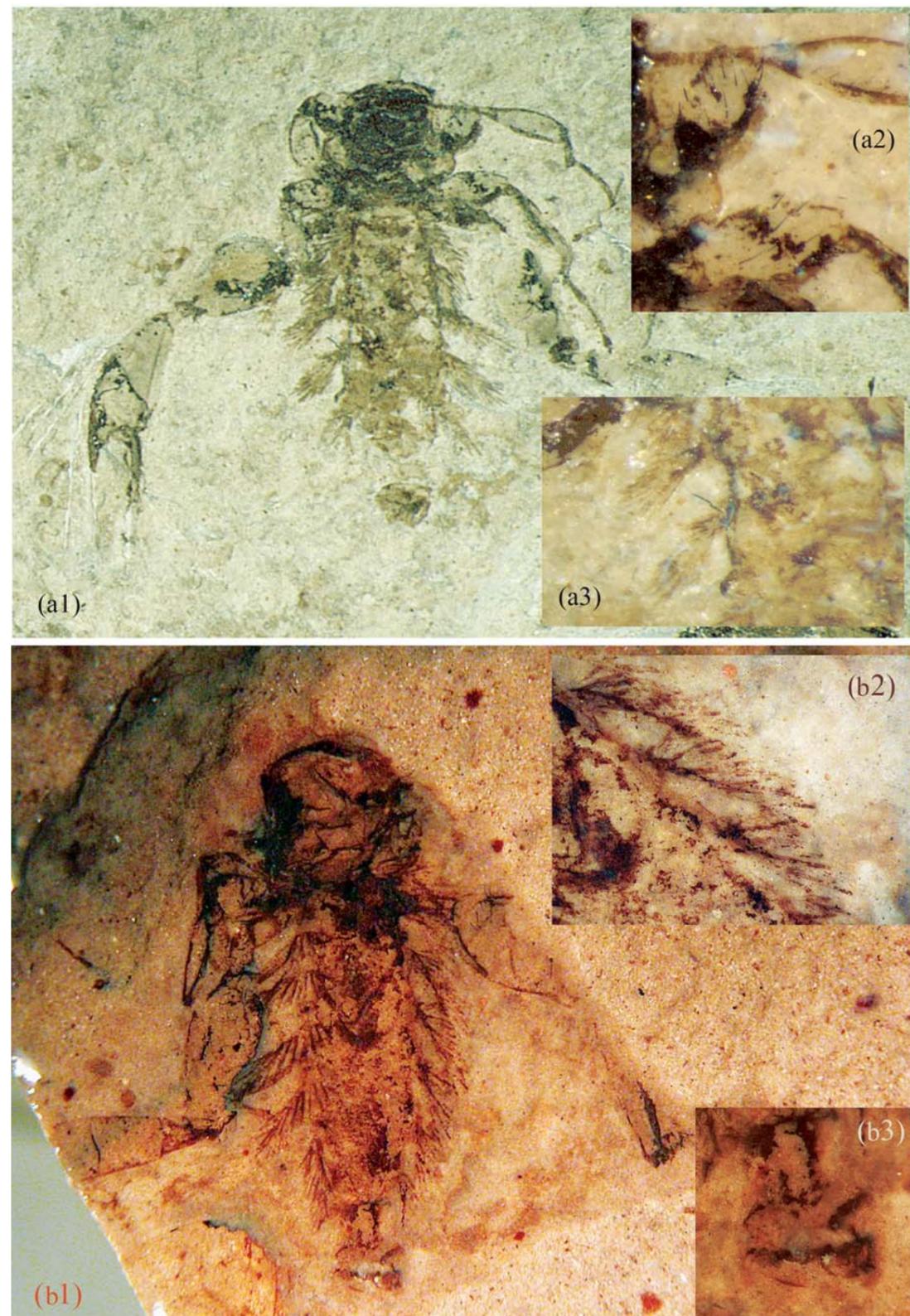
Even based on only four specimens, it must be noted that the sex is most commonly female-biased in ectoparasites. One possible explanation comes from the preservation potential, influenced by water content, which is significantly higher in fed males: CO<sub>2</sub> emission rates of the larvae exceed that of the adults by 2.6-fold and the pupae by 7.3 times. Water content differed between fed (range approx. 67–69% of body mass) and newly emerged adults (range approx. 73–75% of body mass). Although no differences were noted between the water content of newly emerged males and females, fed males had significantly higher water content than fed females. Adult males being the lightest 0,102mg when unfed and fed adult females ca. 0,263mg (0,210 unfed) being the heaviest. The decrease in water content of the females compared to the males may reflect a greater accumulation of fat for subsequent egg production (Fielden et al 2004).

Krasnov et al. (2005c) validated the nutritional and/or energetic cost of host resistance, measured as host-mediated parasite fitness loss, as well as possible adaptive stress-induced immunosuppression (egg production was significantly higher in fleas parasitizing underfed than control animals. Survival of new generation imagos was lowest in fleas from parents on hosts with the highest food limitation. By contrast, survival of parent fleas was highest on hosts offered 30% of maintenance energy intake. Food availability for hosts affected the survival of eggs and larvae produced by fleas on these rodents, but did not affect the survival of pupae. The highest larval survival was recorded in fleas on rodents with 30% of maintenance energy intake).

The rarity of fossil parasites is not necessarily associated with the rarity of host. Based on 57 flea-mammal associations from Slovakia, Stanko et al. (2006) suggests that different flea-host associations are governed by different regulating mechanisms, but different regulation mechanisms may act simultaneously within the same flea-host associations (relationships between flea abundance or prevalence and host abundance were either negative (23) or absent (34)).

The same source data (Krasnov et al. 2006b) reveal that mean abundance and species richness of fleas increased with an increase in host age, although the pressure of flea parasitism in terms of number of fleas per unit host body surface decreased with host age. They also found two different patterns - a peak of flea aggregation and a trough of flea prevalence in animals of middle age classes, and an increase of both flea aggregation and flea prevalence with host age.

*Host size* can be investigated by analogy - according to a positive relationship between body size and hair-shaft diameter (e.g., in pocket gophers), a positive relationship between body size and head-groove width (in chewing lice) and a positive relationship between gopher hair-shaft diameter and louse head-groove width. Changes in body size of chewing lice are driven by a mechanical relationship between the parasite's head-groove dimension and the diameter of the hairs of its host. Louse species living on larger host species may be larger simply because their hosts have thicker hairs, which requires that the lice have



**Figure 3.** Supposed pterosaur parasites of the order Nakridletia ord.n. (Vosilidae), Middle Jurassic, Daohugou, Inner Mongolia, China: *Vosila sinensis* Vršanský et Ren, gen. et sp.n. Holotype CNU-PARA-001. a1) general habitus; a2) detail of fore and middle femur and tarsus with sensillae; a3) gill-like appendages (a2-3 submerged in alcohol). Abdomen 5mm long. b) *Parazila saurica* Vršanský et Ren, gen. et sp.n. Holotype. CNU-NN-PARA-002 submerged in alcohol; b1) general habitus b2) gill-like appendages. Overall body length 5.7mm.



**Figure 4.** Supposed pterosaur parasite of the order Nakridletia ord.n. (Strashilidae): *Strashila incredibilis* Rasnitsyn, 1992. Late Jurassic, Mozgon near Chita, Siberian Russia. Holotype PIN 3084/60 submerged in alcohol, under polarized light. a1) general habitus; a2) details of head and antenna; a3) terminalia; a4) hind tarsus (PIN 3084/60 counterpart). Body 7mm long.

a wider head groove. The study of gopher hair-shaft diameter and louse head-groove dimensions suggests that there is a 'lock-and-key' relationship between these two anatomical features (Morand et al. 2000).

Reed et al. (2000) examined the relationship between mammalian hair diameter and body mass at interordinal, intrafamilial, intrageneric, and intraspecific taxonomic levels and showed a significant, positive allometric relationship between hair diameter and body size. The allometric coefficient ( $\alpha$ ) ranged from 0.13 to 0.33. Within pocket gophers (Geomyidae), a significant positive relationship exists between hair diameter and rostral groove dimensions of their chewing lice, *Geomydoecus*, which use the rostral groove to grasp the hairs of their host. Coupled with previous evidence of a strong allometric relationship between rostral groove width and louse body size, findings suggest that hair diameter of the host is an important determinant of body size in chewing lice that parasitize pocket gophers.

Large-bodied host species often harbor large-bodied parasites (Harrison's rule). Whatever the reason, this rule does not hold true in all body lice possibly because selection on body size is mediated by community-level interactions between body lice (Johnson et al. 2005).

The absence of nutrition finally resulting in the death of the host might result in a decrease in size of the parasite (lice are variable in size because conditions might change – Saxena 1988). Therefore, by analogy, it is possible that the preserved specimens are on the lower levels of the size variability scale.

Lice cannot establish viable populations on novel hosts that differ in size from the native host. Lice could remain attached to, and feed on, hosts varying in size by an order of magnitude. However, they could not escape from preening on novel hosts that differed in size from the native host (Clayton et al. 2003), which might be further support for the strict specificity of the Strashilidae. This general prediction that parasites of large-bodied host species, which tend to be long-lived, should specialize on these hosts, whereas parasites of small host species, which represent more ephemeral and less predictable resources, should become generalists appears supported by independent living fleas (Krasnov et al. 2006ac).

Fleas also develop specific anatomical features such as sclerotised helmets, ctenidia, spines and setae which anchor the flea within the host fur to resist the host's grooming efforts, which correlates with particular characteristics of the host's fur and grooming pattern (Traub 1985).

Additionally, there is a positive correlation between body size and range size (Brown 1995, Gaston and Blackburn 1996a, Gaston and Blackburn 1996b). Habitat specialization of a parasitic species can be considered the equivalent of its host specificity, because a host represents the habitat for a parasite. In general, host specific fleas have more restricted geographical ranges than host opportunistic fleas. Flea species with a broad geographic range are not only capable of exploiting more host species, but they also exploit host species from a wider range of taxa (Krasnov et al 2005e)

Further support for the specificity of the Strashilidae is within flea hosts - larger hosts have fewer flea species, but fleas were more prevalent. Increased host species richness correlated with flea species eye size (Bossard 2006), extremely well developed in the Strashilidae. Interestingly, increased flea species richness was correlated with larger geographical ranges and the stable locomotion of hosts. Hosts from habitats of moderately low productivity (sage and grass) and size 10-33 g, had the highest flea species richness.

The effect of blood sucking parasites on the pterosaur host was perhaps significant. Fifty fleas feeding on a gerbil consumed 3.68±/1.19 mg of blood, in total amounting to 34.3±/1.8% of body mass of a starving flea and only about 0.17% of the blood volume of the host. The average daily metabolic rate of the parasitized gerbils (7.75 kJ g<sup>-1</sup>d<sup>-1</sup>) was 16% higher than that of non-parasitized gerbils (6.69 kJ g<sup>-1</sup>d<sup>-1</sup>). In addition, at zero metabolizable energy intake, the parasitized gerbils lost body mass at a faster rate than the non-parasitized gerbils (4.34 vs 3.95% body mass d<sup>-1</sup>) (Khokhlova et al. 2002).

The host represents a geographic locality for the parasite, and the distance between hosts - an extrinsic barrier – allopatric *speciation* in one geographical area (Mc Coy 2003). More species are known to have originated on the same host, such as human lice, and also some lchnocerans (Cruickshank et al 2001).

Phylogenetically, Strashilidae are more related to fleas, as holometabolans, rather than lice, but the life cycle, by morphological analogy, is presumed to be similar to lice. Lice are the only permanent insect ectoparasites, exhibiting a high degree of host specificity, having no parallel in most other metazoans. Their transmission occurs mostly opportunistically when hosts are in close contact with each other, such as during breeding. Specializations of ~3000 species in the diet of lice underpin their major taxonomic divisions and they can be broadly separated into those that feed on skin debris, feathers and fur, and those that have specialized in blood feeding.

The origin of parasitism in Strashilidae appears to have a similar pattern to lice. While Pthirapterans are abundant on birds, only 6% of the almost 2000 flea species parasitize birds (Marshall 1981).

The superficial resemblance with the primate attacking Pediculidae is surprising, being most probably the result of the social life of pterosaur or eventually an unknown group of flying homeothermous vertebrates. Anoplura and also Pediculidae indicate close relationships between hosts of related taxa.

The Strashilidae exhibit a high degree of specialisation: Vosilidae in possessing unique gill-like filaments, Strashilidae with a pinsette-like nipper being adapted for phoresy by attachment on plain hairs.

Nevertheless, sharing a host can not be excluded – e.g., a significant positive relationship between the numbers of host species infested by flea sister species was found (Mouillot et al. 2006).

The rationale for the nestedness (the nestedness-anti-nestedness continuum observed in endoparasites is via selective accumulation of parasite species rather than interactions among those parasite species (Poulin and Valtonen 2001)) in parasite communities is that nested species subsets are a common pattern in many types of communities found in insular or fragmented habitats (Patterson and Atmar 1986, Bolger et al. 1991). Hosts can be considered as biological islands at three levels: host individual influenced by epizootical processes, host population influenced by biogeographical processes, and host species (Kuris et al. 1980).

Lice can infest all places with trichia, including eyelashes (Shan 1990). Apparent asymmetry in hidlegs of both species is also notable where the right femur is significantly more robust. This might be the result of lateral crab-like movements, similar to that of Pthirus pubis (Pediculidae) which also resembles crustaceans in notum fusion and in the nipper.

Earlier, it was presumed, that parasites, with their reduced morphological complexity fitted well into their mode of life and were good examples of evolution's inexorable march into dead ends (Noble and Noble 1976). Nevertheless, transitions from specialist to generalist strategies have occurred more frequently than the reverse during the evolutionary history of tachinid flies, a group of endoparasitoids of insect hosts - generalist tachinid species tend to be the most derived, i.e., they tend to occupy branch tips in the phylogeny of the group (Stireman 2005).

Among flea species, generalists exploiting many host species consistently achieve a higher abundance (mean number of fleas per individual host) than specialists using only one or very few host species (Krasnov et al. 2004c) and evolutionary changes in host specificity are clearly reversible (Krasnov et al 2006c). Asymmetrical competition where the generalist is expected to be more sensitive to competition than the specialist is supported for parasites (Dawson et al. 2000; Perlman & Jaenike, 2001).

Nevertheless, the extinction of the present order might have been caused by their presumed strict specialisation, which disallowed host switching, as was commonly observed in population peaks of living fleas (Krasnov et al. 2004b).

Additionally, Poulin et al. (2006) found positive relationships between the number of host species used and clade rank across all of his 297 studied species, as well as within one of four large families and one of seven large genera investigated separately, suggesting the specificity may have tended to decrease in many flea lineages, a process that could have been driven by the benefits of exploiting a wide range of host species.

Krasnov et al. (2004a) suggests that host specificity in fleas is to a large extent phylogenetically constrained, while still strongly influenced by local environmental conditions - in the majority of cases, the taxonomic distinctness of the hosts exploited by a flea is no different from that of random subsets; host specificity varies significantly more among flea species than within flea species and in the vast majority of flea species, neither of our two measures of host specificity correlated with either the regional number of potential host species or their taxonomic distinctness, or the distance between the sampled region and the center

of the flea's geographical range. However, in most flea species host specificity correlated with measures in the deviation of climatic conditions (precipitation and temperature) between the sampled region and the average conditions computed across the flea's entire range. Although there was a conducted and experimental interspecific hybridization between *Nosopsyllus fasciatus* and *N. mokrzeckyi* (Yakunin & Kunitskaya 1992), the genetic differentiation between populations of conspecific lice on different host species in two studied genera of lice identified substantial, 10-20% sequence divergence - in the range of that often observed between species of these two genera. (Johnson et al. 2002). The louse 12S rRNA domain III secondary structure displays considerable variation compared to other insects, in both the shape and number of stems and loops, which confirms the highly distinctive nature of molecular evolution in these insects (Page et al. 2002).

Extant insect ectoparasites can be attributed to two main ecological groups, each represented by a separate order: 1) hemimetabolous lice – i.e., without pupa, living the entire cycle on the host and 2) holometabolous fleas with alternating periods on the hosts and periods in the hosts' burrows or nests – the larvae are free-living, feeding on organic debris.

According to the morphology (see below), the *life cycle* of the Strashilidae was perhaps more similar to lice – i.e., certain stages spend their lives on the host, unlike most fleas, in which all immature stages except adults are spent off the host. Specifically, like, restricted to mammals Anoplura, feeding solely on blood, unlike Amblycera which chew away at younger feathers and soft areas of the skin, causing localized bleeding from which some can drink, and also unlike the avian site specific Ischnocera drilling through thick skin.

Nevertheless, many flea larvae also feed not only on organic debris but also on the dried blood of the host obtained through the faeces of adults (Krasnov et al. 2005d).

In contrast to fleas, which survived separated from their host (*Meles meles*) for 89 days, with 50% mortality at 35 days, lice survived only 3 days, which can significantly support the badger's habit of frequently swapping dens with a mean period of return of 6 days. This is unlikely to bring about significant mortality of adult fleas but may effectively eradicate lice (Cox et al. 1999). *Pthirus pubis*, is relatively immobile when on the host, remaining attached and feeding for hours or days on one spot without removing its mouth parts from the skin. Neither larvae nor adults can survive more than twenty-four hours without feeding - bluish-gray discoloration of the skin is due to poisonous saliva injected by the crab louse, similar to the melanoderma caused by the body louse (Riley & Johannsen 1938).

The mature adults live for about 15 to 25 days. Neither nymphs nor adults move about very much. While feeding, a crab louse grabs human hairs with at least one of its second or third legs which are adapted for this purpose. Lice do move about slowly after molting.

Dispersion is mostly by adult stages, and is unaffected by sex, age and blood gender of host and neither population density nor hunger (Takano-Lee et al. 2005). Low infestation is also characteristic for time after hibernation (Sosnina & Davidov 1975).

After emergence from the pupa and cocoon, adult fleas must locate a suitable host to complete their life cycle (Ioff 1941). Since a host may

not always return in a regular or predictable manner to its nest or resting area, the survival of fleas depends in part on their ability to use other host species (Sarfati et al. 2005). This is apparently not the case for Vosilidae, which are presumed to be strictly specific.

By analogy, birds in arid regions have fewer ectoparasitic lice than birds in humid regions. Low humidity reduces the number of lice, even when host defenses are held constant, which confirms this abiotic factor being substantial for parasite pressure and suggests that humidity may influence host life history evolution through its impact on ectoparasites (Moyer et al. 2002).

Dispersal of avian ectoparasites can occur through either vertical transmission from adult birds to their offspring in the nest or through horizontal transmission between adult birds or through phoresy. Chewing lice are mainly horizontally transmitted among adults (bee-eater) and mainly among pair members, whereas vertical transmission between parents and nestlings is less frequent (Darolova & Křištofik 2001).

Parasites face a trade-off between the choice to attack less defended but lower-quality, vs more defended but higher-quality hosts. The reproductive output of a parasite will be higher when exploiting energy deprived hosts if the fitness increment due to reduced host defences is higher than the fitness decline due to lower quality of resources extracted from a host (Krasnov et al. 2005cd).

Darskaya (1970b) and Vatschenok (1988) proposed a classification of fleas based on their annual cycle patterns as follows: (1) adult fleas active and reproduce all year-round; (2) adult fleas active all year-round, but reproduce in warm season only; (3) adult fleas active and reproduce in warm season only; (4) adult fleas active and reproduce most of the year, except for the hottest and driest periods when fleas survive in cocoons; and (5) adult fleas active and reproduce only in the cold season.

The parasite population might have multiple peaks, and/or activity may be restricted to a particular season such as winter in arid areas. At the beginning of the activity, it is often female-biased, often cocooning during the summer. The female bias during the early phase of activity may be considered as reproductive pre-adaptation allowing for a fast population increase (Krasnov et al. 2002b).

Hawlena et al. (2005) found flea distribution changed as a function of flea density-from juvenile-biased flea parasitism (the "poorly fed host" hypothesis) at low densities to adult-biased flea parasitism (the "well-fed host" hypothesis) at high densities. Other factors that influenced flea preference were soil temperature and the presence of ticks.

The host may not always return in a regular or predictable manner to its nest or resting area where the immature fleas develop. The survival and reproduction of fleas are therefore dependent on a combination of environmental factors, including favourable climatic conditions for the development of the immature stages and for adults to survive unpredictable and sometimes lengthy periods without a bloodmeal. This dependence results in seasonal changes of flea life history parameters, e.g. their abundance, pattern of parasitizing of hosts and rate of reproduction (Marshall 1981).

Insect ectoparasites such as the present extinct species, were exposed to strong and/or specific *immune attacks* because of the association with host major immune defence systems in blood and skin associated

lymphoid tissues (Wikel 1996). Additionally, digestion in ectoparasites such as fleas is intracellular and they lack a peritrophic membrane (Vatschenok 1988) which, in many arthropods, separates ingested food from the gut epithelium and, thus, may restrict penetration of ingested immune effector components (Eiseman & Binnengton 1994).

Even surface feeding sheep louse (*Bovicola ovis*) ingesting lipid, scurf, bacteria and loose stratum corneum squames, stimulate an immune response in sheep and this response may play a part in regulating the size of louse populations (James 1999).

Apparently, even the weak attack of a parasite triggers the immune system. However, this system could not overcome an attack by a large number of fleas, perhaps due to their additive immunosuppression effect and the cost of the immune system (Schmid-Hempel & Egert 2003).

Activation of an immune response and even maintenance of a competent immune system is an energetically demanding process that requires trade-off decisions among competing energy demands for growth, reproduction, thermoregulation, work and immunity (Sheldon & Verhulst 1996).

As a result, in many non-tropical vertebrate animals, disease prevalence is increased during periods of food shortage compared with periods when food is readily available (Lochmiller, Vestey & McMurray 1994). However, if food limitation occurs in a predictable manner (e.g., seasonally), it can be advantageous to suppress other functions, including reproduction, rather than suppress the immune function. Indeed, the 'winter immunoenhancement hypothesis' was suggested by Nelson & Demas (1996) to explain the increase in the immune parameters during winter reproduction break in small mammals from temperate environments (Lochmiller & Dabbert 1993; Lochmiller *et al.* 1994).

Furthermore, stress, such as food limitation, may activate the hypothalamic–pituitary–adrenal axis and increase plasma levels of glucocorticoid steroids (Råberg *et al.* 1999) which are largely immunosuppressive. Indeed, reduced food availability was shown to elevate corticosterone concentrations and suppress immune function (Demas & Nelson 1998). Råberg *et al.* (1999) argued that immunosuppression via neuroendocrine mechanisms is adaptive because it allows the avoidance of hyperactivation and subsequent immunopathology during stressful situations.

An important link to the living host includes males being generally less immunocompetent and more susceptible to parasites than females (e.g. Olsen and Kovacs, 1996; Poulin, 1996; Schalk and Forbes, 1997), resulting from the immunosuppressive function of androgens (Folstad and Karter, 1992) and a higher level of circulating immune complexes in females than in males (Khokholova *et al.* 2004).

Some components of host immune defences may operate simultaneously against all kinds of parasites, whereas investment by the host into specific defences against one type of parasite may come at the expense of defence against other parasites, which suggests the existence of a process of apparent facilitation among unrelated taxa in the organization of parasite communities (Krasnov *et al.* 2005b). Authors proposed explanations based on host immune responses, involving acquired cross-resistance to infection and interspecific variation in immunocompetence among hosts.

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