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Host-parasite relationship of birds (Aves) and lice (Phthiraptera) – evolution, ecology and faunistics

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Vas Zoltán

“He [Bonpland] wanted to know what statistics about lice were good for.

One wanted to know, said Humboldt, because one wanted to know.”

Daniel Kehlmann: Measuring the World [Vermessung der Welt, Rowohlt Verlag GmbH, 2005]; English translation by C. B. Janeway, Quercus, 2007

Content

Abstract

The host-parasite relationship is one of the most complex and intimate associations in nature. In this thesis I present a multidisciplinary approach to investigate the host-parasite relationship of lice (Insecta: Phthiraptera: Amblycera, Ischnocera) and their avian (and sometimes mammalian) hosts (Vertebrata: Aves, Mammalia). I apply both modern statistical methodologies of evolutionary comparative analysis and classical zoological methodologies such as sampling in the field for faunistical purposes.

The understanding of the diversity component of host-parasite relationships is a major and yet scarcely discovered field of evolutionary ecology. Here I present a review of the previous literature and three original studies published by myself and my co-authors concerning the factors that shape louse diversity at macroevolutionary level (Chapter 1). I show a positive co-variation found between avian cognitive capabilities and Amblyceran louse richness; a decrease in louse richness due to the brood-parasitic life-style of the hosts; and a positive diversity interaction between Ischnoceran louse richness and foster species richness of brood-parasitic cuckoos. The supposed positive co-variation between host and parasite diversity – an assumption originating from Eichler (1942, the so called Eichler's rule) – were revisited and tested for the first time with modern methodologies across a wide range of avian and mammalian hosts and their lice, and showed to be the strongest and most general diversity pattern of host-parasite evolution found so far.

Chapter 2 incorporates papers related to different aspects of louse faunistics as well as the review of their background. First, I summarize the Hungarian louse fauna based on formerly published records. Second, I report that this checklist was significantly extended by my own recent collections. The third paper is a methodological contribution that points out a formerly overlooked bias in currently widespread sampling projects: the handling of avian host individuals during the bird ringing procedure can reduce the louse burden. Finally, in the last paper I provide global checklist of critically endangered species of parasitic lice.

Preface

The host-parasite relationship is one of the most complex and intimate associations in nature. Given the astonishing diversity of parasitic animals, as well as that of their hosts, a huge variety of interactions evolved between the two partners. These interactions can be studied from several different point of view, each field contributing to the general understanding of host-parasite relationships. At an ecological level, this relationship is often characterized as an arms race – emphasizing the conflicting adaptations and counter-adaptations of the partners. Nevertheless, often the present partners' ancestors have already been associated through evolutionary ages, raising the possibility to study how host and parasite lineages have affected each other's adaptation and diversification. However, none of these studies is able to draw reliable inference without a sound classical zoological background: faunistics, taxonomy, and systematics.

In this PhD thesis I present a multiple approach investigating the relationship of parasitic lice and their avian hosts. The two main chapters indicate the two fields I was most concerned in the recent years: the linkage between host and parasite diversity at a macroevolutionary level and louse faunistics. At first sight, these two main topics may seem distinctly related; however, they are rather deeply bounded. Evolutionary ecological studies on diversity interactions depend on the underlying diversity data that have been produced by faunistical studies published through decades or even centuries.

The structure of my thesis follows the two topics described above; each main chapter includes several case studies published by me and my co-authors in scientific journals. These are presented here exactly as they appeared in the published papers, except for a few necessary changes in the format and citations to integrate them into this thesis. A few sentences were added to the papers' text – both in brackets and in italics – where the reviewer of the thesis requested clarification.

As a consequence, there are inevitable recurrences among some case studies, mainly in the introduction and methods sections. However, as each study has its unique set of background and methodology they cannot be pooled and overviewed together. The references are pooled together in the 'References' chapter to avoid duplications. Acknowledgements of the original papers are also combined and shortened. Figure and table numbering starts form 1 in each chapter. Spacious lists from the case-studies (i.e. checklists) are in the Appendices, as well as the co-authors' affiliations and addresses. The case studies were originally written either in American or in British English; however, to ensure a consistent language usage within the thesis I used American spelling – an arbitrary choice based on my preferences.

General introduction

Birds have fascinated people at all times. They dominate even the earliest written records of natural history, and constantly attract more attention by researchers and amateur naturalists than any other group of animals (Perrins 2003). Several disciplines of supra-individual biology such as ecology, ethology, behavioral ecology, and conservation biology had emerged and evolved, in the main, by studying birds (see e.g. Krebs and Davies 1981, Standovár and Primack 2001). Why are they so attractive to naturalists, researchers, and even artists? Birds live their life more similar to mankind in many ways, than our much closer relatives, mammals do. While the majority of mammals are nocturnal, and live in a world experienced by olfactory senses, birds are mainly diurnal, visually perceiving a colorful world similar to that of people. And, literally, they appear almost everywhere. Birds, the only living descendants of dinosaurs, are the most successful and diverse group of terrestrial vertebrates. The nearly 10.000 avian species double the species richness of mammals, and have adapted to the most various environmental conditions including urban habitats.

However, despite the huge scientific and public interest, only relatively few authors considered that wild birds represent also habitats for other animals such as parasites (I emphasize *wild* birds because the extermination of parasites infesting domestic poultry has been in the human interest for a long time). Nevertheless, a huge diversity of pathogens, endoparasites, and ectoparasites live in an intimate relationship with their avian hosts, affecting each others' life history, life expectancy, reproductive success, and even diversity (see e.g. Marshall 1981, Clayton and Moore 1997, Poulin and Morand 2004).

Parasitism

Parasitism is a successful way of life, as roughly 6-50% of known animal species are parasites – depending on the definition of parasitism used (Poulin and Morand 2004, Rózsa 2005). The broader definition (Price 1980) – emphasizing the general feature that parasites usually do not kill directly their hosts but decrease their fitness – covers the herbivorous insects, the occasionally blood-suckers such as mosquitoes, and the social parasites (e.g. brood parasitic cuckoos, and many arthropod species parasitizing the colonies of social insects) along with parasites like endoparasitic worms or ectoparasitic fleas, and lice. Here I adopt the narrower and more conventional definition of parasites characterized by several strict criteria: (i) parasitism is a long-lasting relationship between the host and parasite individuals (that lasts minimum as long as a developmental period in the parasite developmental cycle, but may last as long as the entire life cycle); (ii) the host individual provides not only nutrients to the parasites, but it also serves as a habitat and the most important natural enemy of the parasites (parasite mortality is mainly caused by host defenses); and (iii) parasites decrease hosts' fitness without usually killing them (see e.g. Poulin and Morand 2004, Rózsa 2005). Hence, herbivorous insects, temporary blood-suckers, and social parasites are not considered as "true" parasites by this definition.

Parasites are usually subdivided into categories according to several aspects (see e.g. Clayton and Moore 1997, Rózsa 2005). The terms microparasites (viruses, bacteria and unicellular eukaryotes) versus macroparasites (multicellular animals) or endoparasites versus ectoparasites reflect differences in size or habitat preferences, respectively. Obligate parasites must use a host at least at some stage of their life cycle while facultative parasites do not require it necessarily. Host specific (euryxene) parasites tend to infest only 1 or a very few closely related host species, while host generalist (stenoxene) parasites are less selective.

Parasitism has evolved in several independent lineages, at least in 9 phyla of metazoans and, additionally, also numerous times independently within certain phyla (e.g. at least 40 times in Arthropoda) (Poulin and Morand 2004). Consequently, the variation of parasitic life-styles among these groups is astonishing (see e.g. Kotlán and Kobulej 1972) and only a few general inferences can be drawn (Rózsa 2005). Parasitic life-style is often characterized by reduced anatomical and morphological complexity as compared to their closest non-parasitic relatives. Most probably this is the reason why vertebrates are hardly ever parasites: their great complexity does not fit well to parasitic way of life. On the other hand, vertebrates are over-represented (according to their species richness compared to invertebrates) as hosts for parasites – the reason is probably the same: their great anatomical and structural complexity offers several habitats for parasites. Given that parasitism has not only medical, veterinary or economic importance but also seriously affects the population dynamics and even diversity of free-living animals, the research for sophisticated patterns in parasite diversity and for factors shaping the evolution of parasitic lineages is a major task in evolutionary biology (Poulin and Morand 2004, Poulin 2007, Krasnov 2008).

Louse biology

In this work I focus on parasitic lice, particularly on avian lice. Lice (Phthiraptera) comprise the largest exclusively parasitic insect order; all members are obligate ectoparasites of birds or mammals. There are about 4500 described louse species, and the majority (more than 85%) of them infests birds (Price et al. 2003). They belong to the Exopterygota group of insects and are classified into 4 suborders: Amblycera, Ischnocera, Rhynchophthirina, and Anoplura. The former division as Mallophaga (chewing lice) and Anoplura (sucking lice) are not in use any more as Mallophaga turned out to be paraphyletic (Johnson and Clayton 2003).

The order of lice is relatively species-rich among the non-holometabolian insect orders. To summarize Phthirapteran diversity below I follow Price et al. (2003). The suborder Ischnocera consists of two families: Philopteridae with 2698 species infesting birds (except 1 species infesting lemurs) and Trichodectidae with 362 species living exclusively on mammals. Amblyceran families are more heterogeneous in life history and distribution: members of the large family Menoponidae (1039 species) as well as Laemobothriidae (20 species with a peculiar host distribution living only on birds of prey, and some members of stork and crane kinship) and Ricinidae (109) infest only birds. Gyropidae (93 species) and Trimenoponidae (18 species) are mammalian lice. Among the 55 species of Boopiidae 54 infest mammals while 1 species lives on cassowaries (*Casuarius casuarius*). Rhynchophthirina with 3 species in a single family and Anoplura with 532 species in 16 families are blood-sucker ectoparasites of mammals. These numbers were obtained from a global overview (Price at al. 2003) published a decade ago and the number of species have slightly increased since then, mostly in Menoponidae and Philopteridae (see e.g. Sychra and Literák 2008, Valim and Palma 2013).

Parasitic lice evolved from Psocopteran-like ancestors (Whiting et al. 1997). Recent Psocopterans often live in the nests of birds and mammals feeding on detritus; hence it is reasonable to suggest that a similar life history of the ancestors of modern lice led to parasitic life-style. More recent molecular taxonomic studies confirmed the close relationship of Psocopterans and Phthirapterans, however, they found that the order of lice is not monophyletic – parasitism arose independently in the ancestors of Amblycera (its sister taxa are the non-parasitic Liposcelid book-lice) and in the ancestors of the other 3 suborders (Johnson et al. 2004, Murrell and Barker 2005). It is still not clear whether lice infested birds or mammals first (Johnson and Clayton 2003). A recent study showed that several louse lineages has already existed in the Cretaceous and passed through the Cretaceous–

Palaeogene boundary (65 million years ago), posing the possibility that lice first emerged on feathered Theropod dinosaurs (Smith et al. 2011). Identifying the first host taxon of lice requires further research and evidence.

The reduction of structural complexity due to a parasitic way of life is quite prominent in this insect order. Lice are secondarily wingless, and their composite eyes are also reduced to quite simple photosensory organs (Johnson and Clayton 2003). Their size varies between 0.8–11 mm; the body is either black or pale brownish or yellowish. Within this range, avian lice tend to have cryptic coloration to avoid visual detection by the host as it was suggested by Rothschild and Clay (1952) and later tested and proved by Bush et al. (2010). Most Amblycerans and Ischnocerans have chewing mouthparts, while Anoplurans and Rhynchophthirinans have sucking mouthparts (Marshall 1981, Johnson and Clayton 2003). The body of avian lice is usually dorsoventrally flattened and either elongate (the guild of the so-called ‘wing lice’) or oval-shaped (so-called ‘body lice’) (Fig. 1). This overall appearance reflects how they avoid host preening in general: elongate lice hide themselves between the barbs of wing and tail feathers, while oval-shaped lice stay mainly on the head and neck (Johnson and Clayton 2003). These two main forms can be found both in Amblycera and Ischnocera (Price el al. 2003). Some Amblycerans utilize more specific refuges to avoid host preening like some *Colpocephalum* lice that chew holes into the feather calamus and spend much time inside these cavities or *Piagetialla* species that live in the pouch of pelicans (Rózsa 2003).

Fig. 1. Louse external morphology. Left: Amblycera: Menoponidae*: Menacanthus rhipidurae* Palma & Price, 2005; right: Ischnocera: Philopteridae: *Naubates ultimate* Palma & Pilgrim, 2002. Copyrights: Museum of New Zealand Te Papa Tongarewa under a CC BY-NC-ND license.

Lice have a hemimetabolous life cycle: the egg is followed by 3 nymphal stages then it develops into an adult insect. The nymphs look quite similar to adults but they are smaller, usually paler, and lack genitals (Marshall 1981). Each nymphal stage lasts about one week, while the adults live for about one month; however, the potential differences in the life span among louse species has not yet been investigated. Males are usually smaller than females, and the sclerotized parts of male genitals are discernible without slide mounting or dissection. The morphology of male genitals is a character of great taxonomic value. In some

Ischnoceran species males have modified antennae to hold the female during copulation (Johnson and Clayton 2003, Rózsa 2003). The reproduction is nearly always sexual, only a very few lineages of mammalian lice are known to be parthenogenic (Johnson and Clayton 2003, Rózsa 2005). Lice don't have identifiable sex chromosomes, the mechanism of sex determination is unknown (Johnson and Clayton 2005).

Amblyceran lice partially feed on dead or living parts of the skin, blood, and other excretions while Ischnoceran lice feed almost exclusively on feathers (Johnson and Clayton 2003; Mey et al. 2007). Members of Anoplura and Rhynchophthirina feed on blood (Marshall 1981). *Rickettsia*-like endosymbiotic bacteria help digesting the keratin in species that feed on feathers and most probably similar bacteria synthetize vitamins in the blood-sucker species (Reed and Hafner 2002). Given that lice usually live in a relatively dry environment (i.e. host plumage or pelage) they have special sclerites between their mouthparts to uptake water vapor from the air (Rudolph 1982). Amblycerans are generally more mobile than Ischnocerans. Members of the latter suborder are so specialized that they can hardly even move on any surface except for feathers (Johnson and Clayton 2003). Hence, the geographical distribution of lice is strictly related to the geographic distribution of avian and mammalian hosts. Louse individuals are hardly ever found off-host; Amblycerans were recorded to abandon dead host individuals; however, as they cannot feed or reproduce among these circumstances, their survival must be quite short (Johnson and Clayton 2003).

Since Crofton (1971) it is widely recognized that parasites have an aggregated distribution among host individuals which can be well estimated by a negative binomial distribution model. This means that the majority of host individuals has zero or very few parasites while a minority of host individuals harbors the majority of parasites. This has far-reaching consequences. First, the mathematical inference that frequently used statistical methods that assume normal distribution of the data cannot be applied here (Rózsa et al. 2000). Second, sampling effort intensity may seriously affect the exploration rate of the parasite faunae of a given host species – a phenomenon that has further sequel on evolutionary ecological investigations (Walther et al. 1995).

Louse-host associations

Lice are quite host-specific parasites (Marshall 1981). Numerous louse species infest only 1 or a few hosts; nevertheless, there are also several species infesting many host species. For example, *Menacanthus eurysternus* (Amblycera: Menoponidae) is harbored by 118 bird species belonging to 70 genera, 20 families, and 2 orders, Passeriformes and Piciformes (Price 1975), and *Anatoecus* (Ischnocera: Philopteridae) species each infests more than 60 species of Anseriformes (Price et al. 2003). However, the understanding of louse host specificity in nature is complicated, at least for two reasons. Firstly, several authors – assuming high host specificity – described new louse species solely on the basis that they were collected from new host species (Mey 2003), resulting in a circular reasoning about host specificity. Clearly, the lumper or splitter attitude of taxonomists greatly affects the interpretation of host specificity (Mey 2003). Secondly, it has to be emphasized that the majority of described louse species are "morphospecies". Given that closely related lice live in more or less similar habitats on different hosts and their morphological complexity is reduced due to the parasitic life-style, it is reasonable to suspect that morphologically similar or even indistinguishable morphospecies may be quite distinct genetically and represent cryptic species in nature. The first molecular taxonomical study on *Menacanthus* species complex is in progress and seems to support this idea (Oldrich Sychra (University of Veterinary and Pharmaceutical Sciences, Brno), personal communication).

The host-parasite associations of birds and lice are relatively well known as compared to several other groups of parasites. This is mainly because birds are very popular animals and their lice can be seen with naked eyes and sampled relatively easily. Hence, it is very common that bird ringers or zoo vets routinely collect lice for the specialists, greatly contributing to louse faunistics. These data – cumulated through centuries – have recently been summarized and extensively reviewed in the monumental work of Price et al. (2003).

One of the greatest challenges for lice is to transmit to a new host individual. Since they are wingless, the transmission usually requires direct physical contact among host individuals (Johnson and Clayton 2003). Hence, obviously, the parent-offspring contacts and the copulation of hosts offer the best opportunity to infest new individuals. The first is called vertical transmission (i.e. among genetically related host individuals) and the latter is called horizontal transmission (i.e. among genetically unrelated host specimens). For avian lice, vertical transmission seems to be most important route to infest new individuals (Clayton and Tompkins 1994); however, there are also evidences of successful horizontal transmission during the copulation of the hosts. Hillgarth (1996) treated the bare parts of the leg (tarsometatarsus) of male pheasants (*Phasianus colchicus*) with glue before copulation with infested females, and found several lice (both Amblycerans and Ischnocerans) attached in the glue trying to infest the male during copulation. Ischnoceran lice – but apparently never Amblycerans – also are known to rely partly on phoretic transmission by hitchhiking on Hippoboscid flies (Clay and Meinertzhagen 1943, Keirans 1975, Harbison et al. 2009);

however, the relative importance of this transmission route in nature has not been clarified yet. Similarly, the behavioral ecology of the decisions in louse transmission (i.e. age, sex and/or intensity of infestation dependence) seems to be a promising field for future studies (see e.g. de Brooke 2010).

Lice have long been considered as relatively harmless parasites for birds (Marshall 1981). However, more recent studies proved that lice can reduce host life expectancy (Brown et al. 1995) mainly by damage flight performance (Barbosa et al. 2002) hence causing a higher mortality during migration. Lice can also increase host metabolism by feeding on down feathers and thus reducing thermoregulation (Booth et al. 1993). Other studies found that louse infestation can reduce sexual attractiveness (Clayton 1990, Kose and Møller 1999, Kose et al. 1999, Pap et al. 2005, Moreno-Rueda and Hoi 2012) hence causing disadvantage in sexual selection.

The host individual does not only provide habitat and food for lice, but also constitutes their natural enemy (Johnson and Clayton 2003). Indeed, host defenses act as predation for lice. These defenses may be grouped as behavioral defenses versus physiological defenses (Rózsa 2005, Clayton et al. 2010). Immunological defenses against avian lice have rarely been studied so far; nevertheless, Amblyceran lice feeding partly on blood and other living tissues seem to precipitate a T-cell mediated immune response (see e.g. Møller et al. 2004, Møller and Rózsa 2005). Though the secretion produced by the uropygial gland is often presumed to play a role in controlling louse burden, and there are correlative evidences supporting this idea (Møller et al. 2010) it has not been tested experimentally so far (Clayton et al. 2010).

Behavioral defenses incorporate preening by the bill (this is usually a targeted attack against louse individuals) (Clayton 1991) and scratching by the feet (which is usually not targeted against certain individuals, but covers body surface areas that are unreachable for preening) (Bush et al. 2012). In several bird taxa there are also some additional methods of behavioral defense such as bathing, dusting (bathing in dust to damage the spiracles of the insect respiratory system), sunbathing (overheating the feathers to distress lice), anting (utilizing ants themselves or their formic acid to reduce the infestation) or using repellent aromatic herbs (Marshall 1981, Clayton and Vernon 1993, Moyer and Wagenbach 1995, Clayton et al. 2010). Molt strategies were also suggested to affect louse populations (Moyer et al. 2002a). Clayton et al. (2010) reviewed the effectiveness of such defenses, pointing out that preening may be the most important and effective method to control ectoparasitic infestations. However, several other methods – which are based on anecdotic observations or contradictory results – have not yet been tested accurately (Clayton et al. 2010) or have recently doubted such as the antiparasitic role of anting (Eisner and Aneshansley 2008).

Louse populations are also affected by environmental conditions outside the host body such as temperature and humidity. Among these, ambient humidity seems to be the most important factor (Johnson and Clayton 2003). There are also hints based on louse diversity on different bird taxa that humidity may affect lice, for example bustards (Otidae) live in arid habitats and harbor quite few louse species as compared to other host taxa of similar size in more humid regions (Price et al. 2003). Moyer at al. (2002b) tested this hypothesis and found that birds living in humid regions of the World have higher louse abundance than birds living in arid regions, even on the same host species with large geographic distribution.

Macroevolutionary approach in studying bird-louse relationships

Macroevolution can be defined simply as the evolution of lineages above species level (Dobzhansky 1937). Naturally, these lineages are abstract entities that had been at all times represented by the genetic and phenetic variability within the populations of species. Environmental challenges exerting selection pressures upon this variability shape populations' allele frequencies and the summation of these microevolutionary changes results in a pattern in the genealogy of higher taxa at a larger evolutionary timescale. The most evident macroevolutionary events are diversification (speciation) and extinctions of higher taxa, acquisition or loss of features and traits in certain lineages. Investigation of such events is termed as a macroevolutionary approach and the broader evolutionary timescale required to recognize such patterns is termed as the macroevolutionary scale. The same logic is applied to the term macroecology; however, the distinction between macroevolution and macroecology is not always clear-cut. The latter refer more to the ecological basis of evolutionary events.

The comparative method – comparing the traits of different taxa to identify macroevolutionary patterns, such as in 'comparative anatomy' – co-appeared along with early evolutionary thinking. However, its proper theoretical and mathematical background was only developed in the 1980's by realizing that the traits compared across taxa are not statistically independent due to their phylogenetic inertia (Felsenstein 2003). To illustrate this statistical non-independence, consider the correlation between average body mass and longevity across 3 mammalian species. Inevitably, two of them are more closely related to each other than to the third taxon, so their character values tend to be more correlated with each other than with the character values of the third one. Hence, phylogenetic relationships must be taken into account in any comparative analysis of macroevolutionary patterns. Felsenstein (1985) proposed the method of independent contrasts to control for the phylogenetic effects in a statistically unbiased way. Since then, a number of different statistical approaches were also developed (Felsenstein 2003, Paradis et al. 2004). The main goal of using phylogenetic control is to distinguish between the two possible causes of observed similarity or difference of a given trait across taxa: phylogenetic inference and independent adaptations since the divergence of the last common ancestor. The first case – closely related taxa are more similar due to character states inherited from their common ancestor – provides a base for taxonomy. Contrarily, however, if two or more characters significantly co-vary on several independent lineages along the phylogeny one would suggest that they are linked by evolutionary effects. By analyzing the distribution of certain traits across taxa we may shed light on how and why those traits evolved as shown by the observed pattern and whether they are related to each other (Garland et al. 1992).

It is always worth noting that even the most modern methodologies of comparative studies lead to correlational evidences; hence the direction of causality between correlated variables cannot be clarified by these tools. Only experimental studies are capable to detect the direction of causality; however, experiments usually involve only a very limited range of taxa during a relatively short time span, hence they are unsuitable to detect macroevolutionary or macroecological patterns. Another possible pitfall of comparative studies may be the lack of plausible phylogenetic information of the investigated taxa (Felsenstein 1985, 2003, Gascuel 2005). Clearly, the results are – at best – as sound as the reliability of the phylogenetic trees they are based on. Birds and mammals have been in the mainstream of molecular taxonomy since the emergence of the field (see e.g. Sibley and Ahlquist 1990) allowing reliable and robust inductions based on mathematically rigorous comparative methods. However, still little is known about the phylogenetic relationships of less known organisms such as the majority of invertebrates. A further problem emerges when studying characters of host-parasite associations. If host and parasite phylogenies do not perfectly mirror each other, which is often the case (Page 2003), it can be hard to define whether one should base the analysis on the host phylogeny or on the parasite phylogeny. A possible solution to this problem is to carry out both analyses and accept results only if they are congruent to each other.

Concerning their life history, lice are excellent candidates for studying evolutionary and ecological patterns of host-parasite relationships partly because they complete their whole life cycle on the host body without any free-living stages. Furthermore, the phylogenies of lice and particularly that of their avian and mammalian hosts are the most resolved phylogenies among any living organisms allowing for evolutionary comparative analyses controlled for phylogenetic effects (Felsenstein 1985). The faunistics and host-parasite associations are also relatively well known as compared to other parasites (Price et al 2003). Due to the remarkable specialization to their hosts and relatively high host specificity lice have had a prominent role in co-speciation studies (Fahrenholz 1913, Hafner and Nadler 1988, Page 2003).

Historically, the early papers about macroevolutionary patterns of the host-parasite relationship predated the development of suitable testing methods and were essentially based on reasoned thinking and generalizations but lacking rigorous tests and phylogenetic control. As for bird-louse relationships, the first macroevolutionary hypotheses were formed in the early and mid-20th century mainly by German authors and termed as the "rules" of parasitological relationships (Klassen 1992). Here I list some of the better known "rules":

- Fahrenholz's rule: host and parasite phylogeny mirror each other (Fahrenholz 1913);
- Eichler's rule: more species-rich groups of hosts harbor more species-rich parasite faunae than host groups with lower species richness (Eichler 1942);
- Manter's rule: the evolution of hosts is faster than that of their parasites (Klassen 1992);
- Harrison's rule: louse body size is correlated with host body size (Harrison 1915).

Many of the proposed relationships turned out to be wrong after rigorous testing (Klassen 1992, Johnson and Clayton 2003, Rózsa 2005). For example, contrary to "Manter's rule", Hafner el al. (1994) found that the rate of molecular evolution of pocket gopher lice is 10 times faster as compared to that of pocket gopher hosts, which is not surprising given that the generation time is about 10 times shorter in the parasites than that of the hosts. Of course, Manter originally proposed his idea referring to morphological evolution; which, however, is not an easily measureable or comparable feature across as distant taxa as hosts and parasites.

However, some of these "rules" proved to be right after testing them with modern methodologies. Both Harrison's (see in Johnson and Clayton 2003) and Eichler's (Vas et al. 2012a, see also in Chapter 1.2.3. of the present thesis) predictions hold across a wide range of avian and mammalian hosts, therefore these are the most robust macroevolutionary patterns that have been demonstrated for lice so far. The attempt of testing "Fahrenholz's rule" created the new and dynamic field of co-phylogenetic studies. Despite the clear reasoning and logic behind “Fahrenholz’s rule”, parasite phylogenies hardly ever mirror that of their hosts (but see Hafner and Nadler 1988) even in relationships characterized by quite strict host specificity. Host switching and independent speciation of either the hosts or the parasites often dismiss the similarity expected on the base of supposed co-speciation events. The investigation of these factors is a promising topic in evolutionary biology (Clayton et al. 2003). Page (2003) gives a comprehensive overview of this field, covering its history, theoretical and methodological background, and illustrated with several case studies.

Chapter 1 – Louse diversity and its macroevolutionary shaping factors

1.1. Introduction to Chapter 1.

“From so simple a beginning” (Darwin 1859) an astonishing variety of life-forms has evolved on Earth. The number of formally described species is over 1.5 million; however, estimations claim that true species richness may be about 10-30 million species globally (see e.g. Janzen 1976, Erwin 1983, May 1988). The more and more commonly used term ‘biodiversity’ embrace the richness of species, the genetic variability within conspecific individuals of a given species, and the variety of ecosystems they live in (Standovár and Primack 2001). Several authors argue that nowadays the expansion of human activities has created a biodiversity crisis, an extinction wave due to rapid human-induced changes in the environment (Eldredge 2000). The recognition of this phenomenon has led to the rise of conservation biology which focuses on practical and applied issues of the protection of endangered population, species, and ecosystems. Nevertheless, there is an obvious need for a well-established theoretical background of biodiversity maintenance as well. From a historical point of view, palaeobiology can offer insight into past changes and fluctuations by analyzing the correlation between biodiversity and environmental changes (see e.g. Pálfy 2000), and drawing the inference for the present situation. Unfortunately, parasites’ fossils are extremely rare (Dittmar 2009) and thus we have to rely on information obtained from extant organisms in order to infer past evolutionary history. Hopefully, such studies may contribute to a better understanding of the formation and maintenance of global biodiversity.

As I stated above, the features of the bird-louse relationship offers a unique system to study the inference of macroevolutionary and macroecological factors shaping two closely associated lineages. In this chapter I focus on the diversity component of host-parasite relationships, using birds (and sometimes mammals) and their lice as a model system. Parasites and pathogens have a quite specific role in the formation and maintenance of biodiversity; they not only represent themselves by their numbers (such as species richness, which is also not negligible) rather they have a unique importance in facilitating the diversity of their hosts as well (Poulin and Morand 2003) hence contributing to the global biodiversity as a whole at a great extent.

Louse richness is remarkably variable among host taxa (Price et al. 2003). Almost all families of birds are infested by some lice (except a very few small families such as Balaenicipitidae and Todidae) while they are absent on several species-rich groups of mammals such as bats (Chiroptera), shrews, moles, hedgehogs and their allies (Insectivora), and whales and their allies (Cetacea). The variation in the taxonomical diversity of louse faunae harbored by different host families is quite high. Among birds, the family of tinamous (Tinamidae) harbor 20 louse genera, followed by the pheasants and their allies (Phasianidae) with 18, then the parrot family (Psittacidae) with 17 louse genera. On the other hand, some other avian families harbor peculiarly species-poor louse assemblages, at least as compared to their closest relative taxa or to non-related birds which are similar in size and general. For example, the shoebill (*Balaeniceps rex*) has no louse record at all, although it is very similar to Ciconiiform birds which in turn harbor several louse taxa. Bustards (Otidae) have also very poor louse faunae as compared to other large-bodied birds.

An evolutionary comparative approach is a potentially useful tool to explore whether this variation in louse richness is caused by host phylogenetic relationship (i.e. the given host clade simply inherited a species-rich louse faunae from its ancestors) or by correlates of host life-style and environment. Up to know only a relatively few comparative studies have been carried out to explore the diversity patterns of ectoparasitic lice. However, before reviewing the literature and presenting our own case studies about the already explored correlates of louse richness two particular methodological problems have to be highlighted, namely the potential bias caused by uneven sampling effort, and the importance of the decision of which measure is used to characterize parasite diversity.

The rate of discovery of the parasite fauna of a certain host species clearly depends on the sampling effort focused on that host (Walther et al 1995), which depends on several factors such as geographic distribution, rarity, body size, and popularity of the host taxon, as well as general research effort focused on the host. Additionally, parasite aggregation, prevalence and intensity of infestation also affect the rate of discovery; the proper sampling of a host species with more aggregated parasite distributions requires larger sample size than the sampling of another host species with less aggregated parasite distributions. Hence, sampling effort should be taken into account when one compares the parasite richness of different host species to avoid the bias caused by uneven sampling.

However, the way how it should be considered is not at all clear-cut. There are several methods how to control for effects of sampling bias on parasite richness, the most widespread among them is, evidently, the residual method (Garland et al. 1992). In this case, the authors perform a linear regression between a host/parasite character and a measure of sampling effort and calculate residuals from the linear model for each data point. Then these residuals are used in the subsequent analysis as a proxy of parasite richness. However, this method has been recently criticized from a mathematical point of view (Freckleton 2002). Freckleton (2009) suggested a more advanced approach by including research/sampling effort as a separate explanatory variable in a multivariate model. Nevertheless, the possibility that controlling for research effort may introduce an extra source of random noise has not been excluded or verified yet.

Another potential source of bias roots in the diversity measures applied. The most commonly used measure is parasite species richness. This measure strongly depends on the more or less arbitrary species concept (Mey 2003). Additionally, as a widely distributed bird species often hosts congeneric louse species, each restricted to different and non-overlapping areas of the host distribution (Clay 1964), parasite species richness may overestimate the actual richness that each bird population harbor locally. Moreover, species richness is more dependent on sampling effort.

Hence, some authors prefer parasite genera richness instead of species richness to avoid the potential bias mentioned above. Uneven sampling arguably affects genera richness to a smaller extent than species richness because the parasite faunae are more precisely explored on the level of genera than on species level. Additionally – at least in the case of avian lice – genera can roughly be interpreted as different ecological guilds in the sense of Simberloff and Dayan (1991) utilizing different environmental refuges to avoid host defenses characterized by distinct body shape and size, such as narrow-bodied 'wing lice' or oval-shaped 'body lice' (Johnson and Clayton 2003). Louse genera fit to this concept, making genera richness a less arbitrary unit.

Another advanced measure is the taxonomic distinctness index (Warwick and Clarke 1995, Clarke and Warwick 1998) that takes into account both the number of parasite species and their taxonomic composition by counting and averaging the required steps up along the Linnaean hierarchy reaching the common node of any given species pairs of the parasite assemblage (Fig. 1). Hence, distinctly related parasites are characterized by a higher value than e.g. the same number of congeneric parasites. One of the biggest advantages of this measure of the richness of parasite faunae is that it depends less on sampling effort (Poulin and Mouillot 2003).

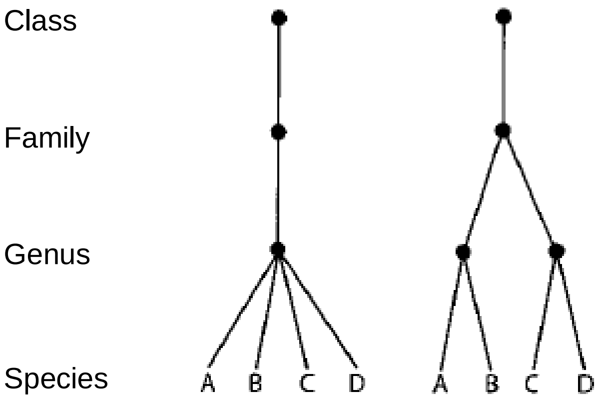

Fig. 1. The calculation of taxonomic distinctness index. Left: all species are congeners thus they average a single step up to the common node, hence the index is 1. Right: steps required up to reach the common node of AB=1, AC=2, AD=2, BC=2, BD=2, CD=1; thus the index is 10/6=1.67. Figure based on Poulin and Mouillot (2003).

The first comparative study on louse richness controlled for both phylogenetic effects and uneven sampling effort was performed by Clayton and Walther (2001). By analyzing a sample of Neotropical birds they found no co-variation between louse species richness and the host characters such as geographical range, population density, microhabitat, body mass, plumage characteristics, and morphology of bill, foot, and toenail. Later on, Hughes and Page (2007) analyzed somewhat similar but more extended host correlates of parasite richness of sea birds (Procellariiformes, Charadriiformes, Pelecaniformes). They examined whether host morphological (body size, body weight, wingspan, bill length), life-history (longevity, clutch size), ecological (population size, geographical range) and behavioral (diving versus non-diving) variables co-vary with louse species and genera richness (controlled for uneven sampling by the residual method). By applying phylogenetic control host population size and geographic range exhibited a significant positive co-variation with species richness and genera richness both in Amblycerans and in Ischnocerans. They also found significant negative correlation between louse richness and host body mass, and confirmed Felső and Rózsa (2006)'s results on the negative effect of diving behavior; however, for some reason the authors only admitted the correlations that were significant both with and without phylogenetic control as reliable results (host population size and geographic range). This approach is quite unsubstantiated and cannot be justified from a mathematical viewpoint (Felsenstein 1985, Garland et al. 1992, Felsenstein 2003, Freckleton 2009).

Felső and Rózsa (2006, 2007) compared the genera richness of lice harbored by aquatic versus terrestrial sister-clades of avian and mammalian hosts. The term ‘aquatic’ means that the hosts dive beneath the water surface with their entire body for food. They found that these diving clades tend to harbor significantly reduced louse faunae as compared to non-diving sister clades both in birds and mammals, indicating that several louse lineages were not able to adapt to the diving life-style of the hosts. Past bottlenecks in host population size – such as artificial introduction of hosts to new continents – were also shown to significantly reduce louse richness most probably due to the fact that the small founder group of a population can not harbor all possible parasite taxa (Paterson et al. 1999, MacLeod et al. 2010).

Another bunch of papers examined the relationship between host defense and louse richness. Cotgreave and Clayton (1994)’s pair-wise comparative approach found a significant positive co-variation between the time spent by grooming (preening and scratching) and louse richness of birds. The authors discussed only one direction of causality by interpreting the results: richer louse burdens may exert a higher pressure on birds hence promote grooming activities.

Studies conducted from a physiological point of view also supported a positive co-variation between host defense and louse richness, at least in case of Amblyceran lice. The authors considered both possible ways of direction of causality in the interpretation of these results (Møller and Rózsa 2005, Møller et al. 2010). The positive correlation may either be explained by the higher selective pressure exerted by parasites upon their hosts or, alternatively, it may be more plausible that increased host defensive capabilities may force parasites to diversify so as to avoid such defenses.

In a comparison across 80 European bird species Amblyceran (but not Ischnoceran) genera richness co-varied positively with the intensity of T-cell mediated immune response of host nestling (Møller and Rózsa 2005). Given the fact that Ischnocerans hardly ever come into direct contact with the living tissues of the hosts, the difference in the results between the two suborders is not surprising. This study was probably the first to point out that the richness of Amblycerans and Ischnocerans should be analyzed separately rather than pooled together as they may response distinctly to certain environmental effects. Similar results were obtained by testing the correlation between the relative uropygial gland size and louse genera richness across 212 bird species (Møller et al. 2010). The uropygial gland produces secretions that are presumed to have anti-ectoparasitic effects (Marshall 1981); hence its relative size may act as a proxy of host defense. Again, these variables co-vary positively in the case of Amblycera, but not in the case of Ischnocera (Møller et al. 2010) confirming that the separate handling of the two suborders in comparative analyses is reasonable.

In the next paragraphs I briefly introduce the three case studies published on this topic by myself and my co-authors.

The first case study entitled "Clever birds are lousy: Co-variation between avian innovation and the taxonomic richness of their amblyceran lice" was published in International Journal for Parasitology. This paper unveils a formerly unexpected positive correlation between the cognitive capabilities and louse richness across avian families. Both large brains and parasitic infestations are highly expensive in terms of energy and nutrient requirements. The costs of parasitism may either come in terms of the damage caused by infestations or in terms of costly defenses against parasitism. Anyway, one could argue that parasites exhibit a negative effect on brain development on a macroevolutionary scale, hence a negative correlation is expected between brain size and parasite richness. On the other hand, a positive correlation is also plausible due to several other reasons. Using data of 108 avian families (controlling for phylogenetic effects, host species richness within a family, body size, and research effort) we found that host cognitive capabilities and brain size co-vary positively with Amblyceran genera richness, but not with Ischnocerans. We proposed several alternative and mutually non-exclusive hypotheses to explain this phenomenon.

The next case study entitled "Avian brood parasitism and ectoparasite richness – scale-dependent diversity interactions in a three-level host-parasite system" was published in Evolution. This paper explores the effect of hosts' brood parasitic life-style and the complex metapopulation structure of foster-generalist cuckoo species on their louse richness. Brood parasitic birds, together with their parasites and their foster birds constitute a complex three-level evolutionary system. Brood parasitic birds harbor host-specific louse species despite the complete lack of the vertical route of louse transmission, as their nestlings never get into direct physical contact with their genetic parents. We showed that host clades' past switches to brood parasitism reduced both Amblyceran and (to a lesser extent) Ischnoceran genera richness, most probably because several louse lineages were unable to adapt to the lack of vertical transmission. On the other hand, we also showed that the supposedly more complex and dynamic subpopulation structure of foster-generalist (i.e. utilizes several to many foster species) cuckoo species facilitates Ischnoceran species richness; hence for the first time we recognized diversity interactions across a three-level host-parasite system.

The final case study in Chapter 1 entitled "Evolutionary co-variation of host and parasite diversity – the first test of Eichler's rule using parasitic lice (Insecta: Phthiraptera)" was published in Parasitology Research. This work re-visits and for the first time tests with modern methodologies the more or less forgotten "Eichler's rule", covering both avian and mammalian lice. Eichler's (Fig. 2) original assumption that more diverse host groups harbor more diverse parasite faunae was strongly supported by the study. Host diversity is most probably the strongest predictor of parasite diversity. We also discuss the potential macroevolutionary and macroecological mechanisms beyond this phenomenon.

Fig. 2. Wolfdietrich Eichler (1912-1994). Photo from phthitaptera.info, copyright expired.

1.2.1. Case study (as published in International Journal for Parasitology 41: 1295-1300., 2011.):

Clever birds are lousy: Co-variation between avian innovation and the taxonomic richness of their amblyceran lice

authors: *Zoltán Vas, Louis Lefebvre, Kevin P. Johnson, Jenő Reiczigel, Lajos Rózsa*

Introduction

Avian lice are interesting candidates to explore environmental factors affecting parasite biodiversity for several reasons. Firstly, animal lice (Insecta: Phthiraptera) are pathogens in the sense that they reduce host life expectancy (Brown et al. 1995) and flight performance (Barbosa et al. 2002), as well as increase metabolism (Booth et al. 1993) and reduce sexual attractiveness (Clayton 1990, Kose and Møller 1999, Kose et al. 1999). Secondly, the diversity and host distribution of avian lice has been extensively reviewed (Price et al. 2003). Finally, avian lice are relatively diverse compared with the species richness of mammalian lice (Johnson and Clayton 2003).

In spite of this, a complete understanding of the taxonomic richness of avian louse fauna is still lacking. One particular methodological problem is that louse species richness data are biased by differences in research effort (Walther et al. 1995). Moreover, parasites can be inherited from host ancestors (Page 2003) and, therefore, host phylogeny limits species composition. Thus studies of parasite richness must always control for potential biases due to differences in sampling effort and host phylogeny.

Some environmental correlates of louse taxonomic richness have already been explored, incorporating some kind of controls for the biases mentioned above. For example, past bottlenecks in host population size may result in a long-lasting reduction of louse richness (Paterson et al. 1999, MacLeod et al. 2010). Moreover, an evolutionary switch to an aquatic way of life (or, more precisely, to diving behaviour) reduces louse richness compared with louse assemblages inhabiting non-aquatic sister-clades of birds (Felső and Rózsa 2006). Interestingly, higher levels of avian physiological defenses such as stronger T-cell immune response or relatively larger uropygial glands co-vary positively with the taxonomic richness of amblyceran lice, while they do not interact with the richness of ischnoceran lice (Møller and Rózsa 2005, Møller et al. 2010). Finally, the population size of marine birds and – to a lesser extent – their geographic range co-varies positively with louse richness (Hughes and Page 2007).

One other intriguing environmental correlate of avian parasites might be host behavioral flexibility. It can be quantified as feeding innovation rates and its neural correlate, relative brain size (Lefebvre et al. 1997). Bird clades that show high rates of novel feeding techniques tend to have large brains (Overington et al. 2009). Both of these traits are associated with a higher prevalence of endoparasites (Garamszegi et al. 2007), as well as a stronger immune response in the form of an enlarged spleen and bursa of Fabricius (Møller et al. 2004). This relationship might be facilitated by the exposure of innovative clades to a wider set of habitats (Overington S.E. 2011. Behavioural Innovation and the Evolution of Cognition in Birds. Ph.D. Thesis. McGill University, Canada), resulting in a higher rate of contact with a diversity of potential parasites. The positive relationship between endoparasite infestation, immune response, innovation rate and relative brain size is all the more intriguing in that it runs counter to the known cost of parasites on brain development. In bats and rodents, Bordes et al. (2008, 2011) followed such logic in predicting a negative effect of parasite species richness on brain size due to a trade-off between energetic costs of immune defense and those of brain maintenance. In contrast, they found a positive association similar to the one reported in birds.

In this paper, we examine the relationship between avian ectoparasite richness, innovation rate and brain size while controlling for host species diversity, body size, phylogeny and research effort. We predict that ectoparasite richness should be positively associated with innovation rate and relative brain size.

Materials and methods

Host taxonomic levels used in the study

We examined variation in avian traits at the family level. Correlates of innovation rate and relative brain size are routinely studied at this level (Sol et al. 2005a,b, Overington et al. 2009). The avian family level is also convenient for the measure of ectoparasite diversity and helps to account for missing information at the species level.

Taxonomic richness of hosts and lice

Species richness of bird families was obtained from the checklist of Sibley and Monroe (1990), because the innovation and relative brain size data also refer to bird families recognized by this checklist. As host species richness among avian families varied across several magnitudes (1–993) we log-transformed species richness data in all subsequent analyses.

We used generic richness as a proxy for louse taxonomic diversity because it has several advantages over species richness. Firstly, a widely distributed bird species often hosts congeneric louse species, each restricted to different non-overlapping parts of the host distribution. Thus, parasite species richness of widely distributed bird species would over-estimate the true parasite richness that each local bird population harbors (Clay 1964). Secondly, taxonomists often use different species concepts to describe louse diversity (Mey 2003), making species richness an unreliable measure. Some taxonomists automatically described congeneric lice from different hosts as distinct species while other authors lump many species into a single one from a wide range of hosts (see Price (1975) as an example). Finally, the bias caused by uneven sampling intensity is stronger at the species level than at the generic level. The number of louse genera found per avian family was obtained from Price et al. (2003).

However, Price et al. (2003) used a bird checklist which differs slightly from that used in the innovation and brain size datasets. Therefore, the louse lists were fitted to the families recognized by Sibley and Monroe (1990) by dividing or unifying certain families. We collected richness data separately for amblyceran and ischnoceran lice. This is because the life histories and the important factors affecting distribution and evolution in these louse suborders are quite different, as already shown by several previous studies (see e.g. Johnson and Clayton 2003, Møller and Rózsa 2005, Felső and Rózsa 2006, Whiteman et al. 2006, Møller et al. 2010). Louse generic richness data was not log-transformed, as it did not vary across several magnitudes (see Section 3).

We controlled for uneven louse sampling effort in two different ways. Firstly, we used generic richness to quantify parasite diversity, which is less biased by sampling than species richness. Arguably, a larger proportion of louse species awaits description than the proportion of unknown louse genera. Secondly, for each host family we calculated a study effort rate defined as the number of species known to be associated with lice divided by the total number of species. Then we excluded all bird families below the 10% effort rate, an arbitrary limit thus reducing the sample size from 108 to 99. As all results in the subsequent analyses were qualitatively identical to those obtained using the whole dataset, we do not report these results.

Quantifying rates of feeding innovation

We used a current extended version of the database on avian innovations collated by Lefebvre and colleagues (Lefebvre et al. 1997, Overington et al. 2009). In birds, feeding innovations are defined as new foods or new ways of searching, handling or ingesting food (Kummer and Goodall 1985, Lefebvre et al. 1997, Reader and Laland 2003). The innovation database currently contains over 2,300 reports for 808 species in six zones of the world (North America, Western Europe, Australia, New Zealand, southern Africa and the Indian subcontinent), compiled from volumes of 64 ornithology journals published mostly between 1960 and 2002. These journals include academic serials (e.g. Auk, British Birds, Ibis, Emu) as well as publications that are edited by local birding organizations (e.g. Florida Field Naturalist, Nebraska Bird Review). Reports are included in the database if they contain keywords such as 'novel', 'opportunistic', 'first description', 'not noted before' or 'unusual' (Lefebvre et al. 1997). Although the degree to which the noted behaviour is a departure from the species’ repertoire may vary, the strength of this database is that it relies on the knowledge of local birders and ornithologists, as well as that of journal editors and reviewers. All of the reports, and the claim of novelty they contain, have thus been subject to some form of peer review. The reliability and validity of the database has been checked for biases stemming from species number per clade, research effort, population size, likelihood of noticing and reporting a case, popularity of a species among observers, inter-classifier (most often blind to the hypothesis) agreement (0.827–0.910), journal identity, geographical zone and historical period (Nicolakakis and Lefebvre 2000, Lefebvre et al. 2001). In this paper, we corrected innovation frequency by research effort, defined as the number of articles listed for each species in the online version of the Zoological Record (available at www.library.dialog.com/bluesheets/html/bl0185.html). Both innovation rate and research effort were summed for families by adding species level data and log transforming the totals.

Relative brain size and body mass for avian families

The avian brain size database includes 1,714 species, comprising both directly measured brain mass and endocranial volumes converted to mass (as described in Mlikovsky 1989a,b,c, 1990, DeVoogd et al. 1993, Székely et al. 1996, Garamszegi et al. 2002, Iwaniuk and Nelson 2002, Iwaniuk (Iwaniuk, A.N. 2003. The Evolution of Brain Size and Structure in Birds. Ph.D. Thesis. Monash University, Australia), Sol et al. 2005a). These data represent mean values of male and female specimens. Previous work (Overington et al. 2009) has shown that the combination of data from multiple sources does not bias the relationship with innovation rate: data on 1,197 species from a single experimenter (Iwaniuk 2003. Ph.D. Thesis, see above) using one technique (endocranial volume, which is not influenced by potential errors related to freezing, desiccation or perfusion that can affect fresh brains) yields similar conclusions to that of the dataset collated from multiple sources. The relationship between innovation rate and relative size of the neural substrate is also robust with respect to both anatomical level and origin of the dataset, yielding similar results at the level of: the whole brain - combined dataset or limited endocranial dataset of Iwaniuk (2003. Ph.D. Thesis, see above), reported in Overington et al. (2009); the cerebral hemispheres – data from Portmann (1947), reported in Lefebvre et al. (1997), or the mesopallium and nidopallium – data from Boire (Boire, D. 1989. Comparaison quantitative de l’encéphale, de ses grandes subdivisions et de relais visuels, trijumaux et acoustiques chez 28 espèces d’oiseaux. Ph.D. Thesis. Université de Montréal, Canada) and Rehkämper et al. (1991), reported in Timmermans et al. (2000). The relationship is also independent of the known confounding effect of development mode of brain size (Bennett and Harvey 1985).

Body mass is a well-known covariate of brain size in birds as well as a potential confounding variable in comparative studies in general (Garland et al. 1992), and particularly in studies focused on avian louse assemblages (Rózsa 1997a). Body mass data were taken from the same sources as brain mass. We averaged brain volumes and body masses within each family and calculated the residuals from a log–log linear regression of the mean body size and brain size of species for each family. As the usage of residuals from linear regression is often criticized (Freckleton 2002, 2009) we also computed the ratio of brain size to body mass. However, as the results obtained by using this ratio were qualitatively identical to the results obtained when analyzing residual brain size, we report only the latter.

Phylogenetic trees

We constructed three different phylogenetic trees of bird families in Mesquite 2.74 (available at www.mesquiteproject.org) to take evolutionary history into account (Felsenstein 1985, 2004). One of these trees was constructed by Sibley and Ahlquist (1990) with branch length values based on DNA-DNA hybridization. This tree was obtained from the Analysis of Phylogenetics and Evolution ('ape') package (Paradis et al. 2004) in R 2.11.1 (available at www.R-project.org). The phylogenetic hypothesis of Sibley and Ahlquist (1990) is often still used in comparative studies because it provides the most complete available tree with real branch lengths (Overington et al. 2009). However, more recent studies based on nuclear and mtDNA sequences suggested that several relationships in the Sibley and Ahlquist (1990) tree might not be correct (Barker et al. 2004, Alström et al. 2006, Hackett et al. 2008).

Therefore, we constructed two other trees, one based on Barker et al. (2004) and Hackett et al. (2008), and another one based on Barker et al. (2004), Alström et al. (2006) and Hackett et al. (2008). The non-passerine branching pattern from Hackett et al. (2008) was combined with passerine topology from Barker et al. (2004) and the latter was modified in one of the trees according to Alström et al. (2006).These trees differ from each other in the phylogeny of Passeriformes. The relationships among these families are still uncertain, possibly due to the rapid radiation of Passeriformes (Barker et al. 2004, Alström et al. 2006). Although these phylogenies provide more up-to-date branching patterns, they come without branch length values. Therefore, we used arbitrary branch lengths computed with PDAP:PDTREE module 1.15 (available at www.mesquiteproject.org/pdap_mesquite) in Mesquite 2.74. This module allows the calculation of arbitrary branch lengths using several methods, e.g. all branch lengths equal to one, branch lengths according to the method of Grafen (1989), Pagel (1992) or Nee (Purvis 1995).

The results obtained by using different trees (and different arbitrary branch lengths in the case of newer trees) were qualitatively identical; therefore, we report only the analysis based on the Sibley and Ahlquist (1990) tree. This choice was reasonable as this was the only phylogenetic model to contain real branch length information and provides a perfect fit to data according to the diagnostic plots (see Section 2.6).

Our phylogenetic trees contained polytomies, probably due to the uncertainty about the true bifurcating patterns. Polytomies in the phylogenetic trees can cause inflation in the type I error in the analysis of independent contrasts (Grafen 1989, Purvis and Garland 1993); however, this problem was resolved by bounded degrees of freedom, as recommended by Purvis and Garland (1993) and tested by Garland and Díaz-Uriarte (1999).

Statistical analyses

We used the method of independent contrasts to control for phylogenetic non-independence (Felsenstein 1985). Calculations were carried out with PDAP:PDTREE module 1.15 in Mesquite 2.74. We plotted the absolute values of standardized phylogenetically independent contrasts versus their S.D.s as the most widespread and reliable diagnostic check to test whether the branch lengths fitted the data (Garland et al. 1992, Díaz-Uriarte and Garland 1996, 1998). According to diagnostic plots, the model using the phylogenetic tree by Sibley and Ahlquist (1990) provided a perfect fit. The more recent trees by Barker et al. (2004), Alström et al. (2006) and Hackett et al. (2008) with arbitrary branch lengths did not provide a perfect fit, probably due to the lack of real branch length information. We simulated character evolution under the Brownian motion model (Felsenstein 1985). Although this model might not perfectly represent the process of evolutionary changes, several authors have shown that even with errors in branch lengths and deviations from Brownian motion the method of independent contrasts is robust and reliable (Díaz-Uriarte and Garland 1996, 1998).

The correlated evolution between two continuous variables can be tested simultaneously by using the method of independent contrasts in Mesquite 2.74. Therefore, we created standardized contrasts for each variable and performed multiple linear regressions to test the explanatory power of all variables on the louse taxonomic richness at the same time. All regressions were computed through the origin (Felsenstein 1985, Garland et al. 1992). Multicollinearity between the explanatory variables was checked by variance inflation factor (VIF) (Reiczigel et al. 2007). These analyses were carried out with R 2.11.1 using the packages 'R Commander' (available at cran.r-project.org/package=Rcmdr) and 'faraway' (available at www.maths.bath.ac.uk/~jjf23). We calculated the *K* phylogenetic signal measure (Blomberg et al. 2003) using the 'picante' package (Kembel et al. 2010). All reported *P*-values are two-tailed and a *P* value of 0.05 was considered significant. The full dataset of all variables is available from the corresponding author.

Results

Both amblyceran (range: 0–10 genera, mean = 1.92) and ischnoceran (range: 0–14 genera, mean = 2.26) richness varied extensively across the 108 avian families involved. The *K* phylogenetic signal measure (Blomberg et al., 2003) of our variables varied between 0.61 and 2.10 suggesting some degree of phylogenetic non-independence. The phylogenetic signal was significant ($P < 0.001$) in residual brain size ($K = 0.99$), body mass ($K = 1.91$), ratio of brain size to body mass ($K = 2.10$), and amblyceran generic richness ($K = 0.80$); hence we controlled for phylogeny in all analyses.

In a phylogenetically controlled comparison, host innovation rate per family, co-varied positively with amblyceran richness ($n = 107$, slope = 0.42, r = 0.30, $P = 0.002$, Fig. 1), but no similar significant relationship appeared with ischnoceran richness ($n = 107$, slope = 0.18, r =

0.08, *P* = 0.388). Relative brain size also showed a significant correlation with amblyceran richness (*n* = 102, slope = 0.37, r = 0.19, *P* = 0.049), however, it did not correlate with ischnoceran richness (*n* = 102, slope = 0.51, r = 0.18, *P* = 0.076).

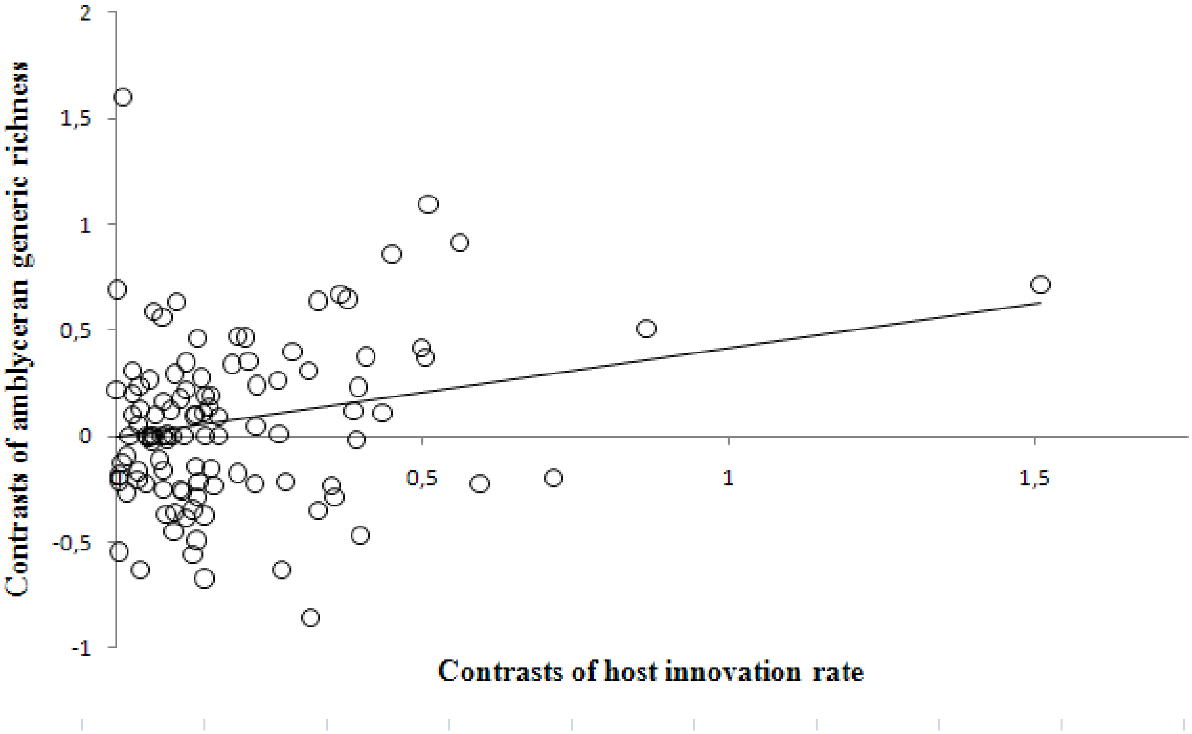

Fig. 1. Co-variation of avian innovation rate and amblyceran richness.

We found a strong positive correlation between amblyceran and ischnoceran richness across avian families (*n* = 107, slope = 0.98, r = 0.65, *P* < 0.001). The (log) species richness of avian families showed a highly significant positive correlation both with amblyceran (*n* = 107, slope = 1.43, r = 0.65, *P* < 0.001) and ischnoceran richness (*n* = 107, slope = 2.05, r = 0.62, *P* < 0.001). However, species richness of avian families co-varied with neither innovation rate (*n* = 107, slope = 0.21, r = 0.14, *P* = 0.161) nor residual brain size (*n* = 102, slope < -0.01, r < -0.01, *P* = 0.992).

One can presume that body mass might act as a confounding variable since more innovative birds may tend to be larger and, consequently, may harbor more diverse louse burdens. Therefore, we checked the relationship between avian (log) body masses and innovative capabilities. Contrary to our expectations, there was no relationship between these variables (*n* = 102, slope = -0.07, r = -0.03, *P* = 0.741). Additionally, we found no correlation between (log) host body mass and either amblyceran (*n* = 102, slope = -0.29, r = -0.09, *P* = 0.345) or ischnoceran generic richness (*n* = 102, slope = -0.39, r = -0.08, *P* = 0.396).

In our multiple linear regression models the response variables were the standardized contrasts of either amblyceran or ischnoceran richness. The explanatory variables were the standardised contrasts of host innovative capability, relative brain size, (log) species richness and (log) body mass of avian families, and the generic-level richness of the other louse suborder. Significant predictors of amblyceran richness were avian (log) species richness (slope = 0.83, *P* < 0.001), innovative capabilities (slope = 0.30, *P* = 0.001), and ischnoceran richness (slope = 0.26, *P* < 0.001, adjusted R^2 of the model = 0.56). There was no multicollinearity between the explanatory variables (VIF values, respectively: 1.64, 1.02 and 1.62). Significant predictors of ischnoceran richness were avian (log) species richness (slope = 1.13, *P* < 0.001), and amblyceran richness (slope = 0.65, *P* < 0.001, adjusted R^2 of the model = 0.48). There was no multicollinearity between the explanatory variables (VIF values, respectively: 1.75, 1.75).

Discussion

To our knowledge, this is the first reported study to explore ecological correlates of the taxonomic richness of louse infestations across a considerably wide range of avian families, comprehensively sampling avian diversity. In particular, we included a large proportion – 108 out of 146 – of the families recognized by Sibley and Monroe (1990).

Our results show that both amblyceran and ischnoceran generic richness co-varied positively with host taxonomic richness. The relationship between host taxonomic richness and louse richness was predicted several decades ago by Eichler (1942). This effect is often called "Eichler’s rule". The positive relationship between amblyceran and ischnoceran richness – independent of the parallel effect of "Eichler’s rule" – has already been reported by Møller and Rózsa (2005) and is strongly supported by our present results. Ecological interpretation of this phenomenon is not well understood. It seems likely that an increase in host diversity might increase amblyceran and ischnoceran richness as parallel but independent effects. However, this effect was not responsible for the relationship of amblyceran richness with innovation rate or residual brain size, as species richness of avian families co-varied with neither of these variables. The lack of co-variation between innovation rates and host species richness was not surprising given the fact that innovation rate was already controlled for research effort which is highly correlated with avian species richness (Lefebvre et al. 2001).

The most surprising result of the present study was a highly significant positive relationship between host residual innovation frequency and the taxonomic richness of amblyceran lice (Fig. 1), in contrast to the lack of a similar relationship in the case of ischnoceran lice. The correlation between host innovative capabilities and amblyceran richness was not influenced by the three outlier points (Fig. 1). According to model diagnostic plots, these points were not influential and results obtained by excluding them were qualitatively identical. This co-variation was robust, as we found qualitatively identical results by using any of the phylogenetic trees and arbitrary branch length transformations described above. This was not a spurious effect of host taxonomic richness, as it was not significantly associated with either innovation rate or residual brain size.

Host behavioral flexibility interacts with amblyceran richness; however, host brain size has only a marginal impact. This finding is paralleled by results of Bordes et al. (2011) who found that only the taxonomic richness of mites, but not the richness of helminths or fleas, was predicted by differences in host brain size. These results again raise doubts about the hypothesis that parasite richness is affected by the high costs of producing and maintaining large brains in the host. It seems more likely that it is not the large brains per se that are important, but cognitive capabilities that co-vary directly with the taxonomic richness of parasite assemblages. In birds, the metabolic costs of maintaining a large brain do not seem to be as high as they are in mammals. Isler and van Schaik (2006a) found a strong association between basal metabolic rate and brain size (both corrected for body size) in 347 mammalian species, but not in 224 species of birds (Isler and van Schaik 2006b).

Here we propose four alternative and mutually non-exclusive hypotheses that might possibly explain the co-variation of host innovative capabilities and amblyceran richness. Firstly, Sol et al. (2005a) have shown that more innovative birds are also better at colonizing new zones in which they have been introduced. Perhaps as a consequence, more innovative species also tend to have more subspecies (Sol et al. 2005b) and innovative parvorders more species (Nicolakakis et al. 2003) than less innovative ones. Host diversity is known to be associated with louse diversity (Eichler 1941), so if innovativeness contributes to avian diversity, then we also expect innovativeness and louse diversity to co-vary. While this effect might partly contribute to amblyceran richness on more innovative taxa, we emphasize that the relationship between amblyceran richness and host innovative capabilities was also significant independently of the parallel effect of "Eichler’s rule".

Secondly, Overington et al. (2011) has shown that more innovative birds exploit a wider diversity of habitats than less innovative ones. These clades might thus have a greater chance of contacting other avian taxa in these habitats, enabling lice specific to other birds to switch more frequently to innovative birds.

Thirdly, birds with more sophisticated cognitive capabilities are also likely to be more social. Logical arguments from resource defense theory, confirmed by a game theory model, suggest that the spatial and temporal predictability of food should drive both sociality and generalism/opportunism in the same direction (Overington et al. 2008). Burish et al. (2004) reported that the volume of the telencephalic portion of the brain is correlated with social complexity in birds; while Emery et al. (2007) show that the birds with the largest brain sizes are those that live in small groups of 5–30 individuals. More social birds likely have more opportunities for louse transmission, which may lead to a higher prevalence of lice in social species as shown by Rékási et al. (1997). This in turn might lower the risk of extinction for lice at low host population sizes (Paterson et al. 2010), leading to higher diversity over time. Additionally, several studies have shown that louse prevalence is higher in more social individuals of the same species (Hoi et al. 1998, Monello and Gompper 2010). In a study comparing prevalence and intensity of Amblycera versus Ischnocera on Galapagos Hawks (*Buteo galapagoensis*), both prevalence and intensity increased with larger group sizes for Amblycera, but not for Ischnocera (Whiteman and Parker 2004). This difference might explain the difference between Amblycera and Ischnocera in the correlation we found between innovation and louse diversity, in which only amblyceran diversity was significantly correlated with innovativeness. Based on these studies, it seems conceivable that in periods of host population bottlenecks, louse extinction rates are higher for Amblycera on more solitary birds.

Finally, birds that show more feeding innovations might also innovate in other domains that affect louse richness, for example grooming. However, this possibility would work against the relationship we have found here, unless these innovations are more efficient against Amblycera than they are against Ischnocera. Former studies have shown that more advanced host defenses increase amblyceran taxonomic diversity (Møller and Rózsa 2005, Møller et al. 2010). Intriguingly, innovative birds such as grackles and starlings have been seen "anting" with a variety of compounds, including marigold flowers (Dennis 1985), moth balls (Borgelt 1960, Clark et al. 1990) and lime (Clayton and Vernon 1993). Clayton and Vernon (1993) experimentally tested the efficiency of lime against ischnocerans and found that a component of lime oil, D-limonene, was lethal to the lice. More research is needed to see whether the innovative use of grooming compounds has an effect that might mitigate some of the parasite risk factors in birds.

To summarize, avian cognitive capabilities co-vary positively with the taxonomic diversity of amblyceran lice – but are not affected by the diversity of ischnoceran lice. Testing the potential causes and consequences of this effect will be a challenging task for future authors.

1.2.2. Case study (as published in Evolution 67(4): 959-968., 2013.):

Avian brood parasitism and ectoparasite richness – scale-dependent diversity interactions in a three-level host-parasite system

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Introduction

Understanding the emergence and maintenance of biological diversity is a major task of evolutionary biology. A relatively large proportion of animals live a parasitic way of life (Poulin and Morand 2004), however, zoologists scarcely address the causes and consequences of their diversity and the authors often conclude their studies with general and over simplified verdicts like "parasite diversity co-varies with host diversity" (see e.g. Hechinger and Lafferty 2005, Vas et al. 2012a). Below we aim to search for some more specific macroevolutionary patterns. How do lineages in historical associations with more than two levels (such as host-parasite-hyperparasite) affect each others' diversity? Do host life history traits affect their parasite richness at different macroevolutionary scales in a similar way? Do different parasite taxa exhibit similar responses to similar changes in host life history? To address these questions, we analyze diversity measures of parasitic lice (Phthiraptera) hosted by brood parasitic birds (Aves), as brood parasitic birds, their foster species and their ectoparasites create a complex co-evolving system built of three hierarchical levels.

Obligate interspecific brood parasites exploit the parental investment of another species so as to obtain nutrition and care for their offspring. This behavioral strategy apparently emerged in seven independent cases during the evolution of birds (Rothstein 1990, Payne 1997, 2005): once in the Black-headed Duck (*Heteronetta atricapilla*), three times in the family of cuckoos (Cuculidae), once in the family of honeyguides (Indicatoridae), and two times among passerines (Icteridae: *Molothrus* spp., and Viduidae).

Interspecific brood parasitism is an intensively studied phenomenon in ornithology; numerous studies address its evolution, ecology, and the emergent co-evolutionary arms-race between brood parasites and their foster species (see e.g. Ortega (1998), Rothstein and Robinson (1998), Davies (2000), and Payne (2005) for reviews). Despite this huge interest and research effort, only a few papers have dealt with the ectoparasites of brood parasitic birds (Clayton et al. 2003). The phenomenon that the chicks of brood parasites never come into physical contact with their own parents raises the questions how do their highly host specific parasites such as parasitic lice (Phthiraptera) maintain their populations on obligate brood parasitic host species, and how do hosts' brood parasitic life-style affect the evolution of their louse lineages. Lice are wingless obligate ectoparasitic insects that complete their entire life-cycle on the body of their hosts. Several authors showed that lice affect both life expectancy (Booth et al. 1993, Brown et al. 1995, Barbosa et al. 2002, Pap et al. 2005) and reproductive success (Clayton 1990, Kose and Møller 1999, Kose et al. 1999) of their hosts, making them excellent model organisms for studying the evolutionary ecology of contagious pathogens.

Vertical transmission (i.e. from parent to offspring) is apparently the most common transmission route of lice (Clayton and Tompkins 1994); however, brood parasitic birds, which lack physical contact between parents and their offsprings, still harbor several host specific louse species (Price et al. 2003). Lice specific to brood parasitic birds must adapt to infest new host individuals via horizontal transmission, either as fledglings or adults (Marshall 1981, de Brooke 2010). Sexual transmission is known to occur in some species of avian lice (Hillgarth 1996). Additionally, body-to-body contact between brood parasites and foster parents constitute a natural experiment of interspecific louse dispersal, potentially initiating host switches among different host species. Previous studies on lice of brood parasitic birds mainly focused on louse dispersal between brood parasitic chicks and their foster parents. Juvenile cuckoos (Lindholm et al. 1998), cowbirds (Hahn et al. 2000) and indigobirds (Balakrishnan and Sorenson 2007) tend to acquire lice specific to their foster species. Nevertheless, it seems that foster-borne infestations cannot establish viable populations on adult brood parasites (Clayton and Johnson 2001, Clayton et al. 2003). In a more focused study on viduid finches, Balakrishnan and Sorenson (2007) found that the successful colonization of brood parasitic finches was constrained by host-specific adaptations (but not dispersal abilities) of louse species specific to estrildid finch foster species.

It is reasonable to suspect that brood parasitic clades may harbor less diverse louse faunas than their non-parasitic sister clades. Take cuckoos as an example; 7 out of the 10 louse genera infesting Cuculid birds do not occur on brood parasitic cuckoos, although some of the louse genera infesting non-parasitic cuckoos are restricted only to small subclades of hosts (Price et al. 2003). Additionally, Balakrishnan and Sorenson (2007) found that *Myrsidea* lice (Amblycera) were entirely absent from brood parasitic indigobirds, although they are common on estrildid finches, which are both their typical foster species and closest non-parasitic sister clade. However, effects of hosts' brood parasitic life-style on the evolution of their louse lineages have never been tested. A phylogenetic analysis comparing brood parasitic avian clades to their non-parasitic sister clades is needed to test whether or not these cases represent a general trend.

In this paper we present two separate analyses (A1, A2) to investigate the effect of hosts' brood parasitic life-style on louse richness at two different macroevolutionary scales. First, we test the hypothesis that louse richness is reduced on brood parasitic host clades compared to non-parasitic sister clades (see sister clades in Fig. 1), considering all the seven independent origins of avian brood parasitism (A1). We assume that brood parasitic life-style affects louse richness negatively due to the lack of vertical transmission routes.

Then, narrowing our scope to the oldest (Hackett et al. 2008) taxa of brood parasites, the cuckoos, we explore which factors shape the richness of their lice communities (A2). Host traits such as body mass, geographic range and habitat diversity may affect cuckoos' louse richness, so too may traits related to brood parasitic life-style such as the number of foster species a brood parasitic cuckoo utilizes. It is reasonable to suspect that foster species-related traits may affect the louse richness of brood parasites as their chicks are exposed to louse transmission from the foster parents. The variance in the number of foster species among cuckoos is remarkable (Payne 2005); hence certain cuckoo species might interact with more diverse foster-borne ectoparasite fauna than others during their evolution.

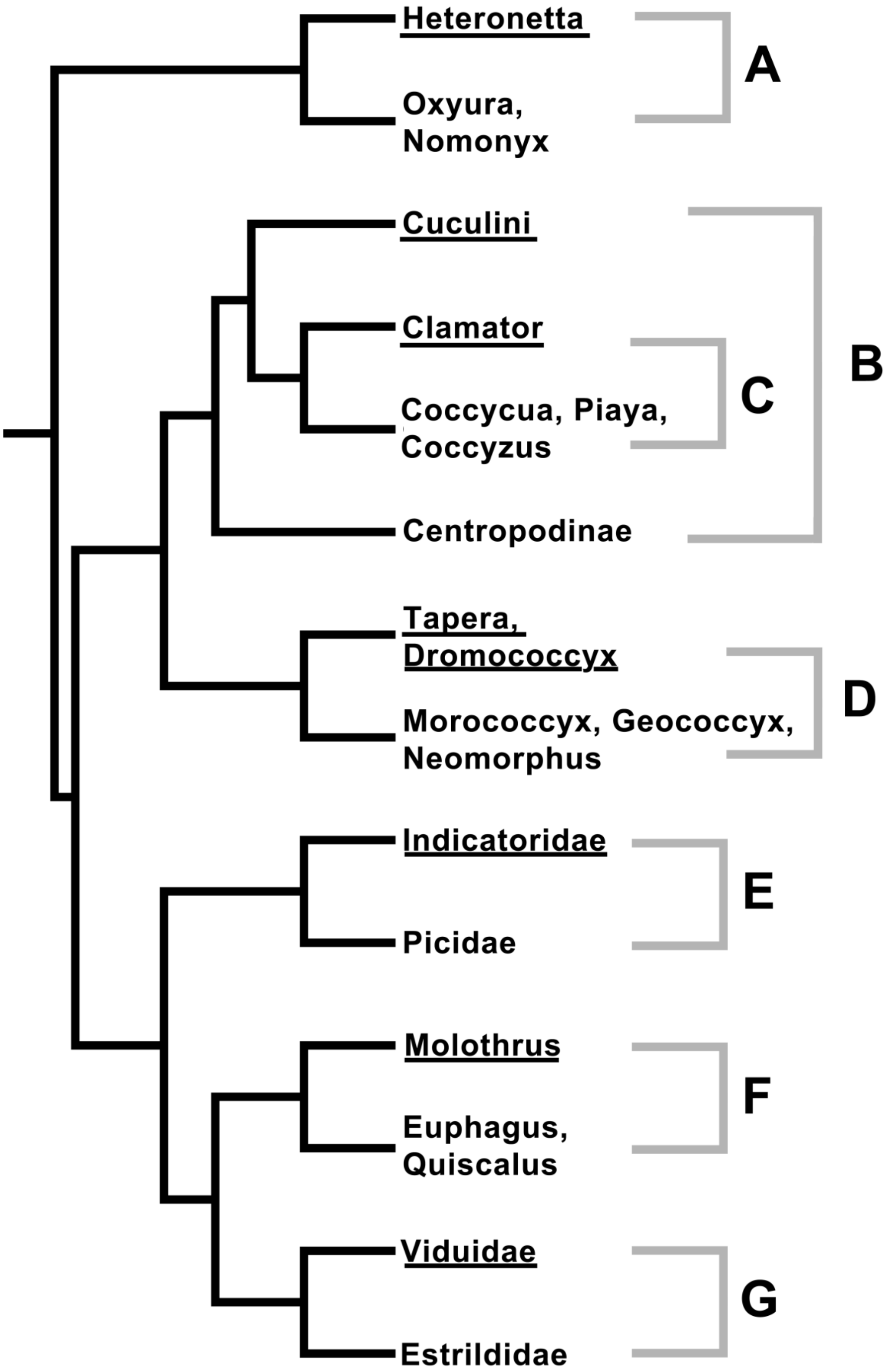

Fig. 1. Phylogeny of the seven avian brood parasitic clades (underlined) and their non-parasitic sister clades (see text for the sources). Grey lines connect the brood parasitic and non-parasitic sister clade pairs (A to G) compared in subsequent analyses (note that the phylogeny is arbitrarily ultrametricized).

Methods

Since Felsenstein (1985) it had been widely accepted that comparative studies have to take evolutionary history into account, as traits of related taxa are statistically non-independent. Additionally, comparative studies focused on parasite diversity among host taxa can also be confounded by uneven sampling effort of parasites (Walther et al. 1995, Krasnov et al. 2005, Poulin 2007); hence researchers need to control both for phylogenetic effects and uneven sampling to recognize relevant macroevolutionary patterns of parasite richness and distribution.

Diversity measures and host-parasite associations

We applied three different measures to describe the diversity of brood parasites, their foster species and their lice, namely genera richness (GR), species richness (SR), and the taxonomic distinctness index (TDI) developed by Warwick and Clarke (1995). These measures are clearly not independent of each other; however, they capture different features of diversity. Patterns of GR and of SR may reflect different scales of evolution. TDI calculates the mean number of steps up the Linnaean taxonomic hierarchy to reach the common ancestor of two given parasite species, computed across all species pairs within a group. In this sense, TDI focuses on the taxonomic structure (i.e. closely related or distinct parasite lineages) of a group rather than the pure number of its associates; hence this index is less dependent on research effort (Clarke and Warwick 1998, Poulin and Mouillot 2003). Furthermore, taxonomists often use different species concepts to describe louse faunas (Mey 2003) making SR a less reliable measure than GR. The biological interpretation of louse GR is quite straightforward as louse genera exhibit distinct body size and body shape according to the specific microhabitats they occupy on hosts (Johnson and Clayton 2003). Therefore, different louse genera can be roughly interpreted as different ecological guilds utilizing different environmental resources (such as topographic refugia to avoid host preening).

We obtained GR and SR data of lice and birds from comprehensive checklists (Dickinson 2003, Price et al. 2003). TDI was calculated with TaxoBiodiv2 software (Poulin and Mouillot 2005). Given that parasitic lice (Phthiraptera) is not a monophyletic group (Jonson et al. 2004, Murrell and Barker 2005, Smith et al. 2011), we collected data separately for Amblyceran and Ischnoceran lice to explore potential differences in their adaptive responses to brood parasitism.

We emphasize here that comparing avian sister clades (rather than sister taxa) is a method that inherently ensures the identical age of compared units (Fig. 1). Therefore, we need not control for the potential age differences between the compared units. Differences in the louse richness of natural sister clades arose along the independent evolution of the sister lineages. In this sense we counted every louse genera and species once – regardless how many host species they infest in a given clade. Characterizing the louse richness of natural sister clades as a whole is unbiased by arbitrary taxonomic decisions such as the uncertain genus-level classification of cuckoos (Dickinson 2003, Payne 2005). In this case confounding effects may arise from factors such as the different diversity of the compared host clades – the effect known as Eichler's rule (Eichler 1942, Vas et al. 2012a), or the different body masses. Hence our model included separate variables describing host clade diversity (SR, GR, and TDI), and average body mass to control for their potential effect.

Despite intensive research into avian brood parasitism, an exhaustive list of brood parasitic birds' foster species is still incomplete (Payne 2005). Here we rely on Lowther's (2011) list to quantify the species richness and TDI of foster species. We deleted all records marked as 'most probably erroneous', 'questionable' or 'misidentified', and all presumed brood parasites without any known foster species. The classification and nomenclature were revised according to Dickinson (2003). Data on host-parasite associations of birds and lice were obtained from Price et al. (2003).

Body mass, distribution and habitat diversity of hosts

We obtained avian body mass data from the literature (Perrins 2003, Payne 2005, Boerner and Krüger 2008, Dunning 2008). Average body mass data for each host species or clade was log-transformed in subsequent analyses. We used the distribution maps of Payne (2005) to estimate the extent of the breeding areas. Initially we georeferenced the maps using QGIS (Quantum GIS Development Team 2011), then calculated the area in square kilometers and log-transformed the value. We also estimated a rough but standard measure of habitat diversity for each cuckoo species from BirdLife International (2011). BirdLife Data Zone lists standard habitat categories (e.g. temperate grassland, dry savanna) used by each species, making the sum of these habitat categories a reliably comparable measure of habitat diversity.

Control for research effort

The research effort focused on each brood parasite species is likely to affect both the number of known foster and the number of known parasite species (Walther et al. 1995, Payne 2005). Nevertheless, GR is a less sampling-biased measure than SR (i.e. a larger proportion of louse species awaits description than louse genera). Similarly, TDI is less sensitive to sampling bias (Walther et al. 1995, Clarke and Warwick 1998), as the discovery of new parasite or foster species – as far as they are congeneric to the formerly known species – will not affect the value.

To control for potential bias caused by uneven sampling, we calculated louse sampling effort measure for brood parasitic clades and their non-parasitic sister clades (A1). We estimated sampling effort as the number of host species known to be associated with lice in a host clade divided by the total number of species in that clade. Then we applied linear regression with each louse richness measure as response and sampling effort rate as an explanatory variable. We obtained the residuals from these linear regression models and used them in the subsequent analyses. This is a common method in comparative studies to control for confounding variables (Garland et al. 1992, Poulin 1992), even though it may sometimes cause bias (Freckleton 2009), particularly when the explanatory variables are strongly correlated (Freckleton 2002). However, as we compared the louse richness of brood parasitic clades and their non-parasitic sister clades, this method was the only possible way to consider the effect of uneven sampling.

When investigating traits that potentially co-vary with cuckoo louse richness (A2), we used a separate variable describing research effort and analyzed it together with other explanatory variables in a multiple regression model, as suggested by Freckleton (2009). We estimated research effort focused on each cuckoo species with the (log-transformed) raw number of the results that Google Scholar returned by searching for their scientific name (e.g. "clamator jacobinus", accessed August 18, 2011. The search terms were not refined as we needed a general measure of research effort on cuckoos covering both the research effort of their ectoparasites and that of their foster species. Including this variable in a multivariate model equally controls for the relationship between study intensity and louse richness and also for the relationship between study intensity and foster species richness in a statistically unbiased way (Poulin 1992, Freckleton 2002, 2009).

Phylogenetic relationships

We constructed a clade-level phylogeny of the seven independent brood parasitic lineages and their non-parasitic sister lineages (regarding A1) following the rule that branches connecting brood parasitic clades to their sister clades should not overlap along the phylogeny. This criterion ensures the phylogenetic independence of comparisons (Purvis and Rambaut 1995, Maddison 2000, Felsenstein 2004). Tree topology and the recognition of appropriate sister clades (Fig. 1, pairs A to G) were based on published phylogenies (Johnson and Lanyon 1999, McCracken et al. 1999, Barker et al. 2004, Sorenson and Payne 2005, Hackett et al. 2008). The species-level phylogeny of cuckoos (attending to A2) was based on Sorenson and Payne (2005). Phylogenies were constructed using Mesquite (Maddison and Maddison 2011). Each tree was subsequently analyzed by using two different arbitrary branch length transformations. Branch length values were either derived from the tree topology as described by Nee (Purvis 1995), or were set to 1. Our results were qualitatively identical by using any of these transformations; however, only the latter setting provided perfect fit according to model diagnostic methods (Garland et al. 1992). Hence, we report only the analyses based on the tree with branch lengths set to 1.

Statistical analysis

We used the method of independent contrasts to control for phylogenetic non-independence (Felsenstein 1985). Analyses were carried out by the 'caper' package (Orme et al. 2011) in R 2.14.0 (R Development Core Team 2011). We used *brunch* (A1) and multivariate *crunch* (A2) functions implemented in this package, originally presented by CAIC (Purvis and Rambaut 1995). Character evolution was simulated under a Brownian motion model (Felsenstein 1985). Although this model may not represent perfectly the process of evolutionary changes, several authors showed that even with errors in branch lengths and deviations from Brownian motion the method of independent contrasts is still robust and reliable (Díaz-Uriarte and Garland 1996, 1998). Louse GR and SR were log-transformed (value + 1) in the *crunch* model to achieve a better fit. The distributional assumptions of all statistical tests were checked graphically (e.g. quantile-comparsion plot), and all tests were two-tailed. Multicollinearity in multivariate models was checked by calculating the variance inflation factor (VIF) using the R package 'faraway' (Reiczigel et al. 2007, Faraway 2011). Our datasets (regarding A1 and A2) are available in Dryad Digital Repository.

Results

Our hypothesis that louse richness is reduced on brood parasites as compared to their non-parasitic sister clades (A1) was supported (Table 1, Fig. 2). Using the *brunch* function of the independent contrast method we found that Amblyceran GR and TDI of brood parasitic clades were significantly lower than those of their non-parasitic sister clades. This effect was weaker in the case of Ischnocerans, where TDI was significantly lower on brood parasitic clades than on non-parasitic sister clades, while GR was only marginally significantly (P = 0.056) reduced on brood parasitic clades. Neither Amblyceran nor Ischnoceran SR differed significantly between avian sister clades. The relationship we found between the emergence of brood parasitic life-style and the reduction of louse richness was not significantly influenced by confounding factors such as host clade diversity (so called Eichler's rule) or body mass (Table 1).

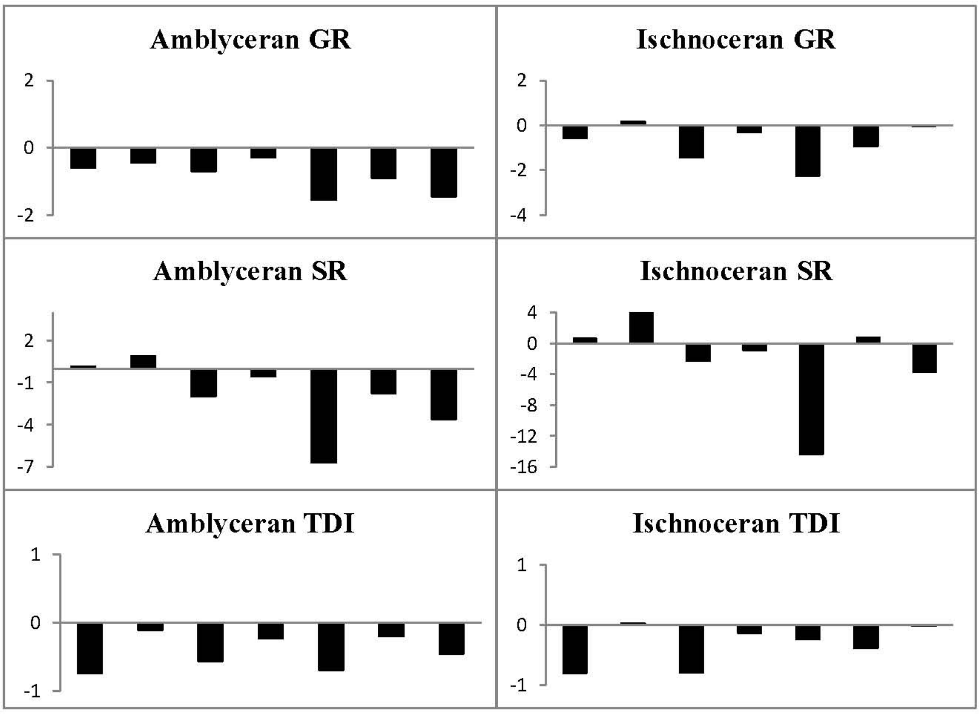

Fig. 2. Standardized contrasts of (residual) louse richness measures between brood parasitic and non-parasitic sister clades. Contrasts on the horizontal axis follow the order (A to G) of Fig. 1 (direction of subtraction by contrast calculation: brood parasitic – non-parasitic, hence negative contrast values indicates lower richness on brood parasitic clades than on non-parasitic sister clades; GR = generic richness, SR = species richness, TDI = taxonomic distinctness index).

Table 1. Results of *brunch* function (direction of subtraction by contrast calculating: brood parasitic – non-parasitic; n = 7; df = 6)

Contrasts between sister clades in:	slope	R^2	*t*	*P*
(residual) Amblyceran GR	-0.84	0.73	-4.50	0.004
(residual) Amblyceran SR	-1.94	0.30	-1.99	0.093
(residual) Amblyceran TDI	-0.42	0.73	-4.52	0.004
(residual) Ischnoceran GR	-0.75	0.40	-2.36	0.056
(residual) Ischnoceran SR	-2.26	< 0.01	-1.02	0.348
(residual) Ischnoceran TDI	-0.33	0.44	-2.56	0.043
(log) body mass	-0.23	0.34	-2.15	0.076
host clade GR	-4.63	0.11	-1.36	0.223
host clade SR	-31.29	0.15	-1.50	0.183
host clade TDI	-0.15	< 0.01	-1.22	0.267

We analyzed which life history traits of brood parasitic hosts affect louse richness at species level (A2) by examining cuckoos, the most intensively studied group of avian brood parasites. Using the *crunch* function of the independent contrast method we found that different factors co-vary with Amblyceran and Ischnoceran richness of brood parasitic cuckoo species (Table 2). The only significant predictor of all Amblyceran richness measures was the research effort focused on hosts. Contrarily, however, both cuckoo body mass and the number of foster species (but not their TDI) co-varied significantly with each Ischnoceran richness measure (Table 2). There was no multicollinearity between the explanatory variables (VIF value = 1.021). Neither the size of the breeding area nor the habitat diversity correlated significantly with louse richness measures (Table 2).

Table 2. Results of *crunch* function: louse richness measures as response variables, and their significant explanatory variables (in italics); louse GR and SR ('value+1') were log-transformed. Non-significant explanatory variables (TDI of foster species, cuckoo breeding area size, cuckoo habitat diversity) are not listed.

	slope	*P*	*F*	R^2
Amblyceran GR (n = 45; df = 41)				
(log) research effort	0.12	0.002	10.58	0.19
Amblyceran SR (n = 45; df = 41)				
(log) research effort	0.13	< 0.001	13.87	0.23
Amblyceran TDI (n = 45; df = 41)				
(log) research effort	0.38	0.002	10.58	0.19
Ischnoceran GR (n = 45; df = 40)				
(log) no. of foster species	0.11	0.017	9.04	0.28
(log) body mass	0.34	0.004		
Ischnoceran SR (n = 45; df = 40)				
(log) no. of foster species	0.12	0.015	10.58	0.31
(log) body mass	0.43	0.001		
Ischnoceran TDI (n = 45; df = 40)				
(log) no. of foster species	0.42	0.013	8.98	0.26
(log) body mass	1.25	0.006		

Discussion

Effects of brood parasitic life-style

We found solid evidence that the brood parasitic life-style reduced GR and TDI of lice as compared to their non-parasitic sister clades (Table 1, Fig. 2). Apparently, only a few louse lineages were able to adapt to the limited transmission possibilities while certain louse taxa became extinct on brood parasites. Louse taxa specific to obligate brood parasites have to rely exclusively on horizontal transmission routes to infest conspecific birds during the short and scarce events of direct physical contact among adult birds such as copulation, aggression or during communal roosting (Marshall 1981, de Brooke and Nakamura 1998).

There is some evidence that both Amblyceran and Ischnoceran lice can transmit during the copulation of birds (Hillgarth 1996). However, our results indicate that several louse lineages went extinct when the vertical transmission route is lacking. It is worth noting that brood parasitic life-style of the hosts may also act as a barrier of successful louse host-switching from other (non-parasitic) bird species *[due to the lack of the possibility of vertical transmission for lice]*.

Amblyceran richness (GR and TDI) appears to be reduced more than Ischnoceran richness (Table 1). This phenomenon may be explained by the difference in Amblyceran and Ischnoceran transmission strategies. Amblycerans may tend to transmit from parents to the chicks earlier and possibly at a greater extent than Iscnocerans (Darolová et al. 2001, de Brooke 2010). Amblycerans partially feed on dead or living parts of the skin, blood, and other excretions (Johnson and Clayton 2003, Mey et al. 2007), while Ischnocerans feed largely on feathers (Johnson and Clayton 2003). For this reason, Amblycerans may be less dependent on chick plumage development than Ischnocerans; hence they are able to infest younger chicks. As nestlings possess undeveloped and hence more-or-less ineffective defenses against parasites, selection may favor early vertical transmission in Amblycerans. Thus it seems conceivable that vertical transmission has a greater importance for Amblycerans, and consequently, they may be less capable of relying on the horizontal transmission routes exclusively. Ischnoceran lice – unlike Amblycerans – also often rely on phoretic transmission using Hippoboscid flies (Harbison et al. 2009) as means of vertical transmission; a behavior known to occur in cuckoo-specific Ischnocerans as well (Clay and Meinertzhagen 1943, Keirans 1975).

Previous studies on factors shaping louse richness found that several host traits affected Amblycerans, but not Ischnocerans (see e.g. Whiteman and Parker (2004), Møller and Rózsa (2005), Whiteman et al. (2006), Møller et al. (2010) and Vas et al. (2011) for examples). To our best knowledge, only 2 former studies found any significant correlates of Ischnoceran richness (Hughes and Page 2007, Vas et al. 2012a). Thus our results indicating that brood parasitic life-style affects both Amblyceran and Ischnoceran richness (at least TDI of the latter) contribute significantly to the poorly understood Ischnoceran macroecology.

Louse richness of brood parasitic cuckoos

Despite GR and TDI were reduced both in Amblycerans and to a lesser extent also in Ischnocerans, SR of lice showed no significant difference between brood parasitic clades and their non-parasitic sister clades in either case (Table 1). This correlational evidence suggests relatively rapid speciation events in the louse lineages adapted to brood parasitic hosts. By narrowing our scope to a species-level phylogeny of brood parasitic cuckoos we identified certain cuckoo traits that significantly co-varied with their louse richness measures. First, research effort focused on cuckoos predicted Amblyceran richness; this is a well-known phenomenon in parasite ecology (Clayton and Walther 2001, Poulin and Morand 2004, Poulin 2007, Krasnov 2008). More importantly, host body mass and the number of foster species co-varied positively with the species richness of Ischnoceran lice on brood parasitic cuckoos (Table 2). Contrarily, cuckoo habitat diversity and geographic range had no effect on the richness measures of their lice (Table 2).

The fact that host body size affects Ischnoceran, but not Amblyceran richness, may possibly be explained by the differences in habitat use between the two louse suborders. Since Ischnocerans live on the surface of feathers and avoid preening by hiding in topographic refugia of the plumage, they depend more on feather size and surface topology of feathers than Amblycerans do. The narrow and elongated body of Ischnoceran "wing lice" is an evolutionary consequence of their strict key-lock mechanism with feather barb size (Johnson and Clayton 2003, Johnson et al. 2005), and this mechanism may prevent successful host switching (Clayton et al. 2003). Johnson et al. (2005) found that both body and feather size of pigeon species correlated positively with the size of their Ischnoceran "wing lice", but not with the size of their Ischnoceran "body lice". They suggested that "body lice" may depend less on host body size, and depend more on microhabitat structures not predicted by overall host body size. The majority of Amblyceran lice also possesses an oval-shaped body and lives partially on the skin and on downy feathers (Johnson and Clayton 2003). Therefore they may not exhibit a high level “key-lock” matching with host feather size. Our results concerning the influence of host body mass on parasite taxonomic richness are consistent with previous studies yielding contradictory results (Poulin and Morand 2004), suggesting that host body mass may not necessarily act as a general predictor of parasite diversity (Krasnov et al. 2004, 2008).

We found a significant positive co-variation between richness measures of Ischnoceran lice infesting cuckoos and the number (but not the TDI) of foster species these cuckoos utilize (Table 2). At least two alternative hypotheses might explain this pattern. First, generalist cuckoo species that exploit more foster species may be more exposed to colonization by foster-borne infestations creating a host switch. Recent evidence suggests that lice of foster species do occur on immature brood parasites (Lindholm et al. 1998, Hahn et al. 2000, Balakrishnan and Sorenson 2007). Their failure to establish viable populations on adult brood parasites does not exclude the possibility that there could have been successful host switches in the evolutionary past. However, the taxonomic composition of cuckoo lice communities falsifies this explanation. Lice infesting parasitic cuckoos form distinct lineages (*Cuculiphilus, Cuculicola, Cuculoecus*) that infest both parasitic and non-parasitic cuckoos, but do not occur on any other birds and, particularly, not on the typical foster species of brood parasitic cuckoos (Price et al. 2003). For this reason we exclude this hypothesis.

Alternatively, we propose that this co-variation emerges due to the higher complexity of subpopulation structure of cuckoos with more foster species. The Common Cuckoo (*Cuculus canorus*) and other generalist cuckoo species tend to form host-specific races (called gentes) each adapted to different foster species (Payne 2005, Starling et al. 2006). Contrary to former beliefs (Marchetti et al. 1998), recent evidence suggests that not only females, but both sexes contribute to the evolution and maintenance of races (Fuisz and de Kort 2007, Fossøy et al. 2011). Hence the gentes are more-or-less separated in space and time (Møller et al. 2011) leading to a certain degree of genetic isolation. These gentes often exhibit quick evolutionary changes to abandon former foster species and to switch to new, naive foster species (Payne 2005). Consequently, both speciation and extinction rates are higher in parasitic than in non-parasitic cuckoos (Krüger et al. 2009).

Foster-opportunistic parasitic cuckoos are likely to have a more complex metapopulation structure built of a dynamically changing network of more or less isolated subpopulations (races, gentes) (Møller et al. 2011). This metapopulation structure may affect the richness of their lice. On one hand, the evolution of lice is much faster than that of their hosts (Page et al. 1998), thus they may speciate rapidly on a network of cuckoo gentes. This process might result in higher louse richness on foster-generalist cuckoos as compared to foster species-specialist ones having a simpler metapopulation structure. On the other hand, complex metapopulation structures may also reduce the risk of louse extinction. Any parasite lineage going extinct from one particular host race – e.g. due to a bottleneck in host population size (Kuris et al. 1980) – has a higher chance to get replaced by conspecific parasites if the host race is embedded into a complex network of populations. These conditions may promote the speciation of lice as well as reduce their extinction risk. This phenomenon may also be responsible for the higher Ischnoceran SR of the Cuculini clade than that of its closest non-parasitic sister clade (Fig. 2, pair B).

Briefly, we conclude that brood parasitic birds, their foster species and their lice form a complex system with three ecological levels interacting with each other in a complex way.

We found that brood parasitic life-style reduced the taxonomic richness of ectoparasitic lice in general, especially Amblyceran richness as compared to that of non-parasitic sister clades. This phenomenon may constitute an overlooked advantage of brood parasitic life-style: it reduces their parasite richness as the vertical transmission of ectoparasites is impossible. Narrowing our scope to brood parasitic cuckoo lice we found that Ischnoceran richness co-varied positively with the richness of utilized foster species, probably due to the complex and dynamic subpopulation structure of the foster-generalist cuckoos. Hence, we found evidence that the same macroecological factor (i.e. hosts' brood parasitic life-style) has opposing effects on louse richness at two slightly differing macroevolutionary scales, i.e. species richness versus genera richness. Additionally, our results suggest that diversity interaction across more than 2 hierarchical levels may contribute considerably to the observed patterns, even when the association between these levels is not obvious, as the diversity interaction we found between the richness of brood parasitic cuckoo lice and that of foster species. Thus it appears that other multi-level systems may offer a great possibility for future studies to understand how 3 or more associated lineages affect each others' diversity during their evolution and contribute to global biodiversity as a whole.

1.2.3. Case study (as published in Parasitology Research 111: 393-401., 2012.):

Evolutionary co-variation of host and parasite diversity – the first test of Eichler's rule using parasitic lice (Insecta: Phthiraptera)

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Introduction

Parasitism is a successful way of life, as – depending on the definition of parasitism – 6-50% of known animal species are parasites (Poulin and Morand 2004). They influence almost every aspect of the life history of non-parasitic species (Thomas et al. 2005). Hence, arriving at an understanding of the factors shaping parasite biodiversity on a global scale is a major task for macroecological and macroevolutionary research. Given that parasites tend to be highly specific to their host resources, it seems reasonable to expect a positive co-variation between the taxonomic richness of hosts and that of their parasites. Eichler (1942) was the first to point out this relationship and it was dubbed as 'Eichler's rule' (Stammer 1957) later on. Admittedly, this co-variation might seem obvious. However, even theoretically expected relationships need to be verified by using a wide range of empirical data and modern methodologies for at least two reasons. Firstly, we expect such tests to yield new information about the strength of the relationship. Secondly, we also hope to obtain information about potential differences among different taxa in the strength of this relationship. Take 'Fahrenholz's rule' (Fahrenholz 1913) as an example. It seemed to be a triviality to presume a topological similarity of host and parasite phylogenetic trees. However, as rigorous tests have later provided contradictory results among different taxa, testing this 'trivial rule' has established a new discipline within evolutionary biology (Page 2003).

Here we set out to test this presumed relationship by using data on the order of lice (Insecta: Phthiraptera). Lice traditionally played an important role in the study of host-parasite evolution (Johnson and Clayton 2003, Page 2003) for two major reasons. Firstly, extensive sampling effort through several centuries resulted in a considerable amount of data concerning their taxonomical richness, distribution and host specificity (Price et al. 2003). Secondly, lice are very intimately related to the host individual spending their entire life-cycle in the host pelage or plumage. Several authors showed that lice affect both the life expectancy (Barbosa et al. 2002, Booth et al. 1993, Brown et al. 1995, Pap et al. 2005) and reproductive success (Clayton 1990, Kose and Møller 1999, Kose et al. 1999) of their hosts. Additionally, lice also act as vectors of virulent microbial infections (see e.g. Clayton et al.

2008, Raoult and Roux 1999). Lice are classified into four suborders: Amblycera, Ischnocera, Rhynchophthirina and Anoplura (Price et al. 2003). However, recent studies (Johnson et al. 2004, Murrell and Barker 2005, Smith et al. 2011) suggested that Phthiraptera do not form a monophyletic group. The parasitic way of life appeared two times independently in parasitic lice: once in the ancestors of Amblycera and once in the ancestors of the other 3 suborders. Diversity and hosts of louse taxa is summarized in Table 1 following Johnson and Clayton (2003). Lice were generally considered quite host specific (Mey 2003), however, it seems that their host specificity varies on a large scale (see e.g. Hellenthal and Price 1991, Price 1975, Price et al. 2003, Zuo et al. 2011).

Table 1 An overview of louse suborders and families (Johnson and Clayton 2003), Anopluran families are not listed separately

	Families	Genera	Species	Hosts
Suborder Amblycera	6	95	1334	birds and mammals
Menoponidae		68	1039	birds
Boopiidae		8	55	mammals [a]
Laemobothriidae		1	20	birds
Ricinidae		3	109	birds
Gyropidae		9	93	mammals
Trimenoponidae		6	18	mammals
Suborder Ischnocera	2	157	3060	birds and mammals
Philopteridae		138	2698	birds [a]
Trichodectidae		19	362	mammals
Suborder Rhynchophthirina	1	1	3	mammals
Suborder Anoplura	16	49	532	mammals

[a] : one louse species also occurs on the other class of hosts

It is reasonable to separate louse suborders (and even families of avian lice) in comparative analyses because their life histories and the factors shaping their distribution and evolution are quite different, as already shown by several former studies (see e.g. Hughes and Page 2007, Møller and Rózsa 2005, Møller et al. 2010, Price et al. 2003, Vas et al. 2011, Whiteman et al. 2006).

Since Felsenstein (1985), it had been widely accepted that comparative studies have to take evolutionary history into account, as traits of related taxa are statistically non-independent.

Moreover, comparative studies focused on parasite richness among host taxa can also be confounded by uneven sampling effort of parasites (Krasnov et al. 2005, Poulin 2007, Walther et al. 1995), hence researchers need to control both for phylogenetic effects and uneven sampling effort while studying macroevolutionary patterns of parasite richness and distribution. Additionally, the uncertainty of louse morphospecies concept and an overestimation of parasite species richness of widely distributed hosts also act as a potential bias in the quantification of louse taxonomic richness (see below).

Previous authors have already explored some factors correlated with the taxonomic richness of lice. Past bottleneck effects of host populations (MacLeod et al. 2010, Paterson et al. 1999, Rózsa 1993) and host aquatic lifestyle (diving under the water surface for food) (Felső and Rózsa 2006, 2007) reduce louse richness. Preening and other behavioral defenses against ectoparasites were also suggested to reduce louse richness, however, the evidence is limited (Clayton and Walther 2001, Clayton et al. 2010). Host innovative capabilities (Vas et al. 2011) and defenses such as stronger immune responses (Møller and Rózsa 2005) or relatively larger uropygial glands (Møller et al. 2010) co-vary positively with Amblyceran taxonomic richness but not with Ischnocerans. Host population size and geographic range of seabirds also correlate positively with the richness of their lice (Hughes and Page 2007).

Some former studies on parasite taxonomic richness have already treated host species richness as a potential confounding factor but found no association between them, possibly due to their relatively narrow host taxonomical range used (Felső and Rózsa 2006, 2007, Hughes and Page 2007). Nunn et al. (2004) found a positive correlation between primate diversification and richness of their viral and protozoan parasites; however, they used a different theoretical and statistical approach to analyze effects of host diversification rates (Agapow and Isaac 2002) rather than recent host diversity. Thus their results do not specifically refer to Eichler's rule (1942). No former studies directly examined the explanatory power of host taxonomic richness on parasite taxonomic richness by using modern methodologies.

The influence of host body mass on parasite taxonomic richness was described by several authors studying various host and parasite taxa. It is often presumed that larger-bodied host taxa may provide more diverse resources, say, more different types of spatial refuges to avoid host defenses. Alternatively, one could also predict a positive co-variation between host body size and parasite richness using the theory of island biogeography (Kuris et al. 1980). However, research on the interaction between host body size and parasite richness yielded contradictory results (see e.g. Poulin and Morand (2004), Poulin (2007) for reviews), suggesting that host body mass may not act as a general predictor of parasite diversity (Bordes et al. 2011, Hughes and Page 2007, Krasnov et al. 2004, Krasnov et al. 2008).

Here we aim to test Eichler's rule (Eichler 1942) on avian and mammalian lice. Our study incorporates all families of birds and mammals recognized by Dickinson (2003) and Bininda-Emonds et al. (2007), respectively. We also examine the relationship between host body mass and louse taxonomic richness on this broad dataframe.

Materials and methods

Taxonomic richness of hosts and parasites

We examined variation in host traits at the family level. Avian and mammalian families form more or less well recognized monophyletic clades according to recent molecular systematic studies, while higher level taxa do not prove to be monophyletic in many case (Baker et al. 2004, Bininda-Emonds et al. 2007, Hackett et al. 2008). Phylogenetic comparisons require well resolved trees, which are much more available at family level than for lower level taxa. Additionally, this level also helps accounting for missing information about louse presence at the species level, which is more complete at the family level.

We described species richness of all 175 avian families recognized by the Howard and Moore checklist (Dickinson 2003) and for all 147 mammalian family-level clades recognized by Bininda-Emonds et al. (2007). Host taxa involved in our analyses are summarized in Table 2 following Dickinson (2003), Perrins (2003) and Wilson and Reader (2005). As species richness of host families varied considerably (see Results) we log-transformed species richness data in all subsequent analyses. Although our results were nearly identical when we used raw species richness (not reported), we preferred to use the log-transformed data because they satisfied all the distributional assumptions of the statistical methods we adopted.

Table 2 A summary of host taxa involved in the analyses (Dickinson 2003, Perrins 2003, Wilson and Reader 2005)

	Orders	Families	Genera	Species
Aves	28	175	2051	9320
Mammalia	29	147	1131	4616

A widely distributed bird species often hosts congeneric louse species each restricted to different and non-overlapping areas of the host distribution. Thus, parasite species richness of widely distributed bird species would overestimate the true parasite richness that each local bird population has to face (Clay 1964). Furthermore, taxonomists often use different species concepts to describe louse faunae (Mey 2003) making species richness an unreliable measure. Some taxonomists automatically described congeneric lice from different hosts as distinct species while other authors lump many species into a single one from a wide range of hosts (see Price (1975) as an example). Therefore, we used generic richness (i.e. the number of louse genera per host families) as a proxy of louse diversity.

Host-parasite associations and parasite generic richness values were obtained from the world checklist of chewing lice (Price et al. 2003) and sucking lice (Durden and Musser 1994). We collected data separately for louse suborders and, in the case of birds, also separately for each avian louse families. Apparently, these louse families are not only phylogenetically distinct but also exhibit marked ecological differences (Johnson and Clayton 2003). In case of mammals, it is not feasible to analyze families separately either because a suborder is represented by a single family (Ischnocera: Trichodectidae) or the families are rather taxon-poor (Amblyceran families) or because the families are ecologically homogeneous (Anopluran families). Therefore, we did not divide mammal lice into families in our analyses. We excluded Rhynchophthirina from the suborder-level analysis of mammalian lice and Boopiidae from the family-level analysis of avian lice, because they do not provide enough variability to justify a comparative analysis (Table 1).

Control for louse research effort

We controlled for uneven louse sampling effort in three different ways. Firstly, we used generic richness, which is less biased by sampling than species richness. Arguably, a larger proportion of louse species awaits description than louse genera (see e.g. Sychra et al. 2010).

Secondly, we calculated a study effort rate as the number of host species known to be associated with lice in a host family divided by the total number of species in that host family. We performed linear regressions using louse generic richness as a response variable and study effort rate as an explanatory variable. We obtained the residuals from these linear regression models and used them in the subsequent analyses. This is a widespread method in comparative studies to control for confounding variables (Garland et al. 1992), even though it can sometimes cause bias (Freckleton 2009), particularly when the explanatory variables are correlated (Freckleton 2002), as in the case of study research effort rate and host species richness. By using this residual analysis method, we may overestimate the effect of sampling effort and underestimate the effect of host species richness on louse generic richness (Freckleton 2002).

Finally, in the avian dataset we excluded all families for which no louse species had been recorded (e.g. Balaenicipitidae, Todidae) and in the mammalian dataset all orders without lice (e.g. Cetacea, Chiroptera). Naturally, this reduced sample sizes.

As the results in the subsequent analyses were identical when any of these three ways to control for uneven sampling effort were used (see only one exception in Results), we report only the analysis based on the raw generic richness.

Average body mass of host families

We quantified the average body mass of each family in two different ways. Firstly, we took body mass data available for 129 avian families from Perrins (2003) and for all mammalian families from Nowak (1999) and Macdonald (2001). *[These sources present body mass data at family level by giving only the minimum and maximum values and/or averages for each family.]* Values were obtained simply by averaging the minimum and maximum values in each family. However, calculating family body mass by averaging the minimum and maximum values may lead to bias, given that the distribution of body masses among species within a family is not even but skewed. Therefore, we also assessed family-level averages by randomly sampling five species from each family using the 'sample' function in R 2.11.1 (R Development Core Team 2010) and averaged their body masses obtained from Dunning (2008) for birds and Silva and Downing (1995) for mammals. *[These sources present body mass data at species level.]* Families below five species were represented by all available data. Averages were log-transformed in all subsequent analyses. As the results in the subsequent analyses were qualitatively identical when any of these two measures were applied (see only one exception in Results), we report only the analysis based on the latter body size estimate.

Phylogenetic trees

To take the evolutionary history into account (Felsenstein 1985, 2004), we constructed a phylogenetic tree of avian families based on Barker et al. (2004) and Hackett et al. (2008). The non-passerine branching pattern from Hackett et al. (2008) was combined with passerine topology from Barker et al. (2004). Naturally, we lost branch length data this way; however, arbitrary branch lengths were calculated using Nee's method (Purvis 1995), as this method provided the best fit according to the most widespread and reliable diagnostic plots recommended by several methodological studies (Díaz-Uriarte and Garland 1996, 1998, Garland et al. 1992).

The phylogenetic relationships of mammalian families were based on a family-level tree published by Bininda-Emonds et al. (2007). Branch length data (proportional to time) were also obtained from the same source. If the family-level clades were different from those accepted by Wilson and Reeder (2005), their taxonomic content was determined using the supplemental information of Bininda-Emonds et al. (2008: Suppl. Fig. 1) (e.g. Geomyidae 1= *Thomomys*, Geomyidae 2= *Geomys*, Geomyidae 3= *Pappogeomys*, Geomyidae 4= *Orthogeomys* and *Zygogeomys*) and louse generic richness and body mass data were corrected accordingly.

As the phylogenetic trees contained some polytomies reflecting the uncertainty of bifurcating patterns, we used the method of bounded degrees of freedom, as recommended by Purvis and Garland (1993) and tested by Garland and Díaz-Uriarte (1999), to avoid inflation of type I errors in the comparative analysis.

We constructed the phylogenetic trees in Mesquite 2.74 (Maddison and Maddison 2010). Basic diagnostic plots, arbitrary branch length transformations and the method of bounded degrees of freedom are also implemented in this software.

Statistical analysis

We controlled for the statistical non-independence of traits of related taxa by using the method of independent contrasts (Felsenstein 1985). These calculations were carried out with PDAP: PDTREE 1.15 module (Midford et al. 2010) in Mesquite (Maddison and Maddison 2010). Character evolution was simulated under a Brownian motion model (Felsenstein 1985). Although this model may not represent perfectly the process of evolutionary changes, several authors showed that even with errors in branch lengths and deviations from Brownian motion the method of independent contrasts is robust and reliable (Díaz-Uriarte and Garland 1996, 1998).

Only two continuous variables can be tested simultaneously by using the method of independent contrasts in Mesquite (Maddison and Maddison 2010). Therefore, in cases when more than one variable had a significant effect on a response variable, we created standardized contrasts and performed multiple linear regressions to test the explanatory power of all variables on the louse taxonomic richness at the same time. All regressions were forced through the origin (Felsenstein 1985, Garland et al. 1992). We checked for multicollinearity between the explanatory variables by variance inflation factor (VIF) (Reiczigel et al. 2007). These analyses were carried out with R 2.11.1 (R Development Core Team 2010) using the package ’faraway’ (Faraway 2009). The distributional assumptions of the statistical tests used were checked graphically (e.g. quantile-comparsion plot). All analyses were two-tailed.

Results

Mean species richness of avian families was 53.3 (range: 1-400), while mean species richness of mammalian families was 31.4 (range: 1-1326). The mean generic richness of lice (whole Phthiraptera) was 3.6 (range: 0-20) on avian families and 1.2 (range: 0-11) on mammalian families.

We investigated whether species richness of host families predicts generic richness of lice. Louse richness values were taken as response variables, while host richness acted as the explanatory variable. In the avian dataset, we found significant positive relationships between host species richness and the generic richness of the whole order (Fig. 1), both suborders and all families of lice, except Laemobothriidae (Table 3). This latter non-significant correlation acted as the only difference in the results of the datasets controlled for louse sampling effort in three different ways (see Materials and methods). This correlation was significant neither when raw generic richness data was used nor when families without louse associations were excluded. However, by residual analysis we found a weak positive correlation (p = 0.042). In the mammalian dataset, we found significant positive relationships between host species richness and the generic richness of the whole order (Fig. 2) and all investigated suborders of lice (Table 3).

We also checked whether host body mass predicts louse generic richness. In the avian dataset we found that generic richness of Ricinidae co-varied negatively with host body mass, while no relationship appeared with other louse taxa (Table 4). However, in case of Menoponids results differed according to different body mass measures. When estimating family body masses by averaging the minimum and maximum values (see Materials and methods), we found a marginally significant positive correlation (*p* = 0.049) between body mass and Menoponid richness. However, even in this case body mass failed to show a significant effect on Menoponid richness in a multiple linear regression model. Body mass of mammals did not predict the generic richness of any of the louse taxa (Table 4).

In the case of Ricinids, both host species richness (Table 3) and body mass (Table 4) had a significant effect on the richness of lice. We therefore performed multiple linear regressions with the standardized contrasts, forced through the origin. Ricinid generic richness co-varied significantly both with host species richness (slope = 0.17, $p < 0.001$) and body mass (slope = - 0.16, $p = 0.006$, $F_{(2,172)} = 15$, adjusted $R^2 = 0.14$). There was no multicollinearity between these explanatory variables (VIF value = 1.02).

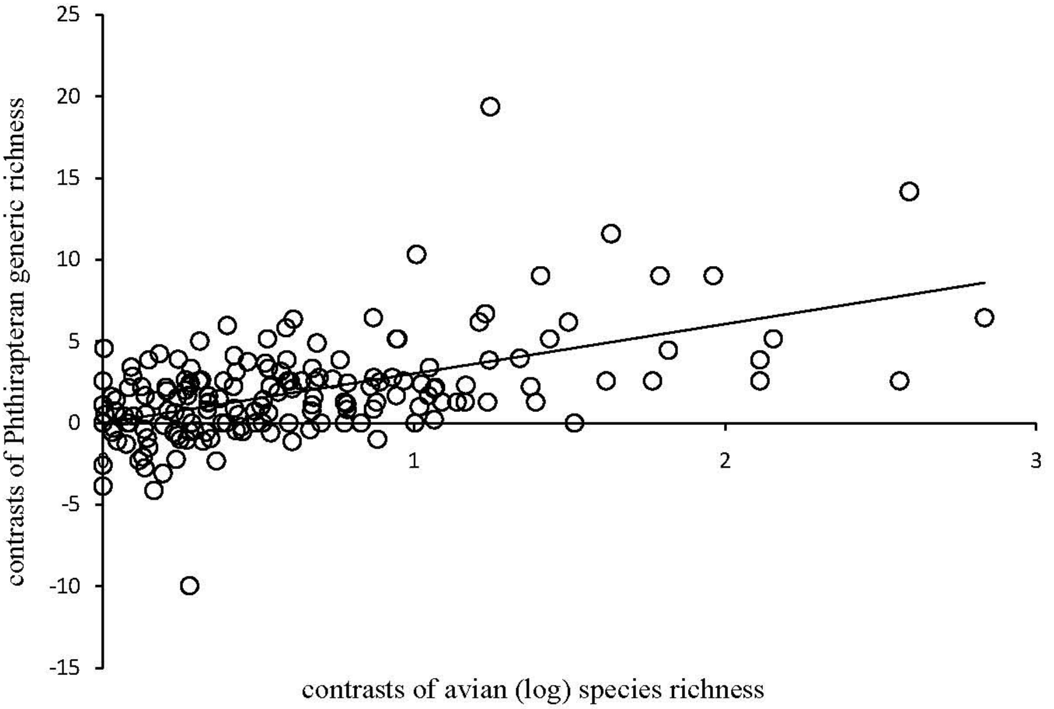

Fig. 1. Regression between contrasts of avian (log) species richness and contrasts of Phthirapteran generic richness.

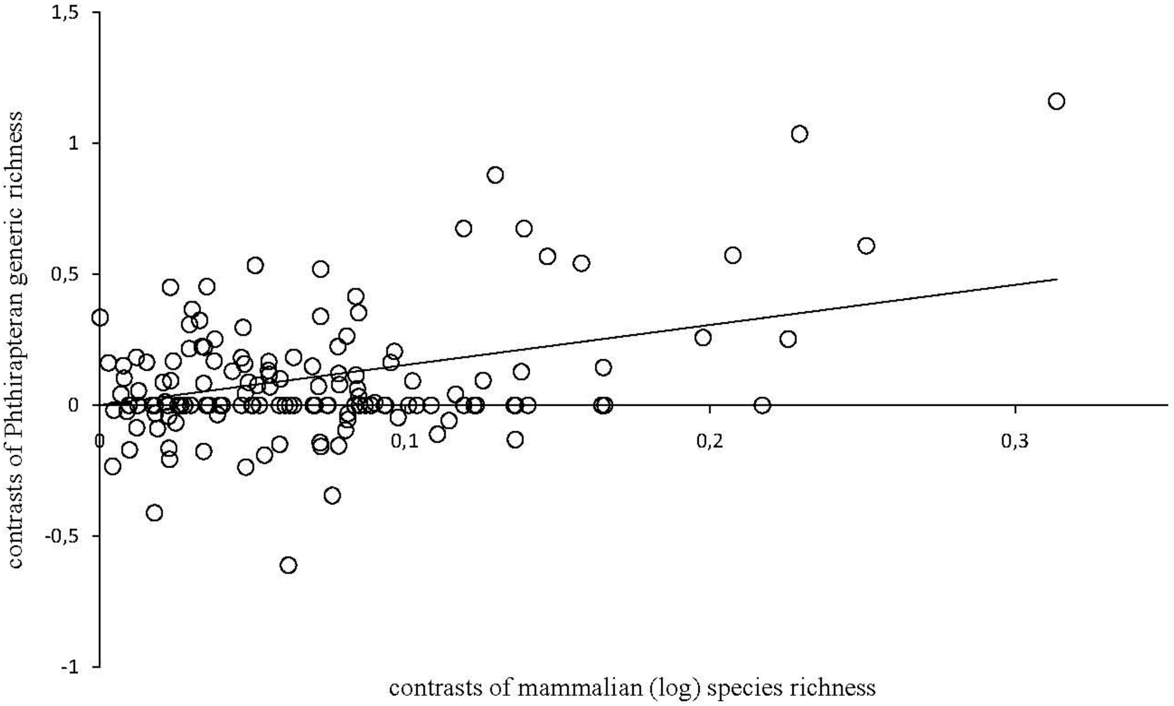

Fig. 2. Regression between contrasts of mammalian (log) species richness and contrasts of Phthirapteran generic richness.

Table 3 Results of linear regression between contrasts of (log) host species richness and contrasts of louse generic richness

	slope	R^2	*F*	*p*
Avian families (*n* = 174; *df* = 172):				
Phthiraptera	3.03	0.48	158.62	< 0.001
Ischnocera : Philopteridae	1.75	0.34	89.84	< 0.001
Amblycera	1.28	0.46	149.54	< 0.001
Amblycera: Menoponidae	1.06	0.38	103.98	< 0.001
Amblycera: Ricinidae	0.19	0.11	21.50	< 0.001
Amblycera: Laemobothriidae	0.04	0.01	2.14	0.146
Mammalian families (*n* = 146; *df* = 128):				
Phthiraptera	1.53	0.29	58.27	< 0.001
Ischnocera	0.30	0.08	11.86	< 0.001
Amblycera	0.45	0.11	17.16	< 0.001
Anoplura	0.78	0.20	37.09	< 0.001

Table 4 Results of linear regression between contrasts of (log) host body mass and contrasts of louse generic richness

	slope	R^2	*F*	*p*
Avian families (*n* = 174; *df* = 172):				
Phthiraptera	-0.33	< 0.01	0.48	0.490
Ischnocera : Philopteridae	-0.14	< 0.01	0.19	0.660
Amblycera	-0.19	< 0.01	0.83	0.468
Amblycera: Menoponidae	< 0.01	< 0.01	< 0.01	0.987
Amblycera: Ricinidae	-0.19	0.05	10.06	0.002
Amblycera: Laemobothriidae	-0.02	< 0.01	0.29	0.591
Mammalian families (*n* = 116; *df* = 98):				
Phthiraptera	-0.37	0.02	2.94	0.090
Ischnocera	-0.09	0.01	1.14	0.288
Amblycera	-0.08	< 0.01	0.57	0.452
Anoplura	-0.23	0.02	2.94	0.089

Discussion

Several recent studies (see e.g. Krasnov 2008) on the environmental correlates of parasite diversity used a ‘diversity concept’ different from the ‘richness concept’ used here. They considered not only the number of parasite taxa, but also a taxonomical distinctness of these taxa as components of parasite diversity. Here we did not follow this line due to three reasons. Firstly, Eichler’s (1942) original hypothesis referred only to the numbers of host and parasite taxa within an assemblage, and not to their distinctness. Secondly, we had no branch length data for the parasite phylogeny, thus we could use only the systematical hierarchy to assess taxonomical distinctness in the sense of Warwick and Clarke’s (1995) – a rough method based on unrealistic presumptions. Finally, if we use the number and distinctness of parasite taxa to quantify the diversity of a parasite assemblage, then we should use the same approach to quantify host diversity as well – a source of substantial further complications.

Thus, for sake of simplicity, we tested strictly what Eichler predicted – i.e. the positive co-variation between the richness of host and parasite taxa and we found strong support for Eichler’s rule.

The biological interpretation of louse generic richness – our measure of parasite richness – is quite straightforward. Co-existing lice taxa exhibit quite distinct body size and body shape differences according to the specific microhabitats they occupy on a particular host species (Johnson and Clayton 2003). Therefore, different louse genera can roughly be interpreted as different ecological guilds utilizing different environmental resources (such as refuges to avoid host defenses) in the sense of Simberloff and Dayan (1991).

The taxonomic richness of avian families showed a significant positive correlation with the generic richness of the whole order of lice (Fig. 1), both suborders and 3 out of 4 families of lice (Table 3). To the best of our knowledge, only one former study (Hughes and Page 2007) succeeded in finding any trait that co-varies with Ischnoceran taxonomic richness showing that population size co-varies positively with Ischnoceran species richness. On the contrary, however, several traits studied by previous authors showed a significant relationship with Amblyceran taxonomic richness and no relationships with Ischnocerans (Clayton and

Walther 2001, Hughes and Page 2007, Møller and Rózsa 2005, Møller et al. 2010, Vas et al. 2011). The generic richness of Laemobothriidae, not surprisingly, failed to co-vary significantly with host taxonomic richness, as this family contains only one genus and has an erratic and still unexplained distribution pattern among birds. They infest several species of Ciconiiformes, Gruiformes, Falconiformes and Strigiformes (Price et al. 2003), though the latter may well be an erroneous host record.

Host species richness of mammalian families co-varied positively with the generic richness of the whole order and all investigated suborders of Phthiraptera (Table 3).

Several explanatory powers (R^2 values) reported in Table 3 are unusually high in comparison with other comparative studies in evolutionary ecology, in which R^2 values were found frequently in the range 0.05-0.10 (Freckleton 2009). However, R^2 values reported here range up to 0.48, reflecting an exceptionally high explanatory power, and strong support for Eichler (1942).

What evolutionary and ecological progresses are behind Eichler's rule? Why do taxon-rich host clades harbor more diverse parasite faunae? Below we propose some alternative hypotheses that may explain the strong correlation between host and parasite taxonomic richness. These hypotheses may not be mutually exclusive, and partly based on former arguments of Eichler (1942), Nunn et al. (2004) and Hughes and Page (2007).

Firstly, from a macroevolutionary viewpoint, the most obvious answer lies in host-parasite cospeciation. In a speciation event of hosts the possibility of horizontal gene transfer breaks not only between host populations but often also between parasite populations infesting them. Reproductive isolation of hosts reduces physical contacts that are often crucial for parasite transmission (Johnson and Clayton 2003). Presuming high host-specificity, we expect host and parasite speciation to follow each other (Page 2003). Given these conditions, taxon-rich host clades would be infested with a taxon-rich parasite fauna, as compared to host clades with little branching (Eichler 1942). However, contrary to early expectations (Fahrenholz 1913), parasites often do not significantly cospeciate with their hosts (see Page (2003) for a review). Indeed, cospeciation events seem to be about as frequent in lice as in any other group of parasites (Page 2003).

One can reasonably change the direction of causality by presuming that parasite richness forces host taxa to increase speciation. Indeed, pathogen taxonomical diversity is an important determinant of selection pressure exerted by parasites (Bordes and Morand 2009), which may increase host speciation through processes such as parasite-mediated sexual selection. These two directions are not mutually excluding each other. Presuming that high parasite richness can increase host diversity and then host diversity can also facilitate subsequent parasite speciation may lead us to hypothesize an autocatalytic process resulting a coevolutionary increase of richness in certain host-parasite lineages.

Secondly, from a macroecological viewpoint, host population size and geographic range may also influence avian (Gregory 1990, Hughes and Page 2007) and mammalian (Poulin 2007) parasite diversity. Species rich host clades may occupy greater area and more diverse habitats, and they may also incorporate a larger number of individuals; hence they have a greater chance of coming into contact with other species. Thus they are more exposed to host switching parasites (Gregory 1990, Hughes and Page 2007, Nunn et al. 2004). This phenomenon may also contribute to the correlation described above.

On the contrary, one could reasonably argue that host taxonomic richness may affect parasite extinction rates rather than speciation rates. Lice – just like many other parasites – exhibit relatively strict host specificity with rare and accidental host-switches during their evolutionary history. The chance of a successful host-switch is likely to be higher if the donor and the recipient host species are closely related phylogenetically and, therefore, morphologically. Arguably, louse taxa parasitizing species-rich host clades are less prone to extinction simply because they have a higher chance to establish parallel populations harbored by different host species. This phenomenon may contribute to the apparent lack of lice on taxon-poor host families like Balaenicipitidae, Rhynochetidae, or Todidae.

In the wide taxonomic range presented by this study, host body mass does not seem a key factor shaping louse richness, as also suggested by several earlier studies (Bordes et al. 2011, Hughes and Page 2007, Krasnov et al. 2004, Krasnov et al. 2008, Poulin 2007). We found, however, that body mass had a strong effect on the generic richness of Ricinids. This is not surprising, given the fact that members of this family infest only hummingbirds and small-bodied passerines (Price et al. 2003). Ricinids are considerably large themselves (Nelson 1972, Rheinwald 1968), hence the factors shaping their peculiar host distribution need further study. Host body mass appears to be more important in shaping other measures of louse infestations, such as prevalence and intensity (Rózsa 1997a,b). However, as it is harder to obtain these kinds of data properly, little is known about how body mass affects infestation measures on a broad phylogenetic scale.

We conclude that exceptionally strong correlational evidence supports the positive co-variation between the species richness of avian and mammalian families and the generic richness of their lice. Given the fact that this relationship is highly significant across all major host and parasite taxa involved in the present study, we propose that it may well be a quite general feature of parasitism and likely also of other historical associations like mutualism. The generality of this phenomenon is also supported by the recent finding that lice represent two independent origins of parasitism (Johnson et al. 2004, Murrell and Barker 2005, Smith et al. 2011). Whatever the driving force and the exact mechanism beyond this phenomenon is, it seems possible that it may greatly contribute to the global biodiversity. Further studies should test the validity of Eichler's rule on a wider range of hosts, parasites and mutualists, and also at other levels of the taxonomical hierarchy.

1.3. Conclusions of Chapter 1

Identifying factors shaping louse diversity is still in an incipient phase as relatively few general inferences can be drawn. Published correlative evidences are summarized in Table 1. Apparently, the studies testing several host characters as explanatory variables either failed to find any significant relationships (Clayton and Walther 2001) or found only rather few significant effects (Hughes and Page 2007). On the other hand, studies testing only fewer or just a single explanatory variable more frequently identified host characters affecting louse diversity (e.g. Felső and Rózsa 2006, Vas et al. 2011). A careful selection of explanatory variables is particularly important in this latter case because potentially influential factors not involved in the model – if correlated with the factors involved – may cause false results. When testing the potential effect of a new host character, an important prerequisite is to control for the effects of all formerly known influential host characters – at least as far as it is possible.

Nevertheless, the macroevolutionary scale of these studies was different (Table 1); some results were obtained by investigating louse species richness controlled for a species-level phylogeny of the hosts (e.g. Clayton and Walther 2001, Møller and Rózsa 2005) while others investigated louse genera richness controlled for a phylogeny of higher host taxa such as families (Vas et al. 2011, 2012a) or sister clades (Felső and Rózsa 2006, 2007, Vas et al. 2013). Furthermore, the diversity measures analyzed also differed; species richness, genera richness, and taxonomic distinctness index – though they are not independent of each other – capture different aspects of diversity, hence they do not necessarily exhibit similar patterns. For example, hosts' brood parasitic life-style affects louse genera richness and species richness differently, and in some cases even oppositely (Vas et al. 2013). Consequently, choosing an inappropriate macroevolutionary scale for a study may seriously affect the results and preclude their generalization. It is reasonable to test a supposed correlation at different macroevolutionary levels.

Table 1. Summary of host characters significantly affecting louse diversity. Characters refer to avian hosts unless marked with asterisk (*) which means that it refer to mammalian hosts as well. + describes positive, – describes negative relationship. Marginally significant effects are in parentheses. (Based on Rózsa and Vas 2013b.)

host character	**Phthiraptera**	**Phthiraptera**	**Phthiraptera**	**Amblycera**	**Amblycera**	**Amblycera**	**Ischnocera**	**Ischnocera**	**Ischnocera**	**reference**
	SR	**GR**	**TDI**	**SR**	**GR**	**TDI**	**SR**	**GR**	**TDI**	
time allocated to grooming	+									Cotgreave and Clayton 1994
diving into water with entire body*		–								Felső and Rózsa 2006, 2007
nestling T-cell immune response					+					Møller and Rózsa 2005
cognitive/innovative capabilities								+		Vas et al. 2011
relative brain size								+		Vas et al. 2011
uropygial gland size								+		Møller et al. 2010
switching to brood parasitism					–	–		(–)	–	Vas et al. 2013
cuckoo foster parent diversity							+	+	+	Vas et al. 2013
cuckoo body mass							+	+	+	Vas et al. 2013
host clade species richness*					+			+		Vas et al. 2011, 2012a
seabird population size				+	+		+	+		Hughes and Page 2007
seabird geographic range				+	+		+	+		Hughes and Page 2007
seabird diving behavior		–								Hughes and Page 2007

Vas et al. (2013) also pointed out that diversity interactions with a third trophic level may also affect parasite diversity as in the case of foster-birds, cuckoos, and their lice. However, given that this study was the first to reveal such a complex interaction affecting louse diversity, the importance and frequency of this phenomenon in nature cannot be assessed yet. In my opinion, the investigation of the strictly associated systems of host insects, parasitoid wasps, and hyperparasitoid wasps may represent a promising system to explore similar diversity interactions across three or perhaps even more trophic levels.

Another inference to be pointed out is that Amblyceran and Ischnoceran lice exhibit rather dissimilar relationships with their hosts (Table 1). Recently it turned out that they represent two lineages that switched to a parasitic way of life independently of each other (Johnson et al. 2004, Murrell and Barker 2005) and their life histories are also quite different (Johnson and Clayton 2003). Unlike Ischnocerans, it seems that Amblycerans co-evolve more closely with host physiological defenses, relative brain size, and cognitive/innovative capabilities, which can at least partly be derived from their more intense interaction with the living tissues of the hosts. Before our own investigations only Hughes and Page (2007) succeeded in finding significant predictors of Ischnoceran richness (host population size and geographic range). Our investigations revealed that Ischnocerans' diversity was affected by the brood parasitic way of life of the hosts in a complex way (Vas et al. 2013), as well as by host clade diversity (Vas et al. 2012a).

An intriguing task is to search for general diversity patterns in parasite evolutionary ecology (Krasnov et al. 2008). An evident idea is that host body size may affect different parasite taxa in a similar way; however, contradictory results were found about the importance and the direction of its effect both between and within certain parasite taxa infesting the same or different host taxa (Krasnov et al. 2004, Hughes and Page 2007, Poulin 2007, Krasnov et al. 2008, Bordes et al. 2011, Vas et al. 2011, 2012a, 2013). It is reasonable to suggest that host body mass is a more important predictor of louse abundance than of louse richness (see e.g. Rózsa 1997a,b).

The positive co-variation of host cognitive capabilities and parasite richness we found (Vas et al. 2012a) may indicate a more general phenomenon. Soon after our work similar results were published by Soler et al. (2012). They found that bird species with higher measures of cognitive abilities (feeding innovation rates and rejection rates of experimental brood parasitic eggs) have higher densities of potentially pathogenic bacteria on their eggshells.

Future studies should test the generality of the phenomenon across other host-parasite systems and particularly in Primates.

The positive co-variation between host and parasite diversity – the so-called Eichler's rule – seems to be the strongest and most general diversity pattern found so far (Eichler 1942, Vas et al. 2012a). Eichler's prediction holds for the whole Phthiraptera infesting both avian and mammalian hosts, and this relationship remains to be exceptionally strong even after controlling for sampling bias and phylogeny. Additionally, an ongoing study on quill mite (Syringophilidae) diversity also supports Eichler's rule (manuscript in preparation, Martin Hromada, Miroslava Klimovičová, Lajos Rózsa, and Zoltán Vas). It is feasible that parasitism – through this effect – may play an important and general role in the creation and maintenance of global biodiversity as a whole.

The understanding of the diversity component of host-parasite relationships is a major and yet scarcely discovered field of evolutionary ecology. Here I presented a literature review and three original studies concerning the host-parasite relationship of lice and their avian and mammalian hosts. Factors decreasing and increasing diversity were both recognized. However, until the full understanding of the macroevolutionary patterns behind parasite diversity there is still a lot to do.

Chapter 2 – Louse faunistics and conservation biology

2.1. Introduction to Chapter 2.

This chapter incorporates papers related to different aspects of louse faunistics. First of all, here I clarify the connection between this chapter and the diversity investigations discussed in the previous chapter. Without a reliable knowledge of parasite faunae the macroevolutionary approach to identify environmental correlates of louse richness is nothing but a pitfall. In particular, if a parasite fauna has been only poorly discovered up to date, there are no meaningful ways to control for uneven sampling in comparative studies. The data on presence or absence of parasite taxa on a given host species, as well as their prevalence, intensity of infestation, and sex ratio – the raw data of evolutionary comparative studies – have been gathered by a handful of dedicated researchers through centuries. In case of lice, such faunistical studies were recently reviewed and summarized by Price et al. (2003) in a monumental world checklist providing valuable data for comparative studies. Naturally, the sampling done by early faunists was never evenly allocated among host species – more attractive and bigger species, and those that can be captured with less effort were always overrepresented. However, in case of well-explored parasite faunae this effect can be taken into consideration (see above).

Local faunistical surveys focusing on smaller areas (say, countries) than Price et al.'s (2003) world checklist are essential to discover the patterns in the geographical distribution of lice, the local variability in louse-host associations and in parasite assemblages. Moreover, even some Western European countries (e.g. France and Italy) have a quite unexplored louse fauna; hence, louse faunistics still has a lot to discover. Although faunistics is often considered to be a low-prestige field of biology nowadays, I argue that it is – and will remain to be – vital to provide basic data about the studied organisms and thus to allow further evolutionary and ecological investigations.

This chapter incorporates papers related to different aspects of louse faunistics. First, I summarize what was formerly published on the Hungarian louse fauna. Second, this list is significantly extended by my own recent collections. The third paper is a methodological contribution that points out a formerly overlooked bias in currently widespread sampling projects. Finally, in the last paper I provide global checklist of critically endangered species of parasitic lice.

2.2.1. Hungarian louse fauna and the history of its investigation

Lice constitute a relatively ‘small order’ within the class of insects, thus there was no Hungarian louse specialist before World War II. Only a few entomological overviews were published by Csiki (1904), Pongrácz (1914), and Dudich (1924) who were respected specialists of other insect groups. Additionally, due to political changes in Central Europe, geographical outline of Hungary – the area their fauna lists were referring to – was subjected to frequent changes and was much larger than present-day Hungary.

The first targeted faunistical surveys after 1945 were carried out on wild birds by the Czech researcher František Balát and his Hungarian colleague György Breuer (Balát and Breuer 1955, Balát 1957). Their contribution, though limited to the western parts of Hungary, proved the occurrence of numerous louse species. Later on, Lajos Schäfer (Sasvári) carried out a more extensive sampling of avian lice and reported several louse species new for the Hungarian fauna (Schäfer 1963, 1964).

Undoubtedly, the greatest contribution to the exploration of the Hungarian louse fauna has been done by József Rékási, ornithologist, phthirapterist, and biology teacher at the Pannonhalma Benedictine School. For 40 years he has been carrying out a remarkably extensive sampling and published more than 50 papers on louse faunistics. He verified the occurrence of 165 louse species in Hungary and established the largest chewing louse collection in Hungary which contains numerous voucher specimens. He has recently donated his valuable collection to the Hungarian Natural History Museum. In recent years some other authors also reported a handful of louse species new to the Hungarian fauna as a byproduct of ecological studies such as Rózsa (1990)’s investigations on Feral Pigeons, Solt (1998)’s work on raptor birds, and Vas et al.’s (2008) study on Barn Swallows.

I started my own faunistical survey on avian lice in 2005 at the Ócsa Bird Ringing Station. Since then, I gathered a quite large collection with the help of my ornithologist and bird ringer colleagues: nearly 600 samples representing 99 wild bird host species. The majority of these samples were collected at Ócsa Bird Ringing Station, however, several samples originate from other locations (mainly Pest and Fejér Counties). I also obtained a considerable Italian material due to a 7-year co-operation with Italian veterinarians and bird ringers. This part of the collection also contains some voucher specimens new for the Italian louse fauna. The methodology we used is discussed in section 2.3.1 below. Though the identification of the samples is far from complete, this collection already incorporates more than 100 identified species involving at least 22 species new for the Hungarian fauna. This collection – along with that of Lajos Rózsa – has also been donated to the Hungarian Natural History Museum recently.

The following two papers summarize the status of the Hungarian louse fauna. The first one (section 2.2.2) is basically a compilation summarizing the previously published faunistical literature to list the louse species formerly documented to occur and those expected to occur (based on host distributions and host specificity). Both avian and mammalian lice are covered in this checklist. Given the page limitations of the present thesis, the spacious list is presented in the Appendices. The second faunistical paper (section 2.2.3) updates and significantly broadens this list with results obtained by me and my co-authors.

2.2.2. Case study (as published in Annales historico-naturales Musei nationalis hungarici 104: 5-109., 2012.):

A checklist of lice (Insecta: Phthiraptera) of Hungary

authors: *Zoltán Vas, József Rékási, Lajos Rózsa*

Introduction

Hungary's sucking louse (Phthiraptera: Anoplura) fauna was summarized by Piotrowski (1970). The chewing louse (Phthiraptera: Amblycera, Ischnocera) fauna was evaluated in two checklists (Rékási 1993a, 1994) summarizing data for avian and mammalian hosts separately. Subsequently, more recent world checklists for sucking lice (Durden and Musser 1994b) and for chewing lice (Price et al. 2003) critically reviewed the nomenclature, taxonomy and host-parasite relationships of this insect order as a whole. Furthermore, genus-level world checklists such as those of Mey (2001) and Bush et al. (2009) were published. These global revisions made it necessary to critically reconsider data at national level again. In the present paper, a critical synthesis of the currently available data on all lice collected after 1945 in the area of present-day Hungary is provided.

This list follows the traditions set out by early Hungarian authors namely Csíki (1904), Pongrácz (1914) and Dudich (1924). However, the forms and methodologies established by modern louse checklists of other countries or areas, such as Kim et al. (1986), Mey (1988), Máca (1991), Smithers et al. (1996), Pajot (2000), Tenquist and Charleston (2001), Ford et al. (2004), Ilieva (2009) and Adam and Sándor (2004, 2005) are also followed.

Materials and methods

We critically reviewed all published literature sources of the Hungarian louse fauna. Our list follows the nomenclature and host-parasite associations of the world checklists of chewing lice (Price et al. 2003) and sucking lice (Durden and Musser 1994b) with a few complements based on Bádr et al. (2005), Sychra and Literák (2008), and Sychra et al. (2008a,b). We involved all bird and mammal species listed in the most recent bird (MME Nomeclator

Bizottság 2008) and mammal (Bihari et al. 2007) checklists of Hungary, except for a few taxa of mammals – e.g. European Mole (*Talpa europaea* LINNAEUS, 1758), bats (Chiroptera), mole rats (*Nannospalax* PALMER, 1903) – that are known to be free of lice.

Several louse records were rejected due to uncertainties of identification. Similarly, we rejected all records before 1945 because these data refer to a geographic area different from present-day Hungary. For the same reason, we have not adopted many data of the previous checklists of Rékási (1993a, 1994). We ignored atypical louse-host associations named ‘stragglers’ or ‘desertoers’ in the literature – i.e. lice collected from atypical host species. Atypical associations may either arise from natural or artificial processes; anyway, they are unlikely to represent self-sustainable louse populations. In the present list, typical associations are those accepted by Price et al. (2003) or Durden and Musser (1994b) as such.

The first part of the text provides data listed by parasites (in an alphabetical sequence, subdivided into avian lice and mammal lice), while the second part repeats the same information listed by hosts. Host lists follow a taxonomical sequence of orders and families, however, genera and species are listed in an alphabetical sequence within families. Bird and mammal taxonomy follows Dickinson (2003) and Bihari et al. (2007) respectively.

At each species, the data published from post-1945 Hungary (marked with “HU:”) are provided first. (In case of host-parasite species pairs with several Hungarian published records, only the earliest publication is mentioned.) This is followed by host or parasite records that have no published data for Hungary; however, their occurrence seems to be likely as judged from the geographic distribution of the host and the parasite. Asterisk (*) marks the type host-parasite relationship. If the original source of data used a louse synonymy that is now considered invalid, synonym names are also given.

Human and domesticated host species are separated from wild ones. Domesticated animals that are also represented by wild populations in Hungary are treated as formally distinct species (e.g. *Anas domesticus*, *Canis familiaris*, *Sus domesticus*) to avoid confusion. Some lice of globally widespread domestic hosts (horse, cattle, and dog) are not included in the present list since they have never been found in the Western Palearctic. Finally, a list of potential host species that are not yet known to harbor lice is also provided.

Results

Our list includes 279 louse species (and subspecies) which have been recorded in Hungary since 1945. Their hosts represent 156 bird and 30 mammal species. Additionally, we also list further 550 louse species whose occurrence may seem to be likely (as judged from geographic and host distribution) but have not been detected yet. Future research will result several new louse species and host records for Hungary.

[See Appendix 1. for the complete lists.]

2.2.3. Case study (as published in Ornis Hungarica 20(1): 44-49, 2012):

New species and host association records for the Hungarian avian louse fauna (Insecta: Phthiraptera)

authors: *__Zoltán Vas__, Csaba Privigyei, Viola J. Prohászka, Tibor Csörgő, Lajos Rózsa*

Introduction

Avian lice (Insecta: Phthiraptera) are wingless obligate ectoparasites that complete their entire life-cycle on the body surface of their hosts. They feed mainly on feathers and dead skin parts and are often highly specific to their hosts (Johnson and Clayton 2003). A recent world checklist of avian lice by Price et al. (2003) critically reviewed their nomenclature, taxonomy and host-parasite associations. They list 3910 louse species infesting 3248 bird species. Most probably a large number of louse species still await description (see e.g. Palma and Price (2010), Sychra et al. (2010), Valim and Weckstein (2012)).

According to a recently published checklist, 279 louse species (and subspecies) have been recorded in Hungary (Vas et al. 2012b). Additionally, this paper also lists over 550 louse species, subspecies, and host associations which have not been detected in Hungary yet; however, their occurrence may seem to be likely as judged from host distribution. Further research shall reveal several louse species new for the Hungarian fauna, as well as new host records. These are new, formerly undocumented associations between host and louse species.

In this paper we report the results of a recent faunistical survey on the Hungarian louse fauna. We identified louse samples from various bird species collected at different locations between 1998-2012. Below we provide a list of louse species new to the Hungarian fauna (as compared to Vas et al. 2012b). Furthermore, we also list host association records that are new either as compared to the Hungarian checklist or new as compared to the world checklist of Price et al. (2003).

Materials and methods

Our faunistical survey of avian lice (Insecta: Phthiraptera) started in 2005 at Ócsa Bird Ringing Station, resulting hundreds of ectoparasite samples collected from over 70 bird species. Other research projects on various bird species (e.g. Barn Swallows (*Hirundo rustica*), European Bee-eaters (*Merops apiaster*), and Red-footed Falcons (*Falco vespertinus*)) provided further hundreds of louse samples. Additionally, a few samples were collected from bird cadavers before taxidermy in the Bird Collection of the Hungarian Natural History Museum (HNHM). All investigated cadavers were known to originate from Hungarian wild populations. Furthermore, many colleagues studying birds collected and sent us samples to help our work.

Lice sampled in focused ectoparasitological research projects (see e.g. Vas et al. (2008) on Barn Swallows) were collected with pyrethroid insecticide in a standardized way to allow further quantitative analyses (Johnson and Clayton 2003, Rózsa 2003). However, some samples we obtained were collected by visual examination without following any standard; hence they satisfy faunistical purposes only. The samples were stored in 70% ethanol. The identification of louse species was made by the first author using a stereoscopic microscope. The samples are presently held by the last author for further research, and will be deposited in the Department of Zoology of HNHM in the future.

Our lists follows the nomenclature and host-parasite associations of the world checklists of chewing lice (Price et al. 2003) with a few complements based on Sychra and Literák (2008), and Sychra et al. (2008). Bird taxonomy follows Dickinson (2003). Asterisk (*) marks the type host-parasite relationship. We also report the locality, date, and collector(s) for each louse sample in brackets. In the case of multiple samples from the same louse species the earliest one's data is given.

Results

New species for the Hungarian louse fauna

AMBLYCERA: MENOPONIDAE

Actornithophilus piceus piceus (DENNY, 1842)

Sterna hirundo LINNAEUS, 1758 [Nagybivalyos lake, Várpalota, 2012.06.08., Ferincz, Árpád; Fuisz, Tibor István; Preiszner, Bálint; Sütő, Szandra; Vas, Zoltán]

Austromenopon atrofulvum (PIAGET, 1880)

Sterna hirundo LINNAEUS, 1758 [Nagybivalyos lake, Várpalota, 2012.06.08., Ferincz, Árpád; Fuisz, Tibor István; Preiszner, Bálint; Sütő, Szandra; Vas, Zoltán]

Colpocephalum subzerafae TENDEIRO, 1988

Falco vespertinus LINNAEUS, 1766 [Kardoskút, 2012.07.07., Fehérvári, Péter; Horváth, Éva; Solt, Szabolcs; Vas, Zoltán]

Menacanthus camelinus (NITZSCH, 1874)

Lanius collurio LINNAEUS, 1758 [Máriahalom, 2006.07.28., Preiszner, Bálint; Vas, Zoltán]

Menacanthus fertilis (NITZSCH, 1866)

Upupa epops LINNAEUS, 1758* [Áporkai tanya, Bugyi, 2012.06.09., Rózsa, Lajos]

Menacanthus obrteli BALÁT, 1981

Locustella luscinioides (SAVI, 1824)* [ringing station, Ócsa, 2007.06.20., Privigyei, Csaba; Prohászka, Viola Judit]

Myrsidea latifrons (CARRIKER & SHULL, 1910)

Riparia riparia (LINNAEUS, 1758)* [sandmine lake, Ócsa, 2008.07., Tóth, Lajos; Vas, Zoltán]

Myrsidea sylviae SYCHRA & LITERÁK, 2008

Sylvia atricapilla (LINNAEUS, 1758)* [ringing station, Ócsa, 2008.08.22., Vas, Zoltán]

Nosopon clayae PRICE & BEER, 1963

Pernis apivorus (LINNAEUS, 1758)* [ringing station, Ócsa, 2008.09.14., Vas, Zoltán]

ISCHNOCERA: PHILOPTERIDAE

Aegypoecus trigonoceps (GIEBEL, 1874)

Gyps fulvus (HABLIZL, 1783)* [Egyed, 2005.09.05., Molnár, Viktor]

Brueelia glizi BALÁT, 1955

Fringilla montifringilla LINNAEUS, 1758* [ringing station, Ócsa, 2006.03.11., Vas, Zoltán]

Craspedorrhynchus dilatatus (RUDOW, 1869)

Buteo lagopus (PONTOPPIDAN, 1763)* [Bugyi, 2010.12.29., Vas, Zoltán]

Degeeriella vagans (GIEBEL, 1874)
Accipiter gentilis (LINNAEUS, 1758)* [ringing station, Ócsa, 2005.07.15., Rózsa, Lajos; Vas, Zoltán]

Falcolipeurus quadripustulatus (BURMEISTER, 1838)
Gyps fulvus (HABLIZL, 1783) [Egyed, 2005.09.05., Molnár, Viktor]

Falcolipeurus sulcifrons (DENNY, 1842)
Haliaeetus albicilla (LINNAEUS, 1758)* [HNHM Bird Collection, 2010.05.20., Vas, Zoltán]

Philopterus modularis (DENNY, 1842)
Prunella modularis (LINNAEUS, 1758)* [ringing station, Ócsa, 2008.10.11., Privigyei, Csaba; Prohászka, Viola Judit]

Philopterus rapax (ZLOTORZYCKA, 1964)
Fringilla montifringilla LINNAEUS, 1758* [ringing station, Ócsa, 2008.01., Vas, Zoltán]

Rallicola minutus (NITZSCH, 1866)
Gallinula chloropus (LINNAEUS, 1758)* [ringing station, Ócsa, 2005.09.01., Vas, Zoltán]

Strigiphilus goniodicerus EICHLER, 1949
Bubo bubo (LINNAEUS, 1758)* [HNHM Bird Collection, 2010.10.08., Vas, Zoltán]

Strigiphilus heterocerus (GRUBE, 1851)
Strix uralensis PALLAS, 1771* [Arka, 1998.10.05., Horváth, Márton]

Host association records new for the Hungarian fauna

AMBLYCERA: MENOPONIDAE

Ciconiphilus decimfasciatus (BOISDUVAL & LACORDAIRE, 1835)
Ardea cinerea LINNAEUS, 1758* [Petőháza, 2006.02., Rózsa, Lajos]

Colpocephalum subzerafae TENDEIRO, 1988
Falco tinnunculus LINNAEUS, 1758 [Kardoskút, 2012.07.07., Fehérvári, Péter; Horváth, Éva; Solt, Szabolcs; Vas, Zoltán]

Menacanthus alaudae (SCHRANK, 1776)

Emberiza citrinella LINNAEUS, 1758 [ringing station, Ócsa, 2008.11.11., Privigyei, Csaba; Prohászka, Viola Judit]

Menacanthus curuccae (SCHRANK, 1776)

Acrocephalus schoenobaenus (LINNAEUS, 1758) [ringing station, Ócsa, 2008.09.29., Privigyei, Csaba; Prohászka, Viola Judit]

Acrocephalus scirpaceus (HERMANN, 1804) [ringing station, Ócsa, 2008.08.01., Privigyei, Csaba; Prohászka, Viola Judit]

Menacanthus eurysternus (BURMEISTER, 1838)

Garrulus glandarius (LINNAEUS, 1758) [ringing station, Ócsa, 2007, Vas, Zoltán]

Lanius collurio LINNAEUS, 1758 [ringing station, Ócsa, 2007.08.11., Privigyei, Csaba; Prohászka, Viola Judit]

Turdus merula LINNAEUS, 1758 [ringing station, Ócsa, 2006.02.11., Vas, Zoltán]

Turdus philomelos BREHM, 1831 [ringing station, Ócsa, 2008.04.03., Vas, Zoltán]

Fringilla coelebs LINNAEUS, 1758 [ringing station, Ócsa, 2008.11.30., Privigyei, Csaba; Prohászka, Viola Judit]

Menacanthus sinuatus (BURMEISTER, 1838)

Parus caeruleus LINNAEUS, 1758 [ringing station, Ócsa, 2006.11.04., Vas, Zoltán]

Nosopon lucidum (RUDOW, 1869)

Circus aeruginosus (LINNAEUS, 1758) [HNHM Bird Collection, 2009.07.20., Vas, Zoltán]

Accipiter nisus (LINNAEUS, 1758) [ringing station, Ócsa, 2011.03.21., Privigyei, Csaba; Prohászka, Viola Judit]

Pseudomenopon pilosum (SCOPOLI, 1763)

Gallinula chloropus (LINNAEUS, 1758) [ringing station, Ócsa, 2005.09.01., Vas, Zoltán]

Trinoton anserinum (FABRICIUS, 1805)

Anser albifrons (SCOPOLI, 1769) [HNHM Bird Collection, 2004.01., Rózsa, Lajos]

AMBLYCERA: RICINIDAE

Ricinus fringillae DE GEER, 1778

Emberiza schoeniclus (LINNAEUS, 1758) [ringing station, Ócsa, 2008.03.15., Vas, Zoltán]

ISCHNOCERA: PHILOPTERIDAE

Degeeriella fusca (DENNY, 1842)

Circus pygargus (LINNAEUS, 1758) [HNHM Bird Collection, 2009.07.20., Vas, Zoltán]

Host association records new for the World fauna (ordered by birds, alphabetically)

Acrocephalus melanopogon (TEMMINCK, 1823)

Philopterus sp. [ringing station, Ócsa, 2006.07.21., Vas, Zoltán]

Carduelis spinus (LINNAEUS, 1758)

Philopterus sp. [ringing station, Ócsa, 2008.12.06., Privigyei, Csaba; Prohászka, Viola Judit]

Emberiza schoeniclus (LINNAEUS, 1758)

Menacanthus sp. [ringing station, Ócsa, 2008.05.03., Privigyei, Csaba; Prohászka, Viola Judit]

Discussion

The most recent checklist (Vas et al. 2012b) reported 279 louse species and subspecies infesting 156 bird species in Hungary. The present study increases theses numbers to 299 louse species and subspecies infesting 170 bird species in Hungary. The species-level identification of the host records new for the World fauna requires further sampling and investigation as the specimens we found were almost exclusively nymphs. Future research will reveal whether these lice are accidentally “stragglers” from other host species or yet unknown host associations. As the louse list is still far from complete further updates to the Hungarian louse fauna are expected, contributing to the understanding of parasite biogeography.

2.3.1. Louse sampling – methods and their limitations

Early phthirapterists simply shot host individuals for sampling. Then, the carcasses were sampled for ectoparasites by visual examination. Since lice tend to emerge from the plumage or pelage of the cooling carcasses there was no need to treat them with fumigants (Fig.1). With some experience, visual examination and sampling with a forceps can be quite effective; however, this method cannot be standardized, hence produces qualitative data optimal for faunistical and taxonomical purposes but relatively poor for quantitative ecological studies. Another problem is the potential cross-contamination of samples if the carcasses are not separated into different bags prior to sampling. Isolating host carcasses from each other is particularly important when different host species are collected in the same time and location; inadequate handling of the carcasses destroys their scientific value from a parasitological point of view, and in a worse case it may lead to misinterpreting host specificity (Price at al. 2003).

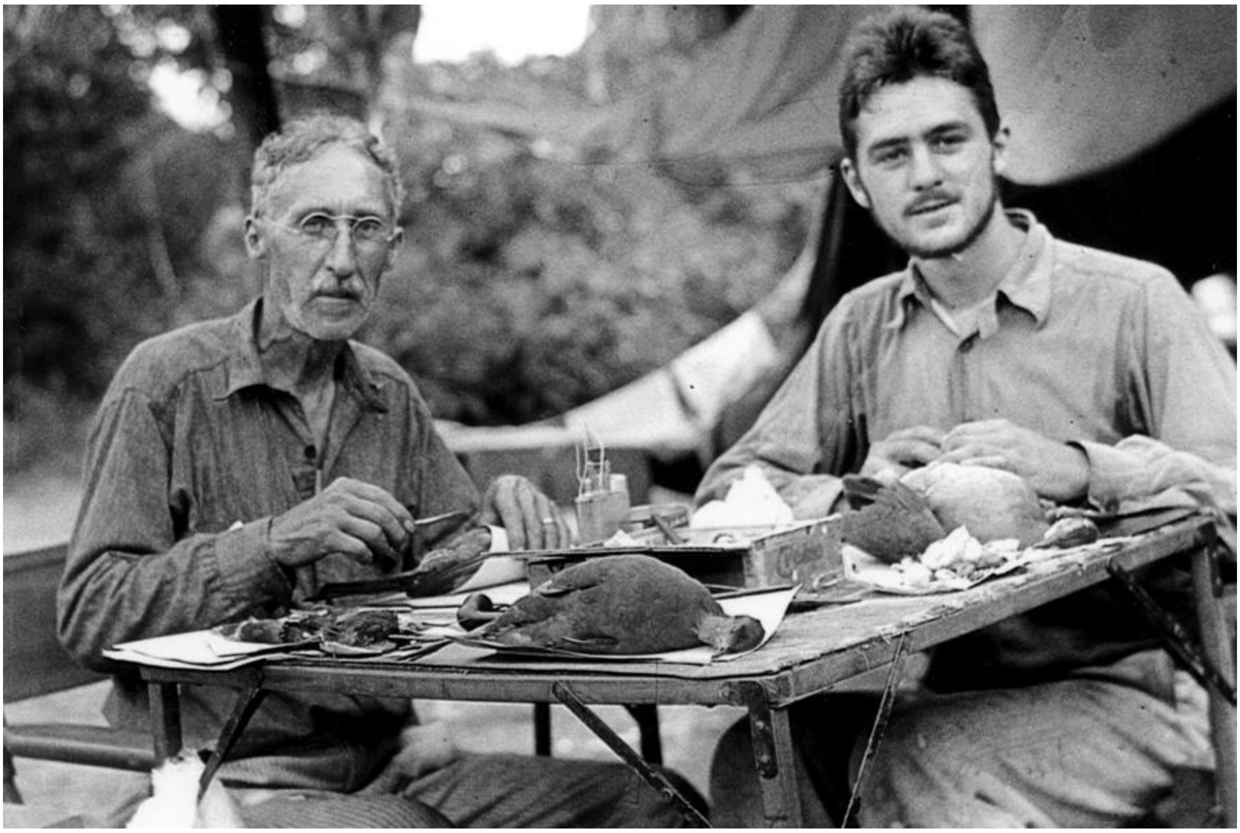

Fig. 1. Meb and Melbourne Carriker, sampling tinamous in Bolivia (1934). Photo from vsmith.info, copyright expired.

At the present time, nature conservation does not allow shooting of hosts in quantities for ectoparasite sampling (except for a few game species). Even the capture of living birds or mammals is strictly prohibited for most citizens. Under such regulations, bird ringing stations offer the most evident possibilities to sample avian ectoparasites. Consequently, ectoparasite sampling from wild birds became bounded with bird ringing activities in several countries all over the World. Bird ringing stations work with the appropriate licenses issued by the relevant conservation authorities and offer excellent conditions for louse sampling as a huge number of birds belonging to several different species are caught there in standardized ways. The handling of birds is also standardized to obtain comparable data on the age, sex, condition and body size measures of birds. Not surprisingly, faunistical data gathered in the last few decades were mostly obtained in parallel with bird ringing.

Another advantage of ectoparasite sampling parallel with ringing is that – as the majority of the investigated bird species (e.g. Barn Swallows) do not moult remiges and rectrices during spring and summer (Svensson 1992), although some irregularities rarely occur (Vas and Fuisz 2010a) –, the observation of the chewing traces on the feathers of captured and recaptured birds may reveal the dynamics of the activity of lice.

The potential cross-contamination has to be also considered in this method, as birds are routinely stored in textile bags before ringing. These bags must hold the birds individually, and be sterilized after each specimen to avoid cross-contamination. However, this latter criterium is hardly ever met in the usual everyday practice of bird ringing stations.

The most common way – and the method that I used – of ectoparasite sampling from living host individuals is treating the feathers with insecticide fumigant or dust that is not harmful for the birds, then collecting the ectoparasites falling out for a standard time period (usually 5 or 10 minutes) from a white tray under the bird (Rózsa 2003). This method is cheap, effective, and easy to standardize. However, only one bird can be sampled simultaneously by one person.

Routinely, ectoparasite sampling is carried out after the ringer has already completed his ringing and measuring procedures. Thus handling of the birds (disengaging them from the net, storing in bags, ringing, measuring, etc.) before the sampling of ectoparasites is quite extensive, posing the possibility of louse losses due to handling before sampling. This assumption was supported by my own field experiences; e.g. I found lice on the ringer’s table or even on his hand. This prompt the question whether there is a significant louse loss caused by handling the birds during the ringing procedure. If yes, the consequences are potentially serious both from a parasitological viewpoint (i.e. biased data in the literature) and from an ecological point of view. By unwittingly removing some of the parasites we may improve the fitness of ringed birds as compared to non-ringed ones. Though this presumed effect may seem to be extremely mild, it may affect millions of birds annually. The next chapter tests for the existence of this effect.

2.3.2. Case study (as published in Acta Ornithologica 45(2): 203-207., 2010.):

Ringing procedure can reduce louse burdens on Barn Swallows *Hirundo rustica*

authors: *Zoltán Vas, Tibor I. Fuisz*

Introduction

Bird ringing is a more than 100 years old method in ornithology. It was originally developed for studying bird migration; however it can be used – especially if combined with color-banding – in other ornithological investigations as well. Bird ringing is applied in population biology, behavioral studies, breeding biology, conservation biology, faunistical studies and even in avian parasitology. Thanks to the co-operation of international organizations (e.g. EURING) the procedures including capture methods, handling of birds and the taking of measurements are standardized and used almost in the same way by every ringer (Svensson 1992). Strict rules are implemented to avoid negative effects on birds caused by catching and ringing. Hereafter the term 'ringing' means the whole ringing procedure from catching with mist nets until releasing.

Birds act as habitat islands for other animals, such as ectoparasitic lice (Insecta: Phthiraptera: Amblycera, Ischnocera). Lice are the most widespread ectoparasites of birds, and the only parasitic insects that complete their entire life cycle on the body surface of birds (Clayton and Tompkins 1994, 1995). Ischnoceran lice (Phthiraptera: Ischnocera) live and feed on feathers, while Amblyceran lice (Phthiraptera: Amblycera) partly feed on feathers and partly also on living tissues (Johnson and Clayton 2003, Rózsa 2003, Mey et al. 2007). A number of influential papers showed that lice affect both life expectancy and reproductive success of hosts (Clayton 1990, Booth et al. 1993, Brown et al. 1995, Clayton et al. 1999, Kose and Møller 1999, Kose et al. 1999, Barbosa et al. 2002). In this paper we test whether ringing procedures reduce louse burdens.

We assumed that catching birds with mist nets, handling and taking measurements can reduce louse burdens on birds, because lice have to cope with unusual mechanical effects and they can fall off the feathers. If this is a remarkable louse loss, it may influence certain aspects of host life history. Furthermore, this phenomenon can have a serious outcome in louse biology. Nowadays, the most evident chance to handle wild birds to collect their lice is offered by ringing sites. When a bird is caught, first a ring is placed on it, then biometrical measurements are taken and its body condition is assessed (Svensson 1992). During this process the feathers are blown apart to view the fat reserves, the brood patch, additionally feathers are spread out on the wings to score moult and to check emarginations and notches. Consequently, ectoparasites living on feathers might be affected. These procedures are usually carried out prior to parasitological sampling. If the ectoparasites fall off the feathers, it may lead to underestimation of lousiness measures.

Møller (1991) described characteristic feather holes found on the rectrices and remiges of the Barn Swallow *Hirundo rustica*. He found that hole counts are highly repeatable, and also showed a positive correlation between the number of holes and the intensity of louse infestation. Hence he suggested that these holes are feeding traces of lice. In some small passerines, including the Barn Swallow, *Brueelia* Kéler, 1936 lice are likely to be causative agents of feather holes (Vas et al. 2008). They also showed that the number of holes increases on the remiges and rectrices of both male and female adult Barn Swallows in the breeding season. As Barn Swallows do not moult remiges and rectrices during spring and summer (Svensson 1992), the observed increase of hole counts can be attributed to the activity of lice. Hereafter we also use hole counts to quantify lousiness in Barn Swallows.

In this paper we compare two experimental groups – one subjected to a standard ringing procedure and another to a reduced ringing procedure (both in terms of handling and measurements taken) – to assess the effect of handling on the number of feather holes of recaptured birds.

Materials and methods

Our study was carried out in a Barn Swallow breeding colony at a cattle farm in Világospuszta (Fejér County, Hungary) in 2009-2010. The birds were caught with mist nets in the stables. All swallows were immediately picked from mist nets and stored in linen bags for a maximum of 15 minutes. We stored each bird separately in sterilized bags to avoid louse transmission. All birds were marked with aluminium rings and sexed by tail length and presence of brood patch (Svensson 1992).

On first capture (30-31 May 2009, 29-30 May 2010) we randomly assigned all adult birds either into the standard or to the reduced ringing procedure group.

Standard ringing procedures included ringing, measuring 3rd primary length, wing length, tail length (all on the left side of the bird) and tail fork length as suggested by Svensson (1992).

Abdominal plumage was blown apart to check subcutan fat and the condition of flying muscles. Moult and abrasion of remiges were also scored. We quantified feather holes on remiges of both wings and on rectrices. We counted the holes on each primaries (18 feathers), secondaries (12 feathers) and tertials (6 feathers) and on each tail feathers (12 feathers). In the analyses each bird was represented by the sum of the holes counted on its tail feathers.

Reduced ringing procedures consisted of marking the bird with an aluminium ring and counting the feather holes on the rectrices only. Feather holes can be counted faster and more reliably on rectrices than on remiges (Z. Vas own data) thus we could collect valuable data on lousiness within a shorter handling period.

On recapture (7-8 July 2009, 2-3 July 2010) feather holes were recounted. The counter was the same person (Z. Vas) on both occasion, however, at the 2nd count he did not know which group the birds were assigned to previously to avoid observer bias.

Hole counts were compared by t-tests. According to quantile-comparsion plots the assumptions of t-test were satisfied. Potential confounders were checked by Kendall’s tau correlation coefficient, because this method treats every concordant and discordant data point with the same weight (Reiczigel et al. 2007). Statistical analyses were carried out with R 2.10.1 (R Development Core Team 2009). Fig. 1 was drawn with Statistica (Statsoft 2009).

Results

We counted the feather holes on the rectrices of captured (n = 60 in 2009 and n = 27 in 2010) and recaptured Barn Swallows (n = 19 in 2009 and n = 15 in 2010). As the there was no significant year effect in the increase of feather holes between capture and recapture (2009: n = 19, mean = 2.3, SD = 1.5; 2010: n = 15, mean = 3.5, SD = 3.0; Welch two sample t-test, two-tailed p = 0.1702), we pooled the data of the two years in further analyses. Individuals included in the experiment in 2009 were excluded from the experiment in 2010. The number of holes increased on rectrices in both groups during the observation period (standard ringing procedure: n = 16; hole numbers at 1st count: mean = 15.5, SD = 12.4; hole numbers at 2nd count: mean = 17.2, SD = 13.0; paired t-test, two-tailed p = 0.0001; reduced ringing procedure: n = 18; hole numbers at 1st count: mean = 12.9, SD = 8.3; hole numbers at 2nd count: mean = 16.8, SD = 9.5; paired t-test, two-tailed p < 0.0001).

We compared the differences in the increase of hole numbers on rectrices during the observation period between the two experimental groups, and we found a significant difference (standard ringing procedure: n = 16; reduced ringing procedure: n = 18; Welch two sample t-test, two-tailed p = 0.0040, Fig. 1).

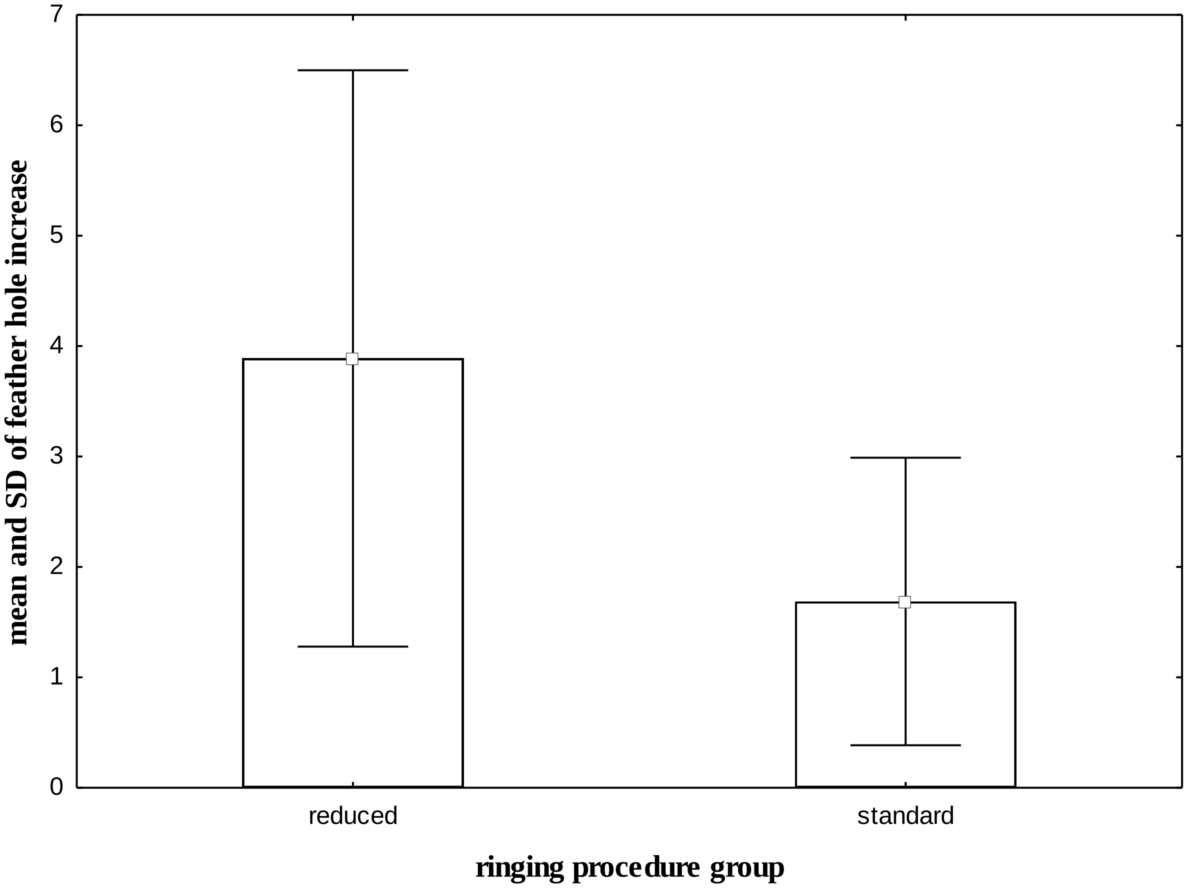

Fig. 1. Feather hole increase in the two experimental groups between capture and recapture

The lengths of tail feathers varied from 89 mm to 125 mm in our sample. We checked whether tail length differences affect our result (e.g. on longer feathers more holes could be found). In addition, according to Svensson (1992) males have longer outermost tail feathers than females (in our sample: males: n = 13, mean = 111.8, SD = 8.5; females: n = 9, mean = 97.1, SD = 5.8; Welch two sample t-test, two-tailed p < 0.0001), therefore we could check the effect of sex by including the outermost tail feather length in the analysis. We found no significant correlation between tail length and the increase of hole numbers (n = 22, Kendall’s tau = -0.1694, p = 0.3057). We also repeated this analysis by excluding all females because the outermost tail feather length in males act as a sexually selected signal indicating higher parasite resistance (Møller 1991). However, no significant correlation was found (n = 13, Kendall’s tau = 0.0857, p = 0.7037). Thus we conclude that tail length and sex did not affect our results.

Discussion

The significant difference in the increase of feather holes in the two experimental groups suggests that ringing (catching, taking measurements and estimating body condition) can cause a measurable louse loss on Barn Swallows. Higher intensity of louse infestations has far-reaching effects on birds. In several species life expectancy of infested birds is lower (Brown et al. 1995, Clayton et al. 1999). Reduced insulation is balanced by higher metabolism rates in feral rock doves *Columba livia* (Booth et al. 1993). In Barn Swallows life history parameters and various individual traits are affected by the presence and intensity of ectoparasites. By chewing feather holes lice may facilitate feather breakage and hence reduce flight capability (Kose and Møller 1999, Barbosa et al. 2002). Pap et al. (2005) showed that female Barn Swallows exhibiting more feather holes are less likely to return next year to their breeding grounds, suggesting that feather holes cause higher mortality during migration, the period characterized by highest mortality in fledged swallows. Birds arriving later in the spring were also characterized by a higher number of feather holes. These birds find pairs later and hence have a reduced chance for producing a second clutch (Kose and Møller 1999, Kose et al. 1999, Møller et al. 2004, Pap et al. 2005). Males having fewer feather holes posses longer tail feathers, a trait strongly preferred by females (Møller 1991). Another sexually selected trait, song is also negatively correlated with the number of feather holes (Garamszegi et al. 2005). Both sexual selection and natural selection favours birds with lower louse burdens, thus researchers through ringing may unconsciously alter the fitness of ringed birds.

Besides effects on the host, bird ringing may also affect population processes of the parasite. The specimens of a louse species inhabiting the same host individual form an infrapopulation. Ringing may act as a stochastic disturbance for louse infrapopulations and may affect transmission chances as well.

As ringing methods are highly standardized, the reduction of louse burdens through ringing can occur not only in *Brueelia* lice of Barn Swallows, but in other bird species and their ectoparasites as well. *Brueelia* spp. are relatively less mobile Ischnoceran lice. In the case of the more mobile Amblyceran lice (Johnson and Clayton 2003) one can presume that ringing influences louse burdens differently. Amblycerans often run from the bird to the hand of the ringer during ringing and measuring (Z. Vas own data). We never observed Iscnocerans doing this, as expected, because Iscnocerans can move only on feathers.

Louse loss due to ringing can have a serious methodological outcome. Most of the lice collected for faunistical studies originate from birds captured for ringing. There are a lot of bird ringing centers, where ringers catch thousands of birds from hundreds of species every year. These camps offer good opportunities for collecting parasitological data. However, as our results suggest, the whole ringing procedure can cause a bias in louse prevalence and intensity of infestation. It may lead to the underestimation of these measures and even an underestimation of parasite species richness. As most phthirapterists collect lice in ringing camps, it may influence results of the louse faunistical literature. Thus it is advisable that birds should be analyzed by phthirapterists before the ringing procedure itself to get more reliable data about louse burden. However, it is possible that birds can get lice from other bird specimens, and maybe from other bird species, if the bird ringers store many bird in the same bag without sterilizing it. This effect can easily be avoided by using sterilized bags and storing only one specimen in a bag.

Several authors have already shown the side-effects of marking techniques on birds (Marion and Shamis 1977, Fuisz 1995, Söhle et al. 2000, Ritchie et al. 2010). However, to our best knowledge, this is the first report to show that bird ringing – the most widespread marking technique – affects ectoparasite infestations. Though our results refer only to Barn Swallows and their *Brueelia* lice, the methods of capture and handling are widespread and highly standardized, so this phenomenon should be tested with other bird species and their lice, including also Amblycerans.

Our study might imply that researchers dealing with feather holes should take into account that ringing and condition measuring of the studied birds might seriously affect their ectoparasite burden. Therefore they are advised to take into account and also publish capture and handling methods. If the phenomenon would prove widespread among other avian and lice taxa, we hypothesize that the widespread use of color ringing as individual identification method in avian behavioral ecology studies might well use birds whose ectoparasite load was considerably affected. Parasitologists also should treat their data carefully, and the description of the collecting method of feather lice should detail the extent of handling of hosts.

2.4.1. Endangered parasites

Conservation biology is mainly focusing on spectacular vertebrates. This phenomenon is partly reasoned by the concept of ‘flagship species’ (Standovár and Primack 2001). This argument claims that protecting these large-bodied vertebrates and their habitats will necessarily protect numerous less spectacular species sharing the same habitat, too. Moreover, these vertebrates have more potential to act as an “icon” for nature conservation. They provoke an emotional response both from the public and politicians. Hence, not surprisingly, the majority of conservation projects are focusing on mammals and birds (Standovár and Primack 2001). This anthropocentric view is also detectable by checking which invertebrates are most commonly protected by law in different European countries: mainly fancy butterflies and beetles. Contrarily, only a relatively few stinging Hymenopterans are protected in spite of their vital role as pollination agents.

Arguably, the worst adjudication is that of parasites. Why should anybody worry about the extinction of parasitic animals? Windsor (1990, 1995) was the first who claimed for “equal rights for parasites”, pointing out that parasites have at least the same biological value as that of free-living animals. An important feature is that parasites exert selective pressure upon their hosts hence facilitating their diversity, and may hold clues about the evolutionary history of their hosts (Rózsa 1992). In a conservational sense, as they are dependent on their hosts, they – or at least their highly host specific species – are more vulnerable than their hosts. Paradoxically, sometimes even the conservation efforts to save the host species may cause the extinction of its specific parasites (see below).

The next chapter is an assessment of the global conservational status of parasitic lice. By combining the known conservational status of the hosts with the published information on the host-specificity of lice I list 6 co-extinct, and 40 (possibly 41) critically co-endangered louse species, and further 2 (but possibly 4) cases of conservation-induced extinction. The purpose of publishing parasite “red lists” is to draw attention to the endangerment of dependent taxa – such as symbionts, parasites and parasitoids – and their biological value.

2.4.2. Case study (as accepted for publication in ORYX):

A list of co-extinct and critically co-endangered species of parasitic lice (Phthiraptera) with remarkable cases of conservation-induced extinction

authors: *Lajos Rózsa, Zoltán Vas*

Gommper and Williams (1998) proposed that a species of Trichodectid lice specific to the black-footed ferret *Mustela nigripes* had gone extinct during the captive-breeding program to save the host. This parasite has become an iconic species often cited in the literature to exemplify the need for parasite conservation. The authors cited Emerson (1964) who suggested that the weasel lice *Neotrichodectes minutus* occurring on this host might represent a “*distinct form*”. However, he also noted that the occurrence of the parasite was based on a single record from 1948 that “*needs confirmation”*. It has never been confirmed subsequently even though lice are easy to collect from stuffed museum specimens. Moreover, even if the lice did occur on the black-footed ferret they did not necessarily represent a separate species. Almost half of the known *Neotrichodectes* species parasitize more than one host species. Actually, there is no reason to believe that the iconic black-footed ferret louse ever existed as a species.

Other erroneous examples have also been used to exemplify the co-extinction of birds and their lice. The louse *Columbicola extinctus* was believed extinct together with its only known host species, the passenger pigeon *Ectopistes migratorius*, until recent genetic analyses showed that the louse was conspecific with those parasitizing an extant species of pigeons (Clayton and Price 1999). Moreover, *Campanulotes defectus* – once also thought to be specific to this host – was shown to be a misidentification of an extant species (Price et al. 2000).

These errors signify the need to develop a reliable taxonomical knowledge about endangered and extinct parasites. Although the co-extinction of host specific 'dependent' taxa (mutualists and parasites) is known to be a major part of the ongoing global wave of extinctions (Stork and Lyal 1993, Koh et al. 2004, Dunn et al. 2009), the magnitude of this threat is often hard to assess. The only 'Red Lists' published for animal parasites are those of ixodid ticks (Durden and Keirans 1996, Mihalca et al. 2011), oestrid flies (Colwell et al. 2009), the helminths of Brazilian vertebrates (Muñiz-Pereira et al. 2009) and New Zealand mites and lice (Buckley et al. 2012). Our purpose is to provide a critical overview of the conservation status of parasitic lice.

We aim to list the louse species that went extinct during conservation efforts to save the host. Furthermore, we provide a list of critically co-endangered or co-extinct species as judged on the basis of known host associations (Durden and Musser 1994b, Price et al. 2003, Mey 2004, 2005, González-Acuña et al. 2007, Stephenson et al. 2008, Mey 2010) combined with the 'extinct', 'extinct in the wild' and 'critically endangered' conservation status of the hosts (IUCN 2011). We do not list lice specific to 'endangered' or 'vulnerable' hosts because of journal space limitations and the markedly reduced threat of conservation-induced extinction in their case.

During the captive-breeding and subsequent release program to save the California condor *Gymnogyps californianus*, the louse *Colpocephalum californici* exclusively specific to this host went extinct probably due to veterinary delousing routines (Dunn 2009).

Similarly, *Rallicola (Aptericola) pilgrimi* probably went extinct when its host, the little spotted kiwi *Apteryx owenii* was translocated to predator-free islands to ensure its survival (Buckley et al. 2012).

We have no information about the fate of *Rallicola (Rallicola) guami*, a louse species known only from Guam rail *Gallirallus owstoni*. Given that this host is extinct in the wild and only captive-bred stocks exist, it seems likely that the parasite might have also been extirpated.

Finally, the status of *Linognathus petasmatus* is unspecified due to uncertainties about its host specificity. It is either specific to the scimitar-horned oryx *Oryx dammah* and likely went extinct due to conservation efforts to save this host in captivity or it may be specific to the addax *Addax nasomaculatus* and has a critically co-endangered status (see below).

The current IUCN Red List (IUCN 2011) names only one critically endangered species of lice and the criteria of selecting this particular species are not known. We considerably expand this list by naming 6 co-extinct and 40 (possibly 41) critically co-endangered species of parasitic lice in Table 1.

There are several reasons why conservationists should care about endangered parasites. They not only constitute a large proportion of global biodiversity but also exert selective pressures to increase host diversity (Rózsa 1992) and thus harboring a unique parasite fauna can increase the conservation value of the host (Pérez and Palma 2001). Furthermore, parasites carry phylogenetic and population genetic information about the evolutionary past of their hosts (Whiteman and Parker 2005, Johnson et al. 2006). Obviously, these justifications are not held for parasites of medical or economic importance.

Naturally, not all parasites are equally important. Some strains may represent arbitrary units that have no conservation value at all. For example, the critically co-endangered gorilla louse *Pthirus gorillae* is of particular value because it is closely related to the human pubic lice *Pthirus pubis* (Reed et al. 2007) thus its potential loss would deprive us from a unique possibility to study the evolution and ecology of an important human pathogen.

In several cases, the IUCN category 'critically endangered' is a clear understatement. Hosts like the Jamaica petrel *Pterodroma caribbaea*, New Caledonian rail *Gallirallus lafresnayanus* and Guadalupe storm-petrel *Oceanodroma macrodactyla* most probably went globally extinct long ago. Consequently, our present list probably underestimates the number of co-extinct or critically co-endangered species. Further sources of uncertainties are the arbitrary nature of the species concept in case of lice (Mey 2003) and the limited information regarding host specificity (Moir et al. 2010, 2011).

Future conservationists should consider preserving also host-specific lice while saving birds or mammals ex-situ. An evident method is to establish in vitro cultures that are relatively easy and cheap to maintain (Saxena and Agarwal 1983). This would open a possibility for a reintroduction of infested hosts. Obviously, the potential costs and benefits of reintroducing infested versus non-infested animals are open for debate.

Table 1. A checklist of louse species specific exclusively to critically endangered or extinct birds or mammals (CE: critically co-endangered, EX: co-extinct, CiE: conservation-induced extinction, * uncertain host idenity)

No.	louse	host species [host family]	status of lice
	Amblycera: Boopidae		
1	*Paraheterodoxus calcaratus* Kéler, 1971	Woylie or brush-tailed bettong *Bettongia penicillata* [Potoroidae]	CE
	Amblycera: Menoponidae		
2	*Austromenopon confine* (Blagoveshtchensky, 1948)	Slender-billed curlew *Numenius tenuirostris* [Scolopacidae]	CE
3	*Austromenopon gregariae*	Sociable lapwing *Vanellus gregarius*	CE

	Timmermann 1954	[Charadriidae]	
4	*Chapinia hoplai* Elbel 1967	Sulu hornbill *Anthracoceros montani* [Bucerotidae]	CE
5	*Colpocephalum californici* Price & Beer 1963	California condor *Gymnogyps californianus* [Accipitridae]	CiE
6	*Colpocephalum davisoni* Price Beer, 1965	White-shouldered ibis *Pseudibis davisoni* [Threskiornithidae]	CE
7	*Colpocephalum eremitae* Price & Beer, 1965	Northern bald ibis *Geronticus eremita* [Threskiornithidae]	CE
8	*Colpocephalum satellitum* (Eichler & Złotorzicka, 1963)	White-rumped vulture *Gyps bengalensis* [Accipitridae]	CE
9	*Franciscoloa (Franciscoloa) thompsoni* Price & Beer, 1966	Philippine cockatoo *Cacatua haematuropygia* [Cacatuidae]	CE
10	*Longimenopon dominicanum* (Kellogg & Mann, 1912)	Guadalupe storm-petrel *Oceanodroma macrodactyla* [Hydrobatidae]	CE
11	*Menacanthus annuliventer* Hopkins 1950	Blue-billed curassow *Crax alberti* [Cracidae]	CE
12	*Myrsidea bakeri* Carriker, 1949	Mariana crow *Corvus kubaryi* [Corvidae]	CE
13	*Myrsidea teraokai* Uchida, 1918	Pohnpei starling *Aplonis pelzelni* [Sturnidae]	CE
14	*Plegadiphilus geronticus* Ledger, 1971	Northern bald ibis *Geronticus eremita* [Threskiornithidae]	CE
15	*Psittacobrosus bechsteini* Mey, 2005	Cuban red macaw *Ara tricolor* [Psittacidae]	EX
	Amblycera: Trimenoponidae		
16	*Philandesia chinchillae* (Werneck, 1935)	Long-tailed chinchilla *Chinchilla lanigera* [Chinchillidae]	CE
17	*Philandesia mazzai* (Werneck,	Long-tailed chinchilla *Chinchilla*	CE

	1933)	*lanigera* [Chinchillidae]	
	Ischnocera: Philopteridae		
18	*Acutifrons caracarensis* (Kellogg & Mann, 1912)	Guadalupe caracara *Caracara lutosa* [Falconidae]	EX
19	*Ardeicola burmanus* Hajela & Tandan, 1970	White-shouldered ibis *Pseudibis davisoni* [Threskiornithidae]	CE
20	*Ardeicola exilis* (Neumann, 1913)	Northern bald ibis *Geronticus eremita* [Threskiornithidae]	CE
21	*Chelopistes craxae* (Carriker, 1945)	Blue-billed curassow *Crax alberti* [Cracidae]	CE
22	*Coloceras hemiphagae* (Tenderio, 1972)	Norfolk Island pigeon *Hemiphaga novaeseelandiae spadicea* [Columbidae]	EX
23	*Coloceras restinctus* (Tenderio, 1972)	Norfolk Island pigeon *Hemiphaga novaeseelandiae spadicea* [Columbidae]	EX
24	*Craspedorrhynchus intermedius* (Piaget, 1880)	Madagascar fish-eagle *Haliaeetus vociferoides* [Accipitridae]	CE
25	*Cummingsiella breviclypeata* Blagoveshtchensky, 1948	Slender-billed curlew *Numenius tenuirostris* [Scolopacidae]	CE
26	*Docophoroides levequei* Timmermann, 1963	Waved albatross *Phoebastria irrorata* [Diomedeidae]	CE
27	*Falcolipeurus hopkinsi* Tandan, 1952	Red-headed vulture *Sarcogyps calvus* [Accipitridae]	CE
28	*Falcolipeurus longiphallus* Złotorzicka, 1963	White-rumped vulture *Gyps bengalensis* [Accipitridae]	CE
29	*Ibidoecus vicinus* (Neumann, 1922)	Northern bald ibis *Geronticus eremita* [Threskiornithidae]	CE
30	*Neopsittaconirmus capreolus* (Gervais 1844)	Yellow-crested cockatoo *Cacatua sulphurea* [Cacatuidae]	CE

31	*Neopsittaconirmus emersoni* Guimarães, 1974	Philippine cockatoo *Cacatua haematuropygia* [Cacatuidae]	CE
32	*Oxylipeurus craxae* Carriker 1944	Blue-billed curassow *Crax alberti* [Cracidae]	CE
33	*Perineus oblongus* Kéler, 1957	Waved albatross *Phoebastria irrorata* [Diomedeidae]	CE
34	*Philopteroides xenicus* Mey, 2004	Bushwren *Xenicus longipes* [Acanthisittidae]	EX
35	*Philopterus acrocephalus* Carriker, 1949	Nightingale reed-warbler *Acrocephalus luscinius* [Acrocephalidae]	CE
36	*Psittoecus hoogstraali* Guimarães, 1974	Philippine cockatoo *Cacatua haematuropygia* [Cacatuidae]	CE
37	*Rallicola (Aptericola) pilgrimi* Clay, 1972	Little spotted kiwi *Apteryx owenii* [Apterygidae]	CiE
38	*Rallicola (Huiacola) extinctus* (Mey, 1990)	Huia *Heteralocha acutirostris* [Callaeidae]	EX
39	*Rallicola (Rallicola) guami* Carriker, 1949	Guam rail *Gallirallus owstoni* [Rallidae]	CiE (?)
40	*Rallicola (Rallicola) insulana* (Carriker, 1949)	Mariana crow *Corvus kubaryi* [Corvidae]	CE
41	*Rallicola (Rallicola) piageti* Clay, 1953	New Caledonian rail *Gallirallus lafresnayanus* [Rallidae]	CE
42	*Saemundssonia (Saemundssonia) fusca* (Giebel, 1874)	Siberian crane *Grus leucogeranus* [Gruidae]	CE
43	*Sturnidoecus stresemanni* Mey, 1989	Bali starling *Leucopsar rothschildi* [Sturnidae]	CE
	Ischnocera: Trichodectidae		
44	*Felicola (Lorisicola) isidoroi*	Iberian lynx *Lynx pardinus* [Felidae]	CE

	Pérez & Palma, 2001		
45	*Tricholipeurus pakenhami* Werneck, 1947	Aders' duiker *Cephalophus adersi* [Bovidae]	CE
	Anoplura: Echinophthiriidae		
46	*Lepidophthirus piriformis* Blagoveshtchensky, 1966	Mediterranean monk seal *Monachus monachus* [Phocidae]	CE
	Anoplura: Haematopinidae		
47	*Hematopinus oliveri* Mishra & Singh, 1978	Pygmy hog *Porcula salvania* [Suidae]	CE
	Anoplura: Linognathidae		
48a	*Linognathus petasmatus* Ferris, 1951	* Addax *Addax nasomaculatus* [Bovidae]	CE (?)
48b	*Linognathus petasmatus* Ferris, 1951	* Scimitar-horned oryx *Oryx dammah* [Bovidae]	CiE (?)
	Anoplura: Pedicinidae		
49	*Pedicinus (Neopedicinus) curtipenitus* Mey, 2010	Grey-shanked douc langur *Pygathrix cinerea* [Cercopithecidae]	CE
	Anoplura: Pthiridae		
50	*Pthirus gorillae* Ewing, 1927	Lowland gorilla *Gorilla gorilla* [Hominidae]	CE

2.5. Conclusions of Chapter 2

The Hungarian louse fauna is far from completely explored; however, it is relatively well described as compared to that of other European countries. The majority of this faunistical work has been carried out by József Rékási and, to a smaller extent, a few other contributors. The compilation of checklists for neglected animal taxa like parasitic lice at a national level typically depends on the presence or absence of one or a few enthusiastic specialists.

In Hungary, faunistical data on lice published before World War II appears to be negligible due to the absence of specialists and also due to the different geographical coverage. After 1945, thanks to the efforts of Rékási, Schäfer, and a few other authors more and more louse species have been detected. Since this information was scattered through marginal journals relatively hard to access, it was necessary to summarize data within a single checklist. For this reason, I critically reviewed the literature by applying standard criteria of record acceptance and updated the nomenclature according to the latest world catalogue (Price at al. 2003).

Our checklist (section 2.2.2., Appendix 1.) includes 279 louse species and subspecies which have been published to occur in Hungary. Their hosts represent 156 bird and 30 mammal species. By studying the material we collected or received in the recent years, I added further 20 species to the Hungarian louse fauna (section 2.2.3., Vas et al. 2012c). Hence, the present status is 299 louse species collected from 170 avian and 30 mammalian hosts. Moreover, the occurrence of further 530 louse species seem to be likely as expected from host distributions (section 2.2.2., Appendix 1, section 2.2.3). Arguably, not all of them will ever occur in Hungary, as a widely distributed bird species often hosts congeneric louse species, each restricted to different and non-overlapping areas of the host distribution (Clay 1964). Anyway, the actual absence of a species that had been expected to occur may also be interesting from a parasitological and biogeographical point of view.

Nevertheless, there are still many unrecorded louse species likely to occur in Hungary. A great advantage of listing the expected species in the checklist is that it helps to draw the attention of future collectors and careful bird ringers to the less explored host species. Arguably, the majority of louse taxa infesting large, attractive, and popular bird species, and lice of host species that can be captured relatively easily have been already recorded in Hungary. The high prevalence and abundance of a louse infestations characteristic to large-bodied host species also facilitate their discovery. On the contrary, several louse species harbored by small passerines such as reed warblers (*Acrocephalus* spp) probably still awaits detection. Their lice are characterized by a low prevalence, hence considerable amounts of host individuals have to be sampled to find these lice. Another problem is that several bird species such as eagles, vultures, swifts, and herons are almost impossible to capture alive after fledging; in these cases there is no reliable way to explore their lice. Though raptors are regularly kept in zoos or bird rehabilitation stations, unfortunately enough, they often share cages with other species; hence cross-contaminations may undermine the reliability of faunistical data obtained from captivity.

As I pointed out in sections 2.3.1-2. (Vas and Fuisz 2010b) a potential louse loss due to the handling of birds during the ringing procedure should also be considered. Optimally, birds should be sampled for ectoparasites as soon as possible after catching, prior to ringing and taking body size measurements. Additionally, the louse loss caused by bird ringing may have a far-reaching effect on ecological studies. Researchers who carry out behavioral ecological studies on wild birds have to consider that simply by catching and marking the birds with rings they may alter their louse burdens, hence – possibly – improve their fitness as compared to non-ringed individuals. Studies focusing on fitness estimations should carefully control for this bias.

The last section (2.4.2., Rózsa and Vas 2013a) lists critically co-endangered and co-extinct louse species, with particular emphasis on parasite species that became extinct due to conservation efforts to save critically endangered hosts. The biological value of parasites and pathogens were discussed above, hence here I intend to mention only some possible consequences of this phenomenon. Conservationists aim to protect the environment of endangered species in order to ensure their survival (Standovár and Primack 2001) often without realizing that endemic (as opposed to introduced or invasive) 'enemies' such as predators, parasites and pathogens constitute an integral part of the endangered species' biotic environment. In very critical situations, such as captive breeding, it is possible that the selective pressure exerted by predators and parasites must be avoided temporarily. However, if the lack of natural enemies becomes permanent (e.g. due to the loss of host-specific parasites), the genetic variability of species reintroduced after successful captive breeding cannot be assured.

Summary

In this thesis I presented a multidisciplinary approach to investigate the host-parasite relationship of lice and their avian (and sometimes mammalian) hosts. I applied both modern statistical methodologies of evolutionary comparative analysis and classical zoological methodologies such as sampling in the field for faunistical purposes.

Here I briefly list the main results of my contribution:

- a positive co-variation was detected between avian cognitive/innovative capabilities and the generic richness of Amblyceran lice;
- avian hosts' switching to brood parasitic way of life was shown to reduce the genera richness and taxonomic distinctness index of both Amblyceran and (to a lesser extent) Ischnoceran lice;
- a positive evolutionary co-variation was found between the diversity measures (species richness, genera richness, and taxonomic distinctness) of cuckoos' Ischnoceran lice and the number of their foster species; this represents the first diversity interaction ever found in a three-level host-parasite system;
- Eichler's assumption that more diverse host groups harbor more diverse parasites was revisited, tested, and judged with modern statistical methodologies covering the global louse fauna; this co-variation represents the strongest predictor of louse diversity recognized so far;
- the Hungarian louse checklist was prepared by critically reviewing the literature;
- 20 louse species were found as new to the Hungarian fauna by identifying the ectoparasite samples collected in the last few years
- bird ringing procedure was shown to reduce avian louse burdens
- a global list of critically co-endangered and co-extinct louse species was provided, with particular emphasis on louse species which became extinct due to conservation efforts focusing on the host.

May I finish my thesis with Douglas Adams's words:

> *"The world is a thing of utter inordinate complexity and richness and strangeness that is absolutely awesome. […] And the opportunity to spend seventy or eighty years of your life in such a universe is time well spent as far as I am concerned."*

Untangling that complexity and richness is a long but fascinating process. And every bit counts, even a lousy bit.

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List of publications

a) published or accepted in peer-reviewed journals with impact factor (2009-2013, related to the present thesis)

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b) published or accepted in peer-reviewed journals without impact factor (2009-2013, related to the present thesis)

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d) conference abstracts (2009-2013, related to the present thesis)

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e) other scientific publications (not closely related to the research topics of the thesis, or published before 2009)

e.1) published in peer-reviewed journals with impact factor

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Appendices

Appendix 1: Lists to 2.2.2 (Vas et al 2012b): A checklist of lice (Insecta: Phthiraptera) of Hungary

CHECKLIST ORDERED BY LICE

Avian lice

Order: PHTHIRAPTERA
Suborder: AMBLYCERA
Family: Laemobothriidae

Laemobothrion *atrum* (NITZSCH, 1818)
Fulica atra LINNAEUS, 1758 * HU: BALÁT (1957)

Laemobothrion biswasi (LAKSHMINARAYANA, 1967)
Porphyrio porphyrio (LINNAEUS, 1758) *

Laemobothrion blagoveshtchenski TENDEIRO, 1963
Porphyrio porphyrio (LINNAEUS, 1758) *

Laemobothrion chloropodis (SCHRANK, 1803)
Gallinula chloropus (LINNAEUS, 1758) *

Laemobothrion maximum (SCOPOLI, 1763)
Buteo buteo (LINNAEUS, 1758) * HU: SCHÄFER (1964, as *L. circi*)
Circus aeruginosus (LINNAEUS, 1758) HU: RÉKÁSI (1990)
Circus cyaneus (LINNAEUS, 1766) HU: RÉKÁSI (1984, as *L. circi*)
Milvus migrans (BODDAERT, 1783) HU: SCHÄFER (1963, as *L. circi*)
Accipiter brevipes (SEVERTZOV, 1850), *Accipiter gentilis* (LINNAEUS, 1758), *Aquila chrysaetos* (LINNAEUS, 1758), *Buteo lagopus* (PONTOPPIDAN, 1763), *Buteo rufinus* (CRETZSCHMAR, 1829), *Circaetus gallicus* (GMELIN, 1788), *Circus pygargus* (LINNAEUS, 1758), *Hieraaetus fasciatus* (VIEILLOT, 1822), *Hieraaetus pennatus* (GMELIN, 1788), *Milvus milvus* (LINNAEUS, 1758), *Pandion haliaetus* (LINNAEUS, 1758), *Pernis apivorus* (LINNAEUS, 1758)

Laemobothrion nocturnum GIEBEL, 1874
Strix aluco LINNAEUS, 1758 *

Laemobothrion simile KELLOGG, 1896
Podiceps nigricollis BREHM, 1831 *

Laemobothrion tinnunculi (LINNAEUS, 1758)
Falco tinnunculus LINNAEUS, 1758 * HU: BALÁT (1957)
Falco columbarius LINNAEUS, 1758, *Falco eleonorae* GENE, 1839, *Falco peregrinus* TUNSTALL, 1771, *Falco subbuteo* LINNAEUS, 1758

Laemobothrion vulturis (Fabricius, 1775)
Aegypius monachus (LINNAEUS, 1766), *Aquila chrysaetos* (LINNAEUS, 1758), *Aquila clanga* PALLAS, 1811, *Aquila heliaca* SAVIGNY, 1809, *Aquila pomarina* BREHM, 1831, *Gyps fulvus* (HABLIZL, 1783), *Haliaeetus albicilla* (LINNAEUS, 1758), *Neophron percnopterus* (LINNAEUS, 1758)

Family: Menoponidae
Actornithophilus *bicolor* (PIAGET, 1880)
Arenaria interpres (LINNAEUS, 1758) *

Actornithophilus canuti PRICE et LEIBOVITZ, 1969
Calidris canutus (LINNAEUS, 1758) *

Actornithophilus flumineus CLAY, 1962
Actitis hypoleucos (LINNAEUS, 1758) *

Actornithophilus gracilis (PIAGET, 1880)
Vanellus vanellus (LINNAEUS, 1758) HU: BALÁT (1957, as *A. svobodai*)

Actornithophilus grandiceps (PIAGET, 1880)
Haematopus ostralegus LINNAEUS, 1758 *

Actornithophilus himantopi BLAGOVESHTCHENSKY, 1951
Himantopus himantopus (LINNAEUS, 1758) *

Actornithophilus hoplopteri (MJÖBERG, 1910)
Charadrius vociferus LINNAEUS, 1758, *Vanellus leucurus* (LICHTENSTEIN, 1823), *Vanellus spinosus* (LINNAEUS, 1758) *

Actornithophilus limosae (KELLOGG, 1908)
Limosa lapponica (LINNAEUS, 1758) *

Actornithophilus lyallpurensis ANSARI, 1955
Tringa ochropus LINNAEUS, 1758 *

Actornithophilus multisetosus BLAGOVESHTCHENSKY, 1940
Lymnocryptes minimus (BRÜNNICH, 1764) * HU: RÉKÁSI (1984)

Actornithophilus nodularis MARTINHO GUIMARÃES, 1988
Charadrius alexandrinus LINNAEUS, 1758 *

Actornithophilus ocellatus (RUDOW, 1869)
Numenius phaeopus (LINNAEUS, 1758) *

Actornithophilus ochraceus (NITZSCH, 1818)
Pluvialis apricaria (LINNAEUS, 1758) * HU: RÉKÁSI (1984)
Pluvialis squatarola (LINNAEUS, 1758) HU: RÉKÁSI (1984, as *A. flavipes*)
Vanellus gregarius (PALLAS, 1771) HU: SCHÄFER (1963)
Charadrius dubius SCOPOLI, 1786, *Charadrius hiaticula* LINNAEUS, 1758, *Charadrius leschenaultii* LESSON, 1826, *Charadrius morinellus* LINNAEUS, 1758, *Pluvialis dominica* (MÜLLER, 1776), *Pluvialis fulva* (GMELIN, 1789)

Actornithophilus paludosus CLAY, 1962
Tringa nebularia (GUNNERUS, 1767) *

Actornithophilus patellatus (PIAGET, 1890)
Numenius arquata (LINNAEUS, 1758) *

Actornithophilus pediculoides (MJÖBERG, 1910)
Arenaria interpres (LINNAEUS, 1758) *

Actornithophilus piceus lari (PACKARD, 1870)
Larus argentatus PONTOPPIDAN, 1763, *Larus canus* (LINNAEUS, 1758), *Larus delawarensis* ORD, 1815, *Larus fuscus* LINNAEUS, 1758, *Larus genei* BRÉME, 1839, *Larus glaucoides* (MEYER, 1822), *Larus hyperboreus* GUNNERUS, 1767, *Larus marinus* LINNAEUS, 1758 *, *Larus minutus* PALLAS, 1776, *Larus pipixcan* WAGLER, 1831, *Larus ridibundus* LINNAEUS, 1766, *Rissa tridactyla* (LINNAEUS, 1758), *Xema sabini* SABINE, 1819

Actornithophilus piceus piceus (DENNY, 1842)
Chlidonias hybrida (PALLAS, 1811), *Chlidonias leucoptera* (TEMMINCK, 1815), *Chlidonias nigra* (LINNAEUS, 1758), *Gelochelidon nilotica* (GMELIN, 1789), *Sterna albifrons* (PALLAS, 1764), *Sterna caspia* PALLAS, 1770, *Sterna hirundo* LINNAEUS, 1758, *Sterna paradisaea* PONTOPPIDAN, 1763, *Sterna sandvicensis* LATHAM, 1787 *

Actornithophilus pustulosus (PIAGET, 1880)
Philomachus pugnax (LINNAEUS, 1758) * HU: RÉKÁSI (1984)

Actornithophilus sedes EICHLER, 1944
Glareola pratincola (LINNAEUS, 1766)

Actornithophilus spinulosus (PIAGET, 1880)
Limosa limosa (LINNAEUS, 1758) *

Actornithophilus stictus (KELLOGG et PAINE, 1911)
Gallinago gallinago (LINNAEUS, 1758) *

Actornithophilus tetralicis CLAY, 1962
Burhinus oedicnemus (LINNAEUS, 1758) *

Actornithophilus totani (SCHRANK, 1803)
Tringa erythropus (PALLAS, 1764) HU: BALÁT (1957, as *A. affinis*)
Tringa glareola LINNAEUS, 1758 HU: RÉKÁSI (1979, as *A. affinis*)
Tringa totanus (LINNAEUS, 1758) * HU: RÉKÁSI (1979)
Tringa flavipes (GMELIN, 1789), *Tringa stagnatilis* (BECHSTEIN, 1803)

Actornithophilus umbrinus (BURMEISTER, 1838)

Calidris canutus (LINNAEUS, 1758) HU: RÉKÁSI (2006)
Calidris ferruginea (PONTOPPIDAN, 1763) * HU: RÉKÁSI (2002)
Calidris alba (PALLAS, 1764), *Calidris alpina* (LINNAEUS, 1758), *Calidris fuscicollis* (VIEILLOT, 1819), *Calidris maritima* (BRÜNNICH, 1764), *Calidris melanotos* (VIEILLOT, 1819), *Calidris minuta* (LEISLER, 1812), *Calidris pusilla* (LINNAEUS, 1766), *Calidris temminckii* (LEISLER, 1812), *Phalaropus fulicarius* (LINNAEUS, 1758), *Phalaropus lobatus* (LINNAEUS, 1758), *Phalaropus tricolor* (VIEILLOT, 1819), *Tryngites subruficollis* (VIEILLOT, 1819)

Actornithophilus uniseriatus (PIAGET, 1880)
Recurvirostra avosetta LINNAEUS, 1758 *

***Amyrsidea** desousai* (KÉLER, 1952)
Numida meleagris (LINNAEUS, 1758) *

Amyrsidea fulvomaculata (DENNY, 1842)
Coturnix coturnix (LINNAEUS, 1758) *

Amyrsidea lagopi (GRUBE, 1851)
Lyrurus tetrix (LINNAEUS, 1758), *Tetrao urogallus* LINNAEUS, 1758

Amyrsidea perdicis (DENNY, 1842)
Phasianus colchicus LINNAEUS, 1758 HU: RÉKÁSI (1984, as *A. megalosoma*)
Perdix perdix (LINNAEUS, 1758) *

***Ardeiphilus** trochioxus* (BURMEISTER, 1838)
Botaurus stellaris (LINNAEUS, 1758) *

Ardeiphilus vittatus (RUDOW, 1866)
Ardeola ralloides (SCOPOLI, 1769) * HU: SCHÄFER (1963, in *Colpocephalum*)

***Austromenopon** aegialitidis* (DURANT, 1906)
Charadrius alexandrinus LINNAEUS, 1758, *Charadrius dubius* SCOPOLI, 1786, *Charadrius hiaticula* LINNAEUS, 1758, *Charadrius leschenaultii* LESSON, 1826, *Charadrius vociferus* LINNAEUS, 1758 *, *Vanellus vanellus* (LINNAEUS, 1758)

Austromenopon alpinum TIMMERMANN, 1954
Calidris alpina (LINNAEUS, 1758) * HU: RÉKÁSI (1984)

Austromenopon atrofulvum (PIAGET, 1880)
Chlidonias hybrida (PALLAS, 1811), *Chlidonias leucoptera* (TEMMINCK, 1815), *Chlidonias nigra* (LINNAEUS, 1758), *Gelochelidon nilotica* (GMELIN, 1789), *Sterna albifrons* (PALLAS, 1764), *Sterna caspia* PALLAS, 1770, *Sterna hirundo* LINNAEUS, 1758, *Sterna paradisaea* PONTOPPIDAN, 1763, *Sterna sandvicensis* LATHAM, 1787

Austromenopon confine (BLAGOVESHTCHENSKY, 1948)
Numenius tenuirostris VIEILLOT, 1817 *

Austromenopon corporosum (KELLOGG et KUWANA, 1901)
Phalaropus fulicarius (LINNAEUS, 1758) *

Austromenopon crocatum (NITZSCH, 1866)
Numenius arquata (LINNAEUS, 1758) * HU: SCHÄFER (1963)

Austromenopon decorosum ZLOTORZYCKA, 1968
Tringa erythropus (PALLAS, 1764), *Tringa totanus* (LINNAEUS, 1758) *

Austromenopon durisetosum (BLAGOVESHTCHENSKY, 1948)
Gallinago gallinago (LINNAEUS, 1758) * HU: RÉKÁSI (1984)
Gallinago media (LATHAM, 1787)

Austromenopon erilis ZLOTORZYCKA, 1968
Calidris maritima (BRÜNNICH, 1764) *

Austromenopon fuscofasciatum (PIAGET, 1880)
Stercorarius parasiticus (LINNAEUS, 1758) HU: SCHÄFER (1964, as *A. circinatum*)
Stercorarius longicaudus VIEILLOT, 1819, *Stercorarius pomarinus* (TEMMINCK, 1815) *

Austromenopon gregariae TIMMERMANN, 1954
Vanellus gregarius (PALLAS, 1771) *

Austromenopon haematopi TIMMERMANN, 1954

Haematopus ostralegus LINNAEUS, 1758 *

Austromenopon himantopi TIMMERMANN, 1954
Himantopus himantopus (LINNAEUS, 1758) *

Austromenopon hystriculum ZLOTORZYCKA, 1968
Actitis hypoleucos (LINNAEUS, 1758) *

Austromenopon icterum (BURMEISTER, 1838)
Scolopax rusticola LINNAEUS, 1758 * HU: RÉKÁSI (1984)

Austromenopon leucurae TIMMERMANN, 1954
Vanellus leucurus (LICHTENSTEIN, 1823) *

Austromenopon limosae TIMMERMANN, 1954
Limosa limosa (LINNAEUS, 1758) *

Austromenopon lutescens (BURMEISTER, 1838)
Calidris canutus (LINNAEUS, 1758) HU: RÉKÁSI (2002)
Philomachus pugnax (LINNAEUS, 1758) * HU: RÉKÁSI (1978*b*)
Arenaria interpres (LINNAEUS, 1758)

Austromenopon meyeri (GIEBEL, 1874)
Limosa lapponica (LINNAEUS, 1758) *

Austromenopon micrandrum (NITZSCH, 1866)
Recurvirostra avosetta LINNAEUS 1758 * HU: RÉKÁSI (1986*b*)

Austromenopon nigropleurum (DENNY, 1842)
Alca torda LINNAEUS, 1758 *, *Fratercula arctica* (LINNAEUS, 1758)

Austromenopon phaeopodis (SCHRANK, 1802)
Numenius phaeopus (LINNAEUS, 1758) *

Austromenopon sohni ANSARI, 1955
Tringa ochropus LINNAEUS, 1758 *

Austromenopon spenceri TIMMERMANN, 1956
Phalaropus lobatus (LINNAEUS, 1758) * HU: RÉKÁSI (2002)

Austromenopon squatarolae TIMMERMANN, 1954
Pluvialis squatarola (LINNAEUS, 1758) * HU: RÉKÁSI (1984)

Austromenopon transversum (DENNY, 1842)
Larus ridibundus LINNAEUS, 1766 HU: RÉKÁSI (1984, as *A. ridibundus*)
Larus argentatus PONTOPPIDAN, 1763, *Larus canus* LINNAEUS, 1758, *Larus delawarensis* ORD, 1815, *Larus fuscus* LINNAEUS, 1758, *Larus glaucoides* (MEYER, 1822), *Larus hyperboreus* GUNNERUS, 1767, *Larus marinus* LINNAEUS, 1758, *Larus minutus* PALLAS, 1776, *Larus pipixcan* WAGLER, 1831, *Rissa tridactyla* (LINNAEUS, 1758) *, *Xema sabini* SABINE, 1819

***Bonomiella** columbae* EMERSON, 1957
Columba livia GMELIN, 1789 * HU: RÓZSA (1990)

Bonomiella concii EICHLER, 1947
Streptopelia decaocto (FRIVALDSZKY, 1838) *

***Ciconiphilus** cygni* PRICE et BEER, 1965
Bucephala clangula (LINNAEUS, 1758), *Cygnus columbianus* (Ord), *Cygnus cygnus* (LINNAEUS, 1758) *, *Cygnus olor* (Gmelin, 1789)

Ciconiphilus decimfasciatus (BOISDUVAL et LACORDAIRE, 1835)
Ardeola ralloides (SCOPOLI, 1769) HU: SCHÄFER (1964, in *Colpocephalum*)
Nycticorax nycticorax (LINNAEUS, 1758) HU: RÉKÁSI (1973)
Ardea alba (LINNAEUS, 1758), *Ardea cinerea* LINNAEUS, 1758 *, *Ardea purpurea* LINNAEUS, 1766, *Bubulcus ibis* (LINNAEUS, 1758), *Egretta garzetta* (LINNAEUS, 1766)

Ciconiphilus pectiniventris (HARRISON, 1916)
Anser albifrons (SCOPOLI, 1769), *Anser anser* (LINNAEUS, 1758) *, *Anser brachyrhynchus* BAILLON, 1834, *Anser caerulescens* (LINNAEUS, 1758), *Anser domesticus* (LINNAEUS, 1758), *Anser fabalis* (LATHAM, 1787), *Anser indicus* (LATHAM, 1790)

Ciconiphilus quadripustulatus (BURMEISTER, 1838)

Ciconia ciconia (LINNAEUS, 1758) * HU: RÉKÁSI (1984)
Ciconia nigra (LINNAEUS, 1758) HU: SCHÄFER (1963, in *Colpocephalum*)

***Clayia** theresae* HOPKINS, 1941

Numida meleagris (LINNAEUS, 1758) *

***Colpocephalum** apivorus* TENDEIRO, 1958

Pernis apivorus (LINNAEUS, 1758) * HU: RÉKÁSI (1984)

Colpocephalum brachysomum KELLOGG et CHAPMAN, 1902

Asio flammeus (PONTOPPIDAN, 1763) *

Colpocephalum ecaudati PRICE et BEER, 1963

Milvus migrans (BODDAERT, 1783)

Colpocephalum eucarenum BURMEISTER, 1838

Pelecanus onocrotalus LINNAEUS, 1758 *

Colpocephalum falconii CARRIKER, 1963

Falco peregrinus TUNSTALL, 1771 *

Colpocephalum flavescens (DE HAAN, 1829)

Haliaeetus albicilla (LINNAEUS, 1758) * HU: SCHÄFER (1963)
Aquila chrysaetos (LINNAEUS, 1758)

Colpocephalum fregili DENNY, 1842

Corvus corone cornix LINNAEUS, 1758 HU: RÉKÁSI (1984, as *C. subaequale*)
Corvus frugilegus LINNAEUS, 1758 HU: SCHÄFER (1963, as *C. subaequale*)
Corvus corax LINNAEUS, 1758, *Pyrrhocorax graculus* (LINNAEUS, 1766), *Pyrrhocorax pyrrhocorax* (LINNAEUS, 1758) *

Colpocephalum gallinulae UCHIDA, 1926

Gallinula chloropus (LINNAEUS, 1758) *

Colpocephalum germanum (EICHLER et ZLOTORZYCKA, 1971)

Accipiter nisus (LINNAEUS, 1758) *

Colpocephalum gypsi (EICHLER et ZLOTORZYCKA, 1971)
Gyps fulvus (Hablizl, 1783) *

Colpocephalum heterosoma PIAGET, 1880
Phoenicopterus ruber LINNAEUS 1758 *

Colpocephalum impressum RUDOW, 1866
Aquila chrysaetos (LINNAEUS, 1758) * HU: RÉKÁSI (2008*a*)
Aquila pomarina Brehm, 1831 HU: RÉKÁSI (2008*a*)

Colpocephalum inaequale BURMEISTER, 1838
Dryocopus martius (LINNAEUS, 1758) * HU: BALÁT (1957)

Colpocephalum leptopygos NITZSCH, 1874
Plegadis falcinellus (LINNAEUS, 1766) * HU: SCHÄFER (1964)

Colpocephalum milvi TENDEIRO, RESTIVO et DEMARTIS, 1979
Hieraaetus pennatus (GMELIN, 1788), *Milvus migrans* (BODDAERT, 1783), *Milvus milvus* (LINNAEUS, 1758) *

Colpocephalum nanum PIAGET, 1890
Accipiter gentilis (LINNAEUS, 1758) HU: RÉKÁSI (2008*a*)
Buteo buteo (LINNAEUS, 1758) HU: RÉKÁSI (1984, as *C. buteonis*)
Accipiter nisus (LINNAEUS, 1758), *Buteo lagopus* (PONTOPPIDAN, 1763)

Colpocephalum napiforme RUDOW, 1869
Pandion haliaetus (LINNAEUS, 1758)

Colpocephalum nigrae PRICE et BEER, 1965
Ciconia nigra (LINNAEUS, 1758) *

Colpocephalum pectinatum OSBORN, 1902
Tyto alba (SCOPOLI, 1769)

Colpocephalum percnopteri PRICE et BEER, 1963
Neophron percnopterus (LINNAEUS, 1758) *

Colpocephalum plataleae PRICE et BEER, 1965
Platalea leucorodia LINNAEUS, 1758 *

Colpocephalum polonum (EICHLER et ZLOTORZYCKA, 1971)
Accipiter gentilis (LINNAEUS, 1758) *

Colpocephalum rosei PRICE et EMERSON, 1974
Phoenicopterus ruber LINNAEUS 1758 *

Colpocephalum salimalii CLAY, 1951
Phoenicopterus ruber LINNAEUS 1758 *

Colpocephalum subzerafae TENDEIRO, 1988
Falco amurensis RADDE, 1863, *Falco columbarius* LINNAEUS, 1758, *Falco naumanni* FLEISCHER, 1818 *, *Falco peregrinus* TUNSTALL, 1771, *Falco tinnunculus* LINNAEUS, 1758, *Falco vespertinus* LINNAEUS, 1766

Colpocephalum tausi (ANSARI, 1951)
Meleagris gallopavo LINNAEUS, 1758

Colpocephalum tirkhan (ANSARI, 1951)
Dendrocopos leucotos (BECHSTEIN, 1802), *Picus canus* GMELIN, 1788

Colpocephalum turbinatum DENNY, 1842
Circus aeruginosus (LINNAEUS, 1758) HU: SCHÄFER (1963)
Columba livia GMELIN, 1789 * HU: RÉKÁSI (1986*a*)
Milvus migrans (BODDAERT, 1783) HU: SCHÄFER (1963, as *C. tricinctum*)
Aegypius monachus (LINNAEUS, 1766), *Buteo buteo* (LINNAEUS, 1758), *Circus cyaneus* (LINNAEUS, 1766), *Gyps fulvus* (HABLIZL, 1783), *Hieraaetus pennatus* (GMELIN, 1788), *Milvus milvus* (LINNAEUS, 1758), *Neophron percnopterus* (LINNAEUS, 1758), *Pandion haliaetus* (LINNAEUS, 1758), *Pernis apivorus* (LINNAEUS, 1758), *Tyto alba* (SCOPOLI, 1769)

Colpocephalum zebra BURMEISTER, 1838
Ciconia ciconia (LINNAEUS, 1758) * HU: SCHÄFER (1963)

Colpocephalum zerafae ANSARI, 1955
Falco peregrinus TUNSTALL, 1771

Comatomenopon *elbeli* EMERSON, 1958
Ardea purpurea LINNAEUS, 1766 *

Comatomenopon elongatum UCHIDA, 1920
Egretta garzetta (LINNAEUS, 1766)

Comatomenopon ibis EMERSON, 1958
Bubulcus ibis (LINNAEUS, 1758) *

Cuculiphilus *fasciatus* (SCOPOLI, 1763)
Cuculus canorus LINNAEUS, 1758 *

Cuculiphilus gypsis (EICHLER, 1944)
Gyps fulvus (HABLIZL, 1783) *

Cuculiphilus snodgrassi (KELLOGG et KUWANA, 1902)
Clamator glandarius (LINNAEUS, 1758), *Cuculus canorus* LINNAEUS, 1758

Dennyus *hirundinis* (LINNAEUS, 1761)
Apus apus (LINNAEUS, 1758) * HU: BALÁT (1957)
Apus pallidus (Shelley, 1870)

Dennyus vonarxi BÜTTIKER, 1954
Tachymarptis melba (LINNAEUS, 1758) *

Eidmanniella *pellucida* (RUDOW, 1869)
Phalacrocorax carbo (LINNAEUS, 1758)

Eucolpocephalum *femorale* (PIAGET, 1880)
Platalea leucorodia LINNAEUS, 1758 * HU: RÉKÁSI (1978*a*)

***Eureum** cimicoides* BURMEISTER, 1838
Apus apus (LINNAEUS, 1758) *

***Gruimenopon** longum* (GIEBEL, 1874)
Grus grus (LINNAEUS, 1758) * HU: RÉKÁSI (1984)

***Heleonomus** elbeli* PRICE, 1970
Anthropoides virgo (LINNAEUS, 1785) *

Heleonomus furgalai PRICE, 1970
Anthropoides virgo (LINNAEUS, 1785)

Heleonomus macilentus (NITZSCH, 1866)
Grus grus (LINNAEUS, 1758) * HU: RÉKÁSI (1984)

***Hohorstiella** gigantea* (DENNY, 1842)
Columba oenas LINNAEUS, 1758 *

Hohorstiella lata (PIAGET, 1880)
Columba livia GMELIN, 1789 * HU: RÓZSA (1990)

Hohorstiella modesta (ANSARI, 1951)
Streptopelia decaocto (FRIVALDSZKY, 1838) *

Hohorstiella streptopeliae EICHLER, 1953
Streptopelia turtur (LINNAEUS, 1758) *

***Holomenopon** acutae* PRICE, 1971
Anas acuta LINNAEUS, 1758 *

Holomenopon bucephalae PRICE 1971
Bucephala albeola (LINNAEUS, 1758) *, *Bucephala clangula* (LINNAEUS, 1758)

Holomenopon cairinae EICHLER, 1943
Cairina moschata (LINNAEUS, 1758) *

Holomenopon clauseni PRICE 1971

Bucephala albeola (LINNAEUS, 1758)

Holomenopon clypeilargum EICHLER, 1943

Anas acuta LINNAEUS, 1758 *, *Anas americana* GMELIN, 1789, *Anas clypeata* LINNAEUS, 1758, *Anas crecca* LINNAEUS, 1758, *Anas penelope* LINNAEUS, 1758, *Anas querquedula* LINNAEUS, 1758, *Anas strepera* LINNAEUS, 1758, *Aythya marila* (LINNAEUS, 1761), *Mergus merganser* LINNAEUS, 1758

Holomenopon leucoxanthum (BURMEISTER, 1838)

Anas crecca LINNAEUS, 1758 * HU: RÉKÁSI (1978*b*)

Anas acuta LINNAEUS, 1758, *Anas americana* GMELIN, 1789, *Anas clypeata* LINNAEUS, 1758, *Anas domesticus* LINNAEUS, 1758, *Anas penelope* LINNAEUS, 1758, *Anas platyrhynchos* LINNAEUS, 1758, *Anas strepera* LINNAEUS, 1758, *Anser anser* (LINNAEUS, 1758), *Anser domesticus* (LINNAEUS, 1758), *Aythya ferina* (LINNAEUS, 1758), *Aythya fuligula* (LINNAEUS, 1758), *Aythya marila* (LINNAEUS, 1761), *Branta canadensis* (LINNAEUS, 1758), *Bucephala albeola* (LINNAEUS, 1758), *Cairina moschata* (LINNAEUS, 1758), *Clangula hyemalis* (LINNAEUS, 1758), *Melanitta nigra* (LINNAEUS, 1758), *Netta rufina* (PALLAS, 1773), *Oxyura jamaicensis* (GMELIN, 1789), *Tadorna tadorna* (LINNAEUS, 1758)

Holomenopon loomisii (KELLOGG, 1896)

Melanitta fusca (LINNAEUS, 1758) *, *Mergus serrator* LINNAEUS, 1758, *Somateria mollissima* (LINNAEUS, 1758), *Somateria spectabilis* (LINNAEUS, 1758)

Holomenopon maxbeieri (EICHLER, 1954)

Anas domesticus LINNAEUS, 1758, *Anas platyrhynchos* LINNAEUS, 1758 *

Holomenopon setigerum (BLAGOVESHTCHENSKY, 1948)

Anas clypeata LINNAEUS, 1758 * HU: RÉKÁSI (1984)

Anas acuta LINNAEUS, 1758, *Anas crecca* LINNAEUS, 1758, *Anas querquedula* LINNAEUS, 1758, *Anas strepera* LINNAEUS, 1758

Holomenopon tadornae (GERVAIS, 1844)

Alopochen aegyptiacus (LINNAEUS, 1766), *Branta bernicla* (LINNAEUS, 1758), *Tadorna ferruginea* (PALLAS, 1764), *Tadorna tadorna* (LINNAEUS, 1758) *

Holomenopon transvaalense (BEDFORD, 1920)
Anas domesticus LINNAEUS, 1758, *Anas platyrhynchos* LINNAEUS, 1758 * HU: RÉKÁSI (1984)

***Kurodaia** cryptostigmata* (NITZSCH, 1861)
Aegolius funereus (LINNAEUS, 1758), *Athene noctua* (SCOPOLI, 1769) *, *Glaucidium passerinum* (LINNAEUS, 1758), *Otus scops* (LINNAEUS, 1758), *Strix aluco* LINNAEUS, 1758

Kurodaia flammei PRICE et BEER, 1963
Asio flammeus (PONTOPPIDAN, 1763)

Kurodaia fulvofasciata (PIAGET, 1880)
Buteo buteo (LINNAEUS, 1758) *, *Buteo lagopus* (PONTOPPIDAN, 1763), *Circaetus gallicus* (GMELIN, 1788), *Circus cyaneus* (LINNAEUS, 1766), *Hieraaetus fasciatus* (VIEILLOT, 1822)

Kurodaia haliaeeti (DENNY, 1842)
Pandion haliaetus (LINNAEUS, 1758) * HU: BALÁT (1957)

Kurodaia longipes (GIEBEL, 1874)
Bubo bubo (LINNAEUS, 1758) * HU: BALÁT (1957)

Kurodaia panjabensis (ANSARI, 1951)
Athene noctua (SCOPOLI, 1769)

Kurodaia platyclypeatum (PIAGET, 1887)
Otus scops (LINNAEUS, 1758), *Strix aluco* LINNAEUS, 1758

Kurodaia subpachygaster (PIAGET, 1880) *
Tyto alba (SCOPOLI, 1769) * HU: SOLT (1998)

***Machaerilaemus** clayae* (BALÁT, 1966)
Riparia riparia (LINNAEUS, 1758) *

Machaerilaemus laticorpus (CARRIKER, 1903)
Emberiza rustica PALLAS, 1776

Machaerilaemus malleus (BURMEISTER, 1838)
Hirundo rustica LINNAEUS, 1758 *

***Menacanthus** abdominalis* (PIAGET, 1880)
Coturnix coturnix (LINNAEUS, 1758) *

Menacanthus affinis FEDORENKO et BELSKAYA, 1977
Oenanthe oenanthe (LINNAEUS, 1758) *

Menacanthus agilis (NITZSCH, 1866)
Muscicapa striata (PALLAS, 1764), *Phoenicurus ochruros* (GMELIN, 1774) *, *Phoenicurus phoenicurus* (LINNAEUS, 1758), *Phylloscopus collybita* (VIEILLOT, 1817), *Phylloscopus trochilus* (LINNAEUS, 1758)

Menacanthus alaudae (SCHRANK, 1776)
Alauda arvensis LINNAEUS, 1758 * HU: SCHÄFER (1963)
Carduelis cannabina (LINNAEUS, 1758) HU: RÉKÁSI (1984, as *M. cannabinae*)
Galerida cristata (LINNAEUS, 1758) HU: RÉKÁSI (1984)
Carduelis carduelis (LINNAEUS, 1758), *Carduelis flammea* (LINNAEUS, 1758), *Carduelis flavirostris* (LINNAEUS, 1758), *Carpodacus erythrinus* (PALLAS, 1770), *Carpodacus roseus* (PALLAS, 1776), *Emberiza citrinella* LINNAEUS, 1758, *Eremophila alpestris* (LINNAEUS, 1758), *Pinicola enucleator* (LINNAEUS, 1758), *Plectrophenax nivalis* (LINNAEUS, 1758)

Menacanthus camelinus (NITZSCH, 1874)
Lanius collurio LINNAEUS, 1758, *Lanius excubitor* LINNAEUS, 1758 *, *Lanius minor* GMELIN, 1788, *Lanius senator* LINNAEUS, 1758

Menacanthus cornutus (SCHÖMMER, 1913)
Gallus gallus (LINNAEUS, 1758) *

Menacanthus curuccae (SCHRANK, 1776)
Sylvia borin (BODDAERT, 1783) HU: RÉKÁSI (1990, as *M. vistulanus*)

Acrocephalus arundinaceus (LINNAEUS, 1758), *Acrocephalus paludicola* (VIEILLOT, 1817), *Acrocephalus schoenobaenus* (LINNAEUS, 1758), *Acrocephalus scirpaceus* (HERMANN, 1804), *Phylloscopus trochilus* (LINNAEUS, 1758), *Sylvia atricapilla* (LINNAEUS, 1758), *Sylvia communis* LATHAM, 1787, *Sylvia curruca* (LINNAEUS, 1758) *, *Sylvia nisoria* (BECHSTEIN, 1795)

Menacanthus eurysternus (BURMEISTER, 1838)
Corvus corone cornix LINNAEUS, 1758 HU: RÉKÁSI (1984, as *M. cornicis*)
Sturnus vulgaris LINNAEUS, 1758 HU: SCHÄFER (1963, as *M. spiniferus*)
Tichodroma muraria (LINNAEUS, 1766) HU: RÉKÁSI (1995, as *M. tichodromae*)
Calcarius lapponicus (LINNAEUS, 1758), *Carduelis chloris* (LINNAEUS, 1758), *Carduelis flammea* (LINNAEUS, 1758), *Corvus monedula* LINNAEUS, 1758, *Fringilla coelebs* LINNAEUS, 1758, *Garrulus glandarius* (LINNAEUS, 1758), *Lanius collurio* LINNAEUS, 1758, *Panurus biarmicus* (LINNAEUS, 1758), *Passer domesticus* (LINNAEUS, 1758), *Pica pica* (LINNAEUS, 1758) *, *Prunella modularis* (LINNAEUS, 1758), *Pyrrhocorax graculus* (LINNAEUS, 1766), *Pyrrhula pyrrhula* (LINNAEUS, 1758), *Remiz pendulinus* (LINNAEUS, 1758), *Sitta europaea* LINNAEUS, 1758, *Sturnus roseus* (LINNAEUS, 1758), *Turdus merula* LINNAEUS, 1758, *Turdus philomelos* BREHM, 1831, *Turdus pilaris* LINNAEUS, 1758, *Turdus viscivorus* LINNAEUS, 1758

Menacanthus exilis (NITZSCH, 1866)
Oenanthe oenanthe (LINNAEUS, 1758) *

Menacanthus fertilis (NITZSCH, 1866)
Upupa epops LINNAEUS, 1758 *

Menacanthus gonophaeus (BURMEISTER, 1838)
Corvus corax LINNAEUS, 1758 * HU: RÉKÁSI (1984)
Corvus frugilegus LINNAEUS, 1758 HU: RÉKÁSI (1984, as *M. laticeps*)
Corvus monedula LINNAEUS, 1758, *Pyrrhocorax pyrrhocorax* (LINNAEUS, 1758)

Menacanthus merisuoi EICHLER, 1953
Nucifraga caryocatactes (LINNAEUS, 1758) *

Menacanthus nogoma UCHIDA, 1926
Motacilla alba LINNAEUS, 1758

Menacanthus numidae (GIEBEL, 1874)
Numida meleagris (LINNAEUS, 1758) *

Menacanthus obrteli BALÁT, 1981
Locustella luscinioides (SAVI, 1824) *

Menacanthus orioli BLAGOVESHTCHENSKY, 1951
Oriolus oriolus (LINNAEUS, 1758) * HU: RÉKÁSI (2002)

Menacanthus pallidulus (NEUMANN, 1912)
Gallus gallus (LINNAEUS, 1758) *

Menacanthus phasiani (MODRZEJEWSKA et ZLOTORZYCKA, 1977)
Phasianus colchicus LINNAEUS, 1758 *

*Menacanthus pici (*DENNY, 1842)
Dendrocopos major (LINNAEUS, 1758) HU: RÉKÁSI (1984, as *M. dryobates*)
Picus viridis LINNAEUS, 1758 * HU: SCHÄFER (1964)
Picus canus Gmelin, 1788

Menacanthus pusillus (NITZSCH, 1866)
Anthus campestris (LINNAEUS, 1758), *Anthus pratensis* (LINNAEUS, 1758), *Anthus spinoletta* (LINNAEUS, 1758), *Anthus trivialis* (LINNAEUS, 1758), *Motacilla alba* LINNAEUS, 1758 *, *Motacilla flava* LINNAEUS, 1758

Menacanthus sinuatus (BURMEISTER, 1838)
Parus major LINNAEUS, 1758 * HU: RÉKÁSI (1973)
Parus palustris LINNAEUS, 1758 HU: BALÁT (1957)
Parus ater LINNAEUS, 1758, *Parus caeruleus* LINNAEUS, 1758

Menacanthus stramineus (NITZSCH, 1818)
Gallus gallus (LINNAEUS, 1758), *Meleagris gallopavo* LINNAEUS, 1758 *, *Numida meleagris* (LINNAEUS, 1758), *Phasianus colchicus* LINNAEUS, 1758

Menacanthus takayamai UCHIDA, 1926

Cettia cetti (TEMMINCK, 1820), *Phylloscopus fuscatus* (BLYTH, 1842)

Menacanthus tenuifrons BLAGOVESHTCHENSKY, 1940
Troglodytes troglodytes (LINNAEUS, 1758) * HU: RÉKÁSI (1984)

Menopon *deryloi* ZLOTORZYCKA, 1972
Lyrurus tetrix (LINNAEUS, 1758) *

Menopon gallinae (LINNAEUS, 1758)
Gallus gallus (LINNAEUS, 1758) *, *Meleagris gallopavo* LINNAEUS, 1758, *Numida meleagris* (LINNAEUS, 1758)

Menopon pallens CLAY, 1949
Perdix perdix (LINNAEUS, 1758) * HU: BALÁT (1957)

Meromenopon *incisum* (GIEBEL, 1866)
Coracias garrulus LINNAEUS, 1758

Meromenopon meropis CLAY et MEINERTZHAGEN, 1941
Merops apiaster LINNAEUS, 1758 * HU: BALÁT (1957)

Myrsidea *abhorrens* (ZLOTORZYCKA, 1964)
Lanius excubitor LINNAEUS, 1758 *

Myrsidea aegithali BLAGOVESHTCHENSKY, 1940
Aegithalos caudatus (LINNAEUS, 1758) *

Myrsidea anaspila (NITSCH, 1866)
Corvus corax LINNAEUS, 1758 * HU: RÉKÁSI (1984)

Myrsidea anathorax (NITZSCH, 1866)
Corvus monedula LINNAEUS, 1758 * HU: RÉKÁSI (1984)

Myrsidea balati MACHACEK, 1977
Passer montanus (LINNAEUS, 1758) *

Myrsidea brunnea (NITZSCH, 1866)
Nucifraga caryocatactes (LINNAEUS, 1758) *

Myrsidea cornicis (DE GEER, 1778)
Corvus corone cornix LINNAEUS, 1758 * HU: BALÁT (1957)

Myrsidea cucullaris (NITZSCH, 1818)
Sturnus vulgaris LINNAEUS, 1758 * HU: SCHÄFER (1963)

Myrsidea dukhunensis ANSARI, 1951
Motacilla alba LINNAEUS, 1758 *

Myrsidea franciscoloi CONCI, 1942
Cinclus cinclus (LINNAEUS, 1758) *

Myrsidea iliaci EICHLER, 1951
Turdus iliacus LINNAEUS, 1766 *

Myrsidea indivisa (NITZSCH, 1866)
Garrulus glandarius (LINNAEUS, 1758) * HU: RÉKÁSI (1984)

Myrsidea islandica KLOCKENHOFF et SCHIRMERS, 1976
Corvus corax LINNAEUS, 1758 *

Myrsidea isostoma (NITZSCH, 1866)
Corvus frugilegus LINNAEUS, 1758 * HU: RÉKÁSI (1973)

Myrsidea latifrons (CARRIKER et SHULL, 1910)
Riparia riparia (LINNAEUS, 1758) *

Myrsidea lyali KLOCKENHOFF, 1984
Fringilla coelebs LINNAEUS, 1758 *

Myrsidea major (PIAGET, 1880)
Plectrophenax nivalis (LINNAEUS, 1758) *

Myrsidea picae (LINNAEUS, 1758)
Pica pica (LINNAEUS, 1758) * HU: BALÁT & BREUER (1955)

Myrsidea proterva (ZLOTORZYCKA, 1964)
Muscicapa striata (PALLAS, 1764) *

Myrsidea quadrifasciata (PIAGET, 1880)
Passer domesticus (LINNAEUS, 1758) *

Myrsidea quadrimaculata (CARRIKER, 1902)
Loxia curvirostra LINNAEUS, 1758 *

Myrsidea rustica (GIEBEL, 1874)
Hirundo rustica LINNAEUS, 1758 * HU: RÉKÁSI (1990)

Myrsidea serini (SÉGUY, 1944)
Carduelis carduelis (LINNAEUS, 1758), *Carduelis chloris* (LINNAEUS, 1758), *Emberiza citrinella* LINNAEUS, 1758, *Serinus serinus* (LINNAEUS, 1766) *

Myrsidea subcoracis KLOCKENHOFF et SCHIRMERS, 1976
Corvus corax LINNAEUS, 1758 *

Myrsidea sylviae SYCHRA et LITERÁK, 2008
Sylvia atricapilla (LINNAEUS, 1758) *

Myrsidea thoracica (GIEBEL, 1874)
Turdus viscivorus LINNAEUS, 1758 * HU: RÉKÁSI (1984)
Turdus merula LINNAEUS, 1758

Myrsidea tibetana KLOCKENHOFF et SCHIRMERS, 1976
Corvus corax LINNAEUS, 1758 *

Myrsidea troglodyti (DENNY, 1842)
Troglodytes troglodytes (LINNAEUS, 1758) *

Myrsidea vinlandica KLOCKENHOFF et SCHIRMERS, 1976

Corvus corax LINNAEUS, 1758 *

Nosopon *clayae* PRICE et BEER, 1963
Pernis apivorus (LINNAEUS, 1758) *

Nosopon lucidum (RUDOW, 1869)
Falco vespertinus LINNAEUS, 1766 * HU: RÉKÁSI (1984)
Accipiter gentilis (LINNAEUS, 1758), *Accipiter nisus* (LINNAEUS, 1758), *Circus aeruginosus* (LINNAEUS, 1758), *Circus cyaneus* (LINNAEUS, 1766), *Circus pygargus* (LINNAEUS, 1758), *Falco columbarius* LINNAEUS, 1758, *Falco peregrinus* TUNSTALL, 1771, *Falco tinnunculus* LINNAEUS, 1758

Nosopon milvus TENDEIRO, 1959
Milvus migrans (BODDAERT, 1783) *

Numidicola *antennatus* (KELLOGG et PAINE, 1911)
Numida meleagris (LINNAEUS, 1758) *

Piagetiella *titan* (PIAGET, 1880)
Pelecanus crispus BRUCH, 1832, *Pelecanus onocrotalus* LINNAEUS, 1758 *

Plegadiphilus *plegadis* (DUBININ, 1938)
Plegadis falcinellus (LINNAEUS, 1766) * HU: SCHÄFER (1964)

Pseudomenopon *concretum* (PIAGET, 1880)
Porphyrio porphyrio (LINNAEUS, 1758) *

Pseudomenopon crecis BECHET, 1963
Crex crex (LINNAEUS, 1758) *

Pseudomenopon dolium (RUDOW, 1869)
Podiceps auritus (LINNAEUS, 1758), *Podiceps cristatus* (LINNAEUS, 1758) *, *Podiceps grisegena* (BODDAERT, 1783), *Podiceps nigricollis* BREHM, 1831, *Tachybaptus ruficollis* (PALLAS, 1764)

Pseudomenopon grebenjukae KASIEV, 1982

Rallus aquaticus LINNAEUS, 1758 *

Pseudomenopon pilosum (SCOPOLI, 1763)
Fulica atra LINNAEUS, 1758 * HU: BALÁT (1957)
Gallinula chloropus (LINNAEUS, 1758)

Pseudomenopon qadrii EICHLER, 1952
Porzana porzana (LINNAEUS, 1766) *

Pseudomenopon scopulacorne (DENNY, 1842)
Rallus aquaticus LINNAEUS, 1758 * HU: RÉKÁSI (1984)
Porzana pusilla (PALLAS, 1776)

Somaphantus *lusius* PAINE, 1914
Numida meleagris (LINNAEUS, 1758) *

Trinoton *alpochen* TENDEIRO, 1960
Alopochen aegyptiacus (LINNAEUS, 1766) *

Trinoton anserinum (FABRICIUS, 1805)
Anser anser (LINNAEUS, 1758) * HU: RÉKÁSI (1978*a*)
Cygnus olor (GMELIN, 1789) HU: RÉKÁSI (2008*a*, as *T. cygni*)
Anser albifrons (SCOPOLI, 1769), *Anser caerulescens* (LINNAEUS, 1758), *Anser domesticus* (LINNAEUS, 1758), *Anser indicus* (LATHAM, 1790), *Branta canadensis* (LINNAEUS, 1758), *Cygnus columbianus* (ORD, 1815), *Cygnus cygnus* (LINNAEUS, 1758)

Trinoton femoratum PIAGET, 1889
Phoenicopterus ruber LINNAEUS 1758 *

Trinoton querquedulae (LINNAEUS, 1758)
Anas crecca LINNAEUS, 1758 * HU: SCHÄFER (1964)
Anas platyrhynchos LINNAEUS, 1758 HU: RÉKÁSI (1973)
Aythya ferina (LINNAEUS, 1758) HU: RÉKÁSI (1979, as *T. nyrocae*)
Bucephala clangula (LINNAEUS, 1758) HU: SCHÄFER (1964)
Anas acuta LINNAEUS, 1758, *Anas americana* GMELIN, 1789, *Anas clypeata* LINNAEUS, 1758, *Anas domesticus* LINNAEUS, 1758, *Anas penelope* LINNAEUS, 1758, *Anas*

querquedula LINNAEUS, 1758, *Anas strepera* LINNAEUS, 1758, *Aythya fuligula* (LINNAEUS, 1758), *Aythya marila* (LINNAEUS, 1761), *Aythya nyroca* (GÜLDENSTADT, 1770), *Bucephala albeola* (LINNAEUS, 1758), *Bucephala islandica* (GMELIN, 1789), *Clangula hyemalis* (LINNAEUS, 1758), *Melanitta fusca* (LINNAEUS, 1758), *Melanitta n*igra (LINNAEUS, 1758), *Mergellus albellus* (LINNAEUS, 1758), *Mergus merganser* LINNAEUS, 1758, *Mergus serrator* LINNAEUS, 1758, *Netta rufina* (PALLAS, 1773), *Oxyura jamaicensis* (GMELIN, 1789), *Polysticta stelleri* (PALLAS, 1769), *Somateria mollissima* (LINNAEUS, 1758), *Somateria spectabilis* (LINNAEUS, 1758)

Family: Ricinidae

***Ricinus** balati* RHEINWALD, 1968
Phylloscopus inornatus (BLYTH, 1842)

Ricinus borin BALÁT, 1952
Sylvia borin (BODDAERT, 1783) *

Ricinus calcarii NELSON, 1972
Calcarius lapponicus (LINNAEUS, 1758)

Ricinus diffusus (KELLOGG, 1896)
Plectrophenax nivalis (LINNAEUS, 1758)

Ricinus dolichocephalus (SCOPOLI, 1763)
Oriolus oriolus (LINNAEUS, 1758) *

Ricinus elongatus (OLFERS, 1816)
Bombycilla garrulus (LINNAEUS, 1758) HU: RÉKÁSI (1984)
Turdus merula LINNAEUS, 1758 HU: BALÁT (1957)
Turdus viscivorus LINNAEUS, 1758 * HU: BALÁT (1957)
Prunella modularis (LINNAEUS, 1758), *Sturnus vulgaris* LINNAEUS, 1758, *Turdus iliacus* LINNAEUS, 1766, *Turdus naumanni* TEMMINCK, 1820, *Turdus philomelos* BREHM, 1831, *Turdus pilaris* LINNAEUS, 1758, *Turdus torquatus* LINNAEUS, 1758

Ricinus frenatus (BURMEISTER, 1838)
Regulus ignicapillus (TEMMINCK, 1820), *Regulus regulus* (LINNAEUS, 1758) *

Ricinus fringillae DE GEER, 1778

Bombycilla garrulus (LINNAEUS, 1758) HU: RÉKÁSI (1978*a*, as *R. bombycillae*)

Emberiza citrinella LINNAEUS, 1758 * HU: BALÁT (1957)

Fringilla coelebs LINNAEUS, 1758 HU: BALÁT (1957, as *R. irascens*)

Anthus pratensis (LINNAEUS, 1758), *Anthus spinoletta* (LINNAEUS, 1758), *Anthus trivialis* (LINNAEUS, 1758), *Carduelis cannabina* (LINNAEUS, 1758), *Carduelis carduelis* (LINNAEUS, 1758), *Carduelis flammea* (LINNAEUS, 1758), *Carduelis flavirostris* (LINNAEUS, 1758), *Emberiza cia* LINNAEUS, 1766, *Emberiza rustica* PALLAS, 1776, *Emberiza schoeniclus* (LINNAEUS, 1758), *Fringilla montifringilla* LINNAEUS, 1758, *Motacilla alba* LINNAEUS, 1758, *Parus ater* LINNAEUS, 1758, *Parus cristatus* LINNAEUS, 1758, *Passer domesticus* (LINNAEUS, 1758), *Passer montanus* (LINNAEUS, 1758), *Plectrophenax nivalis* (LINNAEUS, 1758), *Prunella collaris* (SCOPOLI, 1769), *Pyrrhula pyrrhula* (LINNAEUS, 1758), *Riparia riparia* (LINNAEUS, 1758)

Ricinus major FRESCA, 1924

Emberiza calandra LINNAEUS, 1758 *, *Plectrophenax nivalis* (LINNAEUS, 1758)

Ricinus pflegeri BALÁT, 1952

Ficedula albicollis (Temminck, 1815) *

Ricinus rubeculae (SCHRANK, 1776)

Erithacus rubecula (LINNAEUS, 1758) *, *Luscinia svecica* (LINNAEUS, 1758), *Monticola solitarius* (LINNAEUS, 1758), *Oenanthe deserti* (TEMMINCK, 1825), *Phoenicurus ochruros* (GMELIN, 1774), *Phoenicurus phoenicurus* (LINNAEUS, 1758), *Prunella modularis* (LINNAEUS, 1758)

Ricinus serratus (DURRANT, 1906)

Alauda arvensis LINNAEUS, 1758, *Emberiza cia* LINNAEUS, 1766, *Emberiza melanocephala* SCOPOLI, 1769, *Eremophila alpestris* (LINNAEUS, 1758) *, *Galerida cristata* (LINNAEUS, 1758)

Ricinus thoracicus (PACKARD, 1870)

Plectrophenax nivalis (LINNAEUS, 1758) *

Suborder: ISCHNOCERA

Family: Philopteridae

***Acidoproctus** moschatae* (LINNAEUS, 1758)
Netta rufina (PALLAS, 1773)

Acidoproctus taschenbergi HOPKINS, 1938
Alopochen aegyptiacus (LINNAEUS, 1766) *

***Aegypoecus** brevicollis* (BURMEISTER, 1838)
Aegypius monachus (LINNAEUS, 1766) *

Aegypoecus perspicuus (KELLOGG, 1914)
Neophron percnopterus (LINNAEUS, 1758)

Aegypoecus trigonoceps (GIEBEL, 1874)
Gyps fulvus (HABLIZL, 1783) *

***Alcedoffula** alcedinis* (DENNY, 1842)
Alcedo atthis (LINNAEUS, 1758) * HU: RÉKÁSI (1984)

***Anaticola** angustolimbatus* (GIEBEL, 1866)
Melanitta nigra (LINNAEUS, 1758) *

Anaticola anseris (LINNAEUS, 1758)
Anser albifrons (SCOPOLI, 1769) HU: BALÁT (1957, as *A. serratus*)
Anser anser (LINNAEUS, 1758) * HU: SCHÄFER (1963)
Branta canadensis (LINNAEUS, 1758) HU: SCHÄFER (1963)
Anser brachyrhynchus BAILLON, 1834, *Anser caerulescens* (LINNAEUS, 1758), *Anser domesticus* (LINNAEUS, 1758), *Anser fabalis* (LATHAM, 1787), *Anser indicus* (LATHAM, 1790), *Branta leucopsis* (BECHSTEIN, 1803)

Anaticola asymmetricus (RUDOW, 1869)
Alopochen aegyptiacus (LINNAEUS, 1766) *

Anaticola beieri EICHLER, 1954
Branta ruficollis (PALLAS, 1769) *

Anaticola branderi EICHLER et HACKMAN 1973

Clangula hyemalis (LINNAEUS, 1758) *

Anaticola cairinensis (MONTEIRO DE BARROS, 1933)
Cairina moschata (LINNAEUS, 1758) *

Anaticola candidus (RUDOW, 1869)
Phoenicopterus ruber (LINNAEUS, 1758) *

Anaticola clangulae (FABRICIUS 1780)
Bucephala clangula (LINNAEUS, 1758), *Bucephala islandica* (GMELIN, 1789) *

Anaticola crassicornis (SCOPOLI, 1763)
Anas clypeata LINNAEUS, 1758 HU: RÉKÁSI (1984, as *A. hopkinsi*)
Anas crecca LINNAEUS, 1758 HU: BALÁT (1957, as *A. sordidus*)
Anas platyrhynchos LINNAEUS, 1758 * HU: BALÁT (1957)
Anas querquedula LINNAEUS, 1758 HU: RÉKÁSI (1984, as *A. sordidus*)
Anas strepera LINNAEUS, 1758 HU: BALÁT (1957, as *A. depuratus*)
Anas acuta LINNAEUS, 1758, *Anas americana* GMELIN, 1789, *Anas domesticus* LINNAEUS, 1758, *Anas penelope* LINNAEUS, 1758, *Cygnus cygnus* (LINNAEUS, 1758), *Oxyura jamaicensis* (GMELIN, 1789), *Somateria spectabilis* (LINNAEUS, 1758)

Anaticola klockenhoffi EICHLER et VASJUKOVA, 1980
Polysticta stelleri (PALLAS, 1769) *

Anaticola magnificus ANSARI, 1955
Tadorna ferruginea (PALLAS, 1764) *

Anaticola mergiserrati (DE GEER, 1778)
Aythya nyroca (GÜLDENSTADT, 1770) HU: RÉKÁSI (1984, as *A. fuligulae*)
Somateria mollissima (LINNAEUS, 1758) HU: RÉKÁSI (1998*b*, as *A. rubromaculatus*)
Aythya ferina (LINNAEUS, 1758), *Aythya fuligula* (LINNAEUS, 1758), *Aythya marila* (LINNAEUS, 1761), *Melanitta fusca* (LINNAEUS, 1758), *Mergus merganser* LINNAEUS, 1758, *Mergus serrator* LINNAEUS, 1758 *, *Netta rufina* (PALLAS, 1773)

Anaticola phoenicopteri (COINDE, 1859)
Phoenicopterus ruber (LINNAEUS, 1758) *

Anaticola rheinwaldi EICHLER et VASJUKOVA, 1980
Branta bernicla (LINNAEUS, 1758) *

Anaticola tadornae (DENNY, 1842)
Tadorna tadorna (LINNAEUS, 1758) * HU: RÉKÁSI (1978*a*)

***Anatoecus** cygni* (DENNY, 1842)
Cygnus columbianus (ORD, 1815) *, *Cygnus cygnus* (LINNAEUS, 1758)

Anatoecus dentatus (SCOPOLI, 1763)
Anas clypeata LINNAEUS, 1758 HU: BALÁT (1957, as *A. ferrugineus*)
Anas platyrhynchos LINNAEUS, 1758 * HU: BALÁT (1957)
Aythya fuligula (LINNAEUS, 1758) HU: RÉKÁSI (2002)
Aythya nyroca (GÜLDENSTADT, 1770) HU: RÉKÁSI (1984)
Alopochen aegyptiacus (LINNAEUS, 1766), *Anas acuta* LINNAEUS, 1758, *Anas crecca* LINNAEUS, 1758, *Anas domesticus* LINNAEUS, 1758, *Anas penelope* LINNAEUS, 1758, *Anas querquedula* LINNAEUS, 1758, *Anas strepera* LINNAEUS, 1758, *Anser albifrons* (SCOPOLI, 1769), *Anser anser* (LINNAEUS, 1758), *Anser caerulescens* (LINNAEUS, 1758), *Anser domesticus* (LINNAEUS, 1758), *Anser erythropus* (LINNAEUS, 1758), *Anser fabalis* (LATHAM, 1787), *Aythya ferina* (LINNAEUS, 1758), *Aythya marila* (LINNAEUS, 1761), *Branta bernicla* (LINNAEUS, 1758), *Branta canadensis* (LINNAEUS, 1758), *Branta leucopsis* (BECHSTEIN, 1803), *Bucephala albeola* (LINNAEUS, 1758), *Bucephala clangula* (LINNAEUS, 1758), *Bucephala islandica* (GMELIN, 1789), *Clangula hyemalis* (LINNAEUS, 1758), *Cygnus olor* (GMELIN, 1789), *Melanitta fusca* (LINNAEUS, 1758), *Melanitta nigra* (LINNAEUS, 1758), *Mergellus albellus* (LINNAEUS, 1758), *Mergus merganser* LINNAEUS, 1758, *Mergus serrator* LINNAEUS, 1758, *Netta rufina* (PALLAS, 1773), *Oxyura jamaicensis* (GMELIN, 1789), *Oxyura leucocephala* (SCOPOLI, 1769), *Polysticta stelleri* (PALLAS, 1769), *Somateria mollissima* (LINNAEUS, 1758), *Somateria spectabilis* (LINNAEUS, 1758), *Tadorna tadorna* (LINNAEUS, 1758)

Anatoecus icterodes (NITZSCH, 1818)
Alopochen aegyptiacus (LINNAEUS, 1766)
Anas clypeata LINNAEUS, 1758 HU: RÉKÁSI (1984)
Anas crecca LINNAEUS, 1758 HU: RÉKÁSI (1984)
Anas platyrhynchos LINNAEUS, 1758 * HU: RÉKÁSI (1984)

Anser albifrons (SCOPOLI, 1769) HU: BALÁT (1957, as *A. brunneiceps*)
Anser anser (LINNAEUS, 1758) HU: RÉKÁSI (1984)
Aythya ferina (LINNAEUS, 1758) HU: SCHÄFER (1963)
Bucephala clangula (LINNAEUS, 1758) HU: RÉKÁSI (1978*a*)
Somateria mollissima (LINNAEUS, 1758) HU: RÉKÁSI (1998*b*)
Anas acuta LINNAEUS, 1758, *Anas domesticus* LINNAEUS, 1758, *Anas penelope* LINNAEUS, 1758, *Anas querquedula* LINNAEUS, 1758, *Anas strepera* LINNAEUS, 1758, *Anser caerulescens* (LINNAEUS, 1758), *Anser domesticus* (LINNAEUS, 1758), *Anser erythropus* (LINNAEUS, 1758), *Anser fabalis* (LATHAM, 1787), *Aythya fuligula* (LINNAEUS, 1758), *Aythya marila* (LINNAEUS, 1761), *Aythya nyroca* (GÜLDENSTADT, 1770), *Branta bernicla* (LINNAEUS, 1758), *Branta canadensis* (LINNAEUS, 1758), *Branta leucopsis* (BECHSTEIN, 1803), *Branta ruficollis* (PALLAS, 1769), *Bucephala islandica* (GMELIN, 1789), *Clangula hyemalis* (LINNAEUS, 1758), *Cygnus olor* (GMELIN, 1789), *Melanitta fusca* (LINNAEUS, 1758), *Melanitta nigra* (LINNAEUS, 1758), *Mergellus albellus* (LINNAEUS, 1758), *Mergus merganser* LINNAEUS, 1758, *Mergus serrator* LINNAEUS, 1758 *, *Netta rufina* (PALLAS, 1773), *Oxyura jamaicensis* (GMELIN, 1789), *Oxyura leucocephala* (SCOPOLI, 1769), *Polysticta stelleri* (PALLAS, 1769), *Somateria spectabilis* (LINNAEUS, 1758), *Tadorna tadorna* (LINNAEUS, 1758)

Anatoecus keleri CLAY, 1962
Phoenicopterus ruber (LINNAEUS, 1758) *

Anatoecus penicillatus KÉLER, 1960
Cygnus olor (GMELIN, 1789) *

Anatoecus pygaspis (NITZSCH, 1866)
Phoenicopterus ruber (LINNAEUS, 1758) *

Anatoecus regina ANSARI, 1955
Tadorna ferruginea (PALLAS, 1764) *

Aquanirmus *americanus* (KELLOGG et CHAPMAN, 1899)
Podiceps nigricollis BREHM, 1831 *

Aquanirmus bahli TANDAN, 1951
Tachybaptus ruficollis (PALLAS, 1764) *

Aquanirmus bucomfishi EDWARDS, 1965
Podiceps auritus (LINNAEUS, 1758) *

Aquanirmus colymbinus (SCOPOLI, 1763)
Podiceps auritus (LINNAEUS, 1758) *

Aquanirmus emersoni EDWARDS, 1965
Podiceps grisegena (BODDAERT, 1783) *

Aquanirmus podicepis (DENNY, 1842)
Podiceps cristatus (LINNAEUS, 1758) * HU: RÉKÁSI (1984)

Aquanirmus runcinatus (NITZSCH, 1866)
Tachybaptus ruficollis (PALLAS, 1764) *

Ardeicola *ardeae* (LINNAEUS, 1758)
Ardea cinerea LINNAEUS, 1758 * HU: BALÁT (1957)

Ardeicola ciconiae (LINNAEUS, 1758)
Ciconia ciconia (LINNAEUS, 1758) * HU: RÉKÁSI (1984)

Ardeicola expallidus BLAGOVESHTCHENSKY, 1940
Ardea alba (LINNAEUS, 1758) HU: RÉKÁSI *et al*. (2002, as *A. albulus*)
Bubulcus ibis (LINNAEUS, 1758), *Egretta garzetta* (LINNAEUS, 1766) *

Ardeicola goisagi UCHIDA, 1954
Nycticorax nycticorax (LINNAEUS, 1758) * HU: BALÁT (1957)

Ardeicola leucoproctus (NITZSCH, 1866)
Ardea purpurea LINNAEUS, 1766 * HU: RÉKÁSI (1973)

Ardeicola maculatus (NITZSCH, 1866)
Ciconia nigra (LINNAEUS, 1758) * HU: RÉKÁSI (1979)

Ardeicola plataleae (LINNAEUS, 1758)

Platalea leucorodia LINNAEUS, 1758 * HU: SCHÄFER (1963)

Ardeicola rhaphidius (NITZSCH, 1866)
Plegadis falcinellus (LINNAEUS, 1766) * HU: RÉKÁSI (1978*a*)

Ardeicola stellaris (DENNY, 1842)
Botaurus stellaris (LINNAEUS, 1758) *

***Brueelia** altaica* MEY, 1982
Montifringilla nivalis (LINNAEUS, 1766) *

Brueelia amsel (EICHLER, 1951)
Turdus merula LINNAEUS, 1758 * HU: BALÁT (1957)

Brueelia annae (ZLOTORZYCKA et EICHLER, 1984)
Prunella modularis (LINNAEUS, 1758) *

Brueelia antimarginalis EICHLER, 1951
Turdus pilaris LINNAEUS, 1758 *

Brueelia apiastri (DENNY, 1842)
Merops apiaster LINNAEUS, 1758 * HU: BALÁT (1957)

Brueelia argula (BURMEISTER, 1838)
Corvus corax LINNAEUS, 1758 * HU: RÉKÁSI (1984)

Brueelia atherae ANSARI, 1957
Corvus corax LINNAEUS, 1758 *

Brueelia balati (KRIŠTOFIK, 1999)
Remiz pendulinus (LINNAEUS, 1758) *

Brueelia biguttata (KELLOGG et PAINE, 1914)
Pyrrhocorax graculus (LINNAEUS, 1766) *

Brueelia biocellata (PIAGET, 1880)

Pica pica (LINNAEUS, 1758) * HU: RÉKÁSI (1984)
Corvus corax LINNAEUS, 1758

Brueelia blagovescenskyi BALÁT, 1955
Emberiza schoeniclus (LINNAEUS, 1758) * HU: RÉKÁSI (1984)

Brueelia borini LUNKASCHU, 1970
Sylvia borin (Boddaert, 1783) *

Brueelia brachythorax (GIEBEL, 1874)
Bombycilla garrulus (LINNAEUS, 1758) * HU: SCHÄFER (1963)

Brueelia breueri BALÁT, 1955
Carduelis chloris (LINNAEUS, 1758) * HU: BALÁT (1957)

Brueelia chrysomytris (BLAGOVESHTCHENKY, 1940)
Carduelis spinus (LINNAEUS, 1758) *

Brueelia conocephalus (BLAGOVESHTCHENSKY, 1940)
Sitta europaea LINNAEUS, 1758 *

Brueelia corydalla TIMMERMANN, 1950
Anthus pratensis (LINNAEUS, 1758) * HU: RÉKÁSI (1984)
Anthus spinoletta (LINNAEUS, 1758)

Brueelia cruciata (BURMEISTER, 1838)
Lanius collurio LINNAEUS, 1758 * HU: RÉKÁSI (1984)

Brueelia currucae BECHET, 1961
Sylvia curruca (LINNAEUS, 1758) *

Brueelia cyclothorax (BURMEISTER, 1838)
Passer domesticus (LINNAEUS, 1758) HU: RÉKÁSI (1973)
Passer montanus (LINNAEUS, 1758) * HU: BALÁT (1957)

Brueelia delicata (NITZSCH, 1866)

Emberiza citrinella LINNAEUS, 1758 * HU: BALÁT (1957)
Emberiza leucocephalos GMELIN, 1771, *Emberiza rustica* PALLAS, 1776

Brueelia densilimba (NITZSCH, 1866)
Carduelis carduelis (LINNAEUS, 1758) *

Brueelia docilis ANSARI, 1956
Pyrrhocorax pyrrhocorax (LINNAEUS, 1758) *

Brueelia domestica (KELLOGG et CHAPMAN, 1899)
Hirundo rustica LINNAEUS, 1758 * HU: (VAS *et al*. 2008)

Brueelia exigua (NITZSCH, 1866)
Phoenicurus ochruros (GMELIN, 1774) *

Brueelia ferianci BALÁT, 1955
Anthus trivialis (LINNAEUS, 1758) *

Brueelia fuscopleura (BLAGOVESHTCHENSKY, 1951)
Sturnus roseus (LINNAEUS, 1758) *

Brueelia glandarii (DENNY, 1842)
Garrulus glandarius (LINNAEUS, 1758) * HU: SCHÄFER (1963)

Brueelia glizi BALÁT, 1955
Fringilla montifringilla LINNAEUS, 1758 *

Brueelia gracilis (BURMEISTER, 1838)
Delichon urbica (LINNAEUS, 1758) * HU: BALÁT (1957)

Brueelia gulabitilyar ANSARI, 1955
Sturnus roseus (LINNAEUS, 1758) *

Brueelia haftorni (BALÁT, 1981)
Turdus iliacus LINNAEUS, 1766 *

Brueelia iliaci (DENNY, 1842)
Turdus iliacus LINNAEUS, 1766 *

Brueelia imponderabilica EICHLER, 1954
Lanius excubitor LINNAEUS, 1758 * HU: RÉKÁSI (1984)

Brueelia infrequens (CARRIKER, 1902)
Calcarius lapponicus (LINNAEUS, 1758) *

Brueelia jacobi EICHLER, 1951
Turdus merula LINNAEUS, 1758 *

Brueelia juno (GIEBEL, 1874)
Coccothraustes coccothraustes (LINNAEUS, 1758) * HU: RÉKÁSI (1973)

Brueelia kistiakowskyi FEDORENKO, 1975
Anthus campestris (LINNAEUS, 1758) *

Brueelia kluzi BALÁT, 1955
Fringilla coelebs LINNAEUS, 1758 *

Brueelia kratochvili BALÁT, 1958
Motacilla flava LINNAEUS, 1758 *

Brueelia lais (GIEBEL, 1874)
Luscinia megarhynchos BREHM, 1831 *

Brueelia limbata (BURMEISTER, 1838)
Loxia curvirostra LINNAEUS, 1758 *

Brueelia limpidus (MEY, 1982)
Eremophila alpestris (LINNAEUS, 1758) *

Brueelia locustellae FEDORENKO, 1975
Locustella luscinioides (SAVI, 1824) *

Brueelia lullulae BECHET, 1961
Lullula arborea (LINNAEUS, 1758) *

Brueelia marginata (BURMEISTER, 1838)
Turdus pilaris LINNAEUS, 1758 * HU: BALÁT (1957)
Turdus torquatus LINNAEUS, 1758 HU: RÉKÁSI (1984, as *B. intermedia*)

Brueelia matvejevi BALÁT, 1981
Turdus viscivorus LINNAEUS, 1758 *

Brueelia melanocoryphae BECHET, 1966
Melanocorypha calandra (LINNAEUS, 1766) *

Brueelia merulensis (DENNY, 1842)
Turdus merula LINNAEUS, 1758 * HU: BALÁT (1957)

Brueelia minor LUNKASCHU, 1970
Lanius minor GMELIN, 1788 *

Brueelia modularis (PIAGET, 1880)
Prunella modularis (LINNAEUS, 1758) *

Brueelia mongolica MEY, 1982
Carduelis flavirostris (LINNAEUS, 1758) *

Brueelia multipunctata (CLAY, 1936)
Nucifraga caryocatactes (LINNAEUS, 1758) *

Brueelia munda (NITZSCH, 1866)
Oriolus oriolus (LINNAEUS, 1758) * HU: BALÁT (1957)

Brueelia nebulosa (BURMEISTER, 1838)
Sturnus vulgaris LINNAEUS, 1758 * HU: SCHÄFER (1963)

Brueelia neoatricapillae PRICE, HELLENTHAL et PALMA, 2003
Sylvia atricapilla (LINNAEUS, 1758) *

Brueelia nivalis (GIEBEL, 1874)
Plectrophenax nivalis (LINNAEUS, 1758) *

Brueelia olivacea (BURMEISTER, 1838)
Nucifraga caryocatactes (LINNAEUS, 1758) * HU: RÉKÁSI (1973)

Brueelia oudhensis ANSARI, 1956
Turdus merula LINNAEUS, 1758 *

Brueelia paratricapillae PRICE, HELLENTHAL et PALMA, 2003
Sylvia atricapilla (LINNAEUS, 1758) *

Brueelia parviguttata (BLAGOVESHTCHENSKY, 1940)
Alauda arvensis LINNAEUS, 1758 *

Brueelia pelikani BALÁT, 1958
Emberiza melanocephala SCOPOLI, 1769 *

Brueelia perforata (ZLOTORZYCKA, 1964)
Corvus frugilegus LINNAEUS, 1758 *

Brueelia pyrrhularum EICHLER, 1954
Pyrrhula pyrrhula (LINNAEUS, 1758) * HU: RÉKÁSI (1984)

Brueelia rosickyi BALÁT, 1955
Sylvia nisoria (BECHSTEIN, 1795) *

Brueelia sexytanum (SOLER CRUZ, BENITEZ RODRÍGUEZ, FLORIDO NAVIO et MUÑOZ PARRA, 1987)
Serinus serinus (LINNAEUS, 1766) *

Brueelia sibrica MEY, 1982
Carduelis flammea (LINNAEUS, 1758) *

Brueelia stadleri EICHLER, 1954

Carduelis cannabina (LINNAEUS, 1758) *

Brueelia straminea (DENNY, 1842)
Dendrocopos major (LINNAEUS, 1758) * HU: SCHÄFER (1963)
Dendrocopos leucotos (BECHSTEIN, 1802), *Jynx torquilla* LINNAEUS, 1758

Brueelia subtilis (NITZSCH, 1874)
Passer domesticus (LINNAEUS, 1758), *Passer montanus* (LINNAEUS, 1758) *

Brueelia tasniemae ANSARI, 1957
Corvus frugilegus LINNAEUS, 1758 * HU: RÉKÁSI (1973)

Brueelia tenuis (BURMEISTER, 1838)
Riparia riparia (LINNAEUS, 1758) *

Brueelia tovornikae (BALÁT, 1981)
Sylvia atricapilla (LINNAEUS, 1758) *

Brueelia tristis (GIEBEL, 1874)
Erithacus rubecula (LINNAEUS, 1758) *

Brueelia turdinulae ANSARI, 1956
Turdus philomelos BREHM, 1831 *

Brueelia uncinosa (BURMEISTER, 1838)
Corvus corone cornix LINNAEUS, 1758 * HU: RÉKÁSI (1984)

Brueelia vaneki BALÁT, 1981
Acrocephalus schoenobaenus (LINNAEUS, 1758) *

Brueelia varia (BURMEISTER, 1838)
Corvus monedula LINNAEUS, 1758 * HU: BALÁT (1957)

Brueelia viscivori (DENNY, 1842)
Turdus viscivorus LINNAEUS, 1758 * HU: RÉKÁSI (1984)

Brueelia weberi BALÁT, 1982
Parus major LINNAEUS, 1758 *

Campanulotes *bidentatus* (SCOPOLI, 1763)
Columba palumbus LINNAEUS, 1758 * HU: BALÁT (1957)

Campanulotes compar (BURMEISTER, 1838)
Columba livia GMELIN, 1789 * HU: RÉKÁSI (1978*a*)

Campanulotes drosti EICHLER, 1950
Columba oenas LINNAEUS, 1758 * HU: RÉKÁSI (1990)

Capraiella *subcuspidata* (BURMEISTER, 1838)
Coracias garrulus LINNAEUS, 1758 * HU: BALÁT (1957)

Carduiceps *cingulatus* (DENNY, 1842)
Limosa limosa (LINNAEUS, 1758) *

Carduiceps fulvofasciatus (GRUBE, 1851)
Xenus cinereus (GÜLDENSTADT, 1775) * HU: RÉKÁSI (2008*b*)

Carduiceps lapponicus EMERSON, 1953
Limosa lapponica (LINNAEUS, 1758) *

Carduiceps meinertzhageni TIMMERMANN, 1954
Calidris alpina (LINNAEUS, 1758) * HU: RÉKÁSI (1984)
Calidris maritima (BRÜNNICH, 1764)

Carduiceps scalaris (PIAGET, 1880)
Philomachus pugnax (LINNAEUS, 1758) * HU: RÉKÁSI (1984)

Carduiceps subscalaris (PIAGET, 1880)
Phalaropus lobatus (LINNAEUS, 1758) *

Carduiceps zonarius (NITZSCH, 1866)
Calidris minuta (LEISLER, 1812) * HU: RÉKÁSI (1984)

Calidris alba (PALLAS, 1764), *Calidris canutus* (LINNAEUS, 1758), *Calidris ferruginea* (PONTOPPIDAN, 1763), *Calidris fuscicollis* (VIEILLOT, 1819), *Calidris melanotos* (VIEILLOT, 1819), *Calidris pusilla* (LINNAEUS, 1766), *Calidris temminckii* (LEISLER, 1812), *Tryngites subruficollis* (VIEILLOT, 1819)

***Chelopistes** meleagridis* (LINNAEUS, 1758)
Meleagris gallopavo LINNAEUS, 1758 *

***Cirrophthirius** recurvirostrae* (LINNAEUS, 1758)
Recurvirostra avosetta LINNAEUS 1758 * HU: RÉKÁSI (1986*b*)

***Coloceras** aegypticum* (KELLOGG et PAINE, 1911)
Columba livia GMELIN, 1789 *

Coloceras alloceratum (TENDEIRO, 1974)
Columba palumbus LINNAEUS, 1758 *

Coloceras britannicum (TENDEIRO, 1973)
Streptopelia orientalis (LATHAM, 1790), *Streptopelia turtur* (LINNAEUS, 1758) *

Coloceras chinense (KELLOGG et CHAPMAN, 1902)
Streptopelia orientalis (LATHAM, 1790), *Streptopelia turtur* (LINNAEUS, 1758)

Coloceras damicorne (NITZSCH, 1866)
Columba palumbus LINNAEUS, 1758 * HU: BALÁT (1957)
Columba livia GMELIN, 1789, *Columba oenas* LINNAEUS, 1758

Coloceras hilli (BEDFORD, 1920)
Streptopelia decaocto (FRIVALDSZKY, 1838)

Coloceras israelensis (TENDEIRO, 1974)
Columba livia GMELIN, 1789 *

Coloceras liviae (TENDEIRO, 1974)
Columba livia GMELIN, 1789 *

Coloceras orientalis (TENDEIRO, 1969)
Streptopelia orientalis (LATHAM, 1790) *

Coloceras piageti (JOHNSTON et HARRISON, 1912)
Streptopelia decaocto (FRIVALDSZKY, 1838) HU: RÉKÁSI (1984, as *C. sofioticus*)

Coloceras tovornikae TENDEIRO, 1973
Columba livia GMELIN, 1789 *

***Columbicola** bacillus* (GIEBEL, 1866)
Streptopelia decaocto (FRIVALDSZKY, 1838) HU: BALÁT (1957, as *C. baculus*)
Streptopelia turtur (LINNAEUS, 1758) * HU: BALÁT (1957, as *C. baculus*)

Columbicola claviformis (DENNY, 1842)
Columba palumbus LINNAEUS, 1758 * HU: BALÁT (1957)

Columbicola columbae (LINNAEUS, 1758)
Columba livia GMELIN, 1789 * HU: BALÁT (1957)
Columba oenas LINNAEUS, 1758 HU: BALÁT (1957)

Columbicola orientalis TENDEIRO, 1965
Streptopelia orientalis (LATHAM, 1790) *

Columbicola tschulyschman EICHLER, 1942
Columba livia GMELIN, 1789

Columbicola turturis (UCHIDA, 1917)
Streptopelia orientalis (LATHAM, 1790) *

***Craspedonirmus** colymbinus* (DENNY, 1842)
Gavia arctica (LINNAEUS, 1758) HU: SCHÄFER (1963)
Gavia stellata (PONTOPPIDAN, 1763) *

Craspedonirmus immer EMERSON, 1955
Gavia immer (BRÜNNICH, 1764) *

Craspedorrhynchus *aquilinus* (DENNY, 1842)
Aquila chrysaetos (LINNAEUS, 1758) * HU: SCHÄFER (1963, as *C. chrysophthalmus*)

Craspedorrhynchus dilatatus (RUDOW, 1869)
Buteo lagopus (PONTOPPIDAN, 1763) *

Craspedorrhynchus fasciati GALLEGO *et al.*, 1987
Hieraaetus fasciatus (VIEILLOT, 1822) *

Craspedorrhynchus fraterculus EICHLER et ZLOTORZYCKA, 1975
Aquila heliaca SAVIGNY, 1809 * HU: RÉKÁSI (2008*a*)

Craspedorrhynchus haematopus (SCOPOLI, 1763)
Accipiter gentilis (LINNAEUS, 1758) *

Craspedorrhynchus macrocephalus (NITZSCH, 1874)
Haliaeetus albicilla (LINNAEUS, 1758) * HU: RÉKÁSI *et al.* (2002)

Craspedorrhynchus melittoscopus (NITZSCH, 1874)
Pernis apivorus (LINNAEUS, 1758) * HU: RÉKÁSI (1984)

Craspedorrhynchus naevius (GIEBEL, 1861)
Aquila pomarina BREHM, 1831 * HU: SOLT (1998)

Craspedorrhynchus nisi (DENNY, 1842)
Accipiter nisus (LINNAEUS, 1758) * HU: BALÁT (1957)

Craspedorrhynchus platystomus (BURMEISTER, 1838)
Buteo buteo (LINNAEUS, 1758) * HU: BALÁT (1957)

Craspedorrhynchus ranjhae ANSARI, 1955
Hieraaetus pennatus (GMELIN, 1788) *

Craspedorrhynchus rotundatus (PIAGET, 1880)
Circus aeruginosus (LINNAEUS, 1758) * HU: RÉKÁSI (1984)

Craspedorrhynchus spathulatus (GIEBEL, 1874)
Milvus migrans (BODDAERT, 1783) * HU: SCHÄFER (1963)

Craspedorrhynchus subbuteonis GALLEGO *et al*., 1987
Falco subbuteo LINNAEUS, 1758 *

Craspedorrhynchus triangularis (RUDOW, 1869)
Circaetus gallicus (GMELIN, 1788) *

Cuclotogaster *cameratus* (DE HAAN, 1829)
Lyrurus tetrix (LINNAEUS, 1758) *

Cuclotogaster cinereus (NITZSCH, 1866)
Coturnix coturnix (LINNAEUS, 1758) * HU: BALÁT (1957)

Cuclotogaster heterogrammicus (NITZSCH, 1866)
Perdix perdix (LINNAEUS, 1758) * HU: BALÁT (1957)

Cuclotogaster heterographus (NITZSCH, 1866)
Gallus gallus (LINNAEUS, 1758) *, *Phasianus colchicus* LINNAEUS, 1758

Cuculicola *latirostris* (BURMEISTER, 1838)
Cuculus canorus LINNAEUS, 1758 * HU: RÉKÁSI (1984)

Cuculicola limbatus TENDEIRO, 1962
Clamator glandarius (LINNAEUS, 1758) *

Cuculoecus *latifrons* (DENNY, 1842)
Cuculus canorus LINNAEUS, 1758 * HU: BALÁT (1957)

Cummingsiella *ambigua* (BURMEISTER, 1838)
Gallinago gallinago (LINNAEUS, 1758) * HU: BALÁT (1957)

Cummingsiella aurea HOPKINS, 1949
Scolopax rusticola LINNAEUS, 1758 * HU: RÉKÁSI (1978*a*)

Cummingsiella brelihi TIMMERMANN, 1969

Scolopax rusticola LINNAEUS, 1758 * HU: RÉKÁSI (1984)

Cummingsiella breviclypeata BLAGOVESHTCHENSKY, 1948

Numenius tenuirostris VIEILLOT, 1817 *

Cummingsiella ovalis (SCOPOLI, 1763)

Numenius arquata (LINNAEUS, 1758) * HU: RÉKÁSI (1973)

Degeeriella *aquilarum* EICHLER, 1943

Aquila chrysaetos (LINNAEUS, 1758), *Aquila clanga* PALLAS, 1811, *Aquila heliaca* SAVIGNY, 1809, *Aquila pomarina* BREHM, 1831

Degeeriella discocephalus (BURMEISTER, 1838)

Haliaeetus albicilla (LINNAEUS, 1758) * HU: RÉKÁSI *et al*. (2002)

Degeeriella fulva (GIEBEL, 1874)

Buteo buteo (LINNAEUS, 1758) HU: BALÁT (1957, as *D. giebeli*)
Buteo lagopus (PONTOPPIDAN, 1763) HU: BALÁT (1957, as *D. angusta*)
Buteo rufinus (CRETZSCHMAR, 1829) HU: SOLT (1998)
Aquila heliaca SAVIGNY, 1809 HU: SOLT (1998)
Hieraaetus pennatus (GMELIN, 1788) HU: SOLT (1998)
Aquila chrysaetos (LINNAEUS, 1758) *, *Aquila clanga* PALLAS, 1811, *Aquila pomarina* BREHM, 1831, *Hieraaetus fasciatus* (VIEILLOT, 1822)

Degeeriella fusca (DENNY, 1842)

Circus aeruginosus (LINNAEUS, 1758) * HU: BALÁT (1957)
Circus cyaneus (LINNAEUS, 1766) HU: BALÁT (1957)
Circus macrourus (GMELIN, 1770), *Circus pygargus* (LINNAEUS, 1758)

Degeeriella leucopleura (NITZSCH, 1874)

Circaetus gallicus (GMELIN, 1788)

Degeeriella nisus (GIEBEL, 1866)

Accipiter nisus (LINNAEUS, 1758) * HU: BALÁT (1957)

Degeeriella phlyctopygus (NITZSCH, 1861)
Pernis apivorus (LINNAEUS, 1758) *

Degeeriella regalis (GIEBEL, 1866)
Milvus migrans (BODDAERT, 1783), *Milvus milvus* (LINNAEUS, 1758) *

Degeeriella rufa (BURMEISTER, 1838)
Falco cherrug Gray, 1834 HU: RÉKÁSI (1987, as *D. quadraticollis*)
Falco peregrinus TUNSTALL, 1771 HU: RÉKÁSI (1993*b*)
Falco subbuteo LINNAEUS, 1758 HU: BALÁT (1957, as *D. nitzschi*)
Falco tinnunculus LINNAEUS, 1758 * HU: BALÁT (1957)
Falco vespertinus LINNAEUS, 1766 HU: SCHÄFER (1963)
Falco amurensis RADDE, 1863, *Falco columbarius* LINNAEUS, 1758, *Falco eleonorae* GENE, 1839, *Falco naumanni* FLEISCHER, 1818

***Esthiopterum** elbeli* TANDAN, 1973
Anthropoides virgo (LINNAEUS, 1785) *

Degeeriella vagans (GIEBEL, 1874)
Accipiter gentilis (LINNAEUS, 1758) *

Esthiopterum gruis (LINNAEUS, 1758)
Grus grus (LINNAEUS, 1758) * HU: RÉKÁSI (1973)

***Falcolipeurus** frater* (GIEBEL, 1874)
Neophron percnopterus (LINNAEUS, 1758) *

Falcolipeurus quadripustulatus (BURMEISTER, 1838)
Aegypius monachus (LINNAEUS, 1766) *, *Circaetus gallicus* (GMELIN, 1788), *Gyps fulvus* (HABLIZL, 1783)

Falcolipeurus sulcifrons (DENNY, 1842)
Haliaeetus albicilla (LINNAEUS, 1758) *

Falcolipeurus suturalis (RUDOW, 1869)

Aquila chrysaetos (LINNAEUS, 1758) *, *Aquila clanga* PALLAS, 1811, *Aquila heliaca* SAVIGNY, 1809, *Aquila pomarina* BREHM, 1831

Falcolipeurus yasminae ANSARI, 1956
Hieraaetus pennatus (GMELIN, 1788) *

***Fulicoffula** gallinula* CARRIKER, 1953
Gallinula chloropus (LINNAEUS, 1758) *

Fulicoffula lurida (NITZSCH, 1818)
Fulica atra LINNAEUS, 1758 * HU: BALÁT (1957)

Fulicoffula rallina (DENNY, 1842)
Rallus aquaticus LINNAEUS, 1758 *

Fulicoffula stammeri EICHLER, 1958
Porzana porzana (LINNAEUS, 1766) *

***Goniocotes** chrysocephalus* GIEBEL, 1874
Phasianus colchicus LINNAEUS, 1758 * HU: BALÁT (1957)

Goniocotes congolensis TENDEIRO, 1989
Numida meleagris (LINNAEUS, 1758) *

Goniocotes gallinae (DE GEER, 1778)
Gallus gallus (LINNAEUS, 1758) *, *Meleagris gallopavo* LINNAEUS, 1758

Goniocotes maculatus TASCHENBERG, 1882
Numida meleagris (LINNAEUS, 1758)

Goniocotes megalocephalus UCHIDA, 1916
Tetrastes bonasia (LINNAEUS, 1758) *

Goniocotes microthorax (STEPHENS, 1829)
Perdix perdix (LINNAEUS, 1758) *

***Goniodes** astrocephalus* (BURMEISTER, 1838)
Coturnix coturnix (LINNAEUS, 1758) *

Goniodes bituberculatus RUDOW, 1869
Tetrao urogallus LINNAEUS, 1758 * HU: RÉKÁSI (1978*a*)

Goniodes capitatus (KÉLER, 1939)
Phasianus colchicus LINNAEUS, 1758 *

Goniodes colchici DENNY, 1842
Phasianus colchicus LINNAEUS, 1758 *

Goniodes dispar BURMEISTER, 1838
Perdix perdix (LINNAEUS, 1758) * HU: RÉKÁSI (1993*b*)

Goniodes dissimilis DENNY, 1842
Gallus gallus (LINNAEUS, 1758) *

Goniodes gigas (TASCHENBERG, 1879)
Gallus gallus (LINNAEUS, 1758) *, *Numida meleagris* (LINNAEUS, 1758)

Goniodes klockenhoffi (TENDEIRO, 1988)
Numida meleagris (LINNAEUS, 1758) *

Goniodes meyi (TENDEIRO, 1988)
Numida meleagris (LINNAEUS, 1758) *

Goniodes numidae MJÖBERG, 1910
Numida meleagris (LINNAEUS, 1758) *

Goniodes reichenowii (TENDEIRO, 1988)
Numida meleagris (LINNAEUS, 1758) *

Goniodes tetraonis (LINNAEUS, 1761)
Lyrurus tetrix (LINNAEUS, 1758) *

***Haffneria** grandis* (PIAGET, 1880)
Stercorarius longicaudus VIEILLOT, 1819, *Stercorarius parasiticus* (LINNAEUS, 1758), *Stercorarius pomarinus* (TEMMINCK, 1815), *Stercorarius skua* (BRÜNNICH, 1764)

***Ibidoecus** bisignatus* (NITZSCH, 1866)
Plegadis falcinellus (LINNAEUS, 1766) * HU: RÉKÁSI (1978*a*)

Ibidoecus plataleae (DENNY, 1842)
Platalea leucorodia LINNAEUS, 1758 * HU: SCHÄFER (1963)

***Incidifrons** curvitrabeculatus* BLAGOVESHTCHENSKY, 1940
Porphyrio porphyrio (LINNAEUS, 1758) *

Incidifrons fulicae (LINNAEUS, 1758)
Fulica atra LINNAEUS, 1758 * HU: BALÁT (1957)

Incidifrons gallinulae BLAGOVESHTCHENSKY, 1951
Gallinula chloropus (LINNAEUS, 1758) *

Incidifrons porzanae BLAGOVESHTCHENSKY, 1951
Porzana parva (SCOPOLI, 1769) *

Incidifrons ralli (SCOPOLI, 1772)
Rallus aquaticus LINNAEUS, 1758 *

***Lagopoecus** colchicus* EMERSON, 1949
Phasianus colchicus LINNAEUS, 1758 *

Lagopoecus lyrurus CLAY, 1938
Lyrurus tetrix (LINNAEUS, 1758) *

Lagopoecus pallidovittatus (GRUBE, 1851)
Tetrao urogallus LINNAEUS, 1758 *

Lagopoecus sinensis (SUGIMOTO, 1930)
Gallus gallus (LINNAEUS, 1758) *

Lagopoecus tetrastei BECHET, 1963
Tetrastes bonasia (LINNAEUS, 1758) *

***Lipeurus** caponis* (LINNAEUS, 1758)
Gallus gallus (LINNAEUS, 1758) *, *Meleagris gallopavo* LINNAEUS, 1758, *Numida meleagris* (LINNAEUS, 1758), *Phasianus colchicus* LINNAEUS, 1758

Lipeurus lawrensis BEDFORD, 1929
Numida meleagris (LINNAEUS, 1758) *

Lipeurus maculosus CLAY, 1938
Phasianus colchicus LINNAEUS, 1758 * HU: BALÁT (1957)
Perdix perdix (LINNAEUS, 1758)

Lipeurus numidae (DENNY, 1842)
Numida meleagris (LINNAEUS, 1758) *

Lipeurus tropicalis PETERS, 1931
Gallus gallus (LINNAEUS, 1758) *

***Lunaceps** actophilus* (KELLOGG et CHAPMAN, 1899)
Calidris alba (Pallas, 1764) * HU: RÉKÁSI (2006)
Calidris alpina (LINNAEUS, 1758) HU: RÉKÁSI (1978*b*)

Lunaceps cabanisi TIMMERMANN, 1954
Calidris ferruginea (PONTOPPIDAN, 1763), *Calidris pusilla* (LINNAEUS, 1766)

Lunaceps drosti TIMMERMANN, 1954
Calidris canutus (LINNAEUS, 1758) *

Lunaceps falcinellus TIMMERMANN, 1954
Limicola falcinellus (PONTOPPIDAN, 1763) *, *Tryngites subruficollis* (VIEILLOT, 1819)

Lunaceps haematopi TIMMERMANN, 1954
Haematopus ostralegus LINNAEUS, 1758 *

Lunaceps holophaeus (BURMEISTER, 1838)
Philomachus pugnax (LINNAEUS, 1758) * HU: RÉKÁSI (1978*b*)
Vanellus vanellus (LINNAEUS, 1758)

Lunaceps incoenis (KELLOGG et CHAPMAN, 1899)
Calidris minuta (Leisler, 1812) HU: RÉKÁSI (2006)
Calidris temminckii (LEISLER, 1812), *Pluvialis squatarola* (LINNAEUS, 1758) *

Lunaceps limosella TIMMERMANN, 1954
Limosa lapponica (LINNAEUS, 1758) *, *Limosa limosa* (LINNAEUS, 1758)

Lunaceps nereis TIMMERMANN, 1954
Calidris maritima (BRÜNNICH, 1764) *

Lunaceps numenii numenii (DENNY, 1842)
Numenius arquata (LINNAEUS, 1758) * HU: BALÁT (1957)

Lunaceps numenii oliveri (JOHNSON et HARRISON, 1912)
Numenius phaeopus (LINNAEUS, 1758) *

Lunaceps numenii phaeopi (DENNY, 1842)
Numenius phaeopus (LINNAEUS, 1758) *

Lunaceps numenii proximus (BLAGOVESHTCHENSKY, 1948)
Numenius tenuirostris VIEILLOT, 1817 *

Lunaceps timmermanni BECHET, 1968
Calidris ferruginea (PONTOPPIDAN, 1763) * HU: RÉKÁSI (2006)

***Meropoecus** meropis* (DENNY, 1842)
Merops apiaster LINNAEUS, 1758 * HU: BALÁT (1957)

***Mulcticola** hypoleucus* (DENNY, 1842)
Caprimulgus europaeus LINNAEUS, 1758 * HU: BALÁT (1957)

***Neophilopterus** incompletus* (DENNY, 1842)
Ciconia ciconia (LINNAEUS, 1758) * HU: SCHÄFER (1963)

Neophilopterus tricolor (BURMEISTER, 1838)
Ciconia nigra (LINNAEUS, 1758) * HU: SCHÄFER (1963)

***Ornithobius** bucephalus* (GIEBEL, 1874)
Cygnus olor (GMELIN, 1789) *

Ornithobius cygni (LINNAEUS, 1758)
Cygnus columbianus (ORD, 1815), *Cygnus cygnus* (LINNAEUS, 1758) *

Ornithobius goniopleurus DENNY, 1842
Branta canadensis (LINNAEUS, 1758) *

Ornithobius hexophthalmus (NITZSCH, 1818)
Branta leucopsis (BECHSTEIN, 1803)

Ornithobius mathisi (NEUMANN, 1912)
Anser anser (LINNAEUS, 1758) * HU: RÉKÁSI (1984)
Anser domesticus (LINNAEUS, 1758), *Anser fabalis* (LATHAM, 1787)

Ornithobius waterstoni TIMMERMANN, 1962
Cygnus columbianus (ORD, 1815)

***Otidoecus** antilogus* (NITZSCH, 1866)
Tetrax tetrax (LINNAEUS, 1758) *

Otidoecus turmalis (DENNY, 1842)
Otis tarda LINNAEUS, 1758 *

***Oxylipeurus** colchicus* CLAY, 1938
Phasianus colchicus LINNAEUS, 1758 * HU: RÉKÁSI (1973)

Oxylipeurus copulentus CLAY, 1938
Meleagris gallopavo LINNAEUS, 1758 *

Oxylipeurus dentatus (SUGIMOTO, 1934) *
Gallus gallus (LINNAEUS, 1758) *

Oxylipeurus minor (ZLOTORZYCKA, 1966)
Lyrurus tetrix (LINNAEUS, 1758) *

Oxylipeurus polytrapesius (BURMEISTER, 1838)
Meleagris gallopavo LINNAEUS, 1758 *

Oxylipeurus tetraonis (GRUBE, 1851)
Tetrao urogallus LINNAEUS, 1758 *

Pectinopygus *bifasciatus* (PIAGET, 1880)
Pelecanus crispus BRUCH, 1832 *

Pectinopygus excornis (BLAGOVESHTCHENSKY, 1940)
Phalacrocorax pygmeus (PALLAS, 1773) *

Pectinopygus forficulatus (NITZSCH, 1866)
Pelecanus onocrotalus LINNAEUS, 1758 *

Pectinopygus gyricornis (DENNY, 1842)
Phalacrocorax carbo (LINNAEUS, 1758) HU: BALÁT (1957)

Penenirmus *affectator* (ZLOTORZYCKA, 1976)
Sylvia borin (BODDAERT, 1783) *

Penenirmus albiventris (SCOPOLI, 1763)
Troglodytes troglodytes (LINNAEUS, 1758) * HU: BALÁT (1957)

Penenirmus auritus (SCOPOLI, 1763)
Dendrocopos leucotos (BECHSTEIN, 1802) HU: SCHÄFER (1964)
Dendrocopos major (LINNAEUS, 1758) * HU: BALÁT (1957)
Dendrocopos minor (LINNAEUS, 1758) HU: RÉKÁSI (1984)
Dendrocopos syriacus (EHRENBERG, 1833) HU: BALÁT & BREUER (1955)

Dendrocopos medius (LINNAEUS, 1758)

Penenirmus barusi BALÁT, 1981
Phoenicurus ochruros (GMELIN, 1774) *

Penenirmus buresi BALÁT, 1958
Emberiza hortulana LINNAEUS, 1758 *, *Emberiza melanocephala* SCOPOLI, 1769 *

Penenirmus deductoris MEY, 1982
Carduelis flavirostris (LINNAEUS, 1758) *

Penenirmus desertus FEDORENKO et BELSKAYA, 1979
Oenanthe deserti (TEMMINCK, 1825) *

Penenirmus digitiformis FEDORENKO et BELSKAYA, 1979
Oenanthe pleschanka (LEPECHIN, 1770) *

Penenirmus gulosus (NITZSCH, 1866)
Certhia familiaris LINNAEUS, 1758 *

Penenirmus heteroscelis (NITZSCH, 1866)
Dryocopus martius (LINNAEUS, 1758) *

Penenirmus hibari (UCHIDA, 1949)
Alauda arvensis LINNAEUS, 1758

Penenirmus incurvatus FEDORENKO et BELSKAYA, 1979
Oenanthe isabellina (TEMMINCK, 1829) *

Penenirmus kuxi BALÁT, 1981
Locustella luscinioides (SAVI, 1824) *

Penenirmus longuliceps (BLAGOVESHTCHENSKY, 1940)
Cettia cetti (TEMMINCK, 1820) *, *Troglodytes troglodytes* (LINNAEUS, 1758) *

Penenirmus nirmoideus (NITZSCH, 1874)

Saxicola rubetra (LINNAEUS, 1758) *

Penenirmus pari (DENNY, 1842)

Aegithalos caudatus (LINNAEUS, 1758) * HU: RÉKÁSI (1984)

Parus ater LINNAEUS, 1758 *, *Parus caeruleus* LINNAEUS, 1758 *

Penenirmus patevi BALÁT, 1958

Anthus campestris (LINNAEUS, 1758) *

Penenirmus pavlovskyi BLAGOVESHTCHENSKY, 1951

Galerida cristata (LINNAEUS, 1758) *

Penenirmus phylloscopi (ZLOTORZYCKA, 1976)

Phylloscopus trochilus (LINNAEUS, 1758) *

Penenirmus pici (FABRICIUS, 1798)

Picus canus GMELIN, 1788 HU: BALÁT (1957)

Picus viridis LINNAEUS, 1758 * HU: RÉKÁSI (1984)

Penenirmus pikulai BALÁT, 1981

Sylvia nisoria (BECHSTEIN, 1795) *

Penenirmus rarus (ZLOTORZYCKA, 1976)

Phylloscopus collybita (VIEILLOT, 1817) * HU: RÉKÁSI (1990, in *Pleurinirmus*)

Penenirmus serrahnensis BALÁT, 1982

Fringilla coelebs LINNAEUS, 1758 *

Penenirmus serrilumbus (BURMEISTER, 1838)

Jynx torquilla LINNAEUS, 1758 *

Penenirmus silvicultrix (MEY, 1982)

Phoenicurus phoenicurus (LINNAEUS, 1758) *

Penenirmus speciosus MEY, 1982

Sylvia curruca (LINNAEUS, 1758) *

Penenirmus visendus (ZLOTORZYCKA, 1946b)
Panurus biarmicus (LINNAEUS, 1758) *

Philopterus *alexanderkoenigi* (EICHLER, 1953)
Galerida cristata (LINNAEUS, 1758) * HU: RÉKÁSI (1973)

Philopterus arboreus FEDORENKO, 1984
Lullula arborea (LINNAEUS, 1758) *

Philopterus atratus (NITZSCH, 1818)
Corvus frugilegus LINNAEUS, 1758 * HU: BALÁT (1957)

Philopterus bischoffi (EICHLER, 1951)
Turdus pilaris LINNAEUS, 1758 * HU: RÉKÁSI (1984, in *Docophorulus*)

Philopterus capillatus (ZLOTORZYCKA, 1964)
Ficedula hypoleuca (PALLAS, 1764) * HU: RÉKÁSI (1990, in *Docophorulus*)

Philopterus cincli (DENNY, 1842)
Cinclus cinclus (LINNAEUS, 1758) *

Philopterus citrinellae (SCHRANK, 1776)
Carduelis chloris (LINNAEUS, 1758) HU: BALÁT (1957)
Emberiza citrinella LINNAEUS, 1758 * HU: BALÁT & BREUER (1955)
Pyrrhula pyrrhula (LINNAEUS, 1758) HU: BALÁT (1957)

Philopterus coarctatus (SCOPOLI, 1763)
Lanius collurio LINNAEUS, 1758 * HU: BALÁT (1957)
Lanius excubitor LINNAEUS, 1758 HU: BALÁT (1957, as *Ph. fuscicollis*)
Lanius minor GMELIN, 1788

Philopterus comatus (MEY, 1982)
Montifringilla nivalis (LINNAEUS, 1766) *

Philopterus corvi (LINNAEUS, 1758)

Corvus corax LINNAEUS, 1758 * HU: SCHÄFER (1963, as *Ph. semisignatus*)

Philopterus crassipes (BURMEISTER, 1838)
Nucifraga caryocatactes (LINNAEUS, 1758) * HU: RÉKÁSI (1973)

Philopterus cumulatus (ZLOTORZYCKA, 1964)
Emberiza calandra LINNAEUS, 1758 * HU: RÉKÁSI (1973)

Philopterus curvirostrae (SCHRANK, 1776)
Loxia curvirostra LINNAEUS, 1758 *

Philopterus desertus (ZLOTORZYCKA, 1964)
Muscicapa striata (Pallas, 1764) * HU: RÉKÁSI (1973)

Philopterus dumani PRICE et HELLENTHAL, 1998
Pyrrhocorax graculus (LINNAEUS, 1766) *

Philopterus emiliae BALÁT, 1955
Prunella collaris (SCOPOLI, 1769) *

Philopterus erythrini (MEY, 1982)
Carpodacus erythrinus (PALLAS, 1770)

Philopterus eurasiaticus (MEY, 1982)
Coccothraustes coccothraustes (LINNAEUS, 1758) *

Philopterus excisus NITZSCH, 1818
Delichon urbica (LINNAEUS, 1758) * HU: RÉKÁSI (1984)

Philopterus fedorenkoae (MEY, 1983)
Acrocephalus arundinaceus (LINNAEUS, 1758) *

Philopterus fortunatus (ZLOTORZYCKA, 1964)
Fringilla coelebs LINNAEUS, 1758 *

Philopterus fringillae (SCOPOLI, 1772)

Passer domesticus (LINNAEUS, 1758) * HU: BALÁT (1957)

Philopterus garrulae (PIAGET, 1880)
Bombycilla garrulus (LINNAEUS, 1758) *

Philopterus garruli BOISDUVAL et LACORDAIRE, 1935
Garrulus glandarius (LINNAEUS, 1758) * HU: SCHÄFER (1963)

Philopterus guttatus (DENNY, 1842)
Corvus monedula LINNAEUS, 1758 * HU: BALÁT (1957)

Philopterus hamatus (PACKARD, 1870)
Plectrophenax nivalis (LINNAEUS, 1758) *

Philopterus hansmuenchi (EICHLER et VASJUKOVA, 1981)
Loxia leucoptera GMELIN, 1789 *

Philopterus hanzaki BALÁT, 1955
Anthus spinoletta (LINNAEUS, 1758) *

Philopterus hercynicus (MEY, 1988)
Parus caeruleus LINNAEUS, 1758 *

Philopterus hungaricus RÉKÁSI, 1998
Tichodroma muraria (LINNAEUS, 1766) * HU: RÉKÁSI (1998*a*)

Philopterus isabellinae (MEY, 1982)
Oenanthe isabellina (TEMMINCK, 1829) *

Philopterus kekilovae FEDORENKO, 1984
Eremophila alpestris (LINNAEUS, 1758) *

Philopterus linariae (PIAGET, 1885)
Carduelis flammea (LINNAEUS, 1758) *

Philopterus lineatus (GIEBEL, 1874)

Certhia brachydactyla BREHM, 1820 *

Philopterus markevichi FEDORENKO et VOLKOV, 1977
Ficedula parva (BECHSTEIN, 1792) *

Philopterus microsomaticus TANDAN, 1955
Hirundo rustica LINNAEUS, 1758 * HU: VAS *et al*. (2008)
Riparia riparia (LINNAEUS, 1758)

Philopterus mirificus (ZLOTORZYCKA, 1964)
Acrocephalus palustris (BECHSTEIN, 1798) *

Philopterus modularis (DENNY, 1842)
Prunella modularis (LINNAEUS, 1758) *

Philopterus montani (ZLOTORZYCKA, 1964)
Passer montanus (LINNAEUS, 1758) * HU: RÉKÁSI (1973)

Philopterus nativus FEDORENKO, 1977
Turdus torquatus LINNAEUS, 1758 *

Philopterus necopinatus (ZLOTORZYCKA, 1964)
Acrocephalus schoenobaenus (LINNAEUS, 1758) *

Philopterus neomajor PRICE, HELLENTHAL et PALMA, 2003
Dendrocopos major (LINNAEUS, 1758) *

Philopterus ocellatus (SCOPOLI, 1763)
Corvus corone cornix LINNAEUS, 1758 * HU: BALÁT (1957)

Philopterus oenanthe FEDORENKO, 1983
Oenanthe oenanthe (LINNAEUS, 1758) *

Philopterus ornatus (NITZSCH, 1866)
Oriolus oriolus (LINNAEUS, 1758) * HU: BALÁT (1957)

Philopterus osborni EDWARDS, 1952
Corvus corax LINNAEUS, 1758

Philopterus pallescens (DENNY, 1842)
Parus major LINNAEUS, 1758 * HU: BALÁT (1957)
Parus palustris LINNAEUS, 1758 *

Philopterus passerinus (DENNY, 1842)
Motacilla alba LINNAEUS, 1758 * HU: BALÁT (1957)

Philopterus pavidus (ZLOTORZYCKA, 1964)
Motacilla flava LINNAEUS, 1758 *

Philopterus peripariphilus (MEY, 1988)
Parus ater LINNAEUS, 1758 *

Philopterus phylloscopi FEDORENKO, 1979
Phylloscopus bonelli (VIEILLOT, 1819), *Phylloscopus sibilatrix* (BECHSTEIN, 1793) *, *Phylloscopus trochilus* (LINNAEUS, 1758)

Philopterus picae (DENNY, 1842)
Pica pica (LINNAEUS, 1758) * HU: BALÁT & BREUER (1955)

Philopterus pleschankae FEDORENKO, 1983
Oenanthe pleschanka (LEPECHIN, 1770) *

Philopterus rapax (ZLOTORZYCKA, 1964)
Fringilla montifringilla LINNAEUS, 1758 *

Philopterus reginae (MEY, 1982)
Phylloscopus fuscatus (BLYTH, 1842) *

Philopterus reguli (DENNY, 1842)
Regulus regulus (LINNAEUS, 1758) * HU: RÉKÁSI (1973)

Philopterus residuus (ZLOTORZYCKA, 1964)

Emberiza schoeniclus (LINNAEUS, 1758) * HU: RÉKÁSI (1973)

Philopterus rubeculae (DENNY, 1842)
Erithacus rubecula (LINNAEUS, 1758) *

Philopterus sibiricus FEDORENKO et VOLKOV, 1980
Emberiza leucocephalos GMELIN, 1771 *

Philopterus sittae FEDORENKO, 1978
Sitta europaea LINNAEUS, 1758 *

Philopterus stadleri (EICHLER, 1959)
Alauda arvensis LINNAEUS, 1758 *

Philopterus stepposus FEDORENKO, 1984
Melanocorypha calandra (LINNAEUS, 1766) *

Philopterus subitus FEDORENKO, 1985
Motacilla cinerea TUNSTALL, 1771 *

Philopterus thryptocephalus (KELLOGG et PAINE, 1914)
Pyrrhocorax graculus (LINNAEUS, 1766) *, *Pyrrhocorax pyrrhocorax* (LINNAEUS, 1758)

Philopterus thuringiacus (MEY, 1988)
Parus major LINNAEUS, 1758 *

Philopterus timmermanni (ZLOTORZYCKA, 1964)
Turdus iliacus LINNAEUS, 1766 *

Philopterus trigonophorus (GIEBEL, 1874)
Lanius senator LINNAEUS, 1758 *

Philopterus troglodytis FEDORENKO, 1986
Troglodytes troglodytes (LINNAEUS, 1758) *

Philopterus turdi (DENNY, 1842)

Turdus merula LINNAEUS, 1758 HU: BALÁT & BREUER (1955, as *Ph. merulae*)
Turdus philomelos BREHM, 1831 * HU: RÉKÁSI (1990, in *Docophorulus*)

Philopterus vernus (ZLOTORZYCKA, 1964)
Turdus viscivorus LINNAEUS, 1758 * HU: RÉKÁSI (1984, in *Docophorulus*)

Philopterus vultuosus (ZLOTORZYCKA, 1964)
Anthus trivialis (LINNAEUS, 1758) *

Philopterus zlotorzyckae (MEY, 1982)
Monticola saxatilis (LINNAEUS, 1766) *

***Physconelloides** zenaidurae* (MCGREGOR, 1917)
Columba livia GMELIN, 1789

***Picicola** candidus* (NITZSCH, 1866)
Picus canus GMELIN, 1788 * HU: RÉKÁSI (1984)
Picus viridis LINNAEUS, 1758 HU: SCHÄFER (1964, in *Degeeriella*)

Picicola snodgrassi (KELLOGG, 1896)
Dendrocopos leucotos (BECHSTEIN, 1802), *Dendrocopos major* (LINNAEUS, 1758)

Picicola superciliosa (NITZSCH, 1866)
Dendrocopos medius (LINNAEUS, 1758) *

***Quadraceps** alcae* (DENNY, 1842)
Alca torda LINNAEUS, 1758 *

Quadraceps anagrapsus (NITZSCH, 1866)
Chlidonias hybrida (PALLAS, 1811) *, *Chlidonias leucoptera* (TEMMINCK, 1815)

Quadraceps annulatus (DENNY, 1842)
Burhinus oedicnemus (LINNAEUS, 1758) *

Quadraceps auratus (DE HAAN, 1829)
Haematopus ostralegus LINNAEUS, 1758 *

Quadraceps baliola (BLAGOVESHTCHENSKY, 1951)
Gelochelidon nilotica (GMELIN, 1789) *

Quadraceps bicuspis (NITZSCH, 1874)
Charadrius dubius SCOPOLI, 1786 * HU: RÉKÁSI (1979)

Quadraceps boephilus (KELLOGG, 1896)
Charadrius vociferus LINNAEUS, 1758 *

Quadraceps caspius (GIEBEL, 1874)
Sterna caspia PALLAS, 1770 *

Quadraceps charadrii (LINNAEUS, 1758)
Pluvialis apricaria (LINNAEUS, 1758) * HU: RÉKÁSI (1984)

Quadraceps connexus (KELLOGG et MANN, 1912)
Phalaropus lobatus (LINNAEUS, 1758) * HU: RÉKÁSI (2002)

Quadraceps decipiens (DENNY, 1842)
Recurvirostra avosetta LINNAEUS, 1758 *

Quadraceps ellipticus (NITZSCH, 1866)
Glareola pratincola (LINNAEUS, 1766) *

Quadraceps eugrammicus (BURMEISTER, 1838)
Larus minutus PALLAS, 1776 *

Quadraceps falcigerus (PETERS, 1931)
Tringa flavipes (GMELIN, 1789) *

Quadraceps fimbriatus (GIEBEL, 1866)
Phalaropus tricolor (VIEILLOT, 1819) *

Quadraceps fissus (BURMEISTER, 1838)
Charadrius hiaticula LINNAEUS, 1758 *

Quadraceps furvus (BURMEISTER, 1838)
Tringa erythropus (PALLAS, 1764) * HU: BALÁT (1957)

Quadraceps grallarius TIMMERMANN, 1954
Vanellus leucurus (LICHTENSTEIN, 1823) *

Quadraceps helgovauki (TIMMERMANN, 1974)
Fratercula arctica (LINNAEUS, 1758) *

Quadraceps hemichrous (NITZSCH, 1866)
Himantopus himantopus (LINNAEUS, 1758) *

Quadraceps hiaticulae (FABRICIUS, 1780)
Charadrius hiaticula LINNAEUS, 1758 *

Quadraceps hoplopteri (MJÖBERG, 1910)
Vanellus spinosus (LINNAEUS, 1758) *

Quadraceps hospes (NITZSCH, 1866)
Pluvialis squatarola (LINNAEUS, 1758) * HU: RÉKÁSI (1984, as *Q. charadii hospes*)

Quadraceps houri HOPKINS, 1949
Sterna paradisaea PONTOPPIDAN, 1763 *

Quadraceps junceus (SCOPOLI, 1763)
Vanellus vanellus (LINNAEUS, 1758) * HU: BALÁT (1957)

Quadraceps kekra ANSARI, 1947
Gelochelidon nilotica (GMELIN, 1789) *

Quadraceps kilimandjarensis (KELLOGG, 1910)
Vanellus gregarius (PALLAS, 1771)

Quadraceps kirghizicus (KASIEV, 1982)
Glareola pratincola (LINNAEUS, 1766) *

Quadraceps lahorensis ANSARI, 1955
Philomachus pugnax (LINNAEUS, 1758) *

Quadraceps lineatus (PIAGET, 1880)
Xema sabini (SABINE, 1819) *

Quadraceps longicollis (RUDOW, 1869)
Sterna sandvicensis LATHAM, 1787 *

Quadraceps macrocephalus (WATERSTON, 1914)
Charadrius alexandrinus LINNAEUS, 1758 HU: RÉKÁSI (1986*b*, as *Q. retractus*)

Quadraceps normifer (GRUBE, 1851)
Stercorarius parasiticus (LINNAEUS, 1758) * HU: SCHÄFER (1964)

Quadraceps nycthemerus (BURMEISTER, 1838)
Sterna albifrons (PALLAS, 1764) *

Quadraceps obscurus (BURMEISTER, 1838)
Tringa glareola LINNAEUS, 1758 * HU: RÉKÁSI (1978*b*)
Tringa stagnatilis (BECHSTEIN, 1803)

Quadraceps obtusus (KELLOGG et KUWANA, 1902)
Tringa totanus (LINNAEUS, 1758) HU: BALÁT (1957, as *Q. conformis*)

Quadraceps ochropi (DENNY, 1842)
Tringa ochropus LINNAEUS, 1758 * HU: RÉKÁSI (1979)

Quadraceps orarius (KELLOGG, 1896)
Pluvialis dominica (MÜLLER, 1776) *, *Pluvialis fulva* (GMELIN, 1789)

Quadraceps ornatus lineolatus (NITZSCH, 1866)
Rissa tridactyla (LINNAEUS, 1758) *

Quadraceps ornatus ornatus (GRUBE, 1851)

Larus canus LINNAEUS, 1758 *

Quadraceps ornatus paulschulzei (TIMMERMANN, 1949)
Rissa tridactyla (LINNAEUS, 1758) *

Quadraceps ornatus striolatus (NITZSCH, 1866)
Larus argentatus PONTOPPIDAN, 1763, *Larus glaucoides* MEYER, 1822, *Larus hyperboreus* GUNNERUS, 1767 *, *Larus marinus* LINNAEUS, 1758

Quadraceps parvopallidus (EICHLER, 1951)
Stercorarius longicaudus VIEILLOT, 1819 *

Quadraceps phaeonotus (NITZSCH, 1866)
Chlidonias nigra (LINNAEUS, 1758) * HU: RÉKÁSI (1984, as *Koeniginirmus nychthemerus phaeonotus*)

Quadraceps phalaropi (DENNY 1842)
Phalaropus fulicarius (LINNAEUS, 1758) *

Quadraceps ptyadis (SÉGUY, 1949)
Charadrius leschenaultii LESSON, 1826 *

Quadraceps punctatus lingulatus TIMMERMANN, 1952
Larus pipixcan WAGLER, 1831

Quadraceps punctatus pallidus TIMMERMANN, 1952
Larus genei BRÉME, 1839 *

Quadraceps punctatus punctatus (BURMEISTER, 1838)
Larus ridibundus LINNAEUS, 1766 * HU: BALÁT (1957)
Larus ichthyaetus PALLAS, 1773

Quadraceps punctatus regressus TIMMERMANN, 1952
Larus argentatus PONTOPPIDAN, 1763 *, *Larus canus* LINNAEUS, 1758, *Larus fuscus* LINNAEUS, 1758, *Larus melanocephalus* TEMMINCK, 1820, *Sterna caspia* PALLAS, 1770

Quadraceps punctatus sublingulatus TIMMERMANN, 1952
Larus delawarensis ORD, 1815 *

Quadraceps punctifer HOPKINS, 1949
Charadrius morinellus LINNAEUS, 1758 *

Quadraceps ravus (KELLOGG, 1899)
Actitis hypoleucos (LINNAEUS, 1758) HU: RÉKÁSI (1984)

Quadraceps sellatus (BURMEISTER, 1838)
Sterna hirundo LINNAEUS, 1758 * HU: BALÁT (1957)

Quadraceps semifissus (NITZSCH, 1866)
Himantopus himantopus (LINNAEUS, 1758) * HU: RÉKÁSI (1978*a*, in *Proneptis*)
Recurvirostra avosetta LINNAEUS, 1758

Quadraceps signatus (PIAGET, 1880)
Recurvirostra avosetta LINNAEUS, 1758 * HU: SCHÄFER (1963)

Quadraceps similis (GIEBEL, 1866)
Tringa nebularia (GUNNERUS, 1767) * HU: BALÁT (1957)

Quadraceps stellaepolaris TIMMERMANN, 1952
Stercorarius pomarinus (TEMMINCK, 1815) *, *Stercorarius skua* (BRÜNNICH, 1764)

Quadraceps strepsilaris (DENNY, 1842)
Arenaria interpres (LINNAEUS, 1758) *

Rallicola *cuspidatus* (SCOPOLI, 1763)
Rallus aquaticus LINNAEUS, 1758 * HU: BALÁT (1957)

Rallicola fulicae (DENNY, 1842)
Fulica atra LINNAEUS, 1758 * HU: BALÁT (1957)

Rallicola lugens (GIEBEL, 1874)
Porphyrio porphyrio (LINNAEUS, 1758) *

Rallicola minutus (NITZSCH, 1866)
Gallinula chloropus (LINNAEUS, 1758) *

Rallicola mystax (GIEBEL, 1874)
Porzana parva (SCOPOLI, 1769), *Porzana porzana* (LINNAEUS, 1766) *

Rallicola ortygometrae (SCHRANK, 1781)
Crex crex (LINNAEUS, 1758) *

Rallicola parani EICHLER, 1954
Gallinula chloropus (LINNAEUS, 1758) *

Rallicola thompsoni TENDEIRO, 1965
Porphyrio porphyrio (LINNAEUS, 1758) *

Rhynonirmus *helvolus* (BURMEISTER, 1838)
Scolopax rusticola LINNAEUS, 1758 * HU: BALÁT (1957)

Rhynonirmus medius TIMMERMANN, 1955
Gallinago media (LATHAM, 1787) *

Rhynonirmus scolopacis (DENNY, 1842)
Gallinago gallinago (LINNAEUS, 1758) * HU: BALÁT (1957)

Rotundiceps *cordatus* (OSBORN, 1896)
Limosa lapponica (LINNAEUS, 1758)

Saemundssonia *africana* TIMMERMANN, 1954
Vanellus leucurus (LICHTENSTEIN, 1823)

Saemundssonia brevicornis (GIEBEL, 1874)
Sterna sandvicensis LATHAM, 1787 *

Saemundssonia celidoxa (BURMEISTER, 1838)
Alca torda LINNAEUS, 1758 *

Saemundssonia cephalus (DENNY, 1841)
Stercorarius parasiticus (LINNAEUS, 1758) *

Saemundssonia clayae HOPKINS, 1949
Scolopax rusticola LINNAEUS, 1758 *

Saemundssonia conica conica (DENNY, 1842)
Charadrius vociferus LINNAEUS, 1758, *Pluvialis apricaria* (LINNAEUS, 1758) *, *Pluvialis dominica* (MÜLLER, 1776), *Pluvialis fulva* (GMELIN, 1789)

Saemundssonia conica naumanni (GIEBEL, 1866)
Pluvialis squatarola (LINNAEUS, 1758) * HU: RÉKÁSI (1984, as *S. naumanni*)

Saemundssonia euryrhyncha (GIEBEL, 1874)
Stercorarius pomarinus (TEMMINCK, 1815) *, *Stercorarius skua* (BRÜNNICH, 1764)

Saemundssonia fraterculae (OVERGAARD, 1942)
Fratercula arctica (LINNAEUS, 1758) *

Saemundssonia gelochelidoni (TOULESHKOV, 1959)
Gelochelidon nilotica (GMELIN, 1789) *

Saemundssonia haematopi (LINNAEUS, 1758)
Haematopus ostralegus LINNAEUS, 1758 *

Saemundssonia inexspectata TIMMERMANN, 1951
Stercorarius longicaudus VIEILLOT, 1819

Saemundssonia intiger (NITZSCH, 1866)
Grus grus (LINNAEUS, 1758) * HU: BALÁT (1957)
Anthropoides virgo (LINNAEUS, 1785)

Saemundssonia kratochvili BALÁT, 1950
Gallinago gallinago (LINNAEUS, 1758) *, *Lymnocryptes minimus* (BRÜNNICH, 1764)

Saemundssonia lari (FABRICIUS, 1780)
Larus argentatus PONTOPPIDAN, 1763 HU: RÉKÁSI (1973, may refer to *Larus cachinnans michahellis* NAUMANN, 1840)
Larus ridibundus LINNAEUS, 1766 HU: BALÁT (1957, as *S. mülleri*)
Larus canus LINNAEUS, 1758, *Larus delawarensis* ORD, 1815, *Larus fuscus* LINNAEUS, 1758, *Larus genei* BRÉME, 1839, *Larus glaucoides* MEYER, 1822, *Larus hyperboreus* GUNNERUS, 1767 *, *Larus marinus* LINNAEUS, 1758, *Larus melanocephalus* TEMMINCK, 1820, *Larus minutus* PALLAS, 1776, *Larus pipixcan* WAGLER, 1831, *Rissa tridactyla* (LINNAEUS, 1758), *Xema sabini* (SABINE, 1819)

Saemundssonia laticaudata (RUDOW, 1869)
Sterna sandvicensis LATHAM, 1787 *

Saemundssonia limosae (DENNY, 1842)
Limosa lapponica (LINNAEUS, 1758) *

Saemundssonia lobaticeps (GIEBEL, 1874)
Chlidonias leucoptera (TEMMINCK, 1815) HU: BALÁT (1957)
Chlidonias nigra (LINNAEUS, 1758) * HU: BALÁT (1957)
Chlidonias hybrida (PALLAS, 1811)

Saemundssonia lockleyi CLAY, 1949
Sterna paradisaea PONTOPPIDAN, 1763

Saemundssonia media MARTENS, 1974
Gallinago media (LATHAM, 1787) *

Saemundssonia melanocephalus BURMEISTER, 1838
Sterna albifrons (PALLAS, 1764) *

Saemundssonia platygaster ashi TIMMERMANN, 1955
Philomachus pugnax (LINNAEUS, 1758) *

Saemundssonia platygaster cordiceps (GIEBEL, 1874)
Tringa glareola LINNAEUS, 1758 *

Saemundssonia platygaster frater (GIEBEL, 1874)
Actitis hypoleucos (LINNAEUS, 1758) *

Saemundssonia platygaster islandica TIMMERMANN, 1951
Calidris canutus (LINNAEUS, 1758) *

Saemundssonia platygaster jadwigae TIMMERMANN, 1969
Calidris alba (PALLAS, 1764) *

Saemundssonia platygaster mollis (NITZSCH, 1874)
Tringa totanus (LINNAEUS, 1758) *

Saemundssonia platygaster nitzschi (GIEBEL, 1866)
Calidris minuta (LEISLER, 1812) HU: RÉKÁSI (1984)
Calidris fuscicollis (VIEILLOT, 1819), *Tringa erythropus* (PALLAS, 1764) *, *Tringa flavipes* (GMELIN, 1789), *Tringa nebularia* (GUNNERUS, 1767), *Tringa ochropus* LINNAEUS, 1758

Saemundssonia platygaster pastoris TIMMERMANN, 1969
Charadrius alexandrinus LINNAEUS, 1758 HU: RÉKÁSI (1986*b*)

Saemundssonia platygaster platygaster (DENNY, 1842)
Charadrius hiaticula LINNAEUS, 1758 * HU: RÉKÁSI (1984)
Charadrius leschenaultii LESSON, 1826

Saemundssonia platygaster semivittata (GIEBEL, 1874)
Charadrius morinellus LINNAEUS, 1758 *

Saemundssonia platygaster stenrami (GIEBEL, 1874)
Arenaria interpres (LINNAEUS, 1758) *

Saemundssonia platygaster temporalis (GIEBEL, 1874)
Vanellus vanellus (LINNAEUS, 1758) * HU: BALÁT (1957, as *S. temporalis*)
Vanellus gregarius (PALLAS, 1771)

Saemundssonia platygaster (ssp. indet.) (DENNY, 1842)

Charadrius dubius SCOPOLI, 1786, *Himantopus himantopus* (LINNAEUS, 1758), *Xenus cinereus* (GÜLDENSTADT, 1775)

Saemundssonia scolopacisphaeopodis humeralis (DENNY, 1842)
Numenius arquata (LINNAEUS, 1758) * HU: BALÁT (1957, as *S. humeralis*)

Saemundssonia scolopacisphaeopodis scolopacisphaeopodis (SCHRANK, 1803)
Numenius phaeopus (LINNAEUS, 1758) *

Saemundssonia sternae (LINNAEUS, 1758)
Sterna hirundo LINNAEUS, 1758 * HU: BALÁT (1957)

Saemundssonia thompsoni TIMMERMANN, 1951
Limosa limosa (LINNAEUS, 1758) *

Saemundssonia tricolor CARRIKER, 1956
Phalaropus tricolor (VIEILLOT, 1819) *

Saemundssonia tringae (FABRICIUS, 1780)
Phalaropus lobatus (LINNAEUS, 1758) HU: RÉKÁSI (2002)
Arenaria interpres (LINNAEUS, 1758), *Calidris alba* (PALLAS, 1764), *Calidris alpina* (LINNAEUS, 1758), *Calidris canutus* (LINNAEUS, 1758), *Calidris ferruginea* (PONTOPPIDAN, 1763), *Calidris fuscicollis* (VIEILLOT, 1819), *Calidris maritima* (BRÜNNICH, 1764) *, *Calidris melanotos* (VIEILLOT, 1819), *Calidris minuta* (LEISLER, 1812), *Calidris pusilla* (LINNAEUS, 1766), *Calidris temminckii* (LEISLER, 1812), *Philomachus pugnax* (LINNAEUS, 1758)

Strigiphilus *aitkeni* CLAY, 1966
Tyto alba (SCOPOLI, 1769) *

Strigiphilus barbatus (OSBORN, 1902)
Asio otus (LINNAEUS, 1758) HU: BALÁT (1957, as *S. asionis*)

Strigiphilus ceblebrachys (DENNY, 1842)
Nyctea scandiaca (LINNAEUS, 1758) *

Strigiphilus crenulatus (GIEBEL, 1874)
Surnia ulula (LINNAEUS, 1758) *

Strigiphilus cursitans (NITZSCH, 1861)
Athene noctua (SCOPOLI, 1769) * HU: RÉKÁSI (1973)

Strigiphilus cursor (BURMEISTER, 1838)
Asio flammeus (PONTOPPIDAN, 1763) * HU: BALÁT (1957)

Strigiphilus goniodicerus EICHLER, 1949
Bubo bubo (LINNAEUS, 1758) *

Strigiphilus heterocerus (GRUBE, 1851)
Strix uralensis PALLAS, 1771 *

Strigiphilus heterogenitalis (EMERSON et ELBEL, 1957)
Otus scops (LINNAEUS, 1758)

Strigiphilus laticephalus (UCHIDA, 1949)
Strix aluco (LINNAEUS, 1758) * HU: RÉKÁSI (1993*b*, as *S. laticeps*)
Strix uralensis Pallas, 1771 *

Strigiphilus pallidus (GIEBEL, 1874)
Aegolius funereus (LINNAEUS, 1758) *

Strigiphilus portigi EICHLER, 1952
Strix aluco (LINNAEUS, 1758) *

Strigiphilus rostratus (BURMEISTER, 1838)
Tyto alba (SCOPOLI, 1769) * HU: BALÁT (1957)

Strigiphilus splendens (GIEBEL, 1874)
Glaucidium passerinum (LINNAEUS, 1758) *

Strigiphilus strigis (PONTOPPIDAN, 1763)
Bubo bubo (LINNAEUS, 1758) *

Strigiphilus tuleskovi BALÁT, 1958
Otus scops (LINNAEUS, 1758) *

Sturnidoecus *aeneas* (PIAGET, 1885)
Motacilla alba LINNAEUS, 1758 * HU: RÉKÁSI (1990)

Sturnidoecus atharea ANSARI, 1955
Luscinia svecica (LINNAEUS, 1758) *

Sturnidoecus blandus ZLOTORZYCKA, 1964
Carduelis carduelis (LINNAEUS, 1758) *

Sturnidoecus carpodaci (BALÁT, 1981)
Carpodacus erythrinus (PALLAS, 1770) *

Sturnidoecus chendoola ANSARI, 1955
Galerida cristata (LINNAEUS, 1758) *

Sturnidoecus hudeci (BALÁT, 1981)
Parus major LINNAEUS, 1758 *

Sturnidoecus irritans ANSARI, 1955
Saxicola torquata (LINNAEUS, 1766)

Sturnidoecus melodicus (EICHLER, 1951)
Turdus philomelos BREHM, 1831 *

Sturnidoecus pastoris (DENNY, 1842)
Sturnus roseus (LINNAEUS, 1758) * HU: RÉKÁSI (1984)

Sturnidoecus pflergi (BALÁT, 1981)
Acrocephalus palustris (BECHSTEIN, 1798) *

Sturnidoecus quadrilineatus (NITZSCH, 1866)
Aegithalos caudatus (LINNAEUS, 1758) *

Sturnidoecus radui BECHET, 1965
Oriolus oriolus (LINNAEUS, 1758) *

Sturnidoecus refractariolus (ZLOTORZYCKA, 1964)
Passer domesticus (LINNAEUS, 1758) *

Sturnidoecus ruficeps (NITZSCH, 1866)
Passer montanus (LINNAEUS, 1758) HU: BALÁT (1957)

Sturnidoecus sturni (SCHRANK, 1776)
Sturnus vulgaris LINNAEUS, 1758 * HU: BALÁT (1957)

Sturnidoecus tulackovae (BALÁT, 1981)
Locustella fluviatilis (WOLF, 1810) *

Syrrhaptoecus *bedfordi* WATERSTON, 1928
Syrrhaptes paradoxus (PALLAS, 1773) *

Syrrhaptoecus emahusaini ANSARI, 1947
Pterocles exustus TEMMINCK, 1825 *

Syrrhaptoecus falcatus WATERSTON, 1928
Pterocles exustus TEMMINCK, 1825 *

Syrrhaptoecus paradoxus (RUDOW, 1869)
Syrrhaptes paradoxus (PALLAS, 1773) *

Turturicola *salimalii* CLAY et MEINERTZHAGEN, 1937
Streptopelia decaocto (FRIVALDSZKY, 1838) *

Upupicola *upupae* (SCHRANK, 1803)
Upupa epops LINNAEUS, 1758 * HU: SCHÄFER (1963)

Mammalian lice

Suborder: AMBLYCERA

Family: Gyropidae

***Gliricola** porcelli* (SCHRANK, 1781)
Cavia porcellus (LINNAEUS, 1758) *

***Gyropus** ovalis* NITZSCH, 1818
Cavia porcellus (LINNAEUS, 1758) *

***Pitrufquenia** coypus* MARELLI, 1932
Myocastor coypus (MOLINA, 1782) *

Family: Trimenoponidae

***Trimenopon** hispidum* (BURMEISTER, 1838)
Cavia porcellus (LINNAEUS, 1758) *

Suborder: ANOPLURA

Family: Enderleinellidae

***Enderleinellus** ferrisi* (TOULESHKOV, 1957)
Spermophilus citellus (LINNAEUS, 1766) * HU: (PIOTROWSKI 1970)

Enderleinellus nitzschi FAHRENHOLZ, 1916
Sciurus vulgaris LINNAEUS, 1758 * HU: (PIOTROWSKI 1970)

Enderleinellus propinquus BLAGOVESHTCHENSKY, 1965
Spermophilus citellus (LINNAEUS, 1766)

Family: Haematopinidae

***Haematopinus** apri* GOUREAU, 1866
Sus scrofa LINNAEUS, 1758 * HU: (PIOTROWSKI 1970)

Haematopinus asini (LINNAEUS, 1758)
Equus asinus LINNAEUS, 1758 *, *Equus caballus* LINNAEUS, 1758

Haematopinus eurysternus (NITZSCH, 1818)
Bos taurus LINNAEUS, 1758 * HU: (PIOTROWSKI 1970)

Haematopinus suis (LINNAEUS, 1758)
Sus domesticus LINNAEUS, 1758 * HU: (PIOTROWSKI 1970)

Haematopinus tuberculatus (BURMEISTER, 1839)
Bubalus bubalis LINNAEUS, 1758 *

Family: Hoplopleuridae

***Hoplopleura** acanthopus* (BURMEISTER, 1839)
Arvicola amphibius (LINNAEUS, 1758) HU: (PIOTROWSKI 1970)
Microtus agrestis (LINNAEUS, 1761) HU: (PIOTROWSKI 1970)
Microtus arvalis (LINNAEUS, 1761) * HU: (PIOTROWSKI 1970)
Microtus oeconomus (PALLAS, 1776) HU: (PIOTROWSKI 1970)
Microtus subterraneus (SÉLYS-LONGCHAMPS, 1836) HU: (PIOTROWSKI 1970)
Myodes glareolus (SCHREBER, 1780) HU: (PIOTROWSKI 1970)

Hoplopleura affinis (BURMEISTER, 1839)
Apodemus agrarius PALLAS, 1771 * HU: (PIOTROWSKI 1970)
Apodemus sylvaticus (LINNAEUS, 1758) HU: (PIOTROWSKI 1970)
Apodemus flavicollis (MELCHIOR, 1834)

Hoplopleura captiosa JOHNSON, 1960
Mus spicilegus PETÉNYI, 1882 HU: (PIOTROWSKI 1970) – not included in DURDEN & MUSSER (1994); as a sibling species of *Mus musculus*, likely to be a regular host
Mus musculus LINNAEUS, 1758 *

Hoplopleura edentula FAHRENHOLZ, 1916
Myodes glareolus (SCHREBER, 1780)

Hoplopleura longula (NEUMANN, 1909)
Micromys minutus (PALLAS, 1771) * HU: (PIOTROWSKI 1970)

Hoplopleura pacifica EWING, 1924
Rattus norvegicus (BERKENHOUT, 1769), *Rattus rattus* (LINNAEUS, 1758)

***Schizophthirus** dryomydis* BLAGOVESHTCHENSKY, 1965
Dryomys nitedula PALLAS, 1778 *

Schizophthirus gliris BLAGOVESHTCHENSKY, 1965
Glis glis (LINNAEUS, 1766) *

Schizophthirus jaczewskii CAIS, 1974
Dryomys nitedula PALLAS, 1778 *

Schizophthirus pleurophaeus (BURMEISTER, 1839)
Dryomys nitedula PALLAS, 1778, *Glis glis* (LINNAEUS, 1766), *Muscardinus avellanarius* (LINNAEUS, 1758)

Schizophthirus sicistae BLAGOVESHTCHENSKY, 1965
Sicista subtilis PALLAS 1773 *

Family: Linognathidae

Linognathus *africanus* KELLOGG et PAINE, 1911
Capra hircus LINNAEUS, 1758, *Ovis aries* LINNAEUS, 1758 *, *Ovis musimon* LINNAEUS, 1758

Linognathus setosus (VON OLFERS, 1816)
Canis familiaris (LINNAEUS, 1758) * HU: (PIOTROWSKI 1970)
Canis aureus LINNAEUS, 1758, *Canis lupus* LINNAEUS, 1758, *Vulpes vulpes* (LINNAEUS, 1758)

Linognathus stenopsis (BURMEISTER, 1838)
Capra hircus LINNAEUS, 1758 * HU: (PIOTROWSKI 1970)
Rupicapra rupicapra (LINNAEUS, 1758)

Linognathus ovillus (NEUMANN, 1907)
Ovis aries LINNAEUS, 1758 *, *Ovis musimon* LINNAEUS, 1758

Linognathus pedalis (OSBORN, 1896)
Ovis aries LINNAEUS, 1758 *, *Ovis musimon* LINNAEUS, 1758

Linognathus vituli (LINNAEUS, 1758)
Bos taurus LINNAEUS, 1758 * HU: (PIOTROWSKI 1970)

Solenopotes *burmeisteri* (FAHRENHOLZ, 1919)
Cervus elaphus LINNAEUS, 1758 * HU: (PIOTROWSKI 1970)

Solenopotes capillatus ENDERLEIN, 1904
Bos taurus LINNAEUS, 1758 * HU: (HORNOK *et al*. 2010.)

Solenopotes capreoli FREUND, 1935
Capreolus capreolus LINNAEUS, 1758 * HU: (BERDÁR 1983)

Family: Pediculidae

Pediculus humanus LINNAEUS, 1758 – both "*P. h. capitis*" and "*P. h. humanus*" ecotypes
Homo sapiens LINNAEUS, 1758 * HU: (PIOTROWSKI 1970)

Family Polyplacidae

Haemodipsus *lyriocephalus* (BURMEISTER, 1839)
Lepus europaeus Pallas, 1778 HU: (BEAUCOURNU 1968)

Haemodipsus ventricosus (DENNY, 1842)
Oryctolagus cuniculus (LINNAEUS, 1758) *, *Oryctolagus domesticus* (LINNAEUS, 1758)

Linognathoides *laeviusculus* (GRUBE, 1851)
Spermophilus citellus (LINNAEUS, 1766)

Neohaematopinus *sciuri* JANCKE, 1932
Sciurus vulgaris LINNAEUS, 1758 *

Polyplax *borealis* FERRIS, 1933
Arvicola amphibius (LINNAEUS, 1758), *Myodes glareolus* (SCHREBER, 1780)

Polyplax bureschi TOULESHKOV, 1957
Spermophilus citellus (LINNAEUS, 1766) *

Polyplax gracilis FAHRENHOLZ, 1910
Micromys minutus (PALLAS, 1771) * HU: (PIOTROWSKI 1970)

Polyplax hannswrangeli EICHLER, 1952

Myodes glareolus (SCHREBER, 1780) *

Polyplax reclinata (NITZSCH, 1864)

Crocidura suaveolens (PALLAS, 1811) HU: (HAITLINGER 1973)

Crocidura leucodon (HERMANN, 1780), *Neomys fodiens* (PENNANT, 1771), *Sorex araneus* LINNAEUS, 1758 *, *Sorex minutus* LINNAEUS, 1766

Polyplax serrata (BURMEISTER, 1839)

Apodemus agrarius PALLAS, 1771 HU: (PIOTROWSKI 1970)
Apodemus flavicollis (MELCHIOR, 1834) HU: (PIOTROWSKI 1970)
Apodemus sylvaticus (LINNAEUS, 1758) HU: (HAITLINGER 1973)
Apodemus uralensis (PALLAS, 1811) HU: (HAITLINGER 1973)
Mus musculus LINNAEUS, 1758 * HU: (PIOTROWSKI 1970)

Polyplax spinigera (BURMEISTER, 1839)

Arvicola amphibius (LINNAEUS, 1758) *

Polyplax spinulosa (BURMEISTER, 1839)

Rattus norvegicus (BERKENHOUT, 1769) *, *Rattus rattus* (LINNAEUS, 1758)

Family Pthiridae

***Pthirus** pubis* (LINNAEUS, 1758)

Homo sapiens LINNAEUS, 1758 * HU: (PIOTROWSKI 1970)

Suborder: ISCHNOCERA

Family: Trichodectidae

***Bovicola** alpinus* KÉLER, 1942

Rupicapra rupicapra LINNAEUS, 1758 *

Bovicola bovis (LINNAEUS, 1758)

Bos taurus LINNAEUS, 1758 * HU: (EGRI & NAGY 1995)

Bovicola caprae (GURLT, 1843)

Capra hircus LINNAEUS, 1758 * HU: (PIOTROWSKI 1970)

Bovicola crassipes (RUDOW, 1866)
Capra hircus LINNAEUS, 1758

Bovicola equi (DENNY, 1842)
Equus caballus LINNAEUS, 1758 * HU: (EGRI 1990)

Bovicola limbatus (GERVAIS, 1844)
Capra hircus LINNAEUS, 1758

Bovicola longicornis (NITZSCH, 1818)
Cervus elaphus LINNAEUS, 1758 * HU: (SUGÁR 1997)

Bovicola ocellatus (PIAGET, 1880)
Equus asinus LINNAEUS, 1758

Bovicola ovis (SCHRANK, 1781)
Ovis aries LINNAEUS, 1758 *, *Ovis musimon* LINNAEUS, 1758

Bovicola tibialis (PIAGET, 1880)
Dama dama (LINNAEUS, 1758) *

***Damalinia** meyeri* (TASCHENBERG, 1882)
Capreolus capreolus LINNAEUS, 1758 HU: (SUGÁR 1985)

***Felicola** hercynianus* KÉLER, 1957
Felis silvestris SCHREBER, 1775 *

Felicola spenceri HOPKINS, 1960
Lynx lynx LINNAEUS, 1758 *

Felicola subrostratus (BURMEISTER, 1838)
Felis catus (LINNAEUS, 1758) * HU: (SZILVÁSSY 2006)

Felicola vulpis DENNY, 1842

Vulpes vulpes (LINNAEUS, 1758) * – RÉKÁSI (1979) collected a single individual from an atypical host *Microtus arvalis* PALLAS, 1778

***Lutridia** exilis* (NITZSCH [in GIEBEL], 1861)
Lutra lutra (LINNAEUS, 1758) *

***Stachiella** ermineae* HOPKINS, 1941
Mustela erminea LINNAEUS, 1758 * HU: RÉKÁSI (1983)

Stachiella jacobi EICHLER, 1941
Mustela putorius LINNAEUS, 1758 *

Stachiella mustelae (SCHRANK, 1803)
Mustela nivalis LINNAEUS, 1766 * HU: RÉKÁSI (1979)

Stachiella octomaculatus (PAINE, 1912)
Procyon lotor (LINNAEUS, 1758) *

Stachiella retusa (BURMEISTER, 1838)
Martes foina (ERXLEBEN, 1777) *

Stachiella salfii CONCI, 1940
Martes martes (LINNAEUS, 1758) *

***Trichodectes** canis* (DE GEER, 1778)
Canis familiaris (LINNAEUS, 1758) * HU: (PIOTROWSKI 1970)
Canis aureus LINNAEUS, 1758, *Canis lupus* LINNAEUS, 1758, *Nyctereutes procyonoides* (GRAY, 1834)

Trichodectes melis (FABRICIUS, 1805)
Meles meles (LINNAEUS, 1758) * HU: RÉKÁSI (1979)

Trichodectes pinguis BURMEISTER, 1838
Ursus arctos LINNAEUS, 1758 *

CHECKLIST ORDERED BY HOSTS

Wild birds with louse associations

Order: GALLIFORMES

Family: Phasianidae

Coturnix *coturnix* (LINNAEUS, 1758)

Cuculotogaster cinereus (NITZSCH, 1866) * HU: BALÁT (1957)

Amyrsidea fulvomaculata (DENNY, 1842) *, *Goniodes astrocephalus* (BURMEISTER, 1838) *, *Menacanthus abdominalis* (PIAGET, 1880) *

Lyrurus *tetrix* (LINNAEUS, 1758)

Amyrsidea lagopi (GRUBE, 1851), *Cuculotogaster cameratus* (DE HAAN, 1829) *, *Goniodes tetraonis* (LINNAEUS, 1761) *, *Lagopoecus lyrurus* CLAY, 1938 *, *Menopon deryloi* ZLOTORZYCKA, 1972 *, *Oxylipeurus minor* (ZLOTORZYCKA, 1966) *

Perdix *perdix* (LINNAEUS, 1758)

Cuculotogaster heterogrammicus (NITZSCH, 1866) * HU: BALÁT (1957)
Goniodes dispar BURMEISTER, 1838 * HU: RÉKÁSI (1993*b*)
Menopon pallens CLAY, 1949 * HU: BALÁT (1957)
Amyrsidea perdicis (DENNY, 1842) *, *Goniocotes microthorax* (STEPHENS, 1829) *, *Lipeurus maculosus* CLAY, 1938

Phasianus *colchicus* LINNAEUS, 1758

Amyrsidea perdicis (DENNY, 1842) HU: RÉKÁSI (1984, as *A. megalosoma*)
Goniocotes chrysocephalus GIEBEL, 1874 * HU: BALÁT (1957)
Lipeurus maculosus CLAY, 1938 * HU: BALÁT (1957)
Oxylipeurus colchicus CLAY, 1938 * HU: RÉKÁSI (1973)
Cuculotogaster heterographus (NITZSCH, 1866), *Goniodes capitatus* (KÉLER, 1939) *, *Goniodes colchici* DENNY, 1842 *, *Lagopoecus colchicus* EMERSON, 1949 *, *Lipeurus caponis* (LINNAEUS, 1758), *Menacanthus phasiani* (MODRZEJEWSKA et ZLOTORZYCKA, 1977) *, *Menacanthus stramineus* (NITZSCH, 1818)

Tetrao *urogallus* LINNAEUS, 1758

Goniodes bituberculatus RUDOW, 1869 * HU: RÉKÁSI (1978*a*)

Amyrsidea lagopi (GRUBE, 1851), *Lagopoecus pallidovittatus* (GRUBE, 1851) *, *Oxylipeurus tetraonis* (GRUBE, 1851) *

Tetrastes *bonasia* (LINNAEUS, 1758)
Goniocotes megalocephalus UCHIDA, 1916 *, *Lagopoecus tetrastei* BECHET, 1963 *

Order: ANSERIFORMES
Family: Anatidae
Alopochen *aegyptiacus* (LINNAEUS, 1766)
Acidoproctus taschenbergi HOPKINS, 1938 *, *Anaticola asymmetricus* (RUDOW, 1869) *, *Anatoecus dentatus* (SCOPOLI, 1763), *Anatoecus icterodes* (NITZSCH, 1818), *Holomenopon tadornae* (GERVAIS, 1844), *Trinoton alpochen* TENDEIRO, 1960 *

Anas *acuta* LINNAEUS, 1758
Anaticola crassicornis (SCOPOLI, 1763), *Anatoecus dentatus* (SCOPOLI, 1763), *Anatoecus icterodes* (NITZSCH, 1818), *Holomenopon acutae* PRICE, 1971 *, *Holomenopon clypeilargum* EICHLER, 1943 *, *Holomenopon leucoxanthum* (BURMEISTER, 1838), *Holomenopon setigerum* (BLAGOVESHTCHENSKY, 1948), *Trinoton querquedulae* (LINNAEUS, 1758)

Anas americana GMELIN, 1789
Anaticola crassicornis (SCOPOLI, 1763), *Holomenopon clypeilargum* EICHLER, 1943, *Holomenopon leucoxanthum* (BURMEISTER, 1838), *Trinoton querquedulae* (LINNAEUS, 1758)

Anas clypeata LINNAEUS, 1758
Anaticola crassicornis (SCOPOLI, 1763) HU: RÉKÁSI (1984, as *A. hopkinsi*)
Anatoecus dentatus (SCOPOLI, 1763) HU: BALÁT (1957, as *A. ferrugineus*)
Anatoecus icterodes (NITZSCH, 1818) HU: RÉKÁSI (1984)
Holomenopon setigerum (BLAGOVESHTCHENSKY, 1948) * HU: RÉKÁSI (1984)
Holomenopon clypeilargum EICHLER, 1943, *Holomenopon leucoxanthum* (BURMEISTER, 1838), *Trinoton querquedulae* (LINNAEUS, 1758)

Anas crecca LINNAEUS, 1758
Anaticola crassicornis (SCOPOLI, 1763) HU: BALÁT (1957, as *A. sordidus*)
Anatoecus icterodes (NITZSCH, 1818) HU: RÉKÁSI (1984)

Holomenopon leucoxanthum (BURMEISTER, 1838) * HU: RÉKÁSI (1978*b*)
Trinoton querquedulae (LINNAEUS, 1758) * HU: SCHÄFER (1964)
Anatoecus dentatus (SCOPOLI, 1763), *Holomenopon clypeilargum* EICHLER, 1943, *Holomenopon setigerum* (BLAGOVESHTCHENSKY, 1948)

Anas penelope LINNAEUS, 1758
Anaticola crassicornis (SCOPOLI, 1763), *Anatoecus dentatus* (SCOPOLI, 1763) *Anatoecus icterodes* (NITZSCH, 1818), *Holomenopon clypeilargum* EICHLER, 1943, *Holomenopon leucoxanthum* (BURMEISTER, 1838), *Trinoton querquedulae* (LINNAEUS, 1758)

Anas platyrhynchos LINNAEUS, 1758
Anaticola crassicornis (SCOPOLI, 1763) * HU: BALÁT (1957)
Anatoecus dentatus (SCOPOLI, 1763) * HU: BALÁT (1957)
Anatoecus icterodes (NITZSCH, 1818) HU: RÉKÁSI (1984)
Holomenopon transvaalense (BEDFORD, 1920) * HU: RÉKÁSI (1984)
Trinoton querquedulae (LINNAEUS, 1758) HU: RÉKÁSI (1973)
Holomenopon leucoxanthum (BURMEISTER, 1838), *Holomenopon maxbeieri* EICHLER, 1954 *

Anas querquedula LINNAEUS, 1758
Anaticola crassicornis (SCOPOLI, 1763) HU: RÉKÁSI (1984, as *A. sordidus*)
Anatoecus dentatus (SCOPOLI, 1763), *Anatoecus icterodes* (NITZSCH, 1818), *Holomenopon clypeilargum* EICHLER, 1943, *Holomenopon setigerum* (BLAGOVESHTCHENSKY, 1948), *Trinoton querquedulae* (LINNAEUS, 1758)

Anas strepera LINNAEUS, 1758
Anaticola crassicornis (SCOPOLI, 1763) HU: BALÁT (1957, as *A. depuratus*)
Anatoecus dentatus (SCOPOLI, 1763), *Anatoecus icterodes* (NITZSCH, 1818), *Holomenopon clypeilargum* EICHLER, 1943, *Holomenopon leucoxanthum* (BURMEISTER, 1838), *Holomenopon setigerum* (BLAGOVESHTCHENSKY, 1948), *Trinoton querquedulae* (LINNAEUS, 1758)

Anser *albifrons* (SCOPOLI, 1769)
Anaticola anseris (LINNAEUS, 1758) HU: BALÁT (1957, as *A. serratus*)
Anatoecus icterodes (NITZSCH, 1818) HU: BALÁT (1957, as *A. brunneiceps*)

Anatoecus dentatus (SCOPOLI, 1763), *Ciconiphilus pectiniventris* (HARRISON, 1916), *Trinoton anserinum* (FABRICIUS, 1805)

Anser anser (LINNAEUS, 1758)
Anaticola anseris (LINNAEUS, 1758) * HU: SCHÄFER (1963)
Anatoecus icterodes (NITZSCH, 1818) HU: RÉKÁSI (1984)
Ornithobius mathisi (Neumann, 1912) * HU: RÉKÁSI (1984)
Trinoton anserinum (Fabricius, 1805) * HU: RÉKÁSI (1978*a*)
Anatoecus dentatus (SCOPOLI, 1763), *Ciconiphilus pectiniventris* (HARRISON, 1916) *, *Holomenopon leucoxanthum* (BURMEISTER, 1838)

Anser brachyrhynchus BAILLON, 1834
Anaticola anseris (LINNAEUS, 1758), *Ciconiphilus pectiniventris* (HARRISON, 1916)

Anser caerulescens (LINNAEUS, 1758)
Anaticola anseris (LINNAEUS, 1758), *Anatoecus dentatus* (SCOPOLI, 1763), *Anatoecus icterodes* (NITZSCH, 1818), *Ciconiphilus pectiniventris* (HARRISON, 1916), *Trinoton anserinum* (FABRICIUS, 1805)

Anser erythropus (LINNAEUS, 1758)
Anatoecus dentatus (SCOPOLI, 1763)

Anser fabalis (LATHAM, 1787)
Anaticola anseris (LINNAEUS, 1758), *Anatoecus dentatus* (SCOPOLI, 1763), *Anatoecus icterodes* (NITZSCH, 1818), *Ciconiphilus pectiniventris* (HARRISON, 1916), *Ornithobius mathisi* (NEUMANN, 1912)

Anser indicus (LATHAM, 1790)
Anaticola anseris (LINNAEUS, 1758), *Ciconiphilus pectiniventris* (HARRISON, 1916), *Trinoton anserinum* (FABRICIUS, 1805)

***Aythya** ferina* (LINNAEUS, 1758)
Anatoecus icterodes (NITZSCH, 1818) HU: SCHÄFER (1963)
Trinoton querquedulae (LINNAEUS, 1758) HU: RÉKÁSI (1979, as *T. nyrocae*)
Anaticola mergiserrati (DE GEER, 1778), *Anatoecus dentatus* (SCOPOLI, 1763), *Holomenopon leucoxanthum* (BURMEISTER, 1838)

Aythya fuligula (LINNAEUS, 1758)
Anatoecus dentatus (SCOPOLI, 1763) HU: RÉKÁSI (2002)
Anaticola mergiserrati (DE GEER, 1778), *Anatoecus icterodes* (NITZSCH, 1818), *Holomenopon leucoxanthum* (BURMEISTER, 1838), *Trinoton querquedulae* (LINNAEUS, 1758)

Aythya marila (LINNAEUS, 1761)
Anaticola mergiserrati (DE GEER, 1778), *Anatoecus dentatus* (SCOPOLI, 1763), *Anatoecus icterodes* (NITZSCH, 1818), *Holomenopon clypeilargum* EICHLER, 1943, *Holomenopon leucoxanthum* (BURMEISTER, 1838), *Trinoton querquedulae* (LINNAEUS, 1758)

Aythya nyroca (GÜLDENSTADT, 1770)
Anaticola mergiserrati (DE GEER, 1778) HU: RÉKÁSI (1984, as *A. fuligulae*)
Anatoecus dentatus (SCOPOLI, 1763) HU: RÉKÁSI (1984)
Anatoecus icterodes (NITZSCH, 1818), *Trinoton querquedulae* (LINNAEUS, 1758)

***Branta** bernicla* (LINNAEUS, 1758)
Anaticola rheinwaldi EICHLER et VASJUKOVA, 1980 *, *Anatoecus dentatus* (SCOPOLI, 1763), *Anatoecus icterodes* (NITZSCH, 1818), *Ciconiphilus pectiniventris* (HARRISON, 1916), *Holomenopon tadornae* (GERVAIS, 1844)

Branta canadensis (LINNAEUS, 1758)
Anaticola anseris (LINNAEUS, 1758) HU: SCHÄFER (1963)
Anatoecus dentatus (SCOPOLI, 1763), *Anatoecus icterodes* (NITZSCH, 1818), *Ciconiphilus pectiniventris* (HARRISON, 1916), *Holomenopon leucoxanthum* (BURMEISTER, 1838), *Ornithobius goniopleurus* DENNY, 1842 *, *Trinoton anserinum* (FABRICIUS, 1805)

Branta leucopsis (BECHSTEIN, 1803)
Anaticola anseris (LINNAEUS, 1758), *Anatoecus dentatus* (SCOPOLI, 1763), *Anatoecus icterodes* (NITZSCH, 1818), *Ciconiphilus pectiniventris* (HARRISON, 1916), *Ornithobius hexophthalmus* (NITZSCH, 1818)

Branta ruficollis (PALLAS, 1769)
Anaticola beieri EICHLER, 1954 *, *Anatoecus icterodes* (NITZSCH, 1818)

***Bucephala** albeola* (LINNAEUS, 1758)
Anatoecus dentatus (SCOPOLI, 1763), *Holomenopon bucephalae* PRICE, 1971, *Holomenopon clanuseni* PRICE, 1971, *Holomenopon leucoxanthum* (BURMEISTER, 1838), *Trinoton querquedulae* (LINNAEUS, 1758)

Bucephala clangula (LINNAEUS, 1758)
Anatoecus icterodes (NITZSCH, 1818) HU: RÉKÁSI (1978*a*)
Trinoton querquedulae (LINNAEUS, 1758) HU: SCHÄFER (1964)
Anaticola clangulae (FABRICIUS, 1780), *Anatoecus dentatus* (SCOPOLI, 1763), *Ciconiphilus cygni* (PRICE et BEER, 1965), *Holomenopon bucephalae* PRICE, 1971

Bucephala islandica (GMELIN, 1789)
Anaticola clangulae (FABRICIUS, 1780), *Anatoecus dentatus* (SCOPOLI, 1763), *Anatoecus icterodes* (NITZSCH, 1818), *Trinoton querquedulae* (LINNAEUS, 1758)

***Clangula** hyemalis* (LINNAEUS, 1758)
Anaticola branderi EICHLER et HACKMAN, 1973 *, *Anatoecus dentatus* (SCOPOLI, 1763), *Anatoecus icterodes* (NITZSCH, 1818), *Holomenopon leucoxanthum* (BURMEISTER, 1838), *Trinoton querquedulae* (LINNAEUS, 1758)

***Cygnus** columbianus* (ORD, 1815)
Anatoecus cygni (DENNY, 1842) *, *Ciconiphilus cygni* PRICE et BEER, 1965, *Ornithobius cygni* (LINNAEUS, 1758), *Ornithobius waterstoni* (TIMMERMANN, 1962), *Trinoton anserinum* (FABRICIUS, 1805)

Cygnus cygnus (LINNAEUS, 1758)
Anaticola crassicornis (SCOPOLI, 1763), *Anatoecus cygni* (DENNY, 1842), *Ciconiphilus cygni* PRICE et BEER, 1965 *, *Ornithobius cygni* (LINNAEUS, 1758) *, *Trinoton anserinum* (FABRICIUS, 1805)

Cygnus olor (GMELIN, 1789)
Trinoton anserinum (Fabricius, 1805) HU: RÉKÁSI (2008*a*, as *T. cygni*)
Anatoecus dentatus (SCOPOLI, 1763), *Anatoecus icterodes* (NITZSCH, 1818), *Anatoecus penicillatus* KÉLER, 1960 *, *Ciconiphilus cygni* PRICE et BEER, 1965, *Ciconiphilus pectiniventris* (HARRISON, 1916), *Ornithobius bucephalus* (GIEBEL, 1874) *

***Melanitta** fusca* (LINNAEUS, 1758)
Anaticola mergiserrati (DE GEER, 1778), *Anatoecus dentatus* (SCOPOLI, 1763), *Anatoecus icterodes* (NITZSCH, 1818), *Holomenopon loomisii* (KELLOGG, 1896) *, *Trinoton querquedulae* (LINNAEUS, 1758)

Melanitta nigra (LINNAEUS, 1758)
Anaticola angustolimbatus (GIEBEL, 1866) *, *Anatoecus dentatus* (SCOPOLI, 1763), *Anatoecus icterodes* (NITZSCH, 1818), *Holomenopon leucoxanthum* (BURMEISTER, 1838), *Trinoton querquedulae* (LINNAEUS, 1758)

***Mergellus** albellus* (LINNAEUS, 1758)
Anatoecus dentatus (SCOPOLI, 1763), *Anatoecus icterodes* (NITZSCH, 1818), *Trinoton querquedulae* (LINNAEUS, 1758)

***Mergus** merganser* LINNAEUS, 1758
Anaticola mergiserrati (DE GEER, 1778), *Anatoecus dentatus* (SCOPOLI, 1763), *Anatoecus icterodes* (NITZSCH, 1818), *Holomenopon clypeilargum* EICHLER, 1943, *Trinoton querquedulae* (LINNAEUS, 1758)

Mergus serrator LINNAEUS, 1758
Anaticola mergiserrati (DE GEER, 1778) *, *Anatoecus dentatus* (SCOPOLI, 1763), *Anatoecus icterodes* (NITZSCH, 1818) *, *Holomenopon loomisii* (KELLOGG, 1896), *Trinoton querquedulae* (LINNAEUS, 1758)

***Netta** rufina* (PALLAS, 1773)
Acidoproctus moschatae (LINNAEUS, 1758), *Anaticola mergiserrati* (DE GEER, 1778), *Anatoecus dentatus* (SCOPOLI, 1763), *Anatoecus icterodes* (NITZSCH, 1818), *Holomenopon leucoxanthum* (BURMEISTER, 1838), *Trinoton querquedulae* (LINNAEUS, 1758)

***Oxyura** jamaicensis* (GMELIN, 1789)
Anaticola crassicornis (SCOPOLI, 1763), *Anatoecus dentatus* (SCOPOLI, 1763), *Anatoecus icterodes* (NITZSCH, 1818), *Holomenopon leucoxanthum* (BURMEISTER, 1838), *Trinoton querquedulae* (LINNAEUS, 1758)

Oxyura leucocephala (SCOPOLI, 1769)

Anatoecus dentatus (SCOPOLI, 1763), *Anatoecus icterodes* (NITZSCH, 1818)

Polysticta *stelleri* (PALLAS, 1769)

Anaticola klockenhoffi EICHLER et VASJUKOVA, 1980 *, *Anatoecus dentatus* (SCOPOLI, 1763), *Trinoton querquedulae* (LINNAEUS, 1758)

Somateria *mollissima* (LINNAEUS, 1758)

Anaticola mergiserrati (DE GEER, 1778) HU: RÉKÁSI (1998*b*)
Anatoecus icterodes (NITZSCH, 1818) HU: RÉKÁSI (1998*b*)
Anatoecus dentatus (SCOPOLI, 1763), *Holomenopon loomisii* (KELLOGG, 1896), *Trinoton querquedulae* (LINNAEUS, 1758)

Somateria spectabilis (LINNAEUS, 1758)

Anaticola crassicornis (SCOPOLI, 1763), *Anatoecus dentatus* (SCOPOLI, 1763), *Holomenopon loomisii* (KELLOGG, 1896), *Trinoton querquedulae* (LINNAEUS, 1758)

Tadorna *ferruginea* (PALLAS, 1764)

Anaticola magnificus ANSARI, 1955 *, *Anatoecus regina* ANSARI, 1955 *, *Holomenopon tadornae* (GERVAIS, 1844)

Tadorna tadorna (LINNAEUS, 1758)

Anaticola tadornae (DENNY, 1842) * HU: RÉKÁSI (1978*a*)
Anatoecus dentatus (SCOPOLI, 1763), *Anatoecus icterodes* (NITZSCH, 1818), *Holomenopon leucoxanthum* (BURMEISTER, 1838), *Holomenopon tadornae* (GERVAIS, 1844) *

Order: GAVIIFORMES

Family: Gaviidae

Gavia *arctica* (LINNAEUS, 1758)

Craspedonirmus colymbinus (DENNY, 1842) HU: RÉKÁSI (1984)

Gavia immer (BRÜNNICH, 1764)

Craspedonirmus immer EMERSON, 1955 *

Gavia stellata (PONTOPPIDAN, 1763)

Craspedonirmus colymbinus (DENNY, 1842) *

Order: PODICIPEDIFORMES

Family: Podicipedidae

Podiceps auritus (LINNAEUS, 1758)

Aquanirmus bucomfishi EDWARDS, 1965 *, *Aquanirmus colymbinus* (SCOPOLI, 1763) *, *Pseudomenopon dolium* (RUDOW, 1869)

Podiceps cristatus (LINNAEUS, 1758)

Aquanirmus podicepis (DENNY, 1842) * HU: RÉKÁSI (1984)
Pseudomenopon dolium (RUDOW, 1869) *

Podiceps grisegena (BODDAERT, 1783)

Aquanirmus emersoni EDWARDS, 1965 *, *Pseudomenopon dolium* (RUDOW, 1869)

Podiceps nigricollis BREHM, 1831

Aquanirmus americanus (KELLOGG et CHAPMAN, 1899) *, *Laemobothrion simile* KELLOGG, 1896 *, *Pseudomenopon dolium* (RUDOW, 1869)

***Tachybaptus** ruficollis* (PALLAS, 1764)

Aquanirmus bahli TANDAN, 1951 *, *Aquanirmus runcinatus* (NITZSCH, 1866) *, *Pseudomenopon dolium* (RUDOW, 1869)

Order: CICONIIFORMES

Family: Phoenicopteridae

***Phoenicopterus** ruber* LINNAEUS 1758

Anaticola candidus (RUDOW, 1869) *, *Anaticola phoenicopteri* (COINDE, 1859) *, *Anatoecus keleri* CLAY, 1962 *, *Anatoecus pygaspis* (NITZSCH, 1866) *, *Colpocephalum heterosoma* PIAGET, 1880 *, *Colpocephalum rosei* PRICE et EMERSON, 1974 *, *Colpocephalum salimalii* CLAY, 1951 *, *Trinoton femoratum* PIAGET, 1889 *

Family: Ciconiidae

***Ciconia** ciconia* (LINNAEUS, 1758)

Ardeicola ciconiae (LINNAEUS, 1758) * HU: RÉKÁSI (1984)
Ciconiphilus quadripustulatus (BURMEISTER, 1838) * HU: RÉKÁSI (1984)
Colpocephalum zebra BURMEISTER, 1838 * HU: SCHÄFER (1963)
Neophilopterus incompletus (DENNY, 1842) * HU: SCHÄFER (1963)

Ciconia nigra (LINNAEUS, 1758)

Ardeicola maculatus (NITZSCH, 1866) * HU: RÉKÁSI (1979)

Ciconiphilus quadripustulatus (BURMEISTER, 1838) HU: SCHÄFER (1963, in *Colpocephalum*)

Neophilopterus tricolor (BURMEISTER, 1838) * HU: SCHÄFER (1963)

Colpocephalum nigrae PRICE et BEER, 1965 *

Family: Threskiornithidae

***Platalea** leucorodia* LINNAEUS, 1758

Ardeicola plataleae (LINNAEUS, 1758) * HU: SCHÄFER (1963)

Eucolpocephalum femorale (PIAGET, 1880) * HU: RÉKÁSI (1978*a*)

Ibidoecus plataleae (DENNY, 1842) * HU: SCHÄFER (1963)

Colpocephalum plataleae PRICE et BEER, 1965 *

***Plegadis** falcinellus* (LINNAEUS, 1766)

Ardeicola rhaphidius (NITZSCH, 1866) * HU: RÉKÁSI (1978*a*)

Colpocephalum leptopygos NITZSCH, 1874 * HU: SCHÄFER (1964)

Ibidoecus bisignatus (NITZSCH, 1866) * HU: RÉKÁSI (1978*a*)

Plegadiphilus plegadis (DUBININ, 1938) * HU: SCHÄFER (1964)

Family: Ardeidae

***Ardea** alba* (LINNAEUS, 1758)

Ardeicola expallidus BLAGOVESHTCHENSKY, 1940 HU: RÉKÁSI *et al*. (2002, as *A. albulus*)

Ciconiphilus decimfasciatus (BOISDUVAL et LACORDAIRE, 1835)

Ardea cinerea LINNAEUS, 1758

Ardeicola ardeae (LINNAEUS, 1758) * HU: BALÁT (1957)

Ciconiphilus decimfasciatus (BOISDUVAL et LACORDAIRE, 1835) *

Ardea purpurea LINNAEUS, 1766

Ardeicola leucoproctus (NITZSCH, 1866) * HU: RÉKÁSI (1973)

Ciconiphilus decimfasciatus (BOISDUVAL et LACORDAIRE, 1835), *Comatomenopon elbeli* EMERSON, 1958 *

Ardeola *ralloides* (SCOPOLI, 1769)
Ardeiphilus vittatus (RUDOW, 1866) * HU: SCHÄFER (1963, in *Colpocephalum*)
Ciconiphilus decimfasciatus (BOISDUVAL et LACORDAIRE, 1835) HU: SCHÄFER (1964, in *Colpocephalum*)

Botaurus *stellaris* (LINNAEUS, 1758)
Ardeicola stellaris (DENNY 1842) *, *Ardeiphilus trochioxus* (BURMEISTER, 1838) *

Bubulcus *ibis* (LINNAEUS, 1758)
Ardeicola expallidus BLAGOVESHTCHENSKY, 1940, *Ciconiphilus decimfasciatus* (BOISDUVAL et LACORDAIRE, 1835), *Comatomenopon ibis* EMERSON, 1958 *

Egretta *garzetta* (LINNAEUS, 1766)
Ardeicola expallidus BLAGOVESHTCHENSKY, 1940 *, *Ciconiphilus decimfasciatus* (BOISDUVAL et LACORDAIRE, 1835), *Comatomenopon elongatum* UCHIDA, 1920

Nycticorax *nycticorax* (LINNAEUS, 1758)
Ardeicola goisagi UCHIDA, 1954 * HU: BALÁT (1957)
Ciconiphilus decimfasciatus (BOISDUVAL et LACORDAIRE, 1835) HU: RÉKÁSI (1973)

Order: PELECANIFORMES
Family: Pelecanidae
Pelecanus *crispus* BRUCH, 1832
Pectinopygus bifasciatus (PIAGET, 1880) *, *Piagetiella titan* (PIAGET, 1880)

Pelecanus onocrotalus LINNAEUS, 1758
Colpocephalum eucarenum BURMEISTER, 1838 *, *Pectinopygus forficulatus* (NITZSCH, 1866) *, *Piagetiella titan* (PIAGET, 1880) *

Family: Phalacrocoracidae
Phalacrocorax *carbo* (LINNAEUS, 1758)
Pectinopygus gyricornis (DENNY, 1842) HU: BALÁT (1957)
Eidmanniella pellucida (RUDOW, 1869)

Phalacrocorax pygmeus (PALLAS, 1773)
Pectinopygus excornis (BLAGOVESHTCHENSKY, 1940) *

Order: FALCONIFORMES

Family: Falconidae

Falco *amurensis* RADDE, 1863

Colpocephalum subzerafae TENDEIRO, 1988, *Degeeriella rufa* (BURMEISTER, 1838)

Falco cherrug GRAY, 1834

Degeeriella rufa (BURMEISTER, 1838) HU: RÉKÁSI (1987, as *D. quadraticollis*)

Falco columbarius LINNAEUS, 1758

Colpocephalum subzerafae TENDEIRO, 1988, *Degeeriella rufa* (BURMEISTER, 1838), *Laemobothrion tinnunculi* (LINNAEUS, 1758), *Nosopon lucidum* (RUDOW, 1869)

Falco eleonorae GENE, 1839

Degeeriella rufa (BURMEISTER, 1838), *Laemobothrion tinnunculi* (LINNAEUS, 1758)

Falco naumanni FLEISCHER, 1818

Colpocephalum subzerafae TENDEIRO, 1988 *, *Degeeriella rufa* (BURMEISTER, 1838)

Falco peregrinus TUNSTALL, 1771

Degeeriella rufa (BURMEISTER, 1838) HU: RÉKÁSI (1993*b*)

Colpocephalum falconii CARRIKER, 1963 *, *Colpocephalum subzerafae* TENDEIRO, 1988, *Colpocephalum zerafae* ANSARI, 1955, *Laemobothrion tinnunculi* (LINNAEUS, 1758), *Nosopon lucidum* (RUDOW, 1869)

Falco subbuteo LINNAEUS, 1758

Craspedorrhynchus subbuteonis GALLEGO *et al*., 1987 *

Degeeriella rufa (BURMEISTER, 1838) HU: BALÁT (1957, as *D. nitzschi*)

Laemobothrion tinnunculi (LINNAEUS, 1758)

Falco tinnunculus LINNAEUS, 1758

Degeeriella rufa (BURMEISTER, 1838) * HU: BALÁT (1957)

Laemobothrion tinnunculi (LINNAEUS, 1758) * HU: BALÁT (1957)

Colpocephalum subzerafae TENDEIRO, 1988, *Nosopon lucidum* (RUDOW, 1869)

Falco vespertinus LINNAEUS, 1766

Degeeriella rufa (BURMEISTER, 1838) HU: SCHÄFER (1963)
Nosopon lucidum (RUDOW, 1869) * HU: RÉKÁSI (1984)
Colpocephalum subzerafae TENDEIRO, 1988

Order: ACCIPITRIFORMES
Family: Accipitridae

Accipiter *brevipes* (SEVERTZOV, 1850)
Laemobothrion maximum (SCOPOLI, 1763)

Accipiter gentilis (LINNAEUS, 1758)
Colpocephalum nanum PIAGET, 1890 HU: RÉKÁSI (2008*a*)
Colpocephalum polonum (EICHLER et ZLOTORZYCKA, 1971) *, *Craspedorrhynchus haematopus* (SCOPOLI, 1763) *, *Degeeriella vagans* (GIEBEL, 1874) *, *Laemobothrion maximum* (SCOPOLI, 1763), *Nosopon lucidum* (RUDOW, 1869)

Accipiter nisus (LINNAEUS, 1758)
Craspedorrhynchus nisi (DENNY, 1842) * HU: BALÁT (1957)
Degeeriella nisus (GIEBEL, 1866) * HU: BALÁT (1957)
Colpocephalum germanum (EICHLER et ZLOTORZYCKA, 1971) *, *Colpocephalum nanum* PIAGET, 1890, *Nosopon lucidum* (RUDOW, 1869)

Aegypius *monachus* (LINNAEUS, 1766)
Aegypoecus brevicollis (BURMEISTER, 1838) *, *Colpocephalum turbinatum* DENNY, 1842, *Falcolipeurus quadripustulatus* (BURMEISTER, 1838) *, *Laemobothrion vulturis* (FABRICIUS, 1775)

Aquila *chrysaetos* (LINNAEUS, 1758)
Colpocephalum impressum RUDOW, 1866 * HU: RÉKÁSI (2008*a*)
Craspedorrhynchus aquilinus (DENNY, 1842) * HU: SCHÄFER (1963, as *C. chrysophthalmus*)
Colpocephalum flavescens (DE HAAN, 1829), *Degeeriella aquilarum* EICHLER, 1943, *Degeeriella fulva* (GIEBEL, 1874) *, *Falcolipeurus suturalis* (RUDOW, 1869) *, *Laemobothrion maximum* (SCOPOLI, 1763), *Laemobothrion vulturis* (FABRICIUS, 1775)

Aquila clanga PALLAS, 1811

Degeeriella aquilarum EICHLER, 1943, *Degeeriella fulva* (GIEBEL, 1874), *Falcolipeurus suturalis* (RUDOW, 1869), *Laemobothrion vulturis* (FABRICIUS, 1775)

Aquila heliaca SAVIGNY, 1809

Craspedorrhynchus fraterculus EICHLER et ZLOTORZYCKA, 1975 * HU: RÉKÁSI (2008*a*)
Degeeriella fulva (GIEBEL, 1874) HU: SOLT (1998)
Degeeriella aquilarum EICHLER, 1943, *Falcolipeurus suturalis* (RUDOW, 1869), *Laemobothrion vulturis* (FABRICIUS, 1775)

Aquila pomarina BREHM, 1831

Colpocephalum impressum RUDOW, 1866 HU: RÉKÁSI (2008*a*)
Craspedorrhynchus naevius (GIEBEL, 1861) * HU: SOLT (1998)
Degeeriella aquilarum EICHLER, 1943, *Degeeriella fulva* (GIEBEL, 1874), *Falcolipeurus suturalis* (RUDOW, 1869), *Laemobothrion vulturis* (FABRICIUS, 1775)

***Buteo** buteo* (LINNAEUS, 1758)

Colpocephalum nanum PIAGET, 1890 HU: RÉKÁSI (1984, as *C. buteonis*)
Craspedorrhynchus platystomus (BURMEISTER, 1838) * HU: BALÁT (1957)
Degeeriella fulva (GIEBEL, 1874) HU: BALÁT (1957, as *D. giebeli*)
Laemobothrion maximum (SCOPOLI, 1763) * HU: SCHÄFER (1964, *as L. circi*)
Colpocephalum turbinatum DENNY, 1842, *Kurodaia fulvofasciata* (PIAGET, 1880) *

Buteo lagopus (PONTOPPIDAN, 1763)

Degeeriella fulva (GIEBEL, 1874) HU: BALÁT (1957, as *D. angusta*)
Colpocephalum nanum PIAGET, 1890, *Craspedorrhynchus dilatatus* (RUDOW, 1869) *, *Kurodaia fulvofasciata* (PIAGET, 1880), *Laemobothrion maximum* (SCOPOLI, 1763)

Buteo rufinus (CRETZSCHMAR, 1829)

Degeeriella fulva (GIEBEL, 1874) HU: SOLT (1998)
Laemobothrion maximum (SCOPOLI, 1763)

***Circaetus** gallicus* (GMELIN, 1788)

Craspedorrhynchus triangularis (RUDOW, 1869) *, *Degeeriella leucopleura* (NITZSCH, 1874), *Falcolipeurus quadripustulatus* (BURMEISTER, 1838), *Kurodaia fulvofasciata* (PIAGET, 1880), *Laemobothrion maximum* (SCOPOLI, 1763)

***Circus** aeruginosus* (LINNAEUS, 1758)
Colpocephalum turbinatum DENNY, 1842 HU: SCHÄFER (1963, as *C. bicinctum*)
Craspedorrhynchus rotundatus (PIAGET, 1880) * HU: RÉKÁSI (1984)
Degeeriella fusca (DENNY, 1842) * HU: BALÁT (1957)
Laemobothrion maximum (SCOPOLI, 1763) HU: RÉKÁSI (1990)
Nosopon lucidum (RUDOW, 1869)

Circus cyaneus (LINNAEUS, 1766)
Laemobothrion maximum (Scopoli, 1763) HU: RÉKÁSI (1984, as *L. circi*)
Degeeriella fusca (DENNY, 1842) HU: BALÁT (1957)
Colpocephalum turbinatum DENNY, 1842, *Kurodaia fulvofasciata* (PIAGET, 1880), *Nosopon lucidum* (RUDOW, 1869)

Circus macrourus (GMELIN, 1770)
Degeeriella fusca (DENNY, 1842)

Circus pygargus (LINNAEUS, 1758)
Degeeriella fusca (DENNY, 1842), *Laemobothrion maximum* (SCOPOLI, 1763), *Nosopon lucidum* (RUDOW, 1869)

***Gyps** fulvus* (HABLIZL, 1783)
Aegypoecus trigonoceps (GIEBEL, 1874) *, *Colpocephalum gypsi* (EICHLER et ZLOTORZYCKA, 1971) *, *Colpocephalum turbinatum* DENNY, 1842, *Cuculiphilus gypsis* (EICHLER, 1944) *, *Falcolipeurus quadripustulatus* (BURMEISTER, 1838), *Laemobothrion vulturis* (FABRICIUS, 1775)

***Haliaeetus** albicilla* (LINNAEUS, 1758)
Colpocephalum flavescens (DE HAAN, 1829) * HU: SCHÄFER (1963)
Craspedorrhynchus macrocephalus (NITZSCH, 1874) * HU: RÉKÁSI *et al*. (2002)
Degeeriella discocephalus (BURMEISTER, 1838) * HU: RÉKÁSI *et al*. (2002)
Falcolipeurus sulcifrons (DENNY, 1842) *, *Laemobothrion vulturis* (FABRICIUS, 1775)

***Hieraaetus** fasciatus* (VIEILLOT, 1822)
Craspedorrhynchus fasciati GALLEGO, MARTIN MATEO *et al.*, 1987 *, *Degeeriella fulva* (GIEBEL, 1874), *Kurodaia fulvofasciata* (PIAGET, 1880), *Laemobothrion maximum* (SCOPOLI, 1763)

Hieraaetus pennatus (GMELIN, 1788)
Degeeriella fulva (Giebel, 1874) HU: SOLT (1998)
Colpocephalum milvi TENDEIRO, RESTIVO et DEMARTIS, 1979, *Colpocephalum turbinatum* DENNY, 1842, *Craspedorrhynchus ranjhae* ANSARI, 1955 *, *Falcolipeurus yasminae* ANSARI, 1956 *, *Laemobothrion maximum* (SCOPOLI, 1763)

Milvus *migrans* (BODDAERT, 1783)
Colpocephalum turbinatum DENNY, 1842 HU: SCHÄFER (1963, as *C. tricinctum*)
Craspedorrhynchus spathulatus (GIEBEL, 1874) * HU: SCHÄFER (1963)
Laemobothrion maximum (SCOPOLI, 1763) HU: SCHÄFER (1963, as *L. circi*)
Colpocephalum ecaudati PRICE et BEER, 1963, *Colpocephalum milvi* TENDEIRO, RESTIVO et DEMARTIS, 1979, *Degeeriella regalis* (GIEBEL, 1866), *Nosopon milvus* TENDEIRO, 1959 *

Milvus milvus (LINNAEUS, 1758)
Colpocephalum milvi TENDEIRO, RESTIVO et DEMARTIS, 1979 *, *Colpocephalum turbinatum* DENNY, 1842, *Degeeriella regalis* (GIEBEL, 1866) *, *Laemobothrion maximum* (SCOPOLI, 1763)

Neophron *percnopterus* (LINNAEUS, 1758)
Aegypoecus perspicuus (KELLOGG, 1914), *Colpocephalum percnopteri* PRICE et BEER, 1963 *, *Colpocephalum turbinatum* DENNY, 1842, *Falcolipeurus frater* (GIEBEL, 1874) *, *Laemobothrion vulturis* (FABRICIUS, 1775)

Pandion *haliaetus* (LINNAEUS, 1758)
Kurodaia haliaeeti (DENNY, 1842) * HU: BALÁT (1957)
Colpocephalum napiforme RUDOW, 1869, *Colpocephalum turbinatum* DENNY, 1842, *Laemobothrion maximum* (SCOPOLI, 1763)

Pernis *apivorus* (LINNAEUS, 1758)
Colpocephalum apivorus TENDEIRO, 1958 * HU: RÉKÁSI (1984)
Craspedorrhynchus melittoscopus (Nitzsch, 1874) * HU: RÉKÁSI (1984)
Colpocephalum turbinatum DENNY, 1842, *Degeeriella phlyctopygus* (NITZSCH, 1861) *, *Laemobothrion maximum* (SCOPOLI, 1763), *Nosopon clayae* PRICE et BEER, 1963 *

Order: GRUIFORMES

Family: Otidae

Otis *tarda* LINNAEUS, 1758

Otidoecus turmalis (DENNY, 1842) *

Tetrax *tetrax* (LINNAEUS, 1758)

Otidoecus antilogus (NITZSCH, 1866) *

Family: Rallidae

Crex *crex* (LINNAEUS, 1758)

Pseudomenopon crecis BECHET, 1963 *, *Rallicola ortygometrae* (SCHRANK, 1781) *

Gallinula *chloropus* (LINNAEUS, 1758)

Colpocephalum gallinulae UCHIDA, 1926 *, *Fulicoffula gallinula* CARRIKER, 1953 *, *Incidifrons gallinulae* BLAGOVESHTCHENSKY, 1951 *, *Laemobothrion chloropodis* (SCHRANK, 1803) *, *Pseudomenopon pilosum* (SCOPOLI, 1763), *Rallicola minutus* (NITZSCH, 1866) *, *Rallicola parani* EICHLER, 1954 *

Fulica *atra* LINNAEUS, 1758

Fulicoffula lurida (NITZSCH, 1818) * HU: BALÁT (1957)
Incidifrons fulicae (LINNAEUS, 1758) * HU: BALÁT (1957)
Laemobothrion atrum (NITZSCH, 1818) * HU: BALÁT (1957)
Pseudomenopon pilosum (SCOPOLI, 1763) * HU: BALÁT (1957)
Rallicola fulicae (DENNY, 1842) * HU: BALÁT (1957)

Porphyrio *porphyrio* (LINNAEUS, 1758)

Incidifrons curvitrabeculatus BLAGOVESHTCHENSKY, 1940 *, *Laemobothrion biswasi* (LAKSHMINARAYANA, 1967) *, *Laemobothrion blagoveshtchenski* TENDEIRO, 1963 *, *Pseudomenopon concretum* (PIAGET, 1880) *, *Rallicola lugens* (GIEBEL, 1874) *, *Rallicola thompsoni* TENDEIRO, 1965 *

Porzana *parva* (SCOPOLI, 1769)

Incidifrons porzanae BLAGOVESHTCHENSKY, 1951 *, *Rallicola mystax* (GIEBEL, 1874)

Porzana porzana (LINNAEUS, 1766)

Fulicoffula stammeri EICHLER, 1958 *, *Pseudomenopon qadrii* EICHLER, 1952 *, *Rallicola mystax* (GIEBEL, 1874) *

Porzana pusilla (PALLAS, 1776)
Pseudomenopon scopulacorne (DENNY, 1842)

Rallus *aquaticus* LINNAEUS, 1758
Pseudomenopon scopulacorne (DENNY, 1842) * HU: RÉKÁSI (1984)
Rallicola cuspidatus (SCOPOLI, 1763) * HU: BALÁT (1957)
Fulicoffula rallina (DENNY, 1842) *, *Incidifrons ralli* (SCOPOLI, 1772) *, *Pseudomenopon grebenjukae* KASIEV, 1982 *

Family: Gruidae
Anthropoides *virgo* (LINNAEUS, 1785)
Esthiopterum elbeli TANDAN, 1973 *, *Heleonomus elbeli* PRICE, 1970 *, *Heleonomus furgalai* PRICE, 1970, *Saemundssonia intiger* (NITZSCH, 1866)

Grus *grus* (LINNAEUS, 1758)
Esthiopterum gruis (LINNAEUS, 1758) * HU: RÉKÁSI (1973)
Gruimenopon longum (GIEBEL, 1874) * HU: RÉKÁSI (1984)
Heleonomus macilentus (NITZSCH, 1866) * HU: RÉKÁSI (1984)
Saemundssonia intiger (NITZSCH, 1866) * HU: BALÁT (1957)

Order: CHARADRIIFORMES
Family: Burhinidae
Burhinus *oedicnemus* (LINNAEUS, 1758)
Actornithophilus tetraclicis CLAY, 1962 *, *Quadraceps annulatus* (DENNY, 1842) *

Family: Haematopodidae
Haematopus *ostralegus* LINNAEUS, 1758
Actornithophilus grandiceps (PIAGET, 1880) *, *Austromenopon haematopi* TIMMERMANN, 1954 *, *Lunaceps haematopi* TIMMERMANN, 1954 *, *Quadraceps auratus* (DE HAAN, 1829) *, *Saemundssonia haematopi* (LINNAEUS, 1758) *

Family: Recurvirostridae
Himantopus *himantopus* (LINNAEUS, 1758)

Quadraceps semifissus (NITZSCH, 1866) * HU: RÉKÁSI (1978*a*, in *Proneptis*)
Actornithophilus himantopi BLAGOVESHTCHENSKY, 1951 *, *Austromenopon himantopi* TIMMERMANN, 1954 *, *Quadraceps hemichrous* (NITZSCH, 1866) *, *Saemundssonia platygaster* (DENNY, 1842)

Recurvirostra *avosetta* LINNAEUS, 1758
Austromenopon micrandrum (NITZSCH, 1866) * HU: RÉKÁSI (1986*b*)
Cirrophthirius recurvirostrae (LINNAEUS, 1758) * HU: RÉKÁSI (1986*b*)
Quadraceps signatus (PIAGET, 1880) * HU: SCHÄFER (1963)
Actornithophilus uniseriatus (PIAGET, 1880) *, *Quadraceps decipiens* (DENNY, 1842) *, *Quadraceps semifissus* (NITZSCH, 1866)

Family: Charadriidae
Charadrius *alexandrinus* LINNAEUS, 1758
Quadraceps macrocephalus (WATERSTON, 1914) HU: RÉKÁSI (1986*b*, as *Q. retractus*)
Saemundssonia platygaster pastoris TIMMERMANN, 1969 HU: RÉKÁSI (1986*b*)
Actornithophilus nodularis MARTINHO GUIMARÃES, 1988 *, *Austromenopon aegialitidis* (DURANT, 1906)

Charadrius dubius SCOPOLI, 1786
Quadraceps bicuspis (NITZSCH, 1874) * HU: RÉKÁSI (1979)
Actornithophilus ochraceus (NITZSCH, 1818), *Austromenopon aegialitidis* (DURANT, 1906), *Saemundssonia platygaster* (DENNY, 1842)

Charadrius hiaticula LINNAEUS, 1758
Saemundssonia platygaster platygaster (DENNY, 1842) * HU: RÉKÁSI (1984)
Actornithophilus ochraceus (NITZSCH, 1818), *Austromenopon aegialitidis* (DURANT, 1906), *Quadraceps fissus* (BURMEISTER, 1838) *, *Quadraceps hiaticulae* (FABRICIUS, 1780) *

Charadrius leschenaultii LESSON, 1826
Actornithophilus ochraceus (NITZSCH, 1818), *Austromenopon aegialitidis* (DURANT, 1906), *Quadraceps ptyadis* (SÉGUY, 1949) *, *Saemundssonia platygaster platygaster* (DENNY, 1842) *

Charadrius morinellus LINNAEUS, 1758

Actornithophilus ochraceus (NITZSCH, 1818), *Quadraceps punctifer* HOPKINS, 1949 *, *Saemundssonia platygaster semivittata* (GIEBEL, 1874) *

Charadrius vociferus LINNAEUS, 1758
Actornithophilus hoplopteri (MJÖBERG, 1910, *Austromenopon aegialitidis* (DURANT, 1906) *, *Quadraceps boephilus* (KELLOGG, 1896) *, *Saemundssonia conica conica* (DENNY, 1842)

***Pluvialis** apricaria* (LINNAEUS, 1758)
Actornithophilus ochraceus (NITZSCH, 1818) * HU: RÉKÁSI (1984)
Quadraceps charadrii (LINNAEUS, 1758) * HU: RÉKÁSI (1984)
Saemundssonia conica conica (DENNY, 1842) *

Pluvialis dominica (MÜLLER, 1776)
Actornithophilus ochraceus (NITZSCH, 1818), *Quadraceps orarius* (KELLOGG, 1896) *, *Saemundssonia conica conica* (DENNY, 1842)

Pluvialis fulva (GMELIN, 1789)
Actornithophilus ochraceus (NITZSCH, 1818), *Quadraceps orarius* (KELLOGG, 1896), *Saemundssonia conica conica* (DENNY, 1842)

Pluvialis squatarola (LINNAEUS, 1758)
Actornithophilus ochraceus (NITZSCH, 1818) HU: RÉKÁSI (1984, as *A. flavipes*)
Austromenopon squatarolae TIMMERMANN, 1954 * HU: RÉKÁSI (1984)
Quadraceps hospes (NITZSCH, 1866) * HU: RÉKÁSI (1984, as *Q. charadrii hospes*)
Saemundssonia conica naumanni (GIEBEL, 1866) * HU: RÉKÁSI (1984, as *S. naumanni*)
Lunaceps incoenis (KELLOGG et CHAPMAN, 1899) *

***Vanellus** gregarius* (PALLAS, 1771)
Actornithophilus ochraceus (NITZSCH, 1818) HU: SCHÄFER (1963)
Austromenopon gregariae TIMMERMANN, 1954 *, *Quadraceps kilimandjarensis* (KELLOGG, 1910), *Saemundssonia platygaster temporalis* (GIEBEL, 1874)

Vanellus leucurus (LICHTENSTEIN, 1823)

Actornithophilus hoplopteri (MJÖBERG, 1910), *Austromenopon leucurae* TIMMERMANN, 1954 *, *Quadraceps grallarius* TIMMERMANN, 1954 *, *Saemundssonia africana africana* TIMMERMANN, 1954

Vanellus spinosus (LINNAEUS, 1758)
Actornithophilus hoplopteri (MJÖBERG, 1910) *, *Quadraceps hoplopteri* (MJÖBERG, 1910) *

Vanellus vanellus (LINNAEUS, 1758)
Actornithophilus gracilis (PIAGET, 1880) HU: BALÁT (1957, as *A. svobodai*)
Quadraceps junceus (SCOPOLI, 1763) * HU: BALÁT (1957)
Saemundssonia platygaster temporalis (GIEBEL, 1874) * HU: BALÁT (1957, as *S. temporalis*)
Austromenopon aegialitidis (DURRANT, 1906), *Lunaceps holophaeus* (BURMEISTER, 1838)

Family: Scolopacidae
***Actitis** hypoleucos* (LINNAEUS, 1758)
Quadraceps ravus (KELLOGG, 1899) HU: RÉKÁSI (1984)
Actornithophilus flumineus CLAY, 1962 *, *Austromenopon hystriculum* ZLOTORZYCKA, 1968 *, *Saemundssonia platygaster frater* (GIEBEL, 1874) *

***Arenaria** interpres* (LINNAEUS, 1758)
Actornithophilus bicolor (PIAGET, 1880) *, *Actornithophilus pediculoides* (MJÖBERG, 1910) *, *Austromenopon lutescens* (BURMEISTER, 1838), *Quadraceps strepsilaris* (DENNY, 1842) *, *Saemundssonia platygaster stenrami* TIMMERMANN, 1969 *, *Saemundssonia tringae* (FABRICIUS, 1780)

***Calidris** alba* (PALLAS, 1764)
Lunaceps actophilus (KELLOGG et CHAPMAN, 1899) * HU: RÉKÁSI (2006)
Actornithophilus umbrinus (BURMEISTER, 1838), *Carduiceps zonarius* (NITZSCH, 1866), *Saemundssonia platygaster jadwigae* TIMMERMANN, 1969 *, *Saemundssonia tringae* (FABRICIUS, 1780)

Calidris alpina (LINNAEUS, 1758)
Austromenopon alpinum TIMMERMANN, 1954 * HU: RÉKÁSI (1984)
Carduiceps meinertzhageni TIMMERMANN, 1954 * HU: RÉKÁSI (1984)

Lunaceps actophilus (KELLOGG et CHAPMAN, 1899) HU: RÉKÁSI (1978*b*)
Actornithophilus umbrinus (BURMEISTER, 1838), *Saemundssonia tringae* (FABRICIUS, 1780)

Calidris canutus (LINNAEUS, 1758)
Actornithophilus umbrinus (BURMEISTER, 1838) HU: RÉKÁSI (2006)
Austromenopon lutescens (BURMEISTER, 1838) HU: RÉKÁSI (2002)
Actornithophilus canuti PRICE et LEIBOVITZ, 1969 *, *Carduiceps zonarius* (NITZSCH, 1866), *Lunaceps drosti* TIMMERMANN, 1954 *, *Saemundssonia platygaster islandica* TIMMERMANN, 1951 *, *Saemundssonia tringae* (FABRICIUS, 1780)

Calidris ferruginea (PONTOPPIDAN, 1763)
Actornithophilus umbrinus (BURMEISTER, 1838) * HU: RÉKÁSI (2002)
Lunaceps timmermanni BECHET, 1968 * HU: RÉKÁSI (2006)
Carduiceps zonarius (NITZSCH, 1866), *Lunaceps cabanisi* TIMMERMANN, 1954, *Saemundssonia tringae* (FABRICIUS, 1780)

Calidris fuscicollis (VIEILLOT, 1819)
Actornithophilus umbrinus (BURMEISTER, 1838), *Carduiceps zonarius* (NITZSCH, 1866), *Saemundssonia platygaster nitzschi* (GIEBEL, 1866), *Saemundssonia tringae* (FABRICIUS, 1780)

Calidris maritima (BRÜNNICH, 1764)
Actornithophilus umbrinus (BURMEISTER, 1838), *Austromenopon erilis* ZLOTORZYCKA, 1968 *, *Carduiceps meinertzhageni* TIMMERMANN, 1954, *Lunaceps nereis* TIMMERMANN, 1954 *, *Saemundssonia tringae* (FABRICIUS, 1780) *

Calidris melanotos (VIEILLOT, 1819)
Actornithophilus umbrinus (BURMEISTER, 1838), *Carduiceps zonarius* (NITZSCH, 1866), *Saemundssonia tringae* (FABRICIUS, 1780)

Calidris minuta (LEISLER, 1812)
Carduiceps zonarius (NITZSCH, 1866) * HU: RÉKÁSI (1984)
Lunaceps incoenis (KELLOGG et CHAPMAN, 1899) HU: RÉKÁSI (2006)
Saemundssonia platygaster nitzschi (GIEBEL, 1866) HU: RÉKÁSI (1984)

Actornithophilus umbrinus (BURMEISTER, 1838), *Saemundssonia tringae* (FABRICIUS, 1780)

Calidris pusilla (LINNAEUS, 1766)
Actornithophilus umbrinus (BURMEISTER, 1838), *Carduiceps zonarius* (NITZSCH, 1866), *Lunaceps cabanisi* TIMMERMANN, 1954, *Saemundssonia tringae* (FABRICIUS, 1780)

Calidris temminckii (LEISLER, 1812)
Actornithophilus umbrinus (BURMEISTER, 1838), *Carduiceps zonarius* (NITZSCH, 1866), *Lunaceps incoensis* (KELLOGG et CHAPMAN, 1899), *Saemundssonia tringae* (FABRICIUS, 1780)

***Gallinago** gallinago* (LINNAEUS, 1758)
Austromenopon durisetosum (BLAGOVESHTCHENSKY, 1948) * HU: RÉKÁSI (1984)
Cummingsiella ambigua (BURMEISTER, 1838) * HU: BALÁT (1957)
Rhynonirmus scolopacis (DENNY, 1842) * HU: BALÁT (1957)
Actornithophilus stictus (KELLOGG et PAINE, 1911) *, *Saemundssonia kratochvili* BALÁT, 1950 *

Gallinago media (LATHAM, 1787)
Austromenopon durisetosum (BLAGOVESHTCHENSKY, 1948), *Rhynonirmus medius* TIMMERMANN, 1955 *, *Saemundssonia media* MARTENS, 1974 *

***Limicola** falcinellus* (PONTOPPIDAN, 1763)
Lunaceps falcinellus TIMMERMANN, 1954 *

***Limosa** lapponica* (LINNAEUS, 1758)
Actornithophilus limosae (KELLOGG, 1908) *, *Austromenopon meyeri* (GIEBEL, 1874) *, *Carduiceps lapponicus* EMERSON, 1953 *, *Lunaceps limosella* TIMMERMANN, 1954 *, *Rotundiceps cordatus* (OSBORN, 1896), *Saemundssonia limosae* (DENNY, 1842) *

Limosa limosa (LINNAEUS, 1758)
Actornithophilus spinulosus (PIAGET, 1880) *, *Austromenopon limosae* TIMMERMANN, 1954 *, *Carduiceps cingulatus* (DENNY, 1842) *, *Lunaceps limosella* TIMMERMANN, 1954, *Saemundssonia thompsoni* TIMMERMANN, 1951 *

***Lymnocryptes** minimus* (BRÜNNICH, 1764)
Actornithophilus multisetosus BLAGOVESHTCHENSKY, 1940 * HU: RÉKÁSI (1984)
Saemundssonia kratochvili BALÁT, 1950

***Numenius** arquata* (LINNAEUS, 1758)
Austromenopon crocatum (NITZSCH, 1866) * HU: SCHÄFER (1963)
Cummingsiella ovalis (SCOPOLI, 1763) * HU: RÉKÁSI (1973)
Lunaceps numenii numenii (DENNY 1842) * HU: BALÁT (1957)
Saemundssonia scolopacisphaeopodis humeralis (DENNY 1842) * HU: BALÁT (1957, as *S. humeralis*)
Actornithophilus patellatus (PIAGET, 1890) *

Numenius phaeopus (LINNAEUS, 1758)
Actornithophilus ocellatus (RUDOW, 1869) *, *Austromenopon phaeopodis* (SCHRANK, 1802) *, *Lunaceps numenii phaeopi* (DENNY 1842) *, *Lunaceps numenii oliveri* (JOHNSTON et HARRISON, 1912) *, *Saemundssonia scolopacisphaeopodis scolopacisphaeopodis* (SCHRANK, 1803) *

Numenius tenuirostris VIEILLOT, 1817
Austromenopon confine (BLAGOVESHTCHENSKY, 1948) *, *Cummingsiella breviclypeata* BLAGOVESHTCHENSKY, 1948 *, *Lunaceps numenii proximus* (BLAGOVESHTCHENSKY 1948) *

***Phalaropus** fulicarius* (LINNAEUS, 1758)
Actornithophilus umbrinus (BURMEISTER, 1838), *Austromenopon corporosum* (KELLOGG et KUWANA, 1901) *, *Quadraceps phalaropi* (DENNY 1842) *

Phalaropus lobatus (LINNAEUS, 1758)
Austromenopon spenceri TIMMERMANN, 1956 * HU: RÉKÁSI (2002)
Quadraceps connexus (KELLOGG et MANN, 1912) * HU: RÉKÁSI (2002)
Saemundssonia tringae (FABRICIUS, 1780) HU: RÉKÁSI (2002)
Actornithophilus umbrinus (BURMEISTER, 1838), *Carduiceps subscalaris* (PIAGET, 1880) *

Phalaropus tricolor (VIEILLOT, 1819)
Actornithophilus umbrinus (BURMEISTER, 1838), *Quadraceps fimbriatus* (GIEBEL, 1866) *, *Saemundssonia tricolor* CARRIKER, 1956 *

Philomachus *pugnax* (LINNAEUS, 1758)
Actornithophilus pustulosus (PIAGET, 1880) * HU: RÉKÁSI (1984)
Austromenopon lutescens (BURMEISTER, 1838) * HU: RÉKÁSI (1978*b*)
Carduiceps scalaris (PIAGET, 1880) * HU: RÉKÁSI (1984)
Lunaceps holophaeus (BURMEISTER, 1838) * HU: RÉKÁSI (1978*b*)
Quadraceps lahorensis ANSARI, 1955 *, *Saemundssonia platygaster ashi* TIMMERMANN, 1955 *, *Saemundssonia tringae* (FABRICIUS, 1780)

Scolopax *rusticola* LINNAEUS, 1758
Austromenopon icterum (BURMEISTER, 1838) * HU: RÉKÁSI (1984)
Cummingsiella aurea HOPKINS, 1949 * HU: RÉKÁSI (1978*a*)
Cummingsiella brelihi TIMMERMANN, 1969 * HU: RÉKÁSI (1984)
Rhynonirmus helvolus (BURMEISTER, 1838) * HU: BALÁT (1957)
Saemundssonia clayae HOPKINS, 1949 *

Tringa *erythropus* (PALLAS, 1764)
Actornithophilus totani (SCHRANK, 1803) HU: BALÁT (1957, as *A. affinis*)
Quadraceps furvus (Burmeister, 1838) * HU: BALÁT (1957)
Austromenopon decorosum ZLOTORZYCKA, 1968, *Saemundssonia platygaster nitzschi* (GIEBEL, 1866) *

Tringa flavipes (GMELIN, 1789)
Actornithophilus totani (SCHRANK, 1803), *Quadraceps falcigerus* (PETERS, 1931) *, *Saemundssonia platygaster nitzschi* (GIEBEL, 1866)

Tringa glareola LINNAEUS, 1758
Actornithophilus totani (SCHRANK, 1803) HU: RÉKÁSI (1979, as *A. affinis*)
Quadraceps obscurus (BURMEISTER, 1838) * HU: RÉKÁSI (1978*b*)
Saemundssonia platygaster cordiceps (GIEBEL, 1874) *

Tringa nebularia (GUNNERUS, 1767)
Quadraceps similis (GIEBEL, 1866) * HU: BALÁT (1957)
Actornithophilus paludosus CLAY, 1962 *, *Saemundssonia platygaster nitzschi* (GIEBEL, 1866)

Tringa ochropus LINNAEUS, 1758
Quadraceps ochropi (Denny, 1842) * HU: RÉKÁSI (1979)
Actornithophilus lyallpurensis ANSARI, 1955 *, *Austromenopon sohni* ANSARI, 1955 *, *Saemundssonia platygaster nitzschi* (GIEBEL, 1866)

Tringa stagnatilis (BECHSTEIN, 1803)
Actornithophilus totani (SCHRANK, 1803), *Quadraceps obscurus* (BURMEISTER, 1838)

Tringa totanus (LINNAEUS, 1758)
Actornithophilus totani (SCHRANK, 1803) * HU: RÉKÁSI (1979)
Quadraceps obtusus (KELLOGG et KUWANA, 1902) HU: BALÁT (1957, as *Q. conformis*)
Austromenopon decorosum ZLOTORZYCKA, 1968 *, *Saemundssonia platygaster mollis* (NITZSCH, 1874) *

Tryngites *subruficollis* (VIEILLOT, 1819)
Actornithophilus umbrinus (BURMEISTER, 1838), *Carduiceps zonarius* (NITZSCH, 1866), *Lunacpes falcinellus* TIMMERMANN, 1954

Xenus *cinereus* (GÜLDENSTADT, 1775)
Carduiceps fulvofasciatus (GRUBE, 1851) * HU: RÉKÁSI (2008*b*)
Saemundssonia platygaster (DENNY, 1842)

Family: Glareolidae

Glareola *pratincola* (LINNAEUS, 1766)
Actornithophilus sedes EICHLER, 1944 *, *Quadraceps ellipticus* (NITZSCH, 1866) *, *Quadraceps kirghizicus* (KASIEV, 1982) *

Family: Laridae

Chlidonias *hybrida* (PALLAS, 1811)
Actornithophilus piceus piceus (DENNY, 1842), *Austromenopon atrofulvum* (PIAGET, 1880), *Quadraceps anagrapsus* (NITZSCH, 1866) *, *Saemundssonia lobaticeps* (GIEBEL, 1874)

Chlidonias leucoptera (TEMMINCK, 1815)
Saemundssonia lobaticeps (GIEBEL, 1874) HU: BALÁT (1957)
Actornithophilus piceus piceus (DENNY, 1842), *Austromenopon atrofulvum* (PIAGET, 1880), *Quadraceps anagrapsus* (NITZSCH, 1866)

Chlidonias nigra (LINNAEUS, 1758)

Quadraceps phaeonotus (NITZSCH, 1866) * HU: RÉKÁSI (1984, in *Koeniginirmus*) *Saemundssonia lobaticeps* (Giebel, 1874) * HU: BALÁT (1957), *Actornithophilus piceus piceus* (DENNY, 1842), *Austromenopon atrofulvum* (PIAGET, 1880)

Gelochelidon *nilotica* (GMELIN, 1789)

Actornithophilus piceus piceus (DENNY, 1842), *Austromenopon atrofulvum* (PIAGET, 1880), *Quadraceps baliola* (BLAGOVESHTCHENSKY, 1951) *, *Quadraceps kekra* ANSARI, 1947 *, *Saemundssonia gelochelidoni* (TOULESHKOV, 1959) *

Larus *argentatus* PONTOPPIDAN, 1763

Saemundssonia lari (Fabricius, 1780) HU: RÉKÁSI (1973, may refer to *Larus cachinnans michahellis* NAUMANN, 1840)

Actornithophilus piceus lari (PACKARD, 1870), *Austromenopon transversum* (DENNY, 1842), *Quadraceps ornatus striolatus* (NITZSCH, 1866), *Quadraceps punctatus regressus* TIMMERMANN, 1952 *

Larus canus LINNAEUS, 1758

Actornithophilus piceus lari (PACKARD, 1870), *Austromenopon transversum* (DENNY, 1842), *Quadraceps ornatus ornatus* (GRUBE, 1851) *, *Quadraceps punctatus regressus* TIMMERMANN, 1952, *Saemundssonia lari* (FABRICIUS, 1780)

Larus delawarensis ORD, 1815

Actornithophilus piceus lari (PACKARD, 1870), *Austromenopon transversum* (DENNY, 1842), *Quadraceps punctatus sublingulatus* TIMMERMANN, 1952 *, *Saemundssonia lari* (FABRICIUS, 1780)

Larus fuscus LINNAEUS, 1758

Actornithophilus piceus lari (PACKARD, 1870), *Austromenopon transversum* (DENNY, 1842), *Quadraceps punctatus regressus* TIMMERMANN, 1952, *Saemundssonia lari* (FABRICIUS, 1780)

Larus genei BRÉME, 1839

Actornithophilus piceus lari (PACKARD, 1870), *Quadraceps punctatus pallidus* TIMMERMANN, 1952 *, *Saemundssonia lari* (FABRICIUS, 1780)

Larus glaucoides MEYER, 1822

Actornithophilus piceus lari (PACKARD, 1870), *Austromenopon transversum* (DENNY, 1842), *Quadraceps ornatus striolatus* (NITZSCH, 1866), *Saemundssonia lari* (FABRICIUS, 1780)

Larus hyperboreus GUNNERUS, 1767

Actornithophilus piceus lari (PACKARD, 1870), *Austromenopon transversum* (DENNY, 1842), *Quadraceps ornatus stratiolatus* (NITZSCH, 1866) *, *Saemundssonia lari* (FABRICIUS, 1780) *

Larus ichthyaetus PALLAS, 1773

Quadraceps punctatus punctatus (BURMEISTER, 1838)

Larus marinus LINNAEUS, 1758

Actornithophilus piceus lari (PACKARD, 1870) *, *Austromenopon transversum* (DENNY, 1842), *Quadraceps ornatus striolatus* (NITZSCH, 1866), *Saemundssonia lari* (FABRICIUS, 1780)

Larus melanocephalus TEMMINCK, 1820

Quadraceps punctatus regressus TIMMERMANN, 1952, *Saemundssonia lari (*FABRICIUS, 1780)

Larus minutus PALLAS, 1776

Actornithophilus piceus lari (PACKARD, 1870), *Austromenopon transversum* (DENNY, 1842), *Quadraceps eugrammicus* (BURMEISTER, 1838) *, *Saemundssonia lari* (FABRICIUS, 1780)

Larus pipixcan WAGLER, 1831

Actornithophilus piceus lari (PACKARD, 1870), *Austromenopon transversum* (DENNY, 1842), *Quadraceps punctatus lingulatus* TIMMERMANN, 1952, *Saemundssonia lari* (FABRICIUS, 1780)

Larus ridibundus LINNAEUS, 1766

Austromenopon transversum (DENNY, 1842) HU: RÉKÁSI (1984, as *A. ridibundus*)
Quadraceps punctatus punctatus (BURMEISTER, 1838) * HU: BALÁT (1957)

Saemundssonia lari (FABRICIUS, 1780) HU: BALÁT (1957, as *S. mülleri*)
Actornithophilus piceus lari (PACKARD, 1870)

***Rissa** tridactyla* (LINNAEUS, 1758)
Actornithophilus piceus lari (PACKARD, 1870), *Austromenopon transversum* (DENNY, 1842) *, *Quadraceps ornatus lineolatus* (NITZSCH, 1866) *, *Quadraceps ornatus paulschulzei* (TIMMERMANN, 1949) *, *Saemundssonia lari* (FABRICIUS, 1780)

***Sterna** albifrons* PALLAS, 1764
Actornithophilus piceus piceus (DENNY, 1842), *Austromenopon atrofulvum* (PIAGET, 1880), *Quadraceps nycthemerus* (BURMEISTER, 1838) *, *Saemundssonia melanocephalus* (BURMEISTER, 1838) *

Sterna caspia PALLAS, 1770
Actornithophilus piceus piceus (DENNY, 1842), *Austromenopon atrofulvum* (PIAGET, 1880), *Quadraceps caspius* (GIEBEL, 1874) *, *Quadraceps punctatus regressus* TIMMERMANN, 1952

Sterna hirundo LINNAEUS, 1758
Quadraceps sellatus (BURMEISTER, 1838) * HU: BALÁT (1957)
Saemundssonia sternae (LINNAEUS, 1758) * HU: BALÁT (1957)
Actornithophilus piceus piceus (DENNY, 1842), *Austromenopon atrofulvum* (PIAGET, 1880)

Sterna paradisaea PONTOPPIDAN, 1763
Actornithophilus piceus piceus (DENNY, 1842), *Austromenopon atrofulvum* (PIAGET, 1880), *Quadraceps houri* HOPKINS, 1949 *, *Saemundssonia lockleyi* CLAY, 1949

Sterna sandvicensis LATHAM, 1787
Actornithophilus piceus piceus (DENNY, 1842) *, *Austromenopon atrofulvum* (PIAGET, 1880), *Quadraceps longicollis* (RUDOW, 1869) *, *Saemundssonia brevicornis* (GIEBEL, 1874) *, *Saemundssonia laticaudata* (RUDOW, 1869) *

***Xema** sabini* (SABINE, 1819)
Actornithophilus piceus lari (PACKARD, 1870), *Austromenopon transversum* (DENNY, 1842), *Quadraceps lineatus* (PIAGET, 1880) *, *Saemundssonia lari* (FABRICIUS, 1780)

Family: Stercorariidae

***Stercorarius** longicaudus* VIEILLOT, 1819

Austromenopon fuscofasciatum (PIAGET, 1880), *Haffneria grandis* (PIAGET, 1880), *Quadraceps parvopallidus* (EICHLER, 1951) *, *Saemundssonia inexspectata* TIMMERMANN, 1951

Stercorarius parasiticus (LINNAEUS, 1758)

Austromenopon fuscofasciatum (PIAGET, 1880) HU: SCHÄFER (1964, as *A. circinatum*)
Quadraceps normifer (GRUBE, 1851) * HU: SCHÄFER (1964)
Haffneria grandis (PIAGET, 1880), *Saemundssonia cephalus* (DENNY, 1841) *

Stercorarius pomarinus (TEMMINCK, 1815)

Austromenopon fuscofasciatum (PIAGET, 1880) *, *Haffneria grandis* (PIAGET, 1880), *Quadraceps stellaepolaris* TIMMERMANN, 1952 *, *Saemundssonia euryrhyncha* (GIEBEL, 1874) *

Stercorarius skua (BRÜNNICH, 1764)

Haffneria grandis (PIAGET, 1880), *Quadraceps stellaepolaris* TIMMERMANN, 1952, *Saemundssonia euryrhyncha* (GIEBEL, 1874)

Family: Alcidae

***Alca** torda* LINNAEUS, 1758

Austromenopon nigropleurum (DENNY, 1842) *, *Quadraceps alcae* (DENNY, 1842) *, *Saemundssonia celidoxa* (BURMEISTER, 1838) *

***Fratercula** arctica* (LINNAEUS, 1758)

Austromenopon nigropleurum (DENNY, 1842), *Quadraceps helgovauki* (TIMMERMANN, 1974) *, *Saemundssonia fraterculae* (OVERGAARD, 1942) *

Order: COLUMBIFORMES

Family: Pteroclididae

***Pterocles** exustus* TEMMINCK, 1825

Syrrhaptoecus emahusaini ANSARI, 1947 *, *Syrrhaptoecus falcatus* WATERSTON, 1928 *

***Syrrhaptes** paradoxus* (PALLAS, 1773)

Syrrhaptoecus bedfordi WATERSTON, 1928 *, *Syrrhaptoecus paradoxus* (RUDOW, 1869) *

Family: Columbidae

Columba *livia* GMELIN, 1789

Bonomiella columbae EMERSON, 1957 * HU: RÓZSA (1990)
Campanulotes compar (BURMEISTER, 1838) * HU: RÉKÁSI (1978*a*)
Colpocephalum turbinatum DENNY, 1842 * HU: RÉKÁSI (1986*a*)
Columbicola columbae (LINNAEUS, 1758) * HU: BALÁT (1957)
Hohorstiella lata (Piaget, 1880) * HU: RÓZSA (1990)
Coloceras aegypticum (KELLOGG et PAINE, 1911) *, *Coloceras damicorne* (NITZSCH, 1866), *Coloceras israelensis* (TENDEIRO, 1974) *, *Coloceras liviae* (TENDEIRO, 1974) *, *Coloceras tovornikae* TENDEIRO, 1973 *, *Columbicola tschulyschman* EICHLER, 1942, *Physconelloides zenaidurae* (MCGREGOR, 1917)

Columba oenas LINNAEUS, 1758

Campanulotes drosti EICHLER, 1950 * HU: RÉKÁSI (1990)
Columbicola columbae (LINNAEUS, 1758) HU: BALÁT (1957)
Coloceras damicorne (NITZSCH, 1866), *Hohorstiella gigantea* (DENNY, 1842) *

Columba palumbus LINNAEUS, 1758

Campanulotes bidentatus (SCOPOLI, 1763) * HU: BALÁT (1957)
Coloceras damicorne (NITZSCH, 1866) * HU: BALÁT (1957)
Columbicola claviformis (DENNY, 1842) * HU: BALÁT (1957)
Coloceras alloceratum (TENDEIRO, 1974) *

Streptopelia *decaocto* (FRIVALDSZKY, 1838)

Coloceras piageti (JOHNSTON et HARRISON, 1912) * HU: RÉKÁSI (1984, as *C. sofioticus*)
Columbicola bacillus (GIEBEL, 1866) HU: BALÁT (1957, as *C. baculus*)
Bonomiella concii EICHLER, 1947 *, *Coloceras hilli* (BEDFORD, 1920), *Hohorstiella modesta* (ANSARI, 1951) *, *Turturicola salimalii* CLAY et MEINERTZHAGEN, 1937 *

Streptopelia orientalis (LATHAM, 1790)

Coloceras chinense (KELLOGG et CHAPMAN, 1902), *Coloceras orientalis* (TENDEIRO, 1969) *, *Columbicola turturis* (UCHIDA, 1917) *, *Columbicola orientalis* TENDEIRO, 1965 *

Streptopelia turtur (LINNAEUS, 1758)

Columbicola bacillus (GIEBEL, 1866) * HU: BALÁT (1957, as *C. baculus*)

Coloceras britannicum TENDEIRO, 1973 *, *Coloceras chinense* (KELLOGG et CHAPMAN, 1902), *Hohorstiella streptopeliae* EICHLER, 1953 *

Order: CUCULIFORMES
Family: Cuculidae

***Clamator** glandarius* (LINNAEUS, 1758)
Cuculicola limbatus TENDEIRO, 1962 *, *Cuculiphilus snodgrassi* (KELLOGG et KUWANA, 1902)

***Cuculus** canorus* LINNAEUS, 1758
Cuculicola latirostris (BURMEISTER, 1838) * HU: RÉKÁSI (1984)
Cuculoecus latifrons (DENNY, 1842) * HU: BALÁT (1957)
Cuculiphilus fasciatus (SCOPOLI, 1763) *, *Cuculiphilus snodgrassi* (KELLOGG et KUWANA, 1902)

Order: STRIGIFORMES
Family: Tytonidae

***Tyto** alba* (SCOPOLI, 1769)
Kurodaia subpachygaster (PIAGET, 1880) * HU: SOLT (1998)
Strigiphilus rostratus (BURMEISTER, 1838) * HU: BALÁT (1957)
Colpocephalum pectinatum OSBORN 1902, *Colpocephalum turbinatum* DENNY, 1842, *Strigiphilus aitkeni* CLAY, 1966 *

Family: Strigidae

***Aegolius** funereus* (LINNAEUS, 1758)
Kurodaia cryptostigmatia (NITZSCH, 1861), *Strigiphilus pallidus* (GIEBEL, 1874) *

***Asio** flammeus* (PONTOPPIDAN, 1763)
Strigiphilus cursor (BURMEISTER, 1838) * HU: BALÁT (1957)
Colpocephalum brachysomum KELLOGG et CHAPMAN, 1902 *, *Kurodaia flammei* PRICE et BEER, 1963 *

Asio otus (LINNAEUS, 1758)
Strigiphilus barbatus (OSBORN, 1902) HU: BALÁT (1957, as *S. asionis*)

***Athene** noctua* (SCOPOLI, 1769)

Strigiphilus cursitans (NITZSCH, 1861) * HU: RÉKÁSI (1973)
Kurodaia cryptostigmatia (NITZSCH, 1861) *, *Kurodaia panjabensis* (ANSARI, 1951)

Bubo *bubo* (LINNAEUS, 1758)
Kurodaia longipes (GIEBEL, 1874) * HU: BALÁT (1957)
Strigiphilus goniodicerus EICHLER, 1949 *, *Strigiphilus strigis* (PONTOPPIDAN, 1763) *

Glaucidium *passerinum* (LINNAEUS, 1758)
Kurodaia cryptostigmatia (NITZSCH, 1861), *Strigiphilus splendens* (GIEBEL, 1874) *

Nyctea *scandiaca* (LINNAEUS, 1758)
Strigiphilus ceblebrachys (DENNY, 1842) *

Otus *scops* (LINNAEUS, 1758)
Kurodaia cryptostigmatia (NITZSCH, 1861), *Kurodaia platyclypeatum* (PIAGET, 1887), *Strigiphilus heterogenitalis* EMERSON et ELBEL, 1957, *Strigiphilus tuleskovi* BALÁT, 1958 *

Strix *aluco* LINNAEUS, 1758
Strigiphilus laticephalus (UCHIDA, 1949) * HU: RÉKÁSI (1993*b*, as *S. laticeps*)
Kurodaia cryptostigmata (NITZSCH, 1861), *Kurodaia platyclypeatum* (PIAGET, 1887), *Laemobothrion nocturnum* GIEBEL, 1874 *, *Strigiphilus portigi* EICHLER, 1952 *

Strix uralensis PALLAS, 1771
Strigiphilus heterocerus (GRUBE, 1851) *, *Strigiphilus laticephalus* (UCHIDA, 1949) *

Surnia *ulula* (LINNAEUS, 1758)
Strigiphilus crenulatus (GIEBEL, 1874) *

Order: CAPRIMULGIFORMES
Family: Caprimulgidae
Caprimulgus *europaeus* LINNAEUS, 1758
Mulcticola hypoleucus (DENNY, 1842) * HU: BALÁT (1957)

Order: APODIFORMES
Family: Apodidae
Apus *apus* (LINNAEUS, 1758)

Dennyus hirundinis (LINNAEUS, 1761) * HU: BALÁT (1957)
Eureum cimicoides BURMEISTER, 1838 *

Apus pallidus (SHELLEY, 1870)
Dennyus hirundinis (LINNAEUS, 1761)

Tachymarptis *melba* (LINNAEUS, 1758)
Dennyus vonarxi BÜTTIKER, 1954 *

Order: CORACIIFORMES
Family: Coraciidae
Coracias *garrulus* LINNAEUS, 1758
Capraiella subcuspidata (BURMEISTER, 1838) * HU: BALÁT (1957)
Meromenopon incisum (GIEBEL, 1866)

Family: Alcedinidae
Alcedo *atthis* (LINNAEUS, 1758)
Alcedoffula alcedinis (DENNY, 1842) * HU: RÉKÁSI (1984)

Family: Meropidae
Merops *apiaster* LINNAEUS, 1758
Brueelia apiastri (DENNY, 1842) * HU: BALÁT (1957)
Meromenopon meropis CLAY et MEINERTZHAGEN, 1941 * HU: BALÁT (1957)
Meropoecus meropis (DENNY, 1842) * HU: BALÁT (1957)

Family: Upupidae
Upupa *epops* LINNAEUS, 1758
Upupicola upupae (SCHRANK, 1803) * HU: SCHÄFER (1963)
Menacanthus fertilis (NITZSCH, 1866) *

Order: PICIFORMES
Family: Picidae
Dendrocopos *leucotos* (BECHSTEIN, 1802)
Penenirmus auritus (SCOPOLI, 1763) HU: SCHÄFER (1964)
Brueelia straminea (DENNY, 1842), *Colpocephalum tirkhan* (ANSARI, 1951), *Picicola snodgrassi* (KELLOGG, 1896)

Dendrocopos major (LINNAEUS, 1758)

Brueelia straminea (DENNY, 1842) * HU: SCHÄFER (1963)
Menacanthus pici (DENNY, 1842) HU: RÉKÁSI (1984, as *M. dryobates*)
Penenirmus auritus (SCOPOLI, 1763) * HU: BALÁT (1957)
Philopterus neomajor PRICE, HELLENTHAL et PALMA, 2003, *Picicola snodgrassi* (KELLOGG, 1896)

Dendrocopos medius (LINNAEUS, 1758)

Penenirmus auritus (SCOPOLI, 1763), *Picicola superciliosa* (NITZSCH, 1866) *

Dendrocopos minor (LINNAEUS, 1758)

Penenirmus auritus (SCOPOLI, 1763) HU: RÉKÁSI (1984)

Dendrocopos syriacus (EHRENBERG, 1833)

Penenirmus auritus (SCOPOLI, 1763) HU: BALÁT & BREUER (1955)

***Dryocopus** martius* (LINNAEUS, 1758)

Colpocephalum inaequale BURMEISTER, 1838 * HU: BALÁT (1957)
Penenirmus heteroscelis (NITZSCH, 1866) *

***Jynx** torquilla* LINNAEUS, 1758

Brueelia straminea (DENNY, 1842), *Penenirmus serrilumbus* (BURMEISTER, 1838) *

***Picus** canus* GMELIN, 1788

Penenirmus pici (FABRICIUS, 1798) HU: BALÁT (1957)
Picicola candidus (NITZSCH, 1866) * HU: RÉKÁSI (1984)
Colpocephalum tirkhan (ANSARI, 1951), *Menacanthus pici* (DENNY, 1842)

Picus viridis LINNAEUS, 1758

Menacanthus pici (DENNY, 1842) * HU: SCHÄFER (1964)
Penenirmus pici (FABRICIUS, 1798) * HU: RÉKÁSI (1984)
Picicola candidus (NITZSCH, 1866) HU: SCHÄFER (1964, in *Degeeriella*)

Order: PASSERIFORMES

Family: Laniidae

Lanius *collurio* LINNAEUS, 1758

Brueelia cruciata (BURMEISTER, 1838) * HU: RÉKÁSI (1984)

Philopterus coarctatus (SCOPOLI, 1763) * HU: BALÁT (1957)

Menacanthus camelinus (NITZSCH, 1874), *Menacanthus eurysternus* (BURMEISTER, 1838)

Lanius excubitor LINNAEUS, 1758

Brueelia imponderabilica EICHLER, 1954 * HU: RÉKÁSI (1984)

Philopterus coarctatus (SCOPOLI, 1763) HU: BALÁT (1957, as *Ph. fuscicollis*)

Menacanthus camelinus (NITZSCH, 1874) *, *Myrsidea abhorrens* (ZLOTORZYCKA, 1964) *

Lanius minor GMELIN, 1788

Brueelia minor LUNKASCHU, 1970 *, *Menacanthus camelinus* (NITZSCH, 1874), *Philopterus coarctatus* (SCOPOLI, 1763)

Lanius senator LINNAEUS, 1758

Menacanthus camelinus (NITZSCH, 1874), *Philopterus trigonophorus* (GIEBEL, 1874) *

Family: Oriolidae

Oriolus *oriolus* (LINNAEUS, 1758)

Brueelia munda (NITZSCH, 1866) * HU: BALÁT (1957)

Menacanthus orioli BLAGOVESHTCHENSKY, 1951 * HU: RÉKÁSI (2002)

Philopterus ornatus (NITZSCH, 1866) * HU: BALÁT (1957)

Ricinus dolichocephalus (SCOPOLI, 1763) *, *Sturnidoecus radui* BECHET, 1965 *

Family: Corvidae

Corvus *corax* LINNAEUS, 1758

Brueelia argula (BURMEISTER, 1838) * HU: RÉKÁSI (1984)

Menacanthus gonophaeus (BURMEISTER, 1838) * HU: RÉKÁSI (1984)

Myrsidea anaspila (NITSCH, 1866) * HU: RÉKÁSI (1984)

Philopterus corvi (LINNAEUS, 1758) * HU: SCHÄFER (1963, as *Ph. semisignatus*)

Brueelia atherae ANSARI, 1957 *, *Brueelia biocellata* (PIAGET, 1880), *Colpocephalum fregili* DENNY, 1842*, Myrsidea islandica* (KELLOGG et PAINE, 1911) *, *Myrsidea subcoracis* KLOCKENHOFF et SCHIRMERS, 1976 *, *Myrsidea tibetana* KLOCKENHOFF et SCHIRMERS, 1976 *, *Myrsidea vinlandica* KLOCKENHOFF et SCHIRMERS, 1976, *Philopterus osborni* EDWARDS, 1952

Corvus corone cornix LINNAEUS, 1758
Brueelia uncinosa (BURMEISTER, 1838) * HU: RÉKÁSI (1984)
Colpocephalum fregili DENNY, 1842 HU: RÉKÁSI (1984, as *C. subaequale*)
Menacanthus eurysternus (BURMEISTER, 1838) HU: RÉKÁSI (1984, as *M. cornicis*)
Myrsidea cornicis (DE GEER, 1778) * HU: BALÁT (1957)
Philopterus ocellatus (SCOPOLI, 1763) * HU: BALÁT (1957)

Corvus frugilegus LINNAEUS, 1758
Brueelia tasniemae ANSARI, 1957 * HU: RÉKÁSI (1973)
Colpocephalum fregili DENNY, 1842 HU: SCHÄFER (1963, as *C. subaequale*)
Menacanthus gonophaeus (BURMEISTER, 1838 HU: RÉKÁSI (1984, as *M. laticeps*)
Myrsidea isostoma (NITZSCH, 1866) * HU: RÉKÁSI (1973)
Philopterus atratus (NITZSCH, 1818) * HU: BALÁT (1957)
Brueelia perforata (ZLOTORZYCKA, 1964) *

Corvus monedula LINNAEUS, 1758
Brueelia varia (BURMEISTER, 1838) * HU: BALÁT (1957)
Myrsidea anathorax (NITZSCH, 1866) * HU: RÉKÁSI (1984)
Philopterus guttatus (DENNY, 1842) * HU: BALÁT (1957)
Menacanthus eurysternus (BURMEISTER, 1838), *Menacanthus gonophaeus* (BURMEISTER, 1838)

***Garrulus** glandarius* (LINNAEUS, 1758)
Brueelia glandarii (DENNY, 1842) * HU: SCHÄFER (1963)
Myrsidea indivisa (NITZSCH, 1866) * HU: RÉKÁSI (1984)
Philopterus garruli BOISDUVAL et LACORDAIRE, 1935 * HU: SCHÄFER (1963)
Menacanthus eurysternus (BURMEISTER, 1838)

***Nucifraga** caryocatactes* (LINNAEUS, 1758)
Brueelia olivacea (BURMEISTER, 1838) * HU: RÉKÁSI (1973)
Philopterus crassipes (BURMEISTER, 1838) * HU: RÉKÁSI (1973)
Brueelia multipunctata (CLAY, 1936) *, *Menacanthus merisuoi* EICHLER, 1953 *, *Myrside brunnea* (NITZSCH, 1866) *

***Pica** pica* (LINNAEUS, 1758)
Brueelia biocellata (PIAGET, 1880) * HU: RÉKÁSI (1984)

Myrsidea picae (LINNAEUS, 1758) * HU: BALÁT & BREUER (1955)
Philopterus picae (DENNY, 1842) * HU: BALÁT & BREUER (1955)
Menacanthus eurysternus (BURMEISTER, 1838) *

***Pyrrhocorax** graculus* (LINNAEUS, 1766)
Brueelia biguttata (KELLOGG et PAINE, 1914) *, *Colpocephalum fregili* DENNY, 1842, *Menacanthus eurysternus* (BURMEISTER, 1838), *Philopterus dumani* PRICE et HELLENTHAL, 1998 *

Pyrrhocorax pyrrhocorax (LINNAEUS, 1758)
Brueelia docilis ANSARI, 1956 *, *Colpocephalum fregili* DENNY, 1842 *, *Menacanthus gonophaeus* (BURMEISTER, 1838), *Philopterus thryptocephalus* (KELLOGG et PAINE, 1914)

Family: Bombycillidae
***Bombycilla** garrulus* (LINNAEUS, 1758)
Brueelia brachythorax (GIEBEL, 1874) * HU: SCHÄFER (1963)
Ricinus elongatus (OLFERS, 1816) HU: RÉKÁSI (1984)
Ricinus fringillae De GEER, 1778 HU: RÉKÁSI (1978*a*, as *R. bombycillae*)
Philopterus garrulae (PIAGET, 1880) *

Family: Paridae
Parus ater LINNAEUS, 1758
Menacanthus sinuatus (BURMEISTER, 1838), *Penenirmus pari* (DENNY, 1842) *, *Philopterus peripariphilus* (MEY, 1988) *, *Ricinus fringillae* DE GEER, 1778

Parus caeruleus LINNAEUS, 1758
Menacanthus sinuatus (BURMEISTER, 1838), *Penenirmus pari* (DENNY, 1842) *, *Philopterus hercynicus* (MEY, 1988) *, *Ricinus fringillae* DE GEER, 1778

Parus cristatus LINNEUS, 1758
Ricinus fringillae DE GEER, 1778

Parus major LINNAEUS, 1758
Menacanthus sinuatus (BURMEISTER, 1838) * HU: RÉKÁSI (1973)
Philopterus pallescens (DENNY, 1842) * HU: BALÁT (1957)

Brueelia weberi BALÁT, 1982 *, *Philopterus thuringiacus* (MEY, 1988) *, *Sturnidoecus hudeci* (BALÁT, 1981)*

Parus palustris LINNAEUS, 1758
Menacanthus sinuatus (BURMEISTER, 1838) HU: BALÁT (1957)
Philopterus pallescens (DENNY, 1842) *

Family: Remizidae
***Remiz** pendulinus* (LINNAEUS, 1758)
Brueelia balati (KRIŠTOFIK, 1999) *, *Menacanthus eurysternus* (BURMEISTER, 1838)

Family: Hirundinidae
***Delichon** urbica* (LINNAEUS, 1758)
Brueelia gracilis (BURMEISTER, 1838) * HU: BALÁT (1957)
Philopterus excisus NITZSCH, 1818 * HU: RÉKÁSI (1984)

***Hirundo** rustica* LINNAEUS, 1758
Brueelia domestica (KELLOGG et CHAPMAN, 1899) * HU: (VAS *et al*. 2008)
Myrsidea rustica (GIEBEL, 1874) * HU: RÉKÁSI (1990)
Philopterus microsomaticus TANDAN, 1955 * HU: (VAS *et al*. 2008)
Machaerilaemus malleus (BURMEISTER, 1838) *

***Riparia** riparia* (LINNAEUS, 1758)
Brueelia tenuis (BURMEISTER, 1838) *, *Machaerilaemus clayae* (BALÁT, 1966) *, *Myrsidea latifrons* (CARRIKER et SHULL, 1910) *, *Philopterus microsomaticus* TANDAN, 1955, *Ricinus fringillae* DE GEER, 1778

Family: Aegithalidae
***Aegithalos** caudatus* (LINNAEUS, 1758)
Penenirmus pari (DENNY, 1842) * HU: RÉKÁSI (1984)
Myrsidea aegithali BLAGOVESHTCHENSKY, 1940 *, *Sturnidoecus quadrilineatus* (NITZSCH, 1866) *

Family: Alaudidae
***Alauda** arvensis* LINNAEUS, 1758
Menacanthus alaudae (SCHRANK, 1776) * HU: SCHÄFER (1963)

Brueelia parviguttata (BLAGOVESHTCHENSKY, 1940) *, *Penenirmus hibari* (UCHIDA, 1949), *Philopterus stadleri* (EICHLER, 1959) *, *Ricinus serratus* (DURRANT, 1900)

***Eremophila** alpestris* (LINNAEUS, 1758)
Brueelia limpidus (MEY, 1982) *, *Menacanthus alaudae* (SCHRANK, 1776), *Philopterus kekilovae* FEDORENKO, 1984 *, *Ricinus serratus* (DURRANT, 1900) *

***Galerida** cristata* (LINNAEUS, 1758)
Menacanthus alaudae (SCHRANK, 1776) HU: RÉKÁSI (1984)
Philopterus alexanderkoenigi (EICHLER, 1953) * HU: RÉKÁSI (1973)
Penenirmus pavlovskyi BLAGOVESHTCHENSKY, 1951 *, *Ricinus serratus* (DURRANT, 1900), *Sturnidoecus chendoola* ANSARI, 1955 *

***Lullula** arborea* (LINNAEUS, 1758)
Brueelia lullulae BECHET, 1961 *, *Philopterus arboreus* FEDORENKO, 1984 *

***Melanocorypha** calandra* (LINNAEUS, 1766)
Brueelia melanocoryphae BECHET, 1966 *, *Philopterus stepposus* FEDORENKO, 1984 *

Family: Sylviidae
***Acrocephalus** arundinaceus* (LINNAEUS, 1758)
Menacanthus curuccae (SCHRANK, 1776), *Philopterus fedorenkoae* (MEY, 1983) *

Acrocephalus paludicola (VIEILLOT, 1817)
Menacanthus curuccae (SCHRANK, 1776)

Acrocephalus palustris (BECHSTEIN, 1798)
Philopterus mirificus (ZLOTORZYCKA, 1964) *, *Sturnidoecus pflergi* (BALÁT, 1981) *

Acrocephalus schoenobaenus (LINNAEUS, 1758)
Brueelia vaneki BALÁT, 1981 *, *Menacanthus curuccae* (SCHRANK, 1776), *Philopterus necopinatus* (ZLOTORZYCKA, 1964) *

Acrocephalus scirpaceus (HERMANN, 1804)
Menacanthus curuccae (SCHRANK, 1776)

Cettia *cetti* (TEMMINCK, 1820)
Menacanthus takayamai UCHIDA, 1926, *Penenirmus longuliceps* (BLAGOVESHTCHENSKY, 1940) *

Locustella *fluviatilis* (WOLF, 1810)
Sturnidoecus tulackovae (BALÁT, 1981) *

Locustella luscinioides (SAVI, 1824)
Brueelia locustellae FEDORENKO, 1975 *, *Menacanthus obrteli* BALÁT, 1981 *, *Penenirmus kuxi* BALÁT, 1981 *

Phylloscopus *bonelli* (VIEILLOT, 1819)
Philopterus phylloscopi FEDORENKO, 1979

Phylloscopus collybita (VIEILLOT, 1817)
Penenirmus rarus (ZLOTORZYCKA, 1976) * HU: RÉKÁSI (1990, in *Pleurinirmus*)
Menacanthus agilis (NITZSCH, 1866)

Phylloscopus fuscatus (BLYTH, 1842)
Menacanthus takayamai UCHIDA, 1926, *Philopterus reginae* (MEY, 1982) *

Phylloscopus inornatus (BLYTH, 1842)
Ricinus balati RHEINWALD, 1968

Phylloscopus sibilatrix (BECHSTEIN, 1793)
Philopterus phylloscopi FEDORENKO, 1979 *

Phylloscopus trochilus (LINNAEUS, 1758)
Menacanthus agilis (NITZSCH, 1866), *Menacanthus curuccae* (SCHRANK, 1776), *Penenirmus phylloscopi* (ZLOTORZYCKA, 1976) *, *Philopterus phylloscopi* FEDORENKO, 1979

Sylvia *atricapilla* (LINNAEUS, 1758)
Brueelia neoatricapillae PRICE, HELLENTHAL et PALMA, 2003 *, *Brueelia paratricapillae* PRICE, HELLENTHAL et PALMA, 2003 *, *Brueelia tovornikae* (BALÁT, 1981) *, *Menacanthus curuccae* (SCHRANK, 1776), *Myrsidea sylviae* SYCHRA et LITERÁK, 2008 *

Sylvia borin (BODDAERT, 1783)

Menacanthus curuccae (SCHRANK, 1776) HU: RÉKÁSI (1990, as *M. vistulanus*)

Brueelia borini LUNKASCHU, 1970 *, *Penenirmus affectator* (ZLOTORZYCKA, 1976) *, *Ricinus borin* BALÁT, 1952 *

Sylvia communis LATHAM, 1787

Menacanthus curuccae (SCHRANK, 1776)

Sylvia curruca (LINNAEUS, 1758)

Brueelia currucae BECHET, 1961 *, *Menacanthus curuccae* (SCHRANK, 1776), *Penenirmus speciosus* MEY, 1982 *

Sylvia nisoria (BECHSTEIN, 1795)

Brueelia rosickyi BALÁT, 1955 *, *Menacanthus curuccae* (SCHRANK, 1776), *Penenirmus pikulai* BALÁT, 1981 *

Family: Timaliidae

***Panurus** biarmicus* (LINNAEUS, 1758)

Menacanthus eurysternus (BURMEISTER, 1838), *Penenirmus visendus* (ZLOTORZYCKA, 1946b)

Family: Regulidae

***Regulus** ignicapillus* (TEMMINCK, 1820)

Ricinus frenatus (BURMEISTER, 1838)

Regulus regulus (LINNAEUS, 1758)

Philopterus reguli (DENNY, 1842) * HU: RÉKÁSI (1973)

Ricinus frenatus (BURMEISTER, 1838) *

Family: Troglodytidae

***Troglodytes** troglodytes* (LINNAEUS, 1758)

Menacanthus tenuifrons BLAGOVESHTCHENSKY, 1940 * HU: RÉKÁSI (1984)

Penenirmus albiventris (SCOPOLI, 1763) * HU: BALÁT (1957)

Myrsidea troglodyti (DENNY, 1842) *, *Penenirmus longuliceps* (BLAGOVESHTCHENSKY, 1940) *, *Philopterus troglodytis* FEDORENKO, 1986 *

Family: Sittidae

Sitta *europaea* LINNAEUS, 1758

Brueelia conocephalus (BLAGOVESHTCHENSKY, 1940) *, *Menacanthus eurysternus* (BURMEISTER, 1838), *Philopterus sittae* FEDORENKO, 1978 *

Tichodroma *muraria* (LINNAEUS, 1766)

Menacanthus eurysternus (BURMEISTER, 1838) HU: RÉKÁSI (1995, as *M. tichodromae*)
Philopterus hungaricus RÉKÁSI, 1998 * HU: RÉKÁSI (1998*a*)

Family: Certhiidae

Certhia *brachydactyla* BREHM, 1820

Philopterus lineatus (GIEBEL, 1874) *

Certhia familiaris LINNAEUS, 1758

Penenirmus gulosus (NITZSCH, 1866) *

Family: Sturnidae

Sturnus *roseus* (LINNAEUS, 1758)

Sturnidoecus pastoris (DENNY, 1842) * HU: RÉKÁSI (1984)
Brueelia fuscopleura (BLAGOVESHTCHENSKY, 1951) *, *Brueelia gulabitilyar* ANSARI, 1955 *, *Menacanthus eurysternus* (BURMEISTER, 1838)

Sturnus vulgaris LINNAEUS, 1758

Brueelia nebulosa (BURMEISTER, 1838) * HU: SCHÄFER (1963)
Menacanthus eurysternus (BURMEISTER, 1838) HU: SCHÄFER (1963, as *M. spiniferus*)
Sturnidoecus sturni (SCHRANK, 1776) * HU: BALÁT (1957)
Myrsidea cucullaris (NITZSCH, 1818) *, *Ricinus elongatus* (OLFERS, 1816)

Family: Turdidae

Turdus *iliacus* LINNAEUS, 1766

Brueelia haftorni (BALÁT, 1981) *, *Brueelia iliaci* (DENNY, 1842) *, *Myrsidea iliaci* EICHLER, 1951 *, *Philopterus timmermanni* (ZLOTORZYCKA, 1964) *, *Ricinus elongatus* (OLFERS, 1816)

Turdus merula LINNAEUS, 1758

Brueelia amsel (EICHLER, 1951) * HU: BALÁT (1957)
Brueelia merulensis (DENNY, 1842) * HU: BALÁT (1957)
Philopterus turdi (DENNY, 1842) HU: BALÁT & BREUER (1955, as *Ph. merulae*)
Ricinus elongatus (OLFERS, 1816) HU: BALÁT (1957)
Brueelia jacobi EICHLER, 1951 *, *Brueelia oudhensis* ANSARI, 1956 *, *Menacanthus eurysternus* (BURMEISTER, 1838), *Myrsidea thoracica* (GIEBEL, 1874)

Turdus naumanni TEMMINCK, 1820
Ricinus elongatus (OLFERS, 1816)

Turdus philomelos BREHM, 1831
Philopterus turdi (DENNY, 1842) * HU: RÉKÁSI (1990, in *Docophorulus*)
Brueelia turdinulae ANSARI, 1956 *, *Menacanthus eurysternus* (BURMEISTER, 1838), *Ricinus elongatus* (OLFERS, 1816), *Sturnidoecus melodicus* (EICHLER, 1951) *

Turdus pilaris LINNAEUS, 1758
Brueelia marginata (BURMEISTER, 1838) * HU: BALÁT (1957)
Philopterus bischoffi (EICHLER, 1951) * HU: RÉKÁSI (1984, in *Docophorulus*)
Brueelia antimarginalis EICHLER, 1951 *, *Menacanthus eurysternus* (BURMEISTER, 1838), *Ricinus elongatus* (OLFERS, 1816)

Turdus torquatus LINNAEUS, 1758
Brueelia marginata (BURMEISTER, 1838) HU: RÉKÁSI (1984, as *B. intermedia*), *Philopterus nativus* FEDORENKO, 1977 *, *Ricinus elongatus* (OLFERS, 1816)

Turdus viscivorus LINNAEUS, 1758
Brueelia viscivori (DENNY, 1842) * HU: RÉKÁSI (1984)
Myrsidea thoracica (GIEBEL, 1874) * HU: RÉKÁSI (1984)
Philopterus vernus (ZLOTORZYCKA, 1964) * HU: RÉKÁSI (1984, in *Docophorulus*)
Ricinus elongatus (OLFERS, 1816) * HU: BALÁT (1957)
Brueelia matvejevi BALÁT, 1981 *, *Menacanthus eurysternus* (BURMEISTER, 1838)

Family: Muscicapidae

Erithacus *rubecula* (LINNAEUS, 1758)
Brueelia tristis (GIEBEL, 1874) *, *Philopterus rubeculae* (DENNY, 1842) *, *Ricinus rubeculae* (SCHRANK, 1776) *

Ficedula *albicollis* (TEMMINCK, 1815)
Ricinus pflegeri BALÁT, 1952 *

Ficedula hypoleuca (PALLAS, 1764)
Philopterus capillatus (ZLOTORZYCKA, 1964) * HU: RÉKÁSI (1990, in *Docophorulus*)

Ficedula parva (BECHSTEIN, 1792)
Philopterus markevichi FEDORENKO et VOLKOV, 1977 *

Luscinia *megarhynchos* (BREHM, 1831)
Brueelia lais (GIEBEL, 1874) *

Luscinia svecica (LINNAEUS, 1758)
Ricinus rubeculae (SCHRANK, 1776), *Sturnidoecus atharea* ANSARI, 1955 *

Monticola *saxatilis* (LINNAEUS, 1766)
Philopterus zlotorzyckae (MEY, 1982) *

Monticola solitarius (LINNAEUS, 1758)
Ricinus rubeculae SCHRANK, 1776)

Muscicapa *striata* (PALLAS, 1764)
Philopterus desertus (ZLOTORZYCKA, 1964) * HU: RÉKÁSI (1973)
Menacanthus agilis (NITZSCH, 1866), *Myrsidea proterva* (ZLOTORZYCKA, 1964) *

Oenanthe *deserti* (TEMMINCK, 1825)
Penenirmus desertus FEDORENKO et BELSKAYA, 1979 *, *Ricinus rubeculae* (SCHRANK, 1776)

Oenanthe isabellina (TEMMINCK, 1829)
Penenirmus incurvatus FEDORENKO et BELSKAYA, 1979 *, *Philopterus isabellinae* (MEY, 1982) *

Oenanthe oenanthe (LINNAEUS, 1758)

Menacanthus affinis FEDORENKO et BELSKAYA, 1977 *, *Menacanthus exilis* (NITZSCH, 1866) *, *Philopterus oenanthe* FEDORENKO, 1983 *

Oenanthe pleschanka (LEPECHIN, 1770)
Penenirmus digitiformis FEDORENKO et BELSKAYA, 1979 *, *Philopterus pleschankae* FEDORENKO, 1983 *

***Phoenicurus** ochruros* (GMELIN, 1774)
Brueelia exigua (NITZSCH, 1866) *, *Menacanthus agilis* (NITZSCH, 1866) *, *Penenirmus barusi* BALÁT, 1981 *, *Ricinus rubeculae* (SCHRANK, 1776)

Phoenicurus phoenicurus (LINNAEUS, 1758)
Menacanthus agilis (NITZSCH, 1866), *Penenirmus silvicultrix* MEY, 1982 *, *Ricinus rubeculae* (SCHRANK, 1776)

***Saxicola** rubetra* (LINNAEUS, 1758)
Penenirmus nirmoideus (NITZSCH, 1874) *

Saxicola torquata (LINNAEUS, 1766)
Sturnidoecus irritans ANSARI, 1955 *

Family: Cinclidae
***Cinclus** cinclus* (LINNAEUS, 1758)
Myrsidea franciscoloi CONCI, 1942 *, *Philopterus cincli* (DENNY, 1842) *

Family: Passeridae
***Montifringilla** nivalis* (LINNAEUS, 1766)
Brueelia altaica MEY, 1982 *, *Philopterus comatus* (MEY, 1982) *

***Passer** domesticus* (LINNAEUS, 1758)
Brueelia cyclothorax (BURMEISTER, 1838) HU: RÉKÁSI (1973)
Philopterus fringillae (SCOPOLI, 1772) * HU: BALÁT (1957)
Brueelia subtilis (NITZSCH, 1874), *Menacanthus eurysternus* (BURMEISTER, 1838), *Myrsidea quadrifasciata* (PIAGET, 1880) *, *Ricinus fringillae* DE GEER, 1778, *Sturnidoecus refractariolus* (ZLOTORZYCKA, 1964) *

Passer montanus (LINNAEUS, 1758)
Brueelia cyclothorax (BURMEISTER, 1838) * HU: BALÁT (1957)
Philopterus montani (ZLOTORZYCKA, 1964) * HU: RÉKÁSI (1973)
Sturnidoecus ruficeps (NITZSCH, 1866) * HU: BALÁT (1957)
Brueelia subtilis (NITZSCH, 1874) *, *Myrsidea balati* MACHACEK, 1977 *, *Ricinus fringillae* DE GEER, 1778

Family: Prunellidae

***Prunella** collaris* (SCOPOLI, 1769)
Philopterus emiliae BALÁT, 1955 *, *Ricinus fringillae* DE GEER, 1778

Prunella modularis (LINNAEUS, 1758)
Brueelia annae (ZLOTORZYCKA et EICHLER, 1984) *, *Brueelia modularis* (PIAGET, 1880) *, *Menacanthus eurysternus* (BURMEISTER, 1838), *Philopterus modularis* (DENNY, 1842) *, *Ricinus elongatus* (OLFERS, 1816), *Ricinus rubeculae* (SCHRANK, 1776)

Family: Motacillidae

***Anthus** campestris* (LINNAEUS, 1758)
Brueelia kistiakowskyi FEDORENKO, 1975 *, *Menacanthus pusillus* (NITZSCH, 1866), *Penenirmus patevi* BALÁT, 1958 *

Anthus pratensis (LINNAEUS, 1758)
Brueelia corydalla TIMMERMANN, 1950 * HU: RÉKÁSI (1984)
Menacanthus pusillus (NITZSCH, 1866), *Ricinus fringillae* DE GEER, 1778

Anthus spinoletta (LINNAEUS, 1758)
Brueelia corydalla TIMMERMANN, 1950, *Menacanthus pusillus* (NITZSCH, 1866), *Philopterus hanzaki* BALÁT, 1955 *, *Ricinus fringillae* DE GEER, 1778

Anthus trivialis (LINNAEUS, 1758)
Brueelia ferianci BALÁT, 1955 *, *Menacanthus pusillus* (NITZSCH, 1866), *Philopterus vultuosus* (ZLOTORZYCKA, 1964) *, *Ricinus fringillae* DE GEER, 1778

***Motacilla** alba* LINNAEUS, 1758
Philopterus passerinus (DENNY, 1842) * HU: BALÁT (1957)
Sturnidoecus aeneas (PIAGET, 1885) * HU: RÉKÁSI (1990)

Menacanthus nogoma UCHIDA, 1926, *Menacanthus pusillus* (NITZSCH, 1866) *, *Myrsidea dukhunensis* ANSARI, 1951 *, *Ricinus fringillae* DE GEER, 1778

Motacilla cinerea TUNSTALL, 1771
Philopterus subitus FEDORENKO, 1985 *

Motacilla flava LINNAEUS, 1758
Brueelia kratochvili BALÁT, 1958 *, *Menacanthus pusillus* (NITZSCH, 1866), *Philopterus pavidus* (ZLOTORZYCKA, 1964) *

Family: Fringillidae

Carduelis *cannabina* (LINNAEUS, 1758)
Menacanthus alaudae (SCHRANK, 1776) HU: RÉKÁSI (1984, as *M. cannabinae*)
Brueelia stadleri EICHLER, 1954 *, *Ricinus fringillae* DE GEER, 1778

Carduelis carduelis (LINNAEUS, 1758)
Brueelia densilimba (NITZSCH, 1866) *, *Menacanthus alaudae* (SCHRANK, 1776), *Myrsidea serini* (SÉGUY, 1944), *Ricinus fringillae* DE GEER, 1778, *Sturnidoecus blandus* ZLOTORZYCKA, 1964 *

Carduelis chloris (LINNAEUS, 1758)
Brueelia breueri BALÁT, 1955 * HU: BALÁT (1957)
Philopterus citrinellae (SCHRANK, 1776) HU: BALÁT (1957)
Menacanthus eurysternus (BURMEISTER, 1838), *Myrsidea serini* (SÉGUY, 1944)

Carduelis flammea (LINNAEUS, 1758)
Brueelia sibrica MEY, 1982 *, *Menacanthus alaudae* (SCHRANK, 1776), *Menacanthus eurysternus* (BURMEISTER, 1838), *Philopterus linariae* (PIAGET, 1885) *, *Ricinus fringillae* DE GEER, 1778

Carduelis flavirostris (LINNAEUS, 1758)
Brueelia mongolica MEY, 1982 *, *Menacanthus alaudae* (SCHRANK, 1776), *Penenirmus deductoris* MEY, 1982 *, *Ricinus fringillae* DE GEER, 1778

Carduelis spinus (LINNAEUS, 1758)
Brueelia chrysomytris (BLAGOVESHTCHENKY, 1940) *

***Carpodacus** erythrinus* (PALLAS, 1770)
Menacanthus alaudae (SCHRANK, 1776), *Philopterus erythrini* (MEY, 1982) *, *Sturnidoecus carpodaci* (BALÁT, 1981) *

Carpodacus roseus (PALLAS, 1776)
Menacanthus alaudae (SCHRANK, 1776)

***Coccothraustes** coccothraustes* (LINNAEUS, 1758)
Brueelia juno (GIEBEL, 1874) * HU: RÉKÁSI (1973)
Philopterus eurasiaticus (MEY, 1982) *

***Fringilla** coelebs* LINNAEUS, 1758
Ricinus fringillae DE GEER, 1778 HU: BALÁT (1957, as *R. irascens*)
Brueelia kluzi BALÁT, 1955 *, *Menacanthus eurysternus* (BURMEISTER, 1838), *Penenirmus serrahnensis* BALÁT, 1982 *, *Philopterus fortunatus* (ZLOTORZYCKA, 1964) *, *Myrsidea lyali* KLOCKENHOFF, 1984 *

Fringilla montifringilla LINNAEUS, 1758
Brueelia glizi BALÁT, 1955 *, *Philopterus rapax* (ZLOTORZYCKA, 1964) *, *Ricinus fringillae* DE GEER, 1778

***Loxia** curvirostra* LINNAEUS, 1758
Brueelia limbata (BURMEISTER, 1838) *, *Philopterus curvirostrae* (SCHRANK, 1776) *, *Myrsidea quadrimaculata* (CARRIKER, 1902) *

Loxia leucoptera GMELIN, 1789
Philopterus hansmuenchi (EICHLER et VASJUKOVA, 1981) *

***Pinicola** enucleator* (LINNAEUS, 1758)
Menacanthus alaudae (SCHRANK, 1776)

***Pyrrhula** pyrrhula* (LINNAEUS, 1758)
Brueelia pyrrhularum EICHLER, 1954 * HU: RÉKÁSI (1984)
Philopterus citrinellae (SCHRANK, 1776) HU: BALÁT (1957)
Menacanthus eurysternus (BURMEISTER, 1838), *Ricinus fringillae* DE GEER, 1778

***Serinus** serinus* (LINNAEUS, 1766)

Brueelia sexytanum (SOLER CRUZ, BENITEZ RODRÍGUEZ, FLORIDO NAVIO et MUÑOZ PARRA, 1987) *, *Myrsidea serini* (SÉGUY, 1944) *

Family: Emberizidae

***Calcarius** lapponicus* (LINNAEUS, 1758)

Brueelia infrequens (CARRIKER, 1902) *, *Menacanthus eurysternus* (BURMEISTER, 1838), *Ricinus calcarii* NELSON, 1972

***Emberiza** calandra* LINNAEUS, 1758

Philopterus cumulatus (ZLOTORZYCKA, 1964) * HU: RÉKÁSI (1973)
Ricinus major FRESCA, 1924 *

Emberiza cia LINNAEUS, 1766

Ricinus fringillae DE GEER, 1778, *Ricinus serratus* (DURRANT, 1906)

Emberiza citrinella LINNAEUS, 1758

Brueelia delicata (NITZSCH, 1866) * HU: BALÁT (1957)
Philopterus citrinellae (SCHRANK, 1776) * HU: BALÁT & BREUER (1955)
Ricinus fringillae DE GEER, 1778 * HU: BALÁT (1957)
Menacanthus alaudae (SCHRANK, 1776), *Myrsidea serini* (SÉGUY, 1944)

Emberiza hortulana LINNAEUS, 1758

Penenirmus buresi BALÁT, 1958 *

Emberiza leucocephalos GMELIN, 1771

Brueelia delicata (NITZSCH, 1866), *Philopterus sibiricus* FEDORENKO et VOLKOV, 1980 *

Emberiza melanocephala SCOPOLI, 1769

Brueelia pelikani BALÁT, 1958 *, *Penenirmus buresi* BALÁT, 1958 *, *Ricinus serratus* (DURRANT, 1906)

Emberiza rustica PALLAS, 1776

Brueelia delicata (NITZSCH, 1866), *Machaerilaemus laticorpus* (CARRIKER, 1903), *Ricinus fringillae* DE GEER, 1778

Emberiza schoeniclus (LINNAEUS, 1758)

Brueelia blagovescenskyi BALÁT, 1955 * HU: RÉKÁSI (1984)
Philopterus residuus (ZLOTORZYCKA, 1964) * HU: RÉKÁSI (1973)
Ricinus fringillae DE GEER, 1778

***Plectrophenax** nivalis* (LINNAEUS, 1758)

Brueelia nivalis (GIEBEL, 1874) *, *Menacanthus alaudae* (SCHRANK, 1776), *Myrsidea major* (PIAGET, 1880) *, *Philopterus hamatus* (PACKARD, 1870) *, *Ricinus diffusus* (KELLOGG, 1896), *Ricinus fringillae* DE GEER, 1778, *Ricinus major* FRESCA, 1924, *Ricinus thoracicus* (PACKARD, 1870) *

Wild mammals with louse associations

Order: SORICOMORPHA
Family: Soricidae

***Crocidura** leucodon* (HERMANN, 1780)

Polyplax reclinata (NITZSCH, 1864)

Crocidura suaveolens (PALLAS, 1811)

Polyplax reclinata (NITZSCH, 1864) HU: (HAITLINGER 1973)

***Neomys** fodiens* (PENNANT, 1771)

Polyplax reclinata (NITZSCH, 1864)

***Sorex** araneus* LINNAEUS, 1758

Polyplax reclinata (NITZSCH, 1864) *

Sorex minutus LINNAEUS, 1766

Polyplax reclinata (NITZSCH, 1864)

Order: LAGOMORPHA
Family: Leporidae

***Lepus** europaeus* PALLAS, 1778

Haemodipsus lyriocephalus (BURMEISTER, 1839) HU: (BEAUCOURNU 1968)

***Oryctolagus** cuniculus* (LINNAEUS, 1758)

Haemodipsus ventricosus (DENNY, 1842) *

Order: RODENTIA

Family: Sciuridae

***Sciurus** vulgaris* LINNAEUS, 1758

Enderleinellus nitzschi FAHRENHOLZ, 1916 * HU: (PIOTROWSKI 1970)

Neohaematopinus sciuri JANCKE, 1932 *

***Spermophilus** citellus* (LINNAEUS, 1766)

Enderleinellus ferrisi (TOULESHKOV, 1957) *, *Enderleinellus propinquus* BLAGOVESHTCHENSKY, 1965, *Linognathoides laeviusculus* (GRUBE, 1851), *Polyplax bureschi* TOULESHKOV, 1957 *

Family: Gliridae

Dryomys nitedula PALLAS, 1778

Schizophthirus dryomydis BLAGOVESHTCHENSKY, 1965 *, *Schizophthirus jaczewskii* CAIS, 1974 *, *Schizophthirus pleurophaeus* (BURMEISTER, 1839)

Glis glis (LINNAEUS, 1766)

Schizophthirus gliris BLAGOVESHTCHENSKY, 1965 *, *Schizophthirus pleurophaeus* (BURMEISTER, 1839)

Muscardinus avellanarius (LINNAEUS, 1758)

Schizophthirus pleurophaeus (BURMEISTER, 1839)

Family: Dipodidae

***Sicista** subtilis* PALLAS 1773

Schizophthirus sicistae BLAGOVESHTCHENSKY, 1965 *

Family: Cricetidae

***Arvicola** amphibius* (LINNAEUS, 1758)

Hoplopleura acanthopus (BURMEISTER, 1839) HU: (PIOTROWSKI 1970)

Polyplax borealis FERRIS, 1933, *Polyplax spinigera* (BURMEISTER, 1839) *

***Microtus** agrestis* (LINNAEUS, 1761)

Hoplopleura acanthopus (BURMEISTER, 1839) HU: (PIOTROWSKI 1970)

Microtus arvalis (LINNAEUS, 1761)
Hoplopleura acanthopus (BURMEISTER, 1839) * HU: (PIOTROWSKI 1970)

Microtus oeconomus (PALLAS, 1776)
Hoplopleura acanthopus (BURMEISTER, 1839) HU: (PIOTROWSKI 1970)

Microtus subterraneus (SÉLYS-LONGCHAMPS, 1836)
Hoplopleura acanthopus (BURMEISTER, 1839) HU: (PIOTROWSKI 1970)

***Myodes** glareolus* (SCHREBER, 1780)
Hoplopleura acanthopus (BURMEISTER, 1839) HU: (PIOTROWSKI 1970)
Hoplopleura edentula FAHRENHOLZ, 1916, *Polyplax borealis* FERRIS, 1933, *Polyplax hannswrangeli* EICHLER, 1952 *

Family: Muridae
***Apodemus** agrarius* PALLAS, 1771
Hoplopleura affinis (BURMEISTER, 1839) * HU: (PIOTROWSKI 1970)
Polyplax serrata (BURMEISTER, 1839) HU: (PIOTROWSKI 1970)

Apodemus flavicollis (MELCHIOR, 1834)
Polyplax serrata (BURMEISTER, 1839) HU: (PIOTROWSKI 1970)
Hoplopleura affinis (BURMEISTER, 1839)

Apodemus sylvaticus (LINNAEUS, 1758)
Hoplopleura affinis (BURMEISTER, 1839) HU: (PIOTROWSKI 1970)
Polyplax serrata (BURMEISTER, 1839) HU: (HAITLINGER 1973)

Apodemus uralensis (PALLAS, 1811)
Polyplax serrata (BURMEISTER, 1839) HU: (HAITLINGER 1973)

***Micromys** minutus* (PALLAS, 1771)
Hoplopleura longula (NEUMANN, 1909) * HU: (PIOTROWSKI 1970)
Polyplax gracilis FAHRENHOLZ, 1910 * HU: (PIOTROWSKI 1970)

Mus *musculus* LINNAEUS, 1758

Polyplax serrata (BURMEISTER, 1839) * HU: (PIOTROWSKI 1970)

Hoplopleura captiosa JOHNSON, 1960 *

Mus spicilegus PETÉNYI, 1882

Hoplopleura captiosa JOHNSON, 1960 HU: (PIOTROWSKI 1970) – not included in DURDEN & MUSSER 1994; as a sibling species of *Mus musculus*, likely to be a regular host

Rattus *norvegicus* (BERKENHOUT, 1769)

Hoplopleura pacifica EWING, 1924, *Polyplax spinulosa* (BURMEISTER, 1839) *

Rattus rattus (LINNAEUS, 1758)

Hoplopleura pacifica EWING, 1924, *Polyplax spinulosa* (BURMEISTER, 1839)

Order: CARNIVORA

Family: Felidae

Felis *silvestris* SCHREBER, 1775

Felicola hercynianus KÉLER, 1957*

Lynx *lynx* LINNAEUS, 1758

Felicola spenceri HOPKINS, 1960 *

Family: Canidae

Canis *aureus* LINNAEUS, 1758

Trichodectes canis (DE GEER, 1778), *Linognathus setosus* (VON OLFERS, 1816)

Canis lupus LINNAEUS, 1758

Linognathus setosus (VON OLFERS, 1816), *Trichodectes canis* (DE GEER, 1778)

Nyctereutes *procyonoides* (GRAY, 1834)

Trichodectes canis (DE GEER, 1778)

Vulpes *vulpes* (LINNAEUS, 1758)

Felicola vulpis DENNY, 1842 * – RÉKÁSI (1979) collected a single individual from an atypical host *Microtus arvalis* PALLAS, 1778

Linognathus setosus (VON OLFERS, 1816)

Family: Ursidae

Ursus *arctos* LINNAEUS, 1758

Trichodectes pinguis BURMEISTER, 1838 *

Family: Mustelidae

Lutra *lutra* (LINNAEUS, 1758)

Lutridia exilis (NITZSCH [in GIEBEL], 1861) *

Martes *foina* (ERXLEBEN, 1777)

Stachiella retusa (BURMEISTER, 1838) *

Martes martes (LINNAEUS, 1758)

Stachiella salfii CONCI, 1940 *

Meles *meles* (LINNAEUS, 1758)

Trichodectes melis (FABRICIUS, 1805) * HU: RÉKÁSI (1979)

Mustela *erminea* LINNAEUS, 1758

Stachiella ermineae HOPKINS, 1941 * HU: RÉKÁSI (1983)

Mustela nivalis LINNAEUS, 1766

Stachiella mustelae (SCHRANK, 1803) * HU: RÉKÁSI (1979)

Mustela putorius LINNAEUS, 1758

Stachiella jacobi EICHLER, 1941 *

Family: Procyonidae

Procyon *lotor* (LINNAEUS, 1758)

Stachiella octomaculatus (PAINE, 1912) *

Order: ARTIODACTYLA

Family: Suidae

Sus *scrofa* LINNAEUS, 1758

Haematopinus apri GOUREAU, 1866 * HU: (PIOTROWSKI 1970)

Family: Cervidae

Capreolus *capreolus* LINNAEUS, 1758

Damalinia meyeri (TASCHENBERG, 1882) HU: (SUGÁR 1985)
Solenopotes capreoli FREUND, 1935 * HU: (BERDÁR 1983)

Cervus *elaphus* LINNAEUS, 1758

Bovicola longicornis (NITZSCH, 1818) * HU: (SUGÁR 1997)
Solenopotes burmeisteri (FAHRENHOLZ, 1919) * HU: (PIOTROWSKI 1970)

Dama *dama* (LINNAEUS, 1758)

Bovicola tibialis (PIAGET, 1880) *

Family: Bovidae

Ovis *musimon* LINNAEUS, 1758

Bovicola ovis (SCHRANK, 1781), *Linognathus africanus* KELLOGG et PAINE, 1911, *Linognathus ovillus* (NEUMANN, 1907), *Linognathus pedalis* (OSBORN, 1896)

Rupicapra *rupicapra* LINNAEUS, 1758

Bovicola alpinus KÉLER, 1942 *, *Linognathus stenopsis* (BURMEISTER, 1838)

Louse associations of humans and domesticated animals

Homo sapiens LINNAEUS, 1758

Pediculus humanus LINNAEUS, 1758 * HU: (PIOTROWSKI 1970) – both “*P. h. capitis*” and “*P. h. humanus*” ecotypes
Pthirus pubis (LINNAEUS, 1758) * HU: (PIOTROWSKI 1970)

Domesticated birds (alphabetically)

Anas domesticus LINNAEUS, 1758

Anaticola crassicornis (SCOPOLI, 1763), *Anatoecus dentatus* (SCOPOLI, 1763), *Anatoecus icterodes* (NITZSCH, 1818)*, Holomenopon leucoxanthum* (BURMEISTER, 1838)*, Holomenopon maxbeieri* EICHLER, 1954, *Holomenopon transvaalense* (BEDFORD, 1920)*, Trinoton querquedulae* (LINNAEUS, 1758)

Anser domesticus (LINNAEUS, 1758)

Anaticola anseris (LINNAEUS, 1758), *Anatoecus dentatus* (SCOPOLI, 1763)*, Anatoecus icterodes* (NITZSCH, 1818), *Ciconiphilus pectiniventris* (HARRISON, 1916), *Holomenopon leucoxanthum* (BURMEISTER, 1838)*, Ornithobius mathisi* (NEUMANN, 1912)*, Trinoton anserinum* (FABRICIUS, 1805)

Cairina moschata (LINNAEUS, 1758)

Anaticola cairinensis (MONTEIRO DE BARROS, 1933) *, *Holomenopon cairinae* EICHLER, 1943 *, *Holomenopon leucoxanthum* (BURMEISTER, 1838)

Gallus gallus (LINNAEUS, 1758)

Cuculotogaster heterographus (NITZSCH, 1866) **, Goniocotes gallinae* (DE GEER, 1778) **, Goniodes dissimilis* DENNY, 1842 *, *Goniodes gigas* (TASCHENBERG, 1879) **, Lagopoecus sinensis* (SUGIMOTO, 1930) **, Lipeurus caponis* (LINNAEUS, 1758) **, Lipeurus tropicalis* PETERS, 1931 **, Menacanthus cornutus* (SCHÖMMER, 1913) **, Menacanthus pallidulus* (NEUMANN, 1912) *, *Menacanthus stramineus* (NITZSCH, 1818)*, Menopon gallinae* (LINNAEUS, 1758) **, Oxylipeurus dentatus* (SUGIMOTO, 1934) *

Meleagris gallopavo LINNAEUS, 1758

Chelopistes meleagridis (LINNAEUS, 1758) **, Colpocephalum tausi* (ANSARI, 1951)*, Goniocotes gallinae* (DE GEER, 1778)*, Lipeurus caponis* (LINNAEUS, 1758), *Menacanthus stramineus* (NITZSCH, 1818) **, Menopon gallinae* (LINNAEUS, 1758), *Oxylipeurus copulentus* CLAY, 1938 *, *Oxylipeurus polytrapesius* (BURMEISTER, 1838) *

Numida meleagris (LINNAEUS, 1758)

Amyrsidea desousai (KÉLER, 1952) *, *Clayia theresae* HOPKINS, 1941 *, *Goniocotes congolensis* TENDEIRO, 1989 *, *Goniocotes maculatus* TASCHENBERG, 1882, *Goniodes gigas* (TASCHENBERG, 1879), *Goniodes klockenhoffi* (TENDEIRO, 1988) *, *Goniodes meyi* (TENDEIRO, 1988) *, *Goniodes numidae* MJÖBERG, 1910 *, *Goniodes reichenowii* (TENDEIRO, 1988) *, *Lipeurus caponis* (LINNAEUS, 1758), *Lipeurus lawrensis* BEDFORD, 1929 *, *Lipeurus numidae* (DENNY, 1842) *, *Menacanthus numidae* (GIEBEL, 1874) *, *Menacanthus stramineus* (NITZSCH, 1818), *Menopon gallinae* (LINNAEUS, 1758), *Numidicola antennatus* (KELLOGG et PAINE, 1911) *, *Somaphantus lusius* PAINE, 1914 *

Domesticated mammals (alphabetically)

Bos taurus LINNAEUS, 1758

Bovicola bovis (LINNAEUS, 1758) * HU: (EGRI & NAGY 1995.)
Haematopinus eurysternus (NITZSCH, 1818) * HU: (PIOTROWSKI 1970)
Linognathus vituli (LINNAEUS, 1758) * HU: (PIOTROWSKI 1970)
Solenopotes capillatus ENDERLEIN, 1904 * HU: (HORNOK *et al*. 2010.)

Bubalus bubalis LINNAEUS, 1758

Haematopinus tuberculatus (BURMEISTER, 1839) *

Canis familiaris (LINNAEUS, 1758)

Trichodectes canis (DE GEER, 1778) * HU: (PIOTROWSKI 1970)
Linognathus setosus (VON OLFERS, 1816) * HU: (PIOTROWSKI 1970)

Capra hircus LINNAEUS, 1758

Bovicola caprae (GURLT, 1843) * HU: (PIOTROWSKI 1970)
Linognathus africanus KELLOGG et PAINE, 1911
Linognathus stenopsis (BURMEISTER, 1838) * HU: (PIOTROWSKI 1970)
Bovicola crassipes (RUDOW, 1866) *, *Bovicola limbatus* (GERVAIS, 1844) *

Cavia porcellus (LINNAEUS, 1758)

Gyropus ovalis NITZSCH, 1818 *, *Gliricola porcelli* (SCHRANK, 1781) *, *Trimenopon hispidum* (BURMEISTER, 1838) *

Equus asinus LINNAEUS, 1758

Bovicola ocellatus (PIAGET, 1880), *Haematopinus asini* (LINNAEUS, 1758) *

Equus caballus LINNAEUS, 1758

Bovicola equi (DENNY, 1842) * HU: (EGRI 1990)
Haematopinus asini (LINNAEUS, 1758)

Felis catus (LINNAEUS, 1758)

Felicola subrostratus (BURMEISTER, 1838) * HU: (SZILVÁSSY 2006)

Myocastor coypus (MOLINA, 1782)

Pitrufquenia coypus MARELLI, 1932 *

Oryctolagus domesticus (LINNAEUS, 1758)
Haemodipsus ventricosus (DENNY, 1842)

Ovis aries LINNAEUS, 1758
Bovicola ovis (SCHRANK, 1781) *, *Linognathus africanus* KELLOGG et PAINE, 1911 *, *Linognathus ovillus* (NEUMANN, 1907) *, *Linognathus pedalis* (OSBORN, 1896) *

Sus domesticus LINNAEUS, 1758
Haematopinus suis (LINNAEUS, 1758) * HU: (PIOTROWSKI 1970)

Potential louse hosts with no lice known to science (alphabetically)

Birds

Acrocephalus agricola (JERDON, 1845), *Acrocephalus melanopogon* (TEMMINCK, 1823), *Anthus cervinus* (PALLAS, 1811), *Anthus richardi* VIEILLOT, 1818, *Aquila nipalensis* HODGSON, 1833, *Calandrella brachydactyla* (LEISLER, 1814), *Carduelis hornemanni* (HOLBOLL, 1843), *Cecropis (Hirundo) daurica* (LINNAEUS, 1771), *Egretta gularis* (BOSC, 1792), *Emberiza cirlus* LINNAEUS, 1766, *Emberiza pusilla* PALLAS, 1776, *Glareola nordmanni* FISCHER, 1842, *Hippolais icterina* (VIEILLOT, 1817), *Iduna (Hippolais) pallida* (EHRENBERG, 1833), *Ixobrychus minutus* (LINNAEUS, 1766), *Larus cachinnans* PALLAS, 1811, *Locustella naevia* (BODDAERT, 1783), *Luscinia luscinia* (LINNAEUS, 1758), *Marmaronetta angustirostris* (MENETRIES, 1832), *Motacilla citreola* PALLAS, 1776, *Oenanthe hispanica* (LINNAEUS, 1758), *Parus montanus* (BALDENSTEIN, 1827), *Phylloscopus proregulus* (PALLAS, 1811), *Phylloscopus schwarzi* (RADDE, 1863), *Sylvia cantillans* (PALLAS, 1764), *Sylvia melanocephala* (GMELIN, 1789)

Mammals

Mustela eversmanni LESSON, 1827, *Neomys anomalus* CABRERA, 1907

Appendix 2: Authors' affiliations and addresses

Here I list the affiliations and addresses of all authors of the published papers presented in the thesis.

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