Review

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Review

Flea (Insecta: Siphonaptera) Family Diversity

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Abstract: This overview of extant Siphonaptera lists 19 families with major hosts and general distribution, estimated numbers of genera, species, and subspecies, with a brief taxonomic and phylogenetic review. With around 10 new species described annually, global flea fauna has an estimated extant 249 genera, 2215 species, and 714 subspecies, mostly mammal parasites but 5% of species are on birds. Host specificity varies from euryxenous (i.e., infesting two or more host orders)(e.g., cat fleas, Ctenocephalides felis felis) to monoxenous (e.g., rabbit fleas, Spilopsyllus cuniculi). The largest family is the paraphyletic Hystrichopsyllidae, making up a third of all flea species. The largest monophyletic family, Ceratophyllidae (rodent and bird fleas), comprise another 20%, and has dispersed to every continent including Antarctica. Fleas descend from scorpionflies (Mecoptera), possibly snow scorpionflies (Boreidae) or Nannochoristidae, and even giant fossils found from the Mesozoic could be Siphonaptera. Flea diversification shows evidence of taxon cycles: "Relict" families such as helmet fleas (Stephanocircidae) have a disjunct distribution reflecting the breakup of Gondwanaland, 70 million years ago. "Niche specialists" include nest fleas (Anomiopsyllus), bat fleas (Ischnopsyllidae), and burrowing fleas, the chigoes (Tungidae). By contrast, Ceratophyllidae fleas could be considered "great speciators". Cat fleas and several other synanthropic flea species are invasive "supertramps". Although those species are intensively studied, many flea species and their hosts require urgent surveys and conservation.

Keywords: ectoparasite; taxon cycle; relict; great speciator; invasive species; supertramp; endangered species; conservation; taxonomy; phylogeny

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Introduction

With about 10 new species of flea discovered each year [1], the worldwide, extant flea fauna is estimated at 19 families, 31 subfamilies, 249 genera, 2215 species, and 714 subspecies [2]. These estimates are in flux with hundreds of flea species likely undiscovered [3].

Fleas have been estimated to originate in the Triassic (252 to 201 million years ago), Jurassic (160 million years ago), or Cretaceous (130 million years ago) [4]. Four fossil families of giant Mesozoic insects were identified as Siphonaptera (Pseudopulicidae, Sauropthiridae, Strashiliidae, Tarwiniidae) [4,5]. Strashilidae is now identified as an amphibious fly (Diptera: Nematocera) [6]. Additionally, several Cenozoic fossil fleas beginning late Eocene (50 million years ago) belong to extant families (Hystrichopsyllidae, Pulicidae) [5,7].

Ancestors of fleas are probably in Mecoptera, an order of mysterious insects with complete metamorphosis, mostly winged, and with candidate families being snow scorpionflies (Boreidae) or aberrant amphibious scorpionflies (Nannochoristidae) [8–10]. Whether Order Siphonaptera should

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be demoted in the taxonomic heirarchy and Order Mecoptera promoted are unresolved questions [9,11]

Flea phylogenies using morphology [12–14] or molecular characters [4,8] have been proposed. Other aspects of fleas including histology, host-finding and feeding, immature stages, life cycle, locomotion, mating, and physiology have not been the subject of comprehensive phylogenies [15,21]

Fleas are ecological engineers. They can increase nest humidity [22], carry "transformer species" such as plague bacteria *Yersinia pestis* (Lehmann & Neumann, 1896) [23], and facilitate forest growth [24]. Only 5% of flea species are associated with birds, most parasitize mammals [8]. Fleas are also associated with a myriad of symbiontes from tapeworms [25] to viruses [26,27].

Host specificity of fleas varies from monoxenous (a flea species restricted to one host species) (e.g., rabbit flea, *Spilopsyllus cuniculi* (Dale, 1878)) to euryxenous (a flea species occurring on 2 or more host orders) [28] (e.g., cat flea, *Ctenocephalides felis felis* (Bouché, 1835)) [29]. Some mammals are free of fleas, such as aquatic mammals (Cetacea, Pinnipedia) and elephants (Proboscidea). Unlike biodiversity in general, fleas are inexplicably most speciose in temperate, not tropical, latitudes [21].

Flea taxa seem to reveal a variety of taxon cycle stages. The taxon cycle theorizes that taxa evolve in genetic differentiation, specialization, geographic range, and habitat from coastal margins to hinterlands to mountains. The taxon cycle is generalized as Stage I including "supertramp species", Stage II "great speciators", Stage III "niche specialists", and Stage IV "relicts". Taxa may skip or repeat stages, such as range expansions and contractions seen with ants and birds [30–32].

With this overview, we summarize the main ecology, epidemiology, phylogeny, and taxonomy of the 19 families in Order Siphonaptera. It is a basic introduction for entomologists and for those unfamiliar with the world of fleas.

Flea families

1. Ancistropsyllidae

(Chevrotain fleas)
1 Genus
3 Species
0 Subspecies

The simple morphology of Ancistropsyllidae resembles both infraorder Ceratophyllomorpha and paraphyletic pulicomorphs and although it has never been analyzed molecularly, suggests an early flea family [4,8,33]. Found in Indo-Malaya and Palearctic on chevrotains (Artiodactylidae: Tragulidae), primitive ungulates that do not appear until the Oligocene (34 to 23 million years ago) [34], many of this flea's original hosts may be extinct.

Conservation status of chevrotains is data deficient but some chevrotains are being rediscovered [35]. This flea family is a niche specialist and relict requiring surveys and conservation.

2. Ceratophyllidae

(Rodent and bird fleas)
51 Genera
435 Species
132 Subspecies

This, the largest monophyletic flea family, has the most recent origin of any flea family. Its diversification coincides with recent radiations of squirrels (Sciuridae) and New World rodents (Cricetidae) [4,8,36]. Leptopsyllidae and Ischnopsyllidae are closely related to this family, with all three families grouped into the monophyletic infraorder Ceratophyllomorpha [4].

With a global distribution including Antarctica where the flea *Glaciopsyllus antarcticus* (Smit & Dunnet 1962) lives on southern fulmars (*Fulmarus glacialoides* (Smith, 1840)) and petrels (Aves: Procellariidae) [37–39], Ceratophyllidae dispersed back and forth several times between the Nearctic

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and Palearctic, as did Hystrichopsyllidae [40]. Cold hardening glycerols found in some ceratophyllids [41] may help explain their wide thermal tolerance and distribution [42].

Ceratophyllidae may have originated in the Eocene (45 million years ago) [4] or Oligocene (38-40 million years ago) [36] on mountain beaver (Rodentia: Aplodontidae), many genera of which are extinct, or Nearctic squirrels (Rodentia: Sciuridae); both are Sciuromorpha [8,36,43].

Ceratophyllid "morphospecies" *Nosopsyllus fasciatus* Bosc d'Antic, 1800 (northern rat flea) and *Nosopsyllus barbarus* (Jordan and Rothschild 1912) are considered the same species based on morphology and molecular data [44]. Local differentiation and phylogenetic inertia appear significant in flea diversity within this family [42]; thus, the Ceratophyllidae family is a great speciator.

The hen flea *Ceratophyllus* (*Ceratophyllus*) *gallinae* (Schrank, 1803) is a common, widespread, and synanthropic flea [45–47], but some Ceratophyllidae are island relicts needing conservation (e.g., *Dasypsyllus* spp. (Marshall and Nelson 1967) and the Manx shearwater flea, *Ceratophyllus* (*Emmareus*) *fionnus* (Usher, 1968) [48,49].

3. Chimaeropsyllidae

(Elephant shrew fleas)
7 Genera
29 Species
5 Subspecies

This flea family, with a monophyletic origin and morphological links to Hystrichopsyllidae, was formerly known as Hypsophthalmidae and appears to be a progenitor to Pulicidae [8]. Fleas belonging to this group are niche specialists for elephant shrews (Macroscelidea: Macroscelididae) and Muridae rodents in arid east and south Africa [33,50]. Some elephant shrews are endangered relicts being rediscovered [51].

4. Coptopsyllidae

2 Genera
18 Species
9 Subspecies

Niche specialists in desert areas of the Palearctic (central Asia and north Africa), these fleas infest gerbils (Rodentia: Gerbillinae) which first appear in the Miocene (23 to 5 million years ago [51–53]. However, this flea family is estimated to originate 50 million years ago in the Eocene [4,8] so its original host is unknown.

Roundworms (nematodes) (Secenentea: Tylenchida) neuter fleas of several families especially Coptopsyllidae [50,53,54].

Because only one species (*Coptopsylla africana* Wagner, 1932) was included in molecular phylogeny [8], this family remains phylogenetically neglected. Along with *Coptopsylla*, a second genus (monotypic) has been recognized with *Neocoptopsylla wassiliewi* (Wagner 1932) [51].

5. Hystrichopsyllidae

47 Genera
634 Species
284 Subspecies

Although the catchall, paraphyletic Ctenophthalmidae is subsumed by recognizing its subfamilies as Hystrichopsyllidae (except Macropsyllinae and Stenoponiinae in their own families), Hystrichopsyllidae remains paraphyletic, but has "natural groupings" that may serve as a basis for a revised taxonomy (*sensu* [13], Ctenophthalmidae in part, [8,55]). This family includes species of "nest

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fleas" that infest micromammals with underground nests and that often lack key diagnostic characteristics apparently due to evolutionary reduction in their sheltered environment [12,56,57].

Confusingly, Hystrichomorph rodents in the Nearctic and Neotropics (i.e., Caviomorpha) tend to be infested with Rhopalopsyllidae and not Hystrichopsyllidae, in fact, Hystrichopsyllidae have the "broadest host spectrum" of any flea family [43]. Hystrichopsyllidae is the largest flea family and includes *Ctenophthalmus* which is the largest flea genus comprising 170 species.

Hystrichopsyllidae probably originated in the Gondwanaland subtropics 75 million years ago (Cretaceous) but is now global except Antarctica [8,28,43,57,58]. Four species are fossils only [5].

This family appears to show a mixture of taxon cycle stages. Fleas such as *Hystrichopsylla orientalis orientalis* (Smit, 1956) could be in Stage I dispersal via invasive hosts [59]. Possible Stage II speciators have a high percentage of subspecies (*Hystrichopsylla* spp., *Typhloceras* spp.). Stage III niche specialists include fleas on "mammals having no permanent shelters (e.g., marsupials and insectivores)" [43] (e.g., Doratopsyllinae spp.), and nest fleas (e.g., *Anomiopsyllus* spp., *Ctenophtalmus* spp., *Neopsylla* spp., and *Rhadinopsylla* spp.). Stage IV relicts are the Nearctic mountain beaver flea, *Hystrichopsylla schefferi* Chapin, 1919, celebrated as the world's largest flea, and Australian endemics on marsupials, the nest flea *Acedestia chera* Jordan, 1937 and *Idilla caelebs* Smit, 1957.

6. Ischnopsyllidae

(Bat fleas)
20 Genera
128 Species
22 Subspecies

With specialized morphology and behavior [19,50,60,61], bat fleas are niche specialists whose evolution onto microchiroptera and megachiroptera followed bat diversification in the Eocene (56 to 34 million years ago). Bat fleas may have originated in Asia as a monophyletic family closely related to Leptopsyllidae and Ceratophyllidae [4,8].

Unusual bat fleas phoretic on earwigs (Dermaptera) were observed in Indo-Malaya caves [62]. Ectoparasites can be used to monitor microbes in bats and other hosts non-invasively [63].

7. Leptopsyllidae

(Scaled fleas)
29 Genera
267 Species
147 Subspecies

Originating in the Palearctic, fleas of this paraphyletic family and Ceratophyllidae are linked by another relict mountain beaver flea *Dolichopsyllus stylosus* (Baker, 1904) [4]. Leptopsyllidae are great speciators and nearly global (except Neotropics and Antarctica) mostly parasitizing rodents with some on birds, insectivores, hares, rabbits, and pikas [8,33,64,65].

One of the most studied Leptopsyllidae species has been the monoxenous house-mouse flea *Leptopsylla segnis* (Schönherr, 1811) that is a supertramp species found worldwide [64–66].

8. Lycopsyllidae

4 Genera
8 Species
0 Subspecies

This flea family is likely primitive within infraorder Pygiopsyllomorpha, a group that also includes Pygiopsyllidae and Stivaliidae [8]. Fleas of this family live on Australian echidna (Monotremata: Tachyglossidae) and marsupials such as wombats (Diprotodontia: Vombatidae) and

Tasmanian devils (Dasyuromorphia: Dasyuridae) with one atypical species (*Uropsylla tasmanica* Rothschild, 1905) having parasitic larvae [67,68].

Lycopsyllidae is monophyletic [8] with few recent studies of its epidemiology and phylogeny [69,70]. This flea family is a relict needing conservation, as do many of its hosts [71,72].

9. Macropsyllidae

(Australian giant fleas)
2 Genera
3 Species
0 Subspecies

These giant fleas infest marsupials and appear primitive with origins in the Cretaceous (95 million years ago) and a disjunct distribution that isolated them from other fleas [4]. Macropsyllidae shares some characters with Hystrichopsyllidae and Stephanocircidae [8,50,73].

Macropsylla novaehollandiae (Hastriter and Whiting, 2002) appears monoxenous on the New Holland mouse, *Pseudomys novaehollandiae* a host that itself is endangered [73,74]. Fleas of this family are vulnerable and threatened relicts requiring conservation [73,74].

10. Malacopsyllidae

(Armadillo fleas)
2 Genera
2 Species
0 Subspecies

Malacopsyllidae genera have one species each, *Malacopsylla grossiventris* (Weyenbergh, 1879) and *Phthiropsylla agenoris* (Rothschild, 1904). These Neotropical fleas attach to the ventral regions of armadillos (Dasypodidae: Cingulata), so the fleas do not bore through osteoderms as do Tungidae. Although Malacopsyllidae are mainly associated with armadillos, these fleas have also been reported on Caviomorpha rodents and Carnivora [75].

Malacopsyllidae have unusually strong legs, expandable abdomens and neosomy, and large eggs [76–79]. From a phylogenetic point of view, there is a close relationship between Malacopsyllidae and Rhopalopsyllidae but Malacopsyllidae is monophyletic [4,79]. Because many Cingulata are extinct, especially the larger ones like pampatheriids and glyptodonts, Malacopsyllidae survive as relictual niche specialist on extant armadillos.

11. Pulicidae

23 Genera
164 Species
38 Subspecies

Diversifying after 65 million years ago (Cretaceous) with the appearence of Afrotheria, Pulicidae have switched hosts via food chain or shared habitats [61] several times as great speciators and niche specialists onto rodents (*Xenopsylla*), carnivores (*Ctenocephalides*), insectivores (e.g., hedgehog flea *Archaeopsylla erinacei* (Bouché, 1835)) [80] humans and domestic animals (*Pulex* sp.), or rabbits and hares (e.g., *Cediopsylla inaequalis* (Baker, 1895), *Spilopsyllus cuniculi* (Dale 1878) [81]). *Neotunga* is a burrowing Pulicidae convergent with Tungidae [82].

This monophyletic family probably has an African origin where it is most diverse, with some authors placing the Pulicidae near to Leptopsyllidae [4,8,13,43]. Several much-studied Pulicidae fleas accompany humans as invasive supertramp species, notably the cat flea *Ctenocephalides felis felis* (Bouché, 1835) [83–94], dog flea *Ctenocephalides canis* (Curtis 1926) [93,95], sticktight flea *Echidnophaga gallinacea* (Westwood, 1875) [96], human flea *Pulex irritans* L., 1758 [11,97–99], *Xenopsylla brasiliensis* (Baker, 1904) [64], and the oriental rat flea *Xenopsylla cheopis* (Rothschild, 1903), the last species an historic plague vector ([100,101], disputed by [102]). These synanthropic flea species are involved as vectors of pathogens associated with emerging and re-emerging diseases in animals and humans [103].

Three species and two genera of Pulicidae are fossils only [5]. The Christmas Island flea *Xenopsylla nesiotes* (Jordan & Rothschild, 1908) is extinct [74].

12. Pygiopsyllidae

10 Genera
56 Species
12 Subspecies

Grouped within infraorder Pygiopsyllomorpha along with Lycopsyllidae and Stivaliidae, Pygiopsyllidae may have its origin on ancient prototherian [4] or metatherian mammals [8]. They show a disjunct distribution in Australia, Indo-Malaya, and Neotropics [104].

Whiting et al. [8] showed a monophyletic origin for this family, with Stivaliidae a sister group. Recent studies of Pygiopsyllidae epidemiology and phylogeny include [105–111]. Some Pygiopsyllidae fleas and their hosts require conservation as vulnerable, endangered, or critically endangered relicts [71,74,112].

13. Rhopalopsyllidae

(Club fleas)
11 Genera
141 Species
30 Subspecies

Rhopalopsyllidae are mostly on Hystrichomorpha and Myomorpha (Cricetidae) rodents in South America (i.e., Caviomorpha and Sigmodontinae) as well as marsupials [43,113]. *Parapsyllus* is a genus associated with seabirds fringing the Southern Ocean [78]. Rhopalopsyllidae can be considered great speciators.

Apparently, Hystrichomorph rodents emigrated from the Afrotropics to the Neotropics perhaps by rafting where they largely escaped their fleas, with the niche taken up by the Rhopalopsyllidae [43]. Both rodents and fleas diversified in the New World. This is reminiscent of other hosts escaping their fleas temporarily such as the hedgehog in New Zealand and squirrels in Europe and South America [3,114,115].

Rhopalopsyllidae is closely related to Malacopsyllidae (both are in the Malacopsylloidea superfamily), and to Vermipsyllidae. Zurita et al. [79] found Rhopalopsyllidae is paraphyletic (*contra* [8]).

14. Stenoponiidae

1 Genus
20 Species
7 Subspecies

These are large, dark fleas with distinct genetics and morphology (e.g., full genal comb, eggs with hard extrachorion), that are related to *Rhadinopsylla* spp. (Hystrichopsyllidae) [8,16,116,117]. They live in the Palearctic, Nearctic, and some Indo-Malaya areas as fall and winter niche specialists on rodents (Muridae and Cricetidae) [43,118,119].

15. Stephanocircidae

(Helmet fleas)
9 Genera

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57 Species
6 Subspecies

The function of these fleas' bizarre helmets and crowns of thorns remains unknown [50]. *Stephanopsylla thomasi* (Rothschild 1903) (Macropsyllidae), and *Smitella thambetosa* Traub 1968 (Stivaliidae) also have helmets but it appears the three families are not closely related [8,120,121].

The disjunct distribution of Stephanocircidae in Australia and the Neotropics appears to result from the Gondwanaland breakup, 70 million years ago [122]. Stephanocircidae's original hosts were likely marsupials now extinct [43]. In South America, these fleas parasitize mainly sigmodontine rodents (Cricetidae) like the grass mouse *Akodon*, which entered the Neotropics during the Great American Interchange, and opossums (Didelphimorphia: Didelphidae) [50,75,123,124]. Whereas in the Neotropics Stephanocircidae has many genera, species, host species, and a wide distribution, in Australia it is a relict with only a few genera and many of its species and their hosts endangered [71,74].

16. Stivaliidae

26 Genera
172 Species
13 Subspecies

This flea family is grouped with Lycopsyllidae and Pygiopsyllidae into the monophyletic infraorder Pygiopsyllomorpha [8]. It is considered an advanced flea family that was able to spread through Australia, Indo-Malaya, Palearctic, and Afrotropics as it "switched from metatherians" onto eutherian mammals such as beautiful squirrels (Sciuridae: Callosciurinae) and treeshrews (Scandentia) [8]. Symbiontes include phoretic mites [125].

Stivaliidae is likely a great speciator, but although a new genus in Stivaliidae (*Musserellus*) was described from Indonesia recently [126], this family remains "incompletely studied" [28,127].

17. Tungidae

(Chigoe fleas)
3 Genera
28 Species
0 Subspecies

Chigoes embed into and live under host skin with female swelling (neosomy) [81,128]. Even bony plates of armadillos (Cingulata) can be bored through [129]; holes in fossilized osteoderms of extinct glyptodont (Cingulata) were likely caused by Tungidae [130–133].

The unusual Tungidae family shows a broad host range, especially affecting edentates (Xenarthra) including armadillos and sloths, rodents, humans, and domestic animals [77,128], and in the case of *Hectopsylla,* bats (Chiroptera) and birds [64,134]. The Tungidae family has proven hard to place phylogenetically [4,8].

Tunga are paradoxically the "most specialized" of flea genera [77], but infest many orders of mammals and birds [128]. There are 14 *Tunga* species, most of them Neotropical with many described only recently [2,77].

A euryxenous supertramp species *Tunga penetrans* L., 1758 was spread by humans from South America to Africa and elsewhere in the 1800s [135]. Tungiasis is affected by public health policy, economics, animal health, and climate change [136,137].

18. Vermipsyllidae

(Ungulate and carnivore fleas)
3 Genera
43 Species

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7 Subspecies

Fleas of this family are niche specialists: *Dorcadia* spp. and *Vermipsylla* spp. parasitize even-toed ungulates (Artiodactyla), and *Chaetopsylla* spp. parasitize predators of Artiodactyla such as the weasel family (Carnivora: Mustelidae) and bears (Carnivora: Ursidae) in the Nearctic and Palearctic [43,139]. This is another example of fleas switching hosts via food chain.

These fleas have unusual frontal tubercles and female swelling (neosomy) while still attached to the host [77]. Vermipsyllidae is related to Malacopsyllidae and Rhopalopsyllidae [4].

19. Xiphiopsyllidae

(Brush furred mouse fleas)
1 Genus
8 Species
2 Subspecies

Though they have never been analyzed molecularly, based on morphology, Xiphiopsyllidae are placed as basal in the Ceratophyllomorpha infraorder [8,50].

Because of host movement and insufficient sampling, Harmsen and Jabbal [139] surmised that these fleas were "unlikely" to be relicts. However, they are niche specialists for the brush furred mouse *Lophuromys* (Rodentia: Muridae), several species of which are fragmented mountain populations in east Africa [140,141]. Both flea and rodent appear to include relict species requiring conservation.

Conclusions

Flea taxa appear to display various stages of taxon cycles. Dispersal onto novel hosts and into new areas, differentiation involving speciation, niche specialization, fragmentation and vicariance, and extinction of fleas and their hosts during tens of millions of years have complicated flea diversification.

Molecular studies of fleas are increasing, but many taxa are described only morphologically and could be re-examined using new techniques in order to clarify their taxonomy. Better knowledge of fleas may help prevent diseases caused by some fleas as pests, parasites, or vectors of pathogens [27,52,83,103,142–146].

Vertebrate hosts can often be aided and conserved by monitoring their fleas [38,63,96,147–156]. Even in well-studied areas like Europe where much biodiversity is still undescribed [155], surveys for vertebrates could also collect voucher specimens of fleas and other parasites [156]; an example is the collecting protocol for non-parasitologists of Galbraith et al. [157].

Conservation is urgently needed for some fleas, their hosts, and ecosystems [158–165] since fleas could play important but poorly understood roles in their communities [166–170]. Therefore, flea surveys would be helpful in every biogeographical realm.

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