




Flea (Insecta: Siphonaptera) Family Diversity

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Abstract: This overview of extant Siphonaptera lists 19 families with major hosts and their general distribution, estimated numbers of genera, species, and subspecies, with a brief taxonomic and phylogenetic review. With around 10 new species described annually, extant flea fauna comprises an estimated 249 genera, 2215 species, and 714 subspecies globally, 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), comprises 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. The diversification of fleas 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, such as 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 species; great speciator; invasive species; supertramp species; endangered species; conservation; taxonomy; phylogeny



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1. Introduction

With about 10 new species of fleas discovered each year [1], the worldwide, extant flea fauna is estimated to comprise 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*, and *Tarwiniidae*) [5], disputed [4]. *Strashiliidae* is now identified as an amphibious fly (Diptera: *Nematocera*). Additionally, several Cenozoic fossil fleas from the late Eocene (50 million years ago) belong to extant families (*Hystrichopsyllidae*, *Pulicidae*, and *Rhopalopsyllidae*) [4–7].

The ancestors of fleas are probably in Mecoptera, an order of mysterious insects with complete metamorphosis, are mostly winged, and whose candidate families are snow scorpionflies (*Boreidae*) or aberrant amphibious scorpionflies (*Nannochoristidae*) [8–10].

Whether or not the order Siphonaptera should be demoted in the taxonomic hierarchy and the order Mecoptera be promoted are unresolved questions [9,11].

Flea phylogenies using morphology [12–14] or molecular characteristics [4,8] have been proposed. Other aspects of fleas, including their histology, host-finding, 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 the nest humidity [22], carry “transformer species” such as the plague bacterium, *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 symbionts, from tapeworms [25] to viruses [26,27].

The 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 two 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 other organisms, fleas are inexplicably most speciose at temperate, not tropical, latitudes [21].

Flea taxa seem to reveal a variety of taxon cycle stages. The taxon cycle theorizes that taxa evolve in their genetic differentiation, specialization, geographic range, and preferred habitats 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 as seen in ants and birds [30–32]. We classified flea taxa subjectively with regard to taxon cycle stage.

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

2. Flea Families

2.1. *Ancistropsyllidae* (Toumanoff & Fuller, 1947)

(Chevrotain fleas)

1 Genus

3 Species

0 Subspecies

The simple morphology of *Ancistropsyllidae* resembles both the infraorder Ceratophylomorpha and paraphyletic pulicomorph fleas, but with a curiously “bent” ctenidium, and although it has never been analyzed molecularly, this suggests an early flea family [4,8,33]. Found in Indomalaya and the Palearctic on chevrotains (Artiodactylidae: Tragulidae), primitive ungulates that did not appear until the Oligocene (34 to 23 million years ago) [34], many of this flea’s original hosts may be extinct.

The conservation status of chevrotains is data-deficient, but some chevrotains have been rediscovered [35]. This flea family is a niche specialist and relict, requiring surveys and conservation.

2.2. *Ceratophyllidae* (Dampf, 1908)

(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 coincided with the recent emergence of squirrels (Sciuridae) and New World rodents (Cricetidae) [4,8,36]. In regard to phylogeny, *Leptopsyllidae* and *Ischnopsyllidae* are closely related to this family, with all three families grouped

into the monophyletic infraorder Ceratophyllomorpha; however, these families can be discriminated by characteristics such as their genal ctenidia and tentoria [4,8].

With a global distribution, including Antarctica, where the Antarctic petrel flea, *Glaciopsyllus antarcticus* (Smit & Dunnet, 1962), lives on southern fulmars (*Fulmarus glacialis*) (Smith, 1840) and petrels (Aves: Procellariidae) [37–39], Ceratophyllidae dispersed back and forth several times between the Nearctic and Palearctic, as did Hystrichopsyllidae [40]. The cold-hardening glycerol found in some Ceratophyllidae [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 (40–38 million years ago) [36] on the mountain beaver (Rodentia: Aplodontiidae), many genera of which are extinct, or on Nearctic squirrels (Rodentia: Sciuridae); both are Sciuromorpha [8,36,43].

The Ceratophyllidae “morphospecies”, *Nosopsyllus fasciatus* (Bosc, 1800) (northern rat flea) and *Nosopsyllus barbarus* (Jordan & Rothschild, 1912), are considered to be the same species based on their morphology and molecular data [44]. Local differentiation and phylogenetic inertia appear to be significant regarding the 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 that need conservation (e.g., *Dasyopsyllus* spp. (Baker, 1905) and the Manx shearwater flea, *Ceratophyllus* (*Emmareus*) *fionnus* (Usher, 1968 [48–50])).

2.3. *Chimaeropsyllidae* (Ewing & I. Fox, 1943)

(Elephant shrew fleas)

7 Genera

29 Species

5 Subspecies

This monophyletic flea family was formerly known as Hypsophthalmidae, and it appears to be a progenitor to Pulicidae, with morphological similarities involving their sensilla and setae [8].

Fleas belonging to this group are niche specialists for elephant shrews (Macroscelidea: Macroscelididae) and Muridae rodents in the arid regions of East and South Africa [51–53]. Some elephant shrews are endangered relicts that have been rediscovered [54].

2.4. *Coptopsyllidae* (Wagner, 1928)

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 appeared in the Miocene (23 to 5 million years ago) [51,55,56]. However, this flea family is estimated to have originated 50 million years ago in the Eocene [4,8], so its original host is unknown.

Certain species of roundworms (nematodes) (Secenentea: Tylenchida) cause castration and neutering when hyperparasitizing female and male fleas from various families, especially Coptopsyllidae [50,57,58].

Because only one species (*Coptopsylla africana* (Wagner, 1932)) was included in the molecular phylogeny [8], this family remains neglected phylogenetically. Along with *Coptopsylla*, a second genus (monotypic) has been recognized with *Neocoptopsylla wassiliewi* (Wagner, 1932) [55].

2.5. *Hystrichopsyllidae* (Tiraboschi, 1904)

47 Genera

634 Species

284 Subspecies

Although the catchall, paraphyletic Ctenophthalmidae (Rothschild, 1915) is subsumed through the recognition of 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]). This family includes species of “nest fleas” that infest micromammals with underground nests and often lack key diagnostic characteristics, apparently due to the evolutionary reduction in their sheltered environment [12,59,60].

Although the family has a cosmopolitan distribution, Hystrichomorpha rodents in the Nearctic and Neotropics (i.e., Caviomorpha) tend to be infested with Rhopalopsyllidae fleas 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 it is now global, except in Antarctica [8,28,43,61,62]. Four species exist as 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 [63]. 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., *Ctenophthalmus* 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 fleas *Acedestia chera* (Jordan, 1937) and *Idilla caelebs* (Smit, 1957).

2.6. *Ischnopsyllidae* (Wahlgren, 1907)

(Bat fleas)

20 Genera

128 Species

22 Subspecies

With their specialized morphology and behavior, bat fleas are niche specialists with distinctive genal ctenidia on adults. Their evolution onto microchiroptera and megachiroptera followed bat diversification in the Eocene (56 to 34 million years ago) [19,51,64,65]. Bat fleas may have originated in Asia as a monophyletic family closely related to Leptopsyllidae and Ceratophyllidae [4,8].

Unusual phoretic bat fleas were observed on earwigs (Dermaptera) in Indomalayan caves [66]. Collecting fleas and other parasites permits the non-invasive surveying of bats’ microbial communities [67].

2.7. *Leptopsyllidae* (Rothschild & Jordan, 1915)

(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 in the Neotropics and Antarctica), mostly parasitizing rodents, with some on birds, insectivores, hares, rabbits, and pikas [4,8,33,68,69].

One of the most studied Leptopsyllidae species has been the monoxenous house-mouse flea, *Leptopsylla segnis* (Schönherr, 1811). It is a supertramp species with a cosmopolitan distribution [68–70].

2.8. *Lycopsyllidae* (Baker, 1905)

4 Genera
8 Species
0 Subspecies

This flea family is likely primitive within the infraorder Pygiopsyllomorpha, a group that also includes Pygiopsyllidae and Stivaliidae [8]. Fleas of this family live on Australian echidnas (Monotremata: Tachyglossidae) and marsupials, such as the wombat (Diprotodontia: Vombatidae) and Tasmanian devil (Dasyuromorphia: Dasyuridae). One atypical species (*Uropsylla tasmanica* (Rothschild, 1905)) has parasitic larvae [43,68,71,72].

Lycopsyllidae is monophyletic [8], with few recent studies of its epidemiology and phylogeny [73,74]. This flea family is a relict that needs conservation, as do many of its hosts [75,76].

2.9. *Macropsyllidae* (Oudemans, 1909)

(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* share some morphological characters with *Hystrichopsyllidae* and some with *Stephanocircidae* [8,51,77].

Macropsylla novaehollandiae (Hastriter, 2002) appears monoxenous on the New Holland mouse, *Pseudomys novaehollandiae*, a host that is endangered itself [77]. Fleas of this family are vulnerable and threatened relicts that require conservation [77,78].

2.10. *Malacopsyllidae* (Baker, 1905)

(Armadillo fleas)

2 Genera
2 Species
0 Subspecies

The *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 the osteoderms like *Tungidae*. Although *Malacopsyllidae* are mainly associated with armadillos, these fleas have also been collected on *Caviomorpha* rodents and *Carnivora* [79].

Malacopsyllidae have unusually strong legs, expandable abdomens via neosomy, and large eggs [80–83]. From a phylogenetic point of view, there is a close relationship between *Malacopsyllidae* and *Rhopalopsyllidae*, but *Malacopsyllidae* is monophyletic [4,83]. Because many Cingulata are extinct, especially the larger ones like pampatheriids and glyptodonts, *Malacopsyllidae* survive as relictual niche specialists on extant armadillos.

2.11. *Pulicidae* (Billberg, 1820)

23 Genera
164 Species
38 Subspecies

After diversifying 65 million years ago (Cretaceous) with the appearance of Afrotheria, *Pulicidae* have switched hosts via the food chain or shared habitats [65] several times as great speciators and niche specialists onto rodents (*Xenopsylla* spp.), carnivores (*Ctenocephalides* spp.), insectivores (e.g., the hedgehog flea, *Archaeopsylla gallinace* (Bouché, 1835)) [84], humans, domestic animals (*Pulex* spp.), rabbits, and hares (e.g., *Cediopsylla*

inaequalis (Baker, 1895), *Spilopsyllus cuniculi* (Dale, 1878) [85]. *Neotunga* is a burrowing Pulicidae that appears morphologically convergent with Tungidae and parasitizes threatened pangolins (Mammalia: Pholidota) [8,81].

This monophyletic family probably has an African origin, where it is most diverse, with some authors placing the Pulicidae near Leptopsyllidae [4,8]. Several well-studied Pulicidae fleas accompany humans as invasive supertramp species, notably the cat flea, *Ctenocephalides felis felis* (Bouché, 1835) [29,86–97]; dog flea, *Ctenocephalides canis* (Curtis, 1926) [29,96,98]; sticktight flea, *Echidnophaga gallinacean* (Westwood, 1875) [99]; human flea, *Pulex irritans* (L., 1758) [11,100–102]; *Xenopsylla brasiliensis* (Baker, 1904) [68]; and the oriental rat flea, *Xenopsylla cheopis* (Rothschild, 1903). The last species is a historic plague vector [103,104], though disputed by [105]. These synanthropic flea species are involved as vectors of pathogens associated with emerging and re-emerging diseases in animals and humans [106].

Three species and two genera of Pulicidae exist as fossils only [5]. The Christmas Island flea, *Xenopsylla nesiotis* (Jordan & Rothschild, 1908), is extinct [78].

2.12. *Pygiopsyllidae* (Wagner, 1939)

10 Genera
56 Species
12 Subspecies

Grouped within the infraorder Pygiopsyllomorpha, along with Lycopsyllidae and Stivaliidae, Pygiopsyllidae may have its origin on ancient prototherian or metatherian mammals [4,8]. They show a disjunct distribution in Australia, Indomalaya, the Neotropics, and sub-Antarctica on a variety of hosts [43,68,107].

There is a monophyletic origin for this family, with Stivaliidae as a sister group [8,43]. Recent studies of Pygiopsyllidae epidemiology and phylogeny include [108–114]. Some Pygiopsyllidae fleas and their hosts require conservation as vulnerable, endangered, or critically endangered relicts [75,78,115].

2.13. *Rhopalopsyllidae* (Oudemans, 1909)

(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 [43,116]. *Parapsyllus* is a genus of Rhopalopsyllidae associated with seabirds fringing the Southern Ocean [82]. Rhopalopsyllidae can be considered great speciators.

Apparently, Hystrichomorpha rodents emigrated from the Afrotropics to the Neotropics, perhaps via rafting, where they largely escaped their fleas, with the niche taken up by Rhopalopsyllidae [43]. Both rodents and fleas diversified in the New World. This is reminiscent of other hosts escaping from their fleas temporarily, such as the hedgehog in New Zealand and squirrels in Europe and South America [3,117,118].

Flea phylogenies tend to show that Rhopalopsyllidae is closely related to Malacopsyllidae (both are in the Malacopsylloidea superfamily) and Vermipsyllidae [8]. Recently, Rhopalopsyllidae was found to be paraphyletic [83], *contra* [8].

2.14. *Stenoponiidae* (Cunha, 1914)

1 Genus
20 Species
7 Subspecies

These are large, dark fleas with distinct genetics and morphologies (e.g., full genal comb, eggs with hard extrachorions) that are related to *Rhadinopsylla* spp. (Hystrichopsylli-

dae) [8,16,119,120]. They live in the Palearctic, Nearctic, and some Indomalayan areas as fall and winter niche specialists on rodents (Muridae and Cricetidae) [43,121,122].

2.15. *Stephanocircidae* (Wagner, 1928)

(Helmet fleas)

9 Genera

57 Species

6 Subspecies

The functions of these fleas' bizarre helmets and crowns of thorns remain unknown [51]. *Stephanopsylla thomasi* (Rothschild, 1903) (Macropsyllidae) and *Smitella thambetosa* (Traub, 1968) (Stivaliidae) also have helmets, but it appears the three families are not closely related [8,123,124].

The disjunct distribution of Stephanocircidae in Australia and the Neotropics appears to result from the Gondwanaland breakup 70 million years ago [125]. The original hosts of Stephanocircidae were likely marsupials that are now extinct [43]. In South America, these fleas mainly parasitize sigmodontine rodents (Cricetidae), like the grass mouse, *Akodon*, which entered the Neotropics during the Great American Interchange, and opossums (Didelphimorphia: Didelphidae) [51,79,126,127]. In the Neotropics, Stephanocircidae has many genera, species, host species, and a wide distribution, whereas in Australia, it is a relict with only a few genera and with many of its species and their hosts endangered [75,78].

2.16. *Stivaliidae* (Mardon, 1978)

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 with characteristic genitalia that was able to spread through Australia, Indomalaya, the Palearctic, and the Afrotropics as it "switched from metatherians" [8] onto eutherian mammals, such as squirrels (Mammalia: Sciuridae) and tree shrews (Mammalia: Scandentia) [8,43,68]. Its symbionts include phoretic mites [128].

Stivaliidae is likely a great speciator, but although a new genus in Stivaliidae (*Musserellus*) was described in Indonesia recently [129], this family remains "incompletely studied" [28,130].

2.17. *Tungidae* (Taschenberg, 1880)

(Chigoe fleas)

3 Genera

28 Species

0 Subspecies

Chigoes embed into and live under their hosts' skin using female swelling (neotomy) [85,131]. Even the bony plates of armadillos (Mammalia: Cingulata) can be bored through [132]; holes in fossilized osteoderms of the extinct glyptodont (Cingulata) were likely caused by Tungidae [133–136].

The unusual Tungidae family shows a broad host range, affecting edentates (Xenarthra), including armadillos and sloths, as well as rodents, humans, domestic animals [81,131], and, in the case of *Hectopsylla*, bats (Chiroptera) and birds [68,137]. The Tungidae family has proven to be hard to place phylogenetically [4,8].

Tunga are paradoxically the "most specialized" of the flea genera [81] but infest many orders of mammals and birds [131]. There are 14 *Tunga* species, most of Neotropical, with many discovered only recently [2,81].

A euryxenous supertramp species *Tunga penetrans* (L., 1758) was spread by humans from South America to Africa and elsewhere in the 1800s [138]. Tungiasis is affected by public health policy, economics, animal health, and climate change [139–141].

2.18. *Vermipsyllidae* (Wagner, 1889)

(Ungulate and carnivore fleas)

3 Genera

43 Species

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), bears (Carnivora: Ursidae), and pumas (Carnivora: Felidae) in the Nearctic and Palearctic [43,142]. This is another example of fleas switching hosts via the food chain.

These fleas have unusual frontal tubercles and female swelling (neosomy) while still attached to the host [81]. Vermipsyllidae is related to Malacopsyllidae and Rhopalopsyllidae [4,8].

2.19. *Xiphiopsyllidae* (Wagner, 1939)

(Brush-furred mouse fleas)

1 Genus

8 Species

2 Subspecies

Though they have never been analyzed molecularly, based on their morphology, Xiphiopsyllidae are placed at the base of the Ceratophyllomorpha infraorder [8,51].

Because of host movement and insufficient sampling, Harmsen and Jabbal surmised that these fleas are “unlikely” to be relicts [52]. However, they are niche specialists for the brush-furred mouse, *Lophuromys* (Rodentia: Muridae), several species of which are in fragmented mountain populations in East Africa [143,144]. Both fleas and rodents appear to include relict species that require conservation.

3. 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 the extinction of fleas and their hosts during tens of millions of years have complicated the diversification of fleas.

Molecular studies of fleas are increasing, but most taxa are described only morphologically. They could be re-examined using new techniques in order to clarify their systematics. Better knowledge on fleas may help manage diseases caused by some fleas that are parasitic pests and vectors of pathogens [27,56,86,106,145–149].

Vertebrate hosts can often be aided and conserved through monitoring their fleas [38,67,99,150–157]. Even in well-studied areas, like Europe, where much biodiversity is still undescribed [158], surveys for vertebrates could also collect voucher specimens of fleas and other parasites [159]. For example, a collecting protocol can be made for non-parasitologists [160].

Conservation is needed urgently for some fleas, their hosts, and their ecosystems [48,49,76–78,116,128,159,161–168], and fleas could play important but poorly understood roles in their communities [169–173]. Therefore, flea surveys would be helpful in every biogeographical realm.

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