Flea Families

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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.

ectoparasite taxon cycle relict species invasive species

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]. Strashilidae 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][5][6][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][9][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][13][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][16][17][18][19][20][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][31][32].

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 Ceratophyllomorpha 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 glacialoides* (Smith, 1840)) and petrels (Aves: Procellariidae) [37][38][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][46][47], but some Ceratophyllidae are island relicts that need conservation (e.g., *Dasypsyllus* spp. (Baker, 1905) and the Manx shearwater flea, *Ceratophyllus* (*Emmareus*) *fionnus* (Usher, 1968 [48][49][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][52][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., *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 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][69][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].

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