Host Specificity of *Strigiphilus* Owl Lice (Ischnocera: Philopteridae), with the Description of New Species and Host Associations

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ABSTRACT   Three new species and 11 new host associations are described for the *cursitans* species group of the genus *Strigiphilus*, the only genus of Mallophaga confined to owls (Strigiformes). The new species are *S. schemskei* ex *Bubo coromandus*, *S. garylarsoni* ex *Otus leucotis*, and *S. petersoni* ex *Ninox punctulata*. This paper completes a taxonomic review of the *cursitans* species group and includes an updated host–parasite list. The host specificity of the group is reviewed, including features of the natural history of lice and their hosts that may have influenced the evolution of host–parasite associations. Although most members of the *cursitans* group are host specific, several cases of secondary transfer among ecologically related hosts are apparent. The significance of such transfers is discussed in light of attempts to employ data on host–parasite associations for host systematics.

KEY WORDS   Insecta, Mallophaga, owls, host specificity

THREE GENERA of chewing lice (Mallophaga) parasitize owls of the world: *Colpocephalum* Nitzsch, *Kurodaia* Uchida, and *Strigiphilus* Mjöberg. *Strigiphilus*, a member of the suborder Ischnocera, is the only genus restricted to owls (Strigiformes). Clay (1966) recognized 29 species of *Strigiphilus* and subdivided them into 9 species groups. Of these, the *cursitans* group is the largest, containing more than half of the species in the genus. Clayton & Price (1984) reevaluated the composition of the *cursitans* group, redescribed its members, and provided a key to the species. The current paper describes three new species and 11 new host associations for the group, and provides an updated host–parasite list (Table 1), thus completing a review of the *cursitans* group.

Members of the *cursitans* group vary in their degree of host specificity from monoxenous (one host species) to pleioxenous (two or more confamilial host genera; terminology from Marshall 1981). The variation in specificity is reviewed below, including a detailed discussion of natural history features that may have influenced the evolution of host specificity in this group. Although most members of the *cursitans* group are host specific, several cases of secondary transfer among ecologically related hosts are apparent. The significance of such transfers is discussed in light of attempts to employ data on host–parasite associations for host systematics.

Materials and Methods

The material examined included approximately 100 museum specimens and 32 fresh specimens collected by the author from owls in Peru. Owls were collected at night with a spotlight and shotgun. Each freshly killed host was exposed to ethyl acetate fumes in a chamber for several minutes to kill its ectoparasites. Its feathers were ruffled vigorously over a large sheet of paper. The parasites were removed and stored in 70% alcohol, and later mounted on microslides for taxonomic study. Taxonomic decisions were made according to the procedures outlined in Clayton & Price (1984). The morphological characters discussed are defined in the first new species description and abbreviated in the two subsequent descriptions. For exact demarcation of characters see figures 3 and 52 of Clayton & Price (1984). Dimensional ratios are indicated by a diagonal—e.g., THW/HL is the ratio of temporal head width to head length. All measurements are in millimeters. When sample sizes fluctuate for different measurements within a taxon, it is usually because characters were not visible in all of the specimens examined. Fig. 1–6 were made from slide-mounted specimens using a phase-contrast compound microscope with a 35-mm SLR camera attachment.

Strigiphilus schemskei Clayton, new species
(Fig. 1–3)

Type host: *Bubo coromandus* (Latham).

Diagnosis. Preconal head margins flat to concave (Fig. 1 and 2); dorsal anterior head plate approximately one-third length of head, with very short blunt posterior projection (Fig. 2). Dorsal submarginal head setae long, ocular setae medium to long. Metanotum with 3–4 + 3–4 posterolateral setae, 2–3 + 2–3 posteromedial setae. Posterior margin of terminal ventral sclerite of female bordered by

Table 1. Host–parasite list for the _S. cursitans_ group (see Discussion)

Host taxa	Strigiphilus taxa
Buboninae	
Otus scops	[1]_tuleskovi_ ⎤ A
O. senegalensis	[1]_tuleskovi_ ⎦
O. leucotis	[1]_garylarsoni_ n. sp.
O. asio	[1]_otus_ ⎤
O. kennicottii*	[1]_otus_ ⎥
O. flammeolus*	[1]_otus_ ⎥
O. trichopsis*	[1]_otus_ ⎦ B
O. guatemalae*	[2]_crucigerus_ ⎤ C
O. cooperi*	[2]_crucigerus_ ⎥
O. choliba	[2]_crucigerus_ ⎥
O. watsonii*	[2]_crucigerus_ ⎥
O. colombianus*	[2]_crucigerus_ ⎥
O. ingens*	[2]_crucigerus_ ⎦
(_O. minimus = ingens_)	[2]_lophostrix_ ⎤ D
Lophostrix cristata	[2]_lophostrix_ ⎦
	[2]_transversifrons?_
Bubo coromandus	[1]_schemskei_ n. sp.
Bubo lacteus	[3]_zumpti_
Bubo virginianus	[1]_syrnii_ ⎤ E
	[3]_oculatus_ ⎥
	[1]_chilensis_ ⎥
	[2]_elutus_ ⎤ F
Pulsatrix perspicillata	[2]_elutus_ ⎦
Nyctea scandiaca	[3]_ceblebrachys_
Glaucidium brasilianum	[2]_microgenitalis_
Micrathene whitneyi*	[1]_otus_
Ninox punctulata	[1]_petersoni_ n. sp.
Ninox novaeseelandiae	[1]_vapidus_
Athene brama	[1]_bramae_
Athene noctua	[1]_cursitans_ ⎤ G
Speotyto cunicularia	[1]_speotyti_ ⎥
Ciccaba virgata	[2]_virgo_ ⎦
Striginae	
Strix butleri*	[1]_cursitans_
Strix nebulosa	[1]_syrnii_
Strix occidentalis	[1]_syrnii_
Strix varia	[1]_syrnii_
Strix rufipes*	[1]_syrnii_
Rhinoptynx clamator	[2]_heterurus_
Asio capensis	[1]_capensis_
Aegolius acadicus	[1]_acadicus_
Aegolius funereus	[1]_pallidus_

Host names and sequence of genera were compiled from Morony et al. (1975), Fitzpatrick & O'Neill (1986), and American Ornithologists' Union (1983). Brackets denote associations of oligoxenous (A, C) and pleioxenous (B, D–G) lice; all other lice are monoxenous. *, new host associations; n. sp., new species. Numbers indicate subgroups of lice: 1, _cursitans_; 2, _elutus_; 3, _ceblebrachys_.

4–5 + 4–5 setae. Forked prolongation of male genitalic apodeme and genitalic dorsal plate as in Fig. 3.

Dimensions of male (_n_ = 5, unless otherwise indicated): total length (TL), 1.90–2.07 (_n_ = 4); head length (HL), 0.59–0.63; preconal head width (PCHW), 0.42–0.48; temporal head width (THW), 0.57–0.60; THW/HL, 0.92–0.98; head plate length (HPL), 0.20–0.23; HPL/HL, 0.34–0.38; head plate width at widest part (HPW), 0.18 (_n_ = 3); anterior head plate width (AHPW), 0.12–0.13 (_n_ = 3); ocular seta length (OSL), 0.20–0.25 (_n_ = 4); dorsal submarginal head seta length (DSHSL), 0.30–0.31 (_n_ = 3); prothoracic width (PW), 0.33–0.38; metathoracic width (MW), 0.47–0.58; abdominal width at segment V (AW), 0.80–0.88; male genitalic width (GW), 0.13–0.15; genital plate "arms" length (GPAL), 0.02–0.03.

Dimensions of female (_n_ = 5, unless otherwise indicated): TL, 2.08–2.59; HL, 0.64–0.69; PCHW, 0.48–0.52; THW, 0.60–0.66; THW/HL, 0.94–0.97; HPL, 0.22–0.25 (_n_ = 4); HPL/HL, 0.34–0.37 (_n_ = 4); HPW, 0.19–0.22 (_n_ = 4); AHPW, 0.12–0.13 (_n_ = 3); OSL, 0.25–0.27 (_n_ = 2); DSHSL, 0.30 (_n_ = 2); PW, 0.35–0.41; MW, 0.55–0.64; AW, 0.78–1.05.

Type Material. Holotype ♂, ex _B. c. coromandus_, India: Rajputana, Bharatpur, 4-I-1952, Meinertzhagen, 19687, B.M. 1952-143, in collection of British Museum (Natural History). Paratypes, 3 ♂♂, 4 ♀♀, same data as holotype; 2 ♂♂, 3 ♀♀, same except Rajputana, III-1937, Meinertzhagen 9035; 10 ♂♂, 9 ♀♀, ex _B. coromandus_, Rajputana, I-1936, Meinertzhagen 4756; 1 ♀, same except Rajastan, Bharatpur, 1-III-1969, KO22, 9EO732; paratypes deposited in the British Museum (Natural History) and at Oklahoma State University, Stillwater.

Remarks. Because the posterior projection of the dorsal anterior head plate of _S. schemskei_ is rather blunt (Fig. 2), it is possible to have specimens key to _S. bramae_ in the first couplet of Clayton & Price (1984). The forked prolongation and dorsal plate of the male genitalic apodeme (Fig. 3) are like _S. bramae_. However, _S. schemskei_ is considerably larger than _S. bramae_ (compare TL, HL, PCHW, THW, HPL, HPW, AHPW, PW, MW, AW). If one proceeds beyond couplet 1, _S. schemskei_ will key to _S. acadicus_, based on similar dimensions. However, the configurations of the dorsal head plate, genitalic forked prolongation, and dorsal genitalic plate clearly separate _S. schemskei_ from _S. acadicus_. _S. schemskei_ is a member of the _cursitans_ subgroup of the _cursitans_ species group (Clayton & Price 1984).

Etymology. This species of louse is named for Douglas Schemske, University of Chicago, in recognition of his research on coevolution and in appreciation for guiding the author's dissertation research.

Strigiphilus garylarsoni Clayton, new species
(Fig. 4–6)

Type host: _Otus leucotis_ (Temminck).

Diagnosis. Preconal head margins concave (Fig. 4 and 5); dorsal anterior head plate more than two-

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Fig. 1–6. Two new species of the _Strigiphilus cursitans_ group. (1) _S. schemskei_ head (scale = 0.50 mm): DSHS, dorsal submarginal head setae; DAHP, dorsal anterior head plate; CS, conus. (2) _S. schemskei_ dorsal anterior head plate (scale = 0.10 mm): FP, forked prolongation; DGP, dorsal genitalic plate. (3) _S. schemskei_ male genitalic apodeme (scale = 0.10 mm): GA, genitalic apodeme. (5) _S. garylarsoni_ dorsal anterior head plate (scale as in Fig. 2). (6) _S. garylarsoni_ male genitalic apodeme (scale as in Fig. 2).
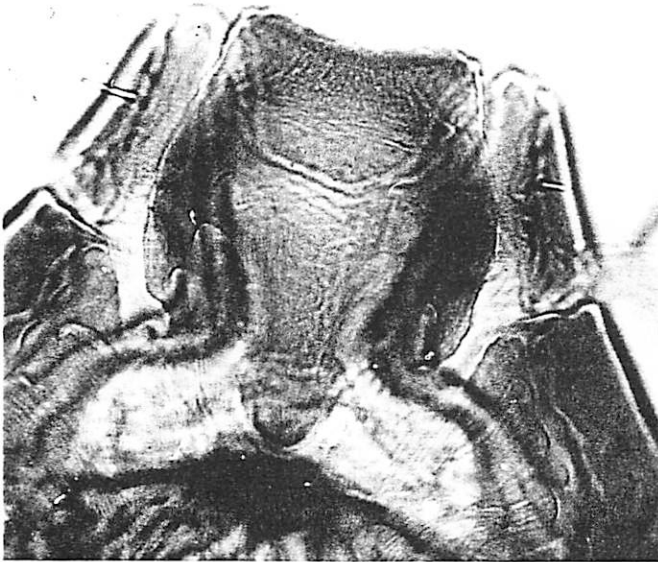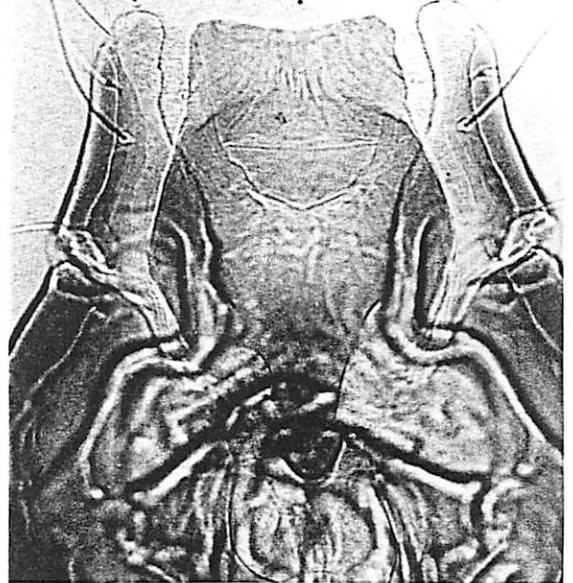
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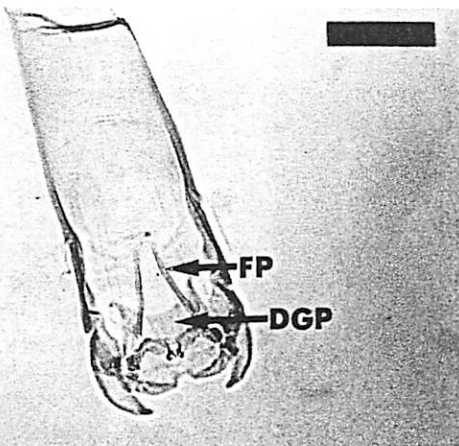DSHS
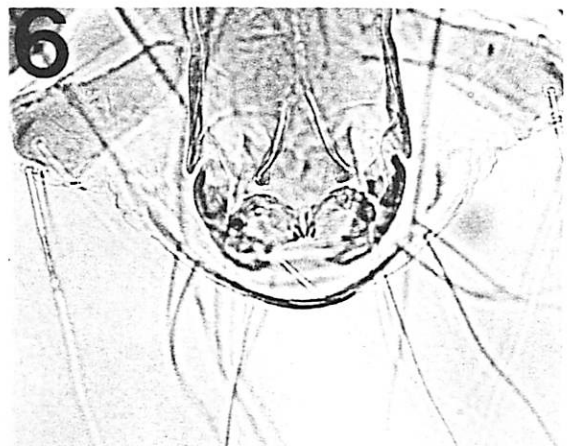DAHP
CS

4

GA

2

5

3

FP
DGP
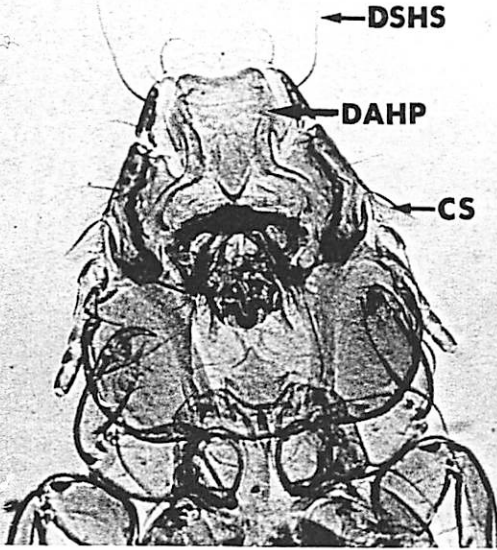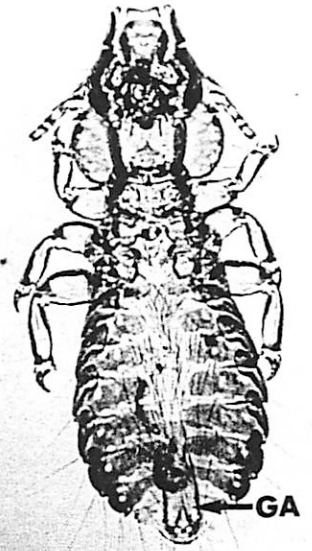
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fifths length of head, with prominent posterior projection. Dorsal submarginal head setae and ocular setae medium length. Metanotum with 3–4 + 3–4 posterolateral setae, 2–3 + 2–3 posteromedial setae. Posterior margin of terminal ventral sclerite of female bordered by 4–5 + 4–5 setae. Forked prolongation of male genitalic apodeme and genitalic dorsal plate as in Fig. 6.

Dimensions of male ($n = 3$ unless otherwise indicated): TL, 1.73–1.82; HL, 0.58–0.60; PCHW, 0.39–0.40; THW, 0.51–0.52; THW/HL, 0.85–0.90; HPL, 0.25–0.26; HPL/HL, 0.43–0.44; HPW, 0.16–0.18; AHPW, 0.09–0.11; OSL, 0.17–0.20; DSHSL, 0.15–0.22 ($n = 8$); PW, 0.32; MW, 0.47–0.49; AW, 0.65–0.67; GW, 0.12–0.13; GPAL, 0.01–0.02.

Dimensions of female ($n = 3$ unless otherwise indicated): TL, 1.93–2.09; HL, 0.63–0.64; PCHW, 0.43–0.44; THW, 0.55–0.57; THW/HL, 0.86–0.90; HPL, 0.26–0.28; HPL/HL, 0.41–0.44; HPW, 0.17–0.19; AHPW, 0.12–0.13; OSL, 0.13–0.20 ($n = 2$); DSHSL, 0.20–0.23 ($n = 6$); PW, 0.32–0.34; MW, 0.51–0.54; AW, 0.80 ($n = 1$).

Type Material. Holotype δ, ex *O. leucotis granti*, N. Rhodesia: N'dola, 20-III-1955, ML/131, British Museum (Natural History) 1956-310. Paratypes, 2 δδ, 3 ♀♀, same data as holotype; 8 δδ, 8 ♀♀, ex *O. l. leucotis*, Somaliland, II-1949, Meinertzhagen 18564. Holotype and all paratypes deposited in the British Museum (Natural History).

Remarks. Specimens of *S. garylarsoni* key to *S. vapidus* in couplet 25 of Clayton & Price (1984), except that the dorsal plate of the male genitalic apodeme (Fig. 6) is like *S. cursitans*, not *S. vapidus*. The major distinguishing feature of *S. garylarsoni* is the dorsal submarginal head setae (Fig. 1), which are much shorter than those of *S. vapidus* and *S. cursitans*. These setae are a conservative character used extensively in the earlier revision. *S. garylarsoni* is a member of the *cursitans* subgroup of the *cursitans* species group (Clayton & Price 1984). An enlarged version of Fig. 4 on p. 171 of Larson (1989) preceded publication herein.

Etymology. This species is named in honor of cartoonist Gary Larson, in appreciation of the unique light he has shed on the workings of nature.

Strigiphilus petersoni Clayton, new species

Type host: *Ninox punctulata* (Quoy and Gaimard).

Diagnosis. Much like *S. garylarsoni* except most dimensions smaller, especially head length and dorsal anterior head plate length. Head relatively wider, as evidenced by somewhat larger ratio of temporal head width (THW) to head length (HL).

Dimensions of male ($n = 3$ unless otherwise indicated): TL, 1.64–1.67; HL, 0.53–0.55; PCHW, 0.35–0.38; THW, 0.50–0.52; THW/HL, 0.91–0.94; HPL, 0.23–0.24; HPL/HL, 0.42–0.44; HPW, 0.15–0.18; AHPW, 0.10–0.11; OSL, 0.15–0.20 ($n = 2$); DSHSL, 0.13–0.17 ($n = 2$); PW, 0.29–0.31; MW,

0.46–0.47; AW, 0.71–0.74; GW, 0.13–0.14; GPAL, 0.01.

Dimensions of female ($n = 3$ unless otherwise indicated): TL, 1.83–1.95; HL, 0.59–0.61; PCHW, 0.40–0.42; THW, 0.55–0.59; THW/HL, 0.93–0.97; HPL, 0.24–0.25; HPL/HL, 0.41–0.42; HPW, 0.15–0.17; AHPW, 0.11; OSL, 0.20–0.23; DSHSL, 0.18–0.19 ($n = 2$); PW, 0.33–0.35; MW, 0.52–0.53; AW, 0.75–0.83.

Type Material. Holotype δ, ex *N. punctulata*, Indonesia: C. Sulawesi, Lake Lindu, 21-I-1972, JTM-6921. Paratypes, 2 δδ, 3 ♀♀, same data as holotype. Holotypes and all paratypes deposited at Oklahoma State University, Stillwater.

Remarks. *S. petersoni* is similar to *S. garylarsoni* but smaller. The head and dorsal anterior head plate of *S. petersoni* are shorter than those of *S. garylarsoni*, but the relative head width of *S. petersoni* is greater than that of *S. garylarsoni*. Because of this difference in head shape, *S. petersoni* will key to *S. vapidus* in couplet 20 of Clayton & Price (1984), whereas *S. garylarsoni* will key to *S. vapidus* in couplet 25. *S. petersoni* is distinguished from *S. vapidus* by the dorsal plate of the male genitalic apodeme, which is like that of *S. cursitans*. In addition, the dorsal submarginal head setae of *S. petersoni* are much shorter than those of *S. vapidus*. *S. petersoni* is a member of the *cursitans* subgroup of the *cursitans* species group.

Etymology. This species is named for the author's friend and colleague A. Townsend Peterson, a promising young avian systematist and parasite collector.

Strigiphilus cursitans (Nitzsch)

New host association: 2 δδ, 12 ♀♀, ex *Strix butleri* (Hume), Palestine, Meinertzhagen 11189.

Remarks. The specimens from *Strix butleri* are in all respects similar to *S. cursitans*, except that the dorsal head plate is slightly longer and the dorsal plate of the male genitalic apodeme is slightly larger. Although males key to *S. cursitans*, females key to *S. vapidus* (Clayton & Price 1984), which has a head plate like that of females from *Strix butleri*. Because the males from *Strix butleri* are nearly indistinguishable from male *S. cursitans*, and given the small number of males available for study from this rare host (see below), it is best to consider lice from *Strix butleri* members of *S. cursitans* sensu lato.

Strigiphilus syrnii (Packard)

New host association: 6 ♀♀, ex *Strix rufipes* King, Chile: Valdivia, 22-VIII-1952, D. S. Bullock.

Remarks. The lice from *Strix rufipes* easily key to *S. syrnii* in Clayton & Price (1984). The only notable difference is that the dorsal head plate is slightly shorter, with a posterior projection that is proportionately longer. Head length and temporal head width are also slightly smaller than those of

S. syrnii. These differences do not justify specific distinction, particularly given the lack of male specimens for study.

Strigiphilus otus Emerson

New host associations: 1 ♂, 5 ♀♀, ex *Otus flammeolus* (Kaup), Mexico: Coahuila, 9-V-1983, J. T. Marshall 7262; 3 ♂♂, 2 ♀♀, ex *Otus trichopsis* (Wagler), Mexico: Michoacan, La Nieve, 21-II-1983, A. R. Phillips; 1 ♂, 3 ♀♀, ex *Micropallus* (=*Micrathene*) *whitneyi* (Cooper), USA: Arizona, Tucson, 16-III-1938, A. R. Phillips.

Remarks. Lice from these 3 hosts key to *S. otus* in Clayton & Price (1984). While those from *M. whitneyi* do not appear to be morphologically distinct from *S. otus*, the genitalia of the single male specimen are difficult to see. The dorsal genitalic plate of male lice from *O. trichopsis* appears to differ slightly from that of *S. otus* lice, but it is difficult to discern in the available specimens. The head, dorsal head plate, and metathorax of lice from *O. trichopsis* and *O. flammeolus* are slightly larger than those of *S. otus*. However, these differences do not justify specific distinction, particularly given the small number of specimens available for study.

The host–parasite list presented by Clayton & Price (1984) did not recognize the recent splitting of *Otus kennicottii* (Elliot) from *Otus asio* (American Ornithologists' Union 1983). The list herein recognizes this split, thus creating a new host association for specimens collected from the former *Otus asio kennicottii.*

Strigiphilus crucigerus Carriker

New host associations: 1 ♂, 2 ♀♀, ex *O. guatemalae* (Sharpe), Peru: Dept. Madre de Dios, Cerro de Pantiacolla, 31-VIII-1985, D. H. Clayton; 4 ♂♂, 4 ♀♀, ex *O. cooperi* (Ridgway), Costa Rica: Guanacaste Pr., Liberia, 6-VIII-1964, 0-3259; 1 ♀, ex *O. watsonii* (Cassin), Peru: Dept. Madre de Dios, Hacienda Amazonia nr. Atalaya, 28-VII-1985, D. H. Clayton; 1 ♀, ex *O. watsonii*, Ecuador: Napo Prov., Río Aguarico, 23-X-1983, R. M. Timm 2692; 1 ♀, ex *O. colombianus*, Colombia: Cauca, El Tambo, D. H. Clayton (from museum skin FMNH 102125); ex *O. ingens*, Peru: Dept. Madre de Dios, Cerro de Pantiacolla, 27-VIII-1985 (5 ♂♂, 2 ♀♀), 5-IX-1985 (7 ♂♂, 5 ♀♀), 6-IX-1985 (6 ♂♂, 3 ♀♀), D. H. Clayton.

Remarks. Clayton & Price (1984) introduced their redescription of *S. crucigerus*: "As with most other members of the *elutus* subgroup, this species is identified best on the basis of its dimensions. . . ." The lice from the five species of *Otus* listed above should clearly be recognized as members of *S. crucigerus*. However, the inclusion of these specimens broadens the dimensional ranges of this taxon, thus complicating identification. Indeed, only the male specimens from *O. ingens* can be identified easily using Clayton and Price's key. Rather than outlin-

ing the dimensional increases here, a modified key is provided for the identification of *S. crucigerus* sensu lato and other members of the *elutus* subgroup, defined in couplet 3 of the key in Clayton & Price (1984).

Key to Species in the *elutus* Subgroup of the *Strigiphilus cursitans* Group

1. Posteromedial setae on male metanotum 5 + 5, on female 3 + 3, and dorsal anterior head plate longer than 0.320 .... *transversifrons*
   Posteromedial setae on male metanotum less than 5 + 5, on female less than 3 + 3, or dorsal anterior head plate shorter than 0.320 2
2. THW/HL less than 0.905 for males, 0.885 for females .... *lophostrix*
   THW/HL greater than 0.905 for males, 0.885 for females 3
3. Male head shorter than 0.625, dorsal anterior head plate shorter than 0.340; female head shorter than 0.680 4
   Male head longer than 0.625, dorsal anterior head plate longer than 0.340; female head usually longer than 0.680 7
4. Ocular setae longer than 0.160 and dorsal anterior head plate over one-half as wide as long (HPW/HPL at least 0.55), with pointed posterior projection; male dorsal genitalic plate with deeply concave anterior margin .... *otus* (=*cursitans* subgroup)
   Not as above 5
5. Head plate with blunt projection; tergocentral setae on II at least 11 for male, at least 13 for female .... *heterurus*
   Head plate with pointed projection; tergocentral setae on II less than 11 for male, less than 13 for female 6
6. Tergal V width greater than 0.22 for males, 0.19 for females; male genitalic width at least 0.12, male head plate length greater than 0.275; female preconal head width greater than 0.360 .... *crucigerus*
   Tergal V width less than 0.22 for males, 0.19 for females; male genitalic width less than 0.12, male head plate length less than 0.275; female preconal head width less than 0.360 .... *microgenitalis*
7. Male head shorter than 0.700, antennae 0.260 long or less; female dorsal head plate not over 0.180 wide, antennae not over 0.260 long .... *virgo*
   Male head at least 0.700 long, antennae 0.260 long or more; female dorsal head plate at least 0.180 wide, antennae longer than 0.260 .... *elutus*

Discussion

Chewing lice are obligate, host-specific parasites that complete their entire life cycle on the host.

List 1. General distribution and habitats of *cursitans* group hosts (from Clark et al. 1978, unless otherwise indicated) (names and sequence from Table 1 sources)

Otus scops: Eurasia, India, China, Indonesia, Philippines (Widespread: woodland, orchards, arid areas, riverine forest, thornbush).

O. senegalensis: Africa south of the Sahara (Savannas and dry woodland) (Burton 1973).

O. leucotis: Africa south of the Sahara (Scrub desert and arid savanna, woodland).

O. asio: Eastern-central N America: S Canada to NE Mexico (Open woodland, deciduous forest, parklands, residential areas in towns, scrub, and riparian woodland in drier regions) (American Ornithologists' Union 1983).

O. kennicottii: Western N America: SE Alaska to central Mexico (Woodland, especially oak and riprarian woodland, and scrub) (American Ornithologists' Union 1983).

O. flammeolus: N America: W U.S.A. to Mexico and Guatemala (Mountain pine forests).

O. trichopsis: SW U.S.A. to Honduras, El Salvador (Mountain pine–oak forest).

O. guatemalae: C America: Mexico to Bolivia (Humid lowland and montane forest, pine–oak association, lowland deciduous forest [both humid and arid], open woodland and plantations [American Ornithologists' Union 1983]).

O. cooperi: C America: S Mexico to NW Costa Rica (Coastal woods, mangroves, palms, Giant Cardon).

O. choliba: C America: Costa Rica to Bolivia, Argentina, SE Brazil (Open woodland, second growth, forest border and clearings, open country with scattered trees, parklands and residential areas [American Ornithologists' Union 1983]).

O. watsonii: Northern S America: Orinoco and Amazonian basins south to N Bolivia (D. Stotz, personal communication) (Tropical rain forests).

O. colombianus: Western S America: Colombia and Ecuador (Subtropical forests) (Fitzpatrick & O'Neill 1986).

O. ingens: Western S America: Bolivia to Venezuela (Subtropical forests).

(*O. minimus:* Known only from the holotype collected in Santa Ana, Bolivia [Peters 1940]).

Lophostrix cristata: S Mexico to Bolivia and Amazonian Brazil (D. Stotz, personal communication) (Lowland mature rain forest).

B. coromandus: India, S China, SE Asia (Riverine forests, wooded plains, plantations, rain forests).

Bubo lacteus: Africa south of Sahara (Dense woodland, riverine forest, savanna).

B. virginianus: N America south of tundra, C America and S America to Tierra del Fuego (Widespread: forests, deserts, mountain forests, rain forests, to limits of woodland, mangroves).

Pulsatrix perspicillata: C America: S Mexico to NW Argentina and SE Brazil (Tropical rain forests, riparian woods, mangroves, plantations, savanna forests).

Nyctea scandiaca: Circumpolar (Arctic tundra).

Glaucidium brasilianum: SW U.S.A. to tip of S America (Riparian woods, shrub seral stages, forest edge, mesquite thickets).

Micrathene whitneyi: N America: SW U.S.A. to central Mexico (Desert with giant cacti, oak woodland and riparian woodland, especially with Sycamores [American Ornithologists' Union 1983]).

Ninox punctulata: Celebes Islands (Open forest and cultivated areas).

N. novaeseelandiae: SE Asia, Islands of East Indies, Australia, New Zealand (Cultivated areas, forest, plantations).

Athene brama: S Iran, India, SW China, SE Asia (Parklands, cultivated fields, desert, lowland tropical rain forest).

A. noctua: Europe, C Asia including Mongolia and N Africa, N China, Arabia (Parklands, orchards, cultivated fields, steppes, semiarid desert).

Speotyto cunicularia: W Canada south through C America locally to Tierra del Fuego, Florida, West Indies (D. Stotz, personal communication) (Grassland, desert, open country).

Ciccaba virgata: C America to S America: Mexico to Bolivia, Paraguay and NE Argentina (Lowland forests, open woodland plantations).

List 1. Continued

Strix butleri: Egypt, Sinai Penninsula, Judean Desert, Saudi Arabia (Goodman & Sabry 1984) (Arid, palm groves).

S. nebulosa: Circumboreal: Eurasia and northern N America (Boreal forest).

S. occidentalis: N America: W Canada to C Mexico (Dense forests and wooded ravines).

S varia: S Canada, E U.S.A. south to Honduras (Dense deciduous or coniferous woods, near lakes, streams, swamps, meadows) (D. Stotz, personal communication).

S. rufipes: S America: Paraguay, Chile, Argentina (Forest [Meyer de Schauensee 1970]).

Rhinoptynx clamator: C America to S America: SE Mexico to Bolivia, Paraguay, N Argentina, Brazil (Savanna, scrub, marshes, plantations).

Asio capensis: Sudan, Ethiopia to S Africa (Flood plains and dambos, semiarid grassland).

Aegolius acadicus: N America: S Canada, S Alaska to Mexico highlands (Dense woodland, cedar and tamarack swamps).

A. funereus: Circumboreal (Coniferous forest, mixed forest).

The close ecological association between Mallophaga and birds has led to extensive host–parasite cospeciation (Brooks 1979), which is responsible for the more or less congruent taxonomic classifications of lice and birds. Lyal (1986) reviewed phylogenetic methods for the analysis of host–parasite cospeciation, including the use of Mallophaga in host systematics. Host–parasite cospeciation is not analyzed in the current paper because a phylogenetic analysis of the *S. cursitans* group has not been performed. Rather, the discussion focuses on ecological factors that may have influenced the patterns of host specificity in the group. It is important to realize, particularly for disjunct distributions, that many potential host species have not been sampled for lice. Furthermore, data on the natural history of some hosts are poor. Information on host distributions and habitats is summarized in List 1.

Most species in the *S. cursitans* group exhibit narrow host specificity. Of 24 species, 17 are monoxenous, 2 are oligoxenous (two or more congeneric host species), and 5 are pleioxenous. The oligoxenous louse *S. tuleskovi* parasitizes the Old World species *Otus scops* and *O. senegalensis* (Table 1, A), which are considered conspecific by some recent workers (Clark et al. 1978). The sharing of *S. tuleskovi* by these owls should not be considered independent support for the conspecificity hypothesis because of the strong possibility that host transfer may have led to secondary colonization (*O. scops* invades the geographical range of *O. senegalensis* during winter). The opportunity for transfer among species of owls is almost certainly high, given their dependence on tree holes or the abandoned nests of other birds for nesting. Nest holes are thought to facilitate louse transfer among species of birds (Hopkins 1939, Eveleigh & Threlfall 1976, Timm 1983). Phoresis of owl lice on hippoboscid flies has also been recorded (Keirans 1975). Phoresis is another suspected interspecific dispersal route for members of the suborder Ischnocera, including *Strigiphilus* (Clay 1957, Marshall 1981, Timm 1983). Although it can be inaccurate to infer host

similarity from shared lice, it is more conservative to infer host dissimilarity from unshared lice. For example, *Otus leucotis*, which is sympatric and syntopic (occupying the same macrohabitat, Lincoln et al. 1982) with *O. senegalensis*, is host to the monoxenous louse *S. garylarsoni*, suggesting that *O. leucotis* differs from *O. senegalensis* more than the latter differs from *O. scops*. This is indeed the case; *O. leucotis* is placed by some workers in the monotypic genus *Ptilopsis* (Eck & Busse 1973).

Five members of the *cursitans* group are pleioxenous and will be discussed, in turn. *S. otus*, a member of the *cursitans* subgroup of the *cursitans* species group, parasitizes five sympatric, syntopic species of North American owls, *Otus asio, O. kennicottii, O. flammeolus, O. trichopsis,* and *Micrathene whitneyi* (Table 1, B). All five species depend on cavities for nesting, particularly abandoned woodpecker holes (Johnsgard 1988). Further south the oligoxenous louse *S. crucigerus*, a member of the *elutus* subgroup, parasitizes six more species of *Otus, O. guatemalae, O. cooperi, O. choliba, O. watsonii, O. colombianus,* and *O. ingens* (Table 1, C). These six owls have sequentially overlapping ranges and habitats, and presumably similar nesting biology, although their natural history is not well known.

A second pleioxenous louse, *S. lophostrix*, also a member of the *elutus* subgroup, has been collected from the southern species *O. minimus* and *Lophostrix cristata* (Table 1, D). *O. minimus*, known only from the holotype described by Carriker (1935), was recently synonymized with *O. ingens* (Fitzpatrick & O'Neill 1986). Although *L. cristata* is sympatric in some localities with *O. ingens*, it seems unlikely that lice could transfer between these species because they occur at different elevations in different habitats (D. Stotz, personal communication). The record of *S. lophostrix* from *O. ingens* is based solely on specimens collected by Carriker from the *O. minimus* holotype. Carriker (1966) described these specimens as *S. minimus*, which Clayton & Price (1984) synonymized with *S. lophostrix*. During fieldwork for the current paper, 28 specimens of *S. crucigerus* were collected from three freshly collected *O. ingens*, but no specimens of *S. lophostrix* were found. Additional collecting from *O. ingens* closer to the type locality of *O. minimus* (La Paz, Bolivia) is needed to confirm the record of *S. lophostrix*. Additional collecting is also needed from *L. cristata* to confirm its host status for *S. lophostrix*, as well as its unresolved status as a possible host for *S. transversifrons* (Emerson 1981).

A third pleioxenous louse, *S. syrnii*, parasitizes the New World species *Bubo virginianus* and four species of New World-circumboreal *Strix, S. nebulosa, S. occidentalis, S. varia,* and *S. rufipes* (Table 1, E), making it the only *cursitans* group member that crosses host subfamilies. *B. virginianus*, one of the world's least habitat-specific birds, is sympatric and syntopic with all four species of *Strix*. Like

them, it nests in holes or abandoned nests of other birds (Johnsgard 1988). A fourth pleioxenous louse, *S. elutus*, also parasitizes *B. virginianus* and the Neotropical species *Pulsatrix perspicillata* (Table 1, F), which is broadly sympatric and syntopic with *B. virginianus* and nests in holes (Burton 1973). *B. virginianus* is also host to the two monoxenous lice *S. oculatus* and *S. chilensis*. The latter is a highly questionable taxon originally described from two female specimens in poor condition (Carriker 1966, Clayton & Price 1984). *S. oculatus*, in contrast, is a distinct species collected from several subspecies of *B. virginianus* from 17 North American localities. In summary, *B. virginianus* is parasitized by three confirmed species of lice representing the three *cursitans* subgroups. *S. elutus*, collected only from Colombia and Venezuela, may be a Neotropical replacement for *S. oculatus*, collected only from the United States and Canada (Clayton & Price 1984). This hypothesis could be tested through additional collecting and identification of lice from *B. virginianus* in Central and South America. The host distributions of *S. oculatus, S. elutus,* and *S. syrnii* suggest that *B. virginianus* is the original host of *S. oculatus*, whereas *S. elutus* and *S. syrnii* may be secondary colonists from *Pulsatrix perspicillata* and *Strix* spp., respectively. This hypothesis could be tested by constructing and comparing host–parasite phylogenies.

The fifth and final pleioxenous species of the *cursitans* group is the nominate species *S. cursitans*, which parasitizes the Old World owls *Athene noctua* and *Strix butleri* (Table 1, G). The latter is a rare species of limited distribution (Goodman & Sabry 1984). *A. noctua*, on the other hand, is a widespread species found in many habitats, again suggesting the possibility of secondary colonization. Its allopatric congener, *A. brama*, is parasitized by the monoxenous louse *S. bramae*.

The allopatric Old World owls *Bubo coromandus* and *B. lacteus* are parasitized, respectively, by the monoxenous species *S. schemskei* and *S. zumpti*, and the allopatric *Ninox punctulata* and *N. novaeseelandiae* are parasitized, respectively, by the monoxenous lice *S. petersoni* and *S. vapidus*. The Nearctic *Aegolius acadicus* and Holarctic *A. funereus* are parasitized by the monoxenous lice *S. acadicus* and *S. pallidus*, respectively, despite considerable overlap in the ranges, microhabitats, and nesting requirements of these hosts in North America (Johnsgard 1988). The 18 specimens of *S. acadicus* redescribed by Clayton & Price (1984) were collected from Canada, whereas the 24 specimens of *S. pallidus* studied were collected from Norway and Sweden, with the exception of two females from Alaska. It seems likely that *S. pallidus* has a geographical distribution superimposed on its host-limited distribution—i.e., *S. pallidus* might be an Old World species. This hypothesis could be tested by collecting and identifying lice (especially males) from North American populations of *S. pallidus*. Clay (1949) reviewed similar geographical

distributions of lice, noting that Mallophaga are sometimes restricted to small portions of their host's range.

The six remaining species of the *cursitans* group, *S. ceblebrachys*, *S. microgenitalis*, *S. speotyti*, *S. virgo*, *S. heterurus*, and *S. capensis*, are all monoxenous parasites of monotypic owl genera—i.e., monotypic in relation to the host taxa included herein. Given the patterns of host association discussed above, it is difficult to understand the restriction of *S. microgenitalis* to *Glaucidium brasilianum*, which is sympatric and syntopic with several other small hole-nesting owls that share lice (hosts of *S. otus* and *S. crucigerus*). Additional collecting from *G. brasilianum* and other New World *Glaucidium* spp. might help to explain the limited distribution of *S. microgenitalis* and clarify why no other *cursitans* group species are found on *G. brasilianum*.

In conclusion, although most members of the *cursitans* species group are highly specific, several cases of transfer among ecologically related hosts are apparent. The six confirmed cases of oligoxenous or pleioxenous species (Table 1, A–C, E–G) all involve lice found on sympatric, syntopic hosts. There are no examples of oligoxenous or pleioxenous lice sharing only allopatric hosts, even closely related hosts. These results argue strongly against the persistent belief that sister species of hosts can be determined by demonstrating shared species of lice (see Elbel and Emerson [1959] for an example involving the *cursitans* group). This practice is based on the assumption that parasites speciate more slowly than hosts, an assumption that is clearly erroneous on genetic grounds (Price 1980). Additional examples of secondary colonization of lice have been reviewed by Clay (1964, 1966), Price & Clayton (1983), and others. Continued documentation of patterns of host specificity in the Mallophaga, especially in light of host ecology, will improve our understanding of the parameters governing host–parasite cospeciation.

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References Cited

American Ornithologists' Union. 1983. Check-list of North American birds. 6th ed. American Ornithologists' Union, Washington, D.C.

Brooks, D. R. 1979. Testing the context and extent of host-parasite coevolution. Syst. Zool. 28: 299–307.

Burton, J. A. (ed.). 1973. Owls of the world. Eurobook Limited, Milan.

Carriker, M. A., Jr. 1935. Descriptions of new birds from Bolivia, with notes on other little known species. Proc. Acad. Nat. Sci. Philadelphia 87: 313–341.

1966. New species and records of Mallophaga (Insecta) from Neotropical owls (Strigiformes). Am. Midl. Nat. 76: 74–99.

Clark, R. J., D. G. Smith & L. H. Kelso. 1978. Working bibliography of owls of the world with summaries of current taxonomy and distributional status. Nat. Wild. Fed. Sci. Tech. Ser. No. 1: 1–319.

Clay, T. 1949. Some problems in the evolution of a group of ectoparasites. Evolution 3: 279–299.

1957. The Mallophaga of birds, pp. 120–155. *In* J. G. Baer [ed.], First symposium on host specificity among parasites of vertebrates. Institut de Zoologie, Université de Neuchâtel, Neuchâtel.

1964. Geographical distribution of the Mallophaga (Insecta). Bull. Br. Ornithol. Club 84: 14–16.

1966. A new species of *Strigiphilus* (Philopteridae: Mallophaga). Pac. Insects 8: 835–847.

Clayton, D. H. & R. D. Price. 1984. Taxonomy of the *Strigiphilus cursitans* group (Ischnocera: Philopteridae), parasites of owls (Strigiformes). Ann. Entomol. Soc. Am. 77: 340–363.

Eck, S. & H. Busse. 1973. Eulen, Die rezenten und fossilien Formen. Neue Brehm–Bucherei. 469: 1–196.

Elbel, R. E. & K. C. Emerson. 1959. The taxonomic position of an Asiatic species of *Otus* (Aves: Strigiformes) as indicated by the Mallophaga. Proc. Okla. Acad. Sci. 39: 76–78.

Emerson, K. C. 1981. Status of five species of Mallophaga described by M. A. Carriker, Jr. Proc. Entomol. Soc. Wash. 83: 137–139.

Eveleigh, E. S. & W. Threlfall. 1976. Population dynamics of lice (Mallophaga) on auks (Alcidae) from Newfoundland. Can. J. Zool. 54: 1694–1711.

Fitzpatrick, J. W. & J. P. O'Neill. 1986. *Otus petersoni*, a new screech-owl from the eastern Andes, with systematic notes on *O. colombianus* and *O. ingens*. Wilson Bull. 98: 1–14.

Goodman, S. M. & H. Sabry. 1984. A specimen record of Hume's Tawny Owl (*Strix butleri*) from Egypt. Bull. Br. Ornithol. Club 104: 79–84.

Hopkins, G. H. E. 1939. Straggling in the Mallophaga. Entomologist 62: 75–77.

Johnsgard, P. A. 1988. North American owls. Smithsonian Institution, Washington.

Keirans, J. E. 1975. A review of the phoretic relationship between Mallophaga (Phthiraptera: Insecta) and Hippoboscidae (Diptera: Insecta). J. Med. Entomol. 12: 71–76.

Larson, G. 1989. The prehistory of The Far Side. Andrews & McMeel, Kansas City, Mo.

Lincoln, R. J., G. A. Boxshall & P. F. Clark. 1982. A dictionary of ecology, evolution and systematics. Cambridge University Press, Cambridge, England.

Lyal, C. H. C. 1986. Coevolutionary relationships of lice and their hosts: a test of Fahrenholz's rule, pp. 77–91. *In* A. R. Stone & D. L. Hawksworth [eds.], Coevolution and systematics. Clarendon, Oxford, England.

Marshall, A. G. 1981. The ecology of ectoparasitic insects. Academic, London.

Meyer de Schauensee, R. 1970. A guide to the birds of South America. Academy of Natural Sciences, Philadelphia.

Morony, J. J., Jr., W. J. Bock & J. Farrand, Jr. 1975. Reference list of the birds of the world. American Museum of Natural History, New York.

Peters, J. L. 1940. Check-list of birds of the world, vol. 4. Harvard University Press, Cambridge, Mass.

Price, P. W. 1980. Evolutionary biology of parasites. Princeton University Press, Princeton.

Price, R. D. & D. H. Clayton. 1983. A review of the genus *Psittaconirmus* (Mallophaga: Philopteridae) from South Pacific parrots (Psittaciformes). Int. J. Entomol. 25: 56–70.

Timm, R. M. 1983. Fahrenholz's rule and resource tracking: a study of host–parasite coevolution, pp. 225–265. *In* M. H. Nitecki [ed.], Coevolution. University of Chicago Press, Chicago.