

Stick-tight fleas in the nostrils and below the tongue: evolution of an extraordinary infestation site in *Hectopsylla* (Siphonaptera: Pulicidae)

STEPHAN M. BLANK^{1*}, CHRISTIAN KUTZSCHER¹, JUAN F. MASELLO^{2,5}, ROBERT L. C. PILGRIM⁴ and PETRA QUILLFELDT^{3,5}

¹Deutsches Entomologisches Institut im ZALF, Eberswalder Strasse 84, 15374 Müncheberg, Germany

²University of Bristol, School of Biological Sciences, Ecology of Vision Group, Woodland Road, Bristol BS8 1UG, UK

³Cardiff University, School of Biosciences, Main Building, Museum Avenue, PO Box 915, Cardiff CF10 3TL, UK

⁴Department of Zoology, University of Canterbury, PB 4800, Christchurch, New Zealand

⁵Max Planck Institute for Ornithology, Vogelwarte Radolfzell, Schlossallee 2, 78315 Radolfzell, Germany

Received August 2005; accepted for publication January 2006

Association with terrestrial mammals as hosts and a sessile mode of life in females are ground plan traits of the stick-tight fleas associated with *Hectopsylla* + *Tunga*. *Hectopsylla* comprises the lineages *H. pulex* + [*H. psittaci*-group + *H. broscus*-group]. The stem species of the *H. psittaci*-group has switched to birds. ***Hectopsylla narium* sp. nov.** infests the nestlings of the burrowing parrot (*Cyanoliseus patagonus patagonus*; Psittacidae). The infestation sites inside the nasal cavity, and later during the breeding season also below the tongue, are unique among fleas. These sites provide a concealed habitat for the sessile, immobile females, where they are safe against cleaning activities of their host and the host's parents. The fleas are able to disperse actively within the bird colony. Their dispersal over long distances can only be assumed to happen accidentally, as fleas have never been found on adult parrots during field studies in Río Negro, Patagonia, Argentina. Data on the species bionomics, morphological descriptions and illustrations, and an identification key for *H. narium* and related taxa are presented. A lectotype is designated for *H. psittaci*. The family group name Tunginae is proposed as a new synonym of Hectopsyllinae. © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, 149, 117–137.

ADDITIONAL KEYWORDS: bionomics – host relationship – identification – morphology – new species – phylogeny – Psittaciformes – spatial dispersal – *Tunga penetrans*.

INTRODUCTION

The pulicid stick-tight fleas are commonly known from the sand flea *Tunga penetrans* (Linné, 1758), which causes a human disease called tungiasis. Females typically infest the feet, where they burrow into the skin and attach with their heavily denticulate maxillary laciniae (Heukelbach, 2004). The sessile mode of life is typical for females of *Tunga* and of its sister-group *Hectopsylla*, although *Tunga* exhibits an extreme

endoparasitic adaptation (Hopkins & Rothschild, 1953; Holland, 1964; Cheetham, 1988). The species of this clade have a Neotropical origin (including Mexico). *Tunga* Jarocki, 1838 comprises eight Neotropical and two Chinese species and *Hectopsylla* Frauenfeld, 1860 13 Neotropical species. *Tunga* and most *Hectopsylla* species appear to be restricted to terrestrial mammals as their primary hosts, but three *Hectopsylla* species are associated with birds and one with bats (Hopkins & Rothschild, 1953; Hastriter & Méndez, 2000; our present data).

In a project ongoing since 1998, extensive studies on the life history of the burrowing parrot *Cyanoliseus*

*Corresponding author. E-mail: blank@zalf.de

patagonus patagonus (Vieillot, 1818) have been conducted in Argentina (e.g. Masello & Quillfeldt, 2004a, b; Masello *et al.*, 2004). In a breeding colony near the village of El C ndor (province of R o Negro, Patagonia) nestlings in particular have been regularly examined for ectoparasites. Two chewing lice species (Phthiraptera; Mey, Masello & Quillfeldt, 2002) and a parasitic bug species (Heteroptera; J. Deckert, ZMHB, Berlin, Germany, personal communication) have been detected. During the investigation single fleas have accidentally been discovered fleeing from nostrils and bills of the nestlings. Closer scrutiny revealed that the fleas infest the nasal cavity and the area below the tongue, which is a unique phenomenon among fleas. The fleas collected from more than 200 parrot nestlings turned out to belong to a new *Hectopsylla* species, *H. narium* sp. nov.

We describe and illustrate this new species and provide a key to the *Hectopsylla* species occurring on birds and bats. The outline of the bionomics of *H. narium* is the most detailed existing for a *Hectopsylla* species. It includes data on the larva, which are the first reported for a species of *Hectopsylla*. A phylogenetic hypothesis for the evolution of the major lineages of *Hectopsylla* is presented, which provides a scenario for the switch of host associations within this taxon. New faunistic and bionomic data and taxonomic notes on selected *Hectopsylla* species are included.

MATERIAL AND METHODS

Adults and larvae of *Hectopsylla narium* were collected during field studies on the breeding biology of the Patagonian race of the burrowing parrot, *Cyanoliseus patagonus patagonus* (Psittacidae). The studies were carried out in the largest colony and most important breeding site of the parrot species from October 1998 to February 1999, November 1999 to January 2000 and November 2001 to January 2002. The studied colony covers 9 km of sandstone cliffs at the Atlantic coast near the village El C ndor, province of R o Negro, Patagonia (Masello & Quillfeldt, 2004a). The cliffs are characterized almost exclusively by grey or yellowish sandstone (Angulo & Casamiquela, 1982). The colony is the largest known colony for the entire Psittaciformes and contains about 35 000 active nests (Masello *et al.*, 2006). The parrots excavate their own nest burrows by tunnelling into faces of the cliff. The nests are 0.8–3.0-m-long, depressed cylinders in the sandstone's softest layers, terminating in the nest chamber (Leonardi & Oporto, 1983).

Continuous observations inside nest tunnels were carried out using a miniature security camera (Masello *et al.*, 2001). Samples of the sandy bottom of the nest chamber were taken using a spoon fixed to a

long stick. Adult fleas (140♂ and 830♀) were collected from nestlings of the parrot and from nest material. For light microscopic study some of the adults were mounted in Canada balsam on slides. Larvae (34) were collected from the sandy bottom of the nest chamber. The larvae were prepared and stained by using Pilgrim's (1992) method and mounted in Canada balsam. The drawings were produced using a camera lucida and digital photographs. For the SEM study of the male genitalia whole specimens were dehydrated stepwise with ethanol (70–98%) and acetone (100%), critical-point dried, mounted on minute pins with conductive glue or fixed on conductive pads, and sputtered with gold and palladium. Coating was repeated after the stepwise dissection of sclerites and control of the dissection result by SEM. Images were made on the SEM JSM-6060LV (JEOL) mostly at 8 kV acceleration voltage.

The following abbreviations are used in the figures (terminology mostly after Snodgrass, 1946; Cheetham, 1988): *bcl*, body of clasper; *cr*, crochet; *dls*, dorsal longitudinal strut; *fs*, Ford's sclerite; *l1*, *l2*, *l3*, distal arm of sternum 9, lobe 1, 2, 3; *lc*, lacinia (maxillary stylet); *man1*, *man2*, manubrium 1 and 2; *msh*, lateral process of mesosternum; *mtp*, metepimeron; *mts*, metepisternum; *mxl*, palpus-bearing lobe of maxilla; *mxx*, maxillary palpus; *p1*, *p2*, *p3*, process 1, 2, 3 of clasper; *pa9*, proximal arm of sternum 9; *pha*, phallosome (= aedeagus); *pmt*, process of metepimeron; *pop*, postoral process; *psp*, lateral process of prosternum; *rd*, rod of closing apparatus of spiracle; *sit*, sclerotized inner tube; *sen*, sensillum; *st*, sternum; *stf*, stalk of the fulcrum; *t1*, *t2* . . . , tergum 1, tergum 2 . . . ; *tra*, trachea; *utp*, unguitractor plate.

Counts of setae and pits refer to one body side unless expressly stated otherwise. Variable ranges are noted in the pattern '7–8 (6–10) setae', meaning that most specimens bear 7–8 setae but 6–10 setae may be observed on the whole sample.

The identification of *H. narium* required the study of some similar taxa. Collection material, which belongs to the following institutions, has been studied: BMNH, The Natural History Museum, London, UK (T. Howard); DEI, Deutsches Entomologisches Institut, M ncheberg, Germany; FMNH, Field Museum of Natural History, Chicago, USA (P. P. Parrillo); NHMW, Naturhistorisches Museum Wien, Vienna, Austria (U. Asp ock); RLCP, R.L.C. Pilgrim Collection, Department of Zoology, University of Canterbury, Christchurch, New Zealand; USNM, United States National Museum, Washington DC, USA (N. Adams); ZSM, Zoologische Staatssammlung, Munich, Germany (E.-G. Burmeister); ZMHB, Museum f ur Naturkunde der Humboldt Universit at, Institut f ur Systematische Zoologie, Berlin, Germany (H. Wendt); ZMUH, Zoologisches Institut und Museum der

Universität Hamburg, Germany (R. Abraham and H. Riefenstahl).

Tunga penetrans (Linné, 1758) and all known *Hectopsylla* species have been included in the phylogenetic analysis: *H. broscus* Jordan & Rothschild, 1906, *H. coniger* Jordan & Rothschild, 1906, *H. cypha* Jordan, 1942, *H. eskeyi* Jordan, 1933, *H. gemina* Jordan, 1939, *H. gracilis* Mahnert, 1982, *H. knighti* Traub & Gammons, 1950, *H. narium* Kutzscher sp. nov., *H. pascuali* Beaucournu & Alcover, 1990, *H. psittaci* Frauenfeld, 1860, *H. pulex* (Haller, 1880), *H. stomis* Jordan, 1925 and *H. suarezi* C. Fox, 1929. The following gaps have occurred when scoring character states for these species. The male of *H. cypha* was not available, but data have been taken from the literature as far as possible. The only known male specimen of *H. broscus* (BMNH) is poorly preserved. The male of *H. knighti* is unknown. Along with Cheetham's (1988) cladogram for the pulicoid genera, two outgroup taxa, *Pulex irritans* Linné, 1758 and *Echidnophaga gallinacea* (Westwood, 1875), have been chosen from the thermastromorph branch of Pulicidae, which also includes *Hectopsylla*. Their association with both terrestrial mammals and in the case of *E. gallinacea* also with birds may well provide the basis for a hypothesis as to how the host association within *Hectopsylla* has evolved. The cladistic analysis has been run in PAUP* 4.0 b10 for Windows (Swofford, 2001; heuristic search). The tree was rooted on *P. irritans*

and *E. gallinacea* as the outgroup as defined in Table 1. Unambiguous character changes (with reference to numbering of nodes, see Fig. 26) and consistency indices (CI) are presented for each character individually in the character descriptions. If a character referred to in the discussion is subject to subsequent change at a higher node, we have marked with a superscript, i.e. 'c' for subsequent changes within the clade other than reversals, 'p' for independent, parallel evolution in an other clade, and 'r' for reversal within the clade.

RESULTS

BIONOMICS OF *HECTOPSYLLA NARIUM*

The fleas have been found on 204 of 380 studied nestlings of the burrowing parrot. An additional 100 adult parrots checked were completely free from fleas. Various larval stages and several teneral moult adults of both sexes have been collected from the sandy bottom of nine nest chambers. Within the studied colony flea larvae have also been found in tunnels of the parrot occupied by a barn owl [*Tyto alba tuidara* (J.E. Gray, 1829), Tytonidae; one nest with five larvae studied] and southern martins [*Progne elegans* (Baird, 1865), Hirundinidae; two nests studied, one with one larva]. Nestlings of the latter two species remained free from adult fleas.

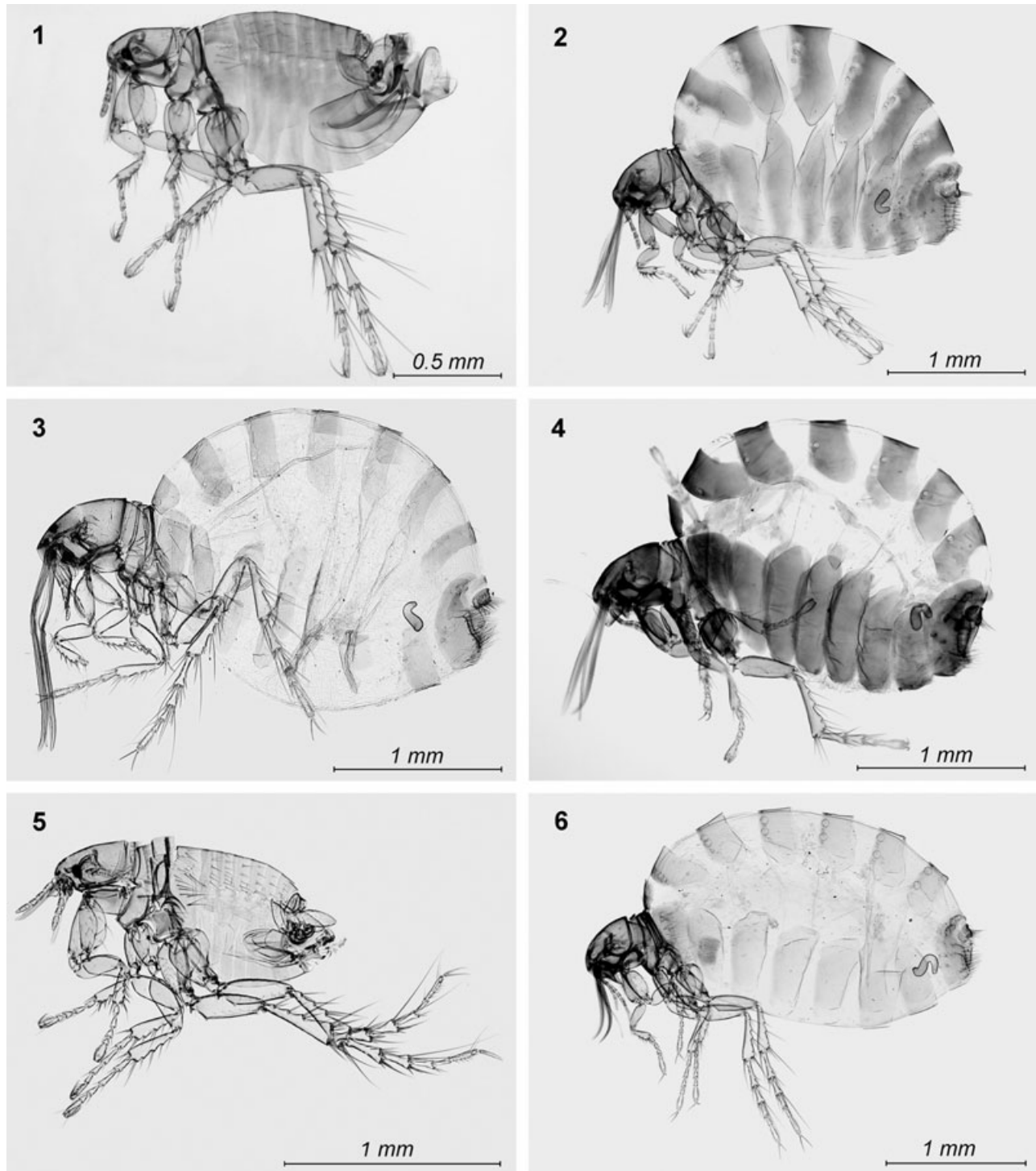
Table 1. Distribution of character states for the phylogenetic analysis of *Hectopsylla*

	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4
1. <i>Pulex irritans</i>	0	0	0	0	0	0	1	0	0	0	0	0	x	0	0	0	0	0	x	0	0	0	0	0
2. <i>Echidnophaga gallinacea</i>	0	0	0	0	0	0	0	?	0	0	0	0	x	0	0	0	0	0	x	0	0	0	0	q
3. <i>Tunga penetrans</i>	1	0	0	0	0	0	0	3	1	0	1	0	x	0	0	0	1	0	x	0	0	0	1	0
4. <i>Hectopsylla pulex</i>	1	0	0	0	0	1	0	1	2	0	2	1	0	1	1	1	1	0	x	0	0	1	1	1
5. <i>Hectopsylla knighti</i>	1	0	?	1	0	1	1	?	2	0	2	?	?	?	?	?	?	?	?	?	?	?	?	2
6. <i>Hectopsylla narium</i>	1	0	0	0	0	1	1	1	2	1	2	1	0	1	1	1	1	1	1	0	0	1	1	2
7. <i>Hectopsylla psittaci</i>	1	0	0	0	0	1	1	1	2	1	2	1	0	1	1	1	1	1	1	0	0	1	1	2
8. <i>Hectopsylla broscus</i>	1	1	0	0	1	1	0	3	2	1	2	1	0	1	1	1	1	1	0	2	0	0	1	0
9. <i>Hectopsylla gracilis</i>	1	0	1	1	1	1	0	2	2	1	2	1	1	1	1	1	1	1	0	2	1	0	1	0
10. <i>Hectopsylla pascuali</i>	1	0	1	1	1	1	0	2	2	1	2	1	1	1	1	1	1	1	0	2	1	0	1	0
11. <i>Hectopsylla stomis</i>	1	0	0	0	1	1	0	2	2	0	2	1	0	1	1	1	1	0	2	0	1	1	0	
12. <i>Hectopsylla cypha</i>	1	0	0	0	1	1	0	1	2	0	2	1	0	1	1	1	1	1	0	2	0	1	1	0
13. <i>Hectopsylla gemina</i>	1	0	0	1	1	1	0	1	2	0	2	1	0	1	1	1	1	1	0	1	0	1	1	0
14. <i>Hectopsylla coniger</i>	1	1	0	0	1	1	0	3	2	0	2	1	0	1	1	1	1	1	0	0	?	?	0	
15. <i>Hectopsylla eskeyi</i>	1	1	0	0	1	1	0	1	2	0	2	1	0	1	1	1	1	1	0	0	1	1	0	
16. <i>Hectopsylla suarezi</i>	1	0	0	0	1	1	0	1	2	1	2	1	0	1	1	1	1	1	0	0	1	1	0	
17. <i>Hectopsylla broscus-group</i>	1	p	p	p	1	1	0	r	2	p	2	1	p	1	1	1	1	1	p	s	p	p	1	0

Legend: 0, 1, 2 – character states; p – 0/1 polymorphism; q – 0/2 polymorphism; r – 1/2/3 polymorphism; s – 0/1/2 polymorphism; x – state not scored; ? – state unknown or uncertain. See text for definitions of character states. In row 17 the character states for the *H. broscus*-group (rows 8–16) are summarized using polymorphic character states where necessary.

Freshly emerged adults of both sexes vivaciously crawl and can jump up to 25 cm in horizontal distance. Females become sessile by anchoring with their heavily denticulate lacinia in the host skin, remaining

fully exposed. The uptake of blood distends their abdomen strongly by stretching the intersegmental membrane between the sclerotized terga and sterna (Fig. 2).



Figures 1–6. *Hectopsylla* species. Fig. 1. *H. narium* sp. nov. (♂, holotype). Fig. 2. *H. narium* sp. nov. (♀, paratype). Fig. 3. *H. knighti* (♀, holotype). Fig. 4. *H. psittaci* (♀). Fig. 5. *H. pulex* (♂). Fig. 6. *H. pulex* (♀).

The female/male sex ratio for the total number of specimens was 5.9 : 1. Females ranged from four to 13 times as abundant as males on individual nestlings. Males were observed mating with females inside the nasal cavities, but they were never found feeding on the nestlings.

Feeding females have usually been found in the nasal cavity (Fig. 27) and on the comparatively dry area under the tongue. Up to 11 live fleas or up to ten live and seven dead fleas were collected from the nostrils of individual nestlings (16 December 1999 to 3 January 2000). The respiration of such heavily infested nestlings was clearly impeded. An infestation under the tongue seems to occur mainly towards the end of the breeding season, when the nostrils are already largely occupied. On 26 December 2004 we found a nestling with 42 live fleas, 32 females and two males below the tongue and seven females and one male in the nostrils. We also found three nestlings with an infestation of the foot with one, one, 18 fleas, respectively. In the third case the fleas formed a crowded assemblage at the base of two toes.

Nestlings become infested at 7–14 days, when the diameter of the nostrils is large enough for fleas to pass (Fig. 27). Females remain on the nestlings until they die *in situ*. Dead fleas are discernible by their darker colour and shrivelled body.

Continuous observations using a miniature security camera inside nest tunnels revealed that adult parrots groom their nestlings approximately every 4 h but not the nestlings' nostrils or oral cavities. Adult parrots have been observed to groom their own nostrils with their claws.

PHYLOGENETIC ANALYSIS

CHARACTER DESCRIPTIONS

1. Club of antenna latero-medially: 0 – with 3 (3–5) setiform sensilla; 1 – with 3 punctiform sensilla. Unambiguous change: 28: 0–1. CI: 1.000.

Pulex irritans with a pair of setae on flagellomeres 4–6 arranged in two rows on inner and outer side of club. Male *P. irritans* with basal and medial flagellomeres separate. Female and other studied species with completely fused flagellomeres. *E. gallinacea* with row of 3 setae in medial position on outer side of club. Setae on inner side absent, 1–2 setae may be present close to setae on outer side or close to ventral edge of club. *Hectopsylla* and *Tunga* with a row of 3 punctiform structures on middle of outer side, but these often hard to recognize. Owing to their position we assume the punctiform structures in *Hectopsylla* and *Tunga* as homologous with the setae found in *P. irritans*.

2. Wedge-shaped occipital lobe in female: 0 – absent; 1 – present (Hastriter & Méndez, 2000: fig. 1). Unambiguous changes: 8: 0–1, 24: 0–1. CI: 0.500.

The lobe becomes evenly wider from top of the head along the occipital margin in ventral direction. It ends between the middle and the lower third of the occiput. In *Hectopsylla broscus* and *H. coniger* it ends in a hook (Hastriter & Méndez, 2000: fig. 1), which is about as wide as the smaller diameter of the antennal torulus. In *H. eskeyi* the lobe is only half as wide and shallowly curved on its ventral side (Hopkins & Rothschild, 1953: fig. 63). Contrary to the statement of Hopkins & Rothschild (1953: 56) an occipital process is also present in *H. stomis*, but it ends close to the ventral end of the occiput. The lobe of *E. gallinacea* is placed on the middle of the occipital margin, and it is not wedge-shaped in its dorsal section. Owing to their position and shape we score the lobes of the latter two species as different structures.

3. Membranous blotch between antennal bases, male: 0 – absent; 1 – present. Unambiguous change: 19: 0–1. CI: 1.000.

The wall of the head usually is evenly thick or widened to a ridge (falx) and evenly sclerotized in *Hectopsylla* species. In *H. gracilis*, *H. pascuali*, *H. gemina* (only in female) and *H. knighti* (male unknown) the wall is thin and pale. The wall seems to be thin also in the male of *H. broscus* but this cannot be determined on the poorly preserved specimen (scored as uncertain). Obviously the blotch is more soft than its surrounding, because in mounted specimens the integument is often wrinkled at this place. Owing to sexual dimorphism observed in *H. gemina*, we have scored the states separately for each sex.

4. Membranous blotch between antennal bases, female: 0 – absent; 1 – present. Unambiguous changes: 5: 0–1, 13: 0–1, 19: 0–1. CI: 0.333.

5. Process on dorso-posterior edge of metepimeron of female: 0 – absent (Fig. 8); 1 – present (Fig. 14). Unambiguous change: 25: 0–1. CI: 1.000.

6. Large basal tooth of hind femur: 0 – absent; 1 – present (Hopkins & Rothschild, 1953: pl. 8C). Unambiguous change: 27: 0–1. CI: 1.000.

7. Insertion of distal plantar seta on article 5 of metatarsus relative to level of proximal edge of unguitactor plate in female: 0 – inserting (short) before proximal edge of inner apodeme of tarsomere (Snodgrass, 1946: pl. 10H); 1 – inserting at or beyond proximal edge of inner apodeme of tarsomere (see Fig. 15: *utp* for male). Unambiguous changes: 1: 0–1, 18: 0–1. CI: 0.500.

In *H. narium* the distal seta may exceptionally be in proximal position if only 3 instead of 4 plantar setae are present on one side of the tarsomere.

8. Number of setae on tergum 5–6, male: 0 – more than 3 setae; 1 – 3 setae; 2 – 2 setae; 3 – 1 seta close to spiracle; 4 – 1 seta in dorso-lateral position. Character states ordered. Unambiguous changes: 3: 1–3, 8: 2–3, 14: 1–3, 21: 1–2. CI: 0.429.

The males of most *Hectopsylla* species have rows of 3 setae on the terga 5–6 (state 1). *Hectopsylla gracilis*, *H. pascuali* and *H. stomis* have 2 setae (state 2). It is evident from the rows of 3 setae on the preceding terga 2–3 that the medial seta is absent. In *H. broscus* a single seta is present close to each spiracle of terga 5–6 (state 3). As we observed a seta and basal ring of a seta on the two preceding terga in a very dorsal position, we conclude that the medial setae are absent in this species and the dorsal seta is absent on terga 5–6. We deduce from the description (Hopkins & Rothschild, 1953: 61) for *H. coniger* ‘abdominal t[erga] II–VII with 1 or 2 bristles each side’ that the pattern is similar in this species. The single seta present in *Tunga penetrans* might be homologous with that in *H. broscus* because it inserts close to the spiracle. *Echidnophaga gallinacea* has a single seta in dorsal position. It is not evident whether the single seta is homologous with that in *H. broscus* but changed in position or whether it represents a character state of its own. *Pulex irritans* usually has more than 3 setae on terga 5–6 (state 0). In the case of variable numbers the character state was scored for the most frequent count. Owing to striking sexual dimorphism the setae counts have been scored separately for the sexes.

9. Number of setae on tergum 5–6, female: 0 – with at least 1 seta in dorsal position; 1 – 1 seta close to spiracle; 2 – setae absent. Character states ordered. Unambiguous change: 27: 1–2, 28: 0–1. CI: 1.000.

Owing to their different position we regard the single seta each of terga 5–6 as not homologous in *Echidnophaga gallinacea* (state 0) and *Tunga penetrans* (state 1). Setae are completely absent in the other species (state 2).

10. Shape of lower quarter of distal (vertical) edge of tergum 8 in female: 0 – straight or slightly convex (Fig. 23), 1 – concave (Figs 22, 24, 25). Unambiguous change: 16: 0–1, 17: 0–1, 20: 0–1. CI: 0.333.

Owing to the presence of a concave section in the lower quarter (state 1), the posterior edge of tergum 8 is trilobate below the stigma in *H. psittaci* and *H. narium*. It is bilobate in *T. penetrans*, *H. knighti* and *H. pulex*. In the *H. broscus*-group both character states occur.

11. Sensillum: 0 – with more than 8 sensory pits, left and right sensillum abut along medial line (Hopkins & Rothschild, 1953: pl. 4 fig. A); 1 – with 8 sensory pits arranged in two lines of each 4 sensory pits, left and right sensillum separated medially (Cheetham, 1988:

fig. 244), 2 – with 8 sensory pits arranged in an anterior line of 5 pits and a posterior line of 3 pits (Figs 22–24), left and right sensillum separated medially (Fig. 20). Character states ordered. Unambiguous changes: 27: 1–2, 28: 0–1. CI: 1.000.

12. Clasper: 0 – with single manubrium; 1 – with dorsal and ventral manubria (Figs 17–19). Unambiguous change: 27: 0–1. CI: 1.000.

The terminology of the manubria is discussed below.

13. Shape of dorsal manubrium: 0 – elongated; 1 – rounded. Unambiguous change: 19: 0–1. CI: 1.000.

Character scored only for species with two manubria (character state 12: 1).

14. Position of base of distal arm of sternum 9 in male: 0 – distal edge of sternum 8 far beyond base of distal arm, not articulating (Hopkins & Rothschild, 1953: fig. 6; Johnson, 1957: pl. 111.1); 1 – at about same level as distal edge of sternum 8, articulating (Figs 17–21). Unambiguous change: 27: 0–1. CI: 1.000.

Tunga and *Hectopsylla* species bear 1–3 prominent lobes on the distal arm of sternum 9. Contrary to the condition in other taxa the lobes are strongly protruding. Only *Tunga* has the basal half of the lobe hidden below sternum 8 (Cheetham, 1988: fig. 244).

15. Width of lateral distal lobe of sternum 9 (*l1*) in male: 0 – narrower than half width of apex of hind tibia; 1 – about as wide as apex of hind tibia (Figs 17–19). Unambiguous change: 27: 0–1. CI: 1.000.

16. Setation on lateral distal lobe of sternum 9 (*l1*) in male: 0 – only with short setae; 1 – with short setae and at least with one stout seta close to base of lobe (Figs 17–19). Unambiguous change: 27: 0–1. CI: 1.000.

The seta is lacking in figure 48 of Hopkins & Rothschild (1953) for *H. stomis*, but we observed it as hardly perceptible but present in several specimens.

17. Proximal arm of sternum 9: 0 – narrowly elongate (Johnson, 1957: pl. 107.2, 109.1); 1 – lobiform (Figs 17, 20: *pa9*; Johnson, 1957: pl. 114.1–2). Unambiguous change: 28: 0–1. CI: 1.000.

18. Distal arm of sternum 9 in male: 0 – with 1 usually setous lobe (Fig. 18), 1 – with lateral setous lobe (*l1*) and mesal glabrous lobe (*l3*; Figs 17, 19; Hopkins & Rothschild, 1953: fig. 52; Cheetham, 1988: figs 227, 232). Unambiguous change: 26: 0–1. CI: 1.000.

In *H. stomis* the lateral lobe *l1* itself is bilobated additionally (Hopkins & Rothschild, 1953: fig. 48). But this particular mesal lobe is homologous neither with *l2* (see character 19) nor with *l3*, which is present additionally in this species. Hopkins & Rothschild (1953) applied their terminology for the lobes of sternum 9 inconsistently, because sometimes the proximal lobe (see character 10) is named lobe 1.

19. Intermediate lobe (*l2*): 0 – absent or very indistinct and membranous; 1 – present, consisting of a fold between lateral and mesal lobes, postero-ventral edge more or less sclerotized (Figs 17, 19, 20, 21; Cheetham, 1988: figs 227, 232). Unambiguous change: 23: 1–0. CI: 1.000.

Character only scored for species with *l1* and *l3* present (character state 18: 1–2).

20. Setation of mesal wall of *l1* close to posterior edge: 0 – glabrous or with few small setae smaller than largest medial setae on lateral wall of *l1*; 1 – with 2 stout setae larger than medial setae on lateral wall of *l1*; 2 – with 1 stout seta. Character states ordered. Unambiguous changes: 22: 1–2, 23: 0–1. CI: 1.000.

21. Tongue-like, glabrous postero-ventral protrusion of *l1*: 0 – absent; 1 – present, protruding beyond postero-ventral edge of *l3* (Mahnert, 1982: fig. 5; Beaucournu & Alcover, 1990: fig. 4). Unambiguous change: 19: 0–1. CI: 1.000.

22. Dorsal longitudinal strut: 0 – absent or very small and indistinct; 1 – present (Fig. 17, *dls*). Unambiguous changes: 20: 1–0, 27: 0–1. CI: 0.500.

The ‘dorsal longitudinal strut’ of Cheetham (1988) corresponds with the ‘dorsal armature’ of Hastriter & Méndez (2000). The character state is not apparent from the only known but poorly preserved *H. broscus* male.

23. Lateral lamina of aedeagal apodeme: 0 – weakly sclerotized, hardly perceptible (Cheetham, 1988: figs 195, 196, 219), 1 – properly sclerotized, outline clearly defined (Fig. 17, *pha*; Cheetham, 1988: figs 229, 249). Unambiguous change: 28: 0–1. CI: 1.000.

24. Host: 0 – terrestrial mammals; 1 – bats; 2 – birds. Unambiguous changes: 4: 0–1, 18: 0–2. CI: 1.000.

The host associations are scored following Hopkins & Rothschild (1953), Galloway, Andruschak & Underwood (2000), Hastriter & Méndez (2000) and our own data. Obviously accidental records like that of *Pulex irritans* on birds (Hopkins & Rothschild, 1953) were excluded. See also discussion.

DATA ANALYSIS

The analysis of 24 unordered characters (Table 1, rows 1–16) by PAUP* produced two trees of 39 steps length (CI: 0.769, RI: 0.848). The topology of the first tree is depicted in Figure 26. The second had *H. gemina* and *H. cypha* arranged in a polytomy with the clade formed by *H. stomis* + (*H. broscus* + (*H. gracilis* + *H. pascuali*)). The first topology was obtained again after ordering characters 8, 9, 11 and 20 (tree length 41 steps, CI: 0.732, RI: 0.845). The unambiguous character changes are mapped on the cladogram (Fig. 26)

as they have resulted from the second analysis. This tree has also been chosen for the computation of the character CI values given in the character analysis section above.

Subsequently, we analysed the unordered data for *Tunga penetrans*, *Hectopsylla pulex*, the *H. psittaci*-group (Table 1, rows 1–7) and a single artificial dataset for the *H. broscus*-group using polymorphic character states for the *H. broscus*-group where necessary (Table 1, row 17). This resulted in a single tree with congruent topology except for the *H. broscus*-group terminating in a single leaf (tree length 23 steps, CI excluding uninformative characters: 0.947, RI: 0.960).

In an additional run for all species character 24 (host associations) has been excluded to avoid possible circular conclusions when discussing the evolution of host changes in *Hectopsylla*. The analysis of the dataset with ordered character states resulted in one tree of 39 steps length (CI: 0.717, RI: 0.841) corresponding to the tree obtained from the analysis of ordered characters above (see Fig. 26).

DESCRIPTION OF *HECTOPSYLLA NARIUM* SP. NOV. AND NOTES ON SELECTED *HECTOPSYLLA* SPECIES

Genus diagnosis: Hind femur with large basal tooth (Hopkins & Rothschild, 1953: fig. 8C; absent in *Tunga*). Base of distal arm of sternum 9 in male at almost same level as distal edge of sternum 8 (distal edge of sternum 8 far beyond base of distal arm in other Pulicidae), lateral distal lobe of sternum 9 about as wide as apex of hind tibia (clearly narrower in other Pulicidae), with short setae and at least one stout seta close to base of lobe (stout setae absent in other Pulicidae; Figs 17–19). Male genitalia with unique clasper type with two manubria (only one present in other flea taxa; Figs 17–19).

HECTOPSYLLA NARIUM KUTZSCHER, SP. NOV.

(FIGS 1, 2, 7, 8, 12, 15, 17, 20–22, 27)

Type locality: Argentina, Patagonia, Río Negro province, El Cóndor near Viedma.

Diagnosis: Distinguished from all *Hectopsylla* species by the absence of a distinct postoral process. Among those lacking a postero-caudal process on the metepimeron, *H. narium* may be further separated by the presence of four lateral plantar setae on the distal tarsomeres (except for *H. pulex* with exceptionally four setae). Females are characterized by the large and strongly sculptured spiracle 8 (Fig. 22). Males have species-specific shapes of clasper and distal arm of sternum 9 (Fig. 17).

Description

Male: HEAD (Fig. 7). Dorsal margin anteriorly slightly rounded, posteriorly straight, slightly concave close to internal incision of frons, dorso-anterior margin widely rounded, ventral margin without definite post-toral process. Preantennal region with several minute setae, 2 large preantennal setae, longer seta in front of eye, shorter seta close to base of maxilla. Postantennal region with 11–20 stout and minute setae. Palpus-bearing lobe of maxilla distally blunt, length *c.* 2.3 width, distally slightly widened (Fig. 7: *mxl*). Apex of maxillary palpus reaching trochanter of fore leg (Figs 1, 7: *mxp*). Lacinia well developed, length *c.* 1.2–1.4 length of fore coxa (Fig. 1). Eye well developed, ventral sinus present. THORAX (Fig. 7). Pronotum with 1 row, 5–9 setae. Mesonotum with 1 row, 4–7 setae. Metanotum narrow, with 1 subdorsal row, 3–5 setae, postero-ventrally with lobe, lobe sometimes with 1 seta. Prosternum with strongly sclerotized, obtusely angled process (*psp*). Mesosternum not divided into

mesepisternum and mesepimeron, caudal process (*mcp*) present below thoracic spiracle 1, antero-dorsally 2–3 minute setae, median subdorsally sometimes 1 stout seta. Metepisternum (*mts*) with long subdorsal seta. Metepimeron (*mtp*) well developed, about as large as head, dorsal margin widely rounded, 3–6 setae below spiracle. LEGS. Fore coxa with 14–16 (12–16) scattered strong lateral setae. Mesocoxa with 3–6 subanterior setae, preapically 1 medial seta and 3–4 (2–4) apical setae immediately in front of ventro-lateral process. Lateral surface of metacoxa with 5–8 scattered proximal and subventral setae, 4–5 distal setae immediately in front of ventro-lateral process, mesal surface with 12–17 (10–17) smaller setae sub-anteriorly. Femora with 1 (2) subapical anterior-marginal seta, metafemur additionally with row of 6–8 (5–9) mesal setae. Dorso-lateral setae on fore tibia and mesotibia stronger than on metatibia. Distal tarsomeres with 4 (3–5) pairs of lateral plantar setae, tarsal claws with slight basal swelling (Fig. 15).

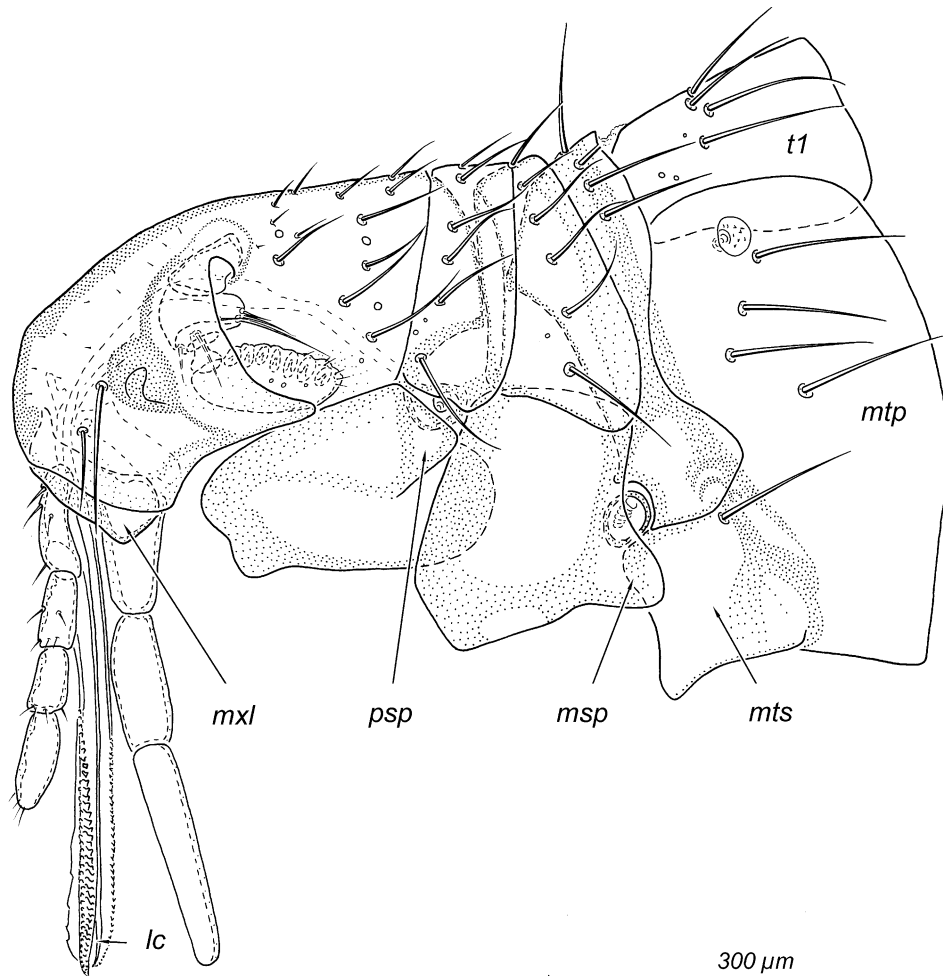


Figure 7. *Hectopsylla narium* sp. nov. (holotype, ♂), head and thorax.

UNMODIFIED ABDOMINAL SEGMENTS (Figs 7, 17). Tergum 1 with 4 setae, terga 2–7 each with 3–4 setae. Abdominal spiracles 1–7 about half width of eye. MODIFIED ABDOMINAL SEGMENTS (Fig. 17). *Tergum 8*: spiracle 8 distinctly elongated, about half length of distal margin. Distal portion of process 1 more or less smoothly convex, without dorsal angle, ventral margin slightly concave, distal portion with *c.* 5 lateral and *c.* 30 marginal setae, inner surface with numerous setae (Fig. 17: *p1*). Processes 2 and 3 short, with a comparatively wide, round tip (Fig. 17: *p2*, *p3*). Process 3 (Fig. 17: *p3*) 1.5 times as long as wide, shallowly curved. *Sternum 8*: subventrally few scattered, very short setae, sometimes 1 long preapical seta. *Sternum 9*: distally with 3 lobes (Figs 17, 20, 21: *l1*, *l2*, *l3*), lobe 1 distally round and bearing numerous setae on lateral surface and with 2–3 long setae near base on medial side, lobe 2 with 1–2 (0–2) setae medially close to antero-dorsal edge. Sclerotized inner tube of phallosome (Fig. 17: *sit*) with small dorsal and larger ventral process, dorsal longitudinal struts (*dls*) strongly sclerotized, distinctly curved in proximal portion, dis-

tally *c.* 2 times as wide as base of stalk of fulcrum (*stf*). Ford's sclerites bilobed, medial lobe longer and wider than lateral lobe (Figs 17, 20: *fs*). Crochet present, dorsal protuberance 4 times longer than wide, with caudally directed lobe (Figs 17, 20: *cr*).

Female (only differences from male described): HEAD (Fig. 8). Dorsal margin slightly and evenly rounded, slightly concave close to internal incursion of frons. Preantennal region with 2, occasionally with 3 large preantennal setae. Palpus-bearing lobe of maxilla distally not significantly widened, length *c.* 2.7 width (Fig. 8: *mxl*). Lacinia 2.5–3.0 width of fore coxa (Figs 2, 8). THORAX (Fig. 8). Pronotum with one row, 7–10 setae. Mesonotum with 1–2 subventral setae. Metanotum with 2 subdorsal setae. Mesosternum with 1 stout, median subdorsal seta. Metepimeron (*mtp*) with 4–6 (3–8) scattered setae below spiracle. LEGS. Fore coxa with 11–16 scattered strong lateral setae. Mesocoxa with 3 (2–4) subanterior setae, 1 medial seta and 2–3 (1–4) apical setae immediately in front of ventro-lateral process. Metacoxa on lateral

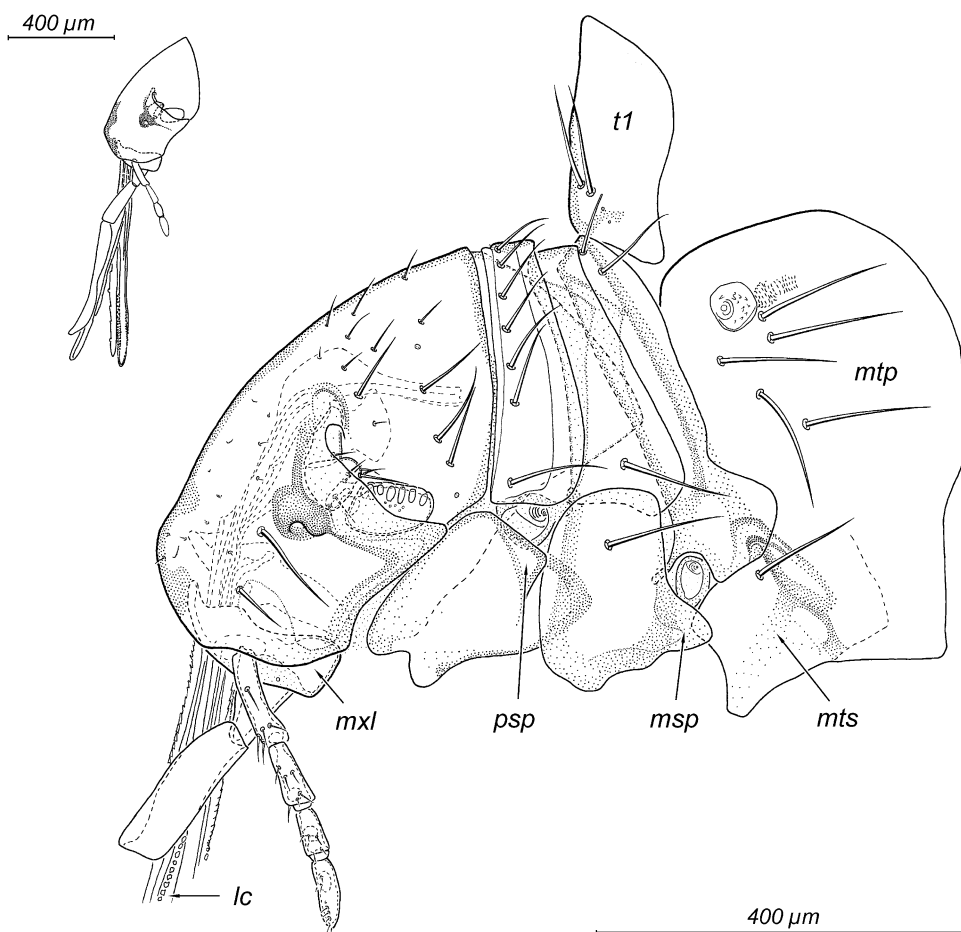


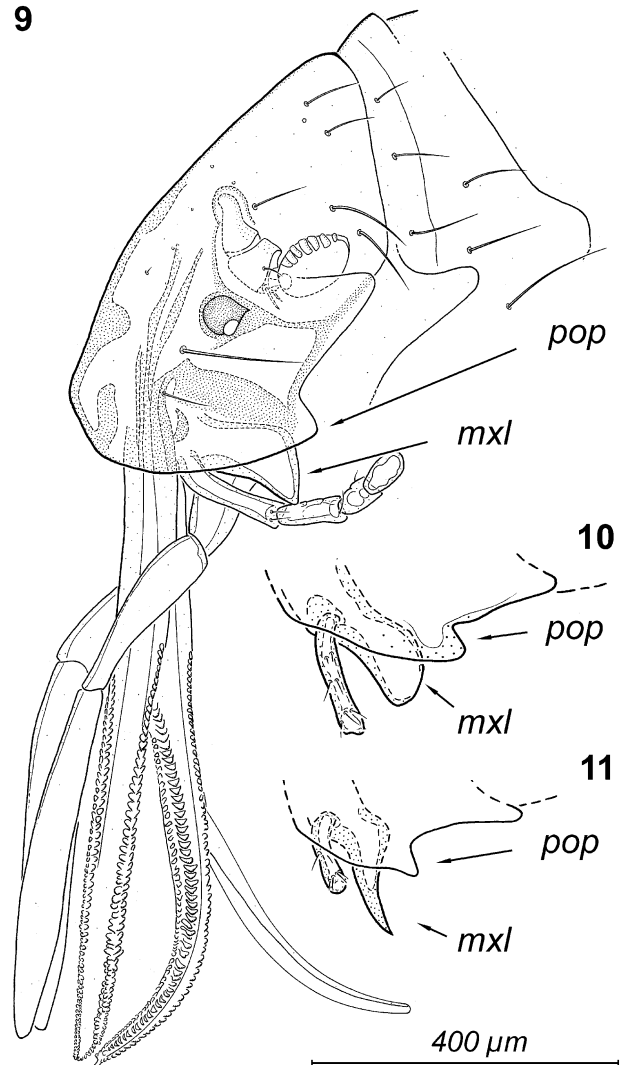
Figure 8. *Hectopsylla narium* sp. nov. (paratype, ♀), head and thorax.

surface 4–6 (4–8) scattered proximal and subventral setae and with 4 distal setae immediately in front of ventro-lateral process, mesal surface subanteriorly with 11–16 smaller setae. Metafemur with row of 5–7 mesal setae. UNMODIFIED ABDOMINAL SEGMENTS (Figs 2, 8). Terga and sterna 2–7 dorso-ventrally comparatively wide, lateral ends touching each other (even in females with distended abdomen). Lateral ends of sterna 3–6 acutely pointed. Terga 2–7 pale surrounding spiracles, posterior margins more sclerotized than anterior. Spiracles larger than eye, trachea widened proximad and distad to rod of closing apparatus (Fig. 22: *tra*). Tergum 1 with 2–3 setae (Fig. 8: *t1*), tergum 2 with 1–2 setae, tergum 3 occasionally with 1 seta. MODIFIED ABDOMINAL SEGMENTS. Tergum 8 (Fig. 22): spiracle strongly sculptured, below spiracle broad and deep sinus, three distinct caudal lobes on medial to ventral edge. Lobes on outer surface with row of *c.* 14 setae, mesal surface along weakly sclerotized line with anterior row of *c.* 11 short stout setae, posterior row with *c.* 8 long setae; longest setae barely longer than length of sensillum. *Sensillum* (Fig. 22: *sen*): with 8 pits, width *c.* 3 times length, caudad *c.* 11 long, 6 small setae. *Spermatheca* (Fig. 12): as in other *Hectopsylla* species except for *H. pulex* (Fig. 13).

Host: *Cyanoliseus patagonus patagonus* (Psittacidae).

Type material. Holotype ♂: 'Argentina, Patagonia, Río Negro province, El Condor near Viedma, 41°03'23"S, 62°48'10"W, 28.xi.1999–5.i.2000, on chicks (in nostrils) of *Cyanoliseus p. patagonus*, leg. J.F. Masello & P. Quillfeldt, 00/36/1'; 'Holotypus ♂ *Hectopsylla narium* nov. spec. det. C. Kutzscher 2001'. Holotype mounted on a slide, DEI. Paratypes (all from the same collecting site): 4♂ 10♀, on *Cyanoliseus p. patagonus* nestlings, xii.1998, leg. J.F. Masello; *c.* 100♂ 400♀, in nostrils of *Cyanoliseus p. patagonus* nestlings, three larvae from a nest of *Cyanoliseus p. patagonus*, 28.xi.1999–5.i.2000, leg. J.F. Masello & P. Quillfeldt; 5♂ 3♀ and 31 larvae from sand in nest of *Cyanoliseus p. patagonus* and 1♀ from leg of *Cyanoliseus p. patagonus* nestling, 3–23.xii.2001, leg. C. Kutzscher & J.F. Masello; 5 larvae from nest of *Tyto alba tuidara* and 1 larva from nest of *Progne elegans*, 3–23.xii.2001, leg. C. Kutzscher & J.F. Masello; *c.* 35♂ 425♀, in nostrils and under tongue of *Cyanoliseus p. patagonus* nestlings, xii.2001–i.2002, leg. J.F. Masello & P. Quillfeldt. Paratypes partly mounted on slides and partly kept in alcohol. Paratype adults deposited among others in BMNH, DEI, FMNH, NHMW, RLCP, ZMHB and ZSM, larvae in DEI and RLCP.

Etymology: The name *narium*, a noun in genitive plural (ICZN, 1999: Art. 11.9.1.3), has been chosen in accordance with a typical niche of the species: *naris* is the Latin name for nostril.



Figures 9–11. Head morphology in *Hectopsylla* species (only postoral process, first article of maxillary palpus and maxilla illustrated in Figs 10, 11). Fig. 9. *H. psittaci* (lectotype, ♀), head. Fig. 10. *H. knighti* (holotype, ♀). Fig. 11. *H. pulex* (♀).

HECTOPSYLLA KNIGHTI TRAUB & GAMMONS, 1950
(FIGS 3, 10, 23)

Hectopsylla knighti Traub & Gammons, 1950: 270–271, ♀, type locality: Mexico, Municipality of Tancitaro, Michoacán.

Material examined: MEXICO: Michoacán, Municipality of Tancitaro, 6000 ft., v.1940 [erroneously reported as 'July 1940' by Traub & Gammons (1950), ex 'head of a swift' [Hirundinidae], 3rd Hoogstraal Mexican Expedition, 1♀ (holotype, FMNH).

Remarks: The male remains unknown. The female is clearly distinguished by the round apex of the palpus-

bearing lobe of the maxilla (Fig. 10: *mxl*). Terga and sterna 2–7 short and very slender, their lateral ends, proximal and distal margins do not touch each other in females with distended abdomen (Fig. 3). The lacinia is extremely long, *c.* 4 times as long as fore coxa (Fig. 3). The distal tarsomeres bear 5–6 pairs of lateral plantar setae.

HECTOPSYLLA PSITTACI FRAUENFELD, 1860
(FIGS 4, 9, 16, 19, 24, 25, 28)

Hectopsylla psittacii Frauenfeld, 1860: 462–465, ♀, type locality: Chile, Santiago de Chile; incorrect original spelling.

Pulex (Hectopsylla?) testudo Weyenbergh, 1881: 267–271, ♂♀, type locality: Argentina; synonymy by Jordan & Rothschild (1906).

Lectotype ♀ (here designated): [the following four labels in the jar containing the tubes of the lectotype and the paralectotypes:] ‘*Hectopsylla psittacii* Frfld. Wien Acad. 1860, XL, pg. 464. Type, Novara Reise. 657, Chile, am Tschoroi’; ‘N.C. Rothschild determinavit *Hectopsylla psittacii* 45’; ‘*Hectopsylla psittacii* Frfld. Tp. det. Rotsch.’; ‘auf *Psittacus*, Chile’; [backside of the label:] ‘*Henicognathus leptorrhynchus* Kunz.’; [label immediately in the tube containing the lectotype:] ‘Lectotypus ♀ *Hectopsylla psittacii* Frauenfeld, 1860, des. C. Kutzscher 2001’. Specimen in alcohol, see below, NHMW. Paralectotypes: 1♀ with damaged head and fragments of 2♀ segregated from lectotype in a separate tube, NHMW; 2♀ each mounted on a slide and labelled ‘*psittacii* ♀ vs. Fr., 1860, St. Jago (Santiago de Chile), Chile’; [red edged:] ‘syntype’; ‘Tschoroi (*Cyanoliseus patagonus* or *Enicognathus leptorrhynchus*) G. von Frauenfeld don. Vienna Mus., C. Rothschild Coll. Brit. Mus. 1923–615’, BMNH.

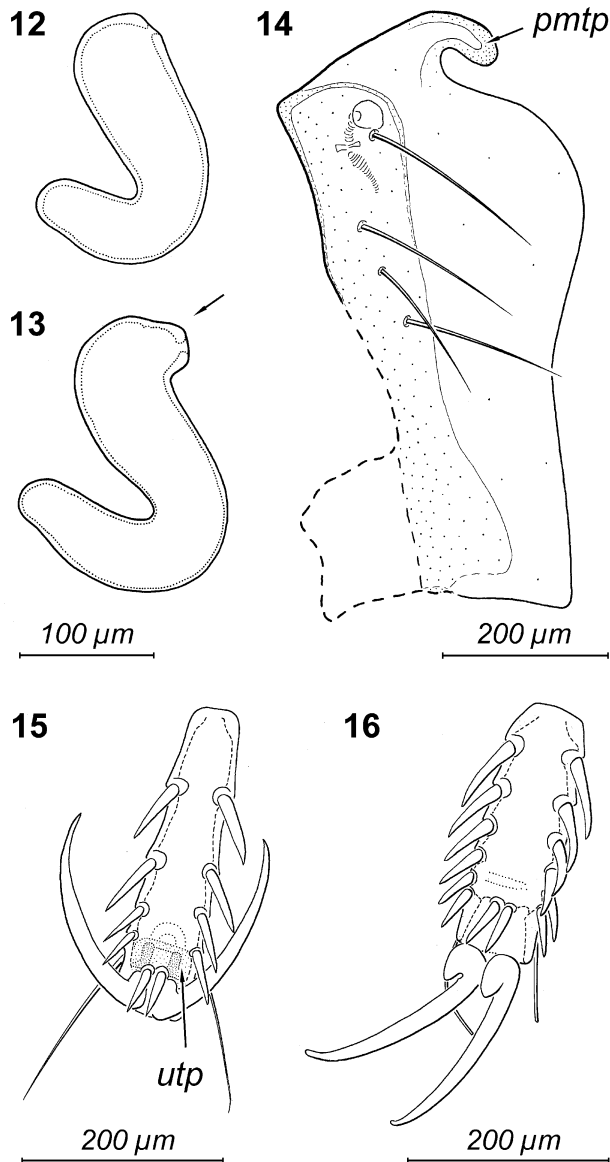
Material examined: ARGENTINA: Buenos Aires, 13.x.1905, ex *Columba livia domestica* [Columbidae], 1♀ (ZSM); Buenos Aires, 1913, ex ‘owl’, 1♀ (BMNH); Buenos Aires Province, Chivilcoy, 2.vi.1936, ex ‘hen’ [= *Gallus domesticus*, Phasianidae], leg. S.J.M. de la Barrera, 2♀ (BMNH); ex *Strix perlata* [= *Tyto alba*, Tytonidae], coll. Weyenbergh, 3♀ (lectotype and 2 paralectotypes of *P. testudo*, BMNH); Las Rosas (B. A.), ex ‘paloma’ [Columbidae], 1♀ (USNM). BRAZIL: Rio de Janeiro, ex *Progne* [Hirundinidae], 1♀ (USNM). CHILE: St. Jago [= Santiago de Chile], Novara Expedition 1857, ex ‘Tschoroi’ [= *Enicognathus leptorrhynchus*, Psittacidae], 4♀ (lectotype and 3 paralectotypes of *H. psittacii*, NHMW); Santiago, 11.ix.1951, ex ‘Turtle dove’ [= *Streptotelia turtur*, Columbidae], leg. José Herrera, 2♀ (USNM). ENGLAND: London, Zoological Gardens, ex *Cittocincla macrura* [= *Copsychus malabaricus* or *Copsychus saularis*, Muscicapidae], 2♀

(BMNH); same collecting site, 15.x.1903, ex ‘birds in western aviary’, leg. E. Ockenden, 2♂ (BMNH). GERMANY: Berlin, Zoological Gardens, 14.ix.1906, ex *Turdus leucomelas* [Turdidae] (from Brazilia), leg. K. Lemm, 2♀ (ZMHB; many additional fleas on pigeon’s head preserved in alcohol, see Fig. 28); same collecting data, ex ‘Hohltaube’ [= *Columba oenas*, Columbidae], 2♀ (DEI), 5♀ (ZMHB). NETHERLANDS: Den Haag, viii.1926, ex *Phasianus* spec. [Phasianidae], 2♀ (BMNH). PERU: [without detailed collecting data] coll. Kiefer, 1♀ (ZSM). URUGUAY: Montevideo, 8.v.1914, ex *Columba livia domestica* [Columbidae], 1♀ (DEI), 6♂ 9♀ (ZSM); same collecting locality, 2.x.1916 and 19.x.1918, ex *Passer domesticus* [Passeridae] and *Columba livia domestica* [Columbidae], leg. Wolfhügel, 5♀ (ZSM). Without collecting data: 2♀ (DEI).

Remarks: *Hectopsylla psittacii* is well defined by the tarsal claws bearing a prominent deep incision at their base (Fig. 16). The shape of the palpus-bearing lobe of the maxilla is species-specific (Fig. 9: *mxl*). Terga and sterna 2–7 short and wide compared with *H. narium*, their lateral ends not touching each other in females with distended abdomen, tips of terga 2–7 distinctly curved backwards (Fig. 4). Distance between tips of manubria 1 and 2 *c.* 2 times width of body of clasper (Fig. 19: *man1*, *man2*, *p1*; see Fig. 18 for measuring length and width of *cl*). Processes 2 and 3 slender, their tips inclined to each other (Fig. 19: *p2*, *p3*). There is a wide variation of several features in the material examined. Position and size of the abdominal spiracle 8 differs conspicuously between the type series and other studied collection material (Figs 24, 25). The size of spiracles 2–7 varies from 0.2 to 0.5 of the eye diameter. The metepimeron may bear 4 (3–6) setae. The number of pairs of lateral plantar setae of the distal tarsomeres ranges from 7 to 8 (6–10). The type series has 6 on average.

The lectotype of *H. psittacii* is designated to ensure the name’s proper and consistent application. Frauenfeld (1860) mentioned six specimens as the original syntype series. Four of them are housed in the NHMW, and two have been donated to the BMNH (Hopkins & Rothschild, 1953). Most specimens received for the present study were so severely damaged previously that positive identifications are almost impossible. Our designated lectotype for *H. psittacii* is the only specimen of the type series in which the head is undamaged. The fore legs and one middle leg are complete; the other legs remaining attached to the body are fragmentary. The agreement of the lectotype and the original description can be confirmed.

It may be pointed out that the lectotype intentionally has not been mounted on a slide. The attempt to



Figures 12–16. Spermatheca, metepimeron and distal tarsomere of metatarsus in *Hectopsylla* species. Fig. 12. *H. narium* sp. nov. (paratype), spermatheca. Fig. 13. *H. pulex*, spermatheca. Fig. 14. *H. broscus* (♀), metepimeron. Fig. 15. *H. narium* sp. nov. (♂, holotype), distal tarsomere. Fig. 16. *H. psittaci* (♀, lectotype), distal tarsomere.

clear a paralectotype of the NHMW series by 6% potassium hydroxide solution resulted in a sudden dissolution of parts of the chitinous structures. The paralectotypes of the BMNH mounted on slides by a former student are similarly damaged. This may have been caused by the age of the material, its former fixation in an unknown and unsuitable preservative, or possibly by its prior desiccation. Attempts to mount

this material should be avoided in the future to preclude its destruction.

The type series was collected from the host ‘Tschoroi’. Hopkins & Rothschild (1953) supposed this name to denote either *Cyanoliseus patagonus* or *Enicognathus leptorhynchus*. Following Johnson & Goodall (1967) and de la Peña & Rumboll (1998), ‘Tschoroi’ or ‘Choroy’ is the popular Chilean name for *Enicognathus leptorhynchus*.

Frauenfeld chose the species name in accordance with the life style and the host of the flea. Therefore, we regard the original spelling of the species name ‘psittaci’ as an inadvertent error. The Latin name for parrot is *psittacus*, and accordingly the species name has to be spelled in the corrected form as ‘psittaci’ (ICZN, 1999: Art. 32.5.1) as it is already in the prevailing use (e.g. Dahl, 1906; Hopkins & Rothschild, 1953).

The type series of *Pulex (Hectopsylla?) testudo* was housed in Córdoba and is obviously lost or destroyed (A.V. Peretti, Departamento de Zoología, Universidad Nacional de Córdoba, Argentina, pers. comm.).

HECTOPSYLLA PULEX (HALLER, 1880)

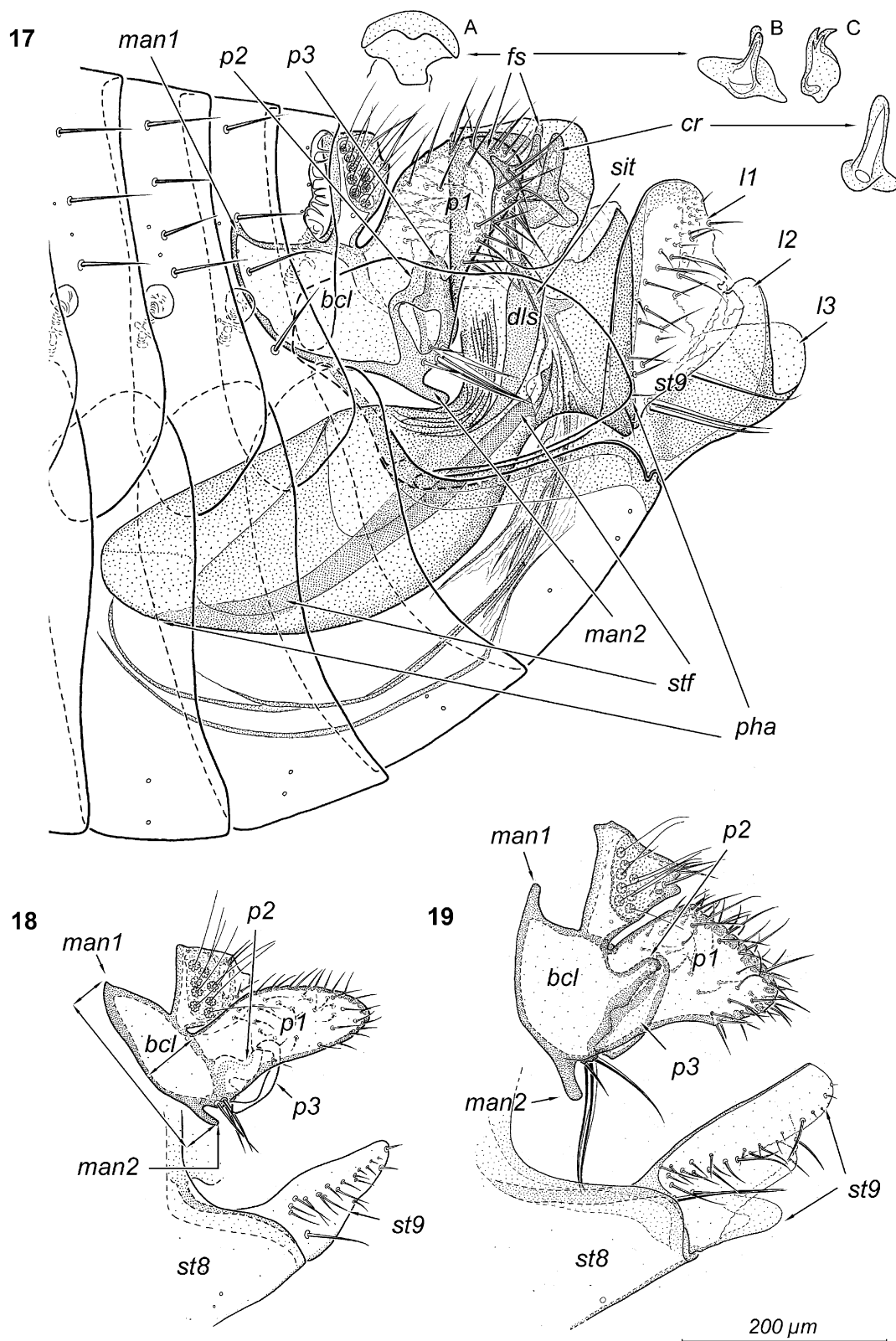
(FIGS 5, 6, 11, 13, 18)

Rhynchopsyllus pulex Haller, 1880: 82, ♀, type locality: Brazil; combined with *Hectopsylla* by Hastriter & Méndez (2000).

Rhynchopsyllus megastigmata Traub & Gammons, 1950: 271–272, ♀, type locality: Peru, Santo Domingo, Puno.

Material examined: BRAZIL: Prov. Paraná, ex *Histiopus velatus* [= *Eptesicus velatus*, Vespertilionidae], 1♀ (DEI), 2♀ (BMNH); ex *Molossus* sp. [Molossidae], 1♀ (paratype of *R. pulex*, BMNH); Lagoa Santa, 2.i.1944, ex *Eumops perotis* [Molossidae], leg. R. Becker, 2♀ (USNM). PANAMA: Pacora, 22.vi.1961 and 27.ii.1962, belfry of church, ex bat guano, coll. Keenan & Tipton, 2♂ (USNM, coll. nos. 7602 and 8824). PARAGUAY: Sta. Trinidad, x.1914, coll. Zürcher, 3♀ (DEI).

Remarks: *Hectopsylla pulex* can be clearly distinguished from similar taxa by the narrow pointed palpus-bearing lobe of the maxilla (Fig. 11: *mxl*). Within *Hectopsylla* the females are characterized by a unique s-shaped spermatheca (Fig. 13). Terga and sterna 2–7 short and wide, lateral ends not touching each other in females with distended abdomen, but in contrast with *H. psittaci*, the successive sterna are spaced (Fig. 6). Process 2 of clasper bluntly rounded, protuberance in the anterior margin of process 3 distinctly below the middle (Fig. 18). Distal tarsomeres with 5 (4–6) pairs of lateral plantar setae.



Figures 17–19. Terminalia in *Hectopsylla* males. Fig. 17. *H. narium* sp. nov. (holotype); crochet (*cr*) and Ford's sclerite (*fs*) of a dissected paratype illustrated separately. A, bridge connecting Ford's sclerites medially, posterior view; B, lateral view; C, posterior view of left Ford's sclerite. Fig. 18. *H. pulex*. Fig. 19. *H. psittaci*.

KEY TO *HECTOPSYLLA* SPECIES ASSOCIATED WITH BIRDS AND BATS

1. Males (unknown for *H. knighti*)..... 2
 – Females 5
- 2(1). Process 1 of clasper evenly rounded distally, dorsal and ventral edges almost parallel (Figs 17, 18: *p1*)..... 3
 – Process 1 of clasper truncate distally, usually dorsal and ventral edges diverging (Fig. 19: *p1*) 4
- 3(2). Distal arm of sternum 9 with single lobe (Fig. 18: *st9*). Palpus-bearing lobe of maxilla long, narrow and pointed (similar to female, Fig. 11: *mxl*). Distance between tips of manubria 1 and 2 more than 3 times width of body of clasper (Fig. 18: *bcl, man1, man2*)..... *Hectopsylla pulex* (Haller, 1880)
 – Distal arm of sternum 9 with three lobes *l1, l2, l3* (Fig. 17: *st9*). Palpus-bearing lobe of maxilla short, wide and distally blunt (Fig. 7: *mxl*). Distance between tips of manubria 1 and 2 less than 2.5 times width of body of clasper (Fig. 17: *bcl, man1, man2*) ***Hectopsylla narium* Kutzscher, sp. nov.**
- 4(2). Distal tarsomeres with 7–8 (6–10) pairs of lateral plantar setae. Tarsal claws with basal tooth present and separated by a deep incision (Fig. 16)..... *Hectopsylla psittaci* Frauenfeld, 1860
 – Distal tarsomeres with at most 6 pairs of lateral plantar setae. If 6 pairs present, then tarsal claws without basal tooth. Males of other *Hectopsylla* species. Usually on terrestrial mammals. See key of Hastriter & Méndez (2000).
- 5(1). Metepimeron with distinct narrow process on dorso-caudal margin (Fig. 14: *pntp*). Females of other *Hectopsylla* species. Usually on terrestrial mammals. See key of Hastriter & Méndez (2000).
 – Metepimeron without process (Fig. 8: *mtp*)..... 6
- 6(5). Palpus-bearing lobe of maxilla distally blunt or round (Figs 8, 10: *mxl*) 7
 – Palpus-bearing lobe of maxilla distally triangularly pointed (Figs 9, 11: *mxl*) 8
- 7(6). Postoral process of head distinct (Fig. 10: *pop*). Abdominal spiracle 8 small and almost unsculptured, trachea not widened proximal and distal to rod of closing apparatus, sinus below spiracle shallow (Fig. 23)
 *Hectopsylla knighti* Traub & Gammons, 1950.
 – Postoral process of head absent or weakly indicated (Fig. 8). Abdominal spiracle 8 large and strongly sculptured, diameter of trachea proximal and distal to rod of closing apparatus conspicuously widened, sinus below spiracle deep (Fig. 22) ***Hectopsylla narium* Kutzscher, sp. nov.**
- 8(6). Spermatheca without projecting cone (similar to Fig. 12). Distal tarsomeres with 7–8 (6–10) pairs of lateral plantar setae. Tarsal claw with basal tooth separated by a deep incision (Fig. 16)
 *Hectopsylla psittaci* Frauenfeld, 1860
 – Orifice of spermatheca placed on a distinctly projecting cone (Fig. 13). Distal tarsomeres with 5 (4–6) pairs of lateral plantar setae. Tarsal claw basally widened, but without incision *Hectopsylla pulex* (Haller, 1880)

DISCUSSION

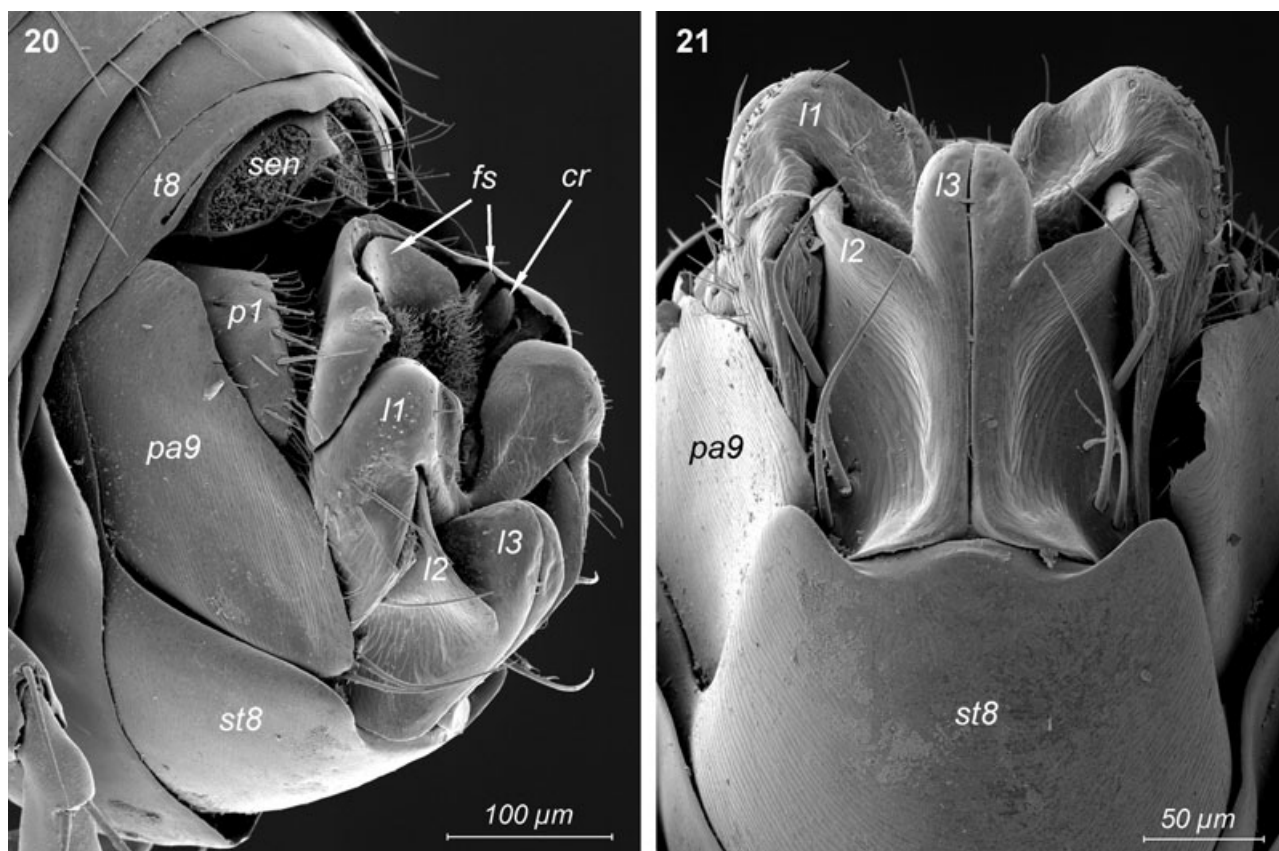
PHYLOGENETIC ASSESSMENT OF *HECTOPSYLLA NARIUM* SP. NOV. AND RELATED TAXA

The phylogenetic analysis supports the monophyly *Tunga* + *Hectopsylla* (Fig. 26). Relevant apomorphies are the presence of punctiform sensilla on the antennal club (1: 1), reduction of the dorsal and medial setae on the abdominal terga of the female (9: 1°), left and right sensillum separated medially and sensory pits being reduced to a number of 8 (11: 1°), lobiform shape of the proximal arm of sternum 9 (17: 1), and properly sclerotized and clearly outlined lateral lamina of the aedeagal apodeme (23: 1). The reduction of the setae on the antennal flagellum (1: 1) might be a consequence of the concealed mode of life.

Tunga and *Hectopsylla* (with *Rhynchopsyllus* separated from *Hectopsylla*) have been treated as *Tunginae* + *Hectopsyllinae* of *Tungidae* by Hopkins & Rothschild (1953) or of *Pulicidae* by Cheetham (1988). These taxa coincide broadly in bionomics and morphology, although *Tunga* displays a number of striking autapomorphies. Both the reduction of the anterior

abdominal spiracles of the female and the elongation of the phallosome of the male might be preadaptations to the concealed feeding habit of the female deep inside the host's skin. The classification under a single common subfamily name appears as sufficient to display the relationships of these comparatively species-poor sister taxa. As the maintenance of *Hectopsyllinae* comprising *Hectopsylla* alone provides no additional information, we propose to treat *Tunginae* Fox, 1925 (p. 130, described as *Tungidae*) as a new junior synonym of *Hectopsyllinae* Baker, 1904 (p. 375, described as *Hectopsyllidae*). The older name *Sarcopsyllinae* Taschenberg, 1880 (p. 43, described as *Sarcopsyllidae*) has not been used possibly since Wagner (1939) stated its synonymy. In accordance with Article 40.2. of ICZN (1999) this name is not to be applied as the valid name of this group in future.

In addition *Hectopsylla* results as monophyletic. For the stem species an enlarged sternum 9 of the male (15: 1) has to be presumed. The distal arm of the sternum 9 abuts at its base the distal edge of the preceding sternum and forms an articulation with the latter (14: 1). It bears one or several long and



Figures 20–21. Terminalia in *Hectopsylla narium* sp. nov. male. Fig. 20. Distal terga and sterna, oblique lateral view. Fig. 21. Sternum 8–9, ventral view.

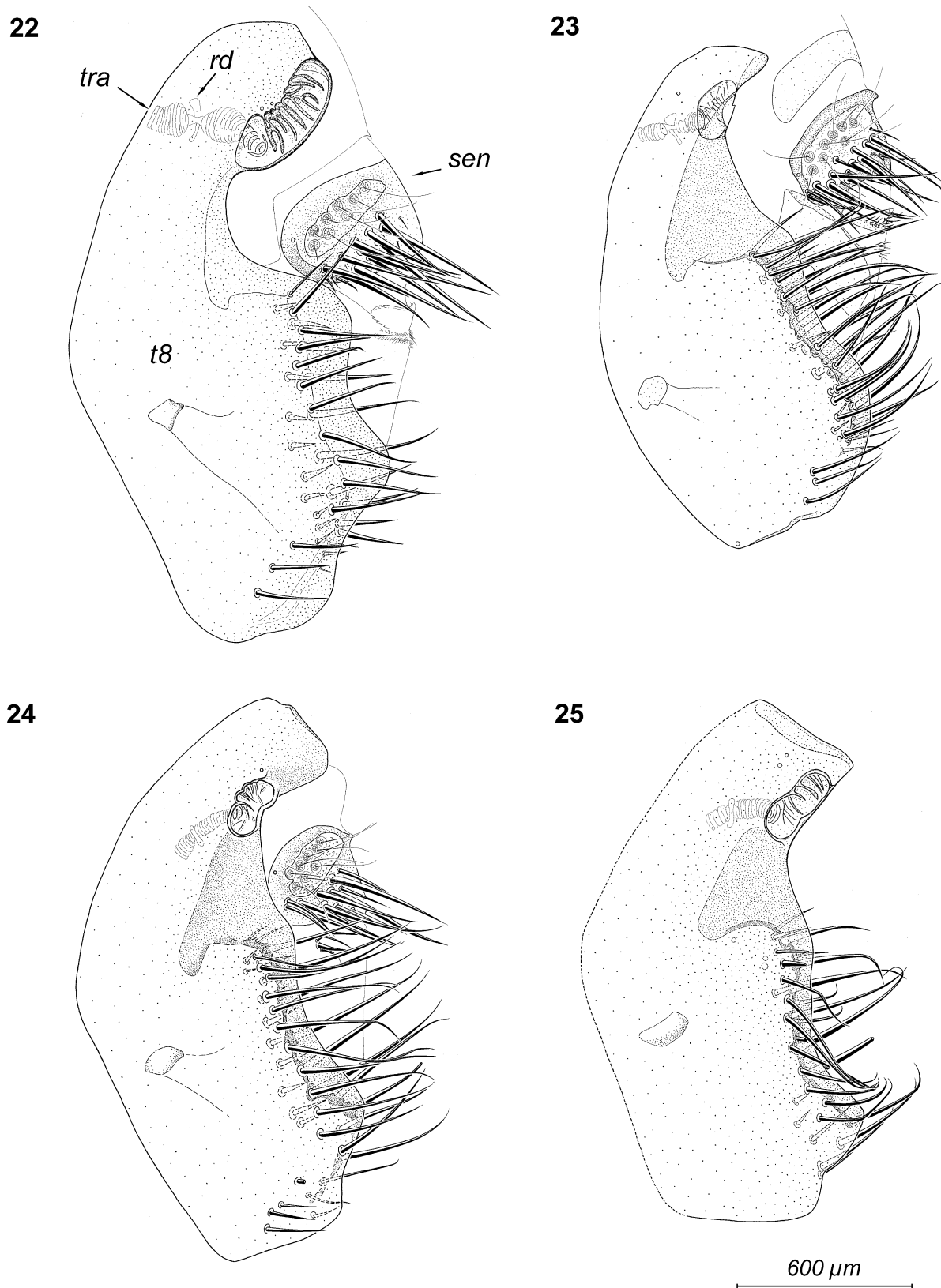
stout setae (16: 1). The sensory pits are arranged in two lines with 5 and 3 pits (11: 2), whereas the two lines contain 4 and 4 in *Tunga*. The hind femur bears a large basal tooth (6: 1) and a dorsal longitudinal strut is present in the phallosome (22: 1^r). Our assumption of the monophyly of *Hectopsylla* agrees in principle with Cheetham's (1988) cladogram, who treated *Rhynchopsyllus* Haller, 1880 as the sister taxon of *Hectopsylla*. The type species of *Rhynchopsyllus* is *H. pulex*, which is here assigned the state of the sister species of the clade formed by all other *Hectopsylla* species. Hastriter & Méndez (2000) synonymized *Rhynchopsyllus* with *Hectopsylla*. We agree with this decision in view of the few species included in *Hectopsylla*, which for practical reason requires no further subdivision.

Hopkins & Rothschild (1953) termed the posteriorly projecting manubrium of *Hectopsylla* as manubrium 2. Its ventral position on the clasper and its rod-like structure suggest that it is homologous with the anteriorly projecting manubrium proper of non-*Hectopsylla* Pulicidae. In consequence the dorsal manubrium, i.e. manubrium 1 of Hopkins & Rothschild (1953), is a new acquisition of the stem species of

Hectopsylla (12: 1). Cheetham (1988) homologized the latter with the apodeme of tergum 9.

The unique shape of the enlarged distal arm of sternum 9 of *Hectopsylla* has further been altered in the stem species of the clade comprising all *Hectopsylla* species except *H. pulex*. These species possess an additional mesal, glabrous lobe *l3* (18: 1). This clade consists of two groups, which are here called the *H. psittaci*-group and *H. broscus*-group (see Fig. 26 for species included in each of these groups).

The *H. psittaci*-group, comprising *H. knighti*, *H. narium* and *H. psittaci*, is monophyletic on the basis of its association with birds as the hosts (24: 2), although the tree topology is not dependent on this character solely. The re-analysis of the data excluding character 24 has produced an identical branching pattern. This clade is also corroborated by the position of the distal plantar setae relative to the unguitactor plate (7: 1^p). Additionally the plantar setae are crowded towards the tip of the tarsomere, i.e. the distances between the proximal setae are wider than between the distal setae. However, we have abstained from including this as an additional character set in the analysis, because character states for 'crowded'



Figures 22–25. Tergum 8 and sensillum in *Hectopsylla* females. Fig. 22. *H. narium* sp. nov. (paratype). Fig. 23. *H. knighti* (holotype). Fig. 24. *H. psittaci*. Fig. 25. *H. psittaci* (lectotype, sensillum not illustrated).

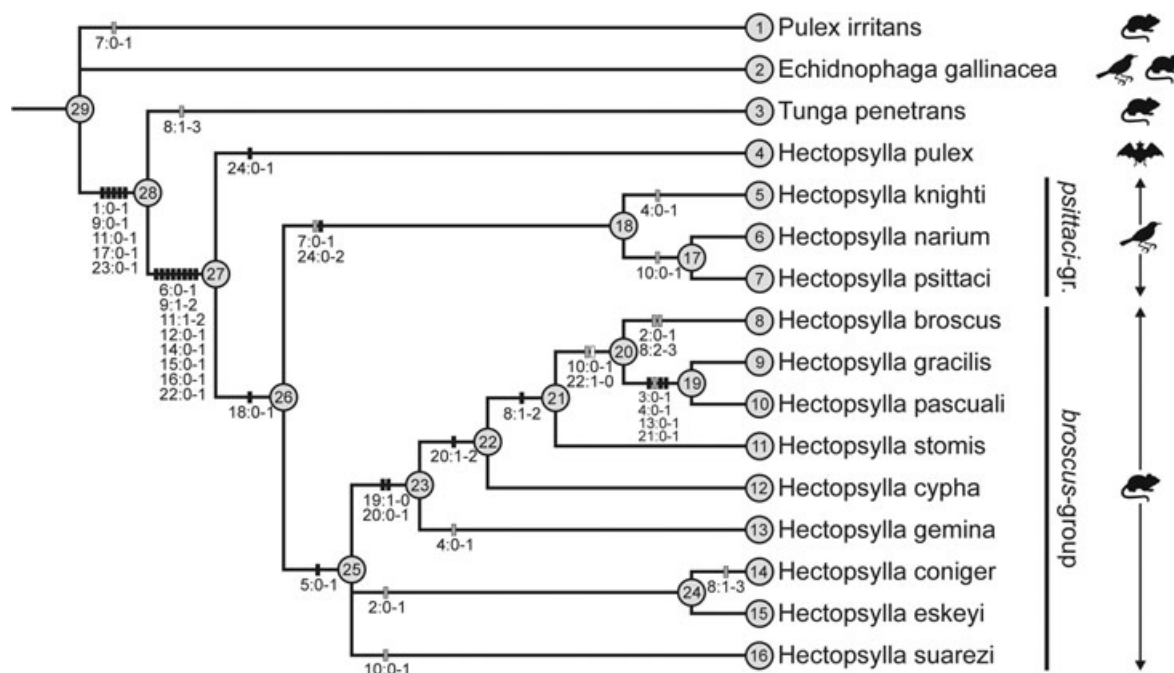


Figure 26. Cladogram of the lineages of *Hectopsylla* and hypothesis of character evolution mapped on it. Tree of 43 steps length produced by ordered analysis in PAUP*. Pictograms on the right side illustrate the association of the flea taxa with birds, bats and terrestrial mammals.

and 'not crowded' are not evidently discernible due to intermediates observed. The crowded arrangement has evolved convergently for many times in flea taxa infesting birds (Holland, 1964), and it must already have been present in the stem species of the *H. psittaci*-group. No reasonable explanation has been offered for this pattern in bird fleas (Holland, 1964).

H. narium is considered to be the sister species of *H. psittaci*, although the support for this assumption is low. Females of both species share the slightly concave lower edge of tergum 8 (10: 1^P), which is straight in *H. knighti* as well as in *H. pulex* and some of the species of the *H. broscus*-group. The native distribution in South America is plesiomorphic for *H. narium* and *H. psittaci*. The occurrence of *H. knighti* more northwards in Mexico (Traub & Gammons, 1950) is an autapomorphy of the latter.

The *H. broscus*-group is characterized by the presence of a dorso-posterior process of the metepimeron as a unique apomorphy (5: 1). Within this clade some branching is not resolved or weakly corroborated by homoplasies and reversals. For example, *H. suarezi*, *H. coniger* + *H. eskeyi* and the clade comprising the remaining species of the *H. broscus*-group are included in a polytomy at the basis of the *H. broscus*-group. Additional, and perhaps non-morphological datasets are required to gain a better resolution. Nevertheless, this deficiency does not have implications for our considerations of the ecological evolution and zooge-

graphy of *Hectopsylla* species, which concern the *H. broscus*-group only. Re-analysis of the data including the *H. broscus*-group as a single taxon with partly polymorphic character states (Table 1, row 17) reveals that the other branching of the tree is independent from the internal topology of the *H. broscus*-group.

Within the *H. broscus*-group the monophyly of *H. coniger* + *H. suarezi* is supported by the presence of a wedge-shaped occipital lobe in the female (2: 1^P). The clade comprising *H. broscus*, *H. cypha*, *H. gemina*, *H. gracilis*, *H. pascuali* and *H. stomis* is corroborated by two apomorphies. The intermediate lobe *l*2 of the distal arm of the sternum (19: 0), which is assumed to be a common ground plan state of the *H. broscus*-group + *H. psittaci*-group, is reduced in the stem species of this clade. The mesal wall of *l*1 of sternum 9 bears enlarged setae: two in *H. gemina* (20: 1) and one in its sister-group comprising *H. broscus*, *H. cypha*, *H. gracilis*, *H. pascuali* and *H. stomis* (20: 2). *H. cypha* is the sister species of the other four species of the latter group, in which the number of setae on the male abdominal terga 5–6 is reduced from three to two (8: 2^S) and in *H. broscus* even to a single seta (8: 3). The monophyly of *H. broscus*, *H. gracilis* and *H. pascuali* is weakly corroborated by a homoplastic character and a character reversal. The concave shape of the lower quarter of the distal edge of tergum 8 in the female (10: 1^P) has evolved in parallel fashion in the stem species of *H. narium* + *H. psittaci* and in *H. pascuali*. The

dorsal longitudinal strut, which is an apomorphy of *Hectopsylla*, is reduced in this clade (22: 0). The monophyly of *H. gracilis* + *H. pascuali* is undoubtedly supported by the presence of a membranous blotch between the antennal bases in the male (3: 1), the rounded dorsal manubrium (13: 1) and the tongue-like glabrous postero-ventral protrusion of *ll* (21: 1). A membranous blotch is also present in the *H. gracilis* and *H. pascuali* females (4: 1^p); among female *Hectopsylla* species this occurs homoplastically in *H. gemina* and *H. knighti*.

HOST RELATIONSHIPS

The high infestation rate within the colony, the high abundance of feeding female fleas on single nestlings, and the observation of flea larvae and teneral adults in the nests strongly indicate that the burrowing parrot is the primary host of *Hectopsylla narium*. From the present data it is not evident, however, whether it is the exclusive host. The observations of larvae in nests of barn owl and southern Martin cannot be assessed properly. Perhaps the barn owl captured a formerly active nest of a breeding parrot pair.

The host relationship to birds has evolved only once in *Hectopsylla*, i.e. in the stem species of the *H. psittaci*-group (character 24: 2; node additionally supported by character 7: 1). The adaptation of fleas to birds is generally regarded as secondary (Holland, 1964). Scarce data on the bionomics of *H. knighti* and the wide host range of *H. psittaci* do not enable reasonable assumptions to be made about host switches within the *H. psittaci*-group.

Tunga and the *H. broscus*-group are associated with terrestrial mammals, which in the present analysis turns out to be the plesiomorphic state for *Hectopsylla*

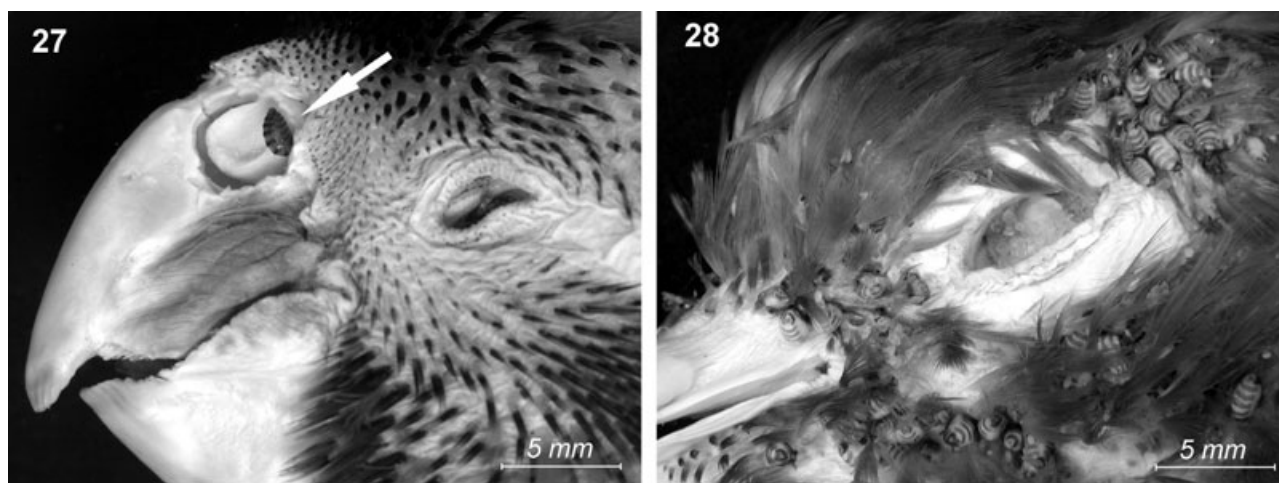
+ *Tunga*. Hopkins & Rothschild (1953) identified material as *T. bondari*, which had been found on the bird red-legged seriama (*Cariama cristata*; Cariamiidae), but the type material of this flea species had been collected from the anteater *Tamandua tetradactyla* (Myrmecophagidae; Wagner, 1932). The observation of *H. stomis* on 'birds' reported by Jordan (1925) might be accidental, because by far most specimens of this species have been found on terrestrial mammals (Hastriter & Méndez, 2000).

The association of *H. pulex* with bats (Hastriter & Méndez, 2000; Esbérard, 2001; character 24: 1) is an autapomorphy of this species.

HABITS OF THE FEMALE

Female *Hectopsylla narium* exhibit a sessile, tick-like behaviour for feeding, which is similar to other *Hectopsylla* species (Figs 27, 28). This behaviour may be assumed for the stem species of *Hectopsylla* + *Tunga*. Hastriter & Méndez (2000) observed autoseverance of body appendages and catabolic scarring in *H. pulex*, which supposedly is an additional ground plan feature of *Hectopsylla* + *Tunga*. This has not been observed in *H. narium*. *Tunga* species have evolved additional morphological preadaptations which provide the licence for concealed, neosomic endoparasitism in the host's skin (Hopkins & Rothschild, 1953; Heukelbach, 2004). The drastic reduction or absence of anterior abdominal spiracles combined with an increase of spiracles 5–7 in *Tunga* (Hopkins & Rothschild, 1953) enables respiration even if the neosome is surrounded by host tissue.

The peculiar infestation site of *H. narium*, i.e. the nasal cavity and the comparatively dry area under the tongue, is unique among Siphonaptera. Other *Hectop-*



Figures 27–28. Infestation sites of *Hectopsylla* species. Fig. 27. *Hectopsylla narium* sp. nov. in the nostril of *Cyanoliseus p. patagonus* chick (nostril dissected). Fig. 28. *H. psittaci* on the head of a 25–30-day-old nestling of *Columba oenas*.

sylla species preferably feed exposed on body regions with sparse hair or plumage close to the head, e.g. *H. pulex* on the ears of *Molossus molossus* (Esbérard, 2001) or *H. psittaci* on a pigeon's head (Fig. 28). The nostrils appear to be the primary infestation site of *H. narium* as we observed the occurrence of fleas below the tongue only in the late season, when the nostrils were already occupied by other fleas. Nostrils and the oral cavity appear to be a suitable, concealed habit for the sessile, immobile *H. narium* females, where they are safe against cleaning activities of their host and the host's parents.

LARVAL DEVELOPMENT

Burrowing parrots do not use nesting material but instead deposit their eggs on the sandy bottom of the nest chamber. The larvae of *Hectopsylla narium* evidently develop there, because we found different larval stages and several teneral adults of both sexes in this substrate. The nestlings remain in the nest for about 63 days until they leave the breeding site gradually, as the young fledge at end of December to end of January (Masello & Quillfeldt, 2002, 2004a). Until then birds and chicks themselves provide sufficient detritus in the nest chamber, which may serve for larval nutrition.

The nesting pairs of the parrot breed once a year. They use the burrows again, which they have dug in previous seasons, and enlarge them (Masello & Quillfeldt, 2002, 2004a; Masello *et al.*, 2002). Obviously the fleas complete their development in the nest chamber. This enables a repeated infestation of nesting birds in subsequent years, perpetuating fleas within the colony.

SPATIAL DISPERSAL

Burrowing parrots are highly gregarious, colonially breeding birds. The colony near El Cóndor has an average of 35 000 active nests (Masello *et al.*, 2006). The first kilometre alone is populated with *c.* 6750 nests. The nest entrances are often very close together and sometimes the tunnels are interconnected (Masello *et al.*, 2002). We have found fleas vivaciously crawling and jumping around, suggesting that they are able to disperse actively within the colony.

In Argentina, the burrowing parrot is distributed from the Andean slopes in the north-west to the arid Patagonian steppes in the south (Bucher & Rinaldi, 1986). The studied Patagonian race occurs in central to south-east Argentina. Southern populations migrate to the north in winter, sometimes reaching as far as Uruguay (Bucher & Rodríguez, 1986). *Hectopsylla narium* is only known to infest this parrot species. The observations have been made in the colony of

El Cóndor solely. This raises the question of the dispersal mechanism of these fleas over long distances, e.g. between geographically separated colonies. The passive dispersal with the help of adult parrots appears most likely, although we have no evidence for this assumption. The sister species, *H. psittaci*, has been introduced to European zoological gardens several times (Wagner, 1936). As with many other parrot species, the burrowing parrot is also valued in the pet trade. It is one of the most frequently sold Psittacidae birds in Europe (Guix, Jover & Ruiz 1997). The official capture rate in the province of Río Negro alone was 3000 individuals in 1998 (R. Cardon, Wildlife Division, Viedma, Río Negro, Argentina, pers. comm.). However, fleas have never been mentioned in the literature in association with captive, adult burrowing parrots. The conditions in *H. narium* possibly resemble those for many other flea species which parasitize birds. *Ceratophyllus gallinae* (Schrank, 1803), for example, may be highly abundant in repeatedly used nests of European birds, but it is only exceptionally found on the adult birds themselves (Peus, 1968). Further studies are required to determine whether *H. narium* occurs in breeding colonies of the burrowing parrot beyond the more restricted coastal zone.

ACKNOWLEDGEMENTS

We thank K. Busse and C. M. Naumann (Bonn) for the interpretation of the vernacular bird name Tschoroi. We are grateful to the curators for the loan of collection material (see Material and methods). Furthermore, we wish to thank P. M. Baena (Madrid), M. Marchesan (Trieste), A. and M. L. Pagnossin (La Plata), and C. Sommer (Berlin) for assistance with the fieldwork. M. Walters (Christchurch) provided the photograph for Figure 27. We appreciate the reviews and detailed comments of M. W. Hastriter (Provo), M. F. Whiting (Provo) and two anonymous reviewers, which helped significantly to improve this work. This project was supported partially by the City Council of Viedma (Río Negro, Argentina), and a grant of the State of Thuringia (Landesgraduiertenstipendium), Germany, a co-operation grant between the International Bureau of the BMBF of Germany (ARG 99/020) and the Argentinean SECyT (AL/A99-EXIII/003), a grant of the World Parrot Trust (WPT), a grant of the Liz Claiborne Art Ortenberg Foundation (LCAOF), and the Wildlife Conservation Society (WCS). The present study was carried out under permission of the Dirección de Fauna de la Provincia de Río Negro, Argentina (Exp. no. 143089-DF-98).

REFERENCES

- Angulo RJ, Casamiquela RM. 1982. Estudio estratigráfico de las unidades aflorantes en los acantilados de la costa

- norte del Golfo de San Matías (Río Negro y extremo austral de Buenos Aires) entre los meridianos 62°30 y 64°30 W. *Mundo Ameghiniano* **104**: 20–73.
- Baker CF. 1904.** A revision of American Siphonaptera, or fleas, together with a complete list and bibliography of the group. *Proceedings of the United States National Museum* **27**: 365–469.
- Beaucournu JC, Alcover JA. 1990.** Pucea récoltées dans la province Neuquén (Argentine); description de 4 nouveaux taxa (Insecta, Siphonaptera). *Annales de Parasitologie humaine et comparée* **64**[1989]: 489–505.
- Bucher EH, Rinaldi S. 1986.** Distribución y situación actual del loro barranquero (*Cyanoliseus patagonus*) en la Argentina. *Vida Silvestre Neotropical* **1**: 55–61.
- Bucher EH, Rodríguez EN. 1986.** Sobre la presencia del loro barranquero (*Cyanoliseus patagonus*) en el Uruguay. *El Hornero* **12**: 303–304.
- Cheetham TB. 1988.** Male genitalia and the phylogeny of the Pulicoidea (Siphonaptera). *Theses Zoologicae* **8**: 1–224.
- Dahl [F]. 1906.** Briefkasten. *Naturwissenschaftliche Wochenschrift N. F.* **5**: 639–640.
- de la Peña MR, Rumboll M. 1998.** *Birds of southern South America and Antarctica. Collins illustrated checklist.* London: Harper Collins Publishers.
- Esbérard C. 2001.** Infestation of *Rhynchopsyllus pulex* (Siphonaptera: Tungidae) on *Molossus molossus* (Chiroptera) in Southeastern Brazil. *Memorias do Instituto Oswaldo Cruz, Rio de Janeiro* **96**: 1169–1170.
- Fox E. 1925.** *Insects and disease of man.* London: H.K. Lewis.
- Frauenfeld G von. 1860.** Diagnosen einiger neuer Insecten und Untersuchung mehrerer Sandproben verschiedener Küstenpunkte, gesammelt während der Reise Sr Maj. Fregatte Novara. *Sitzungsberichte der Mathematisch-Naturkundlichen Classe der Kaiserlichen Akademie der Wissenschaften Wien* **40**: 447–468.
- Galloway TD, Andruschak A, Underwood RM. 2000.** *Echidnophaga gallinacea* (Siphonaptera: Pulicidae) recorded in Canada for the first time. *Proceedings of the Entomological Society of Manitoba* **56**: 5–7.
- Guix JC, Jover L, Ruiz X. 1997.** Muestreos del comercio de psitácidos neotropicales en la ciudad de Barcelona, España: 1991–1996. *Ararajuba* **5**: 159–167.
- Haller G. 1880.** *Rhynchopsyllus*, eine neue Puliciden-Gattung, in einigen Worten gekennzeichnet. *Archiv für Naturgeschichte* **46**: 72–87.
- Hastriter MW, Méndez E. 2000.** A review of the flea genera *Hectopsylla* Frauenfeld and *Rhynchopsyllus* Haller (Siphonaptera: Pulicidae). *Proceedings of the Entomological Society of Washington* **102**: 613–624.
- Heukelbach J. 2004.** Tungiasis. *Orphanet Encyclopedia*, <http://www.orpha.net/data/patho/GB/uk-Tungiasis.pdf> (downloaded December 2004).
- Holland GP. 1964.** Evolution, classification, and host relationships of Siphonaptera. *Annual Review of Entomology* **9**: 123–146.
- Hopkins GHE, Rothschild M. 1953.** *An illustrated catalogue of the Rothschild collection of fleas (Siphonaptera) in the British Museum (Natural History), 1. Tungidae and Pulicidae.* London: British Museum (Natural History).
- ICZN [International Commission on Zoological Nomenclature]. 1999.** *International code of zoological nomenclature*, 4th edn. London.
- Johnson PT. 1957.** A classification of the Siphonaptera of South America. *Memoirs of the Entomological Society of Washington* **5**: 1–299.
- Johnson AW, Goodall JD. 1967.** *The birds of Chile and adjacent regions of Argentina, Bolivia and Peru*, Vol. 2. Buenos Aires: Platt Establecimientos Gráficos.
- Jordan K. 1925.** New Siphonaptera. *Novitates Zoologicae* **32**: 96–112.
- Jordan K, Rothschild NC. 1906.** Notes on the Siphonaptera from the Argentine described by the late Professor Dr. Weyenbergh. *Novitates Zoologicae* **13**: 170–177.
- Leonardi G, Oporto NR. 1983.** Biogenetic erosion structures (modern parrots' nests) on marine and fluvial cliffs in southern Argentina. *Anais de Academia Brasileira de Ciências* **55**: 293–295.
- Mahnert V. 1982.** Two new flea species in the genera *Plocopsylla* Jordan and *Hectopsylla* Frauenfeld (Insecta, Siphonaptera) from Argentina. *Revue Suisse de Zoologie* **89**: 569–572.
- Masello JF, Pagnossin GA, Lubjuhn T, Quillfeldt P. 2004.** Ornamental non-carotenoid red feathers of wild Burrowing Parrots. *Ecological Research* **19**: 421–432.
- Masello JF, Pagnossin GA, Palleiro GE, Quillfeldt P. 2001.** Use of miniature security cameras to record behaviour of burrow-nesting birds. *Vogelwarte* **41**: 150–154.
- Masello JF, Pagnossin ML, Sommer C, Quillfeldt P. 2006.** Population size, provisioning frequency, flock size and foraging range at the largest known colony of Psittaciformes: The Burrowing Parrots of the north-eastern Patagonian coastal cliffs. *Emu*. **106**: 69–79.
- Masello JF, Quillfeldt P. 2002.** Chick growth and breeding success of Burrowing Parrots in the wild. *Condor* **104**: 574–586.
- Masello JF, Quillfeldt P. 2004a.** Consequences of La Niña for the survival and growth of nestling Burrowing Parrots on the Atlantic coast of South America. *Emu* **104**: 337–346.
- Masello JF, Quillfeldt P. 2004b.** Are haematological parameters related to body condition, ornamentation and breeding success in wild burrowing parrots *Cyanoliseus patagonus*? *Journal of Avian Biology* **35**: 445–454.
- Masello JF, Sramkova A, Quillfeldt P, Epplen JT, Lubjuhn T. 2002.** Genetic monogamy in Burrowing Parrots *Cyanoliseus patagonus*? *Journal of Avian Biology* **33**: 99–103.
- Mey E, Masello JF, Quillfeldt P. 2002.** Chewing lice (Insecta, Phthiraptera) of the Burrowing Parrot *Cyanoliseus p. patagonus* (Vieillot) from Argentina. *Rudolstädter Naturhistorische Schriften, Supplement* **4**: 99–112.
- Peus F. 1968.** Zur Kenntnis der Flöhe Deutschlands. II. Faunistik und Ökologie der Vogelflöhe (Insecta, Siphonaptera). *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere* **95**: 571–633.
- Pilgrim RLC. 1992.** Preparation and examination of flea

- larvae (Siphonaptera) by light and electron microscopy. *Journal of Medical Entomology* **29**: 953–959.
- Snodgrass RE. 1946.** The skeletal anatomy of fleas (Siphonaptera). *Smithsonian Miscellaneous Collections* **104**: 1–89.
- Swofford DL. 2001.** *PAUP*. 4.0. Phylogenetic analysis using parsimony*. Champaign: Illinois State Natural History Survey [update to PAUP* 4.0 b10 downloaded February 2002].
- Taschenberg O. 1880.** *Die Flöhe. Die Arten der Insectenordnung Suctoria nach ihrem Chitinskelet monographisch dargestellt*. Halle: Niemeyer.
- Traub R, Gammons JG. 1950.** Two new fleas of the family Tungidae. *Journal of Parasitology* **36**: 270–273.
- Wagner J. 1932.** *Tunga bondari*, eine neue Art der Sandflöhe. *Novitates Zoologicae* **38**: 248–249.
- Wagner J. 1936.** 23. Ordnung: Flöhe, Aphaniptera (Siphonáptera, Suctória). In: Brohmer P, Ehrmann P, Ulmer G, eds. *Die Tierwelt Mitteleuropas. Band VI Insekten, 3 Teil*. Leipzig: Quelle & Meyer, 1–24.
- Wagner J. 1939.** Ordnung: Aphaniptera Kirby & Spence 1818. In: Bronn HG, ed. *Klassen und Ordnungen des Tierreichs. Fünfter Band: Arthropoda. 3. Abteilung: Insecta. XIII. Buch, Teil F*. Leipzig: Akademische Verlagsgesellschaft, 1–114.
- Weyenbergh H. 1881.** Sobre la familia Pulicidae con descripción de algunas nuevas especies. *Periódico Zoológico* **3**: 261–277.