On morphology, taxonomy, ecology, and distribution of *Bothriometopus* Taschenberg (Phthiraptera, Ischnocera, Philopteridae *sensu lato*)

Armando C. Cicchino* and Eberhard Mey**

With 13 Figures and 1 Table

Resumen

Acerca de la morfología, taxonomía, ecología y distribución de *Bothriometopus* Taschenberg (Phthiraptera, Ischnocera, Philopteridae *sensu lato*)

Los caracteres morfológicos de este género se estudiaron comparativamente con los de otros dos géneros afines con *Bothriometopus* – el cual parasita únicamente a especies of Anhimidae –, *Ornithobius* Denny, 1842 and *Acidoproctus* Piaget, 1878 – parásitos de especies de Anatidae: Anserinae y Tadorninae respectivamente Anseranatidae y Anatidae: Dendrocygninae, Stictonettinae, Tadorninae und Anatinae – tanto es su estado aulto como en sus estados preimafinales. Los estados adultos y preadultos de las dos especies en él incluidas, *Bothriometopus macrocnemis* (Burmeister, 1838) (tipo del género) y *B. simillimus* (Giebel, 1874) se describen e ilustran adecuadamente, proveyendo además comentarios acerca de su alimentación, dispersión sobre el cuerpo de sus hospederos, prevalencia y distribución geográfica. Finalmente, se añaden comentarios generales acerca de sus relaciones morfológicas entre los géneros arriba citados las las distribuciones en sus hospederos respectivos.

Zusammenfassung

Zur Morphologie, Taxonomie, Ökologie und Verbreitung von *Bothriometopus* Taschenberg (Phthiraptera, Ischnocera, Philopteridae *sensu lato*)

Bothriometopus ist eine recht eigentümliche ischnozere Gattung, die – nach bisheriger Kenntnis – in zwei Arten nur auf neotropischen Wehrvögeln (Anhimidae) vorkommt. Ihre ungewöhnliche Morphologie teilt *Bothriometopus* weitgehend mit den gleichfalls nur auf anseriformen Wirten vorkommenden Gattungen *Ornithobius* Denny, 1842 (auf Anatidae: Anserinae and Tadorninae) und *Acidoproctus* Piaget, 1878 (auf Anseranatidae und Anatidae: Dendrocygninae, Stictonettinae, Tadorninae und Anatinae), wie in einer vergleichenden Übersicht gezeigt wird. Beide *Bothriometopus*-Arten, *B. macrocnemis* (Burmeister, 1838) (= Generotype) und *B. simillimus* (Giebel, 1874), werden ausführlich beschrieben sowie Angaben über ihre Nahrung, Topographie und Extensität des Befalls und ihre geographische Verbreitung gegeben.

Summary

The morphological characters of the ischnoceran genus *Bothriometopus* occurring on Anhimidae in the Neotropic only are studied in a comparative study. *Bothriometopus* show some morphological affinities with both *Ornithobius* Denny, 1842 (on Anatidae: Anserinae and Tadorninae) and *Acidoproctus* Piaget, 1878 (on Anseranatidae and Anatidae: Dendrocygninae, Stictonettinae, Tadorninae and Anatinae). Adult and preadult stages of the two included species, *Bothriometopus macrocnemis* (Burmeister, 1838) (genero type) and *B. simillimus* (Giebel, 1874) are fully described and illustrated, along with comments on their feeding, dispersion on their host bodies, prevalence and geographic distribution. General remarks on morphological relationships of the three cited genera and host distribution are also given.

Keywords: *Bothriometopus*, adult, nymphal and egg morphology, oviposition sites, Anhimidae, South America.

* A. C. Cicchino, Laboratorio de Artrópodos, Departamento de Biología, Universidad Nacional de Mar del Plata, Funes 3300,7600 Mar del Plata, Buenos Aires Province, Argentina. Research Career of the National Council of Scientific and Technical Research (CONICET). E-mail: chicchino@copetel.com.ar

** Dr. E. Mey, Naturhistorisches Museum im Thüringer Landesmuseum Heidecksburg, D-07407 Rudolstadt.
E-mail: museum@heidecksburg.de oder mey-rudolstadt@t-online.de

Introduction

The genus *Bothriometopus* has been erected by TASCHENBERG (1882:188), and include two nominate species: »*Lipeurus macrocnemis* BURMEISTER, 1838« (= genero type) and »*Lipeurus simillimus* GIEBEL, 1874«, both parasitic on Screamers species (Aves, Anhimidae), confined to the Neotropics. Despite these two species were frequently mentioned or cited, their specific status has not been properly clarified. In addition, nothing is known about their preimaginal instars, feeding, niche, and relationship with allied genera, in particular *Ornithobius* DENNY, 1842 and *Acidoproctus* PIAGET, 1878. By this, it is our aim to state the generic characters of *Bothriometopus* in a comparative form with representatives of these two related genera, along with descriptions of adults and all preimaginal instars of both species, giving also comments on feeding, dispersion on their host bodies, prevalence and geographic distribution.

Material and methods

The birds used in this study were captured with buckshot gun. Each bird was immediately wrapped with an absorbent paper, placed in individual plastic bags containing *ca.* 10 mls. ethyl acetate to kill lice *in situ*, and then frozen as soon as possible. In the laboratory each bird was carefully searched for lice feather-by-feather. Location of individual lice in particular pterylae or apteria was mapped in pre-printed cards, paying special attention to the sites of oviposition. Lice were slide-mounted in Canada Balsam following conventional procedures. The eggs were stored in vials with 70 % ethanol. Lice for scanning microscopy were cleaned in an ultrasonic vibrator, then repeatedly rinsed in distilled water, dehydrated in graded to absolute ethanol, mounted in stubs, coated with gold-palladium, observed and photographed at different magnifications in a Jeol/EO 1.1 Scanning Electron Microscope of the Electronic Microscopy Laboratory of the Museo de La Plata. Nomenclature of chorionic structures follows CICCHINO & CASTRO (1994). Drawings were made by A. C. using a *camera lucida* attached to a Bausch & Lomb compound microscope. All measurements were taken from mounted specimens by means of a calibrated eyepiece, all expressed in millimetres and identified by the following abbreviations:

HL   = head length,
OW = maximum width of the head,
PW = prothorax width,

PTW = pterothorax (mesometathorax) width,
AW   = maximum width of the abdomen,
TL   = total body length,
GL   = male genitalia length (taken from the apex of the basal plate to the tip), and
       GW maximum width of the male genitalia.

Nomenclature of head setae follows CLAY (1951). Repository of specimens: most of the specimens studied are in the collection of Museo de La Plata, La Plata, Buenos Aires Province, Argentina, and in the Museum of Natural History of the Thuringian State Museum Heidecksburg at Rudolstadt (Germany).

Results and discussion

Genus *Bothriometopus* TASCHENBERG, 1882

Bothriometopus TASCHENBERG, 1882: 188. Type species: *Lipeurus macrocnemis* BURMEISTER, 1838. – Attributed by TASCHENBERG to NITZSCH (in GIEBEL), 1874. The name »*Lipeurus macrocnemis*« dates from a manuscript written by C. L. NITZSCH. BURMEISTER (1838) has made these and many broader manuscript names of NITZSCH nomenclaturical available and must be regarded as author of the same after the code.)
Bothriometopus TASCHENBERG, 1882, HOPKINS & CLAY, 1952: 52.
Bothriometopus TASCHENBERG, 1882, CICCHINO & CASTRO 1998: 108
Bothriometopus TASCHENBERG, 1882, PRICE et al. 2003: 15, 152, fig. 122.

This genus comprises two species, which are easily recognized by the following combination of characters:

1) the forwardly directed and unique shaped projections of the forehead flanking the osculum (figs. 1 a, 1 b, 2 a–c, 3 a–c);

2) marginal carina interrupted by osculum from nymph II to adults (figs. 1 a, 1 b, 8 b, 8 c), and by an hyaline area in N I (fig. 8 a);

3) ventral carina is interrupted medially and extends anteriorly to fuse with the marginal carina at the base of the osculum;

4) anterior dorsal seta (ads) replicated 4–10 times in male, not in female and nymphs;

5) head length and width subequal in nymphs and adults;

6) coni well-developed and pigmented but short and almost rectangular in nymphs and adults, arising from the anterior margin of the antennal socket and slightly directed outwards and reaching the anterior margin of the antenna;
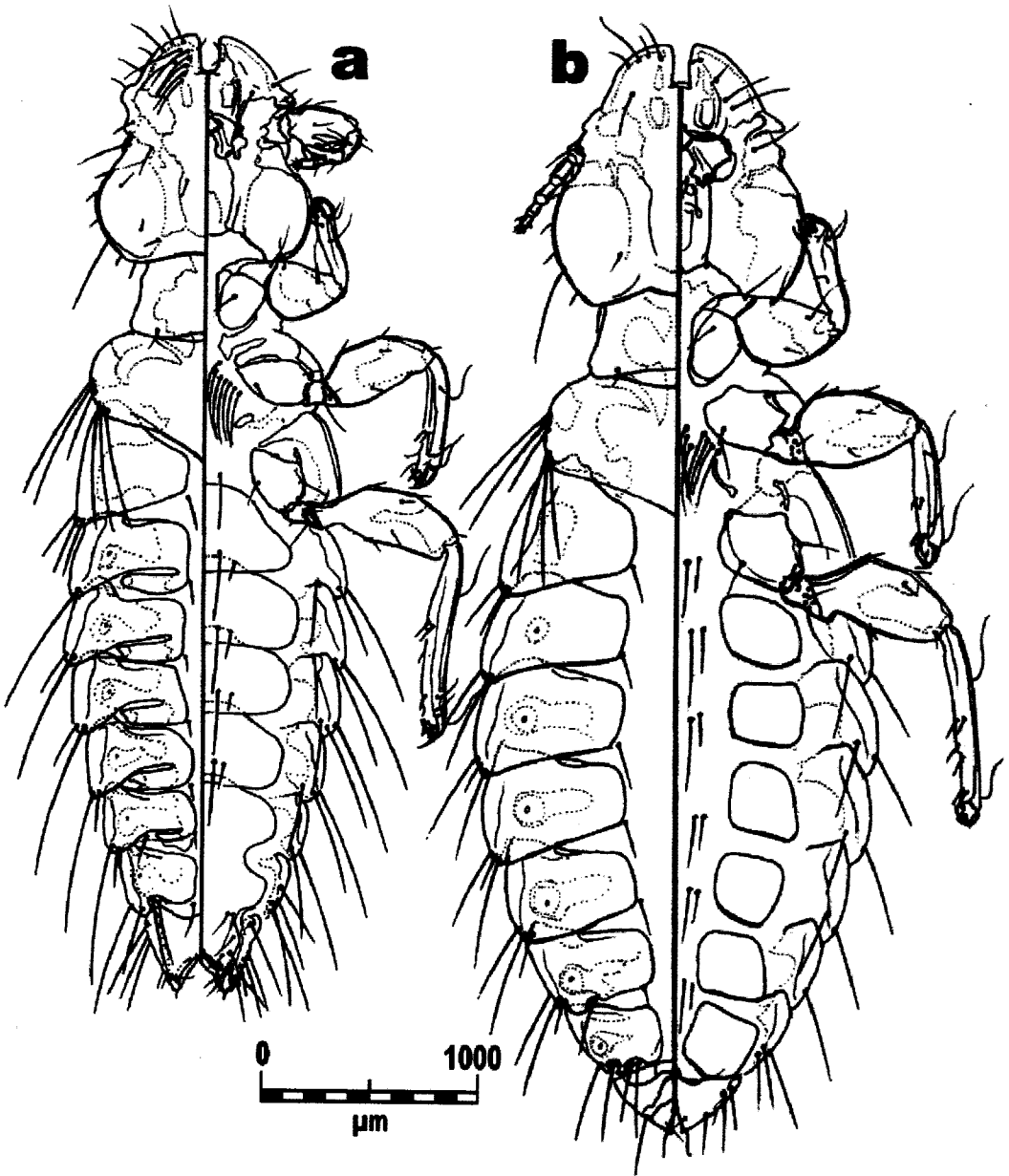
Fig. 1. *Bothriometopus macrocnemis* (BURMEISTER, 1838) ex *Anhima cornuta* (= type host), **a** male, **b** female, dorsal-ventral views.

7) antennae strongly dimorphic, bearing a significantly developed process on anterior lateral margin of the male scape (fig. 4 a);

8) pterothorax (mesometathorax) with three pairs of long setae slightly behind middle on lateral margin and three long pairs of long setae near posterolateral angle (pattern 3 + 3);

9) unique male genitalia, comprising a tapered and posteriorly rounded basal plate lacking discrete paramera and mesosomal complex, with a well-developed and variously spiculated genital sac bearing a pair of parabasal and a medium unpaired pigmented sclerites, which do not fit with phallosome typologies studied by YOSHIZAWA & JOHNSON (2006) (figs. 4 g, 5 a–f);
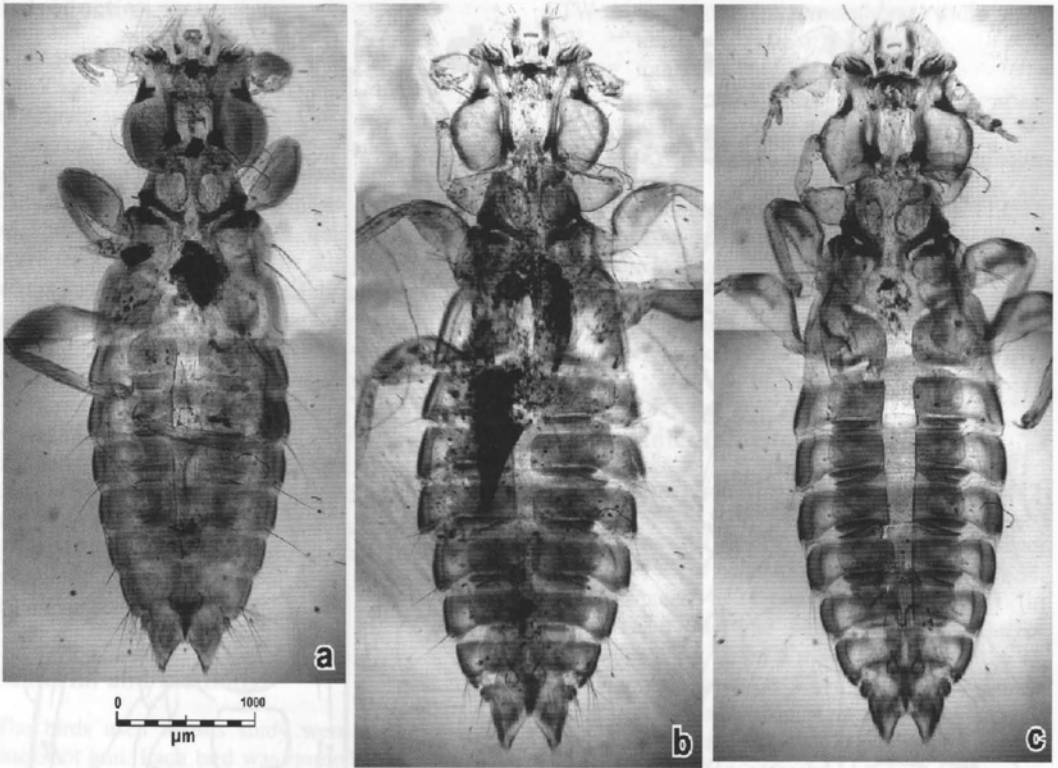
Fig. 2. *Bothriometopus* spp., ♂; **a** *B. macrocnemis* (BURMEISTER) ex *Anhima cornuta*, **b** *B. simillimus* (GIEBEL) ex *Chauna chavaria* (= type host), **c** *B. simillimus* ex *Chauna torquata* from Argentina. – Photos: A. C. CICCHINO.

10) female vulva simple, slightly bilobed, with two irregular rows of sensillae and very small and short setae (fig. 4 f),

11) apex of abdomen deeply bilobed in nymphs and adults.

12) posterior margin of femur III noticeably notched near base in both sexes (figs. 4 b, 4 c), not in nymphs;

13) development of abdominal tergites and paratergites from nymphs to adults fit well MEY's (1994) Gruppe III b;

14) abdominal tergites ii-viii divided medially and typically pigmented in both sexes (figs. 1 a, 1 b, 2 a–c, 3 a–c);

15) abdominal sternites iii-vi entire in males, vii-x integrated in a laterally notched subgenital plate (figs. 1 a, 4 d–e), and sternites iii–viii medially divided in females, vii–viii not forming a discrete subgenital plate (fig. 1 b);

16) sutural seta present in abdominal segments vii–viii in adults and nymphs, being minute in N II and N III;

17) very large size, adults ranging from 4,40 to 5,77 mm, being both sexes very variable in size, even within the same individual host population;

18) tibia III much longer than tibia II in both sexes and N III (less so in N I and N II);

19) eggs flattened, cemented obliquely on the dorsal face of the feather (figs. 10 a–b).

Relationships: Only two other genera show some morphological affinities with *Bothriometopus* in adults and preimaginal instars, *Ornithobius* DENNY and *Acidoproctus* PIAGET both parasitic on members of the Anatidae, differing in a number of characters as shows in Table 1. These affinities have been pointed out by a number of authors (CLAY 1975, TIMMERMANN 1962, EICHLER 1941, 1963, SMITH 2001). These genera share, from N II to adults, a derived state of the forehead by a modification of the ancestral status of circumfasciate forehead consisting in a deep indentation (osculum) in the anterior margin of the head, which interrupts the marginal carina
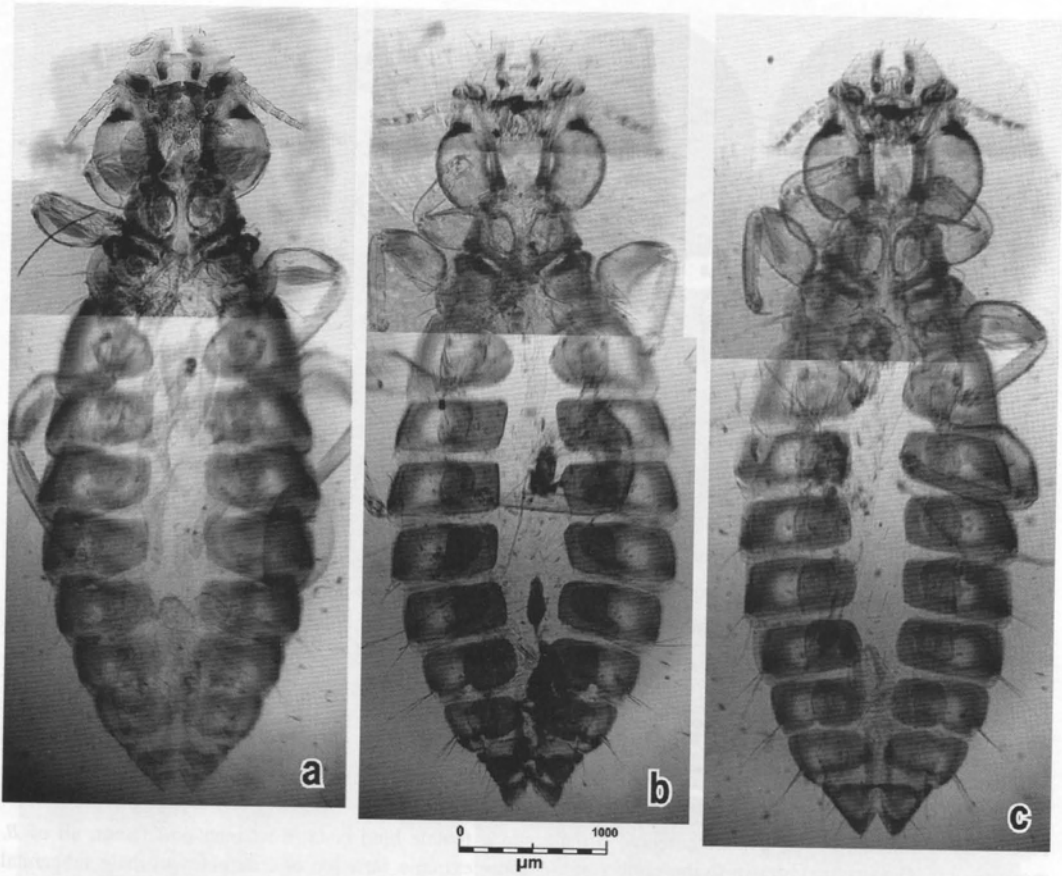
Fig. 3. *Bothriometopus* spp., ♀; **a** *B. macrocnemis* (Burmeister) ex *Anhima cornuta* (= type host), **b** *B. simillimus* (Giebel) ex *Chauna chavaria* (= type host), **c** *B. simillimus* ex *Chauna torquata* from Argentina.

medially, forcing the preantennal portion of the head largely to take on characteristics common to non-circumfasciate taxa (Smith 2001). In these instars, the marginal carina and its associated set of setae (see Clay 1951) are conserved in the so generated paired productions of the forehead. Development of the osculum is easily traceable along the two last nymphal instars of species of these genera. In all them the center of the forehead remains emarginated and bears a sclerotized plate, large and convex in *Ornithobius* and less developed and almost straight in *Acidoproctus* and *Bothriometopus*. In N I dorsal marginal carina encloses most of the forehead, being interrupted in the middle by a subtriangular hyaline area. Paired frontal projections, osculum and the central sclerotized plate begin to be insinuated in the transit to formation of pharate of N II. Whether the central sclerotized plate is or is not a derivative of the central portion of the marginal carina it is

not clear with the available specimens., needing further study. By this, the probable primary circumfasciate condition sustained by Smith (2001) for *Acidoproctus* – extensive to *Ornithobius* and *Bothriometopus* by presumed monophyly – cannot be solved, deserving further studies.

The unusual morphology of these three genera makes their classification difficult. Timmermann (1962) highlighted the close association of *Acidoproctus* and *Ornithobius*, and the classification presented in Clay's unpublished key (1975) supports this. The latter author placed these genera with *Heteroproctus* Harrison (probably no more than a subgenus of *Acidoproctus*, see Hopkins & Clay, 1952: 172), and *Bothriometopus*. Eichler's classification precludes also close relationships, including *Acidoproctus* and *Ornithobius* in the subfamily Acidoproctinae and *Bothriometopus* in the subfamily Bothriometopinae all as part of the Acidoproctidae (Eichler 1941, 1963).
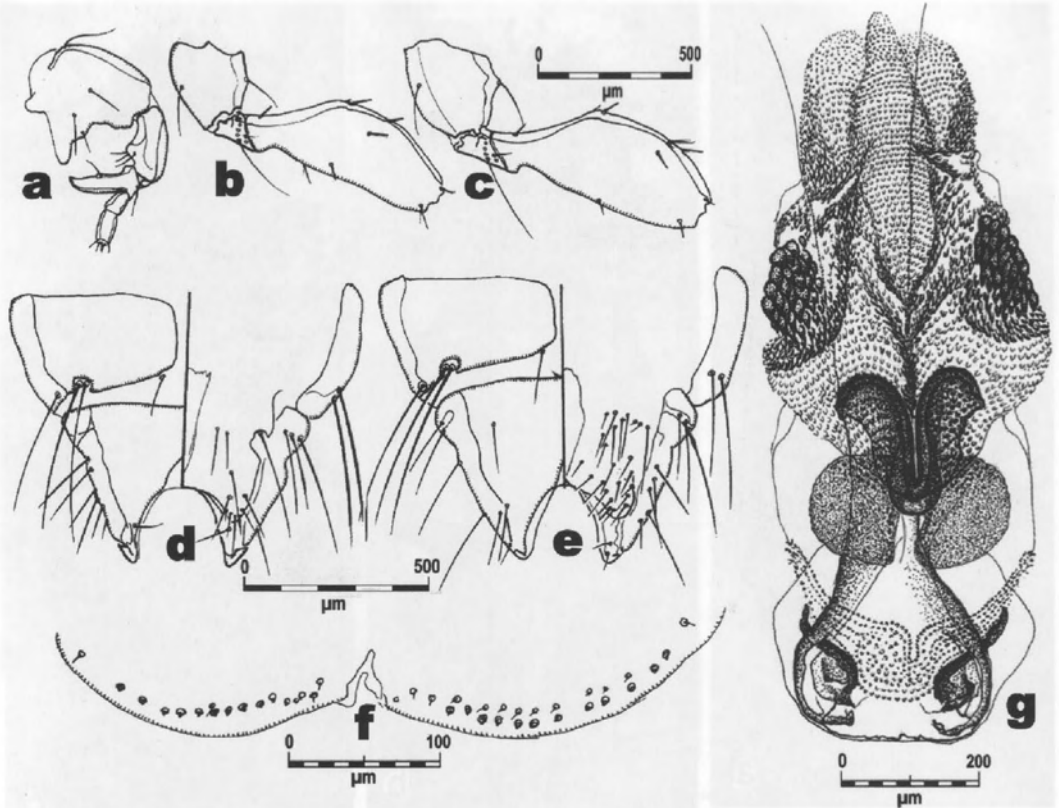
Fig. 4. *Bothriometopus* spp.; **a** male antenna, **b** male and **c** female hind coxa, trochanter and femur, all of *B. macrocnemis* (BURMEISTER), drawn to the same scale, **d** and **e** extreme variation of chaetotaxy of male subgenital plates (**d** *B. macrocnemis* ex *Anhima cornuta*, **e** *B. simillimus* ex *Chauna chavaria*), **f** vulva of *B. macrocnemis*, **g** male genitalia of *B. simillimus* (GIEBEL) ex *Chauna torquata*.

SMITH (2001) made a preliminary examination of the morphology of the vulval margin and preantennal region of specimens of *Acidoproctus* and *Ornithobius*, suggesting also that they are closely related. However, their position within the ischnoceran phylogeny built up by SMITH (2001) remains uncertain because of their association with *Saemundssonia*- and *Philopterus*-complex is absolutely unexpected, particularly as these two genera groups lacks many of the gross morphological characteristics shared with most members of this clade. This suggests that too much remains to be done to clarify their position within the ischnoceran clade. Apart of the mode of solution of this, a situation is clear: *Bothriometopus* possess two unique apomorphic characters (restricted to males), consisting in a replication (4–10 times) of the anterior dorsal seta (ads) (fig. 1 a) and the structure of the genitalia (figs. 4 g, 5 a–f), not present in any other known

ischnoceran genus parasitic on Galliformes and Anseriformes.

Feeding: A female and nymphs I, II and III of. *B. macrocnemis* off *Anhima cornuta* from Bolivia showed a large amount of articles of legs of feather mites (Acari: Analgoidea), together with fragments of egg shells of these mites in their crop and digestive tracts. Other nymphs I to III of the same collection as well as other N I and N III of *B. simillimus* off *Chauna torquata* from Argentina contains mite remains and rests of feather barbules in the crop. Philopterids have a diet consisting of fragments of the feathers (barbs and barbules) (ROTHSCHILD & CLAY 1952, JOHNSON & CLAYTON 2003). It is interesting to note that WATERSTON (1926) did not report mite fragments when studying the alimentary content of chewing lice, although this phenomenon has been observed later repeatedly by several
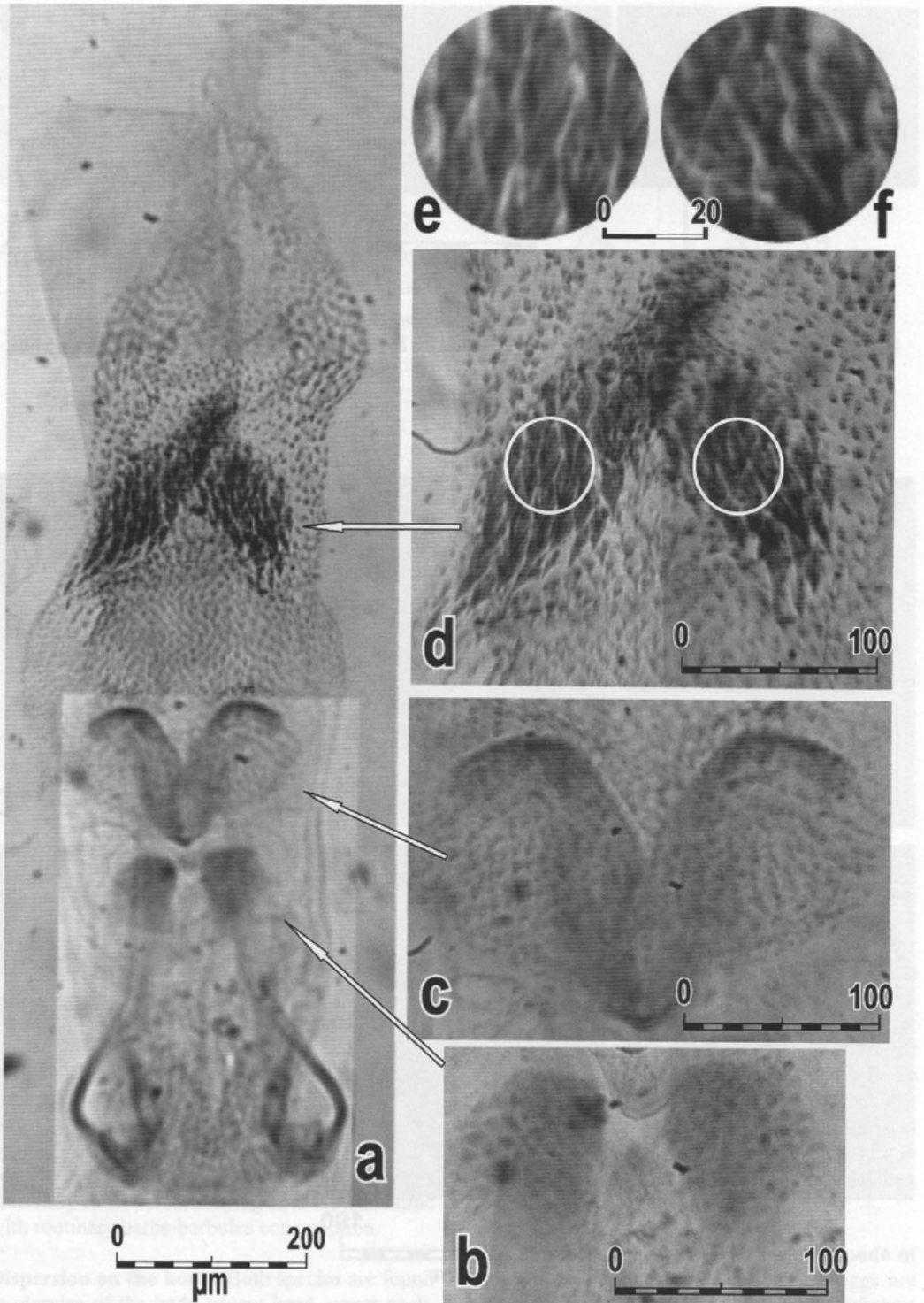
Fig. 5. *Bothriometopus macrocnemis* (BURMEISTER) from Brazil, male genitalia; **a** whole genitalia, **b** paired sclerites, **c** unpaired sclerite, **b** patches of pigmented scales, **e–f** details of the latter.
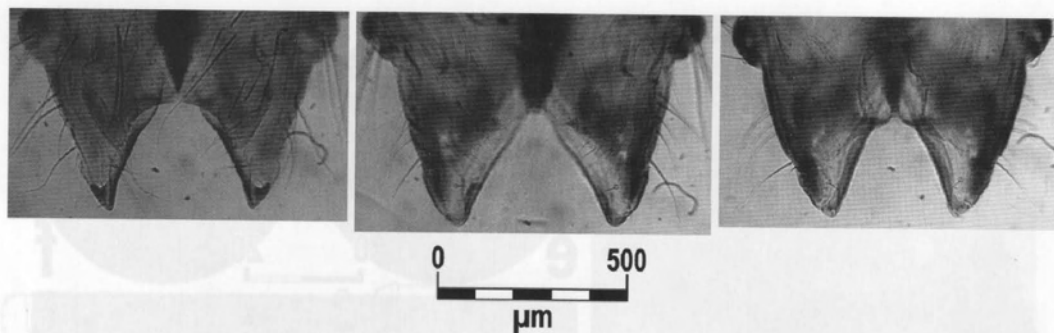
Fig. 6. *Bothriometopus* spp., terminalia, ♂; **a** *B. macrocnemis* (BURMEISTER) ex *Anhima cornuta* (= type host), **b** *B. simillimus* (GIEBEL) ex *Chauna chavaria* (= type host), **c** *B. simillimus* ex *Chauna torquata* from Argentina.
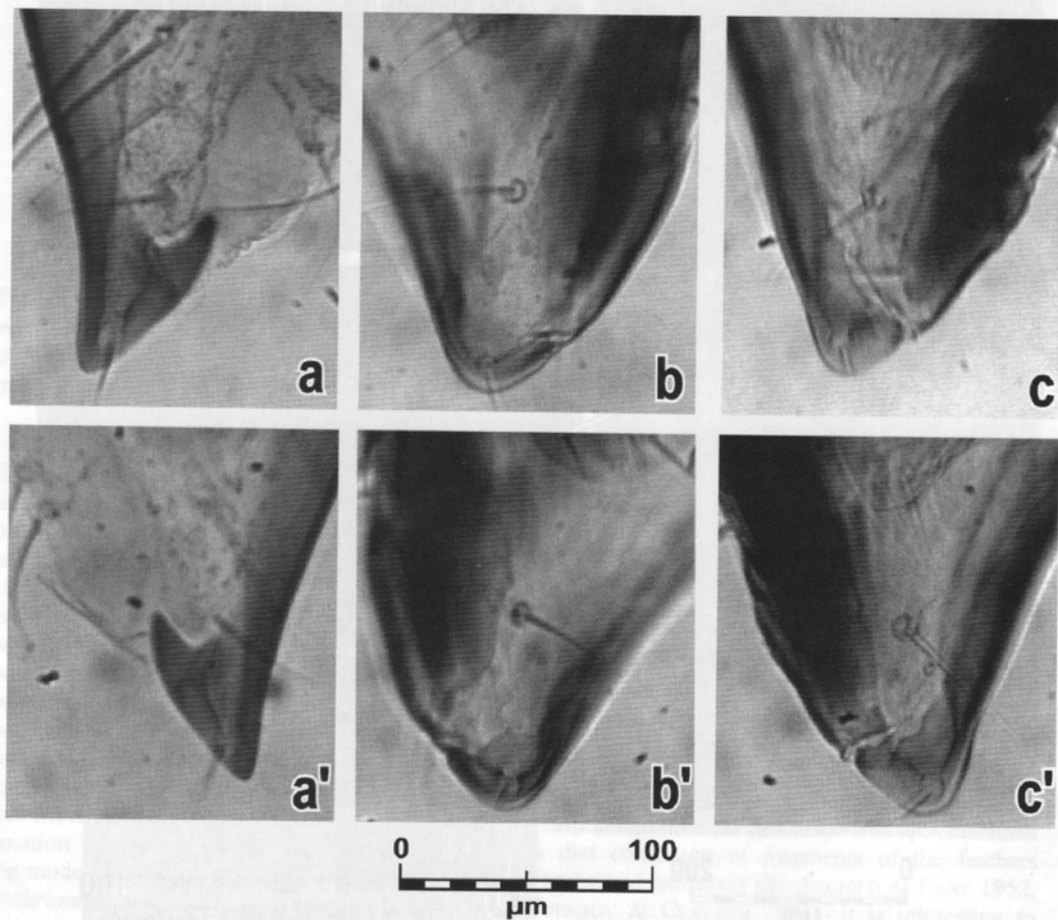

Fig. 7. *Bothriometopus* spp., ♂, apices of the last abdominal segment; **a** *B. macrocnemis* (BURMEISTER) ex *Anhima cornuta* (= type host), **b** *B. simillimus* (GIEBEL) ex *Chauna chavaria* (= type host), **c** *B. simillimus* ex *Chauna torquata* from Argentina.
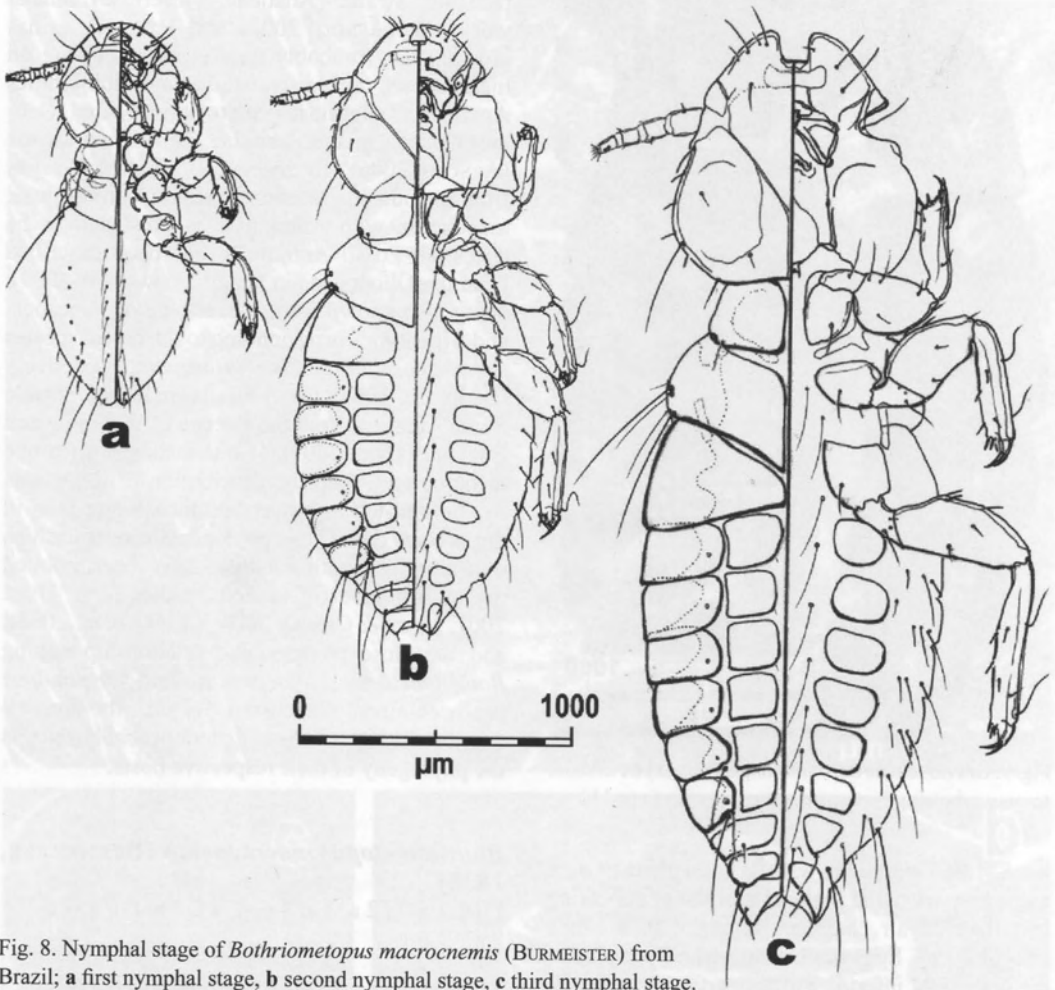
Fig. 8. Nymphal stage of *Bothriometopus macrocnemis* (BURMEISTER) from
Brazil; **a** first nymphal stage, **b** second nymphal stage, **c** third nymphal stage.

authors (e. g. ROTHSCHILD & CLAY 1952, ONIKI &
BUTLER 1989, MEY 1990). Recently VALIM (2006)
observed that a *Tyranniphilopterus* species did not
contain fragments of barbules inside the crop but
articles or fragments of feather mites eggs, legs
and other body remains, concluding that they may
be accidentally ingested. Our findings strongly
suggest that fragments of exuviae are either
accidentally ingested during the feeding process
or usually eaten before starting or at the same time
with routinary barbs-barbules consumption.

Dispersion on the hosts: Both species are found
in pterylae of the body except head, upper neck,
lower abdomen and remiges. Although they
wander predominantly in the chest, patagium
and axillary's feathers. We observed than when

disturbed, they move faster than other ischnoceran
lice sliding sideways between feathers, facilitated
by the structure and length of the last two pair of
legs. This strategy seems to represent an advantage
in avoiding the host's preening. The presence
of osculum since nymph II to adults clearly
represents and advantage in helping to channel
and accommodate the feather barbs/barbules into
the mouth (KÉLER 1938, SMITH 2001) for feeding
of resting.

**Characters of the eggs and sites and mode of
oviposition:** General characters of the eggs are
shown in a comparative form with *Ornithobius*
and *Acidoproctus* in Table 1. Eggs are flattened –
being this condition visible even by transparence
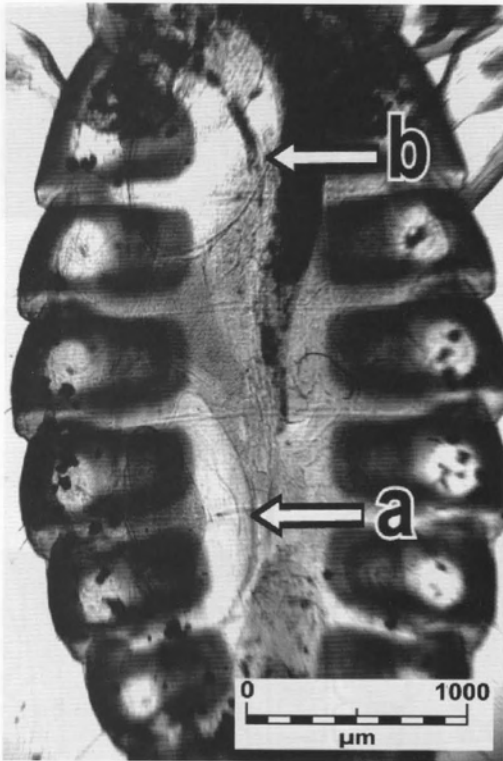in gravid females, fig. 9 – short (ratio length/width

Fig. 9. Gravid female of *B. simillimus* (GIEBEL) ex *Chauna torquata* showing by transparence two eggs (**a** and **b**).

~ 1.8–1.9). Operculum with its basal plane in right angle respect to the main axis of the egg, bearing less than 25 air chambers arranged in a single irregular row. Eggs are laid in ventral pterylae of the patagium, inferior wing coverts and axillary's portion of the pectoral pterylae, involving contour as well as down feathers (figs. 10 a–b). In all three examined bird specimens eggs, one per feather, are glued to the dorsal face of the feather, in angle of 33–45 ° respect of the feather shaft. Spumaline covers more than 2/3 of the exposed surface of the egg (fig. 11 a).

Prevalence: 100 %, for both species. *B. macrocnemis* was present in the three individuals examined, two from Brazil and one from Bolivia. *B. simillimus* was found on the five individuals examined, all from Argentina.

Distribution: *Bothriometopus* is an exclusive South American genus with two species, occurring on the three species of Screamers (Anhimidae), whose complexive distribution ranges from NW Colombia south to central and E Argentina and Brazil (fig. 13). *Ornithobius* comprises eight species

parasitic Swans (Anatidae, Anserinae) almost worldwide (ARNOLD 2005), and *Acidoproctus* has nine species (probably only eight) occurring on members of the Anseranatidae and subfamilies Anatinae, Tadorninae, Stictonettinae, and Dendrocygninae in the Anatidae, almost worldwide (ARNOLD 2006). In absence of *Bothriometopus* from any other member of the extant Anseriformes, association with Anhimidae is presumed to be ancestral. Fossil Anhimidae has been described from the Oliogocene in Brazil (ALVARENGA 1999), being also known from Pleistocene of Venezuela and Argentina, corresponding to the recent species *Anhima cornuta* and *Chauna torquata*, respectively (BRODKORB 1964). Older fossils are known outside South America, from the Eocene of Wyoming and England (DYKE 2001). If our assumptions prove to be correct, then the distribution of this genus by the mid-tertiary must be much larger than in the present day. Close phylogenetic relationships of Anhimidae with Anatidae have been pointed out by a number of modern studies (*e. g.* DYKE 2001, MAYR & CLARKE 2003; CLARKE *et al.* 2005), and the close phylogenetic relationship among *Bothriometopus*, *Acidoproctus* and *Ornithobius* has been already discussed. By this, the present-day distribution of these genera probably reflects the phylogeny of their respective hosts.

Bothriometopus macrocnemis (BURMEISTER, 1838)

Figs. 1 a–b, 2 a, 3 a, 4 a–d, 4 f, 5 a–f, 6 a, 7 a, 7 a', 8 a–c

Lipeurus macrocnemis BURMEISTER 1838: 433.
Lipeurus macrocnemius N.[ITZSCH], GIEBEL 1866: 382. »*macrocnemius*« is a misspelling by GIEBEL. See above.
Lipeurus macrocnemius NITZSCH 1866, GIEBEL 1874: 231
Lipeurus macrocnemis N.[ITZSCH in GIEBEL 1874], PIAGET 1880: 376
Bothriometopus macrocnemis (N.[ITZSCH) in GIEBEL 1874], TASCHENBERG 1882: 188–191, plate VI, figs. 11, 11a, 11b.
Bothriometopus macrocnemis (BURMEISTER, 1838), HOPKINS & CLAY 1952: 52.
Bothriometopus macrocnemis (BURMEISTER, 1838), Price *et al.* 2003: 152.

Type host: Horned Screamer *Anhima cornuta* (LINNAEUS, 1766). It has a wide geographical range, from the Orinoco basin south to central Colombia, center and W of Ecuador, W Peru, N Bolivia and Paraguay to E Brazil (fig. 13) (SICK 1993). **Other hosts**: PRICE *et al.* (2003) mention
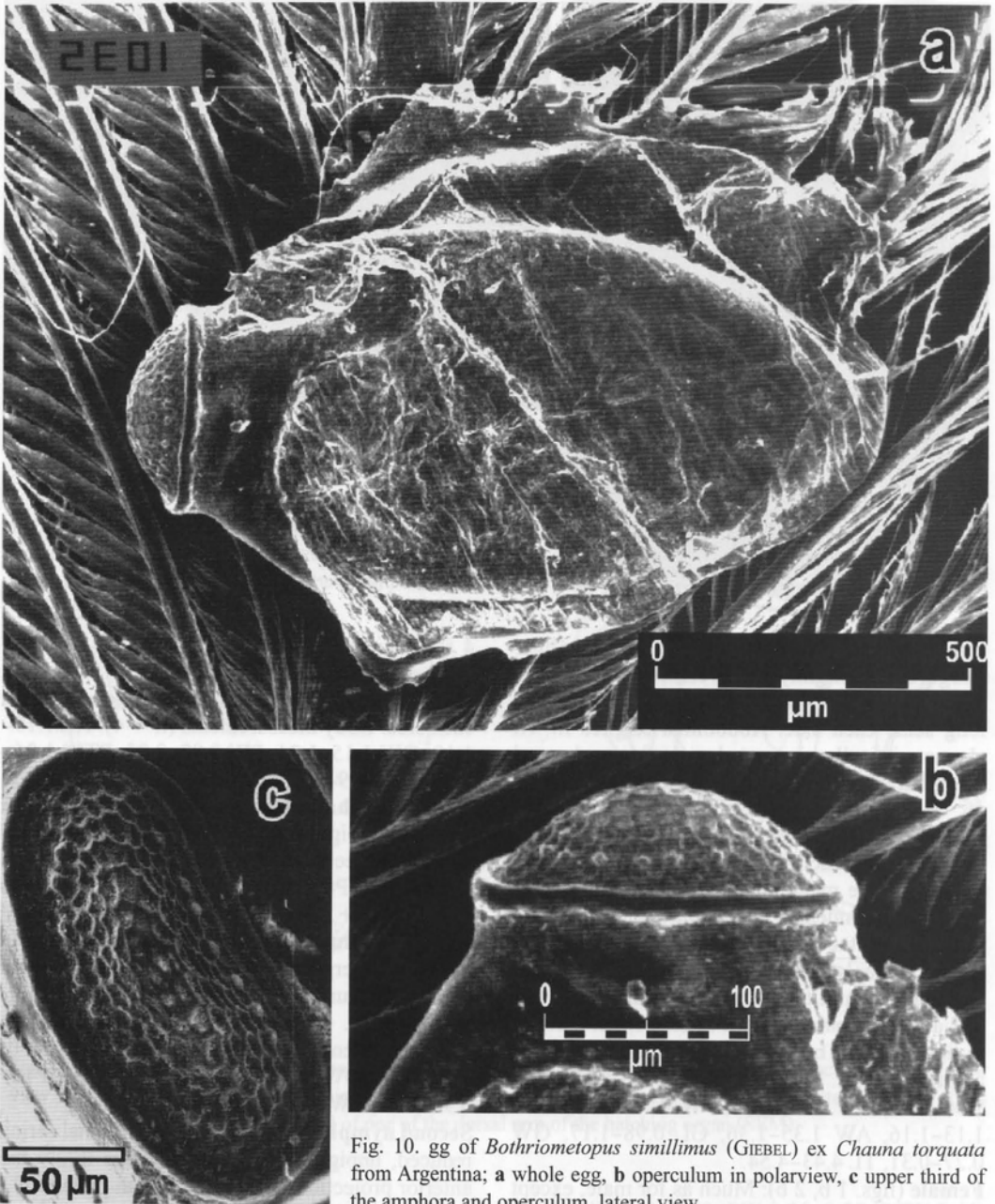
Fig. 10. gg of *Bothriometopus simillimus* (GIEBEL) ex *Chauna torquata* from Argentina; **a** whole egg, **b** operculum in polarview, **c** upper third of the amphora and operculum, lateral view.

Chauna chavaria – the type host of *B. simillimus* – and *C. torquata* as hosts for this species, but taking in mind the close morphological affinities of *B. macrocnemis* with *B. simillimus* this records (without reference) must be taken as provisional. Although, these records may be reliable because *A. cornuta* is partially sympatric with *C. chavaria* in E Colombia and W Venezuela and with *C.*

torquata (the other host for *B. simillimus*) in the center of Brazil, N Paraguay and Bolivia and SW Peru (see fig. 13), so local colonization within these areas between these hosts may occur.

Descriptions – male (fig. 1a, 2a): Marginal carina reduced, almost unpigmented but continuous throw the anterior projections. Pterothorax (me-
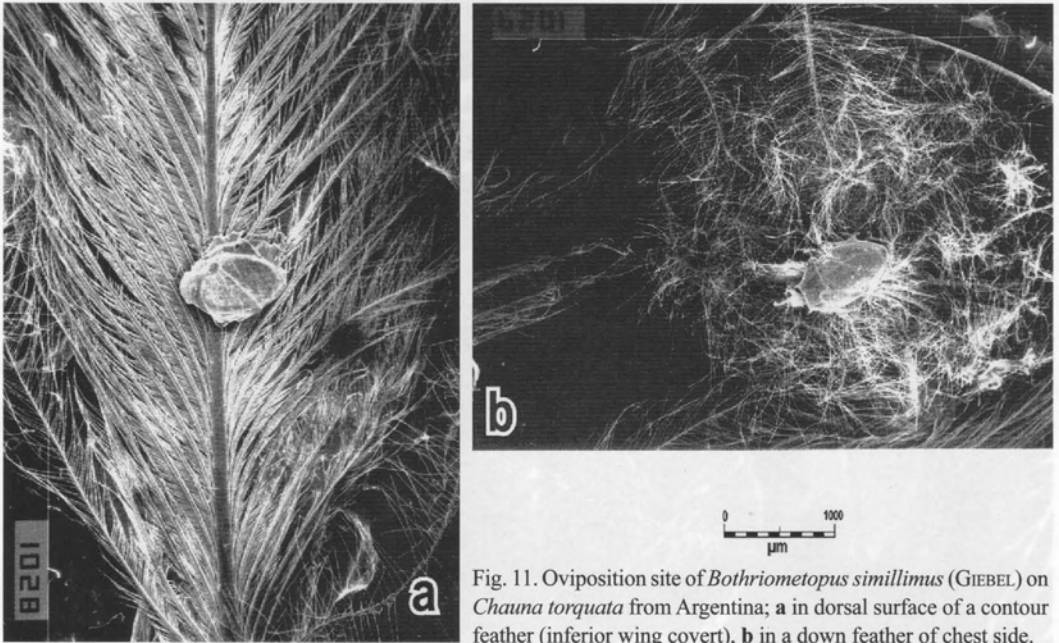
Fig. 11. Oviposition site of *Bothriometopus simillimus* (GIEBEL) on *Chauna torquata* from Argentina; **a** in dorsal surface of a contour feather (inferior wing covert), **b** in a down feather of chest side.

sometathorax) with pattern of 3 + 3 setae. Outer margin of tibia slightly concave. Mesometasternum with no definite plate, bearing 7–8 medium long setae each side. Abdominal tergites iii–vii characteristically pigmented, as in figures 1 a and 2 a. Abdominal chaetotaxy – postspiracular setae on vi–viii, sutural setae short to medium long present on ii–viii; paratergal setae: ii–iii 3, iv–viii 4; sternal setae each side: ii 1–2, iii–vi 2, being the outermost one much shorter. Discrete, elongated and laterally indented subgenital plate, bearing a number of setae arranged as in figure 4 d. Last segment deeply forked, with a subterminal spur-like outgrowth of the external margin (figs. 6 a, 7 a, 7 a'). Chaetotaxy pattern of subgenital plate as in figures 4 d-e, but some individuals show some additional setae. Body measurements (n = 7): HL 1.06–1.07, OW 1.07–1.19, PW 0.74–0.75, PTW 1.13–1.16, AW 1.35–1.36, GL 0.98–1.17, GW 0.27–0.31, TL 4.43–4.54.
Female (figs. 1 b, 2 b): Much as for male, except in dimensions, usual sexual dimorphism, tergal plates differently pigmented, relative lengths of setae in some abdominal segments (figs. 1 b, 3 a) and sternites iii–vi widely divided in the middle, being vii–viii also divided and not forming a subgenital plate. Outer margin of tibia III from slightly convex to slightly concave. Sutural short to medium long setae present on abdominal segments ii–viii. Sternal setae each side: ii–vii 2, being the outermost one much shorter. Vulva (fig.

4 f) with a superior irregular row of 4–10 small setae each side, and an inferior one of 11–13 short sensillae each side, both flanked by a short seta each side. Body measurements (n = 4): HL 1.15–1.19, OW 1.15–1.24, PW 0.82–0.85, PTW 1.26–1.34, AW 1.59–2.07, TL 4.89–5.27.
Third nymphal instar (fig. 8 c): Marginal carina reduced, unpigmented but continuous throw the anterior projections, which are more swollen than those of N II. Pterothorax with pattern of 2 + 3 (less frequently 2 + 2) setae. Abdomen with sclerotized and well-pigmented paratergal plates present in ii–viii. Paratergal setae: ii 0, iii 3, iv 3–4, v–viii 3. Minute sutural setae present on abdominal segments ii–viii. One sternal medium long seta on sternal segments ii–viii. Body measurements: HL 0.85–0.90, OW 0.87–0.91, PW 0.61–0.64, PTW 0.91–0.94, AW 1.08–1.20, TL 3.10–3.33.
Second nymphal instar (fig. 8 b): Marginal carina reduced, unpigmented but continuous throw the anterior projections. Pterothorax with pattern of 1 + 3 (less frequently 1 + 2) setae. Abdomen with sclerotized and well-pigmented paratergal plates present in ii–viii. Paratergal setae: ii 0, iii–v 1, vi–viii 2. Minute sutural setae present of ii–viii. Body measurements (n = 8): HL 0.64–0.65, OW 0,63–0.66, PW 0.44–0.45, PTW 0.64–0.67, AW 0.81–0.93, TL 1.82–2.31.
First nymphal instar (fig. 8 a): Dorsal marginal carina encloses most of the forehead, being interrupted in the middle by an subtriangular
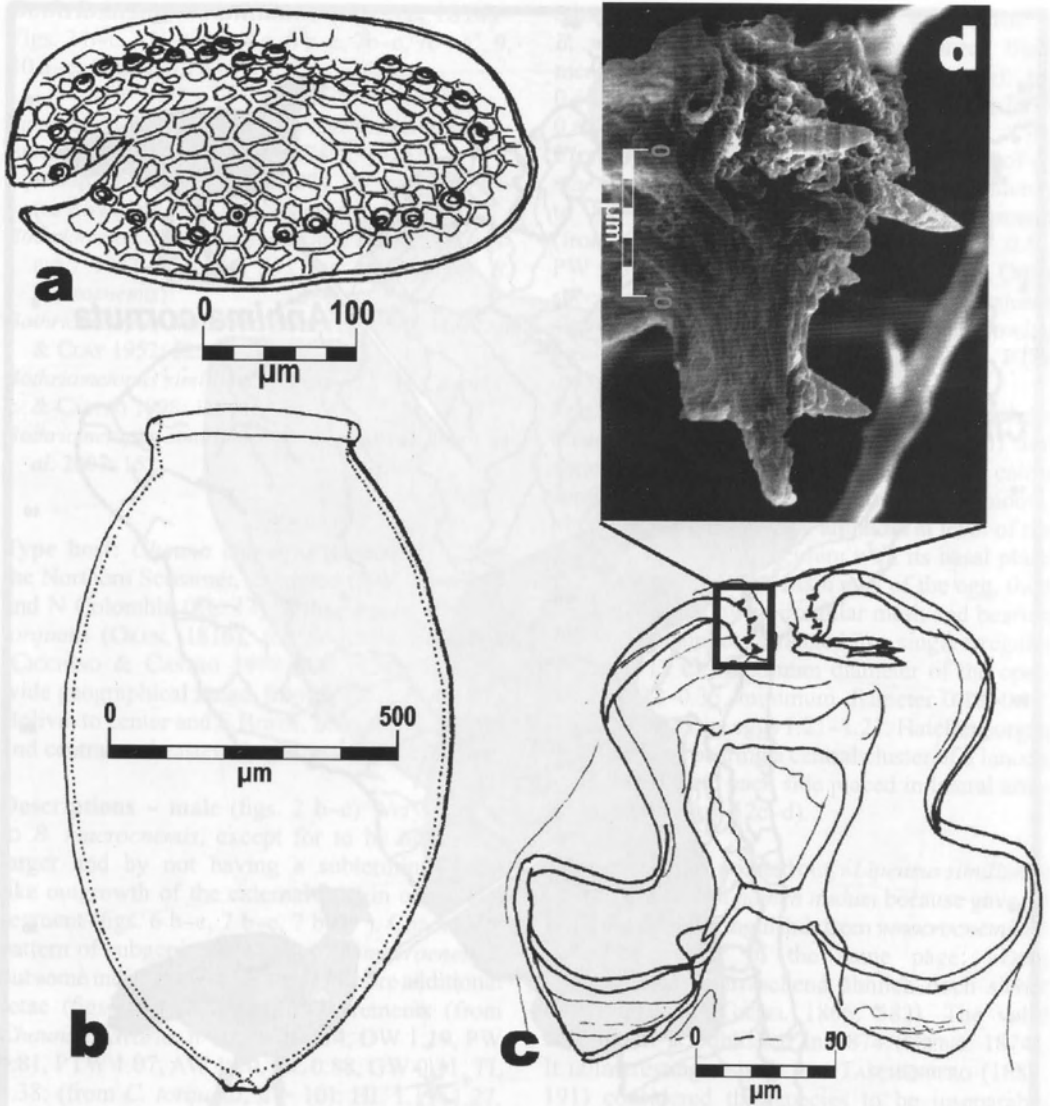
Fig. 12. Egg of *Bothriometopus simillimus* (GIEBEL) ex *Chauna torquata* from Argentina: **a** operculum in semipolar view showing arrangement of the 24 air chambers, **b** outline of the amphora in lateral view, **c** hatching organ of the embryo, **d** detail of one of the dorsal arm of the hatching organ (SEM).

hyaline area. Paired frontal projections, osculum and the central sclerotized plate begin to be delimited. As for most Ischnocera, the pterothorax bears only one very long posterior seta each side, and the abdomen lacks sclerotized paratergal plates (MEY 1994). Abdominal dorsal segments ii–vii with one medium long sutural seta each side, ventral segments ii–viii with one medium long sutural seta each side. Paratergal setae: ii 0, iii–viii 1. Body measurements (n = 3): HL 0.49–

0.50, OW 0.51–0,52, PW 0,36–0-38, PTW 0.46–0.50, AW 0.56–0.59, TL 1.58–1,65.

Egg: Flattened, similar to that of *B. simillimus* (see fig.12), as revealed by field observations, but eggs not conserved for a more detailed study.

Specimens examined (all from the type host): 1 ♀, 3 N I, 8 N II and 3 N III, Santa Cruz de la Sierra, Bolivia, 20-I-1920, leg. A. STEINBACH; 7 ♂ and 4 ♀, Río Pacaraí, Paraná, Brazil, 18-I-1954, leg. DENTE & SERAGLIA.
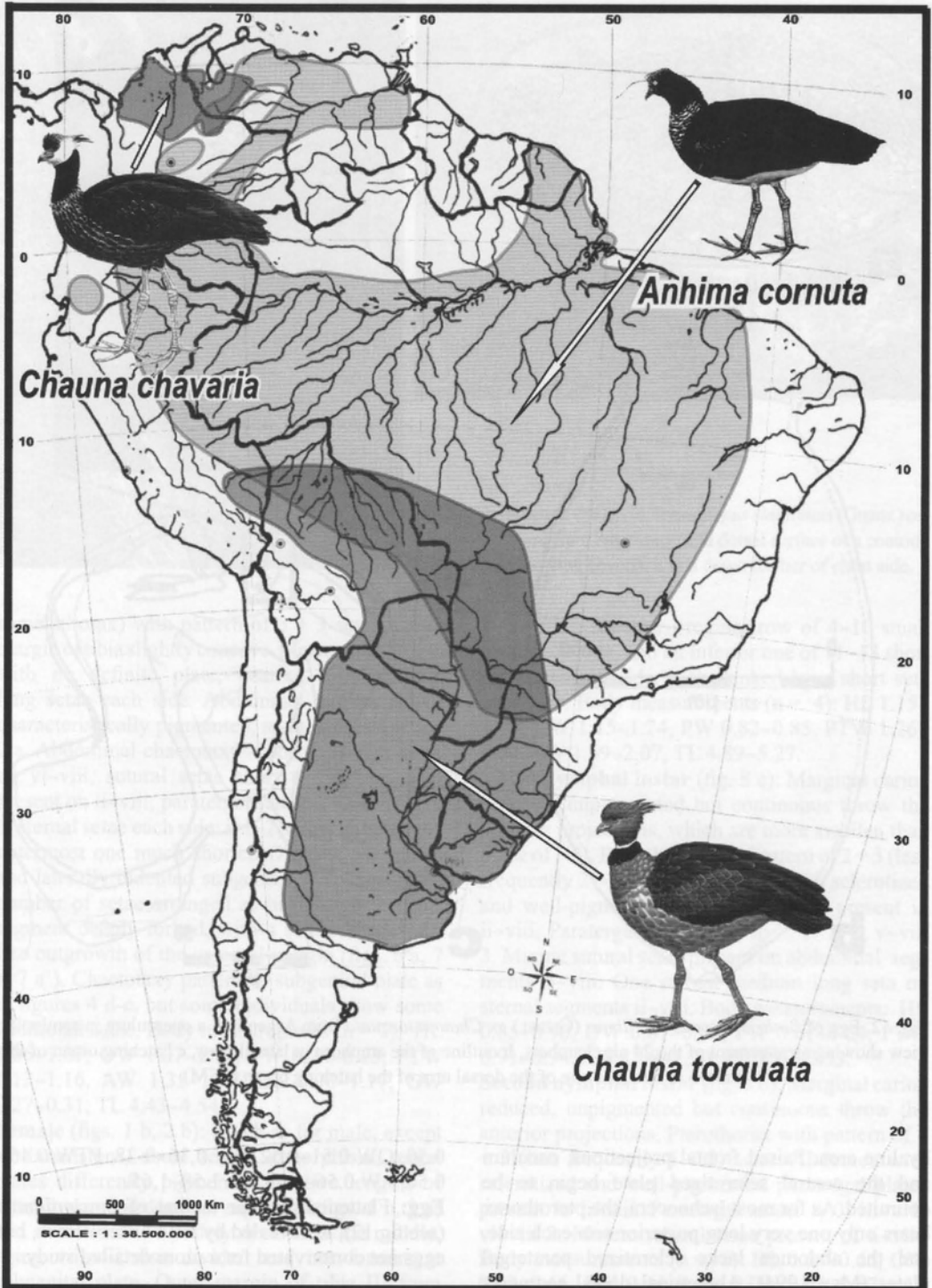
Fig. 13. Approximate geographical range of the three species of Screamers (Anhimidae), compiled from various sources.

Bothriometopus simillimus (GIEBEL, 1874)
Figs. 2 b–c, 3 b–c, 4 e, 4 g, 6 b–c, 7b–c, 7b'–c', 9,
10 a–c, 11 a–c, 12 a–d

Lipeurus simillimus GIEBEL, 1866:382 (*nomen nudum*)
Lipeurus simillimus GIEBEL, 1874: 231–232
Lipeurus simillimus GIEBEL, 1874, PIAGET 1880: 376
(as a »variety« of *L. macrocnemis*)
Bothriometopus simillimus (GIEBEL, 1874), TASCHEN-
BERG 1882: 188 and 191 (as synonym of *B.*
macrocnemis)
Bothriometopus simillimus (GIEBEL, 1874), HOPKINS
& CLAY 1952: 52.
Bothriometopus simillimus (GIEBEL, 1874). CICCHINO
& CASTRO 1998: 118, 124.
Bothriometopus simillimus (GIEBEL, 1874). PRICE *et*
al. 2003: 152.

Type host: *Chauna chavaria* (LINNAEUS, 1766),
the Northern Screamer, restricted to W Venezuela
and N Colombia (fig. 13). **Other hosts:** *Chauna*
torquata (OKEN, 1816), the Southern Screamer
(CICCHINO & CASTRO 1998: 118, 124). It has a
wide geographical range, from SW Peru, N and E
Bolivia to center and E Brazil, Paraguay, Uruguay
and central and eastern Argentina (fig. 13).

Descriptions – male (figs. 2 b–c): Very similar
to *B. macrocnemis*, except for to be noticeably
larger and by not having a subterminal spur-
like outgrowth of the external margin of the last
segment (figs. 6 b–c, 7 b–c, 7 b'–c'). Chaetotaxy
pattern of subgenital plate as in *B. macrocnemis*,
but some individuals show some to more additional
setae (figs. 4 d–e). Body measurements (from
Chauna chavaria, n = 1): HL 1.14, OW 1.19, PW
0.81, PTW 1.07, AW 1.70, GL 0.88, GW 0.31, TL
5.38; (from *C. torquata*, n = 10): HL 1.19–1.27,
OW 1.21–1.31, PW 0.83–0.95, PTW 1.24–1.38,
AW 1.68–1.76, GL 1.13–1.21, GW 0.31–0.33, TL
5.24–5.56.

Female (figs. 3 b–c): Very similar to *B. macro-*
cnemis, except for larger dimensions. Body
measurements (from *Chauna chavaria*, n = 1): HL
1.23, OW 1.24, PW 0.88, PTW 1.32, AW 2.10, TL
5.51; (from *C. torquata,* n = 15): HL 1.12–1.26,
OW 1.17–1.33, PW 0.79–0.95, PTW 1.27–1.40,
AW 1.60–2.02, TL 4.76–5.77.
Third nymphal instar: Much as for that of *B.*
macrocnemis, except for tendency to be somewhat
larger. Body measurements (from *C. torquata,* n =
9): HL 0.90–1.07, OW 0.92–1.02, PW 0.61–0.74,
PTW 0.95–1.05, AW 1.15–1.49, TL 3.33–4.13.

Second nymphal instar: Much as for that of
B. macrocnemis, being somewhat larger. Body
measurements (from *C. torquata,* (n = 6): HL
0.69–0.75, OW 0,70–0.74, PW 0.48–0.52, PTW
0.68–0.75, AW 0.81–1.00, TL 2.42–2.71.
First nymphal instar: Much as for that of *B.*
macrocnemis, except for a very slight tendency
to be somewhat larger. Body measurements
(from *C. torquata,* n = 1): HL 0.50, OW 0.51,
PW 0.38, PTW 0.50, AW 0.62, TL 1.64. Other
specimen beginning molting process, containing
almost mature pharate of N II, has the following
measurements: HL 0.52, OW 0.59, PW 0.48, PTW
0.63, AW 0.88, TL 2.04.
Egg (figs. 10 a–b, 11 a–c, 12 a–b): Amphora
broadly ellipsoid (1.16–1.19 x 0.69–0.70) and
noticeable constricted in proximity of the callus
conforming a short neck, being its surface smooth.
Maximum diameter of the amphora at level of the
callus 0.37–0.38. Operculum with its basal plane
in right angle with the main axis of the egg, their
surface covered by an irregular mesh and bearing
19–23 air chambers arranged in a single irregular
row (fig. 12 e). Maximum diameter of the oper-
culum 0.32–0.35, minimum diameter 0.18–0.19.
Total length of the eggs 1.21–1.27. Hatching organ
of the embryo bearing a central cluster of 3 lancets
and 4 small teeth each side placed in lateral arms
of the organ (figs. 12c–d).

Remarks: As we pointed out, »*Lipeurus simillimus*
GIEBEL, 1866« is a *nomen nudum* because gave no
differences to distinguish it from »*macrocnemius*«
described earlier in the same page: »Dem
vorigen zwar überraschend ähnlich doch sicher
unterschieden« (GIEBEL 1866: 382). The valid
description is published in 1874 (GIEBEL 1874).
It is interesting to note that TASCHENBERG (1882:
191) considered this species to be inseparable
from *B. macrocnemis*, and PIAGET (1880: 376)
judged it as a »variety« of the latter. Female
body measurements given by GIEBEL (1874: 231),
2'''~ 2,17 mm, and alleged differences in the
conformation of abdominal tergites suggest us
that specimens used are recently molted or too
immature individuals.

Specimens examined – Off *Chauna chavaria*: 1
♂ and 1 ♀, Narosi, Estado Bolívar, Colombia, 13–
III–1949, leg. M. A. CARRIKER, jun. Off *Chauna*
torquata: 6 ♂and 13 ♀, Partdo de General Lavalle,
Buenos Aires Province, Argentina, 15–IX–1975, leg.
A. C. CICCHINO; 4 ♂, 8 ♀, 2 N I, 6 N II , 9 N III
and 9 eggs, Partdo de General Lavalle, Buenos Aires
Province, Argentina, 6–I–1973, leg. A. C. CICCHINO.

Table 1. Adult and preadult morphological characteristics and egg-laying behaviour exhibited by members of the genera *Bothriometopus* Taschenberg, 1882, *Ornithobius* Denny, 1842 and *Acidoproctus* Piaget, 1878. See more explanations in the text.

Character/genus	*Bothriometopus*	*Ornithobius*	*Acidoproctus*
Head length and head width	subequal in adults and nymphs	subequal in adults and nymphs	head length much greater than width
Projections of the front of the head	rounded, inconspicuously directed inward	pointed and inwardly directed	rounded and almost straight
Osculum	narrow and deep	wide, never deep	wide, from moderate to deep
Antenna in male	strongly dimorphic, scape with a well developed process on anterolateral margin	slightly dimorphic to dimorphic, scape without such process	slightly dimorphic to dimorphic, scape without such process
Temporal setae (T) of the head	T1 medium, T2 short, T3 long, T4 short, T5 short but noticeable longer than T4)	T1 medium, T2 very short, T3 long, T4 very short, T5 short and slightly longer than T4	T1 medium, T2 very short, T3 long, T4 very short, T5 short and slightly longer than T4
Setal pattern of pterothorax in adults	3+3	2+3	2+3
Setal pattern of pterothorax in nymphs II and III	N II 1+3, less frequent 1+2 N III 2+3, less frequent 2+2	N II 1+3 N III 2+3	N II 1+3 N III 2+3, less frequent 2+2
Characters of male genitalia	tapered and posteriorly rounded basal plate lacking discrete paramera and mesosomal complex, with a well-developed and variously spiculated genital sac bearing a pair of parabasal and a medium unpaired pigmented sclerites	basal plate with well developed paramera and definite endomeral complex, with no obvious genital sac	basal plate with well developed paramera and definite endomeral complex, with no obvious genital sac
Tip of the abdomen in adults	deeply bilobed	not bilobed	not bilobed
Tip of the abdomen in nymphs II and III	deeply bilobed	inconspicuously bilobed	inconspicuously bilobed
Length of tibia III in adults	much longer than tibia II (ratio = 1.3-1.4)	much less so (1.1-1.2)	subequal (ratio = 1.0-1.1)
Body size	very large, 4.4-5.8 mm	large, 3.2-5.0 mm	large, 3.0-4.3 mm
Posterior margin of femur III in adults	noticeably notched near base in both sexes. Not produced posteriad	not notched. It is produced posteriad in males of *O. pricei*	not notched. It is produced posteriad in males of *A. rostratus*
Replication of anterior dorsal seta (ads) in males	replicated 4-10 times	not replicated	not replicated

Character/genus	*Bothriometopus*	*Ornithobius*	*Acidoproctus*
Chaetotaxy of the vulva	with two poorly defined rows, the inner of minute setae and the outer of small sensillae	with two definite rows of setae, or setae (outer row) and strong spines (inner row)	with two definite rows, being setae (outer row) and strong spines (inner row)
Sternites iii-vi in females	Largely divided in the middle	entire	entire
Sternites vii-viii in females	independent and medially divided, not forming a subgenital plates	forming a well definite subgenital plate	forming a well definite subgenital plate
Egg	short, flattened and widely ellipsoid (ratio ~ 1.8-1.9)	elongated, approximately cylindroid and fusiform (ratio ~ 3.0-3.2)	elongated, approximately cylindroid and fusiform (ratio ~ 4,2-4.7)
Operculum	operculum with its basal plane in right angle respect to the main axis of the egg. Air chambers arranged in a single and irregular row	operculum with its basal plane in oblique angle respect to the main axis of the egg. Air chambers arranged in multiple and irregular rows	operculum with its basal plane in oblique angle respect to the main axis of the egg. Air chambers arranged in multiple and irregular rows
Egg: mode of cementation to the feathers	eggs are glued to the dorsal face of the feather, in angle of 33-45° respect of the feather shaft. Spumaline covers more than 2/3 of the exposed surface of the egg	eggs are glued to the ventral face of the feathers, parallel to the barbs and between two contiguous ones. Spumaline, at most, covers only the lateral margins of its exposed surface	eggs are glued to the ventral face of the feathers, parallel to the barbs and between two contiguous ones. Spumaline, at most, covers only the lateral margins of its exposed surface

Literature

ALVARENGA, H. (1999): A fossil screamer (Anseriformes: Anhimidae) from the Middle Tertiary of southeastern Brazil. - Smithsonian Contributions in Paleobiology **89**, 223-230.

ARNOLD, D. C. (2005): Review of the genus *Ornithobius* (Phthiraptera: Ischnocera: Philopteridae), with descriptions of two new species. - Journal of the Kansas Entomological Society **78** (2), 158-166.

- (2006): Review of the genus *Acidoproctus* (Phthiraptera: Ischnocera: Philopteridae), with descriptions of a new species. - Journal of the Kansas Entomological Society **79** (3), 272-282.

BRODKORB, P. (1964): Catalogue of fossil birds. Part 2 (Anseriformes through Galliformes). - Bulletin of the Florida State Museum, Biological Sciences **8**, 195-335.

BURMEISTER, H. C. C. (1838): Handbuch der Entomologie. Band 2. - Berlin.

CICCHINO, A. C. & D. C. CASTRO (1998): Ischnocera. Capítulo 9. Pp 104-124. - In MORRONE, J. J. & S.

COSCARÓN (eds.): Biodiversidad de Artrópodos argentinos. - Buenos Aires.

CLARKE, J., C. P. TAMBUSSI, J. I. NORIEGA, G. M. ERICKSON & R. A. KETCHAM (2005): Definitive fossil evidence for the extant avian radiation in the Cretaceous. - Nature **433**, 305-308.

CLAY, T. (1951): An introduction to a classification of the avian Ischnocera (Mallophaga): Part I. - Transactions of the Royal Entomological Society of London **102**, 171-195.

- (1975): Th Transactions of the Royal Entomological Society of London 102: 171-195.

Clay, T. 1975. A key to the genera and generic groups of the Ischnocera. Unpublished, available on-line from http://www.phthiraptera.org/Publications/4317pdf (access 25 January 2006).

DYKE, G. J. (2001): The Fossil Waterfowl (Aves: Anseriformes) from the Eocene of England. - American Museum Novitates **3354**; 15 pp.

EICHLER, WD. (1941): Zur Klassifikation der Lauskerfe (Phthiraptera HAECKEL: Rhynchophthirina, Mallophaga

und Anoplura). – Archiv für Naturgeschichte **10** (3), 345–398.

– (1963): Mallophaga. – Bronns Klassen und Ordnungen des Tierreichs, Fünfter Band, III. Abteilung, 7. Buch, b) Phthiraptera, 1. Teil. – Leipzig.

GIEBEL, C. [G.A.] (1866): Die im zoologischen Museum der Universität Halle aufgestellten Epizoen nebst Beobachtungen über dieselben. – Zeitschrift für die Gesammten Naturwissenschaften **28**, 353–400.

– (1874): Insecta epizoa. Die auf Säugethieren und Vögeln schmarotzenden Insecten nach Chr. L. Nitzsch's Nachlass bearbeitet. – Leipzig.

HOPKINS, G. H. E. & T. CLAY (1952): A check list of the genera & species of Mallophaga. – London.

JOHNSON, K. P. & D. H. CLAYTON (2003): The biology, ecology, and evolution of chewing lice. Pp. 449–476. – In: PRICE, R. D., R. A. HELLENTHAL, R. L. PALMA, K. P. JOHNSON & D. H. CLAYTON (eds.): The chewing lice: world checklist and biological overview. –Illinois Natural History Survey Special Publication 24.

KÉLER, S. (1938): Baustoffe zu einer Monographie der Mallophagen. I. Teil: Überfamilie Trichodectoidea. – Nova Acta Leopoldina, Neue Folge, **5**, 395–467.

MAYR, G. & J. CLARKE (2003): The deep divergences of neornithine birds: a phylogenetic analysis of morphological characters. – Cladistics **19**, 527–553.

MEY, E. (1990): Eine neue ausgestorbene Vogel-Ischnozere von Neuseeland, *Huiacola extinctus* (Insecta, Phthiraptera). – Zoologischer Anzeiger **224**, 49–73.

– (1994): Beziehungen zwischen Larvenmorphologie und Systematik der Adulti bei den Vogel-Ischnozeren (Insecta, Phthiraptera, Ischnocera). – Mitteilungen aus dem Zoologischen Museum in Berlin **70** (1), 3–84.

ONIKI, Y. & J. F. BUTLER (1989): The presence of mites and insects in the gut of two species of chewing lice (*Myrsidea* sp. and *Philopterus* sp., Mallophaga): accident or predation? – Revista Brasileira de Biologia **49**, 1013–1016.

PIAGET, E. (1880): Les Pédiculines. Essai monographique. Supplément. – Leide[n].

PRICE, R. D., R. A. HELLENTHAL & R. L. PALMA (2003): World Checklist of Chewing Lice with Host Associations and Keys to Families and Genera. Pp. 1–488. – In: PRICE, R. D., R. A. HELLENTHAL, R. L. PALMA, K. P. JOHNSON & D. H. CLAYTON (eds.): The Chewing Lice: World Checklist and Biological Overview. – Illinois Natural History Survey Special Publication 24.

ROTHSCHILD, M. & T. CLAY (1952): Fleas, Flukes & Cuckoos A Study of Bird Parasites. – London.

SICK, H. (1993): Birds in Brazil A natural history. Translated from Portuguese by WILLIAM BELTON. – Princeton.

SMITH, V. (2001): Avian louse phylogeny (Phthiraptera: Ischnocera): a cladistic study based on morphology. – Zoological Journal of the Linnean Society **132**, 81–144.

TASCHENBERG, O. (1882): Die Mallophagen mit beson-derer Berücksichtigung der von Dr. Meyer gesammelten Arten. – Nova Acta der Kaiserlich Leopoldinisch-Carolinisch-Deutschen Akademie der Naturforscher **44** (1), 1–245.

TIMMERMANN, G. (1962): Gruppen-Revisionen bei Mallophagen. V / Zur näheren Kennzeichnung des *Ornithobius*-Komplexes (Philopteridae), parasitisch bei Entenvögeln. – Zeitschrift für Parasitenkunde **22**,133–147.

VALIM, M. P. (2006): *Tyranniphilopterus caiolukasi* sp. n. (Phthiraptera: Philopteridae) from the yellow-olive flycatcher (Aves: Tyrannidae), with observations on gut contents. – Lundiana **7**(1), 55–58.

WATERSTON, J. (1926): On the crop contents of certain Mallophaga. – Proceedings of the Zoological Society of London **4**, 1017–1020.

YOSHIZAWA, K. & K. P. JOHNSON (2006): Morphology of male genitalia in lice and their relatives and phylogenetic implications. – Systematic Entomology **31**, 350–361.