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MICROSPALACINAE, A NEW SUBFAMILY OF THE FEATHER MITE FAMILY ALLOPTIDAE GAUD (ACARINA, ANALGOIDEA)

W. T. ATYEO and J. GAUD

Department of Entomology, University of Georgia, Athens, Georgia, U.S.A., and Laboratoire de Parasitologie, Faculté de Médecine, 06034 Nice cedex, France

Abstract. Microspalacinae subfam. n. (Analgoidea, Alloptidae) is established for the feather mite genus *Microspalax* Mégnin et Trouessart (= *Connivelobus* Dubinin, new synonymy). Morphologies of the species are described and illustrated with line drawings and SEM micrographs, and taxonomical comments are given for named species. The mites are known from shearwaters (Procellariidae) and stormpetrels (Hydrobatidae); host associations are discussed. The alloptid subfamily Thysanocercinae Atyeo et Peterson is elevated to familial rank.

Many feather mites associated with the more ancient lineages of birds are often similar in general appearance. A common conformation is an ovoid idiosoma with well developed dorsal shields and coxisternal apodemes, and ventrally positioned posterior legs. Mites with this form, encountered on wading birds, sea birds and waterfowl, have historically been placed in the family Freyanidae. Through time and re-evaluation of character states, genera formally placed in the Freyanidae have been reassigned to other families.

Primarily on the bases of chaetotaxy and pretarsal modifications *Kramerella* Trouessart, *Freyanella* Dubinin, and *Freyanopterolichus* Dubinin have been placed in the Kramerellidae (Gaud and Mouchet 1961); *Microchelys* Trouessart in the Eustathiidae (Gaud and Atyeo 1967); and *Echinacarus* Dubinin, *Microspalax* Mégnin et Trouessart (including *Connivelobus* Dubinin, new synonymy) in the Alloptidae (Gaud 1968).

Currently the subfamilies of the Alloptidae are Alloptinae Gaud, Echinacarinae Peterson, Oxyalginae Peterson et Atyeo, and Thysanocercinae Atyeo et Peterson. The first three subfamilies are commensals of shore and sea birds, and the Thysanocercinae are associated with the Apodidae. With the recognition of a new subfamily, we believe that with the exception of the Thysanocercinae, these mites form a natural assemblage. For the Thysanocercinae, it will be elevated to the familial level.

Concerning *Microspalax*, the subject of this paper, Mégnin and Trouessart (1984) described it as a subgenus of *Freyana* and later Trouessart (1916) elevated it to generic rank. Dubinin (1949) established *Connivelobus* as a subgenus of *Microspalax* and in 1953, he recognized both as genera. Finally, Gaud and Till (1961) re-established *Connivelobus* as a subgenus of *Microspalax*. New characters discovered with phase, differential interference contrast, and scanning

electron microscopy, allow us to demonstrate a continuum of character states between *Microspalax* and *Connivelobus* (sensu Dubinin), thus the synonymy *Microspalax* (=*Connivelobus*) can be justified. We will define the Microspalacinae, a new subfamily in the Alloptidae, and discuss the included species.

MATERIALS AND METHODS

This study is based on approximately 1,500 microslides and 12 SEM mounts (each with samples from two hosts) prepared from collections taken from museum study skins, with each collection equal to all mites taken from one skin (technique of Atyeo and Braasch 1966). From the Procellariidae, 218 collections were taken from 721 skins examined (prevalence = 30 %) and from the Hydrobatidae, 69 samples from 519 skins examined (prevalence = 13 %). The most common species in the samples, arranged by frequency of collections, are *Zachvatkinia* Dubinin (Avenzoariidae, see Dubinin 1949, 1953), *Microspalax*, and *Brephosceles* Hull (Alloptinae, see Peterson 1971). Not all collections contain species of the 3 genera, but considering all collections from a host species, usually all genera were represented. For *Microspalax*, species were collected from 13 of the 13 species of *Puffinus*, 15 (of 17 species examined) of the 26 species of *Pterodroma*, plus other taxa of the Procellariidae and Hydrobatidae.

The museum collected mites often have setae broken or absent. Even so, all specimens were cleaned in an ultrasonic cleaner for about five seconds; this short period did not always clean the specimens completely, but did minimize damage to setae and ambulacra. For microslides, specimens were rehydrated and cleared with lactophenol, and mounted in Hoyers medium (see Krantz 1978). For scanning electron microscopy, specimens were dehydrated with alcohol and pentane, and mounted on SEM stubs with double-sticky tape. Signatures for idiosomal setae follow Griffiths et al. (1990), and for the gnathosoma, Johnston (in Atyeo and Braasch 1966).

A species revision, which is beyond the scope of this paper, is badly needed. Dubinin's revisions (1949, 1953) were based on collections from ornithological collections and a few field collected birds from Russia. On a worldwide basis, our collections include undescribed *Microspalax* species associated with the Procellariidae and Hydrobatidae. We lack *Microspalax* specimens from some type hosts, therefore, some species determinations herein are tentative.

We have new information and new interpretations of the morphology of these mites, therefore, after defining the new subfamily, characters and their states are discussed. Line drawings produced under phase microscopy (Fig. 1) are included to show chaetotaxy and internal thickenings of the tegument.

MICROSPALACINAE subfam. n.

Description: Ovoid alloptid mites with heavily sclerotized regions associated with coxae; gnathosoma elongated with apical podomere extending anterolaterally, bearing long solenidion; external scapular setae widely separated, short; hysterosoma with lateral flanges; setae c1 absent; level of setae c2 far anterior to level of setae d1, approximately same level as c3; setae cp setiform to triangular; epimerites I Y-shaped; epimerites II converge mesally; epimerites I, II in W-configuration; prodorsal and hysterosomal shields fused; ambulacra with apical point; femora and genua of all legs fused, often with dorsal crests; legs II subequal to larger than legs I, if larger, femorogenu II may be more than two times wider than I (except heteromorphic male with leg form 2, see below); legs III, IV ventral,

subequal, not extending to level of anus; ambulacra III, IV arising subapically on paraxial surface of truncated tarsi.

Male: Posterolateral idiosoma with 4–5 pairs of setae: ps1 as microseta; h3 short, h2 very long, microseta f2 present or absent, ps2 long; terminal margin convex, straight or with broad, shallow cleft; genital organ between coxae IV, either exposed and supported by external aedeagal guides or internal basally; genital setae minute; setae 4a, ps3 inserted on small plates which may connect epiandrum anteriorly; small pair platelets between setae ps3, adanal discs with narrow, sclerotized corollae, each with large tooth anteriorly (plus numerous small teeth circumferentially in *Microspalax major*). Heteromorphic male, if present, similar to homeomorph except slightly larger, legs II with larger crests, and with coxal spines.

Female: Proterosoma, coxae III, IV similar to male; setae g, ps3 absent; sperm-pore terminal or between setae h1; posterior idiosoma rounded with 4 pairs of setae: ps1, ps2 as microsetae, h2, h3 long; epigynum often connected to epimerites I and/or anterior and posterior epimerites of legs II; epigynum with anterior margin relatively straight, posterior margin slightly to strongly curved.

Type genus: *Microspalax* Mégnin et Trouessart, 1884.
Included genus: *Microspalax* (= *Connivelobus* Dubinin).

Relationships: The alloptid subfamilies (see above), except Thysanocercinae Atyeo et Peterson, 1972, are associated with birds of the orders Gaviiformes, Procellariiformes, Pelecaniformes, Ciconiiformes, Anseriformes, Gruiformes and Charadriiformes. Species of more than one subfamily can co-occur on single hosts assigned to the various listed orders.

The relationships between the Microspalacinae and the other subfamilies associated with sea and shore birds are obscured by the different modifications for life on these birds, presumably adaptations for different microhabitats. Males of the Oxyalginae and Alloptinae have fused or separate terminal lobes, often legs IV are noticeable larger than legs III, and the genital organ is usually posterior, or surrounded by well-developed apodemes. The females of the two subfamilies are normally elongate, with or without terminal lobes. The Echinacarinae, with 2 species, has heavily sclerotized adults with some of the terminal setae blade-like, and the males have a huge genital capsule which can be everted in its entirety. The Microspalacinae are singular among the Alloptidae in the modifications of the anterior legs, the male genital organ, the idiosomal configuration, and the ventrally positioned legs.

The species of the monogeneric subfamily Thysanocercinae, restricted to the Apodidae (Apodiformes), have been included in the Alloptidae because of the similarities of the male idiosoma to *Alloptes* Canestrini, the fusion of the femora and genua in all legs, the elongated gnathosoma, and the deep bilobation of the female opisthosoma. However, other character states, such as the bipectinate ensiform appendages prolonging the opisthosomal lobes of females, the differently

modified pseudorutellar processes, and differently positioned ventral setae of males are sufficient to elevate this group of apodid feather mites to familial level, the Thysanocercidae (see Gaud and Peterson 1987 for additional characters).

CHARACTERS AND CHARACTER STATES OF THE MICROSPALACINAE

Gnathosoma: The elongated gnathosoma consists of the subcapitulum, chelicerae, and palpi. The lateral walls of the subcapitulum may be straight (Pl. I, Fig. 1) or expanded laterally into various configurations (Pl. I, Figs. 2–4); some expansions are difficult to discern under light microscopy unless the anterior legs have been displaced laterally during microslide preparation.

The pseudorutellar processes are modified as a series of small platelets subtending the palpi (Pl. I, Figs. 1–3). The characteristic apical podomere of the palpus is attenuated, directed away from the meson, and bears elongated solenidion *omega* 1 (Pl. I, Figs. 1–4). Finally, the chelicerae are thin with small chelae.

Posterior idiosomata of males: Dubinin (1949) distinguished the subgenera *Microspalax* and *Connivelobus* primarily on the form of the posterior margin of male opisthosomata, broadly cleft for the former subgenus (Pl. I, Figs. 5–6), straight or rounded for the latter (Pl. II, Figs. 1–2) with a small, narrow cleft at the meson. On microslides, an O- or U-shaped internal sclerotization can be seen at the meson (supranal concavity *sensu* Atyeo and Braasch 1966) (Fig. 1A). In males of the subgenus *Connivelobus* (*sensu* Dubinin), these internal sclerotizations are U-shaped and extend almost to the opisthosomal margin. Dubinin (1949, 1953) hypothesized that the broad terminal lobes of the subgenus *Microspalax* males represented the primitive condition, and that these lobes were secondarily fused to form the derived subgenus *Connivelobus*, and that the lobe fusion was indicated by a small cleft between the U-shaped sclerotization. With SEM, it can be seen that the posterior margin of the male opisthosoma is uninterrupted and the supranal concavity may be indicated by a slight depression (Pl. II, Fig. 3).

Dorsal idiosoma: Sexual dimorphism of the dorsal idiosoma is expressed posterior to legs IV. Shield ornamentation can be similar for both sexes or very different. Females and many males have elevated ridges forming polygons (Pl. II, Figs. 2, 4, 5; Pl. III, Fig. 1). Other males have polygons with small patterns within each polygon (Pl. 2, Fig. 3), scalelike tegument (Pl. I, Figs. 5, 6), beadlike elevations (Pl. II, Fig. 1), or any combination of the three types (e.g., Pl. IV, Fig. 5).

The male terminus may be rounded, straight or concave (Pl. I, Figs. 5, 6; Pl. II, Figs. 1–4), and the female terminus may be slightly convex to rounded (Pl. II, Figs. 5, 6). Except for males of *Microspalax major* Trouessart et Neumann (Pl. II, Fig. 3), males and females have gently curving hysterosomal margins with lateral flanges of varying widths (Pl. III, Figs. 1, 2).

Dorsal idiosomal setae: Griffiths et al. (1990) have shown that the larval chaetome of astigmatid mites consists of a maximal number of setae and specific

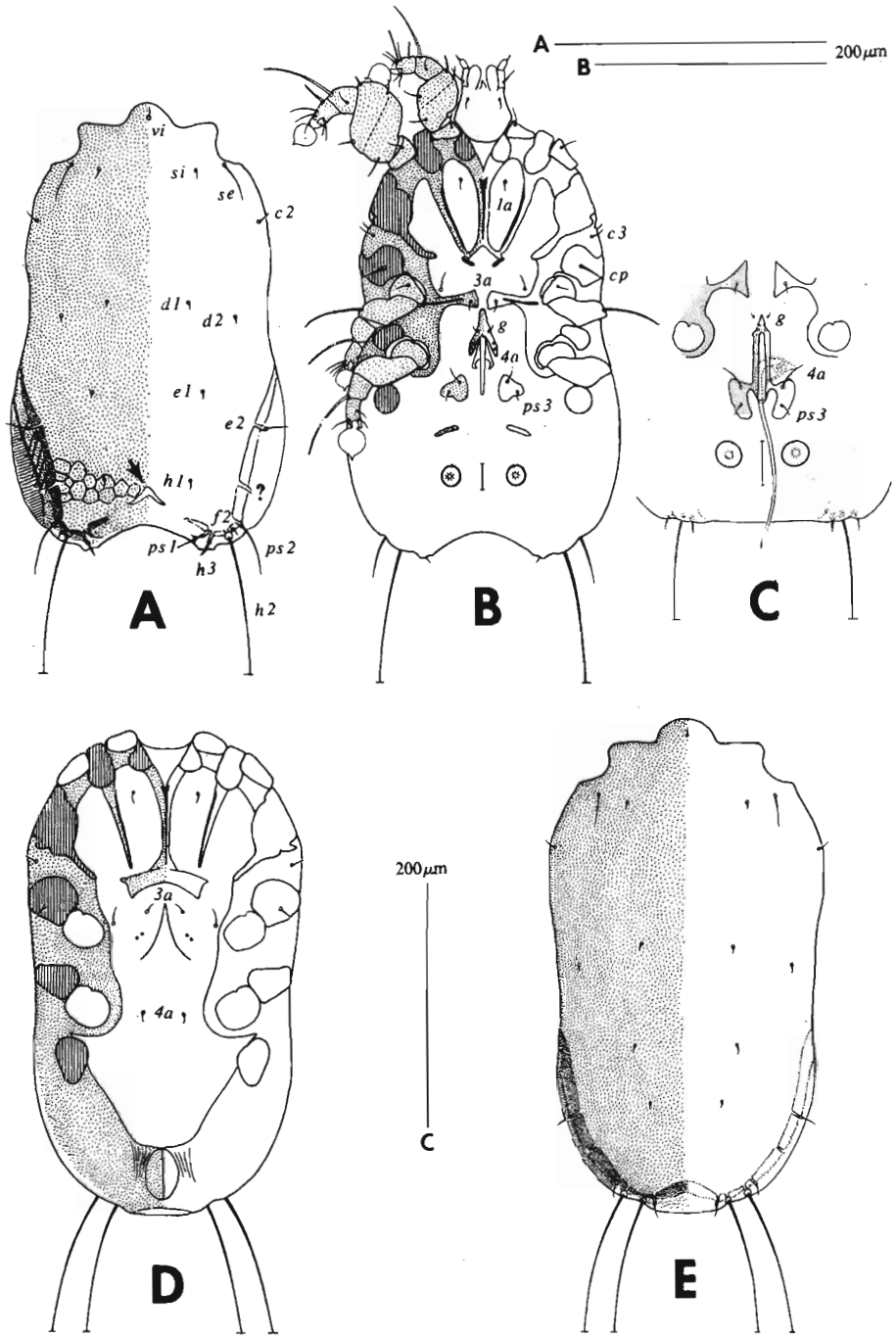

Fig. 1. A, B – *Microspalax* near *ardennae* male. A – dorsal idiosoma, arrow = supranal concavity; B – ventral aspect; C – *Microspalax* near *brevipes*, genital organ extended; D, E – *Microspalax* near *ardennae* female, dorsal and ventral idiosoma. Setal signatures follow Griffiths et al. (1990). Scales: A = Figs. 1A, B; B = Fig. 1C; C = Figs. 1D, E.

setae are added in subsequent molts. In *Microspalax*, as in many other Alloptidae, the larvae and all additional life stages lack setae c1. In the protonymph, 3 rather than the expected 5 pairs of dorsal setae and zero rather than 1 pair of ventral setae are added, that is, setae f2, ps3 and g are absent. Protonymphal setae are maintained in the tritonymph and female (Fig. 1D, E), but in the male, ps3 and g, and sometimes f2, make delayed appearances (Fig. 1A–C). In this sex, the genital setae (g) are minute, ps3 are distant from the adanal discs, and f2, when present, is a microseta inserted near the alveolus of seta h2. Because of the differential sclerotization associated with the male terminus, microsetae ps1 and f2 are difficult to observe. In micrographs of a male *Microspalax* nr. *cymochoreae* Dubinin, setae ps1 and f2 are visible (Pl. III, Figs. 1, 2), but with light microscopy, we have never seen f2 in this species. It is possible that all microspalacine males have setae f2.

Four pairs of cupules are associated with the astigmatid larval chaetome. In the taxa under consideration, typically positioned cupules are not observed. However, in both males and females there is a pair of structures between setae e2 and ps2 which appear under light microscopy structurally similar to setal bases (Fig. 1A, E), but under electron microscopy there are no external indications of them; these probably represent remnants of cupules in or ip. It should be noted that Dubinin (1949, 1953) illustrated a seta emerging from each of these.

Aedeagus: Scanning electron microscopy was used to study males of various species of the Microspalacinae, including *Microspalax brevipes* Mégnin et Trouessart and *M. bulweriae* Dubinin, both of which have long genital organs.

The aedeagus is supported by a U-shaped aedeagal or genital arch (phallobase of Popp 1967) which rotates downward from the posterior articulations, thus causing the aedeagus to move posteriorly (Fig. 1B, C). In the Microspalacinae, there are two unusual modifications.

The first consists of a pair of external aedeagal guides supporting the posterior portion of an aedeagus exposed for its entire length (Fig. 1B; Pl. III, Figs. 3, 4). The articulations of the guides appear to be flexible, so presumably as the aedeagus is rotated posteriorly the guides are not disengaged. Dubinin (1949, 1953) illustrates each guide as ending in a trifurcation.

The second modification is best explained with males having long genital organs. In these, the posteriorly directed portion of the aedeagus is internal from the arch apex to the level of setae ps3, at which point it emerges through a small pore in the idiosomal wall (Fig. 1C). The pore is easily seen with SEM (Pl. III, Figs. 5, 6), but with light microscopy, the only indication of a pore is a slight thickening of the body wall. Narrow internal sclerotizations of the tegument define an internal aedeagal groove (Fig. 1C, epiandrum of authors and aedeagal guides by Dubinin 1949, 1953). As in the first modification, the aedeagus moves posteriorly by the rotation of the aedeagal arch. When an aedeagus, which in repose reaches the level of the anus, is moved posteriorly by the full rotation of the genital arch, it extends well beyond the opisthosomal margin. The emergence pore of males with

short genital organs is not as obvious, especially when comparing genital organs of different diameters (Pl. IV, Figs. 1, 2).

Females associated with males with long genital organs have the spermpore positioned anterior to the terminus. Those associated with males having short genital organs have terminal spermpores between setae ps1.

Ventral idiosomal setae: The positions of the ventral setae of females are stable (Fig. 1D), as are setae 1a, 3a, 3b and g of males (Fig. 1B). The remaining ventral setae of males, 4a and ps3, are variously positioned between the adanal and genital discs. As observed on microslides, males have a pair of platelets bearing setae 4a and ps3; the platelets may or may not be connected to an epiandrum which bears the genital setae and discs (Fig. 1B, C). In some species, setae ps3 may be positioned internal to 4a.

For males with external aedeagal guides, setae 4a and ps3 are positioned slightly posterior to the genital arch, regardless of the aedeagal length (Fig. 1A; Pl. III, Figs. 3, 4; Pl. IV, Figs. 1, 2). For males with long, partially internal genital organs, the emergence pore is near setae ps3 (Pl. III, Figs. 5, 6); this pore can be midway between the adanal discs and genital discs, nearer to the adanal discs than the genital discs, or *vice versa*. In both cases, setae 4a and ps3 are in the same positions relative to the opening for the genital organ. Males with short genital organs have these setae distant from the adanal discs and near the aedeagus, genital discs and setae g (Pl. III, Fig. 3; Pl. IV, Figs. 1, 2).

Coxisternal apodemes: Males and females have similar propodosomata and lateral elements of coxae III and IV (Fig. 1B, D). The anterior epimerites, remnants of the coxae, are especially characteristic for the Microspalacinae. The articulations of the trochanters are heavily sclerotized, and coxal fields I and II may be closed by secondary sclerotizations. In males these sclerotizations may extend across the venter and in females, they may connect with the epigynum (pregenital sclerite of authors). Coxal fields III of males may be closed by mesally directed secondary sclerotizations anterior to the genital region.

Legs: Legs I and II are not oriented in dorsal-ventral planes characteristic of most astigmatid mites. Rather, they are inclined toward the meson so that femorogenua I form a partial canopy over the gnathosoma (Pl. II, Figs. 1–5). This configuration decreases the idiosomal height, thus allowing these mites to occupy spaces between the barbules of the outer (anterior) veins of the outer primaries. These barbules are independent of each other and form narrow, parallel interspaces that can be inhabited by flattened feather mites.

The genua and femora of all legs are fused with the line of fusion weakly evident. These combined segments of legs I and II are enlarged (widened) dorsoventrally, with a concomitant size reduction of the cylindrical tibiae and tarsi (Fig. 1A). Most species have legs II much larger than legs I, and many have the dorsal walls of femorogenua II expanded as thin plates or crests with those of males usually larger than those of females (compare Pl. IV, Figs. 4–6).

In most feather mites the tarsal stalks (*sensu* Atyeo 1978) that support the ambulacra arise from the apicoventral surfaces on the tarsi, that is, ventral to the apicodorsal setae d, e, and f. However, in the Microspalacinae the stalks of the ventrally positioned legs III and IV arise from the paraxial surfaces of truncated tarsi (Fig. 1B). These modifications are often not apparent as the ambulacra of legs III and IV are often missing from museum-collected specimens.

Male polymorphism: In species exhibiting polymorphism, the homeomorph and female have thickened legs II lacking well developed dorsal crests (Pl. IV, Fig. 5), and the lateral margins of epimerites II each lacks a spine. The heteromorph has femorogena II with dorsal crests (Pl. 1, Figs. 4, 6; Pl. 4, Fig. 6), and a spine of coxal origin near the base of trochanter II (Pl. I, Fig. 4); additionally, in comparing the heteromorph to the homeomorph, the idiosoma is larger, the opisthosoma wider, and the terminal cleft is differently shaped (Pl. I, Figs. 5, 6).

Legs II of the heteromorphs usually have the same proportional lengths as the females and homeomorphs, and the dorsal crests usually form an almost continuous arc (leg form 1) (Pl. I, Fig. 4), however, an undescribed heteromorph has differently proportioned segments and has the dorsal crests limited to the apical half of each segment (leg form 2) (Pl. I, Fig. 6; Pl. IV, Fig. 6).

A question arises about the heteromorph with leg form 2: is it truly a heteromorph of *Microspalax ardennae* Dubinin or is it a separate species? To date, we have one form of female and two types of males from *Calonectris leucomelas* (Temminck) (Pl. I, Figs. 5, 6). Both males have similar dorsal ornamentation, genital organs and ventral apodemes; they differ in the width of the posterolateral flanges, the size and depth of the terminal clefts, and the segment proportions and crests of legs II (Pl. IV, Figs. 5, 6). Dubinin's illustrations (1953, Fig. 151) of *M. ardennae* males appear to be a composite of the two forms: the ventral aspect of the male shows crested legs II and coxal spines of a heteromorph and the narrow idiosoma of a homeomorph; his detailed illustration of leg II has crests but lacks the coxal spine. We make the assumption that the two forms of males in our collection are conspecific, representing homeomorphs and heteromorphs.

Heteromorphs exhibiting leg form 1 and their homeomorphs can occur in single collections, or either one can constitute the total population of males in other samples. Heteromorphs with leg form 2 are rare and are found in the same samples as their homeomorphs.

Microspalax Mégnin et Trouessart, 1884

(Syn.: *Freyana* (*Microspalax*) Mégnin and Trouessart, 1884: 152–153; Trouessart and Mégnin, 1885a: 16–17; Trouessart and Mégnin, 1885b: 43; Canestrini and Kramer, 1899: 34. *Microspalax*: Trouessart, 1916: 215; Radford, 1950: 152. *Microspalax* (*Microspalax*): Dubinin, 1949: 201–202. *Microspalax* (*Connivelobus*) Dubinin, 1949: 207; Gaud and Till, 1961: 236. *Microchelys* (*Microspalax*): Radford, 1953: 200. *Microspalax*: Dubinin, 1953:

341–343; Turk, 1953: 83; Gaud and Mouchet, 1959: 485; Gaud and Till, 1961: 229, 236; Atyeo and Peterson, 1970: 137). *Connivelobus*: Dubinin, 1953: 350–355; Turk, 1953: 83; Atyeo and Peterson, 1970: 137.)

Type species (*Microspalax*): *Freyana* (*Microspalax*) *manicata* Mégnin et Trouessart from *Procellaria* (= *Puffinus*) *cinerea* Gmelin (subsequent designation, Trouessart 1916, see Comments below.)

Type species (*Connivelobus*): *Freyana* (*Microspalax*) *manicata* var. *brevipes* Mégnin et Trouessart from *Puffinus assimilis* Gould [= *Puffinus obscurus* (Gmelin)] (by original designation).

Included species: *Microspalax manicatus* Mégnin et Trouessart, *M. ardennae* Dubinin, *M. brevipes* Mégnin et Trouessart, *M. bulweriae* Dubinin, *M. cymochoreae* Dubinin, *M. longipenis* Dubinin, *M. major* Trouessart et Neumann, *M. pterodromae* (Dubinin) (n. comb.), *M. puffini* Dubinin, and *M. thyellodromae* Dubinin.

Comments: – Only a few species are assigned to *Microspalax*, but this reflects the lack of collections, and possibly the broad species definitions of Dubinin for which he did not designate types (1949, 1953). With our larger study collections and better optical equipment, we believe that many of Dubinin's illustrations represent composites of different species and/or morphotypes.

Microspalax manicatus Mégnin et Trouessart, 1884

(Syn.: *Freyana* (*Microspalax*) *manicata* Mégnin and Trouessart, 1884: 153–154, Fig. 26 (1, 2); Trouessart and Mégnin, 1885a: 17–18, Fig. 4 (1, 2); Trouessart and Mégnin, 1885b: 43; Berlese, 1897, Fasc. 82, no. 5; Canestrini and Kramer, 1899: 35; Dubinin, 1949: 202–204, Fig. 1. *Microchelys* (*Microspalax*) *manicata*: Radford, 1953: 200. *Microspalax manicatus*: Trouessart, 1916: 213; Vitzthum, 1929: 39, Fig. 3; Dubinin, 1953: 343–345, Figs. 11, 12, 148, 152; Radford, 1958: 110; Gaud and Till, 1961, Fig. 146; Atyeo and Peterson, 1970: 138, Figs. 36–38.)

Comments: – This species is an unknown entity as the location of the type is unknown. Mégnin and Trouessart (1884) said that the species was taken from puffins, particularly "sur le Puffin cendré (*Puffinus cinereus*), des côtes de France". But what is this host? If the synonym *Procellaria cinerea* (= *Puffinus cinereus*) is correct, then how does one explain that *P. cinerea* occurs circumpolar between 25 °S and 60 °S (Jouanin and Mougin 1979)? If the "Puffin cendré" is *Calonectris diomedea* (Scopoli) as given by Peterson et al. (1983), a species known from Europe and the Far East, then *Microspalax manicatus* was probably described by Dubinin (1949, 1953) as *Microspalax ardennae* from 2 males and 3 females from *C. diomedea*.

Dubinin (1949) had limited specimens that he identified as *Microspalax manicatus* from *Fulmarus glacialis* (L.), 1 female, Novaya Zemlya, 1905; *Thalassoica* (= *Priocella*) *antarctica* (Gmelin), 1 male, Cape Horn, 1840; *Procellaria* (*Adamastor*) *cinerea* (Gmelin), 1 male, New Holland, 1841; *Puffinus griseus* (Gmelin), 1 male, 2 females, Monterrey, California, 1897; *Puffinus tenuirostris* (Temminck), 1 male, Chukotka, Bay of Provideniya, 1938; *Puffinus opisthomelas* Coues, 2 males, 7 females, Guadaloupe, Lesser Antilles, 1906. The illustrations of Dubinin are most similar to species associated with species of *Puffinus*, from which he had the most males.

If we consider that "le Puffin cendré" is *Calonectris diomedea*, we have collected females and three forms of males from both species of *Calonectris* Mathews et Iredale, *C. diomedea* (Scopoli) and *C. leucomelas* (Temminck). First, there are homeomorphs and heteromorphs of a species near or conspecific with *Microspalax ardennae* (Pl. I, Figs. 5, 6) and a species similar to *M. brevipes* (see below).

Microspalax brevipes (Mégnin et Trouessart, 1884) Pl. I, Fig. 1; Pl. II, Figs. 5, 6

(Syn.: *Freyana* (*Microspalax*) *manicata* var. *brevipes* Mégnin and Trouessart, 1884: 154–155, Fig. 26(3); Trouessart and Mégnin, 1885a: 18–19, Fig. 4(3); Trouessart and Mégnin, 1885b: 43; Berlese, 1898, Fasc. 85, no. 3; Canestrini and Kramer, 1899: 35. *Microspalax brevipes* Vitzthum, 1929: 85; Radford, 1958: 110, 111. *Microspalax* (*Connivelobus*) *brevipes*: Dubinin, 1949: 207–208, Figs. 5, 6. *Microchelys* (*Microspalax*) *brevipes*: Radford, 1953: 200. *Connivelobus brevipes*: Dubinin, 1953: 355–357, Figs. 75, 152–154; Atyeo and Peterson, 1970: 137, Figs. 33–35.)

Comments: – The type series is lost, but we have many specimens from the type host, *Puffinus assimilis* (Bonaparte) (= *P. obscurus*), which agree with the original description (Mégnin and Trouessart 1884) and the redescription of Dubinin (1949, 1953). A second species with polymorphic males has also been collected from *P. assimilis* (see Male polymorphism). The *brevipes*-type males are also known from other species of *Puffinus* and both species of *Calonectris*.

Dubinin's study specimens were from *Calonectris leucomelas*, 3 males and 2 females, Mollucas, 1881; *Puffinus gravis*, Massachusetts, 1883 and the Faeroe Islands, 1891; and *Daption capense*, one female, Cape Horn. The last association is probably in error and the two other associations probably represent one or two new species.

Microspalax ardennae Dubinin, 1949 Pl. I, Figs. 5, 6; Pl. 3, Fig. 4; Pl. IV, Figs. 4–6.

(Syn.: *Microspalax* (*M.*) *ardennae* Dubinin, 1949: 206–207, Fig. 4. *Microspalax ardennae*: Dubinin, 1953: 348–350, Figs. 75, 151; Radford, 1958: 110).

Comments: – Dubinin (1949) presumably considered the type host to be *Calonectris* [Syn. *Puffinus* (*Ardenna*)] *diomedea* (Scopoli), the only host from which he had males, and this host with two others, also considered to be in the subgenus *Ardenna*, was the basis for the specific epithet of the mite. Today, the combination for the type host is *Calonectris diomedea* and the other hosts are considered as *Puffinus* (*Hemipuffinus*) species. Using the original combinations, Dubinin's study collection was taken from *Puffinus* (*Ardenna*) *diomedea*, 2 males, 3 females, Atlantic Ocean 40°50′ N 29°40′ E; *P.* (*A.*) *creatopus* Coues, 6 females, Monterrey, California, 1897; *P.* (*A.*) *carneipes* Gould, 1 female, Australia, 1889.

We believe that Dubinin's (1949, 1953) illustrations are composites of homeo- and heteromorphic males. The ventral view of the male shows crests on legs II and a large spine at the base of the trochanters II, yet the enlargement of leg II to illustrate the details of the crests lacks the spine. Lastly, the opisthosoma is rather narrow, which is a characteristic of homeomorphs. We also believe that this species may be conspecific with *M. manicatus* originally described from *C. diomedea*.

In our collections, there are many *Puffinus* hosts with homeo- and heteromorphic males near or conspecific with *M. ardennae* and *M. brevipes*; at least some of these represent new species.

Microspalax bulweriae Dubinin, 1949 Pl. I, Fig. 3; Pl. II, Fig. 2; Pl. III, Fig. 5.

(Syn.: *Microspalax* (*Connivelobus*) *bulweriae* Dubinin, 1949: 211, Fig. 5. *Connivelobus bulweriae*: Dubinin, 1953: 361–362, Figs. 11, 152, 155; Radford, 1958: 111.

Comments: – Dubinin (1949) described this species from a single male collected from *Bulweria bulweriae* (Jardine et Selby) from the Bonin Islands, western Pacific Ocean, 1874. There is no doubt that the association is correct because *Microspalax bulweriae* is the only species having males with narrowed and terminally rounded opisthosomata. Dubinin's illustration of the male venter (1953) lacks small coxal spines and the crests of legs II are represented incorrectly (see Pl. II, Fig. 2). Females of this species lack any evidence of leg crests.

Microspalax cymochoreae Dubinin, 1949 Pl. III, Figs. 1, 2; Pl. IV, Fig. 3

(Syn: *Microspalax* (*Connivelobus*) *cymochoreae* Dubinin, 1949: 209–211, Figs. 5, 6. *Connivelobus cymochoreae*: Dubinin, 1953: 359–361, Figs. 152, 153, 155; Radford, 1958: 111).

Comments: – Although Dubinin (1949, 1953) placed this species in *Connivelobus*, he mentioned that the genital organ was of the *Microspalax* type. Interestingly, the original illustration of the male opisthosoma (1949) does not show a small terminal cleft and except for the straight posterior opisthosomal

margin, should have been placed in *Microspalax*. Dubinin (1953) illustrated the male venter and in this illustration, a terminal cleft is (incorrectly) added.

The type host is probably *Oceanodroma leucorhoa* (Vieillot) as Dubinin had collections from three subspecies of this host: *Oceanodroma* (*Cymochorea*) *l. leucorhoa*, 2 males, Commodore Islands, 1905; *O.* (*C.*) *l. beali* Emerson, 17 males, 1 female, southern Alaska, 1908; *O.* (*C.*) *l. socorroensis* Townsend (=*kaedingi* Anthony), 10 males, 1 female, California, 1857. Dubinin also had specimens from *O.* (*C.*) *castro* (Harcourt), 2 males, St. Helena, 1887.

This is the smallest of the *Microspalax* species and legs I and II of males and females are essentially subequal and lack crests (Pl. IV, Fig. 3). We have *Microspalax* collections from six species of *Oceanodroma*, and as in other instances, these may represent more than one species.

Microspalax longipenis Dubinin, 1949

(Syn.: *Microspalax* (*Connivelobus*) *longipenis* Dubinin, 1949: 211, Figs. 5, 6. *Connivelobus longipenis*: Dubinin, 1953: 362, Figs. 152, 153, 155; Radford, 1958: 110.

Comments: – This species was originally collected from *Puffinus lherminieri* Lesson, 10 males and 10 females, from the Baema Island, Bahama Islands, 1904. Dubinin (1949, 1953) illustrated the male with a genital organ extending beyond the opisthosomal terminus and a glabrous dorsum. Our 6 collections from the same host are similar to *Microspalax brevipes* in that the genital organ does not extend to the opisthosomal margin and the dorsal shields are ornamented with polygons.

Microspalax major Trouessart et Neumann, 1888. Pl. II, Fig. 3

(Syn.: *Freyana* (*Microspalax*) *manicata* var. *major* Trouessart and Neumann, 1888: 336; Canestrini and Kramer, 1899: 35. *Microspalax* (*Connivelubus*) *major*: Dubinin, 1949: 208. *Microchelys* (*Microspalax*) *major*: Radford, 1953: 200. *Microspalax major*: Gaud and Till, 1961: 237. *Connivelobus major*: Dubinin, 1953: 357; Radford, 1958: 110, 111; Atyeo and Peterson, 1970: 137).

Comments: – We have the type slide of this species from the Trouessart Collection (no. 33 F 5) with 3 males and one female from "le Pétrel du Cap, *Daption capense*, Cap de B. Esp.", southern Atlantic Ocean; a second Trouessart slide (no. 33 F 4) with the same collecting data, identified as *Freyana* (*Microspalax*) *manicata* Var., contains 2 males and 1 female. The males are easily recognized as they have uniquely expanded opisthosomata and have dorsal crests on the apical segments of legs III and IV (Pl. II, Fig. 3).

Dubinin reported 1 tritonymph of this species from *Daption capense*, Cape Horn, 1842, and 1 tritonymph from *Fulmarus g. glacialis*, Novaya Zemlya, 1905. We believe both host associations are in error. We examined 38 skins of *Fulmarus glacialis* and 47 skins of *Daption capense* and have never collected any feather mites.

We believe that the true hosts for *Microspalax major* are *Procellaria* (*P.*) *aequinoctialis* L. and *P.* (*P.*) *parkinsoni* Gray as we have numerous collections from these birds from South America. It is anticipated that *P.* (*P.*) *westlandica* Falla, the third species of the subgenus *Procellaria*, will be a host of *M. major*. The fourth species of *Procellaria*, *P.* (*Adamastor*) *cinerea* Gmelin is reported to be the type host of *Microspalax manicatus* (Mégnin et Trouessart, 1884), but we believe this is in error (see Comments under *M. manicatus*).

Microspalax pterodromae Dubinin, 1949 Pl. II, Fig. 1; Pl. IV, Fig. 2

(Syn.: *Microspalax* (*Connivelobus*) *pterodromae* Dubinin, 1949: 208–209, Fig. 5. *Connivelobus pterodromae*: Dubinin, 1953: 357–359, Figs. 152, 155; Radford, 1958: 111.

Comments: – *Microspalax pterodromae* is a representative of a common form associated with species of *Pterodroma*. Males (Pl. II, Fig. 1) have the idiosomal terminus truncated and legs II are usually adorned with crests. We have collections from 15 of 26 species of *Pterodroma*, including the type host, *P. mollis* (Gould). Among the feather mites, obvious species differences are punctate to reticulate dorsal ornamentation, the presence or absence of coxal spines, and stylet-form (Pl. IV, Fig. 2) versus very thick (Pl. IV, Fig. 1) genital organs. Dubinin's (1953) report of *M. pterodromae* from *Pterodroma leucoptera* is probably incorrect as the males from this host have thick genital organs.

Microspalax puffini Dubinin, 1949

(Syn.: *Microspalax* (*M.*) *puffini* Dubinin, 1949: 204–205, Fig. 2. *Microspalax puffini*: Dubinin, 1953: 345–347, Fig. 149; Radford, 1958: 110).

Comments: – Based on our collection of 13 males and 9 females, there is only one form of male and it is equivalent to a heteromorph of leg form 1 with widened opisthosoma, coxal spines, and well developed crests on legs II. Dubinin (1953), although omitting the coxal spines, illustrated a heteromorphic male with an external genital organ extending to the adanal discs.

Dubinin (1949) described the species from *Puffinus tenuirostris* (Temminck), 1 male from Chukotka, USSR, 1938, and 7 males, 11 females, 14 tritonymphs, 12 larvae, Wrangel Island, USSR, 1939; *P. puffinus yelkouan* (Acerbi), 1 female, Sevastopol, 1878; and *P. l. lherminieri* Lesson, 1 female, Baema Island, 1904. In 1949, the host species were assigned to the subgenus *Puffinus*, hence the specific epithet; currently, the type species is assigned to *Puffinus* (*Neonectris*), the remaining two species to *Puffinus* (*Puffinus*).

Microspalax thyellodromae Dubinin, 1949

(Syn.: *Microspalax* (*M.*) *thyellodromae* Dubinin, 1949: 205–206, Fig. 3. *Microspalax thyellodromae*: Dubinin, 1953: 347–348, Fig. 150; Radford, 1958: 110.

Comments: – This species was described from *Puffinus* (*Thyellodroma*) *pacificus* (Gmelin), 1 male and 7 females from Réunion Island, 1897, and 18 males, 91 females, 23 tritonymphs, 3 protonymphs, Bonin Island, 1897. Later, Dubinin (1953) mentioned collecting this mite species from the same host from the Black Sea. Our collections from this host and the second species in the subgenus *Thyellodroma, P. bulleri* Salvin, as well as 7 additional species of *Puffinus* have homeo- and heteromorphic males. Dubinin's (1953) illustrations of the male venter and leg II are probably composites of the two male forms as the terminus is relatively narrow and the coxal spines are absent (homeomorph character states), but the crests on legs II are well developed (heteromorph character state).

DISCUSSION

Whenever possible, Dubinin attempted to demonstrate congruence between the systematics of feather mites and their hosts and often created specific epithets based on higher-level categories of birds. Most of Dubinin's 1949 species of the Microspalacinae were named for genera of the Procellariiformes and subgenera of *Puffinus* Brisson and *Oceanodroma* Reichenbach as arranged by Peters (1931, see Table 1); for genera, *Microspalax pterodromae* and *M. bulweriae*, and for subgenera, *Microspalax puffini, M. ardennae, M. thyellodromae*, and *M. cymochoreae*.

These names epitomize Dubinin's concept that mite species are associated with all species of higher-level host taxa. Presumably Dubinin consulted Peters (1931) for the systematics of the Procellariiformes, but major revisions for these birds have been completed after Dubinin, namely, Morony et al. (1975) and Jouanin and Mougin (1979). Major differences exist between the taxonomic arrangements of Peters and Jouanin and Mougin, especially for the subgenera of *Puffinus* (Table 1). If the later classification is phylogenetically correct, names of feather mites based on older classifications now have little meaning. To exemplify these problems, the host associations of four microspalacine species are included in Table 1.

Establishing host-commensal associations are often hazardous. Many previously defined species are in reality complexes of sibling species, and with small series from limited geographic regions, it is sometimes impossible to define the taxa. Many systematists (including Dubinin and the authors) have based systematic studies and host associations on collections from museum study skins. Such collections often contain only a few individuals and unless the mite species are collected more than one time, preferably from different museums, the validity of an association can be suspect. These facts, coupled with Dubinin's belief that commensal species were commonly restricted to higher-level taxa of birds has created many questionable associations. For example, Trouessart and Neumann (1888) listed *Daption capensis* as the host for *Microspalax major*; we have never collected any mites from this host, but routinely find *M. major* on skins of *Procellaria aequinoctialis* (new record) and *P. parkinsoni* (new record).

Table 1. *Puffinus* species as arranged by Peters (1931) (left column) and Jouanin and Mougin (1979) (right column). Subgenera of *Puffinus* in parentheses with host-commensal associations as superscripts, with capital letters indicating type hosts: A, a = *Microspalax ardennae*, B, b = *M. brevipes*, C, c = *M. thyellodromae*, D, d = *M. puffini*.

(*Ardenna*) Reichenbach	*Calonectris* Mathews & Iredale
leucomelas (Temminck)	*leucomelas*[a,b]
diomedea (Scopoli)	*diomedea*[A]
	(*Hemipuffinus*) Iredale
creatopus Coues	*creatopus*[a]
carneipes Gould	*carneipes*[a]
	(*Ardenna*)
gravis (O'Reilly)	*gravis*[b]
(*Thyellodroma*) Stejneger	(*Thyellodroma*)
pacificus (Gmelin)	*pacificus*[c]
bulleri Salvin	*bulleri*
(*Puffinus*) Brisson	(*Neonectris*) Mathews
griseus (Gmelin)	*griseus*[b]
tenuirostris (Temminck)	*tenuirostris*[D]
nativitatis Steele	*nativitatis*
	(*Puffinus*)
heinrothi Reichenow	*heinrothi*
puffinus (Brünnich)	*p. puffinus*[d]
opisthomelas Coues	*p. opisthomelas*
auricularis Townsend	*p. auricularis*
reinholdi Mathews	*gavia* (Forster)
r. huttoni Mathews	*huttoni*
assimilis Gould	*assimilis*[B]
lherminieri Lesson	*l. lherminieri*[d]
persicus Hume	*l. persicus*

We have had considerable success in obtaining feather mites from species of the Procellariiformes. Notable exceptions include zero feather mites from *Fulmarus glacialis* (38 skins examined) and *Daption capensis* (47 skins examined), both recorded as microspalacine hosts.

There are many undescribed species of microspalacine feather mites, and we suspect that many *Puffinus* species will have two microspalacine-associated species. These mites can be readily collected from museum study skins, therefore, systematic studies should be undertaken with a large data base. Limited field work could answer questions as to preferred microhabitats, an important consideration, especially when two or more congeners are associated with one host species.

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F. Sierra: A laboratory guide to *in vitro* transcription. *In: Biomethods (A. Azzi, J. M. Polak and H. P. Saluz, Eds.), Vol. 2, Birkhauser Verlag, Basel, 1990, 148 pp., Price 98 DM.*

The book is involved in a series of manuals dealing with modern methods, which have been widely employed in medicine, biochemistry and biotechnology over last years. It represents a typical example of up date laboratory guides that have become powerful tools for number of experimental workers. Like other manuals, the book is focused on practical approaches. It contains step-by-step protocols of diverse procedures directly used in or related to the complex strategy of *in vitro* transcription.

In vitro transcription was developed in the early 80s. Together with gel retardation and footprinting techniques it provides a unique approach to study events taking place in the cell nucleus. Cascade of differential gene activity is generally accepted as a mechanism responsible for cell differentiation, embryonal pattern formation, morphogenesis and many other processes. In most cases, transcription of DNA to RNA proves to be the crucial regulatory point. Transcriptional activation/inactivation of genes involves both cis- and trans-activating elements. The cis-elements are constituted by target DNA sequences (enhancers, hormone responsive elements and other structures of eukaryotic promoters). The trans-elements, on the other hand, are represented by a wide spectrum of proteins including transcription factors and hormone receptors. These molecules are, under appropriate conditions (e.g. presence of a hormone), capable of interaction with cis-elements and often possess specific DNA-binding domains. Moreover, structures of chromatin also appear to be of a great importance in ruling the gene expression. The goal of *in vitro* transcription is to discover those protein-DNA interactions resulting in gene transcription, the trans-elements being its main subject. Preparation of nuclear extracts surrounding the DNA *in vivo* and containing putative transcription factors is therefore the critical point of the experiment.

The book is organized in six major sections: (I) Introduction, (II) The biology of transcription, (III) Experimental, (IV) Condensed protocols for benchtop use, (V) Trouble-shooting guide and (VI) Appendix: Suppliers of special items and construction of commercially unavailable equipment. The Introduction provides a short historical review of the development of the method and its main achievements. Although the second chapter is only brief (8 pages), it is very useful in providing comprehensive information on the basic features and constituents of transcription in living cells.

The Experimental section is the largest part of the book, being subdivided in two groups. First, General considerations introduce a user into practice by a detailed description of the laboratory equipment required for both nuclear extract preparations and *in vitro* transcription itself. Basic aspects to be kept in mind working with biological

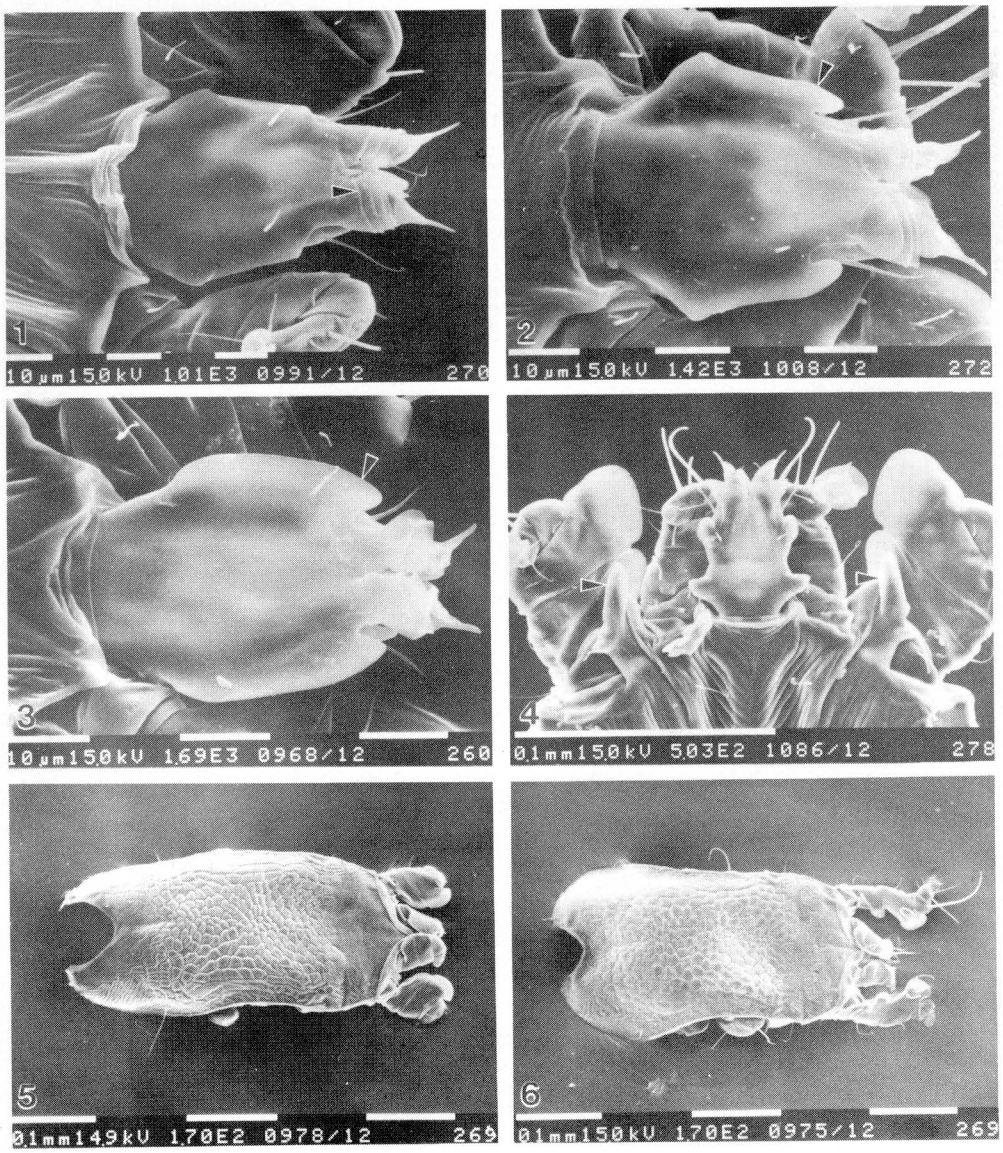
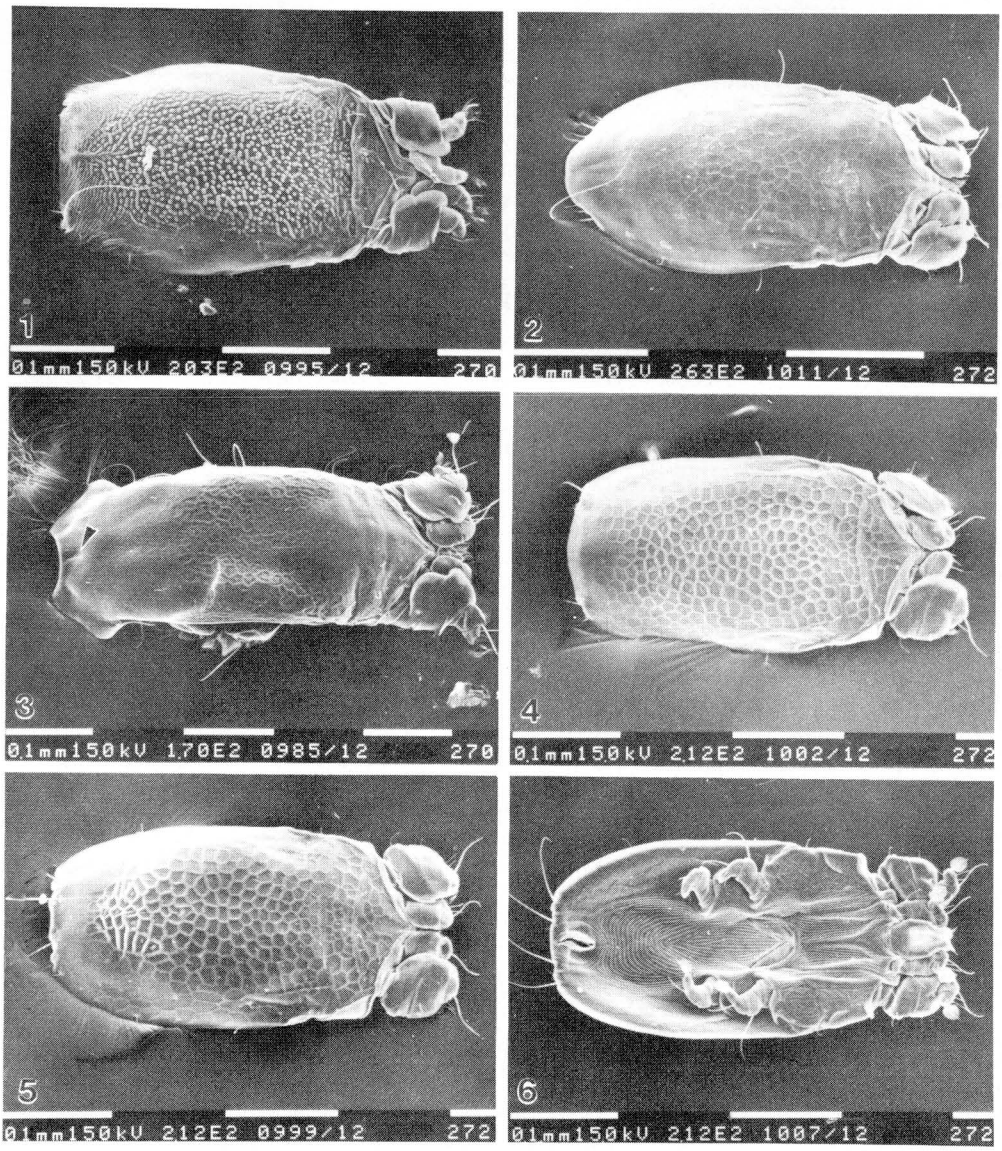


Fig. 1. *Microspalax brevipes* female, ventral gnathosoma, arrow = pseudorutellar process. **Fig. 2.** *Microspalax* sp. male from *Puffinus bulleri*, ventral gnathosoma, arrow = lateral flange. **Fig. 3.** *M. bulweriae* male, ventral gnathosoma, arrow = lateral flange. **Fig. 4.** *Microspalax* sp. male from *Pterodroma rostrata*, ventral gnathosoma, arrows = coxal spines. **Fig. 5, 6.** *M. ardennae*, dorsal aspects of homeo- and heteromorphic males.



Dorsal aspects. **Fig. 1.** *Microspalax* near *pterodromae* male from *Pterodroma cooki*. **Fig. 2.** *M. bulweriae* male. **Fig. 3.** *M. major* male; arrow = supranal concavity. **Fig. 4.** *M. brevipes* male. **Figs. 5, 6.** *M. brevipes* female, dorsal and ventral aspects.

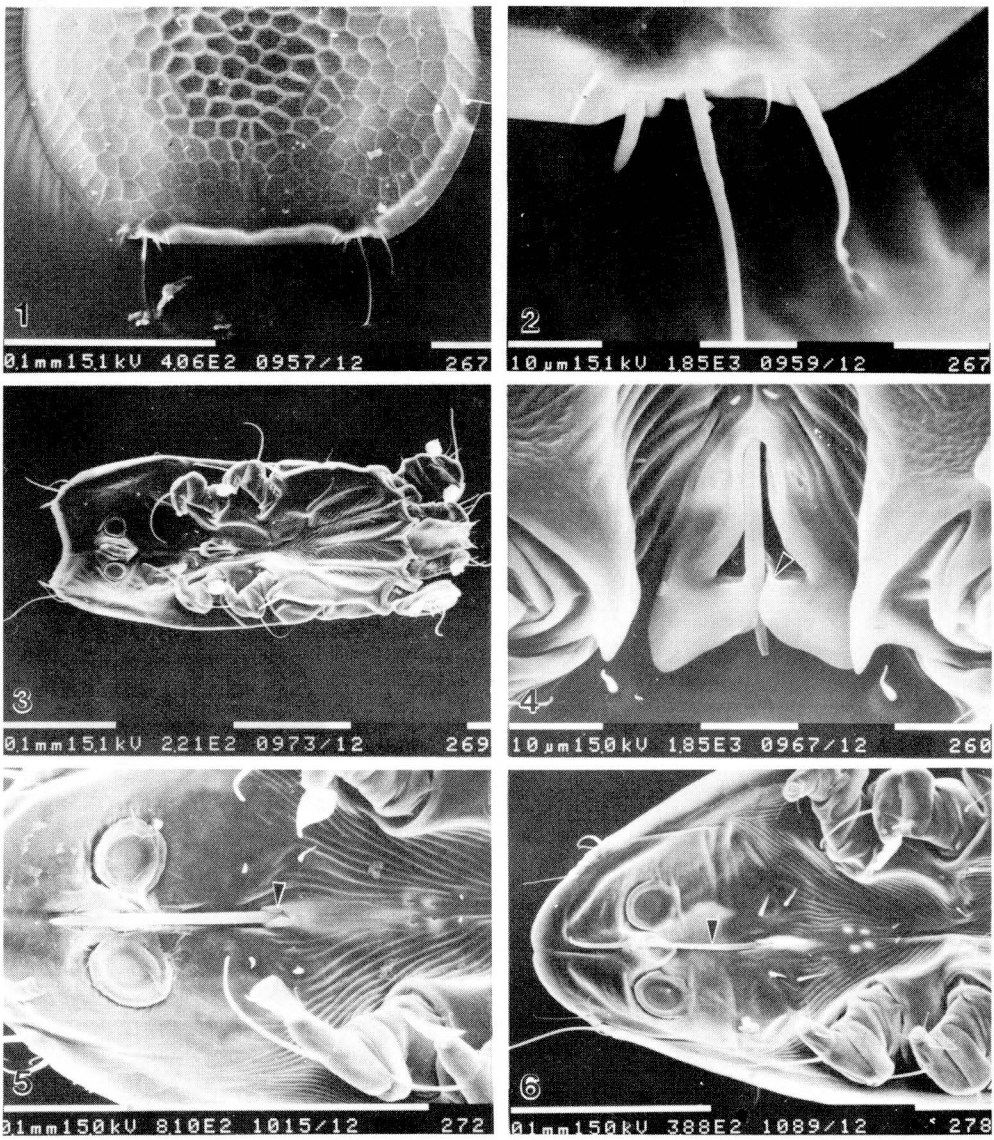


Fig. 1. *Microspalax cymochoreae* male, dorsal opisthosoma. **Fig. 2.** Enlargement of right posterolateral margin of Fig. 1 showing 5 setae, from left to right ps1, h3, h2, f2, ps2. **Fig. 3.** *M. ardennae* male, ventral aspect. **Fig. 4.** *M. ardennae* homeomorph, genital organ, arrow = aedeagal guides. **Fig. 5.** *M. bulweriae* male, ventral opisthosoma, arrow = genital organ emerging through idiosomal wall. **Fig. 6.** *M.* near *brevipes* male from *Pterodroma rostrata*, ventral opisthosoma, arrow = genital organ.

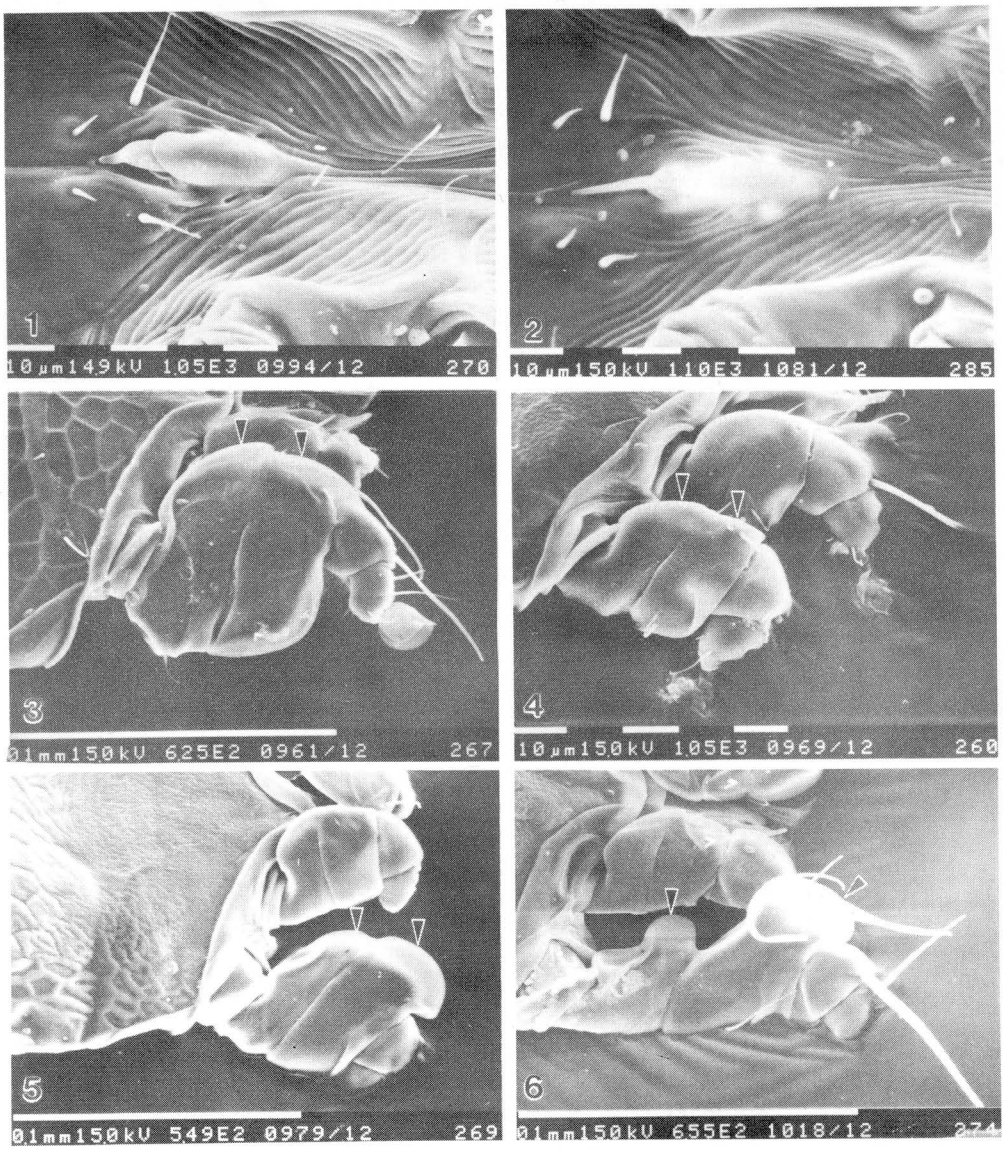


Fig. 1. *Microspalax* near *pterodromae* male from *Pterodroma cooki* with short, thick genital organ. **Fig. 2.** *M. pterodromae* male with short, thin genital organ. **Fig. 3.** *M. cymochoreae* male, leg II. **Fig. 4.** *M. ardennae* female, legs I and II. **Figs. 5, 6.** *M. ardennae*, legs I and II of homeomorphic (5) and heteromorphic (6) males. Figs. 3–6, left arrows = femora II, right arrows = genua II.