

Discheramocephalini, a new pantropical tribe of featherwing beetles (Coleoptera: Ptiliidae): description of new taxa and phylogenetic analysis

VASILY V. GREBENNIKOV^{1,2}

¹Entomology Research Laboratory, Ottawa Plant Laboratories, Canadian Food Inspection Agency, Ottawa, Ontario, Canada and ²Entomology Group, Institut für Spezielle Zoologie und Evolutionbiologie, Friedrich-Schiller-Universität, Jena, Germany

Abstract. Two new genera and eight new species of featherwing beetles (Coleoptera: Ptiliidae) possessing a remarkable horizontal perforation of the mesoventral keel are described: *Skidmorella vietnamensis* sp.n. (Vietnam), *S. memorabilis* sp.n. (Indonesia), *S. serrata* sp.n. (Vietnam), *Fenestellidium capensis* gen. et sp.n. (South Africa, type species), *F. kakamegaensis* sp.n. (Kenya), *Cissidium okuensis* sp.n. (Cameroon), *Dacrysoma usambarensis* gen. et sp.n. (Tanzania, type species) and *D. felis* sp.n. (Madagascar). A phylogenetic analysis of 24 taxa and 37 parsimony-informative characters supports the hypothesis of a single origin of the mesoventral perforation, thus uniting *Discheramocephalus*, *Skidmorella*, *Africoptilium*, *Fenestellidium*, *Cissidium* and *Dacrysoma* into a pantropically distributed clade, for which a new tribe Discheramocephalini (type genus *Discheramocephalus*) is proposed. Identification keys to Discheramocephalini genera and, in some cases, to species are provided. Each new species is illustrated with scanning electron microscopy images.

Introduction

The family Ptiliidae comprises beetles with the smallest body length and volume: the length of most species is between 0.6 and 1.2 mm, with a reported minimum of about 0.40 mm (Sörensson, 1997) or even 0.34 mm (Hall, 1999). Such extremely small organisms have suffered taxonomic neglect compared with other beetle families of similar diversity. This family includes about 635 species in 89 genera: 45 genera were established for a single species, and only 13 genera have 10 or more species (Johnson, 2007a; Newton & Thayer, 2007a; this paper). These numbers are very close to those for the hymenopteran family Trichogrammatidae, which also comprises small and very small insects: 30 of 80 genera are monotypic, and only 14 genera have 10 or more species (Pinto, 1997). Such a disproportionately high number of monotypic genera in families with smaller-than-average species is probably an artefact reflecting the taxonomic obscurity

of such groups. This implies that among small insects there are many new taxa to be discovered and described.

This assumption of taxonomic obscurity was correct for the Ptiliidae I collected recently in South Africa, Kenya, Tanzania and Cameroon. All specimens were united by possessing a perforation of the mesoventral keel between and slightly anterior of the mesocoxae (Figs 2I; 3I; 4I; 5E; 6E; 7G; 9H; 10F). Moreover, some could not be assigned to any known genus. The character of the ventrally extended mesoventral keel bearing a transparent opening in lateral view is a morphological attribute recorded just recently in the genus *Discheramocephalus* Johnson, 2007 (Grebennikov, 2008). A more extensive search has revealed that species with this character have been collected, but never described, from many tropical and subtropical parts of the world, including Florida, Central and South America, Africa, Madagascar, and the Asian-Australian tropics from Vietnam to Queensland in Australia. Furthermore, at least three previously known genera, namely *Africoptilium* Johnson, 1967, *Cissidium* Motschulsky, 1855 and *Skidmorella* Johnson, 1971, possess this remarkable feature. It was plausible to assume that such a novel and unique character was unlikely to be acquired more than once within Ptiliidae, thus offering a potentially valuable synapomorphy to define a previously

Correspondence: Vasily V. Grebennikov, Entomology Research Laboratory, Ottawa Plant Laboratories, Canadian Food Inspection Agency, K.W. Neatby Bldg., 960 Carling Avenue, Ottawa, Ontario K1A 0C6, Canada. E-mail: vasily.grebennikov@inspection.gc.ca

undetected clade. Thus, following descriptive work, a phylogenetic analysis was undertaken.

This paper presents: (i) descriptions and illustrations of eight new species of Ptiliidae from Africa, Madagascar and Southeast Asia possessing such perforated mesoventral keels; (ii) assignation to three previously known and two newly established genera; (iii) an identification key to genera, and, in most cases, to species, of all taxa sharing this morphological peculiarity; (iv) a cladistic analysis of Ptiliidae focused on those taxa with a perforated mesoventral keel, testing monophyly; and (v) the formal introduction of a new tribe comprising species with a perforated mesoventral keel.

Material and methods

Museum abbreviations

All specimens, including types of the new species (unless otherwise stated), are stored in the Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada (CNC). The following abbreviations of entomological collections in various museums are used throughout the text (with the name/s of the contact person/s, when applicable, in parentheses):

FMNH – Field Museum of Natural History, Chicago, U.S.A. (Alfred Newton);

MMUE – Manchester University Museum, Manchester, U.K.;
MNHN – Muséum National d'Histoire Naturelle, Paris, France (Louis Deharveng, Anne Bedos);

MVMA – Museum of Victoria, Melbourne, Australia;

MRAC – Musée Royal de l'Afrique Centrale, Tervuren, Belgium (Marc De Meyer);

NHM – Natural History Museum, London, U.K. (Maxwell V. L. Barclay);

NMW – Naturhistorisches Museum Wien, Wien, Austria (Harald Schillhammer, Heinrich Schönmann);

NZAC – New Zealand Arthropod Collection, Auckland, New Zealand;

OPU – Entomological Laboratory, Osaka Prefecture University, Osaka, Japan;

TMSA – Transvaal Museum, Pretoria, South Africa;

UQIC – University of Queensland Insect Collection, Brisbane, Australia;

ZMMU – Zoological Museum, Moscow University, Moscow, Russia;

ZMUC – Zoological Museum, University of Copenhagen, Copenhagen, Denmark.

Specimen collecting, handling and imaging

Most new species of Ptiliidae species described were collected by sifting forest leaf litter. All material was stored originally in 70% ethanol and then examined under a dissecting microscope to assign specimens to morpho-species. After preliminary assessment, a few (two to six, depending on the availability of material) specimens of each new species were

cleared with hot potassium hydroxide (KOH) to dissolve all non-cuticular parts, treated with isopropanol overnight, and then mounted in Euparal under a cover slip on microscope slides. For scanning electron microscopy (SEM), beetle specimens were allowed to dry and then glued by their elytra to the point of a fine entomological pin. This technique allowed rotation and tilting of the object in the SEM chamber, thus permitting many different SEM views, which are impossible to achieve with a regular table-mounting technique. Beetles were not coated for SEM, and therefore remain available for microscope slides or dry-mounts. KOH-treated whole-mounts in Euparal on microscope slides were studied with a compound microscope with magnification up to 900×. Morphological line drawings were made with the aid of a camera lucida attached to a compound microscope. Images of free or whole-mounted beetles were captured by a digital camera and then assembled in Photoshop onto a single plate. Some images were captured at different focal depths to create a combined image with the maximum depth of focus using COMBINEZ5 software (Hadley, 2007).

Rationale and implementation of phylogenetic analysis

The ingroup taxa include all new and previously known species possessing a horizontally perforated mesoventral keel (or a semi-perforated one, because it seems that in some species a thin membrane separates the bases of the two fossae in the vertical plane). This notable and previously undescribed feature initially was hypothesized to be a synapomorphy of a monophyletic assemblage of ptiliid genera. The choice of the outgroup taxa was less straightforward, because the basal branching events within Ptiliidae have never been reconstructed using phylogenetic analysis. This ambiguity necessitated the inclusion of other Ptiliid taxa as multiple outgroups to test the monophyly of the species with perforated mesoventral keels. For example, some ptiliids with a seemingly non-perforated mesoventral keel (*Cissidium*) closely resemble others with a perforated keel (members of the new genus *Dacrysoma* described below), suggesting inclusion of the former genus in the analysis. In addition, habitually dissimilar *Millidium minutissimus* (Ljungh, 1804) possesses differently shaped foveae in the mesoventrum, necessitating the inclusion of this species. Members of the two recognized groups of genera, namely the tribe Ptiliini (= Pterycini of Hall, 2003), the subfamily Acrotrichinae, and some other distantly related taxa of Ptiliidae were included to represent different branches of the family (see below for species names and label data). Members of two genera with wide hindwing membranes, believed to be a sister-group (or two consequent sister-groups) to the rest of the family, were used to root the tree: *Motschulskium sinuatocolle* Matthews, 1872 and *Nossidium pilosellum* (Marshall, 1802).

Label data for outgroup taxa included in the analysis

Ptenidium gressneri Erichson, 1845: Sweden, Östergötland, Nykvarnparken, 14.xi.2001 (*Jansson*).

Ptiliola kunzei (Heer, 1841): Sweden, Södermanland Bylsjöns norra inlopp, 10.ix.1997 (Viklund).

Ptilium modestum Wankowicz, 1869: Sweden, Skåne, Hallands Väderö, 13.x.1984 (Sörensson).

Ptilium schwarzi (Flach, 1887): Sweden, Skåne, Maltesholm, 28.vii.1984 (Sörensson).

Millidium minutissimus (Ljungh, 1804): U.S.A., Illinois, Will Co., 1mi E of Frankfort, 6.ix.1952 (Dybas). (FMNH). U.S.A., Illinois, Kenosha Co., Kenosha, 16.vi.1966 (Suter). (FMNH).

Limulopteryx loebli Hall, 2003: data from Hall, 2003.

Ptinella aptera (Guérin-Méneville, 1839): Germany, Großschönaus Umgebung, 27.vii.1985 (Sieberg).

Nephanes titan (Newman, 1834): Sweden, Höör, 5.xi.2000 (Ericson).

Acrotichis atomaria (DeGeer, 1774): Sweden, Maltesholm, 11.viii.1985 (Sörensson).

Motschulskium sinuatocolle Matthews, 1872: U.S.A., California, San Mateo Co., Pillar Point, 31.x.2005 (Seago & Shepard). U.S.A., California, Diego Co., San Diego, 30.v.1975 (Baranowski). U.S.A., California, Del Norte Co., Del Norte Coast Redwoods State Park, False Klamath Cove, 17.vi.2000 (Newton & Thayer).

Nossidium pilosellum (Marshall, 1802): Bulgaria, Albena, 24.viii.1986 (Leiler).

Cissidium sp.: Kenya, Kakamega forest, 10–12.xi.2002 (Grebennikov).

Phylogenetic analysis was performed using a matrix (Table 1) comprising 27 terminal taxa and 37 parsimony-informative characters compiled in WINCLADA version 1.00.08 (Nixon, 2002), and analysed using HENNIG86 (Farris, 1988). Two different analyses were implemented. For analysis one, all characters were equally weighted and the most parsimonious trees were searched using the exhaustive search option (implicit enumeration, command 'ie*' in HENNIG86). For analysis two, the successive approximation approach (Farris, 1969) was implemented by the cyclical use of the commands 'mh*', 'bb*' and 'xs w' until the tree statistics stabilized. For both analyses, the multi-state characters were not ordered. Examination of the obtained trees, their consensus, and bootstrap analysis using 1000 replications were performed with WINCLADA.

Terminology

Most of the terms used in this paper are those generally adopted for Ptiliidae (see, for example, Sörensson, 1997). The terms 'mesoventrite' and 'metaventrite', however, follow Lawrence (1999) for the misapplied terms 'mesosternum' and 'metasternum'; 'mesosternal' and 'metasternal' lines of Ptiliidae are therefore called 'mesoventral' and 'metaventral' lines.

Discheramocephalini trib.n.

Type genus. *Discheramocephalus* Johnson, 2007.

Diagnosis. Members of the tribe Discheramocephalini are unique among Ptiliidae for their horizontally oriented

deep fossa on each side of the mesoventral keel opening laterad, each fossa deeper than its external diameter, thus seemingly perforating the mesoventral keel and making it transparent in lateral view. Only in *Cissidium* is the layer of the exoskeleton separating the two fossae not transparent in lateral view, and the fossae are not deeper than the diameter of their external openings. Most of the species' body is rather high or circular in cross-section, with height/width ratio 0.85–0.95. Many, but not all, Discheramocephalini species have the posterior edge of the pronotum concave at middle, and an externally obliterate suture between the meso- and metaventrum.

Description. Body 0.4–1.1 mm in length; elongate, nearly cylindrical and not flattened dorso-ventrally; eyes present, in some species large and with large protruding facets; antennae 11-segmented; head with or without two deep vertical fossae or transverse grooves behind eyes; pronotum with or without longitudinal grooves, with or without transversely oriented line of depressions along posterior edge, posterior margin in some species concave at middle; procoxae almost contiguous; proventrum without propleural suture; mesocoxae not contiguous; mesoventral keel with deep horizontally oriented fossae opening laterally with their bottoms contiguous inside beetle, thus forming transparent opening in lateral view; mesoventrum in some with deep fossa in anterior lateral corners; suture separating meso- and metaventrum between mesocoxae and laterad of them either visible externally or completely obliterated; meso- and metaventral lines absent or present; elytra covering entire abdomen, not truncate apically; scutellum with or without longitudinal keel at middle, with or without deep fossa on each side; alacrista without spur; hindwings present, abdominal glands absent; pygidial teeth present, variable in shape, or absent; parameres absent; spermatheca and aedeagus of variable shape.

Monophyly and phylogenetic relationships. The tribe Discheramocephalini was supported consistently as a monophyletic group (Fig. 14) in the phylogenetic analysis. No attempt was made to identify sister-group relationships of Discheramocephalini within the apparently non-monophyletic subfamily Ptiliinae.

Composition and geographical distribution. The tribe Discheramocephalini currently includes six genera and 28 species (of these, two genera and eight species are newly described here): *Discheramocephalus* Johnson, 2007 (*D. semisulcatus* Johnson, 2007 from Solomon Islands; *D. brucei* Grebennikov, 2008 from Cameroon; *D. elisabethae* Grebennikov, 2008 from Cameroon; *D. mikaeli* Grebennikov, 2008 from Tanzania; *D. stewarti* Grebennikov, 2008 from Bolivia; *D. jarmilae* Grebennikov, 2008 from Bolivia; *D. minutissimus* Grebennikov, 2008 from Indonesia); *Skidmorella* Johnson, 1971 (*S. magnifica* Johnson, 1971 from Papua New Guinea, the Solomon Islands and Japan; *S. amamiana* Sawada & Hirowatari, 2003 from Japan; *S. quadrisulcua* Sawada & Hirowatari, 2003 from Japan;

S. vietnamensis sp.n. from Vietnam; *S. memorabilis* sp.n. from Indonesia; *S. serrata* sp.n. from Vietnam); *Africoptilium* Johnson, 1967 (*A. marginatum* Johnson, 1967 from the Democratic Republic of Congo; *A. mimicum* Johnson, 1967 from Tanzania; *A. concinnum* Johnson, 1967 from the Democratic Republic of Congo); *Fenestellidium* gen.n. (*F. capensis* sp.n. from South Africa; *F. kakamegaensis* sp.n. from Kenya); *Cissidium* Motschulsky, 1855 (*C. basale* Motschulsky, 1855 from Panama; *C. rufescens* Motschulsky, 1855 from Panama; *C. matthewsi* Johnson, 2007 from Japan; *C. adustipenne* Motschulsky, 1869 from India; *C. scutellaris* (Deane, 1931) from Australia; *C. crowsoni* Johnson, 1982 from New Zealand; *C. foveolatum* Johnson, 1982 from New Zealand; *C. okuensis* sp.n. from Cameroon); *Dacrysoma* gen.n. (*D. usambarensis* sp.n. from Tanzania; *D. felis* sp.n. from Madagascar). I have seen other undescribed species of the genera *Discheramocephalus* and *Cissidium* (for details, see below under the respective genera), and representatives of presumably undescribed genera belonging to this tribe. The true diversity of Discheramocephalini taxa remains to be discovered.

The tribe Discheramocephalini is pantropical in distribution, including at least two speciose genera, *Discheramocephalus* and *Cissidium*, that are recorded from all the main tropical regions of the world. Each of the remaining genera seems to be confined to a single zoogeographical region, although this pattern is likely to change as more species become known. A few species of the genera *Discheramocephalus*, *Skidmorella* and *Cissidium* were found just north of the Tropic of Cancer (U.S.A.: Florida; Japan: mainland and the Okinawa Archipelago), and one species of the genus *Fenestellidium* gen.n. was recorded just south of the Tropic of Capricorn (southern part of South Africa).

Bionomics. All specimens of Discheramocephalini with known habitat data were collected in flight intercept traps or by sifting leaf litter in primary, or mature secondary, wet and semi-wet forests. At least one specimen of *Africoptilium* sp. had fungal spores in the gut, suggesting mycophagy among Discheramocephalini, which is widespread in Ptiliidae (Hammond & Lawrence, 1989). All known Discheramocephalini have large eyes, which implies that vision may play an important role in their behaviour. No data about Discheramocephalini suggest parthenogenesis, wing reduction, wing polymorphism, or strong association with social insects, fungal sporocarps, running water, endogean or subcortical habits.

Identification key to the genera of the tribe Discheramocephalini

1. Pronotum on each side with one or two longitudinally oriented grooves extending for at least half of pronotal length (Figs 1D; 2D) 2
 - Pronotum without longitudinally oriented grooves (Fig. 5A), or at maximum, with round basal depressions that extend for less than half of pronotal length (Fig. 8F) 3
2. Hind coxae almost contiguous and separated by less than one-tenth of metaventral width (Fig. 1B); head posterior of eyes with deep transverse groove extending ventrad on lateral surface of head (Fig. 1D, G, E); scutellum and dorsal surface of head between eyes each without two deep fossae in a transverse row (Fig. 1D) *Discheramocephalus* Johnson, 2007
 - Hind coxae not contiguous, clearly separated by more than one-quarter of mesoventral width (Fig. 3D); head posterior of eyes with deep transverse groove not extending ventrad on lateral surface of head (Fig. 3E); scutellum and dorsal surface of head between eyes each with two deep fossae in a transverse row (Fig. 11 A–C) *Skidmorella* Johnson, 1971
3. Pronotum with a transverse row of four to eight poorly delimited depressions along posterior margin as in Fig. 8F (not the much smaller, clearly delimited and round punctures each bearing a small seta as in Fig. 7F found in some *Fenestellidium*); external perimeter of mesocoxal cavities with serrations extending halfway laterad along clearly delimited meso-metaventral suture (Fig. 8E, H) *Cissidium* Motschulsky, 1855
 - Pronotum without a transverse row of depressions along posterior margin (Fig. 9E); external perimeter of mesocoxal cavities regularly shaped and without serration (Fig. 9H); meso- and metaventral junction laterad of mesocoxae obliterated externally and only visible as a line of cuticular thickness in transparent light (Fig. 9H) 4
4. Body behind pronotum about 1.8× as wide (or as high) as pronotum (Fig. 9A); apical antennomere with median constriction separating basal and distal swollen parts and thus resembling a dumbbell (Fig. 10B); the meso-metaventral suture between middle coxae forming a clearly delimited border between two sclerites (Fig. 10F) *Dacrysoma* gen.n.
 - Body behind pronotum at most about 1.5× as wide (or as high) as pronotum (Fig. 7A); apical antennomere without median constriction (Fig. 7G); the meso-metaventral suture between middle coxae not or poorly visible externally, thus not forming a clearly delimited border between two sclerites (Fig. 7I) 5
5. Pronotum without punctures in basal half, not pubescent, with a few (8–12) long and symmetrically located setae on each side (Fig. 5G); perforation of mesoventral keel circular in lateral view (Fig. 5F); meso- and metaventral longitudinal lines present (Fig. 5C); hind margin of metaventrum between metacoxae without teeth (Fig. 5I) *Africoptilium* Johnson, 1967
 - Pronotum with at least some punctures in basal half, pubescent, without long and symmetrically located setae on each side (Fig. 7F); perforation of mesoventral keel ellipsoid in lateral view, about 3× higher than wide (Fig. 7I); meso- and metaventral longitudinal lines absent (Fig. 7C); hind margin of metaventrum between metacoxae with two large teeth pointed posteriorly (Fig. 6D) *Fenestellidium* gen.n.

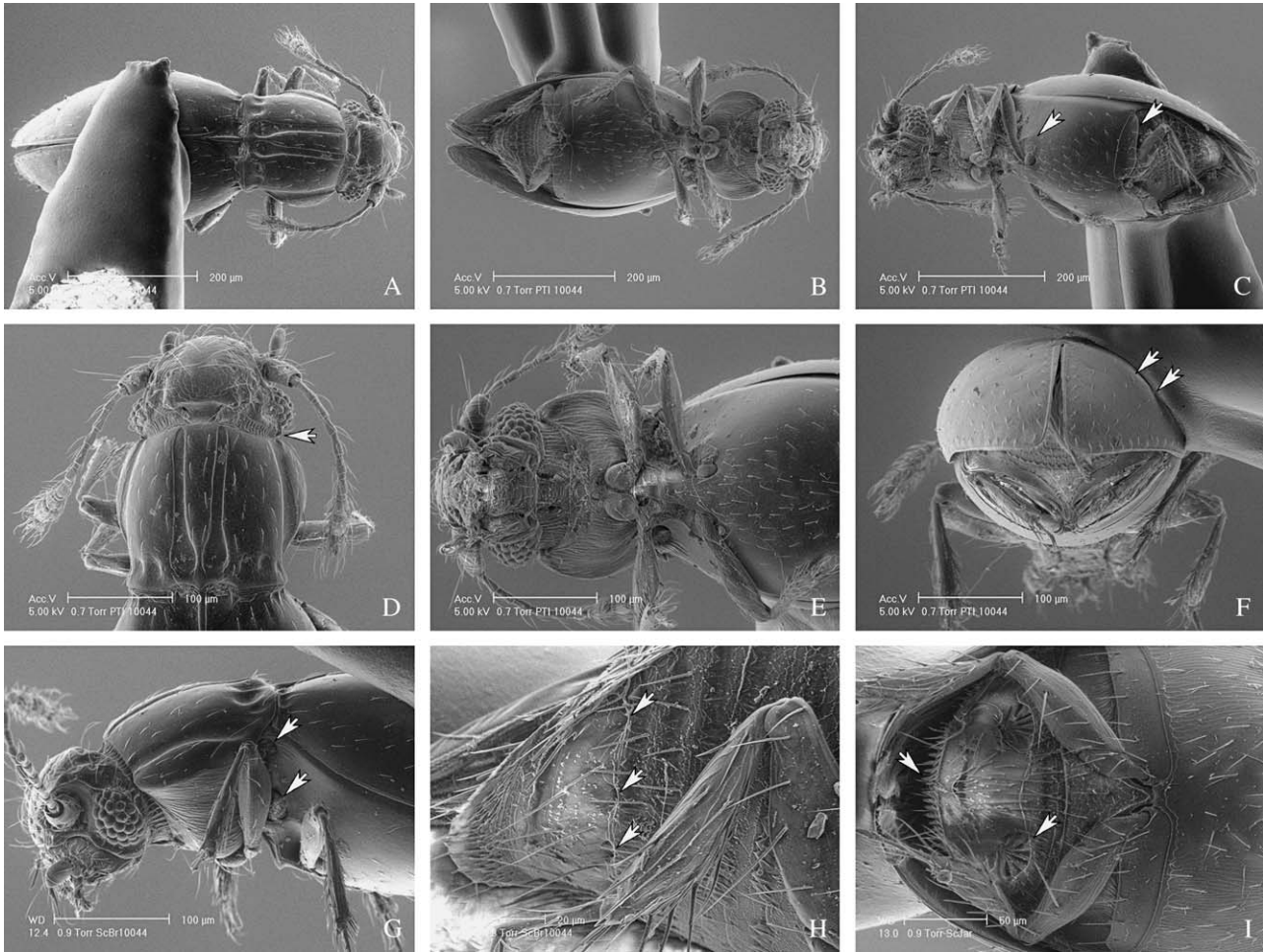


Fig. 1. *Discherocephalus brucei* (A–H) and *D. jarmilae* (I) (Coleoptera: Ptiliidae) from Cameroon and Bolivia, respectively; paratypes, scanning electron microscopy images (from Grebennikov, 2008). (A) habitus, dorsal view; (B) habitus, ventral view; (C) habitus, left ventro-lateral view (left arrow indicates lack of visible meso-metaventral suture, right arrow indicates markedly transverse metacoxae); (D) anterior half of body, dorsal view (arrow indicates transverse postocellar groove); (E) anterior half of body, ventral view; (F) abdomen, posterior view (arrow indicates elytral setae arranged in longitudinal rows); (G) anterior half of body, left lateral view (upper arrow indicates vertical fossa in anterior corner of mesoventrum, lower arrow indicates horizontal fossa in mesoventral keel); (H) abdomen, right latero-ventral view (arrows indicate three of five cavities on abdominal sternite VIII); (I) posterior half of body, ventral view (left arrow indicates serration on pygidium, right arrow indicates one of two large cavities on abdominal sternite VIII).

***Discherocephalus* Johnson, 2007** (Fig. 1)

Type species. *Discherocephalus semisulcatus* Johnson, 2007, original designation.

Diagnosis. Members of the genus *Discherocephalus* are easily recognizable within all of Ptiliidae by having a deep transverse groove on the head behind the eyes, which crosses the dorsal surface of the head (Fig. 1D), extending to the ventral surface (Fig. 1E). The possession of two or more deep cavities on sternite VIII is also unique among Ptiliidae (Fig. 1H, I). Within the tribe Discherocephalini,

species of *Discherocephalus* are unique in possessing almost contiguous metacoxae (Fig. 1B, C, I).

Monophyly and phylogenetic relationships. The genus *Discherocephalus* is a strongly supported monophyletic group with a bootstrap value above 95% and five synapomorphies, as indicated in Fig. 14. It is a member of the *Discherocephalus* + *Skidmorella* clade, which may include *Africoptilium* (Fig. 14).

Remarks. This pantropical genus has seven recently described species; for generic re-description, keys to species, bionomics and distribution, see Grebennikov (2008).

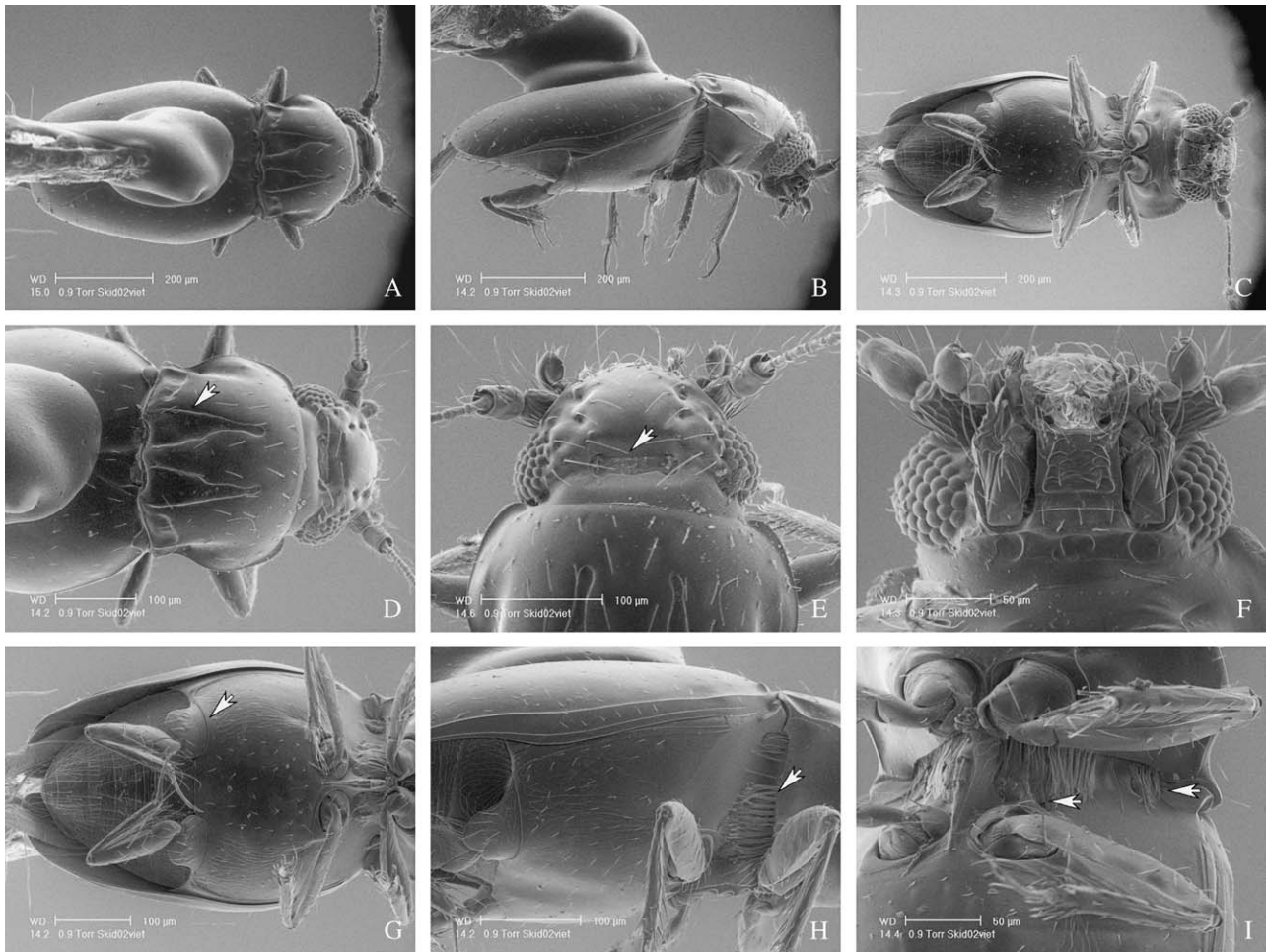


Fig. 2. *Skidmorella vietnamensis* sp.n. (Coleoptera: Ptiliidae) from Vietnam; holotype, scanning electron microscopy images. (A) habitus, dorsal view; (B) habitus, right lateral view; (C) habitus, ventral view; (D) head and pronotum, dorsal view (arrow indicates pronotal grooves markedly widened posteriorly); (E) head, dorsal view (arrow indicates transverse groove connecting two dorsal fossae); (F) head, ventral view; (G) posterior half of body, ventral view (arrow indicates nearly subquadrate metacoxae); (H) middle part of body, right latero-ventral view (arrow indicates posteriorly directed hair-like projections); (I) mesoventral keel, left latero-ventral view (left arrow indicates fossa in mesoventral keel; right arrow indicates fossa in anterior corner of mesoventrum).

Skidmorella Johnson, 1971

Type species. *Skidmorella magnifica* Johnson, 1971, by original designation.

Diagnosis. Within the tribe Discheramocephalini, members of the genus *Skidmorella* can be distinguished easily by the presence of deep fossae on the head behind the eyes (Fig. 4G) and two more on the scutellum (Fig. 11A–C). Moreover, *Skidmorella* is the only genus of Discheramocephalini with the combination of markedly developed longitudinal pronotal grooves (Figs 2A; 3A; 4A) and separate metacoxae (Figs 2G; 3D; 4D).

Description. Body between pronotum and elytra in dorsal view constricted; body behind pronotum not swollen later-

ally and vertically; longitudinally oriented micro-ridges on ventral surface of prothorax absent; elytral setae forming seven or eight longitudinal rows; transversely oriented deep depression behind eyes present, as two large fossae; group of 100–200 small punctures forming transverse band on head behind eyes absent; apical antennomere not dumbbell-shaped; longitudinal depressions of labium present; posterior edge of pronotum at middle straight or slightly convex or concave; depressions on pronotum present as grooves as long as half, or more, pronotal length; longitudinal keel on scutellum absent or present; transverse row of 12–13 round punctures on base of elytra and scutellum absent; two deep exoskeletal fossae on scutellum present; meso-metaventral suture between mesocoxae not visible externally; meso-metaventral suture laterad of mesocoxae not visible externally, present as internal thickening of cuticle; posteriorly pointed serration along meso-metaventral suture laterad of

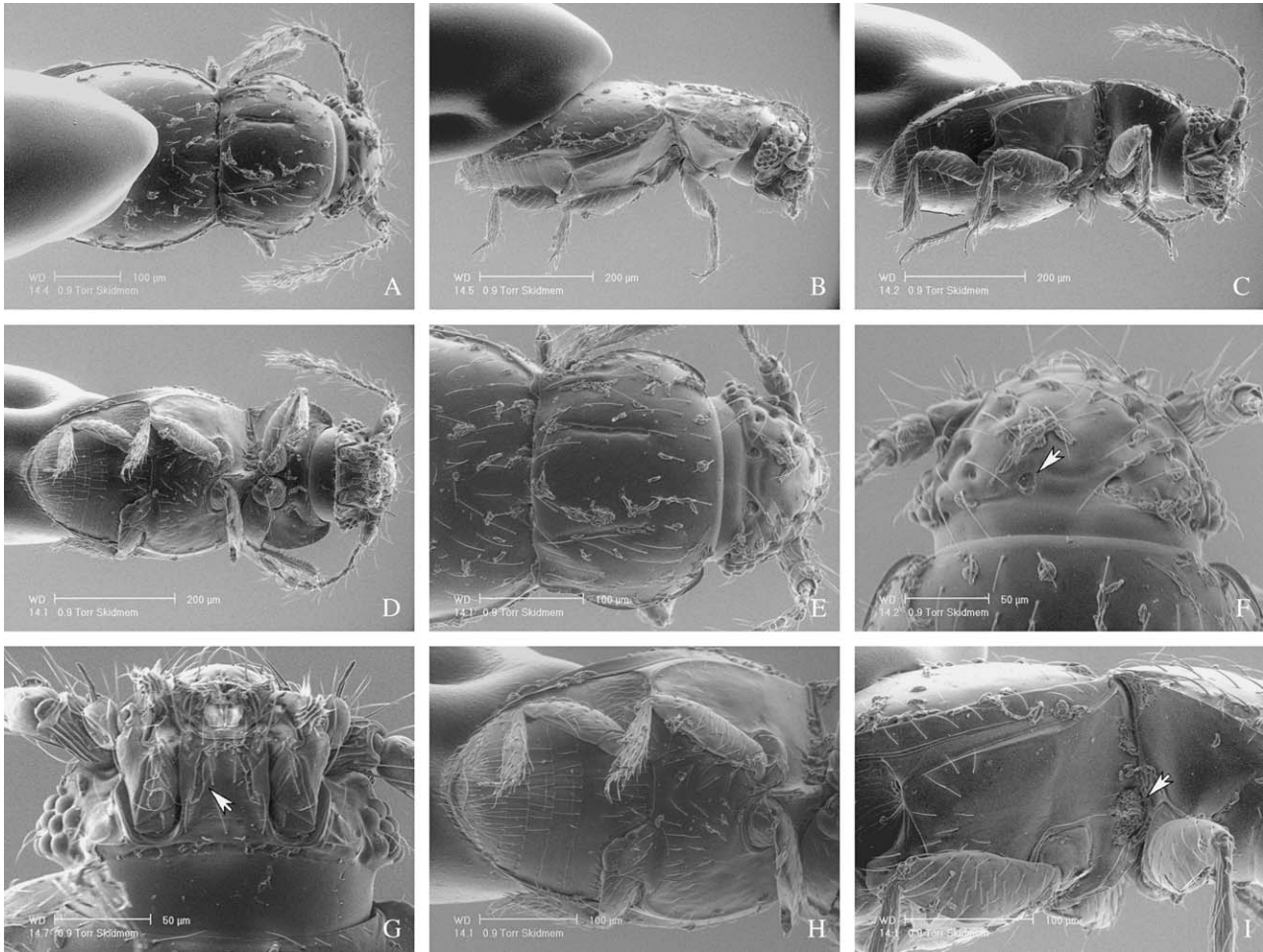


Fig. 3. *Skidmorella memorabilis* sp.n. (Coleoptera: Ptiliidae) from Indonesia; paratype, scanning electron microscopy images. (A) habitus, dorsal view; (B) habitus, right lateral view; (C) habitus, right latero-ventral view; (D) habitus, ventral view; (E) head and pronotum, dorsal view; (F) head, dorsal view (arrow indicates left dorsal fossa); (G) head, ventral view (arrow indicates left longitudinal groove on labium); (H) posterior half of body, ventral view; (I) meso- and metaventrites, right lateral view (arrow indicates fossa in mesoventral keel).

mesocoxae absent; metaventral longitudinal lateral lines absent; horizontal perforation of mesoventral keel as visible in lateral view round, transparent in lateral view; mesoventrum without transverse grooves; alacrista of metathorax at middle without short setae along margins; metacoxae not transverse, separated by one-quarter of metaventral width; posteriorly oriented projection of metaventral plate between metacoxae without two large lateral teeth or with two relatively large and sharply pointed lateral teeth; transversely oriented group of about 50–70 closely adjacent round micropores along posterior edge of tergite VIII absent; cavities on abdominal sternum VIII absent; single elongate internal sclerite alongside aedeagus absent; spermatheca mainly globular (as in Fig. 13J), rarely tube-shaped (Fig. 13K).

Composition and geographical distribution. The genus *Skidmorella* includes, alongside three new species from Vietnam and Indonesia described herein, three other valid

species: *S. magnifica* Johnson, 1971: 44 (from Bismarck Archipelago of Papua New Guinea, the Solomon Islands, and Shikoku, Japan; holotype in ZMUC; examined); *Skidmorella amamiana* Sawada & Hirowatari, 2003: 312 (from the Okinawa Archipelago, Japan; holotype in OPU; not examined); and *Skidmorella quadrisulcua* Sawada & Hirowatari, 2003: 313 (from the Okinawa Archipelago, Japan; holotype in OPU; not examined).

Monophyly and phylogenetic relationships. The genus *Skidmorella*, as presently defined, is certainly a non-monophyletic assemblage incorporating all *Discherocephalini* species with longitudinal furrows on the pronotum that do not belong to *Discherocephalus*. Two *Skidmorella* species, namely *S. vietnamensis* sp.n. and *S. serrata* sp.n., differ from the rest of the genus in having differently shaped pronotal furrows, serrate pronotal lateral margins (*S. serrata*), non-globular spermatheca (*S. serrata*; state of this character is unknown in

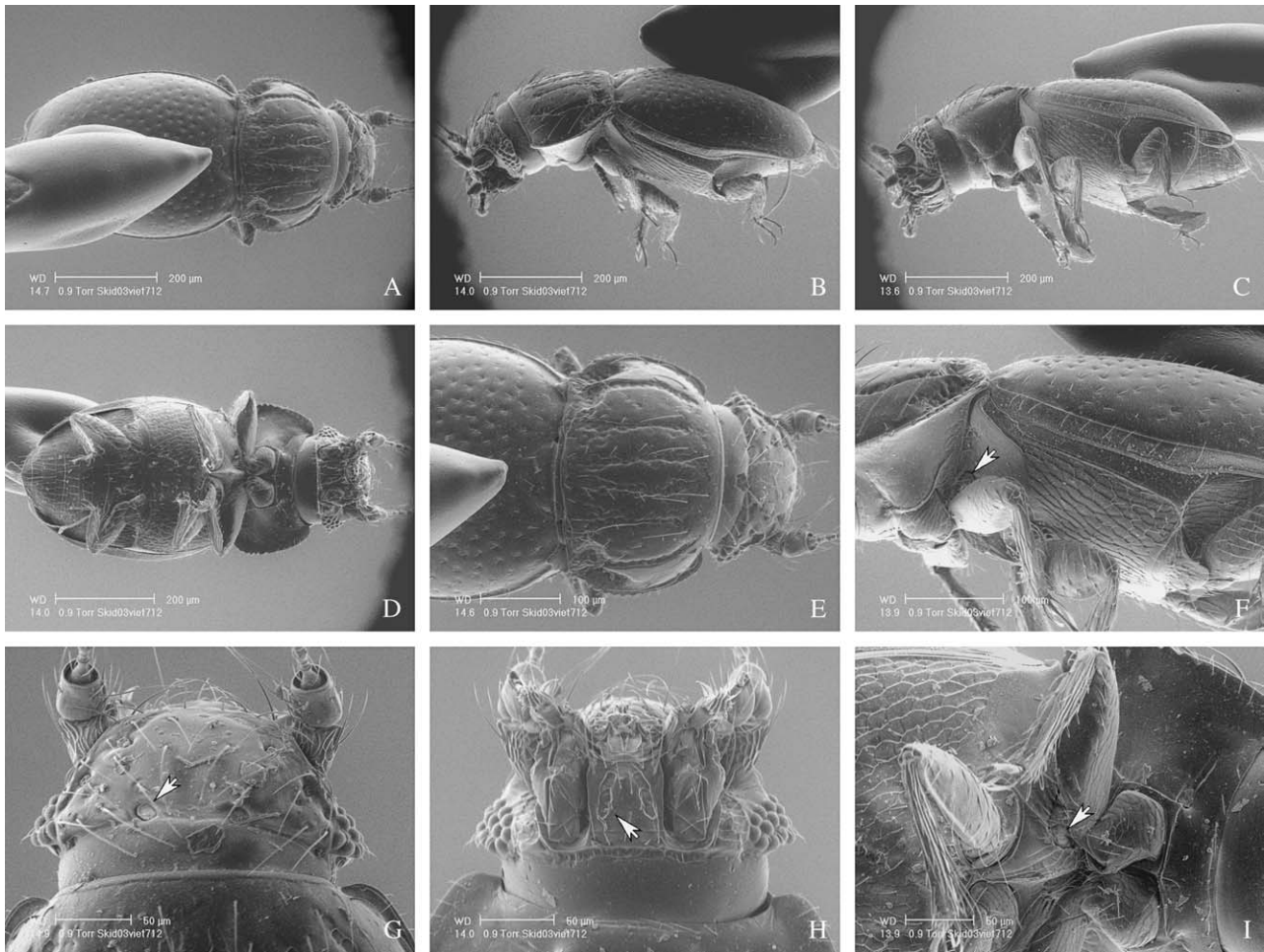


Fig. 4. *Skidmorella serrata* sp.n. (Coleoptera: Ptiliidae) from Vietnam; paratype, scanning electron microscopy images. (A) habitus, dorsal view; (B) habitus, left lateral view; (C) habitus, left latero-ventral view; (D) habitus, ventral view; (E) head and pronotum, dorsal view; (F) middle part of body, left lateral view (arrow indicates fossa in mesoventral keel); (G) head, dorsal view (arrow indicates dorsal fossa); (H) head, ventral view (arrow indicates left longitudinal groove on labium); (I) mesoventral keel, right ventro-lateral view (arrow indicates fossa in mesoventral keel).

S. vietnamensis), a transverse groove connecting dorsal fossae on the head (*S. vietnamensis*) and an extra pair of deep fossae in the anterior lateral corners of the mesoventrum (*S. vietnamensis*). Most probably, the genus *Skidmorella* is paraphyletic with respect to *Discheramocephalus*. Exclusion of the two above-named species would probably leave the rest of *Skidmorella* monophyletic; such action is, however, postponed until more *Discheramocephalini* species are discovered.

Bionomics. All known specimens of this genus were collected from forest leaf litter.

Identification key to Skidmorella species
(modified from Sawada & Hirowatari, 2003)

1. Disc of pronotum with two longitudinal furrows (Fig. 2A) 2

– Disc of pronotum with four or six longitudinal furrows (Fig. 4A) 5

2. Head behind eyes with two deep fossae connected by transverse groove (Fig. 2E); pronotal furrows at base about 4× wider than at apex (Fig. 2A); mesoventrum on each side with deep fossa in anterior lateral corners (Fig. 2I) *S. vietnamensis* sp.n. (Vietnam)

– Head behind eyes with two deep fossae not connected by transverse groove; pronotal furrows at base not wider than at apex; mesoventrum on each side without deep fossa in anterior lateral corners 3

3. Base of pronotal furrows nearly contiguous to basal edge on pronotum; pronotal furrows sinuate, long, extending for some 80% of pronotal length 4

– Base of pronotal furrows clearly separated from basal edge of pronotum by distance subequal to eye diameter (Fig. 3E); pronotal furrows nearly straight, slightly

- convergent anteriorly, short, of about 50% of pronotal length (Fig. 3E) *S. memorabilis* **sp.n.** (Indonesia)
4. Pronotal furrows sinuate and distance between them smallest at their middle; aedeagus without sclerite internally *S. magnifica* Johnson, 1971 (Bismarck Archipelago of Papua New Guinea, the Solomon Islands, Shikoku, Japan)
 - Pronotal furrows sinuate and distance between them smallest distally; aedeagus with sinuate sclerite internally *S. amamiana* Sawada et Hirowatari, 2003 (Okinawa Archipelago, Japan)
 5. Disc of pronotum with four longitudinal furrows, the medial being half the length of lateral ones; posterior half of pronotal margins not serrate; spermatheca globular *S. quadrisulcia* Sawada et Hirowatari, 2003 (Okinawa Archipelago, Japan)
 - Disc of pronotum with six longitudinal furrows subequal in length (Fig. 4E); posterior half of pronotal margins finely serrate (Fig. 4E); spermatheca a long and coiled tube (Fig. 13K) *S. serrata* **sp.n.** (Vietnam)

Skidmorella vietnamensis **sp.n.**
(Figs 2; 11A; 13A)

Diagnostic description. Body length 0.80 mm ($n = 1$); two transverse fossae on head dorsally behind eyes connected by groove; disc of pronotum on each side with one longitudinal furrow not shorter than half of pronotal length; pronotal margins in posterior half not serrate; setae in anterior part of pronotum not longer than those in posterior part; mesoventrum with deep fossa on each side at anterior corners; posteriorly oriented projection of metaventral plate between metacoxae without two teeth adjacent to, and mediad of, coxae; aedeagus Fig. 13E; spermatheca unknown.

Etymology. The specific epithet *vietnamensis* derives from Vietnam, the type locality of this species.

Type material. *Holotype* (male; deposited in MNHN) mounted on Euparal microscope slide and previously used for SEM (antennomeres 3–11 were lost after SEM): VIETNAM, Lam Dong Dalat, Bi Doup, Nui Gia Rich, 1440 m, 18.xii.1998 (*L. Deharveng & A. Bedos*).

Skidmorella memorabilis **sp.n.**
(Fig. 3; 11B; 13C, J)

Diagnostic description. Body length 0.69–0.70 mm ($n = 2$); two transverse fossae on head dorsally behind eyes not connected by groove; disc of pronotum on each side with one longitudinal furrow not shorter than half of pronotal length; pronotal margins in posterior half not serrate; setae in anterior part of pronotum not longer than those in posterior part; mesoventrum without deep fossa on each

side at anterior corners; posteriorly oriented projection of metaventral plate between metacoxae with two teeth adjacent to, and mediad of, coxae; aedeagus Fig. 13C; spermatheca Fig. 13J.

Type material. *Holotype* (female; deposited in MNHN) mounted on Euparal microscope slide: INDONESIA, Sulawesi Selatan, Latimojong, 1980 m, 28.vii.1990 (*L. Deharveng & A. Bedos*). *Paratypes*: two, with the same data as holotype; one unsexed specimen in 70% ethanol and another male mounted on Euparal microscope slide (CNC).

Etymology. The specific epithet is the Latin adjective *memorabilis*, *-e* (remarkable, worthy to be remembered) and refers to the history of the species discovery. Reading about *Skidmorella* in the advanced stages of preparation of this paper I suspected that it might be a member of the clade here called the tribe Discheramocephalini. Because a perforated mesoventral keel was not mentioned in the description of this genus, I needed to request the types to check for this character. Almost simultaneously I remembered the existence of a large sample of unsorted Ptiliidae from Southern Asia received from Louis Deharveng, MNHN. Some minutes later I was going through the samples and much to my joy one vial indeed contained specimens of the genus *Skidmorella*. Moreover, a clear perforation of the mesoventral keel was observed immediately.

Skidmorella serrata **sp.n.**
(Figs 4; 11C; 13B, K)

Diagnostic description. Body length 0.78–0.80 mm ($n = 2$); two transverse fossae on head dorsally behind eyes not connected by groove; disc of pronotum on each side with three longitudinal furrows not shorter than half of pronotal length; pronotal margins in posterior half serrate; setae in anterior part of pronotum 2–3× longer than those in posterior part; mesoventrum without deep fossa on each side at anterior corners; posteriorly oriented projection of metaventral plate between metacoxae with two teeth adjacent to, and mediad of, coxae; aedeagus Fig. 13B; spermatheca Fig. 13K.

Etymology. The specific name is the Latin adjective *serratus*, *-a*, *-um* (saw-shaped, serrated), referring to the serrated margins of the pronotum in this species.

Type material. *Holotype* (male; deposited in MNHN) mounted on Euparal microscope slide: VIETNAM, Lam Dong Dalat, Lang Bian, 2130 m, 21.xii.1998 (*L. Deharveng & A. Bedos*). *Paratypes*: 21, with the same data as holotype; five are mounted on four Euparal microscope slides (two slides in MNHN, two in CNC) and 16 in 70% ethanol (eight in MNHN and eight in CNC).

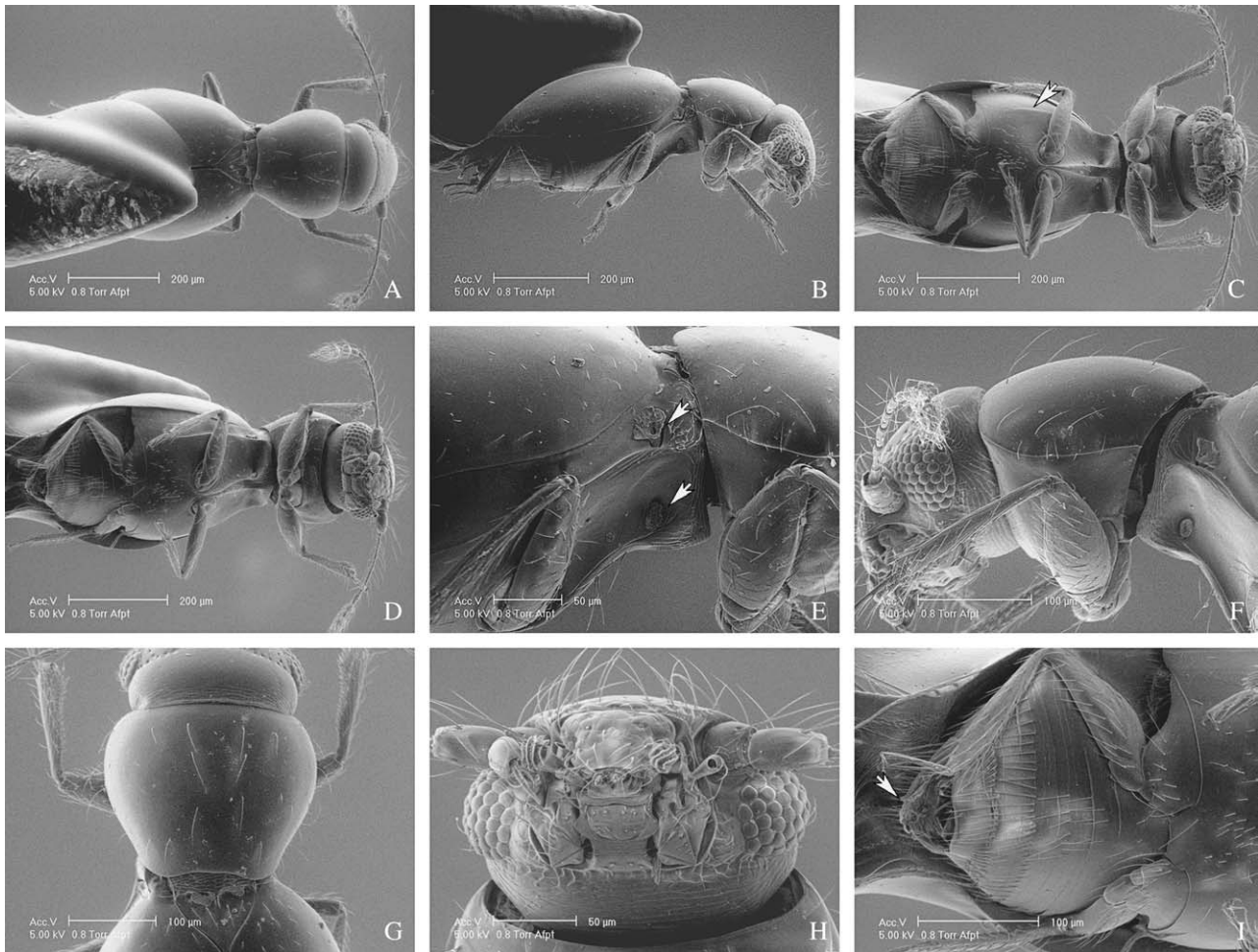


Fig. 5. *Africoptilium* sp. (Coleoptera: Ptiliidae) from DRC, scanning electron microscopy images. (A) habitus, dorsal view; (B) habitus, right lateral view; (C) habitus, ventral view (arrow indicates longitudinal metaventral line); (D) habitus, right ventro-lateral view; (E) middle part of body, right lateral view (upper arrow indicates fossa in anterior corners of mesoventrum; lower arrow indicates fossa of mesoventral keel); (F) anterior part of body, left lateral view; (G) pronotum, dorsal view; (H) head, ventro-frontal view; (I) hind legs and abdomen, ventral view (arrow indicates one of two pygidial teeth).

***Africoptilium* Johnson, 1967**
(Figs 5; 11D–F; 12A–C)

Type species. *Africoptilium marginatum* Johnson, 1967, by original designation.

Diagnosis. Species of *Africoptilium* have a constriction between the pronotum and elytra (Fig. 12A–C) resembling that in *Discheramocephalus* specimens; those of *Africoptilium* differ from the latter by their clearly separated metacoxae and by lacking pronotal grooves. Among *Discheramocephalini* genera without pronotal grooves (*Fenestellidium*, *Cissidium*, *Dacrysoma*), *Africoptilium* species are recognizable by their elongate and constricted body along with sparsely located and short dorsal pubescence, which gives *Africoptilium* specimens a ‘non-hairy’ appearance.

Other unique features of *Africoptilium* within the tribe are the pygidium with two apices (Fig. 5I) and (among the genera with non-contiguous metacoxae) the lack of a posteriorly oriented sharp projection of the metaventrum adjacent to the mesal side of each metacoxal plate.

Description. Body between pronotum and elytra in dorsal view constricted; body behind pronotum not swollen laterally and vertically; longitudinally oriented micro-ridges on ventral surface of prothorax absent; elytral setae forming seven or eight longitudinal rows; transversely oriented deep depression behind eyes absent; group of 100–200 small punctures forming transverse band on head behind eyes absent; apical antennomere not dumbbell-shaped; longitudinal depressions of labium absent; posterior edge of pronotum at middle concave; depressions on pronotum absent; longitudinal keel on scutellum present, short, about

one-third of its length; transverse row of 12–13 round punctures on base of elytra and scutellum absent; two deep exoskeletal fossae on scutellum absent; meso-metaventral suture between mesocoxae not visible externally; meso-metaventral suture laterad of mesocoxae not visible externally, present as internal thickening of cuticle; posteriorly pointed serration along meso-metaventral suture laterad of mesocoxae absent; metaventral longitudinal lateral lines present; horizontal perforation of mesoventral keel circular and transparent in lateral view; mesoventrum without transverse grooves; alacrista of metathorax at middle without short setae along margins; metacoxae not transverse, separated by one-eighth of metaventral width; posteriorly oriented projection of metaventral plate between metacoxae without two large lateral teeth; transversely oriented group of about 50–70 closely adjacent round micropores along posterior edge of tergite VIII absent; cavities on abdominal sternum VIII absent; single elongate internal sclerite alongside aedeagus absent; spermatheca as a coiled tube.

Composition and geographical distribution. The genus *Africoptilium* is known only from Eastern Africa (Tanzania and eastern part of the Democratic Republic of Congo).

Monophyly and phylogenetic relationships. Monophyly of *Africoptilium* was not tested in the present analysis. The remarkable similarity among *Africoptilium* species, however, indirectly suggests that this genus might indeed be monophyletic (or, alternatively, a highly conservative paraphyletic grade). A position of *Africoptilium* as a member of the *Skidmorella* + *Discheramocephalus* clade (Fig. 14) could be an artefact resulting from presumably convergent evolution of similarly located structures such as metaventral longitudinal lateral lines and exoskeletal fossae in anterior lateral corners of mesoventrum. These character states were scored as homologous for *Africoptilium* and some members of the *Skidmorella* + *Discheramocephalus* clade, even though some minor consistent differences were observed. Acceptance of the evolutionary scenario (Fig. 14) implies that the deep longitudinal furrows on the pronotal disc synapomorphic for the *Skidmorella* + *Discheramocephalus* clade could become secondarily obsolete in *Africoptilium*, which appears unlikely.

Bionomics. All specimens of *Africoptilium* with known biological information were collected by sifting leaf litter in tropical forests. One specimen from the West Usambara Mountains in Tanzania mounted on a microscope slide contained fungal spores in its gut (Fig. 11E).

Remarks. Johnson (1967) described the genus *Africoptilium* and all of its three species, *A. marginatum*, *A. mimicum* and *A. concinnum*, based on 13, 3 and 1 specimen, respectively, and provided an identification key. No new findings of *Africoptilium* have been reported. I studied the short type series (including holotypes) of *A. marginatum* (Fig. 12A) and *A. mimicum* (Fig. 12B) stored in MRAC and NHM,

respectively (the allotype of *A. marginatum* is mounted on a Euparal microscope slide). The holotype of *A. concinnum* was reportedly stored in NMW (Johnson, 1967); however, curators' attempts to locate it were unsuccessful. I have seen at least five more *Africoptilium* specimens in the collection of MRAC, all collected during the colonial period in the eastern part of the former Belgian Congo. One of these specimens, labelled 'Congo Belge: P.N.A., 31-iii-1-iv-1955, P.Vanschuytbroeck 12.733-42, Secteur Nord, riv. May ya Moto, 1.040 m, ex P.N.A.', was used for SEM (Fig. 5) and then mounted on a Euparal microscope slide (MRAC). I also collected two unidentified specimens of *Africoptilium* while sifting leaf litter in partly human-disturbed forest in the Lushoto district of the West Usambara Mountains, Tanzania, in October 2002 at an altitude of 1660 m (Figs 11 E; 12C, D). Of these two specimens, the female is mounted in a microscope slide in Euparal and stored in CNC, and the male is stored in the collection of M. Sörensson, Lund, Sweden. I did not make an effort to delimit species boundaries of *Africoptilium* owing to the inadequate number of available specimens. Specimens of this genus have never been collected en masse.

***Fenestellidium* gen.n.**

Type species. *Fenestellidium capensis* sp.n., here designated.

Diagnosis. This genus is unique among Ptiliidae by having the largest known internal size of the horizontally oriented perforation of the mesoventral keel. This perforation is oblong in vertical dimension (Figs 6E; 7G) and, in lateral view, its internal size is subequal to the cross-section of the mesofemur in its thickest part. Among Discheramocephalini without pronotal longitudinal grooves, members of *Fenestellidium* can be distinguished from those of *Africoptilium* by not having meso- and metaventral longitudinal lines; and from those of *Cissidium* and *Dacrysoma* by the shape of the body, which is much less swollen in both horizontal and vertical dimensions. Moreover, males of the known *Fenestellidium* species have groups of setae on abdominal sternite VIII (Fig. 7C, H), which is apparently a case of sexual dimorphism.

Description. Body constricted between pronotum and elytra in dorsal view; body behind pronotum not swollen laterally and vertically; longitudinally oriented micro-ridges on ventral surface of prothorax absent; elytral setae not forming clearly demarked longitudinal rows; transversely oriented deep depression behind eyes absent; group of 100–200 small punctures forming transverse band on head behind eyes absent; apical antennomere not dumbbell-shaped; longitudinal depressions of labium absent; posterior edge of pronotum at middle straight or slightly convex; depressions on pronotum absent; longitudinal keel on scutellum absent; transverse row of 12–13 round punctures

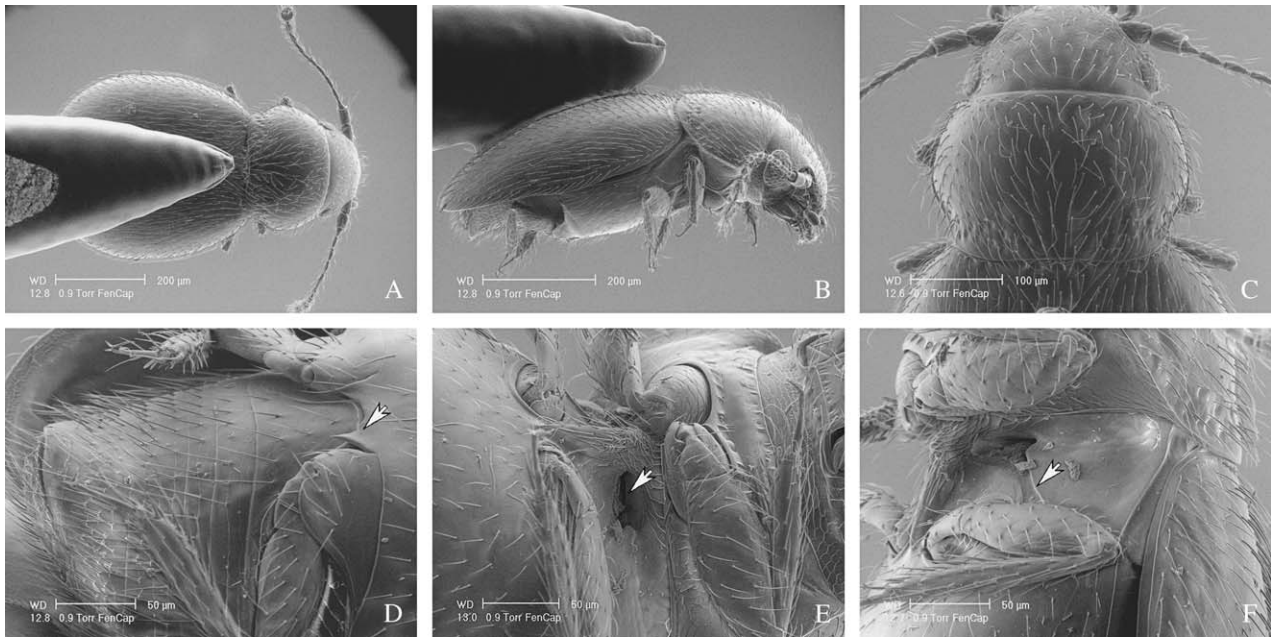


Fig. 6. *Fenestellidium capensis* sp.n. (Coleoptera: Ptiliidae) from South Africa; paratype, scanning electron microscopy images. (A) habitus, dorsal view; (B) habitus, right lateral view; (C) anterior half of body, dorsal view; (D) abdomen, left ventro-lateral view (arrow indicates posterior tooth of metaventrums medially of metacoxa); (E) thorax, left ventro-lateral view (arrow indicates fossa in mesoventral keel); (F) thorax, left ventro-lateral view (arrow indicates oblique groove on mesoventrum).

on base of elytra and scutellum present; two deep exoskeletal fossae on scutellum absent; meso-metaventral suture between mesocoxae not visible externally; meso-metaventral suture laterad of mesocoxae clearly visible externally as projecting keel; posteriorly pointed serration along meso-metaventral suture laterad of mesocoxae absent; metaventral longitudinal lateral lines absent; horizontal perforation of mesoventral keel as visible in lateral view vertically elongate, almost parallel-sided, about 2× longer than wide; mesoventrum with transverse grooves originating from fossae of mesoventral keel and extending laterad absent; alacrista of metathorax at middle with short setae along margins; metacoxae not transverse, separated by one-sixth of metaventral width; posteriorly oriented projection of metaventral plate between metacoxae with two relatively large and sharply pointed lateral teeth; transversely oriented group of about 50–70 closely adjacent round micropores along posterior edge of tergite VIII absent; cavities on abdominal sternum VIII absent; single elongate internal sclerite alongside aedeagus absent; spermatheca either globular (Fig. 13I) or as a coiled tube (Fig. 13H).

Etymology. The generic epithet *Fenestellidium* is a combination of the Latin noun *fenestella*, -ae, f., (a small opening in the wall, a little window) and the suffix *-idium*. The name refers to the remarkably large horizontal perforation of the mesoventral keel, which somewhat resembles a window. Gender neuter.

Composition and geographical distribution. The genus *Fenestellidium* is established for *F. kakamegaensis* sp.n. and *F. capensis* sp.n. from Kenya and South Africa, respectively.

Monophyly and phylogenetic relationships. The genus *Fenestellidium* is a well-supported clade with a bootstrap value above 95% supported by four synapomorphies as indicated in Fig. 14. Its sister-group relationships, however, have not been clarified.

Bionomics. All known specimens of *Fenestellidium* were sifted from the forest leaf litter.

***Fenestellidium capensis* sp.n.**
(Figs 6; 11D; 12E, F; 13E, G, I)

Diagnostic description. Body length 0.78–0.86 mm ($n = 3$). Body densely pubescent dorsally and ventrally; individual hairs 1.2–1.7× longer than the distance between them; pronotum more transverse; disc of pronotum not punctate; mesoventrite on each side with oblique groove originating from perforation of mesoventral keel and extending postero-laterad; males without deep depression along mid-line of apical abdominal sternites; aedeagus Fig. 13E; spermatheca Fig. 13I.

Etymology. The specific epithet *capensis* derives from the name of the Cape Region in South Africa, the type locality of this species.

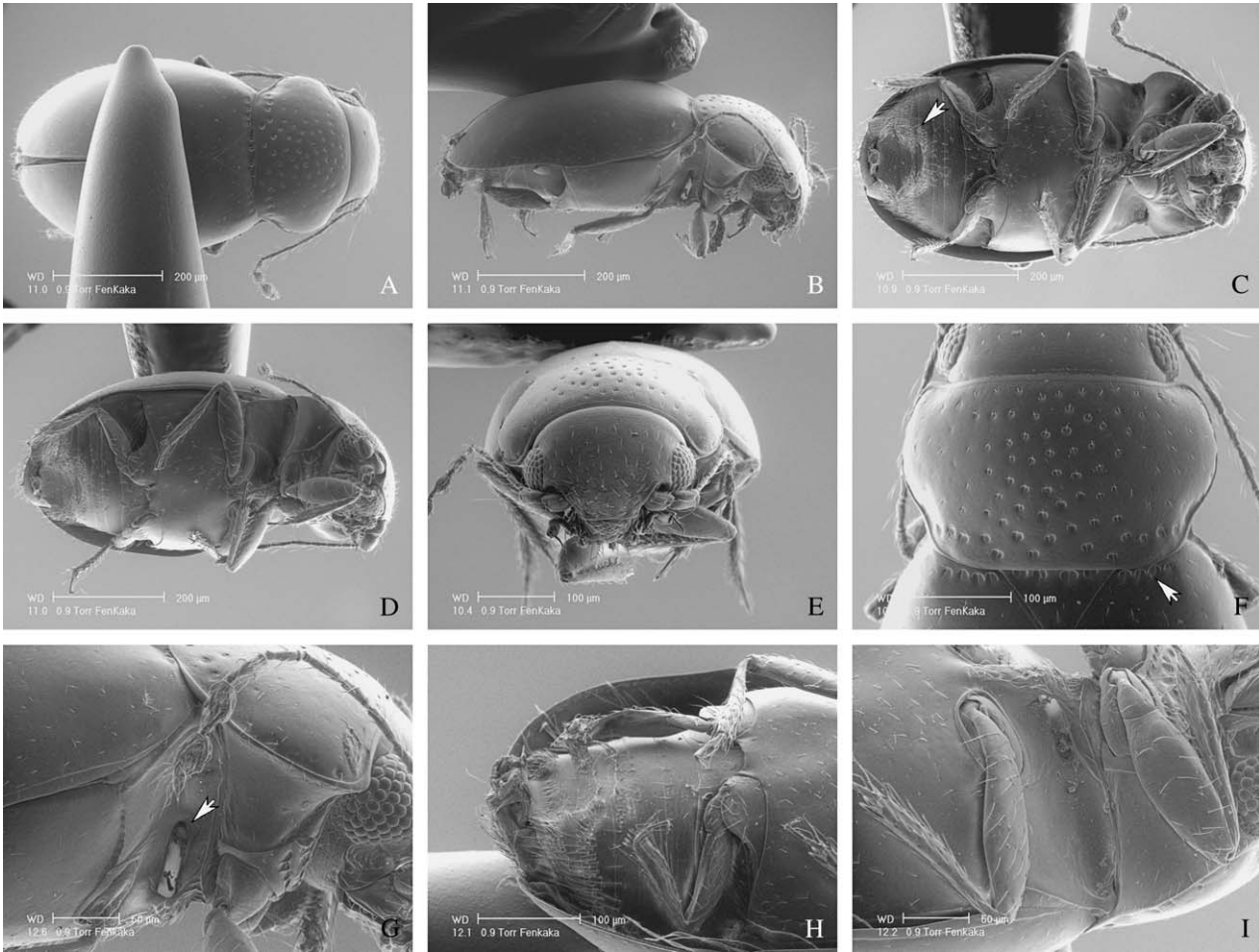


Fig. 7. *Fenestellidium kakamegaensis* sp.n. (Coleoptera: Ptiliidae) from Kenya; paratype, scanning electron microscopy images. (A) habitus, dorsal view; (B) habitus, right lateral view; (C) habitus, ventral view (arrow indicates male secondary sexual features on abdomen); (D) habitus, right ventro-lateral view; (E) anterior part of body, frontal view; (F) pronotum, dorsal view (arrow indicates transverse row of round punctures on base of elytra and scutellum); (G) thorax, right lateral view (arrow indicates fossa in mesoventral keel); (H) abdomen, left ventro-lateral view; (I) thorax, left ventro-lateral view.

Type material. *Holotype* (female) mounted on a Euparal microscope slide: SOUTH AFRICA, Western Cape, Cape Town, Table Mt., 10–11.viii.2002 (*V. Grebennikov*). *Paratypes*: 12; seven specimens are mounted on four Euparal slides. (Three females are mounted on three slides, and the remaining three males and one female are mounted all together on the same slide; this slide has an additional non-congeneric specimen of Ptiliidae mounted among four paratypes of *Fenestellidium capensis* and bears an additional statement on the label: ‘Single teneral male/mounted does not belong to the genus *Fenestellidium*’.) Five specimens are stored in 70% ethanol.

Remarks. This species was collected on the eastern slope of Table Mountain, Cape Town, South Africa, 200–300 m higher than the campus of the University of Cape Town. Two males and one female of a species closely resembling *F. capensis* were collected in Grahamstown in the Eastern Cape, South Africa are mounted on Euparal (Fig. 11H).

Their only difference from the Cape Town population of *F. capensis* is found in the shape of the spermatheca. At this point it is impossible to assess whether these three specimens from Grahamstown represent a conspecific population of *F. capensis* or a congeneric species.

Fenestellidium kakamegaensis sp.n.
(Figs 7; 11I; 12G–H; 13D, H)

Diagnostic description. Body length 0.73–0.76 mm ($n = 2$). Body sparsely pubescent with length of individual hairs 0.5–0.3× distance between them; pronotum less transverse; disc of pronotum punctate with each puncture bearing a short hair; mesoventrite on each side without oblique groove originating from perforation of mesoventral keel; males with deep depression along mid-line of apical abdominal sternites flanked by dense groups of setae; aedeagus Fig. 13D, spermatheca Fig. 13H.

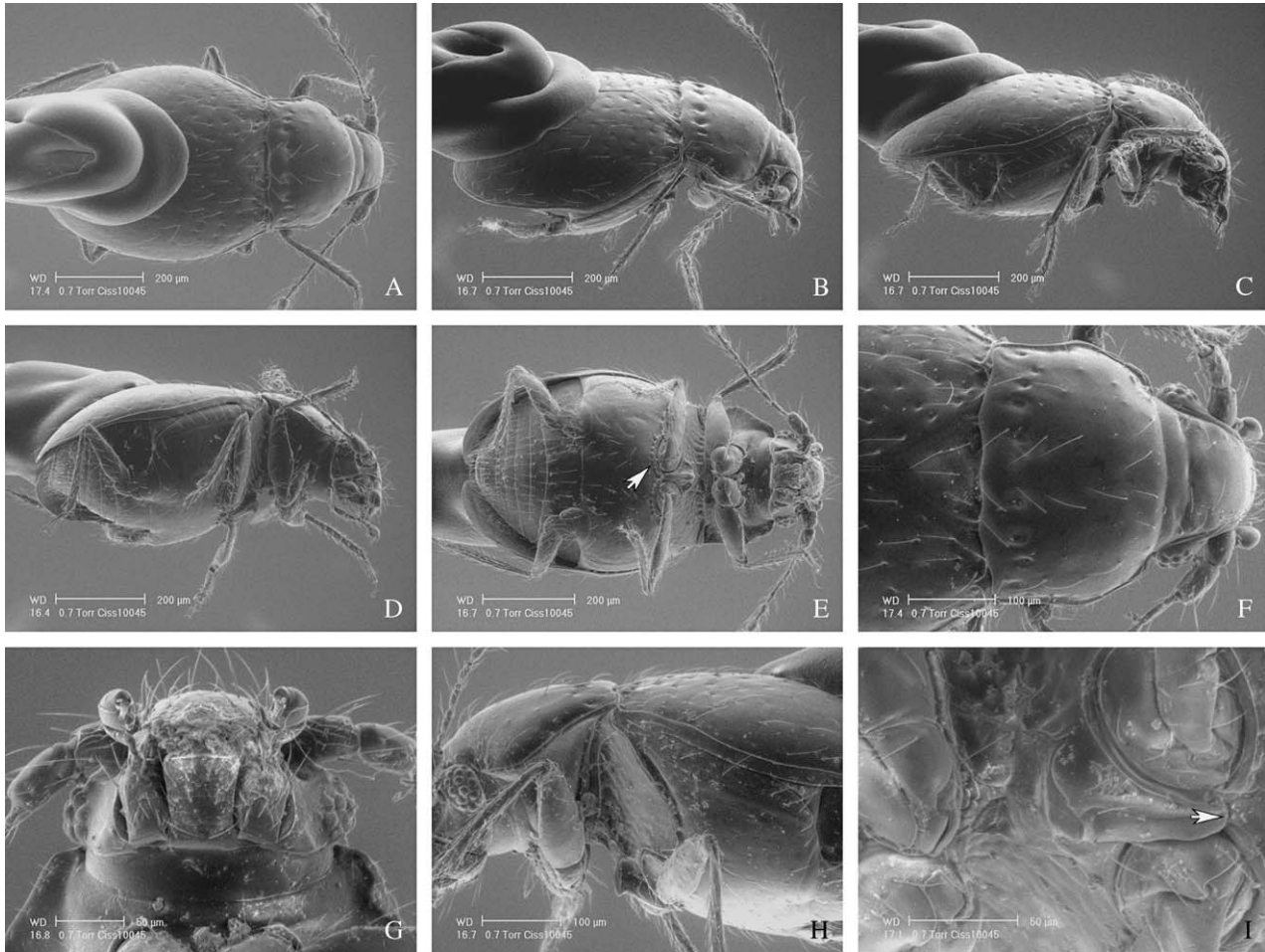


Fig. 8. *Cissidium okuensis* sp.n. (Coleoptera: Ptiliidae) from Cameroon; scanning electron microscopy images. (A) habitus, dorsal view; (B) habitus, right dorso-lateral view; (C) habitus, right lateral view; (D) habitus, right ventro-lateral view; (E) habitus, ventral view (arrow indicates serration); (F) pronotum and head, dorsal view; (G) head, ventral view; (H) thorax, left lateral view; (I) meso- (to the left) and metacoxae (to the right), left ventro-lateral view (arrow indicates clearly visible meso-metaventral suture between mesocoxae).

Etymology. The specific epithet *kakamegaensis* derives from the name of the Kakamega forest in western Kenya, the type locality of this species.

Type material. *Holotype* (male) mounted on Euparal microscope slide: KENYA, Kakamega forest, Udo's bandas, 10–12.xi.2001 (V. Grebennikov). *Paratypes*: six, with the same data as holotype; three in 70% ethanol and three more mounted on three Euparal microscope slides.

***Cissidium* Motschulsky, 1855**

Type species. *Cissidium basale* Motschulsky, 1855, designated by Lucas, 1920: 187 (not seen; cited after Newton & Thayer, 2007b).

= *Camptodium* Motschulsky, 1869: 189; type species *Camptodium adustipenne* Motschulsky, 1869. Synonymy established by Johnson (1982: 358).

= *Dimorphella* A. Matthews, 1889: 190; type species *Dimorphella reitteri* A. Matthews, 1889. Synonymy established by Johnson (1982: 358).

= *Epibaptus* Deane, 1931: 228; type species *Epibaptus scutellaris* Deane, 1931. Synonymy established by Johnson (1982: 358).

Diagnosis. Members of the genus *Cissidium* have a pronotum with a transverse row of four to eight poorly delimited depressions along posterior margin (Fig. 8F). Another unique feature is their posteriorly pointed serration along the meso-metaventral suture laterad of the mesocoxae (Fig. 8E). Within Discheramocephalini, species of *Cissidium* are unique by having poorly developed horizontal perforation of the mesoventral keel, which is not transparent in lateral view. Most of the *Cissidium* and all the *Dacrysoma* species have dumbbell-shaped antennomere 11. Unlike *Dacrysoma*, *Cissidium* species have the meso-metaventral suture clearly delimited and not obliterated externally (Fig. 8H).

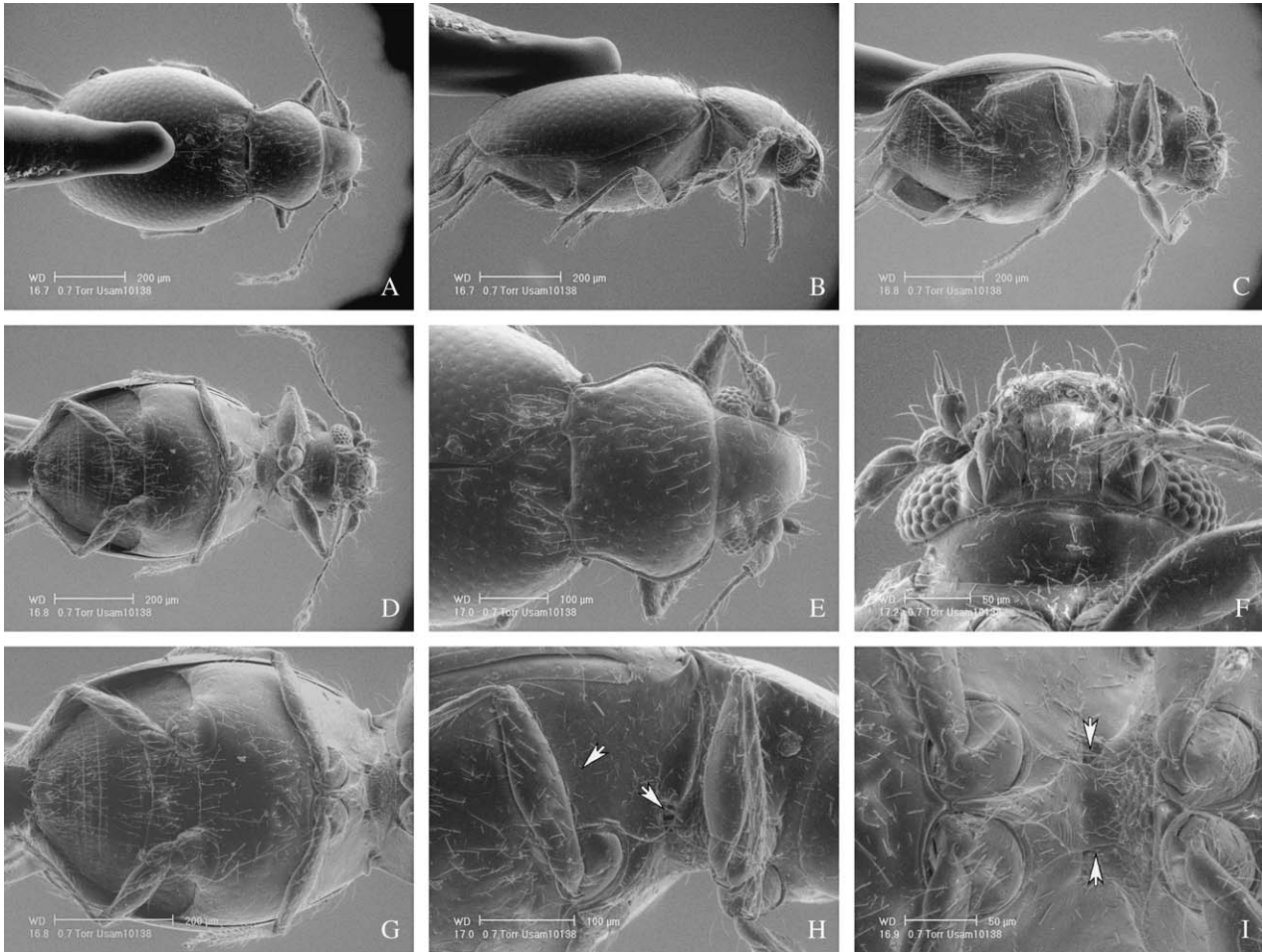


Fig. 9. *Dacrysoma usambarensis* sp.n. (Coleoptera: Ptiliidae) from Tanzania; holotype, scanning electron microscopy images. (A) habitus, dorsal view; (B) habitus, right lateral view; (C) habitus, right latero-dorsal view; (D) habitus, ventral view; (E) pronotum and head, dorsal view; (F) head, ventral view; (G) posterior part of body, ventral view; (H) thorax, right ventro-lateral view (left arrow indicates lack of visible meso-metaventral suture; right arrow indicates fossa in mesoventral keel); (I) pro- (to the right) and mesocoxae (to the left), left ventral view (arrows indicate lateral openings of fossae in mesoventral keel).

Description. Body between pronotum and elytra in dorsal view not or slightly constricted; body behind pronotum swollen laterally and vertically; longitudinally oriented micro-ridges on ventral surface of prothorax absent; elytral setae not forming clearly demarcated longitudinal rows; transversely oriented deep depression behind eyes absent; group of 100–200 small punctures forming transverse band on head behind eyes absent; apical antennomere dumbbell-shaped; longitudinal depressions of labium absent; posterior edge of pronotum at middle concave; depressions on pronotum present as rounded basal depression; longitudinal keel on scutellum absent; transverse row of 12–13 round punctures on base of elytra and scutellum absent; two deep exoskeletal fossae on scutellum absent; meso-metaventral suture between mesocoxae clearly visible forming delimited border between plates; meso-metaventral suture laterad of mesocoxae clearly visible externally as projecting keel; posteriorly pointed serration along meso-metaventral suture

laterad of mesocoxae present; metaventral longitudinal lateral lines absent; horizontal perforation of mesoventral circular in lateral view, not transparent; mesoventrum without transverse grooves; alacrista of metathorax at middle without short setae along margins; metacoxae not transverse, separated by one-quarter of metaventral width; posteriorly oriented projection of metaventral plate between metacoxae with two relatively large and sharply pointed lateral teeth; transversely oriented group of about 50–70 closely adjacent round micropores along posterior edge of tergite VIII present; cavities on abdominal sternum VIII absent; single elongate internal sclerite alongside aedeagus absent; spermatheca small and nearly spherical in shape; aedeagus as in Johnson (1982: fig. 57).

Composition and geographical distribution. The genus *Cissidium* includes eight valid species, including the new species described below: *C. basale* Motschulsky, 1855

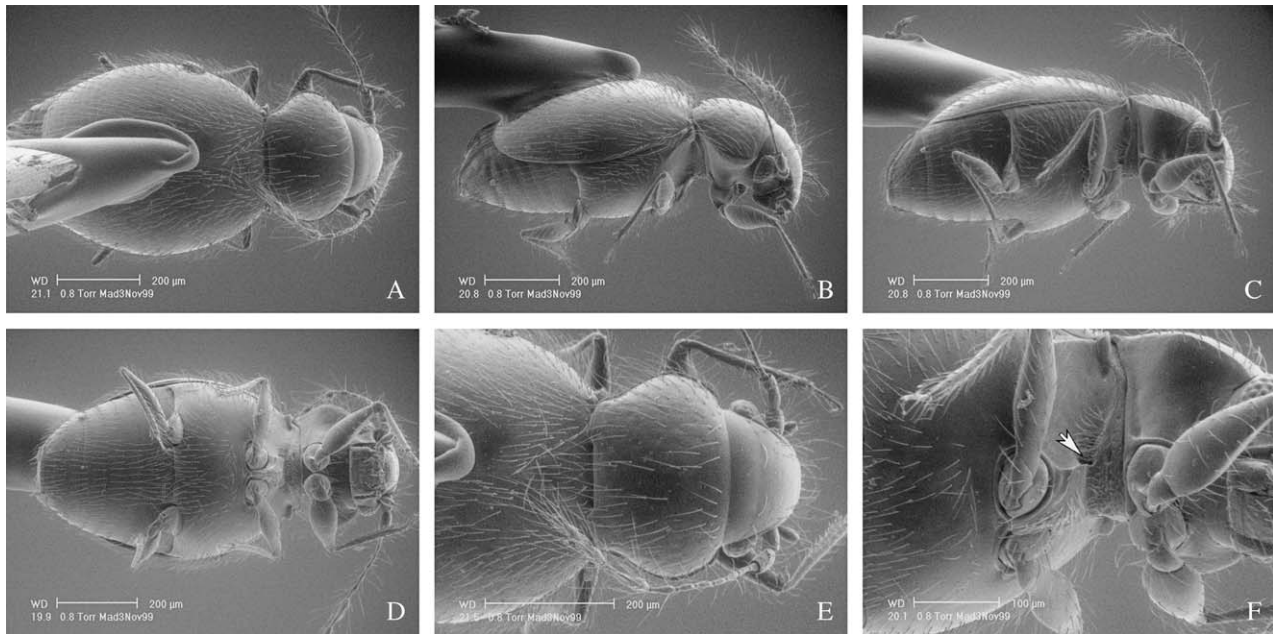


Fig. 10. *Dacrysoma felis* sp.n. (Coleoptera: Ptiliidae) from Madagascar; holotype, scanning electron microscopy images. (A) habitus, dorsal view; (B) habitus, right lateral view (arrow indicates dumbbell-shaped apical antennomere); (C) habitus, right latero-ventral view; (D) habitus, ventral view; (E) pronotum and head, dorsal view; (F) thorax, right ventro-lateral view (arrow indicates fossa in mesoventral keel).

(from Panama; holotype in ZMMU; not examined); *C. rufescens* Motschulsky, 1855 (from Panama; holotype presumably in ZMMU; not examined); *C. matthewsi* Johnson, 2007b: 22 (= *C. matthewsi* Johnson, 2004:25, nomen nudum) (from Japan; holotype in MMUE; not examined); *C. adustipenne* Motschulsky, 1869 (nec *adustipenne* A. Matthews, 1884) (from eastern India; holotype presumably in ZMMU; not examined); *C. scutellarus* (Deane, 1931: 228) (from Australia: Victoria; holotype either in MVMA or UQIC as cited by Johnson, 1982; not examined); *C. crowsoni* Johnson, 1982:359 (from New Zealand; holotype in NZAC; not examined); and *C. foveolatum* Johnson, 1982:359 (from New Zealand; holotype in NZAC; not examined). Johnson (1982: 359) noted that there were about 70 additional species from tropical and subtropical areas of the world. I have seen at least one undescribed species of this genus from Kenya, one from Cameroon, and another from Bolivia.

Monophyly and phylogenetic relationships. The genus *Cissidium* was consistently supported as monophyletic based on four synapomorphies with bootstrap values above 95% (Fig. 14). Only two of its species were included in the analysis, which might be seen as an inadequate sampling for arguing its monophyly. The genus *Cissidium* is hypothesized to be a sister-group of *Dacrysoma*.

Cissidium okuensis sp.n.
(Figs 8; 11J; 13N)

Diagnostic description. Body length 1.03–1.09 mm ($n = 3$). Pronotum marginate, sides subparallel in posterior half.

With external morphological features as depicted in Figs 8; 11J; aedeagus unknown; spermatheca Fig. 13N.

Etymology. The specific epithet *okuensis* derives from the name of Oku Mountain in Cameroon, the type locality of this species.

Type material. *Holotype* (female) mounted on Euparal microscope slide: CAMEROON, North-West province, Mt. and lake Oku, N06°12.218', E010°27.596', 6.v.2006, 2200 m (V. Grebennikov). *Paratypes*: four, with the same data as holotype; two in 70% ethanol and two mounted on two Euparal microscope slides. The specimen used for SEM was subsequently lost.

***Dacrysoma* gen.n.**

Type species. *Dacrysoma usumbarensis* sp.n., here designated.

Diagnosis. Members of *Dacrysoma* share with at least some species of *Cissidium* a unique feature within Ptiliidae, namely the dumbbell-shaped antennomere 11 (Fig. 10B). *Dacrysoma* species differ from those of *Cissidium* by a clearly visible horizontal perforation of the mesoventral keel (Figs 9H; 10F) and by the lack of serration of the meso-metaventral suture laterad of mesocoxae (Figs 9G; 10F).

Description. Body between pronotum and elytra in dorsal view constricted; body behind pronotum swollen



Fig. 11. Discherocephalini spp. (Coleoptera: Ptiliidae); light compound microscopy images, dorsal views. (A) *Skidmorella vietnamensis* sp.n., holotype; (B) *Skidmorella memorabilis* sp.n., holotype; (C) *Skidmorella serrata* sp.n., holotype; (D) *Africoptilium marginatum*, paratype; (E) *Africoptilium* sp. (specimen used for SEM in Fig. 5); (F) *Africoptilium* sp. (Tanzania: W. Usambara Mts); (G) *Fenestellidium capensis* sp.n., holotype; (H) *Fenestellidium* pr. *capensis* (South Africa: Grahamstown); (I) *Fenestellidium kakamegaensis* sp.n., holotype; (J) *Cissidium okuensis* sp.n., holotype; (K) *Dacrysoma usambarensis* sp.n., paratype; (L) *Dacrysoma felis* sp.n., paratype.

laterally and vertically; longitudinally oriented micro-ridges on ventral surface of prothorax absent; elytral setae not forming clearly demarcated longitudinal rows; transversely oriented deep depression behind eyes absent; group

of 100–200 microscopic punctures forming transverse band on head behind eyes present; apical antennomere dumb-bell-shaped; longitudinal depressions of labium absent; posterior edge of pronotum at middle concave; depressions

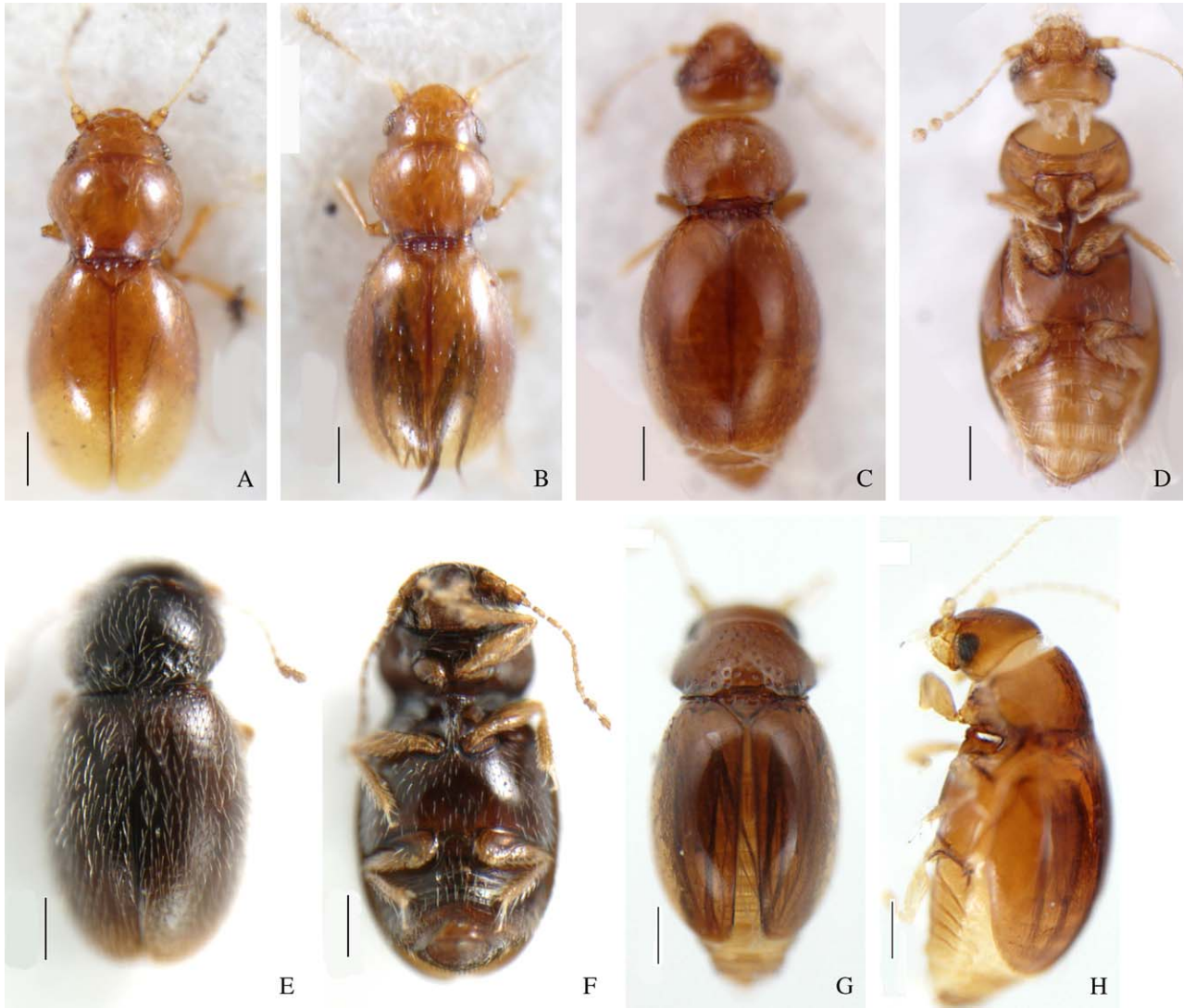


Fig. 12. *Africoptilium* spp. and *Fenestellidium* spp. (Coleoptera: Ptiliidae: Discheramocephalini); light dissecting microscopy images. (A) *Africoptilium marginatum*, holotype, dorsal view; (B) *Africoptilium mimicum*, holotype, dorsal view; (C–D) *Africoptilium* sp. (Tanzania: W. Usambara Mts.), dorsal (C) and ventral (D) view; (E–F) *Fenestellidium capensis* sp.n., dorsal (E) and ventral (F) view; (G–H) *Fenestellidium kakamegaensis* sp.n., dorsal (G) and left lateral (H) view. Scale bars: 0.1 mm.

on pronotum absent; longitudinal keel on scutellum absent; transverse row of 12–13 round punctures on base of elytra and scutellum absent; two deep exoskeletal fossae on scutellum absent; meso-metaventral suture between mesocoxae clearly visible externally forming delimited border between plates; meso-metaventral suture laterad of mesocoxae not visible externally, present as internal thickening of cuticle; posteriorly pointed serration along meso-metaventral suture laterad of mesocoxae absent; metaventral longitudinal lateral lines absent; horizontal perforation of mesoventral keel as visible in lateral view round, transparent in lateral view; mesoventrum with transverse grooves originating from fossae of mesoventral keel and extending laterad; alacrista of metathorax at

middle without short setae along margins; metacoxae not transverse, separated by one-quarter of metaventral width; posteriorly oriented projection of metaventral plate between metacoxae with two relatively large and sharply pointed lateral teeth; transversely oriented group of about 50–70 closely adjacent round micropores along posterior edge of tergite VIII absent; cavities on abdominal sternum VIII absent; single elongate internal sclerite alongside aedeagus absent; spermatheca globular.

Etymology. The generic epithet *Dacrysoma* is a combination of two Greek words δακρυον (a tear) and σωμα (body). The name refers to the somewhat tear-shaped body of these beetles. Gender neuter.

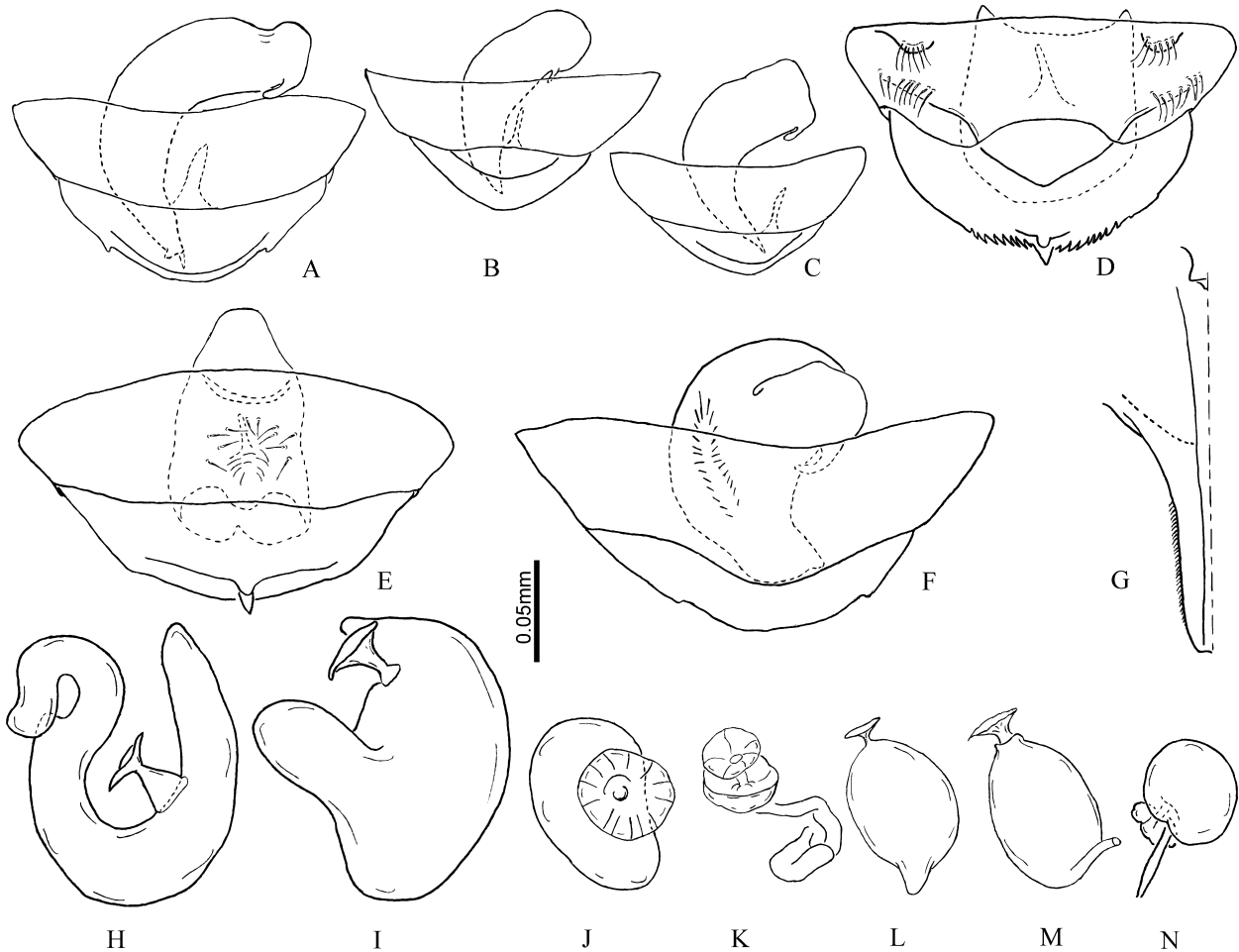


Fig. 13. *Discheramocephalini* spp. (Coleoptera: Ptiliidae); ventral (A–F, H–N) and dorsal (G) views; male genitalia and abdominal sternites VIII and IX (A–F, H–N), spermatheca (H–N), left half of alacrissa (G). (A) *Skidmorella vietnamensis*; (B, K) *Skidmorella serrata*; (C, J) *Skidmorella memorabilis*; (D, H) *Fenestellidium kakamegaensis*; (E, G, I) *Fenestellidium capensis*; (F, L) *Dacrysoma felis*; (M) *Dacrysoma usambarensis*; (N) *Cissidium okuensis*.

Composition and geographical distribution. The genus *Dacrysoma* is established for one African (Tanzania) and one Madagascar species.

Monophyly and phylogenetic relationships. The genus *Dacrysoma* was supported consistently as a monophyletic with three synapomorphies and bootstrap values above 90%, as indicated in Fig. 14. The genus *Dacrysoma* is hypothesized to be a sister-group of *Cissidium*.

***Dacrysoma usambarensis* sp.n.**
(Figs 9; 11K; 13M)

Diagnostic description. Body length 0.97–1.03 mm ($n = 2$); pronotal disk and elytra sparsely pubescent (Fig. 9E); aedeagus unknown; spermatheca Fig. 13M.

Etymology. The specific epithet *usambarensis* derives from the name of the Usambara Mountains in Tanzania, the type locality of this species.

Type material. *Holotype* (sex unknown) dry-mounted on the point of an entomological pin and used for SEM: TANZANIA, E. Usambara Mts., 12–16.x.2002, 950 m, Amani Nature Reserve, headquarters (V. Grebennikov). *Paratypes*: three, with the same data as holotype; two specimens are mounted on two Euparal microscope slides and one in 70% ethanol.

***Dacrysoma felis* sp.n.**
(Figs 10; 11L; 13F, L)

Diagnostic description. Body length 0.88–0.89 mm ($n = 3$); pronotal disk and elytra densely pubescent (Fig. 10E); aedeagus Fig. 13F; spermatheca Fig. 13L.

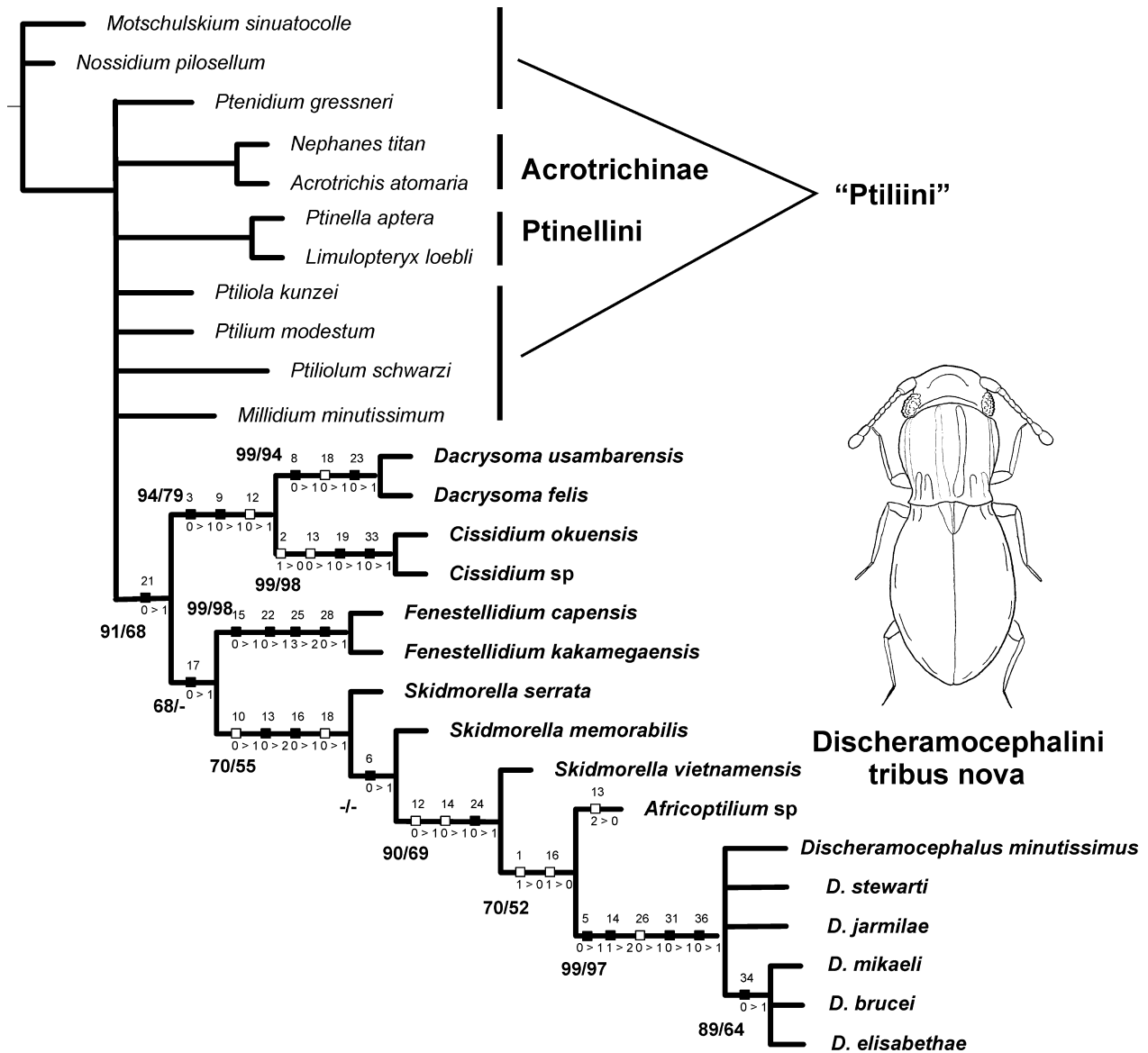


Fig. 14. Phylogeny of Ptiliidae: Discheramocephalini inferred from exhaustive parsimony analysis of 37 morphological characters scored for 27 terminal taxa. Basal nodes of the tree (except for inside the Discheramocephalini clade) represent strict consensus topology found in both Analysis 1 and Analysis 2. Note that the tribe Ptiliini is markedly non-monophyletic. Internal topology of the Discheramocephalini clade is represented by one of 3387 shortest trees with tree length 66; consistency index 66, retention index 87. Discheramocephalini taxa are in bold; generalized habitus of a *Discheramocephalus* species illustrates the type genus of the tribe. Only unambiguously optimized evolutionary events are mapped on the internodes; closed black squares represent unique evolutionary events; white open squares represent convergences or subsequent reversals; character numbers are given above; the direction of character state changes is indicated by two subsequent numbers below. Bootstrap values for Discheramocephalini clades above the 50% threshold are indicated as two values separated by a slash for unweighted and successively weighted analysis, respectively; bootstrap values below 50% are indicated by a dash '-'.

Etymology. The specific epithet is the Latin noun *felis*, -is, f (cat), in apposition.

Type material. *Holotype* (sex unknown; deposited in FMNH) dry-mounted on the point of an entomological pin and used for SEM: MADAGASCAR, province Antsira-

nana, reserve Manongarivo, 20.4 km SW219° Antanambao, 1860 m, 14°2.73S, 48°24.06'E, 3.x.1999, FMNH#98-375 (*B.L. Fischer*), BLF#1990. *Paratypes*: 22, with the same data as holotype; 16 of them in 70% ethanol (six in CNC and ten in FMNH) and the other six mounted on six Euparal microscope slides (three in CNC and the other three in FMNH).

Table 1. Morphological data matrix for phylogenetic analysis of the family Ptiliidae (Coleoptera) focused on testing monophyly of the tribe Discherocephalini ('-' indicates unapplicable characters; '?' indicates missing data).

	000000001	111111112	222222223	3333333
	1234567890	1234567890	1234567890	1234567
<i>Motschulskium sinuatocolle</i>	2001000000	0000000000	0-00010000	00000000
<i>Nossidium pilosellum</i>	2000000000	0000000000	0-00000000	00000000
<i>Ptenidium gressneri</i>	1000000000	1000000000	0-00300001	00000001
<i>Ptinella aptera</i>	2000000000	1000000000	0-00301001	01000001
<i>Limulopteryx loebli</i>	2000000000	1000000000	0-0030?001	01000001
<i>Nephanes titan</i>	2000000000	1000000000	0-00300011	00001010
<i>Acrotichis atomaria</i>	2000000000	1000000000	0-00301011	00001010
<i>Millidium minutissimus</i>	2100000000	1011000000	0-00300001	00000001
<i>Ptiliola kunzei</i>	2001000000	1000000000	0-00300001	00000001
<i>Ptilium modestum</i>	2001000000	1000000000	0-00300001	00000001
<i>Ptiliolium schwarzi</i>	2001000000	1000000000	0-00101001	00000001
<i>Discherocephalus brucei</i>	0100113000	1122001100	1001010001	10010111
<i>D. elisabethae</i>	0100113000	1122001100	1001010001	10010111
<i>D. mikaeli</i>	0100113001	1122001100	1001010001	10010111
<i>D. stewarti</i>	0100113000	1122001101	1001010001	10000111
<i>D. jarmilae</i>	0100113000	1122001101	1001010001	10000111
<i>D. minutissimus</i>	0100113001	1122001101	1001010001	10000111
<i>Skidmorella vietnamensis</i>	1100012001	1121011100	1001300001	00000001
<i>Skidmorella memorabilis</i>	1100011001	1020011100	1000301001	00000001
<i>Skidmorella serrata</i>	1100001001	1020011100	1000301001	00000001
<i>Africoptilium</i> sp.	0100010000	1101001101	1001100001	00000001
<i>Fenestellidium capensis</i>	1100000000	1000101000	1100201101	00000001
<i>Fenestellidium kakamegaensis</i>	1100000000	1000101000	1100201101	00000001
<i>Cissidium okuensis</i>	0010000010	1110000010	1000301001	00100?21
<i>Cissidium</i> sp.	0010000010	1110000010	1000301001	00100001
<i>Dacrysoma usambarensis</i>	0110000110	1100000100	1010301001	00000?21
<i>Dacrysoma felis</i>	0110000110	1100000100	1010301001	00000001

List of morphological characters of Ptiliidae used for the phylogenetic analysis

1. Body in cross-section, height/width ratio: (0) 0.85–0.95 (Fig. 1E); (1) 0.65–0.85; (2) 0.55–0.65 (Fig. 7E).
2. Body between pronotum and elytra in dorsal view: (0) not or only slightly constricted (Fig. 11J); (1) constricted (Fig. 12A).
3. Body behind pronotum: (0) not swollen laterally and vertically (Fig. 2A); (1) markedly swollen laterally and vertically (Figs 9A; 10A).
4. Scale-like microsculpture on pronotum, elytra, and most of the body: (0) absent; (1) present.
5. Longitudinally oriented micro-ridges on ventral surface of prothorax: (0) absent (Fig. 5F); (1) present (Fig. 1E).
6. Elytral setae: (0) not forming clearly demarcated longitudinal rows (Fig. 10A); (1) forming seven or eight longitudinal rows (Fig. 1F).
7. Transversely oriented deep depression behind eyes: (0) absent (Fig. 10E); (1) present, as two large fossae not connected by a groove (Fig. 4G); (2) present, as two large fossae connected by a groove (Fig. 2E); (3) present as deep groove extending laterad and ventrad (Fig. 1D, E).
8. Group of some 100–200 small punctures forming transverse band on head behind eyes: (0) absent; (1) present.
9. Apical antennomere: (0) not constricted at middle, not dumbbell-shaped; (1) constricted at middle, dumbbell-shaped (Fig. 10B).
10. Two longitudinal or anteriorly convergent grooves on labium: (0) absent (Fig. 8G); (1) present (Fig. 3G).
11. Propleural suture: (0) present; (1) absent (Fig. 1E).
12. Posterior edge of pronotum at middle: (0) straight or convex (Fig. 6C); (1) concave (Fig. 9E).
13. Lateral depressions (not punctures bearing single setae as in Fig. 7F) of pronotal disc: (0) absent (Fig. 10E); (1) rounded, present along posterior edge (Fig. 8B); (2) present as developed grooves of at least half pronotal length (Fig. 2A).
14. Longitudinal keel on scutellum: (0) absent (Fig. 6C); (1) present, either short (one-third of the length, Fig. 5G) or long and weak (Fig. 2D); (2) present, sharp, about as long as scutellum (Fig. 1A).
15. Transverse row of 12–13 round punctures on base of elytra and scutellum: (0) absent (Fig. 3E); (1) present (Fig. 7F).
16. Two deep exoskeletal fossae on scutellum: (0) absent (Fig. 11L); (1) present (Fig. 11A–C).

17. Meso-metaventral suture between mesocoxae: (0) clearly visible and forming a delimited border between sclerites (Fig. 10F); (1) obliterated, both sclerites fully amalgamated (Fig. 1E).
18. Meso-metaventral suture laterad of mesocoxae: (0) present and clearly visible externally as an externally projecting keel (Fig. 8H); (1) present only as internal thickening of cuticle, not visible externally (Fig. 9H).
19. Serration along meso-metaventral suture laterad of mesocoxae: (0) absent (Fig. 9D); (1) present (Fig. 8E).
20. Metaventral longitudinal lateral lines: (0) absent (Fig. 1E); (1) present (Fig. 5C).
21. Horizontally oriented perforation of mesoventral keel: (0) absent; (1) present (Figs 2I; 3I; 4I; 5E; 6E; 7G; 9H; 10F).
22. Shape of the horizontal perforation of mesoventral keel as visible in lateral view: (0) round (Fig. 5E); (1) vertically elongate, almost parallel-sided, about 2× longer than wide (Figs 6E; 7G).
23. Grooves on mesoventrum originating from fossae of mesoventral keel and extending laterad: (0) absent (Fig. 5E); (1) present (Fig. 10F).
24. Fossae in anterior lateral corners of mesoventrum: (0) absent (Fig. 6F); (1) present (Figs 1G; 2I; 5E).
25. Metacoxae: (0) separated by one-fifteenth of metaventral width (Fig. 1B); (1) separated by one-eighth of metaventral width (Fig. 5C); (2) separated by one-sixth of metaventral width (Fig. 7C); (3) separated by one-quarter of metaventral width (Fig. 8E).
26. Metacoxae: (0) not transverse, less than 2× as wide as long (Fig. 2G); (1) transverse, more than 2× as wide as long (Fig. 1C).
27. Posteriorly oriented projection of metaventral plate between metacoxae: (0) without two lateral teeth (Fig. 5I); (1) with two lateral teeth (Fig. 6D).
28. Alacrista of metathorax at middle: (0) without setae along margins; (1) with short setae along margins (Fig. 13G).
29. Metascutellar spur on alacrista (Hall, 2003: 97): (0) absent (Fig. 13G); (1) present.
30. Hindwing membrane: (0) not or partly narrowed, individual trichia of the fringe not longer than wing width; (1) narrowed, individual trichia of the fringe longer than wing width.
31. Cavities on abdominal sternum VIII: (0) absent (Fig. 6D); (1) present (Fig. 1H, I).
32. Abdominal glands (Hall, 2003: 95): (0) absent; (1) present.
33. Group of about 50–70 closely adjacent round micropores transversely oriented along posterior edge of tergite VIII: (0) absent; (1) present.
34. Transverse rows of teeth-like serration of abdominal sternites: (0) absent (Fig. 3H); (1) present (Grebennikov, 2008: fig. 14).
35. Tergites XI and X: (0) free, separated from each other; (1) merged together into a single plate.
36. Single elongate internal sclerite parallel to aedeagus: (0) absent (Fig. 13A–F); (1) present (Grebennikov, 2008: fig. 75).
37. Parameres: (0) present; (1) absent.

Results

The present phylogenetic analysis with equally weighted unordered characters aimed to test the monophyly of Discheramocephalini resulted in the overflow of 3387+ most-parsimonious trees of 66 steps (consistency index 66, retention index 87). A second analysis with successive character weighting resulted in 305 most-parsimonious trees of 402 steps long (consistency index 82, retention index 94). The strict consensus tree of both analyses retained Discheramocephalini as a monophyletic group. Bootstrap values for this clade were 91 and 68 in analysis 1 and 2, respectively.

The grouping of taxa inside Discheramocephalini was consistent and mainly resolved by both analyses. The genera *Cissidium* and *Dacrysoma* form a clade supported by three synapomorphies and a bootstrap value varying between 79 and 94% (Fig. 14). Monophyly of *Skidmorella* and *Discheramocephalus* is moderately well supported by four synapomorphies (Fig. 14); however, the inclusion of *Africoptilium* in this clade is apparently an artefact, as discussed above under *Africoptilium*. Therefore, the most conservative current evaluation of the internal relationships of the Discheramocephalini taxa is that the tribe has the basal polytomy of four clades: (i) *Africoptilium*, (ii) *Fenestellidium*, (iii) *Cissidium* + *Dacrysoma* and (iv) *Skidmorella* + *Discheramocephalus*.

Discussion of phylogenetic analysis and current classification of Ptiliidae

Projecting these results to the family Ptiliidae, the internal relationships and classification remain disordered. This problem is mainly because no comprehensive attempt was made to make a phylogenetic analysis of the whole family or to propose a cladogram-based classification. The classification adopted in this work derives from that used by Newton & Thayer (2007a) and reflects a conservative approach aimed at minimizing the number of non-monophyletic taxa. This classification recognizes three subfamilies: Ptiliinae, Acrotrichinae and Cephaloplectinae. Subfamily Acrotrichinae includes the 12 genera listed by Hall (2005) arranged into two tribes, namely Acrotrichini and Nephanini; none of these three taxa has been demonstrated to be monophyletic. Subfamily Cephaloplectinae includes five genera (Hall, 2005); monophyly of this subfamily has also never been demonstrated. Subfamily Ptiliinae contains the rest of the family and is a non-monophyletic assemblage of four tribes: Nanosellini, Ptinellini, Discheramocephalini **trib.n.** and Ptiliini. Among them, only Nanosellini and Discheramocephalini have been hypothesized to be monophyletic as a result of phylogenetic analyses (Hall, 1999 and the present paper, respectively), whereas Ptinellini (under the name Pterycini, nomen nudum) has been extensively discussed (Hall, 2003) and also hypothesized to represent a clade. The tribe Ptiliini remains, however, a taxonomic 'dumping ground' for members of the family that share no apomorphies of the remaining three tribes and cannot be assigned to

Acrotrichinae or Cephalopectinae. Johnson (2004) and Hall (2005) resurrected from synonymy the tribe Ptenidiini without providing cladistic justification; this taxonomic action is not followed here and all its genera listed by these two authors are considered to belong to the non-monophyletic Ptiliini.

The bootstrap support statistics for monophyly of the tribe Discherocephalini might appear unconvincing for validating the existence of a new tribe. Monophyly of Discherocephalini is, however, the only consistently supported hypothesis within the framework of the present analysis. With the present level of knowledge it is hardly possible to rely exclusively on high and convincing values of the formalized cladistic approach when inferring the internal branching pattern of Ptiliidae. The family remains remarkably neglected taxonomically, with the majority of non-monotypic genera neither having been revised nor having had their monophyly tested phylogenetically. Only one attempt to combine a taxonomic review of a subgroup of Ptiliidae with phylogenetic analysis (tribe Nanosellini (Hall, 1999)) resulted in the tribe Nanosellini hypothesized to be monophyletic, including 41 species in 26 genera, 21 of the latter being monotypic. Such a high number of monotypic genera suggests that research into the taxonomy of Ptiliidae still requires description and documentation of the diversity of these beetles. It also means that any phylogeny-based internal groupings of Ptiliidae at the present stage will be hampered by the lack of a pre-existing phylogenetic hypothesis to root the trees and by the absence of a framework of well-understood morphological characters surveyed throughout a wide spectrum of taxa. In other words, the attempt of phylogenetic reconstruction implemented here is meant to serve mainly as a preliminary basis for future studies, rather than to provide definitive answers, in particular regarding the monophyly of the new tribe.

Acknowledgements

Mikael Sörensson (Lund, Sweden) introduced me to the Ptiliidae. He was the first to recognize the new peculiar African genus named here as *Fenestellidium*, coining this generic epithet. He also identified and supplied all species of all non-Discherocephalini ptiliids used in the present analysis, hosted my two visits to Lund, and commented on two early drafts of this manuscript. Louis Deharveng and Anne Bedos (Paris, France) collected and made available Ptiliidae from Berlese samples taken in Vietnam and Indonesia, which contained new species of *Skidmorella*. Bruce D. Gill (Ottawa, Canada) accompanied me during the fieldwork in Cameroon, which resulted in the discovery of a new *Cissidium* species. Elisabeth Hintelmann (Munich, Germany) funded my fieldwork in Cameroon through a scientific foundation which she established at the Zoologische Staatssammlung München in memory of her late husband, Robert J. H. Hintelmann (http://www.zsm.mwn.de/events/wiss_preise.htm). My 2001–2002 fieldwork in South Africa, Kenya and Tanzania was performed during

my appointment as a postdoctoral fellow at the University of Pretoria (South Africa) and was partly supported by the following grants: Visiting Fellowship from the Canadian Museum of Nature (administered through Robert Anderson, Ottawa, Canada), Visiting Fellowship from the Field Museum of Natural History (Chicago, IL), and Ernst Mayr Visiting Fellowship from the Museum of Comparative Zoology (Cambridge, MA). This study was initiated during my tenure as an Alexander von Humboldt Fellow at the Friedrich-Schiller-Universität Jena hosted by Rolf G. Beutel (Jena, Germany). Maxwell V.L. Barclay (The Natural History Museum, London, U.K.) and Marc De Meyer (Royal Museum for Central Africa, Tervuren, Belgium) made *Africoptilium* holotypes available for re-examination. Harald Schillhammer and Heinrich Schönmann (Naturhistorisches Museum, Wien, Austria) searched (unsuccessfully) through the Franz material in their museum for the *Africoptilium concinnum* holotype. Ainsley Seago (Berkeley, CA) supplied specimens of *Motschulskium sinuatocolle* used for the analysis. Hume Douglas (Ottawa, Canada) commented on an early draft of this manuscript. All the above people are sincerely acknowledged for their contributions to the completion of this project.

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Accepted 15 May 2008