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Ptilophorus purcharti sp. nov., the first ripiphorid from Socotra Island, with an account of the biogeography of the Ptilophorini (Coleoptera: Ripiphoridae)

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Abstract. *Ptilophorus purcharti* sp. nov. (Coleoptera: Ripiphoridae) from Socotra Island, Yemen, is described and figured. It is compared with all known Afrotropical and Palaearctic species of the genus and is considered to be a relictual species with Asian relatives. The distribution of the species seems to be restricted to the Afromontane forest habitats in Al Hagher mountain range. A preliminary phylogenetic analysis of Ptilophorini is performed and discussed. The density and length of setation on the antennal rami of Ptilophorini males are shown to be characters of potential phylogenetic importance which may help to understand the biogeography of the tribe. A preliminary hypothesis of Ptilophorini biogeography is proposed.

Key words. Coleoptera, Ripiphoridae, Ptilophorinae, Ptilophorini, *Ptilophorus*, *Toposcopus*, biogeography, new species, phylogeny, Yemen, Socotra

Introduction

Ptilophorinae is a subfamily with world-wide distribution containing seven described genera in two distinct clades (currently recognized as tribes; FALIN 2003). The tribe Ptilophorini sensu FALIN (2003) represents one of the least explored groups of the Ripiphoridae. The nominotypical genus *Ptilophorus* Dejean, 1834 with 22 described species is distributed in the Old World and Australia with the following distributional pattern: central and south Europe, north Africa and Near East (1 species), Near East and Central Asia (5 species), Afrotropical Region (5 species) and Australia (11 species). The genus is absent from the Oriental Region. A revision of the genus is available (SCHILDER 1925) although the diagnoses of the species are sometimes based on characters of little phylogenetic significance. Three additional species were described subsequently (PIC 1945, KASZAB 1957, IABLOKOFF-KHNZORIAN 1973) and some new species known to me await description. The second genus of Ptilophorini, the monotypic *Toposcopus* LeConte, 1868 with isolated occurrence in the southern part of the U.S.A., was

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synonymized with *Ptilophorus* by SCHILDER (1925). RIVNAY (1929) regarded it as a distinct genus and FALIN (2003) again questioned its validity (but see Discussion). Nothing is known about the biology of these two genera.

The discovery of an undescribed species of *Ptilophorus* on the main island of the Socotra Archipelago situated in the Western Indian Ocean was rather unexpected. Socotra lies about 250 km east of Cape Guardafui in Somalia and 300 km south of Cape Ras Fartaq in Yemen, about 12°30′N by 53°50′E. From the zoogeographical point of view it is therefore situated in a very isolated position between the Afrotropical and the Palaearctic Regions. Even though the Socotran arthropod fauna contains mainly East African elements (e.g. UVAROV & POPOV 1957, MAHNERT 2007, TAITI & CHECCUCCI 2009, HACKER & SALDAITIS 2010), Socotran beetles are sometimes catalogued within the Palaearctic Region (e.g. LÖBL & SMETANA 2008).

Described Afrotropical species of *Ptilophorus* are distributed in the South-West of the continent (i.e., Angola, Namibia, Republic of South Africa, and Zambia). And although additional unidentified and possibly undescribed species from Botswana, Kenya, Mozambique, Tanzania and Zimbabwe are present in collections, no Afrotropical *Ptilophorus* species known to me occurs north of the equator. In the Northern Hemisphere, only the Palaearctic *P. dufourii* (Latreille, 1818) reaches to 'Maghreb' countries in the North Africa and to Jordan and Iran in the Near East at the southern extreme of its range (BATELKA 2007). Within current knowledge of distribution of the genus, the here-described Socotran *Ptilophorus* therefore shows isolated and probably relictual distributional pattern. The species is diagnosed, described and figured in this paper.

Preliminary phylogenetic analysis including Palaearctic, Afrotropical, Australian and Nearctic species of Ptilophorini is performed and polarity of some characters is discussed. A biogeographic hypothesis for the current distribution of Ptilophorini is proposed based on characteristic setation of male antennal rami.

Material and methods

The figures of the holotype were taken at the Department of Zoology, Charles University, Prague using an Olympus Camedia C-5060 digital camera attached to an Olympus SZX9 binocular microscope. Differently focused images were combined using Helicon Focus 3.20.2.Pro software.

SEM microphotographs of male antennal rami of dry specimens were made at the Department of Palaeontology of the National Museum in Prague using a Hitachi S-3700N scanning electron microscope. The number of main setae (i.e. microsetae excluded) in a randomly selected line segment of 100 μm, erection and erection-angle of setae with respect of ramus, and protrusion of setae on inner side of ramus with respect of the width of ramus were measured from the pictures. Several measurements for each species were repeated, areas with damaged setation or anomalies were omitted.

The map of World Pacific Ocean centring was downloaded from d-maps.com, free outline & blank maps at http://d-maps.com.

The holotype is deposited in the National Museum, Prague, Czech Republic, one paratype is stored in The Natural History Museum, London, United Kingdom (BMNH); the remaining paratypes are deposited in the author's collection (JBCP). Exact label data are cited as follows: Lines on the label are separated by a single slash (/), different labels are separated by a double slash (//), comments appear in square brackets. The holotype and three paratypes are dry-mounted, two paratypes are stored in 96% ethanol.

The data matrix was analysed using the program TNT version 1.1, described and discussed in Goloboff et al. (2008). The character matrix (Table 1) consists of 13 unweighted and unordered characters, 12 are related to males, one to females. Parameters setup for calculation: traditional (heuristic) search with 1000 replicates; Wagner trees; random seed: 11; 20 trees to save per replication; tree bisection reconnection (TBR); collapse trees after the search. The consensus tree was obtained using the strict procedure (Nelsen). Characters were mapped on this tree using the WinClada program (Nixon 2002).

Subfamilial and tribal classification of Ripiphoridae follows Falin (2003). Although his study remains unpublished, conclusions and subfamilial rearrangements from this work were adopted by Lawrence et al. (2010). Subfamily Ptilophorinae as it is defined by Falin (2003) contains two tribes: Ptilophorini with genera *Ptilophorus* (10 species included in the present analysis) and *Toposcopus* (the only known species analysed), and an unnamed tribe containing four genera including the speciose *Trigonodera* Dejean, 1834 (one species *T. conicollis* (Laporte, 1840) analysed) and *Micropelecotoides* Pic, 1910 (two species *M. rufithorax* Pic, 1924 and *M. fulvus* (Pic, 1950) analysed). *Clinops spectabilis* Schaufuss, 1872 from Pelecotominae, sister subfamily to Ptilophorinae, was chosen for rooting of trees.

Locality data of unidentified *Ptilophorus* species figured and used in the phylogenetic analysis (all from JBCP) are as follows:

Ptilophorus sp. 1: Australia, W. Australia, Darling Range, Lane Pool C.R., 33°8.51′S, 116°22.15′E, 29.xii.1999.
Ptilophorus sp. 2: Botswana, Gaborone, 6.ii.1997.
Ptilophorus sp. 3: Kenya, eastern of Thika, SW Kangonde, 28.xii.2007.
Ptilophorus sp. 4: Mozambique NW, 15 km SSE Manje, 15°29′S, 33°16′E, 530m, 2.–4.xii.2005.
Ptilophorus sp. 5: Zambia, Southern province, 15 km E of Kalomo, 31.i.–1.ii.2006.
Ptilophorus sp. 6: Zimbabwe, East Zimbabwe, Mutare, Dorowa env., 29.xi.1998.

Table 1. Character state matrix. Character state is marked (?) when information is not available and (-) when the character is not applicable. Autapomorphic characters were excluded from the analysis.

	1	2	3	4	5	6	7	8	9	10	11	12	13
Clinops	1	1	1	0	3	1	?	0	1	0	0	-	1
Micropelecotoides	1	1	1	0	3	1	?	0	1	0	0	1	1
Trigonodera	1	1	1	0	3	1	?	0	1	1	0	1	1
Toposcopus wrightii	0	0	0	1	0	0	0	1	1	1	0	0	0
Ptilophorus fallax	0	0	0	1	2	1	0	1	0	1	1	0	0
Ptilophorus fischeri	0	0	0	1	2	1	0	1	0	1	1	0	0
Ptilophorus purcharti sp. nov.	0	0	0	1	0	0	0	1	0	1	1	0	?
Ptilophorus sp. 6 (Zimbabwe)	0	0	0	1	2	1	1	0	0	1	1	0	?
Ptilophorus sp. 2 (Botswana)	0	0	0	1	2	1	1	0	1	1	0	0	?
Ptilophorus dufourii	0	0	0	1	1	1	1	0	0	1	1	0	0
Ptilophorus sp. 3 (Kenya)	0	0	0	1	1	1	1	0	0	1	1	0	?
Ptilophorus sp. 4 (Mozambique)	0	0	0	1	1	1	1	0	0	1	1	0	?
Ptilophorus sp. 1 (Australia)	0	1	0	1	2	1	1	0	1	0	1	1	?
Ptilophorus sp. 5 (Zambia)	0	0	0	1	1	1	1	0	1	1	0	0	?

List of characters used in the analysis.

Males. *Head.*

1. Temples: developed (0); absent (1).
2. Tooth on incisor edge of mandibles: present (0); absent (1).
3. Impression on mandibles: present (0); absent (1).
4. Eyes: slightly incised (0); deeply emarginated (1).
5. Antennal club: strongly arched (0); arched apically (1); straight (2); not developed (3).
6. Antennae: antennal rami distinctly curved outward (0); antennal rami straight or indistinctly curved (1).
7. Number of main setae in the line segment of 100 µm: three at most (0); more than four (1).
8. Protrusion of setae on inner side of antennal rami reach: at most 2/3 of the thickness of the ramus (0); more than 1.5 of the thickness of the ramus (1).
9. Brush of setae on frons: present (0); absent (1).

Thorax.

10. Lateral pronotal carina: present (0); absent (1).

Elytra.

11. Epipleura: present (0); absent (1).

Legs.

12. Distal apices of metatibiae: expanded outward (0); narrowly bordered (1).

Females.

13. Frons: with smooth oval area (0); completely covered by setae (1).

Results

Ptilophorus purcharti sp. nov.

(Figs. 1–5, 13)

Type locality. Yemen, Socotra Island, Hagghier Mts., Skant [= Skand, Skent] Mt. env., 1450 m a.s.l., 12°34′33″N, 54°01′31″E.

Type material. Holotype: ♂, 'YEMEN, SOCOTRA Island / Skant area, 1300-1500 m / N 12°34'33'', E 54°01'31'' / 31.i.-1.ii.2010, L. Purchart lgt. [printed label]'. Paratypes: **YEMEN**, Socotra Island: same data as the holotype, 1 ♂; 'YEMEN, Socotra Isl. / Hagher [sic!] Mts, Skant, / N 12°34,557', E 54°01,514' / 7.-8.vi.2010, / V. Hula & J. Niedobová leg. // collected on / Cephalocroton / socotranus [printed labels]', 1 ♂; 'SOCOTRA Is. (YE) / Al Haghier Mts. / wadi Madar, 1180-1230 m / 12°33.2'N, 54°00.4'E, / Jan Batelka leg. 12.xi.2010 [printed label]', 1 ♂; 'SOCOTRA Is. (YE) / Al Haghier Mts. / wadi Madar, 1180-1230 m / 12°33.2'N, 54°00.4'E, / Luboš Purchart leg. 13.xi.2010 [printed label]', 1 ♂ (all JBCP); 'SOCOTRA: / Kishin. / 700 m. / 18.iv.1967 / K. Guichard. [printed] / B.M. 1967 – 455 [handwritten]', 1 ♂ (BMNH). Specimens of the newly described species are provided with one red printed label: '*Ptilophorus purcharti* sp. nov. / HOLOTYPE [or PARATYPE] / Jan Batelka det. 2012'.

Diagnosis (male). Antennae distinctly uniflabellate, scapus long, widening apically, covered by long semi-erect setae, pedicel lenticular, covered by short sparse setae, antennomeres 3–10 compressed, bearing each one long ramus, antennomere 11 prolonged and fused basally with antennomere 10, equal in length and shape to ramus of antennomere 10. Antennal rami long, distinctly curved outward in their posterior third, covered with long erect setae.

Pronotum without lateral carina. Elytra long, 2.25 × longer than wide at the base, without epipleuron, setae on elytra arranged outward and backward along suture, not combed into separate rows. Pretarsal claws each with 6–9 teeth depending on the size of specimen. Body length 5.5–9.0 mm.

Ptilophorus purcharti sp. nov. differs from all other members of the genus by the antennal rami curved outward in their posterior third and by the highest length ratio between antennal rami and the antennal club among all Ptilophorini. From all African species it differs by its antennal rami covered by long erect setae (probable synapomorphy with all Asiatic species). At least from Afrotropical *P. atricornis* (Pic, 1923), *P. rufomarginatus* (Pic, 1945) (types examined in Muséum national d'Histoire naturelle, coll. M. Pic, Paris), *P. capensis* Gerstaecker, 1855 and *P. pygmaeus* Schilder, 1923 the newly described species differs by the absence of elytral epipleura (a fifth Afrotropical species *P. herero* Schilder, 1923 from Namibia was not examined). In the density, protrusion and length of setae on the antennal rami it is similar to *Ptilophorus* species from Central Asia, from which it further differs by shape and ratio between length and width of the pronotal disc (cf. IABLOKOFF-KHNZORIAN 1975).

Description (male holotype). Body brown, covered by long semi-erect golden pubescence, all appendages dark brown.

Head. Eyes finely faceted, deeply incised by projections of the convex densely pilose genae, dorsal and ventral eye-lobes completely disconnected. Frons broad, with medial brush of short erect setae between antennae insertion. Tempora large, with long dense golden setae. Vertex upraised. Labrum transverse, with slightly incised anterior margin, slightly concealed beneath clypeus. Mandibles prolonged, triangular in section, with several semi-erect setae along posterior half of its outer margin and with convex ridge along outer margin; incisor edge with distinct tooth. Maxillae with very long and large lacinia bearing brush of long dense cilia and without galea. Maxillary palps with apical palpomere narrowly obovate. Labium bears long labial palps.

Antennae with 11 antennomeres, inserted near margins of eyes in deep sockets, antennal club (i.e. antennomeres 3–10 combined) is strongly arched ventrally, antennal rami about 5.25 × longer than length of antennal club, covered with long erect setae, in average 2–3 main setae in the line segment of 100 μm, almost all setae semi-erect in about 40°–80° angle, protrusion of setae on inner side of antennal rami reach about 1.5 of the thickness of ramus.

Prothorax. Pronotum more or less bell-shaped, lateral pronotal carinae absent, pronotal disc 1.2 × wider than long, with doubly notched posterior margin. Setae on pronotal disc combed mainly toward posterior margin, without clusters or partings. Prosternal process narrow and acute.

Mesothorax. Mesoscutellar shield posteriorly truncate.

Elytra rugose, concealing entire abdomen, conjointly rounded apically, densely pilose, with golden setae directed obliquely outward and backward along suture, 2.25× longer than wide at base and 1.15× wider than posterior margin of pronotum, with protruding humeral tubercles, elytral epipleura absent.

Legs long, metatibial apex spread outwards, tibial spurs formula 2–2–2, spurs spatulate, outer posterior spur widely rounded apically, tarsi 5–5–4, length ratios as follows: protarsi

Figs. 1–5. Holotype of *Ptilophorus purcharti* sp. nov. 1 – habitus, dorsal view; 2 – pretarsal claws; 3 – detail of the antennal club; 4 – detail of the head; 5 – internal abdominal segments dorsally: apical part of tergite 8 with erect setae and apical part of aedeagus (medial lobe with parameres); basal part of aedeagus and abdominal segment 9 are not figured.

3.0–1.2–1.2–1.0–3.2 / mesotarsi 3.3–1.3–1.2–1.0–2.8 / metatarsi 2.7–1.4–1.0–2.2, pretarsal claws dentate, each claw with one long seta basally.

Abdomen narrow, with five ventrites (i.e. sternites 3–7). Tergite 8 weakly sclerotised, consisting of two longitudinal plates connected medially by membraneous cuticle, each plate with some 20 long erect setae apically. Sternite 8 wider than longer, simple, slightly trapeziform, with short golden pubescence. Abdominal segment 9 reduced, spiculum gastrale long, straight and simple.

Aedeagus narrow and tubular, parameres bare, fused along middle, drawn into long processes at both ends, slightly curved inward apically. Medial lobe wider than parameres, extended just before sharp apex.

Female. Unknown, sexual dimorphism is expected.

Etymology. The newly described species is dedicated to Luboš Purchart (Mendel University, Brno), specialist in beetles of the family Tenebrionidae and leader of our Socotra expedition.

Habitat. All specimens were collected in Al Hagghier mountain range on three different sites. The localities of Scant Mt. at 1,450 m a.s.l. and Wadi Madar at 1,180–1,230 m a.s.l. are covered by Afromontane forest. The locality of Scant (see Batelka 2012: Fig. 14) belongs to Leucado hagghierensi-Pittosporetum viridiflorum association, and that of Wadi Madar (see Batelka 2012: Fig. 15) to Trichodesmo scotii-Cephalocrotonetum socotrani association (Kürschner et al. 2006). According to Habrova et al. (2007) the site at 1,450 m is the coldest place in Socotra (lowest recorded temperature is 8.2°C in 30th January 2005). Although the timing of the monsoons and their influence on different habitats of Socotra has been recently evaluated (Scholte & De Geest 2010), I am not able to provide conclusions about the seasonality of *Ptilophorus purcharti* sp. nov. based on limited available data and owing to climatic anomalies caused by the 2010 El Niño event worldwide.

Collecting circumstances. Males collected by L. Purchart were swept from the vegetation, V. Hula and J. Niedobová collected their male on *Cephalocroton* (= *Cephalocrotonopsis*) *socotranus* Balf. f., and the specimen collected by myself was captured by hand in the late afternoon, sitting on inflorescence of an unidentified Lamiaceae about 0.5 m above the ground.

Discussion

Ptilophorus sex ratio in collections

Only males are known for *P. purcharti* sp. nov. In respect of the available material of other *Ptilophorus* species this is obviously not accidental. Using the data from my collection as a reference, not a single female is present in a sample of 30 specimens from Africa, only four females are present among 39 specimens of *P. fischeri* (Ménétriés, 1848) from Uzbekistan, and only 12 females are present in my material of *P. dufourii* from 13 countries (96 specimens in total). This unbalanced sex ratio, when males outnumber females in the collections seems to be a sampling artefact caused by collecting methods used and by different behaviour of males and females of *Ptilophorus*. While males are easy to capture by sweeping or even by hand when they are sitting on vegetation (see above for *P. purcharti* sp. nov.; identical behaviour was observed by myself in *P. dufourii* in Bulgaria and Tunisia), females apparently spend most of their life in hidden, so they are only accidentally collected. An unusual sample, that undoubtedly originated in one collecting event, consisting of 30 females and only a single male of *P. dufourii* is stored in the Museum für Naturkunde (Berlin). One of these specimens has an original handwritten label '30 melandria [= former misidentification], H. 28.4.21', and all 31 specimens were later (probably in the 1960's or 1970's) provided with a label 'Hara, 28.4.1921, Palästina' [most probably = Al Harrah, ca. 33°04′N, 35°58′E, now situated in Syria]. Although the correctness of the subsequent label transcription cannot be verified, it is clear that the series must have been collected by some special technique or during some exceptional circumstance.

Preliminary phylogenetic analysis of Ptilophorini

Historical delimitation of Ptilophorini. Both intra- and inter-specific variability of some external characters complicate the phylogenetic analysis of the genus *Ptilophorus*. A good example of intra-specific variability is the number of teeth of the pretarsal claws which positively correlates with the size of specimen. For example the number varies between 13–16 in *P. fischeri* (body length 7–12 mm), 10–18 in *P. dufourii* (body length 5–11 mm), and 6–9 in *P. purcharti* sp. nov. On the contrary, some characters may be convergent in different species groups, as e.g. the pubescence of elytra (combed into longitudinal partings in Asian *P. fischeri* but uncombed in the closely related *P. fallax* Iablokoff-Khnzorian, 1973, but also combed into partings in unrelated *P. atricornis* from Zambia or *P. nervosus* Gerstaecker, 1855 from Australia). Another example of such convergence may be the shortening of the ramus of the 3rd antennomere, which is transformed into a short process in *P. dufourii* or reduced to about 4/5 of the length of the following ramus in *Toposcopus wrightii* LeConte, 1868.

The first suggestion of the affinity of the *Ptilophorus* species was provided by Schilder (1925) who arranged all Ptilophorini species into two species-groups according to the presence or absence of an elytral epipleuron. The group without epipleura has been further divided in two subgroups according to the presence or absence of a brush of setae on the male frons. Although both characters may be of phylogenetic importance, Schilder (1925) probably derived the diagnoses of some species solely from incomplete original descriptions which resulted in incorrect placement of some species, e.g. in *P. atricornis* in which the epipleuron is actually present based on my examination of the type specimen.

A previously overlooked character important for delimiting Palaearctic species of *Ptilophorus* was discovered by Iablokoff-Khnzorian (1975), who pointed out that *P. dufourii* may be separated from all other Asian species by its 'appressed hairs ... with a few very short semierect hairs' in male antennal rami, while male antennal rami bear only 'erect hairs' in Asian species. Detailed examination of antennal setation in 11 Ptilophorini species by scanning electron microscope (Figs. 6–16) showed that these characters may be of phylogenetic significance within the tribe and may elucidate its present distribution.

Results of the analysis. Strict consensus tree (Fig. 17) was calculated from the three most parsimonious trees retained (best score hit 1000 times out of 1000, best score 20). According to the analysis, Ptilophorini can be preliminarily divided into two main groups based on protrusion and density of setae on antennal rami (characters 7 and 8). The hereby so-called 'Southern Group', represented in the analysis by five Afrotropical species, one Australian species and by the Palaearctic *P. dufourii*, is basal and paraphyletic in respect to the species from Socotra, Central Asia and U.S.A. Remaining Ptilophorini species (*Ptilophorus fallax*, *P. fischeri*, *P. purcharti* sp. nov. and *Toposcopus wrightii*), i.e. those with distribution North of the Equator (with exception of *P. dufourii*), form a monophyletic clade (the so-called 'Northern Group').

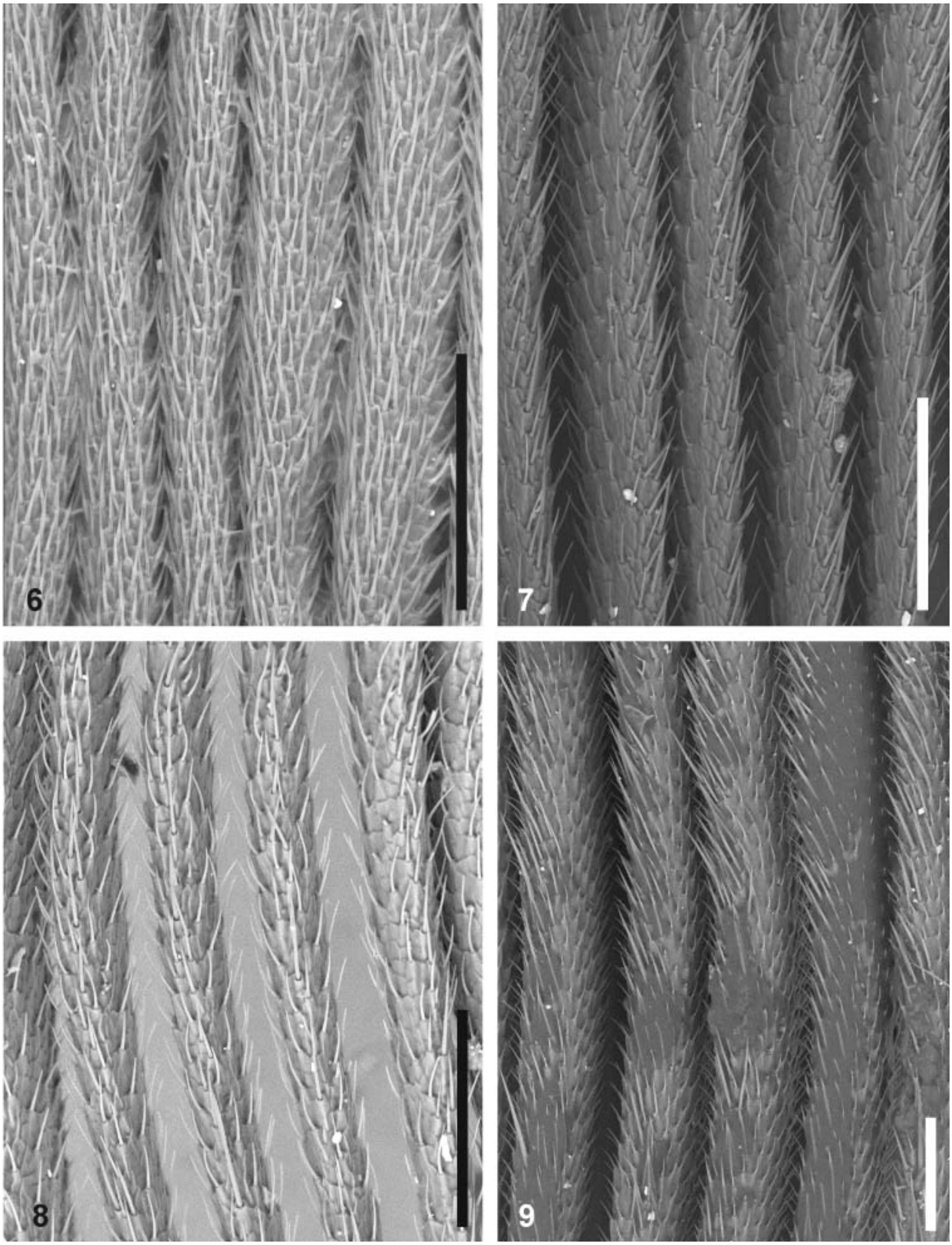
***Southern Group* (SG).** On average 5–6 main setae in the line segment of 100 µm (excepting 4–5 in species from Botswana and eight in *Ptilophorus* sp. 1 (Australia)). Protrusion of setae on inner side of antennal rami distinctly shorter than the thickness of the ramus. Two species-groups may be distinguished based on direction/protrusion of setae:

- Subgroup I. Setae more or less appressed, all in the same direction, protrusion of setae on inner side of antennal rami do not overreach 1/3 of the thickness of the ramus. Species examined: three unidentified species *Ptilophorus* sp. 1 (Australia), *Ptilophorus* sp. 2 (Botswana) and *Ptilophorus* sp. 5 (Zambia), and *P. dufourii* from Greece (JBCP) (Figs. 6–9).
- Subgroup II. Most of the setae semi-erect in about 60°–90° angle, protrusion of setae on inner side of antennal rami do not overreach 2/3 of the thickness of the ramus. Species examined: three unidentified species *Ptilophorus* sp. 3 (Kenya), *Ptilophorus* sp. 4 (Mozambique) and *Ptilophorus* sp. 6 (Zimbabwe) (Figs. 10–12).

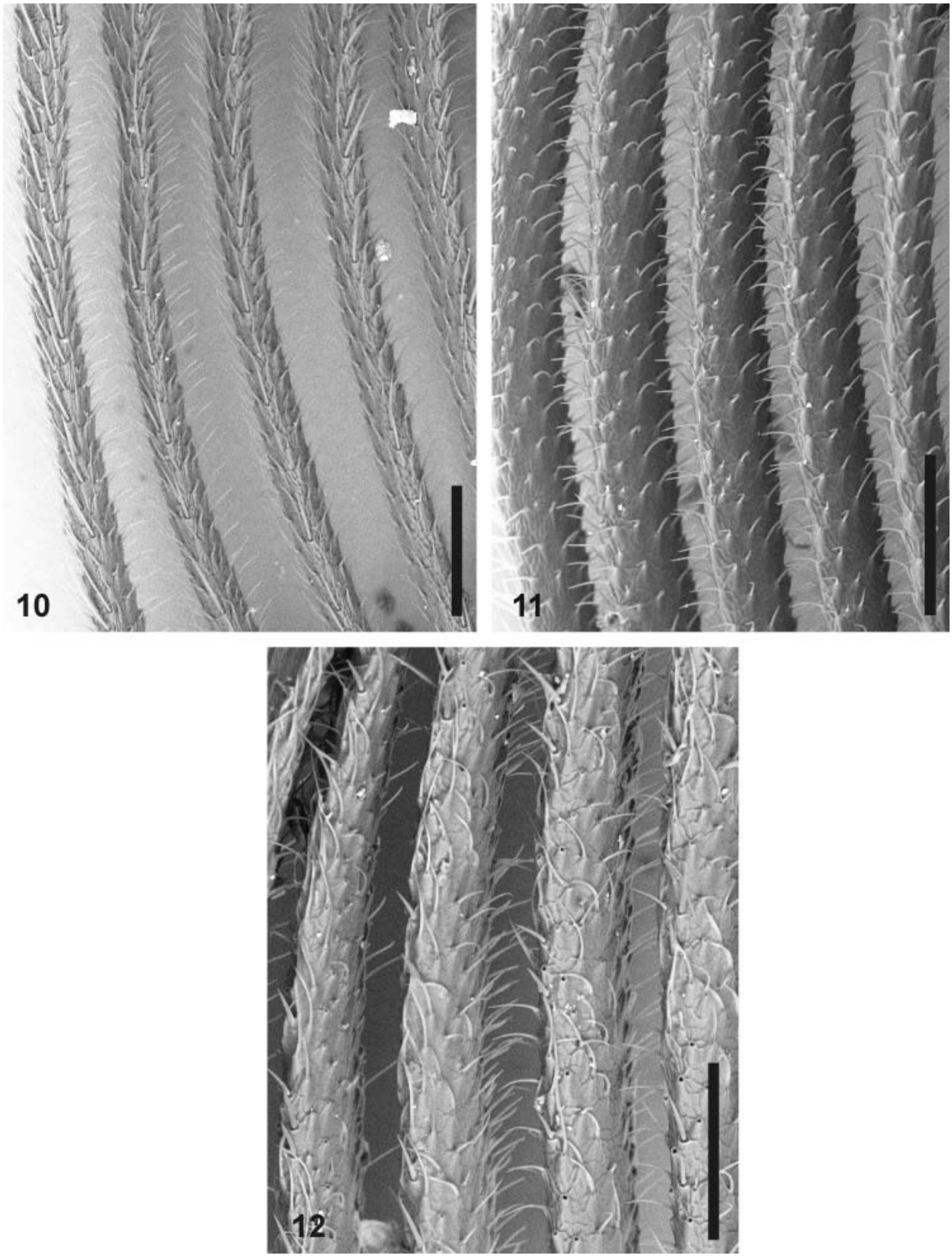
Delimitation of SG into two subgroups was also supported by the analysis (excepting the position of *P. dufourii*) although protrusion of setae in both subgroups (i.e. appressed vs. semi-erect setae) was not distinguished in the analysis.

***Northern Group* (NG).** On average 2–3 main setae in the line segment of 100 µm, almost all of the setae semi-erect at an angle of about 40°–90°, protrusion of setae on inner side of antennal rami reach about 1.5 of the thickness of the ramus (2.0 in *Toposcopus wrightii*). Species examined: *Ptilophorus purcharti* sp. nov., *P. fischeri* from Kazakhstan, *P. fallax* from Tajikistan and *Toposcopus wrightii* from Texas (all JBCP) (Figs. 13–16).

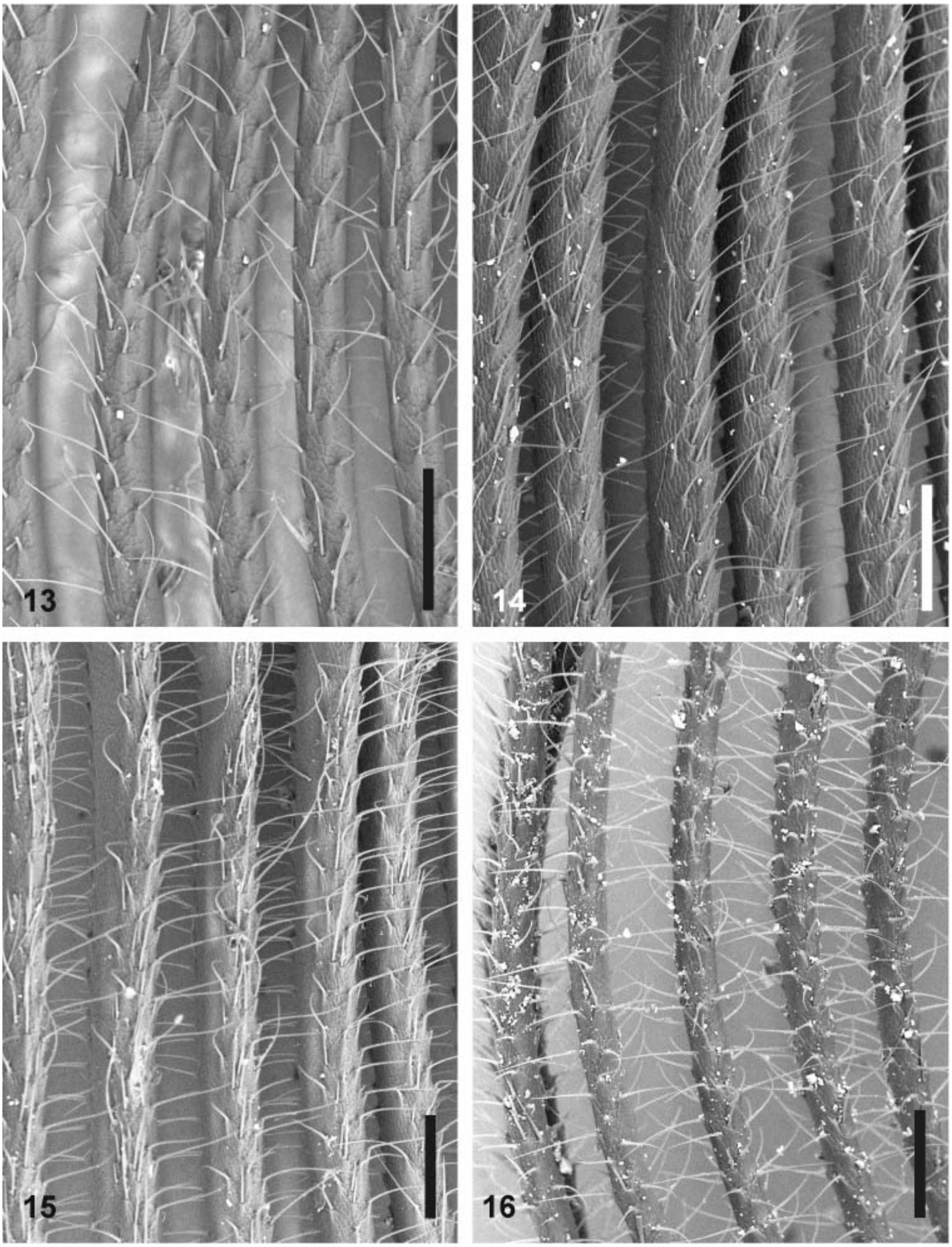
Polarity of characters. The Northern Group is well characterised by apomorphic prolonged protrusion of antennal setae and simultaneously by reduction of their density. It is of note, that *Ptilophorus* sp. 1 (Australia) with the highest density of setae among the examined Ptilophorini is placed most basally in the cladogram although this particular character for this species was coded within the same variability range as it was coded in the rest of the SG species. The direction and length of setae on the antennal rami is at first sight a specific character in the most Ptilophorini I examined. Although described Australian and Afrotropical species are underrepresented in the sample, the preliminary clustering of given sets of characters in all 11 examined species could hardly be accidental. From Australia only one, possibly undescribed, representative was included in the sample and described Australian species remain to be examined if they all match with the proposed criteria. Should they turn out to be distinct



Figs. 6–9. Setation of antennal rami, Southern Group, subgroup I. 6 – *Ptilophorus* sp. 1, Australia, 7 – *Ptilophorus* sp. 2, Botswana, 8 – *Ptilophorus* sp. 5, Zambia, 9 – *Ptilophorus dufourii* (Latreille, 1818). Scale bars: 100 µm.



Figs. 10–12. Setation of antennal rami, Southern Group, subgroup II. 10 – *Ptilophorus* sp. 3, Kenya, 11 – *Ptilophorus* sp. 4, Mozambique, 12 – *Ptilophorus* sp. 6, Zimbabwe. Scale bars: 100 µm.



Figs. 13–16. Setation of antennal rami, Northern Group. 13 – *Ptilophorus purcharti* sp. nov., 14 – *Ptilophorus fischeri* (Ménétriés, 1848), 15 – *Ptilophorus fallax* Iablokoff-Khnzorian, 1973, 16 – *Toposcopus wrightii* LeConte, 1868. Scale bars: 100 µm.

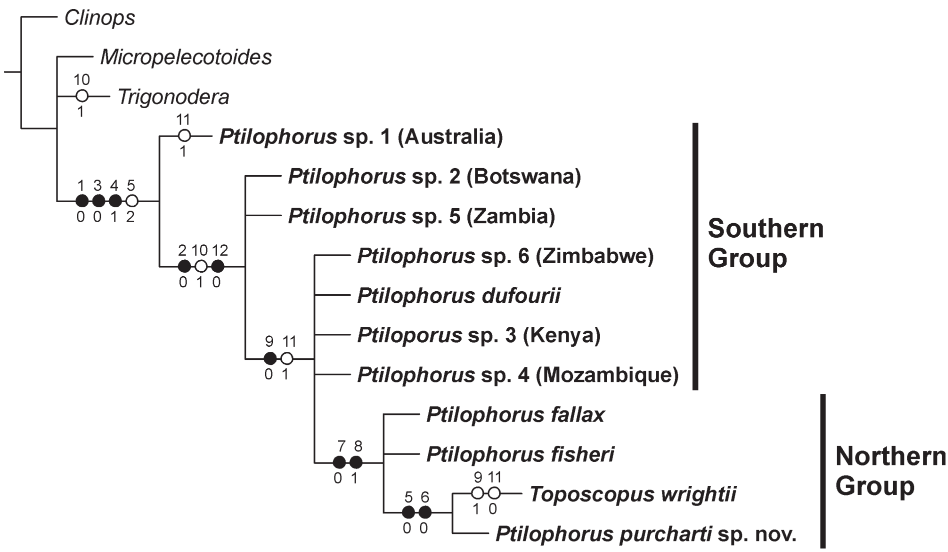


Fig. 17. Strict consensus tree of Ptilophorini with mapped synapomorphies.

to some extent (the examined Australian species possess the highest number of setae within Ptilophorini), the definition of SG subgroups might change. Some species were available only as old pinned specimens (including types) which caused technical complications for preparation of SEM microphotographs. However, their examination using a binocular microscope did not show any apparent difference from the proposed criteria for each group.

Proposed delimiting characters seem to be independent for example of climatic conditions in the areas inhabited by the species of both groups. *Ptilophorus dufourii* (SG) survives in localities with hot and dry climate (e.g. mountain and desert oases in Algeria or Southern Tunisia, southern coast of Crete), as well as in cold mountains up to 2,000 m a.s.l. (High Atlas in Morocco and Eastern Turkey) or in temperate Central Europe (Hungary, regionally extinct in the 19th century). On the contrary, *P. purcharti* sp. nov. (NG) is restricted to remnants of Afromontane forest, where the temperature probably never drops below 0°C, *Toposcopus wrightii* (NG) occurs in the deserts of Arizona, New Mexico and Texas (U.S.A.), while *Ptilophorus* species from the Central Asia (NG) inhabit the high mountain ranges of the Tien-Shan and the Pamirs where the hard winters are similar to those in Moroccan or Turkish mountains. Considering different climatic conditions in all these extralimital localities of particular species/groups, possible morphological adaptations with respect to these conditions can most probably be ruled out.

Systematic position of *Toposcopus*. Falin (2003) synonymised the monotypic *Toposcopus* with the speciose *Ptilophorus*. However, in his phylogenetic analysis of Ripiphoridae, he did not use nor mention the above discussed character on male antennae introduced for Ptilophorini by IABLOKOFF-KHNZORIAN (1975). In addition to *Toposcopus*, FALIN (2003) chose for the analysis a small and unbalanced sample of four *Ptilophorus* species (Palaearctic *P. dufourii*, Afrotropical *P. pygmaeus* and two Australian species *P. nervosus* and *P. signatus* Schilder, 1925). *Toposcopus* then appeared as a terminal branch/taxon sister to *Ptilophorus pygmaeus* from Angola to which it is undoubtedly not related. However, the position of *Toposcopus* is similar in his work as in the present cladogram (Fig. 17), i.e., making the genus *Ptilophorus* paraphyletic with respect to *Toposcopus*, and the two genera should indeed be treated as synonyms, as proposed by SCHILDER (1925). However, for confirmation of this, comprehensive morphological or molecular analysis including more Ptilophorini species from both the Northern and Southern Groups is required. Interestingly FALIN's cladogram is also similar to results obtained in the present study with respect to the position of the Australian species which are those placed the most basally followed by African species, i.e. (*P. nervosus* + (*P. signatus* + (*P. dufourii* + (*P. pygmaeus* + *Toposcopus*)))).

Biogeography of the Ptilophorini

Based on the arrangement of setae on the male antennal rami, Ptilophorini could be divided into two different groups with distinct distributional patterns (Fig. 18). The Southern Group should include 16 described and several undescribed species distributed south of the Equator. *Ptilophorus dufourii* distributed in the northern hemisphere is the only exception within the group. The Northern Group includes seven species which are distributed exclusively north of the Equator. The members of the SG seem to be of the Gondwanan origin and their current distribution in the Afrotropical region and Australia is most probably a result of the Mesozoic break-up of the supercontinent Gondwana. The presence of one isolated species (*P. dufourii*) in the Northern hemisphere is here considered to be the result of range expansion of the Afrotropical members northward. The NG currently has its centre of diversity in the mountain chains of Central Asia and the Near East, and is represented in both Socotra and North America by single relictual species. Although members of the NG came out from the analysis as descendants of African species (including *P. dufourii*), and this seems to be the most probable scenario, their exact origin cannot be proposed because of incomplete taxon sampling.

Consequently, the following three ancient expansion events within Ptilophorini could be proposed:

1) <u>Mediterranean-southern African disjunct model.</u> Owing to its short appressed setae on antennal rami and their high density, the Palaearctic *P. dufourii* is supposed here to be derived from southern African stock. Migration northward (probably in Neogene period) of *P. dufourii*'s ancestor from tropical Africa with subsequent speciation and colonization of the Mediterranean may best explain current disjunct distribution of this morphotype. A similar scenario in Coleoptera is predicted for the meloid genera *Actenodia* Laporte de Castelnau, 1840 and *Ceroctis* Marseul, 1870 (BOLOGNA et al. 2008a, b) and the chrysomelid *Longitarsus capensis* species-group (BIONDI & D'ALESSANDRO 2008). Another chrysomelid *Oxylepus boroveci* Borowiec, 2001 from southern Tunisia seems to be more closely related to its southern African congeners than it is to another two Mediterranean species (BOROWIEC

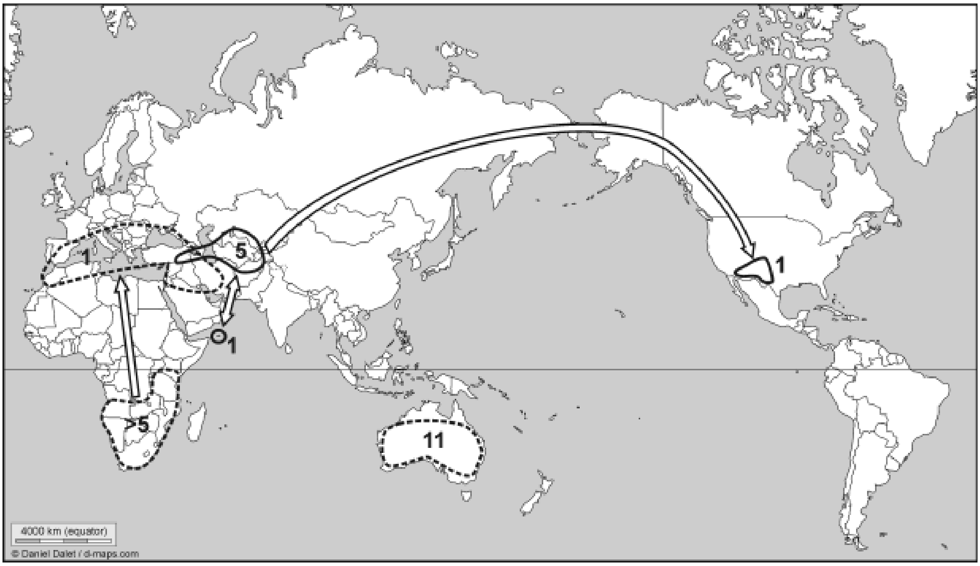


Fig. 18. *Ptilophorini* distributional map. Northern Group - full line, Southern Group - interrupted line, numbers indicate number of known species in the particular range, arrows correspond to supposed expansion events.

2001). In Ripiphoridae a possible example of this disjunct distributional pattern is the genus *Clinops* Gerstaecker, 1855 with one species distributed in Greece and Turkey and one species known from southern Africa ('Caffraria') (Batelka 2005).

2) Asiatic-Arabian faunal interchange. The isolated occurrence of *Ptilophorus purcharti* sp. nov. seems to be an example of a derived endemic Socotran taxon with Asian relatives. Two genera of freshwater crabs (Potamidae) – *Socotrapotamon* Apel & Brandis, 2000 and *Socotra* Cumberlidge & Wranik, 2002 – show affinities to Eurasian potamids and their occurrence in Socotra supposed to be a result of the early Miocene connections of Arabia (including Socotra) with continental Asia (Apel & Brandis 2000; Cumberlidge & Wranik 2002). Another example of this expansion scenario are land snails of the genera *Pseudonapaeus* Westerlund, 1887 and the monotypic *Mordania* Bank & Neubert, 1998 from Oman which are related to species of 'the inner-Asiatic steppe areas and can be characterised as Irano-Turanian elements' (Neubert 1998: 444). However, the direction of putative *Ptilophorus* expansion between Socotra and Central Asia can not be inferred from the morphological and distributional data, as they are currently available.

3) Asiatic-American faunal interchange. *Toposcopus wrightii* from the southernmost U.S.A. (Arizona, New Mexico and Texas) appears to be a relictual successor of an Asian *Ptilophorus* invader which expanded to the New World through Beringia. Similarly, the ancestors of some Mexican endemic beetle genera like the goliathini *Ischnoscelis* Burmeister, 1842 and *Neoscelis* Schoch, 1897 (Scarabaeidae: Cetoniinae) (Morón & Ratcliffe 1989, Mudge et

al. 2003) or the cavernicolous ground beetle *Miquihuana* Barr, 1982 (Carabidae: Sphodrini) (CASALE 1988) are considered to be linked to the Miocene faunal expansion through Beringia followed by subsequent isolation and speciation.

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