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Earwigs (Dermaptera) of Socotra Island: checklist, distribution, and description of a new genus and four new species

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Abstract. The Dermaptera fauna of Socotra Island is reviewed. Based on the study of material collected during expeditions of Czech naturalists in 1999–2012, a new genus, *Socotralabis* gen. nov. with the type species *S. hulai* sp. nov., and an additional species *S. bezdeki* sp. nov. have been recognised, and two new species of the genus *Anisolabella* Zacher, 1911: *A. haasi* sp. nov., and *A. planata* sp. nov. are described. Additionally, a new combination, *Guanchia sokotrana* (Burr, 1905) comb. nov. (from *Anechura* Scudder, 1876), is proposed, and the species *Guanchia bituberculata* (Brindle, 1966) stat. restit., described from the Democratic Republic of the Congo, is removed from synonymy with *G. sokotrana* and reinstated as a valid species. Thirteen species have been found to occur in the Socotra Archipelago, while seven species (54 %) appear to be endemic, all to Socotra Island. Endemic taxa are associated with the mountain areas of Hagher, Homhil and Dixam, which are hot spots of the island's biodiversity. An updated checklist, distribution maps and new data on the Dermaptera species are presented to extend the knowledge of the Dermaptera of Socotra.

Key words. Dermaptera, Anisolabididae, Labiduridae, Forficulidae, *Socotralabis*, *Anisolabella*, *Guanchia*, taxonomy, description, new genus, new species, new combination, new records, Congo, Socotra, Yemen

Introduction

The Socotra Archipelago is a group of four main islands – Abd el Kuri, Darsa, Samha and Socotra, located in the western region of the Arabian Sea. Like Madagascar, the Seychelles, south Arabia, and Africa, the Socotra Archipelago is of east Gondwanan origin. The archipelago was believed to split from what is presently the Dhofar region in southern Arabia between 30–16 Mya

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during the separation of Africa and the Arabian Peninsula and the widening of the Gulf of Aden (for summary, see Batelka 2012). The long isolation of these islands has led to the development of a very specific fauna with a high proportion of endemic taxa. Approximately 50 genus-level taxa of insects are known to reside exclusively in the Socotra Archipelago (Batelka 2012).

So far, nine species of Dermaptera were known from the Socotra Archipelago, two of which (*Forficula redempta* Burr, 1905 and *Marava socotrana* Haas, 2004) were considered to be endemic (Haas et al. 2004). These authors also mentioned the occurrence of an unknown species of Anisolabididae that was provisionally assigned to the genus *Anisolabis* Fieber, 1853; its precise identification was not possible because only females and nymphs were available.

In 1999–2012 during various biological projects, Czech naturalists collected many insects (see Hájek & Bezděk 2012), including specimens of Dermaptera. This material includes also specimens of four undescribed species. Based on a detailed study of the male genital armature, two of the new species are included in the genus *Anisolabella* Zacher, 1911; and for two species with specifically shaped parameres, a new genus, *Socotralabis* gen. nov., is proposed. An updated checklist, distribution maps and new data on Dermaptera species collected during the Czech expeditions are presented to extend the knowledge of the Dermaptera of the Socotra Archipelago.

Materials and methods

The nomenclature and morphological terminology follow those used by Srivastava (2003). The specimens of newly described taxa were dry-mounted, examined, and photographed with an Olympus SZ61 stereomicroscope (20–40× magnification) equipped with an ocular grid and an Olympus E-410 camera. Micrographs of 10 layers of focus of the same specimen were combined with Quick Photo Camera 2.3 software. The dissected body parts (the penultimate sternites) were mounted with methylcellulose glue on the same card with the specimen. A genital armature of male specimens was mounted in dimethyl hydantoin formaldehyde resin (DMHF, a water-soluble mounting medium) on the same label as the specimen.

The specimens studied are deposited in Národní muzeum, Prague, Czech Republic (NMPC); in Moravské zemské muzeum, Brno, Czech Republic (MMBC); in Musée royal d'Afrique centrale, Tervuren, Belgium (MRAC); and in the private collection of the author (PKCO). Local geographic names are mentioned as on the locality labels. For their interpretations, see Bezděk et al. (2012).

Taxonomy

ANISOLABIDAE

Socotralabis gen. nov.

(Figs 1–5)

Type species. *Socotralabis hulai* sp. nov., designated here.

Description. Head as long as wide; antennomere 1 long, narrowed basally, widened terminally, as long as length of antennomeres 2–4 combined; antennomere 2 transverse, only slightly longer than wide; antennomere 3 longer than antennomere 4. Antennomeres 2–4

cylindrical, other antennomeres conical. Pronotum approximately as long as wide, widened posteriorly, meso- and metanotum transverse; mesonotum truncate posteriorly, metanotum broadly emarginate. Prosternum longer than wide, constricted laterally in posterior third, posterior margin truncate; mesosternum approximately as long as wide, posterior margin rounded; metasternum approximately as long as wide, trigonal, widest at base and tapering to truncate tip. Tegmina and wings entirely absent. Legs comparatively long, femora stout; tibiae clad with thick and fine setae; metatarsomere 1 nearly as long as metatarsomeres 2–3 combined. Abdominal tergites, except for ultimate tergite, convex, somewhat widened posteriorly; lateral glandular folds not visible. Ultimate tergite transverse. Pygidium flat. Both branches of male forceps remote and stout at base, gradually tapering apically, apices gently hooked, inner margin finely crenulated, trigonal in basal half, and depressed posteriorly. Right branch more curved in distal third than left branch. Female forceps with contiguous branches, simple and straight. Male genitalia with short parameres, 1.6–1.8 times longer than wide, narrowed apically; external apical angle and margin convex, tip with a remarkable incision in middle. Incision of parameres situated at interface of inner and outer membranes, with median membrane extending to deepest part of incision. Longer genital lobe between 1.5–1.6 times longer than length of paramere.

Differential diagnosis. The new genus corresponds to the general body shape of Anisolabidinae, but differs from the other genera in the structure of the male genitalia with characteristically excised parameres. Except for *Socotralabis* gen. nov., excised parameres occur only in the monotypic Oriental genus *Ornatolabis* Steinmann, 1988, in which the excision of the tip of the parameres is situated entirely in the outer membrane. In *Socotralabis* gen. nov., the excision is situated in the inner membrane near the interface of the inner and outer membranes.

Etymology. The name is modified from the name of the family Anisolabididae, -*labis*, using the Greek prefix *Socotra*-, which refers to Socotra Island; gender feminine.

Key to the genera of the subfamily Anisolabidinae
(based on males)

1 (2) Parameres long, narrow, more than 10 times longer than wide. ..... ***Epilandex*** Hebard, 1927

2 (1) Parameres less than 10 times longer than wide.

3 (12) Parameres entire, not excised or armed internally or externally.

4 (19) Parameres approximately 1.0–2.5 times longer than wide, broad and flattened.

6 (7) Parameres approximately as long as wide or only slightly longer than wide. ..... ***Euborellia*** Burr, 1910

7 (6) Parameres approximately 1.5–2.0 times longer than wide.

8 (11) Parameres approximately 1.5 times longer than wide, wider in middle, narrowed apically.

9 (10) Outer margin of parameres with obtuse or acute angle, somewhat square, or sometimes with inner margin oblique, narrowed towards apex, forming a snout; apical angle projecting or spiniform. ..... ***Mongolabis*** Zacher, 1911

10 (9) Parameres oval to squarish, narrowed apically but not forming a snout; tip pointed or obtuse; external margin semi-circular or forms a continuous arch. ..... ***Anisolabella*** Zacher, 1911

11 (8) Parameres approximately 2.5 times longer than wide, almost of uniform width throughout. ..... ***Gonolabis*** Burr, 1900

12 (3) Parameres excised apically, or armed along internal or external margin.

13 (16) Parameres excised apically in outer membrane. ..... ***Ornatolabis*** Steinmann, 1988

14 (13) Parameres excised apically in inner membrane near interface of inner and outer membranes. ..... ***Socotralabis*** **gen. nov.**

16 (13) Parameres not excised apically.

17 (18) Parameres armed internally at base, or middle with a tooth. ..... ***Aborolabis*** Srivastava, 1969

18 (17) Parameres armed on external margin with a broad recurved flange. ..... ***Canarilabis*** Steinmann, 1985

19 (4) Parameres 3.0–7.0 times longer than wide, generally narrower.

20 (21) Parameres with tip recurved apically. ..... ***Flexiolabis*** Steinmann, 1988

21 (20) Parameres not recurved apically.

22 (23) Parameres with tip bifid, both distal lobes equally long. ..... ***Indolabis*** Steinmann, 1988

23(22) Parameres with the tip entire, one of distal lobes shorter.

23 (24) Parameres three times longer than wide or slightly less, widened at base externally; tip acuminate. ..... ***Apolabis*** Burr, 1915

24 (23) Parameres more than four times longer than wide; tip acute or obtuse.

25 (26) Parameres with tip acute, external and internal margins convex or with a faint sinuation. ..... ***Carcinophora*** Scudder, 1876

26 (25) Parameres with tip obtuse, often slightly broadened in middle. ..... ***Anisolabis*** Fieber, 1853

Socotralabis hulai **sp. nov.**

(Figs 1–5, 28)

Type locality. Yemen, Socotra Island, Wadi Matyaf [= Mathif], 12°27′28.38″N, 54°18′22.32″E, ca. 50 m a.s.l.

Material examined. Holotype: ♂, 'Republic of Yemen / Socotra Isl., Wadi Mathif / N12°27′28.38″, E54°18′22.32″ / V Hula lgt. 20.6.2009 // HOLOTYPUS / *Socotralabis* / *hulai* sp. nov. / det. P. Kočárek 2013' (NMPC). Paratypes: 2 ♂♂ 1 ♀, same label data as holotype (NMPC, PKCO); 4 ♂♂ 3 ♀♀, 'Yemen Socotra Island / Hagher Mts., Scand Mt. env. / montane evergreen woodland / 16.-18.vi.2012 / 12°34.6′N, E54°01.5′E, 1450 m // Socotra expedition 2012 / J. Bezděk, J. Hájek, V. Hula, P. Kment, I. Malenovský, J. Niedobová & L. Purchart lgt.' (MMBC, NMPC, PKCO). Each of the paratype specimens is provided with an additional printed red label: 'PARATYPUS / *Socotralabis* / *hulai* sp. nov. / det. P. Kočárek 2013'.

Description. ***Male.*** Body reddish brown, shiny; antennae unicolor, pronotum reddish brown with paler sides, legs yellowish brown, forceps reddish brown. Cuticle punctured, shiny; tegmina and wings entirely absent.

Head (Fig. 1) as long as wide; postfrontal and coronal sutures fine but distinct; frons convex; posterior margin of head feebly emarginate in middle. Eyes blackish brown, approximately 0.5 times as long as head length posterior to eyes. Antennae of male holotype with 19 antennomeres, female paratype with 20 antennomeres (both incomplete); antennomere 1 long, narrowed basally, widened terminally, as long as antennomeres 2–4 combined; antennomere 2 transverse, only slightly longer than wide; antennomere 3 longer than antennomere 4. Antennomeres 2–4 cylindrical, other antennomeres conical. All antennomeres pubescent.

Pronotum (Fig. 1) smooth, approximately as long as wide, widened posteriorly; anterior margin nearly straight, lateral and posterior margins straight. Median sulcus fine but distinct. Meso- and metanotum transverse, smooth; mesonotum truncate posteriorly, metanotum broadly emarginate. Median sulcus visible on mesonotum, absent on metanotum. Prosternum longer than wide, constricted laterally in posterior third, posterior margin truncate; mesosternum approximately as long as wide, posterior margin rounded; metasternum approximately as long as wide, trigonal, widest at base and tapering to truncate tip. Legs comparatively long, yellowish brown; femora stout; tibiae with thick and fine setae; length of metatarsomere 1 nearly equal to metatarsomeres 2–3 combined.

Abdomen (Fig. 1) sparsely punctulate. Tergites (except for ultimate tergite) convex, somewhat widened posteriorly; lateral glandular folds not visible; antero-lateral parts of tergites with pairs of small longitudinal smooth areas. Tergites 7–9 rugoso-striate at sides, each with low blunt rugoso-striate lateral longitudinal ridge. Ultimate tergite transverse; sides convex, slightly narrowed anteriorly, and slightly depressed medially with visible median longitudinal furrow; lateral longitudinal ridge rugoso-striate, posterior margin in middle slightly concave. Penultimate sternite narrowed posteriorly, with posterior margin subtruncate or slightly emarginate (Fig. 2). Pygidium flat. Forceps asymmetrical, right branch more curved in distal third than left branch; both branches subcontiguous and stout at base, gradually tapering apically, nearly straight in basal two thirds, and slightly incurved afterwards; apices gently hooked, inner margin finely crenulated, dorsally trigonal in basal half, depressed posteriorly.

Genitalia (Figs 4, 5) with short parameres, 1.6 times longer than wide, broadened in middle and narrowed apically; external apical angle and margin convex. Tip of parameres with a remarkable incision in middle (Fig. 5); incision situated at interface of inner and outer membranes, with median membrane extending to deepest part of incision. Longer genital lobe 1.5 times longer than length of paramere (Fig. 4).

Female. Agrees with male in most characters except for: penultimate sternite with posterior margin regularly rounded; posterior margins of all tergites smooth, or only middle parts of tergites 6–7 gently rugoso-striate, but with not developed lateral longitudinal ridge; ultimate tergite comparatively narrowed posteriorly with posterior margin slightly emarginated; forceps with simple and straight contiguous branches (Fig. 3).

Measurements. Total body length without forceps: ♂♂: 9.4–15.6 mm, holotype 14.8 mm; ♀♀: 11.2–18.7 mm. Length of forceps: ♂♂: 1.6–2.7 mm, holotype 1.7 mm; ♀♀: 2.2–2.9 mm.

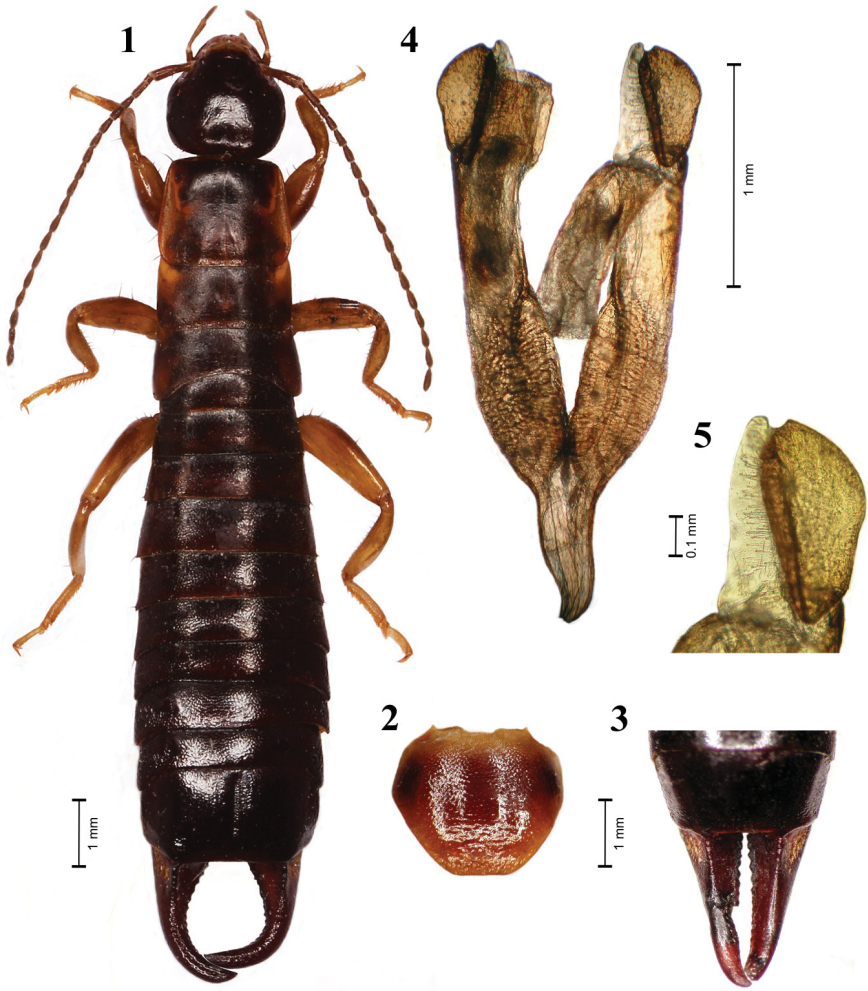
Differential diagnosis. *Socotralabis hulai* sp. nov. differs from *S. bezdeki* sp. nov. in the following combination of characteristics: *S. hulai* sp. nov. is a thicker species with posteriorly

widened abdomen; male tergites 7–9 are rugoso-striate at the sides, and each has a low blunt rugoso-striate lateral longitudinal ridge; the parameres of the male genitalia are wider, 1.5 times longer than wide.

Etymology. The species is named after one of its collectors, Vladimír Hula (Brno, Czech Republic).

Bionomy. Unknown. The species was collected in an area of a montane evergreen woodland.

Distribution. Yemen, Socotra Island (Fig. 28). Most likely an endemic species.



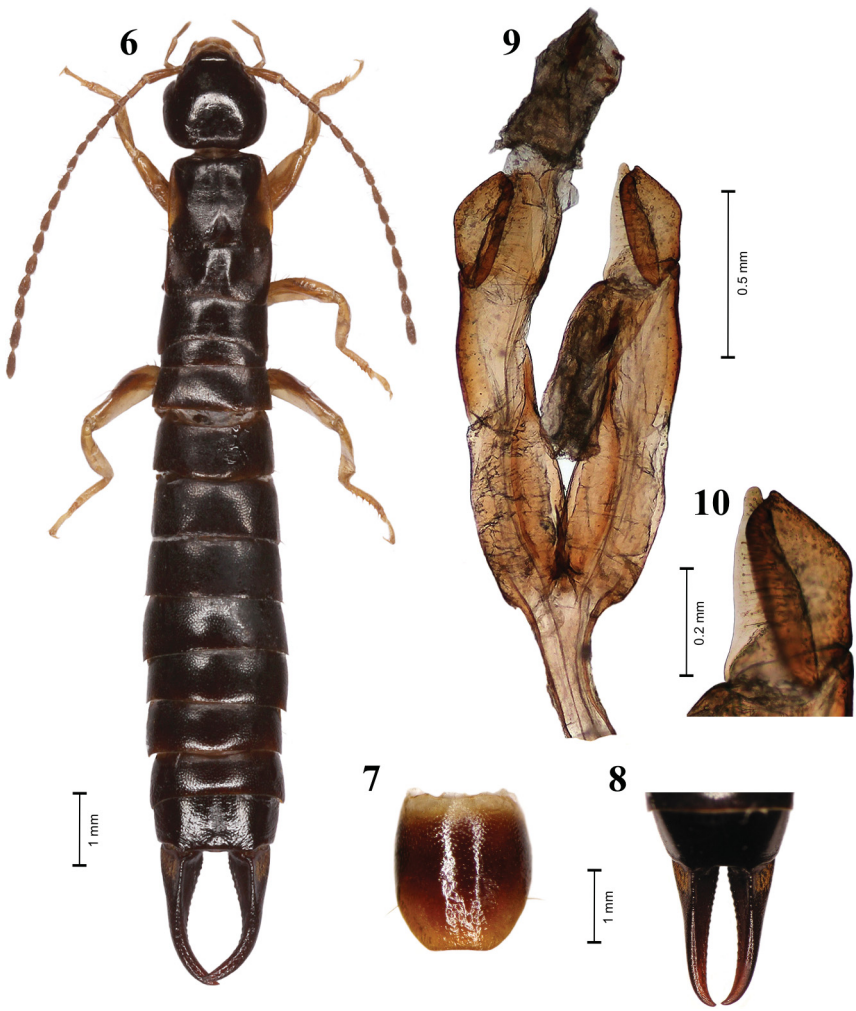
Figs 1–5. *Socotralabis hulai* sp. nov. 1 – habitus of male holotype; 2 – male penultimate sternite, ventral view; 3 – ultimate tergite and forceps of female paratype; 4 – male genitalia; 5 – right paramere of male genitalia.

Socotralabis bezdeki sp. nov.

(Figs 6–10, 29)

Type locality. Yemen, Socotra Island, Hagher Mts., Scand Mt., 12°34.6′N, E54°01.5′E, 1,450 m a.s.l.

Material examined. Holotype: ♂, 'Yemen Socotra Island / Hagher Mts., Scand Mt. env. / montane evergreen woodland / 16.-18.vi.2012 / 12°34.6′N, E54°01.5′E, 1450 m // Socotra expedition 2012 / J. Bezděk, J. Hájek, V. Hula, P. Kment, I. Malenovský, J. Niedobová & L. Purchart lgt. // HOLOTYPUS / *Socotralabis* / *bezdeki* sp. nov. / det. P. Kočárek 2013' (NMPC). Paratypes: 1 ♂ 8 ♀♀, same label data as holotype (MMBC, NMPC, PKCO). Each of the paratype specimens is provided with an additional printed red label: 'PARATYPUS / *Socotralabis* / *bezdeki* sp. nov. / det. P. Kočárek 2013'.



Figs 6–10. *Socotralabis bezdeki* sp. nov. 6 – habitus of male holotype; 7 – male penultimate sternite, ventral view; 8 – ultimate tergite and forceps of female paratype; 9 – male genitalia; 10 – right paramere of male genitalia.

Description. ***Male.*** Body brown to blackish brown, shiny; antennae unicolour; pronotum brown to blackish brown with paler sides; legs yellowish brown; forceps reddish brown. Cuticle punctured, shiny; tegmina and wings entirely absent.

Head (Fig. 6) as long as wide, postfrontal and coronal sutures very fine, but distinct; frons convex, posterior margin of head feebly emarginate in middle. Eyes blackish brown, approximately 0.5 times as long as length of head posterior to eyes. Antennae pubescent, with 20 antennomeres (in holotype incomplete); antennomere 1 long, narrowed basally, widened terminally, as long as length of antennomeres 2–4 combined; antennomere 2 transverse, as long as wide; antennomere 3 longer than antennomere 4. Antennomeres 2–3 cylindrical, other antennomeres conical.

Pronotum (Fig. 6) smooth, about as long as broad, widened posteriorly; margins nearly straight with rounded corners. Median sulcus fine but distinct. Meso- and metanotum transverse, smooth; mesonotum truncate posteriorly, metanotum broadly emarginate. Median sulcus visible on mesonotum, on metanotum absent. Sternal plates typical for genus. Legs comparatively long, yellowish brown; femora stout; tibiae with thick and fine setae; metatarsi with metatarsomere 1 slightly longer than length of metatarsomeres 2–3 combined.

Abdomen (Fig. 6) sparsely regularly punctulate; tergites (except for ultimate tergite) convex, slightly widened posteriorly; lateral glandular folds invisible; antero-lateral parts of tergites with pairs of small longitudinal smooth areas; posterior margins of all tergites smooth, without keels or striation. Ultimate tergite transverse, sides convex, narrowed posteriorly, with shallow median longitudinal furrow; posterior margin in middle straight. Penultimate sternite narrowed posteriorly, with posterior margin concave (Fig. 7). Pygidium flat. Forceps slightly asymmetrical, right branch little more curved in posterior half than left one; both branches remote and stout at base, gradually tapering apically, almost straight in basal two thirds, both slightly incurved afterwards, apices gently hooked, inner margin finely crenulated, dorsally trigonal in basal half, cylindrical posteriorly.

Genitalia (Figs 9, 10) with parameres short, 1.8 times longer than broad, broadened in middle and narrowed apically, external apical angle and margin convex, tip with remarkable incision in middle (Fig. 10). Incision of parameres situated at interface of inner and outer membrane, median membrane extending to deepest part of incision. Longer genital lobe 1.6 times longer than length of paramere (Fig. 9).

Female. Agrees with male in most characters except for: penultimate sternite gradually narrowed posteriorly, with posterior margin rounded; ultimate tergite comparatively narrowed posteriorly with posterior margin slightly emarginated; forceps with branches contiguous, simple and straight, inner margin finely crenulated (Fig. 8).

Measurements. Total body length without forceps: ♂♂: 10.6–11.4 mm, holotype 14.8 mm; ♀♀: 11.0–12.1 mm. Length of forceps: ♂♂: 1.8–1.9 mm, holotype 1.9 mm; ♀: 1.8–2.2 mm.

Differential diagnosis. *Socotralabis bezdeki* sp. nov. differs from *S. hulai* sp. nov. in the following combination of characteristics: *S. bezdeki* sp. nov. is a more slender species with the abdomen nearly parallel sided and not remarkably widened posteriorly; tergites 7–9 are smooth, not rugoso-striated at the sides; the parameres of the male genitalia are slender and they are two times longer than wide.

Etymology. The species is named after one of its collectors, Jan Bezděk (Brno, Czech Republic) as thanks for kind collecting earwigs for my studies.
Bionomy. Sifted from wet leaf litter in a montane evergreen woodland, association *Leucado hagghierensi-Pittosporetum viridiflorum*.
Distribution. Yemen, Socotra Island (Fig. 29). Most likely an endemic species.

Anisolabella Zacher, 1911

Anisolabella planata sp. nov.

(Figs 11–15, 27)

Type locality. Yemen, Hagher Mts., Scand Mt, 12°34.6′N, 54°01.5′E, 1,450 m a.s.l.
Material examined. Holotype: ♂, 'Socotra Is. (YE) / Al Haghier Mts. Scant Mt. env. / 12°34.6′N, 54°01.5′E, 1450 m / Jan Batelka leg. 12-13.xi.2010 // HOLOTYPUS / *Anisolabella* / *planata* sp. nov. / det. P. Kočárek 2013' (NMPC). Paratypes: 1 ♂ 1 ♀, same label data as holotype (NMPC); 1 ♂, 'Yemen Socotra Island / Hagher Mts., Scand Mt. env. / montane evergreen woodland / 16.-18.vi.2012 / 12°34.6′N, 54°01.5′E, 1,450 m // Socotra expedition 2012 / J. Bezděk, J. Hájek, V. Hula, P. Kment, I. Malenovský, J. Niedobová & L. Purchart lgt.' (PKCO). Each of the paratype specimens is provided with an additional printed red label: 'PARATYPUS / *Anisolabella* / *planata* sp. nov. / det. P. Kočárek 2013'.

Description. ***Male.*** Body dorsoventrally depressed, reddish brown, shiny; head dark reddish brown, antennae, pronotum, mesonotum, metanotum and legs pale reddish brown, abdomen and forceps blackish brown. Cuticle punctured, shiny; tegmina and wings entirely absent.

Head (Fig. 11) as wide as long, postfrontal and coronal sutures fine, but distinct, frons convex, vertex flattened, posterior margin of head feebly emarginate in middle. Eyes reddish brown, approximately 0.5 times as long as length of head posterior to eyes. Antennae of paratype male with 21 antennomeres (in holotype incomplete), in female paratype with 22 antennomeres; antennomere 1 shorter than distance between antennal bases, narrowed basally, widened terminally, slightly longer than antennomeres 2–4 combined; antennomere 2 transverse, wider than long; antennomere 3 nearly as long as antennomere 4–5 combined. Antennomeres 2–21(22) cylindrical; distal antennomeres long and thin, 6–7 times longer than wide. All antennomeres pubescent, setae long, as long as, or longer than width of antennomeres.

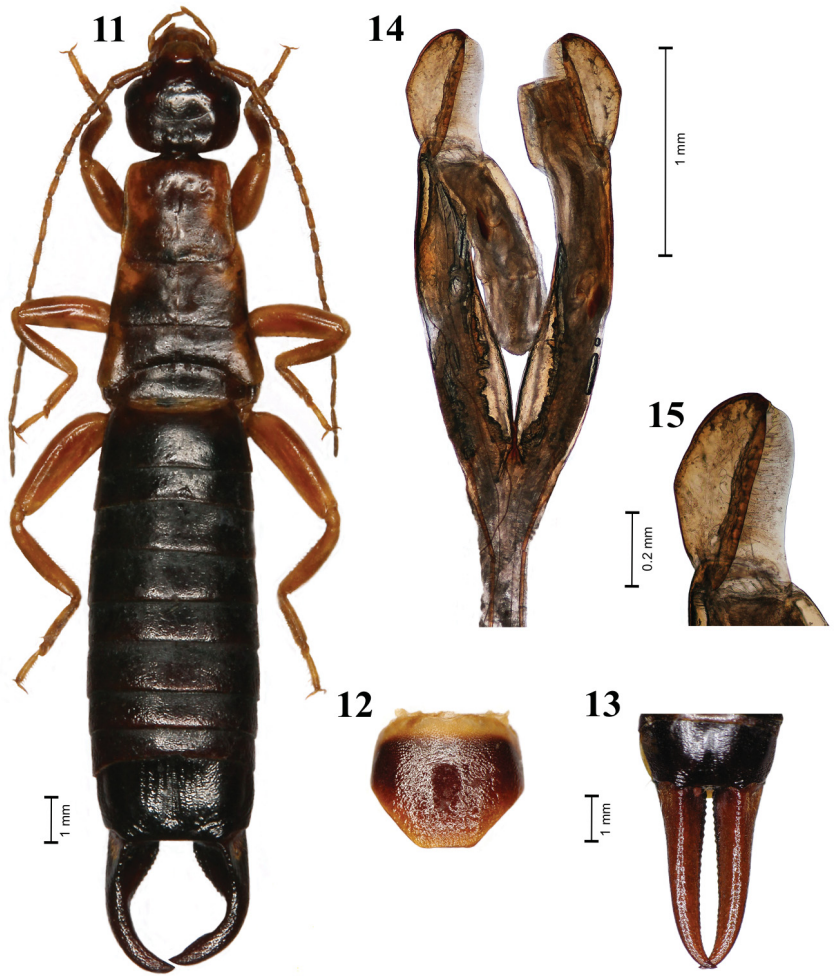
Pronotum (Fig. 11) smooth, about as long as broad, slightly widened posteriorly; anterior margin nearly straight, lateral margins slightly concave, posterior margin nearly straight. Median sulcus fine but distinct. Meso- and metanotum transverse, smooth; mesonotum posteriorly truncate, metanotum broadly emarginate. Median sulcus visible on mesonotum, on metanotum absent. Legs comparatively long, pale reddish brown; femora stout; tibiae with thick and fine setae; metatarsi with metatarsomere 1 of almost equal length as metatarsomeres 2–3 combined.

Abdomen (Fig. 11) sparsely punctulate, tergites (except for ultimate tergite) convex, somewhat widened posteriorly; lateral glandular folds invisible. Tergites 6(7)–9 rugoso-striate at posterior margins. Ultimate tergite transverse, rugose, sides convex, slightly narrowed posteriorly, depressed medially with weak striate median longitudinal furrow, lateral sides and posterior margin rugoso-striate. Penultimate sternite narrowed posteriorly, with posterior margin subtruncate and slightly emarginate (Fig. 12). Pygidium flat. Forceps asymmetrical, right branch more curved in middle than left one; right branch noticeably widened interiorly in distal

quarter. Both branches remote and stout at base, tapering apically, with apices gently hooked; inner margin finely crenulated, dorsally trigonal in basal half, depressed posteriorly.

Genitalia (Figs 14, 15) with oval short parameres, parameres 1.8 times longer than broad, broadened in middle and narrowed apically, external apical angle and margin convex; tip of parameres rounded (Fig. 15). Longer genital lobe 1.7 times longer than length of paramere (Fig. 14).

Female. Agrees with male in most characters except for: posterior margins of tergites 6(7)–9 smooth, not rugoso-striate; penultimate sternite narrowed posteriorly, with posterior margin subtruncate and broadly rounded; ultimate tergite comparatively narrowed posteriorly



Figs 11–15. *Anisolabella planata* sp. nov. 11 – habitus of male holotype; 12 – male penultimate sternite, ventral view; 13 – ultimate tergite and forceps of female paratype; 14 – male genitalia; 15 – left paramere of male genitalia.

and forceps with branches contiguous, simple and straight, with crenulated inner margin (Fig. 13).

Measurements. Total body length without forceps: ♂♂: 15.2–17.8 mm, holotype 17.8 mm; ♀: 12.9 mm. Length of forceps: ♂♂: 2.5–3.1 mm, holotype 3.1 mm; ♀: 3.9 mm.

Differential diagnosis. *Anisolabella planata* sp. nov. differs from the other species of the genus *Anisolabella* based on the following combination of characteristics: the body is flattened with a noticeably flattened vertex of the head; antennomeres 2–22 are cylindrical, the distal antennomeres are long and thin, 6–7 times longer than wide; the right branch of the male forceps is widened interiorly in the distal quarter, and the abdominal tergites of male lack keels or ridges laterally; the penultimate sternite of male is narrowed posteriorly, with the posterior margin subtruncate and slightly emarginate. The parameres of the male genitalia are specific, oval, and broadened in the middle, 1.8 times longer than wide. It can be distinguished from the other *Anisolabella* species occurring on Socotra Island, *A. haasi* sp. nov., using the identification key below.

Etymology. The Latin adjective, *planatus* (*-a*, *-um*; = flattened) is given in reference to the dorsoventrally flattened body of the new species, which is unusual in *Anisolabella*.

Bionomy. Sifted from wet leaf litter in a montane evergreen woodland, association *Leucado hagghierensi-Pittosporetum viridiflorum*, see also the preceding species.

Distribution. Yemen, Socotra Island (Fig. 27). Most likely an endemic species.

Anisolabella haasi sp. nov.

(Figs 16–19, 27)

Type locality. Yemen, Homhil basin, 12°34.5′N, 54°18.5′E, 360-500 m a.s.l.

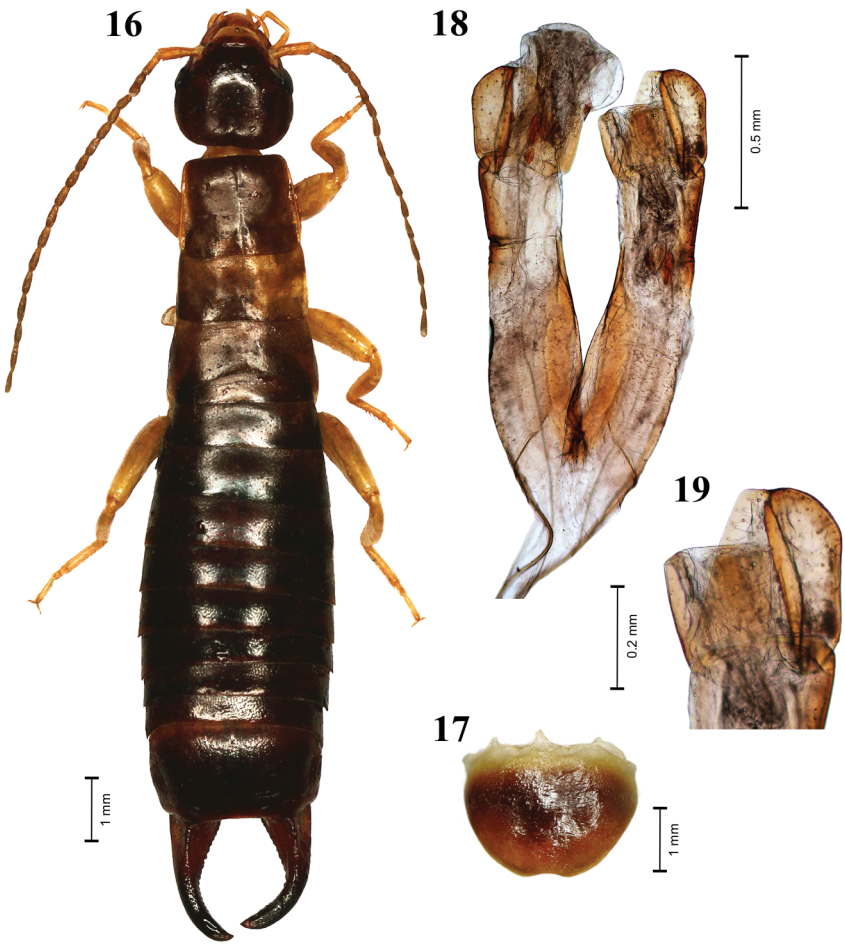
Material examined. Holotype: ♂, 'Yemen, Socotra Island / Homhil protected area / open woodland with *Boswellia* & / *Dracaena* trees; 10.-11.vi.2012 / 12°34.5′N, 54°18.5′E, 360-500 m // Socotra expedition 2012 / J. Bezděk, J. Hájek, V. Hula, P. Kment, I. Malenovský, J. Niedobová & L. Purchart lgt. // HOLOTYPUS / *Anisolabella* / *haasi* sp. nov. / det. P. Kočárek 2013' (NMPC).

Description. ***Male.*** Body pale yellowish to reddish brown, shiny; head reddish brown, antennae, pronotum, mesonotum, metanotum and legs yellowish brown, abdomen and forceps reddish brown. Cuticle regularly punctured, shiny; tegmina and wings entirely absent.

Head (Fig. 16) as long as wide, postfrontal and coronal sutures fine, but distinct, frons and vertex convex, posterior margin of head feebly emarginate in middle. Eyes blackish brown, approximately 0.5 times as long as length of head posterior to eyes. Antennae of holotype with 20 antennomeres (incomplete); antennomere 1 shorter than distance between antennal bases, narrowed basally, widened terminally, as long as antennomeres 2–4 combined; antennomere 2 transverse, slightly longer than wide; antennomere 3 shorter than antennomeres 4–5 combined. Antennomeres 2–20 conical, distal antennomeres relatively short, 3.0–3.5 times longer than wide. All antennomeres pubescent, setae short.

Pronotum (Fig. 16) smooth, about as long as broad, slightly widened posteriorly, margins nearly straight; median sulcus well-distinct. Meso- and metanotum transverse, smooth; mesonotum slightly emarginate posteriorly, metanotum broadly emarginate. Median sulcus visible on mesonotum, on metanotum absent. Legs comparatively short, yellowish brown; femora stout; tibiae with thick and fine setae; metatarsi with metatarsomere 1 slightly longer than length of metatarsomeres 2–3 combined.

Abdomen (Fig. 16) densely regularly punctulate, tergites (except for ultimate tergite) convex, somewhat widened posteriorly; lateral glandular folds not visible. Ultimate tergite transverse, punctate, sides convex, slightly narrowed posteriorly, slightly depressed medially, median longitudinal furrow not visible, posterior margin rugoso-striate. Penultimate sternite widely rounded posteriorly with posterior margin roundly emarginate (Fig. 17). Pygidium flat. Male forceps bicoloured, proximal half reddish brown, distal part blackish brown, asymmetrical, right branch more curved in middle than left one. Both branches remote and stout at base, tapering apically, with apices gently hooked; inner margin finely crenulated, dorsally trigonal in basal half, cylindrical posteriorly.



Figs 16–19. *Anisolabella haasi* sp. nov. 16 – habitus of male holotype; 17 – male penultimate sternite, ventral view; 18 – male genitalia; 19 – right paramere of male genitalia.

Genitalia (Figs 18, 19) with oval short parameres, parameres 1.4 times longer than broad, broadened in the distal third, rounded apically and weakly emarginate in middle (Fig. 19). Longer genital lobe robust and short, 1.6 times longer than length of paramere (Fig. 18).

Female. Unknown.

Measurements. Total body length without forceps 11.4 mm, length of forceps 2.0 mm.

Differential diagnosis. *Anisolabella haasi* sp. nov. differs from the other species of the genus *Anisolabella* in the following combination of characters: antennomeres 2–20 are conical, distal antennomeres are short, 3.0–3.5 times longer than wide; all abdominal tergites of male are densely regularly punctulate, without keels or ridges laterally, penultimate sternite of male is widely rounded posteriorly, with posterior margin roundly emarginate; parameres of male genitalia are oval, broadened in the distal third, rounded apically and weakly emarginate in the middle. From the other *Anisolabella* species occurring on Socotra Island, *A. planata* sp. nov., it can be distinguished using the identification key below.

Etymology. The species is dedicated to Fabian Haas (Germany), my dermapterist colleague, who first revisited the earwigs of Socotra and thus inspired this study.

Bionomy. Unknown. Collected in an open woodland with *Boswellia elongata* and *Dracaena cinnabari* trees on limestone plateau.

Distribution. Yemen, Socotra Island (Fig. 27). Most likely an endemic species.

Key to the Anisolabididae species recorded from Socotra Island
(based on males)

1 (2) Tegmina fully developed or present as narrow lateral ovate flaps on mesonotum. ..... ***Euborellia femoralis*** (Dohrn, 1863)

2 (1) Tegmina absent.

3 (4) Parameres approximately as long as wide, genital lobes with strongly sclerotized denticulated pads; legs yellow, usually with dark bands on femora and tibiae. .... ***Euborellia annulipes*** (Lucas, 1847)

4 (3) Parameres 1.4–4.0 times longer than wide, genital lobes without sclerotized denticulated pads; legs uniformly yellowish or reddish brown.

5 (6) Parameres more than three times longer than wide. .... ***Anisolabis maritima*** (Bonelli, 1832)

6 (5) Parameres 1.4–1.8 times longer than wide.

7 (10) Parameres with a remarkable deep incision on acute tip, middle antennomeres cylindrical.

8 (9) Body stout, widest abdominal tergite 1.6–1.8 times wider than pronotum width; sides of abdominal sternites 7–9 rugoso-striate. ..... ***Socotralabis hulai*** sp. nov.

9 (8) Body slender, widest abdominal tergite 1.4 times wider than pronotum width; abdominal sternites 7–9 regularly punctate. ..... ***Socotralabis bezdeki*** sp. nov.

10 (7) Parameres oval, with tip rounded or weakly emarginate; middle antennomeres conical.

11 (12) Distal antennomeres 6–7 times longer than wide, cylindrical; right branch of forceps widened internally in distal quarter. ..... ***Anisolabella planata*** **sp. nov.**

12 (11) Distal antennomeres 3.0–3.5 times longer than wide, conical; right branch of forceps simple. ..... ***Anisolabella haasi*** **sp. nov.**

FORFICULIDAE

Guanchia sokotrana (Burr, 1905) comb. nov.

(Figs 20–23, 28)

Anechura sokotrana Burr, 1905: 493

Type locality. Yemen, Socotra Island.
Type material. Not studied. The deposition of type material is not stated in the original description of Burr (1905). Haas et al. (2004) suggested that the holotype could be deposited in The Natural History Museum, London. There is a specimen (male) labelled as *Anechura fedchenkoi* Saussure, 1874 (now *Oreasiobia fedschenkoi* (Saussure, 1874)); but this specimen is marked by an additional label stating 'described as new / *A. sokotrana* / Burr inedit / Type MB'.
Material examined. Wadi Mathif, N12°27′28.4″, E 54°18′22.3″, 20.vi.2009, 3 ♀♀, V. Hula lgt. (NMPC, PKCO); Al Haghier Mts., Scant Mt. env., N12°36.4′N, E54°01.5′, 1,450 m a.s.l., 12.–13.xi.2010, 3 ♂♂ 4 ♀♀, J. Batelka lgt. (NMPC); Hagher Mts., Scand Mt. env., N12°34.6′N, E54°01.5′, 1450 m a.s.l., montane evergreen woodland, 16.–18.vi.2012, 4 ♂♂ 5 ♀♀, J. Bezděk, J. Hájek, V. Hula, P. Kment, I. Malenovský, J. Niedobová & L. Purchart lgt. (NMPC, PKCO).

Comments. The sternal plates of this species have structure typical for the subfamily Forficulinae with a quadratic, as wide as long mesosternum (Fig. 21). The shape of the mesosternum is the only diagnostic characteristic that subdivides Forficulinae and Anechurinae. Therefore, *Anechura sokotrana* must be moved to the subfamily Forficulinae, within which the species fits well with the generic diagnosis of the genus *Guanchia* Burr, 1911, characterised by abbreviated, obliquely posteriorly truncate tegmina (Fig. 20).
Distribution. Yemen, Socotra Island (Fig. 28). Most likely an endemic species.

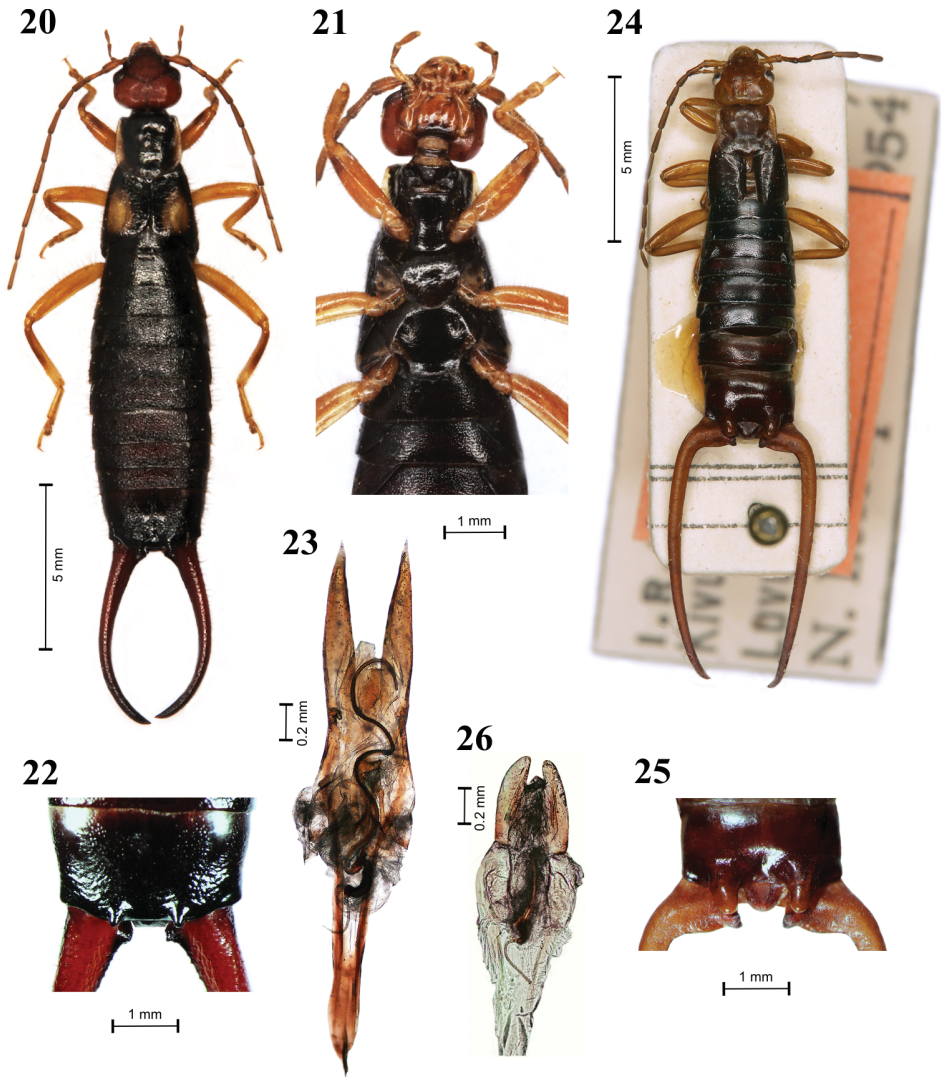
Guanchia bituberculata (Brindle, 1966) stat. restit.

(Figs 24–26)

Anechura bituberculata Brindle, 1966: 43.
Forficula bituberculata: Brindle (1973: 261).
Guanchia bituberculata: Steinmann (1993: 560).
Anechura sokotrana: Haas et al. (2004: 413).

Type locality. Congo [= Democratic Republic of the Congo], Kivu.
Type material. Holotype: ♂, 'HOLOTYPUS // I.R.S.A.C.-MUS. CONGO / Kivu: Terr. Uvira, Ht / Luvubu, 2750 m. (humus) / N. Leleup V-1954 // Anechura / bituberculata Brindle / det. A. Brindle / holotype // Type // Digitised by / F. Haas for / SYNTHESIS / Aug. 06 // MRAC ENT 000017410' (MRAC). Paratypes: 1 ♀, 'ALLOTYPUS // I.R.S.A.C.-MUS. CONGO / Kivu: Terr. Uvira, Ht / Luvubu, 2750 m. (humus) / N. Leleup V-1954 // Allo / type // Anechura / bituberculata Brindle / det. A. Brindle / allotype // Digitised by / F. Haas for / SYNTHESIS / Aug. 06 // MRAC ENT 000017410' (MRAC); 1 ♂, 'Paratypus // I.R.S.A.C.-MUS. CONGO / Kivu: Terr. Uvira, Ht / Luvubu, 2,750 m. (humus) / N. Leleup V-1954 // Para- / type // Anechura / bituberculata Brindle / det. A. Brindle / paratype // Digitised by / F. Haas for / SYNTHESIS / Aug. 06 // MRAC ENT 000017410' (MRAC).

Comments. Haas et al. (2004) synonymised *Anechura bituberculata* with *A. sokotrana* (currently *Guanchia sokotrana*). Based on the comparison of the type material of *Guanchia bituberculata* with specimens of *G. sokotrana* (see above) and the detailed photographs of the male of *G. sokotrana* published by Haas et al. (2004), these two species were recognised to be distinct. Therefore, *G. bituberculata* is removed from the synonymy and considered to be a valid species. These two species can be distinguished based on the following combination of characters: *Guanchia sokotrana* (Figs 20–23): the legs, pronotum, abdomen and forceps are pubescent; the middle antennomeres are eight times longer than wide; the pronotum and tegmina are blackish brown, the pronotum



Figs 20–26. *Guanchia sokotrana* (Burr, 1905) comb. nov. (20–23) and *Guanchia bituberculata* (Brindle, 1966) stat. restit. (24–26). 20 – habitus of male, dorsal view; 21 – male sternal plates, ventral view; 22 – detail of the end of male ultimate tergite; 23 – male genitalia; 24 – habitus of male holotype, 25 – detail of the end of male ultimate tergite; 26 – male genitalia of holotype.

has yellowish sides, each tegmen has a yellowish central spot; the pronotum is as long as it is wide; the ultimate tergite has two narrow conical tubercules, the distal end of the tergite between them is straight (Fig. 22); the forceps are rounded, regularly tapering from the base to the tip; the male genitalia (Fig. 23) have long parameres, 5.5–6.0 times longer than wide, regularly tapering

to the tip. *Guanchia bituberculata* (Figs 24–26): smooth, not a pubescent body; the middle antennomeres are 4–5 times longer than wide; the pronotum and tegmina are entirely reddish brown; the pronotum is wider than long; the ultimate tergite has two large conical tubercles with a weak concavity between them (Fig. 25); the branches of the forceps are dilated and angled basally; the male genitalia are robust (Fig. 26) with short parameres that are 3.0–3.5 times longer than wide, with a rounded tip.

Distribution. Democratic Republic of the Congo, Uganda (Brindle 1973).

New records of Dermaptera species from Socotra Island

Labidura riparia (Pallas, 1773)

(Fig. 27)

Material examined. Hadiboh env., N12°39′00″, E54°01′10″, 6.–24.ix.1999, 1 ♀, V. Bejček & K. Šťastný lgt. (NMPC); Wadi Faar, N12°25′36″, E54°11′51″, 3.xii.2002, 1 ♀, V. Bejček & K. Šťastný lgt. (NMPC); Wadi Deneghen, N12°36′55″, E54°03′49″, 85 m a.s.l., 27.xii.2003, 1 ♂ 1 ♀, D. Král lgt. (NMPC); Hadiboh env., N12°39′02″, E54°02′04″, 10–100 m a.s.l., 21.xi.–12.xii.2003, 1 ♂, D. Král lgt. (NMPC); Qualansiah env., Khayrha mts., N. slopes, N12°38′50″, E53°27′45″, 85–592 m a.s.l., 9.–10.xii.2003, 1 ♀, D. Král lgt. (NMPC); Noged plain, N12°21′09″, E54°01′47″, 11 m a.s.l., sand dunes, 5.–6.xii.2003, 1 nymph, D. Král lgt. (NMPC); Noged plain, Sharet Halma vill. env., N12°21.9′, E54°05.3′, 20 m a.s.l., sand dunes, 10.–11.xi.2010, 1 ♂, J. Batelka lgt. (NMPC); Gubbah vill. env., N12°36′35″, E53°46′56″, 7 m a.s.l., 23.xi.2003, 1 nymph, D. Král lgt. (NMPC); Momi – Homhil, 14.vi.2009, 1 ♀,V. Hula lgt. (NMPC); Wadi Mathif, N12°27′2″, E 54°18′5″, 20–30 m a.s.l., 20.iv.2009, 1 ♂ 3 ♀♀, 3 nymphs, L. Purchart lgt. (NMPC); Halla area, Arher, 12°33.0´N, 54°27.6´E, 5 m a.s.l., freshwater spring in sand dune, *Tamarix nilotica* shrubs, 9.–10.+15.vi.2012, 1 ♂ 11 ♀♀, 1 nymph, J. Bezděk, J. Hájek, V. Hula, P. Kment, I. Malenovský, J. Niedobová & L. Purchart lgt. (NMPC); Deiqub cave, 12°23.1´N, 54°00.9´E, 115 m a.s.l., *Croton socotranus*, *Jatropha unicostata* shrubland, 12.vi.2012, 1 ♂ 2 ♀♀, 1 nymph, J. Bezděk, J. Hájek, V. Hula, P. Kment, I. Malenovský, J. Niedobová & L. Purchart lgt. (NMPC).

Published records from Socotra. Dixey et al. (1898), Burr (1903), Haas et al. (2004).

Distribution. Cosmopolitan species.

Marava socotrana Haas, 2004

(Fig. 28)

Material examined. Homhil protected area, N12.587° E54.302°, 330 m a.s.l., 20.–21.xi.2000, 1 ♂, V. Bejček & K. Šťastný lgt. (PKCO); Homhil protected area, N12°34′27″, E54°18′32″, 364 m a.s.l., 28.–29.xi.2003, 1 ♂, D. Král lgt. (PKCO); Homhil protected area, N12°34′27″, E54°18′32″, 364 m a.s.l., 28.–29.xi.2003, 2 ♀♀, D. Král lgt. (NMPC); Qualansiah env., Khayrha mts., N. slopes, N12°38′50″, E53°27′45″, 85–592 m a.s.l., 9.–10.xii.2003, 2 ♂♂, D. Král lgt. (NMPC, PKCO); Firmihin plateau, N12°28′46.5″, E 54°00′89.8″, *Dracaena* tree forest, 22.–25.vi.2009, 1 ♀,V. Hula lgt. (NMPC); Dixam plateau, Firmihin, N12°28.6′, E 54°01.1′, 490 m a.s.l., *Dracaena* woodland, 14.–15. vi.2012, 3 ♀♀, J. Bezděk, J. Hájek, V. Hula, P. Kment, I. Malenovský, J. Niedobová & L. Purchart lgt. (NMPC).

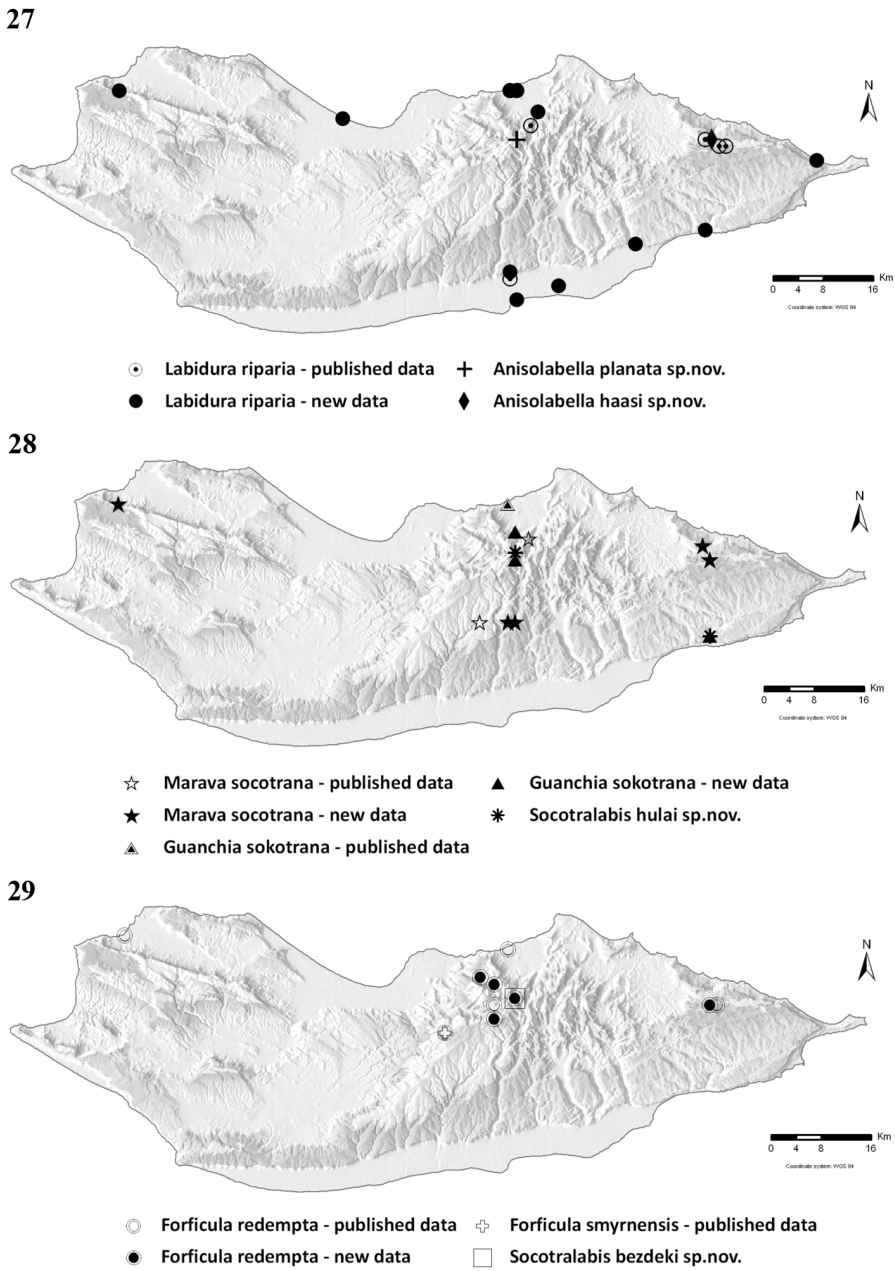
Published records from Socotra. Species previously known only from the type specimens (Haas et al. 2004).

Distribution. Endemic to Socotra Island.

Forficula redempta Burr, 1905

(Fig. 29)

Material examined. Wadi Ayhaft, N12°36′38″, E 53°58′49″, 190 m a.s.l., 24.–26.xi.2003, 2 ♀♀,D. Král lgt. (NMPC); Homhil protected area, N12°34′27″, E54°18′32″, 364 m a.s.l., 28.–29.xi.2003, 2 ♂♂ 2 ♀♀, D. Král lgt. (PKCO); Al Haghier mts., W slopes, Skant area, N12°35′52″, E 54°00′01″, 1240 m a.s.l., 2.xii.2003, 2 ♀♀, D. Král lgt. (PKCO);



Figs 27–29. Sketch maps of Socotra Island displaying the known and newly recorded distribution of Dermaptera. Published records are based on Haas at al. (2004); the occurrence of *Labidura riparia* (Pallas, 1773) on Samha Island published by these authors is not displayed.

Ayhaft, 3.xii.2000, 1 ♀, V. Bejček & K. Šťastný lgt. (PKCO); Dixam plateau, Tudhen, N12°32.7′, E 53°59.9′, 1135 m a.s.l., shrubland with *Commiphora planifrons*, 18.+22.vi.2012, 1 ♂1 ♀, J. Bezděk, J. Hájek, V. Hula, P. Kment, I. Malenovský, J. Niedobová & L. Purchart lgt. (NMPC); Hagher Mts., Scand Mt. env., N12°34.6′N, E54°01.5′, 1450 m a.s.l., montane evergreen woodland, 16.–18.vi.2012, 1 ♀, J. Bezděk, J. Hájek, V. Hula, P. Kment, I. Malenovský, J. Niedobová & L. Purchart lgt. (NMPC).

Published records from Socotra. Burr (1905), Haas et al. (2004).

Distribution. Endemic to Socotra Island.

Checklist of Socotran Dermaptera

The Dermaptera fauna of the Socotra Archipelago consists of 13 species belonging to the families Anisolabididae (7 species), Labiduridae (1 species), Spongiphoridae (1 species), and Forficulidae (4 species). Seven species and one genus of Dermaptera have been described from Socotra, and all are endemic to this island. Endemic species, listed in **bold** in the checklist below, comprise 54 % of the Dermaptera fauna of Socotra. The occurrence of *Anisolabis maritima* (marked by asterisk) must be verified by further findings (for details see Discussion).

ANISOLABIDAE
- ***Anisolabella haasi* nov.**
- ***Anisolabella planata* sp. nov.**
- **Anisolabis maritima* (Bonelli, 1832)
- *Euborellia annulipes* (Lucas, 1847)
- *Euborellia femoralis* (Dohrn, 1863)
- ***Socotralabis bezdeki* sp. nov.**
- ***Socotralabis hulai* sp. nov.**

LABIDURIDAE
- *Labidura riparia* (Pallas, 1773)

SPONGIPHORIDAE
- ***Marava socotrana* Haas, 2004**

FORFICULIDAE
- *Forficula lucasi* Dohrn, 1865
- ***Forficula redempta* Burr, 1905**
- *Forficula smyrnensis* Audinet-Serville, 1839
- ***Guanchia sokotrana* (Burr, 1905) comb. nov.**

Discussion

Thus far, approximately 50 genus-level taxa of insects are known to occur exclusively in the Socotra Archipelago, and such remarkable rate of endemism indicates that the insect biota has undergone a long and uninterrupted period of isolation (Batelka 2012). Socotra, with its unique history and natural conditions, cannot be directly compared with any other African insular biota because all islands in the eastern Atlantic Ocean (such as St. Helena or Ascension Isl.) are of volcanic origin with different histories of colonisation and geological events. The same is true for the Comoros Islands and Mascarenes in the western part of the Indian Ocean. More similar are the granitic islands of the Seychelles, but they are older (63–64 Mya) and more isolated (approximately 1,600 km east of Africa and 3,000 km from India) (Batelka 2012). Based on available databases (Haas 2006), the Dermaptera fauna of the Seychelles comprises 23 species, with only four endemic species (17 %) and a large number of Oriental (8 species) or cosmopolitan species (7 species). Such a high proportion of alien species (65 %)

could be due to the pattern of ocean currents, as the Seychelles lie in the Equatorial Current downstream from Java and the rest of the East Indies, as well as due to the long-term extensive naval communication between the Seychelles and the countries of SE Asia. The species could survive thanks to the climatic/microclimatic conditions on the Seychelles that are similar to the tropical areas of the alien species' origin. Some earwigs are successful 'tramp' species; they have spread throughout the tropics and are usually accidentally introduced along with plant matter, such as fruits, seedlings, or raw wood (e.g., subcortically living *Platylabia major* Dohrn, 1867 introduced to the Seychelles from SE Asia). If we subtract the alien species, the proportion of endemic species on the Seychelles is 50 %, but the absolute number of endemic species is little higher in Socotra (7 species) than on Seychelles (4 species).

The Dermaptera fauna of the Socotra Archipelago comprises seven endemic species (see above), three cosmopolitan species (*Anisolabis maritima*, *Euborellia annulipes*, *Labidura riparia*) and one Oriental species (*Euborellia femorata*). The endemic species have an Ethiopian/Palaearctic origin (genera *Marava*, *Guanchia*, *Forficula*). Because *Anisolabis maritima* has been recorded from Socotra based on only one female (Haas et al. 2004), we must consider its occurrence uncertain until a male is found. The females of Anisolabidinae are very similar to each other, and the specimen could refer to one of the new species described in this contribution. If we subtract the alien species, as in the case of the Seychelles, the proportion of endemic species in Socotra is 77 %. The distribution of the cosmopolitan and alien species remains associated with the coastal zone and the towns in Socotra (see Fig 26 for the distribution of *Labidura riparia*), while the occurrence of endemic taxa seems to be restricted to the inland mountain areas of Hagher, Homhil and Dixam (see Figs 27–29). Our study focused on the diversity of Dermaptera in Socotra resulted in the description of one new genus and four new species from the Anisolabididae. The family has been known on the island based on the occurrence of three cosmopolitan/alien species; however, according to the high rate of similarity between the species, some of the previous records could be misidentified and thus refer to one of the new species described there. Haas et al. (2004) mentioned the occurrence of an unknown species of Anisolabididae, which was provisionally assigned to the genus *Anisolabis* because only females and nymphs were available. This species most likely belongs to one of the newly described species.

The family Anisolabididae is widespread and cosmopolitan containing predominantly wingless earwigs, usually dark with non-contrasting coloration. Forceps are usually simple, trigonal basally, and asymmetrical in males. Specific characteristics of the Anisolabididae include the male genital armature bearing two genital lobes, with one of the lobes directed distally and the second lobe directed basally (Steinmann 1989b, Srivastava 1999). According to recent phylogenetic studies based on morphological as well as the molecular evidence, the family appears to be monophyletic (Haas 1995, Jarvis et al. 2005, Tworzydlo et al. 2010, Kočárek et al. 2013), but the authors included only a few species from the Anisolabidinae. The Anisolabididae is subdivided into 13 subfamilies (sensu Srivastava 1999), and comprises approximately 400 species in 31 genera (Steinmann 1989a,b; Srivastava 1999). The Anisolabidinae, to which all of the described species belong, comprises 128 species in 13 genera (Anisyutkin 1998a,b, 2003; Srivatava 1999, 2003a,b; Nishikawa 2008, 2013; Kočárek 2011a,b); the species are difficult to distinguish based on external morphology because of the

uniform habitus and relatively large variability (Steinmann 1989b). The generic classification is based exclusively on the shape of the male genitalia and especially on the shape and size of the parameres (Srivatava 1999).

Zacher (1911) and then Burr (1915) published comprehensive works in which they defined genera in Anisolabidinae based on differences in the parameres of the males. Popham & Brindle (1966) synonymised the genera described by these authors and placed most species in two genera, *Anisolabis* and *Euborellia*. This concept was not widely accepted by later authors (see Steinmann 1989a,b; Sakai 2000). Srivastava (1999) revisited the classification of the Anisolabididae, and his classification of the Anisolabidinae followed that of Burr (1915), i.e., diagnostic characteristics are based exclusively on the morphology of the male genitalia and especially on the length and shape of the parameres.

The Anisolabididae as well as the Anisolabidinae have not been assessed using numerical or cladistic methods. Because the classification has only been repeatedly compiled within comprehensive monographs (Steinmann 1989b, Sakai 2000), the taxonomic positions of individual genera are uncertain, as are the phylogenetic relationships within the subfamily. A rigorous phylogenetic analysis of the subfamily based on molecular evidence is necessary to clarify the relevance and the relationships of the genera that have been described to date.

Acknowledgements

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