Bees of the Socotra Archipelago (Hymenoptera: Anthophila),
their biogeography and association with parasites

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Abstract. Taxonomy of bees (Hymenoptera: Anthophila) of the Socotra Archipelago is evaluated based on historical and newly available specimens. Four new species of Halictidae are described from the Socotra Island: Austronomia socotrana Pauly & Straka sp. nov., Lasioglossum (Hemihalictus) boswelliae Pauly & Straka sp. nov., Lasioglossum (Sphecodogastra) dioscoridis Pauly & Straka sp. nov., and Lasioglossum (Ctenonomia) dracaenae Pauly & Straka sp. nov. The correct original spelling of Eucera wkirbyi Kohl, 1906 is restored, Eucera kirbyi Friese, 1909 being its unjustified emendation and junior objective synonym. Identity of both Socotran species of Xylocopa Latreille, 1802 is clarified. Lasioglossum (Evylaeus) kowitense (Cockerell, 1937), Nomioides facilis (Smith, 1853), and Nomioides rotundiceps Handlirsch, 1888 are removed from the list of bees of Socotra. In total, 28 species in 16 genera are reported from the archipelago, of which nearly two thirds are considered endemic at the species level. Biogeographic origin of Socotran bees is analysed and proposed. Host associations with beetle parasites of the families Meloidae and Ripiphoridae (Coleoptera) and cleptoparasitic bees are evaluated for the Socotran bee fauna. Obligate bee parasitoid Ripiphorus arabiafelix arabiafelix Batelka, 2009 (Coleoptera: Ripiphoridae) is reported from the archipelago (Socotra Island) for the first time.

Key words. Hymenoptera, Apidae, Colletidae, Halictidae, Megachilidae, Coleoptera, Meloidae, Ripiphoridae, taxonomy, new species, new combination; biogeography, insularity, endemism, host-parasite association, Yemen, Abd el Kuri, Darsa, Samha, Socotra
Introduction

Most flowering plants are reproductively dependent on bee foraging for pollen and nectar, and due to these pollinating services, bees are of special scientific interest. High energetic investment of bees in collecting pollen for their larvae brings an opportunity for many insect parasites and parasitoids from various orders (e.g. Coleoptera, Diptera, Hymenoptera, Strepsiptera) to utilize bees as their hosts. Cleptoparasites usually depend with their development on the accumulated pollen storage, and parasitoids and some parasites on bodies of bee larvae.

Bees have always been in focus of naturalists and it is not surprising, that the first account of Socotran Aculeata was published as early as 1881 (Kirby 1881). However, the list comprised only four species of which only one was a bee. In the first decade of the 20th century, two comprehensive publications with descriptions of new species of Socotran bees were published by Kirby (1900, 1903) and Kohl (1906, 1907). Since then, only a few taxonomic contributions with descriptions of further endemic species have been published (Blüthgen 1925, Baker 1999, Kuhlmann 2003).

We had the opportunity to revise new and interesting material accumulated by the Czech biological expeditions and partially also by Wolfgang Wranik (Germany) in Socotra during the last two decades (Wranik 2003; Hájek & Bezdek 2012, 2014) which resulted in the discovery of multiple new species. In addition, we revised all bee species so far described and recorded from Socotra and the adjacent islets during the past expeditions (e.g. Forbes 1903, Kohl 1906), with an attempt to clarify their taxonomic status and nomenclature where necessary.

Although no bionomic data is available for any Socotran bee (e.g., host plant association, nesting behaviour, mating, etc.), in this account we provide the first list of likely associations of Socotran pollen-collecting bees with cleptoparasitic bees, and parasitic and parasitoid beetles. We also analyse the diversity of Socotran bees, their distribution and zoogeographical affinities to give a comprehensive picture of the origin of the bee fauna of the Socotra Archipelago according to recent data and information. Last but not least, our publication can also serve as a simplified field guide to Socotran bee species, because we present photographs of all species known to date.

Material and methods

Acronyms of collections housing the specimens studied are as follows:

BMNH The Natural History Museum, London, United Kingdom (David Notton);
NHMW Natural History Museum, Vienna (Manuela Vizek);
NMPC National Museum, Prague, Czech Republic (Ján Macek).

The nomenclature of bees is based on Pauly (1990, 2017) and Michener (2007). In the Systematics chapter only references to descriptions and taxonomic and faunistic contributions related to Socotra are considered.

Images were taken using a Canon EOS 550D digital camera with an MP-E 65 mm macro-lens. Each figure was stacked from more than 20 layers of photos with different focus using Zerene photo stacker software (Zerene Systems LLC, Richland, USA).
Systematics

Apidae

**Amegilla (Micamegilla) pyramidalis** (Kirby, 1900)
(Figs 1–3, 8, 9)

*Podalirius pyramidalis* Kirby, 1900: 24 (type locality: Abd el Kuri); Kirby (1903): 257 (redescription).

*Podalirius albigenus* (Lepeletier, 1841): Kohl (1906): 5 (as senior subjective synonym of *P. pyramidalis*); Kohl (1907): 173.


**Material examined.** Ab-del Kari, 6 ♀♂, i.1899, O. Simony lgt.; Sokotra, 1 ♂, i.1899, O. Simony lgt.; Sokotra, Ras Shoab, 1 ♂, i.1899, O. Simony lgt., H. Friese et F. Kohl det. as *Podalirius albigenus* (all in NHMW).

**Remarks.** Wrani (2003: 373) presents the figure of *A. pyramidalis* taken from Kirby (1903) and incorrectly interprets it as *Eucera* sp. The species is closely related to *Amegilla albigena* (Lepeletier, 1841). Due to the similarities of *A. pyramidalis* to *A. albigena*, we suspect their close relationship and origin of *A. pyramidalis* in the Palaearctic Region.

**Distribution.** Possibly endemic to Socotra Archipelago. Recorded from Abd-el-Kuri (Kirby 1900, 1903; Kohl 1906, 1907) and Socotra: Ras Shoab (Kohl 1906, 1907). Reported also from ‘Südarabien, Makálla’ by Kohl (1906, 1907), however considered restricted to the Socotra Archipelago by Engel (2007).

**Amegilla (Amegilla) quadrifasciata** (de Villers, 1789)
(Figs 4–7, 10, 11)


**Material examined.** Sokotra, 1 ♀, i.1899, O. Simony lgt., F. Kohl det.; J. Samha, 3 ♀♂, i.1899, O. Simony lgt., H. Friese et F. Kohl det.; Sokotra, Ras Shoab, 1 ♂, i.1899, O. Simony lgt., F. Kohl det. (all in NHMW); wadi Deneghan, 1 ♀, 19.ii.2000, W. Wrani lgt. (NMPC).

**Remarks.** Wrani (2003: 454) presents a photograph of *A. quadrifasciata* from Hadiboh and incorrectly interprets this species as *Eucera* sp.

**Distribution.** A species widely distributed in the entire Palaearctic Region, but absent in the Arabian Peninsula (Ascher & Pickering 2017). In Socotra reported from Moukaradia (= Gebel Raggit), Homhil, Dinehan Valley, Adho Dimellus (Kirby 1903); Ras Shoab, Haghier Mts., and from Samha island (Kohl 1906, 1907).

**Anthophora (Paramegilla) inclyta** Walker, 1871
(Figs 12–14)

*Podalirius fulvitectus* Kirby, 1900: 22 (type locality: Socotra, various places); Kirby (1903): 253, plate xvi, fig.14 (redescription); Kohl (1906): 4; Kohl (1907): 173.


**Material examined.** Sokotra, Hagier mountains, 2 ♀♂, no date, O. Simony lgt., F. Kohl det. (NHMW).

**Distribution.** The species occurs in North Africa and the Arabian Peninsula (Kohl 1906, 1907; Ascher & Pickering 2017; Kuhlmann 2017). In Socotra reported from Moukaradia
Apis (Apis) mellifera Linnaeus, 1758
(Figs 15, 16)

Apis fasciata Latreille, 1804: Kirby (1903): 254.

Apis mellifera Linnaeus, 1758: Kohl (1906): 4; Kohl (1907): 172.


Distribution. A cosmopolitan species, native in the entire Old World. In Socotra reported from Hadibu Plain, Adho Dimellus (Kirby 1903), and Ras Shoab (Kohl 1906, 1907).

Eucera (Tetralonia) wfkirbyi Kohl, 1906
(Figs 17, 18)

Podalirius antennatus Kirby, 1900: 24 (type locality: Homhil, E. Socotra, 2500 ft); Kirby (1903): 253, plate xvi, fig. 11 (redescription).

Eucera (Macrocera) W. F. Kirby Kohl, 1906: 7 (new combination, replacement name, nec Eucera antennata Fabricius, 1793).

Eucera (Macrocera) W. F. Kirby Kohl, 1907: 175 (junior homonym and objective synonym).

Eucera (Tetralonia) kirbyi Friese, 1909: 379 (461) (new subgeneric combination, unjustified emendation), syn. nov.

Material examined. Sokotra, 1 ♀, ii.1899, O. Simony lgt., F. Kohl det.; Sokotra, Ras Shoab, 1 ♀, i.1899, O. Simony lgt., F. Kohl det. (all in NHMW).

Remarks. All species names associated with this taxon are missing in the world bee checklist (Ascher & Pickering 2017). The species belongs to the nominotypical subgenus of the genus Tetraloniella Ashmead, 1899, according to characters presented by Michener (2007). However, genus Tetraloniella is synonymized with Tetralonia and placed as a subgenus of Eucera based on molecular phylogeny (Dorchin et al. 2017).

Species name Eucera W. F. Kirby (Kohl 1906, 1907) is available as “wfkirbyi” according to ICZN article 32.5.2.4.4 (ICZN 1999), Eucera kirbyi Friese, 1909 being its unjustified emendation and junior objective synonym.

Distribution. Endemic to Socotra. Reported from Homhil (Kirby 1900, 1903) and Ras Shoab (Kohl 1906, 1907).
**Thyreus histrionicus** (Illiger, 1806)

(Figs 19, 20)

*Crocisa major* Morawitz, 1875: **Kohl** (1906): 20; **Kohl** (1907): 188.  

**Material examined.** Sokotra, Ras Shoab, 1 ♂, i.1899, O. Simony lgt., F. Kohl det. as *Crocisa major* (NHMW).

**Distribution.** A widely distributed Palaearctic species, reported from Europe and North Africa (including the Canary Islands) to China (**Lieftinck** 1968). From Socotra reported from Ras Shoab (**Kohl** 1906, 1907) and Hadibo (**Lieftinck** 1968).

**Thyreus uniformis** (Kirby, 1900)

(Figs 21, 22)

*Crocisa uniformis* Kirby, 1900: 21 (type locality: Socotra, various places); **Kirby** (1903): 252, plate xvi, fig. 10 (redescription); **Kohl** (1906): 20; **Kohl** (1907): 188.  
*Thyreus uniformis* (Kirby, 1900): **Lieftinck** (1968): 97 (lectotype designation).

**Material examined.** Sokotra, Ras Shoab, 1 ♀, i.1899, O. Simony lgt., F. Kohl det., M. A. Lieftinck revid. (NHMW).

**Remarks.** Only females are known.
Distribution. Endemic to Socotra: Moukaradia (= Gebel Raggit), Dinehan Valley, Adho Dimellus (Kirby 1900, 1903); Ras Shoab, Hagher Mts. (Kohl 1906, 1907); Alitspan [= Adho Dimellus?] (Lieftinck 1968).

Xylocopa (Ctenoxylocopa) sulcatipes Maa, 1970
(Figs 23, 24)

Xylocopa hottentota Smith, 1854: Kohl (1906): 5; Kohl (1907): 173.

Material examined. Not available.

Remarks. The specimen presented by Kohl (1906, 1907) has not been found in NHMW. Wránik (2003: 454) presents a photograph of Xylocopa sp. from Socotra, Hadiboh, which can be associated with X. sulcatipes, rather than with X. hottentota, which belongs to the considerably different subgenus Xylomelissa Hurd & Moure, 1963. In the Middle East, specimens of X. hottentota were commonly confused with X. sulcatipes in the past century (Hannan et al. 2012). We examined very old specimens labelled as X. hottentota from Aden (Yemen) deposited in BMNH (Figs 23, 24). These specimens belong to X. sulcatipes, which corresponds with the proposed past practice of confusing the names of both species. Without examination of specimens, we cannot identify the species with certainty, but X. sulcatipes is the most probable Socotran species.

Distribution. Distributed in the Arabian Peninsula, Israel, and Egypt (Ascher & Pickering 2017). Recorded from Abd-el-Kuri island (Kohl 1906, 1907) and Hadiboh (Wránik 2003).

Xylocopa (Koptortosoma) pubescens Spinola, 1838
(Figs 25–28)


Remarks. Wránik (2003: 454) presents a photograph of a male of Xylocopa sp. from Hadiboh, which very likely represents X. pubescens. The species was often considered a synonym of X. aestuans, but the species significantly differ from each other (Lieftinck 1964, Hannan et al. 2012).

Distribution. The species is widely distributed in Africa, Turkey and eastwards to the eastern part of India (Ascher & Pickering 2017), but missing in southern parts of the Arabian Peninsula (Hannan et al. 2012). In Socotra reported from Hadibu Plain, Goahal Gorge, Adho Dimellus (Kirby 1903), Ras Shoab (Kohl 1906, 1907), and Hadiboh (Wránik 2003).
Colletidae

Colletes hiekejuniori Kuhlmann, 2003
(Fig. 29)

Colletes hiekejuniori Kuhlmann, 2003: 729 (type locality: Socotra, Gubbet-Koppansija) (both spellings ‘hiekejuniori’ and ‘hiekejuniori’ were used in the paper).


Material examined. Not available.

Remarks. Species known from the holotype male only.

Distribution. A species endemic to Socotra (Kuhlmann 2003).

**Colletes inconspicuus** Kirby, 1900
(Figs 30–33)

*Colletes inconspicua* Kirby, 1900: 23 (type locality: Abd el Kuri); KIRBY (1903): 256, pl. xvi, fig.15 (redescription); KOHL (1906): 6; KOHL (1907): 174.


*Colletes inconspicuus*: KUHLMANN (1998): 567 (*C. pusillus* proposed as a junior subjective synonym of *C. inconspicuus*, lectotypes for both taxa were designated).

**Material examined.** Ab-del Kari, 1 ♀ 1 ♂, i.1899, O. Simony lgt., Noskiewicz det. as *C. pusillus*, lectotype (♀) and paralectotype (♂) designed by M. Kuhlmann (NHMW).

**Remarks.** Species known from four specimens only.

**Distribution.** A species endemic to Abd el Kuri island (KIRBY 1900, 1903; KOHL 1906, 1907; NOSKIEWICZ 1936; KUHLMANN 1998).

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**Halictidae**

*Austronomia socotrana* Pauly & Straka sp. nov.
(Figs 34–43)


**Description. Female.** Species of medium size: total body length 8.0 mm, forewing length 6.0 mm, intertegular distance 2.25 mm. Body black, apical margin of terga distinctly discoloured and transparent, hind legs brown orange (Figs 34, 35).

*Head* wider than long (Length / width = 0.85) (Fig. 36). Measurements (mm): length of clypeus 0.63; clypeus apical width 1.00; lower interocular distance 1.33; upper interocular distance 1.50; clypeo-antennal distance 0.38; length of eye 1.75; interantennal distance 0.58; interocellar distance 0.50; ocellocular distance 0.40; antennocellar distance 0.70; antennocular distance 0.40. Mandibles bidentate, light brown, black at base and apex. Labrum light brown. Clypeus with large punctures less than half to one and half diameter apart, slightly denser apically than basally, interspaces between punctures shiny and smooth. Supraclypeal area dull, microsculptured, with thin punctures, punctures smaller than on clypeus, interspaces between punctures equivalent to diameter of punctures. Front and paraocular area with indistinct or ill-defined small punctures, medially more distinct than laterally, interspaces slightly shiny, frons sparsely covered with white plumose setae, setae about one third of scape length. Vertex narrow, strongly reduced. Ocelli relatively large (Fig. 36). Gena narrow, shiny and superficially punctured. Malar space missing. Scape black, flagellum black dorsally, brown ventrally, flagellomere I and II short, shorter than flagellomere III, or any other subsequent flagellomere.

*Mesosoma.* Pronotum narrow, without carina. Punctuation of scutum medium-sized, dense, punctures well developed, less than one diameter apart, interspaces between punctures well developed, shiny (Fig. 37). Scutellum slightly convex, sculpture similar to scutum, but punctures larger. Pubescence of scutum and scutellum formed of short erect plumose setae, not covering punctuation. Metanotum convex, slightly declining toward propodeum, with dense
pubescence covering sculptures medially. Pleurae and hypoepimeral area coriaceous, dull. Horizontal area of propodeum in form of horizontal gutter with longitudinal ridges (Fig. 38). Vertical part of propodeum with punctuation similar to that of scutum except dorsomedial impunctate area.

Legs. Fore and middle legs brown black, posterior legs brown orange, scopa light orange (Fig. 39). Metabasitarsus about three times as long as wide. Basimetatibial plate completely carinate, broad and rounded (Fig. 40). Inner metatibial spur minutely serrate (Fig. 41).

Wings relatively short, not exceeding end of metasoma. Membranes hyaline. Veins, stigma and tegulae testaceous.

Metasoma broad, oval (Fig. 42). Tergum I with dense regular punctation medially, top of sloping base and apical margin, punctures about one diameter apart, interspaces shiny (Fig. 43). Terga II–IV with a similar punctuation, but slightly sparsely punctate medially. Posterolateral parts of terga I–III with narrow fringe of pubescence, tergum IV with light felted but nearly complete white band. Posterior half of apical margin of terga transparent, showing below white pubescent fringe of base of subsequent tergum: this gives impression that species has apical bands on apical part of terga. Apical margins of terga I–III strongly depressed, with carina at base. Tergum I with pubescence similar to frons, other terga with short setae. Sterna brown, deeply punctate, apical part with dense short erect setae of pale orange colour.

Male unknown.

Differential diagnosis. This species belongs to the group of African and Oriental Austronomia Michener, 1965, characterized by complete basitibial plate of the female, lack of a continuous carina across the pronotum, small tegula, metanotum without projections, terga without enamel-like apical bands, and minutely serrate inner metatibial spur. It differs from described sub-Saharan species in its larger size, polished metasoma, and translucent apical margins of the terga. It differs from the Oriental species in the combination of three characters: propodeal area longer, with horizontal part surrounded by a carina, tergum I smooth between punctures, and metatibia orange. The genus Austronomia sensu lato includes about 20 sub-Saharan species (PAULY 1990), only half of them described, and 18 described Oriental species (PAULY 2009).

Etymology. Latin adjective socotranus (-a, -um) derived from Socotra Island.

Remarks. The species resembles the Afrotropical species more than the Oriental ones, thus we suspect Ethiopian origin of the species.

Distribution. Endemic to Socotra.

Crocisaspidea forbesii (Kirby, 1900)
(Figs 44, 45)

Crocisaspidea forbesii Kirby, 1900: 21 (type locality: Socotra, various places); Kirby (1903): 251, plate xvi, fig. 9 (re-description).

Nomia forbesii: KOHL (1906): 11 (new combination); KOHL (1907): 179.


Material examined. Socotra: Hadiboh env., ca. 10–100 m, 12°65′02″N, 54°02′04″E, 1 ♀, 21.xi.–12.xii.2003, D. Král lgt.; Deiqb cave env., 1 ♂, 10.vi.2010, V. Hula & J. Niedobová lgt.; Zemhon area, 270–300 m, 12°21′14.4″N 54°06′41.0″E, 1 ♂, 16.–17.vi.2010, V. Hula lgt.; Noged plain, Sharet Halma vill. env., sand dunes, 20 m, 12°21.9″N, 54°05.3″E, 1 ♀, 10.–11.xi.2010, J. Hájek lgt.; Dixam plateau, Firmihin, Dracaena forest, 490 m, 12°28.6″N, 54°01.1″E, 1 ♂ 3 ♀♀, 15.–16.xi.2010, J. Batelka lgt. (all NMPC).
Remarks. A species described from Socotra, but not endemic.

Distribution. Known from the Arabian Peninsula, the Socotra Archipelago (Abd el Kuri, Socotra), and East Africa from Sudan to Kenya (DATHE 2009, PAULY 2016b). In the Socotra Archipelago reported from Hadibu Plain, Homhil (Kirby 1900, 1903); Ras Shoab (Kohl 1906, 1907); and Hamadara, Hamhill [sic!], and Abd el Kuri (PAULY 1990).

*Lasioglossum (Ctenonomia) arabs* (Pérez, 1907)
(Figs 46, 47)


Material examined. Not available.

Remarks. Specimens shown here (Figs 46, 47) are from the Arabian Peninsula.

Distribution. The species occurs in the Arabian Peninsula, Ethiopia, and Eritrea (PAULY 2016a). From Socotra reported without a precise locality data (PAULY 1984) and from Ras Shoab (EBMER 1985).

*Lasioglossum (Afrodialictus) bellulum* (Vachal, 1909)
(Figs 48–50)

Material examined. Socotra: Kishin, 700 m, 2 ♂ 1 ♀, 18.iv.1967, K. M. Guichard lgt. (BMNH); Adho Demalu, 1000 m, 5 ♀♀, 24.iv.1967, K. M. Guichard lgt. (BMNH); Al Haghier Mts., Skant Mt., 1400 m, 12°34′36.0″E, 9′1′′N, 31.i.–1.ii.2010, L. Purchart lgt. (NMPC); Al Haghier Mts., Skant Mt., 1400 m, 12°34′36.0″E, 9′1′′N, 12.–13.xi.2010, J. Batelka lgt. (NMPC).

Distribution. The species is known from mountains in South and East Africa, and from the Arabian Peninsula. Reported from Socotra by PAULY (2017) without precise locality data.

*Lasioglossum (Hemihalictus) boswelliae* Pauly & Straka sp. nov.
(Figs 51–59)


Description. Female. Small species: total body length 6.0 mm, forewing length 4.5 mm, intertergular distance 1.25 mm. Black body with beige pubescence, apical margins of terga brown to reddish (Figs 51, 52).

Head almost as long as wide (Length/width = 0.96) (Fig. 53). Measurements (mm): length of clypeus 0.35; width of clypeus apically 0.38; lower interocular distance 0.78; upper interocular distance 0.95; clypeo-antennal distance 0.28; length of eye 1.18; interantennal distance 0.20; interocellar distance 0.35; ocellocular distance 0.20; antennocular distance 0.58; antennocellular distance 0.28. Mandibles black, dark brown in middle. Labrum black. Clypeus shiny with large irregular punctures, punctures less than half diameter apart basally, but more than...
three diameters apart apically, longitudinal swellings among punctures ill-defined. Supraclypeal area dull, irregularly microsculptured, with fine punctures; punctures one to less than one diameter apart. Frons with fine and dense punctures, interspaces hardly visible (Fig. 53). Paraocular area variably punctate, punctures one and half to less than half diameter apart, interspaces slightly shiny. Ocelli of medium size (Fig. 54). Vertex narrow, nearly missing. Gena thin, finely longitudinally microsculptured ventrally. Scape black, flagellum black dorsally, pale ochraceous ventrally.

**Mesosoma.** Scutum with fine and dense punctation, punctures one to less than one diameter apart, interspaces between punctures brightly shiny (Fig. 55). Scutum laterally, anteriorly and posteriorly with tomentum, center with short sparse and thin setae and may appear glabrous. Scutellum punctate like scutum on margins and medially, but with two sparsely punctate areas in centre, with punctures up to five diameters apart, with thin erect setae and without tomentum. Metanotum covered with tomentum. Mesopleura irregularly punctate, punctures ill-defined and evanescent in coarse microsculpture, dull. Hypoepimeral area with fine and dense punctures, dull. Propodeum not carinate, dorsal propodeal area in form of crescent, finely plicate (Fig. 56).

**Legs.** Black, base of pro- and mesotibiae with small yellow spot. Inner metatibial spur with five teeth of decreasing length (Fig. 57). Scopa of hind legs white.

**Wings** relatively long, well exceeding end of metasoma. Membranes hyaline. Tegulae, stigma and veins testaceous.

**Metasoma.** Tergum I with sloping base and centre completely striate and dull, only posterolaterally with fine and dense punctuation, punctures well defined, about one diameter apart or less, sides of tergal base with patch of tomentum. Apical margin of tergum I smooth, punctate as main part of tergum, but impunctated in middle (Fig. 59). Apical depressions not developed. Apex and also base of terga II–VI light brown to orange-brown. All apical margins of tergites largely discoloured, translucent (Fig. 60). Terga II–III with basolateral patch of tomentum. Terga V–VI with light yellowish to white setae. Sterna black with half apical part pale brown, with white setae.

**Male** unknown.

**Differential diagnosis.** This species belongs to the Holarctic subgenus *Hemihalictus* Cockerell, 1897 based on the weakened distal wing venation, the second submarginal crossvein narrower than the first, the posterior surface of propodeum without carina. It is close to *L. ablenum* (Blüthgen, 1934) from the Sahara, *L. kowitense* (Cockerell, 1937) from Sudan and an undescribed species found in northern Ethiopia. The head is longer in *L. boswelliae* (length / width = 0.96) than in *L. ablenum* (L / 1 = 0.86) and *L. kowitense* (L / 1 = 0.90). From *L. ablenum* it differs in the punctuation of the lateral parts of tergum I reaching the apical margin, the basolateral parts of the tergum I with allied tomentum. From *L. kowitense* it differs in the tergum I, with its dorsal base completely striated and without punctuation (densely striato-punctuated in *L. kowitense*), punctuation limited to the sides, the middle of the apical margin is not punctated (in *L. kowitense* it is striato-punctated). The plumose pubescence of the baso-lateral parts of tergum I is denser in *L. boswelliae*. The pubescence of the scutum is denser in the middle in *L. kowitense* but denser in the periphery in *L. boswelliae*.

**Etymology.** Named after the Frankincense Trees (*Boswellia* spp.), as this bee was collected in an area with *Boswellia ameero* and *B. elongata* trees; noun in apposition in genitive case.
Remarks. The species resembles the Afrotropical species. We suspect its Ethiopian origin. It was previously reported from Socotra, based on three females, under the name *Lasioglossum (Evylaeus) kowitense* by EBMER (2000).

Distribution. The species is endemic to Socotra: Adho Demalu [= Adho Dimello], Hamadara [= Hamadero] (EBMER 2000), Aloove area, Dixam plateau and environment of Kesa (this paper).
Lasioglossum (Sphecodogastra) dioscoridis Pauly & Straka sp. nov.
(Figs 60–68)

Material examined. Holotype: ♀, ‘SOCOTRA Is. (YE) wadi Ayhaft / 12°36.5′N, 53°58.9′E, 200 m / Jan Batelka leg. 7-8.xi.2010’ (NMPC). Paratypes: Socotra: Firmihin, 400–500 m, 12°28′27.1″N 54°00′54.0″E, 2 ♀♀, 6–7. ii.2010, yellow pan traps, L. Purchart & J. Vybíral lgt. (NMPC).

Description. Female. Species of medium size: total body length 7.0–7.5 mm, forewing length 5.5 mm, intertegular distance 1.5 mm. Black body, apical margin of terga slightly discolored, basolateral part of terga II–IV with white patch of tomentum, but reduced on tergum IV (Figs 60, 61).

Head wider than long (length / width = 0.90) (Fig. 62). Measurements (mm): length of clypeus 0.40; clypeus apical width 0.53; lower interocellar distance 1.20; upper interocellar distance 1.28; clypeo-antennal distance 0.40; length of eye 1.38; interantennal distance 0.15; interocellar distance 0.40; ocellocular distance 0.33; antennocellar distance 0.68; antennocular distance 0.43. Mandibles dark brown, apically brown reddish. Labrum black. Clypeus narrow and fairly prominent, shiny, smooth with spaced punctuation, punctures ill-defined, one and half to half diameter apart basolaterally and more than three diameters apart in other areas. Supraclypeal area shiny smooth, distinctly convex, punctures variable in size, rather ill-defined, but deep, one and half to half diameter apart. Frons slightly convex, densely punctate, punctures well defined, some interspaces distinct, dull, median ridge developed in ventral half and continues as slightly shiny line up to median ocellus. Paraocular area superficially imbricately punctate, punctures ill-defined. Ocelli of medium size. Vertex narrow (Fig. 63). Gena finely longitudinally ridged, sparsely microsculptured among ridges and ventrally. Scape black, flagellum black dorsally, pale ochraceous ventrally.

Mesosoma. Pronotum short, with tomentum along its dorsal area and pronotal tubercles. Scutum with dense punctuation, punctures well defined, less than half diameter apart laterally, but about one diameter apart in central area, interspaces between punctures shiny (Fig. 64). Scutellum slightly convex, flattened medially, punctated similarly to scutum, but with two sparsely punctated areas in centre, punctures up to two diameters apart. Metanotum with dense white tomentum. Pleura and hypopemeral area dull, coriaceous. Propodeum carinate on all its posterior face but not on lateral parts. Dorsal propodeal area finely irregularly rugose to plicate, interspaces between ridges slightly shiny (Fig. 65).

Legs dark to light brown, apical third of metatarsus darker than base. Scopa of hind legs light yellowish. Inner metatibial spur with short lobed teeth (Fig. 66).


Metasoma. Tergum I smooth in middle and sloping base, punctuation rich, punctures very fine, one to four diameters apart, interspaces shiny, apical margin slightly depressed, finely punctate as main part of tergum and very finely striate, lateral swelling nearly impunctate, isolated punctures larger than any other puncture on tergum I (Fig. 67). Terga II and III similarly sculptured to tergum I, but punctures are ill-defined and interspaces among punctures are finely microsculptured, terga appears slightly shiny to dull, sparsely punctate lateral swellings are also developed, apical margins slightly impressed. Terga IV and V are sparsely punctate, punctures ill-defined and larger than on preceding terga, interspaces microsculptured, dull.
Apical margin of terga I–IV narrowly discoloured. Terga II–IV with basolateral patch of tomentum, patch on tergum IV is reduced (Fig. 68). Terga V–VI with dense light yellowish setae. Sterna entirely light brown, with white setae.

*Male* unknown.
Differential diagnosis. This species belongs to the Holarctic subgenus Sphecodogastra Ashmead, 1899 based on the weakened distal wing venation, the second submarginal crossvein narrower than the first, the posterior surface of propodeum margined at side by vertical carina that extends upwards, and the discolored apical margin of the terga. It resembles Lasioglossum mediterraneum (Blüthgen, 1926), but differs in narrower and more prominent clypeus (Fig. 62). It also resembles L. epipygiale (Blüthgen, 1924) but differs in the fine punctuation on tergum I (Fig. 67).

Etymology. The species is named after the ‘Dioscoridis Insula’, the name of the island of Socotra in the ‘Periplus of the Erythrean Sea’, a first-century AD Greek navigation aid; noun in apposition

Remarks. The species resembles the Palaeartctic species more than the Afrotropical ones, thus we suspect its Palaeartctic origin.

Distribution. Endemic to Socotra.

Lasioglossum (Ctenonomia) dracaenae Pauly & Straka sp. nov. (Figs 69–77)


Description. Female. Relatively large species: total body length 8.0 mm, forewing length 6.5 mm, intertergal distance 2.05 mm. Body black, metatibia, meso- and metatarsus orange, terga II and III with white basal bands of tomentum, and base of apical depression of tergum IV with fine transverse tomentum (Figs 69, 70).

Head almost as long as wide (length / width = 0.94) (Fig. 72). Measurements (mm): length of clypeus 0.45; clypeus apical width 0.68; lower interocular distance 1.20; upper interocular distance 1.35; clypeo-antennal distance 0.50; length of eye 1.65; interantennal distance 0.25; interocellar distance 0.48; ocellocular distance 0.35; antennocular distance 0.78; antennocular distance 0.43. Mandibles black, brown reddish in centre. Labrum black to brown. Clypeus with large punctures half diameter apart basally and half to two diameters apart apically, interspaces between punctures shiny. Supraclypeal area prominent, with large and strong punctures, punctures half to two diameters apart, interspaces between punctures shiny, microsculptured or not. Frons densely punctate, punctures about half diameter apart, interspaces coarsely microsculptured, dull, medial ridge well developed in basal half. Paraocular area imbricately punctate, dull. Vertex narrow (Fig. 71), but gena thicker than eye, longitudinally ridged ventrally. Ocelli of medium size. Scape black, flagellum black dorsally, ochraceous ventrally.

Mesosoma. Dorsolateral angles of pronotum produced and carinate, with tomentum on dorsal area up to lateral tubercles. Scutum elevated and bilobed anteriorly, anteromedially impressed line, central part of scutum with smooth integument, punctuation consisting of larger and finer punctures intermixed, punctures two to less than half diameter apart, interspaces...

Shiny, lateral area of scutum densely punctate, interspaces microsculptured, dull (Fig. 73). Scutellum very sparsely punctate in centre, punctures numerous puncture diameters apart, interspaces glabrous, laterally densely punctate, punctures posteriorly larger than laterally. Metanotum dull, coriaceous, covered with white tomentum. Mesopleura and hypoepimeral area coarsely rugose. Posterior side of propodeum with hexagonal carina. Dorsal propodeal area plicate or irregularly ridged over its entire surface, interspaces between ridges slightly shiny (Fig. 74).
Legs. Protarsi, inner face of protibias, meso- and metatarsi orange. Inner calcar of metatibia with three long teeth (Fig. 75). Scopa of hind leg pale orange.


Metasoma. Whole tergum I densely microsculptured, tessellated, dull, fine punctures developed, but ill-defined and scattered on sides and sloping base, punctures about one to three diameters apart, apical depression slightly impressed, without punctures, but with same microsculpture, dull (Fig. 76). Terga II–III with similar dull sculpture as on tergum I. Tergum IV more coarsely punctured and more finely microsculptured than preceding terga. Apical depressions of terga I–IV developed. Base of terga II–III with narrow and entire white band of tomentum (Fig. 77). Base of apical depression of tergum IV with fine transverse tomentum in fresh specimen (paratype), in others indistinct. Dense setae on terga V and VI light brown to pale orange. Sterna brown, with pale orange plumose and rather long setae.

Male unknown.

Differential diagnosis. This new species belongs to the Palaeotropical subgenus *Ctenonomia* Cameron, 1903 based on the weakened distal wing venation, the second submarginal crossvein as strong as the first, the pectinate inner hind tibial spur, the posterior surface of propodeum surrounded by hexagonal carina. It belongs to the group of large *Ctenonomia* such as *Lasiglossum nairobicum* (Cockerell, 1945) of sub-Saharan Africa and *L. albescens* (Smith, 1853) of the Oriental Region. From *L. nairobicum* it differs in the orange coloration of the hind leg, from *L. albescens* in the angles of propodeum covered with rugose wrinkles (smooth or microsculptured in *L. albescens*).

Etymology. Named after one of the most striking plants of Socotra, the dragon’s blood tree (*Dracaena cinnabari*), as this bee was collected in a woodland with *Dracaena*. ‘Dragon’s blood’, the resin of this tree has been used as dye, since antiquity. Noun in apposition in genitive case.

Remarks. The species resembles the Afrotropical species more than the Oriental ones, thus we suspect Ethiopian origin of the species.

Distribution. Endemic to Socotra.

*Nomoiodes (Erythronomioides) socotranus* Blüthgen, 1925

(Figs 78–81)

*Nomoiodes socotranus* Blüthgen, 1925: 84 (type locality: Socotra, Ras Shoab).


Material examined. Sokotra, Ras Shoab, 1 ♂ (lectotype), 1 ♂2 ♀♀ (paralectotypes), i.1899, O. Simony lgt., type material determined by P. Blüthgen, lectotype and paralectotypes designated by Yu. Pesenko (NHMW).

Remarks. Described and known from three males and three females only.

**Nomioides (Nomioides) squamiger Saunders, 1908**  
(Figs 82–85)


**Material examined.** Socotra: Wadi Ayhaft, 200 m, 12°36.5′N, 53°58.9′E, 1 ♀, 7.–8.xi.2010, J. Bezděk lgt.; Dixam plateau, Firmihin (canyon), 490 m, 12°28.6′N, 54°01.1′E, 2 ♀♂ 41 ♀♀, 15.–16.xi.2010, J. Batelka lgt. on flowers of _Ochradenus_ sp.; Dixam plateau, Firmihin (_Dracaena_ forest), 490 m, 12°28.6′N, 54°01.1′E, 1 ♀ 6 ♀♀, 15.–16.xi.2010, J. Hájek lgt., 2 ♀♂ 2 ♀♀, J. Bezděk lgt. Dixam plateau, Wadi Dirhor, open woodland with _Boswellia_ trees, 340 m, 12°28.0′N, 54°00.5′E, 2 ♀♀, 15.vi.2012 et 22.vi.2012, J. Hájek lgt. (all in NMPC).

**Remarks.** Identification of _Nomioides_ (s. str.) in Socotra is slightly confusing in previous publications. Pesenko & Pauly (2005: 207) reported _N. facilis_ from Socotra, but simultaneously, they noted that: ‘Socotra is also particular with the endemic _Nomioides_ subg. _Erythronomioides_ Pesenko, 1983. Another species found on the island has been formerly identified as _N. facilis_ (see Pesenko 1983), but it is instead _N. squamiger_ by its geographical position and the identity of the specimens checked.’ (Pesenko & Pauly 2005: 209). In the taxonomic part of the same paper, they however reported _N. facilis_ from Socotra (Pesenko & Pauly 2005: 180), while _N. squamiger_ has been reported from North Africa, Israel, and the Arabian Peninsula only. In their study published four years later, they again reported from Socotra both _N. facilis_ (Pesenko & Pauly 2009: 224) and _N. squamiger_ (Pesenko & Pauly 2009: 232) from a single female. In the same paper they moreover reported that: ‘The first information on Nomioiidi-nae from the Arabian Peninsula and its adjacent islands was published by Blüthgen (1925), who described _N. socotranus_ and recorded _N. rotundiceps_ Handlirsch, 1888, from the Island of Socotra.’ (Pesenko & Pauly 2009: 218). In Blüthgen (1925), however, no such Socotran record of _Nomioides rotundiceps_ was published. Three voucher specimens from Firmihin (see Material examined), were identified by one of us (AP) as _N. squamiger_, therefore we use this name for this species that was apparently previously reported from Socotra as _N. rotundiceps_ or _N. facilis_ by mistake.


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**Patellapis (Zonalictus) flavovittata** (Kirby, 1900)  
(Figs 86–88)

_Habictus_ [sic!] _flavovittatus_ Kirby, 1900: 20 (type locality: Socotra, Adho Dimellus).


**Material examined.** Socotra: Kishen, 1 ♀, viii.1956, Oxford Expedition (BMNH); Al Haghier Mts., Skant Mt., 1400 m, 12°34’36.0″N 54°01’30.0″E, 1 ♀, 31.i.–1.ii.2010, L. Purchart lgt.; Al Haghier Mts. env., wadi Madar, 1180–1230 m, 12°33.2’N 34.00.4’E, 1 ♀ 1 ♂, 12.–14.xi.2010, J. Batelka lgt., 1 ♀, J. Hájek lgt. (all NMPC).

**Remarks.** _Zonalictus_ Michener, 1978 is a typical African subgenus of _Patellapis_ Friese, 1909 with a single Arabian species (Ascher & Pickering 2017). An endemic Socotran species resembles the Afrotopical species more than the Arabian one, thus we suspect its Ethiopian origin.

**Distribution.** Endemic to Socotra: Adho Dimellus (Kirby 1900, 1903; Kohl 1906, 1907).
Pseudapis (Pseudapis) anomala Kirby, 1900
(Figs 89, 90)

*Pseudapis anomala* Kirby, 1900: 16 (type locality: Socotra, various places); *Kirby* (1903): 242.

Nomia anomala: Kohl (1906: 7–8) (new combination); Kohl (1907): 176–177.


Remarks. *Pseudapis anomala* was described by Kirby (although with some doubts about its placement) as a new monotypic genus within ‘Sphegidae’ (= Sphecidae) and it was subsequently recognised as a bee by Kohl (1906, 1907).

Distribution. Reported from the Socotra Archipelago and the Arabian Peninsula (Aden) by Kohl (1906, 1907). In the Socotra Archipelago reported from Moukaradia (= Gebel Raggit); Homhil (Kirby 1900, 1903); Ras Shoab; Abd-el-Kuri; and Samha (Kohl 1906, 1907).

Megachilidae

Megachile (Eutricharaea) forbesii Cockerell, 1937
(Figs 91–93)


Material examined. Sokotra: Thentud, 11.i.1899, 1 ♀ (holotype) (BMNH).

Remarks. A species described from a single female specimen (Cockerell 1937). Pasteels (1985) redescribed the female and described the male based on four females and a single male.

Distribution. Endemic to Socotra: Thentud (Cockerell 1937); Kalansiya (Pasteeels 1985).

Megachile (Eutricharaea) naevia Kohl, 1906
(Figs 94–98)

*Megachile argentata* Fabricius, 1793: Kirby (1903): 250 (misidentification).


Megachile naevia Kohl, 1907: 183 (junior homonym and objective synonym).

Material examined. Sokotra: Ras Shoab, 1 ♂ (lectotype), 1 ♀, i.1899, O. Simony lgt., F. Kohl det., D. B. Baker revid. (NHMW); Noged plain (sand dunes), Sharet Halma vill. env., 20 m, 12°21.9′N, 54°05.3′E, 1 ♀, 10.–11. xi.2010, J. Hájek lgt. (NMPC).

Distribution. Endemic to Socotra: Jena-agahan, Homhil (Kirby 1903); Ras Shoab (Kohl 1906, 1907).

Megachile (Callomegachile) paucipunctulata Kirby, 1900
(Figs 99, 100)

*Megachile paucipunctulata* Kirby, 1900: 21 (type locality: Socotra, Homhil); Kirby (1903): 251, plate xvi, fig. 3; Kohl (1906): 17 (*M. sokotrana* proposed as junior subjective synonym of *M. paucipunctulata*); Kohl (1907): 185; Cockerell (1907): 132 (*M. sokotrana* proposed as junior subjective synonym of *M. paucipunctulata*); Cockerell (1937): 218 (comments on the species recognition).

Material examined. Socotra: 1 ♀ (holotype of *M. sokotrana*), i.1899, O. Simony lgt., F. Kohl det., H. Friese revid. (NHMW); Qualentiah env., slopes 5 km SE from Quaysoh, 12°39′41.5″N 53°26′39.5″E, 1 ♀, 4.–5 vi.2010, V. Hula & J. Niedobová lgt. (NMPC); Noged plain (sand dunes), Sharet Halma vill. env., 20 m, 12°21.9′N, 54°05.3′E, 2 ♀♀, 10.–11.xi.2010, J. Hájek lgt., 3 ♀♀, J. Bezděk lgt. (NMPC).

Remarks. Most species of the subgenus *Callomegachile* Michener, 1962 are distributed in Africa and the east Oriental Region, and no species is distributed in the Arabian Peninsula (ASCHER & PICKERING 2017), thus we suspect Ethiopian origin of the endemic Socotran species of this subgenus.
**Distribution.** Endemic to Socotra: Homhil (Kirby 1900, 1903); without a precise locality (Fries 1903; Kohl 1906, 1907).

*Megachile (Chalicodoma) wfkirbyi Kohl, 1906*  
(Figs 101–103)

*Megachile punctatissima* Kirby, 1900: 20 (type locality: Socotra, Homhil); Kirby (1903): 250, plate xvi, fig. 1 (redescription).


*Megachile grantiana* Cockerell, 1907: 132 (replacement name, nec *M. punctatissima* Spinola, 1806).

*Megachile kirbyi* Friese, 1909: 384 (463) (unjustified emendation)

*Chalicodoma grantiana:* Cockerell (1937): 191 (new combination).


**Material examined.** Sokotra, 1 ♂, i.1899, O. Simony lgt., F. Kohl det.; J. Samha, 1 ♀, i.1899, O. Simony lgt., F. Kohl det.; Sokotra, Ras Shoab, 2 ♀♂, i.1899, O. Simony lgt., F. Kohl det. (all in NHMW).

**Remarks.** The subgenus *Chalicodoma* Lepeletier, 1841 is distributed mainly in the Palaeartic Region with a few African species distributed mainly in southern Africa and a single Arabian species (Ascher & Pickering 2017). For this reason we suspect Palaeartic origin of this Socotran endemic species.

Species name *Megachile W. F. Kirbyi* (Kohl 1906, 1907) is available as “wfkirbyi” according to ICZN article 32.5.2.4.4 (ICZN 1999). The nomenclatural history of *M. wfkirbyi* was completely and correctly presented by Ascher & Pickering (2017), however without explanation.

**Distribution.** Endemic to Socotra Archipelago. Recorded from Socotra: Homhil (Kirby 1900, 1903), Ras Shoab (Kohl 1906, 1907), and from Samha (Kohl 1906, 1907).

*Protosmia megaceps* (Kohl, 1906)  
(Figs 104, 105)


*Osmia megaceps* Kohl, 1907: 182 (junior homonym and objective synonym).


**Material examined.** Sokotra: Ras Shoab, 1 ♂ 1 ♀, i.1899, O. Simony lgt., F. Kohl det. (NHMW).

**Remarks.** Known from one male and one female of the type series only. *Protosmia* Ducke, 1900 is a widely distributed Holarctic genus of bees that is missing in Africa (except the north) with a few rare Arabian species (Ascher & Pickering 2017). For this reason we suspect Palaeartic origin of this endemic Socotran species.

**Distribution.** Endemic to Socotra.

*Xenostelis polychroma* Baker, 1999  
(Figs 106, 107)


**Material examined.** Not available.
Remarks. *Xenostelis* Baker, 1999, with a single species *X. polychroma*, is known from the female holotype only.

**Distribution.** Endemic to Socotra: without a precise locality (Baker 1999).

**Excluded uncertain records**

*Anthophora* sp. (Taschenberg 1883: 176): Socotra (without locality).

*Halictus* sp. (Kirby 1903: 250): Homhil, 25.i.1899.

**Origin and distribution of Socotran bees**

There are 28 species of bees known from the Socotra Archipelago to date and 17 of them are endemic. Only one of them is missing in the main Socotra Island: *Colletes inconspicuus*, endemic to Abd el Kuri Island. Three species are known from Samha and six species are reported from Abd el Kuri. A single species is known from Darsa.

**Table 1.** Distribution of Socotran bees on the individual islands (presence is marked by ‘+’, absence according to the current knowledge is marked by ‘–’), endemism to archipelago and putative origin of the species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Socotra</th>
<th>Darsa</th>
<th>Samha</th>
<th>Abd el Kuri</th>
<th>Endemic</th>
<th>Origin</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amegilla pyramidalis</td>
<td>+</td>
<td>–</td>
<td>–</td>
<td>+</td>
<td>+</td>
<td>Palaearctic</td>
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<tr>
<td>Amegilla quadrifasciata</td>
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<td>Anthophora inclyta</td>
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<td>Eucera wfkirbyi</td>
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<td>Xylocopa sulcatipes</td>
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<td>Arabian</td>
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<td>Colletes inconspicuus</td>
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<td>+</td>
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<td>Arabian/Ethiopian</td>
</tr>
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<td>Lasioglossum dioscoridis</td>
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<td>Ethiopian</td>
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<td>Nomioides squamiger</td>
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<td>–</td>
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<td>–</td>
<td>Arabian/Ethiopian</td>
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<td>Patellapis flavovittata</td>
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<td>–</td>
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<td>Ethiopian</td>
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<td>Pseudapis anomala</td>
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<td>Arabian</td>
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<td>Megachile paucipunctulata</td>
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<td>Protosmia megaceps</td>
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<td>Xenostelis polychroma</td>
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<td>–</td>
<td>+</td>
<td>unknown</td>
</tr>
</tbody>
</table>
All bees were assigned to four groups based on their biogeographic distribution: sub-Saharan Africa (Ethiopian origin), the Arabian Peninsula (Arabian origin), Eurasia (Palaearctic origin), or endemic. The fifth category is “unknown origin”, for species where reliable data are not available. Some endemic species can also be putatively allied with closely related species, or lineage (subgenus, species group) with defined historical distribution.

Most species (12) are of Arabian-Ethiopian origin, of which six came from Africa, rather than from the Arabian Peninsula, and two species arrived from the Arabian Peninsula. The other four are of unidentified Ethiopian-Arabian origin. Seven species are Palaearctic faunal elements. Nine species were impossible to ally reliably to any biogeographic origin. A summary of the species and their likely origin is presented in Table 1.

**Bee parasites and their host association**

Based on the available material and published records, we can analyse host associations of cleptoparasitic bees (Hymenoptera) as parasites of other bees, and beetle (Coleoptera) parasites of bees (Table 2).

**Apoidea: Apidae.** *Thyreus histrionicus* is a known parasite of *Amegilla quadrimaculata* within its distribution area (Liese 1968). The presence of both species suggests that the association also exists on Socotra. The endemic *T. uniformis* is smaller than *T. histrionicus* and thus the species is probably parasite of smaller host species than *A. quadrimaculata*. Considering the size of other potential Anthophorini, the endemic species *A. pyramidalis* is most likely the host of *T. uniformis*.

**Apoidea: Megachilidae.** *Xenostelis polychroma*, with a possible relationship to *Afrostelis* Cockerell, 1931, belongs to the *Stelis* Panzer, 1806 clade, which includes parasites of other megachild bees (Michener 2007). According to a molecular phylogenetic analysis of anthidiine bees (Litman et al. 2016), *Afr steerlis* is close to *Euaspis* Gerstaecker, 1857 and *Stelidomorpha* Morawitz, 1875, a subgenus of *Stelis*. The host of *Afr steerlis* is *Heriades* Spinola, 1808 (Taylor 1965), but *Euaspis* and *Stelidomorpha* are parasites of large species of the genus *Megachile* (Michener 2007). Thus, the likely hosts of *Xenostelis* are *M. paucipunctulata* or *M. wfkirbyi*, because *Heriades* does not occur in Socotra.

**Table 2.** Bee families in Socotra with cleptoparasitic bees (Apoidea) and parasitoid beetles (Coleoptera) recorded from the archipelago potentially parasitizing them.

<table>
<thead>
<tr>
<th>Host bee family</th>
<th>Parasites reported from Socotra and their possible host association</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apidae</td>
<td>Apidae: <em>Thyreus histrionicus, T. uniformis</em></td>
</tr>
<tr>
<td></td>
<td>Meloidae: <em>Meloe lefevrei, M. trapeziderus</em></td>
</tr>
<tr>
<td>Colletidae</td>
<td>no parasites reported</td>
</tr>
<tr>
<td>Halictidae</td>
<td>Meloidae: <em>Meloe lefevrei, M. trapeziderus</em></td>
</tr>
<tr>
<td></td>
<td>Ripiphoridae: <em>Ripiphorus arabiafelix arabiafelix</em></td>
</tr>
<tr>
<td>Megachilidae</td>
<td>Megachilidae: <em>Xenostelis polychroma</em></td>
</tr>
<tr>
<td></td>
<td>Meloidae: <em>Meloe lefevrei, M. trapeziderus, Zonitoschema kaszabi</em></td>
</tr>
</tbody>
</table>
**Coleoptera: Meloidae.** Two species of *Meloe* Linnaeus, 1758, of the Afrotropical subgenus *Afromeloe* Schmidt, 1913, have been reported from Socotra: the endemic *M. trapeziderus* Gahan, 1907 and *M. lefevrei* Guérin-Méneville, 1849, which was reported also from Ethiopia (Bologna & Pinto 1998). Larvae of *Meloe* develop on larvae of various bees, mainly on Apidae and Andrenidae, but occasionally also on Halictidae, Megachilidae, and Colletidae, and they are not necessarily specialized on a single bee genus (Mayer & Johansen 1978, Mliczky 1988: 12, Bologna 1991: 288, Fellendorf et al. 2004: 312). Primary larvae of *Meloe (Afromeloe) caffer* Péringuey, 1886 were found on bees of the genus *Rediviva* Friese, 1911 (Melittidae) in South Africa (Bologna & Pinto 1998). Given the absence of Melittidae and Andrenidae in Socotra, and the small size of Socotran *Colletes* Latreille, 1802, *Megachile* Latreille, 1802 of the subgenus *Eutricharaea* Thomson, 1872, and *Protosmia*, members of Apidae, *Crociaspidia* Ashmead, 1899 or large species of *Megachile* are likely hosts of both Socotran *Afromeloe*. For the material examined see Appendix.

*Zonitoschema kaszabi* Batelka & Bologna, 2014, described as endemic to Socotra, could develop on larvae of Megachilidae, as do its congener in the Arabian Peninsula or elsewhere (Bologna 1991, Batelka & Bologna 2014).

**Coleoptera: Ripiphoridae.** *Ripiphorus arabiafelix arabiafelix* Batelka, 2009 was first reported from south Yemen as *Ripiphorus caffer* Gerstaecker, 1855 (Gahan 1896). Based on re-examination of Gahan’s specimens from BMNH it was described as a different species (Batelka 2009). This species is common and widespread through the south and southeast of the Arabian Peninsula, usually collected on inflorescences of *Aerva javanica* (Batelka 2010, 2014, unpublished records), which is also present in lower levels all over the Socotra Island (JB, pers. observ.). The closely related *Ripiphorus caboverdianus* Batelka & Straka, 2011 from the Cape Verde Islands was currently downgraded to a subspecies level of *Ripiphorus arabiafelix* (Batelka et al. 2016) because of very low genetic difference, although morphological differences between both taxa can be observed. Old World species of *Ripiphorus* Bosc, 1791 are known to develop on larvae of several genera of Halictidae (Batelka & Straka 2011). Association of *Ripiphorus arabiafelix caboverdianus* with *Halictus* (*Seladonia*) *lucidipennis* Smith, 1853 in Cape Verde is expected based on field observations (Batelka & Straka 2011). For this reason, we predict that one or multiple bee species from the family Halictidae will be host(s) of this *Ripiphorus* in Socotra. The species is reported here from Socotra from a single female (see Appendix).

**Discussion**

Observed bee diversity of the Socotra archipelago is slightly higher in comparison to the bee faunas of other larger isolated islands in the Atlantic and Indian Ocean: Cape Verde (20), Comoros (22), Madeira (14), or Mascarenes (11) (Ascher & Pickering 2017). Fauna of isolated islands is largely unbalanced in relation to the presence of higher taxa as well as their biogeographic origin. Two families (Andrenidae and Melittidae) and many genera of Apidae, Colletidae, Halictidae and Megachilidae, which are present in the Arabian Peninsula (Dathe 2009), have not been recorded in Socotra, yet. Nearly two thirds of species diversity
consists of endemics (Table 1), including also two taxa of generic rank (*Erythronomioides*, *Xenostelis*) (BATELKA 2012). A review of the biogeographic origin of bees recorded in Socotra (Table 1) shows that most bees apparently came from the Arabian Peninsula or the Ethiopian Region. However, a significant number of species has Palaeartic, or maybe Mediterranean origin. These Palaeartic species might have immigrated either from the Arabian Peninsula or from Africa, however, they possibly disappeared or became very rare in the surrounding mainland area, because they are not known from the Arabian Peninsula (DATHE 2009, ASCHER & PICKERING 2017). These Palaeartic elements often remain isolated in the region. Thus, islands can serve as Noah’s Ark for some species or even all lineages in the region. Another potential island effect seen on Socotra is size shift of small species of the tribe Nomiidini. The monotypic subgenus *Erythronomioides* of the genus *Nomioides* Schenck, 1867 from Socotra with length 5.0–5.5 mm is ‘much bigger’ than any remaining African species of the genus *Nomioides* with their length of 3.0–4.4 mm (PESENKO & PAULY 2005). Similarly, two endemic species of *Ceylalictus* Strand, 1913 (subg. *Atronomioides* Pesenko, 1983) from Cape Verde Islands are the largest species of Nomioidinae in the world (PESENKO & PAULY 2005). The parasite of one of them, *Chiasmognathus batelkai* Straka & Engel, 2012, with its 3.2–4.2 mm in length, is the largest species of its genus (STRAKA & ENGEL 2012). However, the size of cuckoo bees usually depends on the size of the host.

Regarding the species pool of bee parasites, we can associate all parasites at least with the host family or even genera or species present in Socotra. Bee parasites widespread in the Arabian Peninsula, such as *Nomada* Scopoli, 1770 cuckoo bees (DATHE 2009), or *Stylops* Kirby, 1802 strepsipteran (BATELKA & STRAKA 2008, STRAKA et al. 2015) are missing in Socotra because their hosts of the bee genus *Andrena* are also missing in the islands. Most of the beetle parasites are probably specialized to family level of their hosts, or may be parasites of bees from different families (probably the case in *Meloe* spp.). Cuckoo bees are very likely specialized on a genus, or even a species of host, as is common within the present cleptoparasitic groups (LIEFTINCK 1968, WESTRICH 1990). Although the host associations of pollen collecting bees and their parasites is uncertain, approximately one third of the bee species present in Socotra may serve (at least occasionally) as hosts of the reported bee and beetle parasites.

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References


Appendix

Studied material of beetle (Coleoptera) parasites of bees in Socotra

Meloidae

*Meloe lefevrei* Guérin-Méneville, 1849

**Material examined.** Socotra: Dixam plateau, Wadi Esgego, 12°28′09″N, 54°00′36″E, 300 m, 2.–3.xii.2003, 1 spec., J. Farkaš lgt.; Homhil protected area, 12°34′27″N, 54°18′32″E, 364 m, 28.–29.xi.2003, 5 spec., J. Farkaš lgt. (all in NMPC).

*Meloe trapeziderus* Gahan, 1907


Ripiphoridae

*Ripiphorus arabiafelix arabiafelix* Batelka, 2009

**Material examined.** Socotra: Qalansiah mount, 6.iv.2008, 1 ♀, A. Carapezza lgt., J. Batelka det. and coll. **First record from the Socotra Archipelago.**