ACTA ENTOMOLOGICA MUSEI NATIONALIS PRAGAE
Published 17.xii.2012 Volume 52 (supplementum 2), pp. 1–26 ISSN 0374-1036

Socotra Archipelago – a lifeboat in the sea of changes: advancement in Socotran insect biodiversity survey

Jan BATELKA

Nad Vodovodem 16, CZ-100 00 Prague 10, Czech Republic; e-mail: janbat@centrum.cz

Abstract. Nature conditions in the Socotra Archipelago are briefly summarised, main factors contributing to the composition and diversity of the insect fauna, i.e. geological history, geographic position, geomorphology, climatic conditions and plant diversity, are circumscribed. Results of the Socotran invertebrate biodiversity research are reviewed, the first annotated list of 40 insect genera and subgenera endemic to the Socotra Archipelago is provided. Recorded high level of endemism in the Socotra Island is in accordance with the estimated geological age and continuous stability of its ecosystem. Brief comparison of biodiversity in Socotra and Seychelles Islands – both granitic archipelagos of Gondwanan origin in the West Indian Ocean – is performed. Difference in composition of insect fauna in Socotra and allied Abd el Kuri Island is commented. Main threats and conservation issues concerning the fragile Socotran ecosystem are summarised, and examples of possible consequences for insect fauna are given. Based on comparison of scarce outputs and research activities concerning the Socotran insect fauna so far with the number of those elaborated for other countries/islands, establishing of a long-term insect survey is recommended.

Key words. Review, insularity, geology, flora, climate, biodiversity, endemism, insect genera, habitat conservation, insect survey, Yemen, Socotra

Introduction

Because of their remarkable richness in endemic forms, study of the isolated biotas (also called ‘insularity’) has been one of the most interesting topics among naturalists and especially evolutionary biologists since the second half of the 19th century (Witt & Maliakal-Witt 2007). Diversity of insular faunas and floras is particularly influenced by the combination of geological history of the respective archipelago or island, its geographical location, isolation and by the past and current climatic conditions (e.g. del-Arco et al. 2006, Fernández-Palacios et al. 2011). During the last several hundred years, composition of insular biotas worldwide has been, however, negatively influenced by the permanent human presence and the increasing exploitation.

HÁJEK J. & BEZDĚK J. (eds.): Insect biodiversity of the Socotra Archipelago. *Acta Entomologica Musei Nationalis Pragae* **52 (supplementum 2)**: i–vi + 1–557.

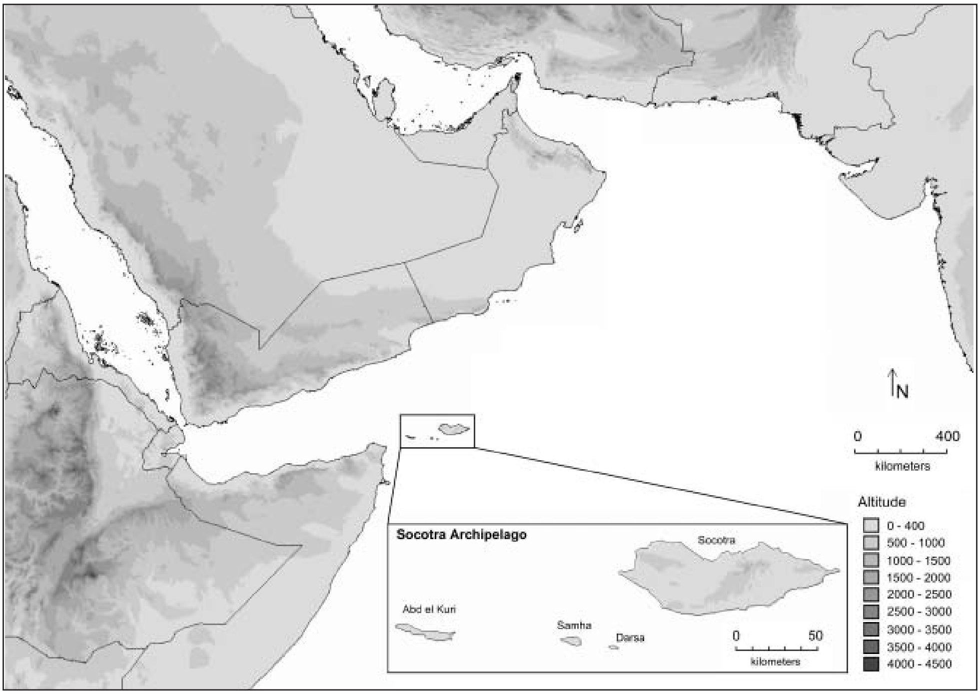


Fig. 1. Location map of the Socotra Archipelago.

Not only endemic vascular plants and vertebrate animals like flightless birds, giant lizards or tortoises were brought to extinction or nearly so (e.g. Fay et al. 1997, Steiner & Sayers 2002, Olson 1973, Machado 1985, Palkovacs et al. 2003, Miralles et al. 2011 – giving just a few examples from insular habitats around Africa). Also many peculiar endemic insect forms known to scientists were exterminated due to destruction of their habitat, like large monotypic ground beetle *Aplothorax burchelli* Waterhouse, 1842 and giant earwing *Labidura herculeana* (Fabricius, 1798) from St. Helena (Ashmole & Ashmole 2004) or many species of dung beetles of the tribe Helictopleurini from Madagascar (Hanski et al. 2007), and certainly many others had been lost forever before they were discovered. Some islands, like Easter Island in Polynesia, are even no longer suitable for research of biodiversity or biogeographic pattern of terrestrial arthropods because of the complete environmental degradation (Desender & Baert 1997).

Socotra Archipelago (also spelt as 'Soqotra' or 'Suqutra') is by its nature and despite some current negative human activities considered a unique spot on the planet and it therefore represents an outstanding place for research of animal and plant diversity and biogeography. To protect all its terrestrial and marine wildlife and original human settlement and cultural heritage, Socotra was designated as a Biosphere Reserve in 2003 and a Natural World Heritage site in 2008 (UNEP-WCMC 2008).

However, the research of the Socotra's fragile biota is far from giving a complete and comprehensive picture. Short-term expeditions of various institutions focused on investigation of the terrestrial invertebrate communities are still bringing to light many species new to science or new island records of species which are naturally present in the region of the Gulf of Aden, and which all undoubtedly represent important although so far overlooked components of this island ecosystem. Much of the fieldwork still needs to be done and many contributions are yet to be published before we obtain data comparable with those available about arthropod faunas of other archipelagos worldwide or adjacent zoogeographic regions.

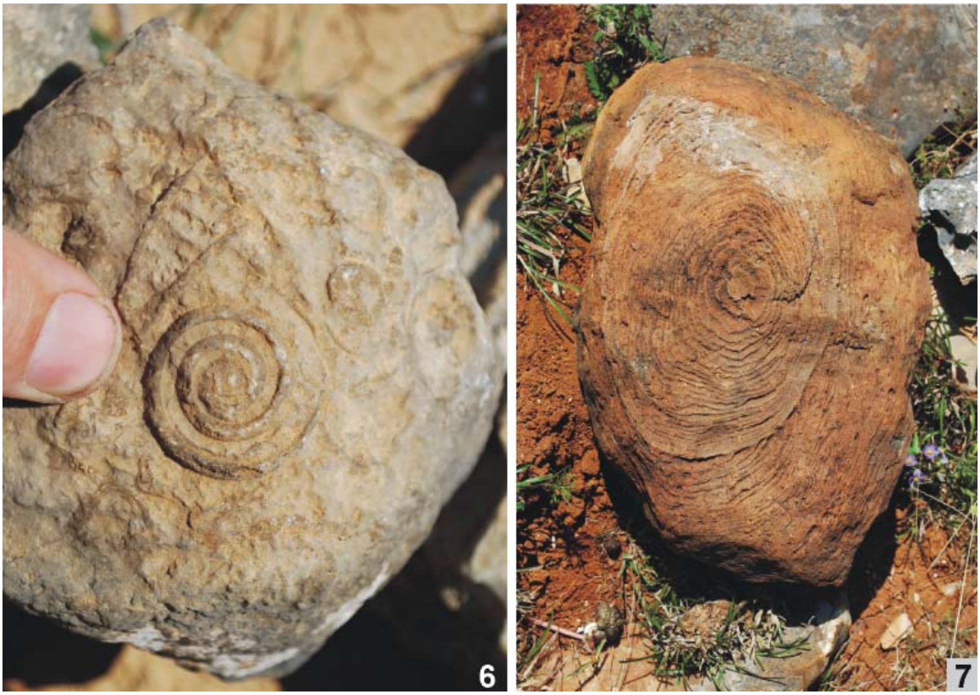
Figs. 2–3. Main landscape features of Socotra Island. 2 – granitic peaks of the Hagher massif (view from Skand to Hadibo); 3 – wadi south of Ba'a village.

Figs. 4–5. Main landscape features of Socotra Island. 4 – Canyons bellow the Diksam plateau (Photo J. Hájek, 2010); 5 – North-East cliffs with sand dunes, close to the Arher spring.

Natural conditions of the Socotra Archipelago

Geography and geomorphology. Socotra Archipelago is situated in the western part of the Arabian Sea and forms the most distinct insular feature on its surface (Fig. 1). The archipelago consists of one main eponymous east-west orientated island (3,625 km^2), two smaller islands Samha (41 km^2) and Darsa (10 km^2) (also known as 'The Brothers' or 'Al Ikhwan') and a bit detached Abd el Kuri (133 km^2) which lies just about 100 km southwest of the main island. All four islands are closer to east Africa than to their place of origin – southern shore of Yemen and Oman. The highest mountain of the archipelago is situated in the eastern half of the Socotra Island in the Haggeher mountain range and reaches slightly above 1,500 m a.s.l. (Fig. 2). The smaller islands with a much more eroded surface reach only 743 m a.s.l. at their highest point in Abd el Kuri (UNEP-WCMC 2008). Three smaller islands are characterized by arid and rocky landscape without any permanent running water or seasonal pools. On the contrary, Socotra has numerous south to north orientated wadis and streams with running water (Fig. 3) which sometimes incised deep canyons into the slopes of the Hagher massive (Fig. 4). Water is abundant during the rainy seasons (see further under Climatic conditions) and scattered pools remain long after the rains. North-west shore is formed by steep cliffs of a limestone plateau (Fig. 5) with some well known cave systems (e.g. Arher, Hoq or Kazekas Cave – for coordinates of these and some other caves see Taiti & Checcucci (2009)). The karstic system in Socotra is remarkably large and complex – altogether 35 different caves with underground galleries with a total length of 25 km were documented (Geest et al. 2005). Both longer edges of the island are bordered by a strip of coastal plains sometimes up to several kilometers wide with occasional sandy dune areas.

Geological and tectonic history. It is beyond the author's competence to comment on or interpret the complex geological and particularly tectonic history of the Socotra Archipelago. However, as such information is often used in biological papers, for example in phylogenetical analyses, short review is in place here. All four islands are situated east of Gulf of Aden on the so-called 'Socotran Platform'. Only Abd el Kuri is detached from the remaining three islands by the Brothers Basin (Birse et al. 1997). The archipelago is of the east Gondwanan origin similarly to the Madagascar and Seychelles in the south (e.g. Krause et al. 2006, Ganerød et al. 2011) and to the neighbouring landmasses of south Arabia in the north and Africa in the west. Between the Socotran Platform and the Arabian Peninsula a deep trench with earthquake epicentres, so-called 'Sheba Ridge' is developed (Matthews et al. 1967). Spreading of the Gulf of Aden is considered to be a result of the anticlockwise rotation of Arabia with respect to the African continent, and the period of 30–17 million years ago (Mya) was chosen for the early spreading phase (Girdler & Styles 1978). D'Acremont et al. (2010) investigated magnetic anomalies in the area between the Alula-Fartak and Socotra-Hadbeen Fracture Zones of the Sheba Ridge and confirmed an oceanic accretion from at least 17.6 Mya just close to the north-west edge of Socotra. Socotra is thus in insular position with respect to Arabia from at least 16 Mya (d'Acremont et al. 2010: Figure 10) while with respect to east Africa its position and distance has only little changed. According to the same authors the rifting between Arabia and Africa started around 35 Mya.



Figs. 6–7. Marine (?) fossils. 6 – Unidentified fossil from Firmihin (490 m a.s.l.); 7 – One of the abundant fossil specimens from the Madboh Sinhin plateau (820 m a.s.l.) which I tentatively identified as a domical 'cabbage-head' stromatolite sensu ANADÓN & ZAMARREÑO (1981); it is probably identical with 'silicified concretions' showed in BEYDOUN & BICHAN (1970, Plate 22, Fig. b).

Date and place of Socotra's splitting-off from the Dhofar region in Oman is interpreted in several different ways in biological papers. Here are some examples: '*The archipelago is of continental origin and was connected to the Arabian plate in the region of today's Dhofar and Al-Mahra prior to the rifting of the Gulf of Aden, at least 15 Myr (at most 35 Myr) ago (Richardson & al. 1995, Samuel & al. 1997)*' (KÜRSCHNER et al. 2006) or '*one unpublished record from Oman ... from an Oligocene site (ca. 32 mio BP) located exactly (in time and space) at the splitting point, where Socotra was separated from the pre-Arabian continental plate (K. van Damme, in prep.)*' (NEUBERT 2009) or '*Although today geographically closer to the Horn of Africa, the Socotran archipelago was separated from the Arabian peninsula 18–15 Ma (Richardson et al., 1995; Fleitmann et al., 2004; Van Damme, 2009)*' (THIV et al. 2011).

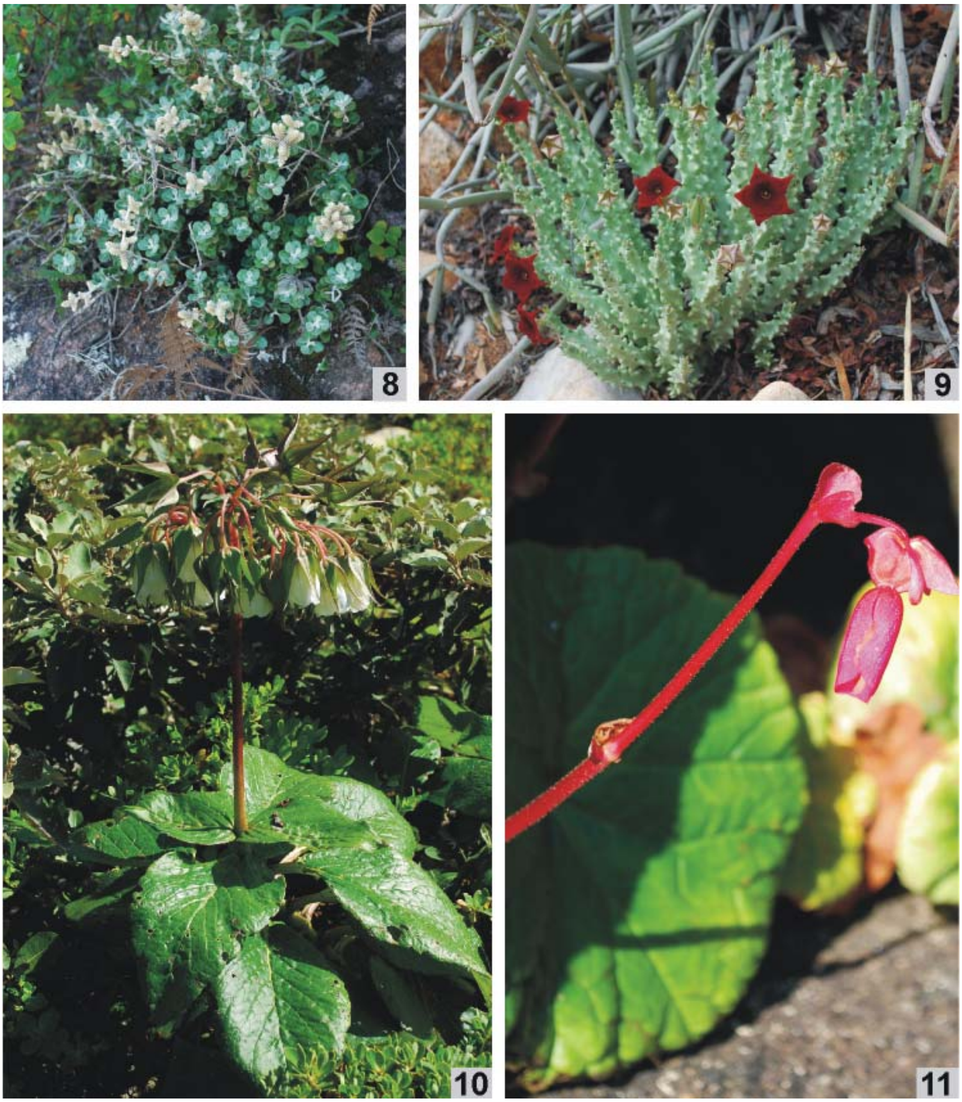
However, historical reconstruction of the **insular nature** of Socotra in geological papers is not so straightforward. Although SAMUEL et al. (1997: Figure 11) found apparent similarities in stratigraphy of Socotra and Dhofar they just pointed out that '*... prior to the Gulf of Aden rifting, Socotra was located adjacent to the Dhofar region...*'. In BIRSE et al. (1997: Figure 7), the Socotran Platform is even figured in isolated position with respect to the neighbouring landmasses since the Late Jurassic. In some other papers insularisation of Socotra is even attributed to isolation from Africa: e.g. '*Kopp (1999) considers isolation from Africa for at least 70 Myr, but minimal estimates are ca. 10 Myr (Laughton et al. 1970). Krupp et al. (2002) hypothesize that the archipelago was separated from Africa "at about the same time as India and Madagascar".*' (Nagy et al. 2003).

Stratigraphy. Three main stratigraphic units dominate the Socotra Island. Paleocene-Eocene plateaus are spread in mid altitudes all over the island and overlay the Proterozoic-Paleozoic granitic basement, which is elevated only in eastern Socotra in the Haggeher massif and in the westernmost part in Qalansiyah and Ras Shúab. It is believed that the highest part of the Haggeher massif was never submerged since the Cretaceous (Fournier et al. 2007) although marine (?) fossils (of age unknown to the author) can be found on limestone plateaus up to 800 m a.s.l. (J. Batelka, pers. observ., Figs. 6–7). Mesozoic outcrops rise along the main wadis and steep edges of Paleocene-Eocene plateaus (Morrison et al. 1997, Fournier et al. 2007). Third, the lowest parts of the island consist either of Quaternary Formations (sensu Fournier et al. 2007) or they are interpreted as Oligocene-Miocene or Lower Cretaceous strata (sensu Morrison et al. 1997).

Climate. Socotra lies within boundaries of the monsoonal precipitation regime (also called Indian summer monsoon). It means that Socotra has bimodal distribution of rainfall due to the seasonal migration of the Intertropical Convergence Zone (Fleitmann et al. 2007). Southwest winds of summer monsoon start in April/May by heavy rains in southern part of the island and usually end between September/October. Shortly after (between October/November), northwest winds bring winter monsoon with precipitation mainly in northern part of the island and this second seasonal peak ends in February. Impacts of both rainy periods are different in different parts of Socotra due to the natural barrier formed by the Haggeher mountain massif (Habrova et al. 2007).

The highest rainfall measured between years 2002–2006 was during September-November and March-May. Fogs are common in the highest parts of the main massif during the southeast summer monsoon, when fog-derived moisture may reach up to 800 mm of precipitation. In several past decades, the precipitation did not reach the mean annual amount in some years, causing droughts some of which are remembered and named by local people (Scholte & de Geest 2010). Recorded air temperature ranged from 8.2 °C in January 2005 in Skant (1,450 m), Haggeher Mts., to 43.5°C in June 2005 in Hadibo. Mean annual records taken by the same weather stations ranged between 17.9°C and 28.0°C, respectively (Habrova et al. 2007). According to Scholte & de Geest (2010) the hottest month is May with the average recorded temperature of 31.2°C.

Paleoclimate. Climatic conditions during the Pleistocene-Holocene period were inferred from the data obtained by analysis of stalagmites from caves in Socotra and Oman (Fleitmann et al. 2007, Shakun et al. 2007). In Pleistocene, interpluvial periods (i.e. dry periods corresponding to glacials in the northern temperate zone) reached its peak ~23 thousand years ago (kya), followed by gradual increase in precipitation (pluvial period) until the following ~16.4 kya dry period. Rainfall increased suddenly again ca. 14.5 kya during the Bølling warming (Oldest and Older Dryas) and was still growing through Allerød. Through Allerød and Younger Dryas, Socotra was exposed to continuous drying, and then precipitation increased suddenly again at the beginning of the Holocene (11.4 kya) (Shakun et al. 2007). During the early Holocene (10.5–9.5 kya), the mean latitudinal position of the Intertropical Convergence Zone expanded rapidly northward and from 7.8 kya to the present it migrated back southward, causing the decrease in summer monsoon intensity and precipitation amount and shortening the rain period duration (Fleitmann et al. 2007).



Figs. 8–11. Endemic flowering plants. 8 – *Aerva revoluta* (Skant); 9 – *Caralluma socotrana* (Wadi Ayhaft); 10 – *Trichodesma scottii* (Skant-Wadi Madar); 11 – *Begonia socotrana* (Skant).

Vegetation. Owing to its complex geomorphology and geological history, the limited area of Socotra holds a remarkably diverse vegetation cover. Král & Pavliš (2006) used satellite data combined with their own field observations and distinguished 19 land-cover classes including e.g. grasslands, shrublands, woodlands, forests and mangroves.

There are about 825 species of vascular plants, 307 of which are regarded as endemic (Figs. 8–13) (Miller & Morris 2004). Fifteen genera are endemic to the archipelago, e.g.

Figs. 12–13. Endemic flowering plants. 12 – *Croton sulcifructus* (Wadi Madar); 13 – *Hypericum scopulorum* (Skant).

Cyanixia Goldblatt & J. C. Manning (Iridaceae), *Nesocrambe* A. G. Mill. (Brassiceae) or *Socotrella* Bruyns & A. G. Miller (Apocynaceae) (Miller & Morris 2004, Goldblatt et al. 2004). Several other genera include high number of endemic taxa due to insular radiations (e.g. *Boswellia* Roxb., *Helichrysum* Gärtn. or *Heliotropium* Linn.) (Orlando & Mies 2004). According to the results of an extensive floristic research conducted by German botanists

14

15

Figs. 14–15. Examples of vegetation cover: Crotonion sulcifructi alliance. 14 – Leucado hagghierensi-Pittosporetum viridiflorum association, Skant Mt. env., forest meadow, 1,450 m a.s.l. (Photo: L. Purchart, 2010); 15 – Trichodesmo scotii-Cephalocrotonetum socotrani association, Wadi Madar, open steppe forest, 1,180–1,230 m a.s.l.

(Kilian & Hubaishan 2006), the vegetation cover of Socotra (so-called Acridocarpo socotrani-Crotonatelia socotrani order) can be further divided in two alliances: (semi)deciduous lowland and low montane communities (i.e. Crotonion socotrani alliance) up to 750–800 m a.s.l., and high montane communities (i.e. Crotonion sulcifructi alliance) above 800–1,500 m a.s.l. (Figs. 14–15) (Kürschner et al. 2006).

Socotran *Dracaena* woodland of mid altitudes with its characteristic flag-species *Dracaena cinnabari* Balf. f. is supposed to be a remnant of the Miocene-Pliocene xerophyllous and sclerophyllous Tethyan flora (Adolt & Pavlis 2004). Although one can thus expect mainly vicariant origin of the endemic plants due to the continental origin of the island, recent studies show that the presence of some endemic taxa (e.g. in the genera *Aerva* Forssk., *Campylanthus* Roth, *Echidnopsis* Hook f. or *Thamnosma* Torr. & Frém) is caused by the long-distance dispersal of their ancestors (Thiv et al. 2006, 2010, 2011; Thiv & Meve 2007). The majority of the flora has East-African or South-Arabian affinities, although some disjunct distributional patterns related for example to Macaronesia are commonly discussed (Andrus et al. 2004).

Insects of the Socotra Archipelago

(Figs. 16–21)

Endemic genera. Endemic species and particularly endemic genera in insular habitats deserve our attention because they could help us, at least to some extent, unveil the history of colonisation and speciation process. In the case of Socotra, the endemic terrestrial forms may be either descendants of species already present on this piece of land before its separation from Oman (speciation by vicariance) or they may have evolved from later colonists that reached the already existing Socotra Archipelago by the over-sea disperse from various mainland sources (speciation caused by founder effect). Natural colonisation of remote islands can happen either by: (1) passive aerial dispersal by wind currents, (2) rafting on organic matter, (3) phoresy on the surface of rafting or flying animals, and (4) active aerial dispersal of winged species (Batelka & Straka 2011). Thus dispersal abilities of insects must also be seriously taken into account when analyzing the origin of island biodiversity (Ashmole & Ashmole 1988). Colonisation of what is now the Socotra Archipelago and what was before its Oligocene-Miocene rifting part of the breaking-up post-Gondwanan landmass was doubtless a complex process. Influence of a substantially increased genetic drift on speciation of the Socotran terrestrial arthropods immediately after the Arabian Sea barrier had developed could be expected because, at least so far, any putative post-rifting connection with Arabia or Africa through possible land-bridges is not evidenced in the reviewed geological literature.

So far altogether 40 genus-level taxa of insects are known exclusively for the archipelago (see Table 1). In addition, three yet undescribed genera of Heteroptera (P. Kment, pers. comm. 2012), one genus of Staphylinidae (Coleoptera) (Hlaváč & Baňař, pers. comm. 2012) and nine genera of Curculionidae (Coleoptera) (Colonnelli, pers. comm. 2012) are known to occur in Socotra as well and will be described in near future, so far making a total of 50 genera and three subgenera in ten insect orders endemic for the Socotra Archipelago. Although their total count shall certainly fluctuate in the future, this remarkable endemism on the genus-taxa level indicates that the insect biota of the main island of the archipelago (see below remark about insects and land-snails in Abd el Kuri) has gone through a long and uninterrupted period of insular isolation. Overall richness corresponds to the estimated antiquity of the island and apparently benefits from preservation of 'one of the oldest forest ecosystem on Earth' (HABROVA et al. 2007).

Genera and subgenera described from the Socotra Archipelago but no longer considered valid or endemic. Nine genera and two subgenera are not mentioned in Table 1 because of the subsequent changes in taxonomy or distribution.

- Monotypic subgenus ***Svatacesta*** Zabransky, 2004 (Coleoptera: Buprestidae: *Strigoptera* Dejean, 1833) from Socotra (ZABRANSKY 2004) is considered invalid by VOLKOVITSH (2012).
- Genus ***Sybrinus*** Gahan, 1900 and its subgenus ***Sokotrosybrinus*** Breuning, 1949 (Coleoptera: Cerambycidae) were established to accommodate a single Socotran species each (GAHAN 1900, BREUNING 1949). As *Sokotrosybrinus* is a junior synonym of *Sybrinus*, which (within current concept) also contains several species from east Africa and Yemen (HÁJEK & KABÁTEK 2012), both names are excluded from the list.
- Genus ***Pseudapis*** Kirby, 1900 (Hymenoptera: Halictidae), described upon one new Socotran species (KIRBY 1900), is no longer endemic to the island having included more than 70 species in the Old World (ASCHER 2012).
- Monotypic Socotran ***Pararhynchomia*** Becker, 1910 (Diptera: Calliphoridae) (BECKER 1910) was subsequently recorded also from east Africa and Oman by DEEMING (1996, spelled there as *Pararhyncomia*).
- Genus ***Goniophthalmus*** Villeneuve, 1910 in BECKER (1910) (Diptera: Tachinidae) is no longer endemic to Socotra having included another species with the Old World distribution (RICHTER & ZHUMANOV 1994).
- ***Crossogaster*** Mayr, 1886 (Hymenoptera: Agaonidae) established by MAYR (1886) as a monotypic Socotran genus is now a speciose Afrotropical genus (VAN NOORT 1994).
- ***Amefrontia*** Hampson, 1899 (= *Palafrontia* Hampson, 1908) (Lepidoptera: Noctuidae) established by Hampson for two Socotran species (HAMPSON 1899, NHM 2012a) now contains also some species from Africa and Arabia (HACKER & SALDAITIS 2010, HACKER et al. 2011).

Three monotypic lepidopteran genera were proposed by REBEL (1907): *Pseudomicra* Rebel, 1907 (Noctuidae) from Abd el Kuri, and *Neosema* Rebel, 1907 (Noctuidae) and *Epimesophleps* Rebel, 1907 (Gelechiidae) from Socotra. None of them is likely to be endemic to the archipelago.

- ***Pseudomicrodes*** Hampson, 1910 (a replacement name for *Pseudomicra* Rebel, 1907 (NHM 2012b)) currently contains nine species distributed elsewhere (NHM 2012b). However HACKER & SALDAITIS (2010) assumed that other 'six [sic!] species ... are not really congeneric' with *Pseudomicrodes* and concept of this genus apparently deserves thorough taxonomic investigation.
- ***Neosema*** is a junior synonym of the speciose genus *Agrotis* Ochsenheimer, 1816 (NHM 2012c).
- Finally, in ***Epimesophleps*** another species was described from Egypt by MEYRICK (1925).

Table 1. List of insect genera/subgenera endemic to the Socotra Archipelago.

Remarks: If not stated otherwise, the particular genus or subgenus has been so far reported from the Socotra Island only. In the Reference(s) column either paper with original description or the latest available review and/or revision of the genus is cited. Given the wide systematic range of the corroborated taxa, it might have happened that some name or some taxonomic change was overlooked in the extensive amount of references.

Order: Family	Endemic genus / subgenus	Sp.	Reference(s)
Collembola: Sminthuridae	*Sokotrasminthurus* Bretfeld, 2005	2	Bretfeld (2005)
Collembola: Bourletiellidae	*Diksamella* Bretfeld, 2005	1	Bretfeld (2005)
Archaeognatha: Machilidae	*Afrochilis* Sturm, 2002	1	Sturm (2002)
Zygentoma: Lepismatidae	*Primacrotelsa* Mendes, 2004	1	Mendes (2004)
Neuroptera: Nemopteridae	*Apocroce* Tjeder, 1974	1	Tjeder (1975)
Neuroptera: Nemopteridae	*Parasicyoptera* Tjeder, 1974	1	Tjeder (1974)
Orthoptera: Acrididae	*Dioscoridus* Popov, 1957	1	Uvarov & Popov (1957)
Orthoptera: Acrididae	*Physemophorus* Krauss, 1907	1	Uvarov & Popov (1957)
Orthoptera: Acrididae	*Oxytruxalis* Dirsh, 1951	1	Dirsh (1951)
Orthoptera: Eumastacidae	*Phaulotypus* Burr, 1899	4	Descamps (1970)
Orthoptera: Eumastacidae	*Socotrella* Popov, 1957	1	Descamps (1970)
Orthoptera: Pyrgomorphidae	*Xenephias* Kevan, 1973	1	Kevan (1973)
Orthoptera: Tettigoniidae	*Pachysmopoda* Karsch, 1886	1	Uvarov & Popov (1957)
Orthoptera: Tettigoniidae	*Phaneroptila* Uvarov, 1957	1	Uvarov & Popov (1957)
Orthoptera: Phalangopsidae	*Socotracris* Desutter-Grandcolas, 2012	1	Desutter-Grandcolas & Felix (2012)
Mantodea: Mantidae	*Teddia* Burr, 1899	1	Burr (1899)
Coleoptera: Cicindelidae	*Socotrana* Cassola et Wranik, 1998	1	Cassola & Wranik (1998)
Coleoptera: Geotrupidae	*Socotrabolbus* Cambefort, 1998	1	Cambefort (1998)
Coleoptera: Scarabaeidae	*Canudema* Lacroix, 1994	1	Lacroix (2002)
Coleoptera: Scarabaeidae	*Canuschiza* Lacroix, 1999	2	Lacroix (2002)
Coleoptera: Scarabaeidae	*Socotraproctus* Král et al., 2012	1	Král et al. (2012)
Coleoptera: Elateridae	*Gahanus* Platia, 2012	1	Platia (2012)
Coleoptera: Elateridae	*Socotrelater* Platia, 2012	1	Platia (2012)
Coleoptera: Tenebrionidae	*Histeromorphus* Kraatz, 1865 (Socotra, Samha, Darsa and Abd el Kuri)	2	Koch (1970), Schawaller (2004)
Coleoptera: Tenebrionidae	*Eusyntelia* Waterhouse, 1881 (Socotra, Samha and Darsa)	6	Koch (1970), Schawaller (2004)
Coleoptera: Tenebrionidae	*Socotropatrum* Koch, 1970 (Socotra and Samha)	2	Koch (1970), Schawaller (2004)
Coleoptera: Tenebrionidae	*Apithesis* Waterhouse, 1881 (Socotra and Samha)	1	Koch (1970), Schawaller (2004)
Coleoptera: Tenebrionidae	*Dioscoridemus* Koch, 1970	1	Koch (1970), Schawaller (2004)
Coleoptera: Tenebrionidae	*Deretus* Gahan, 1900	6	Purchart (2012)
Coleoptera: Tenebrionidae	*Socotralia* Novák, 2007	7	Novák & Purchart (2012)
Coleoptera: Tenebrionidae	*Nanocaecus* Schawaller & Purchart, 2012	1	Schawaller & Purchart (2012)
Coleoptera: Tenebrionidae	*Gahanosis* Penrith, 1983 (as subgenus of *Zophosis* Latreille, 1802) (Abd el Kuri)	1	Penrith (1983)
Coleoptera: Cerambycidae	*Sokothesthes* Adlbauer, 2002 (as subgenus of *Chariesthes* Chevrolat, 1858)	1	Adlbauer (2002)
Coleoptera: Chrysomelidae	*Beenenia* Bezděk, 2012	2	Bezděk (2012)
Coleoptera: Chrysomelidae	*Bezdekaltica* Döberl, 2012	1	Döberl (2012)
Coleoptera: Chrysomelidae	*Erythraella* Zoia, 2012	1	Zoia (2012)
Hymenoptera: Halictidae	*Erythronomioides* Pesenko, 1983 (as subgenus of *Nomioides* Schenck, 1866)	1	Pesenko & Pauly (2005)
Hymenoptera: Megachilidae	*Xenostelis* Baker, 1999	1	Baker (1999)
Lepidoptera: Plutelliidae	*Genostele* Walsingham, 1900	1	Walsingham (1900), Robinson & Sattler (2001)
Lepidoptera: Geometridae	*Mimaplasta* Herbulot, 1993	1	Herbulot (1993)

Endemism on the family-rank level. For the orthopteran genus *Socotrella* Popov, 1957 (in Uvarov & Popov 1957), whose name should not be confused with the vascular plant name *Socotrella* (Apocynaceae), a separate subfamily Socotrellinae was established to accommodate the sole species of the genus owing to its unusual combination of characters (Uvarov & Popov 1957). However, the name is no longer valid as Socotrellinae was synonymised with Thericleinae by Descamps (1970) and there is currently no endemic insect taxon on the family-rank level in the archipelago.

Comparison with other insular biota. Socotra Archipelago with its unique history and natural conditions cannot be directly compared with any other African insular biota. All islands in the eastern Atlantic Ocean are of the volcanic origin, so they have completely different history of colonization and geological events. The same is true for the Comoros Islands and Mascarenes in western part of the Indian Ocean. The only possible candidates for a comparison with Socotra in respect of evolutionary processes are thus granitic islands of Seychelles. Their oceanic isolation from the breaking eastern Gondwana (in their case from the Indian subcontinent) is supposed to be much older (63–64 Mya according to Ganerød et al. 2011), however, until recently they were part of a much larger microcontinent (Seychelles Bank, 55,000 km^2), and their current isolation by the ocean barrier is much stronger (some 1,600 km east of Africa and 3,000 km from India) (Cumberlidge 2008). Even though the four granitic islands of Seychelles are currently much smaller than Socotra (larger Mahé and smaller Praslin, Silhouette and La Digue have a combined area only 454 km^2 (Cumberlidge 2008)) with the highest point slightly above 900 meters in Mahé, they harbour almost the same number of vascular plant species as Socotra (850 flowering plants and ferns); however, only 69 species are supposed to be endemic. Some of them are placed in only 10 endemic, usually monotypic genera (Stoddart 1984).

Surprisingly, Seychelles have much higher rate of endemism in insect genera than Socotra – altogether 215 endemic genera in 10–12 orders (Stoddart 1984). Similarly to Socotra, the most diverse order is Coleoptera with 85 endemic genera out of the total 387 genera present there, but the order and total generic counts of other orders in spite of endemism differ markedly. E.g., Seychelles harbour 24 endemic genera of Diptera, eight genera of Psocoptera and four genera of Trichoptera – all three orders have so far no endemic genus recorded from Socotra. On the contrary, Seychelles has no endemic genus of Neuroptera (Stoddart 1984).

General colonisation model applicable for insular biotas within the frame of long geological time-scale which would include speciation opportunities, immigration and extinction rates, population divergence, host or habitat shifts, anagenetic and phylogenetic changes leading to speciation and diversification and other phenomena is still under hot debate (e.g. Whittaker et al. 2007, 2008; Witt & Maliakal-Witt 2007). It seems that the only way how to test and answer these questions in insular environments is analyses of phylogenies of multiple taxa including insular forms (Whittaker et al. 2007, Witt & Maliakal-Witt 2007). From this point of view we can now only superficially and tentatively comment on the current composition of the Socotran insect biota in comparison with other insular systems or neighbouring continents simply because any such dataset for any insect group including Socotran taxa is not available.

Figs. 16–17. Endemic insects. 16 – *Amitermes socotrensis* Harris, 1954 (Termitidae) – chambers inside the ground nest, Madboh Sirhin plateau, 12.xi.2010; 17 – *Azuragrion granti* (McLachlan, 1903) (Coenagrionidae) – mating pair, Ayhaft, 7-8.xi.2010 (Photo J. Hájek).

Figs. 18–21. Endemic insects. 18 – *Pachysmopoda abbreviata* (Taschenberg, 1883) (Tettigoniidae), female, Madboh Sinhin plateau, 12.xi.2010; 19 – *Julodis clouei* Buquet, 1843 (Buprestidae), Noged plain, 10.xi.2010 (Photo J. Hájek); 20 – *Mallodon arabicum* Buquet, 1843 (Cerambycidae), male, Firmihin plateau, 16.xi.2010; 20 – *Acraea neobule socotrana* Rebel, 1907 (Nymphalidae), mating pair, Skant, 12.xi.2010.

Origin and different composition of fauna among Socotran islands. Composition and presence of some insect families or for example land snails, whose biological requirements and colonisation history are at least to some extent comparable with those of some groups of insect, may reflect important events in geological history of Socotra. Predominant Pimeliinae (Coleoptera: Tenebrionidae) may indicate that the fauna is older than Miocene because this subfamily is supposed to be placed phylogenetically more basally contrary to e.g. Tenebrioninae which is predominant in the Madeira Archipelago (Schawaller 2006). Some terrestrial invertebrate groups may also reflect possible different geological history of Socotra and Abd el Kuri. Differences in composition of the Tenebrionidae fauna on both islands (Schawaller 2006) or in distribution of land snails of the genera *Zootecus* Westerlund, 1887 (Neubert 2003: 158–159), *Achatinelloides* G. Nevill, 1878 (Neubert 2005: 248) and *Guillainia* Crosse, 1884, *Lithidion* Gray, 1850 and *Platypoma* Neubert, 2009 (Neubert 2009: 122) are supposed to be result of independent separation of Socotra and Abd el Kuri from the Arabian Peninsula.

Absence of single-island endemic insect genera in Samha and Darsa and only one single-island endemic subgenus presented in Abd el Kuri (Table 1), may be result of some sudden bottleneck-event after which the insect biota of these islands (contrary e.g. to the land-snails in Abd el Kuri) has never fully recovered again, rather than indicate a unique geological history. It is of interest that, in comparison, even some of the smallest and the most arid islets of the Madeira Archipelago, like Porto Santo (one islet with several allied rocks, 43 km^2 in total), Desertas (three islets, 13.5 km^2 in total) and Selvagens (several islets and fragment rocks, 2.73 km^2 in total), keep remarkable single-island endemic insect genera until their almost last subaerial stage and despite irreversible destruction of their habitats by man (Becker 1992, Borges et al. 2008).

Gaps in our knowledge of Socotran insect fauna. Endemic insect genera and their radiations are often considered flag-ships of insular biodiversity and prime examples of adaptations to the natural conditions ruling in their insular habitat (e.g. Geisthardt 1995, Gressitt 1978, Ritchie & Macías Garcia 2005). However, in this regard our information about Socotran insect fauna is still regrettably scarce. Five endemic genera of a total number of 40 generic rank taxa were described simultaneously with this contribution (Table 1), and the corroborated families still represent only part of the Socotran insect biota. Until very recently our knowledge of some endemic genera on a species-level was not much better either. Of the six known species of endemic *Deretus* Gahan, 1900, five species (i.e. 83 %) were described in the years 2004 and 2012 (Purchart 2012) and all seven species of the endemic *Socotralia* Novák, 2007 were described in 2007 and 2012 (Novák & Purchart 2012). All these genera and species can be identified by common methods, no special techniques like molecular barcoding or statistic morphometry are necessary. Neither any collecting technique unknown in the past has to be used to discover the species. Also, it should be mentioned that for none of the described Socotran insect endemic genera either molecular or morphological phylogenetic analysis of its particular group has been performed until now.

Although the first attempts to corroborate material collected in Socotra are dated back to the second half of the 19^{th} century, the fact is that the previous research works resulted in only limited number of publications in the 20^{th} century altogether insufficiently covering the

Socotran biodiversity heritage. We may speculate about the reasons, the most dominant role among which undoubtedly played inaccessibility of the archipelago, especially between years 1968–1990 due to the political situation in Yemen (Orlando & Mies 2004, Scholte et al. 2011). It is therefore no surprise that from all those above listed genera (subgenera) endemic to the Socotra Archipelago, 50 % have been described during the last 20 years, i.e. within the period which began soon after the Socotra had been opened up to foreign visitors. Lack of skilled taxonomists with knowledge of the complex biogeography in some groups (Löbl & Leschen 2005) or insufficient distribution of material collected during previous surveys may also have had negative influence on low number of elaborated outputs.

Conclusions

Nature conservation issues. Major threats to until now well-preserved natural habitats of the Socotra Island are the increase in tourism causing road and infrastructure development, increasing immigration and import of goods from mainland Yemen, and pollution by irreducible waste around settlements (Damme & Banfield 2011). Countryside is exposed to overgrazing by increasing herds of goats and other livestock (Scholte et al. 2011; shortly after the rain period, we saw some areas almost completely devoid of herbs and grass due to intensive grazing) followed by subsequent aridisation and soil erosion (e.g. cattle trails on Skant). Another problem is a woodland fragmentation and commercial collection of fire wood (Orlando & Mies 2004; e.g. we saw bundles of collected wood (for commercial purposes?) by the road from Hadibo to Shibhon).

Giving an example, *Dracaena* populations, which are growing between 300–1,500 m a.s.l., are one of the well known cases of Socotra's conservation issues. Desintegration and decline of *Dracaena* woodlands is expected within some 30–77 years. As the available data indicate, overmaturity and insufficient regeneration of *Dracaena* growths happened either because of the change of climatic conditions or because of overgrazing by the increasing population of livestock (Adolt & Pavlis 2004). As the number of goats does no longer depend on fluctuation of natural conditions due to human support (drought anomalies usually caused livestock losses in the past (Scholte et al. 2011)), both grazing and prolonged drought periods represent almost impenetrable barrier for the recovery of vegetation, and *Dracaena* seedlings show extremely low survival capacity in open habitats if they are not protected against goats (Attore et al. 2007, Habrova et al. 2009). Impact on the arthropod fauna restricted to this type of habitat could be fatal. In Firmihin *Dracaena* forest, we found at least three endemic beetle species associated exclusively with the mature *Dracaena* trees: *Corticeus socotranus* Purchart & Schawaller, 2012, *Deretus necopinatus* Purchart, 2012 (both Tenebrionidae; Purchart 2012, Purchart & Schawaller 2012) and one undescribed species of *Mechistocerus* Fauvel, 1863 (Curculionidae; Colonnelli, pers. comm.). Some other endemic beetles have been found associated with the very same old trunks: e.g. the large prionid *Mallodon arabicum* Buquet, 1843 (Cerambycidae), scarabaeid *Oryctes vicinus* Gahan, 1900 (Scarabaeidae), *Calais sulcicollis* (Gahan, 1900) (Elateridae) and others (J. Batelka, pers. observ.). All these species are therefore endangered as well although they are also able to develop in other trees in the same habitat (e.g. *Boswellia*). Suddenly, *Boswellia* trees, especially those belonging to the ground-rooted group, also show poor regeneration and may be subject to a progressive decline because of overgrazing, similarly to *Dracaena* (Attore et al. 2011). As a memento we can remind of another Tertiary survivor, *Dracaena draco* (L.) from the Macaronesian islands, which had been completely brought to extinction on some islands (or nearly so on others) within several hundred years after colonisation by Europeans (Marrero et al. 1998, Sziemer 2010: 75–76). Putative insect fauna associated with these disappeared *Dracaena* forests in the Macaronesia archipelagos had not been recorded before its decline and remaining scattered solitary trees (often cultivated) no longer support any specific fauna.

Last but not least, native organisms are exposed to competition with numerous introduced alien and sometimes highly invasive species (Damme & Banfield 2011). Senan et al. (2010) reported in Socotra presence of 87 alien plant species with invasive potential which might to a large extent replace the indigenous host plants of herbivore insects. Introduced birds, rodents or livestock could be also serious direct (predation) or indirect (overgrazing of host-plants) threat for some arthropods (e.g. Peck 2006: 58).

Future prospects of insect surveys. Socotra represents an island ecosystem with long and complex geological and ecological history. Various organisms both of vicariant and dispersal origin have found here suitable shelter against the world of turbulent changes on near continents and many of them have had even enough time to develop into remarkable endemic forms. However this preserved 'Lost World' is changing rapidly.

As it was highlighted above, insect communities are in general endangered by changes and degradation of their habitats but not by sampling or collecting whatsoever. Giving just one example from Socotra (although concerning a non-endemic species): large and hard-to-overlook Afrotropical dragonfly *Rhyothemis semihyalina* (Desjardins, 1832) is supposed to be locally extinct in the island due to the waste accumulation and pollution of its former water habitats in Hadibo plain (Damme & Banfield 2011: 39). In a similar way, many endemic species may disappear before they are discovered. While endangered plants could be preserved in botanical gardens and nurseries or their seeds could be stored in a seed bank, for insects the only chance to survive is the continuous preservation of localities they inhabit.

It should be noted here, that almost all so far published papers about Socotran insects were written from the purely taxonomical perspective, often represented by sole descriptions of particular taxon without any other biological information (e.g. for the endemic genera *Mimaplasta* or *Xenostelia* the only available data is a holotype female of each genus labeled 'east Socotra, 500m, 5–25.i.1993' and 'Socotra' respectively). This is hardly more than a starting point. Little or nothing is known about phylogeny, biology, genetic variability or ecological fitting of the so far described and recorded species. More complete knowledge and understanding of the biology of the species are undoubtedly essential for any future conservation efforts focused on the Socotran insect biodiversity. Establishing of a long-term arthropod survey similar to those which have been conducted already e.g. in the United Arab Emirates, to name the most influential biodiversity project ever established in the Arabian Peninsula (Harten 2008, 2009, 2010, 2011), or in Galápagos Islands, to give an insular example (Peck 2006), is highly recommended for documentation of insect fauna of Socotra and adjacent islands.

Acknowledgements

I am obliged to Luboš Purchart and Jan Bezděk (both Mendel University, Brno) for the possibility to join the Socotra research project. I thank Martin Fikáček, Jiří Hájek (both National Museum, Prague), Antonius van Harten (Portugal), Mike Thiv (State Museum of Natural History, Stuttgart, Germany), David Král (Charles University, Praha), Jan Bezděk and Luboš Purchart who kindly commented upon early version of the manuscript. Martin Fikáček, Jan Bezděk, Antonius van Harten and Jiří Hájek also helped obtain numerous references and Luboš Purchart created the maps. Mike Thiv provided identification of some figured endemic plants.

References

ADLBAUER K. 2002: A new Chariesthes species from the Socotra-islands and transfer of another Tragocephalini into the genus Keirochariesthes Teocchi, 1989 (Coleoptera, Cerambycidae, Lamiinae). *Entomologia Africana* **7**: 19–22.

ADOLT R. & PAVLIS J. 2004: Age structure and growth of Dracaena cinnabari populations on Socotra. *Trees* **18**: 43–53.

ANADÓN P. & ZAMARREÑO I. 1981: Paleogene nonmarine algal deposits of the Ebro Basin, Northeastern Spain. Pp. 140–154. In: MONTY C. (ed.): *Phanerozoic stromatolites. Case histories.* Springer Verlag, Berlin, Heidelberg, New York, 249 pp.

ANDRUS N., TRUSTY J., SANTOS-GUERRA A., JANSEN R. K. & FRANCISCO-ORTEGA J. 2004: Using molecular phytogenies to test phytogeographical links between East/South Africa-Southern Arabia and the Macaronesian Islands – a review, and the case of Vierea and Pulicaria section Vieraeopsis (Asteraceae). *Taxon* **53**: 333–346.

ASCHER J. 2012: Pseudapis – Discover Life. http://www.discoverlife. org/mp/20q?search= Pseudapis. (Accessed 13.iii.2012).

ASHMOLE N. P. & ASHMOLE M. J. 1988: Insect dispersal on Tenerife, Canary Islands: high altitude fallout and seaward drift. *Arctic and Alpine Research* **20**: 1–12.

ASHMOLE N. P. & ASHMOLE M. J. 2004: *Guide to invertebrates of Prosperous Bay Plain, St Helena and illustrated account of species found on the Eastern Arid Area (EAA), including Prosperous Bay Plain, Holdfast Tom and Horse Point Plain.* Peebles, Kidston Mill, 66 pp. http://209.85.129.104 /search?q=cache:Q4UxqB6f9psJ: kidstonmill.org.uk /docs/PBP. (Accessed 11.ii.2010).

ATTORRE F., FRANCESCONI F., TALEB N., SCHOLTE P., SAEED A., ALFO M. & BRUNO F. 2007: Will dragonblood survive the next period of climate change? Current and future potential distribution of Dracaena cinnabari (Socotra, Yemen). *Biological Conservation* **138**: 430–439.

ATTORRE F., TALEB N., DE SANCTIS M., FARCOMENI A., GUILLET A. & VITALE M. 2011: Developing conservation strategies for endemic tree species faced with time and data constraints: Boswellia spp. on Socotra (Yemen). *Biodiversity Conservation* **20**: 1483–1499.

BAKER D. B. 1999: On new stelidine bees from S.W. Asia and N.W. Africa, with a list of the Old-World taxa assigned to the genus Stelis Panzer, 1806 (Hymenoptera, Apoidea, Megachilidae). *Mitteilungen aus dem Museum für Naturkunde in Berlin, Deutsche Entomologische Zeitschrift* **46**: 231–242.

BATELKA J. & STRAKA J. 2011: Ripiphorus caboverdianus sp. nov. – the first ripiphorid record from the Macaronesian volcanic islands (Coleoptera: Ripiphoridae: Ripiphorinae). *Zootaxa* **2792**: 51–62.

BECKER P. 1992: Colonization of islands by carnivorous and herbivorous Heteroptera and Coleoptera: effects of island area, plant species richness, and 'extinction' rates. *Journal of Biogeography* **19**: 163–171.

BECKER Th. 1910: Dipteren aus Südarabien und von der Insel Sokótra. *Denkschriften der Kaiserlichen Akademie der Wissenschaften*, *Mathematisch-Naturwissenschaftliche Klasse* **71(2)**: 1–30. [Published as reprint in 1910, re-published in the journal in 1931 with pagination 131–160].

BEYDOUN Z. R. & BICHAN H. R. 1970: The geology of Socotra, Gulf of Aden. *Quarterly Journal of the Geological Society London* **125**: 413–446.

BEZDĚK J. 2012: Galerucinae (Coleoptera: Chrysomelidae) of Socotra Island, with a review of taxa recorded from Yemen. Pp. 403–428. In: HÁJEK J. & BEZDĚK J. (eds.): Insect biodiversity of the Socotra Archipelago. *Acta Entomologica Musei Nationalis Pragae* **52 (supplementum 2)**: i–vi + 1–557.

BIRSE A. C. R., BOTT W. F., MORRISON J. & SAMUEL M. A. 1997: The Mesozoic and Tertiary tectonic evolution of the Socotra area, eastern Gulf of Aden, Yemen. *Marine and Petroleum Geology* **14**: 675–683.

BORGES P. A. V., ABREU C., AGUIAR A. M. F., CARVALHO P., JARDIM R., MELO I., OLIVEIRA P., SÉRGIO C., SERRANO A. R. M. & VIEIRA P. 2008: *A list of the terrestrial fungi, flora and fauna of Madeira and Selvagens archipelagos*. Direcção Regional do Ambiente da Madeira and Universidade dos Açores, Funchal and Angra do Heroísmo, 440 pp.

BRETFELD G. 2005: Collembola Symphypleona (Insecta) from the Republic of Yemen. Part 2: samples from the Isle of Socotra. *Abhandlungen und Berichte des Naturkundemuseums Görlitz* **77**: 1–56.

BREUNING S. 1949: Notes systématiques sur les lamiaires (Coleoptera Cerambycidae). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* **25(38)**: 1–32.

BURR M. 1899: [The expedition to Sokotra.] VIII. Descriptions of two new genera and six new species of Orthoptera. *Bulletin of the Liverpool Museums* **2**: 42–45.

CAMBEFORT Y. 1998: A new genus of Bolboceratidae from Socotra (Coleoptera, Scarabaeoidea). Un nouveau genre et une nouvelle espèce de Bolboceratidae de Socotra (Coleoptera, Scarabaeoidea). *Bulletin de la Société Entomologique de France* **103**: 443–446.

CASSOLA F. & WRANIK W. 1998: A remarkable new tiger beetle from Socotra Island, Republic of Yemen (Coleoptera, Cicindelidae). *Deutsche Entomologische Zeitschrift* **45**: 265–268.

CUMBERLIDGE N. 2008: Insular species of Afrotropical freshwater crabs (Crustacea: Decapoda: Brachyura: Potamonautidae and Potamidae) with special reference to Madagascar and the Seychelles. *Contributions to Zoology* **77**: 71–81.

D'ACREMONT E., LEROY S., MAIA M., GENTE P. & AUTIN J. 2010: Volcanism, jump and propagation on the Sheba ridge, eastern Gulf of Aden: segmentation evolution and implications for oceanic accretion processes. *Geophysical Journal International* **180**: 535–551.

DAMME K. VAN & BANFIELD L. 2011: Past and present human impacts on the biodiversity of Socotra Island (Yemen): implications for future conservation. *Zoology in the Middle East, Supplementum* **3**: 31–88.

DEEMING J. C. 1996: The Calliphoridae (Diptera: Cyclorrhapha) of Oman. *Fauna of Saudi Arabia* **15**: 264–279.

DEL-ARCO M., PÉREZ-DE-PAZ P. L., ACEBES J. R., GONZÁLEZ-MANCEBO J. M., REYES-BETANCORT J. A., BERMEJO J. A., DE-ARMAS S. & GONZÁLEZ R. 2006: Bioclimatology and climatophilous vegetation of Tenerife (Canary Islands). *Annales Botanici Fennici* **43**: 167–192.

DESCAMPS M. 1970: Les Eumastacidae de Socotra (Orth.). *Bulletin de la Société Entomologique de France* **75**: 123–134.

DESENDER K. & BAERT L. 1997: Conservation of terrestrial Arthropods on Easter Island as exemplified by the beetle fauna. *Conservation Biology* **11**: 836–838.

DESUTTER-GRANDCOLAS L. & FELIX R. P. W. H. 2012: Socotracris kleukersi n. gen. n. sp., a new troglobitic cricket from Socotra (Yemen) (Orthoptera: Grylloidea, Phalangopsidae). *Zootaxa* **3252**: 57–65.

DIRSH V. M. 1951: Revision of the group Truxales (Orthoptera, Acrididae). *EOS, Revista Española de Entomologia*, **Tomo extraordinario 1950**: 119–247.

DÖBERL M. 2012: Alticinae (Coleoptera: Chrysomelidae) of Socotra Island. Pp. 429–447. In: HÁJEK J. & BEZDĚK J. (eds.): Insect biodiversity of the Socotra Archipelago. *Acta Entomologica Musei Nationalis Pragae* **52 (supplementum 2)**: i–vi + 1–557.

FAY M. F., SWENSEN S. M. & CHASE M. W. 1997: Taxonomic affinities of Medusagyne oppositifolia (Medusagynaceae). *Kew Bulletin* **52**: 111–120.

FERNÁNDEZ-PALACIOS J. M., DE NASCIMENTO L., OTTO R., DELGADO J. D., GARCÍA-DEL-REY E., ARÉVALO J. R. & WHITTAKER R. J. 2011: A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests. *Journal of Biogeography* **38**: 226–246.

FLEITMANN D., BURNS S. J., MANGINI A., MUDELSEE M., KRAMERS J., VILLA I., NEFF U., AL-SUBBARY A. A., BUETTNER A., HIPPLER D. & MATTER A. 2007: Holocene ITCZ and Indian monsoon dynamics recorded in stalagmites from Oman and Yemen (Socotra). *Quaternary Science Reviews* **26**: 170–188.

FOURNIER M., HUCHON P., KHANBARI K. & LEROY S. 2007: Segmentation and along-strike asymmetry of the passive margin in Socotra, eastern Gulf of Aden: Are they controlled by detachment faults? *Geochemistry Geophysics Geosystems* **8**: 1–17.

GAHAN C. J. 1900: [The expedition to Sokotra. XI.] Descriptions of the new genera and species of Coleoptera. *Bulletin of the Liverpool Museums* **3**: 8–13.

GANERØD M., TORSVIK T. H., HINSBERGEN D. J. J. VAN, GAINA C., CORFU F., WERNER S., OWEN-SMITH T. M., ASHWAL L. D., WEBB S. J. & HENDRIKS B. W. H. 2011: Palaeoposition of the Seychelles microcontinent in relation to the Deccan Traps and the Plume Generation Zone in Late Cretaceous–Early Palaeogene time. Pp. 229–252. In: HINSBERGEN D. J. J. VAN, BUITER S. J. H., TORSVIK T. H., GAINA C. & WEBB S. J. (eds.): The formation and evolution of Africa: a synopsis of 3.8 Ga of Earth history. *Geological Society, London, Special Publications* **357**: 378 pp.

GEEST P. DE & members of the Soqotra Karst Project 2005: Revealing the caves of Soqotra island (Yemen), the Soqotra Karst Project (2000–2005). P. 669. In: *Oral presentation at the 14th International Congress of Speleology, Abstract Book W2*. Kalamos, Greece.

GEISTHARDT M. 1995: Die Gattung Dinas von den Kapverden und Beschreibung einer neuen Art (Coleoptera: Curculionidae: Brachyderinae). *Mitteilungen des Internationalen Entomologischen Vereins* **20**: 23–29.

GIRDLER R. W. & STYLES P. 1978: Seafloor spreading in the western Gulf of Aden. *Nature* **271**: 615–617.

GOLDBLATT P., MANNING J. C., DAVIES J., SAVOLAINEN V. & REZAI S. 2004: Cyanixia, a new genus for the Socotran endemic Babiana socotrana (Iridaceae–Crocoideae). *Edinburgh Journal of Botany* **60**: 517–532.

GRESSITT J. L. 1978: Evolution of the endemic Hawaiian cerambycid beetles. *Pacific Insects* **18**: 137–167.

HABROVA H., CERMAK Z. & PAVLIS J. 2009: Dragon's blood tree – Threatened by overmaturity, not by extinction: Dynamics of a Dracaena cinnabari woodland in the mountains of Soqotra. *Biological Conservation* **142**: 772–778.

HABROVA H., KRAL K. & MADERA P. 2007: The weather pattern in one of the oldest forest ecosystems on Earth – Dragon's blood tree forest (Dracaena cinnabari) on Firmihin – Soqotra Island. 10 pp. In: ROŽNOVSKÝ J., LITSCHMANN T. & VYSKOT I. (eds.): *Klima lesa. Sborník referátů z mezinárodní vědecké konference. Křtiny 11.–12.4.2007*. Česká bioklimatologická společnost, Praha, 44 pp.

HACKER H. H., HOPPE H., LEHMANN L. & STADIE D. 2011: Neue Noctuidae-Arten aus Südarabien und Ostafrika (Lepidoptera). *Esperiana* **16**: 233–253, 310–313.

HACKER H. H. & SALDAITIS A. 2010: Noctuidae of the Socotra Archipelago (Yemen) with notes on the fauna of the southern Arabian Peninsula (Lepidoptera, Noctuoidea). *Esperiana Memoir* **5**: 172–241, 510–521.

HÁJEK J. & KABÁTEK P. 2012: Synonymical notes on the genus Sybrinus from Socotra Island (Coleoptera: Cerambycidae: Lamiinae). Pp. 365–372. In: HÁJEK J. & BEZDĚK J. (eds.): Insect biodiversity of the Socotra Archipelago. *Acta Entomologica Musei Nationalis Pragae* **52 (supplementum 2)**: i–vi + 1–557.

HAMPSON G. F. 1899: [The expedition to Sokotra.] VI. Descriptions of one new genus and fourteen new species of moths. *Bulletin of the Liverpool Museums* **2**: 35–39.

HANSKI I., KOIVULEHTO H., CAMERON A. & RAHAGALALA P. 2007: Deforestation and apparent extinctions of endemic forest beetles in Madagascar. *Biology Letters* **3**: 344–347.

HARTEN A. VAN (ed.) 2008: *Arthropod fauna of the United Arab Emirates, Volume 1*. Multiply Marketing Consultancy Services, Abu Dhabi, 754 pp.

HARTEN A. VAN (ed.) 2009: *Arthropod fauna of the United Arab Emirates, Volume 2*. Multiply Marketing Consultancy Services, Abu Dhabi, 786 pp.

HARTEN A. VAN (ed.) 2010: *Arthropod fauna of the United Arab Emirates, Volume 3*. Multiply Marketing Consultancy Services, Abu Dhabi, 700 pp.

HARTEN A. VAN (ed.) 2011: *Arthropod fauna of the United Arab Emirates, Volume 4*. Multiply Marketing Consultancy Services, Abu Dhabi, 816 (+ 16) pp.

HERBULOT C. 1993: Mimaplasta canui, n. gen. et n. sp. de l'île de Socotra (Lepidoptera Geometridae Geometrinae). *Bulletin de la Société Entomologique de Mulhouse* **1993**: 49–50.

KEVAN D. K. McE. 1973: A new genus of Pyrgomorphidae (Acridoidea: Orthoptera) from the Island of Socotra. *Canadian Entomologist* **105**: 1169–1173.

KILIAN N. & HUBAISHAN M. A. (eds.) 2006: Biodiversity of Socotra Forests, Woodlands and Bryophyte. *Englera* **28**: 1–175.

KIRBY W. F. 1900: [The expedition to Sokotra. XII.] Descriptions of the new species of Hymenoptera. *Bulletin of the Liverpool Museums* **3**: 13–24.

KOCH C. 1970: Die Tenebrioniden (Coleoptera) des Archipels von Socotra. *Monitore Zoologica Italiano, Nuova Serie* **Supplemento III**: 69–132.

KRÁL D., SEHNAL R. & BEZDĚK A. 2012: Tanyproctini (Coleoptera: Scarabaeidae: Melolonthinae) of Socotra Island. Pp. 153–182. In: HÁJEK J. & BEZDĚK J. (eds.): Insect biodiversity of the Socotra Archipelago. *Acta Entomologica Musei Nationalis Pragae* **52 (supplementum 2)**: i–vi + 1–557.

KRÁL K. & PAVLIŠ J. 2006: The first detailed land-cover map of Socotra Island by Landsat/ETM+ data. *International Journal of Remote Sensing* **27**: 3239–3250.

KRAUSE D. W., O'CONNOR P. M., ROGERS K. C., SAMPSON S. D., BUCKLEY G. A. & ROGERS R. R. 2006: Late Cretaceous terrestrial vertebrates from Madagascar: implications for Latin American biogeography. *Annals of the Missouri Botanical Garden* **93**: 178–208.

KÜRSCHNER H., HEIN P., KILIAN N. & HUBAISHAN M. A. 2006: Diversity and zonation of the forests and woodlands of the mountains of northern Socotra, Yemen. Pp. 11–55. In: KILIAN N. & HUBAISHAN M. A. (eds.): Biodiversity of Socotra forests, woodlands and bryophyte. *Englera* **28**: 1–175.

LACROIX M. 2002: Melolonthidae (Coleoptera: Scarabaeoidea) of Socotra Island, Yemen. *Fauna of Arabia* **19**: 399–414.

LÖBL I. & LESCHEN R. A. B. 2005: Demography of coleopterists and their thoughs on DNA barcoding and the phylocode, with commentary. *Coleopterists Bulletin* **59**: 284–292.

MACHADO A. 1985: Hypothesis on the reasons for the decline of the large lizards in the Canary Islands. *Bonner Zoologische Beiträge* **36**: 563–575.

MARRERO A., ALMEIDA S. R. & MARTÍN-GONZÁLEZ M. 1998: A new species of the wild Dragon Tree, Dracaena (Dracaenaceae) from Gran Canaria and its taxonomic and biogeographic implications. *Botanical Journal of Linnean Society* **128**: 291–314.

MATTHEWS D. H., WILLIAMS C. & LAUGHTON A. S. 1967: Mid-ocean ridge in the mouth of the Gulf of Aden. *Nature* **215**: 1052–1053.

MAYR G. 1886: Feigeninsecten. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* **35** (1885): 147–250.

MENDES L. F. 2004: Zygentoma (Insecta) from the Socotra Archipelago. *Fauna of Arabia* **20**: 357–398.

MEYRICK E. 1925: Descriptions of twenty-four new Egyptian Microlepidoptera. *Bulletin de la Société Royale Entomologique d'Egypte* **9**: 206–219.

MILLER A. G. & MORRIS M. 2004: *Ethnoflora of the Soqotra Archipelago.* Royal Botanic Garden, Edinburgh, 759 pp.

MIRALLES A., VASCONCELOS R., PERERA A., HARRIS D. J. & CARRANZA S. 2011: An integrative taxonomic revision of the Cape Verdean skinks (Squamata, Scincidae). *Zoologica Scripta* **40**: 16–44.

MORRISON J., BIRSE A., SAMUEL M. A., RICHARDSON S. M., HARBURY N. & BOTT W. F. 1997: The Cretaceous sequence stratigraphy of the Socotran platform, the Republic of Yemen. *Marine and Petroleum Geology* **14**: 685–699.

NAGY Z. T., JOGER U., WINK M., GLAW F. & VENCES M. 2003: Multiple colonization of Madagascar and Socotra by colubrid snakes: evidence from nuclear and mitochondrial gene phylogenies. *Proceedings of the Royal Society B, Biological Sciences* **270**: 2613–2621.

NEUBERT E. 2003: The continental malacofauna of Arabia and adjacent areas, II. The genus Zootecus Westerlund 1887. (Gastropoda: Pulmonata: Subulinidae). *Archiv für Molluskenkunde* **132**: 153–160.

NEUBERT E. 2005: The continental malacofauna of Arabia and adjacent areas, V. Revision of the family Cerastidae in the Soqotran Archipelago, II: The genera Achatinelloides G. Nevill 1878 and Microscintilla Neubert 2002, with description of a new genus and species (Gastropoda: Pulmonata: Cerastidae). *Archiv für Molluskenkunde* **134**: 223–259.

NEUBERT E. 2009: The continental malacofauna of Arabia and adjacent areas: VI. Pomatiidae of Arabia, Socotra and Northeast Africa, with descriptions of new genera and species (Gastropoda: Caenogastropoda: Littorinoidea). *Fauna of Arabia* **24**: 47–127.

NHM 2012a: PALAFRONTIA – Butterflies and Moths of the World. http://www.nhm.ac.uk/research-curation/research/projects/butmoth/search/GenusDetails... (Accessed 14.iii.2012).

NHM 2012b: PSEUDOMICRODES – Butterflies and Moths of the World. http://www.nhm.ac.uk/research-curation/research/projects/butmoth/search/GenusDetails... (Accessed 22.iii.2012).

NHM 2012c: NEOSEMA – Butterflies and Moths of the World. http://www.nhm.ac.uk/research-curation/research/projects/butmoth/search/GenusDetails... (Accessed 22.iii.2012).

NOVÁK V. & PURCHART L. 2012: New species of the genus Socotralia and first record of the genus Alogista from Socotra Island (Coleoptera: Tenebrionidae: Alleculinae). Pp. 323–336. In: HÁJEK J. & BEZDĚK J. (eds.): Insect biodiversity of the Socotra Archipelago. *Acta Entomologica Musei Nationalis Pragae* **52 (supplementum 2)**: i–vi + 1–557.

OLSON S. L. 1973: Evolution of the Rails of the South Atlantic Islands (Aves: Rallidae). *Smithsonian Contributions to Zoology* **152**: 1–53.

ORLANDO G. & MIES B. 2004: Vanishing forests and sustainable development of an arid island. Soqotra (Yemen): an example. *Insula, International Journal of Island Affairs* **13**: 95–98.

PALKOVACS E. P., MARSCHNER M., CIOFI C., GERLACH J. & CACCONE A. 2003: Are the native giant tortoises from the Seychelles really extinct? A genetic perspective based on mtDNA and microsatellite data. *Molecular Ecology* **12**: 1403–1413.

PECK S. B. 2006: *The Beetles of the Galápagos Islands, Ecuador: Evolution, ecology and diversity (Insecta: Coleoptera).* National Research Council of Canada Research Press, Ottawa, xiii + 313 pp.

PENRITH M.-L. 1983: Revision of the Zophosini (Coleoptera: Tenebrionidae). Part 8. The Palaearctic species group of the subgenus Oculosis Penrith, the subgenus Cheirosis Deyrolle, and a monotypical subgenus from Socotra. *Cimbebasia, Series A* **6**: 369–384.

PESENKO Yu. A. & PAULY A. 2005: Monograph of the bees of the subfamily Nomioidinae (Hymenoptera Halictidae) of Africa (excluding Madagascar). *Annales de la Société Entomologique de France (Nouvelle Série)* **41**: 129–236.

PLATIA G. 2012: Contribution to the knowledge of the click-beetles from the Socotra Island (Yemen) (Coleoptera Elateridae). *Arquivos Entomolóxicos* **7**: 129–153.

PURCHART L. 2012: Biodiversity research of darkling beetles on Socotra Island. Part I. The genus Deretus Gahan, 1900 (Coleoptera: Tenebrionidae). *Zootaxa* **3153**: 57–68.

PURCHART L. & SCHAWALLER W. 2012: A new species of the genus Corticeus (Coleoptera: Tenebrionidae) from Socotra Island. Pp. 315–322. In: HÁJEK J. & BEZDĚK J. (eds.): Insect biodiversity of the Socotra Archipelago. *Acta Entomologica Musei Nationalis Pragae* **52 (supplementum 2)**: i–vi + 1–557.

REBEL H. 1907: Zoologische Ergebnisse der Expedition der Kaiserlichen Akademie der Wissenschaften nach Südarabien und Sokótra im Jahre 1898/99. Lepidopteren. *Denkschriften der Kaiserlichen Akademie der Wissenschaften. Mathematisch-naturwissenschaftliche Klasse* **71(2)**: 1–100 [published as reprint in 1907, re-published in journal in 1931 with pagination 31–130].

RICHTER V. A. & ZHUMANOV B. 1994: The tachinid genus Goniophthalmus new to the fauna of Middle Asia (Diptera: Tachinidae). *Zoosystematica Rossica* **3**: 146.

RITCHIE M. G. & MACÍAS GARCIA C. 2005: Explosive speciation in a cricket. *Heredity* **95**: 5–6.

ROBINSON G. S. & SATTLER K. 2001: Plutella in the Hawaiian Islands: Relatives and host-races of the Diamondback moth (Lepidoptera: Plutellidae). *Bishop Museum Occasional Papers* **67**: 1–27.

SAMUEL M. A., HARBURY N. A., BOTT W. F. & THABET A. M. 1997: Field observations from the Socotran Platform: their interpretation and correlation to Southern Oman. *Marine and Petroleum Geology* **14**: 661–672.

SCHAWALLER W. 2004: New species and records of Tenebrionidae (Coleoptera) from the Socotra Archipelago. *Fauna of Arabia* **20**: 439–458.

SCHAWALLER W. 2006: Darkling beetles (Coleoptera: Tenebrionidae) from Madeira and Socotra: a comparison of the faunas. *Cahiers Scientifiques* (Lyon) **10**: 91–93.

SCHAWALLER W. & PURCHART L. 2012: Nanocaecus hlavaci gen. & sp. nov. – first record of the tribe Gnathidiini (Coleoptera: Tenebrionidae: Diaperinae) from the Socotra Archipelago. Pp. 303–314. In: HÁJEK J. & BEZDĚK J. (eds.): Insect biodiversity of the Socotra Archipelago. *Acta Entomologica Musei Nationalis Pragae* **52 (supplementum 2)**: i–vi + 1–557.

SCHOLTE P., AL-OKAISHI A. & SAED SULEYMAN A. 2011: When conservation precedes development: a case study of the opening up of the Socotra archipelago, Yemen. *Oryx* **45**: 401–410.

SENAN A. S., SOMASHEKAR R. K., ATTORRE F., TALEB N. & BRUNO F. 2010: Exotic species of Socotra Island, Yemen: A first contribution. *Annali di Botanica* **2010**: 1–11.

SCHOLTE P. & GEEST P. DE 2010: The climate of Socotra Island (Yemen): A first-time assessment of the timing of the monsoon wind reversal and its influence on precipitation and vegetation patterns. *Journal of Arid Environments* **74**: 1507–1515.

SHAKUN J. D., BURNS S. J., FLEITMANN D., KRAMERS J., MATTER A. & AL-SUBARY A. 2007: A high-resolution, absolute-dated deglacial speleothem record of Indian Ocean climate from Socotra Island, Yemen. *Earth and Planetary Science Letters* **259**: 442–456.

STEINER S. & SAYERS D. 2002: Appendix 1. Endemic flora of St Helena. Pp. 145–156. In: STEINER S. (ed.): *St. Helena, Ascension, Tristan da Cunha. The Bradt Travel Guide*. Bradt Travel Guides Ltd, Bucks, England & The Globe Pequot Press Inc, Guilford, USA, 182 pp.

STODDART D. R. (ed.) 1984: *Biogeography and ecology of the Seychelles Islands. Monographiae biologicae. Vol. 55.* Dr. W. Junk Publishers, The Hague, 692 pp.

STURM H. 2002: A new genus and species of jumping bristle-tails (Insecta: Archaeognatha: Machilidae) from the Socotra Archipelago, Yemen. *Fauna of Arabia* **19**: 391–397.

SZIEMER P. 2010: *Madeira's natural history in a nutshell. 2nd edition.* Francisco Ribeiro & Filhos, Lda., Funchal, 288 pp.

TAITI S. & CHECCUCCI I. 2009: New species and records of terrestrial Isopoda (Crustacea, Oniscidea) from Socotra Island, Yemen. Pp. 73–103. In: NEUBERT E., AMR Z., TAITI S. & GÜMÜS B. (eds.): Animal Biodiversity in the Middle East. Proceedings of the First Middle Eastern Biodiversity Congress, Aqaba, Jordan, 20–23 October 2008. *ZooKeys* **31**: 1–252.

THIV M. & MEVE U. 2007: A phylogenetic study of Echidnopsis Hook. f. (Apocynaceae-Asclepiadoideae) – taxonomic implications and the colonization of the Socotran archipelago. *Plant Systematics and Evolution* **265**: 71–86.

THIV M., THULIN M., HJERTSON M., KROPF M. & LINDER H. P. 2010: Evidence for a vicariant origin of Macaronesian-Eritreo/Arabian disjunctions in Campylanthus Roth (Plantaginaceae). *Molecular Phylogenetics and Evolution* **54**: 606–616.

THIV M., THULIN M., KILIAN N. & LINDER H. P. 2006: Eritreo-Arabian affinities of the Socotran flora as revealed from the molecular phylogeny of Aerva Forssk. (Amaranthaceae). *Systematic Botany* **31**: 560–570.

THIV M., NIET T. VAN DER, RUTSCHMANN F., THULIN M., BRUNE T., & LINDER H. P. 2011: Old–New World and trans-African disjunctions of Thamnosma (Rutaceae): intercontinental long-distance dispersal and local differentiation in the succulent biome. *American Journal of Botany* **98**: 76–87.

TJEDER B. 1974: Nemopteridae from the Island of Socotra (Neuroptera) with descriptions of two genera. *Entomologica Scandinavica* **5**: 291–299.

TJEDER B. 1975: A new species name in the Crocinae (Neuroptera: Nemopteridae). *Entomologica Scandinavica* **6**: 133.

UNEP-WCMC 2008: Socotra Archipelago, Yemen. UNESCO Fact Sheet. World Heritage Sites – Protected Areas and World Heritage. United Nations Environment Programme & World Conservation Monitoring Centre, 11 pp. www.unep-wcmc.org/sites/wh/pdf/Socotra%20revised.pdf. (Accessed 15.vi.2009).

UVAROV B. P. & POPOV G. B. 1957: The saltatorial Orthoptera of Socotra. *Journal of the Linnean Society of London (Zoology)* **43**: 359–389.

VAN NOORT S. 1994: Systematics of the sycoecine fig wasps (Agaonidae, Chalcidoidea, Hymenoptera), 3 (Crossogaster). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen Biological Chemical Geological Physical and Medical Sciences* **97**: 83–122.

VOLKOVITSH M. G. 2012: Polycestinae (Coleoptera: Buprestidae) of Socotra Island. Pp. 195–208. In: HÁJEK J. & BEZDĚK J. (eds.): Insect biodiversity of the Socotra Archipelago. *Acta Entomologica Musei Nationalis Pragae* **52 (supplementum 2)**: i–vi + 1–557.

WALSINGHAM LORD 1900: [The expedition to Sokotra. X.] Descriptions of the new species of Micro-Lepidoptera. *Bulletin of the Liverpool Museums* **3**: 1–7.

WHITTAKER R. J., LADLE R. J., ARAÚJO M. B., FERNÁNDEZ-PALACIOS J. M., DELGADO J. & ARÉVALO J. R. 2007: The island immaturity–speciation pulse model of island evolution: an alternative to the ''diversity begets diversity'' model. *Ecography* **30**: 321–327.

WHITTAKER R. J., TRIANTIS K. A. & LADLE R. J. 2008: A general dynamic theory of oceanic island biogeography. *Journal of Biogeography* **35**: 977–994.

WITT C. C. & MALIAKAL-WITT S. 2007: Why are diversity and endemism linked on islands? *Ecography* **30**: 331–333.

ZABRANSKY P. 2004: Ein neuer Prachtkäfer aus der unterfamilie Polycestinae: Strigoptera (Svatacesta subgen. n.) socotra sp. n. (Coleoptera: Buprestidae). *Zeitschrift der Arbeitsgemeinschaft Österreichischer Entomologen* **56**: 115–123.

ZOIA S. 2012: Eumolpinae (Coleoptera: Chrysomelidae) of Socotra Island. Pp. 449–501. In: HÁJEK J. & BEZDĚK J. (eds.): Insect biodiversity of the Socotra Archipelago. *Acta Entomologica Musei Nationalis Pragae* **52 (supplementum 2)**: i–vi + 1–557.