

## Bats (Mammalia: Chiroptera) of the Eastern Mediterranean and Middle East. Part 14. Bat fauna of the Socotra Archipelago, Yemen

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**Abstract.** A complete list of bat records available from the Socotra Archipelago was compiled from the literature and from new records, based on field studies and examination of museum specimens. The record reviews of the particular species are complemented with distribution maps, summaries of distributional status, notes on field data and on taxonomic status. From the Archipelago, at least 54 records of four bat species belonging to four families are known; viz. *Rhinopoma cystops* Thomas, 1903 (34 record sites), *Rhinolophus clivosus* Cretzschmar, 1828 (6), *Asellia italosomalica* De Beaux, 1931 (9), and *Hypsugo lanzai* Benda, Al-Jumaily, Reiter et Nasher, 2011 (5). While the latter three species are known only from the island of Socotra, *R. cystops* was documented also from two other larger islands, Abd El Kuri and Samha. The Socotran populations of *R. clivosus* were found to be morphologically and genetically unique and therefore are here described as a separate subspecies, *Rhinolophus clivosus socotranus* subsp. nov.

**Key words.** Distribution, ecology, taxonomy, Rhinopomatidae, Rhinolophidae, Hipposideridae, Vespertilionidae, Socotra, Yemen, Middle East, Palearctic, Afrotropics.

### INTRODUCTION

The Socotra Archipelago comprises six islands (including two islets) clustered at the southern margin of the Gulf of Aden in the eastern continuation of Cape Guardafui, the easternmost point of the Horn of Africa (Figs. 1, 2). More politically than geographically, the Archipelago is considered a southernmost part of the Middle East, being a distant component of the Republic of Yemen. Anyway, the Archipelago lies on the Socotra Platform, a part of the Somali Plate (being its northernmost piece of dry land), separated from the Arabian Plate by the Aden-Sheba Ridge, the central line of the Gulf of Aden. The Gulf of Aden is 350 km wide at its border with the Arabian Sea between the Socotran and Yemeni shores and up to 5,375 m deep in the Alula-Fartak Trough in its eastern part (Fig. 1).

The area of the Archipelago reaches some 3,800 km<sup>2</sup> of which Socotra itself, the easternmost, largest and most diversified island, exceeds 3,600 km<sup>2</sup> in its area (the exact data on the area vary, 3,625 km<sup>2</sup> is a value reported by Wranik 2000 and De Geest 2006; Fig. 3). However, Socotra is also the largest island of the whole western part of the Indian Ocean after Madagascar. The surface of this island is covered by rugged plateaus at various sea levels and with a central high massif

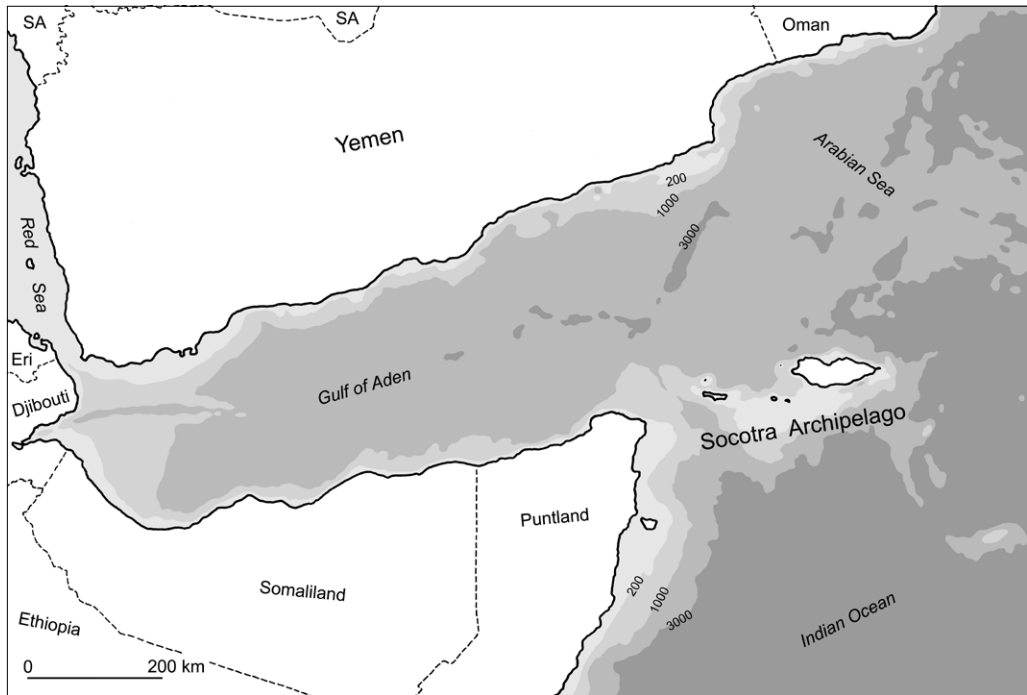


Fig. 1. Bathymetrical map of the north-western part of the Indian Ocean with localisation of the Socotra Archipelago and the Gulf of Aden; SA = Saudi Arabia, Eri = Eritrea.

of the Hagher Mts. (with the highest point *Jebel Skand*, 1,550 m a. s. l.; Cheung et al. 2006). The vegetation comprises mainly dry shrublands (Popov 1957, Miller & Morris 2004, Cheung et al. 2006, Banfield et al. 2011), the croton shrublands in lowland plains, succulent shrublands and semi-evergreen woodlands are on the slopes and plateaus up to 700 m a. s. l., sub-montane shrublands are situated higher (up to 900 m a. s. l.), and above them, there is a mosaic of evergreen woodlands, grasslands and dwarf shrublands. The other islands of the Archipelago (besides *Kal Farun* and *Sabunya* representing only rocky outcrops) are much drier and also lower in altitude, reaching less than a half of the largest island's highest point. They are covered by shrublands and patches of semi-evergreen woodlands. The environment of Socotra is rich in active and inactive karst phenomena, number of caves, of which at least six are longer than 1 km and the whole measured underground of the island exceeds 23 km (De Geest 2006). The climate of the Archipelago is tropical and dry, locally and altitudinally variable, and particularly influenced by seasonally reversing monsoons.

Although the Socotra Archipelago could be seen as a part of the Afrotropics, its biota has characteristics and influences of all surrounding biotas, Afrotropical, Palaearctic and Oriental, besides the extremely high proportions of endemics. For instance, 37% of species of the Socotran flora are endemics, which is a ratio comparable with that of the Galapagos and higher than those found e.g. in Mauritius, Rodrigues, or the Canary Islands (Miller & Morris 2004). Similarly, at least 27% of the breeding bird taxa of the Archipelago are local endemics (Martins 1996, Kirwan

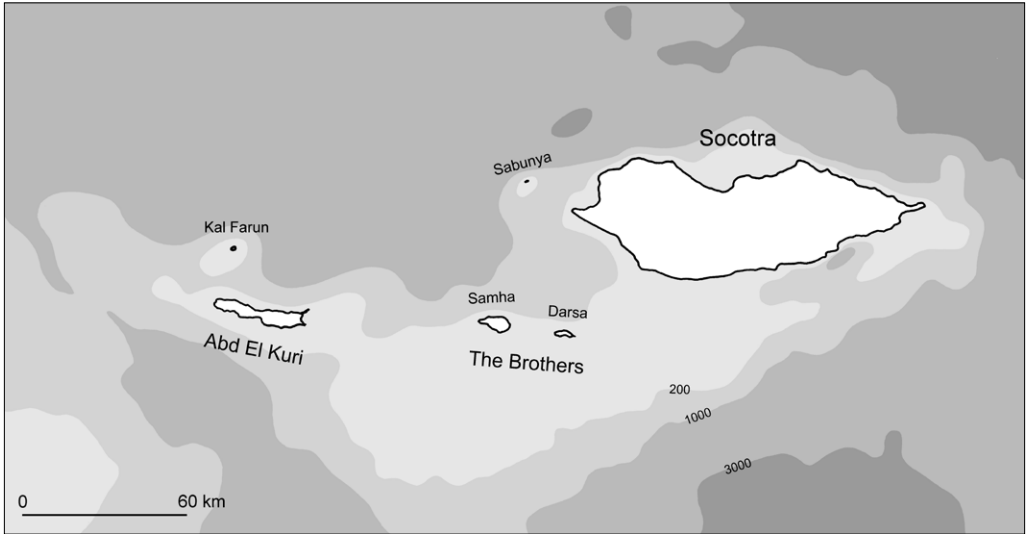


Fig. 2. Map of the Socotra Archipelago.

2007). Large proportions of endemics are reported also for the faunas of reptiles (90%), land snails (95%), spiders (60%) or isopods (60%) (Cheung et al. 2006).

The same is true also for the fauna of bats, which comprises both African and Asian elements as well as a certain portion of endemics. Bats are the only mammal group indigenous to the Archipelago, while all terrestrial mammal species other than bats are considered to be introduced

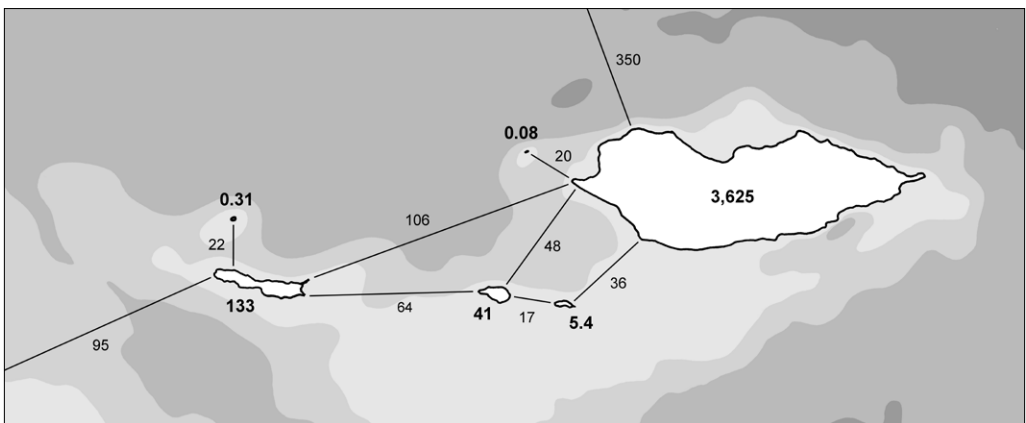


Fig. 3. Map of the Socotra Archipelago with areas of (large bold numerals) and distances between (small numerals at lines) particular islands and islets of the Archipelago and to the closest mainlands; Africa (left) and Arabia (top).

by man. The fauna consists mostly of domesticated and semi-domesticated forms (*Bos taurus*, *Capra hircus*, *Ovis aries*, *Camelus dromedarius*, *Equus asinus*, *Felis catus*, *Viverricula indica*) or commensal species (*Mus musculus*, *Rattus rattus*) (Taschenberg 1883, De Winton et al. 1903, Wranik 1986, 1999, Feiler et al. 2000, Bejček et al. 2001, Wranik et al. 2003, Nasher & Al Jumaily 2004, Cheung et al. 2006, etc.). These species were reported to occur on Socotra, while *Mus musculus* also on Samha (Wranik et al. 2003) and Abd El Kuri (Nasher & Al Jumaily 2004), and *Rattus rattus* on four larger islands of the Archipelago (Wranik et al. 2003). A rather special case is a shrew, known from only two specimens collected on Socotra. The first one, collected by Guichard (1992) in 1967, was published by Hutterer & Harrison (1988) as *Suncus etruscus* (Šavi, 1822) and its indigenous origin has not been doubted. Another specimen found in 1999, first mentioned by Evans (2000), was identified as *Suncus madagascariensis* (Coquerel, 1848) by Hutterer (2005) and reported as an alien species, spread by human activities across the Indian Ocean (Cheung et al. 2006, R. Hutterer ad verb.).

The bat fauna of the Socotra Archipelago has not been studied systematically yet, a big part of the available data are rather accidental records and the history of bat research can be traced “specimen by specimen”; slightly more extensive surveys of bats, covering few weeks, were conducted only twice. However, the first report of bats falls into the era of pioneer investigations of the islands in the 1880s, when a series of *Rhinopoma* was collected by German explorers Emil Riebeck (1853–1885) and Georg August Schweinfurth (1836–1925) in 1881 (Taschenberg 1883). This collection, originally deposited in the Halle Museum and some years later exchanged to the Hamburg Museum (Noack 1891), represented for a long time the only bats known from the island. Further records of bats from Socotra were made by Russian-British entomologist Georg Basil Popov (1922–1998) in 1953, during the expedition of the Desert Locust Survey Nairobi; he collected three bat species (*Rhinopoma cystops*, *Asellia italosomalica*, *Hypsugo lanzai*), two of them were briefly published by Harrison (1957, 1964), one remained overlooked until almost recently and was published by Benda et al. (2008). Two other bats of two species (*Asellia italosomalica*, *Hypsugo lanzai*) were collected by British entomologist Kenneth M. Guichard (1914–2002) during the Middle East Command Expedition in 1967 (Guichard 1992); the latter specimen was published already by Corbet (1978). Another record was made absolutely accidentally by German marine biologist Wolfgang Wranik (\*1950), who collected two *Asellia* bats entering his hotel room in Hadiboh through an open window in search for their prey in March 1985 (Wranik 1986). Despite more frequent expeditions of various naturalists to Socotra in the 1990s, when an extensive, systematic and multidisciplinary survey of the Socotran biota started, only two bat records were made until 1999, both of *Rhinopoma* in 1997, one from a cave in the Diksam plateau (Wranik 1998) and other from Hadiboh (Wranik 1999).

At the turn of the millenium, a new era of bat investigations in the Socotra Archipelago started, also due to a detailed biospeleological research. Between 1999 and 2004, more than fifty new records of bats were made in Socotra and also the first records in two other islands of the Archipelago. In 1999, a fourth bat species was discovered on Socotra, *Rhinolophus clivosus* (Wranik et al. 1999). Some of these new findings are spread across various small papers and unpublished reports (Wranik et al. 1999, Bejček et al. 2001, Al-Jumaily 2004, Nasher & Al-Jumaily 2004) or general works (Wranik 2000, Wranik et al. 2003). About twenty new records of three bat species were reported by Cesarini (2003, 2007) who spent a month in trip to investigate bats of Socotra in summer 2003. Nevertheless, a big part of the records remains still unpublished, namely more than twenty records made in May 2004 (see Original data in the Records chapters below). However, no new bat record from Socotra is available after 2004.

Although the composition of the bat fauna of the Socotra Archipelago is already known (see Wranik et al. 2003, Benda et al. 2006a), the data on distribution and ecology of the bats of the

Archipelago as well as their phylogenetic relations to the mainland populations have not yet been summarised. The presented review tries to fill this information gap.

## MATERIAL AND METHODS

### Records

The lists of records (arranged in alphabetical and/or chronological orders) include, for each item, the following information: name of the locality (each record is primarily listed by a name of the nearest settlement or notable physical feature) [in brackets, serial number of the locality is given as indicated in the map], and/or description of the record site, date, number of recorded bats with indication of their sex and age (for details see Abbreviations below), and a reference to collection. Geographical names follow the original naming of the particular sites in published sources, otherwise they follow Bezděk et al. (2012); exceptions are noted in Appendix I.

### Comparisons

The specimens were examined in a standardised way with the use of mechanical or optical calipers. The evaluated external, cranial and dental dimensions are listed in Abbreviations. External measurements were taken from freshly collected material in the NMP specimens, in other specimens only the forearm lengths were taken from museum preparations (see Material examined under particular species and Appendix II). Tooth-row and dental dimensions were taken on tooth cingulum margins. Bacula were extracted into 6% solution of KOH and coloured with alizarin red. Statistical analyses were performed using the Statistica 6.0 software. For the detailed description of methods of the molecular genetic analysis of *Rhinolophus* Lacépède, 1799 see Benda & Vallo (2012: 71–72).

## ABBREVIATIONS

### Dimensions

EXTERNAL. LC = head and body length; – LCd = tail length; – Lat = forearm length; – LA = auricle length; – LT = tragus length; – LaFE = horseshoe width.

CRANIAL. LCr = greatest length of skull incl. praemaxillae; – LOc = occipitocanine length of skull; – LCb = condylobasal length of skull; – LCc = condylocanine length of skull; – LaZ = zygomatic width; – Lal = width of interorbital constriction; – LaInf = rostral width between infraorbital foramina; – LaNc = neurocranium width; – LaM = mastoidal width of skull; – ANc = neurocranium height; – ACr = cranial height (incl. tympanic bullae); – LBT = largest horizontal length of tympanic bulla; – CC = rostral width between canines (incl.); – P<sup>4</sup>P<sup>4</sup> = rostral width between last upper premolars (incl.); – M<sup>3</sup>M<sup>3</sup> = rostral width between third upper molars (incl.); – CM<sup>3</sup> = length of upper tooth-row between canine and third molar (incl.); – M<sup>1</sup>M<sup>3</sup> = length of upper tooth-row between first and third molars (incl.); – CP<sup>4</sup> = length of upper tooth-row between canine and large premolar (P<sup>4</sup>) (incl.); – LMd = condylar length of mandible; – ACo = height of coronoid process; – I<sub>1</sub>M<sub>3</sub> = length of lower tooth-row between first incisor and third molar (incl.); – CM<sub>3</sub> = length of lower tooth-row between canine and third molar (incl.); – M<sub>1</sub>M<sub>3</sub> = length of lower tooth-row between first and third molars (incl.); – CP<sub>4</sub> = length of lower tooth-row between canine and large premolar (P<sub>4</sub>) (incl.).

DENTAL. LI<sup>2</sup> = largest mesio-distal length of the first upper incisor; – LI<sup>3</sup> = largest mesio-distal length of the second upper incisor; – LCs = largest mesio-distal length of upper canine; – LaCs = largest palato-labial width of upper canine; – LP<sup>2</sup> = mesio-distal length of small upper premolar; – ACn = height of the palato-mesial cingular cusp of the second upper premolar (P<sup>4</sup>); – LP<sup>4</sup> = largest mesio-distal length of large upper premolar on the labial cingulum; – LP<sup>4</sup>2 = mesiodistal length of large upper premolar on palatal cingulum (largest dimension taken over the palato-mesial to palato-distal points of the talon); – LP<sup>4</sup>3 = smallest mesio-distal length of large upper premolar taken over the talon constriction; – LaP<sup>4</sup> = largest palato-labial width of large upper premolar taken over the mesio-labial and palato-distal cingulum margins; – LM<sup>1</sup> = largest mesio-distal length of first upper molar taken over parastyle and metastyle; – LaM<sup>1</sup> = largest palato-labial width of first upper molar taken over parastyle and palato-distal part of talon; – LM<sup>3</sup> = largest mesio-distal length of third upper molar; – LaM<sup>3</sup> = largest palato-labial width of third upper molar taken over parastyle and palatal cingulum; – LI<sub>1</sub> = largest mesio-distal length of the first lower incisor; – LI<sub>3</sub> = largest mesio-distal length of the third lower incisor; – LCI = largest mesio-distal length of lower canine; – LP<sub>2</sub> = largest mesio-distal length of first lower premolar; – LaP<sub>2</sub> = largest labio-lingual width of first lower premolar; LP<sub>3</sub> = mesio-distal length of (second) small lower premolar; – LP<sub>4</sub> = largest mesio-distal length of last lower premolar; – LaP<sub>4</sub> = largest labio-lingual width of last lower premolar; – LM<sub>1</sub> = largest mesio-distal length of first lower molar taken over paraconid and hypoconulid.

RELATIVE DENTAL. CSR = relative length of upper canine (LM<sup>3</sup>/LCs); – CsR1 = relative width of upper canine: (LaCs/LCs); – P<sup>4</sup>R = relative length of large upper premolar across labial cingulum (LP<sup>4</sup>/LaP<sup>4</sup>); – P<sup>4</sup>R2 = relative length of large upper premolar across talon constriction (LP<sup>4</sup>3/LaP<sup>4</sup>); – P<sup>4</sup>R3 = relative length of large upper premolar across talon constriction II (LP<sup>4</sup>3/LP<sup>4</sup>); – M<sup>3</sup>sq = crown square of third upper molar (LM<sup>3</sup>×LaM<sup>3</sup>); – M<sup>1</sup>R = relative width of first upper molar (LaM<sup>1</sup>/LM<sup>1</sup>); – M<sup>3</sup>R = relative width of third upper molar (LaM<sup>3</sup>/LM<sup>3</sup>); – CiR = relative length of lower canine (LM<sub>1</sub>/LCi);

– P<sub>2</sub>Sq = crown square of first lower premolar (LP<sub>2</sub>×LaP<sub>2</sub>); – P<sub>4</sub>Sq = crown square of third lower premolar (LP<sub>4</sub>×LaP<sub>4</sub>); – PR = relative size of the first lower premolar crown square (P<sub>2</sub>Sq/P<sub>4</sub>Sq).

### Collections

BCSU = Biological Collection of the Sana'a University, Sana'a, Yemen; – BMNH = Natural History Museum, London, United Kingdom; – CDIS = Christian Dietz private collection, Herb, Germany; – DM = Durban Natural Science Museum, Durban, South Africa; – EBD = Doñana Biological Station, Seville, Spain; – FMNH = Field Museum of Natural History, Chicago, U. S. A.; – HUJ = Hebrew University, Jerusalem, Israel; – MHNG = Natural History Museum, Geneva, Switzerland; – MNHN = National Museum of Natural History, Paris, France; – MSNG = Civil Natural History Museum Giacomo Doria, Genoa, Italy; – MZUF = Natural History Museum, Zoology Section "La Specola", Florence, Italy; – NMB = National Museum, Bloemfontein, South Africa; – NMP = National Museum (Natural History), Prague, Czech Republic; – NMW = Natural History Museum, Vienna, Austria; – SMF = Senckenberg Research Institute and Natural History Museum, Frankfurt am Main, Germany; – TAU = Tel Aviv University, Tel Aviv, Israel; – TM = Ditsong National Museum of Natural History, Pretoria, South Africa; – ZFMK = Zoological Research Museum Alexander Koenig, Bonn, Germany; – ZMH = Zoological Museum, University Hamburg, Germany.

### Other abbreviations

A = alcoholic preparation; – a = adult individual; – B = dry skin (balg); – F = F-value of ANOVA; – f = female; – j = juvenile individual; – M = mean; – m = male; – min, max = dimension range margins; – p = statistical probability; – S = skull; – s = subadult individual; – SD = standard deviation.

## LIST OF SPECIES

### *Rhinopoma cystops* Thomas, 1903

RECORDS. **Original data:** Diksam plateau, Diksam lake [1], 11 May 2003: det. calls of 1 foraging ind. above and around the lake surface; – Diksam plateau, Marshim cave [2], rocks around the cave entrance, 8 May 2004: obs. & det. 3 foraging inds.; – Homhil [3], 23 March 1999: coll. 1 ma, 1 fa, MHNG; – Kam oasis [4], small karst cave, 5 May 2004: obs. 1 ind.; – Keisu oasis [5], small cave in a slope above the oasis, 22 May 2004: obs. a nursery colony of ca. 100 inds. (incl. juveniles), coll. 1 fa, NMP (cf. Benda et al. 2009); – Timre village [6], rocky crevice, 6 May 2004: obs. a colony of ca. 30 inds., coll. 3 ma, NMP (cf. Hulva et al. 2007, Benda et al. 2009); – Wadi Azro, 3 km N of the Keze village [7], rocky overhang, 14 May 2004: obs. 1 roosting ind.; – Wadi Darho, Desmoiten village [8], goat stable, 13 May 2004: obs. a group of ca. 5 inds., coll. 1 ma, NMP (cf. Benda et al. 2009, 2012); – Wadi Darho, Desmoiten village [9], small pseudokarst cave, 13 May 2004: obs. a colony of ca. 200 inds.; – Wadi Zerig [10], cave system, 5 March 2000: coll. 1 ma, NMP, 2 September 2001: obs. several tens of inds., coll. 1 ma, NMP, 12 May 2004: obs. a scattered colony of ca. 300 inds., coll. 5 ma, BCSU, NMP (cf. Bejček et al. 2001, Šťastný et al. 2002, Hulva et al. 2007, Benda et al. 2009). – **Published data:** Abel, Ghelemeneten [11], 20 August 2003: obs. 30–40 inds., exam. 1 m, 5 f (Cesarini 2003, 2007 [as *R. hardwickii*]); – Bat Cave [12], Mahlez plateau, 9 January 2001: obs. (De Geest 2006 [as *R. hardwickii*]); – De Fareho, Qatanen I [13], 27 August 2003: obs. 30–40 inds., exam. 2 m, 1 f (Cesarini 2003, 2007 [as *R. hardwickii*]); – Dehasas, Devegach [14], 19 August 2003: obs. 4 inds., exam. 1 f (Cesarini 2003, 2007 [as *R. hardwickii*]); – Deksam plateau / Diksamplateau [15], Bedouin camp, a cave used as a livestock shelter, autumn 1997: 3 m (Wranik 1998, 1999, 2000 [as *R. hardwickei*]), Diksam, cave, small group (Wranik et al. 2003 [as *R. hardwickii*]); – Dexam Plateau, Wadi Zerik [10], 4 March 2000: obs. a colony of 60–80 inds., 25 and 26 March 2001: obs. 6–8 inds. (Bejček et al. 2001, Šťastný et al. 2002 [as *R. hardwickei*]); – Shibhon, Jalad / Wadi Zaerig, tunnel system, 8 September 2003: obs. ca. 50 inds., exam. 3 m, 2 f (Cesarini 2003, 2007 [as *R. hardwickii*]); – Dilhailhe Cave [16], Mahlez plateau, 11 January 2004: obs. a large colony (De Geest 2006 [as *R. hardwickii*]); – Haggher, Reshom [17], 14 September 2003: obs. 60–80 inds., exam. 2 m, 2 f (Cesarini 2003, 2007 [as *R. hardwickii*]); – Haggher, Shesor [18], 15 September 2003: obs. ca. 20 inds., exam. 4 m, 1 f (Cesarini 2003, 2007 [as *R. hardwickii*]); – Haif, Gorf cave [19], 3 September 2003: obs. ca. 100 inds., exam. 3 f (Cesarini 2003, 2007 [as *R. hardwickii*]); – Hardwicki Cave [20], Mahlez plateau, 11 January 2004: obs. a very large colony [9 inds. on a photograph] (De Geest 2006 [as *R. hardwickii*]); – Kam [4], [1 April 1953]: 1 ind., BMNH (Benda et al. 2009); – Lahas, Halolaighan [21], 27 August 2003: obs. 25–50 inds. exam. 1 m, 2 f (Cesarini 2003, 2007 [as *R. hardwickii*]); – Medhobo, Desberhe [22], 25 August 2003: obs. 15–20 inds., exam. 3 m, 1 f (Cesarini 2003, 2007 [as *R. hardwickii*]); – Momi area, cave [= Dahaisi cave] [23], [9 February 1999:] obs. (Wranik et al. 2003); – Moumi, De Qaseqas [24], big cave, 24 August 2003: obs. ca. 35 inds., exam. 1 m, 1 f (Cesarini 2003, 2007 [as *R. hardwickii*]); – De Kazakaz Cave, 15 January 2003: 1 ind., BCSU (Nasher & Al Jumaily 2004 [as *R. hardwickii*]); – Neet, cave [25], 9 March 2000: obs. ca. 10 inds. (Bejček et al. 2001 [as *R. hardwickei*]); – Noged, large cave [= Deiqab Cave] [26], [22 November 1999:] obs. (Bejček et al. 2001 [as *R. hardwickei*]); – Shab, Hovagh [27], 3 September 2003: obs. 20–25 inds., exam. 3 m, 2 f (Cesarini 2003, 2007 [as *R. hardwickii*]); – Shab, Terbak [= stable] [28], 3 September 2003: obs. 8 inds., exam. 2 m, 1 f (Cesarini 2003, 2007 [as *R. hardwickii*]); – Shesehar, Shesehar cave [29], 19 August 2003: obs. 3 inds., exam. 1 m, 1 f

(Cesarini 2003, 2007 [as *R. hardwickii*]); – Sirhin, Dixam / Serhin [30], 24 February 1999: 2 m, 3 f, BCSU (Al-Jumaily 2004, Nasher & Al Jumaily 2004 [as *R. hardwickii*]), Diksam Plateau, Sirhin, 24 February 1999: coll. 2 ma, 1 fa, BCSU, SMF (Benda et al. 2009); – Tāiti’s Cave [31], Mahlez plateau, 19 January 2003: obs. a large colony (De Geest 2006 [as *R. hardwickii*]); – bei Tamarida [= Hadiboh] [32], 1881: numerous inds. (Taschenberg 1883 [as *R. microphyllum*]); bei Tamaridah oder Hadibu, 18 inds., ZMH (Kock 1969 [as *R. hardwickei*]); Hadiboh, cave, autumn 1997: obs. a small group of ca. 10 inds., perhaps all males (Wranik 1999, 2000 [as *R. hardwickei*], Wranik et al. 2003 [as *R. hardwickii*]); – Socotra Island (Noack 1891, Anderson 1902 [as *R. microphyllum*], Harrison 1964, Corbet 1978, Koopman 1982a, 1993, Qumsiyeh 1985, Nowak 1991, 1994, 1999, Borisenko & Pavlinov 1995 [as *R. hardwickei*], Simmons 2005, cf. Harrison & Bates 1991 [as *R. hardwickii*]); Socotra Island, 55 inds., [~38 inds., BMNH] (Hill 1977 [as *R. hardwickei*]); Socotra, 9 inds., ZMH (Van Cakenberghe & De Vree 1994 [as *R. hardwickei*]); – Abd al Kuri, [19 February 1999: obs.] (Wranik 2000 [as *R. hardwickei*], Wranik et al. 2003 [as *R. hardwickii*]); – Samha Island (Wranik 1999, 2000 [as *R. hardwickei*], Wranik et al. 2003 [as *R. hardwickii*]); Samha Is., small cave, 15 February 1999: coll. 1 fa, BCSU/SMF (Al-Jumaily 2004, Nasher & Al Jumaily 2004 [as *R. hardwickii*], Benda et al. 2009).

**DISTRIBUTION.** *Rhinopoma cystops* is a very common bat in Socotra, it is known from 32 sites scattered over the whole island (Fig. 4). This species is by far the most frequent bat of the island (see also Wranik et al. 2003), the number of its records from Socotra is three times higher than that of the second most common bat species, *Asellia italosomalica* (Table 27).

*R. cystops* was the first bat species reported to occur in Socotra (under the name *R. microphyllum*), a series of these bats was collected at Hadiboh by E. Riebeck and G. A. Schweinfurth in 1881 (Taschenberg 1883). The Taschenberg’s report remained for a long time the only data on bats from the island (Noack 1891, Anderson 1902), while additional records of this (and also other) bat species were made on the island more than 70 years later (Harrison 1957, 1964).

*R. cystops* is the only bat species which was recorded also from other islands of the Socotra Archipelago; besides Socotra, it was documented from the two larger islands of the group, Abd El Kuri and Samha, in 1999 (Wranik 1999, 2000, Al-Jumaily 2004). Although only a single record is available from each of these islands, permanent occurrence of *R. cystops* can be expected there. In Abd El Kuri, the species was observed in the central areas of the island close to the southern shore between Kilmia and Ras Nabaineh (Wranik 1999, orig. data). Al-Jumaily (2004: 60) reported a female captured “in a small cave, off the seashore, on Samha Island”.

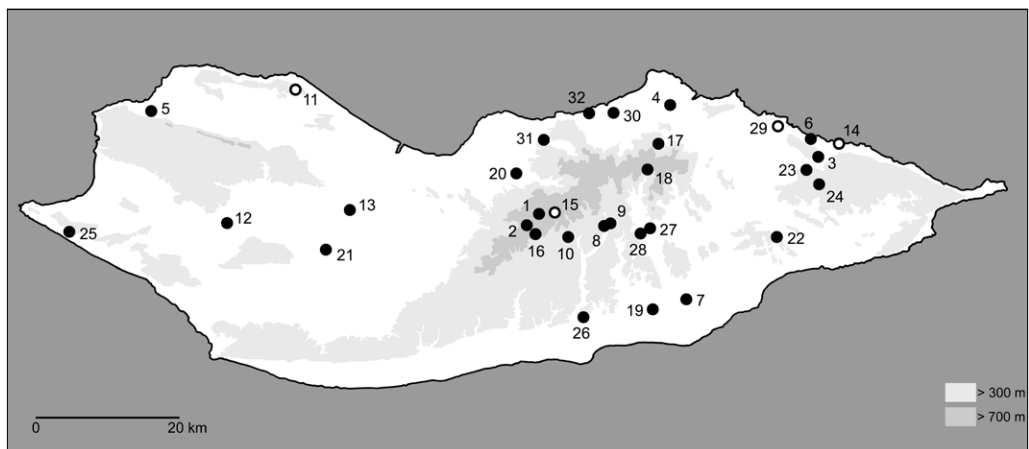


Fig. 4. Records of *Rhinopoma cystops* Thomas, 1903 in Socotra. Open symbols denote uncertain localisations of records.

*R. cystops* is distributed widely across deserts and dry steppes of the northern and north-eastern parts of Africa and the western and southern parts of Arabia, in the broad belt from Morocco and Senegal to the Levant, South Sudan, Somalia and western Oman (Harrison & Bates 1991, Van Cakenberghe & De Vree 1994, Aulagnier 2013, Benda et al. 2014, etc.). The occurrence in Socotra, along with the distribution in the coastal part of Dhofar, south-western Oman, represents the easternmost extension of the species distribution range. (The definitely easternmost distribution point of *R. cystops* is Sadah, Dhofar (55° 05' E; own unpubl. record), lying some 80 km east of the easternmost sites in Socotra.)

In Socotra, *R. cystops* is distributed over a very broad range of altitudes (985 m; Table 1). The records are available from almost all altitudinal levels of the island, from the sea level to higher mountains, although the majority of the records come from rather low to medium altitudes (altitude median 169.0 m, altitude mean 314.1 m a. s. l.; Table 1). The highest area of recorded occurrence of *R. cystops* in Socotra is the Diksam plateau, situated above 900 m a. s. l., where the bat finds both roosts and foraging grounds (Wranik 1998, orig. data). The prevailing majority of the records of this bat from Socotra were made in roosts (90.6%, n=29) and the altitudinal range of the roost sites more or less corresponds to the range of all records (940 m) as well as the median and mean altitude values (165.0 m and 299.7 m a. s. l.; Table 1).

Concerning the distribution of *R. cystops* in Socotra, Al-Jumaily (2004: 60) reported as follows: “Also common in Socotra Island, in low areas (Hadiboh) as well as in the mountains (Sirihin, 1000 m).” This mention indicates a record at the area of Sirihin, Diksam plateau, at 805 m a. s. l. (12° 31' 05" N, 53° 59' 08" E; cf. Bezděk et al. 2012), which was listed by this author in the review of records (p. 59): “Sirihin, Dixam, Socotra Island”. However, in the gazetteer in the same paper, for this site name Al-Jumaily (2004: 58) mentioned coordinates of another locality, the village of Sirihin near Hadiboh at ca. 15 m a. s. l. (12° 39' N, 54° 03' E). Therefore, for calculation of the



Fig. 5. Diksam lake on the Diksam plateau (990 m a. s. l.), the highest site of recorded bat occurrence on Socotra; echolocation calls of *Rhinopoma cystops* were recorded at this site in May 2004. All photos by A. Reiter.



Table 1. Numbers of record sites and altitudinal characteristics of the occurrence of the particular bat species in Socotra

species	record type	n	min	max	range	median	mean
<i>Rhinopoma cystops</i>	all sites	32	5	990	985	169.0	314.1
	roosts	28	5	945	940	165.0	299.7
<i>Rhinolophus clivosus</i>	all sites	6	60	945	885	476.5	493.8
	roosts	5	120	945	825	588.0	580.6
<i>Asellia italosomalica</i>	all sites	9	10	325	315	85.0	123.9
	roosts	7	10	325	315	115.0	149.3
<i>Hypsugo lanzai</i>	all sites	5	5	365	360	10.0	137.0
all sites		43	5	990	985	155.0	285.0

values in Table 1, we used the altitude of the latter site, i.e. according to the coordinates given; when the former site is used instead, the descriptive altitude values for the species in Socotra are slightly higher; altitude median being 176.5 m and altitude mean 338.8 m a. s. l., respectively.

FIELD NOTES. The prevailing majority of records of *Rhinopoma cystops* in Socotra was made in or at roosts, as it was stated already above. There is only one exception (moreover, the type of finding was not defined in some other records), when calls of a foraging bat were detected at the Diksam lake in the highest part of the Diksam plateau (ca. 990 m a. s. l.; Fig. 5). *R. cystops* forms rather small-sized aggregations in Socotra, the documented groups and colonies were composed of 3–300 individuals (median 22 bats in an aggregation, mean 50.2 bats). Only a few roost findings represented more than 50 individuals (groups of ca. 60–300 bats; n=5), smaller groups composed of between several individuals and few tens of bats were found in the majority of the roosts, while only at two sites solitarily roosting individuals of *R. cystops* were observed. Due to large number of this bat in the caves of Socotra noted by speleologists, one roost was named Hardwicki Cave (De Geest 2006).

The largest aggregation of *R. cystops*, representing at least 300 bats, was found in the subterranean system of Wadi Zerig on 12 May 2004 (orig. data); the colony was scattered in smaller groups over walls of several perpendicularly oriented corridors with various influence of daylight. The system is situated in a low side wall of the wadi (Fig. 6) and although it is principally a karst cave, it perhaps combines karst and pseudokarst phenomena. During other checks of this extensive cave system, much smaller aggregations of *R. cystops* were found; tens of individuals were observed there on 4 March 2000 and 2 September 2001 (Bejček et al. 2001) as well as on 8 September 2003 (Cesarini 2003, 2007) and only a small group of some 6–8 bats was found there on 25–26 March 2001 (Bejček et al. 2001) (Fig. 7).

A colony of ca. 200 individuals of *R. cystops* was discovered in a small pseudokarst cave (ca. 15 m deep) temporarily used as a livestock shelter near the Desmoiten village in Wadi Darho on 13 May 2004 (orig. data). A group of five bats was discovered in a man-made goat stable in the respective village on the same day, which perhaps originated from the large colony in the cave nearby and the artificial shelter was used by some individuals only irregularly (one male was examined from the artificial roost). Another large colony of *R. cystops*, composed of ca. 100 bats, both adults and juveniles, was discovered in a small cave in the steep rocky slope above the oasis of Keisu (Kheyra; Fig. 16) in the western part of the island on 22 May 2004. Cesarini (2003, 2007) observed two colonies of a similar size, one composed of ca. 100 individuals (from which he examined three females) in the Gorf cave in southern Socotra on 3 September 2003, and the other, of 60–80 bats (two males and two females were examined) at Reshom in the upper part of the Hagher Mts. (at almost 700 m a. s. l.) on 14 September 2003.



Fig. 6. Wadi Zerig, in the south-eastern slope of the Diksam plateau (660 m a. s. l.); a cave system on the right (opposite side of the wadi hosts a large colony of *Rhinopoma cystops*. During several checks between 2000 and 2004, various numbers of this species were found there (Bejček et al. 2001, Šťastný et al. 2002, Cesarini 2003, 2007, orig. data), up to some 300 individuals on 12 May 2004 (orig. data).

Medium-sized groups of up to 50 individuals of *R. cystops* were observed in Socotra most frequently by Cesarini (2003, 2007) in the period between 20 August and 3 September 2003 (see Records). This author found seven colonies ranging in size between 15 and 50 bats; two to six bats were examined from all these colonies, and in all samples both sexes were presented. Unfortunately, Cesarini (2003, 2007) did not define the type of these roosts, only in two cases he specified them as caves (Ghelementen and De Qaseqas; from the latter cave the species was documented also by Nasher & Al Jumaily 2004). Another colony of a similar size (ca. 30 individuals) was discovered in a crevice near the village of Timre, some 15 m deep but a rather narrow cave in a rock facing the sea shore plain covered by a sparse forest (Fig. 8); three examined individuals from this colony were adult males (orig. data; Fig. 9).

Most probably, such a medium-sized aggregation of *R. cystops* was discovered also by E. Riebeck and G. A. Schweinfurth at/in Hadiboh in spring 1881 (see Taschenberg 1883); from the series collected by these explorers, there are still 18 specimens in the ZMH (Kock 1969) that could have been perhaps collected from a single roost. Unfortunately, no data are available concerning the circumstances of this record (Taschenberg 1883, ZMH evidence). Additionally, in Hadiboh, in a pseudokarst cave in the conglomerate stone with the entrance ca. 1.5 m high but several metres broad, situated under a house inside the town (cf. Wranik et al. 2003: 156, Pl. 36), a small group of around 10 individuals of *R. cystops* was observed to roost in the autumn 1997 (Wranik 1999).

Small groups of *R. cystops*, less than ten individuals in size, were observed at nine sites (see Records; Wranik 1998, 1999, Bejček et al. 2001, Cesarini 2003, 2007, Al-Jumaily 2004, De Geest

et al. 2005, orig. data). The roosts were situated in natural caves in five cases, and in man-made livestock shelters in two cases (the two remaining roosts were not specified by the respective authors). The sex composition of the examined samples of bats from these groups suggested both unisexual and bisexual aggregations (Wranik 1999, Cesarini 2003, 2007, Al Jumaily 2004, orig. data). Bejček et al. (2001) observed a small group of about ten bats in a large cave with a very high ceiling at Neet on 9 February 2000. Wranik (1998) found three male specimens of *R. cystops* roosting in a cave used as a livestock shelter in a Bedouin camp on the Diksam plateau at the altitude of about 900 m, and this record represents the highest roost of this bat found in Socotra.

Only in two roosts, solitary individuals of *R. cystops* were observed; in a small karst cave at the oasis of Kam on 5 May 2004 and in a rocky overhang in Wadi Azro near Keze on 14 May 2004 (orig. data).



Fig. 7. An individual of *Rhinopoma cystops* Thomas, 1903 roosting on the wall of a cave in Wadi Zerig (see Fig. 6).





Fig. 8. A rocky crevice at Timre, on the north-western shore of Socotra (35 m a. s. l.); a roost of a small colony of *Rhinopoma cystops*.

Of the thirteen aggregations of *R. cystops* discovered in Socotra by Cesarini (2003), at least eight were considered “most likely to be reproductive colonies” by Cesarini (2007: 140), despite the late summer term of the roost checks and no mention of an observation of juveniles there. The roost preferences of this bat and its roost characteristics in Socotra were described by Cesarini (2007: 140) as follows: “*R. [cystops]* demonstrates an impressive adaptability in selecting roost site. We found *R. [cystops]* in large caves (De Qaseqas), tunnels systems (Wadi Zaerig), small caves, crevices between large rocks, and man-made buildings. // Even the conditions inside the roosts showed a fair variability. The temperatures ranged from 25.1 to 36.6 °C [mean 30.0 °C], and the range of relative humidity varied from 48 to 77% [mean 63%]. We found colonies in almost every monitored area of the island, and in all the main different environments. [...] the roosts appear more widespread at lower altitudes. Five sites were used by humans as stores or goat enclosures [...], and in three of these people even made fires inside the site, in order to sterilize the milk of their goats. In two sites the guano was collected by people to be used as fertilizer for their vegetable gardens.”

In summary, the roosts of *R. cystops* in Socotra were found in the prevailing majority in natural caves, both karst and pseudokarst, some of them rather fissure-like, and in overhangs; only two documented findings of roosting bats come from artificial shelters (livestock stables). Also the finding of *R. cystops* from the island of Samha was made in a small cave off the seashore (Al-Jumaily 2004).

Some three individuals of *R. cystops* were observed (and their calls detected) foraging in the dark at the entrance to the Marshim cave at the Diksam plateau during the netting session on

8–9 May 2004 (orig. data). The Marshim cave is a deep and extensive cave (Fig. 14). However, it is not clear whether the bats left the cave during the evening emergence or just foraged near the rock wall around the entrance.

Common roosting of *R. cystops* with other bat species was documented three times in Socotra. Cesarini (2003) reported on a finding of *Asellia italosomalica* colony (composed of ca. 50 individuals) in the Gorf cave at Haif on 3 September 2003, where also a colony of *R. cystops* of ca. 100 bats roosted at the time of the visit. An individual of *R. cystops* used a cave at the Kam oasis as a temporal night roost, where a nursery colony of some 200 individuals of *A. italosomalica* was observed on 5 May 2004 (orig. data, see below). Wranik et al. (2003) reported a finding of one individual of *Rhinolophus clivosus* together with an individual or individuals of *R. cystops* in the Dahaisi cave at the Momi plateau.

In the Wadi Darho, where two roosts of *R. cystops* were found close nearby to each other (in a cave and a livestock stable, see above), a roosting individual of *Rhinolophus clivosus* was dis-



Fig. 9. An individual of *Rhinopoma cystops* Thomas, 1903 discovered in the crevice at Timre (see Fig. 8).

covered in a house and foraging activity of *Hypsugo lanzai* was documented above a pool (see below). Thus, common foraging of all three bat species could be expected in the wadi. During the netting session at the Marshim cave on 8 May 2004, when the foraging calls of several *R. cystops* were detected around the cave entrance, a group of *R. clivosus* was caught emerging from the cave; common roosting of the two species in the cave cannot be excluded.

Despite the relatively high number of records, reproduction of *R. cystops* was documented in Socotra only twice. In the nursery colony of ca. 100 bats, discovered in the cave at Keisu on 22 May 2004, almost fully grown and volant young were present along with adults. A single examined female from this colony was in the lactation stage (orig. data). The ZMH series, collected at Hadiboh in April/May 1881, is composed of six males and twelve females; if the series was collected from one site, it represents a part of a nursery colony. It contains a pregnant female (containing a foetus of the crown-rump length of 12.0 mm), a very small (non-volant) juvenile male with the forearm length of 34.8 mm (= 59.3% of the average adult length), and three subadult females and one subadult male; however, none of the remaining females was in the lactation stage.

MATERIAL EXAMINED. 1 ♂ (NMP 90588 [S+A]), Desmoiten, 13 May 2004, leg. P. Benda & A. Reiter; – 1 ♂, 1 ♀ (MHNG 1756.098 [S+A], 1756.099 [A]), Homhil, 23 March 1999, leg. B. Schätti; – 1 ind. (BMNH 54.993 [S]), Kam, 1 April 1953, leg. G. B. Popov; – 1 ♀ (NMP 90594 [S+A]), Keisu, 22 May 2004, leg. P. Benda & A. Reiter; – 2 ♂♂, 1 ♀ (BCSU 120, SMF 91018, 91019 [S+B]), Diksam Plateau, Sirhin, 24 February 1999, leg. M. Al-Jumaily; – 3 ♂♂ (NMP 90576 [A], 90577, 90578 [S+A]), Timre, 6 May 2004, leg. P. Benda & A. Reiter; – 1 ♂ (NMP 96151 [S+A]), Wadi Zerig, 5 March 2000, leg. B. Pražan; – 1 ♂ (NMP 92105 [S+A]), Wadi Zerig, 2 September 2001, leg. B. Pražan; – 5 ♂♂ (NMP 90585, 90586, BCSU pb2741, pb2742 [S+A], NMP 90584 [A]), Wadi Zerig, 12 May 2004, leg. P. Benda & A. Reiter; – 1 ♀ (SMF 91017 [S+B]), Samha Is., Socotra Archipelago, 15 February 1999, leg. M. Al-Jumaily; – 6 ♂♂, 12 ♀♀ (ZMH 6552–6566 [S+A], T646[a–c] [A]), Socotra, Anat. Mus. Halle 1891 [bei Tamarida (= Hadiboh), 1881, leg. E. Riebeck & G. A. Schweinfurth].

TAXONOMIC REMARKS. The taxonomic affiliation of the Socotran populations of *Rhinopoma cystops* has changed several times, together with the changing view of the taxonomic structure and content of the whole genus and/or family, respectively. Originally, these bats were referred to *R. microphyllum* (Taschenberg 1883, Noack 1891, De Winton et al. 1903), a name used at that time for all *Rhinopoma* populations inhabiting the Afro-Arabian area (Dobson 1878, Anderson 1902, Thomas 1903, etc.). However, Taschenberg (1883) attributed the name *R. microphyllum* to the authorship of Geoffroy (not Brünnich); thus, he in fact reported (although it is not clear whether intentionally) a name representing a synonym of *R. cystops* Thomas, 1903 (cf. Dobson 1878). On the other hand, Anderson (1902) attributed the Socotran populations of *Rhinopoma* to the species name *microphyllum* Brünnich, which – in his opinion – comprised all African and Arabian populations of the genus, indivisible into more than one species.

Another opinion on taxonomic position of the Socotran populations of *Rhinopoma* was mentioned first by Harrison (1964), who marked an occurrence point at the Socotra position in his map of distribution of *R. hardwickei* Gray, 1831 in Arabia (Harrison 1964: 61). This opinion was most probably based on his examination of the BMNH specimens of *Rhinopoma* collected in Socotra by G. B. Popov in 1953 (see Hill 1977). Harrison (1964) assigned the Socotran populations to the smaller of the two species of the genus then recognised to occur in Africa and the Middle East, *R. hardwickei* (then comprising also several currently accepted species, including *R. cystops*, *R. muscatellum* and *R. macinnesi*) and *R. microphyllum* (Ellerman & Morrison-Scott 1951).

Kock (1969) revised taxonomy of the genus *Rhinopoma* Geoffroy, 1818, in its African and West Asian ranges; he examined the ZMB series from Socotra and found these bats larger in body size than bats from the surrounding areas of Arabia and the Horn of Africa, but in a closely similar size category as the bats from Mount Nuba at the transition of the Sahel and Savannah zones in Sudanese Kordofan. Kock (1969) classified the Socotran populations as a part of the species rank

Table 2. Basic biometric data on the examined Socotran and comparative samples of *Rhinopoma cystops* Thomas, 1903. For abbreviations see p. 103

	n	M	min	max	SD	n	M	min	max	SD
	Socotra					southern Arabia				
LC	10	<b>65.7</b>	61	68	2.452	36	<b>61.2</b>	56	67	2.724
LCd	10	<b>73.6</b>	70	77	2.271	35	<b>70.3</b>	62	78	3.816
LA <sub>t</sub>	35	<b>59.24</b>	56.0	63.3	1.995	52	<b>54.92</b>	50.5	58.9	2.016
LA	10	<b>21.23</b>	20.2	22.8	0.812	36	<b>20.51</b>	18.9	22.1	0.679
LT	10	<b>7.33</b>	6.7	8.0	0.356	36	<b>7.41</b>	6.4	8.3	0.530
LCr	30	<b>18.06</b>	17.34	18.98	0.434	54	<b>17.26</b>	16.26	18.82	0.524
LOc	26	<b>17.72</b>	16.89	18.54	0.450	28	<b>16.78</b>	15.98	17.46	0.421
LCb	23	<b>16.70</b>	15.98	17.48	0.428	34	<b>15.76</b>	14.95	16.38	0.431
LCC	28	<b>16.01</b>	15.24	16.73	0.385	45	<b>15.27</b>	14.39	16.32	0.406
LaZ	28	<b>10.39</b>	9.74	10.91	0.253	50	<b>9.92</b>	8.96	10.46	0.278
LaI	30	<b>2.69</b>	2.36	2.92	0.154	56	<b>2.53</b>	1.95	2.87	0.155
LaInf	30	<b>4.87</b>	4.52	5.25	0.205	56	<b>4.53</b>	3.92	4.99	0.223
LaNc	30	<b>7.69</b>	7.34	8.11	0.222	56	<b>7.32</b>	6.72	7.85	0.230
LaM	24	<b>9.00</b>	8.25	9.47	0.291	36	<b>8.60</b>	7.96	9.08	0.261
ANc	28	<b>5.78</b>	5.31	6.21	0.204	55	<b>5.47</b>	4.95	6.10	0.218
ACr	24	<b>7.83</b>	7.25	8.34	0.308	44	<b>7.44</b>	6.83	8.03	0.222
LBT	28	<b>4.68</b>	4.41	4.93	0.156	50	<b>4.73</b>	4.44	5.13	0.153
CC	30	<b>4.40</b>	4.11	4.93	0.181	56	<b>4.16</b>	3.62	4.71	0.189
M <sup>3</sup> M <sup>3</sup>	29	<b>7.98</b>	7.58	8.37	0.204	55	<b>7.54</b>	6.60	7.95	0.230
CM <sup>3</sup>	30	<b>6.17</b>	5.74	6.57	0.214	56	<b>5.77</b>	4.51	6.18	0.252
M <sup>1</sup> M <sup>3</sup>	29	<b>3.83</b>	3.62	4.17	0.126	53	<b>3.57</b>	3.29	3.82	0.130
CP <sup>4</sup>	28	<b>2.67</b>	2.42	2.93	0.159	44	<b>2.54</b>	2.27	2.83	0.129
LMd	30	<b>12.36</b>	11.83	13.11	0.369	57	<b>11.64</b>	10.83	12.55	0.343
ACo	30	<b>4.63</b>	4.33	4.89	0.149	57	<b>4.33</b>	3.79	4.75	0.197
CM <sub>3</sub>	30	<b>6.64</b>	6.37	6.93	0.173	57	<b>6.24</b>	5.82	6.58	0.182
MiM <sub>3</sub>	29	<b>4.30</b>	4.11	4.49	0.092	54	<b>4.01</b>	3.77	4.56	0.118
CP <sub>4</sub>	28	<b>2.54</b>	2.31	2.76	0.115	44	<b>2.38</b>	2.18	2.76	0.119
	Somaliland					Ethiopia				
LA <sub>t</sub>	12	<b>62.92</b>	59.7	67.0	2.826	3	<b>56.43</b>	54.5	57.8	1.721
LCr	12	<b>18.75</b>	17.91	19.34	0.350	2	<b>16.68</b>	16.55	16.81	0.184
LCC	12	<b>16.63</b>	15.97	16.98	0.294	3	<b>15.11</b>	14.95	15.33	0.199
LaZ	10	<b>10.67</b>	10.17	11.07	0.261	2	<b>9.69</b>	9.31	10.07	0.537
LaI	12	<b>2.62</b>	2.28	2.87	0.147	3	<b>2.44</b>	2.17	2.75	0.291
LaInf	12	<b>5.11</b>	4.54	5.37	0.230	3	<b>4.40</b>	4.38	4.42	0.021
LaNc	12	<b>7.99</b>	7.75	8.37	0.195	3	<b>7.40</b>	7.19	7.53	0.181
ANc	12	<b>5.86</b>	5.60	6.07	0.122	3	<b>5.58</b>	5.54	5.63	0.047
ACr	10	<b>7.80</b>	7.41	8.28	0.243	2	<b>7.20</b>	7.02	7.38	0.255
LBT	11	<b>4.93</b>	4.62	5.12	0.152	3	<b>4.63</b>	4.53	4.75	0.111
CC	12	<b>4.44</b>	4.14	4.74	0.206	2	<b>4.39</b>	4.36	4.41	0.035
M <sup>3</sup> M <sup>3</sup>	12	<b>8.12</b>	7.76	8.50	0.226	3	<b>7.65</b>	7.51	7.87	0.191
CM <sup>3</sup>	12	<b>6.41</b>	6.18	6.65	0.145	3	<b>5.66</b>	5.52	5.82	0.151
M <sup>1</sup> M <sup>3</sup>	12	<b>4.00</b>	3.73	4.27	0.134	3	<b>3.58</b>	3.45	3.76	0.163
CP <sup>4</sup>	12	<b>2.73</b>	2.58	2.84	0.091	3	<b>2.45</b>	2.36	2.56	0.101
LMd	12	<b>12.70</b>	12.29	13.15	0.274	3	<b>11.23</b>	10.88	11.42	0.301
ACo	12	<b>4.82</b>	4.57	5.18	0.167	3	<b>4.08</b>	3.87	4.26	0.197
CM <sub>3</sub>	12	<b>6.97</b>	6.82	7.17	0.135	3	<b>6.29</b>	6.12	6.42	0.155
MiM <sub>3</sub>	12	<b>4.51</b>	4.41	4.66	0.070	3	<b>4.05</b>	3.93	4.12	0.107
CP <sub>4</sub>	12	<b>2.63</b>	2.48	2.80	0.104	2	<b>2.41</b>	2.39	2.42	0.021

of *R. hardwickei*, although for the subspecies assignment he used slightly confusedly two names, *R. hardwickei cystops*, a small-sized form described from Egypt (type locality [t.l.] Luxor), and *R. h. sennaariense* Fitzinger, 1866, a large-sized form described from eastern Sudan (t.l. Sennaar and Fazuglo, restricted to Fazughli by Kock 1969). The latter name was shown a nomen nudum by Koopman (1975), who suggested instead to use the name *arabium* Thomas, 1913 (t.l. Wasil, Yemen).

The status and distribution of particular taxa of the genus *Rhinopoma* was completely reviewed by Hill (1977); this author examined the BMNH series of these bats from Socotra and attributed them to *R. hardwickei arabium*. He found these specimens to be the largest in body size among the samples from the Afro-Arabian area, along with the bats from Lower Egypt and Sudan. Hill (1977: 37) described the range of this subspecies as follows: “through Mauritania, Morocco, Algeria, Tunisia, Niger, Sudan, Lower Egypt, Ethiopia and French Somaliland [...]; it extends to the island of Socotra and to Israel, Jordan and Arabia, eastward to Iran.” Hayman & Hill (1971) and Corbet (1978) considered both Afro-Arabian forms of *R. hardwickei* recognised by other authors (Kock 1969, Gaisler et al. 1972, Koopman 1975, Hill 1977, etc.), i.e. *R. h. cystops* and *R. h. arabium*, to be rather consubspecific, representing a single taxon *R. h. cystops*, to which Corbet (1978) assigned also the bats from Socotra.

Several subsequent authors (Koopman 1982a, 1993, Qumsiyeh 1985, Harrison & Bates 1991, Nowak 1991, 1994) referred the Socotran populations of *Rhinopoma* (without examination of any specimen from Socotra) just to *R. hardwickei*, not providing a direct assignment to any subspecies. On the other hand, Qumsiyeh & Knox Jones (1986), in their monograph on *R. hardwickii* (they used the correct original Gray’s spelling of this name), did not mention Socotra within the species range of this bat at all.

Van Cakenberghe & De Vree (1994) published another taxonomic revision of the genus *Rhinopoma*, carried out with the help of a multivariate morphometric analysis. They examined the ZMB series of Socotran samples again and assigned them to *R. hardwickei arabium*, a subspecies accepted in the identical geographical distribution range as reported already by Hill (1977). The Socotran populations of *Rhinopoma* were referred to this species and/or subspecies, respectively, by most of recent authors, see the synonymy review below.

Hulva et al. (2007) performed a combined analysis of morphologic and genetic characters of the genus *Rhinopoma* from a large part of its distribution range. Three NMP specimens from Socotra were included into the molecular genetic part of the analysis, which showed them to be a component of the West Arabian sublineage of an Afro-Arabian species. This species was found to be rather deeply distant (8.2–9.5% of uncorrected genetic [*p*] distance in the partial cytochrome *b* gene) from the Iranian populations of *R. hardwickii*, and thus, representing a separate species, *R. cystops*. On the other hand, the morphological variation in the Afro-Arabian populations of this species, formerly considered to represent two subspecies defined by differences in body size, was demonstrated to be just a metric plasticity, caused perhaps by local environmental influences and not affecting the intraspecific structure that should be expressed in taxonomy. However, the Socotran haplotype, found also in the mainland of Yemen (Ma’rib), was found to be closely related to other Arabian haplotypes of *R. cystops* (0.2–1.0% of *p* distance, both from the north and south), while more distant from the African haplotypes within the *cystops* lineage (3.0–3.5%). Thus, the Arabian populations of *R. cystops* distributed from northern Israel in the north to Yemen, Socotra and western Oman in the south, were suggested by Hulva et al. (2007) to represent the subspecies *R. cystops arabium*, while the African populations, occurring in the whole northern Africa to the north of the Sahel zone (inclusive), the nominotypical subspecies *R. cystops cystops*. These relations between and within the Afro-Arabian and Irano-Indian lineages of the former *hardwickii* rank were again confirmed by a more profound analysis by Benda et al. (2012).



External and cranial dimensions of the available samples of *R. cystops* from the Socotran Archipelago (35 adult specimens including one from the Samha island; for the material examined see above) are shown in Table 2. A simple metric comparison of the Socotran specimens and samples from the surrounding regions showed a relatively large body size of the Socotran bats in relation to the samples from southern Arabia and Ethiopia (Table 2, Fig. 10). On the other hand, the specimens from the lowland Somaliland are in the longitudinal skull dimensions even larger than the Socotran bats and almost do not overlap in dimension ranges with the Arabian samples (Table 2, Fig. 10); in the rostrum parameters the Somalian samples rather conform to the Socotran bats (Fig. 11). The dimensions of the individual from Samha lie in the middle of the ranges of the Socotran samples (Figs. 10, 11). So, the Socotran populations of *R. cystops* represent a size transition between the Arabian and Somalian populations and in some aspects are closer to the Somalian bats. It is thus possible that the Somalian lowlands are inhabited by the same form which inhabits Socotra and Arabia (i.e. the lineage referred to *R. cystops arabium* by Hulva et al. 2007) and not by the form of the rest of the African species range (*R. c. cystops*) that is also geographically distant.

In the skull size, the Socotran and Somalian samples of *R. cystops* conform to the samples from northern Libya, and oversize other large-sized populations, i.e. those from Lower Egypt, the Maghreb and Levant (see Benda et al. 2004, 2006b, 2014). However, due to the extreme size plasticity known in *R. cystops* (cf. Kock 1969, Van Cakenberghe & De Vree 1994, Benda et al. 2004, 2006b, Hulva et al. 2007, etc.), the similarity of Socotran, Somalian and Libyan populations could represent convergent adaptations to similar environmental conditions. Nevertheless, the

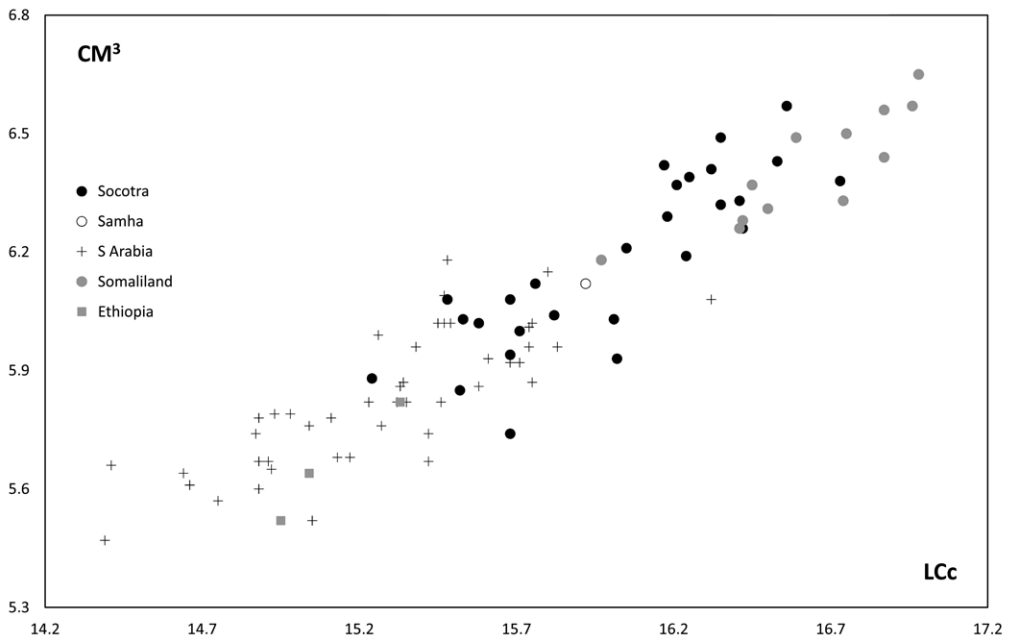


Fig. 10. Bivariate plot of the examined Socotran and comparative samples of *Rhinopoma cystops* Thomas, 1903: condylocanine length of skull (LCc) against the length of the upper tooth-row (CM<sup>3</sup>).

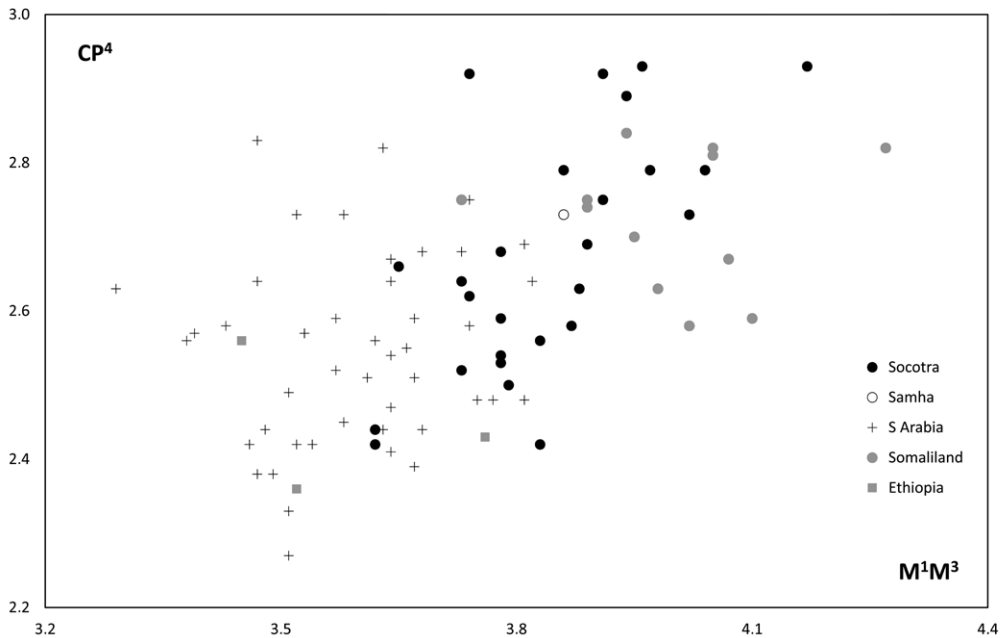


Fig. 11. Bivariate plot of the examined Socotran and comparative samples of *Rhinopoma cystops* Thomas, 1903: length of the upper molar-row ( $M^1M^3$ ) against the length of the upper unicuspidal tooth-row ( $CP^4$ ).

clarification of this question remains a task for another genetic comparison, the only approach which can determine the level of relationship among populations of *R. cystops* with certainty.

SYNONYMY REVIEW.

*Rhinopoma microphyllum* Geoff.[roy, 1818]: Taschenberg 1883: 160; Noack 1891: 133; De Winton et al. 1903: 6.

*Rhinopoma microphyllum* Brünnich, 1782: Anderson 1902: 147.

*Rhinopoma hardwickei* Gray, 1831: Harrison 1964: 56; Kock 1969: 35; Hayman & Hill 1971: 14; Hill 1977: 36; Corbet 1978: 40; Koopman 1982a: 127; Qumsiyeh 1985: 19; Wranik 1986: 15; Nowak 1991: 232; Koopman 1993: 155; Nowak 1994: 86; Van Cakenberghe & De Vree 1994: 14; Borisenko & Pavlinov 1995: 73; Al-Jumaily 1998: 481; Wranik 1998: 145; Nowak 1999: 305; Wranik 1999: 97; Wranik et al. 1999: 35; Bejček et al. 2001: 137; Šťastný et al. 2002: 30.

*Rhinopoma hardwickei sennaariense* Kock, 1969: 51.

*Rhinopoma hardwickei cystops* Thomas, 1903: Kock 1969: 44, 50; Corbet 1978: 40.

*Rhinopoma hardwickei arabium* Thomas, 1913: Hill 1977: 37; Van Cakenberghe & De Vree 1994: 16–17.

*Rhinopoma hardwickii* Gray, 1831: Harrison & Bates 1991: 29; Cesarini 2003: 6–17; Wranik et al. 2003: 85; Al-Jumaily 2004: 60; Nasher & Al Jumaily 2004: 70; Benda et al. 2005: 19; Simmons 2005: 380; Benda et al. 2006a: 139; De Geest 2006: 33; Cesarini 2007: 140.

*Rhinopoma cystops* Thomas, 1903: Hulva et al. 2007: 3, 8; Benda et al. 2009: 67; Benda et al. 2011b: 24; O'Brien 2011: 262, 287; Benda et al. 2012: 194.

*Rhinopoma cystops arabium* Thomas, 1913: Hulva et al. 2007: 3; Benda et al. 2009: 67.

### *Rhinolophus clivosus* Cretzschmar, 1828

RECORDS. **Original data:** Diksam plateau, Fornise area, Hofur cave [1], 8 May 2004: coll. 1 fs, NMP; – Diksam plateau, Marshim cave [2], at the cave entrance, 8 May 2004: net. 4 ma, 1 fs, BCSU, NMP (cf. Benda & Vallo 2012), 17 May 2004:

obs. & det. 5 foraging inds.; – Keisu oasis [3], at a stream in gardens, 21 May 2004: obs. 5–7 foraging inds., net. 2 fa, BCSU, NMP (cf. Benda & Vallo 2012); – Wadi Ayhaft, lower part [4], ceiling niche in a rocky overhang in the lower part of the wadi, 23 May 2004: obs. a roosting group of 7 inds.; – Wadi Darho [5], Desmoiten village, living house, 14 May 2004: coll. 1 fs, NMP. – **Published data:** Diksam, Hafur Cave [1], 8 September 2003: obs./exam. 1 m (Cesarini 2003, 2007); – Momi area, hillside cave [= Dahaisi cave] [6], [9 February] 1999: 1 fs (Wranik et al. 1999, 2003).

**DISTRIBUTION.** *Rhinolophus clivosus* is a rather rare bat in Socotra, only six known sites of its occurrence are available from the island (Table 1). Despite the rather small number of records, the sites are scattered over the whole island (Fig. 12).

*R. clivosus* has been the last bat species so far discovered to occur in Socotra, Wranik et al. (1999) reported a finding of a female in a hillside cave in the Momi area in the eastern part of Socotra. According to the photograph of the cave by Wranik et al. (2003) and mainly according to our field notes, we are able to localise this record precisely to the Dahaisi cave in the northern part of the Momi plateau, where the bat was found in February 1999. Another individual was discovered by Cesarini (2003) in the Hofur cave at the Diksam plateau in central Socotra in September 2003. The latter record suggests that the species survives on the island and creates there a viable population and that the first record did not represent an accidental arrival of a stray individual. In 2004 this supposition was confirmed since *R. clivosus* was documented from five sites scattered across Socotra, including the Hofur cave again. Hence, *R. clivosus* represents a rather rare but regular component of the island fauna (Benda et al. 2006a).

In a traditional view, *R. clivosus* is a species distributed across a huge area of rather dry habitats of the eastern part of Africa, in a broad belt stretching from South Africa to Egypt and southern Algeria, and in the adjacent western part of the Middle East, up to southern Levant, central Saudi Arabia and south-western Oman (Csorba et al. 2003, Simmons 2005, Bernard & Happold 2013). Considering this view, Socotra constitutes an organic part of this belt, continuing both to the north and west, to southern Arabia and the Horn of Africa. Along with the distribution in Dhofar, south-western Oman, the island of Socotra represents the easternmost area of the species range. (The definitely easternmost distribution point of *R. clivosus* is Mirbat, Dhofar (54° 41' E; Benda & Vallo 2012), lying some 42 km east of the Dahaisi cave, the easternmost site in Socotra.)

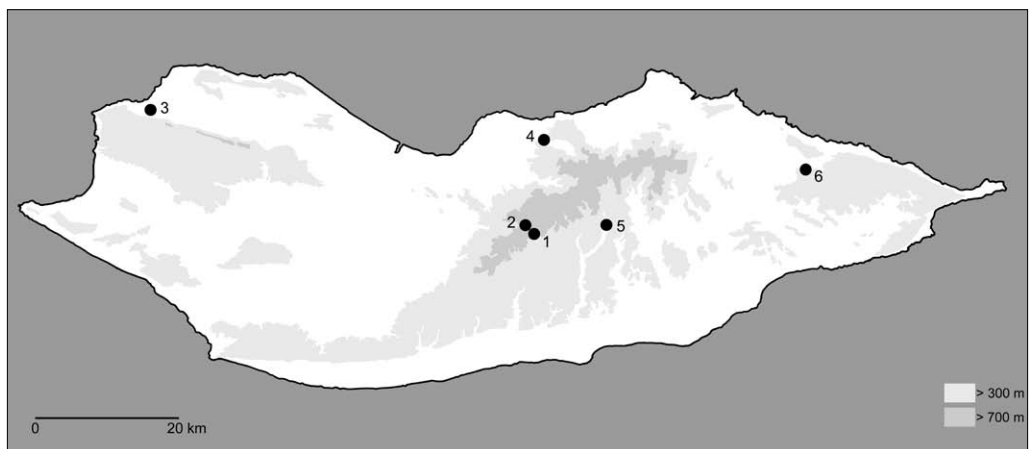


Fig. 12. Records of *Rhinolophus clivosus* Cretzschmar, 1828 in Socotra.

However, the results of the molecular genetic analysis by Benda & Vallo (2012) suggested that this traditional taxonomic concept of *R. clivosus* should be abandoned and this morphotype should be rather regarded a mixture of more lineages, representing several separate species (see below). In this view, *R. clivosus* s.str. represents a species occurring mostly in the Palaearctic part of the former geographical conception, in the Sahara and in the Middle East, and the island of Socotra represents the southernmost part of this range.

In Socotra, *R. clivosus* is distributed over a broad range of altitudes (885 m; Table 1), its records were made both in lower areas (Keisu oasis, 60 m a. s. l.) and in higher mountains (Diksam plateau, two sites situated above 850 m a. s. l.). However, *R. clivosus* could be considered as the most montane bat species in Socotra, the descriptive values of the record altitudes are the highest among the Socotran bats (Table 1), viz. altitude median 476.5 m, altitude mean 493.8 m a. s. l. The majority of the records of *R. clivosus* were made in roosts (83.3%, n=5) and the altitudinal range of the roost sites is only slightly narrower than the range of all records (825 m). However, the median and mean altitude values of the roosts are significantly higher than those of all records (588.0 m and 580.6 m a. s. l.; Table 1). These data clearly demonstrate that *R. clivosus* prefers high situated areas of Socotra, at least in comparison with other bat species.

FIELD NOTES. *Rhinolophus clivosus* was documented in Socotra mostly in or at its roosts, while only once at its foraging grounds. The majority of the roost findings represented solitary individuals, a roosting group was found once and another group of bats was netted when leaving their roost.



Fig. 13. An overhang in the lower part of Wadi Ayhaft, north-western slope of the Hagher massif (120 m a. s. l.); a roost of a small colony of *Rhinolophus clivosus*, composed of at least seven individuals, was discovered in the overhang in May 2004.



Fig. 14. Rocks at the entrance to the Marshim cave, Diksam plateau (945 m a. s. l.); five individuals of *Rhinolophus clivosus* were netted and echolocation calls of *Rhinopoma cystops* were detected at the entrance in May 2004. The type locality of *Rhinolophus clivosus socotranus* subsp. nov.

With only one exception, all documented roosts of *R. clivosus* in Socotra were natural karst caves. The roosting group of *R. clivosus* was discovered in the lower part of Wadi Ayhaft (at ca. 120 m a. s. l.) on 23 May 2004 (orig. data). The group of seven separately hanging adult individuals was found in a ceiling niche of a shallow rocky overhang eroded from the north-facing wadi slope (Fig. 13). However, the bats flew out of the niche before they were caught for examination. The shelter was a relatively shallow cavern (some 2–3 m deep) full of daylight and the bats were visible without using a torch.

Four adult males and one subadult female of *R. clivosus* were netted at the entrance to the Marshim cave at the Diksam plateau during the netting session on 8–9 May 2004 (orig. data). The male individuals were netted when leaving the cave during the evening emergence within 40 minutes after sunset, the female was caught when entering the cave from outside in the morning just before sunrise. The Marshim cave (Fig. 14) is a deep and extensive cave comprising also a subterranean river in a huge corridor (dry at the time of the check), full of roosting opportunities for a colony of *R. clivosus*.

At three sites, solitary individuals of *R. clivosus* were found. The first individual of this species from the island, a young female, was documented from the Dahaisi cave (“a hillside cave”) of the Momi area on 9 February 1999 by Wranik et al. (2003), who, however, did not give any close data on the finding. Cesarini (2003: 11–12) reported on another record as follows: “We found this species once, in Hafur Cave [= Hofur cave, 8 September 2003]. We captured just a solitary male. We saw other two flying bats in the huge cave, but it was impossible the[ir] species recognition. //



[...] The only relevant data is that we found “our” bat in a big cave [...].” Cesarini (2007) added climatic characteristics of this roost at the time of his visit in September 2003 – the air temperature inside the cave was 21.9 °C and relative humidity 89%. A single female of *R. clivosus* was found in the Hofur cave, the same roost as by Cesarini (2003, 2007), during day on 8 May 2004 (orig. data). The individual was in a deep torpor, hanging from a ceiling in the left part of the cave. The cave represents a low but spacious room with a broad entrance (Fig. 15); a larger and spacious part, situated to the right from the entrance, was used as a shelter for livestock and also (temporarily?) for locals.

The only artificial shelter of *R. clivosus* in Socotra was documented in the Wadi Darho on 14 May 2004 (orig. data); a subadult female was found in the Desmoiten village by the locals and given to us for examination. The bat roosted alone in a dwelling house in the centre of the village, the building was a simple wooden-stone house.

A group of several individuals of *R. clivosus* was observed foraging in fast flight above a small stream and among palm trees and other vegetation in the gardens of the Keisu oasis during sunset on 21 May 2004 (orig. data). The bats used echolocation calls with the maximum energy at ca. 90.5 kHz as shown by a heterodyne detector. Due to a very strong wind in the oasis after the sunset, the horseshoe bats hunted only among trees in the gardens for ca. 1.5 hour and then finished foraging. Two adult females of *R. clivosus* were caught by a hand net at this occasion in the gardens of the Keisu oasis. This group foraging at one spot very early after sunset indicates presence of a colony roost in a relatively close vicinity of the oasis; most probably, such roost could be situated in the northern slope (Kheyra) of the Maaleh hills rising just above the oasis (Figs. 16, 17), where a roost of another bat colony was found (*Rhinopoma cystops*, see above).

*R. clivosus* was found in a common roost with other bat species only once in Socotra, Wranik et al. (2003) reported a finding of one horseshoe bat together with an individual or individuals of



Fig. 15. Entrance to the Hofur cave, Diksam plateau (885 m a. s. l.); a solitary individual of *Rhinolophus clivosus* was twice discovered in this cave (Cesarini 2003, orig. data).



Figs. 16, 17. Two views of the oasis of Keisu, north-western Socotra (ca. 60 m a. s. l.), from the sea and from the Kheyra slope; in the oasis, a group of foraging individuals of *Rhinolophus clivosus* was recorded and in the Kheyra slope, a roost of a medium-sized colony of *Rhinopoma cystops* was discovered in May 2004.

*Rhinopoma cystops* in the Dahaisi cave. In Wadi Darho, where a roosting individual of *R. clivosus* was discovered in a house, two roosts of *R. cystops* were found nearby and also foraging of *Hypsugo lanzai* was documented there (see above and below). Thus, common foraging of all three bat species could be expected in the wadi, as the wadi represents a local centre of vegetation and habitats with a relatively high humidity, where the concentration of prey is certainly the highest within a considerable area. During the netting session at the Marshim cave on 8 May 2004, when the group of *R. clivosus* was caught, the foraging calls of several individuals of *Rhinopoma cystops* were detected around the cave entrance.

No direct signs of reproduction were recorded in the observed and/or examined Socotran individuals of *R. clivosus*.

**MATERIAL EXAMINED.** 1 ♀ (NMP 90589 [S+A]), Desmoiten, house, 14 May 2004, leg. P. Benda & A. Reiter; – 1 ♀ (NMP 90580 [S+A]), Hofur cave, Diksam plateau, 8 May 2004, leg. P. Benda & A. Reiter; – 2 ♀♀ (NMP 90593 [S+A], BCSU pb2751 [A]), Keisu, 21 May 2004, leg. P. Benda & A. Reiter; – 4 ♂♂, 1 ♀ (BCSU pb2736, NMP 90581, 90582 [S+A], BCSU pb2737, NMP 90583 [A]), Marshim cave, Diksam plateau, 8 May 2004, leg. P. Benda & A. Reiter.

**TAXONOMIC REMARKS.** The population of *Rhinolophus clivosus* inhabiting Socotra has been discovered only recently and limited data are available on its systematic position and taxonomy.

Cesarini (2003, 2007) examined a male of *R. clivosus* from the Hofur cave (the second individual of this bat known from the island) and compared its dimensions with those published by Harrison

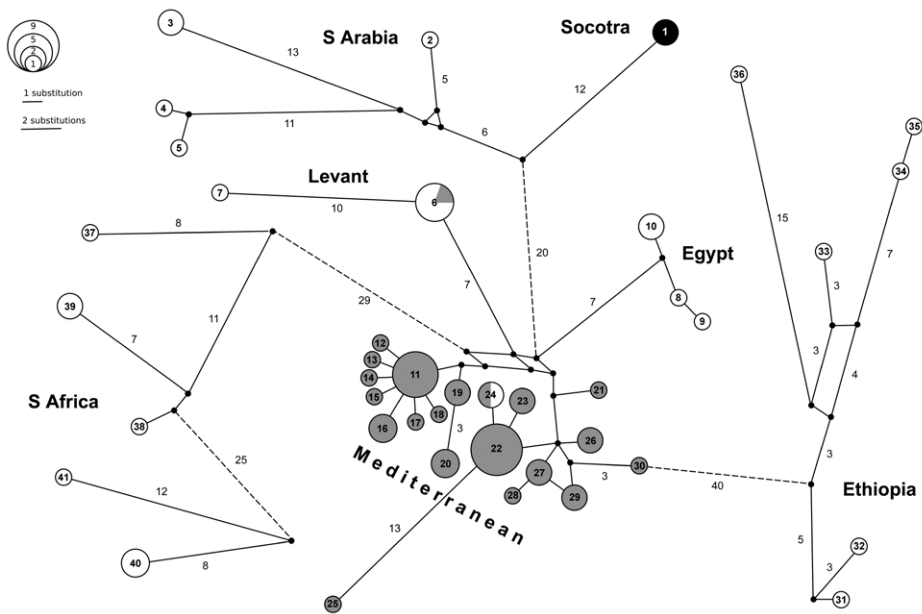


Fig. 18. Haplotype network of the *Rhinolophus ferrumequinum* / *clivosus* complex based on sequences of the mitochondrial gene for cytochrome *b*. The network was reconstructed using median-joining method in the Network v.5 program (Fluxus Technology Ltd, Suffolk, England). Legend: black circle = Socotran haplotype; white circles and sections = other haplotypes of *Rhinolophus clivosus* s.l.; grey circles and sections = haplotypes of *R. ferrumequinum*. The size of circles corresponds to frequencies of particular haplotypes. Numbers of haplotypes correspond with the numbering in Appendix III; numbers of substitutions between haplotypes are indicated by numbers next to the connecting lines. Dots indicate hypothetical missing haplotypes.



& Bates (1991) from the species samples of Arabia; Cesarini (2007: 142) described this observation as follows: “it is evident that its morphometrical measurements are closer to the northern subspecies (*Rhinolophus clivosus clivosus*, Israel and northern Saudi Arabia), and partially below the minimum in the range of variability of the southern subspecies (*Rhinolophus clivosus acrotis*, southern Saudi Arabia and Yemen).” Benda et al. (2006a) briefly examined and compared a series of *R. clivosus* from Socotra with other conspecifics. They referred the Socotran bats to “*R. aff. clivosus*” and stressed their extremely small body size, the smallest among the bats of the *clivosus* group. Besides the small body size, they also found some differences in skull characters, such as the relatively high coronoid process of mandible and relatively wide nasal swellings. Due to these distinctions and the geographical isolation on the island, Benda et al. (2006a) suggested the Socotran populations of *Rhinolophus* to represent a separate species.

Additionally, Benda & Vallo (2012) carried out molecular genetic analysis of the *Rhinolophus ferrumequinum / clivosus* complex including the samples from Socotra. In the comparison of a mitochondrial marker (complete sequences of the gene for cytochrome *b*), the Socotran haplotype was shown to be a part of the *R. clivosus* lineage, comprising also the samples of populations from southern Arabia (Yemen, Oman), but separated from the lineages from sub-Saharan Africa, which represent separate taxa, perhaps even species (but traditionally considered subspecies of *R. clivosus*, viz. *R. (c.) acrotis* von Heuglin, 1861 from the Ethiopian Highlands and *R. (c.) augur* Andersen, 1904 from southern and south-eastern Africa). Other two lineages, comprising also specimens nominally belonging to *R. clivosus*, were also separated from the Arabian-Socotran lineage; one deeply independent of the *R. ferrumequinum / clivosus* complex was described as a species of its own, *R. horaceki* Benda et Vallo, 2012, and the other comprising the Saharan and Levantine samples (i.e., also the nominotypical population of *R. clivosus*)

Table 3. Relative pairwise uncorrected genetic distances among and within the reconstructed *Rhinolophus* phylogroups (after Benda & Vallo 2012, modified). M = morphotype (after Benda & Vallo 2012): C = *R. clivosus* Cretzschmar, 1828 s.l. (including *R. horaceki* Benda & Vallo 2012), F = *R. ferrumequinum* (Schreber, 1774), H = *R. horaceki* Benda et Vallo, 2012. For legend see Fig. 19

sample set	M	Socotra	Yemen	Oman	Levant	Egypt	Ethiop.	E Africa	S Africa	Levant	Iran	Crimea	Crete	Europe	NW Afr.	Cyren.
Socotra	C	-														
Yemen	C	2.2-2.9	0.3-2.3													
Oman	C	2.5-2.6	0.1-2.3	0.1												
Levant	C	3.5-4.1	3.5-4.6	3.6-4.5	0.9-2.2											
Egypt	C	3.3-3.4	3.5-4.3	3.7-3.9	0.9-2.0	0.1-0.4										
Ethiopia	C	5.4-6.2	4.8-6.0	4.8-5.8	4.6-5.8	4.7-5.6	0.2-2.2									
E Africa	C	6.1-6.2	5.6-6.5	5.6-5.7	5.3-6.1	5.6	5.8-6.5	1.8								
S Africa	C	4.6-5.5	4.4-5.5	4.5-5.1	3.9-5.2	4.0-5.0	5.1-5.8	3.1-3.9	0.9-2.3							
Levant	F	3.0-3.4	3.2-3.9	3.4-3.6	0.1-2.3	1.2-1.6	4.3-5.2	4.9-5.6	3.6-4.8	0.2-1.3						
Iran	F	3.0-3.2	3.0-3.8	3.1-3.6	0.4-2.2	1.1-1.4	4.1-4.8	5.1-5.6	3.9-4.8	0.2-1.1	0.1-0.5					
Crimea	F	3.1	3.3-3.9	3.4-3.5	0.4-2.1	1.2-1.3	4.4-4.9	5.4-5.5	4.0-4.7	0.1-1.0	0.1-0.4	-				
Crete	F	3.0-3.3	3.0-3.7	3.3-3.7	1.2-2.1	1.4-1.7	4.1-5.0	4.9-5.2	3.6-4.6	0.2-1.3	0.9-1.2	1.0-1.1	0.2-0.3			
Europe	F	3.1-3.2	3.1-3.6	3.4-3.6	1.1-2.0	1.3-1.6	4.2-4.9	5.0-5.1	3.7-4.5	0.1-1.3	0.8-1.1	0.9-1.0	0.1-0.3	0.1-0.2		
NW Africa	F	3.2-3.5	3.2-3.9	3.5-3.9	1.0-2.2	1.3-1.7	4.3-5.2	4.9-5.4	3.6-4.7	0.4-1.3	0.7-1.2	0.8-1.1	0.4-0.7	0.3-0.6	0.3	
Cyrenaica	H	9.0-9.1	8.3-8.9	8.7-8.9	8.7-9.4	8.6-9.1	8.5-9.1	9.3-9.9	8.2-8.8	8.2-8.9	8.2-8.5	8.3-8.4	8.6-8.9	8.7-8.9	8.6-8.8	0.1

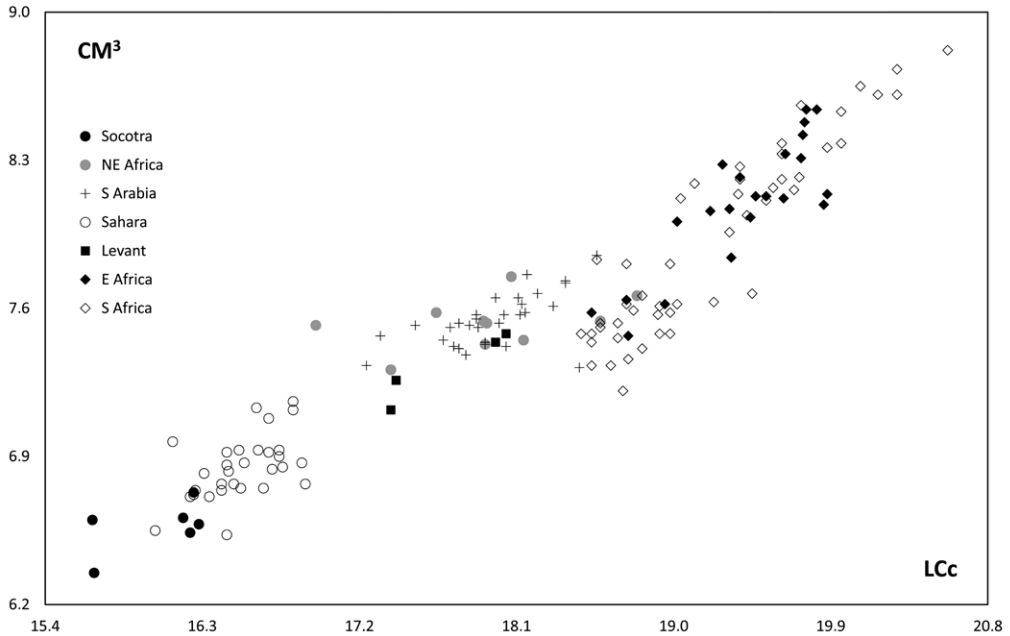


Fig. 19. Bivariate plot of the examined Socotran and comparative samples of *Rhinolophus clivosus* Cretzschmar, 1828: condylocanine length of skull (LCc) against the length of the upper tooth-row (CM<sup>3</sup>). Legend: NE Africa = samples of *R. (c.) acrotis* von Heuglin, 1861 from Ethiopia, Eritrea and Sudan; S Arabia = samples from Yemen and Oman; Sahara = samples from Algeria and continental Egypt; Levant = samples from Sinai, Saudi Arabia and Jordan; E Africa = samples of *R. (c.) augur* Andersen, 1904 from Kenya, Uganda, Tanzania, Rwanda, and Malawi; S Africa = samples of *R. (c.) augur* Andersen, 1904 from Lesotho, Mozambique and South Africa.

was shown to be a part of mixed lineage of *R. ferrumequinum* and *R. clivosus*, which contained three sublineages with unresolved relationships; viz. *R. clivosus* from Egypt and the Levant, *R. ferrumequinum* from the Middle East, and *R. ferrumequinum* from the central and western Mediterranean and from Cyprus.

These preliminary results gave certain evidence for a peculiar position of the Socotran populations of *R. clivosus* within this species or even genus. The position of the Socotran haplotype (identical from two specimens, see Appendix III) within the cytochrome *b* gene network of the *R. ferrumequinum* / *clivosus* complex (Fig. 18) is close to other haplotypes from southern Arabia (Yemen and Oman), which are the closest also geographically, and this group is markedly separated from all other haplotype groups of the complex (Fig. 18). The uncorrected genetic distance of the Socotran haplotype from the genetically closest haplotypes from southern Arabia is 2.2–2.9% (Table 3) and the internal distances within the southern Arabian haplotype group lie in the interval of 0.1–2.3% (Table 3). The separation of the Socotran populations from the Arabian populations is thus larger than that of particular haplotypes within southern Arabia. Interestingly, the Socotran haplotype is positioned closer to the haplotypes of *R. ferrumequinum* (3.0–3.5%) than to the haplotypes of *R. clivosus* (in its traditional sense) from sub-Saharan Africa (4.6–6.2%), including the geographically closely positioned Ethiopian samples (5.4–6.2%), as well as from the Levant and Sahara (3.3–4.1%), see Table 3.

The genetic separation of the southern Arabian populations (including the Socotran one) from the Saharan and Levantine haplotypes (which represent the nominotypical population of *R. clivosus*) suggest also their separate evolutionary position. However, the Levantine and Egyptian haplotypes of *R. clivosus* create a mixed group with the haplotypes of *R. ferrumequinum* from the whole western Palaearctic range of this species (Fig. 18), moreover, two haplotypes were found to be shared by individuals of *R. clivosus* and *R. ferrumequinum* from Jordan (Fig. 18). This situation suggests an irregularity in the mitochondrial pattern of the Mediterranean populations of the *R. ferrumequinum* / *clivosus* complex as it cannot indicate the species differences, which are clear from the morphologic characters of these named forms (see also Benda & Vallo 2012). An introgression of the mtDNA from one species to another cannot be excluded and thus, the mitochondrial marker seems to be insufficient for description of the inter- and intraspecific relations of the group in the Levant and adjacent areas. On the other hand, the southern Arabian populations (including the Socotran one) of *R. clivosus* could be perhaps considered as the genuine *clivosus* lineage without an influence of the *R. ferrumequinum* genome. Anyway, this speculation could be tested only by an analysis of the nuclear markers of the whole complex (for this problematics in other populations of the complex see Dool et al. 2016).

However, the position of the Socotran populations as the genetically most distant part of the southern Arabian haplotype group of *R. clivosus* seems to be sufficiently apparent. Further, the results of the genetic analysis do not correspond with the opinions by some authors (Harrison 1964, Nader 1990, Harrison & Bates 1991, Al-Jumaily 1998, Kock et al. 2002) on the occurrence of the Ethiopian form *R. c. acrotis* in the south of the Arabian Peninsula – the Ethiopian and Ara-

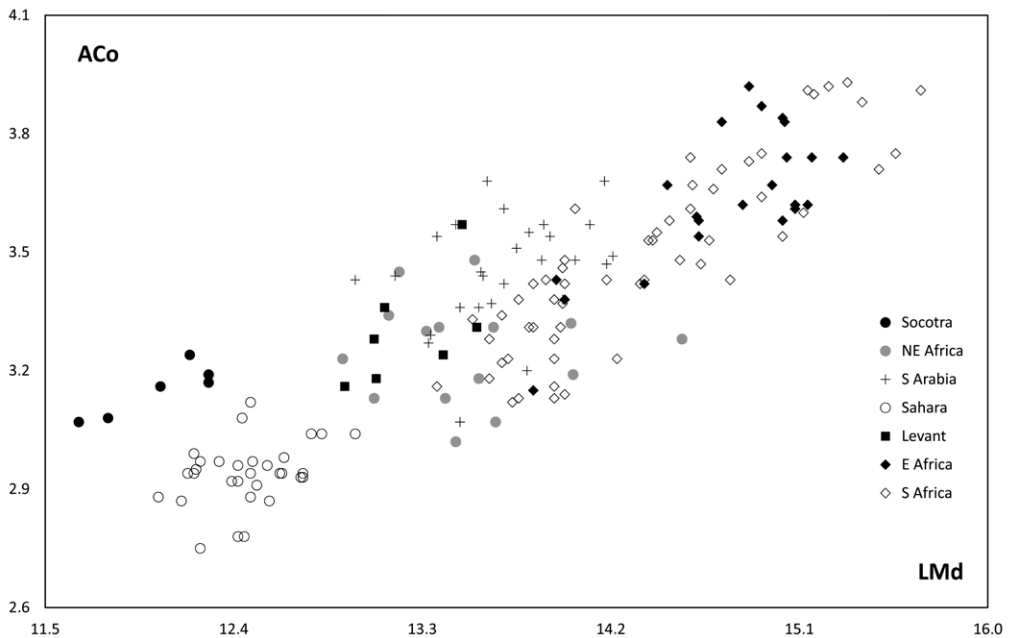


Fig. 20. Bivariate plot of the examined Socotran and comparative samples of *Rhinolophus clivosus* Cretzschmar, 1828: length of mandible (LMd) against the height of the coronoid process (ACo). For legend see Fig. 19.

Table 4. Basic biometric data on the examined Socotran and comparative samples of *Rhinolophus clivosus* Cretzschmar, 1828 and *R. horraceki* Benda et Vallo, 2012. Part 1: external and skull dimensions. For abbreviations see p. 103

	Socotra						Southern Arabia						Levant						Sahara						
	n	M	min	max	SD	n	M	min	max	SD	n	M	min	max	SD	n	M	min	max	SD	n	M	min	max	SD
LC	9	<b>53.8</b>	52	57	1.787	23	<b>59.1</b>	55	65	3.094	5	<b>58.6</b>	53	64	4.722	2	<b>55.0</b>	54	56	1.414	2	<b>55.0</b>	54	56	1.414
LCd	9	<b>31.6</b>	27	35	2.651	23	<b>34.4</b>	30	39	2.350	5	<b>33.2</b>	29	37	3.194	2	<b>29.0</b>	24	34	7.071	2	<b>29.0</b>	24	34	7.071
LAt	9	<b>45.54</b>	44.3	46.6	0.767	37	<b>49.55</b>	47.2	52.2	1.249	7	<b>48.71</b>	46.7	49.9	1.288	32	<b>47.21</b>	44.0	49.1	1.291	32	<b>47.21</b>	44.0	49.1	1.291
LA	9	<b>21.14</b>	19.8	21.8	0.629	23	<b>23.23</b>	21.1	24.2	0.850	5	<b>23.20</b>	22.0	24.6	1.056	2	<b>20.35</b>	20.0	20.7	0.495	2	<b>20.35</b>	20.0	20.7	0.495
LaFE	9	<b>7.67</b>	7.4	8.0	0.180	23	<b>8.33</b>	7.7	8.9	0.296	5	<b>8.26</b>	7.7	8.7	0.416	21	<b>6.61</b>	6.20	7.40	0.314	21	<b>6.61</b>	6.20	7.40	0.314
LCr	6	<b>18.74</b>	17.83	19.23	0.533	29	<b>20.96</b>	20.12	21.62	0.384	4	<b>20.86</b>	20.42	21.33	0.448	29	<b>19.36</b>	18.78	19.93	0.313	29	<b>19.36</b>	18.78	19.93	0.313
LCc	6	<b>16.05</b>	15.67	16.28	0.292	30	<b>17.96</b>	17.24	18.56	0.309	4	<b>17.70</b>	17.38	18.04	0.356	30	<b>16.53</b>	16.03	16.89	0.224	30	<b>16.53</b>	16.03	16.89	0.224
LaZ	6	<b>9.42</b>	9.19	9.64	0.168	30	<b>10.41</b>	10.02	10.93	0.220	4	<b>10.04</b>	9.65	10.26	0.269	29	<b>9.78</b>	9.33	10.24	0.204	29	<b>9.78</b>	9.33	10.24	0.204
LaI	6	<b>2.18</b>	1.94	2.51	0.186	30	<b>2.16</b>	1.81	2.61	0.232	7	<b>2.29</b>	2.08	2.54	0.181	31	<b>2.36</b>	2.19	2.58	0.105	31	<b>2.36</b>	2.19	2.58	0.105
LaInf	6	<b>4.75</b>	4.67	4.80	0.043	30	<b>5.53</b>	5.27	5.82	0.161	7	<b>5.40</b>	5.14	5.53	0.131	31	<b>4.88</b>	4.64	5.12	0.117	31	<b>4.88</b>	4.64	5.12	0.117
LaNc	6	<b>7.80</b>	7.52	7.96	0.169	30	<b>8.35</b>	8.04	8.67	0.152	4	<b>8.24</b>	8.14	8.38	0.104	30	<b>8.17</b>	7.88	8.47	0.153	30	<b>8.17</b>	7.88	8.47	0.153
LaM	6	<b>8.74</b>	8.62	8.90	0.105	30	<b>9.33</b>	8.95	9.68	0.194	4	<b>9.19</b>	9.05	9.48	0.199	30	<b>8.86</b>	8.65	9.09	0.115	30	<b>8.86</b>	8.65	9.09	0.115
ANc	6	<b>5.54</b>	5.29	5.74	0.146	31	<b>6.13</b>	5.52	6.57	0.264	4	<b>6.12</b>	5.86	6.39	0.287	30	<b>5.98</b>	5.64	6.35	0.174	30	<b>5.98</b>	5.64	6.35	0.174
ACr	6	<b>7.07</b>	6.77	7.31	0.197	30	<b>7.54</b>	7.13	7.89	0.166	4	<b>7.43</b>	7.19	7.56	0.167	30	<b>7.35</b>	7.07	7.76	0.193	30	<b>7.35</b>	7.07	7.76	0.193
LBT	6	<b>3.03</b>	2.81	3.35	0.195	22	<b>3.62</b>	3.21	3.84	0.143	5	<b>3.44</b>	3.22	3.59	0.151	28	<b>3.08</b>	2.81	3.42	0.157	28	<b>3.08</b>	2.81	3.42	0.157
CC	6	<b>4.91</b>	4.67	5.04	0.136	30	<b>5.63</b>	5.25	5.94	0.156	6	<b>5.39</b>	5.23	5.52	0.118	30	<b>5.10</b>	4.82	5.36	0.143	30	<b>5.10</b>	4.82	5.36	0.143
M3M <sup>3</sup>	6	<b>6.69</b>	6.62	6.82	0.068	30	<b>7.75</b>	7.34	8.22	0.181	7	<b>7.45</b>	7.18	7.65	0.190	30	<b>7.19</b>	6.93	7.66	0.183	30	<b>7.19</b>	6.93	7.66	0.183
CM <sup>3</sup>	6	<b>6.57</b>	6.35	6.73	0.124	32	<b>7.53</b>	7.16	7.85	0.144	6	<b>7.33</b>	7.12	7.48	0.133	31	<b>6.85</b>	6.53	7.16	0.148	31	<b>6.85</b>	6.53	7.16	0.148
M1M <sup>3</sup>	6	<b>4.25</b>	4.11	4.38	0.093	32	<b>4.78</b>	4.54	5.01	0.120	7	<b>4.62</b>	4.42	4.75	0.126	29	<b>4.40</b>	4.08	4.63	0.102	29	<b>4.40</b>	4.08	4.63	0.102
Cp <sup>+</sup>	6	<b>2.52</b>	2.44	2.70	0.097	22	<b>2.98</b>	2.74	3.28	0.147	6	<b>3.09</b>	2.87	3.26	0.158	30	<b>2.67</b>	2.52	2.89	0.117	30	<b>2.67</b>	2.52	2.89	0.117
LMd	6	<b>12.04</b>	11.66	12.28	0.261	32	<b>13.70</b>	12.98	14.21	0.303	7	<b>13.24</b>	12.93	13.56	0.243	31	<b>12.47</b>	12.04	12.98	0.222	31	<b>12.47</b>	12.04	12.98	0.222
ACo	6	<b>3.15</b>	3.07	3.24	0.066	28	<b>3.45</b>	3.07	3.68	0.140	7	<b>3.30</b>	3.16	3.57	0.138	31	<b>2.94</b>	2.75	3.12	0.081	31	<b>2.94</b>	2.75	3.12	0.081
CM <sub>5</sub>	6	<b>7.10</b>	7.01	7.24	0.091	32	<b>8.13</b>	7.76	8.49	0.159	6	<b>7.87</b>	7.61	8.13	0.181	31	<b>7.38</b>	7.05	7.62	0.144	31	<b>7.38</b>	7.05	7.62	0.144
M1M <sub>3</sub>	6	<b>4.71</b>	4.62	4.88	0.095	32	<b>5.46</b>	5.16	5.74	0.124	7	<b>5.27</b>	4.96	5.38	0.146	30	<b>5.00</b>	4.67	5.34	0.145	30	<b>5.00</b>	4.67	5.34	0.145
CP <sub>4</sub>	6	<b>2.44</b>	2.42	2.46	0.015	22	<b>2.81</b>	2.59	3.08	0.118	6	<b>2.69</b>	2.57	2.96	0.138	30	<b>2.53</b>	2.31	2.78	0.115	30	<b>2.53</b>	2.31	2.78	0.115

Table 4. (continued)

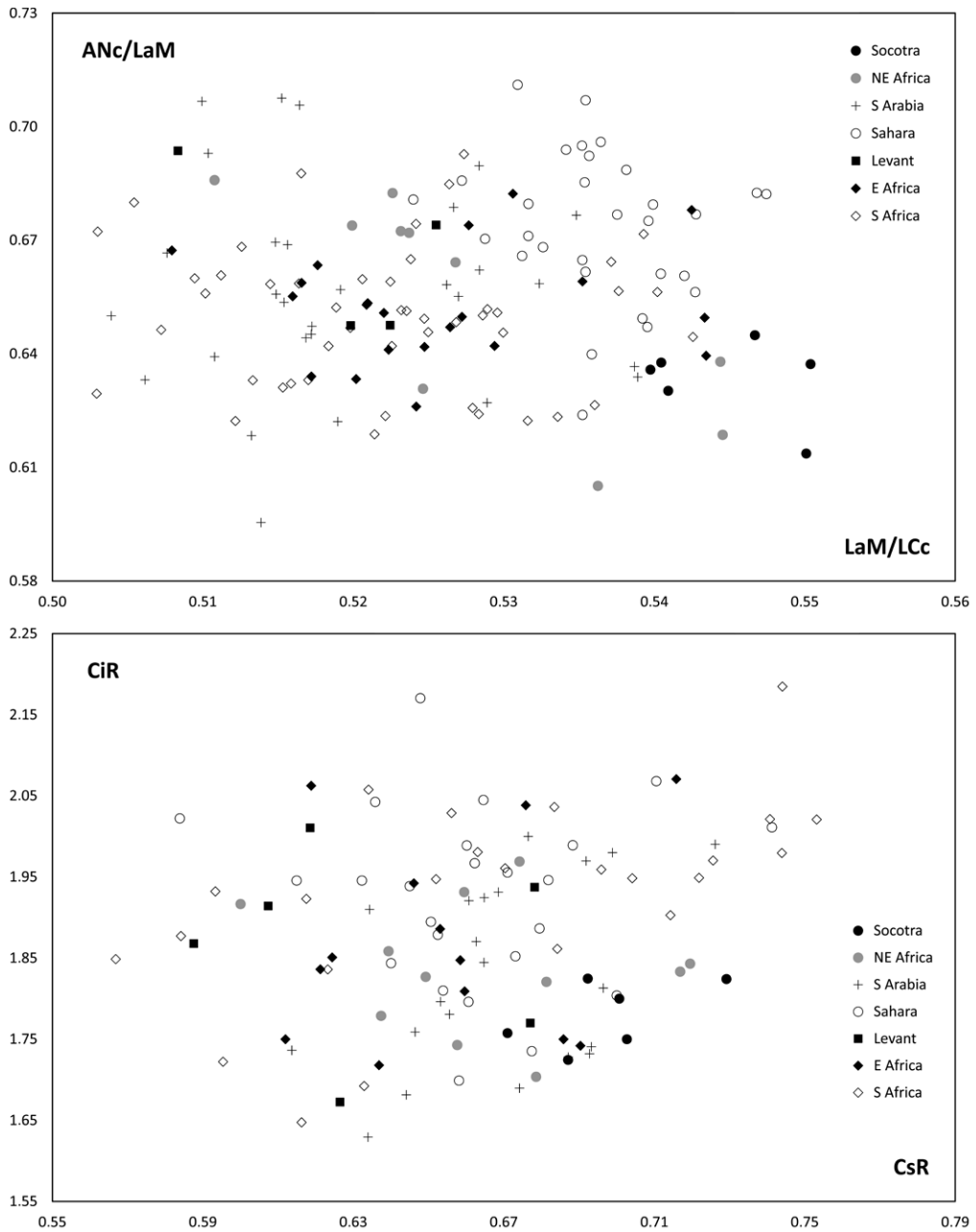
	<i>R. (c.) acrotis</i>					<i>R. (c.) augur</i>					<i>R. (c.) augur</i>					<i>R. horaceki</i>									
	North-eastern Africa					East Africa					Southern Africa					Cyrenaica									
	n	M	min	max	SD	n	M	min	max	SD	n	M	min	max	SD	n	M	min	max	SD	n	M	min	max	SD
LC	6	66.7	64	71	2.805	3	57.6	55	59	2.228	13	72.8	69	78	2.651	8	59.9	56	63	2.100	8	59.9	56	63	2.100
LCd	6	31.2	29	33	1.602	3	34.0	31	36	2.646	14	33.4	28	41	3.589	8	31.8	26	38	4.097	8	31.8	26	38	4.097
LAt	13	50.24	44.6	53.2	3.092	23	54.58	52.3	56.9	1.400	61	53.46	49.2	57.4	1.725	8	48.74	47.7	50.2	0.857	8	48.74	47.7	50.2	0.857
LA	6	22.12	20.5	23.1	0.966	3	21.47	20.0	23.0	1.501	13	23.18	22.8	23.6	0.273	8	21.48	20.6	22.7	0.742	8	21.48	20.6	22.7	0.742
LaFE	8	7.76	6.8	8.8	0.655	20	8.07	6.8	8.9	0.586	22	8.41	7.4	9.1	0.438	5	7.18	6.9	7.5	0.217	5	7.18	6.9	7.5	0.217
LCr	13	20.98	19.93	22.11	0.624	17	22.57	21.42	23.31	0.506	37	22.28	20.63	23.57	0.650	5	20.54	20.16	20.88	0.262	5	20.54	20.16	20.88	0.262
LCC	9	18.04	17.38	18.79	0.434	22	19.40	18.53	19.88	0.395	49	19.22	18.47	20.57	0.559	8	17.72	17.48	18.07	0.231	8	17.72	17.48	18.07	0.231
LaZ	11	10.60	9.94	10.93	0.271	22	11.51	10.87	12.04	0.285	54	11.15	10.12	12.06	0.527	8	10.79	10.67	10.96	0.113	8	10.79	10.67	10.96	0.113
LaI	14	2.46	2.16	2.75	0.182	22	2.65	2.39	3.11	0.169	57	2.67	2.29	2.98	0.183	8	2.35	2.21	2.48	0.099	8	2.35	2.21	2.48	0.099
LaInf	14	5.26	4.93	5.48	0.164	22	5.81	5.34	6.16	0.223	56	5.60	5.28	5.92	0.164	8	5.71	5.64	5.77	0.052	8	5.71	5.64	5.77	0.052
LaNc	13	8.54	8.22	8.93	0.241	22	9.26	8.82	9.81	0.240	53	9.04	8.47	9.65	0.288	8	8.53	8.26	8.66	0.136	8	8.53	8.26	8.66	0.136
LaM	13	9.47	9.01	9.83	0.222	21	10.19	9.86	10.53	0.179	49	10.03	9.42	10.60	0.211	8	9.49	9.29	9.63	0.129	8	9.49	9.29	9.63	0.129
ANc	12	6.20	5.64	6.61	0.305	21	6.65	6.38	7.07	0.201	49	6.52	5.93	7.09	0.257	8	6.20	6.02	6.44	0.145	8	6.20	6.02	6.44	0.145
ACr	11	7.59	7.32	7.83	0.141	12	7.98	7.62	8.38	0.291	42	7.94	6.57	8.52	0.338	5	7.64	7.52	7.80	0.121	5	7.64	7.52	7.80	0.121
LBT	12	3.32	2.81	3.79	0.306	21	3.29	2.93	3.75	0.220	52	3.49	3.06	4.08	0.240	8	3.41	3.07	3.73	0.200	8	3.41	3.07	3.73	0.200
CC	14	5.50	5.19	5.76	0.158	22	6.04	5.61	6.37	0.212	55	5.80	5.12	6.60	0.401	8	5.92	5.81	6.07	0.090	8	5.92	5.81	6.07	0.090
M3M <sup>3</sup>	14	7.66	7.29	7.98	0.190	22	8.27	7.63	8.74	0.280	55	8.06	7.23	8.96	0.456	8	7.84	7.71	8.08	0.117	8	7.84	7.71	8.08	0.117
CM <sup>3</sup>	14	7.52	7.31	7.75	0.112	22	8.09	7.47	8.54	0.307	57	7.85	7.09	8.82	0.447	8	7.39	7.28	7.57	0.092	8	7.39	7.28	7.57	0.092
M1M <sup>3</sup>	14	4.78	4.62	4.97	0.115	13	5.15	4.74	5.58	0.216	44	4.99	4.64	5.59	0.270	5	4.77	4.67	4.87	0.083	5	4.77	4.67	4.87	0.083
CP <sup>4</sup>	14	2.88	2.42	3.17	0.174	13	3.19	3.05	3.47	0.118	44	3.12	2.78	3.58	0.205	5	3.18	2.93	3.32	0.146	5	3.18	2.93	3.32	0.146
LMD	14	13.55	12.92	14.54	0.420	22	14.76	13.83	15.31	0.416	57	14.34	13.37	15.68	0.597	8	13.50	13.23	13.93	0.272	8	13.50	13.23	13.93	0.272
ACo	14	3.24	3.02	3.48	0.133	22	3.64	3.15	3.92	0.182	57	3.48	3.12	3.93	0.233	8	3.41	3.28	3.61	0.108	8	3.41	3.28	3.61	0.108
CM <sub>3</sub>	14	8.04	7.77	8.49	0.209	22	8.65	7.98	9.09	0.285	57	8.40	7.64	9.56	0.534	8	8.09	7.91	8.29	0.140	8	8.09	7.91	8.29	0.140
M1M <sub>3</sub>	14	5.42	5.24	5.79	0.141	13	5.80	5.51	6.19	0.231	44	5.71	5.17	6.43	0.332	5	5.42	5.39	5.47	0.035	5	5.42	5.39	5.47	0.035
CP <sub>4</sub>	14	2.72	2.58	2.88	0.099	13	2.98	2.63	3.19	0.174	44	2.94	2.45	3.43	0.260	5	2.96	2.84	3.06	0.087	5	2.96	2.84	3.06	0.087

Table 5. Basic biometric data on the examined Socotran and comparative samples of *Rhinolophus clivostus* Cretzschmar, 1828 and *R. horaceki* Benda et Vallo, 2012. Part 2: relative skull dimensions. For abbreviations see p. 103

	Socotra				Southern Arabia				Levant				Sahara							
	n	M	min	max	n	M	min	max	n	M	min	max	n	M	min	max	SD			
LaZ/LCc	6	<b>0.587</b>	0.575	0.594	0.007	<b>0.580</b>	0.555	0.605	0.013	4	<b>0.567</b>	0.554	0.581	0.011	29	<b>0.592</b>	0.569	0.613	0.011	
LaInf/LCc	6	<b>0.296</b>	0.293	0.303	0.004	29	<b>0.308</b>	0.293	0.324	0.008	4	<b>0.305</b>	0.295	0.315	0.009	30	<b>0.295</b>	0.284	0.311	0.007
LaInf/CM <sup>3</sup>	6	<b>0.723</b>	0.707	0.748	0.015	30	<b>0.734</b>	0.699	0.774	0.017	6	<b>0.735</b>	0.708	0.770	0.021	31	<b>0.713</b>	0.674	0.769	0.018
LaN/LCc	6	<b>0.486</b>	0.473	0.501	0.009	29	<b>0.465</b>	0.444	0.481	0.010	4	<b>0.466</b>	0.459	0.471	0.005	30	<b>0.494</b>	0.480	0.513	0.008
LaM/LCc	6	<b>0.545</b>	0.539	0.550	0.005	29	<b>0.520</b>	0.504	0.539	0.010	4	<b>0.519</b>	0.508	0.526	0.008	30	<b>0.536</b>	0.524	0.547	0.005
ANe/LCc	6	<b>0.345</b>	0.338	0.353	0.006	30	<b>0.341</b>	0.306	0.365	0.015	4	<b>0.345</b>	0.337	0.354	0.009	30	<b>0.362</b>	0.334	0.379	0.010
ANe/LaM	6	<b>0.634</b>	0.614	0.645	0.011	30	<b>0.657</b>	0.595	0.708	0.027	4	<b>0.666</b>	0.648	0.694	0.022	30	<b>0.674</b>	0.624	0.711	0.019
LBT/LCc	6	<b>0.189</b>	0.173	0.214	0.014	22	<b>0.202</b>	0.176	0.214	0.009	4	<b>0.197</b>	0.195	0.200	0.002	28	<b>0.186</b>	0.171	0.206	0.009
LBT/LaM	6	<b>0.347</b>	0.320	0.388	0.024	22	<b>0.388</b>	0.342	0.414	0.018	4	<b>0.380</b>	0.375	0.393	0.008	28	<b>0.347</b>	0.320	0.383	0.018
LBT/ANc	6	<b>0.547</b>	0.507	0.609	0.036	22	<b>0.584</b>	0.511	0.637	0.033	4	<b>0.571</b>	0.559	0.582	0.011	28	<b>0.515</b>	0.459	0.596	0.033
CC/CM <sup>3</sup>	6	<b>0.747</b>	0.708	0.775	0.023	30	<b>0.748</b>	0.708	0.788	0.020	6	<b>0.735</b>	0.720	0.751	0.012	30	<b>0.745</b>	0.711	0.782	0.021
CC/CP <sup>4</sup>	6	<b>1.953</b>	1.867	2.049	0.063	22	<b>1.903</b>	1.759	2.062	0.090	6	<b>1.746</b>	1.622	1.906	0.098	29	<b>1.914</b>	1.712	2.044	0.079
M <sup>3</sup> /LCc	6	<b>0.417</b>	0.410	0.425	0.006	29	<b>0.432</b>	0.410	0.447	0.010	4	<b>0.418</b>	0.412	0.425	0.005	29	<b>0.435</b>	0.413	0.471	0.011
M <sup>3</sup> /CM <sup>3</sup>	6	<b>1.019</b>	1.003	1.049	0.016	30	<b>1.030</b>	0.977	1.081	0.026	6	<b>1.019</b>	0.989	1.043	0.019	30	<b>1.050</b>	1.022	1.137	0.025
M <sup>3</sup> /LCc	6	<b>0.442</b>	0.432	0.452	0.008	30	<b>0.454</b>	0.428	0.468	0.008	4	<b>0.445</b>	0.438	0.451	0.006	30	<b>0.446</b>	0.435	0.464	0.007
CP <sup>4</sup> /CM <sup>3</sup>	6	<b>0.383</b>	0.370	0.401	0.012	22	<b>0.394</b>	0.364	0.424	0.016	6	<b>0.422</b>	0.394	0.456	0.023	30	<b>0.390</b>	0.370	0.429	0.015
ACo/LMd	6	<b>0.262</b>	0.258	0.266	0.003	28	<b>0.252</b>	0.228	0.270	0.010	7	<b>0.249</b>	0.242	0.265	0.008	31	<b>0.236</b>	0.223	0.250	0.006

	<i>R. (c.) acrois</i> North-eastern Africa				<i>R. (c.) augur</i> East Africa				<i>R. (c.) augur</i> Southern Africa				<i>R. horaceki</i> Cyrenaica							
	n	M	min	max	n	M	min	max	n	M	min	max	n	M	min	max	SD			
LaZ/LCc	9	<b>0.589</b>	0.564	0.614	0.015	22	<b>0.593</b>	0.570	0.617	0.011	49	<b>0.583</b>	0.546	0.615	0.015	8	<b>0.609</b>	0.599	0.619	0.006
LaInf/LCc	9	<b>0.292</b>	0.265	0.306	0.012	22	<b>0.299</b>	0.285	0.313	0.008	49	<b>0.292</b>	0.275	0.313	0.008	8	<b>0.322</b>	0.314	0.326	0.004
LaInf/CM <sup>3</sup>	14	<b>0.699</b>	0.654	0.728	0.019	22	<b>0.718</b>	0.693	0.747	0.013	56	<b>0.714</b>	0.642	0.778	0.031	8	<b>0.773</b>	0.762	0.787	0.010
LaN/LCc	9	<b>0.475</b>	0.464	0.484	0.006	22	<b>0.478</b>	0.456	0.498	0.012	49	<b>0.472</b>	0.447	0.497	0.012	8	<b>0.482</b>	0.471	0.488	0.005
LaM/LCc	9	<b>0.526</b>	0.511	0.544	0.010	21	<b>0.526</b>	0.508	0.543	0.009	48	<b>0.522</b>	0.503	0.543	0.010	8	<b>0.536</b>	0.530	0.541	0.004
ANe/LCc	9	<b>0.346</b>	0.325	0.357	0.011	21	<b>0.343</b>	0.328	0.368	0.010	48	<b>0.340</b>	0.317	0.365	0.011	8	<b>0.350</b>	0.333	0.362	0.009
ANe/LaM	12	<b>0.656</b>	0.605	0.706	0.033	21	<b>0.652</b>	0.626	0.682	0.015	48	<b>0.650</b>	0.619	0.693	0.018	8	<b>0.654</b>	0.625	0.674	0.017
LBT/LCc	9	<b>0.183</b>	0.151	0.213	0.019	21	<b>0.170</b>	0.155	0.190	0.011	49	<b>0.182</b>	0.157	0.220	0.015	8	<b>0.193</b>	0.176	0.206	0.010
LBT/LaM	12	<b>0.350</b>	0.291	0.416	0.037	21	<b>0.323</b>	0.291	0.364	0.021	49	<b>0.347</b>	0.299	0.417	0.026	8	<b>0.360</b>	0.329	0.387	0.019
LBT/ANc	11	<b>0.541</b>	0.432	0.659	0.069	21	<b>0.495</b>	0.449	0.574	0.034	49	<b>0.536</b>	0.436	0.660	0.048	8	<b>0.551</b>	0.498	0.620	0.035
CC/CM <sup>3</sup>	14	<b>0.732</b>	0.702	0.758	0.015	22	<b>0.746</b>	0.719	0.790	0.016	55	<b>0.737</b>	0.685	0.799	0.023	8	<b>0.802</b>	0.787	0.821	0.013
CC/CP <sup>4</sup>	14	<b>1.917</b>	1.779	2.306	0.139	13	<b>1.899</b>	1.798	1.990	0.058	43	<b>1.885</b>	1.673	2.062	0.096	5	<b>1.874</b>	1.810	1.993	0.075
M <sup>3</sup> /LCc	9	<b>0.429</b>	0.407	0.446	0.014	22	<b>0.426</b>	0.407	0.445	0.009	48	<b>0.422</b>	0.385	0.455	0.016	8	<b>0.442</b>	0.430	0.456	0.009
M <sup>3</sup> /CM <sup>3</sup>	14	<b>1.019</b>	0.986	1.060	0.022	22	<b>1.023</b>	0.994	1.057	0.019	55	<b>1.025</b>	0.975	1.077	0.021	8	<b>1.061</b>	1.026	1.093	0.022
CM <sup>3</sup> /LCc	9	<b>0.450</b>	0.434	0.472	0.013	22	<b>0.446</b>	0.426	0.460	0.009	49	<b>0.440</b>	0.413	0.476	0.018	8	<b>0.457</b>	0.450	0.468	0.006
CP <sup>4</sup> /CM <sup>3</sup>	14	<b>0.383</b>	0.325	0.409	0.021	13	<b>0.394</b>	0.368	0.418	0.013	44	<b>0.392</b>	0.356	0.430	0.014	5	<b>0.429</b>	0.398	0.441	0.018
ACo/LMd	14	<b>0.239</b>	0.224	0.262	0.012	22	<b>0.246</b>	0.228	0.264	0.009	57	<b>0.242</b>	0.225	0.258	0.009	8	<b>0.253</b>	0.245	0.269	0.008



Figs. 21, 22. Bivariate plots of the examined Socotran and comparative samples of *Rhinolophus clivus* Cretzschmar, 1828. 21 (top) – relative width of neurocranium (LaM/LCc) against the relative height of neurocranium (ANc/LaM). 22 (below) – relative length of the upper canine (CsR) against the relative length of the lower canine (CiR); the canine lengths are in relation to the molar length of the respective jaw (see pp. 103–104). For legend see Fig. 19.

Table 6. Basic biometric data on the examined Socotran and comparative samples of *Rhinolophus clivosus* Cretzschmar, 1828 and *R. horraceki* Benda et Vallo, 2012. Part 3: tooth dimensions. For abbreviations see pp. 103–104

	Socotra					Southern Arabia					Levant					Sahara				
	n	M	min	max	SD	n	M	min	max	SD	n	M	min	max	SD	n	M	min	max	SD
LCs	6	<b>1.565</b>	1.51	1.63	0.051	21	<b>1.809</b>	1.71	1.92	0.062	6	<b>1.784</b>	1.69	1.85	0.069	24	<b>1.640</b>	1.50	1.77	0.062
LaCs	6	<b>1.360</b>	1.32	1.43	0.041	21	<b>1.541</b>	1.44	1.70	0.064	6	<b>1.423</b>	1.31	1.61	0.102	23	<b>1.360</b>	1.24	1.49	0.066
LP <sub>2</sub>	0	—	—	—	—	1	0.22	—	—	—	0	—	—	—	—	0	—	—	—	—
LP <sub>4</sub>	6	<b>1.288</b>	1.24	1.36	0.043	21	<b>1.581</b>	1.49	1.77	0.065	7	<b>1.473</b>	1.34	1.63	0.091	24	<b>1.418</b>	1.32	1.56	0.065
LP <sub>2</sub>	6	<b>0.902</b>	0.87	0.98	0.045	20	<b>1.029</b>	0.90	1.13	0.069	7	<b>0.889</b>	0.75	1.01	0.091	24	<b>0.901</b>	0.81	1.03	0.058
LP <sub>3</sub>	6	<b>0.710</b>	0.66	0.75	0.038	20	<b>0.819</b>	0.69	0.92	0.060	7	<b>0.743</b>	0.61	0.84	0.094	24	<b>0.712</b>	0.66	0.86	0.046
LaP <sub>4</sub>	6	<b>2.056</b>	2.00	2.12	0.044	21	<b>2.385</b>	2.26	2.51	0.071	7	<b>2.289</b>	2.15	2.52	0.122	24	<b>2.135</b>	1.97	2.35	0.091
LM <sub>1</sub>	6	<b>1.761</b>	1.67	1.83	0.059	21	<b>1.986</b>	1.84	2.05	0.052	7	<b>1.936</b>	1.82	2.03	0.077	24	<b>1.801</b>	1.67	1.93	0.060
LaM <sub>1</sub>	6	<b>2.518</b>	2.41	2.62	0.075	21	<b>2.963</b>	2.85	3.07	0.071	7	<b>2.800</b>	2.65	2.94	0.102	24	<b>2.669</b>	2.38	2.88	0.127
LM <sub>3</sub>	6	<b>1.091</b>	1.06	1.13	0.024	21	<b>1.208</b>	1.13	1.29	0.042	7	<b>1.143</b>	1.04	1.24	0.073	24	<b>1.085</b>	0.98	1.14	0.042
LaM <sub>3</sub>	6	<b>1.772</b>	1.70	1.84	0.056	21	<b>1.997</b>	1.87	2.12	0.071	7	<b>1.955</b>	1.63	2.11	0.158	24	<b>1.861</b>	1.69	1.98	0.073
LCi	6	<b>1.005</b>	0.95	1.04	0.030	21	<b>1.122</b>	1.03	1.21	0.062	6	<b>1.072</b>	0.98	1.18	0.074	24	<b>0.986</b>	0.92	1.08	0.054
LP <sub>2</sub>	6	<b>0.565</b>	0.51	0.60	0.030	21	<b>0.706</b>	0.60	0.88	0.061	6	<b>0.625</b>	0.49	0.72	0.080	24	<b>0.617</b>	0.50	0.73	0.057
LaP <sub>2</sub>	6	<b>0.700</b>	0.65	0.74	0.033	21	<b>0.908</b>	0.65	1.08	0.096	6	<b>0.805</b>	0.60	0.96	0.131	24	<b>0.808</b>	0.74	0.95	0.054
LP <sub>3</sub>	0	—	—	—	—	1	0.17	—	—	—	0	—	—	—	—	1	0.14	—	—	—
LP <sub>4</sub>	6	<b>1.075</b>	1.04	1.12	0.028	21	<b>1.204</b>	1.13	1.28	0.041	7	<b>1.113</b>	1.02	1.19	0.062	24	<b>1.114</b>	0.98	1.24	0.065
LaP <sub>4</sub>	6	<b>0.949</b>	0.92	1.02	0.038	21	<b>1.123</b>	0.98	1.25	0.082	7	<b>1.044</b>	0.86	1.17	0.116	24	<b>0.950</b>	0.82	1.09	0.072
LM <sub>1</sub>	6	<b>1.789</b>	1.74	1.85	0.043	21	<b>2.047</b>	1.97	2.15	0.051	7	<b>1.987</b>	1.85	2.10	0.083	24	<b>1.896</b>	1.71	2.01	0.062
CsR	6	<b>0.697</b>	0.671	0.729	0.019	21	<b>0.669</b>	0.614	0.726	0.027	6	<b>0.633</b>	0.588	0.678	0.037	24	<b>0.662</b>	0.584	0.741	0.032
CsR1	6	<b>0.869</b>	0.840	0.884	0.018	21	<b>0.852</b>	0.809	0.906	0.029	6	<b>0.798</b>	0.743	0.885	0.051	23	<b>0.829</b>	0.756	0.910	0.034
P <sup>a</sup> R	6	<b>0.551</b>	0.521	0.587	0.022	20	<b>0.517</b>	0.462	0.573	0.033	7	<b>0.503</b>	0.433	0.554	0.043	24	<b>0.503</b>	0.436	0.607	0.039
P <sup>a</sup> R2	6	<b>0.626</b>	0.605	0.642	0.012	21	<b>0.663</b>	0.628	0.742	0.025	7	<b>0.644</b>	0.605	0.691	0.026	24	<b>0.665</b>	0.617	0.725	0.029
P <sup>a</sup> R3	6	<b>0.345</b>	0.325	0.372	0.018	20	<b>0.343</b>	0.305	0.387	0.025	7	<b>0.325</b>	0.276	0.365	0.035	24	<b>0.334</b>	0.304	0.375	0.022
M <sup>a</sup> R	6	<b>1.431</b>	1.389	1.497	0.039	21	<b>1.493</b>	1.409	1.621	0.051	7	<b>1.447</b>	1.381	1.487	0.044	24	<b>1.482</b>	1.381	1.581	0.052
M <sup>a</sup> R	6	<b>1.625</b>	1.577	1.663	0.039	21	<b>1.653</b>	1.563	1.718	0.042	7	<b>1.713</b>	1.451	1.911	0.140	24	<b>1.716</b>	1.632	1.867	0.055
CiR	6	<b>1.780</b>	1.724	1.825	0.042	21	<b>1.830</b>	1.629	2.000	0.114	6	<b>1.862</b>	1.673	2.011	0.122	24	<b>1.927</b>	1.699	2.170	0.112
P <sub>2</sub> Sq	6	<b>0.396</b>	0.333	0.444	0.037	21	<b>0.644</b>	0.442	0.949	0.108	6	<b>0.511</b>	0.294	0.696	0.140	24	<b>0.500</b>	0.416	0.698	0.064
P <sub>4</sub> Sq	6	<b>1.021</b>	0.955	1.138	0.062	21	<b>1.352</b>	1.158	1.512	0.105	7	<b>1.164</b>	0.899	1.351	0.163	24	<b>1.059</b>	0.881	1.281	0.100
PR	6	<b>0.389</b>	0.323	0.441	0.043	21	<b>0.478</b>	0.305	0.628	0.082	6	<b>0.447</b>	0.269	0.515	0.089	24	<b>0.474</b>	0.355	0.613	0.062



Table 6. (continued)

	<i>R. (c.) acrotis</i>						<i>R. (c.) augur</i>						<i>R. (c.) augur</i>						<i>R. horaceki</i>							
	North-eastern Africa			East Africa			Southern Africa			Cyrenaica			East Africa			Southern Africa			Cyrenaica			Cyrenaica				
	n	M	SD	n	M	SD	n	M	SD	n	M	SD	n	M	SD	n	M	SD	n	M	SD	n	M	SD		
LCs	10	1.859	1.72	2.00	0.094	0.094	13	2.010	1.86	2.12	0.090	24	1.938	1.65	2.27	0.196	5	1.893	1.83	1.94	0.047	5	1.893	1.83	1.94	0.047
LaCs	10	1.410	1.28	1.59	0.085	0.085	13	1.687	1.51	1.87	0.110	24	1.517	1.24	2.03	0.220	5	1.564	1.53	1.60	0.037	5	1.564	1.53	1.60	0.037
LP <sup>2</sup>	3	0.244	0.24	0.25	0.006	0.006	12	0.325	0.28	0.41	0.035	23	0.332	0.25	0.45	0.052	4	0.356	0.35	0.38	0.015	4	0.356	0.35	0.38	0.015
LP <sup>4</sup>	10	1.373	1.29	1.51	0.084	0.084	13	1.502	1.30	1.63	0.113	24	1.540	1.34	1.74	0.125	5	1.435	1.37	1.53	0.073	5	1.435	1.37	1.53	0.073
LP <sup>4</sup> 2	10	1.055	0.90	1.19	0.082	0.082	13	1.059	0.90	1.19	0.080	24	1.050	0.89	1.26	0.108	5	0.970	0.91	1.03	0.055	5	0.970	0.91	1.03	0.055
LP <sup>4</sup> 3	10	0.775	0.68	0.88	0.053	0.053	13	0.872	0.79	1.01	0.062	24	0.804	0.68	1.02	0.097	5	0.888	0.79	0.96	0.068	5	0.888	0.79	0.96	0.068
LP <sup>4</sup> 4	10	2.189	2.03	2.40	0.112	0.112	13	2.461	2.23	2.63	0.123	24	2.452	2.03	2.83	0.237	5	2.430	2.37	2.51	0.057	5	2.430	2.37	2.51	0.057
LM <sup>1</sup>	10	1.886	1.81	2.03	0.069	0.069	13	2.109	1.97	2.29	0.095	24	2.038	1.88	2.32	0.128	5	1.870	1.82	1.92	0.041	5	1.870	1.82	1.92	0.041
LaM <sup>1</sup>	10	2.774	2.62	2.93	0.120	0.120	13	3.040	2.80	3.28	0.123	24	2.955	2.60	3.31	0.244	5	3.009	2.96	3.05	0.037	5	3.009	2.96	3.05	0.037
LM <sup>3</sup>	10	1.239	1.10	1.30	0.059	0.059	13	1.313	1.17	1.42	0.071	24	1.301	1.18	1.67	0.097	5	1.213	1.20	1.24	0.014	5	1.213	1.20	1.24	0.014
LaM <sup>3</sup>	10	1.991	1.89	2.12	0.074	0.074	13	2.174	1.95	2.34	0.104	24	2.125	1.97	2.40	0.139	5	2.084	2.07	2.09	0.008	5	2.084	2.07	2.09	0.008
LCi	10	1.074	1.01	1.13	0.039	0.039	13	1.166	1.01	1.30	0.086	24	1.122	0.96	1.36	0.114	5	1.150	1.08	1.20	0.046	5	1.150	1.08	1.20	0.046
LP <sub>2</sub>	10	0.783	0.68	0.82	0.039	0.039	13	0.830	0.73	0.92	0.068	24	0.854	0.68	1.03	0.102	5	0.720	0.69	0.73	0.017	5	0.720	0.69	0.73	0.017
LaP <sub>2</sub>	10	0.921	0.81	0.99	0.057	0.057	13	0.952	0.80	1.09	0.082	24	0.906	0.56	1.13	0.143	5	0.838	0.81	0.88	0.028	5	0.838	0.81	0.88	0.028
LP <sub>3</sub>	4	0.152	0.09	0.19	0.041	0.041	3	0.234	0.21	0.25	0.022	7	0.217	0.18	0.26	0.029	1	0.23	—	—	—	1	0.23	—	—	—
LP <sub>4</sub>	10	1.130	0.98	1.23	0.065	0.065	13	1.240	1.13	1.37	0.078	24	1.222	1.06	1.36	0.098	5	1.326	1.29	1.39	0.040	5	1.326	1.29	1.39	0.040
LaP <sub>4</sub>	10	1.031	0.88	1.32	0.117	0.117	13	1.181	1.06	1.32	0.070	24	1.103	0.86	1.34	0.155	5	1.085	1.04	1.14	0.039	5	1.085	1.04	1.14	0.039
LM <sub>1</sub>	10	1.971	1.92	2.06	0.048	0.048	13	2.172	2.07	2.28	0.073	24	2.153	1.97	2.39	0.136	5	2.052	1.98	2.12	0.049	5	2.052	1.98	2.12	0.049
CsR	10	0.667	0.600	0.720	0.036	0.036	13	0.654	0.612	0.716	0.032	24	0.667	0.567	0.753	0.056	5	0.641	0.627	0.657	0.013	5	0.641	0.627	0.657	0.013
CsR1	10	0.761	0.714	0.927	0.065	0.065	13	0.840	0.731	0.909	0.047	24	0.781	0.702	0.928	0.054	5	0.827	0.793	0.864	0.032	5	0.827	0.793	0.864	0.032
P <sup>R</sup>	10	0.565	0.500	0.612	0.040	0.040	13	0.583	0.493	0.667	0.051	24	0.522	0.442	0.601	0.042	5	0.621	0.524	0.697	0.063	5	0.621	0.524	0.697	0.063
P <sup>R</sup> 2	10	0.628	0.562	0.744	0.048	0.048	13	0.610	0.553	0.659	0.032	24	0.631	0.538	0.806	0.054	5	0.590	0.569	0.610	0.019	5	0.590	0.569	0.610	0.019
P <sup>R</sup> 3	10	0.354	0.333	0.382	0.016	0.016	13	0.354	0.325	0.382	0.015	24	0.328	0.289	0.369	0.024	5	0.365	0.319	0.396	0.028	5	0.365	0.319	0.396	0.028
M <sup>R</sup>	10	1.472	1.343	1.554	0.064	0.064	13	1.442	1.381	1.517	0.037	24	1.449	1.347	1.570	0.059	5	1.610	1.559	1.674	0.050	5	1.610	1.559	1.674	0.050
M <sup>R</sup>	10	1.610	1.503	1.830	0.089	0.089	13	1.659	1.422	1.756	0.093	24	1.656	1.551	1.815	0.084	5	1.718	1.691	1.735	0.016	5	1.718	1.691	1.735	0.016
CiR	10	1.872	1.704	1.969	0.084	0.084	13	1.870	1.718	2.071	0.124	24	1.929	1.648	2.185	0.120	5	1.787	1.713	1.893	0.074	5	1.787	1.713	1.893	0.074
P <sub>2</sub> Sq	10	0.722	0.625	0.795	0.062	0.062	13	0.793	0.600	0.992	0.111	24	0.783	0.413	1.161	0.198	5	0.604	0.572	0.645	0.030	5	0.604	0.572	0.645	0.030
P <sub>4</sub> Sq	10	1.161	0.976	1.299	0.091	0.091	13	1.468	1.208	1.782	0.163	24	1.360	0.917	1.768	0.287	5	1.439	1.335	1.590	0.094	5	1.439	1.335	1.590	0.094
PR	10	0.625	0.483	0.691	0.066	0.066	13	0.544	0.411	0.696	0.083	24	0.575	0.424	0.684	0.073	5	0.420	0.397	0.466	0.028	5	0.420	0.397	0.466	0.028

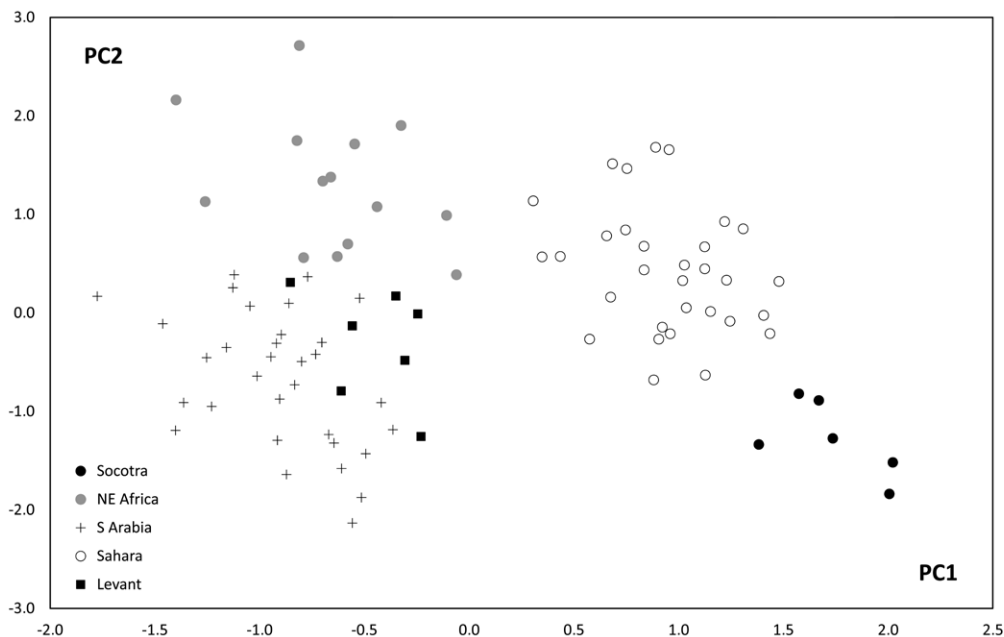


Fig. 23. Bivariate plot of the examined Socotran and comparative samples of *Rhinolophus clivosus* Cretzschmar, 1828 (besides the samples of *R. (c.) augur* Andersen, 1904 from Southern Africa and East Africa): results of the principal component analysis of the skull dimensions including tooth-rows. For legend see Fig. 19.

bian samples belong to two deeply separated lineages. The sub-Saharan *Rhinolophus* populations traditionally considered a part of the *R. clivosus* species rank (e.g. Ellerman et al. 1953, Koopman 1966, 1975, 1994, Csorba et al. 2003, Simmons 2005, etc.) represent two lineages of their own well separated from each other and from the rest of the species content (Table 3, Fig. 18), and they may represent independent species, *R. acrotis* and *R. augur* (see also Benda & Vallo 2012). However, also this view should be tested by an analysis of the nuclear genetic markers only, although the separation of these populations at least at the subspecific level is suggested by results of a morphological comparison (see below) besides the analysis of the mtDNA.

External and cranial dimensions of the available samples of *R. clivosus* from Socotra and of the comparative sample sets are shown in Tables 4–6. The Socotran samples are on average the smallest bats from the compared sample sets of the *R. clivosus* s.l. in most of the external, skull and tooth dimensions examined (Figs. 19, 20); only four exceptions were among the skull and tooth dimensions, their values are very similar to each other in all compared sets (LaI, LBT, ACo, LP<sup>4</sup><sub>2</sub>; Tables 4, 6). With the exception of six dimensions concerning the height of braincase (ANc, ACr) and dentition (LP<sup>4</sup><sub>3</sub>, LCi, LaP<sub>2</sub>, LaP<sub>4</sub>), the ranges of skull and tooth dimensions of the Socotran bats do not overlap with dimension ranges of the southern Arabian samples, which were shown to be their closest relatives by the genetic analysis (see above). Although on average smaller, the Socotran bats are in the body, skull and tooth sizes most similar to the samples of *R. clivosus* from Sahara (Tables 4, 6, Figs. 19, 20), i.e. to the populations formerly referred to *R. c. brachygnathus* Andersen, 1905, now regarded a small desert morphotype of the nominotypical form (Benda & Vallo 2012). The ranges of dimensions of these two sample sets overlap in all

dimensions (Tables 4–6). However, the skull shapes differ between the two morphotypes, the Socotran bats have absolutely and relatively higher coronoid processes of mandible (Fig. 20), but relatively and absolutely lower and relatively wider braincases (Fig. 21) and relatively narrower rostra than the Saharan bats (Table 5); the upper canine crowns are relatively longer, but the lower canine crowns relatively shorter in the Socotran bats than in the Saharan bats (Fig. 22, Table 6). Hence, although these two forms are close in their body, skull and tooth size, they represent two separate morphotypes; this separation is supported also by the results of the principal component analysis of the skull dimensions (Fig. 23; PC1=69.84% of variance, PC2=8.42%).

According to the described results of genetic and morphometric comparisons, the Socotran populations of *R. clivosus* represent a unique evolutionary unit within the species rank. Therefore, it is formally described here as a new subspecies endemic for the island:

***Rhinolophus clivosus socotranus* Benda, Reiter et Vallo, subsp. nov.**

TYPE MATERIAL. **Holotype:** ♂ ad. (NMP 90581 [field No. pb2733] [S+A]), Marshim cave, Diksam plateau, 8 May 2004, leg. P. Benda & A. Reiter. – **Paratypes:** 1 ♀ (NMP 90580 [field No. pb2732] [S+A]), Hofur cave, Diksam plateau, 8 May 2004, leg. P. Benda & A. Reiter; – 2 ♀♀ (NMP 90593 [field No. pb2750] [S+A], BCSU pb2751 [A]), Keisu, 21 May 2004, leg. P. Benda & A. Reiter; – 3 ♂♂, 1 ♀ (BCSU pb2736, NMP 90582 [field No. pb2734] [S+A], BCSU pb2737, NMP 90583 [field No. pb2735] [A]), Marshim cave, Diksam plateau, 8 May 2004, leg. P. Benda & A. Reiter.

SYNONYMY REVIEW.

*Rhinolophus clivosus* Cretzschmar, 1828: Wranik et al. 1999: 35; Cesarini 2003: 6–17; Wranik et al. 2003: 86; Cesarini 2007: 142; O’Brien 2011: 262, 286; Benda & Vallo 2012: 80–95.

*Rhinolophus* aff. *clivosus*: Benda et al. 2005: 19; Benda et al. 2006a: 139.

TYPE LOCALITY. Marshim cave, Diksam plateau, Socotra island, Republic of Yemen; 12° 30’ 32” N, 53° 56’ 19” E, ca. 945 m a. s. l.



Figs. 24, 25. Two portraits of *Rhinolophus clivosus socotranus* subsp. nov. 24 (left) – lateral view of the head and noseleaf, an adult specimen from the Marshim cave, Diksam plateau. 25 (right) – frontal view of the face with noseleaf, a subadult female from Desmoiten, Wadi Darho.

DESCRIPTION. *Rhinolophus clivus socotranus* subsp. nov. is a medium-sized horseshoe bat, the smallest form of *R. clivus* Cretzschmar, 1828 (Fig. 19) and in most respects similar to other forms of *R. clivus* from the Middle East and North Africa, including the structure and relative size of the nose-leaf. Forearm length 44–47 mm, ear length 19.8–21.8 mm, horseshoe width 7.4–8.0 mm, condylocanine length of skull 15.6–16.3 mm, length of the upper tooth-row 6.3–6.8 mm.

The horseshoe of *R. c. socotranus* subsp. nov. is relatively wide (Figs. 24, 25), the connecting process of the nose-leaf is high and rounded, the sella is constricted in the middle, tip of the sella is pointed, lancet is narrow at basis. One medial groove is present in the lower lip.

Skull is relatively wide (LaZ 9.9–11.0 mm; LaZ/LCc 0.575–0.594), rostral part of the skull including the nasal swellings is relatively narrow (LaInf 4.6–4.8 mm; CC 4.6–5.1 mm; M<sup>3</sup>M<sup>3</sup> 6.6–6.9 mm; LaInf/LCc 0.293–0.303; M<sup>3</sup>M<sup>3</sup>/LCc 0.410–0.425), the braincase is relatively low and wide (LaN 7.5–8.0 mm; LaM 8.6–8.9 mm; ANc 5.3–5.8 mm, ACr 6.7–7.3 mm; LaN/LCc 0.473–0.501; LaM/LCc 0.539–0.550; ANc/LCc 0.338–0.353; ANc/LaM 0.614–0.645). The coronoid processes of mandible are relatively high (ACo 3.0–3.3 mm; ACo/LMd 0.258–0.266). Sagittal crest is moderately developed, infraorbital foramen is large and infraorbital bar is long and thin. Nasal swellings are moderately developed, separated from the frontals by a shallow concavity. The posterior median swellings are equally long as the anterior swellings, the anterior lateral swellings are slightly smaller in area than the anterior median swellings.

The teeth are relatively slender (Table 6); upper molars are relatively narrow (LaM<sup>1</sup>/LM<sup>1</sup> 1.389–1.497; LaM<sup>3</sup>/LM<sup>3</sup> 1.577–1.663), large upper premolars (P<sup>4</sup>) are relatively short and mesio-distally wide (LP<sup>4</sup>1/LaP<sup>4</sup> 0.605–0.642), with rather shallow concavity in the distal margin of talon (LP<sup>4</sup>3/LP<sup>4</sup>1 0.521–0.587). Large lower premolars (P<sub>4</sub>) are small (LP<sub>4</sub> 1.04–1.12 mm), but very large in relation to the size of smaller lower premolars (P<sub>2</sub>) (LP<sub>2</sub> 0.51–0.60 mm; LP<sub>2</sub>×LaP<sub>2</sub>/LP<sub>4</sub>×LaP<sub>4</sub> 0.323–0.441). The minute upper and second lower premolars (P<sup>2</sup>, P<sub>3</sub>) are missing in all examined specimens of *R. c. socotranus* subsp. nov.

Baculum of *R. c. socotranus* subsp. nov. is a relatively large bone, dorso-ventrally flattened in its distal two-thirds, creating a lancet-form shape, while its proximal epiphysis is massive and laterally bifurcated (Fig. 26). Total length of baculum 3.02–3.08 mm, largest width of the proxi-

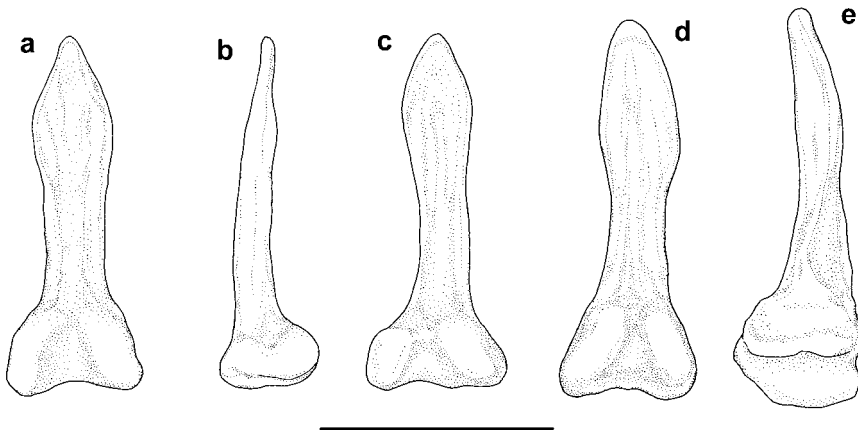


Fig. 26. Baculum preparations of *Rhinolophus clivus socotranus* subsp. nov. (a–c) and a comparative sample of *R. clivus* (d, e) from Egypt. Legend: a – NMP 90581 (holotype); b, c – NMP 90582; d, e – ZFMK 59304; a, c, d – ventral views; b, e – lateral views. Distal epiphyses up; scale bar – 2 mm.

mal epiphysis 1.18–1.21 mm, largest (dorso-ventral) height of the proximal epiphysis 0.84 mm, largest width of the lancet 0.61–0.68 mm.

The adult dorsal pelage of *R. c. socotranus* subsp. nov. is pale brownish-grey, ventral pelage is pale brown to beige (Fig. 24). Nose-leaf and ears are dark brown or dark greyish-brown, distal parts darker than the proximal ones. Wing membranes are dark greyish-brown.

**Genetics.** In the group of *R. clivosus* haplotypes from southern Arabia, *R. c. socotranus* subsp. nov. shows a unique base position within the mitochondrial gene for cytochrome *b* (1140 bp) at 16 sites: 795, 930, 945, 966, 984 (A→G), 106, 165, 384 (C→T), 78, 345, 504, 519, 748, 1014, 1020 (T→C), and 1038 (C/G→A). At 34 other sites, *R. c. socotranus* subsp. nov. shows variance with the particular haplotypes of the southern Arabian haplotype group: 55, 67, 114, 232, 282, 414, 501, 903 (A→G), 147 (A→T), 31, 672, 687, 789, 891, 908, 993, 999, 1104, 1125, 1129 (C→T), 72, 115, 453, 612 (G→A), 291, 327, 351, 393, 561, 756, 780, 996, 1068, and 1074 (T→C).

**DIMENSIONS OF THE HOLOTYPE** (in millimetres). **External:** LC 52; LCd 29; LA 45.0; LA; 20.9; LaFe 7.7. **Cranial:** LCr 19.23; LCc 16.25; LaZ 9.64; LaI 1.94; LaInf 4.76; LaN 7.93; LaM 8.79; ANc 5.54; ACr 7.11; LBT 2.80; CC 5.04; P<sup>1</sup>P<sup>4</sup> 5.82; M<sup>3</sup>M<sup>3</sup> 6.82; CM<sup>3</sup> 6.73; M<sup>1</sup>M<sup>3</sup> 4.38; CP<sup>4</sup> 2.70; LMd 12.28; ACo 3.17; I<sub>1</sub>M<sub>3</sub> 7.95; CM<sub>3</sub> 7.24; M<sub>1</sub>M<sub>3</sub> 4.88; CP<sub>4</sub> 2.42. **Dental:** LCs 1.63; LaCs 1.40; LP<sup>2</sup> –; LP<sup>4</sup> 1.36; LP<sup>2</sup> 0.98; LP<sup>3</sup> 0.75; LaP<sup>4</sup> 2.12; LM<sup>1</sup> 1.83; LaM<sup>1</sup> 2.62; LM<sup>3</sup> 1.13; LaM<sup>3</sup> 1.84; LCi 1.02; LP<sub>2</sub> 0.60; LaP<sub>2</sub> 0.74; LP<sub>3</sub> –; LP<sub>4</sub> 1.08; LaP<sub>4</sub> 0.93; LM<sub>1</sub> 1.85.

**MITOCHONDRIAL SEQUENCE OF THE HOLOTYPE** (complete sequence of the mitochondrial gene for cytochrome *b*; GenBank Accession Number KC579387; 5' end). atg acc aac att cgc aag tcc cac cca cta ttc aaa atc atc aac gac tca ttc gtc gac cta ccc gcc cca tca agc atc tct tcc tga tga aac ttc gga tcc tta cta ggg atc tgc cta gct atc caa att ctc aca gga ctt ttc cta gca ata cat tat aca tca gat acc gcc aca gcc ttc cac tcc gta acc cac att tgc cga gac gtc aac tac ggc tga gtc ctg cgc tat ctc cac gcc aac gga gcc tcc ata ttc ttt atc tgc ctg ttc cta cac gta gga cga gga atc tac tac ggc tcc tat aca ttc tca gaa aca tga aac atc gga atc atc ctc ctc ttc gcc gtc ata gcc aca gca ttt ata ggc tac gta ctc cca tga ggt caa atg tcc ttc tga gga gca aca gtt atc aca aac ctt ctc tca gcc att cca tat att gca aca act cta gtc gaa tga gtc tga ggc ggg ttc tca gtc gat aaa gcc aca ctc acc cga ttc ttc gct gtc cac ttc cta tta ccc ttc atc atc gca gcc ata gtc ata gtc cac cta ctt ttc ctc cac gaa aca gga tca aac aac cca atc gga atc cca tca gac gca gac ata atc cca ttc cac ccc tac tat acc att aaa gac att cta ggc ctc gta cta ata ctc ata gca cta ctg tcc ttg gtc cta ttc gcc ccc gat cta cta ggc gac cca gac aac tac act cca gcc aac cca cta aat act cgc ccc cac att aac cca gaa tgg tac ttt cta ttt gcc tac gca atc cta cgt tca atc cca aat aaa ctc ggc gga gtt gta gcc cta gtc cta tct atc ctt atc ctg gct gtc atc cca cta ctc cac aca teg aaa caa cgc agc atg aca ttc cga ccc cta agc cag tgc tta ttc gta ctc ctg gta gca gat atc ctt aca cta acc tga atc gga ggc caa cct gtc gaa cat cca ttc att atc atc gga caa cta gcc tct atc cta tac ttc cta att atc cta gtc cta ata cca ctt gca agc atc gca gaa aac cat cta ttg aaa tga aga.

**ETYMOLOGY.** The subspecies name refers to the island of Socotra, the only area of occurrence of *R. c. socotranus* subsp. nov.

### *Asellia italosomalica* De Beaux, 1931

**RECORDS. Original data:** Hadiboh [1], guest house, 1 February 1999: 1 ind. (W. Wranik in litt.); – Kam oasis [2], small karst cave, 5 May 2004: obs. a nursery colony of ca. 200 inds. (ads. & juvs.), coll. 10 fa, BCSU, NMP (cf. Benda et al. 2011a); – Suq village [3], water pool in a wadi, 7 May 2004: obs. ca. 10 foraging inds., net. 1 ma, NMP (cf. Benda et al. 2011a); – Wadi Darho, Mazaaba village [4], a cave above the village, 14 May 2004: obs. a nursery colony of ca. 1000 inds., coll. 4 ma, BCSU, NMP (cf. Benda et al. 2011a); – Wadi Shaab, Heloma village [5], small cave ca. 2 km E of the village, 14 May 2004: obs. 1 ind. – **Published data:** Chesa (Noged) [6], 1 ind. (Cesarini 2003, 2007 [as *A. tridens*]); – De Fareho (Abel) [7], Qatanen II, 27 August 2003: obs. 250–350 / 500–600 inds., exam. 4 m, 5 f (Cesarini 2003, 2007 [as *A. tridens*]); – Hadibo [1], house, March 1985: coll. 2 fa flew into a hotel room (Wranik 1986, 1999, Wranik et al. 1991, 2003 [as *A. tridens*]); – Haif [8], Gorf, 3 September 2003: obs. ca. 50 inds., exam. 3 f (Cesarini 2003, 2007 [as *A. tridens*]); – Hawlaf [9], Rhahr Cave, 29 August 2003: obs. 250–350 / 500–600 inds., exam. 3 m, 2 f (Cesarini 2003, 2007 [as *A. tridens*]); – Suq [3], palm grove, 1967: shot 1 ind. (Guichard 1992 [as *A. tridens*]); – Socotra Island [= Socotra, Kam] [2], 1 ind., BMNH (Harrison 1957 [as *A. tridens*]); Kam, 1 ind., BMNH (Benda et al. 2011a); – Socotra Island (Harrison 1964, Kock 1969, Koopman 1982b, 1993, 1994, Duff & Lawson 2004, Simmons 2005, cf. Harrison & Bates 1991 [as *A. tridens*]).

**DISTRIBUTION.** *Asellia italosomalica* is an uncommon bat in Socotra, it is known from nine sites scattered over a large (central) part of the island (Fig. 27). The occurrence of *Asellia* in Socotra

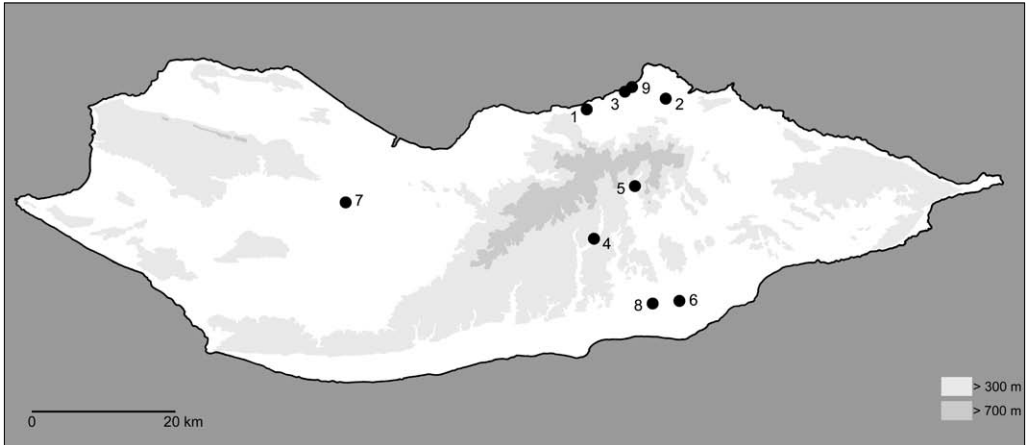


Fig. 27. Records of *Asellia italosomalica* De Beaux, 1931 in Socotra.

was for the first time suggested by W. R. Ogilvie-Grant (in De Winton et al. 1903: 6), who reported his observation as follows: “One night at Adho Dimellus (3,500 feet), while going round the sugared posts in search of moths, a small bat flew several times across the front of the lantern within a few yards of me. It was not flying very fast and I saw it very clearly, but, of course, can only hazard a guess as to the species. By the time I had returned to the spot with a collecting gun the Bat was nowhere to be seen; and, even if I had succeeded in shooting it, it would probably have been lost among the grass and stones. It resembled and may possibly have belonged to the species *Hipposiderus tridens*, which is common in South Arabia.” However, the occurrence of *A. italosomalica* at Adho Dimellus (= Adho Dimello pass, 12° 34' 15" N, 54° 02' 50" E, ca. 1050 m a. s. l.; see Bezděk et al. 2012) seems to be rather less probable, since this locality is extremely high situated, considering the altitudinal distribution of this bat in the island (see below); the above observation perhaps belongs to a different bat species. The first indubitable record of *A. italosomalica* in Socotra was made by G. B. Popov in the Kam oasis in 1953, and the respective specimen was published by Harrison (1957) as coming just from Socotra. However, this report was accepted as an evidence of the species from the island by subsequent authors, although under a different name, *A. tridens* (Harrison 1964, Kock 1969, Hayman & Hill 1971, DeBlase 1980, Koopman 1982b, 1993, 1994, Harrison & Bates 1991). Interestingly, another individual of *A. italosomalica* was collected in Socotra also by an entomologist, K. M. Guichard, who shot it “in the palm groves of Suq” (Guichard 1992: 187). Five additional records of *Asellia* in Socotra were made by Wranik (1986) and Cesarini (2003) and five others are presented here.

*A. italosomalica* is an endemic of the Horn of Africa (Benda et al. 2011a), besides Socotra it is distributed only across deserts and dry steppes of the southern and eastern parts of Somalia, i.e., of former Italian Somaliland/Somalia (see Lanza et al. 2015: 515). The occurrence of *A. italosomalica* in the Socotra island represents a separate and easternmost part of the species range (Benda et al. 2011a). This bat thus could theoretically occur also in other islands of the Socotra archipelago, as these islands create a geographical transition between two parts of the known range now separated for ca. 500 km (Lanza et al. 2015).

In Socotra, *A. italosomalica* is distributed over a very narrow range of altitudes (315 m; Table 1), the narrowest among the Socotran bats. The records are available only from low altitudes of the

island, from the sea level to the foothills of mountains (altitude median 85.0 m, altitude mean 123.9 m a. s. l.; Table 1). The highest site of recorded occurrence of *A. italosomalica* is a cave near the Mazaaba village, situated at 325 m a. s. l. in Wadi Darho in central Socotra, where a large colony of this bat roosts. The majority of records of *A. italosomalica* from Socotra was made in roosts (77.8%, n=7) and the altitudinal range of the roost sites corresponds fully to the range of all records, while the median and mean altitude values are slightly above the values of all records of this species (115.0 m and 149.3 m a. s. l.; Table 1).

FIELD NOTES. *Asellia italosomalica* was documented in Socotra mostly in its roosts, foraging individuals were observed only at two sites. Majority (five) of the roost findings represented tens or even hundreds of individuals, solitarily roosting individuals were found twice. This species creates the largest bat aggregations in Socotra, the documented colonies were composed of 50–1000 individuals (median 300 bats, mean 420 bats).

The largest aggregation of *A. italosomalica* in Socotra, containing some thousand bats, was found in a narrow (ca. 1.5 m) but deep cave situated in a rocky slope above the village of Mazaaba in Wadi Darho on 14 May 2004 (Figs. 28, 29). The colony was composed mainly of adult females nursing their young of all age stages, but also of males; four adult males were examined from the colony (orig. data).

Cesarini (2003, 2007) reported on findings of two roosts of large colonies of *A. italosomalica* in late August 2003, in the Qatanen II cave at De Fareho and the Rhahr cave at Hawlaf. While



Fig. 28. Mazaaba village in Wadi Darho, southern slope of the Hagher mountains (325 m a. s. l.); in a cave above the village (its obliquely oriented entrance is visible across the whole upper part of the picture), a large colony of *Asellia italosomalica* was discovered in May 2004.



Cesarini (2003) reported the numbers of 250–350 bats for both roosts, Cesarini (2007) mentioned 500–600 bats. Since in all other numbers of bats from other Socotran sites these two sources do not differ substantially, it is not clear, why such a large difference is presented for these two sites. Anyway, both intervals indicate very large colonies of *A. italosomalica*. According to Cesarini (2003, 2007), bats of both sexes were examined from both colonies (their ratio was 4:5 and 3:2, respectively).

A nursery colony of some 200 individuals of *A. italosomalica*, composed mainly of adult females and their young of various growth stages (10 adult females from the colony were examined), was discovered in a small cave in the oasis of Kam on 5 May 2004 (orig. data). The roost was a relatively small cave, constituted by a single room, ca. 12 m deep and 4 m high, with a low and broad entrance, ca. 1×4 m in size (Figs. 30, 31). The cave served also as a temporal night roost of one individual of *Rhinopoma cystops*.

Cesarini (2003) reported on a finding of a colony of *A. italosomalica* composed of ca. 50 individuals in the Gorf cave at Haif, in the cliff above Noged plain in southern Socotra, on 3 September



Fig. 29. A colony of *Asellia italosomalica* De Beaux, 1931, composed of ca. 1000 individuals, discovered in a cave above the Mazaaba village in May 2004 (Fig. 28).





Figs. 30, 31. Kam oasis, Wadi Kam (55 m a. s. l.); entrance to a small cave is situated in the eastern slope above the wadi.

2003 (three females were examined from the colony). At the time of the visit, the roost was shared with a colony of *Rhinopoma cystops* of ca. 100 bats (Cesarini 2003) and this is the only record of common roosting of an *A. italosomalica* aggregation with an aggregation of other bat species.

The three colonies of *A. italosomalica* discovered by Cesarini (2003) in Socotra (Qatanen II cave, Gorf cave, Rhahr cave), were considered “most likely to be reproductive colonies” (despite the late summer term of the roost checks) by Cesarini (2007: 140–141). These roosts were described in the latter source as follows: “The entrance of the roost hall is always less than 1–1.5 square mt, and inside it is completely dark with no filtering light. The range of temperatures varies between 29.0 and 33.4 °C [mean 31.9 °C], and the range of humidity varied from 67 to 78% [mean 74.0%]. The caves used by *A. tridens* [= *A. italosomalica*] were not-man made; however, they are not underground wadis. [...]. In the sites Rhahr and De Fareho the guano is collected by the people for their vegetable gardens or for profit.” Some of these features are rather at variance with the characteristics of the remaining two colony roosts of *A. italosomalica* found in Socotra. In the caves at Kam and at Mazaaba, the entrances were much larger than only 1–1.5 square metres, and thus, the daylight penetrated more or less to the cave spaces used by bats as roosts.

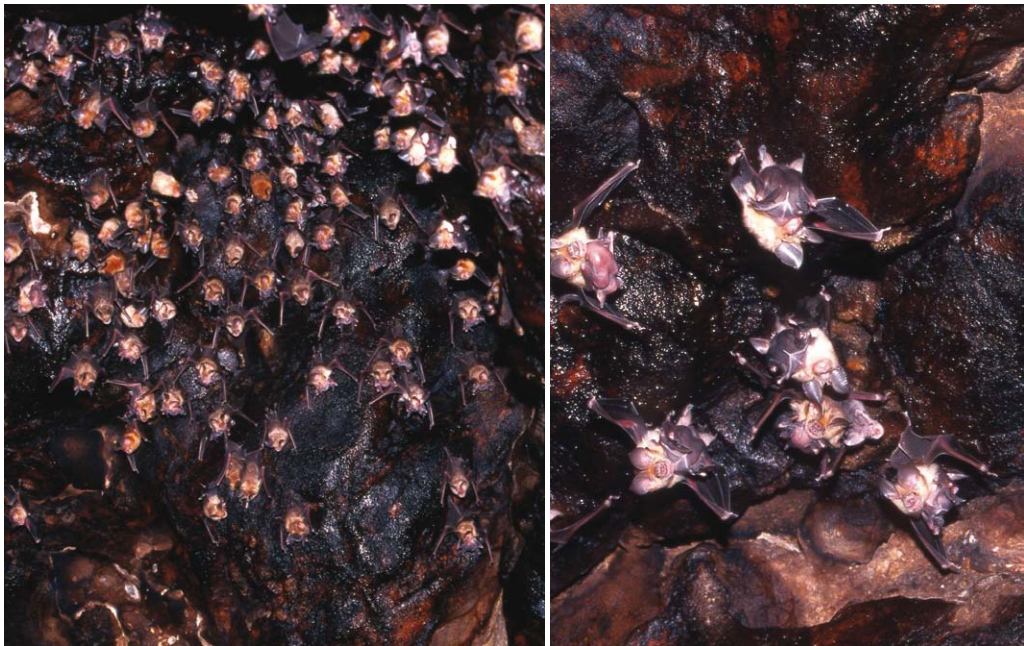
One individual of *A. italosomalica* was found hidden in a small pseudokarst cave near (ca. 2 km east of) the Heloma village in Wadi Shaab during a daytime visit on 14 May 2004 (orig. data). W. Wranik (in litt.) observed a roosting individual of this species in a guest house in Hadiboh on 1 February 1999; this record comprises the only artificial shelter of *A. italosomalica* documented from Socotra. However, most probably, neither of the latter records represents a regularly used roost but only a temporal daytime shelters. Large colonies of *A. italosomalica* were found in relatively short distances of few kilometres from these shelter (see Fig. 27), which can indicate permanent roosts of the (randomly) found solitary individuals of this sociable species.

Foraging individuals of *A. italosomalica* were documented only sporadically; Guichard (1992: 187) reported on a collection of a specimen in 1967 to be: “shot at dusk in the palm groves of

Suq.” On 7 May 2004, at the same site, in the palm oasis of the Suq village and at a water pool in the small wadi surrounded by palms (Fig. 36), foraging of approximately ten individuals of *A. italosomalica* was observed shortly after the sunset; one adult male was netted on this occasion just above the pool (orig. data). Wranik (1986) reported a collection of two specimens of *Asellia* in Hadiboh in March 1985; later on, he specified (Wranik 1998, 1999) that the bats were caught in an illuminated hotel room, to which they flew in search for their prey.

The remaining two records of *A. italosomalica* from Socotra are not accurately specified concerning the type of finding. A BMNH specimen was collected by G. B. Popov at Kam in 1953 (Benda et al. 2011a, cf. Harrison 1957); this bat could have been collected from the colony roosting in a cave situated in the oasis at this village (see above), or could have been shot on wings, which was the most common way of bat collection at that time. Cesarini (2003) reported another individual of this bat that was brought to him by a child from the Chesa village in Noged and speculated about the possible presence of a roost at this village. However, later on, Cesarini (2007: 141) described the finding of this individual as follows: “One female was captured in Chesa (Noged) by mistnetting in open space; [...]” The type of this record thus remains uncertain.

Reproduction of *A. italosomalica* was documented in Socotra twice in May 2004 (orig. data). In the nursery colony discovered in the cave at Kam on 5 May 2004, the young were associated with ca. 80% of the adult bats of the colony, together composed of ca. 200 individuals (Figs. 32–35). The young were in various stages of growth, from hairless and pinkish newborns (with body size of ca. 20 mm) to full grown and volant individuals. Among ten examined females from the Kam colony, six were in lactation, one was pregnant (containing a full grown foetus of the



Figs. 32, 33. Colony of *Asellia italosomalica* De Beaux, 1931 composed of ca. 200 adults and juveniles, discovered in a small cave in the oasis of Kam.





Figs. 34, 35. Female of *Asellia italosomalica* De Beaux, 1931 from the colony discovered in a small cave in Kam.

crown-rump length of 19 mm), and three remaining were adult females not reproducing this year (with no signs of pregnancy or lactation, but with developed pubic nipples). A similar observation was made in the nursery colony found in the cave at Mazaaba in Wadi Darho on 14 May 2004, i.e. nine days later than the Kam colony. In the Mazaaba colony, also the juveniles in various stages of growth were observed, including very small and pinkish young (Fig. 29).

**MATERIAL EXAMINED.** 1 ind. (BMNH 54.1010 [S]), Kam, date unlisted [1953], leg. G. B. Popov; – 10 ♀♀ (BCSU pb2718, 2719, 2721, NMP 90571–90575 [S+A], BCSU pb2720, NMP 90570 [A]), Kam, 5 May 2004, leg. P. Benda & A. Reiter; – 4 ♂♂ (BCSU pb2749, NMP 90590, 90592 [S+A], NMP 90591 [A]), Mazaaba, Wadi Darho, 14 May 2004, leg. P. Benda & A. Reiter; – 1 ♂ (NMP 90579 [S+A]), Suq, 7 May 2004, leg. P. Benda & A. Reiter.

**TAXONOMIC REMARKS.** The Socotran populations of the genus *Asellia* Gray, 1838 were first mentioned and for a long time treated under the species name *A. tridens* (Geoffroy, 1813), see the Synonymy review below, and their current taxonomic position has been determined only recently (Benda et al. 2011a).

Until the 1980s, only one specimen of *Asellia* from Socotra was available, a bat collected at Kam in 1953 and deposited at BMNH. This bat was first examined by Harrison (1957), who identified it as a very small individual of *A. tridens tridens*, the small-sized form of this species. He compared it with a specimen of *Asellia* from the Dhofar region of Oman (currently referred to *A. arabica*, see below and Benda et al. 2011a) and noted as follows (p. 3): “A single specimen from the cave of Sahaur, Qara Mountains, Dhufar in the B. M. collection is very small and so is another from Socotra Island. It is of interest to note here that the form *A. t. italosomalica* de Beaux (1931), Type Locality Oddur, Somaliland is also a very small form [...]” Although very simple



Fig. 36. The oasis of Suq, at the northern shore of Socotra (ca. 10 m a. s. l.); a site of repeated findings of *Asellia italosomalica* and a finding of *Hypsugo lanzai* (Guichard 1992, orig. data).

and rather vague, this is the first mention of the name *italosomalica* in relation to the Socotran *Asellia* population – in the first source, where its Socotran occurrence was published. Later on, Kock (1969: 128) referred the respective Socotran specimen directly to *A. t. tridens*, again along with the Dhofar specimen: “Eine Serie aus Hofuf (Saudi-Arabien) und kleinwüchsige Einzelstücke aus Dhufar (Süd-Arabien) sowie von der Insel Sokotra [...] stehen näher zu der Population von Oman [...] und können ebenfalls zu *Asellia tridens tridens* gerechnet werden.”

Numerous subsequent authors (see Synonymy review below) referred the Socotran populations of *Asellia* just to *A. tridens* without the subspecies specification. Wranik et al. (1991) affiliated two newly collected Socotran specimens to *A. tridens*, however, they noted their smaller size compared to those from the Arabian mainland. Al-Jumaily (1998) referred all *Asellia* populations from Yemen, including the samples collected by Wranik from Socotra, to *A. tridens tridens*.

Cesarini (2007: 144) reviewed the findings on variation in the Socotran *Asellia* and his new observations as follows: “[...], the Socotran population of *A. tridens* seems to have morphological measurements (forearm, body length and tail) on average shorter than the specimens of the species mentioned by Harrison & Bates (1991), but nevertheless almost within the species range. Such a result confirms that this species shows evident variations between different populations [...]. A morphological analysis conducted on a limited sample of specimens from Socotra and South Yemen (Wranik *et al.*, 1991) showed that the two specimens from Socotra Island were smaller than those from the mainland. Our study seems to confirm these results. The 18 individuals captured by us show forearm, body length and tail on average smaller than the Arabian widespread populations studied by Harrison & Bates (1991) and the specimens from southern Yemen [...]. The partial isolation of the bats on the island could establish the conditions for a genetic segregation of their populations.” Thus, Cesarini (2007) interpreted his observations on the Socotran bats

Table 7. Basic biometric data on and results of statistic comparison (univariate analysis of variance) of the examined Socotran and comparative samples of *Asellia* Geoffroy, 1838. For abbreviations see p. 103; Soc = Socotra, Som = Somalia, Dhof = Dhofar

	n	<i>Asellia italosomalica</i>								ANOVA				
		Socotra				Somalia				Soc×Som		Soc×Dhof		
	M	min	max	SD	n	M	min	max	SD	F	p	F	p	
LC	15	<b>52.9</b>	50	57	1.751	–	–	–	–	–	–	–	–	
LCd	15	<b>22.9</b>	20	28	2.086	–	–	–	–	–	–	–	–	
LAt	15	<b>45.62</b>	44.0	48.2	1.189	15	<b>45.17</b>	43.4	47.5	1.606	0.75	0.394	<b>7.55</b>	0.009
LA	15	<b>18.93</b>	16.9	20.2	0.697	–	–	–	–	–	–	–	–	
LCr	13	<b>17.58</b>	16.94	18.04	0.325	13	<b>17.28</b>	16.42	18.21	0.463	3.60	0.070	<b>54.29</b>	0.000
LOc	13	<b>17.17</b>	16.63	17.65	0.325	15	<b>17.19</b>	16.21	17.98	0.450	0.01	0.929	<b>25.83</b>	0.000
LCc	13	<b>15.17</b>	14.79	15.55	0.205	13	<b>15.26</b>	14.48	15.76	0.397	0.51	0.483	<b>19.21</b>	0.000
LaZ	12	<b>9.46</b>	9.08	9.92	0.244	12	<b>9.60</b>	8.98	10.35	0.397	1.03	0.321	<b>44.32</b>	0.000
LaI	13	<b>2.04</b>	1.79	2.23	0.125	16	<b>2.27</b>	1.88	2.52	0.186	1.40	0.225	<b>37.43</b>	0.000
LaInf	13	<b>5.51</b>	5.21	5.77	0.142	16	<b>5.40</b>	5.13	5.67	0.136	4.12	0.056	<b>19.87</b>	0.000
LaNc	13	<b>6.84</b>	6.52	7.26	0.187	15	<b>6.97</b>	6.36	7.42	0.305	1.92	0.177	<b>9.63</b>	0.004
LaM	12	<b>7.99</b>	7.77	8.17	0.140	15	<b>8.16</b>	7.84	8.49	0.202	3.79	0.065	0.68	0.416
ANc	12	<b>4.97</b>	4.71	5.24	0.187	14	<b>5.03</b>	4.67	5.49	0.223	0.50	0.487	1.95	0.173
ACr	12	<b>6.73</b>	6.51	7.02	0.173	12	<b>6.68</b>	6.01	7.38	0.349	0.22	0.645	<b>21.26</b>	0.000
LBT	13	<b>2.85</b>	2.72	2.97	0.080	13	<b>2.71</b>	2.48	3.09	0.182	3.35	0.082	<b>8.93</b>	0.006
CC	13	<b>4.95</b>	4.76	5.24	0.141	15	<b>4.98</b>	4.64	5.45	0.259	0.14	0.715	<b>75.34</b>	0.000
M <sup>3</sup> M <sup>3</sup>	13	<b>6.82</b>	6.62	7.27	0.181	14	<b>6.72</b>	6.39	7.09	0.164	2.44	0.131	<b>32.57</b>	0.000
CM <sup>3</sup>	13	<b>6.19</b>	5.98	6.42	0.147	16	<b>6.29</b>	6.02	6.50	0.147	2.91	0.100	<b>26.14</b>	0.000
M <sup>1</sup> M <sup>3</sup>	13	<b>3.86</b>	3.74	4.02	0.105	16	<b>3.80</b>	3.68	3.93	0.068	3.45	0.074	<b>49.94</b>	0.000
CP <sup>4</sup>	13	<b>2.62</b>	2.47	2.85	0.124	16	<b>2.62</b>	2.41	2.86	0.117	0.00	0.963	<b>21.11</b>	0.000
LMd	13	<b>11.70</b>	11.38	12.11	0.235	15	<b>11.88</b>	11.49	12.51	0.342	2.57	0.121	<b>44.32</b>	0.000
ACo	13	<b>3.70</b>	3.45	3.84	0.099	16	<b>3.45</b>	3.18	3.67	0.156	2.47	0.135	<b>55.64</b>	0.000
CM <sub>3</sub>	13	<b>6.86</b>	6.63	7.18	0.170	15	<b>7.00</b>	6.57	7.27	0.220	3.54	0.071	<b>19.71</b>	0.000
MiM <sub>3</sub>	13	<b>4.53</b>	4.28	4.81	0.161	15	<b>4.51</b>	4.19	4.70	0.133	0.08	0.780	<b>15.96</b>	0.000
CP <sub>4</sub>	13	<b>2.54</b>	2.43	2.74	0.095	16	<b>2.67</b>	2.45	2.92	0.152	3.06	0.113	<b>23.34</b>	0.000
CC/LCc	13	<b>0.326</b>	0.317	0.341	0.007	12	<b>0.329</b>	0.300	0.349	0.016	0.19	0.668	<b>40.13</b>	0.000
LaInf/LCc	13	<b>0.363</b>	0.348	0.379	0.008	13	<b>0.354</b>	0.342	0.372	0.009	3.94	0.061	<b>5.55</b>	0.025
LaZ/LCc	12	<b>0.624</b>	0.606	0.652	0.013	12	<b>0.630</b>	0.604	0.657	0.016	1.14	0.297	<b>19.48</b>	0.000
CM <sup>3</sup> /LCc	13	<b>0.408</b>	0.396	0.420	0.008	13	<b>0.412</b>	0.402	0.422	0.006	1.79	0.194	<b>6.11</b>	0.019
LaNe/LCc	13	<b>0.451</b>	0.441	0.477	0.010	13	<b>0.456</b>	0.425	0.480	0.015	1.45	0.241	0.10	0.756
CC/CM <sup>3</sup>	13	<b>0.800</b>	0.774	0.836	0.018	15	<b>0.794</b>	0.739	0.844	0.029	0.38	0.545	<b>24.16</b>	0.000

just as a dissimilarity of a local form of a generally very variable species, without any attempt to evaluate his data taxonomically.

On the other hand, based on the extraordinarily small body size of the Socotran samples of *Asellia*, Benda et al. (2005, 2006a) suggested to consider these populations as a species separated from *A. tridens*, for which the relevant name is *A. italosomalica* De Beaux, 1931. Benda et al. (2006a: 139) reviewed this opinion as follows: “Socotra individuals of *Asellia* are much smaller than all known Saharan and Middle Eastern specimens of *Asellia tridens*. Socotran trident bats are similar in size to *A. tridens italosomalica* which has been described from Southern Somalia. However, trident bats of this size live also in Yemen where the large-sized *A. tridens* also occurs. Due to the sympatric occurrence of these two forms in Southern Arabia, we consider *A. italosomalica* to be a distinct species. While individuals of the Socotran populations are slightly larger than those of the mainland, further analysis is needed to determine whether or not they

Table 7. (continued)

	<i>Asellia arabica</i> Dhofar				<i>Asellia tridens</i> southern Arabia				<i>Asellia patrizii</i> north-eastern Africa						
	n	M	min	max	SD	n	M	min	max	SD	n	M	min	max	SD
LC	23	<b>53.5</b>	49	59	2.447	13	<b>62.1</b>	59	66	2.060	–	–	–	–	–
LCd	23	<b>20.2</b>	17	25	1.614	13	<b>22.6</b>	19	25	2.256	–	–	–	–	–
LAt	28	<b>44.71</b>	43.1	46.5	0.944	25	<b>51.48</b>	48.7	54.3	1.439	12	<b>39.29</b>	36.70	40.80	1.082
LA	23	<b>18.85</b>	17.7	19.9	0.647	13	<b>19.72</b>	18.8	20.8	0.622	–	–	–	–	–
LCr	21	<b>16.77</b>	16.21	17.37	0.302	25	<b>19.15</b>	18.22	20.52	0.707	16	<b>15.05</b>	14.38	15.62	0.341
LOc	19	<b>16.60</b>	15.91	17.13	0.310	27	<b>19.15</b>	18.04	20.54	0.722	13	<b>14.92</b>	14.58	15.27	0.251
LCc	21	<b>14.82</b>	14.22	15.24	0.242	27	<b>16.96</b>	16.13	18.14	0.649	14	<b>13.16</b>	12.57	13.57	0.322
LaZ	20	<b>8.97</b>	8.68	9.29	0.178	28	<b>10.62</b>	10.06	11.51	0.459	16	<b>7.98</b>	7.43	8.31	0.252
LaI	22	<b>2.27</b>	2.09	2.44	0.097	28	<b>2.30</b>	2.06	2.62	0.133	16	<b>1.83</b>	1.71	2.04	0.090
LaInf	22	<b>5.25</b>	5.06	5.67	0.178	29	<b>6.04</b>	5.58	6.63	0.336	16	<b>4.75</b>	4.51	5.04	0.156
LaNc	21	<b>6.65</b>	6.39	6.97	0.153	28	<b>7.40</b>	7.04	7.88	0.218	16	<b>6.17</b>	5.93	6.49	0.166
LaM	21	<b>7.95</b>	7.68	8.21	0.150	28	<b>8.85</b>	8.44	9.61	0.288	15	<b>7.30</b>	7.01	7.69	0.209
ANc	20	<b>4.89</b>	4.73	5.10	0.122	27	<b>5.55</b>	5.11	6.09	0.232	14	<b>4.53</b>	4.23	4.82	0.157
ACr	21	<b>6.50</b>	6.28	6.67	0.121	25	<b>7.27</b>	6.82	8.03	0.272	14	<b>5.96</b>	5.47	6.37	0.253
LBT	19	<b>2.78</b>	2.64	2.86	0.057	25	<b>2.98</b>	2.76	3.22	0.138	15	<b>2.51</b>	2.34	2.87	0.160
CC	22	<b>4.57</b>	4.39	4.87	0.115	29	<b>5.51</b>	4.87	6.22	0.335	16	<b>4.06</b>	3.86	4.36	0.133
M <sup>3</sup> M <sup>3</sup>	22	<b>6.51</b>	6.24	6.87	0.135	29	<b>7.63</b>	6.97	8.06	0.273	16	<b>5.65</b>	5.21	5.98	0.223
CM <sup>3</sup>	23	<b>5.95</b>	5.74	6.19	0.131	29	<b>7.09</b>	6.57	7.49	0.265	16	<b>5.32</b>	5.11	5.53	0.148
M <sup>1</sup> M <sup>3</sup>	23	<b>3.62</b>	3.41	3.82	0.099	29	<b>4.16</b>	3.91	4.45	0.145	15	<b>3.24</b>	3.03	3.44	0.126
CP <sup>4</sup>	20	<b>2.45</b>	2.34	2.68	0.088	28	<b>3.08</b>	2.68	3.42	0.196	15	<b>2.22</b>	2.04	2.38	0.097
LMd	23	<b>11.18</b>	10.70	11.71	0.219	28	<b>13.01</b>	12.24	13.88	0.551	15	<b>9.94</b>	9.44	10.28	0.239
ACo	23	<b>3.43</b>	3.23	3.61	0.106	28	<b>4.20</b>	3.79	4.73	0.271	15	<b>2.97</b>	2.75	3.24	0.155
CM <sub>3</sub>	23	<b>6.60</b>	6.24	6.88	0.169	28	<b>7.86</b>	7.34	8.33	0.276	16	<b>5.87</b>	5.54	6.37	0.210
M <sub>i</sub> M <sub>3</sub>	23	<b>4.31</b>	4.01	4.71	0.156	28	<b>5.04</b>	4.67	5.39	0.176	15	<b>3.84</b>	3.53	4.16	0.171
CP <sub>4</sub>	20	<b>2.35</b>	2.21	2.67	0.119	27	<b>3.01</b>	2.56	3.43	0.246	15	<b>2.30</b>	2.13	2.74	0.175
CC/LCc	21	<b>0.309</b>	0.297	0.324	0.008	27	<b>0.323</b>	0.298	0.345	0.012	14	<b>0.309</b>	0.298	0.326	0.007
LaInf/LCc	21	<b>0.355</b>	0.339	0.381	0.011	27	<b>0.354</b>	0.338	0.375	0.010	14	<b>0.361</b>	0.349	0.375	0.009
LaZ/LCc	19	<b>0.606</b>	0.589	0.622	0.009	27	<b>0.625</b>	0.594	0.659	0.016	14	<b>0.608</b>	0.581	0.633	0.014
CM <sup>3</sup> /LCc	21	<b>0.402</b>	0.391	0.415	0.006	27	<b>0.417</b>	0.407	0.432	0.006	14	<b>0.404</b>	0.390	0.417	0.007
LaNe/LCc	20	<b>0.450</b>	0.431	0.466	0.010	27	<b>0.436</b>	0.413	0.463	0.013	14	<b>0.470</b>	0.450	0.495	0.012
CC/CM <sup>3</sup>	22	<b>0.768</b>	0.737	0.802	0.018	29	<b>0.777</b>	0.730	0.833	0.026	16	<b>0.762</b>	0.731	0.793	0.017

are sufficiently distinct to be a new subspecies.” Although this view was later shown to be too preliminary in several aspects, the name *A. italosomalica* was demonstrated to be applied for the Socotran populations correctly.

Based on these observations and comparisons with numerous population samples from the whole range of *Asellia*, Benda et al. (2011a) performed a revision of the phylogenetic relations and taxonomy within this genus. According to the results of the molecular genetic part of this analysis, the Socotran samples represented the most distant lineage of the genus, in a sister position to a pair of lineages (12.3–13.4% of Kimura two-parameter [k2p] distance in the complete cytochrome *b* gene), one composed of the samples from the Dhofar region of the Yemeni-Omani border area, the other of the samples from a large range stretching from western Sahara (Morocco and Mauritania) to the eastern Middle East (southern Iran and Oman). According to the morphometric part of this analysis, the Socotran samples were very similar to the samples from Somalia (comprising also the type series of *A. tridens italosomalica* de Beaux, 1931), and in body size close also to the samples from Dhofar (although being somewhat larger), while the African and Middle

Eastern samples of *Asellia*, other than those from the latter two limited regions (and including all examined type specimens of *Asellia* other than of *italosomalica*), were metrically very distinct from the Socotran bats. Thus, the taxonomic position of the Socotran populations of *Asellia* was apparent, they were considered as a part of the Somalian species *A. italosomalica*, being genetically, morphologically and also geographically well separated from the other populations of the genus. The Dhofar samples of *Asellia*, in body size similar to *A. italosomalica* but differing from it in skull shape and very deeply in genetic characters (12.4–12.8% of k2p distance), were described as a new species, *A. arabica* Benda, Vallo et Reiter, 2011 (see Benda et al. 2011a).

External and cranial dimensions of the Socotran specimens of *A. italosomalica* are shown in Table 7. For the material examined see above. The size relations of the available Socotran and Somalian samples of *A. italosomalica* to each other and to other *Asellia* species of the southern Afro-Arabian transition, i.e to *A. patrizii*, *A. arabica* and *A. tridens*, are presented in Table 7 and Fig. 37. Considering body size, *A. italosomalica* along with *A. arabica* represent the medium-sized forms of the genus, significantly smaller than *A. tridens* and significantly larger than *A. patrizii*. No size overlap was found among the sample sets of the medium-sized forms and the larger and smaller species, respectively (Fig. 37); on the other hand, the sample sets *A. italosomalica* and *A. arabica* partially overlap in most of dimension ranges (Table 7). However, the latter two species could be distinguished due to a different shape of skull, besides the on average smaller body and skull size in *A. arabica*. The skull and rostrum of *A. arabica* are absolutely and also relatively

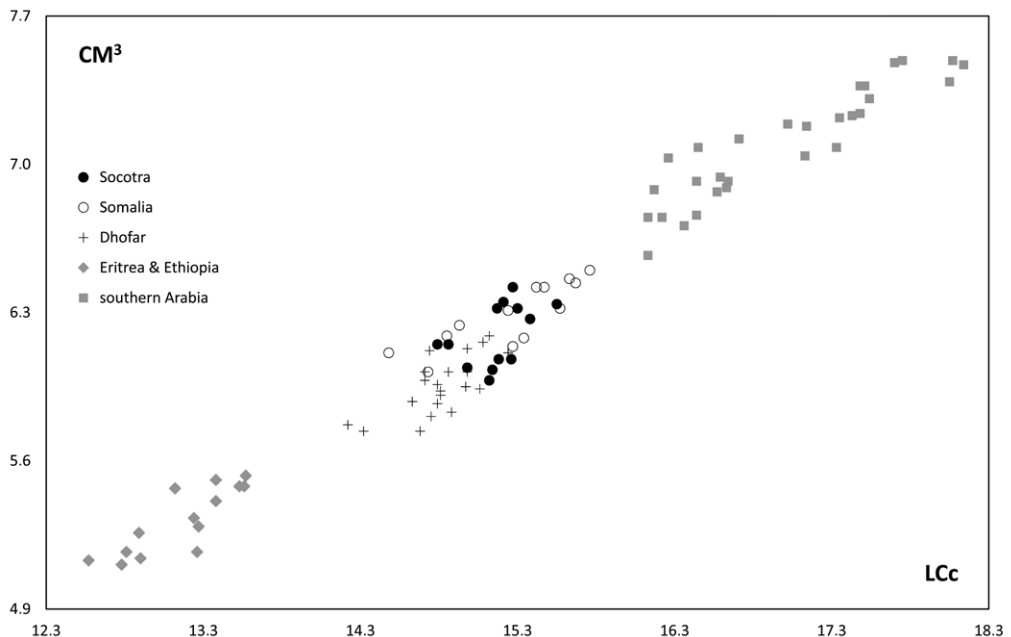
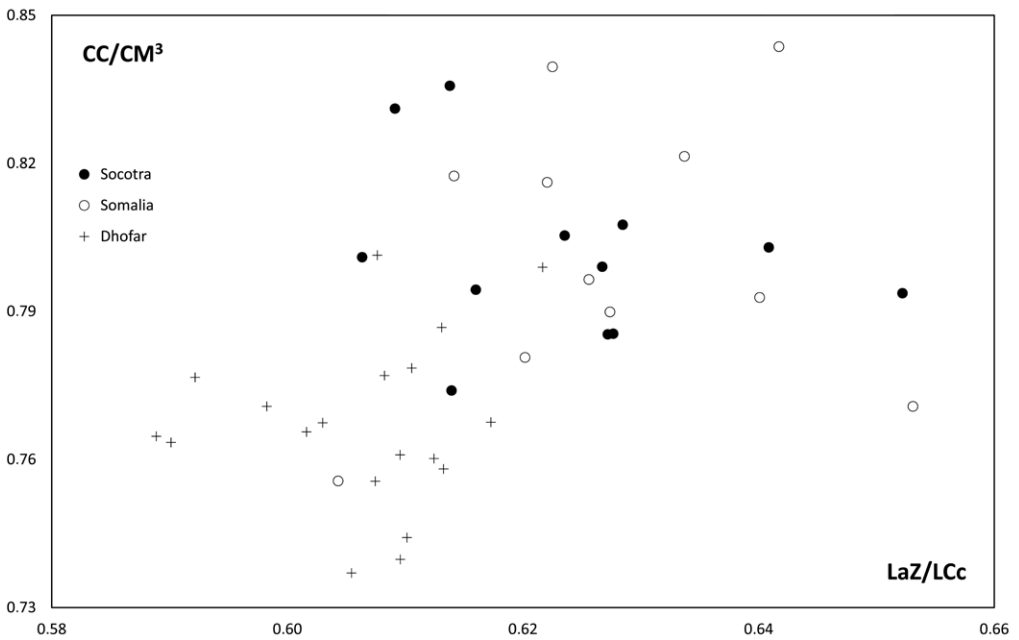
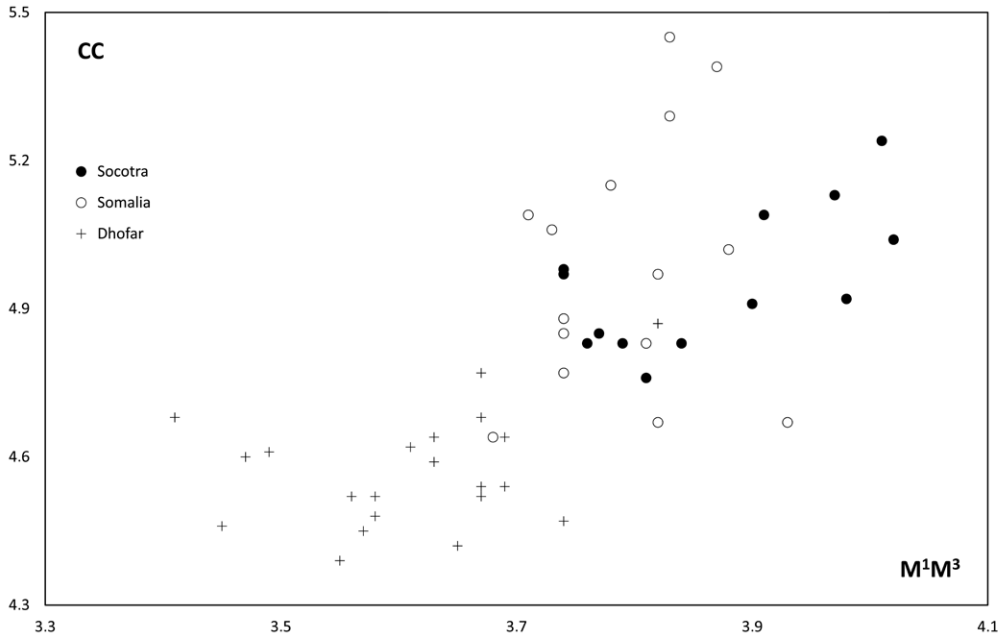


Fig. 37. Bivariate plot of the examined Socotran and comparative samples of *Asellia* Gray, 1838 from the region of the Afro-Arabian transition (Ethiopia, Somalia, Eritrea, southern Arabia): condylocanine length of skull (LCc) against the length of the upper tooth-row (CM<sup>3</sup>). Legend: Socotra and Somalia = samples of *A. italosomalica* De Beaux, 1931; Dhofar = samples of *A. arabica* Benda, Vallo et Reiter, 2011; Eritrea & Ethiopia = samples of *A. patrizii* De Beaux, 1931; southern Arabia = samples of *A. tridens* (Geoffroy, 1813).



Figs. 38, 39. Bivariate plots of the examined Socotran and comparative samples of *Asellia* Gray, 1838. 38 (top) – length of the upper molar-row ( $M^1M^3$ ) against the width of rostrum across the upper canines (CC). 39 (below) – relative width of skull ( $LaZ/LCc$ ) against the relative width of rostrum ( $CC/CM^3$ ). For legend see Fig. 37.



narrower, the rostrum is also shorter than in *A. italosomalica* (Figs. 38, 39). The univariate analysis of variance showed significant differences in the forearm length and all absolute and relative skull dimensions, with exceptions of the braincase characters (Table 7). On the other hand, this analysis did not reveal any significant difference between the limited sets of the Socotran and Somalian samples of *A. italosomalica* (Table 7; see also Figs. 37–39). This indicates that the island of Socotra is inhabited by the identical morphotype as the African mainland, i.e. the nominotypical form of *A. italosomalica*, and thus, this species remains to be considered as monotypic.

SYNONYMY REVIEW.

*Asellia tridens* (Geoffroy, 1813): Harrison 1957: 3; Harrison 1964: 96; Kock 1969: 122; Hayman & Hill 1971: 29; DeBlase 1980: 121; Koopman 1982b: 136; Wranik et al. 1991: 211; Harrison & Bates 1991: 53; Guichard 1992: 187; Koopman 1993: 170; Koopman 1994: 67; Al-Jumaily 1998: 482; Wranik 1998: 145; Wranik 1999: 97; Wranik et al. 1999: 35; Šťastný et al. 2002: 30; Cesarini 2003: 6–17; Wranik et al. 2003: 87; Al-Jumaily 2004: 61; Duff & Lawson 2004: 155; Benda et al. 2005: 19; Simmons 2005: 366; Cesarini 2007: 140; Benda et al. 2011b: 25; O'Brien 2011: 262, 287.

*Asellia tridens tridens* (Geoffroy, 1813): Harrison 1957: 5; Kock 1969: 129; Al-Jumaily 1998: 483.

*Asellia italosomalica* De Beaux, 1931: Benda et al. 2006a: 139; Benda et al. 2011a: 254–267; Lanza et al. 2015: 123.

***Hypsugo lanzai* Benda, Al-Jumaily, Reiter et Nasher, 2011**

RECORDS. **Original data:** Wadi Darho, Desmoiten village [1], at a pool in the wadi, 13 May 2004: det. calls of 1–2 foraging inds.; – Wadi Erher, Faka spring [2], at a stream in the oasis, 24 November 2002: net. 1 ma, NMP (cf. Benda et al. 2008, 2011b), 19 May 2004: obs. 2 foraging inds.; – Wadi Es Gego [3], at and above a stream, 12 May 2004: obs. & det. ca. 10 foraging inds., net. 1 fa, NMP (cf. Benda et al. 2008, 2011b). – **Published data:** Ghadeb [= Qadub] [4], 1 ind., BMNH (Benda et al. 2008 [as *H. ariel*], 2011b); – Ile Socotra [= Socotra, Suq] [5], 1 ind., BMNH (Menu 1987 [as *H. bodenheimeri*]); Suq, palm grove (Guichard 1992 [as *Pipistrellus bodenheimeri*]); Suk, 1 ind., BMNH (Hooper et al. 2006 [as *Hypsugo bodenheimeri*]); Suq, 16 April 1967: 1 m, BMNH (Benda et al. 2008 [as *H. ariel*], 2011b); – perhaps/possibly Socotra Island (Corbet 1978, Harrison & Vernier 1982, Nowak 1991, 1994, 1999, Koopman 1993 [as *Pipistrellus bodenheimeri*], Simmons 2005 [as *H. bodenheimeri*]); ? Socotra Island (Corbet & Hill 1980, Riskin 2001 [as *Pipistrellus bodenheimeri*], Horáček et al. 2000 [as *H. bodenheimeri*]); Socotra (Koopman 1994 [as *Pipistrellus bodenheimeri*]).

DISTRIBUTION. *Hypsugo lanzai* is a rare bat in Socotra, it is an endemic of the island, known only from four specimens and from five sites scattered over the eastern half of the island (Fig. 40).

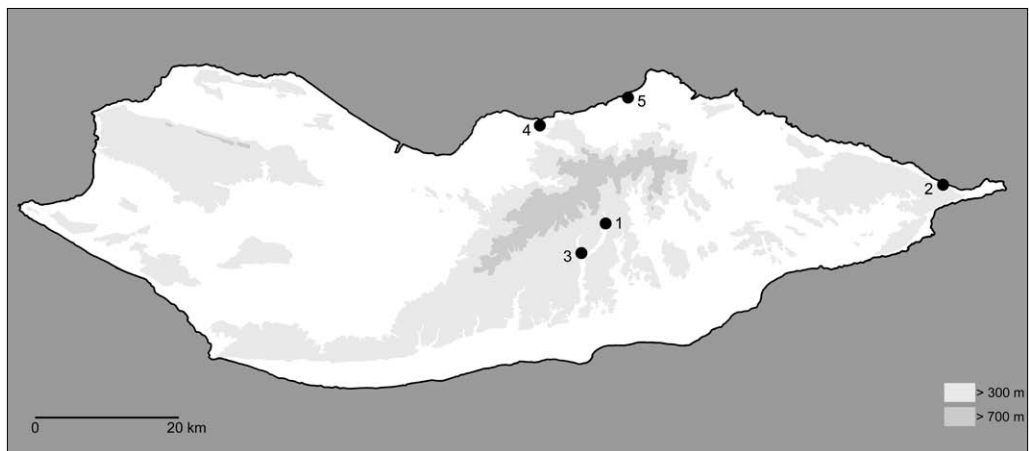


Fig. 40. Records of *Hypsugo lanzai* Benda, Al-Jumaily, Reiter et Nasher, 2011 in Socotra.



Figs. 41, 42. Two views of the Faka spring in Wadi Eher, east-north-eastern shore of Socotra (5 m a. s. l.); site of repeated findings of *Hypsugo lanzai*, in November 2002 and May 2004 (orig. data).

Although a pipistrelle-like bat was collected in Socotra for the first time in 1953 and again in 1967 (both specimens were deposited in the BMNH), and first published in 1978, its occurrence in the island was considered rather doubtful by some authors until almost recently. Corbet (1978: 54) identified the bat of the 1967 catch preliminarily as *Pipistrellus bodenheimeri* (in its broader concept, covering the currently recognised species *Hypsugo ariel* and *H. lanzai*, see below), which he mentioned as follows: “Known only from the type locality, S. W. Arabia and perhaps the island of Socotra. (A single specimen from Socotra in the British Museum is possibly referable to this species but is very dark.)”. Based on this mention, Corbet & Hill (1980) and Harrison & Vernier (1982) reported *P. bodenheimeri* from Socotra with a question mark. The BMNH specimen collected by K. M. Guichard at Suq in 1967 (see Guichard 1992: 187) was identified as *P. bodenheimeri* by Menu (1987). Following this publication, some authors in their reviews reported the occurrence of this species in Socotra (Koopman 1994, Al-Jumaily 1998, Wranik 1999, Wranik et al. 1999, 2003, Hooper et al. 2006, Cesarini 2007), while others regarded its occurrence in Socotra still rather uncertain (Nowak 1991, 1994, 1999, Koopman 1993, Horáček et al. 2000, Riskin 2001, Cesarini 2003, Simmons 2005, etc.). Finally, two additional bats were collected in Socotra in 2002 and 2004 and all available specimens were examined again (Benda et al. 2005, 2006a, 2011b), the occurrence of a pipistrelle-like bat was thus confirmed in the island, albeit as of a very rare inhabitant.

*H. lanzai* is distributed over a narrow range of altitudes (360 m; Table 1). The records are available only from low altitudes of the island, from the sea level to the foothills of mountains (altitude median 10.0 m, altitude mean 137.0 m a. s. l.; Table 1). The highest locality of recorded occurrence

of *H. lanzai* is the Desmoiten village in Wadi Darho at 365 m a. s. l., where the echolocation calls of a foraging individual were detected (no roost of this bat was found, see below).

FIELD NOTES. *Hypsugo lanzai* was recorded in Socotra only at its foraging grounds, no roost of this species was documented. An adult male was captured into a net installed among sparse bush vegetation at the Faka spring in the easternmost part of the island (Figs. 41, 42) on 24 November 2002 (orig. data). Another attempt to net bats at the same place failed because of a strong wind on 19 May 2004; however, two foraging individuals of pipistrelle bats were observed flying a few metres above the vegetated spring area just before sunset. Some ten foraging individuals of *H. lanzai* were observed and their calls detected during a netting session in the Wadi Es Gego on 12 May 2004 (orig. data), where finally one adult female was caught (later on, it was indicated as the holotype specimen of this species). The bats foraged at a small height above a stream and a sparse riparian vegetation and among palm trees in the wadi during sunset and in early dark (Fig. 43). The calls were detected using a heterodyne detector, the maximum energy of the calls was in the range of 45–47 kHz. Very similar calls of foraging bats were detected at a pool on the stream in the Desmoiten village in the Wadi Darho in the dark on 13 May 2004 and we consider them also to belong to *H. lanzai*. Guichard (1992: 187) reported a shot of a foraging individual “at dusk in the palm groves of Suq” (a male collected on 16 April 1967, now deposited in the BMNH collection, cf. Corbet 1978). The last record of this species is represented by a specimen, now also deposited in the BMNH, collected at Ghadeb in 1953. Although no data concerning its collection circumstances are available on the latter specimen, it was most probably also shot on wings, as it was a common way of bat collection at that time.



Fig. 43. Wadi Es Gego, southern slope of the Hagher mountains (295 m a. s. l.); type locality of *Hypsugo lanzai*, an adult female was collected there on 12 May 2004.

Table 8. Basic biometric data on the examined Socotran and comparative samples of *Hypsugo Kolenati*, 1856. Part 1: external and skull dimensions. For abbreviations see p. 103

	n	<i>Hypsugo lanzai</i>				n	<i>Hypsugo ariel</i>				n	<i>Hypsugo arabicus</i>			
		M	min	max	SD		M	min	max	SD		M	min	max	SD
LC	1	46				34	<b>39.76</b>	35	45	2.400	38	<b>44.05</b>	37	48	2.438
LCd	1	42				33	<b>37.91</b>	32	44	2.876	38	<b>39.84</b>	37	44	2.163
LAt	3	<b>31.87</b>	31.1	32.7	0.802	44	<b>30.24</b>	28.1	33.7	1.047	39	<b>31.44</b>	28.9	34.3	0.969
LA	1	14.2				34	<b>13.09</b>	12.2	14.1	0.533	38	<b>12.15</b>	10.5	13.5	0.621
LT	1	4.8				34	<b>4.91</b>	4.1	5.6	0.405	38	<b>5.14</b>	4.7	5.8	0.275
LCr	4	<b>12.26</b>	12.10	12.38	0.123	37	<b>11.48</b>	10.63	12.12	0.323	32	<b>11.51</b>	10.97	12.09	0.244
LCb	4	<b>11.72</b>	11.64	11.89	0.118	37	<b>10.99</b>	10.19	11.71	0.363	31	<b>10.89</b>	10.36	11.26	0.238
LaZ	2	<b>7.43</b>	7.31	7.55	0.170	32	<b>7.00</b>	6.41	7.39	0.217	29	<b>7.27</b>	6.93	7.56	0.196
LaI	4	<b>2.97</b>	2.91	3.06	0.067	37	<b>2.64</b>	2.42	2.88	0.101	32	<b>2.90</b>	2.69	3.15	0.104
LaInf	4	<b>3.83</b>	3.75	3.88	0.054	37	<b>3.56</b>	3.22	3.92	0.172	32	<b>3.31</b>	3.07	3.56	0.125
LaNc	4	<b>6.09</b>	6.04	6.13	0.045	37	<b>5.56</b>	5.10	5.87	0.154	32	<b>5.83</b>	5.59	6.10	0.145
LaM	4	<b>6.42</b>	6.33	6.48	0.077	37	<b>6.07</b>	5.44	6.38	0.185	32	<b>6.23</b>	5.96	6.48	0.140
ANc	4	<b>4.43</b>	4.35	4.47	0.055	37	<b>3.94</b>	3.66	4.25	0.137	32	<b>4.06</b>	3.76	4.35	0.118
ACr	4	<b>5.56</b>	5.45	5.66	0.088	33	<b>5.14</b>	4.55	5.41	0.176	32	<b>5.31</b>	5.04	5.52	0.110
CC	4	<b>3.63</b>	3.58	3.69	0.051	37	<b>3.43</b>	3.20	3.78	0.153	32	<b>3.33</b>	3.01	3.62	0.132
M <sup>3</sup> M <sup>3</sup>	4	<b>5.03</b>	4.92	5.08	0.076	35	<b>4.69</b>	4.23	5.18	0.178	31	<b>4.66</b>	4.35	5.09	0.142
CM <sup>3</sup>	4	<b>4.28</b>	4.19	4.41	0.092	35	<b>3.92</b>	3.62	4.28	0.158	31	<b>3.94</b>	3.72	4.13	0.112
M <sup>1</sup> M <sup>3</sup>	4	<b>3.05</b>	2.97	3.08	0.050	32	<b>2.78</b>	2.53	3.05	0.122	31	<b>2.77</b>	2.58	2.97	0.097
CP <sup>4</sup>	4	<b>1.70</b>	1.64	1.80	0.070	33	<b>1.70</b>	1.50	1.84	0.081	32	<b>1.71</b>	1.59	1.86	0.066
LMd	4	<b>8.32</b>	8.02	8.63	0.252	37	<b>7.80</b>	7.42	8.22	0.231	32	<b>7.76</b>	7.38	8.15	0.212
ACo	4	<b>2.42</b>	2.24	2.58	0.140	37	<b>2.33</b>	2.12	2.57	0.099	32	<b>2.30</b>	2.11	2.47	0.088
CM <sub>3</sub>	4	<b>4.47</b>	4.35	4.57	0.090	35	<b>4.15</b>	3.64	4.47	0.181	32	<b>4.17</b>	3.93	4.48	0.118
MiM <sub>3</sub>	4	<b>3.30</b>	3.21	3.34	0.058	32	<b>3.03</b>	2.66	3.29	0.143	32	<b>2.95</b>	2.76	3.11	0.098
CP <sub>4</sub>	4	<b>1.42</b>	1.36	1.47	0.046	31	<b>1.39</b>	1.25	1.53	0.073	31	<b>1.43</b>	1.35	1.67	0.058

*H. lanzai* was always found to forage above relatively humid grounds, in wadis or spring areas with an active water stream and more or less dense vegetation cover and surrounded by rocky or desert habitats. Guichard (1992) reported a collection of a specimen of *Asellia* at the same site as *H. lanzai* at Suq; however, it is not clear whether it was a simultaneous catch. In Wadi Derho, *H. lanzai* was recorded to forage at a village, where the roosts of *Rhinopoma cystops* and *Rhinolophus clivosus* were found. However, neither roosting of the former species nor common foraging of the three species was documented at the site, although it could be expected there (see above).

The female of *H. lanzai* caught on 12 May 2014 was in the lactation stage. Other signs of reproduction have not yet been documented in *H. lanzai* from Socotra.

MATERIAL EXAMINED (type series of *Hypsugo lanzai* Benda, Al-Jumaily, Reiter et Nasher, 2011). 1 ind. (BMNH 54.1031 [S]), Ghadeb, date unlisted [1953], leg. G. B. Popov; – 1 ♂ (BMNH 67.1255 [S+B]), Suq, 16 April 1967, leg. K. M. Guichard; – 1 ♂ (NMP 92106 [S+A]), Wadi Erher, Faka Spring, 24 November 2002, leg. B. Pražan & A. K. Nasher; – 1 ♀ (NMP 90587 [S+A], holotype of *H. lanzai*), Wadi Es Gego, 12 May 2004, leg. P. Benda & A. Reiter.

TAXONOMIC REMARKS. The Socotran specimens of small vespertilionid bats were first mentioned and for a long time treated under the species name *Pipistrellus bodenheimeri* Harrison, 1960, see the Synonymy review below. The final taxonomic position of this Socotran endemic has been evaluated and suggested only recently (Benda et al. 2011b).

As mentioned above (see Distribution), the first specimen of a pipistrelle bat from Socotra was mentioned by Corbet (1978), who referred it only tentatively as *P. bodenheimeri*, since the Socot-

Table 9. Basic biometric data on the examined Socotran and comparative samples of *Hypsugo Kolenati*, 1856. Part 2: relative skull dimensions. For abbreviations see p. 103

	<i>Hypsugo lanzai</i>				<i>Hypsugo ariel</i>				<i>Hypsugo arabicus</i>						
	n	M	min	max	SD	n	M	min	max	SD	n	M	min	max	SD
LaZ/LCr	2	<b>0.604</b>	0.598	0.610	0.008	30	<b>0.609</b>	0.565	0.628	0.015	29	<b>0.631</b>	0.605	0.648	0.011
LaI/LCr	4	<b>0.242</b>	0.237	0.248	0.006	37	<b>0.230</b>	0.207	0.253	0.010	32	<b>0.252</b>	0.239	0.271	0.009
LaInI/LCr	4	<b>0.312</b>	0.310	0.314	0.002	37	<b>0.310</b>	0.283	0.339	0.014	32	<b>0.288</b>	0.270	0.301	0.008
LaNe/LCr	4	<b>0.497</b>	0.490	0.507	0.007	37	<b>0.484</b>	0.461	0.516	0.013	32	<b>0.506</b>	0.481	0.532	0.013
LaNe/LCb	4	<b>0.520</b>	0.511	0.527	0.007	37	<b>0.506</b>	0.480	0.550	0.015	31	<b>0.536</b>	0.509	0.567	0.015
LaM/LCr	4	<b>0.523</b>	0.521	0.526	0.002	37	<b>0.528</b>	0.503	0.558	0.011	32	<b>0.541</b>	0.524	0.564	0.009
ANe/LCr	4	<b>0.361</b>	0.360	0.363	0.002	37	<b>0.343</b>	0.323	0.365	0.010	32	<b>0.353</b>	0.335	0.383	0.010
ACo/LMd	4	<b>0.291</b>	0.279	0.299	0.009	37	<b>0.299</b>	0.274	0.315	0.010	32	<b>0.297</b>	0.279	0.313	0.009
CC/CM <sup>3</sup>	4	<b>0.847</b>	0.825	0.864	0.017	35	<b>0.870</b>	0.820	0.916	0.026	31	<b>0.843</b>	0.770	0.895	0.028
CM <sup>3</sup> /LCr	4	<b>0.349</b>	0.343	0.358	0.007	35	<b>0.342</b>	0.323	0.365	0.009	31	<b>0.343</b>	0.325	0.353	0.006
CP <sup>4</sup> /M <sup>1</sup> M <sup>2</sup>	4	<b>0.557</b>	0.533	0.588	0.023	32	<b>0.614</b>	0.571	0.674	0.027	31	<b>0.617</b>	0.552	0.699	0.035
M <sup>1</sup> M <sup>2</sup> /CM <sup>3</sup>	4	<b>0.711</b>	0.692	0.723	0.014	32	<b>0.709</b>	0.675	0.745	0.017	31	<b>0.703</b>	0.663	0.743	0.019
CP <sub>1</sub> /M <sub>1</sub> M <sub>3</sub>	4	<b>0.432</b>	0.411	0.444	0.015	31	<b>0.458</b>	0.425	0.486	0.017	31	<b>0.485</b>	0.450	0.605	0.027

ran bat had a very dark pelage colouration in comparison to the creamy whitish specimens from the Levant, the area of the originally reported distribution of this form (Harrison 1960, 1964). Menu (1987) mentioned again this name for the respective specimen, however, he used this bat as an example of the taxon and did not mention other specimens or even type of this name.

Table 10. Basic biometric data on the examined Socotran and comparative samples of *Hypsugo Kolenati*, 1856. Part 3: tooth dimensions. For abbreviations see pp. 103–104

	<i>Hypsugo lanzai</i>				<i>Hypsugo ariel</i>				<i>Hypsugo arabicus</i>						
	n	M	min	max	SD	n	M	min	max	SD	n	M	min	max	SD
LI <sup>2</sup>	4	<b>0.469</b>	0.46	0.48	0.010	32	<b>0.421</b>	0.35	0.50	0.044	31	<b>0.465</b>	0.39	0.58	0.048
LI <sup>3</sup>	4	<b>0.325</b>	0.30	0.35	0.019	33	<b>0.325</b>	0.23	0.39	0.038	32	<b>0.347</b>	0.25	0.46	0.051
LCs	4	<b>0.869</b>	0.87	0.87	0.000	30	<b>0.877</b>	0.76	1.02	0.070	31	<b>0.848</b>	0.75	0.90	0.042
LaCs	4	<b>0.848</b>	0.82	0.88	0.044	30	<b>0.815</b>	0.61	0.93	0.071	31	<b>0.680</b>	0.61	0.79	0.038
ACn	4	<b>0.073</b>	0.04	0.10	0.044	27	<b>0.087</b>	0.00	0.20	0.041	31	<b>0.091</b>	0.03	0.16	0.029
LP <sup>2</sup>	4	<b>0.183</b>	0.15	0.22	0.052	30	<b>0.212</b>	0.16	0.28	0.034	30	<b>0.236</b>	0.18	0.31	0.035
LP <sup>4</sup>	4	<b>0.806</b>	0.76	0.85	0.059	30	<b>0.838</b>	0.70	0.91	0.048	31	<b>0.789</b>	0.69	0.88	0.048
LaP <sup>4</sup>	4	<b>1.089</b>	1.09	1.09	0.000	30	<b>1.096</b>	0.95	1.31	0.087	31	<b>1.092</b>	0.99	1.21	0.052
LM <sup>1</sup>	4	<b>1.215</b>	1.16	1.27	0.074	30	<b>1.132</b>	1.01	1.25	0.059	31	<b>1.145</b>	1.04	1.26	0.048
LaM <sup>1</sup>	4	<b>1.398</b>	1.39	1.40	0.007	30	<b>1.344</b>	1.20	1.51	0.073	31	<b>1.326</b>	1.25	1.40	0.051
LM <sup>3</sup>	4	<b>0.738</b>	0.73	0.74	0.007	30	<b>0.668</b>	0.61	0.75	0.035	30	<b>0.660</b>	0.59	0.72	0.032
LaM <sup>3</sup>	4	<b>1.560</b>	1.53	1.59	0.044	30	<b>1.385</b>	1.21	1.57	0.081	30	<b>1.303</b>	1.19	1.39	0.053
LaI <sub>1</sub>	4	<b>0.398</b>	0.39	0.41	0.015	29	<b>0.378</b>	0.35	0.43	0.019	31	<b>0.379</b>	0.32	0.43	0.023
LaI <sub>3</sub>	4	<b>0.346</b>	0.34	0.36	0.015	29	<b>0.326</b>	0.25	0.46	0.036	30	<b>0.355</b>	0.29	0.40	0.023
LCi	4	<b>0.597</b>	0.60	0.60	0.000	29	<b>0.594</b>	0.47	0.70	0.055	30	<b>0.586</b>	0.51	0.63	0.025
LP <sub>3</sub>	4	<b>0.346</b>	0.34	0.37	0.022	28	<b>0.358</b>	0.27	0.46	0.044	31	<b>0.369</b>	0.30	0.43	0.029
LM <sub>1</sub>	4	<b>1.168</b>	1.10	1.24	0.096	29	<b>1.081</b>	0.96	1.17	0.049	31	<b>1.078</b>	0.96	1.15	0.041
LM <sub>3</sub>	4	<b>1.126</b>	1.10	1.15	0.037	29	<b>1.017</b>	0.92	1.13	0.057	31	<b>0.968</b>	0.89	1.04	0.038
M <sup>3</sup> sq	4	<b>1.152</b>	1.121	1.183	0.044	30	<b>0.925</b>	0.770	1.103	0.084	30	<b>0.861</b>	0.700	0.962	0.070
P <sup>3</sup> /Cs	4	<b>0.211</b>	0.169	0.253	0.060	30	<b>0.242</b>	0.184	0.314	0.039	30	<b>0.279</b>	0.202	0.390	0.044
P <sub>3</sub> /Ci	4	<b>0.588</b>	0.561	0.614	0.037	28	<b>0.600</b>	0.431	0.746	0.075	30	<b>0.630</b>	0.517	0.745	0.057



Figs. 44, 45. *Hypsugo lanzai* Benda, Al-Jumaily, Reiter et Nasher, 2011 (female, holotype).

Horáček et al. (2000) first used a different genus name concerning the Socotran pipistrelle population, *Hypsugo* Kolenati, 1856 instead of *Pipistrellus* Kaup, 1829, and this change was accepted by Simmons (2005). However, the species affiliation remained unchanged until Benda et al. (2008) published a revision of the complex of *Hypsugo bodenheimeri*, where they suggested the latter name to be a junior synonym of *Hypsugo ariel* (Thomas, 1904).

Originally (see e.g. Harrison 1964, Qumsieh 1985, Harrison & Bates 1991, Koopman 1994, etc.), *H. ariel* was considered a very rare species, known from three bats (including type series) from Sudan and other few specimens from Israel. It shared most morphological traits with *H. bodenheimeri* (size, colouration, skull characters and most of dental characters, baculum size and shape), with the exception of the structure of the first upper incisor ( $I^2$ ). In *H. ariel*, this tooth was reported to be unicuspidal while in *H. bodenheimeri* bicuspidal. However, Benda et al. (2008), using a larger series of examined specimens from the whole distribution range, demonstrated these two states of the upper incisor structure to be just extreme variations of a continuum of several intermediate states. Thus, they suggested to consider both taxon names as synonyms. Later on, a molecular genetic analysis (Benda et al. 2016) showed the Yemeni and Egyptian samples of *H. ariel* to represent a single lineage of a mitochondrial gene (originally, only *H. ariel* was reported from Africa, and only *H. bodenheimeri* from Yemen), which conformed with the view by Benda et al. (2008).

Concerning the Socotran populations, although Benda et al. (2006a: 139) suggested to consider them a part of the species rank of *H. ariel*, they mentioned some differences compared to the mainland populations. Similarly, Benda et al. (2008), who analysed morphometric traits of the *Hypsugo ariel* complex (see above), regarded the taxonomic status of the Socotran populations



under *H. ariel* in a need of revision. Finally, Benda et al. (2011b) thoroughly analysed morphologic traits of all four known Socotran specimens of *Hypsugo* and compared them with a large series of *H. ariel* from all parts of its range (NE Africa, Levant, S Arabia) and of *H. arabicus* (Harrison, 1979), a similar bat living in north-eastern Oman and south-eastern Iran (see Benda et al. 2012). Benda et al. (2011b) indicated several groups of characters, in which the Socotran and mainland populations differ; viz. pelage colouration, body and skull sizes, skull shape, tooth size and shape, and baculum size and shape. Based on states of these characters, representing a mosaic of unique traits and traits similar to either *H. ariel* or *H. arabicus*, these authors described the Socotran populations as a separate species, *H. lanzai*.

The characters typical for *H. lanzai*, which differentiate it from two very similar mainland species, *H. ariel* and *H. arabicus*, could be summarised as follows; (1) the colouration of *H. lanzai* is dark, the pelage is brown to dark brown with rusty tinges and naked parts are dark brownish-grey (Figs. 44, 45), while the colouration of the two mainland species is pale, with dorsal pelage from creamy to very pale brownish-grey and wing membranes, face and ears are unpigmented to brown (see also Harrison 1960, 1964, Harrison & Bates 1991, Gaucher & Harrison 1995, Riskin 2001, Benda et al. 2011b). (2) *H. lanzai* is the largest form of the *ariel-arabicus* complex (Fig. 46), some of its external and skull dimensions do not overlap in their ranges with the ranges of dimensions of the two smaller species (which are in their dimensions very similar to each other, Tables 8, 10), and where they do overlap, the average values are larger than those of the two smaller species (Tables 8, 10). (3) the skull of *H. lanzai* is relatively narrow, the braincase is relatively

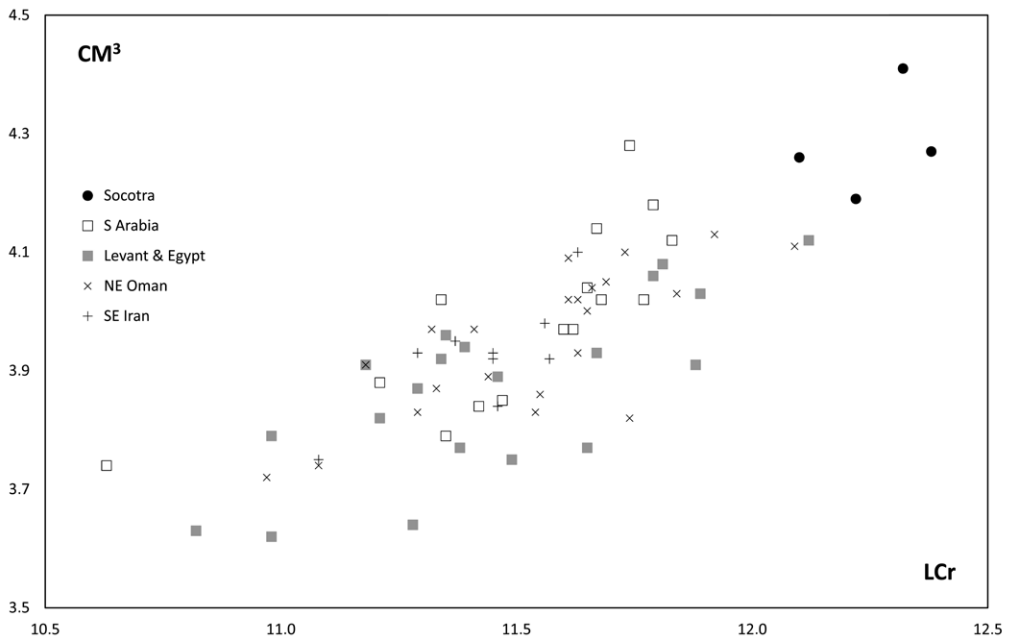
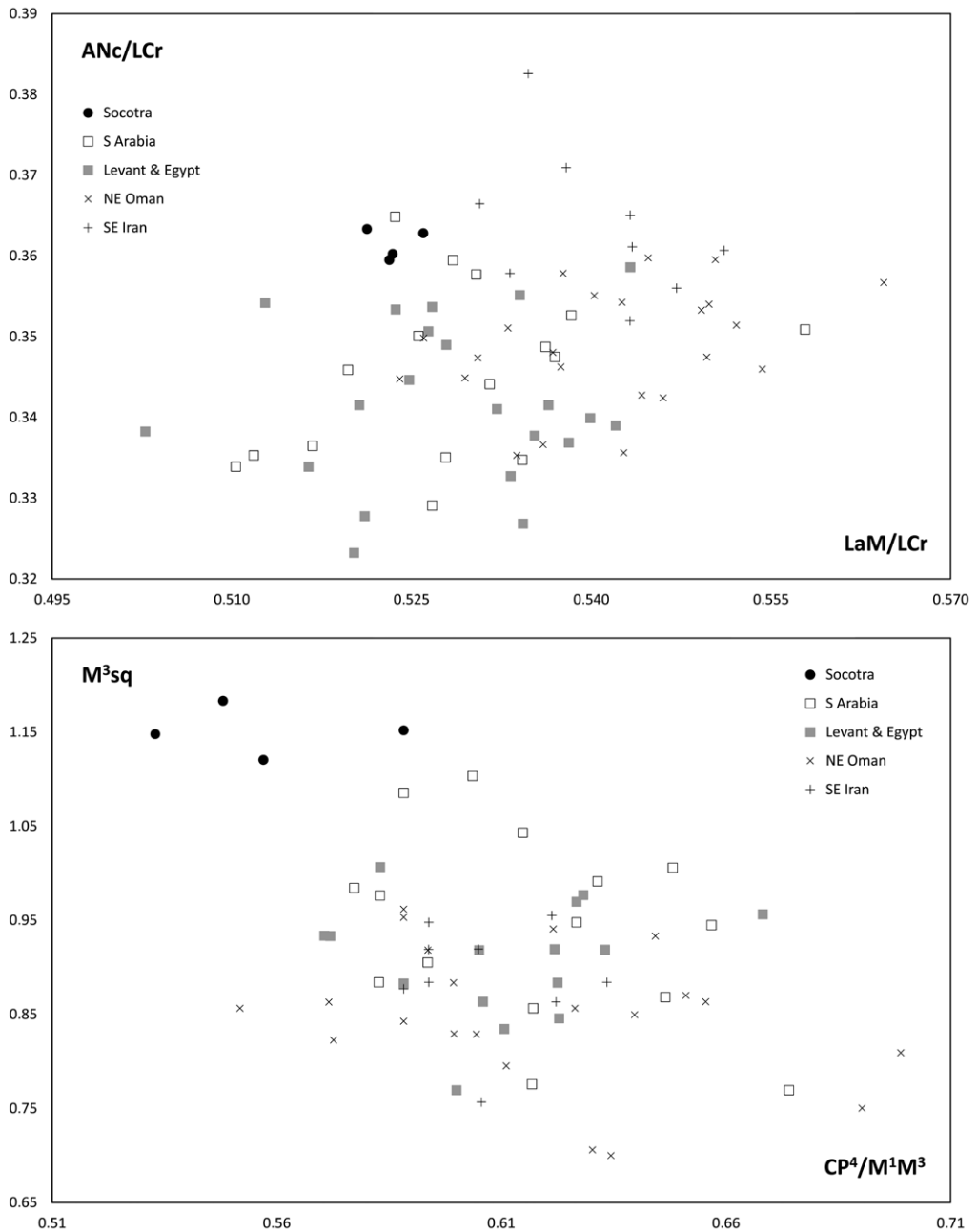


Fig. 46. Bivariate plot of the examined Socotran and comparative samples of *Hypsugo* Kolenati, 1856: greatest length of skull (LCr) against the length of the upper tooth-row (CM<sup>3</sup>). Legend: S Arabia, Levant & Egypt = samples of *H. ariel* (Thomas, 1904); NE Oman, SE Iran = samples of *H. arabicus* (Harrison, 1979) (after Benda et al. 2011b, modified).



Figs. 47, 48. Bivariate plot of the examined Socotran and comparative samples of *Hypsugo Kolenati*, 1856. 47 (top) – relative width of neurocranium (LaM/LCr) against the relative height of neurocranium (ANc/LCr). 48 (below) – relative length of the upper unicuspidal tooth-row (CP<sup>4</sup>/M<sup>1</sup>M<sup>3</sup>) against the crown square of the third upper molar (M<sup>3</sup>sq). For legend see Fig. 46 (after Benda et al. 2011b, modified).



narrower in comparison to *H. arabicus*, but relatively higher in comparison to *H. ariel* (Fig. 47); the rostrum of *H. lanzai* is relatively longer and wider than that of the two mainland species (Table 9). (4) The molars and molar rows of *H. lanzai* are absolutely and relatively larger than those of the two mainland species (Fig. 48, Table 10); the small premolars ( $P^3$  and  $P_3$ ) are relatively ( $P_3$  also absolutely) very small in *H. lanzai*, while the crowns of upper canines are large in *H. lanzai* (Table 10). (5) The baculum of *H. lanzai* is an elongated, flattened manger-like stick (2.14 mm in the only examined specimen; Fig. 49), similar in size to that of *H. arabicus* and larger than that of *H. ariel*, simply pointed in its distal epiphysis (while in *H. arabicus* it is tridentally divided) and slightly broadened in its diaphysis (similarly to *H. ariel*, while in *H. arabicus* it is equally wide along its whole length); the largest width of the baculum diaphysis represents 18% of the baculum length of *H. lanzai*, while 25–28% of that of *H. ariel* (Fig. 49; see also Harrison 1982, Hill & Harrison 1987, Harrison & Bates 1991, Benda et al. 2011b, 2016).

#### SYNONYMY REVIEW.

*Pipistrellus bodenheimeri* Harrison, 1960: Corbet 1978: 54; Corbet & Hill 1980: 67; Harrison & Vernier 1982: 197; Menu 1987: 126; Nowak 1991: 340; Guichard 1992: 187; Koopman 1993: 220; Koopman 1994: 115; Nowak 1994: 194; Al-Jumaily 1998: 484; Wranik 1998: 145; Nowak 1999: 427; Wranik 1999: 98; Wranik et al. 1999: 35; Wranik 2000: 121; Riskin 2001: 1; Šťastný et al. 2002: 30; Cesarini 2003: 7–18; Wranik 2003: 88; Cesarini 2007: 136.

*Hypsugo bodenheimeri* (Harrison, 1960): Horáček et al. 2000: 127; Simmons 2005: 490; Hoofer et al. 2006: 991.

*Hypsugo ariel* (Thomas, 1904): Benda et al. 2005: 19; Benda et al. 2006a: 139; Benda et al. 2008: 32, 95; O'Brien 2011: 270, 290.

*Hypsugo lanzai* Benda, Al-Jumaily, Reiter et Nasher, 2011: Benda et al. 2011b: 37; Mlíkovský et al. 2011: 136; Suchomel 2013: 91; Fasola et al. 2014: 53.

#### DISCUSSION

The present review summarises at least 54 records of four bat species of four families from the Socotra Archipelago. Although the various types of shrubland which are the prevailing vegetation type of the island (Popov 1957) cannot be regarded as a harsh desert, all four bat species belong to

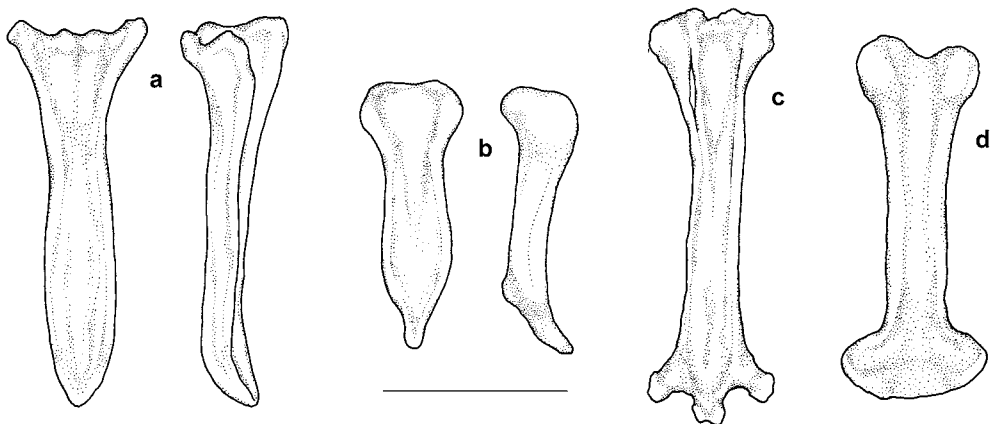


Fig. 49. Baculum preparations from the Socotran and comparative samples of *Hypsugo* Kolenati, 1856: a – *Hypsugo lanzai* Benda, Al-Jumaily, Reiter et Nasher, 2011 (NMP 92106, Socotra, Faka Spring); b – *Hypsugo ariel* (Thomas, 1904) (TAU M8054, Israel, En Gedi); c – *Hypsugo arabicus* (Harrison, 1979) (NMP 48418, Iran, Pir Sohrab); d – *Hypsugo savii* (Bonaparte, 1837) (NMP 48069, Syria, Slinfeh). Distal epiphyses below; scale bar = 1 mm (after Benda et al. 2011b).

desert forms. Their mainland populations (or their closest relatives in the case of *Hypsugo lanzai*) are inhabitants of the most arid environments, in which bats can survive. The most abundant bat of the Archipelago, *Rhinopoma cystops*, representing almost two-thirds of the available bat records (63.0%), is a typical desert bat, commonly occurring also in the inner parts of the Arabian Desert and Sahara. It seems that bats perceive the rather densely vegetated island of Socotra as a desert, and only the bats well adapted to desert life can inhabit it.

Despite the closest geographical proximity of the Socotra Archipelago to the Horn of Africa (that was even more pronounced during the glacial maxima, when the sea level was significantly lower and the gaps between land patches were smaller than today, see Beydoun & Bichan 1969, Van Damme 2006), the bat fauna of Socotra demonstrates its phylogenetic affinities to both mainlands that lie in the island's vicinity. The phylogenetically closest relatives of *Rhinopoma cystops*, *Rhinolophus clivosus* and *Hypsugo lanzai* occur in southern Arabia, i.e., in southern Yemen and south-western Oman. On the other hand, the Socotran populations of *Asellia italosomalica* are a part of the rank of this species occurring in southern and eastern Somalia. The rather surprising prevailing phylogenetic affinity of the bat fauna suggests a different way of colonisation of Socotra than only from the Horn of Africa with the use of stepping-stones of the smaller islands of the Archipelago. Perhaps also the monsoons, namely the winter north-west winds from southern Asia, played a role in the spreading of bats from the mainland to Socotra. After all, such a scenario was already suggested for the colonisation events of flying foxes (*Pteropus* Brisson, 1762) from Asia to the islands of the western part of the Indian Ocean (O'Brien et al. 2009).

The available results of molecular genetic analyses (comprising three of the four bat species of Socotra) showed a variable pattern concerning the age of colonisation of Socotra by the mainland populations. For *Rhinopoma cystops*, Hulva et al. (2007) demonstrated a very close phylogenetic position of the Socotran bats to the Yemeni populations, as the samples from both populations shared identical haplotype of the examined mitochondrial marker (partial sequence of the cytochrome *b* gene). This result suggests a recent arrival of the species to Socotra or very recent continental additions to the island populations, which theoretically could have been established earlier. Although perhaps less probable, this may also suggest a continual gene exchange between the island and mainland populations, which implies a migratory (at least irregularly) behaviour in *R. cystops*. However, this species is considered a sedentary bat which can hardly cross the extreme distance across sea in other way than only accidentally. For *Rhinolophus clivosus*, the genetic divergence of the Socotran populations from the Yemeni ones suggests an older colonisation event than in the previous species, perhaps occurring roughly at the Pliocene-Pleistocene transition (~2.0 Ma). Such a period, spent in the island isolation, was enough for this bat to develop a separate evolutionary unit that is here described as a new taxon. The deepest genetic divergence was demonstrated for *Asellia*, the Socotran populations of *A. italosomalica* were shown to be distant from *A. arabica* and *A. tridens* of the Middle East by 12.3–12.8% of the k2p distance in the complete cytochrome *b* gene; based on this divergence, the split in the Socotran *Asellia* lineage was dated at 12.3 Ma, to middle Miocene (Benda et al. 2011a). This age roughly corresponds to the beginning of the oceanisation of Socotra, for which the latest estimate lies at 15 Ma (Fleitman et al. 2004). Despite the lack of molecular data on the Somalian populations of *A. italosomalica*, their morphological conformity with the Socotran populations allowed a speculation on the colonisation of the Horn of Africa from Socotra in more recent times (Benda et al. 2011a). During Pleistocene the sea level dropped periodically (e.g. by ca. 120 m during the last glacial maximum; Beydoun & Bichan 1969, Van Damme 2006) and the connection between Socotra and Cape Guardafui became easier for bats. Thus, this hypothesis expects even the Socotran origin of *A. italosomalica*. To summarise the available data, the appearance of the particular bat species in the Socotra Archipelago is a result of different and independent colonisati-

Table 11. The fauna of bats and other mammals (as No. of species) of the islands of the western Indian Ocean larger than 100 km<sup>2</sup> (besides Madagascar); based on the data by Cheke & Dahl (1981), Pakenham (1984), Goodman et al. (2009), Kock & Stanley (2009), O'Brien (2011), Happold & Happold (2013), etc.

NOTE. Numbers of introduced mammals were taken from Russell et al. (2016), who, however, did not consider larger herbivores other than goat (i.e. cattle, sheep, camel, ass) among introduced species

island	area [km <sup>2</sup> ]	inhabitants (thousands)	fruit bats	insecti- vorous bats	other indigenous land mammals	introduced mammals
Socotra	3,625	~50	0	4	0	6
Réunion	2,511	843	2	3	0	10
Mauritius	1,865	~1,200	3	2	0	11
Zanzibar	1,554	897	5	20	19	9
Grand Comore	1,025	~350	2	1	0	8
Pemba	988	407	4	13	6	7
Mafia	435	47	5	8	12	5
Anjouan	424	~300	3	3	0	7
Mayotte	368	213	1	1	0	7
Moheli	211	~40	3	0	0	7
Mahé	157	~80	1	1	0	7
Aldabra	155	~0.02	1	3	0	5
Rodrigues	108	42	2	1	0	7

on events and the history of bat origins in Socotra has a similar pattern to that showed e.g. for the much more diversified fauna of the Socotran reptiles (see Macey et al. 2008, Gómez-Díaz et al. 2012, Sindaco et al. 2012, Šmíd et al. 2013, etc.). At least a half of the bat fauna of Socotra is now represented by island endemics.

The number of bat species recorded from the Socotra Archipelago may seem quite low, considering the area of the largest island (more than 3,600 km<sup>2</sup>). For instance, much more bat species can be found on the islands of such size in the Mediterranean (e.g. 15 species on Mallorca with 3,648 km<sup>2</sup>; see Palomo & Gisbert 2002). However, in the western part of the Indian Ocean, the diversity of bat fauna known from Socotra remains well comparable with those of other oceanic islands (Table 11). The exceptions are Madagascar, which resembles rather a smaller continent by its (bat) diversity (see Peterson et al. 1995, O'Brien 2011, etc.), and the Spice Islands lying off the shore of East Africa, in which the bat fauna composition resembles rather that of the close African mainland than of isolated islands (Kock & Stanley 2009, Happold & Happold 2013).

The bat species numbers documented from the larger oceanic islands of the western Indian Ocean (Mascarenes, Comoros, Seychelles) are mostly similar to that found on Socotra (Table 11), also the absence of indigenous terrestrial mammals other than bats in these islands is identical. Actually, the main dissimilarity from other oceanic islands is not the number of species, but the absence of any fruit bat in Socotra. Indeed, remains of an early Holocene fossil of a fruit bat, identified as *Rousettus aegyptiacus* (Geoffroy, 1810), were found in Socotra (Van Damme et al., in press). This finding demonstrates ability of fruit bats to spread to Socotra, but also the impossibility of fruit bats to survive in the conditions of Socotra. With the exception of the Socotra Archipelago, all tropical oceanic islands of the western Indian Ocean are covered by forest, which can well support their populations of fruit bats, composed of even more than one species in some cases (Table 11).

However, some of the previous authors (Wranik 1986, 2000, Cesarini 2003) speculated about a higher number of bat species in the Socotra Archipelago than that currently known. The surrounding mainland areas of Arabia and Africa possess a high diversity of bat fauna, viz. 33 bat species in the continental Yemen (Benda et al. 2011a, b, 2016, Vallo et al. 2011) and 49 bat species in

Somalia (Lanza et al. 2015). Since the four bat species known to occur on Socotra represent the desert forms (see above), other potential members of the Archipelago fauna should be traced among the forms occurring in deserts of the mainland. Although most of the Yemeni and Somalian species represent savannah dwelling bats which can be hardly expected to occupy the dry shrublands of Socotra, some of these species inhabit deserts or semi-deserts, and moreover, 16 bat species are known from both countries. Some of these species could be considered as potential candidates for enrichment of the fauna of Socotra, e.g. *Hipposideros tephurus* Cabrera, 1906, *Triaenops afer* Peters, 1877 (or *T. persicus* Dobson, 1871), *Coleura afra* (Peters, 1852), *Taphozous perforatus* Geoffroy, 1818, *T. nudiventris* Cretzschmar, 1830, *Nycteris thebaica* Geoffroy, 1818, and *Nycticeinops schlieffenii* (Peters, 1859). Among these bats, six representatives (*Triaenops* spp., *Coleura afra*, *Taphozous perforatus*, *T. nudiventris*, *Nycteris thebaica*, *Nycticeinops schlieffenii*) were recorded in the lowland deserts both of eastern Somalia (Puntland) and of southern Yemen, i.e. in the regions geographically closest to the Socotra Archipelago and where the environmental conditions can perhaps best resemble those in these islands. Some bat species have a potential to spread across the sea also in the recent era, see e.g. the famous case of *Coleura afra* (Harrison 1967).

Until now, the survey of bats in Socotra was carried out rather accidentally than as a regular research and the number of records still remains low. The densities of the island populations are generally lower than in the mainland and theoretically, some bat species of Socotra can still remain hidden to our knowledge. A more profound study of bats covering more seasons of a year is needed in Socotra to be able to establish a more realistic picture of its bat fauna than we could bring here.

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APPENDIX I  
Gazetteer

site name	coordinates	altitude [m a. s. l.]
Abd El Kuri	12° 10' 45" N, 52° 13' 49" E	~15
Abel, Ghelemeneten	12° 41' 41" N, 53° 39' 01" E†	~20
Adho Dimello pass	12° 34' 15" N, 54° 02' 50" E*	~1050
Adho Dimellus ... see Adho Dimello pass		
Bat Cave, Mahlez plateau	12° 30' 23" N, 53° 33' 27" E*	175
Chesa (Noged)	12° 23' 42" N, 54° 07' 46" E†	~60
Dahaisi cave	12° 34' 03" N, 54° 17' 22" E*	590
De Fareho, Qatanen I	12° 32' 03" N, 53° 42' 41" E*	75
De Fareho (Abel), Qatanen II	12° 31' 57" N, 53° 42' 48" E*	115
De Kazakaz Cave ... see Moumi, De Qaseqas		
Dehasas, Devegach	12° 36' 16" N, 53° 19' 32" E†	~5
Deiqab Cave	12° 32' 13" N, 54° 01' 01" E	205
Deksam plateau, Bedouin camp, cave	12° 31' 16" N, 53° 58' 00" E†	~900
Dexam Plateau, Wadi Zerik ... see Wadi Zerig		
Diksam, Hafur Cave ... see Diksam Plateau, Fornise Area, Hofur cave		
Diksam [Dixam] Plateau, Diksam lake	12° 31' 24" N, 53° 57' 14" E	990
Diksam [Dixam] Plateau, Fornise Area, Hofur cave	12° 29' 55" N, 53° 56' 46" E	885
Diksam [Dixam] Plateau, Marshim cave	12° 30' 32" N, 53° 56' 19" E	945
Diksamplateau ... see Deksam plateau, Bedouin camp		
Dilhailhe Cave, Mahlez plateau	12° 29' 55" N, 53° 56' 45" E*	880
Faka Spring ... see Wadi Erher, Faka Spring		
Fornise Area ... see Diksam Plateau, Fornise Area		
Ghadab ... see Qadub		
Hadibo ... see Hadiboh		
Hadiboh	12° 39' 00" N, 54° 01' 25" E	10
Hadibu ... see Hadiboh		
Hafur cave ... see Diksam Plateau, Fornise Area, Hofur cave		
Hofur cave ... see Diksam Plateau, Fornise Area, Hofur cave		
Haggher, Reshom	12° 36' 20" N, 54° 05' 49" E*	705
Haggher, Shesor	12° 34' 36" N, 54° 05' 13" E*	665
Haif, Gorf cave	12° 23' 56" N, 54° 05' 49" E*	155
Hardwicki Cave, Mahlez plateau	12° 34' 25" N, 53° 55' 28" E*	208
Hawlaf, Rhahr Cave	12° 40' 13" N, 54° 04' 08" E	85
Homhil	12° 34' 35" N, 54° 17' 57" E†	345
Jalad ... see Wadi Zerig		
Kam oasis, cave	12° 39' 42" N, 54° 07' 05" E	55
Keisu [Qeysoh] oasis	12° 39' 32" N, 53° 28' 12" E	60 / 120
Keze village ... see Wadi Azro, 3 km N of the Keze village		
Lahas, Halolaighan	12° 28' 29" N, 53° 41' 00" E*	95
Marshim cave ... see Diksam Plateau, Marshim cave		
Medhobo, Desberhe	12° 28' 53" N, 54° 15' 07" E*	440
Momi area, cave ... see Dahaisi cave		
Moumi, De Qaseqas	12° 33' 20" N, 54° 18' 33" E*	520
Neet, cave	12° 30' 06" N, 53° 21' 50" E	40
Noged, large cave ... see Deiqab Cave		
Qadub	12° 38' 04" N, 53° 57' 04" E	10
Samha	12° 09' N, 53° 02' E	
Serhin ... see Sirhin, Dixam / see Sirhin		
Shab, Hovagh	12° 29' 38" N, 54° 05' 24" E*	180
Shab, Terbak	12° 29' 33" N, 54° 04' 58" E*	165
Shibhon, Jalad ... see Wadi Zerig		
Shesehar, Shesehar cave	12° 37' 58" N, 54° 15' 14" E†	~10

site name	coordinates	altitude [m a. s. l.]
Sirhin	12° 39' 24" N, 54° 02' 04" E	15
Sirhin, Dixam	12° 31' 05" N, 53° 59' 08" E*	805
Suk ... see Suq		
Suq [Sheq], water pool	12° 39' 59" N, 54° 03' 40" E	10
Taïti's Cave, Mahlez plateau	12° 36' 57" N, 53° 57' 24" E*	110
Tamarida ... see Hadiboh		
Tamaridah ... see Hadiboh		
Timre area, rocky crevice	12° 36' 44" N, 54° 17' 34" E	35
Wadi Ayhaft, lower part	12° 36' 58" N, 53° 57' 24" E	120
Wadi Azro [Di Azerho], 3 km N of the Keze village, cave	12° 24' 26" N, 54° 07' 58" E	60
Wadi Darho, Desmoiten village	12° 30' 13" N, 54° 02' 16" E	365 / 395
Wadi Darho, Mazaaba village, cave	12° 28' 57" N, 54° 01' 45" E	325
Wadi Erher [Arher], Faka Spring	12° 33' 01" N, 54° 27' 36" E	5
Wadi Es Gego [Esgego], lower part	12° 28' 06" N, 54° 00' 38" E	295
Wadi Shaab, Heloma village, cave	12° 32' 50" N, 54° 04' 18" E	295
Wadi Zaerig ... see Wadi Zerig, cave		
Wadi Zerig, cave	12° 29' 21" N, 53° 59' 20" E	660
Wadi Zerik ... see Wadi Zerig, cave		

N.B. The names in parentheses [] represent the transliteration mode of the respective name preferred by Bezděk et al. (2012) which differs from that used by us; otherwise, the transliteration modes used by us and by Bezděk et al. (2012) agree. The asterisk \* denotes data taken from literature, the cross † denotes only approximate data identification.

## APPENDIX II

### List of comparative material examined

#### *Rhinopoma cystops* Thomas, 1903

**Ethiopia:** 1 ♂, 2 ♀♀ (MZUF 6528, 6537, 6540 [S+B]), Metahara, 11–12 April 1971, leg. B. Lanza. – **Oman:** 4 ♀♀ (NMP 94049–94051 [S+A], 94052 [A]), Ain Hamran Cave, 28 March 2012, leg. P. Benda, A. Reiter & M. Uhrin; – 1 ♀ (NMP 94071 [S+A]), wadi 1 km E of Sadah, 31 March 2012, leg. P. Benda, A. Reiter & M. Uhrin; – 1 ♀ (NMP 92696 [S+A]), wadi 2 km W of Rakhut, 25 October 2009, leg. P. Benda, A. Reiter & M. Uhrin. – **Saudi Arabia:** 4 ♂♂, 3 ♀♀ (SMF 60891–60894, 60896–60898 [S]), bei Medina, 19 November 1971, leg. I. Nader. – **Somaliland:** 3 ♂♂, 9 ♀♀ (MZUF 9919–9922, 9925, 9927, 9929, 9930, 9932, 9933, 9935, 9937 [S+A]), Taleh, 18–19 April 1980, leg. B. Lanza. – **Yemen:** 2 ♂♂, 6 ♀♀ (NMP pb2947–pb2954 [S+A]), Al Azhlaniya, Wadi Haramawt, 10 October 2005, leg. P. Benda; – 2 ♂♂ (SMF 91021, 91022 [S+B]), Al Dimnah, Najd Khamran, Lahej Governorate, 29 March 1999, leg. E. Sadik & I. Al-Qubati; – 1 ♂, 1 ♀ (NMP pb3672, pb3673 [S+A]), Al Makha, Taiz, 29 October 2007, leg. P. Benda & A. Reiter; – 1 ♂ (SMF 91020 [S+B]), Al Mazahen, Ibb Governorate, 22 May 1997, leg. A. A. Galeb & H. M. Ibrahim; – 3 ♂♂ (BCSU 319–321 [S+B]), Al Yousifeen, Al Qubaita, Lahj Governorate, 20 December 2002, leg. A. Al-Qubati; – 2 ♂♂, 2 ♀♀ (NMP pb3622, pb3623, pb3625 [S+A], pb3624 [A]), Am Rija', Wadi Am Rija', 25 October 2007, leg. P. Benda & A. Reiter; – 1 ♂ (BCSU 174 [S+B]), Bani Hshaish, Sana'a, 1 June 1999, leg. J. Bahluli; – 4 ♂♂, 2 ♀♀ (BCSU 184, 185, 199, 200, 213, 222 [S+B]), Duhlan, Al Qubaita, Lahj Gov., 11 August 1998, 10 March 2001, leg. M. Al-Qubati; – 4 ♂♂, 4 ♀♀ (NMP pb2920–pb2927 [S+A]), Ma'arib, 8 October 2005, leg. P. Benda; – 1 ♂, 1 ♀ (BMNH 99.11.6.29., 99.11.6.32. [S+B]), Myba, near Aden, date unlisted, leg. W. Dodson; – 3 ♂♂, 5 ♀♀ (NMP pb3763, pb3765, pb3766 [S+A], pb3764, pb3767–pb3770 [A]), Shuhayr, Hadramaut, 6 November 2007, leg. P. Benda & A. Reiter; – 1 ♂, 2 ♀♀ (MHNG 1872.092, 1872.093 [S+A], 1872.091 [A]), Wadi Sam, Bagil, 3 May 1977, leg. F. Meier; – 1 ♀ (MHNG 1872.094 [A]), Wadi Sardud, Bagil, 3 May 1977, leg. F. Meier; – 5 ♂♂, 2 ♀♀ (BMNH 13.6.19.1.–13.6.19.5., 13.6.19.7., 13.6.19.8. [S+B]), including holotype of *Rhinopoma cystops arabium* Thomas, 1913), Wasil, 4000 ft., 6 March 1913, leg. G. W. Bury.

#### *Rhinolophus clivosus* Cretzschmar, 1828 s.str.

**Algeria:** 3 ♀♀ (MNHN 2006-246–248 [S]), type series of *Rhinolophus acrotis schwarzi* Heim de Blasac, 1934), Djanet, Tassili des Adjers, date unlisted, leg. Dr. H. Foley. – **Egypt:** 1 ♀ (NMP 91994 [S]), Abu Rawash, 15 April 1959, leg. H. Roer; – 1 ♂ (NMP 92584 [S+A]), Aswan, 24 January 2010, leg. P. Benda, I. Horáček & R. Lučan; – 1 ♀ (NMP 92596

[S+A]), El A'aqab, 25 January 2010, leg. P. Benda, I. Horáček & R. Lučan; – 1 ♂ (BMNH 92.9.9.7. [S], holotype of *Rhinolophus acrotis brachygnathus* Andersen, 1905), Ghizeh, 16 December 1891, leg. J. Anderson; – 24 ♂♂ (ZFMK 59.274–59.278, 59.290–59.297, 59.299, 59.300, 59.301, 59.304, 59.306–59.308 [S+A], 59.298, 59.302, 59.303, 59.305 [A]), Kairo, Aburawasch, 15 April 1959, leg. H. Roer; – 1 ♂ (MSNG 44290 [S+A]), Korosko, Alto Egitto, date unlisted, leg. Messedaglia Bey; – 1 ♂ (MSNG 44854 [S+A]), Sakkara presso il Cairo, 5 May 1906, leg. W. Innes Bey; – 1 ♂ (SMF 41810 [S+A]), Saqqara, 14 June 1971, leg. I. Helmy & D. Kock; – 1 ♀ (NMP 90498 [S+A]), Sinai, Wadi El Feiran, 10 September 2005, leg. M. Andreas, P. Benda, J. Hotový & R. Lučan; – 1 ind. (NMP 91987 [S+B]), W of Abu Rihal, 90 km E of Idfin Shalatein, date & collector unlisted. – **Jordan**: 2 ♀♀ (NMP 92495 [S+A], 92496 [A]), Jabal Al Bayda, 19 May 2009, leg. P. Benda, J. Obuch & A. Reiter; – 1 ♂ (NMP 92447 [S+A]), Jebel Masuda, Ain Amshit, 15 May 2009, leg. P. Benda, J. Obuch & A. Reiter; – 1 ♂ (NMP 92843 [S+B]), Petra, 4 May 1983, leg. P. Boye; – 1 ♂ (NMP 92425 [S+A]), Wadi Ghuweir, 2 km E of Khirbet Feynan, 13 May 2009, leg. P. Benda, J. Obuch & A. Reiter. – **Oman**: 1 ♂ (NMP 92736 [A]), Ain Tabruq, 28 December 2009, leg. P. Benda, A. Reiter & M. Uhrin; – 1 ♂ (NMP 92755 [S+A]), Mirbat, 30 October 2009, leg. P. Benda, A. Reiter & M. Uhrin; – 1 ♂ (NMP 92695 [S+A]), Mudhai, 25 October 2009, leg. P. Benda, A. Reiter & M. Uhrin. – **Saudi Arabia**: 2 inds. (SMF 4371, 12296 [S+B]), lectotype and paralectotype of *Rhinolophus clivosus* Creutzschmar, 1828), Mohila [= Al Muwaylih], 1826, leg. E. Rüppell. – **Yemen**: 6 ♀♀ (NMP pb3079, pb3081–pb3084 [S+A], pb3080 [A]), 7 km S of Najd An Nashamah, 25 October 2005, leg. P. Benda; – 2 ♀♀ (NMP pb3060, pb3061 [S+A]), Al Hadr, 8 km W of Lawdar, 22 October 2005, leg. P. Benda; – 1 ♂ (NMP pb3059 [S+A]), Al Nueimah, 20 October 2005, leg. P. Benda; – 1 ♀ (BCSU 272 [S+B]), Al Theeba, 28 January 2002, leg. A. Al-Dumaini; – 1 ♂ (BCSU 173 [B]), Bani Ash-Shamakh, Al-Miftah, 13 November 2000, leg. I. Ash-Shamakh; – 1 ♂ (BCSU 250 [S+B]), Bani Ukab, 28 January 2002, leg. A. Al-Dumaini; – 1 ♂ (NMP pb3042 [S+A]), Damqawt, 16 October 2005, leg. P. Benda; – 5 ♂♂, 4 ♀♀ (NMP pb2962, pb2963, pb2992, pb2993, pb3000, pb3001, pb3032, pb3033 [S+A], pb2994 [A]), Hawf, 13–15 October 2005, leg. P. Benda; – 1 ind. (SMF 91025 [S+B]), Iss Khurd, coastal Hadramaut, 13 March 2000, leg. A. K. Nasher; – 1 ♀ (SMF 91024 [S+B]), Jarf Uraiq Cave, Madam, Hamdan, Sana'a Province, 9 August 2000, leg. M. Alban; – 1 ♂ (NMP pb3120 [S+A]), Jebel Bura, W of Riqab, 30 October 2005, leg. P. Benda; – 1 ♂, 3 ♀♀ (BCSU 085, 088, 094, 096 [S+B]), Madam, Hamdan, 9 May 1999, leg. M. Alyan; – 1 ♂ (BCSU 175 [S+B]), Saraf, Bani Hashaish, 11 June 2001, leg. N. Al-Sarfi; – 1 ♂ (BCSU 230 [S+B]), Shahara, 15 March 2002, leg. M. Kaswa; – 2 ♂♂ (BCSU 251, 252 [S+B]), Shamsan, 15 February 2002, leg. A. Al-Dumaini; – 1 ♀ (SMF 55331 [A]), Strasse zwischen Hodeidah und Sanaa, 5 February 1978, leg. J. U. Heckel; – 1 ♂, 2 ♀♀ (MZUF 13175–13177 [A]), Umm Laylah, ca. 50 km NW of Sa'dah, 2350 m, September 1979, leg. C. Borri, B. Lanza & M. Poggesi.

#### *Rhinolophus (clivosus) acrotis* von Heuglin, 1861

**Eritrea**: 1 ♀ (MZUF 6000 [A]), Asmara, October 1937, leg. Ignesti; – 1 ♂ (MSNG 44312 [S+A]), Assab, July 1893, leg. G. Pestalozzo; – 1 ♂ (MSNG 27583 [S+B]), Assab, Dancalia, February 1929, leg. S. Patrizi. – **Ethiopia**: 1 ♂ (NMP 95891 [S+A]), Aksum, 1 November 2012, leg. P. Benda; – 1 ♂ (NMP 95962 [S+A]), 15 km E of Bonga, 26 November 2012, leg. P. Benda; – 3 ♀♀ (NMP 95937–95939 [S+A]), Dangola Washa Caves, 5 km SW of Kesa, 12 November 2012, leg. P. Benda; – 1 ♂ (MZUF 6029 [S]), Gorgora, Lago Tana, 1828 m, 13 March 1937, leg. G. Dainelli; – 3 ♀♀ (MSNG 18243 [S+B], 45630a, 45630b [S+A]), Harrar, date unlisted, leg. P. Felter, 1893, leg. Salimbeni; – 1 ♂ (MZUF 5649 [S]), Lago Tana, 1937, leg. G. Dainelli; – 1 ♀ (NMP 95913 [S+A]), Simien National Park, Aman Amba, 5 November 2012, leg. P. Benda. – **Sudan**: 1 ♂ (BMNH 4.11.4.2. [S+B]), E. Egypt Desert, 22° N, 35° E, holotype of *Rhinolophus andersoni* Thomas, 1904), 3 August 1903, leg. M. Mackilligin; – 1 ♀ (MSNG 46965 [S+A]), Port Sudan, Mar Rosso, January 1908, leg. G. Nicolosi.

#### *Rhinolophus (clivosus) augur* Andersen, 1904

**Kenya**: 1 ♂, 1 ♀ (MHNG 1873.046, 1873.047 [S+A]), Chepnyalil Cave, Mount Elgon, 3 February 1977, leg. F. Meier; – 1 ♂, 2 ♀♀ (SMF 38521 [A], 39427, 39431 [S]), Naibei's Great Cave, Kapasakwany, Süd Seite des Mt. Elgon, 12 & 16 December 1970, 17 May 1971, leg. Dr. Mutuku. – **Lesotho**: 2 ♀♀ (NMB 7350, 7355 [S+B]), Ha Natla, Thaba Tseka, 19–20 October 1989, collector unlisted; – 2 ♂♂, 1 ♀ (MSNG 42305, 44908a, 44908b [A]), Hermon (Basutos), October 1891, leg. Rev. Christol; – 1 ♂ (NMB 8222 [S+B]), Mount Moorosi, Quthing, 13 November 1991, collector unlisted; – 2 ♂♂, 1 ♀ (NMB 6980–6982 [S+B]), Nkokomele, 15 km east of Mateanong, 1–10 February 1989, collector unlisted; – 1 ♀ (NMB 8300 [S+B]), Phallang, Maseru (Semonkong), 12 December 1991, collector unlisted; – 5 ♀♀ (NMB 6983–6986, 6894 [S+B]), Mateanong, Mokhotlong, 1–10 February 1989, collector unlisted; – 2 ♀♀ (NMB 6863, 6864 [S+B]), Sahlebathebe National Park, lodge, 13 November 1988, collector unlisted; – 1 ♂, 12 ♀♀ (NMP pb5586–pb5596 [S+A], pb5585, pb5597 [A]), Sehlabathebe National Park, lodge, 17 February 2013, leg. N. Avenant, P. Benda & J. Červený; – 1 ♂ (NMB 8418 [S+B]), Ski Lodge, Butha-Buthe (Oxbow), 20 February 1992, collector unlisted. – **Malawi**: 1 ♂ (BMNH 97.10.1.18. [S+B]), holotype of *Rhinolophus augur zambesiensis* Andersen, 1904), Fort Hill, N. Nyasa, July 1896, leg. A. Whyba; – 1 ♂ (MHNG 1971.057 [S+A]), Mt. Mulanje, Minunu Plateau, 27 September 2007,

leg. M. Curran & M. Kopp; – 1 ♂ (MHNG 1971.058 [S+A]), Mt. Mulanje, Minunu River, 31 October 2007, leg. M. Curran & M. Kopp; – 1 ♂, 2 ♀♀ (NMP mw199, mw231 [S+A]), Ntchisi Forest Reserve, 8–9 July 2008, leg. J. Škliba. – **Mozambique**: 2 ♂♂ (MHNG 1971.054, 1971.055 [S+A]), Mt. Mabu, 18–19 October 2008, leg. M. Curran & M. Kopp; – 1 ♂ (MHNG 1971.059 [S+A]), Mt. Namuli, NL Ukalini Forest, 21 November 2008, leg. M. Curran & M. Kopp; – 1 ♀ (MSNG 18316 [S+B]), Quilimane, 5 November 1908, collector unlisted. – **Rwanda**: 1 ind. (SMF 92961 [S+Sk]), Lava-Höhle Ubuvumo, 11 December 2004, leg. Laumanns. – **South Africa**: 1 ♀ (SMF 55037 [S+B]), Doornhoek, Pietermaritzburg, Natal, 27 March 1976, leg. I. W. Espie; – 4 ♂♂, 3 ♀♀ (DM 8373–8379 [S+A]), Fort Yolland Farm, Eshowe-Melmoth, Entumeni District, KwaZulu-Natal, 14–15 May 2005, leg. P. J. Taylor et al.; – 4 ♂♂, 3 ♀♀ (NMW 26126–26132 [S+B]), Guano Cave, Tsitsikama, Coastal NP, Cape Province, 4 December 1975, leg. F. Spitzenberger & B. Herzig; – 1 ♂ (TM 46882 [S+A]), Haffenden Heights, Limpopo, 3 November 2002, leg. L. Cohen; – 1 ♂, 1 ♀ (NMB 7626, 7638 [S+B]), Jagersfontein, Commonage, Free State, 12–16 February 1990, collector unlisted; – 1 ♀ (BMNH 4.5.1.8. [S+B]), holotype of *Rhinolophus augur zuluensis* Andersen, 1904), Jususic Valley, 20 mi NW of Eshowe, Zululand, 17 November 1903, leg. C. H. B. Grant; – 1 ♂ (TM 47619 [S+A]), Kaalrug, Mpumalanga, 25 October 2004, leg. L. Cohen; – 1 ♂ (MSNG 44467 [S+A]), Kenilworth, soborgo della Citta del Capo, 15 March 1906, leg. W. L. Sclater; – 2 ♂♂ (NMB 11072, 11075 [S+B]), Koegelbeen Caves, Hay (Griekwastad), Northern Cape, 22 February 1997, collector unlisted; – 1 ♂ (BMNH 4.10.1.1. [S+B]), holotype of *Rhinolophus augur* Andersen, 1904), Kuruman, Bechuana, 19 April 1904, leg. R. B. Woosnam; – 2 ♀♀ (NMB 10573, 10638 [S+B]), Merrimietzie, Winburg District, Free State, 6 February 1996, collector unlisted; – 1 ♂ (SMF 44809 [S+A]), Rhin. Z., Transvaal, 27 December 1952, leg. Zumpt; – 1 ♀ (TM 46643 [S+A]), Sudwala Caves, Mpumalanga, 18 December 2008, leg. H. C. Schoeman & S. Stoffberg; – 1 ♂ (MSNG 42112 [A]), Sud Africa, Rhodesia Mus., date & collector unlisted; – 1 ♀ (SMF 19558 [S]), Transvaal, 1 June 1958, leg. J. Meester; – 1 ♀ (SMF 19557 [S]), Uitkoms, Transvaal, 19 January 1958, leg. J. Meester; – 1 ♂ (MSNG 44381 [A]), Wunderfontein Caves, Petchepont District, Transvaal, April 1907, collector unlisted. – **Tanzania**: 2 ♂♂ (SMF 91227, 91228 [S+A]), Amani-Sigi Forest Reserve, Eastern Usambara Mts., Tanga Reg., 05° 07' S, 38° 39' E, 14 March 1999, leg. Frontier; – 1 ♂ (SMF 92505 [S+A]), Nilo Forest Reserve, 3 August 2000, leg. Frontier; – 1 ♀ (NMW 19822 [S]), Uganda, Ruvumq Province, 1935–1936, leg. H. Zerny. – **Uganda**: 1 ♀ (SMF 44092 [S+A]), Kisoro, Kigezi District, 1° 17' S, 29° 42' E, 30 October 1975, leg. A. B. C. Killango; – 2 ♂♂, 1 ♀ (MHNG 1873.043, 1873.044 [S+A], 1873.045 [A]), Rukungu / Kisoro, 30 October 1976, leg. F. Meier.

#### *Rhinolophus horaceki* Benda et Vallo, 2012

**Libya**: 1 ♂ (NMP 49861 [S+A]), Al Bardiyah, 12 May 2002, leg. M. Andreas, P. Benda, V. Hanák, A. Reiter & M. Uhrin; – 1 ♀ (NMP 49915 [S+A]), Wadi Al Kuf, 20 May 2002, leg. M. Andreas, P. Benda, V. Hanák, A. Reiter & M. Uhrin; – 2 ♂♂ (NMP 49879, 49880 [S+A]), incl. the holotype of *Rhinolophus horaceki* Benda et Vallo, 2012), Wadi Darnah, 15 May 2002, leg. M. Andreas, P. Benda, V. Hanák, A. Reiter & M. Uhrin; – 1 ♀ (NMP 49882 [S+A]), Wadi Darnah, 10 km S of Darnah, 16 May 2002, leg. M. Andreas, P. Benda, V. Hanák, A. Reiter & M. Uhrin; – 1 ♂, 2 ♀♀ (NMW 30106–30108 [S+B]), Wadi Kuf, Prov. Beida, 22 August 1981, leg. A. Mayer, F. Spitzenberger & E. Weiß.

#### *Asellia italosomalica* De Beaux, 1931

**Somalia**: 1 ♀ (MSNG 32582 [S+B]), Bender-Cassim, January–February 1932, leg. I. Zanetti; – 1 ♀ (MZUF 8277 [S+A]), Callis, 20 October 1973, leg. Granchi & B. Lanza; – 2 ♂♂, 2 ♀♀ (MSNG 12232a–d [S+B]), incl. the paratype of *A. tridens italosomalica* De Beaux, 1931), Dolo, May–July 1911, leg. C. Citerni; – 2 ♂♂ (MZUF 9940, 9941 [S+A]), Mahas, 12 February 1977, leg. A. Simonetta; – 1 ♀ (MSNG 30942 [S+B]), holotype of *A. tridens italosomalica* De Beaux, 1931), Oddur, 1929, leg. N. Mosconi Bronzi; – 1 ♀ (MZUF 9942 [S+A]), Pozzi di Mahas, 11 April 1977, leg. A. Simonetta; – 1 ♂, 1 ♀ (MZUF 6291 [S+B], 6305 [S+A]), Run, 15 & 18 August 1969, leg. B. Lanza; – 2 ♂♂, 2 ♀♀ (MZUF 13099, 13100, 15728, 15734 [S+A]), Showli Berdi, 15 March 1984, 15 November 1985, leg. L. Chellazi & Messana.

#### *Asellia arabica* Benda, Vallo et Reiter, 2011

**Oman**: 5 ♂♂, 3 ♀♀ (NMP 94053–94056, 94058–94060 [S+A], 94057 [A]), Ain Hamran Cave, Dhofar Province, 28 March 2012, leg. P. Benda, A. Reiter & M. Uhrin; – 2 ♂♂, 2 ♀♀ (NMP 92721–92724 [S+A]), Ain Jarziz, Dhofar Province, 27 October 2009, leg. P. Benda, A. Reiter & M. Uhrin; – 1 ♀ (NMP 92753 [A]), Ain Tabruq, Dhofar Province, 29 October 2009, leg. A. Reiter; – 1 ind. (BMNH 34.8.4.1 [S+B]), Cave of Sahaur, Qara Mts., SE Arabia, date unlisted, leg. B. S. Thomas. – **Yemen**: 2 ♂♂, 2 ♀♀ (NMP 92795, 92796, 92798 [S+A], 92797 [A]), paratypes of *A. arabica* Benda, Vallo et Reiter, 2011), Damqawt, Al Mahra Province, 16 October 2005, leg. P. Benda; – 4 ♂♂, 2 ♀♀ (NMP 92790, 92791, 92792–92794 [S+A], 92789 [A]), holotype and paratypes of *A. arabica* Benda, Vallo et Reiter, 2011), Hawf, Al Mahra Province, 14–15 October 2005, leg. P. Benda; – 1 ♂ (BCSU 013 [B]), Ryan, Hadramaut Province, July 1995, leg. A. Basmaidi; – 2 ♂♂, 1 ♀ (BCSU 128, 136, 195 [S+B]), Shikhwai, Hadramaut Province, 12 March 2000, leg. A. K. Nasher.

### *Asellia tridens* (Geoffroy, 1813)

**Oman:** 1 ♂ (NMP 94007 [S+A]), small oasis to SE of Mudhai, 25 March 2012, leg. P. Benda, A. Reiter & M. Uhrin; – 5 ♂♂, 7 ♀♀ (NMP 92683–92692, 92694 [S+A], 92693 [A]), Shisr, 24 October 2009, leg. P. Benda, A. Reiter & M. Uhrin. – **Saudi Arabia:** 1 ♂ (BMNH 1950.33. [S+B]), Jeddah, 20 October 1949, leg. A. C. Trott. – **Yemen:** 3 ♂♂, 8 inds. (BMNH 95.6.1.11.–95.6.1.14., 99.11.6.93., 99.11.6.94., 99.11.6.97. [S]), BMNH 99.3.14.25., MSNG 33197a, b, 33198 [S+B]), Aden, 1883, 1892, 1895, 1899, leg. Ruspoli, V. Ragazzi, R. O. Grant, J. W. Yerbury, A. B. Percival & W. Dodson; – 1 ♂ (BCSU 312 [S+B]), Bayt Al-Faqeh, Al-Hodeida Province, October 2002, leg. A. As-Sabri; – 2 ♂♂ (MSNG 33196a, b [S+B]), Moka, 1891, leg. G. Pestalozza; – 1 ♂ (MSNG 33199 [S+B]), presso Aden, 1893, leg. A. Pogliani; – 2 ♀♀, 1 ind. (BMNH 95.6.1.50., 95.6.1.51., 99.11.6.12. [S+B]), Lahej, 9 & 28 March 1895, 9 May 1899, leg. J. W. Yerbury, A. B. Percival & W. Dodson; – 1 ♂ (BMNH 57.426. [B]), Qatn, E. Aden Prot., Arabia, 2000<sup>5</sup>, 5 June 1956, leg. D. J. Greathead.

### *Asellia patrizii* De Beaux, 1931

**Eritrea:** 3 ♂♂, 1 ♀ (MSNG 33203, 33204 [S+B], 31315a, 31315b [S+A]), incl. three paratypes of *A. patrizii* De Beaux, 1931), Assab, July 1893, leg. G. Pestalozza, October 1906, leg. P. Felter; – 1 ♂, 1 ♀ (MSNG 31313, 31314 [S+A]), incl. holotype of *A. patrizii* De Beaux, 1931), Gaarre, Dancalia, December 1928, leg. S. Patrizi; – 2 ♀♀ (BMNH 70.2288., 70.2289. [S]), Nocra Island, Dahlak Islands, 27 December 1969, leg. M. J. Lagen. – **Ethiopia:** 2 ♂♂ (MZUF 6546, 6547 [S+B]), Awash National Park, 4.5 km from Metahara, 08° 54' N, 39° 55' E, 12 April 1971, leg. M. L. Azzaroli & B. Lanza; – 1 ♂, 1 ♀ (MZUF 6545 [A], 6548 [S+A]), Dint. Metahara, Mte. Fantalle, 14 April 1971, leg. M. L. Azzaroli & B. Lanza; – 1 ♂ (BMNH 70.475. [S]), North bank of river, Awash River Valley, Awash National Park, Shoa, 8.50 N, 40.01 E, 25 September 1968, leg. P. Morris; – 1 ♀ (SMF 52377 [S+B]), W of Metahara, Shoa, 28 December 1970, ded. M. Lagen; – 1 ♂, 1 ♀ (SMF 44998, 44999 [S]), “an der Bahnlinie westl. zw. Metahara und Lake Basaka, Awash River Gebiet”, 11 September 1973, leg. H. Rupp. – **Saudi Arabia:** 1 ♀ (MHNG 1719.070 [S+A]), Iles Farasan, 28 May 1989, leg. B. Schätti.

### *Hypsugo ariel* (Thomas, 1904)

**Egypt:** 2 ♀♀ (NMP 92597, 92598 [S+A]), El A'aqab, N of Aswan, 25 January 2010, leg. P. Benda, I. Horáček & R. Lučan; – 1 ♂ (CDIS 946 [S+A]), Sinai, Ain Hudra, 4 August 2005, leg. C. Dietz; – 1 ♂ (CDIS 945 [S+A]), Wadi El Arbacin, Sinai, 1 August 2005, leg. C. Dietz; – 1 ♂, 1 ♀ (NMP 90493, 90494 [S+A]), Wadi El Feiran, Sinai, 8 September 2005, leg. M. Andreas, P. Benda, J. Hotový & R. Lučan. – **Israel:** 1 ♂, 2 ♀♀ (HUJ M6182 [S+A], TAU M6866 [B], M8054 [A]), En Gedi, May 1975, 11 April 1976, 19 October 1987, leg. Y. Barak, Z. Greenberger, H. Mendelssohn & Y. Yom-Tov; – 1 ♀, 1 ind. (BMNH 67.1229. [S+B]), TAU M8639 [S], incl. holotype of *Pipistrellus bodenheimeri* Harrison, 1960), Yotvata, Wadi Araba, 13 October 1959, leg. D. L. Harrison, August 1989, collector unlisted. – **Jordan:** 7 ♂♂, 1 ♀ (NMP 92488–92494 [S+A], 92487 [A]), Al Ghal, 17 May 2009, leg. P. Benda & A. Reiter; – 1 ♀ (NMP 92380 [S+A]), Tall Numeira, 17 October 2008, leg. P. Benda & J. Obuch; – 1 ♀ (NMP 92804 [S+A]), Wadi Al Hassa, Hammamat Borbatah, 5 July 2010, leg. P. Benda & A. Reiter; – 1 ♂ (NMP 92095 [S+A]), Wadi Rum, 24 October 2004, leg. R. Lučan. – **Oman:** 1 ♂ (NMP 92754 [S+A]), 4 km W of Jufa, 29 October 2009, leg. P. Benda, A. Reiter & M. Uhrin; – 3 ♂♂, 1 ♀ (NMP 94074–94076 [S+A], 94073 [A]), Wadi Gharah, 12 km SE of Rima, 2 April 2012, leg. P. Benda, A. Reiter & M. Uhrin. – **Sudan:** 1 ♂, 1 ♀ (BMNH 4.11.4.6., 4.11.4.7. [S+B]), incl. holotype of *Pipistrellus ariel* Thomas, 1904), Wadi Alagy, E Desert of Egypt, 22 N, 35 E, 2000 ft, 12 August 1903, leg. A. M. Mackilligin. – **Yemen:** 1 ♂ (NMP pb3058 [S+A]), Al Nueimah, 20 October 2005, leg. P. Benda; – 2 ♂♂, 1 ♀ (NMP pb3050, 3051 [S+A], 3052 [A]), Damqawt, 16 October 2005, leg. P. Benda; – 5 ♂♂, 4 ♀♀ (NMP pb3022–3025, 3027–3030 [S+A], pb3026 [A]), Hawf, 14 October 2005, leg. P. Benda; – 1 ♂, 1 ♀ (NMP pb3054 [S+A], 3055 [A]), desert ca. 25 km WSW of Sayhut, 17 October 2005, leg. P. Benda; – 1 ♂, 1 ♀ (BMNH 54.423., 54.424. [B]), Seiyun, E. Aden Prot., 2000 ft, leg. J. Greathead.

### *Hypsugo arabicus* (Harrison, 1979)

**Iran:** 4 ♂♂, 8 ♀♀ (NMP 48409, 48410, 48414–48420 [S+A], 48411–48413 [A]), Pir Sohrab, Beluchestan, 12 April 2000, leg. P. Benda & A. Reiter. – **Oman:** 1 ♂ (NMP 92624 [S+A]), Al Aqar, 2 km S of Wakan, 17 October 2009, leg. P. Benda, A. Reiter & M. Uhrin; – 2 ♂♂, 2 ♀♀ (NMP 93739–93741 [S+A], 93742 [A]), Al Aqar, Wadi Tiwi, 4 April 2011, leg. P. Benda, A. Reiter & M. Uhrin; – 2 ♂♂ (NMP 92665, 92666 [S+A]), Al Nakhar, 22 October 2009, leg. P. Benda, A. Reiter & M. Uhrin; – 2 ♀♀ (NMP 93822, 93823 [S+A]), Al Zihaymi, 14 April 2011, leg. P. Benda, A. Reiter & M. Uhrin; – 1 ♂ (NMP 92779 [S+A]), wadi 7 km W of Dibab, 2 November 2009, leg. P. Benda, A. Reiter & M. Uhrin; – 2 ♀♀ (NMP 93760, 93761 [S+A]), Ghab, Wadi Al-Hawasina, 7 April 2011, leg. P. Benda, A. Reiter & M. Uhrin; – 2 ♂♂, 1 ♀ (NMP 92782, 92783 [S+A], 92784 [A]), Mansaft, 3 November 2009, leg. P. Benda, A. Reiter and M. Uhrin; – 1 ♂, 2 ♀♀ (NMP

93785, 93786 [S+A], 93787 [A], Misfat Al Khawater, 9 April 2011, leg. P. Benda, A. Reiter & M. Uhrin; – 1 ♀ (NMP 92774 [S+A]), Muqal, 1 November 2009, leg. P. Benda, A. Reiter & M. Uhrin; – 1 ♂ (NMP 93997 [S+A]), Sal Aalah, 15 March 2012, leg. P. Benda, A. Reiter & M. Uhrin; – 3 ♀♀ (NMP 93812, 93813 [S+A], 93814 [A]), Subakh, Hatta Pools, 12 April 2011, leg. P. Benda, A. Reiter & M. Uhrin; – 2 ♀♀ (NMP 93733, 93734 [S+A]), Wadd, 3 April 2011, leg. P. Benda, A. Reiter & M. Uhrin; – 1 ♀ (NMP 94001 [S+A]), Wadi Banah, 16 March 2012, leg. P. Benda, A. Reiter & M. Uhrin; – 1 ♂ (BMNH 80.393. [S+B], holotype of *Pipistrellus arabicus* Harrison, 1979), Wadi Sahtan, 23°22'N, 57°18'E, 18 March 1979, leg. M. D. Gallagher.

APPENDIX III  
List of specimens examined in genetic analysis

hapl.	morphotype	voucher	country	site	GenBank Accession Number
1	<i>clivosus</i>	NMP 90581	Yemen	Socotra, Marshim Cave	KC579387
–	<i>clivosus</i>	NMP 90593	Yemen	Socotra, Keisu Oasis	–
2	<i>clivosus</i>	NMP pb3079	Yemen	Najd An Nashamah	KC579390
3	<i>clivosus</i>	NMP pb2994	Yemen	Hawf	KC579388
–	<i>clivosus</i>	NMP pb3032	Yemen	Hawf	–
–	<i>clivosus</i>	NMP 92695	Oman	Mudhai, ruins	–
4	<i>clivosus</i>	NMP pb3060	Yemen	Lawdar, Al Hadr	KC579389
5	<i>clivosus</i>	NMP pb3120	Yemen	Jebel Bura	KC579391
6	<i>clivosus</i>	NMP 90498	Egypt	Sinai, Wadi El Feiran	KC579392
–	<i>clivosus</i>	NMP 92447	Jordan	Ain Amshit	–
–	<i>clivosus</i>	NMP 92495	Jordan	Jabal Al Bayda	–
–	<i>ferrumequinum</i>	NMP 92562	Jordan	Milka, cave	–
–	<i>clivosus</i>	NMP 92811	Jordan	Wadi Al Dharih	–
7	<i>clivosus</i>	NMP 92496	Jordan	Jabal Al Bayda	MH029814
8	<i>clivosus</i>	ZFMK 59297	Egypt	Cairo, Abu Rawash	KC579393
9	<i>clivosus</i>	ZFMK 59304	Egypt	Cairo, Abu Rawash	KC579394
10	<i>clivosus</i>	NMP 92584	Egypt	Aswan	MH029817
–	<i>clivosus</i>	NMP 92596	Egypt	Al A'aqab	–
11	<i>ferrumequinum</i>	NMP 48762	Syria	Qala'at Najm, castle	MH029806
–	<i>ferrumequinum</i>	NMP 49049	Greece	Pili, Zahariani Cave	–
–	<i>ferrumequinum</i>	NMP 91800	Lebanon	Faraya, El Qana Cave	–
–	<i>ferrumequinum</i>	NMP 92293	Greece	Crete, Gerani Cave	–
–	<i>ferrumequinum</i>	NMP 92296	Greece	Crete, Sarakinas Cave	–
–	<i>ferrumequinum</i>	NMP 92332	Greece	Crete, Moni Kato Preveli	–
–	<i>ferrumequinum</i>	NMP 90229	Montenegro	Bar, castle	–
12	<i>ferrumequinum</i>	NMP 91178	Greece	Crete, Omalos, Tsanis Cave	KC579399
13	<i>ferrumequinum</i>	NMP 48927	Syria	Qatura, ruins	MH029809
14	<i>ferrumequinum</i>	NMP pb831	Slovakia	Silická Brezová, Milada Cave	KC579400
15	<i>ferrumequinum</i>	NMP 48729	Greece	Kombotades, bunker	MH029804
16	<i>ferrumequinum</i>	NMP 91103	Greece	Crete, Milatou Cave	MH029811
–	<i>ferrumequinum</i>	NMP 92342	Greece	Crete, Gaidourtrypa Cave	–
17	<i>ferrumequinum</i>	NMP pb2080	Kosovo	Mrasor, cave	MH029810
18	<i>ferrumequinum</i>	NMP 92343	Greece	Crete, Gaidourtrypa Cave	MH029812
19	<i>ferrumequinum</i>	NMP 49856	Libya	Ain Az Zarqa	KC579398
–	<i>ferrumequinum</i>	NMP 49967	Libya	Nanatalah	–
20	<i>ferrumequinum</i>	NMP 90035	Morocco	Talkout, mine	KC579397
–	<i>ferrumequinum</i>	NMP 90425	Cyprus	Cinarli, Incirli Cave	–
–	<i>ferrumequinum</i>	EBD 24818	Spain	Cádiz	EU436673 (Zhou et al. 2009)
21	<i>ferrumequinum</i>	NMP 48352	Iran	Deh Bakri, cave	MH029805
22	<i>ferrumequinum</i>	NMP 48270	Syria	Nimrud Castle	KC579395
–	<i>ferrumequinum</i>	NMP 48855	Syria	Bosra, citadel	–
–	<i>ferrumequinum</i>	NMP 91892	Lebanon	Afqa Cave	–
–	<i>ferrumequinum</i>	NMP 92408	Jordan	Dibbine Forest, mine	–



hapl.	morphotype	voucher	country	site	GenBank Accession Number
22	<i>ferrumequinum</i>	NMP 92404	Jordan	Zubiya Cave	–
–	<i>ferrumequinum</i>	NMP 93683	Lebanon	Aamchite, Saleh Cave	–
–	<i>ferrumequinum</i>	NMP 93705	Lebanon	Wadi Jilo, Jilo Cave	–
–	<i>ferrumequinum</i>	NMP 92504	Jordan	Tabaqat Fahl, tomb	–
–	<i>ferrumequinum</i>	NMP 93573	Lebanon	Khirbet Anafar, cave	–
23	<i>ferrumequinum</i>	NMP 93550	Lebanon	Aanjar, Aanjar Cave	MH029818
–	<i>ferrumequinum</i>	NMP 93551	Lebanon	Aanjar, Aanjar Cave	–
24	<i>clivus</i>	NMP 92425	Jordan	Wadi Ghuweir	MH029813
–	<i>ferrumequinum</i>	NMP 92507	Jordan	Zubiya Cave	–
25	<i>ferrumequinum</i>	NMP 92506	Jordan	Zubiya Cave	MH029815
26	<i>ferrumequinum</i>	NMP 48858	Syria	Bosra, citadel	MH029808
–	<i>ferrumequinum</i>	NMP 48928	Syria	Qatura, ruins	–
27	<i>ferrumequinum</i>	NMP pb4351	Ukraine	Crimea, Kuuk-Koba Cave	MH029816
27	<i>ferrumequinum</i>	NMP pb4404	Ukraine	Crimea, Kamenskoe, mine	–
28	<i>ferrumequinum</i>	NMP 90490	Turkey	Muradiye, cave	MH029819
29	<i>ferrumequinum</i>	NMP 48804	Syria	Dura Europos, tunnel	MH029807
–	<i>ferrumequinum</i>	NMP 48936	Syria	Qala'at Samaan, castle	–
30	<i>ferrumequinum</i>	NMP 48122	Iran	Chuplu	KC579396
31	<i>clivus</i>	NMP 95891	Ethiopia	Aksum, King Basen's Tomb	KC579377
32	<i>clivus</i>	NMP 95913	Ethiopia	Simien NP, Aman Amba	KC579378
33	<i>clivus</i>	NMP 95938	Ethiopia	Kesa, Dongola Washa Cave	KC579380
34	<i>clivus</i>	NMP 95939	Ethiopia	Kesa, Dongola Washa Cave	KC579381
35	<i>clivus</i>	NMP 95937	Ethiopia	Kesa, Dongola Washa Cave	KC579379
36	<i>clivus</i>	NMP 95962	Ethiopia	Bonga	KC579382
37	<i>clivus</i>	biopsy	South Africa	Die Hel, Windhoek Mts.	KC579384
38	<i>clivus</i>	biopsy	South Africa	Kruger NP, Sudwala Cave	KC579385
39	<i>clivus</i>	NMW 26131	South Africa	Tsitsikama, Guano Cave	KC579383
–	<i>clivus</i>	NMW 26132	South Africa	Tsitsikama, Guano Cave	–
40	<i>clivus</i>	NMP mw199	Malawi	Ntchisi Forest Reserve	KC579386
–	<i>clivus</i>	NMP mw230	Malawi	Ntchisi Forest Reserve	–
–	<i>clivus</i>	NMP mw231	Malawi	Kasito Lodge	–
41	<i>clivus</i>	FMNH 151424	Tanzania	Chome Forest	EU436674 (Zhou et al. 2009)

