



The continental malacofauna of Arabia and adjacent areas, VII. The family Achatinidae (Coeliaginae, Subulininae) in the Socotran Archipelago (Gastropoda, Pulmonata)

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Abstract

The endemic fauna of achatinoid terrestrial molluscs for the Socotran Archipelago (Yemen) is revised. The main group falls into two genera, viz. *Riebeckia* E. v. Martens, 1883 with five species and *Balfouria* Crosse, 1884 with seven species, two of which are here described as new to science, i.e. *Balfouria nitida* n. sp., and *Balfouria minima* n. sp. Another globally distributed species could be found, and the endemic *Zootecus* species of the outer island of Abd el-Kuri is illustrated. The highly specialised shell structure of *Balfouria* is discussed, which is used to camouflage the animals with a mixture of clay and mucus protecting the shell during the individual lifetime of a specimen.

Keywords Terrestrial malacology · Socotra · Achatinidae · *Riebeckia* · *Balfouria*

1 Introduction

This paper continues the series on the terrestrial malacology of Arabia and north-eastern Africa (Neubert 1998, 2002, 2003a, b, 2004, 2005a, b, 2009). In this area, the Achatinidae form a major faunal element, with enigmatic species and genera inhabiting the humid and cold Abyssinian Highlands to the arid coastal plains of Southern Arabia. One of the evolutionary hotspots is certainly the Socotran Archipelago, home to almost 100 endemic species of terrestrial molluscs (own data).

This revision is based on the results of two visits of the authors to Socotra, i.e. February 1999 (Neubert) and February 2013 (Neubert and Bochud). In addition, until today,

several visitors and researchers collected snails to be identified, so a quite rich portfolio of localities could be checked critically also for Achatinidae. It has to be stressed that the region east of the Haggihr Mountains has not been visited by shell collecting people so far; thus, the gap that appears on the distribution maps is artificial, it does not necessarily reflect the natural distribution patterns of species.

As most other snail species, the Achatinidae of Socotra aestivate during the dry seasons, which is the most attractive visiting time for collectors. Living generally on the ground, these snails hide for aestivation in cracks in the substrate or deep in rock crevices. As a result, only very few specimens could be found alive. Unfortunately, the recent 2019 trial to sequence the few specimens failed because of the small amount and quality of the DNA remaining. Under *Riebeckia* sp., Wade et al. (2006: 596, figs. 1, 2) successfully sequenced the COI, 28S, and 5.8S markers of a specimen of *Balfouria sordida* (Neubert 2002), proving the position of this genus in the Subulinidae. Fontanilla et al. (2017: Fig. 1) detected Subulinidae sensu auct. to be paraphyletic with regard to Achatinidae sensu auct., and subordinated this group with a number of subfamilies under a rearranged family Achatinidae (Bouchet et al. 2017). For this reason, the genus *Balfouria* is shifted to the subfamily Coeliaginae Pilsbry, 1906. We provisionally move the genus *Riebeckia* E. v. Martens, 1883 under this subfamily assuming that this group also derived from a common coeliagine ancestor on Socotra.

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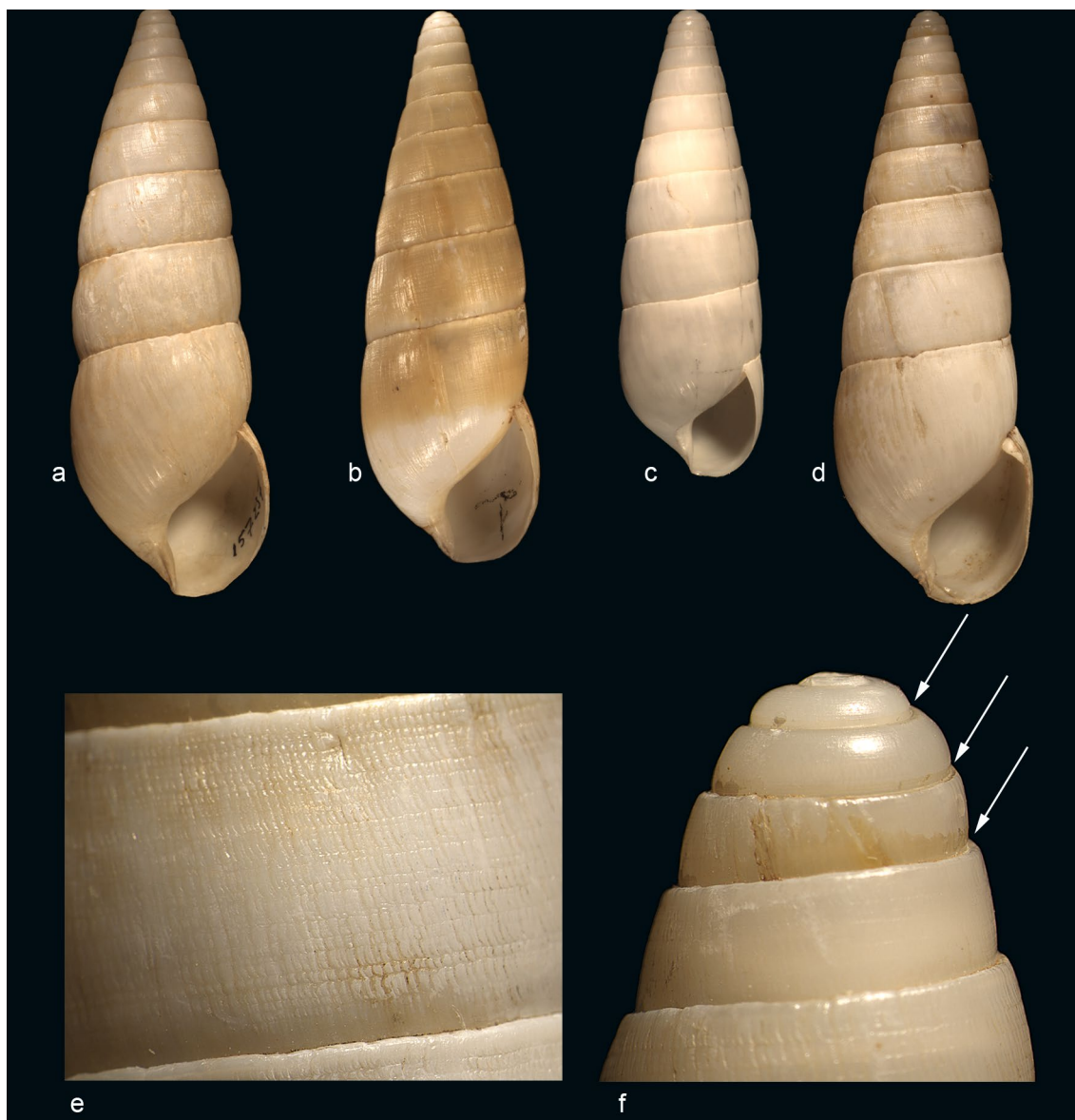


Fig. 1 a–f *Riebeckia sokotorana* (E. v. Martens, 1881). **a** lectotype *Achatina sokotorana*, SMF 157237, “Sokotra”, original specimen of E. v. Martens (1884: plate 29, Fig. 3), $H=63.5$ mm; **b** syntype *Stenogyra fumificata*, NHM 1881.12.14.46, $H=59.6$ mm; **c** holotype *Riebeckia lavranosi*, $H=50.4$ mm; **d** SMF 358856, stony slope with large boulders in front of the cave entrance of Hoq, 50–320 m alt.,

5.6./2.1999, leg. E. Neubert, $H=64$ mm; **e** detail of SMF 358856, section taken from a medium whorl showing the reticulate sculpture of the shell’s surface; **f** detail of SMF 358856, apical part of shell with protoconch showing the deeply channelled suture of the protoconch indicated by arrows. All phot. $\times 1.5$, details not to scale

2 Materials and methods

All specimens were collected by hand, carefully cleaned and stored. All photos were made in the lab of the NMBE under a binocular microscope and a Leica camera (Model MC 190 HD) and produced using the stacked image technology.

Material from the following collections was used:

MNHN—Museum National d’Histoire Naturelle, Paris.

SMF—Forschungsinstitut Senckenberg.

NHM—Natural History Museum, London.

NMBE—Naturhistorisches Museum der Burgergemeinde Bern.

ZMB—Zoologisches Museum Berlin, Germany.

All measurements are done with a Mitutoyo Digimatic Caliper and given in mm. Measured specimens have been adult and were chosen randomly. Abbreviations used: n is the number of specimens; H is the average shell height, H_{\min} is the minimum measured height, H_{\max} is the maximum

measured height, D is the shell diameter, D_{\min} is the minimum measured diameter, D_{\max} is the maximum measured diameter; W is the number of whorls, and \pm is the standard deviation.

Systematic part.

Achatinidae Swainson, 1840.

Subfamily Coeliacinae Pilsbry, 1906

Genus *Riebeckia* E. v. Martens, 1883

1883 *Riebeckia* E. v. Martens, *Conchologische Mitteilungen*, II: 148.

Diagnosis: Elongated, heavy and big shells, usually smooth or with a characteristic reticulate microsculpture on the surface of the teleoconch; protoconch large, dome-shaped or mamillate; columella usually truncate, the median tooth of the radula is of medium size and weakly tricuspidate (cf. Martens 1883); male copulatory organ with penis and epiphallus, penial papilla present, retractor muscle massive, branching off opposite the entrance of vas deferens into epiphallus; vagina, a broad and muscular tube with some longitudinal ridges. Type species: *Achatina sokotorana* E. v. Martens, 1881 by original designation.

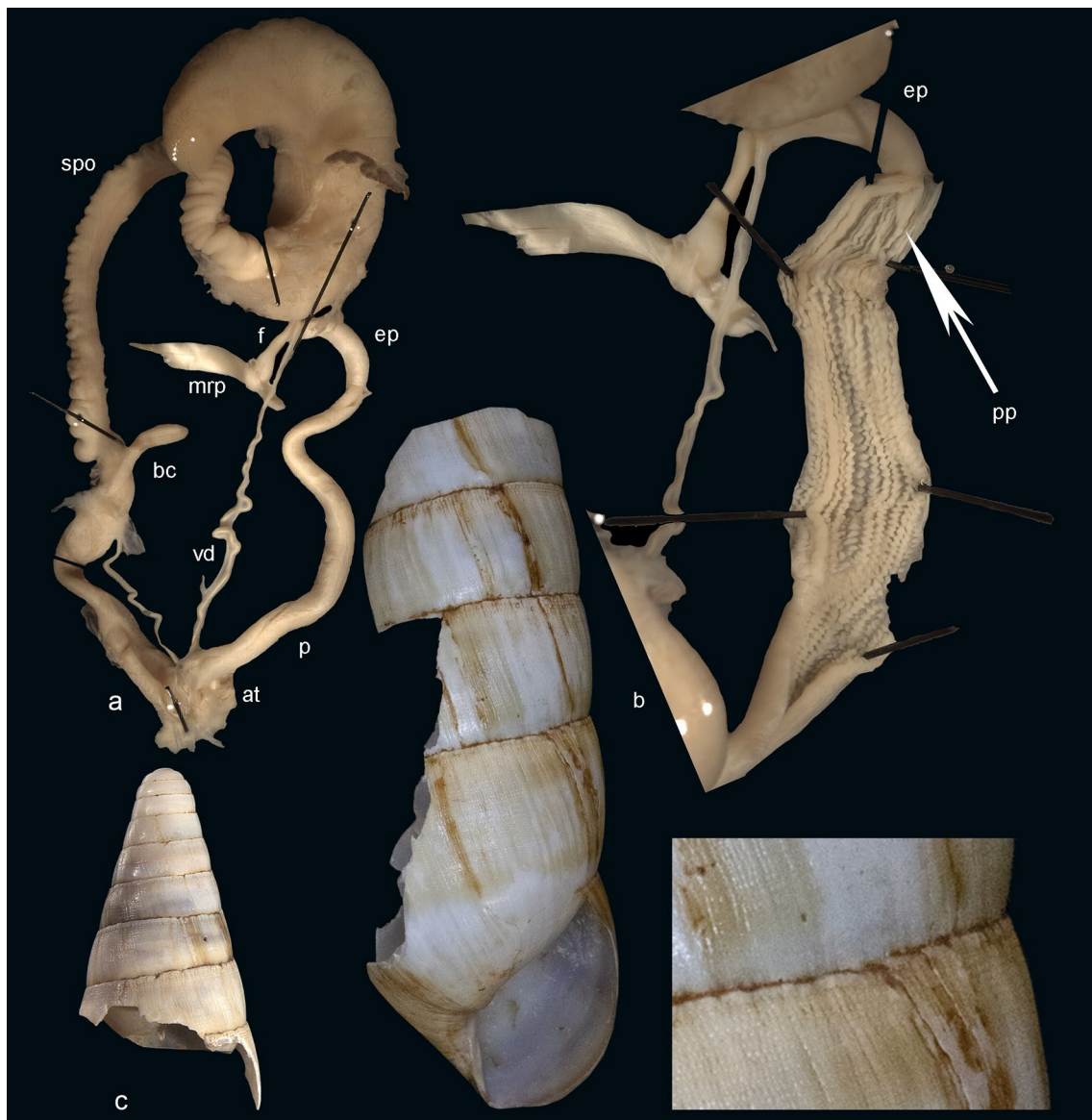


Fig. 2 a–c *Riebeckia sokotorana* (E. v. Martens, 1881). Genital organs and shell; NMBE 563589, Hadibo to the Deksam plateau, teleoconch remain, $H=74.4$ mm, $\times 1.5$; **a** situs of genital organs; **b** male copulatory organ, showing the lumen of penis with internal sculture; **c** shell remains of dissected specimen. All phot. $\times 1.5$, details of genital organs and protoconch not to scale. at genital atrium, bc bursa copulatrix, ep epiphallus, f flagellum, mrp musculus retractor penis, p penis, pp penial papilla, spo spermooviduct, vd vas deferens

c shell remains of dissected specimen. All phot. $\times 1.5$, details of genital organs and protoconch not to scale. at genital atrium, bc bursa copulatrix, ep epiphallus, f flagellum, mrp musculus retractor penis, p penis, pp penial papilla, spo spermooviduct, vd vas deferens

Riebeckia sokotorana (E. v. Martens, 1881)

Figs. 1a–f, 2a–c

1881 *Achatina sokotorana* E. v. Martens, *Nachrichtsblatt der deutschen malakozologischen Gesellschaft*, 13: 135 (Sokotra).

1881 *Stenogyra fumificata* Godwin-Austen, *Proceedings of the Zoological Society of London*, 1881: 810, pl. 69, fig. 2, 2a (Sokotra, common on limestones at the east end of the island, leg. Baily-Balfour).

1884 *Stenogyra (Riebeckia) sokotorana*,—E. v. Martens, *Conchologische Mittheilungen*, 2 (3/4): 146, Taf. 29, Figs. 1,2,3,4,5,6,7,8.

1903 *Stenogyra (Riebeckia) sokotorana*,—E. A. Smith, *Special Bulletin of the Liverpool Museums*, 1903: 131, pl. 13, fig. 15.

1969 *Reibeckia*[sic!] *lavranosi* Salvat, *Bulletin du Muséum National d'Histoire Naturelle, Zoologie*, 41 (3): 750, pl. 1, Figs A, B (Sokotra, leg. Lavranos, 1969).

Type specimens: *sokotorana*: lectotype SMF 157237 [here designated], "Sokotra", coll. K.L. Pfeiffer ex Mus. Berlin 1935, leg. Riebeck (=original specimen of E. v. Martens 1883, plate 29, Fig. 3). *fumificata*: syntype NHM 1881.12.14.46. *lavranosi*: holotype MNHN.

Specimens examined: Wadi Ayhaft, 08.X.2000, leg. Bejček & Šťastný CZ/15; Deksam plateau, hill saddle, 12.548750° N 53.912240° E, 496 m alt., 2 XI.1999, leg. Bejček & Šťastný, XYZ/2 (WGS 84) = 12° 32,56' N 53° 58,20' E, CZ/01; Camp Shebehan Plateau, 6.1.2003, 12.4315° N 53.9551° E, 612 m alt., leg. K. Van Damme, NMBE 563179; Hoq Cave, along hiking path midway up, 16.2.2013, 12.5908° N 54.3594° E, 218 m alt., leg. NeuBo, NMBE 563182; Southern Dixam plateau N of Steroh, 17.2.2013, 12.3956° N 53.9324° E, 436 m alt., leg. NeuBo, NMBE 563183; Southern Dixam plateau N of Steroh, 17.2.2013, 12.3956° N 53.9324° E, 436 m alt., leg. NeuBo, NMBE 563175; Central Mumi area,

Fig. 3 a–e *Riebeckia decipiens* (E. A. Smith, 1897). **a** Syntype *Stenogyra (Riebeckia) decipiens* No. 1, NHM 1897.7.21.1–2, $H=87.3$ mm. **b** Syntype No. 2, NHM 1897.7.21.3–5, $H=74.8$ mm. **c** NMBE 563399, Sokotra, Firmihin, 25.2.1999, leg. A. Miller, $H=78$ mm. **d**, **e** Details of NMBE 563399; **d** section taken from a medium whorl showing the almost smooth surface of teleoconch; **e** apical part of shell with protoconch showing the shallow suture of the protoconch. All phot. $\times 1.5$, details not to scale

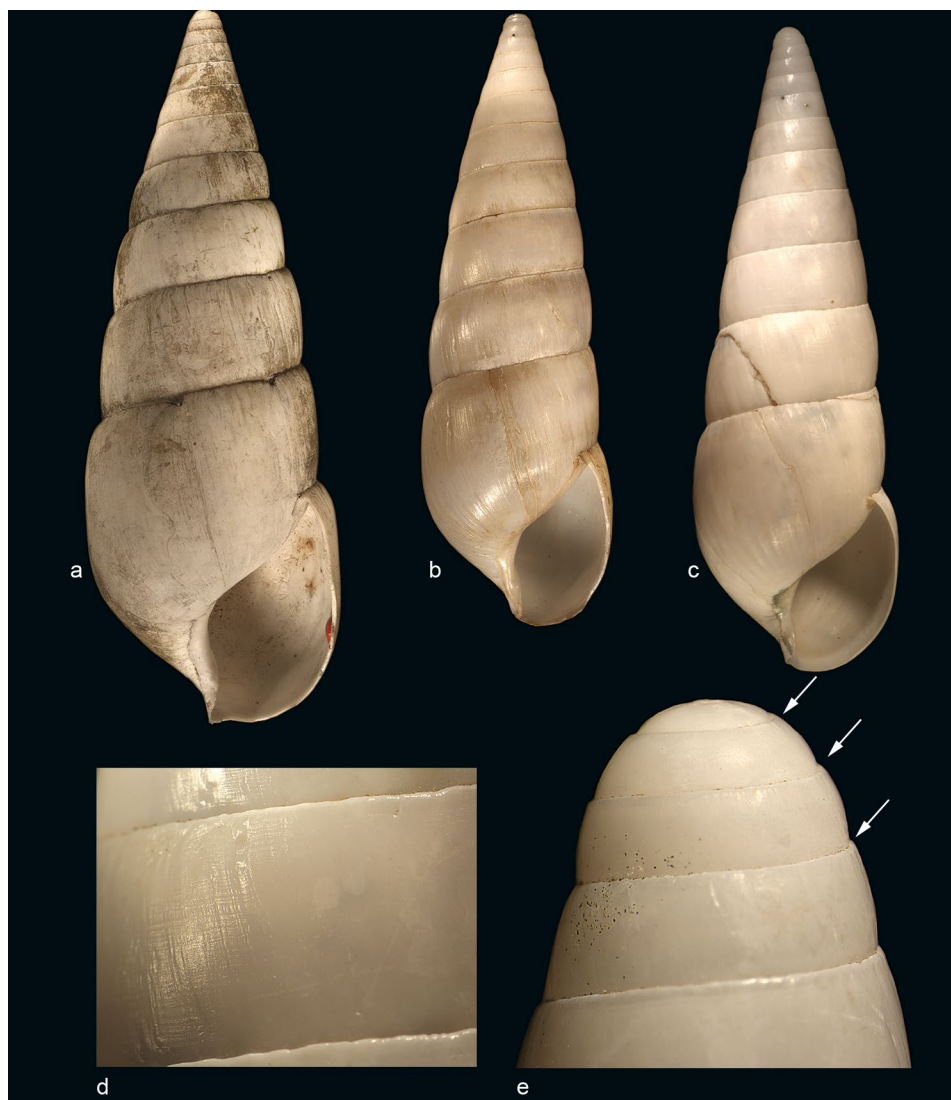


Fig. 4 a–e *Riebeckia gollonsi-rensensis* (Godwin-Austen, 1881). **a** Syntype *Stenogyra gollonsi-rensensis*, NHM 1881.12.19.45, $H=59.9$ mm; **b** detail section taken from a medium whorl showing the almost smooth surface of teleoconch; **c–e** NMBE 563397, Ta' aqs; **c** section taken from a medium whorl; **d** protoconch; **e** different views of complete shell, $H=70.9$ mm. All phot. $\times 1.5$, detail not to scale



Felkanah, 18.2.2013, 12.5369° N 54.3278° E, 494 m alt., leg. NeuBo, NMBE 563177; Southern Dixam plateau, 20.2.2013, 12.4108° N 53.9392° E, 515 m alt., leg. NeuBo, NMBE 563176; Northern Dixam plateau, 20.2.2013, 12.5163° N 53.9363° E, 960 m alt., leg. NeuBo, NMBE 563178; Southern Dixam plateau above slope, 20.2.2013, 12.5428° N 53.8643° E, 480 m alt., leg. NeuBo, NMBE 563180; Central Ma'hli plateau, 25.2.2013, 12.5865° N 53.5150° E, 676 m alt., leg. NeuBo, NMBE 563181; new road to Dixam, on plateau, 20.5.2003, 12.5455° N 53.8506° E, 413 m alt., leg. U. Zajonz, A. Saaed, N. Carpenter, NMBE 563390; new road to Dixam, on plateau, 20.5.2003, 12.5174° N 53.9079° E, 827 m alt., leg. U. Zajonz, A. Saaed, N. Carpenter, NMBE 563391; Ghiniba Cave, 7.1.2003, 12.4341° N 53.9367° E, 404 m alt., leg. K. Van Damme, NMBE 563392; en route to Adho Dimelho through Wadi Danegan, granite, dense shrubs, 2.2.1999, 12.5666° N 54.0333° E, 200–500 m alt., leg. E. Neubert,

NMBE 563393; upper part Wadi Zeewef, plain of Homhil and western mountains, limestone with dense Dracena forest, 7.-8.2.1999, 12.5876° N 54.3025° E, 320–640 m alt., leg. E. Neubert, NMBE 563394; Wadi Desfaf, from Hadibo plain to Haghier ridge, 22.5.2003, 12.5796° N 54.0291° E, 400–1200 m alt., leg. U. Zajonz, A. Saaed, A. Al-Okaishi, SMF 358852; Deksam plateau, campsite, 22.-24.2.1999, 12.5406° N 53.9891° E, 1020 m alt., leg. E. Neubert, SMF 358853; Rewgid, camp site, 3.3.1999, 12.5985° N 53.9919° E, 650 m alt., leg. K. Van Damme, NMBE 563395; Wadi Ayhaft, 21.1.2003, 12.6072° N 53.9926° E, leg. K. Van Damme, NMBE 563396; at the road from Hadibo to the Deksam plateau, 22.2.1999, 12.5373° N 53.9265° E, 800 m alt., leg. E. Neubert, SMF 358854; at the road between Homhil and Kilisan, small unknown village with waterpool on the plateau, 9.2.1999, 12.5356° N 54.3280° E, 540 m alt., leg. E. Neubert, SMF 358855; Hoq, coastal plain to entrance of cave, few

granite rocks with limestone boulders with deep crevices, a few big trees, 5.-6.2.1999, 12.5999° N 54.3499° E, 50–320 m alt., leg. E. Neubert, SMF 358856; Firmihin, 25.2.1999, 12.4814° N 54.0093° E, leg. T. Miller, SMF 358857; *Dracaena* forest N Kilisan, 9.-10.2.1999, 12.5301° N 54.3138° E, 360 m alt., leg. E. Neubert, SMF 358858; Qaysoh W of Qualaansiyah, slope of Jebel Ma'lih, 12.1.2001, 12.6517° N 53.4408° E, 600 m alt., leg. K. Van Damme, NMBE 563400; coastal road E Hadibo, flat area in a dry wadi, dense shrubs of *Croton*, 4.2.1999, 12.6301° N 54.2298° E, 90 m alt., leg. E. Neubert, NMBE 563401; Qaysoh W of Qualaansiyah, slope of Jebel Ma'lih, 12.1.2001, 12.6552° N 53.4411° E, 480 m alt., leg. K. Van Damme, SMF 358859; Wadi Ayhaft, 5.4.1999, 12.6076° N 53.9877° E, 266 m alt., leg. R. Janssen, SMF 358860; Wadi Ayhaft, 5.4.1999, 12.615° N 53.9583° E, 141 m alt., leg. R. Janssen, SMF 358861; Spider Rock, 12.1.2003, 12.5876° N 53.5113° E, 677 m alt., leg. K. Van Damme, NMBE 563402; new road to Dixam, on plateau, 20.5.2003, 12.5375° N 53.8716° E, 472 m alt., leg. U. Zajonz, A. Saaed, N. Carpenter, NMBE 563403; Western Ma'ahli plateau, 25.2.2013, 12.5965° N 53.4852° E, 730 m alt., leg. NeuBo, NMBE 563173.

Description: shell big, elongate, dull, dextral and conical shaped; whorls growing fast in width, towards the apex slightly tapered; periostracum light brown with irregular dark brown axial stripes; protoconch broad, blunt and smooth; suture of protoconch is deep, whorls shouldered below the suture; teleoconch surface with a reticulate microsculpture; aperture oval and small; peristome simple and sharp, with a white internal parietal callus, columella truncate.

Measurements: $n = 25$; $H = 71.21 \pm 10.71$, $H_{\min} = 51.26$, $H_{\max} = 88.70$; $D = 21.00 \pm 2.19$, $D_{\min} = 18$, $D_{\max} = 25.5$; $W = 12.00$.

Morphology of the genital organs: male copulatory organ subdivided in penis and epiphallus, penis extremely long, reaching three times the length of the vagina, penial lumen with several interdigitating ridges; epiphallus separated from penis by a penial papilla, consisting of a short upper part and an elongated triangular flap; epiphallus a muscular tube, lumen filled with fine longitudinal pilasters (not shown); retractor muscle very strong, attaching at the entrance point of the vas deferens, splitting in two arms, probably connecting to the columellar muscle; genital atrium simple, smooth inside; vagina a broad and muscular tube with some longitudinal ridges, bursa copulatrix adhering on a swelling of the vagina at the transition between vagina and spermoviduct; bursa copulatrix a small elongate vesicle on a short stem.

Distribution (Fig. 7): This species is recorded from the western to the eastern part of the island. It seems to miss in the central part of the island. There are also no specimens found at the southern coastal plain. Most of the animals were

found in the region of the Haggier Mountains, and additionally in the far west in the mountainous region of Jebel Ma'lih. In the far east, it is mainly known in the *Dracaena* forest north of Kilisan, and in the region of Hoq and Homhil.

Remarks: In 1884, E. v. Martens reports this species from several localities on Sokotra: Keregnigi [= Wadi Manifo east of Hadibo]; at Balini in the Wadi Dilac [locality not identified yet]; Wadi Kischen from 650 to 1000 m altitude [= Wadi Danegan], collected by Riebeck and Schweinfurth (Bezdek et al. 2012). Already Smith (1903) established the synonymy of *S. fumificata* with *A. sokotorana*. This species can easily be confounded with *R. decipiens*, which has a shell that is on average broader, lacks the typical sculpture on the teleoconch, and usually has deeply channelled suture in the protoconch.

Riebeckia decipiens (E. A. Smith, 1897)

Fig. 3a–e

1897 *Stenogyra* (*Riebeckia*) *decipiens* E. A. Smith, The Journal of Malacology, 6 (3/4): 37 (Sokotra).

Type specimens: *decipiens*: 5 syntypes, NHM 1897.7.21.1-2, NHM 1897.7.21.3-5.

Specimens examined: Haggier, 12.553250 N 54.006620° E (= 12° 33.2' N 54° 0.4'E), 1196.5 m alt., 4.-8.XI.2000, WGS 84, leg. Bejček & Šťastný CZ/09; Haggeher Granite Peak, 22.1.2003, 12.5918° N 54.0901° E, 987 m alt., leg. K. Van Damme, NMBE 563174; Street to camp/Skend, 20.2.2013, 12.5193° N 53.9948° E, 840 m alt., leg. NeuBo, NMBE 563169; Central Dixam plateau, 20.2.2013, 12.4871° N 53.9912° E, 691 m alt., leg. NeuBo, NMBE 563167; Skend area near campside, 24.2.2013, 12.5468° N 53.9981° E, 1160 m alt., leg. NeuBo, NMBE 563171; Skend area uphill, 24.2.2013, 12.547° N 53.9996° E, 1210 m alt., leg. NeuBo, NMBE 563172; Skend area first pass, 24.2.2013, 12.5488° N 54.0006° E, 1224 m alt., leg. NeuBo, NMBE 563168; Firmihin, 26.2.2013, 12.4814° N 54.0093° E, 584 m alt., leg. NeuBo, NMBE 563170; between Tar Qarezhun and Dalaqhen, S of Skend, scarce vegetation, under *Buxus*, 23.5.2003, 12.5373° N 53.9867° E, 900 m alt., leg. U. Zajonz, A. Saaed, A. Al-Okaishi, SMF 358862; close to Demereh Qado, at Skend, 23.5.2003, 12.5685° N 54.0194° E, 1350 m alt., leg. U. Zajonz, A. Saaed, A. Al-Okaishi, SMF 358863; at the road from Hadibo to the Deksam plateau, 22.2.1999, 12.5373° N 53.9265° E, 800 m alt., leg. E. Neubert, NMBE 563398; en route to Adho Dimelho through Wadi Danegan, granite, dense shrubs, 2.2.1999, 12.5666° N 54.0333° E, 200–500 m alt., leg. E. Neubert, SMF 358864; close to Dehepeqa, S of Skend, scarce vegetation, under *Buxus*, 12.5280° N 53.9817° E, 600 m alt., leg. U. Zajonz, A. Saaed, A. Al-Okaishi, SMF 358865; Firmihin, 25.2.1999, 12.4814° N 54.0093° E, leg. T. Miller, NMBE 563399; hills and meadows in the eastern part of the plain of Homhil, 9.2.1999, 12.5695° N 54.3255° E, 540 m alt.,

leg. E. Neubert, SMF 358866; Deksam plateau, campsite, 22.–24.2.1999, 12.5406° N 53.9891° E, 1020 m alt., leg. E. Neubert, SMF 358867; camping site below Adho Dimelho, granite, dense shrubs and meadows, small creek, 3.2.1999, 12.5760° N 54.0485° E, 940 m alt., leg. E. Neubert, SMF 358868.

Description: shell elongate, dull and conical shaped; periostracum light brown; protoconch slender, blunt and smooth; suture of protoconch is shallow, transition between the whorls flat; teleoconch surface smooth with no reticulate microsculpture; aperture oval and small; peristome simple and sharp, with a white internal parietal callus, columella truncate.

Measurements: $n = 13$; $H = 64.09 \pm 7.82$, $H_{\min} = 53.68$, $H_{\max} = 78.73$; $D = 21.4 \pm 2.97$, $D_{\min} = 17.64$, $D_{\max} = 27.12$; $W = 12.00$.

Morphology of the genital organs: so far not collected alive.

Distribution (Fig. 7): This species lives restricted to the central to eastern part of the island, with a clear focus to the Haggier Mountains. The highest so far recorded altitude was 1224 m. There is only a single locality far from this range in the plain of Homhil. However, this gap in the distribution pattern may be artificial.

Remarks: *Riebeckia decipiens* and *R. sokotorana* occur in sympatry in several places in the Haggier Mountains.

Riebeckia gollonsirens (Godwin-Austen, 1881)

Fig. 4a–e

1881 *Stenogyra gollonsirens* Godwin-Austen, Proceedings of the Zoological Society of London, 1881: 809, pl. 69, fig. 1 (Sokotra, on limestones at an altitude of over 1000 feet on the top of the ridge overlooking Gollonsir village).

Type specimens: *gollonsirens*: syntype NHM 1881.12.19.45.

Specimens examined: Ta'aqs, 2.1999, 12.6719° N 53.5756° E, 210 m alt., leg. Lavranos, NMBE 563397.

Description: shell elongate, slender and conical shaped; protoconch broad, blunt and smooth; suture of protoconch is deep, whorls shouldered below the suture; teleoconch with a reticulate microsculpture, second last whorl has it at least in the suture region; teleoconch whorls growing regularly, suture shallow; aperture small and oval shaped, peristome simple and sharp.

Measurements: $n = 3$; $H = 62.92 \pm 6.97$, $H_{\min} = 53.88$, $H_{\max} = 70.85$; $D = 17.40 \pm 1.56$, $D_{\min} = 15.54$, $D_{\max} = 19.36$; $W = 11.5$.

Morphology of the genital organs: so far not collected alive.

Distribution (Fig. 7): Until now, this species is only known from two localities in the northwest of the island. One of it is the type locality of the species on the mountain ridge above Qualaansiyah village, and the other is in the

Ta'aqs area. The latter locality needs reconfirmation, the current position is only an estimate.

Remarks: The shell of *Riebeckia gollonsirens* is generally slender and the last whorl is not that dominant as in the similar species *R. sokotorana* and *R. decipiens*. In both, *R. gollonsirens* and *R. sokotorana*, the protoconch shape is very similarly broad and blunt, while *R. decipiens* has a slender protoconch. The last whorl is not broadened and thus has not a dominant appearance as in *R. decipiens* and *R. sokotorana*. Also in their distribution pattern, *R. gollonsirens* is clearly separated and has only been found so far restricted to the hillside on the northern boundary of the valley of Qualaansiyah.

Riebeckia adonensis (Godwin-Austen, 1881)

Fig. 5a–d

1881 *Stenogyra adonensis* Godwin-Austen, Proceedings of the Zoological Society of London, 1881: 810, pl. 69, fig. 4, 4a (Sokotra, Hadibu near Adona, altitude over 1500 feet, rock granite).

Type specimens: *adonensis*: syntype NHM 1881.12.14.52-3.

Specimens examined: Haggeher Granite Peak, 22.1.2003, 12.5918° N 54.0901° E, 987 m alt., leg. K. Van Damme, NMBE 563135; camping site below Adho Dielho, 940 m alt., granite, dense shrubs and meadows, small creek, 3.2.1999, 12.5760° N 54.0485° E, leg. E. Neubert, NMBE 563136; hills and meadows in the eastern part of the plain of Homhil, 9.2.1999, 12.5695° N 54.3255° E, 540 m alt., leg. E. Neubert, SMF 358869; Deksam plateau, campsite, 22.–24.2.1999, 12.5406° N 53.9891° E, 1020 m alt., leg. E. Neubert, SMF 358870; Deksam plateau, above campsite, limestone hills, 22.–24.2.1999, 12.5333° N 53.9833° E, 1200 m alt., leg. E. Neubert, SMF 358871; dense shrubs below the peak, 23.2.1999, 12.5594° N 54.0079° E, 1500 m alt., leg. K. Van Damme, SMF 358872; Central Dixam plateau, 20.2.2013, 12.4871° N 53.9912° E, 691 m alt., leg. NeuBo, NMBE 563139; Northern Dixam plateau, 20.2.2013, 12.5163° N 53.9363° E, 960 m alt., leg. NeuBo, NMBE 563143; Skend area near campside, 24.2.2013, 12.5468° N 53.9981° E, 1160 m alt., leg. NeuBo, NMBE 563141; Skend area first pass, 24.2.2013, 12.5488° N 54.0006° E, 1224 m alt., leg. NeuBo, NMBE 563142; Firmhin, 26.2.2013, 12.4814° N 54.0093° E, 584 m alt., leg. NeuBo, NMBE 563140; new road to Dixam, on plateau, 20.5.2003, 12.5174° N 53.9079° E, 827 m alt., leg. U. Zajonz, A. Saaed, N. Carpenter, NMBE 563137; Manhor (herders huts) at Skend, lush vegetation of *Dracaena*, 22.5.2003, 12.5757° N 54.0270° E, 1483–1500 m alt., leg. U. Zajonz, A. Saaed, A. Al-Okaishi, NMBE 563138; close to Demereh Qado, at Skend, 23.5.2003, 12.5685° N 54.0194° E, 1350 m alt., leg. U. Zajonz, A. Saaed, A. Al-Okaishi, SMF 358873; between Tar Qarezhun & Dalaqhen,

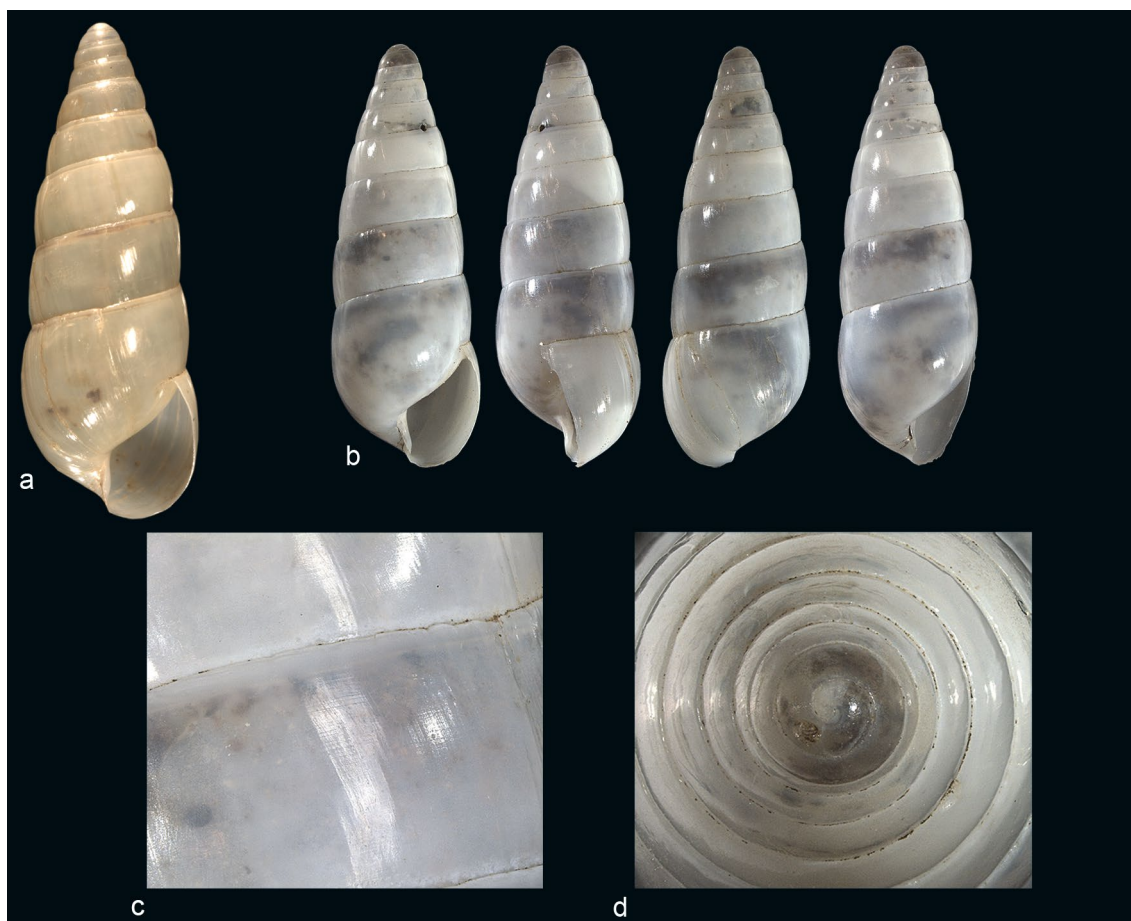


Fig. 5 a–d *Riebeckia adonensis* (Godwin-Austen, 1881). **a** Syntype *Stenogyra adonensis*, NHM 1881.12.14.52-3, $H=25.4$ mm; **b–d** NMBE 563139, Central Dixam plateau; **b** different views of com-

plete shell, $H=21.6$ mm; **c** detail section taken from a medium whorl showing the almost smooth surface of teleoconch; **d** protoconch. All phot. $\times 3$, detail not to scale

S of Skend, scarce vegetation, under *Buxus*, 23.5.2003, 12.5373° N 53.9867° E, 900 m alt., leg. U. Zajonz, A. Saaed, A. Al-Okaishi, SMF 358874; close to Dehepeqa, S of Skend, scarce vegetation, under *Buxus*, 12.5280° N 53.9817° E, 600 m alt., leg. U. Zajonz, A. Saaed, A. Al-Okaishi, SMF 358875; Firmihin, 25.2.1999, 12.4814° N 54.0093° E, leg. T. Miller, SMF 358876.

Description: shell shining, translucent to whitish, often with brown periostracum and some faint reddish axial lines, relatively short and broad, towards the apex often slightly tapered; protoconch broadly dome shaped, smooth, transition between protoconch and teleoconch invisible; suture simple and shallow; teleoconch whorls slightly and evenly curved, generally smooth, only some very faint growth lines visible; teleoconch often with axial grooves combined with a white axial internal callus; aperture short broadly oval, peristome simple and sharp, seldom with a white internal palatal callus, columellar side of the aperture straight, faintly decussate.

Measurements: $n=20$; $H=23.89 \pm 2.07$, $H_{\min}=21.3$, $H_{\max}=27.82$; $D=8.06 \pm 0.61$, $D_{\min}=7.26$, $D_{\max}=9.18$; $W=9.00$.

Morphology of the genital organs: so far not collected alive.

Distribution (Fig. 7): This species seems to be confined to altitudes above 600 m on limestone, but also populates the granite central part of the Haghier Mountains up to the peaks.

Remarks: This species can hardly be confused with any other *Riebeckia* species because of its relatively short and stumpy shell habitus, which easily differentiates it from *R. enodis*. For more differences, refer to the latter species. Both species occur in the Haghier Mountains, but they obviously follow a mainly allopatric pattern. The species have only single sympatric occurrence on the central Dixam plateau.

Riebeckia enodis (Godwin-Austen, 1881)

Fig. 6a–d

Fig. 6 a–d *Riebeckia enodis* (Godwin-Austen 1881). **a** Juvenile syntype of *Stenogyra* (*Subulina*?) *enodis*, NHM 1881.12.14.1, $H=12.6$ mm; **b** NMBE 563148, Central Mumi area, Qadamanoh $H=29.2$ mm; **c** NMBE 563149, Firmhin, $H=33.8$ mm; **d** NMBE 563156, Central Dixam plateau, $H=34.4$ mm. All phot. $\times 3$, detail not to scale



1881 *Stenogyra* (*Subulina*?) *enodis* Godwin-Austen, Proceedings of the Zoological Society of London, 1881: 811, pl. 69, fig. 5 (Sokotra, south side of the island, from limestone rocks, altitude 1000 feet).

1881 *Stenogyra socotorana* E. v. Martens, Nachrichtenblatt der deutschen malakozoologischen Gesellschaft, 13: 137 (Sokotra, in Granitspalten, 1000 Meter über dem Meer).

Type specimens: *enodis*: syntype NHM 1881.12.14.1 [juvenile specimen]. *socotorana*: could not be found in ZMB (pers. comm. Dec. 2019, C. Zorn); probably lost. The type is said to be 20–22 mm long, 6–6.5 mm width.

Specimens examined: Deksam plateau, hill saddle, 12.548750° N 53.912240° E, 496 m alt., 2 XI.1999, leg. Bejček & Šťastný, XYZ/2; Camp Shebehan Plateau, 6.1.2003, 12.4315° N 53.9551° E, 612 m alt., leg. K. Van Damme, NMBE 563155; Ghiniba Cave, 7.1.2003, 12.4341° N 53.9367° E, 404 m alt., leg. K. Van Damme, NMBE 563158; Dil'Euthi Cave, 8.1.2003, 12.4660° N 53.9843° E,

655 m alt., leg. K. Van Damme, NMBE 563159; Homhil (Hamaderoh plateau), walk up the hills SE of village Di-Hamir, Dracaena-woods, 10.1.2001, 12.5836° N 54.3102° E, 480 m alt., leg. K. Van Damme, NMBE 563160; Qaysoh W of Qualaansiyah, slope of Jebel Ma'lih, 12.1.2001, 12.6517° N 53.4408° E, 600 m alt., leg. K. Van Damme, NMBE; upper part Wadi Zeewef, plain of Homhil and western mountains, limestone with dense Dracena forest, 320–640 m alt., 7.-8.2.1999, 12.5876° N 54.3025° E, leg. E. Neubert, NMBE 563144; hills and meadows in the eastern part of the plain of Homhil, 9.2.1999, 12.5695° N 54.3255° E, 540 m alt., leg. E. Neubert, NMBE 563146; canyon and Wadi Kilisan, 120 m alt., 10.2.1999, 12.4866° N 54.3278° E, leg. E. Neubert, NMBE 563147; wadi with palm plantations, en route Hadibo in direction to Nogad, 180 m alt., 14.2.1999, 12.4408° N 54.1553° E, leg. E. Neubert, NMBE 563145; climb to Homhil through the valley of Zeewef until the pool, dense shrubs on limestone, 30–320 m alt, 7.2.1999,

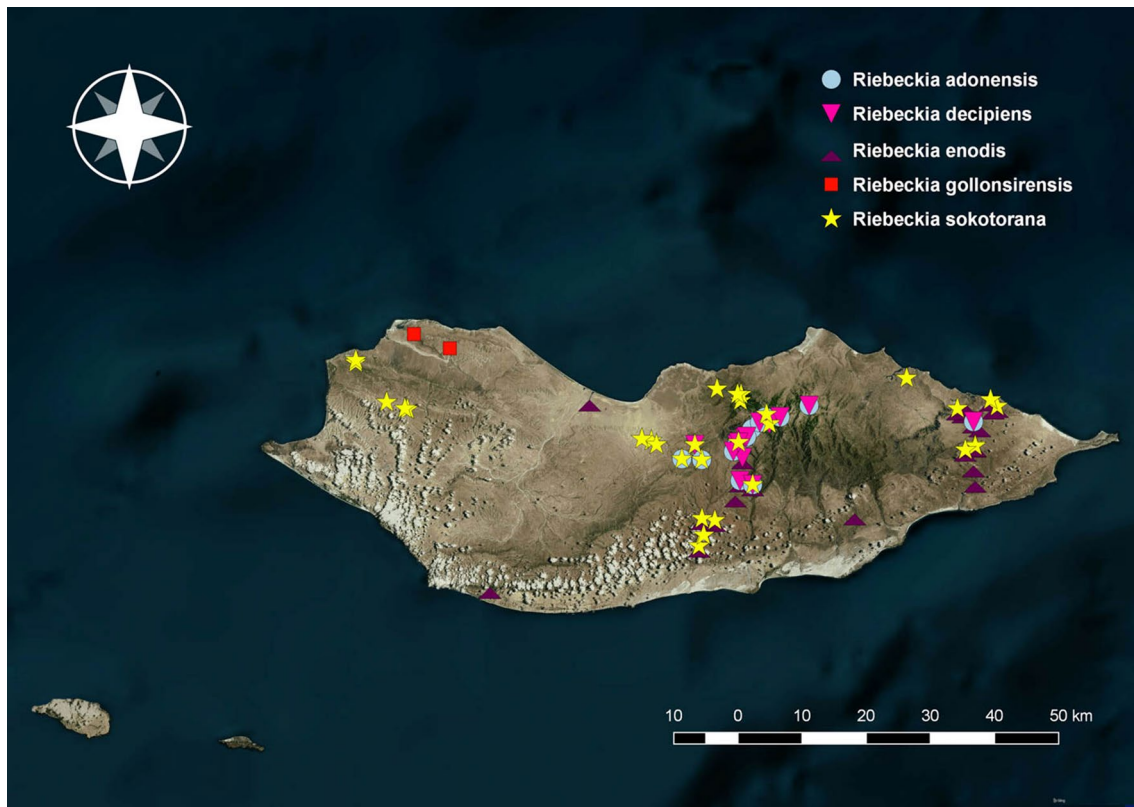


Fig. 7 Distribution records of all species of *Riebeckia*

12.5933° N 54.3146° E, leg. E. Neubert, SMF 358877; en route between Homhil and Kilisan, limestone boulders with low and dense shrubs, ca. 200 m alt., 9.2.1999, 12.5641° N 54.3346° E, leg. E. Neubert, SMF 358878; at the road between Homhil and Kilisan, small unknown village with waterpool on the plateau, 9.2.1999, 12.5356° N 54.3280° E, 540 m alt., leg. E. Neubert, SMF 358879; Dracaena-forest N Kilisan, 9.-10.2.1999, 12.5301° N 54.3138° E, 360 m alt., leg. E. Neubert, SMF 358880; southern coastal plain, surroundings of waterfall at the escarpment, 9.4.1999, 12.3378° N 53.6332° E, leg. R. Janssen, SMF 358881; Khor Ghirma at IT-173, .4.1999, 12.5997° N 53.7757° E, leg. R. Janssen, SMF 358882; Hoq Cave, along hiking path midway up, 16.2.2013, 12.5908° N 54.3594° E, 218 m alt., leg. NeuBo, NMBE 561352; Hoq Cave, area around entrance, 16.2.2013, 12.5886° N 54.3535° E, 380 m alt., leg. NeuBo, NMBE 563150; Southern Dixam plateau N of Steroh, 17.2.2013, 12.3956° N 53.9324° E, 436 m alt., leg. NeuBo, NMBE 563151; Central Mumi area, Felkanah, 18.2.2013, 12.5369° N 54.3278° E, 494 m alt., leg. NeuBo, NMBE 563154; Central Mumi area, Qadamanoh, 18.2.2013, 12.508° N 54.3255° E, 361 m alt., leg. NeuBo, NMBE 563148; Street to camp/Skend, 20.2.2013, 12.5193° N 53.9948° E, 840 m alt., leg. NeuBo, NMBE 563153; Central Dixam plateau, 20.2.2013, 12.4871° N 53.9912° E, 691 m alt., leg. NeuBo, NMBE

563156; Firmhin, 26.2.2013, 12.4814° N 54.0093° E, 584 m alt., leg. NeuBo, NMBE 563149; Firmihin, 25.2.1999, 12.4814° N 54.0093° E, leg. T. Miller, SMF 358883.

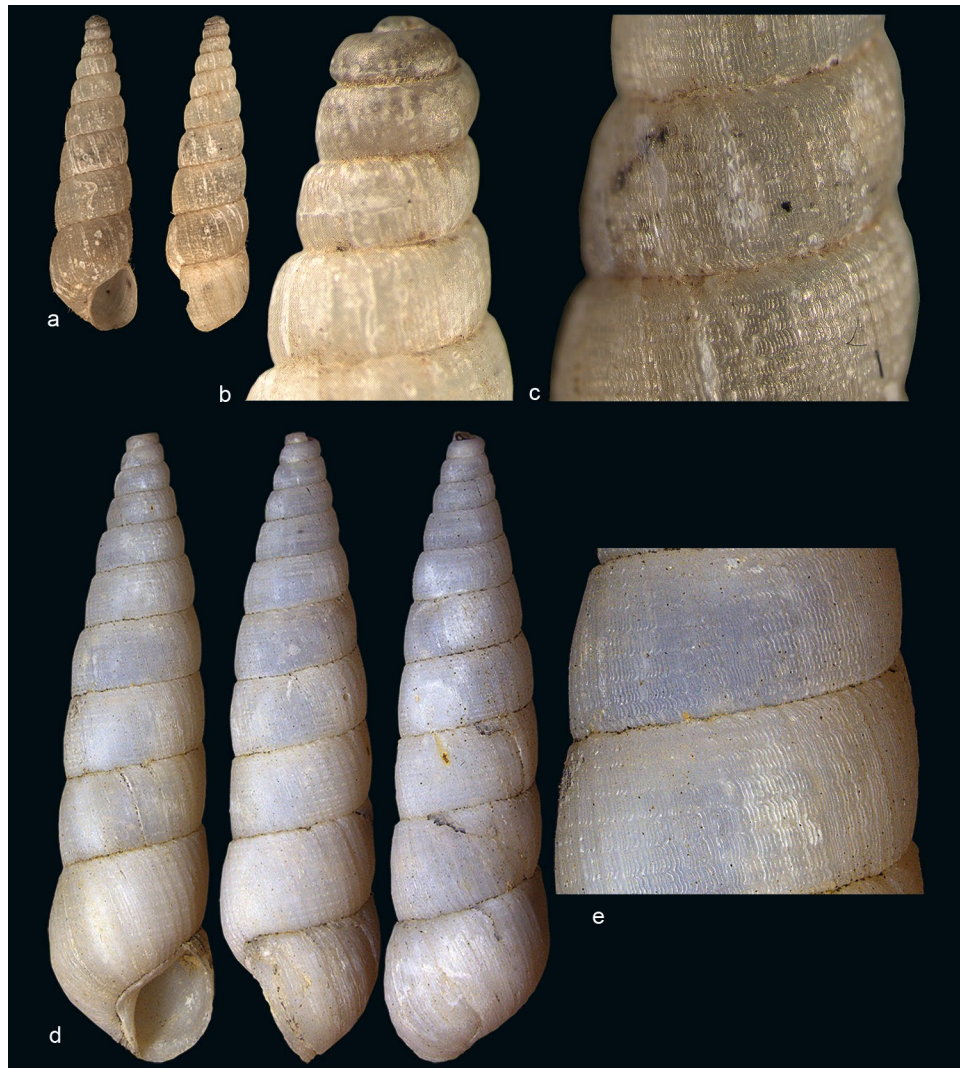
Description: shell shining, translucent or white, needle-like, long and slender; protoconch mamillate, smooth, transition between protoconch and teleoconch invisible; suture simple and shallow; teleoconch whorls slightly and evenly curved, generally smooth, only some very faint growth lines visible; teleoconch often with axial grooves combined with a white axial internal callus; aperture oval elongate, peristome simple and sharp, often with a white internal palatal callus (presence depends on the growth stage of the animal), columellar side of the aperture straight, connecting to the basal part with a faint decussation (often missing).

Measurements: $n = 31$; $H = 31.46 \pm 2.89$, $H_{\min} = 24.40$, $H_{\max} = 36.92$; $D = 6.95 \pm 0.68$, $D_{\min} = 5.61$, $D_{\max} = 8.05$; $W = 12.00$.

Morphology of the genital organs: so far not collected alive.

Distribution (Fig. 7): This species is confined to the eastern part of the island, where it inhabits lowland areas to places up in the granite part of the Haggier Mountains. The large central gap in the distribution pattern is a collecting artefact.

Fig. 8 a–e *Balfouria hirsuta* (Godwin-Austen, 1881). **a** Syntype *Stenogyra* (*Opeas*?) *hirsutus* NHM 1881.12.14.2, $H=11.6$ mm; **b** detail of upper whorls and protoconch; **c** details of central whorls. **d** SMF 358884, Noked plain, surrounding of the waterfall at the western escarpment, $H=23.1$ mm; **e** detail of central teleoconch whorls. All phot. $\times 5$, details not to scale



Remarks: The syntype of this species is a juvenile shell (Fig. 6a), but superimposition of this shell with an adult specimen demonstrates that it is in a subadult stage. The original description of *S. socotorana* suggests that it is simply a synonym of *S. enodis*. Crosse (1884) already recognised this synonymy. Many shells found are decollated, but a diaphragm to close the apical part of the shell is missing. Hence, this seems to be a *postmortem* phenomenon.

This species can probably be confused with *Riebeckia adonensis*. However, fully adult shells of *R. enodis* are somewhat longer but more slender than shells of *R. adonensis*. In *R. enodis*, the shells are growing regularly in width, while in *R. adonensis*, the fifth to seventh whorls suddenly increase in shell width. As a result, the *R. adonensis* shell is more cylindrical than that of *R. enodis*. The main difference can be found in the form of the protoconch, which is mamillate in *R. enodis*, but regularly dome-shaped in *R. adonensis* (Fig. 5).

***Balfouria* Crosse, 1884**

1884 *Balfouria* Crosse, *Journal de Conchyliologie*, 32: 356.

Diagnosis: shells small to medium sized, usually with a pattern of very small riblets on the teleoconch, often interrupted by larger ribs (major rib); periostracum often hairy, used to camouflage the shell with clay; protoconch always with a deeply incised suture. Type species: *Stenogyra* (*Opeas*?) *hirsuta* Godwin-Austen, 1881 by monotypy.

***Balfouria hirsuta* (Godwin-Austen, 1881)**

Fig. 8a–e

1881 *Stenogyra* (*Opeas*?) *hirsutus* Godwin-Austen, *Proceedings of the Zoological Society of London*, 1881: 808, pl. 69, fig. 8 (Sokotra, from underneath granite boulders on hills above Adona, altitude over 2000 feet).

Type specimens: syntype NHM 1881.12.14.2.

Specimens examined: Camp Shebehan Plateau, 6.1.2003, 12.4315° N 53.9551° E, 612 m alt., leg. K. Van Damme, NMBE 563163; southern coastal plain,

surroundings of waterfall at the escarpment, 8.4.1999, 12.3378° N 53.6332° E, leg. R. Janssen, SMF 358884.

Description: shell relatively small, fresh specimens greenish-brownish, eroded specimens white, needle like, long and slender; protoconch mamillate, granulated, with a deep suture; teleoconch covered with a hairy periostracum, underneath with a sculpture of small, comma-like axial riblets, arranged in spirals; riblets serving as adhering structure for the thick periostracum and the bristles inducing a waving pattern on the surface of the shells; aperture small, rounded to suboval, peristome simple and sharp, columellar side of the aperture straight; umbilicus slit-like open to closed.

Measurements (syntype only): $H = 11.6$; $W = 10.00$.

Morphology of the genital organs: not collected alive so far.

Distribution (Fig. 14): The distribution pattern for this species is not yet clarified because of the taxonomic ambiguity (see remarks).

Remarks: *Balfouria hirsuta* shows a quite unique waving or undulating pattern of small riblets on the teleoconch (Fig. 5c), which is an autapomorphic character state of this species and of *B. sordida* from Samha Island. On the one hand, the few specimens from Shebehan Plateau and the waterfall at the western end of the Noged plain are the only shells that show this unmistakable shell sculpture. On the other hand, the area at Adona (type locality) and above is a quite well-documented place, because it is alongside the classical route from Hadiboh to the high plateau and the peaks. Despite the dense collecting grid, not a single shell of *B. hirsuta* was ever found there.

It also has to be remarked that the shells from the two localities show some other shell differences if compared to the type: the shells are larger and particularly longer than the single-type specimen, and the aperture has a strong parietal and columellar callus, which is absent in the type of *B. hirsuta*. It might well be possible that the shells from the two localities belong to another undescribed species. However, currently, there are not enough specimens available to be sure, and a description of a new taxon is postponed until more sites with better preserved specimens will be available. The species probably lives on the more or less unexplored plateau above the southwestern escarpment.

Balfouria insculpta (E. A. Smith, 1897)

Fig. 9a–f

1897 *Stenogyra insculpta* E. A. Smith, The Journal of Malacology, 6 (3/4): 37, pl. 5, fig. 7 (Sokotra).

Type specimens: syntypes *Stenogyra insculpta* NHM 1897.7.21.26–30.

Specimens examined: hills and meadows in the eastern part of the plain of Homhil, 9.2.1999, 12.5695° N 54.3255° E, 540 m alt., leg. E. Neubert, SMF 358886; Hoq Cave,

along hiking path midway up, 16.2.2013, 12.5908° N 54.3594° E, 218 m alt., leg. NeuBo, NMBE 563166.

Description: shell very long if compared to other species in the genus, needle like, slender; protoconch mamillate, smooth, with a deep suture; teleoconch probably covered with a hairy periostracum, sculpture consisting of a dense grid of axial riblets with several major ribs per whorl, which are regularly notched or indentate; suture quite deep, indentate; aperture small, rhomboidal to suboval, peristome simple and sharp, columellar side of the aperture straight to slightly curved; umbilicus slit-like open.

Measurements: $n = 9$; $H = 24.22 \pm 1.65$, $H_{\min} = 22.18$, $H_{\max} = 27.35$; $D = 4.74 \pm$, $D_{\min} = 4.55$, $D_{\max} = 5.07$; $W = 14.00$.

Morphology of the genital organs: not collected alive so far.

Distribution (Fig. 14): This species seems to be a narrow range endemic of the northeastern part of Socotra Island. It is recorded from only two localities so far.

Remarks: *Balfouria insculpta* is an unmistakable species, which is well characterised by its teleoconch sculpture. An outstanding character state is the presence of the comb-like major ribs on the shell. Even on the rather eroded syntype specimens, the special form of the major ribs can be found.

Balfouria jessica (Godwin-Austen, 1881)

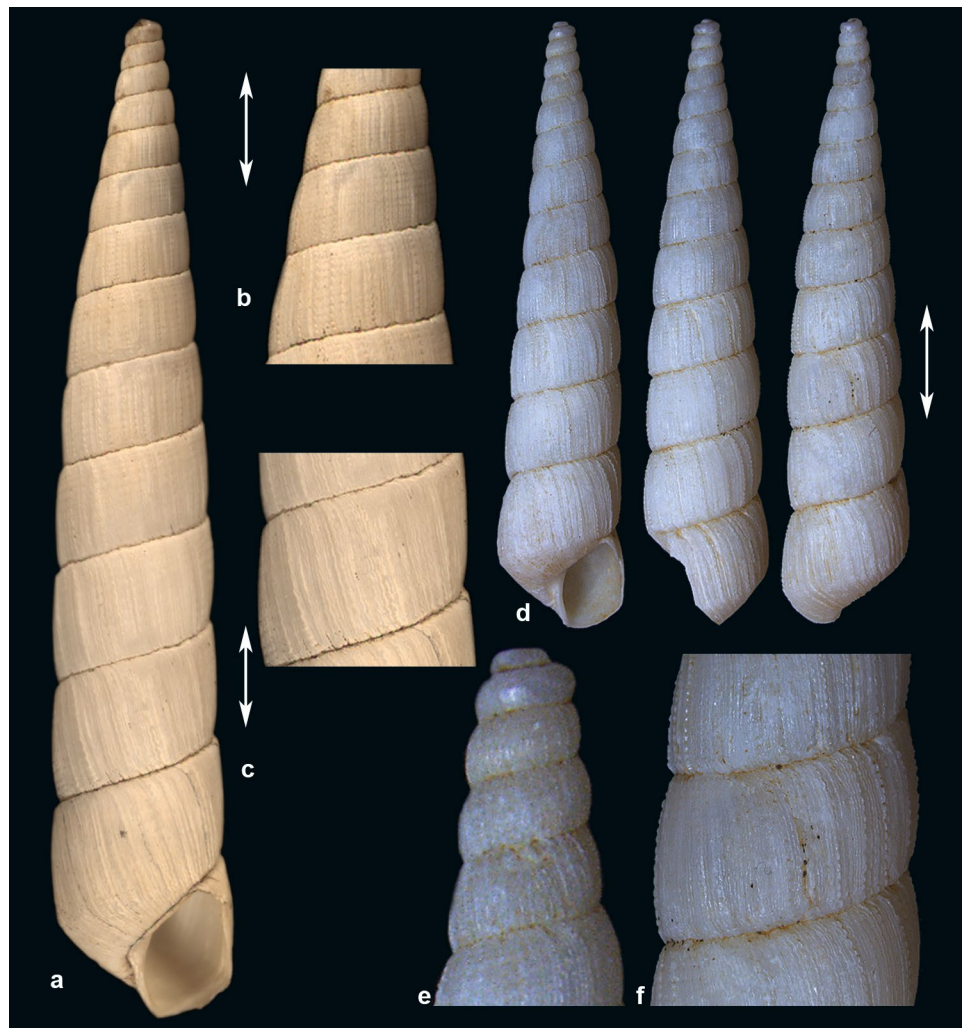
Fig. 10a–e

1881 *Stenogyra jessica* Godwin-Austen, Proceedings of the Zoological Society of London, 1881: 810, pl. 69, fig. 3 (Sokotra, on limestone ridge S.W. of Gollonsir at high altitude; at 1000 feet on south side of the island).

Type material: *jessica*: syntype NHM 1881.12.14.50–51.

Specimens examined: Damdedoh, Southwest, between Road Junction and Lahes, 13.1.2003, 12.4862° N 53.6681° E, leg. K. Van Damme, NMBE 563132; Duhaher Cliff, 12.1.2003, 12.5624° N 53.5419° E, 547 m alt., leg. K. Van Damme, NMBE 563125; Wadi Lahes, 13.1.2003, 12.4716° N 53.6879° E, 94 m alt., leg. K. Van Damme, NMBE 563126; Road Junction, 13.1.2003, 12.4484° N 53.7527° E, 150 m alt., leg. K. Van Damme, NMBE 563132; Amtar Village, 14.1.2003, 12.4370° N 53.4813° E, 440 m alt., leg. K. Van Damme, NMBE 563130; Fherrodzu, 14.1.2003, 12.4509° N 53.4804° E, 435 m alt., leg. K. Van Damme, NMBE 563129; Abris, Dry Wadi, 13.1.2003, 12.4249° N 53.4833° E, 359 m alt., leg. K. Van Damme, NMBE 563127; Qaysoh W of Qualaansiyah, slope of Jebel Ma'lih, 12.1.2001, 12.6552° N 53.4411° E, 480 m alt., leg. K. Van Damme, NMBE 563128; Khor Ghirma at IT-173, 4.1999, 12.5997° N 53.7757° E, leg. R. Janssen, SMF 358887; Western Nogad Plain between Ghishub and Steroh, 17.2.2013, 12.3167° N 53.6995° E, 30 m alt., leg. NeuBo, NMBE 563133; Road Gubbah to Shuab, slope of Salalah Mt., 19.2.2013, 12.5166° N 53.4672° E,

Fig. 9 a–f *Balfouria insculpta* (E. A. Smith, 1897). **a** Syntype *Stenogyra insculpta* NHM 1897.7.21.26–30, $H=36.6$ mm; **b, c** details of upper and last whorls. **d** SMF 358886, Homhil, $H=22.3$ mm; **e, f** detail of central teleoconch whorls showing the comb-like ribs. All phot. $\times 5$, details not to scale; arrows indicate the sector of the shell showing in the magnified pictures



185 m alt., leg. NeuBo, NMBE 563134; Southern Dixam plateau above slope, 20.2.2013, 12.5428° N 53.8643° E, 480 m alt., leg. NeuBo, NMBE 563124; Skend area uphill, 24.2.2013, 12.547° N 53.9996° E, 1210 m alt., leg. NeuBo, NMBE 563131 new road to Dixam, on plateau, 20.5.2003, 12.5455° N 53.8506° E, 413 m alt., leg. U. Zajonz, A. Saaed, N. Carpenter, SMF 358886; new road to Dixam, on plateau, 20.5.2003, 12.5375° N 53.8716° E, 472 m alt., leg. U. Zajonz, A. Saaed, N. Carpenter, SMF 358888; new road to Dixam, on plateau, 20.5.2003, 12.5174° N 53.9079° E, 827 m alt., leg. U. Zajonz, A. Saaed, N. Carpenter, NMBE 563131.

Description: shell broadly elongate, rather large; protoconch mamillate, covered by an extremely fine pitting, reaching almost three whorls, with a deep suture; teleoconch covered by a dense and regular grid of axial riblets, which are finely beaded; suture deep and irregularly indented; aperture small, triangular to suboval, peristome simple and sharp, columellar side of the aperture straight to slightly curved; umbilicus closed.

Measurements: $n = 16$; $H = 23.41 \pm 1.56$, $H_{\min} = 20.81$, $H_{\max} = 26.28$; $D = 6.66 \pm 0.45$, $D_{\min} = 5.79$, $D_{\max} = 7.47$; $W = 10.00$.

Morphology of the genital organs: not collected alive so far.

Distribution (Fig. 14): This species is known from Central to Western Socotra; it has a broad overlap with *B. arguta* in the western pre-mountain plateau of the Haggiehr Mts.

Balfouria arguta (E. v. Martens, 1881)

Fig. 11a–e

1881 *Stenogyra arguta* E. v. Martens, *Nachrichtsblatt der deutschen malakozologischen Gesellschaft*, 13: 135 (Sokotra).

Type specimens: *arguta*: syntype ZMB 34232a.

Specimens examined: Deksam plateau, hill saddle, 12.548750° N 53.912240° E, 496 m alt., 2 XI.1999, leg. Bejček & Šťastný, XYZ/2 (WGS 84) = 12° 32,56' N 53° 58,20' E, CZ/01; Camp Shebehan Plateau, 6.1.2003, 12.4315° N 53.95512° E, 612 m alt., leg. K. Van Damme,

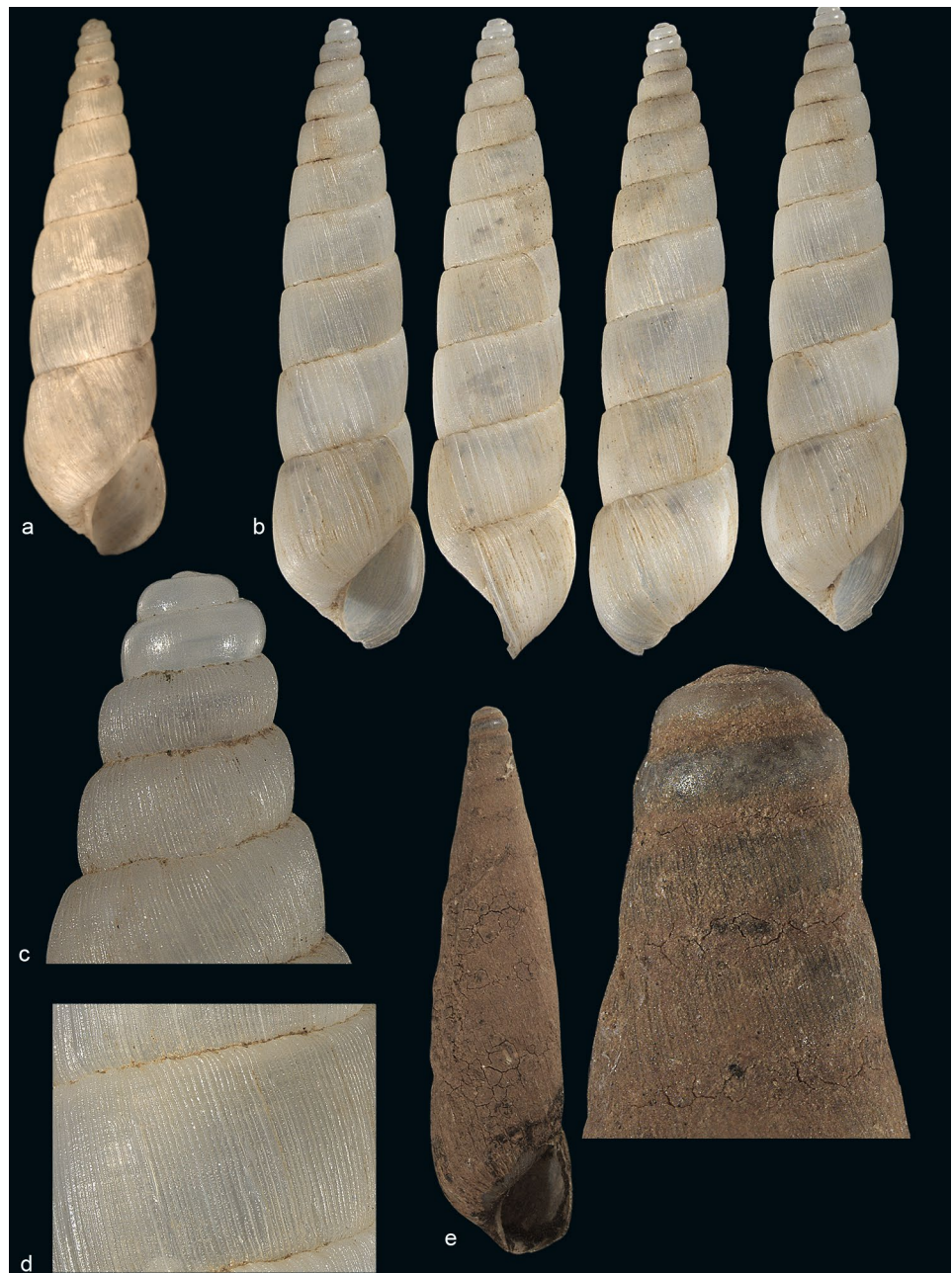
Fig. 10 a–e *Balfouria jessica* (Godwin-Austen, 1881). **a** Syntype *Stenogyra jessica* NHM 1881.12.14.50, $H=19.4$ mm; **b** NMBE 563131, Dixam, new road, on plateau, 827 m alt., $H=21.4$ mm; **c, d** protoconch and central teleoconch whorls of NMBE 563131; **e** NMBE 563124, Southern Dixam plateau above slope, 480 m alt., $H=23.1$ mm. All phot. $\times 5$, details not to scale



NMBE 563113; Ghiniba Cave, 7.1.2003, 12.4341° N 53.93672° E, 404 m alt., leg. K. Van Damme, NMBE 563105, SMF 358889; Dil'Euthi Cave, 8.1.2003, 12.4660° N 53.98432° E, 655 m alt., leg. K. Van Damme, NMBE 563118; Mega Canyon, 12.1.2003, 12.626° N 53.50922° E, 624 m alt., leg. K. Van Damme, NMBE 563120; Spider Rock, 12.1.2003, 12.5876° N 53.51132° E, 677 m alt., leg. K. Van Damme, NMBE 563107; Wadi Ayhaft, 21.1.2003, 12.6072° N 53.99262° E, leg. K. Van Damme, NMBE 563101; Haggeher Granite Peak, 22.1.2003, 12.5918° N 54.09012° E, 987 m alt., leg. K. Van Damme, NMBE 563103; Homhil (Hamaderoh plateau), walk up the hills SE

of village Di-Hamir, Dracaena-woods, 10.1.2001, 12.5836° N 54.31022° E, 480 m alt., leg. K. Van Damme, NMBE 563111; Qaysoh W of Qualaansiyah, Croton-shrubland on hills SW Qaysoh, 12.1.2001, 12.6588° N 53.45972° E, 70 m alt., leg. K. Van Damme, NMBE 563115; Qaysoh W of Qualaansiyah, slope of Jebel Ma'lih, 12.1.2001, 12.6517° N 53.44082° E, 600 m alt., leg. K. Van Damme, NMBE 563114; Qaysoh W of Qualaansiyah, slope of Jebel Ma'lih, 12.1.2001, 12.6569° N 53.43542° E, 670 m alt., leg. K. Van Damme, NMBE 563116; Hoq, coastal plain to entrance of cave, few granite rocks with limestone boulders with deep crevices, a few big trees, 5.-6.2.1999, 12.5999° N 54.34992°

Fig. 11 a–e *Balfouria arguta* (E. v. Martens, 1881). **a** Syntype *Stenogyra arguta* ZMB 34232a, $H=19.9$ mm. **b** NMBE 563105, Ghiniba Cave, $H=23.9$ mm; **c, d** protoconch and central teleoconch whorls of NMBE 563105; **e** NMBE 563116, Qaysoh, slope of Jebel Ma'lih, $H=20.2$ mm. All phot. $\times 5$, details not to scale



E, leg. E. Neubert, SMF 358890; climb to Homhil through the valley of Zeewef until the pool, dense shrubs on limestone, 7.2.1999, 12.5933° N 54.31462° E, leg. E. Neubert, SMF 358891; upper part Wadi Zeewef, plain of Homhil and western mountains, limestone with dense *Dracena* forest, 7.-8.2.1999, 12.5876° N 54.30252° E, leg. E. Neubert, SMF 358892; hills and meadows in the eastern part of the plain of Homhil, 9.2.1999, 12.5695° N 54.32552° E, 540 m alt., leg. E. Neubert, SMF 358893; at the road between Homhil and Kilisan, small unknown village with waterpool on the plateau, 9.2.1999, 12.5356° N 54.32802° E, 540 m alt., leg. E. Neubert, SMF 358894; *Dracaena* forest N Kilisan,

9.-10.2.1999, 12.5301° N 54.31382° E, 360 m alt., leg. E. Neubert, SMF 358895; canyon and Wadi Kilisan, 10.2.1999, 12.4866° N 54.32782° E, leg. E. Neubert, SMF 358896; road from Hadibo in direction to Airport, Kadub, date palm plantation, 12.2.1999, 12.6333° N 53.95002° E, leg. E. Neubert, SMF 358897; wadi with palm plantations, en route Hadibo in direction to Nogad, 14.2.1999, 12.4408° N 54.15532° E, leg. E. Neubert, SMF 358898; at the road from Hadibo to the Deksam plateau, 22.2.1999, 12.5373° N 53.92652° E, 800 m alt., leg. E. Neubert, SMF 358899; Deksam plateau, campsite, 22.-24.2.1999, 12.5406° N 53.98912° E, 1020 m alt., leg. E. Neubert, SMF 358900; Deksam

plateau, above campsite, limestone hills, 22.–24.2.1999, 12.5333° N 53.98332° E, 1200 m alt., leg. E. Neubert, SMF 358901; dense shrubs below the peak, 23.2.1999, 12.5594° N 54.00792° E, 1500 m alt., leg. K. Van Damme, SMF 358902; Firmihin, 25.2.1999, 12.4814° N 54.00932° E, leg. T. Miller, SMF 358903; Road Qalaansiyah to Gubbah, pass at Thaaks, 15.2.2013, 12.6266° N 53.61452° E, 250 m alt., leg. NeuBo, NMBE 563106; Southern Dixam plateau N of Steroh, 17.2.2013, 12.3956° N 53.93242° E, 436 m alt., leg. NeuBo, NMBE 563110; Southern Dixam plateau N of Steroh, 17.2.2013, 12.3956° N 53.93242° E, 436 m alt., leg. NeuBo, NMBE 563108; Central Mumi area, Felkanah, 18.2.2013, 12.5369° N 54.32782° E, 494 m alt., leg. NeuBo, NMBE 563100; Southern Dixam plateau, 20.2.2013, 12.4108° N 53.93922° E, 515 m alt., leg. NeuBo, NMBE 563123; Central Dixam plateau, 20.2.2013, 12.4871° N 53.99122° E, 691 m alt., leg. NeuBo, NMBE 563122; Northern Dixam plateau, 20.2.2013, 12.5163° N 53.93632° E, 960 m alt., leg. NeuBo, NMBE 563112; Skend area near campside, 24.2.2013, 12.5468° N 53.99812° E, 1160 m alt., leg. NeuBo, NMBE 563117; Skend area uphill, 24.2.2013, 12.547° N 53.99962° E, 1210 m alt., leg. NeuBo, NMBE 563121; Skend area uphill, 24.2.2013, 12.547° N 53.99962° E, 1210 m alt., leg. NeuBo, NMBE 563121; Skend area first pass, 24.2.2013, 12.5488° N 54.00062° E, 1224 m alt., leg. NeuBo, NMBE 563119; Central Ma'ahli plateau, 25.2.2013, 12.5865° N 53.51502° E, 676 m alt., leg. NeuBo, NMBE 563102; Western Ma'ahli plateau, 25.2.2013, 12.5965° N 53.48522° E, 730 m alt., leg. NeuBo, NMBE 563104; Firmihin, 26.2.2013, 12.4814° N 54.00932° E, 584 m alt., leg. NeuBo, NMBE 563099; new road to Dixam, on plateau, 20.5.2003, 12.5174° N 53.90792° E, 827 m alt., leg. U. Zajonz, A. Saaed, N. Carpenter, SMF 358904; Wadi Desfaf, from Hadibo plain to Haghier ridge, 22.5.2003, 12.5796° N 54.02912° E, 400–1200 m alt., leg. U. Zajonz, A. Saaed, A. Al-Okaishi, SMF 358905; Manhor (herders huts) at Skend, lush vegetation of *Dracaena*, 22.5.2003, 12.5757° N 54.02702° E, 1483–1500 m alt., leg. U. Zajonz, A. Saaed, A. Al-Okaishi, SMF 358906; close to Demereh Qado, at Skend, 23.5.2003, 12.5685° N 54.01942° E, 1350 m alt., leg. U. Zajonz, A. Saaed, A. Al-Okaishi, SMF 358907.

Description: shell slender elongate, rather large; protoconch broadly mamillate, covered by an extremely fine pitting, reaching almost three whorls, with a deep suture; teleoconch covered by a dense and regular grid of axial riblets, which are finely beaded; regularly larger riblets occurring on the teleoconch surface; suture deep and irregularly indented; aperture small, obliquely suboval, peristome simple and sharp, columellar side of the aperture slightly curved; umbilicus closed.

Measurements: $n = 17$; $H = 22.36 \pm 1.33$, $H_{\min} = 20.27$, $H_{\max} = 25.12$; $D = 5.83 \pm 0.50$, $D_{\min} = 5.12$, $D_{\max} = 6.78$; $W = 10.50$.

Morphology of the genital organs: not collected alive so far.

Distribution (Fig. 14): *Balfouria arguta* is recorded from almost all areas on the island. The gap in the centre of the island may be a sampling artefact.

Remarks: This species can be confused with the other axially striated *Balfouria* species; however, it differs from *B. insculpta* by lack of combed axial riblets and the smaller and more narrow shell, from *B. jessica* by the constantly broader shell and the presence of major riblets, and from *B. minima* by the much larger shell and the differing form of the aperture.

Balfouria nitida n. sp.

Fig. 12a–b

Type specimens: holotype NMBE 563164; paratypes NMBE 563165/4.

Type locality: Qaysoh W of Qalaansiyah, slope of Jebel Ma'lih, 12.1.2001, 12.6517° N 53.4408° E, 600 m alt., leg. K. Van Damme.

Specimens examined: only known from the type locality.

Description: shell elongate, dextral and conical-shaped with a glossy surface; whorls growing regularly in width, convex; protoconch smooth, blunt and broad; protoconch whorls strongly convex; teleoconch whorls slightly and evenly curved, generally smooth, faint growth lines visible; suture deep, transition to the next whorl shouldered; aperture pointed oval and small; peristome simple and sharp.

Measurements: holotype: $H = 16.18$; $D = 4.28$; $W = 9.50$. paratypes: $n = 1$: $H = 12.51$; $D = 3.94$; $W = 8.00$.

Etymology: latin *nitidus* <a, um>: shiny, shimmering, pretty.

Distribution: It is only from the type locality, Qaysoh W of Qalaansiyah in the northwest of the island recorded so far.

Remarks: Only the holotype seems fully grown, the paratypes are juvenile to subadult. More specimens would be needed to show the range of intraspecific variation. Compared to all other *Balfouria* species, *B. nitida* has a glossy and smooth surface, without a reticulate or axial microsculpture.

Balfouria minima n. sp.

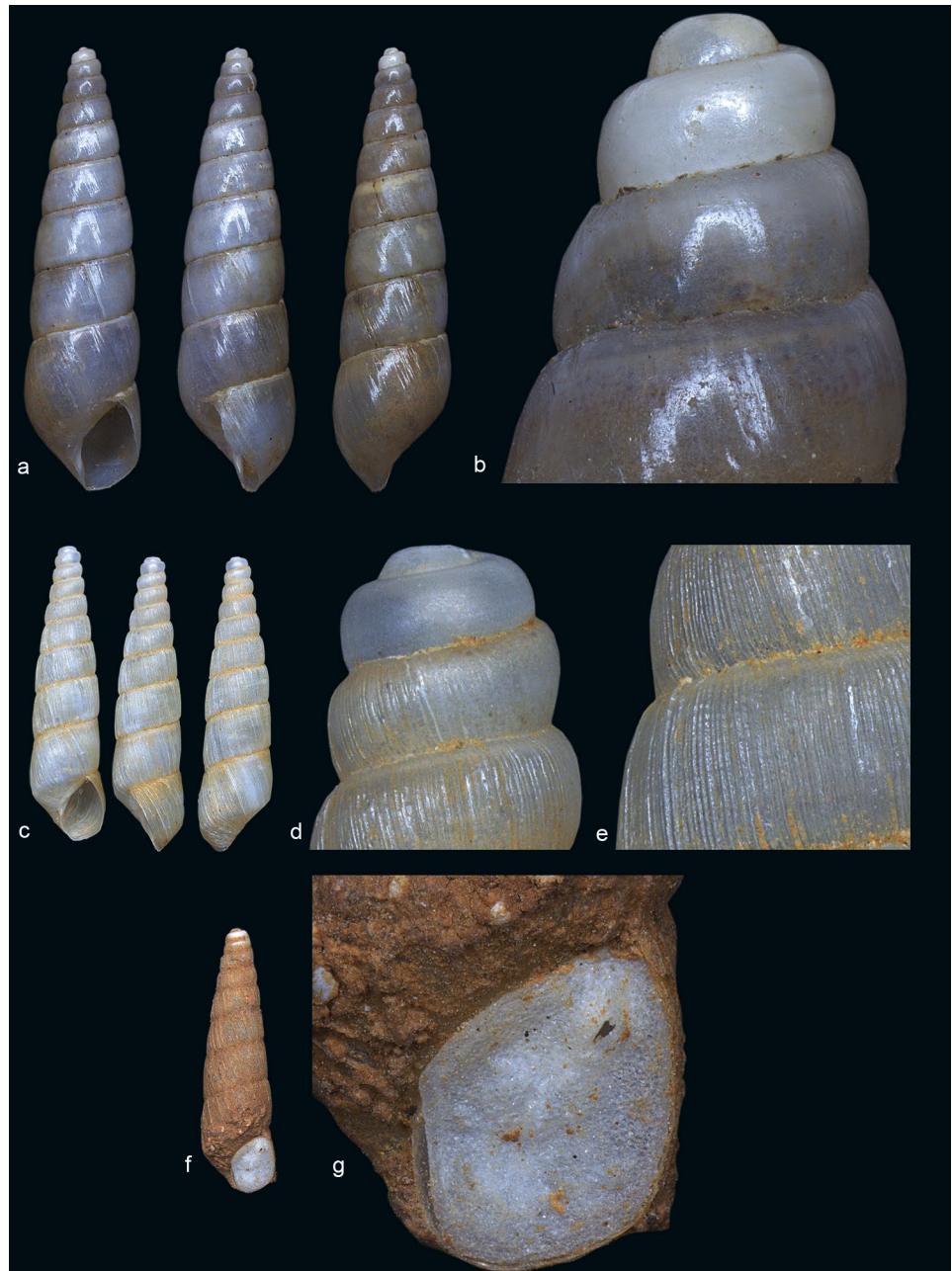
Fig. 12c–g

Type specimens: holotype NMBE 563404; paratypes NMBE 563162/26, SMF 358908/3, NHM xxxx/3.

Type locality: Qaysoh W of Qalaansiyah, slope of Jebel Ma'lih, 12.1.2001, 12.6552° N 53.4472° E, 320 m alt., leg. K. Van Damme.

Specimens examined: Qaysoh W of Qalaansiyah, slope of Jebel Ma'lih, 12.1.2001, 12.6517° N 53.4408° E, 600 m alt., leg. K. Van Damme, NMBE 563404, NMBE 563162.

Fig. 12 a–g *Balfouria* spp.
a, b *Balfouria nitida* n. sp.
a Holotype NMBE 563164, $H = 16.4$ mm. **b** detail of upper whorls and protoconch. **c–g** *Balfouria minima* n. sp. **c** holotype NMBE 563404, $H = 10.9$ mm; **d** detail of upper whorls and protoconch; **e** detail of central teleoconch whorls; **f, g** paratype NMBE 563162, $H = 9.8$ mm; **f** complete shell covered by dried concrete of mud and mucus; **g** aperture with diaphragm and clumps of concreted clay. All phot. $\times 5$, details not to scale



Description: shell elongate, dextral and conical shaped with axial ribs; whorls convex, growing regularly in width; protoconch smooth surface, blunt and broad; protoconch whorls strongly convex; teleoconch whorls less convex, slightly and evenly curved; teleoconch ribs axial, fine and regular, after a short interval of fine ribs (3–9) one rib stronger developed and stick out; suture deep, transition to the next whorl shouldered; aperture ovoidal and small; peristome simple and sharp; diaphragma bright, granular in structure and with a small opening in the upper right corner that was pressed out from the inside.

Measurements: holotype: $H = 10.85$; $D = 3.17$; $W = 9$. paratypes: $n = 13$; $H = 10.42 \pm 0.60$; $H_{\min} = 9.40$, $H_{\max} = 11.32$; $D = 2.82 \pm 0.1$; $D_{\min} = 2.65$, $D_{\max} = 3.04$; $W = 8.50$.

Etymology: latin *minimus* <a, um>: small, little.

Distribution (Fig. 14): Until now, there is only one location known in the northwest of the island: Qaysoh W of Qualaansiyah, slope of Jebel Ma'lih. The specimens have been collected at an altitude between 320 and 600 m over sea level.

Fig. 13 a–c *Balfouria sordida* (Neubert, 2002). **a** Holotype SMF 322977, $H=25.1$ mm; **b** detail of upper whorls and protoconch; **c** detail of central teleoconch whorls. All phot. $\times 5$, details not to scale



Remarks: This new species occurs in sympatry with the superficially similar but much larger *B. jessica* and *B. arguta*.

Balfouria sordida (Neubert, 2002)

Fig. 13a–c, Fig. 14

2002 *Riebeckia sordida* Neubert, Fauna of Arabia, 19: 253, Fig. 20 (Samha Island, north-western slope of the escarpment below the plateau, vicinity of the cave, $12^{\circ} 09.61'N$ $53^{\circ} 02.47'E$, 600 m).

Measurements: holotype (SMF 322977): $H=24.84$; $D=5.27$; $W=12.00$. $n=9$: $H=22.87 \pm 1.19$; $H_{\min}=21.08$, $H_{\max}=24.99$; $D=5.36 \pm 0.26$; $D_{\min}=4.77$, $D_{\max}=5.72$; $W=11.50$.

Remarks: This species is adequately documented by Neubert (2002); for this reason, only the illustration of the species is repeated. No additional information is available since then.

Subfamilia Subulininae P. Fischer & Crosse, 1877

Genus *Allopeas* H. B. Baker, 1935

1935 *Lamellaxis (Allopeas)* H. B. Baker, Nautilus 48 (3): 84.

Diagnosis: Type species: *Bulimus gracilis* T. Hutton, 1834 by original designation.

Allopeas gracile (T. Hutton, 1834)

Fig. 15a–c

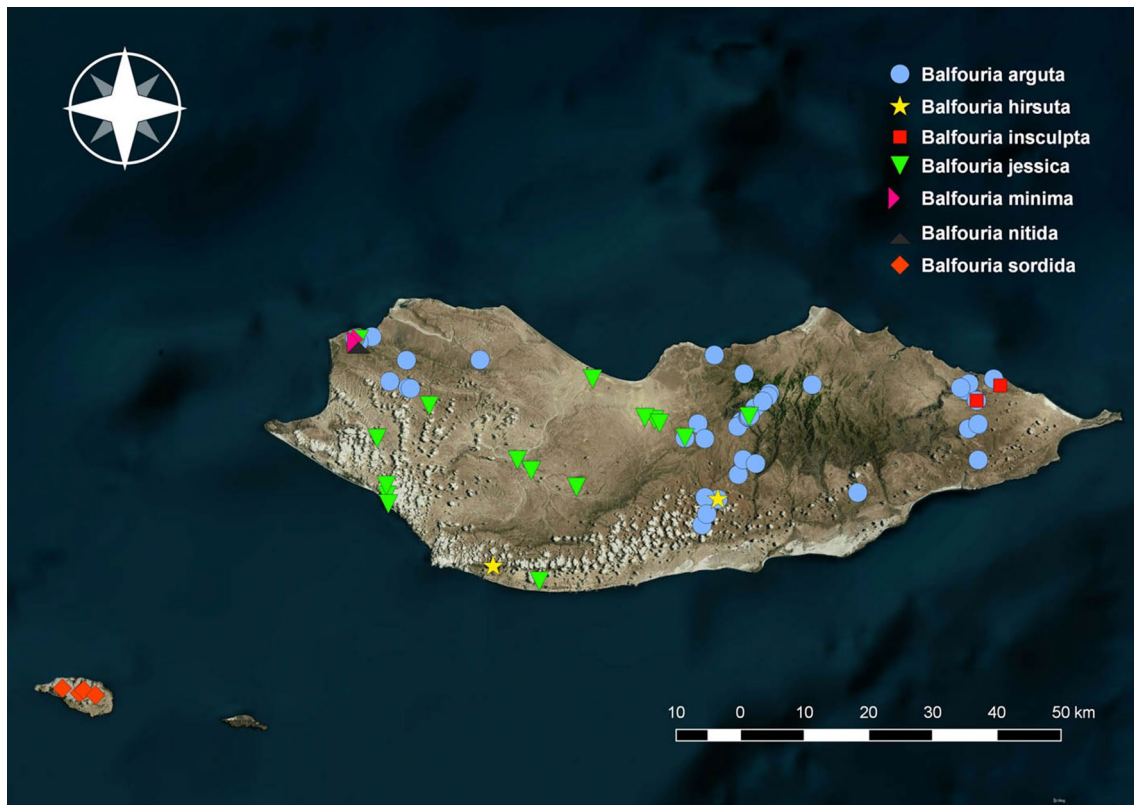


Fig. 14 Distribution records of all species of *Balfouria*

1834 *Bulimus gracilis* T. Hutton, Journal of the Asiatic Society of Bengal, 3: 93.

Specimens examined: roadside Hadiboh to Homhil, vegetated river floodplain of Wadi Mayero, 09.01.2001, leg. K. Van Damme, NMBE 563590.

Remark: A single specimen of this pan-tropical tramp species was found so far on Socotra Island. It is widespread on the southern coast of Yemen and Oman. The shell characters do not vary that much in this species, particularly the beaded sub-sutural line is well pronounced in the Socotran specimen. For more information refer to Neubert (1998: 374, Figs. 64, 67).

Genus *Zootecus* Westerlund, 1887

1887 *Zootecus* Westerlund, Fauna palaeart. Binnenconch. III: 3.

Diagnosis: Cylindrical to pupoid shell with a conical apex. The teleoconch surface is sculptured by wavy growth line. The aperture is considerably small with a thickened peristome (*Pupa insularis* Ehrenberg 1831 by subsequent designation by Pilsbry 1906).

Zootecus contiguus (Reeve, 1849)

Fig. 15d–f

1849 *Bulimus contiguus* Reeve, Conchologica Iconica, V: pl. 79, fig. 582 (Island of Sokotra, Mus. Cuming) [Sept. 1849].

1849 *Bulimus teres* L. Pfeiffer, Zeitschrift für Malakozoologie, 6 (6): 90 (Habitat Zanzibar orae Arabicae (Larg.), in insula Socotora (Cuming)) [non *Bulimus teres* Olivier 1801].

2003 *Zootecus contiguus*,—Neubert, Archiv für Molluskenkunde, 132 (1/2): 155, Fig. 3.

Remarks: This species was adequately documented by Neubert (2003a, b); for this reason, only the illustration of the species is repeated. No additional information is available since 2003.

3 Discussion

The taxonomic position of the genus *Balfouria* as a member of the Coeliacinae is remarkable. Next to *Balfouria*, this subfamily harbours the genus *Coeliaxis* Adams & Angas, 1865, with one extant and one fossil species. *Coeliaxis blandi* (L. Pfeiffer, 1854) lives in South Africa in a small restricted area, buried in the soil (Pilsbry 1906: 338). It should be stressed that the position of the genus *Riebeckia* in the same subfamily Coeliacinae is tentative as there are

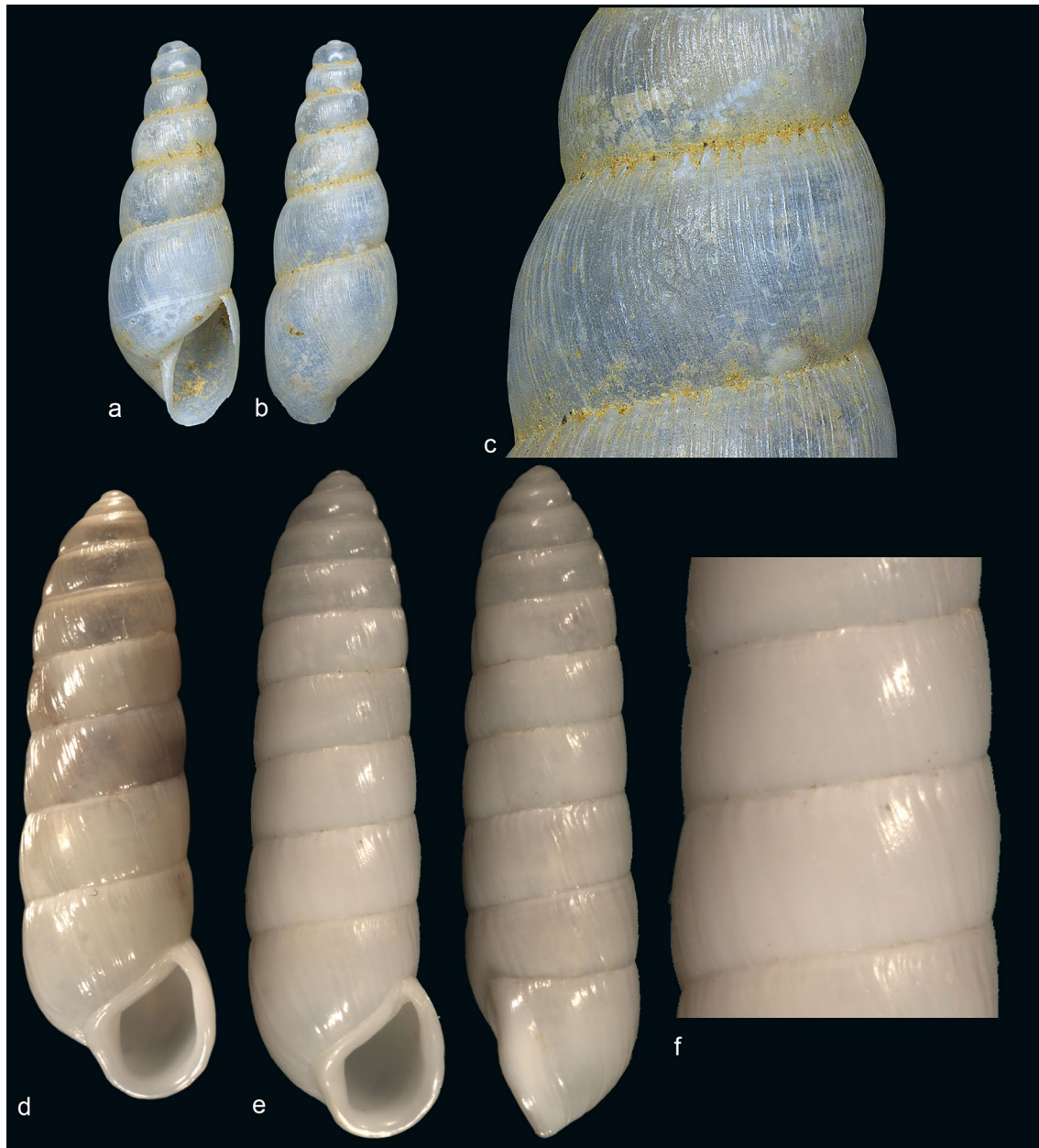


Fig. 15 a–f Species of Socotran Subulininae. a–c *Allopeas gracile* (T. Hutton, 1834). a, b NMBE 563590, Wadi Mayoero, $H=6.45$ mm; c details of teleoconch. d–f *Zootecus contiguus* (Reeve, 1849). d Syn-

type *Bulimus contiguus* NHM 1987.033, Abd el-Kuri, $H=12.8$ mm; e SMF 320188, Abd el-Kuri, $H=14.1$ mm, f details of teleoconch. Phot. a, b $\times 10$, d, e $\times 8$, details not to scale

no genetic data from any of the species available so far. It is also unclear whether *Riebeckia* as presented here forms a monophylum or not. The shells are not informative enough, and it might well be that the thin-walled species *R. adonensis* and *R. enodis* form a separate generic unit.

All species mentioned here are endemic to the Socotran archipelago with the exception of *A. gracile*, which is a global tramp species, and is also found in the closer surrounding like for example on the southern Arabian coast (Neubert 1998: 374, Figs. 64, 67). Remarkably, the whole

group is restricted to Socotra Island, there is only a single member of the group which lives on Samha Island. As can be seen on the maps, some are live restricted to small places like *B. insculpta*, a microendemic species for the Homhil area. A prominent place is again the western slope of the Jebel Ma'lih in the west of the island. Here, two hitherto unknown species of *Balfouria* could be detected. From the same area, the enigmatic microendemic *Cinnabarica excellens* Neubert 2009, is recorded. The slope is inhabited by five species of Achatinidae, and several other groups of

terrestrial molluscs as well, and can be considered a hotspot for this group. This compares to the five species of Achatinidae, which populate the Hagghier Mts.; however, this is a multifold time larger area.

Shells do not decompose that fast in the mainly limestone environment, and empty shells at all stages of erosion can be found scattered on the ground, sometimes in large deposits. This does not necessarily reflect a large population of living animals. In general, we have no idea on ecological requirements of the animals, the shape of their specific niches nor do we have any clue on the individual ages of the large shelled species, their life cycle, diet, reproductive strategy, etc. Living specimens are only very rarely encountered, and all species are obviously ground dwellers hiding in the soil or deep in cracks of rocks. An outstanding feature is the camouflage behaviour of almost all species within the genus *Balfouria*. All the shells show various shell adaptations serving the same purpose to function as adherence sites for clay: whether it is hairy periostracum as seen in *B. sordida* and *B. hirsuta*, or the beaded fine axial riblets as in *B. arguta* and *B. jessica*. The shells are usually covered by a mixture of soil and mucus, which can be as hard as concrete and even longer softening in water does not readily dissolve this layer. The advantage of such a layer, which is unknown in all the *Riebeckia* species, is obvious: the white shells are not directly exposed to the sun, and this probably supports water retention during arid climate periods. It also may serve to protect the animals against predators like birds. During aestivation, the species close their aperture with a diaphragm, which consists of calcified foam that probably can solidify during the drying process (Figs. 8e, 12f, g). However, there is always a small hole or a tube or a similar breathing device left that connects the animal to the outer world.

The species are endangered in many of their habitats by rats; cracked shells at any growth stages are very abundant in all populations of the larger species. It should be observed whether or not birds like the Socotra and Somali Starling also use these animals as prey species as can often be observed in *Achatinelloides*. However, these snails often aestivate on the stems of *Dracaena cinnabarica* or *Adenium socotrana* in the shaded area below the branching point, and thus are easily accessible for larger birds with a strong bill. Usually, species of Subulinidae are bottom dwellers, and thus probably better protected against bird predation.

Molluscs living on islands are often strictly endemic to this particular piece of land independent of the size of the islands, its climate, soil conditions and other factors. They are susceptible against any larger impact to their environment, and thus can well be used to document changes invisible to the untrained eye. For this reason, it is very important to collect as many data on the species as possible, being it biological, ethological or distributional data, and then

observe any changes to the system throughout a certain time period. With this *procedere*, the extinction risk of any species according to the IUCN redlisting process can be evaluated. Applying these methods to the molluscs of Socotra, a rather high percentage of species will be flagged with an elevated conservation concern. This is caused by the relatively high number of species, which are known from a single spot only or have a very restricted distribution. A second driving factor raising the extinction risk are threats directly affecting the animals, or severely impacting their habitats. It is a well-known fact that Socotra is completely overgrazed by livestock, with a number of adverse effects. Plants are food for many molluscs, so there is a certain competition in this field; but grazing also changes the species composition of the vegetation, so potential feeding plants are reduced; reduced vegetation diminishes the shading of the soil, which as a result dries up much faster. Plant species like particular robust grasses of small shrubs producing harder stalks and branches serve as possible place for aestivation, and these are not only reduced by animals but also by humans harvesting fire wood. Other serious threats are increasing urbanisation with reducing habitats for snails, asphalt road construction particularly in mountainous areas with inconsiderate backfill of gravel production, and intensive water retention with adverse effects on soil humidity. Another serious threat to molluscs is the overwhelmingly large population of rats on all islands of the archipelago, which substantially feed on the terrestrial molluscs. This is particularly the case on the islands of Samha, and more prominent, on Darsa, where actually each shell shows biting marks of rats. These islands have their local endemic species, and in combination with completely uncontrolled grazing, the populations of these snails would immediately be listed as critically endangered (CR). Other factors like climate change or increasing hurricane activities add on top of this impressive list of threats, not to speak of the political situation that hampers any control of land use and prevents sustainable use of the resources of the islands fostering conservation of nature for the sake of all, humans and animals.

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Compliance with ethical standards

Conflict of interest There is no conflict of interest.

References

- Baker HB (1935) Jamaican land snails. *Nautilus* 48(3):83–88
- Bezděk J, Purchart L, Král K, Hula V (2012) List of local Socotran geographical names used in entomological literature. *Acta Entomologica Musei Nationalis Pragae* 52(supplementum 2):27–67
- Bouchet P, Rocroi JP, Hausdorf B, Kaim A, Kano Y, Nützel A, Parkhaev P, Schrödl M, Strong EE (2017) Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia* 61(1–2):1–526
- Crosse H (1884) Faune malacologique terrestre et fluviatile des îles de Socotora et d'Abd-el-Goury. *J Conchyliol* 32(4):341–375
- Fontanilla IK, Naggs F, Wade CM (2017) Molecular phylogeny of the Achatinoidea (Mollusca: Gastropoda). *Mol Phylogenet Evol* 114:382–385
- Godwin-Austen H (1881) On the land shells of the island of Soqotra, collected by Prof. Bayley Balfour. Part II: Helicaceae. *Proc Zool Soc Lond* 1881:801–812
- Hutton T (1834) On the land shells of India. *J Asiatic Soc Bengal* 3:85–93
- Martens E (1881) Land-Schnecken von Sokotora. *Nachrichtsblatt der deutschen malakozoologischen Gesellschaft* 13(10):134–138
- Martens E (1883) III Mollusken von Sokotra. *Conchologische Mitteilungen* 2(3/4):140–152
- Neubert E (1998) Annotated checklist of the terrestrial and freshwater molluscs of the Arabian Peninsula. *Fauna Arab* 17:333–461
- Neubert E (2002) The continental malacofauna of Arabia and adjacent areas. I. Terrestrial molluscs of Samha and Darsa Islands (Al-Ikhwan), Socotra Archipelago, Yemen. *Fauna Arab* 19:245–259
- Neubert E (2003a) *Otopoma* Gray 1850—a few words to add to a 150 years old debate. *Archiv für Molluskenkunde* 132(1/2):93–96
- Neubert E (2003b) The continental malacofauna of Arabia and adjacent areas, II. The genus *Zootecus* Westerlund 1887. *Archiv für Molluskenkunde* 132(1/2):153–160
- Neubert E (2004) The continental malacofauna of Arabia and adjacent areas, III. The Streptaxidae of Soqotra, with description of seven new species (Gastropoda: Pulmonata: Streptaxidae). *Archiv für Molluskenkunde* 133(1/2):173–183
- Neubert E (2005a) The continental malacofauna of Arabia and adjacent areas, IV. Revision of the family Cerastidae in the Soqotran Archipelago, I: The genus *Passamaella* L. Pfeiffer 1877, with description of a new genus and species (Gastropoda: Pulmonata: Cerastidae). *Archiv für Molluskenkunde* 134(1):21
- Neubert E (2005b) The continental malacofauna of Arabia and adjacent areas, V. Revision of the family Cerastidae in the Soqotran Archipelago, II: The genera *Achatinelloides* G. Nevill 1878 and *Microscintilla* Neubert 2002, with description of a new genus and species (Gastropoda: Pulmonata: Cerastidae). *Archiv für Molluskenkunde* 134(2):223–259
- Neubert E (2009) The continental malacofauna of Arabia and adjacent areas. VI. Pomatiidae of Arabia, Socotra and northeast Africa, with descriptions of new genera and species (Gastropoda: Caenogastropoda: Littorinoidea). *Fauna Arab* 24:47–127
- Pilsbry HA (1906) Achatinidae: Stenogyrinae and Coeliarinae. In: Tryon, GW (ed) *Manual of Conchology*, vol 18, pp 1–357, 51 plates. Philadelphia
- Reeve LA (1848–1850) Monograph of the genus *Bulimus*. *Conchologica Iconica* 5:58–84
- Salvat B (1969) Mollusques terrestres de Socotra et d'Abd-El-Kuri (Océan Indien) récoltes de M. Lavranos. *Bulletin du Muséum National d'Histoire Naturelle Zoologie* 41(3):743–751
- Smith EA (1897) On some new species of land shells from the island of Soqotra. *J Malacol* 6(3/4):33–38
- Smith EA (1903) The Land and freshwater shells of Sokotra and Abd el-Kuri. In: Forbes HO (ed) *The Natural History of Sokotra and Abd-el-Kuri: Being the report upon the results of the conjoint expedition to these islands in 1898–9*. Special Bulletin of the Liverpool Museums, Liverpool, pp 111–159
- Wade CM, Mordan PB, Naggs F (2006) Evolutionary relationships among the Pulmonate land snail and slugs (Pulmonata, Stylommatophora). *Biol J Linn Soc* 87:593–610
- Westerlund CA (1887) Fauna der in der paläarktischen Region (Europa, Kaukasien, Sibirien, Turan, Persien, Kurdistan, Armenien, Mesopotamien, Kleinasien, Syrien, Arabien, Egypten, Tripolis, Tunesien, Algerien und Marocco) lebenden Binnenconchylien. *Gen Buliminus Sesteria Pupa Stenogyra Cionella* 3:1–183

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