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Palaeogene continental molluscs of Oman

Eike Neubert & Dirk van Damme

ABSTRACT

The Zalumah Formation in Dhofar, Oman, of Terminal Eocene age contains a highly diversified and well preserved land and freshwater snail fauna. This is the earliest known terrestrial malacofauna of the Afrotropical Region. The fossil assemblages show close affinities with the Modern intertropical African fauna and seem as well to show distinct links with the snail fauna that radiated on Soqotra after the Soqotra Plate broke away from Oman in Oligocene times. Three freshwater gastropods belonging to the Ampullariidae and eight species of land snails belonging to several tropical families are described here. The following species are described as new: *Lanistes tricarinatus* sp. nov., *Lanistes thaytinitiensis* sp. nov., *Cyclotopsis praecursor* sp. nov., *Succinea omanensis* sp. nov., *Limicolaria omanensis* sp. nov., *Achatina sculpturata* sp. nov., *Cerastus pseudoena* sp. nov., *Cerastus praeinsularis* sp. nov., *Trochozonites arabica* sp. nov.

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Keywords: Palaeogene, ancestral fauna, aequatorial, Late Priabonian age, Eocene-Oligocene boundary, faunal continuum, Soqotra Archipelago.

Introduction

During the late 1980s, a team of French and Omani palaeontologists under the direction of Hubert Thomas (MNHN) started to investigate the rich vertebrate bearing deposits of the Shizar Member, Ashawq Formation at Taqah and Thaytiniti (Dhofar, Oman) (Thomas & al. 1989, 1999). The age of these freshwater/brackish water deposits has recently been revised to the earliest Oligocene (ca. 34 Ma) (Seiffert 2006).

Part of the underlying Zalumah Formation, of Terminal Eocene age, is also of freshwater/brackish origin. This formation was known to contain a diversi-

fied fossil freshwater and terrestrial malacofauna. But of this fauna only a simple and largely erroneous species list was available (Roger & al. 1989, 1994). The original molluscan samples remained undescribed and were subsequently discarded (Roger, in litt. 2012). In the late 1980s, the members of the Thomas group focused exclusively on the Ashawq Formation and had no interest in the snail fossils. Finally, only a handful of snail fossils, picked up by Martin Pickford, member of the Thomas team, were preserved. These were passed on to D. van Damme in 1994 but remained largely unstudied. It was by sheer coincidence, due to the cooperation of Eike Neubert and Kay van Damme on the Modern fauna of Soqotra, that E. Neubert was able to study these Omani fossils. The presence of a representative of the pomatiid genus *Cyclotopsis*, a close relative of the land snail taxa with an endemic radiation on Soqotra, in the small collection was considered to be of major zoogeographic interest. The Soqotran plate originally was part of Oman and broke away from the Dhofar region during Oligocene times (van Damme 2009). Hence, the fossil malacofauna of the Zalumah Formation could contain the ancestors from which the Soqotra fauna originated. Thus, the two present authors decided to team up and to visit Oman for a short trip to make a more extensive collection of fossils. This article contains the taxonomical descriptions of the fossil specimens collected during this visit, and presents some zoogeographic and evolutionary conclusions.

Material and methods

Material

The fossil material here described was mainly collected in the Wadi Darbat region (along the road between 17.2514°N 53.9826°E and 17.2586°N 54.0060°E, ca. 30 km NNW of Salalah in February 2012 (Figs. 1–3). In this region the Zalumah Formation is exposed as erosional remnants along an E-W trending fault system over a length of ca. 30 km and a width of 1–3 km as the locally youngest Palaeogene formation. The outcrops were identified based on the geological map sheet Habarut. The authors attempted to also find the more westerly situated exposure at Thaytiniti but failed. Only the small sample collected by M. Pickford in the early 1990's is hence incorporated in the present study.

In both regions the fossiliferous beds have an accumulated thickness of ca. 20–30 m, some beds are very poor in molluscs, containing virtually *Lanistes* only, while a few layers mainly consist of snail fossils in an excellent

Figs. 1–2: Outcrops of the white fossiliferous beds in the Zalumah Formation at Wadi Darbat, Dhofar, Oman. Photos: R. Bonifer.

1

2

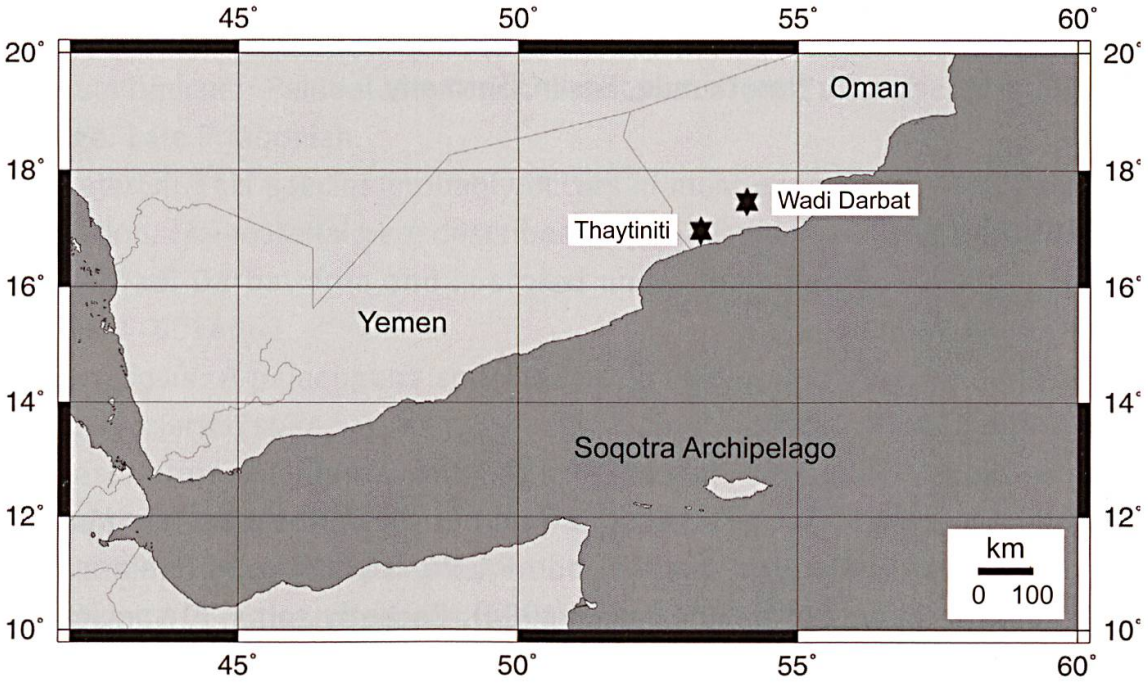


Fig. 3: Map showing the position of the localities.

state of preservation, at least in the Wadi Darbat region. In the Thaytiniti area the fossils are partly dissolved, the shell sculpture gone or barely visible. In both regions biomicritic white to beige paludal limestone is the main matrix in which the fossils are preserved. On the basis of the presence of the charophyte *Rabdochara* aff. *cauliculosa,* the Zalumah Formation is considered to be of Terminal Eocene age, i.e. Late Priabonian (34–35 Ma) (Sénut 1988).

All specimens were exported under a license released by the Directorate General of Minerals of the Sultanate of Oman, Muscat, and are now stored at the NMBE.

Method

The matrix around the fossils was removed as much as possible using fine chisels and a HW25 pneumatic air scribe. Measures taken were total length (H) and Width (W) of the shell and height (h) and width (w) of the aperture (all measurements are in mm; Wh = number of whorls).

Photos of larger fossils were taken using a Canon 50D, small objects and detail photos were made by using the multifocus technique with a Leica DFC 465; photos were then processed with the ImageAccess software.

Abbreviations used:

MNHN	Muséum national d'Histoire naturelle, Paris, France
NHMUK	Natural History Museum, London, United Kingdom
NMBE	Naturhistorisches Museum der Burgergemeinde Bern, Switzerland
SMF	Research Institute Senckenberg, Frankfurt am Main, Germany
ZMB	Museum für Naturkunde, Berlin, Germany

Systematic part

Family Ampullariidae

Genus ***Pila*** RÖDING, 1798

The genus recently occurs all over Africa from the Nile Delta to northern Mozambique and also in Madagascar, the Indo-Pacific islands and S. Asia including southern China and Japan (Brown 1994). Recently some 30 species are known. Most *Pila* species live in swampy habitats such as floodplains and are able to aestivate in the mud during the dry season. The earliest African fossils

Fig. 4: *Pila* sp. Wadi Darbat NMBE 5018961, frontal and apical view. The remains of the operculum can still be seen in the frontal view, lower part of the aperture.

date from the Lower Cretaceous of Niger, though it is impossible to ascertain if these belong to the genus *Pila* (Palaeotropical realm) or to the genus *Pomacea* PERRY, 1810 (Neotropical realm but presently introduced in N. America and S. Asia) or should be considered the ancestral stem of both taxa due to the near identical shell morphology. It is here assumed that the taxa had split in Eocene times.

Pila sp. (Fig. 4)

Stratum typicum: Paludal biomicritic limestones of the Zalumah Formation.

Age: Late Priabonian.

Material: This species probably occurs in most exposures of the Zalumah Formation. The material here described was collected in 2012 by both authors in the Wadi Darbat area and is stored under the catalogue number NMBE 5018961–5018962.

Diagnosis: A palaeogene species of *Pila* with a very globose shell and a slightly exserted spire.

Description: Medium sized *Pila* species with dextral very globose shell with a short spire consisting of five evenly rounded, strongly convex whorls, not flattened but slightly depressed at the deep suture; aperture very large, occupying 4/5 of the total height; umbilical margin strongly reflected; umbilicus relatively narrow; shell surface smooth with regular fine growth lines only.

Measurements: Specimen figured: H = 59 mm, W = 52 mm, h = 46 mm; w = ca. 30 mm; a second relatively well preserved specimen but with the lower part of the mouth missing measures as follows: H = 67 mm, W = 55.4 mm; h = 45 mm; w = 32.3 mm.

Remarks: Referred to by Roger & al. (1994) as *Pila* cf. Sudan form, by which these authors mean *P. wernei* (PHILIPPI, 1851) (terra typica: Sudan). This Modern African species indeed superficially resembles the Eocene Omani species as to the general form and small spire but distinguishing features such as the strongly malleate surface and spiral lines (Brown 1994) are absent in the fossils. In addition, *P. wernei* reaches a size of 115 × 103 mm, hence it is about twice the size of the Omani specimens. At the moment it can be concluded that the fossils cannot be placed in *P. wernei* or any other known Modern or fossil African *Pila*. They actually quite closely resemble the Asian *Pila ampullacea* (LINNAEUS, 1758). Better material is necessary before it can be decided if the fossils do belong to a still extant (Asiatic) species or that it is a distinct one. In the lower part of the Zalumah Formation large gastropods occur (ca. 90 × 80 mm), resembling a *Pila* species with a relatively high spire, but these shells probably belong to the marine family Ampullinidae COSSMANN, 1919 (Naticoidea).

Genus ***Lanistes*** MONTFORT, 1810

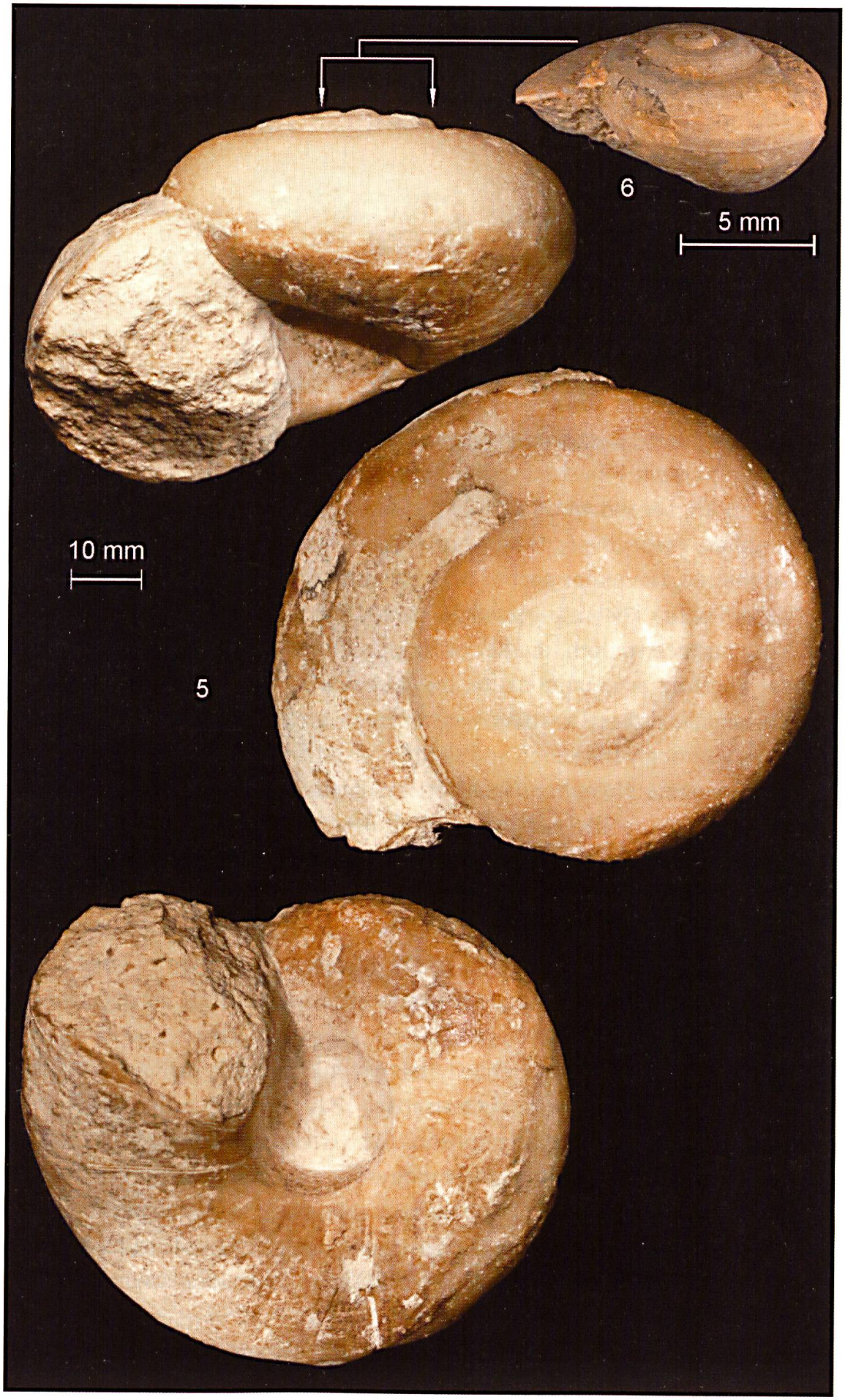
Species with a sinistral shell but the animals are dextral (hyperstrophic growth). Modern occurrence is limited to Africa (Nile Delta to Natal) and Madagascar (Brown 1994), fossil occurrence also includes Arabia (this article). The genus is hence exclusively Afrotropical (Africa + Arabia). The ampullariid genus *Mesolanistes* YEN, 1945 from Cretaceous-Palaeogene deposits in N. America and S. Asia bears no apparent relationship except that it is also sinistral.

Time range of *Lanistes*: (Palaeocene) Eocene-Modern (Mayer-Eymar 1893; Abbas 1967; Gautier 1973).

Lanistes tricarinatus sp. nov. (Figs. 5–6)

Type specimens: Holotype NMBE 5018963; paratypes NMBE 5018964–5018965, 5019037.

Figs. 5–6: *Lanistes tricarinatus* sp. nov. Fig. 5: Wadi Darbat, holotype NMBE 5018963 in frontal, apical and ventral view. Fig. 6: Parataype NMBE 5018964 showing a specimen with the carinae.


6
5 mm
10 mm
5

Type locality: Wadi Darbat, Dhofar, Oman.

Stratum typicum: Paludal biomicritic limestones of the Zalumah Formation.

Age: Late Priabonian.

Material: This species probably occurs in most exposures of the Zalumah Formation. The material here described was collected in 2012 by both authors in the Wadi Darbat area.

Etymology: Named after the three carinae on the third whorl.

Diagnosis: A palaeogene species of *Lanistes* of the *L. carinatus* type, i.e. characterized by a depressed shell with a peripheral carina on the upper whorls and a very large open umbilicus. Such shells were formerly ranged in the subgenus *Lanistes* s.str. (Mandahl-Barth 1954).

Description: With a diameter of 77.3 mm this is the largest *Lanistes* species known, but most specimens do not exceed 60 mm. Depressed shell consisting of 5¾ rapidly increasing whorls; spire little exserted, apex blunt; first whorl smooth, second whorl with two sharp keels at the base and the top of the periphery respectively, third whorl with one keel at the base and a double keel at the top, the upper part of these whorls sunk below the rim formed by the upper keel or keels; fourth whorl evenly rounded, except for a faint central keel; surface smooth, marked with growth-lines only, no spiral sculpture visible; aperture acuminate ovate, pointed at the base, outer margin evenly curved, umbilical margin straight; umbilicus wide, deep and funnel-shaped, bound by a strongly thickened and slightly raised angle; operculum unknown.

Measurements: Holotype (Fig. 5): H = 45.8 mm; W = 77.3 mm, h = 42.2 mm; w = 34.0 mm; Paratype NMBE 5018965: H = 34.8 mm; W = 49.2 mm; h = 30 mm; w = 23.3 mm.

Remarks: The record by Roger & al. (1994) of *Lanistes subcarinatus* (nomen nudum) in their geological study of the Dhofar region seems to pertain to this species. It is the most common of the few fresh water snails present in the Zalumah Formation. In large specimens the apex is strongly eroded and the carination no longer visible.

The Palaeogene fossils mentioned from Egypt and Sudan, namely *L. antiquus* Mayer-Eymar, 1893; *L. olivieri* Montfort, 1810, and *L. sodaensis* Abbass, 1967 (Abbass 1967) and *L. grabhami* Cox, 1933, redescribed by Gautier (1973) have all the same *L. carinatus* morphology. They do differ from *L. tricarinatus* sp. nov. by their smaller size. But these fossils are badly preserved (mainly inner moulds) and the ornamentation on the first whorls is not visible. It hence cannot be excluded that some of that NE African material may pertain to *L. tricarinatus*.

Fig. 7: *Lanistes thaytinitiensis* sp. nov. Thaytiniti, holotype NMBE 5018966 in frontal, apical and ventral view.

Lanistes thaytinitiensis sp. nov. (Fig. 7)

Type specimens: Holotype NMBE 5018966; paratypes NMBE 5018967–5018969, MNHN/2, SMF 340185/2.

Type locality: Thaytiniti, Dhofar, Oman.

Stratum typicum: Paludal biomicritic limestones of the Zalumah Formation.

Age: Late Priabonian.

Material: This species was only recovered from the Zalumah exposures at Thaytiniti. Collected by M. Pickford during one of the palaeontological missions led by H. Thomas in 1988–1990.

Etymology: named after the type locality.

Diagnosis: A palaeogene species of *Lanistes* characterized by the discoid shape and flattened upper side.

Description: Medium sized *Lanistes*; discoid shell consisting of 4½ whorls with virtually no exserted spire, apex pointed; upper part of the gradually increasing whorls completely flattened, lower part convex, forming a peripheral angle accentuated by a ridge; at the base the periphery of the whorls form a second angle with the flattened walls of the umbilicus, in which the whorls wind downwards (or upwards being hyperstrophic) in a regular spiral; aperture horizontal at the top, the outer margin convex, the upper part of the inner margin, connected to the shell, concave and the free lower part straight, basal margin pointed; growth lines regular and fine, no spiral sculpture; operculum unknown.

Measurements: Holotype (Fig. 7): H = 12.5 mm; W = 38.2 mm; h = 12.0 mm; w = 11.5 mm. Paratype (NMBE 5018967): H = 11.2 mm; W = 32.2 mm; h = 11.2 mm; w = 10.3 mm.

Remarks: We did not find any fossils of this species in the Salalah region, while in the Zalumah exposures at Thaytiniti is seems to be the most common of the two *Lanistes*. This indicates either a difference in age or in environmental conditions between these two sites. *Lanistes thaytinitiensis* sp. nov. is the only flattened discoid *Lanistes* species known.

Family Pomatiidae

Genus ***Cyclotopsis*** BLANFORD, 1864

Having been used as a dumping ground for several Indopacific pomatiid species, the range of this genus has recently been restricted to a few species living in India today (Neubert 2009). This is the first fossil species recorded for this genus, which thus has a time range from Oligocene to Modern.

Cyclotopsis praecursor sp. nov. (Figs. 8–9)

Type specimens: Holotype NMBE 5018970; paratypes NMBE 5018971–5018973, MNHN/25, SMF 340184/25; paratypes Wadi Darbat, NMBE 5018974, 5019038–5019043.

Type locality: Thaytiniti, Dhofar, Oman.

Stratum typicum: Paludal biomicritic limestones of the Zalumah Formation.

Age: Late Priabonian.

Material: This species is very abundant at Thaytiniti and Wadi Darbat.

Etymology: praecursor from Latin for predecessor, a noun in apposition.

Diagnosis: A fossil species of *Cyclotopsis* with a slightly elevated spire and an operculum with a lamella-like coiled spiral.

Description: Shell much broader than high, spire slightly elevated; protoconch relatively large, consists of 2 whorls, surface sculpture not preserved; teleoconch of 3.5–4 rapidly increasing whorls; surface sculpture of 3–5 strong spirals (only preserved on the upper whorls); last whorl only slightly descending before the aperture; aperture almost circular, with a slightly thickened lip; umbilicus very large, broad dish-like, umbilical walls very probably smooth; operculum multispiral, spiral consisting of a broad raised lamella of at least 3 whorls.

Measurements: Holotype (Fig. 8): H = 6.73 mm; W = 9.18 mm; h = 4.42 mm; w = 4.25 mm; Wh = 5.5.

Remarks: Roger & al. (1994) probably refer to eroded specimens of this species as 'cf. *valvata*'. The preservation state of the specimens from the type

Figs. 8–10: *Cyclotopsis praecursor* sp. nov. Fig. 8: Thaytiniti, holotype NMBE 5018970 in frontal, apical and ventral view; Fig. 9: Wadi Darbat, paratype NMBE 5018974 in frontal, apical and ventral view; Fig. 10: *Cyclotopsis semistriatum* (SOWERBY, 1843), syntype NHMUK 20030591, India, Poona.

locality in Thaytiniti is quite poor and mainly consists of internal casts. However, in a few cases, remains of the shells themselves are preserved, allowing reconstructing of some details of the surface sculpture. These specimens

display the same teleoconch sculpture as the specimens from Wadi Darbat (Fig. 9), where the preservation state is much better (but no specimen with an operculum could be traced there).

This fossil species is placed in the extant genus *Cyclotopsis*, because it is almost indistinguishable from the few species from India (for comparison see the syntype of *Cyclostoma semistriatum* SOWERBY, 1843 (Fig. 10), the type species of *Cyclotopsis*). It shares autapomorphic details of umbilicus and operculum together with the spiral sculpture of the teleoconch. It differs from most of the Soqotran species of *Dioscopoma* NEUBERT, 2009, which usually have a reticulate surface sculpture, a more narrow umbilicus, and an operculum with a flat sutural line and not a raised spiral; also, most of the species of *Dioscopoma* display a spiral sculpure on the inner umbilical wall, which is very probably smooth in *C. praecursor* sp. nov. Today, the Dhofar area is inhabited by two species of the genus *Rochebrunia* BOURGUIGNAT, 1881, but these have larger shells with a closed umbilicus and an almost smooth operculum. For a more detailed discussion of the pomatiid genera and species of the area see Neubert (2009), and for pomatiid operculum structure Wilmsmeier & Neubert (2012).

Family Succineidae

Succinea omanensis sp. nov. (Figs. 11–12)

Type specimens: Holotype NMBE 5018975; paratypes NMBE 5018976, 5019044; paratypes Thaytiniti NMBE 5019045–5019047.

Type locality: Wadi Darbat, Dhofar, Oman.

Stratum typicum: Paludal biomicritic limestones of the Zalumah Formation.

Age: Late Priabonian.

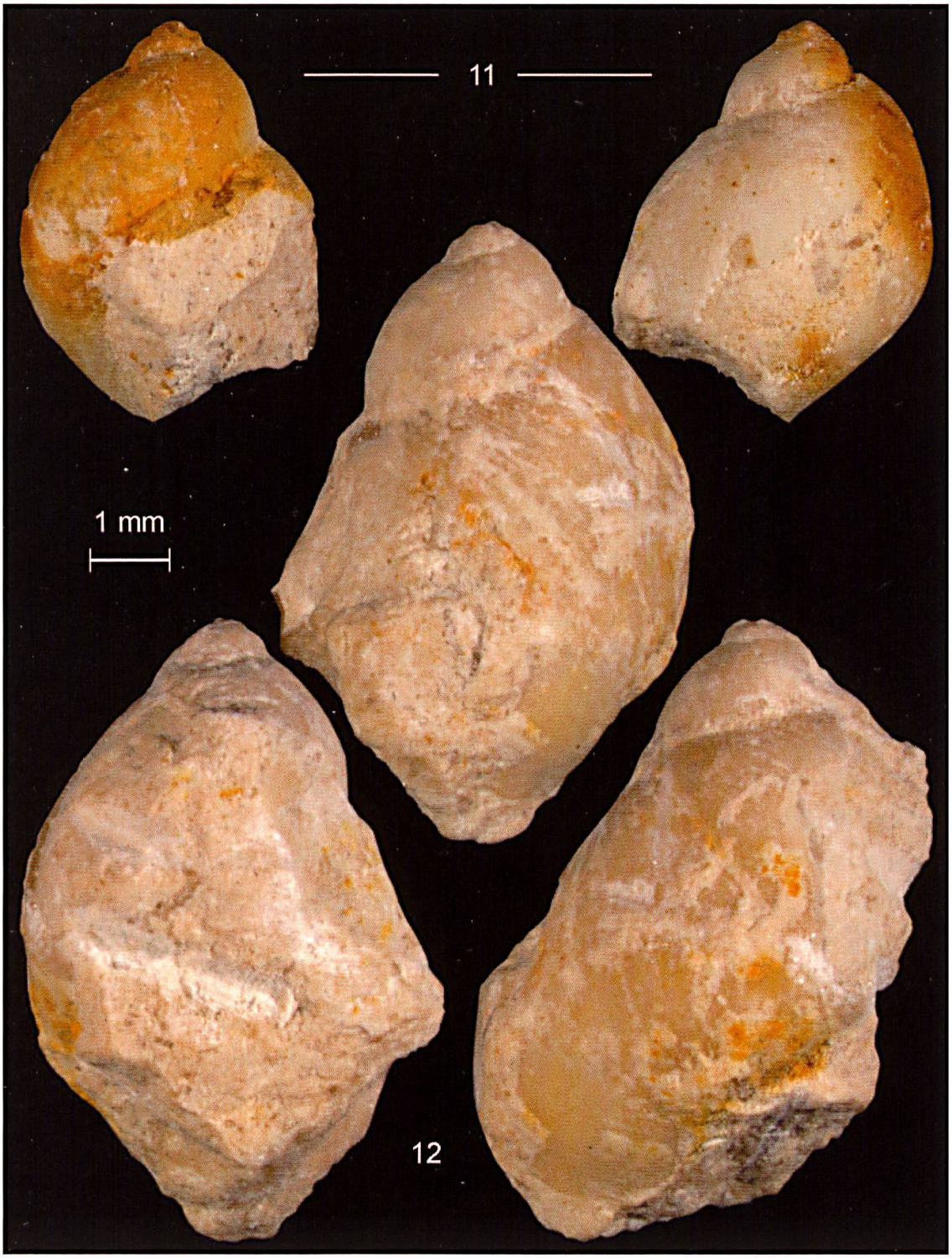
Material: Only known from the type locality.

Diagnosis: A small shelled member of *Succinea*, with a rapidly growing teleoconch and the last whorl exceeding half of the complete height of the shell.

Etymology: *omanensis* refers to the provenance of this new species.

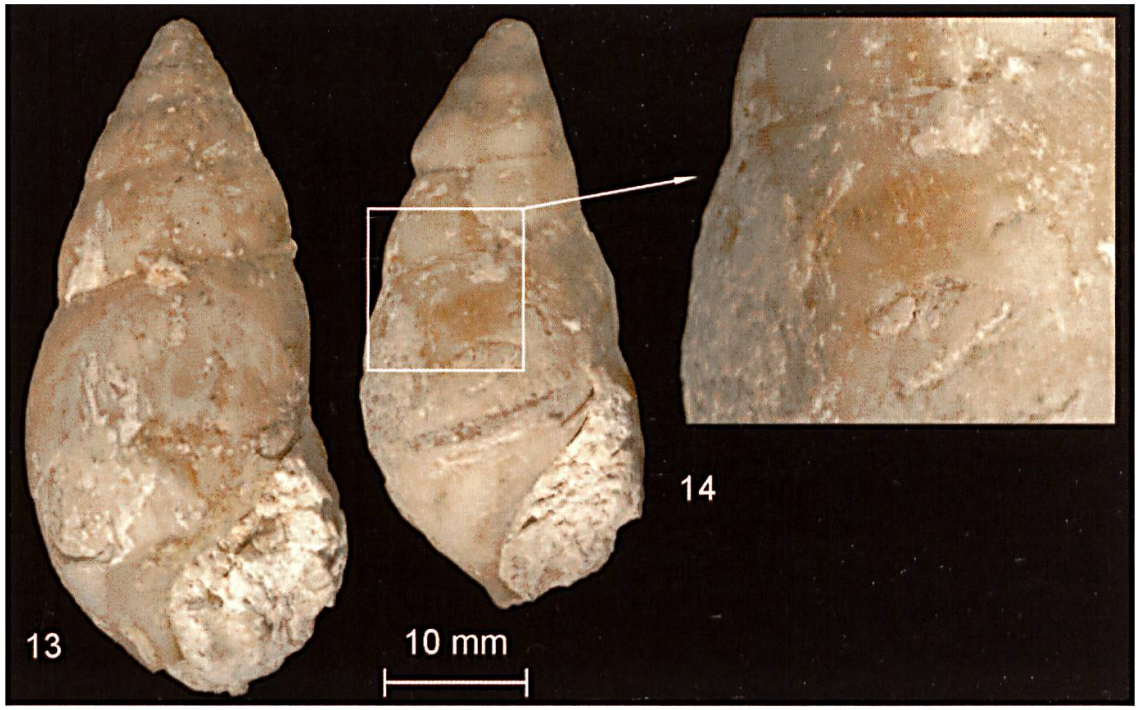
Description: Small shells with a rapidly growing teleoconch, shells probably reach a total shell length of about 10 mm; preserved paratype shell with almost 4 whorls, protoconch eroded; suture shallow, well-marked and somewhat reinforced, subsuturally slightly crenulate; teleoconch covered by a regular pattern of fine, axial growth riblets; last whorl amply open, constituting more than half of the complete height of the shell.

Measurements: Holotype (Fig. 11): H = 4.94 mm; Wh < 3; paratype (Fig. 12): H = 7.67 mm; Wh > 3.5.



Figs. 11–12: *Succinea omanensis* sp. nov. Fig. 11: Wadi Darbat, holotype NMBE 5018975 in frontal and ventral view. Fig. 12: Paratype NMBE 5018976, same locality.

Remarks: It has to be stressed that the affiliation of this species to the extant genus *Succinea* is debatable. However, the shells are in fact quite similar to a number of Modern species within *Succinea* and related genera, which today are defined by using anatomical and molecular data, inapplicable to fossils. Creating a fossil genus to harbour these shells seems not to be advisable as



Figs. 13–14: *Limicolaria omanensis* sp. nov. Fig. 13: Wadi Darbat, holotype NMBE 5018977 in frontal view. Fig. 14: Paratype NMBE 5018980, same locality, detail not to scale.

long as material is so meagre and good arguments in favour of such a genus are available. Today, there are only two records of an extant succineid species from the Arabian Peninsula, i.e. *Quickia concisa* (Morelet, 1848). The shell of this species is smaller, and it has a deep and simple suture, and thus cannot be identified with the fossil specimens from Wadi Darbat (Neubert 1998: 370, fig. 63).

Family Achatinidae

Limicolaria omanensis sp. nov. (Figs. 13–14)

Type specimens: Holotype NMBE 5018977; paratypes NMBE 5018978–5018979, MNHN/5; paratypes Wadi Darbat NMBE 5018980–5018981, 5019048–5019049.

Type locality: Thaytiniti, Dhofar, Oman.

Stratum typicum: Paludal biomicritic limestones of the Zalumah Formation.

Age: Late Priabonian.

Material: This species is also known from the fossil beds of Wadi Darbat.

Etymology: *omanensis* to describe the provenance of this new species.

Diagnosis: A medium sized fossil species of *Limicolaria* Schumacher, 1817, with a peculiar teleoconch pattern of axial riblets and a sutural cord.

Description: Shell turreted, fusiform; small protoconch (only preserved as stone core); teleoconch of ca. 7 whorls; whorls slightly rounded, with a sculpture of fine

axial riblets running over the complete whorl; suture moderately deep, with a subsutural cord; below the cord, a small zone of spirals crossing the riblets and thus producing a characteristic reticulate pattern; aperture oval, upper right part acute.

Measurements: Holotype (Fig. 13): H = 46.6 mm; W = 21.75 mm; h = 19.7 mm; w = 12.5 mm; Wh = 8; parataype (Fig. 14): H = 40.56 mm.

Remarks: The species is mentioned by Roger & al. (1994) as *Bulimus*. The supraspecific affiliation of this species may be debatable. The endemic subulinid genus *Riebeckia* MARTENS, 1883 from Soqotra comprises several very large species, which are conchologically quite close to the afrotropical achatinoid *Limicolaria* species. They differ from those by their truncate columella, which is rounded and usually continuous in *Limicolaria*. Moreover, the species of *Riebeckia* are either smooth, or have a faint pattern of a reticulate sculpture on the teleoconch. None of those species has a subsutural cord nor clear axial riblets. Unfortunately, there is no fully grown specimen of *Limicolaria omanensis* sp. nov. with a preserved lower aperture, so it is not possible at the moment to judge about this character state. At the time being, this species is confined to the Achatinidae because of the resemblance in their teleoconch sculpture with some extant *Limicolaria* species from Eastern Africa.

Achatina sculpturata sp. nov. (Fig. 15)

Type specimens: Holotype NMBE 5018982; paratypes NMBE 5018983–5018984.

Type locality: Wadi Darbat, Dhofar, Oman.

Stratum typicum: Paludal biomicritic limestones of the Zalumah Formation.

Age: Late Priabonian.

Material: This species is only known from its type locality.

Etymology: *sculpturata* refers to the quite unusual (for *Achatina*) teleoconch sculpture of this new species.

Diagnosis: A medium sized fossil species of *Achatina* LAMARCK, 1799, with a peculiar teleoconch pattern of axial riblets and a sutural cord.

Description: Shell medium sized, fusiform; protoconch comparatively small (only preserved as a stone core); teleoconch of ca. 7 whorls; whorls only slightly rounded, with a sculpture of fine axial ribs running over the complete whorl, ribs usually granular; suture moderately deep, strongly reinforced by a subsutural cord; ribs do not fuse with the cord; aperture obliquely lunulate, narrow, lower part of columella not preserved.

Measurements: Holotype (Fig. 15a): H = 66.9 mm; Wh > 7.

Remarks: So far, this species is only recorded from Wadi Darbat, where it occurs sympatrically with *Limicolaria omanensis* sp. nov. Even juvenile or subadult specimens of both species can be separated by the size of the proto-

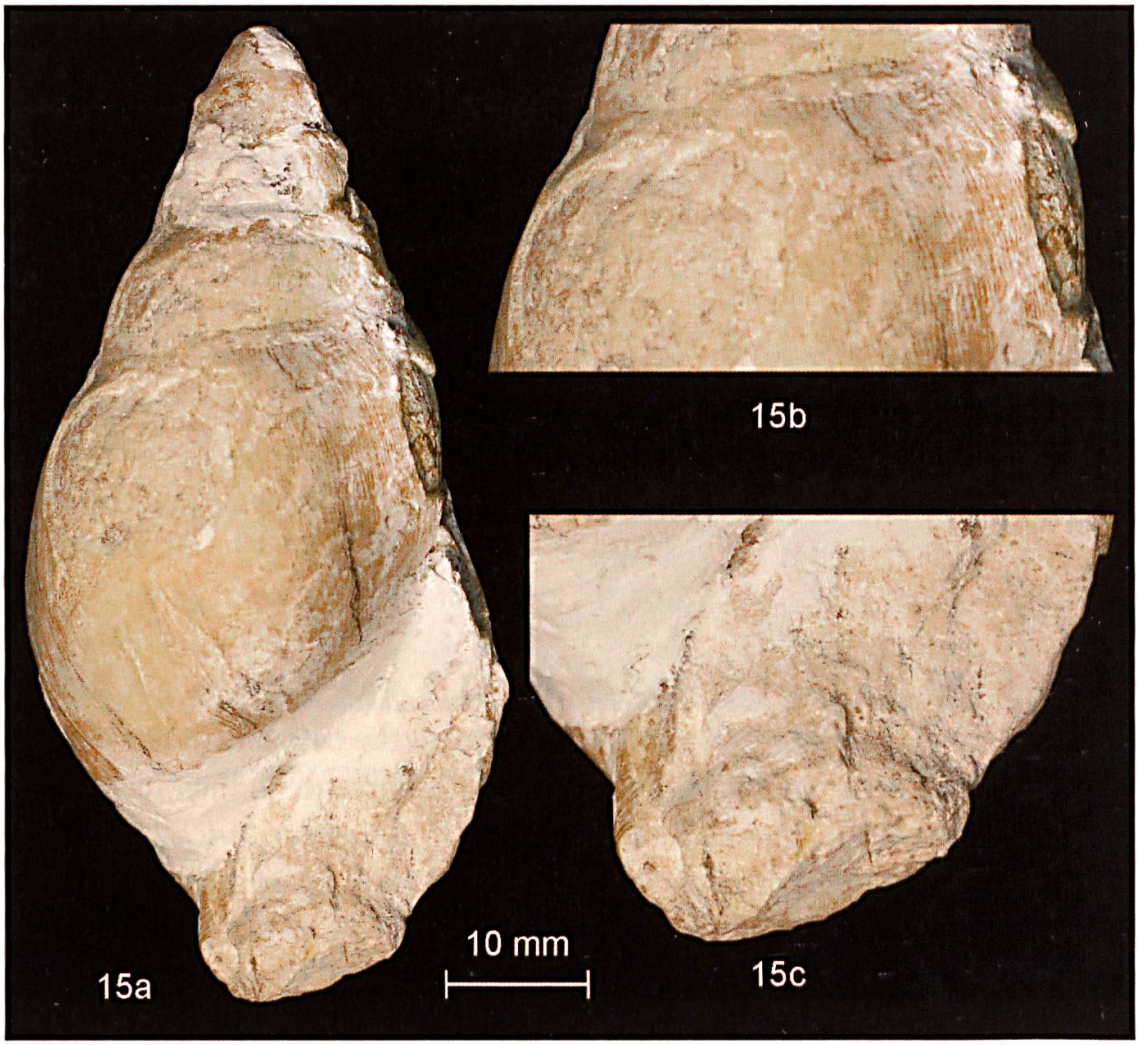


Fig. 15a: *Achatina sculpturata* sp. nov. Wadi Darbat, holotype NMBE 5018982 in frontal view. Figs 15b and 15c show details of the holotype shell; details not to scale.

conch (larger in *A. sculpturata* sp. nov.), the more slender upper teleoconch of *L. omanensis* sp. nov., and the smaller size of adult specimens. It is quite interesting to see the similarity in the surface sculpture, but the formation of the subsutural cord also helps to differentiate the two species.

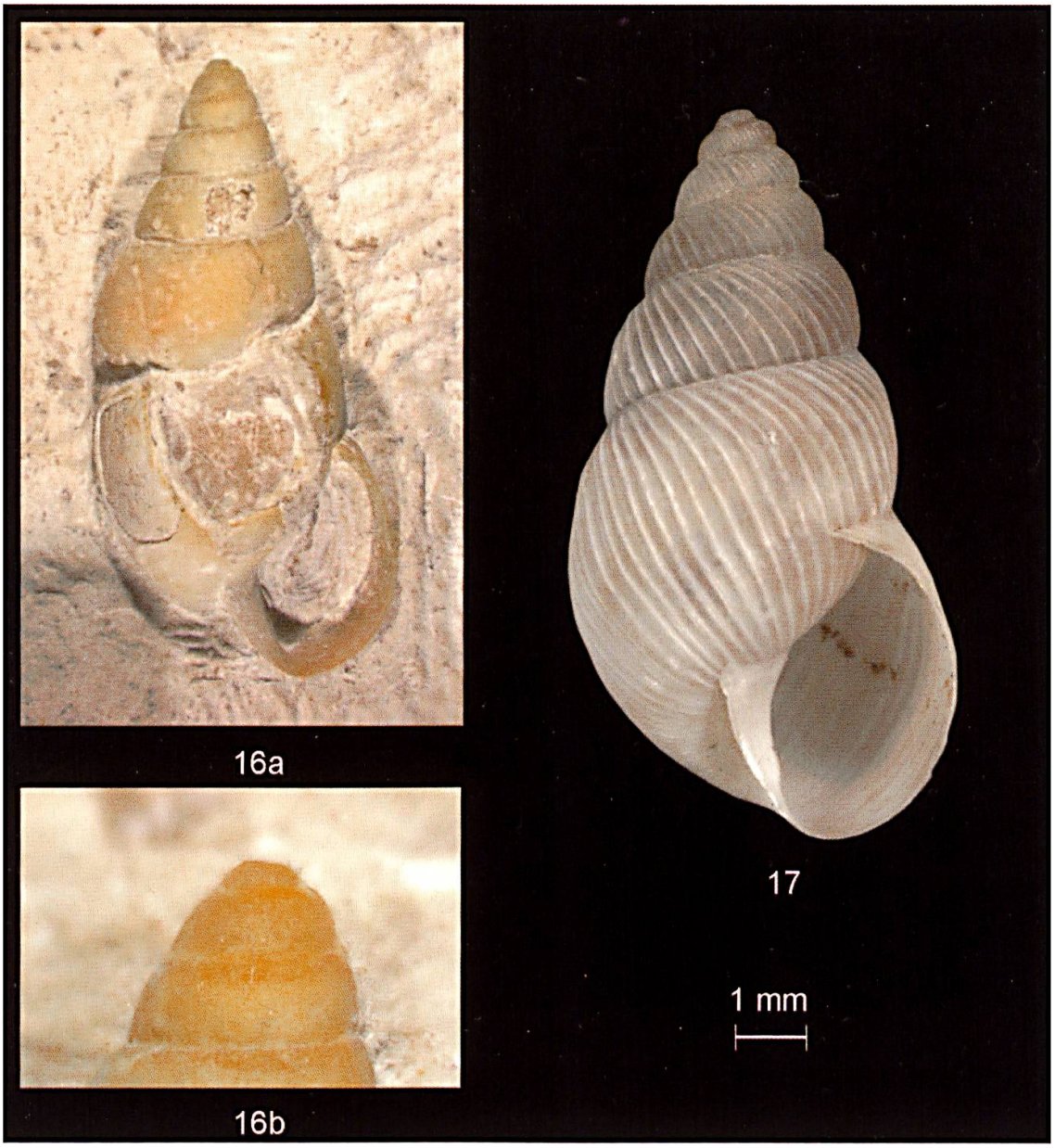
This new species is here attributed to *Achatina* and not *Archachatina* Albers, 1850 because of the relatively small size of the protoconch of *A. sculpturata* sp. nov.

Family Cerastidae

Cerastus pseudoena sp. nov. (Fig. 16)

Type specimens: Holotype NMBE 5018985.

Type locality: Wadi Darbat, Dhofar, Oman.



Figs. 16–17: Species of Cerastidae. Fig. 16a: *Cerastus pseudoena* sp. nov., Wadi Darbat, holotype NMBE 5018985 in frontal view. Fig. 16b: ditto, detail of protoconch and upper teleoconch whorls; detail not to scale. Fig. 17: *Cerastus girwanensis* Connolly, 1941, SMF 311620, Saudi Arabia, Asir province, Wadi al-Sharan S of Bani Sa'ad, 1750 m alt, leg. E. Neubert.

Stratum typicum: Paludal biomicritic limestones of the Zalumah Formation.

Age: Late Priabonian.

Material: This species is only represented by the holotype specimen.

Etymology: *pseudoena* refers to the superficial similarity of this species with the Modern European enid species *Ena montana* (Draparnaud, 1801).

Diagnosis: A small species of Cerastidae with a unique formation of aperture, slight ribbing pattern on teleoconch whorls, and partly obscured umbilicus.

Description: Shell slender, turreted; protoconch small, obtuse (not preserved as shell); upper teleoconch whorls elongate conical, last three whorls

more rapidly increasing; a fine pattern of axial riblets covering the whorls (only partly preserved, Fig. 16b); aperture elongate oval, columellar part triangular, broad, peristomial rim slightly reinforced by lip formation, somewhat flared; umbilicus open, partly obscured by triangular columellar shield.

Measurements: Holotype (Fig. 16): H = 13.78 mm; Wh > 8.

Remarks: This new species is placed in the family Cerastidae, because it matches very well the enoid shell form of most of the Modern species in this family. The correct separation between Cerastidae and Enidae is based on several anatomical details (Mordan 1992). However, all cerastid species recorded from the Arabian peninsula share the shell morphological detail of shells that are ribbed on the upper teleoconch, at least. This holds also true for *C. pseudoena* sp. nov., which thus supports its affiliation to that family. It is described under the genus *Cerastus* Albers, 1860, because this genus has a long-lasting history as suggested by its distribution that ranges from Ethiopia via the southwestern Arabian Peninsula to northwestern India. *Cerastus girwanensis* Connolly, 1941, a Modern endemic species from the Southwest of Saudi Arabia is shown here (Fig. 17) to facilitate comparison.

Cerastus praeinsularis sp. nov. (Figs. 18–19)

Type specimens: Holotype NMBE 5018986, paratype NMBE 5019050.

Type locality: Wadi Darbat, Dhofar, Oman.

Stratum typicum: Paludal biomicritic limestones of the Zalumah Formation.

Age: Late Priabonian.

Material: This species is only represented by the holotype specimen.

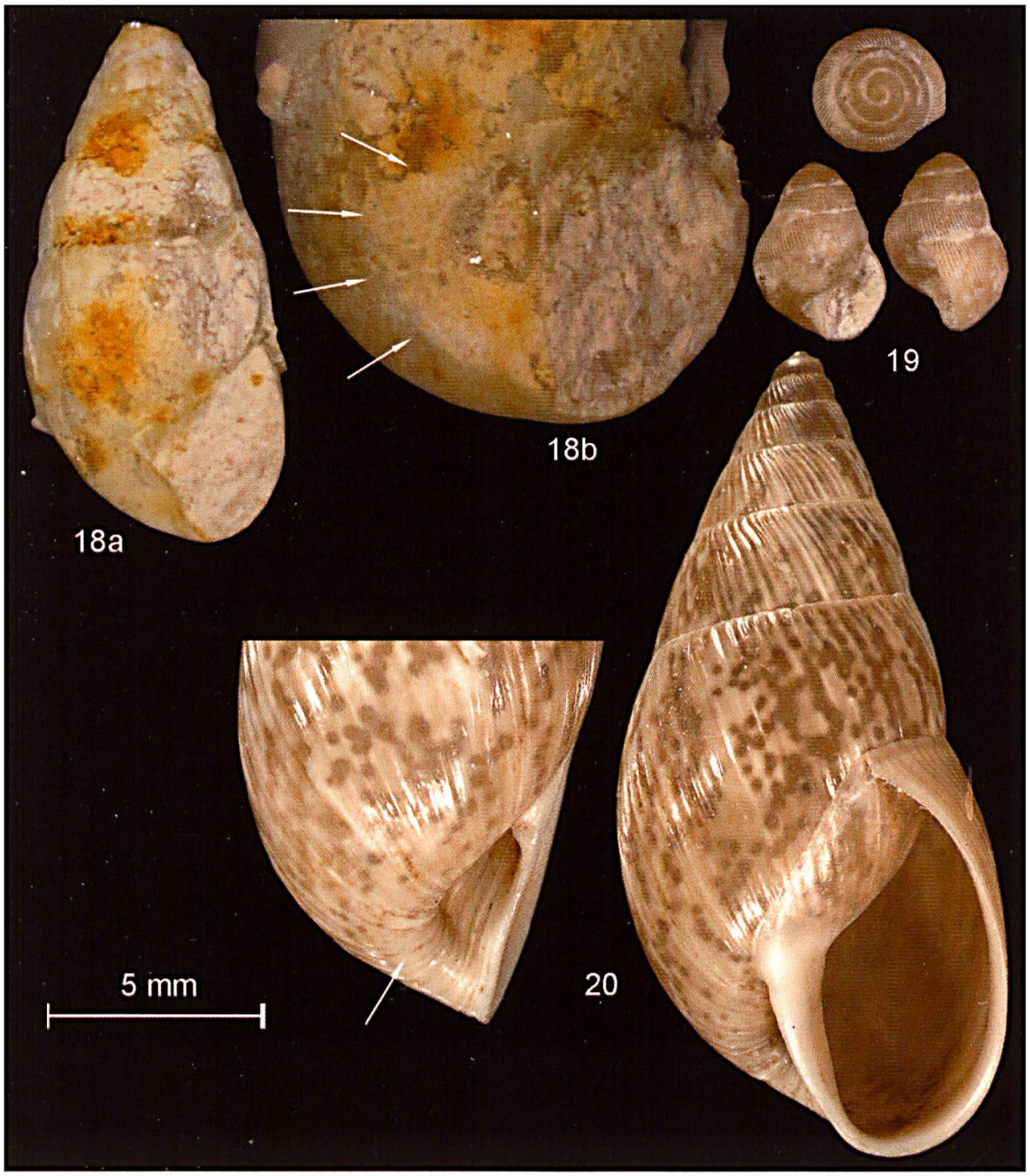
Etymology: *praeinsularis* to pinpoint the early presence of this species in the area, which later gave rise to the Soqotra Archipelago, Yemen.

Diagnosis: Species characterised by the large periomphalum.

Description: Shell elongate turreted, with regularly increasing whorls (protoconch and first teleoconch whorl not preserved); upper teleoconch whorls covered by a fine axial sculpture of ribs; aperture broadly oval, columellar part triangular, partly covering the umbilicus; umbilicus broadly open, with a large periomphalum, delimited by a blunt crest (see arrows in Fig. 18b).

Measurements: Holotype (Fig. 18a): H = 11.81 mm; Wh > 5.

Remarks: For the familial and generic affiliation, the same rationale is used as in *C. pseudoena* sp. nov. However, the peculiar form of the umbilicus of *C. praeinsularis* sp. nov. clearly differs from that of its fossil congener, but is quite similar to species from the Soqotran cerastid radiation. In this respect, it particularly resembles shells of the Modern endemic Soqotran genera *Achatinelloides* Nevill, 1878, and *Passamaella* Pfeiffer, 1877 (Neubert 2005a,



Figs. 18–20: Species of Cerastidae. Fig. 18a: *Cerastus praeinsularis* sp. nov., Wadi Darbat, holotype NMBE 5018986 in frontal view. Fig. 18b: ditto, detail of last teleoconch whorls with the periomphalum. Fig. 19: *C. praeinsularis* sp. nov., only upper whorls preserved, Wadi Darbat, paratype NMBE 5019050. Fig. 20: *Achatinelloides hadibuensis*, Yemen, Soqotra Isl., Wadi Ayhaft, leg. K. van Damme. Details not to scale.

2005b). This is here shown by a comparison with *Achatinelloides hadibuensis* (Godwin-Austen, 1881) (Fig. 20), which shows a very similar umbilicus formation with a large periomphalum delimited by a blunt crest (see arrow in Fig. 20).

In our material, we also found a small shell consisting of a small protoconch and almost four teleoconch whorls, which are also covered by a dense pattern of axial ribs (Fig. 19). The imperfect formation of the aperture makes

it very probable that this is a juvenile shell. Superimposing this fossil with the holotype of *C. praeinsularis* sp. nov. reveals that the diameter and growing increment of both shells match almost perfectly. For this reason we interpret this shell as a juvenile of *C. praeinsularis* sp. nov. (NMBE 5019050).

Family Subulinidae

? *Zootecus* sp. (Fig. 21)

Locality: Wadi Darbat, Dhofar, Oman.

Stratum typicum: Paludal biomicritic limestones of the Zalumah Formation.

Age: Late Priabonian.

Material: This species is only represented by the single cast, NMBE 5018987.

Measurements: Figured cast specimen: H = 7.29 mm.

Remark: This species has an elongated, turreted cylindrical shell, the cast shows six whorls, at least. The magnified detail shows some faint axial riblets on the upper whorl. The preservation of this species is too poor to justify a description, although this is for sure a new species. At the moment, the shell form and size give rise to the hypothesis that this is probably an ancestral species to the little radiation of the genus *Zootecus* WESTERLUND, 1887 in the area. The three Modern species are all larger, but at least the upper teleoconch whorls are also striped (Figs. 22–24).

It should be stressed that *Zootecus insularis* (EHRENBERG, 1831) has a wide distribution ranging from the Cape Verde Islands to Northwest India (Kashmir). Today, it is the most common pulmonate snail species in southern Arabia. The other two species are local endemics, with *Z. lucidissimus* (PALADILHE, 1873) living in the mountains of southern Yemen and the Dhofar area, Oman, while *Z. contiguus* (REEVE, 1849) is endemic to Abd al-Kuri, the westernmost island of the Soqotran Archipelago (Neubert 2003; Fig. 24).

Family Helicarionidae

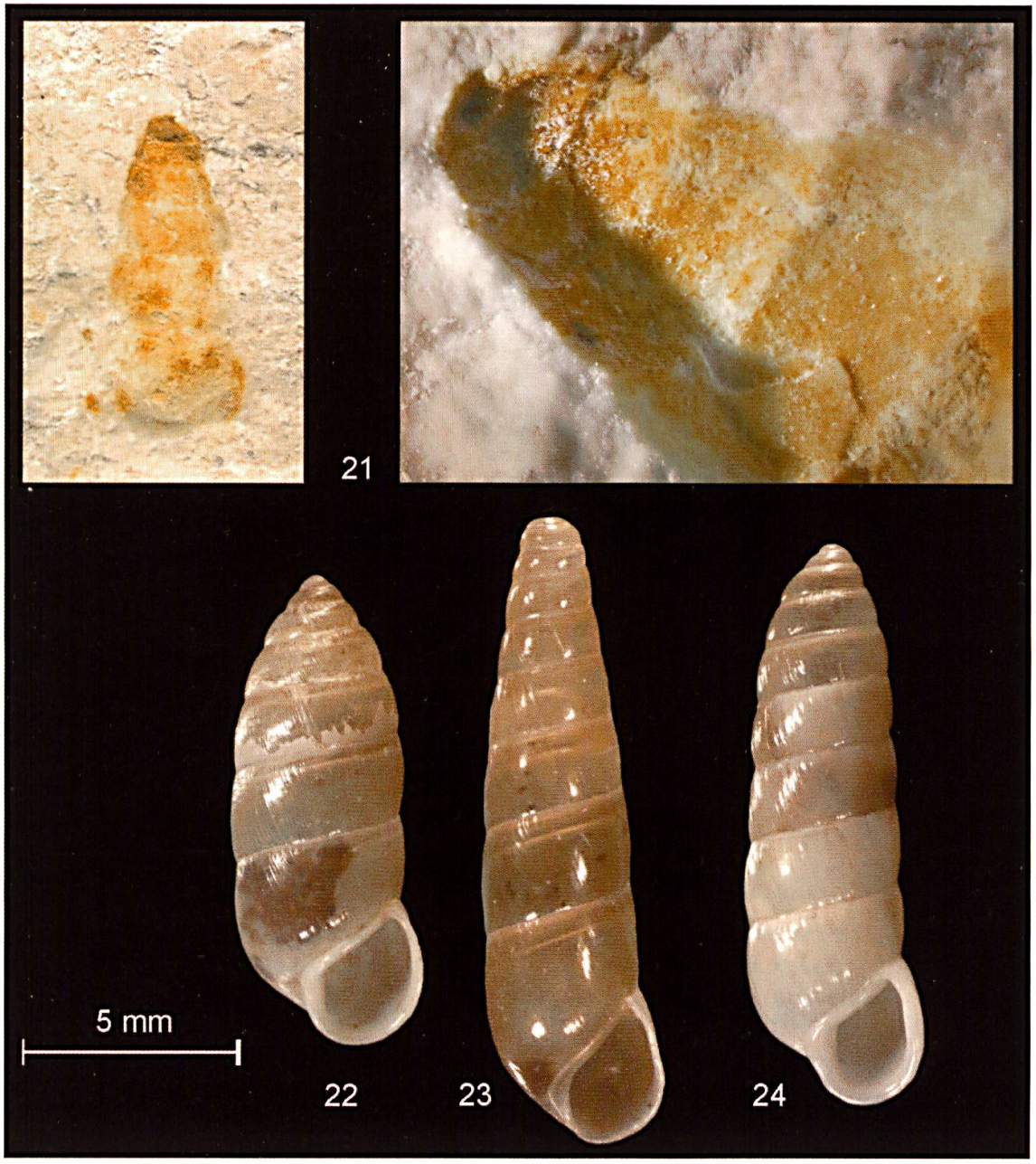
Trochozonites arabica sp. nov. (Fig. 25)

Type specimens: Holotype NMBE 5018988.

Type locality: Wadi Darbat, Dhofar, Oman.

Stratum typicum: Paludal biomicritic limestones of the Zalumah Formation.

Age: Late Priabonian.



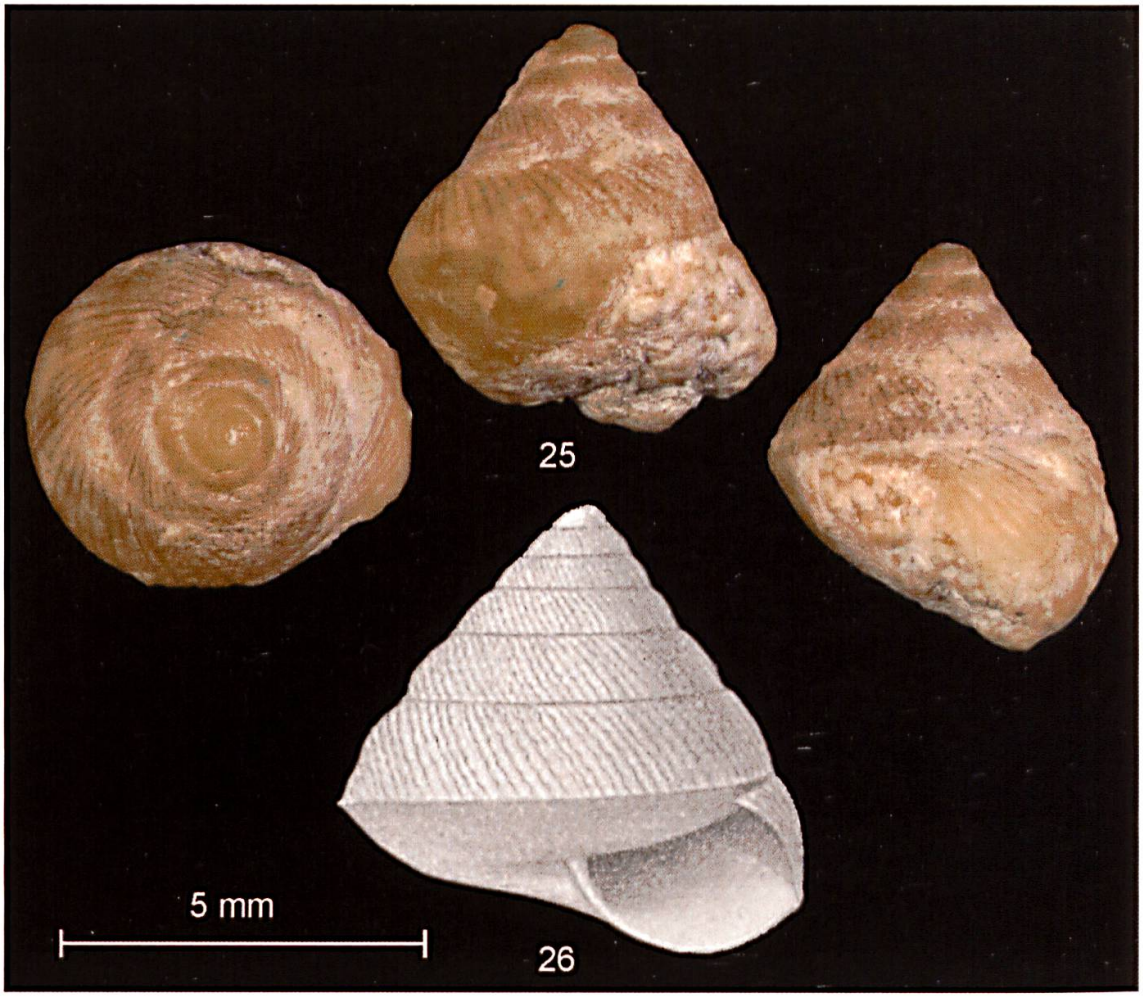
Figs. 21–24: Species of Subulinidae. Fig. 21: Cast of ? *Zootecus* sp., Wadi Darbat NMBE 5018987. Fig. 22: *Zootecus insularis*, lectotype ZMB 109990, Yemen, Insula Cameran. Fig. 23: *Zootecus lucidissimus*, SMF 320191, Yemen, Sana'a, Wadi beni Mansur close to al-Hajima, 15°05.105'N 43°52.818'E, leg. Neubert. Fig. 24: *Zootecus contiguus*, syntype NHMUK 1987.033, Yemen, Socotra Archipelago, Abd el-Kuri. Detail not to scale.

Material: This species is only represented by the holotype specimen.

Etymology: *arabica* for its presence on the Arabian Peninsula.

Diagnosis: Broad conical shell with strong opisthocline ribs.

Description: Shell broad conical; protoconch blunt, consisting of ca. 2 whorls without any obvious sculpture; last teleoconch whorl rapidly increasing, with a sharp peripheral keel; whorls only slightly rounded, suture simple and shallow; teleoconch whorls covered by strong opisthocline ribs; lower part of the shell (below the periphery) smooth; aperture depressed oval, peristome



Figs. 25–26: Species of Helicarionidae. Fig. 25: *Trochozonites arabica* sp. nov., Wadi Darbat, holotype NMBE 5018988 in frontal, apical and lateral view. Fig. 26: *Trochozonites plumaticostata*, Ituri Forest, Penge (from Pilsbry 1919).

(probably) simple, sharp; form of umbilicus not clearly discernible, however, it seems to be quite narrow.

Measurements: Holotype (Fig. 25): H = 5.04 mm; W = 5.27 mm; Wh > 5.

Remarks: The specific opisthocline ribs discriminate this shell from all cerastid shells, which have orthocline ribs. The shell form immediately recalls the shells of the afrotropical helicarionid genus *Trochozonites* PFEFFER, 1883. To facilitate comparison, the figure of *Trochozonites plumaticostata* PILSBRY, 1919 from the Congo Basin is here provided (Fig. 26). In his diagnosis of the species, Pilsbry (1919: 251) explicitly describes the "oblique, rather widely spaced, retractive, undulating riblets", which is close to what can be seen in *T. arabica* sp. nov. Nonetheless, the affiliation to such a badly understood genus remains with some doubts, because important character sets like the protoconch sculpture and microrelief are not preserved.

Discussion

The Omani fossil assemblages have yielded 11 species with 9 of them being described as new to science, originating from two localities situated in south-western Dhofar. This is a remarkable result, because our investigation was only brief, and thus it is to be expected that more intensive further field work will increase that number considerably. Most common are the freshwater gastropods *Lanistes* and *Pila* and the land snails *Limicolaria*, *Achatina* and *Cyclotopsis*. While the first are more evenly dispersed through the deposits, the land snails are found in local vast accumulations of thousands of shells mixed with juvenile ampullariids. Though intensely sought for, no freshwater bivalves were found. Brackish water species, indicative for lagoonal conditions were absent in the Wadi Darbat deposits and rare in the Thaytiniti collection.

The palaeo-environmental setting appears to be one of extensive freshwater swamps rather than lakes or rivers with a very marked seasonal difference in dry and rainy season water level, explaining the massive accumulations of land snails in seasonally flooded areas. There are no indications of water currents and the snails probably were deposited in fine limy mud. As a rule, swampy tropical environments are not suited for fossilization of molluscs. The high acidity from dissolving plant material causes shells to dissolve very rapidly. Large accumulations of land snails, usually virtually monotypic, are mainly known from subarid regions with a distinct wet/arid periodicity. In such regions, e.g. in southern Sudan, large dry areas will be flooded during the rainy season. As a result, shells of snails that died during aestivation will rise from the mud and start to float, are converged by the winds and finally being covered with suspended mud. The excellent, exceptional fossilization of the Omani paludal fossils is due to their preservation in limestone with a relatively high pH. Hence we conclude that the extraordinary richness of preserved shell may be the result of a climate that is not fully tropical, or had such a distinct periodicity.

The main importance of this fossil molluscan fauna is that it dates from the Palaeogene or Lower Cenozoic, a period of which our palaeontological knowledge of the Afro-Arabian fauna sensu lato is extremely fragmentary and virtually non-existent, as far as the malacofauna is concerned. Of this fauna, only some paludal-shallow lacustrine species are known. Virtually all fossils belong to 3 ampullariid genera *Pila, Lanistes* and *Pseudoceratodes* (†), except for a single specimen of '*Hydrobia*' and one unidentified planorbid shell ('*Planorbis*') (van Damme 1984). We had hoped that the Oman deposits would have yielded a richer freshwater fauna but it only confirms all other

findings, namely that the freshwater fauna of northeastern Africa and of Arabia was appallingly poor during the Early Cenozoic.

The Late Eocene terrestrial snail fauna on the other hand appears to be quite diversified. Until now, our knowledge of African terrestrial molluscs only extended to the Lower Miocene and was confined to the region of Kenya-Uganda. The prolific Bernard Verdcourt, a botanist, described the diversified and well preserved Early to Middle Miocene terrestrial malacofauna of Rushinga Island (L. Victoria, Kenya) (Verdcourt 1963), using these fossil snails as proxies for remarkably detailed palaeo-environmental reconstructions, including the type of vegetation, amount of rainfall in mm/year, altitude, humidity...). Subsequently Pickford (1995, 2002, 2004) and Pickford & al. (1986) kept using Verdcourt's approach, e.g. for the Lower Miocene of Napak (Uganda) and Mount Elgon.

Though we fully agree that terrestrial molluscan communities can be important palaeo-environmental indicators, most researchers using them confine themselves safely to Holocene and Pleistocene assemblages. The problem with Verdcourt's proxy methodology is that it was conceived at a time when our knowledge on the taxonomy and ecology of the Modern African snail fauna was still very incomplete (see comments in Rowson & al. 2010 and in van Bruggen 2011). The example cited by O'Brien (2012) on the difference of palaeo-environmental interpretation when a fossil is either identified as *Achatina* (indicative for the availability of perennial water) or as *Limicolaria* (occurring also in semi-arid environments) constitutes a caveat.

In the present article we hence tried to avoid the taxonomic trap to identify 35-million-year-old fossils with Modern species on the basis of morphological resemblances and we also did not risk developing a highly detailed environmental reconstruction.

That said, there is no doubt that a faunal continuum – at least at the genus level – can be observed in the Afrotropical terrestrial malacofauna from the Terminal Eocene to the present. The same conclusion was reached by Otero & Gayet (2001) in their study on the freshwater ichthyofauna from the Early Oligocene Ashawq Formation at Thaytiniti and Taqah. This fauna, containing such tropical African freshwater genera as *Hepsetus*, species of Alestinae, *Bagrus*, *Synodontis* and *Clarias,* corresponds, according to these authors, to 'a fraction of a Modern intertropical ichthyofauna from an African river or lake environment', more specifically to that of the Nilo-Sudanese region. These authors hypothesize that the present equatorial fish fauna was widely Afrotropical (Tropical Africa + NE Africa + Arabia) until at least Early Oligocene times, subsequently became greatly impoverished in the later phase of the Oligocene and Early Miocene on the Arabian Peninsula, with the onset of climatic cool-

ing in Oligocene times, and still later, with the formation of the Sahara and the desertification of Arabia, became restricted to equatorial Africa (Otero & Gayet 2001). The lack of post-Eocene fossil terrestrial snail material from Arabia and Africa, with the exception of the few Miocene sites in Kenya and Uganda does not allow us to make such broad generalizations.

However, from a malacological point of view, the presence of the Afrotropical family Achatinidae and the tropical Afro-Asian Cerastidae is here doubtlessly evidenced. The Pomatiidae are well known in the fossil record of Europe, and show a global distribution pattern with two major branches, a European and an Indopacific clade, the latter inhabiting all coastal areas bordering the Indian Ocean (Neubert 2009). Thus, the presence of a fossil *Cyclotopsis* in both Omani assemblages is not that amazing. The identification of the two other families, i.e. Subulinidae and Helicarionidae follows this picture. All these terrestrial families, except the Achatinidae, still have representatives in the area. Of particular interest was the question, whether there are any elements of the rich Modern malacofauna of the Soqotra Archipelago visible in the Omani assemblages. Although 10 million years before the Soqotra plate is assumed to have been definitely separated from the continent (van Damme 2009), the most important players were already present. Namely the Pomatiidae and Cerastidae, which today form the major part of the terrestrial malacofauna of the islands, had representatives living in the area. Still, ancestral forms of the large Subulinidae and some smaller groups are missing.

This documents shows that an intensive further research in Oman is necessary to complete our knowledge on this enigmatic Eocene fossil fauna. This site promises to be the most proliferous assemblage of Afro-Arabian fossil freshwater and terrestrial molluscs, and thus deserves protection by the Omani law as well as more scientific efforts in the future.

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