Late Cretaceous to ?Paleocene freshwater, brackish-water and marine molluscs from Al-Khodh, Oman

Simon Schneider, Heinz A. Kollmann & Martin Pickford

Bivalvia and Gastropoda from the late Campanian to Maastrichtian deltaic Al-Khodh Formation and from the overlying ?Paleocene shallow marine Jafnayn Limestone Formation of northeastern Oman are described. Freshwater bivalves include three species of Unionidae, left in open nomenclature, due to limited preservation. These are the first pre-Pleistocene unionids recorded from the Arabian Peninsula, where large freshwater bivalves are absent today. Brackish-water bivalves are represented by two species of Cyrenidae. *Geloina amithoscutana* sp. nov. extends the range of *Geloina* to the Mesozoic and to ancient Africa. *Muscatella biszczukae* gen. et sp. nov. has a unique combination of characters not shared with other genera in the Cyrenidae. Brackish-water gastropods comprise *Stephaniphera coronata* gen. et sp. nov. in the Hemisinidae; *Subtemenia morgani* in the new genus *Subtemenia* (Pseudomelaniidae); *Cosinia* sp. (Thiaridae); *Pyrazus* sp. (Batillariidae); and Ringiculidae sp. indet. From the Jafnayn Limestone Formation, several marginal marine mollusc taxa are also reported. The fossils are assigned to four mollusc communities and associations, which are indicative of different salinity regimes. • Key words: Unionidae, Cyrenidae, Pseudomelaniidae, Hemisinidae, taxonomy, palaeobiogeography.

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Globally, the evolution and phylogeny of freshwater and brackish-water molluscs is currently a topic of great interest, mostly due to the importance of these taxa for conservation biology (*e.g.* Lopes-Lima *et al.* 2016, 2018; Do *et al.* 2018; Zieritz *et al.* 2018). Most freshwater mollusc clades show a high degree of diversification, endemism and environmental restrictedness, and, as a result, species have a high risk of extinction (*e.g.* Cuttelod *et al*. 2011). Brackish-water taxa, although often more widespread, show similar patterns and face similar problems, as suitable habitats are often confined to river deltas, which are restricted in extent and usually densely populated by humans (*e.g.* Barnes 1999, Szabo *et al*. 2016). Consequently, combined molecular and morphologic studies of freshwater and brackish-water molluscs are en vogue, and for several groups, comprehensive phylogenies at global scale are gradually becoming available.

In contrast, the fossil component of freshwater and brackish-water mollusc evolution is significantly understudied and comparatively poorly understood. There are several reasons for this. Most importantly, the fossil record of these taxa is scattered and discontinuous, since the preservation potential of the strata enclosing them is low (*e.g.* Dunhill *et al*. 2014). As a result, many species or genera are only known from their type locality (*e.g.* Henderson 1935, p. 4) and phylogenetic relationships remain enigmatic. Additionally, the level of convergence in many of the higher taxa of freshwater and brackish-water molluscs is an issue, as new and surprising cases are continuously revealed by molecular studies (*e.g.* Bolotov *et al*. 2017, 2018). Last, but not least, many freshwater and brackish-water species are highly variable and shells react plastically to changes in habitat or water chemistry.

Whoever is not put off by these caveats and attempts to apply rigorous taxonomy and systematics to fossil freshwater and brackish-water shells is, however, often rewarded with interesting results concerning evolutionary relationships and pathways, palaeobiogeography or palaeoecology. Moreover, fossils supply the component of time to molecular phylogenetics and are thus essential for the calibration of evolution. Such a case, exemplified by a restricted, low diversity fauna from the latest Cretaceous of northern Oman, is presented herein.

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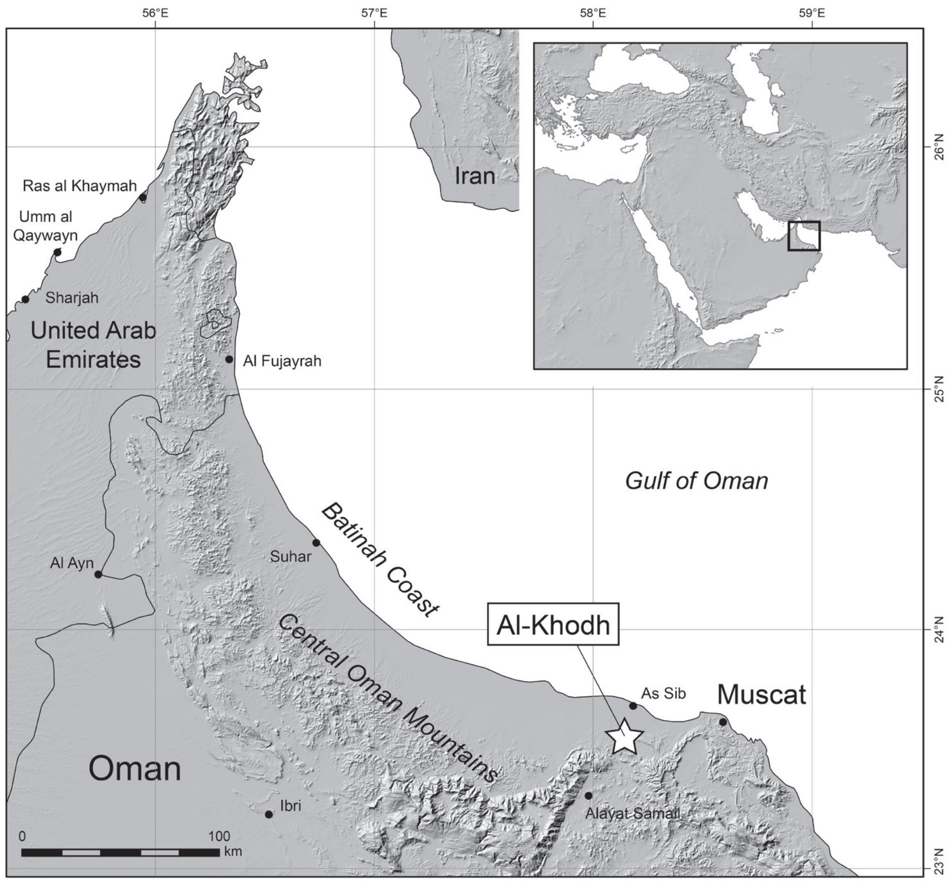

Figure 1. Map of the northern coast of Oman. The area of Al-Khodh is indicated by a star.

The study area around Al-Khodh is near Muscat, the capital of Oman. The outcrops are located approximately 10 km west of Muscat Airport, close to the Batinah Coast in the foreland of the Central Oman Mountains (Fig. 1). The Al-Khodh Formation, which yielded most of the studied fossil assemblages, was defined by Nolan *et al*. (1990; originally spelled 'Al-Khawd Conglomerate Formation'). It comprises a succession of polymict conglomerates, lithic sandstones, shale and subordinate microcrystalline carbonates, and has been interpreted as a fan delta complex by Nolan *et al*. (1990). The Al-Khodh Formation is up to 860 m thick and bounded by unconformities. It was deposited on top of the Semail Ophiolite and is overlain by the marine Jafnayn Limestone Formation. No comprehensive dating is available for the Al-Khodh Formation. However, the Semail Ophiolite was obducted onto the Oman margin during the middle to late Campanian, and the basal Jafnayn Limestone Formation is supposed to be late Palaeocene in age (Nolan *et al*. 1990, and references therein). Given that ornithischian dinosaur remains have been found in the Al-Khodh Formation, a pre-Cenozoic, potential late Campanian to Maastrichtian age was deduced by Nolan *et al*. (1990). The Jafnayn Limestone Formation is dominantly composed of nodular limestones, with minor marly intervals. It is concordantly, but presumably paraconformably overlain by the shale- and marl-dominated Rusayl Formation (Nolan *et al*. 1990). The stratigraphy of both formations is based on echinoids, which define a late Palaeocene to basal Eocene age range for the Jafnayn Limestone Formation (Nolan *et al*. 1990).

From the coarser-grained beds of the Al-Khodh Formation, articulated 'corbiculid bivalves' and gastropods were mentioned by Nolan *et al*. (1990). Pickford (2017) remarked that freshwater molluscs are confined to the lower half of the succession, and become gradually replaced by brackish-water and finally fully marine fauna up-section. Two species of the freshwater gastropod genus *Lanistes* were described in open nomenclature by Pickford (2017). The remaining mollusc taxa, with exclusion of the Ostreoidea, are studied herein for the first time.

Material and methods

The fossils described herein were collected in February 2015 at the following localities at Al-Khodh, Oman (Tab. 1; GPS WGS 84 grid).

Specimens were cleaned with water, brush and needles. All specimens were coated with ammonium chloride for photographs.

All fossils are curated at the Oman Natural History Museum, Muscat (ONHM), under collection numbers ONHM-F-4411 to 4433.

Systematic palaeontology

The systematic arrangement of the Bivalvia is adopted from MolluscaBase (2018). The systematic arrangement of the Gastropoda follows Bouchet *et al.* (2017). Where permitted by preservation, measurements were taken with callipers to the nearest half millimetre. Measurements have only been taken from complete or near-complete specimens in bivalves. Thickness measurements for single valves have been doubled. Abbreviations: AA – apical angle; H – height; HB – height of last whorl; L – length; T – thickness; W – width.

Class Bivalvia Linnaeus, 1758
Subclass Palaeoheterodonta Newell, 1965
Order Unionida Stoliczka, 1871
Superfamily Unionoidea Rafinesque, 1820
Family Unionidae Rafinesque, 1820

Remarks. – The three species of Unionidae described below come from a single fossil assemblage. The original, nacreous aragonite of the shells is recrystallized as sparry calcite. All shells are disarticulated and their surfaces and hinges are more or less strongly worn. No hinge teeth are preserved, preventing assignment at genus or species level. Typical unionid shell features include the generally elongate oval to slightly kidney-shaped outlines of the shells; long, slender nymphs (Fig. 2B2, C2); deeply engraved anterior adductor muscle scar and distinct pedal retractor muscle scar (Fig. 2D); and fine radial striation of inner shell layers (Fig. 2A, C1, E).

Unionidae sp. indet. 1
Figure 2A, C, E

Material. – 17 left valves and 4 right valves, all fragmentary, from the Al-Khodh Formation at locality MP3 (ONHM-F-4428).

Description. – Shell elongate-oval in outline, weakly inflated. Umbo blunt, barely protruding; positioned almost centrally, only slightly shifted towards the anterior end; faintly prosogyrate. Outer shell layer only preserved in patches; smooth where seen. Second shell layer with commarginal growth lines and slightly undulating radial striation, as often seen in corroded (fossil) unionoids. Hinge plate prominent; hinge teeth eroded. Nymph elongate, relatively long, submerged below dorsal shell margin.

Table 1. Localities and communities/associations. For each locality the locality name; GPS coordinates; and the taxa recorded are given. Colours indicate the four mollusc communities/associations: green = unionid community; yellow = *Geloina* association; blue = *Muscatella* association; red = marine community.

Locality	Latitude	Longitude	Unionidae	*Geloina*	Ringiculidae	Oysters	*Subtemenia*	*Lanistes*	*Muscatella*	*Stephaniphera*	*Ceratodus*	*Torquesia*	*Cosinia*	*Pyrazus*	*Amaurellina*	Tellinidae	Euheterodonta
AK33	23°32′45.6″ N	58°09′19.4″ E					x										
AK51	23°33′05.5″ N	58°08′42.6″ E				x	x	x	x	x							
MP1	23°32′53.4″ N	58°08′37.8″ E		x													
MP2	23°32′55.4″ N	58°08′36.3″ E		x			x										
MP3	23°33′02.4″ N	58°08′36.6″ E	x														
MP4	23°33′05.3″ N	58°08′16.9″ E		x													
MP5	23°32′50.9″ N	58°08′39.7″ E		x			x	x									
MP6	23°32′51.0″ N	58°08′39.1″ E		x													
MP7	23°32′52.6″ N	58°08′38.4″ E		x	x	x	x										
MP8	23°33′04.7″ N	50°08′36.1″ E							x								
MP9	23°32′57.6″ N	58°08′33.9″ E		x													
MP10	23°32′59.6″ N	58°08′31.9″ E		x		x											
MP13	23°33′09.6″ N	58°08′31.2″ E					x		x		x						
MP14	23°33′07.8″ N	58°08′36.1″ E							x	x							
Fanja Back	23°26′26.7″ N	58°10′39.8″ E										x	x	x	x	x	x

Remarks. – The shells of this species, although incompletely characterised, are quite distinct from those of Unionidae sp. indet. 2 and 3 with regard to general shell shape. The present species has oval shells with barely protruding umbos. Species 2 is trigonally ovate with markedly protruding umbos. Species 3 has a slight but distinct incurvature of the ventral shell margin, and thus is faintly kidney-shaped in outline.

Unionidae sp. indet. 2
Figure 2B

Material. – A single, almost complete right valve, from the Al-Khodh Formation at locality MP3 (ONHM-F-4429a).

Description. – Shell high trigonally ovate in outline. Umbo blunt, distinctly protruding, faintly prosogyrate; positioned at approximately 25% of shell length. Shell outside smooth, with regular commarginal growth lines only. Nymph elongate, long (more than one third of shell length), submerged below dorsal shell margin. Shell interior unknown.

Remarks. – For differences between the three unionid species, see remarks for Unionidae sp. indet. 1 above.

Unionidae sp. indet. 3
Figure 2D, F

Material. – A single left valve and a single right valve, both fragmentary, from the Al-Khodh Formation at locality MP3 (ONHM-F-4430a, b).

Description. – Shell oval kidney-shaped in outline. Umbo blunt, barely protruding, faintly prosogyrate; positioned at approximately 30% of shell length. Ventral shell margin distinctly incurved shortly before mid-length. Outer shell layer incompletely preserved; smooth with commarginal growth lines where seen. Shell rather thick. Hinge plate prominent and wide; hinge teeth eroded. Anterior adductor muscle scar deep and internally structured. Pedal retractor muscle scar distinct; positioned directly below anterior adductor muscle scar.

Remarks. – For differences between the three unionid species, see remarks for Unionidae sp. indet. 1 above. Kidney-shaped shells are common in species belonging to the family Margaritiferidae, which is sister clade to the Unionidae. However, the shape of the hinge plate in Unionidae sp. indet. 3 suggests that there is insufficient space directly above the anterior adductor muscle scar for the strong pseudocardinal cusps commonly seen in Margaritiferidae. More importantly, the pedal retractor muscle scar is clearly positioned below the anterior adductor muscle scar, not directly behind the latter, as in Margaritiferidae. We thus consider a placement in the morphologically much more diversified Unionidae more likely.

Subclass Heterodonta Neumayr, 1884
Infraclass Euheterodonta Giribet & Distel, 2003

Euheterodonta indet.

Material. – Two internal moulds of articulated specimens, from the Jafnayn Limestone Formation at locality Fanja Back (ONHM-F-4432a, b).

Remarks. – The larger specimen is ovate in outline, distinctly inflated, with relatively pointed, sub-terminal, distinctly prosogyrate umbos, and faint commarginal growth lines. The smaller specimen seems to be similar in shape, but is encrusted with diagenetic calcite. These characters are not indicative at genus or even family level, and could occur both in Imparidentia and Anomalodesmata. We refrain from figuring these poorly preserved specimens.

Superorder Imparidentia Bieler, Mikkelsen & Giribet *in* Bieler *et al.*, 2014
Order Cardiida Férussac, 1822
Superfamily Tellinoidea Blainville, 1814
Family Tellinidae Blainville, 1814

?Tellinidae indet.

Material. – A single fragmentary internal mould of an articulated specimen, from the Jafnayn Limestone Formation at locality Fanja Back (ONHM-F-4431a).

Remarks. – The specimen is poorly inflated, slightly inequilateral and ovate-triangular in shape, with rather pointed, slightly projecting umbos and faint commarginal growth lines. This combination of traits is most common in the Tellinidae, but could occur in a number of other euheterodont bivalve families, which renders the family assignment tentative. We refrain from figuring this fragment.

Order Venerida Gray, 1854
Superfamily Cyrenoidea Gray, 1840
Family Cyrenidae Gray, 1840

Remarks. – The classification of fossil Cyrenidae is far from settled. Some 30 genus-level names are available in this family, but several of them are only vaguely defined (*e.g.* Keen & Casey 1969, Fang *et al.* 2009). Most of these taxa are restricted to the Cenozoic, but several genera extend back into the Mesozoic, or are entirely Mesozoic, in their distribution. Taxa with and without serrated hinge teeth occur throughout, and the phylogenetic significance

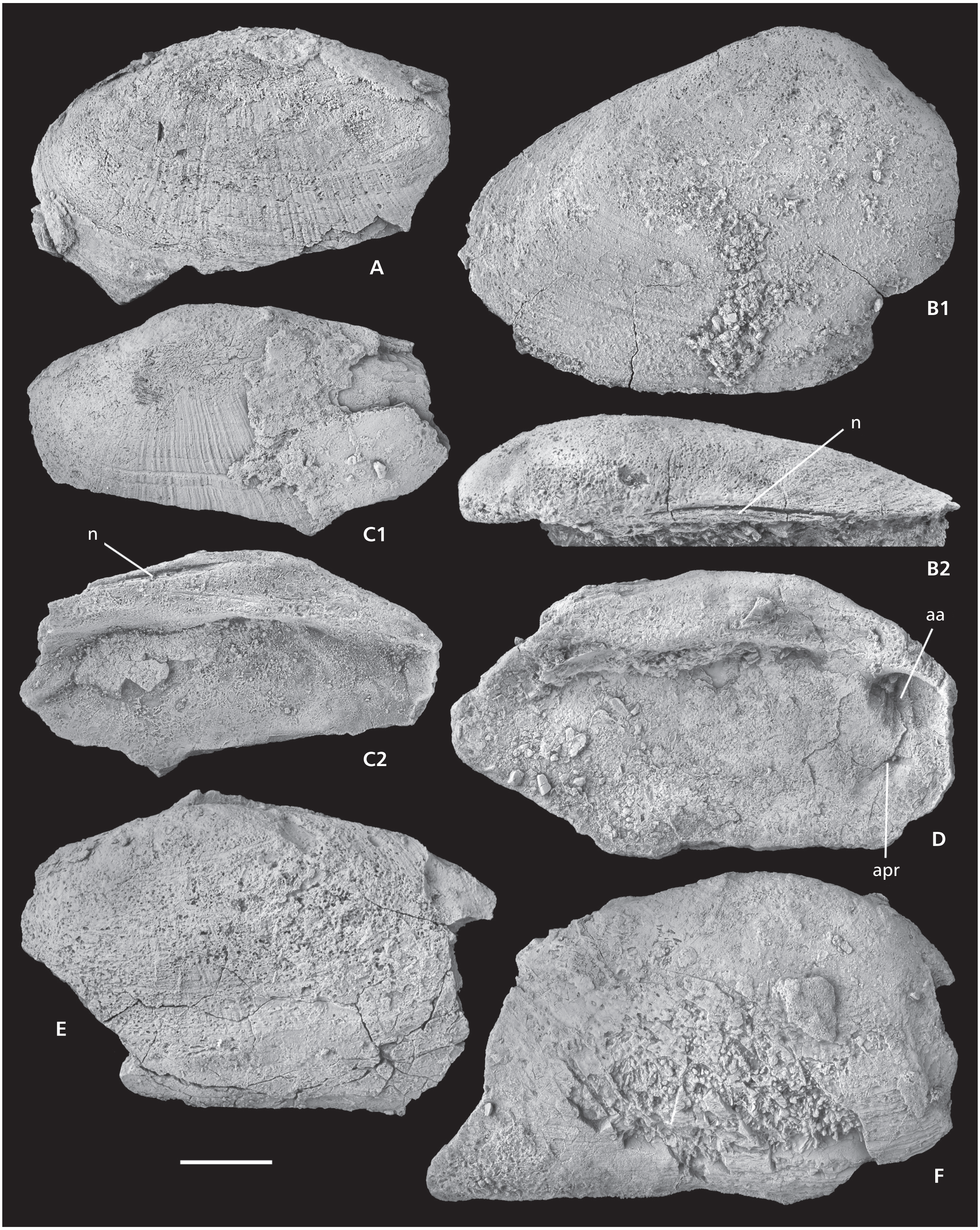

Figure 2. Unionidae from the Al-Khodh Formation at locality MP 3. • A, C, E – Unionidae sp. indet. 1; A – right valve, ONHM-F-4428a; C – left valve, ONHM-F-4428b; E – left valve, ONHM-F-4428c. • B – Unionidae sp. indet. 2, ONHM-F-4429a. • D, F – Unionidae sp. indet. 3; D – left valve, ONHM-F-4430a; F – right valve, ONHM-F-4430b. Abbreviations: aa – anterior adductor muscle scar; apr – anterior pedal retractor muscle scar; n – nymph. Scale bar = 10 mm.

of this character is unclear. Likewise, the phylogenetic significance of the presence or absence of a pallial sinus has not been clarified. In order to avoid making unsupported phylogenetic inferences, both characters are herein treated as significant for generic assignment, which leads to the establishment of a new genus below. Most cyrenid taxa are of broadly veneroid shape, *i.e.* short ovate, or rounded triangular. Some genera, however, have elongate ovate or elongate trigonally ovate shells of tellinoid to donacoid shape.

Genus *Geloina* Gray, 1842

Type species. – *Cyclas zeylanica* Lamarck, 1806 (Recent; Sri Lanka), by subsequent designation by Gray (1847).

Geloina amithoscutana **sp. nov.**
Figures 3A–J, 4A–I

Types. – Holotype, left valve (Fig. 4A); locality MP 10; ONHM-F-4411a. Paratype 1, right valve (Fig. 4B); locality MP 10; ONHM-F-4411b. Paratype 2, right valve (Fig. 4H); locality MP 10; ONHM-F-4411c. Paratype 3, right valve (Fig. 4C); locality MP 10; ONHM-F-4411d. Paratype 4, fragmentary right valve (Fig. 4G); locality MP 6; ONHM-F-4412a. Paratype 5, fragmentary left valve (Fig. 4F); locality MP 6; ONHM-F-4412b. Paratype 6, right valve (Fig. 4D); locality MP 6; ONHM-F-4412c. Paratype 7, right valve (Fig. 4I); locality MP 6; ONHM-F-4412d. Paratype 8, double-valved specimen (Fig. 3H); locality MP 6; ONHM-F-4412e. Paratype 9, double-valved specimen (Fig. 3J); locality MP 6; ONHM-F-4412f. Paratype 10, double-valved specimen (Fig. 3A); locality MP 1; ONHM-F-4413a. Paratype 11, double-valved specimen, Fig. 3B; locality MP 6; ONHM-F-4412g. Paratype 12, double-valved specimen (Fig. 3C); locality MP 6; ONHM-F-4412h. Paratype 13, double-valved specimen (Fig. 3D); locality MP 1; ONHM-F-4413b. Paratype 14, double-valved specimen (Fig. 3E); locality MP 10; ONHM-F-4411e. Paratype 15, double-valved specimen (Fig. 3F); locality MP 10; ONHM-F-4411f. Paratype 16, double-valved specimen (Fig. 3G); locality MP 1; ONHM-F-4413c. Paratype 17, double-valved specimen (Fig. 3I); locality MP 10; ONHM-F-4411g. Paratype 18, right valve (Fig. 4E); locality MP 10; ONHM-F-4411h.

Type horizon and locality. – Al-Khodh Formation, locality MP 10 (see Tab. 1).

Additional material. – Several hundred juvenile and adult left and right valves and articulated specimens, from the Al-Khodh Formation at localities MP 1, MP 2, MP 4, MP 5, MP 6, MP 7, MP 9 and MP 10.

Etymology. – *Amithoscuta* was the earliest mentioned unique name, used by Gaius Plinius Secundus ('Pliny the Elder'), for Muscat, the present-day capital of Oman (Forster 1844).

Diagnosis. – Small, up to 35 mm long, thick-shelled *Geloina* with short-subtrigonal, markedly inequilateral and prosogyrate shells; lowest point of shell distinctly anterior of mid-length. Lateral teeth and nymphs particularly strong and sturdy.

Description. – Shells very small for group, up to 35 mm in length (see Tab. 2 for measurements); thick and solid. Shell outline short subtrigonal, inaequilateral; umbo positioned distinctly behind mid-line; lowest point positioned at approximately one third from anterior end. Anterior-dorsal margin slightly incurved, almost straight; anterior and anterior-ventral margin well-rounded; posterior-ventral margin almost straight, subtly incurved in most specimens; posterior margin faintly rounded, almost straight, meeting posterior-ventral margin in well-rounded corner; posterior-dorsal margin almost straight, at blunt angles to posterior margin, forming a posterior shoulder. Shell distinctly inflated; umbos slightly protruding, moderately prosogyrate. Blunt posterior edge extending from umbo to posterior shoulder. No lunule, no escutcheon. Outside of shell ornamented with densely spaced, narrow, fairly regular commarginal costellae.

Hinge formula of right valve: AIII, AI, 3a, 1, 3b, PI, PIII. Cardinal teeth 1 and 3b prominent, of almost equal size, high and narrow; cardinal tooth 3a much weaker,

Table 2. Measurements of *Geloina amithoscutana* sp. nov., in mm. Abbreviations: H – height; L – length; T – thickness.

Specimen	L	H	T
Holotype, ONHM-F-4411a (Fig. 4A)	22	20	15
Paratype 1, ONHM-F-4411b (Fig. 4B)	18	16.5	12
Paratype 2, ONHM-F-4411c (Fig. 4H)	19	18	12.5
Paratype 3, ONHM-F-4411d (Fig. 4C)	18	16.5	12
Paratype 8, ONHM-F-4412e (Fig. 3H)	31	27	16.5
Paratype 9, ONHM-F-4412f (Fig. 3J)	29.5	26.5	16
Paratype 10, ONHM-F-4413a (Fig. 3A)	24	20	11.5
Paratype 11, ONHM-F-4412g (Fig. 3B)	25	19.5	13.5
Paratype 12, ONHM-F-4412h (Fig. 3C)	23	21.5	13.5
Paratype 13, ONHM-F-4413b (Fig. 3D)	34	31.5	[16.5]
Paratype 14, ONHM-F-4411e (Fig. 3E)	16	13.5	9.5
Paratype 15, ONHM-F-4411f (Fig. 3F)	18	16	11
Paratype 16, ONHM-F-4413c (Fig. 3G)	28	25	15
Paratype 17, ONHM-F-4411g (Fig. 3I)	14	12	8.5
Paratype 18, ONHM-F-4411h (Fig. 4E)	17.5	16.5	11

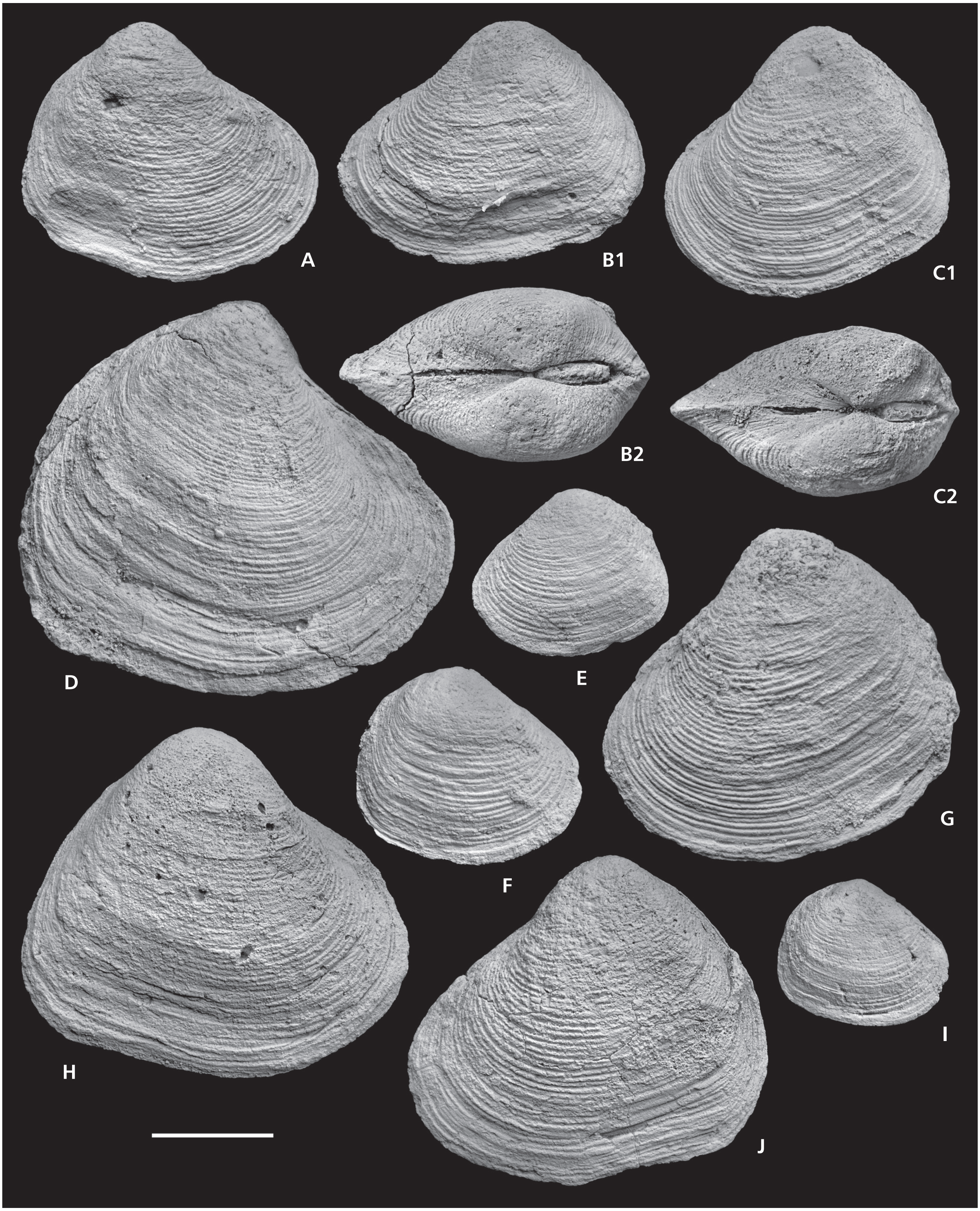

Figure 3. Cyrenidae from the Al-Khodh Formation. *Geloina amithoscutana* sp. nov. Outside view of several double-valved shells, displaying ontogenetic and intraspecific variability; A – paratype 10, locality MP 1, ONHM-F-4413a; B – paratype 11, locality MP 6, ONHM-F-4412g; C – paratype 12, locality MP 6, ONHM-F-4412h; D – paratype 13, locality MP 1, ONHM-F-4413b; E – paratype 14, locality MP10, ONHM-F-4411e; F – paratype 15, locality MP10, ONHM-F-4411f; G – paratype 16, locality MP 1, ONHM-F-4413c; H – paratype 8, locality MP 6, ONHM-F-4412e; I – paratype 17, locality MP10, ONHM-F-4411g; J – paratype 9, locality MP 6, ONHM-F-4412f. Scale bar = 10 mm.

more or less fused with anterior lateral tooth AIII, which forms a narrow, slightly elevated, incurved ridge close to anterior-dorsal shell margin. Anterior lateral tooth AI prominent, relatively long, markedly incurved. Posterior lateral tooth PI equally prominent; PIII faint and narrow. Hinge formula of left valve: AII, 2a, 2b, 4b, PII. Cardinal teeth 2a and 2b prominent, of almost equal size, high and narrow; cardinal tooth 4b much weaker. Later teeth AII and PII prominent. All hinge teeth smooth, not serrated. Nymphs prominent, high, but generally not protruding over shell margin. Pallial line entire, non-sinuate. Anterior and posterior adductor muscle scars of equal size, positioned directly below anterior and posterior ends of hinge plate, respectively. Posterior adductor muscle scar moderately deep; anterior adductor muscle scar shallow. Anterior pedal retractor muscle scar positioned on ventral surface of hinge plate; deep.

Remarks. – The species shows the general characteristics of Cyrenidae regarding shell shape, ornamentation and dentition. Characters that are of value for generic assignment are (1) the absence of a lunule and escutcheon; (2) smooth, non-serrated hinge teeth; (3) three entire, non-bifid cardinal teeth in each valve; (4) an entire, non-sinuate pallial line. The combination of these traits argues for a placement in *Geloina*. Huber (2015) records a weak pallial sinus for *Geloina* and depicts it for one species, while Morton (1976), in a detailed morphological-anatomical study of the genus, reported no pallial sinus. We thus regard the new species as falling within the limits of the variability of the genus.

At the specific level, the following features distinguish the new species from other fossil and modern representatives of *Geloina*. (1) The shells are rather thick and heavy, but small for the genus. Extant species reach adult sizes between 70 and 150 mm (Huber 2015). (2) The umbos are distinctly prosogyrate, and the shells markedly inequilateral, with a faint posterior shoulder; the lowest point of the shell is positioned distinctly anterior of mid-length. (3) The lateral teeth and nymphs are unusually strong and prominent for the genus.

The wealth of material available makes it possible to display the intraspecific and ontogenetic variability of the species (Figs 3, 4). Intraspecific variability is expressed in slightly variable length/height ratios, more or less inaequilateral shells and slightly wider or narrower umbos. Juvenile shells are usually strongly inaequilateral, have very low umbos and the ventral margin is not yet incurved (Fig. 3E, F, I).

Genus *Muscatella* gen. nov.

Type species. – *Muscatella biszczukae* sp. nov., by original designation herein.

Etymology. – From Muscat, the present-day capital of Oman.

Diagnosis. – Moderately large, up to 19.5 mm high Cyrenidae of regular elongate ovate, tellinoid shape. No lunule or escutcheon. Right valve hinge with three cardinal and four lateral teeth (AIII, AI, 3a, 1, 3b, PI, PIII); left valve hinge with three cardinal and two lateral teeth (AII, 2a, 2b, 4b, PII); all teeth smooth, not serrated. Cardinal teeth 1, 2a, 2b and 3b prominent, incipiently bifid at the base. Nymphs elongate, low but prominent. Pallial line entire or very shallowly sinuate.

Remarks. – *Muscatella* shows the general characteristics of Cyrenidae regarding ornamentation and dentition, but is rather elongate in outline. Characters that are of value for generic assignment are (1) the elongate ovate shell outline, (2) the absence of a lunule and escutcheon; (3) smooth, non-crenulated hinge teeth; (4) three distinct, cardinal teeth in each valve, some of them incipiently bifid; (5) an entire or very shallowly sinuate pallial line. All single valves in our samples are either broken posteriorly or are too poorly preserved to determine the condition of the pallial line. However, if present, the sinus must be very shallow, judging from the specimen displayed in Fig. 5F.

The combination of these traits is unique among the Cyrenidae, and thus the new species described below accords with none of the genera previously included in the family. Only four genera assigned to the Cyrenidae are elongate ovate or elongate trigonally ovate in outline, *i.e.* have a tellinoid to donacoid shape. Among these, the type species of Palaeocene to Eocene western European *Loxoptychodon* Sandberger, 1872, *Donacopsis* Sandberger, 1872 and *Tellinocyclas* Dall, 1903 differ in outline shape from elongate ovate to trigonal donaciform, but all have distinctly serrated anterior lateral teeth and a sinuate pallial line. In Late Cretaceous *Baidunoconcha* Gu *in* Gu & Yu, 1999 from the Nenjiang Formation of Jilin, northeastern China, the lateral teeth are serrated, and the conditions of the cardinal teeth and pallial line are unknown (not preserved in the type material).

Muscatella biszczukae sp. nov.

Figure 5A–H

Types. – Holotype, fragmentary right valve (Fig. 5F); locality MP 14; ONHM-F-4414a. Paratype 1, fragmentary left valve (Fig. 5D); locality MP 13; ONHM-F-4415a. Paratype 2, fragmentary left valve (Fig. 5G); locality MP 14; ONHM-F-4414b. Paratype 3, double-valved specimen (Fig. 5B); locality MP 8; ONHM-F-4416a. Paratype 4, double-valved specimen (Fig. 5A); locality MP 8; ONHM-F-4416b. Paratype 5, fragmentary right valve (Fig. 5H);

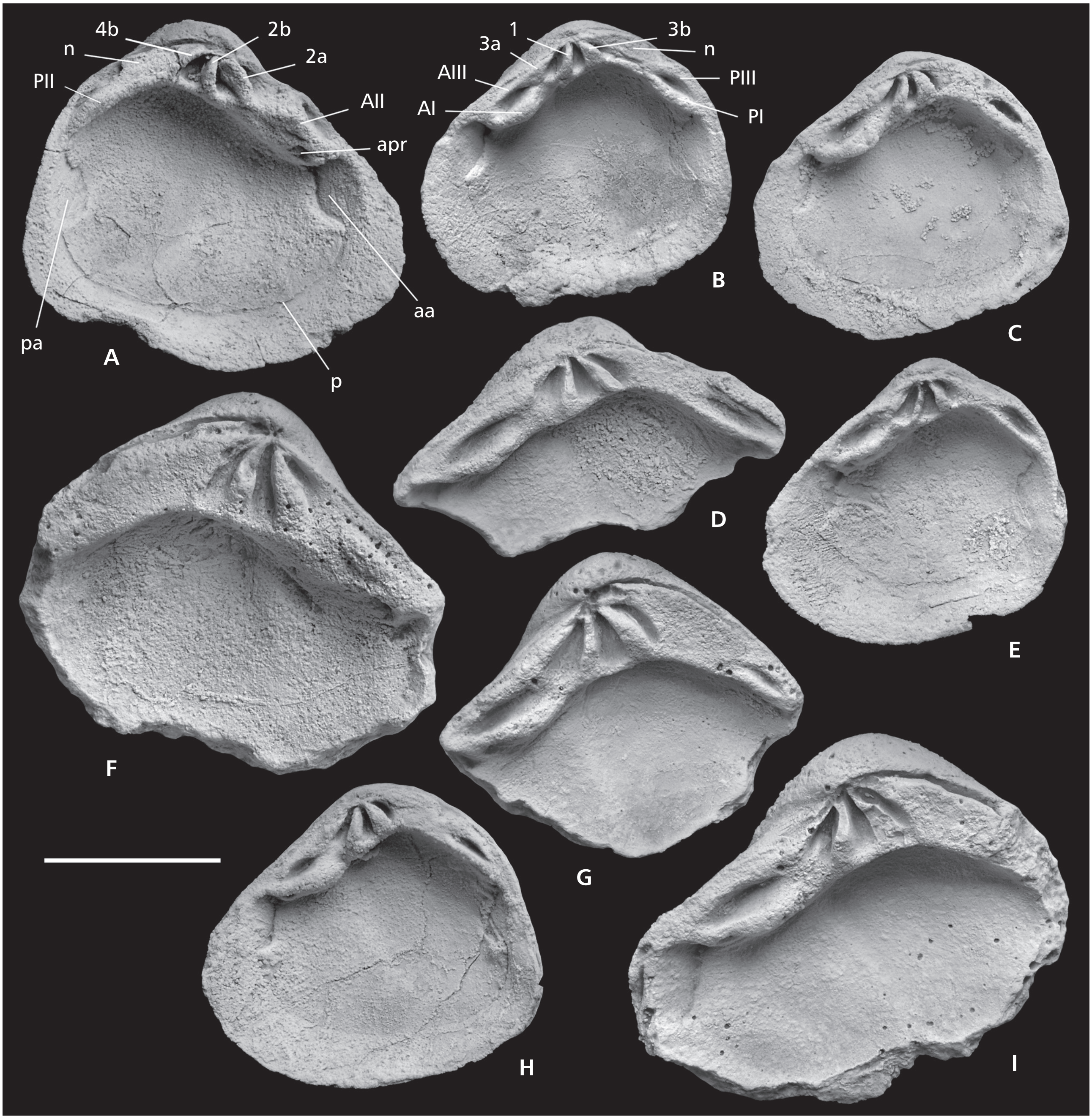

Figure 4. Cyrenidae from the Al-Khodh Formation. *Geloina amithoscutana* sp. nov. Inside views of several shells, displaying ontogenetic and intraspecific variability; A – left valve, holotype, locality MP10, ONHM-F-4411a; B – right valve, paratype 1, locality MP10, ONHM-F-4411b; C – right valve, paratype 3, locality MP10, ONHM-F-4411d; D – fragmentary right valve, paratype 6, locality MP 6, ONHM-F-4412c; E – right valve, paratype 18, locality MP10, ONHM-F-4411h; F – fragmentary left valve, paratype 5, locality MP 6, ONHM-F-4412b; G – fragmentary right valve, paratype 4, locality MP 6, ONHM-F-4412a; H – right valve, paratype 2, locality MP10, ONHM-F-4411c; I – fragmentary right valve, paratype 7, locality MP 6, ONHM-F-4412d. Notation of hinge teeth is AIII, AI, 3a, 1, 3b, PI, PIII for right valves, and AII, 2a, 2b, 4b, PII for left valves. Abbreviations: aa – anterior adductor muscle scar; apr – anterior pedal retractor muscle scar; n – nymph; p – pallial line; pa – posterior adductor muscle scar. Scale bar = 10 mm.

locality MP 14; ONHM-F-4414c. Paratype 6, fragmentary left valve (Fig. 5C); locality MP 13; ONHM-F-4415b. Paratype 7, double-valved specimen (Fig. 5E); locality MP 14; ONHM-F-4414d. Paratype 8, double-valved specimen (Fig. 5I); locality AK 51; ONHM-F-4433a.

Type horizon and locality. – Al-Khodh Formation, locality MP 14 (see Tab. 1).

Additional material. – Numerous additional double-valved specimens and single valves from the Al-Khodh

Formation at localities MP 8, MP 13, MP 14 and AK51.

Etymology. – Named after Magdalena Biszczuk, former GIS specialist at CASP, Cambridge, UK, who kindly prepared the map for Fig. 1, and many other maps before.

Diagnosis. – As for genus.

Description. – Shells up to 19.5 mm in height, moderately solid (see Tab. 3 for measurements). Shell outline ovate; umbo positioned slightly anterior to mid-line. Anterior-dorsal margin faintly incurved; all other margins gently and regularly rounded. Shell weakly inflated; umbo faintly protruding, slightly prosogyrate. No lunule, no escutcheon. Outside of shell ornamented with densely spaced, narrow, fairly regular commarginal costellae.

Hinge formula of right valve: AIII, AI, 3a, 1, 3b, PI, PIII. Cardinal teeth 1 and 3b prominent, of almost equal size, high triangular in shape, incipiently bifid at base; cardinal tooth 3a weak. Anterior lateral tooth AIII forming narrow, slightly elevated, almost straight ridge close to anterior-dorsal shell margin. Anterior lateral tooth AI prominent, markedly incurved. Posterior lateral tooth PI equally prominent; PIII faint and short. Hinge formula of left valve: AII, 2a, 2b, 4b, PII. Cardinal teeth 2a and 2b prominent, of almost equal size, high triangular in shape, incipiently bifid at base; cardinal tooth 4 weak. All hinge teeth smooth, not serrated. Nymphs elongate and distinct, not protruding over shell margin. Pallial line either entire, or with a very short sinus. Anterior and posterior adductor muscle scars of equal size, positioned directly below anterior and posterior ends of hinge plate, respectively. Anterior pedal retractor muscle scar positioned on ventral surface of hinge plate.

Class Gastropoda Cuvier, 1795
Subclass Caenogastropoda Cox, 1960
Unassigned to superfamily *sensu* Bouchet *et al.* (2017)
Family Pseudomelaniidae R. Hoernes, 1884

Remarks. – The genus *Pseudomelania* Pictet & Campiche, 1862 and consequently the family Pseudomelaniidae R. Hoernes, 1884 have been the subject of discussion since they were established. According to Pictet & Campiche (1862, p. 266), *Pseudomelania* is ‘turriculate, large, with a high spire, anomphalous, broad, with the ornament generally reduced to growth lines; the elliptic aperture possesses a rounded base and is adapically more or less acute angular, without a sinus or a canal. Without having internal plaits, the shape of the thick columella coincides with the general outline of the aperture. The labrum is smooth without being reinforced or dentate’ (translated from French; slightly modified).

Table 3. Measurements of *Muscatella biszczukae* sp. nov., in mm. The value in squared brackets is an estimate for maximum length in *M. biszczukae*. Abbreviations: H – height; L – length; T – thickness.

Specimen	L	H	T
Paratype 3, ONHM-F-4416a (Fig. 5B)	19	13	8
Paratype 4, ONHM-F-4416b (Fig. 5A)	12.5	8.5	5
Paratype 5, ONHM-F-4414c (Fig. 5H)	[33]	19.5	\
Paratype 7, ONHM-F-4414d (Fig. 5E)	20.5	13.5	8.5
Paratype 8, ONHM-F-4433a (Fig. 5I)	21.5	12	8

Within the new genus, Pictet & Campiche (1862) described three new species, *Pseudomelania gresslyi* (p. 266, pl. 70, figs 1, 2), *P. jaccardi* (p. 268, pl. 70, figs 3–5) and *P. germani* (p. 269, pl. 70, figs 6–8), which are all based on internal moulds, and, as a result, show only a few distinctive characters.

Pictet & Campiche (1862) did not select a type species for *Pseudomelania*. Subsequently, P. Fischer (1887, p. 697) designated *Chemnitzia normaniana* d’Orbigny, 1851 (p. 40) as type species, which, however, was not originally included in *Pseudomelania* by Pictet & Campiche (1862), and is thus not available as a type. After half a century of taxonomic confusion, Wenz (1938, p. 372) finally selected one of the three originally included species, *Pseudomelania gresslyi*, as type species of *Pseudomelania*. Among the species described by Pictet & Campiche (1862), *Pseudomelania gresslyi* is most complete and thus definitely the primary choice for the type species. It differs from the other two species by its cyrtoconoid outline and convex whorls, of which the final one is about half the total height. Actually, these features do not fully agree with the general description of *Pseudomelania* given by Pictet & Campiche (1862), but the moulds attributed to *Pseudomelania jaccardi* and *P. germani* are not adequately preserved for determining their generic position.

In this context, it is striking that Wenz (1938, p. 372) reproduced the well-preserved *Chemnitzia heddingtonensis* as figured by d’Orbigny (1851, pl. 244, fig. 3) (= *Melania heddingtonensis* J. Sowerby, 1813) to illustrate this genus. However, Gründel (2012) introduced the new genus *Torusiana* with *Melania heddingtonensis* J. Sowerby, 1813 as type species. According to Gründel (2012), the characteristic morphological feature of the new genus is a bulge at the adapical suture, delimited abapically by a constriction of the whorl surface. This adapical bulge is located in the continuation of a small expansion of the aperture. Due to the consistence of this morphological feature a connection with the soft-part anatomy can be assumed. It obviously represents an adapical widening of the mantle cave, which may have served the expelling of water loaded with faeces. There is no trace of the bulge on internal moulds.

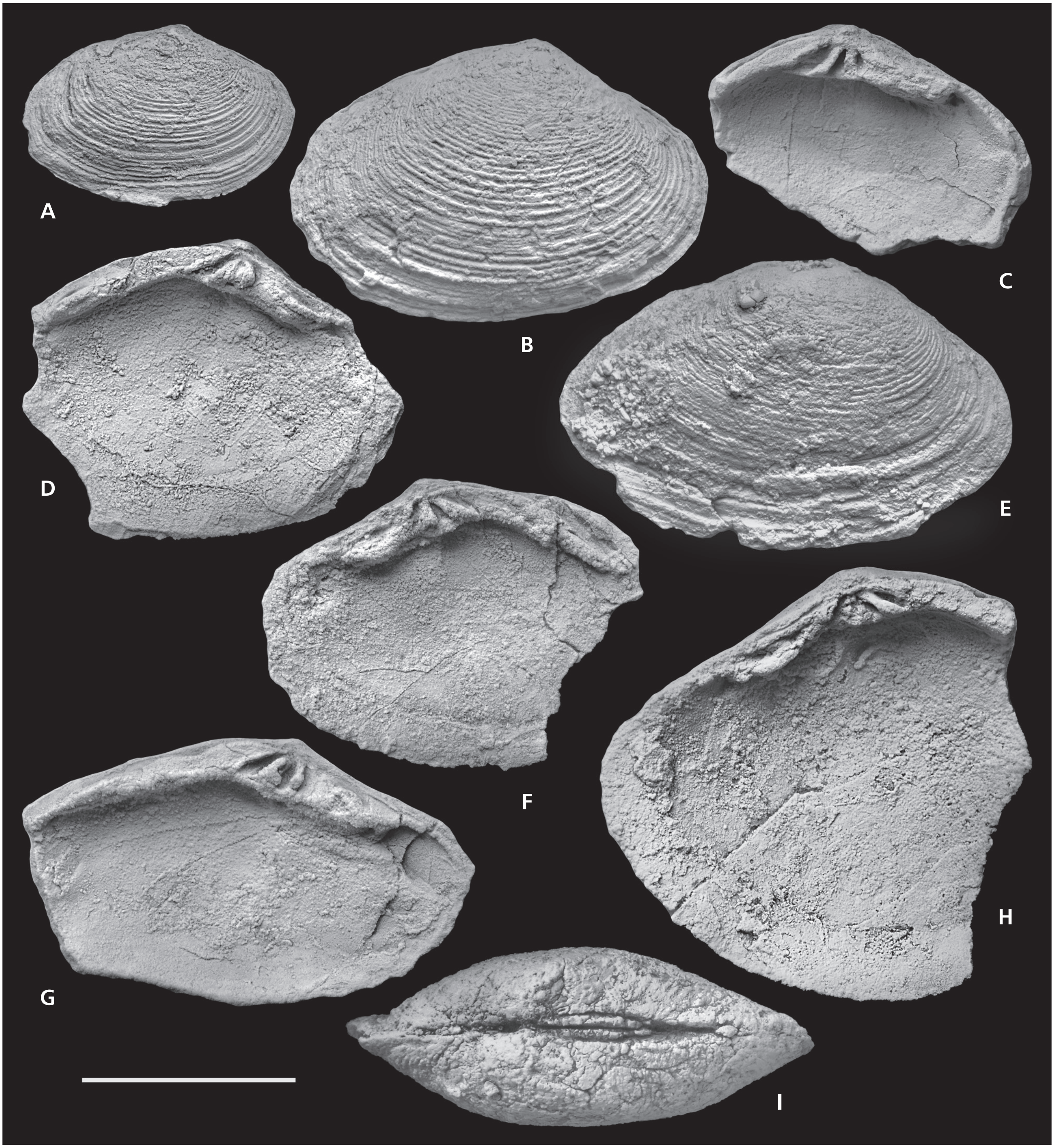

Figure 5. Cyrenidae from the Al-Khodh Formation. *Muscatella biszczukae* gen. et sp. nov.; A – subadult double-valved specimen, right-lateral view, paratype 4, locality MP 8, ONHM-F-4416b; B – double-valved specimen, right-lateral view, paratype 3, locality MP 8, ONHM-F-4416a; C – fragmentary left valve from inside, paratype 6, locality MP 13, ONHM-F-4415b; D – fragmentary left valve from inside, paratype 1, locality MP 13, ONHM-F-4415a; E – double-valved specimen, right-lateral view, paratype 7, locality MP 14, ONHM-F-4414d; F – fragmentary right valve from inside, holotype, locality MP 14, ONHM-F-4414a; G – fragmentary left valve from inside, paratype 2, locality MP 14, ONHM-F-4414b; H – fragmentary right valve from inside, paratype 5, locality MP 14, ONHM-F-4414c; I – double-valved specimen, view from top, paratype 8, locality AK 51, ONHM-F-4433a. Scale bar = 10 mm.

The adapical bulge had already been mentioned by J. Sowerby (1813) in the original description of *Melania lineata* ('a very slight contraction towards the upper part of each whorl'), and in fact, the majority of species hitherto assigned to *Pseudomelania* shows this feature. Ten Jurassic species described by d'Orbigny under *Chem-*

nitzia and assigned to *Pseudomelania* by Fischer & Weber (1997), as well as *Pseudomelania feruglioi* Ferrari, 2013 from the Early Jurassic of Argentina, were included in *Pseudomelania* by Gründel (2012).

Genus *Subtemenia* gen. nov.

Type species. – *Paryphostoma morgani* Douvillé, 1904 (p. 328; Maastrichtian; Iran), by original designation herein.

Etymology. – From the Latin word for thread, *subtemen*, referring to the linear suture.

Diagnosis. – Shells large, broadly turriculate, with generally flat whorls and linear sutures. Last whorl high, with broadly rounded or subangular periphery. Growth lines slightly opisthocyrt. Aperture broadly rounded at the base and angular adapically, with a moderately broad and reinforced outer lip.

Remarks. – Following the attribution of the type species by Douvillé (1904), *Subtemenia* gen. nov. is assigned to the Pseudomelaniidae. Douvillé (1904) stated: 'We provisionally unite under the name (pseudomelaniids) all these elongate marine shells with an entire aperture, which resemble melaniids in shape.' [translated from French]

The broad turriculate outline, the flat to moderately convex whorls, the proportions of the last whorl, the opisthocyrt growth lines, which indicate a slightly sinuous labrum, and, last but not least, the large size support the systematic position of *Subtemenia* gen. nov. In contrast to *Pseudomelania*, *Subtemenia* possesses no subsutural bulge. The specimens figured by Douvillé (1904) show a change of morphology during ontogeny. The whorl flank is delimited towards the base by a rounded periphery in smaller specimens, which becomes more or less angular in large ones.

Douvillé (1904) originally assigned his new species to *Paryphostoma* Bayan, 1873, which was established to replace *Keilostoma* Deshayes, 1848, according to Bayan (1873) because of the great similarity of this name with *Chilostoma* Fitzinger, 1833 (Helicidae). Cossmann (1921) followed Bayan in his argumentation. However, since the spelling of the two names is significantly different, *Paryphostoma* Bayan, 1873 is an unnecessary replacement name, and thus invalid. This was already acknowledged by Wenz (1939), who treated *Paryphostoma* as a junior synonym of *Keilostoma*. Members of the latter genus are usually small to very small and possess an almost circular aperture in which the outer lip is heavily reinforced.

Subtemenia morgani **(Douvillé, 1904)**

Figure 6A–F

*1904 *Paryphostoma Morgani* n. sp.; Douvillé, p. 328, pl. 46, figs 12–17.
1928 *Keilostoma* (*Paryphostoma*) *morgani*. – Lees, p. 651.
1929 *Paryphostoma morgani*. – Kühn, p. 19.
1995 *Paryphostoma morgani* Douvillé. – Smith *et al*., p. 119.

Material. – Several fragments have been extracted from sandstone and granule-sized conglomerate of the Al-Khodh Formation at localities AK 33 [ONHM-F-4420a, b], AK 51 [ONHM-F-4422a–d], MP 2 [1 spec.], MP 5 [ONHM-F-4434a], MP 7 [ONHM-F-4435a] and MP 13 [ONHM-F-4421a].

Description. – Apical angle of shell approximately 15°. Body whorl moderately convex; earlier whorls flat; sutures hardly impressed. Sculpture consisting of sporadic remains of nodose spiral threads, obviously originally covering the entire surface. Last whorl showing orthocline impressions of growth rugae. Whorl sides passing smoothly into rounded base. Base of aperture rounded. Adapical angle of aperture approximately 50°. Columella low, concave. Parietal lip slightly expanded and reinforced. Margin of labrum acute. Measurements are listed in Tab. 4.

Remarks. – In the specimens figured by Douvillé (1904), the sculpture of spiral threads is well-preserved. The large specimen (figs 14, 15) and one of the smaller ones (fig. 13) possess a blunt peripheral angle. In the small specimen of figures 12 and 16, the periphery is evenly rounded, as in most of the specimens collected in Oman. The slight variability with regard to the shape of the whorl periphery is attributed to intraspecific variability.

Occurrence. – *Paryphostoma morgani* was originally described from Maastrichtian strata in Lorestan Province, western Iran (Douvillé 1904). The species has previously been recorded from the Maastrichtian of Oman, from highly diverse shallow marine assemblages in the area of Al Ayn (Lees 1928, Kühn 1929, Smith *et al*. 1995).

Superfamily Cerithioidea Fleming, 1822
Family Hemisinidae P. Fischer & Crosse, 1891

Genus *Stephaniphera* gen. nov.

Type species. – *Stephaniphera coronata* gen. et sp. nov.

Etymology. – From the Greek words for crown and carrying, *stephanos* and *phero*, referring to the ornamentation of the shells.

Diagnosis. – Shell large (up to 45 mm high); whorls high and cylindrical in outline. Early ontogenetic whorls possessing subsutural collar; later ones possessing broad, depressed ramp with strong nodes at its outer margin.

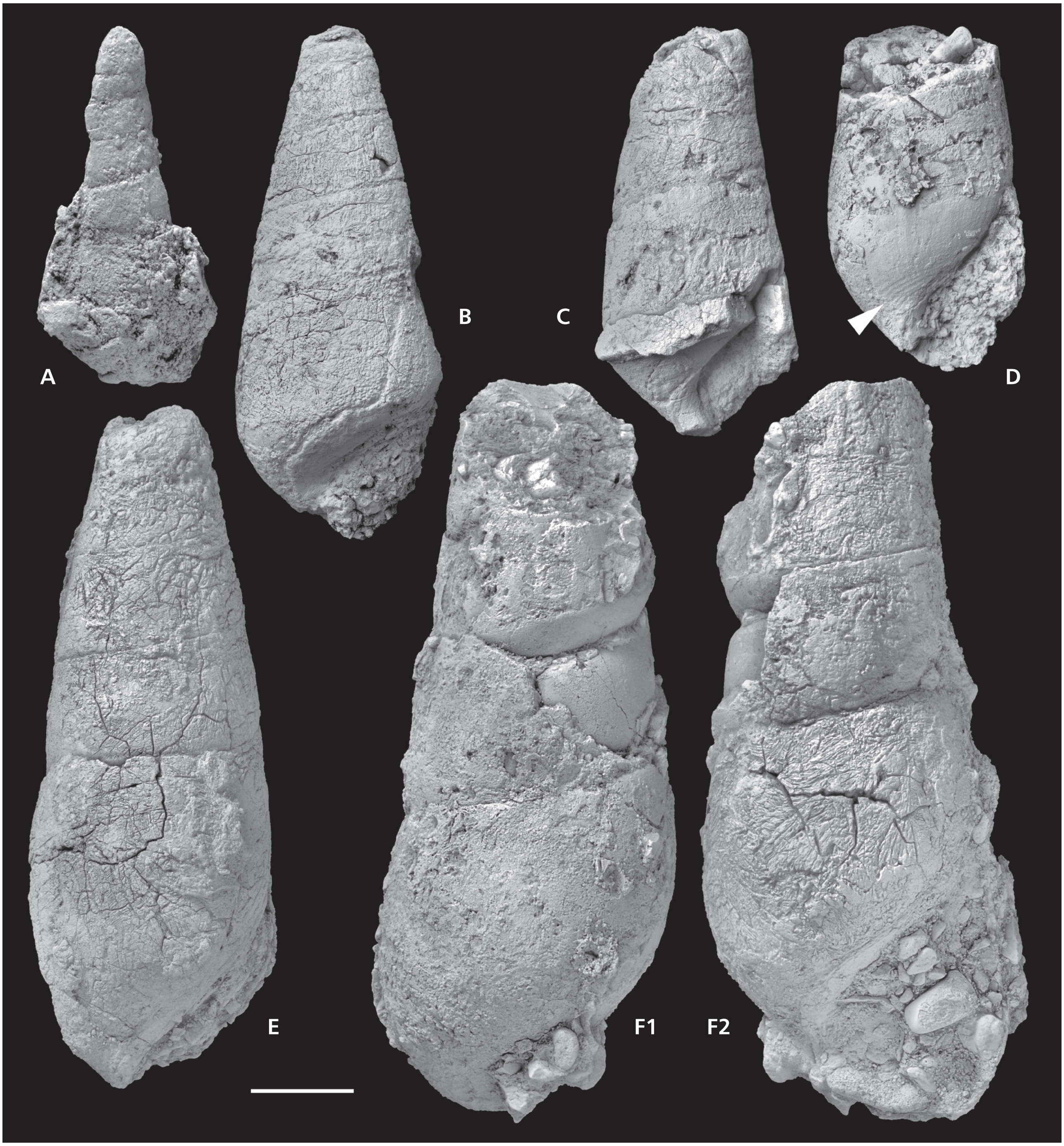

Figure 6. Pseudomelaniidae from the Al-Khodh Formation. *Subtemenia morgani* (Douvillé, 1904); A – apical fragment, locality MP 5, ONHM-F-4434a; B – almost complete specimen from front, locality AK 51, ONHM-F-4422a; C – fragmentary specimen from front, locality AK 51, ONHM-F-4422b; D – fragmentary specimen from front, with delicate spiral furrows on adabical part of last whorl indicated by white arrow, locality AK 51, ONHM-F-4422c; E – fragmentary specimen from front, locality AK 33, ONHM-F-4420a; F – fragmentary specimen from back (F1) and front (F2); locality MP 7, ONHM-F-4435a. Scale bar = 10 mm.

Aperture high, narrow elliptic. Columellar lip concave, truncated towards the deep basal notch.

Remarks. – *Stephaniphera* is distinguished from the Purpurinidae Zittel by its truncated columella, the deep basal notch and the broad subsutural ramp. As in *Stephaniphera* gen. nov., a truncated columella and a deep basal notch are morphological characters of *Hemisinus* and other genera combined in the subfamily Hemisininae P. Fischer & Crosse, 1891, which was treated as a syno-

Table 4. Measurements of *Subtemenia morgani* (Douvillé, 1904), in mm. Abbreviations: AA – apical angle; H – height; HB – height of last whorl; W – width.

Specimen	H	HB	W	AA
ONHM-F-4434a (Fig. 6A)	17	12.5	8	15
ONHM-F-4422a (Fig. 6B)	49	24.5	19.5	25
ONHM-F-4422b (Fig. 6C)	39	15	19	21
ONHM-F-4422c (Fig. 6D)	33	16.5	18	\
ONHM-F-4420a (Fig. 6E)	61.5	38	25.5	26
ONHM-F-4435a (Fig. 6F)	71.5	42.5	29	17

Table 5. Measurements of *Stephaniphera coronata* sp. nov., in mm. Abbreviations: AA – apical angle; H – height; HB – height of last whorl; W – width.

Specimen	H	HB	W	AA
Holotype, ONHM-F-4417a (Fig. 7A)	42	25	26.5	76
Paratype 1, ONHM-F-4417b (Fig. 7B)	37.5	21	25	68
Paratype 2, ONHM-F-4418a (Fig. 7C)	26.5	20.5	15	53
Paratype 3, ONHM-F-4417c (Fig. 7D)	43	27	30.5	88
Paratype 4, ONHM-F-4417d (Fig. 7E)	44	29	33	85
Paratype 5, ONHM-F-4417e (Fig. 7F)	39	25	25	\

nym of Thiaridae Gill, 1871 by Bouchet & Rocroi (2005). Recently, Hemisinidae P. Fischer & Crosse, 1891 was re-established at family rank by Bouchet *et al.* (2017). The morphological features show a close affinity of *Stephaniphera* to *Hemisinus* Swainson, 1840 and other related genera. *Pyrgulifera* Meek, 1871, differs by its almost circular aperture and a small basal notch.

***Stephaniphera coronata* gen. et sp. nov.**
Figure 7A–F

Types.–Holotype (Fig. 7A); locality AK 51; ONHM-F-4417a. Paratype 1 (Fig. 7B); locality AK 51; ONHM-F-4417b. Paratype 2 (Fig. 7C); locality MP 14; ONHM-F-4418a. Paratype 3 (Fig. 7D); locality AK 51; ONHM-F-4417c. Paratype 4 (Fig. 7E); locality AK 51; ONHM-F-4417d. Paratype 5 (Fig. 7F); locality AK 51; ONHM-F-4417e.

Type horizon and locality. – Al-Khodh Formation, locality AK 51 (see Tab. 1).

Additional material. – Several specimens from the Al-Khodh Formation at locality AK 51; ONHM-F-4417f–j.

Etymology. – From the Latin word for crowned, *coronatus*, referring to the row of prominent nodes on the outer margin of the subsutural ramp.

Diagnosis. – As for genus.

Description. – Shells high with last whorl taking approximately two thirds of total height. Early whorls almost flat, with inclined subsutural collar, later passing into broad, depressed ramp. Ramp delimited by distinct edge with large rounded, abapically extended nodes. Nodes decreasing in size at approach to aperture; simultaneously, distance between nodes reduced to almost zero. Shell with distinct growth lines. Aperture high, narrow elliptic; outer margin sharp. Columellar lip concave, slightly expanded, abapically truncated, leaving space for deep basal notch. Measurements are listed in Tab. 5.

Remarks. – The sculpture of *Stephaniphera coronata* gen. et sp. nov. is comparable to that of *Chemnitzia inflata* d'Orbigny, 1842. Despite the small basal notch in the type species (see Roman & Mazeran 1920, Kollmann 2005), the figure by d'Orbigny (1842, p. 156, fig. 2) shows a rounded base. This obviously motivated Roman & Mazeran (1920) and Delpey (1937) to assign *Chemnitzia inflata* to *Microschiza* Gemmellaro, 1878 and to *Coronatica* Blanckenhorn, 1927, respectively. The species differs from *Stephaniphera coronata* gen. nov. sp. nov. by its oblique columella, which is not truncated but decreases in thickness towards the base. Kollmann (2005) attributed *Chemnitzia inflata* to the Melanopsidae genus *Megalonoda* Kollmann, 1984 (see also Neubauer *et al*. 2016).

Family Turritellidae Lovén, 1847

Genus *Torquesia* Douvillé, 1929

Type species. – *Turritella granulata* J. de C. Sowerby, 1827 (Eocene, England), by subsequent designation; Opinion 493 (1957).

Remarks. – *Torquesia* Douvillé 1929 is distinguished from *Turritella* by the deep sinus of the growth lines, with its vertex around mid-whorl and points of inflection below and above. The whorls are flat with beaded spiral cords, of which the adapical one ist most prominent.

***Torquesia contumescens* (Stoliczka, 1868)**
Figure 8A–D

1868 *Turritella contumescens*, Stoliczka, p. 221, pl. 16, fig. 17; pl. 19, fig. 17.

Material. – Four fragmentary specimens from the Jafnayn Limestone Formation at locality Fanja Back; ONHM-F-4423a–d.

Description. – Shell narrow turriculate. Growth lines forming deep sinus at mid-whorl, with points of in-

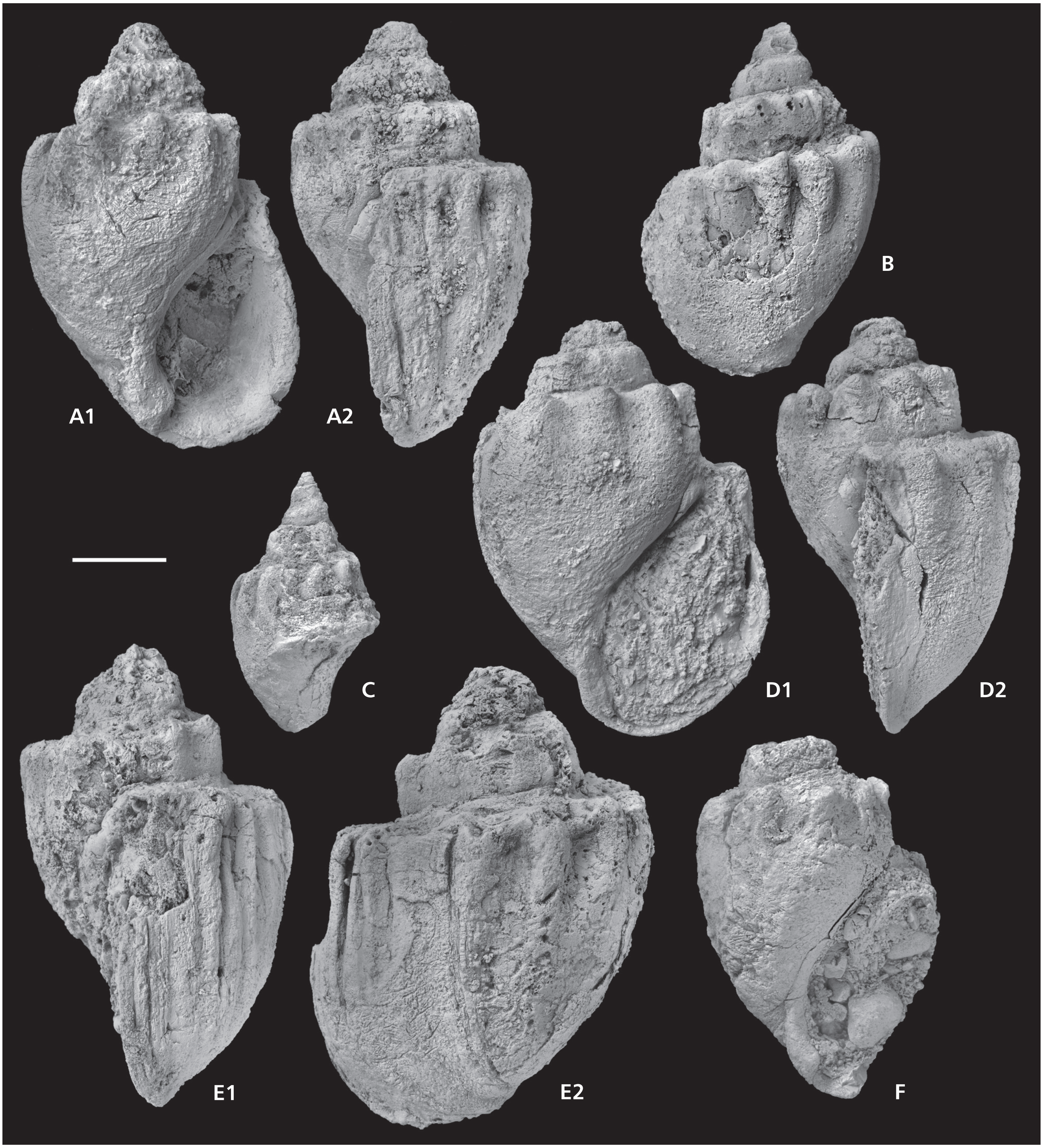

Figure 7. Hemisinidae from the Al-Khodh Formation. *Stephaniphera coronata* gen. et sp. nov.; A – adult specimen from front (A1) and right (A2), holotype, locality AK 51, ONHM-F-4417a; B – subadult specimen from back, paratype 1, locality AK 51, ONHM-F-4417b; C – fragmentary juvenile from front, paratype 2, locality MP 14, ONHM-F-4418a; D – adult specimen from front (D1) and right (D2), paratype 3, locality AK 51, ONHM-F-4417c; E – adult specimen from right (E1) and back (E2), paratype 4, locality AK 51, ONHM-F-4417d; F – fragmentary adult specimen from front, paratype 5, locality AK 51, ONHM-F-4417e. Scale bar = 10 mm.

flection adapically and abapically. Whorls slightly depressed around vertex of growth lines. Four specimens representing different growth stages with changing sculpture. Whorl heights of smallest specimen between 7 and 10 mm, with sculpture consisting of two prominent beaded cords adapically, two less prominent ribs and threads on depressed portion, and two stronger cords abapically, the lower one located at margin towards flat base. At whorl height of approximately 15 mm, broad, pillow-like nodes developing at the two adapical cords. Numerous weak ribs and threads developed in median concave zone; abapically, numerous beaded threads occurring between the two cords. Two adapical cords transforming into prominent adapical bulge at whorl height of 20 mm. Numerous threads of variable strength covering space between bulge and single cord delimiting the base.

Measurements: H (incomplete) = 26.5–44 mm; HB = 11.5–18 mm; W = 12.5–20 mm; AA = 10–11°.

Remarks. – The specimens are assigned to *Torquesia contumescens* because of the deep sinus of the growth lines and the prominent adapical bulge developing from two cords of earlier whorls. The two figures of a single whorl provided by Stoliczka (1868) show three beaded cords, a smooth cord at the abapical suture and threads between them. The figure by Stoliczka agrees in general with that of the medium-size whorls described here.

Occurrence. – This species was originally described by Stoliczka (1868) from the Ariyalur Group in the surroundings of Ariyalur in Tamil Nadu, southeastern India. An additional record by Dartevelle & Brebion (1956) comes from Gabon, West Africa.

Family Thiaridae Gill, 1871

Genus *Cosinia* Stache, 1880

Type species. – *Paludomus cosinensis* Stache *in* Sandberger, 1871 (Cretaceous; Slovenia), by subsequent designation by Cossmann (1909).

***Cosinia* sp.**
Figure 9B

Material. – A single specimen from the Jafnayn Limestone Formation at locality Fanja Back; ONHM-F-4424a.

Description. – Specimen incomplete, of medium size, almost as broad as high. Whorls generally convex, with moderately inclined narrow adapical ramp. Last whorl comprising approximately two thirds of total height. Remains of sculpture of delicate spiral threads preserved at base. Growth lines around the centre yielding evidence of narrow basal notch. Aperture narrow elliptic with straight parietal lip and concave columella.

Measurements: H = 15.3 mm; HB = 9 mm; W = 12.2 mm; AA = 75°.

Remarks. – Stache (1889) described several species under *Cosinia*. As in the fragmentary remains of the present specimen, the sculpture consists of delicate spiral threads. However, the whorls of the species attributed to *Cosinia* by Stache possess a broad adapical shoulder (not a narrow, inclined ramp as in *Cosinia* sp.); the profile of the transition to the abapical part of the whorls varies from angular to rounded in Stache's material. Because of their similar morphologies the species described by Stache are regarded as varieties of *Cosinia bicincta* Stache, 1889 herein. The basal notch was figured in pl. 1, figs 21a and 25a.

Stache (1889) attributed *Cosinia* to his newly established subfamily Stomatopsinae. Indeed, *Cosinia* possesses the narrow basal notch that is characteristic of this subfamily, which corroborates this assignment. Bouchet & Rocroi (2005) considered the Stomatopsinae to be synonymous with the Melanopsidae H. Adams & A. Adams, 1854. Following remarks by Neubauer (2016), Bouchet *et al*. (2017) re-established Stomatopsinae and moved it to the Thiaridae.

Family Batillariidae Thiele, 1929

Genus *Pyrazus* Montfort, 1810

Type species. – *Pyrazus baudini* Montfort, 1810 (Recent; Australia), by original designation [= *Pyrazus ebeninus* (Bruguière, 1792)].

***Pyrazus* sp.**
Figure 9A

Material. – A single specimen from the Jafnayn Limestone Formation at locality Fanja Back; ONHM-F-4425a.

Description. – Shell narrow turriculate. Ontogenetically early whorls convex with narrow subsutural collar. Sculpture incompletely preserved; consisting of 10 orthocline collabral ribs, aligned on successive whorls and crossed by three spiral threads. In ontogenetically later whorls, strong nodes developing at crossing points of collabral ribs with external angle of collar; spiral threads distributed all over the whorls. Breadth of subsutural collar and its angle towards shell axis increasing on final whorl; nodes becoming more prominent. Nodes decreasing in number and size towards aperture; finally replaced by squamous ledge. Abapical part of last whorl fragmentary. Preserved part of columellar lip strongly reinforced. Expansion of peristome triangular; located at margin towards (not preserved) parietal lip, enclosing narrow adapical canal. Growth lines opisthocyrt. Ventrolateral varix opposite aperture not elevated above shell surface, but contrasting with growth lines due to its lighter colour.

Measurements: H = 41.5 mm; HB = 22 mm; W = 17.5 mm; AA = 24°.

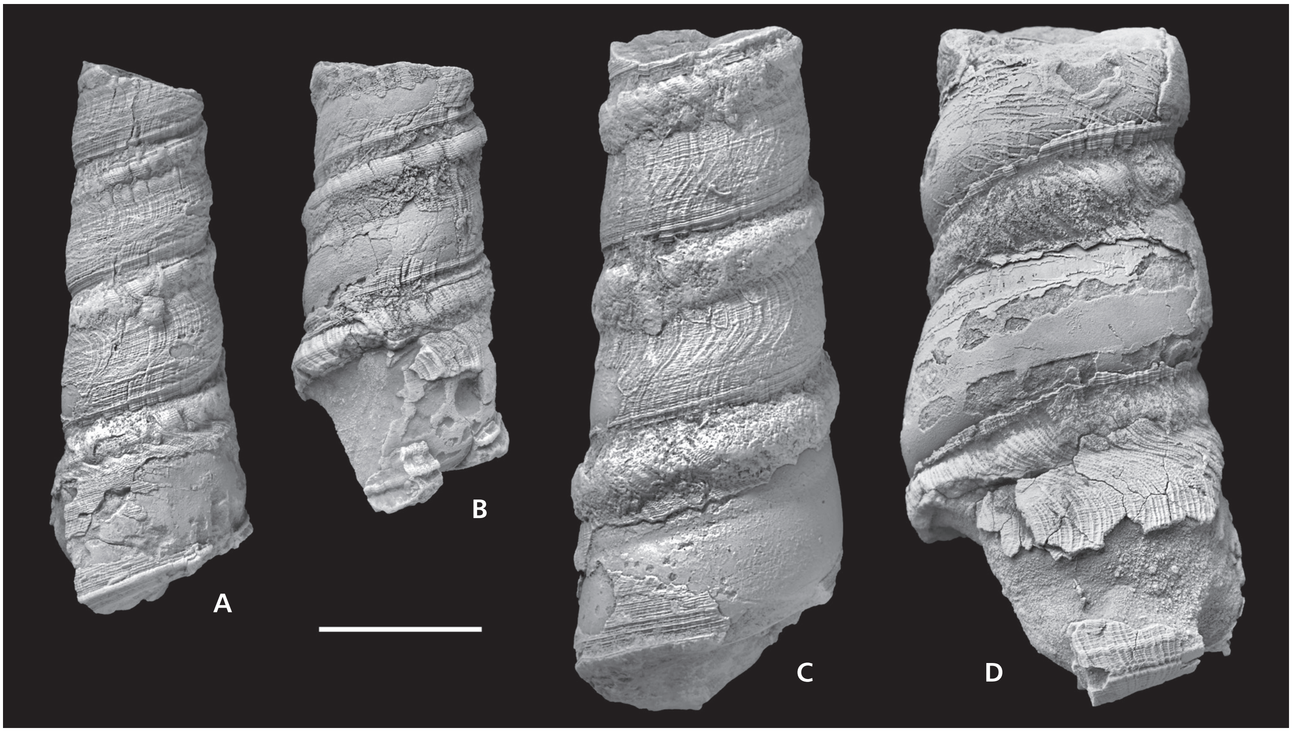

Figure 8. Turritellidae from the Jafnayn Limestone Formation at locality 'Fanja Back'. *Torquesia contumescens* (Stoliczka, 1868); A – ONHM-F-4423a; B – ONHM-F-4423b; C – ONHM-F-4423c; D – ONHM-F-4423d. Scale bar = 10 mm.

Remarks. – The taxonomic distinction and systematic position of *Pyrazus* were the subject of extensive discussion (see Ozawa *et al*. 2009 and references therein). According to Ozawa *et al.* (2009), who provided the latest opinion on this matter, *Pyrazus* belongs to the family Batillariidae. It is distinguished from members of the Potamididae by its straight columella lacking twists or folds, and the absence of varices on the spire whorls (Ozawa *et al*. 2009). *Pyrazus* differs from other batillariid genera by the presence of a ventrolateral varix on the final whorl. Both *Pyrazus* and *Pyrazisinus* Heilprin, 1887 possess an adapical canal, but are distinguished by the shape of their whorls, which are strongly convex with deep sutures in *Pyrazisinus*, but angular with moderately deep sutures in *Pyrazus*.

Originally, the genus *Pyrazus* comprised only extant species (see Healy & Wells 1998). However, Marwick (1929) and Powell & Bartrum (1929) described three new Pleistocene species from New Zealand under this generic name (*Pyrazus weitemaetensis*, *P. consobrinus* and *P. sutherlandi*). Of these, *P. weitemaetensis* was later attributed to the cerithiid genus *Gourmya* by Houbrick (1984), and Beu *et al*. (2004) transferred all three species to the Potamididae genus *Terebralia* Swainson, 1840. However, based on the figures published by Powell & Bartrum (1929), Ozawa *et al*. (2009) inferred close affinities of *Pyrazus consobrinus* and *P. sutherlandi* with *Pyrazus ebeninus* (Bruguière, 1792), the type species of the genus. The new record from the Jafnayn Limestone Formation (if not a case of convergence) considerably extends the range of the genus into at least the Palaeocene, if not the latest Cretaceous (see discussion below).

Family Ampullinidae Cossmann *in* Cossmann & Peyrot, 1919

Genus *Amaurellina* Bayle *in* P. Fischer, 1885

Type species. – *Ampullaria spirata* Lamarck, 1804 (Eocene; France), by monotypy.

***Amaurellina nuttalli* (Douvillé, 1929)**
Figure 9C

*1929 *Naticina nuttalli*; Douvillé, p. 59, pl. 9, figs 25–28.

Material. – A single specimen from the Jafnayn Limestone Formation at locality Fanja Back; ONHM-F-4426a.

Description. – Shell consisting of convex whorls with narrow subsutural ramp. Suture impressed. Last whorl accounting for approximately two thirds of total height, almost globular in shape. Aperture elongate elliptical; columellar lip thin, moderately convex. Strong lamella extending from base into umbilicus.

Measurements: H = 21.5 mm; HB = 15.5 mm; W = 17 mm; AA = 90°.

Remarks. – Douvillé (1929) figured several specimens of variable size of this species. In small specimens, the umbilicus is narrow with a rounded margin (Douvillé 1929, fig. 28), while fig. 26 shows a well-developed lamella extending into the umbilicus as is recorded here. This morphological character, the high spire and the broad aperture suggest assignment to *Amaurellina*, and distinguish *Amaurellina nuttalli* from other Naticoidea.

Occurrence. – This species was originally described from the Maastrichtian or Danian '*Cardita beaumonti* Beds' of Balochistan Province in southwestern Pakistan (Douvillé 1929; see Crame 2013 and discussion below).

Infraclass Euthyneura
Order Ringiculimorpha
Superfamily Ringiculoidea Philippi, 1853
Family Ringiculidae Philippi, 1853

Ringiculidae sp. indet.
Figure 9D

Material. – A single specimen from the Al-Khodh Formation at locality MP 7; ONHM-F-4427a.

Description. – Shell outline elliptic. Spire low. Earliest preserved whorls moderately convex, with narrow, inclined subsutural ramp and remains of delicate collabral ribs. Traces of delicate spiral threads are preserved on last whorl. Aperture high elliptical, with narrow adapical channel. Narrow basal channel only partly preserved. Callous inner lip bearing two blunt columellar plaits and a thin, incompletely preserved parietal plait or tooth. Labrum not preserved.

Measurements: H = 15.5 mm; HB = 12.5 mm; W = 10 mm; AA = 40°.

Remarks. – Due to the rather poor preservation of the single specimen from Oman, we refrain from generic or specific assignment. *Ringinella acuminata* Stoliczka, 1868 from the Ariyalur Group at Comarapolliam near Ariyalur in Tamil Nadu, southeastern India, differs by its higher spire 'consisting of numerous, slightly convex volutions' (Stoliczka 1868, p. 423). Its variability, however, is unknown.

Discussion

Palaeobiogeography and biostratigraphy

Today, the Arabian Peninsula has a hot, arid climate and thus has hardly any lakes or permanent rivers. As a result, the peninsula is devoid of any larger freshwater bivalves, and forms a distribution gap between the Nile bio-province of Afrotropica and the Middle East bio-province of Palaearctica (Neubert 1998, Graf & Cummings 2007, Bogan 2008). During the latest Pleistocene, short-lived, shallow lakes existed in the Rub'al Khali desert of Saudi Arabia, approximately 150 km north of the present-day border to Yemen (McClure 1984). Fossil freshwater molluscs from these lakes had first been reported by Philby (1933) and later figured by McClure (1984). These include the only previous record of unionids from the Arabian Peninsula we are aware of, *Unio terminalis* Bourguignat, 1852. The status and (current) distribution of this species in the Middle East are unresolved (Araujo *et al*. 2018), but it is part of a clade of Western Palaearctic origin, and thus certainly not closely related to the fossil unionids from Al-Khodh.

At the time of deposition of the Al-Khodh Formation, the Arabian Plate was still part of Africa. Rifting of the Red Sea had not started until the late Oligocene, when also the seaway connecting the Mediterranean Sea and the Indian Ocean started to close (*e.g*. Harzhauser *et al*. 2002, Bosworth 2015). During the latest Cretaceous, the study area in Oman was situated on the north coast of a large island at the eastern margin of a wide epicontinental sea covering large areas of the present-day Arabian Peninsula, and was facing the Tethys Ocean to the northeast (*e.g.* Scotese 2013).

The fossil unionids described herein thus possibly had closer affinities to the African freshwater fauna than to the Asian biota. Van Damme *et al*. (2015) recently reviewed the African Mesozoic fossil record of the Unionida. All species described are significantly older than the fossils from Oman, the youngest ones being Coniacian to Santonian in age. Due to both the limited preservation of our material and the poor fossil record of unionids in the wider region, the specimens from Oman currently have no implications beyond adding a dot – though a valuable one – on the map.

A look at the freshwater to brackish-water Cyrenidae is more informative. The extant freshwater genus *Corbicula* Megerle von Mühlfeld, 1811, includes several invasive species and has a near-global distribution. On the Arabian Peninsula, *Corbicula* is represented by a single native species, *Corbicula fluminalis* (O.F. Müller, 1774) (synonym: *Corbicula purpurea* Prime, 1867; see Huber 2015), in coastal Saudi Arabia between Kuwait and Qatar (Neubert 1998). The same species occurred in short-lived shallow lakes in the Rub'al Khali desert in southern Saudi Arabia, not far from the border to Yemen, during the latest Pleistocene (listed as *Corbicula crassula* by McClure 1984). Although cyrenid phylogeny is still poorly resolved (*e.g*. Graf 2013, Huber 2015), it is evident that the Quaternary *Corbicula fluminalis* and the fossil species from Al Khodh are only distantly related.

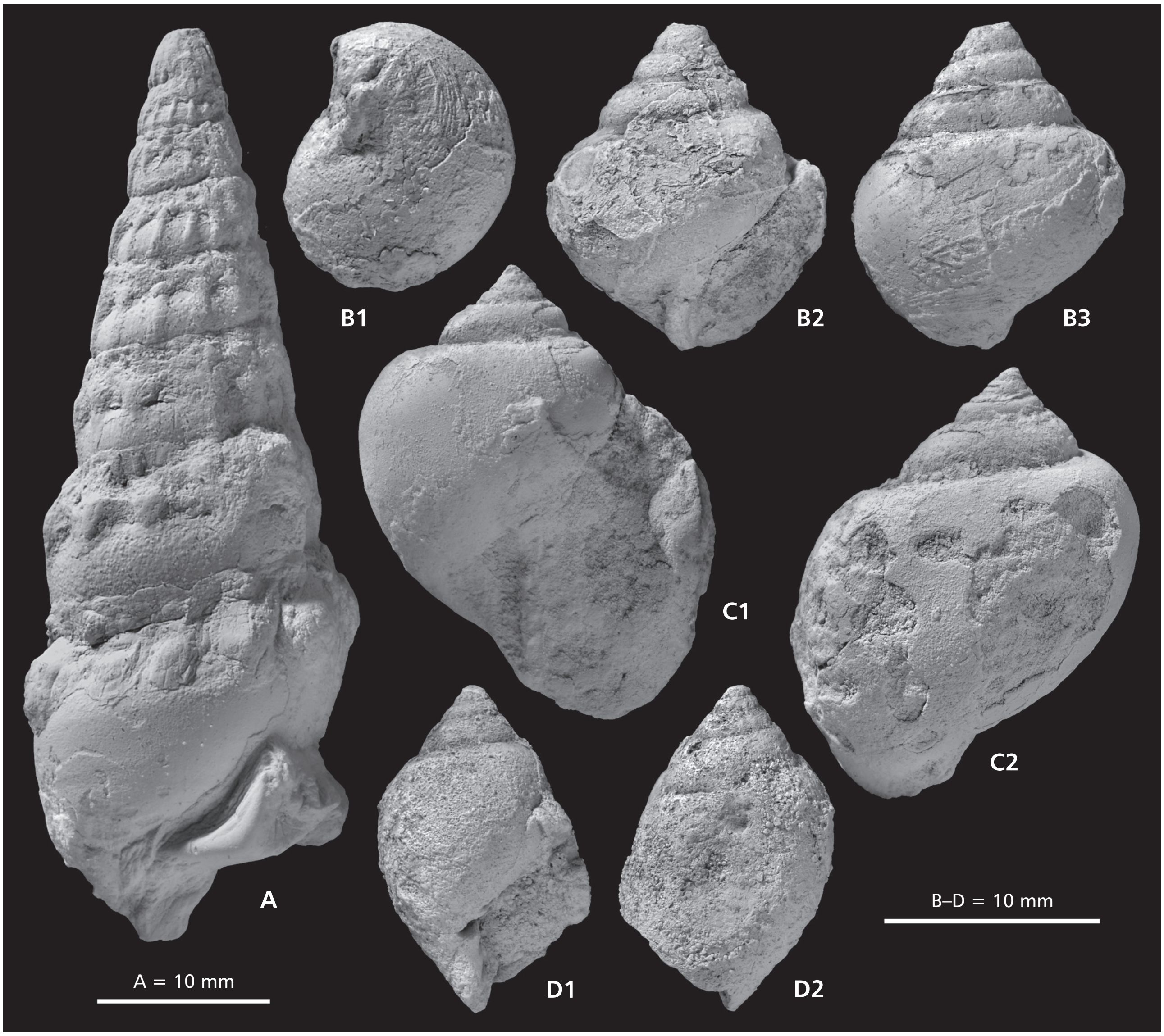

Figure 9. Molluscs from the Jafnayn Limestone Formation at locality 'Fanja Back'. • A – *Pyrazus* sp.; ONHM-F-4425a. • B – *Cosinia* sp.; ONHM-F-4424a. • C – *Amaurellina nuttalli* (Douvillé, 1929); ONHM-F-4426a. • D – Ringiculidae gen. et sp. indet.; ONHM-F-4427a. Scale bars = 10 mm.

However, Cyrenidae have a fossil record dating back to the Early Jurassic and were widespread in Europe and Asia during the Cretaceous (Casey 1955, Keen & Casey 1969), although, as is common for fresh- to brackish-water taxa (*e.g*. Dunhill *et al*. 2014), their fossil record is patchy.

Necessarily, the immediate phylogenetic relationships of the newly established genus *Muscatella* are enigmatic. Fossil bivalves assigned to *Geloina*, however, occur throughout the Cenozoic. The earliest representative, *Geloina rutoti* (Cossmann, 1908) comes from the Danian (Palaeocene) of Mons in southern Belgium (Glibert & Van de Poel 1973). It is thus only slightly younger than the specimens from Oman. *Geloina lunulata* (Deshayes, 1858) from the Thanetian (Palaeocene) of Châlons-sur-Vesle in northern France again is not much younger (Pacaud 1994). Interestingly, both Palaeocene species are small (maximum length of 25 mm), like the new species from Al-Khodh. Several other species of *Geloina* were reported from the Eocene and Oligocene of France and England (Glibert & Van de Poel 1966). No younger records are available from Europe. Extant *Geloina* has an Oriental to Australasian distribution, occurring from Pakistan eastward to New Caledonia (Huber 2015). The genus has been present in Asia at least since the Eocene (Japan, Malaysia; Nagao & Otatume 1943, Suzuki 1949, Kanno 1978, Matsubara *et al*. 2010), and also has a scattered Neogene fossil record (Oostingh 1935; Taguchi 1981, 2002; Matsubara *et al*. 2004).

Summarising this information, the occurrence of *Geloina* in the Campanian or Maastrichtian of Oman indicates either an early faunal link between Arabia and Eurasia, or suggests an African origin for the genus. For a brackish-water taxon, propagation of the larvae along the coastline or across narrow seaways, probably during phases of high freshwater run-off and associated layering of sea and river water, should be relatively straightforward. Accordingly, both an African origin and a Eurasian invasion of *Geloina* seem plausible. However, given that Africa has no fossil or extant record of *Geloina*, a Eurasian origin of the genus is considered to be more likely. Accordingly, *Geloina amithoscutana*, while being the oldest representative of the genus currently known, supposedly had earlier congeners in Asia and possibly Europe.

Of the brackish-water gastropod taxa, the palaeogeographical links of *Subtemenia morgani* are most revealing. This species was originally described from western Iran by Douvillé (1904) and has been reported earlier from Oman, some 200 km to the northwest of our study area (Smith *et al*. 1995). It seems that *S. morgani* was common during the Maastrichtian in the north and south of the Tethys. Although it is advisable to treat biostratigraphic insight provided by gastropods with caution, these occurrences seem to underpin a Maastrichtian age for the sampled strata of the Al Khodh Formation. The second species, *Stephaniphera coronata* is the only species in the new genus *Stephaniphera*. The Hemisinidae in general have a rather wide tropical to subtropical distribution range. Likewise, Ringiculidae had a wide spatial and temporal range in the Cretaceous. As a result, the latter two taxa offer little insight into the biogeographic relationships of the fauna from Al Khodh.

Of the marginal marine fossil community from the Jafnayn Limestone Formation only two taxa are determined at species level: *Torquesia contumescens* was first described from the Campanian to Maastrichtian Ariyalur Group in southeast India (Stoliczka 1868). In addition, *T. contumescens* was recorded from Gabon (West Africa) by Dartevelle & Brebion (1956). Considering the extensive and rather complicated dispersal route around the northern half of the African continent, this record might represent a different species. The type locality of *Amaurellina nuttalli* is situated relatively close to northern Oman, in Balochistan Province of southwestern Pakistan (Douvillé 1929). The type stratum, the '*Cardita beaumonti* Beds', was originally considered to be Danian in age (Cossmann & Pissarro 1927, Douvillé 1929), but, according to Crame (2013, appendix s1), it might actually be slightly older, probably Maastrichtian. The Jafnayn Limestone Formation is currently dated as late Paleocene to basal Eocene, based on echinoids (Nolan *et al*. 1990). The records of *Torquesia contumescens* and *Amaurellina nuttalli*, in contrast, would argue for an earlier, possibly even Maastrichtian onset of this unit. We consider the biostratigraphic evidence from both the echinoids and the gastropods as rather weak, and thus regard the age of the mollusc assemblage as unsettled (Maastrichtian/?Paleocene).

Palaeoecology

The molluscs described herein were part of four different mollusc communities, which thrived at different salinity levels. In succession, these communities testify to an overall transgressive trend in northern Oman during the Campanian to Maastrichtian, and thus corroborate previous results from sedimentology (Nolan *et al*. 1990).

(1) The unionid community, composed of the three indeterminate species of unionids, is indicative of freshwater. Given that the shells are disarticulated and strongly eroded the unionids probably lived in a fluvial environment. The unionid community occurs only at one locality (MP3).

(2) The *Geloina* association is dominated by *Geloina amithoscutana*. At three localities, *Subtemenia morgani* also occurs. Oysters are associated with these two species and a ringiculid at locality MP 7, and further occur at locality MP10. Additionally, the small planispiral ampullariid gastropod *Lanistes* sp. of Pickford (2017) is present at locality MP7. Extant *Geloina* occur in estuaries and mangroves, commonly at or above the tide line, at the land-water interface, exposed to significantly lowered levels of salinity (11 to 22 practical salinity units; Morton 1976). Presumably, the *Geloina* association thus indicates lower mesohaline conditions. As at Al-Khodh, the preferred substrate of modern *Geloina* is coarse sand (Morton 1976). The *Geloina* association is the most common association in the samples from Al-Khodh, occurring at eight localities (MP1, 2, 4–7, 9 and 10). It should be noted that modern *Lanistes* species are restricted to freshwater. The presence of these gastropods at locality MP7 might

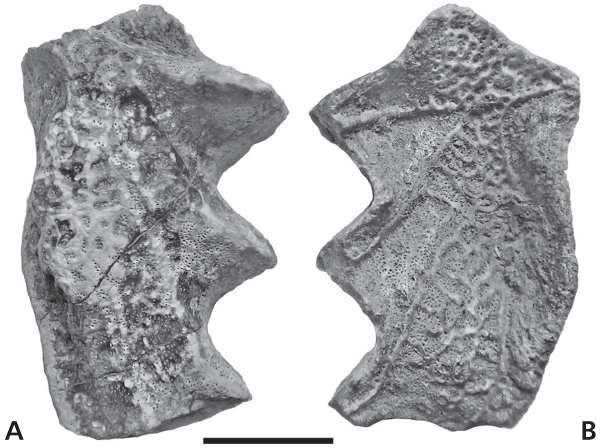

Figure 10. Dental plate of lungfish *Ceratodus* sp., locality MP 13; A – external view; B – internal view. Scale bar = 10 mm.

thus indicate that they have been washed in from nearby freshwater habitats.

(3) The *Muscatella* association occurs at four localities (MP 8, MP 13, MP 14 and AK 51). It is dominated by *Muscatella biszczukae*, which is associated with *Subtemenia morgani* at two localities. Additionally, *Stephaniphera coronata* occurs at two localities with *Muscatella*. Oysters and the small planispiral *Lanistes* of Pickford (2017) are present at locality AK51 (see comments on this species above). At locality MP13, a tooth plate of a lung fish (*Ceratodus*) was found together with the molluscs (Fig. 10). Modern lungfish commonly prey on shellfish and crustaceans (*e.g.* Kemp 1987, Witte & de Winter 1995), and the fossil species may thus have also fed on the molluscs described herein. An upper mesohaline or polyhaline regime seems likely for this association. It should be noted that *Subtemenia morgani* has also been recorded from marine strata in Oman (Smith *et al*. 1995), suggesting that it was an opportunistic, highly adaptable species.

(4) A marginal marine mollusc community is recorded from a single locality, 'Fanja Back', and composed of five taxa: the gastropods *Torquesia contumescens*, *Amaurellina nuttalli* and *Pyrazus* sp., and a questionable tellinid as well as other heterodont bivalves. Together, these taxa indicate shallow marine, nearshore conditions. Recent Batillariidae, including *Pyrazus*, occupy sandy and rocky habitats within the lower tidal regime in warm-temperate latitudes (Ozawa *et al*. 2009).

Conclusions

During the latest Cretaceous (late Campanian to Maastrichtian) the deltaic complex of the Al-Khodh Formation (northern Oman) harboured a mollusc fauna that is remarkable in several aspects. A freshwater community of three species of Unionidae represents the earliest record of large freshwater bivalves from the Arabian Peninsula – from an island bounding a vast epicontinental sea to the southwest and the Tethys Ocean to the northeast during the time of deposition. Two brackish-water associations are indicative of different salinity regimes. The *Geloina* association, inhabiting mesohaline high-energy coarse-grained sandy environment, is dominated by the cyrenid *Geloina amithoscutana* sp. nov., the earliest representative of the genus *Geloina*, and the first one recorded outside Eurasia. Oysters and three gastropods, *Subtemenia morgani*, *Lanistes* (?allochthonous) and an undetermined ringiculid, share this habitat. A second cyrenid, *Muscatella biszczukae* gen. nov. sp. nov., dominates the upper mesohaline to polyhaline *Muscatella* association. *Subtemenia morgani*, *Stephaniphera coronata* gen. nov. sp. nov. and *Lanistes* (?allochthonous) form its gastropod component. The molluscs were probably preyed upon by ceratodontid fish. These molluscs document the transition from freshwater to marine habitats within a single, relatively short-lived, deltaic succession, opening a window in the fossil record that is not often preserved. Shallow marine environment is exemplified by a Maastrichtian/?Paleocene mollusc community from the overlying Jafnayn Limestone Formation, where the gastropods *Torquesia contumescens*, *Amaurellina nuttalii* and *Pyrazus* are accompanied by heterodont bivalves.

Moreover, *Subtemenia morgani*, *Torquesia contumescens* and *Amaurellina nuttalii* document palaeobiogeographic relationships to Iran and Pakistan at the time on the northern coast of the Tethys, and to the still relatively distant shores of southeastern India. *Geloina*, which was thought to be of entirely Eurasian distribution, provides additional evidence for faunal relationships to the opposite side of the Tethys. As a whole, the mollusc fauna from Al-Khodh is an important piece in the still rather incomplete puzzle of faunal development in the Middle East.

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