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TRACING BACK THE ORIGIN OF THE INDO-PACIFIC MOLLUSC FAUNA: BASAL TRIDACNINAE FROM THE OLIGOCENE AND MIOCENE OF THE SULTANATE OF OMAN

by MATHIAS HARZHAUSER*, OLEG MANDIC*, WERNER E. PILLER†, MARKUS REUTER† *and* ANDREAS KROH*

*Natural History Museum Vienna, Burgring 7, A-1010 Vienna, Austria; e-mails: mathias.harzhauser@nhm-wien.ac.at; oleg.mandic@nhm-wien.ac.at; andreas.kroh@nhm-wien.ac.at

†Institute of Earth Sciences – Geology and Palaeontology, Graz University, Heinrichstrasse 26, A-8010 Graz, Austria; e-mails: werner.piller@uni-graz.at; markus.reuter@uni-graz.at

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Abstract: Two new tridacnine species are described from the Chattian and Aquitanian of the Arabian Peninsula. For these, the new names *Omanidacna eos* gen. et sp. nov. and *Tridacna evae* sp. nov. are erected. *Omanidacna* is interpreted as an Oligocene ancestor of *Hippopus*, being the oldest record of this tridacnine lineage. The Aquitanian *Tridacna evae* is the first occurrence of the genus *Tridacna*. These Arabian taxa imply that the modern tridacnine lineages are rooted in the Palaeogene and early Neogene of the East African-Arabian Province, although their Eocene ancestors, such as *Byssocardium*, are Western Tethyan taxa. During the Neogene they successfully settled the Indo-Polynesian Province and became typical elements of the entire Indo-West Pacific Region. The tridacnines are thus an example of a successive transformation and gradual eastward dispersal of an originally Tethyan element contributing to late Neogene diversity in the Indo-West Pacific.

Key words: Bivalvia, Chattian, Aquitanian, Western Tethys, Arabia, Biogeography.

TRIDACNINES are attractive bivalves owing to their exceptional size, their utilisation of photosynthetic symbionts, and the increasing importance of these bivalves in aquaculture and scuba-diving-tourism. Despite their solid shells and sometimes gregarious settling, their fossil record is poor. Fossil assemblages comparable in density and composition with modern tridacnine occurrences are not known before the Pliocene and Pleistocene. At that time, however, most of the extant taxa were already present, giving little insight into the evolution and radiation of the giant clams. The Miocene record, in contrast, is scanty and obscured by a sometimes very vague or simply wrong stratigraphic allocation. The latest phylogenetic attempts to reconstruct the history of the tridacnines, though partly integrating the flawed fossil record, were thus mainly based on molecular phylogeny or cladistic analysis of modern species (Benzie and Williams 1998; Schneider and Foighil 1999). A 'no-record' gap of more than 15 million years had to be bridged in former investigations between the already modern-type tridacnines of the late Miocene and their hypothetical Palaeogene ancestors. This stratigraphic gap coincides with a hitherto unresolved geographic gap that separates the Western European Palaeogene occurrences from those of the Neogene Indo-West Pacific.

The Oligo-Miocene of the Arabian Peninsula is a promising field to close both gaps. During that time it was part of the Tethys Ocean (Rögl 1998; Harzhauser *et al.* 2002) and was situated at the junction between the western Tethyan faunas and those of the Proto-Indo-Pacific.

LOCALITY AND STRATIGRAPHY

The material described was collected during a field trip that focused on Oligocene and Miocene shallow-water carbonates of the Dhofar Group (Shuwayr Formation) and the Fars Group (Warak and Ghubbarah formations) in the area of Madrakah, Sultanate of Oman (Text-fig. 1). A first geological framework for the area was provided by Platel *et al.* (1992) and Béchennec *et al.* (1993), who defined the lithostratigraphic units used herein. Both tridacnine species were found at Gebel Madrakah (N 19° 02′ 19.11″, E 57° 45′ 12.22″) close to Ra's Madrakah, a

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TEXT-FIG. 1. Geographic position of Ra's al Madrakah on the eastern coast of the Sultanate of Oman. The Gebel Madrakah section lies on the Madrakah Plain about 3 km to the west of the coast (see GPS data in Text-fig. 2 for detailed position).

small peninsula on the south-eastern shore of Arabia. There, a 22-m-thick succession of bioclastic limestones is exposed, lying as an erosional relic about 3 km inland on a vast plain formed by the dolomitized limestones of the Shuwayr Formation (Platel *et al.* 1992). This formation yields *Eulepidina formosoides* (Douville, 1925) at the base and *Nephrolepidina* cf. *morgani* (Lemoine and Douville, 1904) in the higher parts, being indicative of a latest Rupelian to earliest Chattian age (Davide Bassi, identification and pers. comm. 2006).

The basal 18 m of the overlying Warak Formation comprise bioclastic limestones (predominantly *Acropora*-bearing packstones). Isolated colonial corals with massive hemispherical growth morphology are sporadically associated with the *Acropora* fragments. Some intercalated beds are characterized by dense populations of the teredinid bivalve *Kuphus* sp. Other conspicuous interbeds consist of pedogenic carbonates, dolomite or attract attention by their red colour. Fossils are abundant and are preserved as calcitic pseudomorphs. The shells of *Omanidacna eos* gen. et sp. nov. derive from the lowermost parts of that unit, where they form dense coquinas (Text-fig. 2). Based on the gastropod assemblage, yielding typical Oligocene taxa, such as *Conorbis protensus* (Michelotti, 1861), *Rhinoclavis submelanoides* (Michelotti, 1861), *Rhinoclavis voglinoi* (Michelotti, 1861), *Gourmya baluchistanensis* (Vredenburg, 1928), *Seraphs* cf. *subconvolutus* (d'Orbigny, 1852) and *Capulus anceps* (Michelotti, 1861), as well as Oligocene to Aquitanian species such *Tectarius elegans* (Faujas, 1817), *Campanile pseudoobeliscus* (Grateloup, 1832) and *Globularia* cf. *compressa* (Basterot, 1825), the Warak Formation has been dated as late Oligocene by Harzhauser (2007). This dating is corroborated by the above-mentioned dating of the underlying Shuwayr Formation.

The top of the section is formed by a prominent cap, more than 5 m thick, of dense floatstones with a diverse mollusc fauna characterised by strombid coquinas. The fauna of this top unit is largely silicified, which distinguishes it from the underlying beds with calcitic preservation. The cap is recorded as the Ghubbarah Formation on the geological map of the Duqm-Madrakah area. Based on the gastropod fauna, which displays a relationship with Miocene faunas of Indonesia and yields species that range from Oligocene to Aquitanian in the Western Tethys, Harzhauser (2007) has considered this part of the succession to be Aquitanian in age. *Tridacna evae* sp. nov. occurs in this upper part of the section. In contrast to the Oligocene *Omanidacna* coquinas, this bivalve is represented only by disarticulated and scattered shells.

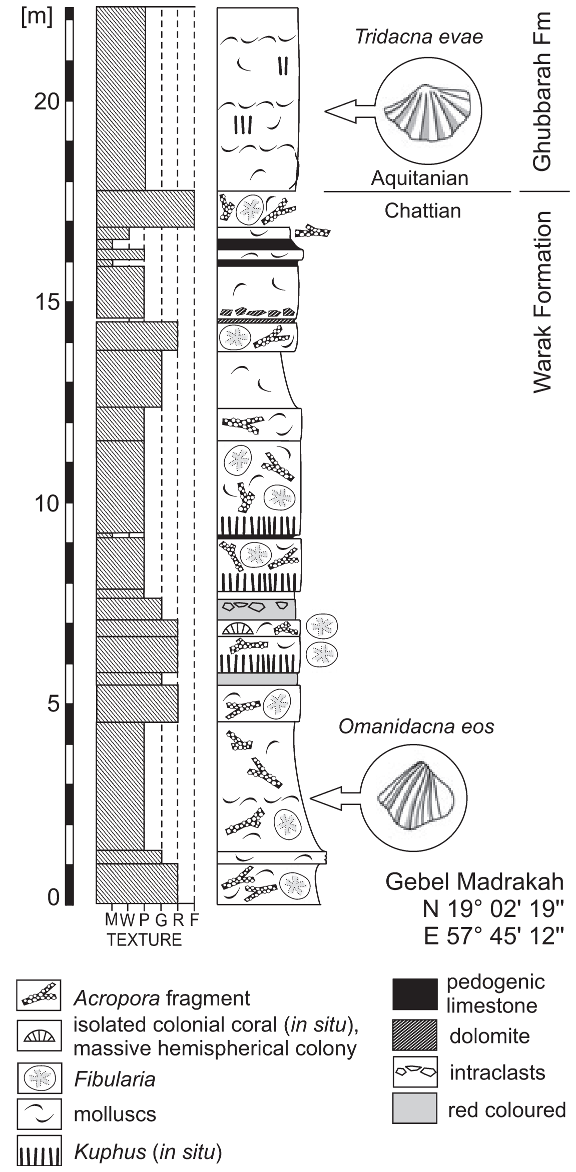
SYSTEMATIC PALAEONTOLOGY

The systematic hierarchy follows Schneider (1992) who considered the tridacnines to be a cardiid subfamily based on cladistic analysis. The terminology is after Schneider (1998) and Stasek (1962). Note that tridacnines are characterised by extensive growth of the posterior shell parts, coinciding with a considerable reduction of all anterior parts. This causes an unusual closeness of dorsal and ventral shell areas (Schneider 1998 and references therein). Text-figure 3 summarizes the terminology used in the descriptions. In the discussion we follow the subgeneric solution of Schneider and Foighil (1999) who demonstrated that *Tridacna gigas*, *T. derasa* and *T. tevoroa* form a monophyletic group, thus rejecting the subgenus *Persikima*. Authorship of all systematic ranks is given in the references.

Class BIVALVIA Linnaeus, 1758
Subclass HETERODONTA Neumayr, 1884
Order VENEROIDA H. and A. Adams, 1856
Superfamily CARDIOIDEA Lamarck, 1809
Family CARDIIDAE Lamarck, 1809
Subfamily TRIDACNINAE Goldfuss, 1820

Genus OMANIDACNA Harzhauser and Mandic gen. nov.

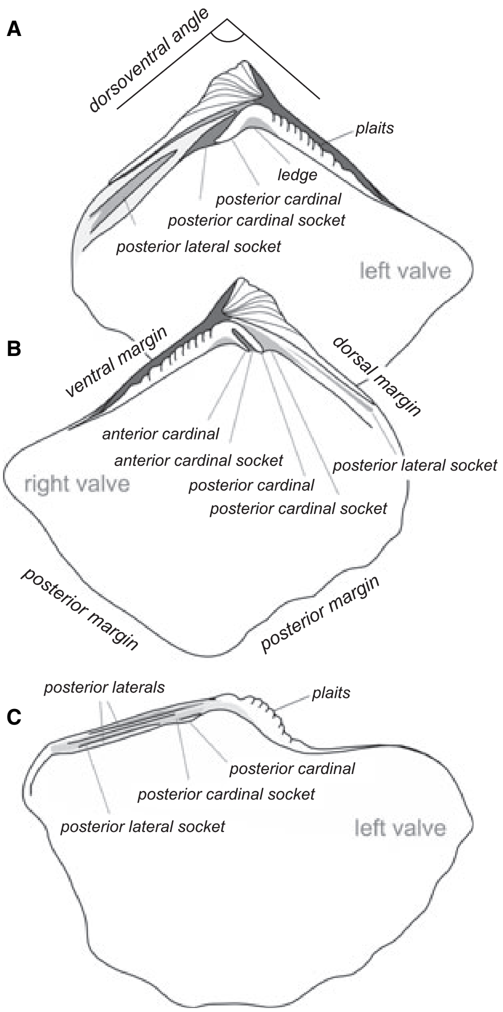
Derivation of name. A mélange of Oman (after the Sultante of Oman) and *Tridacna*, referring to its tridacnine nature.



TEXT-FIG. 2. Lithological succession at Gebel Madrakah. The *c.* 20-m-thick succession comprises bioclastic limestones of the Oligocene Warak and Aquitanian Ghubbarah formations. The position of the two tridacnine occurrences is indicated.

Type species. Omanidacna eos gen. et sp. nov. from the late Oligocene Warak Formation at Gebel Madrakah, Sultanate of Oman.

Diagnosis. Medium-sized, subquadrate tridacnine bivalve with sharp pseudocarina (*sensu* Schneider 1998), narrow dorsoventral angle and closed byssal gape. Pseudocarina with keel-like accentuated primary rib. Sculpture differentiated into broad primary ribs and weaker secondary ribs. Right hinge with a blunt posterior cardinal tooth and a very weak, largely reduced anterior denticle; left valve only with strong posterior cardinal tooth. Left valves develop a deeper posterior lateral socket and stronger laterals than the right valves.



TEXT-FIG. 3. Simplified drawings of the interior valves of A–B, *Omanidacna eos*, and C, *Tridacna evae*. The terminology follows Stasek (1962), Keen (1969) and Schneider (1998).

Remarks. The morphologically closest extant relative is the tridacnine genus *Hippopus* Lamarck, 1799, represented by the two living species *Hippopus hippopus* (Linnaeus, 1758) and *Hippopus porcellanus* Rosewater, 1982. *Hippopus* and *Omanidacna* develop strongly angular pseudocarinas with angles of *c.* 80–90 degrees. This similarity is lost in *Hippopus* during growth when this break in slope becomes successively rounded. The dorsoventral angle, though '*Hippopus*-like', is smaller in *Omanidacna*, whereas it ranges around 100 degrees even in subadult *Hippopus* (Stasek 1962). *Hippopus* is characterised by an extensive growth of the posteroventral wing, causing the valves to have a symmetrically elongate outline. This wing is absent in *Omanidacna*. The primary ribs of *Hippopus* are raised and round in cross section but moderately raised and flat to weakly convex in *Omanidacna*. *Hippopus* lacks the small anterior cardinal denticle (Rosewater 1982) and socket of *Omanidacna* and develops a broader nymph plate. Both genera differ from *Tridacna* by the absence of a byssal gape.

In the fossil record only *Byssocardium* Munier-Chalmas, *in* Fischer 1882 is somewhat reminiscent and might belong to the ancestors of *Omanidacna*. The Eocene–Oligocene *Byssocardium* species all differ, especially in their elongate trigonal outline and homogenous sculpture. *Byssocardium* develops coarse plaits, a deeper anterior cardinal socket and a protruding, free umbo.

Omanidacna eos Harzhauser and Mandic sp. nov.
Plate 1; Text-figure 4

Derivation of name. After Eos, the Goddess of Dawn in Greek mythology; referring to the basal position of the described tridacnine species.

Holotype. Natural History Museum, Vienna, NHM 2006z0272/0001, left valve; length of ventral margin VM, 45 mm; length of pseudocarina PC, 54 mm (Pl. 1, figs 1–3).

Paratypes. NHM 2006z0272/0011, right valve, VM, 62 mm; PC, 63 mm (Pl. 1, figs 4–6); NHM 2006z0272/0004, left valve, VM, 65 mm (Pl. 1, figs 13–14); NHM 2006z0272/0010, right valve, VM, 54 mm; PC, 62 mm (Pl. 1, figs 7–10).

Material. Nine left valves, 11 right valves; all shells are calcitic pseudomorphs with moderately well-preserved surfaces; the ventral margins and posterior hinge area are usually more or less complete; the posterior margins are always weathered and broken.

Type locality and age. Gebel Madrakah, Sultanate of Oman; N 19° 02′ 19.11″, E 57° 45′ 12.22″: *Acropora*-bearing bioclastic limestones of the Warak Formation, Oligocene (Chattian).

Diagnosis. As for genus.

Description. Medium-sized, heavy shells of subquadrate outline. The dorsoventral angle ranges from 80 to 85 degrees during juvenile stages of growth and increases to 100–105 degrees in fully grown specimens. A marked pseudocarina divides the shell into a narrow, slightly concave, steeply dipping ventral area (= inferior slope) and a large, convex posterodorsal area (= superior slope). The markedly angular pseudocarina coincides with a slightly raised keel formed by a primary rib. The angle along the pseudocarina between the inferior and superior slopes ranges around 85 degrees throughout growth. The inferior slope is composed of a strongly convex central field that passes via a shallow concavity into a small posterior ventral wing. Up to 20 narrowly spaced and strongly bent ribs cover the ventral field; in late stages of growth, smaller secondary ribs are intercalated between the primary-pairs, being separated by deep, narrow furrows from the primaries. The main part of the shell develops 8–10 broad, slightly rounded, primary ribs. Subadult shells display a single row of indistinct, widely spaced nodes on each primary rib (these could be the bases of weathered scales). Narrow secondary ribs appear soon in the interspaces within the first 10 mm of growth. Up to three rounded secondaries may be intercalated, each being separated by marked grooves. Usually, however, only one or two such ribs appear; these are highly variable in width and sometimes amalgamate again into a single broader secondary rib. The predominant primary ribs also seem to be accentuated by very vague secondary ribs. Along the margin, the primary ribs give rise to a deeply serrated, wavy commissure.

The hinge area of the right valve consists of a prominent, elongate, posterior cardinal and a short, reduced, anterior cardinal denticle separated by a narrow anterior cardinal socket. An indistinct nymph plate is followed by a long, deep posterior lateral socket. A broad, smooth, concave ledge spans the area between the anterior cardinal and the ventral margin. The left valve lacks any anterior cardinal tooth or socket but displays a very strong posterior cardinal tooth accompanied by a very deep socket. On the available material, the left valves develop a deeper posterior lateral socket and stronger laterals than the right valves. The ventral margin is straight and serrated by blunt plaits, suggesting a closed commissure.

The position of the muscle scar and the exact course of the posterior margin are unclear because of the poor preservation. Nevertheless, the posterior margin displays a slight angulation, which is the cause of the subquadrate outline. This angle changes from 120 degrees in juvenile shells towards 105 degrees in adults.

Remarks. No comparable species is known from the Eurasian-African Oligocene or Miocene. All *Byssocardium* species differ considerably in their trigonal outline,

EXPLANATION OF PLATE 1

Figs 1–15. *Omanidacna eos* Harzhauser and Mandic gen. et sp. nov. 1–3, left valve, holotype, NHM 2006z0272/0001, internal, external and dorsoventral views respectively. 4–6, right valve, paratype, NHM 2006z0272/0011, external, internal and dorsoventral views, respectively. 7–10, right valve, paratype, NHM 2006z0272/0010, external, internal, ventral and dorsoventral views respectively. 11–12, right valve, NHM 2006z0272/0006a, external and dorsoventral views. 13–14, left valve, paratype, NHM 2006z0272/0004, external and ventral views. 15. NHM 2006z0272/0006a, fragment of a left valve showing the plaits of the ventral margin. All scale bars represent 10 mm.

PLATE 1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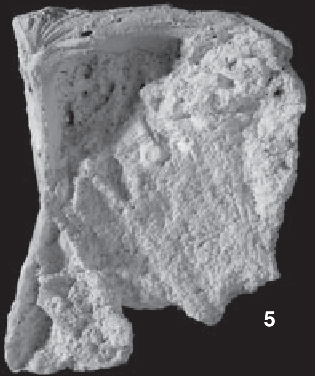
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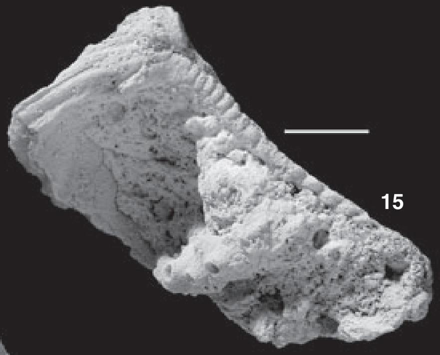
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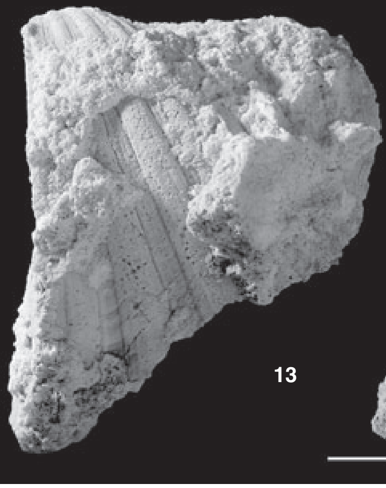
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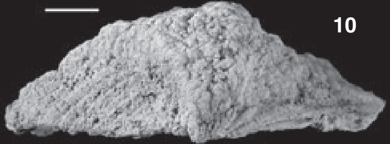
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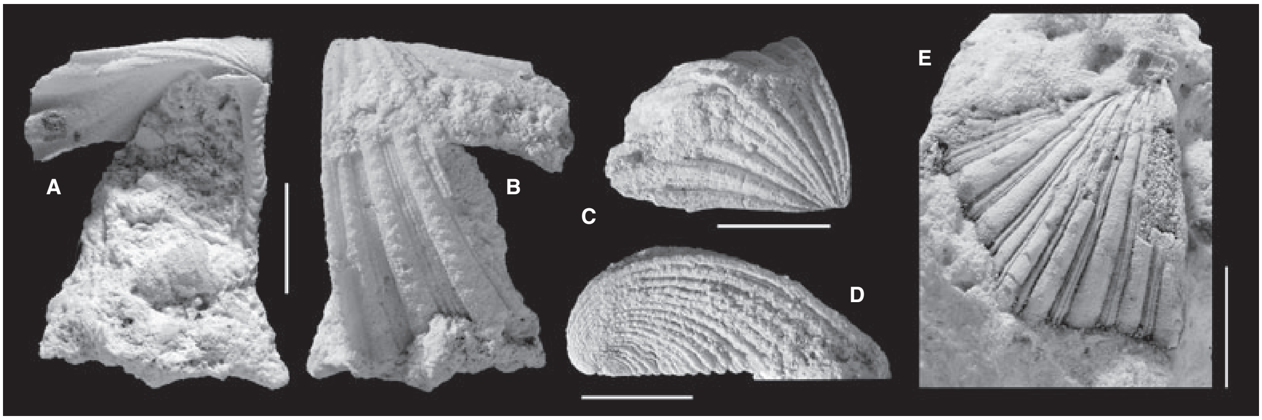
HARZHAUSER *et al.*, *Omanidacna*



TEXT-FIG. 4. A–E, subadult shells of *Omanidacna eos* Harzhauser and Mandic gen. et sp. nov. A–D, NHM 2006z0272/0006b, left valve in A, internal, B, external, C, dorsoventral, and D, ventral views. Note the nodes on the surface of the primary ribs in B. E, NHM 2006z0272/0005b, external view of a right valve. All scale bars represent 10 mm.

homogenous sculpture and the very broad ventral margin with coarse plaits. *Avicularium* clearly differs in its elongated trigonal shape, the presence of an anterior adductor muscle scar and the larger anterior cardinal. *Omanidacna eos* is the earliest record of a tridacnine with 'modern' *Hippopus* sculpture. Morphologically it is a link between *Byssocardium* and *Hippopus*, fitting well into the proposed (*Byssocardium* (*Hippopus*)) relationship pattern of Stasek (1962) and Schneider (1998), which should be extended to (*Byssocardium* (*Omanidacna* (*Hippopus*))). Therefore, the separation of an *Omanidacna–Hippopus* lineage from a *Tridacna* lineage can be traced back into the Oligocene.

The younger *Hippopus*? *gunteri* Mansfield, 1937 from early Miocene deposits in Florida might be a second representative of *Omanidacna* (Table 1). Mansfield (1937) doubted the generic affiliation of the strange casts. They are highly reminiscent of *Omanidacna eos* with respect to the differentiated sculpture and the pseudocarina. A specific separation is evident based on the high number of intercalated secondary ribs (up to five), the low number of primary ribs, and the absence of the small posterior ventral wing. No information on the hinge structures is available; hence, a decision about the status of this American tridacnine remains unsolved. Accepting it as an *Omanidacna* causes an extremely disjunct distribution of this genus, with a gap spanning the entire Atlantic and Western Tethys, because no related species is known from the otherwise well-studied French, Italian, Greek and Pakistani localities. Interestingly, the supposed ancestor *Byssocardium* is represented in this Western Tethys core area, being documented by Eocene and Oligocene occurrences in France and Italy.

Palaeoecology. The shells are concentrated in a coquina layer at the base of the section (Text-fig. 2). All specimens are disarticulated and float within a packstone with numerous fragments of *Acropora* and masses of the tiny echinoid *Fibularia* sp. The co-occurring mollusc fauna comprises strombids, various cerithiids, lucinids, *Periglypta* sp. and *Campanile* spp. Therefore, a very shallow marine environment with *Acropora* carpets and sea grass patches is suggested as the habitat for *Omanidacna eos*. The accumulation of the shells is interpreted as within-habitat transportation.

Genus TRIDACNA Bruguière, 1797

Type species. *Chama gigas* Linnaeus, 1758, Recent, Indo-Pacific; by subsequent monotypy (Lamarck 1799).

Tridacna evae Harzhauser and Mandic sp. nov.
Text-figure 5

Derivation of name. After Eva Mrazek (Vienna), who generously supported our studies for several years.

Holotype. Natural History Museum Vienna, NHM 2006z0272/0002, left valve, maximum shell width, 68 mm (Text-fig. 5C–E).

Paratype. NHM 2006z0272/0003, left valve, maximum length, 45 mm (Text-fig. 5A–B).

Material. Two steinkern specimens with corresponding silicone moulds showing internal features of the valves.

Type locality and age. Gebel Madrakah, Sultanate of Oman; N 19° 02′ 19.11″, E 57° 45′ 12.22″. Packstones of the Ghubbarah Formation, Miocene (Aquitanian).

TABLE 1. Fossil and recent tridacnines with synonymies of fossil taxa and stratigraphic ranges (excluding *Goniocardium*). The list is an extension and partial improvement of the lists of Rosewater (1965) and Schneider and Foighil (1999) including following references: 1, Cossmann and Pissarro 1904; 2, Cossmann and Pissarro 1906; 3, Cossmann 1921; 4, Oppenheim 1896; 5, Oppenheim 1901; 6, Cox 1941; 7, Matheron 1867; 8, Sandberger 1868; 9, Fuchs 1870; 10, Gripp 1922; 11, Karagiuleva 1964; 12, Tournouer 1882; 13, Schneider and Foighil 1999; 14, Beets 1986; 15, Cloud *et al.* 1956; 16, Martin 1879; 17, Rosewater 1965; 18, Taylor 1978; 19, Crame 1986.

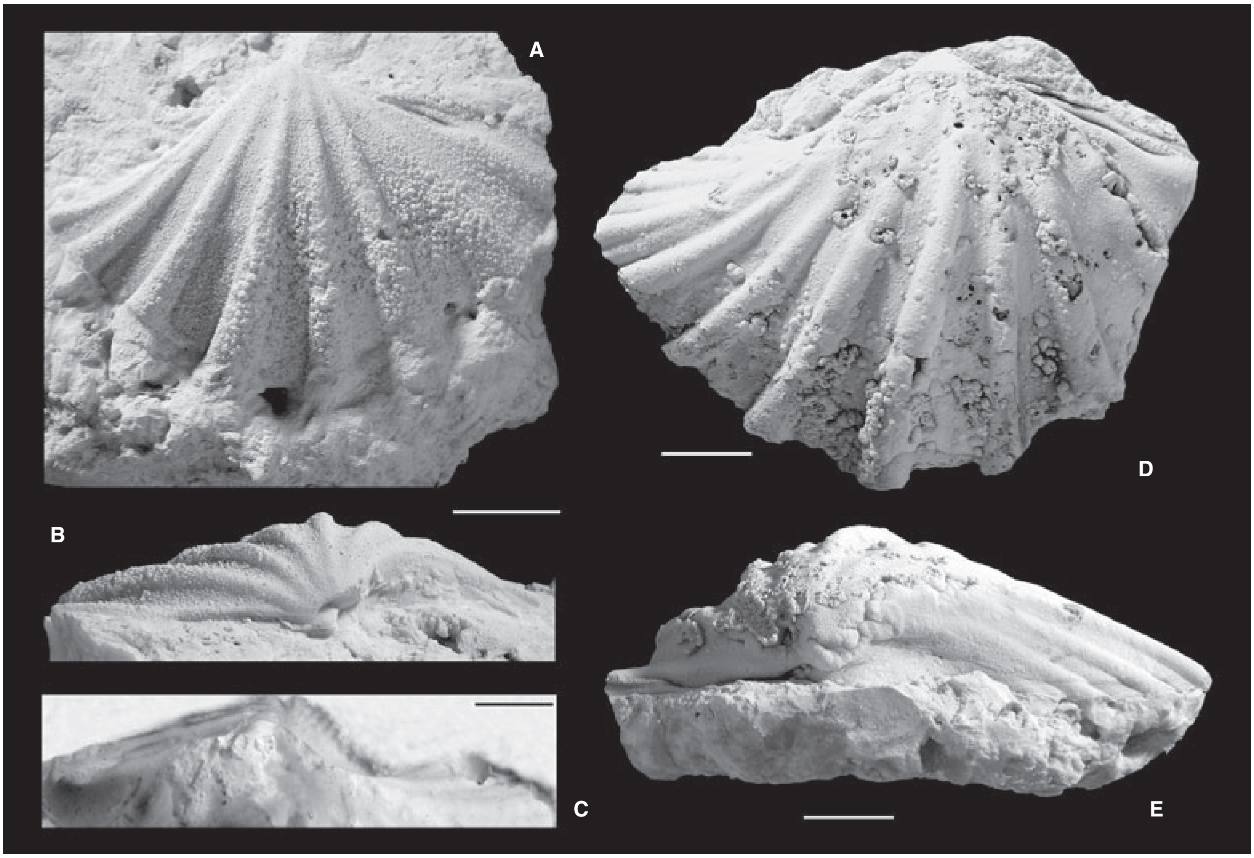
Eocene – Holocene tridacnid taxa (excl. *Goniocardium*)	Stratigraphic range	Important fossil occurrences and references
Avicularium aviculare (Lamarck, 1805)	Middle Eocene	France (Paris Basin) - 1
Avicularium cymbulare (Defrance, 1817)	Middle Eocene	France (Paris Basin, Normandy) - 1–2
Avicularium dilatatum (Cossmann and Pissarro, 1906)	Middle Eocene	France - 3
Avicularium erroris (Oppenheim, 1901)	Middle – late Eocene	Italy - 4–5
Avicularium granuligerum (Cossmann and Pissarro, 1904)	Middle Eocene	France (Normandy) - 1
Avicularium superbum (Cossmann and Pissarro, 1904)	Middle Eocene	France (Normandy) -1
Avicularium trentinum (Oppenheim, 1901)	Middle – late Eocene	Italy (Trentino) - 4–5
Avicularium trechmanni Cox, 1941	Late Eocene	Jamaica - 6
Avicularium carinatum (Bronn, 1831) °	Oligocene	France, Switzerland, Italy, Macedonia, Bulgaria - 3–4, 7–11
Byssocardium emarginatum (Deshayes, 1829)	Middle Eocene	France (Paris Basin) - 2
Byssocardium andreae Tournouer, 1882	Oligocene	France - 12
Omanidacna eos sp. nov.	Late Oligocene (Chattian)	Sultanate of Oman, this paper
Omanidacna? *gunteri* (Mansfield, 1937)	Early Miocene (Burdigalian)	Florida - 13
Hippopus hippopus Linnaeus, 1758	Miocene – Holocene	Borneo - 14
Hippopus porcellanus Rosewater, 1982	Holocene	No fossil record
Tridacna evae sp. nov.	Early Miocene (Aquitanian)	Sultanate of Oman, this paper
?*Tridacna* sp. °°	Early Miocene	Saipan, Mariana Island - 15
Tridacna (*Tridacna*) *gigas* (Linnaeus, 1758) *	Late Miocene – Holocene	Borneo, Indonesia - 14, 16
Tridacna (*Tridacna*) *derasa* (Röding, 1798)	Late Miocene – Holocene	Borneo - 14
Tridacna (*Tridacna*) *tevoroa* Lucas, Ledua and Braley, 1990	Holocene	No fossil record
Tridacna (*Chametrachea*) *squamosa* (Lamarck, 1819) **	Late Pliocene – Holocene	Kita-Daito Island - 13
Tridacna (*Chametrachea*) *maxima* (Röding, 1798) ***	Late Miocene – Holocene	Indonesia - 16
Tridacna (*Chametrachea*) *crocea* Lamarck, 1819	Late Pleistocene – Holocene	Eniwetok, Aldabra Atoll, Kenya - 17–19
Tridacna (*Chametrachea*) *rosewateri* Sirenko and Scarlato, 1991	Holocene	No fossil record

° = *A. difficile* (Michelotti, 1861); *A. girondicum* (Matheron, 1867).
°° = referred to as *Hippopus hippopus* by Schneider and Foighil, 1999.
* = *T. wolfarti* Chenu, 1845.
** = *T. loczyi* Kutassy, 1934; *T. aegyptica* Chenu, 1845; *T. mbalavuana* Ladd, 1934.
*** = *T. besairiei* Collignon, 1951; *T. media* Pusch, 1837; *T. rudis* in Martin, 1879.

Diagnosis. Suboval, rather small *Tridacna* with up to nine rounded ribs separated by wider interspaces. Sculpture also strongly expressed in the interior shell. Concave ventral margin with byssal gape. Hinge reduced with narrow posterior laterals and very weak and posteriorly displaced posterior cardinal tooth (left valve).

Description. Only left valves are available, indicating a comparatively small *Tridacna* with slightly posteriorly displaced umbos. Suboval outline; dorsoventral angle attaining 130 degrees. Eight (small specimen) and nine (large specimen) rounded ribs are present, separated by broader, flat interspaces. Ribs are widely spaced in the posterior field and successively more narrowly spaced towards the ventral margin. The surface sculpture is largely unknown owing to insufficient preservation. Small grooves on the casts, however, suggest the existence of at least four secondary ribs in the interspaces. The ventral margin is steep and strongly concave with a short crenulated part bearing about eight delicate plaits. The posterior cardinal is strongly reduced and posteriorly displaced; the anterior cardinal socket is absent. The nymph plate forms a narrow ledge passing into bipartite, very thin posterior laterals. The posterior lateral socket is shallow and narrow. No muscle scars are recognizable. A byssal gape is present and probably increased in width during growth owing to the expanding ventral wing. The small size and the delicate hinge structures might point to a subadult stage of growth.

Remarks. Based on the few morphological data, *Tridacna evae* seems to be closer to the extant subgenus *Chametrachea* Mörch, 1852 than to *Tridacna sensu stricto*. Its size, the strongly concave ventral margin, the high number and strength of the primary ribs, and the asymmetric distribution of the width of these ribs (wide in the posterior



TEXT-FIG. 5. A–E, *Tridacna evae* Harzhauser and Mandic sp. nov. A–B, paratype, NHM 2006z0272/0003, internal mould of a left valve. A, external, and B, dorsoventral views. C–E, holotype NHM 2006z0272/0002, internal mould of a left valve. C, a silicone mould of the holotype showing hinge features. D, external, and E, dorsoventral views. All scale bars represent 10 mm.

and narrow in the ventral parts) resemble the characters of extant *Tridacna* (*Chametrachea*) *maxima* (Röding, 1798) or the late Miocene *T.* (*Chametrachea*) *mbalavuana* Ladd, 1934 (= *T. squamosa* according to Schneider and Foighil 1999) but differ considerably from those of *T.* (*Tridacna*) *gigas* (Linnaeus, 1758).

Nevertheless, the reduced, slender hinge and the strongly developed impressions of the ribs in the interior shell surface have no equivalent in extant tridacnines; we therefore refrain from assigning the Aquitanian species to an extant subgenus. Differences from modern species are manifold: *T.* (*Chametrachea*) *maxima* (Röding, 1798) has a much smoother interior surface that does not reflect the primary ribs even in subadult shells. The hinge plate is broader and bears a prominent posterior cardinal tooth and a strong interior lateral tooth. Its byssal gape is even broader. *Tridacna* (*Chametrachea*) *crocea* Lamarck, 1819 is distinguished by its huge byssal gape and blunt posterior laterals; *T.* (*Chametrachea*) *squamosa* Lamarck, 1819 develops a broader ventral margin with blunt plaits, and bears a single lateral in the left valve; *T.* (*Chametrachea*) *rosewateri* Sirenko and Scarlato, 1991 has a strongly undulating margin; *T.* (*Tridacna*) *derasa* (Röding, 1798) displays a reduced sculpture, differing fundamentally from the prominent ribbing of *Tridacna evae*, and bears a prominent cardinal tooth; *T.* (*Tridacna*) *gigas* (Linnaeus, 1758) differs in its low number of ribs; and *T.* (*Tridacna*) *tevoroa* Lucas *et al.*, 1990 has a more displaced umbo, smooth shells and a broad hinge plate (see Lucas *et al.*, 1991).

Despite the coincidence of geographic occurrence, this species is significantly different from the stratigraphically older *Omanidacna eos*. Whilst the latter is related to the *Hippopus*-lineage, bearing a straight ventral margin and a closed byssal commissure, *T. evae* is a typical *Tridacna*, with its byssus gape and characteristic ovate shape. Its Aquitanian age indicates that *T. evae* is the earliest known *Tridacna*.

Palaeoecology. The disarticulated specimens were found as rare elements within the packstones of the Ghubbarah Formation (Text-fig. 2). They occurred in association with the huge *Dilatilabrum sublatissimus* (d'Orbigny, 1852) and a second very frequent large strombid

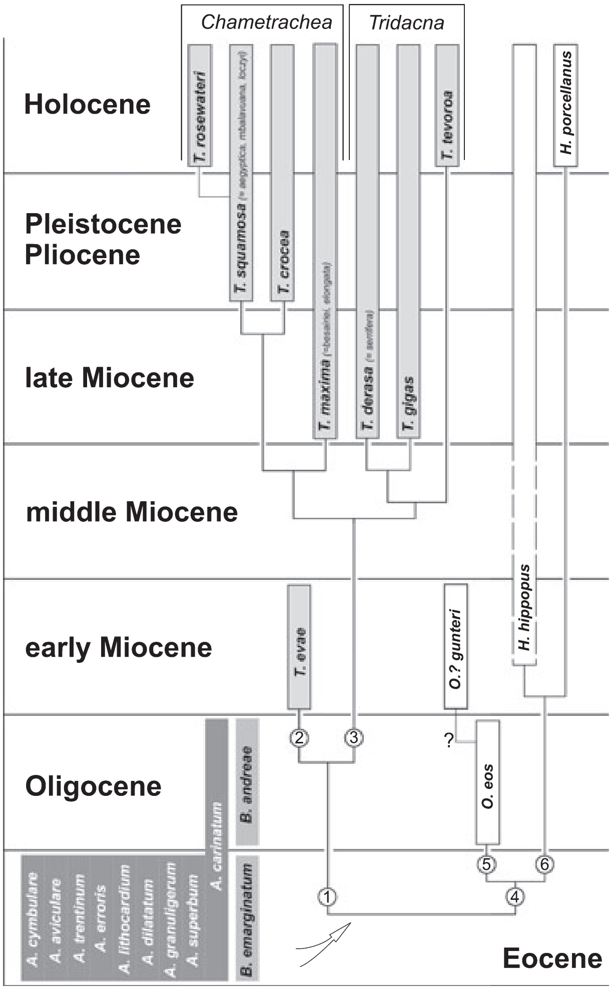
(*Strombus* sp. nov.). Globulariids, *Cerithium rude* Sowerby, 1840, *Gourmya delbosi* (Michelotti, 1861) and scattered small coral-heads are found in the soritid-bearing limestones. *Acropora* thickets, which are typical of the underlying Warak Formation, are rare. This fauna, with the masses of huge strombids, indicates a shallow marine, probably lagoonal environment with sea grasses.

DISCUSSION

Palaeogene prelude

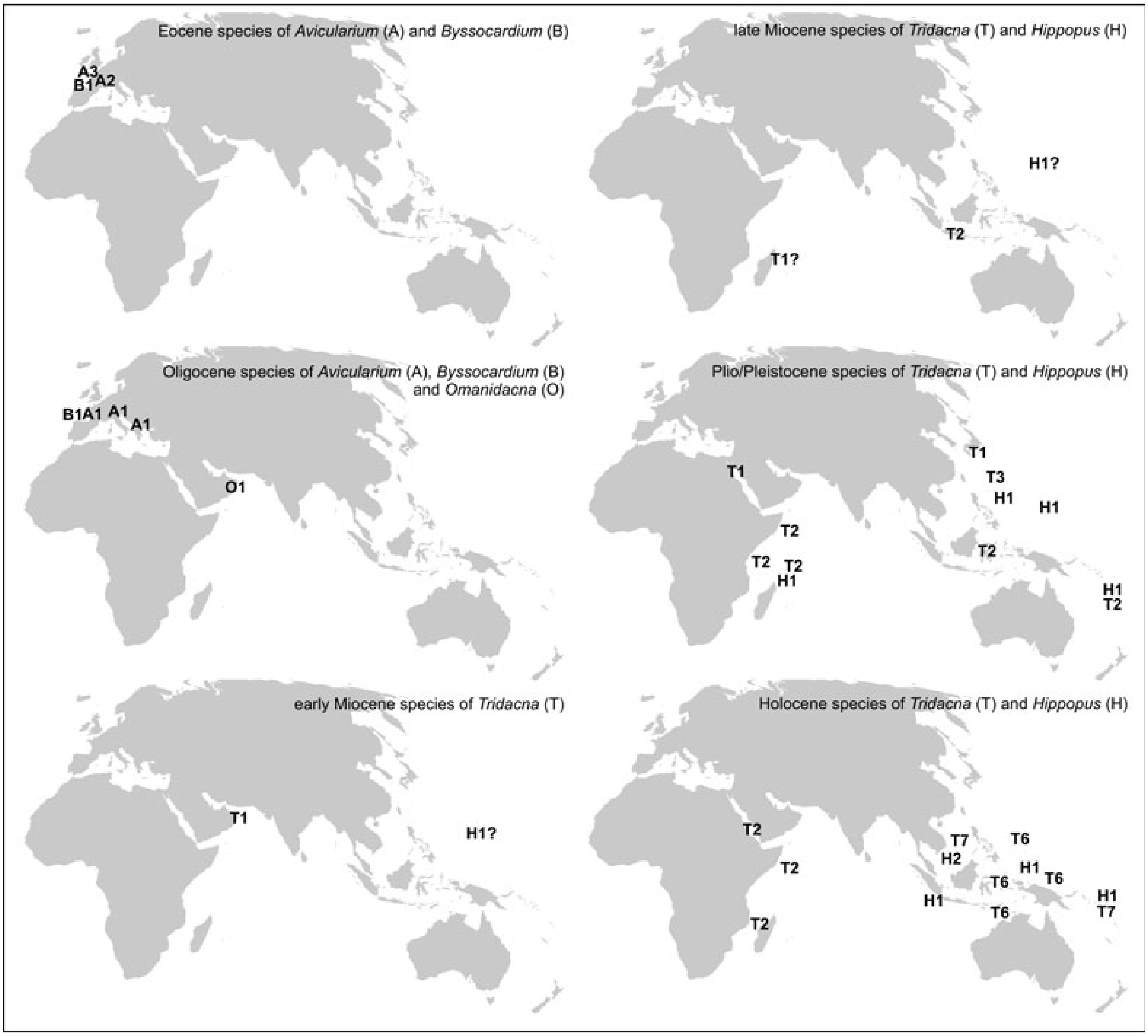
Tridacnines appear in the Eocene, represented by *Goniocardium* Vasseur, 1880, *Avicularium* Gray, 1853 and *Byssocardium* Munier-Chalmas, *in* Fischer 1882. *Goniocardium*, as the most primitive type, is restricted to the Eocene of the westernmost Western Tethys (e.g. France). The slightly more advanced *Avicularium,* with reduced anterior shell, trigonal outline and dominant posterior adductor, displays its maximum diversity in the middle Eocene, when there were about nine species (Text-fig. 6 and references in the caption). This Palaeogene diversity is roughly equivalent to that of extant tridacnines. *Byssocardium*, with its quite modern *Tridacna*-like features, such as a reduced anterior shell and a ventral margin with plaits, is only known from a single Eocene species (see Schneider 1998 for morphological descriptions of the genera). *Sawkinsia* Cox, 1941 from the Eocene of Jamaica was described as another potential Palaeogene tridacnine by Jung (1976). Schneider (1998, 2002), however, documented its relationship with the Cardiinae; it is, therefore, excluded here from the Tridacninae.

After the Eocene boom, the diversity declined dramatically. *Avicularium* was reduced to a single species that was widespread in the Western Tethys during the Oligocene. *Byssocardium* is also known only from a single Oligocene species and seems to have been geographically restricted to the westernmost part of the Western Tethys. The range of *Byssocardium* was erroneously given as Eocene–early Miocene by Stasek (1962) and Rosewater (1965), who considered *Byssocardium andreae* (Tournouer, 1882) to be early Miocene. This species, however, derives from the Oligocene of Gaas in France, as previously indicated by Tournouer (1882). Hence, both genera became extinct at the dawn of the Miocene.



TEXT-FIG. 6. Stratigraphic ranges of the 'modern' tridacnines *Omanidacna, Hippopus* and *Tridacna* compared with the basal tridacnines *Avicularium* and *Byssocardium*. The occurrence data are summarized in Table 1. After eliminating the dubious and obviously erroneous Miocene European tridacnine records, a clear gap in the record is evident in the middle Miocene (see text for discussion). The phylogeny of the extant species largely follows Schneider and Foighil (1999). Numbers on lineages refer to morphological and supposed ecological features that distinguish clades: 1, wide byssal gap, large dorsoventral angle; 2, reduced hinge, strong interior ribs, sea grass habitat; 3, solid shells, broad, solid hinge structure, associated with corals; 4, sharp pseudocarina with steep break in slope, narrow dorsoventral margin at least during early stages of growth; 5, strong hinge with remnants of anterior cardinal; 6, fully reduced anterior part of the hinge, extensive growth of posteroventral wing, rounded ribs.

It is generally accepted that modern tridacnines might be derived from *Byssocardium* or a *Byssocardium*-related taxon (Stasek 1962; Schneider 1998). *Byssocardium andreae* can, however, be excluded as the ancestor because it is also Oligocene in age. Therefore, the separation from the hypothetical *Byssocardium*-like ancestor may be rooted in the Eocene or early Oligocene. The fossil-record data plotted in Text-figure 7 point to a gradual eastward expansion of the Palaeogene tridacnines, laying the foundation for the Neogene success of the tridacnines in the Indo-West Pacific area.



TEXT-FIG. 7. Geographic occurrence patterns of tridacnine taxa based on the same data-set as Text-figure 6. Numbers after the genus abbreviations indicate the number of species of each genus. A concentration in the Western Tethys is evident in the Eocene and Oligocene. By the early Miocene, the tridacnines had shifted into the proto-Indo-Pacific area and were absent in their former centre of origin. From the late Miocene onwards the maximum species diversity was established in the western Pacific.

Unveiling the Miocene history of tridacnines

The Palaeogene vector of stratigraphically successive tridacnine occurrences, starting with an Eocene diversity centre in the westernmost part of the Western Tethys and ending with the appearance of *Omanidacna* on the Arabian shelf during the Oligocene, indicates a gradual decrease of tridacnines in the circum-Mediterranean area (Text-fig. 7). The extinction of the basal European tridacnine genera *Byssocardium* and *Avicularium* at the Oligocene/Miocene boundary amplified that trend. Nevertheless, Miocene occurrences of tridacnines in Europe are frequently reported in the literature, seemingly contradicting the 'go-east' scenario. Beginning with Stasek (1962), all investigations dealing with fossil tridacnines incorporated two references on fossil species of *Tridacna* from the European Miocene. Both *Tridacna media* Pusch, 1837, allegedly from the Miocene of Poland, and *Tridacna wolfarti* Chenu, 1845, from Germany, are based on single specimens of unclear origin. Pusch (1837) emphasized that the exact locality was unknown and that he had obtained the shell from a collector. These references induced Rosewater (1965, pp. 354, 369) to state: 'the occurrence … indicates the presence in that area during the Tertiary of a flourishing tropical fauna' and 'these fossil species inhabited this area during the middle Tertiary apparently when arms of warmer seas extended into northern Europe'. Although he recognized that these specimens are quite reminiscent of extant *Tridacna gigas* and *T. maxima*, none of the investigators doubted their origin (subsequently, *T. media* was considered to be a synonym of *T. maxima* by Schneider and Foighil 1999).

Both occurrences are, however, extremely unreliable. No middle or upper Miocene marine sediments occur in the German Hesse Basin, which was dry land after the Oligocene. The marine connection to the southern seas, such as the Paratethys and the Western Tethys, via the Rhine Graben, was very restricted during the Chattian and Aquitanian (Rögl 1998). Reef facies are absent from the entire Rhine Graben, the Mainz Basin and adjacent depositional areas. Therefore, we reject *Tridacna wolfarti* Chenu, 1845 as a European Miocene fossil. *Tridacna media* Pusch, 1837 (= *T. maxima*) might be from the Miocene of the Polish Carpathian Foredeep. In that area, only a short ecological window is available for a possible occurrence, as this sea was closed off during the late middle and late Miocene, coinciding with a highly endemic mollusc fauna (Rögl 1998). Subsequently, during the Langhian and early Serravallian, no coral reefs developed in the Polish Foredeep (Pisera 1996) and the mollusc fauna lacked highly thermophilous tropical taxa (Harzhauser *et al.* 2003). Furthermore, in the more southern seas with flourishing reef systems (e.g. southern Paratethys Sea and Western Tethys) no tridacnine has ever been found, despite numerous investigations (see Harzhauser *et al.* 2002 for an overview and references). Even Pliocene records of *Tridacna* and *Hippopus* from Europe, as reported by Brambilla and Galli (1992) from Italy, have subsequently been rejected by Taviani (1994) as anthropogenically imported Recent material; the two specimens concerned might have been imported during the Renaissance or the Baroque Period and discarded later. *Tridacna* shells have been used, for example, as out-door decoration in the Belvedere Palace of Prince Eugen of Savoy in Vienna and as pillar tops in the menagerie of Esterhazy Palace in Eisenstadt (Austria). One of the latter was found by a fossil collector in the 1970s, who erroneously considered it to be a fossil when he brought the shell to the Museum of Natural History in Vienna. Imported shells of *Tridacna* are even recorded from archaeological sites such as Milet in Asia Minor, where the shells have been carved and were used as boxes for cosmetics in the seventh century BC (Heinz 1999).

Hence, Miocene *Tridacna* records of undoubted origin are exclusively known from the Indo-Pacific area. The Indonesian locality O of Martin (1879), from where two *Tridacna* species have been described, is dated as late Miocene (Hoek Ostende *et al.*, 2002). The misdating of these occurrences as early Miocene in Rosewater (1965) introduced another tridacnine ghost to the literature.

In stratigraphical terms, this 'cleaning' eliminates all early and middle Miocene occurrences of *Tridacna* mentioned by Stasek (1962), Rosewater (1965), Keen (1969), and Braley and Healy (1998), which more or less clearly refer to misdated European and Indonesian records. A single dubious Cretaceous record from Madagascar, described as *Tridacna besairiei* by Collignon (1951), is also based on a mixing of Neogene shells with Cretaceous material (see Schneider 1998 for a detailed discussion). The geological history of *Hippopus* is still unclear. Rosewater (1965) mentioned an early Miocene *Hippopus hippopus* from the Togpochau Limestone of the Marianas Islands. In the corresponding paper of Cloud *et al.* (1956), however, only a *Tridacna* sp. is mentioned. The first undoubted *Hippopus* is, therefore, that recorded by Beets (1986) from late Miocene deposits in Borneo.

Evolutionary pathways

Omanidacna eos is clearly reminiscent of a *Hippopus*. The step from *Omanidacna* to *Hippopus* required the reduction of the already insignificant anterior cardinal tooth, an elongation of the posterior cardinal tooth, the expansion of the posterior cardinal socket, an increase in the dorsoventral angle, and an extensive growth of the posterior ventral wing during post-juvenile stages of ontogeny. Considering the outline alone, *Hippopus* seems to be an example of heterochrony, recapitulating the *Omanidacna* stage as a juvenile up to a size of *c.* 3 cm characterised by a sharp pseudocarina and a poorly developed wing. This simple (*Omanidacna* (*Hippopus*)) relationship is not paralleled by the Omani *Tridacna* and its potential relatives. Its reduced hinge and the distinct impression of the ribs in the interior of the shell have little in common with the hypothetical *Tridacna* ancestor *Byssocardium.* This combination of features is also unusual for extant *Tridacna* (*Tridacna*) and *Tridacna* (*Chametrachea*). Nevertheless, the overall shape and rib pattern is reminiscent of the latter. The stratigraphically oldest *Tridacna* species after the Aquitanian *T. evae* derive from upper Miocene strata. All are extant species: *T.* (*Tridacna*) *gigas* from Indonesia and Borneo (Martin 1879; Beets 1986), *T.* (*Tridacna*) *derasa* from Borneo (Beets 1986) and *T.* (*Chametrachea*) *maxima* from Indonesia (Martin 1879). This indicates that the extant subgenera were already fully established in the late Miocene, giving no clue as to their pre-late Miocene history.

The contradicting morphologic features fit two evolutionary possibilities (Text-figs 5–6):

1. *Tridacna evae* is an early offshoot and represents a sister taxon of the monophyletic group *Tridacna* (*Tridacna*)

+ *Tridacna* (*Chametrachea*). It would, therefore, require at least subgeneric status. The last common ancestor of all these tridacnines is thus expected to have lived in the Oligocene. This interpretation is supported by the stratigraphic position of a very basal representative of *Tridacna* and by the derived hinge structures. The reduced hinge and strong ribbing of the interior shell surface of *T. evae* cannot be considered to be primitive features. Neither *Byssocardium* nor *Avicularium* share these characters with *T. evae*. This derived character-complex is not seen in any extant tridacnine species either. Therefore, *T. evae* might represent an early Miocene offshoot that inhabited sea grass environments.

2. *Tridacna evae* is a representative of *Chametrachea*, being then a sister taxon of the monophyletic group (*Tridacna maxima* (*T. squamosa* + *T. crocea*)) as defined by Schneider and Foighil (1999). This interpretation is supported by the gross morphology of the shell and would place the separation of the subgenera into the Oligocene. The last common ancestor would then have lived in the Eocene or early Oligocene. This solution is, however, unrealistic with respect to the dominance of the evolutionarily quite basal *Avicularium* and *Byssocardium* at that time. Moreover, it would be surprising that no *Tridacna* shell was found in the European Palaeogene.

Go east! – a tridacnine biogeography

Tridacnines originated as elements of the Tethys Realm and displayed a centre of diversity in the Eocene Mediterranean Region of Popov (1993). Their virtual absence in the Eocene Western Indian-Eastern African Province or the Proto-Indo-Polynesian Province suggests a quite restricted distribution.

This western centre was also present during the Oligocene, but by then the tridacnines had spread over large parts of the Western Tethys, being common elements of the Eastern Atlantic Province and the Mediterranean-Iranian Province (following the biogeographic scheme of Harzhauser *et al.* 2002). The record of *Omanidacna* in Chattian deposits of the Arabian shelf documents the first dispersal of tridacnines towards the Middle East. At that time, a broad connection between the Mediterranean and the Indo-Pacific basins still existed via the Mesopotamian Trough and the Zagros Zone (Rögl 1998). Despite this distributional pulse, they never managed to settle the Proto-Eastern Atlantic Boreal Region in the north-west or the Danube Province of the Paratethys Sea in the north-east.

The western tridacnines became extinct at the Palaeogene/Neogene boundary. Their absence in the Aquitanian of the Mediterranean-Iranian Province and the fact that first restrictions of the Tethyan seaway occurred then, indicated by widespread evaporites in central Iran and the Mesopotamian Trough (Rögl 1998; Jones 1999 and references therein), suggests that the centre of evolution had already shifted to the east. As the Omani occurrence is the earliest for *Tridacna* (aside from a questionable reference in Cloud *et al.* 1956 to an early Miocene tridacnine on the Mariana Islands) this genus seems to have originated in the East African-Arabian Province. Tridacnines are virtually absent from Oligocene and early Miocene deposits of the Western Indian Province (e.g. Pakistani and Indian faunas in Vredenburg 1928 and Dey 1961). Moreover, the absence of any tridacnine records in coeval deposits of the Proto-Indo-Polynesian Province (Martin 1899–1906, 1916, 1921) supports this interpretation. There, the tridacnines are undoubtedly represented in late Miocene deposits (Beets 1986) but are still rather rare, considering the low number of published records of these otherwise eye-catching bivalves. A modern pattern of distribution was not developed before the Pliocene and Pleistocene, reflecting the final shift of the centre of diversity into the western Pacific (Text-fig. 7). The fossil record of the tridacnines is thus a good example of the gradual eastward migration of an originally Tethyan group that ended up in the Indo-Polynesian Province during the late Neogene. This process contradicts an overly simple interpretation of the East Indies as a historical Centre of Origin, as proposed by Briggs (1995, 2000), in documenting that the high diversity was also fed by Miocene arrivals of Tethyan elements. It also indicates that the pre-Pleistocene roots of dispersal are not evident in modern gene flow studies as documented by Benzie (1998). These suggest ‘a movement of material from the Pacific to SE Asia’ (Benzie 1998, p. 197). It is, therefore, extremely dangerous to extrapolate geological dispersal patterns from modern population structures.

CONCLUSIONS

The earliest record of Indo-West Pacific tridacnines is of *Omanidacna eos*, documented from the Chattian of the Arabian Shelf. *Omanidacna* is closely related to extant *Hippopus* and its potential ancestor. At that time, the *Hippopus* lineage was already well distinguished from *Tridacna*, which was considered as a sister group by Schneider and Foighil (1999). This group is represented by *Tridacna evae* in the Aquitanian of the Arabian shelf, being the oldest known *Tridacna*. Whilst *Omanidacna* was associated with coral carpets, much like its modern descendants, the basal *Tridacna* inhabited sea grass environments. Its derived hinge morphology and the unusual habitat, by comparison with modern *Tridacna*, might indicate that *T. evae* was already a specialized early Miocene offshoot. If it is indeed a sister-taxon of the *Tridacna*

(*Tridacna*) + *Tridacna* (*Chametrachea*) group, the separation of *T. evae* from the crown group would have to be searched for in the Oligocene. These interpretations suggest that the last common ancestor of the *Tridacna* and *Hippopus* lineages might have lived in the Eocene.

Palaeogene tridacnines display an Eocene centre of maximum diversity in the Paris Basin and Normandy (Text-fig. 7). In the Oligocene this diversity decreased but was compensated by a geographic expansion into the entire Western Tethys. At that time, tridacnines gained a foothold in the east, infiltrating the faunas of the East African-Arabian Province (EAAP). With the onset of the Miocene, the tridacnine 'experiment' came to an end in the circum-Mediterranean area. The earliest *Tridacna* appears in early Miocene deposits on the Arabian shelf, indicating that the tridacnines were already well established in the EAAP.

A partly intermittent Tethyan seaway, beginning in the Aquitanian (Jones 1999) and ending with its final disintegration in the early Middle Miocene (Rögl 1998), may thus have been the vicariance event that separated the Palaeogene Western Tethyan tridacnine lineages from the Palaeogene–Recent Indo-West Pacific lineages.

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