Annali dell'Università degli Studi di Ferrara
Museologia Scientifica e Naturalistica

ISSN 1824-2707
volume speciale 2005

Bivalve reefs from the Upper Triassic of Iran

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Abstract

In the Upper Triassic Nayband Formation of east-central Iran, bivalves repeatedly form small patch reefs on a mid to outer mixed carbonate-siliciclastic ramp in close stratigraphic neighbourhood to coral and coral-sponge reefs. In contrast to other Triassic-Jurassic bivalve-dominated patch reefs, the bivalve reefs of the Nayband Formation are characterized by a comparatively high diversity of framebuilding taxa. These include taxa from three different families, i.e., the ostreids *Umbostrea emamii*, *U. iranica* and *U.*? aff. *parasiticum*, the prospondylids *Newaagia stocklini* and *Persia monstrosa*, and the plicatulids *Eoplicatula parvadehensis* and *Pseudoplacunopsis asymmetrica*. The bivalve reef constructors may have had a competitive advantage over coral and calcareous sponges in environments characterized by a higher degree of turbidity and/or higher nutrient contents.

Keywords: Triassic, bivalves, reefs, Iran.

Introduction

Throughout the Phanerozoic, the groups of organisms that substantially contributed to reef growth varied considerably in their taxonomic composition (e.g. Fagerstrom 1987; Wood 1999). It is well known that bivalves, represented by rudists and to a lesser extent by oysters, were the main framebuilders during the Middle and Late Cretaceous (e.g., Steuber and Löser 2000; Johnson et al. 2002) and that the oysters continued to build reef structures, especially in marginal marine environments, up to the present day (e.g. Wells 1961; Bahr and Lanier 1981). What is less well known is the fact that some members of this class contributed substantially to reef growth already in the early and middle Mesozoic by acting as framebuilders soon after they acquired a cementing life habit. The earliest example of bivalves acting as framebuilders may even come from the Palaeozic. Jux and Omara (1983) described the oyster-like pseudomonotid bivalve *Pachypteria sinaitica* from the Lower Carboniferous of the Sinai Peninsula. This thick-shelled bivalve was cemented with its right valve to the substrate and formed layers, several centimetres thick, within marls. However, it is not clear, whether the bivalves formed a true framework or merely concentrations of largely disarticulated valves. Probably the best documented examples of the early phase of reef growth involving bivalves are the small patch reefs that consist of the ?prospondylid *„Placunopsis"* and that are common in the Upper Muschelkalk (Middle Triassic) of the Germanic Basin (e.g., Hölder 1961; Bachmann 1979; Duringer 1985; Hagdorn and Simon 2000). However, *„Placunopsis"* was by no means the only bivalve that acted as framebuilder in the Triassic and Jurassic. The purpose of this paper is to describe patch reefs from the Late Triassic Nayband Formation of east-central Iran, in which bivalves were the principle reef organisms, and to summarize the information available on bivalve reefs in the early and middle Mesozoic. Reefs as defined in this paper exhibit a framework of cemented taxa. Banks built by mud stickers such as *Lithiotis* or by epibyssate taxa such as *Isognomon* and *Mytilus* are therefore not regarded as true bivalve reefs.

Geological framework

The Norian-Rhaetian Nayband Formation of east-central Iran is a mixed siliciclastic-carbonate unit, up to 3,000 m in thickness, that overlies, with

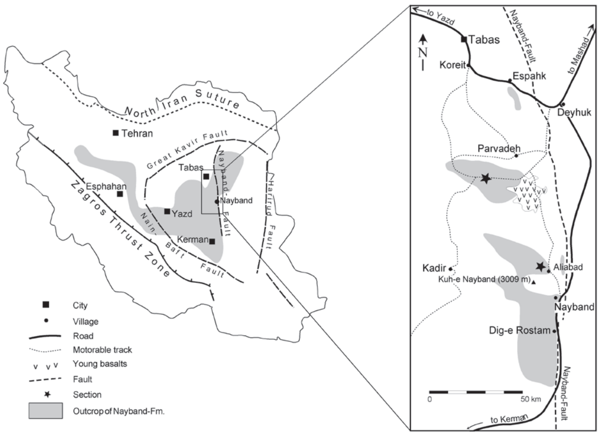


Fig. 1. Locality map.

an unconformity, Middle Triassic shallow water carbonate platform sediments (Shotori Formation). The formation post-dates the Early Cimmerian orogenic movements, which were the result of collision of parts of the so-called Cimmerian Micro-Continent Collage (to which the east-central Iran belonged) with the Turan Plate as part of Eurasia. Originally thought to represent the sediments of a foreland basin (e.g., Alavi 1996, Seyed-Emami 2003), recent studies suggest that the Nayband Formation was deposited in several basins that experienced extensional tectonics (e.g., Fürsich et al. 2005).

In the area of the type locality, around Kuh-e-Nayband and further north towards Parvadeh (Fig. 1), the Nayband Formation consists of several members. Siliciclastic sediments (silts, sandstones) dominate in the Gelkan and Howz-e-Sheikh members, whereas carbonates are a characteristic feature of the Bidestan and Howz-e-Khan members (Fig. 2). Within the carbonates, reefs occur at several levels. Most of them are dominated by corals and/or sponges (e.g. Senowbari-Daryan 1996), but in some of them bivalves constitute a conspicuous element or are the main framebuilders. This is true of the Howz-e-Sheikh Member at Aliabad and particularly of the Bidestan Member south of Parvadeh (Pl. 1, Fig. 1-7). These reefs are briefly described in the following.

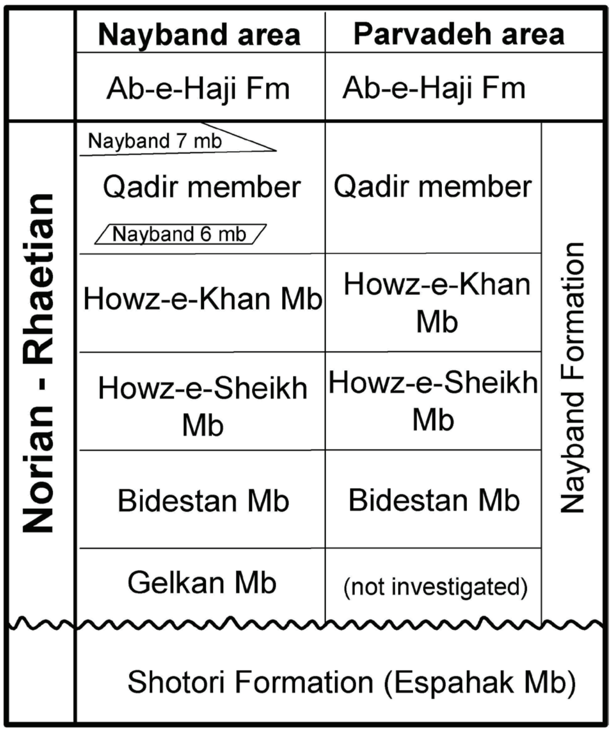


Fig. 2. Stratigraphy of the Nayband Formation.

Description of the bivalve reefs

Probably the most striking character of the bivalve reefs of the Nayband Formation is the large number of taxa which were involved in constructing the framework. Seven bivalve species, belonging to three different families, have been identified as constituents of these bioconstructions: The ostreids *Umbrostrea emamii* Hautmann, 2001, *U. iranica* Hautmann, 2001 and *Umbrostrea*? aff. *parasiticum* (Krumbeck, 1913), the prospondylids *Newaagia stocklini* (Repin, 1996) and *Persia monstrosa* Repin, 1996, and the plicatulids *Eoplicatula parvadehensis* Hautmann, 2001 and *Pseudoplacunopsis asymmetrica* Hautmann, 2001. A comprehensive description and taxonomic discussion of these species is given in Hautmann (2001a, b), to which the reader is referred for details. Therefore, a short description of some morphological peculiarities will suffice here.

Newaagia stocklini is a large and thick-shelled prospondylid with a posteroventrally elongated disc. Its most conspicuous character is the giant dimension of the ligament area of adult individuals (Pl. 2, Fig. 1b). This ligament area carries a broad and shallow resilifer that occasionally shifted during growth, thereby sometimes bifurcating or becoming supplemented or replaced by abruptly inserting additional resilifers. The outer side of the valves is fitted with radial ribs of different strength continuing in prominent spines (Pl. 2, Fig. 1a), which were probably advantageous in supporting attachment as well as in defence and in competition for space.

The left (upper) valve of *Persia monstrosa* is characterized by an abrupt change in ornamentation during ontogeny (Pl. 2, Fig. 6), which probably coincided with the transition from a cementing to a 'free' (i.e., not in contact with the substrate) growth of the opposite valve. The presence of distinct ears in *P. monstrosa* might indicate that a byssally attached state preceded the cemented attachment. A faint ridge on the ligament area (Pl. 2, Fig. 3), representing the growth track of a weak tooth, probably hints at a phylogenetic relationship between advanced prospondylids and plicatulids.

Eoplicatula parvadehensis (Pl. 2, Fig. 2) is a comparatively large plicatulid with a tear-like shape and strong crura, whereas *Pseudoplacunopsis asymmetrica* (Pl. 2, Fig. 4-5) is relatively small, has asymmetric crura and carries spines on the outer surface of the valves. The presence of a secondary ligament in the latter taxon justifies its generic separation from the former.

Umbrostrea emamii (Pl. 2, Figs. 8, 10), *U. iranica* (Pl. 2, Fig. 9), and probably also *Umbrostrea*? aff. *parasiticum* (Pl. 2, Fig. 7) differ from Jurassic and later oysters by an originally aragonitic inner shell layer. Fine laminar structures that are occasionally preserved in spite of recrystallization indicate that its original microstructure probably was nacreous.

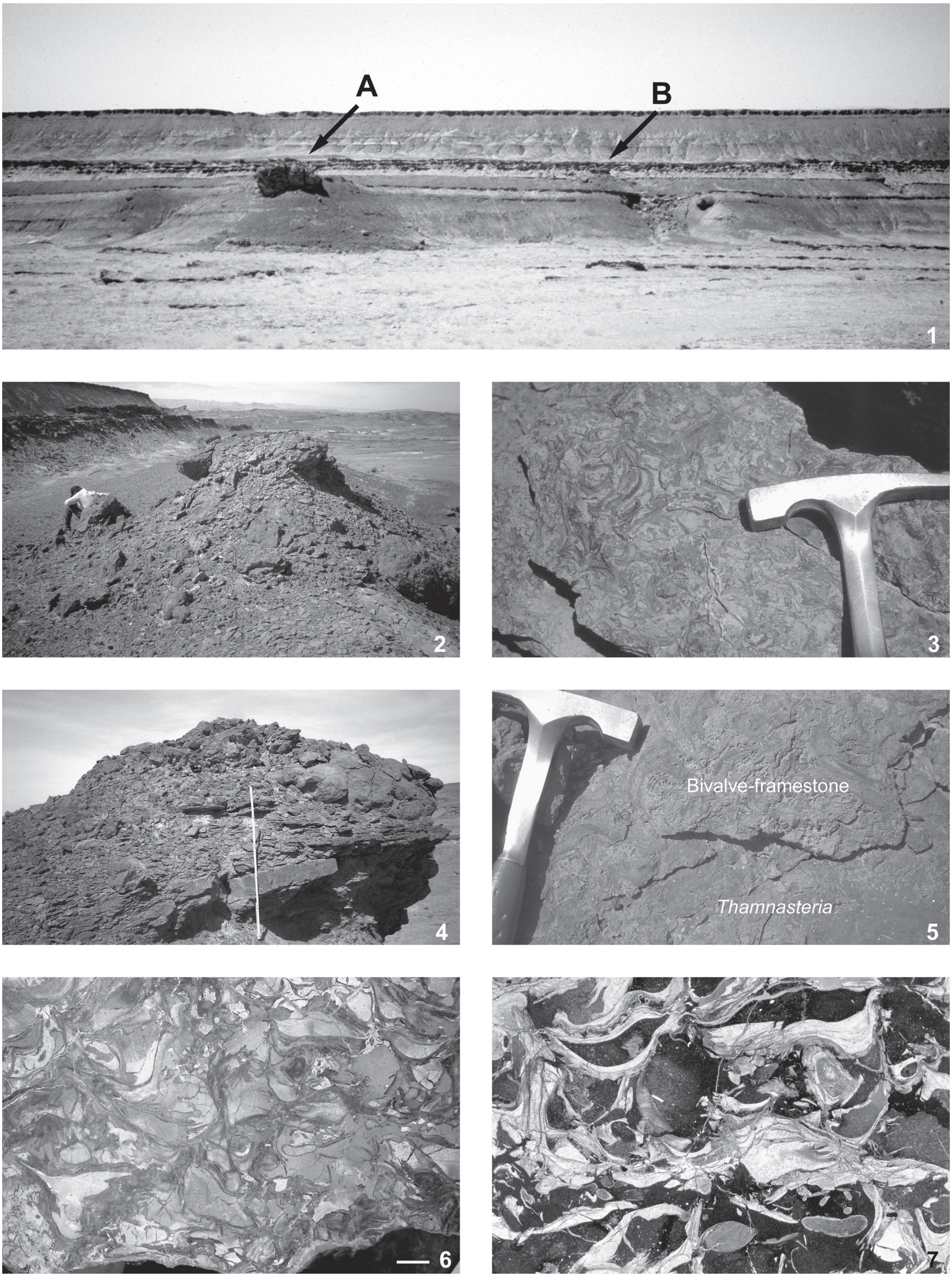
Estimating the relative abundance and spatial distribution of the different species in each reef is difficult, because mutual overgrowth of the reef-forming bivalves and recent weathering under desert conditions makes it nearly impossible to determine specimens *in situ*. Most information about the taxonomic composition therefore comes from specimens that were separated from the reef and have been deposited in laterally interfingering beds. The vast majority of these specimens are disarticulated upper valves (i.e. right valves of the three oyster species and left valves of the prospondylids and plicatulids), whereas most of the lower (cemented) valves obviously remained attached on the reef. Judging from collecting these disarticulated valves, *Umbrostrea emamii* was the most abundant species, followed by *Persia monstrosa*.

The bivalve reefs of the Nayband Formation are commonly associated with solitary and colonial corals. However, associated corals are more abundant at the base of the reefs, where they might represent the pioneer stage of reef development (see below). Corals occasionally are completely replaced by bivalves in later stages of reef development, whereas the opposite has never been observed. Apart from corals, small terebratulid brachiopods occasionally settled in interspaces of the framework (Pl. 1, Fig. 7, lower centre). The surfaces of the reefs occasionally exhibit signs of bioerosion, in particular *Trypanites*-like borings (Pl. 1, Fig. 3).

In spite of the taxonomic richness of the framework constructors, the species involved do not markedly differ in their growth strategies. In life position, the plane of commissure of all species was more or less parallel to the substrate. This resulted in a comparatively slow upward-growth of the reef and thus in reef bodies that are distinctly broader than high. Typical dimensions are heights between 1-2 m and lateral extensions up to 5 m (Pl. 1, Figs. 1-2, 4).

The internal structure of the bivalve reefs consists of a comparatively loose framework formed chiefly by articulated bivalves. Using the charts of Flügel (1975, p. 155), bivalve shells are estimated to form approximately 30% of the rock volume. The interspaces of the framework is completely filled with micrite.

Reef growth started nearly exclusively on the top of shell concentrations or skeletal rudstones, which provided a sufficiently hard and stable substrate for initiating settling. Some bivalve reefs rest directly on such shell beds without other framework constructors being significantly involved. In others, however, growth of bivalve reefs started together with development of small coral patches, or after the surface of the shell beds had been colonised by pioneering corals (Pl. 1, Fig. 5).


A
B
1
2
3
4
Bivalve-framestone
Thamnasteria
5
6
7

Discussion

Palaeoenvironments and sequence stratigraphic position of the reefs

The Nayband Formation of the central Tabas Block of the Central-East Iranian Microcontinent, i.e. at the type area south of Kuh-e-Nayband and towards the north around Parvadeh, has been deposited in a rapidly subsiding basin that received sediment from a northeasterly source (Fürsich et al. 2005). Supply and subsidence were at near-equilibrium and environments ranged from the inner to the outer ramp. The basin shallowed both towards the north and with time. Thus, the upper part of the Nayband Formation of the study area represents marginally marine to delta plain environments with coastal swamps, whereas the basal parts of the formation in the Nayband area characterize middle to lower siliciclastic ramp environments, partly below storm wave-base. The sedimentation pattern exhibits a distinct cyclicity and the sedimentary package can be subdivided into numerous transgressive-regressive sequences. Reef growth in the Bidestan and Howz-e-Khan members of the Nayband Formation characteristically occurs during the late transgressive systems tract (TST), although some coral and coral-sponge reefs also started to grow during early TST. Whereas the early TST is generally characterized by shelly biograin- to biorudstones, which were clearly deposited above the fair weather wave-base in shallow, high energy waters, deposits of the late TST including the bivalve reefs clearly reflect a comparatively low energy, albeit by no means quiet water, environment. This is corroborated by the fact that the bivalve reefs are overlain by clays and silty clays of the early highstand systems tract (HST) (Fig. 3). It appears that while the limited sediment supply during the transgressive phase promoted reef growth, the onset of siliciclastic sedimentation during the early HST was responsible for its termination.

One question remains to be solved: which factors determined the growth of oyster reefs as opposed to the more widespread and larger coral and coral-sponge reefs? Environmental conditions cannot have differed drastically, because apart from bivalve reefs and coral reefs there are patch reefs in which corals and bivalves were major framework constructors. Both reef types apparently required skeletal substrates and occur during the transgressive systems tract. Maybe differences in the degree of turbidity of the water, not easily reconstructed from the rock record, played some role. Also, as opposed to coral reefs which are known to prefer oligotrophic conditions, bivalves might have preferred waters with a higher nutrient content. Clearly, this question cannot be fully answered with the present information.

Comparison with other Triassic-Jurassic bivalve reefs

The bivalve reefs from the Nayband Formation are not the earliest reefs known to be dominated by bivalves. Small patch reefs of the ?prospondylid *„Placunopsis" ostracina* Schlotheim are common at some levels in the Upper Muschelkalk (Anisian) of the Germanic Basin, in particular southwestern Germany and eastern France (e.g., Hölder 1961; Bachmann 1979; Hagdorn and Mundlos 1982; Duringer 1985; Hagdorn and Simon 2000). These reefs are small, cushion- to pillow-shaped structures (usually less than 1 m in diameter; the largest ones reach 10 m in diameter and a height of 4.5 m, Krumbein 1963; Hagdorn and Mundlos 1982), and the framework consists overwhelmingly of the cemented right valves of *„Placunopsis"*. The cementing bivalve *Enantiostreon spondyloides* may also contribute to the reef framework, which may be reinforced by spirorbids and sessile foraminifers (Hagdorn and Mundlos 1982). A characteristic feature of these reefs is that the framework only consists of right valves of successive generations of *„Placunopsis"*. Apparently, any attempt of larvae of

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Plate 1

Fig. 1, Field photographs of two bivalve reefs (Parvadeh section). Details of left (lower) reef (A) are shown in Pl. 1, Figs. 4-5, details of right (upper) reef (B) in Pl. 1, Figs. 2-3. For stratigraphic position of reefs see Fig. 3. Fig. 2, Typical shape of a medium-sized bivalve reef (B in Pl. 1, Fig. 1). Bahram Najafian (Beheshti University, Tehran) for scale. Fig. 3, Close-up of reef B, showing *Trypanites*-like borings in bivalve shells. Fig. 4, Larger bivalve reef (A in Pl. 1, Fig. 1), associated with colonies of the coral *Thamnasteria*. Fig. 5, Close-up of reef A, showing pioneering corals (*Thamnasteria*) overgrown by bivalves. Fig. 6, Polished and etched section of reefal limestone (reef C in Fig. 3), showing articulated bivalves and mud-filling of interspaces. Scale: 1 cm. Fig. 7, Acetate peel taken from the specimen of Fig. 6, showing details of bivalves and a small terebratulid brachiopod (lower centre). Width of photograph: 3.5 cm.

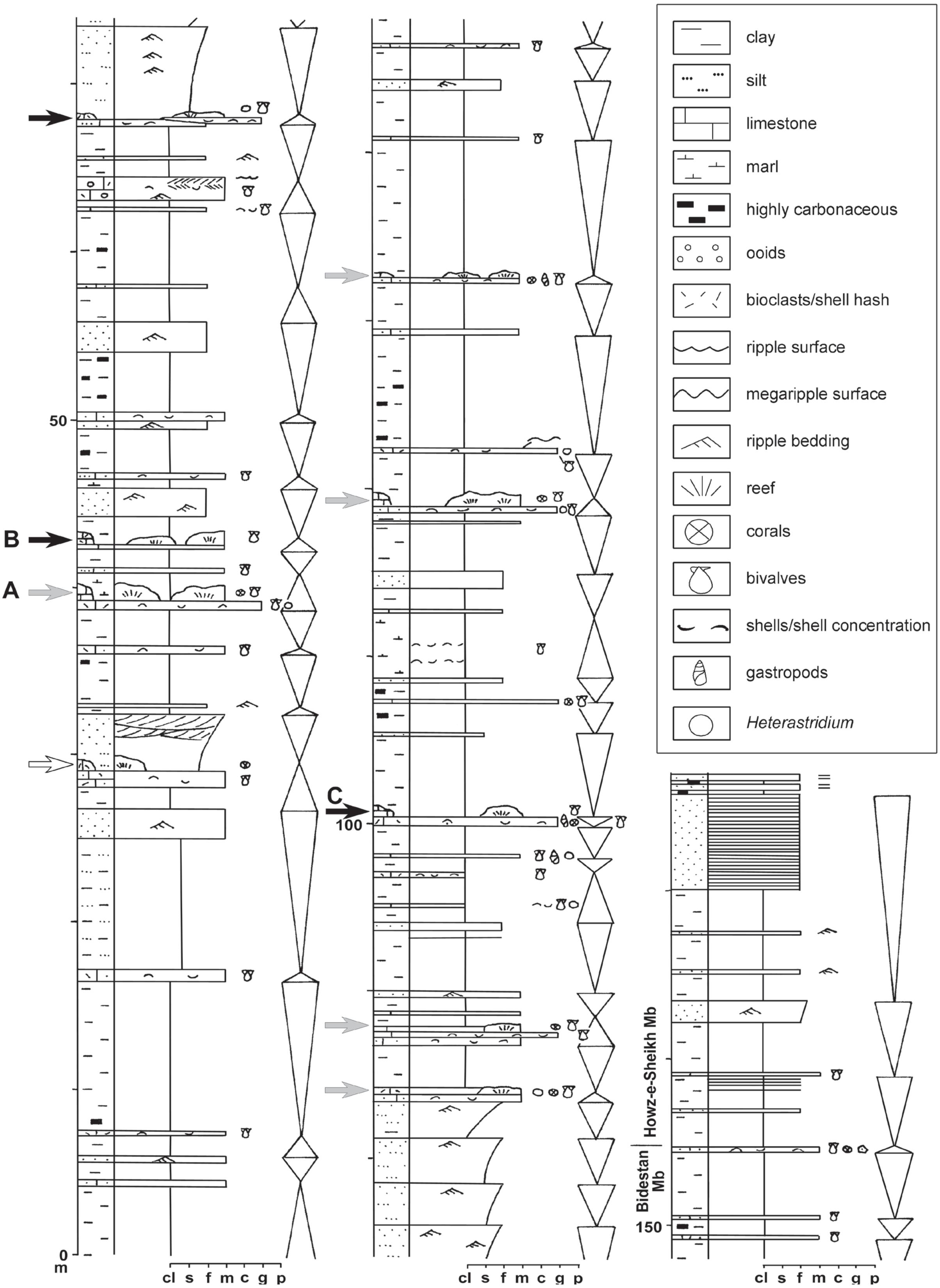


Fig. 3. Section through the Bidestan Member of the Nayband Formation south of Parvadeh (PAR-I). Arrows indicate position of reefs. Black arrows: bivalve reefs; grey arrows: bivalve reefs with associated corals; white arrows: coral reefs.

the bivalves to settle on the upper, left valves were doomed, because these upper valves easily became detached after death and were removed from the reefs by currents. The result is a very solid and dense reef framework.

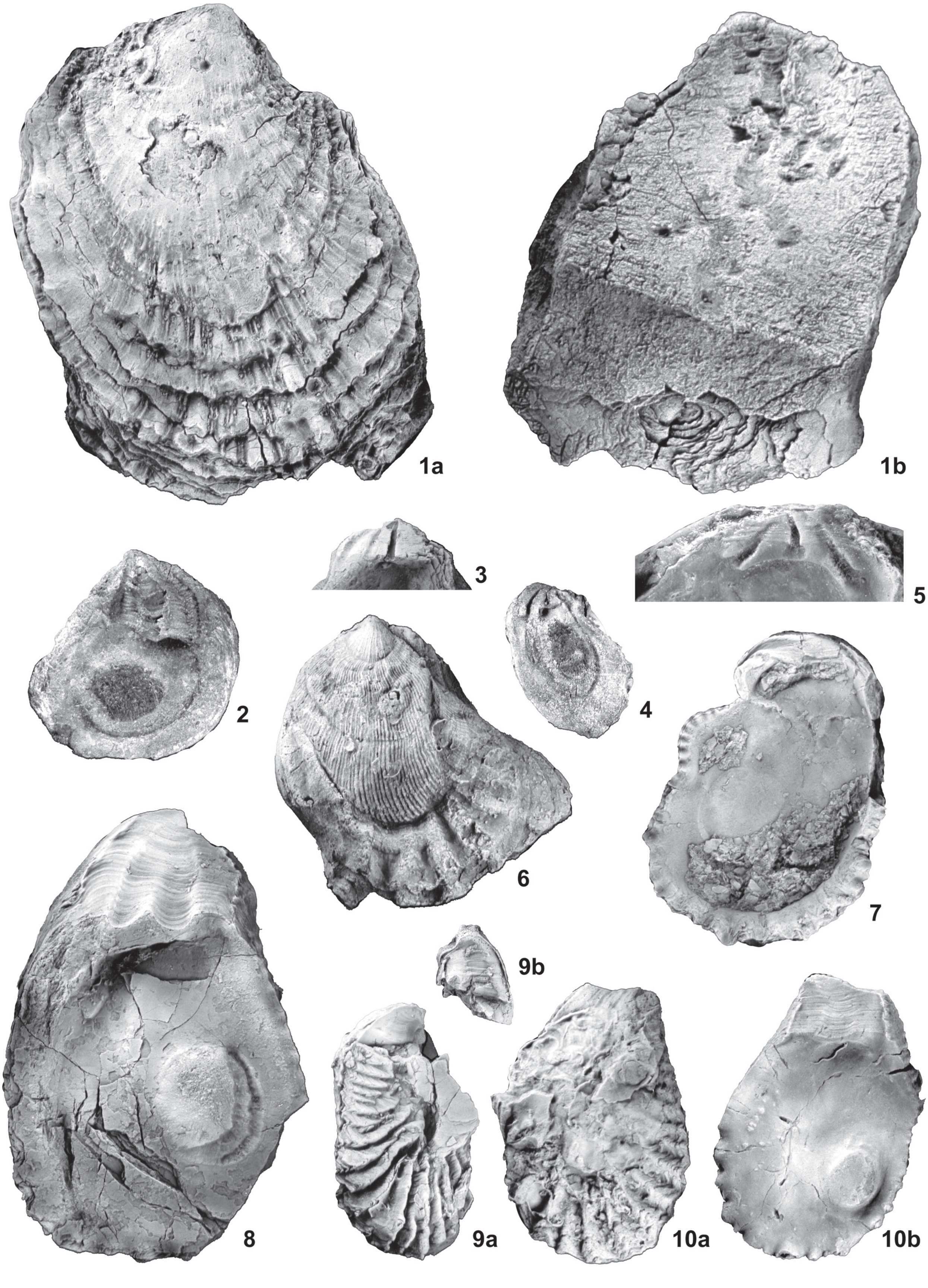
Bivalves also contributed to small patch reefs occurring in the Upper Muschelkalk of northern Baden-Württemberg, the framework of which consists predominantly of cemented roots of the crinoid *Encrinus liliiformis* (Hagdorn 1978; Hagdorn and Mundlos 1982). These reefs form lenticular bodies comparable in size with that of *„Placunopsis"* reefs. The cementing bivalves *Enantiostreon difforme*, *Newaagia noetlingi,* and *„Placunopsis" ostracina* usually form the basal framework of these reefs, in which epibyssate bivalves such as "*Myalina*", *Plagiostoma* and "*Mytilus*" as well as the terebratulid *Coenothyris* formed secondary reef dwellers. Both the *„Placunopsis"* and the bivalve-*Encrinus* patch reefs required a firm substrate and are generally found on top of shell beds or coarse bio-rudstones, more rarely on hardground surfaces. In this respect they closely resemble the reefs found in the Nayband Formation.

In the Jurassic, bivalve-dominated reefs are generally rare and inconspicuous. A lenticular patch reef, 70 cm in diameter, was found by one of the authors (FTF) on top of Lower Pliensbachian biorudstones northeast of Albarracin, Celtiberian Chain (northeastern Spain). The reef is monospecific and consist of a small oyster, probably *Catinula*, and was covered by silty marl.

Small lenticular patch reefs dominated by small oysters occur at several levels within the Kamar-e-Mehdi Formation (Middle Callovian-Lower Kimmeridgian) of the Kamar-e-Mehdi area southwest of Tabas, east-central Iran. The framework of these patch reefs consists either solely of the small grypheid oyster *Nanogyra nana* or else of *Nanogyra nana* associated with a highly diverse fauna of calcareous sponges and hydrozoans. The monospecific *Nanogyra* patches range in height from 0.2 to 0.3 m, the sponge-*Nanogyra* reefs reach up to 1.5 m in height and laterally extend for 2-3 m. The matrix filling the framework is bioclastic marlstone or bio-wackestone and this is also the substrate on which the reefs started to grow. Associated faunal elements are the bivalves *Trichites* and *Radulopecten* as well as crinoid debris. The general environment of the Kamar-e-Mehdi Formation is that of a large shelf lagoon (Wilmsen et al. 2003) and the patch reefs apparently grew in a low energy setting below the fair weather wave-base. Small coral patch reefs occur in close stratigraphic proximity with the oyster reefs in the same facies. The environmental parameters operating during growth of the various patch reefs do not seem to have differed substantially and the composition of these reefs may have been largely controlled by stochastic processes such as fluctuations in the larval pool of the framework-constructing taxa.

Oysters are also the dominant framebuilder of patch reefs that occur in brackish water lagoons and embayments in the Upper Jurassic of the Lusitanian Basin, for example at the coastal sections south of Santa Cruz and at Consolação (Fürsich 1981; Fürsich and Werner 1986; Werner 1986). Typically, these reefs occur in silt and marly silt and vary in height between 0.6 and 0.8 m and have a lateral extent of 1-3 m. The dominant framebuilder is the oyster *Praeexogyra pustulosa*, a minor element in some of the reefs is *Nanogyra nana*. Within the fine-grained substrate the oysters required some secondary hard substrate for initiating reef growth. This was provided by large shells of epibyssate or semi-infaunal bivalves such as bakevelliids, *Trichites* and *Isognomon*, which served as nuclei that became densely overgrown by *Nanogyra* and *Praeexogyra*. The species diversity of these reefs is very low. Associated with the framework occur some byssate and cemented bivalves (*Arcomytilus*, *Juranomia*), mobile grazing gastropods (*Metriomphalus*), and the echinoid *Pseudocidaris*. Framework-enforcing organisms are absent, whereas framework-destructing organisms are represented by some borings (*Gastrochaenolites*, *Talpina*). The low diversity has been explained as a result of high environmental stress, and the patch reefs are thought to have grown in low energy, mesohaline to brachyhaline environments (e.g. Fürsich and Werner 1986), similarly to those of some modern *Crassostrea virginica* reefs (e.g., Parker 1959).

A last reef type dominated by bivalves in the Jurassic has been recorded from the Upper Jurassic Portland Stone in the upper part of the Portland Freestone Member (Portland Limestone Formation) of the Isle of Portland, southern England (Fürsich et al. 1994). The reefs are up to 4 m high and 8 m across and are dominated by the bivalves *Liostrea expansa* and *Plicatula damoni*, whereby *Liostrea* predominates in the reef core and *Plicatula* at the reef edges. Additional framebuilders are the red


1a
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10b

alga *Solenopora* and, in some cases, the cyclostome bryozoan *Hyporosopora*. Bivalves also constitute accessory framebuilders, in particular *Nanogyra nana*, and are important elements of the framework destroyer guild (*Lithophaga*, *Gastrochaenopsis*, *Carterochaena*). The reefs exhibit a high diversity of accessory framebuilders, nestling and boring taxa, which indicate that they grew in a fully marine, shallow water environment.

Concluding remarks

Of the various groups of bivalves that in the early and middle Mesozoic started to form reefs only one group, the oysters, successfully occupy this niche until today. Part of the reason for their success as framework constructors may be that several of the taxa, such as *Crassostrea*, acquired the ability to grow upwards and evolved into a cone-shaped morphology, which is advantageous when competing for space and food and when coping with elevated rates of sedimentation. In this respect they resemble the most successful reef constructors among the bivalves, the rudists.

Plate 2
Fig. 1, *Newaagia stocklini* (Repin, 1996). PIW1999II/6. Aliabad. Left valve; a: exterior, b: interior, note the giant ligament area; x 1. Fig. 2, *Eoplicatula parvadehensis* Hautmann, 2001. PIW1999II/10. Parvadeh, sample PAR-I 107.5 m. Interior of left valve; x 1. Fig. 3, *Persia monstrosa* Repin, 1996. PIW1999II/210. Parvadeh, sample PAR-II 110.5 m. Ligament area of left valve, note the crus-like ridge; x 1. Fig. 4, *Pseudoplacunopsis asymmetrica* Hautmann, 2001. PIW1999II/17. Parvadeh. Interior of right valve; x 1. Fig. 5, *Pseudoplacunopsis asymmetrica* Hautmann, 2001. PIW1999II/18. Aliabad, sample (3f). Hinge of right valve, note the asymmetric crura; x 4. Fig. 6, *Persia monstrosa* Repin, 1996. PIW1999II/9. Parvadeh, sample PAR-II 113 m. Exterior of left valve, note the change in the ornamentation; x 1. Fig. 7, *Umbrostrea*? aff. *parasiticum* (Krumbeck, 1913). PIW1999II/29. Parvadeh, sample PAR-II at 126.5 m. Interior of left valve; x 1. Fig. 8, *Umbrostrea emamii* Hautmann, 2001. PIW1999II/24. Parvadeh, section PAR-I. Interior of right valve, note the multiple resilifer and the division of the adductor muscle scar reflecting position of quick and catch muscle; x 1. Fig. 9, *Umbrostrea iranica* Hautmann, 2001. PIW1999II/21. Parvadeh, sample PAR-II at 126.5 m. Articulated specimen; a: exterior of left valve and exposed ligament area of right valve; b: ligament area of left valve ; x 1. Fig. 10, *Umbrostrea emamii* Hautmann, 2001. PIW1999II/23. Parvadeh, sample PAR-I at 109.5 m. Right valve; a: exterior; b: interior; x 1.

All specimens except those of Pl. 2, Figs. 2 and 4 have been blackened with graphite emulsion and subsequently coated with magnesium oxide.

Acknowledgements

Field work for this project was financially supported by the Deutsche Forschungsgemeinschaft (grant Fu 131/19). We acknowledge, with gratitude, the hospitality of the National Iranian Steel Company at Tabas, and the logistic support by the Geological Survey of Iran.

References

Alavi M. (1996): Tectonostratigraphic synthesis and structural style of the Alborz Mountain system in northern Iran: J. Geodynam. 21: 1-33.

Bachmann G.H. (1979): Bioherme der Muschel „*Placunopsis*" *ostracina* und ihre Diagenese. N. Jb. Geol. Paläont. Abh. 158: 381-407.

Bahr L.M., Lanier W.P. (1981): The ecology of intertidal oyster reefs of the South Atlantic coast: a community profile. U.S. Fish and Wildlife Service, Blot. Program, Washington D.C. FWS/OBS 81/15, 105 pp.

Duringer P. (1985): Stratégie adaptive de la croissance de *Placunopsis ostracina* Schlotheim, épizoaire du Muschelkalk supérieur (Trias germanique, Est de la France). N. Jb. Geol. Paläont. Mh. 1985: 1-22.

Fagerstrom J.A. (1987): The evolution of reef communities. John Wiley and Sons, New York, 600 pp.

Flügel E. (1975): Mikrofazielle Untersuchungsmethoden von Kalken. Springer, Berlin, 454 pp.

Fürsich F.T. (1981): Salinity-controlled benthic associations from the Upper Jurassic of Portugal. Lethaia 14: 203-223.

Fürsich F.T., Werner W. (1986): Benthic associations and their environmental significance in the Lusitanian Basin (Upper Jurassic, Portugal). N. Jb. Geol. Paläont. Abh. 172: 271-329.

Fürsich F.T., Palmer T.J., Goodyear K.L. (1994): Growth and disintegration of bivalve-dominated patch reefs in the Upper Jurassic of southern England. Palaeontology 37: 131-171.

Fürsich F.T., Hautmann M., Senwobari-Daryan B., Seyed-Emami K. (2005): The Upper Triassic Nayband and Darkuh formations of east-central Iran: Stratigraphy, facies patterns and biota of extensional basins on an accreted terrane. Beringeria, in press.

Hagdorn H. (1978): Muschel/Krinoiden-Bioherme im Oberen Muschelkalk (mo1, Anis) von Crailsheim und Schwäbisch Hall (Südwestdeutschland). N. Jb. Geol. Paläont. Abh. 156: 31-86.

Hagdorn H., Mundlos, R. (1982): Autochthonschille im Oberen Muschelkalk (Mitteltrias) Südwestdeutschlands: N. Jb. Geol. Paläont. Abh. 162: 332-351.

Hagdorn H., Simon T. (2000): *Placunopsis*-Riffe im Oberen Muschelkalk der Süd-Eifel. Zbl. Geol. Paläont. Teil I 1999 (3-4): 293-314.

Hautmann M. (2001a): Die Muschelfauna der Nayband-Formation (Obertrias, Nor-Rhät) des östlichen Zentraliran. Beringeria 29: 1-181.

Hautmann M. (2001b): Taxonomy and phylogeny of cementing Triassic bivalves (families Prospondylidae, Plicatulidae, Dimyidae and Ostreidae). Palaeontology 44: 339-373.

Hölder H. (1961): Das Gefüge eines *Placunopsis*-Riffs aus dem Hauptmuschelkalk. Jber. u. Mitt. Oberrhein. geol. Ver., N.F. 43: 41-48.

Johnson C.C., Sanders D., Kauffman E.G., Hay W.W. (2002): Patterns and processes influencing Upper Cretaceous reefs. Soc. Econ. Paleont. Mineral. Spec. Publ. No. 72: 549-585.

Jux U., Omara S. (1983): *Pachypteria sinaitica* n. sp. – eine aufgewachsene, austernähnliche Muschel aus dem Unterkarbon Ägyptens. Paläont. Z. 57: 79-91.

Krumbein W. (1963): Über Riffbildung von *Placunopsis ostracina* im Muschelkalk von Tiefenstockheim bei Marktbreit in Unterfranken. Abh. Naturwiss. Ver. Würzburg 4: 1-15.

Parker R.H. (1959): Macro-invertebrate assemblages of central Texas coastal bays and Laguna Madre. Bull. Am. Ass. Petrol. Geol. 43: 2100-2166.

Senowbari-Daryan B. (1996): Upper Triassic reefs and reef communities of Iran. In Reitner, J., Neuweiler, F. and Gunkel, F. (eds), Global and regional controls on biogenic sedimentation. I. Reef evolution. Research reports. Göttinger Arb. Geol. Paläont., Sonderband 2: 299-304.

Seyed-Emami K. (2003): Triassic in Iran. Facies 48: 91-106.

Steuber T., Löser, H. (2000): Species richness and abundance patterns of Tethyan Cretaceous rudist bivalves (Mollusca: Hippuritacea) in the central-eastern Mediterranean and Middle East, analysed from a palaeontological database. Palaoegeogr. Palaeoclimatol. Palaeoecol. 162: 75-104.

Wells H.W. (1961): The fauna of oyster beds, with special reference to the salinity factor. Ecol. Monogr. 31: 239-266.

Werner W. (1986): Palökologische und biofazielle Analyse des Kimmeridge (Oberjura) von Consolação, Mittelportugal. Zitteliana 13: 3-109.

Wilmsen M., Fürsich F.T, Seyed-Emami K. (2003): Revised lithostratigraphy of the Middle and Upper Jurassic Magu Group of the northern Tabas Block, east-central Iran. Newsl. Stratigr. 39: 143-156.

Wood R. (1999): Reef evolution. Oxford University Press, Oxford, 432 pp.

Riassunto

[*Reefs* a bivalvi del Trassico Superiore dell'Iran]

Durante il Fanerozoico i gruppi di organismi che hanno contribuito in modo sostanziale allo sviluppo di scogliere (*reefs*) variarono considerevolmente dal punto di vista della loro composizione tassonomica. È ben noto che durante il Cretaceo Medio e Superiore i bivalvi, rappresentati da rudiste e da ostriche, costituivano i principali costruttori e che le ostriche continuarono a costruire fino al Recente strutture tipo reef, specialmente in ambienti marini marginali,. Ciò che risulta essere meno noto è che alcuni membri di questa classe contribuirono allo sviluppo delle scogliere già nel Mesozoico inferiore-medio agendo come costruttori poco dopo che essi divenirono forme cementate.

Le finalità di questo studio sono (a) descrivere i *patch reefs* della Formazione di Nayband (Triassico Superiore, Iran centro-orientale) nella quale i bivalvi erano i principali organismi costruttori e (b) riportare le informazioni riguardanti le scogliere a bivalvi durante il Mesozoico inferiore-medio. Le scogliere (*reefs*), come definite in questo studio, mostrano una struttura costituita da taxa cementati. I banchi costruiti da taxa "*mud stickers*" quale *Lithiotis* o da taxa epibissati quale *Isognomon* e *Mytilus* sono tuttavia non considerati come vere e proprie

scogliere a bivalvi.

Nella Formazione di Nayband associazioni a bivalvi costituiscono piccoli *pach reefs* localizzati nella parte mediana ed esterna di una rampa a sedimentazione mista carbonato-silicoclastica. Queste associazioni sono in stretta vicinanza stra-tigrafica con coralli e reefs a coralli e spugne. Rispetto ad altri pach reefs del Triassico-Giurassico dominati da bivalvi, i *reefs* a bivalvi della Formazione di Nayband sono caratterizzati da un'alta diversità di taxa costruttori.

Questi sono rappresentati da tre diverse famiglie quali gli ostreidi *Umbostrea emamii*, *U. iranica* e *U.*? aff. *parasiticum*, i prospondilidi con *Newaagia stocklini* e *Persia monstrosa*, ed i plicatulidi con *Eoplicatula parvadehensis* e *Pseudoplacunopsis asymmetrica*. I bivalvi costruttori di reefs potrebbero aver avuto un vantaggio competitivo sui coralli e sulle spugne calcaree in ambienti caratterizzati da un maggiore grado di torbidità e/o un più alto contenuto di nutrienti.

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Aut. Trib. Ferrara n. 36/21.5.53
Comitato di Redazione della Sezione Museologia Scientifica e Naturalistica: D. Bassi, S. Capitani, C. Peretto, G. Zini.

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