Ecology and adaptive strategies of corals in unfavourable environments: Examples from the Middle Jurassic of the Kachchh Basin, Western India

By


With 19 figures and 1 table in the text


Abstract: In the Bathonian to Callovian sedimentary sequence of Kachchh autochthonous corals are relatively rare elements of the benthic fauna except for two levels at which they dominate and record contrasting strategies and adaptations to cope with conditions generally regarded as unfavourable for coral growth. The monospecific *Amphiprora perforata* field consists of globular to platy coral heads which apparently tolerated turbid water conditions and occasional reworking, and managed to thrive on sandy, intermittently shifting substrates. The highly diverse *Microsolenia amorpha-Montlivaltia frustriformis* association formed meadows on soft lime mud in low energy, turbid, possibly poorly lit environments subject to moderate rates of sedimentation. The lack of large reef bodies within the Jurassic of the Kachchh Basin can be explained largely by unsuitable substrate conditions and relatively high rates of sedimentation and not so much by generally unfavourable palaeo-oceanographic conditions.

Introduction

Hermatypic corals are generally regarded as stenotypic, confined to a well-known range of environmental parameters such as salinity, turbidity, temperature, light, and substrate conditions. Nevertheless, a number of Recent corals are known to occur and apparently thrive in environments thought to be unsuitable for coral growth, due to particular morphological or physiological adaptations (e.g. fungiids). The aim of the present paper is to document two cases from the fossil record, in which corals successfully colonized such environments, the crucial factors apparently being largely substrate conditions.

The Jurassic of Kachchh is famous for its rich faunas of ammonites and benthic invertebrates, chiefly bivalves and brachiopods. Corals are rare or absent except for two notable horizons which are characterized by prolific coral growth. The first of these horizons contains large heads of *Amphistegina pteroforina* which apparently lived on unconsolidated, periodically reworked sandy substrates. In the second horizon, a highly diverse association of colonial and solitary corals lived on soft bioclastic lime mud. In both cases the coral density is so high that some authors used the term reef to describe the coral assemblages (e.g. Kanjilal 1990). We would like to discuss in the following the morphological adaptations which enabled the corals to thrive in these environments.

The coral fauna of Kachchh has been monographed by Gregory (1902) who described 71 taxa. Recently, this fauna has been revised by Pander & Fürsich (1993) in order to obtain a sound taxonomic basis for palaeoecological investigations.

Geological framework

During the Jurassic, the basin of Kachchh formed part of an embayment extending from the southern margin of the Tethyan Ocean in a southeasterly direction (Fig. 1). Situated at the western margin of the Indian plate, the basin formed as a E-W oriented half graben system in connection with the breaking up of Gondwana (e.g. Biswas 1982, 1991) which, initiated in the Late Jurassic, finally led to separation of India from Africa (e.g. Rabinowitz et al. 1983, Boccaletti et al. 1988). The sea inundated the basin by Mid-Jurassic (Bajociian) times (Singh et al. 1982) and persisted until the Mid-Cretaceous. During this period, the basin received nearly 2000 m of predominantly siliciclastic sediments. These sediments range from nearshore coarse-grained sands and conglomerates to storm-influenced shallow shelf silts, and mid-shelf clays and silts situated below storm wave base. Carbonate sediments are confined to the Bathonian and represent skeletal, oolitic or intralastic pack- to grainstones of shallow shelf origin, mid-shelf argillaceous micrites punctuated by distal storm layers, and shelly packstones resulting from reworking processes during transgressive events (Fürsich et al. 1992, Fürsich & Oschmann 1993).

Jurassic sediments form two outcrop belts in the district of Kachchh (Fig. 1): a series of east-west running 'islands' along the Great Rann of Kachchh and a number of domes on the so-called Kachchh Mainland. Both represent domal structures formed in connection with the Deccan Trap volcanism and Jurassic rocks are exposed as a result of erosion of younger sediments on and in the vicinity of these domes. The two coral horizons occur in Middle Jurassic rocks of Kachchh Mainland and belong to the Patcham Formation (Bathonian) and Chari Formation (Callovian-Oxfordian) of earlier authors respectively (Fig. 2). The Patcham Formation is a carbonate-dominated unit representing...
shallow to mid-shelf environments, whereas the Chari Formation is characterized by low energy mid-shelf argillaceous silts with intercalated sand bodies deposited during relative sea level lowstands. According to Fürsich et al. (1992) and Fürsich & Oeschmann (1993) the relative sea level within the basin rose from the Late Bathonian to the Oxfordian. This general deepening trend is composed of shallowing-deepening cycles of at least two orders of magnitude, the smaller unit corresponding to parasequences. The two coral levels discussed here occur in the shallowing phases of the larger-scale cycles (possibly corresponding to third order eustatic cycles; see Fürsich & Oeschmann 1993; Fig. 3).

On the whole, corals are relatively rare elements of the rich benthic shelly macrofauna of the Kachchh Basin which is dominated by bivalves. Apart from the two occurrences which are the subject of this paper, corals are common at only few horizons and usually occur either as scattered autochthonous or abundant, but reworked and transported individuals (Pandey & Fürsich 1993).

**Localities**

The _Amphiastraea piformis_ Bed occurs along the crest of Habo Dome (Fig. 1), in the middle of a thick sandstone unit which divides the Chari Formation in a lower and upper argillaceous unit (Jilikadi Mb of Kanjilal 1978; the _Amphiastraea piformis_ Bed corresponds to his bed no. 9). The level can be followed laterally for several 100 m. The high diversity coral meadow occurs in two closely adjacent horizons in the Patcham Formation at Jamara Dome (Fig. 1), close to the centre of the eroded core. Intensive weathering of the flatly lapping wackestone to packstone beds produced lags of fossils which allowed bulk collecting. At both horizons the coral concentrations have been observed to cover several thousand square metres, although small-scale faulting makes it difficult to trace the beds.

**Material and methods**

At both coral localities detailed sections were measured (Figs. 4, 5, 8). In the case of the _Amphiastraea piformis_ Bed, several coral heads were collected and dissected in the laboratory. At Jamara, statistical sampling of the fossil contents was possible due to extensive outcrops. For this purpose, four subsamples were taken at each horizon (A, B) each covering 1 m² to assess the degree of

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Fig. 3. Generalized section of Jurassic sediments of Kachchh Mainland with tentative curve of relative sea level and position of coral layers discussed in the paper. Note that in many sections of Kachchh Mainland the sandstone in the middle Chari Formation consists of two units separated by fine-grained shaley mudstones. A third, thinner sandstone unit occurs within the upper part of the formation.
patchiness. Within these areas, the total faunal content was collected and identified, where possible, to species level. This way more than 2500 specimens were identified and used to define the Microsclera amorpha-Montlivaltia frustulifera association (see below). To account for the large differences in size among the specimens, an adjusted relative abundance was calculated (as an approximation of biomass) by multiplying the number of individuals with a size factor (1 = small; 2 = medium; 3 = large; 4 = very large) (see also FÜRSEICH & WERNER 1991). In the case of small encrusting taxa (serpulids, bryozoans, scleractinians) the occurrence on each host was counted to represent one individual.

For corals the distribution of encrusting and boring organisms on the upper and lower surfaces was noted in order to recognize different growth strategies among the epizoans and endobions.

**Preservation**

The coral material is generally well preserved. In the *Amphiastrea* heads, the interior is often recrystallized so that morphological features are confined to the outermost few millimetres of the heads. The other corals suffered occasionally from weathering which caused partial abradion of encrusts and morphological features of the surface. Some of the material is fragmented; most of this fragmentation took place in the Bathonian. Similarly, abrasion is not solely a weathering phenomenon, but partly affected the corals after their death on the sea floor. The associated bivalves, gastropods and brachiopods are generally well preserved except for the thin elongate bivalve *Gervilla* (*Cuturepis*) which is usually fragmented.

**The *Amphiastrea* piriformis Bed**

**Description**

The *Amphiastrea* piriformis Bed (Fig. 4) occurs about 60 m above the base of the thick sandstone unit (KANHAIL 1978) which is partly bioturbated, partly crossbedded, and usually unfossiliferous. This sandstone, the middle member of the Chari Formation, represents a shallowing episode where the sea floor was exposed to fair weather waves, wedged in between deeper, storm-dominated argillaceous silts. The coral layer is 15-85 cm thick and rests with a distinct (but not erosion!) base on a heavily bioturbated fine-grained sandstone. This sandstone, more than 1.5 m thick, is unfossiliferous except at locality (g) (Fig. 5) where small heads of *Amphiastrea* piriformis in growth position occur scattered throughout the sediment. Within the coral layer, heads of *Amphiastrea* occur usually closely packed (except at section f), where they are small and scattered, but do not encrust each other. The heads reach up to 60 cm in length and up to 20 cm in height, but usually are around 10-20 cm in diameter. Platy and globular morphotypes occur, whereby the second type is more abundant. Coral heads are rarely encrusted or bored. The sediment between the coral heads consists of heavily bioturbated bioclastic fine-grained sandstone with pockets of shell debris. Associated with the corals are scattered shells of bivalves and gastropods such as *Palaeoconcha*, *Plagiostoma*, and *Plicatula*, as well as echinoid spines. Some of the corals occur in position of growth, others are upside down. At several of the sections, the corals form a jumbled mass of randomly oriented heads. A particular feature of the coral heads is that their calices often cover the whole surface of globular growth forms indicating growth in all possible directions. In some cases (Fig. 6) it can be demonstrated that the coral had been overturned and continued to grow again (possibly due to recolonization) in the opposite direction.

The coral layer is overlain by a 10-40 cm thick poorly sorted calcareous fine-grained sandstone rich in bivalve shells. The base is sharp and erosional, the sediment between the shells bioturbated. At section (b) (Fig. 8) *Ophiomorpha nodosa* can be seen to extend from the top of the layer downwards, but clearly belongs to the overlying depositional unit. The fauna is dominated by *Modiolus imbricatus*, most of which are articulated and many of which are found in life position except at sections (d) and (h), where disarticulated shells prevail. Additional faunal elements are clusters of a large *Plicatula*, apparently also in life position, the bivalves *Plagiostoma* cf. *oeybohli*, *Catunula sandalina*, *Nanogyra nana*, *Indogrammatodonta virgatus*, *Trachites* sp., *Isognomon* sp., and the gastropods *Pseudomelanida* sp. and *Globularia* sp. At section (b) scattered small heads of *Amphiastrea* occur at the base. Most likely, they have been reworked from the coral layer.

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**Fig. 4. Section through the *Amphiastrea* piriformis Bed and adjacent sediments.**
Coral from the Middle Jurassic of the Kachchh Basin, Western India

Fig. 6. Sketch of Amphiastrea perforata in cross-section showing recolonisation by a second generation of polyps after the initial coral head had been overturned. Arrows indicate growth direction of corallites.

The Modiolus shell bed is followed, after a sharp erosional base, by a coarse-grained, large-scale crossbedded, quartzose sandstone. This unit is devoid of fossils except at sections (a), (b) and (c) where a thin basal shell lag is developed consisting, in the case of section (b), of articulated Modiolus imbricatus. In section (g), Ophiomorpha occurs in low density as do large wood fragments.

Discussion: The depositional environment. The sections in Figure 5 reflect an environment subject to a siliciclastic sedimentation regime. Up-section, the rate of sedimentation increased as did the energy level. This is supported by (1) the heavily bioturbated sandstone at the base compared to the cross-bedded sandstone at the top, (2) the increase in grain size up-section, (3) the presence of Ophiomorpha nodosa in the upper part of the section at three localities, a form generally found in shallow-water, high energy environments, (4) the reworking of large coral heads in the coral layer in contrast to the scattered occurrence of corals in life position in the underlying bed in section (f), and (5) the preservation of semi-infaunal (Modiolus imbricatus) and epifaunal (Plicatula) bivalves in life position. The last point might be taken as indication of low energy conditions. Such conditions surely must have existed during growth of the bivalves. The preservation of epifaunal and semi-infaunal elements in their growth positions, however, only possible when they are rapidly covered by sediment while still alive. The presence of these bivalves thus points to episodic phases of rapid sedimentation. Similarly, the presence of erosion surfaces and shell lags indicate that reworking and rapid burial played a major role and that the rate of background sedimentation probably differed considerably from the rate of net sedimentation.

Thus, the depositional environment of the bioturbated sandstone can be envisaged as moderate to low energy shelf below fair-weather wave base and within the reach of distal storms only, so that there was ample time for freshly deposited sediment to become thoroughly bioturbated (Fig. 4). It was in this
facies that small heads of *Amphithraea* started to grow (e.g. Fig. 5g). At a later stage, coral growth became more widespread and heads up to 60 cm in diameter formed. At the same time, the energy level increased and storm events became more frequent resulting in repeated reworking of the coral heads. Kanjilal (1990) interpreted the coral occurrence as reef and in his Fig. 2 sketched a solid coral mass in the crevices of which a number of epibysate and infaunal bivalves lived. Careful examination of the coral layer revealed however that, although the packing of the coral heads can be quite dense, they usually do not encrust each other, but are separated by thin veneers of sediment.

Most likely, coral growth stopped due to a heavy influx of sediment killing the polyps. On the frequently scoured sea floor nests of *Modiolus imbricatus* grew. This biofacies persisted for some time, but was frequently interrupted by reworking events that disarticulated, concentrated and fragmented the *Modiolus* shells. Finally, a migrating high energy subtidal sand dune covered the last colonisation phase of the *Modiolus imbricatus*-dominated community, reworked relics of which are found at the base of the coarse-grained cross-bedded sand body.

**Ecology of *Amphithraea***: The cerioid scleractinian coral *Amphithraea piriiformis* (Fig. 7) apparently is one of those corals that were able to tolerate a broader range of environmental conditions than most other corals. Whereas most hermatypic corals are known to depend on clear water conditions with negligible clastic influx, its high abundance in a fine-grained sandstone at the top of Habo Dome strongly suggests that the coral was able to cope with increased rates of sedimentation and possibly also with turbid water. Moreover the sandy sea floor did not provide a suitable substrate for cementing organisms. Indeed, in none of the *Amphithraea* heads an attachment area could be seen which must have been therefore tiny. It appears that the coral heads rested loosely on the substrate, after the juveniles had outgrown their tiny initial attachment areas. With this mode of life the coral were prone to become reworked during storm events. However, the fact that in many of the corals all the surface is covered by corallites growing outward indicates that reworking events and overturning did not seriously hamper coral growth, as often polyyp growth continued on the side facing upwards. The example shown in Figure 6 demonstrates this strategy which is found not only in globular, but also in platory forms.

Efficient removal and rejection of sediment by *A. piriiformis* may have been possible by polyps with mucus and ciliary cleaning abilities. Such cleaning mechanisms have been observed in Recent corals living in comparable environments (e.g. Loya 1972, 1976).

This is not the only case where *Amphithraea piriiformis* occurs in environments apparently adverse for coral growth: Försch & Werner (1986) recorded the coral as a characteristic element of the *Isognomon rugosus-Amphithraea* subset of their *Isognomon rugosus* association. The species occurs in the Lusitanian Basin (Portugal) within marginally marine, silty to fine sandly sediments of Kimmeridgian age. Försch & Werner (1986: 289) suggested that the coral not only tolerated turbid waters, but was also able to withstand moderate salinity fluctuations. Rosendahl (1985) reported *A. piriiformis* from fine-grained sediments indicative of soft substrates in very shallow but quiet environments from the Upper Jurassic of southern Portugal. There, *A. piriiformis* is associated with stoutly branching compound corals and solitary corals (*Montipora* sp., *Axosmilia* A. Piriiformis). In the Upper Jurassic of Terriente (Iberian Chains, Spain) *A. piriiformis* occurs, associated with other small corals, in fully marine low energy ooid-bearing marls (Erbenst 1990). Apparently the species was a rare constituent of Jurassic coral reefs.

In modern environments comparable coral occurrences (coralliths, "Rollkorallen") have been mentioned repeatedly (e.g. Glynn 1974, Pichon 1974, Gill & Coates 1977), but only limited information is available on their ecology. Whether live polyps cover the whole surface or only part of it largely depends on the frequency of disturbance (Pichon 1974). In frequently disturbed corals, polyps manage to survive short periods during which they come to rest against the substrate. Judging from the irregular growth form and the distinct discontinuity surfaces found in *A. piriiformis* from Habo Dome, disturbance was not frequent enough to allow continuous growth across the whole coralum.

In summary, in the Middle Jurassic of the Kachchh Basin, the coral *Amphithraea piriiformis* was able to live on sandy, intermittently shifting substrates
in a shallow, nearshore environment subject to influx of sediment and turbid water conditions in connection with frequent storm events. The high density of corals and the large size of the coral heads indicate that *Amphistaera piriiformis* was, unlike most other corals, a generalist, successfully adapted to cope with these, for corals generally very unfavourable, conditions.

**High diversity coral meadows of the Patcham Formation**

**Sediments and general features**

Entering the core of the dome at Jumara, the Patcham Formation is characterized by well bedded mudstones to wackestones (biomericite) alternating with thin layers of marl or bioclastic marl. Typical faunal elements in the upper part of this sequence are hexactinellid sponges which occur in high densities for about 25 m of the rock column and apparently formed widespread sponge meadows. The sponge facies is underlain by about 6 m of echinoderm packstone with a layer of bored and encrusted reworked carbonate nodules at its base. The packstone is underlain by 14 m (base not seen) of bioclastic wackestone and marlstone with intercalations of thin (1-3 cm thick) graded beds of skeletal debris corresponding to distal tempestites. Several coral-rich levels occur in the lower 6 m of this sequence (Fig. 8). The lowermost layer is dominated by large (up to 20 cm in diameter), flat, elliptical heads of *Microsolenia* (Fig. 8). The coral diversity is considerably lower than that of the following two levels which are discussed in detail in the following. The levels are 10 cm thick each and consist of heavily bioturbated bioclastic wackestone with remnants of thin layers of packstone. The packstone most likely corresponds to reworking events resulting in skeletal concentrations subsequently largely destroyed by bioturbation. Bioclasts consist of coral, echinoderm, mollusc, and brachiopod debris. Occasionally remnants of lithistid sponges and litooid foraminifera occur.

Apart from the fine skeletal debris, numerous complete specimens of bivalves, brachiopods, corals, and gastropods are the characteristic feature of the two levels (Table 1 and Appendix). The most diverse group are the corals (42 species), followed by bivalves (32 species), gastropods (11 species), brachiopods (7 species) and serpulids (6 species). Comparatively rare elements are coralline sponges, hydrozoans, crinoid ossicles, and echinoid spines. In terms of relative abundance, corals account for 43.3% of the macrofauna, followed by bivalves (14.3%), brachiopods (13.7%), coralline sponges (4.3%), and gastropods (1.6%). Taking size of specimens into account (as an approximation of biomass) corals dominate even more (see weighed relative abundance in Table 1 and Appendix).

Preservation of the fauna is very variable. Nearly pristine shells occur next to shells which show signs of abrasion. Bivalves are partly articulated, partly disarticulated. Very fragile shells such as the thin, elongate *Gerullia* (*Cultriptis*) *tatumosavrus* are commonly fragmented.

**Fig. 8.** Section through part of the upper Patcham Formation (Upper Barroonian) at Jumara Dome. Arrow indicates position of the two adjacent high diversity coral layers.
Table 1. Trophic nucleus of the Microsolenia amorpha-Montlivaltia frustiformis association. pres. %: presence percentage; rel. abund.: relative abundance; troph. group: trophic group, mc: microcarnivores; s: suspension-feeders; eb: epibystes; ec: epifunal cemented.

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<th>weighted rel. ab.</th>
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Palaeocological analysis

The Microsolenia amorpha-Montlivaltia frustiformis association

Nine statistical samples were obtained from the two coral levels, five from the lower one (A) and four from the upper one (B) (see Appendix). For each sample 1 m² of weathered surface was collected to allow inferences about changes in density of the fauna and about the degree of patchiness. Although the nine samples differed considerably in density, the relative abundance of the most abundant taxa was sufficiently similar both within each horizon as well as between the two horizons to combine the samples into a single association. According to its dominant members, the association is termed Microsolenia amorpha-Montlivaltia frustiformis association. Within the trophic nucleus, which consists of 15 taxa, eight corals occur, the most abundant of which are the two name-giving taxa (Table 1; Fig. 9). Apart from Montlivaltia frustiformis all corals are of the compound type. The only brachiopod within the trophic

Fig. 9. Characteristic taxa of the Microsolenia amorpha-Montlivaltia frustiformis association at Junara Dome. a: Microsolenia amorpha (Gregory), x 1; b: Collignonastrea jumarenensis (Gregory), x 2; c: Locbaurosmilia trapeziformis (Gregory), x 1; d, h: Stylinus kachensis Gregory, top view (d) and lower surface view (h), x 2; e: Paeonia cf. crenuligera Cossmann, x 2; f, g: Montlivaltia frustiformis Gregory, top view (f) and side view (g), x 1.5; i: Evginus rollandi Douville, x 2; j: Cryptoporphyina pulcherrima (Ketchin), x 3.

Fig. 9 (Legend see p. 282)
nucleus, *Cryptorrhynchia pulcherella*, occurs in all samples and reaches here the acme of its distribution within the Kachchh Basin. Bivalves are represented by the epibyssate *Eligius rollandi* and the shallow infraunal *Praecynthia cf. creasligera*. Two species of serpulids and the sclerosponge *Neonopus* occur commonly as encrusters on corals.

In terms of trophic groups, microcarnivores (i.e. corals) dominate with 67.2% (weighed relative abundance) followed by suspension-feeders (most bivalves) with 31.6%. Deposit-feeders (0.8%) and herbivores/omnivores (0.4%) are not significant.

Among bivalves more than half (54.2%, unmodified rel. abundance) are epibyssate (e.g. *Eligius*, *Spondyluspecten*, *Gervillia* (*Carditaopina*), *Especten*), 30% are shallow burrowers (*Praecynthia*, *Protocardia*, *Sphaerodonta*), 7.5% mobile infraunal deposit-feeders (*Nuculana*, *Palcomuscula*), and 6.3% cemented (*Lopha*, *Namagwa*). Boring bivalves (1.6%) are underrepresented, because the number of boreholes is considerably higher than the number of shells. Deep burrowing forms (*Pholadomya*) are very rare (0.3%).

Between 0 and 22% (on average: 7.12%) of the coral-associated fauna is encrusted by serpulids, the oyster *Namagwa*, the sclerosponge *Neonopus*, and a nubeculindelliform *Ctenostoma*. Shells bored by cirripedes are very rare.

**Analysis of the coral fauna:** The dominant element of the *M. amorphus-M. frustriformis* association are corals. Compound forms are about three times as abundant as solitary forms, but never reach a large size: most are smaller than 5-10 cm, they rarely exceed 20 cm in diameter. Most compound corals are cestoid, plocoid, or thamnasteroid. The 42 coral taxa have been grouped in 17 morphotypes, ten of which are compound forms, the remaining seven are solitary forms (Fig. 10). Criteria to recognize these morphotypes are the overall shape and the size of the attachment area and resting area. As with all classifications there are some specimens which were difficult to place in one or the other category, but on the whole the corals could be easily assigned to one of the 17 morphotypes.

The relative abundance of the various morphotypes hardly differs between level (A) and (B) (Fig. 11). Flat and umbrella-shaped types dominate, followed by subpatellate, globose, and turbinate types. Tympooid, conical and branching morphotypes are, in contrast, very rare. In general, morphotypes with a small attachment area (e.g. flat, umbrella-shaped, tubinarian, and globosic forms) are more abundant than those with a large attachment area (e.g. crustose and cylindrical forms).

The distribution pattern of the morphotypes in the nine samples varies surprisingly little and the overall composition in the samples is nearly identical (Fig. 12). The major difference lies in a distinctly lower coral density of the samples from level (B).

In a second step of our analysis the relative size of the attachment areas and resting areas has been investigated (Fig. 13). As Fig. 13 shows, the attachment areas vary between small and large: In six of the morphotypes it is less than

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Fig. 10. Coral morphotypes, their characteristic features, and examples. High diversity coral meadows of the Patcham Formation of Junara Dome.
20 % of the maximum diameter of the coral, in eleven morphotypes it is less than 50 %, and only in two morphotypes it exceeds 80 %. In compound corals the attachment area is nearly half of that of solitary corals. Taking all corals together, the average attachment area reaches only 26 % of the maximum diameter.

On average, solitary corals have an attachment area of 40 % as compared to a resting area of 44 %. Thus the resting area is only marginally larger than the attachment area. This is different in compound corals where the average resting area is about twice as large as the attachment area (22 % as compared to 54 %), but this ratio varies substantially according to morphotype. Combining all coral data, the mean resting area reaches half the mean maximum diameter (Fig. 13). In most cases the attachment area is very irregular showing that the corals attached themselves to the biecclast-rich sediment surface and only rarely to larger objects such as big oyster shells. In several cases small pebbles, no longer preserved, were encrusted.

**MORPHOTYPE DOMINANCE**

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Fig. 11. Relative abundance of the 17 morphotypes in the two coral layers (A, B) at Jamara Dome. Compound corals account for three-fourth of the specimens. Note the dominance of morphotypes with small attachment areas. Numbers in brackets refer to investigated specimens.

**Corals from the Middle Jurassic of the Kachchh Basin, Western India**

![Graph showing coral and coral morphotype density (per 1 m²)](image)

Fig. 12. Density of coral morphotypes per square metre in the eight sampled bed surfaces (A1-A4 and B1-B4) of the Patchatt Formation at Jamara Dome. 1-17 refer to coral morphotypes of Figure 10.

Around 50 % of corals are encrusted, but never very densely. As one would expect, encrusting organisms are far more common on the lower side of corals than on the upper surface (Fig. 14). As upper surface encrusters usually settle only after the death of the corals, post-mortem encrustation is not very common. In several cases, pre-mortem encrustation could be verified by growth reaction of the encrusted coral (e.g. Fig. 18b). Between 3 % (level A) and 1 % (level B) of the attachment areas are encrusted and testify that reworking was rare. Among the encrusters, serpulids dominate (Fig. 15). They are represented by six taxa belonging to the form genera **Cycloserpula**, **Doroserpula**, and **Tetraceratula**. The sclerosponge **Neopora** is also relatively common, whereas small oysters are rare. The crustose bryozoan **Beronicus** is the only bryozoan present. **Stomatopora**, another Jurassic bryozoan and ubiquitous encruster on shells and corals in the Jurassic of Europe and usually associated with **Beronicus** does not occur. Apart from the obvious difference in abundance, no pronounced polarisation between lower and upper surface colonisation can be detected in our specimens (Fig. 15).

Similarly neither the distribution of the individual types of encrusters on the various morphotypes nor the encrusters on the whole show a pronounced
Fig. 13. Size of attachment and resting areas of the 17 coral morphotypes of Figure 16.

Fig. 14. Distribution of encrusting organisms on corals of the high diversity coral association, Patcham Formation of Junara Dome. Given are the relative abundances of corals encrusted altogether and encrusted by the various encrusting taxa.
pattern (Fig. 14). Solitary and compound corals exhibit the same degree of encrustation. Those morphotypes which show either extreme low (conical forms) or high degrees (tympanoid forms) of encrustation occur only in low numbers and are therefore not representative. The relatively high degree of encrustation shown by pedunculate forms can be explained by the comparatively large lower surface ideally suited for shade-loving organisms.

More than two-thirds of the corals exhibit signs of bioerosion. The most abundant ichnotaxon is Gastrochaenolites, flask-shaped holes of lithophagid bivalves (Fig. 18f), followed by irregular holes, up to several mm in diameter, the origin of which is not clear (Fig. 16). Common is also Enzelus (Fig. 18c), a sponge boring, in this particular case, judging from the borehole morphology, most likely excavated by haplosclerid sponges rather than by clionids (e. g. Reitner & Keupp 1991); diagnostic spicules were, however, not found. Less common are cylindrical holes around 1 mm in diameter, which belong to straight or slightly curved tubes and can be assigned to Trypanites isp.. Inconspicuous are small sack-shaped borings of acrothoracidian barnacles (Rogerella isp.). In some corals, the epitheca is damaged by shallow scoop-like depressions which in some cases occur in pairs. They are here interpreted as bite marks of vertebrates, possibly fishes. Although most corals are bored, the density of borers is never very high. The boring organisms do not exhibit a preference for the upper or lower surfaces of corals. Similarly, the borings are fairly evenly distributed among the different morphotypes (Fig. 17). Rare bored attachment areas record cases of reworking.

Deep radial incisions of coral skeletons are widespread (Figs. 18c, d). Apart from their occurrence in the trochoid morphotype they are restricted to compound corals, in particular to pedunculate, umbrella-shaped, and wedge-shaped morphotypes (e. g. Dimorphopora stellata). Most likely, they are the result of parasitic organisms which caused cessation of coral growth in their vicinity. Evidence supporting a parasitic relationship is (1) the presence of epitheca along the incised radial slits demonstrating that the slits are not borings, and (2) the reaction of the coral towards the parasite, which in some cases ended with the coral partially or fully overgrowing and thus closing the slits distally (Fig. 18c). Parasitic relationships between polychaete worms and corals are well known from the Recent. Zibrowius et al. (1975) described such a relationship between the polychaete Lumbrineris and various ahermatypic corals. In this example, the polychaetes caused distinct grooves on the epitheca of corals such as Caryophyllia and Flabellum, which are also found on fossil material. In the present material, the parasitic organisms must have grown straight upwards and, with continued radial growth of the host corallum, occupied gradually a position further away from the growth edge. Similar slits as the ones described here but far less pronounced have been recorded by Hoeksema & Mora (1989) in Fungia granosa and were attributed to particular environmental factors such as lack of turbulence. The authors failed, however, to offer a more specific explanation of the feature. An alternative explanation for radial slits would be that they facilitated removal of sediment similarly to the way slits and holes in some irregular echinoids serve to shorten the transport distance of food particles from the upper to the lower side.

Discussion: The diverse coral association at Jumara Dome does not represent a reef structure; the coral heads are usually isolated, corals encrusting each other

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**Fig. 15.** Distribution of encrusting organisms on the upper and lower surfaces of corals in coral levels A and B, Patchen Formation of Jumara Dome.

**Fig. 16.** Distribution of bioerosion on the upper and lower surfaces of corals in coral levels A and B, Patchen Formation of Jumara Dome.
are rare. The corals are best described as forming a meadow on a sea floor consisting of soft lime mud with a variable amount of bioclasts and shell debris. As is shown by their high diversity, many corals were obviously well adapted to such an environment. However, the small to tiny size of most corals except for few taxa such as Microsolenia amorph, Lochnaeosanthes trapeziformis, and Styline kasbemis suggests that some environmental parameter controlled and restricted growth. The distribution and shape of shallow water corals is generally related to the light intensity, the hydrodynamic conditions, the sedimentation rate, and the degree of subaerial exposure (e.g. Chappell 1982, Köhmann 1984). As these environmental parameters are often correlated with depth (whereby the wave stress decreases with depth in contrast to the light stress) a typical depth zonation of reef corals is usually observed (e.g. Geister 1975, 1977, Shepard 1982, Chevalier 1987). Accordingly, deeper parts are represented by dome-shaped and globular corals whereas at intermediate depths branching types dominate (Chappell 1982). However, in the case of the Jamara corals, the substrate, not conforming to the hard substrate most reef corals require, must have been a major environmental parameter greatly influencing selection for shape and size.

Many of the corals from Jamara Dome apparently managed to encrust a soft to firm, bioclast-rich sediment which is shown by the irregular attachment surfaces. The energy level must have therefore been sufficiently low to prevent overturning of the loosely attached coral heads. Others had only a tiny attachment area, probably only large enough to cement to single sand-sized particles. These forms attained a stable position either by building a large, flat resting area, or by anchoring themselves partly in the sediment. Again, successful growth required a low energy environment.

The high abundance of the solitary coral Montlivaltia also suggests soft rather than hard substrate. According to Gill & Lafuste (1971) Montlivaltia lived exclusively on non-lithified substrate. Two different strategies, both represented by species occurring in Jamara Dome, ensured a stable growth position: Long cylindrical or turbinate forms were sediment stickers, whereas tympanoid or sub-turbinate forms simply rested on the soft sea floor. The dominance of the former morphotypes as compared to the latter ones in Jamara Dome supports Gill & Lafuste's (1971) notion that the turbinate forms occurred in finer-grained sediment, whereas the tympanoid and sub-turbinate forms preferred somewhat coarser substrates rich in quartz grains, intraclasts, or ooids. Patellate, sub-patellate, umbrella-shaped and wedge-shaped morphotypes, so widespread in Jamara Dome, probably also represent adaptations to a semi-infaunal growth position within soft substrate. Comparable examples can be found on modern sand or sea grass flats (e.g. Mucida areolata, Trochophylla gregoryi; Pichon 1974, Köhmann 1984). In morphology, many corals resemble in overall shape Recent fungids which are adapted to life on soft substrate. It is, however, questionable whether the morphology of solitary fungids can be directly compared with that of compound corals from Kachchh. Never-
theless, certain features such as a convex upper surface should have, as in Recent fungoids and their homeomorphs (e.g. WISJMAN-BEERS 1974, HÖFLING & MOYA 1989), facilitated the removal of sediment and righting after having turned over (see also GILL & COATES 1977). Studies of the Recent compound coral *Manticula aequata* on the Bahama Bank (e.g. FABRICIUS 1964) showed that a semiglobular shape facilitated righting of overturned corals. *Manticula* living on soft substrates usually have a conical shape, comparable to that of our morphotypes 4, 5, and 14. FABRICIUS (1964) showed that such *Manticula* were able to rise upwards within soft sediment thus counteracting increased rates of sediment influx. Similar morphotypes as the ones described here were recorded by HöFLING (1989) from the Upper Cretaceous Goseau Formation of the Eastern Alps. HöFLING (1989) assumed that these corals lived on a soft substrate for which they showed several adaptations such as being small and having skull-cap-shaped, mushroom-shaped and pedestal-producing growth forms.

Although many corals are encrusted and bored, the density of encrustation and boring is comparatively low. As many of the epif- and endobionts apparently colonised the heads before the corals died (this is indicated by their preference for the lower surfaces of the corals) post-mortem colonisation is even less common. This suggests that the corals did not serve as substrates for encrusters and borers for considerable length of time. Otherwise they would have become extensively attacked by such organisms, because they represented the only reasonably-sized hard substrates on the muddy sea floor. This implies that the rate of sedimentation of fine mud, possibly augmented by sediment stirred up by burrowing organisms, was sufficiently high to cover dead skeletons with a thin film which prevented in many cases further colonisation. This line of argument is supported by the scarcity of cases where corals encrust each other. Out of the > 2000 corals investigated only in 12 cases did corals encrust each other. In a single case the succession *Stylina* - *Stylina-Collignonastrea* was observed. Similarly, there are only rudimentary signs of succession among the

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Fig. 18. Examples of species interactions and of bioerosion in corals from coral layer A and B, Patcham Formation, Jumara Dome. a: *Microsolena subtilihinata* GREGORY with three circular holes caused by commensal (parasitic), non-preservable encrusting organisms. Species interaction is indicated by the raised rims of the holes which show that the coral reacted to and grew around the commensals. x 4. b: The sclerosponge *Neopora* sp. (x 4) encrusted the solitary coral *Trachyphyllum patelliforme* GREGORY while the coral was alive. This is indicated by the reaction of the coral producing an overhanging rim (arrowed). c: *Dimorphosclera stellata* GREGORY with deep radial incisions which are interpreted to have been caused by non-preservable, encrusting, possibly parasitic organisms. x 2. d: *Triangulocystis triangularis* GREGORY with incised margin interpreted as the product of a non-preservable encrusting, possibly parasitic organism. x 2. e: Irregular holes interpreted as the work of boring haplosclerid sponges in *Monticulita frustriformis*; polished transverse section, x 5.

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encrusting and boring organisms. They refer to corals overgrowing serpulids and *Neuropora* encrusting serpulids and vice versa. In a single case the succession coral - serpulid - *Neuropora* - *Trypanites* was observed. All these features point to a relatively short residence time of the corals on the sea floor. This does not necessarily imply rapid complete burial of the coral heads, but - as suggested above - a thin veneer of sediment would have been sufficient to prevent further colonisation.

Burial by sediment may also have been responsible for the cessation of growth observed on parts of some coral surfaces, although a biogenic origin such as grazing fish or other coral-eating organisms cannot be excluded.

Despite the low energy conditions which seem to have prevailed for most of the time, there are also signs of occasional disturbance of the coral community. Such signs include broken corals whose broken surfaces are encrusted by *Neuropora* and serpulids, and encrusting surfaces which have been colonised subsequent to uprooting and overturning of the corals. That such reworking events are the result of storm action is supported by the remains, within the lower part of the coral beds, of a 3 cm thick bed packed with shells and shell debris and with a sharp erosive base. Most of the shell bed was subsequently destroyed by bioturbation. Count of 118 coral heads within the coral layer showed 71% of them still in growth position, the remaining 29% were overturned. Cylindrical solitary corals (41 counts) invariably occupy a position with the long axis parallel to the bedding surface. Thus, it appears that not every of the intermittent physical disturbances caused uprooting of corals. In the majority of cases it may have remained confined to gentle winnowing.

It is interesting that neither the relatively high density of corals nor the presence of distal storm lags promoted pronounced taphonomic feedback (sensu Kidwell & Jablonski 1983). The bivalve fauna consists largely of shallow infaunal and epibyssate forms and the latter may well represent an initial stage of such feedback. Most likely, a moderate rate of sedimentation producing a veneer of sediment on dead corals prevented large-scale succession towards a cementing hard substrate community.

Within the coral layer rare *Pleolophyra*, a deep burrowing bivalve, occur in life position. Quite clearly the bivalve belongs to a different time plane burrowing at a later stage when the coral layer had been covered by several centimetres or even decimetres of sediment.

Depositional environment of the *Microsolenia amorpha-Montlivaltia fruticiformis* association

The coral association at Jumara colonised a muddy sea floor in a low energy environment only occasionally disturbed by the fringes of storms. The high diversity of corals and associated organisms indicates that the fauna grew in warm, well aerated, fully marine environments well below the fair weather wave base. The sedimentation rate probably was sufficiently high to impair coral growth to some extent and to prevent large-scale succession toward a true reef structure. The lack of algal envelopes, microbial crusts, algal borings or remains of macroalgae (except for a single solenoporean fragment), which are usually ubiquitous elements of shallow water reef microfacies suggests that poor illumination was a limiting factor. This view is supported by the lack of a distinct polarisation of the fauna encrusting and boring the corals. Such polarisation is a characteristic feature of well-lit shallow water environments at least since the Jurassic (e.g. Palmer & Fürsich 1981). It is known from the Recent, that this polarisation decreases when the degree of illumination diminishes (e.g. Riedl 1966). In addition, sedimentation may have contributed to the lack of microbial crusts, which are known to thrive in poorly illuminated areas, because cyanobacteria appear to be sensitive towards high rates of sedimentation (e.g. Leinfsfelder et al. 1993). Apart from influx of clay-sized terrigenous particles, micritic cement, stirred by burrowing organisms, probably contributed considerably to the turbidity.

Thus intermediate rates of sedimentation could, on one hand, explain the turbidity (and hence could have contributed to the postulated low illumination), the soft nature of the substrate, the composition of the coral fauna, the morphotype pattern, the dominance of small individuals, the scarcity of successional stages, and the lack of microbial crusts. On the other hand, the sedimentation rate must have been still sufficiently low to provide suitable living conditions for a high diversity coral fauna adapted to life on soft substrate.

**Genesis of coral layers at Jumara Dome**

A thin shell bed (distal tempestites) cover a sea floor of soft lime mud

After renewed sedimentation of lime mud much of the shell bed is destroyed by bioturbation

During a period of reduced sedimentation coral growth takes place, interrupted by minor reworking events

Final burial of the coral layer

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Fig. 19. Sequence of events leading to the formation of high diversity coral layers in the Patcham Formation of Jumara Dome.
In summary, we envisage an offshore midshelf position of the corals, beyond the influence of coarse terrigenous sediments and fair weather waves, and only subject to occasional slight disturbance caused by the fringes of major storms. The *Micromyxa anatopha-Monticrinita fruthiformis* associations thus represent the in-situ relict of a coral-dominated community which possibly grew, subject to intermediate rates of sedimentation, under poorly illuminated conditions on a soft sea floor (Fig. 19).

**Lack of coral reefs in the Jurassic of western India**

Despite the widespread occurrence of shallow-water environments on the western shelf of the Indian craton during the Jurassic, no coral reefs or other reefs are known. At that time, the Kachchh and Rajasthan Basins were situated roughly at 30° south, and opened to a southerly embayment of the Tethyan Ocean. Considering the equable climate of the Jurassic with a weak latitudinal temperature gradient (e.g. HALLAM 1985, 1993) water temperatures must have been sufficiently high for growth of coral reefs. Coral reefs occur, for example, in Middle and Upper Jurassic strata of Central Europe which occupied a comparable palaeolatitude in the northern hemisphere. The European coral reefs were largely confined to widespread carbonate platforms and the lack of coral reefs on the western Indian shelf can be mainly explained by the scarcity of such platforms. The only major carbonate units are the Bathonian Patcham Formation of Kachchh and the Bathonian Amarsagar Member of the Jaisalmer Formation of Rajasthan (Das Gupta 1975), which account only for few percent of the total Jurassic sediment package. On the whole, high silicilastic input into these basins prevented widespread formation of carbonates. The resulting muddy to sandy environments were characterized by unstable soft or shifting substrates and turbid waters. According to FÜRSICHT & OSCHMANN (1993) sedimentation in the Kachchh Basin was controlled by cyclic changes in relative sea level whereby regressive phases with increased rates of sedimentation alternated with transgressive events during which lag deposits formed. During these transgressive events, characterized by low input of silicilastic material, one might have expected the growth of coral reefs (e.g. LEINFEELDER 1993), but large parts of the basin were apparently too deep for reef growth.

The carbonate sediments consist largely of offshore mud- and wackestones with intercalations of thin grainstones (distal tempestites), which again must have been unsuitable for coral reef growth and supported only the reef meadows discussed here and meadows of hexactinellid sponges. Shallow water carbonates are rare and record either proximal storm events (hummocky crossbedded calcarentites) or shallow water shifting sand dunes. The only suitable substrates for reef growth were hardgrounds, that existed in the Bathonian of the Jaisalmer Basin (FÜRSICHT et al. 1992), but apparently were not widespread enough to trigger reef growth.

Thus, it was the prevailing sedimentary regime which prevented growth of coral reefs on the shelf of the Indian craton in the Jurassic and not palaeo-oceanographic features such as unsuitable water temperatures nor biological factors such as lack of larval swarms.

**Conclusions**

1. Corals, albeit rare autochthonous components of benthic faunas in the Jurassic of the Kachchh Basin, are the dominant elements at two horizons within the Bathonian-Callovian sedimentary sequence forming distinct associations: the monospecific *Amphistegia porifera* Bed of the Callovian Chari Formation of Habo Dome and the high diversity coral meadows in the Patcham Formation (Bathonian) of Junara Dome.

2. Both coral occurrences document cases where corals managed to flourish, although the prevailing environmental factors are generally regarded as unsuitable for coral growth.

3. In the case of the *Amphistegia porifera* Bed, the coral was able to flourish on a sandy, intermittently mobile substrate subject to turbid water conditions in connection with frequent storm events.

4. In the case of the high diversity coral meadows, the corals successfully colonised a soft to firm substrate, in low energy, possibly poorly lit environment, subject to moderate rates of sedimentation.

5. Although the Kachchh Basin is represented to a large extent by shallow water sediments which must have been deposited under subtropical to tropical conditions, the two coral occurrences represent the acne of coral growth in the basin. The reason for the lack of true coral reefs is seen in relatively high rates of sedimentation and lack of extensive hard substrates that only allowed colonisation by coral specialists adapted to these conditions.

**Acknowledgements**

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**References**


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### Appendix

Number of taxa in the 9 samples of the *Microsolenia amerya* - *Montefelidella fractiferaformis* association and their presence percentage, relative abundance, and modified relative abundance within the association.

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**Species List:**

- *Microsolenia amerya*
- *Montefelidella fractiferaformis*
- *Cryptonemia pulcherrima*
- *Systyla kocheri*
- *Dimorphocysta stylla*
- *Colligymnospora junarunsis*
- *Lockmanospora traperiformis*
- *Elymnus rollandi*
- *Serpula (Cyclospora) cf. fiacellus*
- *Tropolopogon tenuilimosa*
- *Serpula (Dorcosporella) cf. bimbaccola *
- *Neurospora sp.
- *Pseudacarinia crenulata*
- *Prorochesia biondii*
- *Cenocarpos crassifolius*
- *Tachecodina paxelfiformis*
- *Sibarastus strophus*
- *Serrula (Cyclospora) pseudoflava*
- *Spondygloecpse (Protosporella) subspinosa*
- *Lobyn ericetosmethylis*
- *Serpula (Tetraspora) quinquangularis*
- *Thyroeciospora triangularis*
- *Metophractopsia trellis*
- *Lopha gregaria*
- *Microcollella subulata*
- *Gyropseudospora myrata*
- *Serrula (Tetraplana) sp.*
- *Montefelidella complanata*
- *Orbi (Trichosporella) sp.*
- *Palaecospora kaetschuisi*
- *Saccospora propinqua*
- *Cryptorhynchus weigeneri*
- *Lophophoria tenuilimosa*
- *Gyropseudospora (Chelysia) tumidaensens*
- *Naenogona nana*
- *Teribulbula planicephala*
- *Tetracapsa (Chelysia) actaefusa*
- *Sporospora sp.*
- *Callicaldyx sp.*
- *Chlamides testorii*
- *Saccus hemiphyrum*
- *Thamnasteria nioldii*
- *Colligymnospora aff. junarunsis*
- *Karyk lanataeula*
- *Cabrospora*
- *hydrospora*
- *Pseudoconiosporoides*
- *Plagiozoonus buckmani*
- *Perisnus elegantis*
- *Naccoloma kymnet*
- *Lecidella sp.*
- *Prosarante sp.*
- *Microthyriopsis sp.*
- *Plagiozoonus c. complanata*
- *Tetrahymenia sp.*
- *Dimorphospora junarunsis*
- *Coelosporis indica*
- *Procordaria striata*
- *Ch. Gomphonema socialis*
- *Plateliae sp.*
- *Entolutes sp.*

**Families:**

- *Dimorphosporaceae*
- *Dimorphosporales*
- *Ichnophyllumidaceae*
- *Rhabdosporales*
- *Neuriellales*
- *Guralsiales*
- *Cladoceriales*
- *Cystelliales*
- *Gastrosporales*
- *Pseudolentiales*
- *Trachycleniales*
- *Asphoreales*
- *Quadrannales*
- *Troposporiales*
- *Epeoxicoralliales*
- *Batrachosporales*
- *Tetralobiales*
- *Opis (Thyoglossales) s. similis*
- *Protosporiales cl. angulata*
- *Actinomorpha bennettii*
- *Insignesia*
- *Fulvales*
- *Spondylosporales (S.) palmatus*
- *Asphora* et al.**
- *Fenestellales*
- *Trigoniales longa*
- *Annelidae incertae*
- *Wolleiaceae*
- *Spahniaceae crassiscutata*
- *Coelosporiales (G.) sp.*
- *Rhipidiales sp.*
- *Tetracapsales sp.*
- *Serrula (Cyclospora) sp.*
- *Vitagoounts (Orthoglossiales) junarunsis*
- *Perisnus aff. galistroni*
- *Colligymnospora microphylleoides*
- *Actinálidas bimaculatata*
- *Montellales olivacea*
- *Psilochorelly (Baccharidiales) cl. freita*
- *Complaceseae turbulence*
- *Psilochorelly cl. suberdiformis*
- *Cleistospores procedecidum*
- *Palaeospora stedechas*
- *Baccharoidei cl. discontinua*
- *Ostraciales sp.*
- *Perisnus cl. nedlertei*
- *Actinomorpha aff. socialis*
- *Trigonellas cl. graea*
- *Dinophæstusia sp.*

**Total number of specimens:** 156,566,494,365,201,173,263,141,116

**Total number of specimens in all samples:** 2475