Palaeoecology of solitary corals in soft-substrate habitats: the example of *Cunnolites* (upper Santonian, Eastern Alps)

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LETHAIA

The upper Santonian Hofergraben Member (Eastern Alps) provides an example of a soft-substrate habitat suited mainly for solitary corals (*Cunnolites*), for colonial forms of solitary coral-like shape (*Placosmilia*, *Diploctenium*), and for colonial corals of high sediment resistance (e.g. *Actinacis*, *Pachygyra*). The Hofergraben Member consists mainly of silty-sandy marls of wave-dominated, low-energy shore zone to shallow neritic environments. Substrates of soft to firm mud supported level-bottoms of non-rudist bivalves, gastropods, solitary corals, rudists, echinoids, and benthic foraminifera. Boring and/or encrustation of fossils overall are scarce. In the marls, *Cunnolites* is common to abundant. Both a cupolate shape and a lightweight construction of the skeleton aided the coral to keep afloat soft substrata. *Cunnolites* taphocoenoses are strongly dominated by small specimens (about 1–3 cm in diameter). *Cunnolites* was immobile and mostly died early in life upon, either, smothering during high-energy events, rapid sedimentation associated with river plumes, or by toppling and burial induced by burrowing. Comparatively few large survivor specimens may show overgrowth margins interpreted as records of partial mortality from episodic sedimentation or tilting on unstable substrate. Scattered pits and scalloped surfaces on large *Cunnolites* may have been produced, in some cases at least, by predators (durophagous fish?). Post-mortem, large *Cunnolites* provided benthic islands to corals, epifaunal bivalves and bryozoans. In a single documented case of probable *in vivo* contact of *Cunnolites* with the colonial coral *Actinastraea*, the latter prevailed. □ *Alps, coral,* Cunnolites, *palaeoecology, Upper Cretaceous.*

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In the geological record and at present, coral assemblages that thrived, and thrive, in permanently or episodically turbid waters as a result of terrigenous input are common (Sanders & Baron-Szabo 2005; see also Kiessling 2002; Perry & Larcombe 2003). Recent turbid-water coral communities consist mainly of pseudocolonial and/or of sediment-resistant colonial forms. Conversely, in pre-Miocene turbid-water assemblages, aside of pseudocolonial and sediment-resistant colonial taxa, solitary scleractinians are a widespread and characteristic element (Sanders & Baron-Szabo 2005). Solitary corals, however, are rarely considered for themselves perhaps because most solitary forms are small and of simple construction relative to colonial forms. In ancient turbid-water habitats, however, the well-defined, ontogenetically (largely) stable shape of solitary corals and their synecological associations allow for inferences on depositional dynamics and styles of sedimentation that are hardly recorded by other fossils.

In the present paper, we describe new aspects of the aut- and synecology of the extinct solitary coral *Cunnolites*, based on collection during several field stays from 1997 to 2005, and on previously unpublished material mainly from the storage depot of the Museum of Natural History in Vienna. In the storage collection, many excellent specimens of large *Cunnolites* were donated by or bought from amateur fossil collectors (collection Schütz, collection Gapp). *Cunnolites* was a cupolate, cosmopolitan, tropical to warm-temperate solitary coral (Baron-Szabo 2002) that thrived typically in great abundance on substrata of muddy sand to sandy-silty mud, in many cases well-remote of coral reefs (e.g. Höfling 1989; Smith *et al.* 1995; Baron-Szabo 1997, 1999, 2003; Sanders *et al.* 1997). The fossils described herein are from an upper Santonian succession of neritic marls rich in well-preserved corals (Figs 1, 2), and a classic location of Alpine invertebrate palaeontology (Reuss 1854; Felix 1903; Oppenheim 1930; Beauvais 1982; Baron-Szabo 2003). For the colonial corals of this succession, features indicating partial mortality due to sedimentation and/or episodic tilting on unstable substrate are well known (e.g. overgrowth margins,
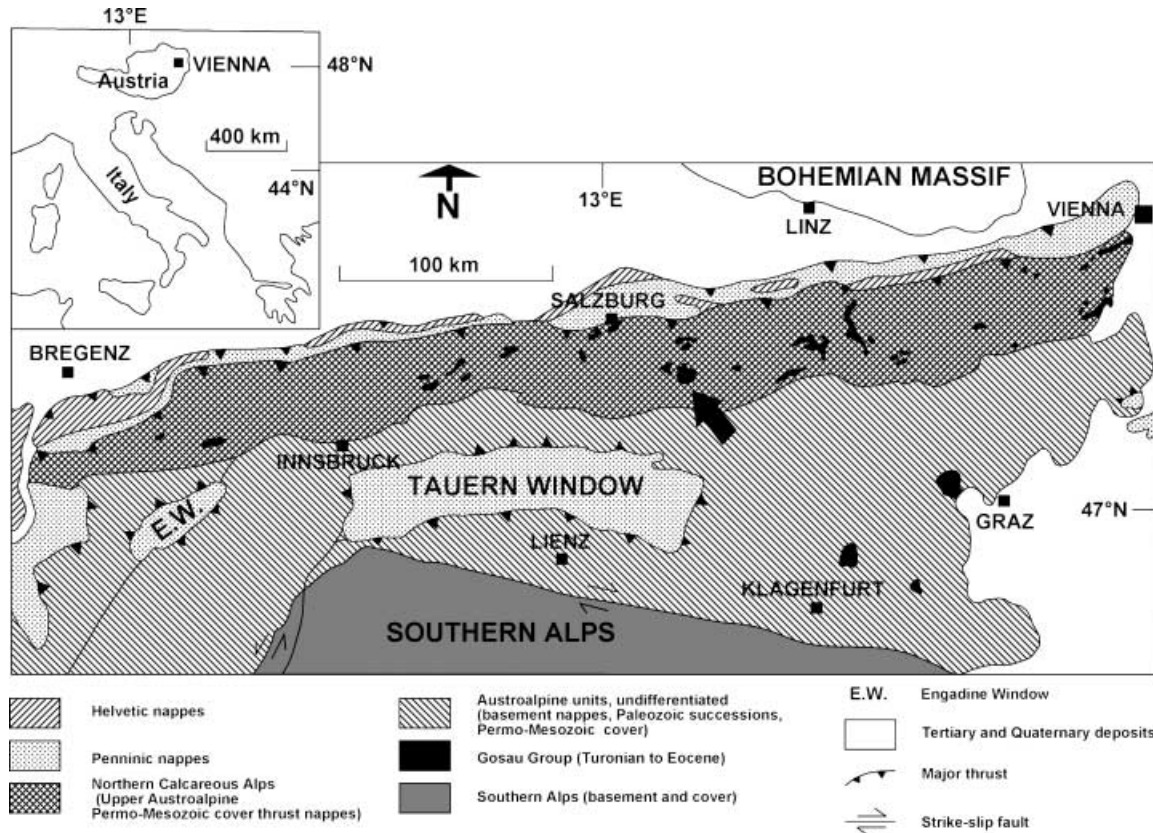
Fig. 1. Geological map of Eastern Alps, with the mixed siliciclastic-carbonate successions of the Gosau Group (middle Turonian to Eocene *pro parte*) in black. The area of Gosau with the investigated succession (Fig. 2) is indicated by heavy black arrow.

tilted overgrowth margins, 'lumpy' shape of massive forms, circumrotatory growth) (Kühn 1925; Höfling 1989; Sanders & Baron-Szabo 2005, and in press). For *Cunnolites*, by contrast, despite an abundance of small specimens, features of partial mortality because of sedimentation are less commonly addressed (Höfling 1989). In addition, partial mortality because of marked tilting, evidence of possible predator attacks, and the potential synecologocial role of this widespread fossil coral taxon to date have not been described. Our results indicate that *Cunnolites* was immobile and shows several distinct styles of partial mortality due to sedimentation and unstable substrate. In addition, herein, for the first time evidence for durophagous predation and of direct competitive interaction with another coral is presented. Finally, the potential synecological role *Cunnolites* took in the turbid-water setting of the Hofergraben Member is discussed.

Geological setting and biofacies

The investigated corals are from the Gosau Group, a middle Turonian to Eocene succession deposited in terrestrial to deep-marine settings on top of the partly emergent Eastern Alpine nappe stack (Fig. 1) (Wagreich & Faupl 1994; Sanders 1998). Today, the Gosau Group is preserved in numerous smaller and larger outcrops scattered along strike of the Northern Calcareous Alps, and in a few larger outcrops in the central-Alpine part of the Eastern Alps (Fig. 1). The depocenters of the Gosau Group formed by extensional faulting and/or by strike-slip faulting in an oblique-convergent plate tectonic regime, and were subject to episodic uplift and compression (see Wagreich 1991, 1995; Neubauer *et al.* 1995; Sanders 1998; Faupl & Wagreich 1999; Ortner 2001; for tectonic setting of the Gosau Group). The Gosau Group transgressively overlies a deeply truncated rock substrate that was characterized by a differentiated morphological relief produced both by subaerial erosion and by syndepositional tectonism (Sanders *et al.* 1997). In the basal part of the Gosau Group, deposits of alluvial fans and fan deltas were nourished from local, small-sized drainage areas. Conversely, siliciclastic input was mainly derived from larger rivers that drained the more internal parts of the Cretaceous Eastern Alpine edifice (Stattegger 1987). As a result of transgression over a morphologically
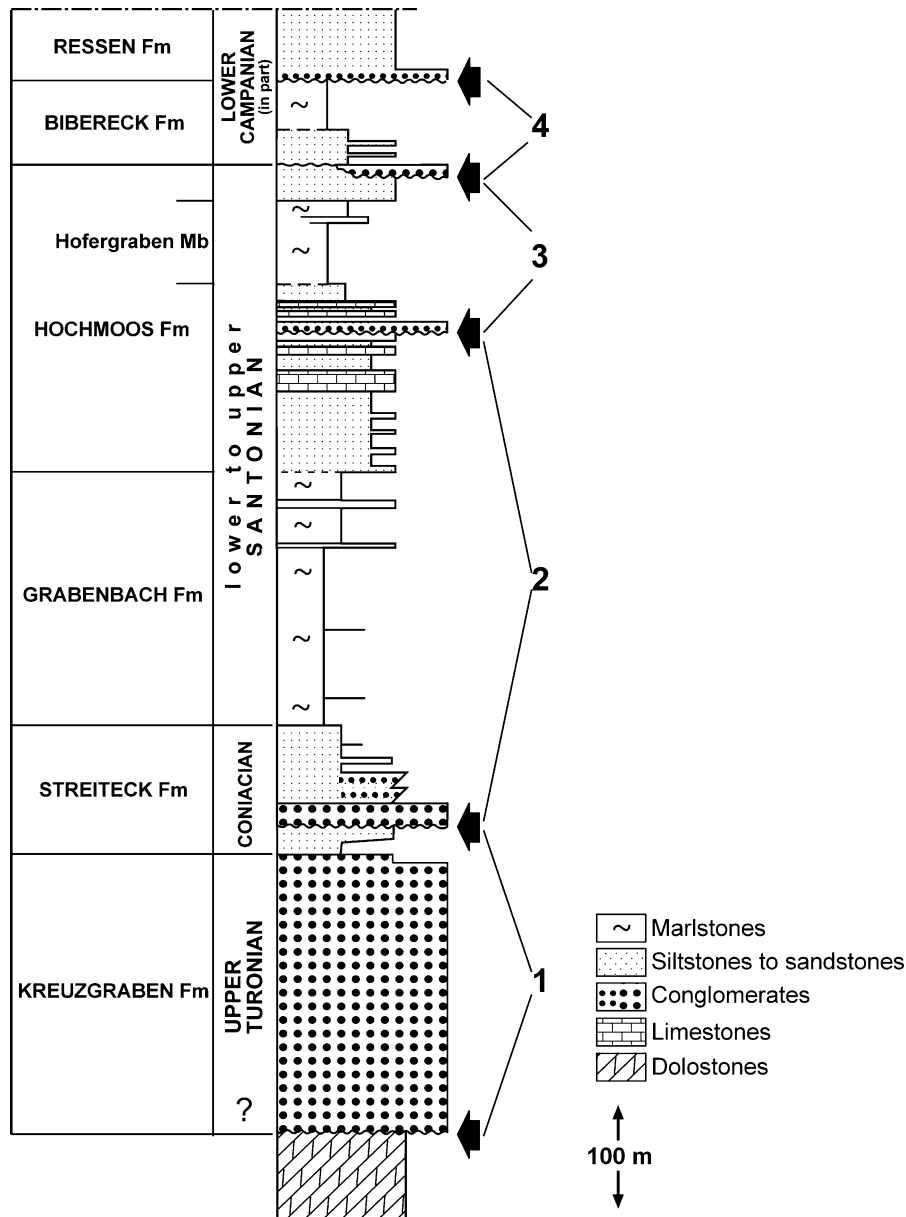
Fig. 2. Upper Turonian to lower Campanian portion of Gosau Group at Gosau (Kollmann & Summesberger 1982; Wagreich 1988). Numbers 1 to 4 indicate preserved tracts of interpreted depositional sequences (Sanders *et al.* 1997). The investigated corals are from the Hofergraben Member (upper Santonian) of the Hochmoos Formation. The marly succession of the Hofergraben Member corresponds to part of the transgressive systems tract and to part of the high-stand systems tract of interpreted depositional sequence 3.

differentiated rock substrate, and of terrigenous input from drainage areas of strongly different size, and as a result of syndepositional tectonism, the Gosau Group is characterized by an exceptionally wide spectrum of facies ranging from terrestrial to deep-marine deposits (see Wagreich & Faupl 1994; Sanders 1998).

The neritic portion of the Gosau Group accumulated on wave/storm-dominated, mixed siliciclastic-carbonate shelves, and locally contains skeletal reefs. Aside of sheet-shaped segment and cluster reefs of rudists and a large coral frame reef, most reefs include (1) mound- to sheet-shaped segment reefs

(see Riding 2002, for terminology of reef fabrics) a few decimetres in thickness of corals, rudists, skeletal sponges and red algae; and (2) segment reefs up to about 10 m thick mainly of colonial corals (Sanders & Baron-Szabo 1997, and in press; Sanders & Pons 1999; Sanders & Höfling 2000). Where present, frame fabrics are typically represented by patches a few decimetres in size of coral boundstone. Many corals are more-or-less intensely bored by clionids and lithophagids; coralline algal encrustation is widespread. Aside of reefs, in the Gosau Group, intervals up to more than 10 m thick of silty-sandy marls are

common that contain level-bottom assemblages of variable amounts of corals, rudists, skeletal sponges, non-rudist bivalves, gastropods, echinoids, foraminifera, and calcareous algae. With respect to abundance, the coral fauna of these marls is typically dominated by solitary forms. Hereunder, for sake of brevity, these marls rich in corals are designated as coral marls. For comprehensive descriptions and interpretations of the stratigraphy and sedimentology of the neritic parts of the Gosau Group, the reader is referred to Wagreich (1988, 1989a, 1998, 2003), Wagreich & Faupl (1994), Sanders (1998, 2001), Sanders *et al.* (1997), Sanders & Pons (1999), Sanders & Höfling (2000), and Sanders & Baron-Szabo (in press).

At the type location of the Gosau Group at Gosau, corals are most abundant in the upper Santonian Hofergraben Member of the Hochmoos Formation (Fig. 2). Integrated biochronostratigraphy (mainly nannofossils, planktonic foraminifera, ammonites, inoceramids) and strontium isotopes from rudist shells all indicate that the Hochmoos Formation spans the early to late Santonian interval, up to the *Paraplanum* Zone (~84 Ma) (see Kollmann & Summesberger 1982; Wagreich 1986, 1988; Steuber 2004; Kroh *et al.* 2006). The Hochmoos Formation includes the interpreted highstand and transgressive systems tract, respectively, of two consecutive depositional sequences (Fig. 2) (Sanders *et al.* 1997), and consists mainly of (1) silty to sandy coral marls (Hofergraben Member) with level-bottoms of corals, molluscs and benthic foraminifera (Table 1); (2) hybrid arenites and wackes of siliciclastic grains, carbonate-lithic grains, and shallow-water bioclasts; (3) sheets to mounds of colonial corals and rudists; (4) shallow-water bioclastic limestones; and (5) shore zone conglomerates (cf. Wagreich 1988; Sanders & Höfling 2000). The fossil assemblage of the Hofergraben Member (Table 1) consists of variable relative proportions of neritic soft-substrate level-bottoms with a potentially reef-building assemblage of corals and rudists. During deposition of the Hofergraben marls, however, reef development was quenched by pulses of sediment input and/or by resuspension, and by toppling and fragmentation of corals during high-energy events and upon burrowing (Sanders & Pons 1999). The marls are bioturbated and contain *Thalassinoides*, and most rudists, corals and non-rudist molluscs are embedded disoriented relative to life position; many bivalves are preserved disoriented but articulated. Intercalated beds of hummocky cross-laminated arenite and of coral/mollusc-clastic rudstone record episodic high-energy events (Wagreich 1989b; Sanders & Pons 1999). Aside of the fossil content indicative of shallow neritic depths (Table 1), local vertical transitions of coral marls into coral-

Table 1. Characteristic fossils of 'coral marls' of Hofergraben Member, Hochmoos Formation (upper Santonian, Gosau Group) (compiled and simplified from Weiss 1977; Kollmann & Summesberger 1982; Höfling 1985; Wagreich 1986; Sanders *et al.* 1997; Pons & Sanders 2000; Baron-Szabo 2003; Kroh *et al.* 2006).

Foraminifera
  Miliolina: *Quinqueloculina, Nummofallotia, Pyrgo, Idalina, Vidalina*
  Textularina: *Cuneolina, Dictyopsella, Haplophragmoides*
  Rotalina: *Daviesina, Goupillaudina*

Non-rudist bivalves
  Cardiaceans, pteriaceans, pholadomyids, veneroids, ostreids

Gastropods
  Actaeonellids: *Actaeonella, Trochactaeon*
  Cerithiacea (e.g. *Cassiope*)
  Aphorrhaidae
  Naticidae
  Neritidae

Rudists (Hippuritacea)
  Hippuritidae
    Vaccinites spp.
    Hippurites spp.
  Radiolitidae
    Lapeirousia
  Plagioptychidae
    Plagioptychus

Echinoids
  Micraster, and undetermined forms

Solitary corals
  Cunnolites (by far most abundant)

Colonial corals adapted in shape to thrive in a 'solitary-like' lifestyle on substrata of sand to mud
  Placosmilia (flabellate to flabello-meandroid)
  Diploctenium (flabelloid)

Other colonial corals (a few typical taxa only)
  Actinacis, Actinastraea, Agathelia, Pachygyra

rudist reefs and, higher up, into shore zone clastics indicate that these marls accumulated in waters a few metres to about 20–25 m in depth (Sanders & Höfling 2000). More calcareous varieties of coral marl are bioclastic wackestones to float stones with a matrix of argillaceous, mixed siliciclastic silt/microbioclastic-peloidal pack stone. At Gosau, the coral fauna of the marls is dominated by taxa of wide geographical distribution and consists mainly of both ecotolerant species (reported from marls to pure limestones) and a subequal share of taxa known only from marls (Baron-Szabo 2003). A total of 28 species of colonial corals and eight solitary taxa have been identified. With respect to abundance, however, the assemblage is typically dominated by *Cunnolites*, whereas solitary and colonial corals of flabelliform, trochoid and conical shape overall are less widespread (Baron-Szabo 2003).

Among the colonial corals, inverted-conical to columnar/club-shaped, plocoid and thamnasterioid massive forms, and flabellate and flabello-meandroid forms comprise a high relative proportion, probably

as a result of the soft-substrate habitat (Höfling 1989; Sanders & Baron-Szabo in press). By far most of the colonial corals are up to about 10 cm in size only, are unbored and unencrusted, and typically show excellently preserved polyparia (Baron-Szabo 1999, 2003). The small size of the colonial corals indicates that the specimens died young; their good preservation and overall lack of boring and encrustation suggest rapid and persistent burial. In some solitary corals (*Rennensismilia*, *Aulosmilia*) skeletal details are similar to extant azooxanthellate deep-water corals, such as *Lophelia pertusa* (Sorauf 1999).

Palaeoecology

Evidence of sedimentation and unstable life position

Both in the Hofergraben Member and in other coral marls of the Gosau Group, by far most of the cupolate solitary corals such as *Cunnolites* are represented by specimens between about 1 and 3 cm in diameter. In the Hofergraben Member, we did not make a quantitative census per stratum on the size distribution of cunnolitids, yet it is obvious in outcrop that small specimens about 1–3 cm in diameter always are overwhelmingly (estimated by us at least a few hundreds to more than 1000 times) more abundant than larger specimens well beyond this size range. The small specimens are practically all well preserved, and evidence for encrustation and partial mortality is practically absent. In a very few cases, specimens of few centimetres in size were observed that are bored by small lithophagids. The overwhelm of small size combined with good preservation imparts an overall monotonous aspect to these faunas. The largest *Cunnolites* known to date from the Hofergraben Member was found by a fossil collector, and has a diameter of 41 cm (H. Summesberger, personal communication, 2003); this is close to the largest observed size of about 50 cm of recent *Fungia* (cf. Littler *et al.* 1997). The largest *Cunnolites* in the collection of the Museum of Natural History in Vienna is about 19 cm in diameter (Fig. 3A). At its underside, this specimen shows a stout pedestal and an overgrowth margin (Fig. 3B).

Among the larger specimens, many show features that can be related to various types of sediment stress. *Cunnolites* with a slightly to distinctly elevated, stout pedestal and/or a single or a few overgrowth margins are relatively common (Fig. 3B–F). The overgrowth margin may be 'tilted' relative to the base of the corallum, i.e. it merges with the basal epitheca on one side of the corallum but, on its opposite side,

is distinctly elevated above the base. Some specimens may show a stout horn-like shape with several tilted overgrowth margins (Fig. 3G–H). Another feature observed on larger specimens is overgrowth margins that had propagated from both the left and the right flanks of the corallum (Fig. 3I). These 'double-fronted' overgrowth margins may be combined with a more-or-less distinct, untilted or tilted overgrowth margin (Fig. 3J–L). Some of the strongly developed (double-fronted) overgrowths are associated with deep scars within the older corallum (Fig. 3M–N).

Interpretation

The overwhelm of well-preserved, unbored and unencrusted, small-sized (~1–3 cm) specimens relative to large ones that show evidence for life crises such as partial mortality strongly suggests that most *Cunnolites* died early during their life. Skewing of coral size-frequency distribution towards small specimens is typical, albeit not diagnostic, for turbid-water habitats with high rates of terrigenous sedimentation (Hunte & Wittenberg 1992). In the Hofergraben Member, the mentioned episodic high-energy events would have led to sediment resuspension followed by fallout; in addition, episodic or seasonal river plumes from the adjacent hinterland may have resulted in periods of rapid sedimentation lethal for many small *Cunnolites* (cf. Cortés & Risk 1985). The good preservation of most of the small-sized specimens suggests that they became rapidly and persistently buried, before providing habitat to macroborers or substrate for hard-ground settlers. In *Cunnolites*, the relation of palaeontological species subdivision to ecophenotypic variations is quite uncertain. Thus, although it is possible that species-related differences in mean size existed, the very rare presence of specimens larger than about 10–15 cm in size suggests that the specimens mostly are small because of early death. This is supported by the size range of recent *Fungia* that mostly is a few centimetres to about 10 cm in diameter, but may attain up to 50 cm in width (Littler *et al.* 1997).

If covered by sediment, recent mobile corals (e.g. *Fungia*, *Manicina*) move up to the sediment surface, and/or push aside the sediment by pumping (Hubbard & Pocock 1972; Gill & Coates 1977; Logan 1988; Stafford-Smith 1993). The ability to cope with sedimentation by active mobility results in very little ecomorphic variation (at least clearly relatable to sedimentation) in mobile corals (Yamashiro & Nishihira 1998; Chadwick-Furman *et al.* 2000). By contrast, the pedestal-based to columnar forms of *Cunnolites* (Fig. 3C), the stout horn-shaped forms (Fig. 3G, H) and the overgrowth margins (Fig. 3B–H) all indicate
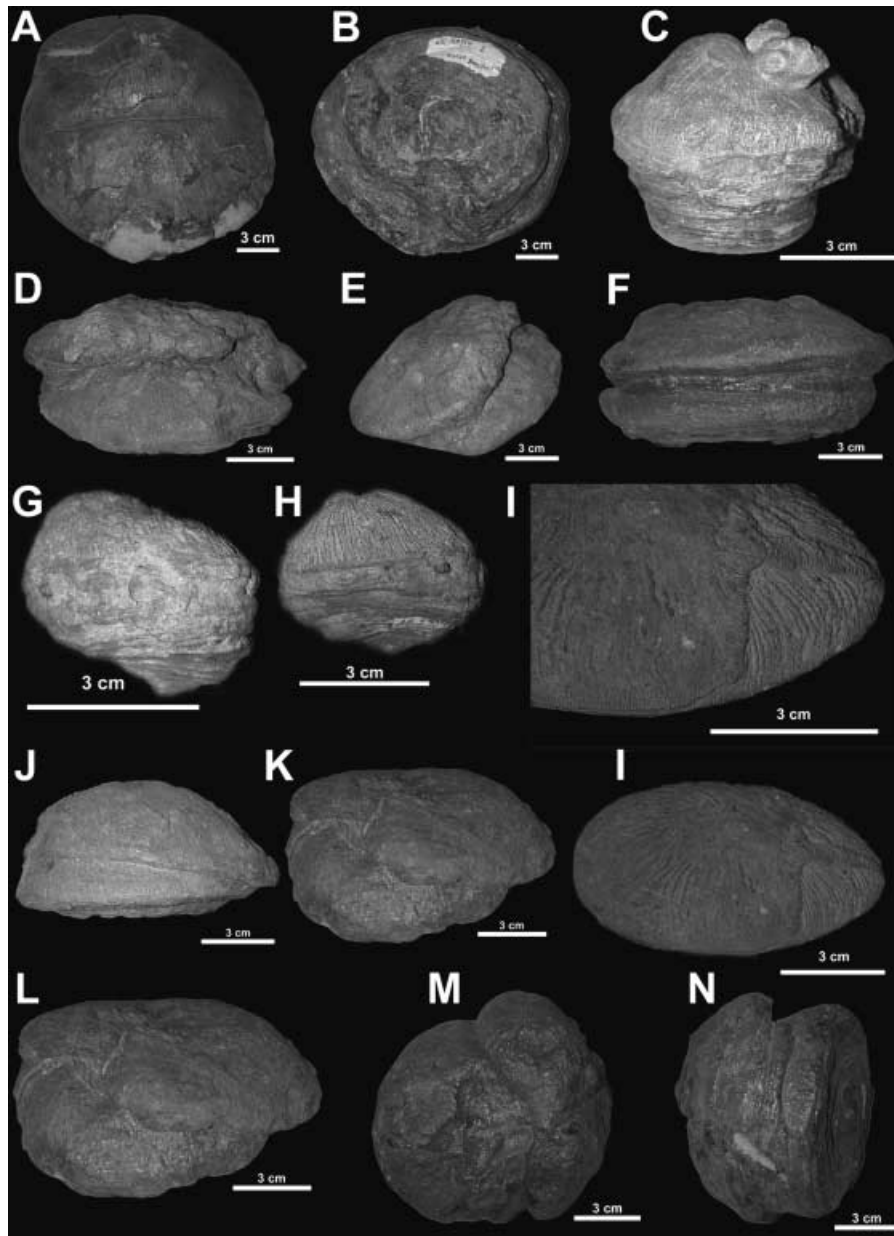
Fig. 3. *Cunnolites* from Hofergraben Member near Gosau and Russbach, Gosau Group, Eastern Alps. □A. Specimen 19 cm in diameter. Sample ob. Neffgr. 2, Kolke Bandmitte, coll. Schütz, MNHV. □B. Underside of specimen shown in A. □C. *Cunnolites* of columnar form and overgrown by a small dendroid coral. Sample 52 Neff.o.F., coll. Schütz, MNHV. □D, E, F. Views of *Cunnolites* with constrictions due to partial mortality. Sample Neff P1 unt. F, coll. Schütz, MNHV. □G, H. Lateral views of *Cunnolites* that grew obliquely upward and formed overgrowth margins. Coll. of MNHV. □I. Specimen with partly overgrown patch shows detail of overgrowth. Coll. of MNHV. □J. Specimen with tilted construction rims and overgrowth rim. Sample AB 8 Neff.o.F., coll. Schütz, MNHV. □K, L. Views of same specimen with distinct overgrowth rim. Sample B40 o.N., coll. Schütz, MNHV. □M, N. *Cunnolites* with marked overgrowth rim. Note lesion in the part of the coral underlying the overgrowth rim. Sample H8 o.N., coll. Schütz, MNHV.

that the ability of this coral to escape sedimentation was very limited or absent; the corals had to cope with sedimentation by partial mortality and modification of skeletal shape. Nevertheless, a comparatively high ability for sediment removal is assumed because of the large polyparia even in the juvenile stage, perhaps enabling sediment rejection by polyp extension and water expellence.

The double-fronted overgrowth margins (Fig. 3I) indicate partial mortality mainly on one side of the corallum. Thus, regrowth of coral tissue propagated not from the centre outwards, as in the case of symmetrical overgrowth margins (see above), but from one side towards the other. The tilted plus double-fronted overgrowth margins (Fig. 3J–L) record both partial mortality by asymmetric sinking into

sediment, or by asymmetric sediment burial for instance due to currents, followed by re-exposure of the dead parts of the corallum. As described, some of the strongly developed (double-fronted) overgrowths are associated with lesions, or scars, of the older corallum (Fig. 3M, N). In these cases, partial mortality may have been brought about by predator attack (see below for further description). The size and area occupied by the overgrowth rims indicate a high recovery potential of partially dead *Cunnolites*. The area from which some of the overgrowth rims propagated is smaller than about half the upper side of the corallum. The described features of partial mortality and regrowth were only observed on the comparatively rare, large specimens, whereas the abundant smaller specimens show no features of partial mortality, disorientation, lesion or other records of environmental change or life crises.

Cunnolites *as settlement substrate*

Large *Cunnolites* were relatively commonly overgrown by other organisms, mainly colonial corals, mussels and bryozoans (Fig. 4A–F). Colonial corals settled include thamnasterioid, cerioid, plocoid, meandroid and flabello-meandroid forms. On each single *Cunnolites*, however, no more than three different taxa of colonial corals were observed as yet; typically, one or two taxa are present. The colonial corals are about one to a few centimetres in size, very well preserved, and do not show evidence for macroboring and encrustation. In a single case, a specimen about 11 cm in diameter is overgrown by five colonial corals of cerioid and thamnasterio-meandroid integration; the size of the colonized patch corresponds roughly to a circle 8 cm in diameter (Fig. 4G, H). In some cases, the surface of the overgrown *Cunnolites* is riddled by pits and scars, whereas the overgrown coral, or corals, commonly are well preserved and unpitted (Fig. 4B, D). At their underside, some *Cunnolites* show the attached valve of a characteristic bivalve taxon (Fig. 4J). It was only this type of bivalve shell that was observed, and it seems to occur exclusively on the flat underside of the coral skeletons. As far as observed, exclusively larger-sized *Cunnolites* skeletons beyond 6–7 cm in diameter were used as settlement substrate by corals, mussels or bryozoans.

Interpretation

In the turbid-water, soft-substrate environment of the Hofergraben Member, hard settlement substrate was scarce, hence skeletons of larger *Cunnolites* provided benthic islands. A benthic island style of colonization is characteristic of soft-substrate habitats with limited settling space (Hattin 1986; Zuschin *et al.* 1999). The number of observed specimens of large *Cunnolites* overgrown by colonial corals is too small to allow for an estimate whether some colonial coral taxa may have preferred or avoided this type of settlement. As far as observed, the colonial corals that overgrew *Cunnolites* all are quite small (Fig. 4). Again, the very good preservation of these colonial forms, and their lack of macroboring and very scarce encrustation (by ostreids, Fig. 4D) suggest that they were choked by rapid sedimentation. In some cases, the difference between *Cunnolites* with a pitted surface and well-preserved, overgrown colonial corals indicates that the solitary form was exposed on the sea floor where it probably was subject to bioerosion (see also below). By their size, also smaller solitary corals about 2–4 cm in diameter should have been suited for settlement of colonial forms. As discussed, however, at least by far most of the small skeletons of dead *Cunnolites* probably were buried. Corals only settled on the upper, convex side of the skeletons, i.e. on the corallum in living position. The bivalves that had attached to the undersides (Fig. 4J), by contrast, indicate that some of the larger coralla had laid in an overturned position before being encrusted by the mussels, and long enough as to allow for the bivalves to grow to size, perhaps even a few years.

Measurement of the colonized patches on *Cunnolites* shows that the size of the settlement area ranged from a few square centimetres (medium-sized specimens) to about 100 cm^2, corresponding to a circle (in plan view) between about 2 to 11 cm in diameter. In this estimate, a potential sediment veneer of the uncolonized marginal portion of the *Cunnolites* skeleton is excluded. Studies of patch colonization (Connell & Keough 1985) in recent shelf habitats indicate a diversity/area-effect, whereby with increasing size of settlement patch the diversity of colonizers increases over some interval of time, then tends to remain stable (see Taylor & Wilson 2003, for review). By comparison to patch colonization in recent, tropical and temperate shelf settings, however, the total diversity of taxa (bivalves, red algae, serpulids, corals) that were observed on *Cunnolites* is quite low, also relative to the deduced size of patches (cf. Taylor & Wilson 2003, p. 39). This may suggest that the low diversity is a result of the turbid-water habitat of the Hofergraben Member. In the Palaeozoic, solitary corals in many cases were crucial in colonizing soft substrata, and provided the starting base for patch reefs of colonial corals (Nield 1982; Watts & Riding 2000; Li *et al.* 2002). In the present case, we observed no case of a demonstrable initiation of a patch reef by colonization of dead solitary corals.
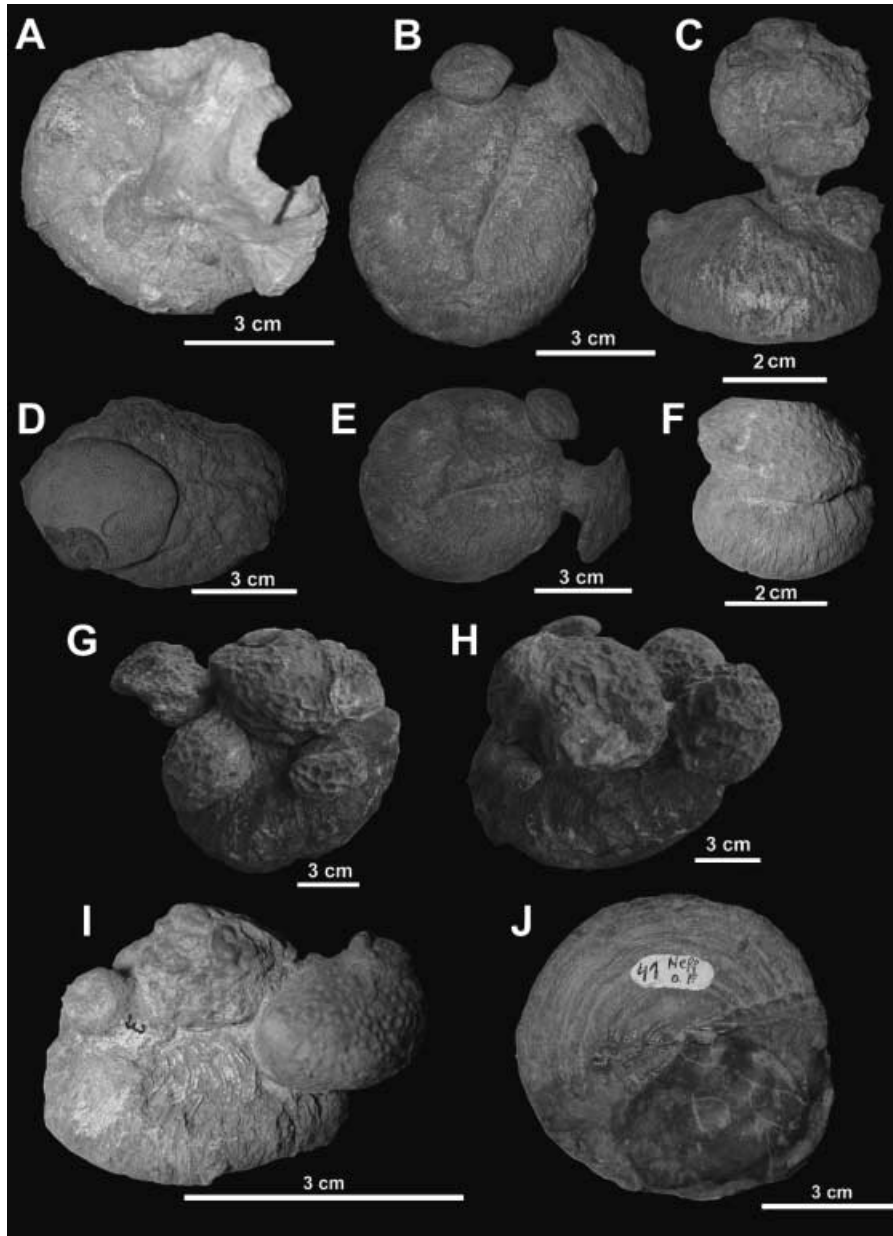
Fig. 4. Cunnolites from Hofergraben Member near Gosau and Russbach, Gosau Group, Eastern Alps. □A. *Cunnolites* as substrate for the foliose-meandroid *Pachygyra princeps* and a small coral head. Sample 9 N. o. F., coll. Schütz, MNHV. □B. *Cunnolites* substrate for two small, mushroom-shaped thamnasterioid corals. Stöcklwaldgraben at Gosau, no sample no. indicated, coll. Schütz, MNHV. □C. *Cunnolites* substrate for small coral heads. Note claviform shape of the larger, cerioid coral heads. Sample 80 N.o.F., coll. Schütz, MNHV. □D. *Cunnolites* substrate for small *Astrocoenia* which, in turn, became encrusted by *Pycnodonte*. Sample 8 N.o.F., coll. Schütz, MNHV. □E. *Cunnolites* substrate for two mushroom-shaped thamnasterioid corals. Sample 19 Neff.u.F., coll. Schütz, MNHV. □F. *Cunnolites* substrate for a small plocoid coral head. Sample N.u.1, coll. Schütz, MNHV. □G, H. Two different views of *Cunnolites* overgrown by five colonial corals. Sample from Nefgraben near Russbach, collected by Martin Gapp, Gosau. □I. *Cunnolites* substrate for three small corals: cerioid (foreground), phaceloid (in center; with branches torn off at base), and ?solitary (left). Sample 40 Neff.o.F., coll. Schütz, MNHV. □J. Underside of *Cunnolites*, as substrate for an unknown bivalve. Cunnolitids with their underside encrusted by these bivalves seem to be fairly common. Sample 41 Neff.o.F., coll. Schütz, MNHV.

Bioerosion

In a few cases, medium- to large-sized *Cunnolites* are bored by lithophagids. Some of these borings had been started from the lower, flat side of the corallum.

Also in large *Cunnolites*, clionid borings are rare and, if present, confined to small patches. At least in the Hochmoos Formation, borings that potentially may be ascribed to worms (sipunculids) were not observed. On larger *Cunnolites*, however,
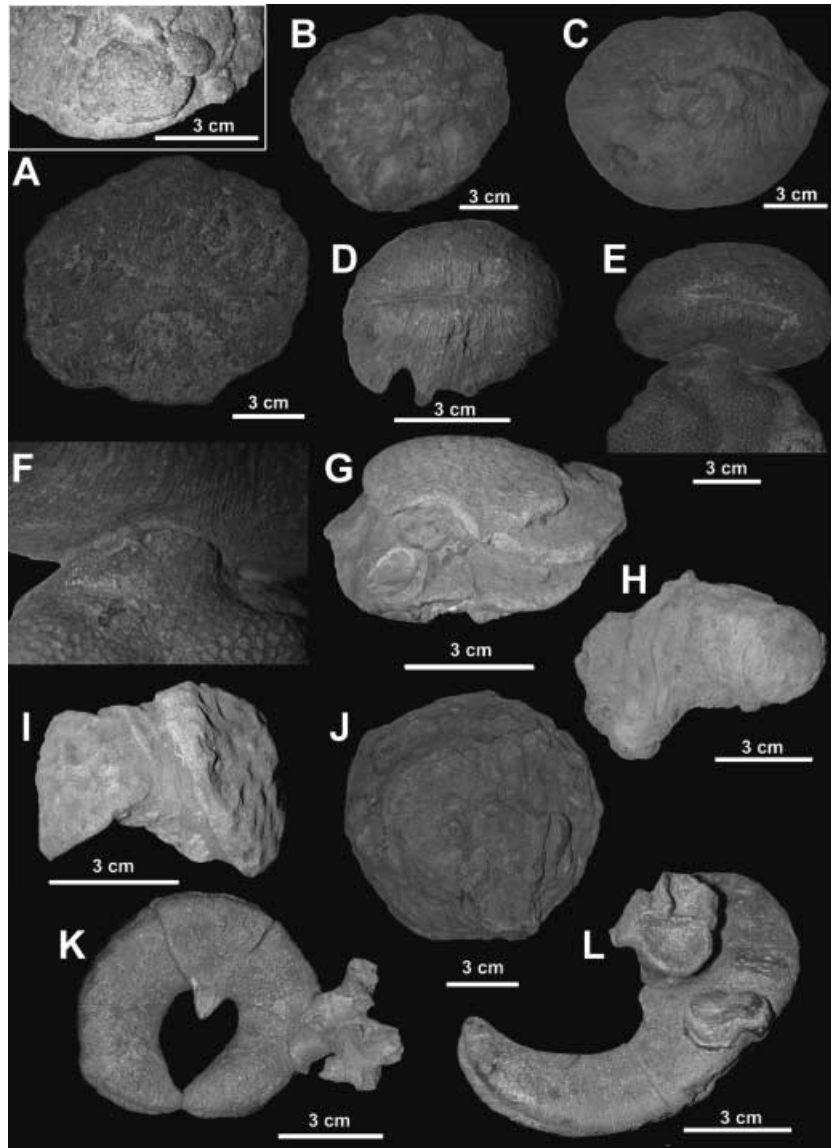
Fig. 5. Patterns of possible bioerosion (predation, ?grazing) on *Cunnolites* from Hofergraben Member near Gosau and Russbach, Gosau Group, Eastern Alps. □A. Cunnolites with pitted and scalloped surface. Inset [above] shows small cerioid colonial corals on flank of same specimen as shown in Fig. 5A. Coll. MNHV. □B. *Cunnolites* with scalloped surface. Sample 50 Neff.o.F., coll. Schütz, MNHV. □C. *Cunnolites* with subcircular scallops. Coll. Schütz, MNHV. □D. Upper side of *Cunnolites* with 'lateral scars'. Sample 65 Neff., coll. Schütz, MNHV. □E. Contact between *Cunnolites* and *Actinacis*. Sample 56 Neff.o.F., coll. Schütz, MNHV. □F. Detail of contact zone of coral ensemble shown in Fig. 6E. □G. Platy grown thamnasterioid coral with constrictions due to partial mortality. One of the dead areas became encrusted by *Pycnodonte*. Edelbachgraben, Hofergraben Mb, Gosau. Coll. of MNHV. □H. Oblique view down a thamnasterioid coral that began in hemispherical shape, but later grew upwards columnar, with many constrictions. Nefgraben, Hofergraben Mb, Russbach. Coll. of MNHV. □I. Marked disorientation of the thamnasterioid coral head. Randograben, Hofergraben Mb, Russbach. Coll. of MNHV. □J. Lower side of a meandroid coral head, with small overgrown *Actinacis*. Hofergraben Mb, Gosau. Coll. of MNHV. □K. *Diploctenium* as substrate for branched coral. Sample 61 NOF, coll. Schütz, MNHV. □L. *Diploctenium* as substrate for a small inverted-conical coral head, and encrusted by *Pycnodonte*. Coll. Schütz, MNHV.

isolated or scattered, roughly subcircular scallops a few millimetres to about 1 cm in depth are fairly common. In addition, some larger *Cunnolites* show a distinctly embayed to scalloped surface and/or a pitted to scalloped outer fringe (Figs 4B, D, 5A–D). Although one might infer that the scallops represent pressure solution pits by lithoclasts, this is precluded by both the marked scarcity of lithoclasts in the coral marls of the Hochmoos Formation and the observation that colonial corals that grew on such specimens are devoid of scallops (Figs 4B, D, 5A). In one specimen, the lower part shows a scallop and a scar, whereas the upper part had regrown from surviving parts of the coral, and shows a distinct, double-fronted overgrowth margin (Fig. 3N).

Interpretation

The marked scarcity of clionid borings in *Cunnolites* may result from the skeletal construction of this coral, consisting of numerous thin, discrete septae. Mere small size of the corals cannot be the reason for lack of clionids, since it is a common observation that bioclasts composed of non-porous calcium carbonate of similar or even smaller size may be densely riddled by clionid borings. By contrast, at least for lithophagids, relative to the size of the mussel, the skeleton also of relatively small cunnolitids appeared massive enough to provide a substrate. As mentioned, in the Hofergraben Member, clionid bioerosion is generally low, also in colonial corals and in mollusc shells. Although quantitative evidence is absent as yet, observations suggest that in recent and ancient turbid-water coral habitats, clionids appear to be low in abundance, whereas lithophagids persist or increase (Sanders & Baron-Szabo 2005). The lithophagid borings that penetrated from the underside of *Cunnolites* most probably were produced post-mortem, when the corallum was lying overturned on the substrate.

The scalloped surfaces of large *Cunnolites* may result from grazing and/or durophagous predation. The scalloped solitary corals overgrown by non-scalloped colonial forms indicate that scalloping occurred before settling and growth of the colonial corals. Grazing by recent gastropods or echinoids typically produces abraded, very gently scalloped, finely scratched surfaces, but not distinct, steeply concave, deep scallops as observed (cf. Bromley 1996). Scalloping of the coral skeleton by crabs also seems less probable. Crabs typically completely disintegrate the shells or skeletons of similar-sized or smaller prey into large fragments, and the scallops seem untypical of crabs. By their size and shape, however, the scallops may broadly resemble cephalopod bites (cf. Bromley 1996; Martire & Torta 2004). After cracking the shell of their prey, however, cephalopods sift out their food; this seems hardly a yielding method in case of a coral with numerous septae. By contrast, durophagous fish typically attack their prey with a single or multiple bites. Solitary corals in low-energy, soft-substrate depositional environments were subject to predator attack – probably by fish – since at least the Devonian (cf. Galle & Mikulas 2003). After the Permian–Triassic extinction, durophagous fish became widespread again since the start of the Late Triassic. The beak-like frontal teeth of these fish scallop the skeleton of attacked corals. Many extant durophagous fish, such as parrotfish and damselfish, that bite into living corals excavate dents into the skeleton, and/or bite up to a few times into the same spot (so-called spot biting),

producing a concave pit typically less than 1 cm in depth (cf. Ogden & Lobel 1978; Miller & Hay 1998). The scallops on *Cunnolites* may result from spot biting, the scarp-bounded lowered fields from patch excavation. Fish bites may pave the way to coral disease and death. At least for densely pitted *Cunnolites*, it is probable that such intense predator attack killed the coral. Conversely, many corals both fossil (Galle & Mikulas 2003) and recent are known to recover even from severe damage by predator attack (Barnes & Hughes 1988; Miller & Hay 1998). Thus, pitted *Cunnolites* with distinct overgrowth margins may result not only from smothering by sediment, but also from regrowth after predator attack.

Interaction with colonial coral

As mentioned, the growth distortions of *Cunnolites* as a result of sedimentation and unstable substrate indicate that this coral was immobile, or at least largely so. In addition, a single fossil ensemble was observed in the collection that consists of a *Cunnolites* in contact with *Actinastraea* (the latter a cosmopolitan, subcerioid colonial coral of the Cretaceous, Baron-Szabo 2002, p. 20 ff.) (Fig. 5E, F). In this ensemble, *Cunnolites* shows a distorted, kidney-like shape in plan view, and the septa are curved away from the contact. Moreover, along the contact, the skeleton of *Cunnolites* shows a distinct retreat. By contrast, the adjacent *Actinastraea* shows an uptilted flange of its skeleton, towards the solitary coral.

Interpretation

The growth distortions of, each, *Cunnolites* that had receded to a kidney-shaped form and *Actinastraea* that had grown against the solitary coral strongly suggest that the colonial coral was digestively dominant (cf. Barnes & Hughes 1988). The kidney shape of *Cunnolites* may further imply that the encounter was not very harmful to the solitary form. Otherwise, by analogy to aggressive encounters among recent corals of quite different digestive rank, *Cunnolites* would have died, at the latest, after gaining direct contact (cf. Barnes & Hughes 1988; Lang & Chornesky 1990). The kidney-shape of the entire *Cunnolites* skeleton suggests that only the portion directly in contact with *Actinastraea* died or suffered, giving rise to the skeletal retreat of the solitary form (cf. Sheppard 1982). The ability of *Cunnolites* to colonize substrata of mud to sand may have reduced the need to be digestively high-ranking, since it only rarely faced direct interaction with other corals. In present-day turbid water settings, digestively low-ranking, but ecotolerant colonial corals are common to prevalent (Potts *et al.*

1985). During the Late Cretaceous, *Actinastraea* was a widespread, highly ecotolerant and morphologically 'plastic' genus found in silty-sandy, friable marls to pure limestones. During the Cretaceous, small-polypar colonial corals resilient to sedimentation and turbid waters appeared, such as *Actinastraea* (Sanders & Baron-Szabo 2005).

Discussion

A summary of evidence related to life history and ecology of *Cunnolites* is given in Table 2. Although a depositional environment like that of the Hofergraben Member may be considered unfavourable to corals, a high total diversity of the coral fauna (Baron-Szabo 2003) and common presence of coral fossils indicate that recruitment occurred geologically continuously. *Cunnolites* preferred soft-substrate habitats off coral reefs. This is shown by closely sampled coral bioconstructions that, if *Cunnolites* were similarly common than within marls, should exhibit many specimens also in cut slabs and thin section; this is not the case (Baron-Szabo 1997; Sanders & Baron-Szabo 1997; Rehfeld & Ernst 1998; Sanders & Pons 1999, 2001; Sanders *et al.* 1999).

In the Hofergraben Member, growth features indicating partial mortality by sedimentation and by tilting on unstable substrate are common on colonial corals, too (Fig. 5G–J). For extant solitary corals, reproduction by fragmentation, dispersal by crawling larvae that settle near the parent, and dispersal by

Table 2. Summary of described aut- and synecological evidence for *Cunnolites.*

(1) *Cunnolites* was immobile.
Evidence: Pedestals, columnar growth, growth distortions, overgrowth margins, direct life encounter with *Actinacis* (colonial coral), size-frequency distribution of *Cunnolites* assemblages

(2) *Cunnolites* provided benthic islands.
Evidence: Larger-sized skeletons of *Cunnolites* are overgrown by colonial corals and/or attached mussels (e.g. ostreids). Up to five colonial corals observed on a single specimen

(3) *Cunnolites* embedded overturned and exposed on the sediment surface over some interval of time.
Evidence: Direct field observations, attached bivalve shells on underside of skeleton, lithophagid borings that started from the underside

(4) Bioerosion by durophagous predation and/or grazing.
Evidence: Pitted and scalloped surfaces and scalloped margins of skeletons

(5) Direct life encounter of *Cunnolites* and *Actinacis* (cerioid colonial coral).
Evidence: *Cunnolites* receded during growth in contact with *Actinacis*, i.e. *Cunnolites* was the digestively subjugate taxon

negatively buoyant larvae may in part explain their common presence in mass accumulations (Goreau & Yonge 1968; Gerrodette 1981; Harrison & Wallace 1990:186; Littler *et al.* 1997), as also characteristic of many fossil solitary forms (Gill & Coates 1977; Rehfeld & Ernst 1998; Baron-Szabo 2003). Marls and sandy marls that formerly represented soft substrata and that are rich in solitary and/or pseudocolonial corals can be considered as an end member of scleractinian assemblages thriving in areas of high sediment input (see Sanders & Baron-Szabo 2005, their fig. 9). Because of its large polyp, *Cunnolites* most probably had a high ability to cope with intermittent sedimentation and to feed on particulate organic matter (cf. Sanders & Baron-Szabo 2005). In the Hofergraben Member, two other fairly common corals are the colonial, flabellate to flabello-meandroid *Placosmilia* and the flabelloid colonial *Diploctenium* that were used as settlement substrate by bivalves and corals (Fig. 5K, L). For mature *Diploctenium*, the crescentic to subcircular flabelloid shape enabled a lifestyle lying on the sea floor, similar to a solitary coral. The Hofergraben marls provide an example of a soft-substrate turbid-water habitat open mainly to (1) solitary corals; (2) to specialized colonial corals of shape and lifestyle similar to solitary corals; and (3) to colonial corals mainly of high sediment resistance. As mentioned, some taxa of solitary corals found in these marls show skeletal features similar to extant azooxanthellate deep-water corals (Sorauf 1999). It is not yet firmly established whether *Cunnolites* was zooxanthellate or not. In the Hofergraben marls many of the corals, solitary and colonial, are still preserved as aragonite; high-precision measurements of stable isotopes of oxygen and carbon thus could help to solve this question (cf. Stanley & Swart 1995) for the perhaps most widespread late Jurassic to Cretaceous solitary coral.

Conclusions

During deposition of the Hofergraben Member (Hochmoos Formation) in a shallow neritic turbid-water environment, soft to firm, silty-sandy muds were colonized by level-bottoms of non-rudist bivalves, gastropods, solitary corals, colonial corals, rudists and echinoids.

Among the corals, the flat-based, subcircular, cupolate solitary form *Cunnolites* is most abundant (locally in mass occurrence). *Cunnolites* faunas are strongly biased towards small specimens about 1–3 cm in diameter, whereas fossils larger than about 5–7 cm are much more rare. For the small specimens, their typical excellent preservation combined with marked

rarity, each, of bioerosion, encrustation, and epibionts suggests that they died from smothering during pulses of sedimentation or sediment resuspension.

Cunnolites was immobile, or at least largely so. Large specimens record partial mortality by stout to columnar pedestals with overgrowth margins, and by diverse types of overgrowth margins on the upper, convex side of the corals. Partial mortality was caused by sedimentation, unstable substrate and, perhaps, by predation.

Large *Cunnolites* provided benthic islands for settlement of colonial corals and/or, less commonly, for non-rudist bivalves (*Pycnodonte*). *Cunnolites* was poorly suited as a substrate for clionid and lithophagid boring. On large specimens, however, scallops and pits suggest predator attacks, possibly by durophagous fish.

In a single documented case of a direct encounter of *Cunnolites* with a cerioid colonial coral, the solitary form was subjugate. By analogy to recent coral faunas, *Cunnolites* perhaps was a digestively low-ranking form that, however, was resistant to input of sediment and particulate organic matter.

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