# The ecological significance of solitary coral and bivalve epibionts on Lower Cretaceous (Valangianian–Aptian) ammonoids from the Italian Dolomites

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ABSTRACT:

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Lower Cretaceous deposits of the Puez section in the Dolomites (northern Italy) yielded a rich ammonoid fauna (28 genera, n = 424) showing unique epifaunal encrustations by the ahermatypic solitary scleractinian ?*Cycloseris* LAMARCK, 1801. The coral encrusted only the outer shell surfaces of the ammonoids; the inner surface remained unaffected. Such a Cretaceous community and the relationship between the two fossil groups are described for the first time. The shells of dead ammonoids sank to the sea bottom and became colonized by the coral larvae, as documented by the location of the epibionts on only one side of the shells. The coral was fixed to the ammonoid shell for its entire life. Only the 'sediment free' upper side of the ammonoid shells could be inhabited by epibionts such as corals and serpulids. The encrustation of ammonoid shells by the bivalve *Placunopsis* represents a different situation in that both sides of the ammonoid shells were affected, pointing to encrustation of floating ammonoids. This long-term infestation in the water column contrasts with coral settlement on the sea-floor. Ammonoid specimens encrusted by *Placunopsis* never exhibit encrustation by corals. The ammonoid-coral relationship from the Dolomites is documented from the Valanginian to Aptian interval. Examples of coral epibionts on ammonoids and other fossil groups throughout the geological column are briefly reviewed.

Key words: Ammonoids, Epibionts, Corals, Autecology, Cretaceous; Dolomites, Italy.

## INTRODUCTION

Epibiosis is one of the few well-preserved biotic interactions in the fossil record and can be traced back to the Early Palaeozoic (PALMER 1982). Studying the spatial relationships among organisms that lived with each other provides insight not only into the autecology of these organisms, but also into their palaeoenvironmental and palaeocommunity structure (LUKENEDER & HARZHAUSER 2003). Fossil and Recent evidence for factors governing the distribution and interaction of fossil sessile animals was summarized by JACKSON (1983).

The Puez section is located in the Southern Alps (Dolomites; Text-fig. 1) of northern Italy. The stratigraphy of the Lower Cretaceous succession here is based on ammonoids (LUKENEDER & ASPMAIR 2006). The latter authors described a Valanginian to Aptian ammonoid fauna from the Puez locality.

The main aim of this study is to show the advantages for palaeoecological interpretations that can be derived from careful examination of sessile epibionts

accompanying an ammonoid assemblage. This relationship between ammonoids and ahermatypic (non-reef constructing) corals yields additional palaeo-ecological information. The coral infestation of ammonoids is shown to be a local phenomenon, caused by special environmental conditions at the Puez section.

GEOLOGICAL SETTING, LITHOLOGY AND DATING

Lower Cretaceous deposits form a major element of the Southern Alps. They have therefore been reported in several papers of the late 19th and early 20th centuries (HOERNES 1876; HAUG 1887, 1889; UHLIG 1887; RODIGHIERO 1919; BACCELLE & LUCCHI-GARAVELLO 1967a, b; STÖHR 1993, 1994; COSTAMOLING & COSTAMOLING 1994; FARAONI & al. 1996). The geology of the Dolomites and adjacent areas has been described and summarized in detail by POZZI (1993), GEYER (1993), HEISSEL (1982), BOSELLINI (1998) and BOSELLINI & al. (2003).

The Southern Alps emerged during the deformation of a passive continental margin (BOSSELINI & al. 2002). The Dolomites (Permian to Cretaceous) are their internal part. The geological landscape of the Puez region is dominated by Triassic carbonate platforms. The top of

these carbonates bears relics of Lower Cretaceous sediments belonging to the Biancone (local name for the Italian Maiolica) and Puez Formations (FARAONI & al. 1996; WIECZOREK 1988, LUKENEDER & ASPMAIR 2006) (Text-fig. 2).

The sequence shows the evolution of the northern-most part of the Trento Plateau at this time. The Trento Plateau extends from the south (around Trento) up to the Puez region and was formerly surrounded by two basins: the Lombardian Basin to the west and the Belluno Basin to the east (BOSSELINI & al. 1981). The reason for the Late Jurassic to Early Cretaceous separation into a basin-plateau-basin succession lies in the rifting history of the Piemonte–Ligurian Tethys Ocean (Penninic Ocean) (MAYER & APPEL 1999).

The Puez section consists essentially of red to grey calcareous marls and grey, silty marlstones of the Puez Formation (Upper Valanginian to Aptian; 150-200 m) underlain by green-grey limestones of the Biancone Formation (Lower Valanginian, 0-5 m) and red nodular limestones of the Ammonitico Rosso (Tithonian to Berriasian; 10-20 m). A remarkable feature of the middle part of the Puez Formation is the large number of cherty and calcareous concretions (Text-fig. 2). The outcrops are generally exposed on steep slopes up to the Piz de Puez (Puezspitzen) and Col de Puez (Puezkofel).
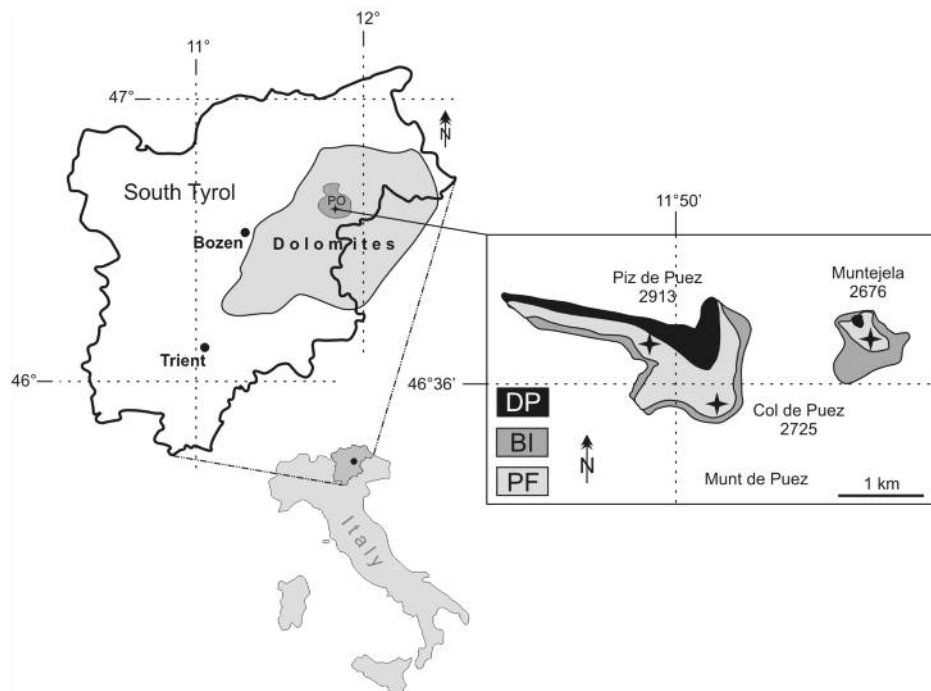
The outcrop is situated on the Puez-Odle-Garde-



Fig. 1. Map of Italy with included locality map of South Tyrol showing the outcrop of Lower Cretaceous sediments around the Puez section investigated within the Dolomites. PO – Puez-Odle nature park. DP – Dolomia principale (Hauptdolomit), BI – Biancone Formation, PF – Puez Formation
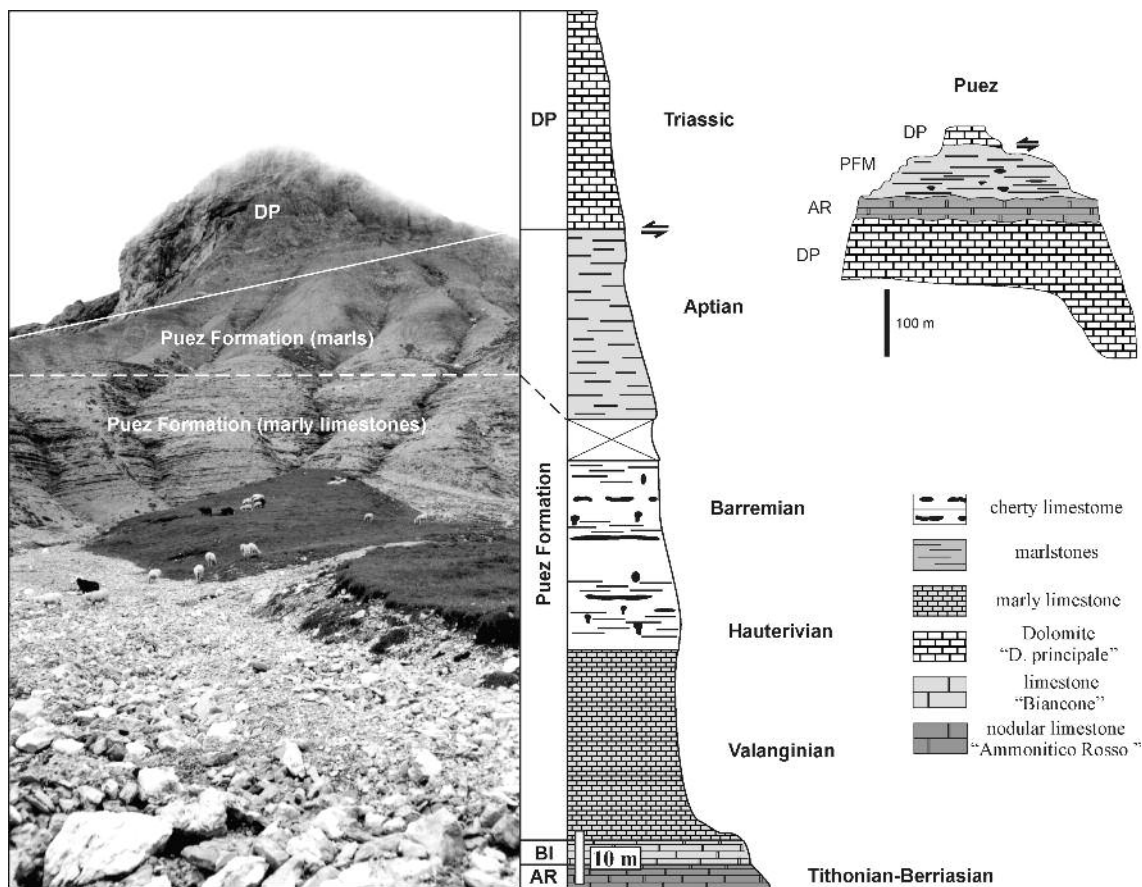
Fig. 2. Exposure of the investigated section and position of the outcrop at the Puez section. Log of the Puez section with indicated age and thickness of the different members. In the right upper corner the overthrusting by Triassic Hauptdolomit is indicated in a synthetic log of the Col de Puez. DP – Dolomia Principale, PFM – Puez Formation, AR – Ammonitico Rosso. Log adapted from (LUKENEDER & ASPMAIR 2006).

naccia Plateau (= Puez Plateau or Puez region) in the Dolomites (Trentino – Alto Adige; South Tyrol), about 30 km northeast of Bozen (Text-fig. 1) (see LUKENEDER & ASPMAIR 2006). The ammonoid-bearing beds are located on the southern side of the Piz de Puez (2846 m, 1:25 000 sheet 05 Val Gardena). The ammonoids described herein were collected on the southern margin of the Puez Plateau. The succession is well-exposed on the steep flanks [GPS (N 46°35'16'', E 11°47'09''; values for '' (seconds) vary due to the 250 metres width of the outcrop and 200 metres of sediment thickness in the investigated area].

The diverse invertebrate fossil assemblage consists of ammonoids, coleoids, aptychi, bivalves, brachiopods, sea urchins, ophiurids, corals, serpulids, benthic/planktonic foraminifera and radiolarians. Relatively fossiliferous parts of the section alternate vertically with parts almost devoid of macrofossils. Radiolarians, ostracods, echinoderms, sponge spicules, brachiopods and foraminifera are the most prominent constituents of the microfauna.

The cephalopod-bearing beds of the Puez Formation range from the Valanginian through to the Aptian (LUKENEDER & ASPAMIR 2006). Future detailed logging by the author should clarify the exact zonation of the Puez locality. No hiatus could be detected so far (Text-fig. 3).

MATERIAL AND METHODS

Most of the material (Pls 1-3) was collected by CH. ASPMAIR, in the context of a project "Puez marls", of the South Tyrolean Museum of Natural Sciences (from 1999 to 2003), and by various collectors for the Natural History Museum Vienna : A. HEINRICH and others 1883-1915 and A. LUKENEDER 2003. During the course of this study, 424 ammonoid specimens, 6 nautiloids, 10 lamellaptychi, 6 belemnites, 26 sea urchins (Disasteroida – Collyritidae), 12 bivalves, 21 brachiopods (*Pygope* and *Triangope*) and several encrusting groups (e.g. corals, bivalves, serpulids) were examined.

## Conventions

NHMW Natural History Museum Vienna (Naturhistorisches Museum Wien; 2005z numbers), NMB South Tyrol Museum of Natural Sciences (Naturmuseum Bozen; PZO numbers). The author follows the basic classification of Cretaceous Ammonoidea by WRIGHT & al. (1996). Unfortunately, many specimens were collected by private collectors or scientists up to one hundred years ago from rock samples only and not bed by

bed. The author can therefore only summarize the specimens now in the collections and cannot provide details from which bed a specimen came. Some specimens in Plates 1-3 were coated with ammonium chloride before they were photographed.

PALAEONTOLOGY

Ammonoids
(Text-figs 4, 5 and Pls 1-3)

MATERIAL: 19 ammonoid specimens encrusted by corals. Nine different genera (*Phylloceras*, *Phyllopachyceras*, *Lytoceras*, *Leptotetragonites*, *Silesites*, *Melchiorites*, *Barremites*, *Crioceratites*, *Ancyloceras*) comprising ten species were encrusted by the solitary coral ?*Cycloseris* sp. (see Appendix).

REMARKS: The ammonoid shapes range from discocone or sphaerocone (involute with ovate whorls), to evolute (with round whorls) and ancylocone to hook-shaped shells. The ribbing of the hosts ranges from fairly dense, as in *Lytoceras subfimbriatum* and *Phyllopachyceras bontshevi*, to strong, as in *Silesites vulpes* and *Phyllopachyceras infundibulum*, to smooth in *Melchiorites cassioides* and *Barremites psilotatus*. Both

| Stages | | Zones | Subzones |
|---|---|---|---|
| APTIAN | Lower | D. furcata | |
| | | D. deshayesi | |
| | | D. weissi | |
| | | D. oglanlensis | |
| BARREMIAN | Upper | P. waagenoides | |
| | | C. sarasini | |
| | | I. giraudi | |
| | | H. feraudianus | |
| | | G. sartousiana | C. provincialis |
| | | | C. sartousiana |
| | | A. vandenheckii | |
| | Lower | C. darsi | |
| | | K. compressissima | |
| | | N. pulchella | |
| | | K. nicklesi | |
| | | T.hugii auct. | |
| HAUTERIVIAN | Upper | P. angulicostata auctorum | P. catulloi |
| | | | P. angulicostata auct. |
| | | B. balearis | |
| | | P. ligatus | |
| | | S. sayni | |
| | Lower | L. nodosoplicatum | |
| | | C. loryi | O. (J.) jeannoti |
| | | | C. loryi |
| | | A. radiatus | |
| VALANGINIAN | Upper | T. callidiscus | |
| | | H. trinodosum | C. furcillata |
| | | | O. (O.) nicklesi |
| | | S. verrucosum | V. peregrinus |
| | | | K. pronecostatum |
| | | | S. verrucosum |
| | Lower | B. campylotoxus | |
| | | T. pertransiens | |
| | | T. otopeta | |

Fig. 3. The stratigraphic position within the Lower Cretaceous (Lower Valanginian to Lower Aptian) of the Puez fauna and its range at Puez (in grey). Table compiled after HOEDEMAEKER & al. (2003) and REBOULET & al. (2006)
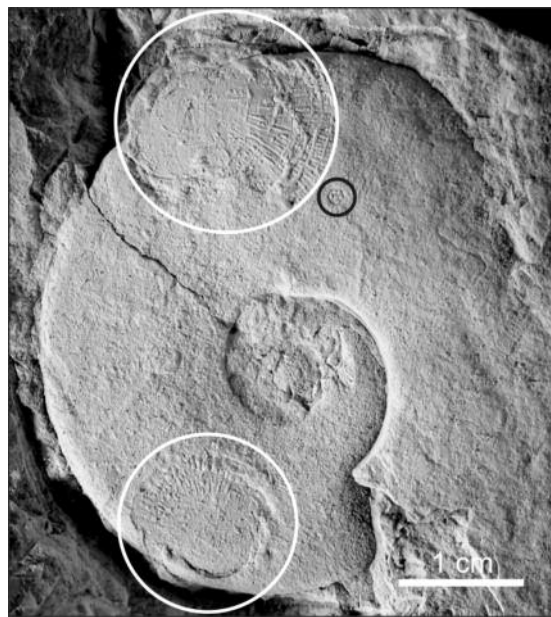


Fig. 4. *Barremites psilotatus* (steinkern; d 38 mm; PZO-CP400) showing three remnants of coral infestation. Two bigger impressions of basal plates (white circles) and a juvenile stage showing six initial chambers (black circle)

micro- and macroconchs (m and M) were similarly encrusted.

Corals – ?*Cycloseris* sp.
(Text-figs 4, 5 and Pls 1-3)

MATERIAL: 30 attached coral specimens were observed on 19 different ammonoid specimens from Valanginian to Aptian beds.

DESCRIPTION: The corals are solitary, discoid to cupolate, from 2 mm up to 43 mm in diameter, with a basal plate thickness of 0.5-3 mm. They are attached to ammonoid shells by their entire basal plate. The attached lower surface xenomorphically copies the ammonoid shell surface morphology (e.g. ribbing). The non-attached side is convex (Text-figs 4-5 and Pls 1-3). The outer shape is circular, comprising a deep calicular fossa that is only visible in the three-dimensional specimens and in the median thin sections (Pl. 1, Figs 4a and 6a). The septa are arranged in six symmetrical sectors. Primary skeletal aragonite has recrystallized to calcite microspar. In most cases only the round basal plate of the corals is visible attached to the steinkerns of the ammonoids. The corallites are preserved, albeit hidden, in the negatives of the ammonoids, which were not normally collected. Only two specimens show three-dimensional preservation of the coral body with its septa (Text-fig. 6). All the corals were attached to ammonoid steinkerns and none was observed isolated in the surrounding sediment. A paper dealing with the coral microstructure and taxonomy is in preparation.

REMARKS: As pointed out by RUSSO & *al*. (1996), the taxonomic status of *Cycloseris* LAMARCK is in need of revision. Confusion remains in the systematics of *Cycloseris* LAMARCK, 1801, *Cyclophyllopsis* ALLOITOU, 1959 and the species "*Cycloseris*" *escosurae* by MALLADA (1887). RUSSO & *al*. (1996) suggested that the latter could possibly be a member of a new genus. The present author therefore uses the name *Cycloseris* in a broad sense only

The morphology is similar to that of Upper Cretaceous solitary corals like *Cunnolites* and *Micrabacia*. Internal structures (septa) and composition are comparable with those of the latter genera. Despite these similar features, corals like *Cunnolites* and *Micrabacia* are not known to have lived attached to ammonoid shells or even to 'normal' hardgrounds such as stones or to a hard substrate. *Connulites* larvae, at least, settled on very small hard substrates, such as individual sand grains or small-sized bioclasts (D. SANDERS, pers. comm.). Later,

when *Connulites* had grown in size, the tiny basal attachment broke off and the coral lay freely on the sea floor. *Connulites* was immobile or at best of very limited mobility, but certainly not as mobile as extant *Fungia* and *Manicina* (SANDERS & BARON-SZABO 2007). Serial thin sections were made and show remarkable differences from other known solitary corals. Detailed microstructural and taxonomic features will be presented by LUKENEDER & STOLARSKI (in prep.). The solitary corals described herein from the Puez section needed years to grow up to their maximal diameter of 43 mm. This assumption is based on the average growth rate for solitary corals. Dome and plate corals show radial growth rates from 0.5 to 2.0 cm a year (BARNES 1980; DODGE & VAISNY 1980). The corals and other encrusters had enough time to grow over the various ammonoid shells. Due to the fact that 30 corals were found attached to ammonoid shells, this seems to have been a relatively common phenomenon (approx. 3 per cent) at the Puez locality. A single ammonoid shell was overgrown by up to five corals (Pl. 3, Fig. 1).

PATTERNS: The adherent corals assigned to ?*Cycloseris* sp. were the most abundant encrusters in the fauna. Virtually all of the ammonoid species were affected. In every encrusted ammonoid specimen the corals are positioned on one side only, namely the outer side, typically laterally. In cases when more than one coral grew on a shell, their arrangement followed no clear pattern. The corals initially settled on the ammonoid shell while it was resting on the sea floor. After embedding and death of the coral, the aragonite of the ammonoids was completely dissolved, in contrast to the primary skeletal aragonite of the coral, which recrystallized to calcite microspar and is therefore preserved. Lithification took place before dissolution of the aragonitic ammonoid shell. Due to the diagenetic solution of the aragonitic shells of the ammonoids, the attached surface of the corallites is visible on the ammonoid steinkerns. In those ammonoids that were prepared by separating the negative and positive pieces, the corallite is always positioned inside the negative part, displaying its basal plate. The corals and their attachment scars are hardly noticeable on the positive of the ammonoid steinkerns.

The preservational stages of the ammonoid/coral community are as follows: (1) Death of the ammonoid; (2) Drifting (incrustation by bivalves) or sinking to seafloor (possible encrustation by corals); (3) Encrustation and growth of corals; (4) Burial and infilling of shell by sediments; (5) Formation of steinkerns; (6) Diagenetically induced dissolution of aragonitic ammonoid shell (only the recrystallized corallite – calcite microspar –
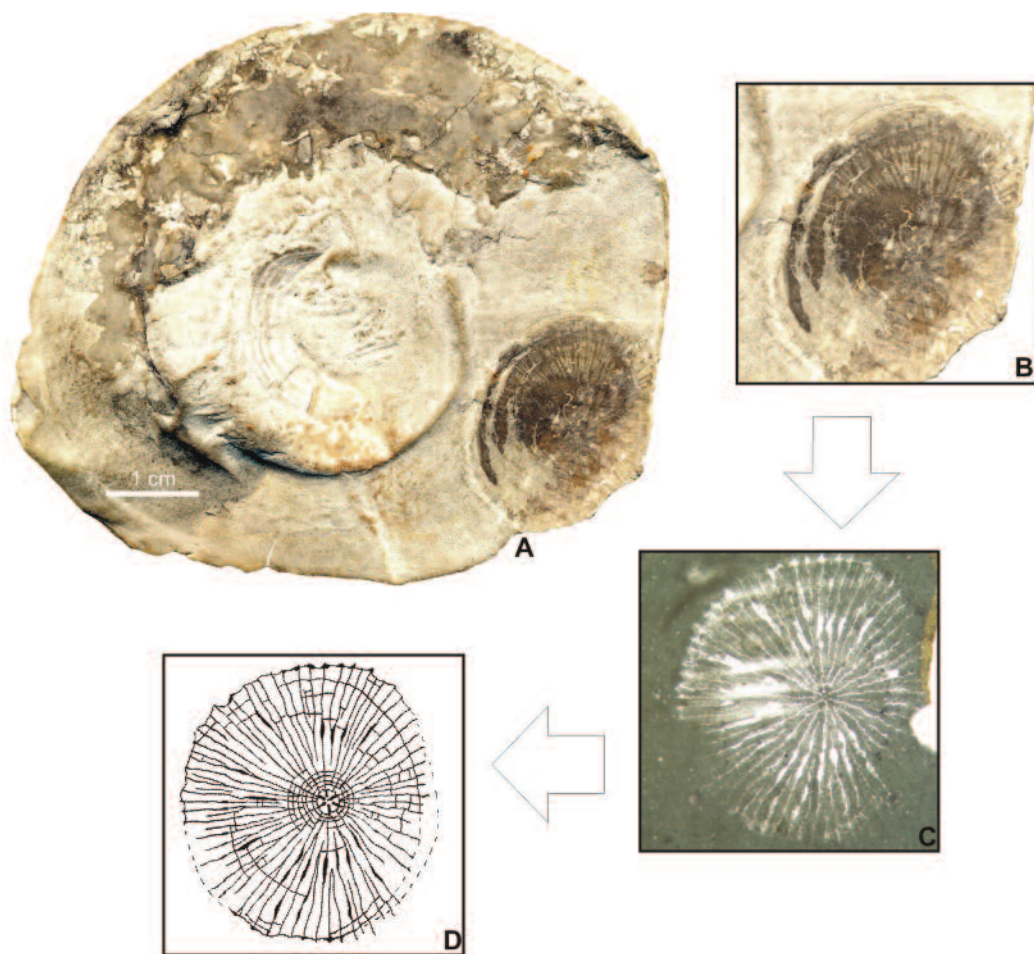
Fig. 5. Encrustation and its lateral position on an ammonite. A – *Lytoceras subfimbriatum*; Puez section; 2006z0149/0001; × 1.5. B – enlargement of the coral in A. C – thin section of the same coral. D – drawing of septal arrangement of the same coral, × 1.5

persisted); (7) Corals appear now as attached on the steinkerns of ammonoids.

**Other epibionts**

Serpulids – *Glomerula* sp.

DESCRIPTION: Numerous tubes of serpulid worms up to 8 mm long and 0.15 mm wide were attached initially to the outer surface of ammonoid shells, now preserved as steinkerns. Only the remnants of the cemented part of the tubes are preserved, these being reminiscent of *Glomerula.* Generic identification, however, is difficult owing to the poor preservation.

Bivalves – *Placunopsis* sp.

DESCRIPTION: Colonies of these encrusting bivalves, which are characterised by a very flat, smooth shell mor-

phology, were frequently found on steinkerns of ammonoids. Ammonoid specimens encrusted by corals were not encrusted by *Placunopsis*. One specimen had up to six valves attached to it. The valves show a preferred orientation on the external side of the ammonoids and are often located ventrally, facing the sea-floor, when the ammonoid was in floating position (Text-fig. 6). Valves attain maximum diameters of 15 mm.

DISCUSSION

The ammonoid assemblage of the Puez region is very similar to ammonoid faunas of the Northern Calcareous Alps, except for the presence of the coral encrustations. The strong similarity of both faunas results from the palaeogeographic position of the Southern Alps in the Early Cretaceous (LUKENEDER & ASPMAIR 2006). The position of the Southern Alps during the Early Cre-

taceous is still enigmatic, but this region was most probably located close to the south of the Northern Calcareous Alps (see CECCA 1997, 1998; LUKENEDER 2004a; VAŠÍČEK & *al*. 1994; Vašíček & MICHALÍK, 1999; STAMPFLI & MOSAR, 1999; STAMPFLI & *al.* 2002, ZHARKOV & *al.* 1998) (Text-fig. 1).

In the Mesozoic, oysters, lanceolate (*Gervillia, Posidonia*), placunopsid (*Placunospsis*) and inoceramid (*Inoceramus*) bivalves were common epizoans encrusting ammonoid shells (SEILACHER 1960; MERKT 1966; SEILACHER & WESTPHAL 1971, COPE 1968, LEHMANN & WIPPICH 1995; WIGNALL & SIMMS 1990). Infestations of Liassic ammonoid shells from Holzmaden (Germany) by serpulids, oysters, gervillid bivalves, the small-sized oyster *Exogyra*, orbiculoid brachiopods and bryozoans are well known (SEILACHER 1960; MERKT 1966; SEILACHER & WESTPHAL 1971). SEILACHER (1960), MERKT (1966) and SEILACHER & WESTPHAL (1971) all inferred that the epizoan settlement took place while the ammonoid shell was still floating. The same hypothesis was put forward by MEISCHNER (1986) for the fixo-sessile bivalve *Placunopsis* attached with its right valve to shells of the Triassic ammonoid *Ceratites*. WIGNALL & SIMMS (1990) proposed the term 'Pseudoplankton' for attached epifaunal species colonizing floating substrates.

There has been considerable debate about whether the attachment of these epizoans to the ammonoid shells occurred during life, after death but while the shell drifted, or on the empty shell after it sank to the sea floor and became a hard substrate suitable for larval settlement (MERKT 1966, KAUFFMAN 1978, KEUPP 1992, SCHINDEWOLF 1934, TAYLOR & WILSON 2002). The organism-substrate relationship and the preferred terminology were summarized by WEST (1977) and later by TAYLOR & WILSON (2002).

The encruster assemblage from Puez is of low diversity and dominated by solitary corals. The pattern of the encrustation reveals the corals to have been solitary-sessile inhabitants utilizing solely the outer surface of ammonoid shells as a habitat. The inner shell surfaces of the ammonoids were unsuitable for settlement by the coral epifauna: traces of coral epizoans here are totally absent. The metabiosis between the latter fossil groups took place after the death of the ammonoid animal, and after the shells had sunk to the sea floor.

In marked contrast to the above-described encrustations of corals on the outer surfaces of ammonoid shells, LUKENEDER & HARZHAUSER (2003) described a remarkable cavity-dwelling palaeocommunity (GINSBURG & SCHROEDER 1973) from Valanginian deposits of Austria (Northern Calcareous Alps) where epibiontic foraminifera lived within the ammonoid body chamber. The

authors demonstrated that the infestation pattern documents an obligate preference of the adherent taxa for the inner shell surface, the outer surface remaining unaffected. Such cryptic habitats shelter sessile and encrusting species from predation and physical disturbance (GISCHLER & GINSBURG 1996). These coelobites (LUKENEDER & HARZHAUSER 2003) were protected within small cavities against other encrusters (e.g. sponges) and enemies. The described foraminifera infested only shells of a single ammonoid species – *Olcostephanus guebhardi*.

Fixosessile solitary corals of the group ?*Cycloseris* sp. have been recorded rarely in Jurassic, Cretaceous and Eocene palaeocommunities in Afghanistan (GILL & LAFUSTE 1971), Austria (DARGA 1992), Borneo (FRITSCH 1878), Croatia (OPPENHEIM 1901), France (MICHELIN 1840-1847; GILL 1970), Hungary (BARTA CALMUS 1973; RUSSO 1996), India (DUNCAN 1880), Indonesia (GERTH 1933), Israel (GILL 1970), Italy (OPPENHEIM 1900; RUSSO 1979), Lebanon (FELIX 1913), Madagascar (GILL 1970), and Spain (RUSSO & *al.* 1996; ALVAREZ PEREZ 1993; as summarized in RUSSO & *al*. 1996). In all of these occurrences, ?*Cycloseris* sp. encrusted foraminifera belonging to the genera *Nummulites, Discocyclina*, *Aktinocyclina*, *Operculina* and *Assilina*. The maximum diameter reported for this disc-shaped solitary coral is 18 mm, which contrasts with the much larger specimens from the Puez section (maximum diameter 43 mm).

RUSSO & *al*. (1996) supposed that the coral larvae settled mainly on palorbitolinid foraminifera but later changed to a mobile, free-living life style. In contrast, the Puez corals were sessile throughout their lifespan. This interpretation is supported by the large diameter of the entirely attached basal plate (up to 43 mm) and the fact that the coral xenomorphically contours the morphology of the ammonoid shell. The corals were attached to the ammonoid by the total area of the basal plate.

The herein-described coral does not fit the scheme of GILL & COATES (1977). The latter authors assumed three different benthic mobility modes for solitary corals: 1) passive motion, 2) towing and 3) auto-mobility. They also supposed a sensitivity of solitary corals to the sediment on which they lived. GILL & COATES (1977) noted that extant *Cycloseris* and the comparable Jurassic *Chomatoseris* are mobile and always linked to soft, sandy or sandy mud substrates. If one accepts this interpretation, then the herein-described sessile coral shows the same shape as that of the above genera but a different life strategy, i.e. attached to hard substrates. The ammonoid shells lying on the seafloor merely served as bioclasts on which the coral larvae could settle.

Several Palaeozoic corals such as *Heliolites*, *Favosites* and *Alveolites* were described by KASE (1986), MCINTOSH (1980) and summarized by DARREL & TAYLOR (1993) as macrosymbionts attached to the walls of large crinoids and sometimes settling on gastropods, nautiloids, bivalves and pebbles (BAIRD & *al*. 1980, 1989; RUSSO & *al*. 1996; JACKSON 1983). The same behaviour is reported from Albian and Recent corals such as *Heteropsammina* and *Heterocyathus*, which encrust dead gastropod shells (STOLARSKI & *al*. 2001). The latter authors noted that the coral larvae settle on small shells, generally gastropods. The solitary Recent coral *Caryophyllia* attaches to polychaete tubes (e.g. *Ditrupa*) and to shells of gastropods such as *Aporrhais*. All the above palaeocommunities apparently inhabited nearshore environments and can now be detected in shallow-water deposits. Jurassic examples from Sicily reported by STOLARSKI & RUSSO (2002) show stylophyllid solitary corals (*Haimeicyclus*) and bivalves encrusted by juvenile specimens of *Haimeicyclus*. BAIRD & *al*. (1989) showed that tabulate corals such as *Alveolites* had grown on cephalopod hosts *synvivo*, based on the orientation of corallites and bryozoan zooecia.

NICOSIA & PALLINI (1977) reported from the Central Apennines Late Jurassic (Tithonian) encrustation of ammonoid shells by mostly colonial forms of hermatypic and ahermatypic corals. They noted encrusting corals such as *Thamnasteria*, *Dimorpharaea* and *Epistreptophyllum* and forms of the suborder Caryophylliina. This is the only previous record of encrustation of ammonoid shells by corals. The greatest similarity with the material described here is the coral they illustrated attached to an Early Tithonian *Ptychophylloceras ptychoicum* (NICOSIA & PALLINI 1977; pl. 3, figs 8-9), for which no name or description was given. From the presence of reworked ammonoids, evidence of reduced sedimentation, occurrence of encrusted pebbles, encrustation of both sides of the ammonoid shells caused by storm waves and high environmental energy, in addition to the coral faunal spectra, they supposed the fauna to be from a shallow water environment.

More recently, GILL & *al*. (2004) determined that pennular corals from the late Jurassic of the Apennines could also inhabit regions from deep neritic to upper bathyal settings. This shows that pennular corals can be found in limestones of the Ammonitico Rosso and the *Aptychus* limestone, both of which were mostly sedimented on intrabasinal highs and locally in basin-margin deposits (GILL & *al.* 2004).

The above-mentioned encrustations of Tithonian ammonoids by corals were by taxonomically diverse and predominantly colonial forms, whereas in the Italian Puez section Cretaceous ammonoid shells belonging to several different taxa were encrusted by a single taxon of solitary coral. There was also a difference in the depositional environment at Puez, where the pelagic depositional environment contrasted with the shallow water environments described by NICOSIA & PALLINI (1977). No coral infestation of ammonoid shells has been reported so far from other Cretaceous localities.

The depositional setting of the Puez section is interpreted as deep shelf or upper slope. Open marine and rather calm conditions are inferred, based on the abundant radiolarian and planktonic foraminifera. Thus, the analysis of the micro- and macrofauna and new data on the cephalopod assemblage support the interpretation of a soft, level bottom habitat with a radiolarian-dominated planktonic fauna in an offshore environment. Recent *Cycloseris* occupy a documented depth range from 0 to 411 m (WELLS 1956).

The interpretation of the origin of the encrusted and fragmented ammonoid specimens is strongly supported by the taphonomy. The well-preserved, unfragmented ammonoid specimens within the limestones and marls apparently did not experience any transport or reorientation, and were therefore deposited in their original environment. The Puez fauna is therefore interpreted as an assemblage comprising exclusively autochthonous benthic (e.g. corals) and parautochthonous pelagic elements (e.g. ammonoids) from the open sea.

The association began in the Valanginian with *Phylloceras thetys, Lytoceras subfimbriatum* and *Leptotetragonites honnoratianus*, and is finally documented in the Aptian with *Ancyloceras matheronianum*.

The main reason why shells of nine different ammonoid genera hosted the corals is because they projected from the mud and acted as hardgrounds on which the coral larvae could settle. Such a distribution precludes encrustation during post-mortem drift (Text-fig. 6).

The encrustation of the ammonoid shells by the fixo-sessile bivalve *Placunopsis* represents a somewhat different scenario. The bivalves became attached on both sides of the shell, indicating attachment while the living ammonoids still floated. In no case do any of the ammonoids encrusted by *Placunopsis* exhibit encrustation by corals. The *Placunopsis* larvae probably did not settle on the deeper depositional area at the sea-floor.

Coral larvae can settle only days after release, but can also survive in the water column under laboratory conditions for one hundred days or more before settling (VERON 1995). The ammonoid-coral relationship at Puez lasted several years based on the assumed average

growth rate for solitary corals. Dome and plate corals show radial growth rates from 0.5 to 2.0 cm a year (BARNES 1980; DODGE & VAISNY 1980). Growth of the calcium carbonate skeleton is species-dependent and strongly related to physical and chemical environmental variables such as water temperature, oxygenation, light intensity and sediment input. This peculiar community died after a few years.

The coral larvae apparently had no preference with regard to shell shape or morphology (e.g. ribbing or smooth). They settled on any hard and sediment-free substrate. Thereafter, their attachment surface contoured the morphology of the ammonoid shell (Text-fig. 6 and Pls 1-3). The position of the corals shows that settlement occurred near the aperture but always on the lateral side, which was the most elevated part.

## CONCLUSIONS AND RESULTS

Exact stratigraphic dating of the ammonoid fauna from the Puez section additionally revealed the Valanginian to Aptian age of the encrusting corals and the autecological history of this new Cretaceous ammonoid/coral community

Nine different genera comprising ten species were encrusted by the solitary coral ?*Cycloseris* sp.: *Phylloceras thetys*; *Phyllopachyceras infundibulum*; *Phyllopachyceras bontshevi*, *Lytoceras subfimbriatum*, *Leptotetragonites honnoratianus*, *Silesites vulpes*, *Melchiorites cassioides, Barremites psilotatus*, *Crioceratites krenkeli*, and *Ancyloceras matheronianum*.

A Cretaceous community comprising ammonoids and attached solitary corals is described for the first time. The encrustation of only one side of the phrag-
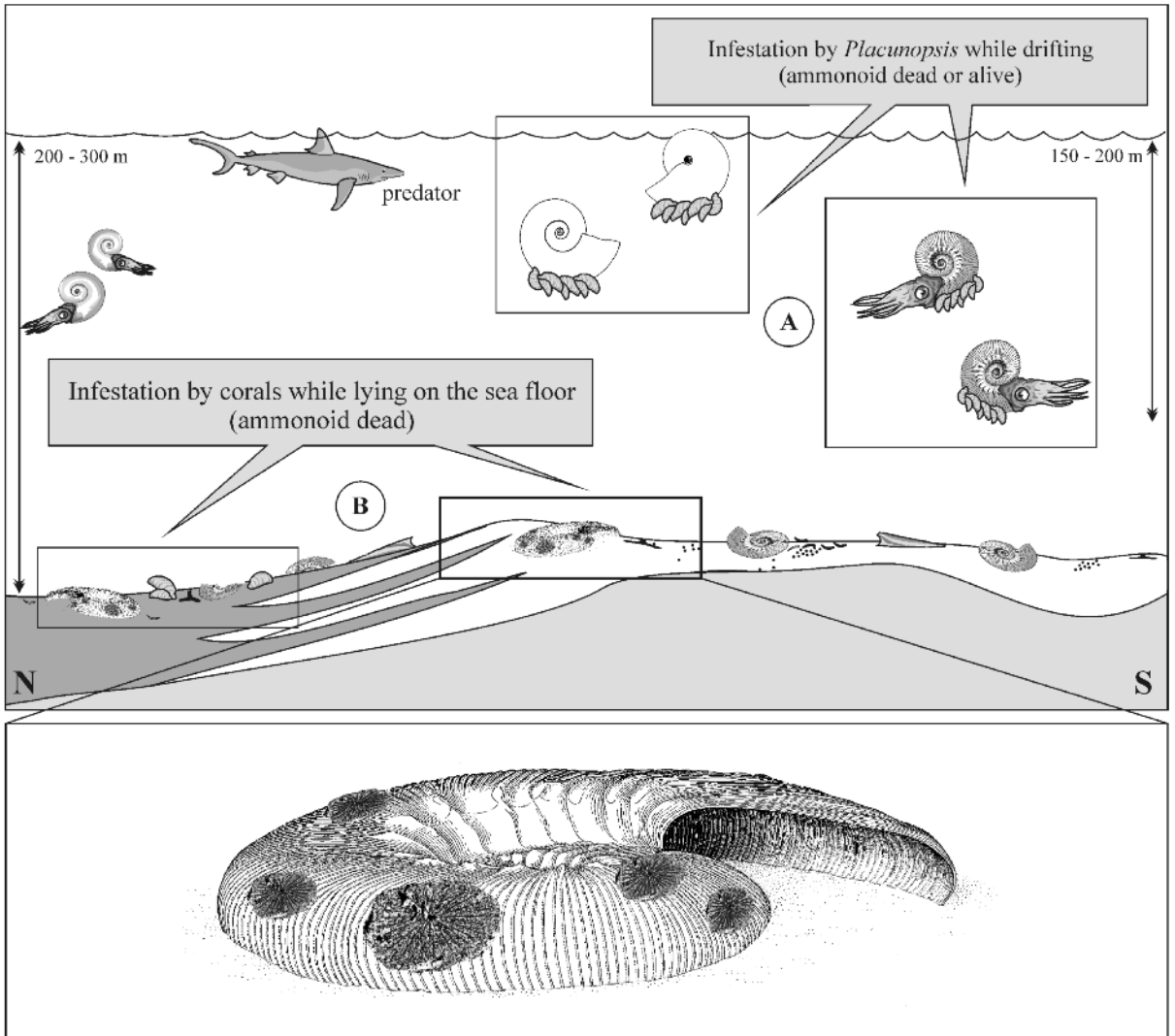


Fig. 6. Reconstruction to show infestation of living or dead ammonoid shell by bivalve *Placunopsis* in water column (A) and infestation by corals of shells of dead ammonoids lying on sea floor (B). Inset shows position of coral specimens on the 'sediment-free' upper parts of ammonoid shells

mocone and the body chamber is evidence for a post-mortem settlement of the corals. ?*Cycloseris* sp., an attached, sessile scleractinian coral, is the predominant encrusting organism. The coral-ammonoid association occurred in deep water settings. The empty ammonoid shells were the only host-islands for settling coral larvae. The coral larvae took advantage unselectively of the most common hard substrate on the muddy surface, the dead ammonoid shells. The ammonoid shells were deposited on the sea-floor, providing a habitat for corals and, to a lesser degree, for serpulids. The ammonoid shells represented benthic islands and opportunities for inhabitation. The shells were ultimately covered by sediment, killing the assemblage and preserving it on the deeper shelf or upper slope.

## Acknowledgements

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# Appendix

Measurements of ammonoid specimens that display infestation. Numbers correspond to individuals. Abbreviations: p, preservation; pos., positive; neg., negative; f, fragment; -, bad preservation, +; well preserved; d, diameter; wh, whorl height; wb whorl breadth; u, umbilicus; c, coral ?*Cycloseris* sp.; cd coral diameter; s, serpulid; Pl., Fig., location of the specimens on plates 1-3 and figure 5. st stratigraphical range of the encrusted ammonoids. Val. Valanginian, Haut. Hauterivian, Barr. Barremian, Apt. Aptian.

| specimen | p. | d | wh | wb | u | c | cd | s | Pl., Fig. | st |
|---|---|---|---|---|---|---|---|---|---|---|
| *Phylloceras thetys* PZO-P23 | - neg. | 104 | 59 | - | 5 | 1 | 38 | - | 1, 1 | Val. |
| *Phylloceras thetys* 2006z0342/0001 | - f neg. | 100 | - | - | - | 1 | 29 | - | 1, 2 | Val. |
| *Phyllopachyceras infundibulum* 2006z0342/0002 | + pos. | 99 | 56 | - | - | 1 | 15 | - | 1, 3 | Haut. - Barr. |
| *Phyllopachyceras infundibulum* PZO-CP112 | + f pos. | 77 | 47 | - | 5 | 1 | 14 | - | 1, 4 | Haut. - Barr. |
| *Phyllopachyceras bontshevi* 2006z0342/0003 | +/- f pos. | 70 | 70 | - | - | 1 | 12 | - | 1, 5 | Barr. |
| *Lytoceras subfimbriatum* 2006z0342/0004 | - f pos. | 119 | 55 | 25 | - | 1 | 23 | - | 1, 6 | Val. - Barr. |
| *Lytoceras subfimbriatum* 2006z0149/0001 | - neg. | 85 | 28 | - | 23 | 1 | 30 | - | 1, 7 | Val. - Barr. |
| *Silesites vulpes* 2005z0245/0041 | + pos. | 83 | 25 | - | 33 | 1 | 25 | - | 1, 8 | Barr. |
| *Silesites Vulpes* PZO-CP91 | - neg | 70 | 22 | - | 34 | 3 | 15-18 | 1 | 1, 9 | Barr. |
| *Melchiorites cassioides* 2005z0245/0045 | + pos. | 163 | 48 | 25 | 55 | 1 | 28 | - | 2, 1 | Barr. |
| *Melchiorites cassioides* PZO-CP51 | + pos. | 124 | 43 | - | 25 | 1 | 11-15 | - | 2, 2 | Barr. |
| *Barremites psilotatus* 2006z034270005 | + pos. | 46 | 20 | - | 6 | 1 | 22 | - | 2, 3 | Barr. |
| *Barremites psilotatus* PZO-CP22 | - neg. | 58 | 23 | - | 17 | 1 | 5 | - | 2, 4 | Barr. |
| *Barremites psilotatus* PZO-CP400 | + pos. | 38 | 17 | 5 | 11 | 3 | 1-15 | - | Text-fig. 5 | Barr. |
| *Barremites* sp. 2006z0342/0006 | + pos. | 72 | 31 | 11 | 22 | 1 | 18 | - | 2, 5 | Barr. |
| *Crioceratites krenkeli* PZO-P2 | - f neg. | 43 | 18 | - | - | 2 | 10-16 | - | 2, 6 | Haut. |
| *Ancyloceras matehronianum* 2005z0245/0047 | +/- f pos. | 310 | 83 | - | - | 5 | 19-26 | - | 3, 1 | Barr. - Apt. |
| *Ancyloceras* sp. PZO-CP92 | - f neg. | 58 | 44 | - | - | 2 | 9-19 | - | 3, 2 | Barr. - Apt. |
| *indet ammo* 2006z0342/0007 | - f neg. | 33 | - | - | - | 1 | 15 | - | 3, 3 | - |
| *indet ammo* 2006z0149/0001 | - f pos. | 140 | - | - | - | 1 | 43 | - | 3, 4 | - |

PLATE 1

**1** – *Phylloceras thetys* with attached coral, PZO-P23; × 0.5; 1a –enlargement of A1, × 2.

**2** – *Phylloceras thetys* with attached coral, × 0.5, 2006z0342/0001. 2a – enlargement of 2, × 2. 2b – same specimen × 4.

**3** – *Phyllopachyceras infundibulum*, 2006z0342/0002; × 0.5; 3a – enlargement of 3, × 2.

**4** – *Phyllopachyceras infundibulum*, PZO-CP112; × 0.5; 4a – enlargement of 4, × 2.

**5** – *Phyllopachyceras bontshevi*, 2006z0342/0003; × 0.5; 5a – enlargement of 5 × 2.

**6** – *Lytoceras subfimbriatum*, 2006z0342/0004; × 0.5; 6a – enlargement of the attached coral, × 2.

**7** – *Lytoceras subfimbriatum*, 2006z0149/0001; × 0.5; 7a – enlargement of 7, × 2; 7b – coated with ammonium chloride.

**8** – *Silesites vulpes*, 2005z0245/0041; × 0.5; 8a – enlargement of the attached coral × 2.

**9** – *Silesites vulpes*; × 0.5; 9a – enlargement of 9, × 2; 9b – enlargement of the attached coral, × 2.

PLATE 2

**1** – *Melchiorites cassioides* with attached coral, 2005z0245/0045; x 0.5; 1a – enlargement of the coral traces on positive ammonoid specimen, × 2; 1b – front view of same specimen, × 0.5; 1c – positive coral specimen in the negative of the ammonoid, 2006z0149/0003, × 2.

**2** – *Melchiorites cassioides* with attached corals, positive, PZO-CP51; × 0.5; 2a – negative of the same specimen, × 0.5; 2b – enlargement of the coral traces on positive ammonoid specimen, × 2; 2c – coated specimen.  [2 looks like a negative and 2a a positive]

**3** – *Barremites psilotatus* with attached coral, 2006z0342/0005; × 0.5; 3a – enlargement of 3, × 3; 3b – enlargement of the attached coral, × 2; 3c – lateral view of coral disc, × 3.

**4** – *Barremites psilotatus* with attached coral, PZO-CP22; × 0.5; 4a – enlargement of 4, × 4.

**5** – *Barremites psilotatus* with attached coral, 2006z0342/0006; × 0.5; 5a – enlargement of 5, × 3.

**6** – *Crioceratites krenkeli* with attached coral, PZO-P2; × 0.5; 6a and 6b – enlargement of 6, × 2.

## PLATE 3

**1** – *Ancyloceras matheronianum* with attached corals, 2005z0245/0047; × 0.5; 1a and 1b
– enlargement of 1, × 2.

**2** – *Ancyloceras* sp. with attached coral, PZO-CP92; × 0.5; 2a – enlargement of the coral
on negative ammonoid specimen, × 2.

**3** – indet. ammonoid specimen with attached coral, 2006z0342/0007; × 0.5; 3a and 3b –
enlargements of 3 (3b coated), × 2.

**4** – indet. ammonoid specimen with attached coral, 2006z0149/0001; × 0.5; 4a – en-
largement of 4, × 2.

1a

1a

1b

2a

1b

3

2

3a

3b

4

4a