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SYNECOLOGY OF AN UNUSUAL LATE CRETACEOUS INOCERAMID-SPONDYLID ASSOCIATION FROM NORTHERN ITALY (*)

Abstract - ANNIE V. DHONDT & IGINIO DIENI - Synecology of an unusual Late Cretaceous inoceramid-spondylid association from Northern Italy.

A large specimen of the Santonian inoceramid *Cladoceramus undulatoplicatus* (F. ROEMER) was found in the Scaglia Rossa Veneta formation at Passo del Brocon, Trento, N. Italy. Both valves of this inoceramid are covered with numerous iso-oriented specimens of *Spondylus fimbriatus* GOLDFUSS. The distribution of the spondylids is explained by the upright position of the living inoceramid specimen.

Key words: Bivalvia, Inoceramidae, Spondylidae, Santonian, Northern Italy, Palaeoecology.

Riassunto - ANNIE V. DHONDT & IGINIO DIENI - Sinecologia di una inconsueta associazione inoceramo-spondili nel Cretaceo superiore dell'Italia settentrionale.

Nella Scaglia Rossa Veneta di età santoniana di Passo del Brocon (Trento) è stato rinvenuto un grande esemplare di *Cladoceramus undulatoplicatus* (F. ROEMER). Entrambe le valve di questo inoceramide sono rivestite di numerosi esemplari isorientati di *Spondylus fimbriatus* GOLDFUSS. La distribuzione degli spondilidi permette di ipotizzare per l'inoceramide una posizione di vita verticale.

Parole chiave: Bivalvia, Inoceramidae, Spondylidae, Santoniano, Italia settentrionale, Paleoecologia.

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Introduction

When studying the ecology of organisms extinct to-day it is often difficult to understand their life habits. The material available generally represents taphocoenoses rather than biocoenoses. Functional morphology or synecological analysis can be used to interpret the possible life position of such extinct animals.

Palaeoecological aspects of life habits of inoceramids have been discussed by several authors [f.i. Hauff (1921), Seilacher & Westphal (1971), Sellwood in McKerrow (1978), Brenner & Seilacher (1978), Tanabe (1983) for Early Jurassic assemblages, Kauffman (1967, 1975, 1978), Kennedy in McKerrow (1978), Hattin (1982), Hessel (1988) for Cretaceous faunas]. Depending on the inoceramid groups different positions have been suggested varying from semi-infaunal [*Mytiloides* spp. (Kennedy in McKerrow, 1978) and even possibly *Sergipia* (Hessel, 1988) in Turonian beds], to pseudoplanktic [easily accepted for larvae as suggested by Kauffman (1978) but less easily understood for the Early Jurassic *Inoceramus dubius* as suggested by Hauff (1921) and others].

Generally most inoceramids are considered to have been byssally attached epifaunal bivalves, such as f.i. the Albian *Birostrina* species or the Cenomanian *Inoceramus crippsi*.

During the Late Cretaceous some inoceramids reached a very large size, frequently with heights of 70-100 cm, especially among species belonging to the genera *Platyceramus* and *Cladoceramus*. The only possible way of life for these bivalves must have been benthic. Their exact life position should be deduced from the distribution of the epibionts which were cemented to the shell when the animal was alive. In the present paper the interpretation of the probable life position of *Cladoceramus undulatoplicatus* is based on a specimen which has numerous spondylids attached on both valves.

Material

Late Cretaceous sediments in the Trento area (N. Italy) are represented by pelagic limestones belonging to the formation generally known as Scaglia Rossa Veneta, a strongly oxygenated sediment deposited according to Bosellini *et al.* (1978, p. 935) at depths extending probably from 400 to 700 m. The Scaglia Rossa is characterised by rich assemblages of planktic foraminifers. Macrofossils on the other hand are rare; echinoids and often fragmentary inoceramids are most frequently quoted. The discovery of a large specimen of *Cladoceramus undulatoplicatus* (F. Roemer, 1849) not far from Passo del Brocon (Fig. 1) was

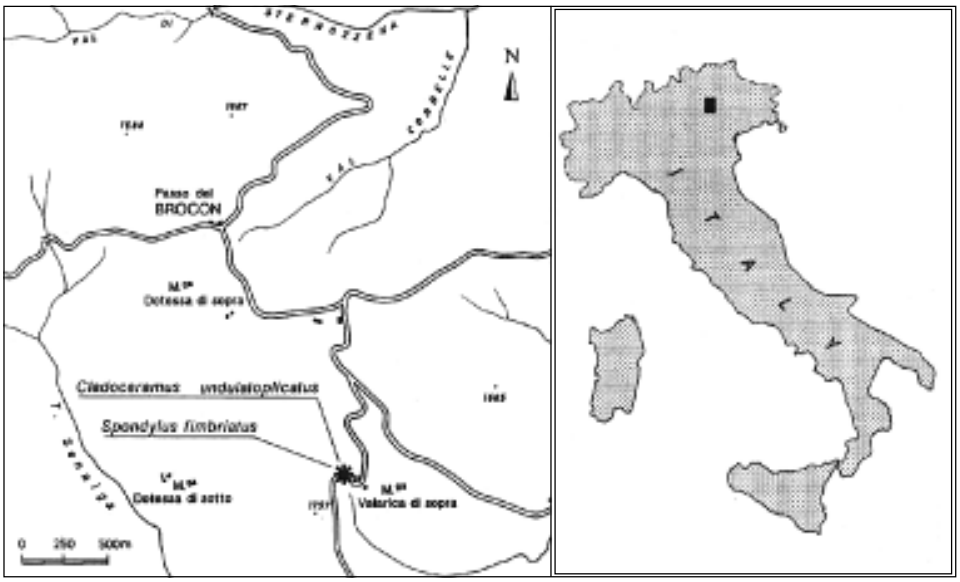

Fig. 1 - Geographic location of the Passo del Brocon area (Trento, N. Italy).

therefore not without importance. The specimen is bivalved, articulated but not complete, and it may have been somewhat compacted. Near it several large fragments have also been found.

The analysis of the planktic foraminiferal assemblage from the matrix indicated the base of the *Dicarinella asymetrica* Zone, corresponding to an Early Santonian age, which confirms that indicated by the inoceramid.

After preparing the specimen it turned out to be covered with many spondylid right valves belonging to *Spondylus fimbriatus* GOLDFUSS, 1835, cemented on it. Also numerous borings made by acrothoracican cirripeds (referable to the ichnogenus *Rogerella* SAINT-SEINE, 1951) are visible.

These synecological facts made us reassess earlier palaeoecologic interpretations of the life position of *Cl. undulatoplicatus*.

DISCUSSION

The *Cladoceramus undulatoplicatus* specimen from Passo del Brocon carries numerous epibiontic specimens of *Spondylus fimbriatus* (Fig. 2) and borings of acrothoracican cirripeds assignable to the genus *Rogerella* SAINT-SEINE, 1951 (Fig. 3).

The spondylids are not distributed randomly. They were found on

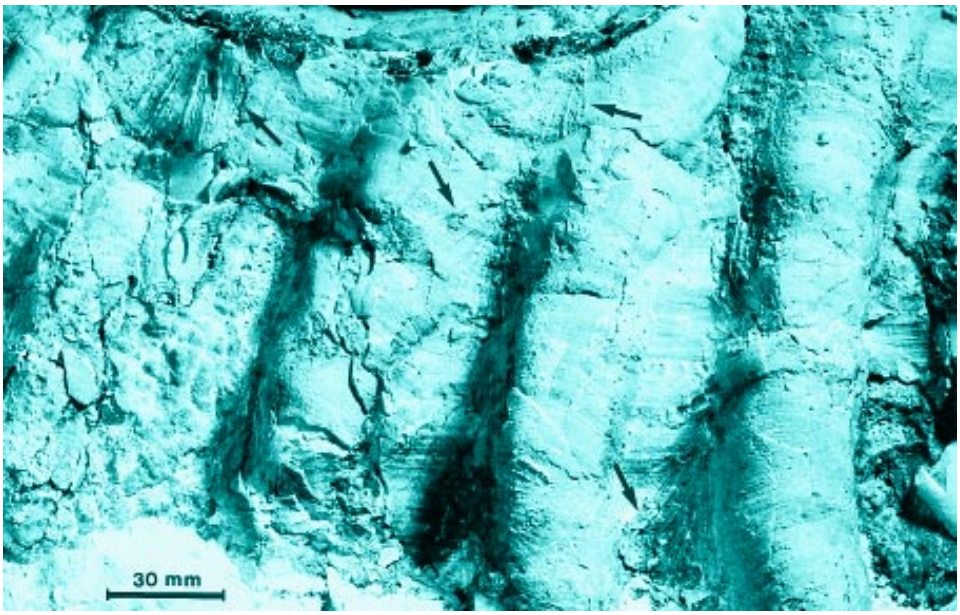

Fig. 2 - Partial view of left valve of *Cladoceramus undulatoplicatus* (F. ROEMER) from Scaglia Rossa, Lower Santonian of Passo del Brocon (N. Italy). The orientation and distribution of the epibiontic *Spondylus fimbriatus* GOLDFUSS specimens (arrows) are visible. Note that the umbo-ventral axis of the spondylids is, as a rule, parallel to the folds of the inoceramid, and located in the intercostal furrows. (Dipart. Geol. Paleont. Geofis. Univ. Padova, n° 26676).

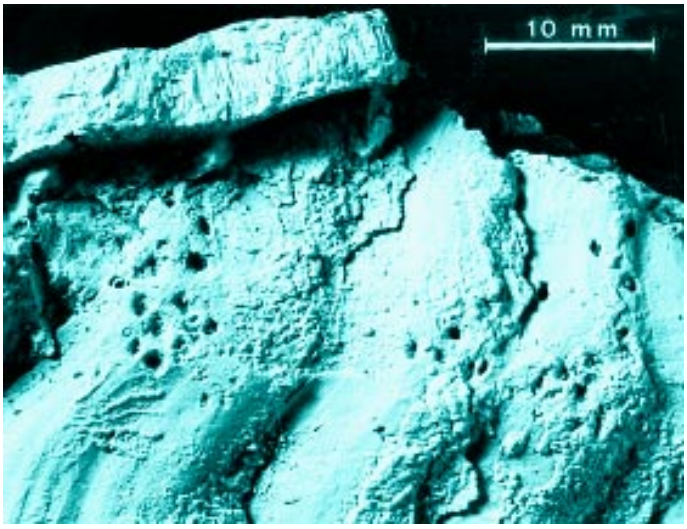

Fig. 3 - Borings of acrothoracican cirripeds assignable to the ichnogenus *Rogerella* SAINT-SEINE on a valve of *Cladoceramus undulatoplicatus* from Scaglia Rossa of the Passo del Brocon area (Trento, Italy). An incomplete cemented small right valve of the epibiont *Spondylus fimbriatus* GOLDFUSS is also visible. (Dipart. Geol. Paleont. Geofis. Univ. Padova, n° 26678).

the external side of *both* valves, mainly located in the radial furrows between folds of the inoceramid shell. Their umbones are generally oriented towards the axial line of the inoceramid on its left as well as on its right valve (Fig. 4).

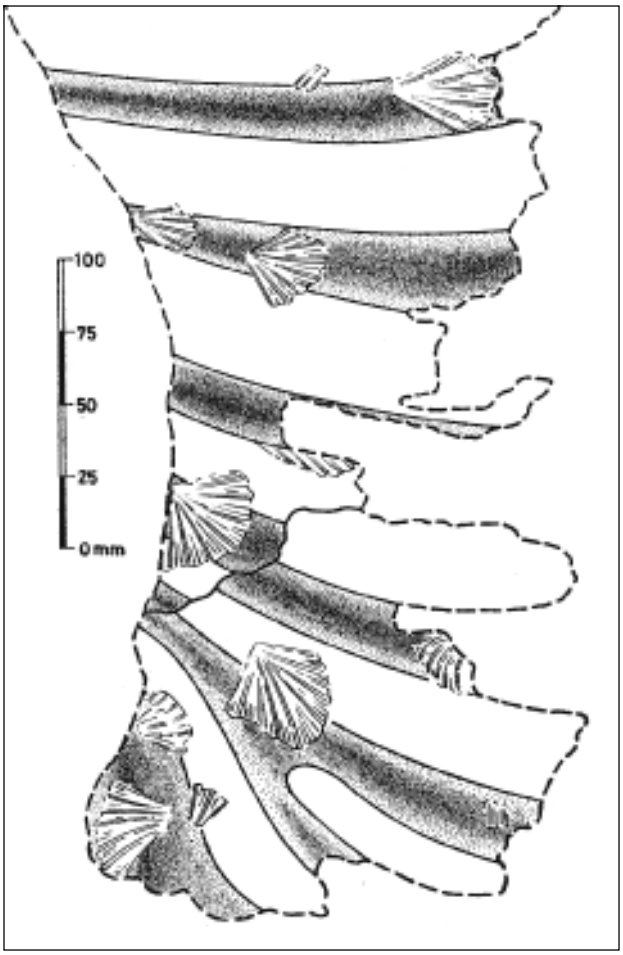

Fig. 4 - Sketch showing the position of right valves of *Spondylus fimbriatus* GOLFUSS cemented to the external side of a left valve of *Cladoceramus undulatoplicatus* (F. ROEMER). Note that the spondylid specimens are located mainly in the intercostal furrows of the inoceramid (in grey) and that they are oriented with their umbo-ventral axis pointed towards the axial line of the host.

Epibionts on Cretaceous inoceramids are not infrequent: oysters, serpulids, boring and pedunculate cirripeds and foraminifers are often mentioned in literature. Only STOLICZKA (1871, p. 447, pl. 33, fig. 5a) mentioned a spondylid valve (*Spondylus arrialoorensis* STOLICZKA, 1871) attached to a fragment of inoceramid.

The most spectacular inoceramid epibiont is seen in the mass occurrence of the oyster *Pseudoperna congesta* (CONRAD in NICOLLET, 1843) cemented on f.i.

Platyceramus platinus (LOGAN, 1898) found frequently in the Smoky Hill Chalk Member, Niobrara Formation (Coniacian-Campanian), in the Western Interior (Kansas-New Mexico-Colorado) (see f.i. BOTTJER *et al.*, 1978).

The life position of large inoceramids has been discussed by KAUFFMAN (1967) and by HATTIN (1982).

– KAUFFMAN (1967, p. 132) interpreted *Inoceramus platinus* and '*Actinoceramus*' *undulatoplicatus* as follows: «These inoceramids must have occupied very soft carbonate substrate where the large area and the light weight of the valves would be adapted to a prone habit on the mud, lacking strong byssal attachment, without sinking in far enough to cover the feeding margin. Radial folds in *Actinoceramus* would further adapt the shell to this habitat. Dense epizoan encrustation normally restricted to the surface of the right valve supports this interpretation of living orientation,…».
– HATTIN (1982, p. 74) re-described the Smoky Hill Chalk Member in Kansas and discussed the palaeoecologic implications of its faunas with particular emphasis on the epibionts of several species of inoceramids. He found numerous articulated specimens of *Platyceramus platinus* [a very large (up to 2 m in diameter) flat, smooth and thin-shelled species] with *Pseudoperna congesta* incrustations on *both* its left and right valves. He excluded the possibility that the inoceramids lived suspended byssally from floating objects such as logs, and concluded (*op. cit.*, pp. 72-75) that *Platyceramus platinus* was «… flat on the sea floor and … colonized simultaneously on both upper and lower valves», and further he specified that «… when deposited the chalk-forming mud initially consisted mostly of water, so that oysters facing downward into the mud actually lived in a predominantly aqueous environment». Such a life position is considered possible by HATTIN because, following the theory substantiated by THAYER (1975), *Pl. platinus* is interpreted as having a «snow-shoe» shape, and could more or less float on the chalk-ooze with its commissural plane oriented horizontally to allow filter feeding.

We have tried to compare these interpretations with the facts which can be gleaned from the Passo del Brocon *Cladoceramus undulatoplicatus* material. In Table 1 a list of characteristics of *Cl. undulatoplicatus*, *Platyceramus platinus* and their epibionts is given.

From these facts we infer that a prone life position for *Cladoceramus undulatoplicatus*, mentioned explicitly by KAUFFMAN (1967) and inferred by HATTIN (1982), does not explain in a totally satisfying way the Scaglia Rossa occurrence because:

1. It is improbable that spondylids could have survived living in the ooze underneath the inoceramid: such an environment must definitely have lacked proper oxygenation. Further, according to CARTER (1972) spondylids in the Chalk lived with the right valve underneath the left valve. A prone position of the

TABLE 1: COMPARISON OF INOCERAMIDS AND SOME OF THEIR EPIBIONTS

	Cl. undulatoplicatus	*Pl. platinus*
Size	– large	– large-very large
Shape	– submytiliform-elongate	– subcircular
Umbonal area	– inflated – thick shelled	– flat – thin shelled
Shell	– folded; away from umbo: thin	– smooth; thin, all over the disk
Substrate	– calcareous ooze	– calcareous ooze
Ornamentation	– commarginal, radial	– commarginal
Epibionts	– spondylids – on both valves – iso-oriented axially – specimens isolated	– oysters – on both valves – oriented near the valve margin only – specimens crowded
Environmental requirements of epibionts	– oxygenated water, above the ooze	– any substrate, possibly in the ooze

inoceramid would mean that the spondylids fixed on its «lower» valve (below the interface water/sediment) would have had their left valve underneath the right one, which is unlikely.

2. If the inoceramid specimen was in a prone position when the spondylids colonized it, the logical place for them to cement to, in order to avoid the mud turbidity, would have been the top of the ribs of its upper valve, and not the bottom of the intercostal furrows as is the case in the Passo del Brocon specimen. Furthermore, these spondylids are placed in the same orientation and position on both inoceramid valves and thus must have lived at the same moment. This excludes the possibility that the spondylids colonized first one valve of the inoceramid, and after overturning it, the second valve of the same living specimen.

3. The shape of *Cladoceramus undulatoplicatus* makes «floating on the mud» difficult to understand in as far that this elongate species did not have an almost equally distributed density as one could imagine to have existed for *Platyceramus platinus*. The heavy hinge-umbonal area of *Cl. undulatoplicatus* was certainly of a much higher relative bulk density than the ventral marginal areas. The «box-effect» on the anterior margin in young shell stages (DHONDT & DIENI, 1990, p. 163) would have enhanced the top-heavy situation which is somewhat contradictory to a floating life position. The deep folds of the adult shell probably strengthened it and made its surface relatively more extensive, but did not de-

crease its density. Relatively, the strongly ribbed and submytiliform *Cl. undulatoplicatus* shell would have been very easily transported by currents, much more so than the very flat and subcircular *Pl. platinus* shells, which certainly also had a very low density.

Differently than the spondylids, the acrothoracican cirriped borings (*Rogerella*) which are present in great numbers (randomly distributed, but clustered in certain areas) on the Passo del Brocon material do not give indications towards the life position of the *Cladoceramus undulatoplicatus* specimen. Their settling undoubtedly followed the death of the inoceramid: they are found on only one valve (the valve which was not hidden by sediment) and then mainly on the most elevated part of the folds. Further they can be seen on the internal side of right valves of *Spondylus fimbriatus*, which means that the cirripeds bored these valves after their disarticulation.

Conclusions

Taking into account the facts discussed above, we consider that a prone life position is unlikely for *Cladoceramus undulatoplicatus*. A different, erect, partly semi-infaunal way of life is more logical because in *Cl. undulatoplicatus*:

1. The heavy umbonal area and box-like antero-dorsal part could have functioned as an anchor in addition to a possible byssal attachment.

2. The radial diverging folds, weakening in the direct vicinity of the ventral margin, are possibly analogous in function to the ribs and spines on recent *Pinna* and *Atrina* species. Especially in its young stages, the cross-section of *Cl. undulatoplicatus* is lenticular as in pinnids.

An erect life-position is the only one we can think of which explains the position of the spondylids. Their symmetrical settling on the inoceramid shell would have allowed them to live in a favourable environment, improved probably by small currents resulting from the pattern of the inoceramid shell folds. In other words, the location (mainly restricted to the deep radial interspaces) and the preferential orientation of the spondylids relative to the commissure of the inoceramid host (dorso-ventral axis parallel to the folds and umbones pointed at the axial line of the inoceramid) suggest, in the inoceramid host as well as in the epizoic spondylids, rheotropism. This is growth in the direction of the approaching currents so as to maximize feeding efficiency.

A *Pinna*-like life position requires a covering with epibionts mainly on the upper (i.e. posterior) part of the shell only. This is the part which was above the water/mud interface when the animal was alive (Fig. 5).

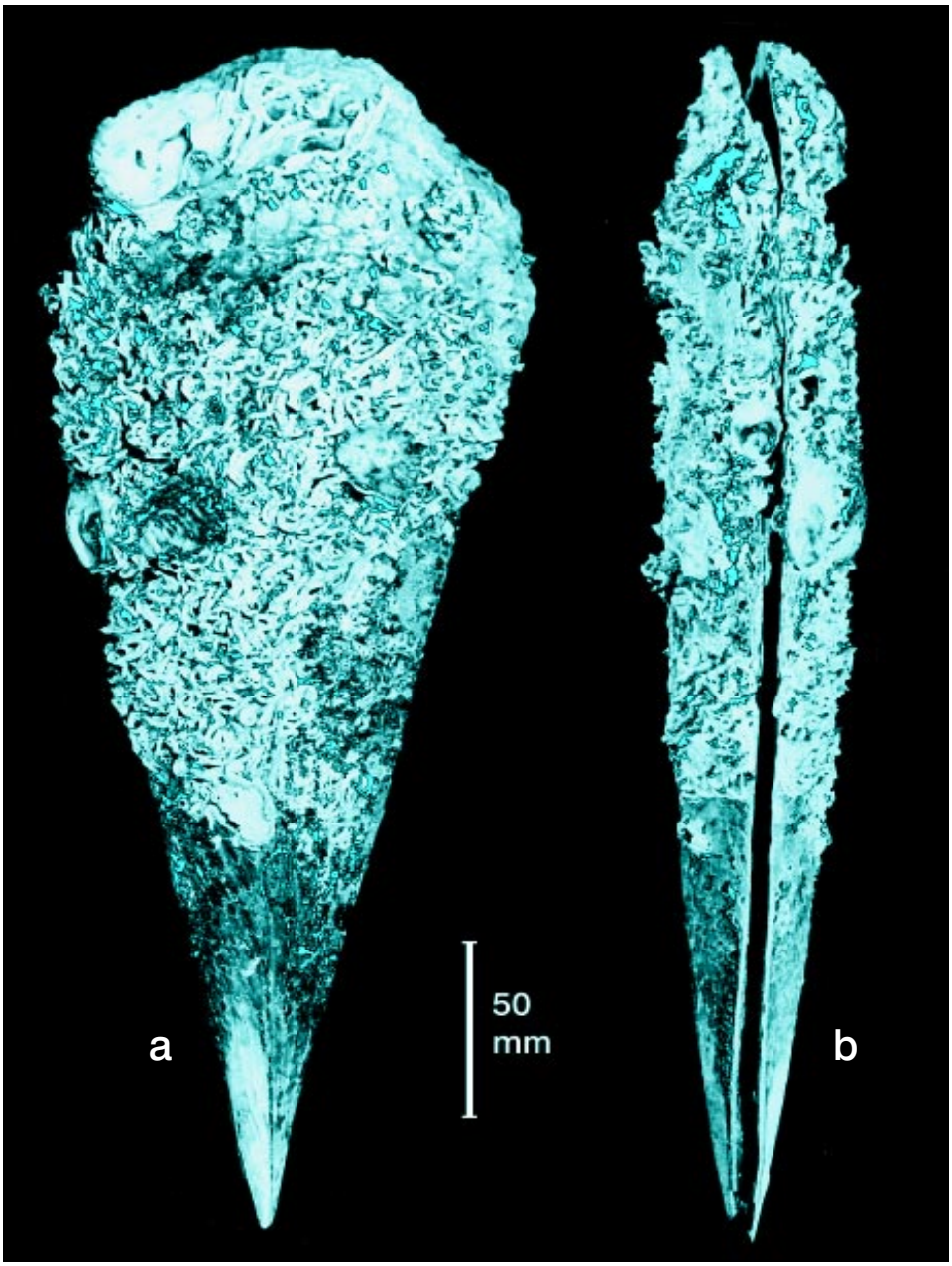

Fig. 5 - *Pinna nobilis* Linné. Right valve (a) and ventral (b) view of an articulated specimen (in life position) totally encrusted by serpulids, balanids and oysters except at the pointed anterior end, which was buried in the sea bottom. Recent, Adriatic Sea. (Dipart. Geol. Paleont. Geofis. Univ. Padova, n° 26683).

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