Taphonomy and palaeoecology of the holotype of *Heterodelphis leiodontus* PAPP, 1905 (Cetacea, Mammalia) from Szentmargita (St. Margarethen, Austria)

by

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Abstract — Investigation of the type specimen of *Heterodelphis leiodontus* PAPP, 1905 and the embedding Leithakalk yielded a taphonomic model and a paleoenvironment reconstruction.

Preservation of an articulated skeleton is exceptional for the Leithakalk. After death the studied specimen underwent rapid burial caused by sudden sediment redeposition, probably due to stormy water movements. The burial took place in a shallow, euphotic, nearshore marine environment. The sediment was coarse, calcareous sand composed mainly of red algal grains. We suppose that fragments of coralline algae have originated from maerl while other microfaunal elements have been transported from a sea-grass meadow community. Reefs were not present in the close vicinity.

Keywords — Miocene, Badenian, Leithakalk, Paratethys, St. Margarethen (Austria), taphonomy, paleoecology, Odontoceti, Heterodelphis

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Introduction

The present paper addresses the taphonomy of a dolphin skeleton that is the holotype of the extinct species *Heterodelphis leiodontus* PAPP, 1905 and gives a reconstruction for the habitat the studied specimen lived in. The fossil skeleton in question is well-known and one of the most famous odontocete remains from the Miocene of Middle Europe (e.g. KELLOGG, 1927; MÜLLER, 1970).

The skeleton was found in the Leithakalk (Leitha limestone, Rákos Formation in Hungary) of Szentmargita (= Szentmargitbánya, today: St. Margarethen) in the Ruster Bergland, close to the Leitha Gebirge (Leitha Mts., Burgenland, Austria) in 1880. The original description (PAPP, 1905) does not give us any clue to retrace the exact location where the fossil remains were excavated. Three quarries expose similar limestones to those preserved with the studied skeleton: the "Hummel" and Roman quarries are located on the north side of the road leading from St. Margarethen to Rust, the "Kummer" quarry is situated on the opposite side of the same road. The skeleton originates most probably from the Roman quarry (Figure 1, A), since limestone had already been exploited in this quarry by the time of the dolphin's discovery.

DULLO (1983, Fig. 5; and Figure 1: B hereby) published a stratigraphic section from the "Hummel" quarry. This section is typical for the Leithakalk in the area. Since the stratigraphic column shows cyclic repetition of five different microfacies types, the origin of the limestone block that yielded the dolphin skeleton cannot be determined. According to DULLO (1983), the stratigraphically younger part of the section is characterised by caliche-like crusts and fine-laminated marls deposited in restricted lagonal environments. He also observed meniscus and dripstone cements referring

to cementation in vadose environment due to early subaerial exposures of the carbonate sand succession. The primary marine cementation was weak, only thin micritic cement is present.



Figure 1 — A: Map showing the locality where the type specimen of *H. leiodontus* was most probably found. B: Lithologic section from the Hummel quarry of St. Margarethen (redrawn after DULLO, 1983). Original position of the limestone bed yielding Ob-258 cannot be determined in the section. The Leithakalk is well known from the Middle Miocene of Austria and Hungary. The Leithakalk of the Ruster Bergland deposited during the Middle Badenian (Sandschaler Zone), the Buliminen–Bolivinen Zone is only represented in the upper layers of the limestones around St. Margarethen (FUCHS 1965).

The depositional environment of the Leithakalk usually was composed of diverse shallow-water and nearshore facies types in patchy, mosaic-like distribution. The local bottom topography caused variable water energy conditions that led to the development of diverse facies types and deposition of different sediments (HÁMOR 1970, 1985). NÉMETH (1999) recognised maerl, calcarenite and rhodolitic Leithakalk types in the subsurface succession of the Ortaháza region (SW Hungary).

Miocene carbonate sediments in Central Europe have traditionally been regarded as indicative of a tropical-subtropical depositional environment (HÁMOR 1985). LELKES & STUDENCKI (1990) and RANDAZZO et al. (1999) suggested more temperate climatic conditions for the Badenian age based on the low diversity of hermatypic corals, lack of calcareous green algae, abundance of a foramol biological association dominated by red algae, and other peculiarities. As CARANNANTE et al. (1988) pointed out, "foramol-type sediments are very abundant on temperate shelves, but they also are present in shallow tropical or subtropical waters where reef corals and calcareous green algae are not developed because of particular environmental or ecological conditions". According to DULLO (1983), the

The type specimen of *Heterodelphis leiodontus* (Inv. number: Ob-258, Geological Museum of the Geological Institute of Hungary, MÁFI) lying on two limestone blocks was used for the study.

The embedding limestone was split into two parts during excavation, breaking the dolphin skeleton approximately along the mediansagittal plane (Plate I: A). As a consequence, the skeleton lies on two halves of the limestone block that complement each other (table 5 and 6 in PAPP 1905). This resulted in the unfavourable condition of most intact bone surfaces being covered by the embedding limestone. Thus, all vertebrae and the right flipper bones exhibit their outlines only. Since the breakage of the skeleton did not occur accurately along the mediansagittal plane (as concluded e.g. from the condition of the skull), intact bones are expected inside the limestone. The distal part of the rostrum, the complete caudal region of the vertebral column, "foraminiferal debris facies types" of St. Margarethen area were formed in a shallow-water environment without reefs.

The Vienna Basin, along with the rest of the Paratethys, underwent a complex tectonic history (FODOR 1995); extensive volcanic activity and regional current system changes characterised the region in the Middle Miocene (RANDAZZO et al. 1999). In the Middle Badenian the Central Paratethys retained a marine connection with the Mediterranean through the "Trans-Tethyan-Trench-Corridor" in today's Slovenia (RÖGL 1998, 1999), which assured normal marine salinity conditions for the Vienna Basin and the entire Central Paratethys. In the Vienna Basin marked facies differentiation took place during the Early Badenian: Baden clay deposited in the basinal part and Leithakalk developed as marginal sediments (TOLLMANN 1955). Extensive carbonate platforms could not be formed due to environmental constraints; smaller marine basins were depositional sites instead (RANDAZZO et al. 1999). Fluvial sediments were transported into the Vienna Basin through smaller deltas in the west (SAUER et al. 1992). A complex basinal geometry, with narrow straits and bays separated by islands and peninsulas characterised the region by that time (RANDAZZO et al. 1999). According to a conceptual paleoenvironmental reconstruction by RANDAZZO et al. (1999), western Hungarian carbonate basins were characterised by patch reefs and rhodolite pavements seawards, while river deltas and volcanic activity influenced the coastal environment.

Material and Methods

posterior lumbar vertebrae and pelvic bones as well as the sternum are missing. The broken surfaces of the rostrum bones and the posteriormost preserved vertebra are clearly visible on the cutting surfaces of both halves of the limestone block. This indicates that the missing parts were lost during excavation and not during the embedding.

Five thin sections were prepared perpendicular to the bedding. Thin sections No. 1–3 originate from the lower block, No. 4–5 from the upper block, numbered from below. The thin sections were studied under petrographic microscope and cathodoluminoscope. Xray was used to trace bony elements inside the limestone blocks. Stable isotope ratios δ^{13} C and δ^{18} O were measured in two samples taken from the upper and lower part of the upper and lower limestone blocks, respectively.

Results

The skeletal assemblage

Vertical extension of the exposed Leithakalk in St. Margarethen is about 30 m (see lithologic section in Figure 1, after DULLO 1983). Shark teeth, cetacean remains and sirenian rib fragments represent the known

marine vertebrate fauna of the Leithakalk in St. Margarethen. The majority of these fossils consists of inarticulated remains and appears to be randomly distributed in the limestone. Only few articulated dolphin skeleton fragments are known from St. Margarethen, the most complete one being Ob-258. Other Leithakalk occurrences (e. g. in Mátraszőlős, North Hungary) show a similar vertebrate fossil composition and pattern, but have never yielded any articulated skeleton fragments (KORDOS 1978, 1985, KORDOS & SOLT 1984).

In his taxonomic paper PAPP (1905) described the condition of the skeleton in detail. Here we restrict ourselves to a brief description, emphasising aspects that are important for the understanding of the taphonomic processes.

The skeleton is almost complete with exception of both missing ends (as discussed earlier)(Plate I: A). The mandibles are attached to the skull and the right tympanic bone lies approximately on its original place. Although the preserved tympanic bone is fragmentary, its surfaces do not show any signs of weathering or rounding. The periotic bone is not exposed at present, but further preparation may prove its presence. The preserved teeth are difficult to count, it is nevertheless clear that most of the teeth are *in situ*. The brain case is highly compressed, roughly dorsoventrally, as concluded from the dorsally exposed tympanic bone. PAPP (1905) asserted that a hyal bone could also be seen on the smaller block. The present authors cannot confirm the existence of this bone.

All seven cervical and all thoracic vertebrae are in their original position. There is, however, one thoracic vertebra (the ninth, according to PAPP 1905) that is slightly hanging out from the arch of the vertebral column. On the larger block, 6 (7?) lumbar vertebrae can bee seen in articular position. The chest is collapsed and the contacts between the preserved ca. 8 ribs and the corresponding thoracic vertebrae are difficult to interpret. This situation may be a result of the distortions of the ribs, or simply due to the fact that the vertebral processes are very fragmented.

The right scapula and flipper bones (humerus, radius, ulna, carpals, metacarpals and some phalanges of three fingers) are preserved on the larger rock slab (Plate I: A). All flipper bones are in articular position, but the

forelimb and the scapula as a whole are slightly shifted cranioventrally.

Although the humerus can only be seen in longitudinal section, it is clear that the proximal epiphysis was completely fused to the shaft in the living animal. Likewise, fusion of vertebral epiphyses to centra was completed in all preserved regions of the vertebral column. In recent *Stenella*, fusion of the humerus is completed by the onset of sexual maturity (PERRIN 1975). Fusion of vertebral epiphyses to centra progresses from the cephalic and caudal ends of the vertebral column. Fusion of thoracic and lumbar vertebrae is not completed until physical maturity is reached (PERRIN 1975). If the ontogeny of *Heterodelphis* was comparable to that of modern spotted dolphins, then we can assume that Ob-258 was physically mature by its death.

The X-ray failed to confirm the presence of any bone elements inside the limestone blocks. Few other fossils were found in close association with the *H. leiodontus* skeleton. In the upper block, cross-section of a single coral polyp was found. One shell of *Pecten (Chlamys) elegans* (PAPP 1905) is situated in the vicinity of the mandibles. Another bivalve shell is located next to the last rib. Among the ribs, concentration of bony fish remains, vertebrae, fin rays and one fish tooth can be seen (figure 7 in PAPP 1905). According to PAPP, the latter belonged to *Chrysophrys* (=*Sparus*, Sparidae, Perciformes). Found in the posterior area of the chest, this concentration is interpreted as a food bolus (see also PAPP 1905).

No traces of encrusting fauna were found on the skeleton. Neither tooth marks nor other evidence of predator or scavenger action could be identified on the bones. This, however, can be misleading since large parts of the skeleton were cut longitudinally (as discussed earlier). Thus, the majority of the bones exhibits their inner structure only, and not the bony surfaces.

In conclusion, all bones are roughly in articular position. Minor distortions of the preserved ribs and slight dislocation of the right flipper are thought to be due to compression during burial. The same might be true for the vertebral column that exhibits a marked breakage between the 8th and 9th thoracic (or between the last thoracic and first lumbar) vertebrae.

The embedding limestone layers

Macroscopic observations — The embedding Leithakalk block consists of porous calcarenite. The limited dimensions of the rock sample do not allow the recognition of larger sedimentary structures, e. g. cross stratification.

There is a notable grain-size contrast between the lower part of the larger slab and the rest. The boundary of these two rock types is indicated with dashed line in Plate I: B. In the lower part of the thicker and larger rock slab the grains and the open pores are definitely smaller than in the upper part of the slab and in the whole thinner slab. The latter parts consist of significantly coarser grains and contain more and larger pores. Because of the noticeable grain-size and porosity contrast, it is highly possible that here we are dealing with a bedding surface between the top, finer section of the underlying layer and the coarser base of the next layer. The dolphin skeleton lies between the two blocks,





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close to the coarse-grained base of the more porous bed. We conclude that the more porous, thinner rock slab is the stratigraphically younger, upper block and the dolphin lies on its right side. The grain-size contrast of the embedding block suggests a rapid sedimentation event.

Table 1 — Stable isotope ratios of the embedding rock

Sample	δ ¹³ C (PDB, ‰)	δ ¹⁸ O (PDB, ‰)	
St. Margarethen, 1	-2.31±0.05	-5.16±0.11	
St. Margarethen, 2	-2.25±0.11	-5.29±0.07	

Stable isotope investigation — Table 1 shows the stable isotope ratios measured in two samples from the vicinity of the skeleton. The depleted carbon reveals meteoric water influence during diagenesis for both samples. Hence, salinity of the palaeoenvironment cannot be calculated and δ^{18} O values cannot be used for palaeotemperature reconstruction.

Microscopic observations — The majority of the elongated grains lie roughly parallel to the bedding that indicates the lack of strong bioturbation in the vicinity of the dolphin skeleton.

The tendency of increase in grain- and pore-size upwards, observed by macroscopic scale, is clearly visible in the thin sections (Plate I: C, Plate II: D). The grain-size varies between 0.1 and 6 mm. The taxonomic composition of the rock forming flora and fauna is similar in all samples. The bedrock and the overlying sediment represent the same facies type.

DULLO (1983) distinguished 10 Leithakalk microfacies types. Our samples could be best correlated with his "foraminiferal algal debris facies", with minor differences. Our samples contain locally more bryozoa and serpulids, but do not contain any rhodolites and peloids. The investigated material is more porous and less cemented than the "foraminiferal algal debris facies" type of DULLO.

The material is weakly cemented bioclastic grainstone and rudstone, containing no mud at all. Halfquantitative measurement of the main components shows the following distribution: red algae 50-60%, foraminifera 3-5%, fragmented bryozoan colonies 5-10%, bivalve shells 0-2%, echinoid fragments 2-6%, serpulids 0-1%. Very few ostracod shells were found. Micrite mud is absent in the material and there were no peloids observed in the thin sections. Micritic envelope around the bioclastic grains is common. The bioclasts are weakly cemented with the 8-10% calcite.

Table 2 — Foraminifer genera identified from the thin sections and their abundances in t he samples. Ecological preferences are based on MURRAY (1976), typical sediments according to NÉMETH (1999). Uncertain occurrences are not listed. (+ found in one sample only; ++ present in at least two samples; +++ present in all samples but not abundant; ++++ abundant in all samples)

Foraminifer genera	Abundance	Ecological preferences	Typical Leithakalk facies
Asterigerina sp.	++++	shallow, warm waters	?
Elphidium sp.	++++	euryhalin; 1–30°C; 0–50 m depth	maerl
<i>Textularia</i> sp.	+++	normal marine; arctic to tropical; 50–640 m depth	calcareous sand
Lenticulina sp.	++	euryhalin; subtropical; shallow waters	?
Quinqueloculina sp.	+++	mainly normal marine; temperate to tropical; 0-40 m depth	maerl
Spiroloculina sp.	++	euryhalin; subtropical; shallow waters	maerl
Triloculina sp.	+	euryhalin; subtropical; shallow waters	maerl

Explanation to Plate I

- A Ob-258 on the larger rock slab. Sliding caliper open at 50 mm.
- B Dashed line indicates the boundary between the fine grained lower part of the larger slab and the more porous parts. The skeleton lies between the two blocks. Scale bar = 50 mm.
- C General view of the thin section No. 1. The material is weakly cemented bioclastic grainstone. Grain sizes are typically smaller than in the upper part of the embedding b lock. Scale bar = 10 mm

The porosity usually measures 15%, in thin section No. 5 it is as high as 20%. Due to compaction, adjacent grains meet in line contact, collapsed bioclasts (e.g. serpulid tubes) were observed regularly (Plate II: E, F). The flat contacts and collapsed bioclasts suggest postdepositional compaction. The majority of red algal clasts is highly fragmented but well-preserved branch fragments can also be observed. Occasionally red algal aggregates of ca. 10 mm occur, however, rhodolites were not found in the samples. Coralline algae form crusts around bioclasts, competition between algae and bryozoan colonies can be observed.

Foraminifer genera observed in the thin sections are listed in Table 2. All identified foraminifera are benthic forms. All five thin sections showed the presence of miliolinas and agglutinated foraminifers of limited abundance. Only *Asterigerina* and *Elphidium* are present in significant numbers in all samples. The latter genus occurs in a wide range of shelf communities including marginal marine environments (MURRAY 1976). Porcelaneous foraminifers or miliolinas (*Quinqueloculina, Spiroloculina, Triloculina*) are abundant in shallow, subtropical seas and they are tolerant to reduced salt conditions (Ágnes GÖRÖG, pers. comm.). Agglutinated foraminifers (*Textularia*) prefer cold and deeper waters (MURRAY 1976).

In conclusion, the embedding rock of Ob-258 is composed of calcareous remains of shallow-water organisms, mostly corallinacean fragments. The rock texture is grainstone and rudstone. The local bottom was soft uncemented sand. The lack of fine mud refers to deposition under strong current conditions. High porosity and coarse grain-size suggest rapid sedimentation. Algal grains are most probably redeposited fragments of branching colonies. Transportation of the corallinacean segments resulted in grain-sizes transitional between that of the maerl and the calcareous sand. Maerl usually develops at depths of 0-25 m but it is sometimes found at 40 m depth in the Mediterranean (BLANC 1968). Calcarenite forms under less energetic current conditions than maerl. It is possible that a seagrass meadow community was established on the calcareous sand, as concluded from the relative abundance of bryozoas. Sea-grass meadows usually develop on soft bottom in the infralittoral zone (ROS et al. 1985). Micritic envelopes around bioclasts are typical in shallow, euphotic environments.

Diagenesis of the embedding limestone was also studied. Marine isopach rim cement is not present. The occurrence of thin micrite cement can not be excluded. If it is present, it is indistinguishable from the micritic envelope. The first observable cement generation is thin dogtooth calcite. It is common on all surfaces, including the fracture faces of the bioclasts. This fact evidences postcompactional origin. Intragranular drusy cement grows inside of the bioclasts, mostly in the bryozoan chambers. Calcite cement filled the tiny pores of the coralline algae as well (best seen under the cathodoluminoscope). The last generation is the late, postcompaction syntaxial cement around echinoids. There is no vadose cement in the samples. Aragonitic fossils were not found in the limestone. The lack of aragonitic fossils indicates diagenetic dissolution, maybe due to meteoric water influence (see also DULLO 1983). Because no biomold cavities after aragonite shells are present, the dissolution must have been an early diagenetic process.

Under the cathodoluminoscope all cement phases show bright orange luminescence (Plate II: E). The syntaxial, and in some cases, the intragranular cements are slightly zoned, while other cement generations show concordant bright luminescence. The calcite shows luminescence when bombarded with electron beam if Mn²⁺ substitute the Ca²⁺ in the crystal lattice (and no Fe²⁺ is present in the system) (MARSHALL 1988). Bright luminescence of the cement refers to manganese substitution. Hence, reductive conditions during diagenesis are assumed. These observations suggest cementation under meteoric phreatic conditions. This is also supported by the stable isotope ratios. DULLO (1983) observed signs of early meteoric vadose aragonite dissolution and calcite cementation, from which the aragonite dissolution could easily be inserted into the diagenetical evolution of the studied samples.

The diagenetic evolution of the sediment could be drawn as follows. Hypothetical early marine cementation took place at first: micritic or isopach rim cement was formed around the grains. Subsequently, meteoric dissolution erased the marine cement and dissolved the aragonite grains. This was followed by compaction and weak cementation by dogtooth calcite under meteoric phreatic conditions. Finally, intragranular and syntaxial calcite cement appeared in the burial setting.

Explanation to Plate II

- D Large red algal fragments in thin section No. 5. Crossed polarisers. Scale bar equals 10 mm.
- E Thin section No. 1 under cathodoluminoscope. Echinoid spine in scross section inserted between collapsed serpulide tube fragments. Bright luminescent thin dogtooth calcite covers the grains including fracture faces. Scale bar equals 5 mm.
- F Thin section No. 2 under cathodoluminoscope. Bryozoan colony on the right. Thin dogtooth calcite can be observed on the grains including fracture faces and the inside of the theca. Scale bar equals 5 mm.





Discussion

Taphonomy

The condition of Ob-258 refers to an uncommon set of taphonomic factors that led to the preservation of the complete skeleton, exceptional for the Leithakalk.

Unlike representatives of the mysticete family Balaenidae, cetacean carcasses are known to sink immediately after death, but will rise to the surface after the peritoneal cavity becomes bloated with gases of decomposition. Mandibles are soon separated from the skull, and as decomposition progresses, the whole skull is likely to drop from the floating carcass (SCHÄFER 1962). The dangling forelimbs are likely targets for predators or scavengers; vertebrae and ribs drop off separately or in groups. The loosely articulated tympano-periotic complexes are subject to loss.

There are, however, cases when the cetacean carcass does not rise to the surface or it is not floating there for long. In small, enclosed seas or if water currents transport the carcass towards the coastline, stranding of the dead body before disintegration is very likely (SCHÄFER 1962). Cold or anoxic waters can inhibit bacterial action and thus, gases of decomposition do not develop. Also, water pressure could prevent the gases of decomposition from attaining a volume sufficient to lift the carcass (LANCASTER 1986). In extreme situations, the carcass of decomposition to develop. In either of these cases, the carcass would be buried in place and decompose slowly (LANCASTER 1986).

The completeness of Ob-258 attests that it did not undergo long floatation and extensive decomposition at the sea surface. The preservation of the tympanic bone (plausibly the whole tympanoperiotic complex) in original position, and the good condition of the preserved surfaces of the tympanic bone clearly indicate the absence of long exposure before burial. A fast burial is supported by other facts, such as the lack of evidence for an epifauna on the skeleton and the preservation of the stomach content.

Since coastal environment is proposed for the Leithakalk, effects of water pressure are unlikely. Nor can we assume a sufficiently cold environment since cold-temperate (RANDAZZO et al. 1999) or tropical-subtropical (HÁMOR 1985) depositional environments were suggested for the Badenian Leithakalk. The lack of preburial decomposition can not be attributed to anoxic conditions because of the presence of a rich benthic fauna.

It is possible that Ob-258 had risen to the surface after its death, but it did not remain there long. In this case either the plausibly buoyant peritoneal cavity was ruptured by predators or scavengers, or the carcass stranded within few days after death. The first hypothesis would provide a possible explanation for the breakage in the vertebral column, although no other evidence refers to predator or scavenger action, and marine predators (primarily sharks) are not likely to break the victim's backbone. There are no evidences suggesting stranding event and burial in terrestrial environment.

We support the hypothesis that the carcass was buried before gases of decomposition could develop. Either this was the case or rupture of the inflated peritoneal cavity made the carcass sink to the bottom, very fast burial must have taken place. Extensive sediment disturbance or sudden redeposition of an undersea dune, induced by vigorous (stormy) water motion, could have buried the carcass within hours, thus preventing scavengers to scatter the bones and encrusting invertebrates to settle. This hypothesis is also supported by the marked grain-size and porosity contrast of the embedding block. We propose that the carcass was snatched and dropped by stormy water movements. The same event disturbed the soft bottom and transported material along with the carcass. Thus, the body was covered by less compacted calcareous sand than the underlying sediment of the seabed (Figure 2: B and C). The unfragmented bivalve shells could have deposited with the sediment. The overlying sediment pile apparently formed a sufficiently thick layer to prevent bioturbation in the vicinity of the dolphin's slowly decomposing body.

One item of the stomach content could be identified as *Sparus* sp. Recent species of the Sparidae are known to be shallow-water fishes. E.g. *Sparus auratus* does not generally go deeper than 30 m. Groups of this species are usually found over mud or sand. The presence of this fish in the food bolus indicates that the last meal of Ob-258 was acquired in coastal waters (Figure 2: A).

Sedimentation and thus, burial of the carcass in the euphotic zone is also evidenced by the abundance of coralline red algae and the accompanying fauna, e. g. benthic forams, bivalves, echinoids, bryozoas that suggest shallow marine, nearshore depositional environment.

The fact that the stomach of the specimen was not empty by its death indicates that the cause of death was most probably not illness or physical weakness. Predator attack is not supported by evidences.

Paleoecology

Ob-258 died and was buried in a shallow, nearshore marine environment. The presence of close coral reefs can be excluded. Figure 2 provides the taphonomic model of the type specimen of *H. leiodontus* and gives a tentative paleoenvironment reconstruction. The seabed was

coarse calcareous sand consisting of allochtonous corallinacean grains and other biogenic fragments. Red algal grains and part of the microfauna (bryozoas, echinoids, foraminifera such as *Elphidium* and miliolinas) took their origin from a branching calcareous red algal assemblage (maerl) nearby, at a depth of 10–40 m. Other microfaunal elements (*Textularia* sp., some bryozoas and echinoids) probably were transported

from a sea-grass meadow community in the infralittoral zone of the area. We propose that the place of burial was located in greater depth, seawards from these communities.

The results presented in this paper do not allow for paleotemperature reconstructions. Likewise salt conditions where Ob-258 was buried can not be established.



Figure 2 — Taphonomic model and a conceptual reconstruction of the habitat of the type specimen of *H. leiodontus*. A: Last hunt of Ob-258 was performed in the euphotic zone of a nearshore marine environment. The prey was *Spanus* sp. The local bottom was coarse calcareous sand; maerl and sea-grass assemblages were located nearby. B: The cause of death of Ob-258 is unknown. Shortly after the intact carcass sank down, it was completely buried. Extensive sediment disturbance or sudden redeposition of an undersea dune induced by strong water motion could have covered the dolphin's body within hours. C: The overlying sedimentary pile was sufficiently thick to prevent bioturbation around the slowly decomposing carcass.

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