



A Speiballen from the Lower Jurassic Posidonia Shale of South Germany

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THIES, D. & HAUFF, R.B. (2013): A Speiballen from the Lower Jurassic Posidonia Shale of South Germany. – N. Jb. Geol. Paläont. Abh., **267**: 117–124; Stuttgart.

Abstract: A Speiballen (regurgitated compacted mass of indigestible stomach contents) from the Lower Jurassic Posidonia Shale of Ohmden, South Germany contains remains of four specimens of the actinopterygian *Dapedium* sp., the specific identity of which remains obscure, and a lower jaw of a specimen identified as *Lepidotes* sp. A list of five suitable characters is proposed to distinguish fossil Speiballen containing specimens from other vertebrate fossils. Large, potentially piscivorous animals in the Posidonia Shale ecosystem comprise chondrichthyans (*Hybodus*), other actinopterygians (pachycormiforms) and marine reptiles (crocodilians, ichthyosaurs, plesiosaurs). Only juvenile ichthyosaurs (*Stenopterygius*) are known to have preyed on *Dapedium*. Available data are, however, insufficient to clearly identify the Speiballen producer. The heavy scale armour of basal neopterygians such as *Dapedium* undoubtedly hampered digestion of these fishes and in this way provided additional protection against predators.

Key words: Jurassic, Fossilagerstätte, Holzmaden, ecosystem, predation.

1. Introduction

Speiballen are understood to be regurgitated compacted masses of indigestible stomach contents. They are released in the form of gastric pellets through the pharynx in contrast to faeces that represent intestinal contents that are excreted through the anus. Speiballen mostly contain indigestible remains of organisms caught and eaten by predators, such as bones, fur or feathers left over in the crop or stomach after other softer components of a prey are macerated and digested. In the fossil record they form together with coprolites and fossilised intestinal fillings a useful source of information on the diets of fossil animals and can thus be used to reconstruct food chains. A precise

English equivalent of the German term ‘Speiballen’ (or ‘Gewölle’, which means the same) does not seem to exist. BURROW & TURNER (2010) described an assemblage of skeletal element, tooth whorls and scales of the acanthodian *Nostolepis scotica* from the Early Devonian of Scotland comparable in terms of taphonomy and preservation to the *Dapedium* specimens 2 and 3 in our fossil as a regurgitate, however, without giving reasons for their view. POLLARD (1990) used the term ‘regurgitates’ for some Carboniferous shell debris probably produced by sharks. As to the diet of a Lower Jurassic ichthyosaur from Lyme Regis, England, he mentioned that only the head and arms of belemnites were eaten whereas the bodies and rostra were bitten off and ‘regurgitated’ (and not swallowed). In ‘Collins

English Dictionary–Complete and Unabridged’ (www.thefreedictionary.com/regurgitates; accessed 20 July 2012) the term ‘regurgitate’ is defined in the zoological sense as ‘to bring back to the mouth (undigested or partly digested food with which to feed the young)’ (occurring in some birds and certain other animals). Thus, the English term ‘regurgitate/s’ is ambiguous. Therefore, and because the translation ‘regurgitated gastric pellet’ for ‘Speiballen’ is a little unwieldy we prefer here to use the German term for the fossil studied below.

Vertebrate Speiballen are well known from several groups of Recent birds such as owls, birds of prey or seagulls, and from carnivorous mammals such as cats. Yielding information on the food sources of the birds or mammals concerned they are helpful in recognizing food chains and webs. Among Recent reptiles Speiballen are known from crocodiles (SCHERPNER 1980) and from egg-eating snakes (Dasypeltinae), which regurgitate broken eggshell remains (REINHARD & VOGEL 1980). Fossil Speiballen appear to be rare in the Jurassic (JANICKE 1969; BARTHEL & JANICKE 1970). JANICKE (1970) and BARTHEL (1978) described fossil remains of the actinopterygian *Caturus* (synonymous *Strobilodus*) from the Solnhofen Plattenkalk (Late Jurassic, Tithonian) and interpreted it as a Speiballen produced by a large fish or crocodile. DIETL & SCHWEIGERT (2001) reported a Speiballen from the Nusplinger Plattenkalke (Late Jurassic, Kimmeridgian) mainly composed of bones of the pterosaur *Rhamphorhynchus*. The pterosaur is assumed to have been caught alive or scavenged by an adequately large predator such as *Caturus* or the crocodilians *Geosaurus* or *Dakosaurus*. KELLER (1977) considered a coiled-up skeleton of an 1.6 m long specimen of the ichthyosaur *Stenopterygius quadriscissus* from the Lower Jurassic Posidonia Shale of South Germany as a Speiballen regurgitated by another large predatory ichthyosaur, *Temnodontosaurus* (synonymous *Leptopterygius*). Another randomly arranged and compacted pile of disarticulated bones of a small ichthyosaur from the Posidonia Shale in South Germany was also suspected by JÄGER (2001) to be a Speiballen produced by a *Temnodontosaurus*. A similar explanation might apply to the assemblage of disarticulated skeletal elements including the skull of a small ornithischian dinosaur found in a concretion within the Posidonia Shale in North Germany and described by HAUBOLD (1990) as *Emausaurus ernsti*. Since dinosaurs were land-bound, in this case a river might have washed the carcass of a small, juvenile dinosaur into the Posidonia Shale sea where it was eaten

by a large ichthyosaur, or a marine crocodile, as proposed by ERNST in 1967. The indigestible bony remains of the little dinosaur were finally regurgitated by the scavenger and preserved as a Speiballen. Otherwise Speiballen seem to be unknown from the Posidonia Shale. The specimen described below appears therefore to be the fourth record of a Speiballen reported from the Posidonia Shale. [M. MAISCH (pers. comm.) considers that it is possible that Speiballen occur more frequently in the Posidonia Shale than is evident from the literature, and that their rareness is only affected by collecting and description biases.]

2. How to recognise a fossil vertebrate Speiballen

Speiballen of Recent owls can easily be identified by the presence of felted masses of hairs (which led to ABEL (1935) defining the German term ‘Gewölle’) containing disarticulated skeletal elements and teeth of small mammals on which the birds preyed. In fossil Speiballen of owls from the glacial epoch preserved in caves in Austria the hairs were decomposed leaving only layered accumulations of small disarticulated bones and teeth of prey. The nature of these bone accumulations as Speiballen remains was revealed by associated Recent Speiballen because the caves were occupied by owls continuously since the Ice Age (ABEL 1935).

Vertebrate fossils older than the glacial epoch cannot be as easily identified as Speiballen. From observations on vertebrate fossils previously interpreted as Speiballen by BURROW & TURNER (2010), ERNST (1967), JÄGER (2001), JANICKE (1970), JANICKE & SCHAIRER (1970), and KELLER (1977), the following list of characters can be derived by which fossil vertebrate Speiballen may be diagnosed:

1. Speiballen may contain skeletal remains of one or several closely packed individuals of one or more species;
2. the skeleton/s of the individual/s are disarticulated to a varying degree;
3. skeletal elements are closely packed and in disorder, not being in accordance with their natural arrangement;
4. the vertebral column if still intact is extremely coiled up;
5. the bony remains of a vertebrate Speiballen often include the skull or skeletal elements thereof (whenever the prey was swallowed whole by the predator). Drifting marine vertebrate carcasses

loose their limbs and skulls while drifting; head, limbs and trunk of such carcass can then be embedded in the sediment at different places (SCHÄFER 1972).

Fossil vertebrate Speiballen may not show all of these characters in the same fossil. For example, the coiled-up specimen of the ichthyosaur *Stenopterygius quadriscissus* from the Lower Jurassic Posidonia Shale of Holzmaden, considered to be a Speiballen by KELLER (1977), agrees with all five characters listed above. By contrast, an accumulation of six coiled-up vertebral columns of the actinopterygian *Leptolepis sprattiformis* from the Upper Jurassic Solnhofen plattenkalks of Bavaria, interpreted as a Speiballen by JANICKE & SCHAIRER (1970), all lack skulls and fin skeletons and is in accordance only with the characters 1, 2 and 4.

It should be mentioned that Speiballen can also be composed of invertebrate remains. Examples of a fossil Speiballen containing echinoid shell and spine fragments were described by GRAWE-BAUMEISTER et al. (2000), and this might also be an example of vertebrate predation. An investigation of such invertebrate-bearing Speiballen, however, is beyond the scope of this paper.

3. The Speiballen

Locality: 'Kromer' Quarry in the village of Ohmden, ca. 1.4 km NNE of Holzmaden, ca 30 km ESE of Stuttgart in South Germany.

Age: Early Jurassic, Early Toarcian, Falciferum Zone.

Horizon: 'Wilder Stein' within the Lower Jurassic Posidonia Shale [= Posidonienschiefer Formation] (Lias ε II₀) (URLICHS et al. 1979).

Preparation and repository: The specimen has been prepared from the bottom and is deposited in the fossil collection of the Urweltmuseum Hauff in Holzmaden, Germany, under the catalogue number UHH 40.

Description: The Speiballen (Fig. 1) measures 285 mm in longitudinal diameter and has a maximum vertical diameter of 160 mm. It contains at least four actinopterygian specimens identified here as *Dapedium* sp. (Neopterygii, Dapediidae) and one lower jaw of an actinopterygian identified as *Lepidotes elvensis* (BLAINVILLE, 1818) (Neopterygii, Semionotidae).

Among the specimens of *Dapedium*, specimen 1 presents its right body side and appears to be preserved best with the squamation and the dorsal and caudal fins still intact. The skull and shoulder girdle are crushed but complete; they still have most of their dermal ossifications in their natural positions. Right and left mandibles are shifted

against each other and the left mandible now reveals the ossification pattern of the medial side of the lower jaw. The specimen measures approx. 18 cm in standard length and 11 cm in maximum dorso-ventral height.

Specimen 2 of *Dapedium* also shows its right side but is less well preserved and posteriorly covered by specimens 1 and 3. Apart from the ventralmost portion the scale armour has disintegrated. The cleithrum pierces out of the Speiballen like a curved spine. The caudal part of the dermal skull (frontal, parietal, dermopterotic) is still present but other bones such as the nasal and the lower jaw seem to have gone or may be hidden underneath other skeletal remains.

Dapedium specimen 3 is even more disintegrated and largely covered by specimen 1. Some cephalic ossifications are preserved. They are, however, broken into pieces and do not allow identification. A number of ribs are visible indicating that a part of the squamation is missing. Some remains extending out of the lower border of the Speiballen may represent elements of the endoskeletal caudal fin support (haemal spines of preural vertebrae and/or hypurals).

Specimen 4 is almost entirely covered by specimen 1 leaving uncovered only the proximal part of the ventral(?) fulcral series of the caudal fin and a narrow strip of the squamation of the caudal peduncle. It cannot be excluded with certainty that the remains here identified as specimens 2 and 4 belong to the same individual. However, the relatively small size of the skull of specimen 2 and the caudal fin of specimen 4 and the long distance between these remains sharply contrasts with the deep-bodied and almost cycloidal body outline that is characteristic for most species of *Dapedium*. We consider, therefore, that it is more likely that the remains concerned represent two different specimens of *Dapedium*.

Finally, it should be noted that all four specimens of *Dapedium* are conspicuously orientated in the same direction. They all have their skulls pointing to the right and their tails showing to the left, as seen in Fig. 1.

The specific identity of the *Dapedium* specimens remains obscure. In specimen 1 the flank scales behind the shoulder girdle are at least twice or even more as high as long. This also seems to be the case in specimens 2 and 3. In specimen 4 the flank scales cannot be observed. According to the flank scale proportions specimens 1, 2 and 3 agree with *D. pholidotum* (AGASSIZ, 1832) and *D. stollorum* THIES & HAUFF, 2011, respectively. Both species of *Dapedium* are well known from the Posidonia Shale of Germany and France (WENZ 1968; THIES 1988; THIES & HAUFF 2011); they differ in the development of the hinder border of the flank scales. In *D. stollorum* the caudal margin is serrated, whereas it is smooth in *D. pholidotum* (see THIES & HAUFF 2011). In the specimens 1 to 3 the caudal margin of the flank scales is either damaged or not visible and thus this leaves the specific identity of the specimens uncertain.

Two bones reaching out of the upper margin of the Speiballen do not agree with ossifications known from *Dapedium*. The bones in question expose their external side and are provided with strong tritoral teeth at their anterior margin. By their shape and dentition these two bones represent the right and left dentalosplenials of a *Lepidotes* sp.. The lower jaw of *Lepidotes* has a wide and high coronoid process formed (laterally) by the angular and supraangu-

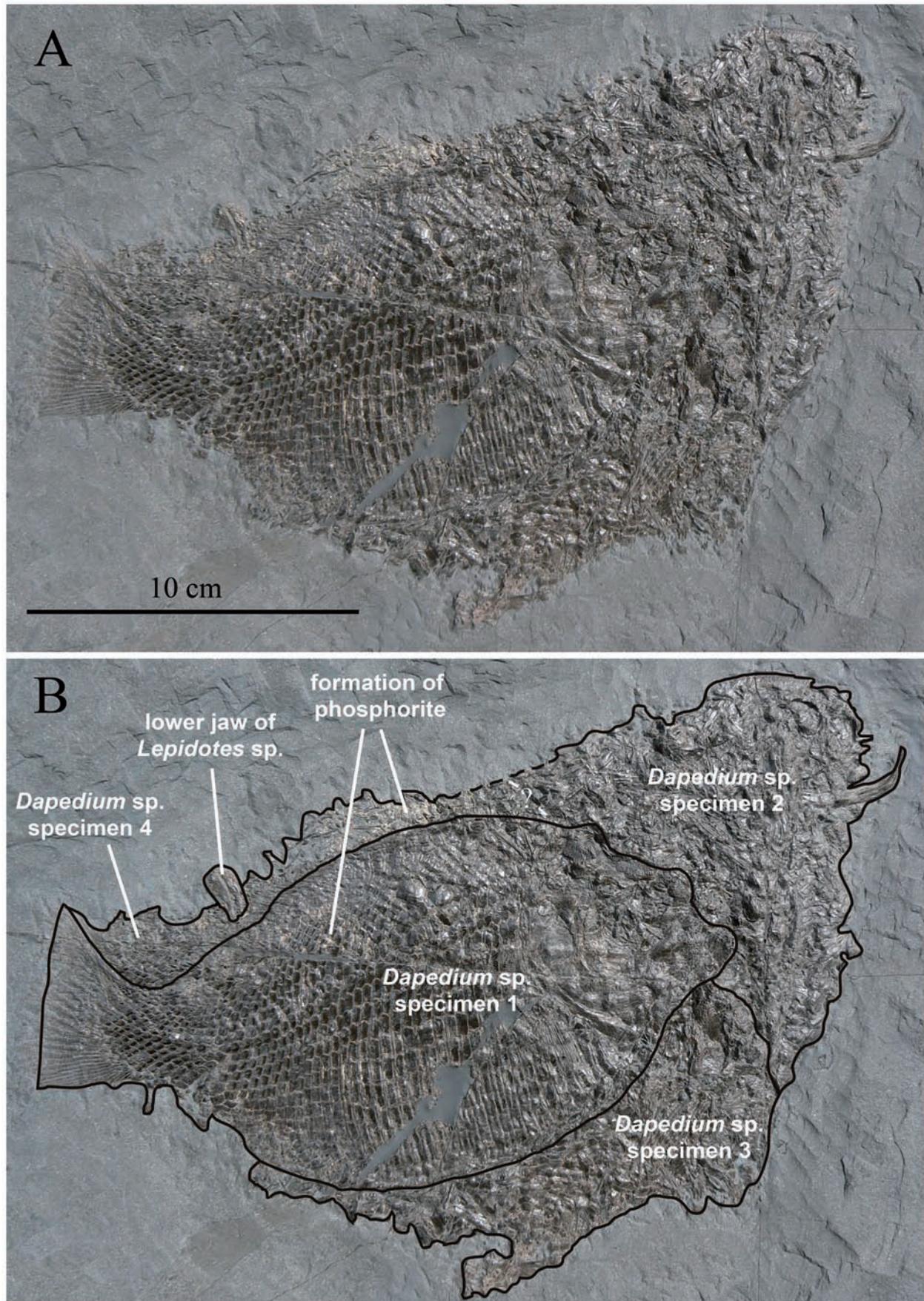


Fig. 1.

lar (WENZ 1968; THIES 1989). These two bones are missing, leaving only the dentalosplenials preserved in the Speiballen being devoid of a coronoid processes.

The specific identity of the enclosed specimen also remains obscure. *L. elvensis* (BLAINVILLE, 1818), *L. gigas* AGASSIZ, 1832, *L. semiserratus* AGASSIZ, 1837 and *L. bülowianus* JAEKEL, 1929 are four species of *Lepidotes* described from the Toarcian of Europe, with *L. gigas* (and *L. elvensis*?) being known from the Posidonia Shale so far (LÓPEZ-ARBARELLO 2012; THIES 1989; WENZ 1968; WOODWARD 1897; for discussion of taxonomical problems related to these species see THIES 1989 and LÓPEZ-ARBARELLO 2012). Because the bones in the Speiballen show no diagnostic characters they cannot be allocated to one of these species of *Lepidotes* with certainty.

L. elvensis reaches a standard length of at least 70 cm as shown by a specimen housed in the collection of the Staatliches Museum für Naturkunde, Stuttgart, and figured by WILD (1994: fig. 83). In this adult specimen the dentalosplenial has a length of approx. 60 mm. The small size of the dentalosplenials in the Speiballen not exceeding 15 mm indicates that they belonged to a juvenile specimen. This is the first record of a juvenile of *Lepidotes* in the Posidonia Shale. The presence of a juvenile in this condition indicates a key piece of evidence for the lack of young within the fossil assemblage if the majority were predated as would be expected before fossilisation.

Formation of phosphorite has occurred to a small extent and is observable on the fossil in two places: (1) at the ventral(?) side of *Dapedium* specimen 4 among an assemblage of disarticulated fulcra of the anal(?) fin and ventral(?) scales; and (2) underneath a small dorso-lateral area of the squamation of *Dapedium* specimen 1 where phosphorite appears in places where scales or parts thereof are broken off (Fig. 1). Formation of phosphorite in *Dapedium* specimen 4 might have been caused by infilling of the intestine and argues for the visible remains actually being the ventral part of specimen 4.

4. Who done it?

The specimen agrees with the criteria 1, 2, 3, and 5 listed above for the identification of fossil vertebrate Speiballen. Also, the squamation and the cephalic skeleton of the *Dapedium* specimen 1 being mostly intact indicate that the remains did not pass through the intestines of a predator but were regurgitated as a Speiballen. The well-preserved caudal fins of specimens 1 and 4 as well as the low degree of formation of phosphorite also support this view.

What animal produced the Speiballen? This question is difficult to answer. Known invertebrates from the South German Posidonia Shale did not reach body sizes that would match the size of the Speiballen described here and can therefore be ruled out. However, all groups of marine vertebrates living in the Posidonia Shale sea include large fish eaters. Considering prevailing or seasonal anoxic conditions at the bottom of the Posidonia Shale sea (e.g., SEILACHER 1982; SCHMID-RÖHL et al. 2002), small and median-sized fishes should have represented one of the most important food sources in the ecosystem.

4.1. Chondrichthyans

Among chondrichthyans, sharks of the genus *Hybodus* are most prominent in the Posidonia Shale. Some Recent sharks, e.g., tigersharks, are known to be opportunistic feeders living on a wide spectrum of prey. The same possibly applied to *Hybodus*, which was certainly large enough (body length up to 3 m) and most taxa had a dentition of multicuspid teeth suited to capture prey such as *Dapedium*. So, it is assumed that a *Hybodus* species preyed on *Dapedium* and other fishes if they were available. Unfortunately, this cannot be proven by stomach contents. One famous specimen of *Hybodus hauffianus* on exhibition in the Staatliches Museum für Naturkunde, Stuttgart, shows a stomach content of approx. 250 belemnite guards (HAUFF & HAUFF 1981; WILD 1994: figs. 73-74). Also, we could not trace any Recent shark taxon in which the regurgitation of Speiballen was observed as part of the natural behaviour. Only one case became well known when a tigershark captured and held in captivity disgorged a human arm (WHITLEY 1940; HUGHES 1989).

4.2. Actinopterygians

Large predatory bony fishes are represented in the Posidonia Shale by the Pachycormiformes. *Saurostomus esocinus* grew up to 2 m body length. Preserved stomach contents of these fishes comprise cuttlefishes and ammonites (HAUFF & HAUFF 1981; WILD 1994). ALDINGER (1965) mentions a specimen of *S. esocinus*

Fig. 1. Speiballen of unknown origin from the Early Jurassic Posidonia Shale of South Germany. The Speiballen contains four specimens of *Dapedium* sp. and the lower jaw of a juvenile *Lepidotes* sp.. A – overview of the specimen; B – same specimen. The individual fish specimens are outlined with black to show their position within the Speiballen. The specimen is housed in the Urweltmuseum Hauff in Holzmaden, Germany, no. UHH 40.

containing six specimens of *Pachycormus curtus* in its stomach. However, *Dapedium* and *Lepidotes* apparently have not been observed so far as prey of pachycormiform fishes. It is also unknown whether these fishes have produced Speiballen. In addition, we could trace no information on whether comparably large Recent predatory bony fishes like the tunas regurgitate Speiballen have ever been noted.

4.3. Marine reptiles

Marine reptiles of the Posidonia Shale include three groups that comprise potential producers of Speiballen: crocodylians, ichthyosaurs and plesiosaurs.

Crocodylians: three genera are known: *Steneosaurus*, *Pelagosaurus*, and *Platysuchus*. Most frequent and best known is *Steneosaurus*. Its long, slender, curved and pointed teeth taking alternating positions in the upper and lower jaw are well adapted to grab and pierce a fish-like prey (MASSARE 1987). JÄGER (2001) actually mentioned and figured a specimen of *Dapedium* showing puncture marks, which he interpreted as the biting marks of a crocodile. The complete and undisturbed squamation of *Dapedium* specimen 1 of our Speiballen, however, does not show any puncture marks. The squamations of specimens 2 and 3 are too disintegrated for such marks to be preserved. Also, in known stomach contents of steneosaurs fish remains are missing (WILD 1994). This might, however, be due to the presence of gastroliths in steneosaurs, which are associated often with skeletal remains of Posidonia Shale crocodylians and which these reptiles in general swallow in order to improve buoyancy and/or digestion.

Ichthyosaurs: Ichthyosaurs are certainly best studied among Posidonia Shale reptiles (e.g., MAISCH 2008). Representatives of the genus *Stenopterygius* are most frequent. As shown by stomach contents *Stenopterygius* changed its diet during ontogeny. Whereas the juveniles were piscivorous up to a body length of approx. 1.7 m, the larger adults fed exclusively on belemnoid cephalopods (KELLER 1976; WILD 1994). Interestingly, *Dapedium* specimens have been found among the fish remains in the stomachs of juvenile stenopterygians. The adults accumulated large gastric masses of undigestible belemnoid hooklets in a certain position in the abdominal cavity indicating that the stomach of stenopterygians was separated into different divisions. That division containing the cephalopod hooklets is assumed to have been a muscular stomach, like that

developed in the digestive tract of some Recent marine mammals (BÖTTCHER 1989), which could have produced Speiballen. However, isolated aggregations of numerous belemnoid hooklets have not yet been discovered in the Posidonia Shale (BÖTTCHER 1989), leaving in doubt whether stenopterygians really vomited Speiballen. Apart from *Stenopterygius* at least three more genera of ichthyosaurs have been discovered in the Posidonia Shale: *Eurhinosaurus*, *Suevoleviathan* and *Temnodontosaurus* (MAISCH 1998a, b). All three genera grew larger than *Stenopterygius* and would therefore have been able potentially to produce Speiballen of the size described here. Stomach contents, however, are still unknown from *Eurhinosaurus* and *Suevoleviathan*, but *Temnodontosaurus* obviously fed on cephalopods and juvenile stenopterygians. This is shown by an 8.7 m-long specimen of *Temnodontosaurus trigonodon* in the collection of the Staatliches Museum für Naturkunde in Stuttgart (cat. No. 50000) that preserves clumped masses of belemnoid hooklets and numerous small stenopterygian vertebrae in its abdominal cavity (BÖTTCHER 1989).

Plesiosaurs: Another group of large marine reptiles to be considered as possible producer of our Speiballen is the plesiosaurs. Better-known genera occurring in the Posidonia Shale include *Rhomaleosaurus*, *Hauffiosaurus*, *Seeleyosaurus* und *Hydrorion*. Comparison of *Hauffiosaurus* with *Peloneustes* (Callovian, Middle Jurassic of England) with regard to jaw and tooth morphology led VINCENT (2011) to the conclusion that *Hauffiosaurus* was a fish eater, after *Peloneustes*. The palaeoecology of *Seeleyosaurus* and *Hydrorion* was studied by GROSSMANN (2006). Functional analysis of skull and tooth morphology as well as cranial musculature allowed her to assume that *Seeleyosaurus* and *Hydrorion* preferred small and soft-bodied prey not exceeding a body length of approx. 10 cm, such as *Leptolepis* and coleoids. Under these circumstances *Dapedium* and other basal neopterygians such as *Lepidotes* possessing a heavy, solid squamation of ganoin scales and growing larger than 10 cm are clearly excluded from the diet of these plesiosaurs (standard length of *Dapedium* specimen 1 in our Speiballen: approx. 18 cm, see above). Unfortunately, direct evidence of the diet of the Posidonia Shale plesiosaurs in the form of stomach contents does not exist and their prey preference therefore remains an assumption (GROSSMANN 2006).

In conclusion, published data on the Posidonia Shale vertebrate fauna does not yield direct evidence indicating to the producer of the Speiballen. The rela-

tively large size of the fossil leaves, in our opinion, only larger predators, such as temnodontosaurus, to have regurgitated the Speiballen.

KELLER (1976) reconstructed a small schematic trophic web of Posidonia Shale organisms. This hypothesis shows *Dapedium* (and other fishes) as feeding on small (unknown) planktonic (epibenthonic?) crustaceans. *Dapedium* itself is preyed on by various ichthyosaurs.

5. Fish meals – healthful or not?

Even though a possible producer of Speiballen cannot be ascertained among large predators of the Posidonia Shale fauna, the Speiballen specimen yields additional information on the function of the massive squamation of *Dapedium*. The heavy ganoid scale armour of basal neopterygians like *Dapedium* is said to have served at least two functions: 1) it provided to some extent protection against the pointed and fang-like teeth of certain predators such as some groups of chondrichthyans (e.g., Orthacodontidae, BEAUMONT 1960), and 2) in the absence of a strongly ossified axial skeleton it served as a dermal skeleton, which gave the body of the fish some stability in the transversal section in order to constrict undulating (wiggling) movements in the horizontal plane (STARCK 1978). To these hypothetical suggestions can now be added a third tangible function. As shown by the Speiballen studied here, fishes of the genus *Dapedium* were clearly difficult to digest because of their solid and firmly jointed ganoid scale armour. This fact may therefore have in principal excluded them from the menu of many larger predatory vertebrates of the Posidonia Shale sea. However, the presence of a Speiballen containing four specimens of *Dapedium* also indicates that some Posidonia Shale predators seem to have developed a strategy to deal with the resistance and indigestibility of heavy scale armours – namely the production of Speiballen.

Acknowledgements

We thank R. KOSMA, Staatliches Naturhistorisches Museum Braunschweig, for information on the nutritional behavior of Recent reptiles. S. TURNER, Brisbane, commented on the manuscript and improved the English. Reviewers M. KOŠŤÁK and T. PŘIKRYL (Prague) and M. W. MAISCH (Tübingen) provided comments that significantly improved the manuscript.

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Manuscript received: July 30th, 2012.

Revised version accepted by the Stuttgart editor: August 30th, 2012.

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