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Autor(en): **Hess, Hans**

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New specimen of the sea star *Testudinaster peregrinus* HESS from the Middle Jurassic of northern Switzerland

HANS HESS[1]

Key words: Sea star, *Testudinaster peregrinus,* Bajocian, Switzerland, description, paleoecology, morphology

ZUSAMMENFASSUNG

Zwei neue Funde des bislang nur durch eine Dorsalseite bekannten Seesterns *Testudinaster peregrinus* HESS (1983) aus dem oberen Hauptrogenstein der Nordschweiz zeigen die Ventralseite. Diese ist geprägt von dicht gedrängten, sehr hohen oralen Zwischenplatten (Ventrolateralia) mit einem Körnerbelag. Die Diagnose von Gattung und Art wird entsprechend ergänzt. Kugelige oder kuppelförmige Seesterne ohne Arme der Ordnung Valvatida wurden als Angehörige der Sphaerasteridae betrachtet. Der Entscheid, ob eine solche Einreihung eher auf Konvergenz als auf Phylogenie beruht, ist nur durch weitere Untersuchungen möglich.

ABSTRACT

New discoveries of the armless sea star *Testudinaster peregrinus* HESS (1983) from the Upper Bajocian of northern Switzerland are described. This species was previously known only from a single specimen in dorsal view. The new fossils show their ventral side, which is dominated by closely set, very high actinal plates; diagnosis of genus and species is correspondingly amended. Spherical and subspherical armless valvatidan asteroids have been grouped together under the Sphaerasteridae; such an alignment might reflect convergence rather than phylogeny, but until further information becomes available, it is accepted here.

Introduction

The Upper Hauptrogenstein (Upper Bajocian), of the now classic quarry of Schinznach, has revealed a rich echinoderm fauna, including 11 species of sea stars. One of these is a heavily armoured, armless form that was described as *Testudinaster peregrinus* (Hess 1983). It is based on a unique, partly disarticulated specimen, which shows the dorsal (aboral, abactinal) side. Last year, two new specimens of this rare species were discovered by Rolf Hirt (Fislisbach) in a quarry northeast of Auenstein (canton of Aargau), not far from Schinznach, again in strata of the Upper Hauptrogenstein. The new specimens fortunately present their ventral (oral, actinal) side. The larger fossil, which is perfectly preserved, has already been figured by Holenweg et al. (1994). The rarity of Jurassic sea stars and their importance for the phylogeny of modern forms render a description of this new specimen important.

[1] Naturhistorisches Museum, Augustinergasse 2, CH–4001 Basel

Geological setting and its fauna

Both specimens of the sea stars lie on the lower side of a bed of a bluish marly limestone, with some molluscan and echinoderm debris. This lenticular bed thins from 15 mm to 2 mm, and it rested on a thin layer of dark-blue marl which could be removed without damage to the fine parts of the fossils. The bed with the sea stars belongs to a number of similar lenses that are overlain by a layer of dark-blue clay. Neighbouring lenses contain, again on their lower surface, small, presumably juvenile individuals of *Pentacrinites dargniesi,* other echinoderms and crustaceans (decapods, crabs, and the cirripedian *Eolepas quenstedti);* other lenses are, however, largely barren of macrofossils, as are the under- and overlying oolitic limestone beds. The horizon with the lenses passes laterally into a cross-stratified oolitic limestone bed. On the lower surface of this bed occur dense patches of the short-stemmed crinoid *Pentacrinites dargniesi* and occasional specimens of the long-stemmed crinoid *Isocrinus nicoleti,* with broken-off stems. A few other fossils are also present, among them possible holothurians; their preservation does not allow further determination.

Material

The smaller specimen of the sea stars, obviously a juvenile individual, has a radius of 2 cm; it is in the collection of R. Hirt. The larger specimen (Fig. 1, 2) has a radius of 4.5 cm and is thus of similar size as the holotype (Natural History Museum Basel, M 9689, illustrated in Hess, 1983). The surface of this bed also contains partly disarticulated remains of echinoids *(Paracidaris charmassei)* and crinoids (*Pentacrinites dargniesi),* as well as of bivalves.

Systematic description of *Testudinaster peregrinus* Hess, 1983

The description (Fig. 1, 2) is based on the larger specimen; the small individual is preserved in exactly the same way. Due to collapse of the pentagonal body and closed ambulacral furrows, which possibly contracted on the death of the animal, the sea star resembles a pancake. The ventral view is dominated by closely set, radially elongate, somewhat spindle-shaped actinal intermediate plates (called "Ventrolateralia" by the author in his previous German language texts). These plates are arranged in imbricated rows parallel to the furrow; those in the interradii are larger than those near the ambulacral furrows. Closer to the margin, the plates are less imbricated but abut; they are indented for close articulation with each other. The actinals in most of the interradial area are very high; they typically measure 3 mm in length, 1 mm in width, and 2 mm in height. They are cuneate, tapering from the surface towards the interior of the disc. The ventral surfaces are covered by granules, which are best preserved in the depressed parts around the mouth; they may have more or less covered the plates in life. At the margin, about 35 rows of these plates can be counted. A similar number is also present in the smaller specimen. True marginals cannot be identified. The adambulacrals are compact, block-like and do not project into the furrow; they carry tufts of small, short spines. There are two actinals for each adjacent adambulacral. The broadly rounded adambulacrals, with only

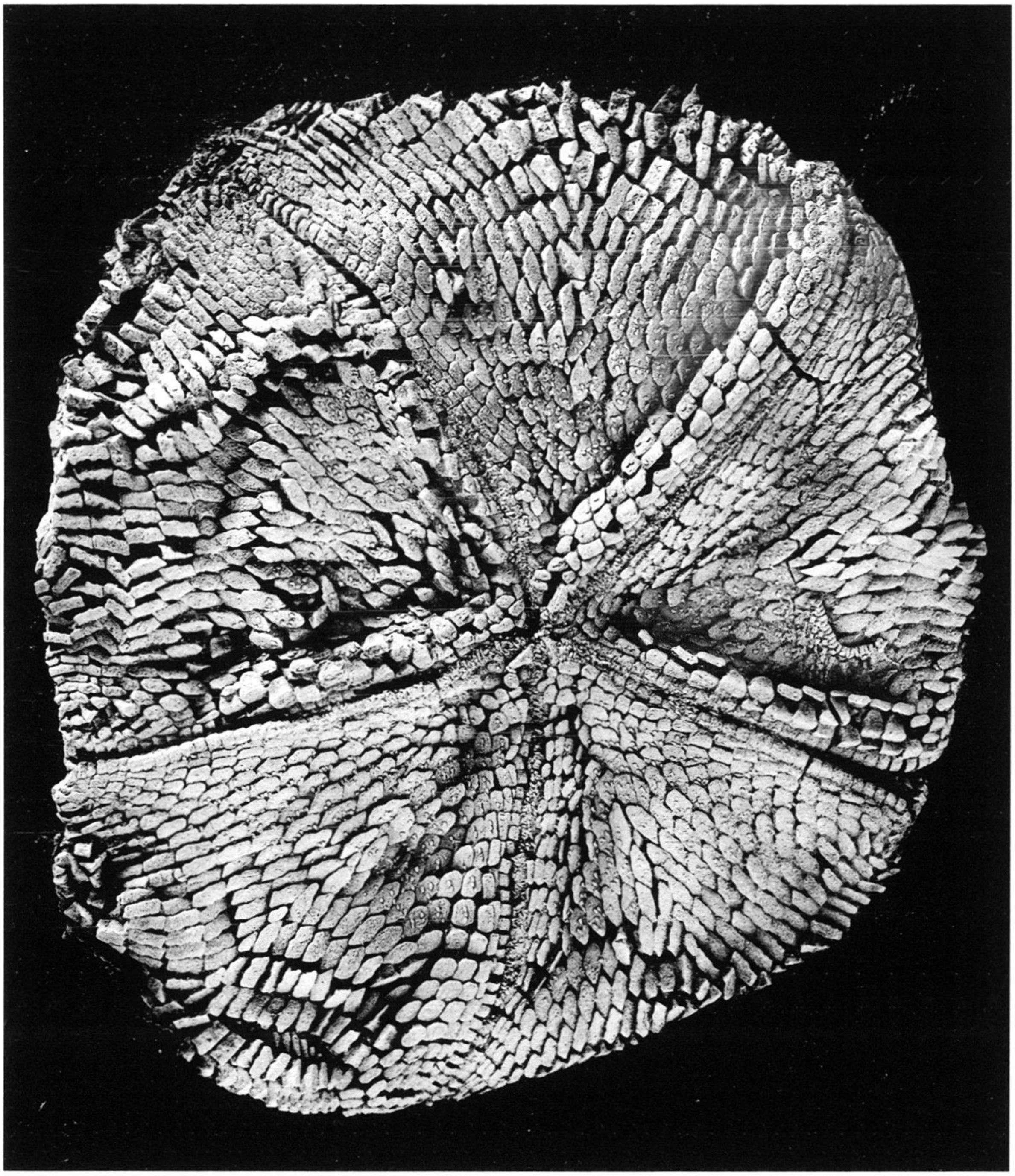

Fig. 1. Ventral (oral, actinal) view of *Testudinaster peregrinus*, Upper Hauptrogenstein (Upper Bajocian), Auenstein (canton of Aargau). On the right interradius an arm fragment of the crinoid *Pentacrinites dargniesi* is preserved. × 1.5. Collection H. Holenweg, CH–4133 Pratteln. Cast No. M 9923 in the Natural History Museum, Basel.

small spines, suggest that the margins of the furrow could be drawn closely together, perhaps as a defense to close the ambulacral furrow against predators. The small, elongated, triangular orals carry small spines similar to those of the adambulacrals.

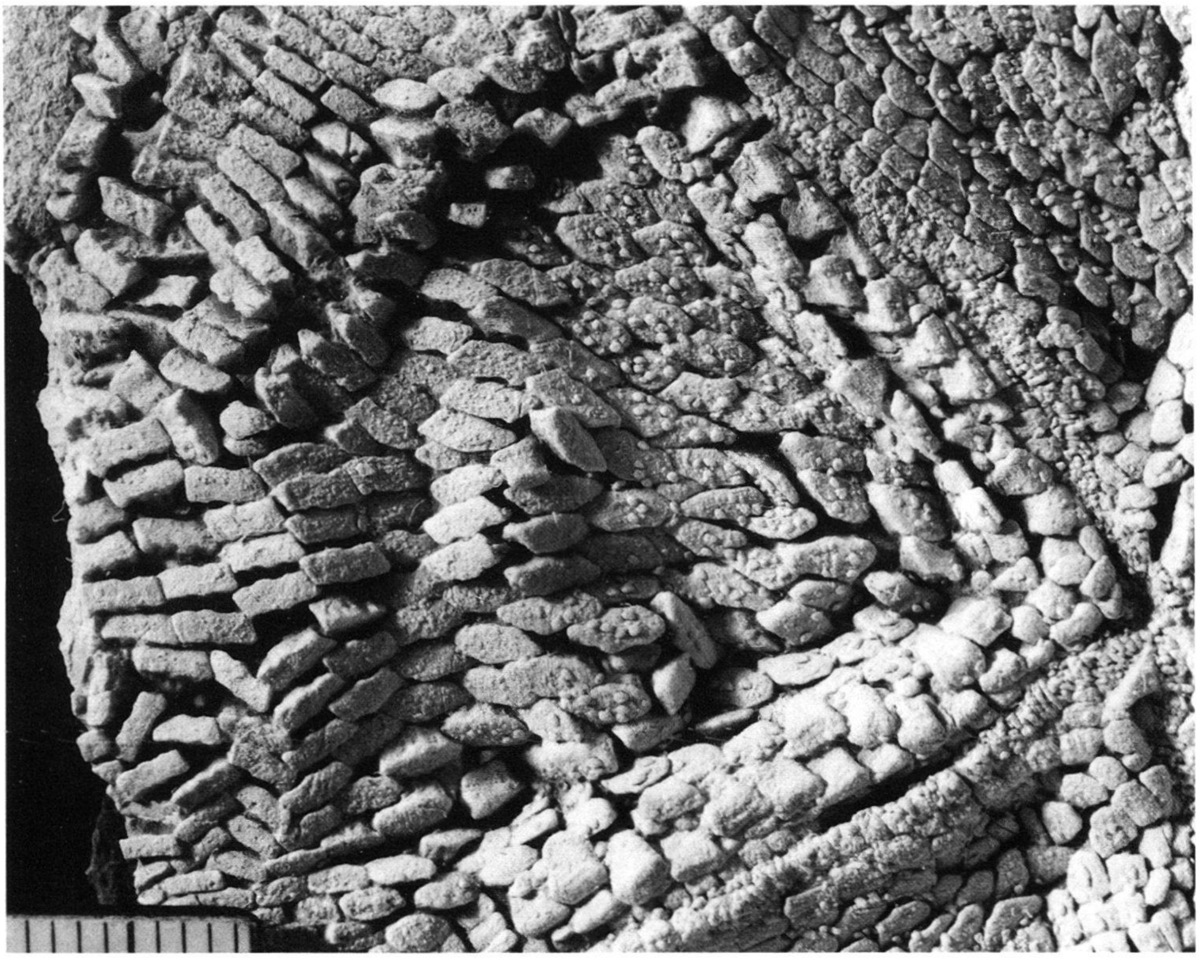

Fig. 2. Detail of fig. 1: Area from mouth (right) to margin (left), note very high actinal ossicles with interlocking sutures. × 3.

Comparison with holotype, affinities

The present fossils and the holotype of *Testudinaster peregrinus* look quite different at first sight. However, the highly typical actinal plates can also be observed on the holotype in some places, so that assignment of the new fossils to the same species is beyond any doubt. The dorsal or aboral plates (abactinals) near the margin of the holotype are also very similar to the actinals of the Auenstein specimens.

In the original description (Hess 1983), *Testudinaster* was provisionally assigned to the Asterinidae, but relationships with the Goniasteridae and the Sphaerasteridae, other families of the order Valvatida, were also mentioned. Body form (a domed pentagon), closely set actinals and dorsals with hinge-like articulations, and compact adambulacrals all suggest a relationship with Sphaerasteridae. However, the radially elongate, high actinals and the equally high, very short (i.e. transversely elongate) dorsal plates near the margin clearly distinguish *Testudinaster* from the Jurassic *Sphaeraster* and the recent *Podosphaeraster*. *Sphaeraster* is characterized by distinct supero- and inferomarginals. The dorsal plates bear abutting ribs and grooves on the adjacent edges for the passage of respiratory papulae in the grooves (Blake 1984a, p. 88, Fig. 8 D,E). Marginals are not differentiated in *Testudinaster*; however, some of the dorsal plates have abutting grooves and ridges for the passage of papulae similar to *Sphaeraster*, while most ossicles are tightly interfingered (Hess 1983, Fig. 1, 3). The third genus assigned to this family, the Upper Cretaceous (Senonian) to Paleocene (Danian) *Valettaster*, has thick, weakly articulated, irregularly rounded plates with low cones; Breton (1985) assumed that this spherical and presumably non-rigid sea star could roll passively on the bottom. Such an assumption seems questionable in view of the soupy nature of the bottom in the Chalk seas where these sea stars mainly lived. The specialized structure and very peculiar form of all three genera make their inclusion in a single family something of a tour de force. Thin sections of dorsal plates of *Testudinaster* and *Valettaster*, similar to those already performed on *Sphaeraster* by Blake (1984, Fig. 4, 5), may shed additional light on the affinities between these fossil sea stars. Common characters of these armless sea stars are a more or less rigid, armoured, arched or domed body and stout adambulacrals which carry only small spines and do not project into the ambulacral furrow. Adambulacrals and ambulacrals fit well within the range of the Valvatida.

Amended diagnosis of the genus ***Testudinaster*** *HESS, 1983*

Body form pentagonal, dorsal ossicles forming dome; marginals not differentiated; both sides completely covered with closely set, indented ossicles; dorsal plates around center of disc irregularly polygonal, some indented for papulae, but most of them closely interfingered; other dorsals transversely elongate and high, arranged in regular rows; spines absent from dorsals; actinals radially elongate, imbricated in central area and very high towards margin, surface covered with granules; adambulacrals compact, not projecting into furrow, with tuft of small spines.

Taphonomy and paleoecology

The sea stars and the other fossils were obviously buried in front of an advancing wave of fine calcareous sand. The fragmentary preservation of the other fossils in this particular lens indicates some transport before burial; the sea stars easily withstood such transport by virtue of their sturdy construction. Their occurrence in life position may be due to their flat lower surface and their probably arched dorsal surface. The sea stars, together with the other animals, lived in somewhat deeper water (the water depth is estimated at 10–15 m), where currents were moderate and clay particles accumulated, at the bottom of a sand wave. Such a setting is indicated by the good preservation of patches of complete crinoids on the lower surface of the adjacent, cross-stratified limestone bed, as well as the occurrence of a marly layer underlying this bed and the lenses. Such places are known from other localities in the otherwise oligotrophic milieu of Lower and Upper Hauptrogenstein (Meyer 1990); they must have provided nutrient-rich habitats for colonies of crinoids, presumably as a result of current eddies (see e.g. Gonzalez 1993, Fig. 2.2, 5.6b). Many of the Schinznach asteroids are found within the beds, which indicates that they were also buried by shifting sediments.

Morphology, habitat and lifestyle of Jurassic sea stars

Both the Auenstein and the Schinznach quarries are situated near the facies boundary between the western platform sediments and the eastern deeper-water marls and tempestites. It is assumed that in both places these sea stars were adapted to life on both firm and soft substrates at the bottom of sand waves (see the reconstruction in Holenweg et al. 1994). As discussed by the author (Hess 1987), astropectinids *(Advenaster inermis, Pentasteria kelleri, Pentasteria [Archastropecten] huxleyi)* are very conspicuous in the Schinznach location. However, sturdier goniasterids with shorter arms *(Tylasteria berthandi)*, goniasterids with large disc and flexible arms *(Noviaster polyplax)*, as well as large *(Argoviaster occultus)* and small, delicate asteriids *(Dermaster boehmi)* also abound. Still another body form is represented by the multi-armed solasterid *Plesiosolaster moretonis*. The rare *Sphaeriaster jurassicus*, with its pentagonal body similar to *Testudinaster*, is reduced to the ambulacral skeleton (ambulacral and adambulacral plates). The rather frequent tremasterid *Mesotremaster felli* is less heavily armoured, but otherwise superficially similar to *Testudinaster* (its ambulacral pores are, however, quadriserial, i.e. arranged in 4 rows). It should be noted that a closely related species, *Mesotremaster zbindeni,* has been found between Oxfordian coral bioherms (Hess 1981). It is therefore difficult to relate body form of these Jurassic sea stars (including armour and flexibility) to a preferred habitat, with the possible exception of food gathering and predation. The presence of the four asteroid orders Forcipulatida *(Argoviaster, Dermaster),* Valvatida *(Mesotremaster, Noviaster, Sphaeriaster, Testudinaster, Tylasteria),* Paxillosida (*Advenaster, Pentasteria)* and Velatida *(Plesiosolaster)* indicates use of different food resources (niche differentiation). As Blake (1990) pointed out, the asteroid orders have adopted different food strategies. Forcipulatida are offensive specialists, typically predators on other invertebrates; Valvatida feed on smaller particles from the substrate; Paxillosida, some of which have developed the ability for self-burial, are partly predatory (astropectinids are known to ingest even large molluscs), whereas others ingest sediment containing small edible particles; Velatida, finally, are known for their predatory activities (probably some of the deeper water forms are small particle feeders). Absent from the platform sediments of the Upper Hauptrogenstein are members of the suspension feeding orders Brisingida and Notomyotida (with *Benthopecten*); it may be assumed that this niche was successfully occupied by the crinoids, which occur here in large numbers. It is interesting to note that a rare benthopectinid *(Xandarosaster hessi)* has been found within a colony of the Lower Hauptrogenstein crinoid *Chariocrinus andreae* (Blake 1984b). Structure of the ambulacrals and adambulacrals as well as body shape, and the heavy armour would have precluded *Testudinaster* to predate on other organisms, such as bivalves. In line with other valvatidans, this sea star lived on mud and sand and directly ingested food, possibly swallowing small animals as a whole.

The peculiar body form of *Testudinaster* is comparable to that of the Oxfordian genus *Sphaeraster,* with its essentially rigid body walls and its dorsal ossicles forming an armless dome. *Sphaeraster* has been interpreted as a reef-dwelling form (Blake 1989, p. 192), but the strata in which two species of this genus occur are made up of carbonate and argillaceous mud deposited in deeper water between algal-sponge mounds (the so-called Argovian or Swabian facies). The Argovian deposits of Switzerland and the similar strata of Southern Germany are dominated by ammonites and siliceous sponges, but have also furnished numerous remains of cyrtocrinids *(Cyrtocrinus, Eugeniacrinites, Gymnocrinus)*. These have developed numerous protective measures, including spines and enrollment of arms; it may therefore be assumed that the body form of *Sphaeraster* was also a protective measure against predation. *Testudinaster* may have developed a similar strategy, but the much more heavily armoured ossicles appear to have been an additional adaptation for life in a high-energy environment, dominated by rapidly changing conditions. In this respect, *Testudinaster* is comparable to *Mesotremaster*.

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