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A new ophiuroid (*Geocoma schoentalensis* sp. nov.) from the Middle Jurassic of northwestern Switzerland and remarks on the family Aplocomidae Hess 1965

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Key words: ophiuroids, Aplocomidae, Mesozoic, Bajocian, shallow-water oolitic platform sediments, obrution Lagerstätte

ABSTRACT

A new ophiuroid species from the Hauptrogenstein Formation (Middle Jurassic, Bajocian) of the Rehhag ridge near Schöntal, northwestern Switzerland, is described based on 34 specimens. The impression of an indeterminate astropectinid sea star has also been found. The fully articulated specimens have been smothered by mobile oolitic dunes or sandwaves. The site can be genetically classified as an obrution deposit and belongs to the widely recognized "Hauptrogenstein type". The remains are assigned to the genus *Geocoma* D'Orbigny 1850, best known from the type species, *G. carinata* (Münster), from the Tithonian Plattenkalk of Zandt. As suggested by Kutscher (1997) this species also includes *Ophiocten kelheimense* Boehm 1889, now documented by numerous well-preserved specimens from the Plattenkalk of Hienheim. Kutscher assigned the Hienheim specimens to the genus *Sinosura* Hess 1964 and used both names though *G. carinata* has priority. Despite rather small differences *Sinosura* is retained as a valid genus besides *Geocoma*, and both are placed in the family Aplocomidae Hess 1965. *Geocoma* and *Sinosura* share small adpressed arm spines with *Aplocoma* D'Orbigny 1852. *Aplocoma* is represented by a number of Triassic and Jurassic species, and the subfamily Aplocominae is proposed herein for the three genera. A second subfamily, Ophiopetrinae, is proposed for the genera *Ophiopetra* Enay & Hess 1962 and *Ophiohybris* Hess 1964, and is characterized by larger, erect arm spines.

ZUSAMMENFASSUNG

Eine neue Ophiurenart aus der Hauptrogenstein Formation (mittlerer Dogger, Bajocian) vom Rehhag bei Schöntal (Kt. Baselland) wird beschrieben. Das Material umfasst 34 Exemplare, neben Armresten und angewitterten Scheiben auch zwei gut erhaltene Scheiben, daneben wurde der Abdruck eines unbestimmbaren Astropectiniden gefunden. Die vollständig artikulierten Schlangensterne wurden von einer migrierenden Sanddüne verschüttet und kann als Obrutions-Lagerstätte („Hauptrogenstein" Typ) klassifiziert werden. Die vorliegenden Funde werden zur Gattung *Geocoma* D'Orbigny 1850 gestellt, welche vor allem durch die meist schlecht erhaltenen Funde von *G. carinata* (Münster) aus den untertithonischen Plattenkalken von Zandt bekannt geworden ist. Kutscher (1997) stellte aufgrund neuer Funde von *G. carinata* eine weitgehende Übereinstimmung mit den ausgezeichnet erhaltenen Funden von *Ophiocten kelheimense* Boehm 1889 aus den etwas jüngeren Plattenkalken von Hienheim fest; er stellte die Form zu *Sinosura* Hess 1964 und verwendete *S. kelheimense* neben *G. carinata*, trotz Priorität der letzteren. *Sinosura* wird trotz geringer Unterschiede als gültige Gattung neben *Geocoma* beibehalten. Beide Gattungen werden zu den Aplocomidae Hess 1965 gestellt; sie teilen mit *Aplocoma* D'Orbigny 1852 die kurzen, anliegenden Armstacheln, und für die drei Gattungen wird die Unterfamilie Aplocominae vorgeschlagen. Eine zweite Unterfamilie, Ophiopetrinae, wird für die Gattungen *Opiopetra* Enay & Hess 1962 und *Ophiohybris* Hess 1964 vorgeschlagen; die entsprechenden Arten tragen längere, abstehende Armstacheln.

Introduction

Intact echinoderms are extraordinary fossils because most of them, such as ophiuroids, quickly disarticulate after death (e.g. Meyer 1988b, Kerr & Twitchett 2004). Therefore, more or less complete specimens with disk plating, oral frame structure and arm spines are rare. Such occurrences are related to storm deposits, submarine channels or migrating sand banks and are classified as obrution Lagerstätten (Meyer 1984, Ausich 2001). The Hauptrogenstein Formation of northwestern Switzerland has long been known for its echinoderm assemblages preserved in situ. More than fifty different Lagerstätten (e.g. Hess 1972, Meyer 1987) have yielded articulated isocrinids, comatulids, asteroids, ophiuroids, echinoids as well as holothurians. We report herein on a new, small asterozoan assemblage that has been preserved in such a context.

Geologic and stratigraphic framework

The present specimens were collected in northwestern Switzerland in the Rehhag area, on the border of a hiking trail 2.5 km north of the small monastery Schöntal near Langenbruck (70° 46' 49.87" E, 47° 22' 36.74" N, Fig. 1). The limestones dip 70° to the north and are part of the northern limb of the Wald-

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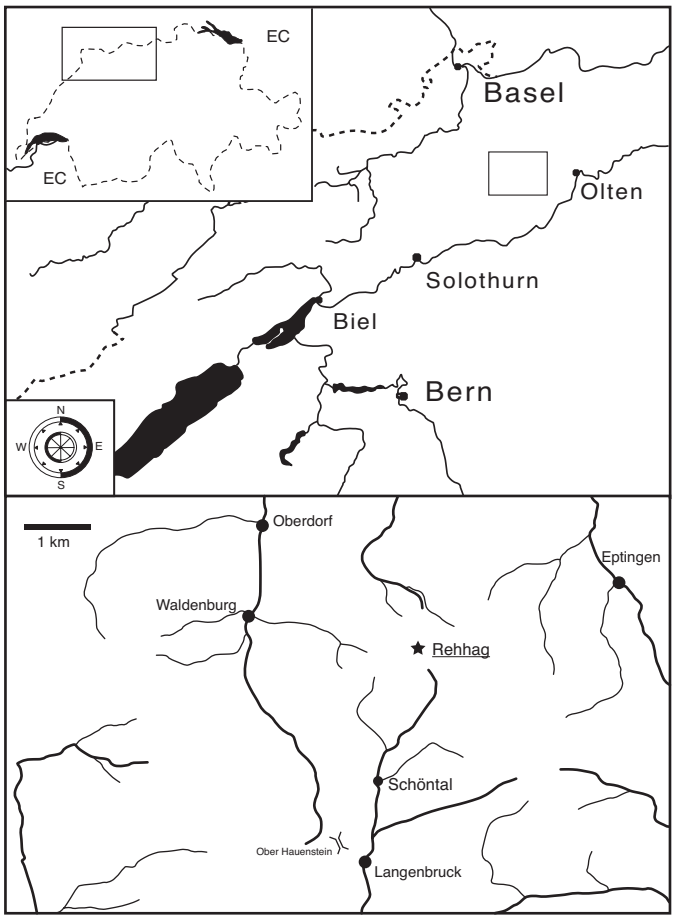

Fig. 1. Geographic and geologic setting of the fossil site. Drawing by C.A. Meyer.

weid – Humbel syncline within the folded Jura mountains. The locality was discovered by a local amateur, Fritz Schmutz (Gelterkinden); his discovery was communicated to the junior author. The locality was visited on two occasions to collect additional material and to examine the geology and sedimentology of the site. The sedimentary rocks belong to the Hauptrogenstein Formation – these predominantly oolitic limestones are Bajocian (Middle Jurassic) in age. More precisely, the fossil-yielding unit can be assigned to the "Obere Oolithische Serien" sensu Gonzalez (1996). This part of the Hauptrogenstein Formation was deposited during the *Parkinsoni* Zone. In the small outcrop, the Hauptrogenstein is only partially exposed. The thickness of the "Obere Oolithische Serien" at the study locality is approximatively 30 m. The Hauptrogenstein was formed in a shallow-water carbonate environment, the so-called Burgundy carbonate platform. Water depth in the study area was around 5–10 m (Gonzalez & Wetzel 1996).

Materials

Several rock specimens are available. A single large block shows ventral and dorsal sides of 28 ophiuroids and a single impression of a sea star (G1. 6281, Fig. 2). The overall outline and the shape and arrangement of the marginals point to a member of the family Astropectinidae (cast G1. 6282). Incomplete preservation precludes attribution to genus or species level. In two of the numerous ophiuroid specimens (called 'a' and 'b'), the ventral side of the disk with the mouth armature and part of the arms are quite well preserved, although the granulation on the disk is missing. In specimen 'a', the two distal oral papillae are well displayed; they are pointed, high and triangular. Specimen 'b' shows adoral shields that are nearly in contact proximally. Arm spines number four, the three dorsal ones are about two thirds as long as the ventral one. No specimen is weathered free, so no specimen shows both sides. The block also contains a number of crinoid brachials. Among them is a symmorphy of an isocrinid, similar to the one figured by Hess (1975c: pl. 7, fig. 4) under *Isocrinus nicoleti* (THURMANN), and a syzygy assignable to *Paracomatula helvetica* HESS (see Hess 1975c: pl. 7, fig. 3). Additionally, three small slabs were found that contain several specimens (slab with holotype and paratype: G1.6278, Fig. 3; slab with two specimens: G1. 6279, Fig. 6; slab with one specimen: G1.6280, not figured). All specimens are in the repository of Museum BL (Liestal).

Systematic palaeontology

Ophiuroidea	GRAY 1840
Ophiuridea	GRAY 1840
Ophiurida	MÜLLER & TROSCHEL 1840
Ophiurina	MÜLLER & TROSCHEL 1840
Chilophiurina	MATSUMOTO 1915
Aplocomidae	HESS 1965

Aplocominae new subfam.
Diagnosis. – see below (section *Overview of Aplocomidae*).

Geocoma D'ORBIGNY 1850
Type species. – *Ophiura carinata* MÜNSTER in GOLDFUSS 1826–33
Diagnosis. – see below (section *Systematic position and relationships*).

Geocoma schoentalensis sp. nov.
(Figs. 3–8)

Etymology. – After the nearby locality Schöntal with its ancient monastery.
Holotype. – Ventral side G1.6278 (Fig. 3, left side; Figs. 4, 5)
Paratype. – Dorsal side G1.6278 (Fig. 3, right side; Figs. 7, 8)
Type locality and stratum. – Rehhag near Schöntal, Canton Basel-Land (Switzerland); Middle Jurassic, Bajocian, Obere Oolithische Serien, Obere Hauptrogenstein Formation.
Diagnosis. – Disk covered on both sides by dense granulation on delicate and imbricating plates; radial shields rather small; oral and adoral shields probably free from granules; oral papillae with two conical proximal and three leaf-like distal papillae;

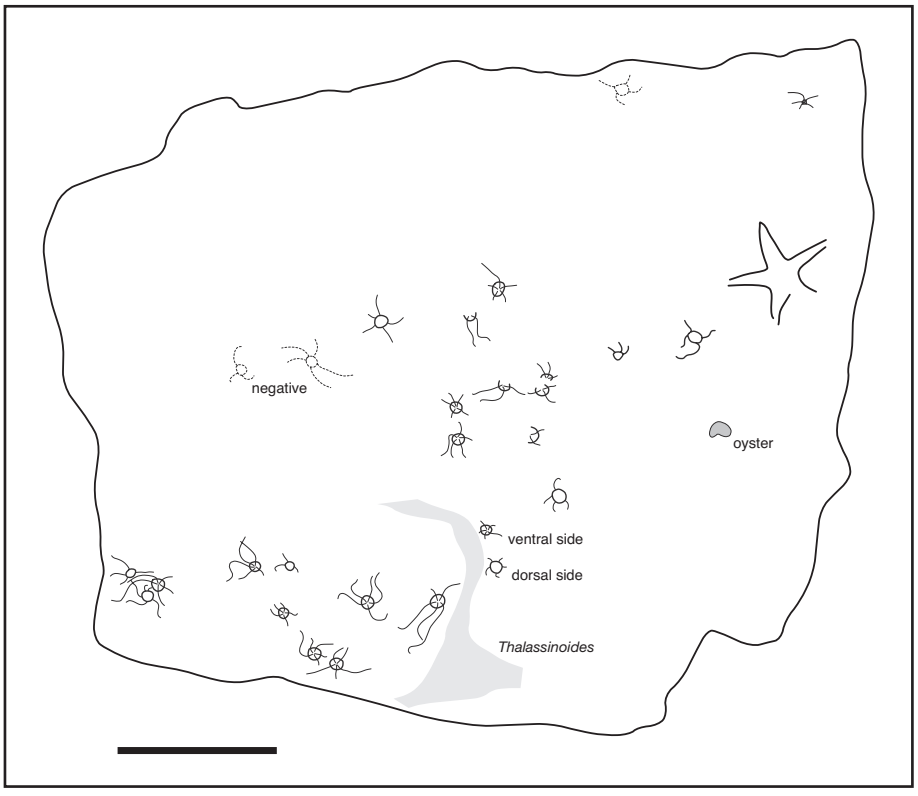

Fig. 2. Overall view of the block with ophiuroids and indeterminate sea star; Museum BL G1.6821. Drawing by C.A. Meyer. Scale bar: 10 cm.

teeth obtuse and larger than proximal papillae; second tentacle pore in the mouth slit; dorsal arms plates at the disk margin short, sickle-shaped; lateral arm plates not swollen, with four short, adpressed spines, the ventral one rounded, the three dorsal ones flattened, spine length two thirds of an arm segment; surface of lateral arm plates at most weakly striated.

Description. – The specimens have a disk diameter of 8–9 mm. The longest, nearly complete arm (specimen G1. 6279) has a length of 32 mm. Arm width at the base is 2 mm (holotype on G1. 6278) or slightly less (paratype on G1.6278).

Disk (Figs. 4, 7). The disk is covered on both sides by dense granulation that is preserved at least partly on most specimens. On the dorsal side of some specimens of the block GL.6281 the granules obscure the underlying plating. It is not certain whether the radial, oral and adoral shields were completely covered by granules. Disk plates are rather delicate and imbricated. Dorsally, a slightly larger central plate is surrounded by smaller, concentrically arranged plates. The radial shields are rather small, they appear to be separated by three single plates. The arm base starts with 2–3 short, sickle-shaped dorsal plates. Genital scales are broad, genital plates are not exposed in any of the specimens. Articulation between radial shields and genital plates is therefore unknown.

Mouth region (Fig. 5). The oral shields are broad, with a small but distinct notch aborally. The adoral shields barely meet adorally. Oral papillae start at the first ventral plate as rather large, broad scales and diminish proximally. The most proximal papilla is pointed, the teeth are obtuse and somewhat larger. Dental plates (tooth plates or torus angularis) are seen ventrally as small triangles but are not exposed as isolated pieces. As in other intact ophiuroids the proximal ends of the oral plates (also called mouth angle plates or jaws) are visible on

Fig. 3. *Geocoma schoentalensis* sp. nov. (Hauptrogenstein Formation, Rehhag near Schöntal). Slab with disk of holotype (ventral side, at left) and paratype (dorsal side, at right); Museum BL G1.6278. Photograph by H. Hess. Scale bar: 1 mm.

the ventral surface; no isolated oral plate has so far been found so that its detailed morphology is unknown. Morphology of the oral frame (including peristomial plates) is not known as none of the specimens is exposed internally.

Arms (Figs. 6–8). Arms plates are rather delicate. Dorsal arm plates are slightly keeled in mid-arm. The lateral plates do not meet dorsally and ventrally for at least half of arm length. They have straight sides and are at most weakly striated. Tentacle pores are large, with two broad, leaf-like tentacle scales, the inner (adradial) one being larger than the outer (abradial) one. The proximal lateral plates carry on their distal border four short adpressed spines, their length is about two thirds of the length of an arm segment, and on distal arm segments the spines are even shorter. The lowermost spine is rounded, the more dorsal ones have a flattened base. Spine sockets are indistinct. Isolated vertebrae are visible dorsally and ventrally where weathering has eliminated the dorsal and ventral plates, their articulation is zygospondylous.

Systematic position and relationships. – The present species is assigned to the genus *Geocoma* D'ORBIGNY 1850. *Geocoma* may be diagnosed as follows: adoral shields in contact; teeth weak, conical; six oral papillae, proximally two conical papillae, distally four leaf-like papillae; arms dorsally slightly keeled; lateral arm plates flat, moderately striated; 4–6 arm spines, length barely reaching that of arm segment; genital plate bar-like.

The set of characters displayed by the new species approaches it to *Geocoma carinata* as defined by Kutscher (1997) and in the present paper (see below). Notable is the nearly identical mouth armature. Arm spines are also quite similar, but those of *G. schoentalensis* sp. nov. have a somewhat different shape. Lateral arm plates are hardly striated in the new species, and the most proximal dorsal arm plates are sickle-shaped.

The Schöntal specimens belong to a group of mostly delicate Mesozoic ophiuroids which share the following characters: disk covered by small scales, overlain on both sides by dense granulation (though granulation may be preserved only in part), oral plates free from granules; radial shields small to moderately large, length not more than one third of disk diameter; mouth armature of contiguous row of leaf-like oral papillae that become conical adorally and thus resemble the teeth; pore of second tentacle facing into mouth opening; arms long, slender and flexible; lateral arm plates not bulging, strongly striated and very thin in some forms; arm spines small, adpressed or larger and erect; dorsal and ventral plates in contact over most of the arms; two leaf-like tentacle scales. These characters are found in the following species represented by more or less intact specimens (in order of stratigraphic appearance):

Aplocoma cf. *agassizi* (MÜNSTER 1839), Ladinian, Spain; see Hess (1965a).
Aplocoma agassizi (MÜNSTER 1839), Rhaetian, Austria, Germany; see Hess (1965a, 1970a).
Aplocoma torrii (DESIO 1951), Rhaetian, Italy; see Hess (1965a).
Aplocoma sp., Rhaetian, England; see Hess (1965a).
Aplocoma mutata HESS 1970, Hettangian, France; see Hess (1970a).
Aplocoma brevispina HESS 1985, Hettangian, Switzerland; see Hess (1985).
Sinosura brodiei (WRIGHT 1866), Toarcian, England, Germany, Switzerland; see Hess (1964, 1991).
Aplocoma aalensis HESS 1991, Aalenian, Germany; see Hess (1991).
Ophiopeza portei GUILLAUME 1926, Bathonian, France; see Guillaume (1926).
Ophiohybris griesbachii (WRIGHT 1854), Bathonian, England; see Hess (1964).
Sinosura wolburgi HESS 1962, Oxfordian, Switzerland; see Hess (1966).
Ophiopetra lithographica ENAY & HESS 1962, Kimmeridgian, France; see also Enay & Hess (1970).
Ophiopsammus? *kelheimensis* (BOEHM 1889); Kimmeridgian, France; see Enay & Hess (1970).
Ophiocten kelheimense BOEHM 1889 = *Sinosura kelheimense* (BOEHM 1889); Tithonian, Germany; see Boehm (1889); Kutscher & Röper (1995); Kutscher (1997).
Geocoma carinata (MÜNSTER IN GOLDFUSS 1826–33), Tithonian, Germany; see Hess (1960a), Kutscher (1997).
?*Geocoma canjuersensis* ROMAN, BRETON & VADON 1993, Tithonian, France. The holotype, a ventral side with a disk diameter of 16 mm, has well-developed spines and thus approaches *Ophiopetra lithographica*, but the adoral shields are quite different according to the authors. However, the corresponding drawing (Roman et al. 1993: fig. 4) appears schematic and unrealistic. No granulation is visible on the disk and the lateral arm plates are said to be in contact from the fifth arm segment (not apparent in the published photographs). The systematic position thus remains unclear.
Ophiopeza buehleri HESS (1970), Hauterivian, Switzerland; see Hess (1970b).

The fossils listed above were assigned to different families. *Aplocoma* and *Ophiopetra* were placed by Hess (1965a) in the newly established family Aplocomidae. This family was compared by Hess (1985) with the extant family Ophioleucidae MATSUMOTO, which consists mostly of abyssal forms; among these is *Ophiernus* LYMAN with two tentacle scales on the arms. Within the Aplocomidae, *Ophiopetra* forms a group of its own

Fig. 4. *Geocoma schoentalensis* sp. nov. (Hauptrogenstein Formation, Rehhag near Schöntal). Disk of holotype (Museum BL G1.6278). Photograph H. Hess (granulation enhanced). Scale bar: 1 mm.

based on the more developed arm spines. *Ophiopeza buehleri* from the Hauterivian of Switzerland and *Ophiopsammus*? *kelheimensis* from the Kimmeridgian of France were considered by Hess (1970b) and Enay & Hess (1970) as belonging to Ophiodermatidae. *Sinosura*, with its type species *S. brodiei* (WRIGHT), was thought by Hess (1964) to belong in Chilophiurina, possibly Ophioleucidae, but final classification was left open because of uncertain disk granulation in *S. brodiei*.

Smith et al. (1995) performed a cladistic analysis of extant ophiuroids. They also included the Aplocomidae in their analysis, but the lack of key internal morphological characters in even intact fossil specimens precluded a classification into higher taxa. Mainly for stratigraphical reasons, the Aplocomidae was taken as a putative plesiomorphic ancestral group to the chilophiurine/gnatophiurine clade. Smith et al. (1995) recommended a classification of Ophioleucinae MATSUMOTO 1915 as a subfamily of Ophiuridae LYMAN 1865. Common to Ophioleucinae and Ophiodermatinae is the cover of disk plates in dense granulation that obscures the underlying plating. Development of arm spines may be an unreliable character for suprageneric classification (Smith et al. 1995). Classification of the fossil forms in modern taxa is thus fraught with problems and we prefer a classification that relies on characters likely to be preserved in fossils. The classification should include characters of isolated lateral arm plates, such as shape, ornamentation and spine sockets because these have proved to be useful for description of fossil faunas (Hess 1960b, 1962, 1963, 1965b, 1966, 1975a, 1975b; Kutscher 1987b; Kutscher 1996; Kutscher & Hary 1991; Kutscher & Jagt 2000; Kristan-Tollmann et al. 1979; Kristan-Tollmann & Gramann 1992). However, these characters are rarely used in the classification of modern forms. Many Mesozoic forms based on fragmentary material were tentatively placed in extant genera.

It is obvious from the above list that the group is in need of revision. Two of the species from this group have recently become available in large numbers and excellent preservation from the Early Tithonian Plattenkalk facies (Moernsheim Formation, Malm ζ 3) of Hienheim, Germany (Kutscher & Röper 1995, Kutscher 1997, Röper & Rothgaenger 1998). One of the Hienheim ophiuroids, classified in these papers as *Ophiopetra lithographica* ENAY & HESS 1962, is characterized by prominent spines. The other form has been described under the names of *Ophiocten kelheimense* and *Ophiopsammus*? *kelheimensis*, but Kutscher & Röper (1995) assigned it to *Sinosura*. *Geocoma carinata* occurs in the somewhat older Solnhofen Formation (Malm ζ 2) of Zandt but the preservation is very rarely sufficient for accurate taxonomy. However, Kutscher (1997) described two well-preserved specimens from Zandt and suggested that *carinata* and *kelheimense* are just states of preservation. He proposed to maintain *Sinosura* with its well-defined species pending final clarification. Because *Geocoma carinata* has priority, *Sinosura kelheimense* would become a subjective junior synonym. The original description of *Geocoma carinata* with figures (Münster in Goldfuss 1826–33: 206, pl. 62, fig. 5) is insufficient to properly define the species and we deem it necessary to designate a lectotype or a neotype. Based on the new specimens from Zandt and the large Hienheim material available, *Geocoma* can now be properly diagnosed, as outlined at the beginning of this section.

Is *Sinosura* a junior synonym of *Geocoma* as suggested by the new studies? *Sinosura* is known from two species represented by more or less intact specimens (*S. brodiei* and *S. wolburgi*) and a number of species based on isolated material, mainly lateral arm plates. *Sinosura brodiei* and *S. wolburgi* differ by some characters. *Sinosura brodiei* has slender, bar-like genital plates (Hess 1964: fig. 39), those of *S. wolburgi* are club-shaped (Hess 1966: fig. 19). Ventral and dorsal arm plates are separated by the lateral plates over a larger part of the arms in specimens of *S. brodiei* from the type locality (Hess 1964: pl. 1), in *S. wolburgi* the ventral plates are more widely in contact (Hess 1966: fig. 18d). However, in specimens of *S. brodiei* from the Toarcian of Germany, the dorsal plates are contiguous on a larger part of the arms (Hess 1991: fig. 5). The reasons for this difference is unknown. Arm spines of *S. brodiei* are inserted on 4–6 weak sockets of similar size, whereas in *S. wolburgi* two ventral, larger sockets are followed dorsally by more than a dozen very fine spines inserted on the jagged, retreating edge of the arm plate (Hess 1966: fig. 19). Both species share very short arm spines, and thin, commonly bent (with angular ventral/dorsal sides) and strongly striated arm plates with a pronounced distal tongue; the inside shows two weak ridges or knobs (Hess 1960b: fig. 30; 1962: fig. 21, 23; 1966: fig. 65; see also Kutscher 1996: pl. 2, fig. 12). *Geocoma carinata* (including the Hienheim specimens) has somewhat longer arm spines; the lateral plates are also bent and have a continuous, distinct ridge on the inside; such a ridge is also shown by lateral plates of *Sinosura derecta* (Hess 1963: fig. 11) considered by Kutscher & Röper (1995, p. 92) to be synonymous with *Geocoma carinata*. The genital plate is slender and bar-like, matching that of *Sinosura brodiei*. *G. carinata* thus more strongly resembles the Early Jurassic *S. brodiei* than the Late Jurassic *S. wolburgi*. Despite the admittedly small differences between the type species of the two genera, *brodiei* and *carinata*, we maintain *Sinosura* as a valid genus.

Overview of Aplocomidae

Family Aplocomidae HESS 1965

Diagnosis. – Disk covered by small scales, overlain on both sides by dense granulation that does not cover the oral shields, except in *Aplocoma brevispina*; adoral shields barely to widely in contact; radial shields small; mouth armature of contiguous row of oral papillae and mostly small, conical to flattened teeth; oral frame without wings; second tentacle pore facing into mouth opening; arms long, slender and flexible, lateral plates flat or bent, not swollen; arm spines mostly few, short and adpressed or longer and erect; dorsal and ventral arm plates contiguous over most of the arms; two leaf-like tentacle scales; genital scale broad and flat, genital plate bar-like to club-shaped. Middle Triassic–Late Jurassic.

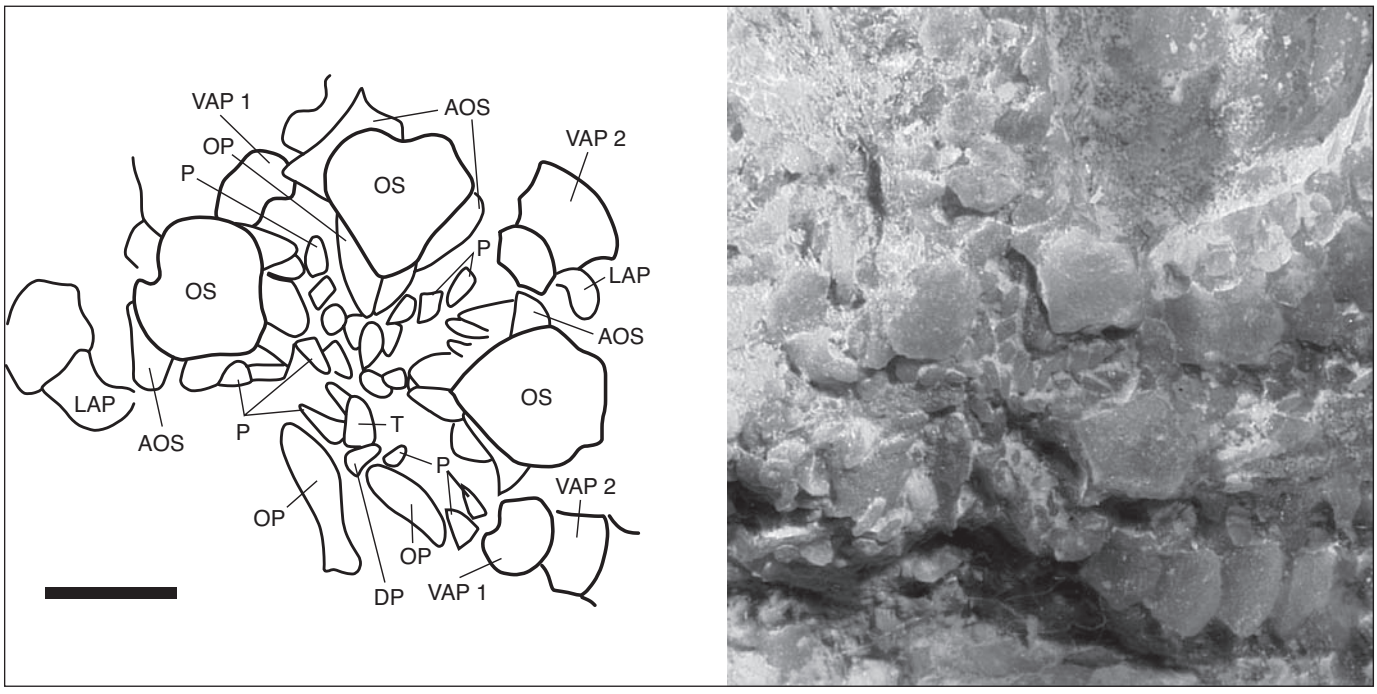

Fig. 5. *Geocoma schoentalensis* sp. nov. (Hauptrogenstein Formation, Rehhag near Schöntal). Drawing (left) and photograph (right) of mouth armature of holotype (Museum BL G1.6278). Abbreviations: AOS, adoral shield; DP, dental plate (torus angularis); LAP, lateral arm plate; OP, oral plate; OS, oral shield; P, oral (mouth) papillae; T, tooth; VAP, ventral arm plate. Photograph M. Knappertsbusch. Scale bar: 1 mm.

Remarks. – Two subfamilies may be distinguished by the development of the arm spines. Within each subfamily species must be distinguished by relatively small differences. These include the shape of teeth and oral papillae, the position of the adoral shields, and the shape of the lateral arm plates with their spines. It has to be born in mind that the paired adoral shields are overridden or partly covered by the oral shield, and preservation may disturb this feature. An exception is *Aplocoma agassizi* with adoral shields widely in contact (Hess 1965a: pl. 14).

Subfamily Aplocominae new

(ex Aplocomidae Hess 1965)

Diagnosis. – Arm spines small, adpressed, inserted on indistinct sockets; arm plates commonly striated.

Genus *Aplocoma* d'Orbigny 1852
Type species. – Acroura Agassiz(*i*) Münster 1839
Diagnosis. – Lateral arm plates either weakly striated or unstriated.

Aplocoma agassizi (Münster 1839)
Diagnosis. – Five leaf-like oral papillae; teeth weak, conical; adoral shields widely in contact; ventral plates narrow; tentacle pores very large, tentacle scales broad; arm spines short, barely reaching length of arm segment.

Aplocoma aalensis Hess 1991
Diagnosis. – Five oral papillae, proximally leaf-like, distally two conical papillae; adoral shields barely in contact; three small arm spines, length about a third of arm segment; ventral arm plates broad; lateral arm plates weakly striated.

Aplocoma brevispina Hess 1985
Diagnosis. – Oral plates probably covered by granules; teeth weak; oral papillae leaf-like proximally, distally two conical oral papillae; ventral arm plates broad in proximal part of arm; three rudimentary arm spines.

Aplocoma buehleri (Hess 1970)

Ophiopeza bühleri – Hess 1970b: 1070, fig. 1, 2; pl. 1; pl. 2, fig. 1–6.

Diagnosis. – 6–7 oral papillae, proximal papillae leaf-like, distal papillae conical; seven arm spines as long as arm segment; dorsal arm plates slightly keeled, ventral and dorsal arm plates very broad.
Remarks. – The species was assigned by Hess (1970b) to the extant genus *Ophiopeza*. However, this genus of Ophiodermatidae has the jaws covered by granules, a continuous row of about 10 oral papillae of similar size, and 10 or more very small arm spines. Its assignment to an extant genus is therefore questionable and we prefer to place it in *Aplocoma*.

Aplocoma mutata HESS 1970
Diagnosis. – Adoral shields widely in contact; oral papillae leaf-like but small, four proximal papillae and two somewhat larger distal ones; teeth cone-shaped, weak; ventral arm plates narrow, but contiguous; three arm spines, somewhat longer than arm segment.

Aplocoma torrii (DESIO 1951)
Diagnosis. – Oral plates probably covered by granules, radial shields partly free from granules; teeth very weak, spine-like; row of oral papillae composed of four small spine-like proximal papillae and two larger distal papillae; adoral shields in contact; four arm spines, length one third to half of arm segment; ventral arm plates narrow, but contiguous; genital plate club-shaped.

Genus *Geocoma* D'ORBIGNY 1850
Diagnosis. – see above (section *Systematic position and relationships*).

Geocoma carinata (MÜNSTER in GOLDFUSS 1826–33)

1826–33 *Ophiura carinata* – Münster in Goldfuss: 206; pl. 62, fig. 5.
1876–80 *Geocoma planata* – Zittel: 446, fig. 316 c,d.
1889 *Ophiocten kelheimense* – Boehm: 274, pl. 5, fig. 6–8.
1970 *Ophiopsammus*? *kelheimensis* (BOEHM) – Enay & Hess: 1095, fig. 1, 2.
1995 *Sinosura kelheimense* (BOEHM) – Kutscher & Röper: 90, pl. 2; 4; 5, fig. 3, 4.
1997 *Sinosura kelheimense* (BOEHM) – Kutscher: 1, pl. 1, fig. 3, 4; pl. 2, fig. 2–5.
1997 *Geocoma carinata* (MÜNSTER IN GOLDFUSS) – Kutscher: 2, text-fig. 1; pl. 1, fig. 1, 2; pl. 2, fig. 1.

Diagnosis. – 5–6 round, slender arm spines; all proximal dorsal arm plates of similar length.
Neotype. – Ventral side, NMB M 10'637 (Fig. 9).

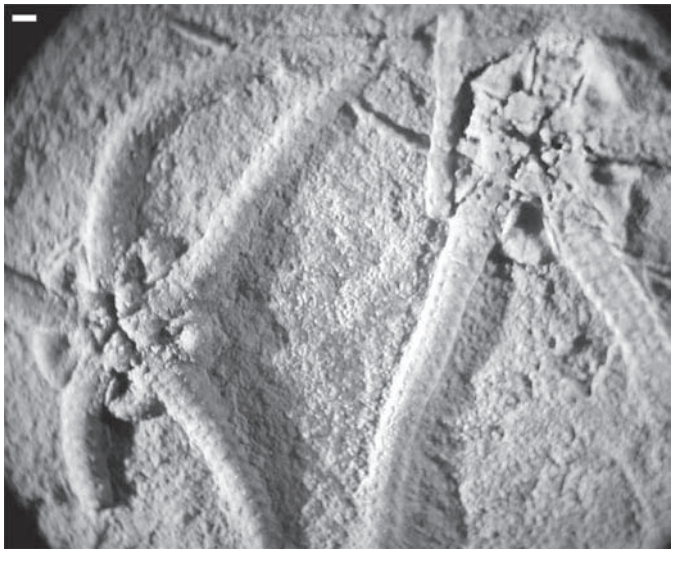

Fig. 6. *Geocoma schoentalensis* sp. nov. (Hauptrogenstein Formation, Rehhag near Schöntal). Two specimens showing their ventral side; Museum BL G1.6279. Photograph H. Hess. Scale bar: 1 mm.

Type locality and stratum. – Zandt Quarry, Germany, Late Jurassic, Early Tithonian, Solnhofen Formation (Malm ζ 2).
Description of the neotype. – The specimen shows the ventral side with two nearly complete arms; they have a length of 27 mm and are composed of 59–60 segments. The disk has a diameter of 3.5 mm, it is not flattened but has a thickened peripheral part where the scales are upright. Disk scales are visible in some parts, granulation is preserved only exceptionally. The teeth are weak, distal papillae are leaf-like; adoral shields are barely in contact proximally. The arms are flattened as commonly observed in *G. carinata*. The tentacle pores are large and have two scales. The ventral arm plates are broad proximally and are contiguous on about half the segments, they rapidly become narrow.
Remarks. – As outlined above, selection of a type specimen for this well-known and important species is highly desirable. In the original description of *Geocoma carinata* with a figure (Münster in Goldfuss 1826–33: 206; pl. 62, fig. 5), only the outline of the species can be recognized. The original material from the Zandt Quarry could not be traced and all specimens from this quarry preserved in old collections do not show the details necessary for comparative work. Over time the Zandt Quarry has furnished abundant specimens; and their overall shape such as disk diameter, arm length and width as well as any additional characters such as granulation of the disk and development of arm spines leave no doubt that they belong to a single species. Selection of a neotype according to the ICZN (1999), Art. 75, is therefore justified.

Geocoma schoentalensis sp. nov.
Diagnosis. – See above. As discussed above the present species differs from *G. carinata*, the only other species assigned to *Geocoma*, by having four arm spines, the dorsal ones flattened, and by the sickle-shaped dorsal arm plates at the base of the arm.

Genus *Sinosura* HESS 1964
Type species. – Acroura Brodiei WRIGHT 1866
Diagnosis. – Oral papillae mostly weak; lateral arm plates very thin and strongly striated, bent, with distal tongue.
Remarks. – This diagnosis is based on the type species and on *Sinosura wolburgi*. A number of species was established on isolated lateral arm plates and assigned to this genus (Hess 1965b, 1966; Kutscher 1996; Kutscher & Jagt 2000, Kutscher & Villier 2003); in some cases the lateral arm plates have stronger dorsal spine sockets and the inside shows a continuous ridge.

Sinosura brodiei (WRIGHT 1866)
Diagnosis. – Oral papillae weak, similar to teeth; radial shields broad.

Sinosura wolburgi HESS 1962
Diagnosis. – Lateral arm plates with two larger ventral spines and numerous very fine dorsal spines attached to jagged distal edge of ornamented part.

Sinosura? *portei* (GUILLAUME 1926)

Ophiopeza portei GUILLAUME 1926

Diagnosis. – Dorsal plates on center of disk small, of similar size; adoral shields small, triangular, not in contact adorally; oral papillae of similar size; five arm spines.
Remark. – Assignment to *Sinosura* is tentative because the lateral arm plates apparently are not bent and striated according to the original description (Guillaume 1926).

Subfamily Ophiopetrinae new

Diagnosis. – Arms spines robust, erect, inserted on distinct sockets; lateral arm plates not striated.

Ophiopetra ENAY & HESS 1962
Diagnosis. – Teeth conical; 3–4 arm spines, length up to two arm segments; dorsal arm plates triangular with convex distal edge, in contact only in proximal part of arms.

Ophiopetra lithographica ENAY & HESS 1962
Diagnosis. – Teeth conical, increasing in size dorsally and becoming flattend; six oral papillae, proximally four leaf-like papillae, distally two conical papillae; surface of lateral arm plates slightly concave; arm spines longer than arm segment; adoral shields barely in contact; genital plate bar-like.

Ophiopetra? *bathonica* HESS 1964
Diagnosis. – Disk and arm plates rather massive; 4–6 leaf-like oral papillae; teeth obtuse; tentacle scales small; three arm spines, length barely reaching arm segment.

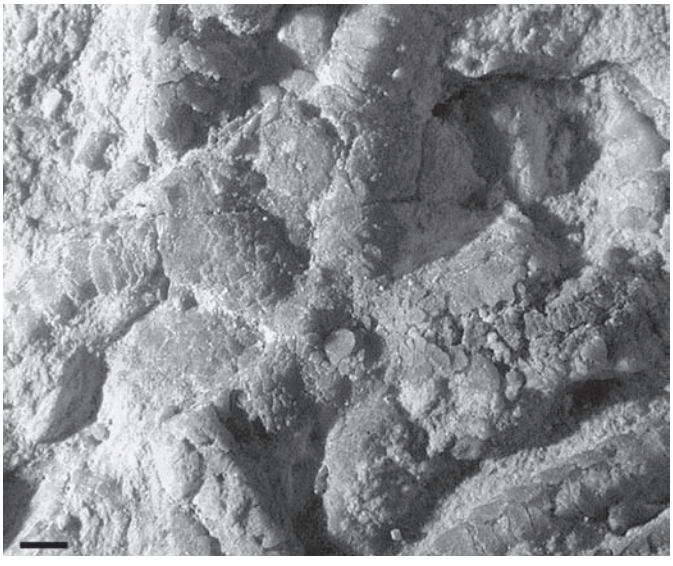

Fig. 7. *Geocoma schoentalensis* sp. nov. (Hauptrogenstein Formation, Rehhag near Schöntal). Disk of paratype, dorsal side (Museum BL G1.6278). Photograph M. Knappertsbusch. Scale bar: 1 mm.

Remark. – Assignment to *Ophiopetra* is uncertain because dorsal side and granulation of disk are unknown in the type specimen.

Ophiohybris HESS 1964
Diagnosis. – Dorsal side unknown; oral plates with raised proximal end; five oral papillae, the two distal papillae conical; teeth obtuse; adoral shields barely in contact; genital scale not flat; 3–4 robust arm spines, length corresponding to arm segment; tentacle pores very large; ventral arm plates narrow but contiguous.

Ophiohybris griesbachii (WRIGHT 1854)
Diagnosis. – See genus (monotypic).

Note on *Arenorbis squamosus* (PICARD 1858)

The Middle Triassic *Arenorbis squamosus*, re-described by Hess (1970a), has some characters of the Aplocominae. It has a granulated disk, a continuous row of oral papillae which increase in size distally up to two smaller papillae covering the second tentacle, and long, flexible arms with three small spines; tentacle pores are moderately large and ventral arm plates rather narrow. In contrast to Aplocominae, the oral plates were covered by granules and carry below the weak teeth infradental papillae of similar size. The tentacle pores have two abradial scales; adradially are three additional, small scales. Ventral and dorsal arm plates are not contiguous, or only near the disk (see Kutscher 2000). The form may easily be recognized by the very slender arms at the disk. The set of characters displayed by *Arenorbis* defies crown group classification as proposed by Smith et al. (1995) but reinforces the notion that the Triassic was a time where diversification into presently accepted clades started.

Note on *Praeaplocoma hessi* (LORIGA & CAVICCHI 1969)

The Early Triassic *Praeaplocoma hessi* has been assigned by Loriga & Cavicchi (1969) to the Aplocomidae. The nearly twenty syntypes on the slab examined belong to a small species, with a maximum disk diameter of about 5 mm. The disk is quite similar to forms of Aplocomidae. It is covered by thin, imbricated plates and both sides are granulated, except the distal part of the radial shields. The oral plates carry small, spine-like teeth and four oral papillae increasing in size distally. The adoral shields are in contact proximally. The arms taper rapidly. The lateral arm plates are swollen, with 3–5 spines slightly longer than an arm segment. The ventral arm plates are narrow, the dorsal arm plates are rudimentary. The tentacle pores are well developed and carry two tentacle scales. The rapidly tapering arms with their rudimentary dorsal plates and bulging lateral plates preclude assignment to Aplocomidae as defined herein. These characters are also found in the Middle Triassic *Aspiduriella* BOLETTE 1998, but the type species of this genus, *A. scutellata* (BLUMENBACH), has a heavily-plated dorsal disk with a ring of large radial shields (see Toula 1887, Calzada &

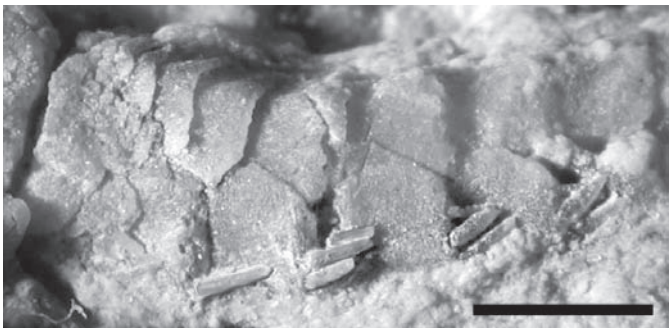

Fig. 8. *Geocoma schoentalensis* sp. nov. paratype (Hauptrogenstein Formation, Rehhag near Schöntal). Enlarged oblique lateral/dorsal view of proximal arm, margin of disk is at left; note short dorsal arm plates near disk and arm spines; Museum BL G1.6278. Photograph H. Hess. Scale bar: 1 mm.

Gutiérrez 1988, Seilacher 1988). This is also true of the closely related *A. streichani* KUTSCHER 1987a. However, *A. streichani* has vertebrae with streptospondylous articulation (M. Kutscher, pers. comm. 2007) so that classification may have to be revised, pending examination of the shape of vertebrae of other Triassic ophiuroids. Other species assigned to *Aspiduriella* have characters that are closer to *Praeaplocoma*. These include *A. ludeni* v. Hagenow with more numerous dorsal disk plates, see also Radwański (2002), and *A. montserratensis* Calzada & Guttiérrez (1988) with largely contiguous dorsal and ventral arm plates; however, in the Spanish species the dorsal disk closely resembles that of *A. scutellata*. It seems possible that *Praeaplocoma* developed into either *Aspiduriella* by shortening of arms and increasing thickness of disk plates, or into *Aplocoma* by lengthening of arms and reducing thickness of arm plates.

Discussion

Sedimentology and taphonomy

The beds that contained the large block consist of medium- to fine-grained oolitic limestone (grainstone) with small-scale cross-bedding; the base of the block shows a large number of trochospiral gastropods and some oncoids. Towards the top the gastropod-rich interval grades into a medium- to fine-grained oolite. The surface shows micritic patches that are most probably the result of subsequent fills of crustacean burrows (*Thalassinoides*). The slabs contain ophiuroids within a layer of approximately 5 mm, and which are either embedded in oolitic or the micritic matrix. The outcrop shows 5 m of thickly bedded grainstones that are laterally discontinuous, a typical feature of the Hautprogenstein Formation. We interpret the sequence as part of a small calcarenitic, subaquatic dune.

The imprint of the sea star on the upper surface is the mould of a body fossil that weathered away, because in one area two body frame ossicles are still in place. The ophiuroids are completely articulated and show no signs of early decay (e.g. missing distal parts of the arms, loosened disk plates). They correspond to the taphonomic grade 1 Echinoderms of Brett et al. (1997), considered as extremely rare in the fossil record. Furthermore, the site can be genetically classified as an obrution deposit and belongs to the widely recognized "Hauptrogenstein type" (Meyer 1988a, Brett & Seilacher 1991, Brett et al. 1997). The presence of both, ventral and dorsal sides on the same slab is another indication of rapid smothering by moving sediment; such conditions are also known from the famous asterozoan Lagerstätte of the middle Oxfordian Effingen Formation of the Weissenstein (Meyer 1984). The presence of widespread blanket-like deposits of echinoderm skeletal grain- and packstones with cross-stratification assigns the present Lagerstätte to the Taphofacies I A of Brett et al. (1997, carbonate dominated skeletal shoals). According to Brett et al. (1997) this taphofacies is usually found during High Stand Transgressive System Tracts. The sequence stratigraphic interpretation of Gonzalez (1996) of the "Obere Oolithische Serien" as deposits of a High Stand Transgressive System Tracts is in accordance with the interpretation of Brett et al. (1997) that the observed taphofacies is usually found during HST System Tracts.

Substrate preferences and feeding of Ophiodermatidae

Because there are no large morphological differences between the fossil species of the family Aplocomidae and the exant species of the family Ophiodermatidae we give a brief summary of substrate preference of aplocomids before continuing with a discussion of the ophiodermatids.

Most of the species of *Aplocoma* of the Muschelkalk facies from Germany or Poland as well as the Tethyan realm occur in fine-grained micritic sediments and in most cases are monospecific mass occurrences (e.g. Radwański 2002).

Ophiopetra? *bathonica* HESS is known from several localities in Europe. The type specimen from Chippenham (Wiltshire, southern England) was recovered from the Forest Marble and is preserved on a calcarenitic slab. A fragmentary specimen of *O.* cf. *bathonica* HESS has been described from the Hauptrogenstein Formation of Schinznach where it occurs together with echinoids, isocrinids, different sea stars and crustaceans (Hess 1972) on oolitic limestone. *Ophiopetra oertlii* HESS occurs as isolated ossicles in many mud-dominated deposits from the Toarcian of France (Kutscher & Villier 2003), the Lower Aalenian and Toarcian of Germany (Kutscher 1996) and the Late Jurassic of Switzerland (Hess 1965b). *Ophiopetra oertlii* HESS is known from articulated specimens from the Late Jurassic Effingen Formation where it occurs together with astropectinid sea stars (*Pentasteria*), *Ophiomusium gagnebini* (THURMANN), *Sinosura wolburgi* HESS and decapod crustaceans on fine-grained calcareous sands (Meyer 1984). *Ophiopetra lithographica* ENAY & HESS is known from the Upper Jurassic Plattenkalk limestones of the Kelheim area (Germany) and from the same facies near Cerin in France (Enay & Hess 1962). These deposits are thought to have been formed under oxygen conditions varying from almost normal to almost anoxic (Etter 2002), and at such times the ophiuroids may have been transported into the

habitat. However, the mass occurrences in the Hienheim area, where hundreds of specimens of *Geocoma carinata* and *Ophiopetra lithographica* have been found, are thought to represent smothered autochthonous communities (Röper & Rothgaenger 1998). *Ophioderma*? *radiatum* KUTSCHER & JAGT and *Ophioderma*? *substriatum* (RASMUSSEN) occur as isolated vertebrae and lateral arm shields in Maastrichtian sediments of the island of Rügen (Germany) (Kutscher & Jagt 2000). Aplocomids were thus not restricted to a particular sediment type.

The autecology of extant members of the family Ophiodermatidae is well known. Most of the tropic species of the genus *Ophioderma* can be found in shallow water environments. *Ophioderma appressum* (SAY), an abundant shallow water species in the Caribbean and off Florida, frequently occurs with other gregarious reef flat species. Its diet includes plant material, calcareous and filamentous algae (Hendler et al. 1995). It is a nocturnal scavenger feeding on fish faeces and other detritus. *Ophioderma brevicaudum* LUETKEN lives in high-energy areas near breaking waves, on beach rock platforms and patch reefs; this habitat is consistent with its short and blunt arms. *Ophioderma brevispinum* (SAY) lives on sea grass, shell-, sand- or mud-bottoms (Hendler et al. 1995). Some of the extant species are considered to be carnivorous; *Ophioderma brevispinum* feeds on small peracarids, brachyuran crustaceans, worms and sponges (Hendler 1982).

Extant ophiuroids with short arm spines use their mobile arms for gathering food such as carrion, detritus or prey (Lawrence 1987) while forms with robust spines are more likely suspensions feeders. *Ophioderma* in particular has been reported to be a predator, scavenger as well as a detritus feeder (Warner 1982).

Geocoma schoentalensis sp. nov. has rather flexible arms as well as short arm spines, therefore it seems likely that it was a detritus feeder but also fed on smaller prey items. The present fossil community constitutes a monospecific assemblage that represents a pioneer fauna in unstable conditions. Unstable environments are often colonized by pioneer communities consisting of opportunistic species (Aigner 1980). The Hauptrogenstein Formation deposited in very shallow water under high energy conditions represents such an unstable environment with its highly mobile substrates.

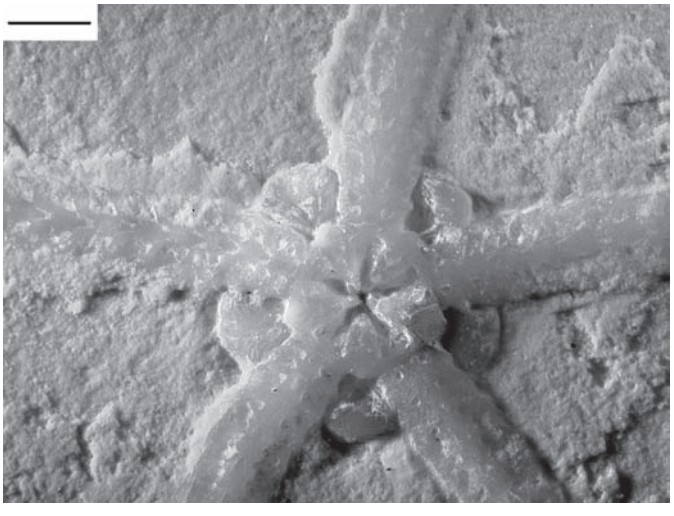

Fig. 9. *Geocoma carinata* (MÜNSTER), neotype (Lower Tithonian Solnhofen Formation, Malm ζ 2, Zandt, Germany). Ventral side of disk and proximal arms; NMB M 10637. Photograph M. Knappertsbusch. Scale bar: 1 mm.

Conclusions

The ophiuroids described are assigned to the genus *Geocoma* D'ORBIGNY 1850, and to a new species *Geocoma schoentalensis* sp. nov. The genera *Geocoma* and *Sinosura* share small adpressed arm spines with *Aplocoma* D'ORBIGNY 1852, and the subfamily Aplocominae is proposed herein for the three genera. A second subfamily, Ophiopetrinae, is proposed for the genera *Opiopetra* ENAY & HESS 1962 and *Ophiohybris* HESS 1964. Diagnostic for this subfamily is the presence of larger, erect arm spines.

The present echinoderm fauna is another example of a small asterozoan communitiy within a highly complex transgressive system tract. The Burgundy carbonate platform with its bahamian-type sediment was a vast platform with a general high-energy water regime under oligotrophic conditions. It is therefore not surprising that the majority of the fossils in this area are echinoderms, a group well adapted to such environments despite their highly delicate multi-element skeletons. The present assemblage may have been a community that colonized the highly mobile substrate for a limited time. Their demise came through sudden smothering by moving oolitic dunes or sandwaves. The taphonomic mode of the present site is in accordance with most *in situ* epibenthic echinoderm communities found in the carbonate deposits of the Hauptrogenstein Formation (e.g. Hess 1972, 1999; Meyer 1987).

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REFERENCES

Aigner, T. 1980: Biofabrics and stratinomy of the Lower Kimmeridge Clay (Upper Jurassic, Dorset, England). Neues Jahrbuch Geologie Paläontologie, Abh. 159, 324–338.

Ausich, W.I. 2001: Echinoderm taphonomy. In: Jangoux, M. & Lawrence, J. M. (Eds.): Echinoderm Studies 6. Balkema, Rotterdam, 171–227.

Boehm, G. 1889: Ein Beitrag zur Kenntnis fossiler Ophiuren. Bericht Naturforschende Gesellschaft Freiburg 4, 232–287.

Brett, C.E. & Seilacher, A. 1991: Fossil Lagerstätten: a taphonomic consequence of event sedimentation. In: Einsele, G. et al. (Eds.): Cycles and Events in Stratigraphy. Springer, New York, 283–297.

Brett, C.E., Moffat, H.A., & Taylor, W.L. 1997: Echinoderm taphonomy, taphofacies and Lagerstätten. In: Waters, J.A. & Maples, C.G. (Eds.): Geobiology of Echinoderms. Paleontology Society Papers 3, Carnegie Museum, 147–190.

Calzada, S. & Gutiérrez, D. 1988: Ofiuras (Echinodermata) del Ladiniense catalàn. Batalleria 1 (1987), 31–38.

Enay, R., & Hess, H. 1962: Sur la découverte d'Ophiures (*Ophiopetra lithographica* n.g. n.sp.) dans le Jurassique supérieur du Haut-Valromey (Jura méridional). Eclogae geologicae Helvetiae 55, 657–673.

Enay, R. & Hess, H. 1970: Nouveaux gisements à Stelléroides dans le Kimméridgien supérieur (Calcaire en plaquettes) du Jura méridional. Eclogae geologicae Helvetiae 63, 1093–1107.

Etter, W. 2002: Solnhofen: Plattenkalk Preservation with *Archaeopteryx*. In: Bottjer, D.J. et al. (Eds.): Exceptional Fossil Preservation. Columbia University Press, New York, 327–352.

Goldfuss, G.A. 1826–1833: Petrefacta Germaniae, v. 1, Divisio secunda, Radiariorum reliquiae [Echinodermata]. Arnz & Co., Düsseldorf, 115–221.

Gonzalez, R. 1996: Response of shallow-marine carbonate facies to third-order and high-frequency sea-level fluctuations: Hauptrogenstein Formation, northern Switzerland. Sedimentary Geology 102, 111–130.

Gonzalez, R. & Wetzel, A. 1996: Stratigraphy and paleogeography of the Hauptrogenstein and Klingau Formations (middle Bajocian to late Bathonian), northern Switzerland. Eclogae geologicae Helvetiae 89, 695–720.

Guillaume, L. 1926: *Ophiopeza portei*, Ophiure nouvelle du Bathonien supérieur de Ranville (Calvados). Bulletin de la Société Géologique de France 26, 17–126.

Hendler, G. 1982: The feeding biology of *Ophioderma brevispinum* (Ophiuroidea; Echinodermata). In: Lawrence, J.M. (Ed.): Echinoderms. Balkema, Rotterdam, 21–27.

Hendler, G., Miller, J.E., Pawson, D.L. & Kier, P.M. 1995: Echinoderms of Florida and the Caribbean – Sea Stars, Sea Urchins, and Allies. Smithsonian Institution Press, Washington & London, 390 pp.

Hess, H. 1960a: Neubeschreibung von *Geocoma elegans* (Ophiuroidea) aus dem unteren Callovien von La Voulte-sur-Rhône (Ardèche). Eclogae geologicae Helvetiae 53, 335–385.

Hess, H. 1960b: Ophiurenreste aus dem Malm des Schweizer Juras und des Departements Haut-Rhin. Eclogae geologicae Helvetiae 53, 385–421.

Hess, H. 1962: Mikropaläontologische Untersuchungen an Ophiuren I, II. Die Ophiuren aus dem Lias (Pliensbachien-Toarcien) von Seewen (Kt. Solothurn). Eclogae geologicae Helvetiae 55, 595–656.

Hess, H. 1963: Mikropaläontologische Untersuchungen an Ophiuren III. Die Ophiuren aus dem Callovien von Liesberg (Berner Jura). Eclogae geologicae Helvetiae 56, 1141–1164.

Hess, H. 1964: Die Ophiuren des englischen Jura. Eclogae geologicae Helvetiae 57, 756–801.

Hess, H. 1965a: Trias-Ophiuren aus Deutschland, England, Italien und Spanien. Mitteilungen Bayerische Staatssammlung Paläontologie Historische Geologie 5, 151–177.

Hess, H. 1965b: Mikropaläontologische Untersuchungen an Ophiuren IV. Die Ophiuren aus dem Renggeri-Ton (Unter-Oxford) von Chapois (Jura) and Longecombe (Ain). Eclogae geologicae Helvetiae 58, 1059–1082.

Hess, H. 1966: Mikropaläontologische Untersuchungen an Ophiuren V. Die Ophiuren aus dem Argovien (unteres Ober-Oxford) vom Guldenthal (Kt. Solothurn) und von Savigna (Dépt. Jura). Eclogae geologicae Helvetiae 59, 1025–1063.

Hess, H. 1970a: Ein neuer Schlangenstern (*Aplocoma mutata* n. sp.) aus dem Hettangien von Ceilhes (Hérault) und Bemerkungen über "*Ophioderma*" *squamosa* aus dem Muschelkalk. Eclogae geologicae Helvetiae 63, 1059–1067.

Hess, H. 1970b: Schlangensterne und Seesterne aus dem oberen Hauterivien "Pierre jaune" von St-Blaise bei Neuchâtel. Eclogae geologicae Helvetiae 63, 1069–1091.

Hess, H. 1972: Eine Echinodermen-Fauna aus dem mittleren Dogger des Aargauer Juras. Schweizerische Paläontologische Abhandlungen 92, 87 pp.

Hess, H. 1975a: Mikropaläontologische Untersuchungen an Ophiuren VI. Die Ophiuren aus den Günsberg-Schichten (oberes Oxford) vom Guldental (Kt. Solothurn). Eclogae geologicae Helvetiae 68, 591–601.

Hess, H. 1975b: Mikropaläontologische Untersuchungen an Ophiuren VII. Die Ophiuren aus den Humeralis-Schichten (Ober-Oxford) von Raedersdorf (Ht-Rhin). Eclogae geologicae Helvetiae 68, 603–612.

Hess, H. 1975c: Die Echinodermen des Schweizer Juras. Veröffentlichungen Naturhistorischen Museums Basel 8, 130 pp.

Hess, H. 1985: Schlangensterne und Seelilien aus dem unteren Lias von Hallau (Kanton Schaffhausen). Mitteilungen Naturforschende Gesellschaft Schaffhausen 33, 1–15.

Hess, H. 1991: Neue Schlangensterne aus dem Toarcium und Aalenium des Schwäbischen Jura (Baden-Württemberg). Stuttgarter Beiträge Naturkunde, Serie B, 180, 11 pp.

Hess, H. 1999: Middle Jurassic of northern Switzerland. In: Hess, H. et al. (Eds.): Fossil Crinoids. Cambridge University Press, New York, 203–215.

ICZN 1999: International Code of Zoological Nomenclature, 4th ed. International Trust for Zoological Nomenclature, London, 306 pp.

Kerr, T.J.V. & Twitchett, R.J. 2004: Experimental decay and disarticulation of *Ophiura texturata*: implications for the fossil record of ophiuroids. In: Heinzeller, Th. & Nebelsick, J.H. (Eds.): Echinoderms. Taylor & Francis, München, 439–446.

Kristan-Tollmann, E. & Gramann, F. 1992: Paleontological evidence for the Triassic age of rocks dredged from the northern Exmouth Plateau (Tethyan foraminifers, echinoderms, and ostracodes). In: Rad U. von et al. (Eds.): Proceedings of the Ocean Drilling Program, Scientific Results 122, 463–474.

Kristan-Tollmann, E., Tollmann, A. & Hamedani, A. 1979: Beiträge zur Kenntnis der Trias von Persien, I. Revision der Triasgliederung, Rhätfazies im Raum von Isfahan und Kössener Fazieseinschlag bei Waliabad SE Abadeh. Mitt. Österr. Geol. Ges. 70 (1977), 119–186.

Kutscher, M. 1987a: *Aspidura streichani* n. sp. – eine neue Ophiuren-Art aus dem Muschelkalk von Rüdersdorf. Zeitschrift geologische Wissenschaften Berlin 15, 703–707.

Kutscher, M. 1987b: Die Echinodermen der Callovien-Geschiebe. Der Geschiebe-Sammler 2–3, 53–104.

Kutscher, M. 1996: Echinodermata aus dem Ober-Toarcium und Aalenium Deutschlands II, Ophiuroidea. Stuttgarter Beitr. Naturk., Ser. B, 243, 33 pp.

Kutscher, M. 1997: Bemerkungen zu den Plattenkalk-Ophiuren, insbesondere *Geocoma carinata* (v. Münster, 1826). Archaeopteryx 15, 1–10.

Kutscher, M. 2000: Schlangensterne (Ophiuroidea) aus dem Oberen Muschelkalk von Atzendorf bei Magdeburg. Aufschluss 51, 301–304.

Kutscher, M. & Hary, A. 1991: Echinodermen im Unteren Lias (Bucklandi und Semicostatum zone) zwischen Ellange und Elvange (SE Luxemburg). Neues Jahrbuch Geologie Paläontologie, Abh. 182, 37–72.

Kutscher, M. & Jagt, J.W.M. 2000: Early Maastrichtian ophiuroids from Rügen (northeast Germany) and Møn (Denmark). Scripta Geologica 121, 45–179.

Kutscher, M. & Röper, M. 1995: Die Ophiuren des "Papierschiefers" von Hienheim (Malm ζ 3, Untertithon). Archaeopteryx 13, 85–99.

Kutscher, M. & Villier, L. 2003. Ophiuroids remains from the Toarcian of Sainte-Verge (Deux-Sèvres, France): paleobiological perspectives. Geobios, 36, 179–194.

Lawrence, J.M. 1987: A functional biology of Echinoderms. Johns Hopkins University Press, Baltimore, 340 pp.

Loriga, C.B. & Cavicchi, A.B. 1969: *Praeaplocoma hessi* n. gen., n. sp., un ofiuro del Werfeniano (Trias Inferiore) del gruppo della Costabella, Dolomiti. Mem. Geopal. Univers. Ferrara 2, fasc. II, 185–197.

Meyer, C.A. 1984: Palökologie und Sedimentologie der Echinodermenlagerstätte Schofgraben (mittl. Oxfordian, Weissenstein; Kt. Solothurn). Eclogae geologicae Helvetiae 77, 733–762.

Meyer, C.A. 1987: Palökologie, Biofazies und Sedimentologie von Seeliliengemeinschaften aus dem unteren Hauptrogenstein des Nordwestschweizer Jura. Unpublished PhD Thesis, University of Bern, 83 pp.

Meyer, C.A. 1988a: Paläoökologie, Biofazies und Sedimentologie von Seeliliengemeinschaften aus dem Unteren Hauptrogenstein des Nordwestschweizer Jura. Revue de Paléobiologie 7, 359–433.
Meyer, C.A. 1988b: Paléoécologie d'une communauté d'ophiures de la région havraise (Seine-Maritime). Bulletin trimestriel de la Société géologique de Normandie et des Amis du Museum du Havre 75, 26–35.
Meyer, C.A. 1990: Depositional environment and paleoecology of crinoid communities from the Middle Jurassic Burgundy platform of Western Europe. In: De Ridder, C. et al. (Eds.): Echinoderm Research. Balkema, Rotterdam, 25–31.
Münster, G. Graf zu. 1839. Beschreibung einiger neuen Radiarien der Flöz-Formation. Beiträge zur Petrefactenkunde 1, 85–90.
Radwański, A. 2002: Triassic brittlestar beds of Poland: a case of *Aspiduriella ludeni* (v. Hagenow, 1846) and *Arenorbis squamosus* (E. Picard, 1858). Acta Geologica Polonica 52, 395–410.
Röper, M. & Rothgaenger, M. 1998: Die Plattenkalke von Hienheim (Landkreis Kelheim). Echinodermen-Biotope im Südfränkischen Jura. Eichendorf Verlag, Eichendorf, 110 pp.
Roman, J., Breton, G. & Vadon, C. 1993: Ophiuridés et astéride (Echinodermata) du Tithonien de Canjuers (Var, France). Annales de Paléontologie 79, 1–18.
Seilacher, A. 1988: Schlangensterne (Aspidura) als Schlüssel zur Entstehungsgeschichte des Muschelkalks. In: Hagdorn, H. (Ed.): Neue Forschungen zur Erdgeschichte von Crailsheim (Sonderbände der Gesellschaft für Naturkunde in Württemberg, Band 1). Schweizerbart, Stuttgart, 85–98.
Smith, A.B., Paterson, H.L.J. & Lafay, B. 1995: Ophiuroid phylogeny and higher taxonomy: morphological, molecular and palaeontological perspectives. Zoological Journal of the Linnean Society 114, 213–243.
Toula, F. 1887: Ueber Aspidura Raiblana nov. spec. Sitz.-Ber. k. Akad. Wiss. math.-naturwiss. Cl., I. Abt. 96, 361–369.
Warner, G.H. 1982: Food and feeding mechanisms: Ophiuroidea. In: Jangoux, M. & Lawrence, J.M. (Eds): Echinoderm nutrition. Balkema, Rotterdam, 161–181.
Zittel, K.A. v. 1876–80: Handbuch der Palaeontologie Abt. I, Bd. I. Oldenburg, München & Leipzig, 765 pp.

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