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A NEW SPECIES OF BRITTLESTAR (OPHIUROIDEA, ECHINODERMATA) FROM THE HUNSRÜCK SLATE (LOWER EMSIAN, LOWER DEVONIAN) OF GERMANY

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Abstract: *Lapworthura lehmanni*, a new species of ophiuroid, is described from four specimens from the Lower Devonian Hunsrück Slate of Germany. It is the only known ophiuroid in the Hunsrück Slate with paired but unfused ambulacrals, and it exhibits unique rows of spine-bearing dorsal arm ossicles. The genus *Lapworthura* Gregory was previously known only from the Ordovician of Scotland and the Silurian of England and Australia.

Key words: Zeugophiurina, Lapworthuridae, Ophiuroidea, Echinodermata, Hunsrück Slate, Lower Devonian, Germany.

THE Lower Devonian Hunsrück Slate of Germany is known for its great diversity of well-preserved invertebrate and vertebrate fossils. The greatest species diversity is present in the echinoderms, and with 48 stelleroid species currently recognized, the Hunsrück Slate preserves the most diverse Palaeozoic stelleroid fauna known (Lehmann 1957; Bartels *et al*. 1998; Glass and Blake 2004; Glass 2006). The Hunsrück Slate fauna is the most diverse ophiuroid fauna known from the Palaeozoic fossil record. Yet despite this important position, many of the most basic questions regarding the morphology, taxonomy and ecology of Hunsrück Slate taxa remain unresolved. The new species *Lapworthura lehmanni* treated here is the first unequivocally new ophiuroid taxon (see note on Südkamp 1994 below) described from the Hunsrück Slate since Lehmann (1957). Discovery of a new species of ophiuroid in existing Hunsrück collections demonstrates that new finds can still be made in older and well-studied collections. Identification of three of the four specimens was facilitated by recent advances in airbrasive preparation techniques. The initial recognition of one of the specimens as an undescribed species was made by studying X-rays taken by W. M. Lehmann that are housed at the Institut für Paläontologie at the Rheinische Friedrich-Wilhelms Universität in Bonn, Germany. Advanced radiography as well as such historical archives of X-rays continue to be of great use for the study of the Hunsrück Slate fauna (see also Bartels and Blind 1995; Briggs and Bartels 2001; Bartels and Poschmann 2002; Haas *et al*. 2003).

Previously, *Lapworthura* Gregory, 1897 had only been reported from the Ordovician of Scotland (Spencer 1925) and the Silurian of England (Salter 1857) and Australia (Withers and Keble 1934). The current find expands the known distribution of the genus to the Lower Devonian of continental Europe.

HISTORY OF STUDY

Ophiuroids were among the first fossils to be described from the Hunsrück Slate (Roemer 1863). Systematic documentation of the diversity and morphology of Hunsrück stelleroids followed most notably in a series of papers by Stürtz (1886*a*, *b*, 1890, 1893, 1899), Schöndorf (1909, 1910*a*, *b*), and finally in the work on Palaeozoic stelleroids by Spencer (1914–40). Lehmann (1951*a*, *b*, 1957, 1958) was the only one to treat comprehensively the Hunsrück Slate stelleroid fauna, and he also popularized the use of X-rays in aiding identification and description. His treatment recognized 15 genera, 21 species and one subspecies of ophiuroid, 14 genera, 22 species and one subspecies of asteroid, and five genera and species of uncertain affinities. Of these five genera (*Eostella*, *Hunsrueckaster*, *Hystrigaster*, *Kyraster* and *Protasteracanthion*), Spencer and Wright (1966) tentatively placed *Eostella* Lehmann, 1957, *Hunsrueckaster* Lehmann, 1957 and *Kyraster* Lehmann, 1957 within the asteroids. Lehmann (1957, pp. 141–147) had already referred to these three genera as 'Seesterne' (seastars in English) but refrained from assigning them to known groups. Both *Protasteracanthion* Stürtz, 1886 and *Hystrigaster* Lehmann, 1957 were labelled 'asterozoans' (Lehmann 1957). *Hystrigaster* Lehmann was placed among the asteroids by Spencer and Wright (1966) and *Protasteracanthion* Stürtz was shown to be an ophiuroid by Hotchkiss (1976) and Haude (1982). Furthermore, in contrast to Stürtz (1890) and Lehmann (1957), Spencer and Wright (1966) first recognized *Medusaster* Stürtz, 1890 as an ophiuroid. However, this assignment went largely unrecognized by subsequent authors (e.g. Bartels and Brassel 1990; Bartels *et al.* 1998; Hotchkiss 2000). Jell and Theron (1999) concluded that the genus *Euzonosoma* Spencer, 1930 is a junior synonym of *Encrinaster* Haeckel, 1866. Lehmann (1958), Kutscher (1970*a*, 1976), Sieverts-Doreck (1978) and Bartels *et al.* (1998) briefly reported on the stelleroid fauna. In his review of the Hunsrück echinoderm collections at the Museum für Naturkunde in Berlin, Südkamp (1994) recognized a new genus and species of ophiuroid with the name *Eschenbachia pinusi*. Unfortunately, the accompanying description is cursory, without a clear generic diagnosis, and preservation of the two figured specimens is poor. Most recently, Glass and Blake (2004) reported on pyritized tube feet and provided a redescription of the Hunsrück protasterid ophiuroids *Bundenbachia beneckei* Stürtz, 1886 and *Palaeophiomyxa grandis* Stürtz, 1886. Glass (2006) synonymized the ophiuroid genera *Miospondylus* Gregory, 1897 and *Palaeophiura* Stürtz, 1890 with *Bundenbachia* Stürtz, 1886 and also redescribed the protasterid ophiuroid *Mastigophiura grandis* Lehmann, 1957.

Despite a long history and comprehensive studies (e.g. Spencer 1914–40; Lehmann 1957) our basic knowledge of Hunsrück Slate stelleroids remains limited and at best superficial. Early studies, including those of Spencer (1914–40), were based on few, often poorly preserved specimens. Lehmann (1957) had access to numerous specimens but examination was limited owing to time-consuming and difficult preparation methods that often allowed only the most surficial exposures. Few workers possessed the preparation skills necessary to prepare fossils completely without causing significant loss of important skeletal detail. For these reasons, the Hunsrück Slate has remained on the fringes of Palaeozoic ophiuroid studies. Fortunately, new and improved preparation methods utilizing airbrasive (Bartels *et al.* 1998; Glass and Blake 2004) now allow detailed systematic analysis of the fauna, and the discovery and documentation of *Lapworthura lehmanni* is part of this effort.

GEOLOGICAL SETTING

Detailed geographical and stratigraphical data for Hunsrück fossils are mostly lacking. This is largely because of historical collecting techniques, in which fossils were discovered during the process of splitting quarried blocks for the production of roofing slates, by which time the exact stratigraphical position had been lost. However, recent studies in the fossiliferous Eschenbach-Bocksberg quarry near Bundenbach have provided a detailed stratigraphic framework for the fossil-rich horizons (see Bartels *et al.* 2002*b*; Schindler *et al.* 2002).

The fossil-producing horizons of slate in the Bundenbach region are found in the middle part of the Lower Devonian, middle Lower Emsian, Kaub Formation (Mittmeyer 1965, 1980; Schindler *et al.* 2002). At least four such horizons with well-preserved pyritized fossils are recognized (Bartels *et al.* 1998; Sutcliffe *et al.* 1999). These layers are dominated by thinly bedded and laminated dark grey clay and silt-sized sediments interpreted to have been deposited by low-density turbidity currents at the distal edge of a submarine fan within the intrashelf Central Hunsrück Basin (Dittmar 1996; Bartels *et al.* 1998, 2002*a*; Sutcliffe *et al.* 1999, 2002). Deposition took place at or just below storm-wave base (Sutcliffe *et al.* 1999). Although sediment anoxia aided in the process of fossil pyritization, the water column was well oxygenated and supported a diverse epifauna (Briggs *et al.* 1996; Sutcliffe *et al.* 1999; Bartels *et al.* 2002*a*). This fauna was periodically overwhelmed and buried by obrution events (e.g. Bartels and Poschmann 2002). The Hunsrück Slate fauna is interpreted as autochthonous, although transport of organisms over limited distances might have taken place (Bartels *et al.* 1998; Sutcliffe *et al.* 1999).

A detailed stratigraphic framework for the middle Kaub Formation was recently published by Schindler *et al.* (2002). Strong biostratigraphic evidence placed the Kaub Formation in the Lower Emsian (see review in Kirnbauer and Reischmann 2001; Schindler *et al.* 2002). Initial radiometric dates obtained from volcaniclastics in the Kuhstäbel Member yielded the questionable age of 388·7 ± 1·2 Ma, which suggested either a Middle Devonian (Eifelian) age or, alternatively, a younger age for the Emsian/Eifelian boundary than previously thought (Kirnbauer and Reischmann 2001). However, the most recently determined date of the same member yielded an age of 407·7 ± 0·7 Ma, which is consistent with the Lower Emsian (Kaufmann *et al.* 2005).

MATERIAL AND METHODS

The current treatment is based on the four known specimens of *Lapworthura lehmanni*. These specimens had previously been identified as *Mastigophiura grandis* Lehmann, 1957 (PWL 2004/5021-LS), *Bundenbachia beneckei* Stürtz, 1886 (PWL 1992/187-LS) and *Palaeophiomyxa grandis* Stürtz, 1886 (Ebo 75, KGM 1983/52). The similarities between *Lapworthura lehmanni* and these protasterid ophiuroids in the Hunsrück Slate strongly suggests that more specimens of the species might exist in collections but remain unidentified.

Of the four specimens, only Ebo 75 and KGM (1983/52) had not been prepared previously using airbrasive. To allow more detailed analysis, all specimens except KGM 1983/52 were further prepared using low-pressure airbrasive (0·5–2·5 bar) with pure iron powder (< 100 mesh); preparation details can be found in Bartels *et al.* (1998) and Glass and Blake (2004). The matrix surrounding KGM 1983/52 proved too resistant for preparation with airbrasive. It is recommended (Bartels, pers. comm. 2004) that following preparation, specimens be stored dry and be brushed and wiped with pure paraffin oil to protect the pyrite against moisture. This oil evaporates within a few months without leaving a residue and it can be reapplied indefinitely. Within Germany this oil can be obtained from any pharmacy as 'Paraffin subliquia', a type of paraffin oil with increased viscosity compared to the low-viscosity paraffin oil that is commonly used as lamp fuel in the United States. This fuel-oil is unsuitable as it is highly volatile and evaporates within hours to days. Paraffin oils of higher viscosities are available through different chemical supply stores, but we have not evaluated brands available in the United States. For the treatment of pyritized Hunsrück Slate specimens already harmed by moisture, see Maus and Wuttke (2003).

The original type material of *Lapworthura miltoni* (Salter, 1857) was unavailable for study. Two specimens of *Lapworthura miltoni* (Salter, 1857) from the Leintwardine channel deposits (Silurian, Ludlow; England) were studied for comparison. These are BMNH 57709 (dorsal) and YPM 14786A (dorsal). Both are preserved as external moulds. A cast of BMNH 57709 was kindly made available to us by David Lewis. Unfortunately, no specimens exposing their ventral surfaces were available. Comparison of the ventral surface was limited to figures provided by Sollas and Sollas (1912, pl. 9, figs 1–4; pl. 10, figs 1–4), Spencer (1925, pl. 19, figs 3–6; pl. 20, figs 2–3; pl. 21, figs 7–8) and Shackleton (2005, pl. 2, figs 10–12).

Institutional abbreviations. BMNH, Natural History Museum, London; Ebo, Institut für Paläontologie, Rheinische Friedrich-Wilhelms Universität, Bonn; KGM, Schlossparkmuseum, Bad Kreuznach; LS, Naturhistorisches Museum, Landessammlung für Naturkunde Rheinland Pfalz, Mainz; YPM, Peabody Museum of Natural History, Yale University, New Haven.

SYSTEMATIC PALAEONTOLOGY

Class OPHIUROIDEA Gray, 1840
Order OEGOPHIURIDA Matsumoto, 1913
Suborder ZEUGOPHIURINA Matsumoto, 1913

Remarks. The names Oegophiurida and Zeugophiurina are widely cited (e.g. Fell 1963; Spencer and Wright 1966) as Matsumoto (1929) and Matsumoto (1915), respectively; however, both have their source in Matsumoto (1913). Indeed, all of the higher-level taxonomic names given by Matsumoto (1929) and some in Matsumoto (1915) originally appeared in Matsumoto (1913). Matsumoto (1929) cited Matsumoto (1913) as the original source of the classification but this was subsequently overlooked.

Family LAPWORTHURIDAE Gregory, 1897

Genus LAPWORTHURA Gregory, 1897

Type species. Protaster miltoni Salter, 1857, by original designation; from the Ludlow of Leintwardine in Herefordshire, England.

Diagnosis. Disc circular. Arms low, flexible, broad, and uniform in width inside and just distal to the disc but tapering evenly toward the tips. Dorsal ambulacrals rectangular, paired across the midline of the arm, and probably unfused (see discussion below). Podial basins large. Laterals curve around the podial basins and attach to the ambulacrals by an elongated process. Vertical spines long and of nearly equal length, some as long as three arm segments. Spines set in rows at wide angles to the arm axis (see 'Remarks' below). Madreporite is ventral.

Included species. Lapworthura miltoni (Salter, 1857); *Lapworthura lehmanni* sp. nov.; *Lapworthura pulcherrima* Withers and Keble, 1934 is not included (see below).

Discussion. The diagnosis proposed here is based on those of Gregory (1897), Spencer (1925) and Spencer and Wright (1966) and supplemented by the observations of Salter (1857, 1861), Schöndorf (1910*b*), Sollas and Sollas (1912) and other literature, as well as specimens of *Lapworthura miltoni*. Emendation of spine length as given by Spencer (1925) is based on personal study of well-preserved specimens of *Lapworthura miltoni*.

Shackleton (2005) provided a new diagnosis for *Lapworthura* based on a cladistic analysis of Ordovician asterozoans. Her characters included an inclined distal margin on the ventral ambulacrals, an 'oral inclined groove running along distal part of perradial region of ambulacral' (Shackleton 2005, p. 87), a large crenulated madreporite, and closely spaced first and second buccal pores with the proximal pore reduced in size and raised dorsally. The last character is unrecognizable in the Hunsrück material described herein. We were unable to discern the exact meaning and nature of the second character and none of the included figures (Shackleton 2005, pl. 2 figs 10–12) was found helpful for this character. The surface of the madreporite is not considered here to be of generic significance. The first character, the inclined oral margin of the ambulacrals, is readily identifiable and discernible in *Lapworthura lehmanni*.

The relationship between the paired ambulacrals in *Lapworthura* has been the subject of disagreement with one side recognizing fused ambulacrals or vertebrae (Stürtz 1890; Gregory 1897) and the other unfused ambulacrals (Schöndorf 1910*b*; Shackleton 2005). The three-dimensional reconstructions of Sollas and Sollas (1912) based on serial sections of *Lapworthura* appear to show separate ossicles, and these authors also claimed to have discovered that in some specimens the ambulacrals exhibit displacement across the midline. However, neither they nor Spencer (1925) could conclusively rule out the possibility of a weak union of the ossicles during life.

The problem of differentiating between unfused and fused ambulacrals is not exclusive to *Lapworthura*. The fact that the vertebrae of *Hallaster* can be broken into two halves (see Spencer 1925) demonstrates that a slight union, presumably in the form of weak calcification, can occur.

The holotype of *L. lehmanni* exhibits slight displacement and rotation of some of the ambulacrals in relation to their counterparts across the midline (Pl. 1, fig. 4), an observation reminiscent of that made in *L. miltoni* by Sollas and Sollas (1912). *Lapworthura* ambulacrals are here considered unfused but some degree of weak calcification between the ossicles cannot be ruled out.

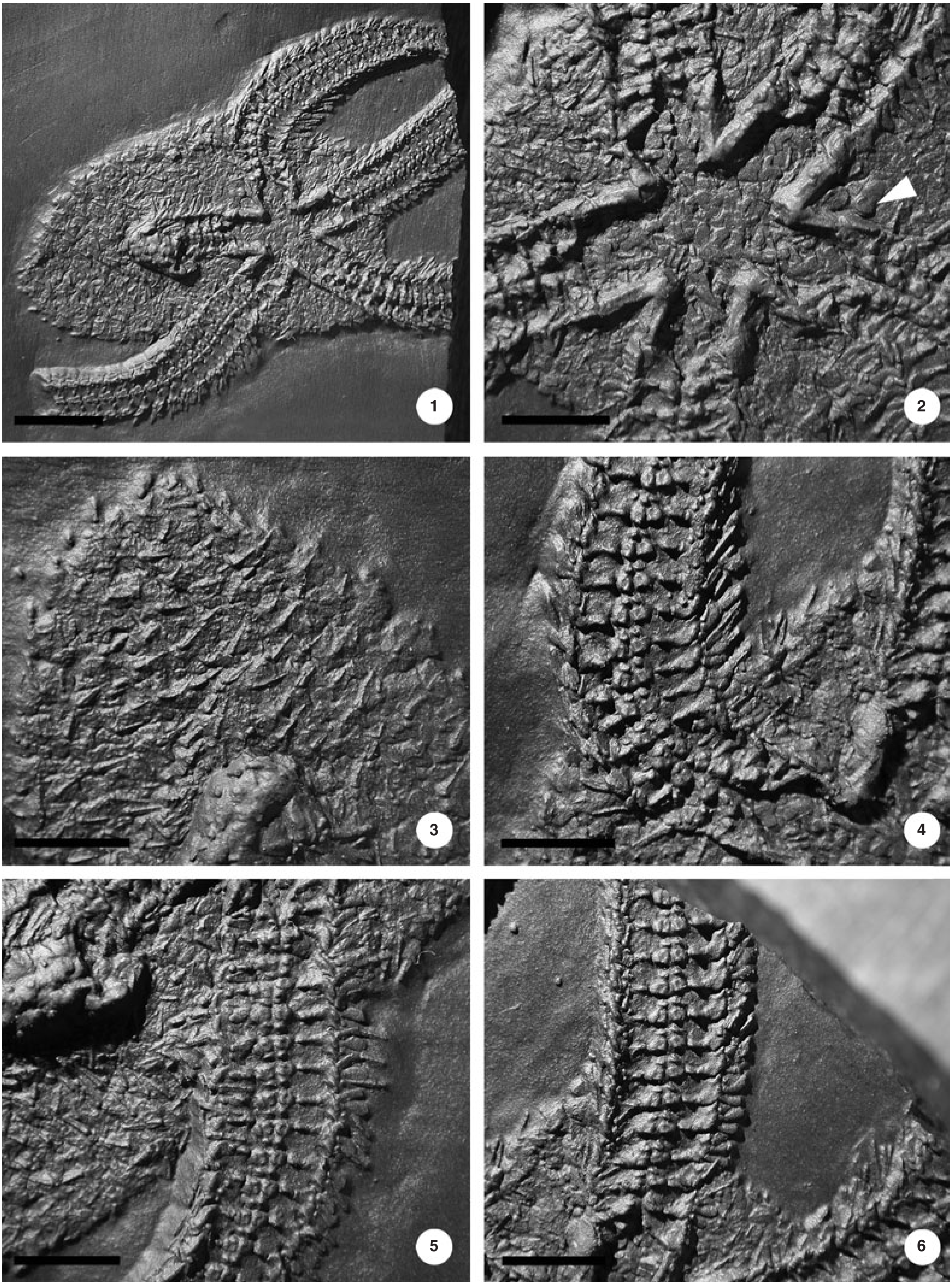
Remarks. Spencer and Wright (1966) divided the suborder Zeugophiurina Matsumoto into four families. Hotchkiss (1976, 1977) removed the families Klasmuridae Spencer and Ophiocanopidae Mortensen from the suborder by reassigning their single genera, *Klasmura* Ruedemann, 1916 and *Ophiocanops* Koehler, 1922 to other groups. This left only the families Lapworthuridae Gregory and Furcasteridae Stürtz. In their division of the Zeugophiurina into families, Spencer and Wright (1966, p. U88) adopted a modified version of Spencer (1925), who had stressed the length, shape, and relative position and angle of the vertical spines to the arm. Specifically, the Lapworthuridae allegedly have 'long conical spines, generally set in rows not parallel to arm axis' whereas Furcasteridae have 'subequal needle-shaped spines in rows close to sides of arms and parallel to arm axes' as diagnostic characters (Spencer and Wright 1966, p. U88). However, the position of the spines in *Furcaster palaeozoicus* Stürtz, 1886 is much more varied than ascribed to it by Spencer and Wright (1966), and it is questionable whether the spines of *Lapworthura miltoni* are best described as conical or needle-like, or whether they lie at an angle or parallel to the arm axis.

Recently, Shackleton (2005) combined the Lapworthuridae and Furcasteridae in the Protasteridae based on a cladistic analysis of Ordovician asterozoans. However, until additional genera are more comprehensively restudied and re-evaluated, the higher-level classification applied here follows Spencer and Wright (1966); family definitions within the Zeugophiurina are in need of further revision.

Four genera of Lapworthuridae are currently recognized. Spencer and Wright (1966) included three, *Lapworthura* Gregory, 1897, *Hallaster* Stürtz, 1886 and *Miospondylus* Gregory, 1897. Glass (2006) has demonstrated that the holotype of *Miospondylus rhenanus* (Stürtz, 1893) is a peculiarly preserved specimen of the common Hunsrück Slate protasterid ophiuroid *Bundenbachia beneckei* Stürtz, 1886. Prokop (1985) re-erected the genus *Hypophiura* Jaekel, 1923, which had been synonymized with *Hallaster* by Spencer (1950). Shackleton (2005) also recognized *Hypophiura* but disagreed with Prokop (1985)

EXPLANATION OF PLATE 1

Figs 1–6. *Lapworthura lehmanni* sp. nov. from the Lower Devonian Hunsrück Slate of Germany, PWL 2004/5021-LS (holotype). 1, ventral surface of exposed specimen with distal ends missing in all five arms; disc has been significantly stretched. 2, close-up of mouthframe with prominent long mouth angle ossicles, small madreporite with circumferential channel in one interradius (white arrow), irregular to stellate dorsal disc scales visible through mouth. 3, stretched section of disc showing scalloped disc ossicles, bearing spines; clear disc granules are absent. 4, proximal section of one arm, showing long processes by which laterals articulate to ambulacrals; slight displacement and rotation of ambulacrals is evidence that these ossicles were not fused across the midline of the arm. 5, proximal section of arm with well-preserved petaloid to paddle-shaped groove spines and some vertical spines; groove spines cover the podial basins on the proximal, left side of the arm. 6, proximal section of one arm showing well-preserved groove spines; consecutive laterals abut via a rounded distal edge; note prominent saddle across distal part of ambulacrals. Scale bars represent 10 mm in 1 and 5 mm in 2–6.



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about how the genus is to be differentiated from *Hallaster*. *Ophiopolytretus* Blake and Glass, 1999 was tentatively assigned to the Lapworthuridae by these authors in Webster *et al.* (1999).

Lapworthura lehmanni sp. nov.
Plates 1–2; Text-figures 1, 2A

Derivation of name. In honour of Walther Maximilian Lehmann (1880–1959), who published the only comprehensive treatment of Hunsrück Slate stelleroids (Lehmann 1957). He also was the first to utilize X-rays systematically in the study of Hunsrück Slate fossils. Among his lasting legacy is his extensive collection of Hunsrück Slate fossils and accompanying X-rays held by the Institut für Paläontologie, Rheinische Friedrich-Wilhelms-Universität Bonn, Germany, where he held an honorary professorship. A review of the life and career of W. M. Lehmann can be found in Gerth (1961) and Kutscher (1970*b*).

Holotype. PWL (2004)/5021-LS, ventral surface (Pl. 1, figs 1–6).

Paratypes. PWL (1992)/187-LS, ventral surface (Pl. 2, fig. 7); Ebo 75, dorsal surface (Pl. 2, figs 1–6, 8–11); KGM 1983/52, ventral surface (Text-fig. 1).

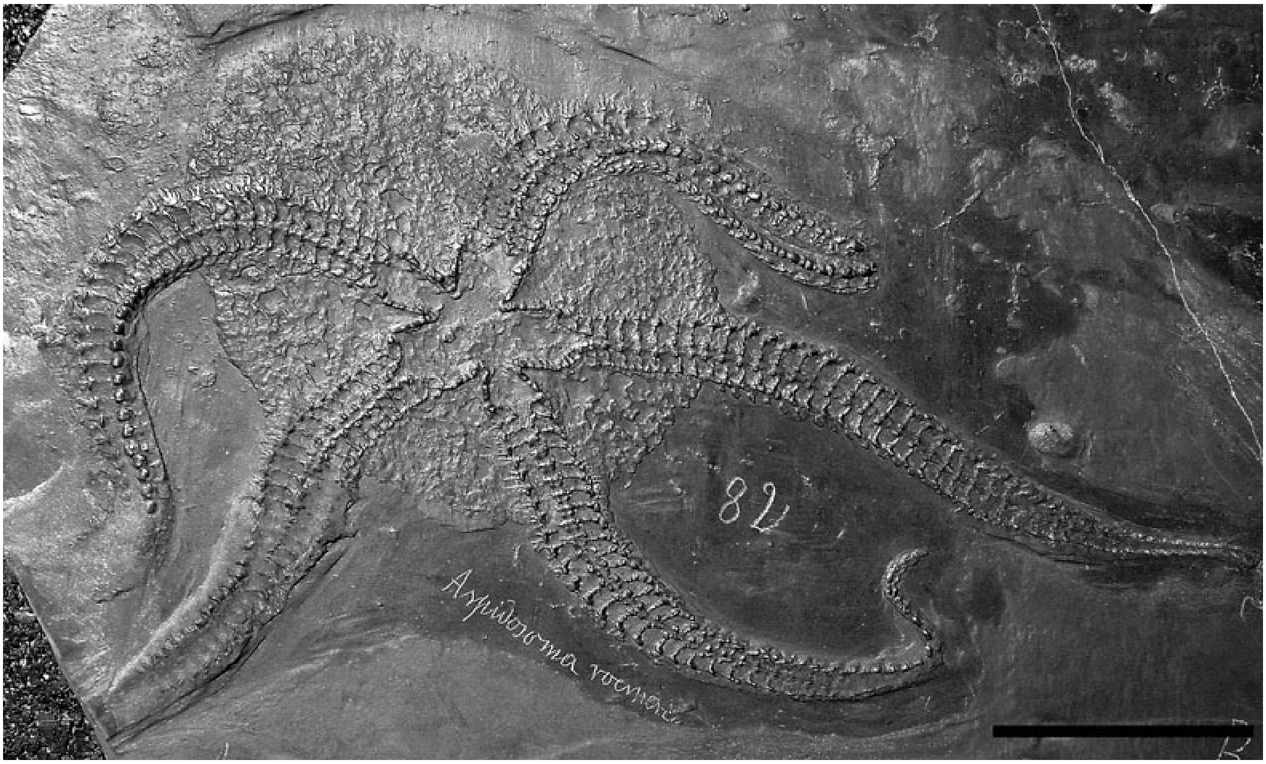
Locality and horizon. Lower Devonian, Lower Emsian, middle Kaub Formation, Hunsrückschiefer. The last fossil-producing slate-mining operation in the Hunsrück region was that of the company Johann & Backes Schieferbergbau south-west of the town of Bundenbach. This company extracted roofing slate from two separate sites known locally as the Eschenbach-Bocksberg and Obereschenbach quarries, until operations ceased in 1999. Historically, the Eschenbach-Bocksberg Quarry is the older of the two operations and presumably most of the well-preserved, pyritized fossil material described since the early publication of Roemer (1863) came from the Eschenbach Member exposed in this pit (Bartels *et al.* 1997). The holotype PWL (2004)/5021-LS is from the Wingertshell Member (*sensu* Schindler *et al.* 2002) of the Obereschenbach Quarry. The rocks here are slightly younger than those exposed in the Eschenbach-Bocksberg pit (see Schindler *et al.* 2002). Locality data for the paratypes PWL (1992)/187-LS and KGM 1983/52 is limited to the town of Bundenbach. Unfortunately, it is not known when these fossils were discovered. Most fossils donated to public collections were from private collections compiled from a number of quarries that have historically operated in the Bundenbach area (see Brassel and Kutscher 1978). Ebo 75 is from the W. M. Lehmann collection and gives 'Eschenbach I' for locality information. This probably refers to the older Eschenbach-Bocksberg Quarry operation because Lehmann consistently distinguished between Obereschenbach and Eschenbach I. Historical differences in quarry labels and their use makes unequivocal assignment to existing sites difficult. For example, the Obereschenbach pit has also been referred to as the Eschenbach Quarry (see Opitz 1932) and smaller mining operations such as the Kuhstäbel Mine were later incorporated into the expanding Eschenbach-Bocksberg Quarry (Schindler *et al.* 2002). Hence, historically different localities are today part of the same operation.

Diagnosis. A species of *Lapworthura* with stout stellate to pentagonal ossicles covering the ventral and dorsal disc. Ossicles have a distinctly scalloped surface texture. Some of these ossicles on both the ventral and the dorsal surfaces carry spines on raised tubercles. Four irregular rows of longitudinally elongated but rounded plate-like ossicles cover the dorsal surface of the arms. The ossicles of at least two rows bear spines at regular intervals along the arm. Laterals on the free arms bear four short, paddle-shaped groove spines and three long thin vertical spines. Madreporite smooth with circumferential channel.

Description. The interradial margin of the disc is rounded but can appear straight when the disc is stretched (Pl. 1, fig. 1; Pl. 2, fig. 7; Text-fig. 1). Disc marginals are absent and there is no differentiation in the size or shape of plating near the disc edges. Both the ventral and the dorsal surfaces of the disc are covered by stout irregular to stellate to pentagonal, partially overlapping or closely abutting, flat ossicles (Pl. 1, figs 2–3; Pl. 2, fig. 11). Accessory disc granulation appears to be absent but the surface of the disc ossicles is distinctly scalloped (Pl. 1, fig. 3; Pl. 2, fig. 11). The stellate and pentagonal ossicles bear a stout tubercle in their centre, which carries a thin, lanceolate, grooved spine (Pl. 1, fig. 3; Pl. 2, fig. 11). This spine reaches lengths up to 1·5 times the length of a proximal ambulacral. A ventral madreporite, of diameter less than the proximal podial basin, lies next to the first lateral (Pl. 1, fig. 2). It is flat and round, with a smooth upper surface and a single circumferential canal. The full extent of this canal cannot be ascertained as the madreporite is partially obscured by an adjacent disc plate.

None of the available specimens exposes the mouth frame from the dorsal surface. Ventrally, the mouth frame is dominated by the prominent long mouth-angle ossicles (Pl. 1, fig. 2). These are of even thickness along most of their length and appear as long, slender rectangles. Their ventral surface is rimmed by low, parallel ridges, the adradial of which carries at least three short petaloid spines on small bump-like bases. The proximalmost ends of the mouth-angle ossicles are slightly raised before abutting the adjacent ossicle across the interradius. Here they form a small, nearly round, scoop-like depression. A torus appears to be absent. At least five short, evenly tapering spines are attached to the dorsalmost edge of two adjacent mouth-angle ossicles, projecting towards the centre of the mouth. Distally, mouth-angle ossicles abut against the first ambulacral and its corresponding lateral. This lateral carries 2–3 short petaloid spines. The first ambulacral is reduced in size adradially but exhibits a nearly full-sized podial basin and lateral. A buccal gap clearly separates the first pair and also perhaps the second pair of ambulacrals.

Arms are widest just distal to the disc margin (Pl. 1, fig. 1; Pl. 2, fig. 7; Text-fig. 1). In PWL (2004)/5021-LS and KGM 1983/52 the arms are broad and exhibit little taper close to the



TEXT-FIG. 1. *Lapworthura lehmanni* sp. nov. from the Lower Devonian Hunsrück Slate of Germany. KGM (1983/52) (paratype); specimen is encased in a very dense silt layer and could not be prepared further using airbrasive. Unfortunately, the specimen was heavily abraded during an earlier preparation and shows only limited surface details. Scale bar represents 40 mm.

disc (Pl. 1, figs 4–6; Text-fig. 1) whereas the arms of the smaller specimens Ebo 75 and PWL1992-187LS taper evenly along their entire length (Pl. 2, figs 1, 7). The complete arms in KGM 1983/52 do not significantly taper until near the arm tips (Text-fig. 1). The dorsal surface of the arms is exposed only in the incomplete and partially disarticulated Ebo 75 (Pl. 2, fig. 1). The ambulacrals are not visible in this specimen because four rows of longitudinally elongated, rounded, overlapping, plate-like ossicles cover the arm surface (Pl. 2, figs 3–6). These ossicles are about as long as the underlying laterals. Their scalloped surfaces are identical to those of the disc ossicles. The outermost row on each side of the arm covers the boundary between the ambulacrals and laterals (Pl. 2, fig. 6). Only the adradialmost dorsal surface of the laterals is covered by these ossicles. The innermost two rows cover the ambulacrals (Pl. 2, figs 3, 5). Some or perhaps all of these ossicles carried spines. Small spines are visible in some places but in others preservation is too poor to tell clearly whether a spine was present or not (Pl. 2, figs 5–6, 10). There are at most four rows of nearly evenly spaced spines across the dorsal arm surface. The spines are identical in shape and form to those of the disc, although they are slightly shorter and decrease in length along the arm. Although the rows of arm ossicles seem to continue into the distalmost preserved regions of the arms, only the centremost rows bear spines here. Unfortunately, the disc of the only dorsally exposed specimen is badly disrupted; as a result it is impossible to observe what happens to the rows of dorsal arm ossicles on the surface of the disc (Pl. 2, fig. 1).

The view of the dorsal surface of the ambulacrals is limited to two pairs in Ebo 75 (Pl. 2, figs 8, 10). They appear wider than long, rectangular, and have raised proximal and distal edges. Their abradial ends are obscured. The number of ambulacrals inside the disc is between five and eight but can be greater where the disc is stretched (Pl. 1, fig. 1; Text-fig. 1).

The ventral shape of the ambulacrals of *Lapworthura miltoni* (Salter, 1857) has been described as L-shaped by Sollas and Sollas (1912) and boot-shaped by Spencer (1925). To facilitate description, the approach and terminology used here follows suggestions by Glass and Blake (2004) for the boot-shaped ventral ambulacrals of protasterid ophiuroids. A typical *L. lehmanni* ambulacral is described just distal to the disc (Pl. 1, figs 4–6; Text-fig. 2A). The width of the foot (W_F) is as long or nearly as long as the leg (L_L). A small rounded depression is present on the ankle of the foot. The edge of the proximal fitting is straight but slightly inclined towards the lateral. The toe is blunt with rounded corners, nearly half as wide (W_T) as the foot (W_F) and nearly half as long (L_F) as the leg (L_L). Toe width decreases distally along the arm. The lace area is gradually rounded from the tip of the toe to the distal fitting. The distal fitting is straight but deeper excavation of sediment between consecutive ambulacrals reveals the presence of an obliquely slanted V-shaped attachment surface for the ventral interambulacral muscle. A saddle crosses the distal part of the leg between an abruptly raised ankle and a gradually raised distal edge. The width of the distal fitting (W_{DF}) is as long as the foot (L_F). The width of the central leg (W_{CL}) is as wide or slightly wider than the distal fitting (W_{DF})

owing to the gradual taper of the lace area. The adradial edge of the leg is straight as is the median suture, although small constrictions exist at the level of the small leg-crossing saddle on both the abradial and the adradial side of the leg.

The ventral view of the laterals is dominated by a long, thin process that connects the ossicle to the toe of the ambulacral (Pl. 1, fig. 5; Text-fig. 2A). The process gradually widens towards the outer shield of the lateral that borders the basins. The process is shifted slightly distally towards the centre of the outer shield, leaving the proximalmost corner of the lateral to take part in cupping the proximally preceding podial basin (Pl. 1, fig. 5; Text-fig. 2A). The shield is slightly curved abradially. Its distalmost tip is sharply and obliquely truncated to match the curvature of the following lateral to which it closely abuts. The ventral edge of the shield rises gradually above the surface of the process but a sharply defined, spine-bearing ridge is absent. Instead, proximal laterals inside and just distal to the disc carry two or three rounded tubercles that bear short petaloid to paddle-shaped groove spines (Pl. 1, figs 5–6). A little further along the arm, the number of groove spines increases to a maximum of four, although three spines are more common. Three vertical spines reaching lengths of up to three ambulacrals articulate to a slightly raised ridge near the centre of the abradial surface of each lateral (Pl. 2, figs 4, 9–10). These spines are slightly lanceolate to evenly tapering with a prominent central groove. The number of vertical spines inside the disc appears to be limited to a maximum of two per lateral.

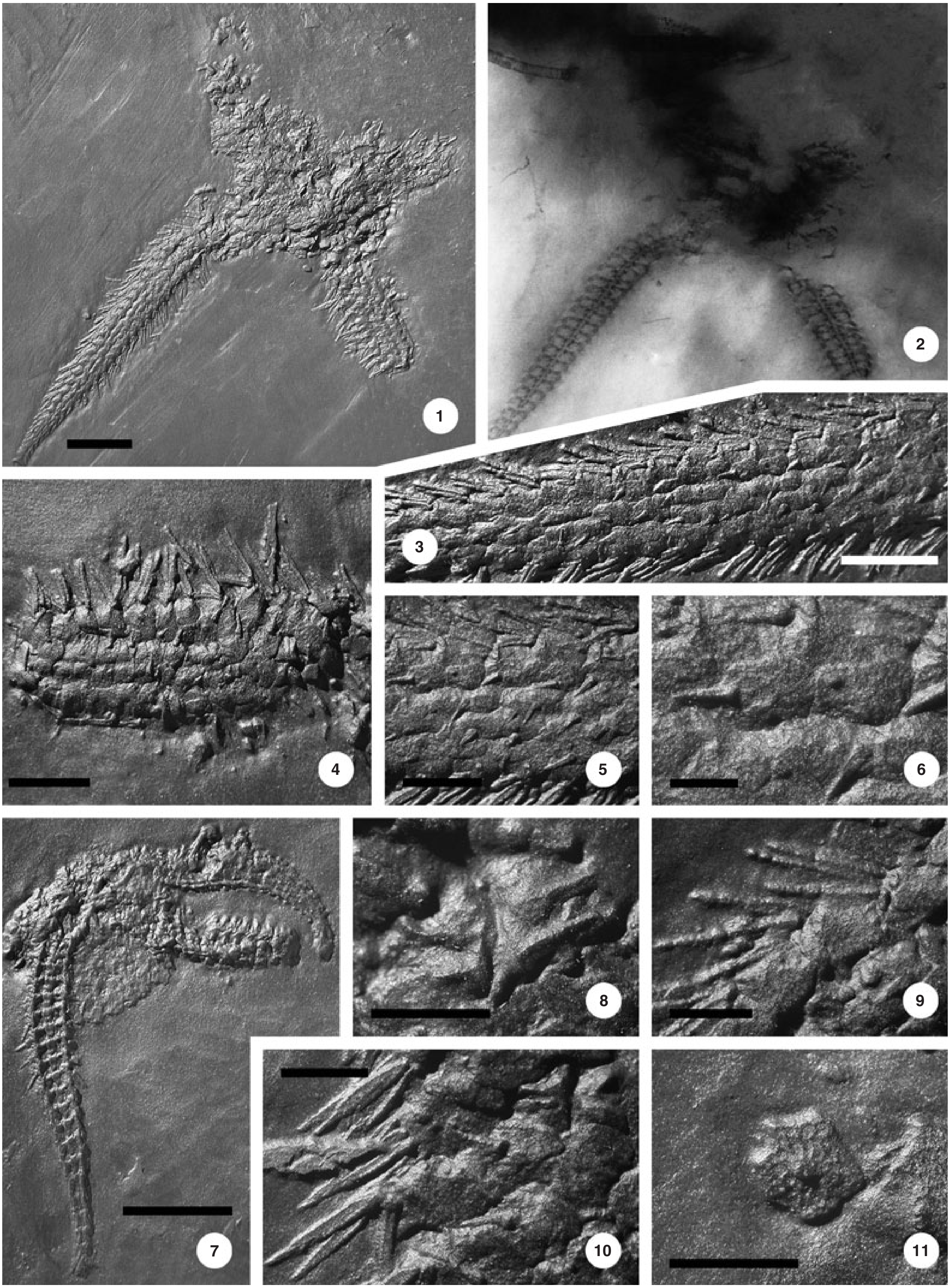
Remarks. Interpreting the shape of spines in the Hunsrück Slate is difficult. Poor preservation, limited exposure, extensive pyritization, and both brittle and ductile tectonic deformation can affect the appearance of spines, and delicate spines, such as those in *L. lehmanni*, are particularly vulnerable. When flattened by compression, originally rounded, evenly tapered spines become petaloid or paddle-shaped. It is, therefore, important to compare morphologies among specimens. Herein groove spines have been described as petaloid to paddle-shaped and vertical spines as slightly lanceolate to evenly tapering. Although intermediate morphologies exist, five common spine shapes are found among Hunsrück Slate ophiuroids (Text-fig. 2B–F). Part of the great diversity of Palaeozoic ophiuroid spine shapes and forms was demonstrated in Boczarowski (2001).

Comparison. The shape of the ventral ambulacrals and laterals, the shape, size and position on the lateral of the vertical spines, the appearance of the ventral mouthframe, and the overall shape and form of the arms are shared by *L. miltoni* and *L. lehmanni*.

The spine-bearing rows of plate-like dorsal arm ossicles differentiate *L. lehmanni* from *L. miltoni*. The arms of all known specimens of *L. miltoni* expose the dorsal surface of the ambulacrals, even in well-preserved, fully articulated specimens that are not preserved as moulds (Sollas and Sollas 1912; Spencer 1925). *Lapworthura miltoni* has a madreporite with a complexly grooved surface (Sollas and Sollas 1912; Shackleton 2005) whereas the madreporite in *L. lehmanni* is smooth, with a narrow circumferential channel. The number of groove and vertical spines in *L. miltoni* is uncertain. Sollas and Sollas (1912) noted the presence of four or five spines on the laterals but they do not differentiate between vertical and groove spines. Spencer (1925, text-fig. 204a) figured three groove spines and two vertical spines. Shackleton (2005) did not provide a specific number for either groove or vertical spines. Specimens of *L. miltoni* studied here appear to carry a maximum of two vertical spines. Hence, the number of vertical spines might also distinguish between the two species. The number of groove spines differs along the arms in *L. lehmanni* and their number could not be clearly established in the available specimens of *L. miltoni*. The nature of the disc ossicles in *L. miltoni* has been the subject of disagreement. They have been described as irregular, small plates with ridges (Salter 1857), as an irregular meshwork of thin rod-like scales (Schöndorf 1910*b*), and as rhomboidal plates with circumferential ridges (Spencer 1925). Shackleton (2005) described the disc ossi-

EXPLANATION OF PLATE 2

Figs 1–11. *Lapworthura lehmanni* sp. nov. from the Lower Devonian Hunsrück Slate of Germany. 1–6, Ebo 75 (paratype). 1, dorsal specimen; disc is partially disarticulated. 2, X-ray clearly shows the shape and arrangement of the ambulacrals and laterals; to scale with 1. 3, close-up of longest preserved arm showing irregular rows of spine-bearing scale-like ossicles. 4, close-up of shortest preserved arm; laterals bear three vertical spines. 5, close-up of part of longest arm with four irregular rows of spine-bearing scales; proximal is to the right. 6, close-up to two dorsal arm scales covering the adradial edge of the laterals (at top); consecutive scales are closely abutted and appear to be offset with scales that cover the ambulacrals (at bottom). 7, PWL1992/187-LS (paratype), poorly preserved, but arm clearly shows the paired ambulacrals. 8–11, Ebo 75 (paratype). 8, exposed dorsal surface of a pair of rectangular ambulacrals with parallel proximal and distal ridges. 9, laterals bear three evenly tapering to lanceolate vertical spines that articulate to a ridge near the centre of each lateral. 10, part of dorsal surface of arm; laterals bear three vertical spines; adradial-dorsal surface of laterals is covered by dorsal arm scales that each bear a small spine; a pair of ambulacrals is exposed in the upper right corner. 11, small isolated pentagonal disc plate; note scalloped surface and central tubercle for spine. Scale bars represent 1 mm in 6, 2 mm in 8–11, 3 mm in 5, 5 mm in 3–4 and 10 mm in 1.



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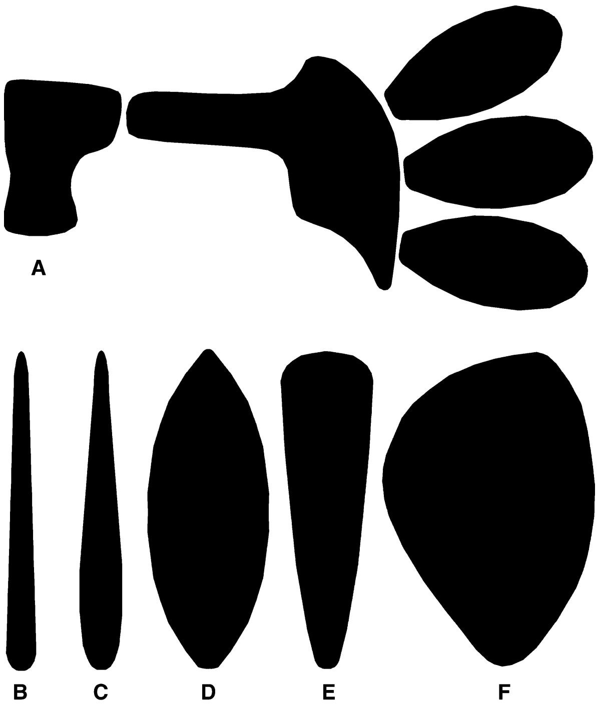

TEXT-FIG. 2. Shape of ventral ossicles in *Lapworthura lehmanni* sp. nov. and common spine shapes of Hunsrück Slate ophiuroids. A, outline of the shape of the ambulacral, lateral and groove spines of *Lapworthura lehmanni*; vertical spines omitted; ossicle shapes just outside of disc; note position of elongated lateral process articulating to ambulacral and protruding proximalmost corner of lateral. B–F, common spine shapes in ophiuroids in the Hunsrück Slate, dimensions not to scale. B, evenly tapering spine, common shape for vertical and disc spines, usually rounded in cross-section, some grooved longitudinally and/or ribbed horizontally. C, lanceolate spine, differs from the evenly tapering spine by a thickened proximal part, common shape for vertical and disc spines, usually flattened, some bearing longitudinal grooves. D, petaloid, or oval spine, found as groove, dorsal arm, or disc spines, always flattened. E, paddle-shaped spine, thickened distally, common groove or vertical spines, always flattened. F, leaf-like spine; Haude (1982, p.18, 'Blattoszikel') first noted these spines in *Furcaster palaeozoicus* from the Hunsrück Slate; lamellae-like banding on abradial surface, always flattened, only known as groove spines.

cles as petaloid, small relative to disc size, and bearing short spines on a central tubercle with both sides of the disc granulated. In contrast, the disc ossicles in *L. lehmanni* are comparably large in relation to the size of the disc. Their shape ranges from small irregular ossicles to large and distinctly stellate or pentagonal, flattened ossicles. Only the larger ossicles bear a single spine on their scalloped surfaces. Specimens of *L. miltoni* studied here exhibit a dense array of very small, irregular ossicles. Spines were not observed. Although disagreements exist over the disc plating in *L. miltoni*, the large size and distinct pentagonal or stellate-shaped, spine-bearing, scalloped ossicles of *L. lehmanni* can be used to differentiate further between the two species.

Occurrence. *Lapworthura lehmanni* is only known from the Hunsrück Slate (Lower Devonian, Lower Emsian) of Germany. *Lapworthura miltoni* (Salter, 1857) was first described from the 'Starfish Bed' in submarine channel deposits (Silurian, Ludlovian) near Leintwardine, England, by Salter (1857). Spencer (1925) also reported the species from the 'Lady Burn Starfish Bed' of the Upper Drummuck Group (Upper Ordovician, Ashgillian) in Threave Glen near Girvan, Scotland. For more details on these two localities, see Goldring and Stephenson (1972), Harper (1982) and Gladwell (2003).

Withers and Keble (1934) reported *Lapworthura miltoni* (Salter) from the Yarravian Series (Silurian) near Kinglake West in Victoria, Australia. They also described a new species, *Lapworthura pulcherrima* Withers and Keble, 1934, from the same rocks but from a different locality in West Brunswick, Victoria. The assignment of *Lapworthura pulcherrima* to the genus is questionable. Unlike *L. miltoni*, this species is described and figured as having alternating ambulacrals and strongly petaloid arms (Withers and Keble 1934, pl. 11, figs 1–2; text-fig. 4). Although their text-figure 5 shows paired proximalmost ambulacrals, this arrangement occurs in other species with alternating ambulacrals, for example the protasterid *Bundenbachia beneckei*. We did not have access to the Australian material, but P. Jell kindly provided observations on this material. We share the view that *L. pulcherrima* should not be included in *Lapworthura* owing to the alternating arm ambulacrals. As for *L. miltoni*, the Australian material appears to be correctly assigned to genus but might represent a new species (P. Jell, pers. comm. 2004). Until a more detailed study is available, assignment of the Australian material to *L. miltoni* by Withers and Keble (1934) is accepted here.

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