A pyritized lepidocoleid machaeridian (Annelida) from the Lower Devonian Hunsrück Slate, Germany

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A machaeridian, *Lepidocoleus hohensteini* sp. nov., is described from the Hunsrück Slate (Lower Emsian) of Germany. The available material includes a unique example preserving evidence of the soft tissues, only the second machaeridian specimen to do so and the first lepidocoleid. This specimen shows that the plates are attached to alternate segments in the trunk. The morphology is consistent with an annelid affinity of the Lepidocoleidae and confirms the unity of the Machaeridia. This discovery adds an important group to the known diversity of this famous late Palaeozoic marine Konservat-Lagerstätte.

Keywords: Annelida; Emsian; Konservat-Lagerstätte; pyritization; soft-tissue preservation

1. INTRODUCTION

Machaeridians are armoured worms with a skeleton of calcite plates which is rarely preserved articulated. They were first discovered by de Koninck (1857) in the Silurian of Dudley, England. Plates of machaeridians are relatively common in benthic marine shelly fossil assemblages from the Lower Ordovician to the Middle Permian. There was controversy about which types of isolated plates should be included in the Machaeridia until Adrain (1992) reviewed the group and demonstrated that three distinct families, Turrilepadidae, Plumulitidae and Lepidocoleidae, form a monophyletic clade. This clade is united by the possession of an exoskeleton of serially arranged plates made up of two differentiated crystalline layers with both rugae and growth lines on their external surface. Nonetheless 150 years of uncertainty about the affinities of machaeridians continued until 2007 when a representative of the family Plumulitidae preserving soft tissues was discovered in the Lower Ordovician of Morocco. The presence of parapodia and chaetae in this specimen showed that the affinities of plumulitids lie with the polychaete annelids (Vinther *et al.* 2008). While plumulitids presumably used the parapodia to locomote on the sediment surface, lepidocoleids differ from other machaeridians in that the mineralized plates enclosed the soft tissues almost completely rather than forming a dorsal armour. Different overlap configurations in the plates of articulated lepidocoleid specimens suggest that they used peristaltic waves to burrow through the substrate (Högström 1997; Vinther & Briggs 2009). A new species of *Lepidocoleus* described here from the Devonian Hunsrück Slate of the Bundenbach area (Rhenish Massif, Germany) includes one specimen that reveals, for the first time, evidence of the nature of lepidocoleid soft tissues.

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The Hunsrück Slate has yielded one of the most significant marine assemblages of Palaeozoic fossils—over 260 species representing 37 classes from 13 phyla, more than half of these species unique to the region (Bartels *et al.* 1998, 2002). The fossils were buried in low-energy turbidite flows carrying clay and silt, and pyritized in anoxic sediment (Briggs *et al.* 1996; Sutcliffe *et al.* 1999, 2002). Escape traces (figure S1 in the electronic supplementary material) show that organisms were alive at the time of burial (Sutcliffe *et al.* 1999). The Hunsrück Slate preserves remarkable morphological details of a diversity of arthropods, echinoderms and vertebrates, as well as rarer taxa (Bartels *et al.* 1998), including soft tissues that rarely survive in other deposits, such as ophiuroid tube feet (Glass & Blake 2004). Exploitation of the Wingertshell Member of the Kaub Formation at Bundenbach for approximately 10 years from the early 1990s has led to new discoveries including the machaeridian described here, as well as a number of other exclusively soft-bodied annelids (Briggs & Bartels in review).

Lepidocoleid machaeridians range from the Middle Ordovician to the Middle Devonian (Sieverts 1935; Wolburg 1938; Sieverts-Doreck 1952; Högström in Hints *et al.* 2004). They are relatively common and diverse in Ordovician and Silurian strata, but few have been reported from the Devonian; this may be due to a greater focus on Lower Palaeozoic machaeridians. The Hunsrück Slate is Early Devonian (Emsian) in age (Schindler *et al.* 2002). The youngest lepidocoleids are from the Middle Devonian of Germany: *Lepidocoleus eifeliensis* (Sieverts 1935), from the Ahrdorf Formation; *Lepidocoleus elongatus* (Sieverts-Doreck 1952), from the Wissenbacher Schiefer, and *Aulakolepos gleidorfense* (Wolburg 1938), from the Fredeburger Schiefer, all based on partial and semi-articulated skeletons. The internal stratigraphy of these units is not well known and the relative ages of these taxa are difficult to resolve. In North America *Lepidocoleus polypetalus* (Clarke 1896) and *Lepidocoleus illinoiensis* (Savage 1913) have been described from the Lower Devonian of

Illinois and *L.* sp. has been reported as a relatively common component in the Lower Devonian (Emsian) Haragan Formation in Oklahoma (Frest *et al.* 1999). *Lepidocoleus rugatus* has been recently described (Klug *et al.* 2008) from the Lower Emsian of Morocco based on a number of partial articulated specimens. *Lepidocoleus* sp. is also known from the Lower Devonian of Victoria, Australia (A. E. S. Högström 2003, personal observation). In addition to these Devonian taxa based on articulated material, there are rare reports of isolated lepidocoleid plates but none from strata younger than the Eifelian (Sieverts-Doreck 1952; Frest *et al.* 1999).

2. MATERIAL AND METHODS

The holotype and seven additional specimens are from the Wingertshell Clayey Slate Member of the Kaub Formation (Schindler *et al.* 2002) in the Obereschenbach Quarry (adjacent to the Eschenbach-Bocksberg Quarry) at Bundenbach. The specimens are held in the Deutsches Bergbau-Museum, Bochum, Bartels collection, abbreviated DBM:HS, and in the Naturhistorisches Museum Mainz, Landessammlung für Naturkunde, abbreviated NM (PH indicates Peter Hohenstein collection). The specimens were X-rayed at the University of Giessen, the Steinmann Institute of the University of Bonn, and the Erdgeschichtliche Denkmalpflege, Mainz; NM:PWL 2002/231-LS was CT scanned (180 kv, 0.250 mA) at the Center for Quantitative Imaging at Pennsylvania State University (movies S3 and S4 in the electronic supplementary material). Terminology follows that of Adrain *et al.* (1991), Adrain (1992), Högström (1997) and Högström & Taylor (2001), but the term 'segment' is not used to refer to external plates as there is no one-to-one correspondence between the two. The plates occur in paired series, where pair 1 is the most anterior. In the case of quadriseriate machaeridians, inner and outer plate pairs alternate in attachment and require separate numbering: inner plate pairs 1-n and outer plate pairs 1-n. In some taxa (especially plumulitids and turrilepadids), the inner plate pairs are more numerous than the outer, as the latter are absent in the anterior region (Jell 1979; Adrain *et al.* 1991). Inflections have been used previously to describe the pattern of rugae in both turrilepadids and plumulitids (Adrain *et al.* 1991; Högström *et al.* 2002) and are used here for the first time to characterize the plates of lepidocoleid machaeridians, i.e. I_1–I_4 present, I_1 being the most dorsal (figure 1). The density of rugae is measured both where they are aligned dorsoventrally (D-V) and antero-posteriorly (A-P) as this illustrates the relative shape of the plate. Where possible, density of rugae is measured in several positions along the skeleton but typically on midbody plates.

3. PRESERVATION

Most Hunsrück Slate fossils are preserved, following transport, in a variety of attitudes to bedding, although many examples, particularly crinoids, have been buried *in situ* (see Bartels *et al.* 1998; Sutcliffe *et al.* 1999). The water column was oxygenated, even though the sediment was normally anoxic (Sutcliffe *et al.* 1999). Most of the lepidocoleid machaeridians are preserved in near lateral as opposed to parallel (i.e. dorsoventral) aspect (figure 2), reflecting their laterally compressed cross section in life (by contrast with other machaeridians), which presumably rendered them more stable in this attitude. However, the dorsal depression is often evident (lateral-oblique aspect: Whittington 1971). Two specimens exhibit enrolment, one partial (figure 2n) and one complete (figure 2g).
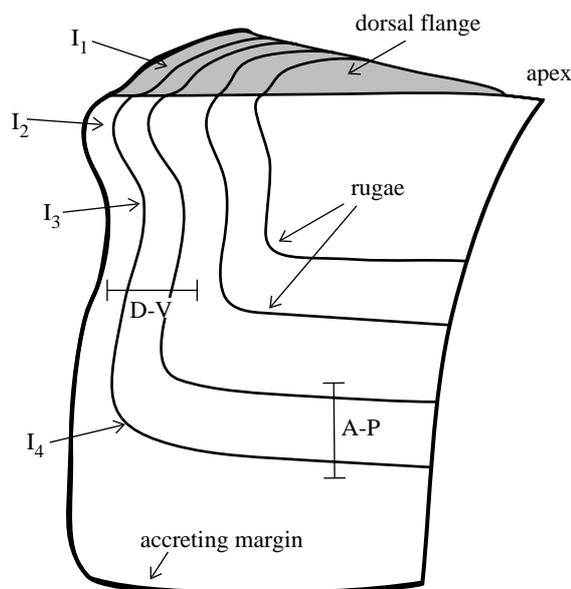
Figure 1. Schematic of inflections in *L. hohensteini* numbered from the most dorsal (I_1) to the most lateral (I_4), and the directions used in measuring density of rugae. Shaded area constitutes the dorsal flange, thicker line the accreting margin, D-V, A-P = lines along which density of dorsoventrally and anteroposteriorly aligned rugae is measured. Not to scale.

Some living polychaetes have been observed to curl up in response to stress (e.g. Abele-Oeschger *et al.* 1994): enrolment in the Hunsrück Slate examples may represent a similar reaction to burial in low oxygen sediment. Alternatively, it may be the result of post-mortem contraction of the ventral longitudinal musculature. Similar configurations have been observed in *Lepidocoleus sarlei* (Högström & Taylor 2001).

Pyritization of the Hunsrück Slate organisms followed rapid burial in sediment with a low concentration of organic matter. Iron and sulphate migrated towards the decaying organisms and rapid mineralization was promoted by the presence of high concentrations of iron reactive to dissolved sulphide (Briggs *et al.* 1996). Where such conditions did not prevail, the decay of soft tissues outpaced pyritization and no evidence of their morphology survives. Thus only one specimen of *Lepidocoleus hohensteini* preserves clear evidence of the soft tissues (figure 3). The trunk is heavily pyritized in the posterior half of the specimen; lighter areas in the X-radiograph (figure 3b) indicate where the pyrite was thinner or less dense. The plates are not uniformly pyritized: those parts dorsal and ventral of the trunk, which lie at a high angle to bedding, are more heavily pyritized than the surfaces near parallel to bedding, creating the appearance of linear structures in the X-radiographs and CT scan (S4 reconstruction). The plates show the effects of subsequent compaction over the pyritized trunk (figure 3a). The plates of the other specimens were also replaced by pyrite to differing degrees. In some cases additional pyrite formed in pressure shadows beyond the plates. The plates were partially replaced by quartz in some specimens and it too precipitated in pressure shadows in places. The infaunal lepidocoleids may have been among those worms that produced strings of faeces within the sediment (e.g. Bartels *et al.* 1998, p. 45, fig. 30).
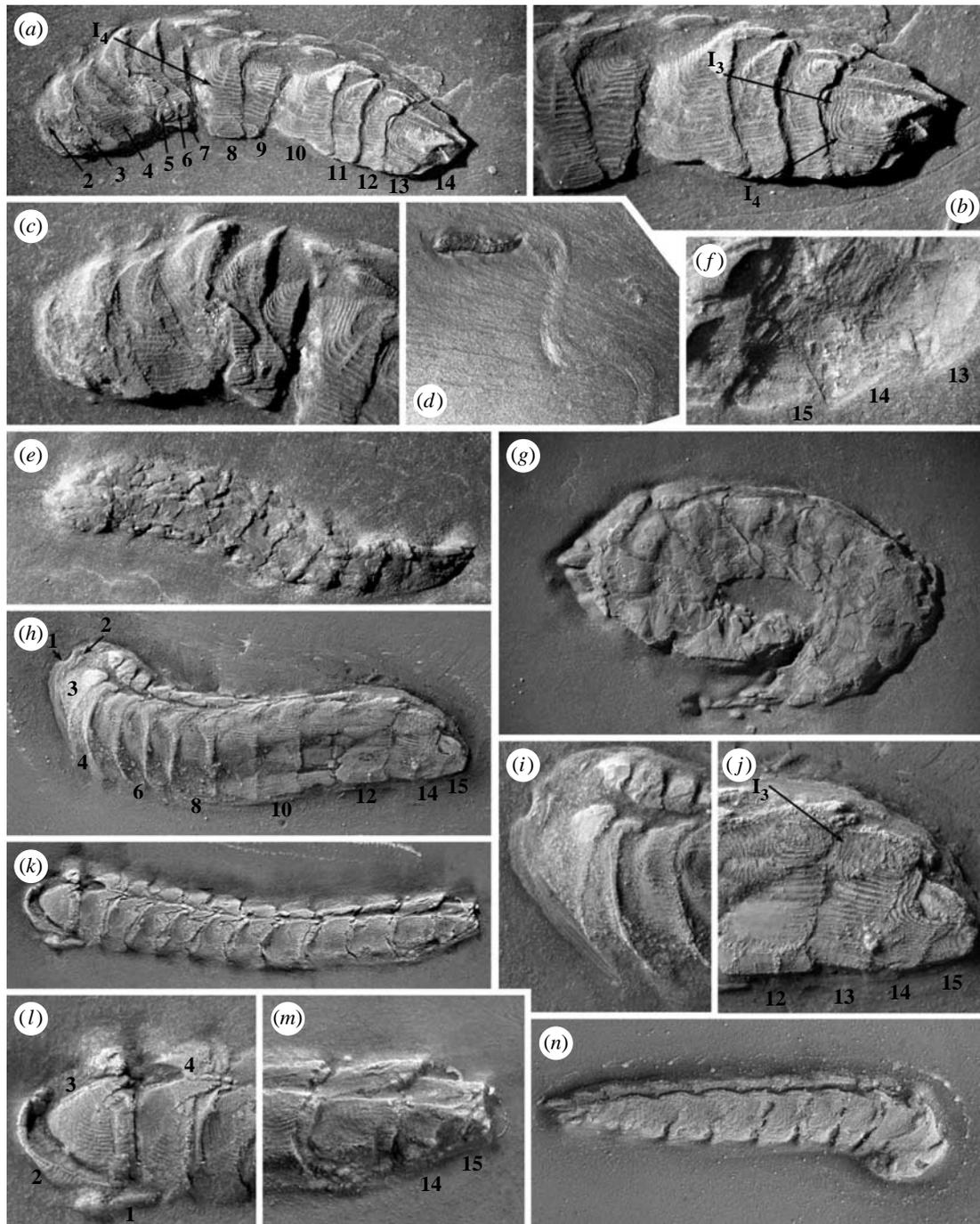
Figure 2. *Lepidocoleus hohensteini*, Early Devonian, Emsian, Hunsrück Shale. (*a*–*c*) Holotype, NM:PH 4.1 598, left lateral. (*a*) Entire specimen, note I_4 and plate numbers, $\times 4.2$; (*b*) posterior part, note I_4 and I_3, and (*c*) anterior part, note relatively 'straight' rugae, both $\times 5.6$. (*d,e*) DBM:HS 735, ventral. (*d*) Specimen with trail, $\times 0.6$; (*e*) entire specimen, $\times 3.0$. (*f,g*) DBM:HS 367, left lateral. (*f*) Posterior end, note plate numbers, $\times 5.4$; (*g*) entire specimen, $\times 3.3$. (*h–j*) NM:PWL 2008/5005-LS, left oblique. (*h*) Entire specimen, note plate numbers, $\times 3.5$; (*i*) anterior and (*j*) posterior end, note I_3 and plate numbers, $\times 5.4$. (*k–m*) NM:PH 0249, left oblique. (*k*) Entire specimen, $\times 2.7$; (*l*) anterior and (*m*) posterior end, note pattern of rugae (especially in plate 3) and plate numbers, both $\times 5.4$. (*n*) NM:PH 0263, right oblique, entire specimen, $\times 4.1$.

4. SYSTEMATIC PALAEONTOLOGY

Phylum: Annelida

Machaeridia Withers 1926 (here regarded as a clade containing three families, following Herringshaw & Raine (2007))

Family: Lepidocoleidae (Clarke 1896)

Diagnosis: Laterally compressed, biseriate or quadriseriate machaeridians with dorsal functional hinge allowing plates to meet ventrally, inner plate surface with dorsolaterally positioned muscle scars.

Genus: *Lepidocoleus* (Faber 1886)

Type species: *Lepidocoleus jamesi* (Hall & Whitfield 1875)

Diagnosis: Biseriate lepidocoleid machaeridians.

Remarks: Two taxa with quadriseriate skeletons are presently included in *Lepidocoleus*: (*Turrilepas*?) *Lepidocoleus ketleyanus* (Reed 1901) and *L*. sp. A (Högström 1997). Future taxonomic revision may show that these should be accommodated in a new genus characterized by the possession of outer plates.
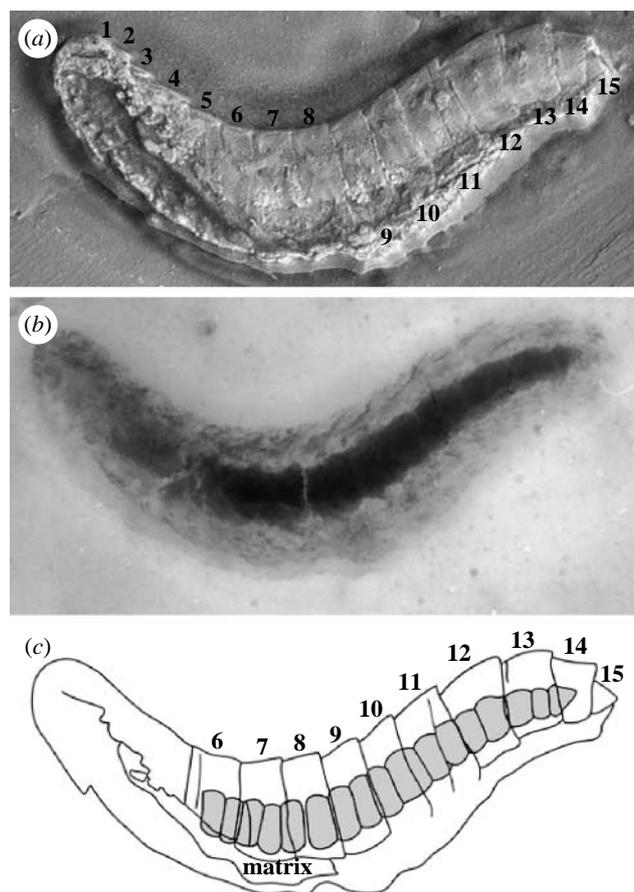
Figure 3. NM:PWL 2002/231-LS, $(a–c) \times 3$, (*a*) specimen exposing left side, note plate numbers, (*b*) X-radiograph, (*c*) explanatory drawing with corresponding plate numbers.

Species: *L. hohensteini* sp. nov.

Derivation of name: for Peter Hohenstein of Lautertal who prepared and provided critical specimens.

Material: Holotype NM:PH 4.1 598 and seven additional specimens (DBM:HS 735; DBM:HS 367; NM:PWL 2008/5005-LS; NM:PWL 2002/231-LS; NM:PH 0263; NM:PH 0249; NM:PH 0857).

Diagnosis. *Lepidocoleus* with 15 paired plates, narrow dorsal depression; dorsal hinge with opposing articulation. Length of complete mature skeleton at least 24 mm. Density of rugae approximately 16–20 per mm (D-V), 8-11 (A-P) on mature midbody plates; total number of rugae at least 30–35 on mature midbody plates. Rugae nearly straight anteriorly with increased curvature towards posterior end. Mature plates in midbody sub-rectangular in outline. Inflections $I_1–I_4$ present, with I_3 distinctly curved and I_4 approximating 90°.

(a) *Skeleton*

The specimens show some flexibility, ranging from straight to dorsally or ventrally curved, laterally twisted or spirally coiled (figures 2 and 3). This presumably reflects the potential for flexure of the body in life. The exoskeleton consists of 15 pairs of plates and ranges in length (in complete specimens) from 16.5 to 24 mm (table 1; S2 in the electronic supplementary material). The degree of overlap between successive plates varies. The dorsal articulation is opposed (not alternate) and the dorsal depression is narrow (figure 2h–n). The midbody

plates are sub-rectangular in outline (figure 2*a*, *g*, *h*), the terminal plates are triangular (figure 2*a*, *b*, *f*, *h*, *j*, *m*). No traces of apical or marginal spines are evident.

The pattern of rugae varies along the trunk: those on the anterior plates are nearly straight (figure 2*l*), whereas those on the more posterior plates display a strongly increased curvature (figure 2*j*). The pattern of rugae also changes as the plates increase in size, with crowding of rugae evident at the accreting margin of large plates. This indicates a reduction in growth increment size with maturity (Högström 2000). The density of rugae is approximately 16–20 per mm where dorsoventrally aligned (D-V) and it is 8–11 per mm where antero-posteriorly aligned (A-P); there are at least 30–35 in total per mature midbody plate. Inflections $I_1–I_4$ (figure 1) are present. I_1 (on the dorsal flange) is often obscured due to the orientation of the specimen in the sediment concealing the dorsal depression, I_3 is distinct particularly in mature specimens, and I_4, which approximates 90°, is clearly evident throughout ontogeny and is prominent in all plates with the exception of the 1st and 15th (figure 2*a–c*, *j*). Further details are provided in the electronic supplementary material S2.

(b) *Soft-part anatomy*

The soft parts are preserved in a single specimen (figure 3) which is lateral-oblique in its attitude to bedding so the right plates project well below the left. The most striking feature is a broad strip of pyrite running along the midline and occupying approximately 40 per cent of the preserved height of the left plates (figure 3*b*, *c*). This structure, which represents the trunk of the animal, is heavily pyritized in the length occupied by the 6th to the 14th plate pairs and more faintly anterior and posterior of this. It tapers gradually posteriorly in proportion to the body. A combination of constrictions and faint transverse lines reflects the segmentation. Approximately 17 segments are evident between the 5th and 14th plate pairs, two corresponding to each of the plates that enclose the trunk (figure 3*c*). The CT scan reveals clear short lateral projections on alternate segments, those on the opposite sides of the trunk offset by the oblique flattening, which represent the attachment of the trunk to the plates that enclose it (figure 4). Above and below the trunk, in contrast, are spaces within the skeleton, which may be original or may reflect some shrinkage of the trunk due to decay (figures 3*b* and 4). Thin linear structures inclined at a low angle to the trunk are apparent, converging anteriorly both above and below it (figures 3*b* and 4). These, however, reflect the plates where they are more heavily pyritized where they traverse the bedding plane at a high angle (figure 4). There is no evidence of parapodia or chaetae.

5. DISCUSSION

Lepidocoleus hohensteini differs from other Devonian lepidocoleids primarily in the number of plate pairs. Other Devonian species have a larger number (*L. elongatus*, for example, has at least 47 plate pairs) and are high and narrow in cross section. *Lepidocoleus hohensteini* is more similar in general habitus to the short Silurian *L. sarlei* (Clarke 1896; Högström & Taylor 2001) and the Ordovician *L. jamesi* (Hall & Whitfield 1875; Högström 2001).

Table 1. Summary of measured parameters for all eight available specimens of *Lepidocoleus hohensteini*. (L=length of skeleton; H=height of skeleton (dorsoventral measurement); W=width of skeleton; WDD=width of dorsal depression.)

specimen no.	L (mm)	H (mm)	W (mm)	WDD (mm)	no. of plate pairs
NM:PH 4.1 598	14.7	∼3.0	—	—	13–14
DBM:HS 735	20.4	—	4.3	—	13–15
DBM:HS 367	∼28.0	∼4.2	—	—	(14-)15
NM:PWL 2008/5005-LS	17.0	3.7	—	∼0.5	(14-)15
NM:PWL 2002/231-LS	24.0	4.3	—	—	15
NM:PH 0263	14.0	—	—	∼0.5	>11
NM:PH 0249	24.0	∼2.7	—	∼0.8	(14-)15
NM:PH 0857[a]	10.0	—	2.2	∼0.3	12

[a]Specimen not figured.

Figure 4. NM:PWL 2002/231-LS, stereo pair of left side based on CT scan, grey arrows point to traces of plates, white arrows to attachments of plates, the two most anterior uncertain in position.

Lepidocoleus hohensteini lacks the dorsal alternate articulation present in *L. sarlei* (Högström & Taylor 2001), however, and has a narrower dorsal depression. Likewise *L. hohensteini* has a narrower dorsal depression than *L. jamesi*, and less pronounced rugae. The recently described *L. rugatus* (Klug *et al.* 2008) is similar in size to *L. hohensteini*, but the number of plates is estimated as larger (at least 16 plate pairs) and the rugae are finer and more closely spaced. *Lepidocoleus rugatus* is described as exhibiting an alternate dorsal articulation (Klug *et al.* 2008, p. 137), but this is not clearly illustrated. *A. gleidorfense* (Wolburg 1938) is too poorly preserved for a detailed comparison but appears to have more than 15 plate pairs.

One individual is associated with a trail (figure 2*d*,*e*) of *Cochlichnus* (Hitchcock 1858) type with a distinct sinusoidal curve. The length of the animal is similar to the wavelength of the trail (table 1; figure 2*d*; and S1 in the electronic supplementary material), excluding the possibility that the machaeridian was moving by lateral undulation as do some annelids. It is likely to represent an escape trail (Vinther & Briggs 2009). Escape trails made by the mitrate *Rhenocystis* have also been reported from the Hunsrück Slate (Sutcliffe *et al.* 2000).

The specimen preserving soft tissues shows clear evidence of segmentation reflected in constrictions in the trunk (figure 3). The distribution of segments and plates reveals a ratio of 2 : 1 (figure 3*c*) and on every second segment there are dorsolaterally positioned paired plate attachments (figure 4), similar to the cirri that carry elytra in living scale worms (Phyllodocida: Aphroditidae). This arrangement is presumably homologous to that in *Plumulites* where the attachment of the inner plates alternates with that of the outer (Vinther *et al.* 2008), strongly supporting the monophyly of the clade Machaeridia. Additional support for the monophyly of machaeridians is provided by the presence of two paired series of plates in *L. ketleyanus* and *L.* sp. A (Dzik 1986; Högström 1997). The lack of evidence for parapodia in both X-radiograph and CT scan indicates that lepidocoleid machaeridians lack the appendages in plumulitid machaeridians. This is consistent with their infaunal lifestyle where the plates were used to gain purchase on the sediment during peristaltic burrowing (Högström 1997; Vinther & Briggs 2009).

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