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

Anette E. S. Högström, Derek E. G. Briggs, Christoph Bartels

1Department of Earth Sciences, Palaeobiology, Uppsala University, Villavägen 16, 752 36 Uppsala, Sweden
2Department of Geology and Geophysics, Yale Peabody Museum of Natural History, Yale University, New Haven, CT 06520, USA
3Deutsches Bergbau-Museum, Am Bergbaumuseum 28, 44791 Bochum, Germany

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 Bendenbach area (Rhenish Massif, Germany) includes one specimen that reveals, for the first time, evidence of the nature of lepidocoleid soft tissues.

Received 16 December 2008
Accepted 28 January 2009
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 Wingertershell Clayey Slate Member of the Kaub Formation (Schindler et al. 2002) in the Oberschenbach 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 quadriseporate 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 turrilipadids), 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 turrilipadids 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. I1–I4 present, I1 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). 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).

![Diagram](http://rsbp.royalsocietypublishing.org/Downloaded from on June 26, 2017)
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: (Turritepas?) 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 2. Lepidocoleus hohensteini, Early Devonian, Emsian, Hunsrück Shale. (a–c) Holotype, NM:PH 4.1598, left lateral. (a) Entire specimen, note I4 and plate numbers, ×4.2; (b) posterior part, note I4 and I5, and (c) anterior part, note relatively ‘straight’ rugae, both ×5.6. (d,e) DBM:HS 735, ventral. (d) Specimen with trail, ×0.6; (e) entire specimen, ×3.0. (f,g) DBM:HS 367, left lateral. (f) Posterior end, note plate numbers, ×5.4; (g) entire specimen, ×3.3. (h–j) NM:PWL 2008/5005-LS, left oblique. (h) Entire specimen, note plate numbers, ×3.5; (i) anterior and (j) posterior end, note I3 and plate numbers, ×5.4. (k–m) NM:PH 0249, left oblique. (k) Entire specimen, ×2.7; (l) anterior and (m) posterior end, note pattern of rugae (especially in plate 3) and plate numbers, both ×5.4. (n) NM:PH 0263, right oblique, entire specimen, ×4.1.
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 I1–I4 present, with I3 distinctly posteriorly aligned (A-P); there are at least 30–35 in total per mature midbody plate. Inflections I1–I4 (figure 1) are present. I1 (on the dorsal flange) is often obscured due to the orientation of the specimen in the sediment concealing the dorsal depression, I3 is distinct particularly in mature specimens, and I4, which approximates 90°, is clearly evident throughout ontogeny and is prominent in all plates with the exception of the 1st and 15th (figure 2a–cj). Further details are provided in the electronic supplementary material S2.

**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 2a,g,h), the terminal plates are triangular (figure 2a,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 2l), whereas those on the more posterior plates display a strongly increased curvature (figure 2j). 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 I1–I4 (figure 1) are present. I1 (on the dorsal flange) is often obscured due to the orientation of the specimen in the sediment concealing the dorsal depression, I3 is distinct particularly in mature specimens, and I4, which approximates 90°, is clearly evident throughout ontogeny and is prominent in all plates with the exception of the 1st and 15th (figure 2a–cj). 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 3b,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 3c). 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 3b and 4). Thin linear structures inclined at a low angle to the trunk are apparent, converging anteriorly both above and below it (figures 3b 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.)

<table>
<thead>
<tr>
<th>Specimen no.</th>
<th>L (mm)</th>
<th>H (mm)</th>
<th>W (mm)</th>
<th>WDD (mm)</th>
<th>No. of plate pairs</th>
</tr>
</thead>
<tbody>
<tr>
<td>NM:PH 4.1 598</td>
<td>14.7</td>
<td>~3.0</td>
<td>—</td>
<td>—</td>
<td>13–14</td>
</tr>
<tr>
<td>DBM:HS 735</td>
<td>20.4</td>
<td>—</td>
<td>4.3</td>
<td>—</td>
<td>13–15</td>
</tr>
<tr>
<td>DBM:HS 367</td>
<td>~28.0</td>
<td>~4.2</td>
<td>—</td>
<td>—</td>
<td>(14–)15</td>
</tr>
<tr>
<td>NM:PWL 2008/5005-LS</td>
<td>17.0</td>
<td>3.7</td>
<td>—</td>
<td>0.5</td>
<td>(14–)15</td>
</tr>
<tr>
<td>NM:PWL 2002/231-LS</td>
<td>24.0</td>
<td>4.3</td>
<td>—</td>
<td>—</td>
<td>15</td>
</tr>
<tr>
<td>NM:PH 0263</td>
<td>14.0</td>
<td>—</td>
<td>—</td>
<td>~0.5</td>
<td>&gt;11</td>
</tr>
<tr>
<td>NM:PH 0249</td>
<td>24.0</td>
<td>~2.7</td>
<td>—</td>
<td>~0.8</td>
<td>(14–)15</td>
</tr>
<tr>
<td>NM:PH 0857a</td>
<td>10.0</td>
<td>—</td>
<td>2.2</td>
<td>~0.3</td>
<td>12</td>
</tr>
</tbody>
</table>

*Specimen not figured.

REFERENCES

Abele-Oeschger, D., Oeschger, R. & Theede, H. 1994
Biochemical adaptations of *Nereis diversicolor* (Polychaeta)


Clarke, J. M. 1896 The structure of certain Palaeozoic barnacles. Am. Geol. 17, 137–143.


Reed, F. R. C. 1901 Woodwardian museum notes: Salters’ undescribed species. J. Geol. 8, 106–110.


