Fossilized soft tissues in a Silurian platyceratid gastropod

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Gastropod shells are common in the fossil record, but their fossil soft tissues are almost unknown, and have not been reported previously from the Palaeozoic. Here, we describe a Silurian (approx. 425 Myr) platyceratid gastropod from the Herefordshire Lagerstätte that preserves the oldest soft tissues yet reported from an undoubted crown-group mollusc. The digestive system is preserved in detail, and morphological data on the gonads, digestive gland, pedal muscle, radula, mouth and foot are also available. The specimen is preserved three-dimensionally, and has been reconstructed digitally following serial grinding. Platyceratids are often found attached to echinoderms, and have been interpreted as either commensal coprophages or kleptoparasites. The new data provide support for an attached mode of life, and are suggestive of a coprophagous feeding strategy. The affinities of the platyceratids are uncertain; they have been compared to both the patellogastropods and the neritopsines. Analysis of the new material suggests that a patellogastropod affinity is the more plausible of these hypotheses.

Keywords: exceptional preservation; Herefordshire Lagerstätte; palaeoecology; phylogeny; Platyceratidae; Wenlock series

1. INTRODUCTION

Marine gastropods are a familiar component of Recent and fossil faunas, with a record extending back to the Cambrian (e.g. Tracey *et al.* 1993). However, this record consists almost entirely of hard parts (i.e. shells and opercula); just one example of marine gastropod soft-tissue preservation is known from the Mesozoic (Casey 1960), and there are no previously reported instances from the Palaeozoic. The phylogeny of Palaeozoic gastropods is therefore based on hard-part (primarily teleoconch) characters and on extrapolation from the soft parts of extant forms; moreover the utility of shell characters for phylogenetic inference is in doubt (Schopf *et al.* 1975; though see also Wagner 2001). The discovery of fossilized soft parts in a Palaeozoic gastropod is hence significant for the evaluation of phylogenetic hypotheses, and as a basis for functional analysis and the interpretation of palaeoecology.

The Platyceratidae are an extinct but long-ranging (Ordovician–Permian, ?Triassic) family whose position within the Gastropoda is unclear (Ponder & Lindberg 1997). They have been placed traditionally within the Archaeogastropoda (see e.g. Knight *et al.* 1960), but this group is now recognized as a grade rather than a clade, and there is currently little consensus about the phylogeny of either extant or extinct ‘archaeogastropods’ (Ponder & Lindberg 1997; Colgan *et al.* 2000; Wagner 2001). Two hypotheses for the phylogenetic position of the Platyceratidae have been championed recently: firstly that they are related to the ‘true limpets’ (Patellidae) and hence lie

within the Patellogastropoda of Ponder & Lindberg (1997); or secondly that they are relatives of the Neritopsidae, and lie within an expanded Neritopsina (Bandel 1992; Bandel & Fryda 1999). Recent morphologically based phylogenetic analyses (Haszprunar 1988; Ponder & Lindberg 1997) placed the Patellogastropoda as the basal clade within the Gastropoda, inferring also a relatively basal position for the neritopsines. However these results are not well-supported by molecular data (Harasewych *et al.* 1997; Colgan *et al.* 2000, 2003), and the exact position of these taxa remains unclear.

There is a substantial literature on the palaeoecology of platyceratid gastropods, which are involved in an unusual but well-documented example of biotic interaction in the fossil record; for reviews and recent contributions see Baumiller (2002, 2003), Gahn & Baumiller (2003) and Lindström & Peel (2003). Platyceratids are found frequently attached to echinoderms (normally crinoids) and preferentially took up a position over the anus. The excrement of crinoids is potentially nutritious, at least in extant comatulids, where it consists of mucus-bound pellets containing micro-organisms and algae (Gislén 1924). Hence, platyceratids have long been interpreted as coprophagous. Recent work (Rollins & Brezinski 1988; Gahn & Baumiller 2003) suggests that they are likely to have been parasitic rather than commensal, and may have functioned as kleptoparasites, extracting partially digested pellets directly from the posterior digestive tract of the crinoid through the anus (Gahn & Baumiller 2003). At least some platyceratids were capable of drilling into their hosts to gain access to their soft tissues (Baumiller 1990; Gahn *et al.* 2003). However it remains unclear whether

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Figure 1. (*Opposite.*) *Platyceras?* sp., OUM C. 29 599. (a), (b), (e)–(i) are ‘virtual’ reconstructions of the specimen; (a), (b), (e), (g), (h) are stereo-pairs. (a) Conventional orientation, $\times 15$. (b) Tilted view into aperture with additional lighting, $\times 15$. (c) Image no. 31 from serial grinding run, $\times 10$. (d) Image no. 57 from serial grinding run, $\times 10$, inset $\times 30$. (e) View from position normal to anterior of viscera, anterior portion of shell removed, $\times 15$. (f) Apical view, $\times 15$. (g)–(i) Digestive system and gonad/digestive gland complex, $\times 20$. (g) Viewing position adaxial of shell, about one-half whorl back from aperture, apex up and right. (h) Viewing position adapical of shell, about one-quarter whorl back from aperture, apex up and away from viewer. (i) Apical view. BR, buccal region; DP, dark phase of gonad/digestive gland complex; Ft, remains of foot; F1–3, first- second- and third-folds of intestines; In, intestine; L1, L2, first and second loops of intestines; LP, light phase of gonad/digestive gland complex; Oe, oesophagus; OO, possible oesophageal outpocketing; PM, pedal muscle; Ra, radula and buccal structures; Re, rectum; St, stomach; Um, Umbilicus. Note that the virtual model has been supplemented by interpretations of the path of the alimentary canal where it is not preserved; interpretations are narrow yellow/orange structures in (g)–(i).

echinoderm symbiosis was the typical mode of life for the family. Specimens have been found attached to cephalopod hosts (Horný 2000), demonstrating a capability for exploiting a broader range of organisms. While there is evidence for a sessile adult ecology (Baumiller 2002) a vagile mode-of-life cannot be excluded for all platyceratid species (Peel 1978; Lindström & Peel 2003).

We describe here a new platyceratid specimen from the lower Silurian (Wenlock Series; approx. 425 Myr) Herefordshire Lagerstätte of England (Briggs *et al.* 1996). This fossil preserves the oldest soft tissues yet reported from an undoubted crown-group mollusc; the co-occurring *Acaenoplax hayae* Sutton *et al.* (2001a) may belong to either the molluscan crown or stem (Sutton *et al.* 2004) and interpretations of older fossils as crown-group molluscs remain controversial (e.g. Vinther & Nielsen 2005). Fossils from the Herefordshire deposit are preserved as three-dimensional calcite in-fills in nodules in a volcanoclastic ash (Orr *et al.* 2000), and preserve high-fidelity details of soft tissues that can be studied through serial grinding and computer reconstruction (Sutton *et al.* 2001b). In addition to molluscs, the deposit has yielded a diversity of sponges, radiolarians (Orr *et al.* 2002; Siveter *et al.* in press), arthropods (Sutton *et al.* 2002; Siveter, David *et al.* 2003; Siveter, Derek *et al.* 2004; Briggs *et al.* 2004, 2005), a polychaete (Sutton *et al.* 2001c), a brachiopod (Sutton *et al.* 2005b), an asteroid (Sutton *et al.* 2005a) and a suite of as-yet undescribed forms.

The Herefordshire gastropod is assigned to the Platyceratidae on the basis of its simple sub-circular aperture, trochiform shell and absence of ornament. The platyceratid fauna from the Wenlock of Britain is in need of revision; no significant taxonomic work has been published on these gastropods since the middle of the nineteenth century (Sowerby 1839; McCoy 1851). Wenlock-aged specimens in collections of the Oxford University Museum of Natural History and Natural History Museum, London, encompass a range of teleoconch morphologies and sizes. Some are closely comparable in both size and form to that described here, and have been assigned by collectors and curators variously to the platyceratid genera *Platyceras*, *Platyostoma* and *Cyclonema*. This morphotype is taller (relatively) and expands less rapidly than ‘typical’ specimens of the best-known contemporaneous species *Platyceras haliotis* (Sowerby 1839), but the true morphological range of *P. haliotis* is poorly known, as is the true stratigraphic range of other species reported from the British Silurian. A resolution of these taxonomic issues is beyond the scope of this study, and the new specimen with soft parts is treated under open nomenclature as *Platyceras?* sp.; this generic assignment is

intended only as a label of convenience, pending a revision of British Wenlock platyceratids. In view of its small size (5 mm in diameter) it may represent a juvenile, although it could be an adult of a small species. Note that *Platyceras* is used here in the sense of Knight *et al.* (1960), incorporating several genera (including *Platyostoma* but excluding *Cyclonema*) as subgenera.

2. MATERIAL AND METHODS

Gastropods are relatively common in the Herefordshire Lagerstätte fauna, but most specimens are small high-spired forms, probably muchisoniids. OUM C.29 599 is the largest gastropod specimen known from the fauna, and the only one known to preserve soft tissues; no other conspecific specimens have yet been recovered. The specimen was serially ground and digitally photographed at 20 μ m intervals, and the resulting datasets were used to generate three-dimensional computerized ‘virtual fossils’ through the approach detailed in Sutton *et al.* (2001b). Images were edited prior to reconstruction in order to remove extraneous material, and to assign all pixels to one of five distinct phases of fossil material. Internal structures (the digestive gland and/or gonad) are preserved in two distinct phases: a dark opaque material (DP in figure 1c), and a lighter speckled material (LP in figure 1c), the latter interpreted as a partial fill of ‘dirty’ sediment. The stomach and intestines are preserved in a light grey opaque material, which may also be sediment contaminated in a different manner. The shell and much of the undifferentiated fill of the whorls is preserved in sparry calcite, translucent and light in colour; soft parts protruding anteriorly are also preserved in this phase, but have been colour-coded separately in reconstructions. The protruding soft parts are poorly preserved, and become increasingly indistinct anteriorly; hence their forward extent is delimited arbitrarily in the figures. An internal cavity (the oesophagus), however, is picked-out clearly in this region by a darker coloration in the sediment that may represent an oxidised area (see figure 1c,d); although interpreted as a cavity, this has been included in the reconstruction as a solid additional phase (dark green in figures), and traced backwards into the viscera. A large light-coloured region is preserved within the pallial cavity (between Re and Oe in figure 1d). It does not record morphology in any direct way and is not included in reconstructions; it probably represents an area of reduction resulting from the decomposition of the head/foot complex. The poorly defined structure attached near the aperture (arrow, figure 1b) is interpreted as a taphonomic artefact, but was too intimately emplaced on the shell to be removed in reconstruction.

Datasets are housed in the University Museum of Natural History, Oxford (OUM).

Figure 1. (*Caption opposite.*)

3. DESCRIPTION

The shell is trochiform, 5.0 mm in diameter and 3.8 mm in height (figure 1*a*). There are about three whorls, although the point of origin is difficult to determine as the protoconch is missing (figure 1*f*). An umbilicus is present, representing

about 15% of whorl diameter (Um; figure 1*b,e*). The last whorl is 2.9 mm in diameter at the aperture, which is prosocline and unmodified. Shell growth-parameters are constant throughout growth. The shell is thin (figure 1*d*), and lacks discernible ornament.

The shell is empty for about one-quarter of a whorl back from the aperture in apical view; at this point a fill of calcite commences, which is interpreted as the visceral mass. The boundary between the viscera and the matrix is poorly defined and difficult to reconstruct; it is subtransverse to the whorl and coincident with the stomach and intestines (figure 1*b*). Other than the rectum and head/foot, no structures are preserved emerging from the viscera.

Material protruding abapically from the visceral region (figure 1*a–c,e*) is interpreted as the remains of the head and foot. Posteriorly it forms a hollow cylinder, open (or not preserved) dorsally, and flexed abapically. The core of the cylinder extends from the viscera, broadening anteriorly from an origin near the first coil of the intestine; this is interpreted as part of the oesophagus (Oe; figure 1*b–e,g–i*). A small subspherical cavity is preserved adjacent to the point where the oesophagus enters the visceral mass; this abuts the oesophagus and may represent an outpocketing or gland (OO; figure 1*c,e,h*). Distally the protruding material is dominated by a substantial ventral mass with a subplanar termination, flanked by poorly preserved lateral extensions (PM; figure 1*a–c,e*); it is interpreted as the distal expression of the columellar (pedal retractor) muscle, the anterior termination and lateral extensions indicating the position of the sole of the foot (Ft). The muscle abuts the oesophagus, but enters the visceral region separately, at the adaxial margin of the aperture (figure 1*b*, at label PM). Where the oesophagus and muscle separate anteriorly, the former widens slightly and becomes indistinguishable from external sediment. At this point (arrow, figure 1*e*) a transverse ‘bar’ is preserved ventral to the oesophagus, from which a straight ribbon-like structure approximately 1 mm long extends anterodorsally (Ra; figure 1*a,b,e*). Although indifferently preserved, serial-grinding images (figure 1*d*) show that this structure is constructed from narrow transverse strips; it is interpreted as a radula, and the strips as remnants of the teeth. These are clearest anteriorly, probably reflecting an ontogenetic increase in sclerotization towards the mouth. At the anterior of the radula, a collection of poorly preserved structures occur (figure 1*a,b,d*; BR in figure 1*e*); these are difficult to interpret and some at least may be taphonomic artefacts. This region almost certainly represents the buccal cavity and mouth, but preservational uncertainties preclude any more detailed interpretation.

The stomach (St) is a well-defined tube 1.6 mm long and 0.4 mm in diameter, aligned ad–abaxially, with anterior axial (oriented towards the viewer in figure 1*a*, downward in figure 1*i*); it occupies nearly all the width of the whorl. No internal structure is evident. The anterior termination of the stomach is well-defined, the presumed oesophagus entering off-centre (figure 1*i*), while the posterior distinction between stomach and intestine (In) is more gradational (figure 1*g,h*). The connection between the section of oesophagus in the head and that entering the stomach is not preserved; it is assumed to have consisted of a loop (L1; figure 1*g–i*) passing behind the stomach and intestine, constricted relative to the stomach and anterior oesophagus. The entire length of the intestine appears constant in diameter (0.2 mm). After egressing the stomach it is folded, abutting the shell, to run adaxially parallel to and apical of the stomach; this fold (F1; figure 1*g,h*) is impermissibly preserved. It then describes a

broad loop (L2; figure 1*g,h*) that passes behind the stomach (left of it in figure 1*i*) axially, in front of it (right of it in figure 1*i*) abaxially, and finishes slightly in front of its starting point. The intestine is then sharply folded (F2; figure 1*g–i*) through 180 degrees to pass abaxially again, abutting both the start and end of loop L2. Preservation stops at this point; a short isolated section occurs near F1, lying between L2 and the rectum, which is directed towards the aperture and runs along the abaxial shell wall. A third fold (F3; figure 1*g–i*) is inferred here, although more complex architectures cannot be excluded. The rectum (Re) passes into the pallial cavity and terminates well short of the aperture; preservation of the rectum in the cavity is clear (figure 1*d*), and hence its termination probably represents the original position of the anus.

Two infill phases (LP, DP; see §2) are intertwined and fill much of the visceral mass behind the digestive system (figure 1*e,g–i*). The morphology is largely undifferentiated, defined by the outline of the shell, extending from around half a whorl to nearly two whorls back from the aperture. The ‘dark phase’ (DP; figure 1*c,e,g–i*) is preserved preferentially adaxially, and extends further back into the shell. These two phases are interpreted as abutting structures, as implied by the nesting of the termination of ‘LP’ inside ‘DP’ (figure 1*e,h*); the lack of continuity of the dark phase is thus probably a preservational artefact. In extant gastropods, both the gonad and digestive gland often occupy a large percentage of the viscera, and are intermingled in some cases (see e.g. Hyman 1967); both of these organs may be represented here, but if so there is insufficient information to determine which phase corresponds to which organ. Connection(s) to the alimentary canal and/or pallial cavity are not evident; these connections may have been thin, and their absence is likely to be an artefact of preservation.

4. DISCUSSION

Although the specimen is exceptionally well-preserved, preservation is incomplete; missing structures include much of the foot, the head (although the position of the buccal cavity is indicated) and structures of the pallial cavity, notably the ctenidium or ctenidia and osphradium or osphradia. The preserved position of the front of the visceral mass is also set further back into the shell than is plausible biologically, as the intestines protrude from it (figure 1*b*). Hence we infer a degree of decomposition prior to the ‘freezing’ of the sediment. The lack of an operculum, in contrast, is interpreted as real; opercula are relatively recalcitrant structures which would have had a high fossilization potential, and a consideration of the taphonomic processes that affect other fossils from this deposit suggests that detachment prior to burial is unlikely.

Findings from our new material are compatible with the model of platyceratid palaeoecology as sessile and coprophagous. The absence of an operculum is suggestive of an attached and hence relatively sessile mode of life; most vagile marine gastropods possess an operculum behind which they can withdraw their soft tissues for protection. The stomach of Recent caenogastropod and heterobranch carnivorous gastropods tends to be a large U-shaped bag; their intestines are greatly reduced (Kay *et al.* 1998). The morphology described here contrasts

with this, suggesting that platyceratids were symbiotic rather than predatory on their hosts. A kleptoparasitic feeding strategy (Gahn & Baumiller 2003) requires the presence of a proboscis or pseudoproboscis (extensile snout). In the Herefordshire specimen, the relatively short, straight radula and position of the buccal region indicate the lack of a substantial proboscis, either retracted or extended. However, the possibility that an unpreserved pseudoproboscis extended beyond the buccal region cannot be excluded.

Of the soft-tissue characters described here, the digestive system is the most informative phylogenetically. Both neritopsines and patellogastropods have coiled intestines (Bourne 1908; Hyman 1967; Lindberg 1998; Sasaki 1998); this morphology is probably plesiomorphic for the gastropods (see e.g. Haszprunar 1988). The intestines of patellogastropods are typically much longer and narrower than that described here, which could represent a juvenile or pedomorphic state, as patellogastropod intestine-coiling increases in complexity with growth and size (Lindberg 1988). Neritopsines have relatively short, inflated and well-differentiated stomachs (Fretter 1965; Sasaki 1998) with many internal structures (gastric caecum, style, gastric shield, corrugated sorting area, intestinal groove) that are not evident in the specimen described here; the stomach-wall is well-defined in our material, and we interpret the absence of these structures as biologically significant, rather than an artefact of preservation. Patellogastropods have a greatly simplified stomach that lacks internal structures and is poorly differentiated from the intestine (e.g. Graham 1949; Hyman 1967, fig. 97a; Ponder & Lindberg 1997; Sasaki 1998). Although the level of stomach-intestine differentiation in the Herefordshire specimen falls between that typical of the two groups, the simple nature of the stomach is far more reminiscent of the patellogastropods than the neritopsines. The relatively posterior placement of the anus is also suggestive of patellogastropod rather than neritopsine affinity (Ponder & Lindberg 1997, character 79).

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