A new crustacean from the Early Devonian Rhynie chert, Aberdeenshire, Scotland

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ABSTRACT: A new crustacean, *Castracollis wilsonae* is described from a loose block of the Early Devonian Rhynie chert, found in the vicinity of Rhynie, Aberdeenshire, Scotland. It differs markedly from *Lepidocaris rhyniensis*, Scourfield 1926, the only other crustacean found in the Rhynie chert.

The material comprises complete individuals up to 8 mm long and fragmentary remains. The head is normally damaged and detached from the body, and damage to the anterior of the trunk suggests the specimens are exuviae. The head appears domed with a labrum, robust mandibles, and long biramous antennae. A few specimens exhibit a probable detached cephalo-thoracic shield. The trunk is multi-segmented, comprising similar ring-like somites. The thorax variably comprises up to 26 segments. The anterior 11 segments possess similar long, phyllopodous appendages, the remainder variably possess 10 to 15 phyllopodous appendages with a disposition of one per somite. The abdomen comprises up to 28 apodous segments. The posterior of the body comprises a telson with two furcal rami.

The crustacean is most probably a calmanostracan branchiopod. It occurs associated with *Lepidocaris*, charophytes, cyanobacteria and coprolites within a 'clotted' chert texture, indicating subaqueous deposition, most probably in a temporary freshwater pool in an area of surficial hydrothermal activity.
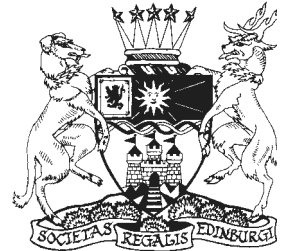
The Early Devonian Rhynie chert Konservat-Lagerstätte is renowned for containing one of the best and most completely preserved early terrestrial and freshwater biotas. Research at the University of Aberdeen (Trewin & Rice 1992; Rice *et al.* 1995, 2002) ascertained that the cherts were undoubtedly deposited as subaerial siliceous sinters within a hydrothermal hot-spring complex.

Since its discovery early last century (Mackie 1913), much of the palaeontological work has concentrated on the remarkable floral content of the chert. Most of the fauna known from the chert was described and diagnosed during the first half of the twentieth century, primarily trigonotarbid and acarid arachnids (Hirst 1923), a crustacean (Scourfield 1926, 1940) and a collembolan (Hirst & Maulik 1926). Recently, during studies at the Universities of Aberdeen and Münster on the Rhynie chert, and on the Windyfield chert (Trewin & Rice 1992) new faunal elements have been found, including two myriapods (Anderson & Trewin 2003) and others that are currently being described. Known problematic forms have also been resolved, primarily the enigmatic arthropod *Heterocrania rhyniensis* (Hirst & Maulik 1926) being recognised as an euthycarcinoid (Anderson & Trewin 2003). To date, only one crustacean has been formally described from the Rhynie chert, the lipostracan branchiopod *Lepidocaris rhyniensis*, Scourfield 1926. This study introduces a new fossil crustacean from the chert representing a completely new branchiopod.

1. Material and methods

The material described herein comes from a loose float block of chert found in the early spring of 2000 during a series of prospective field studies across the northern outlier at Rhynie.

The block in question was discovered within scattered float material located just to the SW of the farm at Castlehill [NJ 3509 8279] some 1500 m E of the Rhynie SSSI (Site of Special Scientific Interest) (Fig. 1). The float material discovered at
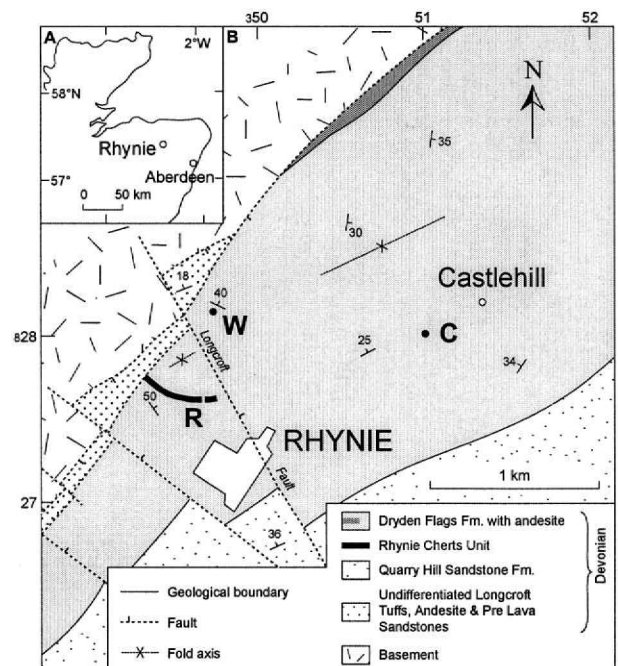

Figure 1   Location map of Rhynie (A) and the geology of the area north of Rhynie village (B), showing the position of the Rhynie chert sub-crop and SSSI (R), the float expression of the Windyfield chert (W) and the area where the float material containing the new crustacean was found (C) (based on Rice *et al.* 2002).

Castlehill is in the vicinity of the projected continuation of the Rhynie Cherts Unit of Rice *et al*. (2002).

The chert block was cut perpendicular to the bedding, initially to determine sedimentology, textures and biota. Cut slabs were studied in hand specimen and under reflected light with a WILD M7 binocular microscope, the cut surfaces applied with a thin film of microscopy immersion oil to bring out surface details. It was at this exploratory stage that the new animal was discovered. Sequential slices of the unit containing the crustacean were cut parallel to the bedding. These slices of chert were then examined using the methods described above to identify any other assemblages of cuticle. Any material discovered was prepared by trimming the slices to an appropriate size and mounting onto unfrosted glass slides using a using a PVU adhesive and cured for 30 minutes over a UV lamp. The mounted slices of chert were then prepared further, examined and photographed using the techniques outlined in Anderson and Trewin (2003).

Most specimens have a three-dimensional aspect and thus not all morphological details are easily resolvable using photography alone. Therefore *camera lucida* illustrations have been used in conjunction with the photomicrographs to add finer details only resolvable under varying focal depths. The explanations for the abbreviations used on these illustrations are listed in Appendix 1.

A sequential series of standard petrographic thin sections was prepared to cover the entire thickness of the chert block. These were used to study lithology, microtextures and biota throughout the sequence of the chert block and to elucidate the palaeoenvironments and diagenetic history.

2. Chert lithology and stratigraphy

The host chert was found as a loose block within surface float material (Fig. 1) and therefore its original field relations with respect to the basin sedimentology and the Rhynie SSSI are unknown. However, it is similar in general structure, colour and appearance to much of the Rhynie chert found in the SSSI locality and as such almost certainly comes from a horizon within the Dryden Flags Formation (Rice *et al*. 2002).

The block itself comprises a composite tabular chert bed 180 mm in thickness, and is internally bedded (Figs 2A, B). The chert block can be broadly subdivided into nine discrete units. These are illustrated in Figure 3, which also summarises details of the chert lithology and textures, the vertical distribution and relative abundance of the biota, and probable environment of deposition for each unit.

The basal unit comprises an irregular, tapering band of massive chert containing common degraded upright and prostrate straws, possibly of *Aglaophyton major* (Fig. 3, unit 1). The framework is relatively open and locally vuggy. The matrix between the straws comprises amorphous finely-disseminated organic matter with minor very fine-grained detrital quartz, mica and clays, and scattered pyrite framboids. It occasionally displays discontinuous, crude internal lamination and commonly forms a meniscate coating binding the plant axes. This unit is sharply truncated and overlain by wavy-laminated, organic-rich, micaceous siltstone to very fine-grained sandstone, up to 15 mm thick, displaying minor water-escape structures (Fig. 3, unit 2). This passes upwards into an irregular unit of vuggy, massive chert (Trewin 1994),
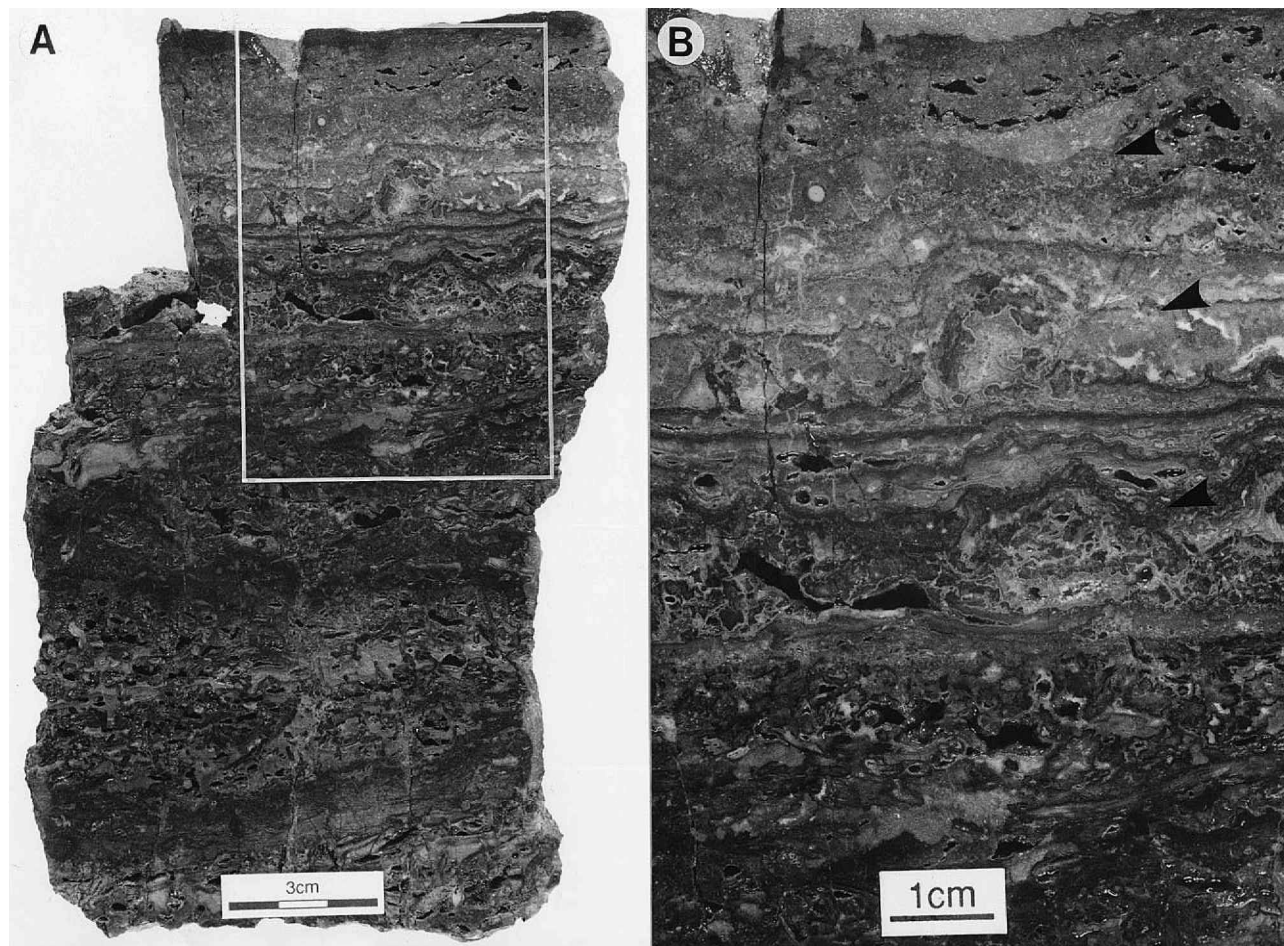

Figure 2　The host chert bed: (A) Polished slab of the chert block, taken perpendicular to the bedding; (B) Detail of inset in (A) showing the units in which *Castracollis* has been found (arrowed).

up to 36 mm thick (Fig. 3, unit 3). It comprises an open framework of partially decayed, para-autochthonous, mainly prostrate axes of *Nothia aphylla*, with a similar patchy, meniscate, organic-rich matrix to that described above. Vuggy porosity variably occurs within plant straws, between stems and occasionally as discrete bubble-like 'fenestrae' within the matrix. Many voids display geopetal layers of very fine sediment and later silica cement.

A predominantly sand-rich chert unit follows (Fig. 3, unit 4), up to 35 mm thick. It is irregular, with discontinuous wavy laminae, micaceous, organic-rich, and contains degraded *Nothia* axes as in Unit 3, though rhizomal axes appear to be more common. The upper surface of the unit is sharp, highly irregular and crenulated. The packing of detrital grains and axes is moderate to loose, and silica cements occlude much of the original porosity. Unit 5 is another thin, massive and vuggy chert unit (Fig. 3), up to 25 mm thick, exhibiting similar textures and biota to those below, however, minor degraded axes of *Asteroxylon mackiei* also occur together with those of *Nothia*. These lower units appear partially brecciated, evidenced in hand specimen by distinct, resealed subvertical, anastomosing fractures (Fig. 3, units 1–5), and also at a finer scale, many of the *in situ* plant axes appear to have been partially silicified, brecciated, and then later resealed by chert.

The partially brecciated upper surface of the massive chert unit is sharply overlain by a conspicuous stromatolitic layer (Fig. 3, unit 6) 22–25 mm thick, and comprising continuous, organic-rich, wavy to crenulated laminae with irregular bubble-like 'fenestrae'; intercalated with discontinuous, wavy to crenulated sandy partings. Internally the organic-rich laminae display variable concentrations of probable cyanobacterial unicells, typically increasing in abundance towards the top of each lamina, and occasional filamentous tufts orientated perpendicular to the laminae. The lower 10–15 mm of this unit includes discontinuous sandy partings with partially decayed prostrate axes of *Nothia aphylla*, often appearing bound by the stromatolitic laminae. Within the uppermost 10 mm of this unit a number of almost complete specimens of the new crustacean have been observed within and bound by the organic-rich laminae (Fig. 4A).

The stromatolitic unit passes upwards into the main arthropod-bearing units (Fig. 3, units 7 and 8). Unit 7 is predominantly massive with occasional discontinuous, wispy, crenulated sandy laminae and is up to 25 mm thick, and has an irregular gradational contact with Unit 8. Unit 8 is similar in texture and biotic content to Unit 7, but exhibits a significantly higher detrital content and is up to 15 mm thick. Both units exhibit a distinctive chert texture, comprising silicified aggregates of amorphous organic matter (Fig. 4B) with coprolites, pervasive clusters of probable cyanobacterial unicells and tufts of multicellular filaments (Figs 4C, D), partially decayed and disaggregated nematophytes (predominantly *Nematoplexus rhyniensis*) (Fig. 4E), and the charophyte *Palaeonitella cranii* (Fig. 4F). Many of the charophyte specimens exhibit attached gametangia. This is the first time fertile charophyte structures have been recorded from the Rhynie chert. The faunal content comprises the new crustacean, *Castracollis wilsonae*, with *Lepidocaris rhyniensis* as a minor component (Fig. 4B). The overall texture is a variation of the 'clotted' chert texture described from arthropod-bearing beds in the Windyfield chert by Anderson & Trewin (2003).

Unit 8 passes upwards into a 5 mm-thick unit of wavy laminated, moderate to tightly packed sandy chert with organo-stylolites (Fig. 3, unit 9), marking the top of the chert block.

3. Taphonomy of the biota

36 near-complete specimens of the new crustacean have been identified, together with at least 41 separate clusters of associated cuticle, apparently from other individuals. Within the sections, at least ten exceptionally preserved lipostracan branchiopods have been identified as belonging to *Lepidocaris rhyniensis*, and although exquisite in their preservation, yield no additional information to the work of Scourfield (1926, 1940).

The main arthropod-bearing unit as a whole exhibits no evidence of compaction prior to preservation, the 'clotted' chert texture and the stromatolitic laminae showing an open framework, although almost all primary porosity has been occluded by pervasive silicification. This suggests that silicification of the organic material was initiated whilst still at the surface and in an aquatic environment.

The specimens of the new crustacean commonly occur with articulated tail, trunk and appendages. The head region is usually present but frequently damaged and slightly detached from the body (Fig. 5), and the anterior of the thorax is also often damaged and twisted. These features, and our own observations of the ecdysis of the notostracan *Triops longicaudatus*, suggest that the majority, if not all, of these specimens are exuviae. Another possible explanation is that the remains represent mortalities, the damage to the anterior of the specimens perhaps reflecting a specific predatory feeding style. However, the first scenario at present appears more likely since all of the specimens lack soft tissues or gut contents, and none of the coprolites in the assemblage appear to contain remains of the animal. Fossils resulting from mortality of individual arthropods previously discovered in the Rhynie and Windyfield cherts tend to exhibit internal structures, such as the gut contents preserved in *Heterocrania rhyniensis* (Hirst & Maulik 1926), and *Leverhulmia mariae* (Anderson & Trewin 2003); and the respiratory structures of trigonotarbid arachnids (Claridge & Lyon 1961).

There is little or no evidence for desiccation prior to preservation, since the majority of near-complete specimens of the new crustacean and associated specimens of *Lepidocaris* appear robust, and the leg appendages, especially the more delicate foliaceous elements, appear to have retained much of their original shape and structure. Experiments by the authors on *Triops longicaudatus* indicate that when removed from the water body, the cephalo-thoracic shields of both exuviae and mortalities curl-up, and the trunk, and especially the limbs collapse and become distorted upon drying. This suggests that the fossil specimens remained in an aqueous environment prior to silicification. Contemporaneous precipitation of iron sulphides during silica deposition is indicated by the presence of scattered framboids of pyrite throughout the chert matrix, suggesting at least mildly reducing conditions at the time of silicification.

Although there are variable amounts of detrital material present within the arthropod-bearing units, mainly in the form of mica laths and quartz grains, the majority of the crustacean specimens and the associated biota appear to be more or less *in situ*. No terrestrial faunal elements have been observed within the units. Many of the crustacean specimens appear to be entombed within filamentous, microbial tufts. These probable cyanobacteria are remarkably well preserved, the filaments exhibiting well-defined chains of cells with little or no evidence
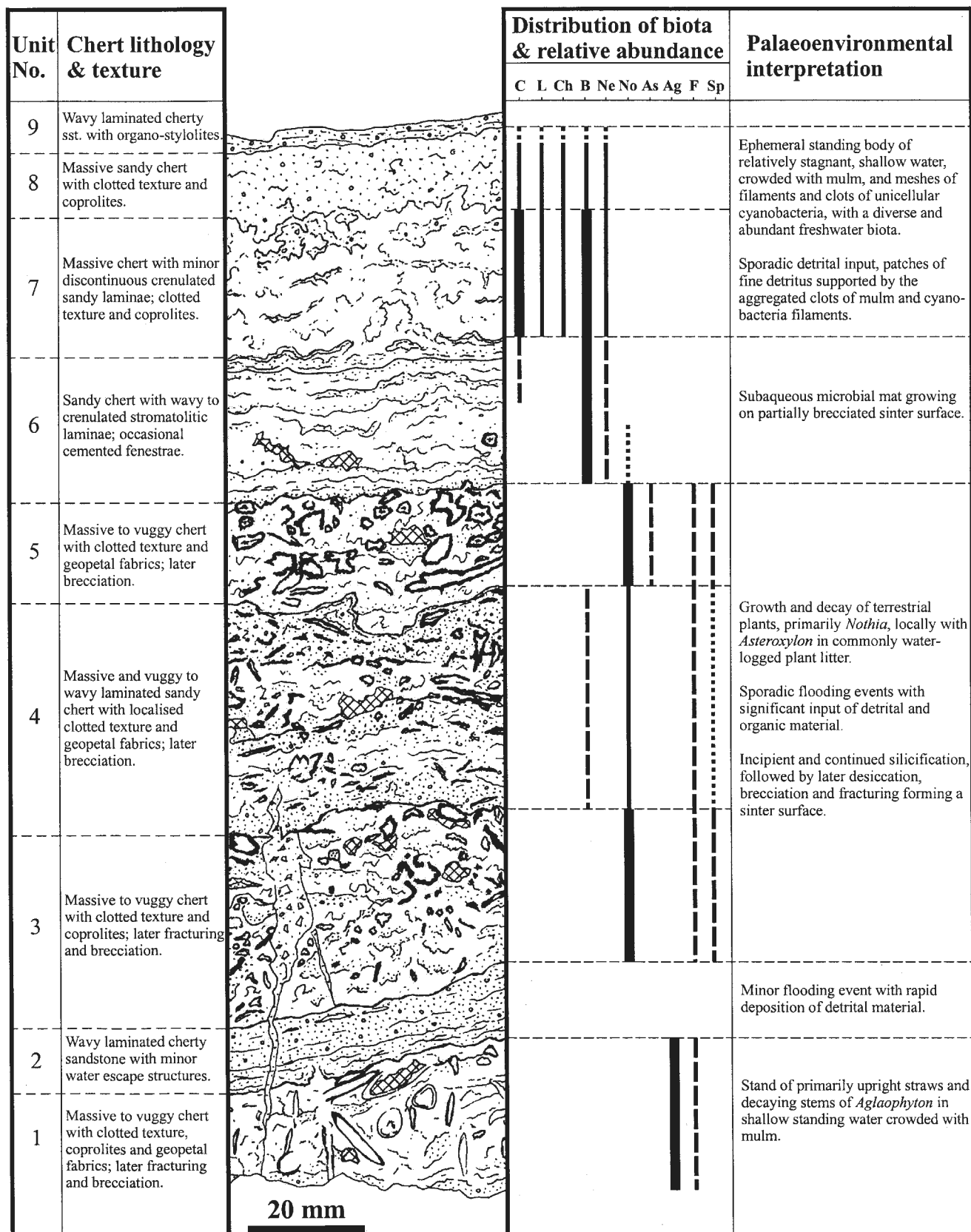
Unit No.	Chert lithology & texture	Distribution of biota & relative abundance	Palaeoenvironmental interpretation
		C L Ch B Ne No As Ag F Sp	
9	Wavy laminated cherty sst. with organo-stylolites.		Ephemeral standing body of relatively stagnant, shallow water, crowded with mulm, and meshes of filaments and clots of unicellular cyanobacteria, with a diverse and abundant freshwater biota.
8	Massive sandy chert with clotted texture and coprolites.		
7	Massive chert with minor discontinuous crenulated sandy laminae; clotted texture and coprolites.		Sporadic detrital input, patches of fine detritus supported by the aggregated clots of mulm and cyanobacteria filaments.
6	Sandy chert with wavy to crenulated stromatolitic laminae; occasional cemented fenestrae.		Subaqueous microbial mat growing on partially brecciated sinter surface.
5	Massive to vuggy chert with clotted texture and geopetal fabrics; later brecciation.		Growth and decay of terrestrial plants, primarily *Nothia*, locally with *Asteroxylon* in commonly waterlogged plant litter.
4	Massive and vuggy to wavy laminated sandy chert with localised clotted texture and geopetal fabrics; later brecciation.		Sporadic flooding events with significant input of detrital and organic material. Incipient and continued silicification, followed by later desiccation, brecciation and fracturing forming a sinter surface.
3	Massive to vuggy chert with clotted texture and coprolites; later fracturing and brecciation.		Minor flooding event with rapid deposition of detrital material.
2	Wavy laminated cherty sandstone with minor water escape structures.		Stand of primarily upright straws and decaying stems of *Aglaophyton* in shallow standing water crowded with mulm.
1	Massive to vuggy chert with clotted texture, coprolites and geopetal fabrics; later fracturing and brecciation.		

20 mm

Figure 3 Composite sketch of the host chert bed (AUGD12404) (Figure 2A) illustrating the internal stratigraphy (Units 1 to 9) (refer to text), chert lithology, textures, vertical distribution of the biota and palaeoenvironmental interpretation. C—*Castracollis*; L—*Lepidocaris*; Ch—charophytes; B—probable cyanobacteria; Ne—nematophytes, No—*Nothia*; As—*Asteroxylon*; Ag—*Aglaophyton*; F—fungi; Sp—spores. Relative abundance: thick lines-abundant; thin lines-common; dashed lines-moderate; dotted lines-rare. Cross-hatched areas denote vugs.

of autolysis prior to silicification (Fig. 4D). Similarly, the pervasive coccoidal unicells, some of which appear to be sheathed, and clusters of daughter cells observed as clotted aggregates, and scattered throughout the matrix, exhibit remarkable preservation. Many of these cells, however, exhibit dark amorphous contents that may represent certain degrees
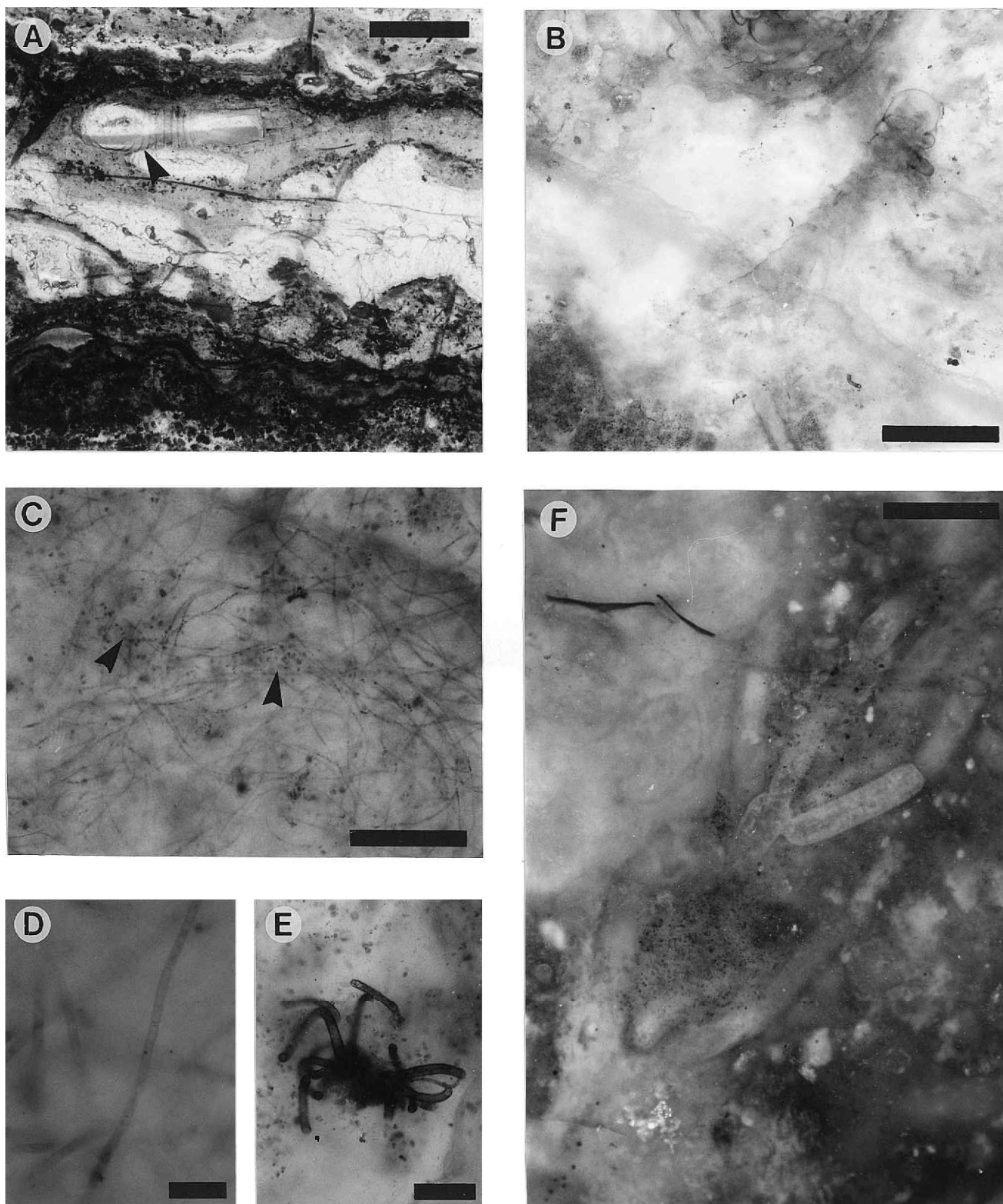
Figure 4 Internal textures and taphonomy of the arthropod-bearing units (Units 6, 7 and 8): (A) Organic-rich stromatolitic laminae towards the top of Unit 6, entombing a specimen of *Castracollis* (arrowed), scale bar = 2 mm; (B) Silicified aggregates of amorphous organic matter (bottom left), charophytes (top), and a near complete specimen of *Lepidocaris rhyniensis* Scourfield 1926, scale bar = 1 mm; (C) Clusters of unicells (arrowed) with multicellular filamentous tufts of probable cyanobacteria, scale bar = 200 μm; (D) Detail of multicellular filaments, scale bar = 50 μm; (E) Isolated branch knot and smooth-walled tubes of the nematophyte *Nematoplexus rhyniensis* Lyon 1962, scale bar = 100 μm; (F) The charophyte *Palaeonitella cranii* exhibiting a well-preserved branch with secondary rays, scale bar = 500 μm.

of shrinkage and degradation of the cell protoplast. On the whole, the majority of these microbes appear to be permineralised rather than occurring as moulds. Cady and Farmer (1996) identified permineralised cyanobacterial sheaths in Recent and sub-Recent sinters as occurring only in microfacies formed at temperatures below 35°C, whereas in sinters from mid- to higher-temperature microfacies, microbial remains were only preserved as moulds.
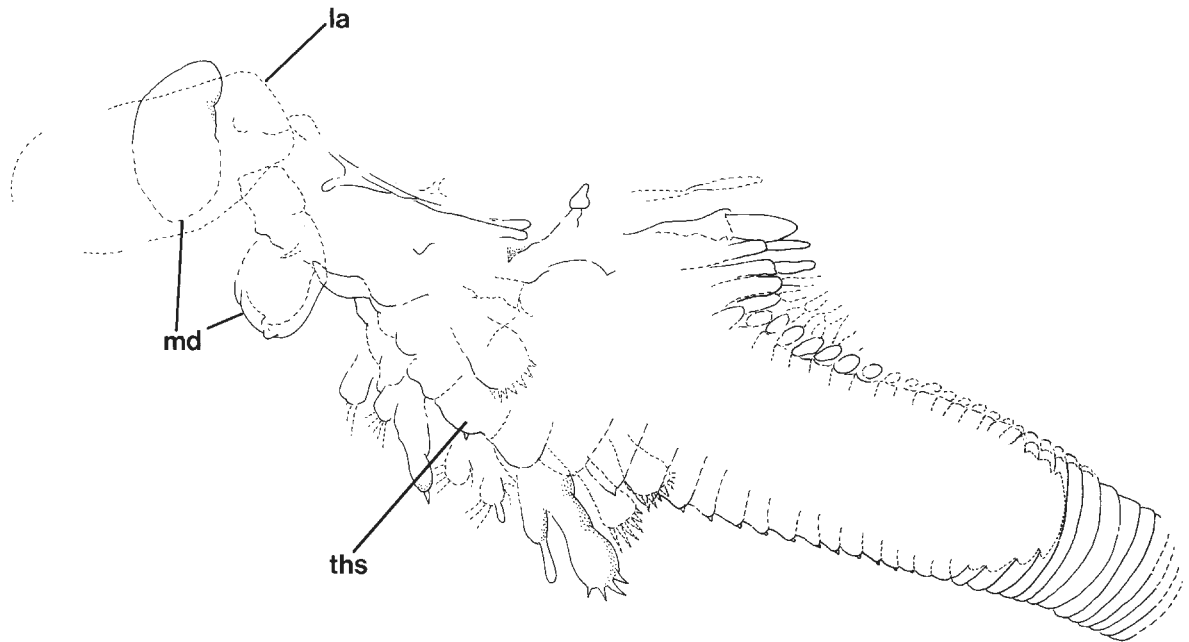
Figure 5 *Castracollis wilsonae* Fayers & Trewin *gen. et sp. nov.*, Pragian, Rhynie, Scotland: (A) An almost complete specimen (AUGD12382d) showing detached partial remains of the head shield and damaged anterior of thorax; (B) Interpretative drawing of (A).

Coprolites are common throughout the unit; their preservation is generally good, comprising sub-cylindrical bodies, between $250\,\mu$m and $1700\,\mu$m in length, containing amorphous organic material and occasionally nematophyte fragments. However, we cannot be certain whether the producer or producers of these faecal pellets were herbivores or
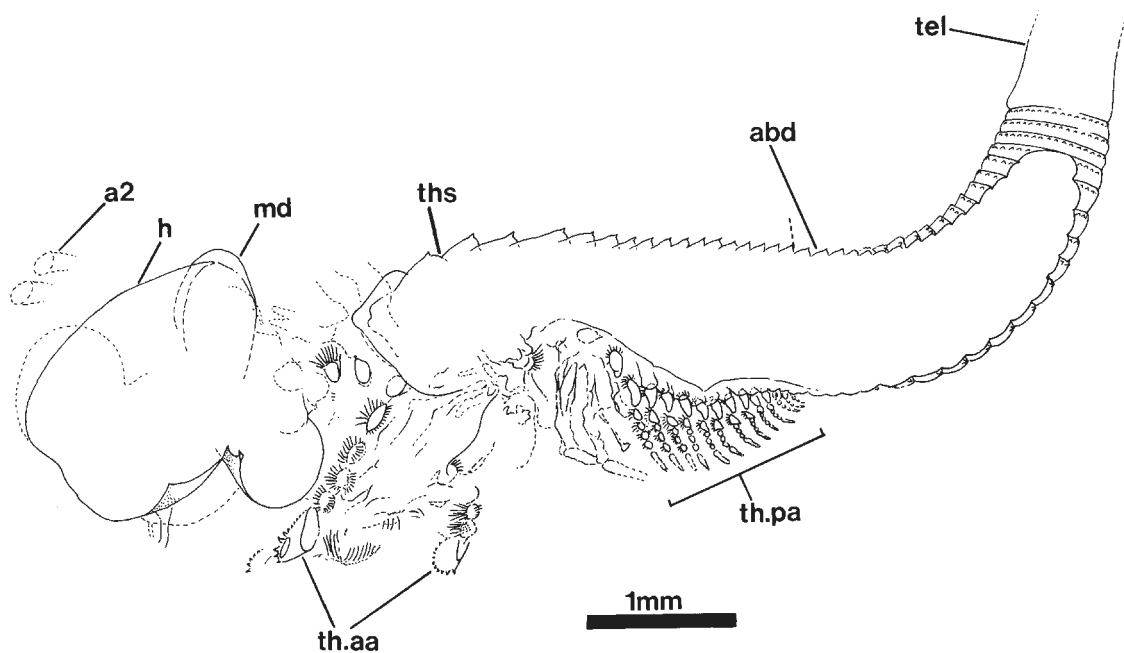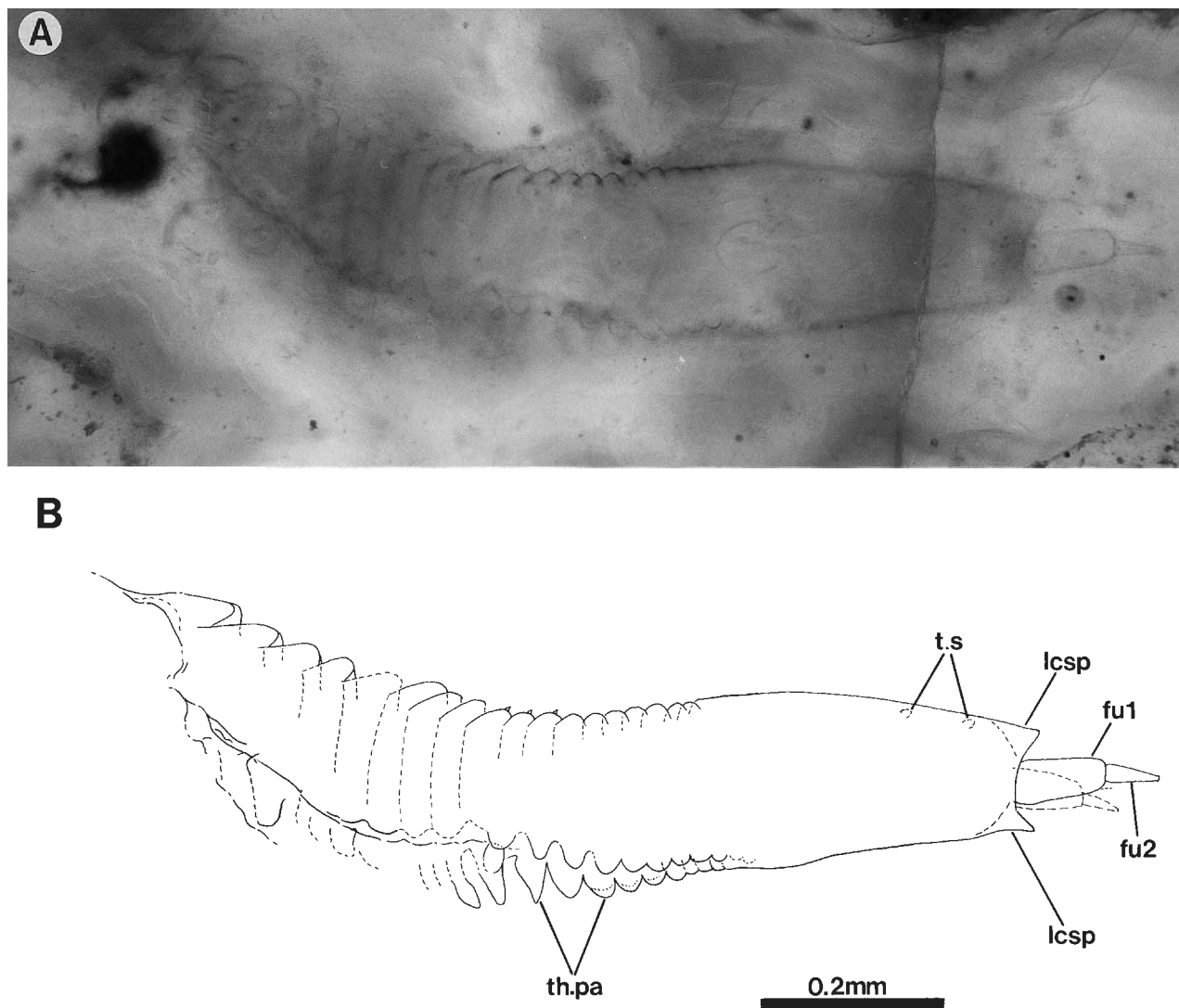
Figure 6 *Castracollis wilsonae* Fayers & Trewin *gen. et sp. nov.*, Pragian, Rhynie, Scotland: (A) AUGD12382a, a longitudinal section through one of the larger specimens, showing the head, multi-segmented trunk, and full posterior series and a partial anterior series of thoracic appendages; (B) Interpretative drawing of (A).

detritivores (Edwards *et al.* 1995). The three-dimensional preservation of the filamentous tufts, cell clusters and coprolites, together with the generally open textural framework of the unit, also tends to suggest that silicification occurred in fully aqueous conditions.

The nematophyte remains are generally highly fragmented, comprising scattered clusters of branch knots and tubes (Fig. 4E). The individual tubes are mostly well preserved, exhibiting the two distinct morphologies described by Lyon (1962) for *Nematoplexus rhyniensis*; the smaller smooth-walled tubes and

Figure 7 *Castracollis wilsonae* Fayers & Trewin *gen. et sp. nov.*, Pragian, Rhynie, Scotland: (A) AUGD12382b, the smallest individual of *Castracollis wilsonae* observed in this study, illustrating the bud-like posterior thoracic appendages, with at most two apodous abdominal segments; (B) Interpretative drawing of (A).

larger tubes with conspicuous spiral thickenings. There are charophytes present, comparable with the described form *Palaeonitella cranii*. The charophytes exhibit good preservation, retaining much of their three-dimensional structure, and appear to be *in situ* (Fig. 4F). As with the fauna, both the nematophytes and charophytes are often entombed by the filamentous microbial tufts and/or enshrouded by clusters of unicells and clots of amorphous organic matter (Fig. 4E).

All these observations tend to suggest the preservation of the bed, its biota and textures occurred rapidly at the surface in an aquatic environment at ambient temperatures and under at least mildly reducing conditions soon after the crustacean remains had accumulated. Silicification may have been initiated whilst some of the aquatic flora, particularly the cyanobacteria, were still living. From experimental studies by other authors (for example, Ferris *et al.* 1988; Cady & Farmer 1996), the timing and silicification rate relative to the death of microbes is significant in the degree of preservation of intact cells. Rapid silicification of both live and lysed microbial cells may lead to the resistance to decay of the cell walls by autolysins and thus preserve the structure and morphology of the cells (Ferris *et al.* 1988; Cady & Farmer 1996; Konhauser *et al.* 1999). The presence of metallic ions, particularly iron, in hydrothermal solutions is also often thought to be significant in the inhibition of autolysis and the retention of microbial cell

structure prior to silicification (Ferris *et al.* 1988). At least some evidence of dissolved iron at the time of preservation is indicated in the arthropod-bearing unit by the presence of contemporaneous pyrite framboids. Such a scenario may help in explaining the remarkable preservation of the microbes and charophytes within the chert.

The pervasive silicification observed would have required a high flux of pore waters supersaturated with respect to silica, the most likely source being the continuous influx of erupted hydrothermal solutions from the local hot springs. However, that said, we have no reason to suspect that the fauna and flora of this unit were particularly adapted to living in hydrothermal environments; instead most likely representing an otherwise normal freshwater biota for Early Devonian times.

4. Systematic palaeontology

Class Branchiopoda Latreille, 1817
Superorder Calmanostraca Tasch, 1969 *incertae sedis*
Genus *Castracollis* Fayers and Trewin *gen. nov.*

Derivation of the name. The generic name *Castracollis* is from the Latin *castrum* meaning castle and *collis* meaning hill or
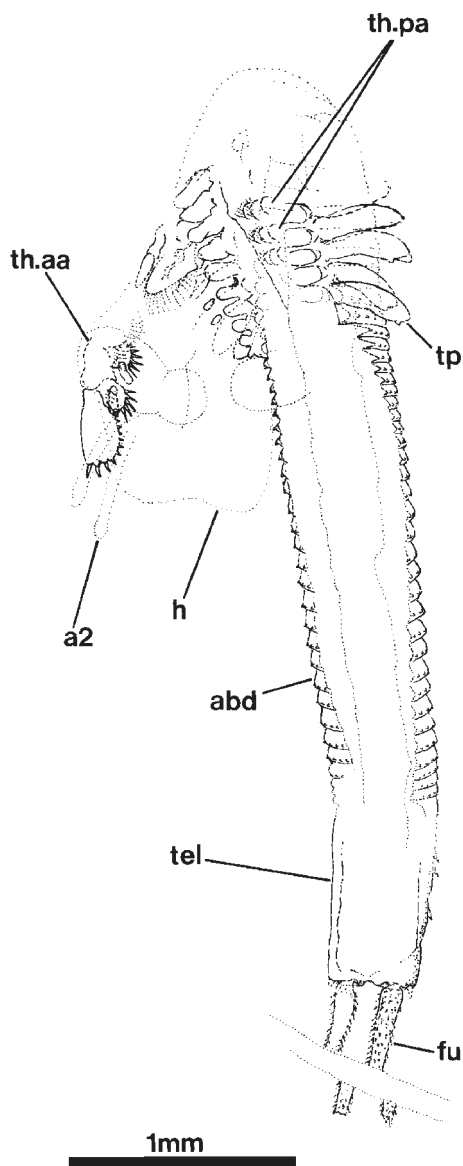
Figure 8 *Castracollis wilsonae* Fayers & Trewin *gen. et sp. nov.*, Pragian, Rhynie, Scotland: AUGD12381a, *camera lucida* drawing of the holotype, a partially enrolled specimen showing the multi-segmented abdomen with 28 apodous segments and the telson with a pair of furcal rami.

high ground, referring to the farm at Castlehill near where the chert block containing the new material was found.

Type and only known species. *Castracollis wilsonae*: Fayers and Trewin *sp. nov.*

Diagnosis. Small branchiopod with long biramous second antennae possessing symmetrical rami. Thorax with two distinct series of thoracopods, the anterior series comprising 11 pairs of similar, long, phyllopodous leg appendages with a robust, raptorial, paddle-like endopod. The posterior leg series variably comprises 10 to 15, though commonly 12, smaller, phyllopodous appendages with a disposition of one leg pair per somite. Leg appendage-bearing somites bear a pair of lateral, tergopleural scales. Thoracopod endites bearing dense plumose setae, the distal four endites also bear a single, long tubular projection or median spine. Multi-segmented abdomen with up to 28 apodous somites, Oblate telson with paired furcae. Probable cephalo-thoracic shield present.

Discussion. The overall morphology of *Castracollis*, namely that of the setose phyllopodous leg appendages, the presence of a ventral food groove, the large and variable number of

trunk segments, the apodous abdomen, together with the presence of paired furcae on the telson, suggests to us that it belongs in the Class Branchiopoda (Latreille 1817). Due to a probable preservation failure, eyes have not been observed for *Castracollis*. The internalisation of the compound eyes is a defining character for the Phyllopoda (Walossek 1993, 1995; Walossek & Müller 1998). However, the overall body plan, the polymetameric trunk and the non-filtratory habit of the anterior trunk limb series (see below) of this animal is strongly reminiscent of calmanostracan phyllopods. Moreover, a calmanostracan affinity is indicated by the development of an anterior series of 11 thoracic appendages quite distinct in appearance from a posterior series of thoracopods, a feature noted by Walossek (1993). However, the presence of long, flagellate biramous second antennae with symmetrical rami seen in *Castracollis* is only known in the Onychura, and has never been observed in calmanostracans. The posterior series of 10–15 thoracopods with a disposition of one pair per somite is also unknown in calmanostracans. Tantalisingly, the presence of a probable cephalo-thoracic shield has only been observed in close association with a few specimens and its disposition to the animal and position of attachment is currently unknown. Tasch (1969) considered the presence of a dorsal cephalo-thoracic shield as a defining character for the Superorder Calmanostraca. Therefore, at this present time, we elect to place this crustacean as Calmanostraca *incertae sedis*.

Castracollis wilsonae sp. nov.
(Figs 5–26)

Derivation of the name. The specific epithet is in recognition of Miss Elizabeth Wilson who discovered the chert block containing *Castracollis*.

Type material. Holotype AUGD 12381a. Early Devonian (Pragian) Rhynie chert, Rhynie, Aberdeenshire, Scotland, UK. It comprises a partially enrolled exuvia, appearing more-or-less intact and articulated. The following 19 specimens have been designated as paratypes: AUGD12381b, 12382a-d, 12383, 12384, 12385, 12386, 12388a-c, 12389, 12391, 12394, 12397a-b and 12401a-b.

Additional material. The following thin section slides contain further crustacean material but have not been designated as type specimens: AUGD12387, 12390, 12392, 12393, 12395, 12396, 12398–12400, and 12402–12403, a polished slab of the chert bed: AUGD12404 (Fig. 2) and a series of four sequential standard thin sections taken through the entire chert bed: AUGD12405–12408.

The type material is housed in the Type and Figured Collections of the Department of Geology and Petroleum Geology, University of Aberdeen.

Diagnosis. As for the genus.

General Description. The specimens are of varying size, most likely representing different stages in ontogeny. Damage to the dorsal head region and anterior thorax (Fig. 5), together with the absence of preserved soft tissues or gut contents, suggests the specimens are exuviae. The largest specimens have an overall length of up to 8 mm (Fig. 6). The smallest specimen observed, AUGD12382b, has a length of approximately 1 mm (Fig. 7). No eggs or larval stages have been identified in this study.

The anterior of the head region appears domed, and ventrally exhibits a conspicuous labrum and a pair of robust mandibles. No eyes or first antennae have been discerned. Long biramous second antennae, with symmetrical rami, are present, together with a pair of slightly reduced maxillulae. No maxillae have been identified. Three or four of the specimens are loosely associated with what may be a detached and generally poorly preserved, cephalo-thoracic shield. The
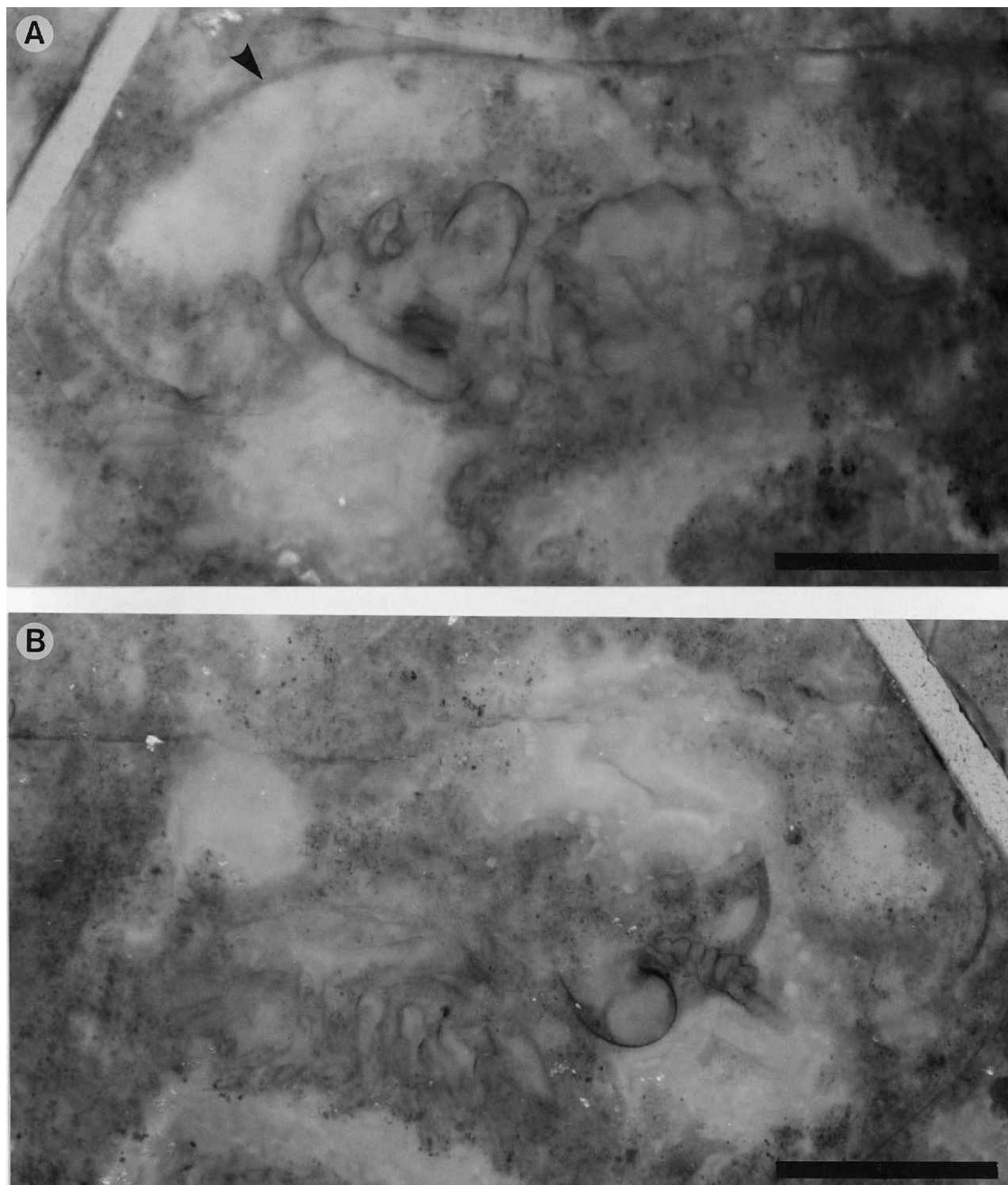
Figure 9 *Castracollis wilsonae* Fayers & Trewin *gen. et sp. nov.*, Pragian, Rhynic, Scotland: (A) AUGD12388a longitudinal section, slightly oblique to the sagittal plane, illustrating the head structure and a possible detached cephalo-thoracic shield (arrowed), scale bar = 1 mm; (B) AUGD12388a reverse of thin section in (A) illustrating the disposition of the second antennae to the mandibles, scale bar = 1 mm.

thorax comprises a series of up to 26 segments with two distinct series of thoracomeres. The anterior series comprises 11 pairs of relatively long, homologous thoracic appendages. The posterior leg series variably comprises 10 to 15, though commonly 12, phyllopodous appendages. Both leg series have a disposition of one leg pair per segment. The abdomen is multi-segmented, comprising up to 28 apodous segments. A distinct tail comprises a telson with two simple caudal furcae (Fig. 8).

5. Anatomical observations

5.1. Head region

The anterior region of *Castracollis* comprises a smooth and dome-like head shield (h), up to $1700\,\mu$m in length and $1500\,\mu$m in width. No clear segmentation or visible fusion between the anterior head shield part and the thoracic segments has been discerned. In the majority of specimens, where observed, the posterior and dorsal surface of the head
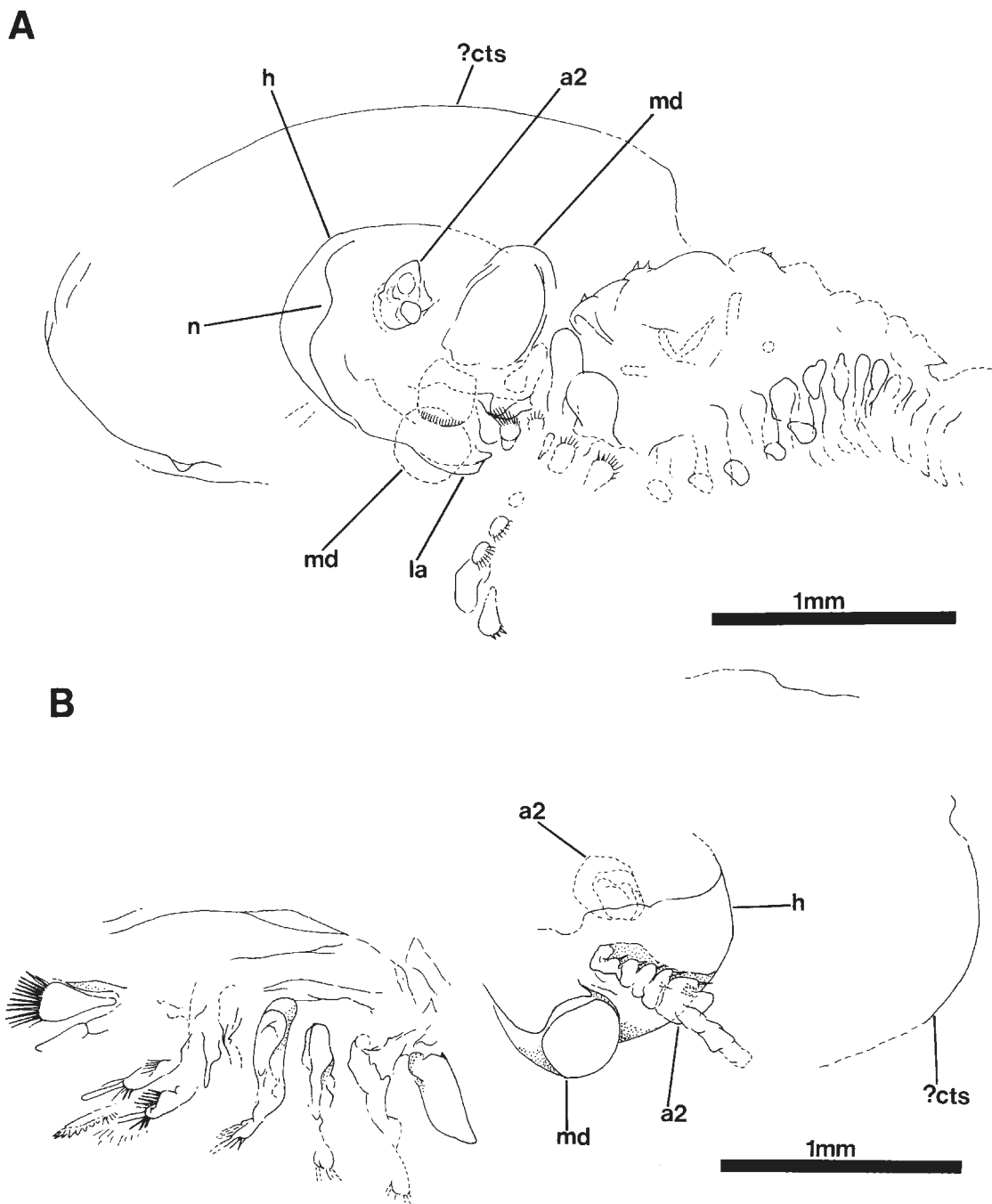
Figure 10 Interpretative drawings: (A) Figure 9A; (B) Figure 9B.

shield is split and heavily damaged. The anterior end of the head shield is rounded with a conspicuous notch (n) or depression along the anterior midline at the apex, giving it a retusoid appearance (Figs 6, 9). Ventrally the cuticle of the head shield forms a distinctive spatulate labrum (la), which begins between the second antennae (a2) and extends to cover the distal ends of the mandibles (md) (Fig. 9).

In a number of specimens, the anterior head shield part is in close proximity to, or is closely associated with, a detached, broad, thin, dome-like sheet of cuticle (Fig. 9), possibly representing a large, posterior cephalo-thoracic shield (cts). The largest of these is observed as being up to $2700\,\mu$m in apparent length, not considering the possible effects of distortion during taphonomy. The integument is predominantly smooth and almost no ornament has been observed, with the exception of one specimen (Fig. 9) which exhibits a single tubercle apparently positioned towards the anterior of

the rather distorted sheet of cuticle. Despite the close association, none of the specimens exhibiting this sheet of cuticle show any indication as to how, if at all, it was attached to the animal.

The anterior-most head appendages observed are a pair of second antennae (a2) (Fig. 10). No first antennae (a1) or eyes have been identified. The second antennae are well developed and robust. They are most often observed isolated, or only loosely associated with the head, within the host matrix (Figs 11B, 12B). However, a few specimens show them attached to the head shield, and therefore their disposition and full morphology can be ascertained (Figs 11A, 12A). The second antennae are ventro-laterally directed and are long and biramous, the rami being symmetrical. The proximal end of the appendage, the basipod, comprises six to seven 'lobes', each being $80\,\mu$m to $120\,\mu$m in length in the larger specimens, the shorter articles being more proximal. At least the five more
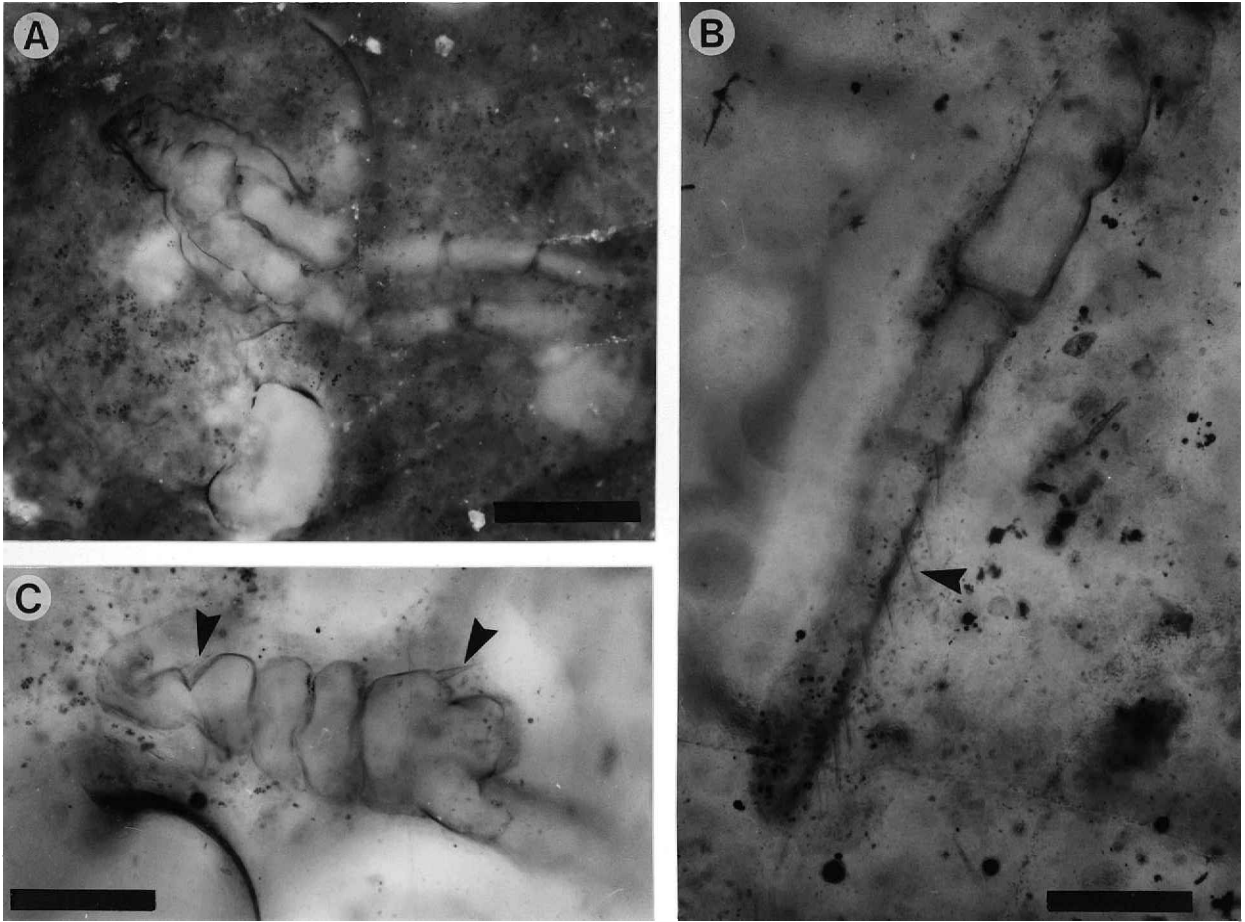
Figure 11 *Castracollis wilsonae* Fayers & Trewin *gen. et sp. nov.*, Pragian, Rhynie, Scotland: (A) AUGD12401b, dorso-lateral view of a fragmented head shield illustrating the right second antenna and its position of attachment, scale bar = 0·5 mm; (B) AUGD12397b, isolated second antenna showing setae (arrowed), scale bar = 0·2 mm; (C) AUGD12388a, basipod of second antenna showing anterior spines (arrowed), scale bar = 0·2 mm.
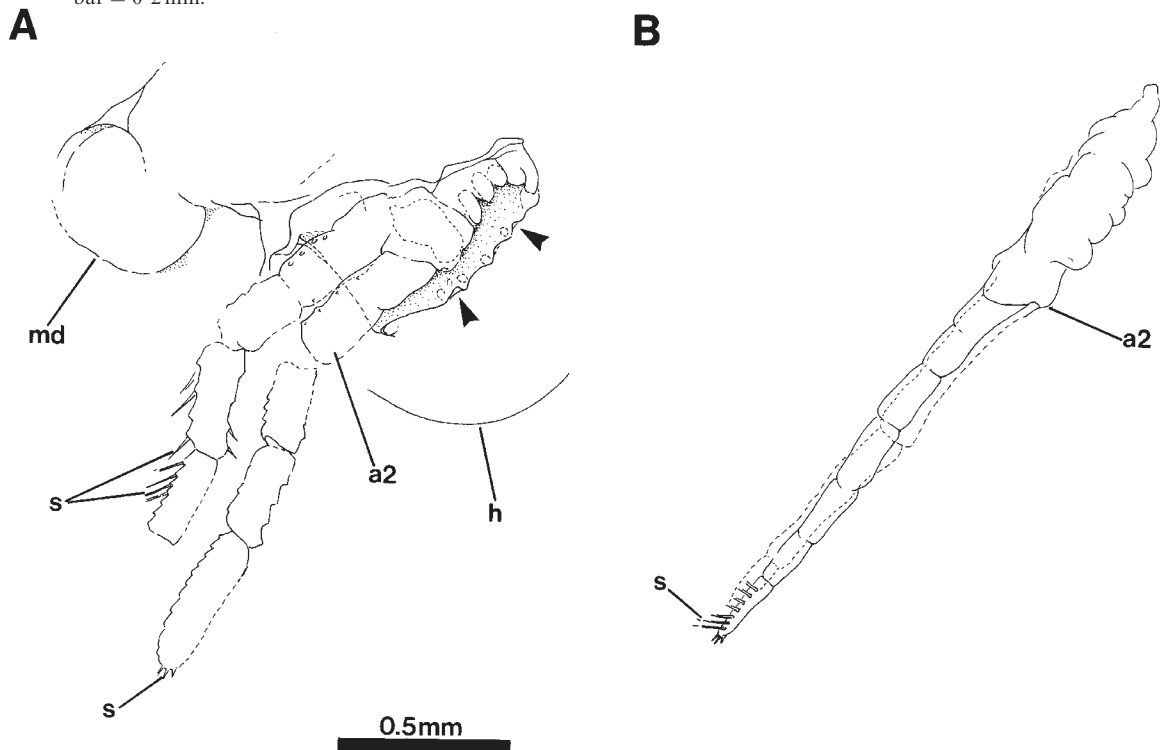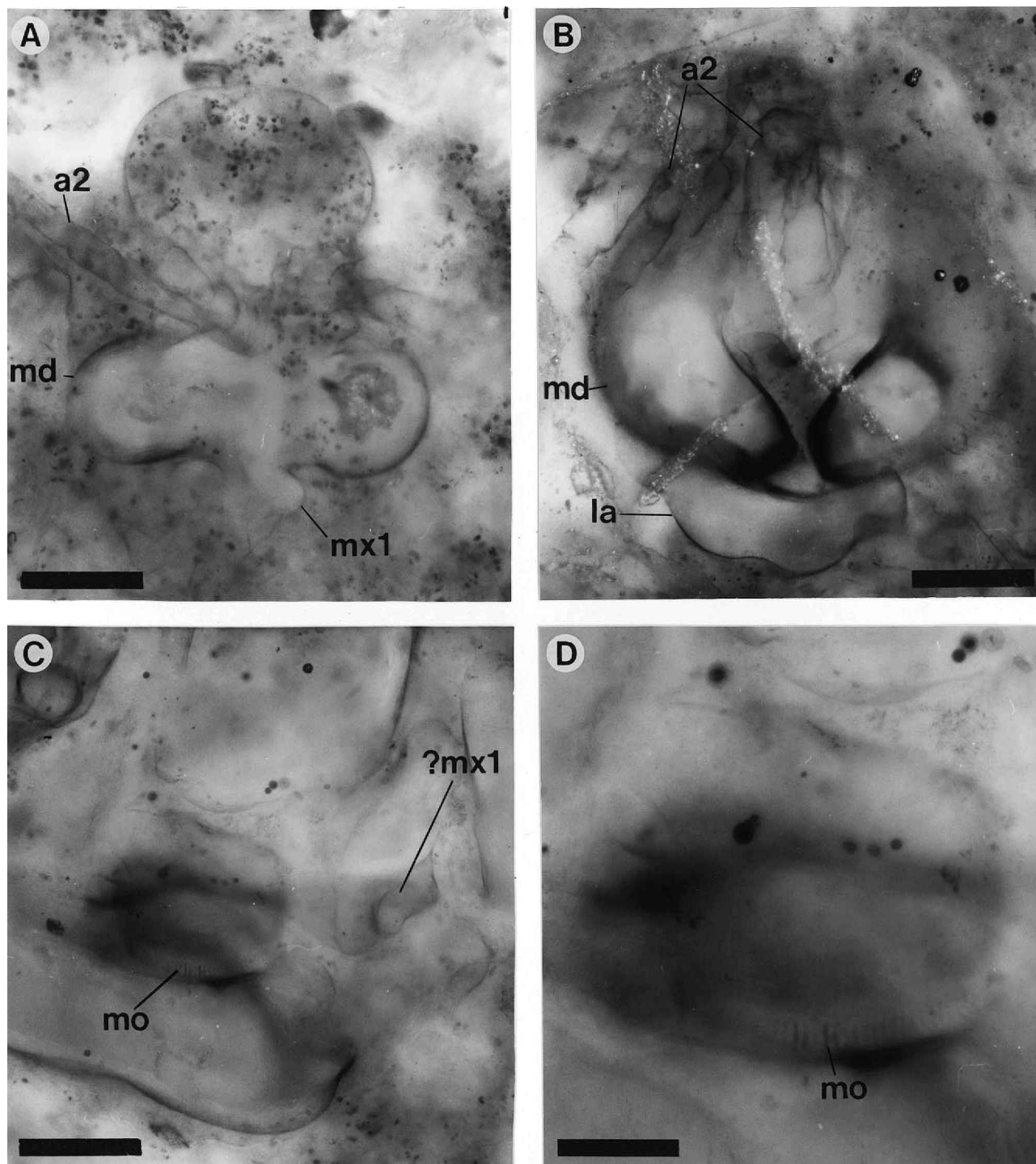

Figure 12 *Castracollis wilsonae* Fayers & Trewin *gen. et sp. nov.*, Pragian, Rhynie, Scotland: (A) AUGD12401b, *camera lucida* drawing of a second antenna attached to a fragmented head shield; (B) AUGD12389, *camera lucida* drawing of an isolated second antenna.

Figure 13 *Castracollis wilsonae* Fayers & Trewin *gen. et sp. nov.*, Pragian, Rhynie, Scotland: (A) AUGD12388c, dorsal view through a head shield showing the disposition of the second antennae, mandibles and maxillulae, scale bar = 0·2 mm; (B) AUGD12397a, ventro-anterior view of the second antennae and mandibles, showing their disposition, scale bar = 0·2 mm; (C) AUGD12388a, showing mandible dentition and possible maxillule, scale bar = 0·2 mm; (D) AUGD12388a, detail of mandible dentition, scale bar = 0·1 mm.

distal lobes possess at least one to three short distally projecting spines on the anterior to mesial surface (up to 40 μm in length) (Fig. 11C). The more proximal 'lobes' become narrower towards the point of attachment with the head shield. One specimen (Figs 11A, 12A) clearly shows the basipod of the second antenna to be partially enveloped medioventrally by a sheath of cuticle. The anterior surface of the cuticle sheath in this specimen appears to be undulate and perforated, although it is not clear whether this feature may be taphonomic. The latter appears to be part of the head shield

cuticle, suggesting the point of attachment for the second antennae is deeply embedded within the head itself. Distal to the basipod are a pair of symmetrical, long, flagellate rami (an endopod and exopod) each comprising five (Figs 11A, 12A) to possibly seven further tubular articles (Fig. 12B), though the latter case could be a taphonomic feature. These articles are generally similar in their morphology. In the larger specimens, most podomeres range between 200 μm and 300 μm in length and appear to generally have a smooth integument, though the anterior and posterior surfaces of each article each support a
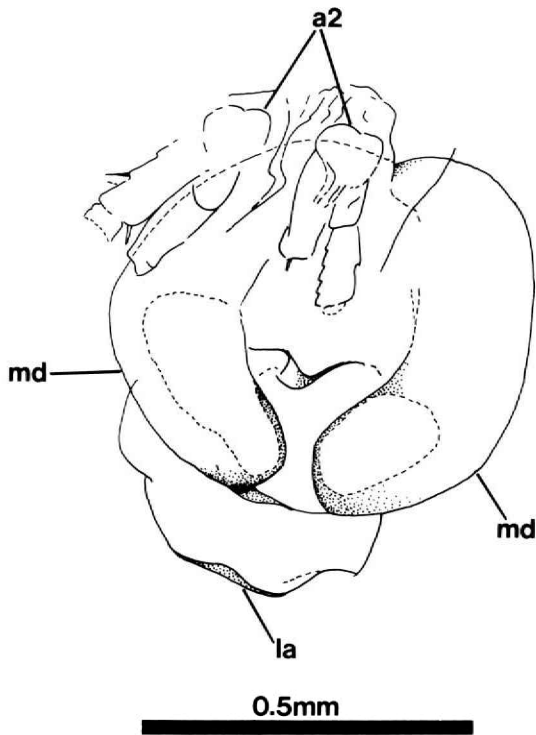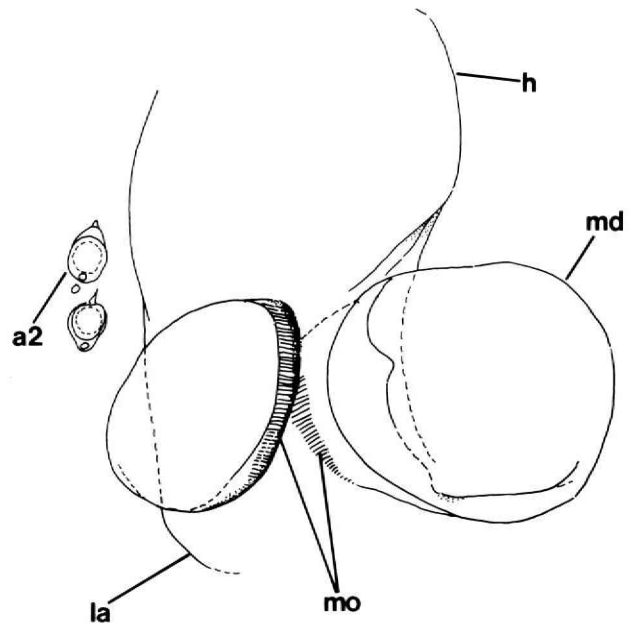
Figure 14 *Castracollis wilsonae* Fayers & Trewin *gen. et sp. nov.*, Pragian, Rhynie, Scotland: (A) AUGD12397a, *camera lucida* drawing of a ventro-anterior view of the mandibles and their disposition; (B) AUGD12382c, *camera lucida* drawing of a dorsal view onto the ventral structures of a head shield illustrating the mandibles and their dentition.

single row of between four and seven distally-directed setae (s) (Figs 11B, 12A). The most distal article is slightly longer and has a conspicuous morphology, tapering towards the distal end; the tip of which possesses three small stout setae (11 μm to 20 μm in length). Along the length of the posterior surface of the article is a single row of comb-like setae (each 50 μm to 60 μm in length) (Figs 11B, 12A, B) of which there appear to be at least 12 in number.

On the ventral side of the head the most conspicuous elements are the mandibles (md) (Figs 9, 10, 13A, B), immediately behind the antennae (Figs 10, 13A, B, 14A). They each comprise one large, robust coxa, almost teardrop-shaped in profile and concavo-convex in transverse section (Fig. 14A). The mandibular coxae are attached far dorsally on the head, and curve downward onto the ventral side where the median gnathic edges meet underneath the labrum. The distal, gnathic edge of each mandible supports a row of very fine, closely spaced ridges (mo) (Figs 13C, D, 14B), typical of Branchiopoda. The mandibles lack palps, as in all adult Branchiopoda.

Possible maxillulae (mx1) have been observed in two specimens (Figs 13A, C); both are preserved as very faint cuticular remains, and therefore much of the morphology is difficult to resolve. In specimen AUGD12388a (Fig. 13C) the maxillulae appear small, simple and comprise a single 'lobe', possibly representing a proximal endite (see Walossek 1993). They are approximately 100 μm in length, with the mesial margin apparently supporting a row of very fine plumose setae. No maxillae (mx2) have been discerned for this crustacean.

5.2. Thorax and abdomen
The trunk appears vermicular (Fig. 15), it is multi-segmented, with all somites in any given individual being of relatively

similar length and morphology, and hence there is little differentiation between thorax and abdomen based on the segmentation alone. The thorax is differentiated from the abdomen by the presence of leg appendages on each segment, whereas the abdomen is apodous.

Many of the specimens exhibit appendages associated with, or attached to, the anterior portion of the trunk, or in detached clusters or in isolation within the host matrix. On the whole, the trunk appendages are preserved as very fine cuticular remains, and as such, their details are faint, and morphology is very difficult to resolve. The following descriptions of the leg appendages have been based on the specimens where the appendage cuticle contrasts enough with the host matrix and chert for morphological details to be accurately recorded.

5.3. Thorax
The total number of thoracic segments (ths) is difficult to resolve, partly due to artefacts of thin section preparation, but more often due to taphonomic damage to the anterior of the trunk, most likely as a result of ecdysis. In what appear to be the more complete or less damaged specimens, the maximum number of thoracic segments appears to have been 26 (Figs 5, 16A, B, 17). Each thoracic segment bears a single pair of leg appendages (Fig. 16B). Of these there are two distinct series, an anterior series of 11 pairs, and a posterior series with between 10 and 15 leg pairs, full descriptions of which are given below. In the majority of specimens, however, only the six posterior segments bearing the anterior leg series appear to be preserved still articulated with the rest of the trunk (Fig. 6). The thoracic segments become more concavo-convex in transverse section towards the anterior (Figs 6, 17, 18). A distinct, but shallow, sulcus is present along the midline of the ventral surface between the leg appendages, most likely representing a ventral food groove (vfg) (Figs 18, 19). The
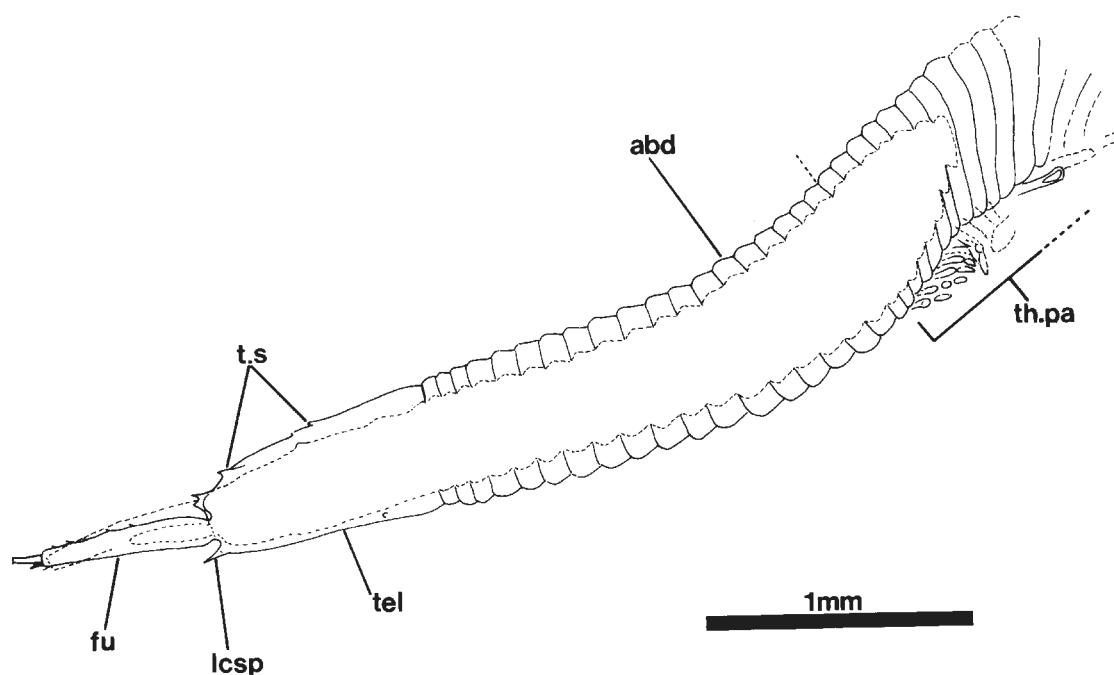
Figure 15 *Castracollis wilsonae* Fayers & Trewin *gen. et sp. nov.*, Pragian, Rhynie, Scotland: (A) AUGD12391, the posterior of *Castracollis wilsonae*, illustrating the ring-like apodous somites of the abdomen, position of the posterior-most thoracic appendages, and telson; (B) Interpretative drawing of (A).

ornament of the thoracic segments comprises a single row of posteriorly projecting spurs towards the posterior of each somite. The spurs are up to 25 μm in length.

Many of the specimens exhibit a pair of faint, laterally and posteriorly-directed oblate lamelliform sheets (tp) with a disposition of one pair per thoracic segment, above and lateral to where the appendages are attached (Figs 8, 16C, 17). The integument of these sheets is smooth with no ornamentation, with the exception of a single short spur just to the posterior of the distal extremity. Their size appears relatively homologous, being up to 800 μm in length and 280 μm in width on the 11 anterior segments. In specimen AUGD12383 they apparently

only occur on the six anterior-most leg-bearing segments of the posterior thoracic appendage series (Fig. 17). In other specimens, however, these sheets also appear to occur on the posterior-most leg-bearing segments. Although probably a taxonomic feature, it is possible that the absence of the posterior-most sheets in specimen AUGD12383 may be an artefact of taphonomy. The size of these sheets on the posterior series is variable between individuals, but generally decreases towards the posterior. The posterior-most sheet on specimen AUGD12383 being 300 μm in length with a maximum width of 90 μm. Since these sheet-like structures do not appear to be directly connected to the appendages, they
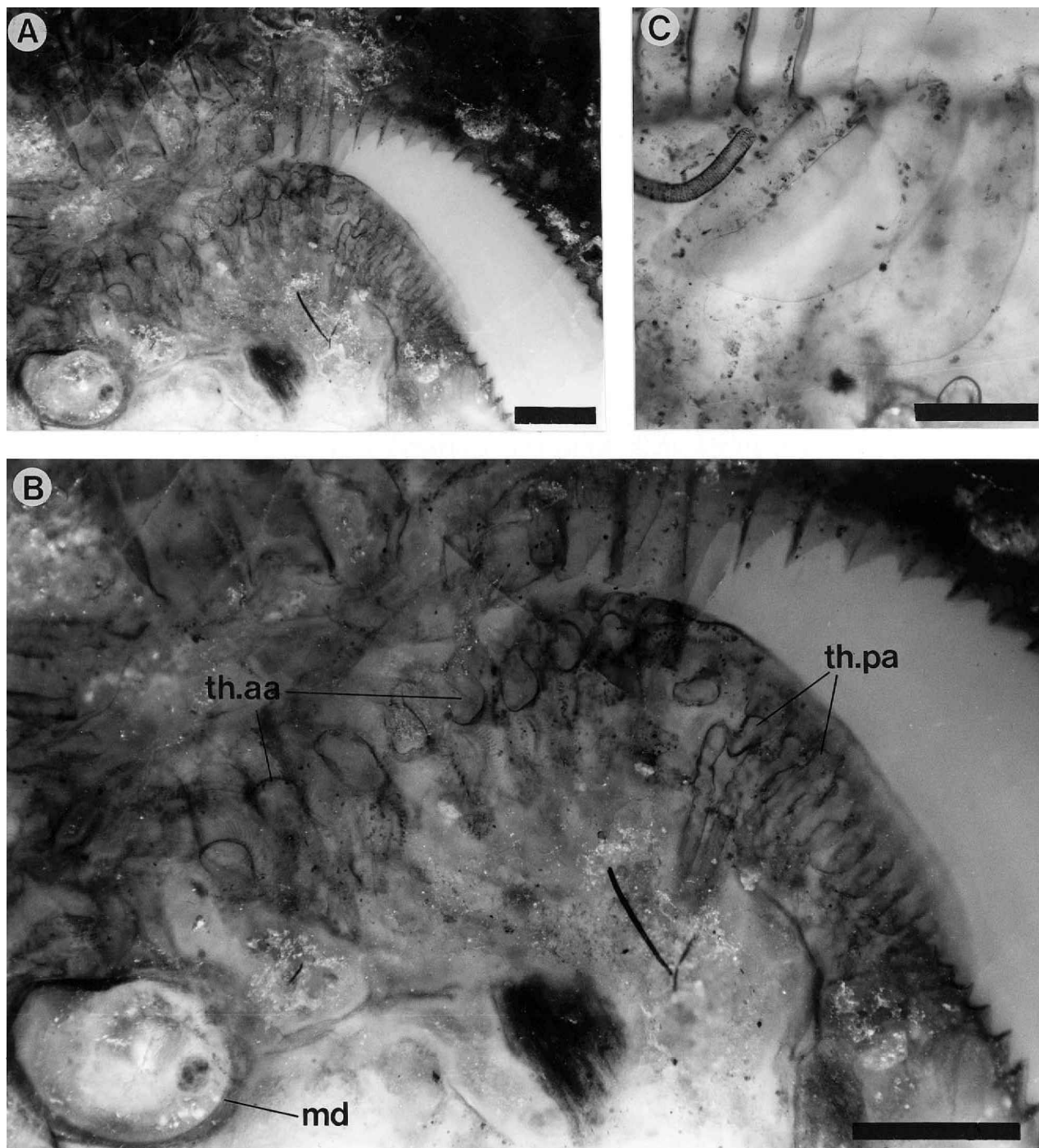
Figure 16 *Castracollis wilsonae* Fayers & Trewin *gen. et sp. nov.*, Pragian, Rhynie, Scotland: (A) AUGD12383, longitudinal section through the trunk of an almost complete individual showing an almost complete series of thoracic leg appendages, scale bar = 0·5 mm; (B) AUGD12383, close up of (A) showing the size difference between the anterior series of larger thoracic appendages (the proximal endites are seen here) and the posterior series of smaller thoracic appendages, scale bar = 0·5 mm; (C) AUGD12383, reverse of section shown in (A) and (B) showing four lateral, tergopleural scales attached to successive trunk segments bearing the posterior leg series. The tubular structure on the left is a nematophyte fragment, scale bar = 0·2 mm.

most likely represent lateral, tergopleural scales rather than epipodites. This is an unusual feature for branchiopods, having only been previously identified in *Lepidocaris rhyniensis*, Scourfield 1926.

5.4. Anterior thoracic appendage series

The anterior series of thoracic appendages (th.aa) are ventro-laterally directed, long, phyllopodous (Fig. 6) and almost raptorial in appearance. The appendages gradually decrease in length towards the posterior of the series. In some of the larger individuals some of the more anterior appendages appear to have attained a length of $1250\,\mu m$ (Figs 17, 20A) and as such may have extended beyond the (probable) posterior cephalo-thoracic shield. The morphology of the appendages appears to be similar on all the thoracic segments and no distinctive genital appendages or apertures are discernible.

The basipod (bas) or protopod, appears to be secondarily divided (Figs 21A, B) into a distinct proximal element and a distal element; together bearing five endites (end). The proximal segment bears the proximal endite (end1). The
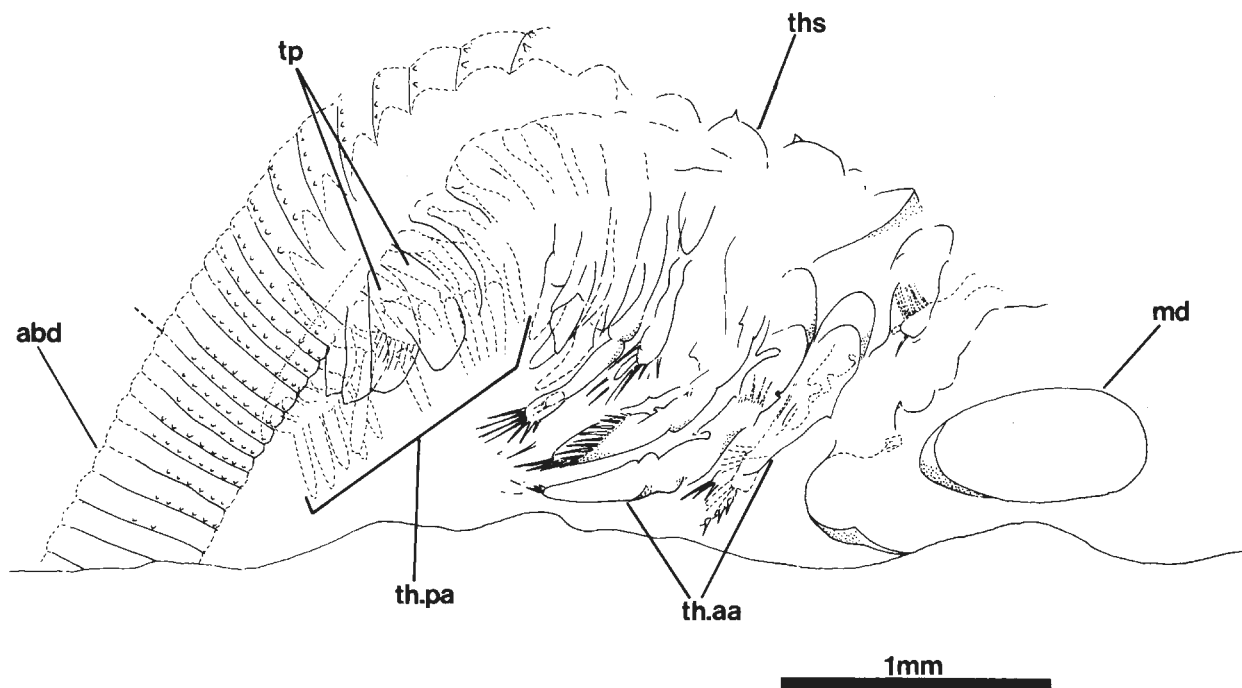
Figure 17 *Castracollis wilsonae* Fayers & Trewin *gen. et sp. nov.*, Pragian, Rhynie, Scotland: AUGD12383, *camera lucida* drawing of reverse of section shown in Figure 16A, showing the disposition of the posterior series of thoracic appendages, lateral tergopleural scales and part of the anterior series of thoracic appendages.

proximal endite is vertically orientated and is heavily setose, comprising a proximal, single row of long, fine, comb-like, plumose setae on the mesial to posterior surface (Figs 20D, 21C). These setae are curved towards the anterior of the thorax. Distal to this row are three successive parallel rows of shorter, slightly more robust setae on the mesial surface of the endite. The distal segment of the basipod bears the remaining four endites (end2–5), a distinctive endopod (en), and an exopod (ex) (Figs 20B, 21B). The four distal endites are similar in their morphology (Figs 21A, C). Each exhibits at least three rows of dense setae or spines (around $50\,\mu$m in length) on the mesial to anterior surface (Figs 20A, 21C) and a single row of plumose setae or 'meshwork spines' (ms) (Fryer 1988) on the posterior surface of the endite (Figs 20A, 21A). Characteristically these four endites also exhibit a large, smooth, tubular element or 'median spine' (end.sp) attached towards the distal end of the mesial surface of each article (Figs 20B, C, 21A, C). Each spine commonly displays up to four short, fine setae at the distal extremity. The length of these elements increases on each distally successive endite, such that the spine of the most distal endite is two thirds to approximately the same length as the endopod (Figs 21A, C). The relative length of the median spines also increases towards the anterior of the thorax.

The endopod (en) comprises a single articulated 'paddle' attached to the distal extremity of the basipod (Figs 20C, 21A, C). The endopod appears relatively robust and raptorial in comparison with the other elements of the appendage. The ornamentation is quite distinctive: the distal edge supports a pectinate row of 12 spines (en.s) that decrease gradually in length and size onto the mesial edge of the element (Fig. 22A), where they pass into four staggered rows of short setae (s) attached mesially onto distinct tubercles (Fig. 22B). The latter ornament is particularly evident and well-developed on the more anterior thoracopods of the larger specimens, which also often exhibit a single seta positioned on a small lobe approximately two thirds along the lateral margin towards the distal end of the article (Fig. 21B). One other feature of the thoracopods of the anterior leg series, seen clearly in a number

of the specimens, is a faint, but large, triangular sheet-like element attached laterally to the proximal end of the distal basipod segment. The lateral and distal edge of this sheet is marked by a single row of plumose setae, becoming shorter on the proximal and mesial edges (Figs 20B, 21B, 23). This structure is quite similar in appearance and disposition to the flabellum observed on the thoracopods of modern notostracans, and fossil kazacharthrans, and equates to an exopod (ex). No proximal, laterally-positioned article that may equate to the epipodite or 'bracht' in notostracans has been observed in this leg series in any of the specimens.

5.5. Posterior thoracic appendage series
The posterior series of thoracic appendages (th.pa) appear variable in number, typically occurring on the 10 to commonly 12 posterior-most segments of the thorax; though in one specimen, AUGD12382c, they appear to occur on as many as 15 segments (Fig. 5), each somite bearing one pair of appendages. They are distinctly smaller than the anterior series of thoracic appendages, the anterior-most appendage of the former generally appearing to be approximately two thirds the length of the corresponding posterior-most appendage of the anterior series (Figs 6, 16A, C, 17). The overall morphology of these appendages appears phyllopodous. They generally seem to be ventro-laterally to posteriorly directed and there is a gradual reduction in appendage size towards the posterior, creating an overall 'basket-like' appearance to the appendage series (Figs 6, 8, 18). Appendage size and degree of development also varies between the largest and smallest specimens. The posterior appendages observed on the smallest specimen, AUGD12382b, for example, appear rudimentary and bud-like (Fig. 7).

The general plan for the posterior series of thoracic appendages, and the morphology and disposition of their various component elements, is very similar to that observed for the anterior series (Figs 6, 19), the main difference being primarily their smaller size and the reduced length and number of setae. The appendages of the posterior series

comprise a basipod with five endites (Fig. 19). The basipod is apparently secondarily divided, the proximal segment bearing the first, proximal endite and the second distal segment bearing the remaining four endites together with an endopod and a flabellum-like exopod. The endites display a variable number of setae. The most proximal endite appears vertically orientated, bearing a row of plumose setae on the proximal mesial margin and a variable number of shorter setae on the mesial surface of the endite (Fig. 19). The four remaining endites on the distal segment of the basipod are also setose with two to three rows of a variable number of short setae on the mesial surface and a faint row of fine setae on the posterior surface. Similarly to the equivalent endites of the anterior series of thoracic appendages, each bears a conspicuous tubular element or 'median spine' on the distal end of the mesial surface. The relative length of these spines increases distally, so that the last, distal endite (end5) bears a spine that is two thirds to half the length of the corresponding endopod. Also, towards the posterior of the body, the spine length decreases relatively with the appendage size, so that on the more posterior appendages the spine either appears not to be present, or is only represented by a small knob.

The endopod (en) of the posterior series of thoracic appendages is similar in plan, but is of a rather simpler and less robust morphology compared with that observed for the anterior appendage series (Fig. 19). It is attached to the distal end of the protopod, and comprises an oblate, flattened, palmate 'paddle'. The distal margin supports a single row of setae, decreasing in size onto the mesial margin. The setae are less robust and raptorial-like, compared to those on the anterior thoracic appendage series. The mesial edge of the endopod apparently bears a single row of short, fine setae and the lateral margin may bear one to two fine setae. The number of setae on the endopods gradually decreases towards the posterior of the leg series.

A very faint, triangular palmate exopod is present, attached laterally at the proximal end of the distal protopod segment (Fig. 19), the lateral margin of which supports at least 28 plumose setae. As with the equivalent element on the anterior series of thoracopods, finer setae appear to continue around the margin onto the proximal and distal mesial edges. One specimen showing a transverse section through a posterior thoracic segment and leg pair, AUGD12386a, shows a tiny knob-like projection, lacking setae, towards the proximal end of the protopod, possibly representing a much-reduced proximal epipodite (Fig. 19).

5.6. Abdomen

The abdomen (abd) in the largest specimens appears to comprise up to 28 apodous ring-like segments (Fig. 8). The somites of the abdomen form complete rings (Figs 15, 18) and range from $90 \mu m$ to $100 \mu m$ in length in larger specimens down to $20 \mu m$ in the smallest specimen. In the smallest specimen the number of post-appendage bearing somites of the abdomen is much reduced, comprising at most two apodous segments (Fig. 7).

The individual somites are rather asymmetric in longitudinal cross-section, the posterior margin of each ring appearing ridged (Figs 6, 8). As with the thoracic segments, each somite exhibits a well-defined single row of equally spaced very fine spines or spurs around the ridged posterior margin. These spurs are more clearly defined and better developed within the larger specimens (Figs 6, 17) and appear to gradually become more robust and generally fewer in number towards the anterior of the abdomen. Spur sizes in the larger specimens range from five

μm to $10 \mu m$ in length on the more posterior abdominal segments to $20 \mu m$ in length towards the anterior.

5.7. Telson

The posterior region of the trunk comprises a telson (tel) with two distinct furcal rami (fu) (Fig. 8). The length of the telson in the larger specimens is 1 mm. The smallest specimen has a telson length of $300 \mu m$ (AUGD12382b, Fig. 7). The morphology of the telson is relatively oblate to cylindrical and is rounded towards the posterior, where in the larger specimens it is sculptured into two distinct bosses or nodes where the furcal rami are attached (Figs 24A, 25A, B). In the larger specimens the telson tends to exhibit sparse to occasionally moderately common, very fine posteriorly projecting spurs (t.s), typically up to $10 \mu m$ in length. These spurs appear to be concentrated on the dorsal surface of the telson (Figs 24B, 25A). Comparing two particular specimens, AUGD12388b (Fig. 25A) and AUGD12381b (Fig. 25B), they appear to be arranged in two longitudinal, sub-parallel rows with up to seven spurs per row. The spurs are evenly spaced, with the exception of the second and third spurs, from the anterior, which appear almost superimposed (Fig. 24). The posterior of the telson displays robust, conspicuous, posteriorly projecting spurs or laterocaudal spines (lcsp) arranged around the points of attachment for the furcae. There are typically six of these spurs; one positioned laterally to each furca, one dorsally and one ventrally. In the larger specimens they exhibit lengths between $20 \mu m$ and $35 \mu m$ (Fig. 24C). In the smallest specimen, AUGD12382b, these spurs are present as poorly developed knobs (Fig. 7). Occasionally, rare isolated spurs of smaller size are positioned between or slightly anterior to these, but apparently have no regular spatial arrangement.

The pair of furcal rami are usually preserved, and range up to $750 \mu m$ in length in the larger specimens (Figs 24B, C) and down to at least $150 \mu m$ in the smallest specimen (Fig. 7). Each ramus comprises two, apparently articulated, elements. In larger specimens the anterior element is up to $650 \mu m$ long (Fig. 24C) with the widest point being just above the point of articulation with the telson at $110 \mu m$, and tapering gently towards the posterior to $50 \mu m$ in width. In many specimens these elements display a slight flexure towards the ventral side. In many specimens this first element displays an integument of very fine ($10 \mu m$ to $20 \mu m$ long) posteriorly projecting setae in an apparently random arrangement over the entire surface (Figs 8, 24C). In the smaller forms, this integument appears either absent or very poorly and sparsely developed, and also, in the smallest forms, this element is much reduced in length relative to the posterior element (Fig. 7). The posterior end of this element, around the point of attachment for the posterior element of the ramus, occasionally exhibits two to three small spines up to $15 \mu m$ in length (Fig. 24C).

The posterior element of the ramus in most of the specimens appears to form an articulated, blunted spine generally up to $100 \mu m$ in length (Fig. 24C), with the exception of one specimen (Figs 24A, 25B), in which the spine is more elongate (up to $200 \mu m$ in length). Therefore, it seems likely that in most of the specimens observed this spine is damaged. In all specimens the integument of this posterior element appears smooth.

6. General Discussion

The presence of different sized individuals in the assemblage suggests to us that these represent various stages of ontogenetic development, regardless of whether the specimens are exuviae or mortalities. From the material discovered in this
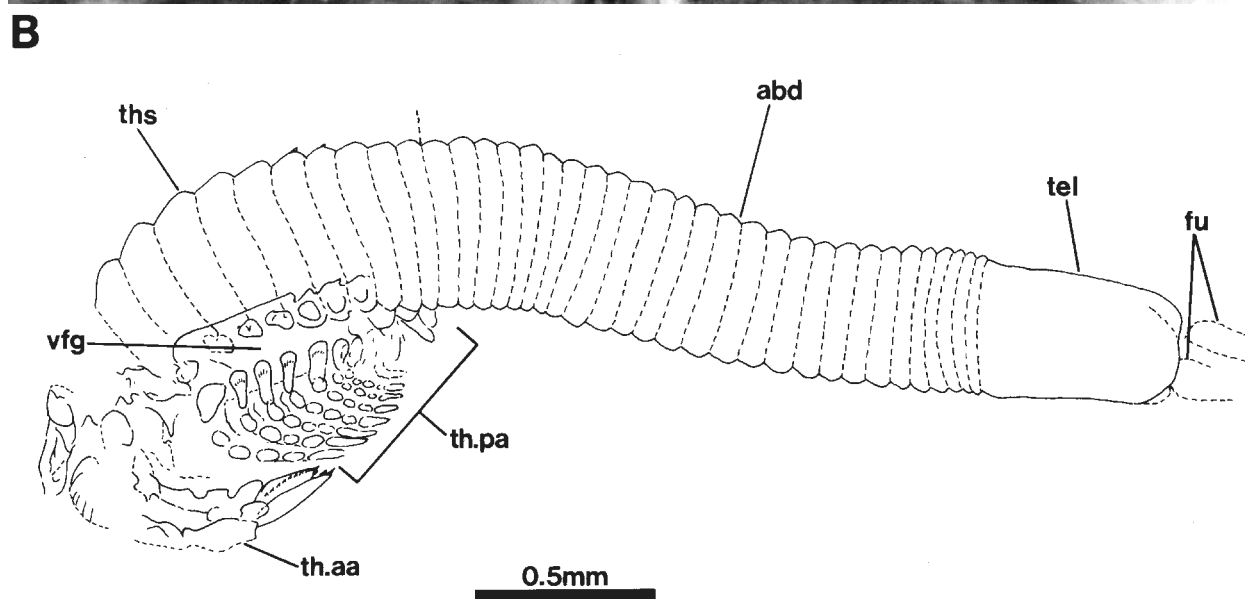
Figure 18 *Castracollis wilsonae* Fayers & Trewin *gen. et sp. nov.*, Pragian, Rhynie, Scotland: (A) AUGD12401a, posterior thorax, abdomen and telson of a small individual, illustrating the gradual reduction in length of leg appendages towards the posterior of a partially complete posterior thoracic appendage series; (B) Interpretative drawing of a (A).

one chert block, we cannot at present ascertain whether the largest specimens of *Castracollis wilsonae* observed represent the adult form of the crustacean. Figure 26 represents a reconstruction of the probable appearance in life of *Castracollis wilsonae*, including reconstructions of typical trunk appendages, together with views of the animal with a hypothetical cephalo-thoracic shield.

A number of morphological characteristics of *Castracollis* are particularly worthy of discussion. The Phyllopoda, comprising the Calmanostraca and Onychura, are considered a monophyletic group based, for example, on the internalisation and dorsal migration of the compound eyes during ontogeny (Walossek 1993, 1995, Walossek & Müller 1998). In *Castracollis,* eyes have not been discerned, but it does not necessarily follow that the animal was blind. The corresponding dorso-anterior region of the head where the eyes are located in the Notostraca, for example, has not been preserved,

or details have been lost as a result of taphonomy in the *Castracollis* specimens, therefore unequivocal comparisons cannot be drawn at this time. Similarly, the lack of preservation or damage to the dorsal surface of the head region in *Castracollis* means that the presence, or absence, of the 'neck organ' and its morphology remains unresolved. It is quite possible the conspicuous notch or depression located on the anterior midline of the head shield may indicate the position of the interior naupliar eye. With the exception of the Notostraca, in which the naupliar eye is enclosed in a pocket together with the compound eyes, the naupliar eye is internal, anterior, or ventral to the eye chamber and 4-cupped in all other members of the Phyllopoda (Walossek 1993, and references therein). This character has not been resolved for the fossil Kazacharthra, the close relatives of the Notostraca.

The presence of long biramous second antennae with symmetrical rami in *Castracollis* is particularly tantalising,
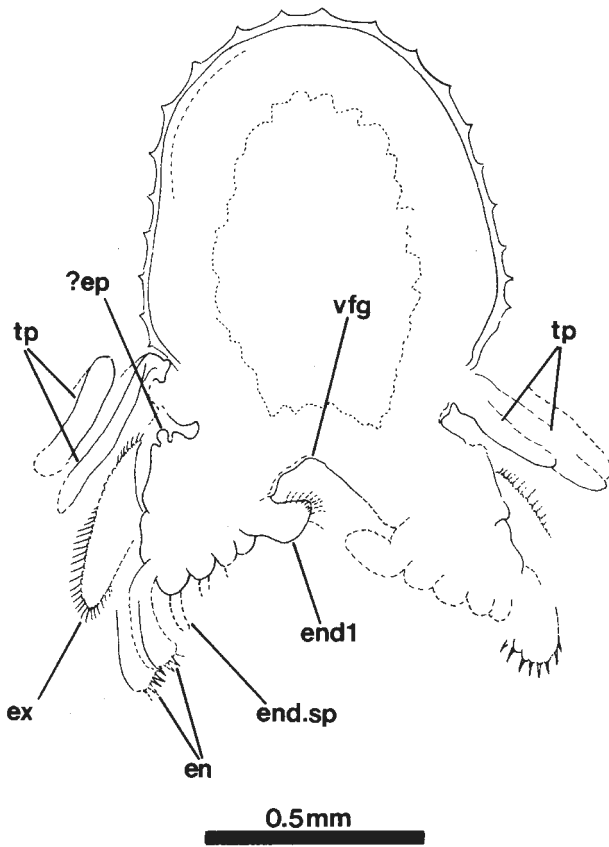
Figure 19 *Castracollis wilsonae* Fayers & Trewin *gen. et sp. nov.*, Pragian, Rhynie, Scotland: AUGD12386, *camera lucida* drawing of a transverse section through a trunk segment bearing a pair of appendages from the posterior thoracic appendage series, illustrating the disposition of the articles. Tergopleural scales are also illustrated originating from segments within and without the thin section.

especially if the larger specimens are adult forms, since this design is not known in calmanostracans. Until the later stages of ontogeny, the second antennae of Notostraca are typically biramous. In the late stages of notostracan ontogeny the second antennae become uniramous, typically reduced, and may even be absent in larger forms (Longhurst 1955). This appears to be a derived character for the Notostraca. In Kazacharthra the second antennae are small and remain biramous (McKenzie *et al.* 1991), but their detailed design remains uncertain. The extant Onychura, however, possess long, biramous second antennae with symmetrical rami. Of these, the Laevicaudata and Spinicaudata are particularly of note since, like those in *Castracollis*, the second antennae are multi-segmented and flagellate. The apparent lack of first antennae in *Castracollis* may be due to a preservational failure.

The presence of two distinct series of thoracic appendages in *Castracollis*, comprising a series of 11 anterior pairs of raptorial, phyllopodous thoracopods, followed by a variable number of progressively smaller phyllopodous appendages, is strongly reminiscent of the Calmanostraca (Tasch 1969), and particularly the Notostraca (Sars 1867). In *Castracollis*, the posterior leg series comprises between 10 and 15 pairs of leg appendages, with a disposition of one pair per segment (trunk segments 12 to 26). This contrasts with notostracans, in which up to six leg pairs may occur on each segment (trunk segments 12 to 17), comprising up to 71 pairs in all (Walossek 1993 and references therein). Although Kazacharthra lack the posterior leg appendage series seen in *Castracollis* and notostracans (McKenzie *et al.* 1991; reconstruction in Walossek 1993), the homologous leg appendage morphology of the anterior leg

series, and the visible segmentation on the ventral surface between the leg pairs of the new crustacean *Castracollis* shows more similarities with the Kazacharthra (Novozhilov 1957).

The morphology of the leg appendages of *Castracollis* is also worthy of note, especially in comparison with those of notostracans and, to an extent, kazacharthrans. With the exception of the first pair of thoracopods in notostracans, which are modified, the thoracopods of any given individual of either of these two orders or in *Castracollis* are all practically identical in their morphology. The phyllopodous thoracopod structure in *Castracollis* is broadly similar to that observed for the second to eleventh pairs of thoracopods in notostracans. However, no dimorphic modifications have been identified in the thoracopods of *Castracollis*, such as those observed in the eleventh pair of thoracopods in modern adult female notostracans, where an expansion of the exopod and epipodite form a brood pouch (Fryer 1988), and in the corresponding thoracopods of kazacharthrans (McKenzie *et al.* 1991). The articulated, robust endopod in *Castracollis* appears to be equivalent to the 'telopod' (Preuss 1957; Pennak 1989) or 'sixth endite' (Borradaile 1958; McLaughlin 1980) in notostracans. This article also equates to the 'carpopodite' of Novojilov (1959) on the thoracopods of kazacharthrans (refer to discussion in Walossek 1993). The large disto-lateral, lamelliform, setose article in *Castracollis* is therefore most likely equivalent to the 'flabellum' or exopod in notostracans. The fleshy, proximal, branchial epipodite of notostracans has not been observed on the thoracopods of *Castracollis*, but the fact that it has not been observed could also simply be due to a failure of preservation, the faintness of the cuticle or the appendage orientation in the thin sections. In contrast to Notostraca, the abdominal appendages of *Castracollis*, despite their comparatively smaller size, are almost identical in their phyllopodous morphology to the thoracopods. In the one specimen, AUGD12386a (Fig. 19), which shows a transverse section through a leg appendage-bearing abdominal segment, the small knob or plate-like protrusion on the proximal lateral margin of the protopod may represent a much-reduced epipodite, but this remains equivocal.

The rather similar and polymetameric segmentation of the abdomen and thorax observed in the specimens, the anterior flattening of the trunk, and the conspicuous integument of the somites shows strong morphological similarities with both notostracans and kazacharthrans. The latter, however, typically exhibit two longitudinal parallel rows of pronounced spines running along the dorsum of the thorax and abdomen. This feature has only been observed in a number of specimens of *Castracollis* on the dorsal surface of the telson. The apparent variation in number of abdominal somites, although in part probably reflective of ontogeny, may also reflect similarities with calmanostracans, which often exhibit a varying number of abdominal segments. *Castracollis* also retains the ventral or sternitic food groove (Fig. 19) that has been lost in the Notostraca. The appearance of lateral, tergopleural scales on the leg appendage-bearing trunk segments of *Castracollis*, however, is interesting, since this feature is not present in either notostracans or kazacharthrans or any of the other extant branchiopod orders. It is, however, a feature observed on the leg-bearing trunk segments of the lipostracan *Lepidocaris rhyniensis* Scourfield 1926.

The telson/furca development of *Castracollis* is also comparable with calmanostracans, comprising an oblate, spurred telson with paired, long, furcal rami. However, in Notostraca and Kazacharthra the furcal rami are cirriform and flagellate. Table 1 shows some of the salient morphological features of

Table 1 Comparative morphological features of *Castracollis wilsonae* (this paper) in its assumed adult form, adult notostracans (Longhurst 1955; Tasch 1969; McLaughlin 1980, 1982; Fryer 1988; Walossek 1993), kazacharthrans (Novozhilov 1957, 1959; Tasch 1969; McKenzie *et al.* 1991; Walossek 1993) and *Lepidocaris rhyniensis* (Scourfield 1926, 1940; Walossek 1993).

Morphological feature	*Castracollis wilsonae*	Notostracans	Kazacharthrans	*Lepidocaris rhyniensis*
Cephalo-thoracic shield	Uncertain	Dorsal, univalve.	Dorsal, univalve	None
Eyes	?Naupliar eye	Paired sessile eyes + naupliar eye	Paired sessile eyes + ?naupliar eye	?Naupliar eye
First antennae (a1)	Unknown	Small, uniramous	Long, uniramous	Small, uniramous
Second antennae (a2)	Long, biramous	Reduced or absent in adult form	Reduced, biramous– remains uncertain	Long, biramous
No. of 'thoracopods' and their disposition	Anterior series: trunk segments 1–11, one pair per segment. Posterior series: trunk segments 12–26, 10–15 leg pairs, one pair per segment	Anterior series: trunk segments 1–11, one pair per segment. Posterior series: trunk segments 12–17, 29–52 leg pairs, < 6 pairs per segment	Trunk segments 1–11, one pair per segment. No posterior leg series	13, one pair per segment (first pair are modified maxillae). Posterior 2 pairs in females are modified to form genital appendages
'Thoracopod' morphology	All similar. Anterior series raptorial. Posterior series phyllopodous	Most similar. Anterior series raptorial. First leg pair long and prehensile in *Triops*. Posterior series phyllopodous	All similar and raptorial	First 3 pairs phyllopodous (first pair are modified maxillae)
Tergopleural scales	Present on leg-bearing segments	Absent	Absent	Present on leg-bearing segments
Abdominal segments	Variable up to 28	Variable up to 33	Variable up to 40	4 ring-like somites
Telson and furcal rami	Oblate telson with two dorsal rows of spurs. Paired furcae	Oblate telson with random spurs, +/− supra-anal plate. Cirriform furcae	Oval telson with spurs on lateral, dorsal and ventral surfaces. Cirriform furcae	Oblate, smooth telson with lateral processes. 2 pairs of primary and secondary furcae

Castracollis in comparison with those for the notostracans, kazacharthrans and the lipostracan *Lepidocaris rhyniensis.*

Considering the current diagnoses of the Notostraca and Kazacharthra, particularly the second antenna morphology, the number, disposition and morphology of the thoracic leg appendages, the presence of tergopleural scales, together with the telson-furca development, *Castracollis* cannot, with any confidence, be placed in either of these taxa. Though care must be taken, especially when considering the taphonomy and remarkable three-dimensional preservation of the Rhynie chert crustaceans, with respect to the level of preservation in otherwise two-dimensional fossil kazacharthrans and notostracans, as direct comparisons may not always be easily drawn.

However, similarities, particularly in the non-filtratory habit of the anterior series of thoracopods, the anterior flattening of the polymetameric trunk, distinctive telson/furcae development and presence of a large, spatulate labrum, indicate that *Castracollis* is most likely to be part of the calmanostracan lineage (Walossek 1993, 1995; Walossek & Müller 1998), these morphological features reflecting modifications for a benthic lifestyle (see below). The loss of the ventral or sternitic food groove, and reduction in antennae in the adult forms of modern notostracans, are derived characters for this group. In *Castracollis*, the retention of the food groove, and the presence of long biramous second antennae with symmetrical rami (in the supposed adult form), would be expected to be plesiomorphic features in the Calmanostraca. Therefore, if *Castracollis* is of the calmanostracan lineage, and if not directly ancestral to the Notostraca and Kazacharthra, it is quite possibly the sister taxon to these two groups. Notostracans are

known since the Upper Carboniferous, Kazacharthrans are only known from the Triassic and Lower Jurassic of Kazakhstan and China, whereas *Castracollis* is of Early Devonian (Pragian) age. Further information is required, particularly regarding the dorsal region of the head, namely the position and morphology of the eyes and 'neck organ', and posterior cephalo-thoracic shield, before the possible phylogenetic relationships of *Castracollis* can be explored further. It is pertinent to note that just as *Lepidocaris* could not be neatly fitted to taxonomic definitions within the Branchiopoda as described in 1926, *Castracollis* does not easily fit within an existing group. These two arthropods might be regarded as early variants of the branchiopod design, and it is quite possible that much greater variation existed in the Devonian than survives to the present day.

The smaller specimens of *Castracollis* generally exhibit a reduction in the number of apodous abdominal segments in progressively smaller specimens, the smallest specimen, AUGD12382b (Fig. 7), appearing to comprise the leg appendage-bearing segments of the thorax and at most two posterior apodous abdominal segments. It is highly likely that this specimen represents a moult of one of the youngest ontogenetic stages of *Castracollis* that we have observed in the chert samples studied, and that posterior apodous segments were added to the abdomen during successive stages of development. Since eggs or larval stages of *Castracollis* have not been identified in this study, at the present time we cannot tell if the animal hatched as an advanced larva or if early larval development was more anamorphic, such as that recorded for modern notostracans (Walossek 1993).
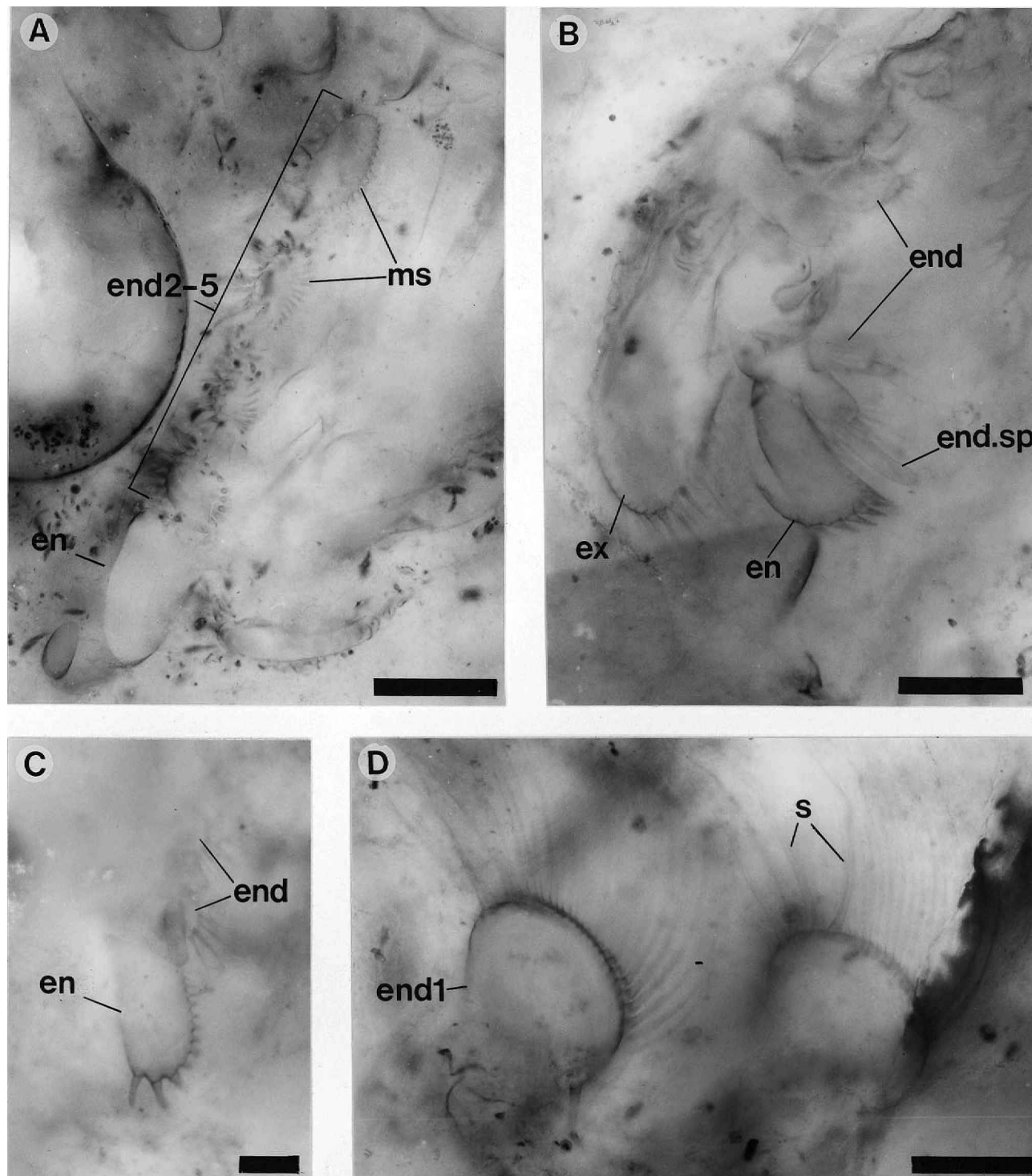
Figure 20 *Castracollis wilsonae* Fayers & Trewin *gen. et sp. nov*., Pragian, Rhynie, Scotland: (A) AUGD12382a, longitudinal section through an anterior thoracic leg appendage showing the disposition of the endites and 'meshwork spines', scale bar = 0·2 mm; (B) AUGD12391, slightly oblique transverse section through two successive, posterior thoracic appendages of the anterior leg series, showing the disposition of the flabellum-like exopod, endopod and endites with tubular elements or 'median spines', scale bar = 0·2 mm; (C) AUGD12381a, partial thoracic appendage from the anterior series showing the endopod, and two endites with 'median spines', scale bar = 0·1 mm; (D) AUGD12383, proximal endites of two successive thoracic appendages, scale bar = 0·1 mm.

7. Palaeoecology

7.1 Environmental interpretation

The existing material of *Castracollis* is only known from a single float block of chert. However, the number and the remarkable preservation of the specimens and the associated biota, together with the distinctive host-chert textures, enable a great deal to be inferred on the palaeoenvironment and mode of life of this crustacean.

Castracollis was undoubtedly an aquatic organism. This is indicated primarily by the morphology of the leg appendages, namely being foliaceous and phyllopodous with lamelliform exopods. The associated biota of *Lepidocaris*, various multicellular, filamentous and unicellular cyanobacteria together
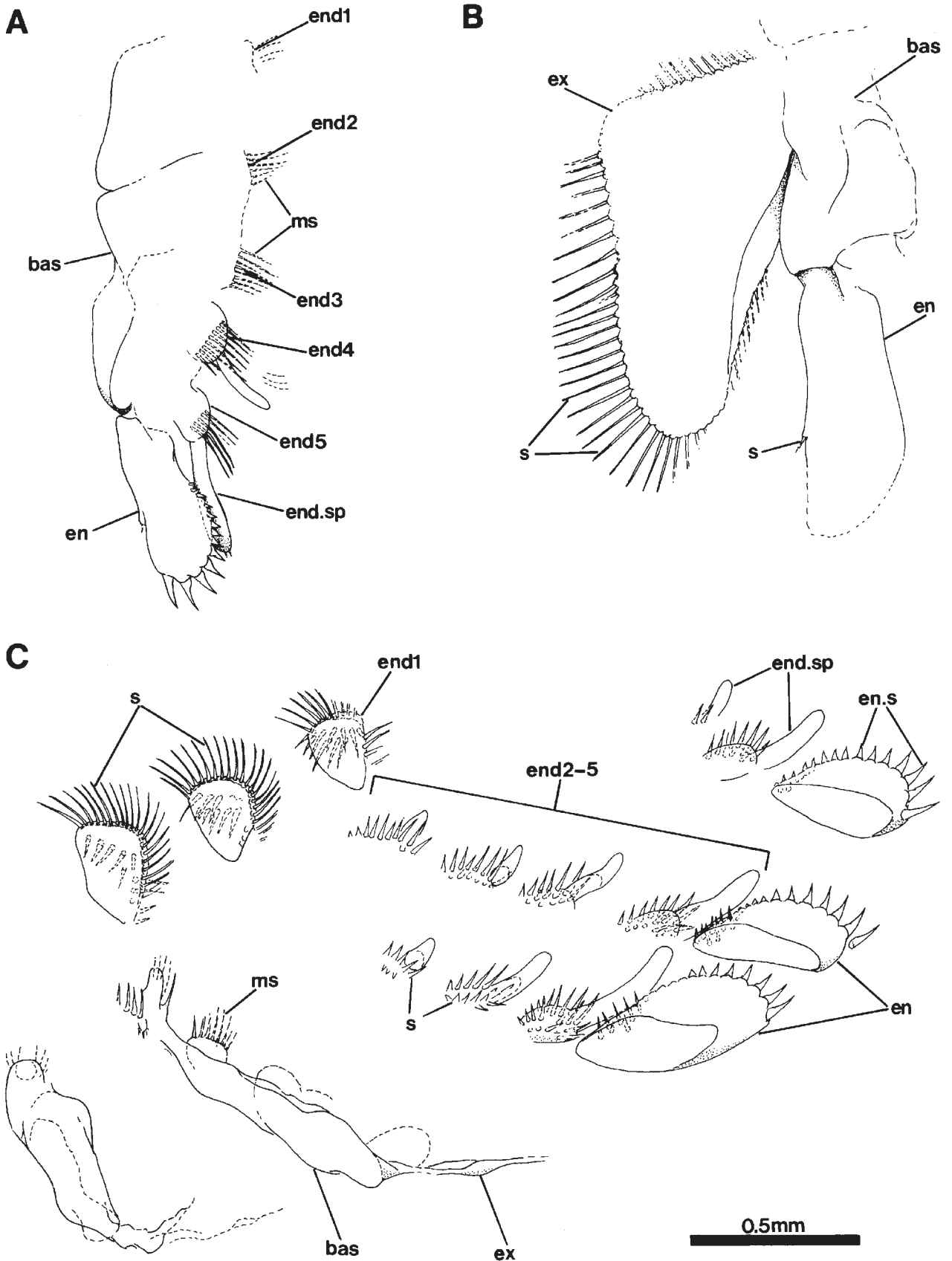
Figure 21 *Castracollis wilsonae* Fayers & Trewin *gen. et sp. nov.*, Pragian, Rhynie, Scotland: (A) AUGD12384, *camera lucida* drawing of an isolated partial thoracic appendage from the anterior leg series, illustrating the segmented basipod, position of the endites and endopod; (B) AUGD12385, *camera lucida* drawing of a partial thoracic appendage from the anterior leg series, illustrating the disposition of the endopod and flabellum-like exopod; (C) AUGD12385, *camera lucida* drawing of a longitudinal section through a series of five thoracic appendages from the anterior leg series, illustrating the proximal and distal endites, and distal portions of the endopods.
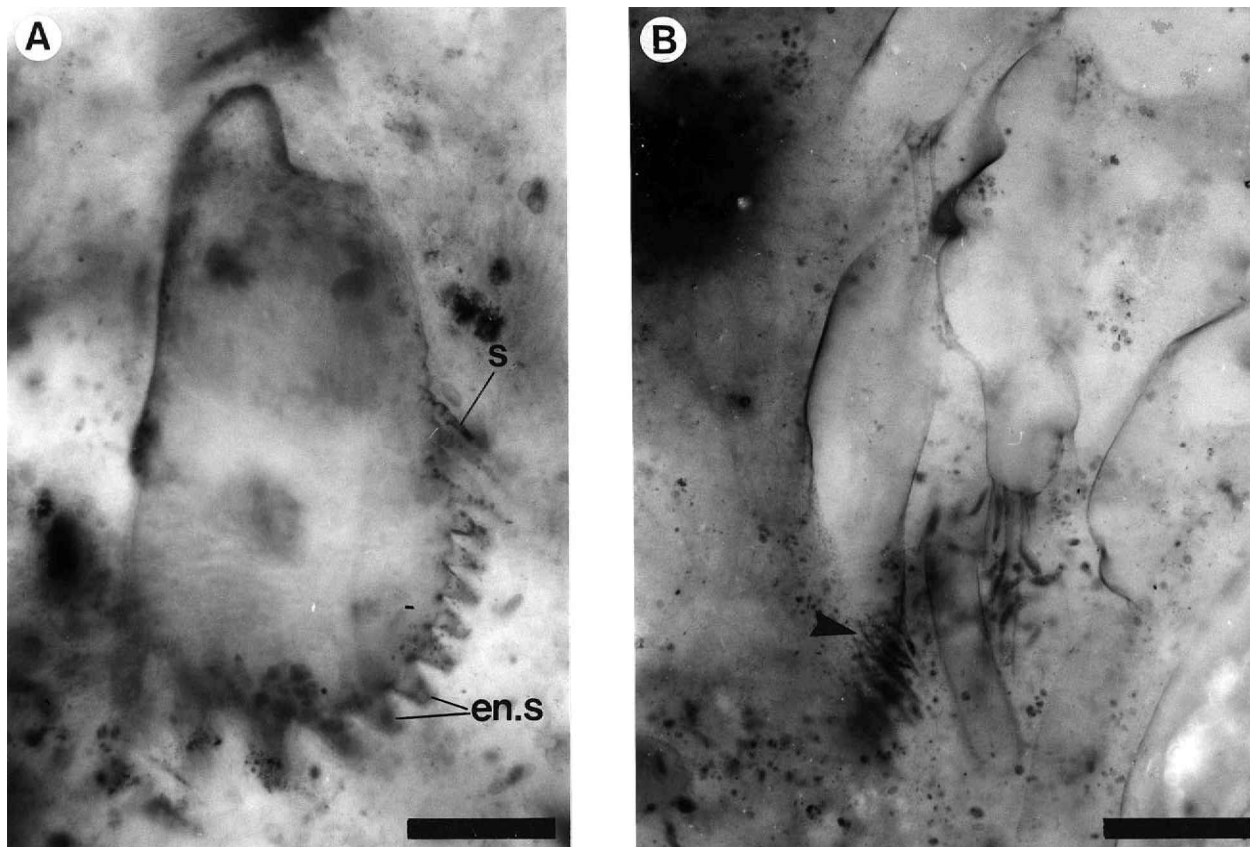
Figure 22 *Castracollis wilsonae* Fayers & Trewin *gen. et sp. nov.*, Pragian, Rhynie, Scotland: (A) AUGD12382c, endopod of an anterior thoracic appendage illustrating robust spurs on the distal to mesial margin, and setae on the mesial margin, scale bar = 0·1 mm; (B) AUGD12394, mesial surface of an endopod of an anterior thoracic appendage illustrating the staggered rows of setae (arrowed), scale bar = 0·2 mm.

with probable charophytes, indicate a freshwater environment. The 'clotted' chert texture of aggregates of amorphous organic matter, coprolites and the filamentous meshes that comprise the matrix of the arthropod-bearing unit is strongly reminiscent of mulm, the fluffy, amorphous organic-rich material found in many modern freshwater ponds (Anderson & Trewin 2003).

7.2. Mode of life

The high concentration of various ontogenetic stages of *Castracollis* in this single, thin chert horizon, could suggest that after hatching the animal moulted and developed rapidly, perhaps having a similar short life cycle to modern notostracans, occupying temporary freshwater ponds. A possible alternative explanation for this assemblage could be they represent an accumulation of debris from selective predation in the overlying water body. However, considering the form of ecdysis in modern notostracans, together with the lack of any soft parts or gut contents in the *Castracollis* specimens, and the lack of cuticle remains within coprolites in the matrix, the former scenario appears more likely.

The phyllopodous thoracic appendages were partly used in locomotion, allowing the animal to crawl over the substrate or swim. Epipodites, although not unequivocally identified in *Castracollis*, would have been used for respiration. The large, laterally directed thoracic appendages were almost certainly utilised in feeding. Their raptorial morphology suggests the appendages were modified for a non-filtratory, predominantly benthic lifestyle, as observed in extant notostracans and postulated for the extinct kazacharthrans (Walossek, 1993, 1995, Walossek & Müller 1998). Although no gut traces have been observed, and the coprolites present in the matrix cannot be unequivocally attributed to the animal, given the abundance
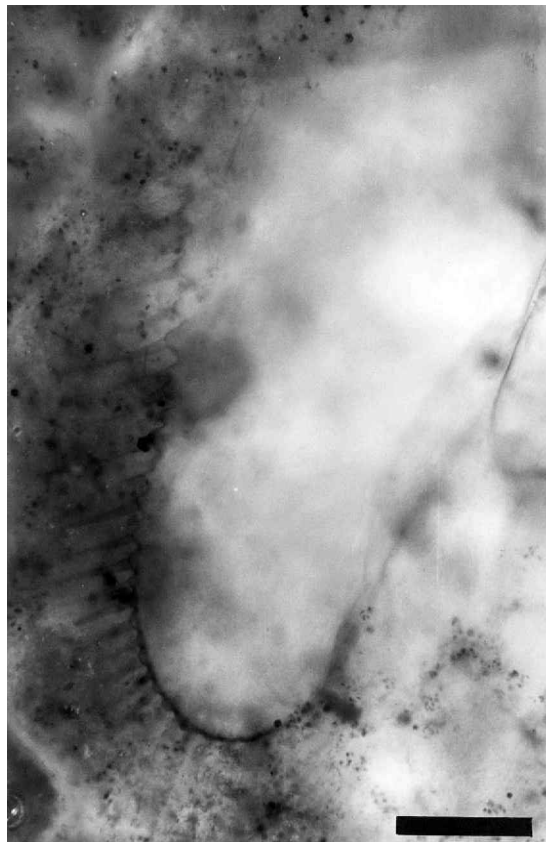

Figure 23 *Castracollis wilsonae* Fayers & Trewin *gen. et sp. nov.*, Pragian, Rhynie, Scotland: AUGD12385, flabellum-like exopod of an anterior thoracic appendage, scale bar = 0·2 mm.
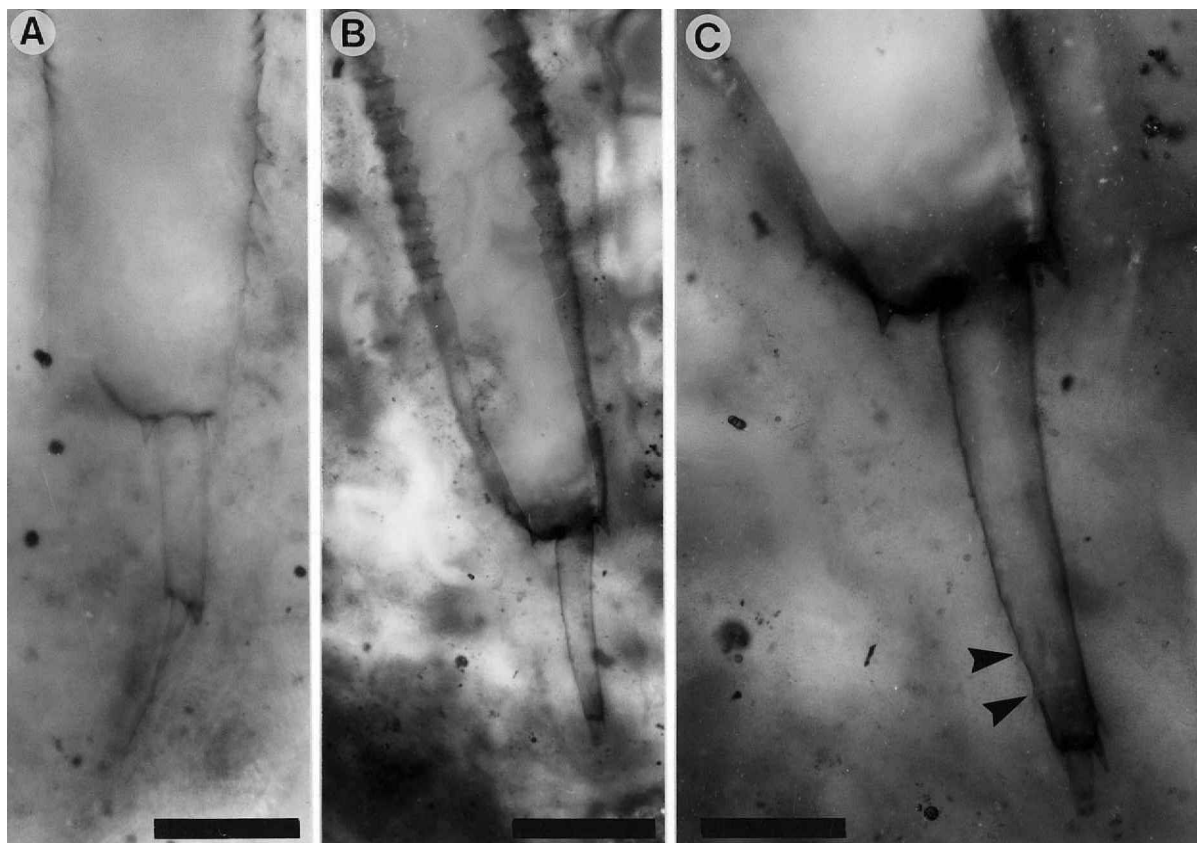
Figure 24 *Castracollis wilsonae* Fayers & Trewin *gen. et sp. nov.*, Pragian, Rhynie, Scotland: (A) AUGD12381b, lateral view of telson of a small specimen, showing the disposition of the furcal rami, scale bar = 0·2 mm; (B) AUGD12391, lateral view of posterior abdomen and telson showing the disposition of the latter, laterocaudal spines, and furcal rami, scale bar = 0·5 mm; (C) AUGD12391, detail of a furcal ramus showing point of attachment with the telson and ornament of fine setae (arrowed), scale bar = 0·2 mm.

of fine organic material in the arthropod-bearing unit, it is likely that *Castracollis* was in part a detritivore. It is also probable that the animal may have also been saprophytic and a facultative predator like modern notostracans (McLaughlin 1980). The robust, raptorial nature of the thoracic endopods, with the development of stout spurs and setae on the distal and mesial margins, would have been well suited to tearing up carrion and prey items. The torn up fragments would have been moved anteriorly along the ventral or sternitic food groove towards the mandibles and mouth by sweeping motions of the plumose setae on the proximal endites. It is quite possible that as well as being used for locomotion, the setose, long biramous antennae of *Castracollis* served a sensory function for locating food items, a function for which the specialised first pair of thoracic appendages in modern notostracans is adapted. The elongate, multi-articulate structure of the first pair of thoracic appendages in notostracans also enable the animal to grasp plant stems and other structures, and therefore notostracans have the ability to climb (McLaughlin 1982). *Castracollis* lacks such prehensile thoracopods and therefore may not have been particularly suited to this method of locomotion. Whether the animal could use its long, multi-articulate antennae for locomotion in such a manner is a point for speculation.

8. Conclusions

Castracollis wilsonae represents the first unequivocal addition to the crustacean fauna of the Rhynie chert since the description of *Lepidocaris rhyniensis* (Scourfield 1926, 1940),
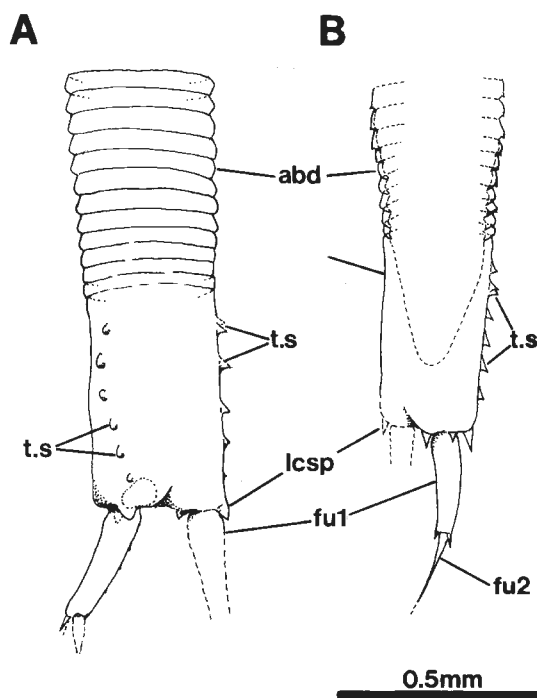

Figure 25 *Castracollis wilsonae* Fayers & Trewin *gen. et sp. nov.*, Pragian, Rhynie, Scotland: (A) AUGD12388b, *camera lucida* drawing showing a near dorsal view of the posterior abdominal segments and telson, illustrating the ornament of two subparallel rows of spurs on the telson and the disposition of the furcal rami; (B) AUGD12381b, *camera lucida* drawing of specimen illustrated in Figure 24A, lateral view showing the posterior abdominal segments, telson and furcal rami.
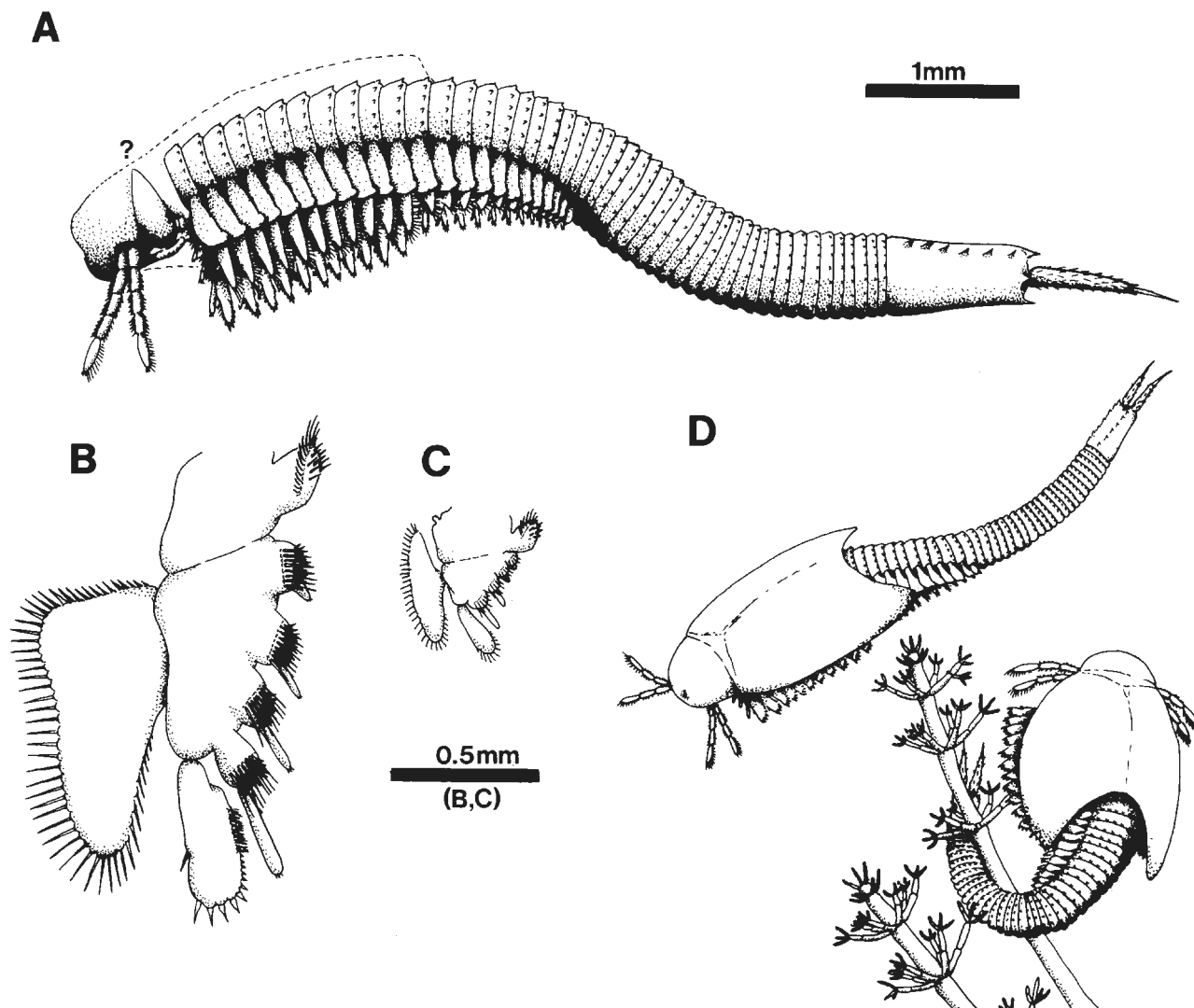
Figure 26 Reconstructions of *Castracollis wilsonae* Fayers & Trewin *gen. et sp. nov.*, Pragian, Rhynie, Scotland: (A) Lateral view of an individual with 23 pairs of thoracic appendages and 25 apodous posterior abdominal segments. A hypothetical cephalo-thoracic shield is indicated by dotted lines; (B) Reconstruction of a leg appendage from the anterior series of thoracopods, viewed from the posterior; (C) Reconstruction of a leg appendage from the posterior series of thoracopods, viewed from the posterior; (D) Views of the animal as it probably appeared in life with hypothetical cephalo-thoracic shield (based upon extant notostracans), in this example illustrated with the charophyte *Palaeonitella cranii.*

expanding yet again the faunal list of this remarkable deposit. A large number of specimens have been discovered in a single float block of chert and concentrated within a distinctive arthropod-bearing unit in the block (Figs 2, 3), comprising a basal stromatolitic layer passing upwards into chert, displaying a clotted texture with an associated, predominantly aquatic, flora and fauna. Although found around 1500 m E of the Rhynie SSSI and not discovered *in situ*, the host chert block, based on its morphology, textures and floral content, is almost certainly from the same stratigraphic unit as the Rhynie chert of the Dryden Flags Formation.

The majority of specimens of *Castracollis* represent different ontogenetic stages, though no eggs or larval stages have been identified in this study. They are associated with a distinctive *in situ* biota, comprising numerous *Lepidocaris*, nematophyte remains, charophytes and pervasive meshes of remarkably well preserved microbial filaments and clusters of unicells and daughter cells of probable cyanobacteria. The microbial remains are contained within and contribute to the 'clotted' chert texture of aggregates of amorphous organic matter and coprolites. The 'clotted' chert texture, strongly reminiscent of

mulm, and biota strongly suggest preservation in an aquatic environment, probably in a shallow, temporary freshwater pool. The remarkable preservation of the biota, particularly the cyanobacteria, would suggest rapid silicification occurring either at or soon after death, or whilst the cells were still living, probably occurring in relatively cool water under slightly reducing conditions.

Castracollis is clearly a branchiopod, possessing the sternitic food groove, and characteristic system of appendages for locomotion and feeding, that are an apomorphy of the Branchiopoda (Walossek 1993, 1995). The non-preservation of internalised compound eyes and 4-cupped naupliar eyes in the *Castracollis* specimens is tantalising, since these characters are considered to be apomorphies of the Phyllopoda (embracing the Calmanostraca and Onychura) (Walossek 1993, 1995; Walossek & Müller 1998). Despite this, the new crustacean shows many features shared by the calmanostracan orders Notostraca and Kazacharthra, particularly the non-filtratory morphology of the anterior series of thoracopods, the flattening of the anterior of the thorax, and the multi-segmented trunk. However, the equivocal presence of a

cephalo-thoracic shield remains to be resolved. Although kazacharthrans possess reduced biramous second antcnnae, the presence in *Castracollis* of long biramous second antennae with symmetrical rami, and tergopleural scales on the thoracopod-bearing segments, has not been previously recorded for calmanostracans. Long, symmetrical biramous second antennae are, however, characteristic of the Onychura. Therefore we elect to place the animal in Calmanostraca *incertae sedis*. We believe *Castracollis* to have been predominantly a detritivore and probably also a facultative predator. It may well have had a short life cycle, similar to modern notostracans, developing and moulting rapidly in temporary freshwater ponds.

9. Acknowledgements

10. Appendix 1: Abbreviations used in the figures

?	Denotes uncertainty
a2	Antenna
abd	Abdominal segments
bas	basipod of Walossek (1993, 1999)
cts	Cephalo-thoracic shield
en	Endopod
en.s	Endopod spurs
end	Endite (end1 = proximal endite)
end.sp	'Median spine' of endite
ep	Epipodite
ex	Exopod
fu	Furca (fu1 = proximal element)
h	Head shield
la	Labrum
lcsp	Laterocaudal spines
md	Mandible
mo	Molar area of mandible
ms	'Meshwork spines' of Fryer (1988)
mx1	Maxillule
n	Anterior notch of head capsule
s	Seta(e)
tel	Telson
ths	Thoracic segments
th.aa	Anterior thoracic appendages
th.pa	Posterior thoracic appendages
tp	Tergopleura or 'lateral scale'
t.s	Telson spurs
vfg	Ventral food groove

AUGD12381: **a (holotype)** near complete partially enrolled specimen, Figs 8, 20C
b (paratype) tail and abdomen, Figs. 24A, 25B Unit 7

AUGD 12382: **a (paratype)** near complete specimen ∼ 8 mm long, Figs 6, 20A
b (paratype) tail and abdomen of a juvenile ∼ 1 mm long, Fig. 7

c (paratype) fragmented specimen, Figs 14B, 22A
d (paratype) near complete specimen with damaged head and thorax, Fig. 5 Unit 7

AUGD 12383: **(paratype)** single, near complete specimen with almost complete leg series, Figs 16A-C, 17, 20D Unit 6

AUGD 12384: **(paratype)** isolated anterior thoracic appendages, Fig. 21A Unit 7

AUGD 12385: **(paratype)** partial anterior thoracic leg appendage series, Fig 21B, C, 23 Unit 7

AUGD 12386: **(paratype)** transverse section through posterior thoracic segments, Fig. 19 Units 6–9 (slide perpendicular to bed)

AUGD 12387: splayed leg appendages of one individual + numerous fragmentary remains, Units 7–9 (slide perpendicular to bed)

AUGD 12388: **a (paratype)** head, anterior thorax and ?cephalo-thoracic shield, Figs 9, 10, 11C, 13C, D
b (paratype) tail and abdomen of small individual, Fig. 25A
c (paratype) small individual with head, part of thorax and abdomen, Fig. 13A Unit 7

AUGD 12389: **(paratype)** isolated second antenna, Fig. 12B + isolated thoracic leg appendages and fragmentary remains Unit 7

AUGD 12390: fragmentary remains, including partial abdomen and isolated second antenna Unit 7

AUGD 12391: **(paratype)** one near complete individual, Figs 15, 20B, 24B, 24C + numerous fragmentary remains Unit 7

AUGD 12392: aggregated fragmentary remains of numerous individuals Unit 6 (parallel slide to AUGD12393)

AUGD 12393: aggregated fragmentary remains of at least two individuals, possible cephalo-thoracic shield + numerous fragments Unit 6 (parallel slide to AUGD12392)

AUGD 12394: **(paratype)** single specimen showing posterior thoracic leg appendages and a number of anterior thoracic leg appendages, Fig. 22B Unit 8

AUGD 12395: fragmentary specimen with partial thoracic appendages, a small specimen with posterior thoracic leg appendage series, and a possible isolated cephalo-thoracic shield Unit 7

AUGD 12396: numerous individuals and fragmentary remains Unit 7 (source for AUGD12381)

AUGD 12397: **a (paratype)** head region with mouthparts and second antennae, Figs 13B, 14A
b (paratype) isolated second antenna, Fig. 11B Unit 8

AUGD 12398: abdomen and tail of an individual Unit 7
AUGD 12399: abdomen and tail of a single specimen (slide perpendicular to bed) Unit 6
AUGD 12400: isolated second antenna Units 6–7
AUGD 12401: **a (paratype)** small individual with tail, abdomen and posterior thorax, Fig. 18
b (paratype) fragmentary head shield with *in situ* second antenna, Figs 11A, 12A + fragmentary remains of larger individual (located next to AUGD12401a) Units 6–7

AUGD 12402: numerous fragmentary remains Unit 8
AUGD 12403: numerous fragmentary remains Units 6–9 (thin section perpendicular to bed)

AUGD 12404: polished slab perpendicular to bedding through chert block R44, Figs 2, 3 Units 1–9

AUGD 12405: standard petrographic thin-section of R44 Units 6–9 (thin section perpendicular to bed)

AUGD 12406: standard petrographic thin-section of R44 Units 4–5 (thin section perpendicular to bed)

AUGD 12407: standard petrographic thin-section of R44 Units 3–4 (thin section perpendicular to bed)

AUGD 12408: standard petrographic thin-section of R44 Units 1–3 (thin section perpendicular to bed)

11. Appendix 2: List of material used in this study

Unit numbers refer to those illustrated in Figure 2. All slides and thin sections are bedding parallel except where indicated.

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