THE 'CASTLECOMER FAUNA': A NEW *KONSERVAT-LAGERSTÄTTE* FROM THE UPPER CARBONIFEROUS OF IRELAND

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Abstract

A large number of boreholes have been drilled through Namurian and Westphalian strata in the Leinster Coalfield of south-eastern Ireland. Core from the Ardra and Hollypark boreholes has yielded an exceptionally preserved fauna, dominated by arthropods. Elements of this fauna have only previously been recorded from the Ardra borehole. The occurrence of the fauna in the Hollypark borehole extends the geographical area over which it is known to occur. The fauna occurs in the Moyadd Coal Formation at or near the level of the *Gastrioceras subcrenatum* marine band, the lowest unit of the Westphalian Series. The most common elements of the fauna are conchostracan branchiopods, many specimens of which display features such as the antennae, mandibles, claspers, trunk appendages, telson, and caudal furca. The anatomical detail preserved in these specimens exceeds that in other conchostracan branchiopods in the fossil record. The 'Castlecomer fauna' clearly merits the term *Konservat-Lagerstatte*.

Introduction: the role of *Konservat-Lagerstätten* in palaeobiology

The fossil record is biased: it is dominated by the most recalcitrant tissues of organisms and plants, often colloquially referred to as the 'hard parts'. The concept of *Konservat-Lagerstatten* (Seilacher 1970; Seilacher *et al.* 1985) includes those exceptional fossil biotas that preserve soft-bodied, or lightly sclerotised, organisms. Such organisms are an important, often the dominant, component of many extant communities *Konservat-Lagerstatten* therefore provide a more complete record of the diversity and palaeoecology of any palaeocommunity than does the 'normal' shelly fossil record. Conway Morris (1986) calculated that up to 86% of genera and perhaps as many as 98% of individuals in the Burgess Shale would not have been preserved in a 'normal' shelly assemblage of Middle Cambrian age. *Konservat-Lagerstatten* may also reveal the morphology of the soft and lightly sclerotised tissues of extinct animals known otherwise as mineralised skeletons. *Konservat-Lagerstätten* therefore assume an importance in palaeobiology disproportionate to the number of examples known and the absolute numbers of fossils that they contain.

Here we describe the biota of the 'Castlecomer fauna', a *Konservat-Lagerstatte*

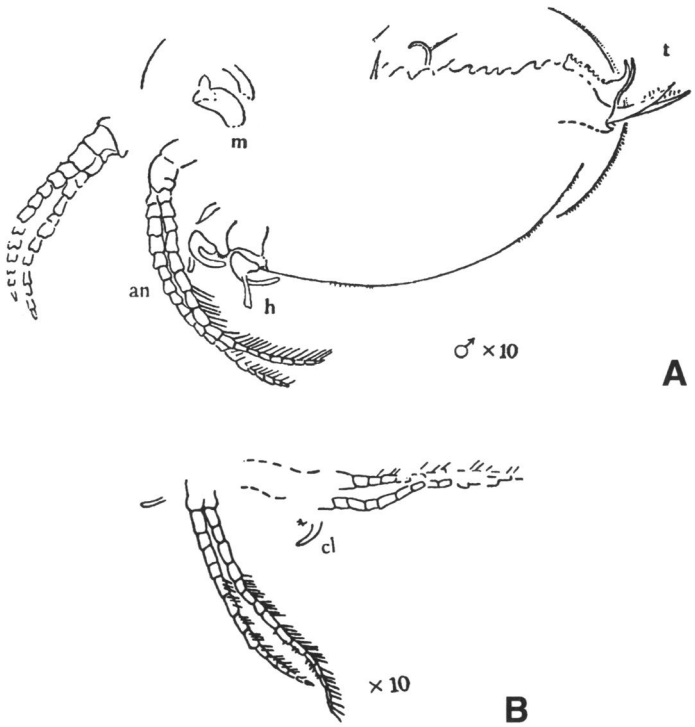


Fig. 1—Interpretative line drawings of specimens of *Limnestheria ardra* Wright, 1920 by Wright (1920). (A) Illustration of holotype specimen (NMING:F14724) by Wright (1920, pl. XXIV, fig. 1). Compare with photographic illustrations in Fig. 4. (B) Specimen (In21096) illustrated in Wright 1920, pl. XXIV, figs 2 and 2a. Compare with photographic illustration in Fig. 5B. Scales indicated are those of Wright (1920).

from the Upper Carboniferous of Ireland. This fauna is dominated by exceptionally preserved arthropods, especially conchostracan branchiopods, and it also includes a number of other, more enigmatic, organisms. Conchostracan branchiopods are relatively common in non-marine lithofacies since the Devonian. In all but a few cases, however, only the bivalved carapace is preserved. Conchostracan branchiopods that preserve anatomical features in addition to the carapace have been recorded as minor components of other *Konservat-Lagerstätten*, including the Triassic (Anisian) Grès à Voltzia fauna from the Vosges of north-eastern France (Gall 1971, 41, pl. IX, fig. 4) and the Kalkschieferzone (uppermost Meride Limestone: Late Ladinian, Middle Triassic) of northern Italy and southern Switzerland (Tintori 1990; Furrer 1995). In neither of these examples does the quality of preservation match that in the Castlecomer fauna. Even though the appendages of arthropods have been recorded from numerous *Konservat-Lagerstätten*, in none of these is the fauna dominated by examples of conchostracan branchiopods.

Here the first photographic illustrations of the fauna are provided; the only previous illustrations are the interpretative line drawings of Wright (1920, figs 1–5, pls XXIV and XXV) (Fig. 1). It is hoped that this contribution will promote the search for similar material in Ireland and elsewhere. This study clearly illustrates the international importance of the collections of the Geological Survey of Ireland.

Conchostracan branchiopods: taxonomy, anatomy, biology and ecology

Taxonomy

Conchostracan branchiopods ('clam shrimps') are small bivalved crustaceans

taxonomically aligned with anostracans ('fairy shrimps'), notostracans ('tadpole shrimps'), cladocerans ('water fleas'), and the extinct lipostracans (Scourfield 1926; 1940) and kazacharthrans (Novojilov 1957; 1959).

The twofold division of conchostracans into the Laevicaudata and Spinicaudata (Linder 1945) is generally accepted. Schram (1986, 385) regarded these two as suborders of the Order Conchostraca; however, Fryer (1987, 368) elevated each to ordinal level and regarded the association of the two as a single entity as 'at least suspect'. In Fryer's scheme, the name Conchostraca is abandoned as a taxonomic unit; it is still useful as a vernacular, descriptive, term, and is employed herein as such. The complex history of the taxonomic classification of branchiopods is summarised by Fryer (1987, 357–65, table 1). The significant anatomical differences between the Laevicaudata and Spinicaudata are summarised in table 2 of Fryer 1987.

Anatomy

The short, laterally compressed conchostracan body is enclosed in a bivalved carapace (Fig. 2). Adults range from 1.7mm to 27mm in length. Externally, the carapace may display concentric growth lines, owing to retention of carapace at moult, as well as other ornamentation. The carapace is attached to the body antero-dorsally by a muscle-containing pedicel ('attachment ligament' of some authors) and by a pair of adductor muscles.

The body is subdivided into a head (cephalon) and a trunk (post-cephalic body). The front of the head may be produced ventrally into a rostrum. The sessile compound eyes are usually closely set; in some taxa, they are fused to form a single large eye. The antennules (first antennae) are uniramous and comprised of a variable number of segments. The antennae (second antennae) are large, biramous, and segmented. They bear setae, which vary in length and number per segment between taxa. The antennae have a variety of uses, most notably natatory; they can also be used for 'walking', burrowing, and, in males, seizing the female carapace during mating. Maxillules and maxillae are reduced; mandibles are of grinding, rolling type, either articulating dorsally on a protuberance (in the Spinicaudata) or not (in the Laevicaudata). The post-cephalic body consists of between 10 and 32 somites, each bearing a pair of foliaceous limbs. The dorsal surfaces of the posteriormost somites may be drawn out into a series of spinelike projections, or denticles. In the Spinicaudata the telson is massive, armed dorsally with spines (the most prominent of which are the posteriormost anal spines), and terminates in a caudal furca. In contrast, in the Laevicaudata the telson is feebly developed, armed only with spinules, and lacks a caudal furca. In males, at least the first pair of post-cephalic appendages are modified into claspers; one or both of the second pair may also be so modified. The claspers are used for

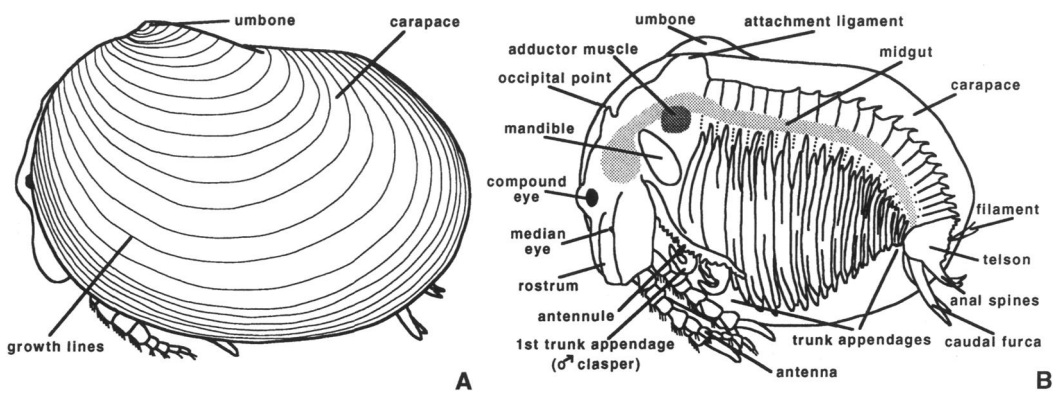


Fig. 2—Anatomy of the extant conchostracan branchiopod *Caenestheriella*: (A) external, lateral, view of bivalved carapace; (B) left valve removed. (After McLaughlin 1980, figs 7A and 7B.)

attachment to females during reproduction. In females modifications for egg-carrying occur on the ninth to eleventh pairs of post-cephalic appendages.

Ecology

Extant conchostracans most commonly occur in temporary, inland, water bodies, the pH of which is neutral to slightly alkaline; optimum water temperature is between 13°C and 25°C; however, they have been recorded from a variety of non-marine and marginal marine environments (see summary in Webb 1979, 260) spanning a range of water temperatures (1–41°C), pH conditions, and fresh to slightly saline (6‰) water.

Populations are usually of high density but low diversity, often monospecific. Conchostracans are non-selective algal and detrital filter feeders. One species of *Cyclestheria* is ovoviviparus; most conchostracans lay thick-shelled 'resting' eggs which can withstand environmental extremes, including desiccation and freezing.

Fossil record

Unequivocal conchostracans first appear in the earliest Devonian, and over 80 fossil genera are known. There was a major diversification during the Carboniferous (resulting in a doubling of the number of families), and almost 90% of fossil taxa date from Namurian or younger rocks. Living species number about 200, divided among four extant families; a further six families are recognised from the fossil record (Briggs *et al.* 1993, 335). Most extant species of conchostracans occur in non-marine environments. Fossil conchostracans are therefore often cited as indicative of freshwater conditions. Co-occurrence with unequivocal marine fossils, including trilobites, brachiopods, and crinoids (Carboniferous, Germany: Kummerow 1939) and ammonoids (Triassic, Russia: Popov 1954), has been recorded. It is possible that the conchostracans are allochthonous components of such faunal assemblages; however, it has been postulated that a shift from marine to freshwater environments occurred during the geological history of the group (Tasch 1969, 147–9). The vast majority of fossil occurrences yield only the relatively thick valves of the carapace.

The Castlecomer fauna: geographical and stratigraphical setting

The Leinster Coalfield is situated in the north-eastern part of County Kilkenny, the south-eastern part of County Laois and the north-west part of County Carlow (Fig. 3); the regional geology was reviewed by Nevill (1956), Eagar (1964) and Higgs (1986).

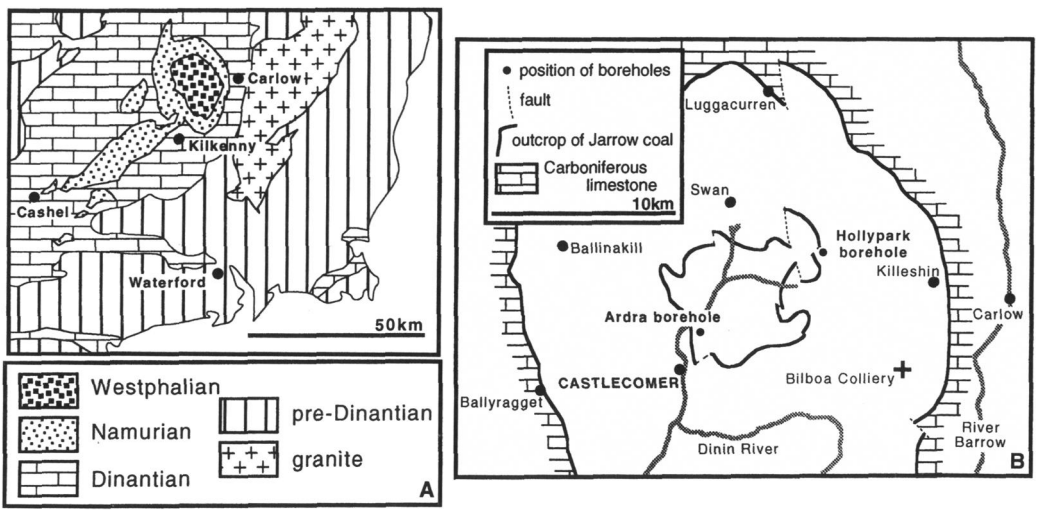


Fig. 3—Location maps of (A) the Leinster Coalfield of south-eastern Ireland and (B) the area around Castlecomer, showing position of the Ardra and Hollypark boreholes. (After Eagar 1964, fig. 1.)

Numerous boreholes have been drilled through the late Namurian and early Westphalian strata of the Leinster Coalfield These include eighteen deep boreholes that were sunk in the central and western parts of the coalfield between 1902 and 1914; the majority, if not all, of these appear to have been at the instruction of, or on behalf of, R.H. Prior Wandesforde. An extensive drilling programme was conducted by the Department of Industry and Commerce between 1959 and 1963; most of these boreholes terminated at levels close to the base of the Westphalian succession (Higgs 1986). The cores recovered from many of these boreholes have been archived by the Geological Survey of Ireland Importantly, they have been discovered to contain an exceptionally preserved, arthropod-dominated fauna. To date, specimens have been recovered from core of two boreholes: the 'Ardra borehole' and the 'Hollypark borehole'. Prior to this study the fauna had only been recorded from the Ardra borehole (Wright 1920). In both boreholes the fauna is dominated by exceptionally preserved examples of conchostracan branchiopods. Representative examples of the fauna from both boreholes are illustrated in Figs 4 to 8.

The Ardra borehole was sunk 'by Mr R. H. Prior Wandesforde at Ardra, a mile and a half N. 30° E. from the crossroads in Castlecomer' (Wright 1920, 192). There is confusion in the geological literature as to the precise age of the strata from which the fauna was recovered Wright (1920, 193) recorded the fossils as having been recovered from 'about eight or nine feet above . . . [the] . . . upper layer' of the 'fleck-rock'. The 'fleck rock' is now recognised as the *Gastrioceras subcrenatum* marine band, which is accepted as the lowest unit of the Westphalian Series, Upper Subsystem of the Carboniferous System However, Eagar (1964, 363, fig. 3) preferred to correlate the interval from which the conchostracans were recovered with the *Gastrioceras subcrenatum* marine band itself, implying a basal Westphalian age. The Geological Survey of Ireland borehole record for the 'Castlecomer No. 8 Bore. Ardra' does not help to resolve this subtle discrepancy. At a depth of *c* 830 feet [249m], 'several species of *Estheria*—probably representing Marine Band' are recorded; however, at depths of between *c.* 840 feet [252m] and 860 feet [258m] notes accompanying the borehole record describe the lithology as 'flecked in places like fleck rock', 'resembling fleck rock' and 'flecked shale'.

The fauna from the 'Hollypark borehole' has been recovered from a series of core slabs inscribed with '*c.* 449′/1, 2, etc'. The cumulative thickness of slabs with the prefix '449' exceeds a foot; it is probable that the slabs were recovered from a series of intervals at or around a depth of 449 feet [135m] in the borehole. Geological Survey of Ireland archives record the fossiliferous slabs as equivalent to the *Gastrioceras subcrenatum* marine band.

In the Leinster Coalfield the lithostratigraphical unit spanning the latest Namurian to earliest Westphalian interval is the Moyadd Coal Formation (Higgs 1986). The occurrence of the fauna in the Hollypark borehole extends the geographical area over which it is known to occur. Further, it suggests that core from other boreholes, and outcrop of the Moyadd Coal Formation in the Castlecomer area, could yield important additional material.

Previous research and new material

Previous research on the Castlecomer fauna is restricted to a brief description of the stratigraphical position, and anatomy, of some of the examples of conchostracan branchiopods from the Ardra borehole (Wright 1920); neither their preservation nor evolutionary significance were considered adequately. Secondly, there have been significant improvements in our understanding of the palaeobiology and taphonomy of arthropods in the intervening period. A re-examination is therefore warranted.

The taxon *Limnestheria ardra* Wright, 1920 was erected to accommodate the specimens examined by Wright (1920); it is the earliest known representative of the Family Limnadiidae Baird, 1849, which includes many living species (Briggs *et al.* 1993). Wright

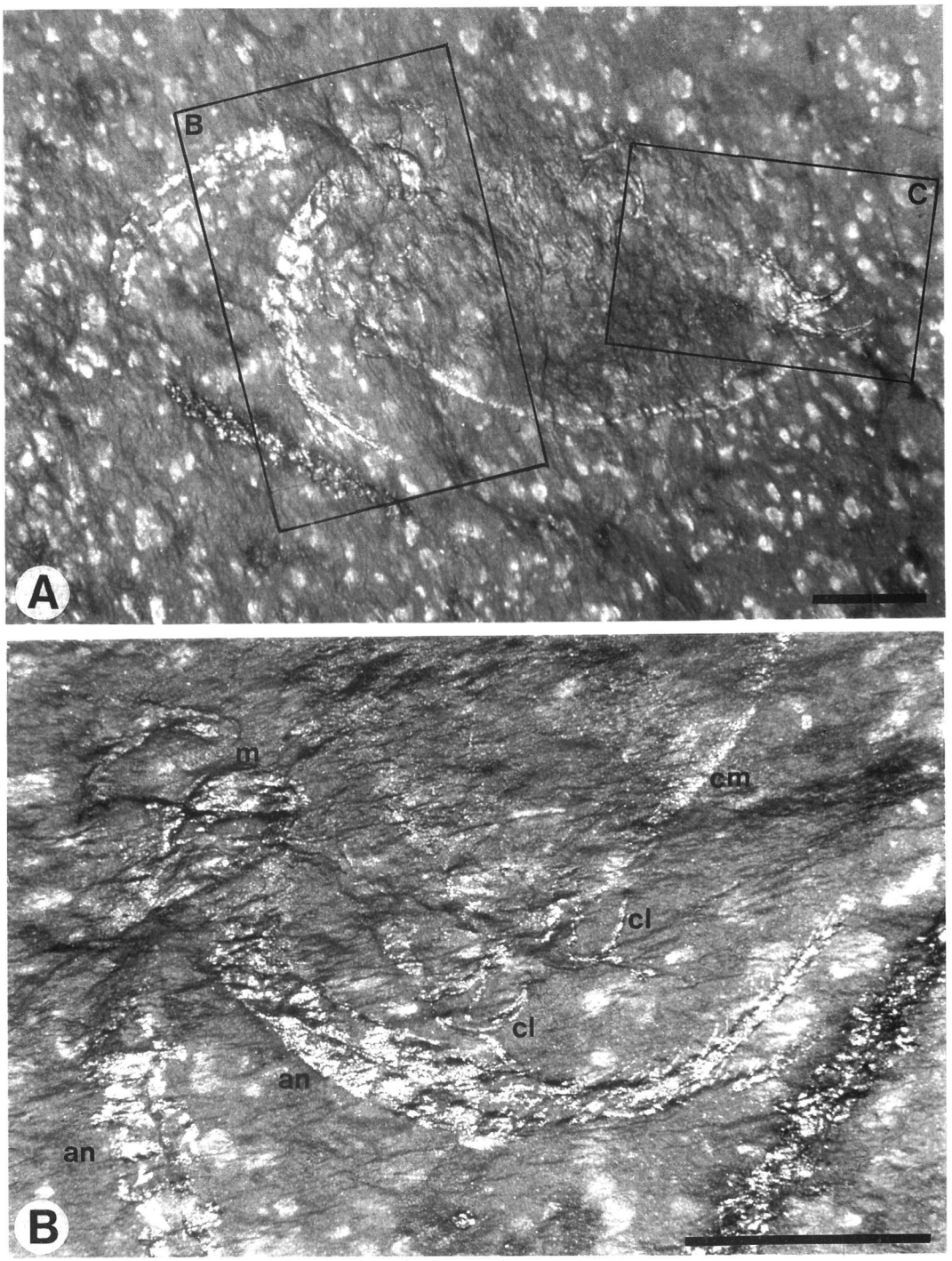
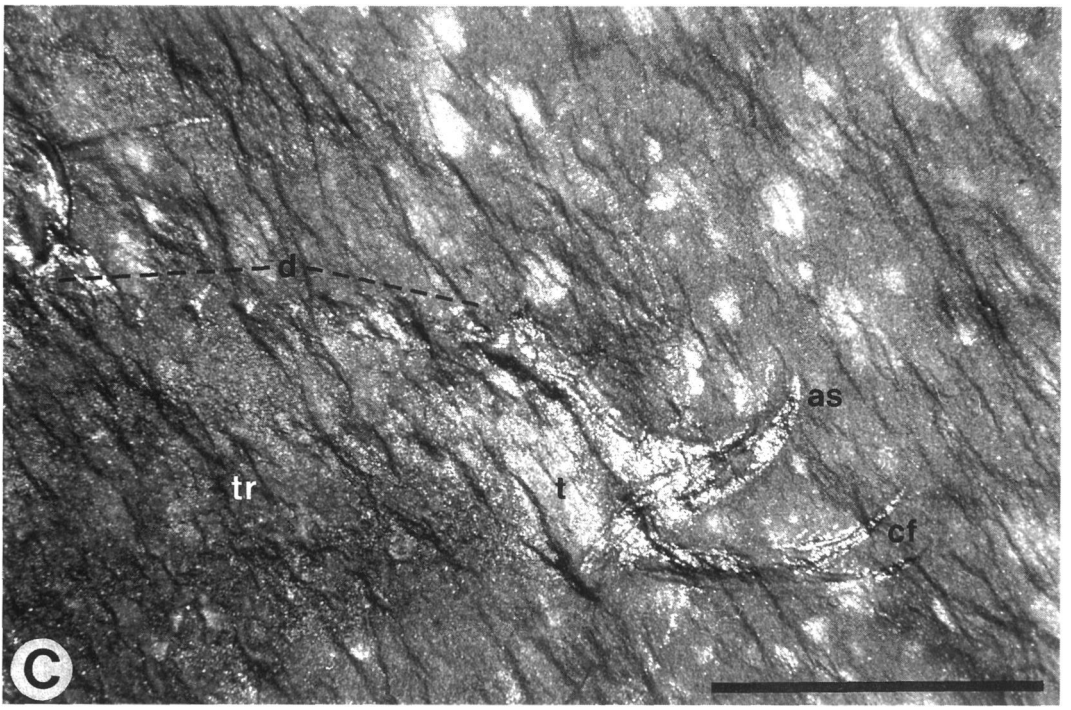


Fig. 4—Conchostracan branchiopods from the Ardra borehole I. Holotype of *Limnestheria ardra* Wright, 1920. (A) Whole specimen (NMING:F14724) in lateral view; areas outlined are enlarged in parts B and C. (B) Anterior of specimen displaying well-preserved segmented, biramous, antennae with setae extending from their lateral margins (an), mandibles (m), two claspers (cl) and the margin of the carapace (cm). (C) Posterior of specimen illustrating telson (t) with anal spines (as) and associated with it a caudal furca (cf); note the series of spines on the dorsal margin of the caudal furca. Dorsal margin of the trunk defined by the series of denticles (d); the trunk (tr) itself possibly displays segmentation along its length. Specimen covered in Canada balsam and glass coverslip. Scale bars = 1mm.



(1920, figs 1–5, pls XXIV and XXV) provided simplified, interpretative, line drawings of some of these specimens. Tasch (1969, R148, figs 48.6a and b) reproduced Wright's fig. 4 and pl. XXIV, fig. 1, respectively. Although Wright (1920, 192) noted that the 'fossils [used in her study] came from a depth of 830 feet', the list of specimens on pp 200–2 (*ibid.*) cites depths of between 827 and 834 feet; it appears that the assemblage she used is a composite derived from at least four discrete horizons. These specimens are currently held by the Geological Survey of Ireland (prefix GSI), the National Museum of Ireland (NMING:F14724 and F14725/1–4), and the Natural History Museum, London (In21096–In21102). Individual specimens have been coated in Canada balsam and covered with glass coverslips (Wright 1920, 192) (Figs 4, 5 and 6A). This precludes examination other than via optical microscope under incident light.

Fortunately, within the Geological Society of Ireland collections are numerous other slabs from the same stratigraphical interval of the Ardra borehole, both with and without accession numbers. Many of these have scratched on them the prefix 'Ard/' followed by three figures, which can confidently be interpreted as representing the depth at which they occurred. Some of these pieces have sawn edges, as do the slabs containing the specimens studied by Wright (1920). Careful examination of over 100 such slabs has revealed that many have examples of exceptionally preserved conchostracan branchiopods on their surfaces; other, more rare, arthropods and more enigmatic fossils also occur. Often several specimens are preserved on a single piece. Our finds have included the counterparts of several of the specimens studied by Wright (1920), including the holotype of *Limnestheria ardra*. The conchostracans typically occur on planes devoid of other organic remains or in association with scattered plant fragments. The surfaces of other planes of splitting within this interval display numerous examples of the carapaces of conchostracans or dense accumulations of fragmented plant debris. On such surfaces conchostracans with their appendages preserved are absent or rare.

A second faunal assemblage has been recovered from the Hollypark borehole.

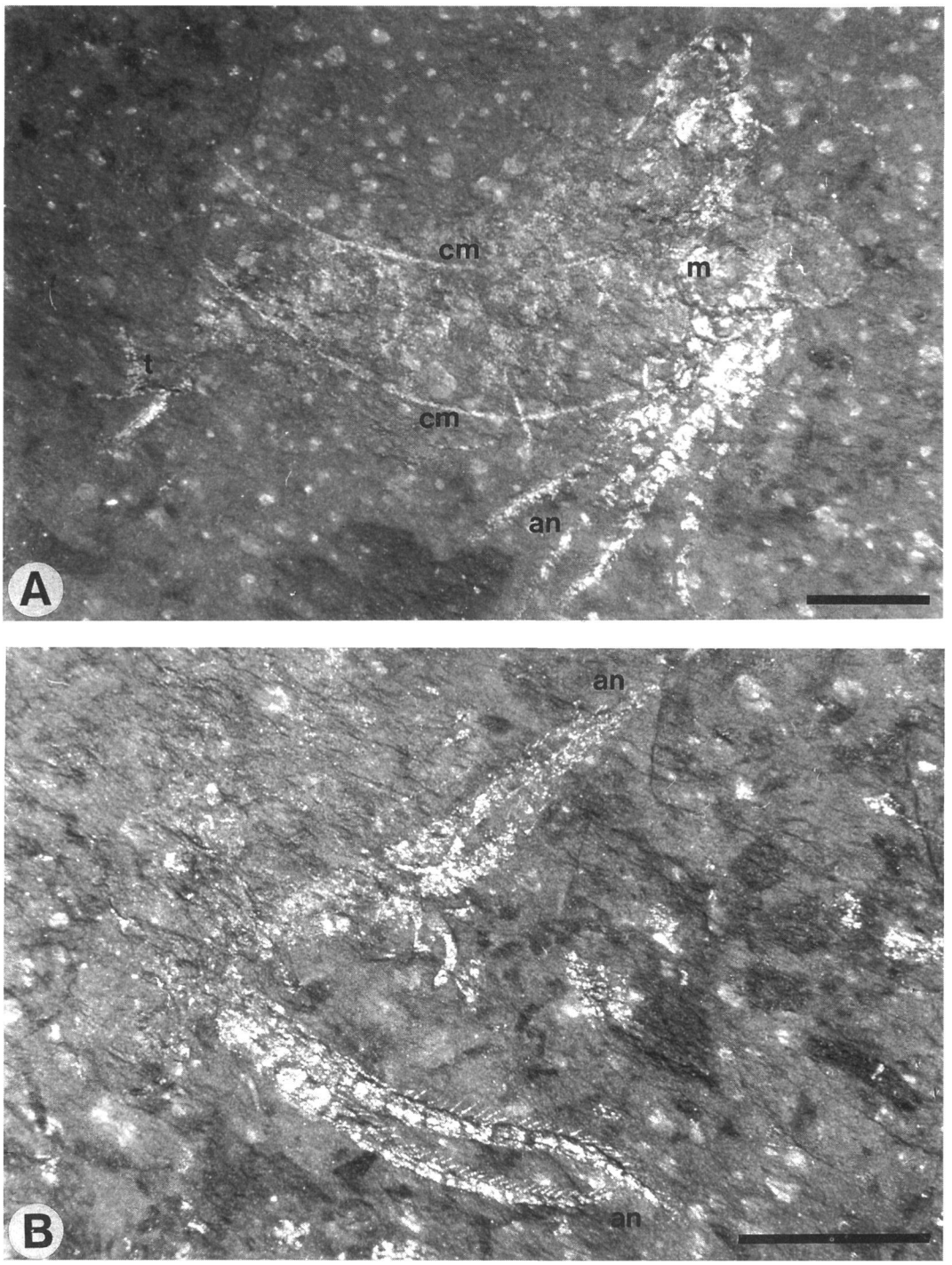


Fig. 5—Conchostracan branchiopods from the Ardra borehole II. (A) Whole specimen (GSI:F00893) in lateral view, displaying antennae (an), mandibles (m), telson (t) and the margins of the bivalved carapace (cm). (B) Segmented, biramous, antennae (In21096), the lower pair of which clearly display setae extending from their lateral margins. Note that the upper pair of antennae lie normal to the well-developed cleavage, while the lower pair of antennae lie parallel or slightly oblique to cleavage. This may explain the variation in the quality of preservation between the two pairs. Specimens covered in Canada balsam and glass coverslip. Scale bars = 1mm.

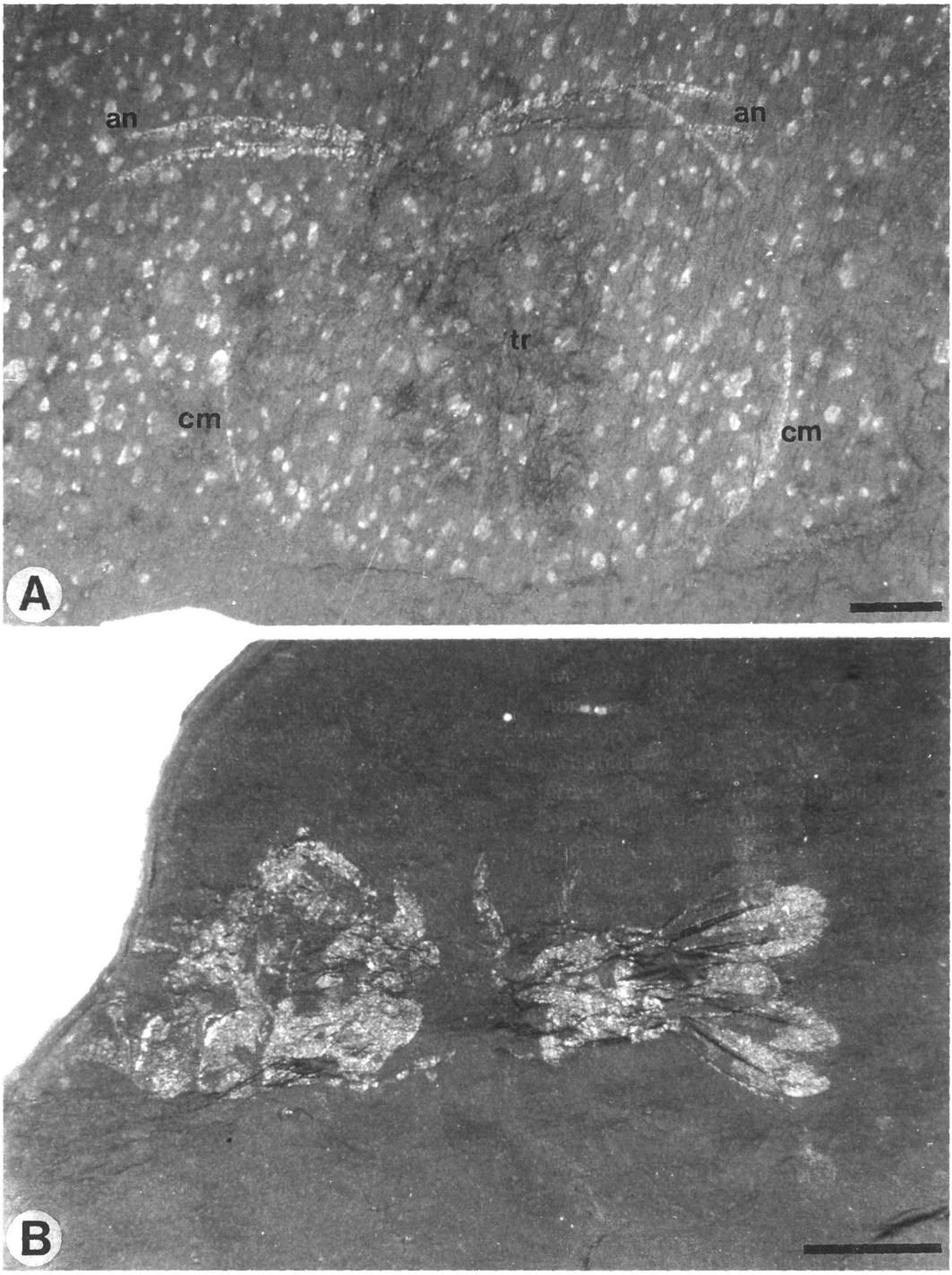


Fig. 6—(A) Whole specimen (GSI:F00897) of conchostracan branchiopod from the Ardra borehole in dorso-ventral view, displaying antennae (an), the margins of the bivalved carapace (cm) and the trunk (tr), defined by the darker-coloured area; contrast this style of preservation with that of the trunk in the specimens in Figs 7A and 7B. (B) As yet undescribed malacostracan crustacean (GSI:F00499) from the Hollypark borehole. Specimens either covered in Canada balsam and glass coverslip (A) or photographed under water and glass coverslip (B). Scale bars = 1mm.

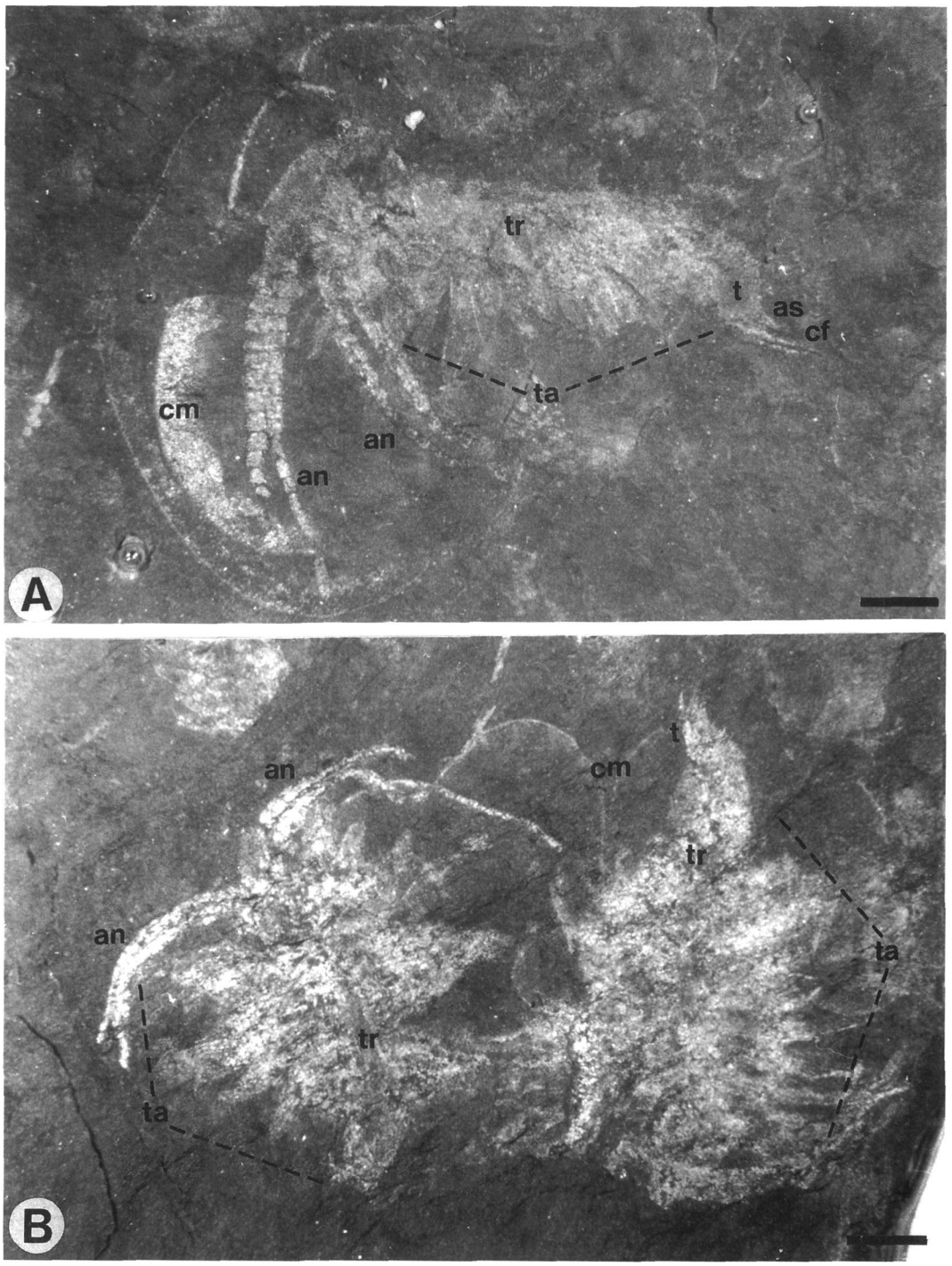


Fig. 7—Conchostracan branchiopods from the Hollypark borehole I. (A) and (B): specimens in lateral view (A and right-hand specimen in B) and dorso-ventral view (left-hand specimen in B), displaying antennae (an), the margins of the bivalved carapace (cm), the telson (t) with anal spines (as) and associated with it a caudal furca (cf) and a series of trunk appendages (ta) on either the ventral margin of the trunk (tr) (A) or displaced to either side of the trunk (B). Contrast the style of preservation of the trunk in these specimens with that of the trunk of the specimen in Fig. 6A. Note also less contortion of the trunk appendages in these specimens than those from the Ardra borehole. Specimens photographed under water and glass coverslip. Scale bars = 1mm. Specimen numbers: (A) GSI:F03486; (B) GSI:F00498.

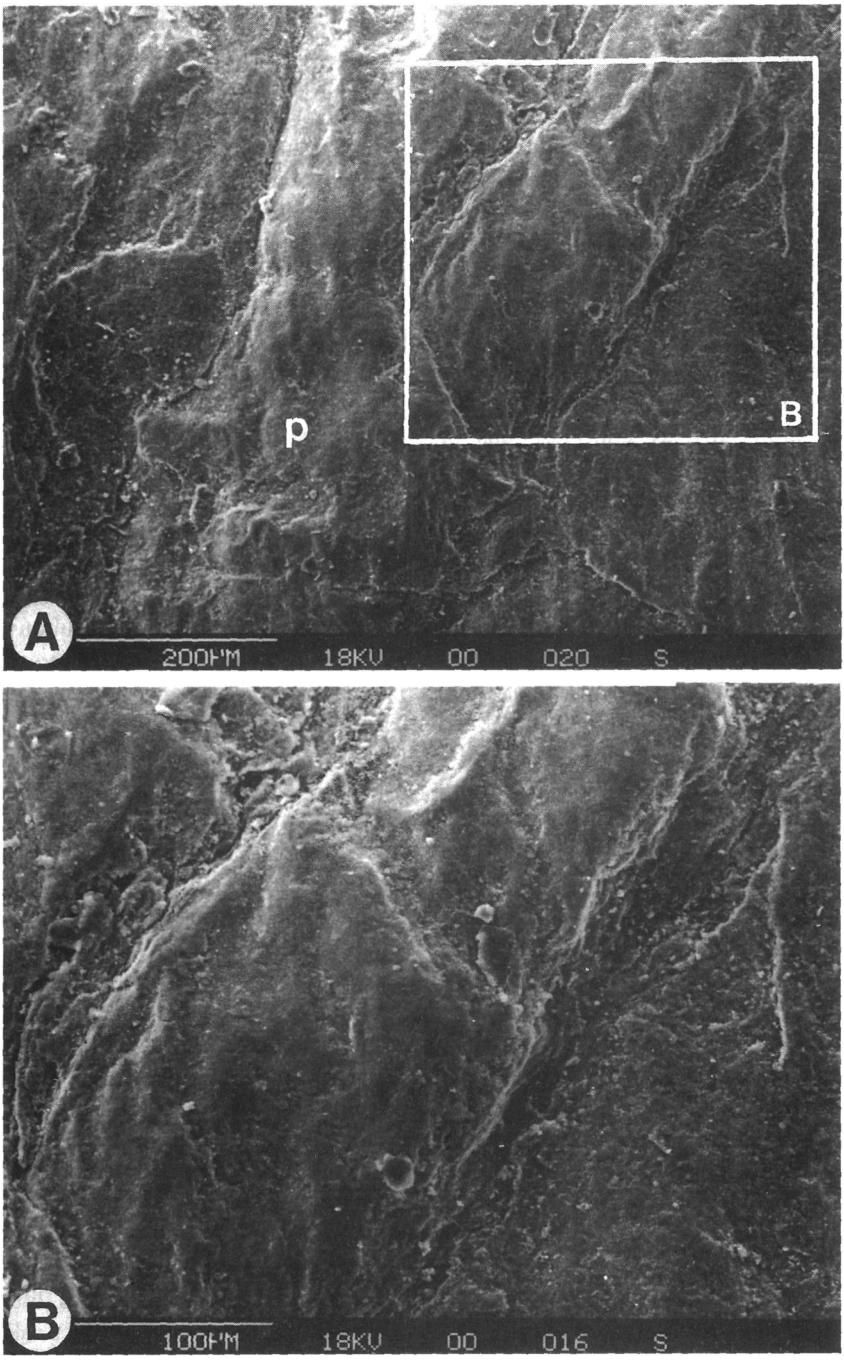


Fig. 8—*SEM* photograph of the basal part of a biramous antenna of a conchostracan branchiopod (GSI:F00197, part a) from the Ardra borehole: note the protopod (p) and clearly defined segmentation of the antennae.

Careful examination of over 30 slabs with the original numbering 'b6/449' has revealed numerous examples of conchostracans in which anatomical features other than the carapace are present (Fig. 7). Other, as yet unstudied, arthropods include a series of malacostracan crustaceans (Fig. 6B). Given the small surface area provided by the 75mm diameter of the core from the Hollypark borehole, the density of exceptionally preserved conchostracans on some planes of splitting is remarkable; up to twelve specimens can occur in an area of less than 4cm^2. Other planes of splitting display concentrations of plant debris.

In both boreholes, the sedimentology of the interval from which the fauna has been collected is similar. The dominant lithology in each is siltstone; the cores separate into 5–10mm-thick slabs along 1–5mm-thick, finer-grained, planes of splitting. These planes of splitting are approximately parallel to bedding; the vast majority of the fauna has been recovered from their surfaces. In the Ardra borehole these planes are black in colour and extensively cleaved; the effect of this cleavage on some of the specimens is typified by the specimen in Fig. 5B. In the Hollypark borehole, these planes of splitting are dark grey or medium grey in colour; there is markedly less development of a cleavage fabric. The exact nature of the depositional facies in each borehole has yet to be elucidated.

In both boreholes, the majority of specimens are observed in lateral aspect. However, there is a high degree of variation in the orientation of specimens with respect to the approximately bedding-parallel planes of splitting (compare, for example, the orientation of the two specimens in Fig. 7B).

Conchostracan branchiopods in the Castlecomer fauna

Populations of extant conchostracan branchiopods are typically monospecific; however, co-occurrence of two or more species or, especially, genera within a population has been documented (see summary in Webb 1979, 261–2). Differentiation of species of conchostracan branchiopods is dependent on subtle morphological differences. A thorough examination of all the fossil material has not yet been completed. It therefore cannot be assumed that the assemblages, even those from the same horizon of the same borehole, are monospecific. Accordingly, the following descriptions are restricted to anatomical details typical of conchostracans in general. This serves to illustrate the exquisite detail preserved; comparison of individual specimens with the anatomy of an extant conchostracan branchiopod (Fig. 2) reinforces this point. The anatomical features most commonly preserved are illustrated in Figs 4–8.

Cephalon

The *mandibles* (Figs 4B and 5A) are clearly evident in numerous specimens. The stout, segmented, *antennae* are ubiquitous; in many examples, their biramous nature, extending from a protopod, is clearly displayed (Fig. 8). The antennae can bear relatively long setae (Figs 4B and 5B).

Post-cephalic body

The outline of the *trunk* is defined in one of two contrasting manners: (a) as a darker-coloured area on the surface of the specimen, contrasting with the highly reflective minerals in which the other anatomical features of the specimen are preserved, or (b) by mineralisation similar to that in which the other anatomical features of the specimen are preserved. The former is more evident in specimens from the Ardra borehole, especially those that are preserved in dorso-ventral, rather than lateral, orientation (Fig. 6A). In contrast, specimens from the Hollypark borehole more usually exhibit the latter style of preservation (Figs 7A and 7B). In both cases, little detail of the trunk can usually be resolved, although the holotype of *Limnestheria ardra* displays possible segmentation of the trunk towards the posterior, in the region underlying the series of *denticles* on its dorsal surface (Fig. 4C).

Claspers are evident in numerous specimens, including the holotype of *Limnestheria ardra* (Fig. 4B). The *trunk appendages* are poorly preserved in most of the

specimens from the Ardra borehole; further, they are often noticeably displaced from their position during life on the dorsal side of the animal. In contrast, the trunk appendages are evident in many specimens from the Hollypark borehole (Figs 6A and 6B) The *telson* is nearly always evident; associated with it is a prominent *caudal furca* (Figs 4C, 5A, 7A and 7B). In life, the dorsal surface of the telson appears to be posterior because of the flexure of the trunk. This orientation is usually retained in specimens preserved in lateral aspect. The *anal spines*, the most prominent of the series of spines that can be developed on the dorsal surface of the telson, are usually evident; in some specimens other shorter spines are also evident. Short spines can also be seen on the dorsal surface of the caudal furca in the holotype of *Limnestheria ardra* (Fig. 4C).

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