

SPECIAL PAPERS IN PALAEOLOGY · 62

**Exceptionally preserved
conchostracans and other**

THE PALAEOLOGICAL ASSOCIATION

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SPECIAL PAPERS IN PALAEOLOGY NO. 62

EXCEPTIONALLY PRESERVED CONCHOSTRACANS
AND OTHER CRUSTACEANS FROM THE UPPER
CARBONIFEROUS OF IRELAND

BY

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with 37 text-figures

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ABSTRACT. The Castlecomer fauna from the Leinster Coalfield in south-eastern Ireland is an arthropod-dominated *Konservat-Lagerstätte* of basal or early Westphalian (Late Carboniferous) age. The fauna has been recovered from finely laminated siltstones and mudstones in core from the Ardra and Hollypark boreholes. Spinicaudatan ('conchostracan') branchiopods are the most abundant exceptionally preserved faunal element: *Limnesteria ardra* Wright occurs in the Ardra core, and *Limnesteria gracilis* sp. nov. in the Hollypark core. The carapace valves of other conchostracans, a single pair of ostracod valves and an elongate, ?setose, problematicum occur in association with *L. ardra*. A more diverse ostracod fauna (some with appendages preserved) occurs with *L. gracilis* together with single specimens of an unidentified eumalacostracan, a probable syncarid and *Waterstonella* sp.

Limnesteria is confirmed as the earliest example of the superfamily Limnadioidea Baird and the family Limnadiidae Baird. The first two pairs of trunk appendages were modified as claspers in the male of *L. ardra*, not solely the first pair as in most previous interpretations. The claspers were prone to displacement from life position during transport and burial; during post-burial decay the claspers rotated and collapsed into more stable attitudes than those at which they were deposited. The strong anatomical similarities between *Limnesteria* and extant spinicaudatans confirm that their external morphology has remained essentially unmodified since at least the Late Carboniferous.

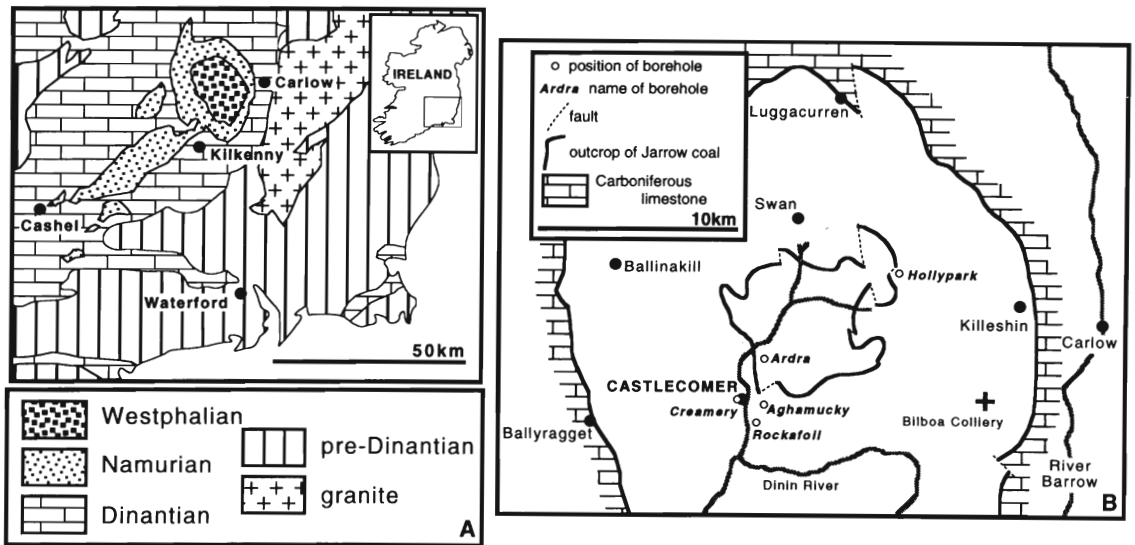
THE fossil record is biased. It is dominated by the most recalcitrant tissues of animals and plants, many of which are biomineralized. 'Soft parts' are represented more rarely as their preservation requires exceptional sedimentological and diagenetic conditions (Allison 1990).

The term 'soft parts' is poorly defined and encompasses a variety of tissue types. Some authors use the term as a collective descriptor for all tissues that are not biomineralized (e.g. Briggs and Kear 1993), whereas Bergström (1990, p. 277) preferred a distinction between 'unmineralized skeletons and true soft parts'. For arthropods, a convenient distinction can be made between structural organic tissues (e.g. cuticle) and more labile tissues such as muscle. As a heavily biomineralized exoskeleton is a feature of only a small proportion of arthropods (e.g. some trilobites, some crustaceans, millipedes), the extensive fossil record of the group (see Briggs and Clarkson 1989; Shear and Kukulova-Peck 1990) reflects the resistance of organic structural tissues to decay. Arthropod cuticle is a complex of chitin and proteins. These components are themselves less decay-resistant than other biomacromolecules, particularly those in vascular plants and algae (Tegelaar *et al.* 1989). The preservational potential of arthropod cuticle, however, may be enhanced by tanning or sclerotization, and by its susceptibility to diagenetic alteration to stable macromolecules (Stankiewicz *et al.* 1997). In contrast with cuticle, more labile tissues such as muscle degrade rapidly. As a result, their preservation necessitates replication by authigenic minerals at an early stage. Replication in calcium phosphate is most common and provides the highest fidelity, although other minerals may be involved (e.g. Gabbott *et al.* 1995).

The concept of *Konservat-Lagerstätten* (Seilacher 1970; Seilacher *et al.* 1985) includes those exceptional fossil biotas that preserve soft-bodied, or lightly sclerotized, organisms. Such organisms are an important, often the dominant, component of many extant communities (see Allison and Briggs 1991, pp. 120–121, table 6.1). *Konservat-Lagerstätten* therefore provide a more complete record of the diversity and palaeoecology of any palaeocommunity than does the 'normal' shelly fossil record (Briggs 1991).

The Castlecomer fauna (Orr *et al.* 1996) is a *Konservat-Lagerstätte* that occurs in early Late Carboniferous strata in the Leinster Coalfield in south-eastern Ireland (Text-fig. 1A). The fauna has been recovered from core from the Ardra and Hollypark boreholes (Text-fig. 1B). It is dominated by arthropods, especially conchostracan branchiopods, and also includes a number of other, more enigmatic, fossils. Musculature and internal organs (with the exception of the gut) are not preserved; however, the non-biomineralized tissues preserved permit detailed reconstructions of the external morphology of the taxa. Fryer (1985) noted that while the fossil record of the Branchiopoda confirms their long geological history, it had not produced much material that is helpful to the functional morphologist; he exemplified this statement by commenting (p. 103) that 'few of the many conchostracan fossils reveal appendages'. The conchostracans from the Castlecomer fauna are the best preserved of the few fossil taxa in which anatomical features other than the carapace are known.

One of the conchostracan taxa, *Limnesteria ardra*, was originally described by Wright (1920). Its restudy is warranted because of subsequent advances in our understanding of the systematics and



TEXT-FIG. 1. Simplified geological maps of A, south-eastern Ireland; inset shows location, and B, the Leinster Coalfield, showing location of boreholes referred to in the text.

taphonomy of arthropods. Wright's (1920) conclusion that in males of *L. ardra* only the first pair of trunk appendages was modified as claspers has been widely accepted (e.g. Raymond 1946; Tasch 1969); only Mattox (1957) has questioned it. This conclusion is at odds with the assignment of the taxon, albeit questionably, to the family Limnadiidae Baird, 1849 (e.g. Tasch 1969; Briggs *et al.* 1993): in males of all extant genera of this family the first two pairs of trunk appendages are modified as claspers. The number of trunk appendages modified as claspers has been employed as an important character in phylogenetic analyses of the 'bivalved' Branchiopoda (e.g. Olesen *et al.* 1996, text-fig. 15). The number, and morphology, of the claspers of *L. ardra* is therefore potentially of evolutionary and phylogenetic significance.

The remainder of the biota has not been studied previously, and the taxa are described here. This paper will be complemented by a second analysing their taphonomy.

CONCHOSTRACAN BRANCHIOPODS

Anatomy and taxonomy

Conchostracan branchiopods (clam shrimps) are small, bivalved crustaceans taxonomically aligned with anostracans (fairy shrimps), notostracans (brine shrimps), 'cladocerans' (water fleas), and the extinct lipostracans (Scourfield 1926, 1940) and kazacharthrans (Novojilov 1957, 1959; McKenzie *et al.* 1991).

The anatomy of conchostracan branchiopods was the subject of pioneering studies by Sars (1896), Calman (1909) and Linder (1945), and of more modern treatments by Tasch (1969), McLaughlin (1980), Belk (1982), Schram (1986) and Martin (1992). The two-fold division of conchostracans into Laevicaudata and Spinicaudata was first recognized (as 'tribes') by Linder (1945, p. 16). These taxa have been retained as suborders by most subsequent authors and are included in the most modern detailed taxonomic treatment of the Conchostraca (Tasch 1969). Later alternative taxonomic schemes (e.g. Kobayashi 1972) have not met with widespread acceptance. Zhang *et al.* (1987, 1990) used a three-fold subordinal division of the Conchostraca: Laevicaudata, Spinicaudata and Leaiina Kobayashi, 1972. Most authors, however, include the last within the Spinicaudata.

The taxonomic status assigned to the divisions Laevicaudata and Spinicaudata and to the higher categories that include them (e.g. Branchiopoda Latreille, 1817; Phyllopoada Latreille, 1825; Conchostraca

Sars, 1867; Diplostraca Gerstaecker, post 1868 (see footnote on p. 358 of Fryer 1987) which takes precedence over Onychura Eriksson, 1934 (Fryer 1987); Calmanostraca Tasch, 1969 and Thoracopoda Hessler and Newman, 1975) has varied among authors. The complex history of the taxonomic classification of branchiopods is summarized by Fryer (1987).

The classification employed here is that of Fryer (1987), which is widely applied to extant conchostracans (e.g. Martin 1992). Fryer (1987) elevated Laevicaudata and Spinicaudata to ordinal level. The significant anatomical differences between them are summarized by Fryer (1987, table 2) and Martin (1992, pp. 32–35). Fryer abandoned Conchostraca as a taxonomic unit but it is still useful as a vernacular, descriptive term. Martin (1992, p. 26) followed Fryer but alluded to naupliar characters of lynceids that suggest that Conchostraca might still be a valid taxon.

The taxonomic status of Branchiopoda was not explicitly considered by Fryer (1987), although he implied that it should be accorded class or subclass status. The former convention is adopted here; intra-ordinal classification follows Tasch (1969).

Ecology

Conchostracans are non-selective algal and detrital feeders. Some extant species of conchostracans can tolerate the low salinities of inland playas or coastal rock pools (Webb 1979). Most occur in freshwater environments which regularly or irregularly dry out, freeze, or show striking changes in water level. Conchostracans exhibit a series of ecological adaptations to such astatic or temporary environments. These include early maturation, obligate oviparity, high fecundity, the production of desiccation-resistant, shelled, dormant embryos (resting eggs or cysts), generation carry-over of propagules in the egg bank by dormancy and hatching at low conductivity (Brendonck and Persoone 1993; Brendonck 1996). Populations are usually of high density but low diversity, often monospecific.

Recurrent faunal associates of Recent conchostracan brachiopods are anostracans, notostracans, copepods, 'cladocerans', crayfish, gastropods, bivalves and tadpoles (Karande and Inamadar 1959; Tasch 1969). Co-occurrence with fish appears to be rare (see discussion in Frank 1988, pp. 399–400); in such cases, conchostracans apparently survive by sheltering among water plants, sometimes exhibiting distinct preferences for certain species (Webb 1979, and references therein).

Fossil conchostracans are often cited as indicative of non-marine conditions. In many cases this conclusion is consistent with the nature of the associated sediments and/or faunal remains (e.g. Tasch 1978; Jell and Duncan 1986). In other cases it is based, at least partly, on an analogy with the ecology of extant conchostracans and the strict application of uniformitarian principles (e.g. Petzold and Lane 1988). Caution should be exercised with the latter approach. Co-occurrence of conchostracans and 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 (Tasch 1969), although a shift from marine to freshwater environments during the geological history of the group, possibly during the Carboniferous, or perhaps more than once has been postulated (Tasch 1969).

Fossil record

Most recent authorities concur that the fossil record of unequivocal conchostracans begins in the lowermost Devonian (Tasch 1969; Schram 1986; Briggs *et al.* 1993). The number of families doubled during the Carboniferous and almost 90 per cent. of fossil taxa date from Namurian or younger rocks. There are about 180 living species in 15 genera (Bowman and Abele 1982, table 1), or 186 species in 13 genera (Brtek 1997).

The number of extant families recognized varies among different authors. The order Laevicaudata is universally accepted to comprise only the family Lynceidae Stebbing, 1902. Most authorities recognize four (Belk 1982, p. 178; Bowman and Abele 1982, p. 7; Martin 1989*a*, p. 123; 1992, p. 27, table 1), or five (the four of the previous authors, plus family Limnadorpsidae Tasch, 1969; Tasch 1969, p. R112; Schram 1986, p. 385) extant spinicaudatan families. However, at least two other spinicaudatan families have been erected; their taxonomic status appears to be uncertain.

The family Metalimnadiidae Straškraba, 1965 is recognized by Roessler (1995*a*, 1995*b*). It is, to date, monotypic (the extant taxon *Metalimnadia serratura* Mattox, 1952) although a second, as yet undescribed, extant species occurs in Brazil (D. Belk, pers. comm., in Roessler 1995*a*, p. 131). Mattox (1952), Straškraba (1965) and Belk (1982, p. 179) included *Metalimnadia* within the family Limnadiidae; Straškraba (1965) accorded it separate sub-familial status.

Roessler (1991), unaware of the description of *Metalimnadia serratura* by Mattox (1952), redescribed the taxon as '*Paraimnadia guayanensis*', and erected the 'Family Paraimnadiidae'. This nomenclatural error was corrected by Roessler (1995*b*) and the subfamily Metalimnadiidae *sensu* Straškraba (1965) was elevated to familial level.

The family Imnadiidae Botnariuc and Orghidan, 1941 is recognized by Roessler (1995*a*, 1995*b*) but not Tasch (1969) and Belk (1982). Straškraba (1965) and Belk (1982, p. 179) assigned the genus *Imnadia* to the family Limnadiidae; Straškraba (1965) assigned it separate sub-familial status.

A further six extinct families are recognized (Tasch 1969, p. R112; Schram 1986, p. 385; Briggs *et al.* 1993, p. 335). More than 80 fossil genera were recorded in the most recent compendium (Tasch 1969).

Most reports of pre-Devonian conchostracans have been disproved. The supposed conchostracan valves of Cambrian age reported by Ulrich and Bassler (1931) are the valves of phosphatocopines (Müller 1979, 1982). Conchostracan valves reported from the Lower Chasmops Shale (Caradoc: upper Ordovician) of the Oslo region, Norway (Soot-Ryen 1960) were discounted by Tasch (1969, p. R163). Other supposed occurrences (e.g. Howell 1963) apparently have not been questioned, but must be regarded as doubtful.

Exceptionally preserved examples

The vast majority of occurrences of fossil conchostracans yield only the relatively thick valves of the carapace. Conchostracan branchiopods that preserve anatomical features in addition to the carapace can be considered to be exceptionally preserved. They have been recorded from the Triassic (Anisian) Grès à Voltzia fauna from the Vosges of north-eastern France (Gall 1971, p. 41, pl. 9, fig. 4) and the Kalkschieferzone (uppermost Meride Limestone: Upper Ladinian, Middle Triassic) of northern Italy and southern Switzerland (Tintori 1990; Furrer 1995). In both of these *Konservat-Lagerstätten* conchostracan branchiopods are locally abundant, but the quality of preservation does not match that described here.

Exceptionally preserved conchostracans have also been described and figured from the Stephanian (Upper Carboniferous) of France (Dechaseaux 1951) and the Jiulongshan Formation (Middle Jurassic) near Zhouyingzi village, Luanping County, Hebei, China (Zhang *et al.* 1987, 1990). Tasch (1987, p. 16, pl. 18, fig. 4) recovered conchostracan appendages and possible conchostracan eggs from Jurassic strata in the Mauger Nunatak section of the Transantarctic Mountains in Antarctica.

Zhang *et al.* (1987, text-fig. 12; 1990, text-fig. 12) also illustrated a number of other examples of soft-part preservation of varying ages. Some of these are considered equivocal herein. Other authors have also questioned some of these examples. Tasch (1956, p. 1249) dismissed the evidence for soft part preservation in conchostracans recorded by Bill (1913, pl. 15, fig. 3) as 'inadequate' and regarded (p. 1248) that reported by Chernyshev (1940) as 'so poorly preserved and figured' as to make verification impossible. However, Kobayashi (1954, p. 10) was 'certain' that the latter material was conchostracan.

TERMINOLOGY

Anatomical terms

The morphological terms used in the description of taxa are those of McLaughlin (1980) as far as possible. Antennule and antenna correspond to the first and second antenna of other authors, and maxillule and maxilla to first and second maxilla. McLaughlin's (1980) 'classical definition' of a telson with or without caudal rami is followed (see discussion in Bowman 1971 and Schminke 1976). Where there are widely used alternatives to McLaughlin's terms, they are given in parentheses when the feature is first mentioned (but see the Appendix). The sources of terms other than those of McLaughlin (1980) are indicated.

There is no universally accepted terminology for the great diversity of crustacean setae and spines (see Felgenhauer 1992; Martin and Cash-Clark 1995); the general terms 'seta(e)' and 'spine(s)' are therefore used. The distinction is partly morphological; the former have a much higher length to breadth ratio. In addition, setae are interpreted as sensory, natatory or filtering, and spines as primarily defensive.

A list of abbreviations and symbols used on the Text-figures is presented in the Appendix.

Specimen orientation

The planes of splitting on which the specimens are observed are parallel or sub-parallel to bedding. The way-up of none of the slabs yielding the specimens is known: where both part and counterpart are available, the slab upon which most of the specimen remains is designated the part. The terminology used to describe the orientation of specimens is modified from Whittington (1971) and Briggs (1981).

Most specimens are preserved with the sagittal axis parallel to bedding, in one of three orientations.

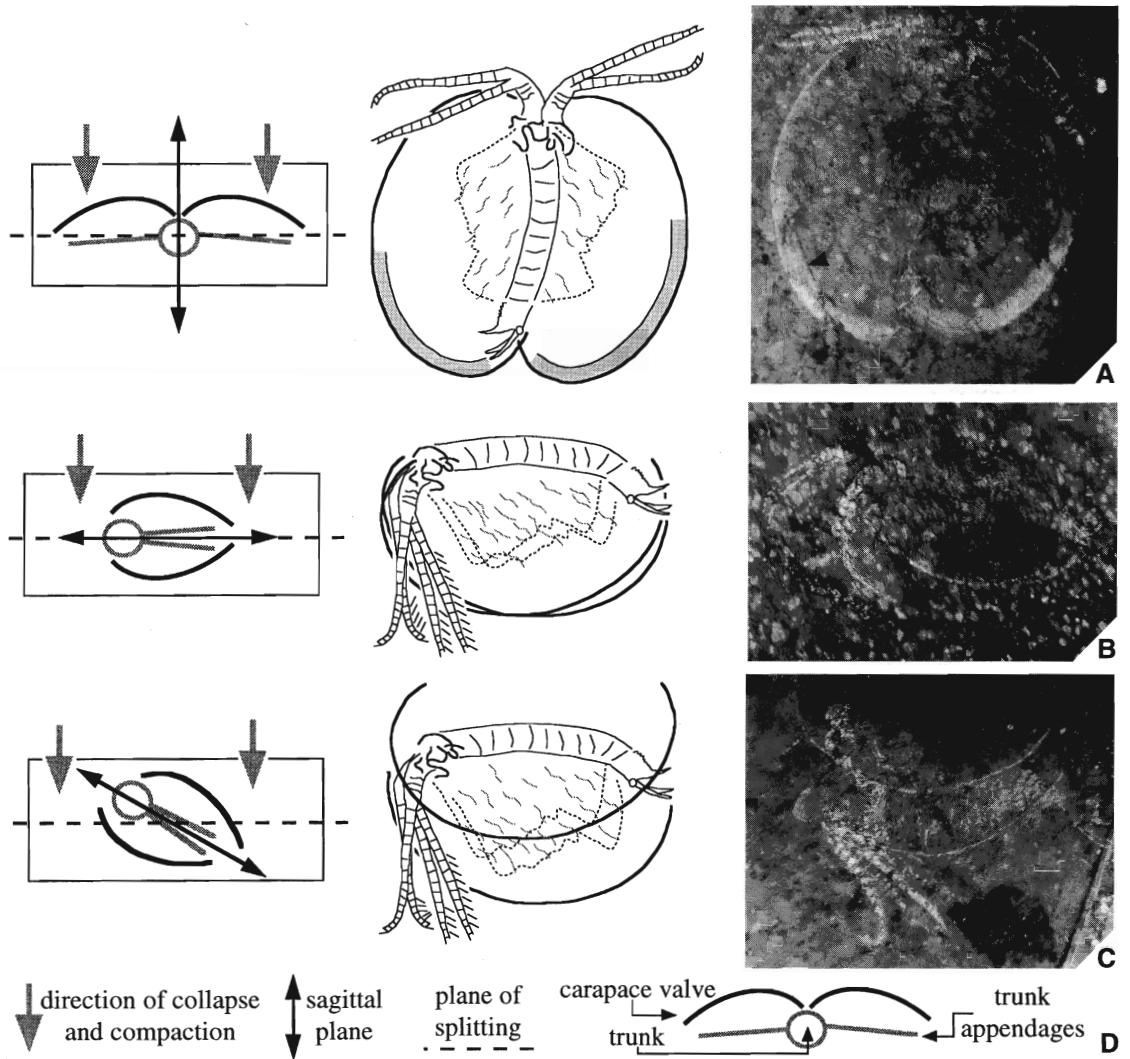
1. Dorso-ventral aspect (parallel aspect *sensu* Whittington 1971): sagittal plane normal, or at a very high angle to bedding; carapace valves typically displaced either side of the trunk (i.e. 'butterfly' position); trunk in medial position; the telson and the posterior part of the trunk usually rotated or collapsed into lateral aspect (Text-fig. 2A).
2. Lateral aspect: sagittal plane parallel or nearly parallel to bedding; carapace valves almost exactly superimposed; trunk in dorsal position (Text-fig. 2B).
3. Oblique aspect: sagittal plane at intermediate angle to bedding; carapace valves typically aligned but offset; trunk in medio-dorsal position (Text-fig. 2C).

Some specimens are preserved with the sagittal axis inclined, rather than parallel, to bedding (compare Text-fig. 3B and 3A, respectively). Specimens in such orientations are identified by condensing or foreshortening of the sagittal length with respect to bedding (e.g. Text-fig. 3C, compare with Text-fig. 9). Where there is evidence that the sagittal axis was inclined to bedding, the aspect descriptor is prefixed by *inclined*.

In most specimens the appendages are displaced to some extent from their position during life. The body of conchostracans is attached to the carapace only by an antero-dorsal attachment ligament (McLaughlin 1980: = muscle-containing pedicel [G. Fryer, pers. comm. 1996; Orr *et al.* 1996]) and an adductor muscle. The posterior of the trunk and the trunk appendages are therefore especially susceptible to *displacement* from life position. The trunk is often rotated anteriorly and elongated normal, rather than parallel, to the long axis of the carapace valve (Text-fig. 3D). Conversely, the anteriorly sited appendages, most obviously the antennae, can be variably orientated but usually exhibit less displacement (e.g. Text-figs 2A–C, 3D).

However, in other specimens simple displacement of the appendages from life position during transport and burial is insufficient to explain the attitudes in which they occur. It is necessary to invoke *distortion* of the specimen before, or during, burial. In specimen GSI:F00898 (Text-fig. 3E) the trunk lies outside, and dorsal to, the perimeter of the carapace valves; the latter are superimposed one upon the other. This configuration can only be derived by one valve having rotated through 180° and become superimposed upon the other. Such distortion is extremely unlikely to have occurred after burial within the sediment column. It may have arisen purely as a result of physical stresses on a living animal during turbulent transport: one valve may have partially separated from the body via rupture of the adductor muscle connecting them. The potential for such rupture to occur would be enhanced in a dead specimen which had partially decayed prior to transport.

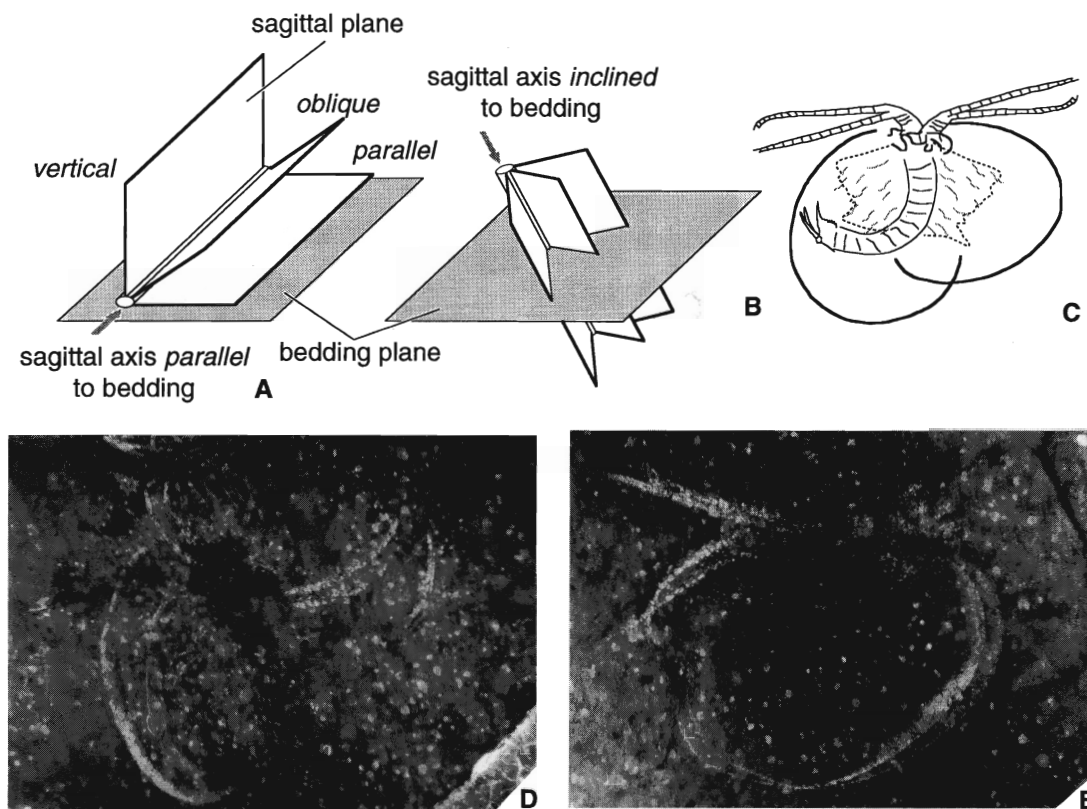
At a finer scale, there can be discrepancies between the orientation of a specimen as a whole and some of its appendages (notably the telson, mandibles and claspers). In specimens in dorsal-ventral aspect, the posterior of the trunk and, especially, the telson are usually in lateral aspect (e.g. Text-fig. 2A). Such discrepancies are attributed to post-depositional *re-orientation* of appendages within the decaying carcass into more stable attitudes than those at which they were originally deposited. This re-orientation was facilitated by decay-induced loss of the structural strength of the cuticle; it occurs preferentially in those appendages, or parts of appendages, with thicker and/or more sclerotized cuticle that degraded less rapidly.



TEXT-FIG. 2. Terminology for the orientation of specimens preserved with their sagittal axis parallel to bedding. Corresponding illustrations represent an idealized vertical section through a specimen at the time of burial (left hand column: key in D), its appearance on the plane of splitting (middle column), and an actual example (right hand column). A, In21097; dorso-ventral aspect; $\times 7$. B, NMING:F:14724; lateral aspect; $\times 6.5$. C, In21099; oblique aspect; $\times 6.5$.

THE CASTLECOMER FAUNA

The only primary research on the Castlecomer fauna prior to this project was by Wright (1920) who erected the genus and species *Limnesteria ardra* Wright, 1920, based on material from the Ardra core (see Orr *et al.* 1996).



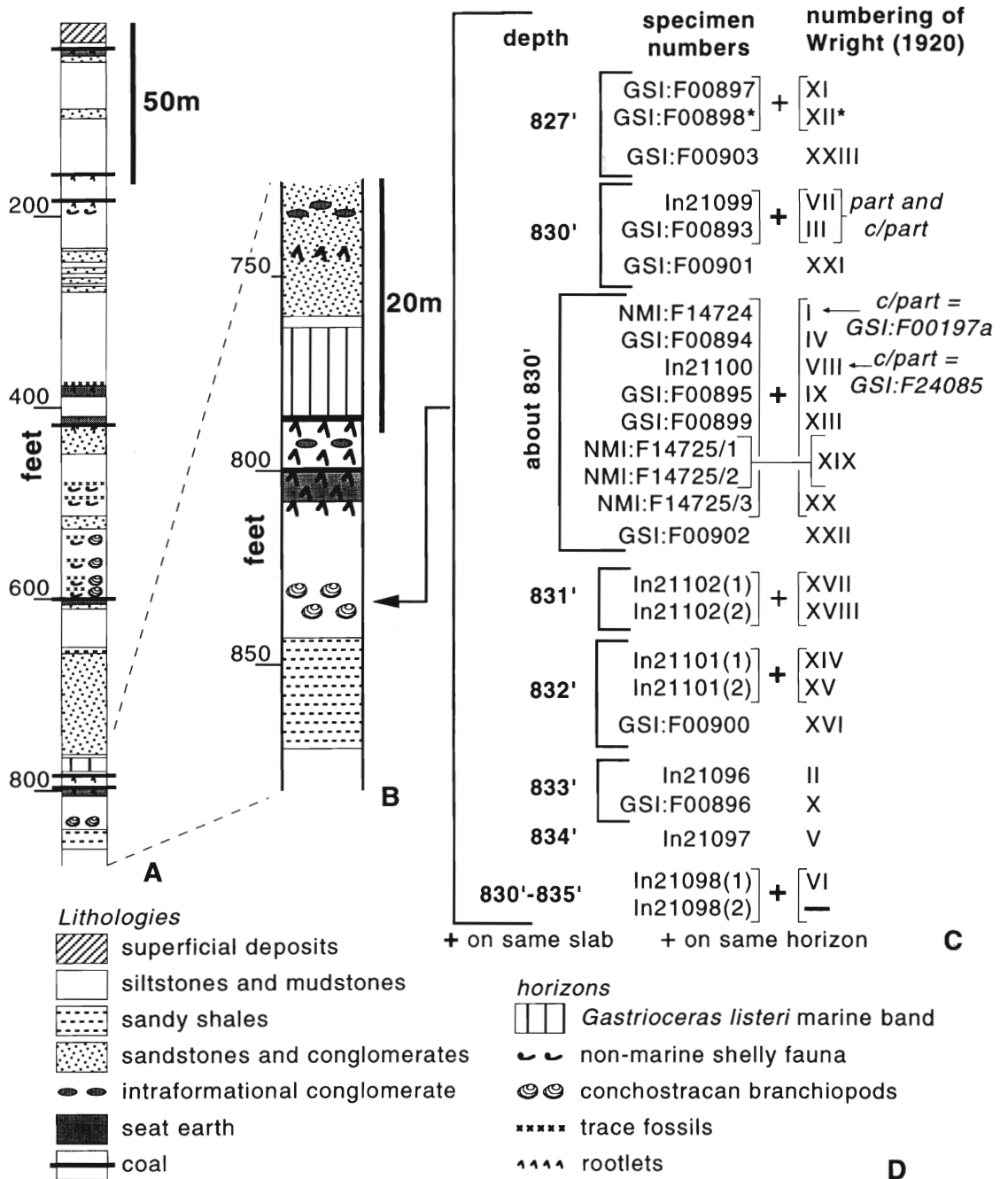
TEXT-FIG. 3. Specimens oriented with their sagittal axis inclined, rather than parallel, to bedding (compare B and A, respectively) appear condensed or foreshortened on the plane of splitting; see idealized example in C. D, NMING: F:14725/2; oblique aspect; note displacement of the posterior of trunk and trunk appendages from life position; $\times 5$. E, GSI:F00898; dorso-ventral aspect, with caveat that one carapace valve has suffered distortion; the two carapace valves are superimposed, but the trunk lies outside their perimeters; $\times 7.5$.

Geographical and stratigraphical setting

The Leinster Coalfield is situated in south-eastern Ireland (Text-fig. 1A); the regional geology was reviewed by Nevill (1956, 1961), Eagar (1964) and Higgs (1986). Numerous boreholes have been drilled through the late Namurian and early Westphalian strata of this area (see Nevill 1956, pl. 4; Eagar 1964, text-fig. 1) including those at Ardra and Hollypark from which the Castlecomer fauna was recovered (Text-fig. 1B).

The precise age of the Castlecomer fauna remains uncertain. In the Ardra borehole the interval with exceptionally preserved conchostracans has been considered to be either the equivalent of (Eagar 1964, p. 363, text-fig. 3), or slightly younger than (Wright 1920, p. 193), the *Gastrioceras subcrenatum* marine band (see discussion in Orr *et al.* 1996). It occurs below the *Gastrioceras listeri* marine band (Text-fig. 4A–B). The *Gastrioceras subcrenatum* marine band is the lowest unit of the Westphalian Series, Upper Subsystem of the Carboniferous System; the fauna is therefore of basal, or early, Westphalian age (c. 315 Ma; Harland *et al.* 1990). The fauna occurs in the Dinin Member of the Moyadd Coal Formation (Higgs 1986, text-fig. 10).

In the Hollypark borehole the fossils occur at or around a depth of 449 feet (135 m). Geological Survey of Ireland archives record it as equivalent to the *Gastrioceras subcrenatum* marine band. There is no indication as to how this conclusion was reached. A lithological log of this borehole is not available.



TEXT-FIG. 4.

In the Leinster Coalfield there are spatial variations in the faunal composition of the *Gastrioceras subcrenatum* marine band: shallower water, brachiopod-dominated, facies were deposited in the southern part of the coalfield and deeper-marine, goniatite-dominated, facies in the northern part (Nevill 1956, pp. 5–6; 1961, p. 455). The boundary between the facies is poorly delineated. It is suggested to have run in a west–east direction through either Rockafoil (Nevill 1956) or Castlecomer (Nevill 1961; Text-fig. 1B).

If the intervals of each borehole that yield the exceptionally preserved conchostracans are considered correlative with the *Gastrioceras subcrenatum* marine band it is difficult to explain the absence of unequivocal marine fossils within them. Both lie within the area in which Nevill (1956, 1961) suggested that deeper-marine, goniatite-dominated, facies accumulated at this time. The Aghamucky, Creamery and Rockafoil boreholes are proximal to, but south of, the Ardra borehole (Text-fig. 1B). In each the *Gastrioceras subcrenatum* marine band is unequivocally present. Lithological logs of these (Eagar 1964, text-fig. 3) divide the *Gastrioceras subcrenatum* marine band into a 'Lower Leaf' and 'Main Leaf' (*sensu* Eagar 1964, text-fig. 2), the latter of which contains a goniatite fauna. In addition, the 'Lower Leaf' of the Aghamucky borehole contains marine bivalves and gastropods (Eagar 1964).

The intervals of each borehole with exceptionally preserved conchostracans may have been correlated with the *Gastrioceras subcrenatum* marine band simply on the basis of their high content of conchostracan material. In the Coal Measures of central and northern England, only some of the intervals with marginal marine to non-marine faunas (*Lingula*, *Carbonicola* and 'Estheria' bands) can be correlated with marine bands with diagnostic goniatite-dominated faunas; others lack any basinal equivalents (Eden 1954; Calver 1968; Flint *et al.* 1995).

Sedimentology

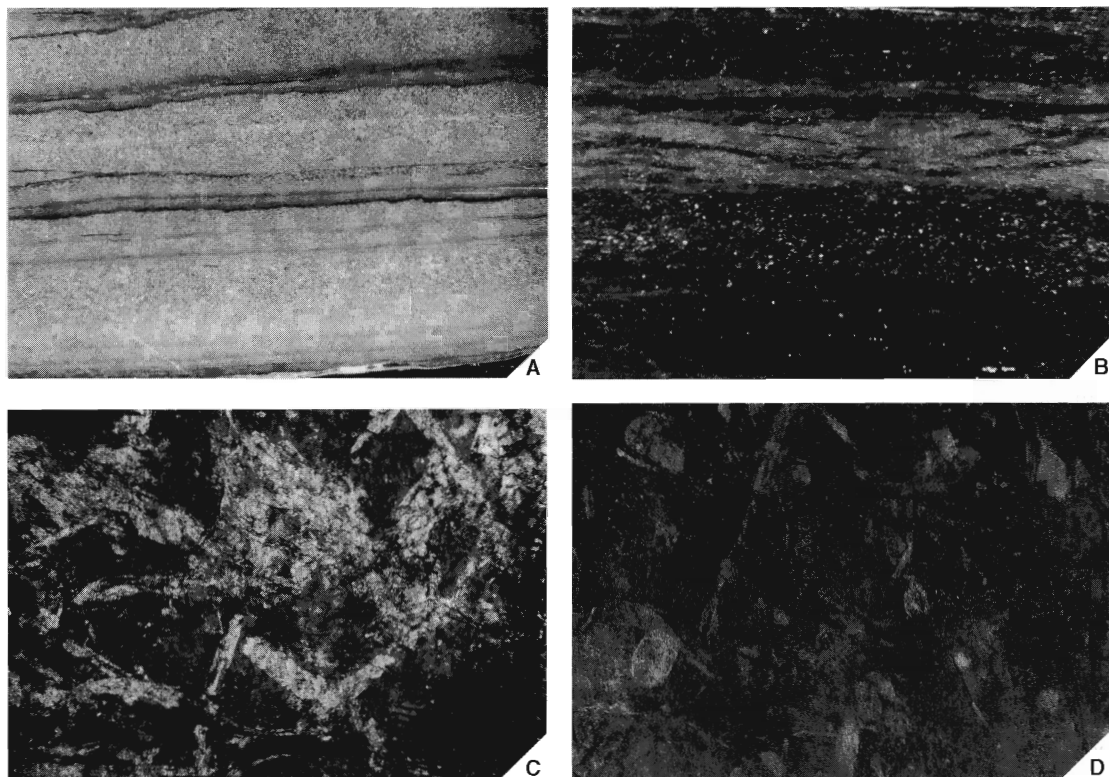
The interval of the Ardra borehole with exceptionally preserved conchostracans comprises finely laminated siltstone and mudstone. Individual laminae are wavy or planar (Text-fig. 5A). The siltstone laminae are slightly thicker (2–5 mm) and medium to dark grey. Fossils, including exceptionally preserved conchostracans, are most common on the surfaces of the black, 1–2 mm thick, mudstone laminae. The core preferentially splits along these laminae; it is therefore possible that a sampling bias has been introduced. The way-up of none of the slabs is known; however, it is probable that the mudstone laminae are contiguous with a subjacent siltstone lamina and the couplet forms a thin, normally graded, or bipartite event bed. There is a pervasive cleavage fabric that is especially well-developed in the finer-grained lithologies.

Core from the Hollypark borehole with exceptionally preserved conchostracans is medium to dark grey. It is dominantly a massive to poorly laminated mudstone, typically in 2–5 mm thick intervals (e.g. at base and top of Text-fig. 5B) separated by thin (1–2 mm thick), horizontal, silt laminae. Planes of splitting are dominantly parallel or sub-parallel to bedding, but the lithology is markedly less fissile than in the Ardra core. A cleavage fabric is less extensively developed.

Palaeoenvironment

In general terms the late Namurian and early Westphalian strata of the Leinster Coalfield represent a progressively shallowing upward sequence (Higgs 1986). The Moyadd Coal Formation represents a paralic coal-forming environment which succeeded the deltaic environments represented by the immediately underlying formations.

TEXT-FIG. 4. The Ardra borehole. A, lithological log of the entire borehole; B, lithological log of the interval from which exceptionally preserved specimens have been recovered; C, grouping of exceptionally preserved specimens into assemblages based on the depth in the borehole at which Wright (1920) recorded them; current accession numbers and numbering used by Wright (1920) to identify specimens are cross-referenced. D, key to lithological logs. *Wright (1920) recorded specimen GSI:F00898 as having occurred at a depth of 827', but the reverse of the specimen has 'Ard833(a)' scratched on it; in all other cases the two separate sources of information are consistent.



TEXT-FIG. 5. Sedimentology and palaeontology of the interval of each borehole with exceptionally preserved conchostracans. A, GSI:F21911; vertical section of finely laminated sediments from the Ardra borehole; $\times 5$. B, GSI:F24084; vertical section of finely laminated sediments from the Hollypark borehole; $\times 14.5$. C, GSI:F00199; dense accumulation of comminuted plant debris on a plane of splitting in core from the Ardra borehole; $\times 7$. D, GSI:F21912; dense accumulation of conchostracan carapaces on a plane of splitting in core from the Ardra borehole; $\times 1.5$.

Intercalated with these facies are goniatite-bearing horizons which represent episodes of marine transgression (Higgs 1986). For reasons outlined above (see *Geographical and stratigraphical setting*), the intervals in each borehole with exceptionally preserved conchostracans are unlikely to correlate with the *Gastrioceras subcrenatum* marine band. The Castlecomer fauna was probably not deposited under fully marine conditions.

Detailed interpretation of the depositional environment of the Castlecomer fauna is difficult. Core provides no opportunity to determine lateral facies associations, and there is no lithological log for the Hollypark borehole. The fine grained laminated sediments in which the Castlecomer fauna occurs are an important lithofacies in numerous environments and sub-environments of paralic successions (Emery and Myers 1996, pp. 134-137, table 1). Possible interpretations include varves in lacustrine settings, episodic sedimentation in temporary terrestrial waterbodies, and tidally influenced environments, including delta-front settings, abandoned tidal channels, tidal flats and estuarine environments (see discussion in Feldman *et al.* 1993).

In both cores the intervals with exceptionally preserved conchostracans are unbioturbated; environmental conditions almost certainly excluded a macroinfauna, and possibly a macroepifauna.

The relevant intervals of both cores show evidence of neither periodic nor episodic emergence; sedimentary structures such as desiccation cracks or salt pseudomorphs have not been identified.

Limited amounts of plant detritus occur on the same surfaces as the exceptionally preserved conchostracans in both cores. Conversely, high concentrations of fragmented plant detritus occur where exceptionally preserved conchostracans are rare or absent (Text-fig. 5C). This negative abundance correlation may indicate temporal (?seasonal) variation in the introduction of biogenic material to the sites of deposition. Other planes of splitting expose high concentrations of conchostracan carapaces (Text-fig. 5D).

In both cores the specimens are preserved in a variety of orientations to bedding. The sediment is therefore interpreted as a series of thin event beds, into which the conchostracans were incorporated. Experiments have demonstrated that freshly killed crustaceans (e.g. *Palaemon* and *Nephrops*) can survive extensive transport without significant disarticulation (Allison 1986). In contrast, extensive disarticulation occurs if the specimens have first decayed. The high degree of articulation of the conchostracans in the Castlecomer fauna therefore does not necessarily imply minimal or no transport, i.e. an autochthonous or para-autochthonous fauna. It does, however, suggest that they were living or recently deceased at the time of burial.

Lithological logs of the Ardra borehole indicate that the strata succeeding the interval with exceptionally preserved conchostracans are siltstones and mudstones with seat earths, an intraformational breccia, and thin coals (Text-fig. 4B). The Castlecomer fauna in the Ardra core is interpreted as the result of transport, and deposition under reducing conditions within an abiotic, semi-permanent, standing body of fresh or brackish origin, within a paralic environment.

There are subtle differences in faunal content between the relevant intervals of the two boreholes. Rare eumalacostracan crustaceans have been recovered from the core of the Hollypark borehole, but not the Ardra core. Ostracod valves are numerous on one plane of splitting in the Hollypark core, but rare or absent on the others. Only a single pair of ostracod valves has been recognized in core from the Ardra borehole. The significance of these faunal variations is unclear. The depositional environment of the interval of the Hollypark borehole in which exceptionally preserved conchostracans occur is uncertain; it may not have been the same as that of the Ardra borehole.

Material

The Ardra borehole (diameter of core 228 mm; few pieces survive intact) yielded the set of specimens on which *Limnetheria ardra* Wright, 1920 was erected. These specimens are currently housed in three institutions: the National Museum of Ireland (NMING:F:14724 and NMING:F:14725/1–4), the Geological Survey of Ireland (GSI:F00893–F00904), and The Natural History Museum, London (In21096–21102).

Wright's (1920) specimens are distinctive; each is covered in Canada balsam and a glass coverslip (the perimeter of which is usually outlined in red paint), and identified by Roman numerals in red paint. Wright (1920, pp. 200–202) summarized the morphology of the specimens numbered I to XXIII; however she (p. 196) noted that 'some twenty four specimens were available, showing body-parts of sufficient similarity to be considered referable to a single genus'. Although no reference was made to a specimen XXV (now GSI:F00904) by Wright (1920), this specimen is prepared in an identical manner to the others. The whereabouts of specimen XXIV, if such originally existed, is not known. To facilitate comparisons between this study and that of Wright (1920) the numbering used by her is cross-referenced against the current accession number in Text-figure 4C. Specimens NMING:F:14725/1 and NMING:F:14725/2 are under the same glass coverslip; Wright (1920, text-fig. 3) identified the former as specimen XIX, although her summary of specimen XIX (p. 202) made reference to both. Specimens In21098(1) and In21098(2) are under the same glass coverslip; the former is specimen VI of Wright (1920).

The assemblages into which these specimens are divided (Text-fig. 4C) are based on the depth (in feet) within the Ardra borehole at which Wright (1920, pp. 200–202) recorded individual specimens. The specimens also have the prefix 'Ard/' followed by three figures scratched on them. In all cases except specimen GSI:F00898 these three figures concur with the depth recorded by Wright (1920). These assemblages almost certainly do not imply that sampling was undertaken systematically. It is likely that the depths are rounded or approximate values; one assemblage is noted by Wright (1920) as from 'about

830'. None of the components of each assemblage can be assumed to be precisely contemporary except for those recorded by Wright (1920) as from the same slab, and possibly those recorded as from the same horizon, as indicated in Text-figure 4c. Wright (1920) was apparently unaware that specimens In21099 and GSI:F00893 (her VII and III, respectively) are part and counterpart of the same animal although she noted that their outlines are very similar.

Geological Survey of Ireland collections include more than 100 pieces of core from the same stratigraphical interval of the Ardra borehole as the specimens studied by Wright (1920). While investigating this material numerous other exceptionally preserved examples of *Limnesteria ardra*, and the counterparts of two of the specimens studied by Wright (1920), were identified: specimen GSI:F00197a is the counterpart of the holotype (NMING:F:14724); specimen GSI:F24085 is the counterpart of specimen In21100.

The fauna from the Hollypark borehole has not been described previously. The 75 mm diameter core from this borehole is archived by the Geological Survey of Ireland. The surfaces of more than 30 pieces (all with the original numbering 'b6/449') were examined; some of the thicker pieces were split to provide additional surfaces.

Methods

All specimens were examined with a Leica Wild M10 stereomicroscope under incident light from a Volpi Intralux 6000 fibreoptic system. Drawings were made using a Wild 308700 *Camera lucida* attached to this microscope. Photographs were obtained with a Wild MPS52 shutterpiece and Wild 35 mm magazine attached to this microscope via a trinocular phototube, and a Wild MPS48 photoautomat. Specimens other than Wright's were covered by water and a glass coverslip prior to photography.

Scanning electron microscopy was carried out at The Natural History Museum, London using an ISI ABT-55 with an environmental chamber, which does not require the samples to be coated prior to examination and can accommodate relatively large specimens; a Robinson backscattered electron (BSE) detector was used to generate images. Secondary electron images (SEI) and backscattered electron images (BSEI) of uncoated, gold-coated and carbon-coated specimens were obtained via the Cambridge Instruments Stereoscan 250 Mk 3 at the Department of Earth Sciences, University of Bristol.

Preparation of partially exposed specimens with drills and fine needles proved unrewarding. The specimens are very small and have minimal or limited vertical thickness. They proved as likely to separate below as along the plane of the fossil.

PRESERVATION

The conchostracans are preserved as organic carbon residues in association with phyllosilicates. The presence of carbon was confirmed by elemental mapping and they appear black in BSEI (Text-fig. 28E). The phyllosilicate minerals have infilled appendages such as the antennae and are responsible for their preservation in three-dimensions (e.g. at arrows in Text-fig. 9). In the Hollypark core, abundant framboidal pyrite (identified on the basis of its characteristic morphology in SEI [Text-fig. 28C and 28D] and brightness in BSEI [Text-fig. 28E]) occurs on the surface of many specimens; the diameter of individual framboids is *c.* 5–12 μm . Polyhedra of pyrite occur more rarely. Pyrite is generally absent from the matrix; a limited amount occurs marginal to specimens. Pyrite is rarely associated with specimens from the Ardra borehole.

A taphonomic model for the Castlecomer fauna, including a discussion of the conversion of organic cuticle into complex inert biopolymers and the origin and role of the associated phyllosilicates, will be the subject of a separate contribution.

SYSTEMATIC PALAEOLOGY

Class BRANCHIOPODA Latreille, 1817
 Order SPINICAUDATA Linder, 1945
 Family LIMNADIIDAE Baird, 1849
 Subfamily ESTHERIININAE Kobayashi, 1954
 Genus LIMNESTHERIA Wright, 1920

Diagnosis. Spinicaudatan 'conchostracan'. Carapace valves limnadiiform, with 'growth lines' but no other ornamentation. Antennal rami similar with high number ($c. 20 \pm 5$) of segments. First two pairs of trunk appendages of males modified as claspers.

Limnesteria ardra Wright, 1920

Text-figures 2–3, 6–17

Holotype. NMING:F:14724, by original designation (Wright 1920, p. 200).

Other material. GSI:F00197a (counterpart of holotype); In21099 (part) and GSI:F00893 (counterpart); In21100 (part) and GSI:F00894 (counterpart); GSI:F00895; GSI:F00897; GSI:F00898; GSI:F00900; GSI:F24085; In21096; In21097; In21098(1); In21101(1); In21102(2); NMING:F:14725/2; NMING:F:14725/3; ? GSI:F00896; ? In21098(2).

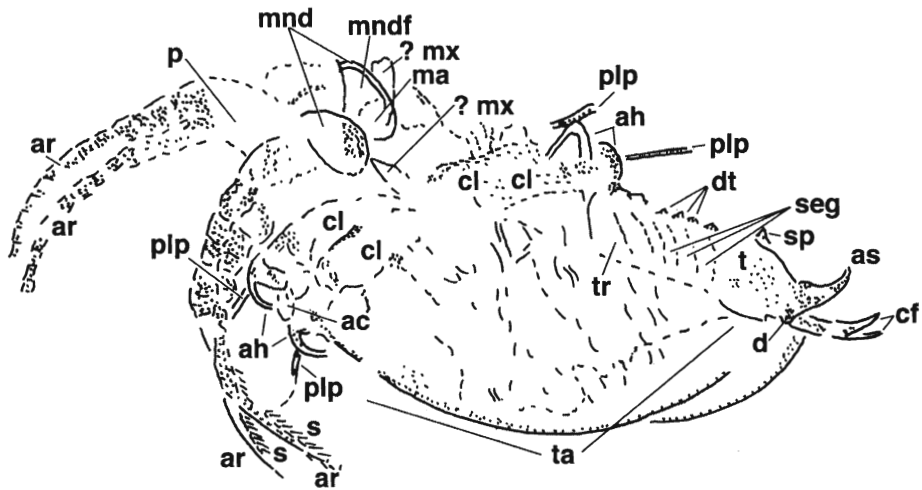
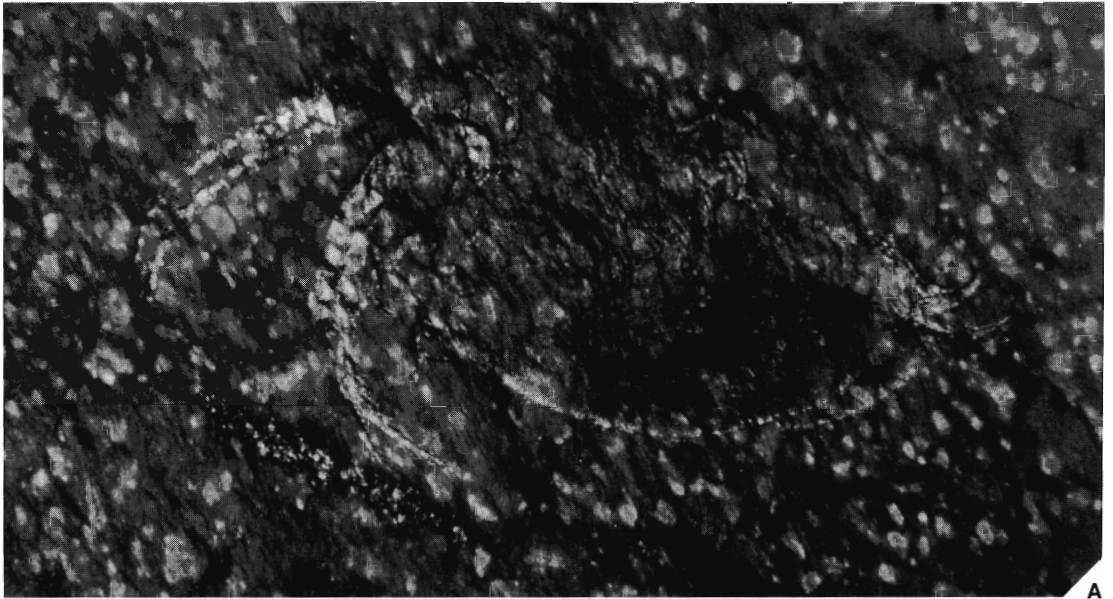
Diagnosis. Head crudely circular in lateral view. Antennal rami of 15 to 20 segments; each expands distally in dorso-ventral view, but is near parallel-sided in lateral view. Distal part of antennal protopod with transverse to oblique furrows. Robust telson: sub-rectangular in lateral view; dorsal margin with two longitudinal rows of stout spines flanking the mid line terminates anteriorly in a paired rounded projection; postero-ventral corner bears a pair of circular 'denticles'.

Description. The carapace comprises two valves, each oval in outline in lateral view, the length 1.5 to 1.75 times the height; the curvature is reduced dorsally along the hinge. There is no evidence for the development of the umbonal region into a beak. The curvature of both the antero-dorsal and postero-dorsal margins is pronounced; the latter identifies the shape of the valves as limnadiiform (*sensu* Tasch 1969, p. R149).

Evidence for the external morphology of the valves is limited (see Remarks, below). In the majority of specimens the outline of the valves is defined by two narrow, reflective lines that represent the intersection of the carapace with the plane of splitting (e.g. Text-fig. 7). These lines are continuous curves; they show no evidence of localized deflections that would indicate the presence of prominent radial ribs. In some specimens, however, these lines enclose a narrow reflective peripheral band, the inner margin of which may be defined by a ridge or groove and is usually parallel or sub-parallel to the outer (e.g. at arrow in Text-fig. 2A). This band is interpreted as part of the carapace surface bordered by a 'growth line'. The surface of these areas is smooth; there was presumably no other ornamentation on the carapace.

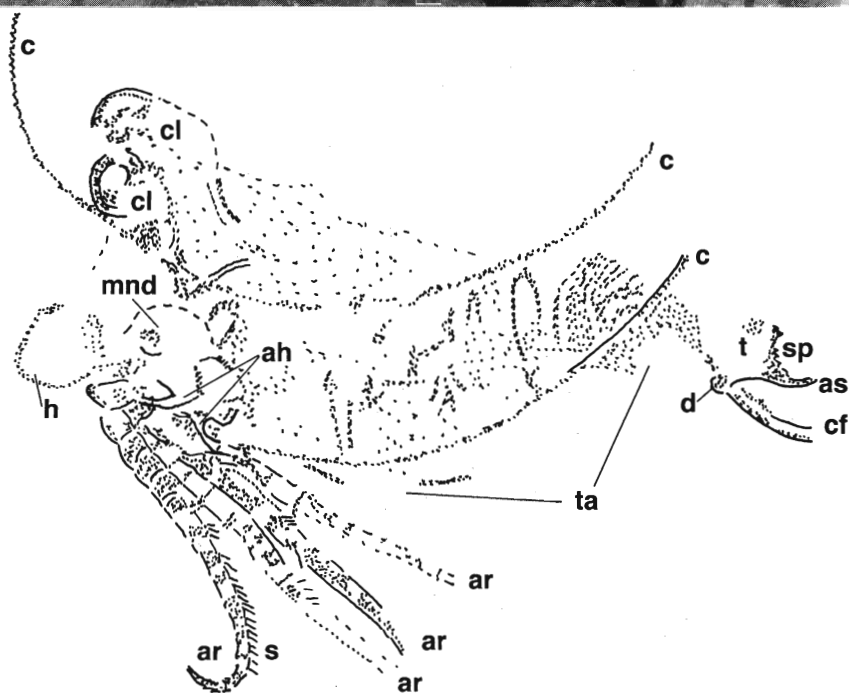
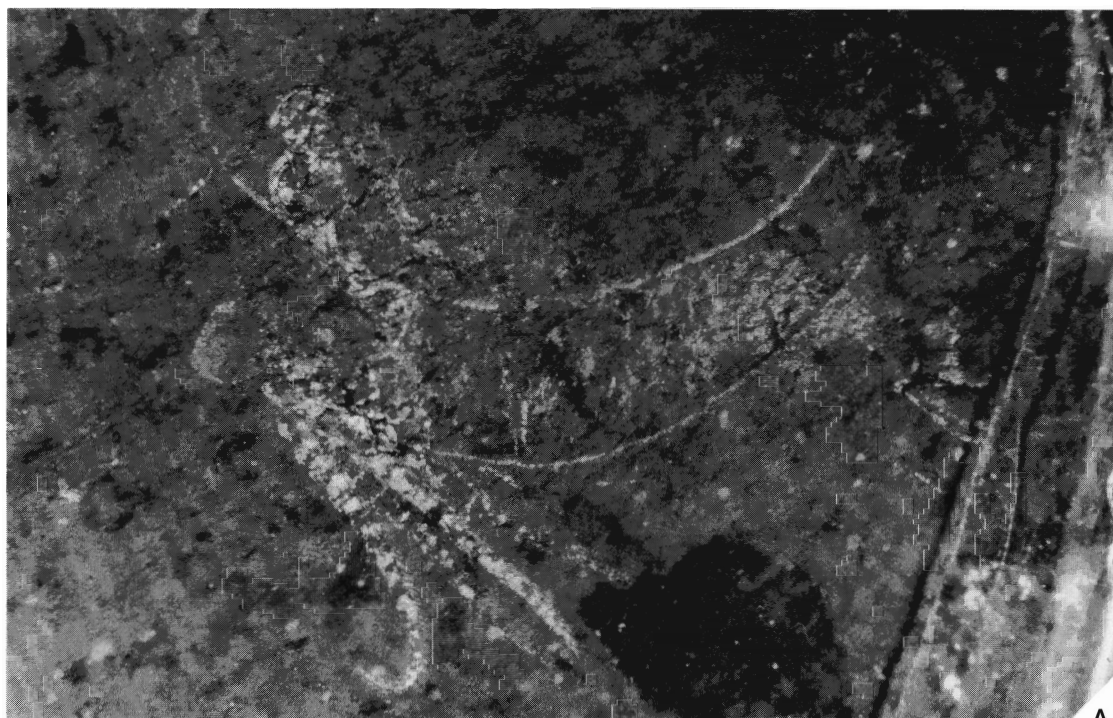
The head is preserved either as an area that is moderately reflective, the perimeter of which is a narrow, more highly reflective, band (Text-figs 7–9), or as an area that is darker in reflected light than the matrix (Text-figs 10, 16). In lateral view the outline is crudely circular. The ventral and antero-ventral margin are convex, and the anterior margin is straight or gently convex, sloping posteriorly dorsally (Text-figs 7–8). There is no evidence of a rostrum. In dorso-ventral aspect, the anterior margin of the head is triangular in outline: two straight, postero-laterally sloping lines meet antero-medially (Text-figs 9–10, 16). These sagittal and transverse views of the head can be combined into a three-dimensional reconstruction (Text-fig. 18A).

A uniramous antennule inserts ventrally medial and slightly posterior of the antenna. One specimen shows both members of the pair (Text-fig. 10). One, preserved projecting anteriorly, is covered distally by matrix, the other, projecting posterolaterally, is obscured by an antenna. Neither shows evidence of tapering along the length preserved, suggesting that they may have been significantly longer. Both antennules, and one antennule, are tentatively identified in specimens GSI:F00895 and In21098(1) (Text-fig. 11A and 11C, respectively).

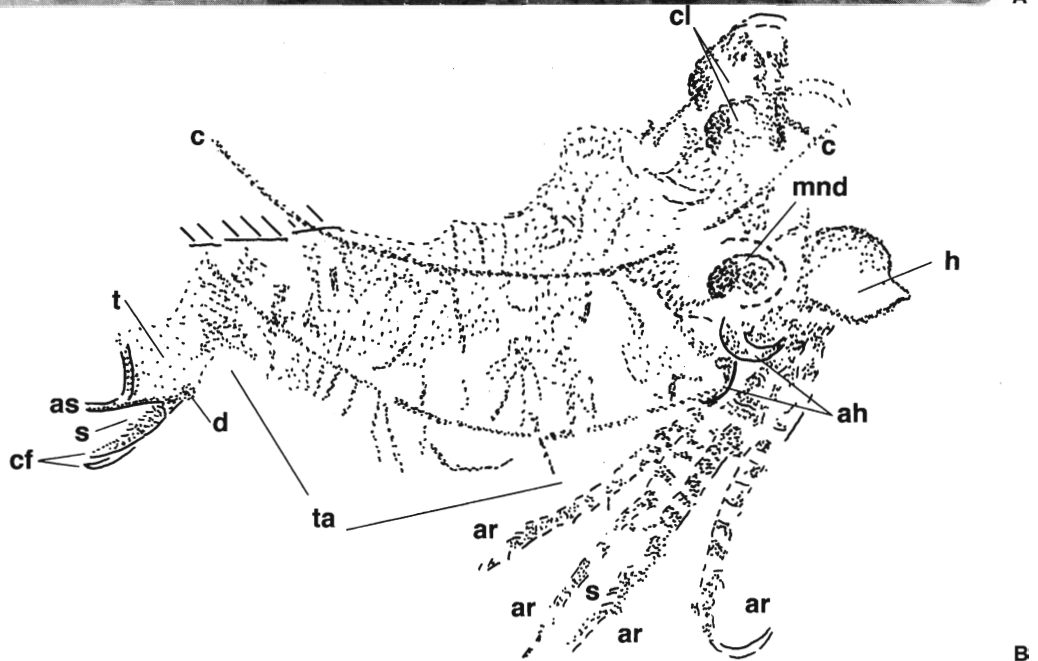
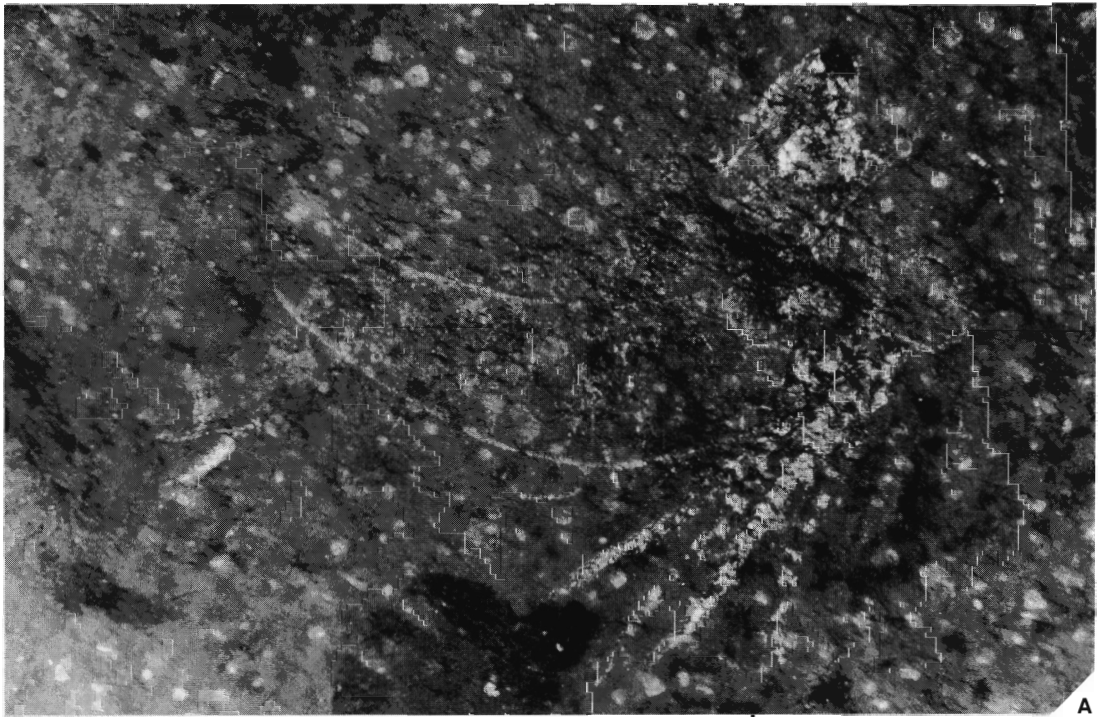


TEXT-FIG. 6. *Limnesteria ardra* Wright, 1920; NMING:F:14724, holotype; lateral aspect; $\times 16.5$.

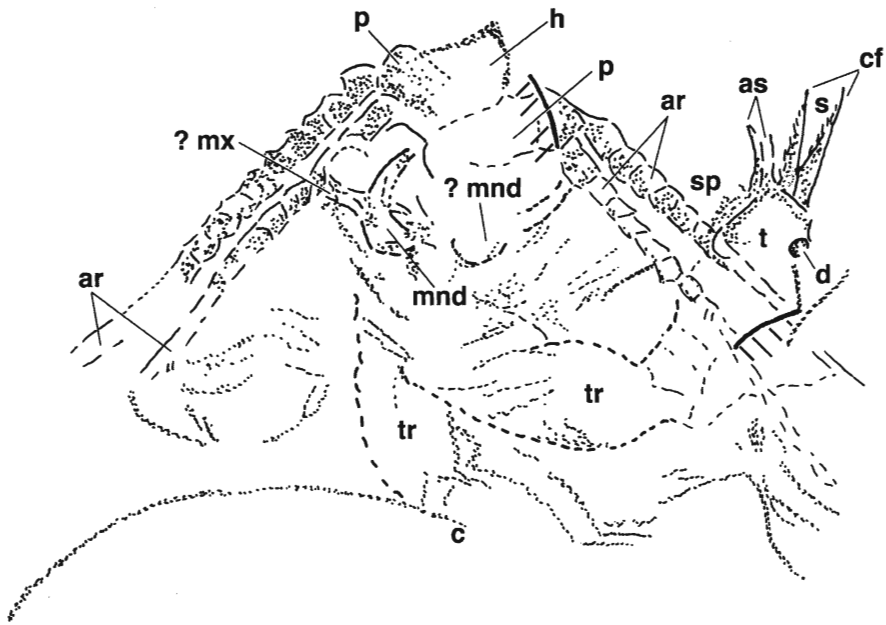
The antenna is biramous: the two similar rami are borne by a relatively long protopod (Text-figs 11, 12A: reconstructions in Text-fig. 18B). The protopod is not obviously segmented, but is traversed distally by a series of transverse or slightly oblique furrows (Text-figs 11C and 12A). The rami are attached to inclined articulating surfaces, one antero-ventral, the other postero-ventral (e.g. left hand antenna in Text-fig. 11C). These articulating surfaces are separated antero-medially by a narrow, transversely oriented, partition. The protopod is less reflective and preserves less relief than the rami, especially their proximal parts (e.g. Text-fig. 16A). This may reflect a thinner more flexible cuticle. The protopod does not exhibit setation. The rami consist of 15 to 20 segments. The segments expand distally in dorsal-ventral view, but are almost parallel sided in lateral view (compare Text-figs 9 and 16A with 6 and 7, respectively). This difference is sufficiently consistent to indicate that it reflects their morphology in life (Text-fig. 18C); the original dimensions are likely to have been retained, even during decay-induced collapse (Briggs and Williams 1981; Briggs 1990). The rami narrow distally beyond the sixth to eighth segment.



TEXT-FIG. 7. *Limnesteria ardra* Wright, 1920; In21099; oblique aspect; $\times 16.5$.

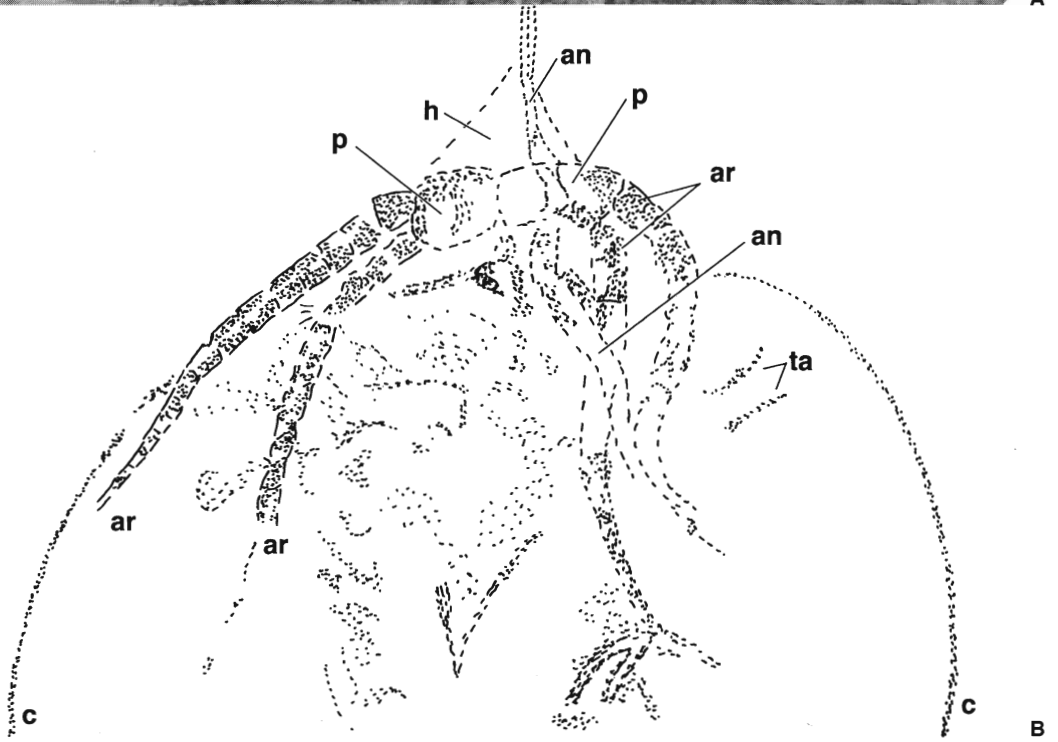
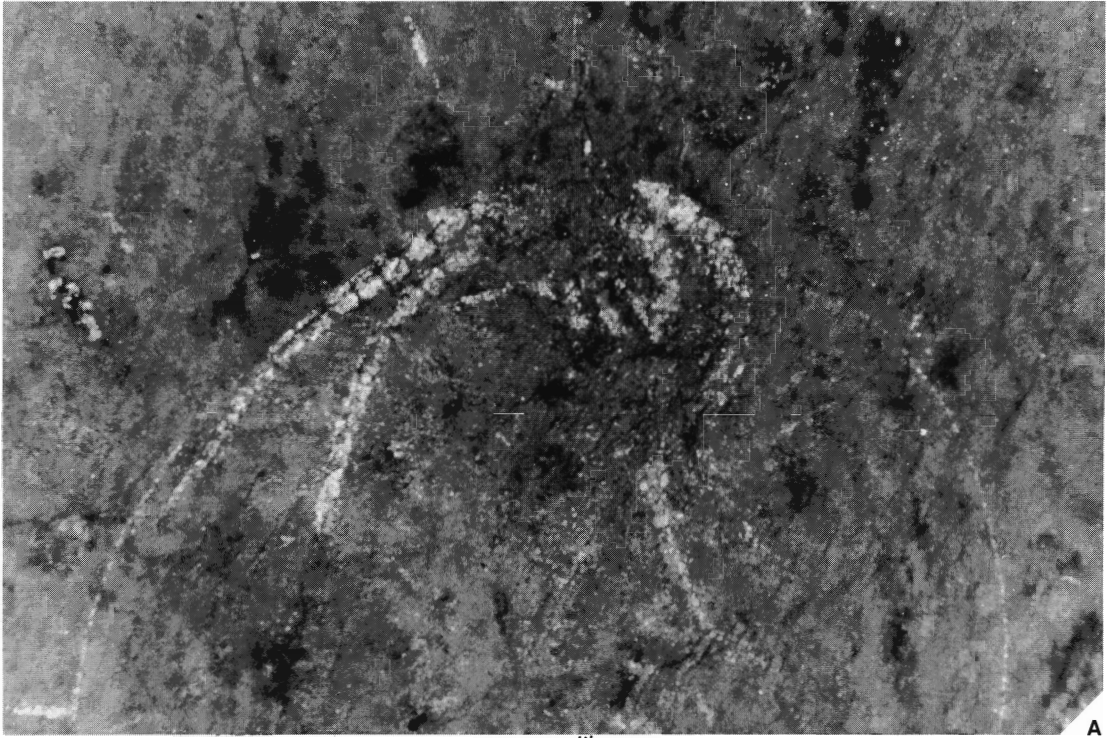


TEXT-FIG. 8. *Limnesteria ardra* Wright, 1920; GSI:F00893; oblique aspect; $\times 16.5$.



TEXT-FIG. 9. *Limnesteria ardra* Wright, 1920; GSI:F00894; inclined dorso-ventral aspect; $\times 18.5$.

The proximal segments of the rami bear fewer setae than the distal. The latter each bear three or four, evenly spaced, setae; these are directed adaxially and distally. Specimens in lateral aspect confirm that the setae were aligned along the mid-line of the posterior-facing margin of the rami; in dorso-ventral aspect, setae are less numerous, appear shorter and are less regularly arranged because their proximal parts are overlain by the segments of the rami (e.g. compare



Text-fig. 12C with Text-figs 9 and 16A, respectively). The morphology of the setae does not vary; each is unbranched, broad proximally, tapers rapidly and has a long slender termination.

The nature of the other cephalic appendages is difficult to resolve. In addition to their small size they are commonly superimposed upon each other, as well as on, or by, other appendages, notably the protopods of the antennae (e.g. Text-figs 11A, 12C). In addition, decay-induced collapse and subsequent compaction have reduced them to near two-dimensional structures.

The mandible is relatively large. In lateral aspect it is asymmetrically lachrymal in outline (Text-fig. 12C). The convex posterior-facing margin and the straight to slightly concave anterior-facing margin converge dorsally in a triangular termination. The distal margin exhibits pronounced ventral convexity. The side that faced laterally was convex (e.g. the more ventral mandible in Text-fig. 12C). A narrow parallel-sided perimeter of cuticle defines the postero-lateral margin of the more dorsal of the two mandibles in specimen NMING:F:14724 (Text-fig. 12C). Medial of this is a sediment-infilled area that may represent the mandibular foramen (McLaughlin 1980: = mandibular cavity [G. Fryer, pers. comm. 1998]). The ovate area in slightly positive relief ventral of this is interpreted as the molar area. It is traversed by narrow, highly reflective lines that may indicate the presence of fine ridges. Specimens in dorso-ventral aspect afford views of the mandible in oblique or transverse planes (e.g. Text-fig. 9). In such orientations, the side of the mandible that faced laterally during life is convex; the proximal two-thirds of the side that faced medially is straight and slopes slightly postero-laterally; it then flexes abruptly and is directed medially. The distal part of each mandible therefore curved medio-transversely to bring the molar areas into opposition. The more proximal part was flattened on the medial facing side, including the dorsal articulation between mandible and head, but convex on the lateral-facing side (reconstruction in Text-fig. 18D).

A poorly preserved, elongate, appendage may represent the maxillule (Text-figs 9, 12C). The maxilla has not been identified.

In *Limnesteria ardra* the first two pairs of trunk appendages in the male are modified as claspers. The claspers making up the two pairs do not vary significantly in size, morphology or quality of preservation. Neither the left and right members of a pair, nor the first and second pairs, differed (in contrast with those in some living conchostracans).

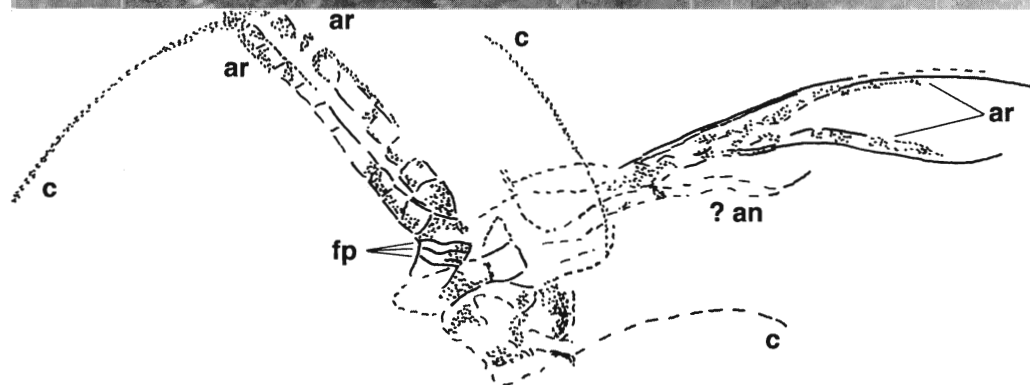
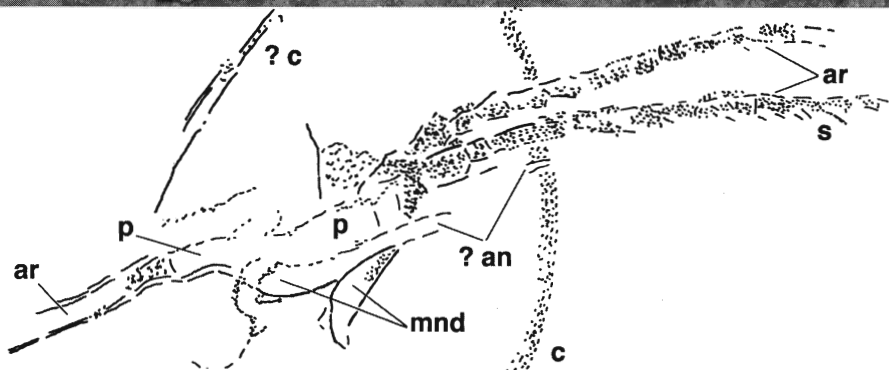
The proximal parts of the claspers are invariably poorly preserved and exhibit no relief. Their margins can sometimes be identified (Text-figs 12C, 13). The proximal part of what is now the posterior-facing margin of the anterior of the two claspers in Text-figure 12A is locally setose. The elongate, tapering, ventrally directed structure immediately distal of these setae is interpreted as the distal part of the exopod.

The distal part of each clasper is almost always well preserved in relief and can be reconstructed in detail (Text-figs 12C, 13: reconstruction in Text-fig. 18E); accordingly, as in extant conchostracans, the cuticle of this part of the clasper is interpreted to have been thicker. The distal part of the clasper comprises the 'hand' (term of Olesen *et al.* 1996), part of which is the apical club (term of Fryer 1987), which carries a palp, the apical hook (term of Fryer 1987) and a second palp; see Appendix 1 for further discussion of this terminology.

The apical hook is arcuate in outline. The margin shared with the 'hand' is slightly convex ventrally; it occupies most of the distal margin of the 'hand'. The ventral margin of the apical hook is semicircular. The proximal part of the antero-dorsal margin is gently convex; it then sharply recurves; distal of this point its course parallels that of the posterior margin. This defines a broad sub-triangular base to the apical hook and a longer, narrow, distal part. The distal end of the apical hook opposes the setiferous, lobate to quadrate, apical club; the setae are short and stout. The apical club has a small narrow palp (Text-fig. 13D–F). A long, narrow, ventrally directed, palp attaches to the ventral margin of the 'hand'. In at least the majority of extant conchostracans this palp is sub-divided into two segments (e.g. Olesen *et al.* 1996, text-figs 11d, 12b, 14e, g). Segmentation of this palp is not evident in *Limnesteria ardra*. This may be taphonomic; the palp is narrow and the lithologies have been deformed; a subtle constriction along its length demarcating two segments is unlikely to be preserved.

The orientation of the claspers is highly variable, even within an individual specimen; for example, the apical hooks in Text-figure 13D–E face in opposing directions. Few occur in what is interpreted, by analogy with extant conchostracans, to have been life position. This is the result of displacement from life position during transport and burial, and post-burial, decay-induced, rotation and collapse of the claspers into more stable attitudes than those in which they were deposited (see Remarks, below).

Two unequivocal claspers are evident in the holotype (Text-figs 6, 12C); two less obvious examples occur in a medio-dorsal position (Text-figs 6, 13A–C). Wright (1920, pl. 24, fig. 1) illustrated the latter but attempted no interpretation. The posterior of the two medio-dorsally sited claspers comprises a curved structure with a narrow, linear structure oriented approximately normal to it. In each of the unequivocal claspers the distal part of the apical hook, and



A

B

C

D

the palp that extends from the ventral margin of the 'hand', have a similar arrangement and size. The margins of the proximal parts of both pairs of claspers are narrow reflective bands; these coalesce centrally and are elongate in opposite directions (Text-fig. 6).

In specimen GSI:F00893 and its counterpart, In21099, the apical hooks of two claspers are juxtaposed with the proximal parts of the antennal rami (Text-figs 7–8, 13b–F); two more complete claspers occur in an antero-dorsal position (Text-figs 7–8, 13G–I). Wright (1920, p. 201, pl. 25, fig. 1) correctly identified the latter and illustrated one of them; she (p. 201) regarded them as belonging to a second animal. Herein all four claspers are interpreted to belong to the same specimen, with the two on the dorsal side significantly displaced from life position (see Remarks, below).

In specimen In21100 (Text-fig. 14) and its counterpart, GSI:F24085, three unequivocal claspers are present; the apical hook of a fourth is less confidently identified. Wright (1920, p. 189) illustrated one in her text-figure 1B and in the text (p. 201) made reference to 'two clasper claws [= apical hooks]'.
 Three apical hooks are evident in specimen In21096 (Text-fig. 15). Wright (1920, p. 200) claimed the 'claw [= apical hook] of one clasper' was present; her illustration (pl. 24, fig. 2) includes the outline of one of the other two, but no indication that she interpreted it as such.

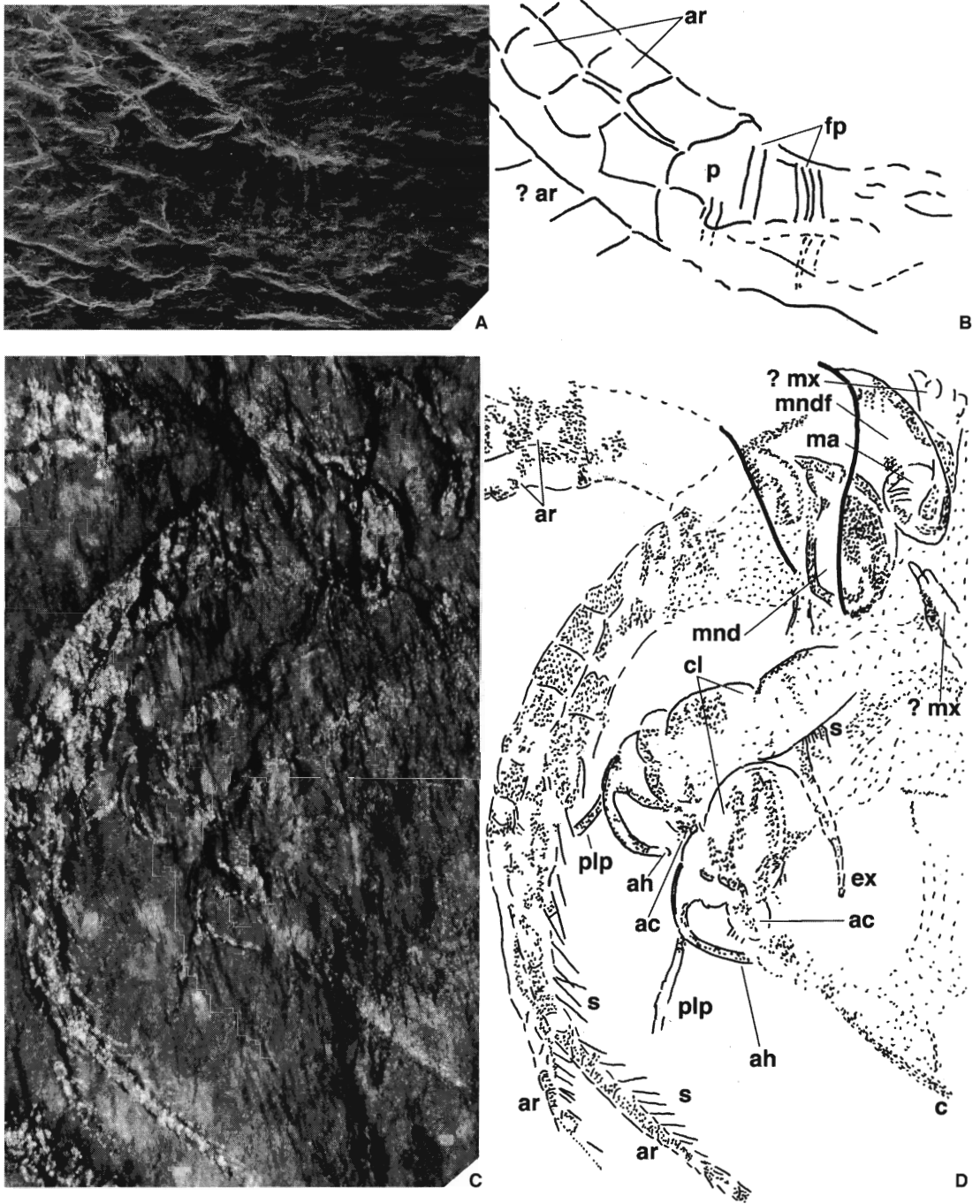
The claspers are the only trunk appendages that preserve any detail. The others are preserved in one of two ways: (1) an area that is moderately reflective (Text-figs 7–8), or (2) an area that is simply darker in reflected light than the matrix (Text-fig. 16B). The shape of these areas indicates that the longest trunk appendages occur approximately one-third from the anterior; either side of this there is a progressive decrease in length. Narrow, ventrally directed, linear structures that occur within, and extend beyond, these areas (e.g. Text-fig. 7) may represent either the exopod, endite 6, or palp (*sensu* McLaughlin 1980: see discussion in Appendix 1) of trunk appendages, or some combination thereof.

The outline of the trunk is preserved in a similar manner to the trunk appendages. Transverse banding defines individual trunk segments (Text-fig. 17A–C). The dorsal margin of each of the posteriormost segments extends into a posteriorly directed projection (= denticle of Fryer 1987) (Text-figs 6, 13B: reconstruction in Text-fig. 18F).

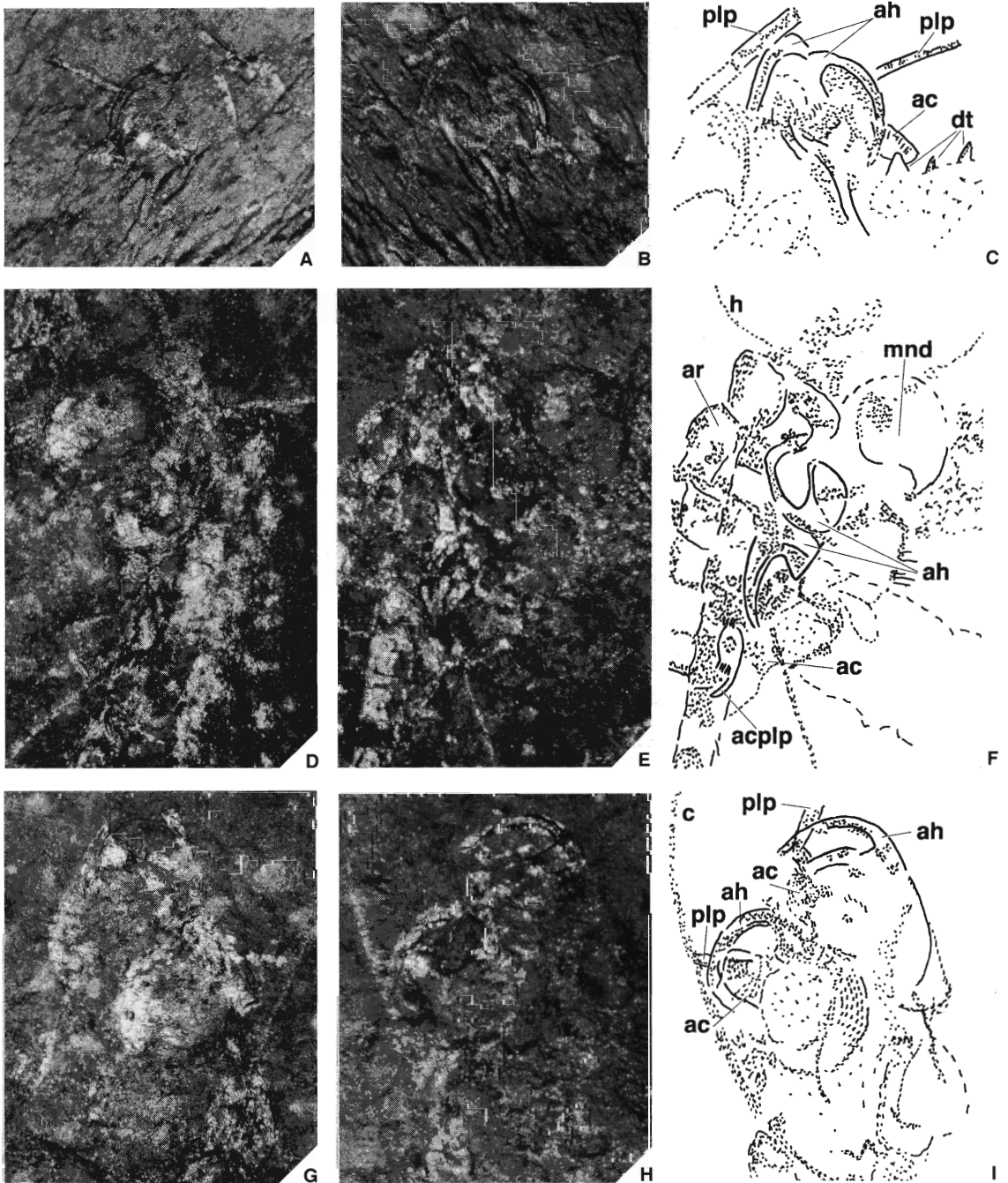
The telson is sub-rectangular in lateral view (Text-figs 6–9, 17: reconstruction in Text-fig. 18F). The dorsal margin, which terminates anteriorly in a paired rounded projection (e.g. Text-fig. 17G, I), bears two longitudinal rows of spines flanking the mid line. The anteriormost, and one about one-third the distance from anterior to posterior, are larger than the rest (e.g. Text-fig. 17H). The telson terminates postero-dorsally in a pair of stout, curved anal spines that bear smaller spines along their anterior margins (e.g. Text-fig. 17E). The posterior margin of the telson is slightly concave. The postero-ventral corner of the telson bears a pair of circular 'denticles' close to the insertion of the caudal rami (e.g. Text-fig. 17E, G–I). These rami curve dorsally and bear a row of posteriorly directed setae along the dorsal margin (e.g. Text-fig. 17H). The ventral and anterior margins of the telson are straight and lack spines.

Remarks. Wright (1920, pp. 196–197) identified only one pair of claspers in *Limmestheria ardra* as opposed to the two identified here. This has significant implications for the taxonomic affinities of *L. ardra* (see below). Wright's error probably arose from a failure to recognize fully the extent to which the orientation of individual appendages can differ from that of the specimen as a whole. She (p. 201) found it necessary, for example, to invoke the fortuitous superimposition of two animals, aligned sub-parallel to each other and facing the same direction, to explain the presence of four claspers in specimen GSI:F00893 and its counterpart In21099; the apparent absence of any anatomical features of the second animal, other than the claspers, was not commented on.

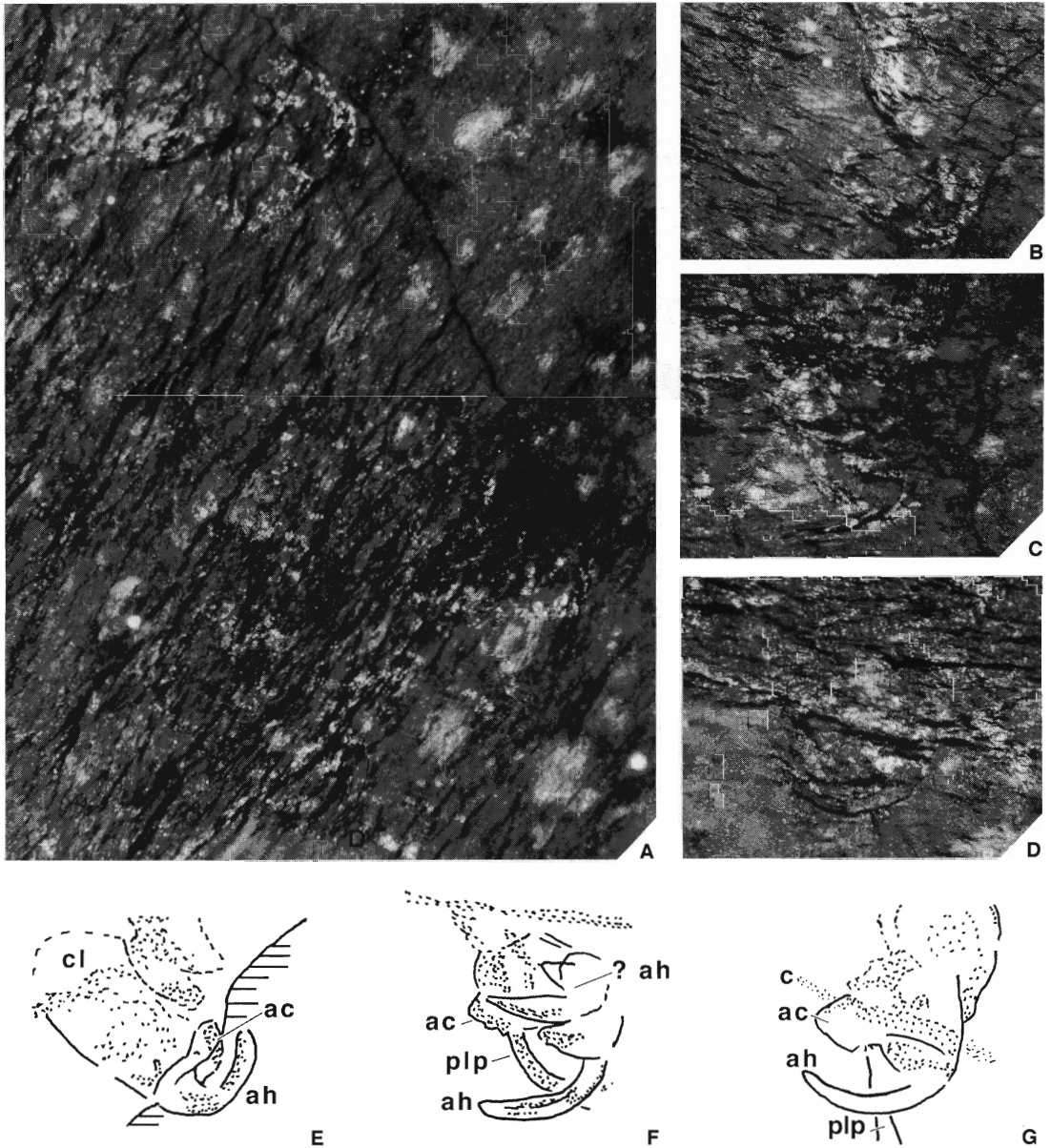
Discrepancies between the orientation of the claspers and the specimen as a whole could have arisen in at least two ways: (1) the anteriormost trunk appendages, including the claspers, were some of the longest, and thus especially prone to simple displacement from life position during transport of a specimen and its incorporation into a depositing event bed (see *Specimen orientation*, above); and (2) experiments indicate that arthropod cuticle becomes flaccid and collapses during decay, due to loss of its structural strength (Briggs and Kear 1994); this would preferentially affect thinner and/or less sclerotized cuticle, such as that covering the proximal parts of the claspers; as the conchostracans decayed, the more robust distal parts of the claspers could be re-oriented into more stable attitudes than those in which they were originally deposited.



TEXT-FIG. 12. *Limnetheria ardra* Wright, 1920. A-B, GSI:F24085; dorso-ventral aspect; $\times 42.5$. C-D, NMING:F:14724; lateral aspect; $\times 37$.

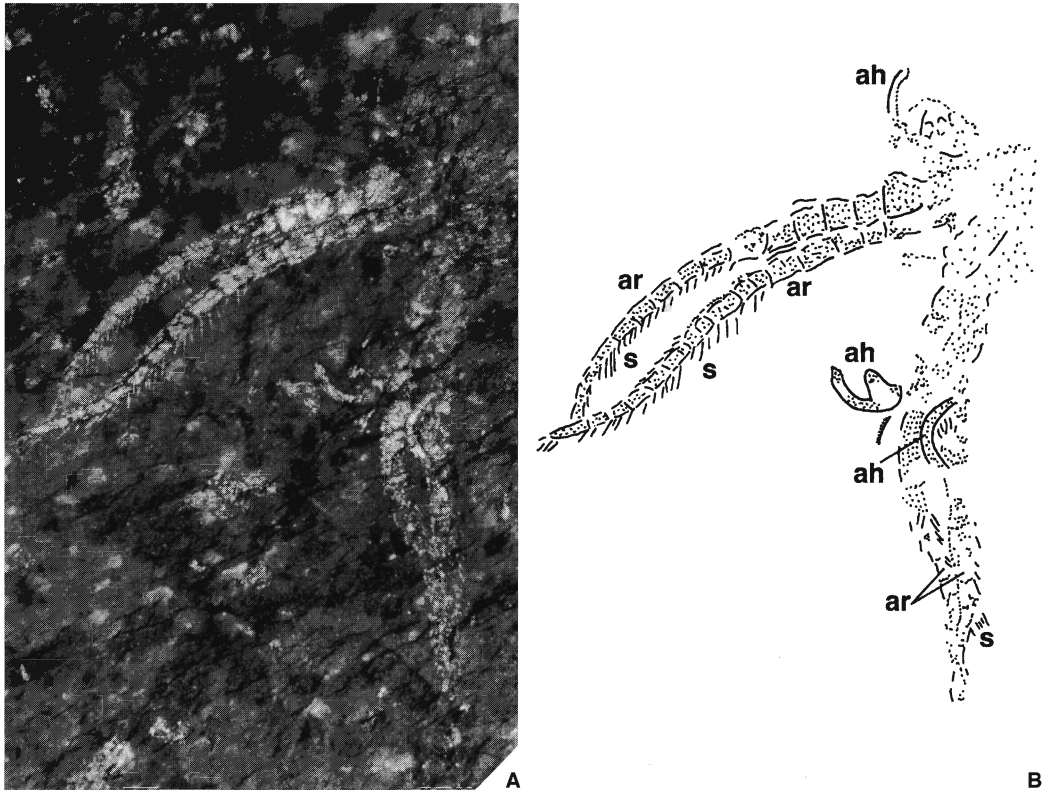


TEXT-FIG. 13. *Limnesteria ardra* Wright, 1920. A, GSI:F00197a. B, NMING:F:14724. C, composite drawing of A (reversed) and B. D, GSI:F00893. E, In21099. F, composite drawing of D (reversed) and E. G, GSI:F00893. H, In21099. I, composite drawing of G (reversed) and H. All $\times 31$.

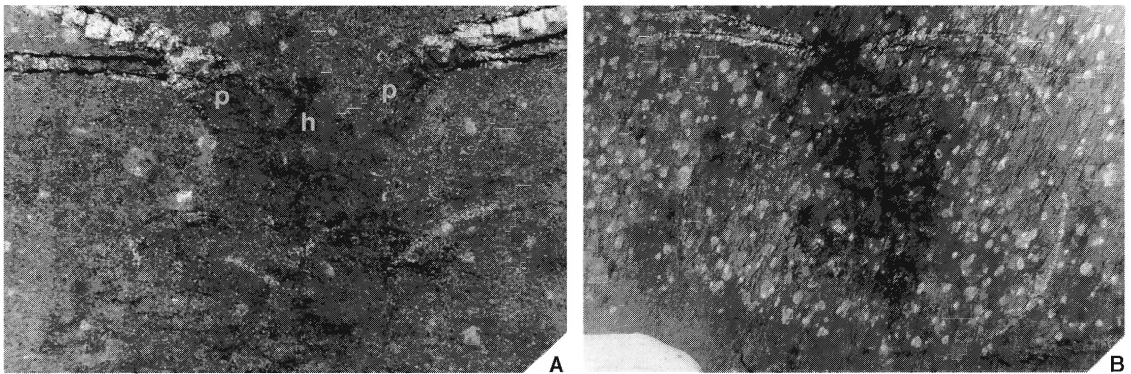


TEXT-FIG. 14. *Limnesteria ardra* Wright, 1920; In21100; dorso-ventral aspect; letters in A indicate the distal parts of claspers that are illustrated in B, C and D, with corresponding line drawings in E, F and G, respectively; A, $\times 31$; B, E, $\times 31$; C–D, F–G, $\times 45$.

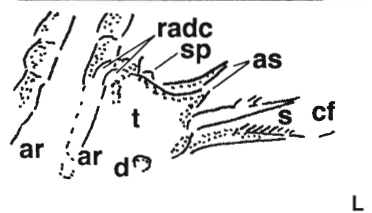
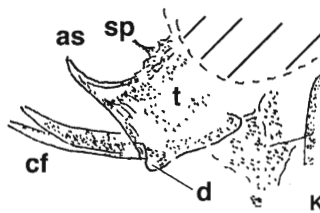
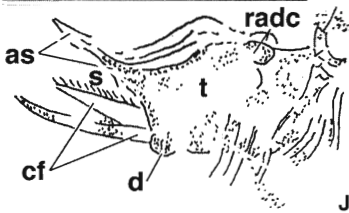
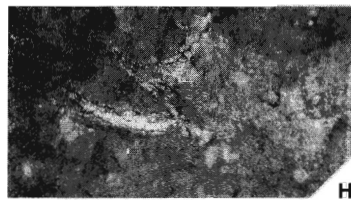
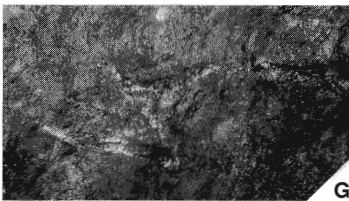
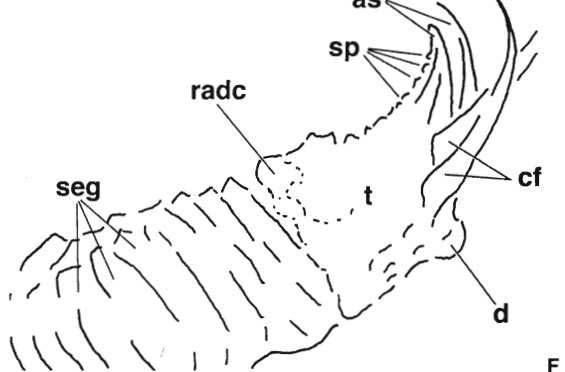
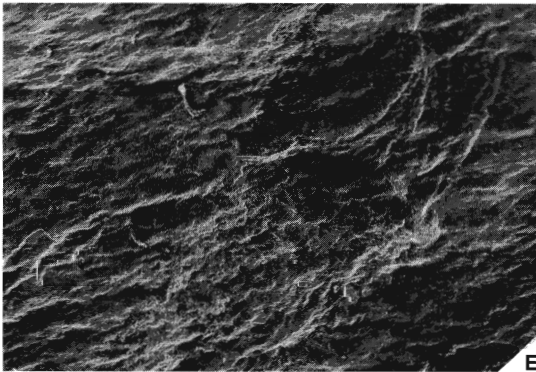
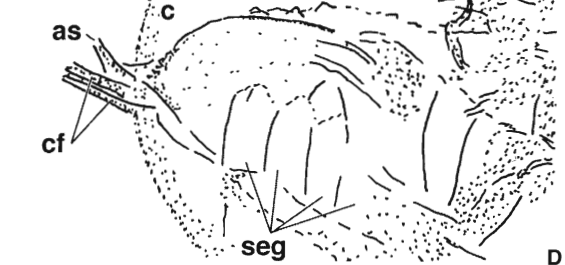
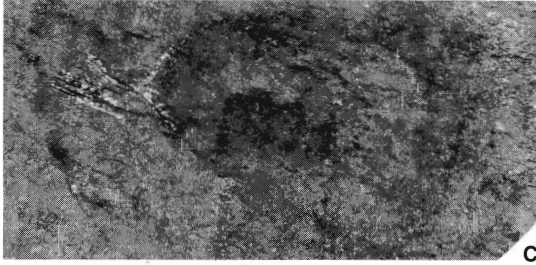
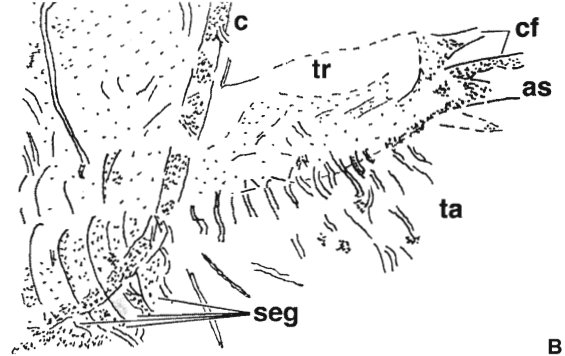
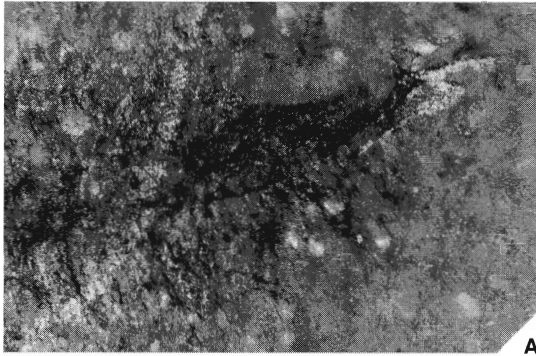
The holotype (Text-fig. 6) is preserved in lateral aspect. The long axis of each of the four claspers is oriented parallel, or at a very shallow angle to, bedding; the preserved length of each is similar and therefore equates to the real length. The two claspers in a medio-dorsal position are interpreted to have been simply 'flipped over' from life position by 180° during transport and deposition of the specimen

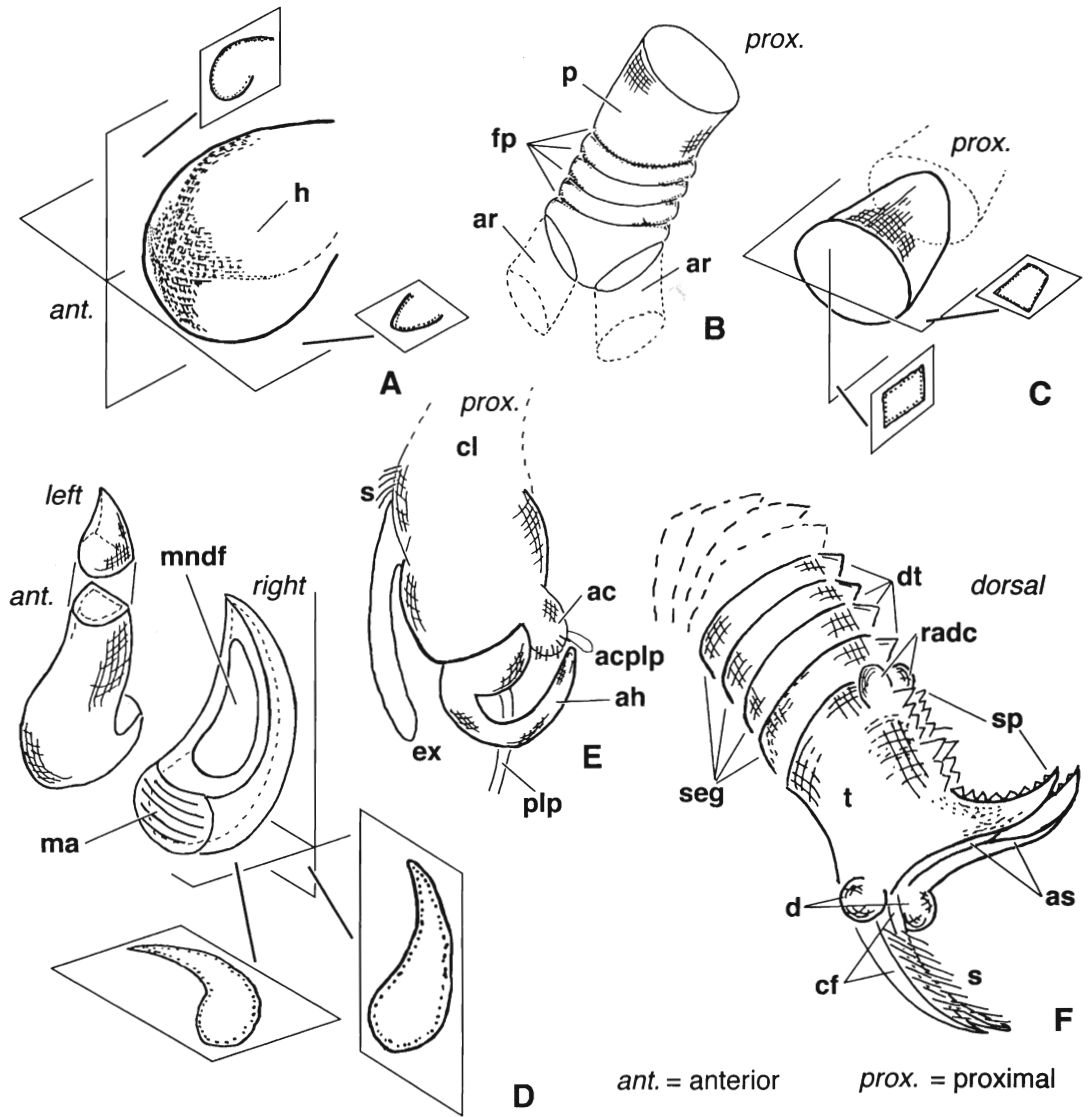


TEXT-FIG. 15. *Limnesteria ardra* Wright, 1920; In21096; incomplete specimen; attitude uncertain; $\times 23$.



TEXT-FIG. 16. *Limnesteria ardra* Wright, 1920. A, In21101(1); dorso-ventral aspect; $\times 17$. B, GSI:F00897; dorso-ventral aspect; $\times 8$.

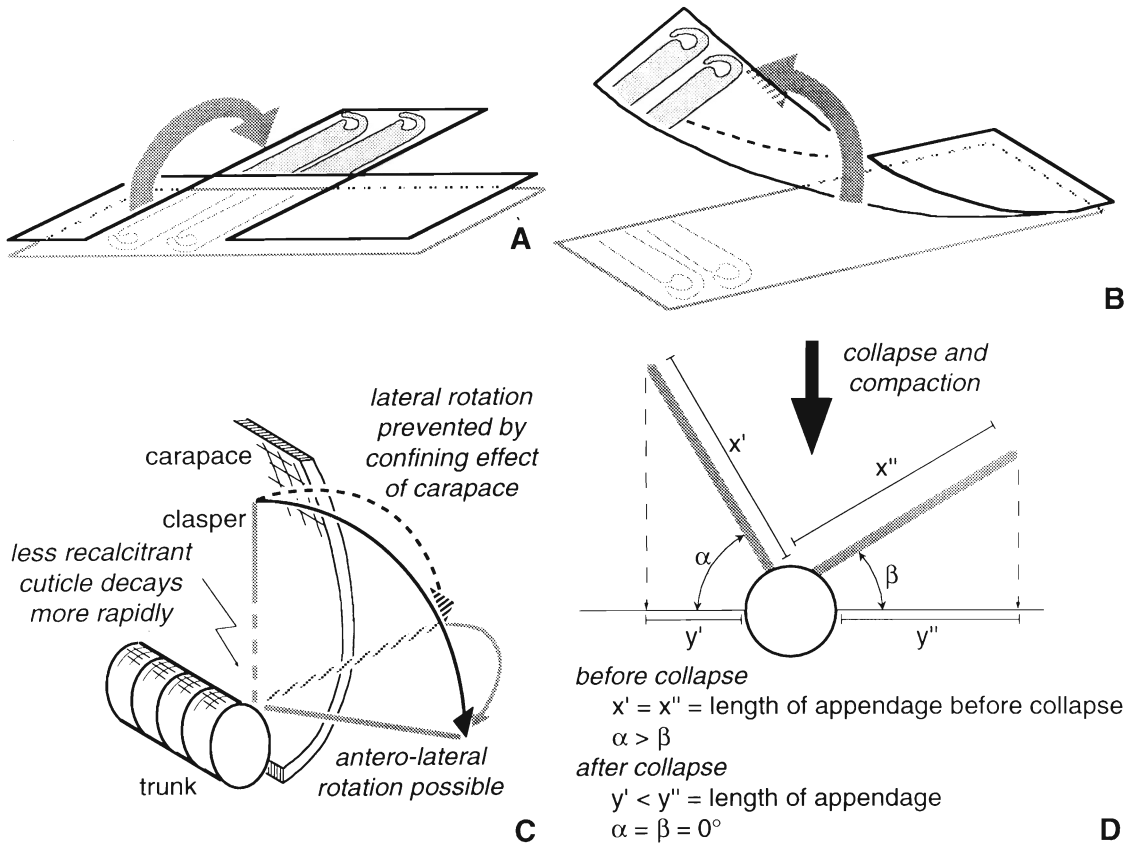




TEXT-FIG. 18. Reconstruction of *Limnetheria ardra* Wright, 1920. A, head. B, protopod of antenna. C, segment of antennal ramus. D, left and right mandibles. E, clasper. F, posterior of trunk and telson. Not to scale.

(Text-fig. 19A; compare with Text-fig. 6). The two claspers in an antero-ventral position appear to be better preserved than the pair in a medio-dorsal position; compare Text-figure 12C with Text-figure 13A–B, respectively. This is considered to be an artefact resulting from subtle differences in position relative to the plane of splitting: the former lie on, and the latter marginally above or below, the plane of splitting. This

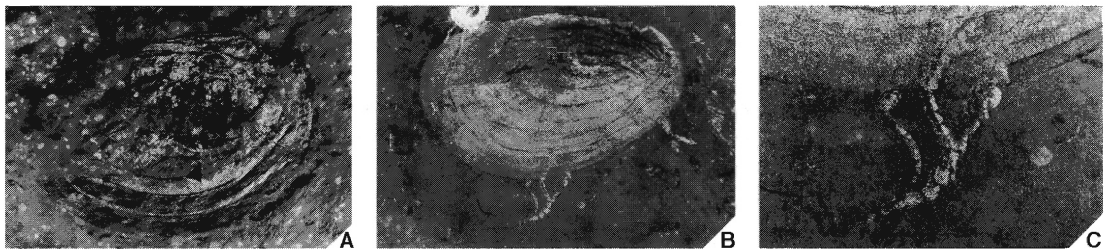
TEXT-FIG. 17. *Limnetheria ardra* Wright, 1920. A–B, NMING:F:14725/2; × 20.5. C–D, NMING:F:14725/3; × 26. E–F, GSI:F24085; × 31.25. G, J, In21097; × 23. H, K, GSI:F00893; × 24. I, L, GSI:F00894; × 22.5.



TEXT-FIG. 19. Models to explain how the variable orientation of claspers in *Limnesteria ardra* Wright, 1920 is the result of displacement during burial and their rotation and collapse after burial; see text for further details.

would be consistent with each pair representing the first and second trunk appendages on the same side of the body.

Specimen GSI:F00893 and its counterpart, In21099, are preserved in oblique aspect. The apical hooks of two claspers are juxtaposed with the proximal parts of the antennal rami (Text-fig. 13D–E); the proximal



TEXT-FIG. 20. Specimens tentatively identified as *Limnesteria ardra* Wright, 1920. A, In21098(2); lateral aspect; $\times 7.25$. B, GSI:F00896; lateral aspect; $\times 4.25$. C, GSI:F00896; lateral aspect; $\times 12.5$.

parts of these claspers cannot be identified. Two other claspers in an antero-dorsal position (Text-fig. 13G–H) are more displaced from life position and their preserved length is greater; their proximal parts merge with an area that represents the trunk and the other trunk appendages (Text-figs 7–8). On the dorsal side of the specimen the perimeter of this area curves postero-ventrally. An outline of this shape can be derived by (1) having the anteriormost trunk appendages on each side of the body in a different orientation, (2) the posterior of each in a similar orientation, and, (3) projecting the resultant outline on to a horizontal plane to simulate the effects of collapse and compaction of the specimen (Text-fig. 19B). The discrepancy in the orientation of the claspers in specimen GSI:F00893 and its counterpart In21099 could therefore have arisen via displacement during transport, and/or deposition at an oblique angle to bedding.

Alternatively, as specimen GSI:F00893 (and its counterpart In21099) is preserved in oblique aspect, it was almost certainly deposited with the long axes of the claspers inclined, rather than sub-parallel, to bedding (cf. the holotype). Decay-induced loss of structural strength of the cuticle may have resulted in rotation of the antero-dorsally sited claspers into a more stable orientation (Text-fig. 19C). The anterior component of rotation would have resulted from the confining effect of the carapace.

These scenarios are not mutually exclusive: re-orientation of the appendages during decay and collapse of the specimen could have been preceded by their displacement during transport and burial.

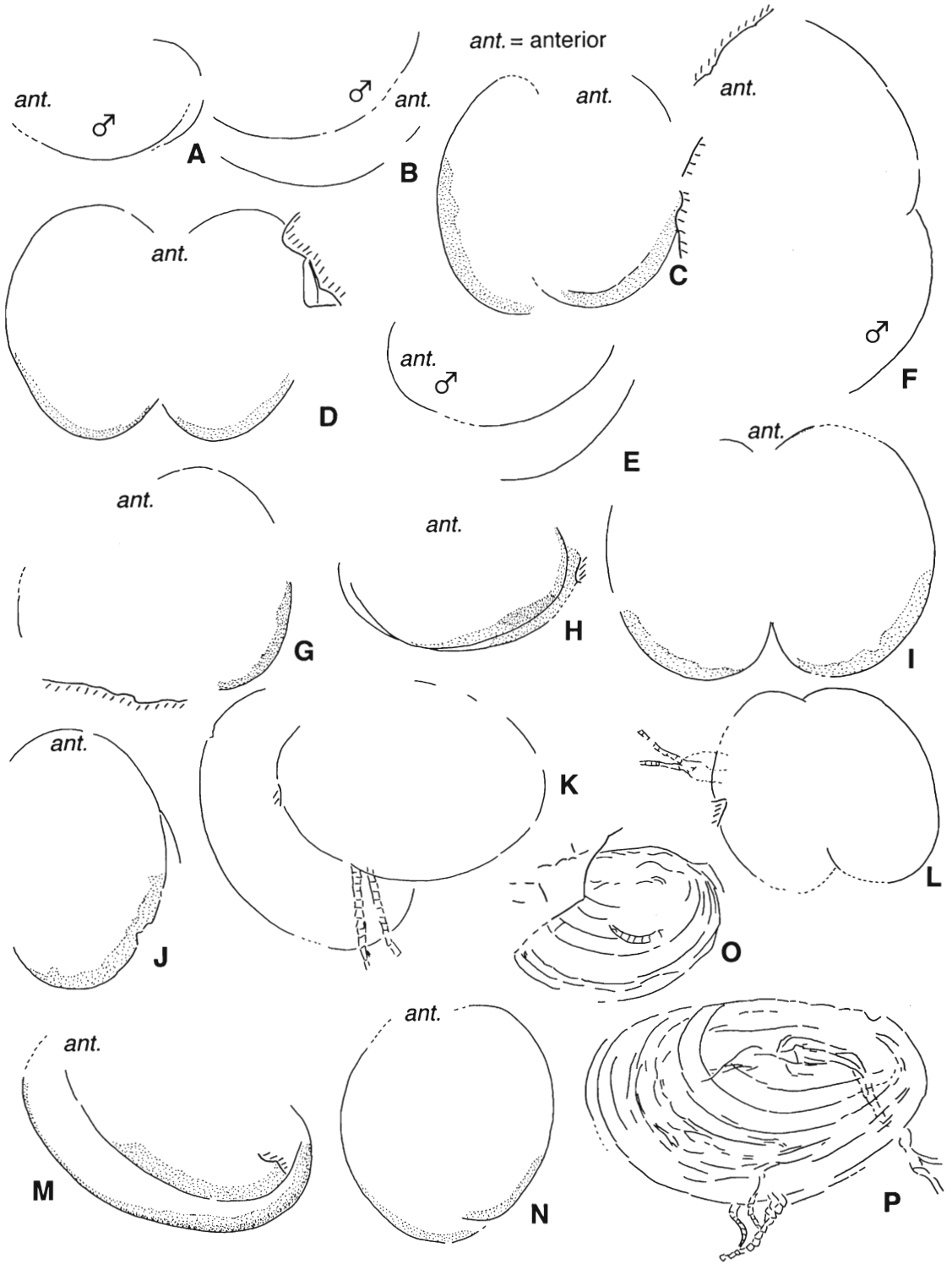
In specimen GSI:F00893 and its counterpart In21099 the four claspers are exposed on the same plane of splitting; however, the preserved length of the two antero-dorsally sited claspers is greater. This difference is consistent with the specimen as a whole being in oblique aspect. If the opposite claspers of a pair were asymmetrically inclined to the plane of bedding, collapse and compaction of the specimen would result in the preserved length of that at a higher angle to bedding being shorter (Text-fig. 19D).

The external morphology of the valves of the carapace is incompletely known. Only two specimens exhibit the exterior of a carapace in association with appendages (Text-fig. 20A–C). Wright (1920) apparently did not recognize the small fragment of antennal ramus present in specimen In21098(2) (at arrow in Text-fig. 20A). Although incomplete, the outline of the carapace is similar to that of *Limnesteria ardra* (compare Text-fig. 21O with Text-fig. 21A–N, respectively); however, insufficient is known of the appendages of the former to confirm that it is similar in other respects. The available evidence, although slight, therefore favours tentatively interpreting specimen In21098(2) as an example of *L. ardra*.

Wright (1920, p. 191) interpreted the association of carapace valve and antennal rami in specimen GSI:F00896 (Text-fig. 20B–C) as fortuitous, resulting from the juxtaposition of two individuals. Despite Wright's interpretation, the carapace valve in specimen GSI:F00896 has subsequently been regarded as *Limnesteria ardra* by several authors (Raymond 1946, p. 268; Tasch 1956, p. 1249, text-fig. 1-1; 1969, p. R148, text-fig. 48.6a; Zhang *et al.* 1987, 1990 left hand specimen in text-fig. 12G).

The antennal rami in specimen GSI:F00896 are very similar to those in other specimens of *Limnesteria ardra*. The proximal ends of the rami lie under the valve, the distal project beyond it. The antennal rami emerge from beneath the carapace near the middle of the ventral side (Text-fig. 20B–C). The significance of this is unclear. In most specimens of *L. ardra* the antennal rami are variably oriented, but usually in an anterior, rather than central, position. There are, however, exceptions (e.g. Text-fig. 21K–L).

As noted by Wright (1920, p. 191) the carapace valve in specimen GSI:F00896 is larger, and a slightly different shape, than those of unequivocal specimens of *Limnesteria ardra* (compare Text-fig. 21P with Text-fig. 21A–N, respectively). Specimens of *L. ardra* display greater symmetry either side of a vertical line from the mid-point of the dorsal side. The curvature of the postero-dorsal margin is less pronounced in specimen GSI:F00896 than in examples of *L. ardra*. Intra-specific variations in carapace morphology occur in extant conchostracans. Roessler (1995b) identified age and environmental conditions as two factors influencing the shape of the carapace in extant species of the family Limnadiidae Baird, 1849 from Colombia. Petrov and Marincěk (1995) documented ontogenetic changes in the shape of the carapace of an extant spinicaudatan. In *Eulimnadia ovisimilis* Martin and Belk, 1989 the carapaces are sexually dimorphic (Martin and Belk 1989). However, the shape of the carapace in *L. ardra* is independent of gender. Taphonomic effects upon the shape of the valve should not be discounted; it may be significant that in specimen GSI:F00896 the carapace valve is in lateral aspect and fully exposed, rather than solely defined as a thin curving line. Accordingly, specimen GSI:F00896 is questionably assigned to *L. ardra*; the most parsimonious interpretation of the carapace and antennal rami is that they belong to the same



specimen. The caveat that the outline of the carapace in specimen GSI:F00896 is different from that in unequivocal examples of *L. ardra* is strongly emphasized.

Wright (1920, text-fig. 3) illustrated specimen NMING:F:14725/1, the right valve of a carapace; no appendages are evident. She claimed (p. 191) that it had a similar size and shape to specimen NMING:F:14725/2 (Text-figs 3D and 21M) which occurs adjacent to it; both are now under the same glass coverslip. Wright (1920) implicitly assigned the latter, in which anatomical features in addition to the outline of the carapace are present, to *Limnesteria ardra*; she regarded specimens 'showing body parts [to be] of sufficient similarity to be considered referable to a single genus' (p. 196). However, she did not assign specimen NMING:F:14725/1 to *L. ardra* citing as her reason (p. 191): 'The danger of judging from mere close association of this nature...'. This decision is supported herein. Specimen NMING:F:14725/1, however, was considered to be *L. ardra* by Raymond (1946, pp. 268–269) who believed it had been assigned as such by Wright (1920).

Limnesteria gracilis sp. nov.

Text-figures 22–30

1996 Conchostracan branchiopods from the Hollypark borehole I, Orr *et al.*, text-fig. 7A–B

Derivation of name. From the Latin 'gracilis' (=slender): to reflect the delicate spination and setation.

Holotype. Geological Survey of Ireland GSI:F03486 (no counterpart).

Other material. GSI:F24069b (part) and GSI:F24070b (counterpart); GSI:F24069c (part) and GSI:F24070c (counterpart); GSI:F24051e (part) and GSI:F03485g (counterpart); GSI:F24051f (part) and GSI:F03485f (counterpart); GSI:F24056a (part) and GSI:F03489a (counterpart); GSI:F03485p (part) and GSI:F24051p (counterpart); GSI:F24051h (no counterpart); GSI:F24070a (part) and GSI:F00513a (counterpart). Numerous fragmentary and incompletely exposed specimens also occur on the surfaces of GSI:F00497–F00498, GSI:F00506, GSI:F00513, GSI:F00515, GSI:F03485, GSI:F03489, GSI:F24051–F24052, GSI:F24056 and GSI:F24069–F24070.

Diagnosis. Carapace valves limnadiiform, with 'growth lines' but no other ornamentation. Outline of head lachrymal in lateral view, with the apex directed antero-ventrally. Antennal rami of c. 19 to 22 cylindrical segments; most of the tapering of each ramus is accommodated distally. First two pairs of trunk appendages in males modified as claspers; stout apical hooks, with well rounded termini. Telson subquadrate in lateral outline: dorsal margin has two longitudinal rows of delicate, acicular spines flanking the mid-line.

Description. Each carapace comprises two valves. In lateral view, the dorsal margin of the valve is virtually straight. The anterior, ventral and posterior margins are a continuous curve; the posterior is slightly more expanded than the anterior. The height of the valve is therefore greatest slightly posterior of its vertical mid-line (Text-fig. 25A–B). Length is 1.3–1.5 times height. There is moderate, sub-equal curvature of both the antero-dorsal and postero-dorsal margins; the latter identifies the shape of the valves as limnadiiform. Antero-dorsally there is a large umbo which does

TEXT-FIG. 21. Outline of carapace in A–N, unequivocal specimens of *Limnesteria ardra* Wright, 1920, and O–P, specimens tentatively assigned to *L. ardra*. Anterior, and male specimens, where known, indicated. A, NMING:F:14724; lateral aspect. B, GSI:F00893; oblique aspect. C, In21097; dorso-ventral aspect. D, In21098(1); dorso-ventral aspect. E, In21099; oblique aspect. F, In21100; dorso-ventral aspect. G, GSI:F00897; dorso-ventral aspect. H, GSI:F00898; dorso-ventral aspect, with caveat that one carapace valve has suffered distortion. I, In21101(1); dorso-ventral aspect. J, In21101(2); lateral aspect. K, GSI:F00900; oblique aspect. L, In21102(2); dorso-ventral aspect. M, NMING:F:14725/2; oblique aspect. N, NMING:F:14725/3; dorso-ventral aspect. O, In21098(2); lateral aspect. P, GSI:F00896; lateral aspect. All $\times 6.25$.

not project dorsally as a beak. Marginal to this umbo, the carapace displays a series of concentric 'growth lines'. The spacing between two adjacent 'growth lines' is greatest in the postero-ventral quarter of each valve. Between the 'growth lines' the surface of the carapace is smooth. No other ornamentation is present.

Most of the head is moderately reflective under incident light, but the perimeter is usually defined as a narrow, more highly reflective, band (Text-figs 22–23, 26, 27A: reconstruction in Text-fig. 30A). The head is relatively large; sagittal length is approximately 20 per cent. of total length. In lateral view, the head is broadly lachrymal in outline, with the apex directed antero-ventrally. The ventral margin is straight or slightly convex and slopes postero-dorsally at a steep angle. The junction between the ventral and anterior margins is accentuated into a short ventrally directed point which is interpreted as a short rostrum. The ventral half of the anterior margin is straight and slopes antero-dorsally at a steep angle; the dorsal half curves posteriorly. The dorsal margin is convex, and elevated slightly above the dorsal margin of the trunk. A small, medial, semicircular elevation of the dorsal margin of the head may mark the position of the attachment ligament (Text-figs 22, 26, 27A). No details can be resolved within the head.

The uniramous antennules can only be identified confidently in two examples. In lateral aspect the antennules attach to the ventral surface of the head a short distance below the antennae (Text-fig. 27A). In dorso-ventral aspect the antennules insert medial to, and slightly posterior of, the antennae (Text-fig. 27C). Their absolute length cannot be determined, but in both these examples they do not narrow significantly along the length observed and may have extended further. One margin of the antennule preserved on the left in Text-figure 27C appears to show a series of lobes; the other is straight. These lobes may be dorsal sensory papillae (*sensu* McLaughlin (1980) = aesthetascs of Martin and Belk (1989) and 'lobes covered by chemosensory papillae' (Schram 1986)).

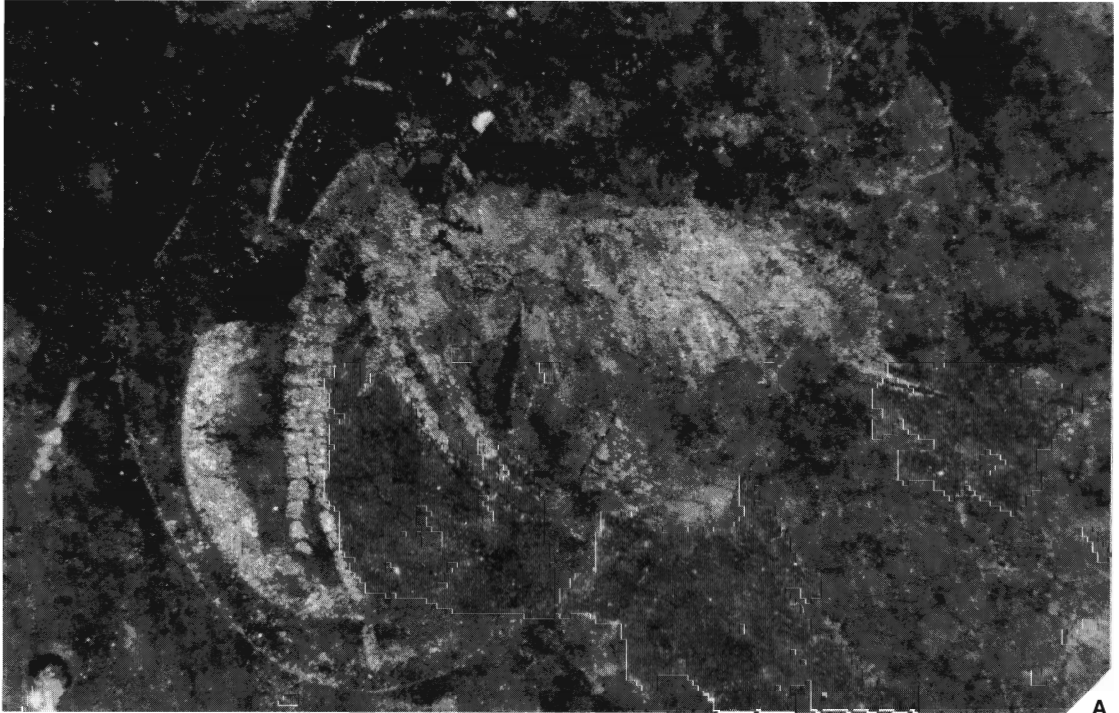
The proximal parts of each antennule are preserved in relief (positive in GSI: F24069b: Text-fig. 27C). Distally, relief is minimal and the antennule is defined as a narrow, elongate structure that is more highly reflective than the trunk appendages. This distinction may identify a division of the antennule into two segments, the proximal shorter with thicker cuticle, the distal longer, with thinner cuticle (reconstruction in Text-fig. 30B). In addition, the antennules are tentatively identified in the holotype (Text-fig. 22) as indistinct, anteriorly directed, elongate structures that are longer and broader than the adjacent trunk appendages.

The antenna is biramous. The protopod is usually indistinct; it is commonly less reflective and preserved in less relief than the attached rami. It is parallel-sided in both lateral and dorso-ventral aspect (Text-figs 22 and 23, respectively), suggesting that it was originally cylindrical. Other structures (e.g. setation or transverse or oblique furrows) are absent. The distal margin of the protopod is straight and normal to the long axis. The proximal parts of the two rami are usually partially superimposed in specimens in dorso-ventral aspect, but not in those in lateral aspect (compare Text-fig. 23 with Text-fig. 22). The two rami therefore joined the protopod one behind the other (reconstruction in Text-fig. 30C).

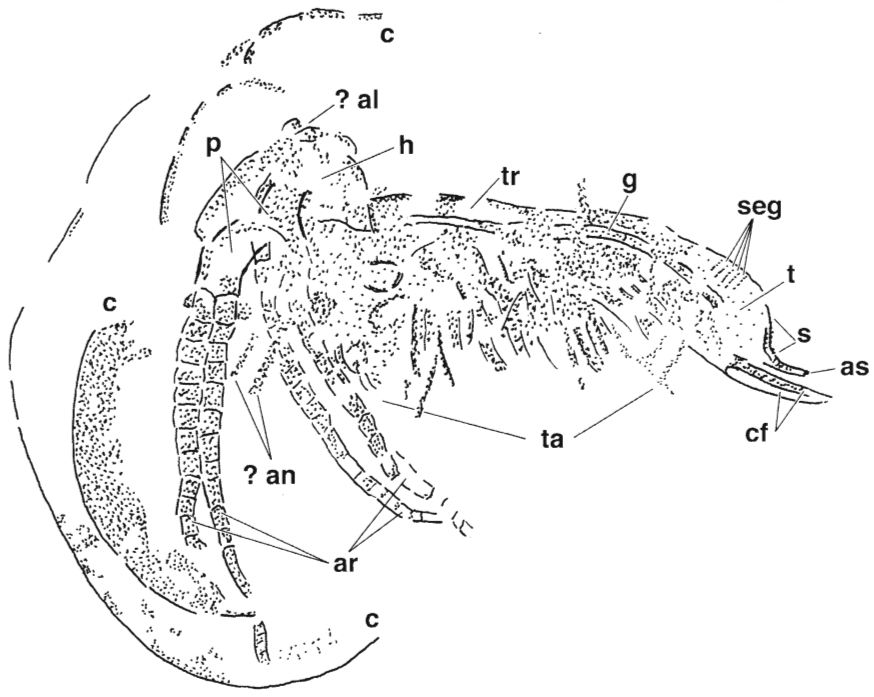
The segmented rami are similar. Individual segments are slightly longer than wide. In both lateral and dorso-ventral aspects they are either parallel-sided or broaden slightly distally. Accordingly, the segments are reconstructed as cylindrical. Most of the tapering of the ramus is accommodated distally. The initial eight to ten segments have a similar length and breadth. The breadth, but not the length, of the succeeding three or four is reduced. Distal of this, the length and breadth of individual segments are progressively reduced; at least another eight segments are present (Text-figs 22, 26). Few specimens reveal the complete, or nearly complete, length of the rami (see Remarks, below).

Setation is absent or scarce on the first five or six segments of each ramus. On the remainder setae occur as a linear, evenly spaced series along the mid-line of the posterior-facing margin; each segment has two to four setae (Text-figs 27A, 28A–B). The anterior facing margin of the ramus and the surfaces of the segments themselves are also setose, but to a markedly lesser extent. Setae on the anterior-facing margin are shorter than the others (at arrows in Text-fig. 28B). As far as can be determined, all setae are of similar type; each is unbranched, broadest at its base and tapers gently to a point. All setae are directed distally.

The mandibles are preserved in greater relief than the adjacent parts of a specimen (Text-figs 23, 25C, 27A, c: reconstruction in Text-fig. 30D). In lateral view the outline of the mandible is asymmetrically lachrymal; the posterior margin is the more convex (Text-fig. 27A). The side that faced laterally during life was smooth and convex (Text-fig. 27A). Its outline is triangular dorsally; it broadens distally and has a curved or straight ventral margin. The ventral margin of the side that faced medially during life is developed as a molar area. This is broadest laterally and constricted slightly medially (Text-fig. 25C). As far as can be resolved, the surface of the molar area is relatively smooth; it certainly lacks any pronounced striations or ridges. Most of the remainder of this side of the mandible is occupied by a large mandibular foramen (Text-fig. 25C). This is broadly triangular in outline; it is flanked laterally by a narrow perimeter of cuticle and dorsally by a triangular area of cuticle. The latter is the site of articulation between the mandible and the cuticle of the head. Specimens in dorso-ventral aspect demonstrate that the distal part of each mandible curved medio-transversely, to oppose the other (Text-fig. 27C). In specimen GSI:F24051f (Text-fig. 25C) the mandible is curved along its length normal to bedding; the proximal and distal ends are elevated further above the

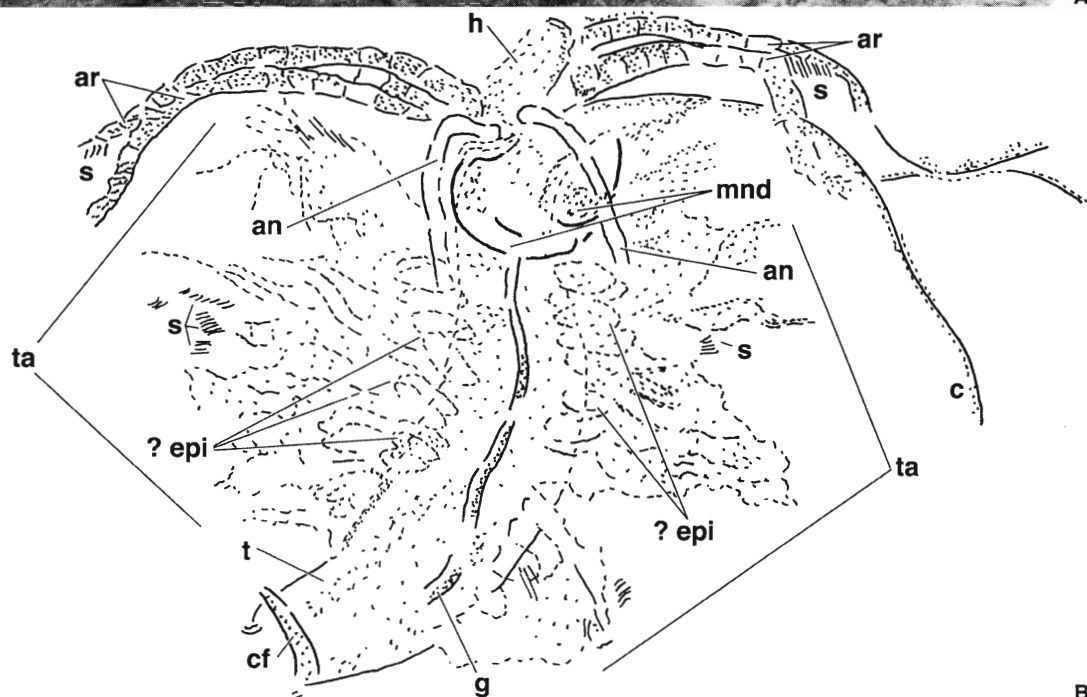


A

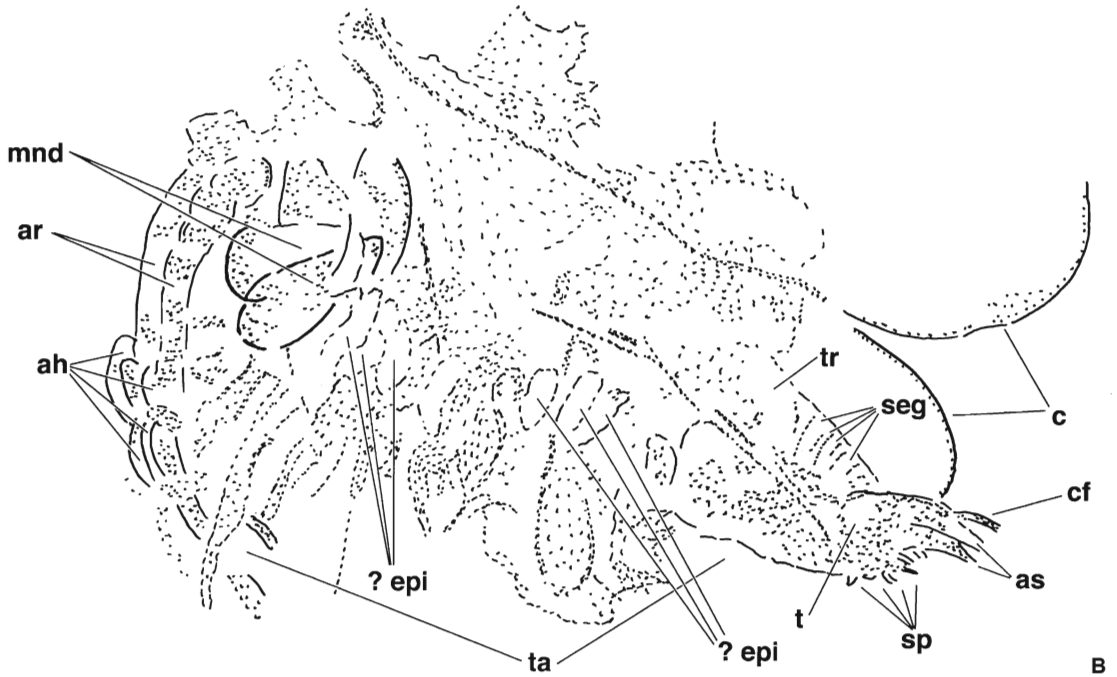
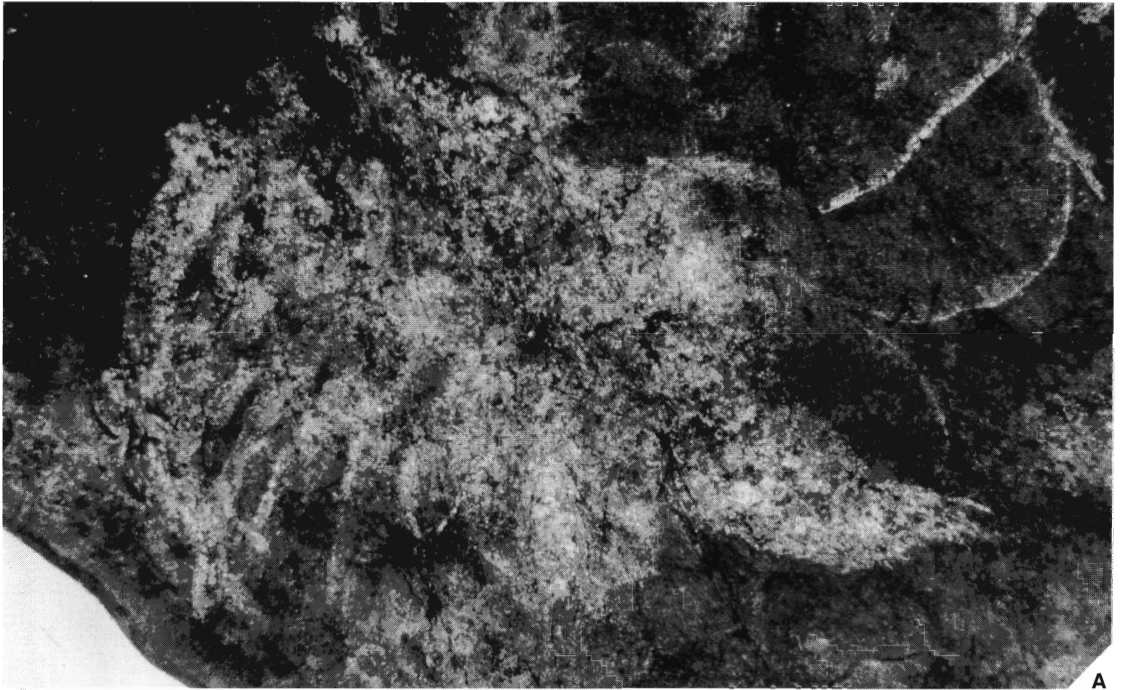


B

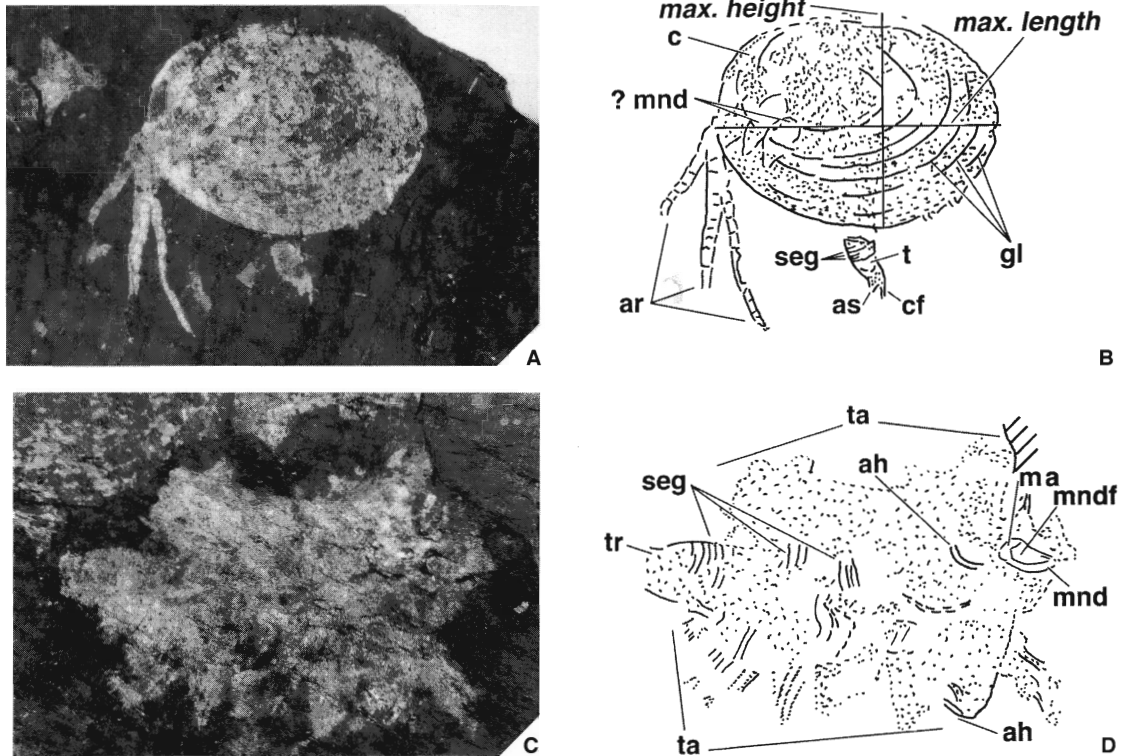
TEXT-FIG. 22. *Linnestheria gracilis* sp. nov.; GSI:F03486, holotype; lateral aspect; $\times 12$.



TEXT-FIG. 23. *Limnesteria gracilis* sp. nov.; GSI:F24069b; dorso-ventral aspect; $\times 17$.



TEXT-FIG. 24. *Limnesteria gracilis* sp. nov.; GSI:F24069c; lateral aspect; $\times 21$.



TEXT-FIG. 25. *Linnestheria gracilis* sp. nov. A–B, GSI:F24051e; lateral aspect; $\times 7.5$. C–D, GSI:F24051f; oblique aspect; $\times 10$.

plane of splitting than the medial parts. As the mandible is in lateral aspect and exhibits the side that would have faced medially during life, this curvature would originally have been in a transverse plane.

The setose lobate structures spatially associated with the mandibles (Text-fig. 27A) are tentatively identified as maxillules. The maxillae have not been identified.

In male specimens of *Linnestheria gracilis* the first two pairs of trunk appendages are modified as claspers (Text-fig. 24: reconstruction in Text-fig. 30E). Usually only the distal part of the apical hook is well preserved; it was robust and a degree of relief has been retained during fossilization (e.g. Text-fig. 28C–E). In specimen GSI:F03485f (Text-fig. 28F) the 'hand' of the clasper can be defined; in addition, the apical club and its palp are preserved in relief. The margin shared by the apical hook and the 'hand' is slightly convex upwards and occupies most of the distal margin of the latter. The posterior and ventral margins of the apical hook are a continuous curve, convex downwards. Proximal of a pronounced deflection, the dorsal margin is rounded and slopes postero-ventrally; distal of this deflection it is recurved anteriorly, convex downward and parallel to the ventral margin. The distal (anterior) termination of the apical hook is a rounded tip. The pronounced deflection in the course of the dorsal margin sub-divides the apical hook into a sub-triangular basal part and an elongate distal part. The apical club is ovate to quadrate in outline in lateral view; a small palp is attached to its ventral margin (Text-fig. 28F). An elongate, narrow, ventrally directed palp extends from the midpoint of the distal margin of the hand (Text-fig. 28C–F).

In an individual specimen, the apical hooks are the same size and shape; their shape is similar between specimens. The morphology of all four claspers is assumed to have been broadly similar.

In virtually all specimens, the remaining trunk appendages occur as a reflective area of irregular outline. In most specimens preserved in lateral aspect the trunk appendages are directed ventrally and those from each side of the body are superimposed (e.g. Text-fig. 22); in most specimens in dorso-ventral aspect, the appendages of each side of the body are separated and extend laterally (e.g. Text-fig. 23). Although their serial similarity along the trunk can be confirmed, it is difficult to resolve the morphology of an individual appendage. The lateral margins of the trunk

appendages are highly setose; individual setae are long (Text-figs 23, 26, 27A). The position, size and shape of a linear series of ovate structures that is preserved marginal to the trunk in some specimens suggests that they are epipods (Text-figs 23–24); see also Text-figure 26. The distal parts of the trunk appendages are usually typified by paired linear structures which are more reflective than the background and in some cases extend beyond the perimeter of the latter. These may represent either the exopod, endite 6, or ‘palp’ (*sensu* McLaughlin 1980) of trunk appendages, or some combination thereof.

The longest trunk appendages are between one-third and half-way along the trunk; either side of this they decrease progressively in length (Text-fig. 23). Marginal to the posterior 15–20 per cent. of the trunk there is either a narrow area that is slightly more reflective than the matrix but lacks identifiable structures (e.g. Text-fig. 29A–B), or there is no indication of appendages (e.g. Text-fig. 29C). An absence of trunk appendages in the posterior 15–20 per cent. of the trunk in *Limnesteria gracilis* would be inconsistent with the anatomy of extant conchostracans (see Remarks, below) and the absence of any trace in some specimens is considered taphonomic rather than real. A reduction in the thickness of the cuticle corresponding to a reduction in size would result in a reduced preservation potential. The posteriormost (? four or five pairs) trunk appendages of *L. gracilis* are therefore interpreted as significantly smaller than those immediately anterior of them.

Segmentation of the trunk is represented by a series of dorso-ventrally oriented bands (Text-figs 25c, 29; reconstruction in Text-fig. 30F). These bands alternate between being very narrow and highly reflective, and slightly broader and less reflective. The former are interpreted as intersomite boundaries rather than as segments themselves. Segmentation is most obvious in the posterior parts of a specimen in those examples where the trunk appendages are not preserved (Text-fig. 29C). Only a single specimen displays segmentation along most of the length of the trunk (Text-fig. 25c); segments have a consistent sagittal length. The relationship between the length of individual segments and that of the trunk as a whole suggests that in excess of 20, and perhaps approaching 30, trunk segments are present.

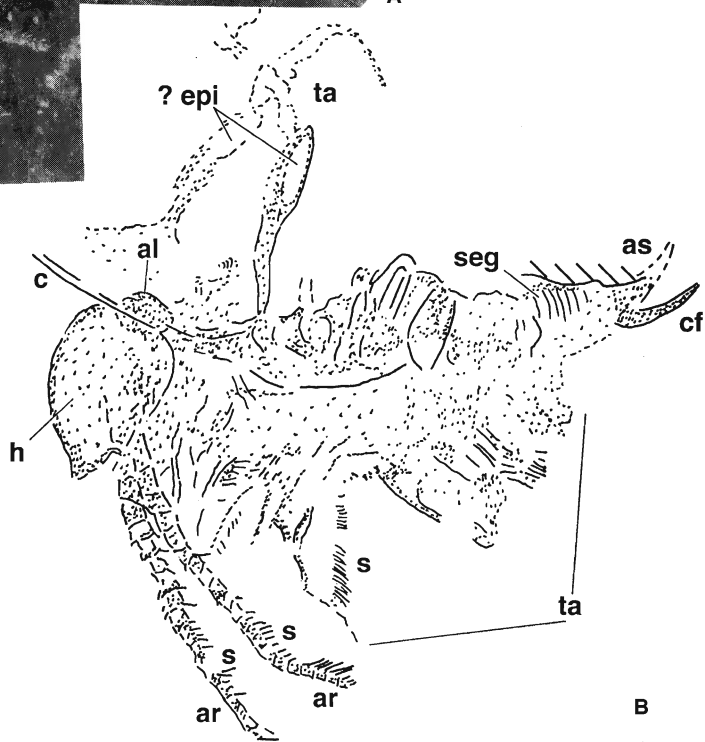
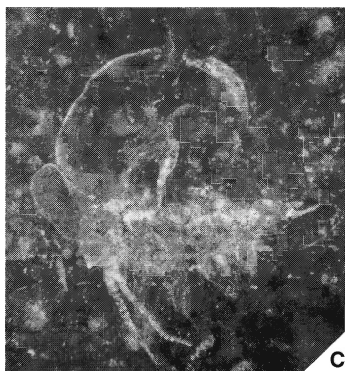
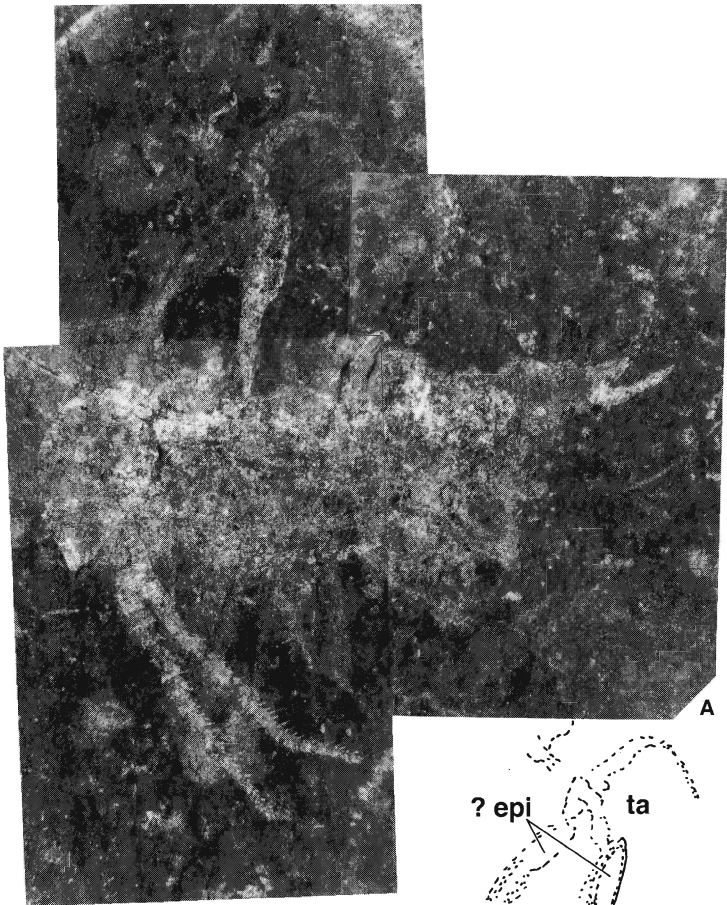
The dorsal margin of at least the posteriormost segments of the trunk is extended into a series of delicate spine-like projections (denticles *sensu* Fryer 1987); the anterior and posterior margins of these slope dorso-posteriorly, the posterior more steeply (Text-fig. 29C).

The gut is usually represented by a narrow, highly reflective, line that is preserved in relief. In lateral aspect it lies slightly dorsal of the mid-line in the anterior part of the trunk; posteriorly, it becomes progressively more ventral in position (e.g. Text-fig. 22). In specimens in dorso-ventral aspect, the gut occupies a medial position (e.g. Text-fig. 23).

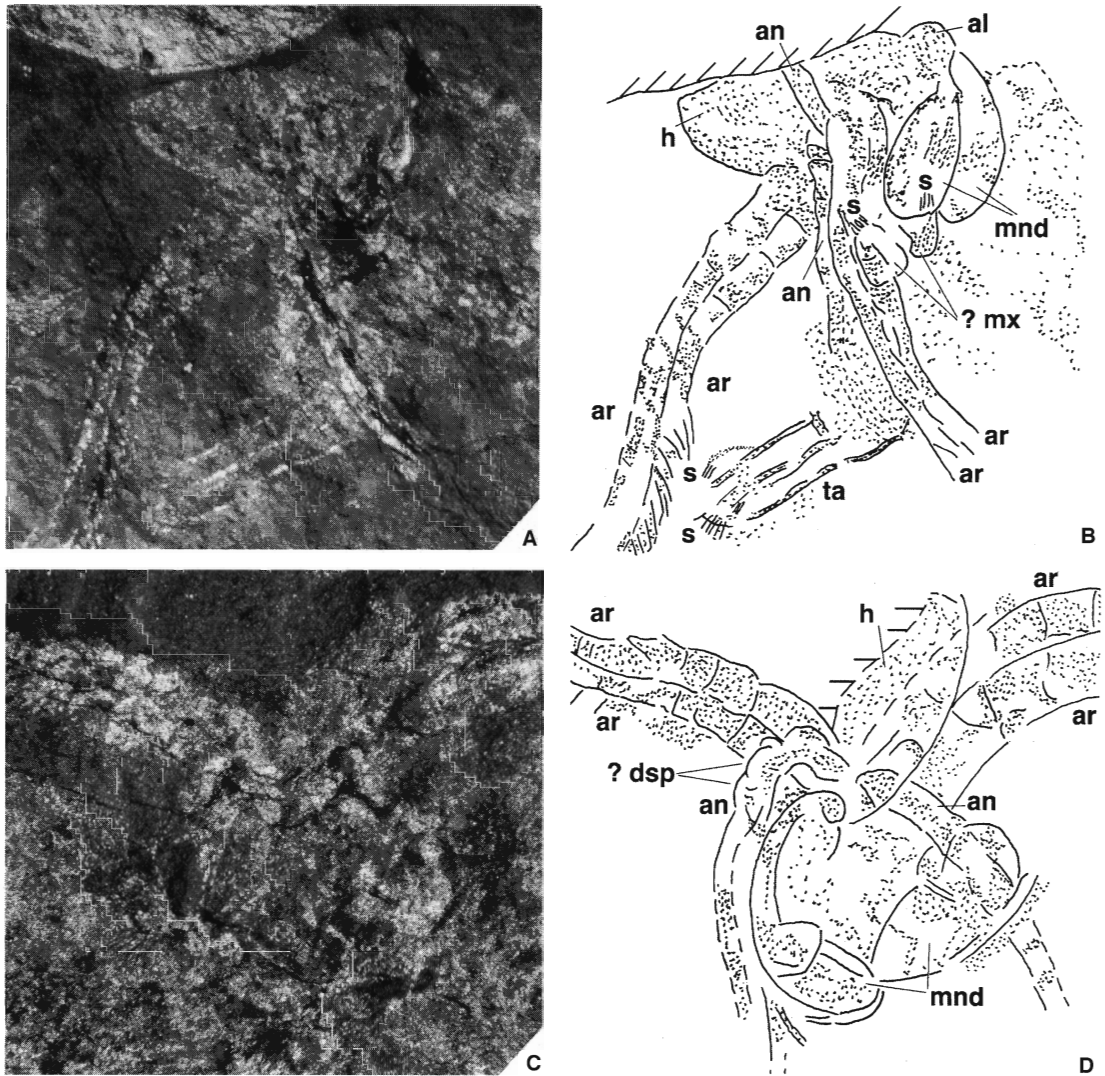
The telson is sub-quadrate in lateral view; length is slightly greater than height (Text-fig. 29; reconstruction in Text-fig. 30). The dorsal margin displays two longitudinal series of numerous spines flanking the mid-line. As each series is clearly outlined (e.g. Text-fig. 29A), the mid-line was presumably depressed. Each spine is delicate, relatively short, needle-like, and elongate normal to the dorsal margin; all are of similar size. There is equivocal evidence in some specimens for the presence of a biramous telsonal filament (Text-fig. 29A). It inserts dorsally slightly anterior of the mid-line and extends normal or oblique to the dorsal margin. As in extant conchostracans, it is presumed to have inserted on to the mid-line between the two longitudinal rows of spines. The dorsal and posterior margins of the telson extend posteriorly into a pair of stout anal spines which curve dorsally. The dorsal margin of each anal spine bears postero-dorsally projecting spines of similar shape and size to those on the dorsal margin of the telson (Text-fig. 29A). The posterior margin of the telson is slightly concave or slopes antero-ventrally. A stout caudal furca inserts at the postero-ventral corner. Each ramus of the caudal furca curves dorsally and bears a series of long narrow spines on its dorsal margin; these point postero-dorsally (Text-fig. 29A). The ventral margin of the telson is straight. The anterior margin is straight or slightly sinuous. Both are unornamented.

Remarks. The antennal rami of *Limnesteria gracilis* repeatedly occur in two preservational states: either the entire, or almost entire, antennal ramus is exposed (e.g. Text-fig. 26) or only the first 12–14 segments are evident (e.g. Text-fig. 25A). Both states can be present within an individual specimen (e.g. Text-fig. 22). It is therefore unlikely that the absence of the distal parts is the result of the decay of thinner cuticle. It is more likely that the distal segments are simply not exposed in some rami; their small size may have been insufficient to induce splitting along, rather than above or below, the plane of the fossil.

The mandibles of *Limnesteria gracilis* tend to be oriented with their longest axis (originally sub-vertical) sub-parallel to the plane of splitting. This is independent of the orientation of the specimen as a whole. For example, the right mandible of the specimen GSI:F24051f (Text-fig. 25c) is preserved with its long axis parallel to the plane of splitting, and the side that would have faced medially during life exposed. The orientation of this mandible is incongruous with the orientation of the specimen as a whole: the mandible has rotated into a more stable orientation.



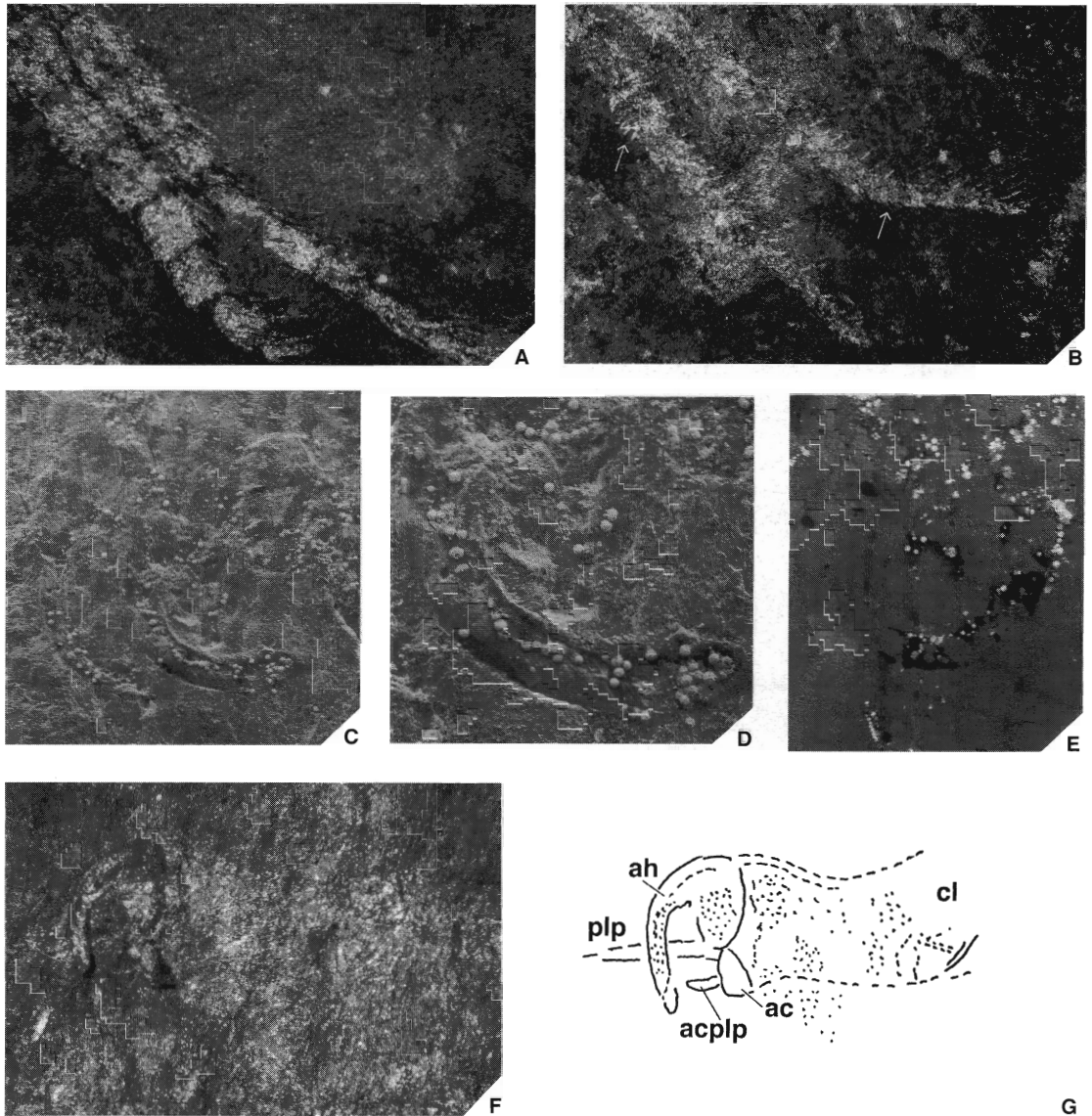
B



TEXT-FIG. 27. *Limnesteria gracilis* sp. nov. A–B, GSI:F03485p; lateral aspect; $\times 25$. C–D, GSI:F24069b; dorso-ventral aspect; $\times 43$.

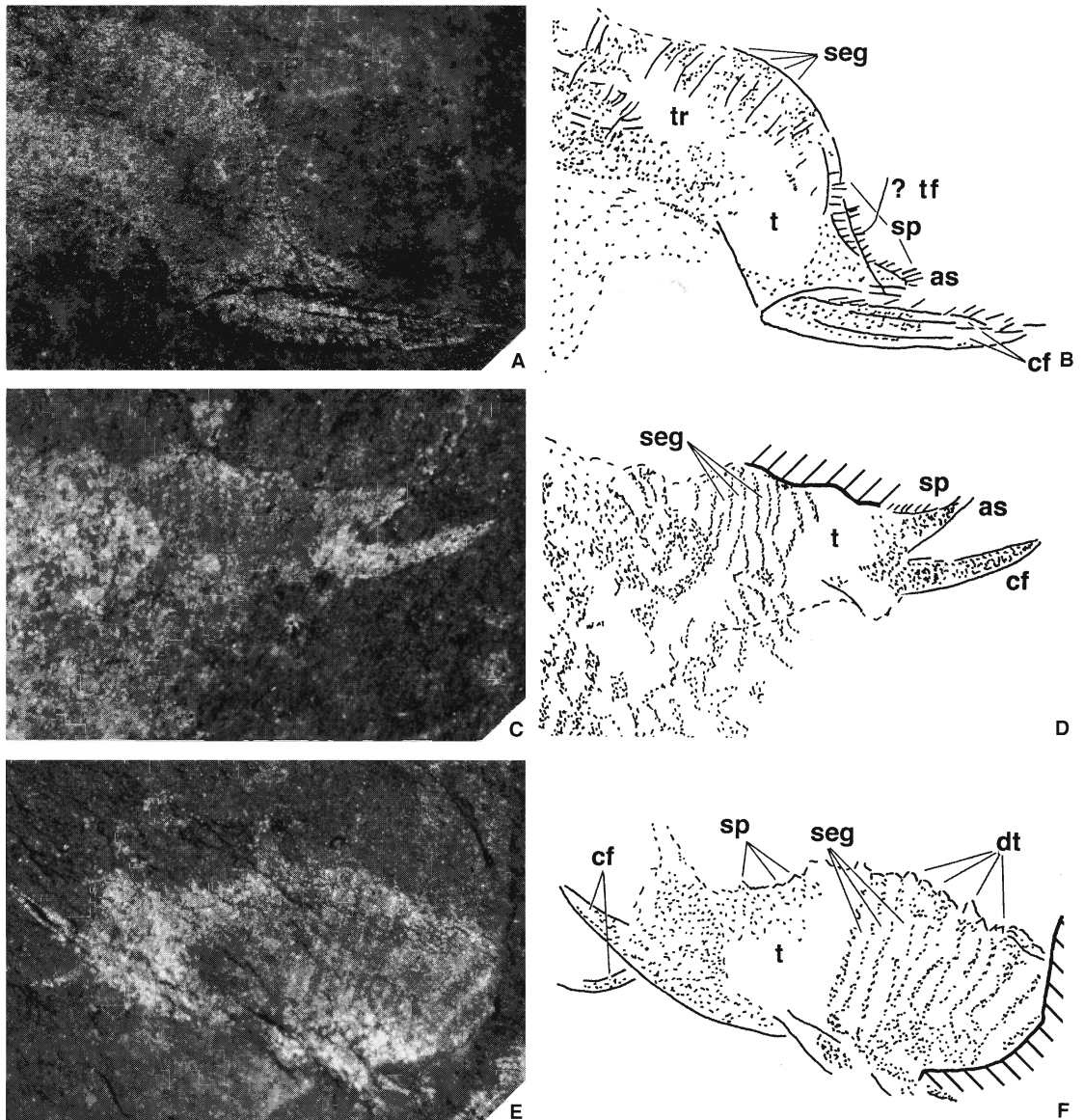
Discrepancies between the orientation of the specimen as a whole and the attitude of the mandibles are more often observed in specimens of *Limnesteria gracilis* than *L. ardra*. The difference between the thickness (and as a result the structural strength) of the cuticle of the head and the mandibles may have been more pronounced in *L. gracilis* than *L. ardra* so that movement of the mandibles was less constrained.

TEXT-FIG. 26. *Limnesteria gracilis* sp. nov.; GSI:F24056a; body in lateral aspect, but valves distorted from life position. A–B, body of specimen; $\times 13.5$. C, entire specimen; $\times 5$.



TEXT-FIG. 28. *Limnesteria gracilis* sp. nov. A, GSI:F03486; $\times 32.5$. B, GSI:F24056a; $\times 30.5$. C, GSI:F24051h; $\times 43$. D, GSI:F24051h; $\times 86$. E, GSI:F24051h; $\times 59.5$. F-G, GSI:F03485f; $\times 26.5$.

In extant conchostracans each somite of the trunk carries a pair of appendages (McLaughlin 1980). In *Eulimnadia ovisimilis* Martin and Belk, 1989 (see Martin 1992, text-fig. 3A [also figured by Martin 1989b, text-fig. 5E, as *Eulimnadia* sp.]) there is a step-like decrease in the size of the appendages of the last four or five trunk somites and those immediately preceding them. A corresponding reduction in their preservation potential is assumed. A similar morphology in *Limnesteria gracilis* would account for the poor preservation of the trunk appendages, or their apparent absence, in the posteriormost 15–20 per cent. of the trunk.

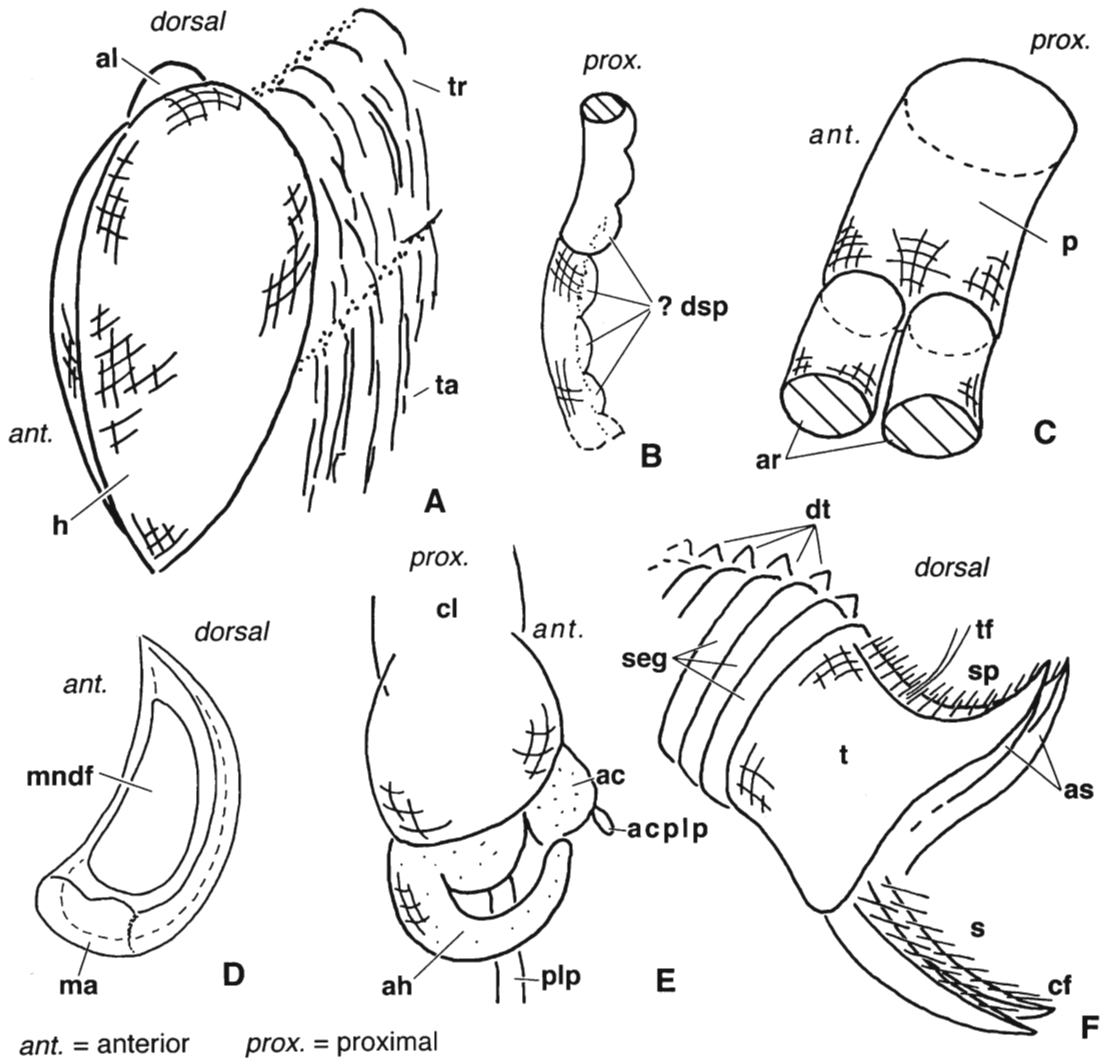


TEXT-FIG. 29. *Limnesteria gracilis* sp. nov. A–B, GSI:F03486; $\times 34.5$. C–D, GSI:F24056a; $\times 30$. E–F, GSI:F24051e; $\times 53.5$. All in lateral aspect.

Taxonomic separation of Limnesteria ardra Wright, 1920 and *Limnesteria gracilis* sp. nov.

The intervals of the two boreholes that yield the exceptionally preserved conchostracan branchiopods have subtly different lithologies and taphonomic histories (see *Sedimentology and Taphonomy*, above). However, the quality of preservation is sufficiently similar to allow the morphological variation between *Limnesteria ardra* and *L. gracilis* to be identified as warranting assignment to different species within the same genus.

Attempts to resolve the taxonomy or phylogeny of branchiopods need to recognize that they exhibit a



TEXT-FIG. 30. Reconstruction of *Limnesteria gracilis* sp. nov. A, head, and anterior of trunk. B, proximal part of antennule. C, protopod of antenna. D, right mandible. E, clasper. F, posterior of trunk and telson. Not to scale.

combination of morphological plasticity and evolutionary stasis (Martin 1992, p. 27). The morphology of extant branchiopods can be modified by varying the conditions under which they are reared (Roessler 1995b). Developing daphniids (Anomopoda: ['Cladocera']) produce spines in response to the waterborne chemical cues of predators; the number of spines increases with predator density (Martin 1992, pp. 27–28, and references therein). In extant conchostracans morphological features that are potential taxonomic characters can also exhibit marked plasticity. Variation in the outline of the carapace and shape of the rostrum can occur between males and females of the same species, for example, *Eulimnadia ovisimilis* Martin and Belk, 1989. *Eulimnadia texana* Packard, 1874 displays variation in rostral morphology that is not sexually dimorphic (Martin and Belk 1989).

In most fossil conchostracans only the valves of the carapace are known and the number of potential taxonomic characters is correspondingly reduced. The shape and ornamentation of these valves is

therefore of paramount importance in deciding their taxonomic affinities. Both *Limnesteria ardra* and *L. gracilis* exhibit significant curvature of the valve margin in the postero-dorsal quadrant of the valve; this characterizes them as limnadiiform. In both (albeit less convincingly demonstrated for *L. ardra*) the exterior of the carapace valves lack ornamentation other than widely spaced 'growth lines'. *Limnesteria gracilis* has a large smooth umbo that does not project dorsally as a beak; there is no evidence for a beak in *L. ardra*. These similarities justify assignment to the same genus.

A number of anatomical features, including the antennae, mandibles, claspers and telson, are repeatedly preserved in both taxa. Differences between the two taxa that separate them at a specific level are:

1. Segments of the antennal rami are virtually cylindrical in *Limnesteria gracilis* (Text-fig. 30C) but more oval in cross section distally in *L. ardra* (Text-fig. 18C).
2. In *Limnesteria gracilis* the distal part of the apical hook of the clasper has a lower length to breadth ratio, and a more rounded termination (compare Text-fig. 28C-E with Text-figs 12C and 13).
3. Spines on the dorsal margin of the telson of *Limnesteria gracilis* are a uniform size; in *L. ardra* they are of variable size and, on the whole, more robust (compare Text-fig. 29 and Text-fig. 17G-I).
4. Compared with the size of the telson, the rami of the caudal furca are proportionally longer in *Limnesteria gracilis* (compare Text-fig. 29 and Text-fig. 17).
5. *Limnesteria gracilis* lacks the pair of rounded denticles that are present at the postero-ventral corners of the telson of *L. ardra* (compare Text-fig. 29 and Text-fig. 17).

Other differences in the anatomy of the species are evident in just a few specimens. In lateral view the outline of the head is lachrymal in *Limnesteria gracilis* but more rounded in *L. ardra* (compare Text-fig. 26 with Text-figs 7 and 8, respectively). Individual segments of the trunk are narrower in *L. gracilis* (compare Text-fig. 29 and Text-fig. 17A-F, respectively). The posteriorly directed spinose projections on the dorsal margins of at least the posteriormost trunk segments are more robust in *L. ardra* (compare Text-figs 6 and 13B with Text-fig. 29E, respectively).

Superfamily ESTHERIELLOIDEA Kobayashi, 1954

Family ESTHERIELLIDAE Kobayashi, 1954

Subfamily ESTHERIELLINAE Kobayashi, 1954

Genus ANOMALONEMA Raymond, 1946

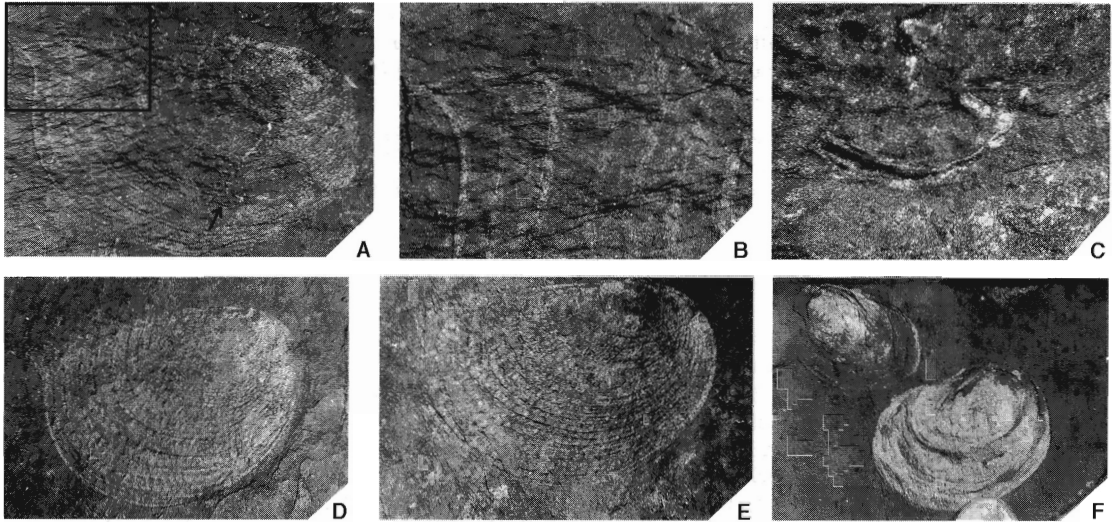
Subgenus ANOMALONEMA Tasch, 1960

Anomalonema (Anomalonema) reumauxi (Pruvost, 1911)

Text-figure 31A-E

Material. GSI:F00208b, GSI:F00208d and GSI:F00208e.

Description. The carapace valves are sub-ovate in lateral outline; maximum length is consistently 1.4 times maximum height (Text-fig. 31A, D-E). The valve margin is moderately convex in the antero-dorsal quadrant of the carapace, the ventral part sloping more steeply. The ventral margin is strongly convex. In the postero-dorsal quadrant the valve margin is initially straight and near-vertical but near its termination it abruptly recurves postero-dorsally; its junction with the dorsal margin therefore defines a small posteriorly pointing triangular projection (Text-fig. 31B). On the postero-dorsal margin, successive 'growth lines' terminate slightly ventral of the preceding; the straight to slightly convex, slightly postero-ventral sloping, dorsal margin is therefore gently serrate (Text-fig. 31B). The antero-dorsally sited umbo is small, smooth, and elevated slightly above dorsal margin. The remainder of the carapace exterior exhibits pronounced 'growth lines'. The ventral margin of the 'growth lines' is tuberculate; these tubercles represent discontinuous, radial costae (Text-fig. 31D). The tubercles can appear locally to be continuous radially, especially in the anterior third of the valve where the interval between successive 'growth lines' is least (Text-fig. 31E). The distal part of a poorly preserved, tectonically deformed, apical hook is evident in specimen GSI:F00208e (Text-fig. 31C).



TEXT-FIG. 31. A–E, *Anomalonema (Anomalonema) reumauxi* (Pruvost, 1911); areas outlined and arrowed in A enlarged in B and C, showing detail of postero-dorsal margin of the carapace valve and apical hook, respectively. A, GSI:F00208e; $\times 5$. B, GSI:F00208e; $\times 12.5$. C, GSI:F00208e; $\times 32$. D, GSI:F00208b; $\times 5$. E, GSI:F00208d; $\times 5.75$. F, *Cyzicus* sp.; GSI:F00903a (lower) and GSI:F00903b; $\times 3.5$. All in lateral aspect.

Superfamily CYZICOIDEA Stebbing, 1910

Family CYZICIDAE Stebbing, 1910

Genus CYZICUS Audouin, 1837

Cyzicus sp.

Text-figure 31F

Material. GSI:F00903a and b.

Description. The carapace valves are ovate, almost circular, in outline; maximum length is approximately 1.25 times maximum height. The relatively large umbo is moderately elevated above the dorsal margin. The anterior margin is therefore longer, but less convex, than the posterior margin. The ventral margin is asymmetrically convex; the posterior part is more convex. The postero-dorsal margin curves anteriorly; the straight, horizontal, dorsal margin is therefore short. On the surface of the valves, fine concentric lines are locally present between the closely spaced 'growth lines'.

Remarks. The valves exhibit pronounced, irregular contortions or wrinkling as a result of compaction. They were probably thin and flexible, possibly with a significant element of lateral convexity. The overall shape of the valves, including the non-terminal umbo elevated slightly above the dorsal margin, the absence of radial ribs, and the presence of fine concentric ornamentation between successive 'growth lines', is consistent with *Cyzicus*, family Cyzicidae (see Tasch 1969, p. R151, text-fig. 50). The specimen is assigned to *Cyzicus* but it does not correspond precisely to any of the subgenera recognized by Tasch (1969, p. R151); in these ornamentation on the surface of the valves is more pronounced than that in specimen GSI:F00903. However, the material is considered inadequate as a basis for the erection of a new subgenus.

Class MALACOSTRACA Latreille, 1806
Subclass EUMALACOSTRACA Grobben, 1892
Order WATERSTONELLIDEA Schram, 1981
Family WATERSTONELLIDAE Schram, 1979
Genus WATERSTONELLA Schram, 1979

Waterstonella sp.

Text-figure 32

Material. GSI:F03490a.

Description. A single specimen is known preserved in lateral aspect. The preserved sagittal length excluding antennules and antennae is 18 mm; as the posterior of the telson and the uropods are poorly preserved the original length was probably slightly greater. The body is elongate, and tapers anteriorly and posteriorly. Only the proximal parts of the poorly preserved antennules are exposed. The scaphocerite is elongate, and ovate in outline. There is no evidence for either setae or spines on the lateral margins but they may be obscured by overlap. The distal margin of neither scaphocerite is exposed. The endopods of the antennae are poorly defined. Anteriorly and dorsal of the antennules there is an ovate area surmounting a short, broad stem. This may represent a pedunculate eye.

The carapace is sub-triangular in outline in lateral view; a rostrum is not evident. Anteriorly the dorsal margin is gently convex; posteriorly, it is straight. The posterior margin of the carapace is sinuous; the outlines of both the left and right hand sides are evident. This reflects a pronounced posterior indentation of the carapace on the dorsal side. The postero-ventral corner of the carapace is rounded. The ventral margin is straight. The carapace has been tilted anteriorly from its position during life. Posteriorly, there is a pronounced vertical separation between the carapace and the dorsal margin of the thorax; this decreases progressively anteriorly. The ventral margin is preserved parallel to the sagittal axis, but would have originally sloped postero-ventrally to cover the bases of the thoracopods.

The anteriormost pair of appendages beneath the carapace is notably shorter than the remainder and may represent the maxillule(s) and maxilla(e). The thoracopods are elongate; there is a slight increase in their length posteriorly. Each is biramous with an exopod, endopod and protopod of subequal length. No other details can be resolved.

There appears to be a narrow tergite associated with at least the last or last two of the thoracic somites; this indicates that the carapace was not entirely fused to the thorax.

There are six abdominal somites. Adjacent tergites overlap by approximately one-quarter of their sagittal length. In lateral aspect, the dorsal margin of each tergite is gently rounded and the ventral margins of at least the first three tergites are developed into rounded pleura.

The articulation between the terminal somite and the telson is narrow. The proximal parts of the telson widen slightly distally; the morphology of its distal parts and the uropods cannot be determined.

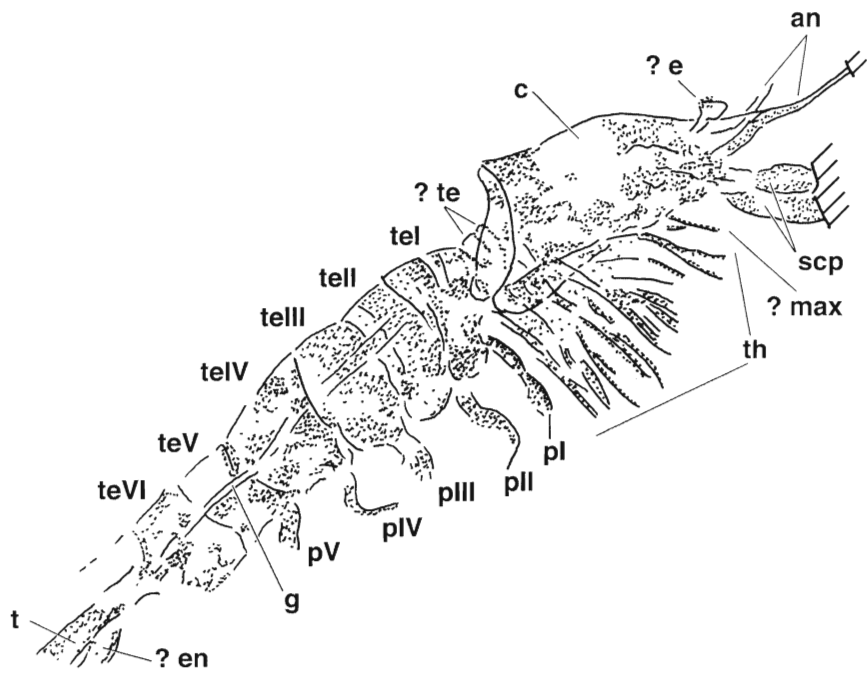
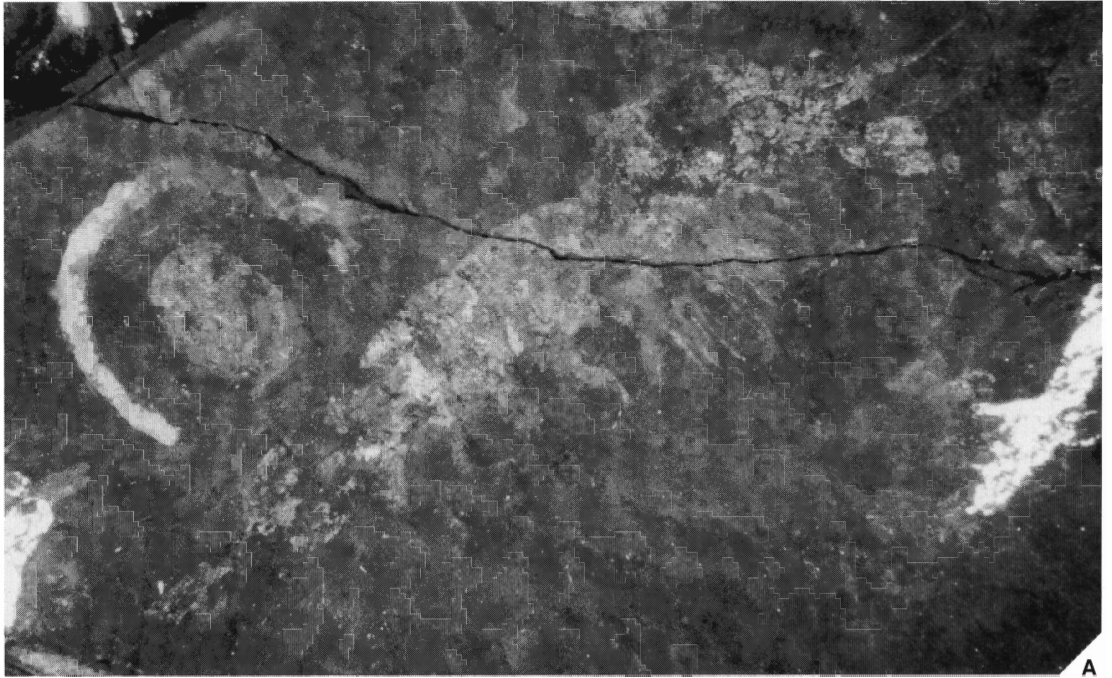
The first five abdominal somites bear pleopods. These decrease in length posteriorly; little other detail is preserved. Putative, posteriorly directed, setation is present on the distal parts of the first and second; an elongate protopod can be identified on the first.

The outline of the gut can be detected along almost the entire length of the specimen, slightly dorsal of the mid-line.

Remarks. The clearly defined gut trace indicates that the specimen is a carcass, rather than a moult. The tilting of the carapace anteriorly was therefore decay-induced, not the result of moulting. The poor preservation suggests that the cuticle was lightly sclerotized.

The carapace and the scaphocerite of specimen GSI:F03490a and *Waterstonella grantonensis* Schram, 1979 are of very similar shape; see examples of the latter in Schram (1979, pp. 72–75), Briggs and Clarkson (1983) and Briggs *et al.* (1991). In both, the thoracopods are biramous and the carapace is not fused entirely to the carapace. Examples (Schram 1979, text-fig. 30; Briggs and Clarkson 1983, pl. 20, fig. 1; pl. 21, figs 2–9; pl. 22, figs 1–5; text-figs 4a–f, 5a–e) and reconstructions (Schram 1979, text-fig. 31; Briggs and Clarkson 1983, text-fig. 6) of *W. grantonensis* demonstrate that the body is very elongate.

Waterstonella grantonensis has been the subject of several recent studies (Schram 1979; Briggs and Clarkson, 1983; Briggs *et al.* 1991). Schram (1979, pp. 72–75) assigned the species separate familial status (family Waterstonellidae Schram, 1979) within the ‘catchall’ (Schram 1986, p. 104) order Eocaridacea



TEXT-FIG. 32. *Waterstonella* sp.; GSI:F03490a; lateral aspect; $\times 6.5$.

Brooks, 1962 (=‘unassignable schizopodous caridoid’ (Schram, 1979, p. 61)). Family and species were diagnosed ‘same as that of the genus’ (p. 72 and p. 73, respectively).

Subsequently Schram (1981) considered the combination of unfused carapace, lack of a brood pouch and schizopodous thoracopods in *Waterstonella* (a combination unique among the Eumalacostraca) to warrant separate ordinal status: the order Waterstonellidea Schram, 1981 was erected. No explicit diagnosis of the order was provided; its ‘distinguishing characteristics’ were summarized as ‘schizopodous thoracopods, no brood pouch’ (Schram 1981, p. 8). Briggs and Clarkson (1983, pp. 174–175) concurred with the assignment of *Waterstonella grantonensis* to the order Waterstonellidea but emphasized that the absence of a brood pouch was ‘impossible to verify’ (p. 175); it could be taphonomic rather than real. In their thorough re-description of *W. grantonensis* Briggs and Clarkson (1983, pp. 174–175) did not provide new diagnoses. Briggs *et al.* (1991) described two additional specimens of *W. grantonensis*.

Specimen GSI:F03490a exhibits schizopodous thoracopods and a brood pouch is not present. Accordingly, it conforms with the distinguishing characteristics of the order Waterstonellidea identified by Schram (1981) and is assigned to it with the following caveats. (1) The absence of a brood pouch in specimen GSI:F03490a may be taphonomic; it shares this complication with *Waterstonella grantonensis*. It is also plausible that specimen GSI:F03490a is male; a brood pouch is an anatomical feature of females. (2) The proportions of the body of specimen GSI:F03490a are broadly comparable to the largest example of *W. grantonensis* known at present (Briggs *et al.* 1991, text-figs 5a, 6a). However, the sixth abdominal segment of the largest example of *W. grantonensis* is proportionally shorter than that in the other examples known, but is still relatively longer than that of specimen GSI:F03490a. Hence the Hollypark specimen probably represents a new species. The erection of a new species on the basis of a single, poorly preserved specimen is not justified. Accordingly, specimen GSI:F03490a is identified as *Waterstonella* sp.

Assignment of specimen GSI:F03490a to *Waterstonella* extends the known geographical and stratigraphical range of the genus. It had only previously been recorded from the Granton ‘shrimp-bed’ a *Konservat-Lagerstätte* from the Lower Carboniferous (Dinantian: Lower Oil Shale Group) of Scotland (Schram 1979; Briggs and Clarkson 1983; Briggs *et al.* 1991).

Order SYNCARIDA Packard, 1885?

Syncarid?

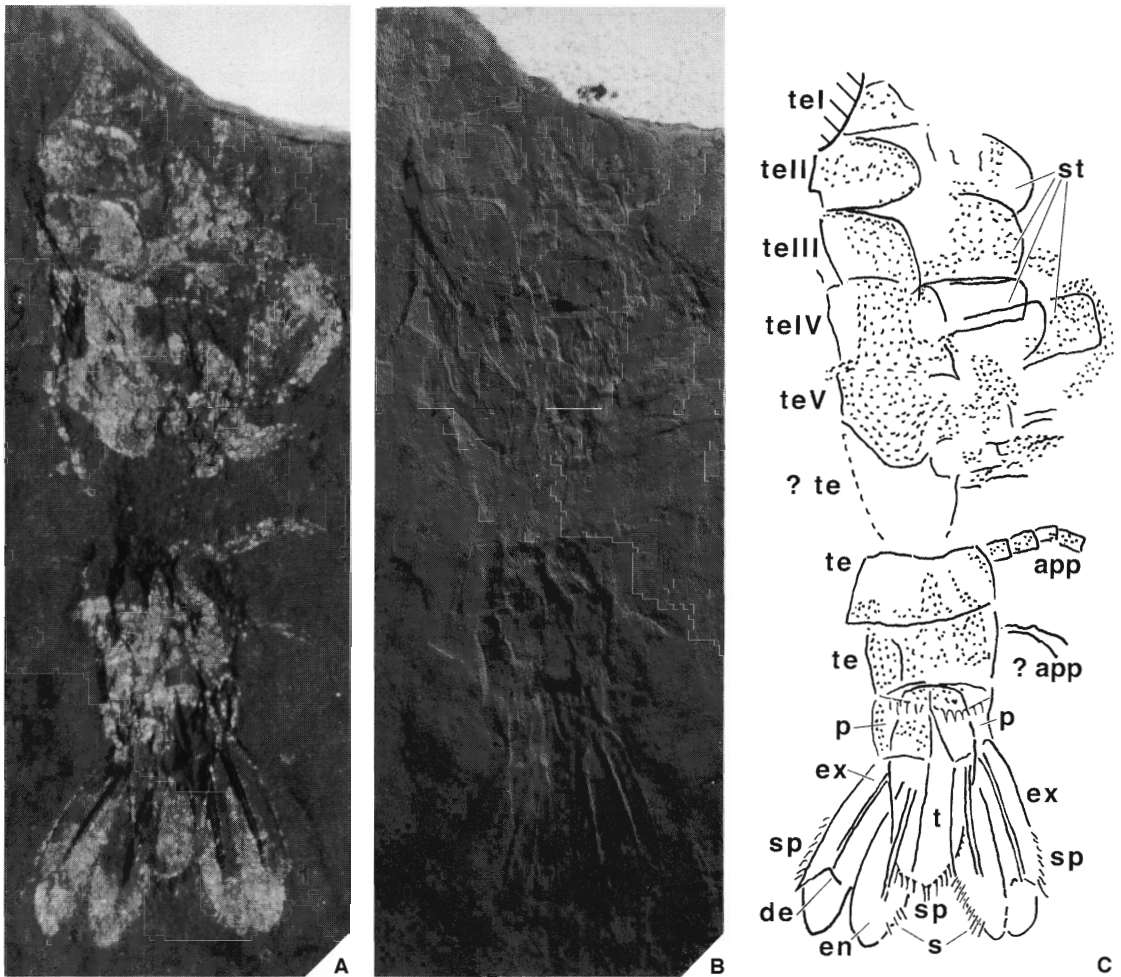
Text-figure 33

Material. GSI:F00499c.

Preservation. Only the incomplete part of a single specimen is known. The attitude of the specimen varies along the preserved length. The posterior is in dorso-ventral aspect. Anteriorly, the somites that can be identified are laterally offset between the left and right hand sides. Those on the left hand side of the specimen are more clearly defined and, under incident light, more highly reflective (Text-fig. 33A). Appendages are only evident on the right hand side of the specimen. The structures on this side are therefore interpreted as a series of sternites. The structures on the left hand side are the tergites; their being more clearly defined and more reflective indicates that the cuticle was more robust. Individual sternites are bilaterally symmetrical and therefore in dorso-ventral aspect. Individual tergites have marked bilateral asymmetry; the left and right hand sides of each are superimposed but in places the outline of each can be identified. The tergites are therefore preserved in lateral or oblique aspect.

This combination of features necessitates (1) lateral flexure or twisting of the specimen along its length, and, (2) lateral rotation of the more anterior sternites to present them in dorso-ventral aspect, lateral to rather than juxtaposed with, the tergites. The first of these is relatively common in fossil crustaceans (e.g. Schram 1979, pl. 1, fig. A). The second would be more easily achieved if the specimen was a moult rather than a carcass; some disarticulation of the cuticle would have occurred during moulting. The absence of a gut trace supports this interpretation.

Description. The anteriormost five tergites (arbitrarily numbered I–V in Text-fig. 33C) are preserved in lateral or oblique aspect. They are sub-quadrate in outline and roughly equal in sagittal length; there is a small degree of overlap



TEXT-FIG. 33. *Syncarid?*; GSI:F00499c; dorso-ventral aspect; $\times 20.5$. A, reflected light; B, secondary electron image; C, line drawing.

between them. The anterior-facing margin of each tergite is slightly convex; the posterior-facing margin is virtually straight and either normal or inclined slightly anteriorly to the dorsal margin. The dorsal margin is gently convex; the ventral margin is asymmetrically convex with greater curvature towards the posterior. The sternites, in dorso-ventral aspect, are sub-rectangular in outline with rounded corners. The proximal parts of segmented appendages can be detected; little detail can be resolved. Appendages cannot be correlated with individual somites.

In the posterior of the specimen two tergites, together with the telson and uropods, are preserved in dorso-ventral aspect. The anterior tergite is sub-trapezoidal in outline; the anterior margin and the longer posterior margin are slightly curved; the lateral margins are straight or slightly convex. The last tergite is longer (sagittally) than the others; the anterior and lateral margins are straight, the width decreasing slightly posteriorly. The posterior margin is convex each side of the midline; a series of short, stout, posteriorly directed spines is present. These spines have swollen bases. An elongate segmented appendage is associated with the anterior of the two tergites. The indistinct appendage to the right of the last tergite also appears to be derived from this segment.

The attachment of the telson occupies three-quarters the width of the terminal abdominal segment. The telson is spatulate in outline; it narrows slightly along most of its length, before terminating in an almost semicircular distal

margin. The posterior half of the telson margin is spinose. These spines are parallel to each other, posteriorly directed, longest at the midline of telson and progressively decrease in length laterally. These spines have swollen bases giving the margin of the telson a beaded appearance. The uropods are approximately the same length as the telson. They insert posterior and lateral to the telson and extend posteriorly beyond it. The large, single segmented, protopod is sub-trapezoidal in outline in dorso-ventral aspect. The endopod and exopod have a prominent medial ridge along the proximal three-quarters of their length. The outer margins of the endopod and exopod are more convex than the inner. Both the endopod and exopod broaden slightly along the first three-quarters of their length; distal of this, they narrow slightly, and terminate in acutely rounded posterior margins. At least the distal parts of the endopods are setose. The proximal three-quarters of the outer margin of the exopod are developed as a narrow ridge with a series of short, postero-laterally directed, spines, giving it a serrated appearance. The most distal of these spines is more robust; immediately distal of its base the margin of the exopod is indented. This indentation is associated with a narrow, V-shaped line which traverses the exopod. This line is interpreted as a diaeresis.

Remarks. The specimen occurs at the periphery of the drill core. The anterior of the specimen is missing.

The absence of a carapace is a defining feature of syncarids; however, the anterior of specimen GSI:F00499c is not preserved. The very high length to width ratio of the body, and the small size of the specimen, are strongly reminiscent of a syncarid. Further, the tailfan is virtually identical to that of the syncarid *Praeanaspides praecursor* Woodward, 1908 figured by Schram (1979, text-fig. 54B), although this example is notably different from the reconstruction of this taxon presented in Schram (1979, text-fig. 55; 1984, text-fig. 19). There is also a resemblance to the syncarid *Minicaris brandi* Schram, 1979 (Clark 1990). Despite the specimen being incomplete it is tentatively regarded as a syncarid. The consensus among more modern treatments appears to be to assign the taxon Syncarida ordinal (Schram 1984, 1986; Briggs *et al.* 1991) rather than superordinal (Schram and Schram 1974; Schram 1979; McLaughlin 1980) status.

The pleopods of fossil syncarids can be biramous or uniramous; the former are flap-like or annulate, the latter annulate (Schram 1986, p. 90). The only abdominal appendage that can be confidently identified in specimen GSI:F00499c is segmented rather than annulate. The significance of this observation cannot be determined on the basis of a single appendage from a single specimen.

Order and Family indet.

Text-figure 34

Material. GSI:F24052a (no counterpart).

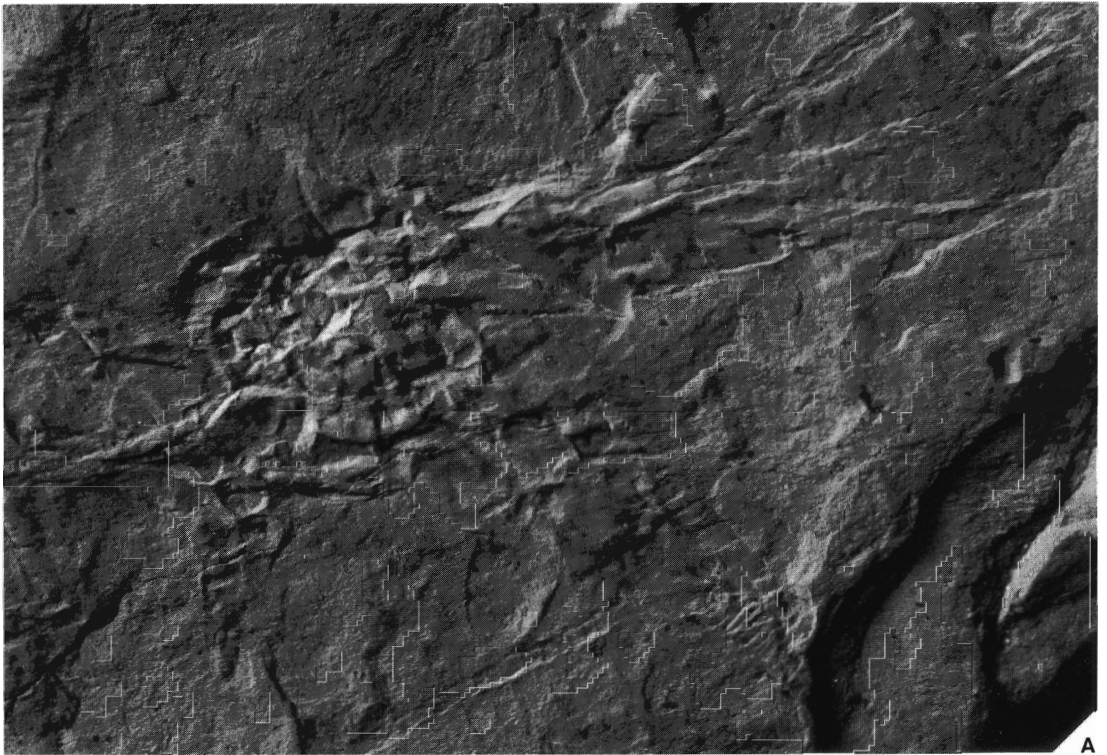
Description. The antennule is biramous. The peduncle is long and slender with at least two segments; the distal margin of the last segment is serrated, and may have been spinose. Both the antennular flagella are long, narrow distally and are segmented; their complete length is unknown.

The antennal peduncle has at least three stout segments (see interpretation in Text-fig. 34B). Each segment is slightly longer than it is wide; they decrease in size distally. The distal margin of the last segment is serrated, and may have been spinose. The antennal flagellum is long and segmented: its complete length is unknown. The ?scaphocerite is broadly ovate in outline with the distal tip more pointed and convex upwards on the plane of splitting. It is setose; individual setae are directed adaxially and distally; they originate a consistent distance inside the margin of the segment and extend beyond it. They are more evident and slightly longer on the posterior-facing margin of the segment.

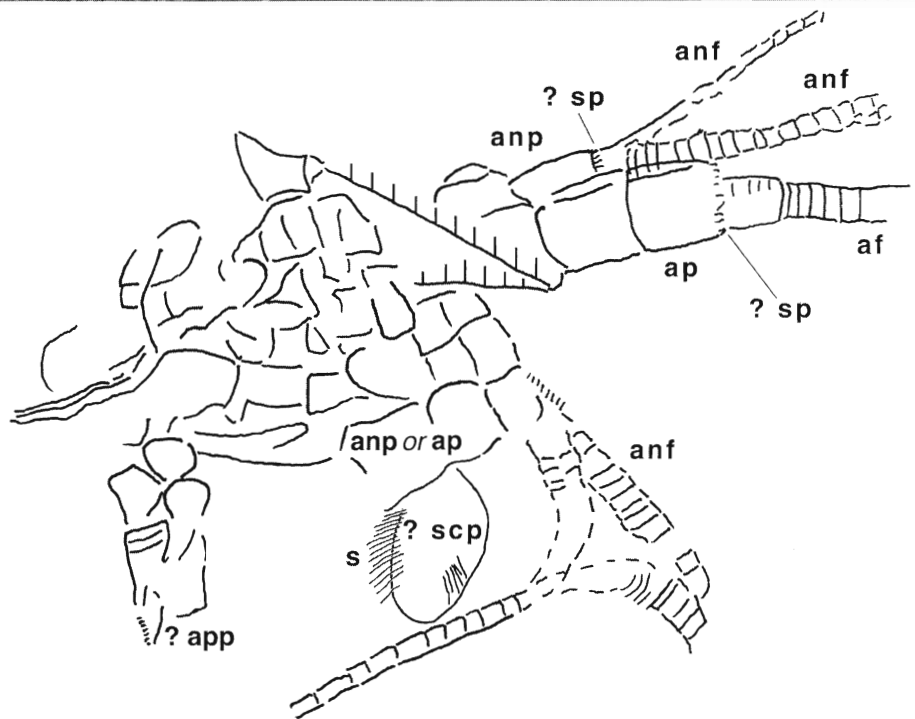
Elongate, segmented structures may represent appendages.

Remarks. The specimen is highly contorted and probably is a moult or exuviae. As the specimen is highly contorted the possibility that the ?scaphocerite is a telson cannot be excluded. The former interpretation is favoured as: (1) the structure is spatially associated with either an antennular or antennal peduncle; and (2) there is no evidence of the uropods of the tailfan.

A more complete identification of this small eumalacostracan cannot be made until additional material is discovered.



A



B

Class MAXILLOPODA Dahl, 1956
Subclass OSTRACODA Latreille, 1806

Order and Family indet.

Text-figure 35

Material. GSI:F24051d (part) and GSI:F03485i (counterpart).

Description. The carapace is preserved in lateral aspect. The two valves are superimposed and the outline of each is difficult to determine. Each valve appears to have been ovate in outline with its maximum length *c.* 1.5 times its height. The crudely concentric furrows and ridges on the surface of the valves are irregular and only occur in a marginal position. They are interpreted as deformation resulting from compaction, rather than ornamentation. Backscattered electron images of specimen GSI:F24051d reveal that some of the appendages are well preserved (Text-fig. 35C–E); their position identifies the right hand side of Text-figure 35A–C as the ventral side. The proximal parts of the two antennules or antennae are segmented. The paired structures adjacent to them are interpreted as the mandibles and mandibular palps. The pair of structures in a medial position on the ventral side are a similar size and shape. They are therefore considered to be appendages, or parts of appendages, rather than artefacts, but identification is not attempted.

Remarks. Ostracods with preserved appendages usually occur as three-dimensional phosphatized specimens (see references in Siveter *et al.* 1995) but can also be preserved as organic remains (e.g. Gocht and Goerlich 1957; Gramann 1962; Braun 1997). They are usually recovered from residues left after the dissolution of the matrix in acid. To our knowledge, this is the first time that the appendages of fossil ostracods have been identified *in situ* using backscattered electron microscopy without any preparation of the sample.

The carapace of extant ostracods is variably calcified; the chitinous inner lamella and the body exoskeleton and endoskeleton are uncalcified (Bate and East 1975; Maddocks 1992). The dark grey and black colour of the appendages of specimen GSI:F24051d in backscattered electron images (Text-fig. 35C–D) contrasts with the lighter greys of the matrix; this implies that the former have a lower atomic number. This would be consistent with, but does not confirm, their preservation as organic carbon residues. However, the appendages of examples of *Limnesteria gracilis* are similarly reflective under incident light; elemental mapping confirms that their exoskeleton is preserved as an organic carbon residue. BSE imaging may have wider applicability in the study of fossils exceptionally preserved as organic compressions.

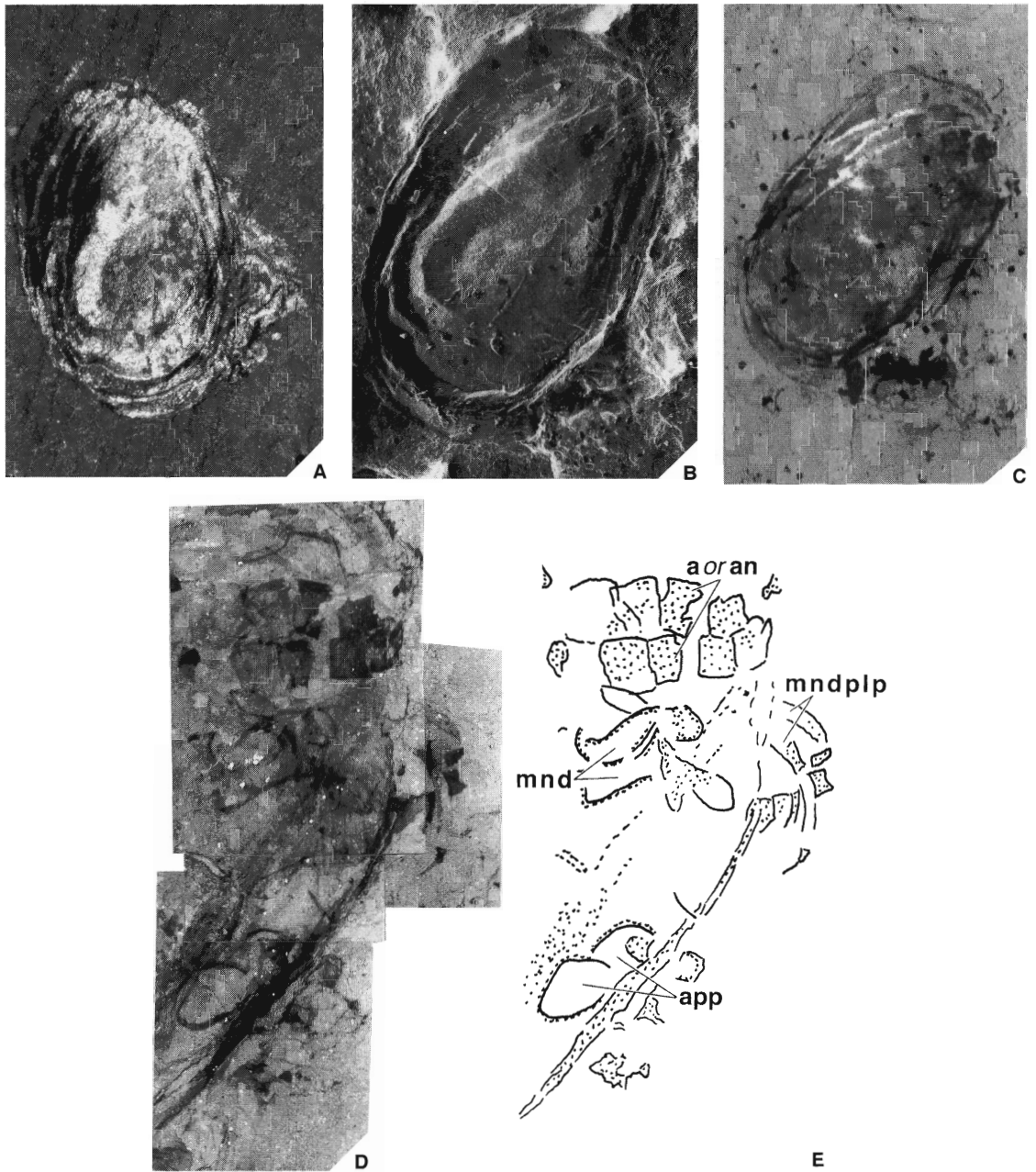
Order PODOCOPIDA Müller, 1894

podocopid

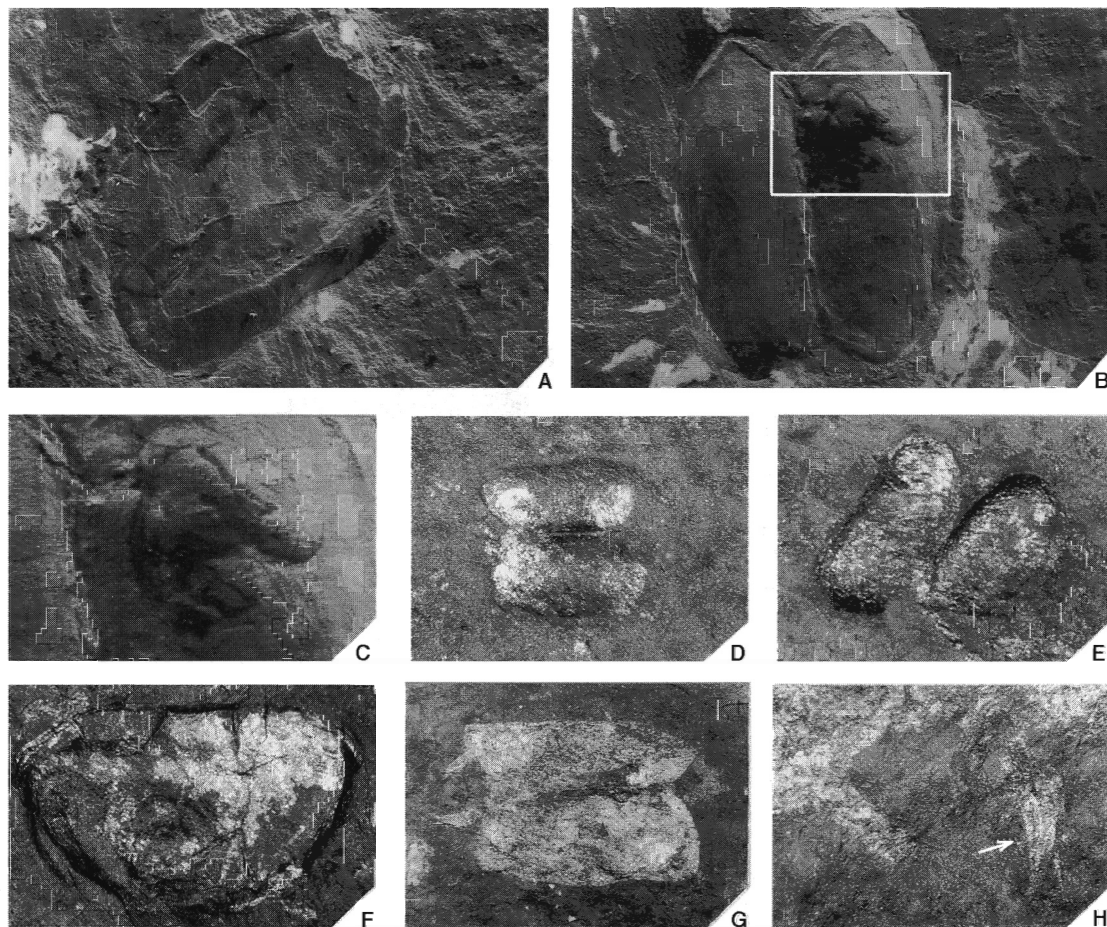
Text-figure 36A–E

Material. GSI:F24051i (part) and GSI:F03485e (counterpart); GSI:F24051j (part) and GSI:F03485d (counterpart); GSI:F03489f (part) and GSI:F24056k (counterpart); NMING:F:14725/4.

Material illustrated here. GSI:F24051i; GSI:F24051j; GSI:F03489f; NMING:F:14725/4



TEXT-FIG. 35. Subclass Ostracoda Latreille, 1806; order and family indet.; GSI:F24051d; lateral aspect. A, reflected light; B, secondary electron image; C–D, backscattered electron image; E, line drawing; D–E, enlargement of right hand side of specimen. A, C, $\times 26.5$; B, $\times 34$; D–E, $\times 79.5$.



TEXT-FIG. 36. Subclass Ostracoda Latreille, 1806. A–E, order Podocopida, Müller, 1894; area outlined in B enlarged in C, showing detail of appendages. F, order Palaeocopida Henningsmoen, 1953? G–H, order Mydocopida Sars, 1866? A, GSI:F24051j; lateral aspect; $\times 37.5$. B, GSI:F24051j; dorso-ventral aspect; $\times 31.5$. C, GSI:F24051j; dorso-ventral aspect; $\times 71.25$. D, GSI:F03489f; in dorso-ventral aspect; $\times 22.25$. E, NMING:F:14725/4; dorso-ventral aspect; $\times 28$. F, GSI:F24053; lateral aspect; $\times 31$. G, GSI:F24069f; dorso-ventral aspect; $\times 6.75$. H, GSI:F24069f; dorso-ventral aspect; $\times 21.25$.

Description. The carapace is broadly ovate to elliptical in outline. The dorsal and ventral margins are straight to marginally convex. The anterior and posterior ends of the valves are slightly obtuse and pointed; this is more evident where valves are preserved lateral to each other rather than superimposed (compare Text-fig. 36B with 36A). The maximum valve length is 2–2.5 times the maximum height. The cardinal angles are obtuse and unequal. The ends and the ventral margin of valves are thickened. The hinge line is straight and 25 per cent. shorter than the long axis of the carapace. The surface of the carapace is smooth. A muscle scar is not evident. A mandible and mandibular palp are preserved in specimen GSI:F24051j (Text-fig. 36B–C).

Remarks. The Ardra borehole has yielded a single pair of associated, but not conjoined, valves (Text-fig. 36E), and the Hollypark borehole several pairs of conjoined valves. These occur in ‘convex-up butterfly position’ on the surface of the rock. The valves usually retain at least most of their original relief, suggesting that, as in most Podocopida, they were well calcified.

The degree of relief in specimen GSI:F24051i (Text-fig. 33A) has been reduced by brittle failure of the valves during compaction. This is the result of preservation in lateral aspect with the valves closed, rather than open in the 'butterfly position'. An infill of detrital sediment may therefore have been absent, making the valves more prone to failure under compaction. Brittle, rather than ductile, failure of the valves would suggest that they were well calcified.

Following Pollard (1966) authorship of the order Podocopida is herein attributed to Müller (1894); it has also been attributed to Sars (1866) (e.g. Sohn 1985).

Order PALAEOCOPIIDA Henningsmoen, 1953?

palaeocopid?

Text-figure 36F

Material. GSI:F24053 (no counterpart).

Description. The valves of the carapace are small. The dorsal margin is straight. The ventral margin is highly convex and continuous with anterior and posterior ends. The ratio of maximum length to height of the valves is c. 1.3:1. There is limited recurvature of the antero-dorsal and postero-dorsal margins: the cardinal angles are obtuse and unequal. The hinge line occupies most of the dorsal margin. The surface of the valves is granulose.

Remarks. The long, straight, hinge line and highly convex ventral margin are suggestive of a palaeocopidan affinity.

Order MYODOCOPIIDA Sars, 1866?

myodocopid?

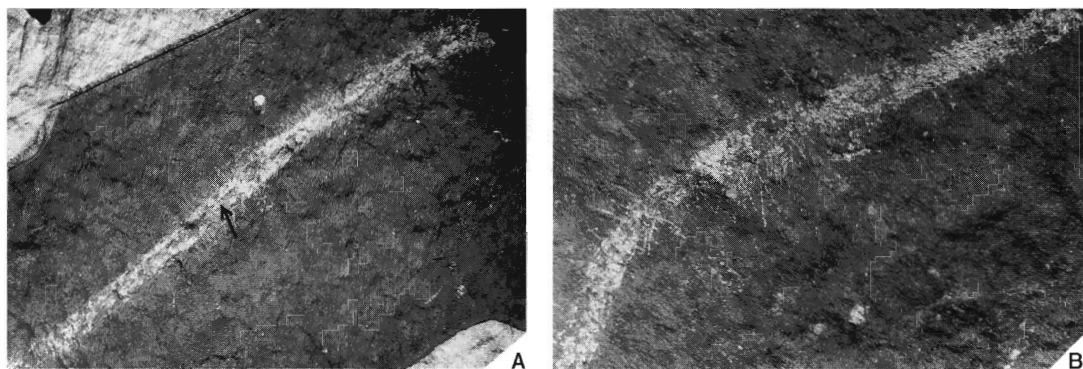
Text-figure 36G-H

Material. GSI:F24069f (part) and GSI:F00498a (counterpart).

Material illustrated here. GSI:F24069f.

Description. The dorsal margin of the valves is slightly convex. The margin on the right hand side of the lower valve in Text-figure 36G appears to be relatively complete; other margins are either incompletely exposed or preserved. This right-hand margin is asymmetrically convex; the dorsal half is steeply sloping, the ventral half virtually normal to the dorsal margin. The narrow, more highly reflective band along the perimeter of this margin may indicate that it was originally slightly thickened. The hinge line is long, and occupies most of the dorsal margin. The length to height ratio of the valves is approximately 3:1. No relief is preserved. Appendages may be represented by a tuft of setae (at arrow in Text-fig. 36H).

Remarks. The overall shape of the valves in specimen GSI:F24069f, and their high length to height ratio, are similar to the material here assigned to the order Podocopida. The shape of the complete margin is, however, different. Secondly, specimen GSI:F24069f is preserved as a thin film that is highly reflective under incident light: only the possible setae are preserved in slight relief. In contrast, specimens assigned to the Podocopida consistently exhibit significant relief or, where this is reduced, evidence of brittle failure of the carapace. There is no evidence for the latter in specimen GSI:F24069f. Dissolution of any carbonate component in the cuticle of specimen GSI:F24069f during fossilization is considered unlikely; the material here assigned to the Podocopida is from adjacent planes of splitting, but is apparently not similarly



TEXT-FIG. 37. Phylum and class unknown. A, GSI:F24074; $\times 3.5$. B, GSI:F24077; $\times 10$.

affected. The absence of relief in specimen GSI:F24069f may indicate that the carapace was thin and poorly mineralized.

Specimen GSI:F24069f is much larger than the other ostracod specimens; its valves measure 4–5 mm long. Recent and fossil myodocopids are characteristically thin-shelled and poorly mineralized. Their carapace often crumples rather than fractures when deformed (Siveter *et al.* 1995). On the basis of the absence of relief, and its relatively large size, specimen GSI:F24069f is tentatively assigned to the Myodocopida.

Phylum and Class unknown

Text-figure 37

The Ardra borehole has yielded several examples of a problematicum (Text-fig. 37). A number of features are evident: a very high length to breadth ratio, a narrow strip along the medial axis (at arrows in Text-fig. 37A), and numerous, setae-like projections from, and normal or oblique to, each lateral margin.

There is no evidence as to whether these specimens represent all or just part of an organism, or which end is anterior. The morphology is similar, and consistent in proportion in all specimens; they are unlikely to represent fragmented plant debris. Further interpretation is not attempted.

AFFINITIES OF *LIMNESTHERIA* WRIGHT, 1920

Previous studies

Wright (1920, pp. 188, 194) did not explicitly erect a higher-level classification for the genus *Limnesteria*. She (p. 202) only compared *Limnesteria ardra* to the extant genera *Cyclestheria* and 'Limnetis' (= *Lynceus*), based upon the supposed absence of a second pair of claspers in all three taxa.

In a taxonomic review of fossil Conchostraca based on carapace morphology, Raymond (1946, pp. 268–269) noted similarities between the carapaces illustrated in text-figures 3 and 4 of Wright (1920) (specimens NMING:F:14725/1 and GSI:F00896, respectively) and the extant genera *Limnadia* and *Eulimnadia*, and assigned *Limnesteria* to the family Limnadiidae Baird, 1849. Based on Wright's (1920) interpretation of *Limnesteria ardra*, Raymond (1946, p. 302) noted the incongruity of *Limnesteria* as 'Limnadiidae with one instead of two pairs of claspers'. Specimen NMING:F:14725/1 (a carapace valve) was not assigned to *Limnesteria* by Wright (1920), a decision supported herein (see *Limnesteria ardra*: Remarks, above). Contrary to Wright (1920), specimen GSI:F00896 has been questionably assigned to *Limnesteria* herein. The caveat that the outline of the carapace is significantly different from that in unequivocal examples of *L. ardra* has been strongly emphasized (see *Limnesteria ardra*: Remarks, above). This specimen cannot be confidently assigned to *Limnesteria*.

Kobayashi (1954, p. 137) included *Limnesteria ardra* within the family Lynceidae. Lynceidae is the only family within the order Laevicaudata; a series of anatomical features demonstrate that *L. ardra* is clearly spinicaudatan, not laevicaudatan (see below).

Mattox (1957, pp. 375–376) incorrectly interpreted discussion of the taxonomic affinities of *Limnesteria ardra* by Wright (1920) (specifically, Wright's interpretation that only a single pair of trunk appendages had been modified as claspers in males) to imply that the latter had assigned this taxon to what is now the lynceids (family Lynceidae Stebbing, 1902). Based on Wright's illustration of the holotype of *Limnesteria ardra* (Wright, 1920; pl. 24, figs 1 and 1b), Mattox (1957, p. 376) argued that (1) the subtle morphological differences between the two claspers illustrated were real and (2) the two claspers were from the same side of the organism's body, not one from each side of the body. These arguments necessitated the first two pairs of trunk appendages to be modified as claspers in males. The second argument and the conclusion are accepted: in the interpretation of *Limnesteria ardra* herein four claspers are identified (see *Remarks*, under *Limnesteria ardra*, above). However, the first of Mattox's arguments cannot be sustained. Obvious morphological differences among the claspers have not been identified; more subtle distinctions are considered as likely to be taphonomic as anatomical. Mattox (1957, p. 376) concluded that familial assignments of fossil conchostracans were difficult, but considered it 'not unreasonable to place them in the family Cyzicidae...'. It is presumed that this over-generalized conclusion was inclusive of *Limnesteria*.

Tasch (1969, p. R145) assigned *Limnesteria* to the family Limnadiidae, but relied heavily, possibly exclusively, on the external morphology of the carapace of specimen GSI:F00896 to do so: the 'large umbo surrounded by few growth lines... that characterizes the valves of *Limnesteria*' is common in the family Limnadiidae Baird, 1849 (see also Tasch 1956, p. 1249, text-fig. 1–1). As outlined above, specimen GSI:F00896 is considered unsatisfactory as the basis for taxonomic assignment of the genus *Limnesteria*.

Tasch (1956, p. 1249, table 1) regarded Kobayashi's (1954, pp. 134–137) two-fold, sub-familial, division of fossil Limnadiidae, as 'needlessly complex' and incorporated both into the subfamily Paleolimnadiinae Tasch, 1956, to which *Limnesteria* was assigned. Subsequently, Tasch (1969, p. R150) considered the subfamily Paleolimnadiinae to be a junior synonym of the subfamily Estheriinae Kobayashi, 1954 and *Limnesteria ardra* was questionably assigned to the latter.

Briggs *et al.* (1993) questionably considered *Limnesteria ardra* the earliest known example of the family Limnadiidae.

Classification of Limnesteria

A revised taxonomy of the genus *Limnesteria* is proposed using the additional information provided by this study and recent studies on extant conchostracans.

Order. Fryer (1987, table 2) tabulated 37 morphological differences between the conchostracan orders Spinicaudata and Laevicaudata. Anatomical features typical of, or restricted to, the Spinicaudata that can be identified in *Limnesteria* include: (1) 'growth lines' on carapace (albeit, less convincingly demonstrated for unequivocal examples of *Limnesteria ardra*); (2) small head; (3) trunk segments with rows of denticles dorsally on at least the posterior segments; (4) massive telson armed dorsally with spines and with a stout caudal furca; (5) first two pairs of trunk limbs modified as claspers in males; (6) elongate antennules; (7) segments of antennal rami elongate; and (8) two or more setae per segment on antennae.

Superfamily. The carapace valves of *Limnesteria* are limnadiiform, a feature typical of, but not restricted to, taxa of the superfamily Limnadioidea Baird, 1849 (Tasch 1969, p. R149). Limited evidence suggests that in *Limnesteria ardra* the exterior of the carapace valves lacked ornamentation and had widely spaced 'growth lines' (see description of *Limnesteria ardra* above). Both of these features are unequivocally present in *Limnesteria gracilis*, as is a large smooth umbo, that does project dorsally as a beak. This combination of characters is sufficient to warrant assignment of *Limnesteria* to the superfamily Limnadioidea.

Family. In the male of *Limnesteria* the first two pairs of trunk appendages are modified into claspers. The genus can therefore be assigned to the family Limnadiidae rather than the monotypic Recent family Cyclestheriidae Sars, 1899. In males of the latter, only the first pair of trunk appendages is modified into claspers (e.g. Olesen *et al.* 1996). *Limnesteria* is therefore the earliest known example of the family Limnadiidae.

This conclusion is consistent with the results of a recent phylogenetic analysis of the ‘bivalved’ Branchiopoda (i.e. the Spinicaudata, Laevicaudata and ‘Cladocera’) by Olesen *et al.* (1996). They (text-fig. 15) united the families Leptestheriidae, Cyzicidae and Limnadiidae by the following apomorphies: (1) presence of non-clasper limbs with palps (not confirmed in *L. ardra* and *L. gracilis*), (2) a lobed antennule (tentatively identified in *L. gracilis*), and (3) two pairs of claspers (unequivocally present in both *L. ardra* and *L. gracilis*) (Olesen *et al.* 1996, text-fig. 15, pp. 311–313). Apomorphies shared by Leptestheriidae and Cyzicidae that are absent in Limnadiidae are a frontal spine (found only in adults of Leptestheriidae but present in juveniles of at least some cyzicids) and the presence, and the shape, of the fornix. Neither has been identified in *Limnesteria*.

Subfamily. The sub-familial classification of the Limnadiidae proposed by Tasch (1969) separates Recent (subfamily Limnadiinae Baird, 1849) and fossil (subfamily Estheriinae Kobayashi, 1954: Carboniferous–Lower Cretaceous) taxa, solely on the criterion that the presence, and morphology, of a ‘pedunculate frontal organ’ is known in the subfamily Limnadiinae, but unknown in the subfamily Estheriinae (Tasch, 1969, p. R150). [The more general term ‘dorsal organ’ is preferred to ‘frontal organ’ by most recent authorities (e.g. Martin 1992; Olesen *et al.* 1996) and is used herein: see Martin (1992, p. 52) for a list of terms considered synonymous with dorsal organ.] A pedunculate dorsal organ has not been identified in either *Limnesteria ardra* or *L. gracilis*, but the head of neither is known in detail. It is plausible that the absence of a pedunculate dorsal organ in both could be taphonomic rather than real, and related to its thin cuticle. Even if the absence of a pedunculate dorsal organ in *Limnesteria* were real, the significance of this character state is uncertain. Martin (1989b, p. 104), in a discussion apparently restricted to extant forms, noted that the dorsal organ is absent in a few, unspecified, members of the family Limnadiidae. Mattox (1952), Straškraba (1965) and Belk (1982) accommodated the extant taxon *Metalimnadia serratura* within the family Limnadiidae, although the dorsal organ is not pedunculate; Mattox (1952, p. 24) described it as ‘rudimentary’ and ‘a rounded knob with a central cavity’. Straškraba (1965) assigned *Metalimnadia* to a separate subfamily. However, Roessler (1995b) used the morphology of the dorsal organ in *Metalimnadia* to support its elevation to separate familial status, whilst Martin (1992, p. 56) considered the pedunculate nature of the dorsal organ diagnostic of the family Limnadiidae.

Classification of *Limnesteria* at sub-familial level must await consensus on the significance of the morphology of the dorsal organ as a character state. The validity of Tasch’s (1969) separation of two sub-families on the basis of a character state that cannot be applied to the vast majority of fossil taxa should also be assessed. In the interim the sub-familial classification of Tasch (1969) is retained.

Genus. In *Limnesteria ardra* the first two pairs of trunk appendages are modified as claspers in males. Although Wright (1920) did not explicitly provide a generic diagnosis of *Limnesteria*, it is clear that this observation removes the single criterion on which she established the genus. The taxonomy of genera within the family Limnadiidae is also confused, and in need of revision (Martin 1989b). There appears to be little consensus on what criteria define even extant genera; for example, whilst Webb and Bell (1979) synonymized *Limnadia* and *Eulimnadia*, Martin (1989b) elected to recognize both. A detailed revision of the taxonomic affinities of *Limnesteria ardra* at the generic level is therefore beyond the scope of this paper. The number of segments in the antennal rami of *Limnesteria ardra* and *Limnesteria gracilis* is higher (c. 20 ± 5 ; 19–22, respectively) than in extant spinicaudatans (usually less than 15 (Olesen 1998, p. 514)). Thus the genus *Limnesteria* is retained, and a generic diagnosis provided.

Independent of the taxonomic uncertainties surrounding *Limnesteria* at the sub-familial and generic levels there are strong similarities between its external morphology (especially that of the antennae, mandibles, distal parts of the claspers and the telson) and that of extant members of the family Limnadiidae. The external morphology of at least some spinicaudatan ‘conchostracans’ has remained

essentially unmodified since at least the Late Carboniferous. Well preserved fossil notostracans and convincing examples of fossil anostracans are also very similar to extant forms (Fryer 1985, pp. 109–110, and references therein). Interpretation of the Branchiopoda as an example of evolutionary conservatism is thus supported.

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APPENDIX

Abbreviations used in text figures and explanatory notes.

The proximal parts of the claspers are not well enough preserved in either *Limnesteria ardra* or *Limnesteria gracilis* to identify the number of endites present. Accordingly, the distal parts of the clasper are coded using general terms (i.e. 'apical club' [ac], 'apical club palp' [acplp], 'apical hook' [ah] and 'palp' [plp]), rather than the endite number to which they correspond in extant spinicaudatans. As outlined below, there is, in some cases, confusion within the literature as to which endite corresponds to these components. There appears to be consensus that the palps of spinicaudatans are true palps and not modified endites (as in laevicaudatans) (see Fryer 1987, pp. 369–370 and Olesen *et al.* 1996 for further discussion).

? denotes uncertainty

a antenna

ac apical club of clasper

The 'apical club' is Fryer's (1987) term for the enlarged, heavily chitinized, endite that opposes the distal tip of the apical hook. The 'apical club' is identified as endite 4 of the spinicaudatan clasper by McLaughlin (1980) and Olesen *et al.* (1996).

acplp palp of apical club

af antennal flagellum

ah apical hook of clasper

McLaughlin (1980, fig. 7F) appears to interpret the apical hook in spinicaudatan claspers as endite 5.

However, others (e.g. Olesen *et al.* 1996) identified the apical hook (= movable finger in their terminology) as the endopod/'endite 6' in spinicaudatan claspers (see ta: trunk appendages, below, for discussion on use of endopod and 'endite 6').

al attachment ligament

an antennule

anf antennular flagellum

anp antennular peduncle

ap antennal peduncle

app appendage(s): undifferentiated

ar antennal ramus

as anal spine(s) of telson

c carapace

cf caudal furca

cl clasper

In male conchostracans the first, and sometimes one, or both of, the second, pair of trunk appendages is modified for grasping the female during mating. The term clasper has been applied both to the entire appendage (e.g. Tasch 1969) and to the distal extremity (e.g. Calman 1909; Olesen *et al.* 1996). Here, following McLaughlin (1980), the term clasper refers to the entire appendage.

d rounded denticle at the postero-ventral corner of the telson

de diaeresis

dsp	dorsal sensory papillae on antennule
dt	posteriorly directed projection of the dorsal margin of the posteriormost trunk segments (= denticle of Fryer 1987)
e	eye
en	endopod
epi	epipod of trunk appendage(s)
ex	exopod
fp	transverse or slightly oblique furrows across protopod of antenna
g	gut
gl	'growth line'
	The informal term 'growth line(s)' is widely used for the concentric line(s) on the exterior of the carapace valves of most conchostracans. The carapace is retained during life, and not shed at moulting; such lines may mark intervals of ecdysis.
h	head
ma	molar area of mandible
max	maxillule(s) and maxilla(e): undifferentiated
mnd	mandible
mndf	mandibular foramen
mndp	mandibular palp
mx	maxillule(s)
p	protopod
pI-V	pleopod, successively numbered posteriorly
plp	palp of clasper
	Although the proximal part of this structure appears to be labelled as 'endite 6' by McLaughlin (1980), most authorities (e.g. Fryer 1987; Olesen <i>et al.</i> 1996) regard this structure as a true palp in spinicaudatans and not a modified endite (as in laevicaudatans).
radc	rounded antero-dorsal margin of the telson
s	seta(e)
scp	scaphocerite(s)
seg	segment(s) of trunk
sp	spine(s)
st	sternite(s)
t	telson
ta	trunk appendage(s)
	(1) McLaughlin (1980) referred to the post-cephalic appendages of conchostracans both as trunk appendages (p. 18, text-fig. 7B) and thoracopods (caption to text-fig. 7B); Olesen <i>et al.</i> (1996) used the latter. The former is used herein; an abdomen (and therefore, by implication, a thorax) cannot be distinguished in conchostracans. Strictly, the term thoracopod(ite) refers to an appendage of any thoracic somite.
	(2) In both <i>L. ardra</i> and <i>L. gracilis</i> , narrow, ventrally directed, linear structures occur within and extend beyond the areas identified as poorly preserved trunk appendages. These were identified as either the exopod, endite 6 or palp of trunk appendages <i>sensu</i> McLaughlin (1980, text-fig. 7E), or some combination thereof. Other authors use differing terminologies. Schram (1986) identified endite 6 <i>sensu</i> McLaughlin as the endopod. The difference is semantic; Olesen <i>et al.</i> (1996, p. 297) noted that the terms 'endite 6' and 'endopod' have been widely used for the same structure, and themselves used the terms interchangeably. Olesen <i>et al.</i> (1996, p. 297) stressed that, technically, the structure is the reduced 'true' endopod of the limb; in some taxa it is separated from the protopod by a suture line; in other taxa the endopod is not demarcated from (i.e. has fused with) the protopod. It remains unclear, however, on what basis Martin and Christiansen (1995) identified the same structure as the distal tip of the protopod. In turn, Martin and Christiansen (1995) identified the palp of endite 5 <i>sensu</i> McLaughlin (1980) as the endopod; note that it is derived from their endite 4, because they identified the first endite <i>sensu</i> McLaughlin (1980) as the proximal endite leaving the second endite <i>sensu</i> McLaughlin (1980) as the first, the third as the second, etc.
	Schram (1986, p. 381) suggested that the palp of endite 5 <i>sensu</i> McLaughlin (1980) is only present in male specimens. McLaughlin (1980) identified it in the first trunk appendage of a female conchostracan, although it is absent in the tenth trunk appendage of the same female (McLaughlin 1980, text-fig. 7E and D, respectively).
te	tergite(s)
tf	telsonal filament
th	thoracopod(s)
tr	trunk