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TAPHONOMY OF EXCEPTIONALLY PRESERVED CRUSTACEANS FROM THE UPPER CARBONIFEROUS OF SOUTHEASTERN IRELAND

PATRICK J. ORR,[1]* DEREK E.G. BRIGGS,[2] and STUART L. KEARNS[3]
[1]University College Dublin, School of Geological Sciences, Belfield, Dublin 4, Ireland; [2]Yale University, Department of Geology and Geophysics, P.O. Box 208109, New Haven, Connecticut 06520-8109, USA; [3]University of Bristol, Department of Earth Sciences, Queen's Road, Bristol, BS8 1RJ, UK
e-mail: patrick.orr@ucd.ie

ABSTRACT

The Castlecomer Fauna, a Konservat-Lagerstätte from the Upper Carboniferous of Ireland, is dominated by two species of exceptionally preserved spinicaudatan conchostracan branchiopod crustaceans; over 300 articulated specimens are known from short lengths of core from two boreholes. The spinicaudatans were entombed at various angles to bedding in thin event beds deposited in a paralic environment. Cuticle is the only tissue represented. The fossils are essentially two-dimensional as specimens collapsed following decay-induced loss of the structural strength of the cuticle. Some three-dimensionality was retained, however, as clay-grade material, probably sediment, infiltrated the carapace during or after burial, preventing the valves from being compacted to the same plane as the body of the specimen. Cuticle-lined voids created by decay of the labile tissues (notably within the tubelike antennal rami) were lined or infilled by authigenic clay minerals that were subsequently metamorphosed. The antennae, mandibles, distal parts of the claspers, and the telson are preserved in excellent detail, often retaining all or most of their original relief. Other anatomical features (antennal protopods, head, proximal part of claspers, trunk appendages) are usually preserved in two dimensions, either as a film of carbon or a dark-colored stain. The antennules, maxillules, and maxillae are rarely preserved. Decay experiments confirm that this variation reflects differences in the recalcitrance (thickness and degree of sclerotization) of the cuticle that covered different parts of the body. Complete decay of certain appendages precedes appreciable deterioration in the morphology of others. Some of the disparity exhibited by exceptionally preserved fossil arthropods is likely to be taphonomic rather than biological in origin.

INTRODUCTION

The Castlecomer Fauna, a Konservat-Lagerstätte of basal or early Westphalian (Upper Carboniferous) age, is preserved in core from the Ardra and Hollypark boreholes in the Leinster Coalfield, southeastern Ireland (Fig. 1). The exceptionally preserved component of the fauna is dominated by spinicaudatan (conchostracan) branchiopods. *Limnestheria ardra* (Wright, 1920) and *L. gracilis* (Orr and Briggs, 1999) occur in the Ardra and the Hollypark cores, respectively. Preservation in the Castlecomer Fauna is exceptional because, unlike the vast majority of occurrences of fossil spinicaudatans, anatomical features in addition to the carapace (notably the trunk and appendages) are preserved. The systematic paleontology was considered by Orr and Briggs (1999). The fauna associated with *L. ardra* in the Ardra core comprises the valves of other conchostracans, a single pair of ostracode valves and an elongate, ?setose problematicum. A more diverse ostracode fauna (including examples in which some of the appendages are preserved), as well as a eumalacostracan, a probable syncarid, and *Waterstonella* sp., occurs with *L. gracilis* in the Hollypark core. This paper describes the taphonomy of the Castlecomer Fauna. The only previous research on the preservation of the fossils was by Wright (1920), who claimed that specimens of *L. ardra* were preserved in pyrite. Unless stated otherwise, comments on the taphonomy of the material described here apply to specimens from both cores. Antennule and antenna refer to the first and second antenna, and maxillule and maxilla to the first and second maxilla (the terminology used by Orr and Briggs, 1999).

Geographic and Stratigraphic Context

Numerous boreholes have been drilled through the late Namurian and early Westphalian strata of the Leinster Coalfield, mainly from 1902 to 1914 and from 1959 to 1963. The Ardra borehole dates from the first of these periods, and the Hollypark borehole from the second. Exceptionally preserved spinicaudatans occur at at least six different levels between ~252 m and 255 m depth in the Ardra core (Fig. 2A) in the Dinin Member of the Moyadd Coal Formation (Higgs, 1986). This interval was considered equivalent to the *Gastrioceras subcrenatum* marine band (i.e., basal Westphalian) by Eagar (1964, fig. 3), although Wright (1920) regarded it as slightly younger, early Westphalian (see Orr et al., 1996). An exceptionally preserved fauna from the Hollypark borehole (first reported by Orr et al., 1996) is preserved in a 75-mm-diameter core held by the Geological Survey of Ireland (GSI) and labeled b6/449; most of the ~30 original pieces were split into thinner slices to recover additional material. Archives at the GSI identify, for unstated reasons, the level at 135 m for the *G. subcrenatum* marine band. Orr and Briggs (1999) noted that there was little evidence that the *G. subcrenatum* marine band was present in either core. This marine band is represented by a shelly fauna (typically bivalves, gastropods, brachiopods, or goniatites) in other boreholes. The Ardra and Hollypark boreholes are in the northern part of the coalfield, in which deeper-marine, goniatite-dominated facies accumulated at this time (Nevill, 1956, 1961). The Castlecomer Fauna was therefore considered more likely to be earliest Westphalian in age. This age is confirmed by the subsequent discovery of a handwritten lithological log of the Hollypark borehole in the archives of the GSI by Dr. Matthew Parkes (reproduced here as Fig. 2B; original author unknown). The fossiliferous interval forms part of a ~3-m-thick interval labeled on the original log as "dark, smooth shales with ironstone bands, ostracodes, non-marine lamellibranches [*sic*], shrimps and plants." The base of this interval is approximately 16.5 m above the top of a unit described on the log as "black sooty shales with coal partings up to 1″ thick" and interpreted to be the No. II coal, which is the combined equivalent of the Skehana and the stratigraphically higher marine band coals that occur in the northeast and northwest of the coalfield, respectively. Both coals are stratigraphically above the Fleck Rock, an informal lithostratigraphic unit that contains the *G. subcrenatum* marine band marking the Namurian-Westphalian boundary. Elsewhere in the coalfield, the marine band coal is succeeded immediately by black shales containing the *G. listeri* marine band of early Westphalian age.

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* Corresponding author.

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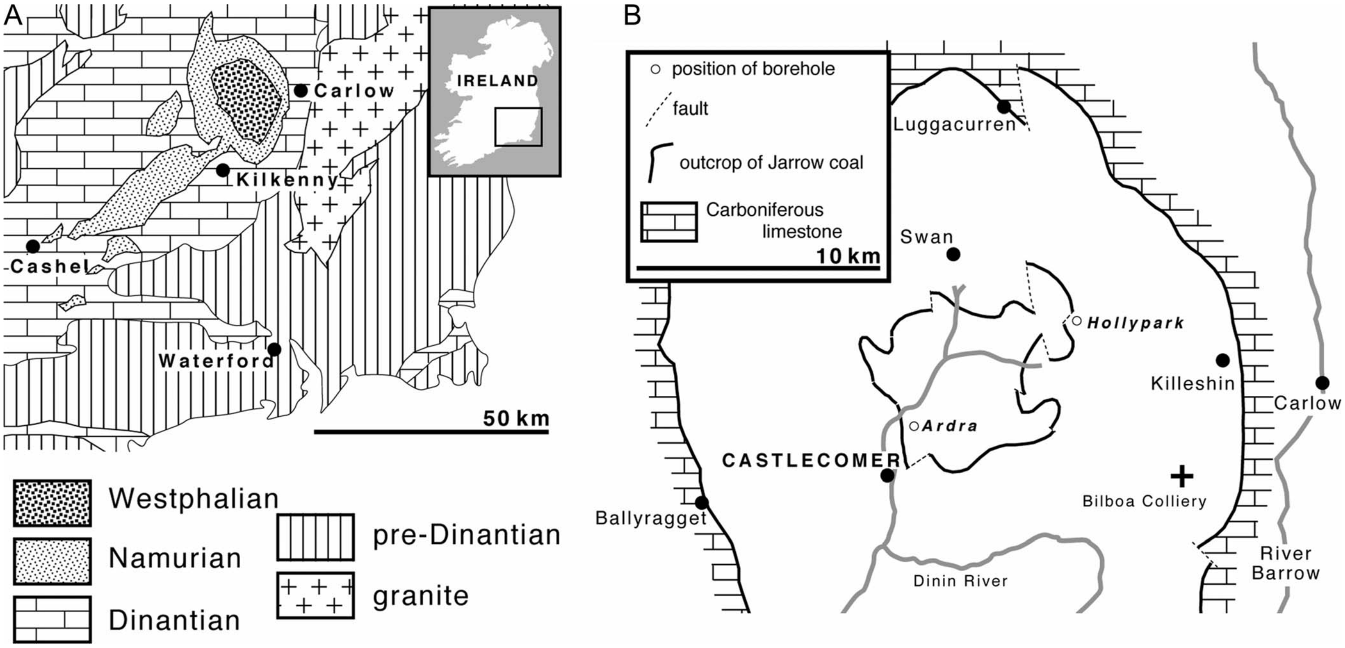

FIGURE 1—Simplified geologic and locality maps. A) Southeastern Ireland. B) The Leinster Coalfield, showing location of the Ardra and Hollypark boreholes.

Sedimentology and Environmental Setting

The fossiliferous interval of the Ardra core consists mainly of 2–5 mm thick intervals of massive or finely planar laminated or wavy laminated light gray siltstone. These intervals are usually separated by 4–6 thin laminae of dark gray to black mudstone (which can be laterally discontinuous) and dark gray, structureless siltstone with a total thickness of 1–2 mm (Fig. 3A). The core splits on the mudstone laminae, which provide almost all the bedding-parallel surfaces. The surface is usually smooth; exceptions (Fig. 3B) have a wrinkled to pustulose texture, reminiscent of microbially bound substrates. Similar textures have been illustrated in modern sediment in the Santa Barbara Basin (Bernhard et al., 2003) and in Ordovician shallow-marine sediments (Noffke, 2000, fig. 2C–D). Plant remains (Fig. 3C) or spinicaudatan carapace valves (Fig. 3D) are abundant on some planes of splitting; exceptionally preserved spinicaudatans, however, tend to occur on surfaces that lack other fossils. Although directionality is unknown, the laminae of dark mudstone and dark gray siltstone together with a subjacent light gray siltstone probably represent a thin (now 7–10-mm-thick), bipartite event bed. Its surface may have been stabilized by a surficial microbial film after deposition. A pervasive cleavage fabric is well developed, especially in the finer-grained lithologies (Fig. 3E).

The fossiliferous interval of the Hollypark borehole comprises mainly massive to poorly laminated, medium to dark gray mudstones that are separated into 2–5 mm thick intervals by thin (1–2-mm-thick) horizontal silt laminae (Fig. 3F). This lithology is markedly less fissile than in the Ardra borehole, although it does tend to split parallel to bedding, and a cleavage fabric is less extensively developed.

The late Namurian and early Westphalian strata of the Leinster Coalfield represent a progressively shallowing-upward sequence (Higgs, 1986). The Moyadd Coal Formation, which yielded the fossils, represents a paralic coal-forming environment that succeeded the deltaic environments represented by the underlying formations. The series of goniatite-bearing horizons within the formation mark marine transgressions (Higgs, 1986). The interval with exceptionally preserved fossils is succeeded in the Ardra borehole by siltstones and mudstones with seat earths (underclays), an intraformational breccia, and thin coals (Fig. 2A). In the Hollypark borehole the fossiliferous interval occurs above a thick sandstone that succeeds an unusually thick seat earth and associated thin coal, within an interval of shales, sandstones, and mudstones (Fig. 2B). In both cores, the spinicaudatans are allochthonous (see below), and thus the ecology of extant examples cannot be used to constrain the environment of deposition. No unequivocal marine fossils are present. There is no evidence of temporary emergence (e.g., desiccation cracks or salt pseudomorphs), and the sediments are unbioturbated. The sediments accumulated under a semipermanent brackish or freshwater body from which a macroinfauna, and possibly a macroepifauna, were excluded. A more precise interpretation of the depositional environment is not possible; fine-grained, laminated sediments are an important lithofacies in numerous environments of paralic successions (Emery and Myers, 1996, table 1). Conodont alteration indices of around five in the Lower Carboniferous rocks in the region indicate anchizone grade (300–400°C) metamorphism after burial (Jones, 1992).

MATERIALS AND METHODS

Fossil Material

The original specimens of *L. ardra* (Wright, 1920; see Orr and Briggs, 1999) are covered in Canada balsam and glass coverslips and can only be examined in incident light. A limited number of new specimens, including the counterpart of the holotype, were present in fragments of core from the same interval of the Ardra borehole (Orr and Briggs, 1999); most of these are smaller, and their morphology is often strongly overprinted by cleavage, making recognition of anatomical features difficult.

Abundant material of *L. gracilis* is available, even though the core of the Hollypark borehole is only 75 mm in diameter. Up to twelve specimens may be exposed in an area of less than 40 mm^2. Scanning electron microscopy (SEM) and electron microprobe analyses were primarily undertaken on material from the Hollypark borehole.

Fossil specimens are held by the Natural History Museum, London (prefix In), the Geological Survey of Ireland, and the National Museum of Ireland (NMING).

Decay Experiments

Specimens of the spinicaudatan *Eulimnadia texana* (Packard, 1871) were hatched in the laboratory from resting eggs. Adults were killed by transferring them to a small beaker filled with deoxygenated water and placing it in an anaerobic cabinet. The exact time of death is unknown; most were dead within 2.5 hours, all within 2.75 hours. Eight individual specimens were then transferred to sterile, transparent, Petri dishes containing a mixture of Milli-Q pure water and a small fraction of the

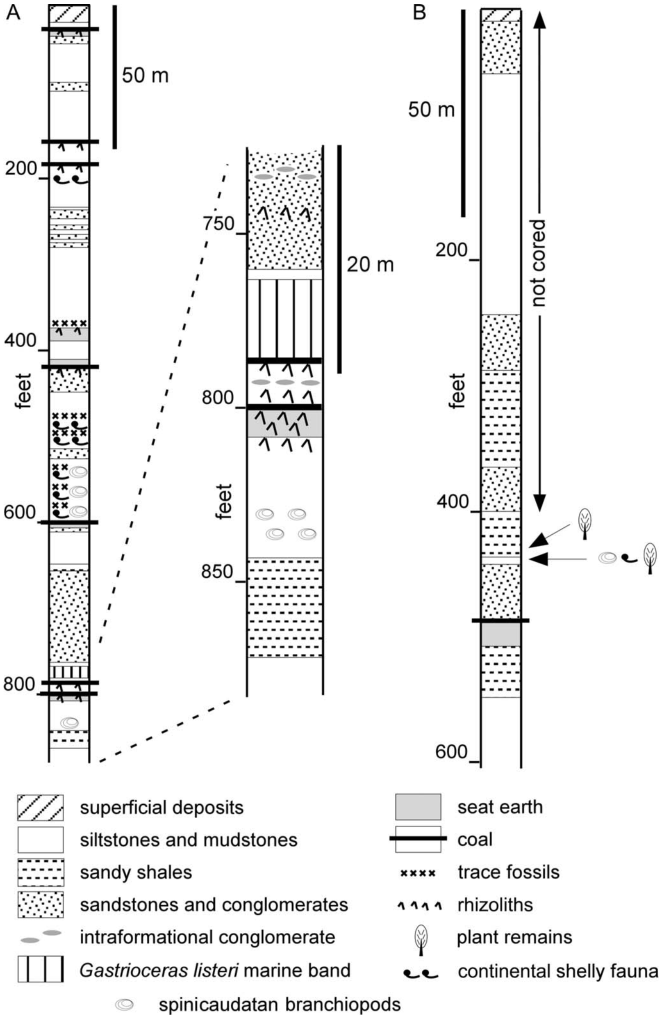

FIGURE 2—Lithological logs of fossiliferous cores. Boreholes are marked in feet, as they were originally measured, but meter scale is also given. A) The Ardra borehole, with a more detailed log of the interval with exceptionally preserved spinicaudatans. B) The Hollypark borehole.

original tank water. The dishes were covered with loose-fitting transparent lids and placed on a laboratory bench in a room with natural summer light (the experiments were carried out during July and August). The lids were removed only for photography and to allow periodic refilling of the water level. Movement of the Petri dishes was restricted to that necessary to position specimens for photography; this had no obvious effect on the specimens' morphology or degree of disarticulation.

Specimens were examined daily and photographed at more irregular intervals over 21 days. The appendages were obscured by the growth of a threadlike bacterial shroud (biofilm) after a few days of decay. Some features of interest could only be recorded by observation and simple sketches. The small size and the location of the maxillules and maxillae made their decay impossible to observe. One specimen was carefully opened up into a butterfly position after 8 days of decay in order to allow the appendages to be photographed. No other specimens were manipulated. Individual experiments were allowed to continue following each examination.

Optical Microscopy

Fossil and experimentally decayed specimens were examined with a Leica Wild M10 stereomicroscope under incident light from a Volpi Intralux 6000 fiber-optic system. Photographs were obtained with a Wild MPS52 shutterpiece and Wild 35 mm camera back attached to this microscope via a phototube and a Wild MPS48 photoautomat. Fossil specimens, other than Wright's original specimens, which were covered in Canada balsam and glass coverslips, were covered by water and glass coverslips prior to photography.

Scanning Electron Microscopy

Secondary electron images of uncoated, gold-coated, and carbon-coated fossil specimens and backscattered electron images of uncoated and carbon-coated fossil specimens were obtained at the Department of Earth Sciences, University of Bristol, with a Cambridge Instruments Stereoscan 250 Mk 3 SEM fitted with a KE Developments solid-state diode backscattered electron detector. Specimens cut from core were mounted on aluminum stubs using self-adhesive carbon discs. Entire pieces of Hollypark core were attached to a specially constructed SEM stage with Blu-Tack™. Specimens were wrapped in aluminum foil with the areas of interest exposed, ensuring that foil and stage were in contact in order to minimize charging. Elemental composition was analyzed qualitatively via energy-dispersive X-ray analysis using Oxford Instruments PCXA-EDX microanalytical facilities linked to the SEM.

Elemental Mapping

Elemental mapping of fossil specimens was performed using a Jeol JXA-8600 superprobe electron microprobe at the Department of Earth Sciences, University of Bristol. Specimens were analyzed uncoated or with selected areas carbon coated; the remainder of the specimen was wrapped in aluminum foil, as was done with the SEM, to minimize charging. Analyses were performed at an accelerating voltage of 5 kV for carbon (Orr et al., 2002) or 15 kV for other elements. All elements were scanned in energy-dispersive mode (Oxford Instruments AN10000) except C, which was scanned in wavelength-dispersive mode. The potential sources of error inherent in analysis of uncoated and rough surfaces (Orr et al., 1998) were considered in the interpretation of the results. Elemental maps indicate the relative abundance of each element; the brightest tones correspond to the maximum levels recorded (counts per 100 seconds live time). These maxima may not be the same between different elements, and the brightness or contrast of the maps was altered, as necessary, to accentuate the differences in tone. Thus identical tones in different maps do not imply similar abundance.

RESULTS OF DECAY EXPERIMENTS

When put in the water-filled Petri dish, all except one of the eight specimens settled to the bottom and came to rest on its side, that is, in lateral aspect. The single exception remained suspended vertically in the water column, dorsal margin uppermost, because an air bubble was trapped between the carapace valves. It came to rest in the same orientation as the others within 3 days. Specimens degraded at different rates. In the latter part of the 21-day period, specimens became coated with a translucent (light-to-white-colored), semicontinuous, fibrous, shroudlike biofilm (see the long arrows in Fig. 4E; short arrows indicate body margin); short green filaments grew vertically from external surface of valves (Fig. 4D). Over the 21 days, slumping of the body of the spinicaudatan into a more stable orientation was facilitated by the separation of the inner lamella from the internal surface of the valves (Figs. 4A–D). Decay-induced shrinkage resulted in cuticle-lined internal voids in as early as 3 days (Figs. 4B, I, J at arrow). Limited disarticulation occurred *in situ*; in some cases the telson separated from the trunk, and the rami of the caudal furca separated from the telson (Fig. 4N). Manipulation of the specimen that was opened into a butterfly position after 8 days (Fig. 4H) did not result in any disarticulation. Subsequent disturbance, however, during the addition of water using a pipette, resulted in extensive disarticulation (Fig. 4I). This included separation of (1) the carapace valves from the remainder, although their physical appearance remained unaltered over the 21 days (Fig. 4O); (2) the head from the rest of the body; (3) the antennal

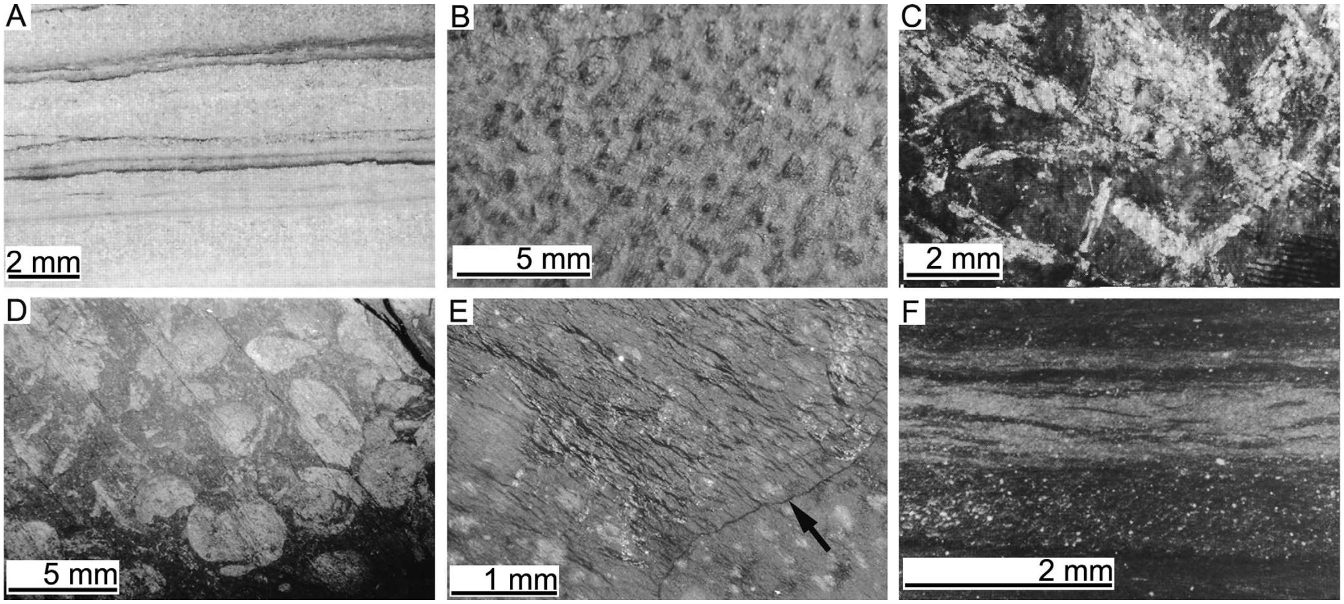

FIGURE 3—Sedimentology and paleontology of the fossiliferous intervals of each core. A–E) The Ardra core. A) Finely laminated sediments in vertical section. B) Some bedding surfaces are pustulose, the probable remains of thin, benthic, microbial mats. C) Fragmented plant remains on a bedding surface. D) Spinicaudatan carapace valves. E) Cleavage is developed more intensely in finer-grained lithologies; such variation can occur between adjacent laminae (arrow). F) Vertical section of fossiliferous lithology in the Hollypark core.

rami from the head by tearing of the cuticle of the protopod; (4) the gut from the body and its fragmentation into several short, solid cylinders; and (5) the rami of the caudal furca from the telson. The antennules remained attached to the head, and the telson, which retained its outline, remained attached to the trunk.

The rate of cuticle decay varied between and within appendages. The outline of the antennules became very indistinct by 8 days (Fig. 4I) but was still evident at the end of the experiment (Fig. 4M, shorter arrow). The outline of the protopod of the antenna was indistinct after 21 days, but the rami remained three dimensional with individual segments clearly identifiable (Fig. 4M). In ~3 days the pinnules of the setae of the antennal rami began to degrade, resulting in a beaded appearance (Fig. 4F, arrows) and reducing the pinnate setae to a single axis. The shape and appearance of the mandibles was unaltered throughout the experiment (Fig. 4M, longer arrow). The outline of the clasper was unchanged after 8 days (Fig. 4G); the cuticle covering the proximal part degraded extensively (Fig. 4K) or completely (Fig. 4L) within 21 days, but the distal part was unaltered. Between 8 days (Fig. 4I) and 21 days (Fig. 4N) the posterior-most trunk appendages degraded completely. The morphology of the telson was unchanged over 21 days, although the telsonal filament disappeared (Fig. 4N).

When removed from the water after 21 days, specimens collapsed into near two-dimensional films of cuticle with the exception of the antennal rami, mandibles, distal parts of the claspers, telson, and carapace valves, in which most or all of the original three-dimensionality was retained. Such collapse of the cuticle has been observed in other experimentally decayed, nonbiomineralized arthropods (Briggs and Kear, 1994). Variation in the recalcitrance of the cuticle is attributed to differences in thickness or the degree of sclerotization. These, in turn, reflect functional differences: thicker or more sclerotized cuticle occurs in the antennae (locomotion), the mandibles (food processing), the spinose telson (protection), the distal parts of the claspers of males (grasping females during mating), and the carapace valves. Similar variations in the structure and thickness of the cuticle occur in the appendages of other small, nonbiomineralized arthropods. In the cladoceran *Daphnia*, the cuticle of the epipods (respiratory structures) is thinner than that covering other parts of the leg (0.2–0.5 μm, as opposed to 1–3 μm; see Peters, 1987); some layers of the cuticle may be absent in regions where gas exchange is important (Martin, 1992). In male anostracans, the cuticle may be 7 μm thick on the clasper (the antenna) but only 1.0–1.5 μm thick in the trunk and thoracopods (Criel, 1991).

FOSSIL PRESERVATION

The lithological differences between the Ardra and Hollypark cores imply that the environment of deposition may not have been identical. Diagenetic conditions did vary; for example, pyrite is associated with specimens of *Limnestheria gracilis*, but not with *L. ardra*. In broad terms, the fidelity of preservation is similar throughout (two-dimensional refractories, *sensu* Allison and Briggs, 1991). There are, however, subtle differences in the extent to which the original three-dimensionality is preserved, which varies among specimens from each core, and between the two cores. Specimens of *L. gracilis*, which is from the Hollypark core, are more frequently preserved in less relief. These differences can be attributed to the different parts of the cuticle varying in its recalcitrance, which, on the whole, was less in *L. gracilis*.

Orientation

Specimens, including adjacent specimens on the same surface (Fig. 5A), occur in various attitudes to the bedding-parallel planes of splitting. Most specimens are preserved with the sagittal axis parallel to bedding, and the sagittal plane, which *in vivo* divides the specimen into equal left and right halves (Fig. 5B), in one of three orientations.

Lateral Orientation.—The sagittal plane is horizontal; that is, the specimen is lying on one side. The trunk is in a dorsal position, and the left and right valves are superimposed vertically and overlap completely. This is the most stable attitude as demonstrated by decay experiments (Fig. 5C).

Oblique Orientation.—The sagittal plane is inclined to bedding. The trunk is in a mediodorsal position, and the left and right valves are offset in the horizontal plane (Fig. 5D).

Dorsoventral Orientation.—The sagittal plane is normal to bedding, with one valve and set of trunk appendages on either side of the medially positioned trunk, that is, in a butterfly position. The telson and the posteriormost part of the trunk are usually rotated into lateral aspect (Fig. 5E). Rare examples are foreshortened in dorsoventral aspect. The sagittal

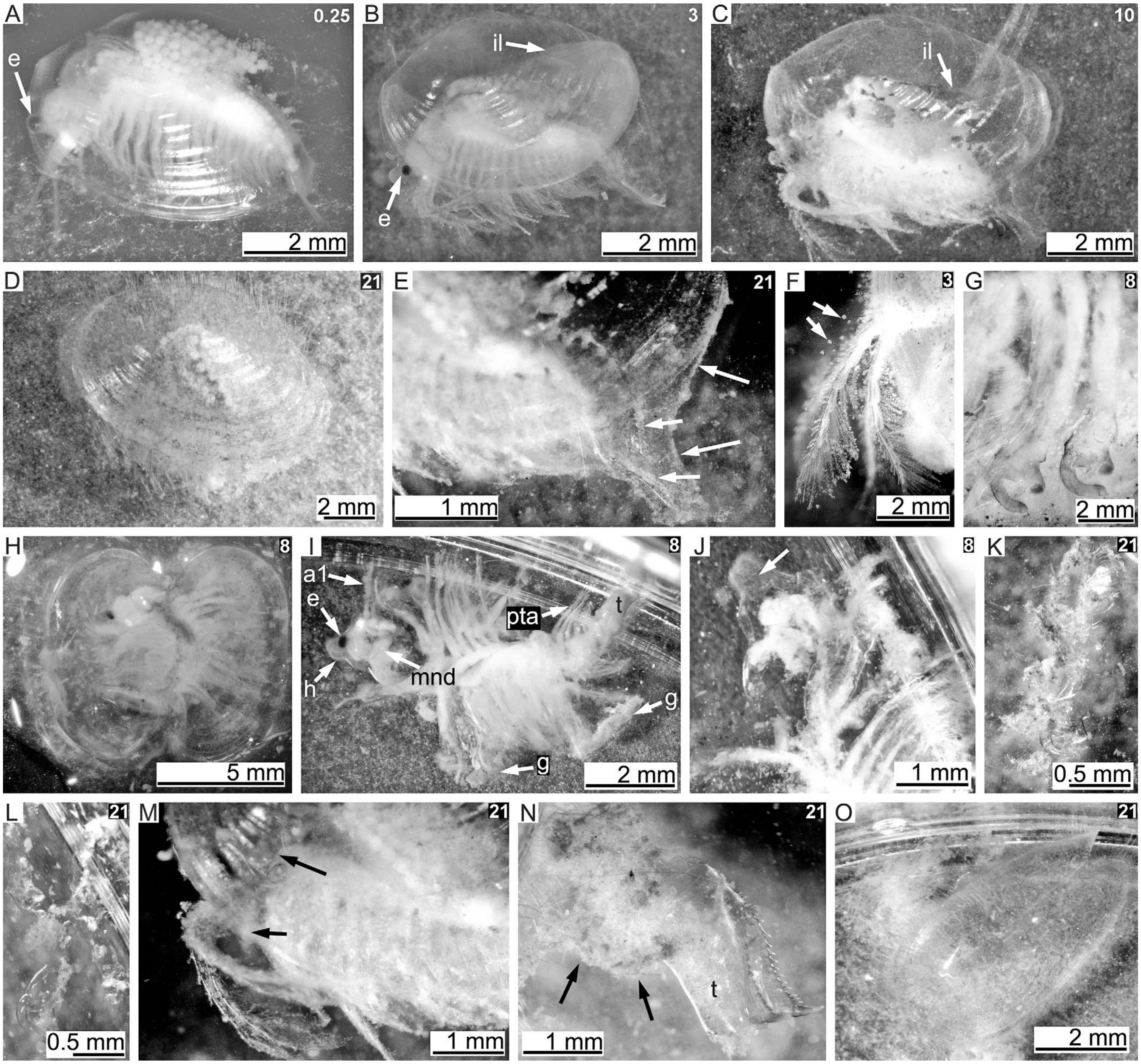

FIGURE 4—Results of decay experiments. Numbers in each image indicate number of days of decay. A–C) The body progressively settles into a more stable orientation as the inner lamella pulls away from the internal surface of the valves. D) Valve with short green filaments growing upward from its external surface. E) Posterior of specimen shrouded in biofilm (long arrows) through which the outline of the telson and caudal furca can be discerned (short arrows). F) Antennal rami in which the pinnules of the setae have degraded into bead-line structures. G) Claspers showing no obvious morphological degradation. H) Decaying specimen opened in butterfly position. I) Disarticulated specimen. J) Anterior of specimen exhibiting cuticle-lined voids (at arrow) resulting from shrinkage of internal tissues. K) Highly degraded clasper with only the distal part exhibiting any morphological detail. L) Distal parts of clasper exhibiting good morphological detail. M) Anterior of specimen with mandible exhibiting no loss of morphological detail (at long arrow) and very indistinct antennule (short arrow). N) Posterior of specimen showing selective degradation of the posterior-most trunk appendages. O) Carapace valves at the termination of the experiment, showing no loss of their original three-dimensionality or morphological detail. a1 = antennule; e = eye; g = short length of gut; h = head; il = inner lamella; mnd = mandible; pta = posterior trunk appendages; t = telson.

axis is inclined to bedding, and the head and the anterior part of the trunk project anteriorly beyond the carapace (Fig. 5F).

Displacement, Distortion, and Rotation

In life, the spinicaudatan trunk runs subparallel and close to the carapace hinge, which is a simple fold, not a true hinge (Martin, 1992, p. 34); the foliaceous trunk appendages are oriented normally to the trunk's long axis (Fig. 5B). The body of a spinicaudatan is attached anterodorsally to the carapace only by a ligament (this is the muscle-containing pedicel of McLaughlin, 1980, and Orr et al., 1996) and a pair of adductor muscles. The posterior part of the trunk and its appendages are especially subject to displacement—that is, preservation can occur in orientations possible but atypical during life. The trunk can be rotated anteriorly and can curve normally, rather than in a parallel manner, to the hinge line (cf. Figs. 6A and 5D, both in oblique aspect). In the specimen in Figure 6B, the left and right trunk appendages are juxtaposed posteriorly and are ventral to the trunk. Toward the anterior, however, the appendages from one side of the body, including the two claspers (numbered 1 and 2) project dorsally from the trunk (Fig. 6C). In general, the head and its appendages exhibit the least displacement from life position, although the antennae occur in various orientations.

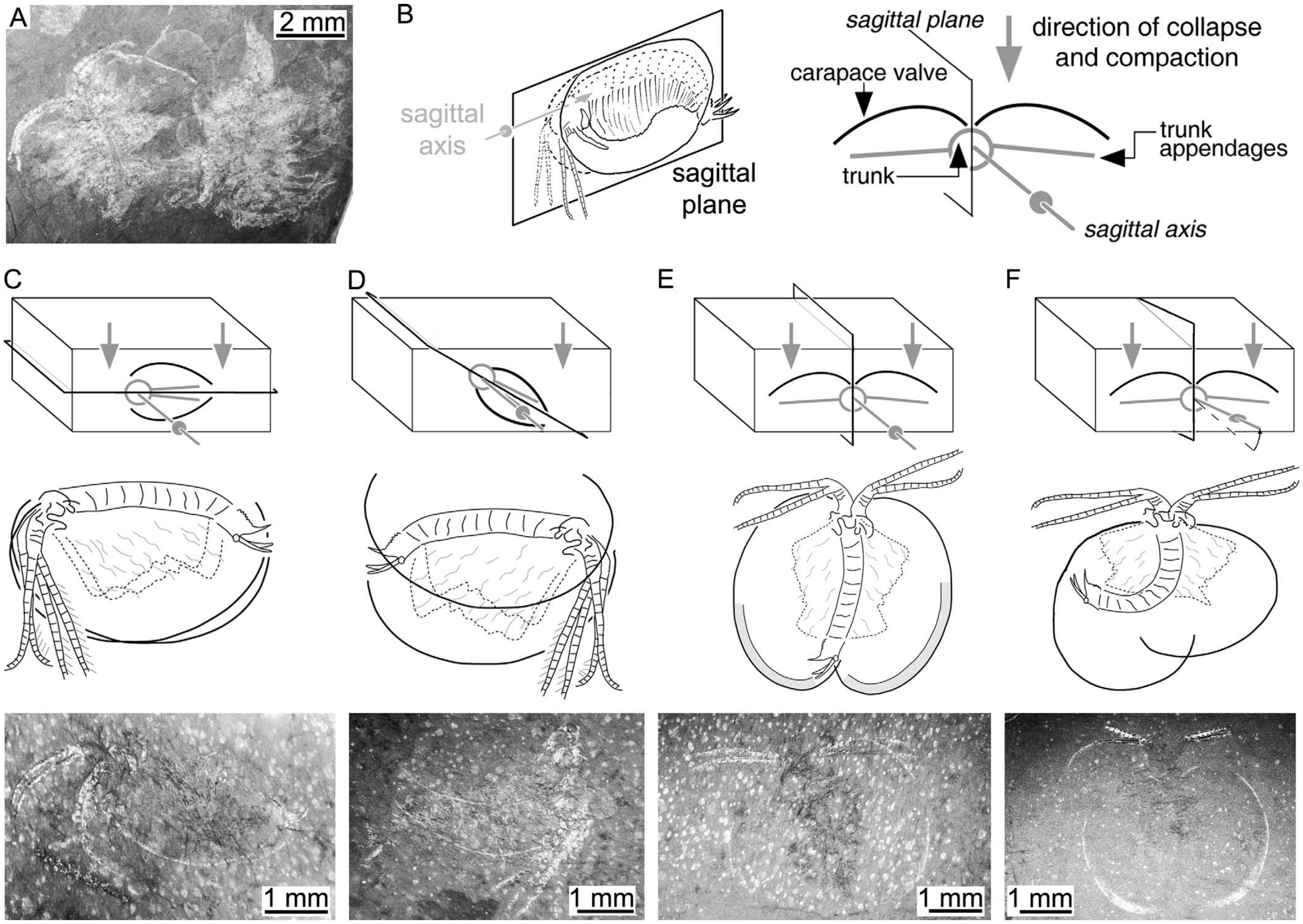

FIGURE 5—Attitude of specimens on the bedding-parallel plane of splitting. A) Two adjacent specimens in different attitudes (GSI:F24069b, left; GSI:F24069c, right). B) Reference terms for attitude of specimens. C–F) Attitude of specimens based on the angle between the sagittal plane and the plane of splitting; in C–E, the sagittal axis is horizontal. C) Lateral aspect (NMING:F:14724). D) Oblique aspect (GSI:F00893). E) Dorsoventral aspect (GSI:F00897). F) Specimen in dorsoventral aspect with the sagittal axis inclined to bedding (In21101[1]).

Some specimens or parts thereof are in orientations that could not occur *in vivo*; it is necessary to invoke distortion of the specimen in these cases. In the specimen in Figure 6D, the trunk lies parallel to, but outside of, the dorsal margin of both carapace valves. This configuration can only be derived by rotating one valve through 360° in the transverse plane, rotating both valves through 180°, or having the two valves separate such that the body slips between and beyond them on the dorsal side. In the specimen in Figure 6E, the two valves are not aligned; one (or both) are rotated in the sagittal plane (Fig. 5B). In both examples the distortion requires rupture of the connection between body and valve on one side or both and must have occurred before or during burial. It is likely that some decay prior to transport affected the more labile tissues, including the attachment ligament and the adductor muscles. Decay, however, did not advance far enough to result in disarticulation during transport.

Certain appendages, notably the mandibles, distal part of the claspers, and the telson, tend to rotate into the bedding plane irrespective of the orientation of a specimen as a whole. These appendages have been rotated relative to the carapace so that the largest surface area possible lies in the bedding plane (see also Aldridge et al., 1993). The specimen in Figure 6F is in oblique aspect, and the preserved trunk appendages on either side of the body differ in length. The mandible (Fig. 6F, shorter arrow) was oriented subvertically *in vivo* and inclined at a high angle to bedding immediately after burial; it has rotated so that its inner face is now parallel to bedding. The distal part of each clasper, including the apical hook (Fig. 6F, longer arrows) lies in lateral aspect irrespective of the attitude of the rest of the specimen (see also Figs. 6B, 11G–I). The telson (and the posterior-most part of the trunk) is often rotated to lie lateral to the bedding plane, although the specimen as a whole is in oblique (Figs. 6A, F) or dorsoventral (Figs. 5E, 6G) aspect.

Mineralogy

Cuticle is the only original tissue represented (Figs. 7–11), often broken into small, parallel-sided pieces by the strongly developed cleavage (see Fig. 11I). No internal tissues or organs other than the outline of the cuticle-lined gut are preserved. The gut, extending the length of the trunk along its midline (arrows in Figs. 7E, 11A, B), is preserved in different ways: (1) without relief as two narrow, parallel lines, slightly more reflective than the surrounding cuticle, and interpreted as the margins of the gut (Fig. 7E, arrows); (2) without relief as a single strip that is slightly more reflective than the surrounding cuticle, and interpreted as the external surface of the gut; and (3) as a convex ridge (groove in the counterpart), either covered in cuticle (Fig. 11A) or, in specimens where the cuticle has degraded, being of fine-grained material, probably sediment (Fig. 11B). Elemental mapping confirms that the cuticle is preserved in organic carbon (Fig. 12C); the absence of a corresponding signal in the elemental map for Ca indicates that a carbonate mineral is not the source of carbon. This is consistent with the dark tone observed in backscattered electron images of the cuticle (Figs. 11H, L; Orr et al., 2002). Its high reflectivity under incident light (Fig. 11J) is the result of graphitization during low-grade metamorphism.

In some specimens of *L. ardra*, the head, protopods of the antennae,

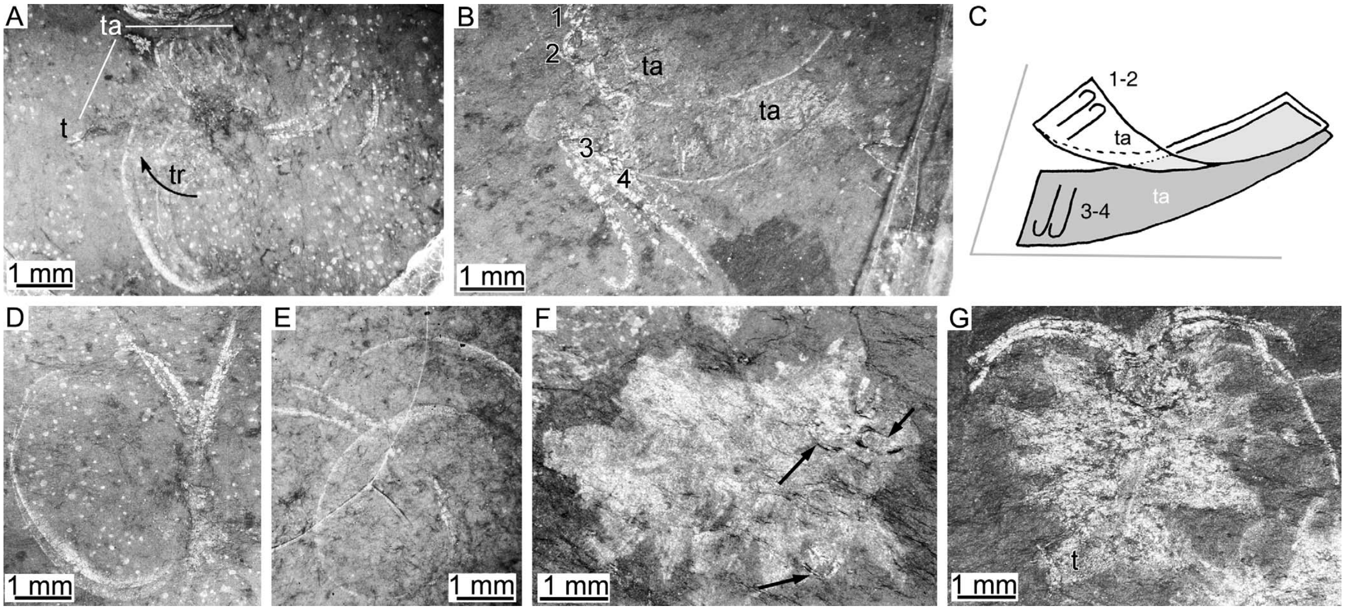

FIGURE 6—Deviation of the spinicaudatan body and appendages from life position results from displacement, distortion, and rotation. A) Rotation of the entire trunk (NMING:F:14725/2). B–C) Rotation of the anterior appendages on one side of the body (In21099). D–E) Distortion of specimens resulting from separation of one or both carapace valves from the body and their rotation in the transverse (D, GSI:F00898) or sagittal planes (E, GSI:F00900). F–G) Rotation of individual appendages including the mandible (F, short arrow), distal part of the claspers (F, longer arrows) and telson (t, in G); their attitudes therefore differ from that of the specimen as a whole (oblique in F, GSI:F24051f; dorsoventral in G, GSI:F24069b).

trunk—including its individual segments (Fig. 11D, arrows)—and trunk appendages lack reflective cuticle and are preserved as dark-colored stains that lack relief but define the shape of the anatomical feature (Figs. 11B–D). More irregularly shaped, dark-colored stains may be present at the distal end of the antennal rami (Figs. 9J–K); others partially overlap and extend ventrally beyond the posterior-most trunk appendages (Fig. 7A, arrow). These dark-colored stains are presumed to be carbonaceous in composition. Such stains are not present in specimens of *L. gracilis*; that is, they are not in the core from the Hollypark borehole. Three-dimensional preservation of the antennal rami, especially proximally, is relatively common in specimens of *L. ardra*. The rami are infilled by fine-grained material (Figs. 11C, E, arrows), which is identical in color and texture to the adjacent matrix; the mineralogy cannot be determined as the specimens are encased in Canada balsam and covered by a glass coverslip. Antennal rami that lack relief, which are in the majority of *L. gracilis* specimens, and the exceptionally preserved ostracodes (Orr et al., 2002, fig. 3) comprise solely carbonaceous cuticle.

Antennal rami of *L. gracilis* that are preserved in relief are infilled by clay minerals (now metamorphosed); the arrows in Figure 11F indicate the margin between the fractured brittle cuticle and the infill. These clay

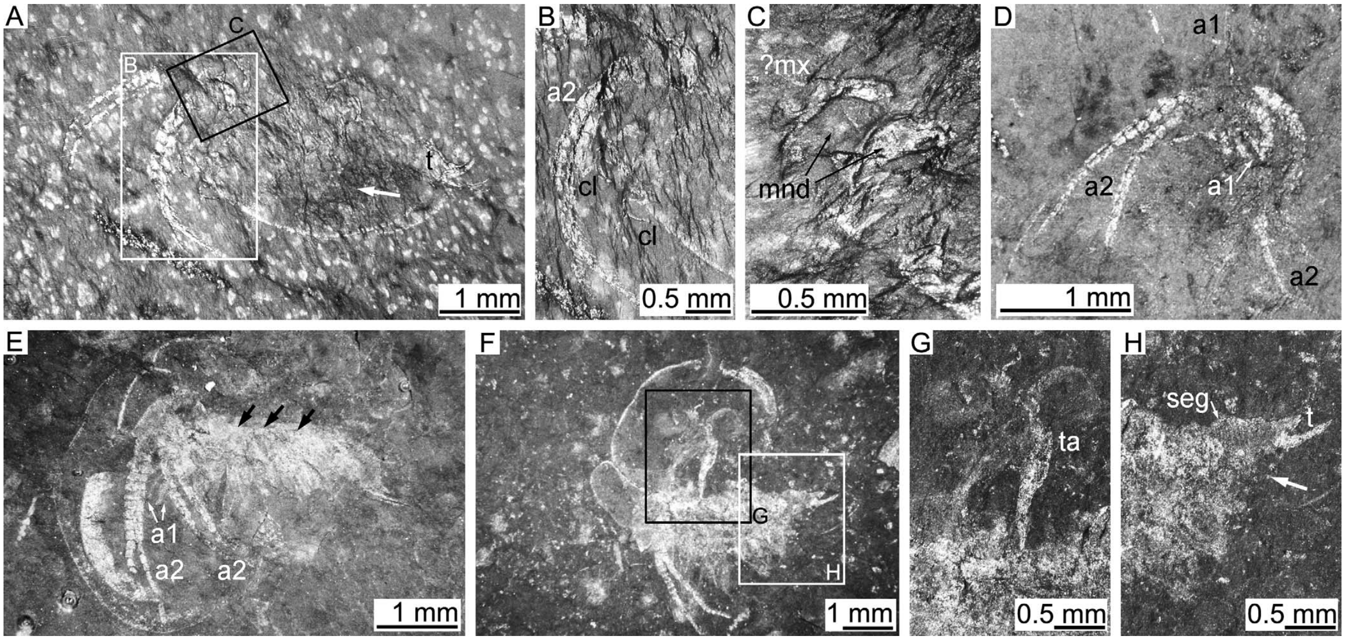

FIGURE 7—Specimens characterized by a high degree of both articulation and completeness. A) Entire specimen, enlarged in B–C (NMING:F:14724). D–E) Specimens showing antennules (a1), which occur in relatively few specimens (D, NMING:F:14725/3; E, GSI:F03486F). F) Entire specimen, enlarged in G–H (GSI:F24056a). a1 = antennules; a2 = antennal rami; cl = claspers; mnd = mandibles; mx = probable maxillules.

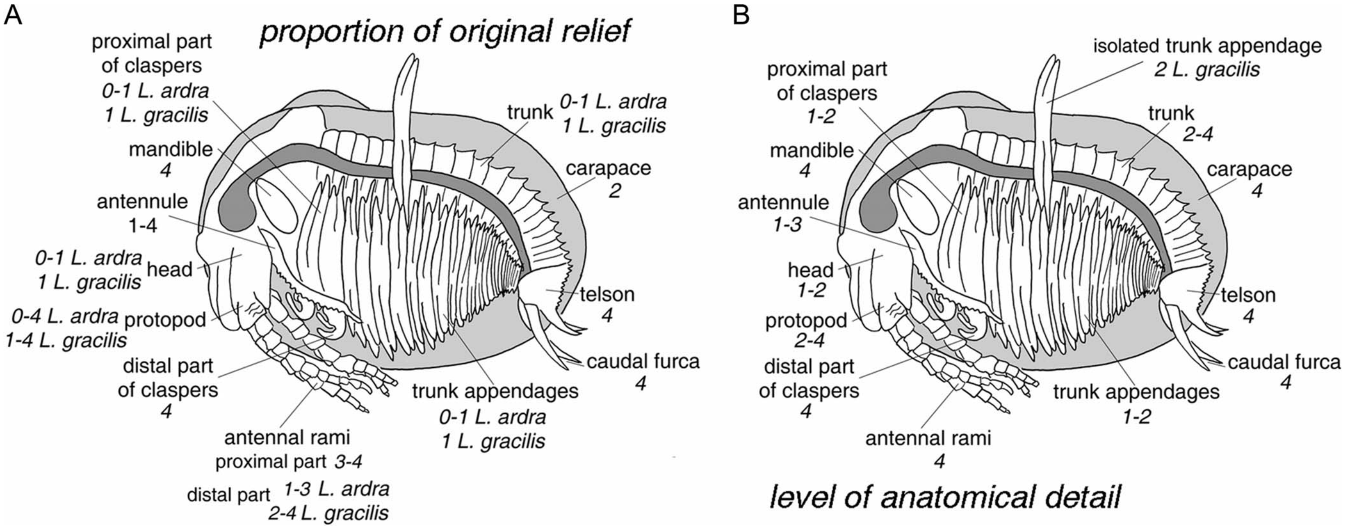

FIGURE 8—Summaries of the proportion of original relief retained (A) and the level of anatomical detail that can be resolved (B). A) 0 = cuticle not preserved; feature defined by dark, presumably organic, stain; 1 = cuticle preserved, no relief; 2 = relief limited; 3 = moderate; 4 = high. B) 1 = little detail observed; 2 = general outline can be resolved; 3 = moderate detail can be resolved; 4 = extensive or all detail can be resolved. Sketch of spinicaudatan after McLaughlin (1980).

minerals can be more Fe rich than the adjacent matrix (Fig. 12C), indicating that they are authigenic, not detrital, in origin. Framboids and smaller octahedra of pyrite (the brightest areas in the map for Fe coincide with elevated abundances of S; see Fig. 12C) precipitated onto the surface of the cuticle and, at much lower density, the immediately surrounding sediment (Figs. 11G–I). Pyrite is rarely sufficiently abundant to define any part of the anatomy. The one exception is the central rachis of some of the setae of an antennal ramus (Fig. 11F). The very sharply defined margins of these setae suggest that the pyrite precipitated inside the rachis. Most of the pyrite, however, precipitated on the external surface of the cuticle, and molds of framboids occur where antennal rami are preserved in negative relief.

Completeness and Articulation

Most specimens show a high degree of articulation and completeness. Isolated telsons and antennae are extremely rare but demonstrate that some specimens disarticulated before or during burial. In most specimens that appear incomplete, part of the specimen is either concealed below the plane of fracture (e.g., the posterior part of the carapace valves in Figs. 9J–K) or is present in the counterpart (e.g., the telson of the specimen in Figs. 9D–E). The complete length of each antennal ramus is not always observed, especially in specimens of *L. gracilis*. Although the length exposed can vary even in a single specimen (Fig. 9E), there is a general pattern: the first 6 to 8 segments are usually evident in *L. ardra* and the first 8 to 12 in *L. gracilis* (Figs. 5F, 9G).

The antennae, mandibles, trunk appendages including the claspers (in males), and telson with caudal furca are evident in almost all specimens (Figs. 7A–C); probable examples of the maxillule have been recognized in a minority (Fig. 7C). The maxilla has not been observed in any specimen of either spinicaudatan; it is obscured because of its small size and posterior position. In marked contrast to antennae, unequivocal examples of antennules are very rare (Figs. 7D–E). Possible examples were observed in about 20 of the >200 specimens examined (Figs. 9H–I). In some specimens of *L. gracilis*, the posterior-most trunk appendages are not preserved (Figs. 7H, 4N).

Preservation in Relief

Figure 8A summarizes the extent to which the original three-dimensionality of the different parts of the body is retained. Although the range of variation in relief is, on the whole, the same in both taxa, more specimens of *L. ardra* are preserved in greater relief. The relief of the antennules and protopods varies most. Even where anatomical features overlap, they can usually be distinguished except where the upper feature is preserved in relatively high relief. Relief can vary between different parts of an appendage: the distal part of the clasper (the so-called hand) is invariably preserved in greater relief that its proximal part (Fig. 9C). The protopods can be preserved in less relief than the contiguous rami (Figs. 11J, E) and the proximal part of a ramus may show greater relief than the distal (Fig. 7D).

There is a strong but imperfect correlation between the extent of relief and the level of anatomical detail preserved (cf. Figs. 8A and B). Antennal rami are often preserved in less relief distally than proximally, but the quality of preservation, including the definition of individual segments and the preservation of delicate, acicular, marginal setae, does not change appreciably. Anatomical detail is difficult to resolve in the trunk appendages, which lack relief, but this is due mainly to overlap along the length of the trunk. Greater detail can be resolved where a trunk appendage is isolated from the remainder (Fig. 7G).

Carapace.—The carapace valves are usually preserved as thin curving lines on the same surface as the remainder of the body (Figs. 5C–D); their outline can continue across steplike breaks that mark changes in the level of the plane of splitting. Alternatively, the periphery of the valves may be preserved as a parallel-sided band of reflective cuticle (Figs. 9F–G). The external surface of spinicaudatan valves frequently displays prominent growth lines (Fig. 9A), marking intervals of ecdysis (the carapace is not shed during molting). The inner margin of the band of reflective cuticle marks the position of a growth line. A single specimen can display both variations (Figs. 5E–F). Both features are present irrespective of specimen orientation, that is, irrespective of their inclination to the plane of splitting. Some of the original curvature of the valves, and some vertical separation from the plane containing the body, have therefore been retained (see Fig. 5, block diagrams). The presence of the body clearly influenced the position of the plane of splitting; if appendages are present, the surface of the valves is rarely evident, although there are exceptions (Figs. 9A–B, D–E). Where the external surface of the carapace valve is exposed, the outline of features below the carapace may be evident (Fig. 9B). Where no features other than the valves are evident, it is likely that they decayed prior to burial (Fig. 3D).

Antenna.—The amount of relief preserved in the antennal rami varies between and within specimens. The ramus is often separated into distinct proximal and distal parts, with less relief in the latter (Fig. 5F). When

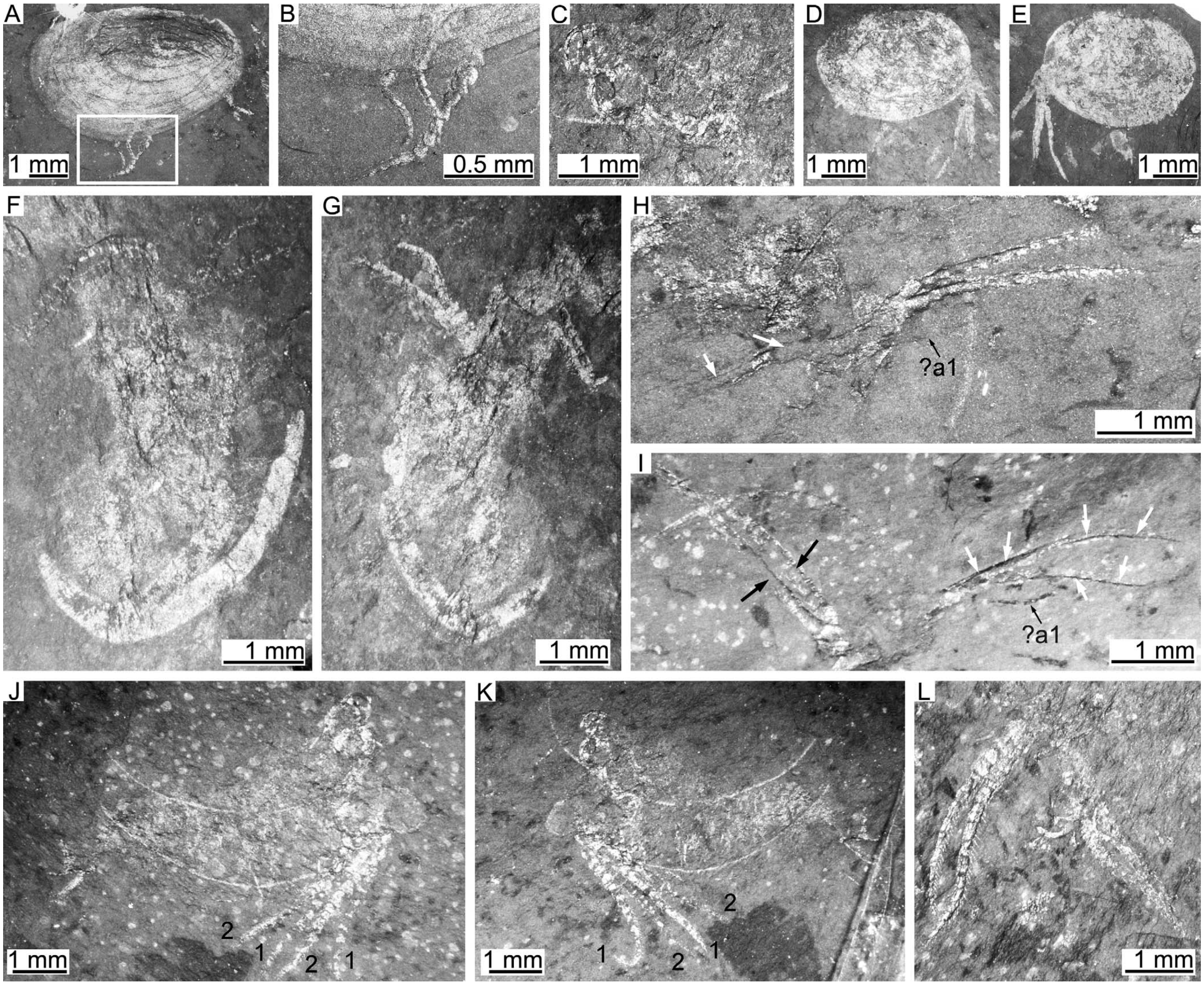

FIGURE 9—Preservation of specimens. A) Rare example in which the plane of splitting passed around the external surface of the carapace valve (GSI:F00896). B) Inset from (A): the presence of the antennal rami can be detected where they continue beneath the carapace. C) The proximal part of the clasper is preserved with much less relief and detail than its distal part (the hand; In21099). D–E) Part and counterpart are mirror images as plane of splitting has passed through the cuticle (except for telson). D) Part (GSI:F03485g). E) Counterpart (GSI:F24051e). F–G) Part and counterpart showing all four antennal rami in positive relief in the part and in negative relief in the counterpart. F) Part (GSI:F00513a). G) Counterpart (GSI:F24070a). H) Antennal ramus on left-hand side of specimen preserved as a broad shallow groove, with lateral margins preserved in positive relief (arrows; GSI:F00895). I) Antennal rami on right-hand side of specimen with creaselike furrows (arrows) along their length; in the upper example the furrow switches position between the sides of the ramus at about the midlength (In21098[1]). J–K) Part and counterpart of specimen in oblique aspect; relief is opposite in the rami of each antenna (labelled 1 and 2). J) Part (GSI:F00893). K) Counterpart (In21099). L) Specimen in which one pair of antennnal rami are in positive relief and the other lacks relief (In21096). ?al = possible antennule.

relief is limited, the plane of splitting can pass through the cuticle, leaving highly reflective cuticle on both part and counterpart (Figs. 9D–E). Where the relief is pronounced, the plane of splitting tends to pass around the external surface of the ramus, resulting in a convex surface covered in cuticle and an external mold lacking it. Some cuticle may be retained in the mold at the junction between segments; for example, compare part and counterpart in Figures 9F and 9G and note that the trunk appendages preserve less relief than the antenna and that their preservation is similar in both part and counterpart.

All four antennal rami usually have the same sense of relief (positive or negative) on the plane of splitting (Figs. 7A, D, 9F–I, 10A), especially if the specimen is preserved in dorsoventral aspect. Occasionally the rami of one antenna are positive and those of the other negative in specimens in lateral and especially in oblique aspect (Figs. 9J–K, compare 1 and 2). In such cases one pair lay above and the other below the plane of splitting (Fig. 10B). Significantly, as cuticle is the only tissue preserved, the rami must therefore have been infilled by sediment or authigenic minerals before they could collapse or be compacted (see Mineralogy, above). The alternative, that the rami of each antenna were at the same horizontal level but collapsed in a different direction (Fig. 10C), is considered implausible. A single specimen preserves the rami of one antenna in positive relief and those of the other without relief (Fig. 9L): the former lie in the plane of splitting, and the latter slightly above or below it.

In some specimens, particularly of *L. ardra*, most of the width of a ramus may be a broad, shallow groove, while the lateral margins are in positive relief (Fig. 9H, white arrows). Alternatively, a sharply defined, creaselike furrow extends along part of the length of the antenna a similar distance from one or other lateral margin (Fig. 9I, white arrows).

Gut.—In some specimens of each taxon, the gut is preserved in moderate to high relief, approaching a semicircular cross section on the plane of splitting (Figs. 11A–B). This requires that the infill, presumably sediment initially, was compacted to a much lesser extent than the host lithology.

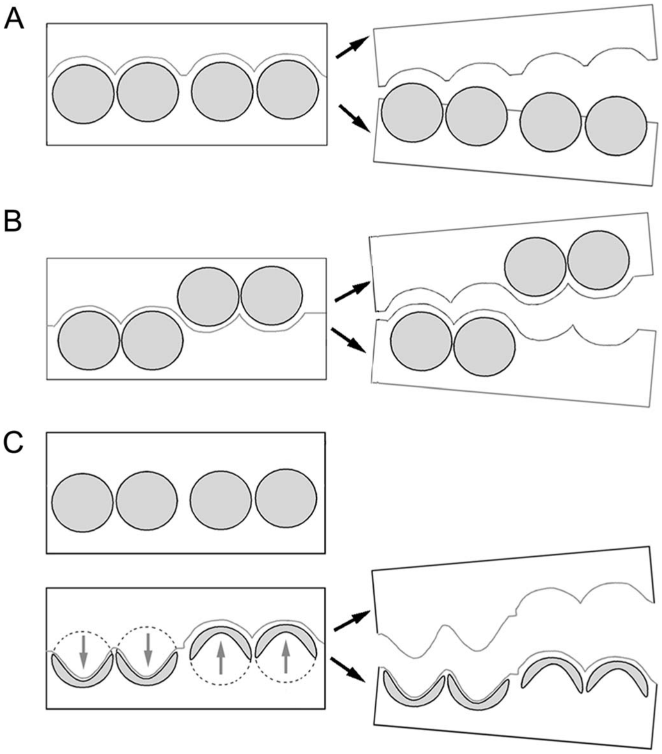

FIGURE 10—Models for the preservation of antennal rami in relief. A) Where all four rami lie on the same horizontal plane, the plane of splitting usually passes around the same side of each generating the part (all rami in positive relief) and counterpart (all rami in negative relief). B) The antennal rami are preserved in full relief, and plane of splitting passes around the upper surfaces of one pair, and the lower surfaces of the other; in the part two rami of one antenna are in positive relief and the other pair in negative relief. Little or no deviation in the vertical position of the plane of splitting is required if each pair of rami is offset from the other by a short vertical distance, as would be expected for specimens preserved in lateral or oblique aspect. C) Preservation on one surface of the two rami of one antenna in negative relief and the other in positive relief via the collapse of the former downward and the latter upward.

TAPHONOMIC MODEL

The Castlecomer spinicaudatans at both sites are preserved similarly, and a model for their taphonomy is presented below as a series of stages, some of which overlapped temporally (Fig. 13).

1. Transport and Burial.—Variation in the attitude of specimens to bedding is strong evidence that they were entombed within event beds represented by silt-mud couplets. Experiments indicate that spinicaudatans disarticulate readily after a short period of decay when subjected to even gentle disturbance (see also Allison, 1986). The Castlecomer spinicaudatans were therefore buried alive or shortly after death. Displacement and distortion of parts of specimens occurred before burial, almost certainly during turbulent transport. Where appendages were rotated into a position at variance with the attitude of the rest of the specimen this must have occurred after burial (stages 3–5).

2. Decay of Labile Tissues.—Decay was initiated shortly after death. The experiments show that the initial stages included shrinkage and decay of tissues, generating voids within the exoskeleton. Extensive degradation of the labile tissues of spinicaudatans occurred over the course of 21 days. Although the experimental conditions do not mimic those under which the fossils were preserved, the results indicate that decay is likely to have been relatively rapid. The intestine and muscles of stomatopod crustaceans became a fluid mass within one week, disintegrating when disturbed (Hof and Briggs, 1997). The irregular dark-colored stain associated with certain specimens (Figs. 7A, 9J–K) may represent decay products that leaked from the body, perhaps similar to the dark stain characteristic of *Marrella splendens* from the Burgess Shale (Whittington, 1971).

3. Loss of Structural Strength of the Cuticle.—Loss of structural strength was protracted, affecting progressively thicker or more sclerotized cuticle and eventually resulted in collapse of the specimen (stage 5).

4. Rotation of Appendages.—The sediment would have had high fluid content and low shear strength during deposition; individual event beds are thin, and dewatering as a result of sediment loading following burial is likely to have been limited. Despite this, sediment did not infill fully the space inside the carapace or infiltrate between different parts of the body, either during or immediately after deposition, unlike, for example, at least the majority of Burgess Shale arthropods (Briggs et al., 1994). It is difficult to envisage how larger parts of the body, such as the posterior part of the trunk and telson (Figs. 5E–F), could have rotated if an extensive infill of fluidized sediment were present, even if additional space were created by collapse of the body (see stage 5 below). Living animals may have reacted to transport by closing the valves, although numerous specimens are in dorsoventral aspect (Fig. 5E). The confining effects of the sediment prevented the carapace from opening after decay of the adductor muscles or attachment ligament (stage 2), thus limiting ingress of sediment after burial, especially to specimens in lateral or oblique aspect. The telson, mandible, and distal part of the clasper are the features most frequently rotated. The morphology of these parts was unaltered after 21 days of decay, indicating that they were covered by the thickest or most sclerotized cuticle.

5. Collapse of the Specimen; Preservation in Relief.—The limited accumulation of sediment inside the carapace allowed the decaying body to collapse into an essentially two-dimensional, bedding-parallel film containing the head, trunk, and appendages of each specimen. In decay experiments the body collapsed as a unit into a more stable orientation as the inner lamella pulled away from the inner surface of the carapace. Collapse affected those parts of the body covered by thinner or less sclerotized cuticle first and facilitated rotation of other parts. In some fossil specimens, cuticle-lined voids created by decay were infilled by sediment or authigenic minerals prior to collapse (see stage 6 below). Three states were observed: (1) features were preserved in or near two dimensions where there is little or no infill, including head, trunk, trunk appendages, proximal part of the clasper, and some of the antennae; (2) high relief resulted where there was extensive infill, including mandible, telson, distal part of the clasper, some protopods, and features of some antennal rami; and (3) collapse was localized to sites where there was incomplete infill, such as in creaselike furrows or broad shallow grooves in some antennae. These different modes of preservation reflect the relative rates of collapse versus infilling by sediment or authigenic minerals, factors that varied very locally.

6. Infill of Appendages.—The relative importance of infill by detrital sediment versus authigenic minerals is unknown. Pyrite is associated with many specimens of *L. gracilis*, both inside and, more often, on the external surface of the cuticle. It rarely occurs in sufficient density to infill cuticle-lined voids, in contrast to preservation in some other exceptional faunas (e.g., Briggs et al., 1996). Pyrite precipitated inside the rachis of some of the setae of an antennal ramus in one specimen of *L. gracilis*; the same feature was observed in arthropod setae from the Lower Cambrian Mount Cap Formation (Butterfield, 2003). The antennal rami of *L. gracilis* are often infilled, particularly proximally, by clay minerals that differ in composition from the surrounding matrix. This material is clearly authigenic in origin and subsequently metamorphosed (stage 8). The surface of the cuticle may have acted as a substrate on which clay minerals precipitated, as in other fossil arthropods (Wills, 1959). Following decay of their internal tissues, the antennal rami represent hollow, tapering cylinders, closed at both ends. Local degradation of less recalcitrant cuticle, such as that of the protopod or head (Fig. 11C; Stage 7), could have created access for fluidized sediment, and negative pressure inside the body caused by decay could result in ingress of this sediment. Significant

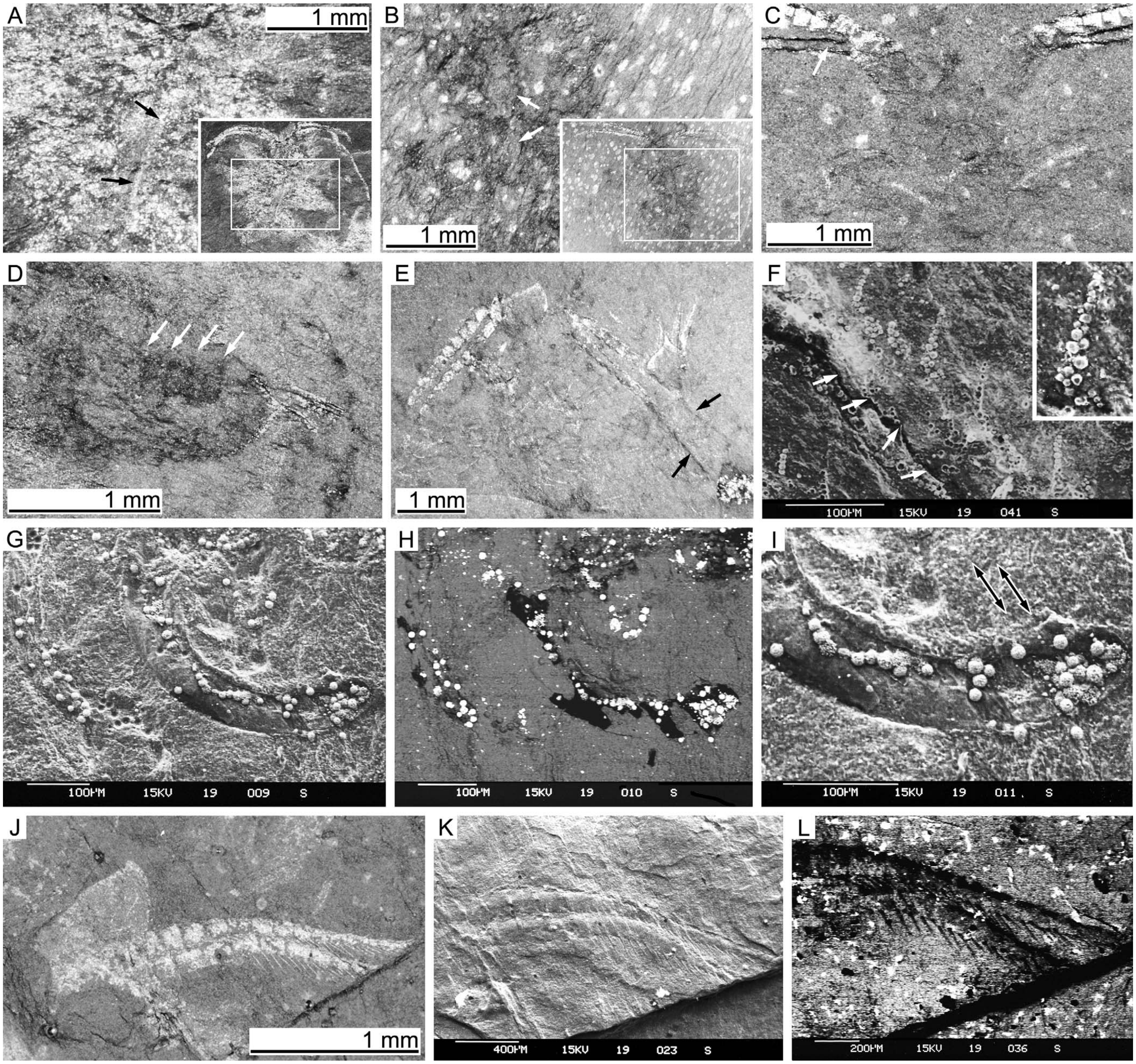

FIGURE 11—Mineralogy of specimens. A–B) Preservation of the gut (arrows) in positive relief; inset shows position in specimen (A, GSI:F24069b; B, GSI:F00897). C) Preservation of head and protopods of the antennae as a dark-colored outline without relief. Arrow indicates area on antennal ramus where cuticle is missing; the ramus is defined by a ridge of fine-grained material similar in appearance to the surrounding sediment (In21101(1)). D) Preservation of posterior part of trunk as a dark-colored outline; arrows = position of segment boundaries along its length (NMING:F:14725/3). E) Distal parts of antennal rami (arrows) lack cuticle and are defined as ridges of fine-grained material similar in appearance to the surrounding sediment (GSI:F00894). F) Secondary electron image of antennal ramus infilled by clay minerals; arrows = broken edge of cuticle. Central rachi of setae are infilled by pyrite octahedra. Inset shows single rachis (GSI:F03485f). G–I) Secondary electron images (G and I) and backscattered electron image (H) of apical hooks showing preservation as dark-colored (carbonaceous) cuticle associated with pyrite framboids. Arrows in I indicate orientation of cleavage, breaking cuticle into smaller, parallel-sided, pieces (GSI:F24051h). J–L) Photograph (J), secondary electron image (K), and backscattered electron image (L) of antennal ramus. The cuticle, highly reflective under incident light, appears dark in the corresponding backscattered electron image (GSI:F24051f).

degradation of the protopod cuticle, however, is not a feature of all specimens in which the antennal rami are preserved in relief (Figs. 9H–I). Further, when degraded completely, the outlines of the protopod and head remain defined, very precisely, as dark stains (Fig. 11C); their preservation is extremely unlikely if adjacent sediment was drawn into the ramus subsequently. The more parsimonious explanation is that, as is in *L. gracilis*, the antennal rami in *L. ardra* were infilled by authigenic clay minerals that were subsequently metamorphosed. The telson, distal part of the claspers, and mandibles usually retain much of their original relief in contrast to the rest of the specimen. Decay of adjacent cuticle may have allowed sediment to infill cavities; for example, the experiments showed that the cuticle of the proximal part of the clasper acquired a very ragged, frayed appearance (Fig. 4K). It is uncertain as to why simple infill by sediment would always be restricted to those parts of the body comprising, or covered by, the most recalcitrant cuticle. The recalcitrance of this cuticle implies that any internal voids would have been retained over an extended period of time, and it is likely that the voids would have been occluded during compaction as a result of burial, not collapse (Stage 8), thus implying sufficient time for their infill by authigenic minerals. The gut is preserved in relief in some specimens. There is no

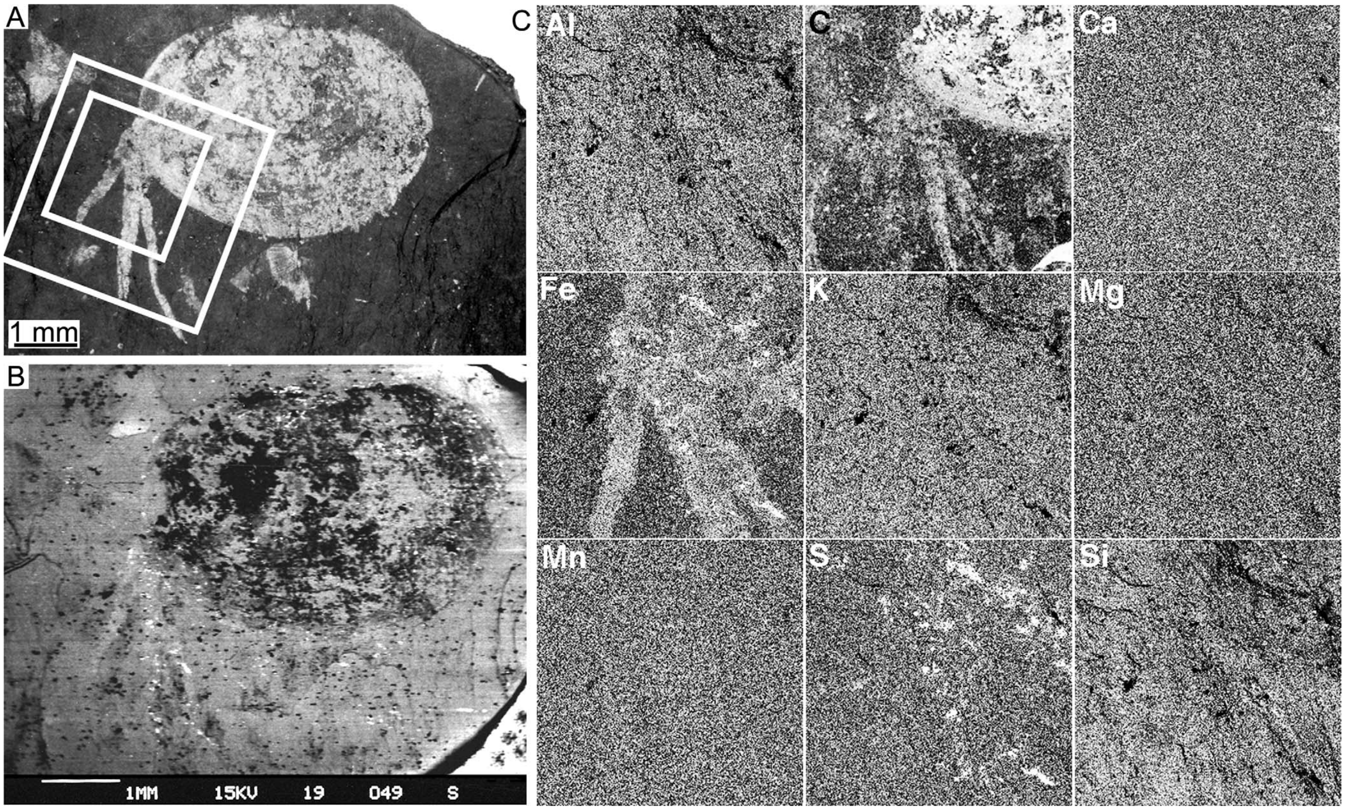

FIGURE 12—Results of X-ray mapping of fossil spinicaudatan (GSI:F24051e). A) Photograph showing areas mapped. B) Backscattered electron image. C) X-ray maps of relative abundance for elements indicated.

evidence that it was the locus of precipitation of authigenic minerals; however, it would be difficult, especially after metamorphism, to distinguish authigenic clay minerals from fine-grained, siliciclastic gut infill present at the time of burial. Decay experiments showed that disarticulation after 8 days resulted in separation of the gut from the remainder of the trunk (Fig. 4I). The gut broke up into short cylindrical fragments that were cohesive enough to retain their circular cross section. Microbial activity may have served to bind the contents together, perhaps with extrapolymeric substances, but in the absence of any authigenic mineralization, microbial activity alone is unlikely to result in the gut retaining its three-dimensionality during burial. It does, however, suggest that even after decay of the cuticular lining, the gut contents will remain *in situ* and not disperse, leaving a longer time period in which to precipitate an authigenic cement.

7. Degradation of the Cuticle.—Thinner cuticle had degraded completely by the end of the decay experiments, including that of the pinnules on the setae of the antennal rami and the posterior-most trunk appendages. The setae on the antennal rami of both *L. ardra* and *L. gracilis* are acicular, almost certainly just the central rachis of an originally pinnate structure. In the decay experiments antennules rapidly became indistinct, but there was no obvious degradation of the antennal rami after 21 days, other than parts of their setae. Similarly, antennules are always poorly preserved in the fossils, in marked contrast to the distal parts of the antennal rami. Thus decay of the fossils was repeatedly arrested between degradation of the cuticle of the antennules and that of the antennae. In some specimens of *L. ardra*, the cuticle covering the protopods, head, trunk, and trunk appendages is not preserved, but its presence is marked by a dark stain, corresponding in shape to the original structure. More rapid decay left less time for the precipitation of authigenic clay minerals (see stage 6, above).

8. Later Events.—Compaction as a result of continued burial resulted in the loss of any remaining internal voids. The carapace valves are the most recalcitrant part of the cuticle, and their morphology was unaltered after 21 days of decay. Loss of most of their three-dimensionality, and probably that of the mandibles, distal part of the claspers, and the telson, is attributed to compaction, not collapse. Metamorphism resulted in graphitization of the cuticle, which rendered it highly reflective, particularly when viewed under incident light under a coverslip, and in the development of a pervasive cleavage, particularly in the Ardra core, and in the finest-grained lithologies.

9. Collection, Sampling, and Splitting.—The lithology, especially in the Ardra core, splits preferentially within the finest-grained laminae in the upper part of each silt-mud couplet; it is not known whether specimens are concentrated in this part or occur throughout the event beds. Rarely, and only in specimens preserved in lateral aspect, the plane of splitting follows the external surface of the carapace valves (Figs. 9A, D–E). The fossil is usually confined to the plane of splitting, with the only recurrent exception being the tendency for the distal part of the antennal ramus to be concealed in the matrix. The cleavage fabric can cause parallel-sided pieces of cuticle to flake off the surface after splitting (Fig. 11I).

DISCUSSION: BURGESS SHALE–TYPE PRESERVATION

The Castlecomer spinicaudatans, like the arthropods from the Burgess Shale (Middle Cambrian, Canada), are essentially two-dimensional on the plane of splitting and are often highly reflective under incident light. The taphonomy of the two faunas is similar in other respects, including (1) burial of organisms in various inclinations within fine-grained event beds, although in different environments; (2) leakage of decay fluids into the surrounding matrix generating a characteristic dark stain; and (3) preservation of arthropods as a combination of carbonaceous compressions (i.e., the most recalcitrant parts of the original tissues were altered to geologically stable organic macromolecules), authigenic clay minerals

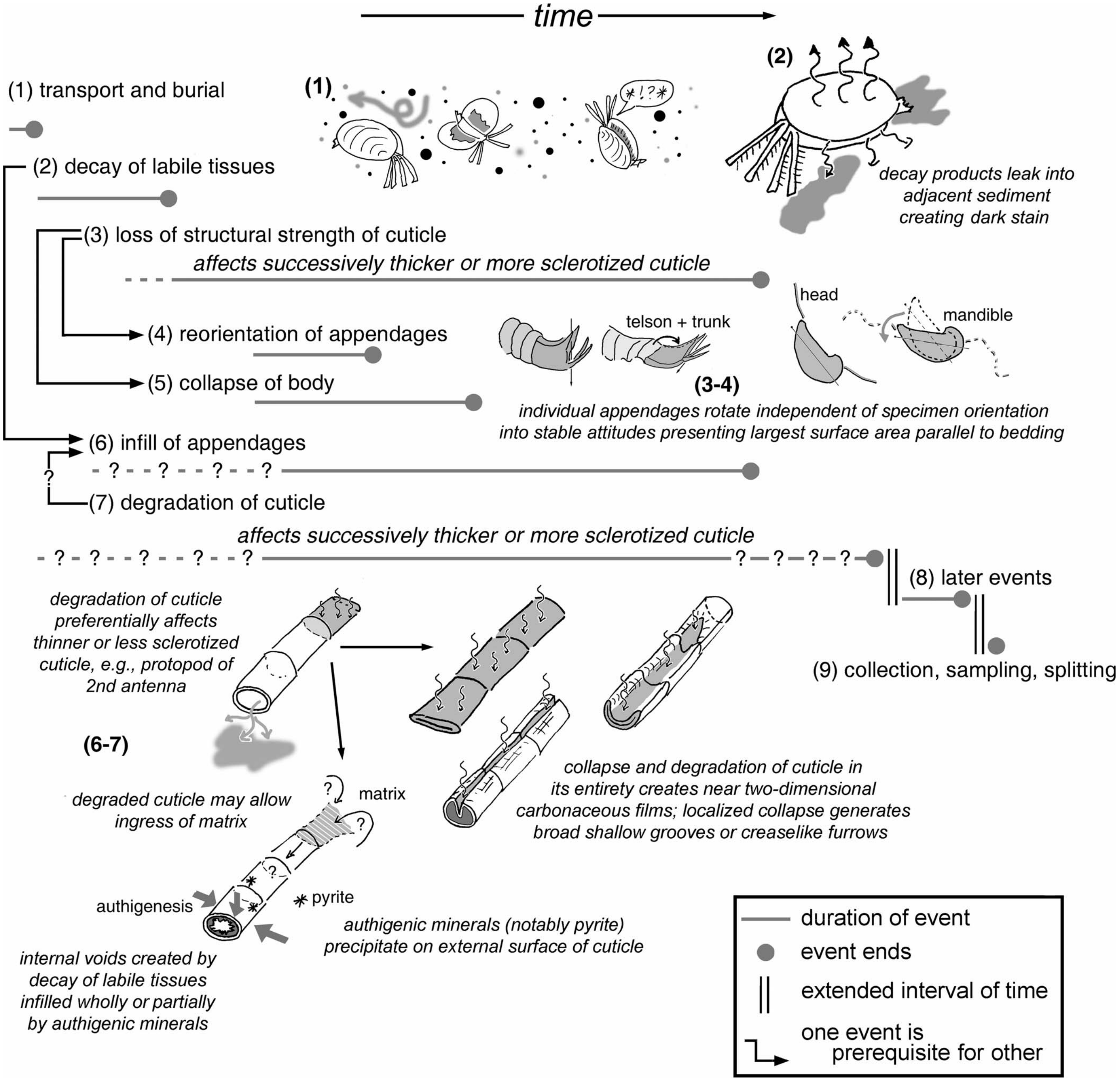

FIGURE 13—Taphonomic model for preservation of spinicaudatans in the Castlecomer fauna.

(subsequently metamorphosed), and pyrite (Orr et al., 1998, and references therein). The postburial history of both localities included metamorphism of the host lithologies and the development of a pervasive cleavage. The Castlecomer spinicaudatans offer potential insights into several aspects of Burgess Shale–type preservation, including postburial diagenetic processes, the fidelity of preservation, the significance of different degrees of decay resistance in parts of the exoskeleton to the interpretation of affinities, and the functional morphology and ecology of the fossil arthropod.

Diagenesis of Burgess Shale Fossils

The postburial history of Burgess Shale fossils is controversial. Debate centers on the relative importance of the organic preservation of original tissues (Butterfield, 1990, 1996) versus replication of features in authigenic clay minerals (Conway Morris, 1990; Orr et al., 1998). Orr et al. (1998) envisaged the authigenic clay minerals (metamorphosed subsequently) to either coat the surface or replace the cuticle of arthropods and outline specific tissues and organs (clay templating, *sensu* Orr et al., 1998). Although it is widely accepted that these clay minerals are diagenetic in origin (Orr et al., 1998; Petrovich, 2001; Butterfield, 2002; Powell, 2003) and do not represent sediment that penetrated the organism during or after burial (Butterfield, 1990; Towe, 1996), there is less consensus on other aspects of Burgess Shale–type preservation. While Orr et al. (1998) considered the clay minerals to have precipitated inside the arthropods, Butterfield (2002, p. 242) argued that they represented "a sedimentary imprint produced during early diagenesis" that "recorded the effects of a decaying carcass on immediately adjacent sediment." Alternatively, clay minerals could have grown in a pressure shadow during later metamorphism (e.g., growth of phyllosilicates in pressure shadows around the organically preserved periderm of graptolites, particularly

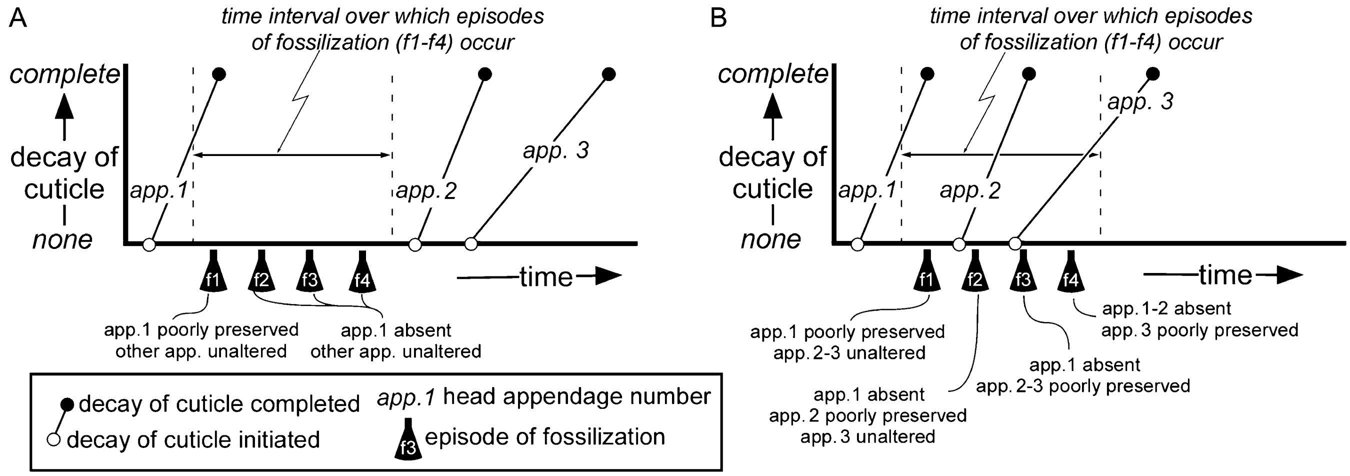

FIGURE 14—Schematic models illustrating how various appendages are preserved and how preservation quality is controlled by the time at which cuticle decay is initiated. The state of preservation of the three appendages (app.) is summarized at each of four episodes of fossilization (f1–f4). A) There is a strong discrepancy in the recalcitrance of the cuticle between appendage 1 and the others and, thus, an extended time period before decay of appendages 2 and 3 is initiated. Fossilization at any time within the time interval indicated will result in the majority of specimens exhibiting the same state of preservation (as in the Castlecomer spinicaudatans). B) Variation in the recalcitrance of the cuticle between appendages is limited; this results in a different state of preservation at each of the four episodes of fossilization.

examples with an infill of pyrite; Underwood, 1992, fig. 3). Butterfield et al. (2007) concluded that the clay minerals grew during metamorphism, simultaneously infilling the void space created by volatilization of the carbonaceous remains.

Specimens of *L. gracilis* provide unequivocal evidence of early diagenetic precipitation of authigenic clay minerals inside the arthropod carcass, infilling cuticle-lined voids created by decay of the labile tissues. Other examples, including the exceptionally preserved ostracodes, are preserved solely as carbonaceous cuticle, indicating that the mode of preservation can vary within individuals, between taxa, between event beds in the same core, and between the two cores. The critical variable is the retention of internal voids long enough to allow them to be infilled by an authigenic phase. The rate at which this occurs is difficult to determine. Other important variables include the resistance of the cuticle to decay and collapse, sediment loading—that is, the frequency of event-bed deposition and thickness deposited—and the rate of mineral precipitation.

Taphonomic Biases in the Disparity of Fossil Arthropods

Variation in the preservation potential of different nonbiomineralized tissues is well established (Briggs and Kear, 1993) and forms the basis for identifying taphonomic thresholds in cases of exceptional preservation, that is, the completeness of soft-tissue preservation (Allison and Briggs, 1991). Although the only tissue preserved in the Castlecomer spinicaudatans is cuticle, its preservation potential is clearly variable. Most important, this variability applies to different appendages, such as the antennule and antenna. Features of the fossil spinicaudatans that are well preserved, including the antennal rami, mandibles, telson, and distal parts of the claspers, are identical to their counterparts in living examples (Orr and Briggs, 1999). The absence of other features in the majority of specimens is undoubtedly taphonomic, not real.

The fossil record of exceptionally preserved arthropods relies on the decay-resistance of the cuticle, so this phenomenon is likely to be more widespread. Thirty-six near-complete specimens and at least 41 separate clusters of cuticle of the notostracan-like crustacean *Castracollis wilsonae* from the Early Devonian Rhynie Chert Lagerstätte were studied by Fayers and Trewin (2003). No antennules (first antennae) or maxillae were recorded, and only two specimens preserved possible maxillulae. Mandibles and antennae (second antennae), in contrast, were common, a situation similar to that found in the Castlecomer spinicaudatans. Fayers and Trewin (2003) suggested that the absence of antennules and epipodites (epipods) on the thoracopods might be taphonomic. Epipods are respiratory or osmoregulatory structures in the Branchiopoda; their cuticle is very thin and may not possess all three layers typical of crustacean integument (Martin, 1992). The number, morphology, and inferred function of the head and trunk appendages of fossil arthropods are important characters in the analysis of interrelationships and disparity. The results of this study show that some of the disparity may be taphonomic in origin, the result of a systematic pattern of selective preservation of certain appendages. It is particularly significant that a continuum of preservational states is not observed in the head appendages of either the Castlecomer spinicaudatans or *C. wilsonae*. Rapid and complete degradation of some appendages before the morphology of others deteriorates appreciably creates an extended time window during which all specimens are similar in appearance (Fig. 14A); fossilization at any time during this process results in most or all specimens being in the same preservational state (e.g., compare f1–f4 between Figs. 14A and B).

The possibility that some appendages have decayed completely should be suspected when the quality of preservation of others varies within a single specimen. In the Castlecomer spinicaudatans, such evidence includes the preferential degradation of the protopods of the antennal rami, trunk, and trunk appendages, including their reduction to dark-colored stains, and the difference in relief between the proximal and distal parts of the claspers. Differences in the preservation of the cuticle may reflect its thickness and strength and therefore correlate with function. The protopods, for example, are key to use of the antennae for swimming, and their cuticle is therefore thin, flexible, and more easily degraded. Thus the state of preservation may offer clues as to the function of the cuticle.

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REFERENCES

Aldridge, R.J., Briggs, D.E.G., Smith, M.P., Clarkson, E.N.K., and Clark, N.D.L., 1993, The anatomy of conodonts: Philosophical Transactions of the Royal Society, London, ser. B, v. 340, p. 405–421.

Allison, P.A., 1986, Soft-bodied animals in the fossil record: The role of decay in fragmentation during transport: Geology, v. 14, p. 979–981.

Allison, P.A., and Briggs, D.E.G., 1991, The taphonomy of soft-bodied animals, *in* Donovan, S.K., ed., The Processes of Fossilization: Belhaven Press, London, p. 120–140.

Bernhard, J.M., Visscher, P.T., and Bowser, S.S., 2003, Sub-millimeter life positions of bacteria, protists, and metazoans in laminated sediments of the Santa Barbara Basin: Limnology and Oceanography, v. 48, p. 813–828.

Briggs, D.E.G., Erwin, D.H., Collier, F.J., 1994, The Fossils of the Burgess Shale: Smithsonian Institution Press, Washington, D. C., 238 p.

Briggs, D.E.G., and Kear, A.J., 1993, Decay and preservation of polychaetes: Taphonomic thresholds in soft-bodied organisms: Paleobiology, v. 19, p. 107–135.

Briggs, D.E.G., and Kear, A.J., 1994, Decay and mineralization of shrimps: PALAIOS, v. 9, p. 431–456.

Briggs, D.E.G., Raiswell, R., Bottrell, S.H., Hatfield, D., and Bartels, C., 1996, Controls on the pyritization of exceptionally preserved fossils: An analysis of the Lower Devonian Hunsrück Slate of Germany: American Journal of Science, v. 296, p. 633–663.

Butterfield, N.J., 1990, Organic preservation of non-mineralizing organisms and the taphonomy of the Burgess Shale: Paleobiology, v. 16, p. 272–286.

Butterfield, N.J., 1996, Fossil preservation in the Burgess Shale: Reply: Lethaia, v. 29, p. 109–112.

Butterfield, N.J., 2002, Perimineralization vs. compression: Disparate modes of exceptional preservation in the Burgess Shale and their palaeobiological significance, *in* DeRenzi, M., Pardo Alonso, M.V., Belinchón, M., Peñalver, E., Montoya, P., and Márquez-Aliaga, A., eds., Current Topics on Taphonomy and Fossilization: Ayuntamiento de Valencia, Spain, p. 241–246.

Butterfield, N.J., 2003, Exceptional fossil preservation and the Cambrian Explosion: Integrative and Comparative Biology, v. 43, p. 166–177.

Butterfield, N.J., Balthasar, U., and Wilson, L.A. 2007, Fossil diagenesis in the Burgess Shale: Palaeontology, v. 50, p. 537–543.

Conway Morris, S., 1990, Burgess Shale, *in* Briggs, D.E.G., and Crowther, P.R., eds., Palaeobiology: A Synthesis: Blackwell, Oxford, UK, p. 270–274.

Criel, G.R.J., 1991, Morphology of *Artemia*, *in* Browne, R.A., Sorgeloos, P.A., and Trotman, C.N.A., eds., *Artemia* Biology: CRC Press, Boca Raton, Florida, p. 119–153.

Eagar, R.M.C., 1964, The succession and correlation of the Coal Measures of southeastern Ireland: Compte Rendu Cinquième Congrès International de Stratigraphie et de Géologie du Carbonifère, Paris, 9–12 Septembre 1963, v. 1, p. 359–374.

Emery, D., and Myers, K.J., 1996, Sequence Stratigraphy: Blackwell Science, Oxford, UK, 297 p.

Fayers, S.R., and Trewin, N.H., 2003, A new crustacean from the Early Devonian Rhynie chert, Aberdeenshire, Scotland: Transactions of the Royal Society of Edinburgh: Earth Sciences, v. 93, p. 355–382.

Higgs, K., 1986, The stratigraphy of the Namurian rocks of the Leinster Coalfield: Bulletin of the Geological Survey of Ireland, v. 3, p. 257–276.

Hof, C.H.J., and Briggs, D.E.G., 1997, Decay and mineralization of mantis shrimps (Stomatopoda: Crustacea)—A key to their fossil record: PALAIOS, v. 12, p. 420–438.

Jones, G.L., 1992, Irish Carboniferous conodonts record maturation levels and the influence of tectonism, igneous activity and mineralization: Terra Nova, v. 4, p. 238–244.

Martin, J.W., 1992, Branchiopoda, *in* Harrison, F.W., and Humes, A.G., eds., Microscopic Anatomy of Invertebrates (Volume 9, Crustacea): Wiley-Liss, New York, p. 25–224.

McLaughlin, P.A., 1980, Comparative Morphology of Recent Crustacea: W.H. Freeman & Co., San Francisco, 177 p.

Nevill, W. E., 1956, The Millstone Grit and Lower Coal Measures of the Leinster Coalfield, with an appendix on the non-marine fauna by R. M. C. Eagar: Proceedings of the Royal Irish Academy, ser. B, v. 58, p. 1–16.

Nevill, W. E., 1961, The Westphalian in Ireland: Compte Rendu Quatrième Congrès pour l'Avancement des Etudes de Stratigraphie et de Géologie du Carbonifère, Heerlen, 15–20 Septembre 1958, v. 2, p. 453–460.

Noffke, N., 2000, Extensive microbial mats and their influences on the erosional and depositional dynamics of a siliciclastic cold water environment (Lower Arenigian, Montagne Noire, France): Sedimentary Geology, v. 136, p. 207–215.

Orr, P.J., and Briggs, D.E.G., 1999, Exceptionally preserved conchostracans and other crustaceans from the Upper Carboniferous of Ireland: Special Papers in Palaeontology, no. 62, Palaeontological Association, London, 68 p.

Orr, P.J., Briggs, D.E.G., and Kearns, S.L, 1998, Cambrian Burgess Shale animals replicated in clay minerals: Science, v. 281, p. 1173–1175.

Orr, P.J., Briggs, D.E.G., and Parkes, M.A., 1996, The ''Castlecomer Fauna'': A new Konservat-Lagerstätte from the upper Carboniferous of Ireland: Irish Journal of Earth Sciences, v. 15, p. 93–106.

Orr, P.J., Kearns, S.L, and Briggs, D.E.G., 2002, Backscattered electron imaging of fossils exceptionally preserved as organic compressions: PALAIOS, v. 17, p. 110–117.

Packard, A.S., Jr., 1871, Preliminary notice of new North American Phyllopoda: American Journal of Science and Arts, v. 102, p. 108–113.

Peters, R.H., 1987, Metabolism in *Daphnia*, *in* Peters, R.H., and DeBernardi, R., eds., *Daphnia*: Memorie dell'Istituto Italiano di Idrobiologia 'Dott. Marco de Marchi' Volume 45, dell'Istituto Italiano di Idrobiologia, Verbania, p. 193–243.

Petrovich, R., 2001, Mechanisms of fossilization of the soft-bodied and lightly armored faunas of the Burgess Shale and of some other classical localities: American Journal of Science, v. 301, p. 683–726.

Powell, W.G., 2003, Greenschist-facies metamorphism of the Burgess Shale and its implications for models of fossil formation and preservation: Canadian Journal of Earth Sciences, v. 40, p. 13–25.

Towe, K.M., 1996, Fossil preservation in the Burgess Shale: Lethaia, v. 29, p. 107–108.

Underwood, C.J., 1992, The preservation and deformation of graptolites: PALAIOS, v. 7, p. 178–186.

Whittington, H.B., 1971, Redescription of *Marrella splendens* (Trilobitoidea) from the Burgess Shale, Middle Cambrian, British Columbia: Bulletin of the Geological Survey of Canada, v. 231, p. 1–21.

Wills, L.J., 1959, The external anatomy of some Carboniferous ''scorpions,'' pt. 1: Palaeontology, v. 1, p. 261–282.

Wright, M.C., 1920, *Limnestheria*: A new conchostracan genus from the Kilkenny Coal-Measures: Proceedings of the Royal Irish Academy, ser. B, v. 35, p. 187–204.

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