trophic groups in the palaeoecology of early communities (Whittington 1985; Conway Morris 1989; see also Section 1.5). As originally exploited by C. Walcott between 1910 and 1921, the fossils came from two quarries on the west slope of a ridge that connects Wapta Mountain and Mount Field, near the town of Field, British Columbia. These excavations are in the basinal shales of the Stephen Formation, and the term 'Burgess Shale' is one of only local significance.

The lower Walcott Quarry, exposing the so-called Phyllopod bed, has been by far the most prolific source of fossils, yielding over 65 000 specimens (Conway Morris 1986). The higher, known as the Raymond Quarry, has been less productive but it provides a distinct assemblage distinguished by a lower diversity and different proportions of taxa in comparison with the Phyllopod bed. In addition, recent searches for comparable soft-bodied biotas elsewhere have yielded a rich harvest. In the vicinity of the Burgess Shale many new localities have been found. More importantly, discoveries elsewhere in the U.S.A., Greenland, and south China have led to a realization that there is a distinctive Burgess Shale-type fauna with a specific and recurrent character that ranges through the Lower and Middle Cambrian.

However, in terms of taphonomic information little is yet known about most of these deposits, and existing insights depend largely on studies of the Phyllopod bed. All the occurrences of Burgess Shale-type biotas share the character of burial in fine-grained sediment, often in catastrophic circumstances, but it would be unwise to assume that their taphonomic histories were similar.

Biota and sedimentary environment

Although studies of the Phyllopod bed biota, which includes both a benthic and pelagic fauna together with associated algae, are not complete, existing estimates of both the number of taxa and individuals (Conway Morris 1986) (Fig. 1) probably will not require radical revision. The benthic fauna (see Conway Morris 1979, 1986; Whittington 1985) is dominated by arthropods, of which only a small fraction are trilobites. In addition, other major groups include priapulid and polychaete worms, cnidarians, sponges, molluscs, echinoderms, and a variety of groups of uncertain taxonomic position (Conway Morris & Whittington 1985; Whittington 1985). As might be expected, the fauna is dominated by relatively few taxa, some nine species accounting

for about 90% of the total. The pelagic fauna is identified largely on adaptations suitable for either a planktic or nektic existence, such as prominent fins, streamlined bodies, or abundance of gelatinous tissue (Conway Morris 1979). In the Phyllopod bed there is strong evidence that much of the biota owes its preservation to catastrophic burial, including occurrence in graded beds, variable orientation of specimens relative to the bedding plane, and seepage of sediment between appendages or other extensions of the body. Because the laminations of the Phyllopod bed lack disturbance or other evidence of bioturbation, it is concluded that the environment of deposition was inimical to metazoan life, and this is confirmed by the exquisite preservation. The excluding factor was most probably anoxic conditions with H_2S, and an alternative possibility of hypersaline waters seems less likely because the specimens do not show obvious osmotic shrinkage or swelling.

The biota clearly lived elsewhere, because it was transported into a hostile environment, and it is useful to recognize this pre-slide environment (Conway Morris 1986). Its exact location is conjectural, but it is probably significant that all the soft-bodied localities in the Stephen Formation, including the Phyllopod bed, were deposited in relatively deep water immediately adjacent to an enormous carbonate bank which rose vertically and acted as a rim to extensive carbonate shoals and lagoons that extended hundreds of kilometres to the east. There is no evidence that any substantial fraction of the biota was derived from the reef top or margins, and it is likely that the pre-slide environment was also adjacent to the reef base. There is also some evidence that the distance of transport between pre- and post-slide environments was relatively small, perhaps a kilometre or so. This figure is based on inferences of local palaeotopography, inferred position of the photic zone relative to the post-slide environment, and survival of partially decayed specimens whose delicate nature could survive only limited transport.

Taphonomic history

The taphonomic history of the Phyllopod bed biota began, therefore, with the failure of the sea bed and its descent towards the post-slide environment. The area of sea floor may have been small, and additional specimens may have been trapped *en route*. As the flows were probably rather weak, extensive erosion and scouring out of the infauna
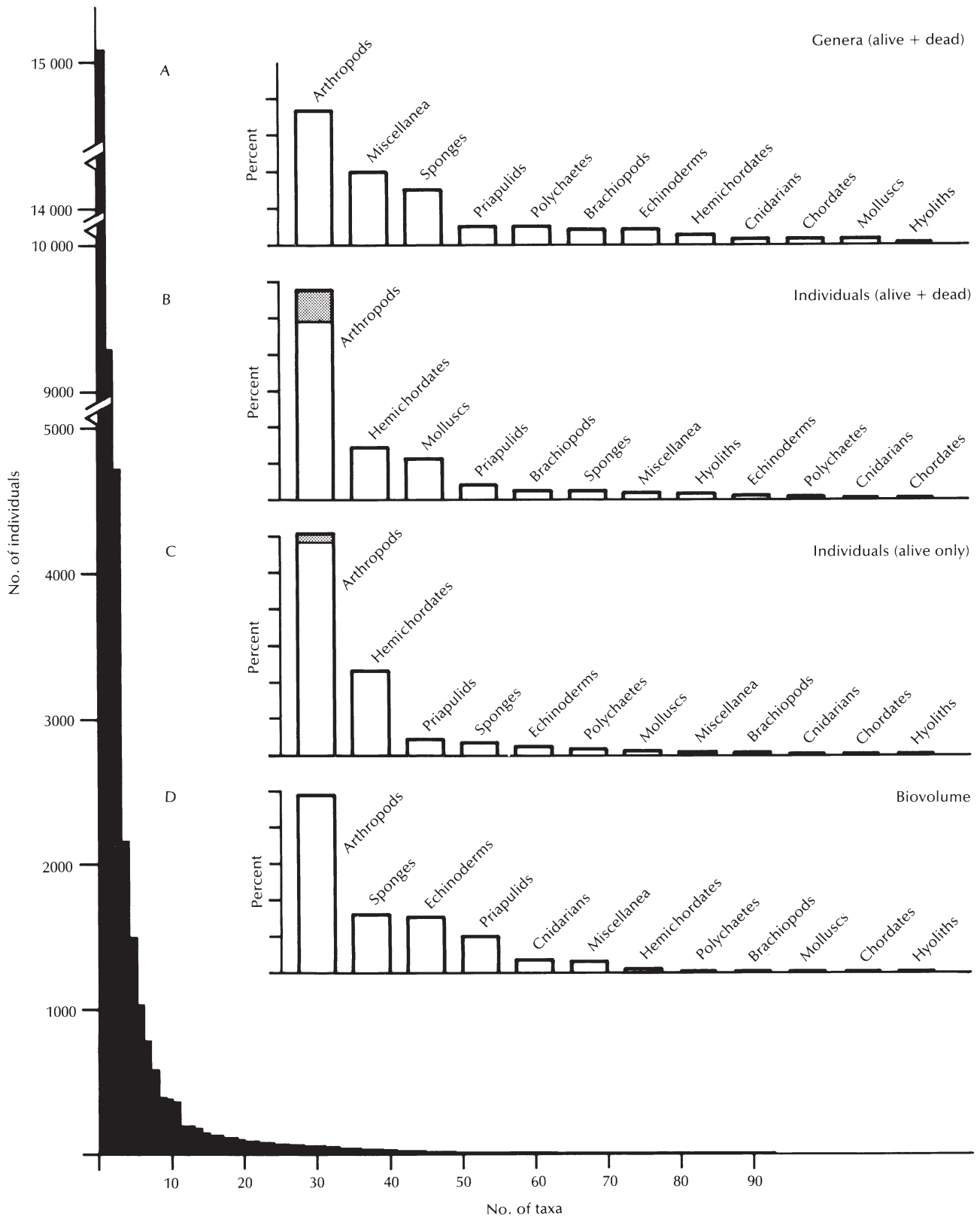
Fig. 1 Frequency distribution of the 93 species that contribute to the benthic community of the Phyllopod bed. Note characteristic 'hollow curve' distribution, and also breaks in scale of ordinate. Inset histograms show relative percentages of the major groups in the Phyllopod bed. A, Genera. B, Individuals, alive and dead (i.e. empty exuviae). C, Individuals alive at the time of burial. D, Estimated biovolumes. Stippled zone in arthropod column represents proportion of trilobites.

seems unlikely, but addition of epifauna and pelagic elements that had strayed close to the sea bed probably occurred. However, other pelagic elements may have descended into the post-slide environment, and there is little doubt that the sampling of this assemblage is very incomplete.

An important principle is that although the benthic flows contained many specimens alive at the time of transport, it also carried a cargo of resistant skeletal parts that had either been discarded (e.g. by ecdysis in trilobites) or remained on death (e.g. in brachiopods, monoplacophorans, and hyoliths). If an accurate census of the original living community is to be undertaken, it is, of course, necessary to subtract these exuviae and empty shells from the specimen totals (Conway Morris 1986). In the case of hyoliths, with attached opercula and helens, and some inarticulate brachiopods with mantle setae extending beyond the valve margins, it is possible to establish whether the individual had been alive at the time of burial. In other cases, such as the monoplacophorans, it is not possible to determine vitality. However, by making reasonable assumptions it can be shown that the shelly component was an insignificant part of the living community, perhaps as little as 2%.

Reasons for death are probably linked to arrival in the inhospitable post-slide environment, but it is likely that much of the fauna was either stunned or dying by the time of deposition. This is because animals placed in an anoxic environment often coil tightly as they enter a metabolic stasis; this feature has not been observed in the Phyllopod bed specimens. Moreover, the lack of evidence for escape activity also supports the notion that the fauna was incapacitated during transport.

In the post-slide environment the majority of specimens were buried, but occasional individuals that show scattering of parts may have lain on the sea floor, where they were disturbed by weak currents. After burial decay commenced, and this is best seen by a dark stain that surrounds an individual and appears to represent body contents that oozed out into the sediment (Whittington 1985). However, decay was evidently limited and, for reasons that are not understood, the processes of fossilization began.

Diagenesis. At present the soft parts of fossils are composed of carbon films (Butterfield 1990) coated by silicate films, principally chlorite and potassium micas (Fig. 2A). In terms of the hard parts, those of calcareous organisms are replaced by similar silicates, although in some cases pyritization has been extensive (Fig. 2C). However, phosphatic species, including the inarticulate brachiopods (Fig. 2B), retain their original composition, while in some cases the sponges retain the siliceous composition of their spicules (Fig. 2D). In many soft-bodied Lagerstätten the role of bacteria is being realized now as a key step in exceptional preservation, especially in the form of coatings that may be subject to rapid mineralization. Although their role in phosphatization has received particular attention (Section 3.11.2), recent work has shown how iron aluminium silicates can also arise during microbial activities (Ferris *et al.* 1987). Fossilized bacteria are now widely known, but have not been recognized

Fig. 2 Back-scattered electron micrographs of Burgess Shale fossils. A, *Eldonia*, surface with potassium mica (dark) and a coating of calcite (light), with a nodule of barium sulphate (very bright), × 65. B, Transverse section of inarticulate brachiopod (*Dictyonina*) with original phosphatic shell and blades of potassium mica, × 125. C, Transverse section of trilobite (*Olenoides*) with exoskeleton partially replaced by pyrite (very bright) enclosing calcite (grey) and elsewhere silicates (light coloured chlorite and dark potassium mica), × 70. D, The sponge *Choia*, surface showing spicules composed of silica and scattered nodules of cerium phosphate (very bright), × 160. (Photographs based on unpublished work with K. Pye.)
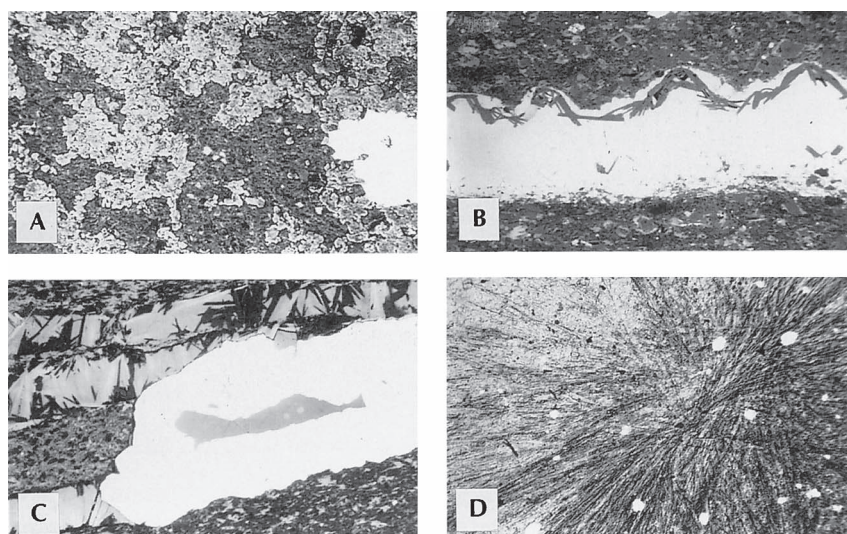
in the Phyllopod bed, perhaps being obliterated during subsequent diagenesis. Indeed, the diagenetic alteration of the Burgess Shale has only received limited study, but in addition to the changes in the silicates, nodules of barium sulphate (Fig. 2A) and cerium phosphate (Fig. 2D) also formed.

The taphonomic history of the Phyllopod bed continued with increasing depths of burial beneath substantial thicknesses of younger sediments. Thrust sheets (including the Cambrian sections with the Stephen Formation on the Simpson Pass thrust sheet) were propelled eastwards as part of a major orogeny during the Mesozoic to Early Cenozoic. Associated with these movements was the development of a strong penetrative cleavage in the argillaceous units. More basinal equivalents of the Stephen Formation were thus affected, and were it not for the massive dolomites of the Cathedral Escarpment providing a tectonic shadow zone, the soft-bodied localities adjacent to this reef would have also been deformed, making recovery of fossils impossible. The final stage of taphonomy, that of its discovery, is to the credit of Walcott, whose chance stumbling on this superb fauna has answered some questions, but set many more.

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3.11.3 Upper Cambrian 'Orsten'

K. J. MÜLLER

Introduction

The Upper Cambrian Alum Shale of southern Sweden first yielded small arthropods with preserved cuticular organs in 1975. Since then, a large variety of such fossils has been recovered at 22 localities from at least five trilobite zones or subzones. They have been discovered over a wide area in Northern and Central Europe, mainly in Västergötland (Kinnekulle, Hunneberg, Falbygden), Skånia, on the island of Öland, in a borehole in northwestern Poland, as well as in drift boulders throughout northern Germany. The fine preservation (Fig. 1) permits detailed comparison not only between the various 'Orsten' animals, but also with extant arthropod orders. Thus the material is important for considerations of the phylogeny of early arthropods and of the relationship between the Recent orders.

Sedimentary environment

'Orsten' is a sulphurous anthraconitic limestone, occurring either as concretions of about 0.1–2.0 m in diameter, or as large flat lenses within the Alum Shale, which may appear as beds in small outcrops. It is commonly banded, because of the fossil layers containing an abundant and varied trilobite fauna represented mainly by exuvia, and/or because of an alternation of lighter, often more sparitic bands with darker, finer-grained ones. There is no apparent difference in the composition of the fauna from either lithology. In general the limestone is rather carbonaceous and often petroliferous. When dissolving such a sample in acid, the oil usually concentrates on top of the liquid. Less carbonaceous beds are beige to light grey. Quartz grains are lacking in both the Alum Shale and the 'Orsten'. Most sediment deposition was under very low-energy conditions. Finely dispersed pyrite indicates the absence of oxygen at the time of deposition. Higher energy sediments composed of fossil hash are rather limited and have not yielded specimens with preserved soft integument.

There is an abundance of calcareous shelly remains; phosphatic fossils are less frequent. Conodonts generally have a dark brown–blackish
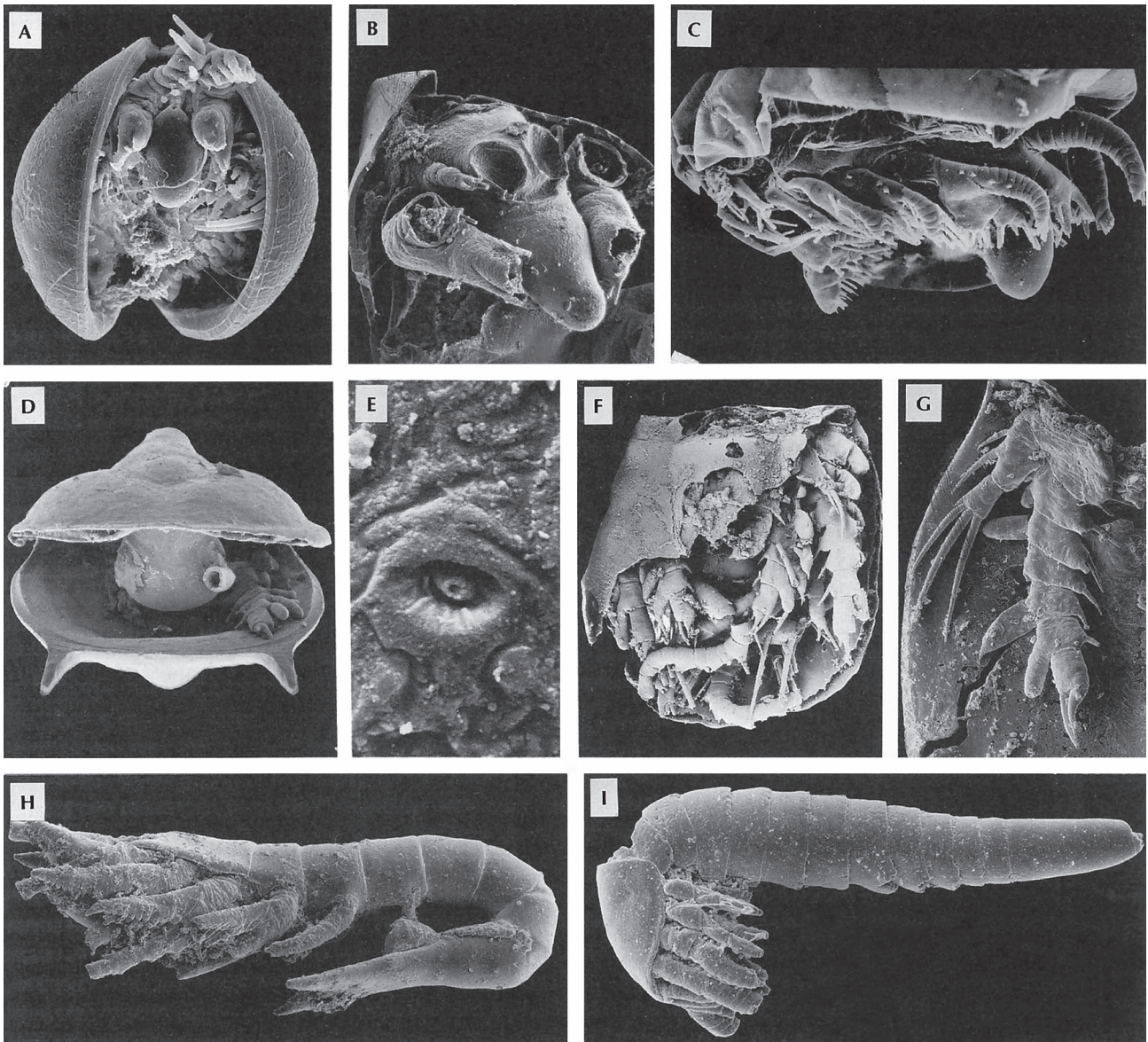
Fig. 1 Examples of 'Orsten' arthropods from the Upper Cambrian of Sweden. A—C, Ostracoda. A, *Falites*, a small growth stage, probably just hatched (× 180). (From Müller 1979.) B, *Hesslandona unisulcata*. Detail with the naupliar eye on collapsed labrum. Small first and large biramous second antennae (× 77). (From Müller 1982.) C, *Vestrogothia spinata*. Preadult stage with six pairs of completely preserved appendages (× 155). (From Müller 1979.) D—G, *Agnostus pisiformis*. (From Müller & Walossek 1987.) D, Larval stage 1b. Hypostome (centre) with proximal parts of antennulae between cephalic and pygidial shields. Left first trunk appendage also evident (× 77). E, Pore on a holaspid (× 1695). F, Larval stage 2a with the appendages snugly packed between the shields (× 220). G, Trunk appendage of meraspid. Note the fusion of proximal podomeres of endo- and exopodites (× 175). H, *Martinssonia elongata* stage 4 (× 77). (After Müller & Walossek 1986.) I, *Skara minuta* (× 90). (After Müller & Walossek 1985 (Reproduced with permission from the *Lethaia* Foundation.)

colour corresponding to the Colour Alteration Index 4—5 (Section 6.2.5). This colour can be produced experimentally by heating the rock to about 300°C. Recrystallization has destroyed the texture in the limestone.

Diagenesis

Dissolution of the limestones in weak acetic acid yields two different types of phosphatic fossils. The first consists of the primarily phosphatic hard parts

of groups such as conodonts, inarticulate brachiopods, phosphatocopine ostracodes, and various problematica. The other type includes secondarily phosphatized fossils or fragments. A thin coating of phosphate may be deposited on the entire surface, in some cases repeatedly. Alternatively, the original chitinous substance may have been replaced by phosphatic matter. Preservation of this kind is generally rare and, except for certain somewhat more widely distributed phosphatocopine ostracodes, most taxa are restricted to a few samples only. The detail preserved by phosphatization varies considerably within samples, let alone between the various occurrences.

The mechanism of phosphatization has not yet been determined (see also Section 3.8.4). It is unlikely that it occurred in the open sea. Many of the 'Orsten' fossils seem to have been phosphatized prior to decay. As even the finest structures have survived, the animals are assumed to have been buried alive or immediately after death.

Extensive picking of residues has produced several thousand specimens with preserved soft integument. Ostracodes such as *Hesslandona unisulcata* (Fig. 1B) are represented by more than one thousand specimens. On the other hand, some other arthropods have yielded only hundreds, tens, or even single individuals. In at least some cases, this difference in preservation potential between the taxa may be attributed to patterns on the cuticle or to variations in original abundance.

The extremely fine preservation even of minor details is due to secondary phosphatization of the body wall, which in most (or all?) cases was chitinous. This may explain the restriction of such preservation to arthropods or arthropod-like organisms and to certain worm-like remains, possibly annelids (see also Section 3.8.4). Other organic matter belonging to an unidentified phylum was not phosphatized at all. The occurrence of internal soft organs is rare.

Most specimens are three-dimensional and show little if any distortion. Others are wrinkled, and were collapsed or inflated before burial. This is perhaps the result of osmotic differences between body liquid and seawater. Flattening or stretching is not evident, and individuals were not compressed significantly after deposition. This enhances the scope for detailed study compared to that afforded by flattened fossils such as those of the Burgess Shale (Section 3.11.2).

Biota

Most representatives of the 'Orsten' arthropod association appear to have been benthic or epibenthic. Their body and appendages indicate that the majority were actively swimming. Forms with legs suitable for walking have not been observed.

A suitable habitat may have been a flocculent bottom layer with a high content of nutrients and low currents. The various morphotypes developed adaptations to different life strategies. They may have lived at different levels on or within the soft bottom layer. The 'Orsten' arthropods represent a thanatocoenosis (death assemblage) (see also Section 3.5). Some of them may be autochthonous, while others have been introduced.

The most widespread soft-bodied fossils are the phosphatocopine ostracodes (Fig. 1A-C). Their appendage morphology indicates that they were filter feeders. *Dala peilertae* and *Rehbachiella kinnekullensis* may have been similar in this respect.

The Skaracarida were cephalomaxillipedal suspension feeders. The more than 100 specimens of the two species of *Skara* (Fig. 1I) represent only adult stages.

Bredocaris admirabilis was most likely a suspension feeder. The retention of many larval features into the adult stage indicates that both larvae and adults fed largely on the same source. This is corroborated by the common occurrence of larvae and adults in the same samples. The paddle shape of thoracopods indicates a swimming mode of life. The habitat may have been on, or closely above, the flocculent bottom layer.

Martinssonia elongata (Fig. 1H) was a bottom dweller that stirred up food with its limbs and its pleotelson-like tail. 'Larva C', a rare form with affinities to the Chelicerata, was ectoparasitic.

The trilobite *Agnostus pisiformis* (Fig. 1D-G) is represented by growth stages from the first instar up to the first holaspid (Müller & Walossek 1987). Although their calcareous exoskeletons are often so abundant as to be rock-forming, phosphatized specimens are extremely rare. *Agnostus* shows characters quite different from the metameric trilobites.

The organization of the Upper Cambrian arthropods as a whole is surprisingly well advanced. Although they are primitive in important respects, many are closely comparable with Recent taxa, even if a direct evolutionary connection is not very likely. In the absence of evidence for the origin of the arthropods in the Precambrian, it is more likely that

the major evolutionary steps were condensed into a time-span of about 80 million years in the Lower and Middle Cambrian.

Small arthropods with preserved soft integument, mainly ostracodes, also occur elsewhere. Similar phosphatization has been found in the Lower Cambrian limestone of Comley, U.K., the Upper Devonian cephalopod limestone in the Carnic Alps, Italy, the Triassic of Spitsbergen, and in the Lower Cretaceous Santana Formation, Brazil. It is likely that further occurrences will be discovered if the techniques used in processing 'Orsten' limestone are more widely applied to such lithologies.

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3.11.4 Hunsrück Slate

J. BERGSTRÖM

Introduction

The Hunsrück Slate (Hunsrückschiefer) occurs mainly in a belt almost 150 km long, south of the River Mosel in West Germany. It is Early Devonian (Early Emsian) in age. Due to synsedimentary tectonism the thickness varies from less than 200 to 3000 m. In the northwest, 'Rhinean' shallow-water sediments are dominated by brachiopods; in the southeast are 'Bohemian' distal sediments with the 'classic' faunas. Much of the clay and silt filling the troughs was derived from a land area to the northwest. Sedimentary structures and trace fossils indicate a depth of more than 200 m (Seilacher & Hemleben 1966), while the well developed eyes of arthropods and vertebrates indicate that the water was probably not much deeper than this (Stürmer & Bergström 1973).

The Hunsrück Slate fossils are pyritized and often preserved as more or less flattened complete individuals. In addition to mineralized skeletal parts, the pyritization has affected unmineralized skeletons and true soft parts (Fig. 1B, C). The latter include cnidarian polyps, arthropod muscles and intestines, and soft parts of annelids and molluscs. The sediment has been transformed to a slate as a result of the Variscan Orogeny, but the cleavage is commonly more or less parallel to bedding, so that the fossils are largely unaffected.

The Hunsrück Slate is a conservation Lagerstätte resulting from rapid burial (or obrution) (see also Sections 3.6, 3.11.4). The dark colour of the rock is partly due to organic carbon, but the sediment is basically a mineral clay and silt deposit.

Sedimentary environment

The average sedimentation rate ranged to a maximum of a couple of millimetres a year. Thus the various well preserved organisms must have been embedded not by normal sedimentation but by very rapid episodic burial. The animals buried in this way were probably alive in many cases; in others they may have been killed by the current transporting the suspended sediment (Stürmer & Bergström 1973; Kott & Wuttke 1987). This explains why many specimens are lying at a high angle to the bedding planes (Fig. 1A). It also explains the strong dominance of benthic organisms in the fauna. A large proportion of the specimens are complete and articulated. It is well known that echinoderms disintegrate within hours of death, and their excellent preservation also indicates rapid burial. Judging from the vertical and lateral distribution of faunas, such events seem to characterize much of the up to 3000 m thick Hunsrück Slate, although fossils are abundant only in the Bundenbach area. Few of the benthic animals seem to have been able to avoid
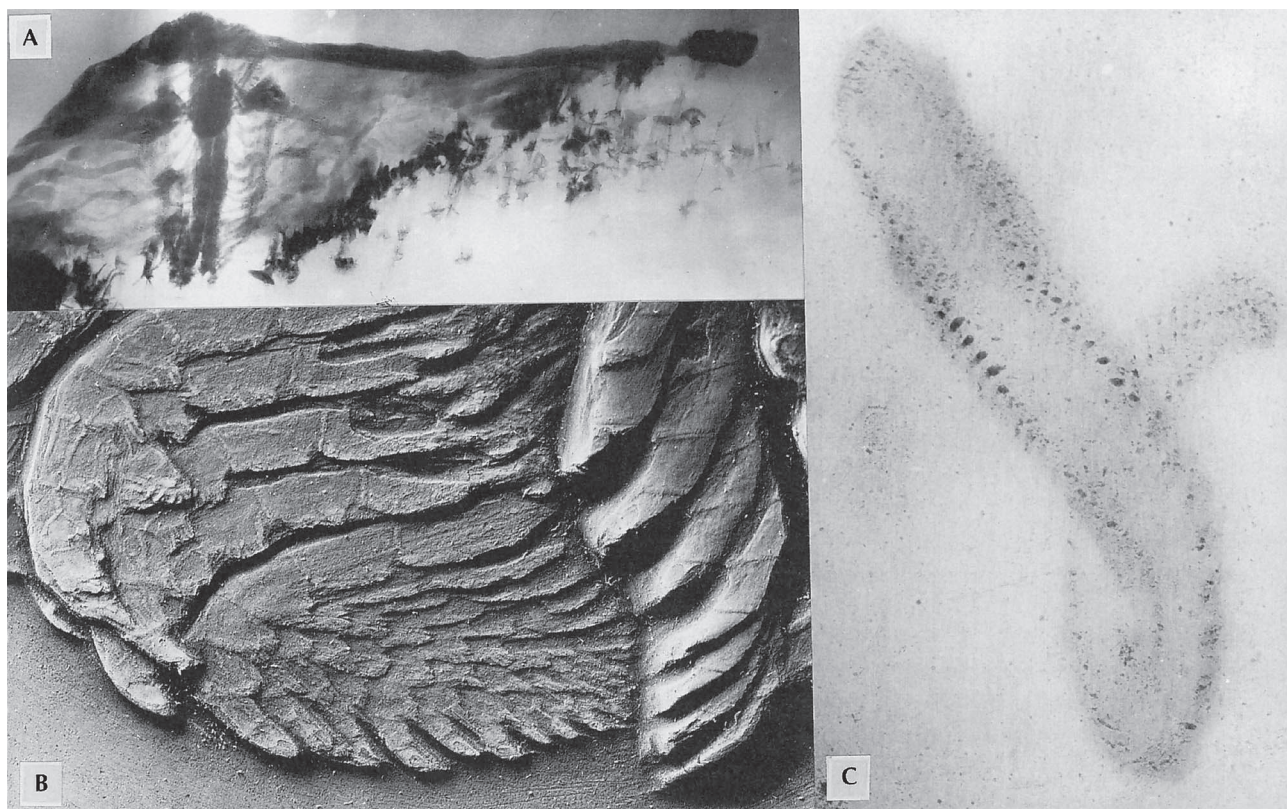
Fig. 1 A, Radiograph of undescribed somasteroid species from Bundenbach. Part of single arm ripped off from rest of body; note isolated skeletal elements on the lower side. The arm is much shortened due to deposition at an angle to sediment surface; tip of the arm above. Contrast due to pyritization of skeleton, × 0.9. (After Stürmer *et al.* 1980.) B, *Phacops* species from Eschenbach. Careful preparation has exposed fine details of pygidial and four thoracic legs of the right side, × 2.9. (Photograph courtesy of S. Stridsberg.) C, Undescribed annelid worm from Bundenbach. Segmental pattern indicated by strongly pyritized chaetae, × 3.5. (Radiograph courtesy of W. Stürmer; no. 12852, Senckenberg Museum, Frankfurt am Main.)

being caught by the suspension currents. Occasionally the currents appear to have been powerful enough to tear bodies apart (Kott & Wuttke 1987) but these may have been weakened by partial decay. A good example of this is illustrated in Fig. 1A, showing a single arm of an undescribed new somasteroid echinoderm.

Part of the Hunsrück Slate sequence includes quite thin lenses and extensive laminae of silt. These are interpreted as indicating a distal density current or turbidite (Seilacher & Hemleben 1966). The undersides of the silt laminae show frequent signs of current activity, such as flute casts and tool marks. These features, in combination with trace fossil evidence, indicate sedimentation in basins in the shelf. The more homogeneous shale is devoid of diagnostic sedimentological features.

Diagenesis

The fossils are usually strongly compressed because of the fine-grained sediment. However, early pyritization has preserved much relief (Fig. 1B), more than in other argillaceous deposits, such as the Burgess Shale (Section 3.11.2). Deposition of small organisms, in particular at high angles to bedding, adds to the deformation caused by compaction. Sliding movements also occurred inside decomposing carcasses. In the arthropod *Cheloniellon*, for example, the ventral side has moved in relation to the dorsal, making the discrimination of the segments difficult (Stürmer & Bergström 1978).

Some authors have suggested that the pyrite was formed mainly in those parts of the animals which contained much organically bound sulphur, e.g. in

the shape of conchiolin, keratin, cystin, spongin, etc. (Fig. 1A, C). The microbial production of H_2S played an important role (Section 3.8.3). In many arthropod specimens the limbs are more extensively pyritized where they extend beyond the carapace, than where they are covered by it. This is probably mainly a function of the high surface area : mass ratio of the exposed limbs, which promotes the reduction of sulphates, compared with that of the main part of the body and adjacent structures.

Biota

In addition to one acritarch and 47 spores, about 400 species of macrofossils are known from the Hunsrück Slate (Mittmeyer *in* Stürmer *et al.* 1980). The fauna is dominated by benthic and nectobenthic species. Thus, echinoderms form the largest group with some 125 species, closely followed by molluscs with around 115 species. Of the molluscs, 92 species are gastropods or bivalves and 31 more or less heavily shelled cephalopods. There are 63 listed species of brachiopods, 31 arthropods, 17 vertebrates, 12 cnidarians, six tentaculite-like forms, six conularids, three bryozoans, one ctenophore, and one red alga. All the arthropods belonged to the benthos, and many of the cephalopods could have done so. The vertebrates are species of agnathans and placoderms which were flattened in life. The flattening provides good evidence that they lived on the substrate. In addition, there is a species of lungfish. A few species form exceptions to this benthic association. These are six species of psilophytes, which must have been derived from a nearby land area, and one pelagic species of each of the hydrozoans and ctenophores.

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3.11.5 Mazon Creek

G. C. BAIRD

Introduction

The Mazon Creek area fossil localities in northeast Illinois yield a diverse biota of Middle Pennsylvanian plants, terrestrial animals, and numerous aquatic taxa including both estuarine marine and non-marine animals. This biota, preserved in sideritic concretions, includes the most important assemblage of soft and lightly skeletonized invertebrate animals known from the Late Palaeozoic (Nitecki 1979). Moreover, it also includes one of the most diverse land plant floras known from North America. Over 350 species of plants, 140 species of insects, and over 100 additional non-marine taxa, including bivalves, millepedes, centipedes, scorpions, spiders, eurypterids, xiphosurans, branchiopods, ostracodes, shrimp-like crustaceans, fish, and tetrapods comprise the non-marine component which is termed the Braidwood Biota (Baird *et al.* 1985a). Estuarine marine organisms, comprising the Essex fauna, are similarly diverse and varied; this component includes medusae, hydrozoans, a siphonophore, chitons, cephalopods with soft parts, diverse polychaetes and crustaceans, a xiphosuran, a holothurian, several agnathan vertebrates, numerous fish species, and various problematical taxa (Fig. 1).

Stratigraphy. Concretions containing the Mazon Creek fossils occur in the Francis Creek Shale Member of the Carbondale Formation which was deposited during the Middle Pennsylvanian Westphalian D stage. The Francis Creek Member is underlain by the widespread and commercially important Colchester (No. 2) Coal Member; strip mining and deep mining of this coal unit account for the numerous spoil dumps which are the usual collecting sources for these fossils. Where the Francis Creek is thin, it is overlain by the Mecca Quarry Member, a thin, fissile, black shale unit which is
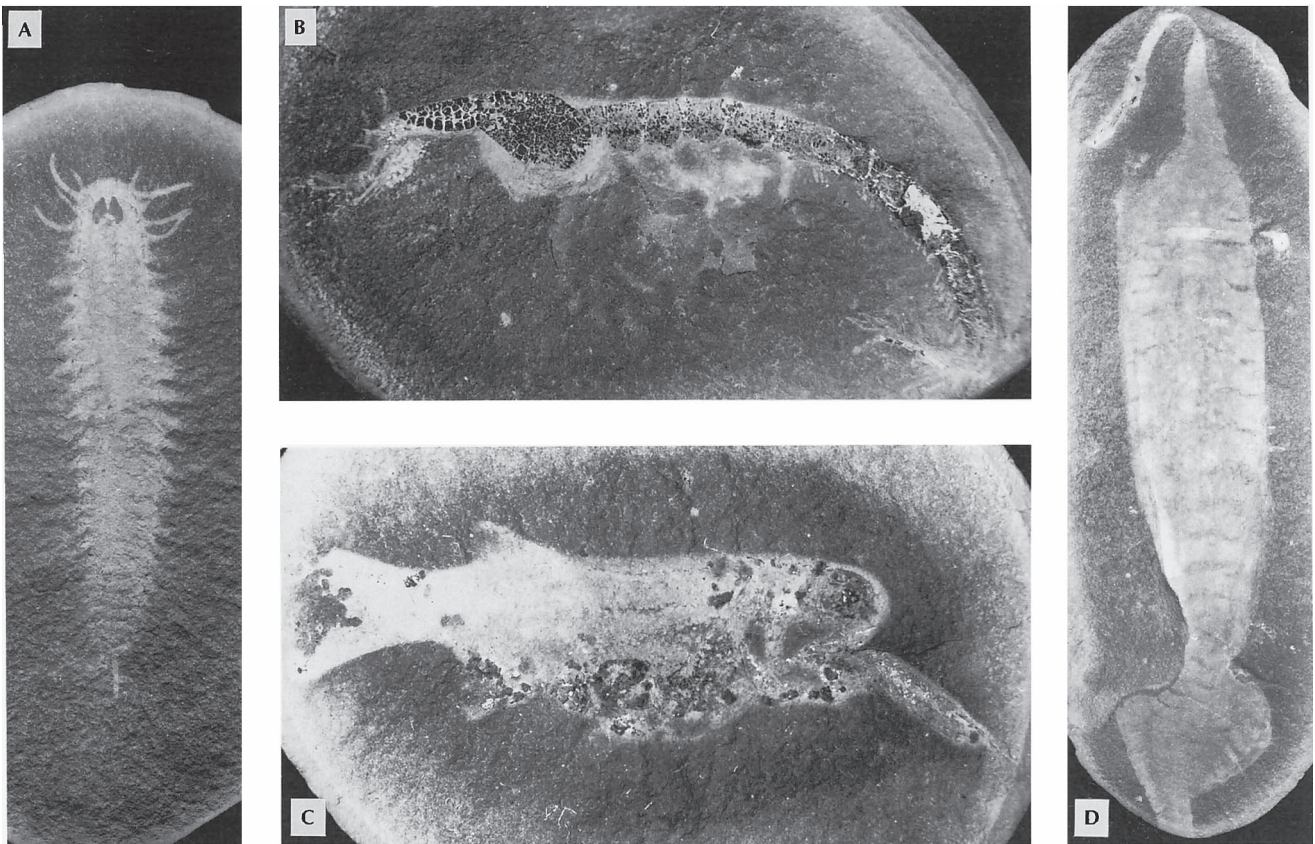
Fig. 1 Marine animals (Essex fauna) from Mazon Creek area, northeast Illinois. All specimens from a large strip mine 'Pit 11' near Essex, Illinois. A, Polychaete annelid *Fossundecima konecniorum* with conspicuous chitinous jaws, × 1.25. B, Phyllocarid crustacean *Kellibrooksia macrogaster*, × 1.4. C, Palaeoniscoid fish *Elonichthys peltigerus*, which has choked on an acanthodian fish, × 1.8. D, Problematic organism *Tullimonstrum gregarium* ('Tully Monster'), × 0.7. (All specimens courtesy of Northeastern Illinois University, Mazon Creek Paleontology Collection.)

locally famous for the occurrence of well preserved marine vertebrates; this unit is absent where the Francis Creek Shale exceeds 10 m in thickness.

The Francis Creek Shale is variable in thickness regionally, and is absent in many parts of Illinois. It reaches a maximum thickness of 25–30 m in northeast Illinois; in the Mazon Creek area it is composed of silty mudstone with local development of coarser deposits, particularly in the upper part of the unit. Fossiliferous sideritic concretions are characteristic of the thickest Francis Creek deposits, and they are usually common in its lowermost four metres. Thin (0–5 m) Francis Creek deposits west and southwest of the Mazon Creek area are composed of grey, argillaceous, and distinctly bio-turbated mudstone deposits which typically lack sideritic concretions (Baird *et al*. 1986).

Localities. More than 100 collecting localities for Mazon Creek fossils exist within the Mazon Creek area, which includes parts of Grundy, Will, Kankakee, Essex, and LaSalle counties. Natural out-crops of the fossiliferous strata are almost completely restricted to Mazon Creek itself near Morris, Grundy County. Virtually all remaining localities are spoil dumps of abandoned strip mines and underground mines exploiting the Colchester Coal. Most fossil collecting is done in strip mine areas, most notably in one large mine area ('Pit 11') near Essex, Illinois. Concretions are continually exposed as the back-piled tip heaps weather and erode; many of these nodules break open along the fossil plane by re-peated frost wedging, but others must be split with a hammer.

Sedimentary environment

The Francis Creek Shale Member in the Francis Creek area is believed to be an estuarine-deltaic deposit recording the progradational advance of

one or more major distributary systems into a shallow epeiric sea (Baird *et al.* 1985a). The presence of numerous thick, distributary channel sandstones with associated crevasse splay and interdistributary bay deposits indicates that an active coastal delta-distributary complex was present. Braidwood aquatic animals inhabited interdistributary bays and waterways bordering this delta complex.

The stratigraphic occurrence of Essex animals in the basal Francis Creek across much of the Mazon Creek area indicates that the delta prograded into a large marine water area. However, the diminutive character of most Essex taxa, the total absence of normal marine shelf organisms (such as corals, bryozoans, articulate brachiopods, trilobites, and crinoids), plus the character of the associated deposits, collectively indicate that Essex organisms inhabited a large river-influenced estuary (Baird *et al.* 1986). Examination of mudstone deposits associated with these organisms reveals the presence of distinctive cyclic repetitions of mudstone and siltstone laminae which appear to record sequential flood- and ebb-tide events within the estuary (Baird *et al.* 1985a).

Detailed census collecting at all Mazon Creek area localities shows that an abrupt boundary separates areas yielding abundant Essex animals from regions yielding no Essex taxa (Baird *et al.* 1985a); non-marine localities near the northeast margin of the census area are abruptly bounded by marine localities to the southwest. However, one-way mixing of plants and non-marine Braidwood animals into areas of Essex animal abundance does occur; this is believed to reflect southwestward (seaward) transport of non-marine taxa by currents from upstream sources (Baird *et al.* 1985a).

Diagenesis

Mazon Creek aquatic animals generally died as a result of episodic incursions of turbid freshwater during periods of flooding (Baird *et al.* 1986). Rapid sedimentation is indicated by engulfment of upright trees, the edgewise burial of plant leaves, and by occasional evidence of escape attempts by bivalves and other organisms (Fig. 2). The rarity of large animal specimens partly reflects a near-absence of large taxa and/or the successful escape of large animals, but it is also a result of the limited availability of interstitial iron and organic nutrients required to produce concretions of sufficient size to enclose large organisms.

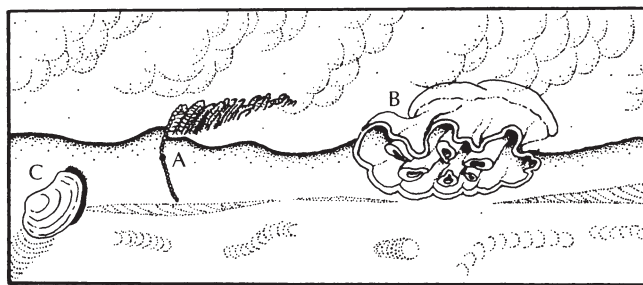Mazon Creek fossils are preserved as variably

Fig. 2 Burial of Mazon Creek organisms. Flood event with torrential sedimentation and incursion of freshwater. Organisms include: A, up-ended pinna of *Pecopteris*; B, partially engulfed medusoid *Essexella asherae*; C, bivalve *Edmondia* attempting to escape smothering. (From Baird *et al.* 1986.)

compressed moulds within concretions. Plant fossils occur as moulds infilled by calcite, kaolinite, or sphalerite with a residue of coaly organic material often present (Baird *et al.* 1986). Mollusc shells, cephalopod and chiton radulas, and holothurian pharyngial rings are also preserved as moulds. Medusae are typically composite moulds which reflect compressive superposition of top surface detail onto the lower surface following burial; convex-downward relief on such impressions reflects weight pressing (loading) of the jellyfish lower surface into subjacent muds (Fig. 2). Most arthropods and some worms retain thin surficial films of variably degraded organic cuticle.

Sideritic concretions enclosing fossils serve as a taphonomic 'window' through which important biological information can be obtained because synjacent mudstone deposits yield few well preserved fossils. These concretions formed very early following fossil burial; they contain up to 80% carbonate, indicating that they formed in water-rich surface muds (Woodland & Stenstrom *in* Nitecki 1979). Most Francis Creek concretions are believed to have nucleated around buried organisms prior to significant decay, and the growth of some may have been triggered or enhanced by decay processes (Fig. 3; see also Section 3.8.2). Precipitation of the siderite is believed to have commenced following depletion of interstitial seawater sulphate by sulphur-reducing bacteria; once it was exhausted, bacterial methanogenesis would have commenced, leading to siderite precipitation (Woodland & Stenstrom *in* Nitecki 1979). Rapid sedimentation, a weak or unsteady sulphate supply within the estuary, and the entrapment of iron and abundant
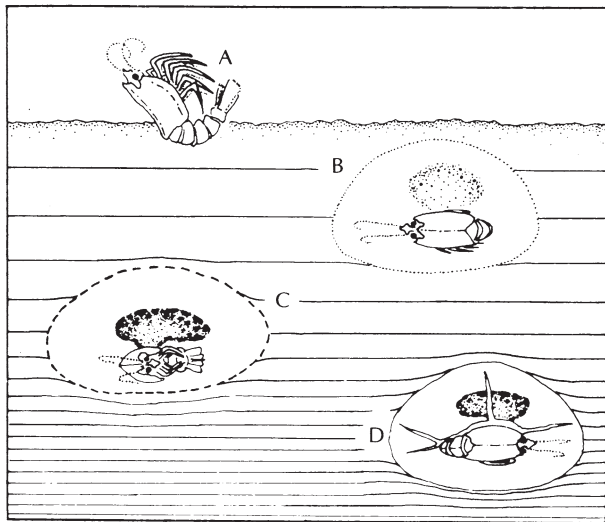
Fig. 3 Early diagenetic events. A, Burial of organism. B, Bacterial sulphate reduction proceeds in local decay centre ('gas vent' zone) above organism prior to depletion of interstitial sulphate. Subsequent bacterial activity produces siderite. C, Continued siderite precipitation hardens proto-concretion which resists compaction. D, De-watering of surrounding muds causes laminae to deform around nodule. Syneresis (de-watering) within concretion produces fractures which break preformed pyrite (or iron monosulphide) halo around decay centre. (From Baird *et al.* 1986.)

organic material, are believed to explain the abundance of sideritic concretions in this deposit (Baird *et al.* 1986).

A regional preservation gradient is observed within the area of Essex animal occurrence; preservation quality of jellyfish, shrimp, worms, and holothurians decreases to the south and west of Grundy, Will, and Essex counties. In eastern LaSalle County jellyfish occur as diffuse and often micro-burrowed impressions, and holothurian remains are sometimes identifiable only from the presence of the coherent pharyngial ring. In western LaSalle County body fossils are rare and the mudstone is highly bioturbated; slower sedimentation near the seaward margin of the delta complex, combined with extensive bottom churning by infauna, account for this poor preservation. Study of similar but younger deposits in Illinois shows that trace-fossil diversity increases seaward of deposits yielding Essex animals, but that body fossils are uncommon between regions of sideritic concretion abundance and normal marine, shell-rich sediments deposited far from shore (Baird *et al.* 1985b; Baird *et al.* 1986).

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3.11.6 Holzmaden

R. WILD

Introduction

The small village of Holzmaden is situated on the northwestern fringe of the Schwäbische Alb, about 30 km southeast of Stuttgart in Baden-Württemberg, West Germany. It lies in an area of Liassic sediments, of which the Lower Toarcian Posidonienschiefer (Fig. 1) contains an abundant, excellently and completely preserved fossil flora and fauna. Fossils have been known since the end of the sixteenth century, at first from Boll, later from the neighbouring Holzmaden region. In this area, which is protected, some quarries still work and fossils are discovered up to this day.

Sedimentary environment and diagenesis

The Posidonienschiefer at Holzmaden consists of 6–8 m of thick black bituminous marls and shaly marls with intercalated bituminous allochthonous limestones. The dark colour of the marls is caused partly by diffusely distributed pyrite and partly by organic material. In some layers the latter exceeds 10%, indicating that stagnant conditions persisted for a long period of geological time. The limestones, calcareous nodules and concretions, however, represent rapid deposition, as shown by obliquely or even vertically embedded uncompressed fossils.
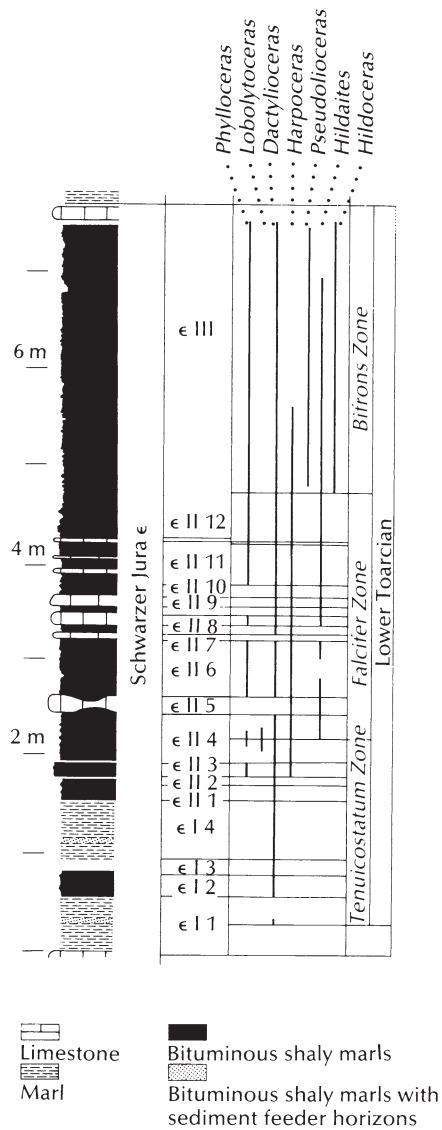
Fig. 1 Stratigraphy of the Posidonienschiefer and distribution of the stratigraphically important ammonites in the quarry G. Fischer, Holzmaden. (After Urlichs *et al*. 1979.)

pressed, broken and flattened, except where they are preserved in calcareous nodules, which originate from the decaying organic material. These layers are often enriched by pyrite (see also Sections 3.8.2, 3.8.3). Bioturbation horizons (ε I 3, ε I 4, top of ε III), consisting mainly of the trace fossil *Chondrites*, indicate that temporary periods conducive to epibenthic life interrupted the otherwise predominantly euxinic conditions. In some beds aligned and mainly juvenile ammonites, or oriented belemnite rostra, point to weak bottom currents. These are also evidenced by the disarticulation of vertebrate skeletons, or those parts of them, which projected above the embedding mud surface.

Benthic organisms are extremely rare in the Posidonienschiefer. They are restricted to some diademoid echinoids, ophiuroids, a few burrowing bivalves (such as *Solemya*, *Goniomya*, *Cucculaea*), and possibly the crustacean *Proeryon*. The reduced benthic life, the proportionally high percentage of bitumen, the undisturbed sedimentation and the preservation of soft tissues, led to the proposal of a stagnation depositional model for the Holzmaden Posidonienschiefer, and comparison with the quiet-water conditions of the modern Black Sea. An upper water body rich in oxygen and life was underlain by euxinic near bottom water. Kauffman (1979), however, supported a depositional model of black shale-type, pointing out that anaerobic conditions were restricted to the sediment itself, or to a boundary fluctuating between the sediment and the water directly overlying it. His views were superseded by a modified stagnation model incorporating storm events (Seilacher 1982) or currents (Riegraf *et al*. 1984).

Biota

In the biotic community the autochthonous flora is represented by coccolithophorids. *Gingko*, the conifers *Pagiophyllum* and *Widdringtonites*, the cycadeans *Pterophyllum* and *Otozamites*, and the newly discovered *Pachypteris*, and the horse-tail *Equisetites* were washed in from the Vindelician continent situated about 100 km south of Holzmaden.

The microfauna, stunted in some layers, consists mainly of radiolarians and foraminiferans. Apart from benthic forms, the bivalves *Gervillia*, *Pseudomytiloides*, *Oxytoma*, *Exogyra*, *Antiquilima* and possibly *Liostrea* were fixed by their byssus to a temporarily hardened mud bottom or to floating

Limestone / Marl

Bituminous shaly marls

Bituminous shaly marls with sediment feeder horizons

The marls are laminated over a distance of kilometres, as a result of an alternation of clay minerals and enriched organic material, consisting mostly of coccolithophorids. They were deposited slowly, primarily as low-density, water-enriched muds, which were later compacted to about 0.17–0.1 of their original thickness. During this early diagenetic process, the pore-water dissolved the aragonite and also partly the calcite of shells, or destroyed microorganic hard tissues, so contributing to the lamination (Einsele & Mosebach 1955). Compaction also resulted in the condensation of shell fragment layers (ε II 3, ε II 12). The enclosed organisms were com-

Fig. 2 *Passaloteuthis paxillosa*. Soft body of a belemnite (Schwarzjura ε II 1, Ohmden, near Holzmaden).

shells of mainly ammonites. The bivalves *Steinmannia*, *Meleagrinella* and *Bositra* (the earlier 'Posidonia', which gave the Posidonienschiefer its name) were pseudoplanktic. The gastropod *Coelodiscus* is numerous in concretions and limestones; it fed on the decaying organic remains of vertebrates. The ammonites and their stratigraphic distribution are listed in Fig. 1 and by Riegraf *et al.* (1984). Coleoids are represented by vampyromorphids (e.g. *Loligosepia*, *Loliginites*, *Teudopsis*, *Phragmoteuthis*, and *Chitinobelus*), and the belemnoids *Dactyloteuthis*, *Youngibelus*, *Salpingoteuthis*, and *Passaloteuthis*. Soft

body tissues of the last are preserved (Fig. 2). The crinoids *Pentacrinites* and *Seirocrinus* lived in colonies, and are often preserved attached to the remains of floating logs. There is a rich ostracode fauna which, together with the crustaceans *Uncina*, *Proeryon*, and *Coleia*, completes the invertebrate fauna of Holzmaden.

Holzmaden is famous for its complete vertebrate skeletons. Sometimes they are preserved with the so-called 'skin' (e.g. in ε II 3–5). This decayed and transformed soft tissue marks the outline of the body as a black film and is found in the sharks *Hybodus* and *Palaeospinax*, the holocephalian *Acanthorhina*, in ganoids and holosteans, but mainly in the many species and specimens of the ichthyosaur *Stenopterygius* (Fig. 3), in the marine crocodile *Steneosaurus* (but not in *Pelagosaurus* and *Platysuchus*), and in the pterosaurs *Dorygnathus* and *Campylognathoides*. The pterosaurs and the saurischian dinosaur *Ohmdenosaurus* are allochthonous faunal elements. Fishes are represented by the ganoids *Lepidotes*, *Dapedium*, *Pholidophorus*, the subholosteans *Ptycholepis*, *Tetragonolepis*, and *Saurorhynchus*, the rare *Chondrosteus* and rare coelacanth *Trachymetopon*, and the teleosts *Leptolepis* and *Euthynotus*, all of which lived in the oxygen-rich upper water. Some, however, are believed to have been allochthonous (e.g. *Lepidotes*, *Dapedium*, *Tetragonolepis*). The plesiosaurs *Plesiosaurus* and *Rhomaleosaurus*, the ichthyosaurs *Stenopterygius* and *Leptopterygius*, and the long-snouted *Eurhinosaurus* seem to have been inhabitants of the open sea, while the crocodiles and the sphenodontid *Palaeopleurosaurus* presumably lived near the coast.

The ichthyosaur *Stenopterygius* is represented by many species and hundreds of specimens, sometimes with stomach and intestine contents (e.g. the hooks of coleoids). There are preserved females giving birth to young (Fig. 4), or containing up to thirteen embryos, or in association with an aborted foetus. The high percentage of pregnant female ichthyosaurs, and of juveniles, may be due to a 'spawning ground' to which the animals migrated periodically over a long geological time to give birth to their young.

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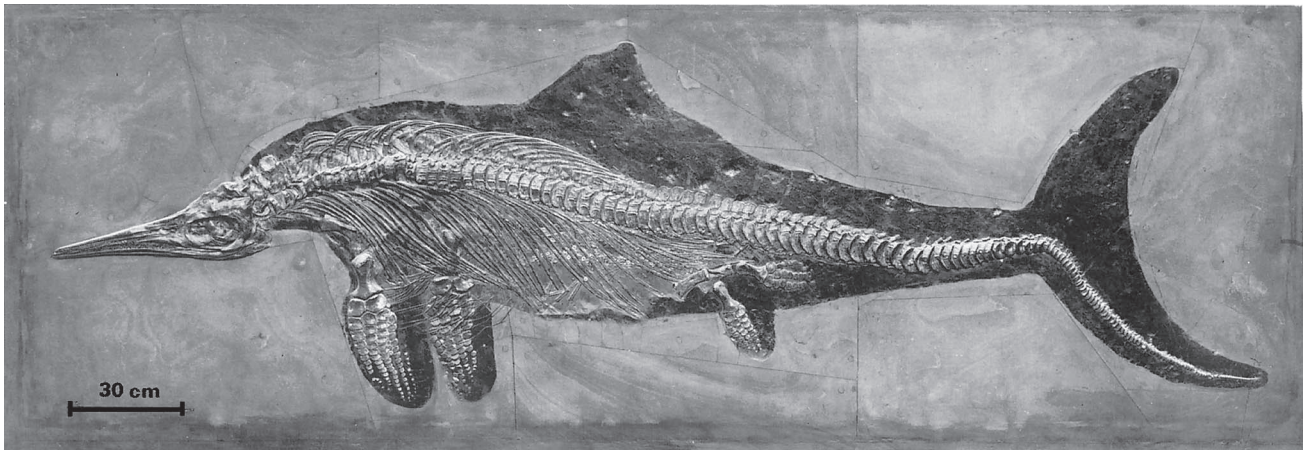
Fig. 3 *Stenopterygius macrophasma.* Soft body of an ichthyosaur with remains of three embryos in its body cavity (Schwarzjura ε II 4, Holzmaden).
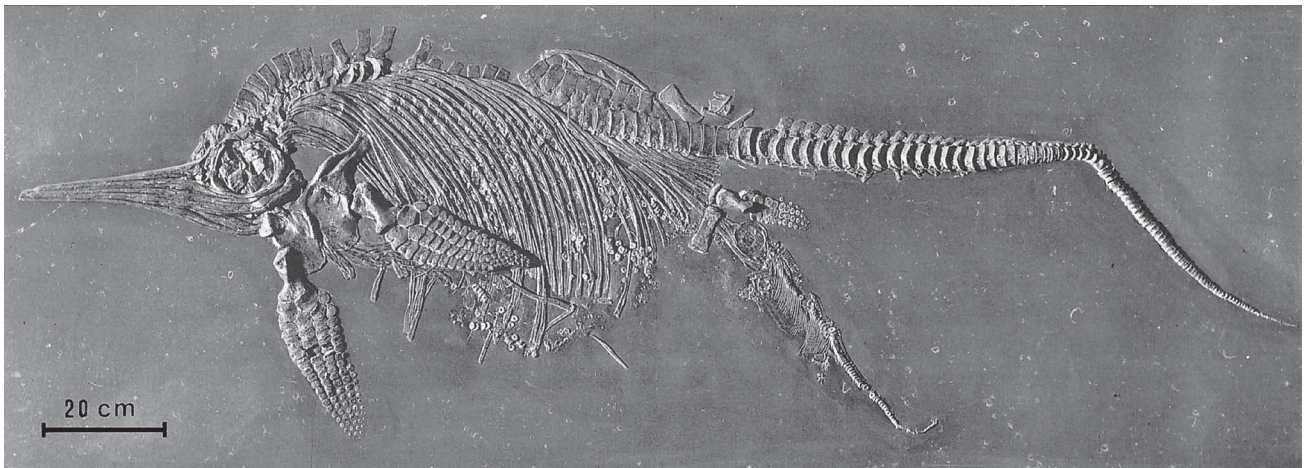

Fig. 4 *Stenopterygius quadriscissus.* Female in the process of giving birth, with the remains of three embryos in its body cavity (Schwarzjura ε II 3, Boll).

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3.11.7 Solnhofen Lithographic Limestones

G. VIOHL

Introduction

The Solnhofen Lithographic Limestones of the Southern Franconian Alb (Bavaria, West Germany) range over an area of about 70 × 30 km and display some differences in facies and preservation of fossils.

The Solnhofen Limestones comprise not more than half an ammonite zone in the lower part of the

Lower Tithonian, representing at most 0.5 myr. The lithology, best described by the German word 'plattenkalke', is characterized by micritic, even-layered limestone slabs ('Flinze') (mostly with an internal microbedding) and irregularly intercalated calcareous fine-layered marls ('Fäulen').

Sedimentary environment

The Solnhofen Limestones were deposited on a sea floor with strong relief, due to algal–sponge reefs. The limestones vary considerably in thickness (0–95 m). The depositional area was backreef in position. It was landlocked to the northwest and separated from the Tethys Ocean by discontinuous coral reefs along its eastern and southern margins.

All the evidence found in the Solnhofen Limestones suggests a semiarid climate (Viohl *in* Hecht *et al.* 1985). High evaporation rates and the restriction of water exchange with the open sea caused a high salinity and the development of a density stratification in the lagoonal waters. This resulted in stagnation and a hostile bottom environment. Even in the surface water layers the organic productivity must have been relatively low, as can be inferred from the scarcity of fossils and the low content of bitumen and pyrite in the sediment. Only episodically was the lagoonal water body completely mixed with waters of the Tethys Ocean.

The origin of the sediment is still controversial. Barthel (1978) regarded the marly layers (Fäulen) as the normal sediment accumulated over a long period, and the limestone layers (Flinze) as representing storm events. In this model, which seems the most probable, carbonate ooze deposited on the seaward margin of the coral reefs was periodically stirred up by storms and pushed into the lagoon as a suspension, where it settled down forming a layer of lime mud. Only the finest fraction was transported as far as the basins of Solnhofen and Eichstätt. Other models explain the limestone layers as a kind of stromatolite built up by cyanobacteria (Keupp 1977) or as the result of coccolithophorid blooms (de Buisonjé *in* Hecht *et al.* 1985).

There are no indications of strong bottom currents. Evidence of currents, such as roll marks of ammonite shells (Seilacher *et al.* 1985), orientation of fossils, and ripple marks (Janicke 1969) are confined to the eastern basins (Painten, Pfalzpaint) or to a few beds in the uppermost Solnhofen Limestones which must be interpreted as turbidites caused by earthquakes. In the area of Solnhofen and Eichstätt settling marks next to the fossils (Mayr

1967), as well as aptychi and fragments of ammonite shells lying convex side down, suggest a very calm environment (see also Section 3.4.1). Other evidence is the high percentage of articulated vertebrates, echinoderms, arthropods (Fig. 1), and ammonites with aptychi in place.

The extraordinarily good preservation, in some instances even of soft parts, also required protection by rapid burial. Swept in during storms, the fossils were buried immediately by suspension fallout, because they settled a little earlier than the micritic particles. This could also explain why most fossils lie parallel to bedding. An exception are the jellyfish found in the quarries of Gungolding–Pfalzpaint, which are embedded within the limestone slabs. Being lighter than other animals, they sank only during deposition of the lime mud.

The Solnhofen Limestones yield not only well preserved fossils but also disarticulated skeletal elements. These are due to decay processes occurring while the carcasses were floating in the water. Particularly long drift times, even after decay of the soft parts, can be inferred for belemnites with attached

Fig. 1 A characteristically complete specimen of the decapod *Eryon arctiformis*. (Scale bar = 1 cm.)

oysters. Their soft parts have never been found, only those of their relative *Acanthoteuthis*.

Some necrolytic features may be due to the hypersaline environment. Mayr (1967) described strongly bent teleostean fishes with the tail fin torn off the vertebral column. This phenomenon can best be explained by dehydration in a brine, and consequent contraction of the ligaments tying together the neural arches. The caudal fin adhered firmly to the bottom, obviously to a cyanobacterial mat; it could not follow the movement of the carcase and became detached (Fig. 2).

The dorsally bent neck, a familiar feature of *Archaeopteryx* (Fig. 3), *Pterodactylus*, and *Compsognathus*, is perhaps better explained by the drifting position in which the carcasses came to rest on the bottom (Rietschel 1976).

Seilacher *et al.* (1985) attributed the *post-mortem* contraction of the crayfish *Antrimpos*, and the coiling of the stemless crinoids *Saccocoma* and *Pterocoma*, to the dehydrating effect of hypersaline waters. The wrinkles seen in some specimens of the jellyfish *Rhizostomites* might also be due to the same cause (de Buisonjé *in* Hecht *et al.* 1985), especially those indistinctly preserved from the Eichstätt quarry area.

Diagenesis

In the Solnhofen Limestones two phases of cementation and correlated compaction must be sharply distinguished:

1 An early cementation of the superficial layer was caused by cyanobacterial mats (Keupp 1977). These were also responsible for the preservation of traces, and they prevented macrofossils from sinking into the underlying soft and mobile sediment. Syneresis phenomena on the bedding planes (Janicke 1969), formerly interpreted as mud cracks and rain-drop imprints (Mayr 1967), suggest that superficial cementation was accompanied by an early dehydration.

2 The main cementation and compaction of the sediment occurred only after the collapse of fossils, which are therefore all flattened (see also Section 3.7). Compaction could not have continued indefinitely after collapse, however, because deformational structures of adjacent bedding planes below and above the fossil have been preserved. These deformations were plastic in the case of fish, crayfish, and squids (de Buisonjé *in* Hecht *et al.* 1985) as well as the body chambers of the ammonites *Glochiceras* and *Aspidoceras*. During the collapse of shells of the ammonite *Perisphinctes*, and of the phragmocones of *Glochiceras* and *Aspidoceras*, the sediment was already stiffened and reacted by fracturing along microfaults (Seilacher *et al.* 1976).

Solnhofen fossils typically lie in a depression in the overlying bed while supported on a pedestal in the underlying bed. Depressions ('collapse calderas' of Seilacher *et al.* 1976) occur on the adjacent bedding planes above and below. Collapse of the fossil certainly plays an important role in the formation of

Fig. 2 A young *Tharsis dubius*, strongly bent by dehydration in a hypersaline environment. The vertebral column has become detached from the tail fin, itself firmly adhered to a cyanobacterial mat, × 0.65.