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PALEOECOLOGY OF THE DEVONIAN-MISSISSIPPIAN
BLACK-SHALE SEQUENCE IN EASTERN KENTUCKY
WITH AN ATLAS OF SOME COMMON FOSSILS

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April 1981

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BLACK-SHALE SEQUENCE IN EASTERN KENTUCKY

by

Lance S. Barron[1] and Frank R. Ettensohn[2]

ABSTRACT

The Devonian-Mississippian black-shale sequence of eastern North
America is a distinctive stratigraphic interval generally characterized
by low clastic influx, high organic production in the water column,
anaerobic bottom conditions, and the relative absence of fossil evidence
for biologic activity. The laminated black shales which constitute most
of the black-shale sequence are broken by two major sequences of inter-
bedded greenish-gray, clayey shales which contain bioturbation and
pyritized micromorph invertebrates. The black shales contain abundant
evidence of life from upper parts of the water column such as fish fos-
sils, conodonts, algae and other phytoplankton; however, there is a lack
of evidence of benthic life. The rare brachiopods, crinoids, and molluscs
that occur in the black shales were probably epiplanktic. A significant
physical distinction between the environment in which the black sediments
were deposited and that in which the greenish-gray sediments were de-
posited was the level of dissolved oxygen. The laminated black shales
point to anaerobic conditions and the bioturbated greenish-gray shales
suggest dysaerobic to marginally aerobic-dysaerobic conditions. A
paleoenvironmental model in which quasi-estuarine circulation compliments
and enhances the effect of a stratified water column can account for both
depletion of dissolved oxygen in the bottom environments and the absence
of oxygen replenishment during black-shale deposition. Periods of
abundant clastic influx from fluvial environments to the east probably
account for the abundance of clays in the greenish-gray shale as well as
the small amounts of oxygen necessary to support the depauparate, oppor-
tunistic, benthic faunas found there. These pulses of greenish-gray
clastics were short-lived and eventually were replaced by anaerobic condi-
tions and low rates of clastic sedimentation which characterized most of
black-shale deposition.

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INTRODUCTION

Paleoecological study of the Upper Devonian-Lower Mississippian black shale is difficult, not only because the depositional environment of these shales is poorly understood, but also because the Late Devonian was a critical time in the evolution and development of life on Earth. For the first time since their initial appearance in the Silurian, land plants evolved to the point that upland forests could develop. Both fresh-water and marine fish underwent rapid evolution, and a few fresh-water forms appparently evolved into amphibians at this time. The enigmatic conodont-bearing animal underwent explosive evolution and radiation whereas large numbers of brachiopod genera became extinct. The underlying environmental controls reflected in these biotic changes may be directly or indirectly related to those responsible for black-shale deposition. Yet, because the shale lacks abundant evidence of metazoan life, and because the contained fossils are generally rare and poorly preserved, any connection with the biotic changes remains unclear. Nonetheless, some significant paleoecological inferences about the included biota can be made using modern analogues, functional morphology, and sediment-organism relationships. It is the purpose of this study to generate a paleoecological overview of the black-shale sequence through integration of the above techniques with observations from the literature and field. Because ecologic studies typically deal with organism habitats, the first part of the study will deal with fossils from the black shale in terms of their larger habitats or environmental preferences. In the second part of the study, the two major facies of the black-shale sequence will be examined in terms of the fossils contained in them.

PLANKTON

Throughout the black-shale sequence, plankton represents the most abundant form of life found. Both phytoplankton and zooplankton are present; phytoplankton typically predominate.

Tasmanites

Tasmanites from the black shales are translucent, amber-to-red-colored discs and spheres, ranging in diameter from 100 to 600 microns. Usually, Tasmanites fossils are collapsed from their normal spherical form into flattened discs by compaction. However, some examples retain their original spherical form because of infill with pyrite, calcite, barite, or phosphate. Specimens viewed with the naked eye appear to lack surface ornamentation and unequivocal trilete or monolete markings. At high magnification, however, a slight rugose nature and inconspicuous punctae are present (Newton, 1875; Schopf and others, 1944; see Plate XII, figures A and B).

In the past, Tasmanites have been misinterpreted for the most part as spores of land plants that were transported by the wind or currents

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into the black-shale sea. Although Dawson (1871a) described similar spore-like discs as Sporangites, Newton (1875) provided a more thorough description of the fossil and named it Tasmanites after the Tasmanian white coal which is composed of these discs. Newton thought that Tasmanites were, "vegetable organs" or spore cases, but he was not certain from which plant they had come. He suggested that they were related to lycopod macrospores. Although Ralph (1865) had suggested earlier that Tasmanites was algal in nature, Newton dismissed this interpretation as improbable. Since that time, Tasmanites generally has been described as a spore of terrestrial origin. Schopf and others (1944), however, discounted any relationship between Tasmanites and higher plants contemporary with the Devonian occurrence of the genus. They concluded that the actual nature and affinities of Tasmanites were unknown.

In 1962, Wall suggested that Tasmanites was algal in origin and was very similar to the modern green alga Pachysphaera pelagica Ostenfield. Pachysphaera was described in detail by Parke (1966) as a planktic, marine green alga of the family Prasinophyceae. Pachysphaera, however, progresses through various life phases, but it is only the encysted phase that resembles the fossil Tasmanites. The encysted stage develops from a motile form that bears four flagellae. The cyst begins with one chloroplast, one nucleus, and one pyrenoid with a starch sheath. Growth continues until the nucleus begins to divide. Nuclear division is accompanied by division of the cell contents. Eventually, motile phases are produced and liberated by breakage of the tough, organic outer wall of the cyst. Each cell of the motile phase contains a single nucleus, chloroplast and pyrenoid. Cells of both the motile and the encysted stages have been reported from depths of 70 meters in the English Channel and North Atlantic (Parke, 1966).

Chaloner and Orbell (1971) and Brooks (1971) supported inclusion of Tasmanites with the Prasinophyceae, but Brooks (1971) was uncertain whether Tasmanites was a marine or fresh-water form. Using δ^{13}C values for an Alaskan tasmanite, Brooks suggested a brackish environment, whereas the δ^{13}C values for Tasmanites punctatus suggested a marine environment. He concluded that the organisms lived in brackish to marine water and were concentrated by currents.

Chemical analyses of the Tasmanites wall have shown that it is composed of sporopollenin, a substance also identified in Carboniferous megaspores as well as in spores and pollen of Recent higher plants. Some chemical analyses of dinoflagellate thecae report properties similar to those from the walls of Tasmanites (Brooks, 1971).

Tasmanites remains occur throughout black shales ranging in age from Middle Devonian to Early Mississippian. On a world-wide basis, Tasmanites ranges from the Silurian to the Cretaceous (Brooks, 1971).

The occurrence of a planktic green alga such as Tasmanites in the upper parts of the black-shale sea suggests the presence of primary producers or phytoplankton which would have been a source of oxygen. The algae also made a significant contribution to the organic matter deposited on the floor of the black-shale sea. Comparisons with other fossil and Recent occurrences suggest a brackish to marine, planktic environment for the probable green alga Tasmanites.

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Acritarchs

Acritarchs are unicellular or colonial organic-walled microfossils that have a spherical, ovoidal, or triangular body or vesicle. The body may possess spines, processes or membranes which project outward (Williams, 1978). These enigmatic, organic-walled microfossils have been reported from the black-shale sequence by Boneham (1970), Wicander (1973a, b), McLaughlin and Reaugh (1974), Reaugh and McLaughlin (1975), and Martin and Zielinski (1978). These fossils occur in both black shales and greenish-gray shales of the black-shale sequence. Although the exact affinities of acritarchs are unknown, they are generally regarded as some form of marine phytoplankton. Acritarchs are thought to reflect marine conditions, even though some Holocene forms are apparently found in fresh-water deposits (Williams, 1978). Wicander (1973a, b) reported an apparent decrease in abundance and diversity of acritarchs upward in the section from a core in the Ohio Shale. Although intervals of increased abundance and diversity were noted in the Chagrin Shale and Cleveland Shale, acritarchs became quite rare in the overlying Bedford Shale. Martin and Zielinski (1978) also reported varying acritarch abundances and diversities accompanying occurrences of Tasmanites and terrestrial spores. An abundance of acritarchs was interpreted to indicate open-marine conditions whereas an abundance of Tasmanites and spores was interpreted to indicate terrestrial environments. It is doubtful that such terrestrial environments are represented in the black-shale sequence, although much of the sediment is certainly terrestrial in origin.

The acritarchs were probably marine phytoplankton, perhaps related to the Chlorophyceae (Downie, 1967). Hence, they not only served as primary producers in the black-shale sea , but also contributed sub-stantially to the organic matter deposited on the sea bottom. In fact, Tasch (1967) has suggested that acritarchs were the leading primary producers of the Paleozoic.

Spores

Spores are included in this section even though most were not native to the marine environment, having been blown or washed into the sea from terrestrial sources. In papers concerned with the study of acid-insoluble, organic-walled microfossils or palynomorphs, spores are generally treated with the acritarchs and tasmanitids. In an environment like that repre-sented by the black-shale sequence, where trees, cones, and other ter-restrial plant materials are preserved, it is certainly not surprising to find spores in the same deposits. Spores, like other terrestrial plant material preserved in the black shale are more indicative of terrestrial conditions than of the marine environment in which they were deposited and preserved (Heusser, 1978). Nonetheless, the relative abundance of spores and other terrestrial plant material may be used as an indicator of relative proximity to shoreline.

Chitinozoans

Chitinozoans are small, hollow, vase-shaped microfossils with organic walls and radial symmetry about a central axis. Their affinities are very

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poorly understood. Reaugh and McLaughlin (1975) reported chitinozoans from the Chattanooga Shale of Tennessee, where they occurred in two distinct associations. In one association they occurred with a diverse biota of acritarchs and scolecodonts, whereas the other assemblage was characterized by abundant terrestrial spores with greatly reduced numbers of acritarchs and scolecodonts. Chitinozoans were apparently marine, but whether they lived high in the water column or on the bottom is uncertain (Jansonius and Jenkins, 1978). They are discussed here as plankton because the nature of the black-shale deposits favors a planktic mode over a benthic one. A relationship between chitinozoans and graptolites has been suggested (Jenkins, 1970), but only one occurrence of graptolites from the black-shale sequence has been reported (Butts, 1922). Nevertheless, this association can not be completely discounted.

Radiolarians

Radiolarians are sarcodine protists which secrete skeletons of amorphous hydrated silica (opal A) (Schopf, 1980); other minerals may have been used in the geologic past. The skeletons are exceedingly intricate and may be radially symmetrical or helmet-shaped (Kling, 1978). Radiolaria possess psuedopodia and divide the contents of the cell into outer and inner zones separated by a membrane, a characteristic that distinguishes them from other protists (Kling, 1978).

Spumellarian radiolarians have been reported from calcareous nodules near the base of the Ohio Shale by Foreman (1959, 1963). Additionally, radiolarians were reported by Conant and Swanson (1961) from phosphate nodules near the top of the Chattanooga Shale. Henbest (1936) reported radiolarians from the Arkansas Novaculite (Upper Devonian) which intertongues with black shales, and also mentioned radiolarians from phosphate nodules in the Tennessee black shale. Pyritized radiolarians have also been found in the black shale (Upper Devonian) of Ontario and Michigan (Mason, 1962). Calcareous, radiolarian-like forms have been reported from silt laminae in the New Albany Shale of Illinois and north-central Kentucky (Harvey and others, 1977; Griffith, 1977). Although these were designated as calcispheres, their distinctive structure suggests that they are radiolarian skeletons replaced by calcite.

The ecology, geographic distribution, and bathymetric range of modern radiolarians are not well understood. In general, radiolarians are marine, planktic protists that feed on various forms of phytoplankton and zooplankton up to the size of copepods. Certainly, a varied assemblage of food material would have been available for radiolarians in upper parts of the black-shale sea. The general absence of radiolarians outside of nodules and concretions is probably related to destruction by compaction. The intricate opalline tests are delicate and easily destroyed by compaction, recrystallization, or solution. It is likely that radiolarians were present in the plankton during most of black-shale deposition, but simply were not preserved (Conant and Swanson, 1961). They are preferentially preserved in chert and various nodules because of pre-compaction lithification.

The presence of the radiolarians further supports the existence of normal-marine conditions in the upper part of the water column in the

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black-shale sea. More importantly, however, radiolarian skeletons and remobilized silica derived from them largely make up the Arkansas and Caballos novaculites, which intertongue with the black shales in Texas, Oklahoma, and Arkansas. The abundant radiolarians apparently reflect the presence of oceanic upwelling near a continental margin. The upwelling of cold, nutrient-rich oceanic water near continental margins results in large plankton blooms, which usually included abundant radiolarians (Schopf, 1980; Koopman, Sarnthein, and Schrader, 1978; Diester-Haass, 1978). Silica from these extremely abundant skeletons apparently saturated the interstitial waters with dissolved silica, and allowed the formation of radiolarian chert. Normally, opalline tests will undergo solution rather than preservation in bottom sediments. However, in areas of abnormally high productivity where interstitial waters become saturated with dissolved silica, opalline tests will be preserved due to recrystallization.

THE NEKTOPLANKTON

The nektoplankton are relatively small organisms that employ both swimming and passive floating mechanisms of locomotion. Included in this ecologic group are fossil organisms having Recent nektoplanktic analogues and a few forms like conodonts which were probably derived from a nektoplanktic organism.

Ostracods

Ostracods are relatively small bivalved crustaceans (Arthropoda) that are known from the fossil record beginning with the early Cambrian. The carapace, which is usually calcified, may possess various elevations (lobes) and depressions (sulci), as well as various forms of sculptural ornamentation such as ridges, tubercles, spines, or other characteristics (Pokorny, 1978; see Plate I, figures C, D, and E).

These small crustaceans have been known for some time from Middle Devonian rocks, but only recently have they been reported from Upper Devonian rocks of the eastern United States. Stewart and Hendrix (1945b) reported ostracods from the Olentangy Shale of Ohio, and Stewart (1944) reported them from the underlying Delaware Formation. More recently Warshauer (1978) and Duffield and Warshauer (1979) have reported ostracods in a core from the black-shale sequence of West Virginia. A genus found in all the above studies is Richterina, an entomozoid (fingerprint ostracod). Recently, the same genus was found in the Three Lick Bed of the Ohio Shale in eastern Kentucky (Barron and Ettensohn, 1980) and is shown in Plate I, figure E.

The entomozoids are interpreted to have been marine plankton. They occur over a wide geographic range and make good Upper Devonian guide fossils (Porkorny, 1978). Duffield and Warshauer (1979) reported that the assemblage of ostracods in the black-shale core of their study showed similarities with European species of Late Devonian age. These ostracods are typically pyritized and are found in the greenish-gray shale intervals of the black-shale sequence. The absence of planktic

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or nektoplanktic ostracods in the black shales themselves is probably the result of preservational bias, and does not indicate absence from the upper part of the water column in the Late Devonian seas where black muds were deposited.

Because the entomozoids were planktic, their carapaces contained less calcite and were thinner than those of benthic ostracods. Therefore, the carapaces of planktic ostracods probably dissolved more easily than those of the more heavily calcified benthic forms. Preservation of these planktic shells in the green shales, even by pyritization, indicates that the depositional environment of the greenish-gray muds was different than that of the black muds. The pH may have been slightly higher in the greenish-gray mud and may have allowed the pyritization to preserve the ostracods prior to solution. In the black sediments, the pH was no doubt lower, and solution of the slightly calcified carapaces probably occurred much more quickly. The presence of ostracods in the upper part of the water column adds additional support to the idea already mentioned that this part of the black-shale sea was oxygenated.

Conodonts

Conodonts are microscopic, toothlike fossils composed of calcium-fluorapatite. Apparently some of the conodont-bearing animals bore more than one type of toothlike element, but neither the functions of the elements nor the nature of the animal is definitely known. Examples of common Upper Devonian conodonts are shown in Plate VII, figures A-H. Because of their nektoplanktic nature and rapid evolution during the Late Devonian, conodonts make excellent Late Devonian index fossils. Although very little work has been done with the Late Devonian conodonts from Kentucky, extensive studies of Late Devonian, black-shale conodonts have been made in Tennessee (Hass, 1956), Ohio (Bond, 1948; Cooper, 1931; Gable, 1973; Hass, 1947a), Indiana (Huddle, 1934; Rexroad, 1969; Rexroad and Scott, 1964), and West Virginia (Duffield, 1978; Duffield and Warshauer, 1979). These workers have found conodonts throughout most of the black-shale sequence. Preliminary work in eastern Kentucky indicates a similar distribution except in some of the basal green shales in the black-shale sequence and in the Bedford Shale, where they become scarce. The conodonts are especially abundant in the well indurated, phosphatic bone beds and lag zones which occur within the black shales. In these lag zones up to 15,000 conodont elements per kilogram of sample have been recovered (Chaplin, personal communication), along with fish remains, Tasmanites, and pyritized or phosphatized gastropods.

The biostratigraphic aspects of conodonts long overshadowed their potential as indicators of biofacies. Early work by Merrill (1965) in the Pennsylvanian of North America developed the idea of facies assemblages of conodonts. Subsequent work in the Devonian of Europe, North America, and Australia has led to a biofacies model for conodont assemblages. Druce (1970) and Seddon (1970) both presented models which were developed from work done in carbonates within the Canning Basin of Australia. In these models, Palmatolepis, Ancyrodella, Ancyrognathus, Playfordia, and Polylophodonta were found only in "deep-water" sedimentary units. Icriodus, Polygnathus, and simple cones came from "shallow-water" facies.

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Druce (1970) suggested that distance from the shore determined the habitats, whereas Seddon (1970) suggested that vertical stratification, which implied some relationship with distance from shore, was the important factor. In Kinderhookian sediments from the same area, Siphonodella, Psuedopolygnathus, and Gnathodus (complex forms) formed the "deep-water" assemblage. Although members of the "shallow-water" assemblage were found in the "deep-water" Palmatolepis-Ancyrodella assemblage, the "deep-water" forms were rare in the "shallow-water" Icriodus-Polygnathus assemblage.

The model further developed by Seddon and Sweet (1971) presented a vertical stratification of conodonts in which the Icriodus assemblage occupied the uppermost part of the water column and where the Palmatolepis assemblage occupied the deeper part. This placed the morphologically simple forms in shallow water above the more complex, deeper-water forms and explained the occurrence of Icriodus in a Palmatolepis assemblage and the absence of Palmatolepis in the Icriodus assemblage.

In Druce's (1973) model, a combination of distance from shore and depth controlled the occurrence of conodonts in three biofacies. Biofacies I represented a very shallow-water facies containing primarily simple cones. Biofacies II represented a facies of intermediate depth (possibly to 50 meters) and contained Icriodus, Pelekysgnathus, and Polygnathus. Biofacies III represented a deeper-water facies (possibly below 50 meters) and contained Palmatolepis, Ancyrodella, Polylophodonta, and Ancyrognathus (see figure 1).

These same biofacies relationships were subsequently observed in North America. In Upper Devonian rocks from western Canada (Chatterton, 1976) from Missouri (Schumacker, 1976), and from the western United States (Sandberg, 1976), Icriodus was shown to occur in shallow-water facies, whereas Palmatolepis, wide-platform polygnathids, or both occurred in deep-water facies. These Late Devonian conodont biofacies have been further substantiated and refined in the work of Sandberg (1980) and Weddige and Ziegler (1976, 1979).

In the black-shale sequence of Kentucky, Griffith (1977) found Polygnathus and some Icriodus elements at the base of the sequence, whereas Palmatolepis and Ancyrodella with a few Polygnathus predominated higher in the section. Griffith (1977) used these occurrences to indicate that the black-shale sea had progressively deepened with time. In the Chattanooga Shale of Tennessee, however, the vertical succession of conodonts did not show the same pattern. Although Polygnathus was found only in the basal sandstone (lag horizon?) of the Chattanooga Shale. Icriodus occurred from the basal sandstone up into upper parts (Gassaway Member) of the Chattanooga (Hass, 1956). Palmatolepis, on the other hand, essentially occurred throughout the entire sequence (Hass, 1956).

Conodonts recovered in reconnaissance samples from a black-shale outcrop on Interstate Highway 64 in Rowan County, eastern Kentucky, supported the findings of Hass in the Chattanooga Shale. Conodonts in the basal sandstone at the bottom of the lower Huron Shale (radioactive unit 5 of Swager, 1978) included Palmatolepis, Polygnathus, a few Icriodus,

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BIOFACIES I

BIOFACIES II

BIOFACIES III

Sea Level

50 Meters
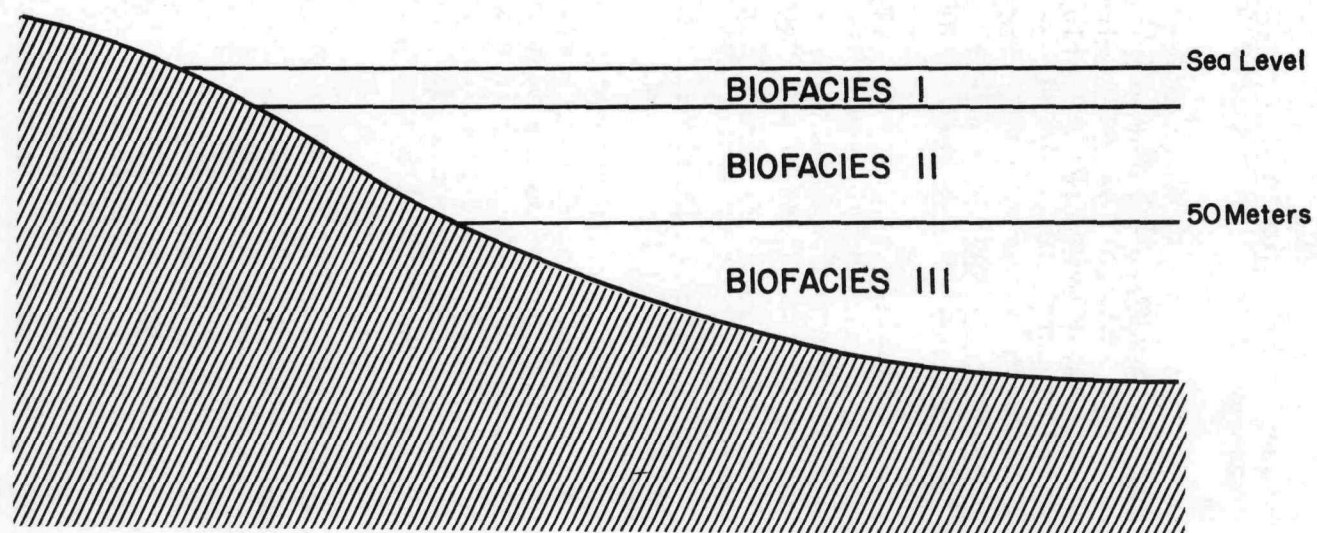
Redrawn from Druce, 1973

Figure 1. Depth stratification of conodont biofacies.

and a few simple cones; this sandstone is probably equivalent to bone bed number 17 of Conkin and Conkin (1979). The bone bed or lag deposit near the top of radioactive unit 5 (Swager, 1978) also contained Palmatolepis, Polygnathus, and Ancyrognathus. Samples from the three greenish-gray shales of the Three Lick Bed contained both Palmatolepis and Spatho-gnathodus. The lag zone at the base of the Sunbury Shale contained numerous Gnathodus (complex forms), Psuedopolygnathus, Polygnathus, and Siphonodella.

The presence of Palmatolepis and the other "deep-water" genera in the black shales of eastern Kentucky is suggestive of deep-water deposition. However, a typical progression from an Icriodus-dominant fauna at the base of the section to a Palmatolepis-dominated assemblage at the top does not appear to be present. All biofacies seem to be concentrated in the lag zones, and the intervening shales seem to be dominated by a Palmatolepis assemblage. This kind of concentration of facies in a basal lag might be expected if the initial transgression of the black-shale sea was relatively rapid, as other evidence suggests in eastern Kentucky. Nonetheless, the conodont biofacies and resulting bathymetric inferences for the black-shale sea of eastern Kentucky must be viewed as tentative until a much more detailed study is undertaken. If Palmatolepis was a deep-water form, the black-shale sea would have been considerably deeper than the 50 meter depth suggested, because the 50 meter depth represents only the top of the Palmatolepis habitat.

THE EPIPLANKTON

Benthic organisms that attached themselves, either permanently or temporarily, to floating objects such as logs or other plant debris constitute epiplankton. Some early researchers used the term psuedoplanktonic in referring to this habitat. Benthic organisms that attached themselves to floating superstrates may have been reacting to a number of possible environmental factors. Floating logs of the size and durability of Callixylon were comparatively new to marine waters in the Late Devonian and presented new, albeit mobile, superstrates for organisms normally found on the sea bottoms. Logs or stems floating in the sea naturally occurred in the upper oxygenated or aerobic zone of the water column, and they may have formed the only habitable surfaces at times when the sea bottom was anaerobic and black euxinic muds were accumulating. The floating plant material probably was derived from a near-shore region of the sea where normal-marine conditions prevailed in all parts of the water column, allowing invertebrate larvae to attach to the floating superstrate. The plant debris continued to float and moved from the near-shore area into deeper parts of the sea where the substrate and lower parts of the water column were anoxic. Eventually the floating material became waterlogged and sank, killing the attached creatures in the toxic bottom waters. For small pieces of flotage, the growth of the attached organisms and the weight that they contributed may have caused relatively early sinking of the material (Thayer, 1974).

Such occurrences in the black-shale sequence include crinoids attached to Callixylon logs (Wickwire, 1936; Wells, 1939, 1941, 1947;

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McIntosh, 1978), pelecypods attached to small pieces of plant matter (Nye and others, 1975) and the association of brachiopods like Lingula, Orbiculoidea, and Leiorhynchus, with plant material indicating a probable epiplanktic life mode (Thayer, 1974).

Brachiopods and Pelecypods

Inarticulate, phosphatic brachiopods such as Lingula, Lingulipora, Orbiculoidea, and Schizobolus (see Plate II) occur in black, laminated shales that otherwise show no evidence of benthic life. These brachiopods generally are thought to have been epiplanktic in the black-shale sea (Rudwick, 1965, 1970; House, 1975b; Thayer, 1974; Newton, 1979). Prosser (1912a) reported receiving a letter from the amateur paleontologist, Rev. Herzer, in which Herzer described finding a calcareous nodule containing a Callixylon log, ". . . with many attached Lingula." Although modern epiplanktic lingulids have not been reported, if the fossil lingulids were similar to modern Lingula and Glottidia, they possessed muscular pedicles coated with a sticky substance that probably was capable of attaching the Lingula to a log or to other plant debris.

If the lingulid died before its superstrate sank or tried to escape during the sinking, the isolated shells might occur far removed from the former superstrate. In this way, the presence of brachiopods on plant debris (Prosser, 1912a), in close association with plant debris (figure 2), and completely dissociated with plant debris or any other flotage (figure 3), can be explained. Very small, thin-shelled lingulids may also represent larval forms that persisted as larval plankton for longer than normal because habitable substrates (superstrates) were not present (Ziegler and others, 1968). After reaching a certain size, the weight prevented further planktic existance, and the organisms sank into the anaerobic bottom waters.

The presence of Lingula and related inarticulate brachiopods has been and still is used to infer a near-shore, shallow-water environment of deposition for the black-shale sequence (Cooper, 1936-1937, 1957; Lewis and Schwietering, 1971). Additionally, Lingula, is commonly regarded as having been a resident of a shallow-water, near-shore environment throughout its entire geologic record (Raup and Stanley, 1971). Regarding the nature of lingulid brachiopods in the fossil record, Rudwick (1965) said, ". . . the occurrence of fossil lingulids without other brachiopods may, if there are no indications of toxic conditions, be taken to reflect littoral (intertidal) conditions of deposition;" he suggested that lingulids found in black shales were attached to plant flotage or to other organisms (Rudwick, 1965, 1970). In any case, Lingula found in black, laminated shales probably were not living on the sea bottom, and as probable epiplanktic organisms, can not be used as indicators of near-shore environments. This conclusion is further supported by the taphonomy of many lingulid specimens found in the shale. Many of the specimens occur only as single valves, of similar size and in preferential orientation, suggesting postmortem transport and orientation of dissociated valves. As epiplanktic organisms, however, they may have initially lived in shallow and/or near-shore waters, but this says nothing about the depth of the sea into which they finally were transported.
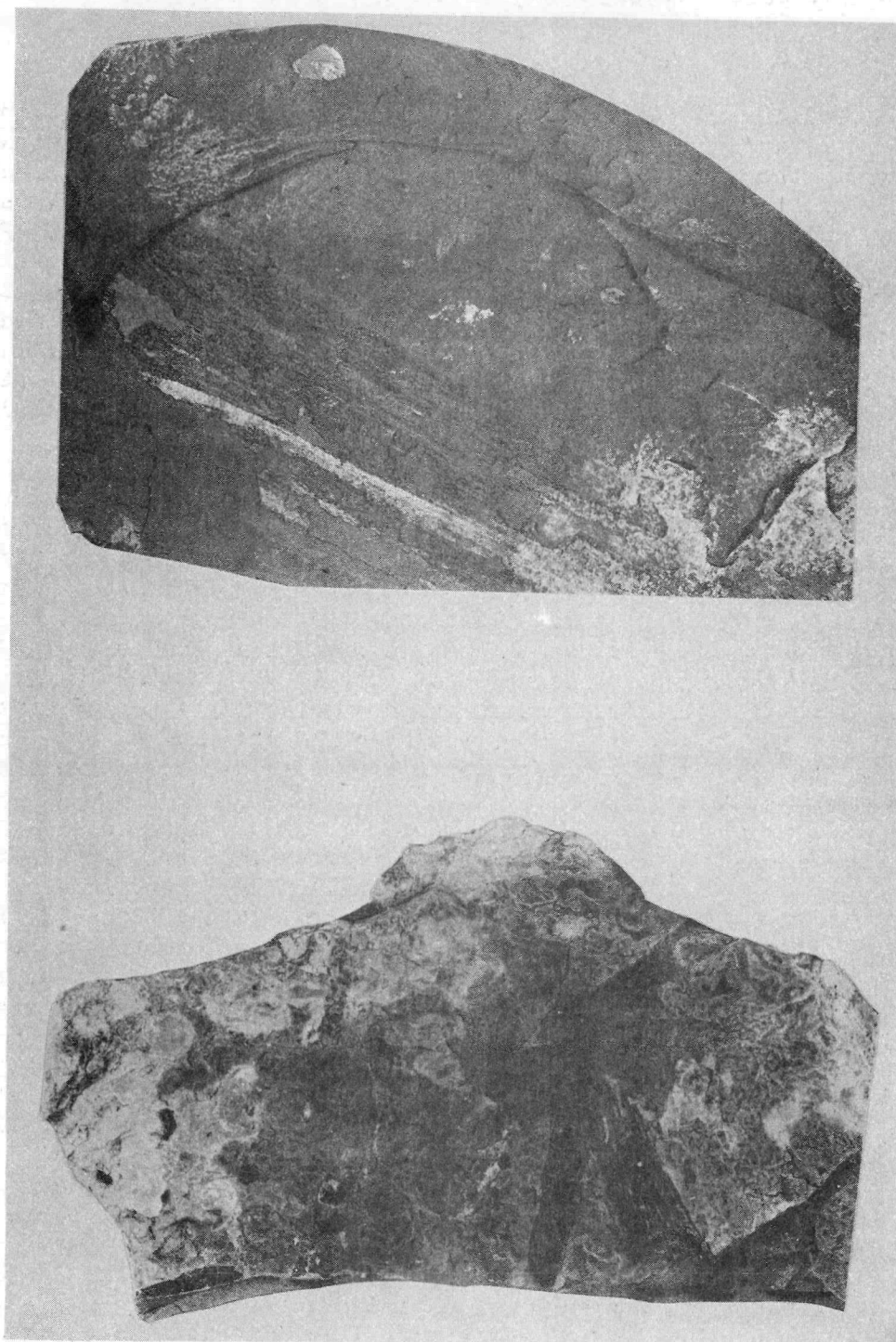
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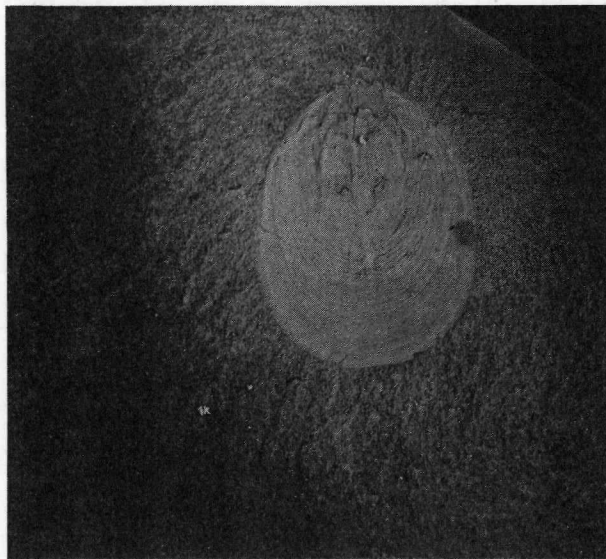Figure 2. Brachiopods in close association with fossil wood.

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Figure 3. Brachiopods not associated with fossil wood.

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Other probable epiplanktic organisms include the articulate brachiopod Leiorhynchus and the inarticulate brachiopods Schizobolus, Orbiculoidea, and Barroisella (Rudwick, 1965; Thayer, 1974), as well as the pelecypods Buchiola (McAlester, 1970) and Lunulacardium (Nye and others, 1975). Forms such as Pterochaenia, Prochasma, and Buchiola which have thin, chitinous shells were probably branchiopods (arthropods) (Thayer, 1974).

Graptolites

Graptolites were colonial, chitinoid organisms preserved generally as flattened carbonaceous films. The colony consisted of branches (stipes) bifurcating from a supporting thread (nema) which hung beneath some type of float. Each stipe bore overlapping cups (thecae) which contained the polypoid animals. Graptolites are known from the Cambrian through the Mississippian, and form excellent guide fossils for the Ordovician and Silurian. Both planktic and benthic forms existed.

Graptolites have been reported only once from the black-shale sequence of eastern Kentucky. Butts (1922) found one Dictyonema specimen from the lower 3 meters of the black shale at Irvine, Estill County, Kentucky. Planktic members of the Graptolithina became extinct in the Silurian, which suggests that Dictyonema was epiplanktic. Moore and others (1952) suggested that the nema was too flimsy to support the rhabdosome (colony) on the bottom, and that it probably supported a colony from above in an epiplanktic life mode. If the previously discussed relationship between the chitinozoans and the graptolites is accurate, then the occurrence of epiplanktic graptolites is possible. Ruedemann and Lochman (1942) reported graptolites from the Lower Mississippian Englewood Formation in the Black Hills of South Dakota, a formation coeval with the Sunbury Shale to the east.

Crinoids

Crinoids are complexly organized and highly varied echinoderms. Although most forms found today are not attached to the bottom, most fossil forms were. They are exclusively marine animals, composed of articulated calcareous hard parts that can number up to several thousand.

Although several reports of epiplanktic crinoids were mentioned earlier, crinoids in the black-shale sequence are considerably less abundant than are inarticulate brachiopods; this may be related to the poor preservation potential of the calcareous crinoidal hard parts which are easily dissolved. Hoover (1960) described crinoids, probably benthic forms, from the greenish-gray Olentangy Shale of Ohio. Although the Olentangy is considered to be part of the black-shale sequence, the greenish-gray color of the shales suggests that they were deposited in oxygenated conditions, which explains the presence of crinoids and other benthic organisms in the Olentangy.

Epiplanktic crinoids have been described from the black Posidonia Shales (Lias) by Seilacher and others (1968), from the Lyme Regis Lias by Jackson (1966) and from the Upper Devonian black shales of Ohio, Indiana, and New York (Wells, 1939, 1941, 1947; McIntosh, 1978; Wickwire, 1936).

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Figure 4 is a photograph of crinoid columnals on a silicified Callixylon
log from the Upper Devonian black shales of Indiana. According to McIntosh
(1978) Melocrinites clarkei Williams was found attached to logs in the
Angola Shale of New York. Wells (1947) reported the same genus on Callixylon
logs in the Huron Shale of Ohio, and this same genus is known also from the
the Olentangy Shale of Ohio (Stewart and Hendrix, 1944).

THE NEKTON

Swimming organisms such as cephalopods, fish, and pteropods are called
nekton, and fossils of these organisms occur throughout the black-shale se-
quence. Usually, however, they are not as abundant as the planktic forms.
Fish fossils are ubiquitous in the black shales and occur most often as
individual scales and teeth (see Plate XI, figures A, B, and C.) Some fish
fossils like those from the Cleveland Shale are preserved in such detail
that muscle fiber and other detailed morphologic features can be observed.
Cephalopods, on the other hand, are not abundant, but they are reported in
the literature and are known from the outcrop and from cores in eastern
Kentucky. The shells are typically preserved by pyritization.

Fishes

By the Devonian Period, and more specifically by the Late Devonian,
the fishes underwent a period of explosive evolution and radiation.
Agnathid (jawless fishes), acanthodian (first jawed fishes), arthrodiran
(armored fishes), chondrichthyan (shark-like fishes), and osteichthyan
(the bony fishes) were all present in various Late Devonian marine and
fresh-water environments (Colbert, 1969; Moy-Thomas and Miles, 1971;
Olson, 1971).

Devonian fossil fishes from North America can be divided into two
basic assemblages: The Scaumenac Bay fauna of Quebec and the Cleveland
Shale fauna of Ohio. The Scaumenic Bay fauna is characterized by placoderms
such as Bothriolepis, lung fishes (Dipnoi), and crossopterygians (tassle-finned
fishes). The Cleveland Shale fauna, on the other hand, is characterized
by giant arthrodires such as Dunkleosteus (Dinichthys) and Cladoselache
(Colbert, 1969). The bony fishes had largely inhabited fresh-water environ-
ments since the Early Devonian (Romer, 1968). The placoderms, however, were
relative newcomers to marine environments since the Late Devonian (Colbert,
1969). The mixture of fresh-water and relatively new marine forms, suggest
that the Scaumenac Bay fauna was fresh-water, estuarine, or brackish in
nature. The sharks and arthrodires that characterize the Cleveland Shale
fauna, are thought to be marine in nature (Colbert, 1969).

The black-shale sequence of Kentucky, Ohio, Indiana, and Tennessee
has long been known for its fish fossils. Though the largest and perhaps
most diverse assemblage of fishes occurs in the Cleveland Shale, remains
are known from the entire sequence, from the basal lag zones to the Sunbury
Shale. Early morphological work with these fossils was carried out by New-
berry (1857 and later) and this work was apparently spurred on by an
itenerant preacher and part-time paleontologist, the Reverend Herzer, who
painstakingly extricated the fish bones from calcareous nodules in the lower
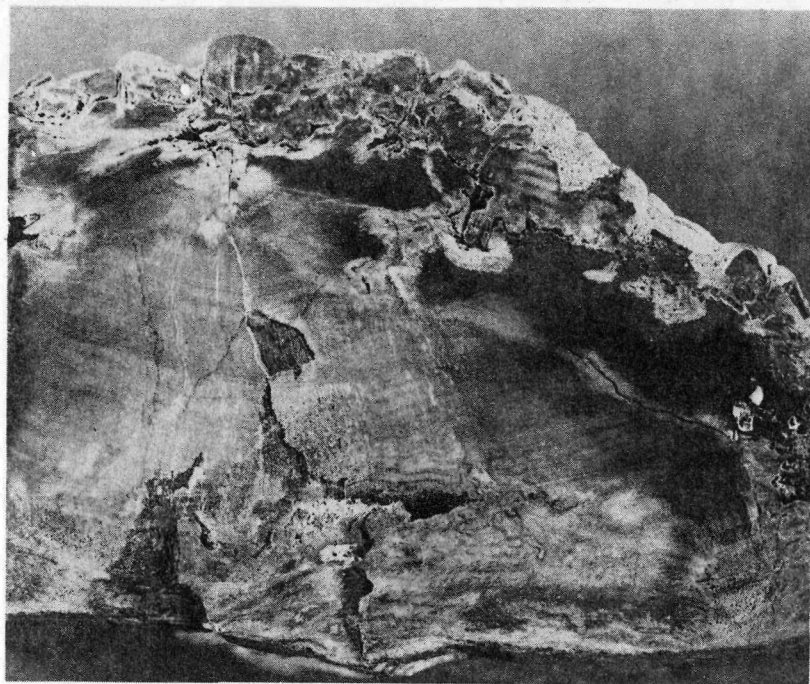part of the black shale.

Figure 4. Callixylon log with crinoids attached. (plan view and cross section).

Foremost among the fishes of the black-shale sea of which we now have record were the sharks and the placoderms. The placoderms are known almost totally from the Devonian with no known Silurian ancestors, and only a few occurrences in the lowermost Mississippian. The most abundant of these armored fishes were the arthrodires, which were characterized by body and head armor, pectoral fins, and a pectoral spine. The body armor and pectoral spine became progressively reduced with time, whereas the pectoral fins became more developed (Romer, 1968). In the Late Devonian, Dunkleosteus (a dinichthyid) was foremost among the arthrodires, and represented some sophistication over its bottom-scavenging predecessors of the Early Devonian. The dorsal-ventral flattening, which characterized most placoderms that dwelt on the sea bottom and some other bottom-dwelling fishes (Gaudant, 1979), was reduced in the genus Dunkleosteus. Using the morphofunctional analysis of Gaudant (1979) and extending it to an extinct group, at some risk, some of the life habits of Dunkleosteus can be inferred. Moy-Thomas and Miles (1971) suggested that Dunkleosteus possessed a powerful bite, with the ability to exert a great deal of pressure upon anterior picks. Based on Gaudant's (1979) analysis, placement of the mouth (buccal opening) was related to the position of the food with respect to the fish. Therefore, the terminal opening of the mouth together with an inferred large bite and the reduction of dorsal-ventral flattening suggests a predatory life in the water column. Colbert (1969) noted that Dunkleosteus had the ability to raise its head as it dropped its jaw due to the presence of a hinge between the head shield and the thoracic shield. This would have allowed large bites. Olson (1971) also pointed out the development of cervical musculature and its role in the action of the head which was important in feeding. The evidence seems to strongly suggest that Dunkleosteus preyed on rather large fish found in the water column. The pectoral fins became more developed in the arthrodires like Dunkleosteus and probably were used as glide planes and controls (Moy-Thomas and Miles, 1971). A life mode within the water column is further supported by reductions of the body armor, which should have made swimming more efficient. Characteristics of the placoderm vertebral column suggest that the swimming was accomplished by eel-like motions (Moy-Thomas and Miles, 1971). The heteroceral tail of most placoderms (Moy-Thomas and Miles, 1971) is suggestive of rapidly swimming pelagic forms, when also supported by other morphological characteristics (Gaudant, 1979). The anaerobic nature of the bottom sediments further suggest that Dunkleosteus lived within the water column.

Two characteristics of placoderms contributed to their eventual replacement by chondrichthyans or sharks in the Mississippian. The modified dermal bone used for cutting and grinding in placoderms instead of true teeth probably became a strong handicap in the later part of an adult placoderm life. When this dermal bone was worn away, it was not replaced (Moy-Thomas and Miles, 1971). Another limiting factor in placoderm development, which was overcome by the chondrichthyans, was the expenditure of energy used to build and maintain the heavily calcified placoderm skeleton and armor. The cartilaginous skeleton of the chondrichthyans required less metabolic effort and additionally was more conducive to nektonic life. The efficiency and versatility conferred by this skeleton allowed the sharks to outcompete their probable ancestors, the placoderms, in the Late Devonian black-shale sea.

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The sharks have often been viewed as primitive fishes primarily because of the cartilaginous skeleton, and the belief that it preceeded ossification. The fossil record contains no evidence of sharks or other elasmobranchs prior to the few scattered teeth in the Middle Devonian. The Osteichthyes (boney fishes) are very well represented in the Early Devonian rocks, so that the cartilaginous skeleton probably appeared after ossified skeletons. One theory suggested that the chondrichthyans evolved from the placoderms. Stensio (according to Romer, 1968) grouped the placoderms with the chondrichthyans into one supergroup called Elasmobranchiomorphii, a classification which was used by Moy-Thomas and Miles (1971).

The sharks are considered to have been marine except for the pleurocanths which apparently invaded fresh-water environments. Pleurocanth remains are poorly known from rocks older than Pennsylvanian (Romer, 1968). A common shark in the black-shale sea was Cladoselache, many examples of which have been found well-preserved in the Cleveland Shale of Ohio. The three chondrichthyan genera Cladoselache, Cladodus, and Ctenacanthus were all very similar and probably very closely related (Romer, 1968). From the excellently preserved cladoselachians in the Cleveland Shale, it is evident that they possessed a torpedo-like shape, a broad heteroceral tail, and extremely well-developed pectoral fins useful in balance and glide-control (Colbert, 1969). Functional morphology based on the interpretations of Gaudant (1979) allows inferences of a rapidly swimming, pelagic, predatory life style for the genus Cladoselache. Large eyes (Colbert, 1969; Moy-Thomas, and Miles, 1971) and an atypically foreshortened snout seem to indicate that sight was more important in prey detection than is the olfactory sense in other sharks, including the Recent forms (Moy-Thomas and Miles, 1971).

Other characteristics of Cladoselache seem to indicate that it could have been the prototype ancestral shark. It possessed a primitive jaw articulation called amphistylic suspension (Colbert, 1969) which did not allow the sawing action of the more modern hyostylic suspension (Moy-Thomas and Miles, 1971). Cladoselache also lacked claspers used in copulation. Claspers are found in sharks that succeeded the cladoselachians in the Mississippian (Romer, 1968). In well-preserved specimens from the Cleveland Shale, the gut contents of Cladoselache included "cladodont" shark teeth and scales of bony fishes (Moy-Tomas and Miles, 1971).

Members of the family Osteichthyes are also known from the black shale, and they include the crossopterygians and actinopterygians. The crossopterygians or tassle-finned fishes possessed paired fins with muscular tissue extending into fins from the body.

It is quite reasonable to expect fresh- to brackish-water bony fishes along with the marine fishes preserved in the black-shale. During floods and periods of large fluvial influx, the resultant large lens of brackish water in the uppermost parts of the water column could have allowed the riverine fish to move into the former marine environments. However, it would be unlikely to find marine fish fossils in continental deposits.

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One question that often arises is why more complete fish fossils are not found in the black shale, given the apparently good conditions for the preservation of organic matter. Schafer (1972) gives an excellent account of the conditions attending the post-mortem phase of the history of a fish. A fundamental difference exists between vertebrates and invertebrates regarding preservation and fossilization. Invertebrates which possess hard parts often are preserved intact because the skeleton is usually in one or a few pieces. Vertebrate hard parts or skeletons generally consist of many smaller hard parts bound together by ligaments, tendons, and other uncalcified tissues which are quite susceptible to decay. Currents which could disarticulate a clam could also disarticulate a fish skeleton. The difference lies in that one valve of a clam is much more readily identified than is one bone of a fish. A crinoid is an example of an invertebrate that like many vertebrates is comparatively rare in articulated form, and is more often found as individual columnals and plates.

Vertebrates, particularly the Osteichthyes which apparently possessed lungs in the Devonian, were likely to float for a length of time after death due to the accumulation of gases. A dead fish may float, sink, and refloat several times. Given such conditions, complete skeletons would be rare. Gas production as a byproduct of decay is particularly high where the water temperature is high, as it would have been in the equatorial, Late Devonian sea. Even fishes such as sharks which did not possess lungs could have floated because of gas accumulation in the abdominal cavity. With a cartilaginous skeleton, a shark would be particularly difficult to preserve intact. In the black-shale sea, the fish may have never touched bottom in a whole state, if the production of gas were fast enough.

Schafer (1972) lists two ways in which complete vertebrate skeletons may be preserved in marine sediments: the skeleton must be buried quickly by rapid sedimentation or else buried in a place unaffected by transportation forces. As suggested in the paleoenvironmental model of Ettensohn and Barron (in preparation), the black shale accumulated under starved-basin conditions so that a skeleton could not have been buried rapidly. The model envisioned is not one of necessarily stagnant bottom waters either, so that preservation of intact fish fossils would be comparatively rare. Schafer (1972) does point out that fish which sink into anaerobic environments do not produce abundant gas, because the rate of decay would have been much slower than in an oxygenated environment. This would have been especially true if the fish sank directly into the anoxic waters immediately after death. In the equatorial region where the black-shale sea was situated (see Ettensohn and Barron, in preparation), the warm temperature may have allowed gas formation to float the fish before it could sink into anoxic waters.

With the difficulty of preserving a fish skeleton intact, the question remaining is why are the fish preserved so well in the Cleveland Shale of Ohio? Again, Schafer (1972) points out that one of the primary causes of catastrophic fish kills is plankton blooms, or the so-called red tides. In these situations several environmental factors act to kill the fish. Schafer (1972) cites Numann (1957) regarding a "red tide" on the west coast of Africa. Those fish killed in the upper ten meters of water were

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killed by toxins from the bloom. Those below the ten-meter depth were either smothered by anoxic waters that resulted from the oxygen demand of the decaying organic matter, or the gills of the fish closed due to irritation from large numbers of microorgaisms, thereby preventing respiration.

Plankton blooms such as these occur in areas of upwelling currents which bring nutrient-rich bottom waters up into the photic zone. The extremely high level of nutrients would allow primary productivity to occur at an explosive rate (Schopf, 1980; Brongersma-Sanders, 1948). In the model of Ettensohn and Barron (in preparation), the deepening black-shale sea would have allowed upwelling to occur during deposition of upper parts of the black-shale sequence. Such an upwelling during Cleveland deposition, and a possible red tide could explain the large numbers of fish remains in the Cleveland Shale. This may also reflect the first time that the water of the black-shale sea became deep enough for upwelling and the resultant plankton blooms to occur.

Cephalopods

Cephalopods are the most advanced of all the invertebrates in that they possess well-developed eyes, prehensile sucker-bearing tentacles, and the ability to swim well. However, the surviving shelled form, Nautilus, is geographically restricted to the southwest Pacific Ocean and may be more stenotypic than its ancestors (Furnish and Glenister, 1964). Although extrapolation from the ecologic characteristics of Nautilus to those of its early ancestors in the Devonian is somewhat risky, it may serve to provide some insight into the ecology of Devonian ammonoids. Modern Nautilus typically occurs at depths of 600 meters or greater, but it apparently moves into shallower water at night. They prey largely on decapod crustaceans, but they also scavenge. The shell contains gas which is used to attain buoyancy and balance, and they use jets of water pulsed through their siphon in order to swim. The buoyancy mechanism, however, only impedes paleoecological interpretation, assuming that the ancestors of Nautilus were similarly disposed. Following death, the buoyant gas-filled chambers allow currents to transport the shell great distances, and thus the shells may be deposited in a facies where cephalopods never naturally occurred in life (Furnish and Glenister, 1964; Miller and Furnish, 1936-1937). Miller (1957) pointed out that, places where various stages of cephalopod ontogenetic development are found preserved together may represent the true habitats of cephalopods.

Reports of cephalopods in the black-shale sequence date from at least 1884 when Linney reported an orthoceratite in a pyritized accumulation near the base of the black shale in Clark County, Kentucky. More recently House (1978) reported a communication from Gorden that a fauna of cephalopods had been discovered near the base of the Cleveland Shale in Ohio by Dr. Hlavin; these fossils were also pyritized. In addition, pyritized cephalopods have been reported from a core in the black shale of Martin County, Kentucky, from greenish-gray shales in the black-shale sequence (Miller, 1978), and from a core in Carrol County, Ohio (Byrer and Rhoades, 1976; see Plate IV). Also, pyritized, micromorph cephalopods have been found in the greenish-gray shales of the Three Lick Bed of the

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Ohio Shale in eastern Kentucky (Barron and Ettensohn, 1980; see Plate V). In general, complete cephalopod shells are rather rare fossils in the black-shale sequence, but in some cores "chitinous" cephalopod aptychi are far more abundant.

The scarcity of cephalopod shells may be related to the aragonitic composition of the shell, which would decrease the likelihood of preservation because of the unstable nature of aragonite. The instability of aragonite would have been more pronounced in the more acid, bottom waters which apparently characterized the sea during most of black-shale deposition. Sensitive as the shells would have been to solution, preservation of those that are found was probably related to temporary improvement (higher pH) of the bottom environment as in the green shales of the Three Lick Bed or because of very rapid replacement of the aragonite with pyrite.

It is difficult to make much of a statement about the paleoecology of the cephalopods from the black-shale sequence. Given the possibility and likelihood of post-mortem transport, some uncertainty exists about their true life habitat, but given the other indicators of marine environmental conditions, it seems that they could have lived in the upper part of the water column. Nonetheless, some of the micromorph or dwarf cephalopods found in the black-shale sequence require further explanation. The significance of similar dwarf faunas has been discussed by Kummel (1948). He pointed out previous studies that showed the stunting effect of high concentrations of iron, low levels of oxygen, presence of hydrogen sulfide, and low salinity. The micromorph forms of the Three Lick Bed could be explained in either of these ways, or by still other mechanisms. Larger cephalopods may have been present but either were not preserved or were transported out of the basin after death. The micromorph forms may have also been preserved because of special conditions in a microscopic burial environment, which did not protect the macroscopic forms. If larger forms were present, the micromorph cephalopods could represent stunted adults, short-lived juveniles, or both.

Nektic Gastropods

Pteropods or nektic gastropods apparently were also present in the black-shale sea. Pteropods often display rather bizarre morphologies as well as those considered to be more normal for gastropods. As pelagic forms, these gastropods possess thinner shells, that would have been more subject to solution. They are presently found only in marine environments to depths of about 500 meters (Herman, 1978).

Styliolina and Tentaculites which are locally abundant in the black-shales have often been reported as pteropods, but they are classed in the Treatise on Invertebrate Paleontology as cricoconarids, or small, straight, narrow cones of uncertain affinity.

Micromorph, pyritized gastropods form a substantial fraction of the microfauna of the greenish-gray shales of the Three Lick Bed. It is possible that these gastropods were pelagic swimmers and were preserved in the less harsh bottom conditions during deposition of greenish-gray muds. These same forms, however, might have been dissolved in the harsher

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conditions of black-shale deposition. Pyritized, micromorph gastropods are also found in the lag zone at the base of the black-shale sequence in eastern Kentucky, which tends to support an interpretation of a pelagic mode of life, since the other major constituents of lag deposits, fish remains, conodonts, and Tasmanites, were most likely pelagic forms.

Phyllocarid Crustaceans

These arthropods, a subclass of the malacostracans, possessed a large, loose carapace and leaf-like appendages. The fossils of these forms are found largely in Paleozoic rocks. Fossils such as Echinocaris and Spathiocaris are commonly reported from the black shales (Campbell, 1946; Hoover, 1961). Some of these forms from the black shale have also been suggested to have been the anaptychi of cephalopods (Ruedemann, 1934). If they were indeed crustaceans, they probably led a nektonic life in the upper part of the water column of the black-shale sea and were associated with flotage as are modern arthropods in the Sargasso Sea. They occur in the black-shale sequence as pyritized carapaces. Campbell (1946) actually named a zone after Spathiocaris, but it is seldom recognized today because of difficulty in finding the fossils.

BENTHOS

Benthic organisms with preservable hard parts apparently were extremely rare in the Devonian-Mississippian black-shale sea. The laminated nature of the black shales in the sequence is strong evidence that even animals with only soft parts were unable to live in or on this sea bottom. The Lingula and Orbiculoidea found in the black shales have been cited as evidence of the shallow-water and near-shore nature of the deposits (Cooper, 1936-1937, 1957), however, these brachiopods were probably epiplanktic during black-shale deposition as previously discussed (Rudwick, 1965, 1970). Had the Lingula lived in or on the black-shale sea bottom, the laminae would almost certainly show disruptive evidence of their presence. An exception to this condition possibly existed in the early stages of black-shale deposition, which are represented by basal portions of the black-shale sequence. Relatively abundant Leiorhynchus, Schizobolus, Chonetes, Barroisella, and other fossils found in the basal portions of the black-shale sequence (Hass, 1956; Campbell, 1946; Lineback, 1968; Wells, 1947; Kindle, 1900) suggest slightly less harsh conditions in the initial depositional environment on the craton. The brachiopods are present locally in such numbers as to suggest aerobic or dysaerobic conditions. Nevertheless, despite the oxygenation, organic matter formed a major sedimentary constituent and accumulated in such quantities that it predominated in the sediment. The aerobic-dysaerobic inferface would have had to be at or very near to the sediment-water interface so that the brachiopods could have survived in a marginally oxygenated environment. The presence of shallow-water sedimentary features such as flaser beds and ripple marks, as well as the presence of carbonates in the Duffin-Harg-Ravenna facies, also supports a shallow-water phase at the beginning of black-shale deposition.

Linney (1884) noted the presence of pyritized fossils near the base

of the black-shale sequence in Clark County, Kentucky, although he inter-
preted the pyritized accumulations as fish coprolites. Butts (1915, 1922)
reported Schizobolus and Leiorhynchus in the "lower few feet" of the section
of Jefferson County, Kentucky, and similar fossils in the basal part (lower
3 to 5 meters) of the sequence at Irvine in Estill County, Kentucky. Savage
(1930) found gastropods which he described as similar to Bellerophon and
Straparollus along with Styliolina in the lower part of the black-shale
sequence. Dolomitic lenses about three meters above the base of the sec-
tion in Estill County, Kentucky, contained Ambocoelia, Chonetes, Gypidula,
Hypothyridina (Hypothyris), and Strophalosia. Savage (1930) after listing
the above fossils also cited a communication from E. M. Kindle that reported
an assemblage of fossils from the basal New Albany Shale of Indiana. Camp-
bell (1946) reported a small variety of fossils from the basal part of his
Portwood Formation (Harg-Duffin-Ravenna facies); Schizobolus was the domi-
nant fossil in the overlying Trousdale Formation. Our observations in Ken-
tucky support those of the above workers, but we have also noted the presence
of reworked Middle Devonian forms in the basal lag deposits.

The basal part of the black-shale sequence, which includes a local
dolomitic facies, seems to represent a shallow-water accumulation during
the initial transgressive phase of the black-shale sea. The bottom condi-
tions that characterized the larger part of the black-shale deposition
were, at best, dysaerobic, with oxygen demand quite high because of the
large amount of organic matter present. The dolomitic facies seem to have
had even higher oxygen levels.

Trace Fossils

Above the basal parts of the black-shale sequence discussed above,
the only evidence of benthic life occurs in greenish-gray shales or dolo-
mites interbedded with black shales in the lower Huron Member, the Three
Lick Bed, or Bedford-Berea (Provo, 1977; Provo and others, 1977; Swager,
1978; see Plates VII and IX). The evidence in the lower Huron Member con-
sists almost exclusively of burrows in the green shales, some of which
penetrate the underlying black shales (figure 5). Jordan (1980) listed the
various genera of trace fossils for the lower Huron Member and from the
gray shales overlying the upper Huron Member. Griffith (1977) also found
trace fossils in the Blocher Member and in the Camp Run Member of the New
Albany Shale in north-central Kentucky. The Blocher is probably correla-
tive with the lower Huron. Trace fossils in the Blocher appear to have
a more vertical orientation whereas those in the Camp Run have a more
horizontal orientation, concentrated along the black shale-green shale
interfaces (Griffith, 1977). The trace-fossil evidence of Griffith (1977)
and the conclusions of Jordan (1980) suggest that the cratonic black-shale
sea became progressively deeper with time and transgression.

As Rhoads and Morse (1971), Griffith (1977), and Byers (1977, 1979)
have pointed out, the presence of bioturbation in an otherwise laminated
shale sequence strongly suggests an influx of oxygen and a change from
anaerobic conditions to at least dysaerobic conditions. The absence of
a calcified fauna and a presence of bioturbation are characteristic of the
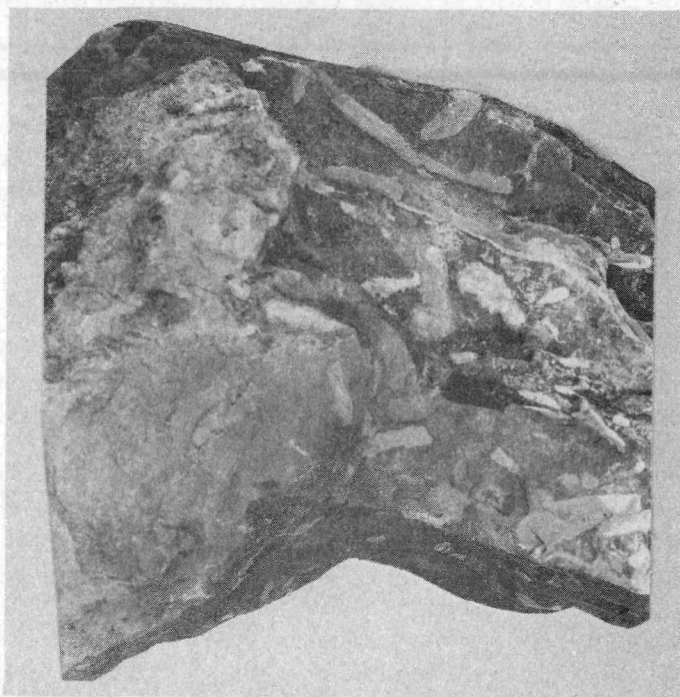dysaerobic zone of Rhoads and Morse (1971).

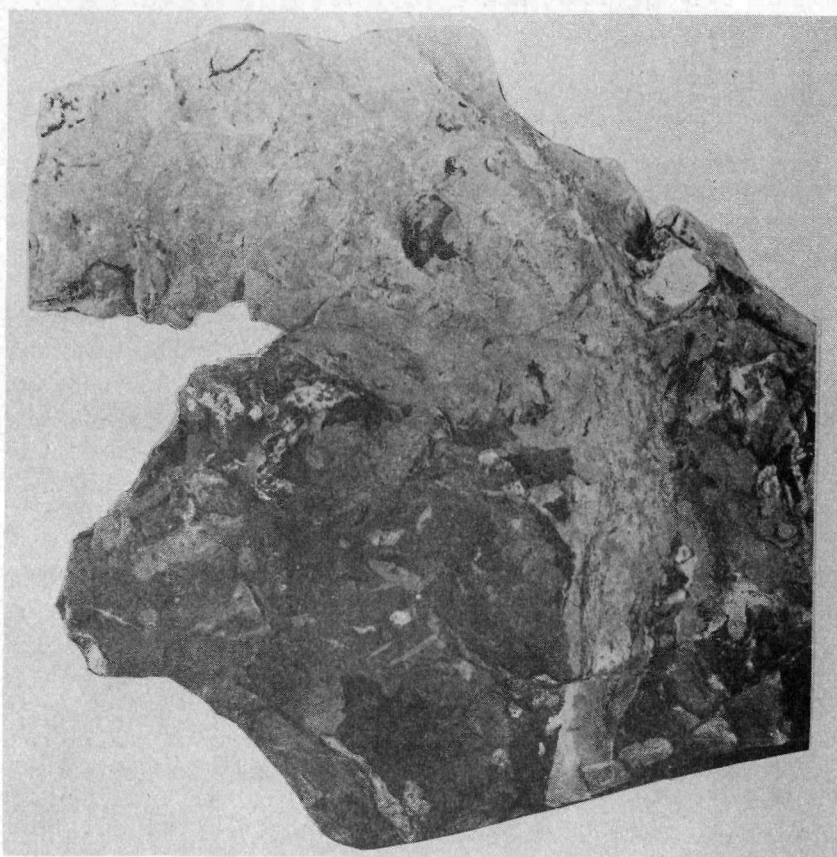Figure 5. Trace fossils filled with greenish-gray shale in a black-shale matrix.

Figure 6. Broad Lingula trail with pedical impression and Lingula shell outlined in green shale.

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In southern Indiana, a change to more oxygenated conditions in the lower Blackiston Member of the black-shale sequence is supported by "worm trails", clams, and preserved goniatite cephalopods reported by Campbell (1946). The lower Blackiston of Campbell (1946) is probably correlative with the lower Huron Member of Provo (1977) and Swager (1978).

Evidence of benthic life is quite strong in the Three Lick Bed of eastern Kentucky. Barron and Ettensohn (1980) reported in situ Lingula, bioturbation, and a pyritized micromorph fauna of clams, gastropods, agglutinated Foraminifera, and ostracods in the three greenish-gray shales of the bed. Burrowing in this bed also extends from the greenish-gray shales into the underlying black shales (figure 5).

Some of the most unusual forms of bioturbation in the Three Lick Bed consist of rather wide (1.5 centimeters) "trails" of green shale in surrounding black shale that end in a comparatively large (2 centimeters) Lingula specimen with a mold or the pyritized remains of the pedicle in the center of the "trail" (figure 6). Complete, in-place Lingula specimens are best known from an outcrop in Madison County, Kentucky, west of Berea, but they have also been found in other sections as well, notably in Rowan County, Kentucky (see Plate X). The Lingula with their phosphatic shells apparently were able to thrive in low-oxygen conditions which were too severe for normal calcified forms.

Lingula

Lingula has often been used to indicate near-shore, shallow-water facies. The Lingula-molluscan assemblage of the Ordovician is widely used to indicate lagoonal conditions (Walker, 1972). The occurrence of rather large Lingula, obviously in place (see Plate VI, figure B), and apparently thriving in the greenish-gray mud deposited in near-reducing conditions does not seem to support a shallow-water, near-shore interpretation; particularly when found with open-marine indicators such as conodonts and goniatite cephalopods.

Cherns (1978) reported Lingula from deep, basinal waters in a Silurian basin in life-position. He also reported a Lingula from shallower, shelf environments. He stated that neither served, in that instance, as a near-shore, shallow- or brackish-water indicator. In addition, Paine (1970) stated that both Lingula and its modern relative Glottidia lived in muddy bottoms at depths of ten meters and greater. He supported that conclusion by showing that Lingula lived in shales which accumulated below wave base. A recent species of Glottidia was known to become most abundant in deeper water. Paine suggested that modern research is biased toward the near-shore, shallow, sandy substrate because of sampling convenience. Because of high-energy conditions and the resulting destruction of shell material, the fossil record is probably biased toward preservation in deeper, lower-energy environments where muds accumulated.

The point of this section is to demonstrate that Lingula and other modern inarticulates have in the past and do presently inhibit the stressful near-shore environments. However, they are not limited to that environment today, and were not likely limited to only that environment in the

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geologic past. As Rudwick (1965) stated, Lingula can be used as an indicator of the near-shore environment in the absence of toxic conditions and other brachiopods. Most of the Lingula in the black shales were not living in the black muds, but were probably epiplanktic. Since Lingula did occupy apparent near-shore environments in the Ordovician and later times, it is likely that they developed very early the capability to survive low levels of oxygen using the pigment hemerythrin which releases bound oxygen to the animal during periods of reduced oxygen levels (Paine, 1970). The capability would have allowed the Late Devonian Lingula to survive and even to thrive in the greenish-gray muds of the Three Lick Bed and other similar horizons in the black-shale sequence.

Molluscs

The micromorph pelecypods (Plate III, figure D) found within the green shales from the black-shale sequence probably were living in or on the bottom as both valves are generally recovered intact and articulated. Alternatively, one can not entirely rule out a possible epiplanktic mode; however, suggestive evidence is not apparent. Scanning electron micrographs of the clams fail to show growth lines or other such details. At higher magnification, the crystallization pattern seems similar to published micrographs of aragonitic structure (Harvey, 1972). If this replacement pattern is correct, the pyritization must have been synsedimentary. Clark and Lutz (1980), Nussman (1975), and Brown (1966) presented evidence suggesting that pyrite replaces aragonite before solution or change to calcite. Berner (1970) and Howarth (1979) stated that pyrite production is related to the activity of sulfate-reducing bacteria; sulfate is reduced through anaerobic bacterial respiration to sulfide, and then the chemically free oxygen is used by the bacteria. The sulfide then combines with iron to form hydrotroilite ($FeS \cdot nH_2O$) which is later changed to pyrite (Lineback, 1968). Such bacterial activity can be inferred to have been at quite a high level in the black-shale sea. Although Clark and Lutz (1980) found surficial pyritization on living mollusc shells, the possibility of such development for fossils from the Three Lick Bed is only speculative at this time. The suggestion by Clark and Lutz (1980) that pyritization seems to coincide with the occurrence of organic material in the mollusc shell is supported by selective pyritization of some burrows which may have been lined with mucous, and by the pyritization of Lingula pedicles. Zangerl and Richardson (1963) reported finding pyritized pelecypods in association with unpyritized phosphatic brachiopods. They attributed the difference in preservation to the presence of phosphate in the brachiopods and its absence in the pelecypods. Schopf (1980), furthermore, stated that the occurrence of pyrite in sedimentary rocks is very strong evidence for the deposition of organic matter which was certainly the case during the deposition of the black shale. In the micromorph fossils from the Three Lick Bed the pattern of pyritization appears to be similar in all the molluscs but different from that of the ostracods (figure 7).

The micromorph gastropods (Plate III, figures A, B, and C) found in the Three Lick Bed probably were benthic, although the possibility of planktic(?) or epiplanktic forms cannot be ruled out. Pteropods have been recovered from Recent anaerobic sediments similar to the black shales in the Santa Barbara Basin (Berger and Soutar, 1970).
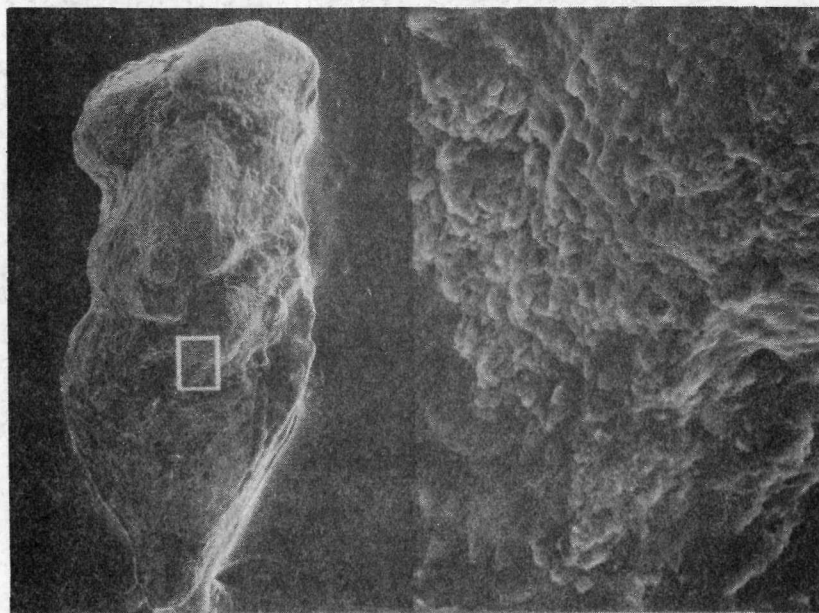
25

Figure 7. Ostracod from Three Lick Bed. SEM micrograph. Area of box magnified 700 times to show pyrite replacement pattern.
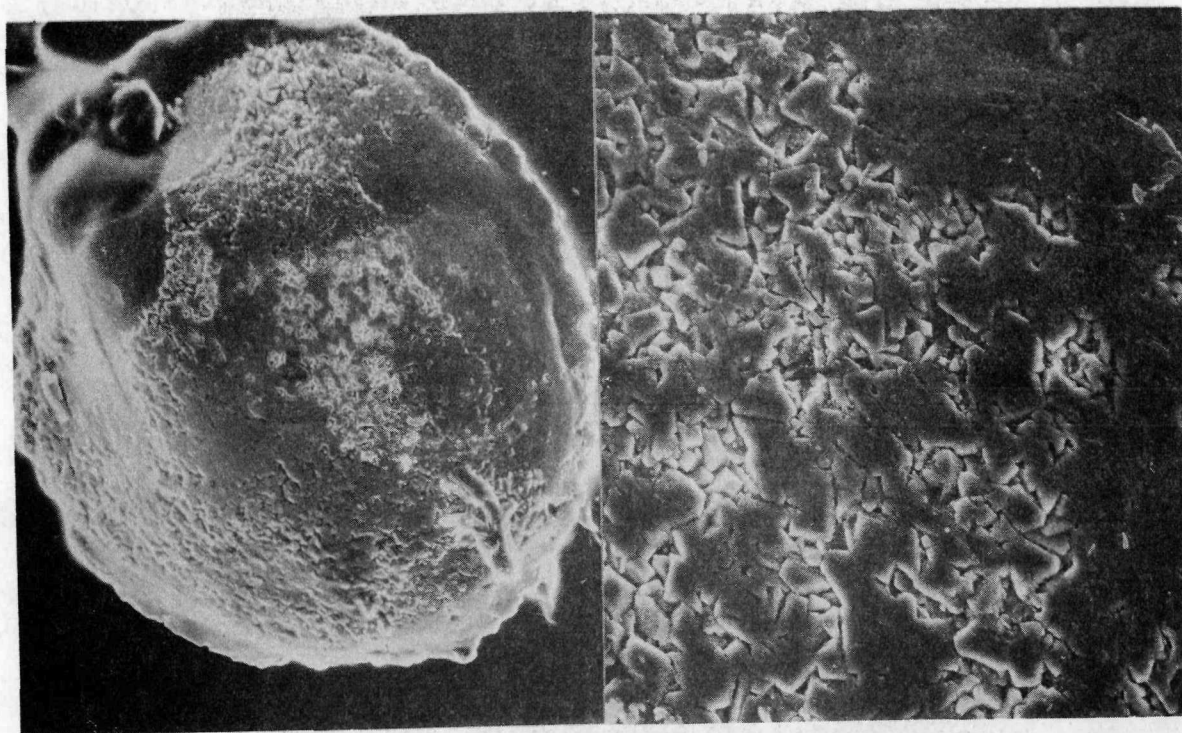

Figure 8. Pyritized pelecypod from Three Lick Bed. Magnified 230 times on left and 950 times on the right to show pyrite replacement pattern.

Foraminifera

Pyritized benthic, agglutinated Foraminifera also occur in the
Three Lick Bed (Plate I, figures A and B)   and include the three
genera: Rhabdammina, Psuedoastrorhiza, and Thurammina. These are in-
terpreted to have been strictly benthic organisms. Similar benthic
Foraminifera have been reported previously by Conkin (1961) and Conkin
and Conkin (1964, 1967, 1977) from   Upper Devonian greenish-gray
shales, and are known from Middle Devonian sediments of Ohio (Stewart
and Lampe, 1947). According to Toomey and Mamet (1978), the Late
Devonian was dominated by the foraminiferal families Saccamminidae and
the Ammodiscidae, both families having single-chambered tests formed of
agglutinated sand or mud particles. Although benthic Foraminifera were
very common during the Devonian, planktic Foraminifera had not yet
developed. Benthic Foraminifera today occupy habitats varying from
ephemeral tidal ponds to abyssal red-clay ocean bottoms. It is possible
that Late Devonian forms were equally opportunistic and could have quickly
moved into the dysaerobic environments which characterized the greenish-
gray muds in the black-shale sequence.

Ostracods

Benthic ostracods are also present in the greenish-gray shales of
the Three Lick Bed (Plate I, figures C, D, and E). Similar forms have
been reported by Stewart (1944) from the Middle Devonian bone beds of
Ohio, by Stewart and Hendrix (1939) from the Olentangy Shale, and more re-
cently by Duffield and Warshauer (1979), and Warshauer (1978) from
greenish-gray shales in the black-shale core from West Virginia. The
latter reported a low diversity of benthic forms and attributed this
low diveristy to harsh bottom conditions. Ostracods from the Three Lick
Bed generally were not heavily ornamented, and as such probably fit into
a deeper-water, off-shore group such as described by Gooday and Becker
(1978).

The ostracods were probably nekto-benthic predators and grazers.
They also formed an important source of food for larger predators. The
ostracods occupy a very wide range of habitats today and probably were
sufficiently eurytopic in the Late Devonian to move into a dysaerobic
environment such as the one in which the greenish-gray muds of the Three
Lick Bed were deposited.

Organism-oxygen Relationships

Pelecypods, gastropods, Foraminifera, and ostracods are generally
considered to have been more eurytopic in nature than were the calcareous
brachiopods. This may explain why the dysaerobic, greenish-gray mud
environment was colonized by molluscs, ostracods, Foraminifera, and
phosphatic brachiopods, whereas heavily calcified benthic organisms are
absent. The absence of heavily calcified benthos is largely related to
a lack of oxygen (Rhoads and Morse, 1971). Rhoads and Morse (1971) in-
dicated that heavily calcified forms are present only where the concentra-
tion of dissolved oxygen was greater than 1.0 milliliter per liter; lightly
calcified organism can exist below this level. Oxygen concentrations of

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about 0.1 to 0.3 milliliters per liter apparently were necessary to support macrofaunal burrowing organisms. At levels below that, aerobic metazoans were largely absent; and, as a result, the sediments retained their original lamination.

Based on this model, the lower Huron Member appears to represent primarily dysaerobic depositional environments with bioturbation providing evidence of the increased oxygen levels compared with the normal anaerobic black-shale sea bottom. The depositional environment of the greenish-gray muds in the Three Lick Bed may have been marginally aerobic-dysaerobic indicated by the presence of burrows and epifauna. This micromorph epifauna may reflect juveniles that died before maturity, or stunted adults that could not develop in a normal manner under dysaerobic conditions.

Other Benthos

Other evidence of benthic life is found in the phosphate-nodule zone near the upper part (Cleveland Shale Member) of the black-shale sequence. Borings attributed to acrothoracic barnacles have been identified in phosphate nodules. Similar borings have been reported by Tomlinson (1969) from the Devonian. The borings were probably made after lithification of the nodule, but prior to burial. Concentrations of some borings on the edges of the nodules may indicate that the nodules were flipped about by currents, leaving only the edges as a safe habitat. That currents were present is further supported by imbrication of the nodules at some locations (Steve Lamb, personal communication). Apparently, the nodules existed for some time in a somewhat soft, semi-consolidated state, because Lingula specimens in apparent life position have been found occupying burrows in some nodules and it is likely the the Lingula made the burrows in which they are found. The trace fossil Lingulichnites Szmuc and others (1976) has a somewhat similar outline in plan view to that of borings made by acrothoracic barnacles. The two types of borings, however, are not always easily distinguishable in plan view.

PLANTS

Terrestrial vegetation began to accumulate in sediments as early as Silurian time. From then until the Middle Devonian, however, preserved plants were comparatively rare. By the Middle Devonian, land plants began to evolve rapidly and became widely dispersed geographically. In the Late Devonian, land plants had become so firmly established that a rather substantial upland forest with large trees (20 meters high) and a diverse and abundant assemblage of lesser plants became an important part of the terrestrial environment. Ancillary to the development of a comparatively lush vegetation, habitats suitable to terrestrial animals were developed and rather quickly occupied. The oldest tetrapod fossil is known from Upper Devonian rocks of Greenland. Likewise some of the earliest insect fossils are from the Late Devonian. This same vegetation seems to have had a great effect on the Late Devonian black-shale sea, the life in that sea, and the sediments deposited therein.

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General

   The plant fossils found in the Upper Devonian-Lower Mississippian
black-shale sequence are preserved by several methods, including
silicification, coalification, pyritization, calcification, phosphatiza-
tion, and in a relatively unaltered state, and each of these methods re-
flect to some degree the environment in which the plant material was de-
posited.

   Silicified, slightly compressed logs probably were buried and
mineralized fairly rapidly in sediment containing silica-saturated in-
terstitial water (Plate XIV, figure A). A mechanism for silica enrich-
ment has been discussed in the section on radiolarians. The coalified
material occurs as carbonized films just a few millimeters thick
Plate XIV, figure B).   Breger and Schopf (1955) reported
coalified woody plant tissue similar to vitrain that essentially ranked
as a high-volatile A bituminous coal. The material came from the upper
Chattanooga Shale in Tennessee. The pyritized material was almost cer-
tainly deposited in anaerobic, reducing conditions where abundant
hydrogen sulfide was produced by bacterial action. Phosphatized wood and
plant material are associated primarily with the phosphate nodules in the
upper parts of the sequence and have been exhaustively treated by Cross
and Hoskins (1951a, b) and Hoskins and Cross (1947, 1951, 1952), Read and
Campbell (1939), Read (1936a, b; 1937), and Scott and Jeffery (1914).
Logs are also known from calcareous nodules near the base of the sequence
in Ohio (Prosser, 1912; Cross and Hoskins, 1951b).

   Although much of the Late Devonian vegetation has been studied in
a classical paleobotanical and systematic sense, very little work has been
done on the ecology of the Late Devonian forests. What work has been done,
is largely from the paleobotanical ecologist C. B. Beck. In 1960, Beck
published a study of the occurrence of Archaeopteris foliage and fructifica-
tions organically connected with Callixylon wood. Prior to that time, the
foliage and fructifications were considered to be one plant, whereas the
wood was thought to be another plant. Together they were the dominant
constituents of many Late Devonian plant assemblages. Beck (1964a) stated
that the Archaeopteris tree was the main constituent of heavily forested
highlands in New York state and Pennsylvania during the Late Devonian.
The presence of forested land areas may have been a contributing cause of
starved-basin conditions in the adjacent black-shale sea because forest
cover no doubt reduced run-off, erosion, and the sediment load of the
rivers discharging through the Catskill Delta.

   Clearly some of the most abundant and diverse assemblages of plant
fossils have been found in the phosphate nodules in upper parts of the
black-shale sequence. Plants preserved in these nodules include both small
bush-like or rush-like plants as well as stems from larger trees like
Callixylon. In addition to plants, animal remains such as brachiopods,
conodonts, crustaceans, and fish remains are found in these nodules.

   Cross and Hoskins (1951b) suggested that the concentration of plants
increased as the crest of the Cincinnati Arch was approached. They noted
that this was less true for Callixylon remains than for smaller forms of

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material found mainly in the phosphate nodules. Distances from either
Ozarkia or the land mass to the east led them to speculate that a low-
lying land mass near Cincinnati may have provided a source for the smaller,
more fragile stems (2.3 millimeters diameter) found in the phosphate
nodules. It is also possible that the smaller stems are preserved only
because of the phosphatization which occurred at this time. If this is
the case, the small stems were not unique to the seas of that time, but
only uniquely preserved by phosphatization.

Protosalvinia

Protosalvinia or Foerstia, a problematic plant fossil common in the
black shales, occupies a controversial place in paleobotany. Even the
generic name is a subject of debate. The thalloid shape and general
resemblance to fucoid algae along with the marine association in the rock
record have led some workers to classify Protosalvinia as a pelagic marine
alga (White and Stadnichenko, 1923; Schopf and Schwietering, 1970;
Schwietering and Neal, 1978; Schopf, 1978). Others have suggested that
Protosalvinia was adapted to a terrestrial environment and that it was not
an alga, but a member of an entirely separate group of plants (Gray and
Boucot, 1978; see Plate XII, figures C and D). A third interpretation
suggested that Protosalvina was related to the Phaeophyta or brown algae
because of similarities in thallus shape and reproduction and that it
inhabited a brackish littoral environment (Niklas and Phillips, 1976).

Although Protosalvinia fossils occur over a geographically broad range
(Ontario, New York, Pennsylvania, Vriginia, West Virginia, Ohio, Indiana,
Oklahoma, Tennessee, and Kentucky), the stratigraphic range is limited to
a narrow zone in the Upper Devonian. In eastern Kentucky, Protosalvinia
occurs in radioactive units 4 and 5, the middle and lower Huron of Provo
(1977) and Swager (1978). That Protosalvinia has been found only in
marine sedimentary units, and not in nonmarine or unequivocally near-shore
marine facies poses some problems for an interpretation as a terrestrial
plant. Gray and Boucot (1978) state:

> "It is possible, therefore, to conclude that a variety of
> circumstances account for the present distribution pattern and
> depositional sites of Protosalvinia rather than the simple
> explanation that the depositional-preservational sites are the
> original life site . . ."

Protosalvinia thalli contain lignin-like long-chain hydrocarbon com-
pounds and the tetrads contain sporopollenin (Niklas and Phillips, 1976).
Gray and Boucot (1978) note the presence of resistant walls with sufficient
durability to withstand transport over long distances and extreme chemical
conditions. Although this argument certainly can explain how these so-
called land plants were transported throughout the basin in one particular
zone, it raises the question, that if these plants were so durable, why
have remains not been found in the nonmarine, Upper Devonian rocks of the
eastern United States? Gray and Boucot (1978) pointed out that uncalcified
algae is very rare in the geologic record and that such durable walls are
unusual for algae. Niklas and Phillips (1976) suggested that the lignin-
like compounds and the production of dessication-resistant spores indicate

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at least some periods of dryness in the life of the plant.

In this short section, we have not tried to put forward one inter-
pretation over another, but have attempted to show some of the complexity
associated with paleoecological interpretations of Protosalvinia.

THE TWO MAJOR FACIES

The so-called homogeneous black-shale sequence contains several dif-
ferent facies, but two facies, the black, laminated fissile shales and
the greenish-gray clayey shales dominate the sequence. Other minor facies
include bone beds, thin layers of vitrain, cone-in-cone limestone, dolo-
mite, and the phosphate nodule zone. A number of characteristics dis-
tinguish the black, fissile shales from the greenish-gray clayey shales.
Color is the most obvious distinction. The greenish-gray shales generally
contain evidence of benthic life; the black shales do not. Directly re-
lated to the presence or absence of benthos is the fact that the green
shales are highly bioturbated, whereas the laminated black shales lack
bioturbation. The black shales contain more organic matter and quartz
than the greenish-gray shales, and the greenish-gray shales contain more
clay (illite) than the black shales. These factors affect the colors of
the two facies.

In figures 9 and 10, the fossils from the two respective facies are
shown in suggested paleoenvironmental reconstructions. The block diagrams
are schematic and not drawn to scale. The black, fissile shale environ-
ment (figure 9) shows laminated, organic-rich sediment undisturbed by
bioturbation, in which syngenetic pyrite nodules formed and into which
necroplanktic logs have sunk with associated epiplanktic life. In the
bottom sediments, anaerobic bacteria, some larger anaerobes and faculta-
tive anaerobes such as blue-green algae and nematodes lived in a primi-
tive sulfide community. A similar community has been described in Recent
sand deposits by Fenchel and Riedl (1970). The dashed lines represent
inferred gradations from anaerobic through dysaerobic to aerobic levels
of oxygen based on the models of Rhoads and Morse (1971) and Byers (1977,
1979). In the aerobic zone (no depth inferred) "normal" nektic, planktic,
nekto-planktic, and epiplanktic life are represented. All fish are
represented in this diagram by the shark Cladoselache. Both shallow-
and deep-water conodont animals are represented by a purely hypothetical,
highly speculative drawing. Additionally, goniatite cephalopods,
Tasmanites, arcitarchs, and epiplanktic brachiopods and crinoids are
shown. Inferred ostracods and radiolarians are also represented.
Tripton is the non-living organic particulate matter found in the water
column.

The diagram representing deposition of greenish-gray shale (figure
10) shows a significant change from the black-shale diagram. The bottom
contains life forms and disrupted or bioturbated sediments which are
greenish-gray and not black. The benthos includes Lingula, unidentified
soft-bodied burrowers, micromorph forms of pelecypods, gastropods, ortho-
cone cephalopods, ostracods, and Foraminifera. Higher in the water column,
the dashed line represents a gradational change from dysaerobic to aerobic
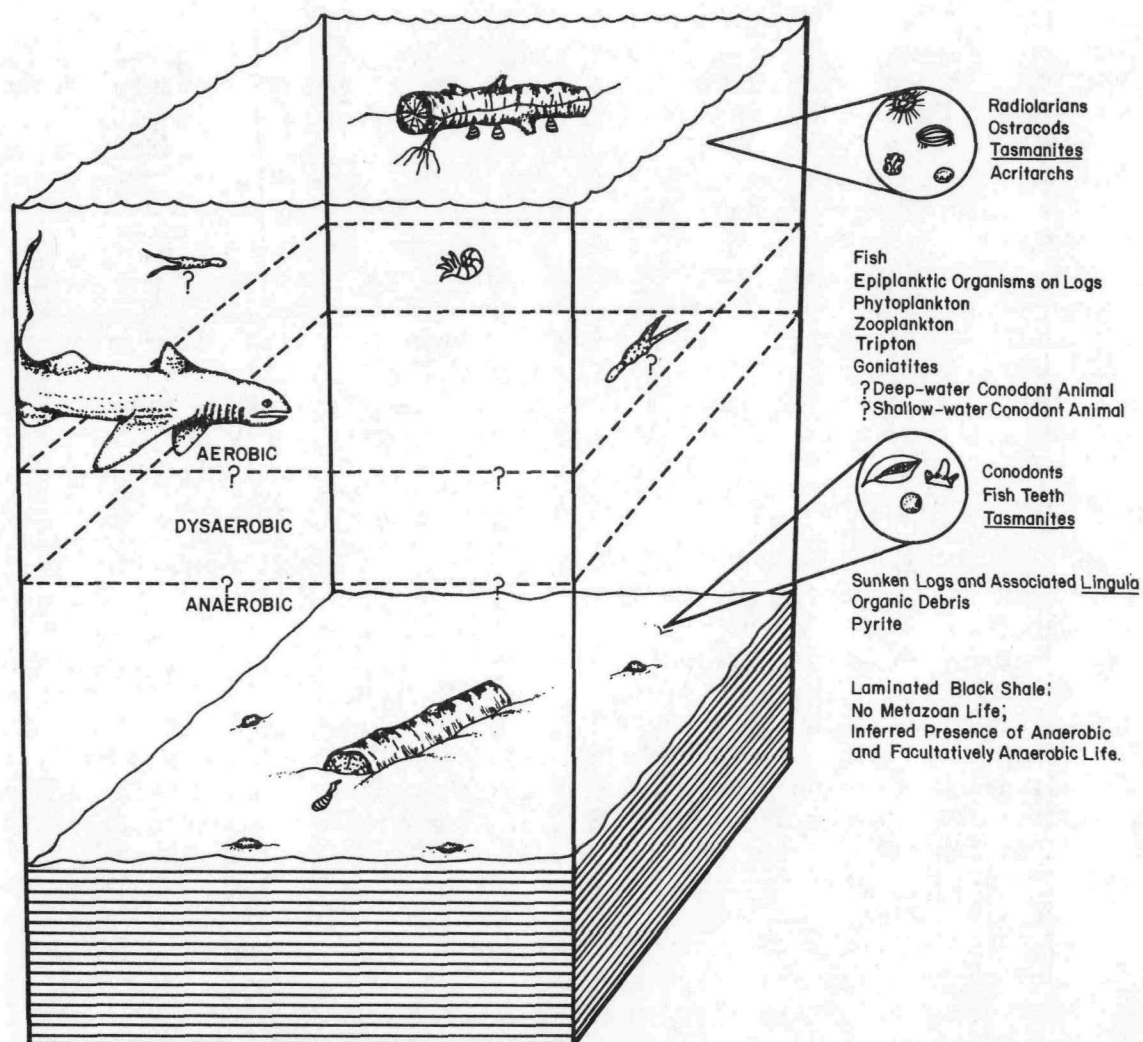
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Figure 9. Schematic block diagram of a reconstructed water column and bottom during black-shale deposition. Continuous lines at base represent laminated black muds. Not drawn to scale.
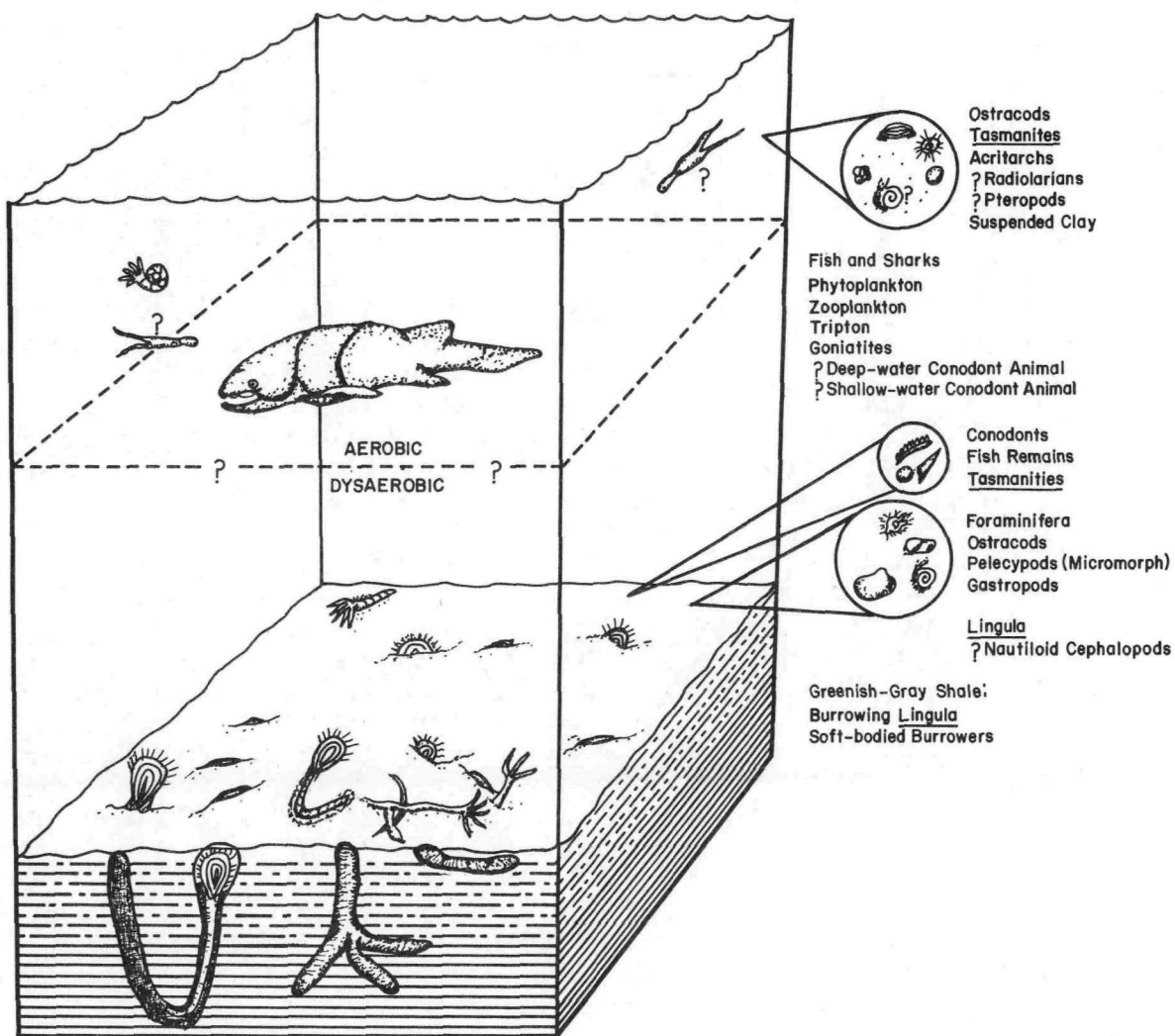
Ostracods
Tasmanites
Acritarchs
? Radiolarians
? Pteropods
Suspended Clay

Fish and Sharks
Phytoplankton
Zooplankton
Tripton
Goniatites
? Deep-water Conodont Animal
? Shallow-water Conodont Animal

Conodonts
Fish Remains
Tasmanities

Foraminifera
Ostracods
Pelecypods (Micromorph)
Gastropods

Lingula
? Nautiloid Cephalopods

Greenish-Gray Shale:
Burrowing Lingula
Soft-bodied Burrowers

AEROBIC

DYSAEROBIC

Figure 10. Schematic block diagram of a reconstructed water column and bottom during the deposition of greenish-gray shale. Dashed lines represent bioturbated green muds. Not drawn to scale.

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oxgyen levels. In the aerobic zone, the life forms are essentially the same as for the black-shale diagram. All fish are represented by the arthrodire _Cladodus_. Represented in this diagram and not in the previous one are an increased suspended clay content and inferred pteropod-like gastropods.

Greenish-gray shales occur in parts of the Olentangy, Huron and Bedford shales, as well as in the Three Lick Bed of the black-shale sequence. We will use the Three Lick Bed as an example to demonstrate a mechanism for deposition of black, laminated muds interbedded with greenish-gray, clayey sediments (see Barron and Ettensohn, 1980). The diagrams in figure 11 show the two mechanisms which we suggest can account for the deposition of these two predominant facies. Figure 11A, shows the establishment of quasi-estuarine circulation related to easterly winds blowing out to sea and carrying surface waters with them; a net deficit of water results in near-shore areas. Water along the bottom moves upward near shore to replace the water blown out to sea. This causes upwelling of cold phosphate-rich, oxygen-poor bottom water. The upwelling brings to the oxygen-rich photic zone abundant nutrients, which support a high level of organic productivity. Oxygen is continually replenished in the upper aerobic zone by mixing due to wind-driven circulation cells and due to the photosynthesis of phytoplankton.

Figure 11B reflects an increase in fluvial discharge and a concomitant increase in clastic input from deltas. The clastic influx enters the adjacent seas both as suspended sediment and in the form of turbidity currents. These currents not only carry oxygen-rich waters to previously oxygen-deficient areas, but also push any upwelling farther seaward, thereby establishing dysaerobic conditions and the deposition of greenish-gray muds on the bottom. Once dysaerobic conditions are established, opportunistic benthic life can colonize the bottom as shown in figure 10. Once the conditions controlling increased fluvial and clastic influx subside, quasi-estuarine circulation would return to reestablish anaerobic bottom conditions.

Three such periods of increased fluvial and clastic input are represented by the three green shales of the Three Lick Bed (Provo and others, 1978). Moreover, the Three Lick Bed represents the southern tongue of the Chagrin Shale, one of the last major progradation of the Catskill Delta. Local turbiditic sandstones are known to be associated with the unit.
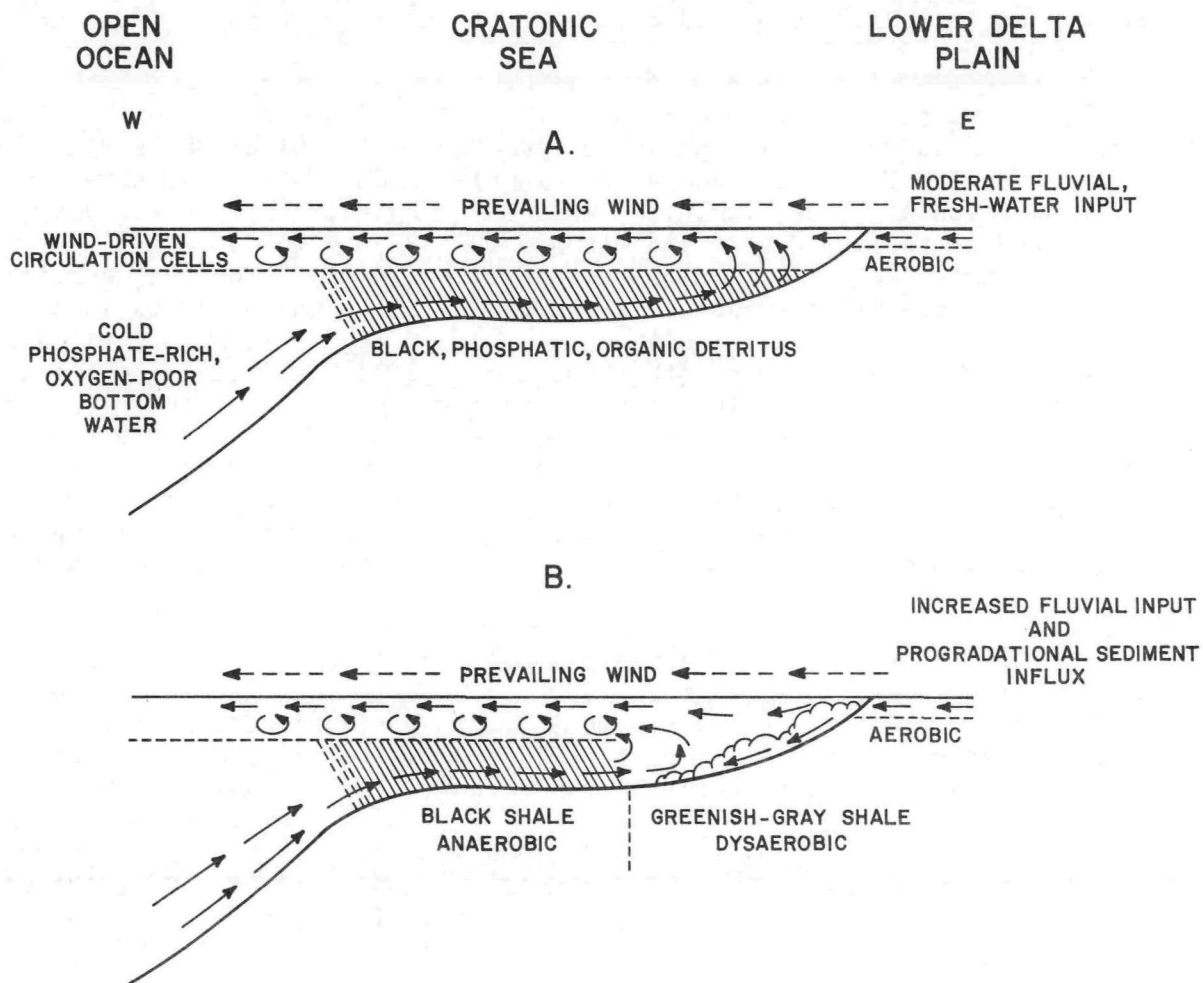
OPEN   CRATONIC   LOWER DELTA
OCEAN   SEA   PLAIN

W   E
                                  A.

                                                       MODERATE FLUVIAL,
            ◄ - - - ◄ - - - PREVAILING WIND ◄ - - - ◄ - - - FRESH-WATER INPUT
WIND-DRIVEN
CIRCULATION CELLS   AEROBIC

   COLD
PHOSPHATE-RICH,   BLACK, PHOSPHATIC, ORGANIC DETRITUS
OXYGEN-POOR
  BOTTOM
  WATER

                                  B.

                                                   INCREASED FLUVIAL INPUT
                                                           AND
                                                   PROGRADATIONAL SEDIMENT
            ◄ - - - ◄ - - - PREVAILING WIND ◄ - - - ◄ - - -   INFLUX

                                                              AEROBIC

              BLACK SHALE   │ GREENISH-GRAY SHALE
              ANAEROBIC   │ DYSAEROBIC

Figure 11.   A.)   Development of quasi-esturaine circulation and upwelling
                   in black-shale sea.

             B.)   Disruption of upwelling through progradation sediment
                   influx.

                   (Adapted from Heckel, 1977).

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A PHOTOGRAPHIC ATLAS OF SOME

COMMON BLACK-SHALE FOSSILS

PLATE I

A. ?Rhabdammina sp. Three Lick Bed, Ohio Shale, Rowan County, Kentucky. Pyritized. x260.

B. ?Thurammina sp. Three Lick Bed, Ohio Shale, Rowan County, Kentucky. Pyritized. x450.

C. Richterina sp. Three Lick Bed, Ohio Shale, Rowan County, Kentucky. Pyritized. x60.

D. Unidentified benthic ostracod. Three Lick Bed, Ohio Shale, Rowan County, Kentucky, SEM micrograph x250.

E. Unidentified benthic ostracod. Three Lick Bed, Ohio Shale, Rowan County, Kentucky, SEM micrograph x60.

PLATE I
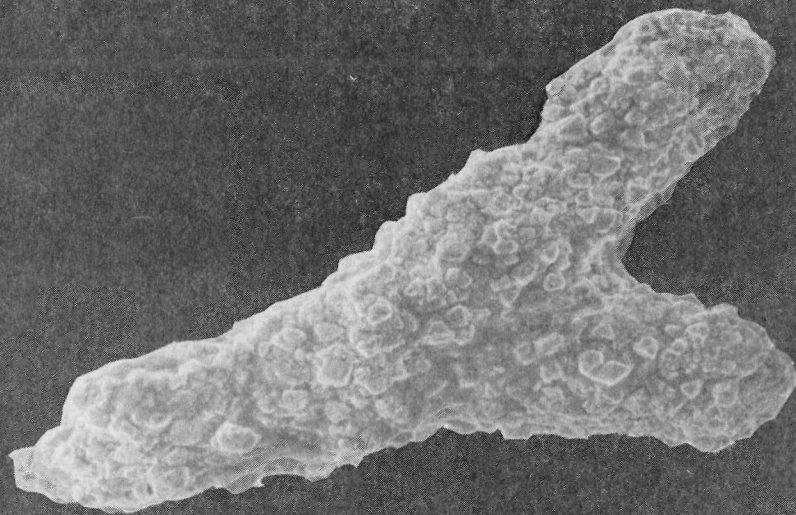
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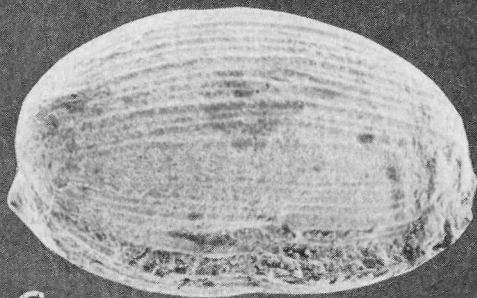
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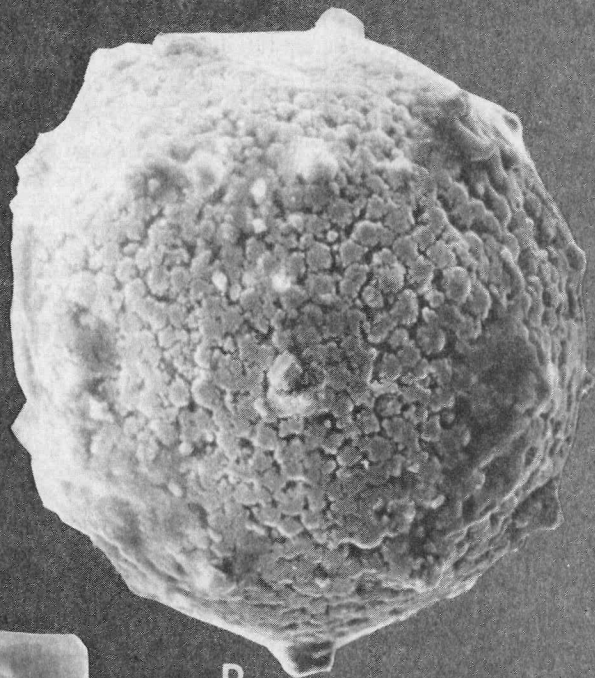
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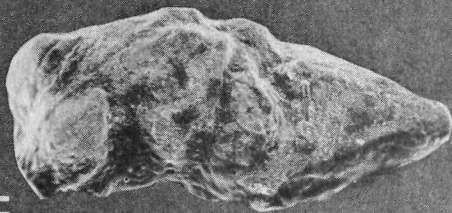
E

PLATE II

A. Lingulipora sp. Ohio Shale, Kentucky. x4.5.

B. ?Barroisella sp. x5.

C. Orbiculoidea sp. Ohio Shale, Burkesville, Kentucky. x4.5.

D. Schizobolus sp. Chattanooga Shale, Clinch Mountain, Tennessee. x3.

E. Orbiculoid brachiopod. Chattanooga Shale, Clinch Mountain, Tennessee. x3.

F. Chonetes sp. New Albany Shale, North Vernon, Indiana. x5.

G. Poorly preserved "Leiorhynchus", New Albany Shale, North Vernon, Indiana. x4.

H. Poorly preserved "Leiorhynchus", New Albany Shale, North Vernon, Indiana. x4.

PLATE II
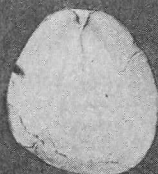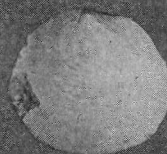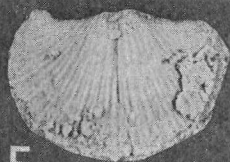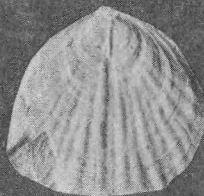
PLATE III

A. Unidentified gastropod . Three Lick Bed, Ohio Shale, Rowan County, Kentucky. SEM micrograph, x240.

B. Unidentified gastropod. Three Lick Bed, Ohio Shale, Rowan County, Kentucky. SEM micrograph, x120.

C. Columella from high-spired gastropod. Three Lick Bed, Ohio Shale, Rowan County, Kentucky. SEM micrograph, x1100.

D. ?Edmondia sp. Three Lick Bed, Ohio Shale, Rowan County, Kentucky. SEM micrograph, x240.

PLATE III
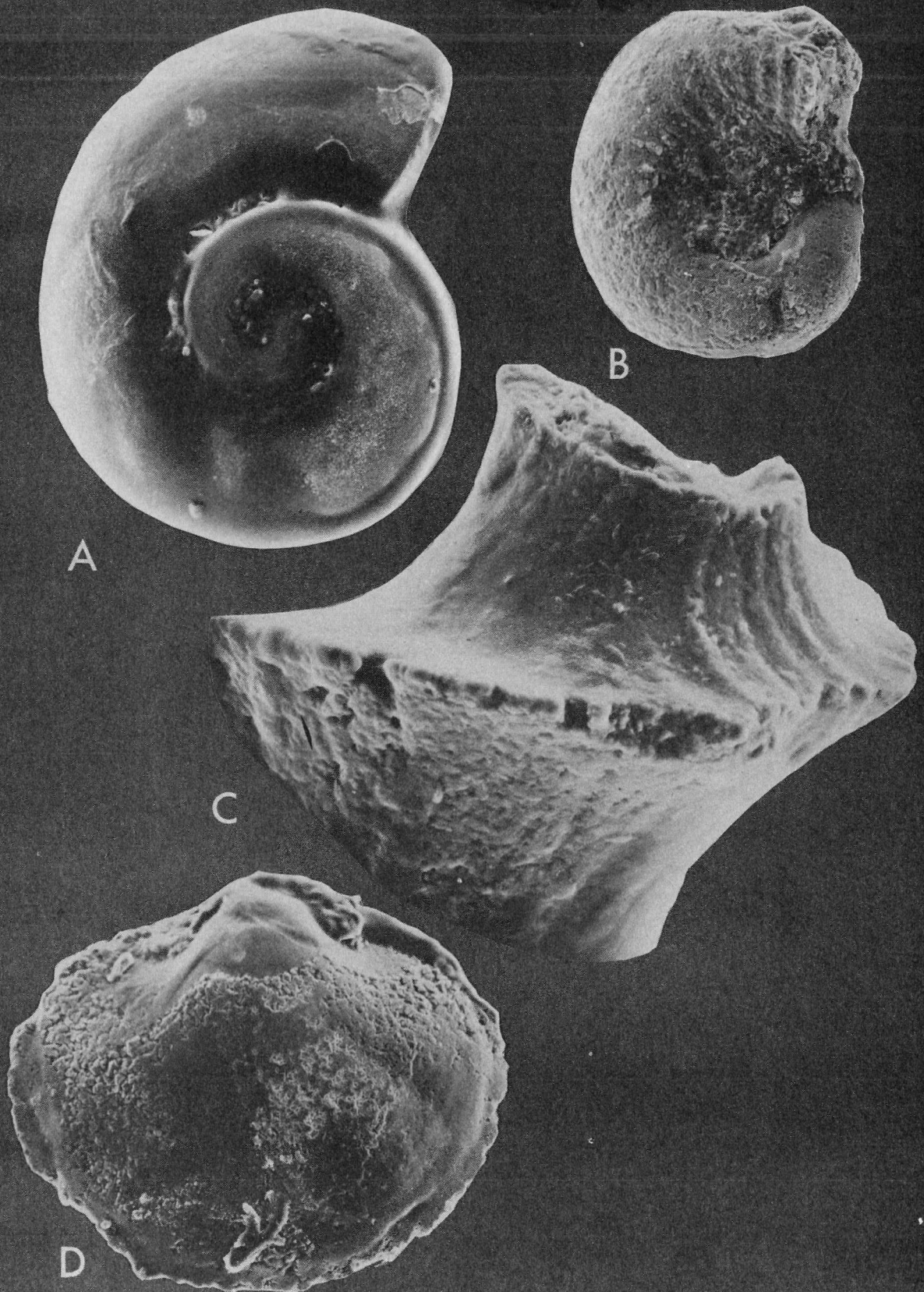
PLATE IV

A. **Unidentified goniatite.** Ohio Shale, core from Columbia Gas well #20336, Martin County, Kentucky; about x2.

B. **Unidentified goniatite .** Ohio Shale, core from Columbia Gas well #20336, Martin County, Kentucky; about x7.

C. **?Anaptychi of a cephalopod.** Black shale core. x3.

D. **Unidentified goniatites.** Ohio Shale, core from Columbia Gas well #20336, Martin County, Kentucky; x1.

PLATE IV

A

B
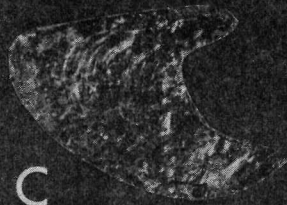
C

D

PLATE V

A. Goniatite cephalopod fragment. Three Lick Bed, Ohio Shale, Rowan County, Kentucky. Pyritized. SEM micrograph, x200.

B. ?Orthoconic cephalopod. Three Lick Bed, Ohio Shale, Rowan County, Kentucky. SEM micrograph, x950.

C. Orthocone cephalopod fragment. Three Lick Bed, Ohio Shale, Rowan County, Kentucky. SEM micrograph, x1000.

PLATE V
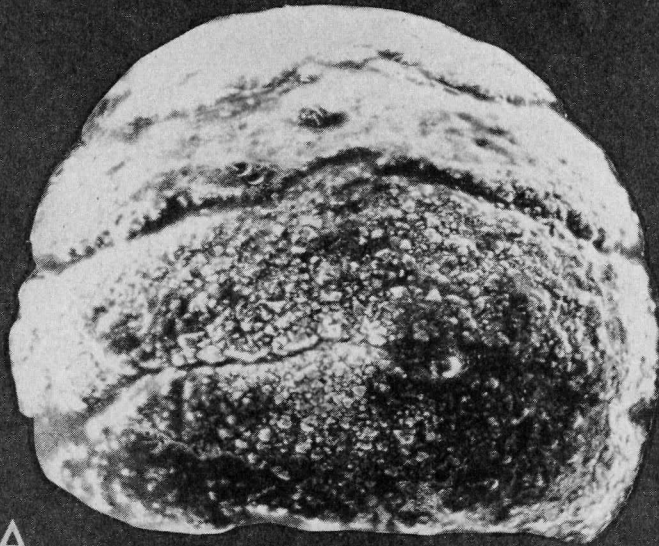
A

B

C

PLATE VI

A. Crinoid fragments associated with <u>Callixylon</u> log. New Albany Shale, Lexington, Indiana. x1. (From University of Cincinnati, Geology Department Collections).

B. <u>Lingula</u> sp. In-place in greenish-gray shale. Three Lick Bed, New Albany Shale, Madison County, Kentucky. x2.5.

PLATE VI
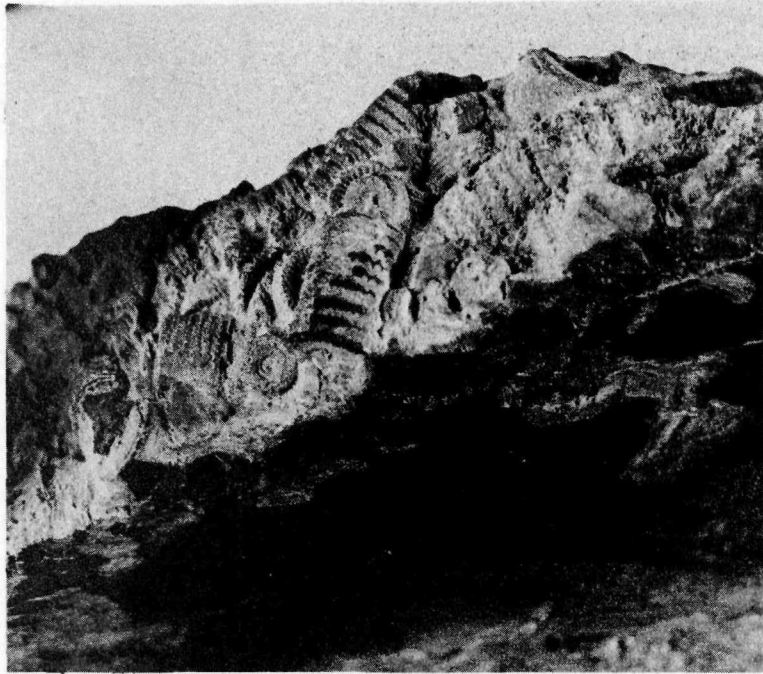
A
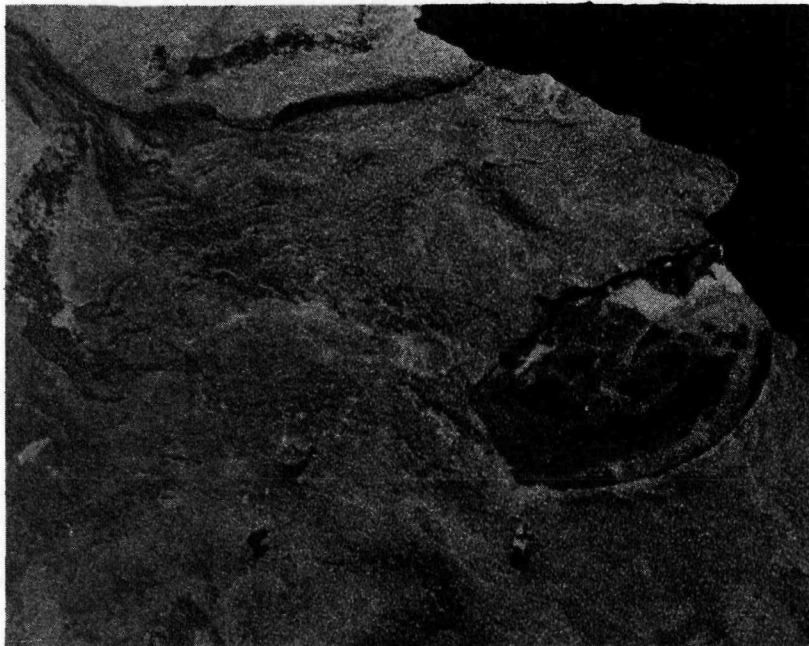
B

PLATE VII

A. Spathognathodus sp. Three Lick Bed, Ohio Shale, Rowan County, Kentucky. x40.

B. Siphonodella sp. Lag deposit at the base of the Sunbury Shale, Rowan County, Kentucky. x40.

C. Gnathodus sp. Lag deposit at the base of the Sunbury Shale, Rowan County, Kentucky. x40.

D., E., F. Palmatolepis sp. Lag deposit at top of the lower inter-bedded unit (Unit 5) of Huron Shale (Swager, 1978), Ohio Shale, Rowan County, Kentucky. x40.

G. Polygnathus sp. Lag deposit at the base of the Ohio Shale, Rowan County, Kentucky. x40.

H. Icriodus sp. Lag deposit at the base of the Ohio Shale, Rowan County, Kentucky. x40.

I. Styliolina sp. Chattanooga Shale, Clinch Mountain, Tennessee. x15.

PLATE VII
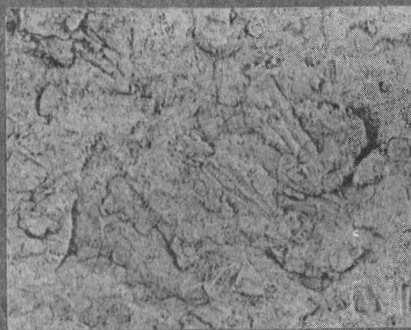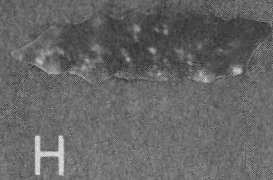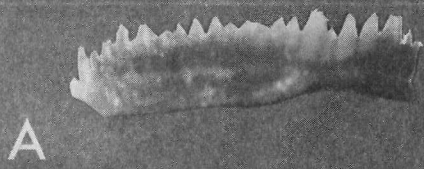
PLATE VIII

A. **Rhizocorallium**, a trace fossil. Ohio Shale, Rowan County, **Kentucky.** x1.

B. **Trace Fossil, Planolites**-like. Kentucky Highway 51, near **Irvine, Kentucky.** x.5.

PLATE VIII
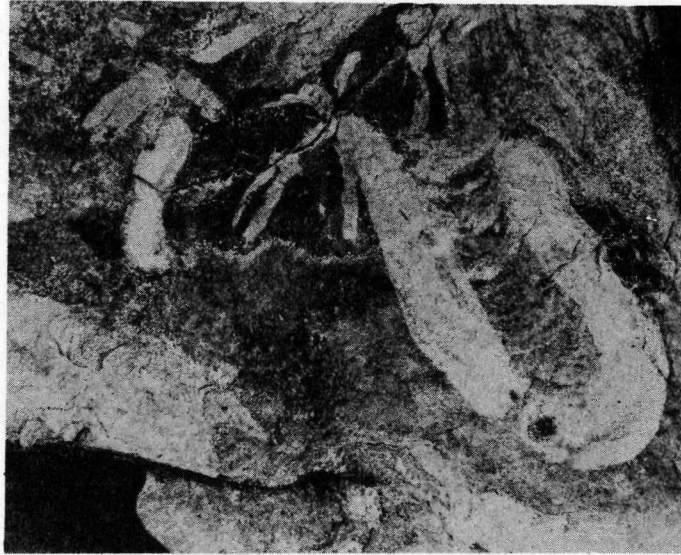
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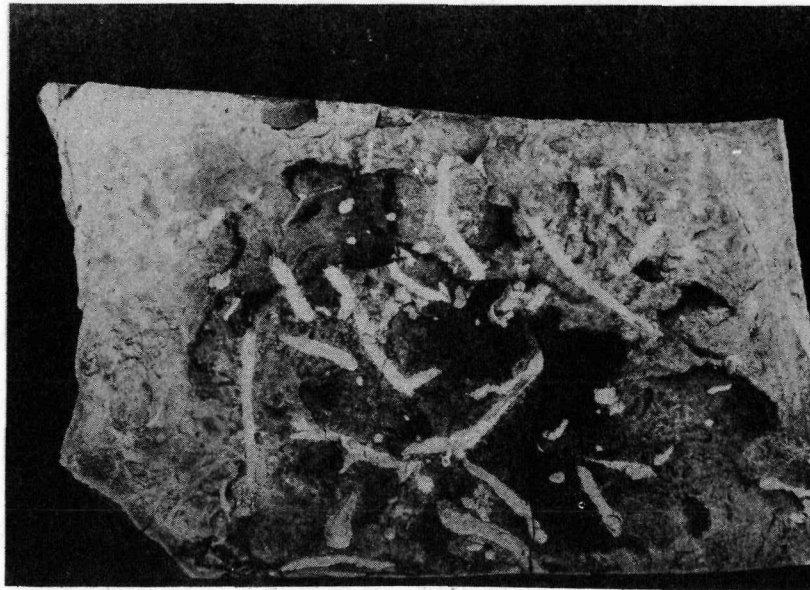
B

PLATE IX

A. <u>Zoophycos</u> trace fossil. Ohio Shale, Rowan County, Kentucky.
    x1.

B. <u>Zoophycos</u> trace fossil. New Albany Shale, Bullitt County,
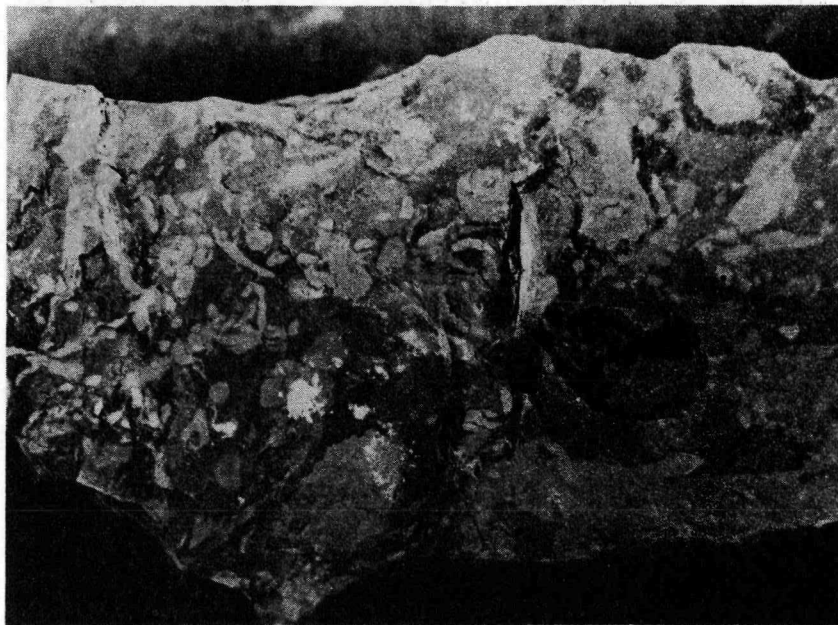   Kentucky, x.5.

PLATE IX

A

B

PLATE X

A. Lingula burrows filled with greenish-gray shale in black shale. Three Lick Bed, New Albany Shale, Madison County, Kentucky. x1.

B. Lingula and Lingulichnites-like trace fossil. Three Lick Bed, New Albany Shale, Madison County, Kentucky. x1.
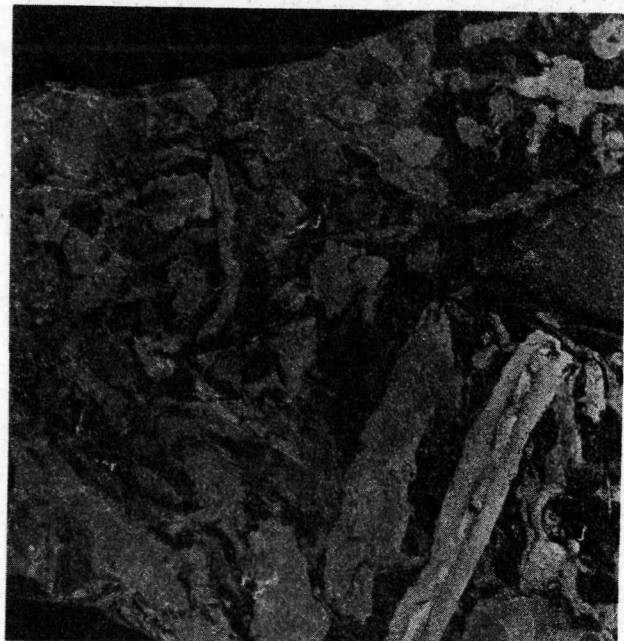
PLATE X

A

B

PLATE XI

A. "Cladodont" shark tooth. Black shale, eastern Kentucky. x10.

B. Fish scale. Black shale, eastern Kentucky. x20.

C. Fish tooth. Black shale, eastern Kentucky. x10.

D. Actinopterygian jaw. New Albany Shale, Madison County, Kentucky. x5.5.

E. Unidentified headless fish. The head may have been bitten off. New Albany Shale, Madison County, Kentucky. x1.5.
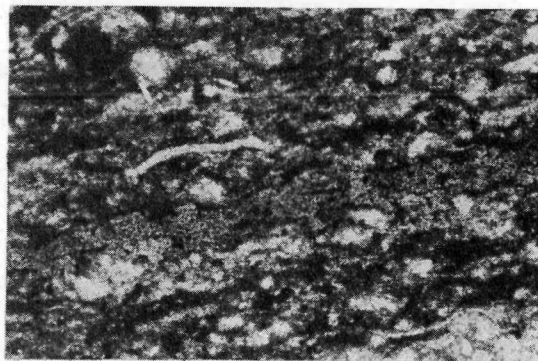
PLATE XI
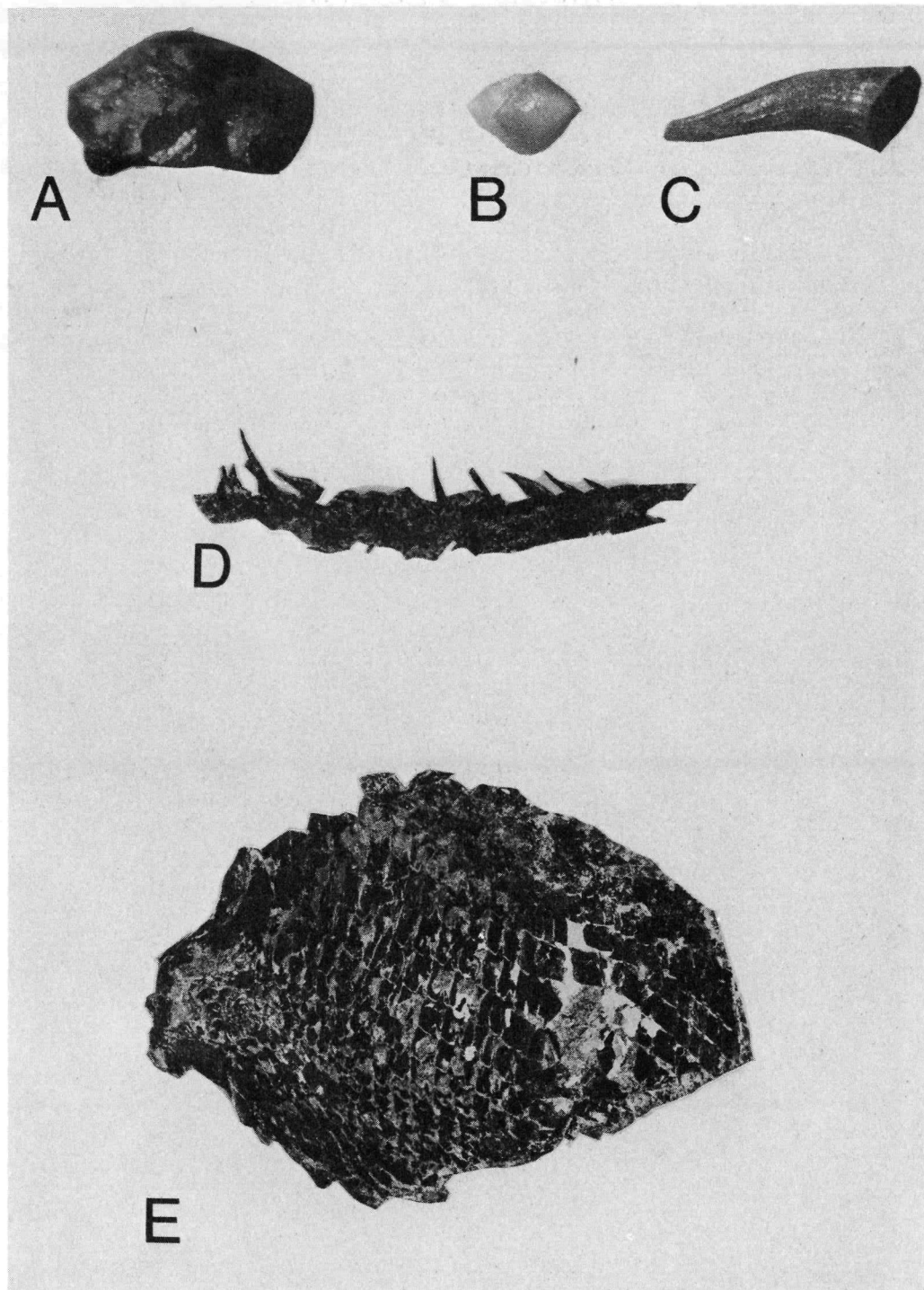
PLATE XII

A. **Tasmanites** sp. Ohio Shale, Rowan County, Kentucky. x150.

B. **Tasmanites** sp. Plane polarized light. Ohio Shale, eastern **Kentucky.** x500.

C. **Foerstia** or **Protosalvinia.** Ohio Shale, Vanceburg, Lewis **County,** Kentucky. x6.

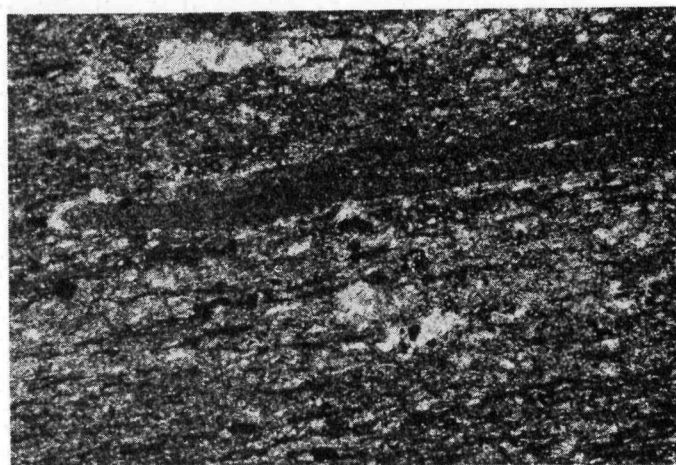D. **Foerstia** or **Protosalvinia.** Plane polarized light. Ohio Shale, **eastern** Kentucky. x500.

PLATE XII
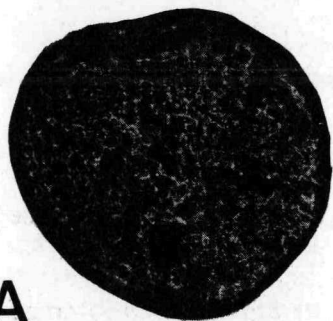
PLATE XIII

A., B. Lepidostrobus sp. New Albany Shale, Madison County, Kentucky. x1.

C. Woody stem preserved in a phosphate nodule from the Falling Run Nodule Zone, New Albany Shlae. x1. From University of Cincinnati, Geology Department Collections.
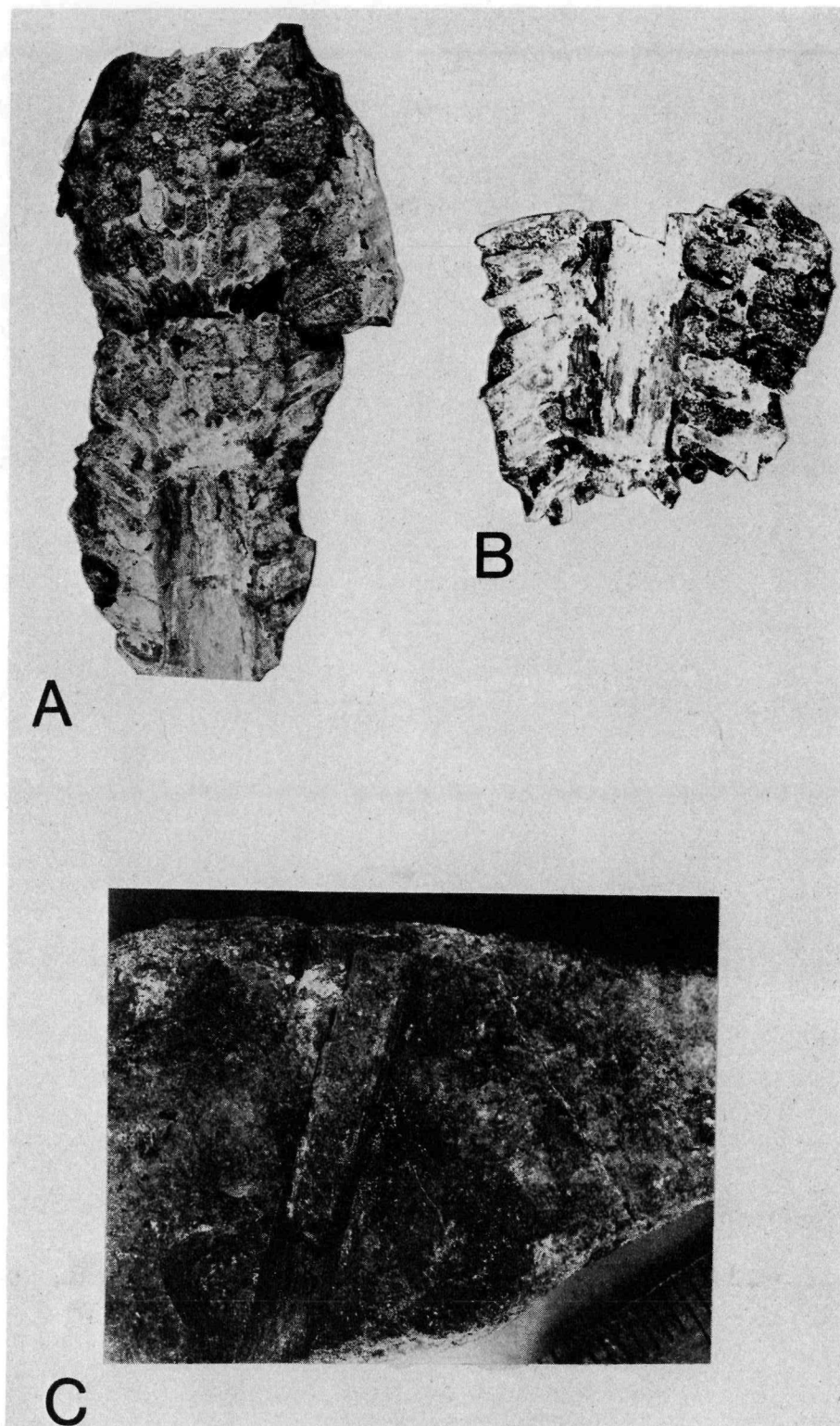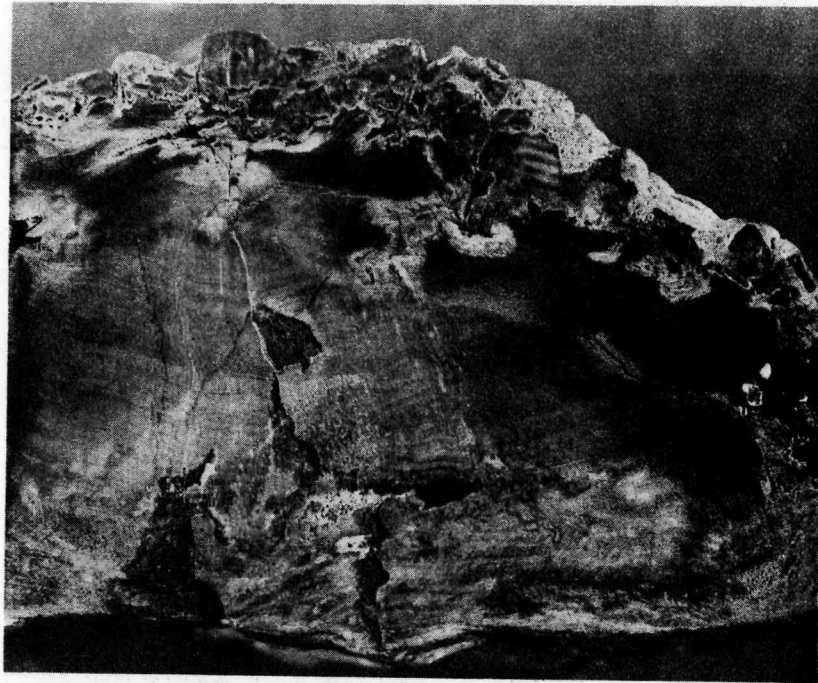
PLATE XIII

PLATE XIV

A. <u>Callixylon</u> wood with associated crinoid columnals. New Al-
bany Shale, Lexington, Indiana. x1. (From University of
Cincinnati, Geology Department Collections).

B. Carbonized films of plant? stems. Chattanooga Shale, Clinch
Mountain, Tennessee. x2.

PLATE XIV

A

B