

Carboniferous echinoderm zonation in the Appalachian Basin, eastern USA

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Abstract

The Carboniferous was a period of major echinoderm evolution, especially during Mississippian (Early Carboniferous) time when crinoids, blastoids, and echinoids increased dramatically in abundance and diversity. The high degree of structural organization and distinctive morphologies of echinoderms make them ideal zonal indicators, and for parts of the Appalachian Basin Mississippian section, they provide greater biostratigraphic resolution than do conodonts or foraminifera. The occurrence of various echinoderm groups in time and space, however, is clearly related to the tectonic and sedimentologic differentiation of the Appalachian Basin through time. By Early Mississippian time on the Laurussian continent, most echinoderms had already made the shift to clastic-rich environments, which predominated in the basin until Middle Mississippian time. Although present, well-preserved Kinderhookian, Osagean, and Meramecian echinoderms are rare in the Appalachian Basin, and most are endemic forms with little diagnostic value. Echinoderms did, however, become especially abundant in the succeeding, late Middle and early Late Mississippian (Late Meramecian–Middle Chesterian), carbonate-rich seas, and it is for this time interval that biostratigraphic resolution, based especially on crinoids and blastoids, is best. By latest Mississippian (Late Chesterian) time, an influx of marginal-marine and terrestrial clastics flooded the Appalachian Basin and continued through Pennsylvanian time. Rare echinoderms are present in these Upper Chesterian and Pennsylvanian rocks and are sufficiently diagnostic to distinguish Mississippian and Pennsylvanian systems; however, the forms are too long ranging to provide smaller scale zonation. Based on a detailed literature search, a chart showing the ranges of diagnostic and relatively common echinoderms throughout the Appalachian Basin is presented.

Keywords: Carboniferous, echinoderm, biostratigraphy, Appalachian Basin, eastern United States.

Introduction and background

The Appalachian Basin is an area of complex sedimentologic, stratigraphic and faunal relationships that reflect its formation as a composite foreland basin during several, Paleozoic, craton-margin orogenies in varying paleogeographic and paleoclimatic settings, and it is in this context that Appalachian, Carboniferous echinoderm faunas must be considered. The Early Carboniferous or Mississippian form of the basin was largely related to the Acadian orogeny,

the last tectophase of which began at the Devonian–Mississippian transition (Etensohn et al., 2002), whereas the Late Carboniferous or Pennsylvanian form of the basin largely reflects subsidence accompanying the Pennsylvanian–Permian Alleghanian orogeny. As for paleogeography and paleoclimate, during Early and Middle Mississippian (Tournaisian–Visean) time, the basin was present on the eastern margin of Laurussia in the warm, subtropical, trade-wind belt at 5–10° south latitude (Scotese, 1998), where echinoderms and other organisms flourished.

By latest Mississippian (Serpukhovian) time, however, the Appalachian basin had moved into the humid, tropical, equatorial zone, and clastic sediments associated with Acadian relaxation and Alleghanian compression flooded the basin; hence, marine organisms of all sorts became comparatively uncommon. By latest Early Pennsylvanian (Late Bashkirian) time, moreover, convergence between Gondwana and Laurussia had generated the Pangean supercontinent, and the basin became isolated (e.g., Ziegler, 1989) with only sporadic access to open-marine waters from the south or west during glacio-eustatic highstands. During much of Mississippian time in the basin, the major response to Gondwanan glaciation was a subtle fourth-order cyclicity in the predominantly shallow-water carbonates (e.g., Al-Tawil & Read, 2003), but during Pennsylvanian time, when marginal-marine and terrestrial environments predominated, the highstand parts of these cycles generated thin, but widespread, marine zones (Chesnut, 1994) in which nearly all marine life was concentrated. The effects of such tectonism and cyclicity, however, were not limited to the Appalachian Basin, for the Carboniferous was a time of global tectonism related to the ongoing formation of Pangea.

Even though the Carboniferous Period was tectonically active, or perhaps because of it, many echinoderm groups experienced a major expansion in diversity and abundance, while some previously important groups like the corals and trilobites underwent major decline. In fact, no period in earth history compares to Mississippian time for diversity and abundance of echinoderm remains. The echinoderm classes Crinoidea and Blastoidea attained their peak abundances during this time, and echinoids became locally abundant for the first time in the Appalachian Basin. Crinoid remains, in particular, are so abundant in many limestones of the period, that the Mississippian has been called the "Age of Crinoids," and regional encrinites are so extensive, especially during Early and Middle Mississippian time, that entire shelf areas must have been dominated by crinoids (Ausich, 1997).

Despite the diversity of form exhibited by various echinoderm classes, echinoderms are among the best characterized and most easily recognized of the invertebrate phyla. They are also relatively abundant and exhibit a high degree of structural organization and distinctive morphological features that make them potentially diagnostic zonal fossils (Moore, 1948). Although the restricted ranges of some U.S. echinoderm species were noted very early by Lyon (1857) and Lyon & Casseday (1860), the first formal use of echinoderms for zonation of Carboniferous rocks in

North America was by Stuart Weller (1926), who used crinoids and blastoids as the basis for five of his 14 Mississippian zones. The zones, however, were largely restricted to the type Mississippian section of the Illinois or Eastern Interior Basin and became the basis for even more detailed zonation in Osagean (Upper Tournaisian–Lower Visean) parts of the section using camerate crinoids (e.g., Laudon, 1931, 1933, 1948, 1973). Other echinoderm-based zones were added by Weller et al. (1948), and some of the more prominent zones were carried into the Appalachian Basin (e.g., Cooper, 1948). Even at present, however, use of these zones in the Appalachian Basin has not been well corroborated with biostratigraphy based on other groups of organisms.

The Carboniferous section in the Appalachian Basin is lithologically diverse and variable, but the rocks can generally be divided into a three-part lithologic succession, including Lower and Middle Mississippian (Tournaisian–Lower Visean) clastics, Middle to Upper Mississippian (Upper Visean) carbonates, and Upper Mississippian through Pennsylvanian (Upper Visean–Gzelian) clastics (Ettensohn et al., 2002). Although echinoderms have been reported from nearly every part of the Appalachian section, they are clearly most abundant and diverse in Middle and Upper Mississippian carbonates, and they decline markedly in both abundance and diversity in uppermost Mississippian and Pennsylvanian parts of the section. Part of this pattern of diversity and abundance may be related to the widespread distribution of shallow, open-marine, carbonate environments that apparently accompanied bulge uplift and moveout during Middle to Late Mississippian phases of Acadian and Ouachita orogeny (Ettensohn, 1993, 1994; Ettensohn and Pashin, 1993), but factors such as predation, siliciclastic tolerance and current-energy preference were also important (Kammer & Ausich, 1987; Waters & Maples, 1991).

The role of depositional facies is of particular significance in the evolution of echinoderms. Early Mississippian echinoderms were especially well adapted to carbonate environments, as epitomized by the diverse and abundant crinoid and blastoid faunas of the Hampton, Gilmore City, Burlington, and Keokuk limestones of the Illinois Basin (Bassler & Moodey, 1943). However, during Early Mississippian time, undoubtedly as a response to environmental changes, echinoderm faunas evolved diverse and abundant communities in siliciclastic facies, such as the late Osagean faunas of the Borden Group at Crawfordsville, Indiana (Van Sant & Lane, 1964; Lane, 1973). The Appalachian Basin faunas are significant because they record the earliest known Mississippian faunas to

make this shift from carbonates to clastics, including those in the Cuyahoga Formation of northeastern and southern Ohio (Hall & Whitfield, 1875; Miller, 1919; Roeser, 1986) and in the Nada Member of the Borden Formation of northeastern Kentucky (Lane & DuBar, 1983; Li, 2000).

Despite the facts that echinoderms evolved very rapidly during Mississippian time and that they may commonly provide higher biostratigraphic resolution than conodonts or foraminifera in parts of the Appalachian section (Ausich et al., 1994), their utility has seldom been exploited. This is probably because species are usually not geographically widespread; thus echinoderm biostratigraphies tend to be regional. Also, preservation of complete echinoderms is rare. Complete or nearly complete echinoderms are typically required for species-level identification, and complete preservation requires special conditions. Echinoderms are composed of multiplated mesodermal skeletons, which are bound together during life by ligaments, muscles, or calcite cementation. Very quickly after death, the connective tissues decay, and unless rapid burial occurs, the echinoderm will disarticulate into its numerous plates (Lewis, 1980; Donovan, 1991; Ausich, 2001).

Although there has been substantial recent work on Carboniferous echinoderms in the Appalachian Basin and nearby areas, there has been little work on their use as diagnostic, zonal indicators. Hence, this report is essentially a survey based on earlier faunal studies, and we have noted as diagnostic below and in Fig. 1 only those forms that are clearly identified and appear to be relatively common across large parts of the basin. We consider faunas extending as far west as the Cumberland Saddle of Kentucky and Tennessee to be within the Appalachian Basin.

Mississippian succession

Kinderhookian

Kinderhookian (Lower and Middle Tournaisian) rocks in the Appalachian Basin consist largely of basinal, black or dark gray shales, commonly included in the Sunbury or Chattanooga shales and deposited in deeper, anoxic to dysoxic conditions during the major basin subsidence that accompanied the final tectophase of the Acadian Orogeny (Ettensohn, 1985, 2001; Ettensohn et al., 1988, 2002). Locally in central parts of the basin, these conditions persisted into Osagean time, but wherever they occurred, faunas of any sort are extremely rare. On the eastern margins of the basin, these dark shales intertongue with coarser,

marginal-marine clastics in which faunas are relatively uncommon.

Kinderhookian–Osagean transition

During Late Kinderhookian–Early Osagean time (Middle to Late Tournaisian), sedimentary facies in the Appalachian Basin were dominated by westwardly prograding, post-Acadian, siliciclastic wedges that extended into the Illinois Basin. The most prominent and extensive of these wedges was the Borden deltaic complex, which prograded from the east and northeast and includes shales, mudstones, siltstones and sandstones deposited in basinal, prodelta, and delta-front environments represented by the Borden Formation of eastern Kentucky, the Logan and Cuyahoga formations of Ohio, the Price-Pocono formations of West Virginia, Virginia, Maryland, and Pennsylvania, and the Grainger Formation of eastern Tennessee and southeastern Kentucky (e.g., Peterson & Kepferle, 1970; Kepferle, 1977; Bjerstedt & Kammer, 1988; Matchen & Kammer, 1994; Ettensohn, 2001, 2004; Ettensohn et al., 2002). Although clastic deposition continued until nearly the end of Osagean time on northern and eastern parts of this complex, by Middle Osagean time in western and southern parts of the basin, decreased clastic influx and delta abandonment permitted the establishment of carbonate and mixed carbonate-clastic facies on the old abandoned delta front.

Although echinoderm faunas of Kinderhookian to Osagean age are rare in the Appalachian Basin, a few faunas are known. The oldest Mississippian echinoderm fauna in the Appalachian Basin is from the Cuyahoga Formation, first comprehensively described by Hall & Whitfield (1875) and more recently revised by Roeser (1986). The age of the Cuyahoga Formation has been equivocal for many years, but it is now generally regarded that the Kinderhookian–Osagean boundary is present within this formation (Sandberg et al., 2002). Thus, the Cuyahoga crinoid fauna is considered to be of Kinderhookian–Early Osagean age here. This fauna is recorded to contain nearly 25 species with more than 67 percent of the specimens recovered by Roeser (1986) belonging to five species: *Aorocrinus helice*, *Cusacrinus helice*, *Cusacrinus daphne*, *Forbesiocrinus communis*, and *Amphoracrinus viminalis*; other prominent species were noted by Bassler & Moodey (1943) and Ausich (1996). Miller (1919) has also noted as diagnostic *Platycrinites sculptus* in rocks of a similar age from southern Ohio and northeastern Kentucky. Unfortunately, the above are all endemic species, so the crinoids offer little biostratigraphic insight for the Cuyahoga Formation, other than being

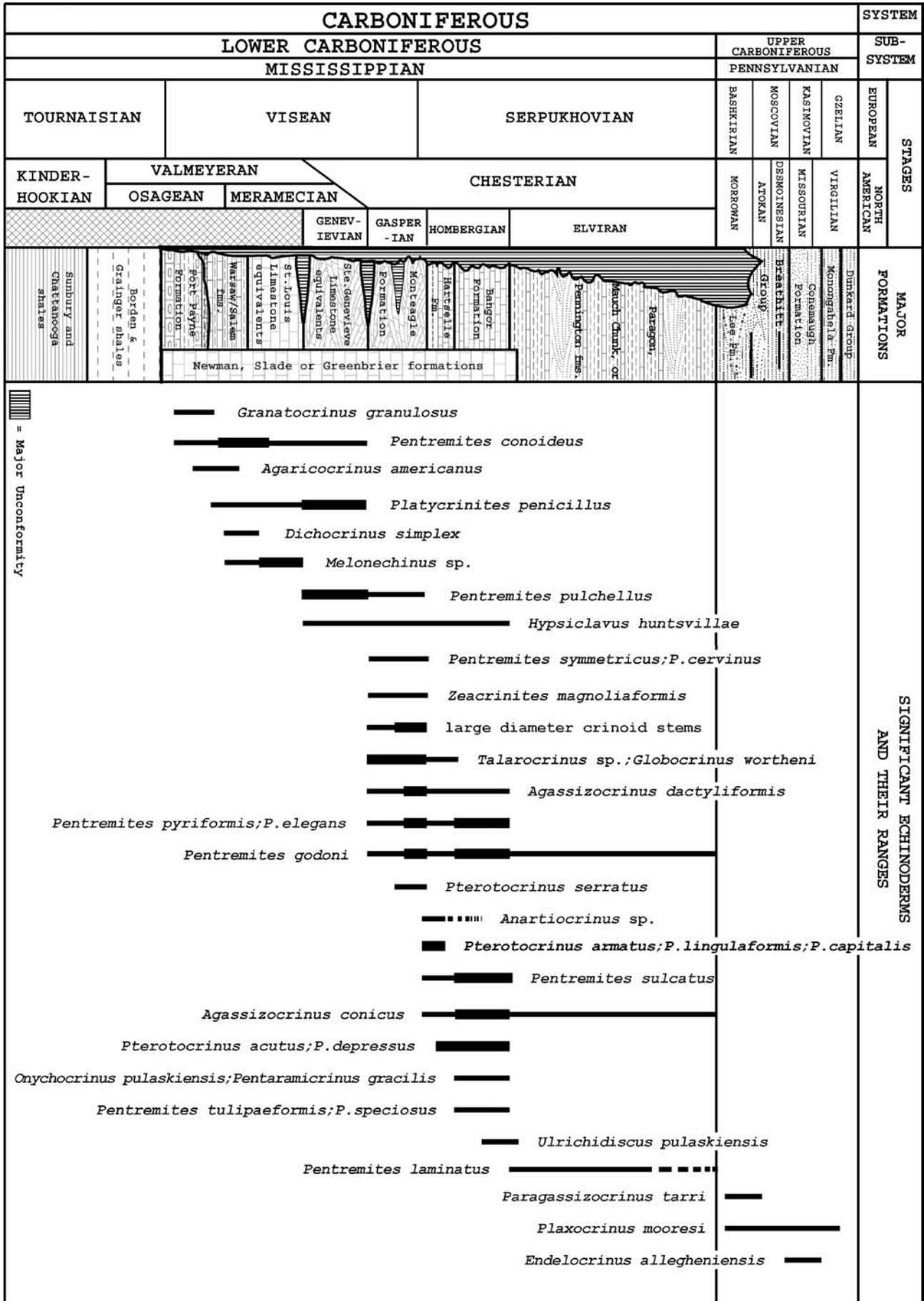


Fig. 1. Stratigraphic distribution of diagnostic, Carboniferous echinoderms in the Appalachian Basin.

consistent with a late Kinderhookian to Early Osagean age.

Other echinoderms from the Cuyahoga Formation include the ophiuroid *Strataster ohioensis*, reported by Kesling & LeVasseur (1971), and two poorly preserved blastoids reported by Ausich & Guenther (1996). Other rare crinoids and edrioasteroids of this age are reported from marine intervals in the Pocono Formation of Pennsylvania and equivalents in New York (Bassler & Moodey, 1943) and from the Price Formation of Virginia (Butts, 1940).

Middle through Late Osagean

By Middle to Late Osagean (Late Tournaisian–Early Visean) time, Borden clastic sedimentation declined substantially in southern and western parts of the basin, and the clastics that did arrive reflect new source areas to the southeast. This was a period of delta destruction and abandonment (Ettensohn et al., 2002), and although echinoderms are relatively uncommon in the resulting facies, notable exceptions are the Nada Member of the Borden Formation from eastern Kentucky and the Ft. Payne Formation of the Cumberland Saddle area in south-central Kentucky and adjacent parts of Tennessee.

The Nada Member is the uppermost member of the Borden Formation and is a mixed carbonate-clastic facies that has been interpreted to represent delta destruction (Ettensohn, 1981a; Ettensohn et al., 2003). The fauna in the unit has been studied by Lane & DuBar (1983) and Li (2000). Age determination for the Borden Formation in northeastern Kentucky has also been problematic, with various ages indicated by different fossil groups in various members of this unit. The crinoids in the Nada Member are characteristic Osagean crinoids, and more specifically, this fauna contains eight species that are known only from the Nada Member and the upper part of the Burlington Limestone in Illinois, Iowa, and Missouri (Li, 2000). These diagnostic, Middle Osagean species include the camerates, *Dorycrinus quinquelobus*, *Gilbertsocrinus tuberosus*, *Macrocrinus konincki*, *Platycrinites glyptus*, *Platycrinites tenuibrachiatus*, and *Rhodocrinites barri*, and the disparids, *Halysiocrinus dactylus* and *Synbathocrinus wortheni*. The most common Nada crinoid species is *Uperocrinus pyriformis*. This species is not confined to the Middle Osagean, but it is characteristic of the fauna of the upper part of the Burlington Limestone. The only other echinoderm recovered from the Nada Member is the blastoid *Granatocrinus* sp., which offers no age-diagnostic information.

After Middle to Late Osagean delta abandonment, deeper water cherty carbonates and carbonate-rich

clastics of the Ft. Payne Formation infilled the basin forward of the abandoned delta front, so that the Ft. Payne Formation predominates in this interval throughout southern and southwestern parts of the Appalachian Basin (Ettensohn et al., 2002). Carbonate buildups and mud mounds are locally common in the Ft. Payne (e.g., Ausich & Meyer, 1990; Meyer et al., 1995), and some of the echinoderm species noted below comprise important parts of the mud-mound faunas.

Late Osagean crinoid faunas are well represented in the Fort Payne Formation of Tennessee, Kentucky, and Alabama. Several Fort Payne facies are dominated by crinoidal remains, and crinoid calyxes and blastoid thecae may be well preserved and relatively abundant. Crinoid faunas were initially reported in the Fort Payne from Tennessee in 1849 by Gerard Troost, and they were recognized then as being Late Osagean (correlative with the Keokuk Limestone of the Mississippi River Valley section) in age (e.g., Bassler, 1926). Modern systematic study of Fort Payne echinoderms is underway, and it verifies the Late Osagean age assignment for Fort Payne crinoids in south-central Kentucky. Fort Payne crinoids that are restricted to other Late Osagean faunas include the camerate genus *Alloprosallocrinus* and the following species: camerates – *Abatocrinus grandis*, *Abatocrinus stereopes*, *Agaricocrinus crassus*, *Dorycrinus gouldi*, *Alloprosallocrinus conicus*, *Eretmocrinus magnificus*, *Gilbertsocrinus tuberosus*, *Uperocrinus nashvillae*, and *Uperocrinus robustus*; cyathocrinine cladids – *Cyathocrinites asperrimus*, *Cyathocrinites glenni*, and *Barycrinus stellatus*; disparids – *Catillocrinus tennesseae*; and flexibles – *Gaulocrinus bordeni*, *Metichthyocrinus tiaraeformis*, *Nipterocrinus monroensis*, *Taxocrinus colletti*; and *Wachsmuthicrinus spinosulus* (Ausich & Meyer, 1992, 1994; Ausich et al., 1994, 1997; Meyer & Ausich, 1997; Meyer et al., 1989). Although *Agaricocrinus americanus* does occur in both Middle and Upper Osagean strata in the Mississippi River Valley (Meyer & Ausich, 1997), it is common and characteristic of Upper Osagean strata in the Appalachian Basin and Midcontinent (Fig. 1).

Ausich & Meyer (1988) reported a diverse but largely endemic blastoid fauna in the Fort Payne Formation of south-central Kentucky, which is therefore of little use for regional biostratigraphy. The one more widely distributed taxon, however, is *Granatocrinus granulatus*, which is also known from the late Osagean New Providence Shale Member of the Borden Formation in north-central Kentucky (Fig. 1). Moreover, blastoids from the Ft. Payne of Georgia, described as *Pentremites cavus* by Allen & Lester (1954), are actually among the earliest forms of the diagnostic species *P. conoideus* (see Galloway & Kaska, 1957) (Fig. 1).

Echinoderm faunas do occur in the Fort Payne Formation elsewhere in the Appalachian Basin (e.g., Butts, 1922, 1926; Allen & Lester, 1954), but these faunas have yet to be studied in detail.

Overall, well-preserved Kinderhookian and Osagean echinoderm faunas are very rare in the Appalachian Basin. However, in some cases, the occurrence of echinoderms, through comparison with the ranges of crinoids in the Mississippi River Valley section (Laudon, 1973), can aid in constraining the age of Appalachian Basin strata. Within the eastern United States, there are a number of crinoid genera, especially camerate crinoids that are either typical of or restricted to Osagean time. Within these genera, species have even shorter durations and can commonly be biostratigraphically useful. Crinoids such as the following camerates, *Aorocrinus*, *Abatocrinus*, *Actinocrinites*, *Alloprosallocrinus*, *Agaricocrinus*, *Azygocrinus*, *Dizgocrinus*, *Dorycrinus*, *Eretmocrinus*, *Eutrochocrinus*, *Macrocrinus*, and *Uperocrinus* are characteristic of the Osagean. Of these, *Azygocrinus* occurred only during Middle Osagean time, and *Alloprosallocrinus* occurred only during Late Osagean time (Fig. 1).

Meramecian

By Meramecian (Middle Viséan) time, the Appalachian Basin had been filled with post-Acadian, deltaic clastics or deeper water, Ft. Payne carbonates and clastics, and a transition to shallow-water, carbonate deposition was ongoing (Ettensohn, 2001, 2004; Ettensohn et al., 2002, 2003). The Meramecian was characterized by a widespread, eastward transgression that produced a gradual onlap of carbonates over Kinderhookian–Osagean clastics. The widespread nature of these carbonates, paralleling the southern flank of the continent in eastern and east-central United States, suggests that shallow-water carbonate deposition may have been related to regional uplift accompanying early Ouachita bulge moveout (Ettensohn, 1993, 1994). In many places there is a substantial unconformity between Osagean and Meramecian rocks (deWitt & McGrew, 1979; Ettensohn et al., 2002), reflecting likely tectonic and eustatic causes (Ettensohn & Pashin, 1993). Because of the unconformity in the Appalachian Basin, Meramecian rocks record less time and are less extensive than their counterparts in the Illinois Basin. As a result, Meramecian echinoderm faunas are relatively rare in the Appalachian Basin.

One of the most remarkable changes in echinoderm faunas at the Osagean–Meramecian boundary is the disappearance of camerate crinoids with large, many-plated calyxes (Laudon, 1948) and their subse-

quent replacement by cladids and smaller, more simply plated camerate crinoids that were cladid homeomorphs (Waters et al., 1993). In the Lower Meramecian Warsaw–Salem interval, one of these cladid homeomorphs, *Dichocrinus simplex*, is the only diagnostic crinoid (Butts, 1922, 1926; Weller, 1931; Bassler & Moodey, 1943) (Fig. 1). In the older literature, *D. simplex* was commonly identified as *Talarocrinus simplex*, but in work by Burdick & Strimple (1982), the species was referred back to the genus *Dichocrinus*. Other diagnostic indicators of the Warsaw–Salem interval include the blastoids, *Metablastus wortheni*, *Tricoelocrinus* and *Pentremites conoideus* (Butts, 1922, 1926; Weller, 1931; Bassler & Moodey, 1943; Kammer et al., 1990) (Fig. 1). *Pentremites conoideus*, in particular, attained its peak abundance in the Warsaw–Salem interval. Although more diagnostic of the St. Louis, the echinoid *Melonechinus*, also known by the junior synonym *Melonites* in the older literature, first appeared in the Appalachian Basin during the Warsaw–Salem interval (Butts, 1926) (Fig. 1).

Another diagnostic crinoid that first makes its appearance in the Warsaw–Salem interval of the Appalachian Basin is *Platycrinites penicillus* (Dever & Moody, 1979; Dever, 1999), also known by the junior synonyms, *P. huntsvillae* or *Platycrinus penicillus*. Although the occurrence of this crinoid is the basis for the *P. penicillus* Zone of Weller (1926) and is commonly thought to be diagnostic only of the Ste. Genevieve and its equivalents (e.g., Moore, 1948; Swan, 1963), the range of this crinoid extends back to the Warsaw–Salem, St. Louis and their equivalents (Weller, 1926; Weller et al., 1948) (Fig. 1). In the Appalachian Basin, the first occurrence of *P. penicillus* is normally reported from upper St. Louis equivalents (e.g., Butts, 1927; Allen & Lester, 1954), but in south-central Kentucky, its first appearance is even earlier (Dever & Moody, 1979; Dever, 1999).

In Upper Meramecian St. Louis equivalents (e.g., Hillsdale and Tucumbia formations), the echinoid *Melonechinus* attains its peak abundance (Fig. 1), and spines of the long-ranging echinoid genus *Archaeocidaris* also become especially abundant in lower parts of the unit (e.g., Butts, 1922, 1927; Dever, 1980).

Chesterian

The Ste. Genevieve and its equivalents (e.g., Denmark and Lower Monteagle formations), long considered to be latest Meramecian in age, are now commonly regarded as earliest Chesterian (Genevievian) in age (Maples & Waters, 1987). This part of the Chester Stage (Upper Viséan–Serpukhovian) generally reflects very shallow-water, commonly oolitic en-

vironments that represent the culmination of Meramecian uplift and shallowing across the southern flank of the continent. Although Genevievian rocks may locally contain several endemic crinoid species (e.g., Butts, 1922; Bassler & Moodey, 1943; Burdick & Strimple, 1982), because of its abundance and widespread distribution, *P. penicillus* is clearly the most diagnostic crinoid species throughout the entire basin during Genevievian time (Butts, 1922, 1926, 1927, 1940, 1948; Reger, 1926; Weller, 1931; Cooper, 1944, 1948; Allen & Lester, 1954; McFarlan & Walker, 1956; Drahovzal, 1967; Englund, 1979; Rice et al., 1979; Thomas, 1979; Ettensohn, 1980a, 1981c; Burdick & Strimple, 1982; Ettensohn et al., 1984; Sable & Dever, 1990; Dever et al., 1990; Dever, 1980, 1999). In addition, the blastoid *Pentremites pulchellus*, which is synonymous with *P. princetonensis*, *P. tuscumbiae*, *P. pediculatus*, and *P. arctibrachiatus* (Horowitz et al., 1981), was thought to occur only in Genevievian rocks in the Appalachian Basin (Butts, 1922, 1926, 1940; Cooper, 1944; Allen & Lester, 1954; Englund, 1979; Burdick & Strimple, 1982), but in Alabama the species also apparently ranges into rocks of Gasperian age (Bassler & Moodey, 1943) (Fig. 1). Moreover, the highest occurrence of *Pentremites conoideus* is in the Genevievian rocks of Alabama (Bassler & Moodey, 1943) (Fig. 1).

Post-Genevievian, Lower Chesterian or Gasperian rocks in the Appalachian Basin are largely high-energy, oolitic and bioclastic calcarenites, which may be difficult to distinguish lithologically from underlying Genevievian rocks. In the older literature these rocks are commonly designated as the "Gasper Formation," and in places an unconformity or paleosol horizon may separate Genevievian and Gasperian rocks (e.g., Ettensohn, 1981c; Ettensohn et al., 1984; Dever, 1999) (Fig. 1). However, the boundary is usually subtle and is more easily identified by changes in echinoderm fauna than in lithology. Most importantly, *P. penicillus* leaves the section at the substage boundary and is replaced by various species of *Talarocrinus*, which are reported only from post-Genevievian, Gasperian rocks across the eastern and central United States. Although *Talarocrinus* is supposedly restricted to Gasperian rocks, the genus has been reported from shaly carbonates just below the Fido Sandstone in Virginia (Butts, 1927), an undescribed species is known from rocks of similar age in northeastern Kentucky, and Burdick & Strimple (1982) indicated that in Alabama *Talarocrinus* occurs just below the *Agassizocrinus conicus* Zone, which begins in mid-Hombergian Glen Dean equivalents. These three occurrences indicate that in the Appalachian Basin, *Talarocrinus* also occurs in post-Gasperian, Golconda-equivalent,

Lower Hombergian rocks (see Swann, 1963) (Fig. 1). *Globocrinus wortheni* apparently has the same range as *Talarocrinus* in the Appalachian Basin (Butts, 1927, 1940; Horowitz & Strimple, 1974). However, an unidentified "large crinoid stem" up to 3 cm in diameter and *Zeacrinites magnoliaformis* are wholly Gasperian in age (Fig. 1). The "large crinoid zone" has its peak occurrence in uppermost Gasperian units (Reelsville-Beech Creek, Tygarts Creek, Union members), but it is also present locally in lower parts of the Gasper (McFarlan et al., 1955; McFarlan & Walker, 1956; Dever, 1980; Ettensohn, 1980a, 1981c; Burdick & Strimple, 1982) (Fig. 1).

The *P. penicillus*-*Talarocrinus* change is the basis for two major Mississippian zones (Weller, 1926; Moore, 1948; Weller et al., 1948; McFarlan & Walker, 1956; Swan, 1963; Burdick & Strimple, 1982), and the fact that both forms occur in similar lithologies indicates that the boundary is not facies controlled, but instead, approaches a true temporal plane (Swan, 1963). This change coincides with a time of major reorganization of echinoderm communities as more large, endemic camerates dropped out, cladids became dominant, cladid-homeomorph camerates like *Talarocrinus*, *Pterotocrinus*, *Dichocrinus*, *Hyrtanecrinus*, *Strimplecrinus*, and *Camptocrinus* became more prevalent, and the blastoid *Pentremites* became extremely abundant (Waters & Maples, 1991; Waters et al., 1993).

Agassizocrinus and *Pterotocrinus* are two other crinoids that are wholly indicative of the Chesterian, and both first appear in Gasperian rocks (e.g., Sutton, 1934; Horowitz & Strimple, 1974). *Agassizocrinus* is a unique stemless cladid crinoid that was common in high-energy, Chesterian environments, but its fused infrabasal cones were easily transported and preserved in many different environments, making them useful biostratigraphic indicators (Ettensohn, 1975). However, the conical infrabasals were apparently subject to great phenotypic variation (Ettensohn, 1981b), and the genus is probably oversplit based on these variations. Despite the many named species, the low-coned *A. dactyliformis*, which is probably synonymous with *A. laevis* and *A. lobatus* (see Ettensohn, 1975; Chesnut & Ettensohn, 1988) is the most diagnostic form in Lower and Middle Chesterian rocks. Although it is apparently common in all Gasperian rocks in the Illinois Basin (McFarlan et al., 1955), in the Appalachian Basin *A. dactyliformis* is relatively rare in Lower Gasperian rocks, reaches its peak occurrence in uppermost Gasperian rocks (Reelsville-Beech Creek, Tygarts Creek, Union members) and lowermost Hombergian Golconda equivalents, and is common through Late Hombergian Glen Dean equivalents (Bangor, Poppin Rock and Lower Bluefield)

(Fig. 1) (Butts, 1922, 1926; Weller, 1931; McFarlan & Walker, 1956; Burdick & Strimple, 1982; Dever, 1980; Chesnut & Etensohn, 1988) (Fig. 1). On the other hand, the high-coned *A. conicus* is the basis for the *A. conicus* Zone of Burdick & Strimple (1982), which ranges from the mid-Hombergian Hartselle, through the Bangor and its equivalents, and probably through the rest of the Chesterian Series (Paragon and Pennington formations) (Fig. 1).

Pterotocrinus is an unusual camerate crinoid that had five, elongated, tegminal, "wing plates" extending outward from the crown at the level of the arms (see Sutton, 1934; Chesnut & Etensohn, 1988); it was the basis for two Upper Mississippian zones (Weller, 1926; Moore, 1948; Weller et al., 1948). Crowns and calyxes are rarely preserved, but the resistant, single-piece wing plates were commonly preserved and easily transported. The shape of these plates is commonly the basis for species designation (Sutton, 1934). However, like *Agassizocrinus* infrabasal cones, *Pterotocrinus* wing plates were also apparently subject to great phenotypic variation, and as a result the genus is probably oversplit. Although Chesnut & Etensohn (1988) synonymized several Hombergian species based on comparison of complete crowns and calyxes, some of the "form species" may still be useful for detailed, local biostratigraphy.

In the Appalachian Basin, *Pterotocrinus* first appears as *P. serratus* in the Upper Gasperian rocks of Virginia, West Virginia and Alabama (Butts, 1940; Reger, 1926; Cooper, 1944; Englund, 1979; Burdick & Strimple, 1982) (Fig. 1), but they are apparently uncommon. In lower Hombergian, Golconda equivalents at various places in the basin, *P. armatus*, *P. linguaformis*, and *P. capitalis* are diagnostic (Butts, 1926, 1948; Drahovzal, 1967; Etensohn, 1975, 1980a; Burdick & Strimple, 1982), whereas in Upper Hombergian Glen Dean equivalents, *P. acutus* (= *P. bifurcatus* and *P. spatulatus*) and *P. depressus* (= *P. wetherbyi*, *P. menardensis*, *P. clorensis*, *P. cuneatus*, and *P. vannus*) are characteristic (Butts, 1922, 1927, 1940; Cooper, 1944; Drahovzal, 1967; Etensohn, 1975, 1980a; Englund, 1979; Burdick & Strimple, 1982; Chesnut & Etensohn, 1988) (Fig. 1). However, the range of *P. depressus* probably also extends throughout overlying parts of the Chester Series (Fig. 1).

Several other crinoid species could be cited as indicative of the Chester Series (see Horowitz & Strimple, 1974; Burdick & Strimple, 1982; Chesnut & Etensohn, 1988), but most seem to be locally endemic and not particularly useful across large parts of the Appalachian Basin. A few less common forms with more widespread distribution include *Anartiocrinus*, a Hombergian genus (Morse, 1911; Burdick & Strim-

ple, 1982; Chesnut & Etensohn, 1988), as well as *Onychocrinus pulaskiensis* and *Pentaramicrinus gracilis*, which are restricted to Upper Hombergian Glen Dean equivalents (Horowitz & Strimple, 1974; Burdick & Strimple, 1982; Chesnut & Etensohn, 1988) (Fig. 1).

The blastoid genus *Pentremites* became especially abundant and diverged into several species by Gasperian time (e.g., Galloway & Kaska, 1957), but apparent diversity has also been artificially increased by oversplitting based on minor characters (Horowitz et al., 1981; Chesnut & Etensohn, 1988). Using current literature and synonymies, ten reported species appear to have diagnostic value in the Chester Series of the Appalachian Basin (Fig. 1). *P. godoni* (= *P. biconvexus*, *P. florealis*, and *P. planus*) apparently ranges through the entire post-Genevian Chester in the basin, whereas *P. symmetricus* (= *P. welleri*, *P. altus*, *P. abruptus*, *P. decipiens*, and *P. buttsi*) and *P. cervinus* are Gasperian species. On the other hand, *P. pyriformis* (= *P. patei*, *P. arctibrachiatus huntsvillensis*, *P. pyramidalis*, *P. lyoni*, and *P. girtyi*) and *P. elegans* (= *P. canalis*) range through the Gasperian and Hombergian. *P. sulcatus* (= *P. cherokeeus*, *P. angularis*, *P. macalliei*, *P. serratus*, and *P. spicatus*) is a wholly Hombergian form but only ranges through Hartselle and Bangor equivalents, whereas *P. tulipaeformis* (= *P. brevis*), *P. robustus* (= *P. johsi*, *P. chesterensis*, *P. hambachi*, and *P. hemisphericus*), and *P. speciosus* (= *P. clavatus* and *P. okawensis*) are restricted to Upper Hombergian, Bangor-Glen Dean equivalents (Fig. 1). *P. laminatus* has been reported only from Elviran parts of the Pennington Formation in Alabama (Drahovzal, 1967) (Fig. 1).

Edrioasteroids are also known from Carboniferous rocks of the Appalachian Basin, but are generally rare to uncommon. The edrioasteroid *Hypsiclavus huntsvillae* is known only from Chesterian rocks of the Appalachian Basin, where it ranges from Genevian to Hombergian (Chesnut & Etensohn, 1988; Sumrall, 1996), and the edrioasteroid *Ulrichidiscus pulaskiensis* is known only from the Upper Hombergian rocks of eastern Kentucky (Chesnut & Etensohn, 1988) (Fig. 1). Kammer et al. (1987) described *Neosorophusella berryi* from the Greenbrier Limestone in Garrett County, Maryland, and *N. carbonarius* from the younger Bluefield Formation near Nemours, West Virginia. Both of these occurrences are also Chesterian in age.

Echinoderm assemblages may also be diagnostic, and some of the most abundant assemblages occur in the Hombergian-Elviran Glen Dean/Poppin Rock/Bangor and equivalent strata of the west-central and southwestern Appalachian Basin. Some of the most important assemblages from this interval come from northwestern Alabama and south-central Ken-

tucky. Although most of the assemblages have been described in a piecemeal fashion over the years, some of the most important assemblage studies are those of Burdick & Strimple (1982) from Alabama and of Ettensohn & Chesnut (1985) and Chesnut & Ettensohn (1988) from Kentucky. For example, Chesnut & Ettensohn (1988) reported 28 crinoid genera, four species of the blastoid *Pentremites*, two edrioasteroid genera, three echinoid genera, two asteroid genera, and two ophiuroid genera. Not only is the assemblage similar to the one from Alabama, but also to time-equivalent assemblages in the southern part of the Illinois Basin in western Kentucky and in southern Indiana and Illinois.

Pennsylvanian succession

Pennsylvanian rocks predominate at the surface in the Appalachian Basin and consist largely of fluvial or marginal-marine-to-terrestrial, coastal-plain, clastic sequences with former sources in the Alleghanian orogen. These generally fining-upward sequences are interrupted by cyclic, coarsening-upward, marine horizons related to glacial eustasy (e.g., Chesnut, 1994), and it is in these horizons that echinoderms occur as rare constituents of low-diversity faunas. Crinoid ossicles, in particular, have been widely reported throughout the Pennsylvanian section (e.g., Morse, 1931; Chesnut, 1991), but most of these are not easily associated with known species and reflect slow burial. However, the crinoid genera, *Aatocrinus*, *Plaxocrinus*, *Delocrinus*, *Endelocrinus*, *Sciadocrinus*, *Metacromyocrinus*, *Diphuicrinus*, and *Paragassizocrinus*, have been reported (Morse, 1931; Bassler & Moodey, 1943; Strimple & Knapp, 1966; Ettensohn, 1980b; Chesnut, 1991; Ausich, 1996), and of these only *Paragassizocrinus*, *Endelocrinus*, *Diphuicrinus*, and *Plaxocrinus* are known from more than one locality in the basin. The stemless *Paragassizocrinus* is an *Agassizocrinus* homeomorph, although unrelated to it. As currently known, *Paragassizocrinus tarri*, the most common species, ranges from Late Morrowan to Early Atokan (Late Bashkirian–Early Moscovian) time in the Appalachian Basin, although beyond the basin it probably ranges into Virgilian (Late Kasimovian) time (Ettensohn, 1980b). *Plaxocrinus* (= *Hydreionocrinus*) *mooresi*, on the other hand, ranges throughout the Pennsylvanian section (Upper Morrowan–Lower Virgilian; Upper Bashkirian–Upper Kasimovian) in Ohio and Kentucky parts of the Appalachian Basin (Morse, 1931; Ausich, 1996), whereas *Endelocrinus allegheniensis* is known only from the Lower Virgilian Ames Limestone in Pennsylvania and West Virginia (Bassler & Moodey, 1943) (Fig. 1).

Echinoid plates and primary spines referable to the genus *Archaeocidaris*? are locally common in some Pennsylvanian strata. However, echinoderms other than crinoids and echinoids have not been reported in the Appalachian Basin.

Summary

The Carboniferous was a period of major echinoderm evolution, especially during Mississippian time when crinoids, blastoids, and echinoids increased dramatically in abundance and diversity. Their high degree of structural organization and distinctive morphologies make them ideal zonal indicators, and during the Mississippian Period they provide greater biostratigraphic resolution in parts of the Appalachian Basin section than do conodonts and foraminifera. Their temporal and spatial occurrence throughout the Appalachian Basin, however, was related to the tectonic and sedimentologic differentiation of the basin through time. Already by Early Mississippian time, they had made the shift to clastic-rich environments, which predominated during Carboniferous time in the basin. However, during a brief interval of Middle and early Late Mississippian carbonate-rich seas, they became extremely abundant throughout the basin and particularly useful for zonal resolution. Hence, echinoderms became very important in the early zonation of the Mississippian Period, a zonation that is still used today.

In general, well-preserved Kinderhookian, Osagean, and Meramecian echinoderm faunas are rare in the Appalachian Basin. However, in some cases through reference to echinoderm ranges in the Illinois Basin section, even rare echinoderm occurrences can aid in constraining the age of Appalachian strata. Although Late Kinderhookian and Early Osagean faunas are present, most are endemic forms of little diagnostic value. By Middle and Late Osagean a number of diagnostic crinoids, mostly camerates living in clastic-rich environments, appear. At the Osagean–Meramecian transition, a major tectonic reorganization occurred across east-central United States as a result of the Ouachita Orogeny, and clastic-rich environments were replaced by shallow-water carbonates. At the same time, most of the larger, many-plated camerate crinoids disappeared only to be replaced by cladids and smaller cladid-homeomorph camerates, while blastoids became more common. In Lower Meramecian, Salem–Warsaw equivalents, for example, the small cladid-homeomorph camerate, *Dichocrinus simplex*, is diagnostic, and three blastoids, *Metablastus wortheni*, *Tricoelocrinus* and *Pentremites conoideus*, attained their peak abundances. Another

cladid-homeomorph camerate, *Platycrinites penicillus*, becomes especially diagnostic in upper Meramecian, St. Louis equivalents and in Lower Chesterian Ste. Genevieve equivalents, and the blastoid genus *Pentremites* becomes abundant for the first time as *P. puchellus* in Ste. Genevieve equivalents across the basin.

In Lower Chesterian, Gasperian parts of the section, another cladid-homeomorph camerate, *Talarocrinus*, replaces *P. penicillus* as the diagnostic form in the same facies, and at this time, there was a brief, but major, evolutionary radiation of cladids, species of *Pentremites*, and species of another cladid-homeomorph camerate, *Pterotocrinus*. In particular, species of the cladid *Agassizocrinus*, of the blastoid *Pentremites*, and of the camerate *Pterotocrinus* provide relatively detailed zonation in lower and middle parts (Gasperian and Hombergian) of the Chesterian section. By Late Chesterian (Elviran) time, an influx of marginal-marine and terrestrial clastics flooded the Appalachian Basin and continued through Pennsylvanian time. Rare echinoderms are present in these Upper Chesterian and Pennsylvanian rocks and are sufficiently diagnostic to distinguish Mississippian and Pennsylvanian systems; however, these forms are too long-ranging to provide any smaller scale zonation.

Acknowledgements

We would like to thank R. Häude and G. Sevastopulo for their constructive criticism and review of an earlier version of the manuscript.

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