

# Post-extinction survivor fauna from the lowermost Famennian of eastern North America

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An earliest Famennian (Late Devonian) shell bed was discovered in the Hanover Shale Member of the Java Formation 1.4 meters above the Frasnian–Famennian (F–F) boundary in western New York. The invertebrate shelly fauna of the shell bed (Lower *Palmatolepis triangularis* conodont Zone), provides information on taxonomy of an outer shelf benthic association during the survival interval of recovery in the Appalachian foreland basin soon after the terminal Upper Kellwasser event marking the F–F mass extinction. Shelly invertebrates are extremely rare in the upper Hanover immediately above and below the shell bed. Abundance of brachiopod valves and remains of other groups in the shell bed reach 80–100 valves/100 cm<sup>2</sup>. Elongate valves of the linguloid brachiopod *Barroisella* cf. *B. campbelli* have preferred alignments roughly parallel to direction of down-slope flow in the deep-water foreland basin depositional setting. The brachiopod fauna is dominated by the representatives of *Retichonetes*, *Barroisella*, *Cyrtospirifer*, *Tylothyris*, and *Praewaagenoconcha*. Rare elements include species of *Thiemella*, *Schizophoria*, *Ripidiorhynchus*?, *Chapinella*?, an indeterminate rhynchonellid, *Ambocoelia*, and extremely rare *Orbiculoidea*. Forms including *Cyrtospirifer hornellensis*, *Tylothyris mesacostalis*, *Praewaagenoconcha speciosa*, and few others are late Frasnian carryovers. The range inception of *Thiemella leonensis* is just above the F–F boundary (Upper Kellwasser horizon) in the upper Hanover Shale shell bed in the western Appalachian foreland basin.

Key words: Brachiopoda, Conodonta, extinction, survivor fauna, Frasnian, Famennian, North America.

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## Introduction

The cause of the terminal Frasnian extinction, one of five major mass extinctions in the Phanerozoic, remains problematic (Walliser 1996; McGhee 1996; Over et al. 1997; Copper 1998). The offshore strata at the Frasnian–Famennian (F–F) boundary in Europe, North Africa, and eastern North America are characterized by an organic-rich horizon, that coupled with an earlier organic-rich interval are referred to as the Lower and Upper Kellwasser horizons, and associated extinction episodes termed the Late Frasnian and Frasnian–Famennian boundary events by Walliser (1996). The Kellwasser beds have been interpreted as eustatic deepening events (Schindler 1990; Joachimski and Buggish 1993; Crick and Ellwood 1997). The late Frasnian extinctions (see Walliser 1996) resulted in the step-wise loss of predominantly shallow water taxa, notably stromatoporoids, rugose corals, trilobites, and brachiopods during or within the Kellwasser intervals (Schindler 1990; McGhee 1996; Rzhonsnitskaya and Modzalevskaya, 1996; Walliser 1996; Copper 1998; Day 1998a; Racki 1998; Racki and Baliński 1998). The ultimate effects of the F–F mass extinction were the complete ecologic and taxonomic restructuring of the benthic marine ecosystem (Droser et al. 2000). The species reduction of the offshore conodont genus *Palmatolepis* and extinctions of tentaculitids, homotrinids, and acrotretid brachiopods at or near the boundary is

puzzling because other deep water and offshore taxa are not as severely affected, nor are more nearshore dwelling conodont taxa of the genera *Icriodus* and *Polygnathus*.

The discovery of a lowermost Famennian brachiopod-rich bed 1.4 m above the F–F boundary in western New York permits us to document a F–F mass extinction survivor fauna from an offshore setting in the Appalachian Basin (Figs. 1 and 2). Conodonts directly associated with the brachiopod fauna in the shell bed and at other nearby localities are correlated with the Lower *Palmatolepis triangularis* Zone (see Over 1997). North American faunas of this age are poorly known, and the Hanover shell bed fauna provides the only definitive information on the nature of lowermost Famennian survivor faunas of the mass extinction from eastern North America. The Hanover survivor fauna displays close similarities with survivor and early recovery faunas in eastern Europe (Baliński 1996, 2002) and those recently reported from western North America (Bratton 1997; Bratton and Day 1997; Whalen et al. 2002).

Specimens are deposited in the New York State Museum, Albany, New York, abbreviated NYSM.

## Stratigraphy

The Frasnian–Famennian boundary and the brachiopod-rich shell bed in the valley of Buffalo Creek are located in the upper

2 m of the Hanover Shale (Figs. 1 and 2). The Hanover Shale Member of the Java Formation, West Falls Group, consists of green-gray pyritic silty mudstone, interbedded with thin black mudshale beds, siltstones, and nodular carbonate beds, that grade eastward into silts and sands of the Wiscoy Member (Fig. 2). The Hanover Shale overlies the Pipe Creek Shale, which is the equivalent of the Lower Kellwasser interval in the northern Appalachian Basin. The Upper Kellwasser bioevent interval is represented by a regionally persistent black shale bed in the upper Hanover that can be traced from Lake Erie to the Buffalo Creek Valley. The Hanover Shale is overlain by the Dunkirk Shale of the Canadaway Group. The Dunkirk is the highest widespread black shale tongue in the Upper Devonian of New York State.

The brachiopod bed is a 5–8 cm thick medium gray siltstone that consists of three fining upward intervals. Brachiopods are present in the under- and overlying strata, but are concentrated in a single 1.0–1.5 cm interval in the middle of the bed, developed in a coarser and more pyritic zone over clay-rich and bioturbated laminae (Fig. 2). The pyrite and shell-rich interval overlies a low relief scour surface, indicating a concentration of coarser and denser material during higher energy conditions. The shell-bearing bed is characterized by low amplitude ripple marks that have a 6–7 cm wavelength with ripple crests oriented NNE–SSW. The fauna is dominated by calcareous brachiopods, with phosphatic lingulate brachiopods, crinoids, ostracodes, bryozoans, fish remains, and conodonts. These cover the entire surface of the shell horizon. The shells of the larger species are disarticulated and convex up, but otherwise there is little evidence of shell abrasion during transport. Some of the larger brachiopod shells are concave up, possibly the result of settling from suspension. Elongate valves of *Barroisella* cf. *B. campbelli* ( $n = 184$ ) have a preferred, but not pervasive, long axes alignment in a NW–SE orientation perpendicular to the current ripple crests (Fig. 2).

The rhythmic bedding, ripple marks, scour surface, shell concentration, and current alignment of brachiopod valves suggest deposition in a turbidity flow. Turbidity flow deposits associated with prograding delta facies and possible development of submarine fans have been described for Upper Devonian strata in western New York and Pennsylvania, including siltstones and silt laminae in the Nunda Sandstone and Hanover Shale (Lundegard et al. 1985; Baird and Lash 1990; Jacobi et al. 1994; Over et al. 1997). The orientation of ripple marks and brachiopods is consistent with a general east to west down-slope flow from the eastern margin of the Appalachian Basin in the Upper Devonian (lower Famennian).

## Brachiopod fauna

The shelly fauna from the Hanover Shale shell bed provides the first record of a biostratigraphically well constrained post-F–F extinction survivor fauna from the lower Famennian of the Appalachian Basin in eastern North America. The majority of brachiopod genera present in the Hanover Shale

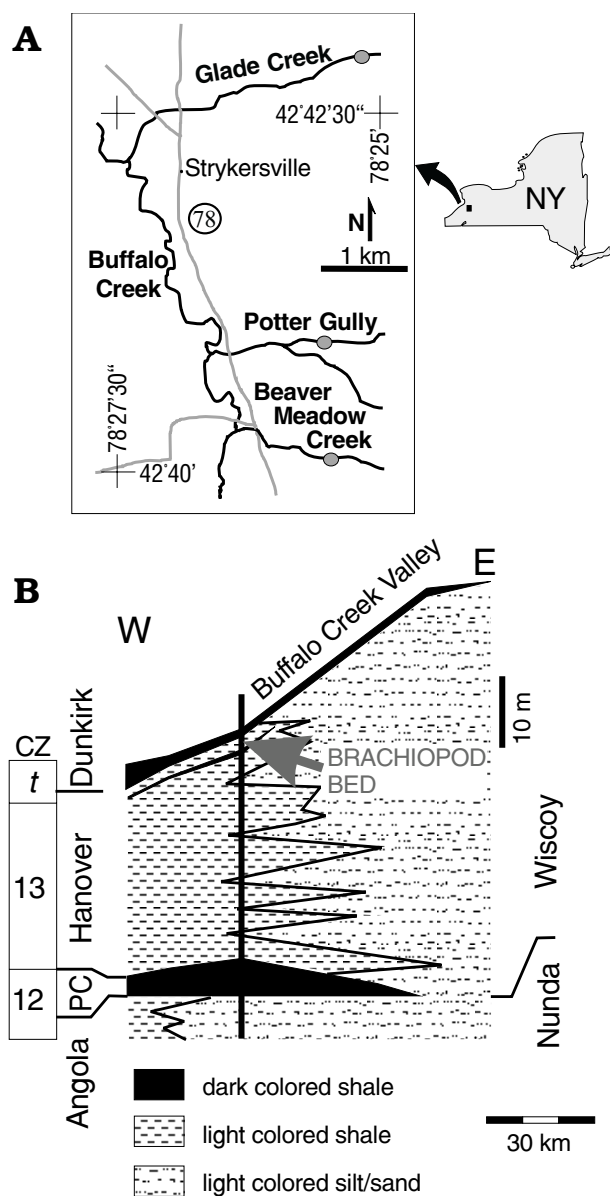


Fig. 1. A. Location of study sites in western New York showing where the Upper Devonian Hanover Shale is exposed. B. Schematic diagram of general facies, lithostratigraphy, and position of the lowermost Famennian brachiopod bed in upper Hanover. Abbreviations: cz, conodont zones; PC, Pipe Creek Shale; t, Lower *Pa. triangularis* Zone; 12 and 13 are Frasnian Montagne Noire conodont zones of Klapper (1989).

shell bed are common to other lower Famennian deposits in the Great Basin (Merriam 1940; Johnson 1977; Johnson and Reso 1966; Johnson et al. 1969; Bratton 1997; Bratton and Day 1997), and western Canada (Warren and Stelck 1956; Sartenaer 1969; Raasch 1989). These lower Famennian North American faunas are typical of faunas dominated by productoid, cyrtospiriferid, and athyridoid brachiopod genera whose subsequent diversification mark the post-extinction recovery of Late Devonian shelly faunas (Racki 1998; Ma and Day 1999, 2000). The Hanover Shale fauna is distinctive as one of, if not, the oldest lowermost Famennian benthic faunas from North America providing information

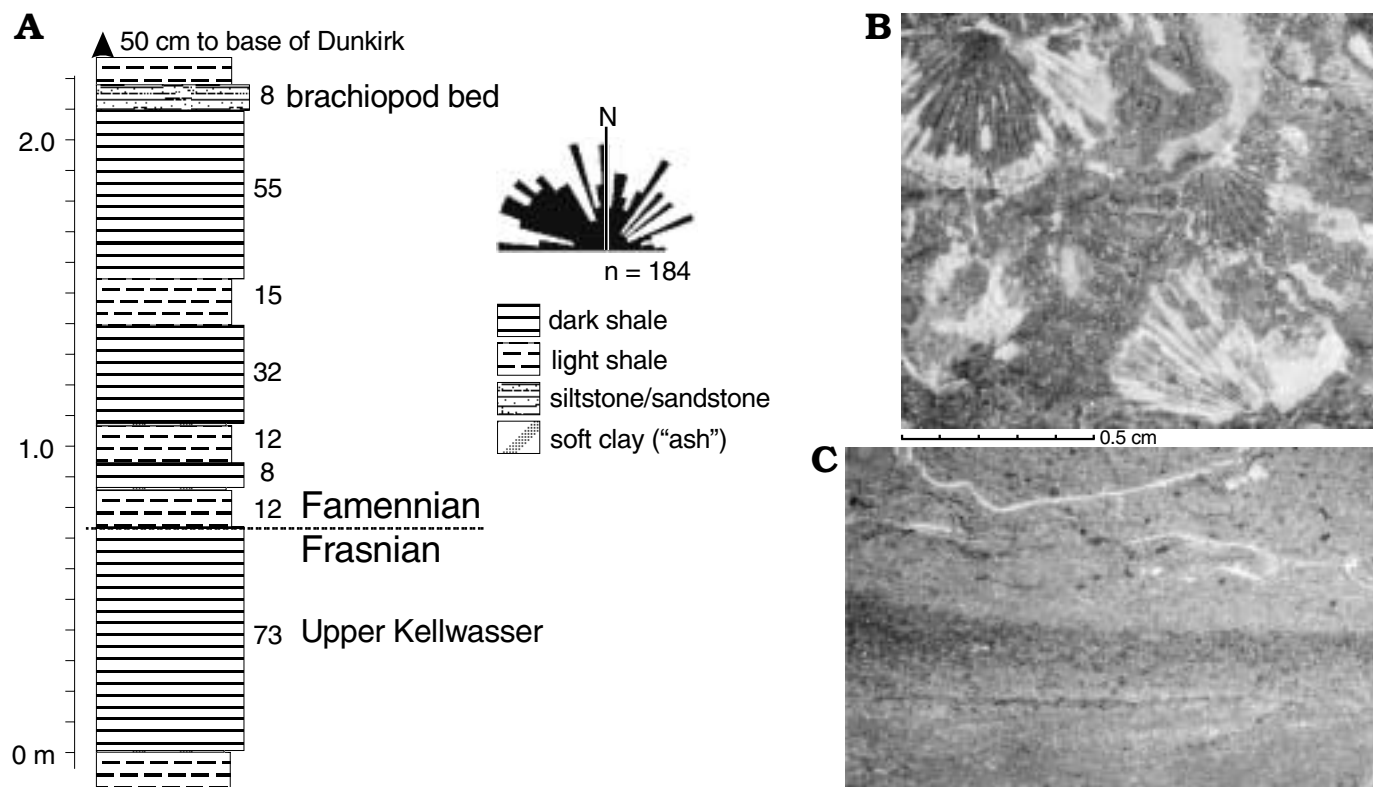


Fig. 2. A. Stratigraphic interval in upper Hanover Shale at Glade Creek that contains Upper Kellwasser Interval, Frasnian–Famennian boundary, and brachiopod bed. Rose diagram is orientation of long axis of lingulid (*Barroisella*) valves on the bedding surface. Numbers to the right of the stratigraphic section denote bed thickness (in cm). B. Photograph of brachiopod-bearing bedding surface showing partially exfoliated ventral valves of the chonetid brachiopod *Retichonetes* aff. *R. obscurus*. C. Cross section of brachiopod-rich horizon. The dark band in the center of the cross section is pyrite-rich.

about the composition of shelly faunas from the survival interval of the early repopulation stage (Kauffman and Harries 1996) following the terminal Frasnian extinction.

**Preservation and composition of the Hanover fauna.**—Shell material of most brachiopod specimens in the Hanover shell bed is relatively well preserved. Moldic preservation is observed where calcite shell material was subject to dissolution at edges of sampled slabs. All specimens were recovered on surfaces of slabs (largest slabs are up to 0.7 square meters in overall dimension) split parallel to bedding to expose the concentrated shell material on resulting parts and counterparts. The abundant brachiopod material (Table 1) is directly associated with less common gastropods, bivalves, pelmatozoan stem plates, tentaculites, fish plates, ostracodes, and conodonts. The conodonts provide a correlation with part of the Lower *Pa. triangularis* Zone providing evidence that the Hanover shell bed fauna is one of the oldest Frasnian–Famennian extinction survivor faunas known from North America.

Whole and disarticulated shells of the small chonetid brachiopod *Retichonetes* aff. *R. obscurus* Cooper and Dutro, 1982 dominate the brachiopod fauna. The second most abundant taxon is *Barroisella* cf. *B. campbelli* Cooper, 1942. The type species (*B. campbelli*) was first described from the *Barroisella* Beds in the Famennian part of the New Albany Shale in southern Indiana (see recent illustrations of *B. camp-*

*belli* by Holmer and Popov 2000: 36, fig. 9: 1a–e). Other calcareous brachiopods common in the Hanover Shale fauna include common *Cyrtospirifer hornellensis* Greiner, 1957, *Tylothyris mesacostalis* (Hall, 1867), and *Praewaagenoconcha speciosa* (Hall, 1867). Additional species present include small numbers of the orthid *Thiemella leonensis* (Hall, 1867); poorly preserved *Ambocoelia* cf. *A. gregaria* (Hall, 1867), a rhychonelloid brachiopod close to *Ripidiorhynchus* Sartenaer, 1966; partial valves of a rhychonellid provisionally assigned to *Chapinella* Savage et al. 1978; *Schizophoria* (*S.*) sp.; and the lingulate brachiopod *Orbiculoidea* sp.

Shells of the spiriferids *Tylothyris*, *Cyrtospirifer*, and *Ambocoelia* are disarticulated with both valves oriented convex side up. Small (3–7 mm wide) concavo-convex shells of the chonetid *Retichonetes* aff. *R. obscurus* are randomly oriented, although significant numbers of specimens are convex side up (Fig. 2). The shells of the medium sized (up to 25 mm) echinoconchoid productid *Praewaagenoconcha* are generally oriented concave side up. As discussed above the disarticulated elongate valves of *Barroisella* display preferred alignment parallel to direction of flow of the turbidity current. Flow velocity and turbulence in the transporting density current was sufficient to exhume the infaunal pediculate lingulates and dislodge and entrain shells of the liberossesile anchored spinose productid *Praewaagenoconcha* and other

Table 1. Brachiopod taxa and their relative abundance in brachiopod bed, upper Hanover Shale, Glade Creek, Wyoming County, New York. Brachiopod count from a 30 × 30 cm area on the oriented split slab from which compass bearing measurements of the long axes of shells of the lingulate brachiopod *Barroisella* cf. *B. campbelli* were taken to construct the rose diagram in Fig. 2A.

| Taxon  | Count |
|--|-------|
| <i>Retichonetes</i> aff. <i>R. obscurus</i>  | 786   |
| <i>Barroisella</i> cf. <i>B. campbelli</i> . | 142   |
| <i>Tylothyris mesacostalis</i>               | 64    |
| <i>Praewaagenoconcha speciosa</i>            | 30    |
| <i>Cyrtospirifer hornellensis</i>            | 15    |
| <i>Chapinella?</i> sp.                       | 4     |
| <i>Ripidiorhynchus?</i> sp.                  | 2     |
| <i>Ambocoelia</i> cf. <i>A. gregaria</i>     | 1     |
| <i>Orbiculoidea</i> sp.                      | 1     |
| Total =                                      | 1045  |

fixosessile pediculate calcareous brachiopods (*Ambocoelia*, *Cyrtospirifer*, *Tylothyris*, and the rhynchonellids). As the shell concentration occurs as part of a turbidite or storm bed muddy nepheloid suspension deposit, it is likely that the fauna of the lower Hanover Shale shell bed represents admixed elements of more than one offshore low-diversity benthic biofacies.

**Distribution of Hanover shell bed taxa in the Frasnian–Famennian of New York.**—The majority (seven, and perhaps nine of eleven) of the brachiopod taxa appear to be Frasnian carryover (survivor) species. The actual stratigraphic ranges and/or systematic status of *Retichonetes*, *Ripidiorhynchus?*, *Chapinella?*, and the indeterminate rhynchonellid are uncertain. These forms may in fact be upper Frasnian carryover taxa, but this can not be confirmed because of the lack of reliable data on biostratigraphic ranges of many brachiopod species described in the older literature from the Frasnian of the Appalachian Basin, and the uncertain systematic status of the aforementioned rhynchonelloids. The only forms from the brachiopod bed fauna whose first occurrence is probably no older than lower Famennian in the Appalachian Basin Upper Devonian brachiopod sequence is the orthoid *Thiemella leonensis* (Hall, 1867).

The base of the range of *Thiemella leonensis* is shown by both Dutro (1981: fig. 7) and Linsley (1994: 103) to begin within the lower part of the Canadaway Group (lower Famennian). Its occurrence in the upper part of the Hanover Shale would place its range inception below that level in the upper part of the Java Formation. *Thiemella leonensis* (see Fig. 3B–D) appears to succeed middle–upper Frasnian *T. danbyi* reported by McGhee and Sutton (1985: 18–19, table 5) from older upper Frasnian deposits (Wiscoy Member) of the Java Formation.

All of the remaining brachiopods, with the possible exception of the species of *Retichonetes* and the rhynchonelloids, are carryover taxa known from upper Frasnian deposits of the Java Formation. Other than the Hanover occurrence, the distribution of species of *Retichonetes* in the Upper

Devonian of New York is essentially unknown. *Retichonetes* is well known from Frasnian deposits in France (Muir-Wood 1962, 1965), Iowa (Day 1989, 1995; Independence Shale and Lime Creek Formation) and New Mexico (Day 1988, Sly Gap Formation). Species of the genus are also described from the lower to upper Famennian of New Mexico (Cooper and Dutro 1982, Percha Formation), and illustrated from the late Famennian Chagrin Shale of eastern Ohio (Schwimmer and Feldmann 1991). Given its widespread distribution in middle–outer shelf brachiopod associations in the upper Frasnian of New Mexico and Iowa, it is likely to occur in similar biofacies in the Upper Devonian of New York.

*Schizophoria* (*S.*) crosses the F–F boundary and is reported from a variety of lower Famennian faunas in the western U.S. and western Canada. In the New York Upper Devonian Dutro (1981: 79, fig. 7) showed “*S. impressa* (Hall)” ranging into the Wiscoy and Hanover Shale members of the Java Formation, and terminating at the presumed position of the F–F boundary. Dutro (1981: fig. 7) also showed the range of “*S. iowensis* (Hall)” beginning in the interval of the Wiscoy–Hanover and ranging into the Conneaut Group (lower Famennian). The single specimen of *Schizophoria* recovered by us from the Hanover Shale shell bed is closest to *S. impressa* (Hall, 1867). A species listed as *S. striatula* was reported from the upper Frasnian faunas of the upper West Falls Group and Java Formation by McGhee and Sutton (1983: table 5). Since the form reported by those authors was not illustrated, its identity cannot be verified. It is likely that their form coincides with forms identified as either *S. iowensis* or *S. impressa* in reports of Dutro (1981) and Linsley (1994). In western Canada, “*Schizophoria iowensis* (Hall)” is listed from the fauna of the lower Famennian *Eoparaphorhynchus* Zone of Sartenaer (1969: 3). The base of Sartenaer’s (1969: fig. 2) *Eoparaphorhynchus* Zone in western Canada is within the upper part of the Lower *Pa. triangularis* Zone. Bratton and Day (1997) and Bratton (1997) reported *S. sp. aff. S. iowensis* (Hall, 1858) from the lowermost Famennian part of the Pilot Shale in Utah. Bratton’s sample WCK-B1 (1997: 131, 236, fig. 7.4.3) from the Coyote Knolls section of the Pilot Shale was taken at the position of sample 9B of Sandberg et al. (1988: fig. 13; 1997: fig. 17), approximately three meters above the F–F boundary, and six to seven meters below the position of the “tsunamiite” debris flow bearing the lowest elements of the *Eoparaphorhynchus walcotti* fauna reported by Sandberg et al. (1988). Consequently, sample WCK-B1 of Bratton (1997) yields the lowest known Famennian shelly fauna just above the F–F boundary (at a position low in the Lower *Pa. triangularis* Zone) in the Great Basin, and is comparable in age to the fauna of the upper Hanover Shale. Ventral valves of juvenile *Schizophoria* (*S.*) *iowensis* (Hall, 1858) from the upper Frasnian Lime Creek Formation of Iowa (Day collection) are similar in shape to the specimen of *S. (S.) sp.* from the Hanover and the form recovered from the Pilot Shale of Utah (Bratton 1997: pl. 5: 7, 8). However the medial adductor ridge of *S. iowensis* from Iowa does not extend anterior of the

impressed lobate diductor platform as seen in the Hanover form (Fig. 3A). The interior of the single specimen collected by Bratton (1997) from the Pilot Shale remains unknown.

Leighton (2000: 185, fig. 2A) illustrated *Praewaagenoconcha speciosa* (Hall, 1867) and discussed the occurrence of the closely related form *P. lachrymosa* (Hall, 1867) from the Java Formation. His report confirms earlier reports of these species in prodelta and open shelf facies of the upper Nunda Sandstone (upper West Falls Group) and Wiscoy Member of the Java Formation by McGhee and Sutton (1985: 18–19, listed as *Productella speciosa* in their table 5). *Praewaagenoconcha speciosa* from the Hanover is closely similar to the somewhat larger specimens of *P. sp.* described by Johnson (in Johnson et al. 1969: 1361–1362, pl. 157: 19–24) from the upper West Range Limestone at Bactrian Mountain in Nevada. At Bactrian Mountain *P. sp.* is associated with *Crinisarina reticulata* (Stainbrook, 1947) and conodonts of the Upper *Pa. rhomboidea* Zone (see Sandberg and Poole 1977: fig. 6). The same form is also known from the upper part of the Guilmette Formation at a position low in the Upper *Pa. triangularis* Zone in Morrow's (2000: fig. 5, table 13) Fox Mountain section in central Nevada. Bratton and Day (1997) reported *Praewaagenoconcha sp.* with *Schizophoria sp. cf. S. iowensis* from the Pilot Shale of western Utah from Bratton's (1997: 131, fig. 7.4.3, also see pl. 1: 1) Coyote Knolls section from a horizon correlated with a position low in the Lower *Pa. triangularis* Zone.

The assignments of the limited number of incomplete rhynchonellid specimens to *Chapinella* Savage et al. (1978) and *Ripidiorhynchus* Sartenaer (1966) are tentative. Further study of both forms (requiring serial sections of additional whole shells) is needed to verify their generic identity. The form identified here as *Ripidiorhynchus?* sp. does share similarities with species of Sartenaer's (1966) genus. *Ripidiorhynchus* is known to range through most of the Frasnian into the lower Famennian (Sartenaer 1985), and is definitely known from the Frasnian West Falls Group of New York (see comments in Sartenaer 1985: 323). Harrington (1972: fig. 1) defined the upper Frasnian *Ripidiorhynchus (?) sp. Zone* on the basis of the range of that form (see his pl. 2: 17–19) in the upper West Falls Group and lower part of the Java Formation in central New York. *Ripidiorhynchus?* sp. in the Hanover may signify survival of that genus into the lower Famennian in western New York. See further remarks on *Ripidiorhynchus?* sp. in the systematic paleontology section below.

Another rhynchonelloid present in the Hanover (Fig. 3G) identified here as *Chapinella?* sp. is very similar externally to the type species of *Chapinella* (*C. bucareliensis*) described by Savage et al. (1978) from the "middle to late Famennian" Port Refugio Formation of southeastern Alaska. There it is associated with the athyrid *Crinisarina milleri* that is most similar to *Crinisarina humerosa* (Stainbrook, 1950) from the late Famennian (see Witzke and Bunker 1996: fig. 5, *Pa. postera* Zone) Aplington Limestone of northern Iowa. Another very similar form is *Chapinella striata* described by Baliński (2002) from the very early Famennian of southern

Poland as an element of the fauna of the *Orbiculatisinuostrium leave* brachiopod interval (Baliński 1996). Brachiopods of the *O. leave* interval occur in strata immediately above beds yielding the lowest F–F survivors that characterize the *Pampoecilorhynchus geniculatus* interval. The occurrence of *Chapinella* in the very early Famennian recovery fauna in southern Poland (Baliński 2002) and possibly in the Hanover Shale Member of the Java Formation of New York constitute the oldest known occurrences of the genus reported to date.

Both *Cyrtospirifer hornellensis* Greiner, 1957, and *Tylothyrus mesacostalis* (Hall, 1867) are reported from upper Frasnian upper West Falls strata and the Wiscoy Member of the Java Formation by McGhee and Sutton (1985). The only other species of *Tylothyrus* known from lower Famennian deposits in North America is *T. compacta* Cooper and Dutro, 1982, described from the phosphatic sandstones of the Thoroughgood Formation of Cooper and Dutro (1982). Thoroughgood Formation of Cooper and Dutro (1982) is now referred to as the Thurgood Sandstone Member of the Contadero Formation after revision by Sorauf (1984). The Thurgood Sandstone in the central and northern San Andres Mountains is a thin (0.89 to 4.0 m thick) condensed transgressive lag deposit (as interpreted by Day 1998b) that accumulated during the initial Famennian transgression and maximum sea level highstand of Devonian Transgressive–Regressive cycle IIe of Johnson et al. (1985). It is reported to yield Lower and Middle *Pa. triangularis* Zone conodont faunas by Sandberg (1979: 94) and Sorauf (1988: 156, fig. 5). The brachiopod fauna of the Thurgood Sandstone in southern New Mexico occurs at or just above the lowest sample yielding conodonts of the Middle *Pa. triangularis* Zone in the central and northern San Andres Mountains (see Sorauf 1988: fig. 5). Consequently its brachiopod fauna is younger than the Hanover fauna reported here.

Upper Devonian species attributed to *Cyrtospirifer* from North America are currently under evaluation based on re-study of the type species of *Cyrtospirifer* and related genera in the Family Cyrtospiriferidae (Ma and Day 2000, in press). Based on revisions of Ma and Day, Greiner's (1957) *Cyrtospirifer hornellensis* is a genuine *Cyrtospirifer*. The only other reports of *Cyrtospirifer* from lowermost–lower Famennian faunas in North America qualifying as potential survivors are *C. portae* (Merriam 1940) reported by Bratton (1997) and Bratton and Day (1997) from Bratton's lowest Famennian sample in the Pilot Shale in Utah (see discussion above). The same form is reported by Day (in Whalen et al. 2002) from the oncoid rudstone bed just above the F–F boundary in the lower part of the Sassenach Formation just south of the Ancient Wall reef platform in western Alberta. *Cyrtospirifer portae* is not a true *Cyrtospirifer* and will be assigned to another related lower Famennian cyrtospiriferid genus (Ma and Day personal communication 2001).

*Ambocoelia cf. A. gregaria* Hall (1867) is close to Hall's species. Hall (1867: 261) described this form from "the shales and shaly sandstones of the Chemung Group" in cen-



tral and eastern New York. Linsley (1994: 104) showed the range for this form beginning near the base of the Sonyea Group (lower–middle Frasnian) extending into the Venango Group (lower Famennian), whereas Dutro (1981: fig. 7) showed its range beginning near the base of the Java Formation and ranging through the entire Famennian of New York. The lowest occurrence of this form in the Java Formation shown by Dutro (1981) is consistent with reports by McGhee and Sutton (1983: table 5) of a sequence of Late Devonian *Ambocoelia* where the range of *A. umbonata* terminates in the upper West Fall Group, succeeded above by *A. gregaria* in the Java Formation. The actual ranges and systematic status of ambocoelids in the New York Late Devonian remain poorly documented and are in need of further study.

Ambocoelids are interpreted as opportunistic species that most frequently occurred as elements of middle and outer shelf associations in the older Middle Devonian (Givetian) Hamilton Group (Goldman and Mitchell 1990: 97). A similar offshore outer shelf association dominated by species of *Ambocoelia* and *Retichonetes* (with the rhynchonellid *Navalicria* and linguloid brachiopods) is reported from dark gray mudstones of the upper Frasnian Sly Gap Formation at Alamo Canyon in the Sacramento Mountains of southern New Mexico (Day 1988: table 17, sample DCAC). The occurrence of *Ambocoelia* in the Hanover fauna would be consistent with the expected occurrence of opportunistic taxa in the “survival interval” of the repopulation stage after mass extinction in the recovery model of Kauffman and Harries (1996).

## Conodont fauna

The conodont fauna is dominated by specimens of *Palmatolepis triangularis*, with lesser numbers of *Icriodus alternatus* ssp., and *Polygnathus* sp. (Fig. 5, Table 2). This fauna is characteristic of the Lower *Pa. triangularis* Zone, which is a low diversity fauna before the radiation of palmatolepids and other conodonts that characterize and define the Middle *Pa. triangularis* Zone. The occurrence of *Pa. delicatula platys* and *Pa. clarki* higher in the Hanover and lower Dunkirk shales in nearby sections supports this zonal assessment (see Over 1997: figs. 3, 7).

Table 2. Conodont taxa represented by P<sub>1</sub> (Pa) elements and their relative abundance in brachiopod bed, upper Hanover Shale, Glade Creek, Wyoming County, New York.

|  |    |
|--|----|
| <i>Palmatolepis triangularis triangularis</i>  | 5  |
| <i>Palmatolepis</i> sp. (upside down P <sub>1</sub> elements that have an outline consistent with <i>P. triangularis</i> ) | 7  |
| <i>Polygnathus</i> sp.   | 3  |
| <i>Icriodus alternatus alternatus</i>  | 3  |
| <i>Icriodus alternatus helmsi</i>  | 1  |
| <i>Icriodus</i> sp.  | 1  |
| Total P <sub>1</sub> elements  | 20 |

## Conclusions

A shell bed recovered 1.4 m above the F–F boundary in the upper part of the Hanover Shale Member of the Java Formation in western New York (Figs. 1 and 2) is lower Famennian based on associated conodonts of the Lower *Pa. triangularis* Zone. Given its position just above the F–F boundary (earliest Famennian age), the Hanover shell bed fauna represents the only shelly fauna from the survivor phase of the early repopulation stage after the F–F mass extinction in eastern North America.

The convex-up orientation of valves or whole shells of *Tylothyris*, *Cyrtospirifer*, *Retichonetes*, *Praewaagenoconcha*, and the preferred alignment of elongate valves of the linguloid *Barroisella* support the interpretation of the shell bed as part of a turbidite deposit. As such the fauna likely includes admixed elements of two or more outer shelf and slope benthic associations occupying the early Famennian sea floor in western New York. The fauna is dominated by *Retichonetes* aff. *R. obscurus*, *Barroisella* cf. *B. campbelli*, *Tylothyris mesacostalis*, *Cyrtospirifer hornellensis*, and *Praewaagenoconcha speciosa*. Rare elements of the fauna include *Thiemella leonensis*, *Ambocoelia* cf. *A. gregaria*, *Chapinella?* sp., *Ripidiorhynchus?* sp., *Orbiculoidea* sp., and an indeterminate rhynchonellid.

Genera of calcareous brachiopods present in the Hanover fauna common to other lower Famennian post-extinction faunas elsewhere in North America include *Retichonetes*, *Praewaagenoconcha*, *Schizophoria* (S.), *Cyrtospirifer*, *Ambocoelia*, *Tylothyris*, and possibly *Ripidiorhynchus?* The systematic status and ranges of other forms present in the Hanover fauna remain uncertain (Figs. 3 and 4). *Cyrtospiriferids* (including *Cyrtospirifer*) and productoids (such as *Praewaagenoconcha*) underwent major radiations later in the early Famennian and are characteristic and dominant elements (together with rhynchonelloid and athyridoid brachiopods) of late post-extinction recovery faunas typical of the remainder of the early Famennian (Racki 1996, 1998, 2001; Baliński 1996, 2002).

## Systematic paleontology

### Brachiopods

Some elements of the Hanover brachiopod fauna are extremely rare and one form (represented by a single specimen) is unknown in the literature on the Devonian brachiopods from North America. Owing to the limited number and poor state of preservation of rhynchonelloid specimens recovered from the Hanover Shale shell bed their systematic status is still open to interpretation.

All specimens are housed at the New York State Museum (abbreviated NYSM) in Albany New York. Lingulate brachiopods discussed above are not illustrated. Classification of the

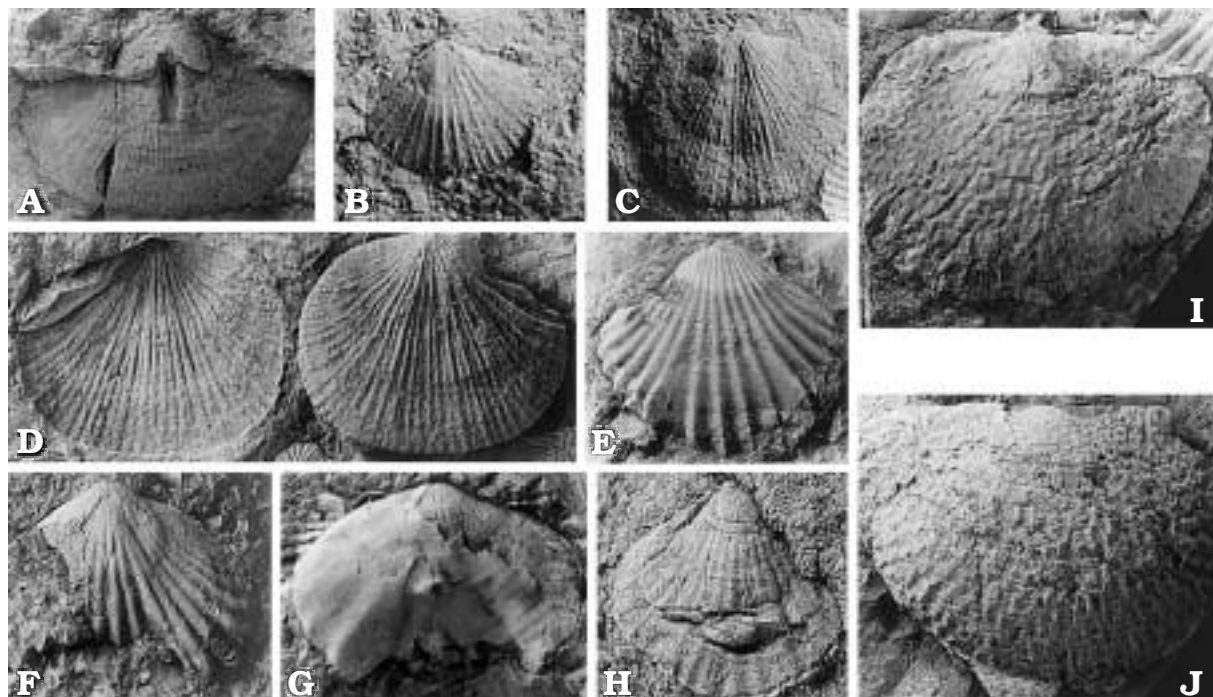


Fig. 3. Brachiopod fauna of the shell bed in upper Hanover Shale Member of the Java Formation. **A.** *Schizophoria* (*S.*) sp. upper view of exfoliated ventral valve, NYSM 15701,  $\times 1.7$ . **B–D.** *Thiemella leonensis* (Hall, 1867). **B.** Dorsal valve of juvenile specimen, NYSM 15722,  $\times 4.6$ . **C.** Ventral valve, NYSM 15694,  $\times 2$ . **D.** Ventral view of nearly complete shell extracted from moldic cavity to left, NYSM 15699,  $\times 2.2$ . **E, F.** *Ripidiorhynchus*? sp. **E.** Upper view of ventral valve with plica extending from anterior margin to beak of valve, NYSM 15723,  $\times 2$ . **F.** Partial ventral valve showing medial and left lateral flank plications, NYSM 15724,  $\times 2$ . **G.** *Chapinella*? sp., ventral valve with lateral plications near shell margin, NYSM 15727,  $\times 2$ . **H.** Genus and species uncertain, ventral valve with radial plica extending from anterior and lateral margins to beak of NYSM 15728,  $\times 4$ . **I, J.** *Praewaagenoconcha speciosa* (Hall, 1867). **I.** Interior of dorsal valve showing bilobed cardinal process, NYSM 15696,  $\times 2$ . **J.** Upper view of ventral valve showing quincuncially arranged spines, NYSM 15697,  $\times 2$ .

spiriferids follows revised classifications of Carter et al. (1994). Classification of the rhynchonellids follows that of Savage (1996). Classification of the other orders follows recent revisions by Brunton et al. (1995) and Williams et al. (1996).

#### Order Orthida Schuchert and Cooper, 1932

Suborder Suborder Dalmanellidina Moore, 1952

Superfamily Enteletoidea Waagen, 1884

Family Schizophoriidae Schuchert and Levene, 1929

Genus *Schizophoria* King, 1850

Subgenus *Schizophoria* (*Schizophoria*) King, 1850

*Schizophoria* (*S.*) sp.

Fig. 3A.

**Material.**—The figured partial ventral valve NYSM 15701.

**Remarks.**—A single partial ventral valve representing *Schizophoria* (*S.*) sp. was recovered from Hanover Shale shell bed. The exfoliated ventral valve does not permit a definite species assignment, although it features molds of the impressed bilobate diductor scars (Fig. 4A) divided by a medial ridge (site of adductor attachment) extending 2–3 mm beyond the diductor muscle field. The only Late Devonian species of *Schizophoria* described from New York with the ventral medial adductor ridge extending well beyond the diductor scars is *S. (S.) impressa* (Hall 1867: pl. 8: 11–19).

#### Family Rhipidomellidae Schuchert, 1913

Genus *Thiemella* Williams, 1908

*Thiemella leonensis* (Hall, 1867)

Figs. 3B–D.

*Orthis leonensis*; Hall 1867: 62, pl. 8: 3–8; Hall and Clarke 1892: 103, pl. 5c: 42, 43.

*Dalmanella leonensis* Hall, 1867; Williams 1908: 48, pl. 2: 1, 2, 5, 6, 9, 10, 13, 24.

*Thiemella leonensis* Hall; Linsley 1994: 103, pl. 116: 13–20.

**Material.**—Figured specimens NYSM 15694, NYSM 15699, NYSM 15722; additional specimens NYSM 15726 (complete shell), NYSM 15700 (dorsal valve in matrix); eight unnumbered specimens on parts and counterparts of split slabs.

**Remarks.**—Thirteen specimens recovered (four complete adult shells) are consistent with Hall's species described originally from the "arenaceous beds of the Chemung group near Leon, Conewego, and Randolph in Cattaraugus county". Consequently the precise origin of his type material remains unknown. See comments on distribution of this form above. Schuchert and Cooper (1932) questionably attributed to William's *Orthis leonensis* to *Thiemella*. Dutro (1981: fig. 7) was the first to definitively attribute this form to *Thiemella*.

Order Rhynchonellida Kuhn, 1949  
 Superfamily Rhynchotrematoidea Schuchert, 1913  
 Family Trigonirhynchiidae Schmidt, 1965  
 Subfamily Ripidiorhynchinae Savage, 1996  
 Genus *Ripidiorhynchus* Sartenaer, 1966  
*Ripidiorhynchus?* sp.

Fig. 3E, F.

*Material*.—Two mature shells NYSM 15699, NYSM 15722, and a juvenile ventral valve NYSM 15694, 15 unnumbered partial compacted ventral and dorsal valves on parts and counterparts of split slabs.

*Remarks*.—The limited material (three partial ventral valves and numerous fragments) do not permit a definitive generic assignment. The angular plications originating near the beak of the ventral valve are a common feature seen in a number of genera known from upper Frasnian–lower Famennian deposits. It is likely that this form represents a species of *Ripidiorhynchus* Sartenaer (1966). The best-preserved ventral valves are close to the Frasnian form *R. kermanensis* Brice (1999) illustrated by her from the Frasnian of Kerman Province of eastern Iran. The Hanover material is provisionally placed in that genus pending discovery of additional well-preserved shells in the Upper Devonian of New York.

The specimens (Fig. 3E, F) also bear an external resemblance to shells of *Sinotectirostrum* Sartenaer (1961a). Of the species described from North America, the limited material (NYSM 15723 with shoulder angle of 115°) from the Hanover Shale is most similar to *S. medicinale deceptum* Sartenaer (1969: his paratype GSC 15900) described from very low in the Sassenach Formation of western Alberta. Raasch (1989) lists species of *Sinotectirostrum* from six of his seven Famennian brachiopod zones (zones DFM1 to DFM6) that span the interval from the Lower *Pa. triangularis* through the *Pa. trachytera* zones of the Upper Devonian Famennian conodont zonation. Sartenaer (1969: fig. 2) portrays the range inception of *S. medicinale deceptum* very low in the Lower *Pa. triangularis* Zone, below species typical of his *Eoparaphorynchus* Zone in western Canada. If the Hanover specimens prove to be *Sinotectirostrum*, then the occurrence of this genus in New York (very low in the Lower *Pa. triangularis* Zone) would be similar to its lowest occurrences in the lowermost Famennian in western Canada. *Ripidiorhynchus?* sp. bears some resemblance to *Rhynchonella* (*Stenocisma*) *contracta* (Hall 1867: 351, pl. 55: 26–39) attributed by Linsley (1994) to *Cupularostrum* Sartenaer (1961b).

Superfamily Pugnacoidea Rzhonsnitskaya, 1956  
 Family Pugnacidae Rzhonsnitskaya, 1956  
 Genus *Chapinella* Savage, Eberlein, and Churkin, 1978  
*Chapinella?* sp.

Fig. 3G.

*Material*.—One partial ventral valve NYSM 15727, numerous unnumbered valve fragments, one ventral, and one par-

tial dorsal valve (both unnumbered) on parts and counterparts of split slabs.

*Remarks*.—This form is a relatively common element of the Hanover Shale fauna, although most frequently represented by broken shell fragments of dorsal and ventral valves. The angular plications bounding the sulcus and upper part of the tongue (Fig. 3G) arise anterior of mid-valve, and do not extend posteriorly to near the beak. External ornament preserved on external molds of partial ventral valves shows very fine concentric growth lines and very fine radial microcapillate micro-ornament. It resembles species of *Chapinella* Savage et al., 1978, and is provisionally placed in that genus pending recovery of sufficient specimens to verify its identity.

Superfamily, family, and genus indet.

Fig. 3H.

*Material*.—A single ventral valve NYSM 15728.

*Remarks*.—This rare brachiopod is unlike anything illustrated by James Hall and other workers on the Devonian of New York. It is provisionally attributed to the Order Rhynchonellida.

Order Productida Sarytcheva and Sokolskaya, 1959  
 Suborder Productidina Waagen, 1883  
 Superfamily Echinoconchoidea Stehli, 1954  
 Family Sentosidae McKellar, 1970  
 Subfamily Caucasiproductidinae Lazarev, 1987  
 Genus *Praewaagenoconcha* Sokoloslkaya, 1948  
*Praewaagenoconcha speciosa* (Hall, 1867)

Figs. 3I, J, 4F, G.

*Productella speciosa*; Hall 1867: 175–176, pl. 25: 2–11.  
 “*Productella*” *speciosa*; Linsley 1994: 103, 225, pl. 119: 1–10.  
*Praewaagenoconcha speciosa*; Leighton 2000: 186, fig. 2A.

*Material*.—Figured specimens NYSM 15695, NYSM 15696, NYSM 15697, NYSM 15706, unfigured specimen NYSM 15698, and an estimated 60–80 unnumbered specimens on parts and counterparts of split slabs.

*Remarks*.—This is a common element of the lower Famennian Hanover brachiopod bed fauna represented by juvenile and adults shells (up to 25 mm in width). The upper Frasnian occurrences of *Praewaagenoconcha speciosa* (Hall, 1867) and the closely related form *P. lachrymosa* (Hall, 1867) in New York (see comments in Leighton 2000) are the oldest documented representatives of the genus in North America. Most other occurrences of the genus, primarily from the Great Basin (Johnson et al. 1969; Bratton and Day 1997; Bratton 1997; Morrow 2000) of western North America are all early Famennian in age (see discussion above).

Suborder Chonetidina Muir-Wood, 1955  
 Superfamily Chonetoidea Bronn, 1862  
 Family Chonetidae Bronn, 1862  
 Subfamily Retichonetinae Muir-Wood, 1962



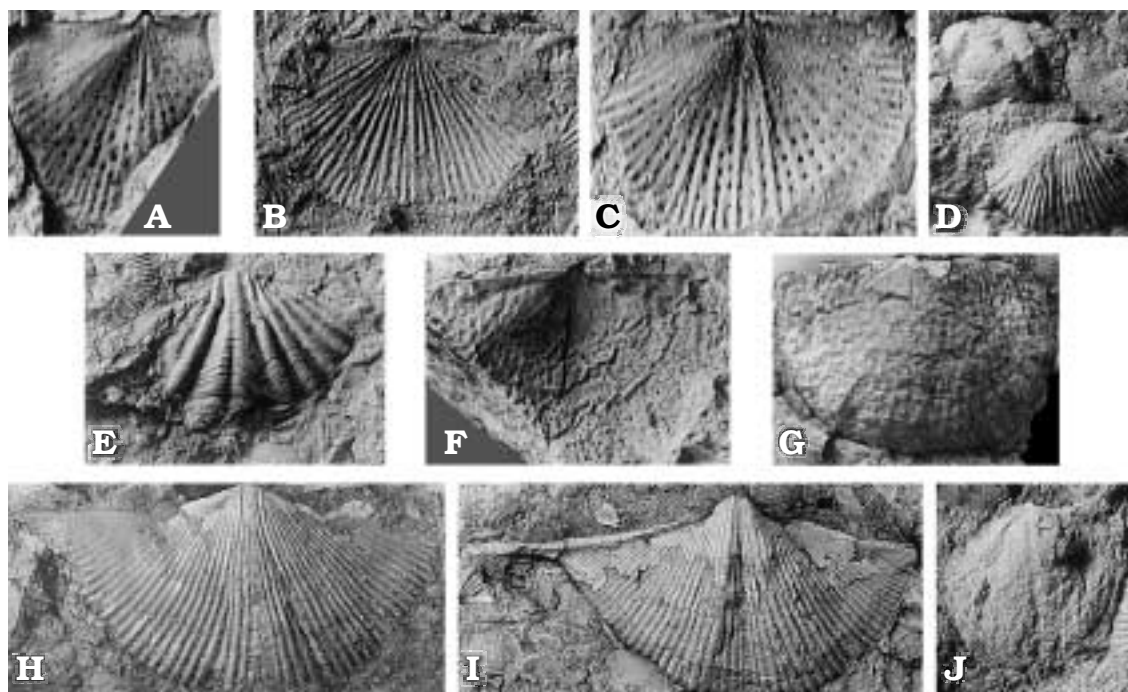


Fig. 4. Brachiopods from the shell bed in the Hanover Shale Member of the Java Formation. **A–D.** *Retichonetes* aff. *S. obscurus* Cooper and Dutro, 1982. **A.** Internal mold of dorsal valve, NYSM 15704 with low medial myophragm, simple sockets flanking the pit near base of cardinal process,  $\times 5.4$ . **B.** Upper exterior view of dorsal valve, NYSM 15710,  $\times 4.8$ . **C.** Internal mold of dorsal valve, NYSM 15705,  $\times 7$ . **D.** Ventral valve showing costellae with crushed and distorted ventral valve of *Ambocoelia* cf. *A. gregaria* in upper left, NYSM 15718,  $\times 3.3$ . **E.** *Tylothyris mesacostalis* (Hall, 1867), view of dorsal valve showing centric lamellose ornament and central groove on fold, NYSM 15711,  $\times 2.3$ . **F, G.** *Praewaagenoconcha speciosa* (Hall, 1867). **F.** Internal mold of dorsal valve with impression of medial myophragm and rugae along the postero-lateral margin, NYSM 15706,  $\times 1.7$ . **G.** External mold of dorsal valve showing radial spine bases with some exfoliated shell material, NYSM 15695,  $\times 1.5$ . **H, I.** *Cyrtospirifer hornellensis* Greiner, 1957. **H.** Exfoliated dorsal valve showing extended postero-lateral extremity, NYSM 15692. **I.** Ventral valve, NYSM 15691; both  $\times 1.8$ . **J.** *Ambocoelia* cf. *A. gregaria* Hall, 1867, upper view of flattened dorsal valve showing dorsal groove, NYSM 15719  $\times 3.5$ .

### Genus *Retichonetes* Muir-Wood, 1962

#### *Retichonetes* aff. *S. obscurus* Cooper and Dutro, 1982

Fig. 4A–D.

*Retichonetes obscurus*; Cooper and Dutro 1982: 58, pl. 11: 19–25.

**Material.**—Figured specimens NYSM 15704, NYSM 15705, NYSM 15718; unfigured specimens NYSM 15708, NYSM 15709, and NYSM 15710; and approximately 2,000 unnumbered complete and partial shells on surfaces of parts and counterparts of split slabs.

**Remarks.**—This small chonetid (4–8 mm in width) is the numerically dominant species in the fauna of the Hanover shell bed. This form was initially interpreted as a new genus by Day (1997). However, careful study of numerous specimens indicates that the chonetid in the Hanover Shale shell bed is a species of *Retichonetes* Muir-Wood (1962) close to *R. obscurus* Cooper and Dutro (1982) described from the Ready Pay and Box members of the Percha Formation of southern New Mexico. Cooper and Dutro (1982: fig. 7) show the Percha as possibly spanning the interval of the Upper *Pa. crepida* Zone to *Po. styriacus* Zone (lower–upper Famennian). The *Po. styriacus* Zone as shown in fig. 7 of Cooper and Dutro (1982) is equivalent to the Lower and Upper *Pa. postera* and Lower *Pa. expansa* zones of the current Famennian conodont zonation

(see revisions by Ziegler and Sandberg 1984: 183–184, figs. 1–4). *Retichonetes obscurus* from New Mexico is similar to the Hanover specimens in overall shape and size and numbers of costellae. The Hanover form differs by the presence of well preserved concentric growth lines on the rounded costellae and in the interspaces, and having a better developed dorsal septum than that shown for *R. obscurus* (Cooper and Dutro 1982: pl. 11: 24).

Another similar form *Retichonetes* sp. is illustrated by Schwimmer and Feldmann (1991: figs. 7.1–7.8) from the Famennian Chagrin Shale of northeast Ohio. Their shells are similar to the Hanover material in overall shape, size, and in the high angle (60 to 90°) that the oblique orthomorph spines arise from the posterior margin of the ventral valve. They do not mention the reticulated ornament typical of species of *Retichonetes* (Muir-Wood 1965: H428, fig. 286). Reticulated ornament is seen on shells of *R. obscurus* with well preserved shell material, produced where fine concentric growth lines cross the radial costellae. Spines along the ventral cardinal margins in both the Hanover specimens and *R. sp.* from the Chagrin Shale of Ohio (Schwimmer and Feldmann 1991) arise at high angles as is typical for the genus (see Muir-Wood 1962: 62, 1965: figs. 285, 286).

## Order Spiriferida Waagen, 1883

## Suborder Spiriferidina Waagen, 1883

## Superfamily Cyrtospiriferoidea Termier and Termier, 1949

## Family Cyrtospiriferidae Termier and Termier, 1949

## Subfamily Cyrtospiriferinae Termier and Termier, 1949

Genus *Cyrtospirifer* Nalivkin in Fredericks, 1924*Cyrtospirifer hornellensis* Greiner, 1957

Fig. 4H, I.

*Cyrtospirifer hornellensis*; Greiner 1957: 28–29, pl. 7: 1–5, 6 (not dorsal valve specimen on right-hand part of image of Yale Peabody Museum number 19435B), and 7.

**Material.**—Figured specimens NYSM 15691 and NYSM 15692.

**Remarks.**—The available specimens are consistent with the species as described by Greiner (1957: 29). It must be pointed out that Greiner (1957) illustrated at least two distinct genera under the name *C. hornellensis*. One of the two dorsal valves (his “larger, presumably gerontic, individual” of Yale Peabody Museum number 19435B) illustrated in his pl. 7 (fig. 6, right-hand specimen) represents a new genus, which will be described (Ma and Day personal communication 2001) from the lower Famennian of South China.

*Cyrtospirifer hornellensis* is about half the size (width), has a narrower sinus and fewer flank plications, and lacks the medial groove on the dorsal fold of the much larger *Cyrtospirifer sulcifer* (Hall and Clarke, 1894). That form serves as the nominal species for the lowest Famennian *C. sulcifer* Assemblage Zone of Dutro (1981: 80, figs. 2, 7). As defined, that zone spans the interval of the Canadaway Group, immediately above the Java Formation of New York. *Cyrtospirifer sulcifer* (Hall and Clarke, 1894) is not a true *Cyrtospirifer* and is considered here a species of *Pripyatospirifer* Pushkin (1996). According to Greiner (1957) his illustrated specimens of *C. hornellensis* were collected 140 feet (42.6 meters) below the top of the upper Frasnian Wiscoy Formation (now Java Formation) and overlying deposits of the lower Famennian “Casaseraga formation” (= Caneadea Formation of the modern nomenclature). Greiner portrays its upper range (see his fig. 4) as somewhere high in the lower Famennian. Thus far, our material represents its lowest Famennian occurrence directly associated with Lower *Pa. triangularis* Zone conodonts in the upper part of the Hanover Shale of eastern North America.

## Superfamily Ambocoelidoidea George, 1931

## Family Ambocoeliidae, George, 1931

Genus *Ambocoelia* Hall, 1860*Ambocoelia* cf. *A. gregaria* Hall, 1867

Fig. 4J.

*Ambocoelia umbonata* var. *gregaria*; Hall 1867: 195, pl. 44: 19–25.

*Ambocoelia gregaria*; Linsley 1994: 104, 233, pl. 126: 1–7.

**Material.**—Figured specimen NYSM 15719, crushed specimen of ventral valve shown in the upper left part of Fig. 5D, three additional specimens on same slab as aforementioned specimens (two ventral, one dorsal valve).

**Remarks.**—The dorsal valve shown in Fig. 5J (NYSM 15719) is comparable to Hall’s (1867) dorsal valve illustrated on his pl. 44 (fig. 19). The two unnumbered specimens of ventral valves have a ventral sinus originating near the beak as seen Hall’s (1867: pl. 44: 19–25) *A. gregaria*. Additional material is required to confirm this provisional species identification.

## Suborder Delthyridina Ivanova, 1972

## Superfamily Delthyridoidea Phillips, 1841

## Family Mucrospiriferidae Boucot, 1959

## Subfamily Tylothyridinae Carter, 1972

Genus *Tylothyris* North, 1920*Tylothyris mesacostalis* (Hall, 1867)

Fig. 4E.

*Spirifer mesacostalis*; Hall 1867: 240, pl. 40: 1, 2, 4–13; Hall and Clarke 1894: 16, 35, pl. 34: 32–34.

*Tylothyris mesacostalis* (Hall, 1867); Cooper 1944: 321–322, pl. 122: 20, 21; Linsley 1994: 234, pl. 127: 6–20.

**Material.**—Figured specimen NYSM 15711, and approximately 180 additional unnumbered specimens on parts and counterparts of split slabs.

**Remarks.**—This is a long ranging species in the Late Devonian of New York. It is the nominal species of Dutro’s (1981: 78, figs. 2, 7) middle Frasnian *Tylothyris mesacostalis* Assemblage Zone. Its range in the New York Upper Devonian is shown to begin in the upper part of the Sonyea Group (mid Frasnian) and terminates in the Conneaut Group at the top of the interval of Dutro’s (1981: figs. 2, 7) Famennian *Spinulicosta arctirostrata* Assemblage Zone.

## Conodonts

## Class Conodonti Branson, 1938

## Order Prioniodontida Dzik, 1976

## Family Icriodontidae Müller and Müller, 1957

Genus *Icriodus* Branson and Mehl, 1938*Icriodus alternatus alternatus* Branson and Mehl, 1934

Fig. 5D–F.

*Icriodus alternatus*; Branson and Mehl 1934: 225–226, pl. 13: 4–6 [fig. 4 = lectotype]; Klapper 1975: 69–70, *Icriodus* pl. 3: 5, 6.

*Icriodus alternatus alternatus* Branson and Mehl, 1934; Sandberg and Dreesen 1984: 158–159, pl. 2: 5, 11; see here for further synonymy.

**Remarks.**—The  $P_1$  (Pa, I) element of *Icriodus alternatus* is straight to slightly curved; the middle row of denticles are low, compressed, or poorly developed, and may alternate with or be fused to outer denticles. The basal cavity is expanded to widely flared under the posterior third of element. *Icriodus alternatus alternatus* is distinguished from *I. alternatus helmsi* by a  $P_1$  element in which the cusp is aligned with the medial denticles. Specimens from the upper Hanover

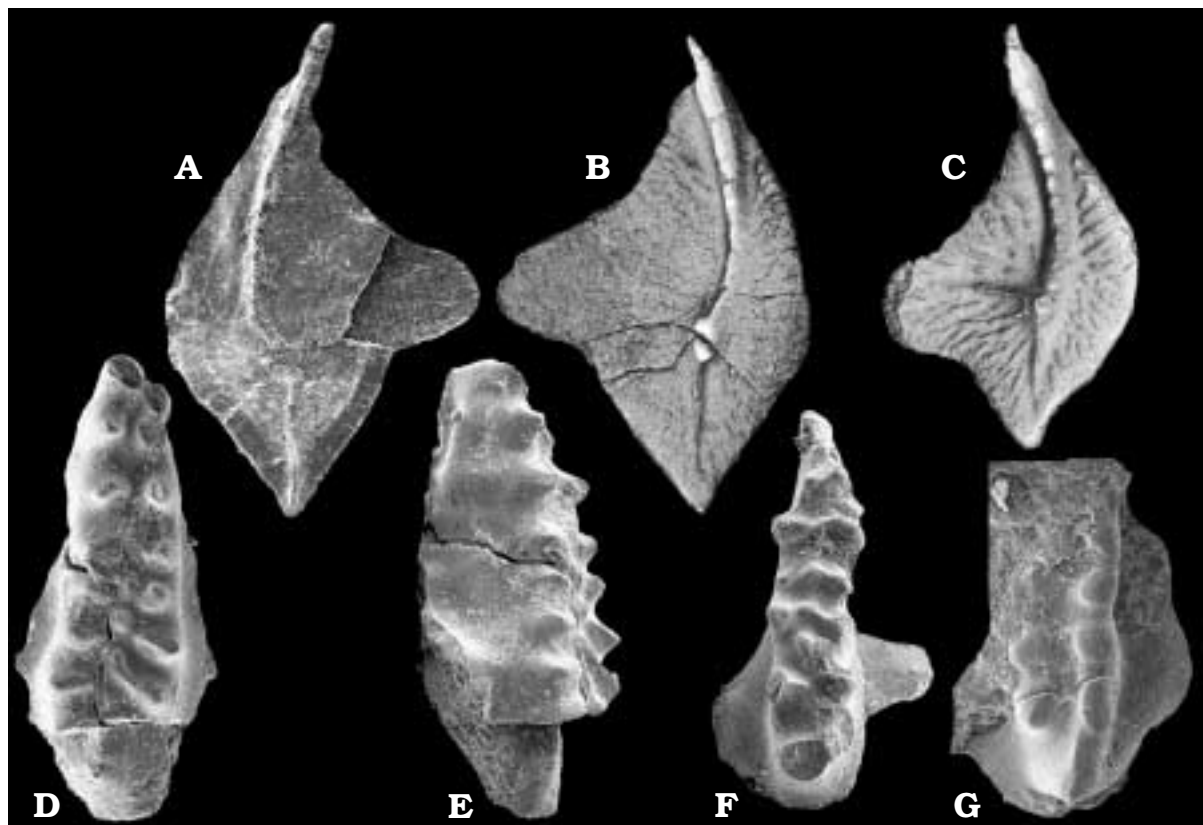


Fig. 5. Digital images from scanning electron microscope of conodont  $P_1$  (Pa) elements from the Hanover Shale Member of the Java Formation, brachiopod bed approximately 1.4 m above the Frasnian–Famennian boundary at Glade Creek, Bartz Road, Wyoming County, New York. All  $\times 60$ . **A–C.** *Palmatolepis triangularis* Sannemann, 1955. **A, B.** Lower view and inverse mirror-image of mold of upper surface of  $P_1$  (Pa) element, NYSM 15682. **C.** Inverse mirror-image of mold of upper surface of  $P_1$  (Pa) element, NYSM 15683. **D–F.** *Icriodus alternatus alternatus* Branson and Mehl, 1934. **D, E.** Upper and oblique outer views of broken  $P_1$  (Pa, I) element showing internal mold of posterior end, NYSM 15684. **F.** Upper view of  $P_1$  (Pa, I) element with missing inner posterior margin, NYSM 15685. **G.** *Icriodus alternatus helmsi* Sandberg and Dreesen, 1984, upper view of fractured and covered  $P_1$  (Pa, I) element, NYSM 15686 (specimen lost).

Shale possess rounded median denticles fused to the lateral denticles. This morphology is suggestive of *I. iowaensis* Youngquist and Peterson, 1947, but the lateral and median denticles are not aligned, as well as the fact that no axial ridge connects the medial denticles.

*Icriodus alternatus helmsi* Sandberg and Dreesen, 1984

Fig. 5G.

*Icriodus alternatus helmsi*; Sandberg and Dreesen 1984: 159, pl. 2: 1–4, 6–7.

**Remarks.**—The  $P_1$  (Pa, I) element of *Icriodus alternatus helmsi* is characterized by alignment of the cusp with the inner lateral denticles. Specimens in which the medial denticles are absent commonly occur in the Lower *Pa. triangularis* Zone through Middle *Pa. crepida* Zone (Sandberg and Dreesen 1984).

Order Ozarkodinida Dzik, 1976

Family Palmatolepidae Sweet, 1988

Genus *Palmatolepis* Ulrich and Bassler, 1926

*Palmatolepis triangularis* Sannemann, 1955

Fig. 5A–C.

*Palmatolepis triangularis*; Sannemann 1955: 327–328, pl. 24: 3 [= holotype]; Over 1997: 172, 10.1, 10.5.

**Remarks.**—The lowest occurrence of *Palmatolepis triangularis* has been used to define the base of the Famennian and the Lower *Pa. triangularis* Zone, although rare specimens occur in the uppermost Frasnian prior to the final extinction event and horizon recognized as the Frasnian–Famennian boundary (Klapper et al. 1994; Schülke 1995; Over 1997). In practice the boundary is recognized by the absence (extinction) of Frasnian conodont species and the lowest abundant occurrence of *Pa. triangularis*.

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