Journal of Paleontology, 87(2), 2013, p. 277–288
Copyright © 2013, The Paleontological Society
0022-3360/13/0087-277$03.00

REVISED TAXONOMY AND AUTECOLOGY FOR THE BRACHIOPOD GENUS *AMBOCOELIA* IN THE MIDDLE AND LATE DEVONIAN NORTHERN APPALACHIAN BASIN (USA)

JAMES J. ZAMBITO IV[1] AND MENA SCHEMM-GREGORY[2]

[1]West Virginia University, Department of Geology and Geography, Morgantown, West Virginia 26506-6300, USA, <james.zambito@mail.wvu.edu>; and [2]Centro de Geosciências e Departamento de Ciências da Terra, Universidade de Coimbra, Largo Marquês de Pombal, P-3000-272 Coimbra, Portugal, <Mena.Schemm-Gregory@dct.uc.pt>

ABSTRACT—Brachiopods belonging to *Ambocoelia* occur ubiquitously in Middle and Upper Devonian strata of the northern Appalachian Basin. Originating during the Eifelian, *Ambocoelia umbonata* persisted through numerous biocrises, but went extinct during the late Frasnian Kellwasser Crisis. *Ambocoelia umbonata* var. *gregaria*, the only other form of this genus that is present within the New York Devonian succession, originated around the time of the Kellwasser Crisis and persisted locally into at least the latest Famennian. Examination of syntypic material of *A. umbonata* var. *gregaria* has resulted in the taxonomic revision of this form and elevation to *Ambocoelia gregaria*. Comparison of ontogenetic stages and environmental preferences of *A. umbonata* and *A. gregaria* suggests that the latter exhibits a paedomorphic morphology that may have evolved from *A. umbonata* through neoteny. Furthermore, these comparisons also give new autecological insights for *Ambocoelia*, suggesting that *A. umbonata* was capable of living in a diversity of environments by using a variety of life positions, whereas *A. gregaria* was likely more specialized. This taxonomic revision provides the necessary framework for revising the biostratigraphic range of *Ambocoelia* and, furthermore, the evolutionary history of this genus in relation to the Lower Kellwasser Event.

INTRODUCTION

AMBOCOELIA GREGARIA Hall, 1860 was originally described from specimens collected from various localities and stratigraphic levels within the Upper Devonian Appalachian Basin of New York State, and distinguished from the Middle Devonian form *Ambocoelia umbonata* Conrad, 1842 (Fig. 1; Hall, 1843, 1857, 1860, 1867). Shortly thereafter, Hall (1867, p. 261) re-described this form as *A. umbonata* var. *gregaria*, noting that its similarity to the Middle Devonian form made him hesitant to classify it as a distinct species. Subsequent studies of the northern and central Appalachian Basin referred to this form inconsistently, as either *A. umbonata* var. *gregaria* (Williams, 1882, 1884, 1907, 1913; Lesley, 1892; Luther, 1901), or *A. gregaria* (Williams, 1903; Williams and Kindle, 1905; Kindle, 1906). Around this same time, Schuchert (1897) synonymized *A. umbonata* var. *gregaria* with *A. gregaria*, although no justification was given. Prosser (1912, p. 539) further described this form and discussed its taxonomic status, however, he ultimately referred to it as *Ambocoelia umbonata* var. *gregaria*. Over the subsequent century, this form was exclusively referred to as *A. gregaria* (Clarke, 1917; Caster, 1934; Stainbrook, 1942; Dutro, 1981; McGhee, 1981; McGhee and Sutton, 1981, 1983; Linsley, 1994). Most recently, Day and Over (2002) made cursory descriptions of this form and noted the inconsistencies regarding the nomenclature of this taxon, and paleoecological studies have simply referred to Frasnian forms as *Ambocoelia* sp. (Bush and Brame, 2010).

Confusion in ambocoeliid brachiopod taxonomy of the Appalachian Basin is perhaps expected, given that Middle Devonian forms were only recently taxonomically revised (Goldman and Mitchell, 1990). As noted by Day and Over (2002), the ranges and systematic status of ambocoeliid brachiopods within the Late Devonian of the northern Appalachian Basin needs further study. This is particularly true in understanding the role of the Kellwasser Crisis (Frasnian/Famennian extinction) in ambocoeliid evolution. As discussed in Day and Over (2002) and summarized in Figure 2, there is uncertainty concerning the range of *A. gregaria* and *A. umbonata* near the Frasnian/Famennian boundary, but the current consensus seems to be that *A. umbonata* goes extinct at or near the Lower Kellwasser Event, and at around the same time, *A. gregaria* first appears. Clarifying the biostratigraphic ranges of these taxa is regionally important, as both *A. umbonata* and *A. gregaria* are the longest-lived ambocoeliids within the northern Appalachian Basin, and are both major components of Middle and Upper Devonian communities throughout the Appalachian Basin (Fig. 2; McGhee and Sutton, 1981, 1983, 1985; Zambito et al., 2008; Bush and Brame, 2010). Furthermore, if the last appearance of *A. umbonata* and the first appearance of *A. gregaria* do indeed correspond to the Lower Kellwasser Event, then ambocoeliid biostratigraphy could allow recognition of this event in coarse siliciclastic-dominated successions in which conodont biostratigraphy is hindered.

Examination of relatively well-preserved material of *A. umbonata* var. *gregaria* from the Famennian of New York has resulted in the taxonomic elevation of this form to *A. gregaria*. The updated description herein provides the taxonomic basis for biostratigraphic revision of ambocoeliids through the Frasnian/Famennian boundary interval. Furthermore, comparison of the morphology and habitat preferences of *A. gregaria* to its probable ancestor, *A. umbonata*, suggests that *A. gregaria* was more specialized. Comparison of ontogenetic sequences of *A. gregaria* and *A. umbonata* are used to infer the evolution of the Late Devonian *A. gregaria* from the Middle Devonian *A. umbonata* through neoteny.

GEOLOGIC SETTING

The Middle and Upper Devonian Appalachian Basin deposits of New York State were deposited in the foreland basin that formed during the Acadian Orogeny, as the Laurentian and

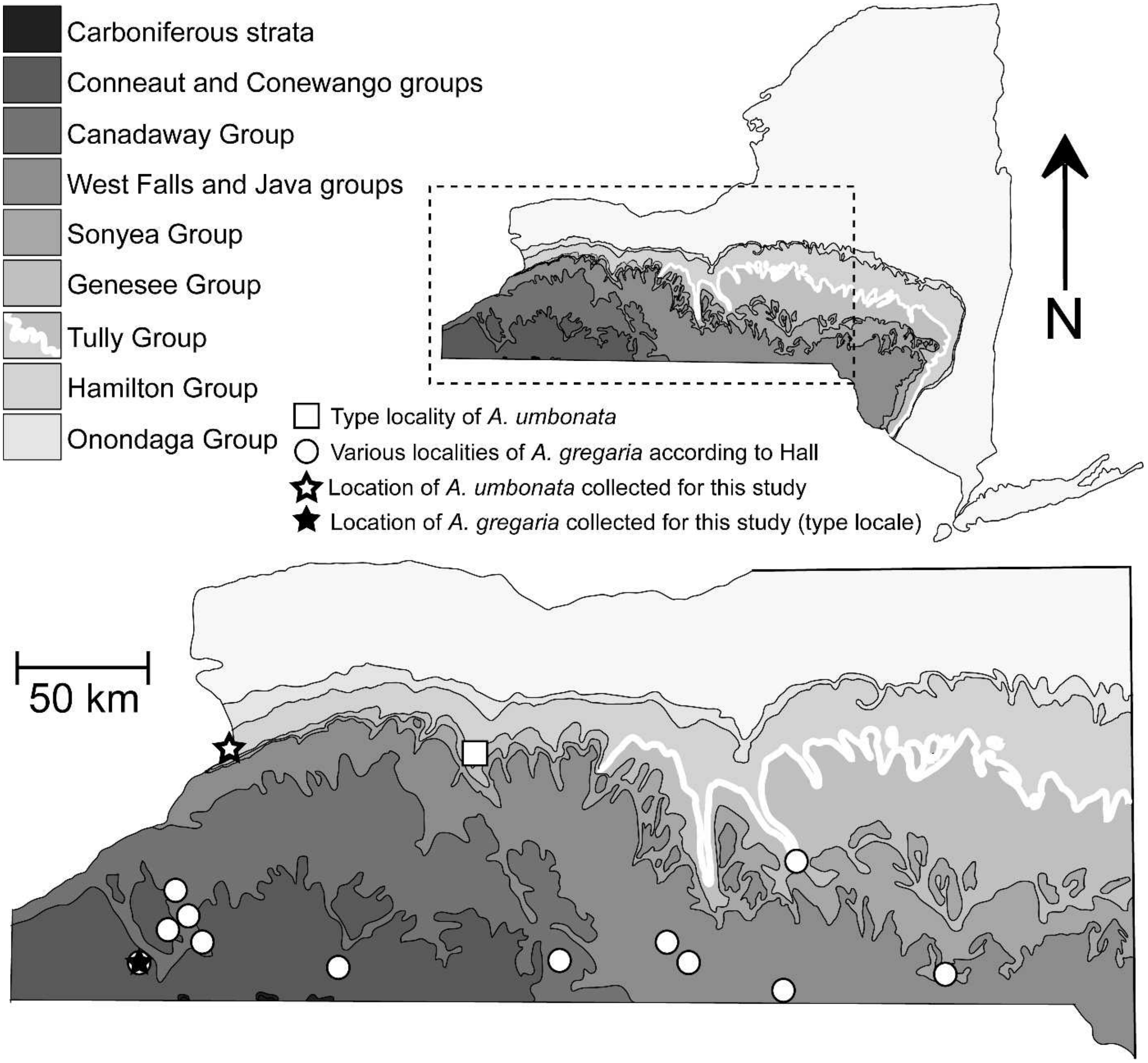

FIGURE *1*—Geologic map of Middle and Upper Devonian strata of New York State (upper) and western and central New York (within dashed box, lower) showing the location of samples collected in this study and the type localities of specimens used in the original taxonomic descriptions. Map is adapted from Rogers and others (1990). Type and other localities as described in Conrad (1842) and Hall (1843, 1860, 1867, 1870).

Avalonian terranes converged obliquely (Ettensohn, 2008; Ver Straeten, 2010). Erosion of the collisional highlands produced a progradational complex, the "Catskill Delta," which advanced in a generally westward direction and largely filled the foreland basin by the early Mississippian. Hall (1860, 1867) described the brachiopod *Ambocoelia gregaria*, and later, as *A. umbonata* var. *gregaria*, from the Upper Devonian "Chemung Group" deposits from localities across New York State (Fig. 1). The "Chemung Group," following recognition that it represented a diachronous facies, has been divided into relatively synchronous stratigraphic units (Fig. 2; Chadwick, 1933, 1935; Baird and Lash, 1990). The term "Chemung facies" is representative of a siltstone-dominated, fossiliferous delta platform setting (Baird and Lash, 1990, and references therein).

MATERIALS AND METHODS

Well preserved specimens of *Ambocoelia gregaria* are difficult to find because most of the Upper Devonian sediments within the Appalachian Basin are siliciclastic-dominated, typically resulting in moldic preservation. Some of the syntypical specimens described by Hall (1843, 1867) were non-moldic, and were reposited with information stating they were collected from Dexterville (now East Jamestown), New York (Whitfield and Holvey, 1898). Although no specific locality information was given by Hall in his descriptions, Caster (1934, p. 64) describes outcrops of the Dexterville Siltstone Member as, "the brick quarries, south of the Chadakoin River in East Jamestown, formerly known as Dexterville." We located a section matching Caster's description, an abandoned quarry at East Jamestown along Allen Street,

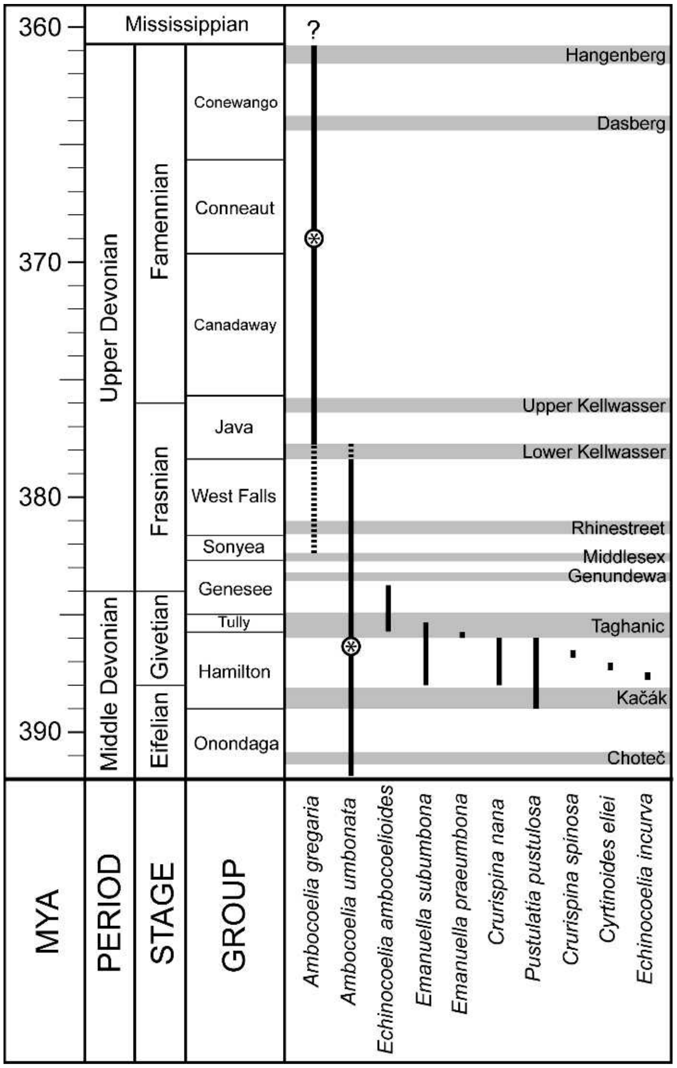

FIGURE 2—Biostratigraphic ranges of Ambocoelioidea in the northern Appalachian Basin during the Middle and Late Devonian. Asterisks represent the stratigraphic position of material collected for this study. Dashed lines represent uncertainty in biostratigraphic range (Day and Over, 2002). Timescale is based on Kaufmann (2006). Stratigraphic nomenclature based on Rogers and others (1990), Over (2007), Over and others (2009), and Baird and others (2009), and placed within the timescale of Kaufmann (2006) using the conodont data provided by Ziegler and others (1976), Over (1997, 2002, 2007), House (2002), DeSantis and others (2007), and Over and others (2009). Biostratigraphic data for Ambocoelioidea was compiled from Williams (1913), Cooper and Williams (1935), Dutro (1981), Goldman and Mitchell (1990), Linsley (1994), Johnson and others (2006), Zambito and Mitchell (2006), Baird and Brett (2008), and Zambito and others (2012). Biocrises recognized in the Northern Appalachian Basin are based on House (1985, 2002), Over (2002), Baird and others (2009), and Brett and others (2009).

south of its intersection with Buffalo Street (Jamestown 7.5 minute USGS quadrangle map), and collected additional specimens for this study. Collections come from the Famennian Dexterville Siltstone Member, Chadakoin Formation, Conneaut Group (Figs. 1, 2) (the following references contain detailed locality and stratigraphic information: Hall, 1843, 1867; Caster, 1934; Baird and Lash, 1990). At this locality, abundant specimens of *A. gregaria* with preserved shell material were found within a lens-like horizon of well-sorted quartz sandstone; however, no articulated specimens were present in this bed. Collection from this horizon resulted in 'crack-outs,' specimens in which the shell material was commonly fractured during the extraction process. To better understand the internal morphology of *A. gregaria*, we collected in situ and float slabs of siltstone and fine-grained sandstone containing moldic material of *A. gregaria*. In his descriptions of *A. gregaria*, Hall also listed numerous localities where he found this form (Fig. 1). Additional syntypic localities exist (Hall, 1843; Whitfield and Holvey, 1898), but were not sampled for this study.

For comparison, specimens of *Ambocoelia umbonata* were collected from the "*Ambocoelia umbonata* Beds," exposed along Buffalo Creek at Bullis Road, near Elma, New York from the Middle Devonian (Givetian) Windom Shale Member, Moscow Formation, Hamilton Group (Figs. 1, 2) (the following references contain detailed locality and stratigraphic information: Grabau, 1898; Zambito and Mitchell, 2006). This is the same stratigraphic level (Moscow Formation) that the type specimens were collected (Conrad, 1842). Specimens of *A. umbonata* were collected from this locality because they are abundant, well preserved, and easily removed from the calcareous mudstone matrix.

All specimens are reposited at the Paleontological Research Institution, Ithaca, New York, U.S.A. Although no articulated material was available, a ventral valve of *A. gregaria* (not


1a
1b
1c
4a
2a
2b
2c
4b
3a
3b
4c
5a
5b
4d
6
7a
7b
8a
8b
8c
9
10
11
10 mm

shown here; PRI 55917) was serially-sectioned transversally. One specimen of *A. umbonata* was also serially-sectioned transversally in order to reconstruct internal shell morphology. Latex casting of moldic material was used to describe the internal structures of *A. gregaria*. Drawings were done with the help of a camera lucida. Specimens were coated with ammonium chloride prior to photographing. Preliminary geometric morphometric analysis of these two species was undertaken but the lack of distinct external landmarks resulted in inconclusive results. Additional specimens of *A. gregaria* are reposited as a bulk collection (PRI 55916).

SYSTEMATIC PALEONTOLOGY

Institutional abbreviations used include: AMNH, American Museum of Natural History, New York, New York, U.S.A.; PRI, Paleontological Research Institution, Ithaca, New York, U.S.A.; YPM, Yale University Peabody Museum, New Haven, Connecticut, U.S.A.

Suborder Spiriferdina Waagen, 1883
Superfamily Ambocoelioidea George, 1931
Family Ambocoeliidae George, 1931
Subfamily Ambocoeliinae George, 1931
Genus Ambocoelia Hall, 1860

Type species.—*Ambocoelia umbonata* (Conrad, 1842).

Remarks.—Although beyond the scope of this paper, it is worth mentioning that the diagnosis of the genus *Ambocoelia* and the species assigned to it are in need of some revision. First, the genus diagnosis is planoconvex to concavoconvex, based on the type species *A. umbonata* (Johnson et al., 2006). However, most other species assigned to *Ambocoelia* are ventribiconvex to planoconvex, including: *A. capillata* Cooper and Dutro, 1982; *A. ectypa* Baranov and Alkhovik, 2006; *A. gregaria* (see below); *A. recidiva* Johnson and Trojan, 1982; and *Ambocoelia* sp. indet. Cooper and Dutro, 1982. Second, although *A. umbonata* does not possess spines, a number of constituent species do, including: *A. recidiva*, with radially arranged spines, transitional to co-occurring forms of *Echinocoelia*; *A. fimbriata* Claypole, 1883, with fine spines in regular concentric rows; and *A. minuta* White, 1862, with surface covered with fine setae (probably spines), which when removed, leave a pustulose appearance. These forms may belong to the Ambocoeliidae genera *Crurispina* or *Echinocoelia*, and possibly even previously described species therein.

AMBOCOELIA GREGARIA (Hall, 1860)
Figures 3.1–3.11, 4.1–4.9

1843 *Orthis unguiculus* Hall, p. 267, fig. 5a–5d.
1860 *Ambocoelia gregaria* Hall, p. 81.
1867 *Ambocoelia umbonata* var. *gregaria* Hall, p. 261, pl. 44, figs. 19–25.
1912 *Ambocoelia umbonata* var. *gregaria* Hall; Prosser, p. 539, pl. 31, figs. 6–9.
1939 *Ambocoelia umbonata* "*gregaria*" Hall; Willard, pl. 22, figs. 12–14.
1942 *Ambocoelia gregaria* Hall; Stainbrook, p. 885, pl. 1, fig. 23.
1994 *Ambocoelia gregaria* Hall; Linsley, p. 104, 233, pl. 126, figs. 1–7.
2002 *Ambocoelia* cf. *Ambocoelia gregaria* Hall; Day and Over, p. 198, fig. 4d, 4j.

Diagnosis.—Differs from *A. umbonata* externally in its larger size, plano- to ventribiconvex rather than plano- to concavoconvex shape, more elongate ventral valve with a less regular convexity, more subangular margins of the sulcus (although both forms have a deeper ventral sulcus than most species assigned to *Ambocoelia*), greater convexity and distinct medial groove in the dorsal valve, and a less incurved umbo which never conceals the delthyrium opening (which in contrast is often partially to completely blocked, and smaller, in *A. umbonata*). Differs from *A. umbonata* interiorly by a well-developed median crest (myophragm) running through the ventral valve muscle field (Figs. 3.9, 3.11, 5.1, 5.2), whereas muscular impressions on the ventral valve of *A. umbonata* are rarely observed and the myophragm is low and located posteriorly (Fig. 6.3; Goldman and Mitchell, 1990); the presence of linear callosities flanking the ventral valve muscle field (Fig. 5.1, 5.2), as Hall (1867, p. 261) noted in describing *A. gregaria*, are a feature not observed in *A. umbonata* (Fig. 6.3; although both possess callosity within the anterior portions of the ventral valve); the position of the adductor muscle scars on the dorsal valve (Figs. 5.3, 6.4, 6.8) which are much less square as well as broader in *A. gregaria*, possibly related to the more defined dorsal myophragm that appears to correspond to the exterior medial dorsal groove, and suggest that *A. gregaria* possessed larger musculature relative to *A. umbonata*.

Differs from *A. recidiva* by its well-developed ventral sulcus and lack of spines; from *A. capillata* by its larger size and lack of distinct costae flanking the sulcus; from *A. ectypa* by its larger size and lack of sharp projections along the shell related to paused shell growth, although pauses in growth are clearly evident in *A. gregaria* (Fig. 3.4a, 3.4c), and even more so in *A. umbonata* (Fig. 6.1a–6.1c).

Description.—Shells ventribiconvex to planoconvex; rather large for *Ambocoelia*, typically greater than or equal to 1 cm. The exterior of shells exhibit varying proportions of length to width, although ventral valve can be elongated relative to dorsal valve; micro-ornamentation of fine concentric growth lamellae and weak radial striae; well-developed ventral sulcus with subangular margins extending from near the beak to the anterior valve margin; dorsal valve typically convex with distinct medial groove; anterior commissure rectimarginate to slightly uniplicate; ventral valve with slightly incurved umbo and apsacline interarea; delthyrium is large, open, extends to near umbo and is bound by thin deltidial lamellae. Interior of ventral valve is posteriorly thickened and has a well-defined myophragm running through muscle field; muscular impressions are limited at their sides by broad linear callosities opposite the myophragm that do not appear to be dental plates; pedicle collar difficult to identify in material available, likely minute, closing apex of delthyrium. Interior of the dorsal valve possesses adductor muscle scars that

←
Figure 3—Ventral valve, *Ambocoelia gregaria* Hall, 1867 from an abandoned quarry at Dexterville (now East Jamestown), New York from the Famennian (Upper Devonian) Dexterville Siltstone Member, Chadakoin Formation, Conneaut Group. All specimens coated with ammonium chloride: *1*, upper (*a*), posterior (*b*), and lateral (*c*) views of external ventral shell, PRI-55918; *2*, posterior (*a*), upper (*b*), and lateral (*c*) views of external ventral shell, PRI-55919; *3*, upper (*a*) and lateral (*b*) views of external ventral shell, PRI-55920; *4*, upper (*a*), posterior (*b*), lateral (*c*) views of external ventral shell, and, detailed view of micro-ornamentation (d), scale bar = 1 mm, PRI-55921; *5*, upper (*a*) and posterior (*b*) views of external ventral shell, note the open delthyrium, PRI-55922; *6*, upper view of external ventral shell, PRI-55923; *7*, upper (*a*) and lateral (*b*) views of external ventral shell, PRI-55924; *8*, upper view of external ventral mold (*a*) and lateral (*b*) and upper (*c*) views of latex cast of it, PRI-55925; *9*, upper view of internal ventral mold, PRI-55926; *10*, upper view of internal ventral mold, PRI-55927; *11*, upper view of internal ventral mold, PRI-55928.

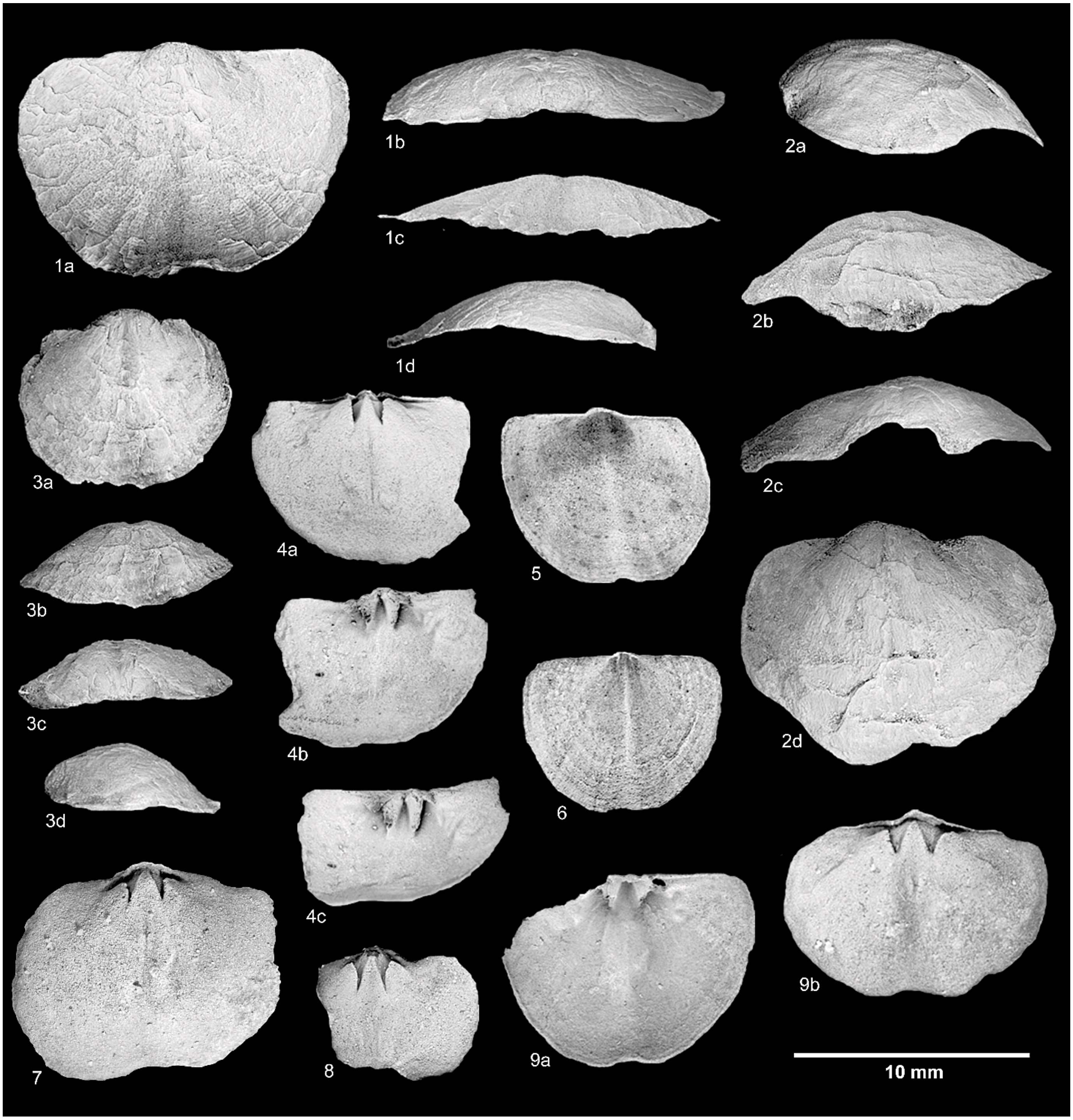

FIGURE 4—Dorsal valve, *Ambocoelia gregaria* Hall, 1867 from an abandoned quarry at Dexterville (now East Jamestown), New York from the Famennian (Upper Devonian) Dexterville Siltstone Member, Chadakoin Formation, Conneaut Group. All specimens coated with ammonium chloride: *1*, upper (*a*), posterior (*b*), anterior (*c*), and lateral (*d*) views of external dorsal shell, PRI-55929; *2*, lateral (*a*), anterior (*b*), posterior (*c*), and upper (*d*) views of external dorsal shell, PR-55930; *3*, upper (*a*), anterior (*b*), posterior (*c*), and lateral (*d*) views of external dorsal shell, PRI-55931; *4*, upper view of internal dorsal mold (*a*) and upper (*b*) and oblique anterior (*c*) views of latex cast of it, PRI-55932; *5*, upper view of external dorsal mold, 55933; *6*, upper view of external dorsal mold, PRI-55934; *7*, upper view of internal dorsal mold, PRI-55935; *8*, upper view of internal dorsal mold, PRI-55936; *9*, upper views of latex cast (*a*) and internal dorsal mold (*b*), PRI-55937.

are typically poorly preserved, broad, somewhat elongated, located anteriorly, and not well incised; dental sockets formed by inner socket ridge and valve wall; outer hinge plates are long and thick; crural plates not observed, but may be underneath outer hinge plates; spires not observed; cardinal process appears to be bilobed, but is poorly represented in latex molds.

Material.—Approximately one hundred specimens of topotypical material from East Jamestown (previously Dexterville), New York State were collected and reposited at PRI. Additional type material of this species was also examined, including: syntype AMNH 6022, Hall (1867; p. 261, pl. 44, figs. 20–22); syntypes AMNH 37459 and AMNH 3760, unfigured specimens

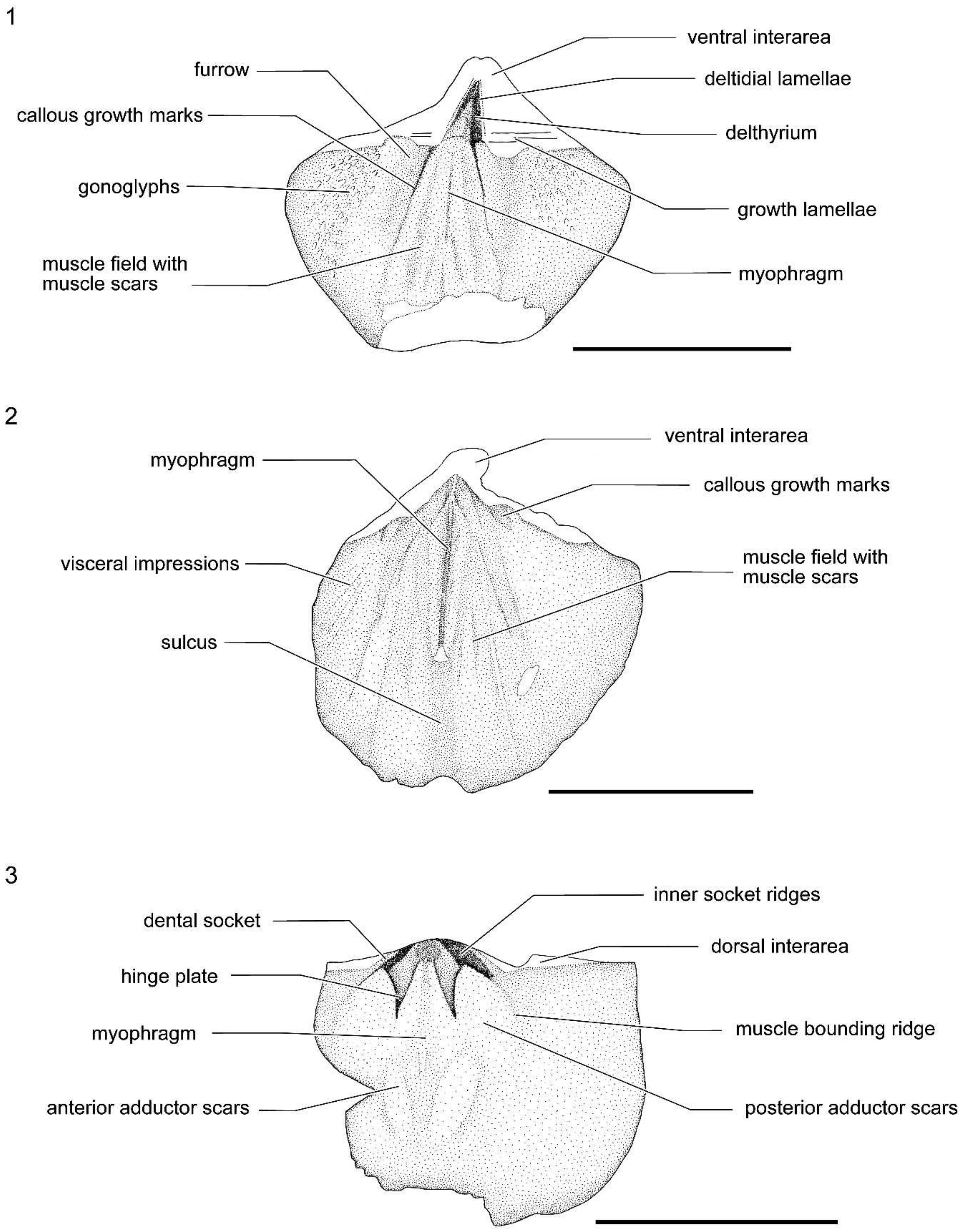

FIGURE *5*—Drawings of internal molds of *Ambocoelia gregaria* Hall, 1867, from an abandoned quarry at Dexterville (now East Jamestown), New York from the Famennian (Upper Devonian) Dexterville Siltstone Member, Chadakoin Formation, Conneaut Group. *1*, ventral internal mold, PRI-55938; *2*, ventral internal mold, PRI-55928; *3*, dorsal internal mold, PRI-55936. Scale bars=0.5 cm. Callous growth marks, muscle fields and scars, deltidial lamellae, growth lamellae, myophragms, muscle bounding ridge, dental sockets, hinge plates, and inner socket ridges are preserved as negative forms.

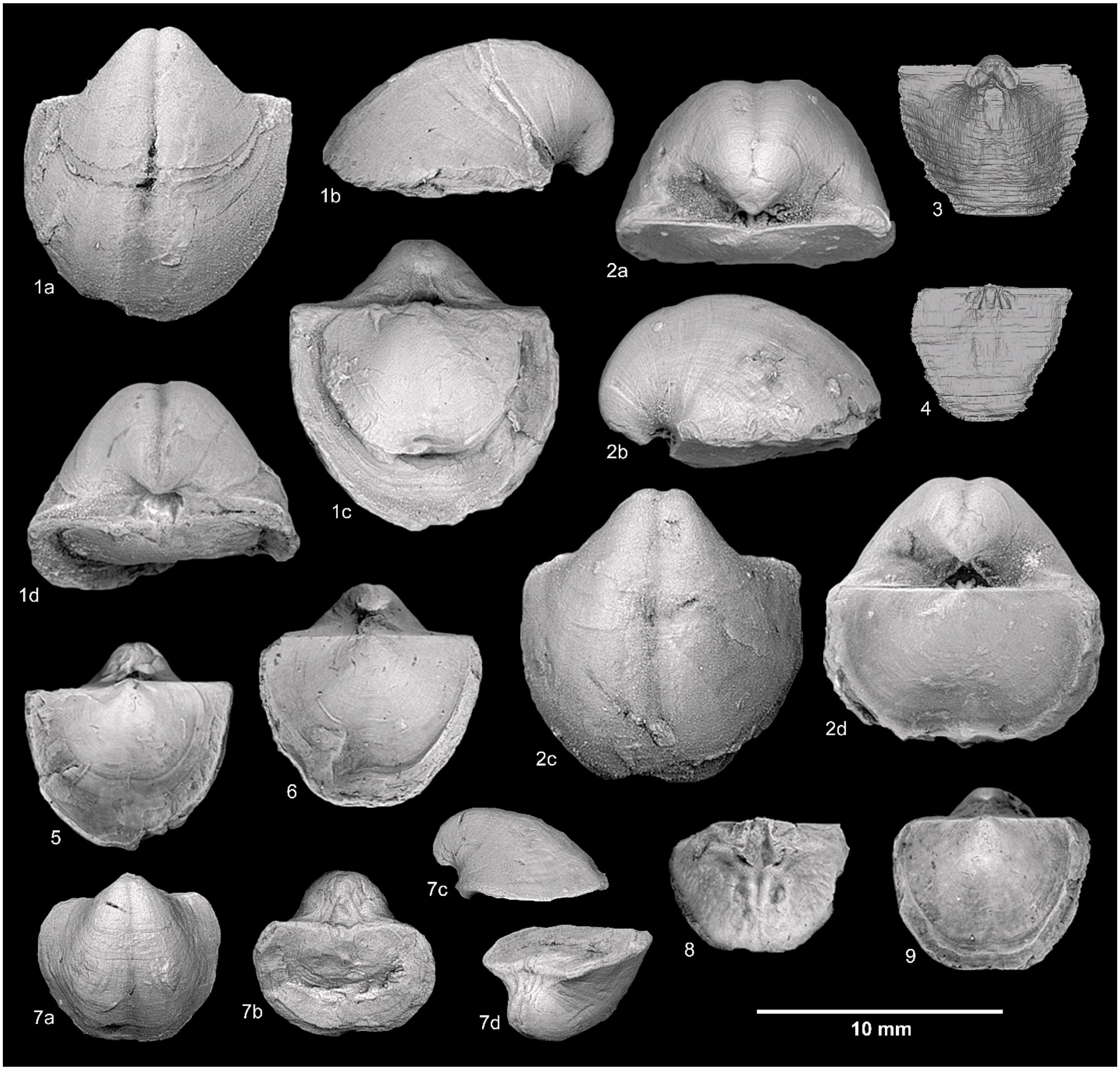

FIGURE 6—*Ambocoelia umbonata* Conrad, 1842, from Elma, New York, from the Givetian (Middle Devonian) Windom Shale Member, Moscow Formation, Hamilton Group. All specimens coated with ammonium chloride except *3* and *4*: *1*, ventral (*a*), lateral (*b*), dorsal (*c*), and posterior (*d*) views of articulated shell, PRI-55892; *2*, posterior (*a*), lateral (*b*), ventral (*c*), and dorsal (*d*) views of articulated shell, PRI-55893, note that shell is fractured and material is missing along commissure; interiors of ventral (*3*) and dorsal (*4*) valves reconstructed from a serial-sectioned, articulated specimen, PRI-55899, note absence of well-developed myophragm and lack of linear callous growths in the interior of ventral valve; *5*, dorsal view of articulated shell, PRI-55894; *6*, dorsal view of articulated shell, PRI-55895; *7*, ventral (*a*), dorsal (*b*), lateral (*c*), and oblique lateral (*d*) views of articulated juvenile shell, PRI-55896; *8*, internal dorsal valve, PRI-55897; *9*, dorsal view of articulated shell, PRI-55898.

associated with AMNH 6022; hypotype YPM S-3626, Stainbrook (1942; p. 885, pl. 1, fig. 23).

Occurrence.—*Ambocoelia gregaria* occurs within the northern Appalachian Basin from at least the Frasnian lower Java Group (though possibly the Frasnian Sonyea Group) to the Fammenian Conewango Group (Figs. 1, 2). *Ambocoelia gregaria* has not been reported post-Devonian in the northern Appalachian Basin, but may occur in the Mississippian (Kinderhookian) of western North America (Crickmay, 1952). This species is also known from the western (Ohio) and central Appalachian Basin during the Frasnian (Prosser, 1912; McGhee and Sutton, 1981, 1983).

Remarks.—In re-examining *A. gregaria*, it is apparent that this form possesses a number of features, both internal and external, that suggest this is not a variation of *A. umbonata*, but a unique species as originally suggested by James Hall.

ORIGIN OF A. GREGARIA

The morphology of *Ambocoelia gregaria* is more similar to juveniles of *A. umbonata* than the mature form. Juvenile specimens of *A. umbonata* possess a delthyrium that is unrestricted by the curvature of the umbo (Fig. 6.7). Similarly, *A. gregaria* never obtains an umbonal curvature greater than that exhibited by juvenile forms of *A. umbonata* (Fig. 3). Furthermore, in some specimens of *A. umbonata* the juvenile portions of the dorsal valve are rather convex (Fig. 6.1c), similar to *A. gregaria*. This may suggest that *A. gregaria* evolved from *A. umbonata* through paedomorphosis. Goldman and Mitchell (1990) suggested that the paedomorphic morphology of *A. umbonata*, i.e., the relatively simplified morphology, small size, and opportunistic ecology evolved through progenesis, the accelerated sexual maturation which causes a suspension of somatic development while the organism is still in a relatively juvenile state compared to its ancestor. Alternatively, paedomorphosis can also result from neoteny, i.e., somatic development that is retarded relative to sexual maturation; species derived through neoteny are larger than their ancestors, exhibit longer generation times, and more specialized ecologies (Gould, 1977). *Ambocoelia gregaria* is generally larger than *A. umbonata* (Figs. 3, 4, 6; Hall, 1867). In our examination of hundreds of mature specimens of each species, we observed that *A. gregaria* typically exhibits more pauses in shell growth than *A. umbonata*, suggesting a relatively longer generation time. Furthermore, McGhee and Sutton (1983) concluded that the less specialized *A. umbonata* was relatively more abundant and also lived in a more diverse suite of environments than *A. gregaria*. Therefore, we propose that *A. gregaria* evolved from *A. umbonata* through neoteny.

MODE OF LIFE

An extensive amount of literature has discussed the life orientation of *Ambocoelia* since this genus is often found in siliciclastic-dominated facies with limited opportunities for pedicle attachment sites, yet possessed an open delthyrium and, presumably, a functional pedicle (Caldwell, 1967; Bray, 1969, 1972; Bowen et al., 1974; Thayer, 1974; Flessa and Bray, 1977; Goldman and Mitchell, 1990; McGhee and Sutton, 1981). However, as noted by Goldman and Mitchell (1990), *A. umbonata* was likely a paedomorphic form, and therefore the presence of an open delthyrium may have no immediate function but was instead a juvenile feature carried forward in the course of paedomorphic evolution. Additionally, Goldman and Mitchell (1990; see also Fig. 6) also noted that the continued umbonal curvature through ontogeny typically results in a blocked delthyrium in mature specimens of *A. umbonata* and suggested the functional loss, or possibly reduction, of the pedicle. However, a smaller, branching pedicle with a rooting morphology like, for example, in Recent *Chlidonophora*, could still have been present (Rudwick, 1970; Bowen et al., 1974). Caldwell (1967) suggested that there was no reason that Middle Devonian *Ambocoelia* could not have had a functional pedicle, but on softer substrates, the ventral valve could have embedded within the substrate. Bray (1969) also argued that *A. umbonata* may have lived in both orientations: 1) attached by a pedicle, and dorsal valve down, on firmer substrates; and 2) on softer substrates the umbo of *A. umbonata* would have sunk into the mud and the pedicle would have pulled free allowing the ventral valve to rotate into a reclined position. In our study of hundreds of specimens of *A. umbonata*, we observed predatory boreholes and encrusting organisms on both the ventral and dorsal valves, suggesting that life orientation was variable.

Although we did not observe a preferred shell orientation within the small clusters of *A. umbonata* from the Windom Member at Elma, Bray (1972) noted that in three different clusters from the slightly older Wanakah Shale Member (Ludlowville Formation, Hamilton Group) in western New York there is a four-fold increase in dorsal valve down orientation from cluster bottom to top. This suggests that when a hard substrate was available, for example, once a cluster was established, *A. umbonata* preferentially lived dorsal-valve down and likely attached by a pedicle (Fig. 7.1). The alternative, ventral valve down orientation, may have been an adaptation for living on the soft substrate at the cluster edge or during initial cluster development. Indeed, *A. umbonata* possesses many morphological features that suggest adaptation for living ventral valve down. The thick, secondary callous shell deposits within the umbonal region of the ventral valve would have likely helped to anchor ventral-down individuals of *A. umbonata* on a soft substrate (Fig. 6.3, 7.1; Richardson, 1981; Goldman and Mitchell, 1990). Furthermore, the concavo-convex shell of *A. umbonata* would have been well-suited for keeping the anterior commissure above the substrate while in a ventral valve down position (Rudwick, 1970).

It is reasonable to infer that *A. umbonata* tolerated different substrate conditions by utilizing varying life orientations given that it was a generalist, widespread in both siliciclastic and carbonate facies, as well as oxygenated and dysoxic environments (McGhee and Sutton, 1981, 1983, 1985; Goldman and Mitchell, 1990; Zambito and Mitchell, 2006; Brett et al., 2007; Zambito et al., 2008; Bush and Brame, 2010). This versatility also enabled *A. umbonata* to act as a pioneer species in muddy, dysoxic settings. Flessa and Bray (1977, p. 353) suggested that clusters of *A. umbonata*, formed through the recruitment of *Ambocoelia* spat through active larval selection of adult *Ambocoelia* shells for attachment, provided "islands of firm substrate amidst a turbid, flocculent mud bottom" for other epifaunal organisms. Additionally, the inferred short generation time, as well as the dominance of *A. umbonata* in low diversity assemblages found in facies representing high stress environments (Goldman and Mitchell, 1990), suggests that this taxa was opportunistic.

Although further paleoecological work is needed, a number of lines of evidence suggest that *A. gregaria* was somewhat less generalized than *A. umbonata*. First, *A. umbonata* was relatively more abundant and also lived in a more diverse suite of environments than *A. gregaria* (McGhee and Sutton, 1983). However, this may be in part because by the Famennian much of the foreland basin had been filled by Acadian sediment, resulting in gradual loss in deep, basinal facies within the foreland (Ver Straeten, 2010). Second, the pedicle of *A. gregaria* would never have become restricted because of its less incurved umbo, and its larger interarea would have made it more difficult to recline to a ventral valve down orientation (Figs. 3, 7.2). Therefore, we reconstruct *A. gregaria* as living pedically attached and ventral valve up, or possibly slightly reclined (Fig. 7.2). Since *A. gregaria* is plano- to ventribiconvex, it would have been less well-suited for keeping the commissure above the substrate in ventral valve down position than the plano- to concavoconvex shape of *A. umbonata*. Similar to *A. umbonata*, a gregarious behavior is also exhibited by *A. gregaria* (*gregarious,* from the Latin meaning living within flocks or loosely organized communities) which is found within clusters of hundreds to thousands of shells which could have served as pedicle attachment surfaces (Bowen et al., 1974; McGhee and Sutton, 1981).

AMBOCOELIA AND THE LOWER KELLWASSER EVENT

Previous studies have suggested that both the last occurrence of *A. umbonata*, and the first appearance of *A. gregaria*, corresponded with the Lower Kellwasser Event (Fig. 2;

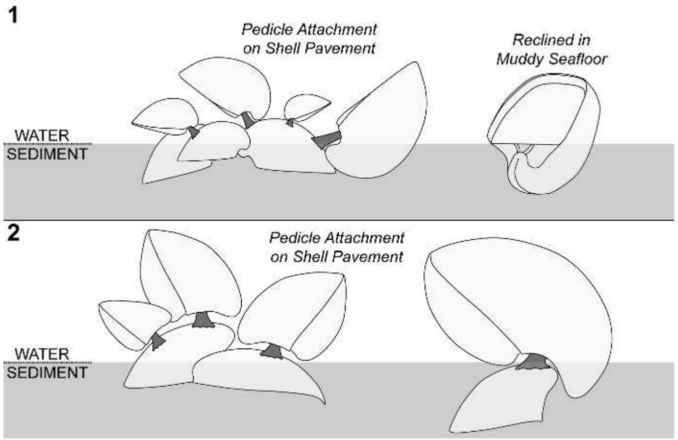

Figure 7—Reconstruction of life positions: *1*, *Ambocoelia umbonata* Conrad, 1842; *2*, *Ambocoelia gregaria* Hall, 1867. Through the ontogenetic sequence of *A. umbonata* the umbo becomes more incurved, to the point that it starts to block the delthyrium. Possible life orientations for *A. umbonata* include pedicle attachment on a shell pavement, and reclined, ventral valve down, within a muddy substrate. Umbonal curvature in *A. gregaria* never blocks the delthyrium, and larger interarea would likely prohibit reclined position as suggested for *A. umbonata*, therefore *A. gregaria* is reconstructed as living attached by a pedicle. Similarities are observed in the morphology between juvenile *A. umbonata* and mature *A. gregaria*. Pedicles are reconstructed here as massive, but could have been branching.

discussion in Day and Over, 2002). Within the northern Appalachian Basin, low oxygen conditions, evidenced by the Pipe Creek black shale (Over, 1997; House, 2002), occurred during the Lower Kellwasser Event. Low oxygen conditions are also inferred globally at this time, as well as climate (temperature) and carbon-cycle changes (Schindler, 1993; Joachimski and Buggisch, 1993, 2002; Joachimski et al., 2009). McGhee (1988) suggested that the Late Devonian extinction was primarily driven by a cessation in new species origination, and, furthermore, Stigall (2010) argued that the range expansion of generalists during this time, and the resulting decreased vicariance, led to a reduction in speciation. Harper and Rong (2001) noted that a shift in brachiopods from shallow forms that lived attached, to deeper water, recumbent forms that lived on soft substrates was also a feature of Late Devonian events.

The extinction of the generalist *A. umbonata* and origination of the less generalized *A. gregaria* is, therefore, counter-intuitive given the environmental and paleoecological changes associated with the Lower Kellwasser Event. Furthermore, the survival of *A. umbonata* through the multiple preceding Middle and Late Devonian biocrises exhibiting similar environmental changes (Fig. 2; House, 2002) would presumably have made this taxon pre-adapted for end-Frasnian events. In fact, *A. umbonata* preceded and out-lived all other Northern Appalachian Basin Ambocoelioidea, only to face extinction during the Lower Kellwasser Event (Fig. 2). One possible explanation is that the earlier ontogenetic stages of *A. umbonata* were better adapted to the environmental changes associated with the Lower Kellwasser Event. Indeed, Harries and others (1996) suggested that paedomorphic features within a given lineage may dominate following an extinction if those features were more resilient to environmental perturbations; though, this is easier to envision as a promoter of progenesis (accelerated sexual maturation), rather than neoteny (retarded somatic development). Alternatively, the ultimate replacement of *A. umbonata* by *A. gregaria* in the Appalachian Basin may have been driven by the general shallowing of the basin as it filled with Acadian sediment through the Famennian and the resulting loss of deeper-water facies. Under this scenario, the more specialized *A. gregaria* may have been better suited than the generalist *A. umbonata* for the dominantly shallow-water settings that were present throughout at least the northern portion of the Appalachian Basin.

Regardless, the taxonomic revision presented herein will enable the future revision of the stratigraphic ranges and environmental tolerances of these taxa. The specimens examined, which were collected with the stratigraphic context of the type material in mind, come from ~8 Ma before (*A. umbonata*) and ~9 Ma after (*A. gregaria*) the transition between these species (Lower Kellwasser Event, Fig. 2). This revised taxonomic framework provides the basis for investigating the intervening time interval, especially the Lower Kellwasser Event and associated strata, to document the rate and mode of transition from paleocommunities dominated by *A. umbonata* to that of *A. gregaria*.

CONCLUSIONS

Taxonomic elevation of *Ambocoelia umbonata* var. *gregaria* to *Ambocoelia gregaria* is warranted based on a distinct morphology that is substantially different from *Ambocoelia umbonata*. The revised taxonomy presented herein should form the basis for revising the biostratigraphic and environmental ranges of these long-lived forms, thereby permitting a better understanding of the relationship of the evolutionary history of these taxa to the Kellwasser Crisis. Morphologic similarity between juvenile individuals of *A. umbonata* and individuals of *A. gregaria* suggest the latter evolved from the former by neoteny. Furthermore, the morphologies and facies distributions of these taxa suggests that *A. umbonata* was more generalized than *A. gregaria*.

ACKNOWLEDGMENTS

This manuscript was substantially improved by the critical comments of the reviewers, A. Boucot and R. Gourvennec, and editor B. Pratt. We are grateful to the Paleontological Research Institute, the American Museum of Natural History, the Peabody Museum of Natural History, and the Field Museum of Natural History for access to specimens of *Ambocoelia*. Research was undertaken with support to JZ from the Paleontological Research Institute, the Evolving Earth Foundation, and the University of Cincinnati. C. Mitchell and H. D. Sheets provided valuable discussion on geometric morphometric methodology in the early phases of this project. T. Phillips assisted with figure drafting.

REFERENCES

Baird, G. C. and C. E. Brett. 2008. Late Givetian Taghanic bioevents in New York State: new discoveries and questions. Bulletin of Geosciences, 83: 357–370.

Baird, G. C. and G. G. Lash. 1990. Devonian strata and paleoenvironments: Chautauqua County region: New York State. Field Trip Guidebook for the New York State Geological Association, 62nd Annual Meeting, p. A1–A46.

Baird, G. C., R. K. Carr, J. T. Hannibal, C. E. Brett, and B. L. Brett. 2009. Uppermost Devonian (Famennian) Stratigraphy of the Cleveland Area, Northeastern Ohio, p. 154–168. *In* C. E. Brett, A. J. Bartholomew, and M. K. DeSantis (eds.), Middle and Upper Devonian Sequences, Sea Level, Climatic, and Biotic Events in East-Central Laurentia: Kentucky, Ohio, and Michigan. Fieldtrip Guidebook for NAPC, 2009.

Baranov, V. V. and T. S. Alkhovik. 2006. Brachiopods of the Family Ambocoeliidae (Spiriferida) from the Givetian of southern Verkhoyanks Region (northeastern Russia). Paleontological Journal, 40:162–167.

Bowen, Z. P., D. C. Rhoads, and A. L. McAlester. 1974. Marine benthic communities in the Upper Devonian of New York. Lethaia, 7:93–120.

Bray, R. G. 1969. The paleoecology of some Middle Devonian fossil clusters, Erie County, New York. Unpublished M.S. thesis, McMaster University, 68 p.

Bray, R. G. 1972. The paleoecology of some Ludlowville brachiopod clusters (Middle Devonian), Erie County, New York. Twenty-fourth International Geological Congress, Section 7, p. 66–73.

Brett, C. E., L. C. Ivany, A. J. Bartholomew, M. K. DeSantis, and G. C. Baird. 2009. Devonian ecological-evolutionary subunits in the Appalachian Basin; a revision and a test of persistence and discreteness. Geological Society Special Publications, 314:7–36.

Brett, C. E., A. J. Bartholomew, and G. C. Baird. 2007. Biofacies recurrence in the Middle Devonian of New York State: an example with implications for evolutionary paleoecology. Palaios, 22:306–324.

Bush, A. M. and R. I. Brame. 2010. Multiple paleoecological controls on the composition of marine fossil assemblages from the Frasnian (Late Devonian) of Virginia, with a comparison of ordination methods. Paleobiology, 36:573–591.

Caldwell, G. E. 1967. Ambocoeliid brachiopods from the Middle Devonian rocks of northern Canada, p. 601–616. *In* D. H. Oswald (ed.), International Symposium on the Devonian System, Alberta Society of Petroleum Geologists, Calgary, Alberta.

Caster, K. E. 1934. The stratigraphy and paleontology of northwestern Pennsylvania; Part 1, Stratigraphy. Bulletin of American Paleontology, 21(71):19–37.

Chadwick, G. H. 1933. Great Catskill Delta, and revision of late Devonic succession. Pan-American Geologist, 60:91–360.

Chadwick, G. H. 1935. Chemung is Portage. Geological Society of America Bulletin, 46:343–354.

Clarke, J. M. 1917. Contributions to the paleontology of New York Devonian glass sponges. New York State Museum Bulletin, 196:177–197.

Claypole, E. W. 1883. On the equivalent of the New York Portage, in Perry County, Middle Pennsylvania. Proceedings of the American Philosophical Society, 21:230–235.

Conrad, T. A. 1842. Observations on the Silurian and Devonian systems of the United States, with descriptions of new organic remains. Journal of the Academy of Natural Sciences of Philadelphia, 8(2):228–280.

Cooper, G. A. and J. T. Dutro Jr. 1982. Devonian brachiopods of New Mexico. Bulletins of American Paleontology, 82/83(315), 215 p.

Cooper, G. A. and J. S. Williams. 1935. Tully formation of New York. Geological Society of America Bulletin, 46:781–868.

Crickmay, C. H. 1952. Discrimination of the late Upper Devonian. Journal of Paleontology, 26:585–609.

Day, J. and D. J. Over. 2002. Post-extinction survivor fauna from the lowermost Famennian of eastern North America. Acta Palaeontologica Polonica, 47:189–202.

DeSantis, M. K., C. E. Brett, and C. A. ver Straeten. 2007. Persistent depositional sequences and bioevents in the Eifelian (early Middle Devonian) of eastern Laurentia; North American evidence of the Kacak events?, p. 83–104. *In* R. T. Becker and W. T. Kirchgasser (eds.), Geological Society Special Publications, Devonian Events and Correlations. The Geological Society of America, Boulder, Colorado.

Dutro, J. T., Jr. 1981. Devonian brachiopod biostratigraphy of New York State, p. 67–81. *In* W. A. Oliver and G. K. Klapper, (eds.), Devonian Biostratigraphy of New York, Part 1, International Union of Geological Sciences, Subcommission on Devonian Stratigraphy.

Ettensohn, F. R. 2008. The Appalachian foreland basin in eastern United States, Chapter 4, p. 105–179. *In* A. D. Miall (ed.), Sedimentary Basins of the World, Vol. 5: The Sedimentary Basins of the United States and Canada. Elsevier.

Flessa, K. W. and R. G. Bray. 1977. On the measurement of size-independent morphological variability: an example using successive populations of a Devonian spiriferid brachiopod. Paleobiology, 3:350–359.

George, T. N. 1931. *Ambocoelia* Hall and certain similar British Spiriferidae. Quarterly Journal of the Geological Society of London, 87:30–61.

Goldman, D. and C. E. Mitchell. 1990. Morphology, systematics, and evolution of Middle Devonian Ambocoeliidae (Brachiopoda), western New York. Journal of Paleontology, 64:79–99.

Gould, S. J. 1977. Ontogeny and Phylogeny. Belknap Press, Cambridge, Massachusetts, 501 p.

Grabau, A. W. 1898. Geology and Palaeontology of Eighteen Mile Creek and the Lake Shore Sections of Erie County New York (Pt. 1: Geology, Pt. 2: Paleontology): Buffalo Society of Natural Sciences Bulletin, No. 6, Kenmore, New York, 403 p.

Hall, J. 1843. Geology of New York. Part IV, Comprising the survey of the fourth geological district. Carrol and Cook, Albany, New York, 683 p.

Hall, J. 1857. Descriptions of Paleozoic Fossils. Tenth Annual Report of the Regents of the University on the condition of the State Cabinet of Natural History, p. 167–168.

Hall, J. 1860. Observations of the genus *Ambocoelia*. Thirteenth Annual Report of the Regents of the University on the condition of the State Cabinet of Natural History, p. 71–72.

Hall, J. 1867. Containing descriptions and figures of the fossil brachiopoda of the Upper Helderberg, Hamilton, Portage, and Chemung groups. Geological Survey of New York, Palaeontology of New York, Vol. IV, Pt. 1, 428 p.

Hall, J. 1870. Preliminary notice of lamellibranchiate shells of the Upper Helderberg, Hamilton and Chemung groups, with others from the Waverly sandstone, Pt. 2. New York State Museum, Albany, New York, 97 p.

Harper, D. A. T. and J.-Y. Rong. 2001. Palaeozoic brachiopod extinctions, survival and recovery: patterns within the rhynchonelliformeans. Geological Journal, 36:317–328.

Harries, P. J., E. G. Kauffman, and T. A. Hansen. 1996. Models for biotic survival following mass extinction. Geological Society of London Special Publications 102:41–60.

House, M. R. 1985. Correlation of mid-Palaeozoic ammonoid evolutionary events with global sedimentary perturbations. Nature, London, 313(5997): 17–22.

House, M. R. 2002. Strength, timing, setting and cause of mid-Palaeozoic extinctions. Palaeogeography, Palaeoclimatology, Palaeoecology, 181:5–25.

Joachimski, M. M. and W. Buggisch. 1993. Anoxic events in the late Frasnian—causes of the Frasnian-Famennian faunal crisis? Geology, 21: 675–678.

Joachimski, M. M. and W. Buggisch. 2002. Conodont apatite $\delta^{18}O$ signatures indicate climatic cooling as a trigger of the late Devonian mass extinction. Geology, 30:711–714.

Joachimski, M. M., S. Breisig, W. Buggisch, J. A. Talent, R. Mawson, M. Gereke, J. R. Morrow, J. Day, and K. Weddige. 2009. Devonian climate and reef evolution: Insights from the oxygen isotopes in apatite. Earth and Planetary Science Letters, 284:599–609.

Johnson, J. G. and W. R. Trojan. 1982. The *Tecnocyrtina* brachiopod fauna (?Upper Devonian) of central Nevada. Geologica et Palaeontologica, 16: 119–150.

Johnson, J. G., J. L. Carter, and H.-F. Hou. 2006. Family Ambocoeliidae, p. 1733–1744. *In* R. L. Kaesler (ed.), Treatise on Invertebrate Paleontology, Vol. 5, Pt. H, Brachiopoda revised. Rhynchonelliformea (part). Geological Society of America and University of Kansas, Boulder, Colorado and Lawrence, Kansas.

Kaufmann, B. 2006. Calibrating the Devonian time scale; a synthesis of U-Pb ID-TIMS ages and conodont stratigraphy. Earth-Science Reviews, 76(3–4): 175–190.

Kindle, E. M. 1906. Faunas of the Devonian section near Altoona, P.A. The Journal of Geology, 14:631–635.

Lesley, J. P. 1892. A summary description of the geology of Pennsylvania, Volume II, Describing the Upper Silurian and Devonian formations. Geological Survey of Pennsylvania, 907 p.

Linsley, D. M. 1994. Devonian paleontology of New York; containing the brachiopods, bivalves, rostroconchs, gastropods, tergomyans, ammonoids, trilobites, eurypterids and phyllocarids, based on the lithographs of James Hall and John Clarke. Special Publication, Paleontological Research Institution, Vol. 21, 472 p.

Luther, D. D. 1901. Stratigraphic value of the Portage Sandstones. New York State Museum, Bulletin 52, Paleontology 6, Report of the State Paleontologist, p. 616–631.

McGhee, G. R. 1981. Evolutionary replacement of ecological equivalents in Late Devonian benthic marine communities. Palaeogeography, Palaeoclimatology, Palaeoecology, 34:267–283.

McGhee, G. R. 1988. The Late Devonian Extinction Event: Evidence for abrupt ecosystem collapse. Paleobiology, 14:250–257.

McGhee, G. R. and R. G. Sutton. 1981. Late Devonian marine ecology and zoogeography of the central Appalachians and New York. Lethaia, 14:27–43.

McGhee, G. R. and R. G. Sutton. 1983. Evolution of late Frasnian (Late Devonian) marine environments in New York and the central Appalachians. Alcheringa, 7:9–21.

McGhee, G. R. and R. G. Sutton. 1985. Late Devonian ecosystems of the lower West Falls Group in New York. Geological Society of America Special Paper 201, p. 199–209.

Over, D. J. 1997. Conodont biostratigraphy of the Java Formation (Upper Devonian) and the Frasnian-Famennian boundary in western New York State. Geological Society of America Special Paper 321, p. 161–177.

Over, D. J. 2002. The Frasnian/Fammenian boundary in central and eastern United States. Palaeogeography, Palaeoclimatology, Palaeoecology, 181: 153–169.

Over, D. J. 2007. Conodont biostratigraphy of the Chattanooga Shale, Middle and Upper Devonian, southern Appalachian Basin, Eastern United States. Journal of Paleontology, 81:1194–1217.

Over, D. J., R. Lazar, G. C. Baird, J. Schieber, and F. R. Ettensohn. 2009. Protosalvinia Dawson and associated conodonts of the upper trachytera zone, Famennian, Upper Devonian, in the eastern United States. Journal of Paleontology, 83:70–79.

Prosser C. S. 1912. The Devonian and Mississippian formations of northeastern Ohio. Geological Survey of Ohio, fourth series, Bulletin 15, 574 p.

Richardson, J. R. 1981. Brachiopods in mud: resolution of a dilemma. Science, 211:1161–1163.

Rogers, W. B., Y. W. Isachsen, T. D. Mock, and R. E. Nyahay. 1990. New York State geological highway map. New York State Museum and Science Service Educational Leaflet, No. 33, 1 sheet.

Rudwick, M. J. S. 1970. Living and Fossil Brachiopods. Hutchinson, London, 199 p.

Schindler, E. 1993. Event-stratigraphic markers within the Kellwasser Crisis near the Frasnian/Famennian boundary (Upper Devonian) in Germany. Palaeogeography, Palaeoclimatology, Palaeoecology, 104:115–125.

Schuchert, C. 1897. A synopsis of American fossil brachiopoda including bibliography and synonymy. Bulletin of the United States Geological Survey 87, 464 p.

Stainbrook, M. A. 1942. The brachiopoda of the High Point Sandstone of New York. American Journal of Science, 240(1):879–890.

Stigall, A. L. 2010. Invasive species and biodiversity crises: testing the link in the Late Devonian. PLoS ONE, 5(12):1–7.

Thayer, C. W. 1974. Marine paleoecology in the Upper Devonian of New York. Lethaia, 7:121–155.

Ver Straeten, C. A. 2010. Lessons from the foreland basin: Northern Appalachian basin perspectives on the Acadian orogeny, p. 251–282. *In* R. P. Tollo, M. J. Bartholomew, J. P. Hibbard, and P. M. Karabinos (eds.), From Rodinia to Pangea: The Lithotectonic Record of the Appalachian Region. Geological Society of America Memoir 206.

Waagen, W. H. 1883. Salt Range fossils, pt. 4(2), Brachiopoda. Palaeontologica Indica Memoir, Ser. 13, 1:547–610.

White, C. A. 1862. Description of new species of fossils from the Devonian and Carboniferous rocks of the Mississippi Valley. Proceedings of the Boston Society of Natural History, 9:8–33.

Whitfield, R. P. and E. O. Holvey. 1898. Catalogue of the types and figured specimens in the paleontological collection of the geological department, American Museum of Natural History. Bulletin of the American Museum of Natural History, Vol. XI, Pt. I, p. 202, 203, 356.

Willard, B. 1939. The Devonian of Pennsylvania: Middle and Upper Devonian. Pennsylvania Geological Survey Fourth Series, Bulletin G 19, 481 p.

Williams, H. S. 1882. Catalogue of the fossils of the Chemung Period of North America. Palaeontological Laboratory, Cornell University, Ithaca, New York, 14 p.

Williams, H. S. 1884. On the fossil faunas of the Upper Devonian along the meridian of 76° 30′ from Tompkins County NY to Bradford County PA. U.S. Geological Survey Bulletin 3, p. 51–86.

Williams, H. S. 1903. The correlation of geological faunas, a contribution to Devonian paleontology. United States Geological Survey Bulletin, Series C, Systematic Geology and Paleontology 210, 147p.

Williams, H. S. 1907. The Devonian Section of Ithaca, N.Y. Part II: the discrimination of the Nunda-Chemung boundary. The Journal of Geology, 15:93–112.

Williams, H. S. 1913. Recurrent Tropidoleptus zones of the Upper Devonian in New York. United States Geological Survey Professional Paper 79, 103 p.

Williams, H. S. and E. M. Kindle. 1905. Contributions to Devonian paleontology, 1903. United States Geological Survey Bulletin, Series C, Systematic Geology and Paleontology 244, 144 p.

Zambito, J. J., IV and C. E. Mitchell. 2006. Life on the edge: death and transfiguration in mud. Field Trip Guidebook for the New York State Geological Association, 74th Annual Meeting, p. 165–179.

Zambito, J. J., IV, C. E. Brett, and G. C. Baird. 2012. The late Middle Devonian (Givetian) global Taghanic biocrisis in its type area (New York State Appalachian Basin): geologically rapid faunal incursion, replacement, recurrence, and extinction as a result of global and local environmental changes, p. 677–703. *In* J. Talent (ed.), Global Biodiversity, Extinction Intervals and Biogeographic Perturbations through Time. Springer, New York.

Zambito, J. J., IV, C. E. Mitchell, and H. D. Sheets. 2008. A comparison of sampling and statistical techniques for analyzing bulk-sampled biofacies composition. Palaios, 23:313–321.

Ziegler, W., J. G. Johnson, and G. Klapper. 1976. Redefinition and subdivision of the varcus-zone (conodonts, Middle-?Upper Devonian) in Europe and North America. Geologica et Palaeontologica, 10:109–140.

Accepted 4 November 2012