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The Ordovician zone index conodont *Amorphognathus ordovicicus* Branson & Mehl, 1933 from its type locality and the evolution of the genus *Amorphognathus* Branson & Mehl, 1933

STIG M. BERGSTRÖM[1,*] & STEPHEN A. LESLIE[2]
[1]School of Earth Sciences, Division of Geological Sciences, The Ohio State University, 155 S. Oval Mall, Columbus, Ohio 43210, USA
[2]Department of Geology and Environmental Science, James Madison University, MSC 6903, Harrisonburg, VA 22807, USA
[*]Corresponding author (e-mail: stig@geology.ohio-state.edu)

ABSTRACT – The 2003 rediscovery of the long 'lost' Ozora, Missouri classical conodont locality of Branson & Mehl (1933b), from which the world's first Late Ordovician conodont fauna was described, has made it possible to obtain topotype specimens of the several important conodont species introduced by Branson and Mehl from this site. A taxonomic reassessment of the Ozora conodont fauna indicates that it includes at least 14 multi-element species, eight of which were previously known from this locality. Several specimens of the taxonomically diagnostic M element of the biostratigraphical key species *Amorphognathus ordovicicus* were recovered. This element was previously not known from the type locality of the species at Ozora. A general review of the evolution of the genus *Amorphognathus* shows that some elements, particularly the M and Pa elements, exhibit relatively rapid gradual morphological changes that are helpfull for distinguishing a series of biostratigraphically useful species through the Upper Ordovician (Sandbian–Hirnantian) interval. No ancestor of *Amorphognathus* has yet been identified but currently available data suggest that the genus appeared in the latest Darriwilian or earliest Sandbian and went extinct in the late Hirnantian. None of the Early Silurian platform genera appears to be closely related to *Amorphognathus*. *J. Micropalaeontol.* **29**(1): 73–80, May 2010.

KEYWORDS: *Ordovician, conodonts, evolutionary trends, North America, Branson and Mehl Ozora locality*

INTRODUCTION

The study of Ordovician conodonts was initiated by Pander (1856), who in his classical monograph described many Floian (Early Ordovician) species from the St Petersburg region in Russia (Tolmacheva, 2006). However, Late Ordovician representatives of this microfossil group remained virtually unstudied for the next 75 years, the only exception being Hinde's (1879) report of five species (representing 3(?) multi-element species) from the Upper Ordovician Lorraine–Dundas formations of Ontario. Probably stimulated by the paper on the classification of conodonts by Ulrich & Bassler (1926), Branson & Mehl (1933a) initiated around 1930 a broad study of conodont faunas ranging in age from the Early Ordovician to the Permian. Their research marks the beginning of the period of detailed study of Palaeozoic conodonts.

One part of their extensive research effort resulted in the description of the first diverse conodont fauna from the Upper Ordovician anywhere in the world. It was recovered from the Maquoketa Shale–Thebes Sandstone boundary interval in eastern Missouri and described in the third paper of their 'Conodont Studies Number 2' (Branson & Mehl, 1933b). This fauna included 10 new single element species from a locality near Ozora, Ste. Genevieve County, four new species from Clarksville, Pike County, and two new species from Grassy Creek west of Louisiana, Pike County. In terms of modern multi-element taxonomy, this fauna comprises about eight multi-element species (Table 1), several of which are now known to be quite widespread geographically and to represent diagnostic taxa of the North American Upper Ordovician.

Among the three localities listed above, that at Ozora is by far the most important, because it is the type locality of six multi-element species, including the globally used zonal index species *Amorphognathus ordovicicus* Branson & Mehl, 1933b, which is the type species of the biostratigraphically important genus *Amorphognathus* Branson & Mehl, 1933b. Branson & Mehl's (1933b) illustrated Ozora specimens are kept at the Department of Geoscience, University of Iowa but, as far as we are aware, the whereabouts of their bulk collections from this locality remain unknown and these collections may be lost.

Because the morphology of some of the elements of the Ozora species, especially *A. ordovicicus*, has remained incompletely known, there has been an urgent need to recollect the Ozora locality and obtain topotypes. The present paper is based on the ultimate success of such an effort that proved far more difficult than was originally envisioned. The second part of the report reviews our interpretation of the evolution of *Amorphognathus* through the Upper Ordovician.

HISTORICAL BACKGROUND

The quarry at the small village of Ozora, which is herein referred to as the Ozora Quarry, is rather remotely located in Ste. Genevieve County in southeastern Missouri (Fig. 1). One may speculate why this unimpressive and obscure locality was selected by Branson & Mehl for conodont study rather than any of the many other exposures of this stratigraphical interval in eastern Missouri. We suggest that there may be two principal reasons for this choice. First, because Branson and Mehl and their students used washing techniques in their early studies to separate the conodonts from the matrix, they had to use relatively unconsolidated clastic sediments. Much of the black to green Maquoketa Shale is well consolidated and the Thebes Sandstone, when unweathered, is a relatively well-indurated rock that is used locally as a building stone. Neither of these rock types is likely to break down in boiling water. However, at the Ozora Quarry, the lowermost Maquoketa is a soft olive to tan clay with abundant sand grains that is disaggregated easily

Species named by Branson & Mehl (1933b)	Name in multi-element taxonomy
Ambalodus triangularis	*Amorphognathus ordovicicus* (Pb)
Amorphognathus ordovicicus	*Amorphognathus ordovicicus* (Pa)
Belodus diminutivus	*Belodina diminutiva*
Belodus(?) *mutatus*	*Dapsilodus*? *mutatus*
Belodus ornatus	*Belodina ornata*
Phragmodus delicatus	*Amorphognathus ordovicicus* (Sc)
Phragmodus dissimilaris	*Protopanderodus insculptus*
Phragmodus insculptus	*Protopanderodus insculptus*
Phragmodus mirus	*Plectodina mira* (Sb)
Phragmodus simplex	*Protopanderodus insculptus*
Total 6 multi-element species	
Additional multi-element species present in our new collection	
Aphelognathus sp.	
Decoriconus sp.	
Drepanoistodus suberectus (Branson & Mehl, 1933b)	
Icriodella superba Rhodes, 1953	
Phragmodus undatus Branson & Mehl, 1933b	
Plectodina florida Sweet, 1979	
Plectodina tenuis (Branson & Mehl, 1933b)	
Pseudooneotodus sp.	
Total 8 additional multi-element species	
Total 14 multi-element species currently known from the Ozora Quarry	

Table 1. Late Ordovician conodonts currently known from Branson & Mehl's (1933b) Ozora locality.

by boiling and washing for isolating the conodonts. Secondly, as mentioned in the 'Introduction' chapter of the 'Geology of Ste. Genevieve County, Missouri' (Weller and St. Clair, 1928), Mehl was engaged in mapping a part of the Weingarten Quadrangle in 1913–14, in all probability including the faulted Ozora area (Fig. 1), which was of special interest as a potential occurrence of economically important lead and copper deposits. That the small quarry on Little Saline Creek (Fig. 2) was in operation in the 1920s is shown by the fact that the sandstone from this quarry was used for the construction of the foundation of the Ozora Church, which has a cornerstone showing the construction year to be 1921. It is most likely that during his mapping Mehl visited this active quarry and noted the clayey nature of the lowermost Maquoketa Shale and, when he and Branson started their conodont studies some 15 years later, he returned to the quarry and collected the samples upon which their Ozora fauna was based.

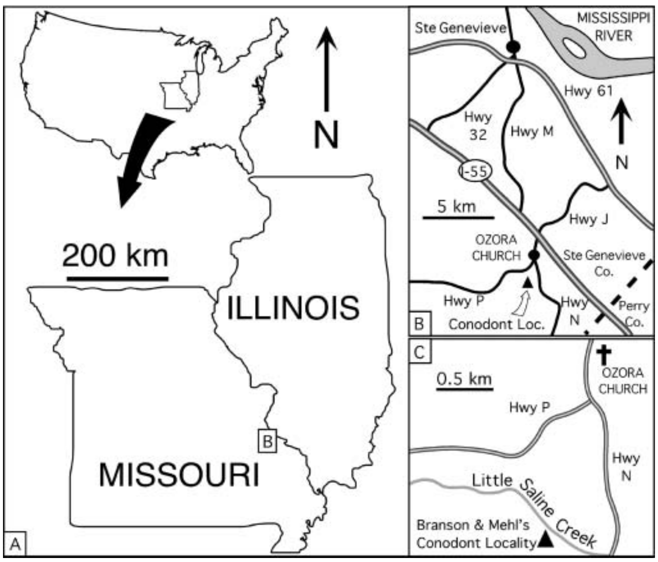

Fig. 1. Geographical orientation maps showing the location of Branson & Mehl's (1933b) classical conodont locality on the south side of Little Saline Creek at Ozora, Ste. Genevieve County, eastern Missouri.

Repeated efforts by several workers since the 1950s to find the imprecisely described Ozora locality were unsuccessful. After several trips we finally located this 'lost' locality in early 2003 (Leslie & Bergström, 2004, 2005). Although the quarry is now overgrown and quite inconspicuous, the principal reason for the failure to locate it was probably the fact that the quarry location given by Branson & Mehl (1933b) as 'one-fourth of a mile above the [road] crossing [of Little Saline Creek]' is not valid anymore because the current road bridge across the creek was constructed some distance downstream of the former crossing.

STRATIGRAPHY OF THE OZORA QUARRY

The stratigraphical succession in the Ozora Quarry is illustrated in Figure 3.

The oldest rocks exposed are small outcrops of the Chatfieldian (early Late Ordovician) Kimmswick Limestone along the south side of Little Saline Creek near the quarry. As noted by Branson & Mehl (1933b), some beds of this unit are locally quite fossiliferous. The unconformable contact between the Kimmswick and the overlying, stratigraphically much younger, Thebes Sandstone is currently not exposed at the quarry, where there is a thin covered interval between the base of the Thebes and the top of the exposure of the Kimmswick. Weller & St. Clair (1928) reported an occurrence of the Cape Limestone (their Fernvale Limestone) with its characteristic Richmondian fauna 'on the south side of Little Saline Creek one and one-fourth mile southwest of Ozora' indicating that the Cape, which ranges in thickness from a few centimetres to less than one metre

Fig. 2. Photos of the abandoned Ozora Quarry, which is the source of Branson & Mehl's (1933b) Upper Ordovician conodont fauna from the lower most Maquoketa Shale: (**a**) view of the quarry face formed by the Thebes Sandstone; (**b, c**) close-up of the topmost part of the Thebes Sandstone and lower-most part of the Maquoketa Shale. The position of Branson and Mehl's conodont bed is marked by the head of the hammer.

in this region, may be present at the top of the Kimmswick in the immediate vicinity of the quarry but we have been unable to confirm this by digging. The Kimmswick and the Cape are closely similar lithologically but are separated by a large stratigraphical gap corresponding to the Edenian and Maysvillian stages (Sweet *et al*., 1975; Goldman & Bergström, 1997; Bergström, 2003).

The succession in the approximately 75 m wide and 10 m deep quarry includes the brownish to grey, lithologically rather uniform, thick-bedded Thebes Sandstone, which is approximately 4.3 m thick and overlain by <0.5 m of exposed thickness of the basal Maquoketa Shale. The poorly exposed base of the Thebes is approximately 4.2 m above the level of the Little Saline Creek. Contrary to previous descriptions, the contact between the Thebes and the Maquoketa is sharp, not gradational, and the smooth top surface of the sandstone is overlain by a sandy, olive green to tan clay of an exposed thickness of about 0.3 m. The top 2–3 cm of the Thebes appears to be a lag concentrate with many dark (phosphatic?) particles, small rounded quartz grains and fossil fragments. Because this layer is relatively resistant, it seems clear that Branson and Mehl's conodont collection came from the thin overlying clay with abundant quartz grains in the lowermost 2–3 cm of the Maquoketa Shale. This is also consistent with Branson & Mehl's (1933b) description, and the fact that our samples from the Maquoketa above the basal 2–3 cm proved to be very poor in conodonts. The condensation bed at the top of the Thebes, the concentration of the conodont elements just above this bed, and the broken condition of the conodont elements suggest a period of very slow deposition, but there is no conglomerate or other evidence of a significant stratigraphical break. However, the Thebes is missing in sections to the north, such as that at Barnhart, where the Maquoketa rests unconformably on the Cape (Sweet *et al.,* 1975). In Figure 3 we illustrate the stratigraphical and biostratigraphical classifications of the Ozora Quarry succession and compare it with the coeval successions at Cape Girardeau and Barnhart in southeastern and eastern Missouri, respectively.

THE CONODONT FAUNA

In general, preservation of the Ozora conodont elements is far from perfect, most specimens being more or less broken. This applies to both the platform and non-platform elements, even the robust ones. It is not clear if this is due to transport along the sea bottom or the effect of having passed through the food digestion system of conodont eaters, or both.

Our samples from the Ozora Quarry produced several hundred conodont elements, representing 14 multi-element species (Table 1), six of which were first described from this locality by Branson & Mehl (1933b). Some of the Ozora taxa are illustrated in Figure 4. There is no record of the size of Branson and Mehl's conodont collection from this locality, but the fact that our collection includes at least eight distinctive multi-element species not recorded by Branson & Mehl (1933b) suggests that our collection, which is based on processing over 10 kg of clay, is substantially larger than theirs. Among Branson & Mehl's (1933b) taxa, the holotypes and currently only known specimens of two species (*Belodina diminutiva* (Branson & Mehl, 1933b) and *Plectodina mira* (Branson & Mehl, 1933b)) remain the only elements so far recognized in the apparatus of these species, and

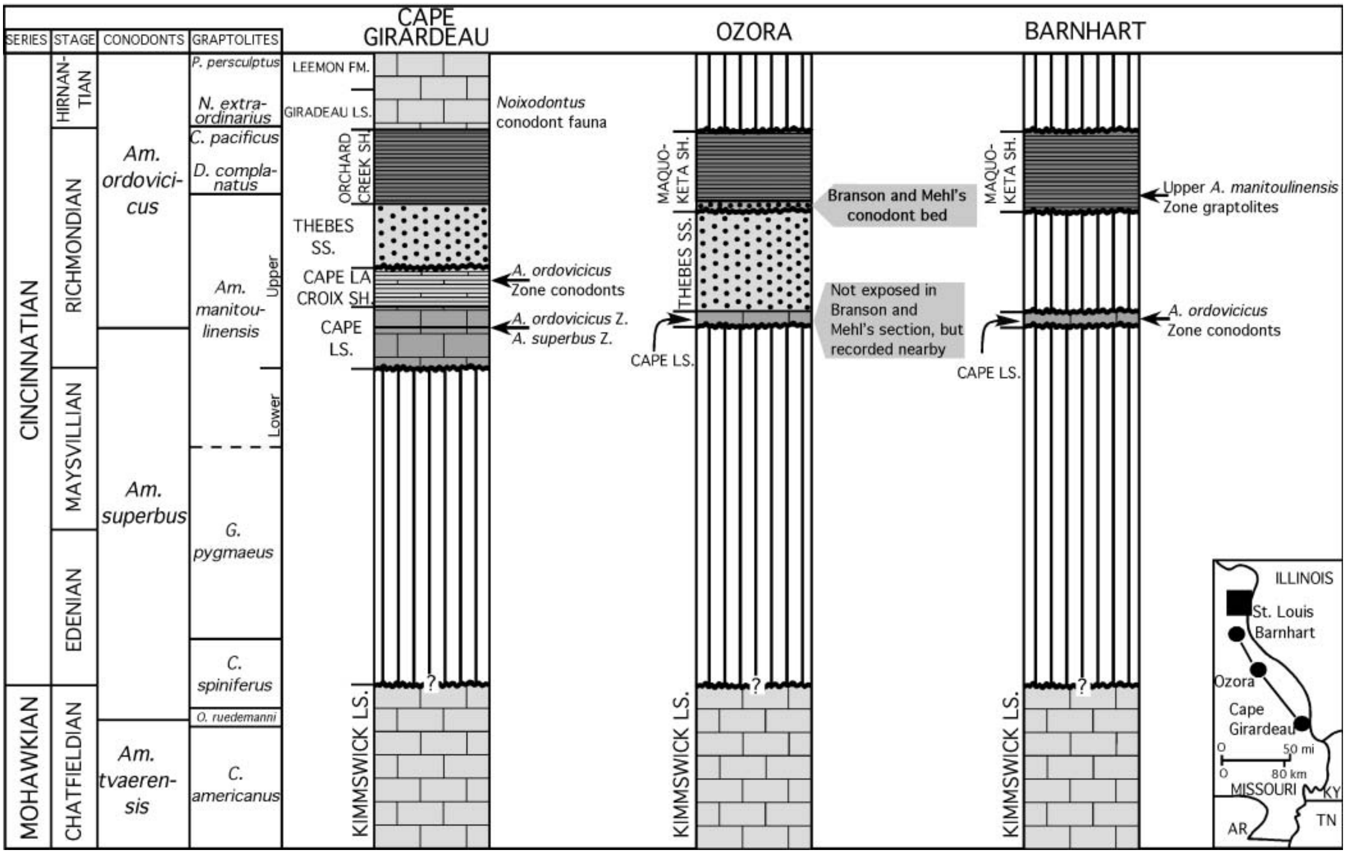

Fig. 3. Stratigraphical diagram showing the succession at the Ozora Quarry compared with the coeval successions at Cape Girardeau and Barnhart (the latter two after Thompson, 1991). For the geographical location of these sections, see inset map. Note the location of Branson & Mehl's (1933b) conodont bed in lowermost 2–3 cm of the Maquoketa Shale at the Ozora Quarry. Vertical ruling indicates inferred stratigraphical gaps. The vertical scale of the three columns is arbitrary.

further studies are needed to clarify their affinities. Neither of these species is represented in our collection. Of special interest in our collection is the presence of several specimens of the diagnostic M element of *Amorphognathus ordovicicus*, which was previously unknown from the Ozora locality. As suggested by several authors based on collections from other localities, this element is characterized by a simple prominent denticle with very poor, if any, development of small denticles lateral to the central one. Because the M element is of critical importance for the identification of several species of *Amorphognathus*, including *A. ordovicicus*, its recovery at the latter's type locality is of significant taxonomic interest.

The Ozora representatives of *Dapsilodus*? *mutatus* (Branson & Mehl, 1933b), *Drepanodus suberectus* (Branson & Mehl, 1933b), *Icriodella superba* Rhodes, 1953, *Plectodina florida* Sweet, 1979, *P. tenuis* (Branson & Mehl, 1933b) and *Protopanderodus insculptus* (Branson & Mehl, 1933b) belong to well-known and repeatedly described taxa in the North American Upper Ordovician conodont faunas. Because our less than perfectly preserved Ozora specimens do not provide significant new morphological information, there is no need to re describe these species herein.

The Ozora species association is characteristic of the *Amorphognathus ordovicicus* Zone, which ranges from the middle Richmondian to Hirnantian (Upper Katian to Hirnantian) interval in North America and elsewhere. The evolutionarily advanced morphology of the M elements of *A. ordovicicus* suggests that the Ozora fauna represents a level well above the base of the *A. ordovicicus* Zone. The abundant occurrence of *A. ordovicicus*, common presence of *Phragmodus undatus* and *Plectodina tenuis* but presence of only rare specimens of *Aphelognathus,* and the lack of representatives of *Oulodus* and *Rhipidognathus*, suggest a moderately deep-water biofacies, specifically the *Amorphognathus* biofacies of Sweet (1988, fig. 7.3). It has been generally assumed that the Thebes Sandstone was deposited in relatively shallow, possibly even deltaic, water (Thompson, 1991) but the presence of the *Amorphognathus* biofacies in the lowermost Maquoketa Shale is consistent with the interpretation that this unit represents a deepening environment that occurred during the early stage of the Maquoketa transgression.

BRIEF COMMENTS ON THE PHYLOGENY OF *AMORPHOGNATHUS*

The genus *Amorphognathus* includes relatively rapidly evolving platform conodont species, many of which had a nearly global distribution. Several of these species are of major biostratigraphical significance in the Upper Ordovician and some serve as zone fossils. Because there has been uncertainty in the classification of some described species, and we have access to topotype specimens of not only *A. ordovicicus*, the type species

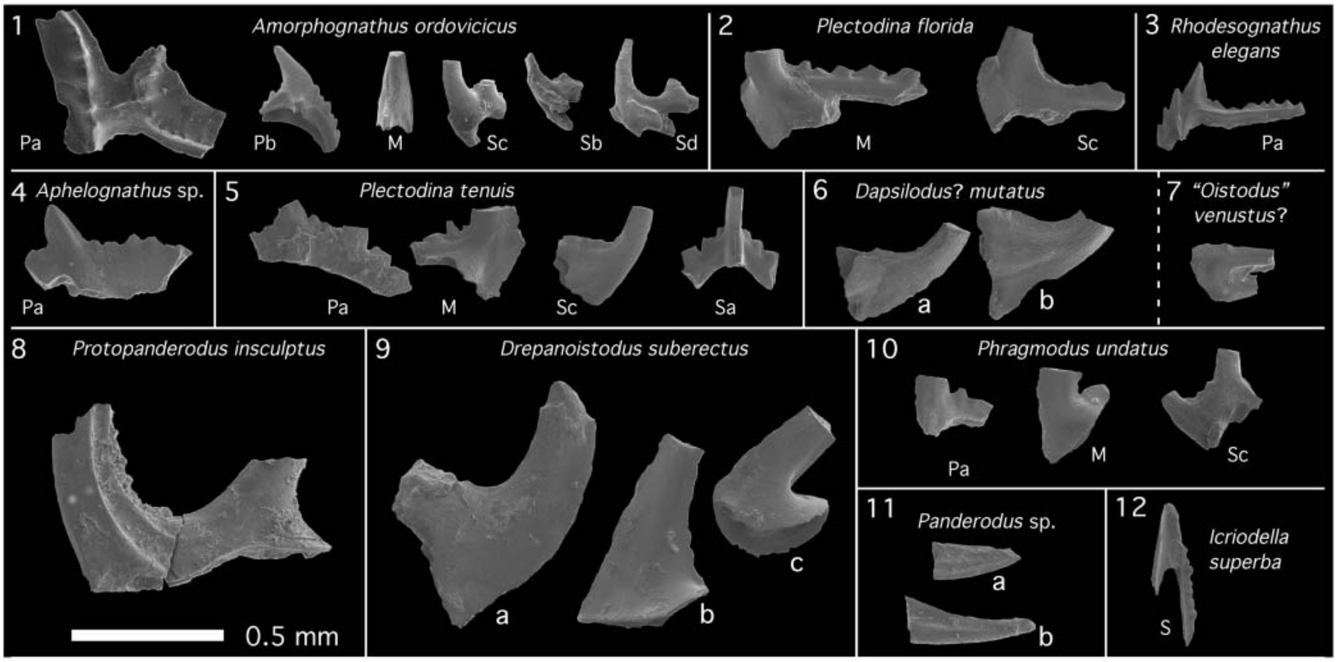

Fig. 4. SEM micrographs of some conodont species recently collected from the Ozora Quarry. The 0.5 mm scale applies to all the illustrated specimens. Note the appearance of the M element of *Amorphognathus ordovicicus*. The illustrated specimens are kept in the type collection of the Orton Geological Museum at The Ohio State University under the following OSU collection numbers: *Amorphognathus ordovicicus* OSU 53656–OSU 53661; *Plectodina florida* OSU 53662–53663; *Rhodesognathus elegans* OSU 53664; *Aphelognathus* sp. OSU 53665; *Plectodina tenuis* OSU 53666–53669; *Dapsilodus*? *mutatus* OSU 53670–53671; '*Oistodus*' *venustus*? OSU 53672; *Protopanderodus insculptus* OSU 53673; *Drepanoistodus suberectus* OSU 53674–53676; *Phragmodus undatus* OSU 53677–53679; *Panderodus* sp. OSU 53680–53681; and *Icriodella superba* OSU 53682.

of the genus, but also to most other species of *Amorphognathus,* it is appropriate to comment on the evolution of this important genus. For previous discussions of this matter, see, for instance, Bergström (1983) and Dzik (1999). Our interpretation of the evolution of *Amorphognathus* is schematically illustrated in Figure 5.

The ancestor of *Amorphognathus* is currently not recognized. Bergström (1983) suggested that the oldest known species of the genus, *A. inaequalis* Rhodes, 1953, might have evolved from a species such as *Sagittodontina*? *kielcensis* (Dzik, 1976) but morphological intermediates are not known. Another possible origin might be from the *Baltoniodus* (cf. Lindström, 1977) or *Lenodus* lineages, but a potential ancestor has not been identified. *A. inaequalis* (Fig. 5) is best known from Wales and northwestern France (Rhodes, 1953; Lindström *et al*., 1974) and it is possible that the origin of the genus is to be found in yet unknown Darriwilian taxa in the Avalonia–Gondwana region. Specimens identified as *A. inaequalis* from Estonia (e.g. Männik & Viira, 2005) have not yet been illustrated. However, it appears that representatives of *Amorphognathus* migrated to Baltoscandia in earliest Sandbian time.

As far as known, *A. inaequalis* has a limited geographical range, being restricted to northern Europe. Its evolutionary successor is *A. tvaerensis* Bergström, 1962 (Fig. 5), which differs morphologically from *A. inaequalis* in details in the M and Pa elements (Lindström, 1977), especially in the number of denticles in the M element. This species has a virtually global range (Baltoscandia, UK, North and South America, Australia, etc.) and is a useful zone index. Its descendant, *A. superbus* (Rhodes, 1953), which differs in lacking the 'extra' postero-lateral process in the Pa element and in having fewer apical denticles in the M element (Fig. 5), evolved from its ancestor in the early Katian Stage (*D. spiniferus* Graptolite Zone). The gradual evolutionary transition from *A. tvaerensis* to *A. superbus* is well illustrated in collections from the Middletown drill-core from southwestern Ohio (Bergström & Sweet, 1966; Richardson & Bergström, 2003).

The distinctive species *A. complicatus* Rhodes, 1953 (Fig. 5), which also evolved from *A. superbus* in the early Katian and differs from the latter species in having a simple, rather than bifid, postero-lateral process in the Pa element, was described from Wales (Rhodes, 1953; see also Orchard, 1980; Savage & Bassett, 1985) and is widely distributed in Baltoscandia (Hamar, 1966; Bergström, 1971, 2007; Merrill, 1980; Männik & Viira, 2005). Specimens that are morphologically intermediate between this species and *A. superbus* have been illustrated from the Pagoda Formation on the Yangtze Platform in China (e.g. An, 1987, fig. 30:12). The stratigraphically youngest known typical specimens of *A. complicatus* are recorded from the basal *A. ordovicicus* Zone in Sweden (Bergström, 2007).

A. superbus underwent a morphological evolution during the middle Katian that is particularly expressed in a decrease in the number of apical denticles in the M element. A stratigraphically late morphotype, which was described as *Holodontus primitivus* by Winder (1966) (Fig. 5) is clearly based on an M element of *Amorphognathus*. However, further studies are needed to clarify if the poorly known *A. primitivus* (Winder, 1966) is distinctive enough to justify a separation from *A. superbus* at the species level.

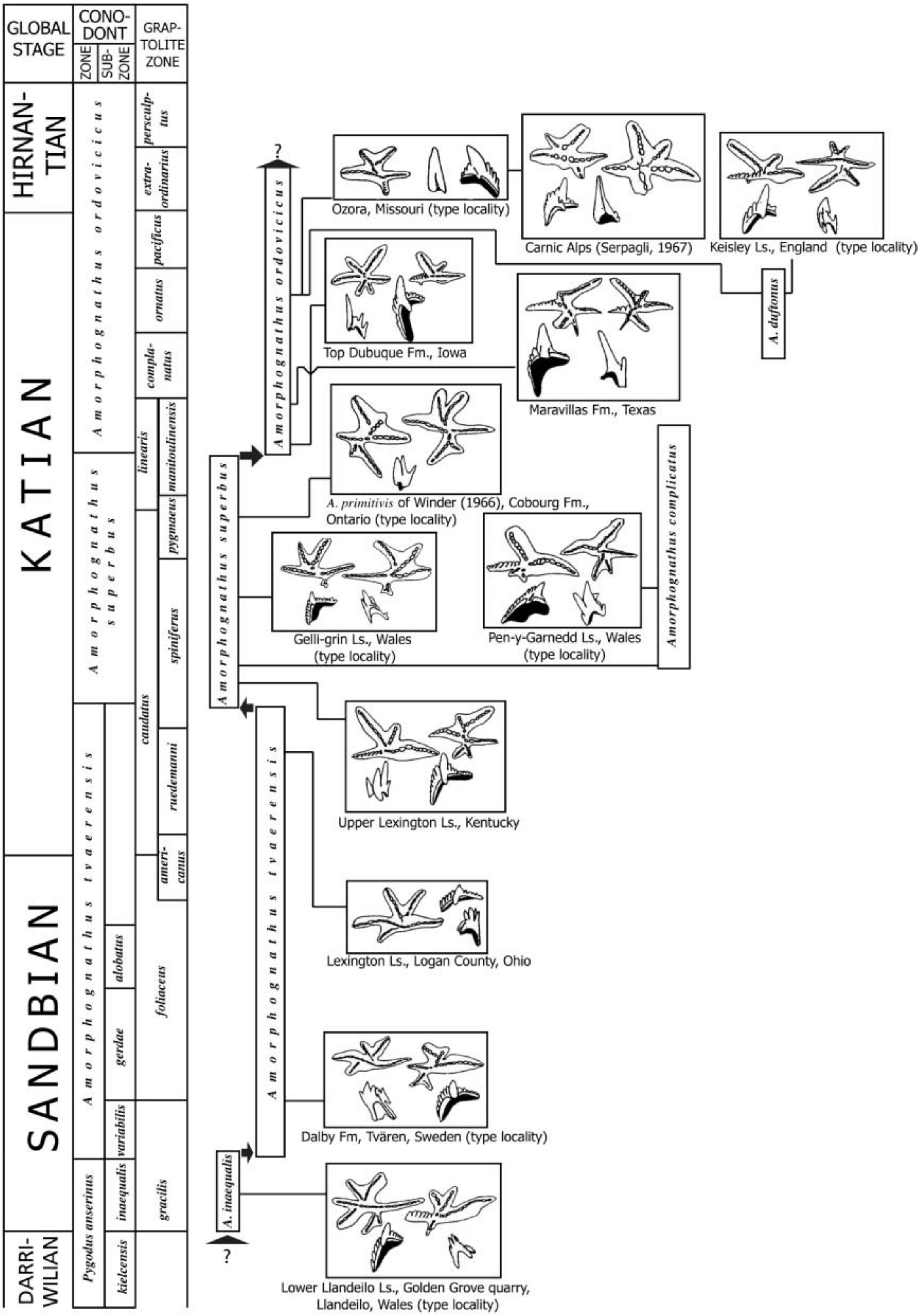

Fig. 5. Schematic chart showing our interpretation of the evolution of the *Amorphognathus* lineage. Only the Pa, Pb and M elements in the apparatus of the various species are illustrated. Figures are based on specimens from the approximate stratigraphical levels shown by the lines connecting the specimen boxes with the vertical range open bars. When not indicated otherwise, the illustrated specimens are from the type stratum of a particular species. Note that evolutionary trends are expressed mainly in a decrease in denticulation of the M elements and in the shape of the platform in the Pa elements.

A. ordovicicus, which is characterized by a single large apical denticle in the M element (Figs 4, 5), evolved from *A. superbus* in late Katian time (middle *A. manitoulinensis* Graptolite Zone). Its very wide geographical range includes the British Isles (Orchard, 1980), Baltoscandia (Bergström, 2007), the Mediterranean region (e.g. Serpagli, 1967; Ferretti & Serpagli, 1998; Del Moral & Sarmiento, 2008), Poland (Dzik, 1994, 1999), China (Wang *et al*., 1983) and North America (e.g. Branson & Mehl, 1933b; Weyant, 1968; Bergström, 1978; Goldman *et al*., 1995; Sweet, 2000) and it is an important zone fossil. At least two proposed *Amorphognathus* species evolved from *A. ordovicicus* in late Katian time, namely *A. duftonus* Rhodes, 1955 (Fig. 5) and *A. ventilatus* Ferretti & Barnes, 1997. The former, which is known from England (Rhodes, 1955; Orchard, 1980) and the Carnic Alps in Italy (Serpagli, 1967; referred to as *Goniodontus lindstroemi*), has a distinctive M element that appears to justify its recognition as a separate species. The latter species, which was described from the *A. ordovicicus* Zone of Thuringia, is known only from its M elements (Ferretti & Barnes, 1997, pl. 2, figs 14–17), and further study is needed to clarify its status. It has been identified from significantly older strata (uppermost *A. tvaerensis* Zone) in Poland (Dzik, 1994) and Estonia (e.g. Männik & Viira, 2005) but we feel it unlikely that these specimens represent the Thuringian species.

A. ordovicicus underwent some evolution during the late Katian, which is expressed mainly in the morphology of the M element (Fig. 5). Stratigraphically late morphotypes, such as that from the type stratum at Ozora, Missouri and the closely similar one from the Carnic Alps (Serpagli, 1967), have greatly reduced denticles and processes in the M element, which in many cases is reminiscent of a straight simple cone.

Representatives of *Amorphognathus* occur high up in the Hirnantian (e.g. Bergström *et al*., 2006) but because there is no confirmed record of the genus from the Silurian, it likely went extinct during the Hirnantian extinction event(s). Apart from the taxa dealt with here, dozens of other species names have been proposed based on single elements, but most of these taxa can now be grouped into the multi-element species dealt with herein (cf. Bergström, 1971, 1983; Lindström, 1977).

CONCLUDING REMARKS

The principal results of the present study may be summarized as follows.

1. The rediscovery of the long 'lost' type locality of *Amorphognathus ordovicicus* and other taxa at Ozora, eastern Missouri now makes it possible to assemble topotype specimens of this and other important species described by Branson & Mehl (1933b).
2. The new collections confirm that the diagnostic M element of the stratigraphically important species *A. ordovicicus* has a simple cone-like shape without well-developed denticles on the sides of the prominent apical denticle. The morphology of this element implies that the Ozora occurrence is rather advanced within the range of this species.
3. Re-classification of Branson and Mehl's Ozora species into multi-element taxonomy indicates that they represent six multi-element species. Our new Ozora collections include at least eight additional multi-element species. Hence, the total number of currently known species from Ozora is 14.
4. The fact that the Ozora fauna represents the *Amorphognathus* biofacies of Sweet (1988), which is characteristic of relatively deep-water environments in the North American Midcontinent, is consistent with the fact that the Ozora conodont fauna occurs at the base of the transgressive Maquoketa Shale.
5. A review of the relatively rapid evolution of *Amorphognathus* through the Upper Ordovician indicates that at least six distinctive species can be recognized. Whereas the Pb and S elements tend to be conservative morphologically, the Pa and M elements exhibit morphological trends useful for species discrimination.

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