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# Evolution of the Late Ordovician high-latitude conodonts and dating of Gondwana glaciations

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*KEY WORDS – Conodonts, Evolution, Late Ordovician, Glaciation.*

*ABSTRACT – The presence of the rapidly evolving conodont lineage of* Amorphognathus *in the Middle and Late Ordovician of the Holy Cross Mountains (Poland) enables correlation of environmental events there with those from other areas of the world. The faunal succession of the conodonts records especially well the profound climatic changes in the Ashgill. The record can be calibrated climatically on the basis of periodic immigrations of species known to be abundant either in the Ordovician subpolar regions (*Sagittodontina, Scabbardella*) or subtropics (*Rhodesognathus, Icriodella, Birksfeldia*). Increased contribution of* Scabbardella *is generally connected with a decrease in taxonomic diversity of the species association. A general trend toward cooling, which is partially reversed close to the end of carbonate sedimentation in the area, is shown. The phyletic succession of* Amorphognathus *chronospecies is shown stratophenetically. This is used to propose a provisional correlation of the events recorded in the Holy Cross Mountains with those within the carbonate sedimentation intervals in areas closer to Gondwana. A late population of* A. tvaerensis, *which shows much similarity to the Thuringian Kalkbank* A. ventilatus *and presumably being ancestral to it, co-occurs in the Holy Cross Mountains with* Rhodesognathus. *This suggests that the Kalkbank warm event was coeval with the topmost phosphate-rich part of the Mójcza Limestone immediately above, where* A. superbus *occurs.* A. *sp. n., which characterizes the lower part of the marly strata above the Mójcza Limestone with a lowest diversity assemblage, is known also from lateral equivalents of the Kullsberg mud mound limestones of Sweden. Its transition to* A. ordovicicus *corresponds to the peak of abundance of cold-water species. The proposed transition from* A. ordovicicus *to* A. duftonus *and a significant increase in contribution of* Dapsilodus *at the expense of* Scabbardella *preceded the cessation of carbonate sedimentation in the area and it seems to be coeval with similar events in the Carnic Alps.*

*RIASSUNTO –* [Evoluzione dei conodonti ordoviciani delle alte latitudini e datazione delle glaciazioni gondwaniane] *– La presenza della linea a rapida evoluzione del genere* Amorphognathus *nell'Ordoviciano medio e superiore delle Holy Cross Mountains (Polonia) permette di correlare eventi ambientali registrati in quest'area con quelli di altre parti della Terra. La successione delle faune a conodonti testimonia molto bene quali profondi cambiamenti climatici siano avvenuti nell'Ashgill. I dati climatici possono essere calibrati sulla base di periodiche immigrazioni di taxa che nell'Ordoviciano sono abbondanti nelle regioni subpolari (*Sagittodontina, Scabbardella*) o subtropicali (*Rhodesognathus, Icriodella, Birksfeldia*). Un progressivo aumento di* Scabbardella *è in genere accompagnato da una diminuzione nella diversità tassonomica. Ne emerge un trend generale di raffreddamento, che è in parte invertito al termine della sedimentazione carbonatica della fine del periodo. La successione filetica delle cronospecie di* Amorphognathus *è illustrata "stratofeneticamente". Questo approccio permette di formulare un primo tentativo di correlazione degli eventi registrati nelle Holy Cross Mountains con quelli degli intervalli carbonatici di aree più vicine al Gondwana. Una popolazione tardiva di* A. tvaerensis, *molto simile ad* A. ventilatus *del Kalkbank (Turingia) e suo probabile predecessore, è presente nelle Holy Cross Mountains assieme a* Rhodesognathus. *Ciò suggerisce che l'evento freddo del Kalkbank sia coevo con la più alta parte ricca in fosfato del Calcare di Mójcza, dove è presente* A. superbus. Amorphognathus *n.sp., che è tipico degli strati marnosi con scarsa diversità specifica al di sopra del Calcare di Mójcza, è noto anche in sedimenti equivalenti ai calcari di scogliera del Kullsberg, in Svezia. La sua evoluzione verso* A. ordovicicus *avviene in corrispondenza di un picco di abbondanza di forme di acque fredde. La transizione da* A. ordovicicus *a* A. duftonus *e un significativo aumento nella presenza di* Dapsilodus *e un calo di quella di* Scabbardella *precedono la fine della sedimentazione carbonatica nell'area e sembrano essere coevi con eventi analoghi nelle Alpi Carniche.*

## INTRODUCTION

The present study is based on three exposures in the Holy Cross Mountains, Poland. All of them have been known for a long time and preliminary descriptions of both their geology and paleontology are available in the literature (reviewed in Dzik & Pisera, 1994). Additional conodont samples have been collected from new trenches dug in the northern wall of the Międzygórz quarry (in 1994), in the Zalesie ravine (also in 1994), and in the field in front of the Mójcza quarry (in 1995).

The Mójcza Limestone, together with the unnamed lower carbonate member of the Zalesie Formation, is an extreme case of stratigraphic condensation. At least 30 million years (according to estimates by Tucker & McKerrow, 1995) are represented by only ten meters of rock succession, with only one biostratigraphically identifiable gap. In fact, the entire Ordovician is extremely condensed in the Holy Cross Mountains. The Zalesie section, with its 38 m of rock sequence, covers the time span from the Late Tremadoc to the end of the Ashgill. Even the Early Ordovician coarse clastics, dominant in Międzygórz and not represented in Zalesie, add only 38 m more to equally condensed Middle and Late Ordovician sections. Such a low rate of sediment accumulation requires that the area of deposition of the Mójcza Limestone and Zalesie Formation carbonates, the Małopolska Massif and the Holy Cross Mountains, was tectonically very quiet. It was earlier peneplained in one of the Late Tremadoc eustatic falls, and isolated from any external source of coarse clastics. Biogeographic and paleomagnetic data suggest that the Małopolska microcontinent was separated from both Baltica and Gondwana by oceanic areas. It was located closer to the South Pole than Baltica, but farther from it than the African parts of Gondwana (Dzik, 1990; Lewandowski, 1993).

### *Mójcza*

The Mójcza section (Text-fig. 1; Tab. 1) provides the best record of conodont evolution in the Holy Cross Mountains (Dzik, 1994). In addition to the part of the section exposed in the quarry, 1.8 m more of Ordovician limestone and 4 m more of Silurian shales with calcareous intercalations have been sampled in a trench dug in the field near the quarry. This is mostly a marly limestone with detritus of ostracodes and echinoderms, especially in the topmost part. The bed about 20 cm below the top of the limestone series contains vertically oriented phosphatic tubes of *Sphenothallus*, and 1.50 m below the top conchs of longiconic orthoceratid nautiloids occur. The Ordovician limestone is covered by a soft sandy marl, 10 cm thick, with mixed Ordovician and Silurian conodonts, very well preserved but fragmented, and a thick bed of a plastic K-bentonite. There are calcareous concretions in the top part of the K-bentonite and a continuous 1-2 cm thick limestone intercalation above it. The limestone contains a typical *Pterospathodus celloni* Zone assemblage, which indicates that the topmost Ashgill and most of the Llandovery strata are missing there. One may guess that these were soft shales and that the erosion that removed them stopped at the topmost limestone bed of the sequence.

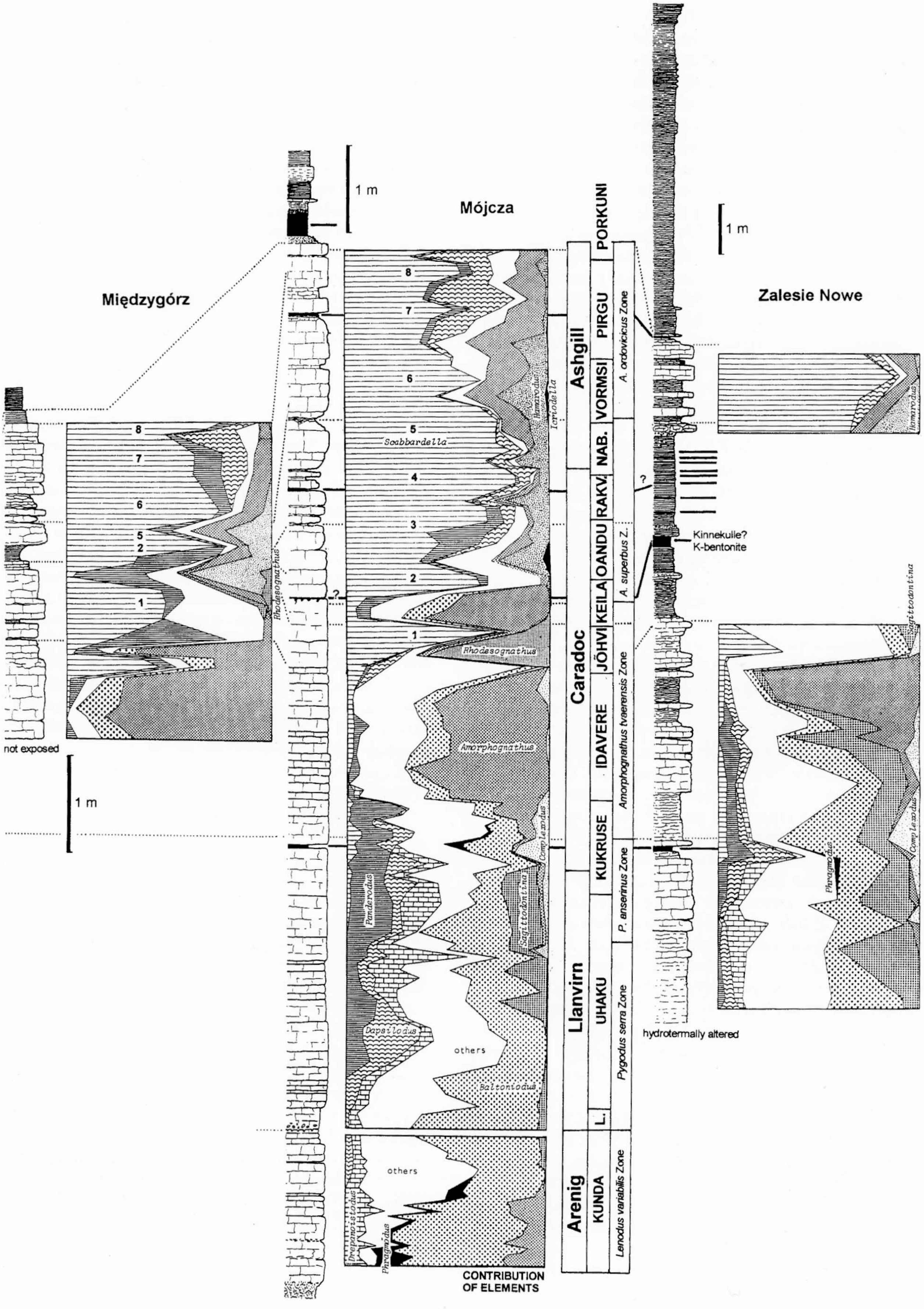
### *Międzygórz*

The strata exposed in Międzygórz (Text-fig. 1) originated in a slightly shallower water sedimentation regime than those at Mójcza. Both belong to the central Kielce facies region, where there was continuous carbonate sedimentation from the end of the Arenig until at least the middle of the Ashgill. The Mójcza Limestone is exposed there in the middle of the northern wall of the quarry (see Dzik & Pisera, 1994). The beds lie in overturned position and Silurian (Middle Llandovery) graptolite shales are below (Tomczyk, 1954). The basal part of the carbonate succession is not exposed. It is hidden under Early Ordovician Bukówka sandstone debris. As the thickness of the limestone units in Międzygórz seems closely similar to that in Mójcza, it may be inferred that about four basal meters of the succession, those below the main Mójcza K-bentonite layer, are not available for study. *Complexodus* and *Eoplacognathus elongatus* occur in the oldest sampled strata. *Amorphognathus tvaerensis* is documented by its diagnostic ne (M) elements somewhat above this horizon (sample MG-48). *Rhodesognathus* is represented (Text-fig. 1), although not as abundantly as in Mójcza (samples MG-41 to MG-37), and is replaced by more abundant *Amorphognathus* above. A single ne (M) element indicates *A. superbus*. The resulting correlation with respective strata in Mójcza is consistent with the presence of phosphatic ooids, which in Mójcza continue to the top of the *A. superbus* Zone. As at Mójcza, the range of *Hamarodus* in Międzygórz overlaps that of *Rhodesognathus*.

A level with a strongly weathered dolomitic mudstone follows and the first bed above it (sample MG-33) contains *Amorphognathus ordovicicus*, as shown by a single ne (M) element. The part of the succession corresponding to that of an unnamed species of *Amorphognathus* (referred to here as *A.* sp. n.) in Mójcza is thus missing in Międzygórz, or is represented by the mudstone. Some support for such a correlation is provided by the abundance of agglutinating foraminifera (indicative of a supply of fine quartz grains to the area, earlier missing), which at Mójcza are restricted in occurrence to the uppermost part of the succession, with *A. ordovicicus* s.s. Elements of the same morphology, with very elongated cusp, in samples MG-21 and MG-17 suggest that the carbonates do not reach the level of *A. duftonus*. The incompleteness of the Międzygórz section may be due to its even stronger stratigraphic condensation than at that of Mójcza or be caused by tectonic dislocations.

In Międzygórz, the Ordovician-Silurian boundary fine clastics are reduced (probably tectonically) to a bed of pale shale a few centimeters thick. The oldest Silurian black graptolite shales represent the middle Llandovery *Monograptus gregarius* Zone (Tomczyk, 1954).

Text-fig. 1 - Correlation of the three main sections of the Middle and Late Ordovician strata in the Holy Cross Mountains, Poland. The Międzygórz and Mójcza sections belong to the relatively shallower-water Kielce facies region, the Zalesie Nowe section belongs to the deeper-water Łagów facies region. General age correlation and recognition of particular time units is based on the evolution of conodonts. Logs of percentage contribution of elements of conodont apparatuses representing particular lineages can be used for finer correlation referring to climatically controlled faunal successions. Climatic gradients are calibrated by using incursions of exotic, subbpolar and tropical species. Numbers in the upper parts of the logs denote episodes of climate cooling identified in the Mójcza succession. Continuous horizontal lines indicate K-bentonite horizons.


1 m
Mójcza
Międzygórz
Zalesie Nowe
1 m
1 m
PORKUNI
PIRGU
VORMSI
NAB.
RAKV.
OANDU
KEILA
JÕHVI
IDAVERE
KUKRUSE
UHAKU
L.
KUNDA
Ashgill
Caradoc
Llanvirn
Arenig
A. ordovicicus Zone
?
A. superbus Z.
Amorphognathus tvaerensis Zone
P. anserinus Zone
Pygodus serra Zone
Lenodus variabilis Zone
8
7
6
5
4
3
2
1
8
7
6
5
2
1
?
Scabbardella
Hamarodus
Icriodella
Rhodesognathus
Amorphognathus
Complexodus
Sagittodontina
Panderodus
Dapsilodus
others
Baltoniodus
others
Drepanoistodus
Phragmodus
CONTRIBUTION OF ELEMENTS
Kinnekulle?
K-bentonite
Hamarodus
Sagittodontina
Phragmodus
Complexodus
hydrotermally altered
not exposed

### *Zalesie Nowe*

The depositional environment in the southern area of the Holy Cross Mountains (the Łagów region) was relatively off-shore with respect to Mójcza and Międzygórz. The carbonate succession at the Zalesie Nowe section (Text-fig. 1) is closely similar to that of Mójcza despite some diagenetic alteration of the rocks, which are more tectonized than in Mójcza, and show greater weathering. The K-bentonite in the middle of the succession is the same as in Mójcza, as proven by an increased contribution of *Phragmodus polonicus* and *Complexodus pugionifer* at that stratigraphic level. Unlike Mójcza, there are numerous marly intercalations (but still with phosphatic ooids) within the upper part of the organodetrital limestone, corresponding presumably to the *Nemagraptus gracilis* transgression. Close to the end of carbonate sedimentation, *Amorphognathus* disappeared almost completely and the assemblage became dominated by species with coniform elements. Initially this was '*Scolopodus*' *peselephantis* (in sample ZA-25) which corresponds to a similar increase in contribution of this species in Mójcza (samples MA-86 to MA-88). The topmost limestone layer (sample ZA-23) contains *Sagittodontina* and numerous *Strachanognathus*, like the horizon immediately preceding the mass occurrence of *Rhodesognathus* in Mójcza (sample MA-91; Fig. 2). Apparently the immigration of this species to the Holy Cross Mountains coincided with the end of carbonate sedimentation in Zalesie.

Above, there are more than three meters of marls and shales with thin dolomitic intercalations and a level with ooids. There is a thick K-bentonite bed, and several minor ones (Chlebowski, 1971 identified six such intercalations), within this series, which ends with purple-red shales with small ferruginous concretions (oxidized pyrite?). Unfortunately, no conodonts have been recovered from this part of the section and its dating remains rather unprecise. It is tempting to correlate the Zalesie K-bentonites with those of the Baltic area (see Bergström *et al.*, 1995, 1997), the Kinnekulle K-bentonite being especially widely distributed (Huff *et al.*, 1992) but they seem to be significantly younger than the Baltic ones. There is also no Baltic equivalent to the main Mójcza bentonite.

Immediately above there is the only bed of pure limestone in the entire section. This is a dark brown nodular rock with numerous darkly stained worm burrows in its basal, muddy part. Conodonts are easily extracted but rather uncommon and represented mostly by *Hamarodus*, specifically indeterminate *Amorphognathus* (almost certainly *A. ordovicicus*), and *Scabbardella*. This is an assemblage similar to that from the topmost Mójcza Limestone at Mójcza and such a correlation has been proposed earlier (Dzik *et al.*, 1994), although the lack of phosphatic ooids may rather suggest its correlation with one of the horizons rich in *Hamarodus* above that formation.

A thin intercalation of a black clay separates the limestone horizon from the series of dolomite and limestone beds. They contain uncommon and rather poorly preserved conodonts, dominated by *Scabbardella* and *Amorphognathus*, which are generally similar to those from the Mójcza section. Unfortunately, no ne (M) element of *Amorphognathus* has been found, which makes a more precise correlation impossible. The two lower dolomite beds are relatively rich in *Hamarodus*, which is very rare in the third one and a little more common in the topmost bed. This may be interpreted as an expression of two warmer epochs separated by a single colder episode, but it has to be kept in mind that the more calcareous dolomite beds are separated by marly intercalations in which conodonts are unknown. It may appear that each of the four dolomite beds corresponds to a separate warm episode recorded in Mójcza. Possibly, this unit corresponds to the entire Ordovician sequence above the Mójcza Limestone at Mójcza.

In Zalesie Nowe, a rather uniform fine-clastic rock continues to the top of the Ordovician, with *Mucronaspis* occurring in its lower part (Czarnocki, 1928; Kielan, 1956, 1960). Sedimentation was continuous across the Silurian-Ordovician boundary. Above the pale shales with K-bentonite intercalations of the Zalesie Formation there is an unfossiliferous black, organic-rich layer, a few centimeters thick, and then a graptolite shale that passes gradually into a radiolarite. Both the latest Ashgill *Normalograptus persculptus* and the earliest Llandovery *Parakidograptus acuminatus* Zones were reported from the shales (Kielan, 1956) although more recent collecting has failed to provide any guide graptolite species in the dominantly normalograptid assemblage.

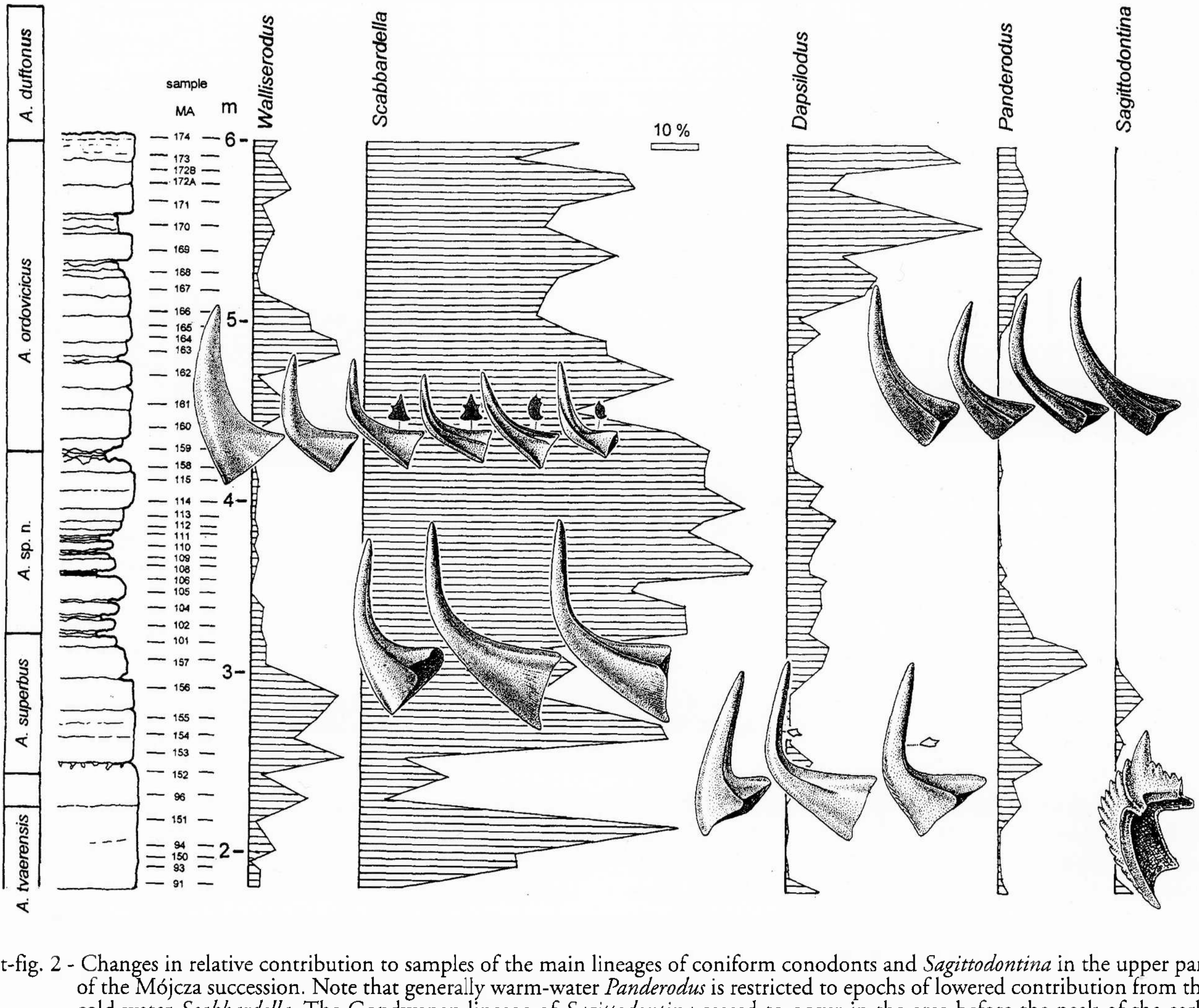
## EVOLUTIONARY CALIBRATION

Although several of the conodont species represented in the Mójcza Limestone and the lower part of the Zalesie Formation have short stratigraphic ranges, in most cases this reflects only their ecological sensitivity and has little to do with evolution or even with a more geographically uniform succession of faunas. Perhaps the only lineage (possibly two parallel lineages) that is of some value in an interregional correlation is that of *Amorphognathus*. Even in this case the more or less continuous succession of populations, typical of the Middle Ordovician part of the Holy Cross Mountains succession, was punctuated in the Late Ordovician by climatic instability. The first such ecological displacement was expressed by an incursion of *Rhodesognathus* (Text-fig. 3), in fact representing an allopatric lineage closely related to *Amorphognathus*. After its disappearance, a morphologically distinct species of *Amorphognathus* occurred in the area, possibly of foreign origin (*A. ventilatus*). The local lineage of *Amorphognathus*, at least when present with *Rhodesognathus*, evolved toward the morphology of *A. superbus*. This was the species that later replaced *A. ventilatus*, which again suggests a migrational event. Perhaps the subsequent series of morphologies, represented by an unnamed chronospecies with a ne (M) element small denticle at the external margin of a high cusp, then *A. ordovicicus*, lacking such a denticle, and finally *A. duftonus*, with a newly formed denticle at the junction of the processes, is a phyletic series. Some uncertainty is introduced, however, by the extremely wide population variability of *Amorphognathus* (see Dzik, 1994) which characterizes especially the population of *A. ventilatus* from Thuringia (see Ferretti & Barnes, 1997). Among specimens found there, forms closely similar to *A. ordovicicus* occur. This may mean that it was a member of an allopatric lineage that invaded the temperate regions during a global cooling.

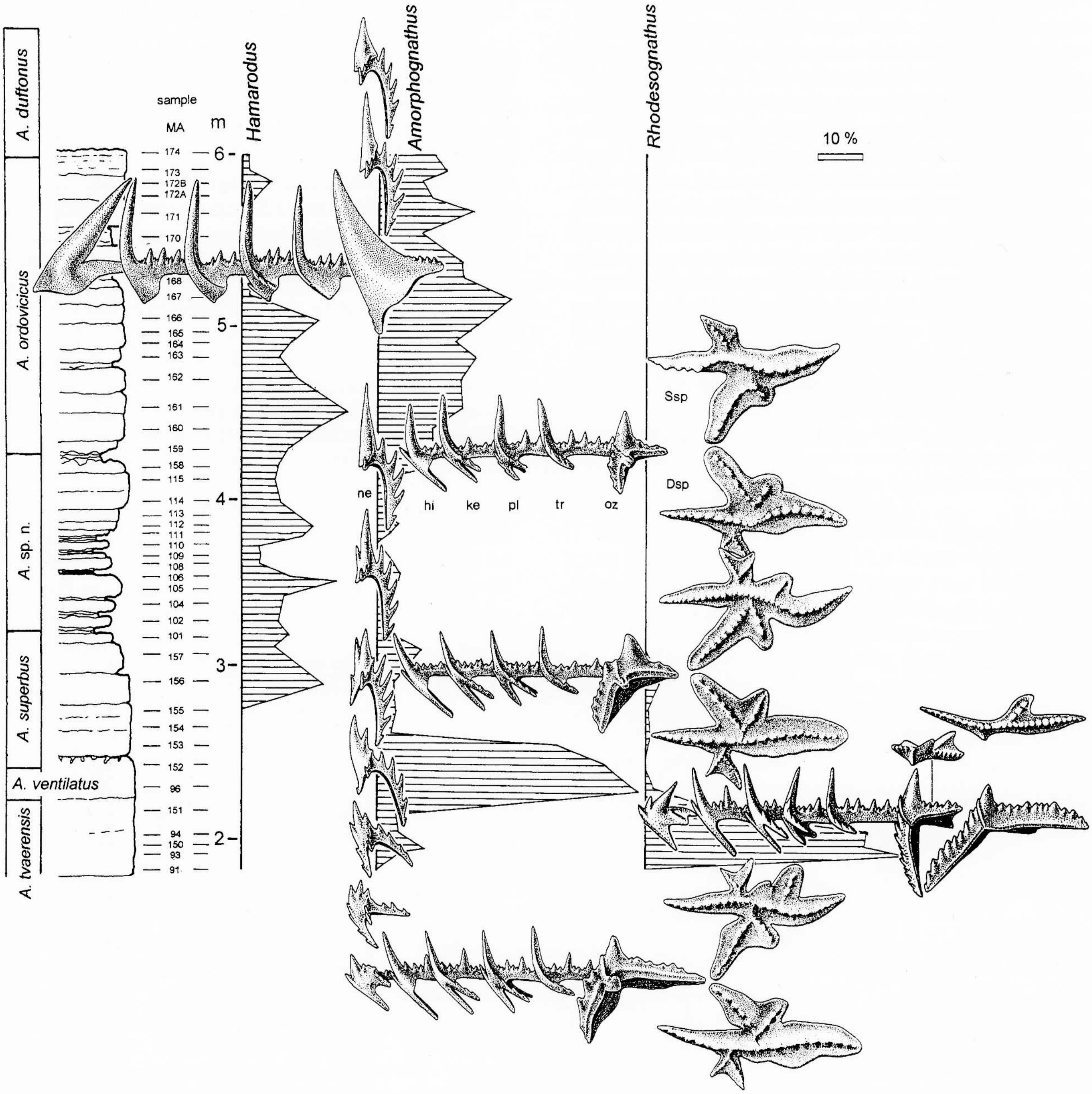
The paleontological basis for the interregional correlation of particular climatic events recognized in Mójcza is very weak. This results mostly from the rarity of small and fragile diagnostic elements of *Amorphognathus* in the studied strata. Unfortunately, there seems to be no alternative to this way of reasoning in correlating the events. Despite all those reservations, a preliminary correlation is here proposed. Problems that result from poor knowledge of the guide species are discussed below.

### *Amorphognathus ventilatus* Ferretti & Barnes, 1997

This species is undoubtedly the most important in the age correlation of the Kalkbank, the only carbonate horizon in the Ordovician of Thuringia. The single ne (M) element in Knüpfer's (1967) collection was



Text-fig. 2 - Changes in relative contribution to samples of the main lineages of coniform conodonts and *Sagittodontina* in the upper part of the Mójcza succession. Note that generally warm-water *Panderodus* is restricted to epochs of lowered contribution from the cold-water *Scabbardella*. The Gondwanan lineage of *Sagittodontina* ceased to occur in the area before the peak of the early Ashgill cooling. Ranges of the *Amorphognathus* species which enable interregional correlation shown on left.



Text-fig. 3 - Changes in relative contribution to samples of the main lineages of conodonts with elaborate apparatuses. Note the restricted occurrences of warm-water Welsh immigrant *Rhodesognathus* and two peaks in abundance of *Amorphognathus*.

classified as *Amorphognathus superbus* Rhodes, 1953 by Dzik (1989) because of its similarity to specimens from the top of the Mójcza Limestone, named '*A. superbus* early form' in Dzik (1990; also Dzik, 1994). This interpretation was not accepted by Ferretti & Barnes (1997), who had at their disposal an extremely large collection of Kalkbank conodonts, including 102 ne (M) elements of *Amorphognathus*. Cusp morphology of ne (M) element is extremely variable in their sample. They introduced the new species, *A. ventilatus*, for elements similar to the one illustrated by Knüpfer (1967) and associated elements with a very prominent cusp without any denticles on its sides were identified as *A. ordovicicus* Branson & Mehl, 1933. On this basis and somewhat arbitrarily, they proposed that the Kalkbank is of early *A. ordovicicus* Zone age. In fact, a complete transition between these morphologies can be traced in their sample, with no evidence of

| Sample MA | 150 | 151 | 190 | 191 | 152 | 153 | 154 | 155 | 156 | 157 | 158 | 159 | 160 | 161 | 162 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Scolopodus* | | | 11 | 7 | | | | | | | 20 | 3 | | 2 | |
| *Walliserodus* | 4 | 47 | 273 | 122 | 4 | 10 | 47 | 64 | 50 | 15 | 3 | 3 | 3 | 51 | 2 |
| *Scabbardella* | 753 | 1862 | 435 | 190 | 39 | 5 | 327 | 318 | 100 | 203 | 1685 | 812 | 384 | 279 | 257 |
| *Dapsilodus* | 3 | 25 | | | 8 | 3 | 4 | 4 | 2 | 33 | 43 | 7 | 18 | 16 | 6 |
| *Panderodus* | 29 | 26 | 152 | 65 | 8 | 5 | 15 | 29 | 14 | 87 | 27 | 6 | | 1 | 1 |
| *Cornuodus* | 54 | 111 | 17 | 2 | 3 | 2 | 23 | 9 | 7 | 3 | 2 | | | | 1 |
| *Strachanognathus* | 9 | 1 | | | | | | | | | | | | | |
| *Staufferella* | 1 | | 3 | | | | | | | | | | | | |
| *Protopanderodus* | | | 1 | | | | | | | 3 | 2 | | 1 | | |
| *Paltodus* | 2 | 3 | 49 | 47 | 2 | | | | | | | | | | |
| *Drepanoistodus* | 31 | 12 | 143 | 42 | 7 | | 44 | 48 | 4 | 8 | 4 | 1 | | | |
| *Pseudooneotodus* | | | | | | | | | | 3 | | | | | |
| *Phragmodus* | | | | | 2 | | | | | | | | | | |
| *Baltoniodus* | 32 | 13 | 179 | 104 | 31 | 5 | | | | | 1? | | | | |
| *Sagittodontina* | | | | | | | 10 | | 17 | | | | | | |
| *Rhodesognathus* | 1056 | 500 | 51 | 14 | | | 5 | 1 | 9 | | | | | | |
| *Amorphognathus* | 224 | 122 | 523 | 414 | 101 | 21 | 18 | 20 | 10 | 43 | 343 | 139 | 69 | 118 | 71 |
| *Icriodella* | | | | | | | | | 6 | | 10 | 4 | 1 | 10 | |
| *Birksfeldia* | | | | | | | | | | | | | | 1 | |
| *Hamarodus* | | 4 | | | | | 1 | | 51 | 35 | 195 | 112 | 96 | 150 | 50 |
| *Spinodus* | 1 | | | | | | | | | 3? | | | | | |

| Sample MA | 163 | 164 | 165 | 166 | 167 | 168 | 169 | 170 | 171 | 172a | 172b | 173 | 174 | 175 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Scolopodus* | | | | 5 | | | | 3 | | 2 | 3 | 2 | 5 | |
| *Walliserodus* | 24 | 42 | 203 | 108 | 7 | 2 | 13 | 48 | 3 | 37 | 67 | 24 | 75 | |
| *Scabbardella* | 71 | 130 | 756 | 393 | 281 | 313 | 460 | 509 | 94 | 317 | 736 | 318 | 832 | 4 |
| *Dapsilodus* | | 3 | 124 | 36 | 118 | 143 | 102 | 551 | 51 | 51 | 168 | 375 | 553 | 5 |
| *Panderodus* | | 1 | 17 | 35 | 28 | 64 | 79 | 40 | 14 | 38 | 75 | 33 | 61 | |
| *Cornuodus* | | 2 | 21 | 16 | 26 | 31 | 16 | 26 | 11 | 4 | 33 | 56 | 17 | |
| *Protopanderodus* | | | 9 | 19 | 16 | 23 | 4 | 1 | 1 | 12 | 15 | 2 | 5 | 2 |
| *Paltodus* | | | | | 1 | | | 1? | | | 8 | | 1 | |
| *Drepanoistodus* | | | | 2 | | | | | | | | | | 3 |
| *Pseudooneotodus* | | | 2 | 4 | 8 | 6 | 10 | 2 | 1 | 4 | 5 | 6 | 15 | |
| *Amorphognathus* | 29 | 43 | 338 | 254 | 215 | 142 | 156 | 122 | 48 | 63 | 127 | 148 | 225 | 11 |
| *Icriodella* | | | | | 1 | | | | | | | | | |
| *Birksfeldia* | | | | | | 1 | 5 | | | | 10 | 1 | | |
| *Distomodus* | | | | | | | | | | | | | | 31 |
| *Pterospathodus* | | | | | | | | | | | | | | 7 |
| *Hamarodus* | 12 | 27 | 246 | 181 | 15 | 17 | 6 | 15 | 1 | 18 | 85 | 17 | 28 | |
| *Plectodina* | | | | | | | | | | 3 | | | | |
| Gen. indet. | | 1 | | | | | | | | 1 | | | | |
| *Drepanodus* | | | | | 1 | | | | | | | | | |

Tab. 1 - Numerical contribution of particular conodont genera to samples taken from the upper part of the Mójcza section.

bimodality in the frequency distribution. Moreover, one element with a denticle on the outer side of the cusp (thus of a morphology typical of *A. superbus*) points to a complex pattern of developmental control of the morphology. In the Kalkbank assemblage the dominating morphology of ne (M) elements is that with one large denticle emerging obliquely from the inner side of the cusp (53 specimens in Ferretti & Barnes, 1995 collection). Elements with two such denticles (the second one usually rudimentary, tips the merging point of internal and posterior processes) include 14 specimens. Specimens without additional denticles on the cusp (thus closely resembling elements in the *A. ordovicicus* s.s. populations, although with a somewhat wider and shorter cusp) are equally common (13 specimens), the distribution seems thus almost Gaussian. Thus it is proposed that only one species of *Amorphognathus* is represented in the Kalkbank assemblage.

The unusually large number of ne (M) elements extracted from the Kalkbank sample by Ferretti & Barnes (1995) cannot alone explain the extraordinary diversity of their morphologies in the assemblage. No doubt that they were much more variable than in any other described Late Ordovician population of *Amorphognathus*. A possible solution to this puzzle may be provided by the apparent immigrational nature of the whole Kalkbank fauna. This can be matched with similar cases of invasion by warm-water conodont assemblages into environments that were ecologically different earlier, which used to be connected with an increase in the population variability. In the Devonian and Carboniferous this pattern of a disparate variability has been explained as an effect of the character displacement that follows complication of a community after its establishment (Dzik, 1997, p. 70). An interesting feature of the associated *Sagittodontina* population is that some ne (M) elements also developed additional oblique denticles close to the tip of the cusp. Sometimes it is difficult to distinguish between the elements of *Sagittodontina* and *Amorphognathus*. This refers also to the oz (Pb) elements, which are extremely variable, and range from morphologies close to those typical of *Rhodesognathus* (and erroneously identified as such by Dzik, 1990) to those with wide, short processes, similar to specimens that occur much lower in the Polish sections (see Dzik, 1994).

A direct relationship of *A. ventilatus* to *A. ordovicicus* is unlikely because of the primitively long external ('anterior') process in ne (M) element of *A. ventilatus* (including specimens classified as *A. ordovicicus* by Ferretti & Barnes, 1997). This process was relatively long and some specimens from the Kalkbank show a small denticle on it. A gradual reduction of the entire process can be seen in the succession from *A. superbus* through *A.* sp. n. to *A. ordovicicus* in the Mójcza section. An independent origin of *A. ordovicicus* from *A. ventilatus* would require that in each of the two separate lineages the reduction proceeded in parallel.

The arched internal process, which is shared by the ne (M) element of all the Ashgill species of *Amorphognathus*, apparently developed already in the late population of *A. tvaerensis*. Perhaps *A. ventilatus* originated directly from *A. tvaerensis* by an almost complete reduction of the external denticulation in the ne (M) elements. The Mójcza specimens from samples MA-96 and MA-97, previously named '*A. superbus* early form' (Dzik, 1994, text-fig. 22, pl. 23, fig. 3), share with those from Kalkbank the very characteristic fan-like arrangement of denticles in the ne (M) elements. Additional sampling at the same level (samples MA-190 and MA-191; Pl. 1, figs. 1-21) yielded 116 ne (M) specimens. Among 42 specimens from sample MA-190 preserved well enough to show the position of the cusp, 27 have the cusp in a marginal position, 13 bear a single external denticle and in two specimens

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EXPLANATION OF PLATE 1

Figs. 1-21 - *Amorphognathus* aff. *ventilatus* Ferretti & Barnes, 1997. Late Caradoc of the Mójcza section, Holy Cross Mountains, Poland. 1) sp (Pa) element ZPAL cVI/819, sample MA-190. 2) oz (Pb) element ZPAL cVI/821, sample MA-190. 3) sp (Pa) element ZPAL cVI/820, sample MA-190. 4) sp (Pa) element ZPAL cVI/805, sample MA-191. 5) sp (Pa) element ZPAL cVI/804, sample MA-191. 6) ne (M) element ZPAL cVI/826, sample MA-190. 7) ne (M) element ZPAL cVI/830, sample MA-190. 8) ne (M) element ZPAL cVI/828, sample MA-190. 9) ne (M) element ZPAL cVI/829, sample MA-190. 10) ne (M) element ZPAL cVI/827, sample MA-190. 11) tr (Sa) element ZPAL cVI/824, sample MA-190. 12) ke (Sc) element ZPAL cVI/822, sample MA-190. 13) hi (Sc) element ZPAL cVI/825, sample MA-190. 14) ne (M) element ZPAL cVI/799, sample MA-191. 15) ne (M) element ZPAL cVI/801, sample MA-191. 16) ne (M) element ZPAL cVI/800, sample MA-191. 17) ne (M) element ZPAL cVI/797, sample MA-191. 18) ne (M) element ZPAL cVI/798, sample MA-191. 19) ne (M) element ZPAL cVI/802, sample MA-191. 20) ne (M) element ZPAL cVI/803, sample MA-191. 21) pl (Sb) element ZPAL cVI/823, sample MA-190.

Figs. 22-26 - *Amorphognathus tvaerensis* Bergström, 1962 late form transitional to *A. superbus* Rhodes, 1953. Late Caradoc of the Mójcza section, Holy Cross Mountains, Poland.
22) sp (Pa) element ZPAL cVI/759, sample MA-152. 23) oz (Pb) element ZPAL cVI/761, sample MA-152. 24) sp (Pa) element ZPAL cVI/760, sample MA-152. 25) ne (M) element ZPAL cVI/765, sample MA-152. 26) ne (M) element ZPAL cVI/764, sample MA-152.

Figs. 27-30 - *Amorphognathus superbus* Rhodes, 1953. Late Caradoc of the Mójcza section, Holy Cross Mountains, Poland.
27) sp (Pa) element ZPAL cVI/758, sample MA-156. 28) oz (Pa) element ZPAL cVI/756, sample MA-156. 29) tr (Sa) element ZPAL cVI/762, sample MA-156. 30) ne (M) element ZPAL cVI/767, sample MA-154.

Fig. 31 - *Pseudooneotodus mitratus* (Moskalenko, 1973). Ashgill of the Mójcza section, Holy Cross Mountains, Poland.
31) element ZPAL cVI/784 in occlusal view, sample MA-172A.

Fig. 32 - Gen et sp. indet. Ashgill of the Mójcza section, Holy Cross Mountains, Poland.
32) element ZPAL cVI/783 in occlusal view, sample MA-172B.

Figs. 33-36 - '*Plectodina*' *alpina* Serpagli, 1967. Ashgill of the Mójcza section, Holy Cross Mountains, Poland.
33) sp (Pa) element ZPAL cVI/781, sample MA-172A. 34) oz (Pb) element ZPAL cVI/780, sample MA-172A. 35) tr (Sa) element ZPAL cVI/714, sample MA-115. 36) ne (M) element ZPAL cVI/782, sample MA-172A.

Figs. 37-39 - *Birksfeldia selli* Serpagli, 1967. Ashgill of the Mójcza section, Holy Cross Mountains, Poland.
37) oz (Pb) element ZPAL cVI/778, sample MA-172B. 38) ke (Sc) element ZPAL cVI/777, sample MA-161.39) ne (M) element ZPAL cVI/779, sample MA-172B.

(All specimens x 70)


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13 bear a single external denticle and in two specimens there are two such denticles (they are then either of *A. superbus* or *A. tvaerensis* morphology). The main difference between the Mójcza and Kalkbank populations is that the modal number of denticles (including cusp) in sample MA-190 is three (21 specimens) while in Thuringia most of the specimens bear only two or even one denticle (cusp alone). Moreover, sinistral sp (Pa) elements in the Mójcza sample still bear a rudimentary lobe at the internal process, which disappeared somewhat higher in the section, wheareas in the Kalkbank this lobe is completely missing (Ferretti & Barnes, 1997). However, the Mójcza population may be ancestral to *A. ventilatus*. Such a taxonomic decision results in a fundamentally different age correlation. Instead of belonging to the early *A. ordovicicus* Zone, the Kalkbank event would be close in age to the *A. superbus* Zone. The presence of similar specimens in the Nabala stage of Estonia may suggest that *A. ventilatus* ranged up to the level of *Amorphognathus* sp. n.

Its origin, if better documented, may appear useful as a marker of at least a regional importance. An emendation to the original diagnosis of *A. ventilatus* is here proposed, as an *Amorphognathus* species characterized by ne (M) elements with a sharp-edged, wide cusp without any external denticulation but with an additional single, obliquely emerging denticle (or two denticles) on its inner margin and a long external process, sometimes bearing a rudimentary denticle.

### *AMORPHOGNATHUS SUPERBUS* RHODES, 1953

In the topmost part of the Mójcza Limestone conodonts are rare and the contribution of *Amorphognathus* to the assemblage is very low. Two ne (M) elements in samples MA-154 and MA-100 (Dzik, 1994, text-fig. 22) show that *A. superbus* was represented there. They are characterized by a relatively short straight cusp associated with parallel strong denticles (Pl. 1, fig. 30).

### *AMORPHOGNATHUS* SP. N.

A series of populations following *A. superbus* in Mójcza (Pl. 2, figs. 1-12) show a gradual transformation towards a rather different morphology of the ne (M) elements. The cusp is much longer and only one denticle is present on the external process. In the early population from samples MA-109 and MA-1 the external process was relatively long, only somewhat shorter than in *A. superbus*. Large specimens may have developed an additional small denticle (Dzik, 1994, Pl. 3, fig. 6a). In samples somewhat above in the section the external process was much shorter, although still pointed, the cusp was even longer and the external denticle attached closer to it.

This segment of the phyletic evolution of the Ashgill *Amorphognathus* was classified earlier (Dzik, 1994) within *A. ordovicicus* but it definitely deserves separation at the chronospecies level.

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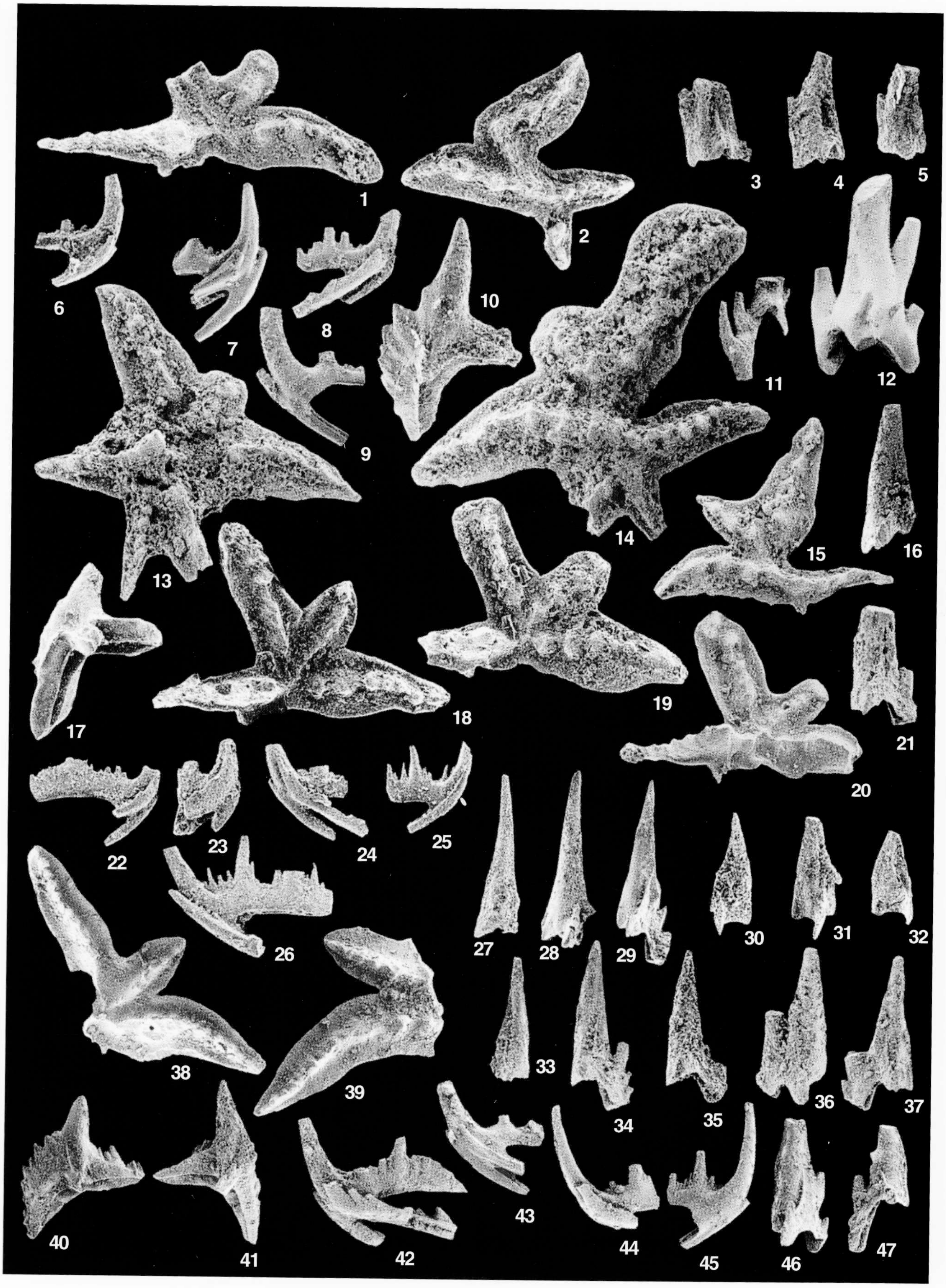
EXPLANATION OF PLATE 2

Figs. 1-12 - *Amorphognathus* sp. n. Earliest Ashgill(?) of the Mójcza section, Holy Cross Mountains, Poland.
1) sp (Pa) element ZPAL cVI/766, sample MA-158. 2) sp (Pa) element ZPAL cVI/767, sample MA-158. 3) ne (M) element ZPAL cVI/774, sample MA-158. 4) ne (M) element ZPAL cVI/773, sample MA-158. 5) ne (M) element ZPAL cVI/775, sample MA-158. 6) tr (Sa) element ZPAL cVI/769, sample MA-158. 7) pl (Sb) element ZPAL cVI/770, sample MA-158. 8) ke (Sc) element ZPAL cVI/771, sample MA-158. 9) hi (Sc) element ZPAL cVI/772, sample MA-158. 10) oz (Pb) element ZPAL cVI/768, sample MA-158. 11) ne (M) element ZPAL cVI/359, sample MA-1. 12) ne (M) element ZPAL cVI/460, sample MA-109.

Figs. 13-37 - *Amorphognathus ordovicicus* Branson & Mehl, 1933. Ashgill of the Mójcza section, Holy Cross Mountains, Poland.
13) sp (Pa) element ZPAL cVI/785, sample MA-163. 14) sp (Pa) element ZPAL cVI/786, sample MA-163. 15) sp (Pa) element ZPAL cVI/788, sample MA-165. 16) ne (M) element ZPAL cVI/776, sample MA-161. 17) oz (Pa) element ZPAL cVI/808, sample MA-165. 18) sp (Pa) element ZPAL cVI/806, sample MA-165. 19) sp (Pa) element ZPAL cVI/807 sample MA-165. 20) sp (Pa) element ZPAL cVI/787, sample MA-165. 21) ne (M) element ZPAL cVI/790, sample MA-166. 22) pl (Sb) element ZPAL cVI/811, sample MA-165. 23) pl (Sb) element ZPAL cVI/810, sample MA-165. 24) ke (Sc) element ZPAL cVI/812, sample MA-165. 25) tr (Sa) element ZPAL cVI/809, sample MA-165. 26) hi (Sc) element ZPAL cVI/813, sample MA-165. 27) ne (M) element ZPAL cVI/815, sample MA-165. 28) ne (M) element ZPAL cVI/817, sample MA-165. 29) ne (M) element ZPAL cVI/816, sample MA-165. 30) ne (M) element ZPAL cVI/789, sample MA-165. 31) ne (M) element ZPAL cVI/814, sample MA-165. 32) ne (M) element ZPAL cVI/818, sample MA-165. 33) ne (M) element ZPAL cVI/796, sample MA-173. 34) ne (M) element ZPAL cVI/793, sample MA-173. 35) ne (M) element ZPAL cVI/794, sample MA-173. 36) ne (M) element ZPAL cVI/792, sample MA-173. 37) ne (M) element ZPAL cVI/795, sample MA-173.

Figs. 38-47 - *Amorphognathus ordovicicus* Branson & Mehl, 1933 transitional to *A. duftonus* Rhodes, 1955. Late Ashgill of the Mójcza section, Holy Cross Mountains, Poland.
38) sp (Pa) element ZPAL cVI/944, sample MA-174. 39) sp (Pa) element ZPAL cVI/943, sample MA-174. 40) oz (Pb) element ZPAL cVI/945, sample MA-174. 41) oz (Pb) element ZPAL cVI/946, sample MA-174. 42) pl (Sb) element ZPAL cVI/948, sample MA-174. 43) ke (Sc) element ZPAL cVI/949, sample MA-174. 44) tr (Sa) element ZPAL cVI/947, sample MA-174. 45) hi (Sc) element ZPAL cVI/950, sample MA-174. 46) ne (M) element ZPAL cVI/951, sample MA-174. 47) ne (M) element ZPAL cVI/952, sample MA-174.

(All specimens x 70)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### *AMORPHOGNATHUS ORDOVICICUS* BRANSON & MEHL, 1933

In samples above MA-119 and MA-159 all the found ne (M) elements of *Amorphognathus* have a very short external process without any denticles (Pl. 2, figs. 13-37). The elements found are invariably of a small size and their adult morphology remains unknown. Still, they are easily distinguishable from the preceding chronospecies at comparable histogenetic stages. Although the material is too sparse to prove this biometrically, there seems to be a progressive reduction of the external process in the lineage, which finally resulted in the complete disappearance of external denticulation. In this respect the origin of *A. ordovicicus* was parallel to the much earlier development of the *A. ventilatus* morphology, which preceded the evolutionary elongation of the cusp and reduction of the external process.

A complete set of element types of this species has been illustrated by Nowlan & Barnes (1981) from the Vauréal Formation of the Anticosti Island, Canada. Both the apparatus reconstruction of *A. ordovicicus* by Armstrong *et al.* (1996) and their identification of the ne (M) element are incorrect. Their oz (Pb) element is actually an incomplete sp (Pa). The specimen identified as ne (M) is too poorly preserved to be identified, it may be a hi element of something else. Instead, their Sb1 element resembles more closely ne elements of *Amorphognathus.* If so, its long external process is suggestive of a proximity to *A. superbus.*

### *AMORPHOGNATHUS DUFTONUS* RHODES, 1955

The topmost limestone layer in Mójcza yielded two ne (M) elements of *Amorphognathus*, one of which has a rather short cusp with a transversely oriented denticle at the merging point of ribs of the internal and posterior processes (Pl. 2, figs. 38-42). Such a denticle develops commonly in specimens from populations of *Amorphognathus* of various ages. Those, which can be found among specimens of *A. ordovicicus*, for instance in sample MA-163 where they seem to be especially common, differ from geologically older ones in that the denticle does not belong to any of the processes but is located in the middle of the flat area spanning between the internal process and its posterior bifurcation. This apparenly resulted from the evolutionary increase of the angle of ramification of the internal process, which was initially rather small (although variable), becoming wider and wider, and finally loosing its connection with the transverse denticle. The denticle probably developed earlier in the histogeny of the element than bifurcation of the processes.

Both the ne (M) elements of *Amorphognathus* from the topmost bed of the Mójcza Ordovician differ from specimens found in older strata (even those bearing the transverse denticle) in having shorter and more robust cusp. Closely similar specimens have been identified in strata of the uppermost Rawtheyan (between shelly zones 7 and 8) Cystoid Limestone of Yorkshire by Orchard (1980) as *Amorphognathus* aff. *lindstroemi*. A conspecific population seems to be represented also in the 2 m thick limestone sequence of the Rifugio Nordio section in the Carnic Alps. Three ne (M) elements of *Amorphognathus* with smooth cusp margins have been found there by Serpagli (1967) and one with an incipient inner denticle. The only ne (M) element of *Amorphognathus* found by Ferretti (1998) in the Králov Dvor Formation immediately below *Mucronaspis* is also *Amorphognathus* aff. *lindstroemi*, which indicates that such a form occurs in strata that immediately precedestrata of Hirnantian age.

In the 3.5 m thick, possibly more complete Monte Zermula Carnic Alps section, three elements with a prominent denticle in this position have been found. This is the type population of *Amorphognathus lindstroemi* Serpagli, 1967. Several ne (M) elements of this kind have been reported (one of them illustrated) by Orchard (1980; also Bergström & Orchard, 1985), in the upper part of the Keisley Limestone of northern England. The Keisley Limestone is covered by shales with *Hirnantia* (Wright, 1985), similarly as the topmost Ordovician limestone units in the Holy Cross Mountains and the Carnic Alps. Bergström & Orchard (1985) pointed out its conspecificity with *Amorphognathus duftonus.*

Although the evidence is obviously very limited, a progressive evolution towards the larger and larger lateral denticle seems likely. The Rifugio Nordio Carnic Alps population, with only an incipient lateral denticle present in some elements, may then be coeval with that from the topmost limestone bed in Mójcza and the Cystoid Limestone of Yorkshire, but slightly older than that of the Monte Zermula and the uppermost(?) Keisley Limestone of northern England. The origin of *A. duftonus* (populations earlier classified as *A.* aff. *lindstroemi* being transitional) may be of some correlative value. In all the samples of late *Amorphognathus* from Mójcza elements ne (M) with the transverse denticle co-occur with elements lacking is, and this is clearly a matter of within-population variability. The main evolutionary change at the emergence of *A. duftonus* was probably a relative reduction in length of the cusp in respect to this denticle.

## ROOTS OF THE SILURIAN CONODONT FAUNAS

In all localities of the world where the Ordovician-Silurian transition is well documented by conodonts, there is drastic faunal change at the boundary. Only the lineages of coniform conodonts *Dapsilodus*, *Panderodus*, and *Pseudooneotodus* occur on both sides of the boundary but their morphological simplicity makes it uncertain if there is truly a continuity at the species level. Possibly, these were extremely opportunistic species, able to withstand even major changes in the environment. Other coniform members of the Ashgill assemblages (thin-crown *Scabbardella*, bizarre *Strachanognathus*), as well as conodonts with complex apparatuses but of the platform series elements with thin crowns (*Hamarodus*, *Ansella*), probably did not become extinct immediately. Rather they moved to cold water refugia and disappeared somewhat later, together with those shrinking environments. The extreme case is the Lazarus-type reappearance of the typically Ordovician *Ansella* in the early Wenlock in Australia (Bischoff, 1997). The lineage of *Icriodella* reinvaded the earlier occupied areas already in the Llandovery, and only slightly later the Pterospathodontidae initiated their rapid evolution. The oldest pterospathodontid with known apparatus structure is *Complexodus* (Dzik, 1994), which is not known from strata younger than the early Caradoc. Rare robust elements of a pterospathodontid resembling the Silurian *Distomodus* occur in the Late Caradoc of the Holy Cross Mountains, which supports the Ordovician origin of the family.

The earliest Silurian *Ozarkodina* and *Aspelundia*, from which probably all the remaining post-Ordovician ozarkodinid branches of the Spathognathodontidae and Prioniodinidae developed, show a biramous symmetrical tr (Sa) element. The biramosity of this element in the Late Ordovician *Yaoxianognathus*, as well as denticulation of the external process in the hi (Sc) element and parallel to the cusp arrangement of denticles in the ne (M) element, makes it a likely relative of the ancestor of the post-Ordovician ozarkodinids (Nowlan *et al.*, 1997).

The only important evolutionary change needed to produce a typical Silurian ozarkodinid would then be the arching of the internal process of the ne (M) element, with a parallel to the cusp arrangement of denticles. From some reason this was perhaps the most conservative feature of the post-Ordovician Ozarkodinida, which persisted unchanged in most lineages until the late Triassic extinction of conodonts (Dzik, 1992). In this respect it is of interest to notice that in the evolution of the ne (M) element of the late Ordovician *Amorphognathus* a closely similar transformation took place. In the Early and Middle Ordovician segment of the lineage, despite basic changes in the shape of the whole element, its internal process remained relatively short and straight, which is the primitive feature of both the Prioniodontida and early Ozarkodinida (Dzik, 1992, 1994). This changed in the late Caradoc, when the denticles close to the cusp developed an orientation parallel to it (*A. superbus* morphology). The internal process elongated significantly and arched, its denticulation becoming prominent with denticle tips pointing in the same direction as the cusp (*A. ordovicicus* morphology). In effect, a shape developed which closely matches the post-Ordovician ozarkodinid 'neoprioniodus' element (e.g. Dzik, 1994, pl. 24, fig. 20).

One may thus wonder, whether this similarity in the morphology of the anteriormost element in the apparatus, as well as the general tendency to molarize the posteriormost elements by developing an elaborate platform, does not express an ecological proximity of *Amorphognathus* to the post-Ordovician ozarkodinids. If so, the main faunistic change at the Ordovician-Silurian boundary would not correspond to any significant difference in the ecology of conodont communities but rather a competitive replacement of one taxonomic group by another.

Only one ozarkodinid species occurs in the Ashgill of the Holy Cross Mountains. Due to time proximity to the earliest Silurian ozarkodinids its taxonomic identity deserves some comments, similarly as the two other poorly known late Ordovician prioniodontids of restricted paleogeographic distribution, *Sagittodontina* and *Birksfeldia*.

### *'PLECTODINA' ALPINA* SERPAGLI, 1967

A few additional elements found in Mójcza in the carbonate equivalent of the Zalesie Formation have helped to clarify relationships of the single specimen classified earlier as a hi (Sc) element *Yaoxianognathus*? sp. (Dzik, 1994, pl. 24, fig. 21). Its surface is obliterated by a cover of an acid resistant clay but it seems now that this is almost certainly a symmetrical tr (Sa) element with one process broken. Such elements occur in the Uqua Limestone population of '*Plectodina*' *alpina* (*Prioniodus ethingtoni* in Serpagli, 1967). The main difference between '*Plectodina*' *alpina* and species of *Yaoxianognathus* is thus its primitive, triramous tr (Sa) element. Whether the medial process disappeared in the evolution from the common ancestor of both lineages at the origin of *Yaoxianognathus* or the latter originated directly from a *Microzarkodina*-like ancestor, remains unknown. Two more oz (Pb) elements and one ne (M) element have been found, which enables reliable taxonomic identification of the species (Pl. 1, figs. 33-36).

'*Plectodina*' *alpina* belongs to an evolutionary branch derived from *Plectodina* but different in lacking a rudimentary process in the oz (Pb) elements and thus similar in this respect to *Aphelognathus*, although differing from it in the morphology of the ne (M) elements, which in *Aphelognathus* have both processes denticulated. '*Ozarkodina*' *rhodesi* Lindström, 1959 and '*Ctenognathus*' *pseudofissilis* Lindström, 1959 from the Crug Limestone of Wales (Lindström, 1959; Orchard, 1980) of an early Ashgill age, the first known also from the Oanduan (late Caradoc) of the Baltic region (Viira, 1974; Dzik, 1983), are among the oldest occurrences of such morphology (Savage & Bassett, 1985). The ne (M) element of '*Prioniodina*' *alpina* does not show the specialization typical for related *Yaoxianognathus* but both show much similarity to the Silurian prioniodinid *Aspelundia* (see McCracken, 1991), perhaps the most primitive in this respect among the Silurian Ozarkodinida.

The *Yaoxianognathus* lineage seems to be rooted in *Y. abruptus* from the Lexington Limestone of Ohio of the Late Caradoc (Sweet, 1979; Bergström, 1990a), which still did not have developed the characteristic external ('anterior') denticle in the hi (Sc) element but its ne (M) element had straight and elongated internal ('posterior') process. *Yaoxianognathus wrighti* from the Clifden Caves Limestone of Australia, dated on the basis of a rather circumstantial evidence as late Caradoc (Savage, 1990), is probably the next in age member of its lineage. In its almost straight base of the ne (M) element and single external denticle in the hi (Sc) element it clearly shows features of the *Yaoxianognathus* lineage. Even more advanced in these respects was '*Ozarkodina*' *sesquipedalis* Nowlan & McCracken, 1988 from the Whittaker Formation of Canada of late Ashgill age (Nowlan *et al.*, 1988). It seems identical with *Yaoxianognathus yaoxianensis* An, 1985 from South China, the type species of its genus (An, 1987).

Most interestingly, the latest Ordovician assemblage with *Yaoxianognathus* from northern Canada does not contain *Amorphognathus* and *Gamachignathus* (Nowlan *et al.*, 1988), which indicates that *Yaoxianognathus* is a truly exotic species in respect to the well known Ashgill conodont faunas. The Australian *Yaoxianognathus* was a member of a probably relatively shallow-water assemblage with robust *Aphelognathus* species and warm-water panderodontids.

### *SAGITTODONTINA* SP.

The last occurrences of *Sagittodontina* in the Holy Cross Mountains (Text-fig. 2) are still of an older age than its type species type horizon. McCracken (1987) discussed Bergström's (1983) suggestion that the North American Midcontinent *Noixodontus girardeauensis* Satterfield, 1971 (Thompson & Satterfield, 1975; McCracken & Barnes, 1982, Lenz & McCracken, 1982) is separate from *Sagittodontina* but it remains poorly known. If the proposed above correlation of the Kalkbank is correct, it would be much younger than the findings of *Sagittodontina* in Europe and probably also in Libya. Lenz & McCracken (1982) reported *Prioniodus*? *girardeauensis* from sample 7217 at the Blackstone River (49.7 m), taken from the top of a limestone unit (about 10 m thick) located between calcareous shale below and a shale with graptolites of the *Glyptograptus persculptus* Zone (index species being absent) above. It was associated there with *Amorphognathus* (no ne (M) element found), *Plectodina tenuis*, *Gamachignathus ensifer*, and *Oulodus rohneri*.

The sp (Pa) element identified as belonging to *Sagittodontina* by Bergström & Massa (1992) is unlike any occurring in the Thuringian Kalkbank assemblage and resembles rather *Rhodesognathus* from Mójcza.

### *BIRKSFELDIA SELLI* (SERPAGLI, 1967)

According to McCracken (1987) *Birksfeldia circumplicata* Orchard, 1980 differs from *Gamachignathus ensifer* McCracken *et al.*, 1980 (as well as *G. hastatus* McCracken *et al.*, 1980) in having a shorter additional (posterior) process in the sp (Pa) element. Bergström (1990) 'it is unclear if the differences are enough to justify separation at the generic level'. Moreover, *Birksfeldia complicata* may be a junior synonym of '*Gothodus*' *selli* Serpagli, 1967 from the Uqua Limestone of Refugio Nordio in the Carnic Alps. The Mójcza material is too incomplete to support any taxonomic decision (Pl. 1, figs. 37-39). In fact, the few fragmentary sp (Pa) or oz (Pb) elements are not diagnostic even at the generic level; that these are elements of *Birksfeldia* is shown by associated ke elements.

*Gamachignathus* occurrences in America are generally younger in age than those of *Birksfeldia* in Europe (McCracken *et al.*, 1980), and species originally attributed to these genera may thus represent the subsequent stages in the evolution of the lineage. In Canada *Gamachignathus* appears in low numbers in the late Ashgill (Richmondian) Vauréal Formation and dramatically increases its contribution to the conodont assemblages with the base of the Ellis Bay Formation (Gamachian). It replaces *Plectodina*, which does not reach the top of the Vauréal Formation, as well as other Midcontinent conodonts (McCracken & Nowlan, 1988). According to those authors '*Gamachignathus* probably favored cool-water environments, and immigrated to areas marginal to Laurentia in the later Ordovician in response to glacial cooling'. In the Malopolska microcontinent, rare appearances of *Birksfeldia* are connected with increases in contribution of *Scabbardella*, which may also indicate association with cooling events.

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