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Conodonts in Ordovician biostratigraphy

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The long time interval after Pander's (1856) original conodont study can in terms of Ordovician conodont biostratigraphic research be subdivided into three periods, namely the Pioneer Period (1856-1955), the Transition Period (1955-1971), and the Modern Period (1971-Recent). During the pre-1920s, the few published conodont investigations were restricted to Europe and North America and were not concerned about the potential use of conodonts as guide fossils. Although primarily of taxonomic nature, the pioneer studies by Branson & Mehl, Stauffer, and Furnish during the 1930s represent the beginning of the use of conodonts in Ordovician biostratigraphy. However, no formal zones were introduced until Lindström (1955) proposed four conodont zones in the Lower Ordovician of Sweden, which marks the end of the Pioneer Period. Because Lindström's zone classification was not followed by similar work outside Baltoscandia, the time interval up to the late 1960s can be regarded as a Transition Period. A milestone symposium volume, entitled 'Conodont Biostratigraphy' and published in 1971,

summarized much new information on Ordovician conodont biostratigraphy and is taken as the beginning of the Modern Period of Ordovician conodont biostratigraphy. In this volume, the Baltoscandic Ordovician was subdivided into named conodont zones whereas the North American Ordovician succession was classified into a series of lettered or numbered Faunas. Although most of the latter did not receive zone names until 1984, this classification has been used widely in North America. The Middle and Upper Ordovician Baltoscandic zone classification, which was largely based on evolutionary species changes in lineages and hence includes phylozones, has subsequently undergone only minor changes and has been used slightly modified also in some other regions, such as New Zealand, China, and eastern North America. The great importance of conodonts in Ordovician biostratigraphy is shown by the fact that conodonts are used for the definition of two of the seven global stages, and seven of the 18 stage slices, now recognized within this system.

Keywords. Conodonts, Ordovician, global biostratigraphy, research history.

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Along with graptolites, conodonts are now considered to be the regionally and locally most useful index fossils in the Ordovician. They are generally well represented in, and easily extracted from, most calcareous marine sediments and are also present in many shales. They are particularly useful biostratigraphically in the vast carbonate-dominated continental platform successions in which graptolites tend to be sparse and represented by species of only limited biostratigraphic utility. Although both these index fossils groups have sometimes been considered facies fossils, the zone classifications based on each group complement each other. Furthermore, there are currently more than 100 direct ties between conodont and graptolite zones as summarized by Bergström (1986).

Conodonts were first described more than 150 years ago by Pander (1856) but their great utility as zone fossils in the Ordovician was not recognized until some 100 years later by Lindström (1955). For convenience, we distinguish three periods of Ordovician conodont biostratigraphic research, which we refer to as the *Pioneer Period* (1856-1955), the *Transition Period* (1955-1971), and the *Modern Period* (1971-Recent). Each of these periods has its own characteristics and the transition from one period to another is marked by a special event that we regard as being of special significance in the history of Ordovician conodont biostratigraphic research. The purpose of the present study is to review major developments in conodont biostratigraphy and to list a selection of important investigations that have had a significant impact on the current status of conodont biostratigraphy around the world. The present paper is an outgrowth of an invited symposium presentation at the Second International Congress on Stratigraphy, which was held in Graz, Austria in 2015.

The Pioneer Period

Out of biostratigraphic point of view, Pander's (1856) classic monograph is not very helpful in that he did not provide much information about the stratigraphic, or even geographic origin, of his Ordovician specimens. This has led to incorrect statements in the literature; for instance, even a well-known handbook states that the specimens came from Estonia, even if a careful reading of his text makes it clear that the Ordovician specimens came from the St. Petersburg region of Russia, where the source was a poorly consolidated glauconitic sand of Floian age (Bergström 1988), which is now known as the Leetsian horizon (or Stage). The few other Ordovician conodont occurrences described up to the 1920s, such as those of Hinde (1879), Wiman (1903), Smith (1907), and Hadding (1913), were based on specimens preserved on shale bedding planes and their potential as guide

fossils remained unexplored. Systematic collecting through shale successions similar to those upon which Lapworth (1878) based his graptolite zone biostratigraphy in South Scotland was not attempted anywhere and apparently, Pander's (1856) washing technique was not used on soft sediments. Conodonts remained as paleontologic curiosities up to the 1920s, when extensive conodont research was initiated at several universities in the American Midwest. At the University of Missouri, Branson & Mehl (1933) and their students started a long and extensive program involving isolating of conodonts by boiling of soft shales present in the local Paleozoic succession and similar studies were carried out by Stauffer (1935a, b) at the University of Minnesota, Furnish (1938) at the University of Iowa, and Cullison (1938) at the School of Mines and Metallurgy in Missouri. This research resulted in the description of numerous new genera and species and general comparisons of the described faunas but no formal conodont zones were proposed.

The rather accidental discovery by Graves & Ellison (1941) that conodonts could survive the breaking down of carbonate rocks by the use of acetic acid had a major impact on conodont investigations. Although the method did not become a standard preparation technique until the 1950s, its importance for conodont studies, including conodont biostratigraphy, cannot be overestimated because for the first time, it made it possible to obtain long series of productive samples through critical stratigraphic intervals. The comparatively late application of acid etching to isolate conodont specimens from the rock matrix is somewhat surprising in view of the fact that it had been known for half a century that organic fossils, such as graptolites (e.g. Holm 1890; Wiman 1895), could be freed from the sediment by means of acid preparation. Although very representative conodont collections obtained by the acetic acid method were assembled around 1950 in North America (e.g. Branson *et al.*1951) and Europe (e.g. Rhodes 1953, 1955), no formal zones were proposed. The use of conodonts in Ordovician biostratigraphy was still restricted to general comparisons of faunas and ranges of taxa, which were classified in terms of single element (form) taxonomy. Hence, the usefulness of conodonts for detailed local and regional biostratigraphy remained unexplored more than a century after the discovery of this enigmatic fossil group.

The Transition Period

What may be considered the initial step in the history of the use of conodonts as zone index fossils in Ordovician biostratigraphy was the publication of Lindström's (1955) monograph on conodonts from the stratigraphically rather complete but quite condensed, dominantly calcareous, Lower Ordovician succession in south-central Sweden. Obviously influenced by Tjernvik's (1952; also see Tjernvik 1956) detailed trilobite investigation in the same interval,

Lindström (1955) carried out virtually bed-by-bed sampling, and using acetic acid in the sample lab preparation, he assembled what is likely to have been the by far largest condont collection existing at that time. His monograph not only includes description of nine new genera and 61 new species (all defined in single element taxonomy) but also, in it he formally established four named conodont zones in a stratigraphic interval ranging from the Tremadocian to the lower Dapingian in terms of current global stage terminology (Bergström et al. 2009). In modern species classification, these well-defined zones would be called the *Cordylodus* angulatus, Paroistodus proteus, Oepikodus evae, and Baltoniodus navis zones. These zones were directly correlated with the trilobite zones established by Tjernvik (1952) in the same stratigraphic interval. We consider Lindström's (1955) study be the beginning of a new era, here referred to as the *Transition Period*, in Ordovician conodont biostratigraphy.

For a few years, no additional Ordovician conodont zones were proposed anywhere in the world but in the following decade, Sergeeva (1964) and Viira (1966) introduced a slightly different set of zones based on sections in the East Baltic. Their work also extended into somewhat younger strata than those initially investigated by Lindström (1955).

The only other region where extensive Ordovician conodont studies were carried out at this time was North America, where in the late 1950s local and

regional investigations were initiated by faculty and students at several Midwest universities, such as The University of Missouri, University of Iowa, and the Ohio State University. Conodonts from numerous formations, geographically ranging from the Great Basin in Utah and Nevada to the Appalachian Mountains in eastern North America, were investigated but no formal North American zone classification was proposed during the 1960s. Major reasons for this were the vast size of the continent, the most considerable thickness of many Ordovician successions, the regionally variable conodont species associations, and the huge amount of taxonomic work required for classification of the largely undescribed faunas. Also in other parts of the world no zone classification similar to that in Baltoscandia was introduced during this period. The focus in the 1960s was more on describing the conodont faunas and less on assessing their regional biostratigraphic significance.

A major event in the history of conodont research was the transformation of the formerly prevailing single element (form) taxonomy into a biologically sounder multielement taxonomy. The first attempt to apply the latter consistently was in a study of the prolific Lexington Limestone fauna (Bergström & Sweet 1966). A similar taxonomic approach was used on some conodont taxa by Webers (1966) in a study on Sandbian and Katian faunas in Minnesota. However, it took several years before this approach became widely used in conodont taxonomy. Using this taxonomy, many generic and species names became obsolete but because the absence of named zones outside Baltoscandia, these name revisions never became a significant problem in the Ordovician conodont biostratigraphy.

Another event that came to have a profound influence on virtually all kinds of conodont research was the 1967 establishment of an informal conodont organization, the Pander Society. This society, which serves as an umbrella organization for all conodont workers, has been very active in sponsoring numerous national and international symposia on many aspects of conodont research, and to keep conodont workers informed about recent progress through comprehensive annual newsletters. Virtually all the symposia have resulted in symposia volumes of lasting value.

The Modern Period

The Columbus Symposium volume

Such a Pander Society-sponsored symposium, held in May, 1969 at the Ohio State University in Columbus, Ohio resulted in a monographic volume entitled 'Symposium on Conodont Biostratigraphy' that was edited by Sweet & Bergström and published as a Memoir of the Geological Society of America. Chapters in this volume summarized the status of Cambrian to Triassic conodont biostratigraphy and contained a vast amount of new information, not least in the case of Ordovician. In view of its importance, we regard the publication of this volume as marking the beginning of the *Modern Period* in Ordovician conodont biostratigraphic research. Four relatively extensive papers in this volume summarized previously known data and much new information on Ordovician conodont biostratigraphy with focus on northern Europe and North America. In his paper on 'Lower Ordovician conodonts of Europe' Lindström (1971) described a Baltoscandic succession of 10 conodont zones in an interval ranging from the Tremadocian to the middle Darriwilian (Fig. 1). He used multielement taxonomy and the zones were correlated with graptolite zones. His zones may be considered assemblage zones with the bases marked by the appearance of the zone index species. No zone reference sections were selected but with relatively minor modifications, this zone succession has later been widely used not only in Baltoscandia but also in other parts of the world, such as Argentina and China.

In a paper entitled 'Lower Ordovician Conodonts in North America' Ethington & Clark (1971) presented a comprehensive review of Tremadocian and Floian conodont biostratigraphy in both the North American Midcontinent and the Great Basin in Utah and Nevada as well as in adjacent part of Canada. The conodont succession was subdivided into Faunas A through E based on the vertical ranges of 39 form species (Fig. 2). It would appear that the intervals of these Faunas are comparable to assemblage zones but no named zone designations were introduced.

A similar approach was used by Sweet et al. (1971), who subdivided the North American Lower to Upper Ordovician (Floian/Dapingian to Hirnantian) into 12 numbered Faunas (Fig. 3). Because the incomplete knowledge of the conodont species succession, the existence of significant stratigraphic gaps, and various correlation problems, they stated that it was premature to present a succession of formal zones. For more than a decade (cf. Sweet & Bergström 1984) these numbered faunas were widely used as a kind of assemblage zones until Sweet (1984), in a paper on graphic correlation, introduced a series of named zone units (Fig. 4). Although the graphic correlation base data have not been published, no reference sections selected, and in some cases zone boundaries are defined only in terms of his graphic correlation system, these units have been widely used as faunal zones. Unfortunately, there are some problems with the definition and correlation of several of these zone units and a re-assessment is clearly needed. In a later paper, Sweet (1988) referred to these units as biozones.

Based mainly on platform conodonts in the stratigraphically relatively complete upper Darriwilian to Hirnantian succession in Baltoscandia, Bergström (1971) introduced a zone sequence of five zones and 10 subzones (Fig. 5). Because these units were based on species in rapidly evolving lineages, they can be

considered phylozones and phylosubzones. Each unit was defined in a precisely measured reference section in the Siljan region of central Sweden. Only key species were originally listed but the complete faunas were much later recorded by Bergström (2007). Although there have been minor modifications of this zone nomenclature, especially in regions lacking some of the key index species, this zone succession has proved to be useful also in many regions far away from Baltoscandia. For instance, it turned out to be applicable to the upper Darriwilian and Sandbian successions in the eastern thrust belts of the Appalachian Mountains in eastern North America (e.g. Bergström 1971, 1973; Bergström & Carnes 1976; Bergström et al. 1974) where their use resulted in a greatly improved understanding of the age relations of many important formations. Whenever possible, the Baltic condont zones were also applied to the Middle and Upper Ordovician successions in the Great Basin of western USA (Harris et al. 1979) and to the graptolite standard succession in the Marathon area in West Texas (Bergström 1978).

Newer developments

During the decades since 1971 extensive work on Ordovician conodonts and conodont biostratigraphy has been carried out in many parts of the world. Page limitations of the present contribution make it impossible to deal with more than a fraction of the hundreds of published papers on local and regional conodont biostratigraphy and we here restrict ourselves to review a selection of investigations that we have found particularly valuable and informative about conodont biostratigraphy in different parts of the world. It is our hope that these records will provide an insight into the current status of conodont biostratigraphy within the main distribution areas of Ordovician rocks in the world. We feel that there is a need for such a global review in view of the fact that no such review has been published previously and that the current conodont literature includes hundreds of papers published in a very large number of geology journals. The currently most used zone classification in six selected regions are summarized in Fig. 7.

Baltoscandia. - A very large amount of Ordovician conodont work has been carried out in Baltoscandia during the past few decades and the biostratigraphy of the various platform successions in that region is now known in greater detail than that of any comparable region in the world. Published papers are too many to list herein but we regard as especially important the studies by Viira (1974, 2011), Löfgren (e.g. 1978, 1985, 1993, 1994, 1995, 2000), Stouge & Bagnoli (1991), Bagnoli & Stouge (1997), Zhang (1998a), Rasmussen (2001), Bergström (2007), Löfgren & Tolmacheva (2008), Bergström & Löfgren (2009), and Männik & Viira (2012).

Poland. - Middle and Upper Ordovician conodont faunas closely similar to coeval ones in Baltoscandia have been described by Dzik (1976, 1990, 1994) from the very condensed but stratigraphically remarkably complete Mójcza succession in southern Poland. Although taxonomy is more important than biostratigraphy in these studies, these reports present much valuable data on species ranges.

British Isles. - Although most of the Middle and Upper Ordovician conodont faunas from this region (e.g. Bergström 1971, 1990a; Orchard 1980; Savage & Bassett 1985; Ferretti *et al.* 2014a, b; Bergström & Ferretti, 2015) contain several species that are common in Baltoscandia, these faunas have their own distinctive provincial character with the presence of some taxa of North American affinities, such as species of *Plectodina*, *Ozarkodina*, and *Icriodella*, which are absent, or very rare, in coeval faunas from the East Baltic. Several late Darriwilian-Sandbian faunas from outcrops near Girvan and Tweeddale in South Scotland (Bergström 1990a; Armstrong 1997) show close affinities with coeval faunas from eastern North America, particularly Newfoundland, but are also very similar to equivalent Baltoscandic faunas. The similarity to North American faunas is in agreement with paleogeographic interpretations that place South Scotland on the western side of the Iapetus near the eastern side of the North American plate.

Southern Europe and North Africa. - Relatively limited conodont biostratigraphic work has been carried out in the dominantly clastic successions in these regions (e.g. Knüpfer 1967; Serpagli 1967; Lindström & Pelhate 1971; Weyant *et al.* 1977; Paris *et al.* 1981; Ferretti & Serpagli 1991, 1999; Bergström & Massa 1992; Ferretti & Barnes 1997; Ferretti & Schönlaub 2001; Serpagli *et al.* 2007, 2008; Del Moral & Sarmiento 2008; Sarmiento *et al.* 2011; Ferretti *et al.* 2014c; Lehnert et al. 2016). Most of these studies deal with Katian and Hirnantian faunas and conodonts from some other parts of the Ordovician are incompletely known which is likely due to the scarcity, or absence, of calcareous intervals in the successions.

Siberia. -The vast Siberian region has some of the most outstanding Ordovician outcrops in the world, but the published conodont information from these successions is somewhat limited and partly out of date. The pioneer work by Abaimova (1971) and Moskalenko (1973, 1983) was based on form taxonomy and as shown by the informative field trip guide of the important Kulyumbo River sections (Kanygin *et al.* 2006), the old conodont taxonomy has not yet been consistently updated in the Middle and Upper Ordovician. In her important review

paper in English, Moskalenko (1983) presented useful information about the stratigraphic ranges of 17 index species, many of which were used for subdivision of the Siberian Ordovician succession into 12 assemblage zones. This zone classification was recently updated by Sennikov et al. (2015) as illustrated in Figure 7. Although a few of these taxa have North American Midcontinent affinities, the Siberian faunas have their own provincial character which makes close correlation to North America difficult (cf. Dumoulin et al. 2002). There is virtual no similarity between the Siberian faunas and possibly equivalent ones from Baltoscandia so close correlation based on conodonts is not possible. Yet, as shown by, for instance, Tolmacheva & Abaimova (2009), Tolmacheva et al. (2009) and Tolmacheva (2014), the Ordovician conodont succession currently recognized in Kazakhstan is rather similar to that in Baltoscandia although the Katian condont faunas appear to be unstudied in Kazakhstan.

New Zealand and Australia. - Conodont faunas ranging in age from the Tremadocian to the Katian have been described from a variety of localities in the South Island of New Zealand (e.g. Zhen *et al.* 2009 and references therein). Because these faunas are dominated by species best known from Baltoscandia, it has proved possible to use the Baltoscandian conodont zone classification. Ordovician conodonts have been described from a considerable number of localities in the vast Australian continent, which represent a variety of depositional environments (e.g. Zhen *et al.* 2003 and references therein). Whereas the deeper water faunas, such as that described from southern Tasmania by Burrett *et al.* (1983), are reminiscent of Baltoscandic faunas, the shallower-water faunas from the continental platform, such as those from the Late Ordovician Cliefden Caves Limestone Group in central New South Wales (Zhen & Webby 1995) are more similar to North American Midcontinent faunas although they also contain Chinese-Siberian taxa. Unfortunately, the absence of regionally useful index species makes it currently impossible to classify these faunas in terms of North American Midcontinent or Baltoscandic conodont zones.

Also the Lower Ordovician conodont faunas from the Australian Platform have their own provincial character (e.g. Druce & Jones 1968, 1971; McTavish 1973; Cooper 1981; Watson 1988). They show some similarity to North American Midcontinent faunas but they also contain some species that are best known from Baltoscandia. A classification into named conodont zones that can be used regionally in Australia has not yet been established. For a now slightly outdated but still informative zone summary, see Young & Laurie (1996). Argentina. - A very large amount of conodont work has been carried out during the past 20 years in the magnificent Ordovician sections in the Precordillera of western Argentina, which is the only extensive region of calcareous Ordovician rocks in South America. In his pioneer monographic work on Floian to Dapingian faunas in the San Juan Limestone, Serpagli (1974) recognized five lettered local assemblage zones containing mixture of taxa of Baltoscandic and North American affinities. Subsequent work by several investigators, including among others, Mario Hünicken, Guillermo Albanesi and his students, Oliver Lehnert, and Suzana Heredia, has led to the establishment of a refined Tremadocian through Sandbian conodont zone biostratigraphy (Fig. 7). For useful summaries of the current Lower and Middle Ordovician conodont biostratigraphy with data on its correlation with the graptolite zone succession, see, for instance, Albanesi & Ortega (2002), Serra et al. (2015), Feltes et al. (2016) and Voldman et al. (2016). Although the faunas tend to be dominated by Baltoscandian taxa, there are also species best known from North America which provide useful links between provincial zone classifications.

Canada. - During the past 50 years, conodont biostratigraphy has been applied to numerous Ordovician successions across Canada and conodonts have served as the major fossil group for the dating and correlation of carbonate stratigraphic units.

Only a very small selection of the numerous publications by, among others, Chris Barnes, Godfrey Nowlan, Sandy McCracken, and S. Zhang can be mentioned here.

Investigations of the Lower and Middle Ordovician successions on western Newfoundland have been of particular global significance. The GSSP of the base of the Ordovician, which is located at Green Point on western Newfoundland, has been the subject of much study. The most recent paper is Miller *et al.* (2014), who presented a detailed conodont zonation across the systemic boundary. The conodont faunas of the Tremadocian and Floian St. George Group, one of the finest carbonate successions of this interval in the world, was monographed by Ji & Barnes (1994), who introduced a detailed zone succession based on taxa of North American Midcontinent affinity. On the other hand, the quite different conodont faunas of the largely coeval Cow Head Group, which was deposited in deeper water, were classified using the Baltoscandic conodont zone succession (Pohler et al. 1987; Stouge & Bagnoli 1988; Pohler 1994; Johnston & Barnes 1999). The conodonts of the Darriwilian Table Head Group were monographed by Stouge (1984), who subdivided the succession into both assemblage and phylozones and described several key index species. Two of these zones, the Histiodella holodentata Zone and the Histiodella kristinae Zone, have turned out to be recognizable in many parts of the world and are useful for long-distance

correlations. As a whole, the Table Head conodont fauna is more similar to those of southern USA and Argentina than to equivalent Baltoscandian faunas.

The faunas of the corresponding Ordovician interval in British Columbia, western Canada (Pyle & Barnes 2001, 2002) are dominated by Midcontinent species but some Baltoscandian taxa are also present. Pyle & Barnes (2002) subdivided the Tremadocian-Darriwilian interval into eight assemblage zones, the Darriwilian zone succession being similar to that used elsewhere in the Midcontinent.

Post-Darriwilian conodont faunas are in Canada best known from southern Ontario and the Hudson Bay region. The conodont faunal successions on Bruce Peninsula and Manitoulin Island have been discussed by several authors (e.g. Zhang *et al.* 2011). The Katian sequence of zones, which is in need of some reassessment, is mainly based on Midcontinent taxa. Of particular interest in this region is the presence of a conodont-producing Hirnantian succession in which the *Ozarkodina hassi* Zone is well developed in the Manitoulin Formation on Bruce Peninsula (Bergström *et al.* 2011). As is the case in the Midcontinent of the United States, uppermost Ordovician strata are rarely found on the Canadian craton although they are well known from Anticosti Island in Quebec, where their conodonts have been investigated by, among others, McCracken & Barnes (1981). A significant amount of work on the Ordovician conodont biostratigraphy of the Hudson Bay region and the Canadian Arctic has been carried out in recent years (e.g. Nowlan 1985; Zhang & Barnes 2007). Also the Ordovician conodont faunas of Greenland (e.g. Armstrong 1990; Smith 1991) and Svalbard (e.g. Lehnert *et al.* 2013) have been subjected to recent investigations.

USA. - The Cambrian-Ordovician boundary interval has been investigated in great detail in the Ibex area in western Utah (e.g. Miller *et al.* 2003, 2012, 2014). Based on very extensive collections, three *Cordylodus* zones have been identified in the uppermost Cambrian, and three zones, including the basalmost Ordovician *Iapetognathus* Zone, have been recognized in the lowermost Tremadocian (Fig. 7). The Ibex area has some of the finest sections across the Cambrian-Ordovician boundary in the world but its diverse conodont faunas are dominated by taxa characteristic of the tropical zone which are difficult to use for correlation with higher latitude faunas.

In an extensive study of Floian, Dapingian, and Darriwilian conodont faunas from the Ibex area, Ethington & Clark (1981) subdivided the succession into 12 intervals named for characteristic species. Younger Ordovician strata in the Great Basin were investigated by Harris *et al.* (1979). Because of the preliminary nature of this regional study, only a few conodont zones were recognized, most of which are from the Baltoscandic zone succession. The thick Katian-Hirnantian carbonate succession in the Great Basin was investigated by Sweet (1979, 1995, 2000) and Sweet *et al.* (2005) using graphic correlation and no named conodont zones were recognized.

One of the finest and best exposed Ordovician successions in North America is in the Arbuckle Mountains in Oklahoma. Its Dapingian and Darriwilian conodont faunas have been described by, among others, Bauer (1987, 2010), who in the interval of the Joins-Oil Creek formations distinguished a series of Histiodella zones similar to those described by Stouge (1984) from the Table Head Group of Newfoundland. The faunas are dominated by Midcontinent taxa and have little in common with the Baltoscandic faunas. The faunas of the overlying McLish, Tulip Creek, and Bromide formations also include mainly Midcontinent taxa (cf. Amsden & Sweet 1983; Bauer 1987). The former authors did not use named conodont zones to subdivide the succession. However, as has recently been shown by Wang et al. (2013, figs. 15-16), based on the recorded species ranges it is possible to interpret the McLish-Bromide succession in terms of North American and Baltoscandic conodont zones.

China. - Conodonts have been studied in the widespread Ordovician deposits in China since at least 1980 and more than 55 papers (Wang & Wang 2013), mostly written in Chinese and published in Chinese journals, record these fossils from a very large number of localities. Prominent early students of Chinese conodonts include An (1981, 1987), An et al. (1983, 1985), An & Ding (1985), and Ni & Li (1987). The many later contributions include, among others, Wang (1993), Wang & Zhou (1998), Zhao et al. (2000), Zhang (1998b), Wang et al. (1996, 2013), Zhan & Jin (2007) and Zhen *et al.* (2009, 2011). As summarized by Wang et al. (1996), the very conspicuous provincial differentiation in the Chinese Ordovician conodont faunas has made it necessary to introduce radically different zone classifications for different parts of the country. Whereas the 28 conodont zones recognized in the South China Province (Fig. 7) are, with a couple of exceptions, basically the same as those in Baltoscandia, the zones recorded in the North China Province are mostly vastly different although they contain a couple of North American index species. Research since the early 1990s has resulted in some modifications of the zone successions. For a modern review of zones recognized in South China, see Zhan & Jin (2007, p. 91-94) and for a recent discussion, with many references, of Middle and Upper Ordovician Chinese conodont biostratigraphy, see Wang *et al.* (2013). Recently, Zhen et al. (2016) revised the Ordovician conodont biostratigraphy of the extensive carbonate successions on the North China platform (cf. Fig. 7) that contain a mixture of endemic, North American Midcontinent, and more or less pandemic species.

Southeast Asia. - Recent work in the relatively thick Ordovician carbonate successions in Thailand and Malaysia by Agematsu *et al.* (2008a, b) has led to the discovery of notable conodont faunas. Whereas those of Tremadocian and slightly younger age are of North American type, the Sandbian - Katian faunas are dominated by taxa best known from Baltoscandia.

Concluding remarks

As shown by, for instance, Sweet (1988), conodont species diversity is much higher in the Ordovician than in any other system. Many of these species combine a short vertical range with abundant occurrence and serve as excellent index fossils. However, the fact that the continental plates with their shallow-water depositional environments occupied a variety of latitudinal positions with different water temperatures and other ecologically important parameters caused a pronounced provincial differentiation of the Ordovician conodont faunas (e.g. Sweet & Bergström 1974, 1984; Bergström 1990b) and the limited geographic distribution of many biostratigraphically key species has resulted in the fact that it has been impossible to produce a globally applicable conodont zone classification and markedly different sets of zones have been defined in, for instance, the North American Midcontinent, Baltoscandia, North China, and Siberia. Recent work in regions with some mixing of the provincial faunas, such as the Appalachians in

eastern North America, the Precordillera of Argentina, and some parts of China has helped tie together parts of the provincial zone classifications but much more work of that type remains to be done. Also, there is a need in some areas, for instance, in the North American Midcontinent, to re-assess and improve the existing zone classifications. However, as is clear from this brief review, the extensive conodont biostratigraphic work carried out during the last half century has resulted in that Ordovician conodont biostratigraphy has reached a relatively mature state in most parts of the world.

A matter of general concern is that compared with that of the last decades of the 20th century, research on Ordovician conodont biostratigraphy has slowed down in recent years in, for instance, North America and Baltoscandia. Only a couple of universities in North America now offer MS or Ph.D. programs in conodont research supervised by a specialist. Taxonomic work is no longer very attractive as student thesis projects. This is alarming in view of the fact that a solid taxonomic background is essential for high-quality biostratigraphic work. The disappearance of conodont specialists is not unique but is shared with quite a few other fossil groups. It may well be that the 'Golden age' of Ordovician conodont biostratigraphic research is not far from its end. Let us hope that in the future, this pessimistic forecast will prove to be in error.

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LEGENDS OF FIGURES

Fig. 1. Lindström's (1971) Lower and Middle Ordovician (Tremadocian-Darriwilian) conodont zone succession in Baltoscandia. From Lindström (1971, fig. 1).

Fig. 2. The subdivision of the North American Tremadocian and Floian interval into five lettered Faunas by Ethington & Clark (1971). From Ethington & Clark (1971, fig. 2).

Fig. 3. The North American subdivision of the post-Tremadocian portion of the Ordovician into 12 Faunas proposed by Sweet et al. (1971, fig. 1). Note that because no Hirnantian conodont fauna was known in 1971, conodont ranges into the youngest Ordovician were omitted.

Fig. 4. The classification by Sweet (1984) of the North American Darriwilian-Katian part of the Ordovician into series, stages, and conodont zones. Numbers at the zonal boundaries are values in Sweet's graphic correlation system. Figure from Sweet (1984, fig. 2).

Fig. 5. The Middle and Upper Ordovician (upper Darriwilian-Hirnantian) conodont zone succession introduced by Bergström (1971) based on sections in Sweden. Also shown are ranges of key taxa. Figure slightly modified from Bergström (1971, figs. 4-5). Current names of some of the taxa illustrated are as follows: 'Bryantodina' n. sp. = Ozarkodina hassi; 'Distomodus' europaeus = Hamarodus *brevirameus; 'Scolopodus'* n. sp. cf. '*S.' insculptus = Protopanderodus liripipus;* 'Scolopodus' varicostatus = Protopanderodus varicostatus; Prioniodus alobatus = *Baltoniodus alobatus; Prioniodus gerdae = Baltoniodus gerdae; Prioniodus* variabilis = Baltoniodus variabilis; Polyplacognathus sweeti = Cahabagnathus sweeti. Also, the base of the Upper Ordovician is now at the base of the *Nemagraptus gracilis* Zone. The former *Diplograptus multidens* Zone and the *Glyptograptus teretiusculus* Zone are now referred to as the *Climacograptus bicornis* Zone and the *Dicellograptus vagus* Zone, respectively.

Fig. 6. Zonal ties between Baltoscandic conodont zones and graptolite zones as known in the mid-1980s. After Bergström (1986, fig. 5).

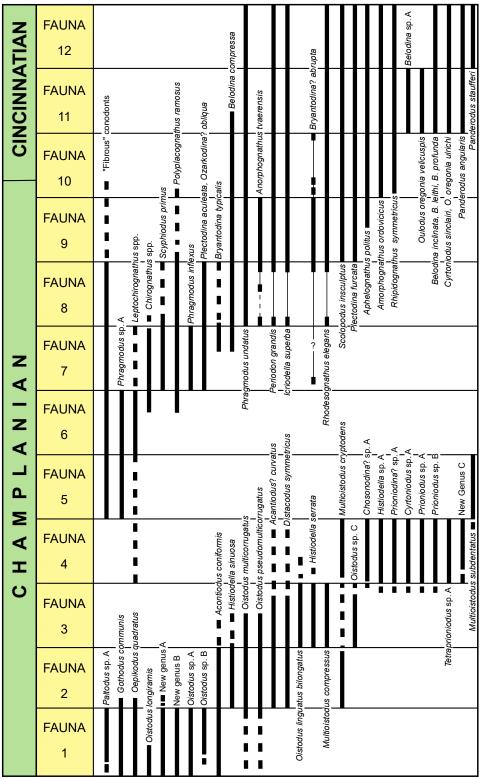
Fig. 7. Comparison between conodont zone classifications of the Ordovician System in six regions. Note the conspicuous difference between some of these zone classifications.

A.: Amorphognathus; Ac.: Acanthodina; Acanth.: Acanthocordylodus; Aph.: Aphelognathus; B.: Baltoniodus; Be: Belodina; C.: Cahabagnathus; Card.: Cardiodella; Ch.: Chosonodina; Cl.: Colaptoconus; Col.: Coleodus; Cor.: *Cordylodus*; *Cu.*: *Culumbodina*; *E.*: *Eoplacognathus*; *E. protoram*.: Eoplacognathus protoramosus; Er.: Erismodus; F.: Fahraeusodus; F. mar.: Fahraeusodus marathonensis; H.: Histiodella; I.: Iapetognathus; Ju.: Jumudontus; L.: Lenodus; M.: Microzarkodina; O.: Oepikodus; O. com.: Oepikodus communis; Ois.: Oistodus; Ois. multicorr.: Oistodus multicorrugatus; Ou.: Oulodus; Oz.: Ozarkodina; P.: Pygodus; Pa.: Paraserratognathus; Pa. paltodifor.: Paraserratognathus paltodiformis; Pal.: Paltodus; Par.: Paroistodus; Pe.: Periodon; Phr.: Phragmodus; Pl.: Plectodina; Pr.: Prioniodus; Pt.: Ptiloconus; R.: Reutterodus; Ro.: Rossodus; Sc.: Scalpellodus; Serr.: Serratognathus; Sp.: Spathognathodus; T.: Tripodus; Tan.: Tangshanodus; Yangtz.: Yangtzeplacognathus; Yaox.: Yaoxianognathus. Subzones: an.: anitae (Pygodus anitae); com.: communis (Oepikodus communis); fo.=foliac.: foliaceus (Eoplacognathus foliaceus); glad.: gladysi (Periodon gladysae); horr.: horridus (Paroistodus horridus); in.: inaequalis (Amorphognathus inaequalis); ki.: kielcensis (Sagittodontina kielcensis); li.=linds.: lindstroemi (Eoplacognathus lindstroemi); ma.: magnus (Polonodus magnus); re.=reclin.: reclinatus

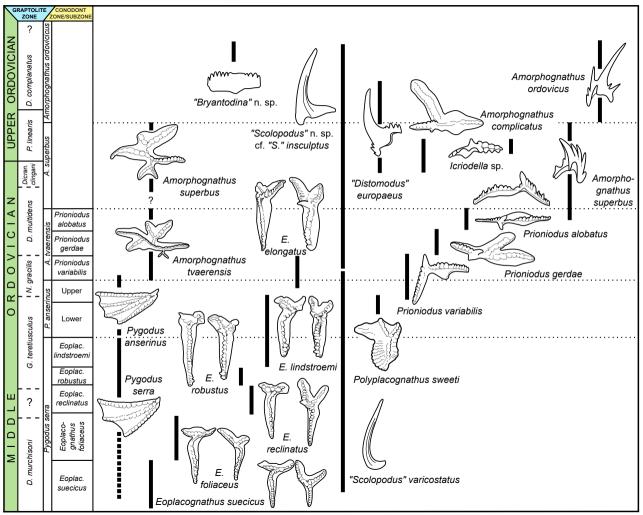
(Eoplacognathus reclinatus); ro.=robus.: robustus (Eoplacognathus robustus); swe.: sweeti (Tropodus sweeti).

INTERNATIONAL	BALTIC SHIELD			Graptolite	Scandinavian	Conodont	
SERIES	Series	Stages	Substages	zones	subzones	zones	
	MIDDLE ORDOVICIAN	Lasnamägian (C lb)		Didymograptus			
LLANVIRNIAN	OR VIRUAN	Aserian (C la)		murchisoni			
			Aluoja (B III Y)	Didymograptus		Amorphognathus variabilis	
		Kundan (B III)	Valaste (Β III β)	bifidus			
			Hunderum (Β ΙΙΙα)				
ARENIGIAN	LOWER ORDOVICIAN		Langevoja (B II Y)	gibberulu		Microzarkodina parva	
		Volkhovian (B II)	Limbata beds (Β ΙΙ β)		lsograptus gibberulus Phyllogr. angustif. elong.	Paroistodus originalis	
	OR		(Β II α)			Baltoniodus navis	
			(=)			Baltoniodus triang.	
	OELANDIAN	Latorpian	Billingen (ΒΙβΥ)		Phyllogr. densus	Prioniodus evae	
				Didymograptus	Tetragr	Prioniodus elegans	
TREMADOCIAN		(B I)	Hunneberg (ΒΙα)	extensus		Paroistodus proteus	
		Ceratopyge beds (A III)		Bryograptus		Paltodus deltifer	
		Pakerortian (A II)		Dictyonema flabelliforme		Cordylodus angulatus	

	 Drepanodus homocurvatus Drepanodus homocurvatus Drepanodus suberectus Drepanodus staufferi Scolopodus cornutiformis Scolopodus quadraplicatus Oistodus linguatus Oistodus sprallelus Oistodus deraglies A Scolopodus gracilis Oistodus defta Oistodus defta Oistodus defta Oistodus defta Oistodus defta
FAUNA E	eertus eertus eertus vasis igularis geularis geularis geularis densus us ppinquus eerturthi Distacodus stola Acontiodus sp. A
FAUNA D	ensis eri mulleri Cordylodus angulatus Cordylodus rotundatus Cyrtoniodus prion Cyrtoniodus prion Cyrtoniodus prion Luxodus bransoni Acanthodus lineatus Paltodus bransoni Acontodus propinquus Chosonodina herfurthi Chosonodina herfurthi Chosonodina herfurthi Aconti
FAUNA C	
FAUNA B	Cordylodus proavus Cordylodus oklahom Proconodontus muli
FAUNA A	



SERIES	STAG	E/SUBSTAGE	CONODONT ZONE			
	6	AMACHIAN	A. shatzeri Zone			
INCINNATIAN	_	CHMONDIAN	A. divergens Zone			
¥		(1197)	A. grandis Zone			
Ž	Μ	AYSVILLIAN	O. robustus Zone			
V			O. velicuspis			
		EDENIAN	Zone LOWER			
		(1065)	B. confluens Zone			
	⊢≓	SHERMANIAN	(1025)			
NA	'TREN ONIAN	KIRKFIELDIAN	P. tenuis Zone Lower			
Т Т	-(966)	ROCKLANDIAN	P. undatus Zone			
OHAWKIAN		UPPER	B. compressa Zone			
Ĥ	BLACK RIVERAN		<i>E. quadridactylus</i> Zone			
MOI		LOWER (=ASHBYAN)	<i>P. aculeata</i> Zone			
		(809)	(807)			
		UPPER	<i>P. sweeti</i> Zone			
z	(=	± CHAZYAN)	<i>P. friendsvillensis</i> Zone			
I ₹		(680)	(680)			
WHITEROCKIAN		MIDDLE	P. "pre-flexuosus" Zone			
			<i>H. holodentata</i> Zone			
		LOWER	H. sinuosa Zone			
			H. altifrons Zone			



BRIT. SERIES	PACIFIC GRAPTOLITE ZONES	ZONAL TIES	NORTH ATLANTIC CONODONT ZONES	ZONAL TIES	BALTOSCANDIC GRAPTOLITE ZONE	S	
	A. inuiti						
ASH- GILL	D. complanatus	<>	Amorphognathus	«»			
	C. manitoulinensis	<>	ordovicicus		D. complanatus		
	C. pygmaeus	«» «»		<>			
	C. spiniferus	€		<>	Pleurograptus linearis		
	O. ruedemanni		Amorphognathus superbus		Dicr. clingani		
CARA- DOC	Corynoides americanus	<>		«»			
	Diplogr. multidens	<>	Amorphognathus tvaerensis		Dipl. multidens		
LLAN- DEILO	Nemagraptus gracilis	<> <>	Pygodus anserinus		Nemagraptus gracilis		
	G. cf. teretiusculus	«» «»	Pygodus serra		Glypt. teretiusculus		
LLAN-		Éŏpl. suecicus ≤−−−−>			Did. murchisoni		
VIRN 	Paragl. tentaculatus	≈\$ <>	Eopl.? variabilis M. flabellum parva	<	Did. "bifidus"		
	I. caduceus		Paroistodus o ^r iginalis Prioniodus navis Prioniodus triangularis	<u><-</u> ? <u>^</u> ?	Did. hirundo		
ARENIG	Did. protobifidus		Oepikodus evae	«» «»	Ph. angustifolius elongatus	sns	
	<i>T. fruticosus</i> (3 + 4 br)	«		<	elongatus Phyllograptus densus		
	<i>T. fruticosus</i> (4 br)	<>	Prioniodus elegans		Did. balticus		
	Tetr. approximatus		Paroistodus proteus	«» «»	Tetragraptus approximatus Tetr. phyllograptoides		
 TREMA-	<> Clonograptus		Drepanoistodus deltifer	<>			
DOC	Anisograptus		Cordylodus intermedius	€	Dictyonema, etc.		

STAGE	CO	NO	DONTZ	ONES	AND	SUBZONES		
ST	BALTOSCANDIA		N. AMERICA	SIBERIA	_{S.} СН	ina _{N.}	ARGENTI PRECORDIL	
HIR.	Oz. hassi		Oz. hassi	Oz. hassi	Oz. hassi			
		Z	Aph. shatzeri					
	Amorphognathus ordovicicus	ATIA	Aph. divergens	Aphelognathus pyramidalis	Aph. pyramidalis		?	
Z		Z	Aph. grandis					
∢		Z	Ou. robustus		Yaox.	Үаох.		
—	Amorphognathus	C N	Ou. velicuspis	Ac. nobilis	yaoxianensis Yaox.	yaoxianensis Yaox.	Amorphogna	athus
	superbus	C		"Sp." dolboricus	neimeng- guensis	neimeng- guensis	superbu	
∢			Be. confluens		Be. confluens	Be. confluens		
\mathbf{x}								
		Z V		Acanth. festus				
	atus	Ϋ́	Pl. tenuis	Cu. mangazeica				
z	alopatrs	ΑW	Phr. undatus	ou. mangazoloa	Phr. undatus	Phr. undatus		
IAN	gnathus ^m	H	Be. compressa		-	Be. compressa	Amorphogna tvaerens	
DB	tvaerensis	0 M	Er. quadridactylus	Phr. inflexus	B. alobatus	Er. quadridactylus		
A N	Amorpho- gnathus tvaerensis B: derdae B: derdae	2	Pl. aculeata		E. elongatus E. jianyeensis	Pl. aculeata		
S	P. anserinus in. ki.		C. sweeti		Pr. variabilis P. anserinus	P. anserinus	P. anserin	us
I A N	P. serra	ΑN	C. friendsvillensis	Pt. anomalis Phr. flexuosus	P. serra E. protoram. E. foliaceus	P. serra	P. serra	linds. robus. reclin.
2	fo. an.	- Y	Phr. polonicus	Phr. polonicus	L. Iollaceus	P. anitae		foliac. anitae
RIWILIA	E. suecicus _{ma.}	C	H. holodentata		E. suecicus	E. suecicus H. holodentata	E. suecicus	kris- tinae
R R	E. pseudoplanus	R O		Card. lyrata -	E. pseudo- planus	Tan. tangshanensis ППППППГППГ	E. pseudopla	
AF	Yangtz. crassus	ш		Polyplacognathus angarense	L. variabilis		Yangtz. cras	-
	Lenodus variabilis	÷		Col. mirabilis	A. antivariabilis		L. variabilis	horr. glad.
IAN	B. norrlandicus	× ≥	H. sinuosa	H. angulata	B. aff. B. navis	•	M. parva	1-
DNI NG	Par. originalis		H. altifrons	2	Par. originalis		B. navis	
DAP	B. navis B. triangularis		M. flabellum - T. laevis	.	Ois. multicorr Pe. flabellum		T. laevis	
Z	O. evae	7	O. evae	Scolopodus warandensis -	O. evae	Ju. gananda Pa. obesus	O. intermedi	
AIC	Pr. elegans	IAN	Ju. gananda -	Glyptoconus sp.	B. communis	Pa. paltodifor.	O. evae Pr. elegans	com. swe.
FL(Par. proteus	×	R. andinus O. com F. mar.		Serr. diversus	Serr. extensus	Par. protei	
TREM. FLOIAN DAPINGIAN	Pal. deltifer	Ш В	Acodus deltatus Macerodus dianae	Loxodus bransoni	Pal. deltifer Cl. quadra-	Sc. tersus Cl. quadraplicatus Ch. herfurthi - Ro. manitouensis	Pal. deltife	er
RE	Cor. angulatus	Ξ	Ro. manitouensis	Cor. angulatus	plicatus	Cor. angulatus I. jilinensis -		
H	Cor. lindstroemi		lapetognathus	?	Cor. angulatus	Cor. lindstroemi		