TREATISE ONLINE

Number 133

Part V, Second Revision, Chapter 8: Paleogeography of the Hemichordata

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2020

KU PALEONTOLOGICAL INSTITUTE
The University of Kansas

Lawrence, Kansas, USA
ISSN 2153-4012
paleo.ku.edu/treatiseonline

PART V, SECOND REVISION, CHAPTER 8: PALEOGEOGRAPHY OF THE HEMICHORDATA

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INTRODUCTION

Nearly all organisms exhibit at least some biogeographic restriction in their distribution, and this aspect has commonly been used to interpret paleogeographic aspects in geology, e.g., plate tectonic configuration, oceanic development, latitudinal differentiation. Plate tectonics is one of the major aspects, initially relying largely on paleontological data and dating back to WEGENER (1915), even though the concepts of continental drift and modern plate tectonics appear to describe somewhat different things. Still, they are based on various geological and paleontological investigations, and modern plate tectonics and paleobiogeography are closely connected (see HARPER & SERVAIS, 2013; TORSVIK & COCKS, 2013).

The Graptolithina, one of the major fossil groups of all marine environments in the early Paleozoic, are not an exception when we, as paleontologists, think of Paleozoic paleobiogeography. However, little is known on the biogeographic distribution of their sister group, the Enteropneusta. Extinct taxa are known only from few specimens and extant taxa have not been in the focus of biologists either, thus, their biogeographical distribution is very incompletely documented. Even the precise biogeographic distribution of the extant Pterobranchia is largely unknown, as the recent description of the first *Rhabdopleura* ALLMAN in NORMAN, 1869 species in the Mediterranean shows (BELI & others, 2018). Equally, not a single species of the non-colonial Cephalodiscida has been discovered in the Mediterranean so far, but a new *Cephalodiscus* M'INTOSH, 1882 species from Sagami Bay, Japan was recently introduced by MIYAMOTO, NISHIKAWA, and NAMIKAWA (2020). Therefore, the remark, that "rhabdopleurids can only be found close to marine research stations" (MALETZ, 2017, p. 12), is not just an oversimplification, but clearly shows that scientific interest often limits our knowledge and that more new records of Pterobranchia may be expected in the future.

EXTANT HEMICHORDATA

The two extant groups of the Hemichordata have not attracted much scientific interest by biologists in a long time and even knowledge of their living taxa is relatively poor, while the fossil Graptolithina, as an exception, gained considerable interest by paleontologists and geologists in the past due to their application in biostratigraphical interpretations and the dating of marine sedimentary sequences.

Extant enteropneusts are widely distributed and occur in marine environments from shallow water shelf regions to the deep waters of the abyssal regions of the oceans and can also be found attached to rocks close to hydrothermal vents at the mid-ocean ridges (WOODWICK & SENSENBAUGH, 1985). Four families can be differentiated, all exclusively found in marine regions, usually burrowing in the sediment and rarely living as epibenthos (CAMERON, 2018). The epibenthic torquaratorids have been

ISSN 2153-4012

Maletz, Jörg. 2020. Part V, Second Revision, Chapter 8: Paleogeography of the Hemichordata. Treatise Online 133:1–12, 4 fig.

Fig. 1. Global distribution of *Rhabdopleura* Allman in Norman, 1869 species (adapted from Beli & others, 2018, fig. 4).

discovered only quite recently. Thus, their record is still extremely spotty and, due to their dwelling in deeper oceanic regions, it is difficult to demonstrate their possibly worldwide biogeographic distribution (Jabr, 2017; Jabr, Archambault, & Cameron, 2018). Valuable zoogeographical conclusions are also not available for the other enteropneust families, as most species have been reported from a single locality only or are known from relatively small geographical regions (Cameron, Deland, & Bullock, 2010). Only few species have been described from larger regions or are reported to show a wider but often patchy and discontinuous distribution. The documented distribution of extant enteropneusts may be interpreted in different ways as relict populations, either of once more widely distributed taxa or as the result of too little systematic search. Cameron, Deland, and Bullock (2010) suggested that the enteropneusts represent an ancient and declining group, which may be supported by their spotty fossil record and their possibly early Cambrian origin (Maletz, 2019a).

Beli and others (2018) discussed the biogeographical distribution of extant rhabdopleurids and differentiated five species, of which *Rhabdopleura normani* Allman, 1869 appears to be the taxon with the widest geographical distribution. It is present in the northern and southern Atlantic Ocean but has also been collected in the Antarctic Ocean (Fig. 1). Rhabdopleurids can be found from the deeper waters of the polar regions to the shallow tropical regions close to the equator and, thus, do not show extensive ecological restrictions. The relatively uneven geographical distribution of the few known taxa (Fig. 1) may be based on lack of scientific interest and the difficulty of collecting these small and inconspicuous organisms.

FOSSIL HEMICHORDATA

Fossil hemichordates are largely known from the tubaria of the Graptolithina, while the fossil Enteropneusta are too rare to provide sufficient information for a paleobiogeographic interpretation. Cameron (2018) discussed the fossil material of the Enteropneusta, of which the most specimen-rich material comes from the Burgess Shale of British Columbia, Canada, and includes specimens of *Spartobranchus tenuis* (Walcott, 1911) and *Oesia disjuncta* Walcott, 1911, also representing the oldest known enteropneusts. None of the fossil taxa

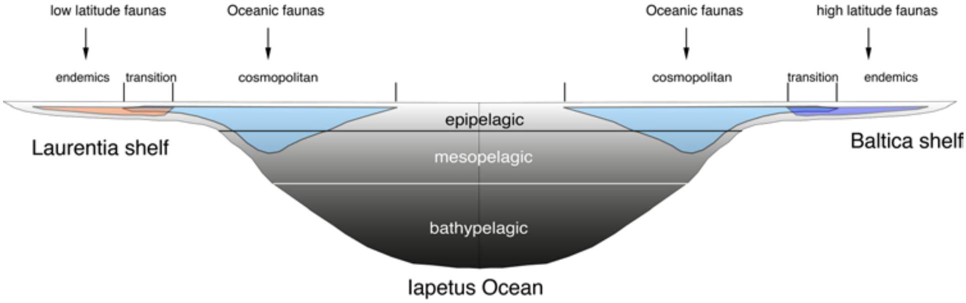

FIG. 2. Biogeographical and paleoecological distribution of the Graptolithina across the Lower Paleozoic Iapetus Ocean, showing endemic and cosmopolitan oceanic graptolite faunas, as well as shallow to deeper water distributions (adapted from Maletz & others, 2011, fig. 9).

is known from more than one locality and most taxa are described from single specimens, except for the Carboniferous *Mazoglossus ramsdelli* BARDACK, 1997 from the Mazon Creek fauna of Illinois, USA, which is a moderately common species (MALETZ, 2014; CAMERON, 2016).

Large data sets on fossil graptolite faunas have been collected in the past and provide a good insight into the ecology and paleobiogeography of the Graptolithina (see COOPER & others, 2004, 2017; GOLDMAN & others, 2013). The problems of precise biostratigraphic correlation between continents in the Lower to Middle Ordovician initiated the research into the paleobiogeography of graptolite faunas. A number of factors were suggested to be responsible for faunal differentiations (e.g., BERRY, 1960, 1962, 1979; BOUČEK, 1972; ROSS, 1961; BERRY & BOUCOT, 1972; CISNE & CHANDLEE, 1982; BULMAN, 1964, 1971), leading to two main competing models explaining the ecological controls on graptolite species distribution. SKEVINGTON (1973, 1974) discussed the cool-temperate Atlantic Province and the paleo-tropical Pacific Province and considered latitudinal variation in surface water temperature as the main control for graptolite provincialism. CISNE and CHANDLEE (1982) suggested a depth stratification model to explain graptolite distribution patterns in the Late Ordovician Utica Shale of the Taconic foreland basin of the northeastern Appalachians (USA), while FINNEY (1986) explained the same pattern by lateral differentiation of water mass specificity and not depth stratification. COOPER, FORTEY, and LINDHOLM, 1991, and COOPER and others (2012, 2017) recognized a shallow epipelagic biotope with cosmopolitan species, combining two models: 1) a deeper mesopelagic biotope, the isograptid biofacies, and 2) an inshore biotope that included largely endemic species, the didymograptid biofacies. MALETZ and others (2011) discussed the faunal differentiation on a transect across the Iapetus Ocean from the moderate to higher latitudes of Baltica to the low latitudes of Laurentia (Fig. 2) during the Darriwilian (Middle Ordovician) and recognized endemic and pandemic faunal elements due to their presence and absence. GOLDMAN and others (2013) stated that both depth and surface temperature play an important role in the biogeographic differentiation of graptolite faunas. The authors also suggested discussing graptolite distributions in terms of low, medium, and high latitudes and abandoning the Atlantic and Pacific Provinces of SKEVINGTON (1973, 1974), which are based on modern geographical concepts and not applicable to plate tectonic configurations in the Paleozoic. The main differentiation of Paleozoic planktic graptolite faunas is clearly based on paleo-latitude, but certain graptolite taxa may be restricted to a certain paleo-continent or restricted depositional basin (GOLDMAN & other, 2013). Thus, a latitudinal gradation from low latitude to high latitude faunas is combined with true endemicity based on other factors in the Paleozoic oceans.

BIOGEOGRAPHY

GOLDMAN and others (2013) provided a current overview on the knowledge of biogeographical differentiation of planktic graptolite faunas through time and should be consulted for details. Paleogeographic interpretations are based on plate tectonic reconstructions of which the Scotese maps (MCKERROW & SCOTESE, 1990; www.Scotese.com) are the best known. Early Paleozoic paleogeography has generated considerable interest in recent years (HARPER & SERVAIS, 2013) and sedimentological and paleontological data still form a considerable part of the interpretations (TORSVIK & COCKS, 2013) to which data on the distribution of individual graptolite taxa may be added (Fig. 3). Biogeographic differentiation of graptolite faunas is best known from the Ordovician, where numerous papers discuss the often high endemicity of graptolite faunas (GOLDMAN & others, 2013).

Unfortunately, there is no information available for the paleogeographical distribution of the dendroid (benthic) graptolites. These are usually described from small fragments of their colonies and complete, undistorted specimens are comparatively rare. It is likely that their distribution is restricted by temperature barriers as is the distribution of some planktic taxa. Otherwise, a restriction of individual species or even genera to certain paleo-continental plates may be supposed, but cannot be verified.

THE ORDOVICIAN

The base of the Tremadocian saw a quick dispersal of early planktic graptolites and any biogeographic differentiation is lacking as can be seen from the easy worldwide correlation of graptolite zones (see COOPER & others, 1998; COOPER, 1999; LOYDELL, 2012). The mid-Tremadocian genus *Bryograptus* LAPWORTH, 1880 demonstrates the start of some faunal differentiation, as it appears to be restricted to the cooler water regions of higher latitudes (MALETZ, EGENHOFF, & ALONSO, 2010), possibly indicating the start of a general biogeographic faunal differentiation. In the upper Tremadocian, *Kiaerograptus supremus* LINDHOLM, 1991 represents another taxon restricted to high latitude regions (LINDHOLM, 1991; MALETZ & EGENHOFF, 2001). The best-known and investigated interval to document Ordovician graptolite biogeography appears to be the Floian to Darriwilian time interval (COOPER, FORTEY, & LINDHOLM, 1991; GOLDMAN & others, 2013). During this time interval, the planktic graptolite faunas attained a diversity and faunal differentiation not seen in this extreme in younger time intervals.

The problems of the differentiation of pendent didymograptids (BERRY, 1960, 1967; SKEVINGTON, 1963; COOPER & FORTEY, 1982; MALETZ, GOLDMAN, & CONE, 2005), commonly used for biostratigraphic purposes, led to the detailed investigation of their proximal end construction and a revision of taxonomy and biostratigraphy of the Floian to Darriwilian graptolite faunas (COOPER & FORTEY, 1982; GUTIÉRREZ MARCO, 1986; MALETZ, 1994, 2010; VANDENBERG, 2018). Thus, a number of graptoloid genera occurring in high latitudes (*Aulograptus* SKEVINGTON, 1965; *Azygograptus* NICHOLSON & LAPWORTH in NICHOLSON, 1875; *Baltograptus* MALETZ, 1994; *Didymograptus* M'COY in SEDGWICK & M'COY, 1851–1854; *Jenkinsograptus* GUTIÉRREZ-MARCO, 1986) and low latitudes (*Didymograptellus* COOPER & FORTEY, 1982; *Paraglossograptus* MU in MU & others, 1962; *Yutagraptus* RIVA, 1994) were differentiated and can be used as biostratigraphical marker species in the individual regions (BECKLY & MALETZ, 1991; MALETZ, 1994; TORO 1996; TORO & MALETZ, 2007). Due to the co-occurrence with other, pandemic faunal elements in mixed assemblages, these endemics can often been correlated indirectly with coeval shallow water endemic faunas from other continental regions. During the Dapingian, the isograptids form the main stock of pandemic faunal elements and were used extensively for long distance biostratigraphic correlations (Harris, 1933; Cooper, 1973; Williams & Stevens, 1988; Maletz, 2011). They were very useful to correlate many largely endemic faunas of this time interval. Fortey and Cocks (1986) even successfully used the presence of isograptids, the isograptid biofacies, to infer the presence of oceanic basins and the rims of ancient continents.

The base of the Darriwilian saw a major rearrangement of graptolite faunas with the evolution of the Axonophora, and faunal differentiation became more difficult due to the apparent similarities of flattened biserial graptolites in shales. However, axonophorans can also be demonstrated to show a considerable provincialism in the Middle and Upper Ordovician, and a number of endemic taxa have been described (Maletz & others, 2007; Goldman & others, 2013). In eastern and southeastern North America the endemic genus *Geniculograptus* Mitchell, 1987 evolved in the late Ordovician, but is absent even in western Laurentia, leading to considerable problems in the intra-continental correlation of Laurentia and to other continents (Riva, 1969, 1974; Berry 1977; Bergström 1978; Goldman, Bergstöm, & Mitchell, 1995). Some of the apparent faunal endemism of the South China platform faunas has been revised by the discovery of species previously considered to be endemic in other regions (e.g., *Tangyagraptus* Mu, 1963; Chen & others, 2005; Goldman & others, 2007).

Provinciality increased throughout the later Ordovician (Katian) due to the onset of climate change leading to the Hirnantian glaciation. Faunal differences made it increasingly difficult to correlate between low latitude and high latitude faunal localities in this time interval (e.g., Williams & others, 2003; Zalasiewicz, Rushton, & Owen, 1995).

A major reorganization of graptolite faunas occurred due to the Hirnantian glaciation in the latest Ordovician. The Dicranograptidae-Diplograptidae-Orthograptidae (or DDO) faunas of Melchin and Mitchell (1991) were rapidly replaced by species of *Normalograptus* Legrand, 1987 (their Monograptidae fauna; now the Neograptina) that invaded from the southern high latitudes (Goldman & others, 2011) and in the *Metabolograptus extraordinarius* to *Metabolograptus persculptus* biozones, neograptine elements dominated the graptolite faunas and the diplograptines were forced into extinction. The neograptines, while already originating in the early Darriwilian, experienced a dramatic radiation and formed the base from which all clades of the Silurian and early Devonian graptoloids (e.g., Štorch & others, 2011; Maletz, 2019b) originated.

Fig. 3. Floian, Lower Ordovician paleobiogeography showing the distribution of *Baltograptus* species in blue (high latitude faunas). Low latitude faunal regions in red. Cross-section line shows approximate position of section in Fig. 2 (adapted from Egenhoff & Maletz, 2007, fig. 2).

THE SILURIAN

Graptolite provincialism in the Silurian has only more recently been explored and often has been considered as of lesser degree than graptolite provincialism in the Ordovician, especially as a standard biozonation was easily applied in the Silurian (e.g., Rickards, 1976; Koren’ & others, 1995, 1996; Loydell, 2012). Štorch (1998) and

Legrand (2009) discussed the endemic graptolite faunas of the northwest African part of Gondwana, interpreted as a distinct cool water paleobiogeographic region through the Llandovery and Wenlock, with the strongest endemicity present in the late Hirnantian to Rhuddanian. Melchin (1989) demonstrated that a number of taxonomic groups were restricted to the paleotropical regions of Laurentia, Baltica, Siberia, Kazakhstan, and China and considered these as a circum-equatorial faunal province, supported by the interpretation of Rickards, Rigby, and Harris (1990). Štorch (1998) noted that the lower paleolatitude regions of Avalonia and southern Baltica represent transitional faunas between the cooler-water faunas of the peri-Gondwanan and circum-equatorial regions. Little is known about biogeographic differences in the Ludlow to Pridoli interval (e.g. Koren', 1979; Berry & Wilde, 1990). However, according to Goldman and others (2013), considerable differences in the faunal composition between Kazhakstan, northern Laurentia, and Bohemia (see Koren', 1989; Lenz, 1988, 1990; Přibyl, 1983) may indicate the presence of faunal provinces in the late Silurian.

THE DEVONIAN

The graptolite faunas of the Devonian show low diversity and no apparent biogeographic provinciality. Jaeger (1978, 1988) discussed a worldwide distribution of Lower Devonian graptolite faunas, but it is clear from new paleogeographic interpretations that these faunas appear to be restricted to equatorial regions (Berry & Wilde, 1990). Lower Devonian graptolites of southwestern Europe are usually restricted to outer shelf regions and are not found in inner shelf areas (Lenz & others, 1996), suggesting that the expanses of the Paleozoic oceans may have been the last refuge of the planktic graptoloids in order to escape from competition with other planktonic organisms. Koren' (1979) suggested that this restriction of Devonian planktic graptolites may have been a significant factor in their final extinction. Lenz (2013) demonstrated that the distribution of early Devonian graptoloids was not limited to tropical, equatorial regions. He indicated a presence also in cold-water sites and suggested a probably universally moderate climate for the early Devonian but regarded the reasons for the graptoloid extinction as not understood.

HISTORICAL BIOGEOGRAPHY

The paleogeographical origin of certain graptolite taxa or groups (clades), or historical paleobiogeography, has rarely been considered in the interpretation of graptolite faunas. Erdtmann (1982) and Cooper (1999, p. 9) discussed the possible origin of the first planktic graptolites of the genera *Rhabdinopora* and *Staurograptus* Emmons, 1855 in a deep water biotope on the continental slope and a subsequent expansion into the shallow water shelf regions. As benthic graptolites appear to be largely limited to the shallow water regions of the oceans, the idea of a deeper water origin of planktic graptoloids might be difficult to explain and needs further investigation. Zhang and Chen (2007, 2008) suggested a deep-water origin and shallow water dispersal model in graptolite evolution, based on the distribution of early Darriwilian pseudisograptids and early axonophorans in China. The authors suggested that the Axonophora evolved in the deep-water regions in which also their ancestors, the isograptids and pseudisograptids, lived. Thus, they favored a model of evolution of certain planktic graptoloids clades from equally planktic ancestors in oceanic regions, in which the planktic graptoloid taxa were supposedly living, but did not discuss the origin of planktic graptolites per se.

Goldman and others (2013) discussed historical biogeography in order to explain the patterns of changes of graptolite faunas through time and to recognize regions of evolutionary innovations and origins of faunal dispersal. The authors used published cladistics trees to pinpoint the evolutionary origin of certain clades to particular regions,

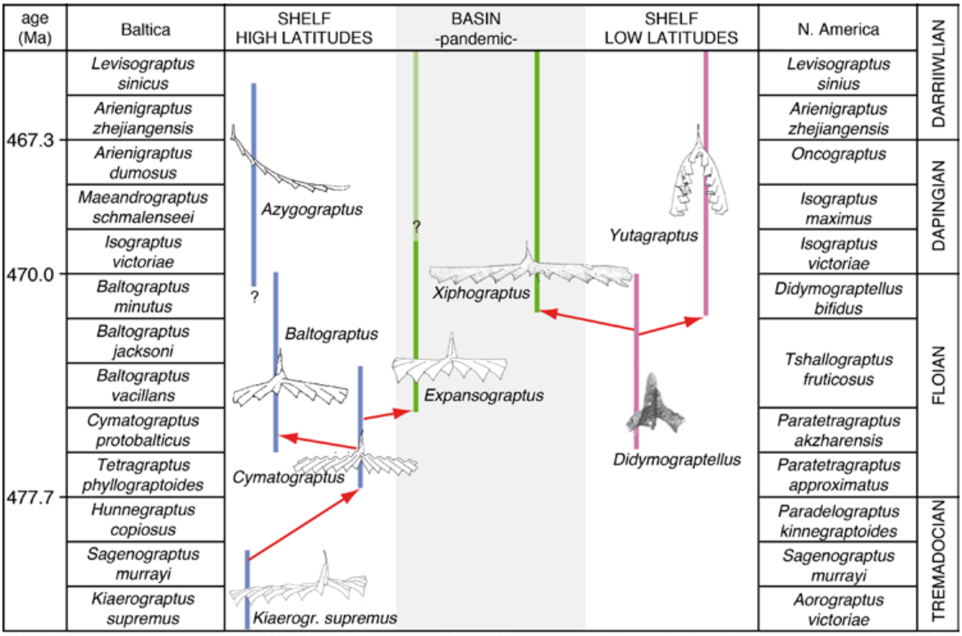

Fig. 4. Historical paleobiogeography of the late Tremadocian to early Darriwilian time interval, showing the introduction of the genera *Expansograptus* Bouček & Přibyl, 1952 and *Xiphograptus* Cooper & Fortey, 1982 into the pandemic graptolite faunas of the marine basins from the respective low latitude and high latitude shelf regions (new; radiometric ages [Ma] from Cooper & Sadler, 2012).

based on a parsimony-based analysis, mapping geographical states to ancestral nodes. They noted a possible origin of early axonophorans in South China, but also recognized a considerable diversification center in high- to mid-latitudinal regions, leading to a number of new clades. These interpretations, however, are regarded as preliminary by the authors, as they consider the available data sets as incomplete.

Goldman and others (2013) provided a number of examples to document historical biogeography of graptolite clades. Thus, the origin of the expansograptids (e.g., *Expansograptus* Bouček & Přibyl, 1952; *Didymograptus; Baltograptus*) was considered to be in the shallow-water regions of the high latitudes, preceded by the two-stiped *Kiaerograptus supremus* (Fig. 4). The genus *Cymatograptus* Jaanusson, 1965 suddenly appeared in middle of the *Tetragraptus phyllograptoides* Biozone, considerably before the origination of the cosmopolitan genus *Expansograptus* (Egenhoff & Maletz, 2007). *Cymatograptus* is present in most high latitude regions, but only a single record has been made in lower latitude regions, in the Cow Head Group of western Newfoundland (Toro & Maletz, 2008, p. 981). The *Expansograptus holmi-Expansograptus suecicus* group in the upper part of the *Cymatograptus protobalticus* Biozone (Egenhoff & Maletz, 2007, fig. 3) made the expansograptids successful on a global scale after several million years of evolution as high latitude faunal elements (Fig. 4) with a probable origin in the mid-Tremadocian. The evolution of xiphograptids in the low latitude regions demonstrates another example of a biogeographically determined origin of clades in graptoloid evolution. The genus *Didymograptellus* in the *Tetragraptus akzharensis* Biozone, as found in western Newfoundland, represents the oldest xiphograptid in the fossil record as an endemic of the low latitude fauna (Maletz, 2010). Global dispersal and invasion of the derived genera *Xiphograptus* COOPER & FORTEY, 1982 and *Pterograptus* HOLM, 1881 into the cosmopolitan oceanic biofacies happened in the Dapingian to Darriwilian, where these taxa enjoyed long-time success until the demise of the group in the Upper Darriwilian. The genus *Didymograptellus,* mainly represented by the short-lived *Didymograptellus bifidus* (HALL, 1865), was only moderately successful in the late Floian in the low latitude fauna. *Yutagraptus* had greater species longevity, originating in the upper Floian and lasting until the early Darriwilian, but was also restricted to the low latitudes or perhaps even endemic to Laurentia (MALETZ, 2010).

The radiation of the Neograptina, and especially of the genus *Normalograptus*, represents an excellent example of the biogeographic component of macroevolutionary processes. *Normalograptus* species are uncommon in the Darriwilian to Sandbian and are widely distributed in high latitudes, but during the early Hirnantian, species of *Normalograptus* invaded the paleotropics and rapidly replaced DDO species during the Late Ordovician extinction event (MELCHIN & MITCHELL, 1991; CHEN & others, 2005). Eventually, only species of *Normalograptus* survived the extinction and re-populated the Early Silurian oceans before a new diversification occurred in the Rhuddanian, early Silurian, initially based on biserial Neograptina, but followed by the origin and radiation of the Silurian Monograptidae.

The genus *Cyrtograptus* CARRUTHERS in MURCHISON, 1867, may in the future provide another useful example to understand the evolutionary history of graptoloids through the late Llandovery and Wenlock (mid-Silurian). The genus *Cyrtograptus* shows significant provincial differences in the distribution during the late Telychian, and MELCHIN (1989) used the distribution of *Cyrtograptus sakmaricus* KOREN', 1968 and related forms as indicator of the circumtropical faunal province. *Cyrtograptus* disappeared completely from the southern paleolatitudes in the mid-Sheinwoodian, but is well documented during this interval in the Canadian Arctic (LENZ & MELCHIN, 1991). In the late Sheinwoodian *Cyrtograptus rigidus* Biozone, *Cyrtograptus* reappears in Avalonia, Baltica, and Bohemia. The reason for this pattern is unclear, especially as the origin and early evolution of the genus *Cyrtograptus* has not been verified. A number of authors discussed a polyphyletic origin of the genus *Cyrtograptus* (e.g., RICKARDS, HUTT, & BERRY, 1977; FU, 1985; WILLIAMS & ZALASIEWICZ, 2004; LENZ & others, 2012). As this question is not resolved, a suitable phylogenetic analysis and paleobiogeographic interpretation is impossible to provide.

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