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The asaphid trilobite fauna: Its rise and fall in Baltica

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ABSTRACT

The Baltica terrane is well known as the Asaphus Province of the Ordovician World. Being situated in intermediate latitudes and surrounded by fairly wide oceans, Baltica had a benthic fauna that developed in a relatively endemic direction. The most common trilobites were the asaphids. The present study discusses how they appeared, evolved in various environments around Baltoscandia and finally disappeared. The total range of the asaphids based on data from 381 species is estimated as extending from the Furongian, latest Cambrian to the end Ordovician. The remnant Cambrian Olenid Fauna, which was adapted to black bituminous shale facies, survived into the Tremadocian. This Cambrian fauna includes the first asaphids (*Promegalaspides*, *Niobella*, *?Eoasaphus*). With a shift to lighter-coloured and carbonatic sediments in the middle Tremadocian, this fauna was replaced by the immigrating *Ceratopyge* Fauna. The latter contains the first five widely distributed asaphid genera *Promegalaspides*, *Niobe*, *Niobella*, *Niobina*, and *Asaphellus*. As carbonate sedimentation became more widespread in many areas from the Floian onwards, the asaphids increased in number and formed a stabilised Asaphid Fauna during the Dapingian. In Baltoscandia a gradual development of endemism related to facies belts is observed during the Darriwilian. Records of the mud-related niobines, *Megistaspis* and *Ptychopyge* faunas, together with some other benthic macrofaunas are not found beyond the boundary of the Kunda/Aseri regional stages (middle Darriwilian). Their disappearance may be due to a catastrophic event. In contrast *Asaphus* s.l. survived this interval. Drift of Baltica towards lower latitudes and fluctuations in sea-level influenced the Asaphid Fauna leading to its gradual collapse by late Sandbian time. Influx of the islotelines during the early Katian gave way to a set of illaenimorph species found together with corals that are related to a reefal environment. This morph disappears prior to the Hirnantian glaciation.

1. Introduction

In 1966, H. B. Whittington gave a superbly illustrated overview on the phylogeny and distribution of the Ordovician trilobites in his presidential address to the Paleontological Society (Whittington, 1966). The phylogeny of families was drawn following their parallel development in different regions, pointing out geographic and climatic influence. He demonstrated that the Tremadoc (then being included within the Late Cambrian) trilobites are widely distributed worldwide, while successive faunas are endemic or with limited distribution. He pointed out that the greatest change ever in trilobite faunas occurred shortly before or during Tremadoc time when the majority of ancient trilobite families vanished and a small relatively short-lived group together with the earliest members of the dominant Ordovician families appeared. These include six geographically recognised faunas defined for the Tremadoc, followed by several more including an Asaphid Fauna during post-Tremadoc times. The Asaphid Fauna is characteristic of the Early Ordovician of Baltoscandia. This term was already used earlier by Whittington (1963) to distinguish the Baltic province from that of North America and Siberia. In these regions the bathyurids and asaphids co-occur along with totally different elements. The Baltoscandian elements were mentioned as those figured in works by Tjernvik (1956), Jaanusson (1953a,b, 1956) and Henningsmoen (1960) but a comprehensive list was lacking. In our study we review all representatives of the family Asaphidae (see for systematics Fortey and Chatterton, 1988; Jell and Adrain, 2003).

The trilobite records from the Ural Mountains and the islands to the north, Vaygach and Novaya Zemlya, which form a further continuation of the chain in the north reflect some similarity with Baltoscandia, including occurrence of some common asaphids (Balashova, 1961, 1967; Burskiy, 1970; Ancygin, 2001; for more detail see Bergström et al., in press; Pärnaste and Bergström, in press). Following this appearance the entire Baltica terrane is considered to represent the Asaphid province in the Arenig and Llanvirn (Whittington and Hughes, 1972) or in modern terms in the Floian, Dapingian and Darriwilian ages (see for global stratigraphy e.g. Bergström et al., 2009). A southern mid-latitude Megistaspidine Realm to include Baltica was introduced by Adrain and others (Adrain et al., 2004) in their new global analysis for the Ordovician radiation of trilobites, because specifically the megistaspidine asaphids are endemic to this region (Cocks and Fortey, 1982, 1990). A family Megistaspididae

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was erected by Balashova (1976) covering the previously established subfamily Isotelinae in sense of Jaanusson (in Moore, 1959) to embrace four subfamilies Megistaspidinae, Asaphellinae, Hoekaspinae, and Thysanopyginae using diagnostic characters different from those chosen by Jaanusson. The systematics of this group is still lacking so we continue to use the term Asaphid Fauna as first introduced, especially since the subfamily Megistaspidinae in sense of Balashova (1976) included the following genera (*Megistaspis*, *Paramegistaspis*, *Megistaspidella*, *Ogygitoides*, *Stenorhachis*, *Plesiomegalaspis*, *Paramegalaspis*, *Ekeraspis*, *Dolerasaphus*, *Kayseraspis*, *Nerudaspis*, *Rhinoferus*, *Hunnebergia*) of which some are also known outside of Baltica, i.e. are not endemic to Baltica.

The aim of this contribution is to reveal the dynamics of distribution and development of different groups of asaphids, which prevailed during the first half of the Ordovician in Baltica. For that we (1) compare the trilobite succession in 13 regions across Baltoscandia throughout 15 intervals from the beginning of the Ordovician to the end of the Darriwilian, when the asaphids were flourishing; (2) review the trilobite occurrences in the Ural Mountains together with Vaygach and Novaya Zemlya—the islands in the north–west (in present-day terms) on the other side of Baltica; (3) detect the distribution of asaphid subfamilies in different regions and time intervals in Baltoscandia; (4) analyse the major events in the diversification of the asaphids until the demise of the family at the end of Ordovician.

2. Geological setting

2.1. Baltica Plate—boundaries and palaeogeographical position

Baltica formed a discrete continental block before the Caledonian collisions (Fig. 1A; see also, e.g., Torsvik, 1998; Cocks and Torsvik, 2002, 2005). A series of Caledonian nappes, the lowest of which contains fossils of Baltic and Avalonian origin and the uppermost those of Laurentian origin (Neuman and Bruton, 1974; Bruton and Harper, 1981, 1988; Bruton et al., 1989) have been transported eastwards from off-shore Norway (Ebbestad, 1999, fig. 2; Harper et al., 2009; Lamminen et al., 2011, fig. 11), and the evidence for litho- and biofacies in these areas is largely destroyed. Magmatic rocks included in some nappes bear evidence of the emergence of island arcs off the coast in

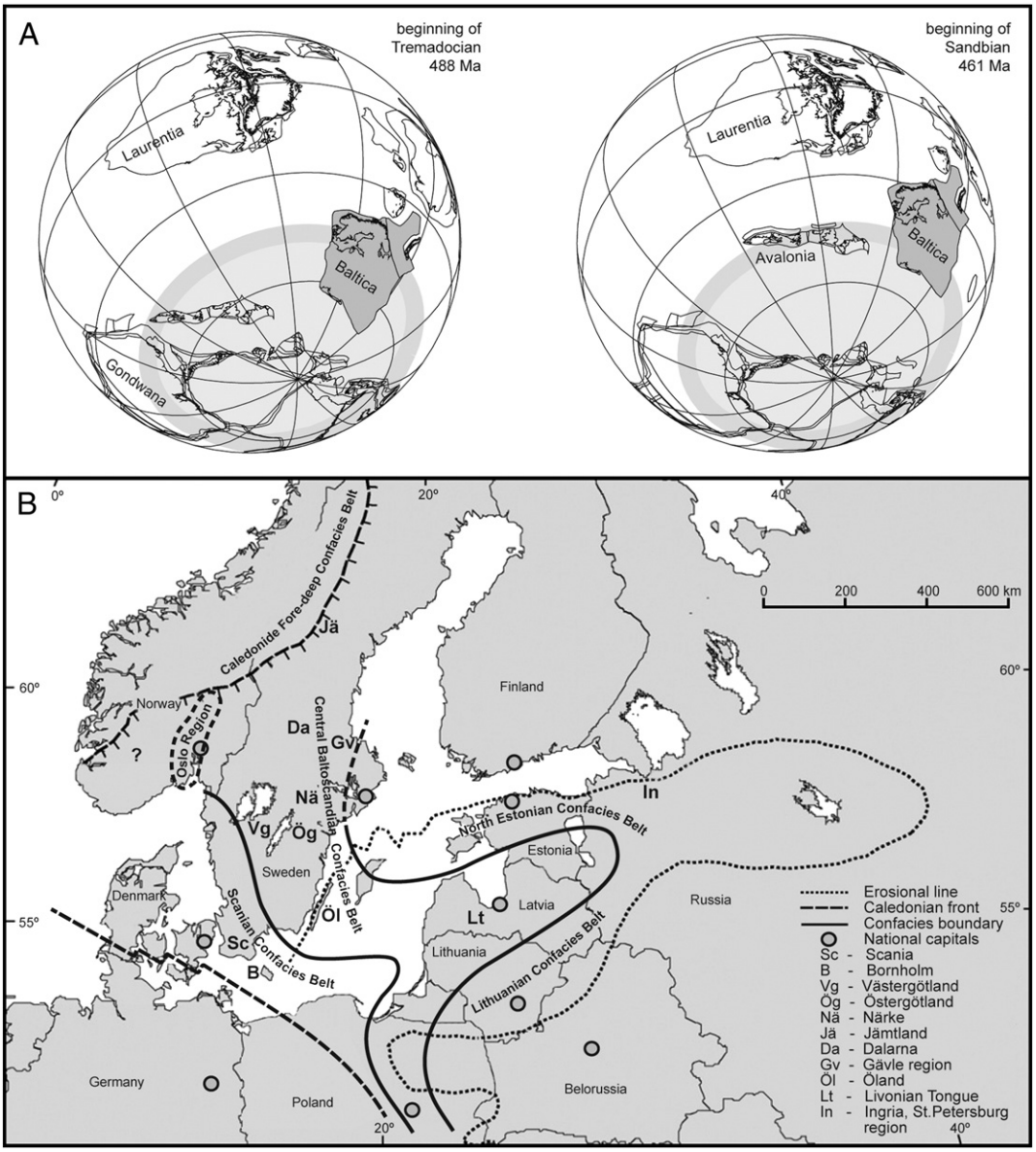

Fig. 1. A. Palaeogeographical reconstruction showing change in position of Baltica from the beginning of the Tremadocian to the beginning of the Sandbian (Map generated using the T.H. Torsvik's GIS-oriented software from 2009, BugPlates: linking biogeography and palaeogeography). Grey circle marks the ocean circulation in cool sea surface temperatures suggested by current circulation in modern oceans, and the wide line indicates the winter–summer amplitude. B. The confacies (bio-lithofacies) belts of Baltoscandia modified from Jaanusson (1982a).