

TÕNN PAISTE

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Amorphognathus and updated Sandbian
(Upper Ordovician) conodont
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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following published papers, which are referred to in the text by Roman numerals. The papers are reprinted with the kind permission of the publishers.

- I Paiste, T., Männik, P., Nõlvak, J. and Meidla, T. 2020.** The lower boundary of the Haljala Regional Stage (Sandbian, Upper Ordovician) in Estonia. *Estonian Journal of Earth Sciences*, **69**, 76–90, DOI: <https://doi.org/10.3176/earth.2020.05>
- II Paiste, T., Männik, P. and Meidla, T. 2022.** Sandbian (Late Ordovician) conodonts in Estonia: distribution and biostratigraphy. *GFF*, **144**, 9–23, DOI: <https://doi.org/10.1080/11035897.2021.2020333>
- III Paiste, T., Männik, P. and Meidla, T. 2023.** Emended Sandbian (Ordovician) conodont biostratigraphy in Baltoscandia and a new species of *Amorphognathus*. *Geological Magazine*, **160**, 411–427, DOI: <https://doi.org/10.1017/S0016756822001005>

Author's contribution:

- I** The author took part in fieldwork, was responsible for the sample preparation, data collection under microscope and SEM, data analysis, interpretation and visualization, as well as the writing of the draft manuscript.
- II** The author was responsible for the sample preparation, data collection under microscope and SEM, data analysis, interpretation and visualization, as well as the writing of the draft manuscript.
- III** The author was responsible for planning original research, data collection under microscope and SEM, data analysis, interpretation and visualization, as well as the writing of the draft manuscript.

ABBREVIATIONS

CAI	colour alteration index (Conodont colour Alteration Index)
CSZ	Conodont Subzone
CZ	Conodont Zone
FAD	first appearance datum
Fm	Formation
GSSP	Global Boundary Stratotype Section and Point
GZ	Graptolite Zone
LAD	last appearance datum
RS	Regional Stage
SEM	scanning electron microscope

1. INTRODUCTION

Global stages defined by their lower boundaries marked by the first appearances of selected graptolite or conodont species are standard units in the global Ordovician stratigraphic scheme. Conodonts and biozonation based on these fossils are particularly essential for dating and correlating carbonate-dominated successions of the Baltoscandian region with the global units as zonal graptolites are rare or missing in this type of rocks (Goldman *et al.*, 2020). Specifically, conodonts can be used for high-resolution biostratigraphy because of their widespread global distribution, high rates of evolution, abundance in the fossil record and fairly robust mineralogy (Henderson, 2020).

The Ordovician conodont research has more than 50 years of history in Estonia (Männik and Viira, 2012) and, as a result, high-resolution biozonation has been worked out for the Lower and Middle Ordovician interval in the region (Meidla *et al.*, 2022). However, Upper Ordovician conodont biozones are still somewhat problematic and any research on this topic holds essential value. Updating the stratigraphic correlation will have a direct influence on the practical geology of Estonia and adjacent areas, allowing improving the quality of the stratigraphic framework and geological maps. The results will facilitate the worldwide correlation of the Upper Ordovician in the areas with poor graptolite record, having thus a fundamental value for the development of the global stratigraphic standard (geochronological table).

The Sandbian is the lowermost stage in the Upper Ordovician (Bergström *et al.*, 2009). It is defined as the interval between the first appearance datum (FAD) of the *Nemagraptus gracilis* Graptolite Zone (GZ) and the FAD of the *Diplacanthograptus caudatus* GZ (Bergström *et al.*, 2000). In the type section of the Sandbian Stage (Bergström *et al.*, 2000), the FAD of the *N. gracilis* GZ is located within the *Pygodus anserinus* Conodont Zone (CZ) and distinctly below the first occurrences of *Baltoniodus variabilis* and *Amorphognathus tvaerensis*. As believed until now, the best estimate for the base of the Sandbian Stage in the conodont succession of Baltoscandia is the base of the *A. inaequalis* Conodont Subzone (CSZ) (Meidla *et al.*, 2022; Nielsen *et al.*, 2023). However, some authors (e.g., Ferretti and Bergström, 2022) state that the occurrence of *A. inaequalis* in Estonian and Swedish sections is problematic.

This thesis is based on critical analysis of the composition and distribution of Sandbian conodont faunas in Baltoscandia and aims to updating the (1) conodont taxonomy, (2) evolutionary patterns of selected lineages and (3) conodont-based biozonation of this time interval. A need for this kind of study became evident when it was realized that not only the occurrence of *A. inaequalis*, and of the eponymous subzone, in Baltoscandia is highly problematic but also the elements of long-ranging *A. tvaerensis* are morphologically highly variable and differ considerably in the lower and upper parts of their distribution interval. Both issues have potentially a major impact on Baltoscandian conodont biostratigraphy if current understandings of them would change.

The main hypotheses of the study are as follows: (I) Baltoscandian conodont material is sufficient and adequately preserved for validating the evolutionary succession of species within biostratigraphically important genera; (II) the investigation of morphological trends within the long-ranging species of the genus *Amorphognathus* will result in further refinements in taxonomy; (III) detailed taxonomic studies will be capable of improving the resolution and applicability of the regional conodont biozonation of the Sandbian.

2. GEOLOGICAL SETTING, STRATIGRAPHY AND CONODONTS OF THE ORDOVICIAN OF BALTO-SCANDIA

2.1 Geological setting

During the Ordovician, the palaeocontinent Baltica existed as an isolated plate surrounded by oceans. Starting from the late Cambrian, Baltica drifted from high southern latitudes towards the equator and by the Late Ordovician was situated at about 30°S (Fig. 1A; Torsvik and Cocks, 2017). The Baltoscandian Palaeobasin was located on the western part of the palaeocontinent. The epicontinental basin was open to the ocean, similarly to the nowadays North Sea, and deepened to the south-west. A clear trend of change is observed in the composition of sediments along the depth profile. Northern Estonia, palaeogeographically termed as the Estonian Shelf, is characterized by limestones formed in shallow-water environments (Fig. 1B). The deeper part of the basin, the western part of the Scandinavian Basin (nowadays north-western Poland and western Sweden), is represented by graptolite-bearing grey and black shales. The transition between these two palaeogeographic regions corresponds to the Livonian Basin and the eastern part of the Scandinavian Basin *sensu* Harris *et al.* (2004) comprising southern Estonia, the western part of Latvia and Lithuania, north-eastern Poland and eastern Sweden, dominated by marls and argillaceous limestones.

During the Sandbian, mostly argillaceous-calcareous muds accumulated all over the Baltic region, with variation in the ratio of argillaceous and calcareous components (Nestor and Einasto, 1997). Argillaceous limestones of the Kõrgekallas Formation (Fm) in the Estonian Shelf (Figs 1B, 2), micritic limestones with intercalation of bioclastic limestones and marls of the Taurupe Fm in the Livonian Basin and Furudal Limestone in the eastern part of the Scandinavian Basin were replaced by more bioclastic limestones at the beginning of the Sandbian (Fig. 2). Namely, by bioclastic limestones of the Pihla Fm and argillaceous bioclastic limestones with intercalations of kukersite of the Viivikonna Fm in the Estonian Shelf, bioclastic Dalby Limestone in the eastern part of the Scandinavian Basin and limestones with dark pyritized skeletal detritus of the Dreimani Fm in the Livonian Basin (Hints, 1997).

In the middle Sandbian, purer bioclastic calcareous sediments of the Tatruse Fm are overlain by argillaceous carbonates of the Kahula Fm in the Estonian Shelf. At the same time, argillaceous bioclastic muds of the Adze Fm and argillaceous muds of the Blidene Fm deposited in the Livonian Basin, overlain by organic-rich marls of the Mossen Fm (Hints and Meidla, 1997a, 1997b). In the eastern part of the Scandinavian Basin, the bioclastic Dalby Limestone was overlain by argillaceous bioclastic carbonates of the Freberga Fm (Ebbestad and Högström, 2007).

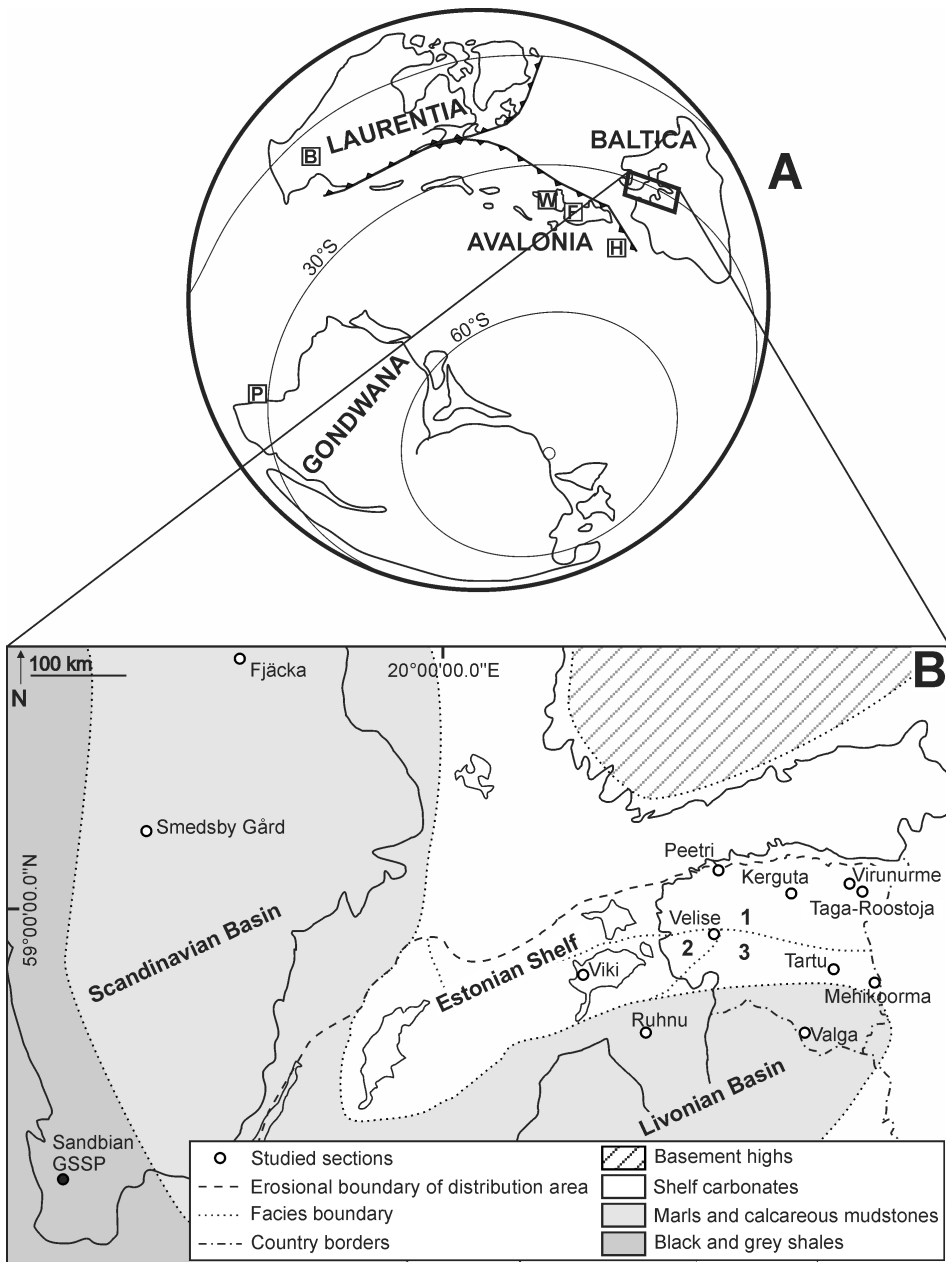


Figure 1. (A) Position of the palaeocontinents at 460 Ma (Sandbian) to 450 Ma (Katian) (modified after Domeier, 2016; Torsvik and Cocks, 2017; Dzik, 2020). B – Black Knob Ridge section; W – Wales; F – West France; H – Holy Cross Mountains; P – Argentine Precordillera. (B) General facies structure of the Baltoscandian Sandbian Ordovician Palaeobasin (modified after Hints, 1997; Harris *et al.*, 2004; Meidla *et al.*, 2022). 1 – northern Estonia; 2 – west-central Estonia; 3 – east-central Estonia; Sandbian GSSP – The Global Boundary Stratotype Section and Point (GSSP) of the Sandbian Stage.

System	Series	Stage	Graptolite zones	Conodont zones	Conodont subzones	Regional stages	Regions / Formations			
							N & C Estonia	S Estonia	Siljan district, Scandinavia	
Ordovician	Upper	Katian	<i>Dicranograptus clingani</i>	<i>Amorphogn. superbis</i>		Rakvere	Rägavere			
				<i>Amorphogn. ventilatus</i>		Oandu	Hirmuse	Variku	Mossen	Freberga
		Sandbian	<i>Diplograptus foliaceus</i>	?		Keila	Kahula		Blidene	Skagen L.
				<i>Nemagraptus gracilis</i>	<i>Amorphogn. tvaerensis</i>	<i>Baltonio. alobatus</i>	Haljala	Tatruse	Adze	Dalby Limestone
						<i>Baltonio. gerdae</i>	Kukruse			
	?	<i>Amorphogn. inaequalis</i>	Uhaku	Kõrgekallas	Taurupe	Furudal Limestone				
	Mid.	Dar.	<i>Gymnograptus linnarssoni</i>	<i>Pygodus anserinus</i>	<i>Sagittodontia kielcensis</i>	Uhaku	Väo			

Figure 2. Generally accepted Upper Darriwilian, Sandbian and lower Katian stratigraphy of Estonia and the Siljan district of Sweden. Chronostratigraphy, biozonations, regional stages and lithological units of Estonia and Sweden are based on Meidla *et al.* (2022) and Nielsen *et al.* (2023), respectively. Mid. – Middle; Dar. – Darriwilian; *Amorphogn.* – *Amorphognathus*; *Baltonio.* – *Baltoniodus*; N & C Estonia – northern and central Estonia; S Estonia – southern Estonia; Skagen L. – Skagen Limestone.

2.2 Stratigraphic framework

The standard chronostratigraphic unit in the Baltoscandian Ordovician stratigraphy is a regional stage (RS), which is used in the stratigraphic schemes of Estonia (Meidla *et al.*, 2022), Sweden (Bergström, 2007; Nielsen *et al.*, 2023), Poland (Dzik, 1999), Lithuania (Stouge *et al.*, 2016) and Ukraine (Saadre *et al.*, 2004). The absolute majority of the RSs are originally defined on the basis of data from the northern Estonian outcrop area, from the sections representing the Estonian Shelf. This region is characterized by an incomplete succession of shallow-water carbonate sediments containing numerous discontinuities and gaps (Männil, 1966; Jaanusson, 1976; Nestor and Einasto, 1997). As a result, the boundaries of RSs in the region correspond to major hiatuses in the succession and, outside the outcrop area, the RSs are more often recognized by their content than by their boundaries (Meidla *et al.*, 2022). This practice, i.e., undefined boundaries of the RSs, makes their recognition difficult in the deeper part of the basin where the succession is more complete. For that reason, the question of their practicality was raised (see Appendix A in Kumpulainen, 2017). Furthermore, new Scandinavian stages were proposed, two of them in the Sandbian (Nielsen *et al.*, 2023). The new stages helped to modernize previous chronostratigraphic charts but are purposely directed to the Scandinavian part of the Baltoscandian Ordovician Palaeobasin. Their use outside the Scandinavian region is thus limited.

In the Estonian succession (Fig. 2), the Sandbian is considered to correspond to the Kukruse, Haljala and lower part of the Keila RSs, although location of its boundaries is tentative due to the scarcity of graptolites in this part of the palaeobasin (Meidla *et al.*, 2022). Similarly, in the eastern part of the Scandinavian Basin (Fig. 1B), where graptolites are rare, the lower boundary of the Sandbian Stage is drawn tentatively and the stage is considered to correspond to the lower part of the Kukruse RS and the Haljala and Keila RSs. Based on the new Scandinavian stages, the Sandbian Stage corresponds to the uppermost part of the Segerstadian Stage and to the entire Dalbyan Stage (Nielsen *et al.*, 2023).

Due to scarcity of graptolites within the Estonian Shelf area, Livonian Basin and eastern part of the Scandinavian Basin (Fig. 1B), the biozonations based on conodonts (Fig. 2) and chitinozoans are the best alternatives for correlating regional units with global Ordovician stages (Meidla *et al.*, 2022; Nielsen *et al.*, 2023). In the conodont succession, the lower boundary of the Sandbian Stage is located within the *P. anserinus* CZ (Bergström *et al.*, 2000), at or near the base of the *A. inaequalis* CSZ, overlain by the *A. tvaerensis* and *A. superbus* CZs. The lower boundary of the Katian Stage lies near the base of the *A. superbus* CZ (Meidla *et al.*, 2022; Nielsen *et al.*, 2023). The short-ranged *A. ventilatus* CZ has been introduced for the Estonian part of the Baltoscandian Palaeobasin just below the *A. superbus* CZ (Meidla *et al.*, 2022). More detailed subdivision of the *A. tvaerensis* CZ is based on the lineage of the genus *Baltoniodus*, with the *B. variabilis* CSZ corresponding to the lower part, *B. gerdae* to the middle part and *B. alobatus* to the upper part of this zone.

2.3 Upper Ordovician complex conodonts

Conodonts are microscopic (~1 mm) bioapatitic elements found in almost any marine sedimentary rock of Cambrian to Triassic age (Sweet, 1988). The first descriptions depicted them as teeth and jaws of a previously unknown group of fishes (Pander, 1856). Their biological affinity remained controversial until the discovery of the first fossil of a small animal with an apparatus comprising various conodont elements in its head part (Fig. 3A; Briggs *et al.*, 1983). However, the biological affinity of conodonts is still debated (Henderson, 2020), although they are commonly affiliated with vertebrates (Aldridge *et al.*, 1993) and reconstructed as a small (5 cm) eel-like animal (Fig. 3B). Size variation between different families is considerable as an element from the apparatus of the genus *Promissum* can be up to 18.8 mm (Aldridge *et al.*, 1995) and the animal itself about 40 cm long (Gabbott *et al.*, 1995). In the present paper, the term ‘conodont’ is used for individual elements of the conodont apparatus, unless stated otherwise.

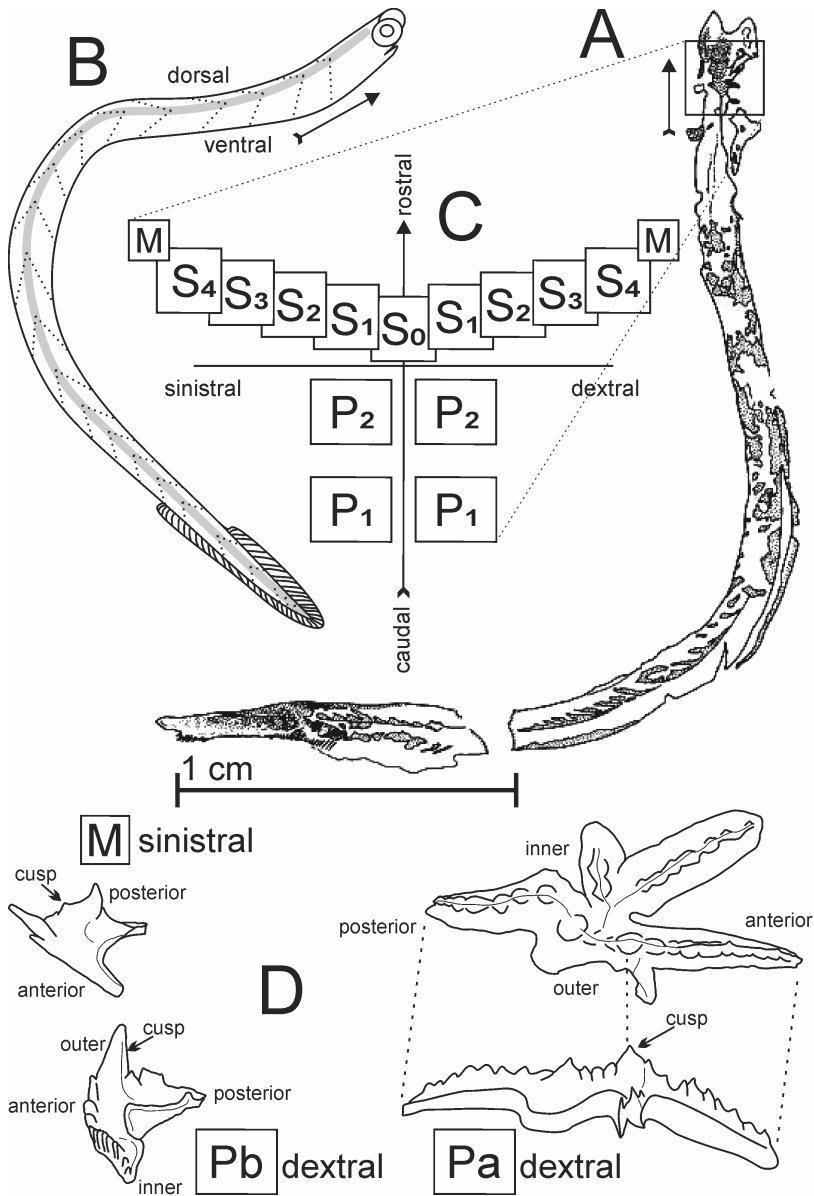


Figure 3. Anatomy of the conodont animal and designation of elements. (A) Sketch of the conodont animal, with a scale bar (modified after Briggs *et al.*, 1983; Prothero, 2013). (B) Author's interpretation of the conodont animal (modified from Aldridge *et al.*, 1993). (C) Relative position of conodont elements of different types in the topological scheme of notation (Purnell *et al.*, 2000). (D) Conventional terminology of Pa, Pb and M elements (modified from Paper III).

Despite the problematic nature of the conodont animal, the practical implications of conodont elements are numerous. For example, the FADs of multiple conodont species define the Global Boundary Stratotype Points of many global Phanerozoic stages (Gradstein *et al.*, 2020); their evolutionary range of around 300 million years is subdivided into at least 240 interregional biozones making them one of the best index fossil groups for biostratigraphy (Henderson, 2020); the thermal maturity studies of conodont elements is widely applied in oil exploration (Epstein *et al.*, 1977); isotope-geochemical studies offer clues for palaeoenvironmental interpretations (Trotter *et al.*, 2016); widespread distribution and rapid evolution are applicable both in palaeoecology and palaeobiogeography (Mei and Henderson, 2001).

Among various types of conodont elements, the term ‘complex conodonts’ is used for species with more complex morphology of elements forming the feeding apparatus of the conodont animal. The term is usually referred to the conodont clade Prioniodontida that includes the Upper Ordovician conodont genera useful for biozonation (Purnell *et al.*, 2000; Donoghue *et al.*, 2008). In practice, conodonts have various shapes, being coniform, ramiform, rastrate and pectiniform (Sweet, 1988). Coniform conodonts are referred to as ‘simple cones’ or elements of conical shape, with the cusp and basal area. Ramiform (‘with branching outgrowth’) conodonts have additional base extensions next to the cusp, in the form of processes, commonly with serrated upper edges. Rastrate (‘rake’) conodonts resemble coniform elements in ramiform features as the extended or extensive base is commonly serrated on the concave posterior margin of the cusp. Pectiniform conodonts combine all ‘blade’, ‘plate’ and ‘platform’ type elements that occupied similar positions in the apparatus and thus were described as the same. Pectiniform conodonts are typically more robust than other element types and occupy the P element position. Current morphological terminology and relative location of conodont elements in an apparatus are based on finds of natural assemblages and fused clusters of elements (Fig. 3C; Purnell *et al.*, 2000).

The orientation and location of individual elements in the apparatuses of the stratigraphically useful Upper Ordovician conodont genera of the clade Prioniodontida, like *Amoprhognathus* and *Baltoniodus*, are appointed tentatively as no fused clusters or bedding plane assemblages of their elements are known (Fig. 3C; Purnell *et al.*, 2000). Even though the different element types are similar to those known from preserved apparatuses of some other genera, the conventional notation of separate elements is still widely in use (Ferretti and Bergström, 2022). Similarly, descriptions in this thesis are compiled without referring to the probable anatomical orientation and position of elements. Instead, the traditional Pa, Pb, Pc, M, Sa, Sb, Sc, Sd notation is employed (Cooper, 1975; Sweet and Schönlaub, 1975; Sweet, 1981, 1988). Additionally, the terms ‘anterior’, ‘posterior’, ‘lateral’, ‘inner’, ‘outer’, ‘upper’ and ‘lower’ are used in the traditional sense for isolated conodont elements (Sweet, 1981, 1988) and do not refer to their biological orientation. The application of these terms in descriptions is illustrated in Figure 3D.

2.4 Conodont biostratigraphy

The identifications of conodont species in this study are based on the general morphology of Pa elements that are commonly used as the holotypes of species. In some cases, Pb and M elements provide also valuable information for species identification, while S elements tend to be the most conservative and only of limited use for identification (Bergström, 1962; Ferretti *et al.*, 2014). The conodont successions described are based on the comparison of the element with the holotype of a species as a reliable identification of a taxon (Fig. 4, index 7); the comparison of the element with the broken holotype element or other than the Pa element (e.g., M) is marked as a questionable identification of a taxon (Fig. 4, index 8).

The Sandbian Stage comprises three conodont zones and five subzones in the Baltoscandian area. The zones are based on phylogenetic lineages of the genera *Pygodus*, *Amorphognathus* and *Baltoniodus*. The distribution interval of the last (youngest) species of the *Pygodus* lineage (Zhang, 1998), *P. anserinus* (Fig. 5A–H), includes the lower boundary of the Sandbian Stage (Bergström *et al.*, 2000). The genus *Amorphognathus* appears near the lower boundary of the Sandbian Stage. Its possible ancestor was *Sagittodontina kielcensis* (Fig. 6A–H; Dzik, 1976) but this is not yet generally accepted (Ferretti and Bergström, 2022). The *Baltoniodus* lineage of the Sandbian follows *B. prevariabilis* (Fig. 5I–P), as apparent from the stratotype section (Bergström *et al.*, 2000).

The *P. anserinus* CZ corresponds to the interval from the first appearance of *P. anserinus* up to the first appearance of *A. tvaerensis* (Bergström, 1971). The *S. kielcensis* and *A. inaequalis* CSZs are distinguished within the *P. anserinus* Zone (Dzik, 1978; Bergström, 1983), with the boundary between the subzones drawn as corresponding to the FAD of *A. inaequalis*. The *A. tvaerensis* CZ corresponds to the interval from the FAD of *A. tvaerensis* (Fig. 6I–Q) up to the FAD of *A. superbus* (Bergström, 1971). The *B. variabilis* (Fig. 5Q–X), *B. gerdae* (Fig. 5Y–AF) and *B. alobatus* (Fig. 5AG–AN) CSZs are distinguished within the *A. tvaerensis* CZ (Bergström, 1971), with the boundaries between the subzones determined by the FADs of *B. gerdae* and *B. alobatus*. The *A. superbus* CZ corresponds to the interval from the FAD of *A. superbus* (Fig. 6AC–AL) up to the FAD of *A. ordovicicus* (Bergström, 1971).

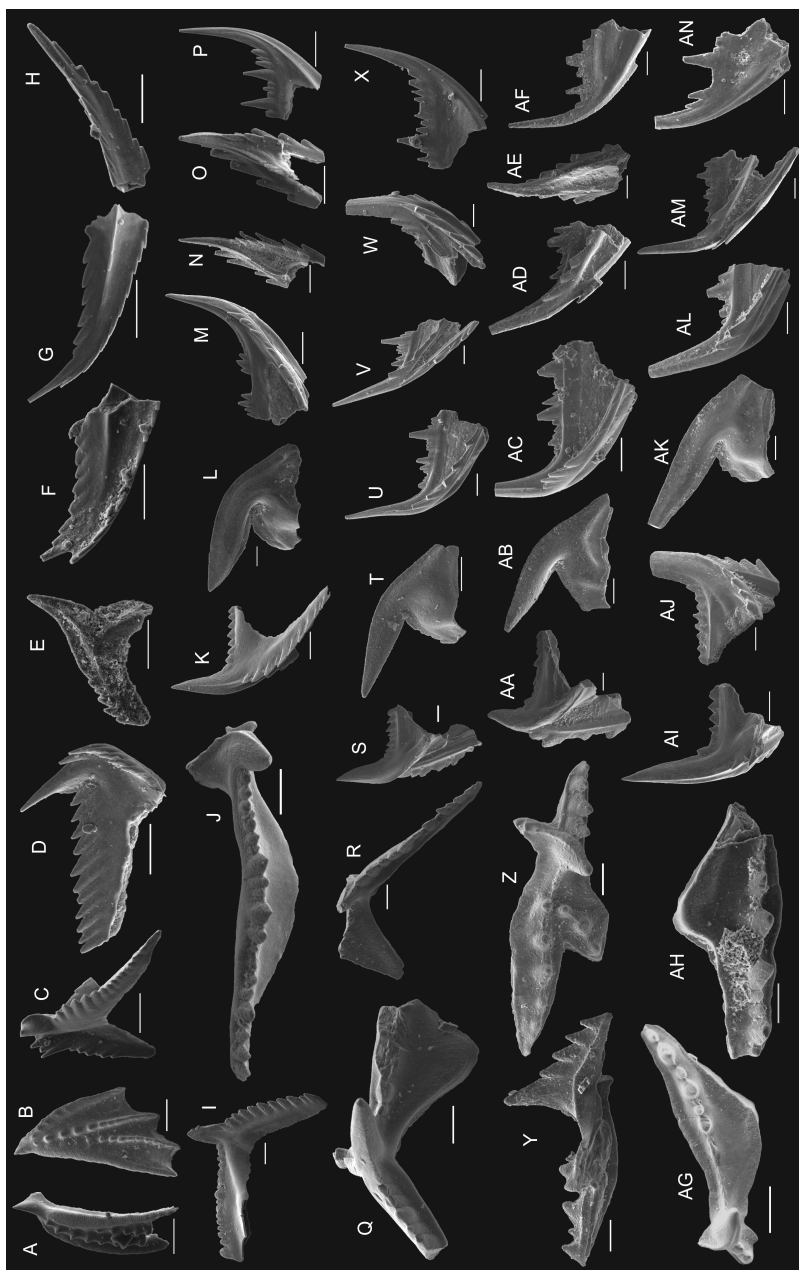


Figure 5. Genera *Pygodus* and *Baltoniodus* in the Sandbian of the Baltoscandian area, a compilation of photos from Paper II. A–H, *Pygodus anserinus* (Lamont and Lindström, 1957): A, B, Pa elements; C, D, Pb elements; E, M? element; F, G, H, S elements. I–P, *Baltoniodus prevariabilis* (Fåhraeus, 1966): I, J, Pa elements; K, Pb element; L, M element; M, N, O, P, S elements. Q–X, *Baltoniodus variabilis* (Bergström, 1962): Q, R, Pa elements; S, Pb element; T, M element; U, V, Q, X, S elements. Y–AF, *Baltoniodus gerdæ* (Bergström, 1971): Y, Z, Pa elements; AA, Pb element; AB, M element; AC, AD, AE, AF, S elements. AG–AN, *Baltoniodus alobatus* (Bergström, 1971): AG, Pa element; AH, Pa element; AI, AJ, Pb elements; AK, M element; AL, AM, AN, S elements.

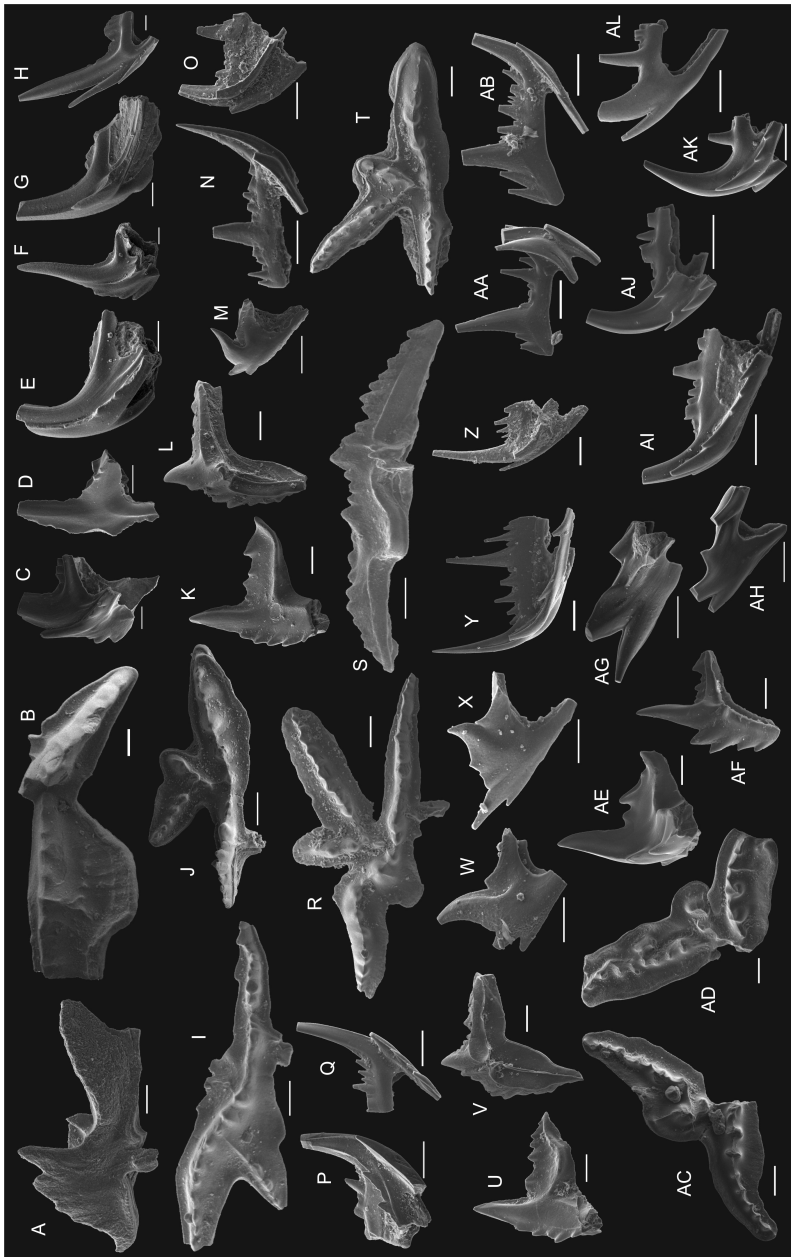


Figure 6. *Amorphognathus* lineage in the Sandbian of the Baltoscandian area, a compilation of photos from Paper II (A–H) and Paper III (I–AL). A–H, *Sagittodontina kielcensis* (Dzik, 1976): A, B, Pa elements; C, Pb element; D, M element; E, F, G, H, S elements. I–Q, *Amorphognathus tvaerensis* (Bergström, 1962): I, dextral Pa element; J, sinistral Pa element; K, dextral Pb element; L, sinistral Pb element; M, sinistral M element; N, O, P, Q, S elements. R–AB, *Amorphognathus viirae* (Paiste, Männik et Meidla, 2023): R, S, dextral Pa elements; T, sinistral Pa element; U, dextral Pb element; V, sinistral Pb element; W, X, sinistral M elements; Y, Z, AA, AB, S elements. AC–AL, *Amorphognathus superbus* (Rhodes, 1953): AC, dextral Pa element; AD, sinistral Pa element; AE, dextral Pb element; AF, sinistral Pb element; AG, AH, dextral and sinistral M element; AI, AJ, AK, AL, S elements.

3. MATERIAL AND METHODS

3.1 Studied sections

This thesis is based on detailed study of conodont successions in three Estonian sections (Fig. 4). The Peetri outcrop (Paper I) is located in the Harju County, west of Tallinn (Fig. 1B). It comprises two separate sections, with about half a metre overlap: an inclined shaft exposing the lower part of the succession (59.364869°N, 24.499064°E) and a trench revealing the upper part of the succession (59.365461°N, 24.499975°E). The Peetri outcrop represents the northern part of the Estonian Shelf of the Baltoscandian Sandbian Palaeobasin and contains argillaceous shelf carbonates. Altogether 15 conodont samples were collected (in 2014–2016), covering the transition from the lower Sandbian (Kukruse RS) to the middle Sandbian (Haljala RS), with ten samples from the Viivikonna Fm and five samples from the Kahula Fm. The average sample weight was about 3.6 kg. Conodont yield was mostly low and the colour alteration index (CAI – see Epstein *et al.*, 1977) of the elements was 1. The total thickness of the section was about 10 m. The Sandbian conodont succession in the north-western part of the Estonian Shelf was previously described based on only few findings (Viira, 1974) and the study of the Peetri outcrop helped to cover the missing part.

The Velise borehole (Paper II) was drilled in the Käriselja village, Rapla County (58.80476°N, 24.51917°E, Fig. 1B). The drill core represents the west-central part of the Estonian Shelf of the Baltoscandian Sandbian Palaeobasin, containing carbonates with various clay content. Ninety-one samples were collected from the studied interval (173.0–218.4 m) comprising the uppermost Darriwilian (middle Uhaku RS), Sandbian (uppermost Uhaku, Kukruse, Haljala and lowermost Keila RSs) and lower Katian (Keila and lower Oandu RSs), corresponding to the Kõrggekallas, Pihla, Tatruse, Kahula and Hirmuse Fms. All the studied samples had been taken earlier (in 2012) and prepared for analysis, but a couple of dozen samples still needed picking for conodont elements from heavy fraction. The average sample weight was about 0.4–0.5 kg, the CAI was 1. The samples yielded mostly well-preserved conodont elements, from six up to several thousands per sample. The conodont succession of the Velise drill core was previously unpublished. The Velise core represents another reference section, along with the Viki core (Männik, 2010; Hints *et al.*, 2014), for the west-central part of the Estonian Shelf.

The Mehikoorma-421 drill core (Paper III) has been previously described in Männik and Viira (2005) from the Mehikoorma settlement, Põlva County (58.24289°N, 27.45231°E, Fig. 1B). The core represents the east-central part of the Estonian Shelf of the Baltoscandian Sandbian Palaeobasin, comprising marls and argillaceous limestones. The studied interval (288–334 m) represents the early evolutionary interval of the genus *Amorphognathus* and includes 45 samples where this genus is present. The interval corresponds to the uppermost Darriwilian (upper Uhaku RS), Sandbian (uppermost Uhaku, Kukruse, Haljala and

lowermost Keila RSs) and lower Katian (Keila, Oandu RSs), assigned to the Kõrgekallas, Dreimani, Tatruse, Kahula and Variku Fms. All the studied samples, weighing 0.25–1.22 kg and with the CAI equalling 1, were collected in 2003–2004. The section yielded well-preserved conodont elements, numbering from ten to several thousand elements per sample. The conodont succession from the Mehikoorma drill core was selected as it yielded a rich conodont collection and contains no significant sedimentary hiatuses.

Additionally, several previously published conodont successions of Estonia (Kerguta – Viira *et al.*, 2006; Ruhnu – Männik, 2003; Taga-Roostoja – Viira and Männik, 1999; Tartu – Stouge, 1998; Valga – Männik, 2001; Viki – Männik, 2010 and Hints *et al.*, 2014; Virunurme – Männik, 2017) and Sweden (Fjäckå main section – Bergström, 2007 and Smedsby Gård section – Bergström *et al.*, 2011) were restudied for comparison (Fig. 1B).

3.2 Laboratory preparation of material and methods of study

The laboratory processing of samples collected from the Peetri outcrop (Paper I) was carried out in the Department of Geology, University of Tartu. In the standard chemical laboratory environment, the limestone samples were washed with water and liquid soap to remove any loose material and broken down to sizable pieces (diameter up to 10–15 cm) for further chemical processing. The weighed samples were soaked in buffered acetic acid according to the approach described by Jeppsson *et al.* (1999). Further treatment with buffered formic acid based on Jeppsson and Anehus (1995) for the removal of dolomite was followed by processing with hydrogen peroxide, to get rid of organics when needed. The remaining residue was subjected to density separation in heavy liquid (bromoform); the light fraction was discarded.

After the laboratory processing, conodonts were picked from the remaining residue under the binocular microscope, at a magnification of $\times 16$ –25. The picking procedure of samples from the Peetri outcrop (Paper I) and several tens of samples from the Velise drill core (Paper II) was carried out in the Department of Geology, University of Tartu.

After picking, the material obtained from each sample was sorted by conodont genera and intact elements of specific interest were separated. The results were recorded in the form of succession figures for documenting successive changes in element morphology. Scanning electron microscopy (SEM, ZEISS EVO MA15) was used for imaging individual elements. The records of successive changes and conodont genera were composed in different universities according to the location of the samples (University of Tartu, Tallinn University of Technology, University of Copenhagen, The Ohio State University).

4. RESULTS

4.1 Conodont successions at Peetri, Velise and Mehikoorma

The Peetri succession includes the *B. variabilis* and *B. alobatus* CSZs of the *A. tvaerensis* CZ (Fig. 4; Paper I). *Amorphognathus viirae* and *B. gerdae* are absent. The sedimentary gap between the Viivikonna and Kahula Fms is marked by a discontinuity surface at a depth of 2 m and comprises the upper part of the Viivikonna Fm, the entire Tatruse Fm and the lower part of the Kahula Fm (Fig. 2).

The Velise succession revealed the *P. anserinus* CZ (*S. kielcensis* CSZ) and the *A. tvaerensis* CZ with the *B. variabilis*, *B. gerdae* and *B. alobatus* CSZs (Fig. 4; Paper II). The probable presence of the *A. superbus* CZ is considered, as the elements of *Amorphognathus* from the Hirmuse Fm resemble typical *A. superbus*. Noticeable is the absence of *A. inaequalis*. The middle and upper parts of the Kahula Fm lack any elements of zonal species and are dominated by long-ranging simple-cone taxa.

The Mehikoorma succession covers the *S. kielcensis* CSZ of the *P. anserinus* CZ, the *B. variabilis*, *B. gerdae* and *B. alobatus* CSZs of the *A. tvaerensis* CZ and the *A. superbus* CZ (Fig. 4; Paper III). *Amorphognathus inaequalis* is absent here as well and the middle and upper parts of the Kahula Fm lack zonal species, similarly to the Velise succession. *Amorphognathus ventilatus* was recorded in three samples from a one-metre interval in the middle of the Variku Fm, within the *A. superbus* CZ.

4.2 Distribution of principal conodont species used in biostratigraphic correlations of the Sandbian within the Baltoscandian region

The FADs and LADs (last appearance datum) of principal conodont species used in Sandbian biostratigraphic correlations of the Baltoscandian region are summarized in Table 1. The data come from the author's restudy of individual successions (Fig. 1B) and differ in some details from the information given in previous publications. Main differences stem from the following observations:

- (1) the appearance of *B. variabilis* is considered transitional from *B. prevariabilis* (Dzik, 1978) and, without any detailed taxonomic study, interpretations by different authors may vary;
- (2) previous identifications of *A. inaequalis* are reinterpreted as *A. tvaerensis*;
- (3) elements from the upper range of *A. tvaerensis* are attributed to *A. viirae*;
- (4) the FAD of *A. superbus* is based on new discoveries of its M elements (Paper III).

Table 1. The FADs and LADs of selected conodont species in the studied sections (Fig. 1B).

Species	Section	Formation	FAD (m)	LAD (m)	Species	Section	Formation	FAD (m)	LAD (m)		
<i>B. variabilis</i>	Peetri	Viivikonna	9.95	2.43	<i>A. viirae</i>	Peetri	—	—	—		
	Kerguta	Kõrgekallas/Viivikonna	169.88	147.75		Kerguta	Tatruse	144.94	144.83		
	Taga-Roostoja	Kõrgekallas/Viivikonna	93.7	71.7		Taga-Roostoja	Tatruse/Kahula	65.9	60.6		
	Virunurme	—	—	Virunurme		—	—	—			
	Velise	Kõrgekallas/Pihla	215.25	205.04		Velise	Tatruse/Kahula	202.54	196.4		
	Viki	Kõrgekallas/Pihla	348	340.2		Viki	Tatruse/Kahula	338.33	334.2		
	Mehikoorma	Kõrgekallas/Dreimani	334	320.8		Mehikoorma	Tatruse/Kahula	316.1	310.6		
	Tartu	Kõrgekallas/Dreimani	341.48	327.3		Tartu	Tatruse/Kahula	325.03	320.5		
	Ruhnu	Taurupe/Dreimani/Adze	669.7	658.8		Ruhnu	Adze	656.8	653.8		
	Valga	Taurupe/Dreimani/Adze	418.04	401.15		Valga	Adze	397.9	396.75		
	Fjäckä main	Dalby	0.00	9.85		Fjäckä main	Dalby	13.30	17.85		
	Smedsby Gärd	Dalby	108.37	97.18		Smedsby Gärd	Dalby	95.29	93.04		
	<i>A. naerensis</i>	Peetri	Viivikonna	9.95		2.43	<i>B. alobatus</i>	Peetri	Kahula	1.94	0.12
		Kerguta	—	—		Kerguta		Kahula	143.47	143.32	
		Taga-Roostoja	Viivikonna	77.97		67.95		Taga-Roostoja	Tatruse/Kahula	64.6	57.5
		Virunurme	—	—		Virunurme		—	—	—	
		Velise	Pihla/Tatruse	211.37		202.95		Velise	Tatruse/Kahula	200.45	194.2
Viki		Pihla/Tatruse	343.8	338.95	Viki	Tatruse/Kahula		337.3	331.5		
Mehikoorma		Dreimani/Tatruse	328.7	316.4	Mehikoorma	Tatruse/Kahula		315	308.95		
Tartu		Dreimani/Tatruse	335.83	325.4	Tartu	Tatruse/Kahula		322.85	318.08		
Ruhnu		Dreimani/Adze	664.8	657.8	Ruhnu	Adze		655.8	652.8		
Valga		Dreimani/Adze	405.22	400.05	Valga	Adze		397.9	395.8		
Fjäckä main		Dalby	6.05	13.10	Fjäckä main	Dalby		14.35	19.34		
Smedsby Gärd		Dalby	103.49	95.35	Smedsby Gärd	Dalby		94.3	91.17		
<i>B. gerdae</i>		Peetri	—	—	<i>A. superbus</i>	Peetri		—	—	—	—
		Kerguta	—	—		Kerguta		Hirmuse/Rägavere	122.25	121.18	
		Taga-Roostoja	Viivikonna/Tatruse	69.9		65.3		Taga-Roostoja	Hirmuse/Rägavere	37.4	34.8
		Virunurme	—	—		Virunurme		Hirmuse	20.6	19.3	
		Velise	Tatruse	204.38		201.5		Velise	Hirmuse/Rägavere	176.75	173
	Viki	Tatruse	339.9	338.18		Viki	Hirmuse	328.45	328.35		
	Mehikoorma	Dreimani/Tatruse	319.85	315.5		Mehikoorma	Variku	296.4	288.2		
	Tartu	Tatruse	326.76	323.21		Tartu	—	—	—		
	Ruhnu	Adze	657.8	656.8		Ruhnu	Blidene/Mossen	646.3	642.05		
	Valga	Adze	400.23	400.05		Valga	Blidene/Mossen	388.85	384.4		
	Fjäckä main	Dalby	10.05	14.10		Fjäckä main	Skagen	1.50	5.00		
	Smedsby Gärd	Dalby	97.1	94.36		Smedsby Gärd	Skagen	80.7	94.2		

The FAD of *A. viirae* in the Mehikoorma section is marked as 316.1 m (Table 1), not as 318.6 m as presented in the original study (Fig. 4; Paper III). The occurrence of *A. viirae* at 318.6 m is here assumed to be a result of contamination as the Mehikoorma section is the only studied succession where *A. viirae* co-occurs with *A. tvaerensis* within the upper range of the latter. Additionally, the full range of *A. superbis* is not determined, as only the lower range of the species is provided.

5. DISCUSSION

The conodont biozonation and the respective correlation of the Sandbian interval in Baltoscandia have been generally unchanged since the publication of Bergström's (1971) paper where he discussed the stratigraphic significance of the Middle and Upper Ordovician conodonts in Europe and Eastern North America. The conodont zones established by him (*P. anserinus*, *A. tvaerensis* and *A. superbus*) are still in use for Baltica (Meidla *et al.*, 2022; Nielsen *et al.*, 2023), Argentine Precordillera (Albanesi and Ortega, 2016) and Avalonia (Bergström and Ferretti, 2018). However, a noticeable change has been made to the proposed conodont subzones in the interval spanning the lower boundary of the Sandbian Stage where the *B. prevariabilis* and *B. variabilis* CSZs established by Bergström (1971) were replaced by the *S. kielcensis* CSZ and *A. inaequalis* CSZ, respectively, by Dzik (1978).

5.1 *Amorphognathus inaequalis* Conodont Subzone in Baltoscandia

The lower boundary of the *A. inaequalis* CSZ has been proposed as the best possible approximation of the lower boundary of the Sandbian Stage in the Baltoscandian and Avalonian regions (Fig. 1A; see Bergström and Ferretti, 2018; Meidla *et al.*, 2022; Nielsen *et al.*, 2023).

The first illustrations of *A. inaequalis* came from Wales (Rhodes, 1953; Ferretti and Bergström, 2022) and West France (Lindström *et al.*, 1974). Later, the species was identified also from Poland (Dzik, 1976), Estonia (Männik, 2003; Männik and Viira, 2005) and Lithuania (Saadre *et al.*, 2004), but none of these papers contains figures of *A. inaequalis*. The recognition of the species in the Baltoscandian sections lent credence to the inclusion of the *A. inaequalis* CSZ in the regional stratigraphic charts (Nölvak *et al.*, 2006; Bergström, 2007 and many subsequent papers). However, *A. inaequalis* has not been found in Swedish sections (Bergström, 2007). Dzik (1976) identified *A. inaequalis* in the Mojca Quarry, Poland, but reassigned the same elements later to *A. tvaerensis* (Dzik, 1994). Viira (2008) suggested that conodonts identified as *A. inaequalis* in Estonia might in reality represent an early morphotype of *A. tvaerensis*.

The Pa elements are most promising for distinguishing *A. inaequalis* from younger species of the genus *Amorphognathus* (Ferretti and Bergström, 2022). The dextral Pa element of *A. inaequalis* (Fig. 7A) has straight posterior and anterior processes (in upper view), whereas those of *A. tvaerensis* (Fig. 7B) demonstrate a slight curvature to outer direction on their posterior processes, resulting in the overall sinusoidal shape of the element. The dextral Pa element of *A. inaequalis* also lacks an extra postero-lateral process on its outer side, however, this is one of the main characteristic features in *A. tvaerensis* (Ferretti and Bergström, 2022).

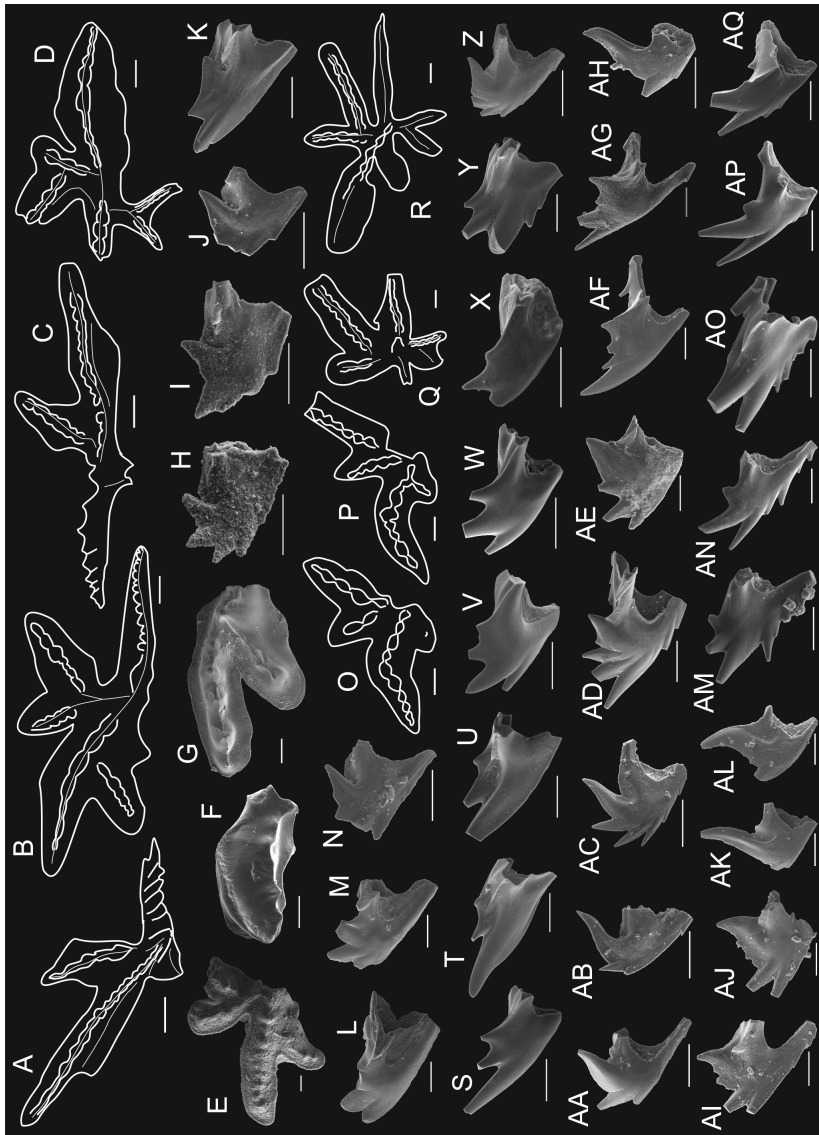


Figure 7. Elements of the genus *Amorphognathus*. **A**, *A. inaequalis* (Rhodes, 1953), outline drawing of dextral Pa element from Lindström *et al.* (1974, pl. 1, fig. 9). **B**, *A. tvaerensis* (Bergström, 1962), outline drawing of dextral Pa element from Bergström (1962, pl. 4, fig. 7). **C**, *A. inaequalis*, outline drawing of sinistral Pa element from Lindström *et al.* (1974, pl. 2, fig. 1). **D**, *A. tvaerensis*, outline drawing of sinistral Pa element from Bergström (1962, pl. 4, fig. 6). **E–N**, *A. tvaerensis*: **E**, dextral Pa element from Paper II; **F**, fragment of posterior process of probable dextral Pa element, from Paper III; **G**, posterior process of dextral Pa element, from Paper III; **H, I**, dextral M elements from Paper III; **J–N**, M elements from Paper III: **J, L, M**, sinistral M elements; **K, N**, dextral M elements. **O–R**, *A. viirae* (Paiste, Männik et Meidla, 2023): **O**, outline drawing of dextral Pa element from Dzik (1994, fig. 22, sample 93); **P, Q**, outline drawings of dextral Pa elements from Dzik (1994, fig. 22, sample 96); **R**, outline drawing of dextral Pa element from Goldman *et al.* (2007, fig. 7: 18). **S–Y**, *A. ventilatus* (Ferretti and Barnes,

1997) M elements from Paper III: **S, V–X**, sinistral elements; **T, U, Y**, dextral elements. **Z–AE**, *A. tvaerensis* M elements from Paper III: **Z**, dextral element; **AA–AE**, sinistral elements; **AD**, dextral element; **AE**, sinistral element. **AF–AL**, *A. viirae* M elements from Paper III: **AF–AH**, sinistral elements; **AI, AJ**, dextral elements; **AK, AL**, sinistral elements. **AM–AQ**, *A. superbis* (Rhodes, 1953) M elements from Paper III: **AM**, dextral element; **AN**, sinistral element; **AO**, dextral element; **AP, AQ**, sinistral elements. All scale bars are 100 µm.

Furthermore, the sinistral Pa element of *A. inaequalis* (Fig. 7C) has a simple inner lateral process and lacks the extra antero-lateral branch that is characteristic of *A. tvaerensis* (Fig. 7D). Additionally, a typical M element of *A. tvaerensis* has a prominent posteriorly directed denticle that has not been observed in M elements of *A. inaequalis* (Ferretti and Bergström, 2022). Still, as all illustrated M elements of *A. inaequalis* are broken (Bergström *et al.*, 1987, pl. 18.1, fig. 10; Ferretti and Bergström, 2022, fig. 9J, K) or shown in only lateral view (Lindström *et al.*, 1974, pl. 2, fig. 7), it is difficult to understand their complete outline.

In Estonia, the *A. inaequalis* CSZ has been identified in the Ruhnu (Männik, 2003) and Mehikoorma (Männik and Viira, 2005) core sections. In order to assess the validity of the identification of the *A. inaequalis* CSZ in the Estonian succession, the collection of conodonts from the Mehikoorma core section was re-investigated (Paper III) and new material from the Velise core was analysed (Paper II). The lowermost Pa element of the genus *Amorphognathus* in the Velise core section (Fig. 4; Paper II) represents morphologically a typical *A. tvaerensis* (Fig. 7E). Similarly, the lowermost dextral Pa elements of *Amorphognathus* in the Mehikoorma section resemble those of *A. tvaerensis*, showing a slight curvature (Fig. 7F, G). Additionally, all M elements from the lowermost part of the *Amorphognathus* range in the Velise (Fig. 7H, I) and Mehikoorma sections (Fig. 7J–N) have a prominent posteriorly directed denticle that is a characteristic feature of a typical M element of *A. tvaerensis*.

Furthermore, *A. inaequalis* was not identified during restudy of collections from numerous Estonian sections (Ruhnu, Kerguta, Taga-Roostoja, Tartu, Valga, Viki – Paper III) although it had been reported earlier from the Ruhnu section (Männik, 2003). Similarly, restudy of collections from the Smedsby Gård and Fjäckå sections showed only the presence of typical *A. tvaerensis* elements (Paper III). The absence of *A. inaequalis* in Swedish sections was confirmed by S. M. Bergström (personal communication, 2021).

It is evident that the *A. inaequalis* CSZ is present in the succession of Avalonia but not on Baltica. The new data suggest the removal of that subzone from the regional stratigraphic schemes. The occurrence of the *A. inaequalis* CSZ in the Bliudziai-150 core section of Lithuania (Stouge *et al.*, 2016) and Kovel-1 section of Ukraine (Saadre *et al.*, 2004) needs to be validated.

5.2 Range of *Amorphognathus tvaerensis* in Baltoscandia

Elements of *A. tvaerensis* are easily recognizable and the species has been reported from numerous sections in Baltoscandia, Avalonia, Laurentia (Bergström, 1971) and Argentine Precordillera (Serra *et al.*, 2015; Fig. 1A). The *A. tvaerensis* CZ *sensu* Bergström, 1971 corresponds to the main part of the Sandbian Stage (Meidla *et al.*, 2022; Nielsen *et al.*, 2023) and supports reliable correlation between all these areas.

Although *A. tvaerensis* is widely known, the morphological variation in elements within the long distribution interval of the species has been poorly studied. This has resulted in the assignment of younger specimens of *A. tvaerensis* to other taxa, e.g., to early *A. superbus* or to *A. aff. ventilatus* Dzik (1994). Additionally, elements from the upper range of *A. tvaerensis* were designated as *A. cf. tvaerensis*, *Amorphognathus* n. sp. and *Amorphognathus* sp. A. by Stouge (1998) in the Tartu succession. Dzik (1999) recognized the so-called ‘late forms’ of *A. tvaerensis*. The variation in the morphology of P and M elements of *A. tvaerensis* has also been noted in some other papers (Dzik, 1990; Viira, 2008; Xu *et al.*, 2010), but no detailed morphological study has been carried out so far.

Detailed study of the conodont collection from the continuous Mehikoorma succession (Fig. 4; Paper III) served as the basis for analysing the evolution and taxonomic composition of the genus *Amorphognathus*. The samples from this section yielded up to several thousands of specimens. Most representative specimens belonging to the species of the genus *Amorphognathus* were sorted by element types and photographed under SEM (Paper III, Supplementary Figures S1–S17) for preparing data for taxonomic and stratigraphic analysis. The obtained figures illustrate the full range of changes in the morphology of *Amorphognathus* elements in the Sandbian and lower Katian.

Within the upper range of *B. gerdae*, *A. tvaerensis* displays a distinct change in the morphology of the dextral Pa element. At this level, the main characteristic of the species (Fig. 6I; Bergström, 1962), the extra postero-lateral process on the outer side of the elements, disappears (Fig. 6R). This change served as a key for distinguishing a new species within the former upper range of *A. tvaerensis*. The new species was named *Amorphognathus viirae*, after the Estonian pioneering conodont specialist Viive Viira (Paper III).

The main diagnosis of *A. viirae* is based on the dextral Pa element (Fig. 6R) that is shaped, in its upper view, as a sinuous curve and possesses bifurcated lateral processes on both sides. Additionally, a small and distinct lateral lobe occurs on the outer side of its posterior process, at the starting point of the sinuous curvature. Along with the distinctive dextral Pa element, the M elements of *A. viirae* can also provide additional criteria for the identification of the species. The prominent posteriorly directed denticle is reclined in M elements of *A. tvaerensis* (Fig. 6M), while in the M element of *A. viirae* its distal part is anteriorly curved or erect (Fig. 6X, W).

In all sections studied (Fig. 1B), the new species appears within the upper range of *B. gerdae*. In sections where *B. gerdae* is missing or where *Amorphognathus* can be identified only at genus level within the *B. gerdae* Subzone, *A. viirae* first appears typically within the lowermost range of *B. alobatus*. The analysis of published figures shows that *A. viirae* evidently occurs also in the Mojeza Quarry, Holy Cross Mountains, Poland (Fig. 7O–Q; Dzik, 1994, fig. 22: samples 93, 96) and in the Black Knob Ridge section, Oklahoma (Fig. 7R; Goldman *et al.*, 2007, fig. 7: 18) sections.

5.3 Morphological variation in M elements of *Amorphognathus*

A detailed succession of M elements of *Amorphognathus* in the Mehikoorma section (Paper III) demonstrates their high morphological variation. Specifically, the number of denticles around the cusp varies. There are also differences in the size of these denticles, in the morphology of the cusp, and the processes may be denticulated or not. All latter morphological variations occur in M elements of *A. tvaerensis* (Fig. 6M; Fig. 7K–N, Z–AE), *A. viirae* (Fig. 6W, X; Fig. 7AF–AL), *A. superbus* (Fig. 6AG, AH; Fig. 7AM–AQ) and *A. ventilatus* (Fig. 7S–Y).

Amorphognathus ventilatus was originally defined on the basis of its M element only (Ferretti and Barnes, 1997). However, Ferretti and Barnes (1997) recorded *A. ventilatus* from the *A. ordovicicus* CZ but the Estonian specimens, described originally as *Holodontus* sp. n. (Viira, 1974, fig. 110), were identified from the older, *A. superbus* CZ, as were the Mehikoorma specimens (Paper III). Besides, no P or S elements of *A. ventilatus* have been found, which could be compared with those of *A. superbus*. Both aspects raise the question of whether the M elements assigned to *A. ventilatus* in Estonian material may simply represent a variety of *A. superbus*. Thus, the zone based on the species (Fig. 2) should also be used with caution. In addition, in the Mehikoorma section (Fig. 4), the first elements of *A. superbus* appear below the first appearance of elements of *A. ventilatus*, being in conflict with the generally accepted succession of conodont zones where the *A. ventilatus* CZ is underlying the *A. superbus* CZ (Fig. 2). However, M elements assigned to *A. ventilatus* occur only in a relatively short interval together with the elements of *A. superbus*, in the lower part of the distribution interval of the latter species and can be used as a useful event marker in the Estonian regional conodont succession. The presence of *A. ventilatus* has been confirmed in the Mehikoorma (291.9–292.9 m), Valga (384.4–385.25 m), Ruhnu (642.05–652.15 m) and Ohesaare (461.95 m, Viira, 1974) sections.

5.4 Key differences between the elements of *Amorphognathus tvaerensis*, *A. viirae* and *A. superbis*

Main morphological characteristics of different elements of *A. tvaerensis*, *A. viirae* and *A. superbis* are shown in Figure 8.

Dextral Pa element. An extra postero-lateral process and a small lateral lobe are present on the outer side of the posterior process of the dextral Pa element of *A. tvaerensis* (Fig. 8A). This extra postero-lateral process is absent on elements of *A. viirae* (Fig. 8B) and both features are missing in *A. superbis* (Fig. 8C). In *A. tvaerensis*, the anterior process of the dextral Pa element is considerably longer than the anterior branch of its inner lateral process (Fig. 8A), while they are almost equal in size in *A. viirae* (Fig. 8B) and the anterior process is clearly shorter in *A. superbis* (Fig. 8C). The main central row of denticles in upper view of the dextral Pa element has a configuration of a sinuous curve in both *A. tvaerensis* (Fig. 8D) and *A. viirae* (Fig. 8E) but is almost straight in *A. superbis*, with its posterior end turned outwards (Fig. 8F).

Sinistral Pa element. The relative length of the anterior branch of the inner lateral process increases from *A. tvaerensis* to *A. superbis* (Fig. 8G–I), similarly to the dextral elements described above.

Dextral Pb element. The inner edge of the posterior process of the dextral Pb element is slightly undulating in *A. tvaerensis* (Fig. 8J) and *A. superbis* (Fig. 8N), but is particularly distinct on elements of *A. viirae* (Fig. 8L). The denticle row on the posterior process of the dextral Pb element is straight in *A. tvaerensis* (Fig. 8K) and *A. superbis* (Fig. 8O), but slightly curved inwards just behind the cusp in *A. viirae* (Fig. 8M). This curvature forms a platform extension on the inner side of the posterior process.

Sinistral Pb element. A narrow basal platform ledge occurs on both anterior and posterior processes of the sinistral Pb element in *A. viirae* (Fig. 8R), while no noticeable outward extensions are present on the sinistral Pb elements in *A. tvaerensis* (Fig. 8P) and *A. superbis* (Fig. 8T). The cusp of the sinistral Pb element of *A. superbis* (Fig. 8U) is of similar size to that of its dextral Pb element (Fig. 8N), but is noticeably smaller in *A. tvaerensis* (Fig. 8Q) and *A. viirae* (Fig. 8S).

M element. The angle between the posterior process and the posterior denticle in the M element increases from 50–75 degrees in *A. tvaerensis* (Fig. 8V, W) to 90–110 degrees in *A. viirae* (Fig. 8X, Y) and is about 130 degrees in *A. superbis* (Fig. 8Z, AA).

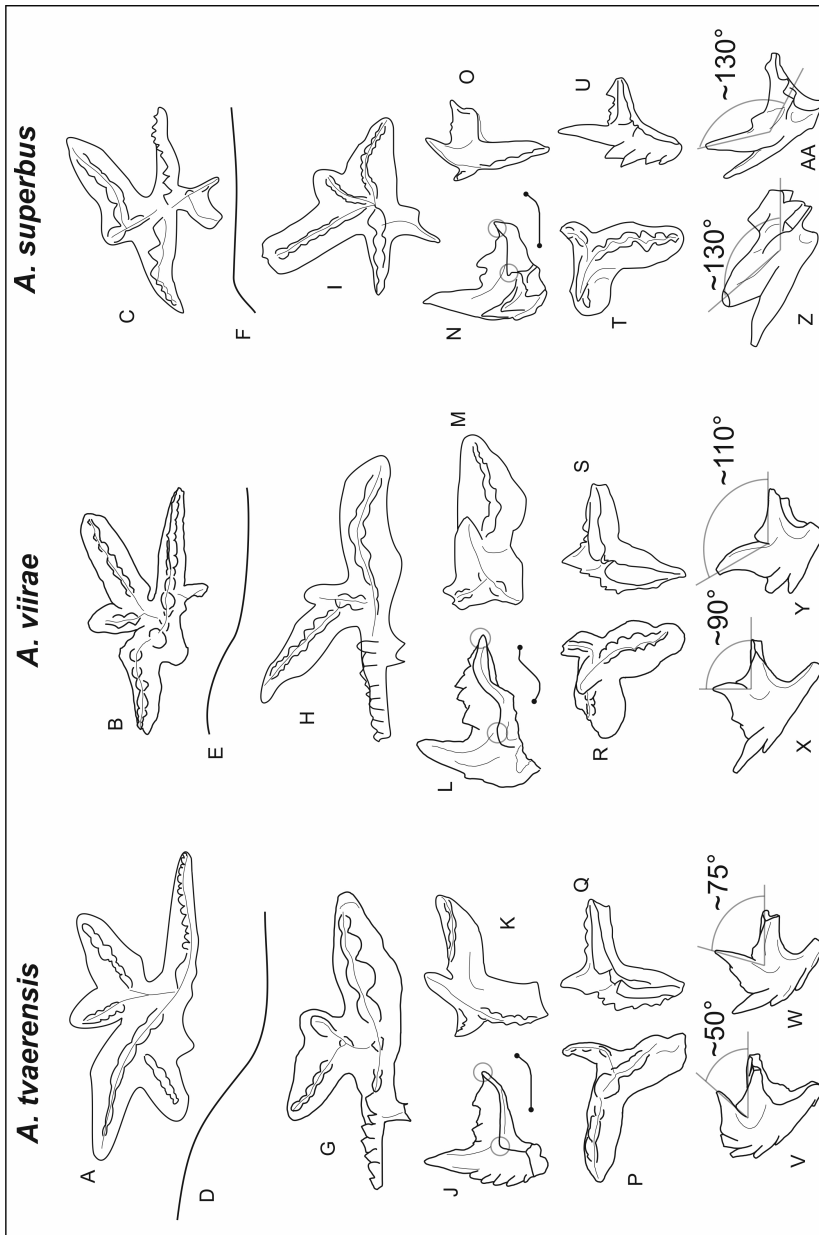


Figure 8. Outline drawings showing main differences between elements of *Amorphognathus tvaerensis*, *A. viirae* and *A. superbus*. Illustrations are based on Paper III if not indicated otherwise. A, G, J, K, P, Q, V, W, *A. tvaerensis* (Bergström, 1962): A, dextral Pa element from Bergström (1962, pl. 4, fig. 7); G, sinistral Pa element; J, K, dextral Pb elements; P, Q, sinistral Pb elements; V, W, sinistral M elements. B, H, L, M, R, S, X, Y, *A. viirae* (Paiste, Männik et Meidla, 2023): B, dextral Pa element; H, sinistral Pa element; L, M, dextral Pb elements; R, S, sinistral Pb elements; X, Y, sinistral M elements. C, I, N, O, T, U, Z, AA, *A. superbus* (Rhodes, 1953): C, dextral Pa element from Bergström (1971, pl. 2, fig. 8); I, sinistral Pa element from Dzik (1976, pl. 28g); N, O, dextral Pb elements; T, U, sinistral Pb elements; Z, AA, dextral and sinistral M elements. D–F indicate the shape of the main central row of denticles on the dextral Pa element in *A. tvaerensis* (D), *A. viirae* (E) and *A. superbus* (F).

5.5 Updated correlation of regional lithostratigraphic units in the Sandbian of Estonia

New conodont data complement earlier correlations of the lithostratigraphic units recognized in the Sandbian interval in Estonia (compare, e.g., Meidla *et al.*, 2014, 2022 and Fig. 9 below). As a result, the following adjustments were made: (1) The lowermost part of the Adze Fm in southern Estonia is younger than the Tatruse Fm; (2) The boundary between the Vão and Kõrgekallas Fms is diachronous in central Estonia – older in the eastern and younger in the western part.

Baltic regional stages	Conodont zones	N Estonia	W-C Estonia	E-C Estonia	N Livonian Basin
Oandu	<i>A. superbus</i>	Hirmuse	Hirmuse	Variku	Mossen
Keila	<i>B. alobatus</i>	Kahula	Kahula	Kahula	Blidene
Haljala	<i>A. viirae</i>	Tatruse	Tatruse	Tatruse	Adze
	<i>B. gerdae</i>				
Kukuruse	<i>A. tvaerensis</i>	Viivikonna	Pihla	Dreimani	Dreimani
	<i>B. variabilis</i>				
Uhaku	<i>P. anserinus</i>	Kõrgekallas	Kõrgekallas	Kõrgekallas	Taurupe
		Vão	Vão	Vão	

Figure 9. Stratigraphy in the Sandbian interval in Estonia. The correlation of the formations in northern Estonia is based on the Peetri outcrop section and the Virunurme, Taga-Roostoja and Kerguta core sections; in west-central Estonia on the Velise and Viki core sections; in east-central Estonia on the Tartu and Mehikoorma core sections; in the northern part of the Livonian Basin on the Valga and Ruhnu core sections.

5.6 Correlation of the Estonian and Swedish sections.

Considering the absence of *A. inaequalis* in Baltoscandia and recognition of the new species *A. viirae*, an improved correlation between regional successions is possible (Fig. 10). The correlation is based on the updated distribution data of the key species *B. variabilis*, *A. tvaerensis*, *B. gerdae*, *A. viirae*, *B. alobatus* and *A. superbus* (Table 1) from the most complete and representative sections of each main facies zone (Fig. 1B).

Baltoniodus variabilis appears in the middle part of the Kõrgekallas Fm in the Estonian Shelf area and in the upper part of the Taurupe Fm in the northern part of the Livonian Basin (Fig. 10). In the Siljan region of the Scandinavian Basin, this level correlates with the lower boundary of the Dalby Limestone. Traditionally, the base of the Dalby Limestone has been correlated with the lower boundaries of the Viivikonna and Dreimani Fms in Estonia (Männik and Meidla, 1994). However, our data suggest that the lower boundary of the Dalby Limestone is younger than the lower boundaries of the Viivikonna and Dreimani Fms in Estonia.

The genus *Amorphognathus*, represented by *A. tvaerensis*, appears in the middle part of the Viivikonna Fm in northern Estonia (Estonian Shelf), in the lower part of the Pihla Fm in west-central Estonia, in the lower part of the Dreimani Fm in the east-central Estonian Shelf and northern part of the Livonian Basin. In the Siljan region of the Scandinavian Basin, *A. tvaerensis* appears in the lower part of the Dalby Limestone. These findings support earlier correlations.

Baltoniodus gerdae appears in the upper part of the Viivikonna Fm in the northern Estonian Shelf, just above the lower boundary of the Tatruse Fm in the west-central Estonian Shelf, in the upper part of the Dreimani Fm in the east-central Estonian Shelf and in the lower part of the Adze Fm in the northern part of the Livonian Basin (Fig. 10). In the Siljan region of the Scandinavian Basin, *B. gerdae* appears in the middle of the Dalby Limestone. The lower boundary of the Adze Fm is younger than that of the Tatruse Fm; they are not coeval as indicated in Meidla *et al.* (2014, 2022).

Amorphognathus viirae appears in the middle part of the Tatruse Fm in the Estonian Shelf area (Fig. 10). In the northern part of the Livonian Basin, it appears in the lower part of the Adze Fm and in the Siljan region of the Scandinavian Basin in the upper part of the Dalby Limestone. The FAD of *A. viirae* adds a new useful biostratigraphic level which agrees with the earlier correlation of these strata.

Baltoniodus alobatus appears in the upper part of the Tatruse Fm in the Estonian Shelf area (Fig. 10). In the northern part of the Livonian Basin, the FAD of *B. alobatus* occurs in the middle part of the Adze Fm and in the Siljan region of the Scandinavian Basin in the upper part of the Dalby Limestone. These data coincide with previous correlations.

Conodonts are rare in the upper part of the Sandbian, particularly in Estonian sections. In the northern and west-central Estonian Shelf area, elements resembling *A. superbus* appear in the Hirmuse Fm (Fig. 10), above the prominent sedimentary hiatus in the succession. The appearance of *A. superbus* along with other typical Katian taxa (e.g., *A. complicatus* Rhodes) is known from the Hirmuse Fm (Männik, 2017). *Amorphognathus superbus* appears in the lower parts of the Variku and Blidene Fms in the east-central Estonian Shelf and the northern part of the Livonian Basin, respectively. In the Siljan region of the Scandinavian Basin, *A. superbus* appears in the lower part of the Skagen Fm. In previous studies, the lower boundary of the *A. superbus* Zone has been marked in a younger interval, above the Skagen Fm in Sweden (Bergström, 2007) and in the formation above the Hirmuse Fm, or in the upper parts of the Variku and Mossen Fms in Estonia (Meidla *et al.*, 2014).

5.7 Updated conodont biozonation, its importance and future applications

Despite rich conodont faunas available, the boundaries of the Sandbian Stage have no good marker in the conodont succession. Based on the data from the Fågelsång section, the stratotype for the base of the Sandbian Stage, the lower boundary of this stage in the conodont succession seems to be drawn within or below the range of *B. variabilis* (Bergström *et al.*, 2000). *Baltoniodus variabilis* has global distribution. In addition to Baltica, it has been reported from Laurentia (Bergström, 1971), Avalonia (Ferretti and Bergström, 2022), Argentine Precordillera (Serra *et al.*, 2015) and South China (Bagnoli and Qi, 2014).

The Sandbian–Katian boundary interval is poor in conodonts in all successions studied. The ranges of *A. viirae* and *A. superbus* are separated by an interval that is barren of *Amorphognathus*. In the stratotype of the lower boundary of the Katian Stage, in the Black Knob Ridge section, the *Amorphognathus* elements just above the Katian boundary have been identified as *Amorphognathus* sp. with probable affiliation to *A. superbus* (Goldman *et al.*, 2007, fig. 7: 15, 16). These illustrated specimens are quite similar to the elements of a typical *A. superbus*, suggesting that at current knowledge the Sandbian–Katian boundary lies near the lower boundary of the *A. superbus* CZ.

An updated zonal scheme for the Sandbian interval in Baltoscandia, based on the results of the restudy and revision of conodont taxonomy, is proposed (Fig. 11). The absence of *A. inaequalis* in the Baltoscandian conodont succession suggests omitting the corresponding subzone from the scheme. It is replaced by the *B. variabilis* CZ. Additionally, the *A. viirae* CZ, corresponding to the upper part of the *B. gerdae* CSZ as identified earlier, is included. The extent of the former *B. gerdae* CSZ is reduced and this unit is used as a conodont zone in the updated scheme. Also, two former subzones of the *A. tvaerensis* CZ are treated in the proposed scheme as zones – the *B. alobatus* CZ corresponding to the interval between the FADs of this species and *A. superbus* and the *B. variabilis* CZ corresponding to the interval of its FAD and that of *A. tvaerensis*.

In summary, the revised conodont zonal scheme proposed for the topmost Darriwilian to lower Katian comprises (from below) the *P. anserinus*, *B. variabilis*, *A. tvaerensis*, *B. gerdae*, *A. viirae*, *B. alobatus* and *A. superbus* CZs (Fig. 11). However, both stratotype sections of the Sandbian and Katian stages lack good biostratigraphic markers in the conodont succession.

System	Series	Stage	Conodont ranges based on studied sections/literature	Nölvak 1997	Nölvak et al. 2006; Meidla et al. 2022	Bergström 2007	Männik et al. 2021	Nielsen et al. 2023	This study			
Ordovician	Upper	Katian	<i>P. anserinus</i> <i>B. variabilis</i> <i>A. tvaerensis</i> <i>B. gerdæ</i> <i>A. viiræ</i> <i>B. alobatus</i> <i>A. superbus</i>	<i>A. superbus</i>	<i>A. ventilatus</i>	<i>A. superbus</i>	Upper <i>A. tvaerensis</i>	<i>A. superbus</i>	<i>A. superbus</i>			
				?	?		?					
				<i>B. alobatus</i>	<i>B. alobatus</i>	<i>B. alobatus</i>	<i>B. alobatus</i>	<i>B. alobatus</i>	<i>B. alobatus</i>	<i>B. alobatus</i>		
				<i>B. gerdæ</i>	<i>B. gerdæ</i>	<i>B. gerdæ</i>	<i>B. gerdæ</i>	<i>B. gerdæ</i>	<i>B. gerdæ</i>	<i>A. viiræ</i> <i>B. gerdæ</i>		
				<i>A. tvaerensis</i>	<i>A. tvaerensis</i>	<i>A. tvaerensis</i>	lower <i>A. tvaerensis</i>	<i>A. tvaerensis</i>	<i>A. tvaerensis</i>			
	Middle	Darrw.			<i>B. variabilis</i>	<i>B. variabilis</i>	<i>B. variabilis</i>	<i>B. variabilis</i>	<i>B. variabilis</i>	<i>A. tvaerensis</i>		
					<i>P. anserinus</i>	<i>P. anserinus</i>	<i>P. anserinus</i>	<i>P. anserinus</i>	<i>P. anserinus</i>	<i>P. anserinus</i>	<i>A. inaequalis</i> <i>B. variabilis</i>	
						<i>A. inaequalis</i>	<i>A. inaequalis</i>	<i>A. inaequalis</i>	<i>A. inaequalis</i>	<i>A. inaequalis</i>		
						<i>S. kielcensis</i>	<i>S. ? kielcensis</i>	<i>S. kielcensis</i>	<i>S. kielcensis</i>	<i>S. kielcensis</i>	<i>S. kielcensis</i>	<i>P. anserinus</i>

Figure 11. The ranges of key conodont species and comparison of the conodont zonation of the topmost Darrwiliian–lower Katian interval in the Baltoscandian region.

6. CONCLUSIONS

1. Detailed restudy of conodont collections from several Estonian and Swedish sections did not confirm the occurrence of *A. inaequalis* in the Baltoscandian succession. Conodonts, earlier identified as *A. inaequalis* in some Estonian sections, represent early forms of *A. tvaerensis*. Previous use of the eponymous Conodont Subzone and correlations based on the assumed presence of *A. inaequalis* in the sections are revised.
2. Conodonts, earlier assigned to *A. tvaerensis* as the youngest representatives of the species, constitute a new species – *A. viirae*. The distribution of *A. viirae* across Baltoscandia has been confirmed by the restudy of collections from different parts of the region and the occurrence of the species adds a new useful datum level in conodont biostratigraphy and correlation.
3. Restudy of *A. superbus* elements allowed us to justify the FAD of this species in the studied Baltoscandian successions to a lower level. Previous correlations of selected sections based on the distribution of *A. superbus* require a revision.
4. The Sandbian conodont zonal scheme in Baltoscandia is revised and a new, updated version is hereby proposed. In the new version of conodont zonation, previous conodont subzones of *B. variabilis*, *B. gerdae* and *B. alobatus* are elevated to the rank of conodont zones, the extent of the *A. tvaerensis* Zone is revised and the new *A. viirae* CZ is added. In summary, the new proposed conodont zonation includes (from below) the *P. anserinus*, *B. variabilis*, *A. tvaerensis*, *B. gerdae*, *A. viirae* and *B. alobatus* CZs.
5. Analysis of conodont ranges shows that the correlation of some Estonian rock units needs to be revised in the correlation chart. The lower boundary of the Adze Fm is older than previously thought and corresponds to levels in the upper parts of the Viivikonna, Pihla and Dreimani Fms. The uppermost part of the Vão Fm is younger in west-central Estonia than in northern or east-central Estonia. The lower boundary of the Dalby Limestone of Sweden correlates with the upper part of the Kõrgekallas and Taurupe Fms, i.e., with older strata than previously assumed.

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SUMMARY IN ESTONIAN

Perekonna *Amorphognathus* varajane evolutsioon
ja Sandby lademe (Ülem-Ordoviitsium) uuendatud
konodondi-biostratigraafia Baltika ürgmandri läbilõigetes

Ajavahemikku 443.8–485.4 miljonit aastat tagasi nimetatakse Ordoviitsiumi ajastuks. Sellest ajastust säilinud kivimkehad moodustavad Ordoviitsiumi ladestu, mis omakorda liigestub seitsmeks globaalseks lademeks. Lademete piirid on määratud teatud graptoliidi- või konodondiliikide esmailmumisega ning need on aluseks ka läbilõigete korreleerimisel. Korrelatsioonidega tegelevat geoloogiat haru nimetatakse stratigraafiaks ning selle peamiseks ülesanneteks on selgitada kivimkehade suhteid ajas ja ruumis. Üheks stratigraafia põhimeetodiks on biostratigraafia, mis tugineb kivimikihtides esinevate fossiilide levikule. Nii graptoliidid kui ka konodondid olid pelaagilised loomad, kuid graptoliidid eelistasid süvaveelisemat keskkonda ning nende fossiile leidub peamiselt süvamere setendites. Eesti ja idapoolse Rootsi Ülem-Ordoviitsiumi läbilõigetes valdavad lubjakivid, mis on moodustunud kunagise Baltoskandia paleobasseini (epikontinentaalne meri, sarnane Põhjamerele) šelfil suhteliselt madalaveelistes tingimustes kuhjunud lubisetetest, milles graptoliidid praktiliselt puuduvad, kuid konodondid on rikkalikult esindatud. Seega karbonaatsete läbilõigete puhul on konodondid kujunenud üheks peamiseks biostratigraafilise korrelatsiooni vahendiks. Konodondiliikide fülogeneesist tulenevad liikide bioloogilised järgnevused on aluseks läbilõigete biotsonaalsetele liigestustele, millel põhineb kivimkehade suhtelise vanuse ja nendevaheliste ajaliste suhete määramine. Globaalne levik, kiire evolutsioon, kõrge arvukus merelistes settekivimites ja vastupidavus geoloogilise aja jooksul ilmnunud mõjutustele on konodontidest teinud ühe peamise biostratigraafia 'tööriista' Vara- ja Kesk-Paleosoikumide läbilõigete liigestamisel.

Konodondid on mikroskoopilised (mõõtmetega valdavalt alla 1–2 mm) biopatiitsed fossiilid, varieeruva väliskujuga hambalaadsed moodustised, mida leidub pea igat tüüpi merelistes setetes alates Kambriumi ladestust kuni Triiase ladestuni. Algselt peeti neid kunagiste kalade lõuaaparaadi osadeks või hammasteks. Täna-seks on leitud ka üksikud looma tervikfossiilid, mis näitavad, et konodontide puhul oli tegemist valdavalt väikeste, mõne kuni mõnekümne sentimeetri pikkuste, väliskujult silmulaadsete, kahe suure silmaga loomakestega, keda peetakse selgroogsete vahetuteks eellasteks. Termin 'konodont' omab kahesugust tähendust. Algselt tähistati sellega üksikelemente, mida kõiki käsitleti ja kirjeldati iseseisvate liikidena. Hiljem, kui selgus, et üksikelementide puhul on tegelikult tegemist ühele organismile kuulunud lõuaaparaati moodustanud osadega (iga aparaat koosnes mitmest morfoloogiliselt erinevast elemendist), hakati terminiga 'konodont' tähistama ka looma kui tervikut. Konodondilooma elemendid jaotatakse P, M ja S elementideks, vastavalt anatoomilisele positsioonile ja lisatähistus (a,b/1,2) määrab järgnevust. Isegi kui konodondilooma täpne kuuluvus loomariigis on siiani mõnevõrra problemaatiline, on tema lõuaaparaadi osad (konodondi

elemendid) mitmele geoloogilisele uurimissuunale, ja eriti biostratigraafiale, hindamatu väärtusega.

Konodondid eksisteerisid ligi 300 miljonit aastat. Selle aja jooksul ilmus ja kadus suurel hulgal erinevaid liike, milledest paljude esmailmumiste põhjal on määratletud mitmeid globaalseid Fanerozoikumi lademeid ja defineeritud vähemalt 240 erinevat biotsooni. Lisaks, konodondi elementide värvus võimaldab tagantjärele hinnata kivimkehi mõjutanud temperatuuri ning see teadmine on kasutatav naftaotsingutel. Elemente moodustava bioapatiidi geokeemilised analüüsid aitavad meil selgitada paleokeskkonnas valitsenud tingimusi ja konodontide laialdane levik ning kiire evolutsioon võimaldavad analüüsida paleoökoloogilisi ja paleogeograafilisi muutusi minevikus.

Ülem-Ordoviitsiumi kõige alumise osa moodustab Sandby lade, mille alumine piir on määratud graptoliidi *Nemagraptus gracilis* esmailmumise järgi ning vastab seega samanimelise biotsooni alumisele piirile. Sandby lademel lasub Katy lade, mille alumine piir on määratud graptoliidi *Diplacanthograptus caudatus* ilmumisega. Sandby ja Katy lademetes piirid on püsitatud vastavalt läänepoolse Roots ja Oklahoma süvameresetetega paljandites. Sandby lademe stratotüüpses paljandis paikneb lademe piir konodondi *Pygodus anserinus* biotsooni sees, allpool konodontide *Baltoniodus variabilis* and *Amorphognathus tvaerensis* esmailmumise tasemeid. Traditsiooniliselt on pea kogu Sandby lade konodontide järjes- tuses loetud vastavaks liigi *A. tvaerensis* biotsoonile.

Sandby eal paiknes Baltoskandia paleobassein subtroopilistel-troopilistel laius- kraadidel (~30 S), Baltika ürgmandri läänepoolses osas, süvenedes edela suunas ja olles avatud ookeani. Sandby eal settisid Baltoskandia paleobasseinis erineva savikusastmega karbonaatsed mudad, mida tänapäeval näeme mitmesuguse koostisega lubjakividena. Põhja Eestis on Sandby lade esindatud madalveelist päritolu šelfilubjakividega. Lõuna-Eestis ning Läti ja Leedu läänepoolseimates osades, Kirde-Poolas ja Ida-Rootsis valdavad savikad lubjakivid ja merglid, mis ladestusid šelfi sügavamas osas. Loode-Poolas ja Lääne-Rootsis, kunagisele avaookeanile lähemal, levivad kiltjad savikivimid.

Ordoviitsiumi konodontide teadusliku uurimise ajalugu Eestis hõlmab rohkem kui 50-aastast perioodi. Uuringute käigus on kinnitust saanud Ordoviitsiumi läbilõigete konodontidel põhinev biotsonaalne liigestus. Täpne ja usaldusväärne biostratigraafia omab otsest mõju geoloogiliste tööde stratigraafilise raamistiku koostamisele ja geoloogiliste uuringute käigus vajalikule lokaalsele ja globaalsele korrelatsioonile, need mõlemad on aga omakorda olulised geoloogiliste kaartide koostamisel.

Seni on arvatud, et Sandby lademe alumine piir asub liigi *A. inaequalis* biotsooni alumise piiri vahetus läheduses või langeb sellega kokku. Lisaks, Sandby lademe ülemises pooles on säilinud konodonte vähe, mis raskendab oluliselt nende kihtide dateerimist ja korrelatsioone. Tinglikult on see intervall varem arvatud liigi *A. tvaerensis* biotsooni koosseisu, ehkki liigi *A. tvaerensis* esinemine siin on küsitav. Käesolev väitekiri baseerub Baltoskandia läbilõigete Sandby lademes esineva konodondifauna detailsele analüüsile, eesmärgiga täpsustada fauna taksonoomilist koosseisu, arengu seaduspärasusi ja intervalli biotsonaalset

liigestust. Töö peamiseks eesmärgideks oli perekonna *Amorphognathus* arengu ja leviku täpsustamine Baltoskandia läbilõigetes ning, vastavalt eelneva tulemustele, konodondi-biotsoonaalsuse ja Sandby-ealiste läbilõigete regionaalsete ja globaalsete korrelatsioonide täpsustamine. Hüpoteesi kohaselt eeldasime konodondiliigi *A. inaequalis* puudumist Baltoscandia läbilõigetes ja liigi *A. tvaerensis* jagunemist mitmeks liigiks.

Käesoleva uurimustöö koostamisel kasutati esmajärjekorras materjali kolmest Eesti läbilõikest: Peetri paljandist Harju maakonnas, Velise puursüdamikust Rapla maakonnas ja Mehikoorma puursüdamikust Põlva maakonnas, kuid täiendavalt analüüsi ka varasemat andmestikku mitmest Eesti läbilõikest (Kerguta, Ruhnu, Taga-Roostoja, Tartu, Valga, Viki, Virunurme) ja Rootsist (Fjäcka, Smedsby Gård).

Konodontidel põhinev biotsoonaalne liigestus on püsinud Baltoskandia regioonis praktiliselt muutumatuna 50 aastat. Siiani on seda tsoonaalsust edukalt kasutatud nii Baltika, Argentiina Precordillera, Avaloonia kui ka Laurentia ürgmandri läbilõigete korreleerimisel. Baltika ja Avaloonia korrelatsiooniskeemidel vastab Sandby lademe alumine piir liigi *A. inaequalis* biotsooni alumisele piirile või asub selle vahetus läheduses, kuigi *A. inaequalis* on seni kindlalt määratud ainult Avaloonia läbilõigetest. Kontrollimaks liigi *A. inaequalis* esinemist Baltika läbilõigetes ja sellele baseeruva biotsoonaalsuse kasutatavust, kontrollisin selle olemasolu kõigis neis Eesti läbilõigetes, milles antud liiki on varem määratud. Töö tulemusena selgus, et liigi *A. inaequalis* esinemist ei olnud võimalik tuvastada ühestki uuritud läbilõikes. Konodondi *A. inaequalis* tõenäolist puudumist Baltoskandia regioonis kinnitas ka Rootsi läbilõigetega tegelenud ning hiljuti antud liigi kohta spetsiaalse uuringu avaldanud S. M. Bergström, Baltoskandia esimese konodondi-biotsoonaalsuse autor (suuline teave, 25.–28.10.2021).

Laia levikuga *A. tvaerensis* on määratud nii Baltika, Avaloonia, Laurentia kui ka Precordillera ürgmandrite läbilõigetes. Liigi pika eksisteerimisaja jooksul toimus selle elementide morfoloogias märgatavaid muutusi ning sellest tingitult on liigi levikut käsitletud mitmeti. Konodonte, mida ühed autorid on lugenud liigi *A. tvaerensis* hilisteks esindajateks, on teised autorid kirjeldanud kui mõnda muud liiki või siis nimetanud liigi *A. tvaerensis* varieteetideks. Ehkki muutusi liigi elementide morfoloogias on sageli täheldatud, ei ole nende detailsemat uuringut seni läbi viidud. Kirjeldamiseks liigisisest variatsiooni ja elementide morfoloogilise arengu üldisi suundumusi, fikseerisin perekonna *Amorphognathus* varajaste esindajate detailse uuringu käigus skaneeriva elektronmikroskoobi fotodel kõik elementide morfoloogias toimunud muutused. Erinevatest läbilõigetest pärinevate andmete detailsel võrdlemisel õnnestus kindlaks teha, et Sandby ea vältel toimunud evolutsioonilised muutused liigi *A. tvaerensis* morfoloogias olid sarnased kogu Baltoskandia regiooni haaravas settebasseinis. Oluline muutus seni liigi *A. tvaerensis* määratud Pa elemendi morfoloogias toimub *Baltoniodus gerdae* biotsoonis, kus kaob iseloomulik elemendi tagajätke välisküljel asunud lisajätke, üks peamisi liigi tunnuseid. See markeerib juba uue liigi, *Amorphognathus viirae* ilmumist. See liik on nimetatud Eestis konodontide uuringutele aluse pannud spetsialisti Viive Viira auks. Uus liik esineb kõigis varem uuritud läbilõigetes nii

Eestis kui ka Rootsis ning selle ilmumine kui biostratigraafiline marker võimaldab täpsustada läbilõigete korrelatsioone kogu Baltoskandia regioonis.

Perekonna *Amorphognathus* varajase evolutsioonilise arengu detailne uuring täiendas ka meie arusaamu noorema liigi *A. superbis* kohta. Kuigi liigi holotüüp on lõuaaparaadi Pa element, on liigi kirjeldamisel lähtunud eelkõige M elemendist ning ka Pb elemendil on mitmeid iseloomulikke tunnuseid. Uued teadmised võimaldavad täpsustada liigi *A. superbis* leviku intervalli, samanimelise biotsooni mahtu ja liigi levikul põhinevaid korrelatsioone.

Perekonna *Amorphognathus* varajaste esindajate taksonoomiliste uuringute tulemused võimaldavad täiendada seni Baltoskandia regioonis kasutuses olnud Sandby lademe biotsonaalset skeemi. Uus, täpsustatud, kogu Sandby ladet hõlmav biotsonaalne skeem koosneb järgmistest biotsoonidest (alates vanematest): *P. anserinus*, *B. variabilis*, *A. tvaerensis*, *B. gerdae*, *A. viirae*, *B. alobatus*. Ehkki kunagise Baltika ürgmandri läbilõiked sisaldavad rikkalikult hästi säilinud konodonte, mis loob head eeldused nende kasutamiseks detailsetel korrelatsioonidel ja taksonoomilistel uuringutel, on Sandby ja Katy lademe stratotüüpsetes paljandites, ja just lademete piiri-intervallides, konodontide levik katkendlik ning see ei võimalda lademepiiride asendi täpset määratlemist konodontide järgi.

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Publications:

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