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Lower Ordovician (Billingenian - Kunda) conodont zonation and provinces based on sections from Horns Udde, north Öland, Sweden

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ABSTRACT – The Hunnebergian to Kunda conodont succession of the lower Ordovician Orthoceras Limestone on northern Öland, Sweden is described. The faunal succession is based on 57563 conodont elements recorded from two representative sections: North of Horns Udde and Horns Udde quarry. The new data allow the recognition and definition of 10 successive interval zones, each characterized by a nominate species and a distinctive conodont association. The interval zones are recommended to substitute the previous assemblage zones in future references to the conodonts of the Öland region. The interval zones are compared with earlier and corresponding zones of the lower Ordovician in neighbouring areas. The interval zones provide an alternative reference to former formally established zones as precise correlation across the East European Platform is possible.

The fauna changed from cosmopolitan in Billingen time to provincial in Volkhov time. The fauna assemblages changed from Pandemic forms to temperate water (Precordilleran) faunas and finally were replaced by cold water (Baltic Province) conodonts of the North Atlantic Realm. The Baltic Province persisted throughout the lower Ordovician on the East European Platform. The change of fauna from Pandemic to provincial is connected with sea level changes and a shallowing of the shelf environs.

One new multielement genus is recognized: *Lundodus*; one multielement genus has been revived: *Gothodus* Lindström, 1955, and two multielement genera are revised: *Lenodus* Sergeeva, 1963 and *Trapezognathus* Lindström, 1955. Four new species are named: *Parapanderodus quietus*, *Protopanderodus floridus*, *Protopanderodus calceatus*, and *Scolopodus princeps*, and 20 species are reported but not formally named because they are of low occurrences but with a known apparatus structure and because the number of specimens available was not adequate for their definition.

RIASSUNTO – [Biozonazione a conodonti e province dell'Ordoviciano inferiore sulla base delle sezioni di Horns Udde, Öland settentrionale, Svezia] – Viene descritta la successione a conodonti dall'Hunnebergian al Kunda dei calcari a *Orthoceras* della parte settentrionale dell'Isola di Öland. Sono stati esaminati 57.563 conodonti provenienti da due sezioni rappresentative: la sezione a Nord di Horns Udde e la sezione della cava di Horns Udde. I nuovi dati emersi permettono di individuare e definire 10 successive biozone di intervallo, ciascuna caratterizzata dalla specie nominale e da una particolare associazione a conodonti. Le biozone a conodonti di intervallo qui introdotte vanno a sostituire le precedenti biozone di associazione per la regione di Öland. Le biozone di intervallo vengono paragonate con le corrispondenti zone dell'Ordoviciano inferiore istituite precedentemente in aree vicine. Queste biozone di intervallo offrono il vantaggio di consentire precise correlazioni attraverso la Piattaforma Est Europea.

La fauna, cosmopolita nel Billingen, diventa provinciale nel Volkhov. Le associazioni faunistiche a conodonti cambiano da forme pandemiche a faune di acque temperate (Provincia della Precordigliera) che vengono successivamente sostituite da faune di acque freddo-temperate (Provincia Baltica) del Reame Nord Atlantico. La Provincia Baltica persiste per tutto l'Ordoviciano inferiore sulla Piattaforma Est Europea. Il cambiamento di fauna da Pandemica a provinciale è connesso con variazioni del livello del mare e con un abbassamento del livello del mare sulla piattaforma.

Viene istituito un nuovo genere a più elementi: *Lundodus*; un genere è stato emendato in termini di tassonomia a più elementi: *Gothodus* Lindström, 1955; *Lenodus* Sergeeva, 1963, and *Trapezognathus* Lindström, 1955 vengono ridefiniti. Sono state istituite 4 nuove specie: *Parapanderodus quietus*, *Protopanderodus floridus*, *Protopanderodus calceatus*, e *Scolopodus princeps*. 20 taxa sono riportati informalmente perché rinvenuti in numero esiguo o perché gli esemplari non consentono una precisa determinazione.

INTRODUCTION

Öland, Sweden, is situated in the western Baltic Sea and is a flat, narrow and long island (Text-fig. 1). It is the key area for the understanding of the lower Ordovician stratigraphy of the East European Platform, northwest Europe (Stouge *et al.*, 1995) and it gives the name to the lower Ordovician Oeland Series of the Baltoscandian chronostratigraphical system (Männil & Meidla, 1994; Stouge *et al.*, 1995).

This study was undertaken for the purposes of establishing conodont faunal zones, correlating measured sections, discussing the provincial af-

finities of the fauna and describing the conodont taxa of the Billingenian Substage through Volkhov Stage in northern Öland, Sweden (Text-fig. 2). Two stratigraphic sections are documented and are designated North of Horns Udde Section and the Horns Udde quarry Section (Text-figs. 3, 4). Each section was measured, described and sampled for microfossils. Selection was based primarily on completeness of exposure and geographic location, and secondarily on data available from former studies (Tjernvik, 1956; Lindström, 1963; van Wamel, 1974; Bagnoli *et al.*, 1988; Nordlund, 1988; Stouge & Bagnoli, 1990). Numerous sections in nearby sea cliffs, active and abandoned quarries and elevated

seacliffs were also studied to obtain an understanding of regional stratigraphic relationships.

PREVIOUS WORK

The well-preserved rocks on Öland form a natural and lateral extension of the East Baltic exposures farther to the East-Northeast. The strata are very rich in fossils and the history of palaeontological research dates back at least 250 years when Linnaeus (1745), during his studies in natural science, noted the abundance of trilobites and cephalopods from the island. Later, the knowledge expanded during geological investigations by Wiman (1807), Holm (1882), Tullberg (1882), Moberg (1890), Anderson (1893), Regnéll (1942), Westergård (1944, 1947), Hadding (1927, 1932, 1958),

Bohlin (1949, 1955), Hessland (1955), Tjernvik (1956), Skevington (1963, 1965) and Jaanusson (1957, 1960a, b) creating the basis for the stratigraphy that is used today (Fig. 2) (van Wamel, 1974; Jaanusson & Mutvei, 1982; Stouge & Bagnoli, 1990; Stouge *et al.*, 1995).

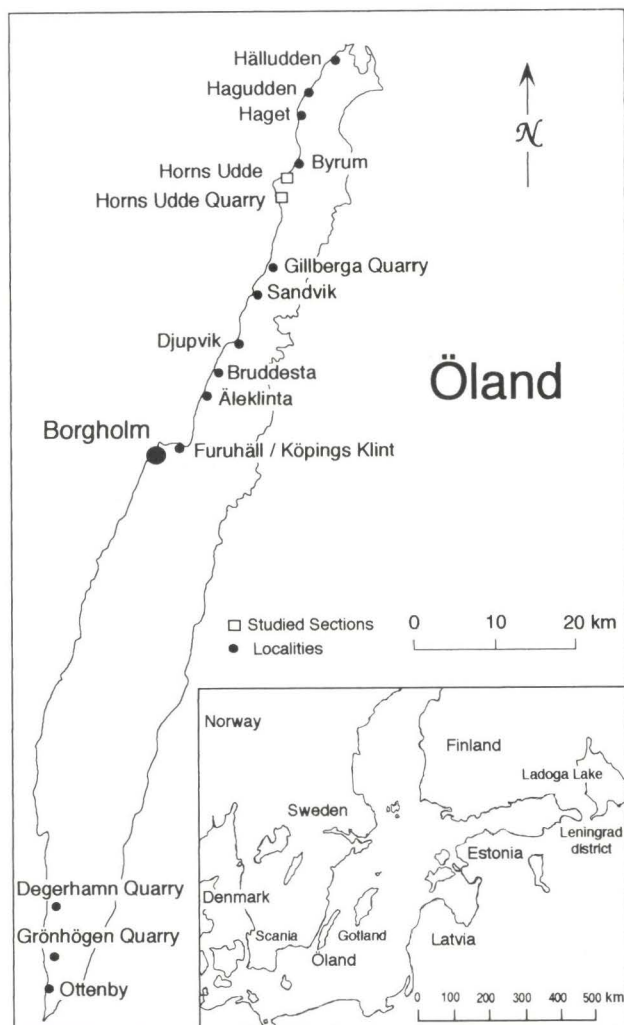
On the island, trilobites are the most common and abundantly represented among the macrofossils. Cephalopods are prominently represented in the rocks and may cover whole bedding planes at certain intervals (Grahn, 1986). Systematic taxonomical work on the different fossil groups (Bohlin, 1955; Tjernvik, 1956; Jaanusson, 1957; Whittington & Bohlin, 1960) has not been completed and work is still in progress (Jaanusson & Mutvei, 1982). Recently, the sediments and allochems have been investigated by van Wamel (1974) and Nordlund (1988) and several fossil groups (Echinodermata, Gastropoda and Brachiopoda) make up the sediments. Graptolites occur in specific horizons (Holm, 1882; Moberg, 1890) and have been described by Bulman (1936), Jaanusson (1960a), and Skevington (1963, 1965).

Among the organic walled microfossils, acritarchs, chitinozoans and tasmanites were first described from northern Öland by Eisenack (1976). The lower Ordovician chitinozoans succession of Öland has been outlined by Grahn (1980, 1982). Recently systematic work and descriptions of the acritarchs have begun (Bagnoli *et al.*, 1988; Paalits, 1994; Ribecai & Tongiorgi, 1994; Playford *et al.*, 1995) and are in progress (Ribecai, in prep.).

Conodonts are abundant in the rocks and modern systematic descriptions have been published by van Wamel (1974), Bagnoli *et al.* (1988) and Stouge & Bagnoli (1990). Earlier, Lindström (1960, 1963, 1971, 1984a, b) included data from the region and additional information from the island appeared in papers by Dzik (1983) and Löfgren (1978, 1990, 1994, 1995).

PURPOSE OF THIS PAPER

The description of the lower Ordovician conodonts from the region by van Wamel (1974) created uncertainties in the understanding of the lower Ordovician stratigraphy on Öland. The uncertainties are due to different interpretations of many taxa and so correlation with other regions became unclear. The work of van Wamel (1974) deviated, especially on the species level, from that of other specialists working on conodonts from north-western Europe (Lindström, 1971; Dzik, 1976, 1994; Löfgren, 1978; Bagnoli *et al.*, 1988; Stouge & Bagnoli, 1990; Rasmussen, 1991).



Text-fig. 1 - Location map.

GREAT BRITAIN STANDARD			BALTO-SCANDIAN REGIONAL STANDARD			
SERIES	GRAPTOLITES		SERIES	STAGE	SUBSTAGE	TRILOBITES
LLANVIRN	<i>Didymograptus artus</i>		O E L A N D	K U N D A	Aluojan	<i>Megistaspis gigas</i> <i>Megistaspis obtusicauda</i>
					Valastean	<i>Asaphus "raniceps"</i>
ARENIG	<i>Didymograptus extensus</i>	<i>Isograptus gibberulus</i>			Hunderumian	<i>Asaphus expansus</i>
				V O L K H O V	Langevojan	<i>Megistaspis (M.) limbata</i>
						<i>Megistaspis (M.) simon</i>
		<i>Didymograptus nitidus</i>			<i>Megistaspis (M.) polyphemus</i>	
				L A T O R P	Billingenian	<i>Megistaspis (V.) estonica</i>
						<i>Megistaspis (M.) dalecarlicus</i>
		<i>Megistaspis (V.) aff. estonica</i>				
		<i>Didymograptus deflexus</i>			<i>Megistaspis (V.) planilimbata</i>	
				<i>T. phyllograptoides</i> <i>T. approximatus</i>	Hunnebergian	<i>Megistaspis (E.) armata</i>
TREMADOC						

Text-fig. 2 - Lower Ordovician chronostratigraphic nomenclature of the Baltoscandian region. The British Chronostratigraphy is from Fortey *et al.*, 1995.

Van Wamel (1974) also established a formal and detailed biozonation system for northern Öland which has not been widely applied, because 1) the recognition of the nominate species was difficult and 2) the biozonation was very detailed in certain intervals. Van Wamel's (1974) biozonation has been interpreted «to be too much influenced by local conditions» (Löfgren, 1978) or to reflect the general faunal succession within a zone (Bagnoli *et al.*, 1988). Whatever the reason, van Wamel's biozones have not been used for correlation over long distances within the Baltoscandian region (Bagnoli *et al.*, 1988; Löfgren, 1994).

The failure in recognition of the detailed zonal system promoted by van Wamel (1974) is probably

due to 1) the lack of comparative detailed work, 2) lateral facies and faunal changes and 3) locally developed hiatuses or 4) a combination of the three. The purpose of this paper is:

1) to describe the conodont succession at North of Horns Udde and Horns Udde Quarry, northern Öland.

2) to revise, where needed, the conodont taxonomy given in van Wamel (1974).

3) to describe the conodont succession from the strata which follow stratigraphically above the sediments described by van Wamel (1974) in the section North of Horns Udde and Horns Udde Quarry.

4) to establish a conodont zonation system that

is valid for the Öland region through the middle and upper part of the Arenig Series.

5) to comment on the provincial affinities of the conodont fauna in the Billingen-Volkhov-Kunda time.

STRATIGRAPHY

CHRONOSTRATIGRAPHY

The regional chronostratigraphy of the Baltoscandian Region has been updated most recently by Männil & Meidla (1994) and reviewed by Stouge *et al.* (1995) and Nielsen (1995). The nomenclature of the series, stages and substages, which are used in this paper is given in Text-fig. 2, where the Chronostratigraphical System of Great Britain (Forrey *et al.*, 1995) is given as a reference.

LITHOSTRATIGRAPHY

The oldest exposed strata on Öland are green siltstones and sandstones of the Middle Cambrian File Haidar Formation (formerly the «Tessini» Sandstone). These are overlain by the Middle and Upper Cambrian to lower Ordovician black shales of the Alum Shale Group (Vejbæk *et al.*, 1994) on southern Öland (Westergård, 1944, 1947). The coeval strata of the Alum Shale Group are either developed as interbedded shales, glauconite sands and limestone lenses or are missing on northern Öland. The strata are referred to the Djupvik Formation following van Wamel (1974). The Cambro-Ordovician System boundary is not preserved on the island and the interval is developed as an extensive hiatus. The hiatus becomes larger towards the North, where the Upper Cambrian is represented by an *Agnostus pisiformis*-bearing conglomerate and the lower Ordovician is recognized by the presence of thin *Dictyonema*-bearing shale of alum shale facies or by the Obolus conglomerate of the Tremadoc. In the late Tremadoc the clastic input diminished and consistent carbonate accumulation of the Orthoceras Limestone started and persisted throughout the lower and into the middle Ordovician on Öland (Moberg, 1890; Jaanusson & Mutvei, 1982; Stouge *et al.*, 1995). The Orthoceras Limestone is a condensed carbonate sequence – usually developed as upwards coarsening units – that was deposited under temperate to cold water conditions and in shallow to deep water environments on the shelf.

Formations investigated in this study include the Köpingsklint Formation (*pars*), Bruddesta Formation, Horns Udde Formation all established by van Wamel (1974) and the informal (allo-) formations A and B (*pars*) of Stouge & Bagnoli (1990).

- Köpingsklint Formation

The Köpingsklint Formation named and described by van Wamel (1974) is characterized by interbedded glauconite sands and glauconitic limestones. The lateral variation of single beds within the formation is remarkable and characteristic. The thickness of the unit varies from 0,20 m to 1,60 m on Öland.

One lithologic unit within the formation – the Ceratopyge Limestone – is a marker horizon which can be recognized from many sections on Öland, but it is missing in northern localities (Bohlin, 1955; Tjernvik, 1956; Tullberg, 1882; Jaanusson & Mutvei, 1982).

The formation spans the interval from the upper Tremadoc to the lower Arenig comprising the *Apatokephalus serratus*, *Plesiomegalaspis armata*, *Plesiomegalaspis planilimbata* trilobite Zones and the *Megistaspis* (V.) aff. *estonica* informal zone of the so-called «Transition Beds» (*sensu* Tjernvik in Tjernvik & Johansson, 1980) (Bagnoli *et al.*, 1988) (Text-fig. 2). The first zone is referred to the regional Ceratopyge Stage (Moberg, 1890); the next two zones are from the Hunnebergian Substage of the Latorp Stage and the informal zone comprising the «Transition Beds» is contained either in the Hunnebergian Substage (Bagnoli *et al.*, 1988; Lindholm, 1991) or the basal Billingenian Substage of the Latorp Stage (Tjernvik & Johansson, 1980; Löfgren, 1994).

- Bruddesta Formation

The beds included in the Bruddesta Formation were earlier named (upper) Planilimbata Limestone and lower Limbata Limestone by Moberg (1890, and workers after him) and subsequently named by van Wamel (1974) from exposures near Bruddesta (Text-fig. 1). It consists of interbedded limestones, marls and marly shales. The formation is persistent over the whole island with a thickness that decreases towards the Southwest (from 4,60 m in the North to 1,60 m in the South).

A series of two to four amphora-shaped hard (or firm-) grounds (locally known as «Blommiga Bladet» = the «Flowery Sheet») are developed within the formation and locally are used as marker horizons. They can be traced from Byxelkrok in the North to Ottenby in the South, but the hard (or firm-) grounds are less prominent in the southern region. The hard (or firm-) grounds represent a shallowing event of regional importance.

The sedimentary folds described by Lindström (1963), probably representing slumped beds, are common in the lower half of the formation. The

folds can be recognized in most sections of Öland, where this part of the formation is exposed.

The Bruddesta Formation comprises the *Megalaspides* (*M.*) *dalecarlicus* and *M.* (*V.*) *estonica* trilobite Zones of the Billingenian Substage of the Latorp Stage and the *Megistaspis* (*M.*) *polyphemus* (formerly *lata*; see Nielsen, 1995) trilobite Zone of the Lower Volkhov Stage (Tjernvik, 1956).

- Horns Udde Formation

Van Wamel (1974) named the Horns Udde Formation after Horns Udde (Text-fig. 1). It conformably overlies the Bruddesta Formation. This unit is multi-colored varying from gray to green to violet and yellow. It is a bedded fossiliferous lime mudstone with abundant closely spaced discontinuity surfaces most of which are developed as load pressure surfaces or stylolites. The Horns Udde Formation is present throughout the studied area and it ranges in thickness from 1,60 m at the type section to 1,00 m at Degerhamn to the South, generally thinning out toward the South and East.

Some of the bedding surfaces within the formation are hematite impregnated and they have a strongly red appearance in outcrop. Limonitic impregnation of the surfaces in the formation is common giving an aspect of yellow stringers. Three closely spaced surfaces are present near the base of the formation in the region and they are known as «Blodläget» (= the «Bloody Layer» by local quarry men; Bohlin, 1949). The «Bloody Layer» beds are diagenetically formed and can be traced laterally for some distance. The «Bloody layers» can not safely be applied as long distance stratigraphical markers without biostratigraphical control, because haematite diagenetic surfaces can be found at different stratigraphic levels (Stouge & Bagnoli, 1990).

The Horns Udde Formation probably comprises the top of the *Megistaspis polyphemus* Zone and the *Megistaspis simon* trilobite Zone of the Volkhov Stage, but the precise position of the zonal boundaries have not been worked out (Stouge & Bagnoli, 1990; Stouge *et al.*, 1995).

- Formations A and B

The Horns Udde Formation is overlain by green to gray glauconitic limestones, glauconite sand and minor shale. The beds are highly bioturbated and phosphatic burrows are common (Nordlund, 1988) and ooids are well displayed (Bohlin, 1955; Stureson, 1986, 1988). The units are developed as cyclic upwards coarsening sequences varying from

0.20 to 0.40 m in thickness. Each cycle concludes with a discontinuity surface or hardground.

Holm (1882) named the generally green limestones Vaginatum Limestone using the terminology of the east Baltic Sequence (Schmidt, 1881; Männil & Meidla, 1994). Later Bohlin (1949) referred the whole unit to the Asaphus Limestone. Stouge & Bagnoli (1990) informally distinguished the green limestones into two lithologically distinct units, formations A and B, which were considered as alloformations.

The limestones are exposed in several quarries on the island. A complete exposure, more than 5 m thick, of both units is displayed in the walls in the Gillberga Quarry (Text-fig. 1). Toward the South the beds of the unit change in colour from green to beige and red. It is a characteristic unit with glauconite and ooids disappearing in the southern region of the island.

The beds comprise the *Megistaspis limbata* Zone (which includes the *Asaphus lepidurus* trilobite Zone of Bohlin, 1949) (Jaanusson, 1960a; Tjernvik in Tjernvik & Johansson, 1980) of the Upper Volkhov Stage and the *Asaphus expansus* Zone (with an extension perhaps into the *A. «raniceps»* trilobite Zones) of the Kundan Stage (Jaanusson & Mutvei, 1982; Stouge *et al.*, 1995).

The unit is very rich in organic walled fossils including graptolites (Skevington, 1963, 1965), acritarchs (Ribecai & Tongiorgi, 1994; Playford *et al.*, 1995), tasmanites and chitinozoans (Eisenack, 1976; Grahn, 1980, 1982).

Overlying and younger strata are present on the island. These younger formations are not the topic of this paper and the stratigraphy of the younger strata is given in Bohlin (1949), Jaanusson (1960a) and summarized by Jaanusson & Mutvei (1982) and for the Kunda sequence by Stouge *et al.* (1995).

LOCATIONS

Twelve sections have been and are being investigated on Öland. These are Hälludden, Haget, Hagudden, Byrum, North of Horns Udde, Horns Udde, Gillberga, Sandvik and Köpingsklint on northern Öland. On southern Öland, the quarries at Grönhögen and Degerhamn and the seacliffs at Ottenby (Text-fig. 1) support the presentation. These investigations have either been published (van Wamel, 1974; Lindström, 1984b; Bagnoli *et al.*, 1988; Stouge & Bagnoli, 1990; Löfgren, 1995) or are in process of being published. In this paper we present the details from two sections near and at Horns Udde.

Horns Udde is situated on the northwest coast of

Öland which is 20 km South of the northern tip of the island or 5 km South of Byrum (Text-fig. 1). The rocks are well displayed along the seashore and in coastal cliffs North of Horns Udde and in active quarries on the Horns Udde itself:

1) Section North of Horns Udde (Text-figs. 1, 3).

This section is the same as Section 14 of van Wamel (1974).

The locality has been investigated and described in detail by numerous authors (Holm, 1882; Hadding, 1927, 1958; Tjernvik, 1956; Lindström, 1963; van Wamel, 1974; Nordlund, 1988) and depicted by Stureson (1986) and Playford *et al.* (1995). The long history of research on this section classifies the section as «a classical locality» in the lower Ordovician stratigraphy of Baltoscandia. The beds of formation A and B (*sensu* Stouge & Bagnoli, 1990), however, have not been biostratigraphically documented previously. The section and the shore are part of a natural reserve.

The exposed sequence begins with the Middle Cambrian sandstones of the File Haidar Formation and extends into the Volkhov limestones of formation A (lower Ordovician). The Middle Cambrian sediments are exposed on the sea bottom and are occasionally accessible in the beachzone. The succeeding interval starting from the base of the Djupvik Formation and ranging into formation A is exposed in the beachzone and in the coastal cliffs. In total, the measured sequence is approximately 9.5 m thick (Text-fig. 3). In all, 55 samples (labelled HU, after Horns Udde) have been investigated from this section yielding a total of 39545 conodont elements (Tab. 1).

Succession – The base of the Djupvik Formation is used as reference for the measured section (= 0 m). The measurements are given in precise values, but a plus/minus of maximum 0.05 m is considered realistic.

Cumulative values:

0.00 - 0.60 m Djupvik Formation (≈ 0.60 m).

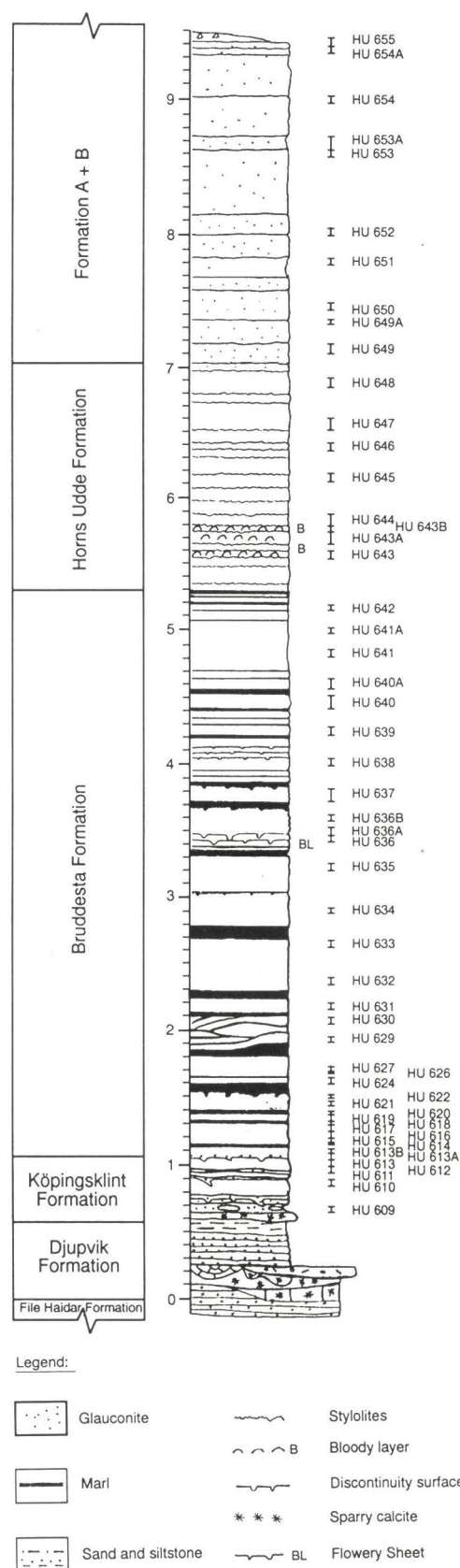
Gray to light-green grainstones and mudstone with calcite prisms (0.0 - 0.20 m).

Gray to black phosphatic discontinuous conglomerates with *Agnostus pisiformis* (0.00 - 0.10 m). Repeated small sequences composed by green glauconitic siltstones to shales (≈ 0.25 m).

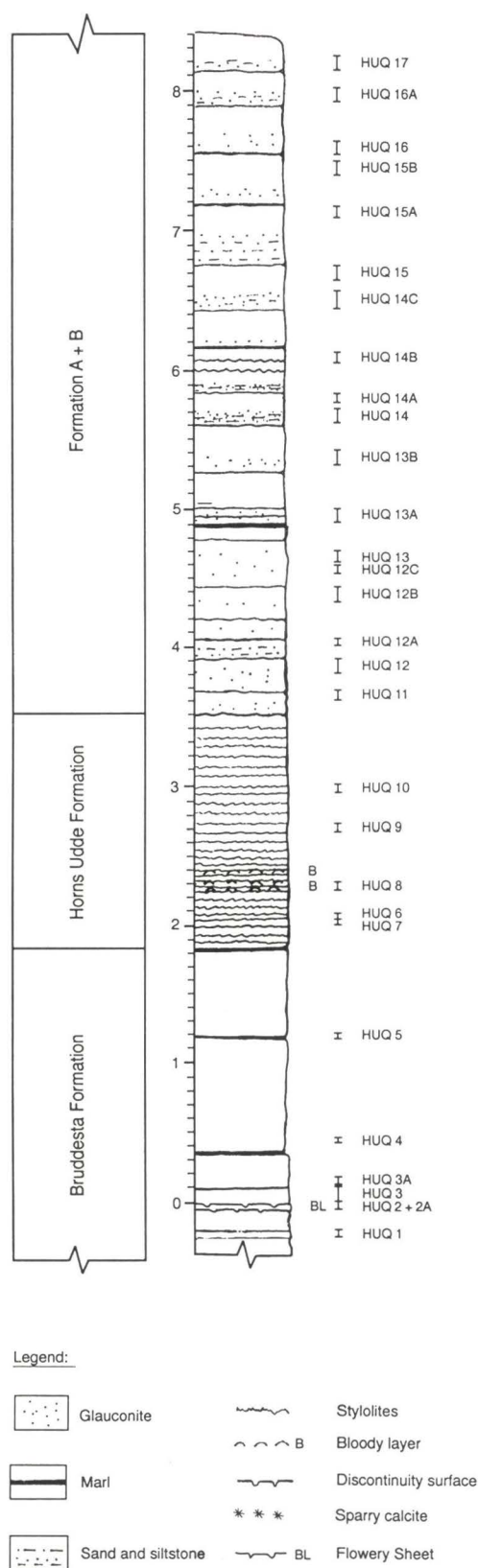
Dark gray bituminous and laminated shale with small brachiopods (0.10 m).

0.60 - 1.05 m Köpingsklint Formation (≈ 0.45 m).

Member Kk2: Gray-green glauconitic sandstone; lime mudstone and recrystallized limestone. Lateral variation of this unit is typical (see van Wamel, 1974) (≈ 0.30 m).



Text-fig. 3 - Section North of Horns Udde.



Text-fig. 4 - Section from the Horns Udde quarry.

Member Kk3: Glauconitic bedded lime mudstone with minor green shaly interbeds (≈ 0.15 m).
Samples HU 609, HU 610, HU 612 and HU 613.

1.05 - 5.31 m Bruddesta Formation (≈ 4.26 m).

Repeated small and upwards coarsening sequences (3-10 cm) composed by marls and fossiliferous lime mudstone. Trilobites are the most common allochems.

The lower 0.95 - 1.00 m are green to red-mottled; the upper two-thirds of the formation is gray to reddish-brown with occasionally green mottled horizons.

Sedimentary folds (Lindström, 1963) (=slumped beds) are prominently displayed in the lower part of the section.

Between 3.40 - 3.50 m: prominently developed hard(firm-) grounds or «Blommiga Bladet». The top of the formation is placed at the top of the last marly bed.

Samples HU 613A, HU 613B and up to HU 642 inclusive.

5.31 - 6.97 m Horns Udde Formation (≈ 1.66 m).

Red to gray lime mudstone to wackestone, stylolitic, with abundant endoceratid cephalopods (≈ 0.87 m).

Between 5.53 - 5.85 m: haematite impregnated surfaces with abundant cephalopods (= «Bloody layer»).

Interbedded gray, green limestone with violet stringers; stylolitic and limonitic surfaces (0.79 m).
Samples HU 643 to HU 648 inclusive.

6.97 - 9.43 m Formations A and B (≈ 2.46 m).

Green gray glauconite lime mudstone to wackestone interbedded with green shale; glauconite silt to sand. Bedding uneven.

Trilobites and endoceratid cephalopods most common allochems.

7.03 - 7.18 m: zone with abundant cephalopods.

7.35 - 7.58 m: massive limestone unit.

The top is covered by shingle and soil. The top of the section finishes within formation A and B.

Samples HU 649 to HU 655 inclusive.

2) Horns Udde quarry Section (Text-figs. 1, 4).

Three active quarries are present on Horns Udde. For this study the southern quarry was investigated and chosen as representative for this part of the peninsula.

The section (Text-fig. 4) covers the interval from the middle of the Bruddesta Formation (ie. «Flowery sheet») into the *Asaphus* limestone *sensu* Bohlin (1949). The section extends stratigraphically higher than at the section North of Horns Udde comprising the total of formation A and continues into formation B (*sensu* Stouge & Bagnoli, 1990). 30 samples (labelled HUQ, referring to Horns Udde Quarry) have been investigated yielding a total of 18018 conodont elements (Tab. 2).

The stratigraphy of the section at Horns Udde quarry has been outlined and the acritarchs have been described by Ribecai & Tongiorgi (1994) and Playford *et al.* (1995).

Samples HU																													
Species		609	610	611	612	613	613A	613B	614	615	616	617	618	619	620	621	622	624	626	627	629	630	631	632	633	634			
<i>Baltoniodus navis</i>																													
<i>Baltoniodus cf. navis</i>	Pa																												
	Pb																												
	M																												
	Sb																												
	Sd																												
<i>Baltoniodus norrlandicus</i>																													
<i>Baltoniodus? triangularis</i>	Pa																												
	Pb																												
	M																												
	Sa																												
	Sb																												
	Sc																												
	Sd																												
<i>Cornuodus longibasis</i>		10	18	13	2	10	15	5	4	6	5	3	2	7	7	7	7	3	12	7	3	1	6	7	11	18			
<i>Drepanodus arcuatus</i>		123	67	45	29	7	21	17	9	7	3		14	7	7	26	19	17	42	42	23	30	32	26	35	19			
<i>Drepanodus planus</i>		4	4			6		38	23	1		1									1			7					
<i>Drepanoistodus basiovalis</i>																													
<i>Drepanoistodus contractus</i>																14			17					15	20				
<i>Drepanoistodus forceps</i>		178	213	168	94	260	183	366	409	485	386	470	481	419	432	323	371	217	267	408	405	496	475	284	453	427			
<i>Gothodus costulatus</i>	Pa					2	4	2	2		16	6	9	5	2	17	9			1									
	Pb					2	1	1	1		9	5	1	4	1	15	2		1										
	M					2	3	1	4		5	14	6	8	5	31	2			1									
	Sa					1					1	2	2	1	2	6	2												
	Sb					3	2	1	1		10	17	3	5	3	14				1									
	Sc						1	1	1		3	12	7	14	1	25	2		1	1									
	Sd						2	4	3	1	13	10	5	10	5	41	7		1				1						
<i>Gothodus cf. costulatus</i>	Pa																												
	Pb																												
	Sc																												
	Sd																												
<i>Jumodontus gananda</i>																									4				
<i>Lenodus antivariabilis</i>	Pa																												
	Pb																												
	M																												
	Sa																												
	Sb																												
	Sc																												
	Sd																												
<i>Lundodus gladiatus</i>	P			1														2	6										
	S			1			1	1										3	6										
<i>Microzarkodina flabellum</i>																													
<i>Microzarkodina parva</i>																													

(continue)

Tab. 1

635	636	636A	636B	637	638	639	640	640A	641	641A	642	643	643A	643B	644	645	646	647	648	649	649A	650	651	652	653	653A	654	654A	655	Total
3		1																												5
	1																													1
																														2
																														1551
17	9					1																								255
21	7					3																								275
2	4																													40
41	10					4																								408
10	4					1																								260
		8	2		1																									11
						2																								2
						1																								1
						1																								1
																				1				4						9
													104	109	168	219	265	343	5		4	79	26			8		4	4	1338
		3	2	1						6																				733
4	5				17	1					3																			37
																														447
	5				11																									16
	4				12																									16
	17	2		1	22																									42
																														50
																														88
						23																								23
						3																								3
						22	1																							23
														2																2
														1																1
														1	1															2
																														23
71	52						46	92	70	126	96	43	158	107	133	53	68	64	66	52	48	129	98	11	68	22	26	16	89	2546
		97	185	87	71	57																								497
		10	48	22	26	30																								136
																														267
																														90
8	9																		6	11	5	5	2							57
	3											3							2	1	2									15

(continue)

Species	Samples HU																												
		609	610	611	612	613	613A	613B	614	615	616	617	618	619	620	621	622	624	626	627	629	630	631	632	633	634			
Microzarkodina n.sp. A	P																									1			
	Sc																												
Oelandodus elongatus		1	1																										
Oepikodus evae		3	23	190	492	180	368	41	21	19	33	21	42	21	58	13	26												
Oistodus lanceolatus	P	2		5	8	6	4	14	9	12	12	10	11	13	5	9	5	4	11	17	9	21	10	7	15	9			
	M	2		3	6	11	5	12	15	11	17	19	11	15	5	12	10	1	5	22	8	14	7	10	10	13			
	Sa			2				4		1	3	2	2	4	2	1	1		2		2	3	3	1	1				
	Sb	2		7	5	15	5	20	10	17	16	28	15	23	13	19	13	4	17	38	9	21	21	9	21	5			
	Sc	2		6	7	14	5	5	21	16	12	8	15	25	10	11	14	2	3	16	3	15	5	11	12	7			
Oistodus sp.																													
Oistodus sp. A	P																												
	M																												
	S																												
Parapaltodus spp.					1					1		1	1																
Paroistodus originalis																													
Paroistodus parallelus		115	165	101	11	44	10	73	67	4	9	15	29	37	21	15	5												
Paroistodus cf. proteus																				1		1				5			
Periodon flabellum							5	7	2	2	15	18	1	3	9	20	27	28	86	22	15	5		46	66	70			
Periodon cf. flabellum	P																												
	M																												
	S																												
Periodon primus		30	20																										
Periodon selenopsis		33	11	38	6																								
Periodon sp. A	P																												
	M																												
	S																												
Periodon sp. B	P																												
	M																												
	S																												
Prioniodus elegans		21	2																										
Protopanderodus rectus											91	61	22	32	68	33	34	22	21	37	28	39	78	87	20	69			
Protopanderodus floridus	acon.																												
	scan.																												
Protopanderodus sulcatus	acon.			41	20	56	49	39	28	34																			
	scan.			11	6	17	18	9	13	16																			
Protopanderodus calceatus	acon.																								10	1			
	scan.																									4			

(continue)

[illegible]

(continue)

(continue)

635	636	636A	636B	637	638	639	640	640A	641	641A	642	643	643A	643B	644	645	646	647	648	649	649A	650	651	652	653	653A	654	654A	655	Total
																							130							130
																														2
																														9
2	4																													6
																								3		4	36	115	158	
										1		1	1	5	12	10	1	3	58	69	28	94	66	39	60	21	104	13	54	640
					2																								2	
7	7					3																							113	
		18	19	35	10																								82	
26	5					14	40	21	15	18	6	9	3		4				2	1			5						444	
5	4	14	16	17	25	20	18	31	19	10	13	12	12	15	22	8	14	7	17	10	1	24	11	6	8	2	4		4	619
																			6	11	13	36	21	19	32	9	59	12	18	236
																													1121	
							17	8	6			9	2	2			1			1	1	2							49	
							4	4	2	1	1	8	1	4	1						2	1							29	
							10	3	3	1		5	2	4	3				1		1	1							34	
							3	3	2	1		2	1	6	2		1			1	1	1							24	
							4	4	1			9	1	2	2														23	
							1	2	1			3	2	1	5														15	
							11	17	3			9	7	7	3	1	1		2		2	5							68	
	3																												54	
	2																												7	
	2																												24	
																													15	
	1																												31	
																													29	
	1																												40	
												1	4	5	15	44	22	17	17	54	33	5							217	
																													2	
																													3	
																													23	
2																														
712	712	739	759	767	689	738	724	724	709	714	717	561	794	563	717	726	721	705	713	717	730	1605	690	755	830	530	1046	334	871	39545

Tab. 1 - Numerical distribution of conodont species from the section North of Horns Udde.

Species	Samples HUQ													
		1	2	2A	3	3A	4	5	7	6	8	9	10	11
<i>Baltoniodus navis</i>									39	133	130	154	218	161
<i>Baltoniodus cf. navis</i>	Pa							19						
	Pb							11						
	M							18						
	Sa							12						
	Sb							16						
	Sc							10						
	Sd							19						
<i>Baltoniodus norrlandicus</i>														7
<i>Baltoniodus? triangularis</i>	Pa				2	1	15							
	Pb						6							
	M				3	4	12							
	Sa				1	2	5							
	Sb					3	8							
	Sc					2	8							
	Sd				1	2	17							
<i>Cornuodus longibasis</i>		4	11	7	6	4	10	17	16	18	6	17	4	15
<i>Drepanodus arcuatus</i>		12	40	13		3	3			2	11	13	16	21
<i>D. repanoistodus basiovalis</i>									19	34	47	142	134	77
<i>Drepanoistodus contractus</i>		45	19	23	50	4	24	36						
<i>Drepanoistodus aff. contractus</i>	drep. oist.													
<i>Drepanoistodus forceps</i>		849	619	264	438	280	378	468	699	475	67			
<i>Drepanoistodus venustus</i>														
<i>Gothodus cf. costulatus</i>	Pa								5					
	Pb								6					
	M								4					
	Sb								3					
	Sc								4					
	Sd								3					
<i>Lenodus antivariabilis</i>	Pa													
	Pb													
	M													
	Sa													
	Sb													
	Sc													
	Sd													
<i>Lenodus sp. A</i>														
<i>Microzarkodina flabellum</i>								92	163	128	66	7		3
<i>Microzarkodina hagetiana</i>														
<i>Microzarkodina parva</i>												42	55	65
<i>Microzarkodina n.sp. A</i>	P	2												
	M	8												
	Sa	1												
	Sb	4												
	Sd	1		1										
<i>Oistodus lanceolatus</i>	P	2	3	1	1									
	M	5	8	7										
	S	7	17	18	4									

(continue)

Tab. 2

12	12A	12B	12C	13	13A	13B	14	14A	14B	14C	15	15A	15B	16	16A	17	Total
																	835
																	19
																	11
																	18
																	12
																	16
																	10
																	19
138	332	314	294	76	338	232	355	222	307	348	192	94	68	217	20	258	3812
																	18
																	6
																	19
																	8
																	11
																	10
																	20
4	3			12							6	1			1		162
17	32	27	19	4	19	16	12	22	12	11	2	5	2	2	2	11	349
66	304	233	283	135	148	129	93	87	79	57	59	51	45	79	17	45	2363
																	201
												1	3		1	5	10
												1	4				5
																	4537
													1			3	4
																	5
																	6
																	4
																	3
																	4
																	3
			3	2	5	1	1	1									13
			4	1	6			1									12
				3	1		2										6
				3	2		2	1									8
					1	1		4									6
				1	1	5	2	3									12
			2	4	5	3	4	5									23
								2	9	27	8	15	10	47	10	48	176
2	12		2	7			1										483
													12	105	7	6	130
140	82	3	3	98	37	13	30	3	3	4	101	2	1				682
																	2
																	8
																	1
																	4
																	2
																	7
																	20
																	46

(continue)

Species	Samples HUQ													
		1	2	2A	3	3A	4	5	7	6	8	9	10	11
<i>Oistodus</i> sp. B	S													
<i>Parapanderodus quietus</i>														
<i>Paroistodus originalis</i>											140	401	168	
<i>Paroistodus</i> cf. <i>proteus</i>			6		3				28					
<i>Periodon</i> cf. <i>flabellum</i>	P		5			1								
	M		2											
	S		4			1								
<i>Periodon</i> sp. B											2			
<i>Periodon</i> sp. C														
<i>Protopanderodus rectus</i>		66	128	28				84	246	70	168	56	17	73
<i>Protopanderodus floridus</i>	acon.				41	31	44							
	scan.				8	7	16							
<i>Protopanderodus calceatus</i>	acon.	6	1	5										2
	scan.	3		1										
<i>Protopanderodus</i> sp.														
<i>Protoprioniodus papillosus</i>		1												
<i>Scalpellodus gracilis</i>														
<i>Scalpellodus latus</i>									6		16	5	8	42
<i>Scalpellodus</i> cf. <i>latus</i>		1			1									
<i>Scandodus furnishi</i>		6	7		3									
<i>Scolopodus princeps</i>						8	42							
<i>Scolopodus rex</i>		10	5	3				7		18	3	1		3
" <i>Scolopodus</i> " <i>peselephantis</i>		3	7	2	3	5		12	34	23	5	3		15
" <i>Semiacontiodus</i> " <i>cornuformis</i>														4
" <i>Semiacontiodus</i> " sp.														
<i>Trapezognathus quadrangulum</i>	Pa							24	5	10	2			2
	Pb							8	4	4				1
	M							4	3	3	1			1
	Sa							2	2	2	1	1		
	Sb							2	1	4	1			
	Sc							4	7	2	2	1	1	
	Sd							8	9	17	3	3	1	
<i>Trapezognathus diprion</i>	Pa	1	1	1										
	Pb		1											
	M			1										
	Sa			1										
	Sc			1										
	Sd	1	1											
<i>Triangulodus brevbasis</i>									8	1	13	24	12	15
<i>Tropodus</i> sp.										3				
Gen. et sp. indet.		3	4											
TOTAL		1041	889	377	565	358	588	873	1314	947	684	870	638	505

(continue)

12	12A	12B	12C	13	13A	13B	14	14A	14B	14C	15	15A	15B	16	16A	17	Total
		2															2
										4	6	7	10		23	35	85
35	26				1	12	1										784
																	37
																	6
																	2
																	5
																	2
		5															5
38	38	30	25	25	18	3	14				4					3	1134
																	116
																	31
	1					2				1							18
																	4
16				11			18										45
																	1
				1		31	95	17	28	4	30	11	12	22	3	16	270
28	31	33	18	14	15	5	1										222
																	2
																	16
																	50
	3																53
11	4	1		1			4				1				1		135
5	6	20	8	6	8	2	11	17	36	45	30	46	47	92	29	89	501
												3	17	45	11	35	111
																	43
																	17
																	12
																	8
																	8
1																	18
1																	42
																	3
																	1
																	1
																	1
																	2
																	73
																	3
																	7
501	873	668	661	404	605	455	646	385	474	501	439	237	232	609	125	554	18018

Tab. 2 - Numerical distribution of conodont species from the Horns Udde quarry.

Succession – The base of the section is the upper amphora-shaped hard (firm-) ground of the «Flowery sheet» that is exposed at the bottom of the quarry. The horizon also serves as the reference level to the section North of Horns Udde.

Cumulative values:

- 0.00 - 1.84 m Bruddesta Formation ($\approx$ 1.84 m).
Red to reddish brown fossiliferous lime mudstone with marly interbeds.
Samples HUQ 1 to HUQ 6.
- 1.84 - 3.51 m Horns Udde Formation (1.67 m).
Red to gray, green lime mudstone to fossiliferous lime mudstone, stylolitic and with endoceratid cephalopods. (Succession similar to the section North of Horns Udde).
Samples HUQ 7 to HUQ 10.
- 3.51 - 8.41 m Formation A and B (4.90 m).
Interbeds of glauconitic, bioturbated, green fossiliferous lime mudstone, massive bedded glauconitic wackestone and glauconitic sand and clay. Cyclic deposition of upwards coarsening sequences and with phosphatic burrowed surfaces at top; each cycle about 0.15-0.40 m. Ooids (Sturesson, 1986) are recorded from $\approx$ 7.50 m to the top of the section.
Samples HUQ 11 to HUQ 17.

CONODONT BIOSTRATIGRAPHY

After compiling the two sections from the Horns Udde quarry and North of Horns Udde into a single composite section, the composite range chart was constructed. The vertical distribution of the taxa is given in Text-fig. 5.

In the Köpingsklint Formation only the uppermost strata were investigated here. Additional information on the biostratigraphy of the unit were given by van Wamel (1974) and Bagnoli *et al.* (1988). The fauna from the upper part of the formation includes *Prioniodus elegans* and *Oelandodus elongatus*. Member Kk3 includes the appearance of *Oepikodus evae* (with *Prioniodus elegans* as reworked and *in situ*), *Periodon primus* and *Periodon selenopsis*.

The basal part of the Bruddesta Formation is characterized by the association of *Oepikodus evae*, *Paroistodus parallelus*, *Stolodus stola* and *Oistodus lanceolatus*. Additional common species include *Drepanoistodus forceps* and species of *Drepanodus*. *Protopanderodus sulcatus*, *Lundodus gladius*, *Gothodus costulatus* and *Periodon flabellum* successively appear in this part of the formation. Higher parts of the formation are characterized by the appearance of *Protopanderodus rectus* and *Trapezognathus diprion* with *Protoprioniodus aranda*, *Jumodontus gananda* and *Tripodus* sp. as rare associates. The genus *Microzarkodina* appears for the

first time below the «Flowery Sheet» and it is represented by *Microzarkodina* n.sp. A.

The *Baltoniodus? triangularis* fauna appears at the «Flowery Sheet». *Baltoniodus? triangularis* is associated with *Protopanderodus floridus* n.sp., *Scolopodus princeps* n.sp., *Periodon* cf. *flabellum* and *Oistodus* sp. The stratigraphically higher beds of the formation are characterized by the appearance of *Microzarkodina flabellum*, followed by *Baltoniodus navis* and *Trapezognathus quadrangulum*. These taxa extend into the following Horns Udde Formation.

The conodont fauna from the Horns Udde Formation is dominated by *Paroistodus originalis*, *Drepanoistodus forceps* and *Drepanoistodus basiovalis*. *Triangulodus brevibasis*, *Microzarkodina parva* and *Baltoniodus norrlandicus* all appear in the formation and range into higher units. *Periodon* sp. B and *Gothodus* cf. *costulatus* have a short but characteristic range in the lower part of the formation. «*Semiaconitodus*» *cornuformis* s.l. appears near the top of the formation and ranges throughout the exposed section. In this material «*S.*» *cornuformis* s.l. comprises two morphotypes both of which probably represent new species which are distinct from «*S.*» *cornuformis* s.s. (see Systematic Palaeontology).

The fauna from formations A and B includes a local occurrence of *Periodon* sp. C and the arrival of *Lenodus antivariabilis* succeeded by *Scalpellodus gracilis*. *Lenodus* sp. A appears in the unit and it is associated higher in the formations by *Parapanderodus quietus*. *Drepanoistodus venustus* and *Microzarkodina hagetiana* appear near the top of the Horns Udde quarry section.

THE CONODONT FAUNA AND ITS PROVINCIAL AFFINITIES

Traditionally in the lower Ordovician two rather unfortunately named main conodont realms (or provinces of some authors), the warm water Midcontinent Realm of North America, Siberian Platform, North China and eastern Australia and the temperate to cold water Atlantic Realm of Europe, the Appalachian region of North America, South China, South America and the Nevada-Utah Sections of North America and northwest Australia have been well established (Bergström, 1990; Bagnoli & Stouge, 1991).

The Öland conodont faunas are referred to the pandemic group and to the North Atlantic Realm (*sensu* Bagnoli & Stouge, 1991). During Billingen times the conodont fauna changed from pandemic taxa of deep water setting to a fauna of relatively more shallow water affinities. The change in the

fauna composition is connected with the appearance of taxa which are characteristic of the Precordilleran Province (*sensu* Bagnoli & Stouge, 1991). This change is probably due to migration of oceanic components onto the East European Platform caused by sea level changes.

At the end of the Billingenian Substage and into beginning of the Volkhov Stage a new stock of conodonts gradually migrated onto the platform. The Volkhov faunas are referred to the deep to shallow water Baltic Province and some taxa are of unknown provincial affinity.

Pandemic Group

Oepikodus, *Periodon*, *Prioniodus*, *Gothodus*, *Lundodus* and perhaps *Oelandodus* are known from several palaeocontinents and belong to the Pandemic Group (*sensu* Bagnoli & Stouge, 1991). The taxa preferred cool to temperate oceanic water conditions and they represent a group of conodonts of cosmopolitan aspect (Bagnoli & Stouge, 1991). The fauna appeared on the East European Platform along with the global «evae transgression» in early Billingen times (Arenig) (Stouge & Bagnoli, 1988; Nielsen, 1992).

Gothodus and *Periodon* of the Pandemic Group returned and disappeared equally fast on the East European Platform in the Volkhov. The short incursions of these pandemic taxa in the Volkhov Stage mark the peaks of transgressions that reached the study area.

Atlantic Realm conodonts

- Precordilleran Province conodonts

In the lower Ordovician the East European Platform was invaded and for a while hosted taxa that are known from the temperate Precordilleran Province (*sensu* Bagnoli & Stouge, 1991). In the investigated sections four, perhaps five, genera which are known from North America (Ethington & Clark, 1982; Repetski, 1982; Ji & Barnes, 1994), the Precordilleran Argentina (Serpagli, 1974; Lehnert, 1995) and Australia (Cooper, 1981) occur and apparently migrated from one of these regions or from a region with a similar fauna. This group of taxa comprises one or more species of *Tripodus*, *Protoprioniodus*, *Jumodontus* (*J. gananda*) and *Tropodus* in Billingen. *Stolodus* is recorded from the uppermost part of Köpingsklint Formation and ranges into the lower third of the Bruddesta Formation. The ancestor of the genus is unknown and the destiny of this distinct taxon is uncertain as the

successor has not been recorded. *Stolodus*, however, may belong to this province.

In the lower part of the Bruddesta Formation and below the «Flowery Sheet» (Billingenian Substage), the succession and appearance of the species in this group imitates the faunal succession of North America (Ethington & Clark, 1982; Repetski, 1982) and the Precordilleran Argentina (Serpagli, 1974; Lehnert, 1995). This Precordilleran Province faunal influx on the East European Platform permits a confident correlation with the Wah Wah and Juab Formations of the Utah-Nevada sections, the El Paso Group of Texas, and the St. Juan Formation of the Precordilleran successions of South America. Moreover, it suggests that the water column in the Öland region changed from oceanic to temperate shelf conditions during Billingen times.

Parapaltodus simplicissimus and *Parapanderodus quietus* appear in formations A and B, respectively in the late Volkhov and Kundan Stages. The genera are recognized from North America (Ethington & Clark, 1982; Stouge, 1984), China (An, 1987) and from Australia (Watson, 1988). The taxa are part of the Table Head - Toquima macrofauna Realm (Ross & Ingham, 1970; Stouge, 1984). This younger incursion of «foreign» conodonts is parallel to the appearance of the temperate Precordilleran Province conodonts in the Billingenian Substage.

- Baltic Province conodonts

From the late Billingen and into the beginning of the Volkhov, a major migration event occurred and associations of new taxa appeared on the Baltica palaeocontinent. The newcomers include *Baltoniodus? triangularis*, *Baltoniodus*, *Microzarkodina*, *Trapezognathus*, *Triangulodus*, *Scalpellodus* and somewhat later «*Semiacontiodus*» and *Lenodus*. *Baltoniodus? triangularis* and the associated fauna represents the arrival of a new stock onto the platform and is an important event in the history of the lower Ordovician faunal succession on the East European Platform.

The genera *Baltoniodus*, *Microzarkodina*, *Lenodus* and *Trapezognathus* migrated to Baltica and settled. The taxa became components of the Baltoscandian fauna during the Volkhov and Kunda and established important evolutionary lineages through the lower and middle Ordovician. The provincial affinity of these taxa is Baltoscandic and so they are referred to as the temperate water Baltic Province of the Atlantic Realm in this paper. The same taxa of the Baltic Province are found in south China (An, 1987). The origin of the Baltic Province fauna – except perhaps for *Microzarkodina* – is un-

certain. Sweet (1988) postulated that *Microzarkodina* originated in North America. This is one possibility; the oldest known species of the genus: *M. buggischi* Lehnert, 1995 is described from Argentina (Lehnert, 1995). So if Precordilleran Argentina should be considered part of North America (Dalla Salda *et al.*, 1992), this statement may be true. Otherwise, the appearance of *Microzarkodina* n.sp. A in the Bruddesta Formation (van Wamel, 1974 and this study) is coeval or nearly so with the appearance of *Microzarkodina* in North America (Sweet *et al.*, 1971; Ethington & Clark, 1981). *Microzarkodina* became a persistent part of the Baltica (and south China) fauna during Volkhov and early Kundan times in contrast with North America where the genus disappeared or is rarely recorded.

The hyaline genus *Triangulodus* from the middle Volkhov is common in Horns Udde Formation. The genus is well known in Australia (Crespin, 1943; Nieper 1969; Cooper, 1981; Stait & Druce, 1993) where it has a long range and is probably represented by several species. It is apparent that this taxon derived from the Australian region of the Gondwana Palaeocontinent. (By this statement it is postulated that the Midcontinent Province genus *Eoneoprioniodus* Mound, 1975 or *Pteracontiodus* Harris & Harris, 1965, emended Ethington & Clark 1982, is not congeneric with *Triangulodus*).

Based on the current knowledge on conodonts from North America (Ethington & Clark, 1982; Repetski, 1982; Stouge, 1982; Ji & Barnes, 1994) the coniform genera *Scalpellodus* and «*Semiacontiodus*» were not present on Laurentia during Arenig times. The taxa reached Baltica in Volkhov times and the origin of these taxa is so far unknown.

EVOLUTIONARY LINEAGES IN THE ÖLAND SECTIONS

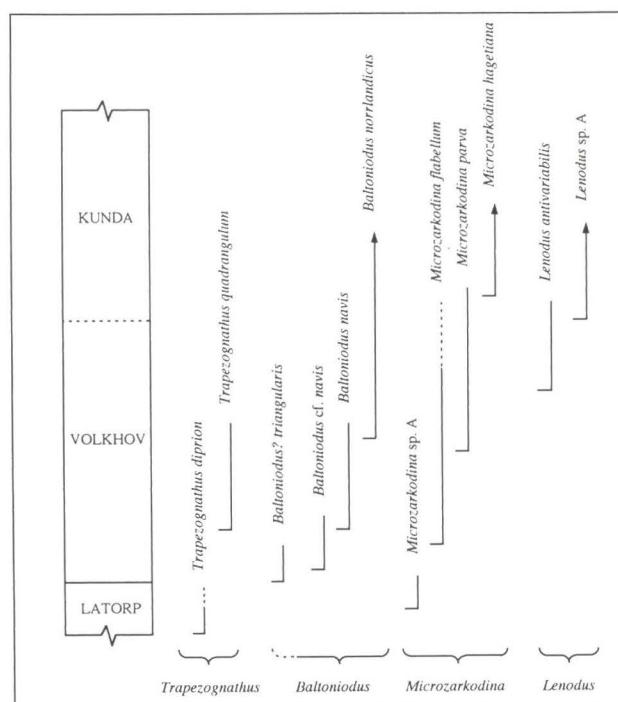
In early applications of conodonts to stratigraphic zonation, the standard technique was to use distinctive marker species of limited range. They were chosen empirically with the aim of seeing that a new species appeared as closely as possible to where the older one died out. Representative examples are the selection of *Paroistodus proteus*, *Prioniodus elegans*, *Oepikodus evae*, and *Baltoniodus? triangularis* as indices of successive zones (Sergeeva, 1964; Lindström, 1971).

The concept of evolutionary lineages is easy to comprehend, for it simply postulates an ancestral form succeeded by divergent progeny which changed in one or more of their physical attributes.

Representative trends might be change in the size of the basal sheath, reduction of basal cavity, inverted basal cavity and change in denticulation. The stages of the development of a given lineage from primitive to advanced provide clues to their stratigraphic levels. By efficient codification and nomenclature of successive development phases of a lineage, its evolution can be utilized for definition of a precise zonal scheme. Combined use of several unrelated lineages is potentially the most reliable basis for zonation.

For this purpose, the evolutionary lineages of the genera *Baltoniodus*, *Lenodus*, *Microzarkodina* and *Trapezognathus* are used.

The appearance of supposedly primitive forms before presumed descendant (stratigraphically higher) advanced ones is essential. Lindström (1971) found, and maintained by Löfgren (1978) and Dzik (1976, 1994), that *Baltoniodus navis* (*sensu stricto*) evolved from *Baltoniodus? triangularis*. In this paper we are cautious and suggest that *Baltoniodus? triangularis* should not be considered a direct ancestor of *Baltoniodus navis*. In our opinion the *Baltoniodus* lineage begins with *Baltoniodus* cf. *navis* which is interpreted as the primitive form. It appeared before the presumed descendant *Baltoniodus navis* and the even more advanced *Baltoniodus norrlandicus*.



Text-fig. 6 - Phylogeny and ranges of *Baltoniodus*, *Lenodus*, *Microzarkodina*, and *Trapezognathus* based on this study.

[illegible]

Text-fig. 5 - Ranges of species from the composite section and distribution of the interval zones. *M. fl.* = *Microzarkodina flabellum*.

Trapezognathus diprion is interpreted to represent the primitive species of the genus and *Trapezognathus quadrangulum* is the advanced descendant.

Microzarkodina n.sp. A is the oldest representative of the genus on Baltica. The successor is represented by *Microzarkodina flabellum* and later by *Microzarkodina parva*.

Lenodus is closely related with *Trapezognathus* but we do not consider *Lenodus* as a direct descendant of the latter genus. *Lenodus antivariabilis* is the ancestor and *Lenodus* sp. A is the more advanced successor.

The phylogeny and ranges of the important lower Ordovician species of *Baltoniodus*, *Microzarkodina*, *Trapezognathus* and *Lenodus* are shown in terms of the Baltoscandian chronostratigraphical divisions in Text-fig. 6.

CONODONT ZONATION

The faunal succession in the sections allows the establishment of a new conodont biozonation. The first occurrences and associations shown in the range chart (Text-fig. 5) were used to construct a conodont zonation (Text-fig. 7). The zonation comprises zones defined on the basis of first occurrences or first appearance datums (FAD's) but containing faunal associations that generally permit recognition of the zones with faunas that lack the zonal index taxon. When possible, the zones are based on evolutionary lineages from several taxa. This is possible for the Volkhov and Kunda conodonts and the lineages of *Baltoniodus*, *Lenodus* and *Microzarkodina* are used in this interval.

The pandemic oceanic fauna of the Billingenian Substage does not permit a subdivision using phyletic lineages (except perhaps for the *Periodon* lineage) and the first occurrences of non-related taxa are considered the best possible approximation for a precise zonation of this substage.

The conodont zonation presented in this study comprises ten zones up to the base of the Kunda Stage compared to the six zones of Lindström's (1971) zonation for the same interval and twelve zones of van Wamel's (1974) zonation for the same interval. This implies a precision about 1.5 times more than that of Lindström's zonation and slightly less as for van Wamel's zonation. Positions exist where the present conodont zonation and the Lindström and van Wamel zone boundaries do not coincide so that the present zonation might be used to subdivide the older zones.

Some of the proposed zones bear the same species names as the older zonations, but with a dif-

ferent diagnosis; for example, the *Microzarkodina flabellum* (Assemblage) Zone of van Wamel (1974) and the *Microzarkodina parva* Zone of Lindström (1971).

The diagnosis, faunal associations, and ages of the zones are tabulated below according to the rules given in Hedberg (1976) and Salvador (1994).

- *Prioniodus elegans* interval Zone

Definition – Interval from the first appearance (FAD) of *Prioniodus elegans* to the first appearance (FAD) of *Oepikodus evae*.

Reference-Section – Section between Äleklinta and Djupvik (Section 6 of van Wamel, 1974).

Reference-strata – The rock interval from 0.00 - 0.35 m above the base of the Köpingsklint Formation (Samples 2-5 of van Wamel 1974)

Description – The biozone is recognized by the partial range of *Prioniodus elegans* from the appearance (FAD) of *Prioniodus elegans* to the first appearance (FAD) of *Oepikodus evae*.

Associated fauna includes species of *Periodon*, *Oelandodus elongatus*, *Oistodus lanceolatus*, *Paroistodus parallelus* and *Stolodus stola*.

Age – Latorp Stage; the zone is either part of the Hunnebergian Substage (Bagnoli *et al.*, 1988; Lindholm, 1991) or at the very base of the Billingenian

SERIES	STAGE	SUBSTAGE	CONODONT ZONES
O E L A N D	KUNDA	Hunderumian	<i>Lenodus</i> sp. A
	V O L K H O V	Langevojan	<i>Lenodus</i> <i>antivariabilis</i>
			<i>Baltoniodus</i> <i>norrlandicus</i>
			<i>Microzarkodina</i> <i>parva</i>
			<i>Baltoniodus</i> <i>navis</i>
			<i>Microzarkodina</i> <i>flabellum</i>
			<i>Baltoniodus?</i> <i>triangularis</i>
		L A T O R P	Billingenian
	<i>Trapezognathus</i> <i>diprion</i>		
	<i>Oepikodus</i> <i>evae</i>		
			Hunnebergian

Text-fig. 7 - Conodont interval zones in this paper.

Substage (Tjernvik & Johansson, 1980; Bergström, 1988; Löfgren, 1985, 1993a, b, 1994).

Remarks – The *Prioniodus elegans* Zone has not been established from the sections dealt with in this study, but it has been recorded from a section at Äleklinta by van Wamel (1974) and from the Furuhall Section (Bagnoli *et al.*, 1988) from the Öland region.

– *Oepikodus evae* interval Zone

Definition – The zone is defined by the first appearance (FAD) of *Oepikodus evae* to the first appearance (FAD) of *Trapezognathus diprion*.

Reference-Section – Section North of Horns Udde.

Reference-strata – The rock interval from a level at about 0.65 m above the base of the section to 1.38 m above the base of the section (Samples HU 609 to HU 619).

Description – The biozone is recognized by the partial range of *Oepikodus evae* from the appearance of *Oepikodus evae* to the first appearance of *Trapezognathus diprion* in the region.

Associated fauna includes species of *Periodon* (*Periodon primus*, *P. selenopsis* and *P. flabellum*), *Oistodus lanceolatus*, *Paroistodus parallelus*, *Protopanderodus sulcatus*, *Stolodus stola* and *Drepanoistodus forceps*. Rare taxa, i.e. *Lundodus gladius* and *Gothodus costulatus* are present; *Oelandodus* and *Prioniodus elegans* from below are present in the basal part of the zone.

Paroistodus parallelus has a partial upper range that coincides with the upper range of the nominate species.

Periodon primus, *Periodon selenopsis*, *Prioniodus elegans*, *Oelandodus elongatus* and *Protopanderodus sulcatus* have their upper ranges within the zone.

Oistodus lanceolatus, *Periodon flabellum*, *Gothodus costulatus*, *Protopanderodus rectus* and *Lundodus gladius* all appear in the zone and extend into higher zones.

Age – Latorp Stage; Hunnebergian(?) – Billingenian Substage (*M. aff. estonica* and *M. dalecarlicus* trilobite Zones).

– *Trapezognathus diprion* interval Zone

Definition – The zone is defined by the FAD of the nominate species to the FAD of *Microzarkodina* n.sp. A.

Reference-Section – Section North of Horns Udde

Reference-strata – The rock interval from about 1.38 m above the base of the section to the level about 2.65 m above the base of the section (Samples HU 620 – HU 632).

Description – The zone is characterized by the first appearance of the nominate species. *Drepanoistodus contractus* and *Paroistodus cf. proteus* have their first appearance within the zone.

Oepikodus evae and *Lundodus gladius* both disappear in this zone and the last occurrence of *Stolodus stola* is at the top of the *Trapezognathus diprion* Zone.

Protoprioniodus aranda is constrained to this zone.

Age – Latorp Stage; Billingenian Substage (*M. estonica* Zone).

– *Microzarkodina* sp. A interval Zone

Definition – The interval from FAD of *Microzarkodina* n.sp. A to the FAD of *Baltoniodus? triangularis*.

Reference-Section – Section North of Horns Udde.

Reference-strata – The rock interval from 2.65 m above the base of the section (≈0.85 m below the upper surface of the «Blommiga Bladet») to 3.48 m above the base of the section (≈top surface of the «Blommiga Bladet») (Samples HU 633 – HU 636; HUQ 1 – HUQ2A).

Description – The zone is characterized by the rare presence of *Jumodontus gananda*, *Tripodus* sp., *Tropodus* sp., and *Protoprioniodus papillosus* which are restricted to the zone. *Periodon flabellum* has its upper range within the zone.

Scalpellodus cf. latus and *Periodon cf. flabellum* appear in the zone and range into the next zone.

Age – Latorp Stage- (?Volkhov Stage); Late Billingenian Substage – ? Early Volkhov Stage (*M. estonica* Zone – ? *M. polyphemus* Zone).

– *Baltoniodus? triangularis* interval Zone

Definition – The zone is defined by the interval between the FAD of *Baltoniodus? triangularis* to the FAD of *Microzarkodina flabellum*.

Reference-Section – Section North of Horns Udde.

Reference-strata – The interval between 3.48 m and 4.12 m above the base of the section (Samples HU 636A – HU 638; HUQ 3 – HUQ 4).

Description – The base of the zone is characterized by the FAD of the nominate species, which is common in the zone.

Microzarkodina n.sp. A, *Scalpellodus cf. latus* and *P. cf. flabellum* have their upper ranges in the zone.

Scolopodus princeps n.sp. and *Oistodus* sp. are constrained to the zone. *Protopanderodus floridus* n. sp. appears at the base of the zone and *Baltoniodus cf. navis* has its first appearance in the zone. Both species extend into the next zone.

Paroistodus parallelus returns to the area and it is represented by a short (partial-) range within the zone.

Age – Early Volkhov (*M. polyphemus* Zone).

Remarks – The sudden appearance of several new taxa suggests that a hiatus is present at the base of the zone in this area.

– *Microzarkodina flabellum* interval Zone

Definition – This zone is defined by the first appearance of the nominate species to the first appearance of *Baltoniodus navis*.

Reference-Section – Section North of Horns Udde.

Reference-strata – The rock interval from 4.22 m above the base of the section to 4.45 m above the base of the section. (Sample HU 639).

Description – The nominate species is characteristic for the zone. *Oistodus* sp. A is constrained to the zone. *Periodon* sp. A has its first appearance in this zone.

Scandodus furnishi, *Oistodus lanceolatus*, *Baltoniodus?* *triangularis*, and *Protopanderodus floridus* have their upper ranges at the top of the zone.

Age – Volkhov Stage (*M. polyphemus* Zone).

– *Baltoniodus navis* interval Zone

Definition – The zone is defined by the first appearance of *Baltoniodus navis* to the first appearance of *Microzarkodina parva*.

Reference-Section – Section North of Horns Udde.

Reference-strata – The rock interval from 4.45 m to 6.13 m above the base of the section (Samples HU 640 - HU 644; HUQ 5 - HUQ 8).

Description – The nominate species is present throughout the zone and extends into the following zone. *Trapezognathus quadrangulum* appears together with the nominate species.

Scalpellodus latus, *Drepanoistodus basiovalis*, *Paroistodus originalis*, and *Triangulodus brevibasis* have their first appearance within the zone and extend into higher strata.

Periodon sp. B and *Gothodus* cf. *costulatus* are restricted to the zone in this region.

Periodon sp. A and *Baltoniodus* cf. *navis* have their upper ranges in the zone.

Paroistodus parallelus returns and has a constrained (partial-) range in the zone.

Age – Volkhov Stage (*M. polyphemus* Zone).

– *Microzarkodina parva* interval Zone

Definition – The zone is defined by the first appearance of *Microzarkodina parva* to the first ap-

pearance of *Baltoniodus norrlandicus*.

Reference-Section – Section North of Horns Udde.

Reference-strata – The rock interval from 6.13 m to 6.53 m above the base of the section (Samples HU 645 - HU 646; HUQ 9 - HUQ 10).

Description – The nominate species is present throughout the zone and extends into higher zones. The species from the older zones extend through the zone.

Age – Volkhov Stage (*M. simon* Zone).

– *Baltoniodus norrlandicus* interval Zone

Definition – The zone is defined as the interval from the first appearance of *Baltoniodus norrlandicus* to the first appearance of *Lenodus antivariabilis*.

Reference-Section – Horns Udde Quarry.

Reference-strata – The rock interval from 3.10 m to 4.50 m above the base of the section (Samples HU 647 - HU 651; HUQ 11 - HUQ 12B).

Description – The nominate species ranges throughout the zone and extends into higher beds. «*Semiacontiodus*» *cornuformis* s.l. (early type, see Stouge & Bagnoli, 1990; Löfgren, 1995), *Baltoniodus navis*, *Trapezognathus quadrangulum*, *Scolopodus rex*, and *Triangulodus brevibasis* have their upper ranges in the zone.

Periodon sp. C and *Oistodus* sp. B are restricted to the zone in this area.

Age – Volkhov Stage (*M. limbata* Zone).

– *Lenodus antivariabilis* interval Zone

Definition – The zone is defined by the first appearance of *Lenodus antivariabilis* to the first appearance of *Lenodus* sp. A.

Reference-Section – Horns Udde Quarry.

Reference-strata – The rock interval from 4.50 m above the base of the section to 6.05 m above the base of the section. (Samples HU 654; HUQ 12C - HUQ14).

Description – The nominate species extends through the zone. *Scalpellodus gracilis* appears in the zone.

Age – Volkhov Stage (*M. limbata* Zone).

– *Lenodus* sp. A interval Zone

Definition – The zone is defined by the first appearance of *Lenodus* sp. A to the first appearance of *Microzarkodina hagetiana*.

Reference-Section – Horns Udde Quarry.

Reference-strata – The rock interval from 6.05 m above the base of the section to 7.35 m, which is near the top of the section. (Samples HUQ 14A - HUQ 15; HU 654A - HU 655).

Description – The nominate species extends through the zone.

Parapanderodus quietus appears in the zone and continues into higher intervals and *Baltoniodus norrlandicus* extends through the zone. *Lenodus antivariabilis* has its upper range into the zone.

Age – Volkhov - Kunda Stages (*M. limbata* - *A. expansus* Zones).

DATUM LEVELS OF CORRELATIVE SIGNIFICANCE

The distribution of certain characteristic species allows the recognition of several intervals which may turn out to be of very precise correlative value. We have however noted that not all of the proposed palaeontological datum events (van Wamel, 1974; Löfgren, 1993b, 1994) can be recognized over larger distances on the East European Platform and so we have not used these events as zonal indicators.

The common occurrence of *Oepikodus evae* and *Prioniodus elegans* (and *Oelandodus elongatus*) at the base of the *Oepikodus evae* interval Zone is very useful for regional and international correlation (Bergström, 1988; Stouge & Bagnoli, 1988). This evidence may prove useful for establishing a concurrent range zone of extensive and precise correlation. *Prioniodus elegans* however is often only found reworked at the basis of the *O. evae* Zone over most of the East European Platform (Lindström, 1971) and we have not taken this interval into consideration at the present time.

The FAD of *Gothodus costulatus* may also be useful for the subdivision of the *O. evae* interval Zone (see van Wamel, 1974 and Löfgren, 1993b, 1994). The taxon is not consistently present across the platform (eg. it is apparently missing in Finngrundet, Löfgren, 1985) but appears only in successions which are closer to the margin of the platform. Therefore this taxon has limited value for correlation across the platform.

Triangulodus brevibasis has been important for the recognition of the *Paroistodus originalis* Zone (Lindström, 1971; Rasmussen, 1991; Löfgren, 1995). The taxon appears on the platform without an ancestor and it is considered a migrating species (Dzik, 1994).

The stratigraphical overlap of *Triangulodus brevibasis* and *Drepanoistodus forceps* appears to be valuable as a potential interval for correlative purpose across the platform (Rasmussen, unpubl. Ph.D. Thesis, Univ. Copenhagen, 1994). Löfgren (1995) described this overlap as «phase 1» of the *Paroistodus originalis* Zone. The concurrent ranges of *Triangulodus brevibasis* and *Drepanoistodus forceps* oc-

curs in samples HU 643 - HU 644 and HUQ 7, HUQ 6, and HUQ 8.

COMPARISON WITH LINDSTRÖM'S (1971) ZONATION

The zonal scheme summarized for the lower Ordovician of Baltoscandia by Lindström (1971) has been applied almost unchanged since 1971, except for minor alterations by Löfgren (1978). Recently, revisions of the scheme have begun (Bagnoli *et al.*, 1988; Stouge, 1989; Stouge & Bagnoli, 1990; Rasmussen, 1991; Löfgren, 1993a, b, 1994, 1995).

During the work on the Lower Ordovician conodont succession and as the knowledge increased, it became clear that some zones introduced by Lindström (1971) in the Arenig can not be applied for correlation everywhere in Baltoscandia (Kohut, 1972; Stouge, 1975, 1989; Rasmussen, 1991). In particular the upper *O. evae* Zone, the *Paroistodus originalis* Zone and the *Microzarkodina parva* Zone appeared to be problematic to recognize and to use for correlation. The problems include for example the definition of the upper *Oepikodus evae* Subzone that was based on the interval with negative evidence of the nominate species. In addition new data showed that ranges of nominate species or important species became extended or the ranges differed from one region to another on the platform.

– *Prioniodus elegans* interval Zone

The *Prioniodus elegans* interval Zone correspond to the *Prioniodus elegans* Zone of Lindström (1971).

– *Oepikodus evae* interval Zone

The basis of the *Oepikodus evae* interval Zone is apparently coeval with the base of the *O. evae* Zone of Lindström (1971). At Horns Udde the lower *O. evae* Zone of Lindström (1971) corresponds to the total range of *O. evae* and the partial range of *Paroistodus parallelus*. Thus, the lower *O. evae* Zone is clearly recognized in the region and elsewhere on the East European Platform (Löfgren, 1993b, 1994).

– *Trapezognathus diprion* interval Zone

The zone can be correlated with the uppermost part of the lower *O. evae* Zone and the lower part of the upper *O. evae* Zone of Lindström (1971) where *O. evae* and *Trapezognathus diprion* have overlapping ranges. Correlation with the upper part of *O. evae* Zone *sensu* Lindström (1971) is not precise.

– *Microzarkodina* sp. A interval Zone

This zone is constrained to the topmost part of the *Oepikodus evae* Zone of Lindström (1971). The *Microzarkodina* sp. A interval Zone is situated below

the «Blommiga Bladet» (= «Flowery Sheet»). Lindström (1971) used the «Flowery Sheet» as the top of the *O. evae* Zone and the base for the Volkov Stage.

Lindström (1971) did notice the presence of «rare» *Microzarkodina* below the «Blommiga Bladet», but did not comment or use this information further.

– *Baltoniodus? triangularis* interval Zone

This interval zone corresponds to the lower part of the *Baltoniodus triangularis* Zone of Lindström (1971). The zone is characterized by a faunal assemblage consisting of several new species.

– *Microzarkodina flabellum* interval Zone

The *Microzarkodina flabellum* interval Zone is coeval with the upper *Baltoniodus triangularis* Zone of Lindström (1971).

– *Baltoniodus navis* interval Zone

This interval zone begins at an horizon that is higher than the base of the *Baltoniodus navis* Zone *sensu* Lindström (1971) because we distinguish *Baltoniodus cf. navis* from *Baltoniodus navis* (see systematic palaeontology).

The *Baltoniodus navis* interval Zone extends into the lower *Paroistodus originalis* Zone of Lindström (1971).

– *Microzarkodina parva* interval Zone

The *Microzarkodina parva* interval Zone corresponds to a level within the *Paroistodus originalis* Zone of Lindström (1971). It can not be precisely correlated with Lindström's (1971) zonation because FAD of *Microzarkodina parva* appears after the appearance of *Triangulodus brevibasis* and after the level where the number of *Drepanoistodus basiovalis* surpasses that of *Drepanoistodus forceps* and after the acme of *Paroistodus originalis*.

The *Microzarkodina parva* interval Zone is older than the *Microzarkodina parva* Zone of Lindström (1971). This is due to the different definition of the zone applied in this paper and by Lindström (1971). The FAD of the nominate species is applied here whereas Lindström (1971) used the common occurrence of *Microzarkodina parva* and «*Semiacontiodus*» *cornuformis* s.l., which appears in the next zone.

– *Baltoniodus norrlandicus* interval Zone

The *Baltoniodus norrlandicus* Zone can be correlated with the *Microzarkodina parva* Zone (pars) *sensu* Lindström (1971) from the level where «*Semiacontiodus*» *cornuformis* s.l. appears.

Baltoniodus norrlandicus appears stratigraphically earlier than «*Semiacontiodus*» *cornuformis* s.l. (Text-fig. 5)

– *Lenodus antivariabilis* interval Zone

The nominate species of this zone is newly revised and direct correlation with Lindström's (1971) zonation is not possible. It is uncertain if this taxon is part of the extensive *Amorphognathus variabilis* Zone *sensu* Lindström (1971) (Stouge, 1989; Stouge & Bagnoli, 1990). *Lenodus antivariabilis* is of late Volkhov age and thus the *L. antivariabilis* interval Zone should be pre-*Amorphognathus variabilis* age according to the definition of Lindström (1971).

– *Lenodus* sp. A interval Zone

Presumably this zone corresponds with the early *Amorphognathus variabilis* Zone of Lindström (1971). *Lenodus* sp. A appears at the lower boundary of or within the Kunda Stage (Stouge & Bagnoli, 1990).

COMPARISON WITH VAN WAMEL'S (1974) ZONATION

In the zonation promoted by van Wamel (1974) the first appearance datum (FAD) and last appearance datum (LAD) or combination of those were used. Van Wamel labelled his zones assemblage zones but they were actually defined as range, interval or concurrent range zones. As the FAD's are used in this study several levels correspond with those of van Wamel (1974).

Van Wamel (1974) focused on the Hunnebergian and Billingenian Substages of the Latorp Stage in his detailed subdivision. The interval from the uppermost part of the Billingenian Substage and the Volkhov Stage was not subdivided in detail and the zones in this interval are rather broad (Text-fig. 8).

– *Prioniodus elegans* interval Zone

Prioniodus elegans interval Zone comprises the *Prioniodus elegans-Oelandodus elongatus* Assemblage Zone, the *Stolodus stola* Assemblage Zone and the *Protopanderodus rectus-Oelandodus costatus* Assemblage Zone. Van Wamel's (1974) assemblage zones represent a subdivision of one zone and are based on the faunal succession within the zone (Bagnoli *et al.*, 1988).

– *Oepikodus evae* interval Zone

This zone includes the *Protopanderodus rectus-Oepikodus evae* Assemblage Zone, the *Oistodus lanceolatus-Prioniodus deltatus* Assemblage Zone and the *Prioniodus crassulus* Assemblage Zone of van Wamel (1974).

CHRONOSTRATIGRAPHY REGIONAL STANDARD			TRILOBITE ZONES	CONODONT ZONES						
SERIES	STAGE	SUBSTAGE	Tjernvik, 1956 Tjernvik & Johansson, 1980	Lindström, 1971		van Wamel, 1974	Löfgren, 1993b 1994, 1995		This study	
O E L A N D	KUNDA	Hunde- rumian	<i>Asaphus expansus</i>	<i>Amorphognathus variabilis</i>			<i>Amorphognathus? variabilis</i>		<i>Lenodus</i> sp.A	
	V O L K H O V	Lange- vojan	<i>Megistaspis (M.) limbata</i>	<i>Microzarkodina parva</i>				<i>Microzarkodina parva</i>		<i>Lenodus antivariabilis</i>
										<i>Baltoniodus norrlandicus</i>
			<i>Megistaspis simon</i>	<i>Paroistodus originalis</i>		<i>Triangulodus brevibasis</i>	<i>Paroistodus originalis</i>		<i>Microzarkodina parva</i>	
			<i>Megistaspis (M.) polyphemus</i>	<i>Baltoniodus navis</i>			<i>Baltoniodus navis</i>	Upper	<i>Baltoniodus navis</i>	
								Middle		
								Lower	<i>Microzarkodina flabellum</i>	
					<i>Baltoniodus triangularis</i>		<i>Microzarkodina flabellum</i>	Upper	<i>Baltoniodus? triangularis</i>	
						Lower				
	L A T O R P	Billin- genian		<i>Megistaspis (V.) estonica</i>	Upper		<i>Drepanoistodus forceps</i> <i>Prioniodus navis-Stolodus stola</i>		Upper	<i>Microzarkodina</i> sp.A
				<i>Megalaspides (M.) dalecarlicus</i>	<i>Oepikodus evae</i>	Lower			<i>Prioniodus navis-Prioniodus crassulus</i>	Upper
			<i>Prioniodus crassulus</i>				Middle			
				<i>Megistaspis (V.) aff. estonica</i>		<i>Prioniodus elegans</i>	<i>Oistodus lanceolatus</i>	Lower Middle	<i>Oepikodus evae</i>	
<i>Oistodus lanceolatus- Prioniodus deltatus</i>		Lower								
<i>Protopanderodus rectus-Oepikodus evae</i>										
		Hunne- bergian				<i>Protopanderodus rectus-Oelandodus costatus</i>	<i>Prioniodus elegans</i>		<i>Prioniodus elegans</i>	
					<i>Stolodus stola</i>					
					<i>Prioniodus elegans-Oelandodus elongatus</i>					

Text-fig. 8 - Comparison with Lindström's (1971), van Wamel's (1974), and Löfgren's (1993b, 1994, 1995) zones with the interval zones in this study.

The *Protopanderodus rectus*-*Oepikodus evae* Assemblage Zone and the *Oistodus lanceolatus*-*Prioniodus deltatus* Assemblage Zone are not considered valid because the ranges of the nominate species, i.e. *Protopanderodus rectus* and *Oistodus lanceolatus*, are different than those found by van Wamel (1974). The *Oistodus lanceolatus* Assemblage Zone could not be established as a distinct unit, because *Prioniodus deltatus sensu* van Wamel (1974), which characterizes the former zone has not been recognized or recorded in this study.

The *Prioniodus crassulus* (= *Gothodus costulatus*) Assemblage Zone is recorded from sample HU 613 to sample HU 615 within the *Oepikodus evae* interval Zone.

– *Trapezognathus diprion* interval Zone

The *Trapezognathus diprion* interval Zone corresponds to the *Prioniodus navis*-*Prioniodus crassulus* Assemblage Zone (we consider the early *Prioniodus navis sensu* van Wamel, 1974 = *T. diprion*), the *Prioniodus navis*-*Stolodus stola* Assemblage Zone and the *Drepanoistodus forceps* Assemblage Zone. The first assemblage zone is recorded in samples HU 620 to HU 631 and it is easy to recognize. The second zone, i.e. *Prioniodus navis*-*Stolodus stola* Assemblage Zone, is recognized in sample HU 632 and the third zone is constrained to an interval between samples HU 632 and HU 633. The boundaries of the two zones are not precisely delineated and are difficult to distinguish (van Wamel, 1974). The two latter zones should probably be abandoned.

The distribution of the taxa from the section North of Horns Udde shows that the species *Trapezognathus diprion*, *Baltoniodus? triangularis*, *Baltoniodus* cf. *navis*, and *Baltoniodus navis* were all referred to *Prioniodus navis* by van Wamel (1974). This taxonomical approach caused problems, because van Wamel (1974) correlated the *Prioniodus navis*-*Prioniodus crassulus*, the *Prioniodus navis*-*Stolodus stola*, the *Drepanoistodus forceps* and the *Microzarkodina flabellum* assemblage Zones with the upper *Oepikodus evae*, *Baltoniodus triangularis* and *Baltoniodus navis* Zones of Lindström (1971). The identification of *Trapezognathus diprion* interval Zone as a pre-*Baltoniodus triangularis* Zone may help to clarify the problematic correlation made by van Wamel (1974).

– *Microzarkodina* sp. A interval Zone

The basis of this zone coincides with the *Microzarkodina flabellum* Assemblage Zone of van Wamel (1974). The *Microzarkodina flabellum* Assemblage Zone is an extensive unit and covers several of the interval zones promoted in this study.

– *Baltoniodus? triangularis* interval Zone.

The zone corresponds to the middle part of the *Microzarkodina flabellum* Assemblage Zone of van Wamel (1974). More precise correlation is not possible, also because van Wamel's concept of *Prioniodus navis* is different from that of this study and corresponds to three or four species in our interpretation.

– *Microzarkodina flabellum* interval Zone

The *Microzarkodina flabellum* interval Zone is completely contained in the *Microzarkodina flabellum* Assemblage Zone of van Wamel (1974).

– *Baltoniodus navis* interval Zone

This interval zone covers the highest part of the *Microzarkodina flabellum* Assemblage Zone and it extends into the following *Triangulodus brevibasis* Assemblage Zone.

– *Microzarkodina parva* interval Zone

This interval zone is completely contained within the *Triangulodus brevibasis* assemblage Zone. Van Wamel (1974) did not distinguish *M. flabellum* from *M. parva* and a further precise correlation is not possible.

– *Baltoniodus norrlandicus* interval Zone

The lower part of this interval zone until the appearance of «*Semiacontiodus*» *cornuformis* s.l. covers the top of the *Triangulodus brevibasis* Zone of van Wamel (1974), who defined the *T. brevibasis* Zone as a range zone. Van Wamel (1974) did not record the top of the zone in his study.

COMPARISON WITH LÖFGREN'S (1993b, 1994, 1995) FAUNAL SUCCESSIONS

Löfgren (1993b, 1994, 1995) presented modifications to Lindström's (1971) zonation based on studies of numerous sections, particularly from the Swedish mainland. The approach of Löfgren in the papers has been variable and her definitions of zones include FAD's, interval zones or relative abundances. In some instances detailed correlation has been carried out by using relative abundance of species in the samples. Löfgren's zonation is a variety of Lindström's (1971) and apparently includes an ecostratigraphic or biofacies approach. Some of the zonal boundaries of Löfgren in the upper Billingenian Substage and the Volkhov Stage and those of this study rarely coincide (Text-fig. 8), because different zonal fossils have been applied.

– *Prioniodus elegans* interval Zone

The *Prioniodus elegans* interval Zone is defined in the same way as Löfgren (1994) did. Therefore the concept of *Prioniodus elegans* Zone of Löfgren (and that of Lindström, 1971) and ours is identical.

– *Oepikodus evae* interval Zone

Löfgren (1993b) informally subdivided the *Oepikodus evae* Zone of Lindström (1971) into four sub-units (lower, lower-middle, upper-middle, upper) which can be (pars) recognized in the *Oepikodus evae* interval Zone. The lower *O. evae*, the lower-middle *O. evae* and the upper-middle (pars) *O. evae* subzones of Löfgren (1993b, 1994) are contained in the *O. evae* interval Zone. Like van Wamel (1974), Löfgren (1993b, 1994) promoted the FAD of *Prioniodus crassulus* (= *Gothodus costulatus*) as a marker for the subdivision of the *O. evae* Zone.

– *Trapezognathus diprion* interval Zone

This zone begins within the upper-middle part of the *Oepikodus evae* Zone *sensu* Löfgren (1993b). It covers most of the upper *O. evae* Zone *sensu* Löfgren (1993b, 1994). The upper *O. evae* Zone of Löfgren (1993b) is identical with the upper *O. evae* Zone of Lindström (1971).

– *Microzarkodina* sp. A interval Zone

This interval zone covers the top of the upper *Oepikodus evae* Zone *sensu* Löfgren (1993b, 1994). Löfgren (1993b, 1994) in her detailed investigations did not record *Microzarkodina* in this interval, nor comment on this. Therefore further precise correlation on the basis of Löfgren's (1993b, 1994) data is not possible.

– *Baltoniodus? triangularis* interval Zone

This zone is equivalent to the lower *Baltoniodus triangularis* Zone of Löfgren (1993b, 1994).

– *Microzarkodina flabellum* interval Zone

This is the upper *Baltoniodus triangularis* Zone of Löfgren (1993b, 1994). The position of the lower boundary of the *Baltoniodus navis* Zone of Löfgren (1993b, 1994) is uncertain, because we distinguish *Baltoniodus* cf. *navis* from *B. navis*. The common occurrence of *B. cf. navis* and *B.? triangularis* in samples HU 638 and HU 639 probably corresponds with the lower *B. navis* Zone *sensu* Löfgren (1993b, 1994, 1995).

– *Baltoniodus navis* interval Zone

This interval zone correlates with the middle *Baltoniodus navis* Zone; the upper *Baltoniodus navis* Zone and part of the *Paroistodus originalis* Zone of

Löfgren (1993b, 1994, 1995). The *Baltoniodus navis* interval Zone covers the lower *Paroistodus originalis* zonal boundary of Löfgren (1995).

– *Microzarkodina parva* interval Zone

This zone is equivalent to a level which is high within the *Paroistodus originalis* Zone of Löfgren (1994, 1995). It appears to correspond to phases 3, 4, and 5 of Löfgren (1995).

– *Baltoniodus norrlandicus* interval Zone

The base of this interval zone is coeval with the base of *Microzarkodina parva* Zone of Löfgren (1995) but *B. norrlandicus* appears before «*Semiacontiodus*» *cornuformis* s.l. in the Öland sections. Apparently, the data presented by Löfgren (1994, 1995) suggest that there is a hiatus at the base of this interval zone in many sections in Sweden.

– *Lenodus antivariabilis* and *Lenodus* sp. A interval Zones

At present and similar to Lindström's (1971) zonation it is not possible to identify the two interval zones on the base of Löfgren's (1978, 1985, 1995) data. Possibly *Lenodus* sp. A is the same species as *Amorphognathus? variabilis sensu* Löfgren (1995) as the species (pars) are of Kunda age.

The correlation of the interval zones of this paper with the zones of Lindström (1971), van Wamel (1974), and Löfgren (1993b, 1994, 1995) is given in Text-fig. 8.

SYSTEMATIC PALAEOLOGY

Limestone samples from the sections were processed for conodonts. A total of 85 limestone samples were dissolved using standard analysis technique, i.e. 10% acetic acid, and washed through a 63µm sieve. The conodonts were recovered from limestone samples weighting 500-1000 gms. The residue was handpicked without using heavy liquid separation.

All samples were found to yield conodonts. The number of conodont elements investigated is given in Tables 1 and 2 and the total number of discrete conodont elements collected from the two sections is 57664.

All the elements are thermally unaltered and yellow in color (CAI 1 of Epstein *et al.*, 1977), most of them are well preserved, and virtually all of them are specifically identifiable. In the higher part of the sequence and within formation A and B the yield and preservation of the discrete conodont elements is lower than below and many specimens are fragmented.

65 species (4 of which are new; 20 are informally recognized) belonging to 30 genera (1 of which is new) are identified.

Repository

All type specimens bear five digit catalog numbers of the Invertebrate Palaeontology Collections, Geological Museum, University of Copenhagen, Denmark (prefix MGUH).

Genus BALTONIODUS Lindström, 1971

Type species – *Prioniodus navis* Lindström, 1955.

BALTONIODUS cf. *B. NAVIS* (Lindström)
Pl. 1, figs. 9-15

cf. 1955 *Prioniodus navis* n.sp. LINDSTRÖM, p. 590 (*partim*), pl. 5, fig. 33 (only).

Remarks – *Baltoniodus* cf. *B. navis* (Lindström) is represented in this collection by few small specimens which are not well preserved. Compared with *Baltoniodus navis*, the denticulation is more discrete and the basal cavity is deeper. The Pb element has a posterior process which is relatively shorter than in *B. navis*. The specimens at hand may be early representatives of *Baltoniodus navis* or are a new species.

Occurrence – Samples HU 638-639; HUQ 5.

Material – 25 Pa elements, 15 Pb elements, 24 M elements, 12 Sa elements, 17 Sb elements, 10 Sc elements, 29 Sd elements.

Repository – MGUH 24018-24024.

BALTONIODUS? TRIANGULARIS (Lindström)
Pl. 3, figs. 1-12

Pa element

1955 *Prioniodus navis* n.sp. LINDSTRÖM, pp. 590-591 (*partim*), pl. 5, figs. 31-32 (only).

?1955 *Prioniodus triangularis* n.sp. LINDSTRÖM, pp. 591-592, pl. 5, fig. 45 (only).

Pb element

1955 *Prioniodus navis* n.sp. LINDSTRÖM, pp. 590-591 (*partim*), pl. 5, figs. 34-35 (only).

Sa element

?1955 *Trichonodella longa* n.sp. var. *minor* nov. LINDSTRÖM, p. 601 (*partim*), pl. 6, figs. 18-19 (only).

Sb element

1955 *Prioniodus triangularis* n.sp. LINDSTRÖM, pp. 591-592 (*partim*), pl. 5, fig. 46 (only).

Sc element

1955 *Prioniodina densa* n.sp. LINDSTRÖM, pp. 586-587, pl. 6, fig. 20.

Sd element

1955 *Trapezognathus quadrangulum* n.sp. LINDSTRÖM, p. 598 (*partim*), pl. 5, figs. 40-41 (only).

Multielement

1971 *Baltoniodus triangularis* (Lindström) - LINDSTRÖM, p. 55, pl. 1, fig. 12.

1974 *Prioniodus navis* Lindström - VAN WAMEL, pp. 89-90 (*partim*), pl. 12, figs. 2, ?3 (only).

1994 *Baltoniodus triangularis* (Lindström) - LÖFGREN, fig. 8: 28, 29.

Description – The elements of *Baltoniodus? triangularis* are denticulated and with a deep basal cavity and a large basal sheath.

The Pa element has a proclined cusp and three processes with apically free denticles. The anterior process is the most commonly preserved and is as long as the cusp and downwards directed. The lateral process can be as long as the anterior one. The posterior process, which is very rarely preserved, carries denticles increasing in size distally.

The Pb element has a stubby cusp and three processes with mostly confluent denticles.

The M element has a suberect cusp which is as long as the anterior edge of the base and a long posterior extension. The anterior edge of the base is frequently serrated on the distal part. In several specimens the tip of the cusp is sigmoidal in lateral view, owing to a slight concavity of the distal part of the anterior edge of the cusp.

The S elements are denticulated and with slender cusp.

The lateral processes of the Sa element are denticulated and quite divergent in posterior view. The anterior face of the base is flat. The posterior margin of the cusp has a keel that continues beyond the aboral margin as a very short adenticulated process.

The Sb and Sc elements are proclined with proclined, small, mostly free denticles on the anterior and posterior processes.

The Sd elements are curved to proclined. The base has two anterior, one lateral and one posterior keels/costae which extend beyond the base as thin denticulated processes, which are however rarely preserved.

Remarks – The type specimen of *Baltoniodus? triangularis* is a Sb element. This element is well denticulated, which is not well displayed by Lindström (1955, Pl. 5, fig. 46). Lindström (1971) stated that this is a robust species. This is true for the P elements, whereas the S elements are quite slender. Denticulation of this species is well developed rather than being sporadic in the S elements. The basal

sheath of P and S elements is thin and fragile and the specimens are frequently incompletely preserved. Some elements of this species, when broken, can be difficult to distinguish from those of *Trapezognathus* Lindström, and we can not exclude that the interval includes some *Trapezognathus* elements.

Material – 173 Pa elements, 55 Pb elements, 124 M elements, 45 Sa elements, 75 Sb elements, 61 Sc elements, 101 Sd elements.

Occurrence – Samples HU 636A-639; HUQ 3-4.

Repository – MGUH 24043-24054

Genus DREPANOISTODUS Lindström, 1971

Type species – *Oistodus forceps* Lindström, 1955.

DREPANOISTODUS aff. *D. contractus* (Lindström).
Pl. 1, figs. 16a-b

aff. 1955 *Oistodus contractus* n.sp. LINDSTRÖM, p. 573, pl. 4, figs. 45-46, text-fig. 3H.

Remarks – The oistodiform element of *Drepanoistodus* aff. *D. contractus* has a small base similar to that of *Drepanoistodus contractus* (Lindström), but it is characterized by an inverted basal cavity.

Occurrence – Samples HUQ 15A-17.

Material – 10 oistodiform elements and 5 drepanodiform elements.

Repository – MGUH 24025.

Genus GOTHODUS Lindström, 1955

Type species – *Gothodus costulatus* Lindström, 1955.

Discussion – The genus *Gothodus* was erected by Lindström in 1955 who selected *Gothodus costulatus* Lindström, 1955 as the type species. Lindström (1971) revised the genus *Gothodus* as a multielement genus with a seximembrate apparatus consisting of P, M and S elements. In this reconstruction *Gothodus costulatus* Lindström, 1955 was the Sb element and *Oepikodus crassulus* Lindström, 1955 was the Sd element.

Sweet & Bergström (1972), however, placed *Gothodus costulatus* Lindström, 1955 in synonymy with *Prioniodus* Pander, 1856. Sweet & Bergström (1972) also queried the elemental composition of the apparatus which, according to Lindström (1971), should be referred to *Gothodus costulatus* Lindström *sensu* Lindström, 1971.

Van Wamel (1974) in his reconstruction of *Prioniodus crassulus* (Lindström) identified seven element types in an apparatus consisting of Pa, Pb, M, and a complete series of S elements. This apparatus included *Oepikodus crassulus* Lindström, 1955, but *Gothodus costulatus* was placed in synonymy with *Prioniodus elegans* Pander, 1856,

EXPLANATION OF PLATE 1

- Figs. 1-8 - *Baltoniodus navis* (Lindström). Section North of Horns Udde.
1) Pa element, sample HU 642, MGUH 24010, ×80.
2) Pb element, sample HU 643, MGUH 24011, ×80.
3) Sa element, sample HU 643, MGUH 24012, posterior view, ×90.
4) Pb element, sample HU 642, MGUH 24013, ×55.
5) Sc element, sample HU 645, MGUH 24014, ×75.
6) Sb element, sample HU 643, MGUH 24015, ×70.
7) Sd element, sample HU 642, MGUH 24016, ×80.
8) M element, sample HU 644, MGUH 24017, ×60.
- Figs. 9-15 - *Baltoniodus* cf. *B. navis* (Lindström). Section North of Horns Udde, sample HU 638.
9) M element, MGUH 24018, ×100.
10) Pa element, MGUH 24019, ×85.
11) Pb element, MGUH 24020, ×100.
12) Sa element, MGUH 24021, posterior view, ×80.
13) Sc element, MGUH 24022, ×90.
14) Sd element, MGUH 24023, ×85.
15) Sb element, MGUH 24024, ×90.
- Figs. 16a-16b - *Drepanoistodus* aff. *D. contractus* (Lindström). Horns Udde Quarry, sample HUQ 17.
16a) Oistodiform element, MGUH 24025, ×45.
16b) Detail of the inverted basal cavity, ×170.
- (Specimens shown in lateral view, if not specified).



thus following Sweet & Bergström (1972). The apparatus reconstruction of van Wamel (1974) was accepted by Lindström (*in* Ziegler *et al.*, 1977) and later confirmed by Bagnoli *et al.* (1988). The latter authors allocated the taxon to *Baltoniodus* Lindström rather than to *Prioniodus* Pander.

Although accepted by many authors including ourselves (van Wamel, 1974; Lindström *in* Ziegler *et al.*, 1977; Löfgren, 1978 (tentatively), Bagnoli *et al.*, 1988), the allocation of the type specimen of *Gothodus costulatus* Lindström, 1955 to *Prioniodus* (i.e. *P. elegans*) was not convincing. The specimens of *Gothodus costulatus* Lindström, 1955 are all Sb elements belonging to *Prioniodus crassulus* (Lindström) *sensu* van Wamel, 1974 and *Baltoniodus crassulus* (Lindström) *sensu* Bagnoli *et al.*, 1988. As a consequence, the genus *Gothodus* Lindström, 1955 is valid and is not considered a junior synonym of *Prioniodus* Pander, 1856 or *Baltoniodus* Lindström, 1971. In addition, *Gothodus* is a taxon phylogenetically independent from *Prioniodus* and *Baltoniodus*. As suggested by Dzik (1994) it is possible that *Gothodus* Lindström, 1955 is related to *Phragmodus* Branson & Mehl, 1933.

Emended diagnosis – The apparatus of *Gothodus* Lindström, 1955 is septimembrate. The Pa and Pb elements are pectiniform, the M element is geniculate coniform, and the S elements form a symmetry transition series including alate, bipennate, tertiopectate and quadriramate ramiform elements.

The P elements may be fully denticulated, the M element is adenticulate and with a pointed antero-basal extension that is markedly shorter than the posterior extension.

The posterior process is denticulated on all S elements. The lateral processes are denticulated on the Sa elements. The anterior and lateral processes of the other S elements are adenticulated and become denticulated distally in younger species of the genus.

Remarks – Several species of *Gothodus* have previously been referred to *Phragmodus* Branson & Mehl, 1933 (Dzik, 1978, 1994 and references therein), *Prioniodus* Pander, 1856 (Cooper, 1981 with a query) or in open nomenclature (Ethington & Clark, 1982).

The apparatus of the type species of *Phragmodus* is unknown. Reconstructions of the *Phragmodus* apparatus on the basis of other species than the type species include elements (Sweet *in* Ziegler, 1981) that are not recognized in *Gothodus*. Probably more than one genus is present within these reconstructions (see discussions in Ethington & Clark 1982; Dzik, 1978, 1994; Sweet *in* Ziegler, 1981).

One group of *Phragmodus* includes angulate and pastinate P elements and dolobrate M elements in the apparatus and this group is not considered to be closely related with *Gothodus*. An other group of *Phragmodus* (i.e. ?*Phragmodus flexuosus* Moskalenko *sensu* Ethington & Clark, 1982) has an apparatus which is similar to the apparatus of *Gothodus* and a generic affinity with *Gothodus* is possible. *Gothodus* is, nevertheless, considered to be a genus in its own right during the early Arenig to the late Llanvirn. The possible ancestor-descendant relationship between *Gothodus* and *Phragmodus* can not be evaluated until the type species of *Phragmodus* has been established as a multielement genus.

The following taxa can be assigned to *Gothodus* Lindström, 1955:

– *Gothodus costulatus* Lindström, 1955 (emended herein) from the Billingenian Substage and *Gothodus* cf. *costulatus* from the Volkhov Stage.

– *Gothodus* n.sp. = aff. *Oepikodus*? *minutus* (McTavish) *sensu* Ethington & Clark, 1982 from the Ninemile Formation and the Vinini Formation, central Nevada (R. Ethington, pers. comm., 1996) and the Cow Head Group, Newfoundland (Stouge, undescribed collection). The species is common within *Isograptus* (v.) *victoriae* graptolite Zone.

– *Gothodus amadeus* (Cooper, 1981) of Volkhov-Kundan age.

– *Gothodus polonicus* (Dzik) is from the Arenig and Llanvirn of Poland. The early form is known also from Scania, Sweden, and Bornholm, Denmark (Stouge, unpublished collection).

Phragmodus? sp. aff. «*Baltoniodus*» *crassulus* (Lindström, 1955) *sensu* Dzik, 1994 is neither *Phragmodus* nor *Gothodus*; it is a new genus with a dolobrate M element (Stouge, undescribed collection from Scania and Bornholm).

GOTHODUS COSTULATUS Lindström, 1955

Pl. 2, figs. 10-17

P element

1955 *Prioniodus acodiformis* n.sp. LINDSTRÖM, p. 591, pl. 5, fig. 42.

M element

1955 *Oistodus linguatus* n.sp. LINDSTRÖM, pp. 577-578 (*partim*), pl. 3, figs. 39-40 (only).

Sa element

1955 *Trichonodella longa* n.sp. LINDSTRÖM, p. 600, pl. 6, figs. 47-48.

Sb element

1955 *Gothodus costulatus* n.sp. LINDSTRÖM, p. 569, pl. 5, figs. 23-25.

Sd element

1955 *Oepikodus crassulus* n.sp. LINDSTRÖM, pp. 570-571 (*partim*), pl. 5, fig. 36 (only).

Multielement

- 1971 *Gothodus costulatus* Lindström - LINDSTRÖM, pp. 54-55 (*partim*), pl. 1, figs. 4, 5 (only).
 1974 *Prioniodus crassulus* (Lindström) - VAN WAMEL, pp. 83-85, pl. 6, figs. 7-14.
 1977 *Acodus deltatus deltatus* (Lindström) - Lindström in ZIEGLER, pp. 7-8 (*partim*), *Acodus* pl. 2, figs. 8-9 (only).
 1977 *Baltoniodus crassulus* (Lindström) - Lindström in ZIEGLER, pp. 69-70, *Baltoniodus* pl. 1, figs. 4-7.
 1988 *Baltoniodus crassulus* (Lindström) - Bagnoli & Stouge in Bagnoli *et al.*, p. 208, pl. 38, figs. 1-7.
 1993b *Prioniodus? crassulus* (Lindström) - LÖFGREN, fig. 6E.

Description - The P elements are pastinate pectiniform elements with three processes. The Pa element is characterized by a sharp bend at the base/cusp junction. The anterior process is downwards directed and denticulated distally. The lateral process is directed downwards and may be distally denticulated. The upper margin of the posterior process is straight and carries minute denticles. The distal ends of the processes are connected by a well developed basal sheath. The aboral margin is convex upwards or straight between the processes. The basal cavity is deep and its tip extends into the cusp. The cusp is erect to reclined, keeled, and laterally compressed. On one side of the cusp there is a costa that continues across the base as a lateral process. The other side of the element is flat.

The Pb element has a straight, suberect cusp and the anterior process is shorter than the other two and may carry denticles distally. The anterior edge of the element is almost straight to uniformly convex in lateral view. The upper margin of the base is straight and denticulated. The denticles are small, pointed, and free. The lateral process is directed outwards and it is denticulated anteriorly. The processes are connected by a well developed basal sheath. *Prioniodus acodiformis* Lindström, 1955 is the Pb element.

The M element is geniculate. The cusp is keeled, reclined and straight with a broad inner carina. Similar to the Pa element, the anterior edge is strongly bent, when seen in lateral view, at the cusp/base junction. The antero-basal corner is pointed and the anterior basal extension is shorter than the posterior extension of the base. The aboral outline is straight to slightly sinuous in lateral view. The posterior upper margin of the base is keeled. The cusp and the posterior extension of the base are about equal in length. There is an inner flare on the base.

The Sa element is *Trichonodella longa* Lindström, 1955. It is alate and denticulated on all processes. The denticles of the lateral processes are minute and apically free. The lateral processes are short and barely extend beyond the aboral margin. The

posterior process is long and straight. The aboral outline is very concave between the lateral processes and the posterior process, when seen in lateral view. The cusp is procurved.

The Sb element is *Gothodus costulatus* Lindström, 1955.

The Sc element has a long and slender cusp which is proclined to procurved. Except for the lack of an outer costa, the Sc element is similar to the Sb element.

The Sd element is *Oepikodus crassulus* Lindström, 1955.

All elements have a tall and slender cusp.

The elements are mostly hyaline with diffuse white matter in the cusp and denticles.

Remarks - *Gothodus costulatus* is distinguished from later species of the genus by having a larger basal sheath in the P elements. The M element is not diagnostic at the species level, but in this species the anterior extension of the base is short. The S elements are also characteristic and the denticles, when preserved, are relatively smaller than in younger species where they become markedly taller distally.

Oistodus linguatus Lindström, 1955 (pl. 3, figs. 39-40 only) is the M element of this species. Lindström (1977) placed the specimen in *Acodus deltatus* as an M element, which is not accepted here.

Although not placed in synonymy by us, the species is probably present in China. Some of the elements referred to by An (1987) as *Baltoniodus triangularis* (Lindström) (pl. 19, figs. ?15, 16, 17, 20, 22, 23, 26, ?27) and *Baltoniodus navis* (pl. 20, fig. 6) appear to be *Gothodus* elements rather than *Baltoniodus* elements. At this stage we cannot with certainty identify the species although *G. costulatus* can not be excluded.

Few specimens of the same genus appear in stratigraphically higher beds (samples HU 643A and HUQ 7). These specimens are included in Table 1, 2, and 3 as *G. cf. G. costulatus* Lindström until better material is obtained. It is likely, however, that they represent a new species.

Occurrence - Samples HU 613-631.

Material - 75 Pa elements; 43 Pb elements; 82 M elements; 17 Sa elements; 60 Sb elements; 69 Sc elements; 103 Sd elements.

Repository - MGUH 24035-24042.

Genus LENODUS Sergeeva, 1963

Type species – *Lenodus clarus* Sergeeva, 1963.

Remarks – The apparatus of *Lenodus* Sergeeva consists of dextral and sinistral Pa, Pb, M and S elements (Stouge & Bagnoli, 1990).

The material recovered from the two sections at Horns Udde allowed a better understanding of some elements of *Lenodus*, particularly of the S elements.

The S elements have a very short and rounded cusp with small knobs at the tip as noted by Löfgren (1990). The lateral processes are folded posteriorly and the basal sheath is strongly reduced anteriorly. These features allow a clear distinction from the S elements of *Trapezognathus* Lindström which have a pointed cusp.

LENODUS ANTIVARIABILIS (An, 1981)

Pl. 4, figs. 1-13

- 1981 *Amorphognathus antivariabilis* n.sp. AN, p. 215, pl. 4, figs. 10-11.
 1985 *Amorphognathus antivariabilis* An - AN, DU & GAO, pl. 9, fig. 11; pl. 14, fig. 17.
 1985 *Amorphognathus antivariabilis* An - AN & DING, pl. 1, fig. 19.
 1987 *Amorphognathus antivariabilis* An - AN, p. 122, pl. 26, fig. 19, pl. 28, figs. 21, 22; pl. 29, figs. 23, 24.
 ?1987 ?*Amorphognathus antivariabilis* An - AN, pl. 18, fig. 18 (only).
 1990 *Trapezognathus* sp. STOUGE & BAGNOLI, pp. 27-28, pl. 10, figs. 6, 11-15, 17.

Description – Pa elements are fragmented and the

posterior process is broken off on all specimens. The cusp is short and stubby. The denticles on the anterior and lateral processes are irregular with rounded tips. The basal cavity is deep and continues into the processes which are connected by a well developed basal sheath. The angle between the posterior and the anterior process is about 180°. The differences between dextral and sinistral elements are not clear because of the fragmentary state of preservation, however, the angle between the lateral and anterior processes is smaller in dextral elements than in the sinistral ones.

Pb elements have an anterior, an antero-lateral, a posterior and a postero-lateral process. The cusp is stubby and the denticles on the processes are discrete and irregular. In most specimens the postero-lateral process does not start at the base of the cusp, but slightly posteriorly to it. The basal cavity is deep and wide and excavates the whole unit. The basal sheath connects all the processes. The anterior and posterior processes are on the same plane. The angle between the anterior and the antero-lateral process is less than 90°.

The M element has a cusp that is almost as wide as the height of the base. The cusp has well developed anterior and posterior keels. The anterior keel continues onto the anterior side of the base which is extended downwards. Distally the anterior edge of the base can be serrated. The aboral margin of the base is directed downwards. The inner side of the base carries a more or less sharp crest. The area between the crest and the aboral margin is almost

EXPLANATION OF PLATE 2

- Figs. 1-2 - *Jumodontus gananda* Cooper. Section North of Horns Udde, sample HU 634.
 1) MGUH 24026, ×65.
 2) MGUH 24027, ×105.
 Figs. 3-9 - *Baltoniodus norrlandicus* Löfgren. Section North of Horns Udde.
 3) Pb element, sample HU 649, MGUH 24028, ×55.
 4) Pa element, sample HU 649A, MGUH 24029, ×75.
 5) M element, sample HU 649, MGUH 24030, ×70.
 6) Sa element, sample HU 649, MGUH 24031, posterior view, ×70.
 7) Sd element, sample HU 649, MGUH 24032, ×75.
 8) Sb element, sample HU 653, MGUH 24033, ×75.
 9) Sc element, sample HU 648, MGUH 24034, ×55.
 Figs. 10-17 - *Gothodus costulatus* Lindström. Section North of Horns Udde.
 10) M element, sample HU 621, MGUH 24035, ×60.
 11) Pb element, sample HU 621, MGUH 24036, ×65.
 12) Pa element, sample HU 621, MGUH 24037, ×80.
 13) Pa element, sample HU 621, MGUH 24038, ×75.
 14) Sd element, sample HU 617, MGUH 24039, ×60.
 15) Sc element, sample HU 621, MGUH 24040, ×60.
 16) Sa element, sample HU 616, MGUH 24041, ×65.
 17) Sb element, sample HU 621, MGUH 24042, ×60.
 (Specimens shown in lateral view, if not specified).



flat and faces posteriorly. The maximum width of the base is in correspondence to the crest, where the aboral margin makes a notch. The basal cavity is deep.

S elements have a very short and blunt cusp. The denticulation on the processes is represented by crenulations and/or low and irregular denticles. The processes of the S elements are connected by thin basal sheath but they are free distally. The oral margin between the processes is concave. The lateral processes continue onto the distal part of the cusp forming a ledge around the knobs.

Sa elements are narrow and denticulated or serrated on the three processes. The lateral processes or the denticles of the lateral processes are folded backwards. The basal sheath is well developed between the lateral and posterior processes, while anteriorly it is strongly reduced.

The Sb element is similar to the Sa element, but it is asymmetrical.

The Sc element has posterior and anterior denticulated processes. The anterior edge is folded backwards producing a furrow on the inner side of the element close to the denticles. The outer side is convex owing to a rounded bulge (or carina). The basal sheath is quite reduced on the inner side. The denticulation of the posterior process is developed as a crenulated keel, rather than being free denticles.

In most Sa, Sb and Sc elements the processes are not complete, but the posterior process seems to be the longest one.

Sd elements are symmetrical to asymmetrical with four posteriorly directed processes. In the most asymmetrical elements the most anteriorly directed

process is reduced to a low rounded costa that does not extend beyond the aboral margin.

Remarks – Specimens from Hagudden described by Stouge & Bagnoli (1990) as *Trapezognathus* sp. are now included in synonymy with *Lenodus antivariabilis* (An). Specimens from Hagudden were assigned to the genus *Trapezognathus* Lindström because no *Lenodus*-like Pb elements were recognized.

Lenodus sp. A *sensu* Stouge & Bagnoli, 1990 differs from *Lenodus antivariabilis* by having a better developed denticulation and a reduced basal sheath on all the elements, and different angles between the processes of the Pb elements.

Material – 30 Pa elements, 21 Pb elements, 13 M elements, 13 Sa elements, 16 Sb elements, 16 Sc elements, 34 Sd elements.

Occurrence – Samples HU 653-655; HUQ 12C-14A.

Repository – MGUH 24059-24071.

Genus LUNDODUS n.gen.

Type species – *Acodus gladius* Lindström, 1955.

Derivation of name – After Lund, Sweden.

Diagnosis – *Lundodus* n.gen. is a multielement genus with adenticulated P elements and den-

EXPLANATION OF PLATE 3

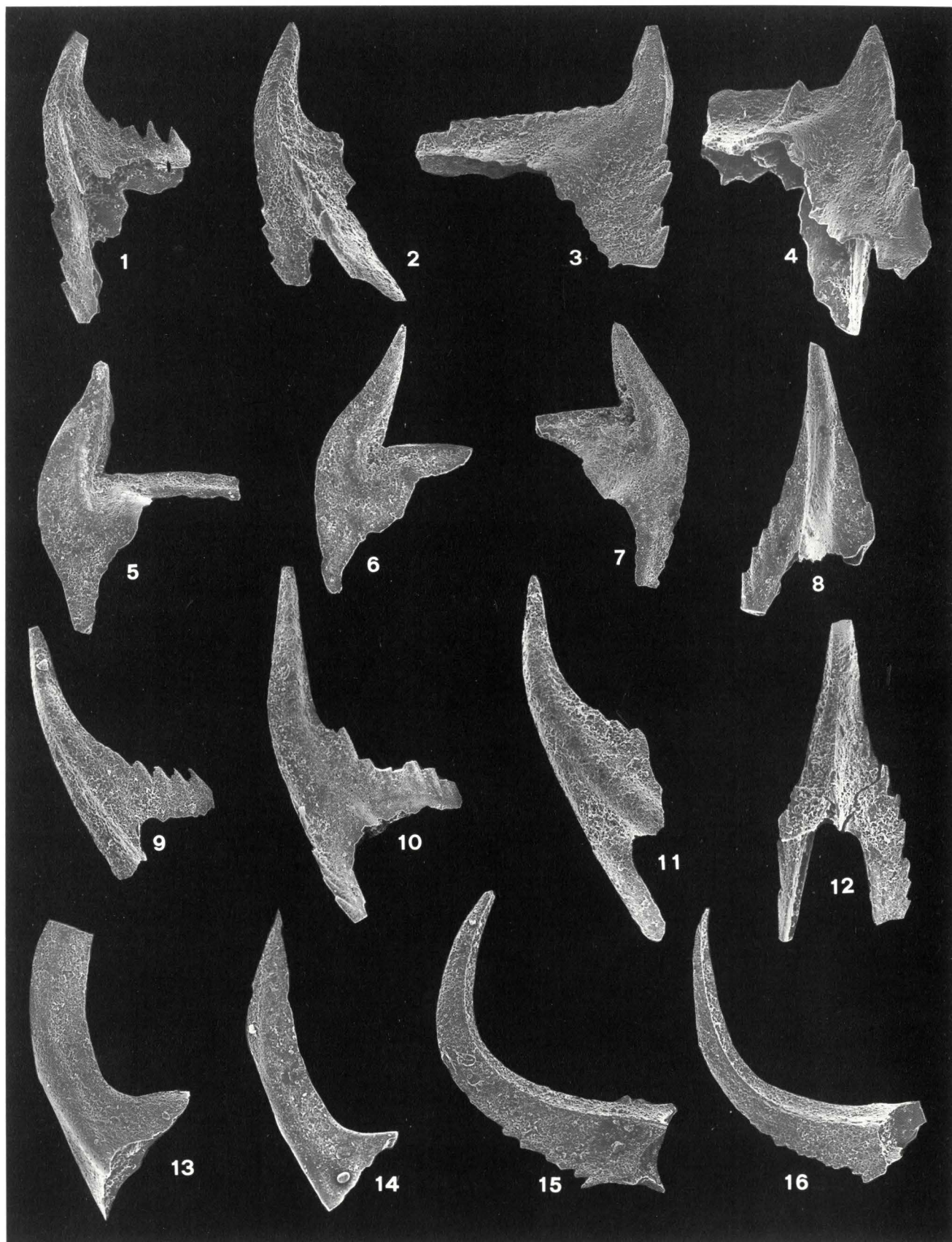
Figs. 1-12 - *Baltoniodus? triangularis* (Lindström). Section North of Horns Udde.

- 1) Pa element, sample HU 636B, MGUH 24043, ×100.
- 2) Pa element, sample HU 636B, MGUH 24044, ×80.
- 3) Pb element, sample HU 637, MGUH 24045, 65.
- 4) Pb element, sample HU 637, MGUH 24046, ×80.
- 5) M element, sample HU636B, MGUH 24047, ×60.
- 6) M element, sample HU 637, MGUH 24048, ×100.
- 7) M element, sample HU 636B, MGUH 24049, ×75.
- 8) Sa element, sample HU 637, MGUH 24050, posterior view, ×75.
- 9) Sb element, sample HU 637, MGUH 24051, ×100.
- 10) Sc element, sample HU 637, MGUH 24052, ×100.
- 11) Sc element, sample HU 637, MGUH 24053, ×100.
- 12) Sd element, sample HU 637, MGUH 24054, posterior view, ×100.

Figs. 13-16 - *Lundodus gladius* (Lindström). Section North of Horns Udde.

- 13) P element, sample HU 624, MGUH 24055, ×85.
- 14) P element, sample HU 626, MGUH 24056, ×80.
- 15) S element, sample HU 626, MGUH 24057, ×85.
- 16) S element, sample HU 613B, MGUH 24058, ×85.

(Specimens shown in lateral view, if not specified).



ticulated S elements. P elements have a long cusp and a relatively small base. S elements have a long base with denticulated edges. The basal cavity is deep and excavates the base and the lower third of the cusp.

Remarks – The genus *Lundodus* n.gen. is similar to *Stolodus* Lindström, 1955 in the sense that M element and Sa element are not present in the apparatus.

The denticulated S elements have been tentatively referred to *Stolodus* (e.g. van Wamel, 1974) based on their overall resemblance. The denticulation of the S elements characteristic of *Lundodus* is not developed in *Stolodus* elements.

To our knowledge the genus comprises only the species *Lundodus gladiatus* (Lindström).

LUNDODUS GLADIATUS (Lindström, 1955)

Pl. 3, figs. 13-16

P element

- 1955 *Acodus gladiatus* n.sp. LINDSTRÖM, pp. 544-545, pl. 3, figs. 10-12.
 1976 *Acodus gladiatus* Lindström - LANDING, p. 629, pl. 1, fig. 7.
 1978 *Prioniodus? gladiatus* (Lindström) - LÖFGREN, p. 78, pl. 10, fig. 10.
 1987 *Acodus gladiatus* Lindström - AN, pp. 118-119, pl. 4, figs. 7-9, 11-13, 19.
 1988 «*Acodus*» *gladiatus* Lindström - STOUGE & BAGNOLI, pp. 111-112, pl. 1, fig. 4 (*cum syn.*).
 1994 «*Acodus*» *gladiatus* (Lindström) - LÖFGREN, fig. 8:48.

S elements

- 1974 «*Stolodus*» sp.1 - SERPAGLI, pp. 88-89, pl. 18, figs. 1a-2c.
 1974 «*Belodella*» sp.B - SERPAGLI, p. 39, pl. 7, figs. 1a-c; pl. 20, fig. 11.

- 1974 *Stolodus stola* (Lindström) - VAN WAMEL, pp. 95-96 (*partim*), pl. 8, fig. 23 (only).
 1976 *Stolodus* sp. aff. *Stolodus stola* (Lindström) - LANDING, pp. 640-641, pl. 4, figs. 17, 18, 21.
 1987 *Acodus gladiatus* Lindström - AN, pp. 118-119, Pl. 4, figs. 7-9, 11-13, 19.
 1987 *Stolodus stola* (Lindström) - AN, pp. 191-192, Pl. 22, figs. 20-23; pl. 23, figs. 1-2.
 1987 *Stolodus stola stola* (Lindström) - OLGUN, p. 55 (*partim*), Pl. 7, fig. 22 (only).
 1988 «*Stolodus*» aff. «*S.*» *stola* Lindström - STOUGE & BAGNOLI, p. 140, pl. 10, figs. 12-13.
 1995 «*Acodus*» *gladiatus* Lindström - LEHNERT, p. 68.

Remarks – All elements of this species have been fully described as form species by several authors (cf. synonymy list) and we do not have further comments.

Occurrence – Samples HU 611, 613A, 613B, 624, 626.

Material – 9 P elements; 12 S elements.

Repository – MGUH 24055-24058.

Genus MICROZARKODINA Lindström, 1971

Type species – *Prioniodina flabellum* Lindström, 1955.

MICROZARKODINA n.sp. A

Pl. 5, figs. 1-5

- ?1981 *Microzarkodina flabellum* (Lindström) - COOPER, pl. 28, figs. 2-4.

EXPLANATION OF PLATE 4

Figs. 1-13 - *Lenodus antivariabilis* (An).

- 1) Sinistral Pa element, section North of Horns Udde, sample HU 653, MGUH 24059, ×140.
- 2) Dextral Pa element, section North of Horns Udde, sample HU 654A, MGUH 24060, ×100.
- 3) Pb element, Horns Udde Quarry, sample HUQ 13A, MGUH 24061, ×80; 3a) inner view; 3a) upper view.
- 4) Pb element, section North of Horns Udde, sample HU 653, MGUH 24062, outer view, M140.
- 5) M element, section North of Horns Udde, sample HU 653, MGUH 24063, ×125; 5a) lateral view; 5b) postero-lateral view.
- 6) M element, section North of Horns Udde, sample HU 653, MGUH 24064, ×120.
- 7) Sa element, section North of Horns Udde, sample HU 653A, MGUH 24065. 7a) posterior view, ×85; 7b) detail of the tip of the cusp, ×450.
- 8) Sb element, section North of Horns Udde, sample HU 653, MGUH 24066, ×100.
- 9) Sd element, Horns Udde quarry, sample HUQ 13B, MGUH 24067, postero-lateral view, ×80.
- 10) Sa element, section North of Horns Udde, sample HU 653A, MGUH 24068, ×65.
- 11) Sd element, Horns Udde quarry, sample HUQ 13A, MGUH 24069.
- 11a) Posterior view, ×85; 11b) detail of the tip of the cusp, ×400.
- 12) Sc element, Horns Udde quarry, sample HUQ 13B, MGUH 24070, outer view, ×80.
- 13) Sc element, Horns Udde quarry, sample HUQ 14, MGUH 24071, inner view, ×100.

(Specimens shown in lateral view, if not specified.)



Description – The P element has a reclined cusp, a denticulated upper margin of the base and an anterior denticle. The anterior margin of the cusp can be crenulated. The aboral margin is convex in lateral view and the antero-basal corner is pointed. The basal cavity is deep with the tip anteriorly directed.

The M element is similar to that of *Microzarkodina flabellum* (Lindström).

S elements have denticles decreasing regularly in size towards the distal part of the processes. The symmetrical Sa element has two to three denticles on the lateral processes. The Sb element has one to two denticles on the anterior process and three denticles on the posterior one.

The Sd element, which is the most characteristic element for this species, has an outer-lateral denticulated process, an antero-lateral denticulated process, and a keeled posterior upper margin of the base. An additional posterior keel, lateral to the main keel, is present on the base.

Remarks – The material recorded from Horns Udde Quarry and from the section North of Horns Udde is represented by very few specimens, but larger collections from the Gillberga section clearly

indicate that the material at hand represents a new species.

The species resembles *Microzarkodina flabellum* (Lindström) from which it differs by the regular denticulation and the relatively larger basal cavity of the P elements. The diagnostic Sd element differs from *M. flabellum*, *M. parva* (Lindström) and *M. hagetiana* Stouge & Bagnoli by the presence of the additional posterior keel.

Material – 7 P elements, 8 M elements, 1 Sa element, 4 Sb elements, 1 Sc element, 2 Sd elements.

Occurrence – Samples HU 633-636A; HUQ 1 and 2A.

Repository – MGUH 24072-24076.

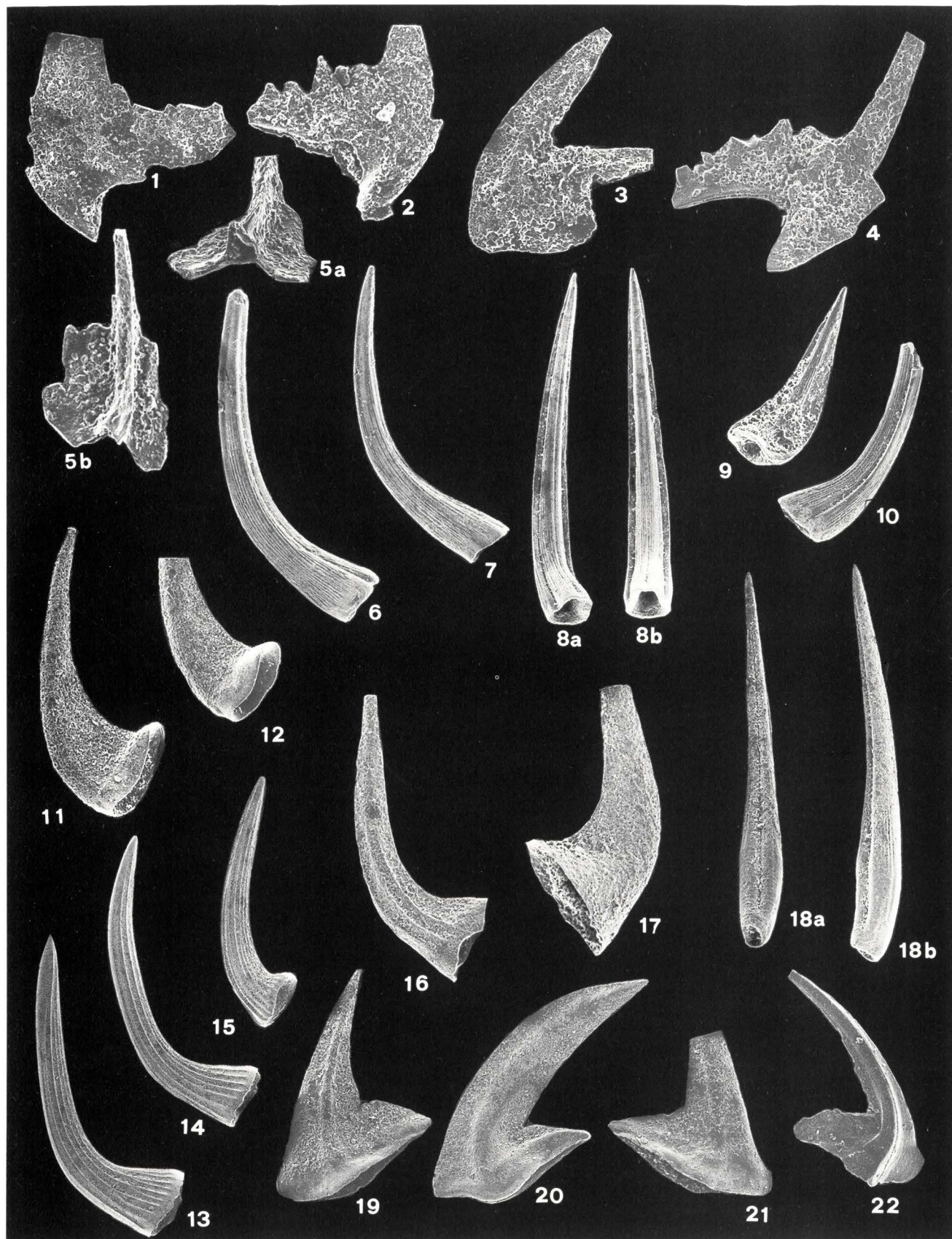
Genus OISTODUS Pander, 1856

Type species - *Oistodus lanceolatus* Pander, 1856.

OISTODUS LANCEOLATUS Pander, 1856

EXPLANATION OF PLATE 5

- Figs. 1-5 - *Microzarkodina* n.sp. A. Section North of Horns Udde, sample HU 635.
 1) P element, MGUH 24072, $\times 125$.
 2) P element, MGUH 24073, $\times 125$.
 3) M element, MGUH 24074, $\times 120$.
 4) Sb element, MGUH 24075, $\times 125$.
 5) Sd element, MGUH 24076; 5a) aboral view, $\times 125$; 5b) posterior view, $\times 80$.
- Figs. 6-10 - *Parapanderodus quietus* n.sp. Horns Udde quarry, sample HUQ 17.
 6) Paratype, slender element, MGUH 24077, $\times 125$.
 7) Paratype, slender element, MGUH 24078, $\times 125$.
 8) Holotype, symmetrical bicostate element, MGUH 24079, $\times 80$; 8a) postero-lateral view; 8b) posterior view.
 9) Paratype, short asymmetrical element, MGUH 24080, posterior view, $\times 105$.
 10) Paratype, symmetrical bicostate element, MGUH 24081, $\times 140$.
- Figs. 11-12 - *Scalpellodus* cf. *S. latus* (van Wamel). Section North of Horns Udde, sample HU 638.
 11) MGUH 24082, $\times 170$.
 12) MGUH 24083, $\times 160$.
- Figs. 13-15 - *Scolopodus princeps* n.sp. Section North of Horns Udde.
 13) Holotype, symmetrical element, sample HU 636A, MGUH 24084, $\times 75$.
 14) Paratype, asymmetrical element, sample HU 636B, MGUH 24085, $\times 65$.
 15) Paratype, asymmetrical element, sample HU 636B, MGUH 24086, $\times 75$.
- Figs. 16-17 - *Parapaltodus* sp. Section North of Horns Udde.
 16) Sample HU 615, MGUH 24087, 95.
 17) Sample HU 617, MGUH 24088, $\times 80$.
- Fig. 18 - Gen. et sp. indet. Section North of Horns Udde, sample HU 633, MGUH 24089, $\times 85$; 18a) posterior view; 18b) postero-lateral view.
- Figs. 19-21 - *Oistodus* sp.A. Section North of Horns Udde, sample HU 639.
 19) S element, MGUH 24090, $\times 75$.
 20) M element, MGUH 24091, $\times 55$.
 21) P element, MGUH 24092, $\times 60$.
- Fig. 22 - *Oistodus* sp.B. Horns Udde quarry, sample HUQ 12B, S element, MGUH 24093, $\times 100$.
 (Specimens shown in lateral view, if not specified.)



- 1856 *Oistodus lanceolatus* n.sp. PANDER, p. 27, pl. 2, figs. 17-19.
 1987 *Oistodus lanceolatus* Pander - AN, p. 160, pl. 12, figs. 10-15, 24.
 1988 *Oistodus* aff. *O. lanceolatus* Pander - Bagnoli & Stouge in BAGNOLI *et al.*, pp. 211-212, pl. 40, figs. 1-4 (*cum syn.*).
 cf. 1988 *Oistodus* aff. *O. lanceolatus* Pander - STOUGE & BAGNOLI p. 123, pl. 6, figs. 1-8.
 1993 *Oistodus lanceolatus* Pander - LÖFGREN, fig. 6: V-X.
 1994 *Oistodus lanceolatus* Pander - LÖFGREN, fig. 6: 38-40.

Remarks – Earlier we assigned the species of *Oistodus* present in the Billingenian to *Oistodus* aff. *O. lanceolatus* Pander, 1856, because we found that some specimens of *Oistodus lanceolatus* depicted by Pander (1856) were different from the material at hand. Later it appeared that the specimens at hand all represent the species that Lindström (1971) revised as *O. lanceolatus* Pander in terms of multielement taxonomy. Because the Pander material is lost (T. Koren, pers.comm., 1994), and we have not been able to record elements similar to those depicted by Pander (1856), we refer the specimens to *Oistodus lanceolatus* Pander, 1856 *sensu* Lindström, 1971.

Oistodus aff. *O. lanceolatus* recorded from western Newfoundland (Stouge & Bagnoli, 1988) differs from the Baltic species by having a well pronounced costa on the anterior side of the Sa elements.

Occurrence – Samples HU 609-639; HUQ 1-3.

Material – 262 P elements; 295 M elements; 44 Sa elements; 440 Sb elements; 270 Sc elements.

OISTODUS sp. A
 Pl. 5, figs. 19-21

Description – The elements of *Oistodus* sp. A have a prominently developed thickened rim just above the aboral margin.

The P element has an erect cusp and a straight outline of the upper margin of the base. The cusp and the upper margin of the base form an angle of 90°. The anterior edge of the base is short and pointed. The posterior extension of the base is only slightly longer than the anterior one.

The M element has a wide and recurved cusp. The base is small and the outline of the aboral margin is sinuous in lateral view.

The S element is recurved and with a well developed cusp. The base is short posteriorly.

Remarks – *Oistodus* sp. A differs from *Oistodus*

lanceolatus Pander by having a smaller base and a wider cusp. The characteristic thickened edge of *Oistodus* sp. A is not present in *Oistodus lanceolatus*.

Occurrence – Sample HU 639.

Material – 2 P elements, 1 M element, 1 S element.

Repository – MGUH 24090-24092.

Genus *PARAPANDERODUS* Stouge, 1984

Type species – *Protopanderodus asymmetricus* Barnes & Poplawski, 1973.

Remarks – The apparatus of *Parapanderodus* Stouge was revised by Stouge & Bagnoli (1990) and Smith (1991). It includes slender elements forming a curvature transition, antero-posteriorly compressed, short, asymmetrical elements, and symmetrical bicostate elements.

PARAPANDERODUS QUIETUS n.sp.
 Pl. 5, figs. 6-10

- 1978 *Scolopodus* aff. *S. gracilis* (Ethington & Clark) - LÖFGREN, p. 110, pl. 8, figs. 10A-B.
 1985 «*Scolopodus gracilis*» Ethington & Clark - LÖFGREN, fig. 4:AG-AJ, non AK.
 1990 *Parapanderodus* n.sp.A STOUGE & BAGNOLI, p. 21, pl. 7, figs. 1-4.

Derivation of name – *Quietus*, lat. = quiet.

Type locality – Horns Udde Quarry.

Type stratum – 8.10 m above base of the section, sample HUQ 17, *Lenodus* sp.A Zone, Kundan.

Holotype – MGUH 24079, a symmetrical bicostate element (Pl. 5, fig. 8a, b).

Diagnosis – The apparatus of *Parapanderodus quietus* n.sp. comprises slender elements with a posterior groove throughout the whole unit, symmetrical elements with two lateral grooves and a posterior carina with a median groove and asymmetrical short elements with prominent keels and an asymmetrically located posterior carina. The slender elements have a nearly circular aboral margin and a nearly straight aboral outline in lateral view.

Description – The slender elements are rounded to laterally compressed. They are long and slim,

procurved to suberect. The posterior groove extends from the apex to the aboral margin. The cusp continues smoothly onto the base. The aboral margin is oval to circular with an indentation on the upper margin of the base due to the longitudinal narrow groove. In lateral view the aboral margin is straight to gently concave. The depth of the basal cavity varies according to the length of the base. The apex is located close to the anterior margin.

The symmetrical bicostate element is slender and procurved. The anterior face is convex. The two costae are flanked by grooves, which are separated by a prominent posterior carina with a median groove that almost reaches the aboral margin. The aboral margin is sub-trapezoid.

The short asymmetrical element is keeled and with a posterior, asymmetrically located carina. The aboral margin is lenticular.

All elements are striated except for a narrow band along the aboral margin and the distal part of the cusp.

Remarks – The asymmetrical element is rare in this collection.

Parapanderodus quietus n.sp. resembles *Parapanderodus arcuatus* Stouge, 1984. *P. quietus* is different from *P. arcuatus* in the outline of the aboral margin. The short extension of the upper margin of the base typical for slender elements of *P. arcuatus* is not developed in *P. quietus*. The sub-trapezoid outline of the aboral margin and the median groove on the posterior carina on the bicostate symmetrical element are diagnostic for *P. quietus*. The asymmetrical short element can not be distinguished at species level between the two taxa.

Occurrence – Samples HUQ 14C-17.

Material – 85 specimens.

Repository – MGUH 24077-24081.

Genus PERIODON Hadding, 1913

Type species – *Periodon aculeatus* Hadding, 1913

PERIODON cf. *P. FLABELLUM* (Lindström, 1955)
Pl. 6, figs. 1-7

cf.1978 *Periodon flabellum* (Lindström) - LÖFGREN, pp. 72-74 (partim), pl. 11, figs. 1-5 (only).

Description – The P elements carry one to two anterior denticles. The Pa element has a prominent

anterior keel on the base. The keel is serrated to denticulated. The Pb element has usually two denticles on the anterior process. The basal sheath extends almost to the distal part of the posterior process.

The M element is reclined and the anterior edge of the base is keeled. The anterior edge is serrated in some specimens.

The S elements are fully denticulated. On the posterior process there is a clear distinction between the largest denticle which is distally located and the denticles between the cusp and the largest one. The number of the smaller denticles is three to four. The basal cavity is restricted and extends beneath the processes as a slit.

Remarks – *Periodon* cf. *P. flabellum* (Lindström) represents an evolutionary stage between *P. flabellum* and *Periodon* sp.A.

Material – 22 P elements, 18 M elements, 47 S elements.

Occurrence – Samples HU 636-638 and HUQ 2 and 3A.

Repository – MGUH 24094-24100.

PERIODON sp. A
Pl. 6, figs. 8, 12-18

cf.1978 *Periodon flabellum* (Lindström) - LÖFGREN, pp. 72-74 (partim), fig. 29 (only).

1993 *Periodon flabellum* (Lindström) - LÖFGREN, fig. 6: M-P.

Description – Pa elements have a constantly short anterior denticulated process. In most specimens there is only one denticle anteriorly which is free and reaches up to or slightly above the base/cusp junction. In some specimens one or two small additional denticles can be present. The upper margin of the base has two, most commonly three reclined denticles which are tilted to the outer side distally. The cusp is reclined and the base has a prominent inner flare. The basal sheath is developed from the distal part of the anterior process and fades toward the distal posterior part of the unit.

The Pb element is sinuous and with one to three denticles on the anterior outward bended process. The cusp is reclined and the upper margin of the base carries three to five reclined denticles. The basal sheath becomes reduced to a shallow groove in the distal part of the base.

The M element is geniculate and with a reclined cusp. The distal part of the anterior edge of the base is serrated and slightly extended to pointed.

The S elements are fully denticulated. There are about four denticles between the cusp and the largest denticle on the posterior extension of the base. The basal cavity is developed beneath the cusp and becomes a slit distally. The outline of the aboral margin in lateral view is strongly concave downwards. The anterior edge of the base is denticulated.

Remarks – *Periodon* sp.A differs from *Periodon flabellum* by the initial extension of the antero-basal corner of the M elements and the development of a free anterior process on the Pa elements. The free anterior process on the Pa elements marks an important change in *Periodon* evolution. After the development of an anterior process was established, the evolution of new *Periodon* species in the interval between *P. flabellum* and *P. aculeatus* became very fast. In the S elements the evaluation of the number of denticles on the posterior process between the cusp and the largest one is hampered by the gradual increase in the size of denticles, which distally become nearly equal in height and width.

Occurrence – Samples HU 639-640.

Material – 23 P elements; 3 M elements; 23 S elements.

Repository – MGUH 24101-24108.

PERIODON sp. B

Pl. 8, figs. 9-12

‡1978 *Periodon flabellum* (Lindström) - LÖFGREN, pp. 72-74 (*partim*), pl. 11, figs. 6-11 (only).

‡1991 *Periodon flabellum* (Lindström 1955) - RASMUSSEN, p. 281, fig. 7: O,P,S.

Remarks – The specimens of *Periodon* sp. B resemble *Periodon* sp. A but the S elements have well defined large sized posterior denticles on the posterior process. The number of denticles between the cusp and the largest denticle is four or five. The S elements are strongly flexed and have an inverted basal cavity.

Material – 4 P elements, 1 M element, 2 S elements.

Occurrence – Samples HU 643A-643B; HUQ 8.

Repository – MGUH 24140-24142.

PERIODON sp. C

Pl. 6, figs. 19-20

1990 *Periodon* sp. - STOUGE & BAGNOLI, p. 22, pl. 7, figs. 11-12.

‡1991 *Periodon aculeatus* spp.A - RASMUSSEN, p. 281, fig. 7: Q,R.

EXPLANATION OF PLATE 6

- Figs. 1-7 - *Periodon* cf. *P. flabellum* (Lindström). Section North of Horns Udde, sample HU 638.
 1) Pa element, MGUH 24094, ×100.
 2) Pb element, MGUH 24095, ×100.
 3) M element, MGUH 24096, ×85.
 4) S element, MGUH 24097, ×100.
 5) S element, MGUH 24098, ×100.
 6) S element, MGUH 24099, ×100.
 7) S element, MGUH 24100, ×100.
- Figs. 8, 12-18 - *Periodon* sp.A. Section North of Horns Udde, sample HU 639.
 8) P element, MGUH 24101, ×90.
 12) P element, MGUH 24102, ×65.
 13) P element, MGUH 24103, ×60.
 14) S element, MGUH 24104, ×95.
 15) S element, MGUH 24105, ×90.
 16) S element, MGUH 24106, ×60.
 17) S element, MGUH 24107, ×60.
 18) M element, MGUH 24108, ×60.
- Figs. 9-11 - *Protopanderodus sulcatus* (Lindström). Section North of Horns Udde.
 9) Symmetrical acontiodiform element, sample HU 612, MGUH 24109, ×85.
 10) Asymmetrical acontiodiform element, sample HU 613, MGUH 24110, ×85.
 11) Scandodiform element, sample HU 613A, MGUH 24111, ×60.
- Figs. 19-20 - *Periodon* sp.C. Horns Udde quarry, sample HUQ 12B.
 19) S element, MGUH 24112, ×80.
 20) P element, MGUH 24113, ×100.
- (All specimens shown in lateral view).



Remarks – Stouge & Bagnoli (1990) distinguished a species of *Periodon* on the basis of few M elements. In this material also Pa and Sc elements have been recorded.

The Pa element has a well developed anterior process with two and three denticles.

Material – 2 P elements, 2 M elements, 1 S element.

Occurrence – Sample HUQ 12B.

Repository – MGUH 24112-24113.

Genus PROTOPANDERODUS Lindström, 1971

Type species – *Acontiodus rectus* Lindström, 1955.

PROTOPANDERODUS CALCEATUS n.sp.

Pl. 8, figs. 13-19

- 1974 *Scolopodus varicostatus* Sweet & Bergström, - VIIRA, p. 123 (partim), pl. 5, figs. 23, 24 (only).
 1974 *Scandodus* cf. *unistriatus* Sweet & Bergström - VIIRA, p. 119 (partim), pl. 5, fig. 30 (only).
 1978 *Protopanderodus* cf. *varicostatus* (Sweet & Bergström) - LÖFGREN, pp. 91-92, pl. 3, figs. 26-31.
 1987 *Protopanderodus* cf. *varicostatus* (Sweet & Bergström) - OLGUN, pl. 7, figs. P-S.
 1990 *Protopanderodus* cf. *P. varicostatus* (Sweet & Bergström) - STOUGE & BAGNOLI, pp. 23-24, pl. 8, figs. 9-12.
 1991 *Protopanderodus* cf. *varicostatus* (Sweet & Bergström) - RASMUSSEN, pp. 283-284, fig. 8:D-E.
 1994 *Protopanderodus* cf. *P. varicostatus* (Sweet & Bergström) - LÖFGREN, fig. 7:3.

Derivation of name – *Calceatus*, lat. = with shoes.

Type locality – Section North of Horns Udde.

Type stratum – 7.10 m, above the base of the section, sample HU 649, *Baltoniodus norrlandicus* interval Zone, Volkhov (Arenig).

Holotype – MGUH 24149, a scandodiform element (Pl. 8, fig. 18).

Diagnosis – The elements of *Protopanderodus calceatus* n.sp. have a low, small and hyaline base. The asymmetrical elements have a prominent antero-lateral groove.

Description – The bicostate symmetrical elements have a suberect to slightly reclined cusp. The base is small and hyaline.

The asymmetrical bicostate and unicostate elements have one lateral, anteriorly located deep groove.

The scandodiform element has a low base and a deep lateral groove situated near the anterior margin.

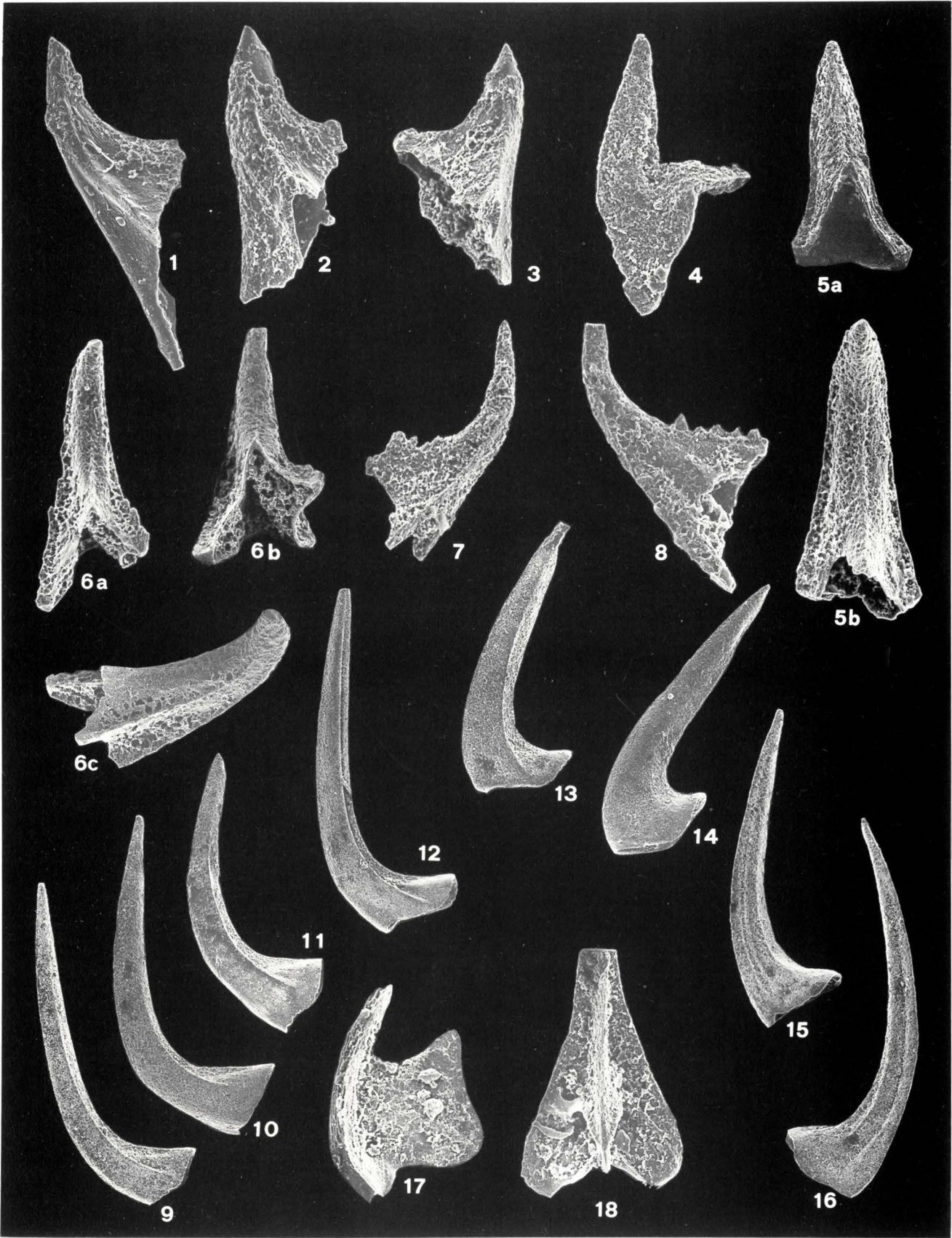
The outline of the aboral margin in lateral view is sinuous to gently curved. The anterior edge of the basal cavity is concave and the tip is anteriorly directed.

All elements are keeled.

Remarks – The species occurs together with *Protopanderodus rectus* (Lindström). It differs from *P. rectus* by having a small and low base and a deep

EXPLANATION OF PLATE 7

- Figs. 1-8 - *Trapezognathus diprion* (Lindström). Section North of Horns Udde.
 1) Pa element, sample HU 621, MGUH 24114, $\times 120$.
 2) Pb element, sample HU 621, MGUH 24115, $\times 120$.
 3) Pb element, sample HU 621, MGUH 24116, $\times 95$.
 4) M element, sample HU 624, MGUH 24117, $\times 120$.
 5) Sa element, sample HU 620, MGUH 24118; 5a) postero-aboral view, $\times 105$; 5b) posterior view, $\times 120$.
 6) Sd element, sample HU 629, MGUH 24119; 6a) posterior view, $\times 100$; 6b) postero-aboral view, $\times 120$; 6c) $\times 120$.
 7) Sb element, sample HU 629, MGUH 24120, $\times 70$.
 8) Sc element, sample HU 629, MGUH 24121, $\times 120$.
 Figs. 9-16 - *Protopanderodus floridus* n.sp. Section North of Horns Udde, sample 636A.
 9) Paratype, acontiodiform element, MGUH 24122, $\times 60$.
 10) Paratype, acontiodiform element, MGUH 24123, $\times 60$.
 11) Paratype, acontiodiform element, MGUH 24124, $\times 60$.
 12) Paratype, acontiodiform element, MGUH 24125, $\times 55$.
 13) Paratype, acontiodiform element, MGUH 24126, $\times 60$.
 14) Paratype, scandodiform element, MGUH 24127, $\times 60$.
 15) Paratype, scandodiform element, MGUH 24128, $\times 65$.
 16) Holotype, scandodiform element, MGUH 24129, $\times 60$.
 Figs. 17-18 - *Protoprioniodus papillosus* (van Wamel). Section North of Horns Udde, sample HU 636.
 17) M element, MGUH 24130, $\times 115$.
 18) Sa element, MGUH 24131, $\times 100$.



lateral groove on asymmetrical acontiodiform and scandodiform elements.

Protopanderodus calceatus n.sp. differs from *Protopanderodus sulcatus* (Lindström) by having the well developed antero-lateral groove on the scandodiform element.

Occurrence – Samples HU 633-651; HUQ 1-14C.

Material – 75 acontiodiform elements and 19 scandodiform elements.

Repository – MGUH 24144-24150.

PROTOPANDERODUS FLORIDUS n.sp.
Pl. 7, figs. 9-16

Derivation of name – *Floridus*, lat. = flowery. The species occurs at the Flowery Sheet on Öland.

Type locality – Section North of Horns Udde.

Type stratum – 3.58 m (= 12 cm above the upper surface of the «Blommiga Bladet»), Sample 636B, Volkhov (Arenig).

Holotype – MGUH 24129, a scandodiform element (Pl. 7, fig. 16).

Diagnosis – A species of *Protopanderodus* with a

scandodiform characterized by an inner prominent costa with a groove on each side.

Description – The species includes symmetrical and asymmetrical bicostate to unicastate elements (acontiodiforms) and asymmetrical unicastate, grooved elements (scandodiforms). The specimens vary from reclined to proclined. The upper margin of the base is keeled in several specimens.

The bicostate acontiodiforms have an anterior and posterior keel. The costae are symmetrically placed on each side of the posterior keel. The costae and the posterior keel extend nearly to the aboral margin of the base. Proclined elements have a relatively long base and the outline of the aboral margin is straight or nearly so in lateral view. The recurved elements have short bases and the outline of the aboral margin is sinuous in lateral view. The difference between asymmetrical and symmetrical acontiodiforms is due to the position of costae and minor torsion of the cusp. The strongly reclined/recurved specimens are unicastate.

The scandodiforms are keeled and skewed. The outer face is smooth. The inner side has a prominent costa with a narrow anteriorly placed groove that fades across the base. The costa becomes a carina in the distal part of the cusp. Posteriorly to the costa, a wide groove is developed.

Remarks – The species resembles *Protopanderodus rectus* (Lindström) from which it differs by

EXPLANATION OF PLATE 8

Figs. 1-8 - *Trapezognathus quadrangulum* Lindström. Section North of Horns Udde, sample HU 643.

- 1) Pb element, MGUH 24132, $\times 140$.
- 2) Pa element, MGUH 24133, $\times 100$.
- 3) M element, MGUH 24134, $\times 90$.
- 4) Pb element, MGUH 24135, $\times 100$.
- 5) Sd element, MGUH 24136, $\times 120$; 5a) lateral view; 5b) posterior view.
- 6) Sb element, MGUH 24137, $\times 105$.
- 7) Sc element, MGUH 24138, $\times 120$.
- 8) Sa element, MGUH 24139, $\times 90$; 8a) posterior view; 8b) postero-aboral view.

Figs. 9-12 - *Periodon* sp. B.

- 9) S element, section North of Horns Udde, sample HU 643B, MGUH 24140, $\times 100$.
- 10) S element, section North of Horns Udde, sample HU 643A, MGUH 24141, $\times 85$.
- 11) Pa element, section North of Horns Udde, sample HU 643A, MGUH 24142, $\times 85$.
- 12) Pb element, Horns Udde quarry, sample HUQ 8, MGUH 24143, $\times 100$.

Figs. 13-19 - *Protopanderodus calceatus* n.sp. Section North of Horns Udde.

- 13) Paratype, scandodiform element, sample HU 636, MGUH 24144, $\times 55$.
- 14) Paratype, scandodiform element, sample HU 649, MGUH 24145, $\times 70$.
- 15) Paratype, bicostate symmetrical element, sample HU 635, MGUH 24146, $\times 85$.
- 16) Paratype, bicostate asymmetrical element, sample HU 649, MGUH 24147, $\times 55$.
- 17) Paratype, bicostate asymmetrical element, sample HU 635, MGUH 24148, $\times 40$.
- 18) Holotype, scandodiform element, sample HU 649, MGUH 24149, $\times 55$.
- 19) Paratype, scandodiform element, sample HU 635, MGUH 24150, $\times 60$.

(Specimens shown in lateral view, if not specified).



having a grooved unicastate scandodiform in the apparatus. The symmetrical bicostate elements are not diagnostic at specific level.

Protopanderodus sulcatus (Lindström) is similar to *P. floridus* n.sp., but the latter species does not have an extra lateral groove in the acontiodiforms.

Occurrence – Samples HU 636A-639; HUQ 3-4.

Material – 613 acontiodiform elements; 167 scandodiform elements.

Repository – MGUH 24122-24129.

PROTOPANDERODUS SULCATUS (Lindström, 1955)
Pl. 6, figs. 9-11

1955 *Acontiodus rectus* var. *sulcatus* LINDSTRÖM, p. 550, pl. 2, figs. 12, 13; text-fig. 3D.

Description – The asymmetrical acontiodiform element has been described by Lindström (1955) as *Acontiodus rectus* var. *sulcatus*. The antero-lateral deep groove on the inner side of the elements is persistently present on the base and on the whole length of the cusp.

The symmetrical acontiodiform elements have two posteriorly located sharp costae.

The scandodiform element is keeled with a wide median carina that extends through the whole element.

Remarks – *Protopanderodus sulcatus* differs from *Protopanderodus rectus* (Lindström) by having an asymmetrical acontiodiform element with a prominent groove located close to the anterior margin.

Occurrence – Samples HU 611-615.

Material – 267 acontiodiform elements; 90 scandodiform elements.

Repository – MGUH 24109-24111.

Genus SCALPELLODUS Dzik, 1976

Type species – *Protopanderodus latus* van Wamel, 1974.

SCALPELLODUS cf. *S. latus* (van Wamel, 1974)
Pl. 5, figs. 11-12

1983 *Scalpellodus* cf. *latus* (van Wamel) - LÖFGREN, pp. 127-128, fig. 4: AQ-AS, AZ, AAA (*cum syn.*).

Remarks – *Scalpellodus* cf. *S. latus* (van Wamel) has been fully described by Löfgren (1983).

Occurrence – Samples HU 638; HUQ1 and 3.

Material – 4 specimens.

Repository – MGUH 24082-24083.

Gen. SCOLOPODUS Pander, 1856

Type species – *Scolopodus sublaevis* Pander, 1856.

SCOLOPODUS PRINCEPS n.sp.
Pl. 5, figs. 13-15

1987 *Scolopodus quadratus* Pander n.sp. - OLGUN, pl. 7, fig. GH (only).

Derivation of name – *Princeps*, lat. = prince.

Type locality – Section North of Horn Udde.

Type stratum – 3.48 m above the base of the section, sample HU 636A, Volkhov (Arenig).

Holotype – MGUH 24084, a symmetrical element (Pl. 5, fig. 13).

Diagnosis – A species of *Scolopodus* with closely spaced costae resulting in the presence of a high number of costae, especially on the base.

Description – *Scolopodus princeps* n.sp. consists of symmetrical, asymmetrical to very asymmetrical elements with a high number of costae. Most costae extend throughout the total length of the elements and almost reach the aboral margin. The elements vary from proclined to recurved. The symmetrical elements have costae on the lateral faces, but the anterior face is rounded and smooth. The number of costae vary from 16 to 18. Elements vary from recurved types with short base to proclined with longer base.

The asymmetrical elements are similar to the symmetrical ones but with a minor torsion of the base. The antero-lateral face is rounded and smooth. The number of costae vary from 16 to 24. The costae are more closely spaced on the inner side than on the outer side and more costae are present on the base than on the cusp. The elements are proclined to recurved.

The very asymmetrical elements are recurved with a short base. The costae vary from 12 to 16 on the base, but become reduced to 6 or 8 on the cusp. The outer lateral face is smooth and between the anterior keel and the first inner lateral costa there is a broad groove.

Remarks – *Scolopodus princeps* n.sp. differs from *Scolopodus rex* Lindström, 1955 by having a higher number of closely spaced costae which are most abundant on the base.

Occurrence – Samples HU 636A-638; HUQ 3A-4.

Material – 132 specimens.

Repository – MGUH 24084-24086.

Genus SEMIACONTIODUS Miller, 1980

Type species – *Acontiodus (Semiacontiodus) nogamii* Miller, 1969

«SEMIACONTIODUS» CORNUFORMIS (Sergeeva, 1963)

1963a *Scolopodus cornuformis* sp.nov. SERGEEVA, p. 93, pl. 7, figs. 1-3; text-fig. 1.

1990 «*Semiacontiodus*» *cornuformis* (Sergeeva) - STOUGE & BAGNOLI, p. 26, pl. 9, figs. 14-18, 20-25 (*cum syn.*).

1994 *Semiacontiodus cornuformis* (Sergeeva) - DZIK, pp. 66-67, pl. 13, figs. 7-10; text-fig. 7a.

Remarks – Stouge & Bagnoli (1990) noted that elements of «*Semiacontiodus*» *cornuformis* changed stratigraphically. The change begins with early types of «*Semiacontiodus*» with simple ornamentation and the apparatus is less variable than younger types (Stouge & Bagnoli, 1990, p. 26, pl. 9, figs. 14-17). These types are restricted to samples HU 648 to HU 653A and HUQ11 to HUQ 13B.

The second group includes specimens with a prominent groove on each side of the posterior carina of the symmetrical element. In addition, the posterior median carina carries a groove (Stouge & Bagnoli, 1990, p. 26, pl. 9, fig. 18). These types of elements range from HU 654A to HU 655 and from HUQ 14 to HUQ 15.

It is likely that new species are to be distinguished.

Occurrence – Samples HU 648-655 and HUQ 11-17.

Material – 64 symmetrical elements; 673 asymmetrical elements.

Genus TRAPEZOGNATHUS Lindström, 1955

Type species – *Trapezognathus quadrangulum* Lindström, 1955.

Remarks – Stouge & Bagnoli (1990) revised *Trapezognathus* Lindström, 1955 in terms of multielement taxonomy. The *Trapezognathus* apparatus comprises P (Pa and Pb), M, and S (Sa, Sb, Sc, and Sd) elements. The most characteristic elements are the Sd and the M elements, while the other elements have an appearance that makes it difficult to distinguish them from closely related genera such as *Baltoniodus* Lindström, 1971. *Lenodus* Sergeeva, 1963 is also possibly related to *Trapezognathus*, but in *Trapezognathus* the P elements are paired and mirror images, whereas P elements of *Lenodus* are not. Moreover, the tips of the cusp of Sa, Sb, and Sd elements of *Lenodus* are blunt and not pointed.

TRAPEZOGNATHUS DIPRION (Lindström, 1955) Pl. 7, figs. 1-8

1955 *Prioniodina diprion* n.sp. LINDSTRÖM, p. 587, pl. 5, fig. 43.

1971 *Gothodus costulatus* Lindström - LINDSTRÖM, pp. 54-55 (*partim*), pl. 1, figs. 1-3 (only).

1974 *Prioniodus navis* Lindström - VAN WAMEL, pp. 89-90 (*partim*), pl. 8, figs. 13, 15 (only).

1977 *Baltoniodus crassulus* (Lindström) - Lindström, in ZIEGLER pp. 69-70 (*partim*), *Baltoniodus* pl. 1, fig. 3 (only).

Diagnosis (emended) – A species of *Trapezognathus* where the elements have a large base and deep basal cavity. P and M elements are adenticulated to vaguely denticulated. S elements have small denticles. All processes are connected by a basal sheath and free processes are not well developed.

Description – The species comprises elements with a large keeled base and short extensions or small processes that extend beyond the aboral margin. The basal cavity is very deep. It excavates the base and extends into the cusp. Denticulation is absent, or, when preserved, it is sporadic or the edges are uneven.

The Pa element has a proclined, keeled cusp, the posterior of which continues as a straight keeled upper margin of the base. The short lateral process is posteriorly directed and continues onto the cusp as a sharp costa. The anterior keeled edge of the cusp curves at the cusp-base junction and continues downwards as a straight, keeled, short process. The basal sheath is large and connects the distal part of the processes and the posterior margin of the base.

The Pb element has a suberect and relatively short cusp with an anterior and posterior keel. A costa is present on the inner side. The keels and the costa continue onto the base as prominent keeled edges. The anterior edge continues nearly straight downwards but with a characteristic concavity to the posterior on the base, when seen in lateral view. The base is large and wide and it is excavated by a deep basal cavity.

In Pa and Pb elements sporadic denticulation or undulating edges have been observed in few specimens on the posterior and lateral edges.

The M element is geniculate with a straight and erect cusp. In lateral view the cusp and the upper margin of the base form an angle of about 90°. The upper margin of the base is sharp and the base has a small inner flare. The outline of the leading edge of the element is convex to the anterior. The lower third of the base has an uneven, nearly serrated edge, but distinct denticles are not present.

The S element are adenticulated to denticulated on the base. The Sa element is proclined with a stubby cusp. Few denticles are present on the lateral processes. The posterior edge is sharp with a weak keel. The Sb element has few denticles on the upper margin of the base and a proclined cusp. The Sc element, described by Lindström (1955) as *Prioniodina diprion*, is procurved with denticulated edges. The anterior edge extends slightly beyond the aboral margin. The Sd elements have a skewed quadratic cross-section of the base and the cusp is recurved.

Remarks – The P elements can be difficult to distinguish from early species of *Gothodus* and perhaps *Baltoniodus*. The P elements of *Gothodus costulatus* Lindström, 1955 *sensu* Lindström, 1971 are interpreted as P elements of *Trapezognathus diprion* in this paper.

Van Wamel (1974) described *Trapezognathus diprion* as «early *navis*».

This early species of *Trapezognathus* is difficult to characterize due to the general or «simple» appearance of especially the P elements. The M and S elements, however, are typical for *Trapezognathus* and they characterize the species.

Occurrence – Samples HU 620-636; HUQ 1-2A.

Material – 57 Pa elements, 8 Pb elements, 25 M elements, 16 Sa elements, 31 Sb elements, 30 Sc elements, 42 Sd elements.

Repository – MGUH 24114-24121.

TRAPEZOGNATHUS QUADRANGULUM Lindström, 1955

Pl. 8, figs. 1-8

- 1955 *Trapezognathus quadrangulum* n.sp. LINDSTRÖM, p. 598 (*partim*), pl. 5, figs. 38-39 (only).
 1977 *Baltoniodus triangularis* (Lindström) - Lindström in ZIEGLER, pp. 81-82 (*partim*), *Baltoniodus*-pl. 2, figs. ?8, ?9, 10-11.
 1978 *Prioniodus* (*Baltoniodus*) *triangularis* Lindström - LÖFGREN, pp. 81-82, pl. 12, figs. 1-7.
 1990 *Trapezognathus quadrangulum* Lindström, 1955 - STOUGE & BAGNOLI, pp. 26-27, pl. 10, figs. 1-5, 7-10).
 ?1991 *Baltoniodus triangularis* (Lindström 1955) - RASMUSSEN, p. 274, fig. 5: V-W.
 1993 *Lenodus?* sp. - LÖFGREN, fig. 6:I.
 1994 *Lenodus?* sp.A - LÖFGREN, fig. 8: 24-27.
 1995 *Lenodus?* sp.A - LÖFGREN, fig. 9: j-n.

Remarks – This species has been fully described by Stouge & Bagnoli (1990).

Material – 92 Pa elements, 46 Pb elements, 46 M elements, 32 Sa elements, 31 Sb elements, 33 Sc elements, 110 Sd elements.

Occurrence – Samples HU 640-650; HUQ 5-12.

Repository – MGUH 24132-24139.

Gen. et sp. indet.
 Pl. 5, figs. 18a-b

- 1985 «*Scolopodus gracilis*» Ethington & Clark - LÖFGREN, fig. 4AK (only).

Description – The elements of Gen.et sp. indet. are slender, highly striated coniforms with a proclined cusp. Posteriorly a deep groove is present through the entire length of the element. The cross section of the cusp is subcircular, modified by the posterior groove.

Gen.et sp. indet. is characterized by a very small and constricted base, with a tiny basal cavity with an anteriorly directed tip.

The cusp is swollen just above the base.

The cusp consists of white matter and the base is hyaline.

Remarks – Gen.et sp.indet. shows similarities with *Striatodontus* Ji & Barnes, 1994 in the peculiar shape of the base, in the striations, and in the presence of a posterior groove. Gen. et sp. indet. possibly belongs to this genus.

«*Scolopodus*» *peselephantis* (Lindström) has a similar appearance and comparable size but it differs in the shape of the base and the deep posterior groove is not present.

Occurrence – Samples HU616-635 and HUQ1-2.

Material – 30 specimens.

Repository – MGUH 24089.

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