

Conodont faunas with *Lenodus variabilis* in the upper Arenigian to lower Llanvirnian of Sweden

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Lenodus variabilis occurs in an interval in the lower to middle Kundan Stage which includes the Arenig–Llanvirn boundary. The lower part of its range constitutes the *L. variabilis* Zone, the upper part, where it co-occurs with *Yangtzeplacognathus crassus*, making up the *Y. crassus* Zone. The conodont faunas of these two consecutive conodont biozones have been investigated in 14 sections from south, south-central and central Sweden, the faunal differences between the areas being mainly expressed in shifts in relative abundance. The taxon which is generally the most abundant, *Baltoniodus*, has comparable abundance maxima at localities representing shallow parts of the basin as well as in deeper parts, indicating that some environmental factor other than water depth has influenced its distribution. *Drepanodus* and *Protopanderodus rectus* prefer areas representing deeper parts of the epicontinental sea. *Scalpellodus* is most abundant at the sites representing intermediate depths. *Semiacontiodus cornuformis* was adapted to shallow water and is lacking at levels representing maximum depths, but at some places (for instance in Skåne) it is replaced by *Semiacontiodus davidi*.

Key words: conodonts, biostratigraphy, biofacies, ecology, Arenigian, Llanvirnian, Sweden.

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Introduction

The lower and middle Kundan Stage (upper Arenigian to lower Llanvirnian) in Sweden has long been described and discussed, the emphasis usually being placed on lithologies and macrofossil biostratigraphy (e.g., Bohlin 1949, 1955; Tjernvik and Johansson 1980; Jaanusson 1982; Jaanusson and Mutvei 1982; Nielsen 1995). Lindström (1971a) included most of the Kundan in the *Amorphognathus variabilis* conodont zone, which was later subdivided and confined to the lower and middle Kundan by Löfgren (1978, 1985). An (1981) distinguished “A.” *antivariabilis*, an ancestor of “A.” *variabilis*, in south-central China, and Bagnoli and Stouge (1997) based a zone in the uppermost Volkhovian on its occurrence.

Zhang (1998a) identified the boundary between the *Lenodus antivariabilis* Zone and the *L. variabilis* Zone in the lower part of the Kundan in the Hällekis section in Västergötland (Fig. 1) and in the Grötlingbo-1 drill-core from southern Gotland. In the Gillberga section on Öland the lower boundary of the *L. variabilis* Zone lies slightly above the base of the Kundan (Löfgren 2000a, b).

In the upper part of its range *L. variabilis* is usually accompanied by another platform-equipped species, *Yangtzeplacognathus crassus* (see Zhang 1997 for description), and Zhang (1998a, b) based a taxon range zone, the *Y. crassus* Zone, on its occurrence. The lower boundary of this zone was considered to be roughly equal to the base of the *Asaphus* “*raniceps*” trilobite zone (Zhang 1998a: table 3). In

the Finngrundet drill-core (Löfgren 1985) the lowermost *Y. crassus* specimen was found ca. 0.8 m above the lowermost specimen of *A. “raniceps”*, so the lower boundary of the *Y. crassus* Zone may actually lie slightly above the base of the *A. “raniceps”* Zone (Fig. 2). The top of the *Y. crassus* Zone is situated within the *A. “raniceps”* Zone (Zhang 1998a).

The entire succession in the Gillberga quarry was described by Löfgren (2000b), including relative abundance data for the conodonts. The aim of the present study is to compare the conodont faunas from the *L. variabilis* and *Y. crassus* zones in that section with faunas of the same age from other parts of Sweden, from Skåne in the south to Jämtland in the north (Fig. 1). This investigation is based on 96 samples from 14 sections, and includes slightly more than 100,000 conodont elements.

Geological setting

During the early to middle Kundan, lime mud was deposited over much of Sweden in a temperate epicontinental sea at depths from ca. 150 to ca. 250 m (Chen and Lindström 1991), extending into shallower waters to the east (e.g., Estonia). This led to the formation of the characteristic “Orthoceratite limestone”, a succession of grey and red limestones with numerous discontinuity surfaces, the result of extremely slow deposition (Lindström 1971b). In deeper waters to the west (Norway) and in southwestern Sweden deposition leading to shale formation prevailed. The division in mainly E-W ex-

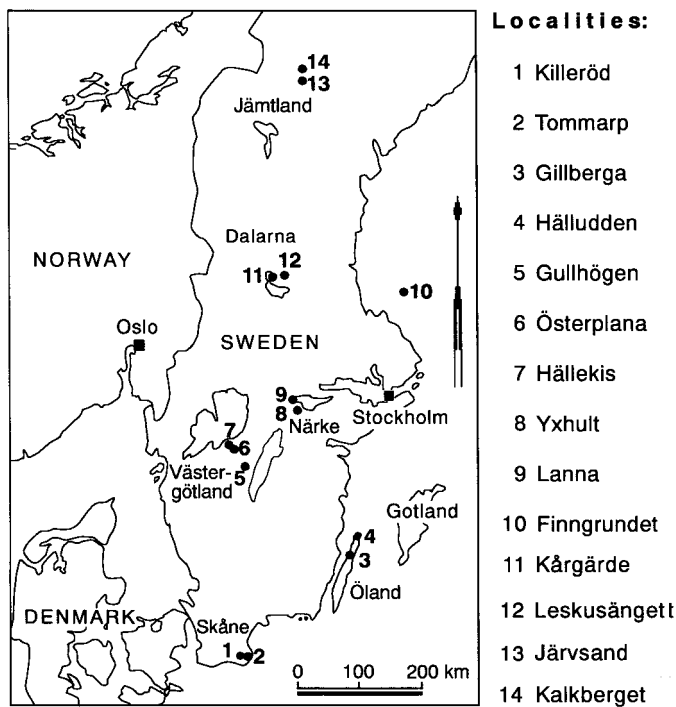


Fig. 1. Location of areas (provinces) and sections in Sweden where samples have been taken.

British series	Baltic substag.	Graptolite intervals	Graptolite zonation Bergstr. and Wang (1995)	Trilob. zonat. Tjernv. and Joh. (1980)	Conodont zonation Zhang (1998a)
Llanvirnian	Aluojan	Da3	<i>Didymogr. artus</i>	<i>M. gigas</i> ----- <i>M. obtusicauda</i>	<i>Eoplacog. pseudoplanus</i> Zone
	Valasteian	Da2		<i>Asaphus</i> "raniceps"	
Arenigian	Hunderumian	Da1	<i>Didymogr. hirundo</i>	<i>Asaphus expansus</i>	<i>Lenodus variabilis</i> Zone

Fig. 2. Chronostratigraphic and biostratigraphic subdivisions in the Kundan. The interval investigated here, the *L. variabilis* and *Y. crassus* zones, approximately equals the lower half (Da 1-2) of the Darriwilian Stage (Da 1-4).

tending facies belts also involved differences in biofacies (Jaanusson 1976). Most of the region discussed here belongs to Jaanusson's Central Baltoscandian Confacies (see map in Jaanusson 1995). Today, erosion has removed most of these mainly biomicritic limestone occurrences from Sweden and only minor outcrop areas remain in Skåne, Öland, Västergötland, Närke, Östergötland, Dalarna, Jämtland and on the

sea floor in the Gulf of Bothnia. Most of these areas are included in this investigation (Fig. 1).

Material and repository

The investigation comprises 96 samples 43 of which have been accounted for in earlier publications: 10 from Järvsand and Kalkberget in the Flåsjö area, Jämtland (Löfgren 1978), 24 from Finngrundet (Löfgren 1985), 7 from Lanna and 2 from Leskusänget (Löfgren 1995a); these samples together yielded 8,540 conodont elements. In addition there are 20 samples from Gillberga with a total of 68,222 elements (Fig. 3), 16 samples from Österplana, Hällekis, Gullhögen, Kårgårde, and Yxhult totalling 19,534 elements (Fig. 4) and eight from "Sylten" with together 2,520 elements. Two samples from Råvanäs, Dalarna, were added to the investigation at a late stage, but the elements have not been included in the Table. From Skåne six samples yielded 1,257 elements. Three samples from Hälludden were originally processed for taxonomical purposes and only absence/presence data and a few abundance estimates have been noted for these.

All samples were dissolved in dilute acetic acid; those prepared since 1983 have been treated according to the buffering method of Jeppsson et al. (1985), and the residues washed through a 63 µm sieve. CAI values (thermal maturity) for the conodont collections vary from five (black, Skåne) and four (dark brown, Flåsjö area) to 1 (unaltered, Öland, Dalarna, Närke and Finngrundet). For an explanation of the CAI scale, see Epstein et al. (1977).

The conodont elements are well to very well preserved. The specimens illustrated are deposited in the type collection at the Department of Geology, Lund University, Sweden (prefix LO).

Comments on the samples

Beds yielding conodonts from the *L. variabilis* Zone have been encountered in all major areas with Ordovician rocks in Sweden. The *Y. crassus* Zone is present in all areas investigated except possibly Jämtland. Information and comments on the samples are given below.

Skåne.—The Killeröd section is a succession through the middle to upper Komstad Limestone in an abandoned quarry in SE Skåne (Scania). The locality was shown on a map published by Regnéll (in Regnéll and Hede 1960: fig. 4), and was described in detail by Nielsen (1995) as "the main quarry at Killeröd". The trilobite biozonation performed by Nielsen (1995: 15) revealed that the upper part of the quarry exposure lies within the trilobite zone of *Asaphus expansus*, and thus not quite extending to the top of the Arenig.

Five test samples from the upper part of the quarry section were collected in 1981, and together yielded 1,157 conodont elements. The conodont faunas recovered include numerous

conodont biozone	taxa	samples																																																		
		total	Ö193-9	Ö183-106	Ö187-3	Ö187-2	Ö193-8	Ö183-105	Ö192-9	Ö172-7	Ö193-7	Ö192-8	Ö183-104	Ö192-7	Ö172-6	Ö183-103	Ö192-6	Ö187-1	Ö192-5	Ö172-5	Ö183-102	Ö192-4	Drepanodus arcuatus	Cornuodus longibasis	Drepanoistodus basiovalis	Drepanoistodus? aff. venustus	Drepanoistodus stougei	Drepanoistodus cf. suberectus	Decoriconus pesequus	Semiacontiodus cornuiformis	Semiacontiodus davidi	Semiacontiodus sp. A	Scalpellodus gracilis	Protopanderodus rectus	Protopanderodus cf. parvibasis	Protopanderodus calceatus	Parapanderodus quietus	Microzarkodina parva	Microzarkodina bella	Microzarkodina hagetiana	Baltoniodus norrlandicus	Baltoniodus medius	Lenodus variabilis	Paroistodus originalis	Parapaltodus simplicissimus	Costiconus mysticus	Dzikodus humanensis	Yangtzeplacognathus crassus	Eoplacognathus pseudoplanus	Ansella jemtlandica	Strachanognathus parvus	Periodon flabellum
Yangtzeplacognathus crassus Zone	total	340	302	5432	811	141	70	363	9407	628	5	3115	396	22	278	430	4425	2295	444	8733	25896	2515	447	80	36	66	1429	1cf	9	13	67	26	68222																			
	Ö193-9	2	24	247	72	--	40	18	2440	--		152	--		43			21	203		5313	74		11	2	26	337					7	9032																			
	Ö183-106	18	15	188	134	--	--	7	537	--		47	46		1			335	69		5257	286		14	3	152							7109																			
	Ö187-3	3	52	672	179	--	--	76	1051	--		92	22		189			17			4620	647		22	26		421		9	67			8165																			
	Ö187-2	8	23	238	123	--	--	8	616	--		329	6		11			150			2792	15		1			338		13	5			4676																			
	Ö193-8	1	10	51	27	--	--	2	445	--		37	5		--			96			638	35		2		3	31				3		1386																			
	Ö183-105	2	4	15	4	--	2	--	117	--		11	2		--			19			236	26		2			--						440																			
	Ö192-9	8	10	208	38	--	16	4	553	--		127	--		24			38			1480	317		3	7	16	130	1cf					2980																			
	Ö172-7	--	--	34	2	--	--	--	59	12		3	--		--			1			57	15				1	3						187																			
	Ö193-7	--	3	36	10	--	--	4	129	--		22	3		--			68			628	82		1			4						990																			
	Ö192-8	1	11	51	22	--	--	2	255	--		25	3		--	1		70			510	93		2		1	5				2		1054																			
	Ö183-104	3	8	240	40	--	--	2	506	57		13	12		2	--		39			866	183		3		9	8						1991																			
Lenodus variabilis Zone	Ö192-7	4	2	47	12	--	1	21	317	--		31	1	--	--		124			349	65		15		3							992																				
	Ö172-6	13	22	135	27	--	--	10	151	144		79	--	--	14		42	159		347	70									2		1215																				
	Ö183-103	27	23	706	--	--	--	13	380	182		135	--	--	94		329	13	35	621	39			4									2601																			
	Ö192-6	5	5	163	36	--	--	3	314	60	2	26	15	2	--	9		25	43	1354	128									2			2192																			
	Ö187-1	8	--	139	11	--	--	2	191	18	2	12	3		--	170		7	--	335	93									3			994																			
	Ö192-5	11	1	50	19	42	8	12	124	14		24	12		--	79		43	--	76	49		1							1			566																			
	Ö172-5	10	1	109	--	6	--	1	59	1		16	--		8	2		13		150	--	5											381																			
	Ö183-102	194	80	1869	18	66	--	174	916	--		1865	265	20		42	4425	598		7274	417	177	447										18847																			
Ö192-4	22	8	234	37	27	3	4	247	140	1	69	1			19		260		1231		116		3	1cf				1				2424																				

Fig. 3. Conodont element distribution in the samples from the Gillberga section.

elements of *Protopanderodus rectus* and *Baltoniodus medius*. *Drepanodus arcuatus* and *Cornuodus longibasis* are more common than in samples from the same interval on Öland. *Drepanoistodus stougei* and *Lenodus variabilis* are also represented by a fair number of specimens in all the samples, while *Semiacontiodus davidi* and *Decoriconus pesequus* were represented in only 3 of the 5 samples. Only a few elements each of *Costiconus mysticus*, *Scalpellodus gracilis*, *Microzarkodina* cf. *parva* and *Erraticodon* sp. were found in the samples from this interval. The fauna indicates the lower to middle part of the *Lenodus variabilis* Zone.

A small Komstad Limestone sample (100 elements) was collected by Maurits Lindström in the mid-1950s at Tommarp, ca. 12 km ESE of Killeröd. The conodont taxa found are: *Baltoniodus medius*, *Cornuodus longibasis*, *Decoriconus pesequus*, *Drepanodus arcuatus*, *Drepanoistodus stougei*, *Dzikodus humanensis*, *Lenodus variabilis*, *Microzarkodina* cf. *hagetiana*, *Protopanderodus rectus*, and *Semiacontiodus davidi*. The presence of a few P elements of *Microzarkodina* with two denticles in front of the cusp (see discussion of simi-

lar elements in Löfgren 2000b) and of *Dzikodus* indicates the upper *L. variabilis* Zone, or even the *Yangtzeplacognathus crassus* Zone although *Y. crassus* is lacking. That the *Y. crassus* Zone is indeed represented in the upper Komstad Limestone of Skåne was recently demonstrated by the recovery of a few elements of the zonal denominator in well cuttings from a drilling at Lyby in central Skåne, ca. 50 km NW of Killeröd (Erlström et al. 2001). The Komstad Limestone in SE Skåne may extend even higher, since a conodont sample from the Killeröd area (Nielsen 1995: 42, table 4) from the base of the overlying shale unit indicated the upper subzone of the *Eoplacognathus pseudoplanus* Zone.

Öland.—The Gillberga section was described by Löfgren (2000b) and in addition to the samples from the *L. variabilis* Zone included there, only one more sample, Ö172-5, has been added to this analysis (Fig. 3), which was collected from the top 5 cm of division K, 13–18 cm above sample Ö183-102 (cf. Löfgren 2000b: fig. 8). The boundary between the *L. variabilis* and the *Y. crassus* zones was placed a few

samples	taxa																											
	<i>Drepanodus arcuatus</i>	<i>Cornuodus longibasis</i>	<i>Drepanoistodus basiovalis</i>	<i>Drepanoistodus? aff. venustus</i>	<i>Drepanoistodus stougei</i>	<i>Drepanoistodus cf. suberectus</i>	<i>Decoriconus pesequus</i>	<i>Semiacontiodus cornuformis</i>	<i>Semiacontiodus davidi</i>	<i>Semiacontiodus sp. A</i>	<i>Scalpellodus gracilis</i>	<i>Protopanderodus rectus</i>	<i>Protopanderodus calceatus</i>	<i>Parapanderodus quietus</i>	<i>Microzarkodina parva</i>	<i>Microzarkodina haegitana</i>	<i>Baltoniodus norrlandicus</i>	<i>Baltoniodus medius</i>	<i>Lenodus variabilis</i>	<i>Paroistodus originalis</i>	<i>Costiconus mysticus</i>	<i>Dzikodus humanensis</i>	<i>Yangtzeplacognathus crassus</i>	<i>Pygodus sp. A</i>	<i>Strachanognathus parvus</i>	<i>Periodon flabellum</i>	others	total 19,534
Österplana:																												
Vg98-4B	132	106	55	--	462		41	28	199	--	670	145		--	269	20	186	110		23	--			48			2	2496
Vg98-4A	87	123	10	--	253		19	8	134	--	525	158		--	71	13	64	64		6	2			25			11	1573
Vg98-3	74	183	15	--	283		31	52	82	2	698	52		--	223	14	120	44		--	--		15			1	1889	
Vg98-2	93	154	72	--	438		34	87	155	3	827	110		4	89	23	196	122		1	--		11	1	46	6	2472	
Vg98-1	59	80	20	--	201		3	22	86	--	282	63		5	27	19	105	39		--	--		1			--	1012	
total Öst.	445	646	172	--	1637		128	197	656	5	3002	528		9	679	89	671	379		30	2		100	1	46	20	9442	
Hällekis:																												
HK88-3*	43	11	79	14	--		5	36	--		68	94	158		--	75	--	222	10		--	12	63			3	12	905
HK88-2*	39	109	18	--	180	14	7	47	222		32	87	2		--	31	--	117	73		--	3	27			--	9	1017
Vg90-3	138	82	194	39	209		103	31	116		204	7	--		--	214	18	132	20		2	--	--			3	8	1520
HK88-1	52	64	20	34	114		--	10	55		158	37	--		--	8	16	101	32	1	--	--	--			--	--	702
total Häll.	272	266	311	87	503	14	115	124	393		462	225	160		--	328	34	572	135	1	2	15	90			6	29	4144
Gullhøgen:																												
Gb81-900*	6	17	68	38	--		--	20	--		24	85	83		--	8	--	199	5		71		176			702	2	1504
Gb81-1100	36	10	27	--	82		--	48	15	1	85	11	--		--	1	--	33	38		4		--	9		--	--	400
Gb81-1200	44	17	219	--	--		2	1	17		39	9	--		--	3	29	15	17	1	1		--			--	--	414
total Gull.	86	44	314	38	82		2	69	32	1	148	105	83		--	12	29	247	60	1	76		176	9		702	2	2318
Kårgårde:																												
D70-102*	--	2	6	2			1	32	--	--	--	2	52		--	--	--	115	--				56			3	1	272
LK-H14	7	--	90	3			--	33	1	2	4	--	--	2	--	1	--	11	4			--	--			--	--	158
LK-H15	48	--	189	--			--	98	--	--	18	16	--	10	94	305	279	12	25			--	--			1	3	1098
total Kår.	55	2	285	5			1	163	1	2	22	18	52	2	10	95	305	405	16	25			56			4	4	1528
Yxhult:																												
Nå90-1	80	48	300	--			157	16	--	--	269	100	1	5	157	--	932	--	36								1	2102

Fig. 4. Distribution of conodont elements in samples from Närke, Dalarna and Västergötland not previously presented. Samples with an asterisk (samples D70-102, GB81-900, HK88-2 and HK88-3) represent the *Y. crassus* Zone; the remaining samples are from the *L. variabilis* Zone.

centimetres lower than that previously depicted by Löfgren (2000b: fig. 8), when three specimens of *Y. crassus* were retrieved from a second piece of sample Ö183-104, and this sample became the basal sample from the *Y. crassus* Zone. Thus nine samples were referred to the *L. variabilis* Zone in this investigation. Two more samples were added to those previously noted from the *Y. crassus* Zone (Löfgren 2000b: fig. 9); sample Ö172-7, collected from the top 5 cm of division M, at approximately the same level as sample Ö192-9, and sample Ö183-105, collected from the basal 5 cm of division N, just below sample Ö193-8. Thus, 11 samples from Gillberga were referred to the *Y. crassus* Zone in this investigation (Fig. 3).

The Hälludden section, situated ca. 27 km N of Gillberga, has been intensely investigated and sampled for many years (see review in Jaanusson and Mutvei 1982). Nordlund (1989) performed a lithostratigraphic and sedimentological investiga-

tion in the section in connection with which a few small conodont samples were collected. A specific, sulphide-impregnated, planar discontinuity surface, "D", had been selected as the 0-level. Samples with a representative *L. variabilis* Zone fauna were collected from 120 cm below the "D" surface and at least up to that surface. At 60 to 70 cm below the "D" surface a fauna with *Baltoniodus medius*, *Drepanoistodus basiovalis*, *Lenodus variabilis*, *Microzarkodina bella*, *Scalpellodus gracilis*, *Semiacontiodus cornuformis*, and *S. davidi* has been encountered. Further details about the conodont succession at Hagudden, situated ca. 10 km S of Hälludden, can be found in Stouge and Bagnoli (1990) and Bagnoli and Stouge (1999).

Gullhøgen.—The Gullhøgen quarry (= the Skövde quarry of Lindström 1984) is situated near the northern end of the Billingen Mountain in Västergötland. A short description was given by Thorslund and Jaanusson (1960), and a more detailed log of the section was published by Jaanusson

(1982). Conodont samples from the lower part of the section have been described and discussed by Löfgren (1995a, 2000a). Two samples, Gb81-1200 and Gb81-1300, belong to the *L. variabilis* Zone (Fig. 4). They were collected from a calcilitic red limestone at 12.00 m and 11.00 m, respectively, below a distinctive level in the Middle Ordovician. Another sample of red limestone, Gb81-900, taken 9.00 m below the same level can be attributed to the *Y. crassus* Zone.

Hällekis.—The Hällekis quarry is situated near the top of the Kinnekulle Mountain in Västergötland (Thorslund and Jaanusson 1960). A short description, conodont biostratigraphy and distribution of conodont elements from this section were presented by Zhang (1998a). Samples from a series taken through the section there by Lars Holmer, Uppsala, in the 1980s have been included here and were briefly discussed by Löfgren (1995a). Some additional sampling took place in 1990. Two samples of red calcilitic limestone derive from the *L. variabilis* Zone. They were collected below a conspicuous, ca. 1.2 m thick, grey limestone interval in the lower to middle Kundan (cf. Zhang 1998a: fig. 2); sample HK88-1 approximately 0.5 m below, and sample Vg90-3 immediately below the base of the grey limestone (cf. Fig. 4). Two samples from the same section can be assigned to the *Y. crassus* Zone. Sample HK88-2 was collected from the middle part of the grey limestone “Täljsten” interval, ca. 1.0 m above sample HK88-1, and sample HK88-3 was collected in the red limestone above the grey interval, at ca. 2.0 m above HK88-2. The ostracod biostratigraphy of the section was recently discussed by Tinn and Meidla (2001).

Österplana/Sylten.—This quarry section is situated ca. 4 km SE of Hällekis, on the southeastern slope of Kinnekulle. Five samples were collected from a ca. 60 cm thick, reddish-brown limestone immediately below the conspicuous grey limestone that was also recognized in the Hällekis quarry section. The interval was sampled by B. Schmitz, Göteborg, in connection with another project to find out if there were any abrupt faunal changes recorded. The 60 cm long sampling column was divided into five consecutive samples; from below: sample Vg98-1 (103 mm thick), sample Vg98-2 (149 mm), sample Vg98-3 (134 mm), sample Vg98-4A (ca. 100 mm) and sample Vg98-4B (ca. 100 mm) (Fig. 4). Eight samples were collected in another part of the same quarry by L. Holmer in the 1980s. These samples (marked “Sylten”, a local name for this part of the quarry), together yielding 2,520 elements, were collected within a 4-m interval, four samples representing the upper *L. variabilis* Zone and four representing the *Y. crassus* Zone.

Lanna.—The Lanna section is situated in the Province of Närke, just outside Örebro (Fig. 1). The ca. 11.5-m-high section was measured and sampled by the late Torsten Tjernvik in the early 1950s. A simplified log and lithologic description of the section was presented in Löfgren (1995a) together with a description of the conodont faunas, focusing on the middle Arenig part of the section. The uppermost metre of

the section (with 7 samples, yielding 3,816 conodont elements in all) consists of an olive-grey to greenish-grey limestone belonging to the *L. variabilis* Zone. Since the conodont element distribution and the discussion of the fauna from this interval have been published previously (Löfgren 1995a: fig. 6, 706–707), only a few comments will be added. The 10 and 7 elements, respectively, in the column headed “others” (Löfgren 1995a, fig. 6) for samples Nä94-32 and Nä94-35, both from the lower half of the interval, all represent *Parapanderodus quietus*. In sample Nä94-34, also from the lower half of the interval, a few of the elements referred to *Drepanoistodus basiovalis* should instead be assigned to *D. stougei*. In sample Nä94-33, from the lowermost part of the interval, a few of the elements referred to *Microzarkodina parva* should be transferred to the column headed *Microzarkodina* cf. *hagetiana* (which includes elements which can now more confidently be referred to *M. hagetiana*). Only one specimen of *Microzarkodina* possibly belongs to *M. bella*. The column with “*Amorphognathus* spp.” only includes records of elements actually belonging to *Lenodus variabilis*. The heading “*Semiacontiodus* sp. A” refers to the species *S. davidi*, formally described by Löfgren (1999).

Yxhult.—From Hällabrottet at Yxhult [locality data in Lindström (1955)], a single sample (Nä90-1, 1400 g) was collected from the greyish-green basal 0.05 m of the Expansus Limestone in the south quarry wall, not far from Lindström’s (1955) section II. The sample can be referred to the lower *L. variabilis* Zone (Fig. 4).

Finngrundet.—The conodont biostratigraphy in the Finngrundet drill-core, Gulf of Bothnia, has been previously published (Löfgren 1985). Fourteen samples from levels 39.00 m through 32.00 m represent the *Lenodus variabilis* Zone and 10 samples from 31.50 m through 27.00 m represent the *Yangtzeplacognathus crassus* Zone. Together these 24 samples yielded 3,818 conodont elements. Conodont element distributions for these intervals have already been presented (Löfgren 1985: fig. 3) and here only some comments will be added. Changes in systematic usage make the following changes in column headings necessary for the interval 39.00 m – 27.00 m: *Scolopodus? peselephantis* should be *Decoriconus pesequus*, *Protopanderodus* cf. *varicostatus* should be *P. calceatus*, “*Scolopodus gracilis*” should be *Parapanderodus quietus*, *Polonodus* sp. should be *Dzikodus hunanensis*, *Drepanodus?* sp. A should be *Parapaltodus simplicissimus*, and *Dapsilodus mutatus* should be *D. viruensis*.

Lenodus variabilis is not common at Finngrundet. In a Table (Löfgren 1985: fig. 3) platform elements as well as a few ramiform and geniculate elements belonging together with these were registered in the column “*Eoplacognathus? variabilis*”. In the interval 39.00 m – 32.00 m all the registered elements actually do belong to *L. variabilis*, but higher up in the sequence some of the elements should be transferred elsewhere. *Yangtzeplacognathus crassus* first appears at 31.50 m (base of the *Y. crassus* Zone) and then co-occurs with *L. variabilis*, being more abundant than that species

near the upper boundary of the *Y. crassus* Zone. In the uppermost sample, at 27.00 m, almost all the elements referred to *E. ? variabilis* in the diagram belong to *Y. crassus*.

Microzarkodina generally occurs in great abundance at Finngrundet, and in the interval 39.00 m – 27.00 m all specimens were previously (Löfgren 1985) referred to *M. parva*. The recognition of two new species, *M. hagetiana* (see Stouge and Bagnoli 1990 for description and Löfgren 2000a: fig. 5c–d for basal cavity outline), and *M. bella* (see Löfgren 2000b for description and Löfgren 2000a: fig. 5e, f for basal cavity outline) necessitates some adjustments in the Table of distribution (Löfgren 1985: fig. 3). In the basal *L. variabilis* Zone, *M. parva* is the only representative of *Microzarkodina* that has been recovered from Finngrundet. At 38.00 m, about one metre above the lower zonal boundary, *M. hagetiana* appears, and from 37.00 m *M. bella* has also been retrieved. From that level upwards *M. parva* is no longer found in the Finngrundet sequence. *Microzarkodina bella* and *M. hagetiana* co-occur in the upper *L. variabilis* Zone, while *M. hagetiana* is lacking in the lower *Y. crassus* Zone. In the upper *Y. crassus* Zone *M. hagetiana* reappears and totally replaces *M. bella*.

In the column for *Semiacontiodus cornuformis* (Löfgren 1985: fig. 3), 8 elements from the sample at 35.50 m, 7 from 34.50, 6 from 34.00, 1 from 33.50, 1 from 33.00, and 2 from 32.50 should instead be referred to *Semiacontiodus davidi*, described by Löfgren (1999). In the columns “*Scalpellodus latus*” and “*Scalpellodus gracilis*” in the same diagram, 18 elements from sample 35.50, 1 from 35.00, 3 from 34.50, 8 from 34.00, 2 from 33.50, 6 from 33.00, 5 from 32.50, 1 from 32.00 and 1 from 31.00 should be transferred to *Semiacontiodus davidi*. The range of *S. davidi* will thus be from 35.50 m to 31.00 m at Finngrundet.

The column for *Drepanoistodus basiovalis* (in Löfgren 1985: fig. 3) should be slightly modified since *Drepanoistodus stougei* has been distinguished as a separate species (Rasmussen 1991). Although *D. basiovalis* is by far the most abundant of the two species in the interval 39.00 m – 27.00 m, a few elements of *D. stougei* occur at 39.00, 38.50, 36.00, 35.50, 34.00, 33.50, 33.00 and 31.00 m.

Dalarna.—Leskusänget is a locality in the northern part of the Siljan area, Province of Dalarna [cf. Fig. 1; for location see also Thorslund and Jaanusson (1960)]. Two samples collected from the uppermost part of the section represent the *L. variabilis* Zone and together yielded 613 conodont elements. The lower of these samples, LÄ2, was taken from the upper part of a grey limestone interval rich in flat limonitic ooids, and the upper sample, LÄ1, was taken ca. 1.0 m higher up, from the lower part of a red limestone interval. The conodont element distribution in these samples has been published previously (Löfgren 1995a: fig. 8). As a comment to that Table: the 3 elements in sample LÄ2 under “others” are *Parapanderodus quietus*.

The Kårgärde section is situated ca. 17 km SW of Leskusänget. From a series sampled by Lars Holmer in the 1980s

two samples, both from a grey limestone, belong to the *L. variabilis* Zone (Fig. 4). The lower sample, DLK-H15, is rich in flat limonitic ooids, whereas ooids are rare in the second sample, DLK-H14, taken ca. 0.5 m higher in the section. DLK-H13 is the next higher (ca. 0.5 m) sample in this sample series, and belonging to the *E. pseudoplanus* Zone. In 1970 a pilot sample series had been taken from the same section, and one of these samples, D70-102, which represents the *Y. crassus* Zone was collected from a level somewhere between samples H13 and H14. The exact vertical distance from DLK-H14 cannot, however, be determined since the position of D70-102 in the section was measured less accurately than the position of samples in the more comprehensive sampling series.

From the section at Rävånäs, ca. 30 km SSE of Leskusänget, one sample from the *L. variabilis* Zone and one from the *Y. crassus* Zone were collected in a ca. 2 m thick interval of grey limestone between sample RÄ4 (from the *B. norrlandicus* Zone) and sample RÄ5 (from the *E. pseudoplanus* Zone). These samples were processed for another purpose when this paper had already been submitted, so they have not been included in any of the diagrams. However, their faunas agree well with those from the other localities in Dalarna.

Flåsjö area.—In the Flåsjö area in Jämtland (cf. Löfgren 1978) 10 samples from the Järvsand and Kalkberget sections (Fig. 1) have been referred to the interval under discussion. Together these samples yielded 293 conodont elements. Only 3 platform specimens and a few associated elements were found in these samples, all referable to *L. variabilis*. The presence of the *Y. crassus* Zone in the area can thus neither be proved, nor refuted.

The elements of *Microzarkodina* found in this interval were all previously assigned to *M. parva* (Löfgren 1978: fig. 38). The youngest specimen retrieved from this interval (in sample J68-615), has after reinvestigation been reassigned to *M. hagetiana*. The elements previously reported as *Drepanoistodus basiovalis* in sample J68-611, in the lower part of the investigated interval, should instead be referred to *D. stougei* and the element referred to “other” in the Table (Löfgren 1978: fig. 38) for the youngest sample in the interval, J70-154, represents *Parapaltodus simplicissimus*. As a whole, the conodont fauna recovered from this interval is meagre. The base of the following zone can with confidence be placed below the next higher samples in the two sections, J68-631 and J70-155, respectively, since they include elements of the zonal species, *Eoplacognathus pseudoplanus*.

Biostratigraphical events

The basal strata of the *Lenodus variabilis* Zone yield a conodont fauna including *Drepanodus arcuatus*, *Cornuodus longibasis*, *Protopanderodus rectus*, *Paroistodus originalis*, *Drepanoistodus basiovalis*, *D. stougei*, *Microzarkodina parva*, *M. bella*, *Semiacontiodus cornuformis*, *S. davidi*,

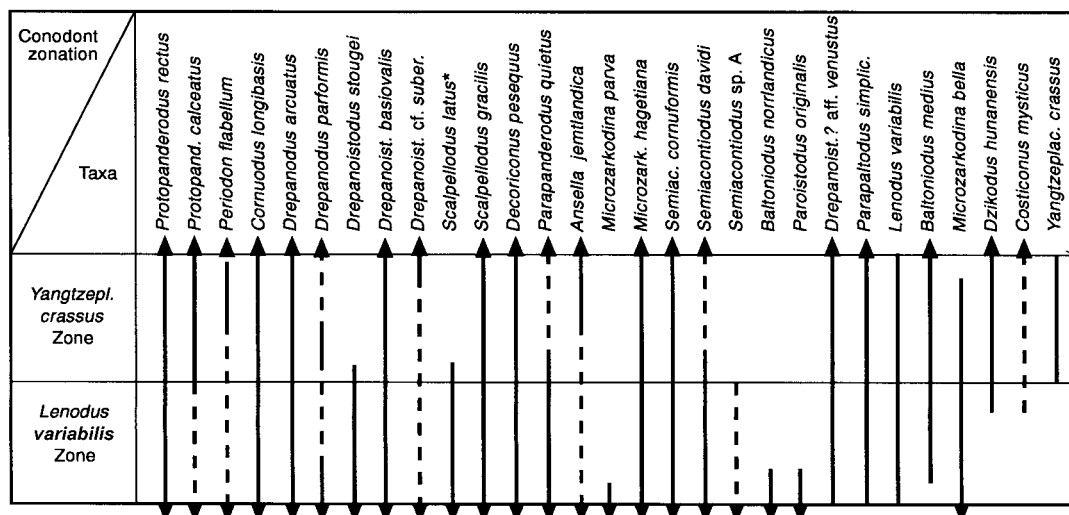


Fig. 5. Stratigraphic ranges of key taxa in Swedish sections. The range of *Scalpellodus latus* applies to Finngrundet only; in other areas, except possibly in Jämtland, the species disappeared before the beginning of the *L. variabilis* Zone interval.

Baltoniodus norrlandicus, *Decoriconus pesequus*, *Scalpellodus gracilis*, and *Parapanderodus quietus*, all of which first appeared in the underlying *B. norrlandicus* Zone or even further down in the succession. The conodont biostratigraphy of the interval following this is based on three main events (Fig. 5):

(1) The first appearance of *Lenodus variabilis*, marking the lower boundary of the zone of that name (Lindström 1971a; Zhang 1998a, b; Löfgren 2000a, b).

(2) The first appearance of *Yangtzeplacognathus crassus*, marking the lower boundary of the zone of the same name (Zhang 1998a, b; Löfgren 2000a, b).

(3) The first consistent occurrence of *Eoplacognathus pseudoplanus*, marking the lower boundary of the succeeding zone (Zhang 1998a, b; Löfgren 2000b)

Remarks.—At the lower boundary of the *Lenodus variabilis* Zone, *Lenodus antivariabilis* has disappeared presumably because it was replaced by its descendant, *L. variabilis*. Löfgren (1995a, 2000a, b) discussed the level at which this replacement took place; it is now fairly certain that the lower boundary of the *L. variabilis* Zone occurs in the lower, but not the lowermost Kundan Stage. The base of this stage, the base of the trilobite *Asaphus expansus* Zone, thus lies in the upper *L. antivariabilis* Zone (cf. Löfgren 2000b).

The first appearance of *Yangtzeplacognathus crassus* in Baltoscandia is probably attributable to an immigration event. However, as far as can be judged this event seems to have been geologically instantaneous in the region and also correlates excellently with the first appearance of the taxon in south-central China (Zhang 1997, 1998a, b). It is not yet clear which taxon was the immediate ancestor of *Y. crassus*, or where its centre of origin was, but morphological evidence indicates that *Lenodus antivariabilis* rather than *L. variabilis* was the ancestral species (Löfgren and Zhang 2002 and in press).

Eoplacognathus pseudoplanus seems to have evolved from *Lenodus variabilis* and occurs very rarely in the upper *Y. crassus* Zone in Sweden together with *L. variabilis* (e.g., Fig. 3). In south-central China there is usually a stratigraphic gap between the last occurrence of *Y. crassus* and the first occurrence of *E. pseudoplanus* (cf. Zhang 1998b).

Besides these three main events there are a number of first and last appearances of conodont taxa in the interval which are of potential use in subdividing the two zones. These bioevents are presented below in stratigraphic order (Fig. 5).

(a) Last appearance of *Microzarkodina parva*. *Microzarkodina parva* is succeeded by either *M. bella* [= *M. sp. nov.* A of Löfgren (2000a)], by *M. hagetiana*, or by both. Here, the time of substitution may differ from area to area and the transitions are probably not suitable for purposes of correlation. The first specimens of *M. bella* and *M. hagetiana* seem to occur in the uppermost *L. antivariabilis* Subzone (Löfgren 2000a: 60), but when and where they evolved has not been ascertained.

At Gillberga, *Microzarkodina bella* is the most common species of *Microzarkodina* found in samples from the uppermost ca. 0.5 m of the *L. antivariabilis* Subzone and through the *L. variabilis* Zone and most of the *Y. crassus* Zone (Löfgren 2000b: 332). *M. bella* has nowhere been found in beds younger than those of the *Y. crassus* Zone. Elements of *M. parva* prevail in sample Ö183-102, 0.2 m above the lower boundary of the *L. variabilis* Zone, but are lacking in higher parts of the Gillberga section. *M. hagetiana* is present in samples Ö183-103 and Ö172-6, both collected from a particularly glauconitic interval in the upper part of division L of the Gillberga section, 1.5–1.8 m from the base of the *L. variabilis* Zone, and then again in the uppermost two samples from the *Y. crassus* Zone. At Hagudden Stouge and Bagnoli (1990) retrieved *M. hagetiana* from the upper to middle *L. variabilis* Zone and upwards in the section; the

holotype is from the *E. pseudoplanus* Zone. In the *L. variabilis* Zone *M. hagetiana* varies in abundance in the Hagudden section from 2 to 6%, but only amounts to 0.5% in a sample from the *Y. crassus* Zone. With such low abundance values, possible incursions of *M. bella* could easily go undetected. Most of the sporadic elements of *Microzarkodina* from the interval corresponding to the *L. variabilis* and *Y. crassus* zones at Hälludden in my collections seem to belong to *M. bella*.

Except for one doubtful find from the Lanna section, Finngrundet is the only Swedish locality outside Öland where *M. bella* has yet been encountered. As described in greater detail under "Comments on the samples", *M. hagetiana* and *M. bella* co-occur at Finngrundet in the middle to upper *L. variabilis* Zone. As at Gillberga, *M. hagetiana* is lacking from the lower *Y. crassus* Zone, reappearing and replacing *M. bella* in the upper part of that zone at Finngrundet.

In the uppermost *L. variabilis* Zone and, particularly, in the *Y. crassus* Zone there is a tendency in both *M. bella* and *M. hagetiana* to develop additional denticles in front of the cusp in P elements, prior to the first appearance of genuine *M. ozarkodella* (Löfgren 2000b: 325, 335). Such "false *M. ozarkodella*" elements, if found outside their stratigraphical context, and particularly if not well preserved, could easily be taken for genuine *M. ozarkodella* elements.

Some events in the evolution of *Microzarkodina* may thus be unsuitable for use in correlation. Löfgren (1993: 204) discussed the first appearance of *M. flabellum* in various Swedish sections and concluded that biostratigraphically it could be used with caution. Bagnoli and Stouge (1997) described rare elements of an even older *Microzarkodina* species, *Microzarkodina* sp. nov. A, from northern Öland. This taxon has subsequently been found in greater numbers in western Russia (Tolmacheva 2001a), but seems to be rare in Swedish areas outside Öland. The replacement of *M. flabellum* by *M. parva* was used to distinguish the beginning of "phase 3" of the *P. originalis* Zone by Löfgren (1995a), while Bagnoli and Stouge (1997) used it to define the base of their *M. parva* Zone. This replacement event is probably reasonably synchronous in Baltoscandia.

(b) Last appearance of *Baltoniodus norrlandicus* and first appearance of *B. medius*. *Baltoniodus medius* first appears at a level within the lower part of the *L. variabilis* Zone. At Gillberga it co-occurs with *B. norrlandicus* through ca. 1.5 m in the lower to middle *L. variabilis* Zone. The entire zone is only ca. 2.5 m thick in that section. *B. medius* is the more common of the two taxa almost from the beginning of its range at Gillberga. At Finngrundet, *B. norrlandicus* is the only *Baltoniodus* species in the lower 3.5 m of the *L. variabilis* Zone above which *B. medius* co-occurs with and exceeds *B. norrlandicus* in abundance for about 2.5 m. In the upper ca. 1.5 m of the ca. 7-m-thick *L. variabilis* Zone, and throughout the *Y. crassus* Zone, only *B. medius* occurs. At Lanna, as at Gillberga, *B. medius* appears within the lowermost 0.5 m of the *L. variabilis* Zone. The interval of co-occurrence with *B. norrlandicus* is very thin at Lanna, at most

0.2 m. The pattern of occurrence of these two species of *Baltoniodus* is less clear in the rest of the sections, since so few samples were collected from the interval. At Kårgårde, Gullhögen and Hällekis the lowermost samples representing the *L. variabilis* Zone yielded both *B. norrlandicus* and *B. medius*, as did the entire suite of 5 samples through 0.6 m at Österplana. The single sample collected from Yxhult yielded a rich *B. norrlandicus* fauna, but no *B. medius* and should probably be regarded as representing the basal part of the *L. variabilis* Zone.

The relationship between *B. norrlandicus* and *B. medius* is decisive for the interpretation of these patterns, *B. norrlandicus* in all probability being the direct ancestor of *B. medius* (Löfgren 1978: 86) since the two species occur consecutively, although with slightly overlapping stratigraphic ranges, and in the same areas. Moreover, their respective elements often resemble one another closely, and it is possible to follow morphological trends that progress from one to the other species and then continue in the even younger species, *B. prevariabilis*. Among such trends are the arrangement of processes in Sb elements and the denticulation of Sc elements. However, Stouge and Bagnoli (1990) described what they recognized as another lineage of *Baltoniodus* subsequent to *B. norrlandicus* in the Hagudden section on Öland. That lineage comprised two species, *B. clavatus* and *B. sp. nov. A*. Typical *B. clavatus* appears to morphologically fall within the limits of variation of *B. medius* and is particularly common at some levels in Öland. In the same way I consider that *Baltoniodus* sp. nov. A of Stouge and Bagnoli (1990) represents younger morphotypes within the limits of variation of *B. medius*. It is not at all clear why Stouge and Bagnoli (1990: 13) should regard the divergent populations that they distinguished as *B. clavatus* as more likely to be ancestral to their *B. sp. nov. A* than less deviating populations of *B. norrlandicus* which morphologically are closer to *B. sp. nov. A*.

Specimens of *Baltoniodus* vary considerably, both within collections from single samples (cf. Dzik 1994: 81, fig. 13) and between faunas from different areas, which has made the delimitation of successive species particularly precarious in some intervals, such as that in the middle Kundan discussed here. Dzik (1994) distinguished *B. parvidentatus* (Sergeeva, 1963) in the early Kundan and *B. medius* (Dzik, 1976) in the late Kundan and Aserian. In his synonymy lists Dzik (1994) included *B. norrlandicus* (Löfgren) as well as *B. clavatus* Stouge and Bagnoli in *B. parvidentatus* and *B. sp. nov. A* Stouge and Bagnoli in *B. medius*. The stratigraphically oldest specimens that I have referred to *B. medius* would probably have been referred to *B. parvidentatus* instead by Dzik (1994). Our conception of these two taxa does not differ greatly, but probably involves the interval which I have interpreted as the co-occurrence of *B. norrlandicus* and *B. medius* in my sections, and possibly also the rest of the *L. variabilis* Zone. Although these differences in interpretation and delimitation of *Baltoniodus* taxa can occur, I consider that the *B. norrlandicus*–*B. medius* transition could be of considerable biostratigraphical use.

(c) *Scalpellodus latus*–*S. gracilis* transition. In most Swedish sections *Scalpellodus latus* had its last occurrence below the base of the *L. variabilis* Zone. This final disappearance was preceded by a period of co-occurrence with the descendant species *S. gracilis*, which at Gillberga lasted throughout most of the *L. antivariabilis* Subzone (Löfgren 2000a: fig. 3). At Finngrundet *S. gracilis* is first met with higher up in the *L. antivariabilis* Subzone, and the co-occurrence with *S. latus* continues even into the basal part of the *Y. crassus* Zone there. In the upper half of the *L. variabilis* Zone of Finngrundet, *S. latus* is actually the only species of *Scalpellodus* present. It has been suggested that the difference in stratigraphic distribution in different areas is the result of slight differences in preferred habitat between ancestor and descendant (Löfgren 2000a). The transition is thus unsuitable for use as a biostratigraphic marker.

(d) Last appearance of *Paroistodus originalis*. This is most certainly facies related, since *P. originalis* is succeeded in some areas by *P. horridus* in the early Llanvirn, while in other areas *P. originalis* appears to be rare, but prevail (cf. Rasmussen 2001).

(e) First appearance of *Dzikodus hunanensis*. This species is not common in Sweden, but its elements are characteristic. Since it is fairly common in some sections in south-central China (Zhang 1998b) it could well prove to be a useful index species for the upper *L. variabilis* Zone.

The other first and last appearances shown in Fig. 5 all appear to be facies dependent, or the taxa are too sparsely or irregularly distributed to prove reliable biostratigraphic markers. These appearances are further discussed in the relative abundance section below.

Conodont palaeoecology

The oceanographic conditions in the Ordovician seas probably differed considerably from those in present-day seas. Outside coastal waters in particular, the seas seem to have been much less productive in the Mid-Ordovician than nowadays (Bambach 1993; Vermeij 1995), conditions possibly being comparable to those in the deep seas of today, and this must influence our interpretation of the living conditions of conodonts. The closest Recent equivalents to conodonts equipped solely with coniform elements could be some carnivorous deep-sea fish (see, e.g., Silcock 1993: 125). These bathypelagic fish are non-specialized in the choice of prey (Bruun 1957), and since they seldom encounter anything edible, every feeding attempt must be successful (Silcock 1993: 108). Their teeth have one purpose: to catch and hold prey with the utmost efficiency. Representatives of *Drepanodus* and *Drepanoistodus* may have had feeding strategies comparable to these fish, but Middle Ordovician conodont faunas also included a number of taxa with more complicated dental apparatuses exhibiting a combination of catching/holding, slicing and (?) crushing parts. The functions of conodont elements have been discussed by Dzik (1976, 1991), Jeppsson

(1979), Aldridge et al. (1987), Purnell (1999), Donoghue and Purnell (1999a, 1999b) and others. The taxa with a more diverse set of elements were probably more selective in their choice of food than those bearing only coniform elements.

Conodont palaeoecology and biofacies models have been discussed since at least the 1970s, when Seddon and Sweet (1971) presented a model where conodont biofacies were based on depth-stratification of the planktic forms. In essence, this model was also used by Zhang (1998b) to explain the distribution of some key forms in her Mid-Ordovician sections from south-central China. Other researchers regarded at least some conodont genera as being nektobenthic (Barnes et al. 1973; Barnes and Fåhræus 1975). Some taxa such as *Periodon* and *Protopanderodus* have generally been considered as being planktic/pelagic (Lindström 1984). Lindström (1984) attempted to use these models to explain the distribution of conodont genera in the Swedish Ordovician. He concluded that the “conodont distribution in the Baltoscandian sections is not easily interpreted in constructive, ecologic terms” (Lindström 1984: 40), a statement that is sadly true, to a great extent, even today. In the 1990s the emphasis was instead on biogeography and biofacies (Bergström 1990; Rasmussen and Stouge 1995; Bagnoli and Stouge 1996; Rasmussen 1998). Sea-level curves for the Ordovician of Baltoscandia have been presented and discussed for instance by Nielsen (1992, 1997). Bagnoli and Stouge’s (1991) division into cold-water, warm-water and pandemic taxa has proved useful in many instances.

Conodont occurrence and relative abundance

Although presence/absence data must provide the basis for conodont biostratigraphy, some useful occurrence patterns can also emerge when relative abundance figures are studied, particularly when slightly dissimilar environments are compared. Detailed relative abundance data from the *L. variabilis* and *Y. crassus* zones have previously been published for the Gillberga section on Öland (Löfgren 2000b: 331–333). Öland can in many instances be regarded as belonging at one extremity of variation in abundance patterns in Sweden. Sections generally representing even shallower conditions can be found to the E, for instance in Estonia (cf. Viira et al. 2001).

These data can be compared with the biofacies patterns over a much more extensive area, from the Scandinavian Caledonian front in the east and to the Laurentian margin in the west (see Rasmussen and Stouge 1995). The shallowest of their biofacies, the *Scalpellodus* biofacies, contained numerous specimens of *Scalpellodus* and *Baltoniodus* (together 30–75%) and 5–10% of *Semiacontiodus cornuiformis*. This combination of frequencies could generally be matched by single samples from almost any of the investigated areas and is not particularly common on Öland (cf. Fig. 6), since

samples \ % taxa	<i>Scalpellodus</i> spp.	<i>Lenodus variabilis</i>	<i>Yangtzeplac. crassus</i>	<i>Baltoniodus</i> spp.	<i>Microzarkodina</i> spp.	<i>Semiacont. cornuformis</i>	<i>Semiacontiodus davidi</i>	<i>Drepanodus arcuatus</i>	<i>Cornuodus longibasis</i>	<i>Drepanoist. basiovalis</i>	<i>Drepanoist. stougei</i>	<i>Drepanoist? aff. venustus</i>	<i>Parapaitod. simpliciss.</i>	<i>Protopanderodus rectus</i>	<i>Protopand. calceatus</i>	<i>Dzikodus hunanensis</i>	<i>Decoric. pesequus</i>	<i>Parapander. quietus</i>	<i>Periodon flabellum</i>	<i>Costiconus mysticus</i>
Skåne: L. var. Z	0-4	3-14	0	4-34	0-9	0	0-28	1-24	0-9	0	4-31	0	0	8-59	0	0-1	0-19	0	0	0-1
Gillberga: u. Y. crass. Z	0.7-7	0.3-8	2-7	46-73	0.2-7	7-32	0	0-0.5	0.2-1	3-8	0	1-3	0-0.5	0-1	0-2	0-0.3	0-1	0	0-1	0-0.3
l. Y. crass. Z	2-4	8-11	0.4-4	30-64	0.5-7	13-31	0-6	0-0.3	0-1	4-18	0	1-2	0-0.3	0-1	0-1	0-0.5	0-0.4	0-0.1	0	0-0.2
u. L. var. Z	1-7	2-7	0	25-62	1-16	12-32	0-12	0.2-1	0.2-2	5-28	0	0-2	0-2	0-1	0	0-0.3	0.1-5	0-4	0	0
l. L. var. Z	1-10	1-9	0	13-51	0.7-27	5-22	0.3-6	1-3	0-0.4	9-28	0.3-7	0-3	0-0.2	0-2	0-2	0	0.2-2	0.2-17	0	0
Gullhögen: Y. crass. Z	2	0.3	12	13	0.5	1	0	0.4	1	5	0	0-3	0	6	6	0	0	0	47	5
L. var. Z	9-21	4-10	0	8-11	0.2-0.7	0.2-1.2	4	9-11	3-4	7-55	0-20	0	0	2-3	0	0-0.5	0	0	0	0.2-1
Sylten: Y. crass. Z	0-11	0-0.4	1-21	19-29	0-5	1-13	0	3-13	0-3	4-15	0	0-1	0	2-32	0.3-38	0-4	0-2	0	0-11	0-5
u. L. var. Z	0-16	5-34	0	3-58	0-1	1-4	0-10	1-15	0-2	3-22	0-25	0	0	9-22	0	0-2	0-1	0	0	0-1
Österplana: l. L. var. Z	27-37	2-5	0	5-12	3-12	1-4	4-9	4-6	4-10	1-3	15-20	0	0	3-10	0	0-0.1	0.3-2	0	0-2	0-1
Hällekis: u. Y. crass. Z	7	1	7	24	8	4	0	5	1	9	0	2	0	10	17	1	1	0	0.3	0
l. Y. crass. Z	3	7	3	11	3	5	22	4	11	2	17	0	0	8	0.2	0.3	1	0	0	0
u. L. var. Z	13-22	1-5	0	10-17	15	1-2	8	7-9	5-9	3-13	14-16	3-5	0	1-5	0	0	0-7	0	0-0.2	0-0.1
Närke: u-m L. var. Z	11-19	1-3	0	11-31	6-14	0.3-15	0-3	3-5	1-13	25-35	0	0	0	1-6	0	0	2-15	0-0.9	0	0-1
l. L. var. Z	11-18	1-2	0	30-50	2-13	0.1-1	0-0.1	3-4	1-2	8-15	0-1	0	0	4-18	0-0.1	0	4-12	0-0.8	0	0
Finngrundet: u. Y. crass. Z	2-11	0	5-13	26-48	6-52	6-19	0	0-4	0-2	1-11	0	1-8	0-2	0-3	0-3	0-2	0	0	0	0
l. Y. crass. Z	3-8	1-4	1	43-57	4-18	3-18	0-0.3	0-4	0-3	3-20	0-0.2	0-4	0-4	0-0.3	0	0-4	0-3	0	0	0
u. L. var. Z	5-16	2-6	0	8-44	0-26	3-22	1-12	0-5	0-6	10-33	0-2	2-11	0-2	0-2	0	0-2	0	0-13	0-6	0-0.3
l. L. var. Z	9-20	0-2	0	14-44	4-23	0-20	0	1-4	0-20	18-33	0-2	0	0	0-7	0-0.2	0	0-3	0-4	0-0.2	0
Dalarna: Y. crass. Z	0	0	20	42	0	12	0	0	1	2	0	1	0	1	19	0.4	0.4	0	1	0
L. var. Z	2-3	0-10	0	7-53	0.3-9	9-24	0-1	4-9	0-1	15-57	0	0-2	0	0-2	0-0.5	0	0	0-1	0-0.1	0
Jämtland: L. var. Z	0-7	0-6	0	20-66	0-17	0-7	0	0-7	0-1	0-13	0-18	0-5	0-7	0-28	0-40	0	0	0	0-5	0

Fig. 6. Relative abundance of major taxa in the samples for different areas and stratigraphic intervals. "Skåne" comprises samples from Killeröd and Tommarp, "Närke" samples from Lanna and Yxhult and "Dalarna" samples from Leskusånget and Kårgårde.

Scalpellodus never quite attains 10% in abundance in the interval there, *Baltoniodus* generally varies from ca. 30 to ca. 60% and *Semiacontiodus cornuformis* usually exceeds 10% in the interval. Most of the shifts in abundance between various taxa in Öland would consequently have to be accommodated at or slightly outside the shallow end of the *Scalpellodus* Biofacies of Rasmussen and Stouge (1995). This biofacies model thus does not seem to provide sufficient resolution in the shallowest environments met with here.

At the deeper end of the inferred oceanic depth-scale we have the Yangtze Platform in south-central China, where faunas of the same age as those discussed here closely resemble those in Baltoscandia. Zhang (1998b) calculated that ca. 80% of the conodont species recorded from Baltoscandia

were also met with in S China. Among those lacking on the Yangtze Platform are *Scalpellodus latus*, *S. gracilis*, and *Semiacontiodus cornuformis*. While *S. cornuformis* generally becomes more common in increasingly shallow environments (cf. Löfgren 1999: 77), species of *Scalpellodus* appear to have reached their peak of abundance in a slightly deeper sea (cf. Löfgren 2000a: 60). The Yangtze Platform, however, probably provided no habitats shallow enough for either *Scalpellodus* or *Semiacontiodus*.

In the comparisons below, Öland constitutes the shallowest and Skåne, Jämtland and at some levels Kinnekulle in Västergötland the deepest parts of the epicontinental sea.

Scalpellodus.—Löfgren (2000a: 60) suggested that the discrepancy in stratigraphic occurrence between *Scalpellodus*

latus and *S. gracilis* (Fig. 7V–X) in different areas (discussed under “Remarks” section c, above) was mainly due to differences in preferred water depth. Finngrundet, representing a slightly deeper part of the basin, would provide a more favourable environment for the older species, *S. latus*, which preferred somewhat deeper waters than its descendant, *S. gracilis*. At Gillberga, with shallower habitats, *S. gracilis* could establish itself earlier than at Finngrundet. The preferred depth interval seems to have been rather narrow. Suitable environments for *Scalpellodus* appear to have been virtually lacking in Skåne, and it is clear that maximum abundance generally occurs at medium depths, that is in areas such as Finngrundet, Närke and parts of Västergötland (Fig. 6). In the *L. variabilis* Zone, *S. gracilis* is most abundant in samples from the sections at Kinnekulle (27–37% at Österplana, 13–22% at Hällekis). In the *Y. crassus* Zone, *Scalpellodus* abundance values lie almost consistently below 10%. In areas where *Scalpellodus* is lacking it may to a certain extent have been replaced ecologically by *Semiacontiodus davidi*, a species of *Semiacontiodus* whose morphology converges with that of *Scalpellodus* (cf. Fig. 7Q, R and V, W).

Lenodus and Yangtzeplacognathus.—*Lenodus variabilis* (Fig. 7A–H) is uncommon (usually from 1 to 10% in abundance) throughout the *L. variabilis* and *Y. crassus* zones at Gillberga with the highest values in the lower half of the *Y. crassus* Zone (cf. Fig. 6). Abundance values for *Y. crassus* (Fig. 8A–E) are even lower at Gillberga, 0.4–7%. In only 2 out of 11 samples from the *Y. crassus* Zone is *Y. crassus* more common than *L. variabilis*. At Finngrundet *L. variabilis* is more numerous than *Y. crassus*, and together they only contribute ca. 1–6% up to the upper *Y. crassus* Zone. In the upper ca. 2 m of that zone, *L. variabilis* is lacking and *Y. crassus* amounts to 5–13% of the fauna.

Samples from Lanna, Yxhult and Kårgårde mainly represent the lower *L. variabilis* Zone and the abundance values of the zonal fossil only amount to 1–3%. Slightly higher values are met with at Gullhögen, Hällekis and Österplana (all in Västergötland) and Finngrundet, where abundances equal those at Gillberga or are slightly higher (up to ca. 10%). At Sylten, in samples representing higher parts of the *L. variabilis* Zone at Kinnekulle, an abundance of up to 34% has been met with. Frequencies of *Y. crassus* are also quite high in the Sylten samples, up to 21%. The samples from Jämtland yielded few specimens of *L. variabilis*, and the *Y. crassus* Zone has not been recorded in the Flåsjö area at all. Elements of *Lenodus* are actually not particularly common in any of the sections in Sweden. Possibly, the ideal habitats for *Lenodus* lay in the deeper part of the basin, but not even at the platform margin of Baltica (Rasmussen 2001) or in south-central China (Zhang 1998b) where environments were generally deeper than in Sweden does *Lenodus* attain to more than 10% in most samples and often considerably less.

In Sweden *Yangtzeplacognathus crassus* appears to have thrived in slightly shallower waters than *Lenodus* (cf. Fig. 6), but at some levels in south-central China it is much more com-

mon than in Sweden (almost 50% abundance; see Zhang 1998b: fig. 17). Probably both these platform-bearing species were higher up in the food pyramid than most of the other conodont taxa and so rarely became very abundant, and may also have been only indirectly dependant on water depth.

Baltoniodus.—*Baltoniodus norrlandicus* (Fig. 9A–H) and its descendant, *B. medius* (Fig. 9I–R), are generally the most abundant taxa in the *L. variabilis* and *Y. crassus* zones. In Jämtland abundance values attain to more than 60% in a few samples, and frequencies around 40% are common. The abundance values for the Gillberga section generally increase upwards, maximum values increasing from 50% in the lowermost *L. variabilis* Zone to about 70% in the upper *Y. crassus* Zone, but values change rather abruptly from sample to sample. The samples from Dalarna include up to 53% of *Baltoniodus*.

At Finngrundet relative abundance values of *Baltoniodus* are slightly lower than at Gillberga (Fig. 6), the highest relative abundance being 57% just above the lower boundary of the *Y. crassus* Zone. At Hällabrottet and Lanna, representing only the *L. variabilis* Zone, *Baltoniodus* yields appear to decrease upwards. The values generally match those at Finngrundet in the same interval.

Considerably lower values were calculated for the sections in Västergötland: Österplana, representing the lower *L. variabilis* Zone, contains between 5 and 12% of *Baltoniodus*, Hällekis and Gullhögen generally 10–17% with a maximum of 24% at Hällekis in the upper *Y. crassus* Zone. Values for Skåne vary, but the maximum abundance of *Baltoniodus* measured is 34%.

If only water depth is considered as a limiting factor for the occurrence of *Baltoniodus*, these abundance figures are confusing. Lindström (1984) explained the comparable abundances of *Baltoniodus* on Öland and in Jämtland by suggesting that in Jämtland *Baltoniodus* elements had been transported from shallow shoals into deeper environments. Another explanation could be that whereas *Baltoniodus* for some reason preferred the shallower parts of the basin it could at times also invade deeper waters opportunistically. Thus the distribution of *Baltoniodus* would not primarily depend on water depth but on some other factor which usually co-varies with depth.

Microzarkodina.—At Gillberga relative abundance values of *Microzarkodina* vary rather abruptly from sample to sample and from 0.7 to 16% (median value 6%), except in Ö183-102, with *M. parva* (Fig. 9S–X), 27%. The relative abundance of *Microzarkodina* elements is higher, often considerably so, in the samples from Finngrundet than in those from Gillberga (Fig. 6). In the Finngrundet drill-core *Microzarkodina* specimens are present in all samples but one in the interval, varying from 4 to 57% with a median of 15%. Elements of *Microzarkodina* vary in abundance in the interval from 3 to 12% at Österplana, 2–15% at Hällekis, Lanna and Yxhult and 0–9% in the other sections. The Öland sections are thus not at all exceptional in their abundance values;

rather it is Finngrundet that has the highest values for *Microzarkodina*.

Microzarkodina is related to *Periodon* and is also fairly close to it morphologically; it could have inhabited a niche comparable to that occupied by *Periodon*, though in waters that were less oceanically influenced. At least by the time *M. hagetiana* and *M. bella* appeared there was a separation into different habitats, *M. bella* (Fig. 9Y–AC) being adapted to shallower parts of the sea than *M. hagetiana* (Fig. 9AD–AI).

Semiacontiodus.—This genus, represented by *S. cornuformis*, *S. davidi* and *S. sp. A*, is probably the one adapted to the shallowest waters represented in Swedish sections in the interval. Rasmussen and Stouge (1995) made the same observation for localities further to the west near the platform margin, where only the shallowest biofacies had more than 5% of *S. cornuformis*. In sections from the Yangtze Platform in S China representing deeper habitats, *Semiacontiodus* is lacking and is apparently replaced by a close relative of the Lower Ordovician species “*Scolopodus*” *rex* Lindström (Zhang 1998b; Tolmacheva 2001b).

The most common of the *Semiacontiodus* species, *S. cornuformis* (Fig. 7J–O), has its lowest abundance in the *L. variabilis*–*Y. crassus* interval at Hällekis, Österplana, Gullhögen, Yxhult and Lanna, where only two of the samples yield more than 5%. The species attains to less than 10% in abundance in the basal *L. variabilis* Zone at Gillberga, in most samples from that zone at Finngrundet, and in all the samples available from Jämtland in the *L. variabilis*–*Y. crassus* interval. Throughout most of the upper *L. variabilis* Zone at Gillberga and in all samples from Dalarna frequencies vary from ca. 12 to ca. 24%. At Finngrundet abundance in the *Y. crassus* Zone increased to around 15% in many samples. At Gillberga the highest values are 25–30% from near the *L. variabilis*–*Y. crassus* zonal boundary and through the lower and middle *Y. crassus* Zone.

Semiacontiodus davidi (Fig. 7P–R) is the dominating *Semiacontiodus* species in only a few samples from Skåne

and Kinnekulle (see below), probably representing the deepest habitats available in the region investigated. In the *L. variabilis* Zone at Finngrundet it can be as abundant as *S. cornuformis* at some levels, up to 12%. In the other areas (including Öland) *S. cornuformis* is the more abundant of the two species, *S. davidi* usually attaining to only 5% or less.

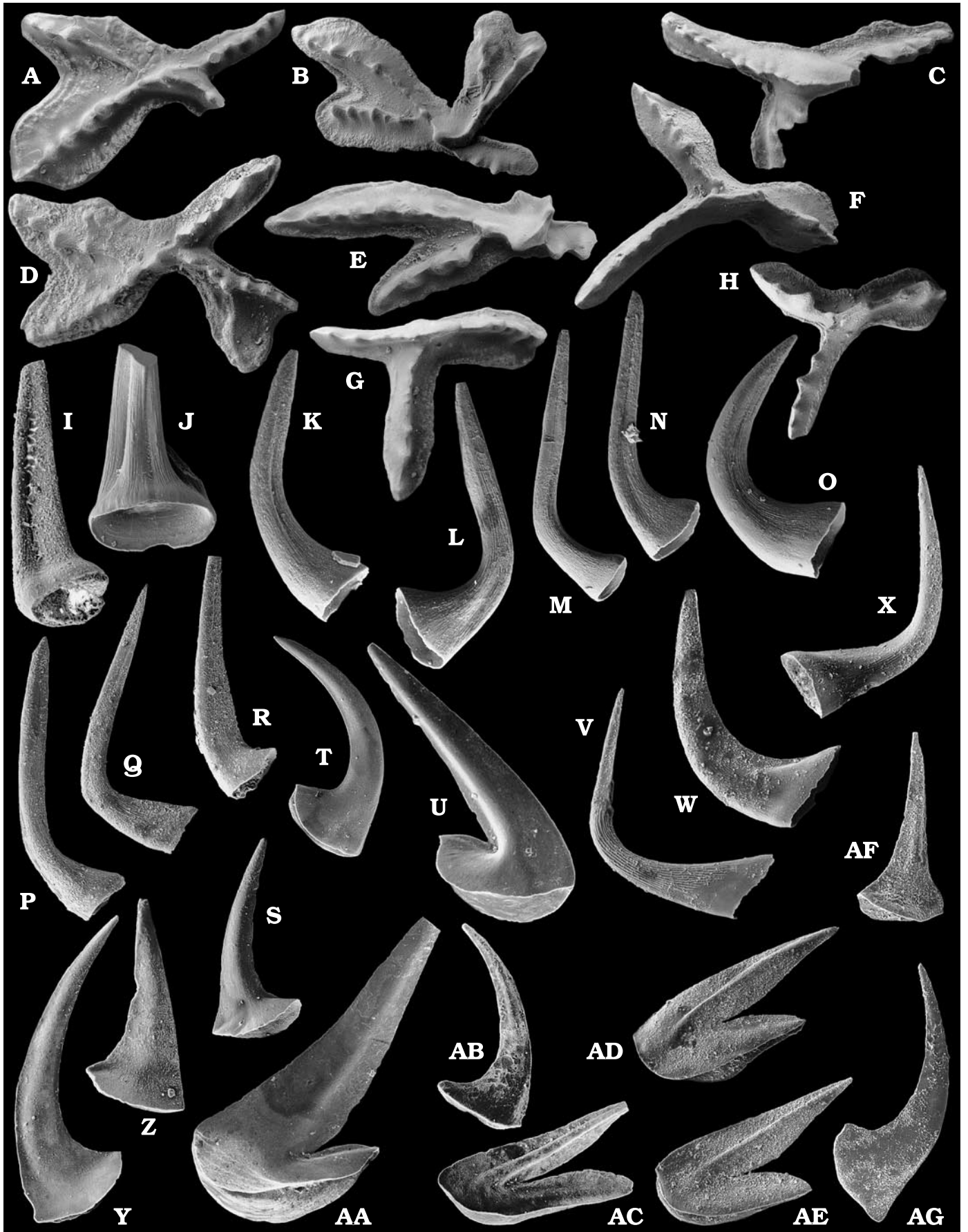
In the Hällekis quarry, Kinnekulle, a level particularly rich in *S. davidi* was encountered in the middle part of the grey “Täljsten” interval that has traditionally been taken as marking the base of the Kundan in lithostratigraphic terms (cf. discussion by Tinn and Meidla 2001). Sample HK88-2, taken from this level, yielded 21.5% of *S. davidi* elements and was chosen as the type stratum of the species (Löfgren 1999: 82). Since this sample clearly derives from the *Y. crassus* Zone, the “Täljsten” interval belongs to the middle rather than to the lower Kundan, as was also indicated by Tinn and Meidla (2001). The great numbers of *S. davidi* in the “Täljsten” interval is an indication of the special facies development there, since in the other sections *S. davidi* is uncommon in the *Y. crassus* Zone (cf. Fig. 6).

The third species of *Semiacontiodus* (Fig. 7I), *S. sp. A* (= *Semiacontiodus?* sp. A in Löfgren 1999: 83) is mainly found in my sections in the (lower) *L. variabilis* Zone; only 14 specimens were found in all (see Figs. 3, 4).

Drepanodus and Cornuodus.—The relative abundance of *Drepanodus arcuatus* at Gillberga lies between 0.2 and 3% (median value 1%) and *Cornuodus longibasis* varies from 0 to 2% with a median of 0.3% in the *L. variabilis* Zone. In the *Y. crassus* Zone *D. arcuatus* is less abundant (not reaching 1%), while values for *C. longibasis* remain virtually unchanged.

The abundance values for *D. arcuatus* from Finngrundet are only slightly higher than at Gillberga; 0–5% (median 2.5%) for the *L. variabilis* Zone and 0–4% (median 1%) in the *Y. crassus* Zone. One specimen of *Drepanodus parformis* Löfgren and Tolmacheva (2003) was found in the lower *L. variabilis* Zone. Abundance values for *C. longibasis* in the

Fig. 7. Conodont elements from the *L. variabilis* and *Y. crassus* zones. **A–H.** *Lenodus variabilis* (Sergeeva, 1963) from sample HK88-2, *Y. crassus* Zone, Hällekis quarry (**A, E, G, H**), sample –15D, *L. variabilis* Zone, Hälludden section (**B**), sample Ö192-6, *L. variabilis* Zone, Gillberga quarry (**C, F**) and sample from Tommarp, *L. variabilis* Zone (**D**). **A.** Dextral Pa element, later form with posterior process longer than postero-lateral process, LO 8694t, × 80. **B.** Sinistral Pa element, early complete specimen with posterior lobes almost united, LO 8691t, × 55. **C.** Dextral Pb element, antero-lateral lobe fragmented, LO 8695t, × 75. **D.** Dextral Pa element, early form with posterior and postero-lateral processes subequally long, LO 8692t, × 70. **E.** Sinistral Pa element, later form with posterior process longer than postero-lateral process, LO 8693t, × 75. **F.** Sinistral Pb element, subadult, LO 8698t, × 75. **G.** Dextral Pb element, LO 8697t, × 60. **H.** Sinistral Pb element, juvenile, LO 8780t, × 70. **I.** *Semiacontiodus* sp. A, Sa element from sample Vg98-2, *L. variabilis* Zone, Österplana quarry, LO 8793t, × 90. **J–O.** *Semiacontiodus cornuformis* (Sergeeva, 1963) from samples Ö183-105 (**J**) and Ö193-9 (**K–O**), *Y. crassus* Zone, Gillberga quarry. **J.** Sa element with divided posterior carina, LO 8781t, × 70. **K.** Sa element with straight profile, LO 8782t, × 100. **L.** Pa element, inner side, LO 8783t, × 95. **M.** Sd element, LO 8784t, × 60. **N.** Pb element, outer side, LO 8785t, × 80. **O.** Sa element with curved profile, LO 8786t, × 95. **P–R.** *Semiacontiodus davidi* Löfgren, 1999 from sample Vg98-4B, *L. variabilis* Zone, Österplana quarry. **P.** Sa element, LO 8794t, × 70. **Q.** Sc element, LO 8795t, × 65. **R.** Pb element, LO 8796t, × 65. **S–U.** *Drepanoistodus* cf. *suberectus* (Branson and Mehl, 1933) from sample HK88-2, *Y. crassus* Zone, Hällekis quarry. **S.** Sa element, LO 8797t, × 60. **T.** Sc? element, LO 8798t, × 50. **U.** M element, LO 8863t, × 108. **V–X.** *Scalpellodus gracilis* (Sergeeva, 1974) from sample Vg98-4B, *L. variabilis* Zone, Österplana quarry. **V.** Sb? Element, LO 8799t, × 85. **W.** P? element, LO 8800t, × 75. **X.** Sd? element, LO 8801t, × 85. **Y–AA.** *Drepanoistodus basiovalis* (Sergeeva, 1963) from sample Ö183-104, basal *Y. crassus* Zone, Gillberga quarry. **Y.** Sc? element, LO 8802t, × 70. **Z.** Sa element, LO 8803t, × 90. **AA.** M element, LO 8864t, × 65. **AB–AC.** *Drepanoistodus?* aff. *venustus* (Stauffer, 1935) from sample Ö187-3, *Y. crassus* Zone, Gillberga quarry. **AB.** Sd? element, LO 8823t, × 85. **AC.** M element, LO 8824t, × 80. **AD–AG.** *Drepanoistodus stougei* Rasmussen, 1991 from sample Vg98-4B, *L. variabilis* Zone, Österplana quarry. **AD.** M element, outer side, LO 8825t, × 70. **AE.** M element, inner side, LO 8826t, × 70. **AF.** Sa element, LO 8827t, × 75. **AG.** Sb? element, LO 8828t, × 60. →



Finngrundet drill-core are also comparable to those from Öland in this interval (Fig. 6). Values from Jämtland are doubtful, since so few specimens were found there.

In all the other sections abundance values for both *D. arcuatus* and *C. longibasis* are higher, and as at Gillberga values are lower in the *Y. crassus* Zone than in the *L. variabilis* Zone. In most sections *D. parformis* occurs together with *D. arcuatus* at some level in the interval, though sparsely. At Kinnekulle (Hällekis, Sylten) and Kårgärde, a small number of specimens of *Drepanodus reclinatus* Lindström were also retrieved at a few levels.

Cornuodus longibasis has noticeably high maximum values in the *L. variabilis* Zone at Finngrundet (20% at 36.5 m) and Lanna (13% in the top sample). It is not impossible that these maxima represent one and the same event that was favourable for *C. longibasis*, and that is possibly much less clearly discernible in the lower part of the *L. variabilis* Zone at Gillberga.

To conclude, *D. arcuatus* is much more common in the sections in south-central Sweden, particularly in Dalarna, than at Gillberga and Finngrundet. Abundance values generally drop from the *L. variabilis* Zone to the *Y. crassus* Zone (cf. Fig. 6). To a lesser degree this also applies to *C. longibasis*.

***Drepanoistodus*.**—In most of the sections *Drepanoistodus basiovalis* (Fig. 7Y–AA) is by far the most common species of the genus in this interval, and one of the most common taxa of all. It varies from ca. 5% to 35% at Gillberga, Lanna, Yxhult and Finngrundet and from 15–57% in Dalarna in the *L. variabilis* Zone; in the *Y. crassus* Zone values are generally lower, below 20% (Fig. 6). *Drepanoistodus stougei* (Fig. 7AD–AG) makes up only 0.3–7% in the four lower samples of the *L. variabilis* Zone at Gillberga, and less than 1% at Lanna and Finngrundet. In samples from Skåne and Österplana as well as most samples from Sylten *D. stougei* is the most common species of *Drepanoistodus* in the *L. variabilis* Zone, with between 15 and 31% in relative abundance, while *D. basiovalis* at most amounts to 3% there. Rasmussen (2001) reported that in his sections *D. stougei* did not extend very far into the lower range of *B. medius*. In Sweden, specimens have been found up to the lower *Y. crassus* Zone. It is uncertain whether this is because it became extinct or whether there are ecological causes. On the basis of the lateral distribution of *D. stougei* it can be inferred that this species preferred a slightly deeper habitat than *D. basiovalis*. However, Rasmussen and Stouge (1995) made the opposite conclusion based on sections representing deeper environments. *Drepanoistodus* cf. *suberectus* is probably a Laurentian immigrant, appearing at a few levels at Gillberga, and notably in the “Täljsten” interval at Hällekis.

***Parapaltodus* and *Drepanoistodus?* aff. *venustus*.**—*Parapaltodus simplicissimus* (Fig. 8V, W) and *Drepanoistodus?* aff. *venustus* (Fig. 7AB–AC) occur in many samples from the base of the *L. variabilis* Zone and throughout the *Y. crassus* Zone. As regards *P. simplicissimus* the first appearance is probably the result of migration since there is no obvi-

ous ancestral species in older rocks in Baltoscandia. Stouge (1984) interpreted it as an open shelf species. *Drepanoistodus?* *venustus* is a controversial taxon name that has been used in Baltoscandia for conodonts that have geniculate elements similar to those of *Drepanoistodus forceps*, but the rest of the apparatus has not been widely recognized. Leslie (2000) described *D. venustus*-like elements from the Laurentian Upper Ordovician as “*Oistodus*” sp. A and referred some Baltoscandian elements to this taxon as well, but it is far from clear whether these are conspecific. I have chosen to call the Baltoscandian taxon *D.?* aff. *venustus*. There is probably an ecological reason for the occurrence of more numerous *D.?* aff. *venustus* elements precisely at the base of the *L. variabilis* Zone, since a few similar geniculate elements occur much lower down in the succession.

Drepanoistodus? aff. *venustus* varies from less than 1% to ca. 3% in the interval at Gillberga. It is lacking in the *L. variabilis* Zone in several of the sections (Fig. 6), and is most abundant at Finngrundet and Hällekis. *Parapaltodus simplicissimus* occurs sparsely throughout the interval, e.g. at Gillberga (Figs. 3, 6).

***Parapanderodus*.**—*Parapanderodus quietus* (Fig. 8J–N) attains its highest abundance in Swedish sections in the *L. variabilis* Zone and only rarely occurs above this zone. Although this may appear to be a stratigraphically restricted taxon that could serve as a biostratigraphic indicator, it should be used with caution (see also Löfgren 2000a). *P. quietus* is probably a Laurentian immigrant, and Smith (1991: 48) discussed its relations with Early Ordovician (Canadian) *Parapanderodus* taxa. It is thus not surprising to find it slightly lower in the Gillberga section than was reported by Bagnoli and Stouge (1999: 34). Löfgren (2000a: fig. 3) noted its occurrence in the middle *L. antivariabilis* Subzone, ca. 0.5 m below the shaly boundary that Bagnoli and Stouge (1999) regarded as lying below its first appearance. Since this lowermost reported occurrence of *P. quietus* at Gillberga consists of 74 elements, the species seems to be well established at this level and could actually have appeared even earlier. Two specimens from the lower *B. norrlandicus* Zone at Kloksåsen, Jämtland (Löfgren 1978) could belong to *P. quietus* or an older species. Stouge and Bagnoli (1988) found species of *Parapanderodus* as low down as in the lower Arenigian of Newfoundland.

From the base of the *L. variabilis* Zone and upwards *P. quietus* is present at every sampled level in the Gillberga section up to the upper 0.5 m of the zone. Relative abundance values vary from 0.2 to 17%, the maximum occurring in the lower part of the zone in the interval 0.4–0.9 m above the distinct boundary between divisions K and L (Löfgren 2000b: fig. 8). A single specimen of *P. quietus* was recovered from the lowermost 0.2 m of the *Y. crassus* Zone at Gillberga, and the species reappears again sparsely towards the top of the section.

Parapanderodus quietus also occurs in the lower *L. variabilis* Zone at Lanna, Yxhult, Leskusänget and Kår-



Fig. 8. Additional conodont elements from the upper *L. variabilis* and *Y. crassus* zones. **A–D.** *Yangtzeplacognathus crassus* Chen and Zhang, 1993 (in Ding et al. 1993) from samples Ö192-9 (**A**) and Ö187-3 (**B–D**), *Y. crassus* Zone, Gillberga quarry. **A.** Dextral Pa element, LO 8708t, $\times 50$. **B.** Sinistral Pa element, LO 8707t, $\times 55$. **C.** Dextral Pb element, LO 8710t, $\times 60$. **D.** Sinistral Pb element, LO 8709t, $\times 40$. **E–I.** *Dzikodus humanensis* Zhang, 1998b from samples HK88-3 (**E, F, H**) and HK88-2 (**I**), Hällekis quarry, and Ö193-8 (**G**), Gillberga quarry, all from the *Y. crassus* Zone. **E.** Sinistral juvenile Pa element, LO 8849t, $\times 90$. **F.** Sinistral subadult Pa element, LO 8850t, $\times 50$. **G.** Dextral? Pb element, LO 8851t, $\times 55$. **H.** Sb element, LO 8852t, $\times 100$. **I.** M element, LO 8853t, $\times 80$. **J–N.** *Parapanderodus quietus* Bagnoli and Stouge, 1997 from sample Ö187-1, *L. variabilis* Zone, Gillberga quarry. **J.** Slender element (?Sb), lateral view, LO 8854t, $\times 75$. **K.** Slender element (?Sb), posterior-lateral view, LO 8855t, $\times 70$. **L.** Small, laterally compressed element (?Sc), LO 8856t, $\times 100$. **M.** Small, asymmetrical element (?Sd), LO 8857t, $\times 105$. **N.** Bicostate element (?Sa), posterior view, LO 8858t, $\times 75$. **O–Q.** *Protopanderodus calceatus* Bagnoli and Stouge, 1997 from sample HK88-3, Hällekis quarry, *Y. crassus* Zone. **O.** Square-based asymmetrical element, LO 8804t, $\times 45$. **P.** Short-based asymmetrical element, LO 8805t, $\times 60$. **Q.** Scandodontiform element, LO 8806t, $\times 45$. **R–U.** *Protopanderodus rectus* (Lindström, 1955) from sample Vg98-4B, *L. variabilis* Zone, Österplana quarry. **R.** Scandodontiform element, LO 8807t, $\times 50$. **S.** Short-based asymmetrical element, LO 8808t, $\times 55$. **T.** Square-based acontiodontiform element, LO 8809t, $\times 50$. **U.** High-based acontiodontiform element, LO 8810t, $\times 60$. **V–W.** *Parapaltodus simplicissimus* Stouge, 1984 from sample Ö187-3, *Y. crassus* Zone, Gillberga quarry. **V.** Scandodontiform element, LO 8829t, $\times 80$. **W.** Drepanodontiform element, LO 8830t, $\times 45$. **X.** *Ansella jemtlandica* (Löfgren, 1978) from sample Ö187-3, *Y. crassus* Zone, Gillberga quarry, LO 8859t, $\times 110$. **Y, Z.** *Periodon flabellum* (Lindström, 1955), late form from sample Ö187-3, *Y. crassus* Zone, Gillberga quarry. **Y.** Sb element, LO 8860t, $\times 80$. **Z.** M element, LO 8861t, $\times 80$. **AA.** *Strachanognathus parvus* Rhodes, 1955 from sample Ö187-2, *Y. crassus* Zone, Gillberga quarry, LO 8862t, $\times 120$. **AB–AD.** *Costiconus mysticus* (Barnes and Poplawski, 1973) from sample GB81-900, *E. crassus* Zone, Gullhögen quarry. **AB.** Multicostate element, LO 8831t, $\times 100$. **AC.** Geniculate element, LO 8832t, $\times 110$. **AD.** Scandodontiform element, LO 8833t, $\times 80$.

gårde, but makes up less than 1% of the conodont fauna there. At Finngrundet, too, the taxon occurs from the lower *L. variabilis* Zone and was retrieved from all sampled levels between 36.5 and 33.0 m, the relative abundance generally being one to two percent, but with a maximum of 13% at 33.5 m. It is tempting to correlate this maximum with that of about the same magnitude at Gillberga which, however, is probably slightly older. *Parapanderodus quietus* is lacking from the top metre of the *L. variabilis* Zone and in most younger beds at Finngrundet, but reappears briefly in the upper *E. pseudoplanus* Zone.

Protopanderodus.—The relative abundance of *Protopanderodus rectus* (Fig. 8R–U) is generally highest in the samples from Skåne and Jämtland, although the species is entirely lacking in some of the smaller samples there. Values of 10–20% appear to be normal. Samples from Lanna and Sylten have comparable values (Fig. 6), while samples from Dalarna and Gillberga only yielded up to 2%. Since most workers consider that the distribution of *P. rectus* is distinctly depth-related, its abundance figures can probably be interpreted as an almost direct reflection of relative depth. The change at Finngrundet from values comparable to those in Skåne and Jämtland in the lower part of the *L. variabilis* Zone to values similar to those in the shallowest parts of the basin in younger beds is noteworthy.

A second species of *Protopanderodus* (Fig. 8O–Q), *P. calceatus* (= *P. cf. varicostatus* of Löfgren, 1978) accompanies or replaces *P. rectus* at some levels which probably represent intervals of slight shallowing. In general, more costate forms of *Protopanderodus* seem to prevail in shallower seas than those where simpler types of *Protopanderodus* species abound. Maximum frequencies of *P. calceatus* were encountered in the *Y. crassus* Zone of Sylten, Hällekis and in Dalarna (Fig. 6).

Dzikodus and Pygodus.—*Dzikodus hunanensis* (Fig. 8E–I), is the oldest species of this lineage so far identified. It first appears sparsely in the upper *L. variabilis* Zone at Gillberga (Fig. 6). Zhang (1998b) reported it from the upper half of the *L. variabilis* Zone and from the *Y. crassus* Zone in south-central China (Zhang 1998b: figs. 20–22) where it is fairly common, particularly in the *Y. crassus* Zone in the deeper depositional environment represented by the Maocao pu section, where it comprises up to 22% of the elements (Zhang

1998b: table 8). Two elements recovered from Österplana (Fig. 4) and 3 from Finngrundet indicate that in Sweden as well the first *D. hunanensis* populations are not uncommon in the upper *L. variabilis* Zone. Abundance values of up to 4% are met with in the *Y. crassus* Zone in Sweden (Fig. 6).

What is probably a new species of *Pygodus*, *P. sp. A*, has been encountered in samples from the *L. variabilis* Zone at Österplana and Gullhögen (Fig. 4). It could well be an ancestor of *Pygodus lunnensis* Zhang, 1998, which is the oldest species of that genus yet identified (Zhang 1998c). The platform element consists of equivalents of the antero-lateral and anterior processes in *P. lunnensis*, but only one entire element of that kind has so far been found. It is accompanied by a set of ramiform elements and, notably, a very characteristic geniculate element type with numerous denticles on the anterior margin. Like *D. hunanensis* this new *Pygodus* species is of potential value for correlation, but additional material is needed for a full description before it can be used.

Costiconus and Ansellia.—*Costiconus* is Rasmussen's (2001) new generic name for "*Walliserodus*" *ethingtoni* (Fähræus) and related species. In the interval investigated an older species, *Costiconus mysticus* (Barnes and Poplawski, 1973) was found from the upper *L. variabilis* Zone upwards, as well as a few doubtful occurrences from the lower part of the zone. Zhang (1998b) reported similar elements from just below the *L. variabilis* Zone in south-central China. *Costiconus mysticus* (Fig. 8AB–AD) occurs somewhat erratically with up to 5% in relative abundance at Gullhögen in the *Y. crassus* Zone (Fig. 6). Rasmussen (2001) referred such elements to *Costiconus costatus* (Dzik), but since there is no evidence that Dzik's (1976) type specimen was associated with M elements like those typical of *C. mysticus* I prefer to use the latter designation, pending further information. Rasmussen and Stouge (1995) found *Costiconus* (then called "*Walliserodus*") typical of outer shelf settings which could explain why it is so rare in my sections.

The first specimens of *Ansellia jemtlandica* (Fig. 8X) were met with in the *Y. crassus* Zone at Gillberga, Hällekis and Kårgårde (Fig. 5). This appearance should probably be regarded as an immigration event, and the taxon is fairly widespread in the *E. pseudoplanus* Zone of western Baltoscandia (Löfgren 1978; Zhang 1998a; Rasmussen 2001). In the Finngrundet drill-core two doubtful specimens were en-

Fig. 9. Elements of *Baltoniodus* and *Microzarkodina* from the *L. variabilis* and *Y. crassus* zones. A–H. *Baltoniodus norrlandicus* (Löfgren, 1978) from sample Nä90-1, lower *L. variabilis* Zone, Yxhult quarry. A. Pa element, LO 8865t, × 60. B. Pb element, LO 8811t, × 70. C. Sa element, LO 8812t, × 60. D. Sc1 element, LO 8866t, × 65. E. Sb element, LO 8813t, × 70. F. Sc2 element, LO 8814t, × 70. G. Sb element, LO 8815t, × 75. H. M element, LO 8816t, × 70. I–R. *Baltoniodus medius* Dzik, 1976 from samples Ö193-9 (I, K–P, R), Ö183-105 (J), and Ö187-3 (Q), all from the *Y. crassus* Zone, Gillberga quarry. I, J. Pa elements, LO 8834t, LO 8835t, × 70 and × 50, respectively. K, L. Pb elements, LO 8836t, × 50 and LO 8837t, × 55, respectively. M. Sb element, LO 8838t, × 70. N. Sc2 element, LO 8839t, × 60. O. Sa element, LO 8840t, × 50. P. Sc1 element, note part of basal sheath, LO 8841t, × 50. Q. M element, LO 8842t, × 70. R. M element, LO 8843t, × 65. S–X. *Microzarkodina parva* Lindström, 1971 from samples Nä90-1, Yxhult quarry (S–T, V–X) and Ö183-102, Gillberga quarry (U), all from the lower *L. variabilis* Zone. S. P element, LO 8817t, × 85. T. Sa element, LO 8818t, × 80. U. Sb2 element, LO 8819t, × 110. V. Sc element, LO 8820t, × 80. W. M element, LO 8821t, × 85. X. Sb1 element, LO 8822t, × 130. Y–AC. *Microzarkodina bella* Löfgren, 2000b from sample Ö187-2, *Y. crassus* Zone, Gillberga quarry. Y. P element, LO 8844t, × 80. Z. Sa element, LO 8845t, × 80. AA. Sc element, LO 8846t, × 110. AB. Sb1 element, LO 8847t, × 130. AC. M element, LO 8848t, × 110. AD–AI. *Microzarkodina hagetiana* Stouge and Bagnoli, 1990 from samples Vg98-4B (AD–AH) and Vg98-3 (AI), lower *L. variabilis* Zone, Österplana quarry. AD. P element, LO 8787t, × 130. AE. Sa element, LO 8788t, × 130. AF. M element, outer side, LO 8789t, × 130. AG. Sb2 element, LO 8790t, × 130. AH. Sb1 element, outer side, LO 8791t, × 150. AI. M element, inner side, LO 8792t, × 130. →



countered as far down as in the middle of the *L. variabilis* Zone and Zhang (1998a) found a specimen of the same age in the Grötlingbo-1 drill-core from southern Gotland. These specimens could either represent an earlier incursion of the species or an ancestor. Zhang (1998b) described the ancestral species *Ansella longicuspica* from the *L. variabilis* Zone and slightly older beds in south-central China, but this older species has not yet been reported from other areas.

Decoriconus.—*Decoriconus pesequus* Löfgren, 1998, is the species of *Decoriconus* that occurs in the *L. variabilis* and *Y. crassus* zones. Since different screen sizes were used in the laboratory at different times, these needle-shaped elements were probably washed out of some of the samples processed in the 1970s and early 1980s. Abundance values in Fig. 6 should be treated with caution and taken as minimum values. The species occurs in frequencies up to ca. 20% and seems on the whole to be more abundant in the *L. variabilis* Zone than in the *Y. crassus* Zone.

Periodon, Erraticodon, and Strachanognathus.—*Periodon flabellum* (Fig. 8Y, Z) has been found in abundances of up to 47% at specific levels throughout the sequences (Figs. 3, 4, 6). *Periodon* has been regarded as occurring in the open seas (e. g. Barnes and Fähræus 1975; Lindström 1984; Stouge 1984; Bagnoli and Stouge 1991; Zhang 1998b), and mass occurrences often seem to be associated with either transgression or “oceanic influx” in the type of environments investigated here. It is difficult to correlate specific maxima unless the sequences to be correlated are sampled at very short intervals. The level that yielded the 47% maximum at Gullhögen, for instance, had probably not been sampled in any of the other sections, except possibly at Österplana (Sylten). In more open oceanic environments such as investigated in south-central China by Zhang (1998b), *Periodon* is a dominating taxon and at some levels can make up more than 90% of the conodont elements. Even in these settings, however, percentages of *Periodon* fluctuate widely from level to level.

Elements of *Erraticodon*, probably *E. balticus* Dzik, have occasionally been encountered in my sections, e.g., at Kille-röd. The highest abundance, 2%, was met with in a sample from the lower *L. variabilis* Zone of Finngrundet; these specimens were described and discussed previously by Löfgren (1985). Zhang (1998b) suggested that *Erraticodon* could have belonged to the same biofacies (pelagic, surface-dwelling) as *Periodon*. Although rare in the sections investigated, the occurrence of *Erraticodon* could be explained by the same kind of “oceanic influx” model proposed for *Periodon*.

Occasional specimens of *Strachanognathus parvus* (Fig. 8AA) were found at Gillberga, Österplana and in Jämtland. The species, with its oldest reported occurrence from the middle Arenig in Sweden (Löfgren 1978), has an obscure distribution, which could also be attributed to instances of “oceanic influx”.

Paroistodus originalis.—A few samples yielded up to 2% of *Paroistodus originalis*, a species which typically disappears

from Baltoscandia in the *Baltoniodus norrlandicus* Zone, the zone preceding the *L. variabilis* Zone. Isolated occurrences higher up in the succession have already been reported (e.g., Löfgren 1978; Rasmussen 2001). In other regions *P. originalis* was replaced by *Paroistodus horridus* (Barnes and Poplawski), with denticulated non-geniculate elements and geniculate elements closely resembling those of *P. originalis* (see e.g., Zhang 1998b). Albanesi and Barnes (1996) described the transition from *P. originalis* to *P. horridus* in an early Llanvirnian sequence from Argentina, but a similar, probably unsuccessful, transition took place as early as in the early Arenig *Oepikodus evae* Zone, documented from Sweden (Löfgren 1995b).

Conclusions

The *Baltoniodus norrlandicus*–*B. medius* transition and the first appearance of *Dzikodus hunanensis* Zhang, 1998 as well as a new species of *Pygodus* will probably be of most use in a further biostratigraphic subdivision of the *L. variabilis* and *Y. crassus* zones. The appearance and disappearance of the other species that are present in the interval as well as differences in relative abundance from area to area are interpreted as being the results of ecological changes and differences. *Semiacontiodus cornuformis* is most abundant in areas representing the shallower parts of the basin, and is replaced in areas where the water was deeper by its close relative *S. davidi*. Abundance maxima of *Scalpellodus* are found where the sea was of medium depth, although different species probably preferred slightly different depths. The same kind of pattern appears to apply to different species of *Drepanoistodus*. *Drepanodus*, and to a lesser extent *Cornuodus longibasis*, seem to have preferred the open seas. *Protopanderodus rectus* is most abundant in areas representing the deeper parts of the basin. Stratigraphic levels where *Protopanderodus calceatus* becomes more abundant are interpreted as indicating slight shallowing. *Periodon flabellum* appears at some levels, probably owing to an increase in oceanic influence. *Microzarkodina* probably inhabited a niche in the epicontinental sea comparable to that *Periodon* is thought to have occupied in the open ocean, and different species of *Microzarkodina* seem to have had different depth preferences. Some other taxa, such as *Erraticodon*, *Costiconus*, *Ansella* and *Strachanognathus*, may also have appeared during periods of “oceanic influx”. The distribution of *Baltoniodus*, *Lenodus* and *Yangtzeplacognathus* is considered as being not primarily dependent on water depth, whereas *Dzikodus* obviously preferred deeper waters.

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