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Morphology, evolution and stratigraphic distribution in the Middle Ordovician conodont genus *Microzarkodina*

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ABSTRACT: *Microzarkodina* is a genus of mainly Middle Ordovician conodonts that has its centre of distribution in Baltoscandia, and much less commonly occurs in southern China, Australia, Argentina and Laurentia. In Baltica a series of species, *Microzarkodina russica* n. sp., *M. flabellum*, *M. parva*, *M. bella*, *M. hagetiana* and *M. ozarkodella*, established themselves successfully. The succession of species ranges from just below the base of the Middle Ordovician (*M. russica*) to the upper part of the Middle Ordovician (*M. ozarkodella*). The species are frequently used for biostratigraphical purposes. The largely contemporaneous species *Microzarkodina bella* and *M. hagetiana* probably both evolved from *M. parva* and mostly occurred in separate areas. *Microzarkodina ozarkodella* probably evolved from *M. hagetiana*. This present investigation is based on a total of 94,208 elements, collected from 20 sections and one drill-core site in Sweden, one drill-core site and one outcrop in Estonia and two sections in the St Petersburg area in Russia. The *Microzarkodina* apparatus probably consisted of 15 or 17 elements: four P, two or four M and nine S elements. The S elements include different Sa, Sb_1, Sb_2, and Sc element types.

KEY WORDS: Baltoscandia, biostratigraphy, Conodonta, *Microzarkodina russica* n. sp., taxonomy

Microzarkodina Lindström, 1971, is a chiefly Middle Ordovician conodont genus with its major area of distribution in Baltoscandia. The first appearance of *Microzarkodina* occurs in the late Floian, the Second Stage of the Ordovician, and in the upper range of its distribution rare, stunted specimens of *M. ozarkodella* have even been retrieved from the late Middle Ordovician *Eoplacognathus robustus* Subzone of the *Pygodus serra* Zone in Poland (Dzik 1994). The main stratigraphic distribution of *Microzarkodina* is more restricted, ranging from the uppermost *Oepikodus evae* Zone (or the *Baltoniodus triangularis* Zone at the base of the Middle Ordovician in many areas) and throughout the *M. ozarkodella* Subzone of the *Eoplacognathus pseudoplanus* Zone.

The six species of *Microzarkodina* treated in this study are morphologically very similar, they occur successively in the sections that have been investigated and elsewhere (Fig. 1) and several of them seem to be largely restricted in distribution to Baltica. In the absence of other, closely related taxa the most probable assumption is that these six species form a lineage with *M. russica* n. sp. as the oldest ancestor. *Microzarkodina flabellum* and, later *M. parva*, follow and seem to be more widely distributed geographically than *M. russica* n. sp. *Microzarkodina parva* is probably directly ancestral to both *M. hagetiana* and *M. bella*, which partly overlap stratigraphically. Morphological and distributional similarities makes it most probable that *M. ozarkodella* evolved from *M. hagetiana*.

Microzarkodina migrated into the Baltoscandian basin at approximately the same time as some other conodont taxa, such as *Trapezognathus* and *Baltoniodus*.

1. Localities and material

Material was collected from the following localities (Fig. 2): From Sweden – N Öland: the Gillberga quarry (Löfgren 2000a, b); province of Västergötland: the Orreholmen quarry (Löfgren 1996), the Gullhögen/Skövde quarry (Jaanusson 1982a; Lindström 1984; Löfgren 1995, 2000a, 2003, 2004), the Hällekis quarry (Thorslund & Jaanusson 1960; Zhang 1998a, Löfgren 2000a, 2003, 2004), Brattefors N near the locality Brattefors of Löfgren (1997) and the Österplana quarry (Löfgren 2003); province of Närke: the Gymninge quarry (Löfgren 1993), the Lanna quarry (Löfgren 1995) and the Yxhult quarry (Lindström 1955; Löfgren 2003); province of Dalarna: the Rävanäs section (Sturesson 1988; Löfgren 1995), the Leskusänget section (Löfgren 1995, 2000a), the Sjurberg section (Löfgren 1994) and the Kårgärde section (Karis *in* Jaanusson 1982b; Löfgren 2000a, 2003, 2004); Gulf of Bothnia: the drill-core from Finngrundet (Tjernvik & Johansson 1980; Löfgren 1985); province of Jämtland: the sections at Gammalbodberget, Sommartjärnen, Kloxåsen, Lunne, Gärde, Gusta and Kalkberget (Löfgren 1978, 1993, 2003, 2004). From Estonia – Mäekalda in N Estonia (Viira *et al.* 2001), and the Tamsalu drill-core in north-central Estonia (Sjöstrand 2003; Löfgren 2004; Viira *et al.* 2006). From Russia – from the St Petersburg region: the Lava and Putilovo sections (Tolmacheva & Fedorov 2001).

The investigation is based on conodont elements from Ordovician limestones that had previously been processed mainly for biostratigraphical purposes. The limestone samples were dissolved in dilute acetic acid. Samples prepared before 1980 were unbuffered and the residues washed through a

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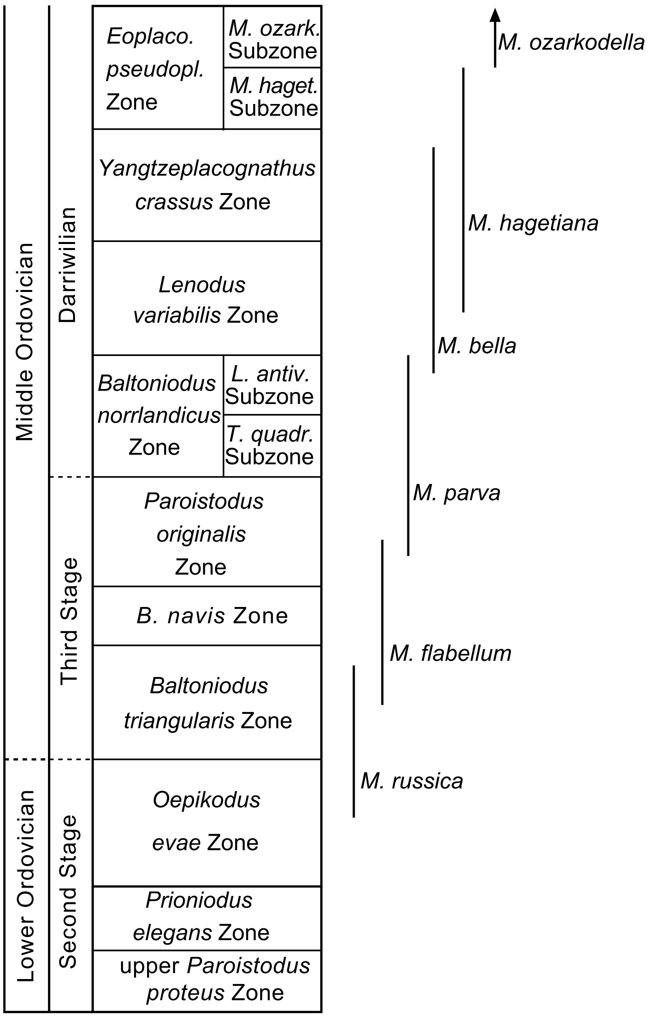

Figure 1 Stratigraphic distribution of species of *Microzarkodina* in Baltoscandia.

90 µm sieve. Since 1983 the buffering method of Jeppsson *et al.* (1985) and later that of Jeppsson *et al.* (1999) has been used and the sample residues washed through a 63 µm sieve, thus achieving a truer proportionality between element types of different sizes as expected.

All elements illustrated in this paper are kept in the Type Collection of the Department of Geology, Lund University (prefix LO-).

2. Other species and relationships

McTavish (1973) argued that '*Microzarkodina? adentata*' McTavish, 1973 from the Canning Basin in Western Australia was the direct ancestor of later *Microzarkodina* species. The Australian species was recovered from beds that are presumably equivalent in age to the middle upper part of the *P. proteus* Zone, i.e. close to the base of the Second Stage of the Ordovician. P elements of '*M.? adentata*' have a bladelike, carinate cusp, a short adentate anterior process strongly deflected inwards, a posterior process with up to six denticles and a short adentate outer lateral process.

Stouge & Bagnoli (1988) selected '*Microzarkodina? adentata*' McTavish, 1973 as the type species of *Fahraeusodus*. Their interpretation of '*M.? adentata*' was based in part on slightly younger material from Newfoundland. Pohler (1994), who also worked on conodont faunas from Newfoundland, placed most of Stouge & Bagnoli's (1988) specimens referred to *Fahraeusodus adentatus* in synonymy with her new species *Texania teras*.

'*Microzarkodina buggischi*' Lehnert, 1995, derives from Argentina and was found in beds of approximately the same age as those yielding *M. russica* n. sp. and early *M. flabellum* in Baltoscandia. In '*M. buggischi*' the P elements lack anterior denticles, while the Sa element differs from those of Baltoscandian *Microzarkodina* in the robust denticulation of the posterior process. The taxon seems to be closely related to taxa referred to *Texania* by Pohler (1994), and should probably be referred to this genus.

Both *Texania* and *Fahraeusodus* are morphologically comparable with *Microzarkodina*, and the respective ancestors of the three genera could well have shown even greater similarities.

Microzarkodina corpulenta Rasmussen, 2001 was based on 21 Norwegian specimens, from a level high up in the range of *M. flabellum* that could probably be correlated with the basal *Paroistodus originalis* Zone in Sweden, for instance. The present authors would like to point out the similarity between the holotype of *M. corpulenta* (see Rasmussen 2001, pl. 8:13) and two of the P elements from New Brunswick referred to *M. flabellum* by Nowlan (1981, pl. 2:1, 5), notably in the thickened lateral ledge on the posterior process. *Microzarkodina corpulenta* may in fact be an immigrant from Laurentia.

The closest relative of *Microzarkodina*, at least in Baltoscandia, is arguably the geographically far more widely spread genus *Periodon* Hadding, 1913, which also has a considerably longer stratigraphic range: from the early Floian, the Second Stage of the Ordovician, to the Late Ordovician.

3. Taxonomy

Lindström (1970) included both *Periodon* and *Microzarkodina* as well as *Phragmodus* and *Plectodina* in the Family Periodontidae Lindström, 1970. Sweet (1988) also placed *Periodon* and *Microzarkodina* in the same family, while in the *Treatise* (Clark *et al.* 1981) *Microzarkodina* was transferred to Cyrtoniodontidae Hass, 1959. In Dzik's (1991) classification the two genera were even placed in separate superfamilies: *Periodon* in the Oistodontacea Lindström, 1970 (Family Periodontidae) and *Microzarkodina* in Chirognathacea Branson & Mehl, 1944 (Family Plectodinidae Sweet, 1988). In later classifications such as those of Aldridge & Smith (1993) and Sweet & Donoghue (2001) *Microzarkodina* has not been listed, but it is taken that these authors agreed with Sweet's (1988) opinion in this matter. Donoghue *et al.* (2008) performed a phylogenetic analysis including more than sixty higher taxa, among which were *Periodon* and *Microzarkodina*. They confirmed that these two genera are, indeed, closely related and placed them firmly together in the 'evolutionary grade' Prionioidontida. There are certain good reasons for separating the two genera, however. For instance, elements of *Periodon* are often considered as parts of a 'symmetry transition series', a term originally coined by Lindström (1964) for *Periodon*, implying gradual morphological boundaries between neighbouring element types. *Microzarkodina* has characteristic, morphologically well delimited element types. Below, the present authors prefer to use the P, Sa–Sc, M homological notation system presented by Sweet (1981, 1988) rather than the topological notations P$_1$, P$_2$, S$_0$, etc. of Purnell *et al.* (2000), thereby stressing their wish to establish homologies rather than positional equivalents to other conodont apparatuses in the Ordovician.

Microzarkodina is characterised by a septimembrate apparatus with bipennate Pa and Pb, alate Sa, digyrate–tertiopedate Sb$_1$ and Sb$_2$, dolabrate Sc and geniculate M elements.

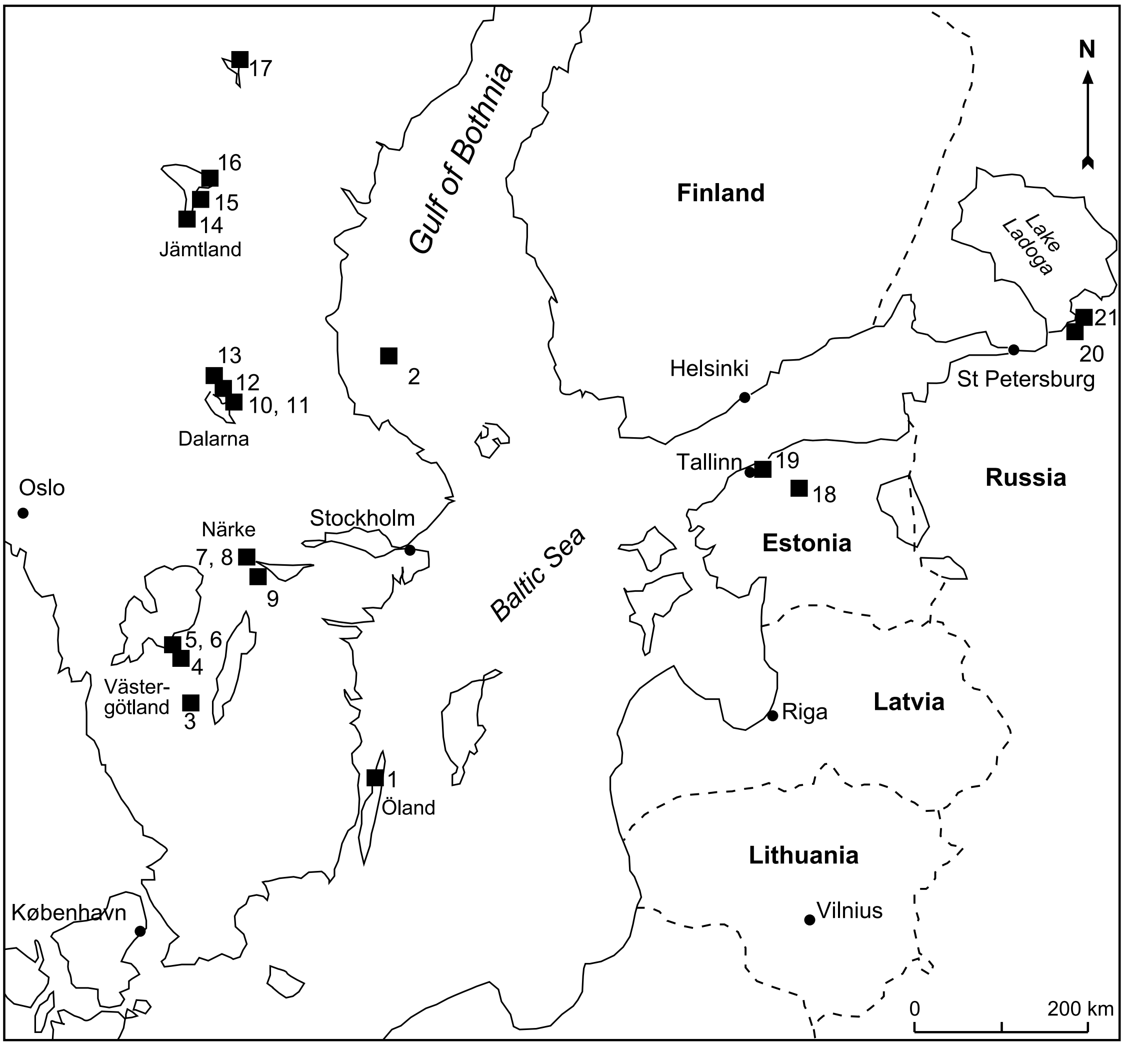

Figure 2 Map showing sampling localities. Localities 2 and 18 are drill-core sites, the rest are outcrops. 1, Gillberga; 2, Finngrundet; 3, Orreholmen; 4, Gullhögen (Skövde); 5, Hällekis; 6, Österplana and Brattefors; 7, Gymninge; 8, Lanna; 9, Yxhult; 10, Sjurberg; 11, Rävanäs; 12, Leskusänget; 13, Kårgärde; 14, Gammalbodberget; 15, Sommartjärnen and Kloxåsen; 16, Brunflo area: Lunne, Gärde and Gusta quarries; 17, Kalkberget; 18, Tamsalu; 19, Mäekalda; 20, Putilovo; 21, Lava River.

Genus *Microzarkodina* Lindström, 1971

Type species. *Prioniodina flabellum* Lindström, 1955

Microzarkodina russica n. sp.
Fig. 3

1997 *Microzarkodina* n. sp. A; Bagnoli & Stouge, p. 146, Pl.5, Fig. 1–5.

2001 *Microzarkodina* n. sp. A; Tolmacheva & Fedorov, Fig. 4: A–D.

2001 *Microzarkodina* sp. A; Tolmacheva, Pl. 4, Fig. 11–22.

Derivation of name. *russica*, after Russia where this species is more abundant than in other parts of Baltoscandia.

Type locality. The Putilovo section, St Petersburg area, Russia (Tolmacheva *et al.* 2003).

Type stratum. 0·1 m below the base of the Volkhov Stage, sample Put–Bg/2 (upper part of Bg layer), *Oepikodus evae* Zone.

Holotype. LO 10000T, a P element (Fig. 3C).

Diagnosis. A species of *Microzarkodina* with P elements bearing from one to five, usually one to three, denticles on the anterior process, and characteristic Sb_2 elements in which the denticulation of the posterior process is often pronounced. Sa and Sb_2 elements do not bear anterior keels.

Description. ***P elements.*** The P element is characterised by a wide cusp with keeled edges and denticulate anterior and posterior processes. Each lateral side of the cusp bears a smooth carina. The number of denticles on the anterior process varies strongly, approximately half the elements in the collection bearing only one anterior denticle, whereas the others have two or more. The greatest number of denticles found in our collection is five. The number of denticles on the posterior processes of large adult elements varies from five to eight. Some elements bear straight discrete denticles of equal size and other elements have irregular denticulation with one or two large and several rudimentary denticles. The aboral margin is straight and there is a slight bulge on the outer side. The anterior process of some elements is directed slightly inwards, which could indicate that these are Pb elements. The basal cavity is triangular and often shallow. In the majority of specimens it occupies no more than half the base height. However, some specimens have a relatively deep basal cavity with a tip that extends as far as the base of the cusp.

Sa elements. The Sa element has a thin posteriorly inclined cusp, two denticulate lateral processes and a usually short adenticulate posterior process. Some rare specimens in the

Figure 3 SEM micrographs of *Microzarkodina russica* n. sp. All elements are from sample Put–Bg/2, upper part of the *Oepikodus evae* Zone, the Putilovo Quarry, western Russia. (A–I) P elements, all elements shown in lateral view: (A) LO 10150, × 118; (B) LO 10151, × 70; (C) LO 10000T (holotype), × 68; (D) LO 10152, × 103; (E) LO 10153, × 84; (F) LO 10154, × 90; (G) LO 10155, × 87; (H) LO 10156, × 67; (I) LO 10157, × 64. (J–L) Sa elements: (J) LO 10158, anterior view, × 85; (K) LO 10159, posterior view, × 55; (L) LO 10160, posterior-lateral view, × 57. (M–O) Sc elements, all elements are shown in lateral view: (M) LO 10161, × 58; (N) LO 10162, × 68; (O) LO 10163, × 65. (P–R) Sb_1 elements: (P) LO 10164, posterior view, × 85; (Q) LO 10165, aboral view, × 85; (R) LO 10166, anterior view, × 64. (S–Z) Sb_2 elements: (S) LO 10167, posterior view, × 85; (T) LO 10168, posterior view, × 100; (U) LO 10169, posterior view, × 89; (V) LO 10170, posterior view, × 68; (W) LO 10171, posterior-lateral view, denticulated posterior process with two denticles, × 72; (X) LO 10172, anterior view, × 80; (Y) Same specimen as (U), aboral view, × 89; (Z) LO 10173, lateral view, denticulated posterior process with four denticles, × 87. (AA–AB) M elements, both shown in lateral view: (AA) LO 10174, × 64; (AB) LO 10175, × 55.

present collection have a longer posterior process, but it always lacks denticles. The two lateral processes are laterally or slightly posteriorly directed and each bears from five to 11 thin, straight and long denticles. The angle between the lateral processes varies considerably from 80 to 130 degrees. There is no anterior process or keel.

***Sb_1* elements.** These elements have two relatively long lateral processes and short posterior and anterior processes. The cusp is slender, straight and slightly inclined towards the inner side. The anterior process is a continuation of a pronounced anterior keel on the cusp. It is always short and lacks denticles. The anterior lateral process starts higher up than the posterior lateral process and is more distinctly downwards-directed. It is usually shorter than the posterior lateral process but is wider and bears fewer denticles, in large specimens two to four, commonly three. The posterior lateral process is relatively long and has up to nine denticles. The short posterior process lacks denticles or has only one or two small denticles.

***Sb_2* elements.** The Sb_2 element is the most distinctive element of this species. It has a slender, straight cusp, two lateral processes and a posterior process. There is no anterior process whatsoever, not even a basal costa. The lateral process on the outer side of the element is small, strongly downwards-directed and occupies an anterior-lateral position. The inner lateral process is long and less downwards-directed and more laterally placed than the outer lateral process. The inner lateral process of large adult specimens bears up to 12 denticles, whereas the outer lateral process usually has no more than two to three compressed denticles. One large and partially broken element in the collection deviates with as many as seven denticles on the outer lateral process.

The posterior process is usually slightly flexed towards the inner side and varies in length as well as in number of denticles. Rarely the posterior process can have up to 10–12 denticles. The majority of Sb_2 elements have an additional small lateral process/costa at the base between the inner lateral and posterior processes. The additional process usually arises at the lateral part of the cusp base, close to the posterior keel and runs subparallel to the posterior process. The processes have regular denticulation with long, straight and thin denticles, the size of denticles decreasing distally.

Sc elements. The Sc element has a slender almost straight cusp; the base has a short anterior extension with a rounded distal margin and a denticulated, well-developed posterior process. The element is almost symmetrical; in rare examples the posterior process is turned slightly inwards. The lateral sides of the cusp have a medial carina that is usually flat and may even be almost invisible on juvenile elements. The posterior process is long and bears up to 12 discrete denticles that are inclined slightly posteriorly and are almost equal in size.

M elements. The M element has a wide reclined cusp with keeled anterior and posterior edges. The base is strongly extended posteriorly. On both sides of the cusp is a smooth carina with a continuation on the upper part of the base. The length of the base of large and complete specimens is almost equal to that of the cusp, but in the majority of M elements the thin distal part of the base is broken. The oral margin is convex and keeled. The aboral margin has a typical sinuous outline in lateral view.

Remarks. *Microzarkodina russica* n. sp. differs markedly from its descendant species *M. flabellum* in often having multiple anterior denticles on P elements and Sb_2 elements that have no anterior keels or processes. Moreover, the symmetry of Sb_2 elements, with an outer lateral process occupying an extremely anterior position, differs from those of any other *Microzarkodina*.

Geographic and stratigraphic occurrence. Lava and Putilovo sections (western part of Russia), rare in Öland and Västergötland (Sweden), Billingen Stage, uppermost part of the *Oepikodus evae* Zone.

Material. 710 elements in all: from Russia 703 elements (259 P, 55 Sa, 70 Sb_1, 27 Sb_2, 65 Sc and 227 M); from Sweden seven elements.

Microzarkodina flabellum (Lindström, 1955)
Figs 4A–U, 5

1955 *Prioniodina flabellum* n. sp.; Lindström, p. 587, p. 6:23–25.
1955 *Cordylodus perlongus* n. sp.; Lindström, p. 552, pl. 6:36–37.
1955 *Trichonodella alae* n. sp.; Lindström, p. 599, pl. 6:38–40.
1955 *Trichonodella? irregularis* n. sp.; Lindström, p. 600, pl. 6:21–22.
1955 *Oistodus linguatus* n. sp. var. *complanatus* nov.; Lindström, p. 578, pl. 3:37–38.
1960 *Cordylodus perlongus* Lindström, 1955; Lindström, fig. 3:1.
1960 *Trichonodella? irregularis* Lindström, 1955; Lindström, fig. 3:2.
1960 *Trichonodella alae* Lindström, 1955; Lindström, fig. 3:5.
1960 *Prioniodina flabellum* Lindström, 1955; Lindström, fig. 3:10.
1964 *Trichonodella alae* Lindström; Lindström, fig. 31L–N.
1967 *Prioniodina flabellum* Lindström; Viira, fig. 1:28.
1967 *Cordylodus perlongus* Lindström; Viira, fig. 1:21.
1967 *Trichonodella alae* Lindström; Viira, fig. 1: 19.
1967 *Trichonodella? irregularis* Lindström; Viira, fig. 1:20.
1971 *Microzarkodina flabellum* (Lindström); Lindström, p. 58, pl. 1:6–11.
?1971 *Prioniodina? flabellum* Lindström?; Sweet *et al.*, pl. 1:12.
1974 *Microzarkodina flabellum* (Lindström); van Wamel, p. 70, pl. 7:18–23.
1974 *Prioniodina flabellum* Lindström; Viira, p. 31, fig. 14a, d, pl. 5:3–4.
1974 *Trichonodella alae* Lindström; Viira, p. 22, pl. 5:5.
1974 *Trichonodella? irregularis* Lindström; Viira, p. 127, pl. 5:6.
1974 *Cordylodus perlongus* Lindström; Viira, p. 22, pl. 5:7–8.
1974 *Oistodus complanatus* Lindström; Viira, p. 22, pl. 5:1–2.
?1981 *Microzarkodina flabellum* (Lindström); Nowlan, p. 14, pl. 2:1–5.
non 1981 *Microzarkodina flabellum* (Lindström); Cooper, pl. 28:2–4.
?1982 *Microzarkodina flabellum* (Lindström); Ethington & Clark, p. 54, pls. 4:2, 5:21, 22, 25, 26.
1985 *Microzarkodina flabellum flabellum* (Lindström); Löfgren, fig. 4H–N.
?1987 *Microzarkodina flabellum* (Lindström); Ni & Li, pl. 60:5.
1987 *Microzarkodina flabellum* (Lindström); An, pl. 22:14,16–17.
1990 *Microzarkodina flabellum* (Lindström); Stouge & Bagnoli, p. 19, pl. 6:1–7.
1991 *Microzarkodina flabellum* (Lindström); Rasmussen, p. 278, fig. 7A–D, F.
1993 *Microzarkodina flabellum flabellum* (Lindström); Löfgren, fig. 6Q–U, Y, Z.
1994 *Microzarkodina flabellum flabellum* (Lindström); Löfgren, fig. 8:43, 44.
1995 *Microzarkodina flabellum* (Lindström); Löfgren, fig. 7i–o.
1996 *Microzarkodina flabellum* (Lindström); Löfgren, fig. 5AD.
2000b *Microzarkodina flabellum* (Lindström, 1955); Löfgren, fig. 4I.
2001 *Microzarkodina flabellum* (Lindström); Tolmacheva, pl. 6:25–32.
2001 *Microzarkodina flabellum* (Lindström, 1955); Rasmussen, p. 88, pl. 8:14.
2005 *Microzarkodina flabellum* (Lindström); Wang *et al.*; fig. 5.

Description. ***P elements.*** The holotype of *M. flabellum*, the type species of the genus, is a P element (see Lindström 1955, pl. 6, figs. 23–24).

Basal cavity. The size and shape of the basal cavity of the P elements seem to be the most distinctive characters in *M. flabellum*. In smaller specimens (including young adults) the tip of the basal cavity is situated just below the junction between the base of the cusp and the anterior denticle. As the cusp grows broader (in an anterior-posterior direction) the additional lamellae eventually cover the anterior denticle, while a new anterior denticle arises further down on the base. Since both the anterior denticle and the cusp are filled with white matter above the level of the basal cavity apex, this process is difficult to trace, except as a poorly defined anterior denticle on the surface of the base and along the anterior edge. In later stages of overgrowth the first developed anterior denticle can sometimes be seen as an indentation of the anterior margin above the new anterior denticle. In extreme cases the anterior edge of the element forms a smooth curve

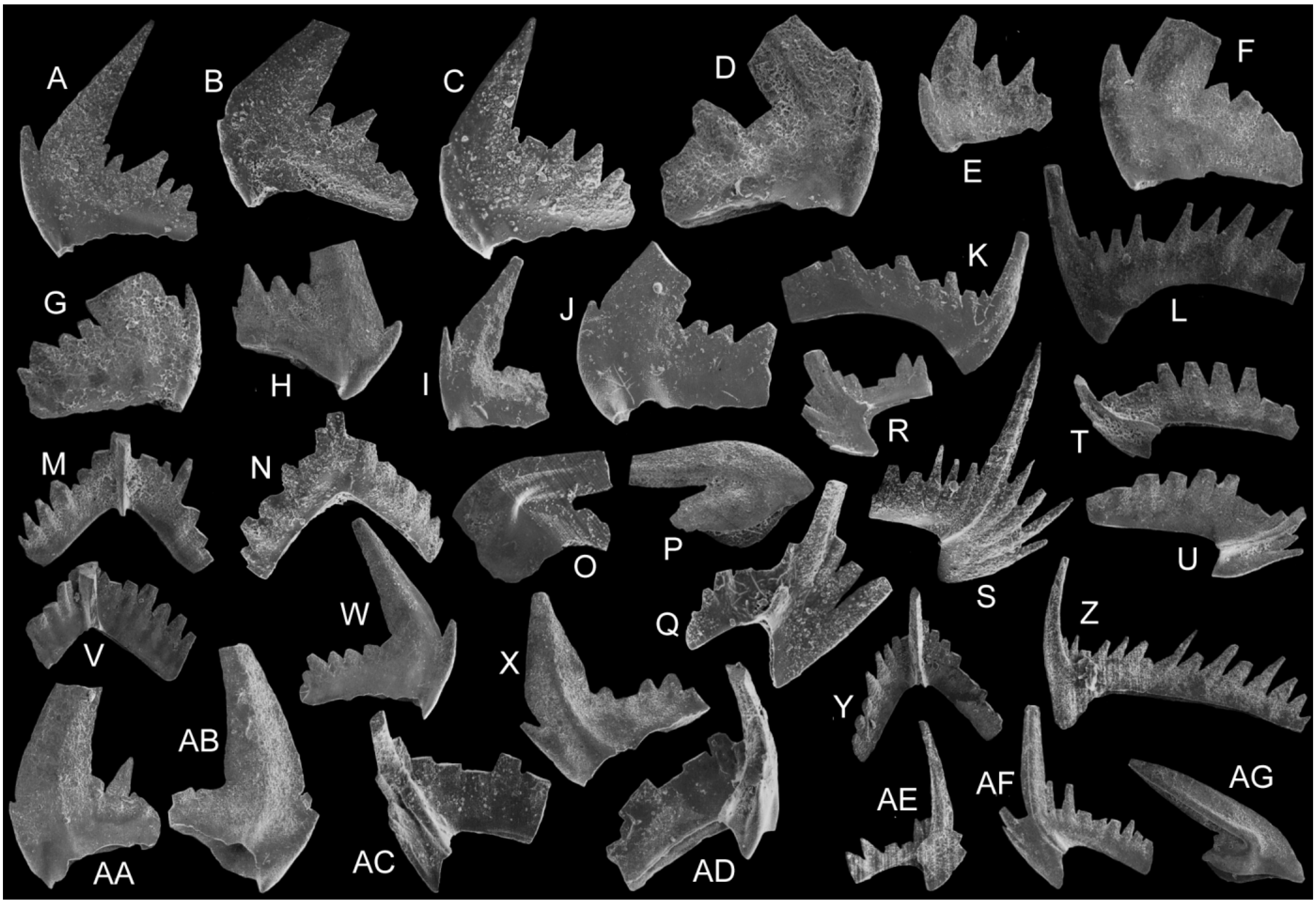

Figure 4 SEM micrographs of normal and aberrant elements of *Microzarkodina*. (A–U) *Microzarkodina flabellum* (Lindström, 1955): (A) LO 9979, P element, × 77, same element as in Fig. 5A, *Baltoniodus navis* Zone, sample DLS 86-H 5·0 m, Sjurberg; (B) LO 9980, P element with one anterior denticle almost overgrown, × 70, same element as in Fig. 5B, same sample as (A); (C) LO 9981, P element, × 70, same element as in Fig. 5C, same sample as (A); (D) LO 9989, P element with two anterior denticles, × 72, same element as in Fig. 5K, *Baltoniodus triangularis* Zone, sample L8, Kårgärde; (E) LO 9996, juvenile P element, × 65, same element as in Fig. 5R, *Baltoniodus triangularis* Zone, sample GB81-50FK, Gullhögen; (F) LO 9993, P element, × 65, same element as in Fig. 5O, same sample as (E); (G) LO 9988, P element with two anterior denticles, × 72, same element as in Fig. 5J, same sample as (D); (H) LO 9995, P element, × 50, same element as in Fig. 5Q, same sample as (D); (I) LO 9987, P element, × 70, same element as in Fig. 5I, *Baltoniodus triangularis* Zone, sample HK 89-0, Hällekis; (J) LO 9994, P element, × 70, same element as in Fig. 5P, same sample as (I); (K) LO 10079, Sc element, × 70, same sample as (I); (L) LO 10080, Sc element, × 65, same sample as (E); (M) LO 10081, Sa element, × 55, same sample as (E); (N) LO 10082, Sa element, outer side, × 70, same sample as (A); (O) LO 10083, M element, inner side, × 62, same sample as (I); (P) LO 10084, M element, outer side, × 60, same sample as (E); (Q) LO 10085, Sb_1 element, × 83, same sample as (A); (R) LO 10086, Sb_1 element, × 55, same sample as (I); (S) LO 10087, Sb_1 element, outer side, × 76, same sample as (A); (T) LO 10088, Sb_2 element, × 62, same sample as (E); (U) LO 10089, Sb_2 element, × 69, same sample as (E). (V–AG) *Microzarkodina parva* Lindström, 1971: (V) LO 10090, Sa element, × 42, *Paroistodus originalis* Zone, sample Lä5, Leskusänget; (W) LO 10025, P element, × 45, same element as in Fig. 6AB, same sample as (V); (X) LO 10024, P element with broken and regenerated anterior denticle, × 48, same element as in Fig. 6AA, *Paroistodus originalis* Zone, sample L2, Kårgärde; (Y) LO10091, Sa element, × 54, same sample as (V); (Z) LO 10092, Sc element, × 60, upper *Paroistodus originalis* Zone, sample Öl88-3, Gillberga; (AA) LO 10028, P element with almost overgrown anterior denticle, × 56, same element as in Fig. 6AE, same sample as (V); (AB) LO 10027, P element with two partly overgrown anterior denticles, × 57, same element as in Fig. 6AD, same sample as (V); (AC) LO 10093, Sb_2 element, × 85, same sample as (Z); (AD) LO 10094, Sb_2 element, × 85, same sample as (Z); (AE) LO 10095, Sb_1 element, × 60, same sample as (Z); (AF) LO 10096, Sb_1 element, outer side, × 60, same sample as (Z); (AG) LO 10097, M element, outer side, × 33, same sample as (V).

completely lacking in denticles, which often results in stubby-looking mature and gerontic elements (Fig. 4B, C, D). The growth process also has another consequence: the basal cavity tip indirectly moving successively backwards in relation to the anterior part of the base and the mid-line of the cusp. In some of the largest specimens the tip of the basal cavity is thus situated approximately on the mid-line of the cusp at its junction with the base.

Sa elements. The Sa element of *M. flabellum* was described as *Trichonodella alae* by Lindström (1955, p. 599, pl. 6, figs. 38–40). It has a short, adenticulate posterior process, two anterior lateral processes with up to eight denticles each, but no anterior process or keel. The angle between the lateral processes exceeds 100° in most elements.

Sb_1 elements. There is a prominent anterior keel. The most anteriorly situated (shorter) lateral process has up to four relatively long denticles. The posterior-lateral process is long with up to ten denticles. The posterior 'process' is directed backwards and in most cases is adenticulate.

Sb_2 elements. There is an anterior keel that can be fairly prominent on the base. The anterior-lateral process can have up to ten almost erect denticles. The generally adenticulate

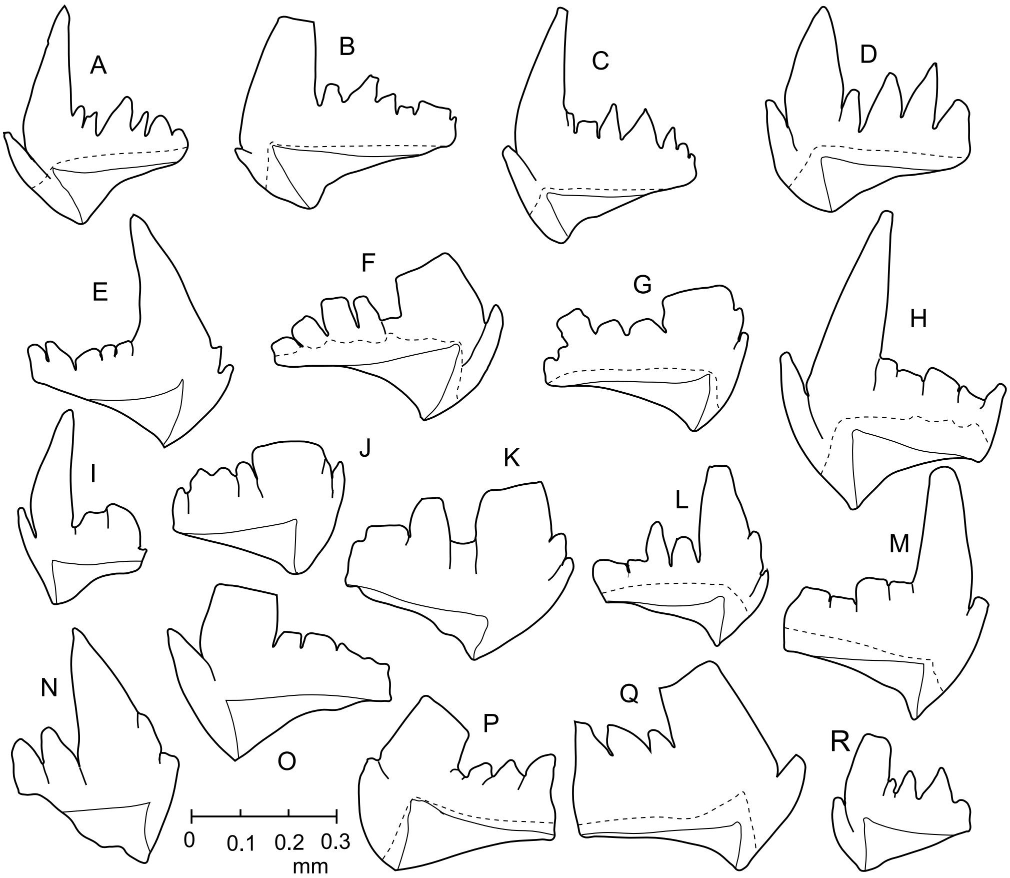

Figure 5 Camera lucida drawings of P elements of *Microzarkodina flabellum* (Lindström, 1955); thin line = outline of basal cavity; broken line = limit of white matter (where visible): (A) LO 9979, same element as in Fig. 4A, *B. navis* Zone, sample DLS 86-H 5.0m, Sjurberg; (B) LO 9980, same element as in Fig. 4B; same sample as (A); (C) LO 9981, same element as in Fig. 4C, same sample as (A); (D) LO 9982, *B. navis* Zone, sample L6, Kårgärde; (E) LO 9983, same sample as (D); (F) LO 9984, same sample as (A); (G) LO 9985, same sample as (A); (H) LO 9986, same sample as (D); (I) LO 9987, same element as in Fig. 4I, *B. triangularis* Zone, sample HK89-0, Hällekis; (J) LO 9988, same element as in Fig. 4G, *B. triangularis* Zone, sample L8, Kårgärde; (K) LO 9989, same element as in Fig. 4D, same sample as (J); (L) LO 9990, *B. navis* Zone, sample EST86-16, Tamsalu drill-core, Estonia; (M) LO 9991, same sample as (L); (N) LO 9992, same sample as (J); (O) LO 9993, same element as in Fig. 4F, *B. triangularis* Zone, sample GB81-50FK, Gullhögen; (P) LO 9994, same specimen as in Fig. 4J, same sample as (I); (Q) LO 9995, same specimen as in Fig. 4H, same sample as (J); (R) LO 9996, same specimen as in Fig. 4E, same sample as (O).

posterior ‘process’ is directed backwards and runs subparallel with the posterior-lateral process which has 1–2 denticles.

Sc elements. The Sc element of *M. flabellum* was designated *Cordylodus perlongus* by Lindström (1955, p. 552, pl. 6, figs. 36, 37). What has not been previously noted is the presence of lateral costae or sharp carinae on one or both sides of the cusp. Such costae are clearly visible in published photos of *M. flabellum* (see, e.g., Stouge & Bagnoli 1990, pl. 6, fig. 5). The posterior process has up to 20, posteriorly inclined denticles that tend to be confluent. The cusp is straight, slightly proclined, erect, or even somewhat reclined.

M elements. M elements of *M. flabellum* were described by Lindström (1955, p. 578, pl. 3, figs. 37–38) as *Oistodus linguatus complanatus* and the description was elaborated on by Löfgren (1978, pp. 61–62). The oral margin has a posterior extension that is shorter than the cusp.

Remarks. Lindström (1971, p. 59) held that the main difference between *M. flabellum* and *M. parva* was that in the P elements of the former the denticles extended to about half the height of the cusp; in the latter to considerably less than half the height of the cusp. Although variable, the denticle/cusp height ratio has been shown to be greater in *M. flabellum* than in later *Microzarkodina* taxa, which has also been demonstrated in subsequent investigations where the material has been reasonably well preserved. Since this difference may be difficult to discern when the cusp and/or denticles are broken (cf. for instance Löfgren 1978, p. 62), Löfgren (1985, p. 127) suggested that the angle between the anterior margin of the base (along the anterior denticle) and the anterior edge of the cusp could be used as an additional criterion for distinguishing between these two taxa. This angle is wider in *M. flabellum* than in *M. parva*. Stated in other words, *M. flabellum* often has a strongly reclined cusp, while in *M. parva* and younger taxa the cusp is more erect. In *M. flabellum* the posterior process carries up to six posteriorly inclined or erect denticles which are often of irregular height.

Geographic and stratigraphic occurrence. Ubiquitous in Baltoscandia; also reported from North America and southern China, upper half of the *Baltoniodus triangularis* Zone, the *B. navis* Zone and lower *Paroistodus originalis* Zone.

Material. 29,671 elements in all: 26,066 from Sweden, 2,566 from Estonia and 1,039 from Russia.

Microzarkodina cf. *M. flabellum* (Lindström, 1955)

Remarks. The elements referred here exhibit characters that are intermediate between those of *M. russica* n. sp. (ancestor) and *M. flabellum* (descendant). The P elements are very variable as in *M. russica* n. sp. The other elements resemble those in early *M. flabellum* populations.

Microzarkodina cf. *M. flabellum* seems to have had a narrower geographical distribution than *M. flabellum*. It provides a link between *M. russica* n. sp. and *M. flabellum*.

Geographic and stratigraphic distribution. Reported from Kinnekulle (Västergötland) in Sweden, only in the lower *Baltoniodus triangularis* Zone.

Material. 391 elements (187P, 16M, 45Sa, 88Sb, and 55Sc) from Sweden.

Microzarkodina parva Lindström, 1971
Figs 4V–AG, 6, 7L, 7N–S, 8

?1960 *Oistodus complanatus* Lindström; Lindström, fig. 4:11.
1961 *Prioniodina* cf. *flabellum* Lindström; Wolska, p. 354, pl. 4:4a–b.
1971 *Microzarkodina parva* n. sp.; Lindström, p. 59, pl. 1:14.
1976 *Microzarkodina flabellum parva* Lindström; Dzik, fig. 35a–h.
1978 *Microzarkodina flabellum* (Lindström); Löfgren, pp. 61–62 (pars), pl. 11:27–35, ?36.
1985 *Microzarkodina flabellum parva* Lindström; Löfgren, p. 127 (pars), fig. 4B, D, G.
1985 *Microzarkodina flabellum* (Lindström); An *et al.*, pl. 15:5–10.
?1985 *Microzarkodina ozarkodella* Lindström; An *et al.*, pl. 13:16.
?1987 *Microzarkodina parva* Lindström; Ni & Li, pl. 60:8, 31.
1987 *Microzarkodina flabellum* (Lindström); An, pl. 29:14, 16–19.
?1987 *Microzarkodina ozarkodella* Lindström; An, pl. 29:15.
1990 *Microzarkodina parva* Lindström; Stouge & Bagnoli, p. 20, pl. 6:8–16.
1991 *Microzarkodina parva* Lindström; Rasmussen, p. 279 (pars), fig. 7E–G, I, J
1994 *Microzarkodina flabellum parva* Lindström; Löfgren, fig. 8:45–46.
1995 *Microzarkodina parva* Lindström; Löfgren, fig. 9o–v.
1995 *Microzarkodina flabellum* (Lindström); Lehnert, p. 97, pl. 6:16–23.
1996 *Microzarkodina parva* Lindström; Löfgren, fig. 5AC.
1998 *Microzarkodina flabellum* (Lindström, 1955); Bednarczyk, pl. 1:3, 8, 16.
1998b *Microzarkodina parva* Lindström; Zhang, p. 75, pl. 12:1–6.
2000a *Microzarkodina parva* Lindström; Löfgren, figs. 4y, 5a, b.
2000b *Microzarkodina parva* Lindström; Löfgren, fig. 4J.
2001 *Microzarkodina parva* Lindström; Tolmacheva, pl. 7:27–33.
2001 *Microzarkodina parva* Lindström; Rasmussen, p. 92, pl. 8:15–20.
2003 *Microzarkodina parva* Lindström, 1971; Löfgren, fig. 9S–X.

Description. ***P elements.*** The holotype of the species is a P element (Lindström 1971, Pl.1:14). The five to seven denticles on the posterior process are more regular than in *M. russica* n. sp. and *M. flabellum*. The basal cavity is deep, and its tip extends into the cusp. In some mature specimens the basal cavity has an extra 'abandoned' tip anteriorly (Fig. 7L, P). The cusp has weak lateral costae. In most specimens there is only one anterior denticle, but there are some instances of multiple anterior denticles as well as overgrowth. Elements from very mature or gerontic individuals can look quite stubby (Fig. 8S), but less so than those of *M. flabellum*.

Sa elements. The lateral processes bear up to nine denticles each and in most specimens diverge less than 100°. The posterior process is short and lacks denticles. There is no anterior process, but there can be a faint keel on the base.

Sb_1 elements. There is a prominent adenticulate anterior keel or process. The anterior-lateral process bears 1–3 denticles. The posterior-lateral process is long and carries up to eight denticles, the posterior process is very short and has only 0–2 denticles.

Sb_2 elements. The anterior keel is developed as a short, undenticulate process on the base. The anterior-lateral process can have up to 12 denticles; the posterior-lateral process is shorter with two denticles at most. The posterior process lacks denticles.

Sc elements. The posterior process bears up to 15 posteriorly inclined denticles. The lateral carinae are often weak on the base. The cusp is slender and recurved.

M elements. The element is more robust than in the other species. As in *M. flabellum*, the cusp seems to be longer than the base in most specimens. The distal part of the base is often broken, however, so its length can be difficult to assess. The lateral carinae are sometimes weak.

Geographic and stratigraphic distribution. Reported from all over Baltoscandia, the Holy Cross Mountains (Poland), Argentina and southern China, upper half of the *Paroistodus originalis* Zone and through the *Baltoniodus norrlandicus* Zone *s.l.*

Material. 40,453 elements in all: 39,351 from Sweden, 258 from Estonia and 844 from Russia.

Microzarkodina bella Löfgren, 2000
Figs 7G–I, 7M, 9AA–AK

2000a *Microzarkodina* n. sp. A; Löfgren, figs. 4x, 5e, f.
2000b *Microzarkodina bella* n. sp.; Löfgren, p. 335, figs. 5S–U, 11A, ?B.
2003 *Microzarkodina bella* Löfgren, 2000; Löfgren, fig. 9Y–AC.

Description. ***P elements.*** The P elements have a shallow basal cavity with the apex situated anteriorly. The cusp is long, slender and suberect and has distinctly carinate sides. The up to five denticles on the posterior process are confluent and posteriorly inclined. There is usually only one, long anterior denticle, rarely more, as in the other stratigraphically older *Microzarkodina* species.

Sa elements. On the cusp and base there is a prominent anterior keel. The lateral processes carry up to seven denticles each. The angle between the lateral processes is obtuse, usually exceeding 100°. The posterior process, that can be fairly long, always lacks denticles.

Sb_1 elements. There is a distinct anterior keel but no denticles. The anterior-lateral process carries up to three denticles and the posterior-lateral process up to six denticles. The posterior process apparently always lacks denticles.

Sb_2 elements. The anterior and posterior processes or keels lack denticulation. The anterior-lateral process bears up to six denticles, the posterior-lateral process 0–2 denticles.

Sc elements. The cusp is slender, carinate and erect to recurved. The posterior process has up to ten confluent denticles.

M elements. The cusp is thin, carinate and rather short, in some specimens even shorter than the base.

Geographic and stratigraphic distribution. Restricted to central Baltoscandia (Öland and Finngrundet in Sweden), from the uppermost part of the *Lenodus antivariabilis* Subzone of the *B. norrlandicus* Zone, through the *Lenodus variabilis* Zone to the upper *Yangtzeplacognathus crassus* Zone.

Material. 3,070 elements from Sweden.

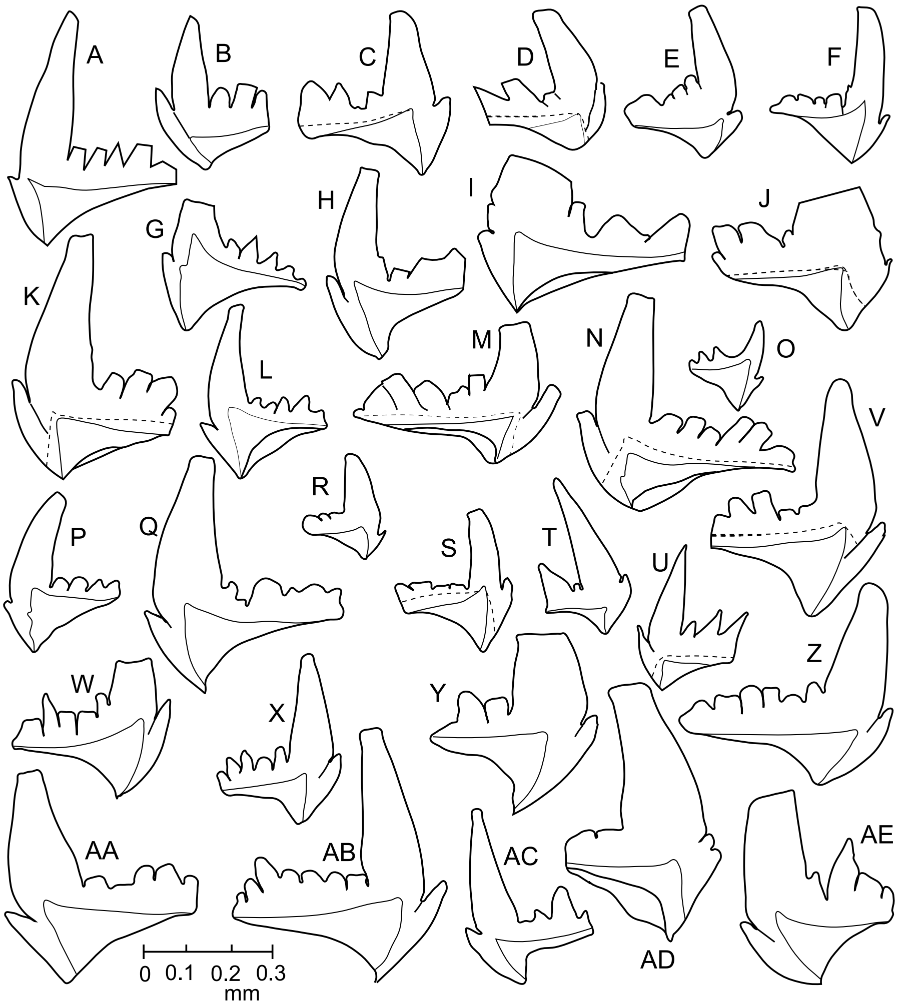

Figure 6 Camera lucida drawings of P elements of *Microzarkodina parva* Lindström, 1971; thin line = outline of basal cavity, broken line = limit of white matter (where visible): (A) LO 9997, same element as in Fig. 8A, *Trapezognathus quadrangulum* Subzone, sample Öl88-4, Gillberga; (B) LO 9998, same element as in Fig. 8K, same sample as (A); (C) LO 9999, same element as in Fig. 8S, *Lenodus antivariabilis* Subzone, sample Öl88-6, Gillberga; (D) LO 10001, same element as in Fig. 8L, same sample as (C); (E) LO 10002, same element as in Fig. 8Q, *Paroistodus originalis* Zone, sample Rä2, Rävanäs; (F) LO 10003, same element as in Fig. 8R, same sample as (E); (G) LO 10004, *Lenodus antivariabilis* Subzone, same element as in Fig. 8N, sample Öl88-5, Gillberga; (H) LO 10005, same element as in Fig. 8M, same sample as (A); (I) LO 10006, same element as in Fig. 8J, same sample as (A); (J) LO 10007, same element as in Fig. 8O, *Lenodus antivariabilis* Subzone, sample Öl93-1, Gillberga; (K) LO 10008, same element as in Fig. 8C, *Paroistodus originalis* Zone, sample Lä5, Leskusänget; (L) LO 10009, same sample as (K); (M) LO 10010, same element as in Fig. 8B, same sample as (K); (N) LO 10011, same sample as (K); (O) LO 10012, same element as in Fig. 8F, *P. originalis* Zone, sample Vg84-11, Orreholmen; (P) LO 10013, same element as in Fig. 8H, same sample as (O); (Q) LO 10014, same element as in Fig. 8I, same sample as (O); (R) LO 10015, same sample as (O); (S) LO 10016, same sample as (O); (T) LO 10017, same element as in Fig. 8E, same sample as (O); (U) LO 10018, same element as in Fig. 8D, same sample as (O); (V) LO 10019, same element as in Fig. 8G, *Paroistodus originalis* Zone, sample Lä4, Leskusänget; (W) LO 10020, *Paroistodus originalis* Zone, sample Öl88-3, Gillberga; (X) LO 10021, same sample as (W); (Y) LO 10022, same sample as (W); (Z) LO 10023, same sample as (K); (AA) LO 10024, same element as in Fig. 4X, *Paroistodus originalis* Zone, sample L2, Kårgärde; (AB) LO 10025, same element as in Fig. 4W, same sample as (K); (AC) LO 10026, same sample as (W); (AD) LO 10027, same element as in Fig. 4AB, same sample as (K); (AE) LO 10028, same element as in Fig. 4AA, same sample as (K).

Microzarkodina hagetiana Stouge & Bagnoli, 1990
Figs 7A–F, 7J, 7K, 9A–W, ?9X–Z, ?10A–E

1974 *Prioniodina* sp. 1+2 Lindström; Viira, fig. 14B.

1978 *Microzarkodina flabellum* (Lindström); Löfgren, pp. 61–62 (pars), fig. 27A–B.

?1983 *Microzarkodina flabellum* (Lindström); Zheng *et al.*, pl. 12:2.

1985 *Microzarkodina flabellum parva* Lindström; Löfgren, p. 127 (pars), fig. 4A, C, E–F.

1990 *Microzarkodina hagetiana* n. sp.; Stouge & Bagnoli, p. 20, pl. 6:17–24.

1991 *Microzarkodina parva* Lindström; Rasmussen, p. 279 (pars), fig. 7H, K.

1998b *Microzarkodina hagetiana* Stouge & Bagnoli; Zhang, p. 76, pl. 12:7–10.

2000a *Microzarkodina hagetiana* Stouge & Bagnoli; Löfgren, fig. 5c, d.

2000b *Microzarkodina hagetiana* Stouge & Bagnoli, 1990; Löfgren, fig. 6M.

2001 *Microzarkodina hagetiana* Stouge & Bagnoli, 1990; Rasmussen, p. 279 (pars), fig. 7H, K.

2003 *Microzarkodina hagetiana* Stouge & Bagnoli, 1990; Löfgren, fig. 9AD–AI.

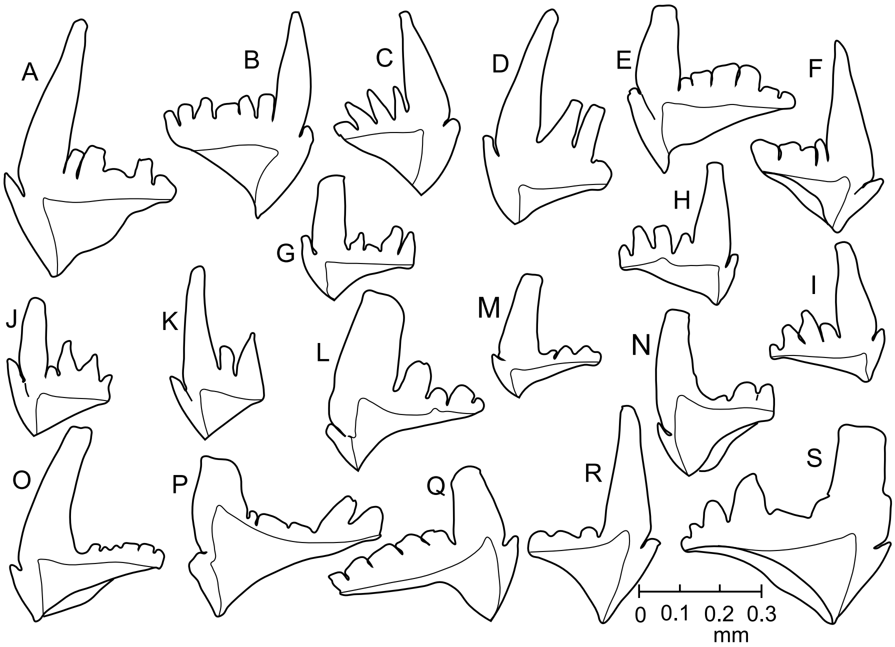

Figure 7 Camera lucida drawings of P elements of stratigraphically younger species of *Microzarkodina*; thin line=outline of basal cavity. (A–F) *Microzarkodina hagetiana* Stouge & Bagnoli, 1990, from the *E. pseudoplanus–M. hagetiana* Subzone: (A) LO 10029, same element as in Fig. 9K, sample Rä5, Rävanäs; (B) LO 10030, same element as in Fig. 9L, same sample as (A); (C) LO 10031, same element as in Fig. 9M, same sample as (A); (D) LO 10032, same element as in Fig. 9Q, sample Öl74-101, Gillberga; (E) LO 10033, same element as in Fig. 9S, same sample as (D); (F) LO 10034, same element as in Fig. 9R, same sample as (D). (G), (M) *Microzarkodina bella* Löfgren, 2000 from the upper *Lenodus antivariabilis* Subzone, sample Öl83-100, Gillberga: (G) LO 10035, same element as in Fig. 9AF; (M) LO 10036, same element as in Fig. 9AG. (H–I) *Microzarkodina bella* Löfgren, 2000, from the upper *Lenodus variabilis* Zone, sample Öl92-7, Gillberga: (H) LO 10037; (I) LO 10038. (J–K) *Microzarkodina hagetiana* Stouge & Bagnoli, 1990, from the upper *Lenodus variabilis* Zone, sample Vg90-3, Hällekis: (J) LO 10039; (K) LO 10040, same element as in Fig. 9B. (L), (N–S) *Microzarkodina parva* Lindström, 1971, from the upper *Lenodus antivariabilis* Subzone, same sample as (G, M): (L) LO 10041; (N) LO 10042; (O) LO 10043; (P) LO 10044, same element as in Fig. 8T; (Q) LO 10045, same element as in Fig. 8V; (R) LO 10046, same element as in Fig. 8U; (S) LO 10047.

2004 *Microzarkodina hagetiana* Stouge & Bagnoli; Löfgren, fig. 12a, c–g ?b.

Description. ***P elements.*** The holotype of the species is a P element (Stouge & Bagnoli 1990, Pl. 6:17). There are 3–6 denticles on the posterior process that decrease successively in size distally. The basal cavity is moderately deep. There is usually only one anterior denticle. Some levels of the upper stratigraphical range of this species, however, yield elements with up to three anterior denticles. Not until this character is firmly established in the majority of adult specimens can the populations be designated as *M. ozarkodella*.

Sa elements. The posterior process is adenticulate, and there is a faint keel anteriorly on the base. Each lateral process has up to eight denticles. The lateral processes diverge at about 90°.

Sb_1 elements. The anterior process lacks denticles. The anterior-lateral process bears up to three denticles, while the posterior-lateral process carries 4–5 denticles. The posterior process is long and can have up to eight denticles, a character shared only with *M. ozarkodella* among the species treated here.

Sb_2 elements. The anterior and posterior processes are adenticulate. The lateral processes have 3–5 denticles; the anterior-lateral process is the longest and has confluent, compressed denticles and the posterior-lateral process bears discrete denticles.

Sc elements. The cusp is thin and recurved with lateral costae. There are up to 14 denticles on the posterior process.

M elements. The cusp is thin, costate and shorter than the base.

Geographic and stratigraphic distribution. Reported from all over Baltoscandia and from southern China, from the lower *Lenodus variabilis* Zone, through the *Yangtzeplacognathus crassus* Zone and the *Microzarkodina hagetiana* Subzone of the *Eoplacognathus pseudoplanus* Zone.

Material. 5,011 elements in all; 4,963 from Sweden and 48 from Estonia.

Microzarkodina ozarkodella Lindström, 1971
Figs 10F–AE, 11, 12

1960 *Prioniodina* n. sp. 1; Lindström, fig. 5:1.
1960 *Prioniodina* n. sp. 2; Lindström, fig. 5:2.
1967 *Prioniodina* sp. 1 Lindström; Viira, fig. 1:29.
1967 *Prioniodina* sp. 2 Lindström; Viira, fig. 1:30.
1971 *Microzarkodina ozarkodella* n. sp.; Lindström, p. 59, pl. 1–15–17.
1974 *Prioniodina* sp. 1+2 Lindström; Viira, p. 31 (pars), fig. 14 g, d, pl. 5:34–38.
1974 *Prioniodina* sp.; Viira, fig. 14 e, f.
1976 *Microzarkodina ozarkodella* Lindström; Dzik, fig. 35 i–l.
1978 *Microzarkodina ozarkodella* Lindström; Löfgren, p. 62, fig. 27C–G, pl. 11:37–47.
?1987 *Microzarkodina ozarkodella* Lindström, 1971; Ni & Li, pl. 22:18.
1994 *Microzarkodina ozarkodella* Lindström; Dzik, p. 113, fig. 31c, pl. 24:5–9.
1998 *Microzarkodina ozarkodella* Lindström, 1971; Bednarczyk, pl. 1:17.
1998b *Microzarkodina ozarkodella* Lindström; Zhang, p. 76, pl. 12:11–13.

Figure 8 SEM micrographs of *Microzarkodina parva* Lindström, 1971: (A) LO 9997, P element, × 70, same element as in Fig. 6A, *Paroistodus originalis* Zone, sample Lä5, Leskusänget; (B) LO 10010, P element, × 60, same element as in Fig. 6M, same sample as (A); (C) LO 10008, P element, × 55, same element as in Fig. 6K, same sample as (A); (D) LO 10018, juvenile P element, × 90, same element as in Fig. 6U, *Paroistodus originalis* Zone, sample Vg84-11, Orreholmen; (E) LO 10017, juvenile P element, × 70, same element as in Fig. 6T, same sample as (D); (F) LO 10012, juvenile P element, × 100, same element as in Fig. 6O, same sample as (D); (G) LO 10019, P element, × 65, same element as in Fig. 6V, *Paroistodus originalis* Zone, sample Lä4, Leskusänget; (H) LO 10013, P element, × 85, same element as in Fig. 6P, same sample as (D); (I) LO 10014, P element, × 50, same element as in Fig. 6Q, same sample as (D); (J) LO 10006, P element, × 70, same element as in Fig. 6I, *Trapezognathus quadrangulum* Subzone, sample Öl88-4, Gillberga; (K) LO 9998, P element, × 90, same element as in Fig. 6B, same sample as (J); (L) LO 10001, P element, × 85, same element as in Fig. 6D, *Lenodus antivariabilis* Subzone, sample Öl88-6, Gillberga; (M) LO 10005, P element, × 70, same element as in Fig. 6H, same sample as (J); (N) LO 10004, P element, × 80, same element as in Fig. 6G, *Lenodus antivariabilis* Subzone, sample Öl88-5, Gillberga; (O) LO 10007, P element, × 80, same element as in Fig. 6J, *Lenodus antivariabilis* Subzone, sample Öl93-1, Gillberga; (P) LO 10098, P element, × 65, same sample as (J); (Q) LO 10002, P element, × 80 same element as in Fig. 6E, *Paroistodus originalis* Zone, sample Rä2, Rävanäs; (R) LO 10003, P element, × 80, same element as in Fig. 6F, same sample as (Q); (S) LO 9999, P element, × 80, same element as in Fig. 6C, same sample as (L); (T) LO 10044, P element, × 80, same element as in Fig. 7P, upper *Lenodus antivariabilis* Subzone, sample Öl83-100, Gillberga; (U) LO 10046, P element, × 70, same element as in Fig. 7R, same sample as (T); (V) LO 10045, P element, × 70, same element as in Fig. 7Q, same sample as (T); (W) LO 10099, M element, inner side, × 60, same sample as (G); (X) LO 10100, M element, outer side, × 50, same sample as (A); (Y) LO 10101, Sa element, anterior side, × 60, same sample as (D); (Z) LO 10102, Sa element, posterior side, × 60, same sample as (T); (AA) LO 10103, Sb_1 element, oblique posterior view; note denticle on posterior process, × 75, same sample as (A); (AB) LO 10104, Sb_1 element, anterior side, × 90, same sample as (A); (AC) LO 10105, Sb_1 element, oblique posterior view, × 90, same sample as (T); (AD) LO 10106, Sb_1 element, oblique posterior view; note denticles on posterior process, × 70, same sample as (T); (AE) LO 10107, Sb_1 element, anterior side; note extended anterior process, × 90, same sample as (T); (AF) LO 10108, Sb_1 element, oblique posterior view; note denticle on posterior process, × 95, same sample as (J); (AG) LO 10109, Sb_2 element, × 80, same sample as (D); (AH) LO 10110, Sb_2 element, × 70, same sample as (J); (AI) LO 10111, Sb_2 element; note denticles on anterior-lateral process to the left, × 70, same sample as (A); (AJ) LO 10112, Sc element, × 55, same sample as (J); (AK) LO 10113, Sc element, × 50, same sample as (G); (AL) LO 10114, Sb_2 element; note denticles on anterior-lateral process to the left, × 70, same sample as (A); (AM) LO 10115, Sc element, × 55, same sample as (A).

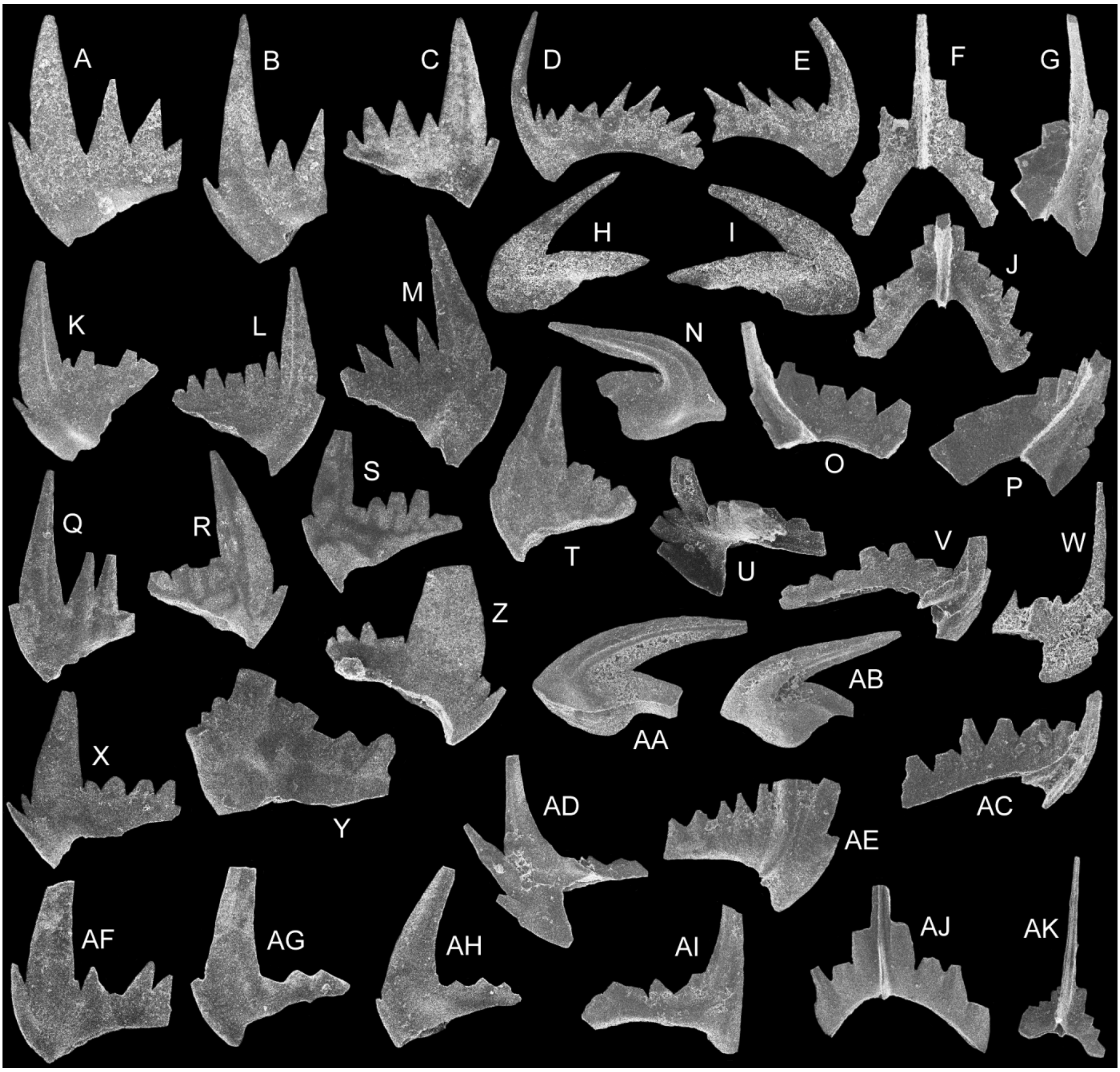

Figure 9 SEM micrographs of later representatives of *Microzarkodina*. (A–W) *Microzarkodina hagetiana* Stouge & Bagnoli, 1990: (A) LO 10116, P element, × 120, upper *Lenodus variabilis* Zone, sample Vg90-3, Hällekis; (B) LO 10040, P element, × 100, same element as in Fig. 7K same sample as (A); (C) LO 10117, P element, × 90, upper *Lenodus variabilis* Zone, sample Öl72-6, Gillberga; (D) LO 10118, Sc element, × 85, same sample as (A); (E) LO 10119, Sc element, × 90, same sample as (A); (F) LO 10120, Sa element, posterior side, × 90, same sample as (A); (G) LO 10121, Sb$_2$ element, × 110, *Eoplacognathus pseudoplanus–Microzarkodina hagetiana* Subzone, sample Rä5, Rävanäs; (H) LO 10122, M element, × 100, same sample as (A); (I) LO 10123, M element, × 85, same sample as (A); (J) LO 10124, Sa element, × 65, same sample as (G); (K) LO 10029, P element, × 60, same element as in Fig. 7A, same sample as (G); (L) LO 10030, P element, × 70, same element as in Fig. 7B, same sample as (G); (M) LO 10031, P element, × 90, same element as in Fig. 7C, same sample as (G); (N) LO 10125, M element, inner side, × 55, same sample as (G); (O) LO 10126, Sb$_2$ element, × 100, *E. pseudoplanus–M. hagetiana* Subzone, sample Öl93-12, Gillberga; (P) LO 10127, Sb$_2$ element, × 100, same sample as (G); (Q) LO 10032, P element, × 65, same element as in Fig. 7D, *E. pseudoplanus–M. hagetiana* Subzone, sample Öl74-101, Gillberga; (R) LO 10034, P element, × 75, same element as in Fig. 7F, same sample as (Q); (S) LO 10033, P element, × 70, same element as in Fig. 7E, same sample as (Q); (T) LO 10128, P element, note overgrown anterior denticle, × 70, same sample as (Q); (U) LO 10129, Sb$_1$ element, note denticulated posterior process, × 90, *E. pseudoplanus–M. hagetiana* Subzone, sample Öl83-109, Gillberga; (V) LO 10130, Sb$_1$ element, note long, denticulated posterior process, × 100, same sample as (G); (W) LO 10131, Sb$_1$ element, note denticulation of posterior process, × 100, same sample as (A). (X–Z) *Microzarkodina* cf. *hagetiana* Stouge & Bagnoli, 1990, P elements with multiple anterior denticles: (X) LO 10049, × 90, same element as in Fig. 8B, *Yangtzeplacognathus crassus* Zone, sample HK88-2, Hällekis; (Y) LO 10052, × 90, *E. pseudoplanus–M. hagetiana* Subzone, same element as in Fig. 8E, sample H13, Kårgärde; (Z) LO 10048, × 100, same element as in Fig. 8A, same sample as (X). (AA–AK) *Microzarkodina bella* Löfgren, 2000: (AA) LO 10132, M element, outer side, × 80, *Lenodus variabilis* Zone, sample Öl83-103, Gillberga; (AB) LO 10133, M element, inner side, × 80, lower *Lenodus variabilis* Zone, sample Öl92-5, Gillberga; (AC) LO 10134, Sb$_2$ element, × 120, lower *Lenodus variabilis* Zone, sample Öl92-4, Gillberga; (AD) LO 10135, Sb$_1$ element, oblique posterior view, × 160, same sample as (AA); (AE) LO 10136, Sb$_1$ element, anterior side, × 130, same sample as (AA); (AF) LO 10035, P element, × 100, same element as in Fig. 7G, upper *Lenodus antivariabilis* Subzone, sample Öl83-100, Gillberga; (AG) LO 10036, P element, × 100, same element as in Fig. 7M, same sample as (AF). (AI) LO 10137, Sc element, × 100, same sample as (AB); (AJ) LO 10138, Sa element, anterior side, note prominent keel, × 120, *Yangtzeplacognathus crassus* Zone, sample Öl87-2, Gillberga; (AK) LO 10139, Sa element, posterior side, × 80, same sample as (AJ).

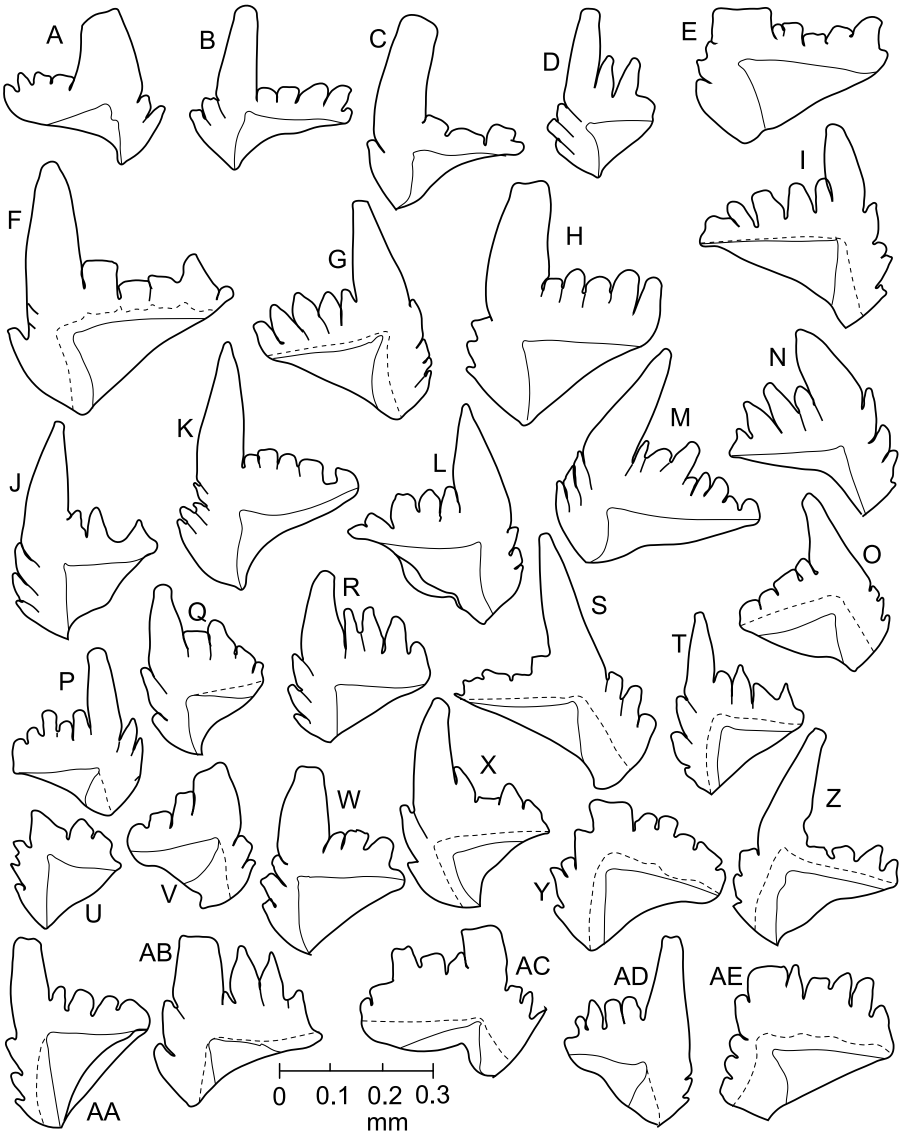

Figure 10 Camera lucida drawings of P elements of *Microzarkodina ozarkodella*-type; thin line = outline of basal cavity, broken line = limit of white matter (where visible). (A–E) *Microzarkodina* cf. *M. hagetiana* (early, probable homeomorphs of *Microzarkodina ozarkodella*): (A) LO 10048, same element as in Fig. 9Z. *Yangtzeplacognathus crassus* Zone, sample HK88-2, Hällekis; (B) LO 10049, same element as in Fig. 9X, same sample as (A); (C) LO 10050, *E. pseudoplanus–M. hagetiana* Subzone, sample H13, Kårgärde; (D) LO 10051, same sample as (C); (E) LO 10052, same element as in Fig. 9Y, same sample as (C). (F–AE) *Microzarkodina ozarkodella* Lindström, 1971, from the *Eoplacognathus pseudoplanus–M. ozarkodella* Subzone: (F) LO 10053, same element as in Fig. 11C, sample H9, Kårgärde; (G) LO 10054, sample H10, Kårgärde; (H) LO 10055, same sample as (F); (I) LO 10056, same element as in Fig. 11H, same sample as (F); (J) LO 10057, same element as in Fig. 11N, sample Öl87-6, Gillberga; (K) LO 10058, same element as in Fig. 11B, same sample as (J); (L) LO 10059, same element as in Fig. 11M, same sample as (J); (M) LO 10060, same element as in Fig. 11A, same sample as (J); (N) LO 10061, same element as in Fig. 11G, same sample as (J); (O) LO 10062, same element as in Fig. 11E, sample H8, Kårgärde; (P) LO 10063, same sample as (O); (Q) LO 10064, same sample as (O); (R) LO 10065, same element as in Fig. 11K, same sample as (O); (S) LO 10066, same element as in Fig. 11L, sample H6, Kårgärde; (T) LO 10067, same sample as (S); (U) LO 10068, sample J70-17, Lunne; (V) LO 10069, same sample as (U); (W) LO 10070, same element as in Fig. 11F, sample J70-18, Lunne; (X) LO 10071, sample J70-11, Lunne; (Y) LO 10072, same element as in Fig. 11D, sample HK89-4, Hällekis; (Z) LO 10073, sample J74-36, Gammalbodberget; (AA) LO 10074, same sample as (Y); (AB) LO 10075, same sample as (Y); (AC) LO 10076, same sample as (Y); (AD) LO 10077, same element as in Fig. 11J, sample H4, Kårgärde; (AE) LO 10078, same sample as (AD).

2000b *Microzarkodina ozarkodella* Lindström, 1971; Löfgren, figs. 6N, O, 11C.
2001 *Microzarkodina ozarkodella* Lindström, 1971; Rasmussen, p. 91, pl. 9:1–6.
2004 *Microzarkodina ozarkodella* Lindström; Löfgren, fig. 12 h–n.

Description. ***P elements.*** The anterior denticles number up to five in mature specimens. In stratigraphically older collections the maximum number is lower (see Fig. 12). The anterior denticles occur either along the anterior edge (Pa) or on an extended anterior process that can be deflected to a greater or lesser degree (Pb). The posterior process carries up to eight denticles.

Sa elements. There is an anterior keel, particularly prominent on the base. The lateral processes bear up to eight denticles each. The posterior process lacks denticles. The lateral processes diverge at less than 90°.

Sb$_1$ elements. The anterior process or keel lacks denticles. The anterior-lateral process carries 3–4, often long, denticles,

Figure 11 SEM micrographs of *Microzarkodina ozarkodella* Lindström, 1971; all elements are from the *Eoplacognathus pseudoplanus–Microzarkodina ozarkodella* Subzone: (A) LO 10060, P element, × 80, same element as in Fig. 10M, sample Öl87-6, Gillberga; (B) LO 10058, P element, × 80, same element as in Fig. 10K, same sample as (A); (C) LO 10053, P element, note crowded anterior denticles, × 70, same element as in Fig. 10F, sample DLK86-H9, Kårgärde; (D) LO 10072, P element, × 90, same element as in Fig. 10Y, sample HK89-4, Hällekis; (E) LO 10062, P element, × 90, same element as in Fig. 10O, sample DLK86-H8, Kårgärde; (F) LO 10070, P element, × 100, same element as in Fig. 10W, sample J70-18, Lunne; (G) LO 10061, P element, × 90, same element as in Fig. 10N, same sample as (A); (H) LO 10056, P element, × 70, same element as in Fig. 10I, same sample as (C); (I) LO 10140, P element, × 100, sample J74-37, Gammalbodberget; (J) LO 10077, P element, × 100, same element as in Fig. 10AD, sample DLK86-H4, Kårgärde; (K) LO 10065, P element, × 130, same element as in Fig. 10R, same sample as (E); (L) LO 10066, P element, × 80, same element as in Fig. 10S, sample DLK86-H6, Kårgärde; (M) LO 10059, P element, × 90, same element as in Fig. 10L, same sample as (A); (N) LO 10057, P element, × 80, same element as in Fig. 10J, same sample as (A); (O) LO 10141, Sb_1 element, × 100, same sample as (A); (P) LO 10142, Sb_1 element, × 130, same sample as (A); (Q) LO 10143, Sc element, × 70, same sample as (A); (R) LO 10144, Sb_1 element, broken posterior process, × 110, same sample as (A); (S) LO 10145, M element, × 90, same sample as (E); (T) LO 10146, M element, × 80, same sample as (E); (U) LO 10147, Sb_2 element, × 100, same sample as (A); (V) LO 10148, Sa element, × 65, same sample as (A); (W) LO 10149, Sb_2 element, × 100, same sample as (A).

the posterior-lateral process up to five denticles and the long posterior process up to eight denticles. Of the older species only *M. hagetiana* is provided with this kind of posterior process.

***Sb_2* elements.** The anterior and posterior processes lack denticulation. The anterior-lateral process is the longest, with up to ten denticles. The posterior-lateral process has up to four denticles.

***Sc* elements.** The cusp is erect or often recurved, and the posterior process carries up to 14 confluent and posteriorly inclined denticles.

***M* elements.** The cusp is thin, carinate and of about the same length as the base.

Geographic and stratigraphic distribution. Reported from all over Baltoscandia, Poland and from southern China, from the base of the *Microzarkodina ozarkodella* Subzone of the *Eoplacognathus pseudoplanus* Zone into the late Middle Ordovician (Poland).

Material. 15,293 elements in all: 15,119 from Sweden and 174 from Estonia.

4. Elements and element types in *Microzarkodina*

The *Microzarkodina* apparatus is basically septimembrate, with morphologically distinct M, Sa, Sb_1, Sb_2 and Sc elements,

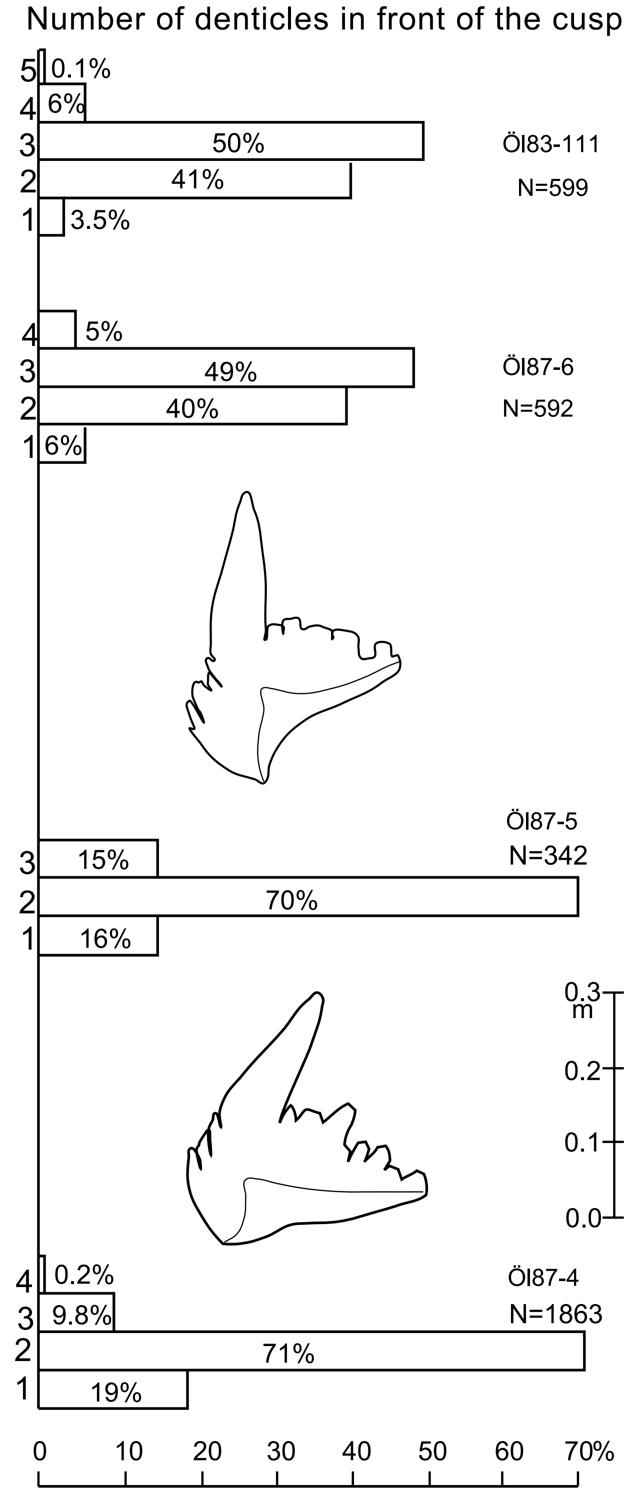

Figure 12 Successively increasing number of denticles anterior to the cusp in P elements of *Microzarkodina ozarkodella* Lindström, 1971 in samples from the upper part of the Gillberga quarry. The lowermost of the four samples used for the calculations, Öl87-4, derives from the base of the *Eoplacognathus pseudoplanus–M. ozarkodella* Subzone, while the uppermost one, sample Öl83-111, was collected c. 0·7 m from the top of the quarry section which ends within the same subzone. The investigated interval measures *c.* 1·6 m in all (see scale to the lower right). N=number of P elements in the sample for which it was possible to count the anterior denticles. The two conodont sketches depict the same elements as in Fig. 11A (below) and 11B (above); both elements are from sample Öl87-6.

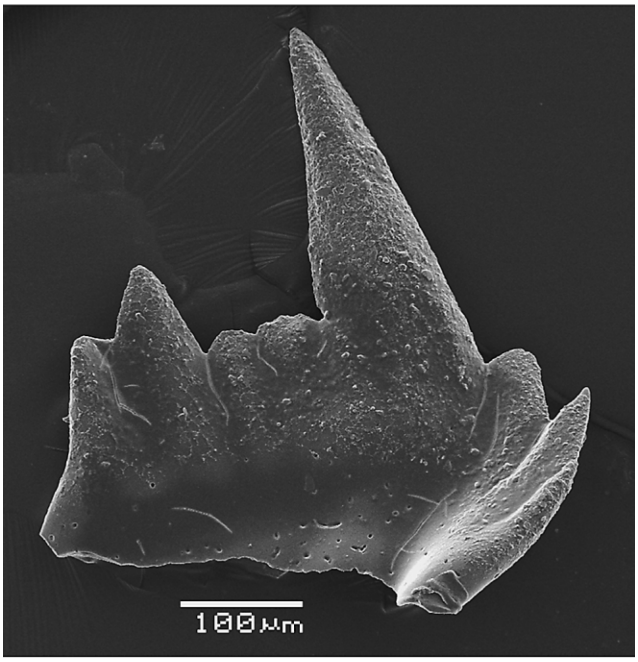

Figure 13 Aberrant Pb element of *Microzarkodina* cf. *M. flabellum* with multiple anterior denticles on an anterior process. Specimen LO 10176 from sample Vg05 B12-4, Brattefors N, lower *Baltoniodus triangularis* Zone.

as well as virtually identical Pa and Pb elements. As will be demonstrated below, the proportion of P elements in the apparatus compares with that in *Baltoniodus* and other septimembrate apparatuses where there are two P element types.

P elements. These are the major element types used to distinguish between species of *Microzarkodina.* The holotype of *M. flabellum*, the type species of the genus, is a P element (see Lindström 1955, pl. 6, figs. 23–24). In his description of the element type, Lindström (1955, p. 587) noted that the anterior denticle is deflected laterally in some specimens. This has also been observed in later species of the genus, and may be the best way to distinguish Pb elements (anterior denticle clearly deflected) from Pa elements (anterior denticle not deflected or only slightly so). The difference is, however, often slight.

Sweet (1988, p. 77) tentatively regarded the single anterior denticle in P elements of *M. flabellum* as part of a short, anteriorly deflected lateral process, and consequently took the anterior margin to be rounded and adenticulate. Figure 13 shows how an aberrant Pb element of *Microzarkodina* cf. *M. flabellum* from the Lower–Middle Ordovician boundary beds at Brattefors, Västergötland, has developed multiple denticles on an anterior process consisting of the strongly deflected anterior margin. This, together with detailed observations on ordinary elements, strengthens the assumption that the denticulation in P elements of *Microzarkodina* is developed on an anterior process.

The differences between P elements in the different species of *Microzarkodina* (see Fig. 14) are pronounced mainly in denticle/cusp height ratio, degree of reclination of the cusp, depth of the basal cavity and number and development of the anterior denticles.

In *M. russica* n. sp. and at least early *M. flabellum* (Fig. 5), a serrated anterior margin is not infrequently observed in mature P specimens. The denticles closest to the cusp represent anterior denticles from older growth stages that have not been covered and obliterated by successive lamellae. In *M. parva*, overgrown denticles and cusps with serrated anterior edges are rarer than in the older species. It is evident that there is still some kind of growth problem in mature and gerontic P elements of *M. parva*, since many specimens have become malformed during the growth process, so that the morphological variation is extreme (see, for instance, Fig. 6).

Two species, *M. bella* and *M. hagetiana*, were derived from *M. parva. Microzarkodina bella* is geographically restricted, its elements are generally small and neither serration nor multiple denticulation has been observed anteriorly in P elements. In *M. hagetiana*, the P elements have deeper basal cavities, with the tip of the basal cavity often directed forwards (Fig. 7A–F, J–K), as in its successor *M. ozarkodella* (Fig. 10F–AE). In *M. hagetiana*, multiple anterior denticulation is clearly evident in some P elements (10A, B, D, E). These specimens appear to belong to animals in a population where the great majority had P elements with only one anterior denticle.

At the base of the *E. pseudoplanus–M. ozarkodella* Subzone there is a rapid increase in the proportion of the number of P elements of *Microzarkodina* with more than one anterior denticle. Moreover, the number of anterior denticles in the elements increases gradually through time. The boundary between late *M. hagetiana* and *M. ozarkodella* must therefore be statistical; it is taken to be where the majority of P elements have more than one anterior denticle. Single isolated P elements can be difficult to determine within the boundary interval, and biostratigraphic interpretations based on only a few elements should be treated with caution. As shown in Figure 12, later representatives of *M. ozarkodella* can have P elements with up to five anterior denticles.

Sa elements. The Sa element of *M. flabellum* has a short, adenticulate posterior process, two denticulate anterior lateral processes, but no anterior process or keel. *Microzarkodina russica* n. sp. also lacks an anterior keel, but rarely *M. parva* has a rudimentary anterior keel, particularly in juveniles. Stratigraphically younger representatives (*Microzarkodina bella*, *M. hagetiana* and *M. ozarkodella*) have developed an anterior keel. Sa elements of *Microzarkodina* also vary in the angle between the lateral processes. Seen in posterior view this angle is generally obtuse (up to *c.* 130°) in older *Microzarkodina* species and acute (sometimes less than 80°) in younger ones, although variation can be considerable even within a single population.

Sb elements. There are two kinds of Sb elements in the apparatus. Lindström (1955) described *Trichonodella irregularis*, which he later included in *Microzarkodina flabellum* (Lindström 1971, p. 58). These elements were referred to as 'a markedly asymmetrical trichonodelliform element with one big and three small processes', thereby describing elements of the kind represented by the type specimen of *T. irregularis*, but also those referred to as 'sannemannula' or tetraprioniodiform elements in the illustrations (Lindström 1971, pl. 1, fig. 11, fig. 20). In van Wamel's (1974, pp. 70–71, pl. 7, figs. 18–23) description of *M. flabellum* as well, these elements were separated and referred to as 'irregularis' and 'sannemannula' elements, respectively. In the *Treatise* (Clark *et al.* 1981) and Stouge & Bagnoli (1990) these element types were designated Sd and Sb, while Dzik (1991, p. 294) referred to them as pl and lo, both homologous with Sb elements in the *Oulodus* plan (cf. Dzik 1991, table 1, p. 279). The present authors prefer the latter homologisation and will use the designation Sb_1 (for 'oulodiforms') and Sb_2 (for 'tetraprioniodiforms').

In Sb_1 elements the posterior 'process' is adenticulate, or has only one to two denticles in stratigraphically older representatives. It is subparallel with the most posterior (longest) of the lateral processes. In the stratigraphically younger species *M. hagetiana* and *M. ozarkodella*, the posterior process is provided with many (up to eight) denticles. The most anterior (shortest) lateral process has a few, relatively long denticles. There is an anterior keel, but no anterior process.

In Sb_2 elements the adenticulate posterior 'process' is also directed backwards. It is subparallel with the most posterior (shortest) lateral process, which sometimes has a few confluent denticles. The posterior and posterior lateral processes are connected by a basal sheath. There is an adenticulate anterior process or keel in all species, except *M. russica* n. sp. The anterior lateral process is the longest process in this element type. The denticles are close together. This element type differs significantly only in *M. russica* n. sp.

Sc elements. These elements are almost identical in all the *Microzarkodina* species described. There is a faint carina on the outer side of the cusp and a distincter carina on the inner side. The long posterior process is straight or slightly arched and has up to 20 denticles inclined towards the posterior end. The cusp is often proclined, erect to reclined in the two oldest species, but often somewhat recurved in the youngest ones.

M elements. The M elements of *Microzarkodina* are fragile, and the long posterior extension of the oral margin in particular is almost always broken, though it is possible to distinguish subtle differences between M elements of different *Microzarkodina* species. In stratigraphically younger representatives, the lateral carinae on the cusp tend to be better developed, and the distal part of the base is longer relative to the cusp and more often preserved.

5. Mosaic evolution in *Microzarkodina*?

The evolution of morphological details in the different element types of *Microzarkodina* can be described as being gradually progressive, for instance the development of anterior multiple denticles in P elements, particularly in *M. ozarkodella* (see Fig 12). The entire evolution in the succession of species, however, must be labelled mosaic.

While the anterior side of the Sa element is completely smooth in *M. russica* n. sp. and *M. flabellum*, and there is only a rudimentary anterior keel in *M. parva*, the three species *M. bella*, *M. hagetiana* and *M. ozarkodella* are keeled anteriorly. This is evident in particular in *M. bella*, whose elements generally are small and have a juvenile appearance even when other morphological details indicate that they are mature. A few juvenile Sa elements of *M. flabellum* have a faint anterior keel.

In *M. russica* n. sp., *M. flabellum*, *M. parva* and *M. bella*, the posterior process of the Sb_1 element is adenticulate or has a single denticle. In *M. hagetiana* and *M. ozarkodella*, the posterior process can have up to eight denticles, which is the best criterion for regarding *M. hagetiana* as the closest ancestor of *M. ozarkodella.*

Microzarkodina bella is provided with small elements with a juvenile appearance, and could be derived from *M. parva* through paedomorphosis (the retention of juvenile characters in adults). *Microzarkodina hagetiana* was probably also derived from *M. parva*, but by a more complicated process whereby some element types were changed by paedomorphosis and some by the opposite process, peramorphosis (which implies evolutionary trends carried beyond that in the ancestral adult). Such heterochronic processes can explain how species in a lineage, such as these, could evolve more or less sympatrically.

Microzarkodina ozarkodella may have evolved from *M. hagetiana* largely by peramorphosis. The two species share considerable similarity of all element types. In *M. ozarkodella*, even juvenile P elements in most cases have several anterior denticles. In *M. hagetiana*, only mature elements rarely carry multiple anterior denticles. If this progressed to earlier ontogenetic stages it would lead to successive stabilisation of the anterior denticulation and eventually an increase in the number of anterior denticles.

6. Numerical proportions of *Microzarkodina* elements

From observations of natural assemblages, it has been shown that the apparatus of ozarkodinids consisted of 15 elements: 2Pa, 2Pb, 1Sa, 4Sb, 4Sc and 2M (see, e.g., Purnell 1993a; Purnell & Donoghue 1997, 1998; Purnell *et al.* 2000). The same general arrangement and number of elements was also present in, e.g., the Ordovician *Paracordylodus gracilis* (see Tolmacheva & Purnell 2002) and in Carboniferous prioniodinids (Purnell 1993b). In the best-preserved prioniodontid, *Promissum pulchrum* Kovács–Endrödy from the Upper Ordovician of South Africa, the apparatus consisted of 19 elements: 2Pc and 2Pd elements in addition to elements that were presumably homologous with those of ozarkodinids. The *Promissum* apparatus is thus more complex than that of the ozarkodinids, and is also much larger, some elements attaining a length of 14 mm (Aldridge *et al.* 1995). If we are to judge from other types of prioniodontids, *Promissum* may be also unusual in the structure of the apparatus. The proportions between preserved isolated elements of Ordovician *Baltoniodus* indicates that there were twice as many Pb elements as Pa elements (see Stouge & Bagnoli 1990; Bagnoli & Stouge 1997; Rasmussen 2001, and Löfgren collections), and Löfgren & Zhang (2003) suggested that the apparatus of species of the platform-equipped genera *Lenodus* and *Eoplacognathus* comprised 17 elements: 2Pa, 4Pb, 1Sa, 4Sb, 4Sc and 2M.

No natural assemblages of *Microzarkodina* have been found, and the closest related taxa with preserved natural assemblage arrangement are *Paracordylodus gracilis* (see Tolmacheva & Purnell 2002), *Phragmodus* (see Repetski *et al.* 1998) and *Promissum pulchrum* (see Aldridge *et al.* 1995). It could be misleading, however, to uncritically regard the element arrangement in any of these taxa as a plesiomorphic model for other Ordovician conodonts, since separate morphologies could have been adopted to different modes of life.

Lindström (1971) provided the first statistical data on the reconstruction of the *Microzarkodina* apparatus. For the 730 elements of *M. flabellum* investigated, he suggested a ratio of 2:1 for P to Sc elements and also of 2:1 for P to Sa+Sb elements. Marsal & Lindström (1972) amplified the statistical method and their calculations suggested a ratio of 2:1:1:1 for P:Sb:Sa:M. Marsal & Lindström (1972) as well as Lindström (1984, p. 37) stressed that these proportions were unlike those to be expected in the animals themselves. We know for instance from experience that many samples are biased towards P elements against all other types because of size differences. Although there are fallacies in interpreting the 'true' proportions of elements from element proportions in samples (for a recent review of this, see Purnell & Donoghue 2005), carefully selected samples can be useful. Such statistics can at least give an indication of changes in proportions between element types in specific lineages (e.g. in *Drepanoistodus*, cf. Lindström 1971, pp. 42–43; Löfgren 1978, p. 55). Löfgren (1978, p. 62) found that the ratio P: (Sa+Sb_1+Sb_2):M:Sc was approximately 5:3:3:1 in *Microzarkodina flabellum* and 4:2:2:1 in *M. ozarkodella.*

The present authors have compared these ratios with those from a number of localities (see Localities and material), using ten samples containing *M. flabellum* from Jämtland, Dalarna, Finngrundet and Öland. The samples comprised 6,396 *Microzarkodina* elements in all; the smallest sample consisted of 145 elements. The best ratio for P:Sa:Sb:Sc:M of whole numbers to fit all the samples was 4:1:2:2:2, but some of the samples, particularly from the upper part of the interval with *M. flabellum*, had more M elements than this, indicating that the number of this element type might have doubled in some populations or parts of populations.

Thirteen samples containing *M. parva* were then investigated (17,718 *Microzarkodina* elements in all, the smallest sample having 135 elements). As in the faunas from the upper range of *M. flabellum*, the oldest *M. parva* faunas had a ratio of 4:1:2:2:2 for P:Sa:Sb:Sc:M, although the previously mentioned surplus of M elements remained constant, indicating that M elements were more numerous in some populations or parts of populations. Close to the levels where *M. hagetiana* Stouge & Bagnoli, 1990 first appears, populations of *M. parva* from Öland and possibly also from Dalarna show a definite increase in M elements, so that the suggested ratio becomes 8:1:2:4:8.

Within the interval of *M. hagetiana*, the ratio for six samples from Öland, Västergötland and Dalarna has been calculated (1,560 *Microzarkodina* elements in all, the smallest sample having 152 elements). The suggested ratio is 8:1:2:2:8 or 8:1:2:2:4, possibly indicating that Sc elements had become less numerous than previously. In a few samples with *M. bella* from Öland, the proportions are similar. Finally, in the interval with *M. ozarkodella*, the calculations were based on seven samples from Öland, Västergötland and Dalarna (11,394 *Microzarkodina* elements in all, the smallest sample having 109 elements). For this interval, too, a ratio of 8:1:2:2:4 or 8:1:2:2:8 is suggested. The possible changes in ratios between the different element types thus seem to have taken place within rather than between species of *Microzarkodina*, and thus do not appear to be associated with morphological change in the elements.

The Sb elements in the samples are consistently twice as common as Sa elements. The Sa element is unpaired in all reconstructions and natural assemblages seen. If the proportions between Sa and Sb elements were natural in the picked samples, this would indicate that each individual had one pair of Sb elements. Since there are two kinds of Sb elements, *viz.* Sb_1 and Sb_2, both with sinistral and dextral versions, this could imply dimorphism. A more probable explanation is that the rather large Sa elements may less easily get broken than Sb elements and thus be considerably overrepresented.

In the absence of natural assemblages, the above calculations provide the basis for reconstructing the original proportions of elements in *Microzarkodina.* Assuming that the large P elements are generally overrepresented and the Sb elements underrepresented, it can be concluded that the most reasonable original proportions were: 4P:1Sa:4Sb:4Sc:4M, 17 elements in all. If, however, for some reason, the M elements are also generally overrepresented, there may have been only one pair of M elements (as in all known natural assemblages) and we thus arrive at the interesting figure of 15 elements, the same number and the same relative proportions of elements as in ozarkodinid and many other apparatuses: 4P:1Sa:4Sb:4Sc:2M (Purnell & Donoghue 1997, 1998; Donoghue *et al.* 2008).

The 'ozarkodiniform' elements (e.g., Pa and Pb elements in *Microzarkodina*, Pb and some Pa elements in ozarkodinids) presumably had a shearing function in food processing. Jeppsson (1979) compared these elements with analogous shark's teeth and assumed that they had had a similar function, and Purnell (1995) found microwear in the form of fine, parallel striations on the surface of one such conodont element, probably caused by a shearing action. As with comparable microwear in mammals, these striations indicate a macrophagous diet (Purnell 1999), so at least those conodont animals that were equipped with this kind of element were probably predators or scavengers or both.

7. Biogeography and ecology

In Baltoscandia, *Microzarkodina* generally seems to have thrived in fairly shallow waters (Löfgren 2003, 2004). *Microzarkodina flabellum* is also present (together with *Periodon* and graptolites) in the Huanghuachang section in Yichang, southern China (Wang *et al.* 2005). Representatives of later species of *Microzarkodina* are rare in the platform seas of Laurentia (Ethington & Clark 1982, p. 54; Ross *et al.* 1997, p. 162, fig. 4) and Australia (Cooper 1981, p. 154, pl. 28, figs. 2–4). They occur, but much less commonly than in Baltoscandia in, e.g., southern China (An *et al.* 1985; An 1987; Ni & Li 1987; Zhang 1998b), where the epicontinental sea was only slightly deeper than in Baltoscandia (Chen & Lindström 1991).

Periodon, on the contrary, is a classic example of an indicator of colder/deeper water (cf. Barnes & Fåhræus 1975; Lindström 1976; Bergström & Carnes 1976; Pohler *et al.* 1987; Bagnoli & Stouge 1991). A predominance of *Periodon* should consequently be expected to occur in deeper water than the *Microzarkodina* optimum.

Microzarkodina russica n. sp. inhabited the Baltoscandian basin during a period of water high stand that was followed almost immediately by regression and a period of nondeposition at the base of the Volkhov Stage (Dronov & Holmer 1999). This led to its restricted distribution in the basin, since sediments from that time are not widely preserved. On the other hand, the environmental changes may have forced the process of evolution and led to the appearance of *M. flabellum.*

In the St Petersburg area, the shallow-water sandy limestone of the upper *Oepikodus evae* Zone yields a conodont assemblage consisting of more than a third of elements of *Microzarkodina russica* n. sp. *Periodon* is absent at this stratigraphic level, whereas it is abundant in the uppermost limestone beds (deposited in the deepest water) of the zone, where *M. russica* n. sp. is absent. The relatively shallow-water glauconitic limestones of the *Baltoniodus navis* Zone of the Volkhov Formation in the St Petersburg area contain abundant *M. flabellum*, whereas the same samples yield only a few *Periodon* elements (Tolmacheva 2001).

A series of 65 samples from different levels in the Gillberga quarry, N Öland, have been investigated (Löfgren 2000b). The samples range from the upper *B. navis* Zone to the upper *E. pseudoplanus* Zone, and most levels can be judged to represent shallower water than their stratigraphic equivalents elsewhere in Sweden. *Microzarkodina* is present in 64 of the 65 samples, while *Periodon* occurs in only ten of these samples. All species of *Microzarkodina* have at most an abundance of *c.* 30%.

Samples from Estonia are generally taken to represent shallower environments than those from Öland. At Mäekalda in N Estonia (Viira *et al.* 2001) *Periodon flabellum* is found in the *O. evae* Zone, with a few occurrences in the lower *P. originalis* Zone as well. *Microzarkodina flabellum* and *M. parva* are fairly common at some levels, but *M. ozarkodella* is rare. In the Tamsalu drill-core from central Estonia (Sjöstrand 2003; Viira *et al.* 2006) there is a maximum of *c.* 13% of *P. flabellum* in the upper *O. evae* Zone; *Microzarkodina* is rare or lacking. Stouge (in Männik 1998) reported *Periodon* only from a level in the upper *O. evae* Zone in the Tartu drill-core from central Estonia, where it was succeeded by species of *Microzarkodina* that occurred consistently into the Kundan.

Three localities from the province of Närke (Gymninge, Lanna and Yxhult) in the main represent conditions comparable in depth with, or slightly deeper than, those found in Öland. The Lanna section (Löfgren 1995) includes beds ranging from the upper *O. evae* Zone to the lower *L. variabilis* Zone. *Microzarkodina* is present in 32 of the 36 samples within its range, and its relative abundance is comparable to that found in Öland. *Periodon* is only present in a third of the samples.

Finngrundet, a shoal in the Gulf of Bothnia at *c.* 60° N where a drill-core has been investigated (Löfgren 1985), has an exceptionally high abundance of *Microzarkodina.* Of the 77 samples investigated from the first occurrence of *M. flabellum* at 56·5 m to the top of the section, within the *E. pseudoplanus–M. ozarkodella* Subzone, only five lack elements of *Microzarkodina*, even though a number of samples yielded less than 100 conodont elements in all. Most species of *Microzarkodina* have relative abundance values like those from Öland.

The *Microzarkodina*-rich sequence at Finngrundet coincides with a dearth of *Periodon.* Only 12 of the 77 samples within the range of *Microzarkodina* yielded *Periodon*, most of the occurrences being in the lower part of the sequence. Below the first occurrence of *Microzarkodina*, *Periodon* is more abundant. In Västergötland, environments representing deeper water are preserved. *Microzarkodina* is about as abundant as in Öland, but *Periodon* is much commoner, being present in eight of 15 samples from Hällekis, eight of 13 samples from Gullhögen, and in eight of 12 samples from Orreholmen. *Microzarkodina* was found in all samples within its range from the three sections.

In the three sections from Dalarna (Leskusänget, Rävanäs and Kårgärde) the relative abundance values for *Microzarkodina* and *Periodon* vary widely. *Microzarkodina* was retrieved from practically all samples. *Periodon* is present about as often in samples from Dalarna as from Västergötland, in three of seven samples from Leskusänget, three of six from Rävanäs and 22 of 26 from Kårgärde.

In samples from Jämtland (Löfgren 1978, 1993) *Periodon flabellum* abounds in the *O. evae* Zone (30% at Sommartjärnen), but at many other levels it is rare or lacking.

Both *Microzarkodina* and *Periodon* occur only sparsely in the *B. norrlandicus*, *L. variabilis*/*Y. crassus* and lower *E. pseudoplanus* zones in Jämtland. In the upper subzone of the *E. pseudoplanus* Zone, however, *Periodon* is much commoner, most of the samples yielding 12–76%. *Microzarkodina ozarkodella* does not appear so regularly in the samples of this subzone as it does in some other areas and is totally lacking from the Gärde samples.

Ozarkodinids such as *Polygnathus* have been designated shallow pelagic (e.g., Chatterton 1976) or nektobenthic. On the other hand, *Microzarkodina*'s closest relative in Baltoscandia, *Periodon*, is generally regarded as being typically planktic/pelagic (see, e.g., Lindström 1984; Bagnoli & Stouge 1991). The respective occurrence patterns could be most easily reconciled if we assume that *Periodon* was, indeed, pelagic and *Microzarkodina* trying out life as a nektobenthic predator.

8. Conclusions

Although the morphological variation within species of *Microzarkodina* is considerable, it is not difficult to distinguish between the species and to use them for biostratigraphical purposes (Fig. 14). *Microzarkodina russica* n. sp. occurs from the uppermost *Oepikodus evae* Zone into the lower *Baltoniodus triangularis* Zone, while *M. flabellum* or *M.* cf. *M. flabellum* prevails in the middle and upper *B. triangularis* Zone. *Microzarkodina flabellum* continues through the *Baltoniodus navis*

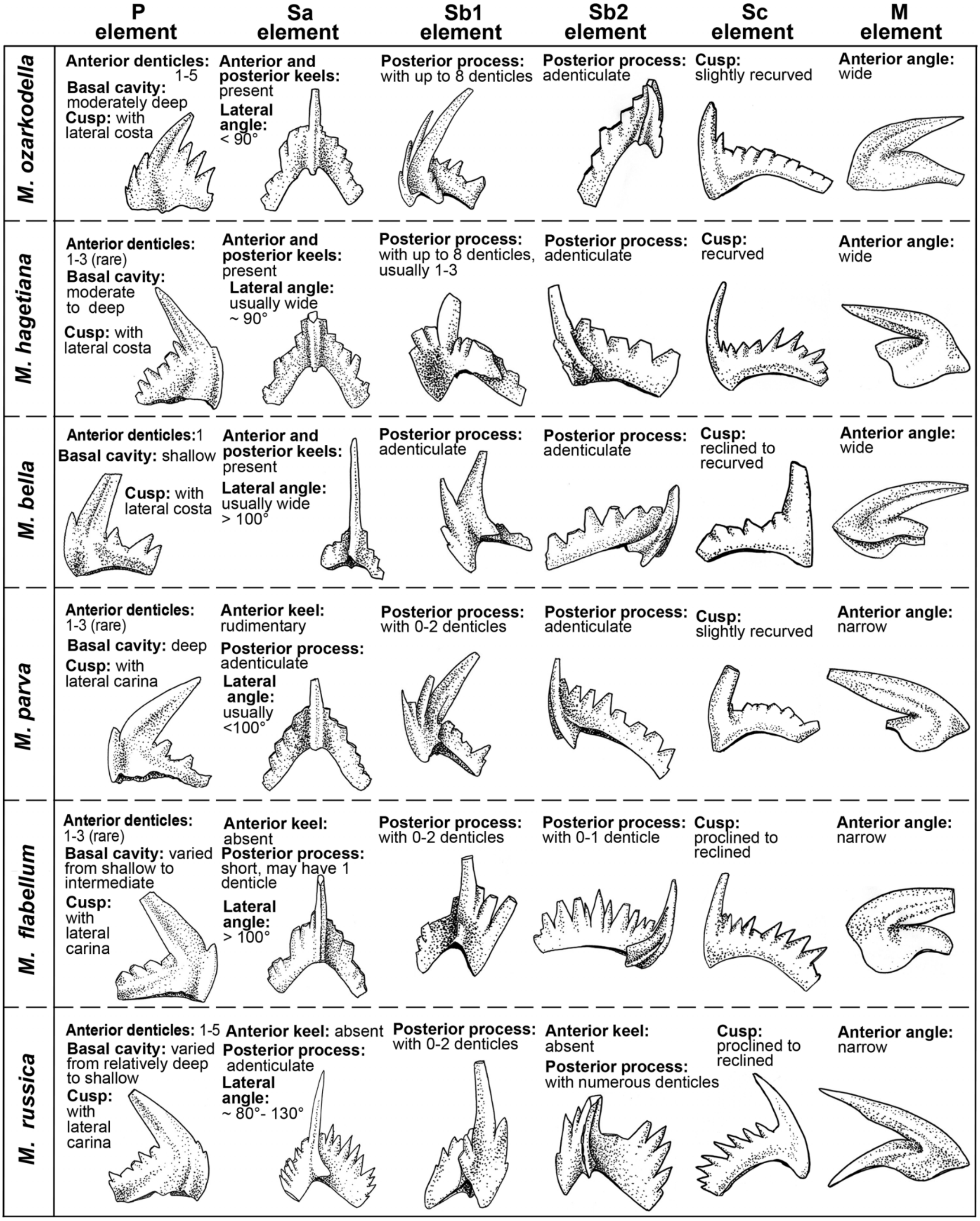

Figure 14 Similarities and differences in the six *Microzarkodina* species treated.

Zone into the lower middle *Paroistodus originalis* Zone. Most of the *P. originalis* Zone and the entire succeeding *Baltoniodus norrlandicus* Zone are characterised by *Microzarkodina parva.* In the upper part of the upper subzone of the *B. norrlandicus* Zone *Microzarkodina bella* appears, displacing *M. parva* in some areas, such as Öland. Within the lower half of the next zone, the *Lenodus variabilis* Zone, *Microzarkodina hagetiana* replaces *M. parva* in other areas, though it can also now and then occur in the same areas as, but rarely in the same samples as, *M. bella.* While *M. bella* disappears in the upper part of the succeeding *Y. crassus* Zone, *M. hagetiana* prevails throughout the lower subzone of the following *Eoplacognathus pseudoplanus* Zone. *Microzarkodina hagetiana* has a far wider geographical range than *M. bella*, and is the putative ancestor of *Microzarkodina ozarkodella* which characterises the upper subzone of the *E. pseudoplanus* Zone.

In addition to the characteristic P elements, some of the S element types can also be used to differentiate between the species. There are some clear trends: the Sa elements lack an anterior keel in *Microzarkodina russica* n. sp., *M. flabellum* and *M. parva*, but have an anterior keel or process in *M. bella*, *M. hagetiana* and *M. ozarkodella*. In *M. hagetiana* and *M. ozarkodella*, the Sb_1 element has a long denticulate posterior process, while in the other species the corresponding process generally lacks denticulation.

All six species treated here can have multiple anterior denticulation in mature P elements. Only in *M. ozarkodella* is this also common in juveniles and is present in practically all adults. If the elements are not well preserved, the basal cavity difficult to observe, and cusp and denticles broken, it is quite possible to make mistakes in the identification of the P elements of these species. Identification of *M. ozarkodella* and subsequent biostratigraphic conclusions should not be based on a few P specimens only. It is better to include co-occurring S elements for identifying this and other species.

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