Upper Wenlock to Lower Přídolí (Silurian) conodont biostratigraphy of Saaremaa, Estonia, and a correlation with Britain

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ABSTRACT – The closely related conodonts *Ozarkodina bohemica*, *O. snajdri* and *O. crispa* form a clade that provides useful biostratigraphical indices through the upper Silurian. Collections from boreholes and surface outcrops on Saaremaa and from a borehole at Kolka, Latvia, contain new morphotypes of *O. bohemica* and *O. crispa*. A new subspecies, *O. snajdri parasnajdri*, is also distinguished, occurring above *O. crispa* in the Kuressaare and lowermost Kaugatuma stages. Evidence from conodonts and other fossils, primarily chitinozoans, ostracods and ichthyoliths, can be used to correlate the upper Silurian succession of Saaremaa with those of the Welsh Borderland and Gotland, although some problems remain to be solved. The microfossil distribution suggests that there may be a major break at the base of the Ludlow Bone Bed Member at Ludlow, equivalent to the Kuressaare Formation on Saaremaa. *J. Micropalaeontol.* **17**(1): 33–50, April 1998.

INTRODUCTION

The study of the Silurian rocks of Estonia dates back to the last century, with the establishment of a Lower Palaeozoic stratigraphical scheme by Schmidt (1858). Details were added in the earlier part of this century, and more recently scientific investigations have been considerably advanced by a group of researchers at the Institute of Geology, Estonian Academy of Sciences, working under the leadership of D. Kaljo. Modern research has been greatly facilitated by the availability of numerous boreholes drilled by the Estonian Geological Survey, and a large number of papers and monographs has been published on Lower Palaeozoic palaeontology, stratigraphy and facies distribution. General summaries of the main results of this work may be found in volumes edited by Kaljo (1970, 1977), Kaljo & Klaamann (1982*a*,*b*) and Kaljo & H. Nestor (1990).

The current understanding of the Silurian stratigraphy of Estonia has been summarised by H. Nestor (1993) and the Wenlock-Přídolí correlation chart is shown in Fig. 1. The main stratigraphical units are regional chronostratigraphical stages, within which separate local lithostratigraphical units are distinguished in different parts of the Baltic basin (Bassett *et al.*, 1989). The local units reflect facies differences: Central Estonia and most of Saaremaa (Fig. 2) are dominated by shallow-water facies, whereas in South Estonia and on the Sörve Peninsula of southern Saaremaa deeper water shelf and outer shelf sediments prevail (H. Nestor & Einasto, 1977; Bassett *et al.*, 1989). Gradual shifts of the facies belts occurred during the evolution of the basin.

The present paper deals with the succession representing the late Wenlock to early Přídolí interval, embracing the Rootsiküla, Paadla, Kuressaare and Kaugatuma stages. In the absence of graptolites, the correlation of these stages and their representative formations with other areas is currently only approximate. The Rootsiküla Formation is considered to correspond to the late Wenlock Klinte Secundo Episode of Jeppsson *et al.* (1995), when very variable shallow-water sediments were deposited with characteristic cyclic alternation of limestones and primary dolomites. The total thickness is 25–32 m, and the sediments

display frequent discontinuity surfaces, mud cracks, ripple marks and trace fossils. Abundant stromatolites and oncolites occur, but the fauna is restricted to eurypterids, thelodonts and conodonts. The Paadla Formation is 26-32 m thick and consists of detrital biomorphous and biohermal stromatoporoid-coral limestones, dolomites and marls. A hiatus beneath the base, established from chitinozoan data, has been reported to eliminate almost all local equivalents of the lower Ludlow Gorstian Stage in parts of the region (Nestor, V., 1982, 1990). The Kuressaare Formation comprises a broadly similar range of lithologies to those found in the Paadla, but there is a rich fauna that includes ostracods and thelodonts, both of which have proved useful in local correlations. Published conodont data are currently limited, with more precision required on the ranges of key taxa (Kaljo, 1990). Indirect correlation suggests that the Kuressaare Stage is at the level of the formosus/balticus standard graptolite biozone (Kaljo, 1990).

In this contribution, we present details of the distribution of key conodont species in exposed sections and borehole cores on the island of Saaremaa, Estonia, and in a borehole from Kolka, Latvia (Fig. 2). The evolving species complex comprising taxa referred to *Ozarkodina bohemica* (Walliser), *O. snajdri* (Walliser) and *O. crispa* (Walliser) is of particular importance, and this group is given especial attention. The conodont data are used in conjunction with information from other fossils to assess the correlations between the Estonian succession and those of Britain and other areas.

BACKGROUND TO CONODONTS

The Ozarkodina bohemica lineage

The oldest reported member of this lineage is *O. bohemica* subsp. nov. of Aldridge (1985, pl. 3.3, figs 13 a, b), from the lowermost Wenlock of Whitfield, Gloucestershire, England. Above this, there is a gap in records until well into the Homerian Stage (upper Wenlock), where *O. bohemica bohemica* is widely distributed. Ludlow representatives of the same lineage include *O. snajdri*, which appears in the upper part of the Gorstian Stage, and *O. crispa*, of latest Ludlow age; these two were



Fig. 1. Current correlation chart of Wenlock-Přídolí stratigraphical units in Estonia and Latvia (from Nestor, 1993).

considered to be important fossils by Walliser (1964) in his conodont biozonation of the Silurian.

Early views of the relationships of these species varied. Walliser (1964) included O. bohemica as a subspecies of O. sagitta (Walliser) and commented that O. snajdri may be a descendant of O. excavata (Branson & Mehl). Pollock & Rexroad (1973) suggested that O. snajdri was ancestral to O. remscheidensis eosteinhornensis (Walliser), or that they shared common ancestry, and Mehrtens & Barnett (1976) also considered O. snajdri to be the ancestor of O. eosteinhornensis. Helfrich (1975) used morphological characteristics of Pa elements and multielement patterns to identify a 'Spathognathodus sagitta bohemicus Lineage' which incorporated taxa that would now be referred to as O. bohemica bohemica, O. bicornuta (Helfrich), O. snajdri, O. tillmani (Helfrich), O. crispa and, tentatively, his N. gen. et n. sp. (Helfrich, 1975, pl. 16, figs 1-3, 6). The latter has subsequently been described as Homeognathodus peniculus (Denkler & Harris, 1988). Helfrich (1975) recorded that all Pa elements of this lineage posess a basal cavity of similar form which closes before the posterior tip of the blade in stratigraphically older forms but extends further posteriorly relative to the posterior blade in successively younger species. A further characteristic of all the Pa elements, except that of O. bicornuta, is a tendency towards fusion of denticles above the basal cavity.

Aldridge & Schönlaub (1989) stated that O. crispa was a direct descendant of O. snajdri, and that the two occurred in

stratigraphical succession. Miller (1995) agreed that *O. crispa* originated in *O. snajdri*, but showed that intermediate forms occurred in the Welsh Borderland at stratigraphically higher levels than the first occurrence of *O. crispa*, so the relationship was not one of simple phyletic transition.

The succession of these conodonts on Saaremaa is comparable with that identified by Helfrich (1975). Ozarkodina bohemica bohemica, O. aff. bicornuta, O. snajdri snajdri and O. crispa are all recognized, and some specimens of O. crispa are transitional to O. tillmani. The youngest representatives, above the last occurrence of O. crispa, are clearly of snajdri affinities and are here referred to as O. snajdri parasnajdri subsp. nov.

Previous records of O. snajdri and O. crispa

The holotype of *O. snajdri* is from Muslovka Quarry, Bohemia, a few metres below the base of the *ultimus* graptolite biozone, while that of *O. crispa* is from Santa Creu, Spain (Walliser, 1964). In his conodont biozonation, Walliser (1964) included a '*crispus* zone' in the uppermost Ludlow, and a '*snajdri*-Horizon' within the upper part of the middle/upper Ludlow *siluricus* zone; *O. crispa* was represented in samples from his reference section at Cellon in the Carnic Alps, whereas *O. snajdri* was not.

Subsequent records produced some uncertainties about the ranges of *O. snajdri*, *O. crispa* and the index taxon of the zone succeeding the 'crispus zone', *O. r. eosteinhornensis*. Fåhraeus (1969) reported the Pa element of *O. crispa* on Gotland in strata above *O. r. eosteinhornensis*, leading Walliser (1971) to question



Fig. 2. Location map of outcrops (triangles) and boreholes (circles) on Saaremaa and northernmost Latvia.

whether the 'crispus zone' lay within the 'eosteinhornensis zone' or whether the two overlapped. In fact, the specimen illustrated by Fåhraeus (1969, pl. 2, figs 13, 14) may belong to O. snajdri, although subsequent work has resulted in records of O. crispa and representatives of the steinhornensis group in association on Gotland (Jeppsson, 1983; Jeppsson et al., 1994) An association of O. snajdri with specimens referred to as primitive O. r. eosteinhornensis was reported by Rexroad & Craig (1971) in the Bainbridge Formation of Lithium, Missouri, and the two taxa were also recorded together in the Kokomo Limestone Member of the Salina Formation in north-central Indiana by Pollock & Rexroad (1973). The specimens illustrated by Pollock & Rexroad (1973, pl. 1, figs 30-34), however, show several characteristics of the Pa element of O. crispa and the specific assignment is equivocal. An overlap of the ranges of O. crispa and specimens referred to O. r. eosteinhornensis in North America was also found by Helfrich (1975) in the Central Appalachians, while Denkler & Harris (1988) reported that the range of O. snajdri in the same region began below that of O. crispa and terminated above it.

In Australia, De Deckker (1976) found some overlap of the ranges of *O. snajdri* and *O. crispa* in the Kildrummie Formation of New South Wales, and was the first to suggest that the range of *O. snajdri* might be longer than previously thought. He also considered a second possibility that the intraspecific variation of Pa elements of *O. crispa* may include specimens of similar

morphology to *O. snajdri*. However, his specimens are rather atypical, and resemble those described by Link & Druce (1972, pl. 9, figs 22–28) from the Yass Basin, New South Wales as *Spathognathodus* cf. *S. ranuliformis* Walliser, a species that is now assigned to the genus *Kockelella*.

In Europe, there are records of overlap between O. snajdri and O. r. eosteinhornensis s. l. in sections near Graz, Austria (Ebner, 1976) and in the uppermost Kopanina Formation of Pozarech Quarry, Bohemia (Mehrtens & Barnett, 1976). Feist & Schönlaub (1974) found O. crispa, O. r. eosteinhornensis s. l. and Pedavis latialatus (Walliser) together in the Montagne Noire, southern France, and Chlupác et al. (1980) demonstrated the overlap of O. crispa and O. r. eosteinhornensis s. l. in the Muslovka Quarry, Bohemia, leading to a proposal to incorporate a crispa subzone within the lower part of an extended eosteinhornensis zone. Chlupác et al. (1980) also showed an overlap in the ranges of O. snaidri and O. crispa in Kolednik Quarry, Bohemia. In Britain, uppermost Ludlow conodont faunas include O. snajdri, O. cf. snajdri, O. crispa, O. cf. crispa, O. r. eosteinhornensis s. l. and O. remscheidensis baccata Miller & Aldridge (Miller, 1995; Miller & Aldridge, 1997). In two sections, at Woolhope and at Tite's Point, Miller (1995) found O. snajdri above O. crispa.

In summary, all possibilities of co-occurrence of *O. snajdri*, *O. crispa* and specimens referred to *O. r. eosteinhornensis* are known; all three may occur together or any pairing. Only in

Bohemia are they represented in clearly succeeding order, in the Muslovka and Kolednik quarries, and even here there is some overlap of the ranges.

SYSTEMATIC DESCRIPTIONS

Systematics are given here for members of the *O. bohemica* lineage, based on material from Saaremaa. As noted by Miller & Aldridge (1997), there is some inconsistency regarding the usage of subspecies and morphotype designations in conodont taxonomy. We have followed the principle of retaining subspecies designations for populations that are separated in space and/or time; for morphological variants that occur together in some samples we have used morphotypes. The exceptions are where we subdivide subspecies or exisiting morphotypes: even if different forms seem to be chronologically or geographically separated, we have designated them as morphotypes.

Order Ozarkodinida Dzik, 1976 Family Spathognathodontidae Hass, 1959 Genus Ozarkodina Branson & Mehl, 1933 Ozarkodina bohemica bohemica (Walliser, 1964)

- 1964 Spathognathodus sagitta bohemicus Walliser: 83, pl. 7, fig. 4, pl. 18, figs 23, 24.
- 1964 Ozarkodina edithae Walliser: 55, pl. 26, figs 12-18.
- 1967 Spathognathodus sagitta bohemicus Walliser; Austin & Bassett: 278, pl. 14, fig. 19.
- 1967 Spathognathodus cf. sagitta bohemicus Walliser; Austin & Bassett: 279, pl. 14, fig. 20.
- ?1967 Spathognathodus sagitta bohemicus Walliser; Flajs: pl. 4, fig. 7.
- 1969 Spathognathodus sagitta bohemicus Walliser; Fåhraeus: pl. 2, figs 15, 16.
- 1975 Spathognathodus sagitta bohemicus Walliser; Helfrich: pl. 1, figs 2-4, 8, 12, 17, 20.
- 1975a Ozarkodina sagitta bohemica (Walliser); Aldridge: 327, pl. 47, fig. 21.
- 1975b Ozarkodina sagitta bohemica (Walliser); Aldridge: pl. 2, figs 18, 19.
- 1976 Ozarkodina sagitta bohemica (Walliser); Barrick & Klapper: 81, pl. 4, figs 1-7, 10, 12.
- 1981 Ozarkodina sagitta bohemica (Walliser); Aldridge, Dorning & Siveter: pl. 2.3, figs 1, 3.
- 1982a Spathognathodus sagitta bohemica Walliser; Viira: text-fig. 5.4, figs 31, 34.
- 1984 Ozarkodina sagitta bohemica (Walliser); Kozur: pl. 2, figs 4, 5.

- 1985 Ozarkodina sagitta bohemica (Walliser); Balogh & Kozur: pl. 2, fig. 5.
- 1985 *Ozarkodina bohemica bohemica* (Walliser); Aldridge: pl. 3.4, fig. 3.
- 1985 Spathognathodus sagitta bohemicus Walliser; Qiu: 32, pl. 2, figs 1-4.
- 1985 Spathognathodus sagitta bohemicus Walliser; Yu: 26, pl. 2, figs 1, 2, pl. 3, figs 1-3, 6, 11.
- 1987 Ozarkodina sagitta bohemica (Walliser); An: 200, pl. 32, figs 21, 22.
- 1990 Ozarkodina bohemica (Walliser); Kleffner: fig. 3, no. 20.
- 1990 Ozarkodina tillmani (Helfrich); Kleffner: fig. 3, nos 21, 22.
- 1993 Ozarkodina bohemica (Walliser), Morphotype 1; Schönlaub (In Kríz et al.): 829, pl. 1, figs 1, 3, 4.
- ?1993 Ozarkodina bohemica (Walliser), Morphotype 2; Schönlaub (In Kríz et al.): 829, pl. 1, fig. 9.
- 1993 Ozarkodina bohemica (Walliser), Morphotype 3; Schönlaub (In Kríz et al.): 829, pl. 1, figs 10-14.

Diagnosis. See Aldridge (1985, p. 88).

Remarks. Three morphotypes of *O. b. bohemica* were distinguished by Schönlaub (*In* Kríz *et al.*, 1993) and numbered 1–3; morphotype 1 has low posterior denticles, similar to *O. sagitta*, whereas morphotype 3 has an abrupt posterior termination and a widely flaring basal cavity. Morphotype 2 is very distinct, with an ornament of ridges of fused denticles on the basal cup. Schönlaub did not mention the specimens originally described by Walliser (1964), with a widely flaring basal cavity extending to the posterior tip, but they appear to be closest to morphotype 3. Because we cannot relate Walliser's specimens or ours to the Bohemian morphotypes we apply a different notation here. The type specimen and associates represent the α morph. Those from Saaremaa have a less flared cavity which does not extend right to the posterior tip and belong to the β morph.

Ozarkodina bohemica bohemica β morph (Pl. 1, figs 1–15)

Description. Pa element: blade long, with 14–20 denticles that are largest posteriorly. Anterior edge gently convex, posterior edge upright. Basal cavity situated beneath posterior part of blade, terminating short of posterior tip. Small specimens shorter and relatively higher than large specimens. Large specimens usually with fused denticles above basal cavity and a longitudinal ledge in the lower third of the blade. All specimens with white matter, deep above basal cavity and narrowing anteriorly and posteriorly so that extreme denticles may be hyaline.

Occurrence on Saaremaa. Rootsiküla Stage: Vesiku borehole

Explanation of Plate 1

Figured specimens on all plates are Pa elements; they are deposited in the Institute of Geology, Estonian Academy of Sciences, Tallinn. **figs 1–15**. *Ozarkodina bohemica (Walliser 1964)* β morph, Rootsiküla Formation. figs 1, 9, 11, 15; lateral views, Cn 1454–Cn 1457, ×120, ×50, ×80, ×65, Viita Beds, Ohesaare borehole, 145.55 m. figs 2, 3; lateral and aboral views, Cn 1458, ×50, Viita Beds, Ohesaare borehole, 142.25 m. figs 4–6, 10; lateral, lower lateral, aboral and oral views, Cn 1459, ×50, ×135, Cn 1460, x50, Viita Beds, Kaugatuma borehole, 100.25 m. figs 7, 8; lateral and aboral views, Cn 1461, ×50, ×85, Viita Beds, Ohesaare borehole, 144.05 m. fig. 12; lateral view, Cn 1462, ×55, Viita Beds, Vesiku borehole, 4.95 m. fig. 13; lateral view, Cn 1463, ×55, Viita Beds, Viita outcrop. fig. 14; lateral view, Cn 1464, ×70, Vesiku Beds, Kaugatuma borehole, 81.4 m. **figs 16–19**. *Ozarkodina* aff. *bicornuta* (Helfrich 1975). figs 16, 17; lateral views, Cn 1465, ×65, ×75, Soeginina Beds, Soeginina cliff, sample 3-87. fig. 18; lateral view, Cn 1467, ×85, lowermost Paadla Formation, Anikaitse outcrop, sample 4-76. fig. 19; lateral view, Cn 1468, ×80, Soeginina Beds, Soeginina Cliff, sample 2-87. figs 20, 21. *Ozarkodina snajdri* cf. *snajdri* (Walliser 1964). fig. 20; lateral view, Cn 1469, ×80, Torgu Formation, Ohesaare borehole, 113.35 m. fig. 21, lateral view, Cn 1470, ×75, Kuressaare Formation, Kolka borehole, 284.2 m.





Explanation of Plate 2

Figs 1–16, 19, 20. Ozarkodina crispa (Walliser 1964) α_2 morph. figs 1, 2; lateral and oral views, Cn 1471, ×70, Sauvere Beds, Kaugatuma borehole, 61.6 m. figs 3, 7, 8; lateral and aboral views, Cn 1472, Cn 1473, ×70, ×85, Kudjape Beds, Kolka borehole, 270.8 m. figs 4, 5; lateral and aboral views, Cn 1474, ×85, Sauvere Beds, Riksu borehole, 33.5 m. Fig. 6; lower lateral view, Cn 1475, ×75, Himmiste Beds, Kaugatuma borehole, 58.5 m. figs 9, 10; lateral and aboral views, Cn 1476, ×70, ×85, Sauvere Beds, Riksu borehole, 35.0 m. figs 11–16, 19, 20; lateral and aboral views, Cn 1477 – Cn 1480, ×65, ×85, ×70, ×90, Himmiste Beds, Karala outcrop. figs 17, 18, 21, 22. Ozarkodina crispa (Walliser 1964) α_3 morph; lateral and aboral views, Cn 1481 – Cn 1483, ×85, ×70, ×85, Himmiste Beds, Karala outcrop.

4.95 m, Sakla borehole 51.86–54.45 m, Kaugatuma borehole 81.4–100.25 m, Ohesaare borehole 142.25–157.2 m, Kolka borehole 362.3 m, Viita outcrop.

Material. Pa element: 44 specimens.

Ozarkodina aff. bicornuta (Helfrich, 1975) (Pl. 1, figs 16–19)

aff. 1975 Spathognathodus bicornutus Helfrich: pl. 1, figs 5-7, 11, 13-16, 18, pl. 2, figs 1, 4, 6, 16.

Description. Pa element: specimens small; blade rather high, denticles wide, usually 10–11 when not fused. Basal cavity beneath posterior part of blade, circular, not extending to posterior tip. Morphologically close to the smallest specimen illustrated by Helfrich (1975, pl. 1, fig. 5).

Remarks. The specimens illustrated by Helfrich (1975) are very variable, but most have a single high denticle at both ends of the blade; between these are 5-10 denticles which show no fusion on any of the figured specimens. The Estonian specimens have an enlarged posteriormost denticle, but the anterior denticle is not markedly different in size from its neighbours; the denticles above the cavity may be fused.

Occurrence. Uppermost Rootsiküla Stage: Soeginina samples 1–3, Anikaitse sampes 4, 8.

Material. Pa element: 9 specimens.

Ozarkodina crispa (Walliser, 1964)

- 1964 Spathognathodus crispus Walliser: 74, pl. 9, fig. 3, pl. 21, figs 7-13.
- ?1969 Spathognathodus crispus Walliser; Fåhraeus: pl. 2, figs 13, 14.
- 1971 Spathognathodus crispus Walliser; Bultynck & Pelhate: pl. 1, figs 19, 20.
- 1971 Spathognathodus crispus Walliser; Drygant: 782, figs 1-3.
- 1974 Spathognathodus crispus Walliser; Feist & Schönlaub: pl. 7, figs 8, 9, 11, 12, 14, 15.
- 1974 *Ozarkodina crispa* (Walliser); Klapper & Murphy: 33, pl. 8, fig. 10.
- 1975 Spathognathodus crispus Walliser; Helfrich: pl. 14, figs 1-4, 9, 14, 19, 21, 24, 27.
- 1977 Ozarkodina crispa (Walliser); Cooper: 188, pl. 16, figs 16, 17.
- 1980 Ozarkodina crispa (Walliser); Chlupác et al.: pl. 25, figs 12-15.
- 1980 Spathognathodus crispus Walliser; Wang: 374, pl. 1, figs 1-3, 14-16, 19-21, 24, 25, text-fig. 4.
- 1984 Ozarkodina crispa (Walliser); Kozur: pl. 4, fig. 4.
- 1984 Spathognathodus crispus Walliser; Drygant: 126, pl. 10, figs 12, 13.
- 1985 Ozarkodina crispa (Walliser); Balogh & Kozur: pl. 3, fig. 3.
- 1986 Spathognathodus crispus Walliser; Jiang et al.: pl. 4-4, fig. 9.
- 1987 Spathognathodus crispus Walliser; An: 202, pl. 34, figs 20, 21.
- 1988 *Ozarkodina snajdri crispa* (Walliser); Denkler & Harris: pl. 1, figs J, K.
- 1989 Ozarkodina crispa (Walliser); Walliser & Wang: 114, textfig. 1, pl. 1, figs 1-16.
- 1990 Ozarkodina aff. snajdri (Walliser); Männik & Viira: pl. 18, fig. 10.
- 1990 Ozarkodina crispa (Walliser) β morphotype; van den

Boogaard: 11, pl. 6, figs 2-7.

1994 Ozarkodina aff. snajdri crispa (Walliser); Viira: pl. 1, fig. 8. 1994 Ozarkodina snajdri (Walliser); Jeppsson et al.: fig. 4d. 1995 Ozarkodina crispa (Walliser); Miller: pl. 3, figs 1–2, 4-5. 1995 Ozarkodina cf. crispa (Walliser); Miller: pl. 3, figs 3, 6–12 **Remarks.** Pa elements that have been assigned to O. crispa show considerable variation, and four morphotypes, designated α , β , χ , δ , were differentiated by Walliser & Wang (1989). The β , χ and δ morphs are all characterized by a furrow on the oral margin of the blade; the α morph lacks the furrow. The holotype selected by Walliser (1964, pl. 21, fig. 12) lacks a furrow and thus belongs to the α morph, as do all the specimens from the northern East Baltic. However, there is major variation within this group, and we distinguish α_1 , α_2 and α_3 morphs, with the holotype belonging to α_1 .

Ozarkodina crispa α_2 morph

(Pl. 2, figs 1-16, 19, 20, Pl. 3, figs 5, 6, 9-11)

Description. Pa element: specimens small; blade high, short with fused denticles towards posterior end. Denticle height decreases posteriorly from anterior end to fused portion. Posterior termination of blade concave to vertical. Basal cavity with wide subcircular lips, underlying posterior half of blade and extending to posterior tip. White matter fills denticles, extending down to tip of cavity beneath fused portion of blade.

Remarks. These specimens differ from the α_1 morph in the subcircular, rather than asymmetrical, shape of the basal cavity. **Occurrence on Saaremaa.** Paadla Stage and lowermost Kuressaare Stage: Sakla borehole 18.0–33.13 m, Riksu borehole 35.0 m, Kaugatuma borehole 49.7–69.3 m, Ohesaare borehole 99.75–100.8 m, Kolka borehole 270.8–284.2 m; Kärla, Roopa, Paadla and Karala outcrops.

Material. Pa element: more than 100 specimens.

$Ozarkodina \ crispa \ \alpha_3 \ morph$

(Pl. 2, figs 17, 18, 21, 22, Pl. 3, figs 1-4, 7, 8)

Description. Pa element: similar to α_2 morph but with posterior denticles unfused or only partly fused. Basal cavity variable in position, normally extending to posterior tip. White matter occupies one-third to one-half of blade.

Remarks. Specimens in which the basal cavity does not extend beyond the posterior end of the blade are similar to *O. s. snajdri*, but differ in the smaller size of the cavity and the shorter blade. The specimens illustrated by Helfrich (1975) encompass the range of variation shown by α_2 and α_3 morphs.

Occurrence on Saaremaa. Paadla Stage and lowermost Kuressaare Stage: Sakla borehole 30.15 m, Riksu borehole 33.5–35.0 m, Kuressaare (Kingissepa) borehole 39.14 m, Ohesaare borehole 100.8 m, Kolka borehole 276.15–284.2 m; Roopa and Karala outcrops.

Material. Pa element: 31 specimens.

Ozarkodina snajdri (Walliser 1964)

- 1964 Spathognathodus snajdri Walliser: 84, pl. 9, fig. 2, pl. 21, figs 14–15, pl. 22, figs 1–4.
- ?1969 Spathognathodus crispus Walliser; Fåhraeus: pl. 2, figs 13, 14.
- ?1969 *Spathognathodus* cf. *snajdri* Walliser; Schönlaub: pl. 1, fig. 29.



Explanation of Plate 3

Figs 1–4, 7, 8. *Ozarkodina crispa* (Walliser 1964) α_3 morph. figs 1–4; lateral and aboral views, Cn 1484, Cn 1485, $\times 70$, $\times 85$, $\times 150$, Sauvere Beds, Sakla borehole, 30.15 m. fig. 7; lateral view, Cn 1486, $\times 80$, Sauvere Beds, Kèrla outcrop. fig. 8; lateral view, Cn 1487, $\times 85$, Himmiste Beds, Roopa cliff. figs **5, 6, 9–11**. *Ozarkodina crispa* (Walliser 1964) α_2 morph. fig. 5; lateral view, Cn 1488, $\times 85$, Sauvere Beds, Sakla borehole, 30.15 m. fig. 6; lateral view, Cn 1489, $\times 85$, Uduvere Beds, Sakla borehole, 18.0 m. figs 9–11; lateral and aboral views, Cn 1490, Cn 1491, $\times 70$, $\times 150$, $\times 95$, Himmiste Beds, Paadla outcrop, sample 3-73. figs **12–21**. *Ozarkodina snajdri parasnajdri* subsp. nov. figs 12, 13; lateral and aboral views, Cn 1492, $\times 50$, Äigu Beds, Ohesaare borehole, 64.65 m. figs 15, 17; lower lateral and oral views, Cn 1495, Cn 1496, $\times 120$, $\times 45$, Äigu Beds, Ohesaare borehole, 61.2 m. figs 18–21, lateral and oral views, oral views of fused denticles and a discrete denticle, Cn 1497, $\times 50$, $\times 850$, Äigu Beds, Ohesaare borehole, 67.4 m.



Explanation of Plate 4

Figs 1–9. Ozarkodina snajdri parasnajdri subsp. nov. figs 1, 2; lateral view, Cn 1498, ×50, detail ×2600, Äigu Beds, Kolka borehole, 263.4 m. figs 3, 4; lateral and aboral views, Cn 1499, Äigu Beds, Kolka borehole, 263.4 m. Figs 5, 6, 8; lateral and aboral views, Cn 1500, Cn 1501, ×85, ×95, ×50, Kuressaare Formation, Ilpla outcrop. fig 7; lateral view, Cn 1502, ×50, Äigu Beds, Kolka borehole, 264.4 m. fig. 9; lower lateral view, Cn 1503, ×45, Tahula Beds, Kaugatuma borehole, 45.5 m. figs 10, 13–17. Ozarkodina remscheidensis eosteinhornensis (Walliser 1964) sensu lato. fig. 10; lateral view, Cn 1505, ×40, Kaugatuma Formation, Ohesaare borehole, 64.65 m. figs 15–17, lateral view, Cn 1508, ×40, details of lateral surfaces of denticles ×600, Kaugatuma Formation, Ohesaare borehole, 67.4 m. figs 11, 12. Ozarkodina confluens densidentata (Viira 1983). Lateral view, Cn 1504, ×50, lateral surfaces of two anterior denticles x650, Viita Beds, Ohesaare borehole, 144.05 m.

- 1971 Spathognathodus snajdri Walliser; Rexroad & Nicoll: pl. 2, figs 4, 5.
- 1971 Spathognathodus snajdri Walliser; Rexroad & Craig: 700, pl. 82, figs 16, 17.
- ?1973 Spathognathodus snajdri Walliser; Pollock & Rexroad: 83, pl. 1, figs 30–34.
- 1975 Spathognathodus snajdri Walliser; Helfrich: pl. 2, figs 3,7, 10-15, 17.
- 1976 Spathognathodus snajdri Walliser; Ebner: 20 (292), pl. 4, figs 1, 2.
- 1976 Ozarkodina remscheidensis snajdri Mehrtens & Barnett (sic); Mehrtens & Barnett: 497, pl. 1, figs 19, 22.
- 1980 Ozarkodina snajdri (Walliser); Chlupac et al.: pl. 25, figs 1, 4-11.
- 1985 Ozarkodina snajdri (Walliser); Aldridge: pl. 3.4, fig. 18.
- 1994 Ozarkodina snajdri (Walliser); Jeppsson et al.: fig. 4e
- 1995 Ozarkodina snajdri Walliser; Miller: pl. 3, figs 14-15, 17-18.
- 1995 Ozarkodina cf. snajdri Walliser; Miller: pl. 3, figs 13, 16.

Remarks. A new subspecies, *O. s. parasnajdri*, is described here. The holotype and all previously described material belong to the nominate subspecies *O. s. snajdri* (Walliser).

Ozarkodina snajdri parasnajdri subsp. nov. (Pl. 3, figs 12-21, Pl. 4, figs 1-9)

Holotype. Specimen Cn 1498, Kolka Borehole 263.4 m; pl. 4, fig. 1,2.

Type stratum. Kaugatuma Formation, Äigu Beds.

Diagnosis. Pa element with large subquadrangular basal cavity extending to posterior end of blade; denticles above cavity fused. Other elements unknown.

Description. Blade commonly long and low, with small denticles, fused above cavity; anterior end higher, posterior portion arched. Posterior termination of blade vertical or oblique concave. Basal cavity with tip a little posterior of centre of blade; lips commonly quadrangular and extending to posterior tip of blade; cavity extends as a narrow groove to anterior tip. White matter deepest above cavity, rising anteriorly and posteriorly; anterior denticles may lack white matter.

Remarks. There is variation in the length of the fused part of the blade and in the position of the basal cavity tip. However, this subspecies differs from O. s. snajdri in always possessing fused denticles and in the more central position of the cavity tip. The cavity lips always extend to the posterior tip of the blade.

Occurrence. Kuressaare Stage and lowermost Kaugatuma Stage: Kaugatuma borehole 28.9–45.4m, Ohesaare borehole 61.2– 93.4m, Kolka borehole 253.6–263.4m; Ilpla and Loode Tammik outcrops.

Material. Pa element: 84 specimens.

Ozarkodina snajdri cf. snajdri (Walliser 1964) (Pl. 1, figs 20,21)

Remarks. Seven specimens in the Ohesaare and Kolka boreholes are close to *O. s. snajdri*. All have fused denticles above the basal cavity, but on unbroken specimens the cavity can be seen to terminate just short of the posterior end of the blade.

CONODONT BIOSTRATIGRAPHY OF SAAREMAA

Samples have been processed for conodont recovery from seven boreholes and nine outcrops (Fig. 2). Spacing of samples in the



Fig. 3. Stratigraphical spans and numbers of samples for the studied boreholes.

boreholes was 1-3 m (Fig. 3), with a standard sample weight of 1-1.5 kg, except in the Kuressaare (Kingissepa) borehole where weights were c. 0.5 kg. All samples yielded conodont elements. The distribution of members of the O. b. bohemica lineage is shown in Fig. 4. In addition, samples from the Rootsiküla Stage contain O. confluens densidentata (Viira) and Ctenognathodus murchisoni (Pander), generally in small numbers. Samples from the Paadla Stage contain O. confluens of Confluens confluens confluentata (Viira), O. excavata (Branson and Mehl), O. roopaensis Viira, Oulodus siluricus (Branson and Mehl), Panderodus spp. and, in the upper part, Coryssognathus dubius (Rhodes), while those from the Kuressaare Stage have O. r. eosteinhornensis s. 1., O. confluens ambigua (Viira) and Oulodus elegans (Walliser) (Viira, 1982 a,b, 1994).

The O. bohemica lineage is most completely represented in the Ohesaare borehole (Figs 5 and 6). In the lower part of the Viita Beds O. b. bohemica β morph appears at a depth of 157.2 m and is found in seven samples through to 142.25 m. The lineage is not represented in the succeeding 29 m, but rare broken specimens of O. s. cf. snajdri are identified at 113.35 m and 106.25 m, in the Torgu Formation of the Paadla Stage. At 100.8 m two specimens of O. crispa α_3 morph occur, and a specimen of O. crispa α_2 morph is found at 99.75 m. In the interval 93.4–61.2 m, seven samples contain O. snajdri parasnajdri. The lowest specimens are small and not well preserved, but have the widely open basal cavity characteristic of this subspecies. The largest specimens occur in the uppermost sample. The lower boundary of the Kuressaare Stage is identified by the occurrence of the thelodont Theolodus sculptilis Gross at 95.15 m, just below the first occurrence of O r. eosteinhornensis at 93.40 m.

The next borehole to the north of Ohesaare is at Kaugatuma, where *Ozarkodina b. bohemica* β morph is represented in two samples at depths of 100.25 m (Viita Beds) and 81.4 m (Vesiku Beds). Four samples from the Paadla Stage at 49.7–69.3 m contain *O. crispa* α_2 morph, with good typical specimens present

	VESIKU	SAKLA		RIKSU	KURESSAARE	KAUGATUMA			OHESAARE				KOLKA			
	8.65 4.95	54.45 51.86	33.13 31.06 30.15 18.0	36.0 35.0 33.5	39.14 4.80	100.25 81.4 69.3 61.6	58.5 49.7	45.4 48.5 37.45 33.75 28.9	157.21 151.7 149.8 149.5 145.55 144.05	113.35 106.25 100.8 99.75 95.95	93.4 90.75 84.95 76.7 73.5 69.9 67.4 67.4	61.20	367.5 362.3 346.6 344.6	289.5 287.4	284.2 276.15 270.8	263.4 253.6
	K1	K1	K ₂	K2	K ₃ a K ₃ a	К1 К	(₂	K ₃ a	K1	K2	K ₃ a	(3a	К1	K2	K ₃ a	K ₃ b
O.b. bohemica β morph	1 1	61	1			4 2		······································	1 1 2 3 11 1 3	L	L I	-	2 ? ?	L]		
O. aff. bicornuta								i								
O. cf. s. snajdri										1 1				1 1	3	
O. crispa $lpha_2$ morph			2 1 14 2	2		14	1 1			1					3 15	
O. crispa $lpha_{3}$ morph			3	131	1					2 ?					13	
O. s. parasnajdri			·		?			2214214] 		2 1 1 1 4 4 14 12	3				28 5



Fig. 4. Distribution of taxa in the Ozarkodina bohemica lineage on Saaremaa and northern Latvia.

in the uppermost Sauvere Beds and the Himmiste Beds. *Ozarkodina s. parasnajdri* occurs in the interval 28.9–45.4 m of the Kuressaare Stage; as noted in the Ohesaare borehole, small specimens are found in the lowest samples and the biggest specimens are from the upper samples.

In the Riksu borehole further to the north, the highest strata are assigned to the Uduvere Beds. The *O. bohemica* lineage is represented only by *O. crispa* α_2 and α_3 morphs at 33.5–36.0 m in the Sauvere Beds. The most northerly borehole sampled from West Saaremaa is at Vesiku, where *O. b. bohemica* β morph has been recovered from two samples in the Viita and Kuusnömme Beds.

The Sakla borehole is situated in East Saaremaa, where the strata are generally dolomitized. Nevertheless, *O. b. bohemica* β morph has been recovered from the Viita Beds and *O. crispa* α_2 and α_3 morphs occur in the Sauvere Beds and in a single sample from the Uduvere Beds (Fig. 7).

In all the boreholes, including the Kolka borehole in northernmost Latvia, O. b. bohemica β morph usually occurs in the Viita Beds and occasionally also in the Kuusnömme and Vesiku Beds of the Rootsiküla Stage. All records of O. crispa on Saaremaa are in the Paadla Stage: in the Sauvere Beds of Riksu, the Sauvere and Himmiste beds of Kaugatuma, and the Torgu Formation of Ohesaare. In the Kolka borehole, *O. crispa* occurs with *O. r. eosteinhornensis* s. 1 in the Kuressaare Stage, with the most typical specimens at a depth of 270.8 m. In general, there is a pattern of increasingly high occurrence of *O. crispa* in the lithostratigraphical sequence from north to south, i.e. towards deeper water facies.

The exposure of Himmiste Beds or uppermost Sauvere Beds at Karala has yielded more than 50 specimens of the Pa element of *O. crispa*, with α_2 morphs dominant, but with some α_3 morphs and transitional forms (Fig. 8). A few specimens of the α_2 morph have also been recovered from Kärla (Sauvere Beds) and Paadla (Himmiste Beds). One specimen from Roopa Cliff (Himmiste Beds) is identified as an α_3 morph.

Small specimens with short blades and large posterior and anterior denticles have been recovered from the Soeginina cliff section (uppermost Rootsiküla Stage) of West Saaremaa and from the outcrop at Anikaitse in East Saaremaa. They are identified as *O*. aff. *bicornuta*. *O*. *bicornuta* was placed in the *bohemica* lineage between *O*. *b. bohemica* and *O*. *snajdri* by Helfrich (1975).

The relative completeness of the *O. bohemica* lineage in the Ohesaare borehole is complemented by evidence that *Coryssognathus dubius* has its longest range in this section. A more



Fig. 5. Distribution of conodonts, icthyoliths (Märss, 1986), chitinozoans (Nestor, 1982) and ostracods (Sarv, 1971) in the Ohesaare borehole. $J_2J_2 - J_{aa}$ Jaagarahu Formation, $K_1Vt - Viita$ Beds, $K_1Kn - Kuusnömme$ Beds, $K_1Vs - Vesiku$ Beds, $K_1Sn - Soeginina$ Beds, $K_2T - Torgu$ Formation, $K_{3a}T - Tahula$ Beds, $K_{3a}K - Kudjape$ Beds, $K_{3b}A - Aigu$ Beds. Lithological column and stratigraphical divisions after Kaljo & Nestor (1990).

complete section in this borehole than in others is also confirmed by occurrences of ichthyoliths and ostracods (Märss, 1986, 1990; Sarv, 1971).

The distribution of conodonts in the Paadla Formation, in particular, suggests the presence of gaps in the Saaremaa succession. V. Nestor (1982) has previously suggested on the basis of chitinozoan data that there is a gap between the Rootsiküla and Paadla stages, and an increase in the scale of this gap northwards has been recognized (Nestor, V., 1990; Nestor, H., 1993). Conodont correlations with Gotland confirm a hiatus at this level (Jeppsson *et al.*, 1994), and the absence of *O. s. snajdri* in all studied sections except Ohesaare provides consistent evidence. A break between the Paadla and Kuressaare stages was also postulated by Einasto (1991) and Märss (1992), and is corroborated by the fact that overlap between *O. crispa* and *O. r. eosteinhornensis* s. l. is apparent in the Kolka section, but has not been found anywhere on Saaremaa. Alternatively, the restricted nearshore facies represented by the Uduvere Beds



Fig. 6. Specimens of Ozarkodina snajdri cf. snajdri O. crispa α_2 and α_3 morphs and O. s. parasnajdri in the Ohesaare borehole.

may be a factor in producing the differences in the observed stratigraphical distributions of the conodonts.

OTHER FOSSIL DATA

Chitinozoans

Chitinozoans are very poorly represented in the Rootsiküla Stage, but a biozonal scheme has been developed for the Paadla and Kuressaare stages (Nestor, V., 1982, 1990). All biozonal species occur in the Ohesaare borehole (Fig. 5). *Conochitina* *latifrons* Eisenack and *Angochitina elongata* Eisenack appear in the lowermost Paadla Formation, and by correlation with the Ventspils borehole, Latvia, Nestor, V. (1982) deduced that strata representing the *nilssoni* and *scanicus* graptolite biozones were absent. In the Ohesaare borehole, *Eisenackitina lagenomorpha* (Eisenack) and *E. philipi* Laufeld range from the uppermost Paadla Stage into the Kuressaare Stage, with *E. lagenomorpha* extending much further upwards. The succeeding biozones of the Kuressaare Stage have as index species *Conochitina granosa*



Fig. 7. Specimens of *Ozarkodina crispa* α_2 and α_3 morphs in the Sakla borehole; all except for the specimen labelled are α_2 morphs.

Laufeld and Sphaerochitina sphaerocephala Eisenack.

In the Ludlow type area, Britain, *C. latifrons* is restricted to the Gorstian, with the highest record at the top of the Lower Bringewood Formation, while *A. elongata* occurs throughout the Gorstian from the uppermost Middle Elton Formation and extends into the Lower Leintwardine Formation (Sutherland, 1994). Sutherland (1994) also showed no overlap between the ranges of *E. lagenomorpha* and *E. philipi*, with the former spanning the Lower Bringewood Formation to Lower Leintwardine Formation and the latter ranging from the Upper Leintwardine Formation to the Upper Whitcliffe Formation. On Gotland, *C. latifrons* and *A. elongata* appear in the topmost Klinteberg Beds, and *E. lagenomorpha* and *E. philipi* appear together in the upper part of the Hemse Beds coincident with the highest occurrence of *C. latifrons* (Laufeld, 1974).

Ostracods

The distribution of ostracods in the Ohesaare borehole has been documented by Sarv (1971), and the ranges of key species are

shown in Fig. 5. Ostracods are rare in the Rootsiküla Stage and absent from the lowermost Paadla Stage, but in the Paadla Stage above a depth of 115 m, rich assemblages occur. Sarv (1971) reported that five species, including *Neobeyrichia nutans* Martinsson, had not been found in the northern East Baltic other than in the Ohesaare borehole, but included a *N. nutans* biozone in the upper Paadla Stage of Saaremaa (Sarv, 1982). In Britain, *N. nutans* occurs in the Lower Leintwardine Formation (Siveter, 1989), but other species recorded in the Ohesaare borehole are not represented.

Ichthyoliths

A microvertebrate biozonation for the Silurian of the northern East Baltic has been established by Märss (1982, 1990), and all the zonal species for the Rootsiküla, Paadla and Kuressaare stages are represented in the Ohesaare borehole (Märss, 1986; see Fig. 5). *Logania martinssoni* (Gross) occurs in the Rootsiküla and lowermost Paadla stages, and has also been found in the Halla, Mulde, Klinteberg and Hemse beds of Gotland (Fred-



Fig. 8. Specimens of *Ozarkodina crispa* α_2 and α_3 morphs in the Karala, Roopa, Kärla and Paadla outcrops.

holm, 1990). *Phlebolepis ornata* Märss characterizes strata assigned to the upper Sauvere Beds by Märss (1986); this species has not been found in the other boreholes, but occurs in the lower Hemse Beds on Gotland (Fredholm, 1988). *Phlebolepis elegans* Pander ranges from the upper Sauvere Beds to the lowermost Uduvere Beds, and has been recorded widely in Estonia and Latvia. *Andreolepis hedei* Gross is restricted to the Uduvere Beds, and is also known from the upper Hemse Beds on Gotland (Fredholm, 1988, 1989) and the Long Quarry Beds (lowermost Přídolí) of South Wales (Märss, 1982).

CORRELATION

The evidence given by conodonts, chitinozoans and icthyoliths for correlations is not always consistent. An attempt to provide the most parsimonious correlation between the succession on Saaremaa and those of the Ludlow type area and of Gotland is shown in Fig. 9. The correlation with Gotland is based on the recent conodont work by Jeppsson *et al.* (1994), who confirmed the presence of gaps in the exposed Saaremaa sequence. One of these gaps is between the Jaagarahu and Rootsiküla stages, embracing strata referred to the upper Slite Beds, Mulde Beds and Halla Beds on Gotland. This results in only part of the O. b. bohemica Biozone being recognized on Saaremaa, here characterized by the β morph.

The gap between the Rootsiküla and Paadla stages on Saaremaa corresponds to the uppermost Klinteberg Beds and lower Hemse Beds of Gotland (Jeppsson *et al.*, 1994). Chitinozoan evidence, particularly the presence of *C. latifrons* in the Ohesaare borehole, indicates that at least the upper part of the Gorstian Stage is represented on Saaremaa; the occurrence of *Phlebolepis ornata* is consistent with this. The hiatus is probably of greater significance in shallower facies away from Ohesaare, where *P. ornata* has not been found, and Kaljo (1990, p. 26) has suggested that the entire Gorstian may be lacking in the shoreward region. The conodont *O. s.* cf. *snajdri* and the ostracod *N. nutans* have also been found only in the Ohesaare borehole.

Jeppsson *et al.* (1994) also determined the presence of a gap between the Paadla and Kuressaare stages, equivalent to the upper Hemse and Eke beds of Gotland. Part of the evidence for



Fig. 9. Correlation of the upper Wenlock to lower Přídolí sequences of Britain (Wenlock Edge and Ludlow area), Estonia (southern Saaremaa) and Gotland.

this is the absence of *Polygnathoides siluricus* Walliser on Saaremaa, although this species is rare in most facies and its distribution may have been environmentally controlled. However, there is a marked change in conodonts at the Paadla/Kuressaare boundary on Saaremaa, with *C. dubius*, *O. excavata* and *O. crispa* disappearing, and a fauna characterized by *O. r.* eosteinhornensis, s. l., *O. confluens, Oulodus elegans* (Walliser) and *O. snajdri parasnajdri* appearing.

Uppermost Ludlow and lowermost Downton conodont faunas from the Welsh Borderland have recently been documented in detail by Miller (1995). He noted that the top of the Upper Whiteliffe Formation in the Ludlow area is characterized by *C. dubius* and *O. s. snajdri*, with less common *O. r. eosteinhornensis* and *O. cf. crispa*. At Ludlow itself, *O. cf.*

crispa rnges 30–15 cm below the top of the formation; the specimens compare with the α_3 morph described in this paper and found in the upper Paadla Stage on Saaremaa. Miller (1995), however, also recovered *O. crispa* from the lower part of the Whitcliffe Formation at Tite's Point, Gloucestershire, and from the lower part of the Upper Perton Beds at Woolhope; these specimens have a narrow furrow on the upper surface and are similar to the β morph of Walliser & Wang (1989).

There is a problem in using the appearance of *O. crispa* in correlating the Saaremaa succession with that of the type Ludlow, as the species is found throughout the upper Sauvere Beds, the Himmiste Beds and the Uduvere Beds. This part of the sequence is usually correlated with the middle part of the Ludlow Series. A revision of this correlation would contradict the evidence from the thelodont *P. elegans*, which has been found by RJA in the Upper Bringewood Formation of the Welsh Borderland, but co-occurs with *O. crispa* in the Sakla Borehole. An explanation may be that the fluctuating nearshore environment of Saaremaa was suited to the earlier evolution of populations of *O. crispa*, which spread into the Welsh Borderland with the onset of appropriate conditions. Further stratigraphical evidence, perhaps from acritarchs or from chemostratigraphy, is required to clarify this question.

The base of the Přídolí Series is commonly identified by the appearance of the ostracod Frostiella groenvalliana Martinsson (Hansch & Siveter, 1994), which occurs in the basal Downton Castle Sandstone Formation of Ludlow (Bassett et al., 1982; Miller, 1995) and in the lower part of the Kaugatuma Stage on Saaremaa (Sarv, 1982). However, the conodont fauna of the Kuressaare Stage suggests a Přídolí age, or at least an age postdating the highest Upper Whitcliffe Formation at Ludlow. One explanation that fits all the fossil data would be the existence of a gap in the succession at Ludlow at the top of the Upper Whitcliffe Formation, as intimated by Jeppsson (1983, p. 137), equivalent to the Kuressaare Stage of Estonia and encompassing the highest part of the Ludlow Series. Bassett et al. (1982, p. 6), however, while noting that the basal contact of the Downton Castle Sandstone Formation is sharp and scoured, considered there to be no indication of a major break in sedimentation at this level.

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APPENDIX: Locality information

Ohesaare borehole – situated in the southern part of the Ohesaare cliff, on the west coast of the Sörve Peninsula.

Kaugatuma borehole – situated near Kaugatuma cliff on the west coast of the Sörve Peninsula.

Riksu borehole – Situated near Riksu lake, Riksu village, southwest Saaremaa.

Vesiku borehole – situated near the mouth of Vesiku brook, westernmost Saaremaa.

Kuressaare (Kingissepa) borehole – situated in the centre of Kuressaare (in the yard of the restaurant 'Tuulik').

Sakla borehole - situated on the south side of Sakla village,

southeast Saaremaa.

Kolka borehole – situated south of Kola village, on the east coast of the Kola cape, northernmost Kuseme Peninsula, Latvia. Anikaitse – small cliff (2.7 m) on the coast of the Kübassaare Peninsula, Anikaitse cape, easternmost Saaremaa.

Ilpla – outcrop on the shore terrace, western part of Ilpla village, south Saaremaa.

Karala – small old quarry at the west end of Karala village, westernmost Saaremaa.

Kärla – outcrop in Kärla brook, central Kärla village, westernmost Saaremaa.

Loode Tammik – small old quarry (1.2 m) in Loode Oak Wood (Tammik), 2 km west of Kuressaare, south Saaremaa.

Paadla – old quarry (1.8 m) in Paadla village, 50 m south of the Kuressaare–Kihelkonna road, central Saaremaa.

Roopa – small cliff (1.5 m) on the southernmost cape of the Atla Peninsula, western coast of Saaremaa.

Soeginina – cliff (4.2 m) on the south-west shore of the Atla Peninsula, westernmost Saaremaa.

Viita – old trench on the shore at Rootsiküla village, 2 km southwest of Kihelkonna, western Saaremaa.

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REFERENCES

- Aldridge, R. J. 1975a. The stratigraphic distribution of conodonts in the British Silurian. Journal of the Geological Society of London, 131: 607– 618.
- Aldridge, R. J. 1975b. The Silurian conodont Ozarkodina sagitta and its value in correlation. Palaeontology, 18: 323-332.
- Aldridge, R. J., Dorning, K. J. & Siveter, D. J. 1981. Distribution of microfossil groups across the Wenlock shelf of the Welsh Basin. In Neale, J. W. & Brasier, M. D. (Eds), Microfossils from Recent and Fossil Shelf Seas, 18-30. Ellis Horwood, Chichester, for British Micropalaeontological Society.
- Aldridge, R. J. 1985. Conodonts of the Silurian System from the British Isles. In Higgins, A. C. & Austin, R. L. (Eds), A Stratigraphical Index of Conodonts, 68–92, 238–241. Ellis Horwood, Chichester, for British Micropalaeontological Society.
- Aldridge, R. J. & Schönlaub, H. P. 1989. Conodonts. In Holland, C. H. & Bassett, M. G. (Eds), A Global Standard for the Silurian System, 274–279. National Museum of Wales, Cardiff.
- An Tai-xiang, 1987. The Lower Paleozoic Conodonts of South China. Beijing University Publishing House, 238 pp.
- Austin, R. L. & Bassett, M. G. 1967. A sagitta zone conodont fauna from the Wenlockian of the Usk Inlier, Monmouthshire. *Geological Magazine*, **104**: 274–283.
- Balogh, K. & Kozur, H. 1985. The Silurian and Devonian in the surroundings of Nekézseny (southernmost Uppony Mts, northern Hungary). Acta Mineralogica-Petrographica, Szeged., 27: 193-205.
- Barrick, J. E. & Klapper, G. 1976. Multielement Silurian (late Llandoverian-Wenlockian) conodonts of the Clarita Formation, Arbuckle Mountains, Oklahoma, and phylogeny of Kockelella. Geologica et Palaeontologica, 10: 59-100.
- Bassett, M. G., Kaljo, D. & Teller, L. 1989. The Baltic region. In Holland, C. H. & Bassett, M. G. (Eds), A Global Standard for the Silurian System, 274–279. National Museum of Wales, Cardiff.
- Bassett, M. G., Lawson, J. D. & White, D. E. 1982. The Downton Series as the fourth Series of the Silurian System. *Lethaia*, 15: 1–24.
- Boogaard, M. van den, 1990. A Ludlow conodont fauna from Irian Jaya (Indonesia). Scripta Geologica, 92: 1–27.
- Branson, E. B. & Mehl, M. G. 1933. Conodonts from the Bainbridge (Silurian) of Missouri. *The University of Missouri Studies*, 8: 39–52.

Bultynck, P. & Pelhate, A. 1971. Découverte de la zone a eosteinhor-

nensis (conodontes) dans le synclinorium médian du Massif Armoricain. Memoires Bureau de Recherches geologiques et Minières, 73: 189-197.

- Chlupác, Kríz, J. & Schönlaub, H. P. 1980. Silurian and Devonian localities of the Barrandian. In Schönlaub, H. P. (Ed.), Second European Conodont Symposium – ECOS II, Abhandlungen der Geologischen Bundesanstalt, Wien, 35: 147–180.
- Cooper, B. J. 1977. Upper Silurian conodonts from the Yarrangobilly Limestone, southeastern New South Wales. *Royal Society of Victoria Proceedings*, 89: 183–191.
- De Deckker, P. 1976. Late Silurian (Late Ludlovian) conodonts from the Kildrummie Formation, South of Rockley, New South Wales. *Journal and Proceedings, Royal Society of New South Wales*, **109**: 59–69.
- Denkler, K. E. & Harris, A. G. 1988. Homeognathodus peniculus (Conodonta), a new earliest Pridolian index species, and the Ludlovian-Pridolian boundary in the Central Appalachian Basin. U.S. Geological Survey Bulletin 1837: C.1-8, pl. 1.
- Drygant, D. M. 1971. Conodont Spathognathodus crispus Zone in Skala Stage (Silurian of Volyno-Podolia). [In Ukrainian with English abstract.] Proceedings of the Academy of Sciences, Ukraine SSR, 5: 780–783.
- Drygant, D. M. 1984. Silurian and Lower Devonian conodonts of Volyno-Podolia [In Russian]. Naukova Dymka, Kiev, 191 pp.
- Dzik, J. 1976. Remarks on the evolution of Ordovician conodonts. Acta Palaeontologica Polonica, 21: 395–453.
- Ebner, F. 1976. Das Silur/Devon-Vorkommen von Eggenfeld ein Beitrag zur Biostratigraphie des Grazer Paläozoikums. Mitteilungen der Abteilung für Bergbau, Geologie und Paläontologie des Landes-Museums Joanneum, 37: 275–305.
- Einasto, R. 1991. Silurian. In Puura, V., Kalm, V. & Puura, J. (Eds), First World Meeting of Estonian Geologists, Tallinn-Lohusalu, 9-14 September 1991. Geology and Mineral Resources of Estonia: Excursion Guide, 7-9. Tallinn.
- Fåhraeus, L. E. 1969. Conodont zones in the Ludlovian of Gotland and a correlation with Great Britain. Sveriges Geologiska Undersökning, C63(2), 1–33.
- Feist, R. & Schönlaub, H. P. 1974. Zur Silur/Devon-Grenze in der östlichen Montagne Noire Süd-Frankreichs. Neues Jahrbuch fur Geologie und Paléontologie Monatshefte, 1974, 200-219.
- Flajs, G. 1967. Conodontenstratigraphische Untersuchungen im Raum von Eisenerz, Nördliche Grauwackenzone. Mitteilungen der Geologischen Gesellschaft in Wien, 59: 157–212.
- Fredholm, D. 1988. Vertebrate biostratigraphy of the Ludlovian Hemse Beds of Gotland, Sweden. *Geologiska Föreningens i Stockholm Förhandlingar*, **110**: 237–253.
- Fredholm, D. 1989. Silurian vertebrates of Gotland, Sweden. Lund Publications in Geology, 76, 47 pp.
- Fredholm, D. 1990. Agnathan vertebrates in the Lower Silurian of Gotland, Sweden. Geologiska Föreningens i Stockholm Förhandlingar, 112: 61–84.
- Hansch, W. & Siveter, D. J. 1994. 'Nodibeyrichia jurassica' and associated beyrichiacean ostracode species and their significance for the correlation of late Silurian strata in the Baltic and Britain. Journal of Micropalaeontology, 13: 81–91.
- Hass, W. H. 1959. Conodonts from the Chappel Limestone of Texas. U.S. Geological Survey Professional Paper 294-J: 365-400.
- Helfrich, C. T. 1975 [dated 1974]. Silurian Conodonts from the Wills Mountain Anticline, Virginia, West Virginia and Maryland. *Geologi*cal Society of America Special Paper, 161.
- Jeppsson, L. 1983. Silurian conodont faunas from Gotland. *Fossils and Strata*, **15:** 121–144.
- Jeppsson, L., Aldridge, R. J. & Dorning, K. J. 1995. Wenlock (Silurian) oceanic episodes and events. *Journal of the Geological Society, London*, 152: 487–498.
- Jeppsson, L., Viira, V. & Männik, P. 1994. Silurian conodont-based correlations between Gotland (Sweden) and Saaremaa (Estonia). *Geological Magazine*, 131: 201–218.
- Jiang Wu, Zhang Fang, Zhou Xiyun, Xiong Jianfei, Dai Jinyie & Zhong Duan. 1986. Conodonts-Palaeontology [in Chinese]. Southwestern Petroleum Institute, 287 pp.
- Kaljo, D. (Ed.) 1970. The Silurian of Estonia [in Russian with English abstracts]. Tallinn, Valgus, 343 pp.

- Kaljo, D. (Ed.) 1977. Facies and Fauna of Baltic Silurian [in Russian with English abstracts]. Academy of Sciences of the Estonian SSR, Tallinn, 286 pp.
- Kaljo, D. 1990. The Silurian of Estonia. In Kaljo, D. & Nestor, H. (Eds), Field Meeting Estonia 1990, an Excursion Guidebook, 21–26. Estonian Academy of Sciences, Tallinn.
- Kaljo, D. & Klaamann, E. (Eds) 1982a. Communities and Biozones in the Baltic Silurian [in Russian with English abstracts]. Tallinn, Valgus, 139 pp.
- Kaljo, D. & Klaamann, E. (Eds) 1982b. Ecostratigraphy of the East Baltic Silurian. Tallinn, Valgus, 112 pp.
- Kaljo, D. & Nestor, H. (Eds), Field Meeting Estonia 1990, an Excursion Guidebook. Estonian Academy of Sciences, Tallinn, 209 pp.
- Klapper, G. & Murphy, M. A. 1974. Silurian-Lower Devonian Conodont sequence in the Roberts Mountains Formation of Central Nevada. University of California Publications in Geological Sciences, 111.
- Kleffner, M. A. 1990. Wenlockian (Silurian) condont biostratigraphy, depositional environments, and depositional history along the eastern flank of the Cincinnati Arch in Southern Ohio. Journal of Paleontology, 64: 319-328.
- Kozur, H. 1984. Preliminary report about the Silurian to Middle Devonian sequences near Nekézseny (southernmost Uppony Mts., northern Hungary). Geologische und Paläontologische Mitteilungen Innsbruck, 13: 149–176.
- Kríz, J., Dufka, P., Jaeger, H. & Schönlaub, H. P. 1993. The Wenlock/ Ludlow boundary in the Prague Basin. Jahrbuch der Geologischen Bundesanstalt, 136: 809–839.
- Laufeld, S. 1974. Silurian Chitinozoa from Gotland. *Fossils and Strata*, **5:** 130 pp.
- Link, A. G. & Druce, E. C. 1972. Ludlovian and Gedinnian Conodont Stratigraphy of the Yass Basin, New South Wales. Bulletin of the Bureau of Mineral Resources, Geology and Geophysics, Australia, 134.
- Männik, P. & Viira, V. 1990. Conodonts. In Kaljo, D. & Nestor, H. (Eds), Field Meeting Estonia 1990, an Excursion Guidebook, 84–89. Estonian Academy of Sciences, Tallinn.
- Märss, T. 1982. Vertebrate zones in the East Baltic Silurian. In Kaljo, D. & Klaamann, E. (Eds), Ecostratigraphy of the East Baltic Silurian, 97– 106. Tallinn, Valgus.
- Märss, T. 1986. Silurian Vertebrates of Estonia and West Latvia [in Russian with English summary]. Tallinn, Valgus, 104 pp.
- Märss, T. 1990. Vertebrates. In Kaljo, D. & Nestor, H. (Eds), Field Meeting Estonia 1990, an Excursion Guidebook, 93–96. Estonian Academy of Sciences, Tallinn.
- Märss, T. 1992. Vertebrate history in the Late Silurian. Proceedings of the Estonian Academy of Science, Geology, 44: 205–214.
- Mehrtens, C. J. & Barnett, S. G. 1976. Conodont subspecies from the Upper Silurian-Lower Devonian of Czechoslovakia. *Micropaleontol*ogy, 22: 491-500.
- Meidla, T. & Sarv, L. Ostracodes. In Kaljo, D. & Nestor, H. (Eds), Field Meeting Estonia 1990, an Excursion Guidebook, 68–71. Estonian Academy of Sciences, Tallinn.
- Miller, C. G. 1995. Ostracode and conodont distribution across the Ludlow/Přídolí boundary of Wales and the Welsh Borderland. *Palaeontology*, **38**: 341–384.
- Miller, C. G. & Aldridge, R. J. 1997. Ozarkodina remscheidensis plexus conodonts from the upper Ludlow and lower Přídolí of the Welsh Borderland and Wales. Journal of Micropalaeontology, 16, 41-49.
- Nestor, H. 1993. Catalogue of Silurian stratigraphic units and stratotypes in Estonia and Latvia. Estonian Academy of Sciences, Tallinn, 23pp.
- Nestor, H. & Einasto, R. 1977. Facies-sedimentary model of the Silurian Paleobaltic sedimentary basin. *In* Kaljo, D. (Ed.), *Silurian Facies and Fauna of East Baltic*, 89–121. Academy of Sciences of the Estonian SSR Institute of Geology, Tallinn [in Russian with English abstract].

- Nestor, V. 1982. Correlation of the East Baltic and Gotland Silurian by chitinozoans. In Kaljo, D. and Klaamann, E. (Eds). Ecostratigraphy of the East Baltic Silurian, 89–95. Academy of Sciences of the Estonian SSR Institute of Geology, Tallinn.
- Nestor, V. 1990. Silurian chitinozoans. In Kaljo, D. & Nestor, H. (Eds), Field Meeting Estonia 1990, an Excursion Guidebook, 80–83. Estonian Academy of Sciences, Tallinn.
- Pollock, C. A. & Rexroad, C. B. 1973. Conodonts from the Salina Formation and the upper part of the Wabash Formation (Silurian) in north-central Indiana. *Geologica et Palaeontologica*, **7**: 77–92.
- Qiu Hong-rong 1985. Silurian conodonts in Xizang (Tibet). Bulletin of the Institute of Geology of the Chinese Academy of Geological Sciences, Beijing, 11: 23-36. [in Chinese, with English abstract].
- Rexroad, C. B. & Craig, W. W. 1971. Restudy of conodonts from the Bainbridge Formation (Silurian) at Lithium, Missouri. Journal of Paleontology, 45: 684–703
- Rexroad, C. B. & Nicoll, R. S. 1971. Summary of conodont biostratigraphy of the Silurian System of North America. In Sweet, W. C. & Bergström, S. M. (Eds), Symposium on Conodont Biostratigraphy. Geological Society of America Memoir, 127: 207-225.
- Sarv, L. 1971. Silurian ostracodes in the Ohesaare boring. Proceedings of the Academy of Sciences, Estonian SSR, Chemistry Geology, 20: 349– 355. [in Russian with English abstract].
- Sarv, L. 1982. On ostracode zonation of the East Baltic Upper Silurian. In Kaljo, D. and Klaamann, E. (Eds). Ecostratigraphy of the East Baltic Silurian, 71–77. Academy of Sciences of the Estonian SSR Institute of Geology, Tallinn.
- Schmidt, F. 1858. Untersuchungen über die silurische Formation von Ehstland, Nord-Livland und Oesel. Archiv fur die Naturkunde Liv-, Est- und Kurlands. Dorpat, Ser. 1, 248 pp.
- Schönlaub, H. P. 1969. Das Paläozoikum zwischen Bischofalm und Hohem Trieb (Zentrale Karnische Alpen). Jahrbuch der Geologischen Bundesanstalt, Wien, 112: 265–320.
- Siveter, D. J. 1989. Ostracodes. In Holland, C. H. & Bassett, M. G. (Eds), A Global Standard for the Silurian System, 252–264. National Museum of Wales, Cardiff.
- Sutherland, S. J. E. 1994. Ludlow chilinozoans from the type area and adjacent regions. *Palaeontographical Society Monograph*, **148**(594): 1– 104.
- Viira, V. 1982a. Shallow water conodont Ctenognathodus murchisoni (Late Wenlock, Estonia). In Kaljo, D. and Klaamann, E. (Eds), Communities and Biozones in the Baltic Silurian, 63–83. Tallin, Valgus [in Russian with English abstract].
- Viira, V. 1982b. Late Silurian shallow and deep water conodonts from the East Baltic. In Kaljo, D. and Klaamann, E. (Eds), Ecostratigraphy of the East Baltic Silurian, 79–87. Academy of Sciences of the Estonian SSR Institute of Geology, Tallinn.
- Viira, V. 1994. A new Upper Silurian conodont species from Estonia. Proceedings of the Estonian Academy of Science, Geology, 43: 32–37.
- Walliser, O. H. 1964. Conodonten des Silurs. Abhandlungen des Hessischen Landesamtes f
 ür Bodenforschung, 41: 106 pp.
- Walliser, O. H. 1971. Conodont biostratigraphy of the Silurian of Europe. In Sweet, W. C. & Bergström, S, M. (Eds), Symposium on Conodont Biostratigraphy. Geological Society of America Memoir, 127: 195–206.
- Walliser, O. H. & Wang, C.-y. 1989. Upper Silurian Stratigraphy and conodonts from the Quijing District, East Yunnan, China. *Courier Forschungsinstitut Senckenberg*, **110**: 111–121.
- Wang, C.-y. 1980. Upper Silurian conodonts from Quijing District, Yunnan [in Chinese with English summary]. Acta Palaeontologica Sinica, 19: 369–378.
- Yu Hongjin 1985. Conodont biostratigraphy of Middle-Upper Silurian from Xainza, Northern Xizang (Tibet). *Contribution to the Geology of the Qinghai-Xizang (Tibet) Plateau*, **16:** 15–31. [in Chinese with English abstract].