

Ozarkodina remscheidensis plexus conodonts from the upper Ludlow (Silurian) of the Welsh Borderland and Wales

C. GILES MILLER* & RICHARD J. ALDRIDGE

Department of Geology, University of Leicester, Leicester LE1 7RH, UK.

*Present address: Department of Palaeontology, Natural History Museum, Cromwell Road, London SW7 5BD, UK.

ABSTRACT – Three subspecies of the conodont *Ozarkodina remscheidensis* Ziegler, 1960, are described from the late Ludlow (Silurian) of the Welsh Borderland and Wales, including a new subspecies *O. r. baccata*. Four discrete element types which occur in association are also described and interpreted as possible members of the *Ozarkodina remscheidensis* apparatus. *J. Micropalaeontol.* 16(1): 41–49, May 1997.

INTRODUCTION

Walliser (1962, 1964) proposed the first Silurian conodont biozonation, based on the Cellon section in the Carnic Alps. This scheme included a late Silurian *eosteinhornensis* Biozone characterized by *Ozarkodina remscheidensis eosteinhornensis* (Walliser). Since then, *O. remscheidensis* plexus conodonts have been recognized in late Silurian and early Devonian sections worldwide (Fig. 1) and a number of authors have suggested revisions to Walliser's original biozonal scheme. A review of early modifications has been given by Cooper (1980). More recent biozonal revisions have included that of Aldridge & Schönlaub (1989, fig. 173), who showed the *eosteinhornensis* Biozone spanning much of the Přídolí, with its base above the last occurrence of *Ozarkodina crispa* (Walliser) and its upper limit at the first occurrence of *Icriodus woschmidti woschmidti* (Ziegler). Kleffner (1989) used graphical correlation on data from 30 sections in America and Europe to establish a composite biozonal scheme including a late Ludlow to late Přídolí *remscheidensis* Biozone.

We have made detailed conodont collections around the Ludlow–Přídolí boundary in the Welsh Borderland and Wales, and these have provided new data on the distribution of conodonts of the *remscheidensis* plexus at this critical level. The majority of the specimens were extracted from limestones or slightly calcareous rocks using 10% acetic acid. Residues were dried and sieved to 75 µm and the heavy fraction (including conodonts) separated out using an aqueous solution of the inert heavy liquid sodium polytungstate (manufactured by Sometu, Berlin) at a specific gravity of 2.80. Locality and sample numbers are those used by Miller & Aldridge (1993, p. 244). All figured specimens are deposited at the Natural History Museum, London.

Previously, Walliser (1966), Collinson & Druce (1966), Aldridge (1975, 1985) and Aldridge & Schönlaub (1989) have reported *O. remscheidensis eosteinhornensis* from the Welsh Borderland. In this contribution we provide the first description of associated members of the *remscheidensis* plexus that occur with *O. r. eosteinhornensis*, including a new subspecies *O. r. baccata*. The use of subspecies in conodont taxonomy has a somewhat chequered history. They have been used to differentiate populations of species that are clearly chronologically (e.g. Walliser (1964) for *Ozarkodina sagitta rehana* and *O. s. sagitta*, now considered index fossils for successive zones

U.S.A.		AUSTRALIA	
California	Savage (1976)	Phillip (1966)	
Indiana	Nicoll & Rexroad (1987)	Link & Druce (1972)	
	Pollock & Rexroad (1973)	Savage (1973)	
Missouri	Rexroad & Craig (1971)	Telford (1975)	
New Hampshire	Harris <i>et al.</i> (1983)	Mawson (1986)	
New Jersey	Barnett (1971, 1972)		
Nevada	Klapper & Murphy (1974)		
	Barnett (1972)		
Oklahoma	Clark & Ethington (1966)		
	Barrick & Klapper (1990, 1992)		
Virginia	Barrick <i>et al.</i> (1990)		
Utah	Helfrich (1975, 1978)		
Yukon	Clark & Ethington (1966)		
	Klapper (1969)		
EUROPE		CHINA	
Welsh Borderland	Walliser (1966)	Wang (1981, 1985)	
	Collinson & Druce (1966)	Wang & Ziegler (1983)	
	Aldridge (1975, 1985)	Wang & Li (1986)	
	Aldridge & Smith (1985)		
France	Bultynck & Pelhate (1971)		
	Feist & Schönlaub (1974)		
	Bultynck (1977, 1986)		
	Borremans & Bultynck (1986)		
Germany	Ziegler (1956, 1960)		
	Walliser (1957)		
Spain	Bultynck (1971)		
	Degardin & Lethiers (1982)		
Sardinia	Serpagli & Mastandrea (1970)		
	Mastandrea (1985a, b)		
	Gnoli <i>et al.</i> (1990)		
	Olivieri & Serpagli (1990)		
Barrandian Basin	Barnett (1972)		
	Walmsley <i>et al.</i> (1974)		
	Mehrtens & Barnett (1977)		
	Chiupác <i>et al.</i> (1980)		
	Jeppsson (1988, 1989)		
Carnic Alps	Walliser (1957, 1962, 1964)		
	Schulze (1968)		
	Jaeger & Schönlaub (1980)		
	Schönlaub (1980, 1986)		
		CANADA / ARCTIC	
		Legault (1968)	
		Klapper (1969)	
		Lane & Ormiston (1979)	
		Uyeno (1981, 1990, 1991)	
		Savage (1982)	
		PAKISTAN	
		Barnett <i>et al.</i> (1969)	
		EUROPE (OTHER)	
		Durdanovic (1967)	
		Wolska (1969)	
		Fahræus (1969)	
		Saladzius (1971)	
		Walliser (1971)	
		Spassov (1971)	
		Mashkova (1972)	
		Jeppsson (1975)	
		Ebner (1976)	
		Viira (1983)	
		Drygant (1984)	

Fig. 1. Publications that figure or document *Ozarkodina remscheidensis* plexus conodonts, arranged geographically.

(Aldridge & Schönlaub, 1989)) or geographically separated (e.g. *Apsidognathus tuberculatus tuberculatus* Walliser, 1964 and *A. t. arcticus* Armstrong, 1990). Subspecies have also been applied to morphological variants that overlap in space and time (e.g. Higgins (1975) for the Carboniferous species *Gnathodus girtyi*). Some authors have preferred to designate morphotypes for the latter situation (e.g. Klapper & Murphy (1974) for *Ozarkodina confluens*), giving each morphotype a different Greek letter. The subspecies designated here, *O. r. baccata*, forms a distinct and potentially biostratigraphically useful population in late Ludlow samples from the Welsh Borderland,

although specimens of the other two subspecies do occur in association. As subspecific categories already exist for *O. remscheidensis*, it is preferential to differentiate this population as a third subspecies, rather than add morphotype letters to one of the existing subspecies.

SYSTEMATIC PALAEOONTOLOGY

Phylum **Chordata** Bateson, 1886

Class **Conodonta** Pander, 1856

Order **Ozarkodinida** Dzik, 1976

Family **Spathognathodontidae** Hass, 1959

Genus **Ozarkodina** Branson & Mehl, 1933

Ozarkodina remscheidensis baccata ssp. nov.

(Pl. 1, figs 1–18; Fig. 2)

1985 *Ozarkodina remscheidensis* subsp. nov. Aldridge: 90, pl. 3.4, fig. 17 (Pa).

Derivation of name. Subspecies named *baccata* (Latin = yew tree) as first specimens were collected from an exposure in the car park opposite the Yew Tree Inn at Prior's Frome near Hereford (loc. 24).

Diagnosis. Pa element with straight blade bearing irregular mostly broad denticles, crowded near to inconspicuous cusp which is central or very slightly to posterior of midlength. Posterior process and denticles decrease in height distally; basal margin weakly concave. Asymmetrically flared cavity with one side more flared and more pinched.

Holotype. Natural History Museum, London, UK, No. PM X 1156 (Pa). Holotype figured in Pl. 1, figs 9, 12.

Material. 20 Pa elements.

Localities and horizons. (Figs 3, 4) Holotype 2m below top of Whitcliffe Formation: sample 39/1, Aston Munslow, Corve Dale, Shropshire, GR SO 5124 8658 (loc. 7a). Upper Whitcliffe Formation: sample 15c/2, Whitcliffe Quarry, Ludlow, Shropshire (loc. 15c); samples 77/2 and 18/1, Ludford Corner, Ludlow, Shropshire (loc. 18). Upper Perton Beds: samples 162/2 and 24a/2a, Prior's Frome, Hereford and Worcester (loc. 24a). Upper Llangibby Beds: sample 33/3, Brook House, Usk, Gwent (loc. 33).

Description. Pa element (Pl. 1, figs 1–18; Fig. 2) carminate with inconspicuous cusp, central or just posterior of cavity. Posterior process with four to six denticles; two proximal denticles of similar shape and size to cusp; one specimen with tiny accessory denticle fused to proximal denticle. Remaining denticles increasingly smaller distally as process diminishes posteriorly

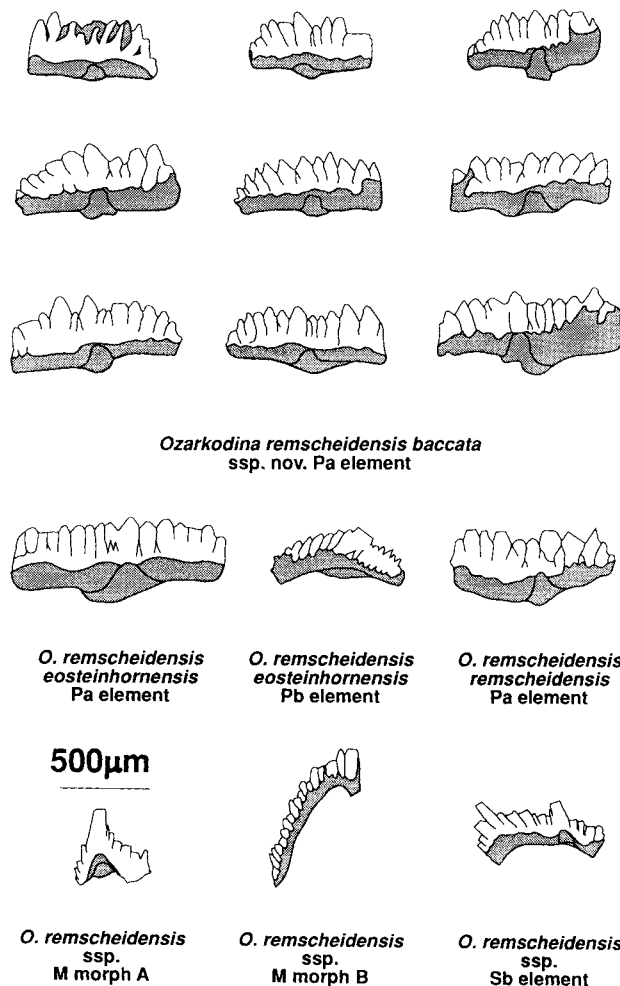


Fig. 2. Camera lucida drawings in lateral view showing white matter distribution in elements of *O. r. baccata*, *O. r. eosteinhornensis*, *O. r. remscheidensis* and *O. r. ssp.* Specimen numbers from top left: PM X 1292, PM X 1293, PM X 1294, PM X 1296, PM X 1295, PM X 1156, PM X 1298, PM X 1297, PM X 1157, PM X 1164, PM X 1259, PM X 1277, PM X 1169, PM X 1180, PM X 1168.

to three quarters medial height; process terminates with small step-like extension beyond last denticle. Posterior aboral surface slightly concave. Anterior process same length as posterior; denticles number four in juvenile specimens and up to six in

Explanation of Plate 1

Figs 1–18. *Ozarkodina remscheidensis baccata* ssp. nov., Pa elements. **Figs 1, 4.** PM X 1292, sample 162/2, Upper Perton Beds, Prior's Frome, Hereford & Worcester (loc. 24a), $\times 55$: Fig. 1. Lateral; Fig. 4. Oral. **Figs 2, 5.** PM X 1293, sample and locality as for Fig. 1, $\times 45$: Fig. 2. Lateral; Fig. 5. Oral. **Figs 3, 6.** PM X 1294, sample and locality as for Fig. 1, $\times 50$: Fig. 3. Lateral; Fig. 6. Oral. **Figs 7, 10.** PM X 1296, sample 161/1, Upper Perton Beds, Perton, Hereford & Worcester (loc. 23b), $\times 45$: Fig. 7. Lateral; Fig. 10. Oral. **Figs 8, 11.** PM X 1295, sample and locality as for Fig. 1, $\times 50$: Fig. 8. Lateral; Fig. 11. Oral. **Figs 9, 12.** PM X 1156, holotype, sample 39/1, Whitcliffe Formation, opposite the Swan Inn, Aston Munslow, Corve Dale, Shropshire (loc. 7a), $\times 45$: Fig. 9. Lateral; Fig. 11. Oral. **Figs 13, 16.** PM X 1298, sample and locality as for Fig. 1, $\times 45$: Fig. 13. Lateral; Fig. 16. Oral. **Figs 14, 17.** PM X 1297, sample and locality as for Fig. 1, $\times 45$: Fig. 14. Lateral; Fig. 17. Oral. **Figs 15, 18.** PM X 1157, sample and locality as for Fig. 8, $\times 40$: Fig. 15. Lateral; Fig. 18. Oral. **Figs 19, 22.** Pa element, PM X 1164, sample 8/1, Whitcliffe Formation, Diddlebury, Corve Dale, Shropshire (loc. 8), $\times 30$: Fig. 19. Lateral; Fig. 22. Oral. **Figs 20, 23.** Fragment showing cavity and posterior process of Pa element, PM X 1190, sample 18/1, Upper Whitcliffe Formation, Ludford Corner, Ludlow, Shropshire (loc. 18), $\times 50$: Fig. 20. Lateral; Fig. 23. Oral. **Figs 21, 24.** *Ozarkodina remscheidensis remscheidensis* (Ziegler, 1960). Pa element, PM X 1277, sample 31b/3, Whitcliffe Formation, foreshore of Severn Estuary, Tite's Point, Gloucestershire (loc. 31b), $\times 45$: Fig. 21. Lateral; Fig. 24. Oral.

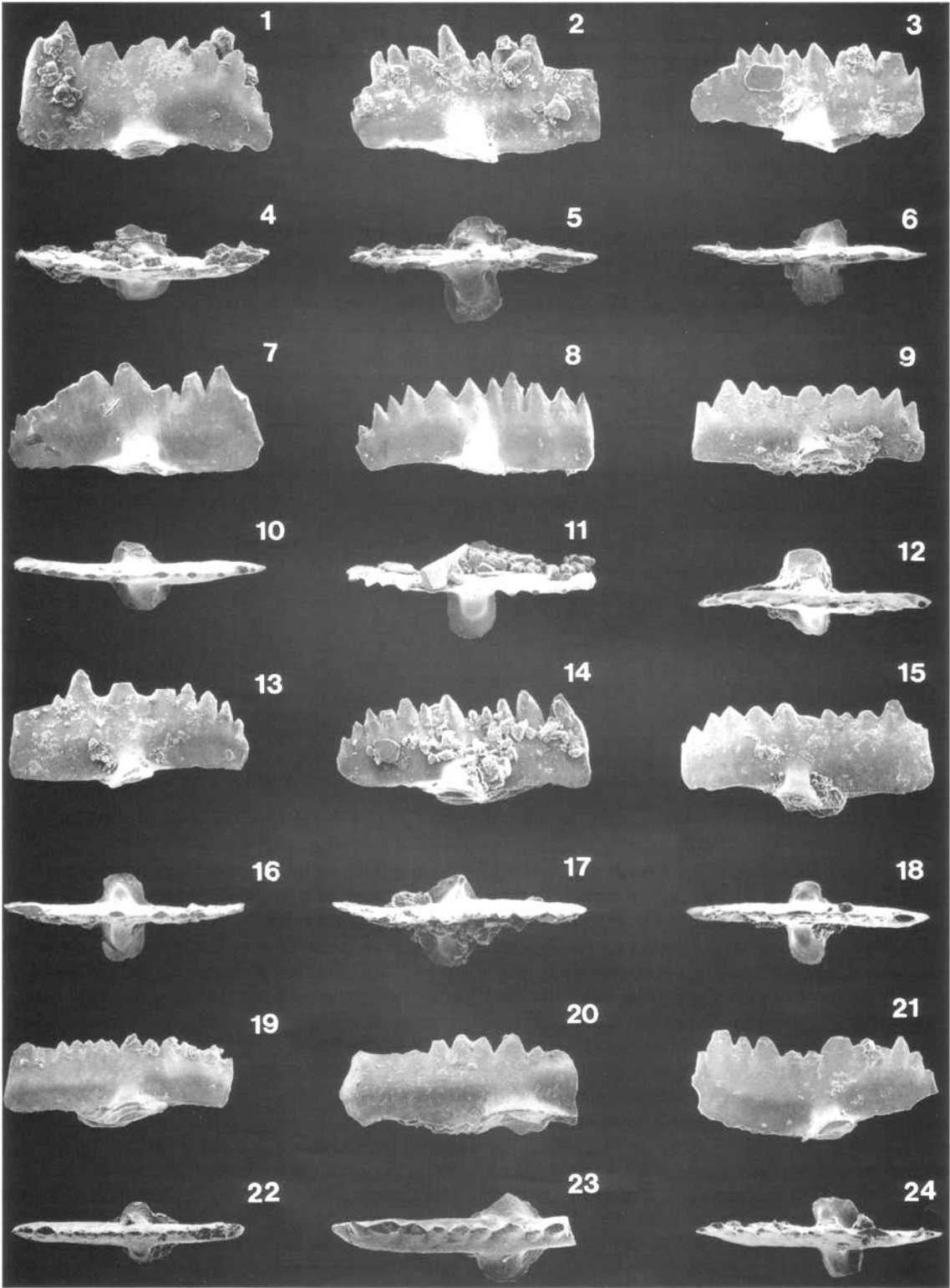


Plate 1

Species	Sample	5c 1	39 1	8 1	14c	74 1	15c 2	77 2	18 1	20 1b	160 1	161 1	24a 2a	162 2	31b 1	31b 3	31b 4	33 2	33 3	33 4
Weight of dissolved sample (kg)		2.45	1.35	0.68	-	0.18	1.31	0.40	0.55	0.50	1.25	1.18	0.91	1.56	1.23	1.74	1.86	1.16	1.51	0.84
Total no. conodont elements		1260	238	57	194	524	261	67	195	551	1320	1627	1010	1744	343	435	486	123	176	45
<i>O. remscheidensis baccata</i>	Pa	2	3			1	1	3					3	1					1	
<i>O. r. cf. baccata</i>	Pa	3	2			1		1					2	1			1			
<i>O. r. eosteinhornensis</i>	Pa	2	2	1	1	6	1	5	1	1	1	1	1		1		2			
<i>O. r. cf. eost.</i>	Pb			1				2	3						1	1				
<i>O. r. remscheidensis</i>	Pa										1					1				
<i>O. r. ssp.</i> Pa element fragments			2	2		1	3	1			2	1	3				1			2
M morph A			1																	
M morph B			2			1	2				2		6				1			
Sb			1	1																

Fig. 3. Frequencies of *O. remscheidensis* elements in samples from the Welsh Borderland and Wales. Samples and localities as listed by Miller & Aldridge (1993).

Ludlow Series																	Pridoli		
Upper Whitcliffe Formation (and lateral equivalents)																	DCS Fm.		
74/1	15c/2	8/1	5c/1	31b/4	33/2	31b/3	33/4	33/3	161/1	31b/1	162/2	24a/2a	20/1b	39/1	160/1	77/2	18/1	14c	Sample
c. 28	c. 28	<10	<10	7.7	c. 7	6.2	c. 6	c. 6	c. 4	2.5	2.5	2.5	2.2	1.9	0.5	0.30	0.15		Height below top of Ludlow Series (m)
<div><div></div><div><i>O. r. eosteinhornensis</i> Pa</div></div>																			
<div><div></div><div><i>O. r. eosteinhornensis</i> Pb</div></div>																			
<div><div></div><div><i>O. r. baccata</i> Pa</div></div>																			
<div><div></div><div><i>O. r. cf. baccata</i> Pa</div></div>																			
<div><div></div><div><i>O. r. cf. eosteinhornensis</i> Pa</div></div>																			
<div><div></div><div><i>O. r. ssp. M</i> morph B</div></div>																			
<div><div></div><div><i>O. r. ssp. M</i> morph A</div></div>																			
<div><div></div><div><i>O. r. ssp. Sb</i></div></div>																			
<div><div></div><div><i>O. r. remscheidensis</i> Pa</div></div>																			

Fig. 4. Stratigraphic distribution of *O. remscheidensis* plexus conodonts from Wales and the Welsh Borderland. Samples are arranged in approximate stratigraphical order with height below the top of the Ludlow Series given when possible. DCS = Downton Castle Sandstone. Lateral equivalents for the Upper Whitcliffe Formation are given by Miller & Aldridge (1993).

more mature specimens, of uneven size, crowded close to cusp, becoming slightly more isolated distally. Terminal denticle slightly lower than adjacent denticle, with anterior margin sloping very slightly to anterior and rounded antero-aborally. Anterior process with straight aboral margin, decreasing much more gradually in height than posterior process. Shallow cavity extends entire length of element, flared at mid-length with rounded lips; flaring asymmetrical, much stronger on one side of element. Oral surface of flare pinched. White matter present in cusp and all denticles, mostly as single solid block; base of white matter parallel to aboral margin of element or rising anteriorly from beneath cusp (Fig. 2).

Dimensions. Length and maximum height (μm) are given for each specimen: PM X 1156 (holotype); 812, 334. PM X 1157; 980, 406. PM X 1292; 720, 380. PM X 1293; 670, 456. PM X 1294; 760, 342. PM X 1295; 811, 342. PM X 1296; 900, 394. PM X 1297; 887, 367. PM X 1298; 932, 444.

Remarks. Before 1974, subspecies of *O. remscheidensis* were

treated by various authors as subspecies of *Ozarkodina steinhornensis* (Ziegler, 1956). Mashkova (1972), however, used a bedding plane assemblage to reconstruct the apparatus of *O. steinhornensis* and showed that it possessed an Sa element with a denticulate posterior process. On Sa elements of the reconstructed apparatuses of the taxa discussed here a posterior process is not developed (see Mashkova (1972), pl. 2), and Klapper & Murphy (1974, pp. 39, 40) argued that the appropriate species name should be *remscheidensis* rather than *steinhornensis*.

O. r. baccata is distinct from other late Silurian subspecies, but is closer to *O. r. eosteinhornensis* than to *O. r. remscheidensis*. There is a clear angle between the basal margins of the anterior and posterior process of the Pa element of *O. r. remscheidensis*, which also displays well developed denticles towards the anterior. The Pa element of *O. r. baccata* is distinct from that of *O. r. eosteinhornensis* as it has a central, asymmetrically flared cavity pinched on one side and broader denticles which are not

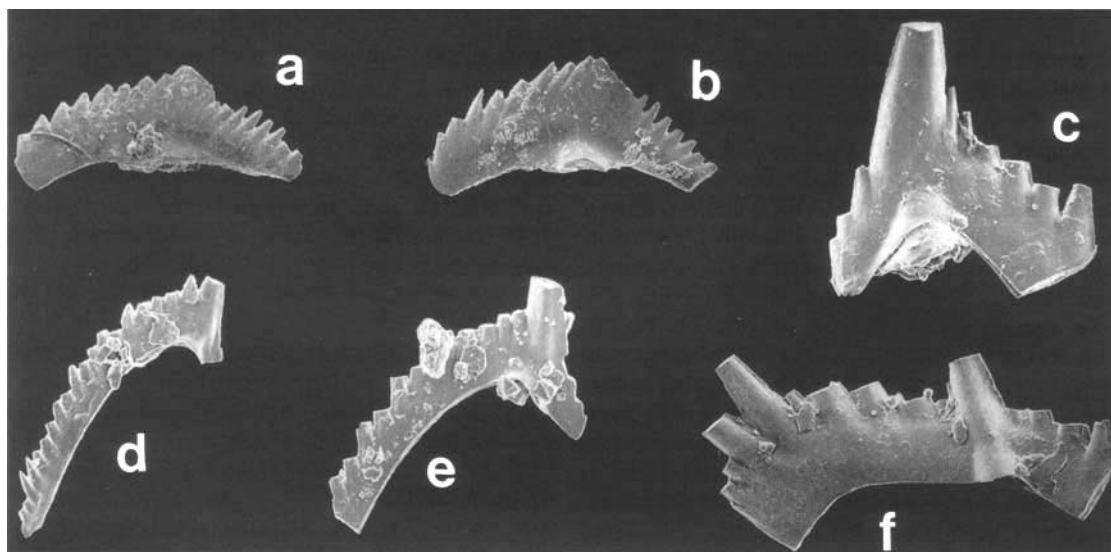


Fig. 5. a, b. *Ozarkodina remscheidensis eosteinhornensis* (Walliser, 1964). a. Pb element, lateral view, PM X 1259, sample 39/1, Whitcliffe Formation, opposite the Swan Inn, Aston Munslow, Corve Dale, Shropshire (loc. 7a), $\times 50$. b. Pb element, lateral view, specimen now lost, sample 24a/2a, Upper Perton Beds, Prior's Frome, Hereford & Worcester (loc. 24a), $\times 45$. c–f. *Ozarkodina remscheidensis* spp. c. M element morphotype A, lateral, PM X 1169, sample 8/1, Whitcliffe Formation, Diddlebury, Corve Dale, Shropshire (loc. 8), $\times 30$. d, e. M element morphotype B. d. Lateral, PM X 1180, sample 15c/2, Upper Whitcliffe Formation, Whitcliffe Quarry, Ludlow, Shropshire (loc. 15c), $\times 50$. e. Lateral, PM X 1265, sample 162/2, Upper Perton Beds, locality as for Fig. 5b, $\times 70$. f. Sb element, lateral, PM X 1168, sample and locality as for Fig. 5c, $\times 70$.

fused above the cavity. Philip (1966, fig. 8A) figured a similar Pa element from the Lower Devonian of Australia as *Spathognathodus steinhornensis buechanensis* Philip, but the denticles vary from relatively large, crowded and almost discrete to small, crowded and fused. The anteriormost denticles of *S. s. buechanensis* are sometimes enlarged (Philip 1966, fig. 8B), whereas the denticles on *O. r. baccata* do not show a marked size increase anteriorly and the anteriormost denticle is always smaller and lower than its neighbour. The majority of *S. s. buechanensis* specimens figured by Philip (1966, pl. 2) are markedly bowed in oral view whereas all the specimens of *O. r. baccata* from the Welsh Borderland have straight to very slightly bowed blades (Pl. 1). Schönlaub (1980, pl. 6, fig. 11 as *O. r. remscheidensis*) and Drygant (1984, pl. 13, fig. 11 as *Spathognathodus eosteinhornensis*) also figured specimens with similar dentition to *O. r. baccata* but the nature of the cavity is unclear on both illustrations.

The apparatus of *O. r. baccata* is unknown. It is probable that the Pb element is indistinguishable from that of *O. r. eosteinhornensis*, which is relatively over-represented in our collections (Fig. 3). Aldridge (1985, p. 90) suggested that the Pa element 'is associated with ramiform elements bearing crowded denticles of alternating size'. An Sb element with appropriate morphology (Fig. 5f) occurs in the Whitcliffe Formation and is possibly from the apparatus of *O. r. baccata*, although it has not yet been found in association with the Pa element. No other unassigned elements with alternating denticulation have been recovered from the late Silurian of the Welsh Borderland. Specimens identified (Figs 3, 4) as *O. r. cf. baccata* or *O. r. cf. eosteinhornensis* are incomplete or abraded. Many of the faunas have been significantly affected by hydrodynamic sorting and Pa element over-representation is common in other species from the same samples. This could explain the poor representation of the

other elements of the apparatus.

Jeppsson (1975) noted that conodonts of the *O. steinhornensis* (*remscheidensis*) group tend to form local populations. *O. r. baccata* probably represents a localized subspecies of *O. remscheidensis* that may have been confined to the Welsh Borderland in the late Silurian.

Ozarkodina remscheidensis eosteinhornensis (Walliser, 1964)

(Pl. 1, figs 19, 20, 22, 23, Fig. 2, Figs 5a, b)

1964 *Spathognathodus steinhornensis eosteinhornensis* Walliser: 85–86, 19–25, pl. 9, fig. 15, pl. 20, figs 7, 8, 12–16 (Pa).

1964 *Ozarkodina typica denckmanni* Ziegler; Walliser: 61, pl. 9, fig. 14; pl. 26, figs 3–11 (Pb). See Walliser (1964, p. 61) for further synonymy of Pb element.

1972 *Ozarkodina steinhornensis eosteinhornensis* Walliser; Mashkova: 83, pl. 2, figs 25–30 (whole apparatus).

1973 *Ozarkodina remscheidensis eosteinhornensis* (Walliser); Klapper: 243–244, pl. 2, fig. 5 (Pa).

For synonymy see Uyeno (1990, pp. 94–95) and add the following:

1976 *Ozarkodina typica typica* Ziegler; Ebner: 289, pl. 4, fig. 11 (Pb).

1989 *Ozarkodina steinhornensis eosteinhornensis* Walliser; Jeppsson: 28, pl. 2, fig. 4 (Pa).

1992 *Ozarkodina remscheidensis eosteinhornensis* (Walliser); Barrick & Klapper: 48, pl. 6, figs 2–4 (Pa).

Diagnosis. 'Pa with a long blade of relatively even denticulation, an inconspicuous cusp; cavity slightly posterior of mid-length with widely flaring lips, commonly pinched' (Aldridge, 1985, p. 90).

Holotype. Geologisch–Paläontologische Institut, Phillips Universität, Marburg/Lahn, FRG., No. Wa 540/4 (Pa). Figured by

Walliser, 1964, pl. 20, fig. 21, from the Cellon section, Carnic Alps.

Material. 28 elements (3 Pa and 25 Pb elements).

Localities and horizons. (Figs 3, 4) Whitcliffe Formation: sample 8/1, Diddlebury, Corve Dale, Shropshire (loc. 8). Upper Whitcliffe Formation: sample 18/1, Ludford Corner, Ludlow, Shropshire (loc. 18). Ludlow Bone Bed Member, Downton Castle Sandstone Formation: Ludford Corner, Ludlow, Shropshire (Walliser, 1966). Platyschisma Shale Member, Downton Castle Sandstone Formation (Přidolí): sample 14c, Downton, Shropshire (loc. 14c).

Description. *Pa element* (Pl. 1, figs 19, 20, 22, 23; Fig. 2) carminate, with uneven denticulation; cavity and indistinct cusp situated slightly to posterior of mid-length. Cusp triangular, posterior edge sloping at 60–70°, anterior edge at 45°. Both processes lenticular in section with distinct thickened area extending entire length of element, parallel with oral margin, at a level confluent with the uppermost extension of the cavity. Posterior process with slightly concave oral margin, decreasing slightly in height distally; second or third denticle from cusp dominant, terminal two denticles more isolated than remainder. Anterior process of constant height with straight aboral margin, longer than posterior, with five fused denticles of roughly similar proportion to anterior of cusp; terminal two denticles larger, broader and more isolated. Termination of anterior process inclined slightly to anterior, rounded postero-aborally. Cavity circular under cusp, drawn out under entire length of both processes, lips pinched and inclined slightly to posterior. Basal body present in some specimens, extending slightly beyond and below cavity lips. White matter fills cusp and all denticles, extending to top of thickened area, parallel with oral margin. Two denticles either side of cusp have accessory white matter patches between them (Fig. 2).

Pb element (Fig. 2, Figs 5a, b) angulate with cusp strongly inclined to posterior. Angle between aboral margins of processes 150–160°. Anterior process taller than posterior with proximal denticles strongly fused to cusp, denticles becoming more isolated and more erect distally, with final three denticles rapidly decreasing in size. Posterior process decreasing in height distally, bearing discrete denticles of similar size and posterior inclination. Cavity elongate, narrow, tapering distally, extending entire length of both processes. Posteriorly inclined distinct white matter patches beneath each denticle decreasing in size distally on anterior process, extending almost to the cavity for entire length of posterior process.

Remarks. The diagnosis given by Walliser (1964, p. 85) is unclear and there is disagreement regarding the limits of this subspecies. Jeppsson (1975, 1989) suggested a restricted definition including only specimens with fused, almost indistinct denticles above the cavity. Barrick & Klapper (1992) argued for a much broader concept to reflect the original inclusion by Walliser (1964) of specimens with fused denticles above the cavity and specimens with even denticulation. The Welsh Borderland material has fused denticles above the cavity but there is no development of denticulation on the basal cavity lips (Jeppsson, 1989, pl. 2, figs 1–3, omitted from synonymy); it is similar to the type material (see particularly Walliser, 1964, pl. 20, fig. 16), although the cavity is not heart shaped but almost spherical in outline and most similar to morphotype A of Bultynck (1971).

***Ozarkodina remscheidensis remscheidensis* (Ziegler, 1960)**

(Pl. 1, figs 21, 24; Fig. 2)

1960 *Spathognathodus remscheidensis* Ziegler: 194–196, pl. 13, figs 1, 2, 4, 5, 7, 8, 10, 14 (Pa).

1969 *Spathognathodus steinhornensis remscheidensis* Ziegler; Fähræus: text-fig. 1 (Pa).

1973 *Ozarkodina remscheidensis remscheidensis* (Ziegler); Klapper: 241–242, pl. 2, fig. 4 (Pa).

1986 *Ozarkodina remscheidensis remscheidensis* (Ziegler); Mawson: 49, pl. 6, figs 1–20 (whole apparatus).

For synonymy see Uyeno (1990, pp. 93, 94) and add the following:

1964 *Spathognathodus steinhornensis* ssp. indet. Walliser: pl. 21, figs 3–6 (Pa).

1969 *Spathognathodus inclinatus inclinatus* Rhodes; Wolska: 585–586, pl. 3, figs 6, 7, 12 (Pa).

1978 *Spathognathodus steinhornensis eosteinhornensis* (Walliser); Helfrich: pl. 1, figs 25–27, 33, 34 (Pa).

1991 *Ozarkodina remscheidensis remscheidensis* (Ziegler); Uyeno: pl. 1, fig. 13 (Pa).

1992 *Ozarkodina remscheidensis remscheidensis* (Ziegler); Barrick & Klapper: 49, pl. 6, figs 5–16 (Pa).

Diagnosis. A subspecies of *Ozarkodina* 'with a straight or slightly curved blade. Denticles are uneven in length, 1–2 directly behind the anterior margin are big and there is a single large denticle above the basal cavity. The margins of the basal cavity are flared and generally symmetrical to almost symmetrical' (translated from Ziegler, 1960, p. 64).

Holotype. Geologisches Landesamptes Nordrhein – Westfalen, Krefeld, FRG., No. G 88 b. Figured by Ziegler, 1960, pl. 13, fig. 4, from Pack 6, sample E, Remscheid Anticline, Germany (see Ziegler 1960, fig. 2).

Material. Two Pa elements.

Localities and horizons. (Figs 3, 4) Whitcliffe Formation: sample 31b/3, Tite's Point, Gloucestershire (loc. 31b). Upper Perton Beds: sample 161/1, Perton, Hereford & Worcester (loc. 23b). A single specimen (identified by RJA) was also reported from 60 cm below the Temeside bone bed in the Ledbury Formation (Přidolí) of the Teme River Section, Ludlow (GR SO 522 742), by Antia (1979, p. 117).

Description. *Pa element* carminate with cusp slightly to anterior of cavity. Aboral margins of processes inclined upwards away from cavity to form angle of 150°. Denticulation uneven. Posterior process decreases in height distally, although termination broken on one specimen; proximal denticle large and similar to cusp with following three denticles decreasing rapidly in size. Posterior and anterior processes thickened parallel to oral margin at level half way between aboral margin and base of denticles. Anterior process longer than posterior, of constant height, with proximal two denticles small, followed by a tiny fused denticle. Fourth, fifth and sixth denticles larger, triangular, more isolated and of roughly equal size. Terminal denticle small, extending to three quarters height of rest of blade. Cavity lips asymmetrical, more laterally flared on one side and slightly obliquely pinched either side of blade; in lateral view, cavity lips inclined parallel to posterior aboral margin. Cavity tapering, extending under entire length of anterior process and unbroken part of posterior process. White matter fills cusp and all denticles with base subparallel to aboral margin. Accessory

white matter patches anteriorly and posteriorly between cusp and first denticle, and between first and second denticles (Fig. 2).

O. remscheidensis ssp.

M element morphotype A

(Fig. 2, Fig. 5c)

?1975 *Hindeodella steinhornensis* ssp. 1. Jeppsson: 43–44, pl. 11, fig. 50.

Material. Three specimens.

Localities and horizons. (Figs 3, 4) Whitcliffe Formation: sample 8/1, Diddlebury, Corve Dale, Shropshire (loc. 8). Upper Perton Beds: sample 160/1, Perton, Hereford & Worcester (loc. 23a).

Description. Bipennate; cusp stout with convex inner face, flatter outer face, sharp anterior and posterior edges. Anterior process as downward extension of cusp with three strongly fused denticles. Posterior process increases in height distally, most complete specimen (Fig. 5c) broken after sixth denticle; proximal denticles slender, small, sharp and crowded, becoming wider and more isolated distally. Cavity flared beneath cusp, tapering gradually to termination of anterior process and present as thin groove under entire preserved part of posterior process. Basal body may be retained within flared cavity, extending below cavity lips. White matter extends under entire element apart from basal cavity lips (Fig. 2).

Remarks. A specimen of this morphology was figured as a subspecies of *O. steinhornensis* by Jeppsson (1975) although alternating denticulation typical of the *remscheidensis* (*steinhornensis*) plexus is absent. The specimen figured by Nicoll & Rexroad (1987, pl. 3.1, fig. 4) as *O. r. eosteinhornensis* is very similar, but the anterior processes on the Welsh Borderland specimens are more pointed and the specimens have a fused denticle next to the cusp on the posterior process (Fig. 5c). This is a candidate M element for the apparatus of *O. r. baccata*, but the available material is too limited to test this possibility.

M element morphotype B

(Fig. 2, Figs 5d, e)

Material. 14 specimens.

Localities and horizons. (Figs 3, 4) Whitcliffe Formation: sample 39/1, Aston Munslow, Corve Dale, Shropshire (loc. 7a); sample 31b/4, Tite's Point, Gloucestershire. Upper Whitcliffe Formation: sample 15c/2, Whitcliffe Quarry, Ludlow, Shropshire (loc. 15c); sample 77/2, Ludford Lane, Ludlow, Shropshire (loc. 17a); sample 18/1, Ludford Corner, Ludlow, Shropshire (loc. 18). Upper Perton Beds: sample 160/1, Perton Lane, Hereford and Worcester (loc. 31b); sample 162/2, Prior's Frome, Hereford and Worcester (loc. 24a).

Description. Bipennate; cusp lenticular in section with sharp anterior and posterior edges. Anterior process directed anteriorly and downwards at 45°, with two or three denticles strongly fused to base of cusp. Posterior process markedly curved downwards, proximal denticles upright and fused, distally becoming more isolated and posteriorly inclined. Cavity lips slightly flared below cusp, extending as groove along entire postero-aboral margin, but only to first denticle on anterior process. Beneath each denticle there is a white matter bar which extends mid-way to the basal margin (Fig. 2).

Remarks. M element morphotype B occurs in association with *remscheidensis* Pa elements and those of *O. snajdri* (Walliser) in

the Welsh Borderland, but is probably part of a *remscheidensis* apparatus. Similar elements have previously been assigned to taxa of the *remscheidensis* plexus (Jeppsson, 1975, pp. 39–43, pl. 10, figs 2, 3, as *Hindeodella steinhornensis scanica* Jeppsson; Savage, 1976, p. 1182, pl. 1, fig. 7 as *O. remscheidensis*; Helfrich, 1978, pl. 1, fig. 22 as *O. steinhornensis eosteinhornensis*; Savage, 1982, p. 986, pl. 1, figs 19–21 as *O. remscheidensis*).

The reconstruction of *O. r. remscheidensis* by Mawson (1986) includes a broadly similar M element, but the Welsh specimens do not possess alternating denticulation. Lane & Ormiston (1979) also figured a similar M element as *O. r. remscheidensis* but with less fused denticles. The specimen figured by Mastandrea (1985a, pl. 1, fig. 4) has a straight, not curved, posterior process, similar to that identified by Bultynck (1971, pl. 4, fig. 7) as *Neoprioniodus bicurvatus* (Branson & Mehl). A specimen figured by Borremans & Bultynck (1986, pl. 1, fig. 20) as *O. r. remscheidensis* has the same distinctive curved posterior process but the specimen is poorly preserved and the denticulation is not evident on the illustration.

Sb element.

(Fig. 2, Fig. 5f)

Material. Two specimens.

Localities and horizons. (Figs 3, 4) Whitcliffe Formation: sample 39/1, Aston Munslow, Corve Dale, Shropshire (loc. 7a); sample 8/1, Diddlebury, Corve Dale, Shropshire (loc. 8).

Description. Bipennate. Cusp lenticular in section, posteriorly inclined; posterior edge rounded, anterior edge sharp. Anterior process curved slightly inwards with alternating denticulation; repeated sequence of two broad denticles followed by narrow fused denticle, denticles increasing in size until break in specimen after fourth large denticle. Posterior process proximally straight but curved downwards distally at about 45°, increasing in height towards abrupt tip; proximal denticle small and fused to base of cusp, followed by two larger denticles. Alternating denticulation on straight part of process, with increasing size until largest denticle in third group of denticles is almost cusp sized; downcurved distal part of process with two large medial denticles flanked by smaller neighbours. Cavity small, lips flared to greater extent on inner margin. White matter reflects the inclination of the denticles on the anterior process and alternating denticulation of the posterior process (Fig. 2).

Remarks. The element possesses alternating denticulation which is a characteristic of some members of the *remscheidensis* plexus. The element possibly belongs to *O. remscheidensis eosteinhornensis*, but its posterior process is curved downwards through 45° and is unlike the Sb element figured from the apparatus of *O. r. eosteinhornensis* by Mashkova (1972, pl. 2, fig. 28). It is a possible candidate Sb element for *O. r. baccata*.

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