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

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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 biozonal scheme, based on the Cellon section in the Carnic Alps. This scheme included a late Silurian eostainhornensis Biozone characterized by Ozarkodina remscheidensis eostainhornensis (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 eostainhornensis Biozone spanning much of the Předolí, with its base above the last occurrence of Ozarkodina crispis (Walliser) and its upper limit at the first occurrence of Icriodus woschmidtii woschmidtii (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 Předolí remscheidensis Biozone.

We have made detailed conodont collections around the Ludlow–Předolí 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 mm 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 eostainhornensis from the Welsh Borderland. In this contribution we provide the first description of associated members of the remscheidensis plexus that occur with O. r. eostainhornensis, 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 (Aldridge & Schönlaub, 1989) or geographically separated (e.g. Apsidognathus taberculatus taberculatus Walliser, 1964 and A. r. 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 confinens), 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,

Table: Subspecies of Ozarkodina remscheidensis

| Country | Subspecies |
|---------|------------|
| California | O. r. remscheidensis remscheidensis (Walliser) |
| Indiana | O. r. remscheidensis remscheidensis (Walliser) |
| Missouri | O. r. remscheidensis remscheidensis (Walliser) |
| New Hampshire | O. r. remscheidensis remscheidensis (Walliser) |
| New Jersey | O. r. remscheidensis remscheidensis (Walliser) |
| Nevada | O. r. remscheidensis remscheidensis (Walliser) |
| Oklahoma | O. r. remscheidensis remscheidensis (Walliser) |
| Virginia | O. r. remscheidensis remscheidensis (Walliser) |
| Utah | O. r. remscheidensis remscheidensis (Walliser) |
| Yukon | O. r. remscheidensis remscheidensis (Walliser) |
| U.S.A. | O. r. remscheidensis remscheidensis (Walliser) |
| Canada | O. r. remscheidensis remscheidensis (Walliser) |
| Australia | O. r. remscheidensis remscheidensis (Walliser) |
| Europe | O. r. remscheidensis remscheidensis (Walliser) |
| Pakistan | O. r. remscheidensis remscheidensis (Walliser) |
| U.K. | O. r. remscheidensis remscheidensis (Walliser) |

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

**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 2 m 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 Liangibby 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 denticles fused to proximal denticle. Remaining denticles increasingly smaller distally as process diminishes posteriorly 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 three quarters medial height.

**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), ×55: Fig. 1. Lateral; Fig. 4. Oral.  
**Figs 2, 5.** PM X 1293, sample and locality as for Fig. 1, ×45: Fig. 2. Lateral; Fig. 5. Oral.  
**Figs 3, 6.** PM X 1294, sample and locality as for Fig. 1, ×50: Fig. 3. Lateral; Fig. 6. Oral.  
**Figs 7, 10.** PM X 1295, sample 161/1, Upper Perton Beds, Hereford, & Worcester (loc. 23b), ×45: Fig. 7. Lateral; Fig. 10. Oral.  
**Figs 8, 11.** PM X 1296, sample and locality as for Fig. 1, ×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), ×45: Fig. 9. Lateral; Fig. 11. Oral.  
**Figs 13, 16.** PM X 1298, sample and locality as for Fig. 1, ×45: Fig. 13. Lateral; Fig. 16. Oral.  
**Figs 14, 17.** PM X 1297, sample and locality as for Fig. 1, ×45: Fig. 14. Lateral; Fig. 17. Oral.  
**Figs 15, 18.** PM X 1157, sample and locality as for Fig. 8, ×40: Fig. 15. Lateral; Fig. 18. Oral.  
**Figs 19, 20, 22, 23.** *Ozarkodina remscheidensis eosteinhornensis* (Walliser, 1964).  
**Figs 19, 20.** Pa element, PM X 1164, sample 8/1, Whitcliffe Formation, Diddlebury, Corve Dale, Shropshire (loc. 8), ×30: Fig. 19. Lateral; Fig. 22. Oral.  
**Figs 21, 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), ×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), ×45: Fig. 21. Lateral; Fig. 24. Oral.
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Plate 1
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, 342. 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 budding plane assemblage to reconstruct the apparatus of *O. steinhornensis* and showed that it possessed a 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

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

| Species                  | Sample | 5c | 39 | 8 | 14c | 74 | 15c | 77 | 18 | 20 | 160 | 161 | 24a | 162 | 31b | 31b | 31b | 33 | 33 | 33 |
|--------------------------|--------|----|----|---|-----|----|----|----|----|----|-----|-----|-----|-----|-----|-----|-----|----|----|----|
|                          | 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 | O. remscheidensis baccata | 1260 | 238 | 57 | 194 | 524 | 261 | 67 | 195 | 551 | 1320 | 1627 | 1010 | 1744 | 343 | 435 | 486 | 123 | 176 | 45 |
|                          | O. r. cf. baccata | 2 | 3 | 2 | 1 | 1 | 1 | 2 | 3 | 3 | 2 | 1 | 1 |
|                          | O. r. eosteinhornensis | 2 | 2 | 1 | 1 | 1 | 1 | 5 | 1 | 2 | 1 | 1 | 1 | 1 |
|                          | O. r. cf. eost. | 2 | 1 | 6 | 1 | 5 | 1 | 1 | 1 | 1 |
|                          | O. r. remscheidensis | 2 | 2 | 1 | 3 | 1 | 1 | 1 | 2 |
|                          | O. r. ss. Pa element fragments | M morph A | 1 | 1 | 1 | 3 | 1 | 1 | 2 |
|                          |                          | M morph B | 2 | 2 | 2 | 2 | 2 | 2 | 2 |

**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).
fused above the cavity. Philip (1966, fig. 8A) figured a similar Pa
element from the Lower Devonian of Australia as Spathognathodus steinhornensis buchanensis Philip, but the denticles vary
from relatively large, crowded and almost discrete to small, 
crowded and fused. The anteriormost denticles of S. s. 
buchanensis 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. 
buchanensis 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; Jepps-
son: 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 Uni-
viersität. Marburg/Lahn, FRG., No. Wa 540/4 (Pa). Figured by
Walliser, 1964, pl. 20, fig. 21, from the Celon 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 Shropshire (loc. 14c).

**Material.** Castle Sandstone Formation (Piidoli): sample 14c, Downton, Shropshire (loc. 14c). Upper posterior edge sloping at 60-70°, anterior edge at 45°. Both carminate, with uneven denticulation; cavity and indistinct cusp confluent with the uppermost extension of the cavity. Extending entire length of element, parallel with oral margin, at dominant, terminal two denticles more isolated than remainder. 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 elongate, narrow, tapering distally, extending to three quarters height of rest of blade. Cavity lips pinched and inclined slightly to posterior. Basal inclination. 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).
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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 _Neopriioniodus bicurvatarius_ (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). Upper Perton Beds: sample 160/1, Pertton, Hereford & Worcester (loc. 23a).

**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, 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 oosteinhorensis_; Savage, 1982, p. 986, pl. 1, figs 19–21 as _O. remscheidensis_).

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