AN *AMORPHOGNATHOIDES* ZONE CONODONT FAUNA FROM THE SILURIAN OF THE RINGERIKE AREA, SOUTH NORWAY

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Aldridge, R. J.: An *amorphognathoides* Zone conodont fauna from the Silurian of the Ringerike area, south Norway. *Norsk Geologisk Tidsskrift,* Vol. 54, pp. 295–303. Oslo 1974.

A limestone sample from 'Stage' 8-Silurian strata of Akerløkken in the Ringerike area has yielded a number of brachiopods and a diversified conodont collection. Faunal lists are presented and the taxonomy of the 49 conodont element-types identified is discussed. A new multi-element species, *Apsidognathus walmsleyi* sp. nov., is named and described. The conodont fauna compares with those of the *amorphognathoides* Zone of Austria and the *P. amorphognathoides* Assemblage Zone of Britain and a high upper Llandovery (C_6) or early Wenlock age is indicated.

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Following the classic work of Walliser (1964) on the Silurian conodonts of Europe, a large number of publications have recorded and described Silurian conodont faunas from many parts of the world. However, much less is known about the stratigraphical and geographical distribution of conodonts in the Silurian than in the more extensively studied Ordovician, Devonian and Carboniferous Systems. The information that has been accumulated to date is sufficient to underline the value of conodonts as tools of Silurian stratigraphy, and the consolidation and extension of present knowledge will undoubtedly increase that value. This contribution adds information on the composition of conodont faunas referable to the *amorphognathoides* Zone and presents the first detailed record of a Silurian conodont fauna from Norway.

In 1965, Dr. V. G. Walmsley collected a number of rock samples from the Silurian of the Ringerike area, Norway. Dr. Walmsley has examined the brachiopods from these samples and the author has processed the rock to recover the associated conodonts. Only four conodont collections were obtained, three of which were not large and provided little stratigraphical or palaeontological information. A single limestone sample, from the northwest end of Steinsfjorden, yielded abundant and diverse conodont elements. The sample was collected from a cliff section 0.2 km along the track leading north from Akerløkken, 1 km WSW of Grantopp, grid reference 733669. The strata here are referable to 'Stage' 8 of the local stratigraphic scheme established by Kiær (1908), whose map of the Ringerike area records them as undifferentiated 8a-b. Kiær and, subsequently, Henningsmoen (1960: pl. 7) have suggested that a broad correlation exists between 'Stage' 8 of the

Oslo and Ringerike areas and the Wenlock of Britain. Bassett & Rickards (1971: 254, fig. 1), however, recognized that Kiær's stages were diachronous and that 'Stage' 8 in the Ringerike area ranged from the uppermost Llandovery (C_6) into the Lower Wenlock. An age within this range is also indicated for the sample by the poorly preserved brachiopods, which have been identified by V. G. Walmsley and M. G. Bassett as:

Atrypa 'reticularis' (Linnaeus)	21 specimens
Leptaena sp.	11 specimens
Isorthis sp.	20 specimens
?Protochonetes sp.	5 specimens
Eoplectodonta sp.	2 specimens
Howellella cf. *H. elegans* (Muir-Wood)	1 specimen
Protomegastrophia walmstedti (Lindström)	1 specimen

Walmsley (1973: pers. comm.) reported that the general fauna indicates a late Llandovery to Wenlock age and that the presence of *P. walmstedti* indirectly suggests a high upper Llandovery (C_6) age. *P. walmstedti* occurs in the Lower Visby Marl of Gotland, where it is associated with *Costistricklandia lirata lirata* (J. de C. Sowerby) and abundant specimens of the coral *Palaeocyclus porpita* (Linnaeus), together indicative of C_6.

The conodont fauna

More than 600 well-preserved conodont specimens were recovered from the limestone sample by acetic acid digestion and bromoform separation. The fauna is diverse, with 49 different element-types identified, but it is at present impossible to estimate the number of natural conodont species these represent. It is now accepted that the conodont-bearing organism was provided with an apparatus comprising several conodont elements, and the reconstruction of a number of such apparatuses has been achieved by the logical and numerical analysis of collections of disjunct elements. In this way, partial or complete reconstructions of several Silurian conodont apparatuses have been proposed (Walliser 1964, 1972, Jeppsson 1969, 1971, 1972, Schönlaub 1971). In the Ringerike collection, only 12 of the element-types can be assigned with confidence to established reconstructed apparatuses, and, with a few exceptions, insufficient evidence exists for attempts to be made at further reconstructions incorporating the remaining forms.

The current situation, with some forms referable to apparatuses while others are not, results in the application of a dual taxonomy to conodonts. Apparatuses that are known from natural occurrences or have been reconstructed carry a single 'multi-element' name, applicable to all their components. Elements which cannot be referred to an apparatus retain their form-taxonomic designations. This approach, despite its present deficiencies, is maintained herein, as it is envisaged that, in time, most conodont elements will be referred to apparatuses and an almost total multi-element taxonomy will be possible.

The conodont fauna recovered from the Ringerike sample may therefore be tabulated as follows:

Multi-element species

Carniodus carnulus Walliser	61 elements
Ozarkodina excavata (Branson & Mehl)	37 elements
Pterospathodus amorphognathoides Walliser	67 elements
Apsidognathus walmsleyi sp. nov.	39 elements

Form-species

Acodus curvatus Branson & Branson	6
Ambalodus galerus Walliser	18
Astrognathus tetractis Walliser	4
Carniodus carnicus Walliser	2
Diadelognathus excertus Nicoll & Rexroad	1
Diadelognathus nicolli Aldridge	1
Diadelognathus? sp.	8
Distomodus? egregius (Walliser)	9
Distomodus kentuckyensis Branson & Branson	3
Distomodus triangularis tenuirameus (Walliser)	1
Distomodus triangularis triangularis (Walliser)	6
Exochognathus caudatus (Walliser)	6
Exochognathus detortus (Walliser)	5
Exochognathus? expansus (Nicoll & Rexroad)	3
Exochognathus latialatus (Walliser)	6
Exochognathus sp.	1
Hadrognathus staurognathoides Walliser	4
Hibbardella? trichonodelloides (Walliser)	1
Ligonodina petila Nicoll & Rexroad	2
Ligonodina salopia Rhodes	12
Ligonodina silurica Branson & Mehl	4
Ligonodina? variabilis Nicoll & Rexroad	12
Ligonodina spp.	14
Lonchodina greilingi Walliser	2
Lonchodina walliseri Ziegler	6
Lonchodina spp.	5
Neoprioniodus costatus costatus Walliser	13
Neoprioniodus planus Walliser	1
Ozarkodina sp.	1
Paltodus costulatus Rexroad	2
Paltodus debolti Rexroad	2
Paltodus dyscritus Rexroad	4
Paltodus migratus Rexroad	5
Panderodus simplex (Branson & Mehl)	41
Panderodus cf. *P. staufferi* (Branson, Mehl & Branson)	3
Panderodus unicostatus (Branson & Mehl)	128
Panderodus sp.	1
Sagittodontus edentatus (Branson & Branson)	1
Spathognathodus cf. *S. gulletensis* Aldridge	9
Synprioniodina silurica Walliser	11
Trichonodella inconstans Walliser	7
Trichonodella symmetrica (Branson & Mehl)	11
Trichonodella spp.	14

The specimens are deposited in the conodont reference collection of the Department of Geology, University of Nottingham. Descriptions and illustrations of almost all the above forms may be found in Aldridge (1972) and in earlier works, particularly Walliser (1964) and Nicoll & Rexroad (1968).

Detailed systematic treatment and illustration of the complete Ringerike collection is considered unnecessary, but some discussion about the constitution and taxonomy of the reconstructed apparatuses is desirable.

The multi-element species *Carniodus carnulus,* according to Walliser's (1964: 14, 1972: 76) reconstruction, comprises the four element-types formerly designated as the form-species *Carniodus carinthiacus* Walliser, *C. carnulus* Walliser, *C. carnus* Walliser and *Neoprioniodus subcarnus* Walliser. All four element-types are present in similar numbers in the Ringerike collection. As partial evidence for this reconstruction, Walliser (1964: 17) cited the apparent fusion of some specimens of the form-species *C. carnulus* with specimens of *C. carnus* and *N. subcarnus,* the resulting elements displaying two basal cavities and two cusps. A similar apparent fusion of *C. carnulus* with *Exochognathus latialatus* was illustrated without comment by Walliser (1964: pl. 6, fig. 15), and was noted by Aldridge (1972: 179). This may indicate that *E. latialatus* elements should be included in the *Carniodus carnulus* apparatus. Although *E. latialatus* is consistently less abundant than the other representatives, the five elements do tend to occur in association (e.g. Walliser 1964, samples 11–12A; Aldridge 1972, sample Cowleigh Park 1, the Ringerike collection).

The reconstructed apparatus assigned to *Ozarkodina excavata* (Branson & Mehl) is well-known, but the confused history of nomenclature of this species serves to illustrate the problems caused by the transition from form taxonomy to multi-element taxonomy. The apparatus was first reconstructed by Walliser (1964: 14), who applied the informal name of Conodonten-Apparat. Jeppsson (1969), as first nomenclatural reviser, assigned the binomen *Hindeodella excavata* (Branson & Mehl), but Lindström (1970) and Klapper & Philip (1971) pointed out that *Hindeodella* was not a valid generic designation for the apparatus and transferred it to *Ozarkodina.* Walliser (1972) pointed out the additional problems that result from the strict application of the law of priority in the choice of specific name. Since it is apparent that different elements within an apparatus commonly evolved at different rates and that closely similar elements may occur in widely different apparatuses, the first-named element may not, in fact, characterise only that apparatus to which its name is subsequently restricted. Walliser (1972: 75), therefore, suggested the application of the following *modus operandi:* – 'For the case that the law of priority is used for uniting the elements of a single taxon, this animal takes the name of the earliest-described characteristic element.' Applying his own approach to the apparatus in question, Walliser rejected the specific name *excavata,* and employed instead the specific name *inclinata,* formerly borne by the spathognathodontan element. This designation, however, has not achieved general acceptance, and the legally valid binomen *Ozarkodina excavata* is used herein. The multi-element species *Ozarkodina excavata* is represented in the Ringerike fauna by all six element-types; spathognathodontan, ozarkodinan, neoprioniodontan, hindeodellan, plectospathodontan and trichonodellan.

Two element-types, one platform and one ozarkodinan, are included in the apparatus of *Pterospathodus amorphognathoides*. Although other elements have not yet been referred to this apparatus, it is probable that these two elements represent only a partial reconstruction (Walliser 1972: 76).

The association of a platform element and a pygodiform element in *Apsidognathus tuberculatus* Walliser was recorded by Walliser (1972: 76), and a similar association is recognised in the Ringerike fauna. The two element-types from Ringerike, however, exhibit morphological differences from those of *A. tuberculatus,* and they are referred to the multi-element species *Apsidognathus walmsleyi* sp. nov. As with *Pterospathodus amorphognathoides,* the *Apsidognathus* apparatuses may be only partially reconstructed and a possible additional candidate for inclusion is the form-species *Ambalodus galerus,* which is commonly found in association with the platform and pygodiform elements (e.g. Walliser 1964, samples 10C–10E, 11A, 11D, 11F, Aldridge 1972, sample Gullet 4, the Ringerike collection).

Several of the other form-species represented in the collection have been referred by authors to multi-element apparatuses. Schönlaub (1971: 44), for instance, suggested a combination of *Hadrognathus staurognathoides* and *Neospathognathodus latus* Nicoll & Rexroad. However, Walliser (1964: 35) recorded 25 specimens of *H. staurognathoides* from the Carnic Alps, but no *N. latus,* and 70 specimens of *H. staurognathoides* have been described from the Welsh Borderland without the association of *N. latus* (Aldridge 1972: 180). As Schönlaub's collections contained very few specimens of these two forms, the evidence for his reconstruction appears to be limited.

The four form-species *Ligonodina salopia, L. silurica, Lonchodina greilingi* and *Trichonodella inconstans* occur in apparatuses of the genus *Kockelella* (Klapper & Philip 1971: 449, Walliser 1972: 77). These form-species occur in the Ringerike collection, but the characteristic platform and ozarkodinan elements of *Kockelella* are absent. It is possible that these forms are from an apparatus ancestral to *Kockelella,* which bore different platform and ozarkodinan elements or lacked them altogether.

Elements of the genus *Panderodus* have been combined into apparatuses from studies on Ordovician collections. Bergström & Sweet (1966), for example, suggested that the form-species *Panderodus gracilis* (Branson & Mehl) and *Panderodus compressus* (Branson & Mehl) formed an apparatus with a ratio of 2:1 between the two element-types. Webers (1966), however, suggested that the *Panderodus gracilis* apparatus consisted of only a single element-type. The two fused clusters of *Panderodus* elements recorded by Pollock (1969) from the Silurian of Indiana appear to be of one element-type, although these almost certainly represent only part of an apparatus. Of the forms common in the Ringerike fauna, *Panderodus unicostatus* may form a single element-type apparatus or may be associated with *Panderodus simplex,* with which it commonly occurs in an approximate 2:1 ratio (e.g. Aldridge 1972: tables 3, 4).

Correlation

The collection contains almost all the forms characteristic of the *amorphognathoides* Zone of Walliser (1964: pl. 6, figs. 6–15), the form-species *Spathognathodus ranuliformis* being the only absentee. With the same exception all forms considered characteristic of the *Pterospathodus amorphognathoides* Assemblage Zone in Britain (Aldridge 1972: 153, fig. 11) are present. However, the association of forms in the Ringerike fauna is a little different from any previously recorded. The *amorphognathoides* Zone of the Carnic Alps has not yielded *Ozarkodina excavata, Diadelognathus* or spathognathodontans of the *gulletensis* type, and the *Apsidognathus* apparatus is different, indicating a geographical or chronological variation in the genus. Elements referable to *Apsidognathus* have not been recorded at all from the *P. amorphognathoides* Zone of the Welsh Borderland. These differences, however, are minor and a correlation with the *amorphognathoides* Zone of the Carnic Alps and the *P. amorphognathoides* Zone of Britain is clear. The *P. amorphognathoides* Zone in Britain occurs in strata of high upper Llandovery (C_6) and lower Wenlock age, although the precise upper limit is unknown (Aldridge 1972). The age of the sampled horizon at Akerløkken thus indicated by the conodont fauna is consistent with that deduced from the brachiopod evidence.

Systematic description

Genus *Apsidognathus* Walliser 1964

Apsidognathus walmsleyi sp. nov.

Figs. 1A–1D.

Holotype. – Specimen WN. 13/2.

Type locality and horizon. – Cliff section, 0.2 km along track north of Akerløkken, Ringerike area (grid ref. 733669). The strata are referred to 'Stage' 8 of Kiær, and the sample is no. WN. 13 of V. G. Walmsley (University College of Swansea).

Material. – 30 specimens of the platform element, 9 specimens of the pygodiform element.

Diagnosis. – Platform element with a short free blade and a sub-elliptical platform that is broader than long and ornamented by a number of rows of nodes which radiate from the carina. Pygodiform element with a short free blade and a flared platform which is steeply inclined posteriorly and bisected by a ridge extending beyond the posterior limit of the platform.

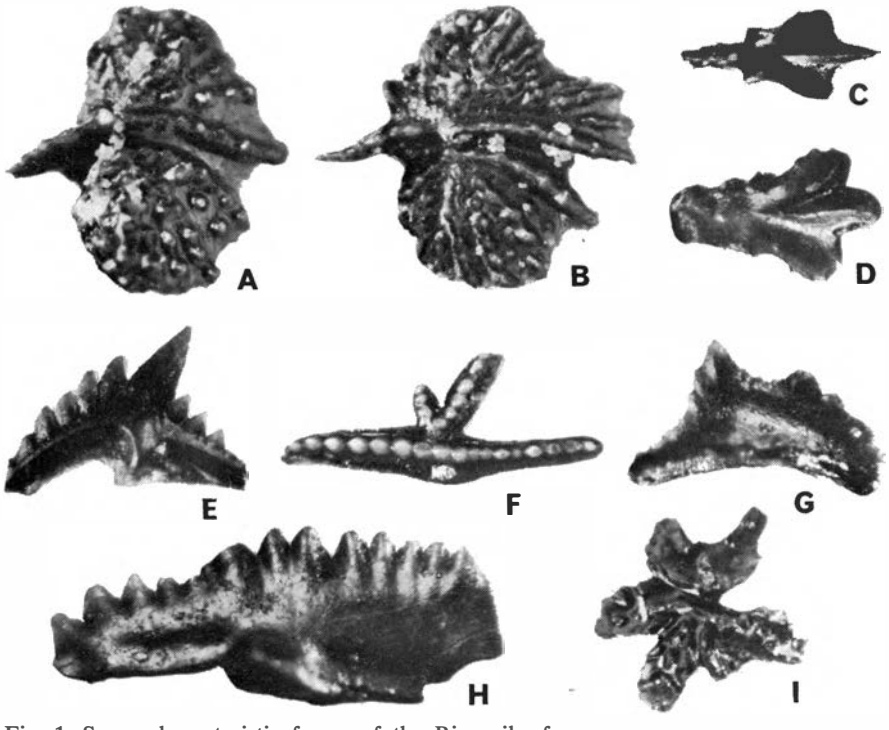

Fig. 1. Some characteristic forms of the Ringerike fauna.
A–D. *Apsidognathus walmsleyi* sp. nov.
A. Platform element. Oral view of holotype WN. 13/2.
B. Platform element. Oral view of specimen WN. 13/1.
C. Pygodiform element. Oral view of specimen WN. 13/4.
D. Pygodiform element. Oral view of specimen WN. 13/3.
E–F. *Pterospathodus amorphognathoides* Walliser.
E. Ozarkodinan element. Lateral view of specimen WN. 13/7.
F. Platform element. Oral view of specimen WN. 13/6.
G. *Ambalodus galerus* Walliser. Lateral view of specimen WN. 13/8.
H. *Spathognathodus* cf. *S. gulletensis* Aldridge. Lateral view of specimen WN. 13/5.
I. *Hadrognathus staurognathoides* Walliser. Oral view of specimen WN. 13/9.
All illustrations × 40.

Description. – The platform element exhibits a short free blade that continues as a gently curved, nodose carina more or less medially across the very broad, arched platform. The margins of the platform are irregular and the outline is sub-elliptical, the lateral extension being up to 1½ times the anterior-posterior length. The entire aboral surface of the platform is deeply excavated and the cavity extends as a groove under the free blade. The oral surface of the platform is ornamented by nodes that are arranged in rows radiating away from the carina. On the inner side of the unit, the two rows of nodes adjacent to the carina meet to form an arcuate ridge, curved convex to the carina and separated from it by a low, unornamented area that is widest at the posterior end. Within the arc, short nodose ridges diverge from the point where the arc is at its closest proximity to the carina, somewhat

anterior of its midpoint. The outer side of the platform also bears nodose ridges, diverging not from a common point but spaced at intervals along the carina. In a few large specimens the nodose ornamentation has coalesced to such an extent that the pattern of distribution is obscured.

The pygodiform element is bilaterally symmetrical about the anterior-posterior axis and consists of a short free blade and a platform that is flared and steeply inclined posteriorly. The blade may be laterally thickened so that the entire unit is platform-like. A central ridge crosses the platform in continuation of the line of the blade, from which it is separated by a smooth, flat area. The ridge increases in height posteriorly, as the platform dips aborally, and extends beyond the posterior limit of the platform to produce a pointed posterior tip. The oral surface of the platform is unornamented, but the lateral margins are commonly a little upturned, and may be serrated. The entire aboral surface of the element is excavated, the cavity being deepest beneath the centre of the platform.

Remarks. – The platform element of *A. tuberculatus* Walliser differs from that of *A. walmsleyi* sp. nov. in being markedly longer than broad and in exhibiting a platform ornamentation that is dominated on each side by two nodose rows which radiate from near the midpoint of the carina (Walliser 1964: pl. 12, figs. 16–22). The pygodiform specimens of *A. tuberculatus* illustrated by Walliser (1964: pl. 12, figs. 8–14) show a shorter free blade and a platform that is conspicuously corrugated at its lateral margins. There is no central ridge to the platform and the posterior end of the unit is indented. Pygodiform elements from the Welsh Borderland referable to *A. tuberculatus* (Aldridge 1972: 210, pl. 3, fig. 2) do exhibit a central ridge, but it is considerably less prominent than that exhibited by the present specimens.

Acknowledgements. – Dr. V. G. Walmsley, who kindly supplied the samples for conodont study, gratefully acknowledges preliminary guidance on the Ringerike area from Dr. J. H. McD. Whitaker and help during fieldwork from Professor G. Henningsmoen. The author is also grateful to Dr. Walmsley and to Mr. A. M. Honeyman for reading and discussing the manuscript. The conodont specimens were photographed by Mr. D. J. Jones.

August 1973

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