

Latest Silurian Conodonts from Klouk, Czechoslovakia

Lennart JEPPSSON

with 1 Text-figure and 3 Plates

JEPPSSON, Lennart: Latest Silurian Conodonts from Klouk, Czechoslovakia. – *Geologica et Palaeontologica*, 23:21–37, 1 Text-fig., 3 Pls., Marburg/Lahn, 30. 9. 1989.

Eight Late Silurian – Early Devonian, often sympatric, species of *Belodella* are limited on the base of their apparatuses, all of which include an undenticulated two-edged element and up to seven other elements. Three of these species are identified at Klouk: *B. mira*, in which all the elements are strongly compressed with a very broad anterior flange on the base; *B. sp. S.*, in which all elements are small with a narrow basal cavity and some elements display denticles on the anterolateral edges; *B. anomalis*, in which some of the elements have a fan. The stratigraphically very important taxon *Ligonodina elegans detorta* is represented by typical elements. *Pseudooneothodus beckmanni*, *Panderodus sp.*, *O. confluens*, *O. e. excavata*, and *Ligonodina sp.* are also present. The *Ozarkodina steinhornensis* group is represented by two very different taxa: *O. eosteinhornensis* s.s. and an off-shore ecotype of *O. s. remscheidensis*.

In many species, populations off-shore of the particular zone of optimal conditions comprise smaller, more gracile elements with neotenic characters. Populations on the nearshore side of the optimal area are also smaller, but are robust and stunted.

Acht spätsilurische bis frühdevonische, oft sympatrische, *Belodella*-Arten werden auf Grund ihrer Apparate abgegrenzt, die alle ein ungezähneltes zweikantiges Element und bis zu sieben weitere enthalten. Drei dieser Arten kommen in Klouk vor: *B. mira*, bei der alle Elemente stark zusammengedrückt sind und einen sehr breiten vorderen Wulst an der Basis besitzen; *B. sp. S.*, bei der alle Elemente klein sind und eine enge Basalgrube haben und einige Elemente Zähnnchen an den anterolateralen Kanten zeigen; *B. anomalis*, bei der einige Elemente einen Fächer besitzen. Die stratigraphisch wichtige *Ligonodina elegans distorta* ist durch typische Elemente vertreten, auch *Pseudooneothodus beckmanni*, *Panderodus sp.*, *O. confluens*, *O. e. excavata* und *Ligonodina sp.* kommen vor. Die *Ozarkodina steinhornensis*-Gruppe ist durch zwei sehr unterschiedliche Taxa vertreten: *O. eosteinhornensis* s.s. und *O. e. remscheidensis* in einer ökologischen Form der offenen See.

Bei vielen Arten enthalten die Populationen aus dem seewärts der Zone optimaler Lebensbedingungen gelegenen Gebiet kleinere, zierlichere Elemente mit neotenenischen Merkmalen. Auch die Populationen, die von landwärts der optimalen Zone stammen, sind kleiner, aber robust und im Wachstum gehemmt.

Address of the author: Lennart Jeppsson, Department of Historical Geology and Paleontology, Sölvegatan 13, S-223 62 Lund, Sweden.

Contents

Autecology	21	<i>Ozarkodina excavata</i>	27
Taxonomy	22	<i>Ozarkodina confluens</i>	27
<i>Pseudooneothodus beckmanni</i>	22	<i>Ozarkodina steinhornensis</i>	27
<i>Belodella</i>	22	<i>Ozarkodina s. eosteinhornensis</i>	28
Elements	22	<i>Ozarkodina s. remscheidensis</i>	28
Element frequencies	23	Acknowledgements	30
Taxonomy	23	Literature	30
Nomenclature	23		
Distribution	24		
Ecology	24		
<i>Belodella mira</i>	24		
<i>Belodella sp. S</i>	25		
<i>Belodella anomalis</i>	25		
<i>Panderodus sp.</i>	26		
<i>Ligonodina elegans detorta</i>	26		
<i>Ligonodina sp.</i>	26		

Autecology

Interpretation of the faunal sequence at Klouk and its representativeness requires knowledge of the characters of the environment in which the faunas lived. Understanding of the autecology of the conodonts involved contributes to that interpretation. Three ecotypes are identified (below) in *O. s.*

remscheidensis. Corresponding ecotypes are found in several other taxa as well and a model that explains their presently known distribution may be formulated. Populations with small delicate elements inhabited the most offshore areas occupied by the taxon, populations with large robust elements are found where the taxon had its ecologic optimum, and populations with stunted, small but robust elements dwelt in sub-optimal shallow water environments. The location of optimal environments varied with the species. In the case of *L. elegans* it was in the low diversity Beyrichienkalk environments south of Gotland (MARTINSSON 1963), where the conodont fauna essentially consists of only *L. elegans* and the *O. steinhornensis* group; *L. elegans* is only represented by rare small delicate elements in environments with a higher conodont diversity. In the latest Silurian and earliest Devonian, *O.s. remscheidensis* had its optimum seaward of *L. elegans* and therefore all three ecotypes are known. The offshore turbidite area at Klonek was inhabited by a population with delicate elements, the shallow water Beyrichienkalk fauna included a population with small but robust elements, while populations with larger elements lived in intermediate environments like Untenruden in the Rheinische Schiefergebirge (ZIEGLER 1960). Judging from the size of the elements, Klonek did not provide optimal conditions for any of the well-known taxa found there. How suitable the environment was for *Belodella* is not resolvable in the present state of knowledge of the ecology of this genus. However, Klonek clearly represents a biofacies where *Belodella* is important, whereas that genus is absent from both the Beyrichienkalk and the Ockerkalk at Untenruden. The biofacies with *Belodella* was the most offshore one identified by ALDRIDGE & JEPPSSON (1984).

Taxonomy

Pseudooneotodus beckmanni (BISCHOFF & SANNEMANN 1958)

The specimens found are small, and are not adequate to permit consideration of the number of species in this genus that may have existed during this time. Therefore they are conventionally referred to *P. beckmanni*.

Belodella

In order to describe the three species represented at Klonek it is necessary to first give some general remarks on the genus. Five different species are well represented in my late Silurian collections from Bohemia and Gotland. Other late Silurian species include *B. silurica* BARRICK 1977, one or more undescribed species represented by rare specimens in my other collections, and possibly *B. erecta* which occurs so close to the Silurian-Devonian boundary that it may well have appeared in the late Silurian. However, my comments below are mainly based on those species which I have been able to study personally.

Elements. – In order to distinguish the different elements in a species and to identify homologous elements, several characters are important. One is the nature of the edges of the cusp, which are continuations of the posterior and inner lateral edges of the base in asymmetric elements. On some elements there is an additional, outer anterolateral edge to the base, ending proximally on the cusp. The tr element differs in that the cusp is also three-edged, with two anterolateral and one posterior edge. All three connect with the edges of the base. The elements within each species differ in the depth of the basal cavity and in the form of the base, which may be

straight or weakly or strongly laterally curved proximally. The cusp may be strongly laterally compressed or rounded in cross section, strong or weak, and proclined or more or less erect. One or more of the edges may be denticulate.

These characters are more or less linked, and some elements have unique combinations that permit identification of homologues. Conflicting opinions regarding the designation of the elements of *Belodella* and related taxa have been published, and I think that, as yet, we lack enough knowledge to apply standard designations. Therefore I will use provisional informal designations here.

One group of elements with one anterior edge – the f elements – is undenticulated in all studied species, has the shallowest basal cavity, and a strongly compressed two-edged cusp. It is certainly homologous with the compressed element of *Panderodus*, which was described as falciform by SWEET (1979). In, for example, *P. recurvatus* and *P. spasovi* this group includes two distinct elements. There is a certain variation in studied species of *Belodella*, and ultimately it may be possible to similarly distinguish two elements. In most species these elements are sickle-shaped with a more or less compressed base, but in *B. mira* the compressed element is specialized (see below), at least in late Pridolian populations. It is the only undenticulated element in most species (compare BARRICK 1977; KLAPPER & BARRICK 1983).

Another easily identified group of elements – u elements – with a single anterior edge has a basal cavity of average depth and the same symmetry as the type specimen of *Panderodus unicostatus*. Thus the anterior edge is markedly anterolateral, the base is markedly curved inwards and the posterior edge is median on the distal part of the base and twisted to an oblique outer lateral position on the proximal parts of the base and cusp. In all studied species of *Panderodus* this group includes two kinds of elements, which in their common ancestor probably only deviated in the location of the anterolateral costa, the direction of its edge, and the curvature of the element (in advanced taxa the two elements may be very different). A variation in the position of the anterolateral edge is found in studied *Belodella* taxa, and it is possible that with larger and better preserved collections it will be possible to distinguish two u elements in *Belodella*.

The f and u elements can be identified in all studied species of *Belodella*, but the identification of homologous elements among the other elements sometimes causes problems, and it is easiest to use one species – *B. resima* – as a reference.

Belodella resima has three kinds of slender elements – d elements – with a basal cavity deeper than that of the u elements and with a weak cusp. Two of them have a base that is slightly curved inwards, the doc element (Pl. 1, Fig. 18) has one anterolateral edge and the dtc element has two anterolateral edges on the base. The third element, the dts element, also has two edges but a straight base.

The a elements (Pl. 1, Fig. 18) of *Belodella resima* are more robust and have a basal cavity of average depth; that is, it is about as deep as in the u elements and much more broadly triangular in cross-section than in the dt elements. The base of the atc element is about as curved as that of the u element, whereas that of the ats element is nearly straight.

I have also found some specimens that have the general shape of the a elements but differ in that both anterolateral edges continue onto the cusp, and the specimens seem to be perfectly symmetrical. They are much rarer than all the other groups of elements; it is likely that these specimens represent the tr element, and below I will use that designation.

The brief description above was based on a collection from strata with *M. ultimus* from Lochkov. These specimens are very small and juvenile, whereas the ones that derive from a toptype sample, kindly sent by Dr. Barry J. Cooper, are much

larger and more mature. No one-edged denticulated element was found in the latter fauna, neither by PHILIP (1965) nor by me. Although my collection is small and preservational bias cannot be ruled out, it may be that the u and doc elements had acquired an outer anterolateral costa too, through ontogenetic growth or through evolution – which makes them similar to the atc and dtc elements, respectively.

In the other studied species the elements are less differentiated, and two or more of the groups may merge. The designations have been adjusted accordingly.

Element frequencies: The relative numbers of recovered elements are influenced by preservational effects so that in each species more robust elements are more abundant than those that are less robust. However, some conclusions regarding the original element frequencies can be drawn. Together the a and d elements are about as frequent as the combined u and f elements. The u and f elements are usually about equally frequent. The tr element is rarest – as expected. In the descriptions below, unexpectedly low frequencies are noted.

Taxonomy: It is to be expected that other populations deviate more or less strongly from those described here. Further, many collections may not include enough specimens for all elements to be well represented. Thus, some characters that definitely establish the presence of a species are useful even if only one or a few elements can be identified. The following characters have been found useful:

Belodella sp. G (Pl. 1, Figs. 16, 17) is the only species with an extra posterior edge on the proximal part of the base in all studied elements except the f elements. In the u element (Pl. 1, Fig. 16) this is found well inside the true posterior edge, but in the other elements it can be so close to the latter that it is very difficult to see, even under high magnification. Distally on the base it becomes fused with the true posterior edge. In my collections the denticulation is so feeble that wear and recrystallisation have obliterated it nearly completely in some specimens. Some specimens lack any trace of denticulation.

Belodella sp. B has an extra anterior edge on some of the elements, so that one element has three edges in the anterior part of the base, one inner anterolateral, one approximately anterior, and one outer anterolateral. The species was found by REXROAD & CRAIG (1971: Pl. 79, Figs. 1–7) although they did not illustrate a specimen of this most characteristic element.

Belodella resima (Pl. 1, Figs. 18, 19) has very delicate and slender d elements with deeper basal cavities than in most other species. Elements are best separated from *B. mira* in having only a narrow anterior flange on the base; the base is not so strongly compressed on elements with two anterolateral edges. The a elements have a pyramid-shaped base and an erect or even slightly recurved cusp.

B. mira (Pl. 1, Figs. 1–5) is easy to identify using the broad flange, the strongly compressed elements and the shape of the f element (Pl. 1, Fig. 1).

B. anomalis (Pl. 1, Fig. 15) is the only species with a fan on some of the elements.

B. sp. S (Pl. 1, Figs. 7–14) is less distinct, except for the doc element. Other characters are the basal cavity, which is rather narrow and thread-like towards its tip, and the fact that the elements are usually slightly smaller than those of other species.

B. silurica BARRICK 1977 has extremely long and slender elements. Specimens illustrated by COOPER (1976a) and BARRICK (1977) have a base that is about four times as long as the basal diameter, and they are more slender than elements of *B. resima*. Further, the cusp is more robust in *B. silurica* and no a elements of the kind described here were found by BARRICK in spite of his very large collections. The a elements of *B. resima* are very different from the d elements, and they could well be-

long to another species. However, both a and d elements occur together in studied collections, and there are no good candidates for a second set of u and f elements.

B. erecta RHODES & DINELEY 1957 (see their Pl. 38, Figs. 8, ?9) is characterized by the proximal part of the base and cusp lacking denticles on the posterior edge (or they are so weak that they are not preserved) and by the presence of rather robust distinct denticles on the middle part of that edge in at least some elements.

A peculiar feature in some specimens of both *B. mira* and *B. sp. S* from Klonek is the presence of hyaline basal cavity deposits (Pl. 1, Figs. 1, 2, 8, 12, 13, 14), which are indistinguishable from the lamellar matter, and round off the tip of the cavity. This contrasts with the normal angular cavity with a more or less thread-like tip (Pl. 1, Figs. 7, 10, 11). It has not been seen in any other collections and a preservational factor must be involved.

Nomenclature: It has been noted for *Panderodus* (see JEPPSSON 1983b, c) that lineages may be very long. If this is the case with *Belodella*, a large number of types, and probably also of «type-populations» must be studied in order to evaluate any previous names that have been applied to these species. I have not had the opportunity to see many of these, so I have used an available name which may not be the oldest for some of the species. Others have been referred to in open nomenclature, in spite of the fact that they are now among the very best known. There are at least 33 available names based on late Silurian and Devonian specimens plus many based on stratigraphically older collections, that have to be considered. Only a few are commented upon below.

The names *B. devonica* STAUFFER 1940, its junior synonym (SERPAGLI 1967, compare KLAPPER & BARRICK 1983) *B. triangularis* STAUFFER 1940, their possible synonym *B. costata* DRUCE 1970b, and *B. staufferi* KLAPPER & BARRICK 1983 are based on taxa with costate elements; thus they need not be considered here as names for any of the taxa found at Klonek. The name *B. erecta* RHODES & DINELEY 1957 is based on a species that is distinct from the late Silurian species discussed here, as noted above.

The name *B. resima* PHILIP 1965 is used herein. The f elements were referred to *Paltodus valgus*, but the holotype of that name seems to be distinct.

B. asiatica MOSKALENKO 1966 and *B. subtriangularis* MOSKALENKO 1966 are junior synonyms of *B. erecta*. The holotype and other specimen of *B. multidentatus* illustrated by MOSKALENKO 1966 cannot presently be referred to a specific taxon. They may well belong to *B. resima*, although neither *B. sp. S* nor a species not discussed here can be excluded.

KHODALEVICH & TSCHERNICH (1973a, b) introduced 15 (sic.) new species names and one new generic name – *Haplobelodella* – based on about 60 specimens. One of these names – *B. mira* – is used herein; the generic name has been shown to be a junior synonym of *Belodella* (by KLAPPER & BARRICK 1983), and three of the species names are placed in synonymy with *B. mira* (see below). Further, it seems likely that *B. ra*, *B. clara*, *B. polydentalis* and *B. ethingtoni* are based on *B. resima* and that *B. philipi* and *B. uralica* are junior synonyms of *B. erecta*.

COOPER (1974) described and named another of the species here reported from Klonek, *B. anomalis*.

SNIGIREVA (1975) added three species names – *B. humilidentata*, *B. prebreviscula*, and *Haplobelodella bicarinata* – and SAPELNKOV & al. (1981) another.

ZHOU & al. (1981) introduced 42 (sic.) new names for Llandovery conodonts, including *B. spatha*.

KOZUR (1986) is the author of the name *B. striata*, which also may be based on *B. resima*.

Distribution: *Belodella mira* is extremely rare in the Ludlow, and only 10 specimens have been found in the Hemse Beds on Gotland, at seven localities. The oldest one is the locality Amlings 1, that is, *B. mira* first appears in or below the *A. ploeckensis* Zone. Collection LM 21 R (Indiana University – Indiana Geological Survey collection 13336) of REXROAD & CRAIG (1971) contains over 25 specimens of *Belodella* (see below) including one of *B. mira*. The youngest Silurian specimens are from Bed 19 at Klonk. LANGE (1968, Pl. 5) illustrated Late Devonian specimens, forming a partial apparatus, found together in a coprolite; these show the broad anterior flange typical of *B. mira* very well. No f element is recognizable. Some other Devonian reports of «*B. devonica*» may be based on this taxon, although the lack of illustrations of the shape of the basal cavity makes it difficult to be sure.

Belodella sp. G is known from the Whitcliffian Eke and Hamra Beds on Gotland. LINK & DRUCE (1972) illustrated a specimen which, judging from their drawing (Fig. 11), has the extra posterior edge. The specimen is from the Hume Limestone Member, which is, at least in part, of *P. siluricus* Zone age, i.e. the specimen is Leintwardinian or younger.

Belodella sp. B is known from strata with *P. siluricus* and *K. variabilis* of the Bainbridge Formation in Missouri (REXROAD & CRAIG 1971).

Belodella resima is known from the Whitcliffian Hamra Beds on Gotland and the latest Ludlovian and early Pridolian at Lochkov in Bohemia. The species is also present in sample 21 R of REXROAD & CRAIG (1971) from their section in Lithium, Missouri. The rest of the fauna indicates that this is much younger than the *P. siluricus* Zone. It is probably to be correlated with a level in the Hamra Beds on Gotland. Devonian specimens which are likely to belong here have been illustrated by PHILIP (1965: Pl. 8, Figs. 7, 8, 15–17, 19, 22, 26–28), RHODES & DINELEY (1957: Pl. 37, Figs. 1–3), and BULTYNCK (1970: Pl. 27, Figs. 7–9).

Belodella anomalis was described from the late Ludlovian in Australia (COOPER 1974), and occurs in strata of similar age in Europe. It ranges at least up into Bed 19 at Klonk; that is, a few centimetres below the top of the Silurian in Bed 20.

The known range of *Belodella* sp. S starts in the earliest Pridolian, and it ranges at least up into Interbed 16/17 at Klonk; that is, into the *L. e. detorta* Zone.

Belodella erecta is widespread in Devonian strata and has been illustrated from Australia (e.g. PHILIP 1966: Pl. 1, Figs. 20?, 22–24; DRUCE 1970 d: Pl. 4, Fig. 2), from the Soviet Union (MOSKALENKO 1966: Fig. 1 a–d, Pl. 11, Figs. 4, 5), from Britain (RHODES & DINELEY 1957: Pl. 38, Figs. 8, 9?), and from Pakistan (BARNETT & al. 1966: Pl. 85, Fig. 1).

Most published pictures of *Belodella* cannot presently be identified with certainty as any of the taxa distinguished herein and the accompanying descriptions are often of little help, since they often deal with characters that distinguish elements and not those that are important for species separation.

Ecology: Most of the taxa discussed here are morphologically very distinct. Excluding samples with 1–10 specimens, any sample typically has two or more species or none at all. Although the distributional data are scattered as yet, at least four of the lineages occurred at the same time from the latest Ludlow to the end of the Silurian. It may be concluded that most or all of these species were ecologically distinct, with sufficient habitat separation that they did not exclude each other in a generically favourable environment. ALDRIDGE & JEPPSSON (1984) concluded that this environment was found in the more offshore areas.

The morphologic distinctness, the morphologic stability through the studied interval, the large number of species, and the co-occurrence of different species, indicating that these

species were not merely vicariant taxa, suggest that the common ancestor was very much older than the studied interval. Several Ordovician taxa have been referred to *Belodella* but they were all excluded by FÄHRAEUS & HUNTER (1985). In addition, they disputed the existence of early Silurian representatives. My results contradict at least the latter part of their opinion. The rarity of early Silurian records may have different causes. Also other Silurian conodont lineages exhibit long gaps in the known record (JEPPSSON 1983 c, 1987).

***Belodella mira* KHODALEVICH & TSCHERNICH 1973 a**
Pl. 1, Figs. 1–5

Four of the names introduced by KHODALEVICH & TSCHERNICH (1973 a) were based on elements which are closely similar to those from Klonk. Thus the type of *B. breviscula* resembles the u element apart from a difference in the cross section of the base (their Pl. 4: 5). That of *B. serrata* agrees well with the tc elements and those of *B. corniformis* and *B. mira* have characters of the ts element. One difference is that the posterior limit of the basal cavity is slightly curved posteriorly whereas it is straight or nearly so in the population from Klonk. At present, these differences are not enough to treat them as distinct species. No specimens of the f element were reported by KHODALEVICH & TSCHERNICH (1973 a, b), but they only recorded a total of 11 specimens of the *B. mira* type. They may have failed to find specimens of the f element, or may not have described them, as they differ considerably from typical f elements of *Belodella*.

The holotype of *B. mira* is the best illustrated specimen, and that name is selected here to have priority; the other three names are considered to be junior synonyms. Further, I refer the collections described herein to *B. mira* in the absence of any evidence to the contrary.

All elements have a strongly compressed base, even those with two anterolateral edges. Only towards the basal opening in mature specimens does the cross section become more broadly elliptical. The most important feature is the broad anterior flange of the base in the f and u elements. In the other elements the feature can better be described as a separation of the anterior margin of the basal cavity from the anterior side of the element by a broad, hyaline, massive «flange». The anterolateral edge(s) is found at the margin of this «flange». Only the posterior edge is denticulated. The rim of the basal cavity is often broken away; thus, the length of an element is often unknown. To separate the denticulated elements the best characters are the opening angle of the basal cavity in lateral outline and whether the element is essentially straight or markedly bowed laterally. In fractured specimens it may not be possible to separate elements with deep and average basal cavities. Further, the base is so strongly compressed that very high magnification is needed to separate elements with one and two anterolateral edges respectively. The difference in lateral curvature of the base is also slight; however, it is possible to separate curved and flat elements. Thus, ts and tc elements can be separated. The more slender basal cavity separates the doc element from the u element.

The f element: The base is short, in lateral view rounded triangular, and the cusp is broad and nearly erect, that is, perpendicular to the direction of the «oral» margin of the basal cavity. The element is bowed and twisted so that the inner side becomes concave at the junction of base and cusp, and the long axis of the cross-section of the cusp is up to at least 45 degrees from the plane of the base. The lower margin of the white matter of the cusp is diffuse along the central part of the upper margin of the basal cavity. In the largest specimen stud-

ied, it is organized there as if consisting of overgrown denticles. The anterior edge – obliquely anterolateral due to the element being twisted – has a flange on the base, broadest at or distally of the middle of the base; the margin of the flange is evenly curved. The oral margin of the base has a narrow flange distally, centrally the flange is wider and directed obliquely outwards at the junction with the cusp.

Typical *f* elements have not been seen in Ludlovian and early Pridolian collections. Although the collections are too small to definitely rule out its presence in faunas of that age, it could also be that it developed after that time. If so, then the *u* element in older populations could not be separated so easily from those of other taxa. Another possibility is that there are two contemporaneous taxa with a broad anterior flange and that further studies are needed to separate their non-*f* elements.

The *u* element: This element resembles the *f* element but differs in the base being more narrow in lateral view, the upper margin of the base and the proximal part of the posterior margin of the cusp being denticulated, and the cusp being rounded in cross-section and equipped with two costae. The anterolateral flange on the base is more or less curved inwards. Even in mature specimens it is sometimes only partly preserved; its absence in more juvenile specimens studied may not be genuine.

The *doc* element: This element differs from the *u* element in the basal cavity being much longer and more slender. The base is strongly curved inwards. In most specimen the cusp is slightly proclined.

The *tc* element: The base is only slightly curved proximally. The angle between the upper margin of the basal cavity and the cusp is about 90°; thus, the cusp is nearly erect. The two anterolateral edges are very close to each other, and often it is necessary to study both sides in high magnification to separate it from the *doc* element.

The *ts* element: The cusp is distinctly proclined and small compared with the long base. The two anterolateral edges are very close to each other, but at least in larger specimens they can be seen in a good microscope. In lateral view the basal cavity occupies less than half of the width of the base in the proximal half of the base. Although not perfectly symmetrical, this element might be confused with the *tr* element, but the fact that the outer edge of the cusp is formed by the posterior edge of the base distinguishes it.

The *tr* element: This is similar to the *ts* element except that all three edges continue symmetrically from the base onto the cusp.

***Belodella* sp. S**

Pl. 1, Figs. 6–14

Most elements lack unique features, the only exception being the *tc?* element. The anterolateral edges are denticulated in some elements, a feature shared with *B. anomalis*, but not with the other taxa discussed here. The elements are rather small, and the basal cavities are narrower than in the corresponding elements of *B. anomalis*.

The identification of the *tc* element is equivocal since the highly distinct element described below has only one anterolateral costa. If the identification is correct, then it is likely that this group includes both *dtc* and *atc* elements.

The *f* element: The range of variation includes two distinct forms. The first (Pl. 1, Fig. 6) has a short base. The depth of

the basal cavity is only slightly larger than its greatest diameter. The laterally compressed, proclined cusp is basally very broad. The edges of cusp and base are both in the median plane.

The second form (Pl. 1, Fig. 7) has a slightly deeper basal cavity. The cusp is more narrow proximally and more proclined. The best character is, however, that the anterior edge is in a distinctly anterolateral position and directed anterolaterally.

The *u* element: The basal cavity is narrow and about as deep as in the second form of the *f* element. The cusp is proclined but directed obliquely inwards; that is, the inward curvature of the base is concentrated at the base-cusp junction and combined with a twist. The anterolateral edge varies in direction and width; it can even be weakly denticulated. The denticles along the posterior edge of the base are slanted.

The *doc* element: The basal cavity is narrow, deeper than in the *u* element and curved posteriorly proximally; otherwise the element is like the *u* element.

The *tc?* element: The base of this element is triangular in cross-section although no outer anterolateral edge is developed. Instead, the transition between the anterior and the outer lateral side is smoothly rounded. The depth of the basal cavity varies, and probably both *dtc* and *atc* elements are included. The row of denticles along the posterior margin is strongly flexed inwards along the proximal part of the base, and strongly curved outwards just behind the cusp. The inner lateral edge is weakly denticulated, and forms a smooth curve from the basal rim onto the side of the cusp. The inner side is distinguished through the fact that in *Belodella* the inner anterolateral edge forms one of the two main edges of the cusp, whereas the outer anterolateral edge usually ends close to the base – cusp junction in all asymmetrical elements. In the flexure of the denticle row and the flatness of the denticles, the inner side looks more like an outer side.

The *dtc* element: Basal cavity deep, narrow and curved posteriorly proximally; otherwise like the *ats* element.

The *ats* element: Base broadly triangular in cross-section. Posterior margin of the basal cavity curved but the anterior side nearly flat. Cusp proclined. The posterior edge of the base curves around and forms an outer posterolateral edge as in other taxa. The outer anterolateral edge continues more distally on the cusp than in most other species. Both anterolateral edges are denticulated. Inner lateral side like that of the *dtc* element.

***Belodella anomalis* COOPER 1974**

Pl. 1, Fig. 15

There is some uncertainty regarding the use of the name *B. anomalis* COOPER 1974 for the third species found at Klonk. COOPER (1974) illustrated several specimens with a well developed fan. However, the holotype has the same symmetry as the *tc?* element of *B. sp. S*. Elements with that symmetry are lacking in my best collection of the fan-equipped species, which includes about 150 specimens. However, the base of the holotype is much more expanded than in the *tc?* element of *B. sp. S* and the element seems to have a one-sided fan like some of the elements of the fan-equipped species. Both species co-occur in many of my samples, and might well do so in the type stratum too, so the taxonomic assignment of the type has to be judged on its morphology alone. Based on that, it probably belongs with the other illustrated specimens. Evidently the Australian and European forms represent different populations, perhaps different subspecies.

In the *tr* element the fan is formed by the cusp and denticles of the two anterolateral edges. However, in the *ats* and *dts* elements only the inner part of the fan has that origin, whereas the outer part is formed by denticles of the posterior edge. The posterior row of denticles is strongly curved close to the cusp so that it connects to the outer side of the cusp.

Only a few specimens are known from Klonk; thus, the description below is based on other collections too. Cooper distinguished only two elements. His description of these therefore includes characters found on different elements.

The base is strong, short and markedly laterally expanded in all elements. The cusp is directed more posteriorly in all elements than in an average *Belodella* and can even be slightly reclined in some *dts* elements.

The denticulation is better developed than in other studied *Belodella* species. The anterolateral edges may also be denticulate, but these denticles are generally short and only evident as a serration in well preserved specimens. The only major exceptions are those denticles which are a part of the fan. The pallsade of denticles along the posterior margin of the base forms a larger part of the lateral face than the basal cavity except distally. A particularly useful character is that the posterior margin of the basal cavity may be expanded like a trumpet.

The *f* element: The base is short and strongly expanded laterally, mostly on the outer side. The basal cavity is only slightly deeper than its greatest diameter. There is a large variation in the size and direction of the cusp. In many specimens a thin sheet, starting at the edge of the base, fills the bay between the base and the slightly proclined, laterally compressed cusp.

The *u* element: Base short, strongly expanded distally, the denticles along the posterior edge constitute more than half of the lateral face. In most specimens the anterolateral edge is directed inwards; in others it forms a broad obliquely anterolaterally directed flange, which in some specimens is denticulated.

The *doc* element: I have only seen one specimen that has the characters of this element. The basal cavity is deep, the posterior edge denticulate. The anterolateral edge may also be denticulate on the base.

The *dtc* element: Basal cavity deep, cusp proclined. The lateral curvature of the base is indistinct, and the best character to separate this element from the *dts* elements is the lack of a fan. My collections are not good enough to exclude the possibility that some specimens may be transitional between this element and the *atc* element, although typical specimens are easily separated.

The *dts* element: Base long and broad. Basal cavity deep. Cusp slightly proclined or erect. Fan slightly less pronounced than in the *ats* element. The differences from the *ats* element are similar to those between the *dtc* and *atc* elements.

The *atc* element: Like the *dtc* element but base shorter, and at least some specimens are more typically curved.

The *ats* element: Base short, strong and broad, posterior denticulation constitutes most of the lateral face except distally. Cusp erect or slightly recurved, with a broad strong fan.

The *tr* element: Similar to the *ats* element except that the fan is formed by the two anterolateral edges, the posterior row of denticles is straight and the element symmetrical.

***Panderodus* sp.**

Species level identifications of *Panderodus* usually require at least one good collection of the population in question, including at least a few well-preserved specimens of several of the different elements. Small or less well preserved collections of the same population can then be identified via direct comparisons. No such collection is available from Klonk. Only rarely are species-specific elements found. One denticulate element is found in the sample from Bed 14 at Klonk; such elements are currently only known in some populations of *P. unicostatus*. The preservation of the other specimens varies but there is no evidence that a second species occurs at Klonk.

***Ligonodina elegans detorta* (WALLISER 1964)**

sensu JEPPSSON 1975

Pl. 3, Figs. 1–4

The difference between *L. e. elegans*, *L. e. detorta* and a third subspecies of that lineage was briefly pointed out by JEPPSSON (1975). The major difference between the three taxa is in the denticulation. In *L. e. detorta* one or two very small denticles are interspersed in one or more of the spaces between the normal-sized ones. *L. e. elegans* lacks such extra denticles, whereas the third subspecies has more than two small denticles on average in each space. The transition between *L. e. elegans* and *L. e. detorta* is gradual, both in the number of individuals affected and in the regularity. Thus it will be necessary to define an arbitrary boundary. The definition may be of the style: Populations in which X% of the *y* elements have at least one small denticle interspersed belong to *L. e. detorta*. In order to make it possible to identify small collections it is necessary that X is not too small or too high and a number between 10 and 50% would be best. A number close to 10% is preferable, since it is the appearance of *L. e. detorta* that is stratigraphically important; thus, the identification would be reliable even with only a few specimens with alternating denticulation. The best element to use is probably the *hi* (Sc) element. Since small denticles appear in most of the elements, other elements can be used to substantiate identification of smaller collections.

At present *L. e. detorta* is the only subspecies known from Klonk, although it is likely that larger collections from the beds below Bed 13 would produce *L. e. elegans*.

All specimens are much smaller than those of *L. elegans* from the Beyrichienkalk, at comparable ontogenetic age.

In the sample from Interbed 16/17 there are small denticles in all studied specimens of all elements except the *ne* (M) element. Further, small denticles are interspersed in every space between the large ones except on one of the processes in a couple of specimens of non-*hi* elements. In a few places there are two small denticles in one space. The average number of small denticles on the posterior process of the *hi* element is somewhere between one and two, probably closest to one.

The number of small denticles can only be studied in a couple of spaces in the single detortiform element from Bed 19. There are two small denticles in one space and probably the same number in another.

***Ligonodina* sp.**

Pl. 3, Figs. 5, 9

The single *hi* element is small with very low processes each bearing only two very widely spaced denticles. The inner lateral process is nearly straight and directed obliquely downwards.

Ozarkodina excavata (BRANSON & MEHL 1933)
sensu JEPPSSON 1969
Pl. 3, Figs. 6–8

A very distinct subspecies – *O. e. wurmi* is found in Devonian faunas (BISCHOFF & SANNE-MANN 1958, PHILIP 1965). It has been found as close to Klonek in time and space as the *M. uniformis* Zone at U topolů (SCHÖNLAUB in CHLUPÁČ & al. 1980: Pl. 19, Fig. 17). It has very long elements; BISCHOFF & SANNE-MANN illustrated one oz element that was about 2,4 mm long, and irregular denticulation is found in some of the elements. *O. e. excavata*, on the other hand, has regular denticulation on all elements and rather short elements (JEPPSSON 1976, Fig. 1). Some Silurian populations approach *O. e. wurmi* in appearance but not in size. Specimens of this type have been found in a sample from the latest Ludlow in the Lochkov quarry (JEPPSSON 1986 b). Typical populations of *O. e. excavata* occur elsewhere in contemporaneous strata.

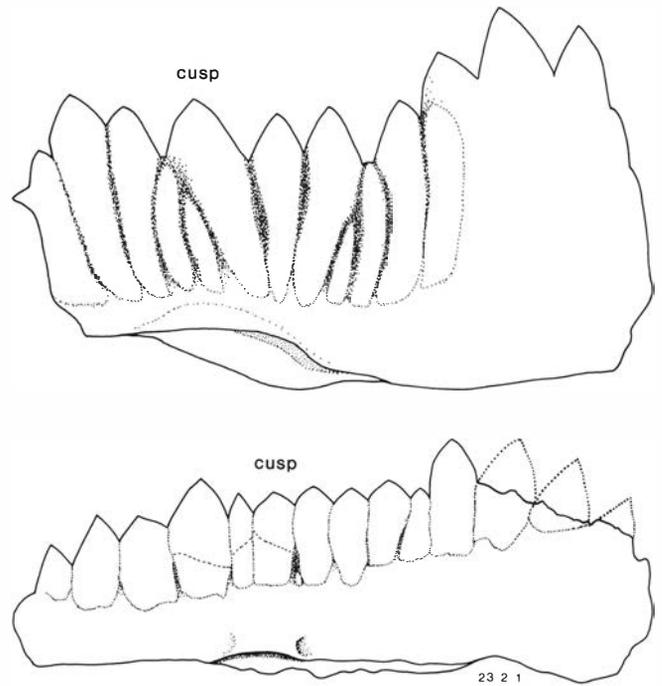
The specimens from Klonek are small like those of other taxa and rather fragmentary; thus, the length cannot be measured, but their size and degree of ontogenetic maturity indicate that they were very short when fully grown. The denticulation is regular indicating a subspecific assignment to *O. e. excavata*. However, the separation of the two subspecies is purely based on morphology, without consideration of whether the pronounced differences are the expression of many genes or if they all may be the consequences of changes in a single character and that more subtle features must be used for separating the taxa. For example, a pygmy population of *O. e. wurmi* would be expected to have regular denticulation.

Ozarkodina confluens BRANSON & MEHL 1933
sensu JEPPSSON 1969
Text-fig. 1

It is sometimes difficult to separate *O. confluens* and *O. steinhornensis*. When it is a matter only of establishing the presence of each taxon, then the most characteristic elements can be used. Thus, fragments of hi and pl elements with the typical alternating denticulation of needle-shaped denticles prove the presence of *O. steinhornensis*. Similarly, mature bar elements of many populations of *O. confluens* with broad, well separated and deep denticle roots are so characteristic that fragments are enough for a reliable identification. Some of the elements in many populations may however be more difficult to identify. Thus, the presence of a distinct poop – a distinctly separated, high anterior end – in the sp (Pa) element of both species may make these elements superficially very similar, especially if the white matter distribution cannot be studied. However, the overgrowth of denticles in *O. confluens* sp elements is sometimes a species-specific character (Text-fig. 1). The innermost denticles on both processes are fanned, and at the contact with the poop one or more is overgrown. Similarly, on the posterior process there is often a cusp-sized denticle, parallel to the cusp, at which the denticle direction changes markedly, and where overgrowth can often be seen in mature specimens. Usually it is necessary to study the white matter to establish overgrowth or change in denticle direction. Once the presence of a taxon is proven it is often possible to identify most of the specimens of it.

In the Klonek faunas *O. confluens* is very rare. It can be identified with confidence only in Bed 11 (Text-fig. 1). The collection studied also includes a pl element with enough unique characters for an identification.

O. confluens is wide-spread and abundant in most Ludlow faunas and in many older ones but is rarer in Pridoli faunas. At Cellon, however, it is not found below the Whitcliffian and



Text-fig. 1: Sp (Pa) elements of *Ozarkodina confluens* (BRANSON & MEHL 1933) sensu JEPPSSON 1969 and *O. s. remscheidensis* (ZIEGLER 1960) sensu nov., from Bed 11 and Bed 12 at Klonek, respectively. See text for a discussion.

The specimens are 0.68 (as broken) and 0,79 mm long, respectively. LO 5869 and LO 5870.

is sporadic in most intervals (WALLISER 1964). The Bohemian faunal sequence seems to be rather typical. A critical evaluation of published data (WALLISER 1964, WALMSLEY & al. 1974, and CHLUPÁČ & al. 1980) indicates that the species was abundant in the Leintwardinian *P. siluricus* Zone and older Ludlow strata and more rare and sporadic in succeeding strata.

***Ozarkodina steinhornensis* s.l.**

A marked tendency to form local populations is characteristic for the *O. steinhornensis* group (JEPPSSON 1975). The taxonomic treatment of the group has varied strongly from typologic, in which every taxon described is treated as a distinct species, to the treatment of the whole group as a single species with several subspecies.

Silurian collections are often referred to only a single subspecies, whereas Devonian populations have usually been treated as several distinct species. More studies are needed before any consensus can be reached. Possibly a study of character combinations and their variation through time might show if one, two or more contemporaneous lineages existed.

It is evident that a large number of contemporaneous populations existed in the Silurian, but there is little evidence for these representing distinct lineages; they may have formed threads in the gigantic web of a single lineage. Thus the species concept adopted herein is the same as that used in 1964 by WALLISER. The only difference is that the non-sp elements are now included.

The most distinct differences found within the group are those between *O. s. eosteinhornensis* s. str. and similar taxa and *O. s. remscheidensis* and similar taxa. The former have oz (Pb) elements with short high processes and sp (Pa) elements with a more or less even row of cusp and denticles perpendicular to the nearly equal processes. Probably they also have ne (M)

elements with the long process directed obliquely downwards.

The taxa of the *O. s. remscheidensis* group have oz elements with long processes, and sp elements with a large cusp, often distinctly different anterior and posterior processes, the anterior often with one or more large cusp sized denticles in mature specimens. The ne elements were probably those with the long process initially directed more or less horizontally and curved obliquely downwards to give a broad U-shaped aboral margin.

The possibility that rare specimens may derive from other populations always makes it difficult to identify the total range of variation in a population. Therefore, identification of subspecies and populations often requires at least ten good sp elements plus some of the other elements.

O. s. eosteinhornensis (WALLISER 1964)
sensu JEPPSSON 1975
Pl. 2, Figs. 1–4; Pl. 3, Fig. 10

The type population: This is from Cellon Bed 40 (WALLISER 1964). The taxon also occurs in Beds 39A to 41. The Cellon conodont elements are dark and the white matter distribution cannot be studied.

The sp (Pa) element (WALLISER 1964: Pl. 20, Figs. 19–22). Basal cavity lips vary in size but their outline is more or less heart-shaped. The cusp does not deviate much from adjacent denticles in size and often it cannot even be identified (probably there are small overgrown denticles adjacent to its root which would have permitted identification, had the strata not been heated). The number of denticles, including the cusp, is 13–14 on small specimens. Larger specimens may have up to about 20 denticles, but these are difficult to count as early in ontogeny the central denticles and the cusp become nearly fused to a wavy edge. In mature elements the fusion is complete. In typical specimens (WALLISER 1964: Pl. 20, Figs. 19–22) there are 1–3 denticles on the outer basal cavity lip; sometimes the inner lip may also bear denticles. This is not limited to mature specimens, although the size of the lateral process increases with age.

The oz (Pb) elements (WALLISER 1964: Pl. 26, Fig. 8) resemble those of *O. sagitta*. They have a short anterior process, triangular in lateral view, with an oral edge forming a continuation of the anterior edge of the cusp. The denticles are fused nearly to the tips, so that they form a serrated edge. The posterior process is short, low and triangular in lateral view. Other specimens are less extreme. However, it is impossible to determine whether there is more than one population represented in these samples and descriptions here are concentrated on the more extreme elements, which undoubtedly belong to *O. s. eosteinhornensis*.

The ne (M) elements (WALLISER 1964: Pl. 30, Fig. 28) have regular denticulation. At its origin the long process is directed downwards, not initially directed laterally and curved downwards under the first denticles as in e.g. *O. s. scanica*.

The other elements (WALLISER 1964: Pl. 31, Fig. 30) have hindodelliform denticulation, usually with 1–3(4) small denticles in each space between large denticles. The lower number is often found near the tip of the posterior process in mature specimens, and in the tr (Sa) element. The posterior process in the hi (Sc) element is curved outwards like that in *O. excavata*. Its anterolateral process is short, obliquely directed inwards and downwards at its origin and curved inwards. The processes of the tr element are directed nearly straight forward and slightly downward and curved outwards and backwards. The angle between them is less than 90°, at least in some specimens.

The population from Klonk: The collection from Klonk, Bed 10, consists of badly broken elements, and only one or two of the sp (Pa) elements have both processes unbroken. That from Bed 11 is better but cooccurrence with *O. s. remscheidensis* prevents an independent identification of the non-sp elements.

Sp elements with and without a lateral process are about equally frequent. In other characters they are closely similar so it is likely that they are members of the same population. In many other taxa left and right sp elements are not mirror images and it might be that individuals had one element with and one without a lateral process. Alternatively the population may have been dimorphic, possibly only in this character. One or both processes are broken on most specimens, thus their length can only be gauged approximately but it seems as if most specimens did not reach more than about 0.6 or 0.7 mm when mature, whereas those from Cellon reached at least 0.9 mm (WALLISER 1964: Pl. 20, Fig. 22) and probably 1.0 mm (WALLISER 1964: Pl. 20, Fig. 19). However this is still less than Cellon specimens of *O. s. remscheidensis* (WALLISER 1964: Pl. 20, Fig. 26), and at Klonk, too, the sp elements of *O. s. remscheidensis* seem to have grown slightly larger. In the most juvenile specimens the lateral «process» consists only of a ridge on the side of the cusp, but in larger specimens well developed denticles occur. In the most mature specimens these are fused to a short ridge. Similarly most of the denticles in the main row are fused to a ridge. The lower ends of the denticle roots form a nearly straight line, parallel both with the upper and lower margins of the blade, except in the anteriormost part where the denticle roots are shorter. In this respect both elements with and without a lateral process are similar and deviate strongly from cooccurring sp elements of *O. s. remscheidensis*, which has a markedly triangular hyaline lower part of the anterior process. The number of denticles seems to be slightly lower than in the Cellon population.

The collection from Bed 11 includes some oz (Pb) elements closely similar to those of *O. s. eosteinhornensis* s.str. from Cellon, and some that are closely similar to those from *O. s. remscheidensis*. Specimens of *O. s. remscheidensis* from Bed 12 are less distinct (Pl. 2, Fig. 11).

Similarly a couple of ne (M) elements lack typical alternating denticulation, although a slight alternation is apparent. Other specimens have typical alternating denticulation with 1–2 small denticles in each space. From a comparison with the collection from Bed 12, the former may be referred to *O. s. eosteinhornensis* s.str. and the latter to *O. s. remscheidensis*.

The remaining elements cannot presently be separated from the corresponding ones of *O. s. remscheidensis*.

Ozarkordina s. remscheidensis (ZIEGLER 1960)

Text-fig. 1; Pl. 2, Figs. 6–11; Pl. 3, Figs. 11–18

To understand the morphology of the population from Klonk and its relationship it is necessary first to discuss three other populations.

The type population: Comments on the population from the type level at the type locality – Untenruden – are chiefly based on my own topotype collection; however, I use the illustrated paratypes as examples. The specimens have been subjected to heating and tectonism: they are so dark that the distribution of white matter can no longer be studied and brittle stress has extended some of them as is evident in the hyaline fusion («healing») bands sometimes adding as much as the breadth of one large denticle to the length. Some elements (e.g. ZIEGLER 1960: Pl. 13, Fig. 15) look as if extended by plastic deformation; however, it cannot be excluded that they are a part of the biologic variation; they occur in my topotype collection

too. There is continuous transition to normal specimens. A few of them look like some specimens illustrated by ZIEGLER (1960: Pl. 13, Fig. 8) that is, the denticles are slightly inclined towards the anterior, which is unlikely to be an original biological feature. In any event, these long low sp elements do belong to *O. steinhornensis*, and not to *O. excavata wurmi* as suggested by Ziegler.

The variation in the type collection also includes sp (Pa) elements which have a posterior process that is nearly a mirror image of the anterior process, instead of showing the more typical morphology in which the denticles become smaller and more slanted distally. The Australian, Baltic and Bohemian collections discussed herein do not contain such specimens, but they may be more frequent in the very latest Silurian and earliest Devonian (cf. specimens illustrated by WALLISER 1964: Pls. 20, 21).

Similarly, the sp element illustrated as *S. frankenwaldensis* by Ziegler belongs here and not to *O. confluens*. (WALLISER 1964 showed that «*S. frankenwaldensis*» belongs to the latter taxon.) The sinuous lower margin is best displayed in mature specimens, but the beginning of it is more subtly evident in many smaller specimens (e.g. ZIEGLER 1960: Pl. 13, Fig. 9). Sometimes one of the processes has a straight lower margin whereas the other has a sinuous lower margin (e.g. ZIEGLER 1960: Pl. 13, Fig. 2). Many specimens are intermediate in this respect, like the holotype. When comparing the type-population with other populations, it is important to note that the individuals grew rather large – the largest illustrated sp element is about 1.51 mm in length (ZIEGLER 1960: Pl. 13, Fig. 4). It should of course also be kept in mind that the high denticles on the anterior end should not be expected to occur in juvenile specimens, although most of these were excluded by ZIEGLER (1960) who illustrated them as *S. cf. canadensis*.

The oz (Pb) element has long processes; the posterior process is low, but the denticle tips of the anterior process form a more or less straight line with the cusp tip.

The ne (M) element has regular denticulation in my specimens, but ZIEGLER (1960: Pl. 15, Fig. 9) illustrated one with well developed alternating denticulation. Usually there are several denticles on the well developed short process and the same u-shaped space between the processes below the cusp as in *O. s. scanica* (JEPSSON 1975). The cusp of the hi element is elliptical and equipped with edges at least basally in most specimens. The posterior process is long, slightly arched distally and has alternating denticulation. The anterior process is smoothly curved obliquely inwards and downwards and regularly denticulated.

The pl and ke elements have alternating denticulation on the posterior process. The anterior process probably has similar denticulation in some specimens but others seem to be regularly denticulated. KUWANO (1982) has shown that there are two kinds of plectospathodontiform elements in *O. excavata*. These can be separated also in other species of *Ozarkodina* and it is possible that they had different denticulation in this population of *O. s. remscheidensis*.

The tr (Sa) element lacks a posterior process and has regular or poorly developed alternating denticulation on the two anterolateral processes.

Completely overgrown denticles cannot be identified due to the thermal darkening of the elements. Therefore, it cannot be excluded that one or more of the processes which here are described as having regular denticulation instead have alternating denticulation with one or two small denticles in each space.

A Nordic and an Australian population: The collections from the upper part of the Buchan Caves Limestone (only) of Australia described by PHILIP (1966) as *S. s. buchansensis*

(including the holotype) and the collections from the upper part of the Beyrichienkalk which I am studying (JEPSSON 1981) are closely similar to each other, although the Australian ones are much younger.

They both consist of smaller individuals than found at Untenruden, and most of the differences probably relate to size. In the sp element, the number of denticles between the cusp and the poop is often only one to three, whereas specimens illustrated by ZIEGLER have four or five, although the range in my topotype collection is from two. Similarly the shortening of the posterior process is accomplished through a lower number of denticles and not through a more needle-like denticle shape. Those Untenruden specimens with the lowest number of denticles on the low part of the anterior process are closely similar to those from the Beyrichienkalk, in all aspects that can be studied (unfortunately the thermal darkening prevents observation of the white matter and overgrowth of denticles in the type material).

The non-sp elements in the Buchan Caves Limestone population (PHILIP 1966: Pl. 3, Figs. 2, 7, 9, 10, 14–17, 21, 25; Pl. 4, Figs. 1–6, 16, 17) agree well with those of the type-population, except that they are smaller. The oz (Pb) element has a long low posterior process, whereas the denticle tips on the anterior process form a nearly straight line with the cusp tip; the other elements have alternating denticulation, best developed on the posterior process and poorly developed or absent on the anterior process of hi, pl and ke elements, the lateral processes of the tr element, and the long process of the ne element.

The Beyrichienkalk population has ne (M) elements with rare alternating denticulation. The lateral processes of the tr element and the anterior processes of the hi, pl and ke elements mostly have alternating denticulation with one small denticle in each space, whereas the posterior process of these elements usually has one to three in each space.

The population from Klouk: The collection from Bed 12 shows little variation but is markedly distinct from those discussed above. All sp (Pa) elements are shorter than 0.9 mm. The general outline is wedge-shaped with many narrow, rather even denticles. The posterior process is distinctly shorter than the anterior. Compared with the type collection those from Klouk have much more slender denticles, up to 12 on the anterior process and up to 5 on the posterior process, more than found in the Untenruden population on much larger specimens. The increase in height distally on the anterior process is gradual to the third or fourth denticle from the end, in respect of denticle tips, points of fusion and root ends; an exception occurs in a few specimens which show a clear break between a poop and an inner part. This feature is best displayed by root height. The poop has four to six denticles, the second of which is highest. The high number of lower denticles distal of the highest one is only slightly greater than found in the Untenruden population, whereas these from Celon, Australia and the Beyrichienkalk usually have only zero to two. The lower margin is more or less evenly arched and different from all the other populations discussed here.

The oz (Pb) element is shorter than in the type-population, and as in the sp element the denticles are narrow and closely packed.

The ne (M) element differs from that of the type population in that the short process is less well developed and may have only one denticle, and that most specimens have alternating denticulation, mostly with only one small denticle in each cycle; in a few specimens there are two small denticles in some cycles.

The hi (Sc) element has a long posterior process with alternating denticulation with up to four small denticles in each cycle.

The pl-ke (Sb, Sd) elements. Some specimens have nearly regular denticulation on the posterior process whereas others have well developed alternating denticulation with up to three small denticles in each cycle.

The processes of the tr (Sa) element vary similarly. Most display alternating denticulation with one small denticle in each cycle, but the number varies between 0 and 2.

Younger collections from Klonk have far fewer specimens that are sufficiently well preserved to be compared. However, in sample Tj 80-7 LJ from Interbed 16/17 the lower margin of the anterior process of one sp element curves upwards very strongly distally; otherwise the population agrees with that from Bed 12.

Discussion: The Klonk population differs from the typical one in a number of characters. Most of these changes can easily be understood as an adaptation to an offshore environment through a decrease in size. As discussed by ALDRIDGE & JEPSSON (1984) nearshore taxa have large robust elements while offshore taxa have small delicate elements. The ontogeny in nearshore taxa exhibits a marked change from delicate juvenile elements to robust mature ones. Thus any population adapted to a more offshore habitat would show both some neotenic aspects and a decreased accentuation of characters developed late in ontogeny. In *O. s. remscheidensis* the

former change would give shorter sp elements with narrower denticles, the latter less overgrowth of denticles and lack of a distinct poop.

Acknowledgements

Samples from Beds 10–14 were kindly provided by Ivo Chlupáč. The Beyrichienkalk faunas referred to were collected by Anders Martinsson. Topotype samples from other localities were provided by James E. Barrick, Stig M. Bergström, Barry Cooper and Anders Martinsson. Otto Walliser kindly allowed access to all his collections during a memorable visit in 1972. Barry Cooper, Alan Horowitz and Carl B. Rexroad arranged loans of type material. James E. Barrick and Stefan Bengtson assisted with references. Most of the samples were processed by Ewa Säll and picked by Doris Fredholm. Richard J. Aldridge and Ann-Sofi Jeppsson improved the language of the manuscript, Claes Bergman drew Text-fig. 1, Sven Stridsberg took the photographs, and Viveka Askeland and Ann-Mari Gayle typed the manuscript. Grants from The Swedish Natural Science Research Council paid my salary, my participation in ECOS II, the laboratory work and other costs. My sincere thanks to everybody.

Literature

- ALDRIDGE, Richard J. & JEPSSON, Lennart (1984): Ecological specialists among Silurian conodonts. – Spec. Pap. Palaeontol. 32: 141–149, text-figs. 1–3, London.
- BARNETT, Stockton G., KOHUT, Joseph J., RUST, Claude C. & SWEET, Walter C. (1966): Conodonts from Nowshera reef limestones (uppermost Silurian or lowermost Devonian), West Pakistan. – J. Paleontol. 40: 435–438, tab. 1, pl. 58, Tulsa/Okla.
- BARRICK, James E. (1977): Multielement simple-cone conodonts from the Clarita Formation (Silurian), Arbuckle Mountains, Oklahoma. – Geologica et Palaeontologica 11: 47–68, text-fig. 1, tabs. 1–2, pls. 1–3, Marburg.
- BISCHOFF, Günther & SANNEMANN, Dietrich (1958): Unterdevonische Conodonten aus dem Frankenwald. – Notizbl. hess. L.-Amt Bodenforsch. 86: 87–110, pls. 12–15, Wiesbaden.
- BRANSON, E. B. & MEHL, M. G. (1933): Conodont studies number 1. – The University of Missouri Studies 8: 1–72, 3 text-figs., pls. 1–4, Columbia, Missouri.
- BULTYNCK, P. (1970): Révision stratigraphique et paléontologique (Brachiopodes et Conodontes) de la coupe type du Couvinien. – Mém. Inst. géol. Univ. Louvain 16: 1–197, text-figs. 1–16, pls. 1–39, Louvain.
- CHLUPÁČ, Ivo (1980): Stop 10. Klonk at Suchomasty. – In: CHLUPÁČ, Ivo, KRÍŽ, Jirí & SCHÖNLAUB, H. P.: Fieldtrip E Silurian and Devonian conodont localities of the Barrandian p. 177–180, text-fig. 16. – In: SCHÖNLAUB, H. P. (ed.): Second European conodont symposium (ECOS II) Guidebook Abstracts, p. 147–180, text-figs. 16, pls. 17–25. – Abh. Geol. Bundesanstalt Austria 35: 1–265, text-figs. 1–84, tabs. 1–8, pls. 1–25, 1 geological map, Wien.
- KRÍŽ, Jirí & SCHÖNLAUB, H. P. (1980): Fieldtrip E Silurian and Devonian conodont localities of the Barrandian. – In: SCHÖNLAUB, H. P. (ed.): Second European conodont symposium (ECOS II) Guidebook Abstracts: 147–180, text-figs. 1–16, pls. 17–25. – Abh. Geol. Bundesanstalt Austria 35: 1–265, text-figs. 1–84, tabs. 1–8, pls. 1–25, 1 geological map, Wien.
- COOPER, Barry J. (1974): New forms of *Belodella* (Conodonta) from the Silurian of Australia. – J. Paleontol. 48: 1120–1125, text-fig. 1, pl. 1, Tulsa/Okla.
- (1976a): Multielement conodonts from the St. Clair Limestone (Silurian) of southern Illinois. – J. Paleontol. 50: 205–217, text-figs. 2, tab. 1, pls. 1–16, Tulsa/Okla.
- DRUCE, E. C. (1970b): Frasnian Conodonts from Mount Morgan, Queensland. – Austral. Bur. Miner. Resour. Geol. Geophys., Bull. 108: 75–89, text-fig. 1, pls. 12–14, Canberra.
- (1970d): Conodonts from the Garra Formation (Lower Devonian), New South Wales. – Austral. Bur. Miner. Resour. Geol. Geophys., Bull. 116: 29–63, text-fig. 1–3, 1 appendix (un-numbered), pls. 4–9, Canberra.
- FÄHRÆUS, Lars E. & HUNTER, David R. (1985): Simple-cone conodont taxa from the Cobbs Arm Limestone (Middle Ordovician), New World Island, Newfoundland. – Can. J. Earth Sci. 22: 1171–1182, text-figs. 1–7, tab. 1, pls. 1–3, Ottawa.
- JEPSSON, Lennart (1969): Notes on some Upper Silurian multielement conodonts. – Geol. Fören. Stockholm Förh. 91: 12–24, text-figs. 1–4, Stockholm. Also in: Publ. Inst. Miner., Paleontol. Quaternary Geol., Univ. Lund, Sweden 157.
- (1975): Aspects of Late Silurian conodonts. – Fossils Strata 6: 1–79, text-figs. 1–6, tabs. 1–2, pls. 1–12, one appendix (date of imprint 1974), Oslo.
- (1976): Autecology of Late Silurian conodonts. – In: BARNES, C. R. (ed.): Conodont Palaeoecology. Geol. Assoc. Can. Spec. Pap. 15: 105–118, text-figs. 1–2, tabs. 1–3. Also in: Publ. Inst. Miner., Paleontol. Quaternary Geol., Univ. Lund, Sweden 211.
- (1981): The conodont faunas in the Beyrichienkalk. – In: LAUFELD, Sven (ed.): Proceedings of Project Ecostratigraphy Plenary Meeting, Gotland 1981. – Sver. Geol. Unders., Rapp. Medd. 25: 13–14. Also in: Publ. Inst. Miner., Paleontol. Quaternary Geol., Univ. Lund, Sweden 243a.

- (1983 b): Simple-cone studies: some provocative thoughts. – *Fossils Strata* 15: 86. Also in: *Lund Publ. Geol.* 26.
 - (1983 c): Silurian conodont faunas from Gotland. – *Fossils Strata* 15: 121–144, text-figs. 1–2, one appendix, Oslo. Also in: *Lund Publ. Geol.* 18.
 - (1986 b): A possible mechanism in convergent evolution. – *Paleobiology* 12: 80–88, text-figs. 1–2, Ithaca, N.Y.
 - (1987): Lithological and conodont distributional evidence for episodes of anomalous oceanic conditions during the Silurian. – In: ALDRIDGE, Richard J. (ed.): *Palaeobiology of Conodonts: 129–145*, text-figs. 9.1–9.4, tab. 9.1, Chichester, England (Ellis Horwood Ltd).
 - (1988): Conodont biostratigraphy of the Silurian-Devonian boundary stratotype at Klonk, Czechoslovakia. – *Geologica et Palaeontologica* 22: 21–31, text-figs. 1–2, tab. 1, Marburg/Lahn.
- KHODALEVICH, A. N. & TSCHERNICH (Chernykh), V. V. (1973 a): Konodonty iz Zivetskikh olozenij vostochnogo sklona juznogo Urala. (Conodonts from the Givetian strata on the east slope of southern Ural). – In: *Fauna i biostratigrafija srednego i verchnego Paleozoja Urala*. – *Trudy Sverdlovskogo ordena trydovoga krasnogo znameni gornogo instituta im V.V. Vachruseva* 93: 27–41, text-fig. 1 (un-numbered), 15 tabs. (un-numbered), pls. 1–4, Sverdlovsk.
- (1973 b): Novoe podsemejstvo Belodellinae (Konodonty). [The new subfamily Belodellinae (Conodonts)]. – In: *Fauna i biostratigrafija srednego i verchnego Paleozoja Urala*. – *Trudy Sverdlovskogo ordena trydovoga krasnogo znameni gornogo instituta im V.V. Vachruseva* 93: 42–47, 1 text-fig. (un-numbered), 3 tabs. (un-numbered) pl. 1, Sverdlovsk.
- KLAPPER, GILBERT & BARRICK, JAMES E. (1983): Middle Devonian (Eifelian) conodonts from the Spillville Formation in northern Iowa and southern Minnesota. – *J. Paleontol.* 57: 1212–1243, text-figs. and pls. 1–12, Tulsa/Okla.
- KOZUR, H. (1984): Preliminary report about the Silurian to Middle Devonian sequences near Nekézseny (southernmost Uppony mts., northern Hungary). – *Geol. Paläont. Mitt. Innsbruck* 13(7):149–176, tabs. 1 a, 1 b, 2–4, pls. 1, II–X, Innsbruck.
- KUWANO, Y. (1982): Element composition of some Silurian ozarkonodids. – In: JEPPSSON, Lennart & LÖFGREN, Anita (eds.) *Third European conodont symposium (ECOS III) Abstracts*. – *Publ. Inst. Miner., Paleontol. Quaternary Geol., Univ. Lund, Sweden* 238: 15–16, Lund
- LANGE, Friedrich-Georg (1968): Conodonten – Gruppenfunde aus Kalken des tieferen Oberdevon. – *Geologica et Palaeontologica* 2: 37–57, text-figs. 1–2, pls. 1–6, Marburg.
- LINK, A. G. & DRUCE, E. C. (1972): Ludlovian and Gedinnian conodont stratigraphy of the Yass Basin, New South Wales. – *Austral. Bur. Miner. Resourc. Geol. Geophys., Bull.* 134: 1–136, text-figs. 1–67, tabs. 1–2, pls. 1–12, 1 map, 1 appendix (un-numbered, in pocket), Canberra.
- MARTINSSON, Anders (1963): *Kloedenia* and related ostracode genera in the Silurian and Devonian of the Baltic area and in Britain. – *Bull. Geol. Inst. Univ. Uppsala* 42: 1–63, text-figs. 1–36, Uppsala.
- MCLAREN, D. J. (1972): Report from the Committee on the Silurian-Devonian Boundary and Stratigraphy. – *Geological Newsletter* 1972 (4):268–280, Haarlem.
- MOSKALENKO, T. A. (1966): First find of Late Silurian conodonts in Zeravshan Range. – *Paleontol. Zhurnal* 1966, 2: 81–91, text-figs. 1–4, 5 un-numbered tabs, pl. 11, Moskva. In: Russian, translated in: *Int. Geol. Rev.* 9: 195–204.
- PHILIP, G. M. (1965): Lower Devonian conodonts from the Tyers area, Gippsland, Victoria. – *Proc. Roy. Soc. Victoria* 79: 95–117, text-figs. 1–2, pls. 8–10, Melbourne.
- (1966): Lower Devonian conodonts from the Buchan Group, eastern Victoria. – *Micropaleontology* 12: 441–460, text-figs. 1–9, tab. 1, pls. 1–4, New York/N.Y.
- REXRoad, Carl B. & CRAIG, William W. (1971): Restudy of conodonts from the Bainbridge Formation (Silurian) at Lithium, Missouri. – *J. Paleontol.* 45: 684–703, text-figs. 1–2, tab. 1, pls. 79–82, Tulsa/Okla.
- RHODES, F. H. T. & DINELEY, D. L. (1957): Devonian conodont faunas from southwest England. – *J. Paleontol.* 31: 353–369, text-figs. 10, tab. 1, pls. 37–38, Tulsa/Okla.
- SAPELNKOV, V. P., MIZENS & SNIGIREVA, M. P. (1981): Brahipydy i konodonty zony Zdimir (Devon) severnoj casti severnogo Urala. – In: *Biostratigrafija i fauna srednego Paleozoja Urala: 75–91*, text-figs. 1–3, pls. 1–2. UNC AN SSSR, Sverdlovsk.
- SERPAGLI, Enrico (1967): I conodonti dell'Ordoviciano superiore (Ashgilliano) delle Alpi Carniche. – *Soc. Paleontol. Ital., Boll.* 6: 30–111, text-figs. 1–8, tabs. 1–6, pls. 1–31, Modena.
- SNIGIREVA, M. P. (1975): Novyye konodonty iz srednedevonskikh otlozheniy Severnogo Urala. – *Paleontol. Zhurnal* 1975, 4: 24–31, 1 text-fig., pl. IV, Moskva. Translated as: New conodonts from Middle Devonian deposits of the Northern Urals. – *Paleontol. J.* 9: 448–455, text-fig. 1, 5 un-numbered tabs., pl. IV.
- STAUFFER, Clinton R. (1940): Conodonts from the Devonian and associated clays of Minnesota. – *J. Paleontol.* 14: 417–435, pls. 58–60, Tulsa/Okla.
- SWEET, Walter C. (1979): Late Ordovician conodonts and biostratigraphy of the Western Midcontinent Province. – *Brigham Young Univ., Geol. Stud.* 26: 45–85, 4 text-figs., tab. 1, 6 pls., numbered 1–10, Provo, Utah.
- WALLISER, Otto H. (1964): Conodonten des Silurs. – *Abh. hess. L.-Amt Bodenforsch.* 41: 1–106, text-figs. 10, tabs. 2, pls. 32, Wiesbaden.
- WALMSLEY, Victor G., ALDRIDGE, Richard J. & AUSTIN, Ronald L. (1974): Brachiopod and conodont faunas from the Silurian and Lower Devonian of Bohemia. – *Geologica et Palaeontologica* 8: 39–47, text-figs. 1–3, tabs. 1–2, one appendix, Marburg.
- ZHOU, Xiyun, ZHAI, Zhiqiang & XIAN, Siyuan (1981): On the Silurian conodont biostratigraphy, new genera and species in Guizhou Province. – *Oil & Gas Geology* 2: 123–146, figs. 1–8, tabs. 1–3, pls. I–II (in Chinese with a short abstract with this title on p. 140).
- ZIEGLER, W. (1960): Conodonten aus dem Rheinischen Unterdevon (Gedinnium) des Remscheider Sattels (Rheinisches Schiefergebirge). – *Paläont. Z.* 34: 169–201, text-figs. 1–2, tabs. 1–3, pls. 13–14, Stuttgart.

Plate 1

Most specimens have been illustrated in inner lateral views in ordinary light (a) supplemented by a SEM picture (b) from the same angle. Most pictures are oriented with the proximal part of the posterior margin of the basal cavity horizontal. Most magnifications are calculated from direct measurements of the specimens. The uncertainty is about 5%. Magnifications indicated by the SEM instrument turned out to deviate, and are not used except that they have to be used for figures of parts of specimens and view like Fig. 15 c. These magnifications may be about 15% too high. All illustrated specimens are deposited in the type collection at the Department of Historical Geology and Palaeontology, Lund.

Figs. 1–5: *Belodella mira* (KHODALEVICH & TSCHERNICH 1973) sensu nov. All specimens from Bed 11 at Klonk.

Fig. 1: An f element. In fig. 1 a, note the incompletely rounded-off basal cavity tip and the broad flange anterior (to the lower right in the picture) of the basal cavity. Fig. 1 a about $\times 100$, fig. 1 b about $\times 102$. LO 5871.

Fig. 2: A u element. Probably only a small amount of the distal part of the base is lost. In fig. 2 a the outline of the basal cavity, which has been rounded off twice, may be seen as well as the broad flange anterior of that cavity, the strong anterior edge of the base (light in fig. 2 a), and the fused part of the denticles. The inward curving of the anterior flange causes its light appearance in fig. 2 b. Figs. 2 a, b about $\times 108$. LO 5872.

Fig. 3: A doc element. The base is incomplete distally. In fig. 3 a can be seen the broad flange (dark in fig. 3 a) anterior of the basal cavity, the anterolateral edge (the narrow light line in fig. 3 a, compare fig. 3 c), and the narrow hyaline strip (dark in fig. 3 a) between the basal cavity and the root tips of the denticles, except near the pointed tip of the basal cavity where there are surface reflections. Fig. 3 c shows the lateral displacement of the edges onto the cusp as compared with the base. Fig. 3 a about $\times 107$, fig. 3 b about $\times 100$, fig. 3 c about $\times 388$. LO 5873.

Fig. 4: A tc element. Much of the distal part of the base is lost. In fig. 4 a the broad anterior flange and the narrow hyaline strip below the denticles can be seen. A comparison of fig. 4 b with fig. 5 b shows that the base is slightly more curved proximally and the cusp is nearly erect. Fig. 4 a about $\times 100$, fig. 4 b about $\times 108$. LO 5874.

Fig. 5: A ts element. The base is incomplete distally. In fig. 5 a can be seen at least seven sack-like extensions of the basal cavity into the broad anterior flange. The narrow light strip along the anterior margin of the base is the thin inner anterior edge. The narrow hyaline strip (dark in fig. 5 a) below the denticle roots marks the straight posterior margin of the basal cavity. The obliquely anterolateral view in fig. 5 c shows that the element is strongly compressed but, in spite of this, that it has an anterior side. See also figs. 5 d and 5 e. The part illustrated in fig. 5 e is found between 23 and 29 mm from the tip of the cusp in fig. 5 c. A faint striation on the base can be seen in fig. 5 d. Fig. 5 a about $\times 104$, fig. 5 b about $\times 98$, fig. 5 c about $\times 100$, fig. 5 d about $\times 415$. LO 5875.

Figs. 6–14: *Belodella* sp. S. from sample Tj 80-7 LJ from a limestone lens 0.05–0.10 m above Bed 16 at Klonk, that is from the lower part of Interbed 16/17. The elements are illustrated in the same order as those of *B. mira*.

Fig. 6: An f 1 element. Note the slightly rounded basal cavity tip. The boundary between hyaline and white matter is difficult to discriminate. The element was probably hyaline up to where the dark streak ends about 10 mm above the basal cavity tip, perhaps except for a narrow strip of white matter just posterior of this streak. The striation is best seen in fig. 6 c. Fig. 6 a about $\times 100$, fig. 6 b about $\times 112$, fig. 6 c about $\times 445$. LO 5876.

Fig. 7: An f 2 element. The basal cavity tip is close to the anterior margin, about 7 mm from the distal end of the cusp (most of which is lost). Fig. 7 a about $\times 103$, fig. 7 b about $\times 115$, fig. 7 c about $\times 445$. LO 5877.

Fig. 8: A u 1 element. Note the rounded tip of the basal cavity and the narrow zone of translucent hyaline matter along the sides of the expanded basal cavity. Fig. 8 a about $\times 109$, fig. 8 b about $\times 122$. LO 5878.

Fig. 9: A u element. In fig. 9 a note the straight margins of the basal cavity and the thin streak of hyaline matter that extends from the basal cavity tip into the base of the cusp. The distal part of the base is markedly reinforced. The anterior lateral margin was probably weakly denticulated. Fig. 9 a about $\times 110$, fig. 9 b about $\times 106$. LO 5879.

Fig. 10: A doc element. In fig. 10 a the narrow zone of hyaline matter (dark in fig. 10 a) delimits the curved basal cavity well. Like in the specimen in fig. 9 a there is a thin streak of hyaline matter extending into the base of the cusp. Fig. 10 a about $\times 108$, fig. 10 b about $\times 114$. LO 5880.

Fig. 11: A tc? element in inner lateral view. The pointed tip and the streak of hyaline matter into the proximal part of the cusp may be seen. Fig. 11 a about $\times 105$, fig. 11 b about $\times 109$. LO 5881.

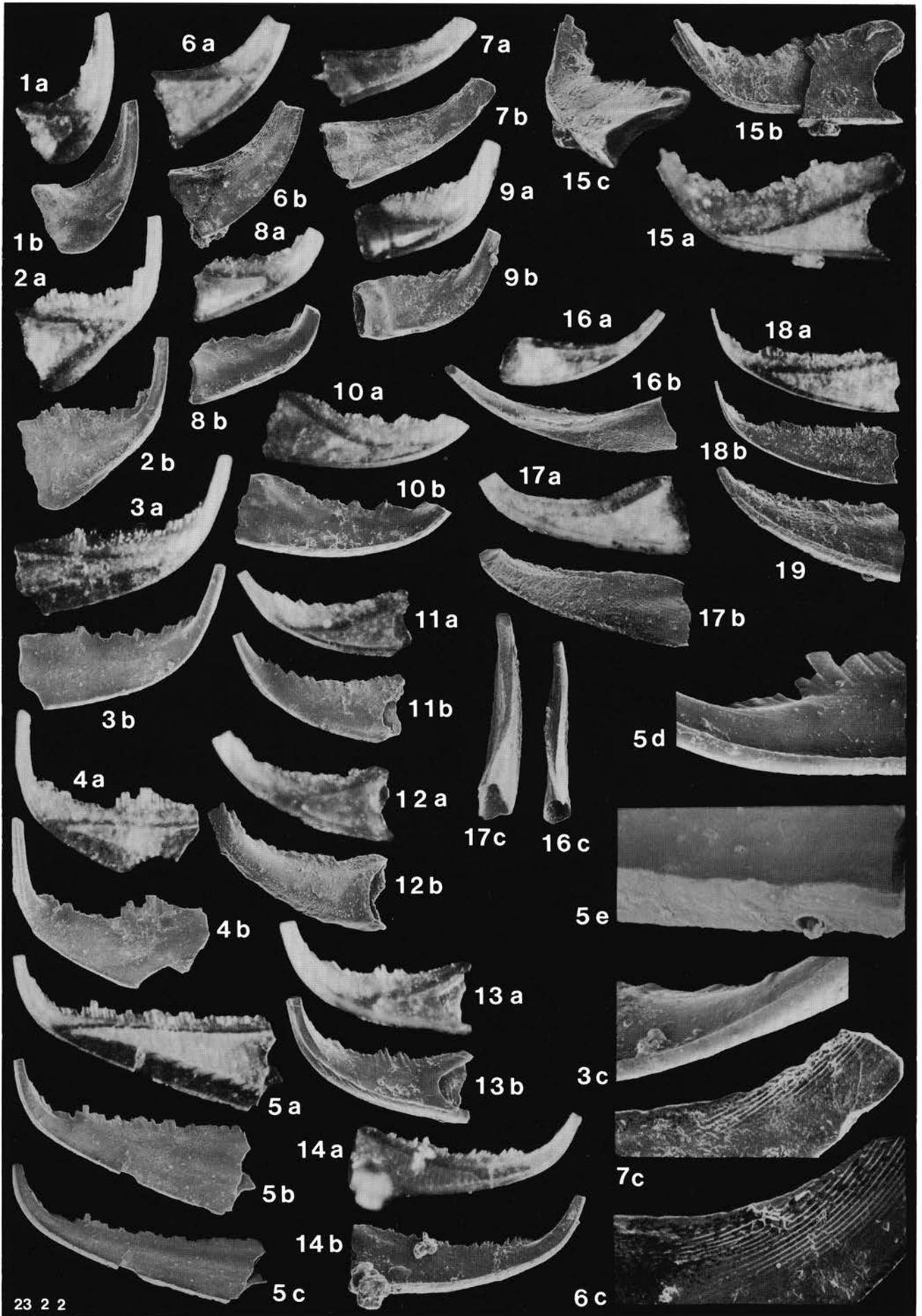
Fig. 12: A tc? element in outer lateral view. Note the rounded-off basal cavity tip. However, when viewed from other angles the original pointed tip can be seen. Fig. 12 a about $\times 108$, fig. 12 b about $\times 110$. LO 5882.

Fig. 13: An ats element. In fig. 13 a can be seen the curved posterior margin of the basal cavity. The narrow zone of hyaline matter along the basal cavity extends about 9 mm beyond the present rounded basal cavity tip. In fig. 13 a note the typical denticulation with long slanted denticles proximally and markedly shorter and slightly less slanted denticles distally on the base. Compare with figs. 8 a–14 a: the shorter base, the more curved posterior basal cavity margin and the more distinct differences in denticle length. In fig. 13 b the denticulation on the inner anterolateral edge is shown. The transverse darker lines on the inside of the basal cavity can be seen on the most distal part of the outer side, where the inner side is lost – compare with fig. 14 a. Figs. 13 a, b about $\times 121$. LO 5883.

Fig. 14: A dts element. In fig. 14 a note the curved posterior basal cavity margin and the obliquely filled basal cavity tip. In slightly differently views it is possible to see that the original basal cavity tip was about 8 mm closer to the cusp. The low, slanted denticles on the posterior edge are clearly visible in fig. 14 a and the denticulation on the anterolateral edge in fig. 14 b. Compare with the corresponding element of *B. mira* in fig. 5. Fig. 14 a about $\times 107$, fig. 14 b about $\times 111$. LO 5884.

Fig. 15: A dts element of *B. anomalis* (COOPER 1974) in inner lateral view from Bed 19 at Klonk. In fig. 15 a the narrow strip of hyaline matter outlines the posterior margin of the basal cavity. The very narrow dark line along the anterior side does not mark the outline of the basal cavity but is caused by the inner lateral edge, compare with fig. 15 b. Unfortunately, the specimen broke during remounting for SEM picturing. The cusp is broken slightly more proximally than the longest denticle of the inner half of the fan; most of the thick cusp is seen anterior of this denticle in fig. 15 b, but a minor part is seen posterior of it. In fig. 15 c the cusp is situated between 2,5 and 5,5 mm from the left margin of the fan. Fig. 15 a about $\times 106$, fig. 15 b about $\times 103$, fig. 15 c about $\times 120$. LO 5885.

continued on p. 34



continued from p. 32

Figs. 16, 17: *Belodella* sp. G from the latest Ludlow Hamra Beds at Kettelviken 5, Gotland, Sweden, sample G77-35LJ.

Fig. 16: Probably a juvenile u element. The posterior margin of the basal cavity is visible proximally in fig. 16 a (about 3 mm from the denticle tips). The light streak about 1 mm from the denticle tips is the extra posterolateral edge, which is better visible in fig. 16 c. Fig. 16 a about $\times 117$, fig. 16 b about $\times 160$, fig. 16 c about $\times 121$. LO 5886.

Fig. 17: Probably a mature ats element. In the inner lateral view in fig. 17 a the posterior margin of the basal cavity is well outlined by the broad hyaline zone, but the thin darker line about 2 mm inside and along the anterior margin of the element is the margin of the lateral edge. The white matter of the cusp ends about 2 mm from where the cusp is broken. There is also a zone about 1 mm wide of white matter along the proximal posterior margin, representing the remains of the denticle roots. The posterior edge can be seen in fig. 17 c as the distinct limit between the illuminated outer side (to the right in the picture) and the darker posterior and inner

sides. The extra posterior lateral edge is similarly illuminated and may be seen about 2 mm to the left of the posterior edge proximally on the base, compare with fig. 16 c. Fig. 17 a about $\times 110$, fig. 17 b about $\times 120$, fig. 17 c about $\times 103$. LO 5887.

Figs. 18, 19: *Belodella resima* (PHILIP 1965) sensu nov. from the same sample as 16 and 17.

Fig. 18: A juvenile doc element. The strongly compressed shape of the element may perhaps be seen at the basal cavity opening in fig. 18 b. The narrow zone of hyaline matter around the basal cavity outlines the latter well in fig. 18 a. Note the narrow anterior flange compared with that of the corresponding element of *B. mira* in fig. 3 a. The thin light line along the anterior margin of the base in fig. 18 a is the anterolateral edge, compare fig. 18 b. Fig. 18 a about $\times 109$, fig. 18 b about $\times 107$. LO 5888.

Fig. 19: An at element in outer lateral view. The broad triangular cross section can best be seen on the broad anterior side. Note that the outer lateral edge does not continue above the proximal part of the cusp. Fig. 19 about $\times 110$. LO 5889.

Plate 2

Sp (Pa) elements of *Ozarkodina steinhornensis* s. l. The specimens have been illustrated perpendicular to the plane of the blade, to avoid letting the development and preservation of the basal cavity lip of the far side determine the angle of view. Two exceptions are figs. 2b and 5a, which are in slightly oblique view – compare the apparent height of the blade with that in figs. 2a and 5b, respectively. Caution is necessary when the length-height proportion of the blade is compared with specimens illustrated in an unstandardized view. Similarly, I have tried to illustrate the oral from straight above the blade. Fig. 6c differs in this respect. Regarding magnifications, see legend to Plate 1.

Figs. 1–4: *Ozarkodina s. eosteinhornensis* (WALLISER 1964) sensu JEPSSON 1975 from Bed 11 at Klonk. Figs. 1–3 illustrate specimens with a well developed lateral process and fig. 4 illustrates a specimen lacking such a process.

Fig. 1: A specimen approximately 0.72 mm long. Fig. 1 a about $\times 75$, fig. 1 b about $\times 77$, fig. 1 c about $\times 74$. LO 5890.

Fig. 2: A specimen approximately 0.66 mm long. Note the successive overgrowth of denticles. The small denticle between the third and fourth functional denticles on the anterior process is well visible, that between the second and third is clearly visible in fig. 2 a and the former existence of one between the first and second can only be deduced from the abrupt lower end of the hyaline streak (dark in fig. 2 a) between the denticles. Judging from irregularities in the white matter of the first denticle, its unusual broad character results from fusion of two or three denticles. Fig. 2 a about $\times 75$, fig. 2 b about $\times 80$, fig. 2 c about $\times 78$. LO 5891.

Fig. 3: A specimen approximately 0.44 mm long. The magnifications of figs. 3 a and 3 c are similar to those of figs. 1 and 2 whereas fig. 3 b is magnified to about the same length as figs. 1 and 2. Comparisons of these figs. show that, apart from the fusion of the cusp and most of the denticles, the proportions are retained during ontogeny. Fig. 2 shows how space for the increase in denticle size is achieved. In fig. 3 a note that the line formed by the lower end of the denticle roots is nearly parallel with the aboral margin. Compare with *O. s. remscheidensis* in fig. 8 a. Fig. 3 a about $\times 75$, fig. 3 b about $\times 117$, fig. 3 c about $\times 80$. LO 5892.

Fig. 4: This specimen is presently about 0.53 mm in length. Fig. 4 a about $\times 73$, fig. 4 b about $\times 77$, fig. 4 c about $\times 75$. LO 5893.

Fig. 5: A specimen approximately 0.55 mm long from Bed 11 at Klonk. The small cusp and the line formed by the lower end of the roots of the denticles and the direction of the denticles relate this incomplete specimen to *O. s. eosteinhornensis* whereas the shape of the

basal cavity is more like that of *O. s. remscheidensis*. The juvenile specimen is probably best interpreted as an extreme specimen of *O. s. eosteinhornensis* or possibly of *O. s. remscheidensis*, not as an intermediate form. Mature specimens in the fauna are well separated. Fig. 5 a about $\times 70$, fig. 5 b about $\times 76$, fig. 5 c about $\times 75$. LO 5894.

Figs. 6–11: *Ozarkodina s. remscheidensis* (ZIEGLER 1960) sensu nov. from Bed 11 (figs. 6 and 7) and Bed 12 (figs. 8–11) at Klonk.

Fig. 6: A specimen approximately 0.66 mm long. Fig. 6 a about $\times 74$, fig. 6 b about $\times 75$, fig. 6 c about $\times 76$. LO 5895.

Fig. 7: This specimen was lost after it was photographed. About $\times 75$.

Fig. 8: A specimen approximately 0.83 mm long. In fig. 8 a note the angle between the lower ends of the denticle roots and the aboral margin of the blade. Compare with fig. 3 a. Reflections from the surface create a false impression of deeper white matter roots in the most anterior denticles. Fig. 8 a is about $\times 72$, fig. 8 b is about $\times 74$, fig. 8 c about $\times 74$. LO 5896.

Fig. 9: A specimen approximately 0.79 mm long. Fig. 9 a is about $\times 73$, fig. 9 b about $\times 76$, fig. 9 c about $\times 77$. LO 5897.

Fig. 10: A specimen approximately 0.68 mm long. Fig. 10 a is about $\times 75$, fig. 10 b about $\times 76$, fig. 10 c about $\times 75$. LO 5898.

Fig. 11: This specimen is presently about 0.60 mm long. Fig. 11 a is about $\times 72$, fig. 11 b about $\times 75$, fig. 11 c about $\times 77$. LO 5899.

Fig. 12: *Ozarkodina s. remscheidensis*? from sample Tj80-7LJ from Interbed 16/17 at Klonk. The specimen is about 0.80 mm long. The lower margin is essentially intact, thus the ascending character of the lower margin on the process to the right – probably the anterior process – is real. See the text for a discussion. About $\times 75$. LO 5900.

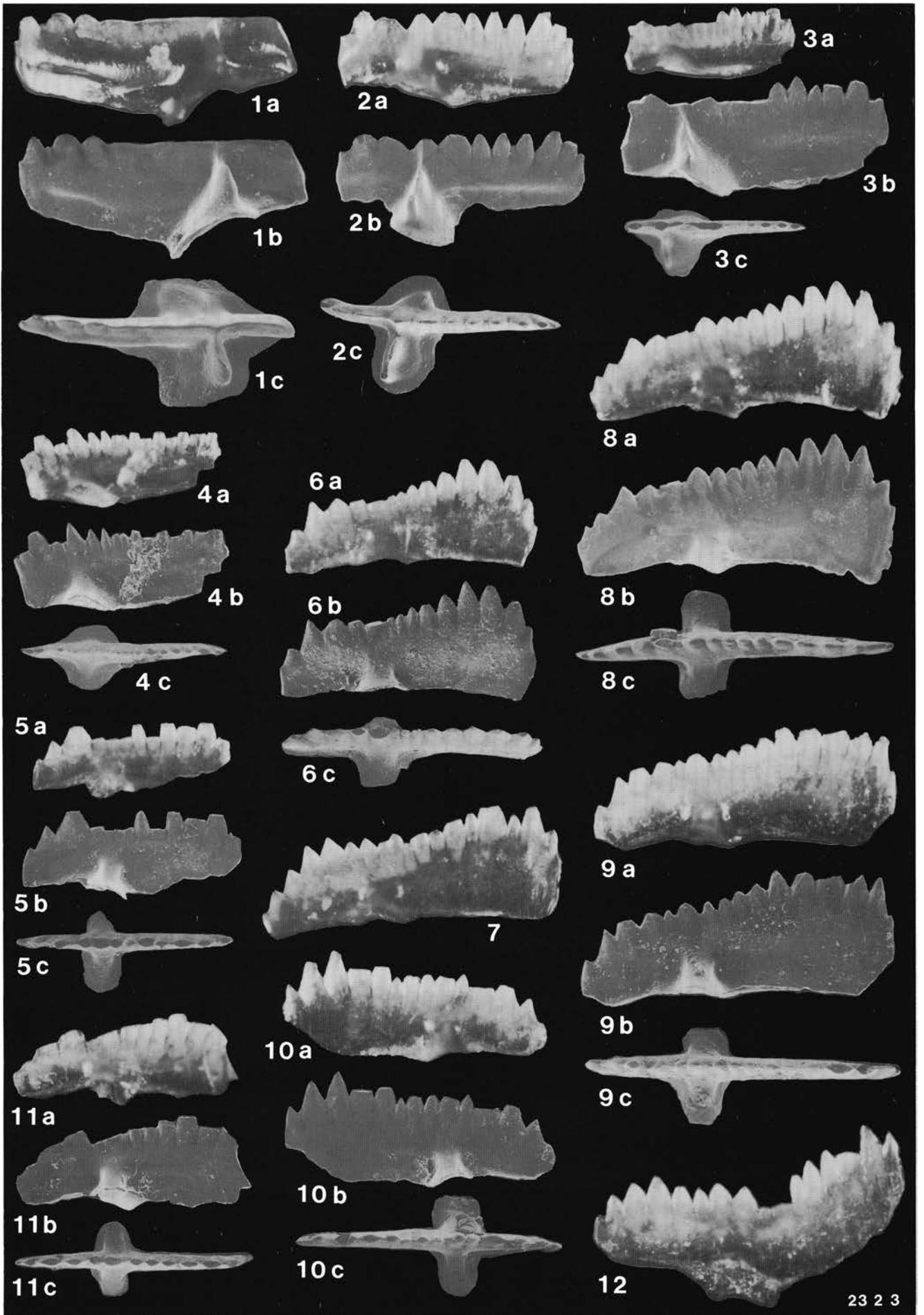


Plate 3

Regarding magnifications see legend to Plate 1.

Figs. 1–4: *Ligonodina elegans detorta* (WALLISER 1964) sensu JEPSSON 1975. The specimen in fig. 2 is from sample Tj80-1LJ from Bed 3 at U topolù, the other three are from sample Tj80-7LJ from Interbed 16/17 at Klouk.

Fig. 1: An hi (Sa) element in oblique lateral view. The total length is about 0.61 mm. In fig. 1 a note the two small denticles (arrows) between those of normal size. Fig. 1 b: same view but about the same magnification as fig. 5 a. Fig. 1 a about $\times 150$, fig. 1 b about $\times 75$. LO 5901.

Fig. 2: A detortiform element with 1–3 small denticles between most of those of normal size. The span from the tip of the longest process to the present end of the cusp is about 0.40 mm. About $\times 150$. LO 5902.

Fig. 3: A fragment, approximately 0.34 mm long, of the posterior process of an hi (Sa) element in which the alternation in denticle size is easily seen. About $\times 150$. LO 5903.

Fig. 4: An ne (M) element. The maximum dimension is about 0.27 mm. About $\times 150$. LO 5904.

Fig. 5: *Ligonodina* sp. A hi element. Fig. 5 a and fig. 5 b in lateral view and fig. 5 c in oblique oral view. The difference between the two views in the impression of the direction of the lateral process is pronounced. Fig. 5 a about $\times 75$, fig. 5 b about $\times 116$, fig. 5 c about $\times 116$. LO 5905.

Figs. 6–8: *Ozarkodina excavata* (BRANSON & MEHL 1933) sensu JEPSSON 1969 from Bed 12 at Klouk.

Fig. 6: An sp (Pa) element in lateral view. Fig. 6 a about $\times 75$, fig. 6 b about $\times 100$. LO 5906.

Fig. 7: A pl or ke (Sb/Sd) element. Fig. 7 a about $\times 75$, fig. 7 b about $\times 100$. LO 5907.

Fig. 8: An ne (M) element. Note the distinct edges on most of the denticles. Fig. 8 a about $\times 75$, fig. 8 b about $\times 95$. LO 5908.

Fig. 9: *Ligonodina* sp. Compare the smooth curvature of the inner margin of the basal cavity with that of the ne element of *O. excavata* in fig. 8. Fig. 9 a about $\times 75$, fig. 9 b about $\times 106$. LO 5909.

Fig. 10: *Ozarkodina s. eosteinhornensis* (WALLISER 1964) sensu JEPSSON 1975 from Bed 11 at Klouk. The maximum dimension as preserved is 0.42 mm. Fig. 10 a about $\times 73$, fig. 10 b about $\times 108$. LO 5910.

Figs. 11–18: *Ozarkodina s. remscheidensis* (ZIEGLER 1960) sensu nov. All specimens are from Bed 12 at Klouk except the specimen in fig. 12 which is from Bed 11.

Fig. 11: An oz (Pb) element, 0.64 mm long. This specimen from Bed 12 is in some respects more similar to the juvenile specimen of *O. s. eosteinhornensis* in fig. 10 than to the mature Bed 11 specimen in fig. 12. However, the appearance is typical for oz elements from Bed 12, where only *O. s. remscheidensis* is identified. The identification of the specimen in fig. 10 as *O. s. eosteinhornensis* is based on the similarity with oz elements from Cellon (WALLISER 1964, Pl. 26, fig. 8). Possibly the less extreme character of the oz element is related to the fact that only *O. s. remscheidensis* existed there at that time whereas both taxa are found in Bed 11. Fig. 11 a about $\times 75$, fig. 11 b about $\times 78$. LO 5911.

Fig. 12: A mature oz (Pb) element. The distance between the tip of the anterior process and that of the cusp is about 0.57 mm. About $\times 79$. LO 5912.

Fig. 13: A juvenile ne (M) element. The maximum dimension is 0.39 mm. Fig. 13 a about $\times 72$, fig. 13 b about $\times 77$. LO 5913.

Fig. 14: This ne (M) element is more mature than that in fig. 13. The specimen is presently 0.77 mm long. Fig. 14 a about $\times 73$, fig. 14 b about $\times 75$. LO 5914.

Fig. 15: A mature tr (Sa) element. The maximum dimension is 0.56 mm. Fig. 15 a about $\times 70$, fig. 15 b about $\times 75$. LO 5915.

Fig. 16: A mature pl/ke (Sb or Sd) element. The specimen is presently 0.69 mm long. Fig. 16 a about $\times 72$, fig. 16 b about $\times 83$. LO 5916.

Fig. 17: A pl/ke (Sb or Sd) element. The posterior process has reached the stage where the end turns obliquely downwards and the increase in length slows down. Compare with fig. 16. The specimen is presently 0.60 mm long. About $\times 78$. LO 5917.

Fig. 18: A 1.15 mm long hi (Sc) element. Fig. 18 a about $\times 75$, fig. 18 b about $\times 77$. LO 5918.

