A Ludlow conodont fauna from Irian Jaya (Indonesia)

M. van den Boogaard

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The conodont fauna extracted from a boulder in the Lorentz River (southern Irian Jaya) is described. Arguments are put forward that the elements of *Distomodus dubius* (Rhodes, 1953) sensu Jeppsson, 1972 are part of the apparatus of species of *Coryssognathus* Link & Druce, 1972, a genus that ontogenetically acquires an apparatus of multidenticulate elements on account of the phenomenon that one coniform element of each of the several (curvature-transition ?) series successively incorporates its – to that time independently growing – coniform neighbours within its lamellae. Attention is called to the fact that probably also the apparatus of *Distomodus kentuckyensis* Branson & Branson, 1947 – as described by Cooper (1975) – had a similar ontogeny and that it needs to be investigated whether other species assigned to *Distomodus* are congeneric.

M. van den Boogaard, Nationaal Natuurhistorisch Museum, Department of Palaeontology, Postbus 9517, NL 2300 RA Leiden, The Netherlands.

Introduction

Ordering part of the museum collection in 1972 I came across a rock sample from western New Guinea (Irian Jaya) described by Martin in 1911. The sample contains some small pygidia of trilobites which Martin could not identify to generic or specific level. He therefore could not give an age estimate other than Palaeozoic. I decided to look for conodonts. The rock – a fine-grained quartz sandstone cemented with lime – indeed yielded conodonts, a fauna dominated by two types of Pa elements up to that time not reported in the literature. The rock sample had been taken from a boulder in the Lorentz (or Noord) River and nothing was known about its derivation. Because of the inaccessibility of that part of Irian Jaya no outcrops of this type of rock have been found. Consequently I decided at that time to let the matter rest, convinced that in due time these conodonts would be published based on material from a genuine type locality. Eighteen years have passed and now both types of Pa elements have been reported, one as an element of *Coryssognathus dentatus* Link & Druce, 1972, the other as sp element beta morph of *Ozarkodina crispa* (Walliser, 1964) by Walliser & Wang (1989). Because several elements of the fauna show some characteristics which may be of interest in phylogenetic considerations I venture the present paper.

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PROVENANCE OF THE SAMPLE

The rock sample was collected in 1906 by the mining-engineer O.G. Heldring – member of a military expedition exploring the Noord (or Lorentz) River in southern New Guinea – from a boulder bed somewhere south of Camp Alkmaar (see Fig. 1). Martin did not give data about the exact locality of that boulder bed but indicated a stretch of the river from Camp Alkmaar down to the confluence with the Schultz river (see Fig. 1 and Martin 1911, pl. 8, loc. 3). Knowledge of the exact locality does not matter much, for it does not restrict the area of provenance. The upper Lorentz River traverses a zone of strata over 400 km long and c. 15 km wide indicated as undifferentiated Palaeozoic of the Central Range on the geological map published by Visser & Hermes (1962, enclosures 1 and 2). No detailed data are available about these strata in the inaccessible, jungle-covered, drainage basin of the Lorentz river, but some 200 km to the west in a road section SW of the Carstenz Toppen, Martodjojo et al. (1975) established the presence of strata of the Kemoem Formation in the southern part of the zone. Lithologically the boulder yielding the conodonts may derive from the Kemoem Formation which, according to Visser & Hermes (1962, p. 63), is a monotonous sequence of phyllitic slates with subordinate intercalations of quartzites and greywackes. In north-central Vogelkop graptolites have been found in situ in the Kemoem Formation indicating that part of the formation has a Late Llandovery age (Visser & Hermes, 1962, p. 52). Besides conodonts the sample contains numerous small gastropods, some brachiopods, bivalves and Ostracoda. Many of these remains, especially the gastropods, are preserved as phosphatized internal moulds.

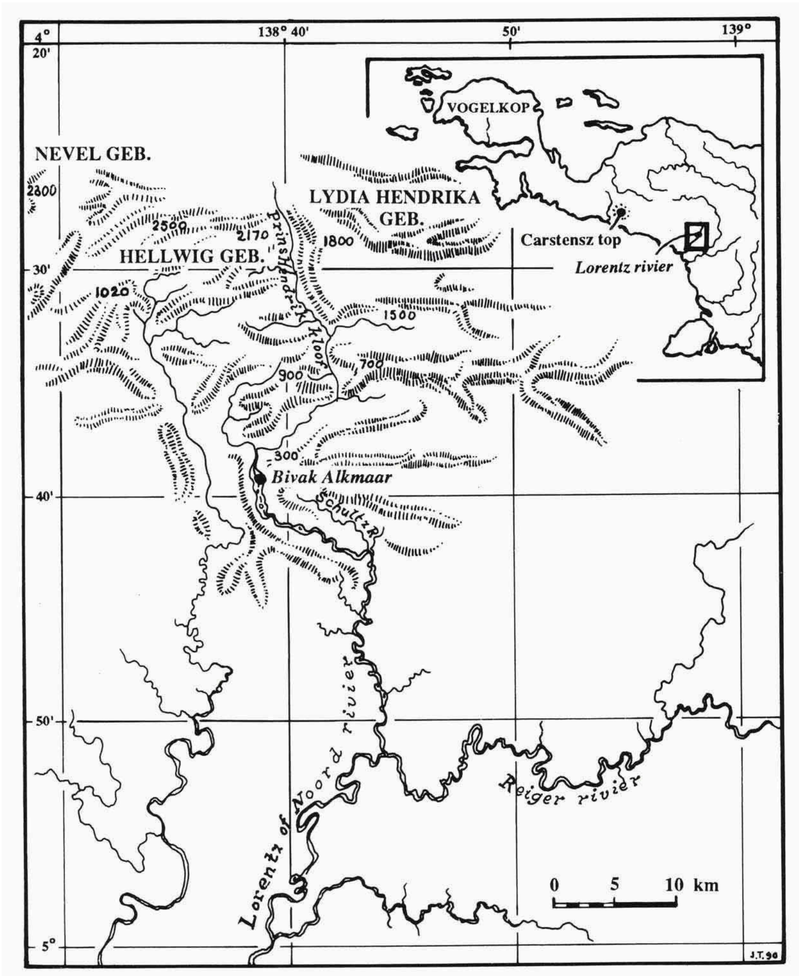

Fig. 1. Sketch map of the upper Lorentz River. Simplified version of the sketch map drawn by A.J. Gooszen in 1908, and published in Hellwig (1908, map XIX).

Systematic palaeontology

Coryssognathus dentatus Link & Druce 1972
Pl. 1, figs. 1-7; Pl. 2, figs. 1, 2.

1972 *Coryssognathus dentatus* sp. nov. – Link & Druce, pp. 31, 32, pl. 2, figs. 13-19, text-fig. 13.

Original description – Unit short, consisting of denticulated posterior bar, apical denticle not prominently larger than denticles of posterior bar, short anterior bar, and lateral bar. Bar denticles blunt, erect, oval in cross-section, and decreasing in size from apical denticle; 2 to 3 denticles on posterior bar, 1 on anterior and 1 on lateral bar. Basal cavity deep, occupying aboral region.

Description of the specimens from the sample from Irian Jaya – Only one element, the Pa element, is currently assigned to *Coryssognathus*. For possible other elements of the apparatus see discussion below. The Pa element has three processes and a cusp with oval cross-section and sharp anterior and posterior edges. The posterior process, which is straight or slightly curved, has two or three denticles which are fused to the cusp and to each other over a large part of their length; the denticles become progressively less fused posteriorly. The denticles may be as large as or even larger than the cusp, are oval in cross-section, and are progressively inclined towards the posterior and sometimes bent to one side, away from the side with the lateral process. The anterior process is very short with one small denticle which may be incorporated in the cusp in mature specimens. The anterior process is bent slightly sidewards in a direction opposite from the eventual curvature of the posterior process; the line from anterior to posterior tip may thus be weakly sigmoidal. Because of the direction of the anterior process with regard to the direction of the posterior one and also because of the direction of the occasional slight bending of some denticles, the lateral process is considered to be an outer process. It is directed posteriorly, and may be slightly shorter, as long as, or even longer than the posterior process. It bears one to three, generally two, denticles which are much less fused than those of the posterior process.

The aboral side of the element is completely occupied by the widely flaring basal cavity in which every denticle has its own basal pit (see Pl. 1, figs. 3, 4 and Pl. 2, figs 1, 2). Pl. 2, fig. 2, a photograph of the aboral side of the specimen on Pl. 1, fig. 3, shows the basal pits of some of the denticles. It is clearly visible that the cusp (lower centre) and the next denticle (left of the centre) first developed some lamellae of their own before being enveloped by joint lamellae. Then, at a later stage, the posterior denticle (top left) and the first denticle of the lateral process (top right) became enveloped by the joint lamellae. Pl. 2, fig. 1 shows that the second denticle of the lateral process (top right) became enveloped by the joint lamellae at a later stage than the first denticle (lower left). For orientation see the dust particle indicated by the arrow, which lies near the boundary of the own lamellae and the joint lamellae of the first denticle (Pl. 2, fig. 2). In fig. 1 it is apparent that several lamellae were added before they started to envelop the second denticle. Thus the element became more denticulate by successively incorporating denticles which had started to develop as isolated denticles. A very juvenile specimen (Pl. 1, fig. 7) has one denticle in front of the cusp (right side of the photograph) which is slightly flexed to the side. The posterior process, still with one denticle, is slightly flexed in the opposite direction. From the tip of the cusp a ridge extends onto the lateral process which in this specimen is broken off. In mature specimens the denticle of the anterior process is generally completely enveloped by the lamellae of the cusp but the anterior edge still shows the slight lateral flexure.

Remarks – *Coryssognathus dentatus* occurs in the Yass Basin (Australia) in strata of early Ludlow age. In upper Ludlow and lower Pridoli strata of Europe the species *Pelekysgnathus dubius* Jeppsson, 1972 is found. *P. dubius* is an element (Aldridge, 1985) "displaying a linear row of few broad discrete denticles and a terminal cusp;

basal cavity deep and widely flared with a marginal fold on the inner side". In my opinion the marginal fold is located on the outer side, for i.a. one specimen photographed by Jeppsson (1975, pl. 2, fig. 2c) shows that the line from the tip of the anterior process over the cusp and the preserved part of the posterior process is convex at the side of the marginal fold. *P. dubius* has a fold of the lateral cavity wall where *Coryssognathus dentatus* has a lateral process, (see also Pl. 3, figs. 3 and 4). In all other aspects they are almost similar: size and shape of the denticles on the posterior process – although less fused – and position of the cusp, which in Jeppsson's original description is considered to be posterior instead of anterior. Also the aboral side is similar, all denticles having a basal pit. Two small specimens (Jeppsson, 1972) do have a denticle on the marginal fold. Klapper & Murphy (1974) considered *P. dubius* not to belong in *Pelekysgnathus* but to be congeneric with *Coryssognathus dentatus*. Clark et al. (1981) synonymize the two species as *Coryssognathus dubius* (Jeppsson, 1972), the epitheton specificum *dubius* Jeppsson, 1972 having priority over *dentatus* Link & Druce, 1972. Jeppsson (1979) and Aldridge (1985) still refer to the late Ludlow form as *Pelekysgnathus dubius*. Sweet (1988) is of the opinion that *Coryssognathus* is not a *Pelekysgnathus* as suggested by Jeppsson (1972). The *Pelekysgnathus* Pa element has a posterior cusp and only the one denticle directly in front of it also has a basal pit, whereas in *P. dubius* all denticles but one are posterior of the cusp and all do have a basal pit. This feature – already observed by Jeppsson (1972) – indicates a phylogenetic history different from that of *Pelekysgnathus*. *C. dubius* and *C. dentatus* do appear to be distinct species. Some rare small specimens of *C. dubius* have a lateral process, but the majority only have a marginal fold. In contrast all the mature specimens of *C. dentatus* from the Yass Basin and from Irian Jaya have a denticulated lateral process. More finds of *Coryssognathus* will be necessary to decide whether the fact that the Australian specimens have only one denticle on the lateral process indicates that they should be assigned to a species different from the specimens from Irian Jaya which have two to three. At present I consider the material from the two areas to be conspecific.

Material – Thirty specimens (storage nrs. RGM 383 519, 383 521 and 383 524). Six specimens were destroyed in an attempt to free them from quartz grains. Of the remaining 24, fifteen are dextral and nine sinistral specimens.

Other elements – As already mentioned above, only the Pa element of *Coryssognathus* is thought to be known, although Nicoll (1982) reported some elements associated with the *C. dentatus* Pa element (which Nicoll referred to as *Pelekysgnathus dubius*) which are nearly identical with the cone elements of *P. index* Klapper & Murphy, 1974 from the Pridoli of the Roberts Mountains in Nevada. In Great Britain (Aldridge, 1975, 1985), in the east Baltic (Viira, 1982), in Sweden (Jeppsson, 1972, 1975, 1979, 1984) and Australia (Link & Druce, 1972) the Pa element of *Coryssognathus* always occurs together with a number of elements of *Distomodus dubius* (Rhodes, 1953) sensu Jeppsson, 1972 (sometimes also referred to as *Rotundacodina dubia*) (for taxonomy see Jeppsson & Aldridge, 1988). This species is missing a Pa element so the most plausible inference would be that they are elements of the same apparatus. A strong argument in favour of this is that all the elements of *Distomodus dubius* occurring in the same faunas as the Pa elements of *Coryssognathus* developed ontogenetically in the same way as the Pa element of *Coryssognathus*. They did not expand from one central basal cavity pit but enlarged and became multidenticulate by successively incorporating neighbouring coniform elements.

I am of course not the first one to suggest that *Coryssognathus* and *Distomodus dubius* are elements of the same apparatus. Aldridge (1975) wrote that it appears possible from the British faunas that the elements placed in *Pelekysgnathus dubius* by Jeppsson (1972) could also be part of the apparatus of *Distomodus dubius*. Jeppsson (1979), who has given the matter considerable thought, rejects this idea, although he had noticed (Jeppsson, 1972) that all denticles of both *P. dubius* and *D. dubius* do have a basal pit.

The Pb element (Pl. 4, figs. 1, 2 and 10, 11; Pl. 7, fig. 1)
A large cusp, bent backwards and inwards, with three processes. A short anterior process with one denticle or no denticle. From this process an edge runs to the tip of the cusp. An outer lateral process with one or two denticles (larger than the one of the anterior process), and a ridge running up the lateral side of the cusp but fading out a short distance from the base. The posterior process bears one denticle about as large as the second denticle of the lateral process. From this denticle a ridge runs to the tip of the cusp. The cusp is lenticular in cross-section. The basal cavity is more or less triangular and large (see Pl. 4, fig. 2). In the same figure one can clearly observe that all denticles have their own basal pit, and that (see Pl. 7, fig. 1) they already had developed several lamellae before being enveloped by the lamellae of the cusp. This element differs from the Pa element in that the cusp is much larger than the other denticles and that the posterior process is short and bears only one denticle. This element differs from those described from Lunnarna (Jeppsson, 1972, i.a. pl. 1, fig. 7), in that the lateral process is less developed, and has no denticle or only one. [See also Pl. 3, figs. 1, 2, a specimen from Lunnarna (Sweden)].

The M element (Pl. 4, fig. 7)
Large cusp with sharp lateral edges, curved backward and inwards. Anterior face rather flat, posterior face more convex. Both lateral edges bear a tiny denticle, the one on the inner side less close to the cusp than the other. The basal cavity is large, and plano-convex in form. The posterior base of the cusp of some specimens bears a tiny denticle. In this element it is also apparent that the tiny denticles had already acquired several lamellae before being enveloped by the lamellae of the cusp. The M elements are similar to the specimen figured by Jeppsson (1972, pl. 1, fig. 1).

The Sa element (Pl. 4, figs. 8, 9)
A symmetrical or almost symmetrical element consisting of a large posteriorly curved cusp with two short lateral processes, both with one small denticle closely oppressed to the cusp, and a posterior process with a much smaller denticle. Basal

cavity large, in outline more or less quadrangular with rounded corners, especially so posteriorly. This element is very similar to the one pictured by Aldridge (1985, pl. 3.4, fig. 14).

The Sb element (Pl. 4, figs. 5, 6)
Asymmetrical element with short lateral processes, generally one with one peglike denticle and the other with two peglike denticles, and a posterior process with a smaller denticle. The cusp is twisted and lenticular in cross-section with two sharp edges near its top. One edge runs down to the lateral process with one denticle, the other towards the denticle on the posterior process but becomes gradually less sharp and often fades out before reaching the posterior process. A third edge coming from the other lateral process fades out about mid-cusp. The basal cavity is large and its outline is like that of the Sa element. The anterior face of the Sa and Sb elements shows a flat V-shaped concavity which in specimens with an undamaged basal rim is manifest as a V- or U-shaped notch on the anterior side. This element differs from the Sb element pictured by Aldridge (1985, pl. 3.4, fig. 15), because the latter has more accessory denticles. It is almost similar to the tr element of Jeppsson (1972, pl. 1, fig. 5; 1975, pl. 1, fig. 4).

The Sc element (Pl. 4, figs. 3, 4)
Long, relatively slender, posteriorly curved cusp with one or two very small, peglike denticles on the posterior edge and – in one well-preserved specimen – three small peglike denticles on the anterior edge. This specimen is very similar to a specimen figured by Jeppsson (1972, pl. 1, fig. 3). The basal cavity is lens-shaped with a sharp anterior and somewhat less sharp posterior corner. As in the other elements the tiny denticles had already acquired several lamellae before being enveloped by the lamellae of the cusp.

Coniform elements
In addition to the elements described above a number of coniform elements with a flat base occur similar to the specimen figured by Jeppsson (1975, pl. 1, fig. 2A-D). They are quite similar to the terminal denticles of the lateral processes of some of the elements. They may represent denticles not reached by the enveloping lamellae of the multidenticulate elements or broken off terminal ones. The elements observed by Nicoll (1982) accompanying the *Coryssognathus* Pa element and resembling elements of *Pelekysgnathus index* (Klapper & Murphy, 1974, pl. 12, figs. 1, 3) are probably such coniform elements.

Material – Twenty seven Pb elements (storage nos. RGM 383 520 and 383 525), 29 M elements (RGM 383 520 and 383 526), 36 Sa elements (RGM 383 520, 383 521 and 383 527), 37 Sb elements (RGM 383 520, 383 521 and 383 528), 27 Sc elements (RGM 383 520, 383 521, 383 522 and 383 529), 11 coniform elements (RGM 383 530), and 23 indeterminable fragments (RGM 383 531).

Remarks – One or two apparatuses? – Jeppsson (1979) noted that in Skåne *P. dubius* is restricted to a much shorter interval than *D. dubius*, and that the elements of *P. dubius* are few compared with those of *D. dubius*. In Skåne the elements of the two apparatuses are also of different growth stages, the *P. dubius* elements being juvenile. Generally in conodont faunas the Pa elements are over-represented. So the numerical ratio here is unusual if all elements are from one species. Merrill & Powell (1980) described faunas from a shaly interval in the Pennsylvanian Drum Limestone from the Kansas City area, where all Pa elements of the species present show a minimum over-representation. All apparatuses in these faunas are juvenile and, – an important observation – the Pa elements are much less developed than the other elements. Compared with the faunas from the limestones from the same section where the Pa elements generally are as large as or larger than the ramiforms, the Pa elements of these juvenile faunas are smaller to considerably smaller than the ramiforms. Merrill & Powell (1980) explained the occurrence of these special faunas by assuming that juvenile conodonts swam or floated into a lethal environment and suggested the following ontogeny for certain platform-bearing conodonts. "Earliest apparatuses consisted only of ramiforms, probably of small size. As the ramiforms became of normal, 'adult' size, small platforms were introduced that grew to their 'adult' size". The ontogeny of *Coryssognathus* may show the same pattern and this may be an explanation for the data presented by Jeppsson (1979) for the Skåne faunas. If we assume that only juvenile conodonts lived and/or died in the Skåne area it will explain the under-representation of the Pa element of *Coryssognathus dubius* and the fact that it is more juvenile than the other (*D. dubius*) elements. That quite a number of faunas with *D. dubius* elements did not yield recognizable Pa elements may be because the coniform elements had not yet "fused" to a multidenticulate element or these multidenticulates were destroyed sometime after the death of the animal because these young Pa elements are rather fragile.

With regard to the above attention should be given to an observation by Aldridge (1975, p. 615) "The morphology of the *Pelekysgnathus dubius* platform elements is very variable and a clear trend is apparent through the interval from upper Bringewood to upper Whitcliffe. The stratigraphically older specimens are small, fragile and commonly have only a single denticle in addition to the cusp. The younger specimens are stouter and commonly have three denticles to the 'anterior' (should be posterior) of the cusp and a single smaller denticle on a short lateral bar".

So it would appear that during phylogeny the Pa element of *Coryssognathus* became stouter and in that process incorporated more coniform elements. However, as early Ludlow *C. dentatus* already is composed of 5 or 6 denticles, one must assume that the observed change is ontogenetic and that from late Bringewood time to late Whitcliffe time the environment became more hospitable for the *Coryssognathus* animal. This may have been the case, for according to Aldridge (1976), *Coryssognathus* ('*P. dubius*' + '*D. dubius*') is only a minor component in upper Bringewood and Leintwardine faunas, but is abundant in all collections from the Whitcliffe Beds, deposits of shallower water. So the change in size of the *Coryssognathus* Pa elements in this succession of Ludlow strata may after all be but a succession of ontogenetic stages because the environment became successively more suitable for more adult specimens. In this respect Jeppsson (1976, p. 111) may be quoted ".....the individuals spent the same part of their life in the same area as their ancestors did when of corresponding age, and generation after generation migrated in the same regular way. The ontogenetic age of the individuals, which died in a given area, could thus remain constant, not only for the time needed for sedimentation of a sampled stratum but sometimes also for the time needed to give many different strata conodont elements with more or less identical size distribution".

This argument involves several assumptions but it explains why we always find '*D. dubius*' in faunas with *Coryssognathus* but not always *Coryssognathus* in faunas with '*D. dubius*'.

The phenomenon that juvenile conodont animals had relatively rather adult ramiforms, elements of the assumed grasping device (Briggs et al., 1983; Aldridge et al., 1987; Aldridge, 1987 and references therein), and less developed platform elements may indicate that juvenile conodonts had another diet of may be softer food that needed less crushing – or whatever the Pa elements were used for – but still needed to be caught.

If can be shown that *Cordylodus*? *dubius* Rhodes, 1953 is an element (the Sc element) of the apparatus of *Coryssognathus dubius* than the name of the species should be *Coryssognathus dubius* (Rhodes, 1953), otherwise it should be *Coryssognathus dubius* (Jeppsson, 1972).

Some other occurrences of Coryssognathus – Aldridge & Mohamed (1982) reported the occurrence of a *Coryssognathus*? sp. at the top of the Llandovery Solvik Formation of Asker in the Oslo region. They do not mention the presence of the other elements of the apparatus. But these may have been assigned to the apparatuses of *Distomodus kentuckyensis* Branson & Branson or *Icriodella discreta* Pollock, Rexroad & Nicoll. For instance the specimen figured by them on pl. 1, fig. 15 as a M? element of *Icriodella discreta* has an anterior process displaying a peninsular shape as described by Jeppsson (1972) for a Sc element of '*D. dubius*' – the peninsular shape caused by the initial stage of annexation of a coniform element by the lamellae of the process.

Aldridge & Mohamed state that their *Coryssognathus* specimens closely compare with a specimen from the Brassfield Formation in the Cincinnati Arch assigned to *Neoprioniodus costatus* Walliser, 1964 by Rexroad (1967, pl. 3, fig. 13). I agree that, that specimen is a *Coryssognathus*. Several specimens figured by Rexroad may be elements of the *Coryssognathus* apparatus, i.a. *Drepanodus*? *arrectus* Rexroad, 1967 (pl. 2, figs. 1-3), one specimen assigned to *Distomodus kentuckyensis* Branson & Branson (Rexroad, 1967, pl. 2, fig. 14) and *Trichonodella* n. sp. (pl. 3, figs. 24-26), but in absence of a distribution chart confirming that they derive from the same samples and having no information about the basal cavity other than that it is expanded, this remains mere speculation.

Mabillard & Aldridge (1983) reported the occurrence of *Rotundacodina* aff. *R. dubia* in the Coralliferous Group (Llandovery-Wenlock) of Marloes Bay, Wales, where eleven faunas with small numbers of specimens were not accompanied by a *Coryssognathus* Pa element. Considering the preservation of the conodonts in these faunas, which according to Mabillard & Aldridge (1983) is mostly poor with distorted and fractured specimens, it may be that Pa elements, more fragile as they are, have become fragmented beyond recognition during tectonic and recovery processes.

In upper Llandovery to lower Wenlock samples from the Cellon section (Austria) Walliser (1964) encountered elements consisting of two or more (4-5) coniform elements which are fused (Walliser, 1964, textfig. 2 and pl. 10, figs. 1-7, 10-12). In my opinion they represent juvenile elements of a species of *Coryssognathus* or are closely related to that genus. Because of this find Walliser suggested, that it might be that some multidenticulate conodont elements originated by fusion of a number of coniform elements.

The apparatus of *Coryssognathus* is in my opinion an example of such a phylogenetic development. It must have had an Ordovician (?) ancestor which possessed some 60-80 coniform elements in its apparatus, possibly an apparatus of the type described by Fåhraeus & Hunter (1975), consisting of curvature-transition series. Somewhere during phylogeny one coniform of each series started to grow faster and/or earlier than its neighbours, incorporated them successively within its lamellae and in doing so attained a more modern shape, morphologically similar to elements of *Distomodus*.

Cooper (1975) described apparatuses of *Distomodus kentuckyensis* Branson & Branson, 1947 and of *Distomodus* sp. cf. *D. kentuckyensis*. He stated that all accessory denticles of the elements of both species have their own basal cavity tip. Thus they are probably related to *Coryssognathus*. The Pb, M and S elements are morphologically rather similar, but the Pa element is quite different from that of *Coryssognathus*. Bischoff (1986), who described several species of *Distomodus* extensively, never mentioned anything about separate basal cavity tips of accessory denticles. I have inspected some elements of *D. staurognathoides* (Walliser, 1964) from Gullet Quarry in the Malvern Hills (U.K.) (see Aldridge, 1972). I did observe some pseudopits – small indentations caused by open lamellar spaces – but no basal cavity tips of accessory denticles. So the question arises whether all species assigned to *Distomodus* are real *Distomodus*. It will be necessary to verify if the accessory denticles of their elements have basal cavity tips or not, for that seems to me the decisive indication whether they are congeneric with *D. kentuckyensis* or not. It will of course be necessary to include the type material of Branson & Branson (1947) in such an investigation.

Walliser & Wang (1989) published a photograph of a specimen of *Dentacodina* sp. (Walliser & Wang, 1989, pl. 2, fig. 16) from the late Ludlow Miaogao Formation from the Qujing District of Yunnan (China), which may be a Pb element of a species closely related to *Coryssognathus*. It seems to be composed of coniform elements which are partly fused except for the terminal cone of one of the processes which only touches its neighbour.

Ozarkodina confluens (Branson & Mehl, 1933)
Pl. 6, fig. 1.

For synonymy see Klapper & Murphy (1974) and Jeppsson (1975).

Description – The Pa element is straight and has a basal cavity at about midlength, or anterior of it, beneath a cusp which is slightly larger than the denticles directly anterior and posterior of it. Two to three denticles at the anterior end are much larger than the others. The denticles are flattened on the left side of the blade and convex on the right side. The Pb elements are incomplete, but do show the large cusp, which is broad and triangular in lateral view.

Material – Eleven Pa elements, 4 Pb elements and 1 fragment of a Sc element, (RGM 383 519, 383 521, 383 532).

Ozarkodina crispa (Walliser, 1964) Pa element beta morph Walliser & Wang, 1989
Pl. 6, figs. 2-7; Pl. 7, figs. 3, 4.

Description – *Ozarkodina crispa* is represented in this fauna by only one type of element, a Pa element, which is similar to the Pa element of *O. crispa* alpha morphotype Walliser & Wang, 1989 but for the posterior half of the upper side. In *O. crispa* alpha morphotype the posterior half of the upper side consists of a row of fused denticles, whereas in the present form the posterior half possesses a median trough bordered on both sides by a smooth ridge. The ridges unite at about the middle of the element and at the posterior end. The trough increases slightly in width in posterior direction, but narrows before reaching the posterior end. In cross-section the trough is V-shaped (see Pl. 7, fig. 4). The denticles of the blade are laterally compressed. The blade thickens slightly downwards, down to about a quarter from the base; from there it becomes thinner. The anterior sides of the large asymmetrical platform meet the blade at right angles. The larger platform of large specimens may show a fold. The basal pit is at the anterior side of the large basal cavity.

Remarks – This element resembles the element described as sp (= Pa) element beta morph by Walliser & Wang (1989, pl. 1, fig. 1). All specimens of this element, encountered in the fauna from Irian Jaya, are straight and in this respect differ from other specimens of the beta morph (figs. 2-3 on pl. 1 of Walliser & Wang, 1989) which have a curved posterior end.

Ozarkodina is reported to have a seximembrate skeletal apparatus (see i.a. Sweet, 1988). *Ozarkodina crispa* beta morphotype may be unimembrate for there are no other elements in the sample that could belong to its apparatus.

Material – Seventy three Pa elements, reg. nr. RGM 383 533, 383 518, 383 521, 383 523.

Age of the sample

The occurrence of *Ozarkodina confluens* restricts the age of this sample from late Early Wenlock into late Pridoli (Sweet, 1988; Jeppsson, 1988). Elements of the type referred to '*Distomodus dubius*' first appear in the early Ludlow (Cooper, 1980) and range into at least the early Pridoli (Higgins & Austin, 1985). According to Cooper (1980) *Coryssognathus dentatus* occurs in strata above the *Kockelella variabilis* Datum and below the *Ozarkodina crispa* Datum, that is from basal Ludlow up to late Ludlow.

Ozarkodina crispa beta morphotype occurs in the Qujing District of East Yunnan (China) only in the middle part of the Miaogao Formation. Its range is according to Walliser & Wang (1989, p. 113-114) restricted to the uppermost Ludlow[1]. Thus, in all probability the age of the sample from Irian Jaya is Late Ludlow.

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[1] At this place should be remarked that Walliser & Wang's 1989 paper suffers from some serious printer's errors which may easily confuse the reader. The paragraphs Occurrence and Material of the beta morph (Walliser & Wang, 1989, pp. 114-115) actually bear upon the alpha morph. Those on Occurrence and Material of the gamma morph (op. cit., p. 115) relate to the beta morph, those on the Occurrence and Material of the delta morph .... and so on.

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Plate 1

Figs. 1-7. *Coryssognathus dentatus* Link & Druce, 1972. Magnification × 100, unless indicated otherwise.

1. Oblique view of outer side of damaged specimen. Free tips of the denticles are missing. RGM 383 519.
2. Aboral side of a specimen with a relatively undamaged cusp. RGM 383 519.
3. Aboral view of a specimen showing basal pits of some denticles and the terminal denticles of the posterior and lateral processes, × 150. RGM 383 521.
4. Aboral view of a specimen of which the posterior process is shorter than the lateral process. Note the oval basal pits of the denticles and the groove-like part of the basal cavity under the anterior process. × 300. RGM 383 519.
5. Lateral view of a specimen of which the free tips of the denticles are broken off. RGM 383 519.
6. Same specimen, oral view. Note that the denticles of the lateral process are more discrete than those of the posterior process. RGM 383 519.
7. Juvenile specimen, lateral process broken off. × 500. RGM 383 521.


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Plate 2

Figs. 1-2. *Coryssognathus dentatus* Link & Druce, 1972. Details of the basal cavity of the specimen of Pl. 1, fig. 3 seen from somewhat different angles. For discussion and meaning of the arrows see descriptive part in the text; 1 × 1000; 2 × 850.

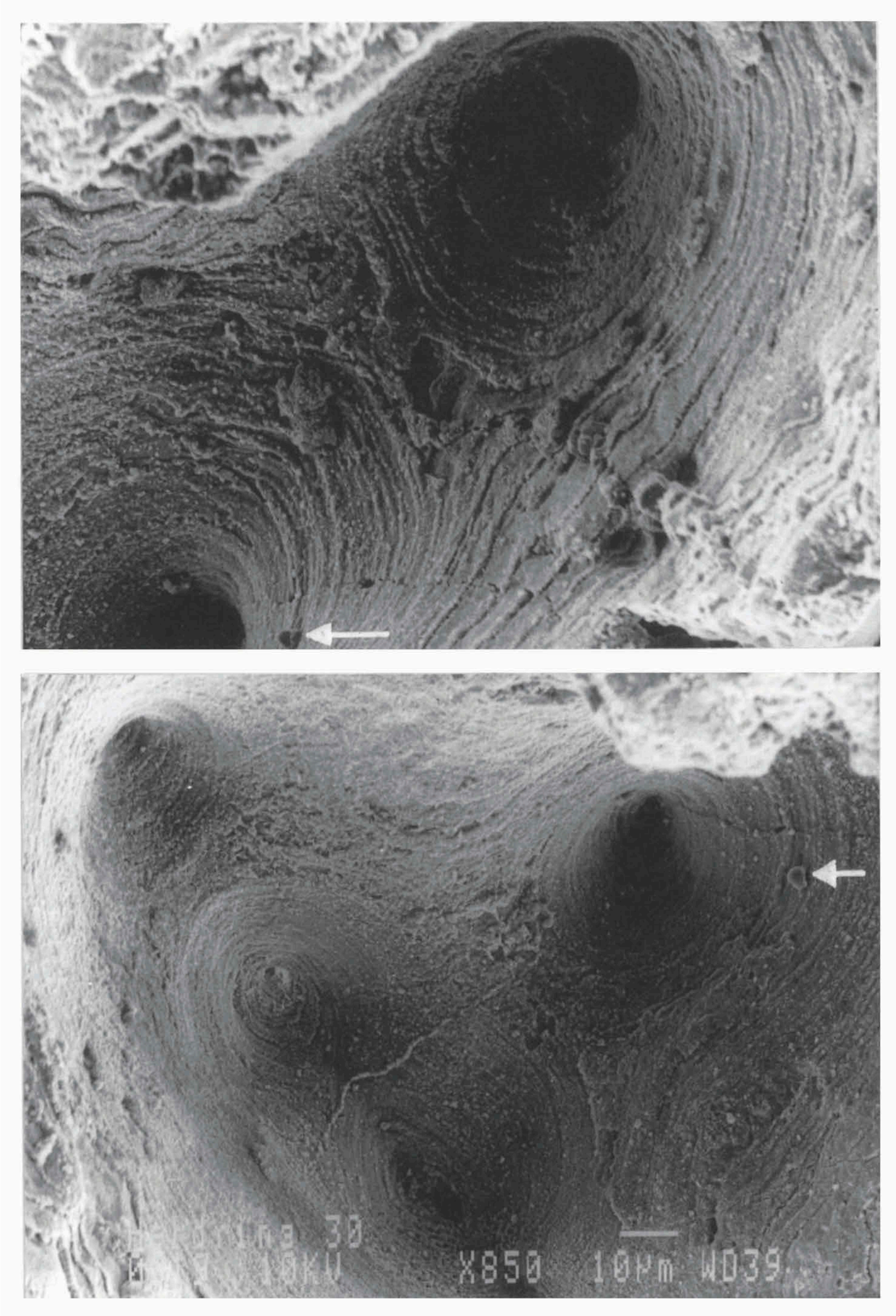
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Plate 3

Figs. 1-2. Pb element of '*Distomodus dubius*' (Rhodes, 1953) sensu Jeppsson, 1972 from Lunnarna, Sweden. RGM 383 534.
1. View of basal side. Note basal cavity pit of denticle of posterior process. Lateral process indicated by fold of cavity wall; × 330 (see detail Pl. 5, fig. 1).
2. Same specimen as Fig. 1, lateral view, × 150. In lateral view this element looks like a M element. However, the M element has a different basal cavity, with one straight and one convex side (compare with Jeppsson, 1972, pl. 1, fig. 1).

Figs. 3-4. Pa element of *Coryssognathus dubius* from Lunnarna, Sweden. RGM 383 534.
3. View of outer lateral side, note narrow basal side of anterior process and deeply excavated basal cavity under the cusp and posterior process, × 200.
4. Same specimen as Fig. 3. View of aboral side, major part of the lamellae covered by basal filling (see detail Pl. 7, fig. 2). Note flexure of the anterior process in a direction opposite to the slight curvature of the posterior process, × 200.

Fig. 5. Partly preserved S element of '*D. dubius*' from the Irian Jaya sample. RGM 383 522, × 150. For detail see Pl. 5, fig.2.


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Plate 4

Figs. 1-11. Elements considered to belong to the apparatus of *Coryssognathus dentatus* from the sample from Irian Jaya, elements which up to now were assigned to the apparatus of '*Distomodus dubius*' (Rhodes, 1953) sensu Jeppsson, 1972.

1-2. Pb element with a lateral process with two denticles. RGM 383 520, × 100; 1: posterior view; 2: same specimen, aboral view.

3-4. Sc elements, RGM 383 520, × 100; 3: view of aboral side; 4: lateral view.

5-6. Sb elements, × 100; 5: postero-lateral view, RGM 383 520; 6: oblique view of anterior side, RGM 383 521.

7. M element, RGM 383 520, × 100, view of aboral and posterior side.

8-9. Sa element, RGM 383 520, × 100; 8. view of posterior side; 9: oblique view of anterior side.

10-11. Pb element with a lateral process with one denticle, RGM 383 520; 10: lateral view, × 100; 11: view of posterior and aboral side of the same specimen, × 150.


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Plate 5

Fig. 1. Detail of the specimen of Pl. 3, fig. 1. Note basal cavity pit of accessory denticle with concentric lamellae (left of centre), enveloped by lamellae of the cusp. Basal cavity pit of the cusp lower right. × 1000.

Fig. 2. Detail of the specimen of Pl. 3, fig. 5. Note concentric lamellae around basal pits of two accessory denticles, one in upper centre, one in lower left. × 500.

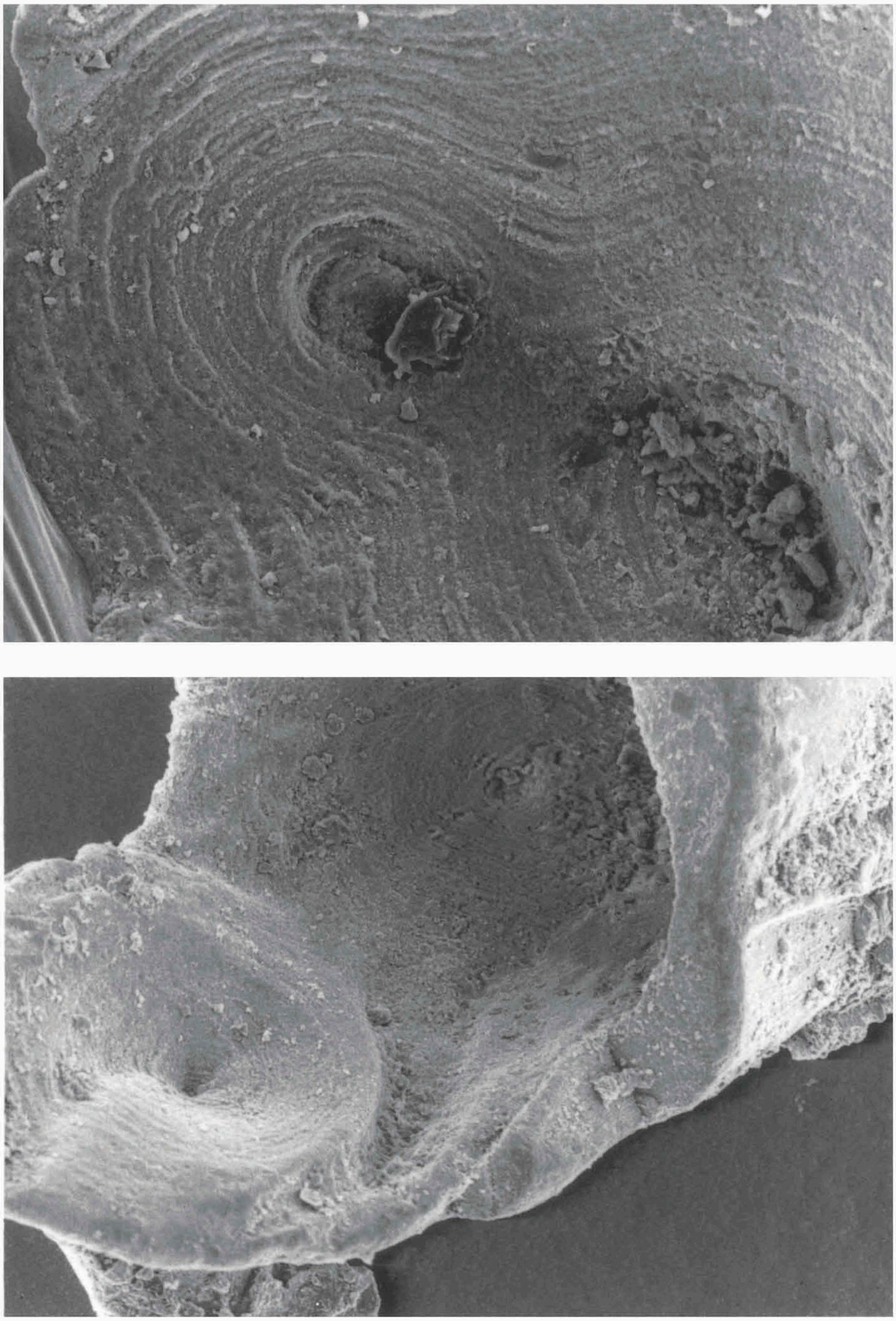

Plate 6

Fig. 1. *Ozarkodina confluens* (Branson & Mehl, 1933). Lateral view of Pa element from the sample from Irian Jaya, RGM 383 519, × 100.

Figs. 2-7. *Ozarkodina crispa* (Walliser, 1964) beta morphotype Walliser & Wang, 1989. Pa elements from the sample from Irian Jaya; 2: view of upper and lateral side of damaged specimen. RGM 383 521, × 100. (see detail Pl. 7, fig. 3); 3: oblique view of specimen missing the anterior part, RGM 383 518, × 100; 4: view of the basal cavity, RGM 383 518, × 100; 5: another specimen, oblique lateral view, RGM 383 518, × 100; 6: almost complete specimen (with some adhering quartz grains), view of upper side, RGM 383 521, × 190; 7: same specimen, lateral view, × 190.


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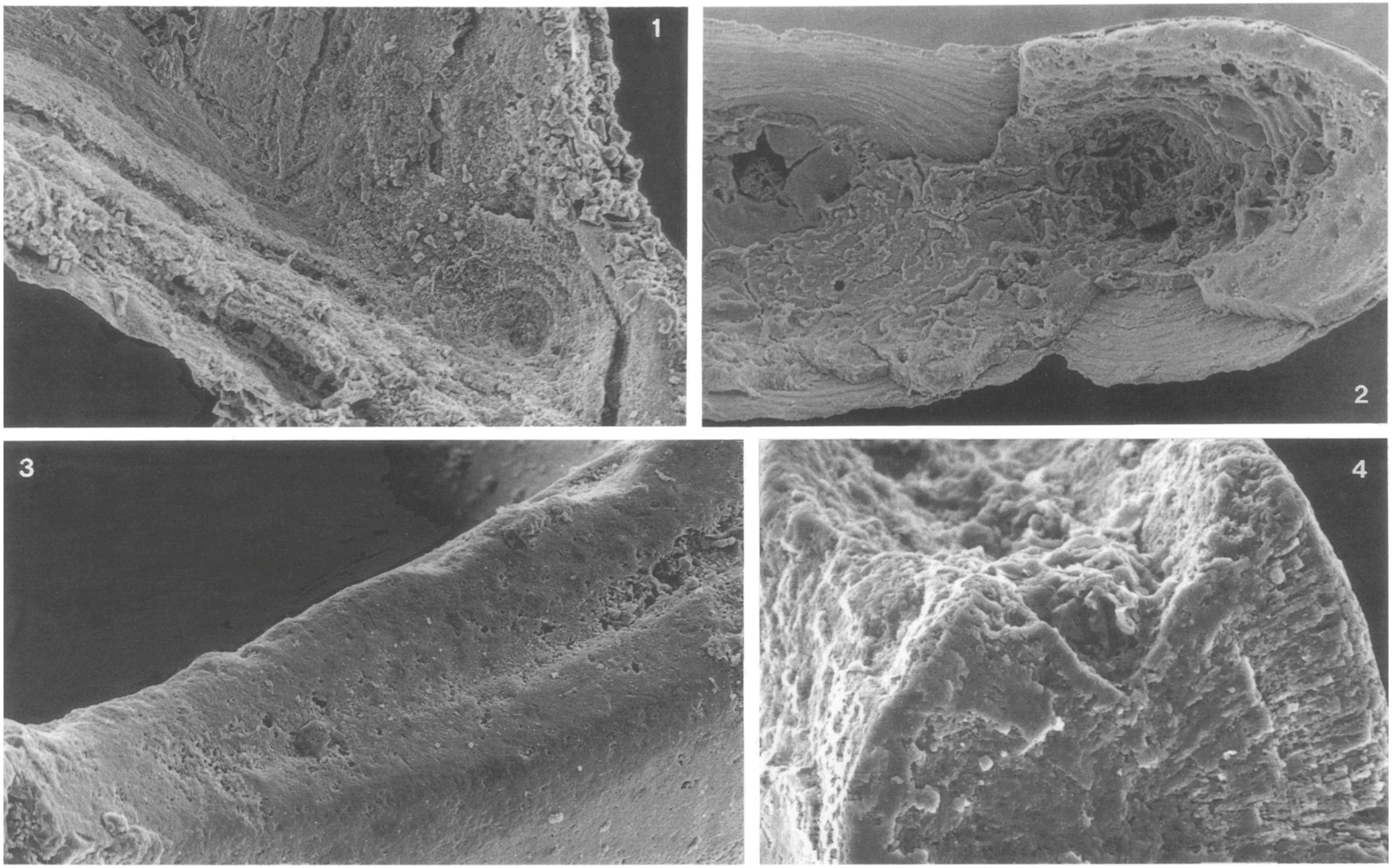
Plate 7

Fig. 1. Detail of the aboral side of the Pb element of Pl. 4, fig. 2. Part of the basal cavity of the cusp and the anterior process. Note concentric lamellae around the pit of the denticle of the process, later on enveloped by the lamellae of the cusp, × 700.

Fig. 2. Detail of the aboral side of the specimen of *Coryssognathus dubius* of Pl. 3, fig. 4. Posterior part of the element, with two basal pits, major part of the lamellae covered by basal filling, × 500.

Fig. 3. Detail of upper side of the specimen on Pl. 6, fig. 2. Anterior part of the median trough, × 1000.

Fig. 4. View at fracture through posterior part of a specimen of *Ozarkodina crispa* beta morphotype. Note V-shaped median trough, × 1170.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