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**Late Devonian (Famennian) jaws:
The icriodid multielement apparatus and its function
(Conodonta, Prioniodontida)**

IMMO SCHÜLKE

Institut für Geologie und Paläontologie, Universität Hannover, Callinstr. 30, 30167 Hannover, Germany
Email: schuelke@geowi.uni-hannover.de

Abstract

In this study the conodont multielement apparatus of Late Devonian (Famennian) *Icriodus alternatus* is described which has been reconstructed from clustered group findings and separated elements. This apparatus is markedly different from classical ozarkodinid apparatuses and needs further consideration of its functional morphology. Since bedding plane assemblages of *Icriodus alternatus* are yet unknown, a spatial reconstruction of this apparatus and a feeding mechanism are proposed which are based on the oropharyngeal apparatus of recent lampreys. Though the extant representatives of petromyzontoids are not close phylogenetic relatives of extinct conodonts, there exist intriguing analogies concerning the morphology of the tooth types and the presumed spatial distribution within the oral cavity of both taxa.

Zusammenfassung

Auf der Basis von Conodonten-Clustern und separierten Einzelementen wird der Multielement-Apparat von *Icriodus alternatus* (Oberdevon, Famennium) beschrieben. Da dieser Apparat sich von z.B. dem klassischen ozarkodiniden Apparat unterscheidet, muß seine Funktion neu überdacht werden. Da bislang keine Schichtflächen-Exemplare von *Icriodus alternatus* gefunden wurden, die über die räumliche Verteilung der Zahnelemente in der Mundhöhle Auskunft erteilen könnten, wird eine Rekonstruktion erwogen, die auf Ähnlichkeiten zur Bezahnung von rezenten Neunaugen basiert. Obwohl beide Organismengruppen keine nahe phylogenetische Verwandtschaft aufweisen, sind die Analogien zwischen den Bezahnungstypen so groß, das sie eine entsprechende Funktion nahelegen.

Keywords: Conodonts, Famennian, multielement reconstruction, *Icriodus*

INTRODUCTION

In the last decades, conodont research has re-focused on areas that deal with them as living animals with their own anatomy, affinities, functional morphology, aut- and synecology, and evolution. They are now considered by many to belong either to more probably early chordates or craniates (e.g. Purnell, 1995; Janvier, 1996; Purnell & Donoghue, 1998 among many others) and to form a taxon far more diverse and better known than any other group of early chordates (Purnell & Donoghue 1998). On the other hand, most of the progress attainable

on the paleobiological features of conodonts is based on group findings of complete oropharyngeal apparatuses - about 1000 (Purnell & Donoghue, 1998) - which are exceptionally rare when compared to the mass of the conodont fossil record as isolated elements. Additionally, the distribution of complete apparatuses between the various groups of conodonts and between the stratigraphic intervals they were attributed to is highly unequal. Today, the bauplan of the ozarkodinid apparatus is the best known concerning its architecture and functional morphology because most of the bedding-plane assemblages or clusters of complete apparatuses belong

to specimens of this order (Purnell & Donoghue 1998). But this statement proves not even true for all variations of the ozarkodinid apparatus known to be present within this order. When focusing on other orders of conodonts, much less is known about apparatuses both in general and in particular. For further reading see Sansom et al. (1994) for Belodellida and Panderodontida, Aldridge et al. (1995) for Prioniodontida, and Purnell & Donoghue (1998) for Ozarkodinida. The prioniodinid apparatus has not yet been analyzed concerning its general features, though there are respective studies in preparation (Purnell & Donoghue, 1998: 60). To which degree general analyses can be applied to e.g. *Icriodus alternatus*, a Late Devonian representative of the Prioniodontida with vastly different apparatus reconstructions (Schülke, 1999a; 1999b) when compared to the best studied species *Promissum pulchrum* from the Ordovician (Aldridge et al., 1995), is yet unsettled. This study has to be understood as a proposal of the lifetime strategy and feeding mechanism of an extinct animal which is based on fairly scarce data taken from the fossil record and some intriguing analogies with recent agnathans. When additional data can be added in the future, the reconstruction presented here will be tested.

THE *ICRIODUS ALTERNATUS* APPARATUS

The few data present about the *Icriodus alternatus* apparatus up until today derive from two clusters one of which has been described by Lange (1968: pl. 6). This cluster consists of two pairs of segminiscaphate Pa elements (form taxon: *Icriodus*) highly unequal in size and a large variety (about 56) of non-geniculate coniform elements (form taxon: *Acodina*). This cluster truly represents faecal matter or stomach ejecta of a conodont predator which presumably consist of the remains of two more or less complete specimens as proposed by Lange (1968). The second partial cluster is formed by a single segminiscaphate Pa element to which three non-geniculate simple cones are attached in the basal cavity of the Pa element. This cluster originates from the upper Kellwasser horizon (bed 23) of the Sessacker trench section (comp. Schindler et al., 1998; Schülke, 1998). Whether this partial cluster has to be interpreted as ejectamenta, faecal matter, or as remnants of a decaying conodont carcass separated by, e.g. bottom currents, bioturbation or scavenging remains uncertain.

Additional data sets are provided by multielement reconstructions based on bed-by-bed examination of separated elements which derive from samples taken at three basal Famennian sections of the Montagne Noire (Schülke, 1999a; c). The results of statistical investigation gave further support to the data, e.g. of Lange

(1968) and led to a refusal of an icriodid apparatus consisting only of a variety of segminiscaphate elements as favored by Bultynck (1972). In his study mainly small Middle Devonian icriodid faunas were analyzed which mostly lack any simple cones formerly assigned to the form taxon *Acodina*. The samples, that contained both form taxa, showed a disagreement in the ratio of simple cone and segminiscaphate elements. This same relationship with simple cones being vastly outnumbered by segminiscaphate elements, was also observed by Klapper & Philip (1971) who reconstructed an apparatus (type 4 apparatus) consisting of both a single pair of segminiscaphate and a single pair of coniform elements.

The multielement reconstruction of Chatterton & Perry (1977) of *Icriodus hadnagyi* Chatterton & Perry generally conforms to that presented here in essential features. Their apparatus consists of a segminiscaphate Pa element and a "number" of simple cones which "appear to form a sort of symmetry transition series" (Chatterton & Perry, 1977: 792). Also, Serpagli's (1983) reconstruction of *Latericriodus woschmidti* provides additional support for my reconstruction of *I. alternatus*. This closely related taxon exposes an apparatus with Pb, S, and M elements completely formed by a single cusp or dominated by a large main cusp and reduced posterior or lateral processes which indicate a phylogenetic and functional relationship. The last reconstruction of an apparatus belonging to the Icriodontidae was put forward by Sandberg & Dreesen (1984) with the description of closely related *Pelekysgnathus inclinatus* from the Late Famennian. This apparatus has been reconstructed displaying a septimembrate apparatus as is the case with *I. alternatus* which yields mainly geniculate and non-geniculate coniform elements and a segminiscaphate Pa element.

In my own samples from the Montagne Noire and also from several other sections in the Rheinische and Thüringische Schiefergebirge there is a positive correlation between the number of segminiscaphate Pa and a variety of coniform elements. On the other hand, extremely unbalanced numbers of elements can also be observed when compared to the clustered icriodids of Lange (1968). Even in a variety of large samples, coniform elements are almost completely lacking. So far my observations correlate well with those of Bultynck (1972) and Klapper & Philip (1971). In contrast to the studies mentioned above, the presence of coniform elements correlates with average specimen size within each sample. The more large, probably adult Pa element specimens are present the higher is the number of simple cones. Otherwise, almost no coniform elements are present if the icriodid fauna has a small average specimen size and no adult

individuals are contained. It is not unusual in the Montagne Noire faunas, that a complete icriodid faunal portion consists of juvenile specimens. These observations can be caused by various processes, e.g. by post mortem water current activity. Generally, this apparatus fractionation process is presumed to have a great influence especially on elements with highly different hydrodynamic properties such as segminiscaphate and coniform types, but in the Montagne Noire basal Famennian successions sedimentological features of bottom currents are lacking (Schülke et al., in press). Another possible reason is a considerable change in the life mode of icriodids connected with a delay in the cristallization of coniform elements as is presumed for basal Famennian palmatolepids (Schülke, 1999b). This contrasts with the clustered grouping described by Lange (1968) which contains at least one small, probably juvenile specimen with tiny coniform elements. These small coniform elements display the same size ratio when compared to the small Pa element pair as the larger coniform elements to the large Pa pair. Therefore, a change in lifetime strategy in icriodids seems improbable. The most probable explanation for the unbalanced presence of coniform elements and the complete lack of very small cones in my samples is a systematic error in the preparation technique. The insoluble residue of acidification process of the broken bulk samples was carefully run through a nested sieve of 125 μ mesh width through which most of the cones with small basis diameters could have passed and, consequently, might have separated from the larger Pa elements. However, the material present in the Montagne Noire sections enables a variety of coniform elements associated with the segminiscaphate Pa element to be distinguished. These elements show some typical characters of a conodont multielement apparatus as described in the below.

SYSTEMATIC PALEONTOLOGY

Phylum Conodontia Pander, 1856

Class Conodonti Branson, 1938

Order Prioniodontida Dzik, 1976

Family Icriodontidae Müller & Müller, 1957

Icriodus Branson & Mehl, 1938

Type species: *Icriodus expansus* Branson & Mehl

Remarks: As stated by Sweet (1988) and Schülke (1999a), the phylogenetic history of *Icriodus* is as yet unsettled. Possibly, there are repeated evolutionary links with other genera of the Icriodontidae, e.g., with *Pelekysgnathus* Thomas (Sandberg & Dreesen 1984), that gave rise to the assumption that *Icriodus* formed a

poly-phyletic taxon. Both genera are distinguished mainly by a single row of denticles on the oral side of the Pa element (*Pelekysgnathus*) and three rows of denticles on the oral surface (*Icriodus*) with the remaining elements of the apparatus formed by geniculate to non-geniculate coniform denticles (comp. Sandberg & Dreesen, 1984; Schülke, 1999a for apparatus descriptions). Therefore, a generic description has to be delayed to a later study when more data provided by other icriodid species can be added and the apparatus proposed here can be confirmed. Nevertheless, the hints for the presence of an advanced septimembrate apparatus in *Icriodus* with a rather typical element distribution of element classes as described below are fairly strong, but not tested yet.

Icriodus alternatus Branson & Mehl, 1934

Figs. 1, 2

1999a *Icriodus alternatus* Branson & Mehl.- Schülke, Famennian multielement reconstructions, Pl. 13, figs. 21-32 (see for further synonymy).

Lectotype: Specimen illustrated by Branson & Mehl (1934) on pl. 13, fig. 4 and selected by Ziegler (1962: 51).

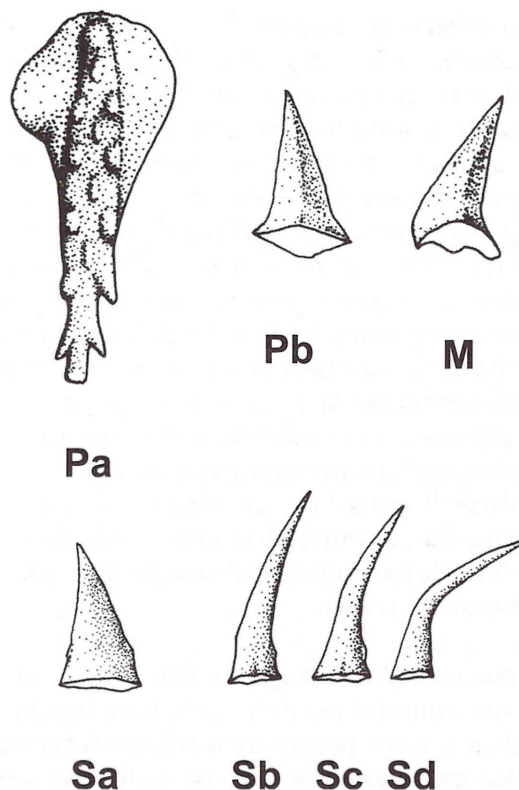


Fig. 1: - Idealized sketch of the *Icriodus alternatus* multielement apparatus. Elements are drawn in natural size ratio.

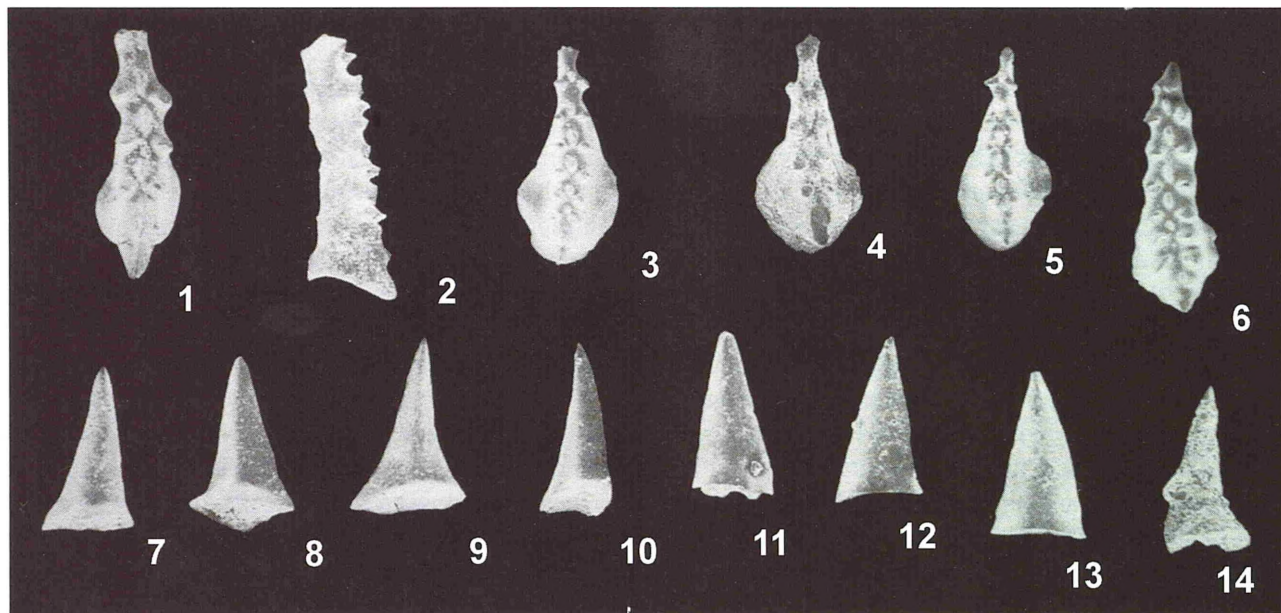


Fig. 2: - Icriodid elements from the Montagne Noire (abandoned Coumiac quarry).

No.1,2: *Icriodus cornutus* Sannemann, 1955; Pa element, upper view (1); lateral view (2); x55.

No.3-6: *Icriodus alternatus* Branson & Mehl, 1934; Pa element, upper view; x35 (3, 6), x45 (4, 5).

No.7-10: *Icriodus alternatus* Branson & Mehl, 1934; Pb element, inner lateral view (7-9), inner posterolateral view (10); x45 (7, 8, 10), x60 (9).

No.11-13: *Icriodus alternatus* Branson & Mehl, 1934; Sa element, lateral view; x55.

No.14: *Icriodus alternatus* Branson & Mehl, 1934; M element, inner lateral view; x60.

All specimens are refigured from Schülke (1999a: Pl. 13, figs. 19-32). See there for further information on origin and reposition of originals.

Revised diagnosis (altered after Schülke, 1999a): The *I. alternatus* multielement apparatus consists of seven element classes. The straight segminiscaphate Pa element displays three rows of denticles on the platform. The denticles of the medial and lateral rows alternate longitudinally. The medial row denticles are reduced in height and diameter when compared to the lateral row denticles, or are completely lacking. The main cusp of the element is either positioned at the posterior end of the medial or the lateral rows of denticles. On the complete aboral side, a large and deep basal cavity is developed which extends to almost three quarters unit height. The (presumed) Pb position is occupied by a coniform non-geniculate element with a deep basal cavity on the aboral side. The basal margin of the unit is elliptical to subtriangular in outline. The cusp is sharply edged, slightly curved posteriorly, and strongly declines in diameter towards its apex.

The (presumed) M element is a coniform non-geniculate unit with a rounded to subtriangular basal margin, that possesses a small, posteriorly positioned bulge which parallels the longitudinal axis and declines in size towards the apex of the cusp extending only onto the lower third of the unit. Its cusp is moderately curved posteriorly. The symmetry transition series is formed by four elements some of which appear more frequently when

compared to other conodont apparatuses with paired S elements. The element presumed to occupy the Sa position in this apparatus is a coniform nongeniculate unit with a subrounded to slightly elliptical basal margin outline and an erect subcylindrical cusp, that are separated by a narrow constriction. The general features of the Sb, Sc, and Sd elements are highly similar. These units are non-geniculate denticles with a rounded to subrounded basal margin outline and a long and slender cusp and a large basal cavity on the aboral surface. The elements are differentiated by the posterior-ward curvature of the cusp. While the presumed Sb element displays a straight to mildly backcurved cusp, the presumed Sc element is moderately bowed posteriorly. The presumed Sd element shows a cusp strongly bent posteriorly at almost one third unit length.

Remarks: The attribution of the different coniform elements to a particular position within the multielement apparatus has been executed on the basis of different traits. The S elements form a curvature transition series the curvature of which increases away from the plane of bilateral symmetry. This type of arrangement seems to characterize almost all conodont apparatuses disregarding their position within higher taxonomic units. Apart from the Sa element, the symmetry elements share a wide variety of characters which make this choice

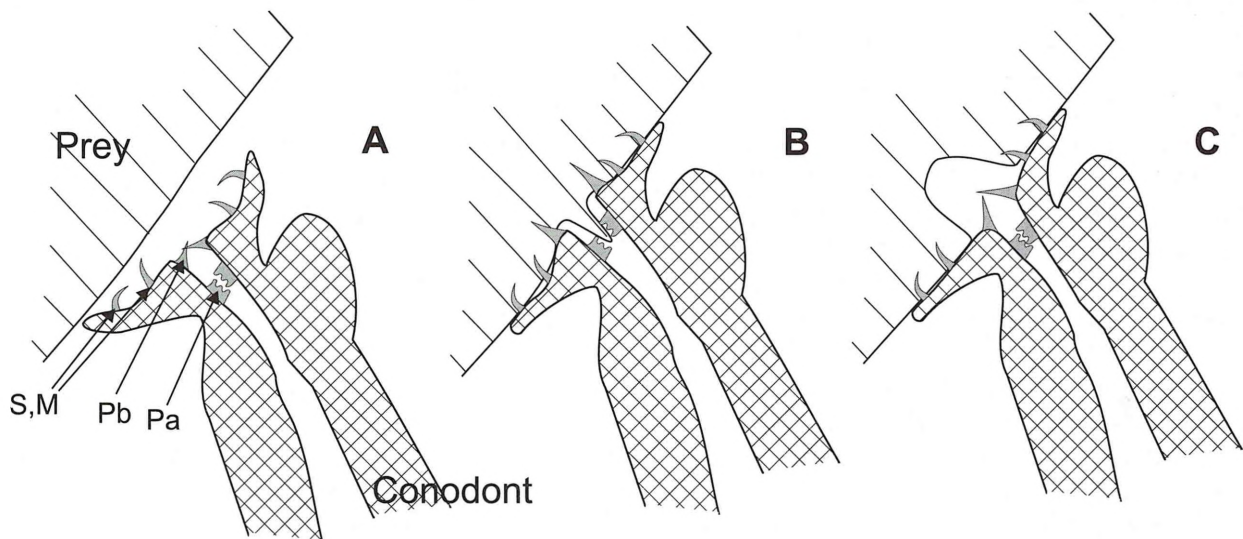


Fig. 3: - Possible icriodid feeding mechanism in analogy to feeding in extant petromyzontoids. (A) S elements in frontal part of mouth opening expanded for grasping. (B) S elements maintain contact to prey; true biting and mashing of food by Pa and Pb elements. (C) Position after biting.

reasonable. The Sa element is presumed to occupy this position because it is the only bilateral symmetrical element assigned to this apparatus. The total number of S elements varies from, e.g. ozarkodinid apparatuses. The presence of multiple Sb to Sd elements has to be assumed conforming to the clustered groupings described and drawn by Lange (1968), which exposed a large number of the respective element types. This fact, the presence of a variable number of elements on certain positions, conforms to the results of Fähræus & Hunter (1985). The assumed M and Pb elements differ greatly from the symmetry elements by the formation of a sharply edged cusp. This difference in element morphology between Pb and M on one hand side and S elements on the other is also typical in most conodont apparatuses. Otherwise, the respective elements position of both units has been attributed by their abundance in the samples which is comparatively high in the presumed Pb elements and much lower in the presumed M elements equal to the abundance of the S skeletal units. Additionally, these elements are shown as present within the drawings of Lange (1968: pl. 6), each represented by a single bilateral symmetrical pair (Pb: uppermost row, first on the left and third row, third from the right; M: third row, second and fifth from the left).

FEEDING MECHANISM AND SPATIAL APPARATUS FORMATION

The spatial reconstruction of the icriodid multielement apparatus presented here is proposed on the basis of a variety of presuppositions. First, conodont apparatuses generally provide evidence for a grasping and food-

processing function (Purnell, 1993 and others) of the oropharyngeal apparatus which makes them predators or scavengers analogous with living cyclostomes rather than suspension feeders. In contrast to the well known ozarkodinid or other apparatuses (Freedman et al., 1998), the simple cone symmetry elements of icriodids do not seem to be well adapted for grasping and retaining of small food particles and transport to the cutting or mashing Pa and Pb elements, since the muscular pressure which triggers element movement is not dispersed among a large number of cusps. They were much more adapted to focus maximum muscular pressure to their pointed tips, as is the case with higher vertebrate predators, in order to penetrate soft (or possibly hard) tissues, maintaining contact with this tissue while the biting, cutting, and mashing of food particles has almost completely to be attributed to pharyngeal Pa and Pb element pairs. If these assumptions prove right, they raise some intriguing analogies with the feeding mechanism of recent adult Petromyzontoidea (Young, 1950; Heintz, 1963; Carrol, 1993). These agnathan fish display an adhesive oral disc upon which a variety of "teeth" are developed which are not homologous with vertebrate teeth due to the lack of dental laminae. The teeth are used for fixing the lamprey onto its prey while the pharyngeal teeth arranged on a "biting apparatus" (buccal apparatus. e.g. Krejsa et al., 1990) penetrate and dissect the soft tissue (Grzimek, 1993). The conodont bodyplan which resembles that of recent cyclostomes to such a degree, that a close relationship between both taxa has been considered (see Janvier, 1996 for review), seems generally to be adapted to such a feeding mode. Even the horizontal bilateral symmetry of biting (Potter & Hilliard, 1987) rather than of rasping is

developed in recent lampreys (Krejsa et al., 1990), which seems to be fundamental to the masticating apparatus of conodonts. Nevertheless, the biting in recent lampreys and hagfishes differs from that presumed in Devonian icriodids by the absence of a dental structure like a palatal tooth (comp. Krejsa et al., 1990). I disagree with the statement of Krejsa et al. (1990) that especially the symmetry elements can be interpreted as counterparts of the lingual tooth rows or laminae and the palatal tooth of cyclostomes, since a function like this would contradict their spatial distribution in the front part of the oral opening and would leave the pharyngeal positioned P elements without any purpose. Krejsa et al. (1990) admitted that extant lampreys and hagfishes deploy no dental structures analogous to the conodont Pb element. Whether the conodont P elements were capable of muscular protrusible (protractile-retractile) movement can only be presumed. Therefore, the feeding mechanism mentioned above for recent cyclostomes can only be taken as a general model of a similar lifetime strategy when compared to that of *Icriodus*, and is not completely homologous.

The spatial architecture of the icriodid apparatus (fig. 4) is proposed here to exhibit two functional units, as is the case with other conodont apparatuses. The symmetry elements (S, M) form a curvature transition series in the front part of the mouth opening. Whether these elements are positioned in a "plane" as reconstructed

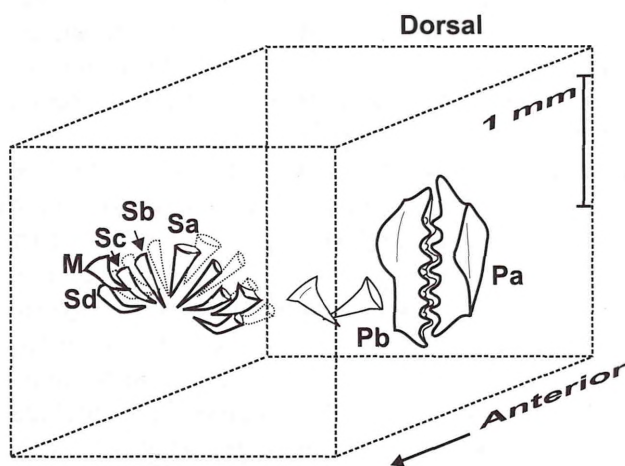


Fig. 4: - Presumed spatial architecture of the *Icriodus alternatus* multielement apparatus; simple cone S elements form a curvature transition series in the anterior part of the oropharyngeal opening. The number of elements may amount up to 30 (Lange, 1968). Coniform Pb and segminiscaphate Pa elements are positioned deeper in the pharynx. Apparatus architecture is based on respective approaches of, e.g., Purnell (1993). Scale bar is approximate.

for other conodont apparatuses (comp. Purnell & Donoghue, 1998 for further literature) or form a semicycle or even a full cycle around the mouth, as is the case with the "teeth" on the oral disc of extant lampreys can only be surmised. Taking reconstructions of other apparatuses into account (e.g. Freedman et al., 1998), an arrangement of the symmetry elements in the upper part of the mouth opening is assumed. Also, in several recent lampreys a concentration of teeth in the upper half of the oral disc can be observed with no detrimental effects on the adhesive capabilities of the lower half (Nikolskii, 1961). The ability of a protractile-retractile muscular movement of the symmetry elements of icriodids which is analogous to that of related *Promissum pulchrum* (Freedman et al., 1998) is probable and crucial to the presumed function of establishing and retaining contact of its oral opening to its macrophagous prey.

The second functional unit in conodont apparatuses are the P elements deeper in the pharynx of the conodont oral cavity. In the icriodid apparatus, the sharply edged non-geniculate Pb element is positioned anterior to the Pa element. Due to its comparatively sharp edges, it seems well adapted for a bilaterally-cutting function dissecting food particles from the prey, while the posteriorly positioned Pa elements with their molar-like platform surface could mash the small particles for further digestion (fig. 3, 4).

AND THE ICRIODID HABITAT ?

The icriodid habitat has frequently been discussed (starting with Seddon & Sweet, 1971) on the basis of its distribution and abundance in Late Devonian shelf settings. Its preferred habitat has been deciphered by e.g., Sandberg & Dreesen (1984) as one to be attributed to shallow water settings possibly within the euphotic zone (Dreesen, 1987). Icriodid enrichments in deeper water settings as e.g., the Montagne Noire sections expose, coincide with third order sequence lowstand phases (Schülke, 1999a, c; Schülke et al., in press). On the other hand, generic faunal portions in conodonts might have been triggered by more ecological factors than simple water depth (e.g. Nicoll, 1984; Belka & Wendt, 1992). A large variety of additional factors have to be considered before we will be able to elucidate conodont (syn-)ecology, some of which are the apparatus architecture, functional morphology and the feeding mechanisms of different species. Consequently, when we discuss conodont (single element) abundance data concerning their significance for possible changes in an ecosystems structure without taking into account mutual interrelations between co-occurring taxa, e.g., based on feeding mechanisms and lifetime strategies, these approaches can only be considered highly speculative.

Most recently, such an approach is exemplified by the survival of the Kellwasser event of *Icriodus alternatus* (House et al., 2000). These authors speculate about “opportunistic takeovers in parallel with the ecological deterioration for other Frasnian conodonts” (House et al., 2000: 67) and “tolerance to low-oxygen and eutrophic conditions” as part of the “*Icriodus* survival success” (House et al., 2000: 67) without any knowledge about how and whether at all the icriodid habitat was affected by Kellwasser crisis conditions and whether opportunistic takeovers were possible in the light of completely different lifetime strategies which are founded, e.g., by different apparatus architecture and feeding mechanisms.

Considering the functional morphology of the icriodid feeding mechanism as a macrophagous predator or scavenger of (soft bodied) benthonic or nectonic marine organisms, the attribution of *Icriodus* to neritic shallow water settings, which seems to me well founded, can also be explained as a function of prey density rather than of other ecological factors. In contrast, this interpretation would explain the rather high icriodid faunal portions within, e.g., deeper marine open shelf settings such as the Montagne Noire sections represent. An additional intriguing observation from these sections and others from the Rheinische Schiefergebirge is the almost parallel abundance development of *Icriodus* and acanthodian remains (Riemann et al., in press), which could be explained following a predator-prey relation.

CONCLUSIONS

The early Famennian *Icriodus alternatus* multielement apparatus is reconstructed based on the spatial distribution and functional morphology following the example of highly similar feeding apparatus of extant petromyzontoids. An analogous lifetime strategy for this extinct conodont animal is proposed which fulfills the postulation that conodonts were carnivorous predators or scavengers. A conclusive reconstruction of the icriodid habitat cannot yet be proposed, but it is quite reasonable to presume that a variety of intrinsic factors including functional morphology of the feeding mechanism, influenced the icriodid lifetime strategy rather than other extrinsic physical properties of the surrounding environment alone.

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