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ANALYSIS OF SYNCHROTRON MICROTOMOGRAPHY 3D IMAGES OF EXCEPTIONAL FUSED CLUSTERS OF *MOCKINA SLOVAKENSIS* (CONODONTS)

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ABSTRACT

Conodonts are the unique hard-parts of a set of teeth-like elements placed in the oral cavity of an eel-shaped soft-bodied organisms. The general architecture of conodonts' oral skeleton is a bilaterally symmetrical array of usually 15 phosphatic elements. There are many controversies regarding the function of those mineralized elements, but novel quantitative computational methods have opened new opportunity to study their function. Following this, the object of the present work is to study the arrangement and the function of the oral skeleton of the late Norian species *Mockina slovakensis* from several fused clusters found in the Dolomia di Forni, Seazza Creek valley, northern Italy. They were imaged using propagation phase-contrast X-ray synchrotron microtomography at the European Synchrotron Radiation Facility of Grenoble (France) and then the individual elements in the clusters were segmented and analyzed in details. Single elements were extracted from each analyzed clusters and then their relative positions were used to build up a revised, animated model of the *M. slovakensis* apparatus. With these results, we proposed a new motion of the apparatus that can be useful in future work to understand better the general function of the condonts' oral skeleton. We lend also additional support to the supposed presence of a lingual cartilage about which the elements were rotated by pair of antagonistic muscles, i.e. a pulley-like mechanism, previously proposed.

Key words: conodont apparatus, modelling, synchrotron microtomography, *Mockina slovakensis*.

RIASSUNTO

I conodonti sono le uniche parti dure di un set di elementi simili a denti posti nella cavità orale di organismi con un corpo formato da tessuti molli di forma simile a quello delle anguille. L'architettura generale dell'apparato masticatorio dei conodonti è una serie di, solitamente, 15 elementi fosfatici a simmetria bilaterale. Ci sono molte controversie riguardanti il funzionamento di questi elementi mineralizzati, ma nuovi metodi quantitativi computazionali hanno aperto nuove opportunità di studio del funzionamento di questi apparati. In riferimento a queste nuove scoperte, l'obbiettivo di questo lavoro è di studiare la disposizione e la funzione dell'apparato masticatorio del specie Norica *Mockina slovakensis.* Questo è stato possibile tramite l'analisi di diversi clusters di *M. slovakensis* trovati nella formazione della Dolomia di Forni, in Friuli Venezia Giulia, Italia. Questi clusters sono stati scannerizzati usando la microtomografia di sincrotrone a contrasto di fase presso l'ESRF (European Synchrotron Radiation Facility) a Grenoble, Francia. Successivamente, i singoli elementi fusi nei clusters sono stati segmentati e analizzati in dettaglio. Le posizioni relative di ogni singolo elemento estratto dai clusters analizzati sono state usate per costruire un modello rivisitato e animato dell'apparato masticatorio della specie *M. slovakensis.* Con questi risultati è stato possibile proporre un nuovo movimento dell'apparato dei conodonti che sicuramente sarà utile in futuri lavori che vorranno comprendere in dettaglio la funzione di questo apparato masticatorio. Con questo lavoro si fornisce un ulteriore supporto per la supposta presenza di una cartilagine linguale che serviva a ruotare tutti gli elementi tramite delle coppie di muscoli antagonisti, con un movimento simile a una puleggia, precedentemente proposta.

Parole chiave: apparato conodonti, modellazione, microtomografia a sincrotrone, *Mockina slovakensis.*

1. Introduction

Conodonts are major components of Early Phanerozoic marine ecosystems and have a wide geographical and temporal distribution (fig. 1.1). Their biozones and the taxonomy on which they are built have long been applied to resolve regional and intercontinental-scale correlations.

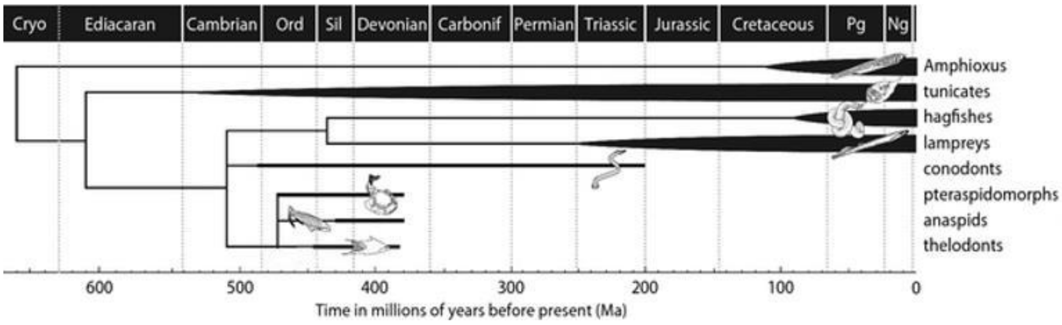

Fig. 1.1. Phylogeny of conodonts compared to other living and extinct chordates.

The fossil record of the true conodonts (euconodonts) ranges from the Upper Cambrian to the uppermost Triassic and consists almost entirely of their dissociated skeletal elements. These became scattered in the sediment on the death and subsequent decay of the animals. In conditions where the conodont carcasses were buried and decayed without disturbances from currents, scavengers or burrowing organisms, the elements of the skeletal apparatus may be preserved in association on bedding surfaces. Partial or complete apparatuses are also found in form of clusters, where the elements lying in juxtaposition have become fused together during diagenesis.

Conodonts have no close living relatives and there are no homologous structures in extant organisms to aid interpretation. Hence, only natural assemblages present the evidence for the original arrangement of the components of their skeleton.

Methods as microwear analysis, computed tomography and finite element analysis are applied to the study of conodont elements and they now can be combined to interpret conodont taxonomy, stratigraphy and phylogeny.

1.1 Anatomy

Conodont-animals were small elongate organisms, few centimeters long. They had no hard skeleton, but a stiffening rod of cartilage along their back and V-shaped blocks of muscles along their side. The anterior end of the body was developed as a distinct cephalic lobe that included two fairly large eyes and the apparatus of mineralized elements by which conodonts are best known (fig. 1.2).

Fig. 1.2. Shape of the conodont animal

In some specimen, Aldrige et al. (1993) found traces of additional soft-tissue morphology in the head region. At start, they were supposed to be the eyes, but are now consider more likely to represent otic capsules. These features mean the possible presence of a nervous system that might include a brain. However, these considerations are still under debate.

The main features of the trunk that can be preserved were the notochord, myomers and caudal fin rays. These elements are part of the so-called soft tissues of the conodont animal.

Notochord. The evidence of the notochord in the fossils is some pair of axial lines, which represent its margins. In specimens heavily phosphatized, the area between these lines is mineralized and preserved in relief. It extended posteriorly to the tip of the tail.

Nerve cord. In some specimens, the anterior part of one of the axial lines delimiting the notochord appears thickened and divided medially by a darker trace. Aldridge et al. (1983) suggested that this feature might represent the dorsal nerve cord.

Myomers. These represent the V-shaped muscles of the animals and their preservation as distinct and separated chevrons can be attributed to postmortem shrinkage of the muscle fibers prior to phosphatization. The evidence from all the specimens in which they are preserved is consistent with an arrangement of laterally paired V-shaped myomeres, their apices directed anteriorly and their limbs converging posteriorly to meet dorsally and ventrally along the midline.

The tail. For every specimen the structure of the tail is different. The notochord can be extended into it or not; the fins can be more developed along one side of the tail than the other side. For these reasons the precise structure of the caudal fin remains equivocal; it may have been symmetrical, or it may have been extended slightly further on the dorsal or ventral margin.

They should have had also four pairs of branchial grooves but there is lack of evidence to confirm their form and position.

In addition of soft tissues, conodont animals had also hard tissues, which are the best-preserved parts in the paleontological record. They form a mineralized phosphatic feeding apparatus (fig. 1.3). The general architecture of the conodont oral skeleton is a bilaterally symmetrical array of usually 15 phosphatic elements. It is composed by one pair of obliquely pointed M elements in rostral position, behind them, one unpaired S_0 element (lying on the axis of bilateral symmetry) and four pair of elements (S_{1-4}) located on both sides of the S_0 and, more caudally, two pairs of pectiniform elements (P_1, P_2) (fig. 1.4). This apparatus may be preserved in a variety of configuration depending on its orientation to bedding.

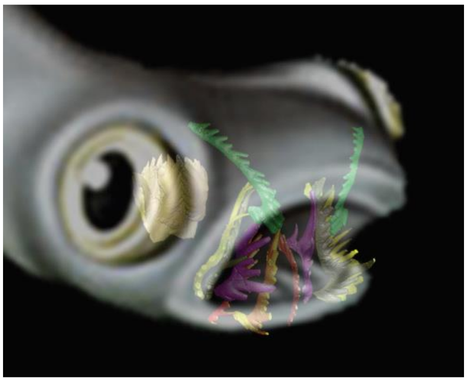

Fig. 1.3. Apparatus within the conodont’s head

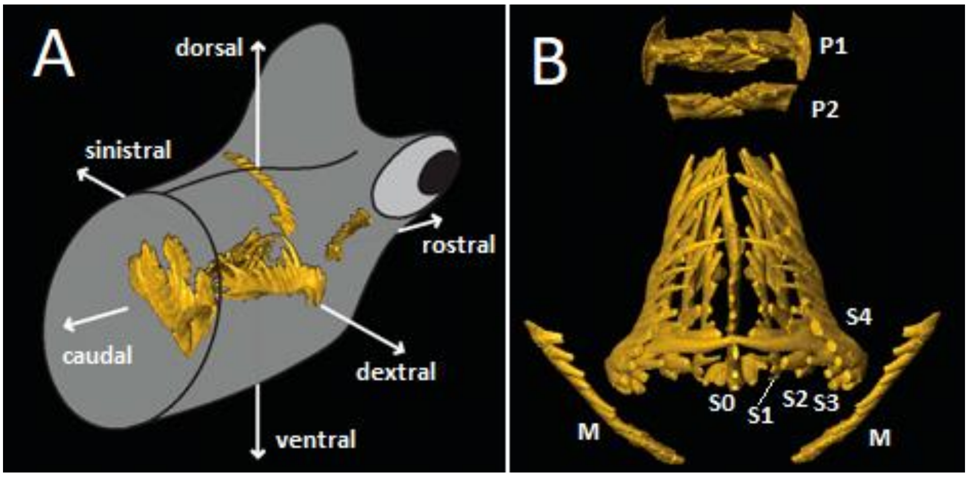

Fig. 1.4. Anatomical orientation and notation. (A) Orientation of the apparatus within the conodont’s head; (B) Dorsal view of a reconstructed conodont's apparatus.

In the years before the discovery of the preserved soft tissues, the affinity of these tooth-like phosphatic elements remained enigmatic. Some paleobiologists had attempted to solve this problem using comparative anatomy of the architecture of the feeding apparatus, element morphology and histology. These studies did not reach an equivocal conclusion regarding conodont affinity because they were without any constraint.

After the discovery of the soft tissues and with a much clearer perception of conodont affinity, the considerations in conodont histology were much better than the previous time. One problem was that not all these studies considered the interactions between the component hard tissues during growth.

Donoghue (1998) is one of the first who made a study regarding the interpretation of hard tissues after the consideration of growth and patterning in the conodont skeleton.

However, conodont elements are constructed from two basic units: the crown and the underlying basal body. The crown can be composed entirely of hyaline *lamellar crown tissue* or of a combination of lamellar crown and *white matter*. The basal body is a single component structure composed from a hard tissue usually called *basal tissue*.

Lamellar crown tissue. This is the most coarsely crystalline tissue and usually comprises the major component of conodont elements. The crystallites are no more than a few microns long and are bounded at each end by the growth lines which define the lamellae. It grew by outer apposition because many elements display evidence of damage and subsequent repair.

White matter. This term derived from the evidence of this tissue in reflecting the light. It is composed by more fine crystallites and it has lower organic content than the lamellar crown tissue. White matter occurs only in denticles as cores and has sharply defined lateral margins. In the cores, there are cavities enclosed within the fine-grained groundmass and they can vary in their size, shape and orientation. It was secreted as a continuous core of mineralized tissue, partly controlled at the margins by the lamellar crown.

Basal tissue. It is often clearly punctuated by growth striae and it is so finely crystalline that individual crystallites cannot be distinguished with a light microscopy. It is the most variable of all conodont hard tissues, both between taxa and within a single taxon. Most basal bodies are atubular and they usually occur within concentric growth increments equivalent to the striae in the lamellar crown tissue. It grew by outer apposition and synchronously with the crown tissue; this is indicates by the confluent passage of incremental growth striae between the two tissues.

1.2 Conodont affinities

The debate about the affinities of conodonts is going on since the first conodont animal specimen was found. At start, it was not so easy to put them in a precise position in the animal world because of the lack of evidences and many authors forwarded many hypotheses.

Heinz Christian Pander, a Russian biologist, discovered the first conodonts fossils in 1856. Initially, he interpreted them as teeth of primitive fish. However, only after the discovery of the first conodont animal in 1981 in the Carboniferous deposits of Edinburgh that was possible to make more accurate considerations about conodonts affinities.

Briggs et al. (1983) established their phylogenetic position with reference of two groups, chordates and chaetognaths. After the discovery of new specimen, he placed them in a separate phylum, Conodonta, following Clark (1981). Other subsequent specimens and the discovery of soft tissues remains led Aldrige et al. (1993) to dismiss the chatognath affinity and to confirm the chordate one.

Some authors strongly argued that conodonts could be part of a separate phylum and their affinity with chordates because of the lack of positive evidence about notochord, dorsal nerve cord and gill slits. Conodonts were also compared to the nemertean worms for the similarity of their soft parts. Other authors proposed a relationship with a Carboniferous mollusk for the similarity of their feeding apparatuses, the trunk and the posterior fins. Someone compared the collapsed, non-operational position of the apparatus of conodonts to that of chaetognaths (marine invertebrates) and seemed that, at least for protoconodonts, there was some relationship especially for the retracted position of the apparatuses. The problem was the definition of a relation between protoconodonts with para- and euconodonts. Finally, some authors listed a number of criteria in support of an affinity between conodonts and cephalochordates: the lack of paraxial or dermal elements, the V-shaped folding of the muscles in the trunk, the level of encephalization demonstrated by the anterior feeding apparatus and the anatomy of the fin rays.

All these hypotheses were refuted by the combined evidence from soft-part anatomy, functionality of the feeding apparatus and element microstructure.

Now, after lots of studies about conodonts remains, their affinity with vertebrates is now widely recognized and they are now considered as a major group of early vertebrates.

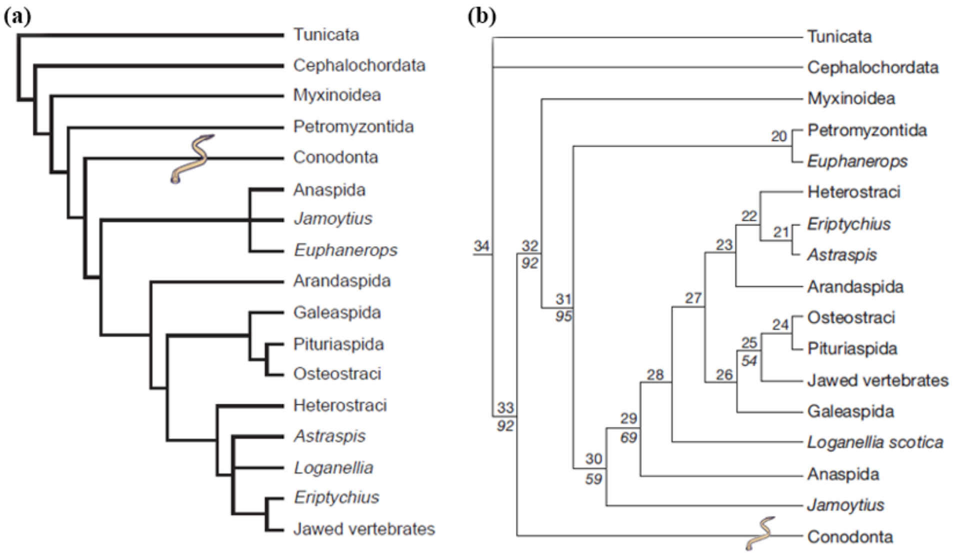

Fig. 1.5. Cladogram showing conodonts as early vertebrates (a) and as basal chordates (b).

1.3 Objectives

The elucidation of the controversies explained above has been slowed down due to the restrictions caused by outdated technologies. This work wants to show a new method to study and interpret the conodonts apparatus based on the analysis of well-preserved clusters, meaning having at least two conodonts elements fused together.

The first aim of this project is to understand better the position and the function of all the single elements of the conodonts apparatus, in particular the one of the M elements that are the most problematic elements, along with the particular position of the elements which would put some constraints on the functional model of the apparatus.

After that, this study wants also to shed light upon the function of the entire conodonts apparatus by making a movie after the analysis of the specimen and the extraction of the elements from the clusters.

Furthermore this work supports the assumption of the presence of a lingual cartilage that might have moved the apparatus helped by some pairs of antagonistic muscles (Goudemand et. al 2011). Consequently, the theory of the conodont affinity with vertebrates would be even more confirmed.

It is expected that the use of new technologies, such as *Propagation Phase-Contrast X-Ray Synchrotron Microtomography,* will allow the acquisition of better and more precise evidence supporting the function and the position of conodonts elements in the apparatus. This will be achieved through obtaining three dimensional virtual model in order to recognize the conodonts elements.

2. History of apparatus' reconstruction

Parallel to all the discussions about affinity and anatomy of conodonts, other studies have been going on since the first conodonts remains were found. They deal with the interpretation of the original three-dimensional arrangement of the elements comprise in the conodont feeding apparatus.

As previously mentioned, the oral skeleton of conodont-animal is composed by 15 phosphatic elements and, for this reason, they are the best preserved parts of the animal in the fossil record. After the death of the animal, these elements became scattered and if not affected by any type of disturbance, they could be preserved in bedding plane association, in form of clusters or as natural assemblages.

Currently, the notation used for the 15 elements of the conodonts apparatus is the one of Purnell et al. (2000) with P_1, P_2, M, S_0, S_1, S_2, S_3 and S_4 (fig. 2.1A) that replaced the one of Orchard and Rieber (1999) with, respectively, Pa, Pb, M, Sa, Sb_1, Sb_2, Sc_1, Sc_2 (Fig. 2.1B).

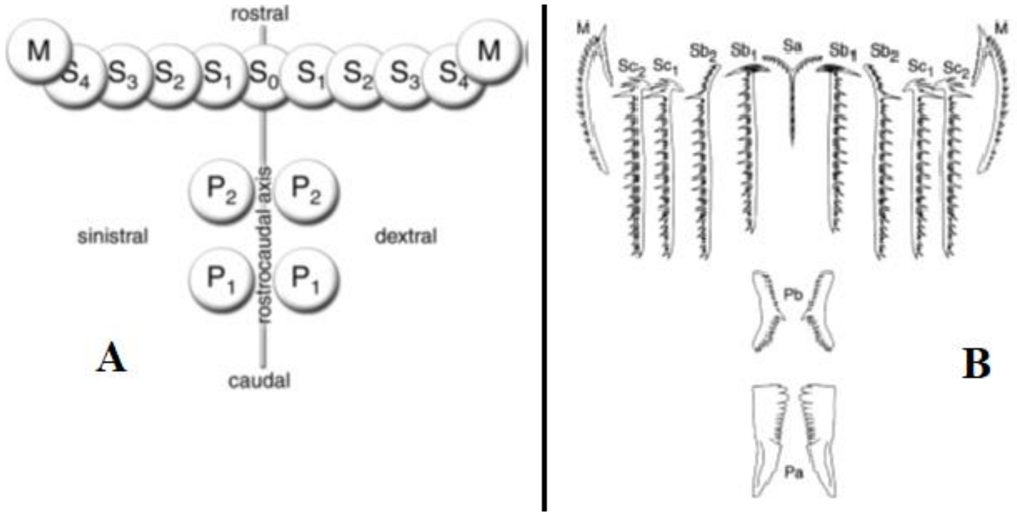

Fig. 2.1. Schematic map of the relative positions of elements in the topological scheme of notation proposed by (A) Purnell et al 2000 and (B) Orchard e Rieber 1999.

Bedding plane assemblages can be found in different type of configuration depending on the orientation of the apparatus relative to the plane of flattening.

This can be modified by any rotation of the elements during the collapse of the apparatus or as a result of a muscular contraction on animal's death.

Fused clusters are potentially more informative than most bedding-plane assemblages because the elements are better preserved, more often intact and may also better record their 3D positions. However, it is very difficult to distinguish all the elements without removing any if more than two or three elements are fused together. A way to bypass this problem is to use a non-destructive inspection method, such as tomography. The principle of tomography is based on the computed reconstruction of a series of 2D-slice images through the studied object under study from radiographs of the specimen acquired during its rotation.

Linear reconstructions

A few studies have based architectural reconstructions on interpretations of function. Lindstrom's hypotheses (1964, 1973 and 1974) were based on the functional interpretation of the conodont apparatus as a lophophore support. Similarly, Nicoll (1995) assessed that the conodont apparatus morphology was placed in an amphioxus-like body.

Almost all the other studies on conodonts apparatuses arrangement were based on analyses of clusters or bedding-plane associations. Schmidt (1934) proposed that *Gnathodus* had a linear array of 14 elements with their long axes approximately parallel to each other. In this reconstruction the M elements flanked the S elements, the denticles of which are directed downwards, inwards and towards the P elements. This configuration was influenced by his interpretation of similarity between the conodont apparatus and the mandibles of a placoderm fish. For this reason he put the Pa elements at the front of the apparatus. Although some errors, he also did not include a Sa (=S_0) element, this reconstruction was ahead for that time and had no real rival until the work of Rhodes in 1952.

Rhodes (1952) proposed a reconstruction for the apparatus of *Idiognathodus.* He did not include a Sa (=S_0) element and did not recognize different morphologies of S elements, but his reconstruction was one of the most influential for that time.

For this reason, many authors re-illustrated his model in successive works only with minor modifications.

Schmidt and Muller (1964) recognized morphological differentiation within the S elements and suggested a linear apparatus similar to that of Schmidt (1934), but with the Pa (= P_1) elements in the opposite position. Many authors re-examined this work and proposed similar arrangement in the next years.

This method of approaching to apparatus reconstruction had lots of weakness, in particular the difficulty to explain the recurrent asymmetrical patterns without considering post-mortem effects on the carcasses of animals.

Three-dimensional reconstructions

Aldridge (1987) tried to understand the three-dimensional architecture of the conodonts apparatus by analyzing some bedding plane associations of Carboniferous polygnathaceans. He demonstrated that the elements are arranged about a dorso-ventral plane of symmetry with the ramiforms in an anterior position and with their long axes close to vertical forming a V-shaped structure; the P elements follow posteriorly and lie vertically and almost normal to the long axis of the trunk. To achieve this result he took some photos of the model from various angles to project the three-dimensional structure onto a two-dimensional plane. He also proposed a functional system for this apparatus, with the anterior elements, the ramiforms, grasping food to be processed later by a shearing action of the P elements. Further reconstructions conflicts with this interpretation, especially for the arrangement of the ramiforms elements.

Aldridge et al. (1995) presented a reconstruction of the architecture and the function of the apparatus of *Promissum pulchrum.* It is a large species of conodont found in the Upper Ordovician Soom Shale Member, Cedarberg Formation, South Africa. They collected and analyzed more than 100 complete apparatuses as natural assemblages on bedding surfaces. This reconstruction presented some problems because sometimes the preservation made impossible to determine the relative superposition of elements. However, they reached some results and the apparatus reconstructed is more complex than the other conodont taxon: the number of elements is large and some of them have a complicated three-dimensional morphology. This apparatus comprises 19 elements in total (two Pa, two Pb, two Pc, two Pd, two M and nine S) and also the arrangement is different form the others. In the recent notation of elements the Pa corresponds to the P_1 and the Pb to the P_2; for the Pc and Pd there is not a notation used, but they can be called P_3 and P_4 respectively. The Pa, Pb and Pc are horizontally aligned, the Pd are positioned below the Pb, the S form an oblique array below the P elements and the M are at the anterior (fig. 2.2). The functionality of this apparatus is even more complex than the reconstruction; probably all the elements worked together to promote the feeding of the animal, the S elements grasped the prey and the P elements crushed them. Understanding the details was not possible, but probably the process must have involved a sequence of events.

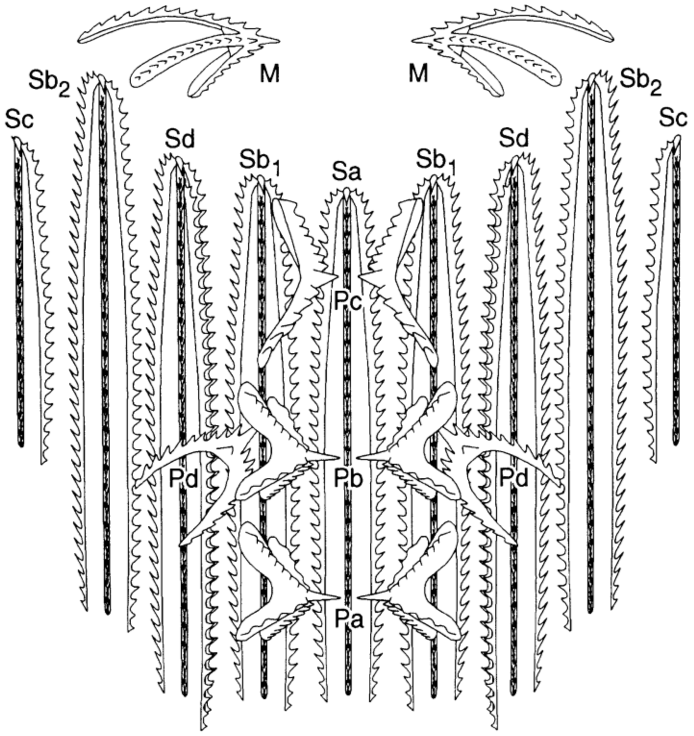

Fig. 2.2. Scheme of the apparatus of *Promissum pulchrum.* Pa = P_1; Pb = P_2; Pc = P_3; Pd = P_4; Sa = S_0; Sb_1 = S_1; Sd = S_2; Sb_2 = S_3; Sc = S_4. From Aldridge et al. (1995).

Purnell and Donoghue (1997) analyzed some natural assemblages of *Idiognathodus* from the Pennsylvanian of Illinois. In this case, they didn't use clusters or bedding plane associations, but natural assemblages. The aim of this methodology was to produce a single model of apparatus architecture based on a variety of these assemblage patterns without recourse to *ad hoc* hypotheses of post-mortem muscle contraction. They achieved a precise scale model of the feeding apparatus of ozarkodinid conodonts. This apparatus is composed at the front by a Sa (= S_0) element, flanked by two pairs of elongate Sb_{1-2} (= S_1 and S_2) and Sc_{1-2} (= S_3 and S_4) elements which were inclined obliquely inward and forwards; above these elements lay the M elements, arched and inward pointing (fig. 2.3). Behind them lay the Pb (= P_2) and Pa (= P_1) elements, they are transversely oriented and bilaterally opposed. This reconstruction differs from the previously proposed in two aspects. First, the position of the Pa elements with the left elements behind the right; second, the arrangement of the S and M elements at the anterior of the apparatus is very different from the one proposed by Aldridge et al. (1987). Purnell and Donoghue placed the S elements in parallel with almost equal forward inclination and no vertical displacement and no inward inclination; the M are located above and are oriented obliquely to the S elements, but the long axis of M and S elements are parallel. These new considerations on the conodonts apparatus were fundamental to analysis of functional morphology and the problem of food acquisition in conodonts. For the function of the apparatus, they confirmed that the P elements processed the food by crushing and/or slicing and that the S and M elements probably had a grasping function. Considering that the position and orientation of the M elements and the inclination of their denticles were markedly different from to S elements, they suggested that the M elements probably worked in a different way. They also proposed that the S and M elements were attached to cartilaginous plates and that the anterior part of the conodonts apparatus is comparable to those of extant agnathans; they did these considerations without any direct evidence.

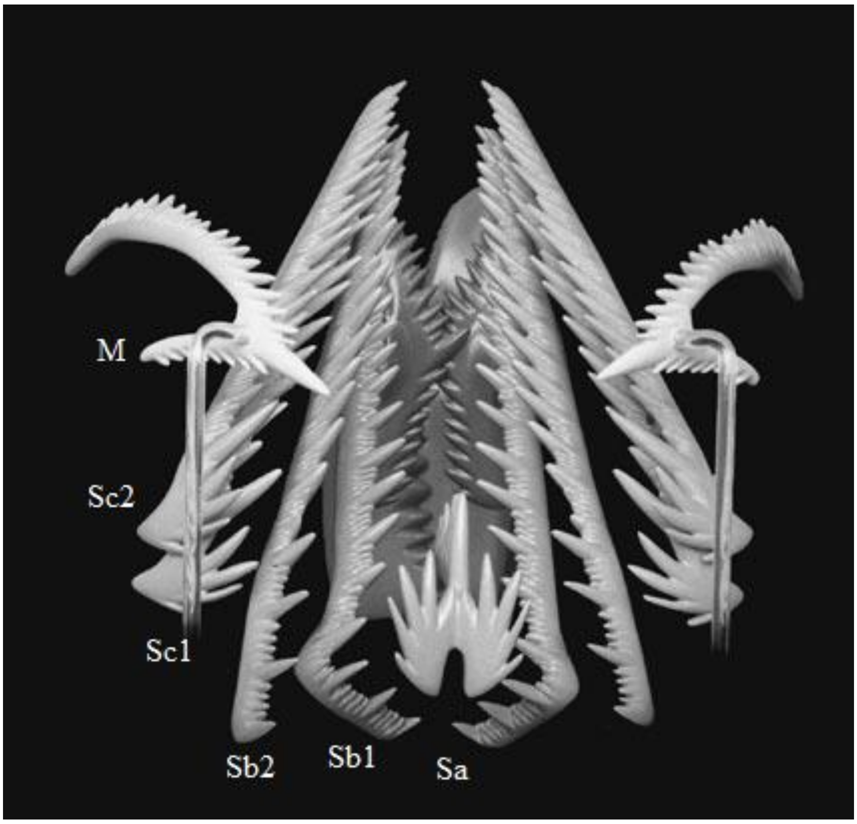

Fig. 2.3. Anterior view of *Idiognathus* apparatus model. From Purnell and Donoghue 1997. Sa = S_0; Sb_1 = S_1; Sb_2 = S_2; Sc_1= S_3; Sc_2 = S_4 in the current notation.

Goudemand et al. in 2011 analyzed exceptional preserved clusters of the Early Triassic *Novispathodus* and provided a new interpretation of the apparatuses for the *Ozarkodinina;* they also proposed the presence of a pulley-shaped lingual cartilage similar to that of extant cyclostomes within the feeding apparatus of euconodonts. They imaged these clusters using propagation phase contrast X-ray synchrotron microtomography. They made lots of consideration about the movement of the elements in the conodont apparatus considering the shape and the position of the elements; for example, they proposed a new position of the S_0 and the M elements, called the pinching position, in which those elements overall a Y-shaped (in rostral view), converging motion that would have performed an efficient pinching and seizing function (fig. 2.4).

At the end they assessed a general movement of the apparatus which is consistent with a presence of some pairs of antagonistic muscles which moved the entire apparatus. They also proposed a movie in which is demonstrated the movement of the apparatus. This work gives a strong support to the vertebrate affinity of conodonts.

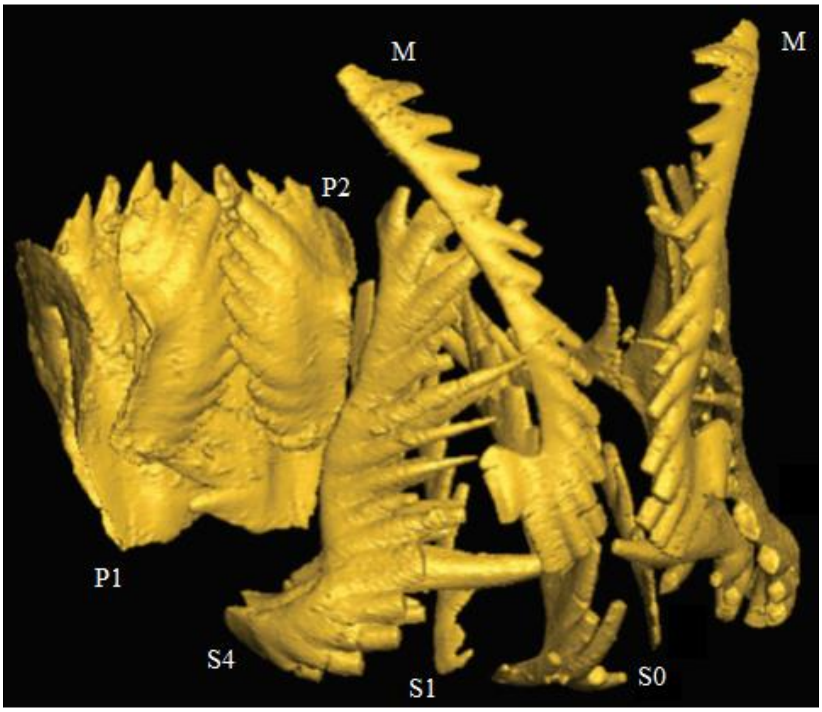

Fig. 2.4. Reconstructed apparatus of *Novispathodus* in the pinching position. Oblique rostral view. From Goudemand et al. 2011.

In 2012, Goudemand et al. published a work about a revision of the architecture of the conodont apparatus of the superfamily *Gondolelloidea*. They recovered several fused clusters of the genera *Neospathodus* and *Novispathodus* from the limestone beds from different localities in South China. With this work, they inverted the position occupied by S_1 and S_2 elements within apparatuses of members of superfamily Gondolelloidea and they did the same things for S_3 and S_4 elements within apparatuses of members of the subfamily Novispathodinae.

Agematsu et al., in 2014, described the apparatus of the *Hindeodus* species, an early Triassic conodont; they found its fossils in a deep-water chert and claystone section in the Mino Terrane, Japan. They recognized 13 natural assemblages comprising at most 13 elements. In detail, they discriminated pairs of P_1, P_2 and M elements, and the single S_0 element. They also found other elements of the S array that are preserved in the S_2 and $S_{3\text{-}4}$ positions, but not a pair of the S_1 elements due to the incompleteness in the natural assemblages. (Fig. 2.5) At the end, they support the theory of the 15 elements' apparatus for the *Hindeodus* species even if with some doubts on the presence of the S_1 elements.

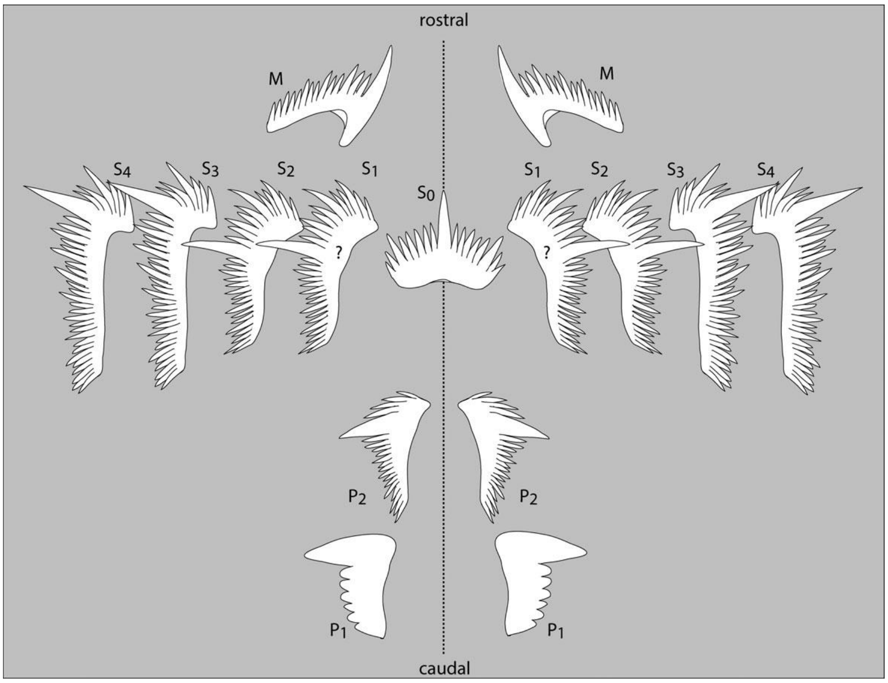

Fig. 2.5. The apparatus composition of Hindeodus parvus and Hindeodus typicalis. From Agematsu et al. 2014.

The last published work about conodont apparatuses is the one of Liu et al. (2017), in which they described the conodonts that they have found in the middle-upper Darriwilian (Middle Ordovician) Winneshiek Konservat-Lagerstätte in northeastern Iowa. The particularity of these fossils is that they are giant and they are preserved with hyaline elements, i.e. the crown and basal bodies (fig. 2.6).

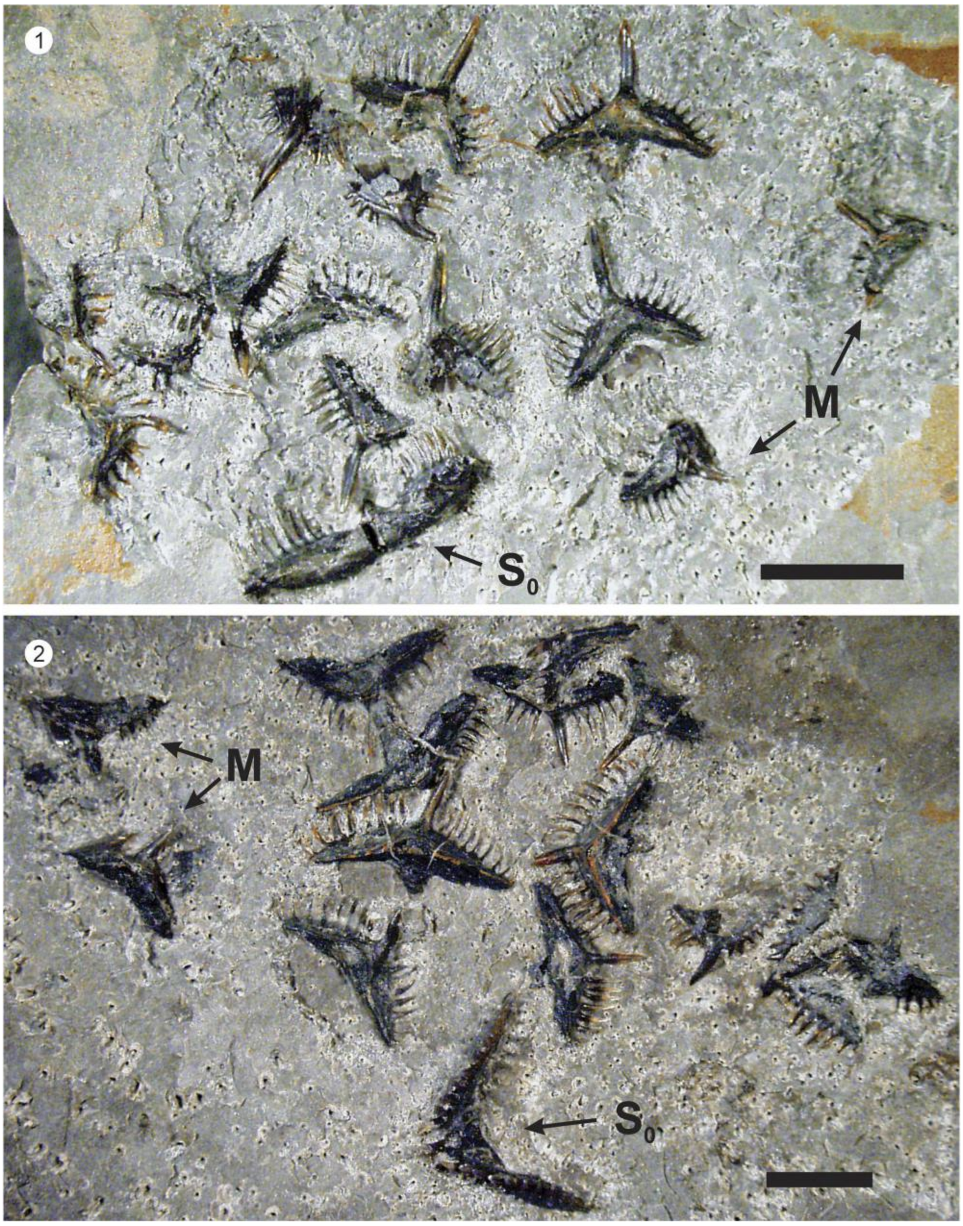

Fig. 2.6. Two apparently complete apparatus of the *Iowagnathus grandis* new genus new spwcies. Scale bar = 2 mm. From Liu et al. 2017.

The main species identified are the *Archeognathus primus* Cullison, 1938 and *Iowagnathus grandis* new genus new species. The *A. primus* apparatus is composed by six elements: two pairs of P and one pair of S elements. On the other hand, the apparatus of the *I. grandis* n. gen. n. sp. consists in 15 elements that comprises 7 pairs of ramiform elements and one single alate ramiform element (S_0). They compared these two apparatuses with the one of the prioniodontid

Promissum; they point out that the *A. primus* apparatus is very different to it; instead, the apparatus of *I. grandis* n. gen. n. sp. shows some similarity to it. They also proposed a new family Iowagnathidae in Conodonta, based on the samples found in the Winneshiek section.

After those there is my study that, it must be remembered, deals with an Upper Triassic conodonts (*Mockina slovakensis*) and, until now, is the unique one; so the complexity of these work is also for the lack of other apparatus of the same age.

2.1 Microwear analysis

Another type of studies that developed parallel to the reconstruction of the apparatus is the analysis of microwear on the denticles of conodont elements. These regard in particular the P_1 elements because they are the easiest to find in the fossil record and for their position in the conodont apparatus. They are in the most caudal position of the apparatus, behind the P_2 and the ramiforms elements, and with the blade of the left element lying behind the blade of the right element with the denticles pointing each other (fig. 2.7).

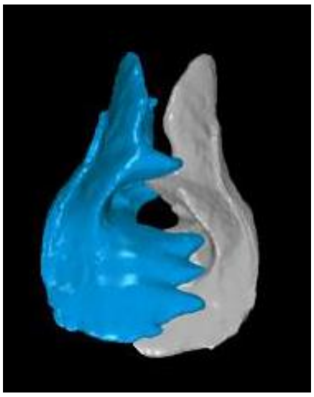

Fig. 2.7. Cluster of P_1 elements useful for the microwear analysis.

Microscopic wear patterns on conodonts elements provide the first unequivocal evidence that they functioned as teeth. These microwear were produced in vivo by abrasives in food and by the compressive and shearing forces that act on enamel during feeding.

Analysis of microwear represents a very powerful and direct tool for investigating feeding in fossil animals, but its application to fossil material is complicated by the problem of post-mortem abrasion. With technology such as Scanning Electron Microscopy (SEM) and Synchrotron Radiation X-Ray Tomographic Microscopy (SRXTM) the identification of microwear is becoming easier than in the past.

The presence of wear in conodonts has a number of implication for models of element growth. Wears have been observed on small, immature elements, indicating that conodonts did not grow their teeth to full size before using them. It is important also for the reconstruction of functional model of the conodonts apparatus; by the joint analyses of microwears and relative position of single conodont elements in fused clusters it is possible to proposed a more precise model of the conodonts oral skeleton and occlusion.

Important works were made by Purnell in 1995 and by Martinez-Perez et al. in 2014 and 2016 that, after the analysis of these microwears, provided a general model for occlusal cinematic in conodonts and assessed a number of important implication on understanding the growth of the conodont elements.

The presence of these microwears is a clear support to the hypothesis that the first vertebrates were predators. In this way, previous hypotheses that assessed that conodonts were microphagous pump-suspended feeders based on comparisons with amphioxus and larval lampreys are discarded.

It is clear that the studies on conodonts are widespread in a number of different topic and there are so many authors that are giving their help on resolving most of them. The work is not easy but with the discovery of new technology suitable for conodonts studies the results will be important in next years.

3. Late Triassic conodont taxonomy

The Triassic Period is divided in Lower, Middle and Upper, and in particular, Upper Triassic covers ca. 75% of the entire duration of the Triassic Period. The Upper Triassic is divided in three stages, that are Carnian, Norian and Rhaetian, and it goes from 227 to 201 My, at the end of which a big mass extinction led to disappearance of the 76% of the living species and to the mass extinction of the conodont fauna.

The taxonomy of the Upper Triassic is generally characterized by an important diversification during the Carnian stage, but only few taxa survived toward the Norian and Rhaetian stages (Rigo et al., 2017).

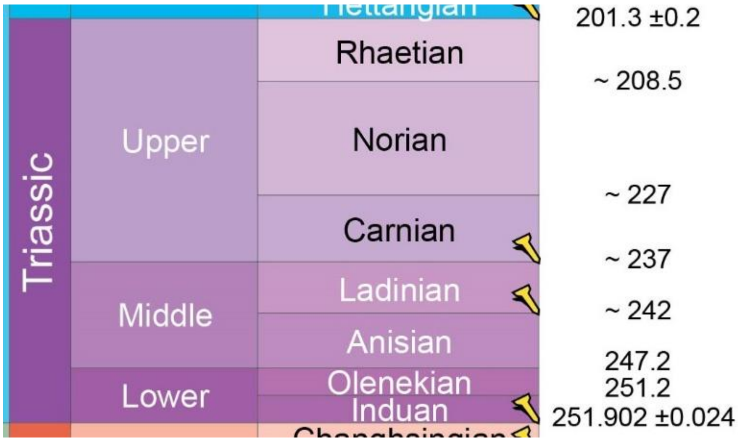

Fig. 3.1. Geological time scale of the Triassic Period.

Conodonts are biostratigraphically very important in the Upper Triassic for their great abundance, worldwide distribution and mineralogical composition that makes them available tools for biostratigraphic and geochemical studies.

The conodont record of the Upper Triassic documents pulses of extinctions followed by recovery events, but testifying a continuous decline of conodonts specific diversity during this period.

In the Late Triassic, conodonts suffer four main extinction events before the final one at the end of the Rhaetian: the first, in the Lower Carnian that is the weak one; the second, in the middle Carnian; the third one, at the Carnian/Norian boundary, which is more similar to a fauna turnover; the fourth, across the Norian/Rhaetian boundary. Each of this extinction is followed by a new speciation and by evident changes in the morphology of conodonts elements.

The Lower Carnian pectiniform species that survive the first extinction are morphologically simple, characterized by elongated platforms without ornamentations and a posterior pit (i.e. paragondolellidis).

The second extinction is more intense and related to the well know humid pulse called Carnian Pluvial Event and the subsequent recovery is slow, but it brings to a new peak of the conodont specific diversity (i.e. genera *Carnepigondolella*, *Metapolygnathus*, and *Epigondolella*). These conodonts have platforms with node or denticle and are characterized by a gradual reduction of the platform and the forward shifting of the pit.

Late Triassic species follow another extinction event around the Carnian/Norian boundary and, after that, conodonts exhibit two different evolutionary trends. The first trend is characterised by the extension of the platform with loss of the lateral margin nodes and of the free blade (i.e. genus *Norigondolella*). The second trend, instead, consists of species (i.e. *Epigondolella* and *Mockina*) that bear high denticles distributed on the platform margins; *Mockina slovakensis* belong to this pulse. After this last pulse, the evolutionary history of conodonts until the end of the Triassic is characterised by a constant decline, both in terms of morphology and diversity.

At the end of the Norian, the tendency to a general simplification of the morphological features may be observed. Even if two different branches evolved from the same species *Mockina bidentata*, all the uppermost Triassic pectiniform conodonts lose the platform and decrease in dimension (genera *Parvigondolella* and *Misikella*). This morphological simplification represented by *Misikella* is no longer successful, and after the disappearance of the last platform-bearing conodonts (such as *Norigondolella*), also platformless genus *Misikella* disappears at the end of Rhaetian.

4. Systematic paleontology

In the following, a description of the *Mockina slovakensis* species is proposed.

Phylum **Chordata** Baetson, 1886

Subphylum **Vertebrata** Linneus, 1758

Class **Conodonta** Eichenberg, 1930

Order **Ozarkodinida** Dzik, 1976

Superfamily Gondollelacea (Lindoström, 1970)

Family Gondollellidea Lindström, 1970

Genus *Mockina* Kozur, 1989

Mockina slovakensis (Kozur, 1972)

1972 *Metapolygnathus slovakensis* n. sp. Kozur, p. 10-11, fig 23

1983 *Epigondolella* n. sp. C population – Orchard, p. 185-186, fig. 9

1990 *Epigondolella multidentata* – Budurov & Sudar, pl. 5, fig. 20-22

1995 *Epigondolella slovakensis* – Roghi et al, pl. 1

2003 *Mockina slovakensis* – Channel et al., pl. A2, fig. 56, 57, 58; pl. A3, fig. 49

2012 *Mockina slovakensis* – Mazza et al., pl. 7, fig. 9,10

2016 *Mockina slovakensis* – Rigo et al., fig. 2, 3

Description of P_1 elements. Compact species characterized by a short blade and thick platform margins. The platform has sharp and high denticles on the anterior lateral margins and, sometimes, other nodes occur on the posterior margin. On the anterior part, there is a free blade with 4-5 denticles. The cusp has the same shape of the other denticles and two or rarely three carinal nodes follow it. The blade is very high anteriorly and it descends abruptly inside the platform before the carina, which is composed by small and well-separated nodes. The last carinal node is usually larger than the other ones and inclined through the posterior. In lateral view, the specimens are characterized by a strong upward bend of the lower side just before the pit. The pit is located in center; the keel is posteriorly prolonged and its termination is pointed.

Description of ramiform elements. In 2005, Orchard published a work in which he described the genus *Cypridodella* that then was revisited and considered to the same genus as *Mockina slovakensis* after some consideration made by several authors (Moix et. al, 2007; Mazza et al., 2012; Rigo et al.). The M has a breviform digyrate shape; both S_3 and S_4 elements have a short, variably inturned anterior process and a joined elongated posterior process. The distal end of the larger process of the S_1 element is characterized by a crest of high, apically curved denticles. In some species, the S_2 element has a basal attachment scar extending apically towards the cusps.

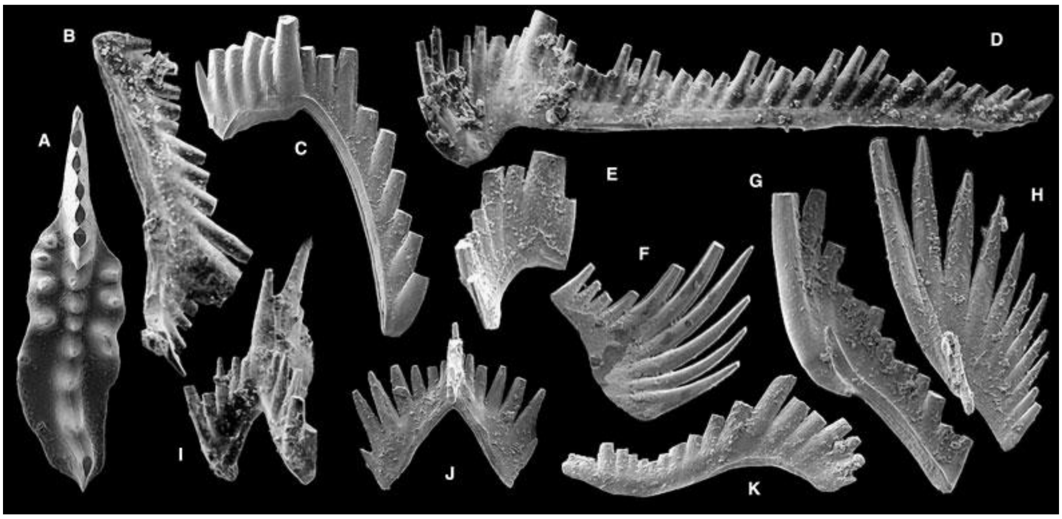

Fig. 4.1. A: P_1; B: P_2; C: M; D: S_4; E: S_3; F: S_1, distal part of long process; G: S_2; H: S_1; I: S_0, antero-lateral view; J: S_0, posterior view; K: S_0: posterior process. From Orchard, 2005.

5. Geological settings

The Dolomia di Forni (Formation) is a lithostratigraphic unit cropping out along the upper valley of Tagliamento river, in the Friuli Venezia Gulia region (fig. 5.1). It is characterized by dark-gray to black or brown bituminous dolostones, usually well bedded, often in thin layers, with chert nodules and lenses. Its importance is due to a particular and rich fossil association constituted mainly of crustaceans, terrestrial plants, fishes and reptiles. The Dolomia di Forni lies on the “dolomia cariate”, which is mostly composed by vuggy dolostones, but the basal contact in the Seazza Creek valley is tectonically disturbed, being in relation with the “Linea dell’ Alto Tagliamento”. The Dolomia di Forni is overlain, for almost all his extension, by black, well and thinly bedded limestones, sometimes cherty, named “Calcare di Chiampomagno”, Rhaetian in age (Roghi et. al 1995).

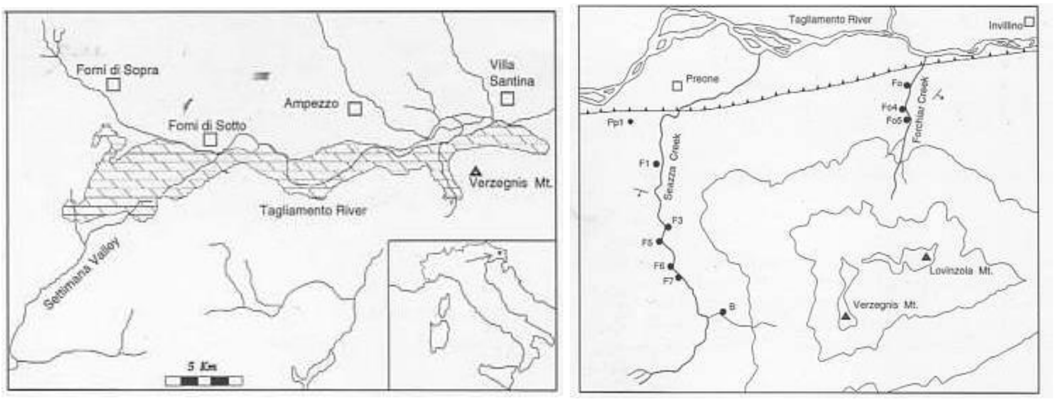

Fig. 5.1. Position of the Dolomia di Forni formation (left) and of the Seazza Creek valley (right). From Roghi et al. 1995.

At the beginning of the XX century was described as a carbonatic unit of thin layers, grey or black, often bituminous that could be a part of the Dolomia Principale (Formation), and few years later, this geological unit was identified as the lower part of the Dolomia Principale. Ferasin et al. (1969) informally called this lithological unit as “Calcare di Caprizzi”.

After that, Mattavelli e Rizzini (1974) changed the name into “Dolomia di Forni” and they made a detailed petrographic and sedimentological study identifying six lithofacies. Dalla Vecchia (1991), in particular studying one of these litofacies, the

Rio Seazza (Preone) one, from a sedimentological point of view. In 1994, Carulli et al. made a series of studies that permitted to understand better the stratigraphic and paleo-environmental characteristics of the bacinale facies of the Norian-Rhaetian in the Prealpi Carniche. At first, in this formation, different lithologies consisting of an association of laminated dolomites, massive dolomites, intraclastic dolomites, stromatolitic dolomites, dolomites breccia and argillitic dolomites were recognized. After more detailed studies, Braga et al. (1971) and Dalla Vecchia (1991) subdivided the Dolomia di Forni in three members: the first on lithological bases and the second basing on the sedimentological characteristics of the Rio Seazza valley. However, this subdivision works only locally. A successive accurate study of the entire basin, which comprises a wide area of the Prealpi Carniche, permitted the distinction of an Upper and a Lower Member in the Dolomia di Forni.

Lower Member

The Lower Member, which is widespread in almost all the area, is mostly made up by not-laminated dolomites without any particular fabric; the rocks have a light gray color. There is a sharp stratification 30-100 cm thick; sometimes there may be little dolomitic layers 20-40 cm thick and stromatolic layers that could reach one meter of thickness.

In the southern area this member is between the Carnian Dolomie Cariate and the Dolomia Principale, while in the northern area it is between the Dolomia Cariate and the Upper Member of this formation. The overall thickness of the Lower Member is more or less about 200-300 m.

This member represent deposits of shallow marine, lagoon or inter-tidal environment, with rare risedimented facies. The organic matter is almost completely absent. The stromatolitic layers, which appear only in this member, are a clear evidence of a shallow marine environment with oxygenation events in an anoxic period (Carulli et al., 1997).

Upper Member

The Upper Member consists in dark-gray dolomite, well stratified and laminated, often with marly intercalation and selciferous layers. The layers have a tabular geometry and are 20 cm thick. When occurs, the lamination is mostly plane parallel and represents the distal deposition of carbonate sediments of a turbiditic current. The dolomitic-marly or argillic interbedded layers may be rich in organic matter. In the transitional areas there are several slump deposits and, in the proximal area, debris flow deposits can occur. Interbedded with the bacinal facies can occur: olistolith of massive dolomite, brecce, bioclastic and dolo-sandstone. This member reach the thickness of 700 m and its boundary with the Lower Member is quite fast (Carulli et al., 1997).

It represents a deeper basinal euxinic environment, as testified by the absence of bioturbation and the abundance of turbiditic sequences and is known for the different fossil associations (Roghi et al., 1995). Most of the fossiliferous outcorps are in the narrow valley of the Seazza Creek, near the village of Preone, and along the northern slope of the Verzegnis Mt massif. The radiolarians, often poorly preserved, came from the upper layers of the water column; instead, the gastropods and the foraminifera are resedimented and from the platform. Much more important is the presence layers with macrofossils, which are not so rich but often significant. Crustaceans, fish, plants and little reptiles represented most of the fossils that are studied from this member; all these fauna are indicative for the Norian stage. There are also many levels very rich in conodonts especially in the medium part of the Upper Member. They are concentrated in dark layers of laminated dolomite and they should indicate phases of positive oscillation of the relative sea level (Carulli et al., 1997).

In conclusion, from the analysis made on these two members it is possible to say that the Dolomia di Forni formation is represented by two different evolutionary moments, at least from the environmental point of view. Low energy narrow tidal environment for the Lower Member and deep bacinale euxinic where the energy was very sensitive for the Upper Member.

The silicoclastic debris was very weak and, for this reason, there are isolated granules of quartz, feldspar and blades of muscovite. This is an evidence for the absence of wide areas subjected to erosion near to the basins (Carulli et al., 1997). From a diagenetic point of view, these litofacies are made by secondary dolomite that have replaced the calcite.

The top of the unit is Norian in age, given from the pollinic association: *Tsugapollenites pseudomassulae, Corollina sp., Corollina meyeriana, Granulopercupatipolis rudis, Ovalipollis pseudoalatus,* and the presence of the mostly monospecific conodont fauna of *Mockina slovakensis* (Roghi et al., 1995).

Several conodont elements of the species *Mockina slovakensis* have been found in this formation. They have been found above the rest of flying reptiles and successively studied by Roghi et al. in 1995, in order to characterize the age of the fossil associations. The rich conodont association, mostly monospecific, consisting of single elements, clusters and apparatuses permits the development of a 3D *M. slovakensis* apparatus, main aim of this thesis.

6. Material and Methods

Exceptionally preserved fused clusters of elements of the Norian (Upper Triassic), along with separate specimens mostly belonging to a monospecific fauna of species *Mockina slovakensis* was collected in the Dolomia di Forni, Seazza Creek valley, northern Italy. Clusters and apparatuses were the subject of this thesis, and they have been thus analyses for the 3D apparatus reconstruction and feeding mechanism.

Propagation Phase-Contrast X-Ray Synchrotron Microtomography. The specimens were scanned at the European Synchrotron Radiation Facility (ESRF) on the beamline ID19. We used a pink beam with a critical energy of 17.68 keV delivered by a U17.6 undulator. This insertion device delivers a single harmonic with a narrow bandwidth (ΔE/E of 5%). The original source monochromaticity is good enough to perform high-quality scans at submicron resolution without a monochromator. It allows rapid scans of microfossils, nearly free of ring artifacts. Regarding the sample size, we used a detector composed of a 6-µm thick GGG scintillator, of a revolver microscope, and of a FReLoN CCD camera. The isotropic voxel sizes ranged from 0.23 to 0.46 microns. Phase contrast was obtained using a propagation distance of 10 mm. Because absorption contrast is often low in fossils, phase contrast can reveal much more in structures.

The ESRF (European Synchrotron Radiation Facility) is the most intense source of synchrotron-generated light, producing X-rays 100 billion times brighter than the X-rays used in hospitals. These X-rays, endowed with exceptional properties, are produced by the high energy electrons that race around the storage ring, a circular tunnel measuring 844 metres in circumference. Thanks to the brilliance and quality of its X-rays, the ESRF functions like a "super-microscope" which "films" the position and motion of atoms in condensed and living matter, and reveals the structure of matter in all its aspects. It provides many opportunities for scientists in the exploration of materials and living matter in many fields.

Fig. 6.1. Photo of the ESRF on the left and organization of the site on the right.

Processing of Raw Data. Radiographs were processed using in-house tools developed at the ESRF (European Synchrotron Radiation Facility), Grenoble (France). They were corrected by flatfield and darkfield reducing ring artefacts. An average of the processed radiographs was computed to obtain a correction map for ring artefacts. The volumes were then reconstructed using a filtered back-projection algorithm. Sample movements were measured and corrected during the tomographic reconstruction. After the reconstruction, the remaining ring artifacts were corrected slice by slice. The final slices were converted into stacks of 16-bit TIFF files for the 3D processing.

3D processing. For the construction of the 3D model was used the commercially available Amira imaging software. The fused clusters were analyzed with that software and all the possible single elements were extracted from them with a process called *segmentation.* Although the clusters were very compacted, all the 15 elements composing the original apparatus were collected almost complete. I made the 3D processing in the Goudemand laboratory at the ENS de Lyon; it was a beautiful period during which I learnt a lot about conodont topic. The 3D processing was not so easy for the stiffness encountered in the segmentation of the clusters related to the high fusion of the single elements, but at the end I managed to extract all the information I needed.

The clusters analyzed were 6 out of 9. For two of them, P9A-3 (fig. 7.3 and 7.4) and P9A-2 (fig. 7.1 and 7.2), was possible to extract all the single elements, instead in the other four, F1 (fig. 7.7 and 7.8), F4-A (fig. 7.9), P9A-5 (fig. 7.10

and 7.11), P9A-7 (fig. 7.5 and 7.6), for the intense grade of fusion, was possible to extract only some elements. Hence, the relative position of these elements can be used to obtain the composition of the complete apparatus.

7. Cluster analysis

In the following, I present all the information I got from the segmentation of the clusters.

P9A-2. In this cluster, there are the right and the left elements for all the S elements, instead is preserved only the right M elements. The P elements are not present (apart for something that could be a P_2 element). The S_0 element is deformed and broken into pieces but its position is fairly well distinguishable. The elements on the right side are moved towards the posterior part compared to the left elements; this means that, during the deposition, the apparatus were subjected to some movement. The cusps of the S_4 and S_3 elements are aligned, instead the cusp of the S_2 elements is orientated more caudally and its largest denticle is sub-parallel to the cusps of the S_3 and S_4. The curvature of the S_1 element seems to follow the curvature of the S_2. The position of the M element relative to the S elements (especially S_3 and S_4) is the one expected from this kind of apparatus.

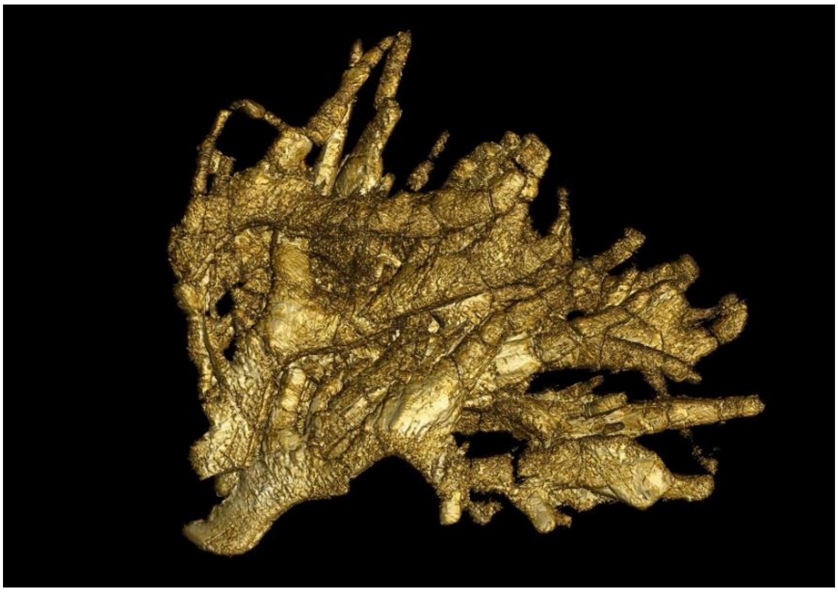

Fig. 7.1. Cluster P9A-2 before segmentation, sinistral view.

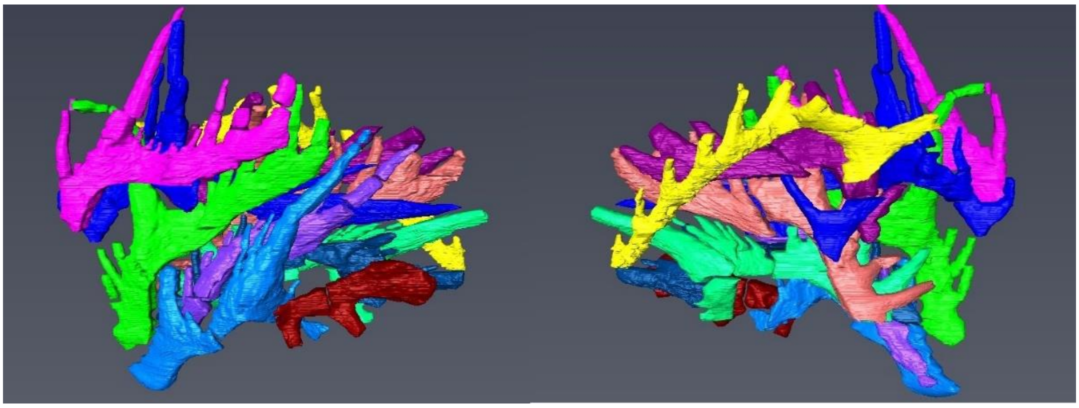

Fig. 7.2. Sinistral and dextral views of the cluster P9A-2 after segmentation. Elements present: M (yellow), S_4 (pink and purple), S_3 (green and light orange), S_2 (aqua and light blue), S_1 (light purple and night blue), S_0 (blue), P_2 (brown).

P9A-3. In this cluster all the ramiforms elements are preserved, from the M to the S_0. There is also a part that could be a P_2 element. The S_0 is the most deformed and broken for the very hard compaction. The elements on the right side are in a lower position than the elements on the left side. The S_3 and S_4 elements of both sides are very attached to each other and this confirm the fact that probably they were located close and sub-parallel to one another in the apparatus and worked together within the living animal. Having both the M elements is very important because we are able to measure their relative position with the S elements and so to reconstruct the apparatus in a better way. It's clear that the elements in this cluster are very long compared to the elements of the other clusters.

Fig. 7.3. Cluster P9A-3 before segmentation.

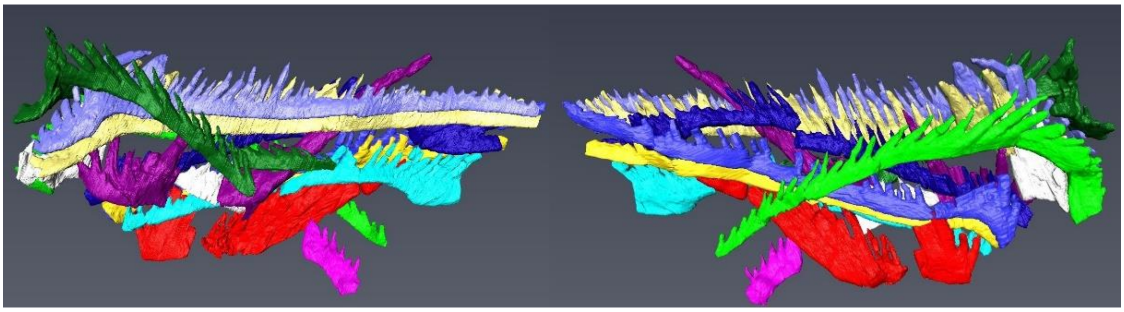

Fig. 7.4. Sinistral and dextral views of the cluster P9A-3 after segmentation. Elements present: M (dark and light green), S_4 (night blue and blue), S_3 (yellow and light yellow), S_2 (red and purple), S_1 (dark blue and light blue), S_0 (white), P_2 (pink).

P9A-7. The element extracted here are the S_2, S_1 and P_2 of both side and a part of the S_0. This cluster is important because there are the P_2 elements preserved, so it is thus possible to put them in a precise anatomical position. I realize that the position of these elements is particular and characterized by the tips of the denticles pointing towards the posterior part of the apparatus.

Fig. 7.5. Sinistral and dextral views of cluster P9A-7 before segmentation.

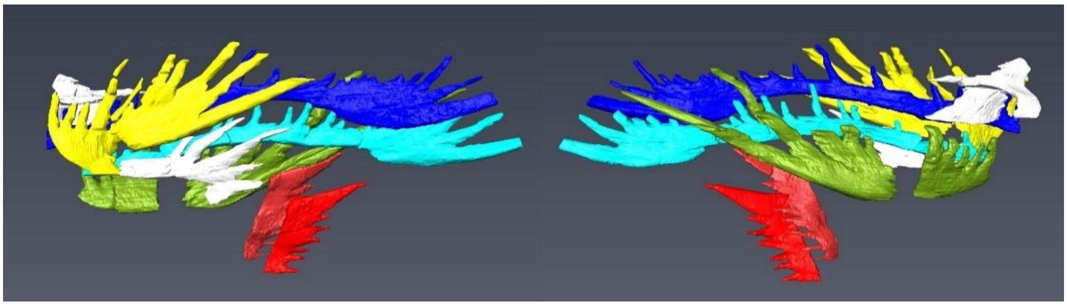

Fig. 7.6. Sinistral and dextral views of the cluster P9A-7 after segmentation. Elements present: S_2 (yellow and green), S_1 (blue and light blue), S_0 (white), P_2 (red).

F1. From this cluster it was possible to extract the M, S_4 and S_2 elements of both sides and only partially the S_0 and the S_1 elements. It is possible to see that the S_2 elements are in a lower position compared to all the other elements. Considering that is evident also in other clusters, I interpret this position as peculiar for the *Mockina slovakensis* apparatus. Another peculiarity is the position of the M elements and the anterior part of the S_0: the M are close to the S_0 and above the other S elements; I thus suppose that this is a particular position of this elements in order to perform a better seizing action, the so-called *pinching position.*

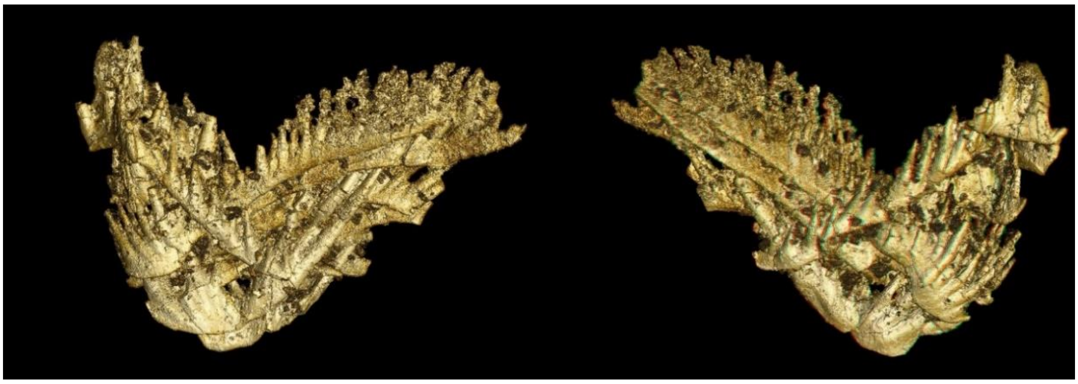

Fig. 7.7. Cluster F1 before segmentation.

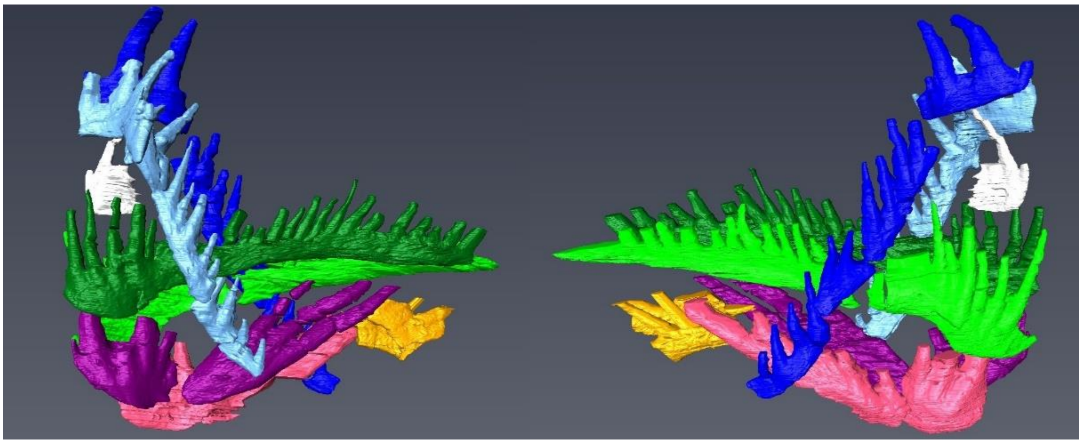

Fig. 7.8. Sinistral and dextral views of the cluster F1 after segmentation. Elements present: M (blu and light blue), S_4 (dark and light green), S_2 (purple and pink), posterior process of S_1 (yellow), anterior process of S_1 (white).

F4-A. We used this cluster to extract the P_1 elements. They are not in a particular position, maybe closer to the S elements than the apparatus of Lower Triassic *Novispathodus*.

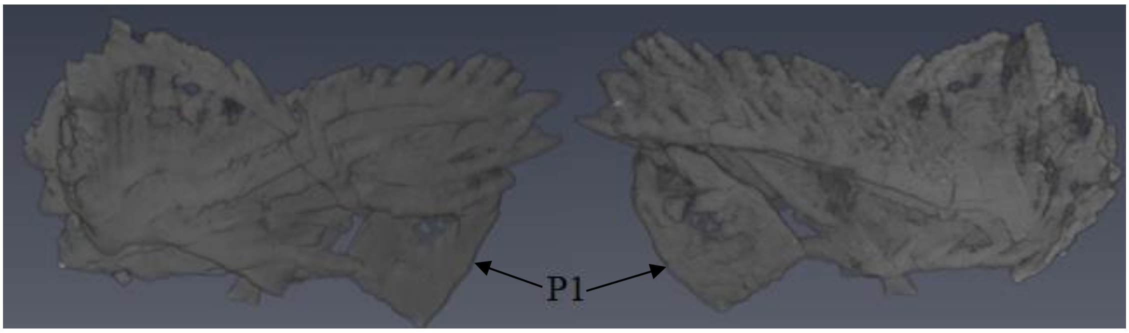

Fig. 7.9. Sinistral and dextral views of cluster F4-A.

P9A-5. From this cluster only the M elements were extracted. However, the position of these M elements is very particular and it is expressed only in this cluster. On the left side it is possible to see the S_4, S_3 and S_2 elements and on the right side the S_4 or S_3 and the S_2 elements. The elements on the right side are moved a little towards the posterior part of the other elements. The M elements are perpendicular to the other element and this could represent a particular position of the apparatus when the animal was grasping food. Considering the configuration of the M elements, we put the S “module” with a certain inclination from a plane parallel to the horizontal to let the apparatus reach this configuration during its motion.

Fig. 7.10. Cluster P9A-5 before segmentation.

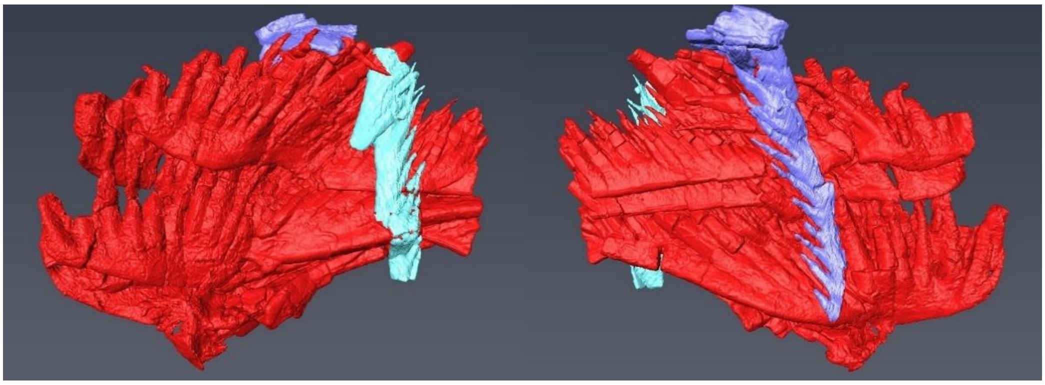

Fig. 7.11. Sinistral and dextral views of the cluster P9A-5 after segmentation. M (purple and light blue), S elements not distinguishable (red).

All this information was fundamental for the achievement of a great functional model of the *Mockina slovakensis* apparatus.

8. Results

For the reconstruction of the *Mockina slovakensis* apparatus, I used the information extrapolated from the clusters of the Dolomia di Forni and the results of the work of Goudemand et al. (2011). In particular, using the position of all the elements of the clusters, especially the ramiforms. I tried to adjust the positions of the elements in the reconstruction made for *Novispathodus* to see if was possible to achieve a similar arrangement (fig. 8.1 and fig. 8.2).

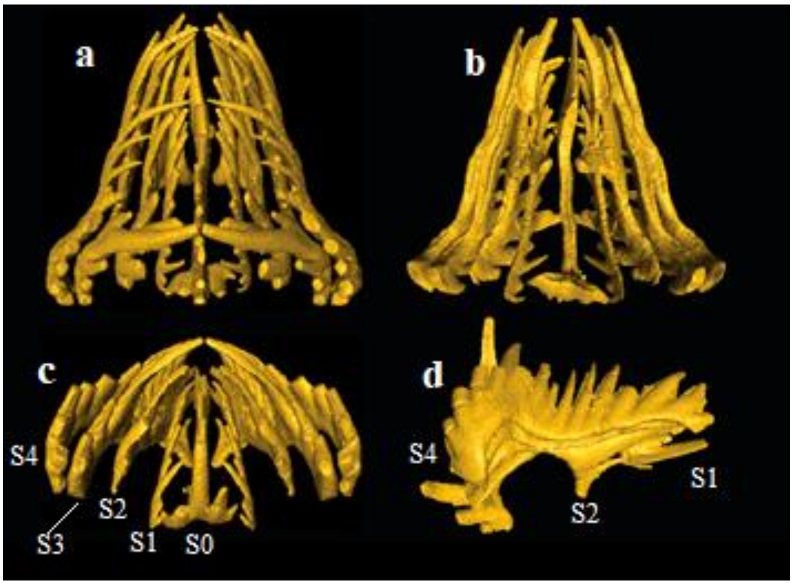

Fig. 8.1. Closed arrangement of S elements of the Early Triassic conodont *Novispathodus.* (a) dorsal, (b) ventral, (c) rostral, (d) sinistral views. From Goudemand et al. 2011.

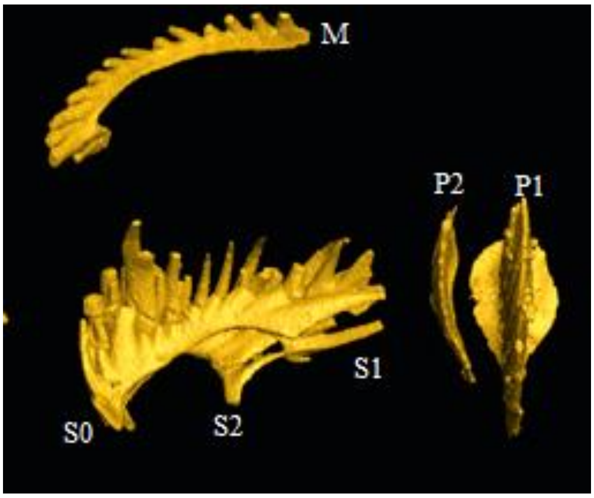

Fig. 8.2. Sinistral view of the reconstructed apparatus of *Novispathodus.* From Goudemand et al. 2011.

The general arrangement of the conodont apparatus was confirmed. The S_0 is in a central position and lying on the axis of bilateral symmetry, next to it there are the other ramiforms elements in pairs, S_1 S_2 S_3 S_4, from the inner to the outer side. Above them and in a rostral position there are the two M elements. Caudally compared to the S elements there are the P_2 and P_1 (fig. 8.3).

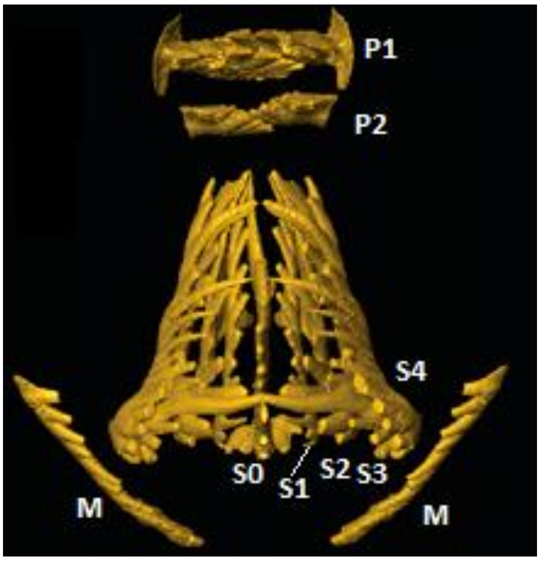

Fig. 8.3. General architecture of a conodonts apparatus.

The S_3 and S_4, in the clusters, are always attached to each other and it is very difficult to find them isolated. This suggests that they were located close and subparallel to one another and had probably a common motion in the living animals. I supposed for them, and of course for also the other S elements (S_1 and S_2), an inclined position of about 20/30 degrees towards the anterior part of the apparatus to a plane parallel to the surface (fig. 8.4D).

The element S_2 is more ventrally than the other elements in order to respect their position in the analyzed clusters. Compared to the other apparatuses, their position is not so much different; the cusp of the S2 is still subparallel to the posterior process of the S_3 and S_4 elements and the largest denticle of its anterior part is aligned with the cusp of the S_3 and S_4.

The S_1 are located near to the S_0 and with the cusps above the P_2 according to the position of these elements in the cluster P9A-7 (fig. 7.5). The curvature of the S_1

follows the one of the S_0 and, for their shape and position, it can be presumed that they should have worked together in the living animal. Per definition, the tip of the cusp of the S_1 always points posteriorly. The S_0 elements was located a little more rostrally than the other elements (fig. 8.4D).

Hence, considering all these position of the S elements a compact arrangement in which all denticle tips end up close to midplane was suggested (fig. 8.4). I consider this spatial configuration as the maximal closing position of the grasping S “module” of the apparatus.

For the position of the P_1 elements I use the information of the cluster F4-A (fig. 7.9) and I supposed for them a common position assessed for most of the conodonts apparatuses. They are in the most caudal position, perpendicular to the S elements and with the tips of the denticles pointing inward.

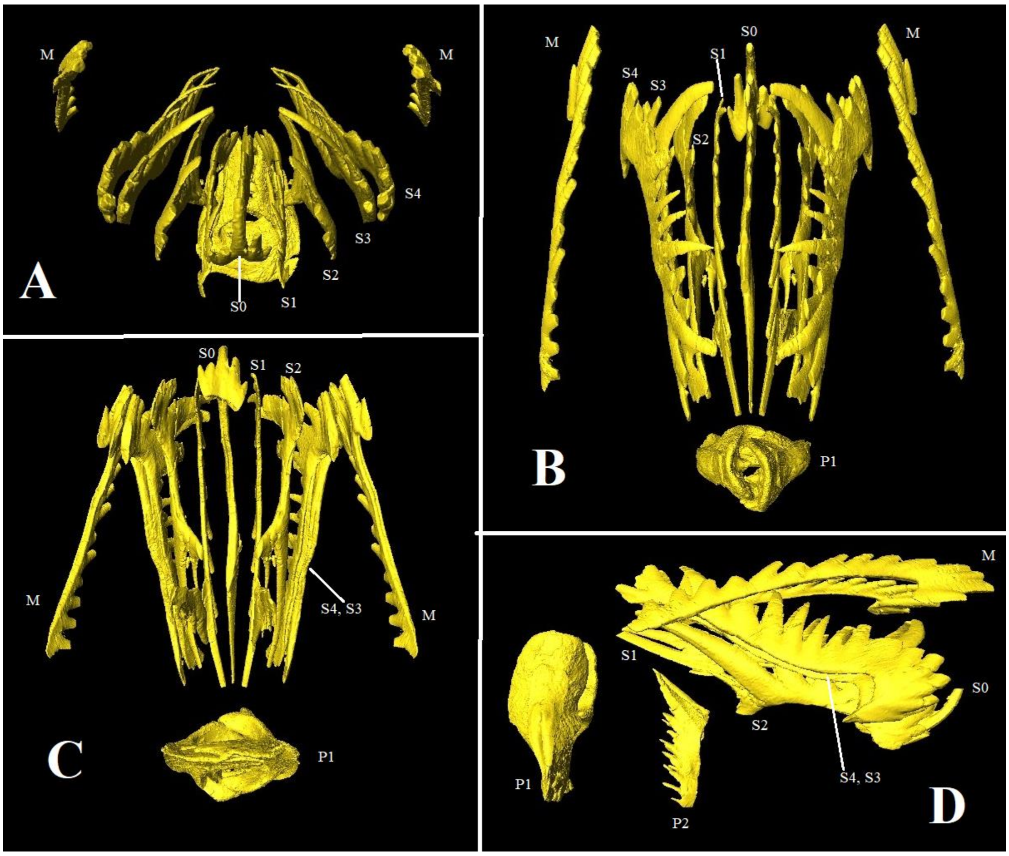

Fig. 8.4. General architecture of *Mockina slovakensis* apparatus. (A) rostral, (B) dorsal, (C) ventral, (D) dextral views.

Considering the arrangement of *Novispathodus* (Goudemand et al., 2011), the position of the P_2 elements is the same as the P_1, but not for *Mockina slovakensis*. I put them parallel to the S elements, more or less under the posterior part of the S elements and with the tips of the denticles pointing towards the P_1. Of course, the distance between P_1 and P_2 is greater than in *Novispathodus* because of the different orientation of the elements. I propose this configuration according to their position in the cluster P9A-7 (fig. 8.5).

Fig. 8.5. Comparison between the positions of the P_2 elements of *Mockina slovakensis* in the cluster P9a-7 (left) and in the reconstructed apparatus (right).

Also the position of the M elements differs a little from previous arrangements. Considering the relative position extrapolated from the clusters I assumed that the M were in a rostral position, inclined with the cusps pointing more dorsally and the posterior part more ventrally than in *Novispathodus* arrangement (fig. 8.6).

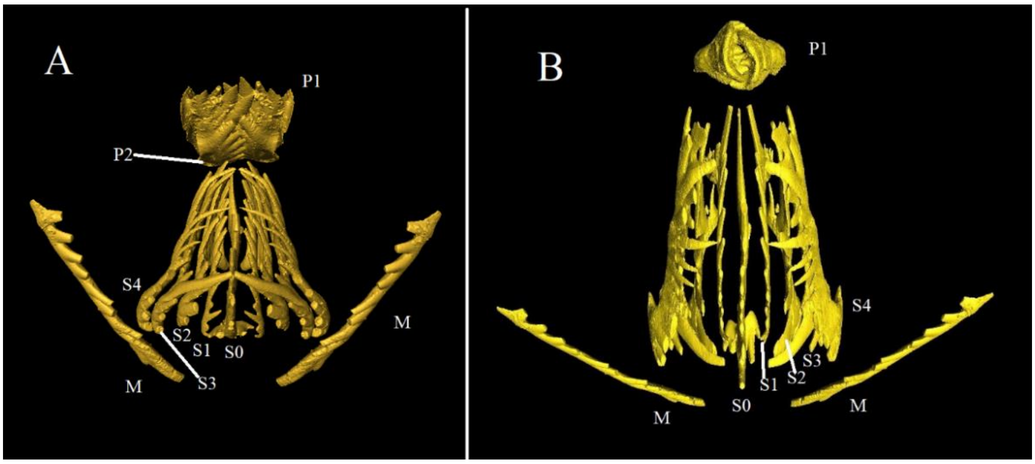

Fig. 8.6. Dorsal view of the reconstructed apparatus of Early Triassic *Novispathodus* (A) and Late Triassic *Mockina slovakensis* (B).

As already said, for the reconstruction of the apparatus I used the scanned elements of *Novispathodus* because the lack of single elements of *Mockina slovakensis* to scan, so I prefer to use those elements to perform a better work. *Novispathodus* was an Early Triassic conodont and I could use its elements for my reconstruction because they are very similar to the elements of *M. slovakensis* even if it is was a Late Triassic conodont. The shapes of their elements are so similar because they belong to the same family *Gondolellidea.*

However, after a first reconstruction with outstanding results, I saw that the elements of the apparatus did not fit too much with the shape of the elements in the clusters, particularly in the length. Thus, I tried to stretch the elements and with little adjustments in the position of the elements, I arranged an apparatus very similar to the first and, in some detail, better than the previous one. With longer elements is necessary an arrangement a little bigger to keep them from touching each other and to allow the movement needed, but in this case the relative position of all the elements seems to recall better the position highlighted in the clusters.

For the movement of the apparatus I made a peculiar research in order to use all the possible information regarding this field of work. However, the principal base is, again, the study made for *Novispathodus*. A video with the suggested apparatus movement is in the attached CD, in rostral, dextral, sinistral and ventral views.

The close position of the apparatus is when the M elements are in their most rostral position, in front of all the other elements and with the cusps pointing towards the center; the S elements are completed retracted towards the P elements, the posterior parts of the elements are above the P_2 and the tips of the denticles converge towards the center (fig. 8.7).

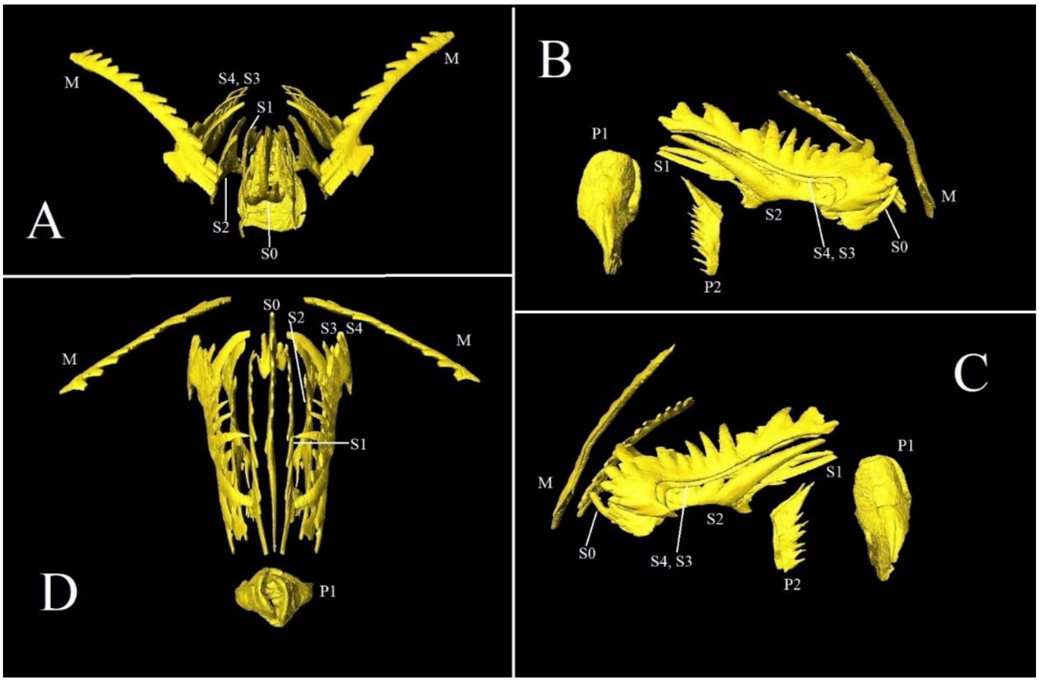

Fig. 8.7. Closed position of the reconstructed apparatus of *Mockina slovakensis.* (A) Rostral, (B) dextral, (C) sinistral, (D) dorsal views.

The opening movement is composed by a caudal retraction, mostly translation, of the M elements and by a rostral displacement of the S elements until the tips of the denticles are pointed towards the front of the apparatus. In order to perform a good hunting, the S_{3-4} and the S_{0-1} elements probably had an additional motion. For the S_{3-4}, considering the shape of their denticles, it was essentially an opening/closing pivot motion around an axis parallel to their posterior part as shown in the movies (see Appendix); in this case the animal could be able to catch the prey in front of it. The curvature of the denticles of the S_{0-1} elements and the shape of the cusp of S_0 suggest both a rotation and an arched antero-posterior translation (see movies in Appendix).

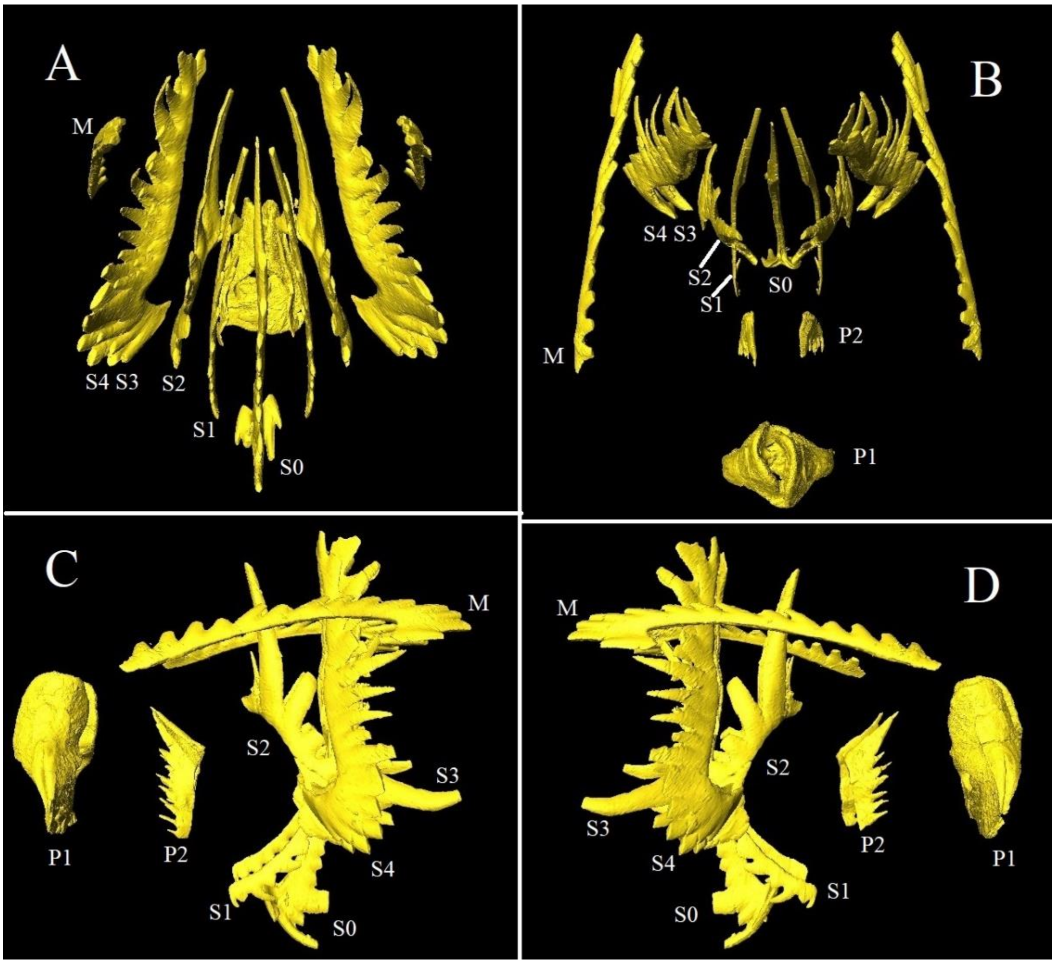

Fig. 8.8. Reconstructed apparatus of *Mockina slovakensis* in opened position. (A) Rostral, (B) dorsal, (C) dextral, (D) sinistral views.

As highlighted by cluster F1 (Fig. 7.7 and 7.8), it was possible that the S_0 and M occupied a particular position that provided an efficient pinching and seizing function. To obtain this position, the rotation of the S_{0-1} should have been synchronized with the closure of the M; at the end of the movement, the cusps of the M and of the S_0 elements converged in the same point (fig. 8.9, 8.10 and movies in Appendix).

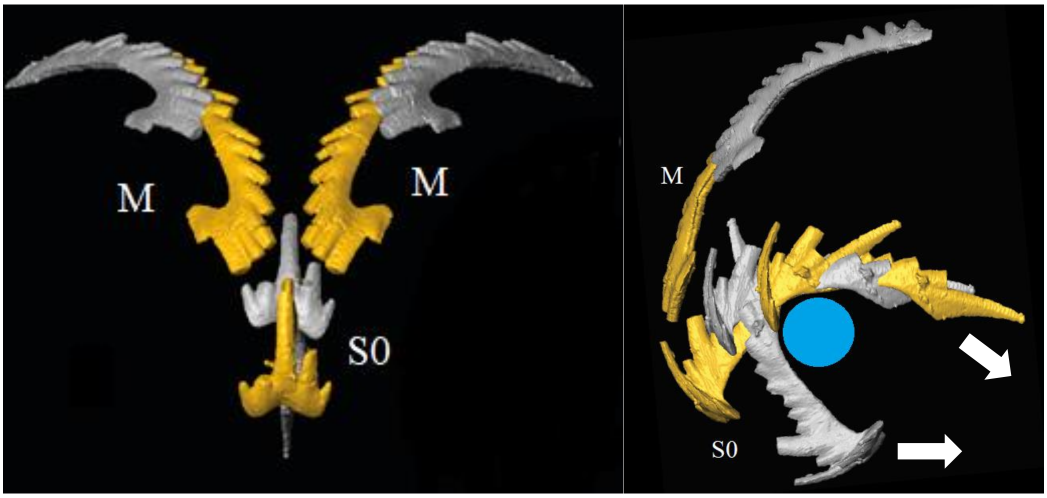

Fig. 8.9. Hypothetical synchronized pinching movement of the M and S_0 elements. Left, rostral view; right, sinistral view. Blue circle: supposed cartilage that should have permitted this movement.

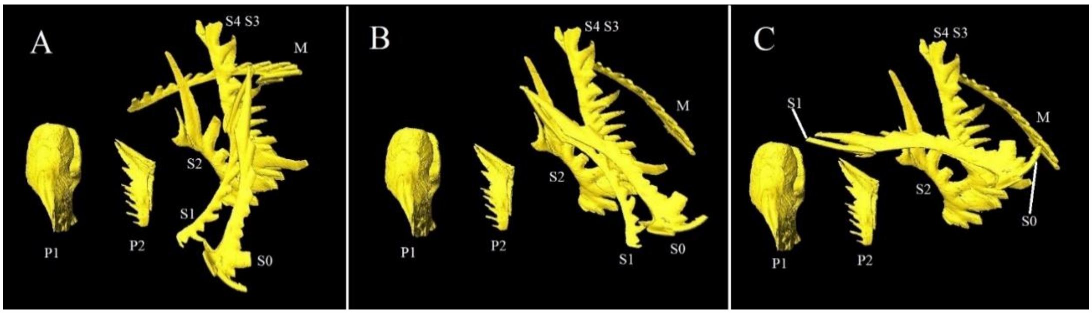

Fig. 8.10. Pinching movement of *Mockina slovakensis apparatus.* (A) Start point, opened position; (B) pinching position; (C) end point, closed position.

The subsequent dorso-caudal retraction of the S_{0-1} elements would have ripped off the tissues of prey and brought them to the P_{1-2} elements. Then, the closure of the other S elements would have helped to put back the food. The function of the P elements was, probably, to crumble the food brought back by the S elements.

I made some movies to show the movement of the complete apparatus. I also tried to make a video in which I combined all the independent movements in order to promote a more complex general movement that the animal could have had in its life. Here I present two movie (Movie1 and Movie2 that you can find in the attached CD-ROM).

In Movie1 are highlighted the independent movements of some elements on which I base my reconstruction. In particular, the opening/closing pivot motion of the S_3 and S_4 elements and the pinching movement of the M and the S_{0-1} elements. They are shown, respectively, in rostral, dextral, sinistral and ventral views.

Otherwise, in Movie2 I have combined the movements of all the elements (except the P_1 and P_2 elements) to proposed a functional motion of the entire apparatus that could have occurred in the living conodonts. The starting point is the closed position of the apparatus and so it is the final one. We present it in the same views of the previous movie.

This reconstruction fit the assumption of a pulley-like system with protractor and retractor muscles that would have moved the elements about a ventral supporting element cylinder-shaped or U-shaped made of an unknown material but most probably of cartilaginous nature as assessed by Goudemand et al. (2011).

It must be remembered that this is the first work which deals with the reconstruction of *Mockina slovakensis* apparatus, so I do not have too many constrains on which base my work.

9. Conclusions

The present study has allowed me to put other constraints in the conodonts apparatus reconstruction. Considering the relative positions measured in the analyzed clusters of *Mockina slovakensis* I confirm previous studies that deals with this topic. In particular, the general arrangement of the conodonts oral skeleton was confirmed and some peculiar positions within the apparatus were found also in our cluster.

First, the pinching position on which the M and S_0 elements converged towards a common point on the frontal part of the apparatus in order to catch and cut the prey; this let me to say that, probably, conodont animals were predators. Moreover, I present a new position for the S_2 elements, which lie more ventrally than the other S elements, and for the S_0 element, which is moved more rostrally compared to the other S elements. The complete S array is inclined of 20/30 degrees towards the frontal part of the apparatus and this configuration is, for me, more suitable for the conodont animal because it permitted a faster opening of the apparatus. Furthermore, I put the P_2 elements under the posterior process of the S elements and, together with the P_1, they are close to the S array; this position make the apparatus more compact and so it could have had a very functional motion. In the end, I assign a new position to the M elements and, therefore, their movement become essentially translational that could be easier to explain.

With this kind of arrangement I support the assumption of the presence of a lingual cartilage that may have moved the entire apparatus together with some pairs of antagonistic muscles. I proposed a motion of the entire conodont apparatus that can be used in future works to improve the knowledge about this area of research.

Furthermore, this study shows the importance of synchrotron microtomography as a method to analyze fused clusters of conodonts elements and to extract very useful information. The application of this technology, together with other analysis, might help shedding light to many controversies related not only in the reconstruction of conodonts oral apparatus, but also in other aspects of their history.

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APPENDIX

Attached in the CD there are the poster and the abstract submitted at the International Conodont Symposium (ICOS4_2017) which took place in Valencia, Spain. There is also the program of the conference and the two movies showing the function of the apparatus (Movie1 and Movie2).