

Evolutionary convergence in conodonts revealed by Synchrotron-based Tomographic Microscopy

Michele Mazza and Carlos Martínez-Pérez

ABSTRACT

The conodont fossil record is well known for its morphological diversity, but the iterative evolution that characterizes conodonts often avoids providing reliable phylogenetic frameworks among species, making unclear if the diagnostic characters of the taxa are indicative of common ancestry or evolutionary convergences. To distinguish homologies from analogies in conodonts, the most reliable method is by studying the ontogenetic development of the single taxa. Until now, the reconstruction of the ontogenetic stages was based on the study of separate individuals at different age from single populations. Nevertheless, the only unequivocal way to describe the ontogenesis of a conodont is to describe it from a single specimen. We achieve this objective by using Synchrotron Radiation X-ray Tomographic Microscopy applied to P₁ elements of species belonging to the Upper Triassic genera *Carnepigondolella* and *Epigondolella*. Our analysis provided internal tomographic information for the reconstruction of the conodont ontogenesis. We focused our study on the posterior platform, where an accessorial node develops behind the cusp. This node resulted in an autapomorphy of the genus *Epigondolella* from previous cladistic analyses and, thus, a diagnostic character for the elaboration of phylogenetic models. The microtomographies showed that this character is instead an evolutionary convergence. These results suggest the revision of the Late Triassic conodont phylogenetic relationships, showing that ontogenesis can be used as a criterion for discriminating homology from homoplasy in conodonts, and demonstrating that Synchrotron Radiation X-ray Tomographic Microscopy is a powerful and reliable tool to investigate conodont ontogenesis, evolutionary processes and phylogenetic relationships.

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INTRODUCTION

The conodont fossil record constitutes a rich archive of evolutionary history, in terms of its temporal extent, from Cambrian to Triassic, and its completeness (Foote and Sepkoski, 1999). Functional analyses have advanced to an extent where conodont taxonomy, based on dental morphology, can be interpreted in terms of feeding ecology (Jones et al., 2012a, 2012b; Purnell and Jones, 2012; Martínez-Pérez et al., 2014a, 2014b, 2016; Murdok et al., 2014). This opens the possibility of interpreting the conodont fossil record as a detailed and comparatively complete record of the evolution of feeding ecology through much of the Phanerozoic, including across some of the most dramatic ecological and environmental crises that have impacted animal life, such as the end-Ordovician, Frasnian-Fammenian, Hangenberg, and Permian-Triassic mass extinction events. Realizing this vision requires a coherent phylogeny for conodonts on which to trace the evolution of feeding ecology. To this end, attempts have been made to establish a phylogeny for conodonts using cladistics (Donoghue, 2001; Zhang and Barnes, 2004; Wickström and Donoghue, 2005; Donoghue et al., 2008; Mazza et al., 2012b), but this aim is challenged by widespread morphological convergence in disparate conodont lineages (Sweet, 1988; Dzik, 2005). Here, we explore the utility of ontogenetic evidence, in the form of growth arrest lines that record the morphogenesis of conodont elements, showing that they can be used to discriminate between homologous and convergent adult morphologies. Until now, the reconstruction of the different ontogenetic stages was based on the study of isolated specimens from single populations, but several problems normally arise in order to distinguish between juvenile specimens of related species that did not develop their characteristic morphologies until more developed stages. Hence, the only unequivocal way to describe the ontogenesis is by describing it from a single element. A first step forward in this direction has recently been made by Mazza and Martínez-Pérez (2015), who used Synchrotron data to test and verify the reconstructions of 10 ontogenetic series of Carnian-Norian (Late Triassic) platform conodont species. In this study a higher level of detail is reached in the use of the X-Ray Tomography Microscopy, reconstructing the ontogenetic mechanisms of a single morphological character in order to unravel homology from homoplasy in conodonts.

MATERIAL AND CASE STUDY

The present work is focused on the P_1 elements of Late Triassic gondolellid conodonts from the Neotethyan Province. Our study is based on seven phylogenetically related species belonging to the genera *Carnepigondolella* (*C. pseudodiebeli*) and *Epigondolella* (*E. miettoi*, *E. quadrata*, *E. violovi*, *E. rigoi*, *E. triangularis*, and *E. uniformis*), ranging from the Upper Carnian (Tuvanian) to the Lower Norian (Lacian) (Table 1). The studied conodonts have Colour Alteration Index (CAI) values of 1.5 or 7 (Epstein et al., 1977). All the specimens are stored at the Dipartimento di Scienze della Terra “A. Desio” of the Università degli Studi di Milano (see Table 1 for the repository numbers).

The material comes entirely from the Upper Triassic (Upper Carnian-Rhaetian) section of Pizzo Mondello (western Sicily, Italy), GSSP candidate for the Norian stage (Muttoni et al., 2001, 2004; Nicora et al., 2007; Balini et al., 2011, 2012, 2015; Mazza et al., 2012a, 2012b; Mazza and Krystyn, 2015).

The *Carnepigondolella*-*Epigondolella* lineage constitutes a worthy case of study, because it is the only conodont phylogenetic lineage encompassing the Carnian/Norian boundary and evolving into the last Middle Norian and Rhaetian taxa (i.e., genera *Mockina*, *Parvigondolella*, and *Misikella*), which are the last conodont representatives (Martínez-Pérez et al., 2014c). In addition, previous innovative studies on this lineage (Mazza et al., 2012b) provide a solid evolutionary framework to be tested. The phylogenetic relationships of the species composing this lineage were first investigated using numerical cladistic analyses (Mazza et al., 2012b; Figure 1). In these analyses, some morphological characters of the posterior platform resulted in autapomorphies that defined the most derived taxa of the *Epigondolella* clade. These were the development of denticles on the posterior platform margin together with the enlargement of the posterior platform, and the occurrence of a large carinal node behind the cusp. In addition, the platform development (ontogenesis) of some carnepigondolellids and epigondolellids, considered also in the present study, were recently described by Mazza and Martínez-Pérez (2015), using both growth series and X-ray tomographies. This study also provided the tools to give a specific taxonomic identity to the most juvenile conodont forms. Nevertheless, those results produced some discrepancies between the new conodont ranges that emerged with the classification of the juvenile specimens and the previous cladistic phylogenetic

TABLE 1. List of the conodonts scanned at the X-ray Synchrotron Microscopy for analyses of the internal structure. Species for which more than one specimen was scanned are provided with a capital letter that, associated with the species name, identify the specimen in the text and in figures. All the specimens are from the Pizzo Mondello section (western Sicily, Italy).

Species	<i>Epigondolella vialovi</i>	<i>Epigondolella quadrata</i>	<i>Epigondolella quadrata</i>	<i>Epigondolella quadrata</i>
Author and year	(Buri, 1989)	Orchard, 1991	Orchard, 1991	Orchard, 1991
Specimen		A	B	C
Range of the species	Upper Carnian - Lower Norian	Upper Carnian - Middle Norian	Upper Carnian - Middle Norian	Upper Carnian - Middle Norian
Sample	NA30	NA60	NA60	NA66
Age of the sample	Uppermost Tuvalian (Upper Carnian)	Upper Lacion (Lower Norian)	Upper Lacion (Lower Norian)	Upper Lacion (Lower Norian)
Repository number	Micro-Unimi no. 2010	Micro-Unimi no. 2011	Micro-Unimi no. 2012	Micro-Unimi no. 2017
CAI	1.5	7	7	1.5
Species	<i>Epigondolella rigoi</i>	<i>Epigondolella rigoi</i>	<i>Epigondolella uniformis</i>	<i>Epigondolella triangularis</i>
Author and year	Noyan and Kozur, 2007	Noyan and Kozur, 2007	(Orchard, 1991)	(Budurov, 1972)
Specimen	A	B		
Range of the species	Lower - Middle Norian	Lower - Middle Norian	Lower - Middle Norian	Lower Norian
Sample	NA61	NA60	NA42	NA44a
Age of the sample	Upper Lacion (Lower Norian)	Upper Lacion (Lower Norian)	Lower Lacion (Lower Norian)	Lower Lacion (Lower Norian)
Repository number	Micro-Unimi no. 2018	Micro-Unimi no. 2014	Micro-Unimi no. 2013	Micro-Unimi no. 2015
CAI	7	1.5	1.5	1.5

model (Figure 1). In particular, the phylogenetic position of *E. vialovi*, *E. quadrata*, *E. rigoi*, *E. uniformis*, and *E. triangularis* became uncertain, because their stratigraphic ranges are now prolonged downwards in the Upper Carnian and not limited to the Lower Norian as before, questioning their previous phylogenetic relationships (Mazza and Martínez-Pérez, 2015, figure 1). It is evident that convergences between species were misinterpreted as homologies with phylogenetic value. In particular, the accessorial node behind the cusp that resulted in an autapomorphy in Mazza et al. (2012b) and defined the *Epigondolella* clade, seemed to be developed at different ontogenetic stages in the epigondolellids (see Mazza and Martínez-Pérez, 2015). Thus, in an attempt to discriminate between homology and homoplasy, we undertook a detailed analysis of the morphogenesis of what seems to be a key character to shed light on the evolutionary scenario of the Late Carnian/Norian conodonts.

METHODS

We characterise the inner growth patterns of the different species using the synchrotron radiation X-Ray Tomography Microscope at the X02DA TOMCAT beamline of the Swiss Light Source, Paul Scherrer Institute (Villigen, Switzerland), a technique that allows non-invasive, high resolution, quantitative and volumetric x-ray tomographies on diverse samples. The specimens were scanned using a 20x objective, with exposure time between 83 to 270 ms at 10-14 keV, acquiring 1501 projections equiangularly over 180 degrees. Isotropic voxel dimensions are 0.325 μm . Projections were post-processed and rearranged into flat- and dark-field-corrected sinograms, and reconstruction was performed on a 60-core Linux PC farm using a Fourier transform routine and a regridding procedure (Marone and Stampanoni, 2012). The reconstructed files were analyzed and manipulated using AVIZO v.8 (VSG), allowing us to extract accurate 3D virtual models, and virtual thin sections that were created using the voltex module, which simulates the casting of light rays from preset sources

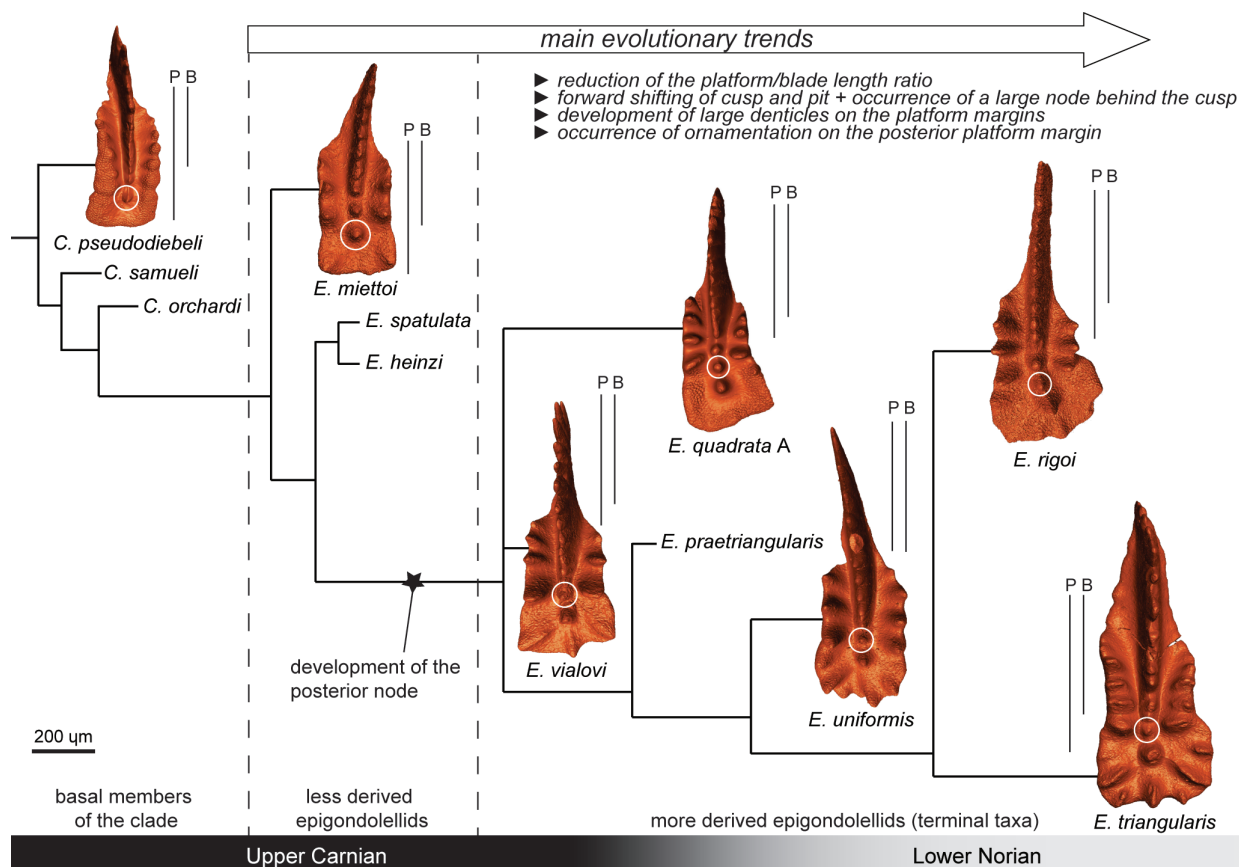


FIGURE 1. Cladogram representing the *Epigondolella* clade of Mazza et al. (2012b), illustrating the phylogenetic relationships between the Upper Carnian-Lower Norian (Upper Triassic) carnepigondolellids and epigondolellids and their main evolutionary trends. Only the species analysed in this work are figured. The specimens of *E. vialovi*, *E. quadrata*, *E. uniformis*, and *E. triangularis* are from Mazza and Martínez-Pérez (2015). Vertical bars beside the specimens indicate the platform (P)/blade (B) length ratio; white circles mark the cusp. All the specimens are at the same scale.

through a volume of data. This technique permitted us to generate multiple sections of the analyzed specimens in all the desired directions, providing a complete control on the area of the conodont that we want to investigate (Figure 2). Horizontal sections of the entire element of the epigondolellids considered in this study were already employed in Mazza and Martínez-Pérez (2015) to verify the reliability of the reconstructed conodont ontogenetic series. The excellent correspondence between the juvenile stages outlined by the growth lines in the X-ray sections and juvenile specimens photographed at the SEM used for the growth series, proved the validity of the technique. In this work, we analyze for the first time cross and longitudinal sections perpendicular to the longitudinal axis of the platform and parallel to the platform surface, respectively (Figure 2).

Microtomographic sections were compared with scanning electron microscopy (SEM) photos

of artificially fractured specimens from the same samples in order to demonstrate the degree of detail of the synchrotron analyses (Figure 3). The artificial fractures have been produced across the longitudinal axes of the platforms with a common needle, etched with 0.5% orthophosphoric acid for 2–4 minutes and coated with gold previous to the SEM analysis.

RESULTS

Tomographic images of the conodonts ultrastructure were obtained from all the scanned elements, but with variable levels of detail from specimen to specimen. The best results were obtained on conodonts with CAI value 7 (see Table 1), probably induced by hydrothermal alteration (Rejebian, 1987). These conodonts show the best contrast between the growth lines and the highest number of visible details in the ultrastructure (Fig-

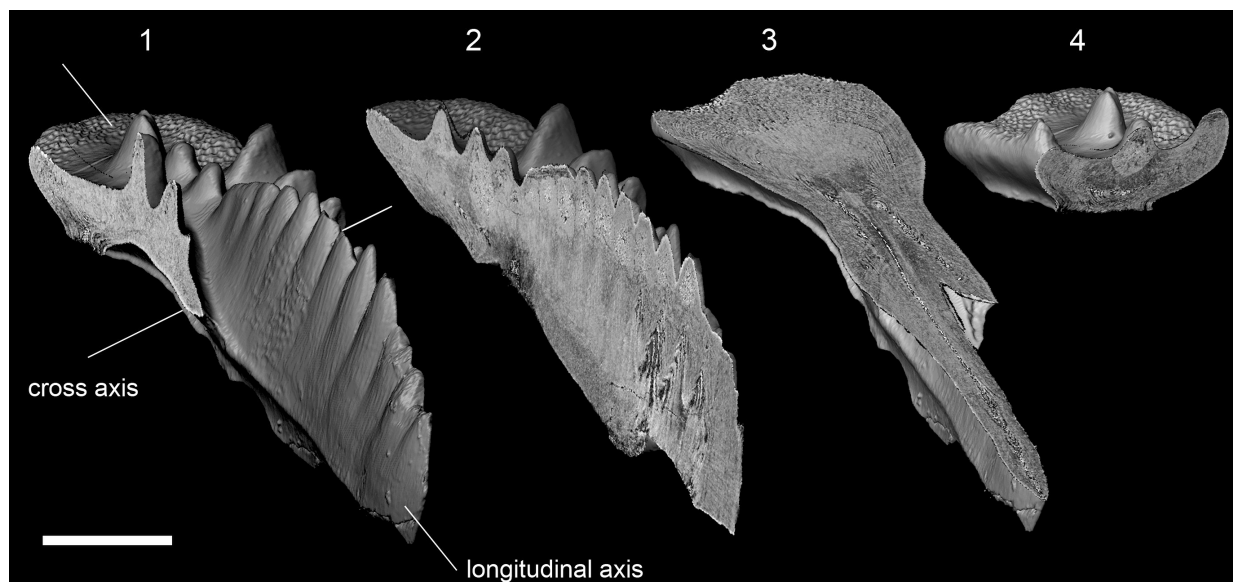


FIGURE 2. X-ray Synchrotron microtomography of *Epigondolella quadrata* specimen A. Three possible sections that can be obtained with the X-ray synchrotron microscopy are shown. 1, 3D model of the specimen; 2, Longitudinal section; 3, Horizontal section; 4, Cross section. Scale bar equals 200 μm .

ure 3.1). No differences of preservation or other sign of alteration were observed on specimens with CAI 1.5 that could affect the X-ray analyses.

Conodont crown tissue is basically constituted by two main components, the hyaline lamellar tissue and the white matter (Donoghue, 1998 and references herein), both clearly recognizable in the tomographic reconstructions. Lamellar tissue is composed by prismatic crystallites organized in growth lines (i.e., lamellae). In the microtomographic sections, these growth lines appear as bright and parallel lines, separated by darker gaps (interlamellar space) of variable thickness (Figure 3). On the other hand, the white matter, a hard tissue that shows a more compact structure than the previous one, is characterized by a dense porous structure that gives to this tissue a typical cancellated appearance (Donoghue, 1998). In the microtomographic sections the white matter is easily distinguishable, being brighter than the lamellar tissue in all the analysed specimens and CAI values, and showing a coarse granulated appearance given by the porosity of the tissue (Figure 3). As shown in the microtomographies, its distribution is limited only to the blade denticles and carinal nodes.

Ontogenesis of the Posterior Node

We focused our X-ray microtomographic analyses on the posterior platform, particularly diagnostic for the terminal taxa of the *Epigondolella* clade (Mazza et al., 2012b; Mazza and Martínez-Pérez,

2015). In *Carnepigondolella pseudodiebeli* and *E. miettoi* the cusp is the last node of the carina but, in the descendant epigondolellids, the cusp shifts forward and a larger carinal node starts developing behind the cusp (Figure 1). This character was interpreted by previous cladistic analyses as an autapomorphy shared by all the most derived epigondolellids (Mazza et al., 2012b). In all the scanned specimens the cusp is always easily distinguishable in longitudinal section due to the massive occurrence of white matter that permeates the entire node from its tip to the basal cavity (Figures 4, 5). Local tomographic sections that longitudinally cuts the cusp and the posterior node of *E. quadrata* show, in all the three analyzed specimens of this species, growth lines developing from the cusp and building a short posterior platform margin (Figure 4.1, 3-4). In the younger growth stages, no carinal nodes occur behind the cusp of *E. quadrata*, as seen in a juvenile specimen of the same species, sampled from an *E. quadrata* monospecific population (Figure 4.2) and illustrated also in the growth series of Mazza and Martínez-Pérez (2015, plate 3, p. 171). The posterior node starts developing only later in age: a series of hypocalcifications, increasing in size with age, may be observed growing from the juvenile posterior platform margin and originating what was previously regarded as a carinal node (Figure 4.4).

In *Epigondolella rigoi*, instead, the supposed direct descendant species of *E. quadrata* (Noyan and Kozur, 2007; Mazza et al., 2012b), the onto-

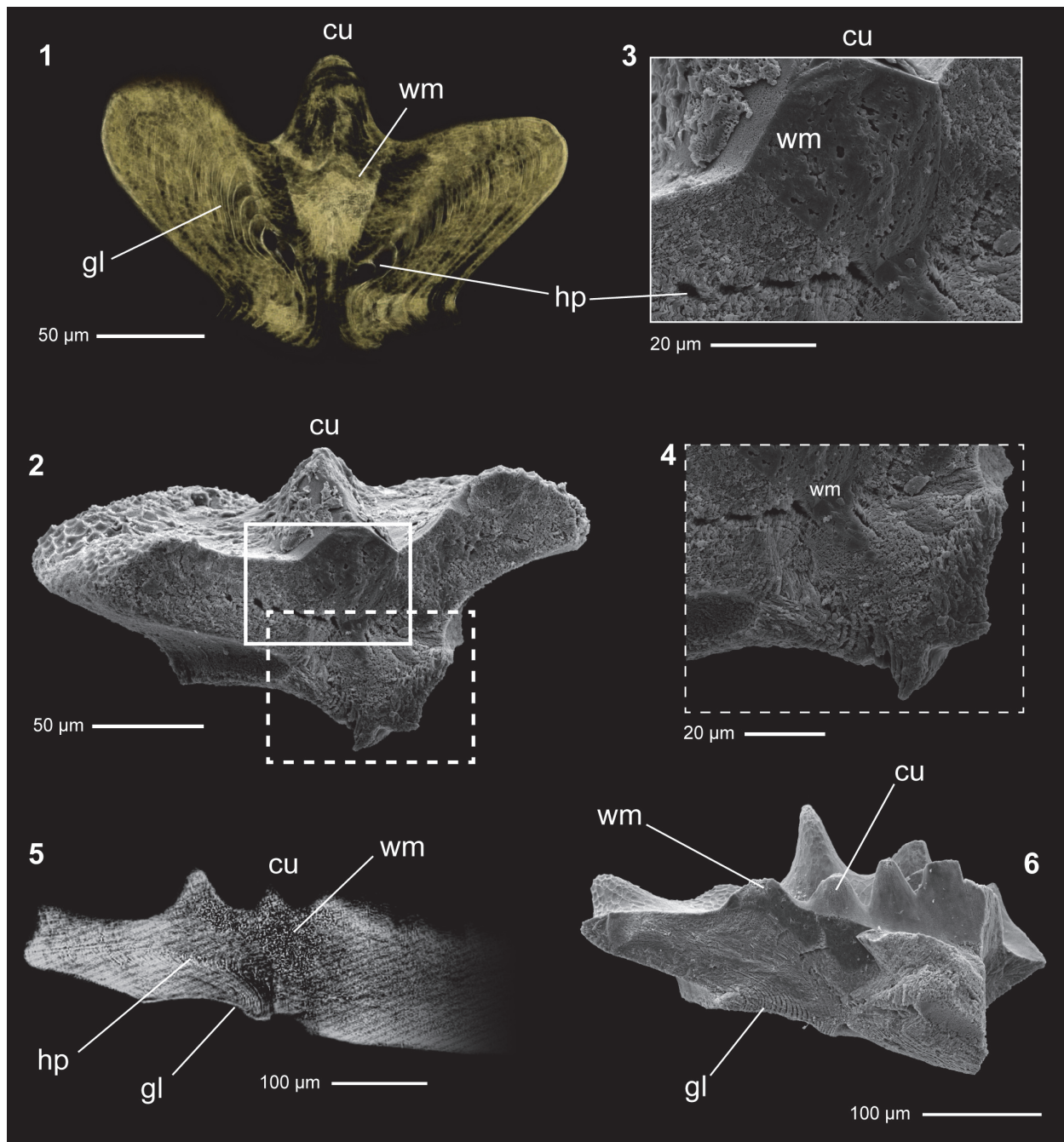


FIGURE 3. X-ray synchrotron microtomographic sections compared to SEM photos of artificially fractured conodont specimens. 1, Tomographic section of *Epigondolella quadrata* specimen A; 2-4, SEM photos of an artificially fractured specimen of *Carnepigondolella carpathica* (sample NA16). Both the specimens are sectioned in correspondence to the cusp; 5-6, Comparison between a tomographic section (5) and an artificially fractured (6) specimen of *E. uniformis* from the same sample (NA42). Legend: cu, cusp; wm, white matter; hp, hypocalcification; gl, growth lines.

genesis of the posterior node is completely different (Figure 4.5-7). A focused longitudinal section of the cusp region of the two analyzed *E. rigoi* specimens reveals that the youngest growth stages of the posterior node are not yet interested by white

matter, and it allows us to observe the early ontogenetic stages of this character (Figure 4.5). The microtomography clearly shows that, unlike in *E. quadrata*, in *E. rigoi* the lamellae constituting the posterior node grow directly from the cusp since

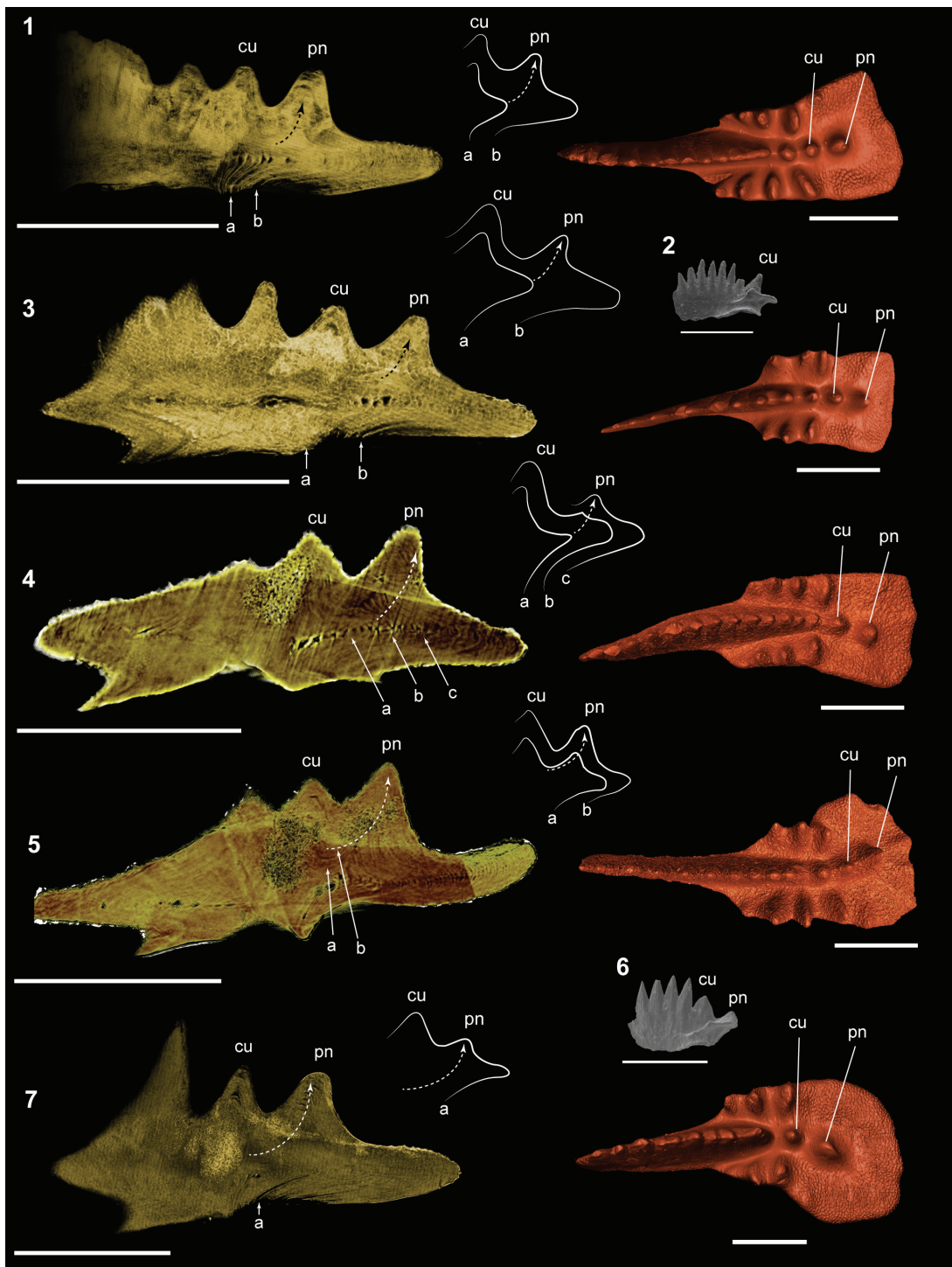


FIGURE 4. Microtomographic longitudinal sections focused on the posterior platform of *Epigondolella quadrata* and *E. rigoi*, aimed to show the ontogenesis of the posterior node growing behind the cusp. For each section a 3D model of the correspondent conodont is provided. Beside the sections, the outlines of selected growth lines are reported, in order to evidence some visible growth stages and show the different ontogenetic processes of *E. quadrata* and *E. rigoi*. Arrows and letters (a, b, c) mark the growth lines considered to draw the stages. 1, *E. quadrata* A; 2, juvenile specimen of *E. quadrata* from sample NA60 (from Mazza and Martínez-Pérez, 2015; repository number Micro-Unimi no. 2001); 3, *E. quadrata* B; 4, *E. quadrata* C; 5, *E. rigoi* A; 6, juvenile specimen of *E. rigoi* from sample NA68 (from Mazza and Martínez-Pérez, 2015; repository number Micro-Unimi no. 2003), showing that the posterior node is already occurring; 7, *E. rigoi* B. Scale bars equal 200 μ m. Legend: cu, cusp; pn, posterior node.

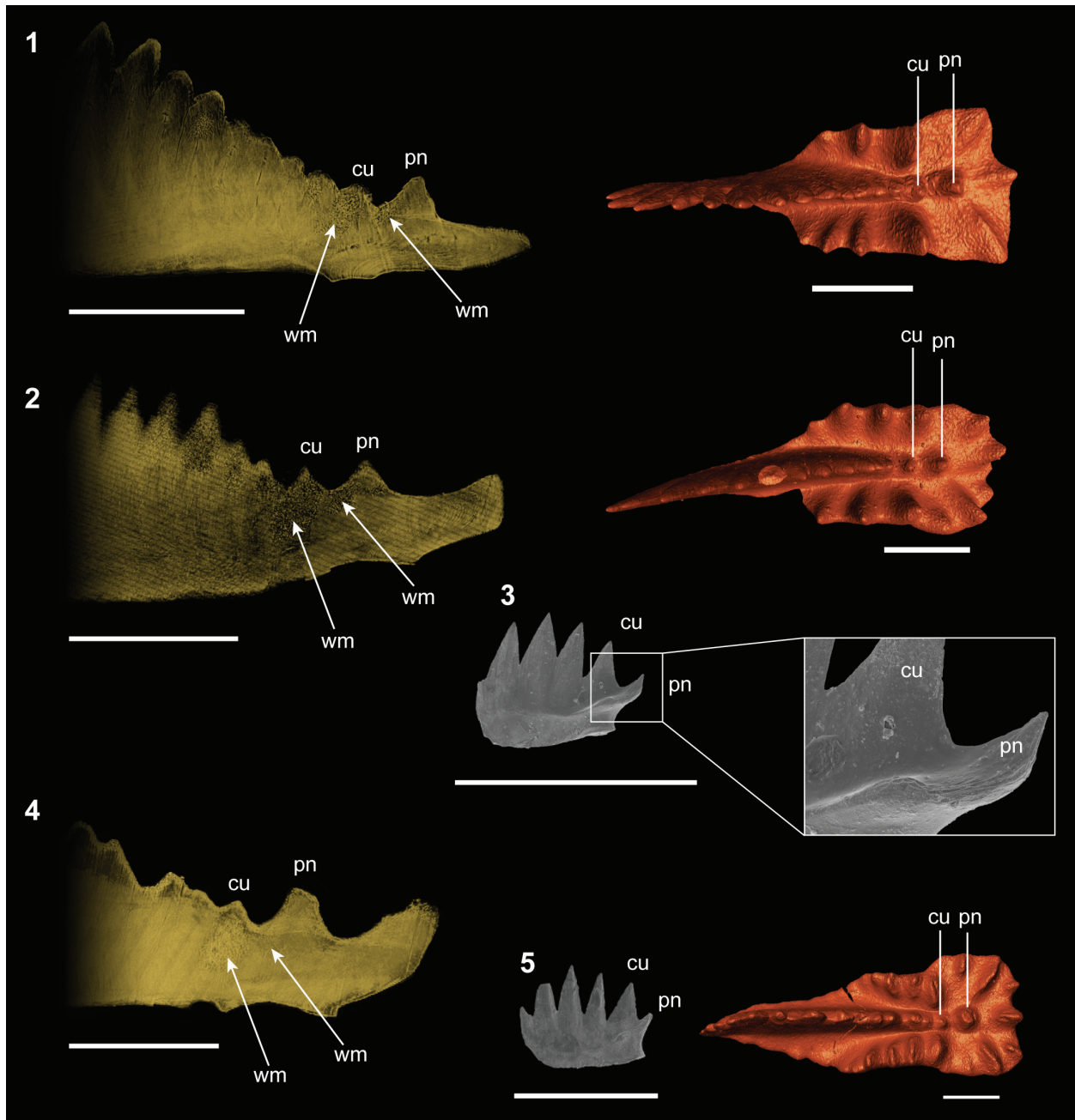


FIGURE 5. Microtomographic longitudinal sections focused on the posterior platform of *Epigondolella vialovi*, *E. uniformis*, and *E. triangularis* aimed to show the ontogenesis of the posterior node growing behind the cusp. For each section a 3D model of the correspondent conodont is provided. 1, *E. vialovi*; 2, *E. uniformis*; 3, juvenile specimen of *E. uniformis* from sample NA43 (from Mazza and Martínez-Pérez, 2015; repository number Micro-Unimi no. 2005); 4, *E. triangularis*; 5, juvenile specimen of *E. triangularis* from sample NA43 (from Mazza and Martínez-Pérez, 2015; repository number Micro-Unimi no. 2004). Scale bars equal 200 μm . Legend: cu, cusp; pn, posterior node; wm, white matter.

the beginning of the ontogenetic process of the species. Very juvenile specimens of *E. rigoi*, in fact, already bear a large carinal node behind the cusp (Figure 4.6).

The same growth process may be observed in the other three epigondolellids analyzed: *Epigondolella vialovi*, *E. uniformis*, and *E. triangularis* (Figure 5). The tomographic sections of these species do not have the same quality of those of *E.*

quadrata and *E. rigoi*, thus the lamellae of the cusp region are not well distinguishable. Nevertheless, in all the three epigondolellids the posterior node is permeated by a massive occurrence of white matter as in *E. rigoi* and, in the same way, in the most anterior part of the node the albid tissue appears to be coalescent with that of the cusp (Figure 5). Thus, even if in *E. vialovi*, *E. uniformis*, and *E. triangularis* the growth lines are not well distinguishable, the internal structure of their posterior node is homologous to that of *E. rigoi* and its ontogenesis is seemingly the same. Comparisons with SEM photos of specimens of *E. uniformis* and *E. triangularis* from monospecific populations, together with the analyses of their growth series (Mazza and Martínez-Pérez, 2015), confirm the occurrence of the posterior denticle already from the early juvenile stages of these species (Figure 5.3, 5.5).

DISCUSSION

The evolutionary trends of the Late Triassic P₁ conodont elements are quite well defined (see Figure 1; Mazza et al., 2012b). One of the most evident trend is the forward shifting of cusp and pit, which is associated with the occurrence of nodes behind the cusp (Orchard, 2014). This trend also characterizes the evolution of the Late Carnian carnepigondolellids into genera *Epigondolella* and, later in the Middle Norian, the development of nodes behind the cusp is a character inherited also by the genus *Mockina* (Mazza et al., 2012a; Mazza and Martínez-Pérez, 2015). The development of the large node behind the cusp in the epigondolellids considerably influenced the phylogenetic model obtained with the cladistic analyses (Mazza et al., 2012b).

The Synchrotron Radiation X-ray Tomographic Microscopy allowed us to investigate in detail the ontogenetic process of this character, revealing that the posterior node of *Epigondolella vialovi*, *E. rigoi*, *E. uniformis*, and *E. triangularis* is a carinal node because it grows directly from the cusp, while in *E. quadrata* this node, even if it has the same morphology and is located in the same position of that of the other mentioned epigondolellids, has the same ontogenetic process that leads to the growth of the nodes/denticles developing on the platform margins. For this reason, the posterior node of *E. quadrata* is a different structure than a carinal node, analogous to other platform ornamentation structures (Figures 4, 5). Thus, the large posterior node growing behind the cusp cannot be considered as indicative of common ancestry, as

supposed before, but as a clear evolutionary convergence.

Consequently, since different ontogenetic processes for the same morphological character indicate evolutionary convergence, the main question that raises is if the position of *Epigondolella quadrata*, *E. rigoi*, *E. uniformis*, and *E. triangularis* in the phylogenetic model previously proposed has to be reconsidered. One hypothesis is that the evolution of *E. quadrata* into *E. rigoi* could proceed by the conversion of the posterior node of *E. quadrata* into a carinal node in *E. rigoi*. Nevertheless, we have to consider that the studies on the Late Triassic conodont growth series (Mazza and Martínez-Pérez, 2015) revealed that *E. quadrata*, *E. rigoi*, and *E. uniformis* first occur quite contemporaneously in the uppermost Carnian and can be found together in a long stratigraphic range until the Middle Norian (Mazza et al., 2012a; Karádi et al., 2013; Mazza and Martínez-Pérez, 2015). Juvenile epigondolellids now classifiable as *E. triangularis* are found in the Tuvallian even below the first occurrences of the other three species (Mazza and Martínez-Pérez, 2015). This suggests that more than being phylogenetically related, these species evolve in parallel lineages, sharing analogous characters. This definitely confirms a new and more articulated scenario for the evolutionary history of the Upper Triassic epigondolellids. Genus *Epigondolella* cannot be considered anymore as a monophyletic group, but a paraphyletic assemblage of species deriving from Carnian taxa that develop similar morphologies but follow different evolutionary and ontogenetic processes. The previous phylogenetic model has necessarily to be revised.

This aspect raises a considerable transcendence in conodont, as far as their morphology is the base for its systematics and phylogenetic relationships, highlighting the importance of discriminating homology from homoplasy. In this sense, Synchrotron Radiation X-ray Tomographic Microscopy represents a unique and versatile instrument for these kind of investigations, providing data that can inform on conodont ontogenesis, evolutionary processes and phylogenetic relationships.

CONCLUSIONS

The application of Synchrotron Radiation X-ray Tomographic Microscopy to reconstruct the ontogenesis of single Late Triassic conodont P₁ elements, suggests that using ontogenesis as a criterion for discriminating homology from homoplasy is actually effective, allowing to identify cryptic

homology between apparently convergent characters in the conodont platform morphology. In particular, our results about the ontogenesis of the posterior node growing behind the cusp of Late Triassic conodont P₁ elements, an autapomorphy characterizing the *Epigondolella* clade, reveal that the studied character is not a homologous character of the epigondolellids but an evolutionary convergence. Therefore, it cannot be considered as evidence of common ancestry anymore, confirming that the genus *Epigondolella* is not a monophyletic clade as previously hypothesized, but a polyphyletic assemblage of taxa with different possible ancestors among the carnepigondolellids as later reconsidered. This result highlights the importance to discriminate homology from homoplasy in conodonts to depict more precisely their ontogenetic and evolutionary dynamics.

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