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Cover image:
X-ray synchrotron tomographic images and SEM photography of a juvenile specimen of *Epigondolella quadrata* (Orchard, 1991), from Mazza & Martínez-Pérez (this volume. Pag. 172: Fig. 2e)

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Unravelling conodont (Conodonta) ontogenetic processes in the Late Triassic through growth series reconstructions and X-ray microtomography

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KEY WORDS - Conodonts, ontogeny, growth series, Late Triassic, X-ray, microtomography, synchrotron.

ABSTRACT - The ontogenetic series of ten Carnian-Norian (Late Triassic) platform conodont species, belonging to the genera Paragondolella*,* Carnepigondolella*,* Epigondolella*, and* Metapolygnathus *are reconstructed in this paper. The growth series are based on rich populations derived from almost monospecific samples from the upper Carnian-Rhaetian succession of Pizzo Mondello (Sicani Mountains, Western Sicily, Italy), a GSSP candidate for the Norian stage. Six to twelve ontogenetic stages have been recognized for each species, based on examination of more than 350 SEM photos, integrated with X-ray synchrotron microtomographic images of their internal structure.*

These findings have given rise to a revaluation of the systematics and the phylogenesis of the Late Triassic conodonts from an ontogenetic perspective, leading to important refinements of their biostratigraphy and to a reinterpretation of their evolutionary processes. Herein it is observed that conodonts develop a morphological identity already in their most juvenile stages, thus, for the first time, they now have a specific taxonomic identity. Changes to the stratigraphic ranges of important Epigondolella *species such as* E. rigoi*,* E. triangularis*, and* E. uniformis *are noted, and their First Appearing Data (FADs) now result younger in age, calling into question previous phylogenetic models. More articulated phylogenetic relationships with the carnepigondolellids have emerged, questioning the hypothesis that* Epigondolella *is a monophyletic group and suggesting the existence of different polyphyletic lineages deriving anagenetically from several Carnian* Carnepigondolella *species.*

Subsequently in the middle Norian the epigondolellids evolve into the genera Mockina*,* Parvigondolella*, and* Misikella*, which show reduced dimensions and neotenic characters. The present study provides a tool for the interpretation of this evolutionary process. We observed that the morphologies of these three genera are analogous to progressive juvenile stages of the epigondolellids: the mockinae are comparable to early adult, late juvenile, and juvenile stages of the epigondolellids, while the parvigondolellids and the misikellae to their early juvenile stages. Consequently, it is deduced that the final evolutionary trend of conodonts in the Late Triassic is thus the result of a gradual process of progenesis that started already in the middle Norian.*

RIASSUNTO - [I processi ontogenetici dei conodonti (Conodonta) nel Triassico Superiore svelati attraverso la ricostruzione delle serie di crescita e la microtomografia a raggi-X] - *In questo articolo vengono ricostruite le serie ontogenetiche di dieci specie di conodonti del Carnico-Norico (Triassico Superiore) appartenenti ai generi* Paragondolella*,* Carnepigondolella*,* Epigondolella *e* Metapolygnathus*. Le serie di crescita sono state ricostruite grazie allo studio di ricche popolazioni provenienti da campioni quasi totalmente monospecifici della successione Carnica superiore-Retica di Pizzo Mondello (Monti Sicani, Sicilia occidentale, Italia), candidata a GSSP del Norico. Per ogni specie sono stati illustrati, attraverso l'ausilio di più di 350 fotografie fatte al SEM, da sei a dodici stadi ontogenetici, fornendo per ognuno di essi la visuale superiore, inferiore e laterale, in modo da poter mostrare l'ontogenesi dei principali elementi morfologici in ogni parte della piattaforma. Al fine di testarne l'affidabilità, le nostre ricostruzioni sono state integrate con immagini microtomografiche a raggi-X della struttura interna di conodonti appartenenti alle stesse specie utilizzate per gli studi ontogenetici. Le analisi sono state eseguite all'SLS (Swiss Light Source) del Paul Scherrer Institute (Villigen, Svizzera).*

I risultati delle nostre ricostruzioni hanno portato a riconsiderare la sistematica e la filogenesi dei conodonti del Triassico Superiore della Neotetide dal punto di vista della loro ontogenesi, suggerendo significative revisioni della loro biostratigrafia e una reinterpretazione dei loro processi evolutivi. Si può osservare quindi che i conodonti sviluppano una loro identità morfologica già a partire dai loro stadi più giovanili, che hanno adesso per la prima volta una loro identità tassonomica; le distribuzioni stratigrafiche di importanti specie del genere Epigondolella*, come* E. rigoi*,* E. triangularis *ed* E. uniformis *sono cambiate, e le loro prime comparse (FADs) risultano ora più giovani, mettendo in discussione i precedenti modelli filogenetici. Emergono così relazioni filogenetiche più articolate con i carnepigondolellidi, svalutando l'ipotesi che il genere* Epigondolella *sia monofiletico e suggerendo invece l'esistenza di più linee filogenetiche che si diramano anageneticamente da diversi carnepigondolellidi carnici.*

Successivamente, nel Norico medio, gli epigondolellidi evolvono nei generi Mockina*,* Parvigondolella *e* Misikella*, contraddistinti da dimensioni ridotte e caratteri neotenici. Con questo lavoro, forniamo una possibile chiave interpretativa di questo ultimo passo evolutivo dei conodonti. Si può infatti osservare che la morfologia di questi tre generi è analoga agli stadi progressivamente più giovanili degli epigondolellidi. In particolare, le mockinae sono confrontabili agli stadi sub-adulti, tardo giovanili e giovanili degli epigondolellidi, mentre i parvigondolellidi e le misikellae ai loro stadi sub-giovanili. Si ritiene quindi che l'ultimo processo evolutivo dei conodonti nel Triassico Superiore sia il risultato di un processo di progenesi che iniziò già nel Norico medio con una riduzione graduale della crescita degli epigondolellidi.*

INTRODUCTION

Conodonts have a kinetic evolutionary history that lasted more than 300 Myr, making them one of the most long-lasting fossil groups known at present (Dzik, 2008). They colonized most of the ecological niches, being nearly ubiquitous in marine sediments from the Cambrian to the end of the Triassic (Sweet, 1988; Aldridge et al., 1993; Purnell & Donoghue, 2005; Rigo & Joachimski, 2010; Trotter et al., 2015).

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1972], *Mockina tozeri* [Orchard, 1991], *Mockina zapfei* [Kozur, 1972], and *Mockina bidentata*). The morphologies of the middle and late Norian mockinae can be related to different ontogenetic stages of the lower Norian epigondolellids, suggesting that *Epigondolella*, not *Metapolygnathus*, is the most probable ancestor of all the late Norian-Rhaetian species (Fig. 4).

We can observe that the first *Mockina* species (i.e., *Mo. tozeri*, *Mo. englandi*, *Mo. slovakensis*) reach the adult age at the GS4 of, probably, *E. triangularis* or *E. uniformis*, with some morphological innovations, such as a further increment of the posterior platform growth, expressed in a still more rapid forward shifting of the pit and prolongation of the keel end, and premature fusion of the blade denticles (Fig. 4). Latermost Norian mockinae (i.e., primitive and less evolved *Mo. bidentata*), stop their growth even earlier at the GS3 and then at the GS2 equivalent epigondolellid stages (i.e., more evolved *Mo. bidentata*), developing only a blade, a posterior carina and a couple of denticles besides the blade (Fig. 4). Finally, the late Norian-lower Rhaetian parvigondolellids, stop their growth at the epigondolellid GS1, developing only a blade and a posterior carina (Fig. 4). In other words, we suggest that the Norian-Rhaetian conodonts evolved through a process of gradual progenesis from the middle Norian epigondolellids, and not through neoteny as supposed before. Neoteny implies that an adult species has the same size of its ancestor but that it does not develop adult characters. Instead, late Norian mockinae do not grow in size, but they reach the adult age at young ontogenetic stages (i.e., progenesis).

The successive evolutionary step is the development of the genus *Misikella* from the mockine or the parvigondolellids, in which the absence of a platform is associated to the development of new characters, such as the enlargement of the basal cavity and the increase of the blade denticles size. This simplification of the P_1 elements morphology of the misikellae is probably the result of the adaptation to some kind of still unknown environmental stress. Seemingly, even if we do not know the causes, a decrease of the size and of the morphological characters constituting the platform elements could help conodonts to face a new ecological crisis in the Late Triassic. We have documented here that this process is not abrupt, but it develops gradually from the middle Norian epigondolellids through progenesis.

CONCLUSIONS

The growth series illustrated in this work open new perspectives to the study of the systematic and evolution of conodonts. Our reconstructions of the conodonts ontogenesis, supported by original X-ray synchrotron tomographic images, show that different morphologies are strictly related to different ontogenetic processes and that certain morphologies can be recognized already from the most juvenile growth stages. In this way we could give, for the first time, a taxonomic identity to the juvenile specimens of Late Triassic biostratigraphically key species such as *Metapolygnathus communisti*, *Epigondolella quadrata*, *Epigondolella rigoi*, *Epigondolella triangularis*, and *Epigondolella uniformis*. The new taxonomy of the juvenile representatives of the analyzed epigondolellids places the FADs of *E. rigoi*, *E. uniformis*, and *E. triangularis* in the uppermost Carnian and not in the lower Norian as believed in the past, changing their biostratigraphic ranges and questioning the previous phylogenetic models. Their phylogenetic relationships result more articulated, suggesting that genus *Epigondolella* is not a monophyletic group as supposed before. Genus *Epigondolella* may be instead composed by several lineages that derive anagenetically from different *Carnepigondolella* species, claiming now more detailed systematic studies of this genus that will probably lead to the establishment of new species that take in account also their ontogenetic processes. Since the GSSP of the Norian stage is under definition, and conodonts may represent a possible marker event (Krystyn & Gallet, 2002; Balini et al., 2010; Mazza et al., 2012b; Karádi et al., 2013; Orchard, 2014), a new and solid conodont biostratigraphy that can take advantage also of classifiable juvenile specimens may give a fundamental contribution to the definition of the base of the Norian.

Our study puts also new light on the evolutionary history of the Late Triassic conodonts after the Carnian Pluvial Event from an ontogenetic point of view. We observed that, from the late Carnian to the middle Norian, the morphogenetic point of the platform shifts gradually from the center of the element backward towards the cusp. At the same time, the platform growth rates increase posteriorly and decrease anteriorly, producing the apparent forward shifting of the pit and lengthening of the blade, which are evolutionary trends that occur cyclically in the family Gondolellidae. This evolutionary process continues until the middle Norian, when the metapolygnathids extinguish and only the epigondolellids continue to evolve into the mockinae. The evolutionary step between the genera *Epigondolella* and *Mockina* is marked by a progenetic process, which characterizes also the evolution of the genera *Parvigondolella* and *Misikella* in the late Norian-early Rhaetian. The epigondolellids thus gradually generate adult individuals that interrupt their ontogenesis at forms that are analogous to the epigondolellids early adult (GS4), late juvenile (GS3), juvenile (GS2) or early juvenile (GS1) growth stages. This is the last evolutionary pulse of conodonts that led them to extinction at the Triassic/Jurassic boundary.

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