

Original Article

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Towards a refined Norian (Upper Triassic) conodont biostratigraphy of the western Tethys: revision of the recurrent 'multidentata-issue'

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Abstract

The issue of oversimplified Norian conodont taxonomy has set back the development of Norian conodont biostratigraphy of the western Tethys Realm for decades. The majority of stratigraphic studies used the name *Epigondolella multidentata*, a North American endemic, to gather specimens indicative of strata from the lower part of the middle Norian substage. Detailed conodont biostratigraphic investigations were carried out on the Norian hemipelagic cherty dolostones of the Mátyás Hill section in the Buda Hills (Hungary) in order to resolve the 'multidentata problem'. The age of the section ranges from the upper part of the lower Norian substage (Lacian-3) to the lower part of the middle Norian substage (Alaunian-1). The new species *Ancyrogondolella manuelei* n. sp. is introduced, and *A. transformis* is documented for the first time in the Tethys. The studied conodont fauna significantly improves the correlation potential between the western Tethys and the eastern Pacific.

1. Introduction

The Norian Age is the longest (~20 million years) within the Triassic Period; however, a well-applicable biostratigraphic subdivision is still pending. The Triassic timescale was originally established based on ammonoid biostratigraphy and biochronology (Balini et al. 2010 and references therein) long before the development of micropaleontological research. Unfortunately, most of the Norian successions, except for some condensed deposits, are remarkably poor in ammonoids. A possible alternative fossil group in Triassic biostratigraphy is represented by conodonts, due to their rapidly changing morphologies, wide paleogeographic distribution and high resistance to diagenetic processes and metamorphic overprint (Rigo & Joachimski, 2010; Rigo et al. 2012, 2018; Trotter et al. 2015).

The research on Norian conodonts dates back to the late 1950s, to the pioneer work by Huckriede (1958). Although several stratigraphic studies have been carried out till recent times, most of them are hampered by the lack of a steady taxonomic framework. This is due to the early recognition of the main evolutionary trends of conodonts during the Norian Age, discussed, for example, by Orchard (1983), Kozur (1989) and Karádi (2021), which allowed the approximate dating of strata based solely on the general characteristics of faunas and, thus, resulted in the oversimplification of Norian conodont taxonomy (see Karádi (2018) for details). This is still a common practice among stratigraphers, who often gather a great variety of morphologies under a single species name and totally ignore the true diversity of the assemblages. It is very well reflected in Figure 1 of Krystyn et al. (2009) which makes the false impression that each timespan within the Norian Age is characterised (besides *Norigondolella* spp.) by a single species of the genus *Epigondolella* having a short overlap with both the preceding and the succeeding species. Studies on conodont evolution (e.g. Mazza et al. 2012a; Chen et al. 2016; Karádi et al. 2020a) clearly prove that evolutionary lineages are more complex, and such a simple situation does not exist. It can hardly be imagined how much information is lost by this act, especially if there is no or only inadequate figuration of the conodonts, which is also typical of stratigraphic papers. Not to mention that newcomers in conodont studies get completely lost when they face a much more diverse material for the first time. Their only option remains turning to the original diagnoses of the few species mentioned in stratigraphic studies. However, these descriptions are usually ambiguous, coupling with incomplete comparisons with other taxa, and sparse and often inappropriate figuration. A more serious problem emerges when non-conodont workers, totally unaware of these taxonomic issues, use the simplified conodont data as reference for dating the subjects of their own research or calibrating their isotope curves in chemostratigraphic studies. Despite these shortcomings, age determination can still turn out to be correct at the end

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(e.g. Roniewicz et al. 2007), but there is a great chance of misinterpretation if ages are based on obsolete data.

Due to the reasons mentioned above, Norian conodont species have seemingly long ranges, and since biozonal schemes of the Tethys Realm are based predominantly on the few taxa introduced in the second half of the twentieth century, conodont zones cover quite long time intervals. This cannot be more evident by looking at the most recent Upper Triassic conodont biozonation of the Tethys (Rigo et al. 2018). There, the Carnian and the Norian stages have almost the same number of zones, with the latter representing two times longer timespan than the former. It must be noted though that the authors were aware that the Norian zonation can most likely be improved, but very few studies of detailed taxonomic investigations were available at that time (e.g. Mazza et al. 2012b); those that presented diverse Norian conodont assemblages were published simultaneously or later (e.g. Karádi, 2018; Orchard, 2018; Karádi et al. 2021).

Precise age determinations are crucial for correlating regional events and understanding the geodynamic evolution of the Tethys Realm during the Norian Age. One significant phenomenon can be observed in the transitional interval between the early and middle Norian (Lacian and Alaunian), which is characterized in the western Tethys, but most probably also in the eastern Tethys, by intense tectonic activity resulting in widespread slump structures, sedimentary breccias and neptunian dykes (e.g. Gawlick & Böhm, 2000; Mazza et al. 2012b; Karádi, 2018; Karádi et al. 2021). Conodont faunas of this period are most of the time simply assigned to the species *Epigondolella spatulata* and one of the various forms used for the 'multidentata population': *Epigondolella* cf. n. sp. C, *E. multidentata*, *E. multidentata* n. ssp. A, *E. 'multidentata'* and *Epigondolella* cf. *multidentata* (Gallet et al. 1992, 1996, 2000; Gawlick & Böhm, 2000; Roniewicz et al. 2007; Krystyn et al. 2009). These species are fairly problematic because the original description of *E. spatulata* (as *Gladigondolella abneptis* var. *spatulata* var. nov. in Hayashi (1968), p. 69) is ambiguous, and specimens identical to the holotype occur in the lower part of the Lacian substage (Mazza et al. 2012b, p. 110) rather than the Lacian/Alaunian transition, whereas *E. multidentata* is suggested to be a North American endemic taxon (Kozur, 2003; Orchard, 2006).

This study presents the conodont biostratigraphy of the Mátyás Hill section, a classic locality in an abandoned quarry of the Buda Hills (eastern Transdanubian Range, north-central Hungary). The aims are to show that the diversity of the conodont assemblages in the Lacian/Alaunian transition is greater than suggested earlier and to illustrate the taxa previously gathered in the 'multidentata population'. A rich figuration of the conodont material is critical because at the moment only a low number of studies exist from this timeframe which can be used for faunal comparisons. The intention of the author is to find the balance between oversimplification (too much lumping) and over-complication (too much splitting) in order to keep the improved biostratigraphic scheme applicable to a wide range of conodont specialists and stratigraphers in the future.

2. Geological setting

The Buda Hills are located in the northeastern part of the Transdanubian Range in north-central Hungary, ranging from the western bank of the River Danube to the western vicinity of Budapest. The area is mainly composed of Triassic carbonate rocks of platform and basin facies, overlain by Eocene and Oligocene

deposits. The Buda Hills were situated on the northwestern shelf of the Tethys during the Late Triassic epoch (Haas et al. 1995). A large part of the Triassic formations was subjected to extensive dolomitization (Haas, 2002; Hips et al. 2016); limestones are preserved in a lesser volume.

The hemipelagic carbonates represent a proximal periplatform depositional environment and are assigned to the Mátyáshegy Formation. Conodont-based age assignment was given by Kozur and Mock (1991), Karádi et al. (2016) and Karádi (2018) suggesting an uppermost Carnian to Rhaetian Age for the sedimentary sequence. The change from dolostone to limestone is in the Sevatian substage (upper Norian). The limestone outcrops at the northwestern edge of the Buda Hills, type locality of the lower Carnian (Julian-2) monospecific *Nicoraella budaensis* conodont assemblage (Kozur & Mock, 1991), represent a different depositional environment (restricted basin) and have no sedimentary and stratigraphic relation to the younger Mátyáshegy Formation.

The subject of the present study is the type section of the Mátyáshegy Formation, exposed by an old trench at the western margin of the abandoned quarry of Mátyás Hill (N47° 32.09', E19° 00.99', Figure 1).

The Norian Age of the section was first proven with conodonts by Kozur and Mock (1991) and later confirmed by Dosztály in Haas et al. (2000) based on radiolarians. Middle Norian conodonts from the succession were already presented by Karádi et al. (2016) and Karádi (2018). At that time, a large part of the section was covered by debris and soil. During the present biostratigraphic investigation, it was cleared to expose an ~19 m thick sequence of greyish-yellow dolostone (Figure 2). The beds are mainly of decimetre scale, but variation in thickness can be observed laterally. Centimetre-sized, red chert nodules are common in the lower half of the section, especially around the middle part (between 7 and 12 m). Disturbed bedding and fractured blocks can be observed at several levels in the upper half of the trench but are more pronounced above the cherty interval.

3. Material and methods

The first sampling campaign of the present research was carried out in 2019 when 13 samples were collected from the exposed parts of the succession (Figure 2; Karádi et al. 2020b). After clearing the section during the second sampling in 2021, 61 beds were consecutively numbered from base to top. Systematic sampling was carried out in order to record the changes in the conodont fauna. A total of 20 samples were taken (Figure 2), ~3.5 kg each. Samples were processed at the Department of Palaeontology of the Eötvös Loránd University, Budapest, Hungary. Since brecciation and the presence of neptunian dykes are common in the lower/middle Norian transition in the western Tethys, the microfacies of each rock sample was analysed in 5 × 5 cm thin sections as an attempt to reveal the causes if any faunal mixing is observed. Rocks were dissolved using diluted (10%) acetic acid, and the washing residues were collected on a 125 µm mesh-size sieve. Fossils were picked manually without preceding density separation. Scanning electron micrographs (SEMs) of the fossils were taken at the Environmental Analytical and Geoanalytical Research Group of the Szentágotthai Research Centre of the University of Pécs using the Jeol JSM-IT500HR scanning electron microscope. The materials are deposited at the Department of Palaeontology of the Eötvös Loránd University in Budapest, Hungary.

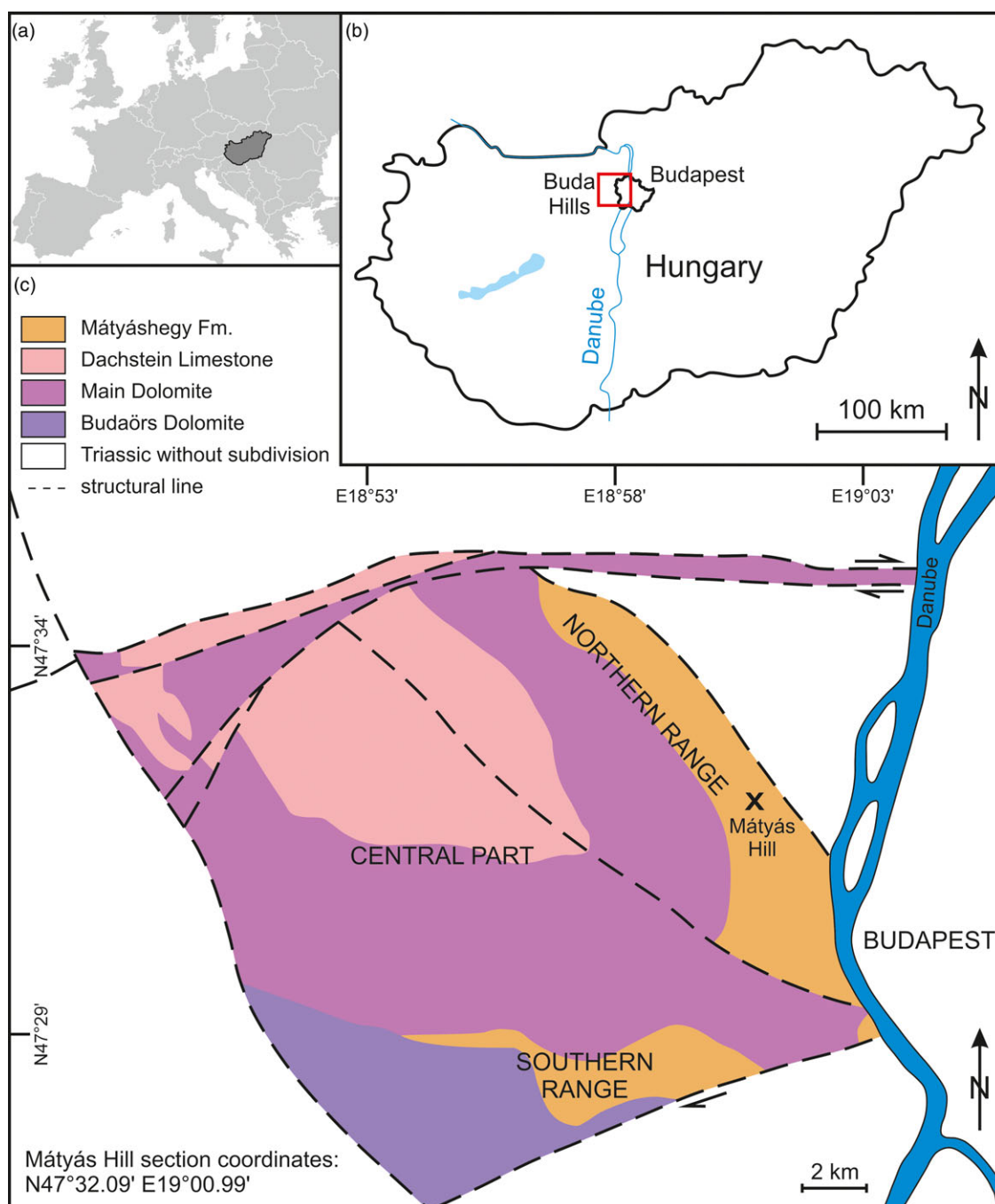


Figure 1. (Colour online) (a) Map of Europe with the position of Hungary indicated. (b) Map of Hungary with the Buda Hills marked by red rectangle. (c) Simplified basement map of the Buda Hills with the Triassic formations indicated (modified after Haas et al. 2000). The studied outcrop is marked by X.

4. Results

Conodont elements were found in every sample; the most abundant fauna occurred in bed 58. Sample MH5/19 (bed 19) yielded only juvenile specimens. Conodonts are pale yellow in colour that corresponds to the Colour Alteration Index (CAI) value of 1 suggesting inconsiderable thermal alteration.

4.a. Biostratigraphy

A large part of the trench, from sample MH1/21 to sample MH54/21, contains conodonts (*Norigondolella navicula*, *N. hallstattensis*, *Ancyrogondolella uniformis*, *Ancyrogondolella*

ex gr. *triangularis*, *Ancyrogondolella* ex gr. *rigoi* and *A. 'spatulata'*) that are characteristic for the Lacián-3 substage (higher part of the lower Norian) (Figure 2). Similar assemblages from the same age interval are known from Austria (e.g. Krystyn et al. 2009), Slovenia (e.g. Karádi et al. 2021) and Hungary (Karádi & Korte, 2023). In certain levels, however, specimens with typical Alaiian morphological features (*Epigondolella/Mockina* spp.) are mixed with the Lacián fauna. These are marked with red symbols in Figure 2.

In sample MH20/21, the mass occurrence of *Ancyrogondolella? bohorensis* and the occurrence of a single specimen of *A. equalis* was observed. In the middle part of the section, some rare species

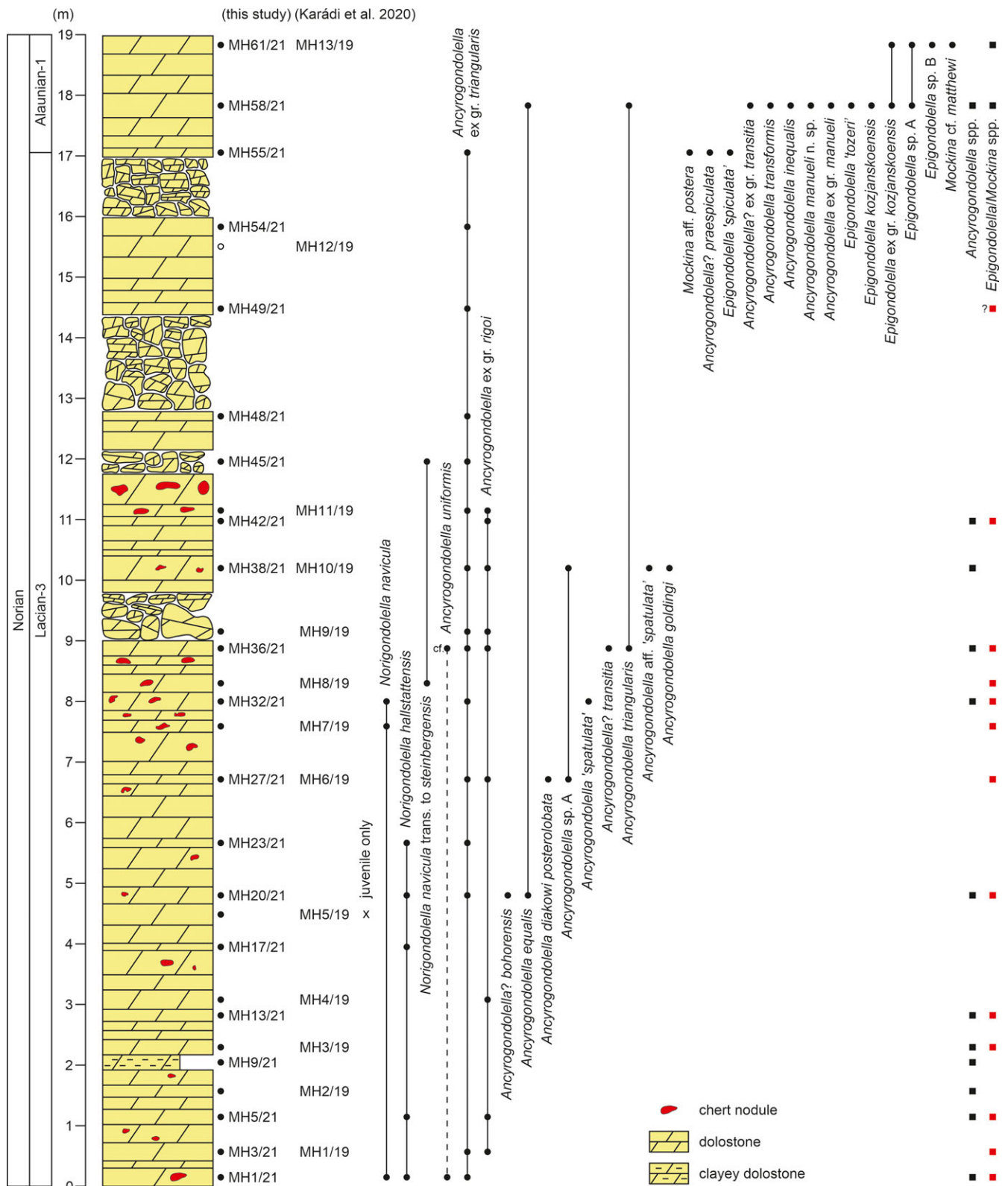


Figure 2. (Colour online) Stratigraphic log of the Mátyás Hill section with the position of the samples (solid circles, conodonts present; open circles, conodonts absent) and the distribution of conodont taxa. Red symbols in the conodont occurrences indicate reworking (see text for discussion). Scale is in metre.

of the genus *Ancyrogondolella* were documented: *A. diakowi posterolobata* (sample MH27/21), *Ancyrogondolella* sp. A (samples MH27/21 and MH38/21), *Ancyrogondolella? transitia* (sample MH36/21), *Ancyrogondolella* aff. 'spatulata' (sample MH38/21) and

A. goldingi (sample MH38/21). Two specimens showing transitional morphology between *N. navicula* and *N. steinbergensis* were also found in this part of the section (sample MH8/19 and sample MH45/21). The highest part of the Laciaan (from sample MH42/21 to

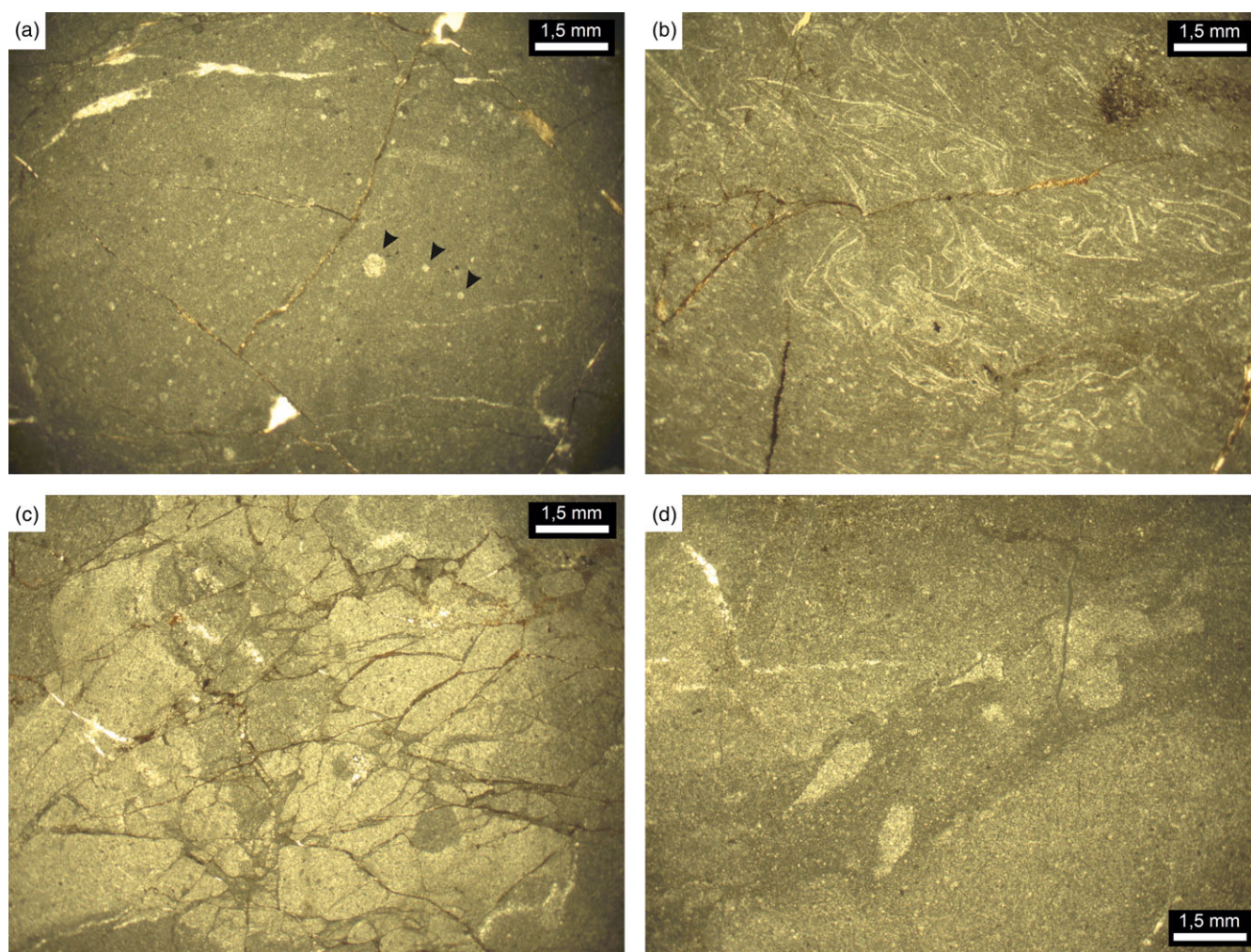


Figure 3. (Colour online) Characteristic microfacies of the cherty dolostone of the Mátyás Hill section. (a) Radiolarian wackestone of sample MH17/21. Black arrowheads point to recrystallized radiolarians. (b) Filament wackestone to packstone of sample MH58/21. (c) Fractured fabric of sample MH55/21. (d) A possible fissure fill (darker area) in sample MH32/21.

sample MH54/21) is characterized by the presence of a less diverse assemblage (assigned here to *Ancyrogondolella* ex gr. *triangularis* and *Ancyrogondolella* ex gr. *rigoi*).

The uppermost part of the section (from sample MH55/21 to sample MH61/21) is assigned to the Alaunian-1 substage (lower part of the middle Norian) based on the dominance of specimens with evident differences in pit position, keel termination and posterior carina from those of the Lacián fauna. This fauna is represented by the species *E. 'spiculata'*, *E. 'tozeri'*, *E. kozjanskoensis*, *Epigondolella* ex gr. *kozjanskoensis*, *Epigondolella* sp. A, *Epigondolella* sp. B, *Mockina* aff. *postera* and *Mockina* cf. *matthewi*. Only *Ancyrogondolella* ex gr. *triangularis* and *A. equalis* from the Lacián assemblage are still present at this level (sample MH58/21); however, other species of this genus (*Ancyrogondolella? praespiculata*, *Ancyrogondolella? ex gr. transitia*, *A. transformis*, *A. inequalis*, *A. manueli* n. sp. and *Ancyrogondolella* ex gr. *manueli*) first appear in the Alaunian-1 interval. Comparable assemblages of this age were documented from Slovenia (e.g. Karádi et al. 2021) and Canada (Orchard, 2018). Samples from the section yielded several specimens, which could not be assigned to any of the existing species. Since all of them are unique in a certain way, they are referred to as *Ancyrogondolella* spp., *Epigondolella* spp. and *Mockina* spp. in this study.

4.b. Microfacies

Thin sections revealed that rocks of the Mátyás Hill section have undergone pervasive dolomitization, which obscures the original texture of the rock and makes it impossible to study primary sedimentary features in most cases. The crystal size varies from finely crystalline to coarsely crystalline dolomite, but finely and medium crystalline dolomite dominates. The recent study does not include the analysis and description of the dolomitic features since this was done in detail by Hips et al. (2016). Ghosts of microfossils sporadically occur in samples MH9/21, MH13/21, MH17/21, MH23/21, MH27/21, MH42/21, MH49/21 and MH58/21. These are classified as radiolarian wackestone (Figure 3a) and filament wackestone–packstone (Figure 3b). A fractured fabric (Figure 3c) was observed in samples MH3/21, MH20/21 and MH55/21. Sample MH32/21 might reveal a possible fissure fill (Figure 3d).

5. Systematic palaeontology

Figures 4–9 show conodonts from the entire section of Mátyás Hill. In the systematic part, however, only taxa of the Alaunian-1 substage (above the mixed and disturbed interval) are discussed. Some of these were previously referred to as 'multidentata' in the

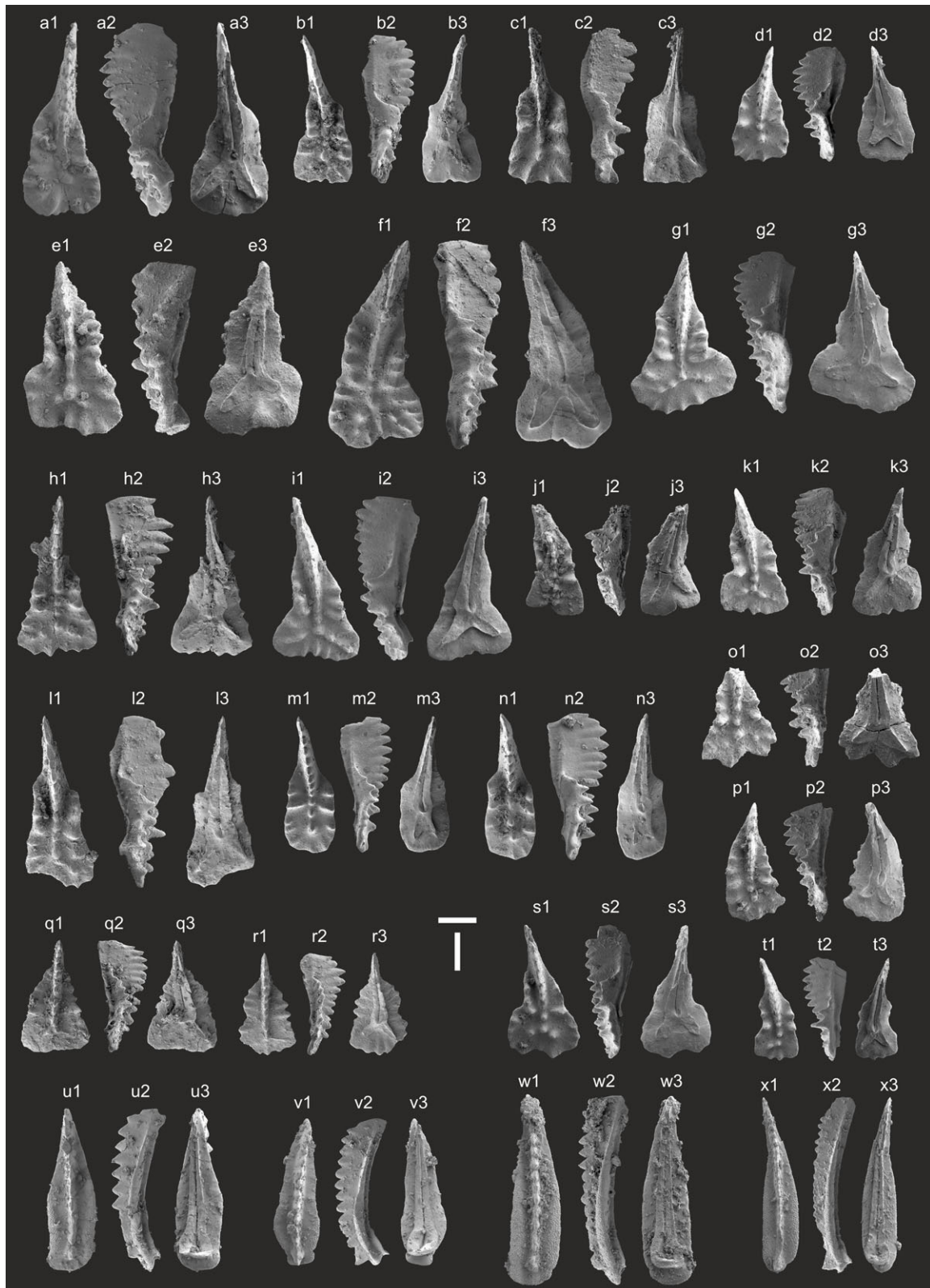


Figure 4. SEM micro-photographs of conodonts of the Mátyás Hill section. Scale bars are 200 μm , and all specimens are on the same scale. Three views (1, upper; 2, lateral; and 3, lower) are provided. (a) *Ancyrogondolella uniformis*, sample MH1/21 (mh1_03). (b–i) *Ancyrogondolella* ex gr. *triangularis*, (b) sample MH20/21 (mh20_24), (c) sample MH58/21 (mh58_37), (d) sample MH38/21 (mh38_03), (e) sample MH27/21 (mh27_12), (f) sample MH36/21 (mh36_08), (g) sample MH27/21 (mh27_08), (h) sample MH36/21 (mh36_12), (i) sample MH54/21 (mh54_03). (j–k) *Ancyrogondolella* ex gr. *rigoi*, (j) sample MH3/21 (mh3_10), (k) sample MH38/21 (mh38_02). (l) *Ancyrogondolella?* *transitia*, sample MH36/21 (mh36_17). (m–n) *Ancyrogondolella?* *bohorensis*, (m) sample MH20/21 (mh20_04), (n) sample MH20/21 (mh20_16). (o) *Ancyrogondolella diakowi posterolobata*, sample MH27/21 (mh27_11). (p) *Ancyrogondolella* aff. *'spatulata'*, sample MH38/21 (mh38_09). (q–r) *Ancyrogondolella 'spatulata'*, (q) sample MH32/21 (mh32_10), (r) sample MH32/21 (mh32_14). (s) *Ancyrogondolella* sp. A, sample MH38/21 (mh38_07). (t) *Ancyrogondolella goldingi*, sample MH38/21 (mh38_05). (u–v) *Norigondolella hallstattensis*, (u) sample MH1/21 (mh1_01), (v) sample MH17/21 (mh17_01). (w) *Norigondolella navicula*, sample MH1/21 (mh1_02). (x) *Norigondolella navicula* transitional to *Norigondolella steinbergensis*, sample MH45/21 (mh45_03).

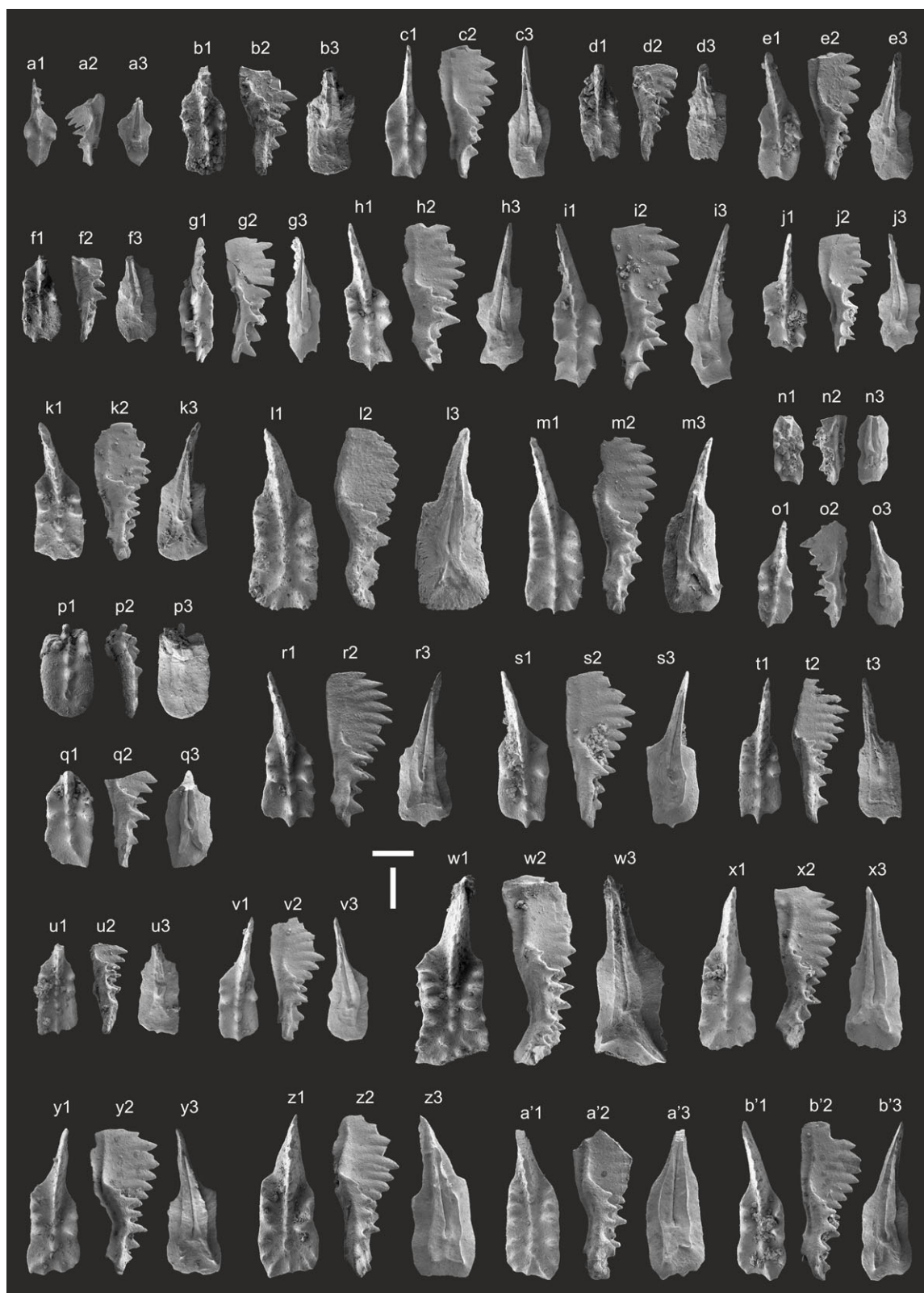


Figure 5. SEM micro-photographs of conodonts of the Mátyás Hill section. Scale bars are 200 μm , and all specimens are on the same scale. Three views (1, upper; 2, lateral; and 3, lower) are provided. (a) *Mockina* aff. *postera*, sample MH55/21 (mh55_01). (b–c) *Epigondolella* sp. A, (b) sample MH61/21 (mh61_01), (c) sample MH58/21 (mh58_36). (d–f) *Epigondolella* sp. B, (d) sample MH61/21 (mh61_11), (e) sample MH61/21 (mh61_13), (f) sample MH61/21 (mh61_10). (g) *Epigondolella* ‘*tozeri*’, sample MH58/21 (mh58_03). (h–i) *Ancyrogondolella transformis*, (h) sample MH58/21 (mh58_07), (i) sample MH58/21 (mh58_17). (j) *Ancyrogondolella?* *transformis*, sample MH58/21 (mh58_10). (k–m) *Ancyrogondolella equalis*, (k) sample MH20/21 (mh20_03), (l) sample MH58/21 (mh58_57), (m) sample MH58/21 (mh58_55). (n) *Ancyrogondolella?* *praespiculata*, sample MH55/21 (mh55_03). (o) *Epigondolella* ‘*spiculata*’, sample MH55/21 (mh55_02). (p) *Mockina* cf. *matthewi*, sample MH61/21 (mh61_05). (q) *Ancyrogondolella* *inequalis*, sample MH58/21 (mh58_58). (r) *Epigondolella kozjanskoensis*, sample MH58/21 (mh58_35). (s–v) *Epigondolella* ex gr. *kozjanskoensis*, (s) sample MH58/21 (mh58_59), (t) sample MH58/21 (mh58_24), (u) sample MH61/21 (mh61_04), (v) sample MH58/21 (mh58_02). (w–b’) *Ancyrogondolella?* ex gr. *transitia*, (w) sample MH58/21 (mh58_39), (x) sample MH58/21 (mh58_44), (y) sample MH58/21 (mh58_20), (z) sample MH58/21 (mh58_54), (a’) sample MH58/21 (mh58_45), (b’) sample MH58/21 (mh58_23).

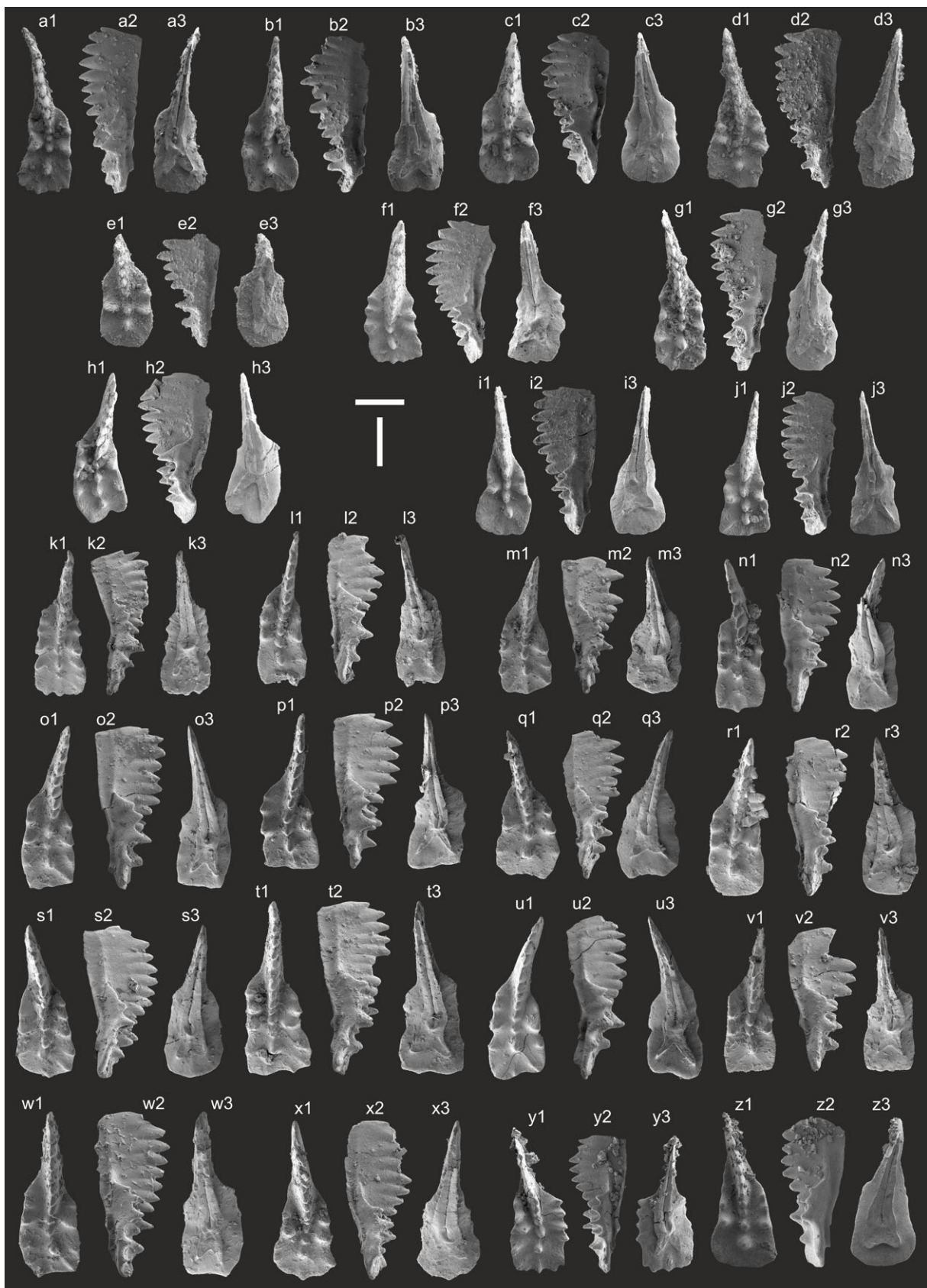


Figure 6. SEM micro-photographs of conodonts of the Mátyás Hill section. Scale bars are 200 μm , and all specimens are on the same scale. Three views (1, upper; 2, lateral; and 3, lower) are provided. (a–z) *Ancyrogondolella* spp., (a) sample MH1/21 (mh1_04), (b) sample MH1/21 (mh1_06), (c) sample MH1/21 (mh1_09), (d) sample MH3/21 (mh3_02), (e) sample MH3/21 (mh3_06), (f) sample MH3/21 (mh3_13), (g) sample MH5/21 (mh5_04), (h) sample MH5/21 (mh5_05), (i) sample MH5/21 (mh5_02), (j) sample MH5/21 (mh5_03), (k) sample MH9/21 (mh9_03), (l) sample MH20/21 (mh20_08), (m) sample MH20/21 (mh20_12), (n) sample MH20/21 (mh20_15), (o) sample MH20/21 (mh20_13), (p) sample MH20/21 (mh20_06), (q) sample MH20/21 (mh20_28), (r) sample MH20/21 (mh20_10), (s) sample MH20/21 (mh20_25), (t) sample MH20/21 (mh20_18), (u) sample MH20/21 (mh20_23), (v) sample MH20/21 (mh20_14), (w) sample MH20/21 (mh20_29), (x) sample MH32/21 (mh32_01), (y) sample MH38/21 (mh38_10), (z) sample MH42/21 (mh42_02).

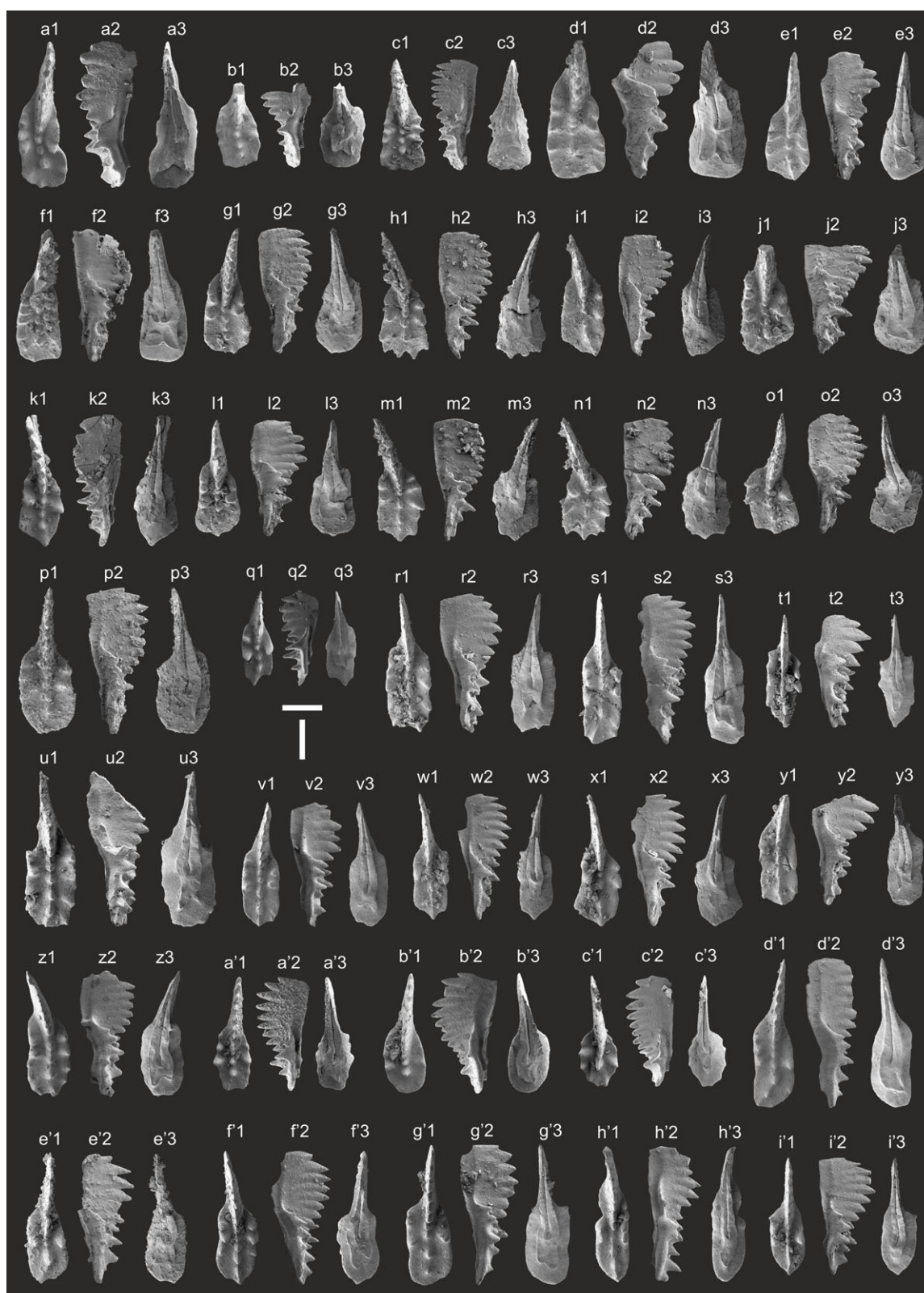


Figure 7. SEM micro-photographs of conodonts of the Mátyás Hill section. Scale bars are 200 μm , and all specimens are on the same scale. Three views (1, upper; 2, lateral; and 3, lower) are provided. (a–z) *Epigondolella* spp., (a) sample MH1/21 (mh1_07), (b) sample MH3/21 (mh3_11), (c) sample MH13/21 (mh13_01), (d) sample MH20/21 (mh20_02), (e) sample MH20/21 (mh20_22), (f) sample MH20/21 (mh20_27), (g) sample MH32/21 (mh32_02), (h) sample MH32/21 (mh32_06), (i) sample MH32/21 (mh32_07), (j) sample MH32/21 (mh32_08), (k) sample MH32/21 (mh32_17), (l) sample MH32/21 (mh32_18), (m) sample MH32/21 (mh32_15), (n) sample MH32/21 (mh32_09), (o) sample MH32/21 (mh32_13), (p) sample MH36/21 (mh36_10), (q) sample MH42/21 (mh42_04), (r) sample MH58/21 (mh58_05), (s) sample MH58/21 (mh58_06), (t) sample MH58/21 (mh58_09), (u) sample MH58/21 (mh58_12), (v) sample MH58/21 (mh58_16), (w) sample MH58/21 (mh58_18), (x) sample MH58/21 (mh58_21), (y) sample MH58/21 (mh58_27), (z) sample MH58/21 (mh58_34). (a'–i') *Mockina* spp., (a') sample MH3/21 (mh3_09), (b') sample MH3/21 (mh3_12), (c') sample MH13/21 (mh13_02), (d') sample MH58/21 (mh58_01), (e') sample MH58/21 (mh58_04), (f') sample MH58/21 (mh58_08), (g') sample MH58/21 (mh58_13), (h') sample MH58/21 (mh58_11), (i') sample MH58/21 (mh58_25).

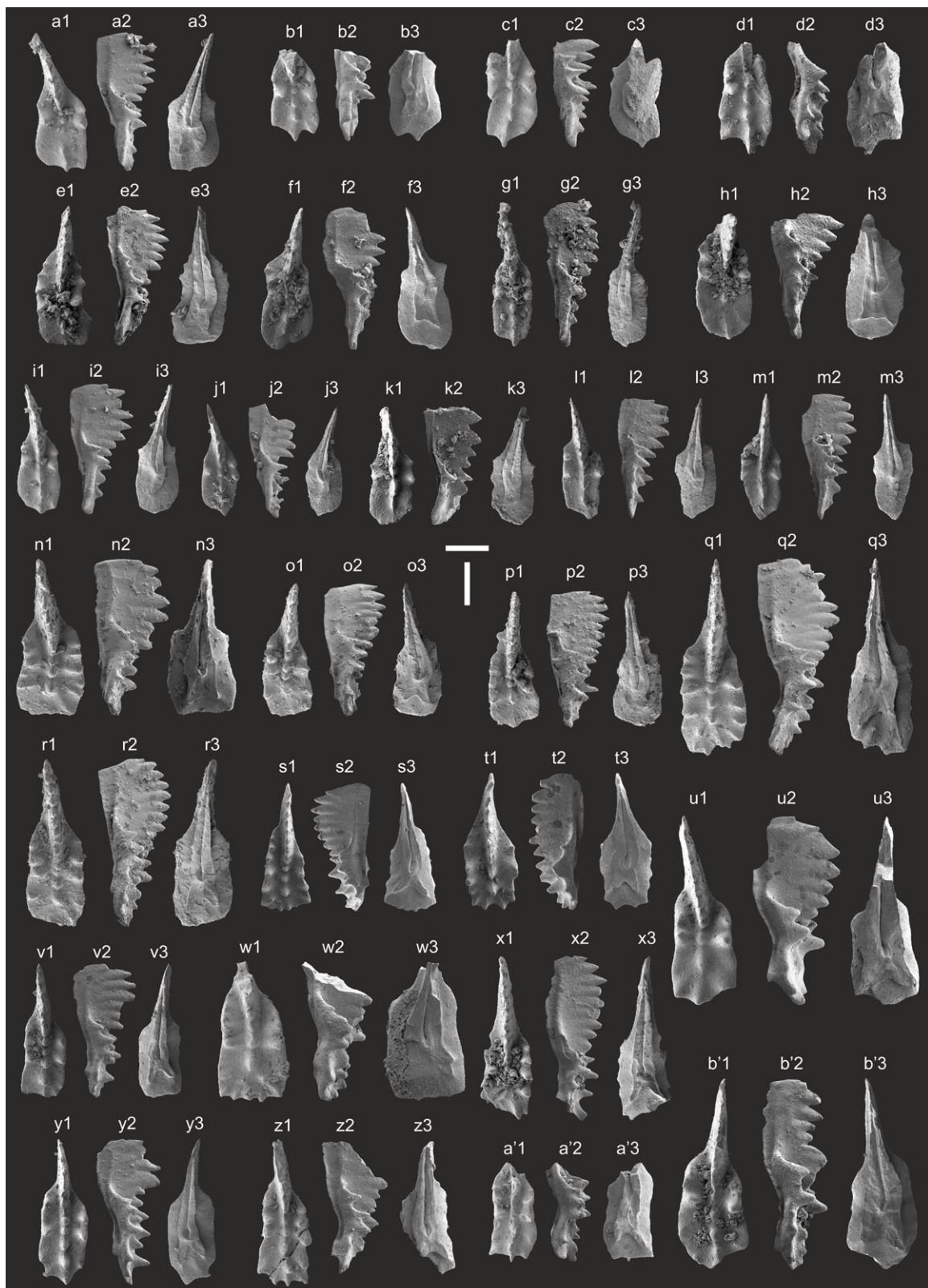


Figure 8. SEM micro-photographs of conodonts of the Mátyás Hill section. Scale bars are 200 μm , and all specimens are on the same scale. Three views (1, upper; 2, lateral; and 3, lower) are provided. (a–f) *Epigondolella* spp., (a) sample MH58/21 (mh58_38), (b) sample MH58/21 (mh58_60), (c) sample MH58/21 (mh58_61), (d) sample MH58/21 (mh58_62), (e) sample MH61/21 (mh61_02), (f) sample MH61/21 (mh61_08). (g–m) *Mockina* spp., (g) sample MH61/21 (mh61_03), (h) sample MH61/21 (mh61_07), (i) sample MH61/21 (mh61_09), (j) sample MH61/21 (mh61_14), (k) sample MH61/21 (mh61_06), (l) sample MH61/21 (mh61_15), (m) sample MH61/21 (mh61_16). (n–x) *Ancyrogondolella?* spp., (n) sample MH20/21 (mh20_26), (o) sample MH20/21 (mh20_05), (p) sample MH32/21 (mh32_04), (q) sample MH36/21 (mh36_02), (r) sample MH36/21 (mh36_14), (s) sample MH42/21 (mh42_01), (t) sample MH42/21 (mh42_03), (u) sample MH58/21 (mh58_53), (v) sample MH58/21 (mh58_33), (w) sample MH58/21 (mh58_46), (x) sample MH58/21 (mh58_40). (y–b') *Epigondolella?* spp., (y) sample MH58/21 (mh58_14), (z) sample MH58/21 (mh58_49), (a') sample MH58/21 (mh58_52), (b') sample MH58/21 (mh58_22).

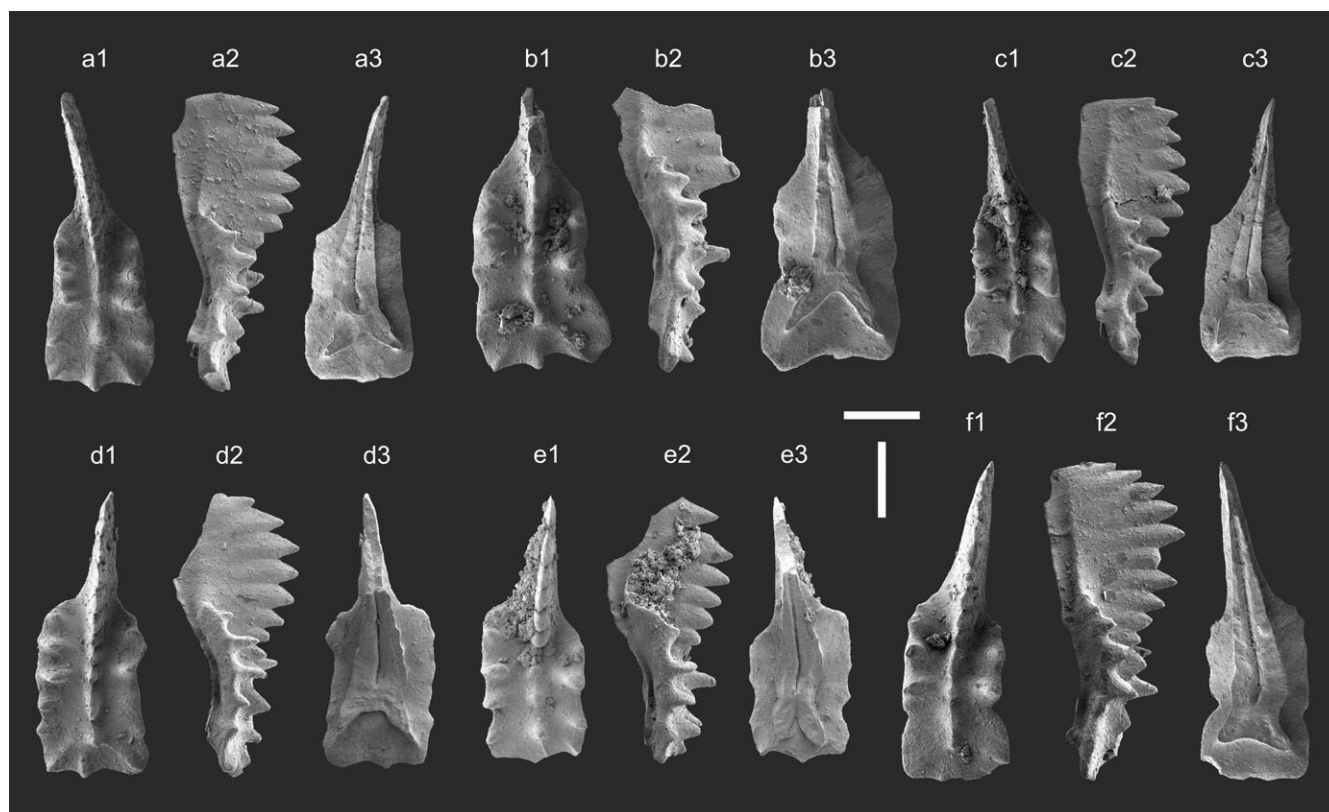


Figure 9. SEM micro-photographs of conodonts of the Mátyás Hill section. Scale bars are 200 μm , and all specimens are on the same scale. Three views (1, upper; 2, lateral; and 3, lower) are provided. (a–d) *Ancyrogondolella manueli* n. sp., (a) holotype, sample MH58/21 (mh58_43); (b) paratype, sample MH58/21 (mh58_32); (c) paratype, sample MH58/21 (mh58_42); (d) sample MH58/21 (mh58_47). (e–f) *Ancyrogondolella* ex gr. *manueli*, (e) sample MH58/21 (mh58_51), (f) sample MH58/21 (mh58_19).

Tethys, whereas some others are relatively recent finds in the Tethys, and their description and figuration are important to allow the comparison with the assemblages of the eastern Pacific. *Mockina* aff. *postera* was discussed in detail by Karádi (2018) and Karádi et al. (2021); therefore, it is not included here. Neither is *A. triangularis* since this taxon is a remnant of the Laciian-type assemblage that needs a thorough revision and will be the subject of a separate study.

Class Conodonta Pander, 1856

Order Ozarkodinida Dzik, 1976

Superfamily Gondolelloidea (Lindström, 1970)

Family Gondolellidae Lindström, 1970

Genus *Ancyrogondolella* Budurov, 1972

Type species: *Ancyrogondolella triangularis* Budurov, 1972

Description. This genus has a broad, symmetrical or asymmetrical platform, which bears high or moderately high denticles all over the margins or only at the anterior portions. The length of the free blade is between 1/2 and 1/3 element length. There is usually one carinal node behind the cusp; only stratigraphically younger species may have a longer posterior carina. The presence of secondary carinae is common. The pit occupies a central position below the platform. The keel termination shows a strong or moderately strong but distinct bifurcation, which starts just behind the pit. The lower margin of the element is arched in lateral view.

Remarks. The stratigraphically younger (i.e. uppermost Laciian – lowermost Alaunian) representatives of the genus may have more than one node behind the cusp, but these are either transitional taxa with still bifid keel termination (e.g. *A. equalis*,

A. inequalis and *A. transformis*) or included in the genus with question due to a much less developed secondary keel lobe (e.g. *Ancyrogondolella? transitia* and *Ancyrogondolella? praespiculata*).

Comparison. Genus *Ancyrogondolella* differs from both genus *Epigondolella* and genus *Mockina* in having a bifid keel termination, a centrally located pit, a short posterior carina and an arched lower profile.

Ancyrogondolella equalis Orchard, 2018

Figure 5k–m

pars 2013 *Epigondolella uniformis* Orchard, 1991 – Karádi et al., pl. 2, Figure 10 (only).

2018 *Ancyrogondolella equalis* n. sp. – Orchard, p. 172; pl. 1, Figures 15–19.

2021 *Ancyrogondolella equalis* Orchard, 2018 – Karádi et al., p. 685; Figures 5/4–5.

Material. Eight specimens in two samples.

Description. This species has a rectangular platform with parallel lateral margins. Denticulation is present all over the platform margins being stronger on the anterior part and weaker towards the posterior. The postero-lateral corners bear two obliquely oriented, ridge-like denticles. The free blade typically occupies 1/2 to 1/3 of the length of the element but closer to 1/3. The blade is high anteriorly and descends gradually towards the carina. The cusp is small and is followed by at least two mostly larger carinal denticles. In some of the more mature specimens, a secondary carina can occur. The pit is located just in front of the middle of the platform. The keel termination is clearly bifid, but in some specimens, the bifurcation does not reach close to the pit, and thus, the keel shows a slight posterior prolongation behind the pit.

The posterior lobes of the keel are a bit curved and outward directed in some specimens. The lower profile is stepped in lateral view.

Comparison. *Ancyrogondolella uniformis* has a shorter platform that is slightly broadening posteriorly and a shorter posterior carina. *Ancyrogondolella inequalis* is similar, but its platform is asymmetrical.

Occurrence. Uppermost Laciian substage to lowermost Alaunian substage of the western Tethys, lowermost Alaunian substage of western North America.

Ancyrogondolella inequalis Orchard, 2018

Figure 5q

pars 1973 *Epigondolella abneptis* (Huckriede) – Krystyn, pl. 4, Figure 3 (only).

2018 *Ancyrogondolella inequalis* n. sp. – Orchard, p. 172; pl. 3, Figures 7–15, 19–24.

Material. One specimen in one sample.

Description. This species has a subrectangular platform with one postero-lateral corner being more developed than the other. The anterior platform margins have two to four high denticles on both sides, and the rest of the platform is either strongly or weakly denticulated. The free blade is between 1/2 and 1/3 element length. The blade is anteriorly high, and it descends gradually towards the cusp, which is moderate in size. The posterior carina behind the cusp is composed of more than one denticle, and it is often bent towards the more developed postero-lateral corner of the platform. The pit is found approximately in the middle of the platform or slightly in front of it. The keel termination is deeply bifid behind the pit, and the two lobes are unevenly developed. The lower margin of the unit is slightly or moderately arched in lateral view.

Comparison. *Ancyrogondolella equalis* has a rectangular and symmetrical platform. The platform shape of *Ancyrogondolella? praespiculata* and of *E. 'spiculata'* is similar, but the former has a weakly developed secondary lobe of the keel, and the latter has a single-lobed keel.

Remarks. Orchard (2018) differentiated two morphotypes in the Canadian material. Both morphotypes A and B were found also in the fauna of the Mátyás Hill section. A specimen similar to morphotype A was figured by Krystyn (1973) from the Alaunian substage of Sommeraukogel, Austria.

Occurrence. Lowermost Alaunian substage of the western Tethys and western North America.

Ancyrogondolella manueli n. sp.

Figure 9a–d

pars 1990 *Epigondolella abneptis spatulatus* (Hayashi) – Wang and Wang, pl. 2, fig. ?8 (only)

2016 *Epigondolella vialovi* (Buryi, 1989) – Karádi et al., pl. IV, Figure 7.

Derivation of name. In honour of Manuel Rigo, University of Padova, for his outstanding contribution to Triassic conodont research.

Holotype. The specimen in Figure 9a, rep.-no. mh58_43.

Type locality. Old trench at the western margin of the abandoned quarry of Mátyás Hill, Buda Hills.

Type stratum. Greyish-yellow dolostone of Alaunian-1 age.

Material. Four specimens in one sample.

Diagnosis. A species with a narrow anterior and broad posterior platform. Large denticles are present on the anterior margins in a number of two to four. The postero-lateral margins have one shorter denticle on each side at the broadest part, and three ridge-like denticles are present on the posterior margin. The free blade is between 1/2 and 1/3 element length. The cusp is followed by one

larger denticle. The pit is central, and the keel termination is bifid. The lower contour of the unit is arched.

Description. The platform of this species is characterized by a narrower anterior half and a broader posterior half. The anterior platform has parallel margins which generally bear three large denticles. In some specimens, there are only two large denticles on one side, and rarely in other specimens, a fourth tiny denticle is developed anterior to the three large denticles on one side. There is a slight constriction just behind the last denticles of the anterior margins. Behind the constriction, the width of the platform increases suddenly and not gradually. The posterior platform is broadest at its midlength and modestly narrows towards the posterior. There is usually one shorter denticle on each side at the broadest part of the platform. On the posterior margin, three short, ridge-like denticles are present: two in the postero-lateral corners oriented obliquely and one in the middle in the continuation of the carina. The length of the free blade is between 1/2 and 1/3 unit length. The blade is anteriorly high and descends gradually towards the cusp, which is small in size. The posterior carina behind the cusp is composed only of one larger carinal denticle. The pit is centrally located, and the keel termination is markedly bifid. The bifurcation does not reach directly to the pit, and thus, the keel shows a very slight posterior prolongation. The lower margin of the element has an arched profile in lateral view.

Comparison. The platform width of *A. equalis* is uniform in its whole length, and its posterior carina is longer. *Ancyrogondolella diakowi* has a different posterior margin with an evident notch in the middle and more numerous denticles. *Ancyrogondolella transformis* is more slender, and the width of its platform is either uniform along the whole length, or it is broadest at the posteriormost part (as in Orchard, 2018, plate 2, Figure 20). *Ancyrogondolella triangularis* has a triangular platform outline that broadens gradually and is widest at the posteriormost part. The platform shape of *A. uniformis* differs in its rounded postero-lateral corners and its slight but gradual broadening towards the posterior. The keel of *E. tozeri* is single-lobed.

Remarks. This species unequivocally belongs to the genus *Ancyrogondolella*. It shows the morphological characters (short posterior carina, centrally located pit and posteriorly not prolonged keel) that are typical of Laciian representatives of the genus. In the Buda Hills, however, this species was always found in association with Alaunian taxa (Karádi et al. 2016, this study). The specimen figured by Wang and Wang (1990) from China is assigned here to *A. manueli* n. sp. with question, because no lower and lateral views were provided.

Occurrence. Lower Alaunian substage of the western Tethys and perhaps also the eastern Tethys.

Ancyrogondolella ex gr. *manueli*

Figure 9e–f

Material. Two specimens in one sample.

Remarks. Some specimens were found in the material, which are basically similar to *A. manueli* n. sp., but have a few characters that are not very well developed or not typical of the species. Such features are, for example, the not-so-obvious denticulation on the posterior platform half and a weak keel bifurcation. These forms came from the same sample as *A. manueli* n. sp. and are referred to as *Ancyrogondolella* ex gr. *manueli* in this study.

Occurrence. Lower Alaunian substage of the western Tethys.

Ancyrogondolella? praespiculata Orchard, 2018

Figure 5n

pars 2018 *Mockina spiculata* (Orchard, 1991b) – Karádi, p. 169–170; pl. 2, Figure 7 (only).

2018 *Ancyrogondolella? praespiculata* n. sp. – Orchard, p. 174, pl. 3, Figures 1–6.

Material. One specimen in one sample.

Description. This conodont has a slender platform that is asymmetric, since one side is straight and the other is curved. Two large denticles are present on both anterior margins. The rest of the platform margins have shorter but distinct denticles that are more numerous on the curved side. The platform shows a slight constriction just behind the denticles of the anterior margins. There are two well-separated denticles in the posterior carina behind the cusp, and a short, ridge-like, obliquely oriented denticle, which is fused with the posterior platform margin and directed towards the postero-lateral corner of the straight side. The pit is located slightly in front of the platform midlength. The keel is bifid with one lobe being more developed than the other. The bifurcation does not reach directly to the pit.

Comparison. *Ancyrogondolella inequalis* has two well-developed keel lobes. The keel of *E. spiculata* is single-lobed. The specimen from the Mátyás Hill section differs from the North American representatives, including the holotype, of the species (Orchard, 2018) in being more slender. It is very similar to the specimen presented by Karádi (2018) as *M. spiculata* morphotype A from another locality of the Buda Hills, which specimen was included in the synonymy of *Ancyrogondolella? praespiculata* by Orchard (2018, p. 174).

Remarks. The only available specimen lacks the blade, and thus, the length of the free blade and the contour of the lower profile cannot be described.

Occurrence. Lower Alaunian substage of the western Tethys and western North America.

Ancyrogondolella transformis Orchard, 2018

Figure 5h–j

2018 *Ancyrogondolella transformis* n. sp. – Orchard, p. 172–173; pl. 2, Figures 8–13, 19–26.

Material. Four specimens in one sample.

Description. The platform of this species is slender and has a slight constriction at or just behind the midlength. The anterior platform margins bear two to three large denticles. Some smaller denticles can be present on the postero-lateral margins, and usually, there is one obliquely oriented denticle in each postero-lateral corner. A small, posteriorly projected denticle can be found in the middle of the posterior margin in the continuation of the carina. The free blade is between 1/2 and 1/3 element length. The blade is anteriorly high and descends rapidly but gradually towards the cusp. The cusp is followed by two well-separated carinal denticles. The pit is located just in front of the middle of the platform. The keel is posteriorly prolonged behind the pit and has a symmetrically or asymmetrically bifid termination. Sometimes one of the keel lobes is strongly reduced. The element shows arched profile in lateral view.

Comparison. *Ancyrogondolella equalis* lacks the platform constriction and has more numerous denticles all over the margins. *Ancyrogondolella manueli* n. sp. has a different platform outline as it rapidly broadens at the beginning of the posterior half. It has only one denticle behind the cusp, and its keel termination is widely bifid. *Orchardella multidentata* lacks the bifurcation of the keel, and it has smooth postero-lateral and posterior platform margins.

Occurrence. Lowermost Alaunian substage of the western Tethys and western North America.

Ancyrogondolella? ex gr. transitia (Orchard, 1991)

Figure 5w–b'

Material. Six specimens in one sample.

Remarks. These specimens from the Mátyás Hill section show an asymmetric platform outline with denticles all around, likewise in *Ancyrogondolella? transitia*. They differ, however, in their keel termination, which is slightly or moderately bifid, whereas the keel of *Ancyrogondolella? transitia* is asymmetric but non-bifid.

Occurrence. Lowermost Alaunian substage of the western Tethys.

Genus *Epigondolella* Mosher, 1968

Type species: *Polygnathus abneptis* Huckriede, 1958

Description. This genus has a platform that varies between broad and narrow, symmetrical and asymmetrical, and bears strong denticulation on the anterior margins, whereas the rest of the margins can be variably ornamented or unornamented. The free blade covers between 1/2 and 1/3 of the whole unit length but usually closer to 1/3. At least two carinal nodes are present in the posterior carina. The pit is slightly to moderately shifted anteriorly relative to the platform midlength. The keel shows a posterior prolongation behind the pit. It is mostly single-lobed with a squared or obliquely truncated termination, but in some cases, the remnant of a secondary lobe is still visible. In lateral view, the lower profile has a stepped or upturned appearance.

Comparison. Genus *Epigondolella* differs from genus *Mockina* in its keel termination and platform outline. See differences from genus *Ancyrogondolella* under genus *Ancyrogondolella*.

Epigondolella 'spiculata' Orchard, 1991

Figure 5o

non 1983 *Epigondolella* n. sp. C – Orchard, p. 185–186; Figure 15/M–O.

non 1987 *Epigondolella multidentata* Mosher, 1970 – Mao & Tian, pl. I, Figures 16–20.

non 1991 *Epigondolella spiculata* n. sp. – Orchard, p. 312–313; pl. 3, Figures 10, 14, 15.

? 2003 *Epigondolella spiculata* Orchard – Channell et al., Figure A2/38, A2/40.

non 2003 *Epigondolella spiculata* Orchard – Ji et al., pl. 1, Figures 4–9.

non 2003 *Epigondolella tozeri* Orchard – Ji et al., pl. 1, Figures 12–16.

non 2005 *Epigondolella spiculata* Orchard – Onoue & Tanaka, Figure 13/18.

non 2005 *Epigondolella* cfr. *spiculata* Orchard, 1991 – Rigo et al., Figure 4/1.

pars 2005 *Epigondolella serrulata* Orchard, 1991 – Rigo et al., Figure ?4/3 (only).

non 2008 *Epigondolella spiculata* Orchard, 1991b – Katvala & Stanley, p. 223; Figures 42/1–7.

non 2016 *Mockina spiculata* (Orchard, 1991) – Karádi et al., pl. I, Figure 1, pl II, Figure 3.

pars 2018 *Mockina spiculata* (Orchard, 1991b) – Karádi, p. 169–170; pl. 2, Figure ?8 (only).

pars 2018 *Epigondolella spiculata* Orchard, 1991c – Orchard, p. 175; pl. 4, Figures 11–16 (only).

non 2021 *Epigondolella spiculata* Orchard, 1991a – Karádi et al., p. 691; Figure 7/9.

Material. One specimen in one sample.

Description. This species has a platform with subparallel margins but an asymmetrically developed posterior end. The anterior margins bear three denticles on the external side and two on the internal side of the element. Short denticles occur on the rest of the platform margins. The free blade is 1/3 element length. The blade is anteriorly high and descends gradually towards the cusp.

The posterior carina behind the cusp consists of two larger carinal denticles and a shorter, ridge-like denticle that is obliquely oriented and outwardly projected giving the posterior margin a pointed appearance and enhancing the asymmetry of the platform. The pit is found slightly in front of the platform midlength. The keel is posteriorly prolonged behind the pit and has an asymmetrically rounded termination. The lower profile is stepped in lateral view.

Comparison. *Ancyrogondolella? praespiculata* has a weakly developed secondary keel. The keel termination of *A. inequalis* is clearly bifid.

Remarks. The specimen assigned to *E. 'spiculata'* is somewhat different from the holotype of *E. spiculata*. It has a less prominent denticulation on the posterior half of the platform and a different keel shape. Orchard (2018, pl 4., Figures 11–16) figured two specimens that also differ from the holotype and are very similar to the specimen presented here (Figure 5o). These specimens figured by Orchard (2018) were found in the lower part of the *multidentata* Zone (lower Alaunian substage) of North America, from a lower stratigraphic position than the FO of true *E. spiculata*. Since no representatives of *E. spiculata* were recovered from the interval between the two occurrences, Orchard (2018) indicated an assumed range of the species and connected the early forms and the late (more typical) representatives with dashed line (see Figure 4 in Orchard, 2018). According to the author, the stratigraphically older specimens might belong to a different species rather than to *E. spiculata*. However, due to the very few available specimens, this problem cannot be resolved at the moment, and therefore, the species name *E. 'spiculata'* is placed in quotation marks, just like in the case of *E. 'tozeri'*.

Occurrence. Lower Alaunian substage of the western Tethys and western North America.

Epigondolella 'tozeri' Orchard, 1991

Figure 5g

non 1991 *Epigondolella tozeri* n. sp. – Orchard, p. 313–314; pl. 5, Figures 1–3, 6–8.

non 2003 *Epigondolella tozeri* Orchard – Ji et al., pl. 1, Figures 12–16.

non 2006 *Epigondolella tozeri* Orchard – Orchard, pl. 8, Figure 17.

non 2008 *Epigondolella tozeri* Orchard, 1991b – Katvala & Stanley, p. 223; Figures 42/26–31.

non 2016 *Mockina* cf. *tozeri* (Orchard, 1991) – Karádi et al., pl. II, Figure 5.

non 2016 *Mockina tozeri* (Orchard, 1991) – Karádi et al., pl. IV, Figure 3.

pars 2018 *Epigondolella tozeri* Orchard, 1991c – Orchard, p. 175–176; pl. 4, Figures 17–22 (only).

2021 *Epigondolella tozeri* Orchard, 1991a – Karádi et al., p. 691–692; Figures 7/10–11.

Material. One specimen in one sample.

Description. This conodont species has a slender, subrectangular platform with a truncated termination. The anterior platform margins bear two to three large or moderately large denticles. The rest of the margins have smaller denticles of which two typically develop at the postero-lateral corners and one in the middle of the posterior margin in the continuation of the carina. The free blade is short, ~1/3 unit length or even less. The blade is anteriorly high and descends gradually but rapidly into the carina. The cusp is small, and it is followed by two larger carinal denticles. The pit is slightly forward shifted in front of the middle of the platform. The keel is posteriorly prolonged behind the pit, and it has a narrowly

rounded or truncated termination which is usually asymmetrical. The lower margin of the element is slightly arched in lateral view.

Comparison. *Ancyrogondolella equalis* is broader, and its keel termination is clearly bifid. *Epigondolella* sp. A n. sp. is broader, and it has weaker denticulation, a longer free blade and a keel that is posteriorly broadly truncated.

Remarks. The specimen assigned to *E. 'tozeri'* is similar to but not identical with the larger and broader holotype of *E. tozeri*. They differ the most in their keel shapes. Orchard (2018, pl 4., Figures 17–22) figured two specimens that also differ from the holotype and are very similar to the specimen presented here (Figure 5g) and to those documented from Slovenia by Karádi et al. (2021, Figures 7/10–11). Both specimens in Orchard (2018) came from the lower part of the *multidentata* Zone (lower Alaunian substage) of North America, from a lower stratigraphic position than the FO of true *E. tozeri*. Since no representatives of *E. tozeri* were reported from the interval between the two occurrences, Orchard (2018) indicated an assumed range of the species and connected the early forms and the late (more typical) representatives with dashed line (see Figure 4 in Orchard, 2018). According to the author, all the above arguments suggest that the stratigraphically older specimens might represent a species different from *E. tozeri*. However, due to the very few available specimens (two from Canada, two from Slovenia and one from Hungary), this problem cannot be resolved at the moment, and therefore, the species name *E. 'tozeri'* is placed in quotation marks, just like in the case of *E. 'spiculata'*.

Occurrence. Lower Alaunian substage in the western Tethys and in western North America.

Epigondolella kozjanskoensis Karádi & Kolar-Jurkovšek, 2021 in Karádi et al. (2021)

Figure 5r

2021 *Epigondolella kozjanskoensis* n. sp. – Karádi et al., p. 690; Figures 6/11–15.

Material. One specimen in one sample.

Description. This species is characterized by a symmetrical, posteriorly slightly widening platform with subparallel margins. The postero-lateral corners can be slightly rounded or more angular. The anterior platform margins bear two to three large denticles. The rest of the platform is weakly ornamented, and often, there is a difference in the denticulation of the two postero-lateral margins. A very low, obliquely oriented, ridge-like denticle develops at the postero-lateral corner at least on one side. The middle of the posterior margin shows a pointed appearance due to a low, posteriorly projected denticle in the continuation of the carina. The free blade is between 1/2 and 1/3 element length. The blade is high anteriorly and lowers posteriorly until the small cusp. The posterior carina behind the cusp is composed of two large, well-separated denticles. The pit is situated clearly in front of the platform midlength. The keel is wide, and it has a broadly (and often obliquely) truncated termination. The posterior margin of the keel can be slightly concave, but this cannot be considered as bifurcation. In lateral view, the element has a stepped profile.

Comparison. This species is similar to true *E. tozeri*, but in *E. tozeri*, the postero-lateral corners of the platform are not rounded, and both bear a sharp denticle. Its postero-lateral platform margins are more strongly denticulated than in *E. kozjanskoensis*. *Ancyrogondolella equalis* differs in having a bifid keel termination.

Occurrence. Lower Alaunian substage of the western Tethys.

Epigondolella ex gr. *kozjanskoensis* Karádi & Kolar-Jurkovšek, 2021, in Karádi et al. (2021)

Figure 5s–v

Material. Four specimens in two samples.

Remarks. Some specimens of the Mátyás Hill section resemble *E. kozjanskoensis*, but they differ in the development of the postero-lateral corners. One of them is rounded, and the other one is angular, which gives the platform an asymmetric appearance. Probably, this can be considered intraspecific variability (especially because they are from the same sample as *E. kozjanskoensis*), but for the time being, these specimens are classified here as *Epigondolella* ex gr. *kozjanskoensis*.

Occurrence. Lower Alaunian substage of the western Tethys.

Epigondolella sp. A

Figure 5b–c

Material. Two specimens in two samples.

Diagnosis. A species with a slender platform that is broader in the anterior half and narrower in the posterior half. The anterior margins bear large denticles, and the narrow part of the platform is undenticulated or very weakly ornamented. The free blade is 1/2 to 1/3 element length. The cusp is followed by two carinal denticles. The pit is found below the anterior half of the platform. The keel is prolonged posteriorly with a blunt end. The lower contour of the unit is stepped.

Description. The platform of this species is slender and has a rectangular posterior termination. The platform is broadest in its anterior half where two to three large denticles are present on the anterior margins. The rest of the platform behind the anterior marginal denticles is narrow and generally unornamented or can have a very low node-like denticle on the posterior margin and even lower nodes at the postero-lateral corners. The free blade is between 1/2 and 1/3 unit length. The blade is high anteriorly and descends slowly and gradually towards the cusp. The posterior carina behind the cusp is composed of two denticles. The pit is forward shifted in front of the middle of the platform. The keel is posteriorly prolonged, and it has a blunt, somewhat asymmetric termination. The posterior edge of the keel is slightly concave, but this cannot be considered as bifurcation. The profile of the lower margin is stepped in lateral view.

Comparison. *Mockina medionorica* has a suboval platform with a rounded posterior end and a rounded keel termination. It also differs in having less anterior marginal denticles than *Epigondolella* sp. A n. sp. *Orchardella multidentata* of western North America is longer with a pointed or narrowly truncated posterior end of the platform. In addition, its keel termination is pointed, and it has a longer posterior carina. True *E. tozeri* has a more denticulated platform that is uniform in width along its length.

Remarks. *Mockina medionorica* is very poorly known, even the holotype is figured only from upper view (Kozur, 2003, pl. 1, Figure 5). The intraspecific variability of *M. medionorica* has to be understood before it can be compared in detail with *Epigondolella* sp. A.

Occurrence. Lower Alaunian substage of the western Tethys.

Epigondolella sp. B

Figure 5d–f

Material. Three specimens in one sample.

Diagnosis. A species with a platform that has a broadly rounded termination and a posterior margin with two posteriorly projecting tips. Denticles are present only on the anterior margins, or a pair of weak nodes can develop behind the anterior marginal denticles. The posterior carina is composed of two denticles. The pit is situated below the anterior half of the platform. The keel has a narrowly truncated, slightly asymmetric end. The lower contour of the unit is stepped.

Description. This species has a platform that is the same width along its length or slightly broader at the posterior half. The posterior end is quite peculiar. It is broadly rounded, and the posterior margin has two posteriorly projected tips, which give the platform a more or less symmetrical appearance. The anterior margins have two to three large denticles. The posterior platform half is unornamented, or a pair of very low nodes may occur just behind the last denticles of the anterior margins. The cusp is small, and it is followed by one large and one small carinal denticles, which are well separated. The pit is located in front of the middle of the platform. The keel is narrow and posteriorly prolonged, and it has a narrowly truncated, slightly asymmetric termination. The unit has a stepped lower profile in lateral view.

Comparison. *Mockina matthewi* has a rounded keel termination and lacks the projecting tips of the posterior margin of the platform. *Orchardella multidentata* differs in its platform outline, the length of its posterior carina and the termination of its keel.

Remarks. The blade was not completely preserved in either of the available specimens; therefore, the length of the free blade cannot be described.

Occurrence. Lower Alaunian substage of the western Tethys.

Genus *Mockina* Kozur, 1989

Type species: *Tardogondolella abneptis postera* Kozur & Mostler, 1971

Description. The platform of this genus is generally biconvex or posteriorly strongly tapering. In stratigraphically young species, it is strongly underdeveloped. The platform margins have variable denticulation, but very often only the anterior margins bear denticles. The length of the free blade is ~1/3 unit length or even shorter. There are at least two carinal nodes in the posterior carina behind the cusp. The anteriorly shifted pit is located in front of the middle of the platform. The single-lobed keel is characterized by a marked posterior prolongation behind the pit and a rounded or pointed termination. The elements have a stepped, straight or rarely upturned lower margin in lateral view.

Comparison. See under the genera *Ancyrogondolella* and *Epigondolella*.

Mockina matthewi (Orchard, 1991)

Figure 5p

1991 *Epigondolella matthewi* n. sp. – Orchard, p. 309; pl. 4, Figures 8–10.

2001 *Mockina* aff. *matthewi* (Orchard, 1991) – Ishida & Hirsch, p. 238, 240; pl. 5, Figure 3.

pars 2001 *Mockina postera* (Kozur & Mostler, 1971) – Ishida & Hirsch, pl. 4, Figure 4 (only).

2002 *Mockina* aff. *matthewi* Orchard – Ishida & Hirsch, pl. 1, Figure 2.

2002 *Mockina postera* (Kozur & Mostler) – Ishida & Hirsch, pl. 1, Figure 3.

2006 *Epigondolella matthewi* Orchard – Orchard, pl. 8, Figure 16.

? 2008 *Epigondolella matthewi* Orchard, 1991b – Katvala & Stanley, p. 222; Figure 42/8.

2016 *Mockina matthewi* (Orchard, 1991) – Karádi et al., pl. IV, Figure 6.

2018 *Mockina matthewi* (Orchard, 1991b) – Karádi, p. 165; pl. 2, Figures 1, 4, 6.

2018 *Mockina* ex gr. *M. matthewi* (Orchard, 1991c) – Orchard, p. 176–177; pl. 3, Figures 17, 18, 25–33.

Material. One specimen in one sample.

Description. This species has a biconvex platform that is broadest at the midlength. The platform termination is rounded.

Denticles are present only on the anterior platform margins; the rest of the margins are unornamented. The cusp is small, and it is followed by three larger, well-separated denticles of the posterior carina. The pit is forward shifted in front of the middle of the platform. The keel is markedly prolonged posteriorly, and its termination is rounded.

Comparison. *Ancyrogondolella? bohorensis* has a keel with an asymmetrically truncated or slightly bifid termination. Its platform outline is also different as it broadens suddenly behind the denticles of the anterior margins. *Mockina* aff. *postera* is smaller, it has less denticles on the anterior margins, and its platform is posteriorly pointed.

Remarks. The only available specimen lacks the blade and the anteriormost part of the platform, and thus, the length of the free blade and the contour of the lower profile cannot be described.

Occurrence. Upper part of Lacia-3 substage to Alaunian substage of the western Tethys, eastern Tethys and western North America.

6. Discussion

As mentioned in Section 1, the subdivision of the Triassic System of the western Tethys Realm was based on ammonoids of predominantly very condensed Alpine sections of Austria. The calibration of the ranges of certain Norian conodont taxa with the standard ammonoid zonation was likewise done in Alpine successions. An integrated ammonoid-conodont zonation including conodont ranges was presented by Krystyn (1980). Later, this scheme was somewhat refined by Krystyn et al. (2009) but with minor changes only. The long range of *E. abneptis* was split, and *E. quadrata*, *E. triangularis*, *E. spatulata* and *E. 'multidentata'* were included to mark distinct intervals of the Lacia-3 and the Alaunian substages. It is clear that the overall picture did not improve much in 29 years (and neither did till today), since almost the same oversimplified taxonomy was used for the Norian *Epigondolella* lineage (*Ancyrogondolella*, *Epigondolella* and *Mockina* in the present study) as before. Representatives of this lineage were only scarcely figured, and thus, other conodont specialists can hardly understand what morphological variety is exactly included by Alpine stratigraphers in the species listed above.

The only species which seem to have ranges quite well calibrated with ammonoid zones in Alpine stratigraphic studies belong to the genus *Norigondolella*. Representatives of this taxon were deep-water dwellers according to Trotter et al. (2015), which lived in a stable environment and probably had a monotonous diet. As a consequence, *norigondolellids* are not really diverse, and they generally have long ranges; therefore, they are less suitable for precise biostratigraphic dating than the *ancyrogondolellids* and related taxa. Fortunately, it is the upper Lacia-3 to lower Alaunian interval where species of the genus *Norigondolella* turned out to be useful stratigraphic markers. *Norigondolella hallstattensis* indicates the Lacia-3 substage as it is coeval with ammonoids of the *Juvavites magnus* Zone, whereas the first appearance of *N. steinbergensis* is around the base of the lower Alaunian *Cyrtopleurites bicrenatus* Zone (Krystyn, 1980; Krystyn et al. 2009). The problem with *norigondolellids* is that their occurrences are controlled either by competition with other taxa (Kozur, 2003; Mazza et al. 2010) or by temperature (Trotter et al. 2015). Nevertheless, when either of these two species are present in a sample, they can be applied to anchor certain levels of a section.

Age assignment of the Mátyás Hill section in the present study leans strongly on the genus *Norigondolella*. The lower part of the

section can be unequivocally assigned to the Lacia-3 substage based on the presence of *N. hallstattensis* up to sample MH23/21. No samples yielded *N. steinbergensis*, but two specimens with transitional characters between *N. navicula* and *N. steinbergensis* are present in samples MH8/19 and MH45/21 (Figure 4x). These are quite slender forms having a large cusp situated close to the posterior margin but still surrounded by a narrow platform brim. It suggests that the base of the Alaunian substage is still a bit higher up in the section. *Ancyrogondolella 'spatulata'* in sample MH32/21 also supports the Lacia-3 age of this level, since this is the same taxon as *E. spatulata* in Figure 1 of Krystyn et al. (2009) used as the index species of the Lacia-3 substage. In the present study, however, '*spatulata*' is written in quotation marks, because the holotype of true *A. spatulata* (pl. 2, Figure 5 in Hayashi, 1968) differs from this upper Lacia-3 taxon, and the original description of the species does not include any figures of specimens other than the holotype. In addition, specimens that resemble the holotype were documented from the lower part of the Lacia-3 substage in the Pizzo Mondello section in Sicily, Italy (Mazza et al. 2012b). Being an issue of Lacia-3 taxonomy and biostratigraphy, it is beyond the scope of this study, but it needs to be resolved soon by the revision of *A. spatulata* in a separate paper.

At this point, the cause of the evident faunal mixing in large part of the Mátyás Hill section has to be discussed. This can be resulted in either by the reworking of older material in the form of sedimentary breccias or by the deposition of younger conodonts in neptunian dykes or fissure fills cross-cutting older beds. Both scenarios are well known from the Lacia-3–Alaunian transition in the western Tethys (e.g. Gallet et al. 1992; Gawlick & Böhm, 2000; Channell et al. 2003; Karádi et al. 2021), but in the case of the Mátyás Hill section, neptunian dykes seem more probable. Unfortunately, the pervasive dolomitization of the rocks does not allow to observe such sedimentary features in most cases neither in the field nor in thin sections. The thin section made from sample MH32/21, however, might reveal a fissure fill (Figure 3d). Hips et al. (2016) states that the characteristic microbreccia fabric in certain beds of the section is the result of the dolomitization and not inherited from the precursor carbonates. According to the author, if the faunal mixing was caused by synsedimentary breccias, the samples should contain a more diverse and abundant Alaunian assemblage (similar to that in sample MH58/21) throughout the Mátyás Hill section, into which the Lacia-3 conodonts have been reworked. In the lower 16 m of the section, however, the assemblage is dominated by the genus *Ancyrogondolella* over specimens assignable to the genera *Epigondolella* and *Mockina*. These latter genera then become dominant in the upper 3 m of the section, which interval is characterized by conodonts with typical Alaunian-1 morphologies.

The true morphological variety of the representatives of the genus *Ancyrogondolella* in the Lacia-3 is yet to be researched. The recently studied conodonts of Mátyás Hill and Dovško revealed that the diversity of the *Ancyrogondolella* population of the western Tethys is much higher than thought before. In every section, several specimens occur, which undoubtedly belong to the genus *Ancyrogondolella* but do not fully fit in any of the already described species of the genus. These conodonts were previously routinely ignored, especially in stratigraphic studies, since they are useless for biostratigraphic dating. This practice leads to a serious information loss and totally obstructs comparative investigations. In the present work, such conodont P1 elements are documented as *Ancyrogondolella* spp. (Figures 6a–z and 8n–x).

In other cases, more precise determinations were possible. In sample MH20/21, for example, a specimen of *A. equalis* was found (Figure 5k). Its occurrence at this level may seem to be a bit low, since this species was described from the lower Alaunian-1 substage of western North America. Likewise, in the Dovško section in Slovenia, it appears only in the Alaunian-1 substage together with *N. steinbergensis* (Karádi et al. 2021). This suggests that the specimen in question is possibly also reworked; however, in the Csővár core (in north-central Hungary), this species was found just below the Alaunian interval accompanied by *A. triangularis* and *A. uniformis* (Karádi & Korte, 2023). Thus, it cannot be excluded that the First Appearance Datum (FAD) of *A. equalis* is somewhat earlier than previously documented. The sample MH20/21 yielded also several specimens of *Ancyrogondolella? bohorensis* (Figure 4m–n), a species showing typical Alaunian morphological characters (i.e. a forward-shifted pit, a posteriorly prolonged keel and a posterior carina with more than one denticle). Interestingly, this species is present at approximately the same level also at Dovško (Karádi et al. 2021), and it was not found higher in the Alaunian-1 substage in either of the sections. These facts make it more likely that this conodont already appeared in the Lacia-3 substage and can be an early representative of the Alaunian-type faunas.

Sample MH27/21 yielded one specimen of *A. diakowi posterolobata*. This subspecies of *A. diakowi* was recently described from Slovenia (Karádi et al. 2021), but it was not abundant in the Dovško section either. There, it was found somewhat above *A. spatulata* and *N. hallstattensis* but still below the diverse Alaunian assemblage. In the Mátyás Hill section, it is present between the last occurrence of *N. hallstattensis* and the single occurrence of *A. spatulata*, stratigraphically a bit lower than in the Slovenian section. Unfortunately, only these two specimens are known from the Tethys so far. Even if it was previously found in other Tethyan sections, it was never figured, and most probably it was assigned to *A. triangularis*, from which it differs in the contour of the posterior platform margin. The peculiar indentation in the outline of this margin characterizes both the western North American *A. diakowi diakowi* (pl. 2, Figures 1–7, 14, 15 in Orchard, 2018) and the Tethyan *A. diakowi posterolobata* (Figure 5/3 in Karádi et al. 2021, Figure 4o in this study). The two subspecies seem to have slightly different but overlapping stratigraphic ranges. *Ancyrogondolella diakowi posterolobata* is present in the Lacia-3 substage (Buda Hills, Hungary) to the lowermost Alaunian-1 substage (Dovško, Slovenia), and *A. diakowi diakowi* is found only in the lowermost Alaunian-1 substage (Pink Mt., British Columbia, Canada); however, the significant difference in their paleobiogeographic distributions is against the ancestor–descendant relation. According to the author, it is more probable that the narrower and longer *A. diakowi diakowi* and the postero-laterally more expanded *A. diakowi posterolobata* represent two ecomorphotypes of the same species. This morphological difference is generally observable between the Upper Triassic conodont assemblages of the Tethys and the eastern Pacific. This phenomenon has never been studied in detail, but it was briefly discussed by Karádi (2021).

A major change in the faunal composition is observed from sample MH55/21 (Figure 2). From here upwards, the Lacia-type representatives of the genus *Ancyrogondolella* strongly decrease in number regarding both species and specimens, and species assignable to the genera *Epigondolella* and *Mockina* dominate. This interval can be definitely assigned to the Alaunian substage. It is an interesting feature that this level is characterized by the mass occurrence of a diverse assemblage, which includes several species,

but none of the species is represented by many specimens. This is exactly the case in the Dovško section, too (Karádi et al. 2021); however the composition of the fauna shows clear differences. The species *E. senovoensis*, *E. slovenica*, *E. buseri*, *E. ritae*, *Mockina? spinosa* and *M. medionorica* were not found in the Mátyás Hill section, although *M. medionorica* and conodonts similar to *E. slovenica* were reported from elsewhere in the Buda Hills (Karádi, 2018).

Epigondolella kozjanskoensis, introduced as a new species in Karádi et al. (2021) from Dovško, was also recovered from sample MH58/21 of Mátyás Hill. Since the intraspecific variability of this species is not yet well known, similar forms of the fauna that show a slight difference in the development of the postero-lateral corners were separated and are indicated here as *Epigondolella* ex gr. *kozjanskoensis*. Another taxon that was found at both Dovško and Mátyás Hill is *E. 'tozeri'*. This species might be identical to that figured by Orchard (2018) in plate 4, Figures 17–22, as *E. tozeri*. Here, it is written in quotation marks to indicate that, according to the author, it is different from the stratigraphically younger holotype of the species (pl. 5, Figures 6–8 in Orchard, 1991). This view is also supported by the fact that there is a gap in the range of the species where no specimens are present between these early forms of *E. 'tozeri'* and the stratigraphically younger, true *E. tozeri* fauna (see Figure 4 in Orchard, 2018). *Epigondolella 'spiculata'* is written here in quotation marks for the same reason.

Karádi et al. (2016, pl. 4, Figure 7) figured a specimen and tentatively named it *E. vialovi* (*A. vialovi*) from the Alaunian outcrop at 45 Rácz Aladár Road in the Buda Hills. Although it was recovered together with unequivocally Alaunian species, this specimen shows typical characters of the Lacia ancyrogondolellids. It has a centrally located pit, a deeply bifid keel termination and only one denticle in the posterior carina behind the cusp. The section was later published in detail by Karádi (2018), but by mistake, this specimen was not marked on the log. Nevertheless, several specimens identical to that of Karádi et al. (2016) were found in the Alaunian part of the Mátyás Hill section, which revealed that this species is most likely a late representative of the genus *Ancyrogondolella* and is described here as *A. manueli* n. sp. Together with *Ancyrogondolella? bohorensis* from the Lacia-3 substage, these species support the view that the replacement of Lacia faunas by markedly different Alaunian assemblages was not caused by a sudden faunal turnover as it may seem in condensed successions but rather by stepwise evolution.

The recovery of the species *A. inequalis* and *A. transformis* in the Alaunian of Mátyás Hill is probably the most important result of this study, not only from stratigraphic aspects but also from a paleobiogeographical point of view. Since these taxa are indicative of the lower Alaunian *A. transformis* Zone of western North America (Orchard, 2018), they clearly improve the correlation potential between the western Tethys and the eastern Pacific. A single specimen similar to morphotype A of *A. inequalis* was figured earlier by Krystyn (1973, pl. 4, Figure 3) as *E. abneptis* from the Bicrenatus Zone (i.e., Alaunian-1 substage) of the Hallstatt region of Austria. Now with its presence in the Alaunian substage of the Buda Hills, too, the further splitting of the formerly so often used '*abneptis* population' is possible, and the overall picture starts to get more refined. As far as the author knows, specimens assignable to *A. transformis* were never figured from any Tethyan sections, although they are most likely present not only in the Buda Hills. Based on the general characteristics of the species and its occurrence in the Alaunian-1 substage, it was previously surely involved in the '*multidentata* population' by European

stratigraphers. The same applies to *Epigondolella* sp. A and *Epigondolella* sp. B that are now separated from the former *E. 'multidentata'*. Despite the extreme diversity of the Alaunian-1 faunas in both the Dovško and the Mátyás Hill sections, not a single specimen of true *E. multidentata* has been recovered. Since figured representatives of this species are not found in the literature either, it can be stated that it is an endemic species of the eastern Pacific and using this name should be avoided in the Tethys Realm.

7. Conclusions

The detailed taxonomic and biostratigraphic investigation of the Mátyás Hill section of the Buda Hills (Hungary) shed light on the great morphological variance of the conodonts of the lower to middle Norian transition and helped to overcome the issue of oversimplified taxonomy, which has hampered the development of Norian conodont biostratigraphy in the Tethys for nearly half a century.

The assemblages of Mátyás Hill show obvious resemblance in the faunal composition and the stratigraphic occurrences and ranges of the taxa with the conodont fauna of the Dovško section in Slovenia. The highly similar results from two separate sections of the western Tethys underline the accuracy and the reliability of the obtained data. The occurrences of *Ancyrogondolella? bohorensis* in the Lacia-3 substage as an early representative of Alaunian-type conodonts and *A. manueli* n. sp. in the Alaunian-1 substage as a late representative of Lacia-type forms suggest that the change from a lower Norian to a middle Norian assemblage was the result of stepwise evolution and not a sudden faunal turnover as it may seem in condensed successions.

The figuration of specimens that cannot be assigned to any already introduced species at the moment avoids information loss and supports future comparative studies that can move Norian conodont taxonomy and biostratigraphy one step further. By the documentation of *A. transformis*, *Epigondolella* sp. A and *Epigondolella* sp. B from the Alaunian-1 substage of the Buda Hills, the 'multidentata-mystery' of the Tethys can be considered as solved, and the refinement of the middle Norian conodont zonation of the western Tethys Realm can begin.

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References

- Balini M, Lucas SG, Jenks JF and Spielmann JA (2010) Triassic ammonoid biostratigraphy: an overview. In *The Triassic Timescale* (ed SG Lucas), pp. 221–62. Geological Society of London, Special Publication no. 334.
- Budurov K (1972) *Ancyrogondolella triangularis* gen. et sp. n. (Conodonta). *Mitteilungen der Gesellschaft der Geologie- und Bergbaustudenten* **21**, 853–60.
- Channell JET, Kozur HW, Sievers T, Mock R, Aubrecht R and Sykora M (2003) Carnian-Norian biomagnetostratigraphy at Silická Brezová (Slovakia): correlation to other Tethyan sections and to the Newark Basin. *Palaeogeography, Palaeoclimatology, Palaeoecology* **191**, 65–109.
- Chen Y, Krystyn L, Orchard MJ, Lai X and Richoz S (2016) A review of the evolution, biostratigraphy, provincialism and diversity of Middle and early Late Triassic conodonts. *Papers in Palaeontology* **2**(2), 235–63.
- Dzik J (1976) Remarks on the evolution of Ordovician conodonts. *Acta Palaeontologica Polonica* **21**, 395–455.
- Gallet Y, Besse J, Krystyn L, Marcoux J and Théveniaut H (1992) Magnetostratigraphy of the Late Triassic Bolücektası Tepe section (southwestern Turkey): implications for changes in magnetic reversal frequency. *Physics of the Earth and Planetary Interiors* **73**(1–2), 85–108.
- Gallet Y, Besse J, Krystyn L and Marcoux J (1996) Norian magnetostratigraphy from the Scheiblkogel section, Austria: constraint on the origin of the Antalya Nappes, Turkey. *Earth and Planetary Science Letters* **140**(1–4), 113–22.
- Gallet Y, Besse J, Krystyn L, Marcoux J, Guex J and Théveniaut H (2000) Magnetostratigraphy of the Kavaalani section (southwestern Turkey): consequence for the origin of the Antalya calcareous nappes (Turkey) and for the Norian (Late Triassic) magnetic polarity timescale. *Geophysical Research Letters* **27**(14), 2033–6.
- Gawlick H-J and Böhm F (2000) Sequence and isotope stratigraphy of Late Triassic distal periplatform limestones from the Northern Calcareous Alps (Kälberstein Quarry, Berchtesgaden Hallstatt Zone). *International Journal of Earth Sciences* **89**, 108–29.
- Haas J (2002) Origin and evolution of Late Triassic backplatform and intraplatform basins in the Transdanubian Range, Hungary. *Geologica Carpathica* **53**(3), 159–78.
- Haas J, Kovács S, Krystyn L and Lein R (1995) Significance of Late Permian–Triassic facies zones in terrane reconstructions in the Alpine-North Pannonian domain. *Tectonophysics* **242**, 19–40.
- Haas J, Korpás L, Török Á, Dosztály L, Góczán F, Hámor-Vidó M, Oravecz-Scheffer A and Tardi-Filáz E (2000) Upper Triassic basin and slope facies in the Buda Mts. – based on study of core drilling Vérhalom tér, Budapest. *Bulletin of the Hungarian Geological Society* **130**(3), 371–421. (in Hungarian with English abstract)
- Hayashi S (1968) The Permian Conodonts in Chert of the Adoyama Formation, Ashio Mountains, Central Japan. *Earth Science* **22**(2), 63–77.
- Hips K, Haas J and Györi O (2016) Hydrothermal dolomitization of basinal deposits controlled by a syndimentary fault system in Triassic extensional setting, Hungary. *International Journal of Earth Sciences* **105**, 1215–31.
- Huckriede R (1958) Die Conodonten der mediterranen Trias und ihr stratigraphischer Wert. *Paläontologische Zeitschrift* **32**(3/4), 141–75.
- Ishida K and Hirsch F (2001) Taxonomy and Faunal Affinity of Late Carnian-Rhaetian Conodonts in the Southern Chichibu Belt, Shikoku, SW Japan. *Rivista Italiana di Paleontologia e Stratigrafia* **107**(2), 227–250.
- Ishida K and Hirsch F (2002) The Izanami Plateau: Pre-Accretionary origin of Japan's low latitude Triassic pelagic carbonates. *Eclogae geologicae Helvetiae* **95**, 43–55.
- Ji Z-S, Yao J-X, Yang X-D, Zang W-S and Wu G-C (2003) Conodont zonation of Norian in Lhasa area, Xizang (Tibet) and their global correlation. *Acta Palaeontologica Sinica* **42**(3), 382–92. (in Chinese with English abstract)
- Karádi V (2018) Middle Norian conodonts from the Buda Hills, Hungary: an exceptional record from the western Tethys. *Journal of Iberian Geology* **44**, 155–74.
- Karádi V (2021) Evolutionary trends of the genus *Ancyrogondolella* (Conodonta) and related Taxa in the Norian (Late Triassic). *Journal of Earth Science* **32**(3), 700–8.
- Karádi V and Korte C (2023) Upper Carnian to Rhaetian (Upper Triassic) conodont and carbon-isotope stratigraphy of the Csóvár borehole succession, Hungary. *Palaeogeography, Palaeoclimatology, Palaeoecology* **630**, 111792.
- Karádi V, Kozur HW and Görög Á (2013) Stratigraphically important Lower Norian conodonts from the Csóvár borehole (Csv-1), Hungary – comparison with the conodont succession of the Norian GSSP candidate Pizzo Mondello (Sicily, Italy). In *The Triassic System* (eds LH Tanner, JA Spielmann and SG Lucas), pp. 284–95. New Mexico Museum of Natural History and Science, Bulletin no. 61.

- Karádi V, Pelikán P and Haas J** (2016) Conodont biostratigraphy of Upper Triassic dolomites of the Buda Hills (Transdanubian Range, Hungary). *Bulletin of the Hungarian Geological Society* **146**(4), 371–86. (in Hungarian with English abstract)
- Karádi V, Cau A, Mazza M and Rigo M** (2020a) The last phase of conodont evolution during the Late Triassic: integrating biostratigraphic and phylogenetic approaches. *Palaeogeography, Palaeoclimatology, Palaeoecology* **549**, 109144.
- Karádi V, Virág A, Kolar-Jurkovšek T and Jurkovšek B** (2020b) Stress-related evolution in Triassic Conodonts and the Middle Norian Juvenile Mortality. In *Morphogenesis, Environmental Stress and Reverse Evolution* (eds J Guex, JS Torday and WB Miller Jr), pp. 37–58. Cham: Springer.
- Karádi V, Kolar-Jurkovšek T, Gale L and Jurkovšek B** (2021) New advances in biostratigraphy of the Lower/Middle Norian transition: Conodonts of the Dovško Section, Slovenia. *Journal of Earth Science* **32**(3), 677–99.
- Katvala EC and Stanley GD** (2008) Conodont biostratigraphy and facies correlations in a Later Triassic island arc, Keku Strait, southeast Alaska. *The Geological Society of America Special Paper* **442**, 181–226.
- Kozur H** (1989) The taxonomy of the gondolellid conodonts in the Permian and Triassic. *Courier Forschungsinstitut Senckenberg* **117**, 409–69.
- Kozur HW** (2003) Integrated ammonoid-, conodont and radiolarian zonation of the Triassic. *Hallesches Jahrbuch für Geowissenschaften* **25**, 49–79.
- Kozur H and Mock R** (1991) New middle Carnian and Rhaetian conodonts from Hungary and the Alps. Stratigraphic importance and tectonic implications for the Buda Mountains and adjacent areas. *Jahrbuch der Geologische Bundesanstalt* **134**(2), 271–97.
- Kozur H and Mostler H** (1971) Probleme der Conodontenforschung in der Trias. *Geologisch-Paläontologische Mitteilungen Innsbruck* **1**(4), 1–19.
- Krystyn L** (1973) Zur Ammoniten- und Conodonten-Stratigraphie der Hallstätter Obertrias (Salzkammergut, Österreich). *Verhandlungen der Geologischen Bundesanstalt* **1973**(1), 113–53.
- Krystyn L** (1980) Stratigraphy of the Hallstatt region. In *Second European Conodont Symposium (ECOS II), Guidebook, Abstracts* (ed HP Schönlaub), pp. 69–98. Abhandlungen der Geologischen Bundesanstalt no. 35.
- Krystyn L, Mandl GW and Schauer M** (2009) Growth and termination of the Upper Triassic platform margin of the Dachstein area (Northern Calcareous Alps, Austria). *Austrian Journal of Earth Sciences* **102**, 23–33.
- Lindström M** (1970) A suprageneric taxonomy of the conodonts. *Lethaia* **3**, 427–45.
- Mao L and Tian C** (1987) Late Triassic conodonts from the uppermost Mailonggang Formation in Mailonggang village of Lhünzhub County, Xizang (Tibet), China. *Bulletin of the Chinese Academy of Geological Sciences* **17**, 159–68. (in Chinese with English abstract)
- Mazza M, Furin S, Spötl C and Rigo M** (2010) Generic turnovers of Carnian/Norian conodonts: climatic control or competition? *Palaeogeography, Palaeoclimatology, Palaeoecology* **290**, 120–37.
- Mazza M, Cau A and Rigo M** (2012a) Application of numerical cladistic analyses to the Carnian–Norian conodonts: a new approach for phylogenetic interpretations. *Journal of Systematic Palaeontology* **10**(3), 401–22.
- Mazza M, Rigo M and Gullo M** (2012b) Taxonomy and biostratigraphic record of the Upper Triassic conodonts of the Pizzo Mondello section (western Sicily, Italy), GSSP candidate for the base of the Norian. *Rivista Italiana di Paleontologia e Stratigrafia* **118**(1), 85–130.
- Mosher LC** (1968) Triassic conodonts from western North America and Europe and their correlation. *Journal of Paleontology* **42**(4), 895–946.
- Onoue T and Tanaka H** (2005) Late Triassic bivalves from Sambosan accretionary complex, southwest Japan, and their biogeographic implications. *Paleontological Research* **9**(1), 15–25.
- Orchard MJ** (1983) *Epigondolella* populations and their phylogeny and zonation in the Upper Triassic. *Fossils and Strata* **15**, 177–92.
- Orchard MJ** (1991) Upper Triassic conodont biochronology and new index species from the Canadian Cordillera. In *Ordovician to Triassic conodont paleontology of the Canadian Cordillera* (eds MJ Orchard and AD McCracken), pp. 299–335. Geological Survey of Canada, Bulletin no. 417.
- Orchard MJ** (2006) Late Paleozoic and Triassic conodont faunas of Yukon and northern British Columbia and implications for the evolution of the Yukon-Tanana Terrane. In *Paleozoic Evolution and Metallogeny of Pericratonic Terranes at the Ancient Pacific Margin of North America, Canadian and Alaskan Cordillera* (eds M Colpron and JL Nelson), pp. 229–60. Geological Association of Canada, Special Paper no. 45.
- Orchard MJ** (2018) The Lower-Middle Norian (Upper Triassic) boundary: new conodont taxa and a refined biozonation. In *Conodont Studies Dedicated to the Careers and Contributions of Anita Harris, Glen Merrill, Carl Rexroad, Walter Sweet, and Bruce Wardlaw* (eds DJ Over and CM Henderson), pp. 165–93. *Bulletins of American Paleontology* no. 395–396.
- Pander CH** (1856) *Monographie der fossilen Fische des silurischen Systems der russisch-baltischen Gouvernements*. St. Petersburg: Buchdruckerei der Kaiserlichen Akademie der Wissenschaften, 91 pp.
- Rigo M and Joachimski MM** (2010) Palaeoecology of Late Triassic conodonts: constraints from oxygen isotopes in biogenic apatite. *Acta Palaeontologica Polonica* **55**(3), 471–8.
- Rigo M, De Zanche V, Gianolla P, Mietto P, Preto N and Roghi G** (2005) Correlation of Upper Triassic sections throughout the Lagonegro Basin. *Bollettino della Società Geologica Italiana* **124**, 293–300.
- Rigo M, Trotter JA, Preto N and Williams IS** (2012) Oxygen isotopic evidence for Late Triassic monsoonal upwelling in the northwestern Tethys. *Geology* **40**(6), 515–8.
- Rigo M, Mazza M, Karádi V and Nicora A** (2018) New Upper Triassic conodont biozonation of the Tethyan Realm. In *The Late Triassic World: Earth in a Time of Transition* (ed LH Tanner), pp. 189–235. *Topics in Geobiology* no. 46.
- Roniewicz E, Mandl GW, Ebli O and Lobitzer H** (2007) Early Norian Scleractinian Corals and Microfacies Data of the Dachstein Limestone of Feisterscharte, Southern Dachstein Plateau (Northern Calcareous Alps, Austria). *Jahrbuch der Geologischen Bundesanstalt* **147**(3–4), 577–94.
- Trotter JA, Williams IS, Nicora A, Mazza M and Rigo M** (2015) Long-term cycles of Triassic climate change: a new $\delta^{18}\text{O}$ record from conodont apatite. *Earth and Planetary Science Letters* **415**, 165–74.
- Wang Z and Wang L** (1990) Several species of the Middle and Late Triassic conodonts from Yushu, Qinghai. In *Devonian-Triassic Stratigraphy and Palaeontology from Yushu Region of Qinghai, China, Part I* (eds Qinghai Institute of Geological Sciences and Nanjing Institute of Geology and Palaeontology, Academia Sinica), pp. 123–34. Nanjing, Zhejiang: Nanjing University Press. (in Chinese with English abstract)