

The evolutionary trend of platform denticulation in Middle Triassic acuminate Gondolellidae (Conodonta)

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Abstract: Acuminate Middle-Late Triassic Gondolellidae are characterized by an ellipsoid platform with a central to posterior amygdaloid basal cavity and an octomembrate apparatus of gondolelloid affinity. Starting with a neospathodiform proteromorph during the Anisian, their anagenetic lineage developed during the Fassanian, Longobardian, and Julian, ending in another neospathodiform proteromorph. As the increase in complexity in the platform denticulation is an important evolutionary trend, three new genera are proposed: *Guexispathodus* n. gen., *Marquezella* n. gen., and *Kirilella* n. gen., which, together with *Pseudofurnishius* and *Mosherella*, represent the subfamily Marquezellinae n. subfam.

Key words: Conodonts, evolution, Middle Triassic, systematic, Marquezellinae

1. Introduction

Triassic Gondolellidae have a rounded or subquadrate posterior end, a basal cavity or keel ending in a rounded loop with a basal pit below the main cusp in the posterior half of the carina, and dominantly smooth platforms. While the evolutionary trend of developing nodose platforms occurred in the Smithian neogondolellid genus *Scythogondolella*, denticulated platform-edges also appeared in the Longobardian acuminate "*Polygnathus mungoensis*" Diebel 1956.

Acuminate platform conodonts without platform ornamentation probably appeared for the first time in the Fassanian, with "*Gladigondolella truempyi*" Hirsch 1971. The development of platform ornamentation is an integral part of evolution for other Triassic conodonts, such as the Carnian genera based on platform ornamentation (Kiliç et al., 2015); no platform denticulation as in *Metapolygnathus*, nodose in *Mazzaella*, and denticulated in *Carnepigondolella*. An acuminate lineage reappears in the Laciian and acuminate ornamented lineages are dominant in Alaunian-Sevatian times. This criterion can be applied as well to Mid-Triassic acuminate genera, and several new taxa are proposed.

The Late Anisian smooth neospathodiform "*Neospathodus shagami*" (Benjamini and Chepstow-Lusty, 1986) is the proteromorph that preceded the Fassanian *Pseudofurnishius murcianus* Van den Boogaard 1966, with strong, denticulated platforms. The Late Anisian "*Pseudofurnishius siyalaensis*" Sadeddin and Kozur 1992 appears intrinsically related to the acuminate smooth platform-bearing Fassanian "*Gladigondolella truempyi*", a relation already perceived by Sadeddin and Kozur (1992). Characteristic for the Longobardian, the acuminate "*Polygnathus mungoensis*" developed a denticulation along its platform borders, a feature that persisted in several successive species into the Early Julian.

Since neither "*Polygnathus*" nor "*Gladigondolella*" were correct generic attributions, Budurov (1973) established the genus *Carinella*. However, as this taxon was found to be preoccupied, the names *Budurovignathus* Kozur (1989) and *Sephardiella* March, Budurov, Hirsch and Márquez-Aliaga (1990) were proposed simultaneously during the ECOS V (European Conodont Symposium) in 1988. Since then, several species have been included in the genus.

However, the significance of smoothness versus platform nodosity, and the evolutionary trend of increase in platform denticulation (as, e.g., in Julian-Tuvalian genera

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Metapolygnathus-Carnepigondolella), made it imperative to propose the Fassanian-Early Longobardian *Marquezella* n. gen. (type species: *Gladigondolella truempyi* Hirsch 1971) for the smooth platform-bearing acuminate lineage and the Late Longobardian-Julian *Kirilella* n. gen. (type species: *Polygnathus mungoensis* Diebel 1956) for the acuminate lineage with platform denticulation. These genera, together with the well-established genus *Pseudofurnishius*, are preceded by the proteromorph *Guexispathodus* n. gen., and that ends with the proteromorph genus *Mosherella* that constitutes the Upper Anisian to Lower Carnian conodont lineage of the subfamily Marquezellinae, former Sephardiellinae Plasencia et al. 2007.

2. Systematic paleontology

Order OZARKODINIDA Dzik, 1976

Superfamily Gondolellacea (Lindström, 1970)

Family Gondolellidae (Lindström, 1970)

Subfamily Marquezellinae n. subfam.

Type genus: *Marquezella* n. gen.

Derivation of the name: after *Marquezella*, one of the new genera.

Diagnosis (modified from Plasencia et al., 2007): Differential criteria of the octomembrate apparatus are the structure of the basal cavity in the P_1 element, of amygdaloid shape and progressively narrow, a relatively high blade, elongated and well denticulated (with at least 7 denticles or more in mature elements); the variable morphology of the P_2 element; and the simple S_3 element.

Description: Octomembrate apparatus composed of a pair of P_1 , P_2 , M, S_1 , S_2 , S_3 , and S_4 elements, with a single S_0 element. The P_1 acuminate element develops several kinds of platforms in the course of its phylogeny; amygdaloid basal cavity, with tendency of the basal pit to shift towards the posterior end of the unit in the course of evolution; early species are platform-less (*Guexispathodus* n. gen.), or with a ridge along the element blade. Later species may develop a platform-like cluster composed of denticles (*Pseudofurnishius*), while others may have the ridge develop into a wide platform, first unornamented (*Marquezella* n. gen.) and later with nodes and denticles (*Kirilella* n. gen.). Anterior denticles of the blade are initially directed upwards and inclined progressively towards the posterior end. Blade denticles are fused at least up to midlength, and in later specimens of *Kirilella* n. gen. posterior denticles are isolated. Basal cavity is of amygdaloid shape, narrow in the central third and gradually narrowing towards both ends; in some specimens of *Kirilella* n. gen. the cavity is wider and in some cases posteriorly bifid.

Preliminary remark: Chen et al. (2016a, 2016b) transcribed the term Pseudofurnishiinae from Pseudofurnishiidae Ramovš 1977, in replacement of Sephardiellinae Plasencia et al. 2007, based on ICZN Article 36.1. However, Ramovš (1977), not providing a

description of the family Pseudofurnishiidae, herewith contradicts the requirements for names published after 1930 as shown in ICZN Article 13.1, which stipulates:

13.1. **Requirements.** To be available, every new name published after 1930 must satisfy the provisions of Article 11 and must

13.1.1. be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon, or

13.1.2. be accompanied by a bibliographic reference to such a published statement, even if the statement is contained in a work published before 1758, or in one that is not consistently binominal, or in one that has been suppressed by the Commission (unless the Commission has ruled that the work is to be treated as not having been published [Art. 8.7]), or

13.1.3. be proposed expressly as a new replacement name (nomen novum) for an available name, whether required by any provision of the Code or not.

This means that the name Pseudofurnishiidae cannot be valid and consequently neither Pseudofurnishiinae. Also, since Ramovš (1994–1995) limits the family to the genus *Pseudofurnishius* it is clear that he considered *Budurovignathus/Sephardiella* to be part of family Gondolellidae.

Similar is the debate between the use of *Sephardiella* or *Budurovignathus*. Based on Kozur (1988) by page priority over March et al. (1988), and presenting no definition of the species, Kozur (1989) describes mainly characteristics of possible forerunners of the genus and some characteristics of different representatives of the genus, but lacks a correct definition that allows for differentiation of the genus from others. This is made clear by the fact that it was not done until Gullo and Kozur (1991), when the diagnosis and description of *Budurovignathus* was published for the first time. As March et al. (1990) present a full diagnosis and description of the genus *Sephardiella*, it has preeminence over the incorrectly defined *Budurovignathus*.

Orchard (2005) included both genera *Sephardiella* and *Pseudofurnishius* in the Subfamily Novispathodinae, after the genus *Novispathodus*. We do not consider the genera *Sephardiella* and *Pseudofurnishius* to be part of the same lineage as the genera *Novispathodus*, nor *Triassospathodus* Kozur, 1988, and we therefore agree with Chen et al. (2016a) in differentiating the two subfamilies.

However, as in this paper the genus *Sephardiella* becomes an emptied genus, since it is now divided into the genera *Marquezella* n. gen. and *Kirilella* n. gen., their lineage having origin in the genus *Guexispathodus* n. gen., it is necessary to establish a new subfamily showing the phylogeny of the subfamily, for which we propose the name Marquezellinae n. subfam. In the phylogeny of the new subfamily Marquezellinae n. subfam. also belongs the genus *Pseudofurnishius*.

2.1. Precedents

After being included in different genera, like *Gondolella*, *Metapolygnathus*, *Epigondolella*, *Carinella*, and some others, March et al. (1990) not only gave the full diagnosis of the genus *Sephardiella* but also described the ontogenetic development of the species *S. mungoensis*, with a model that was later slightly modified by Plasencia (2009) to include *S. truempyi*, *S. hungarica*, *S. mostleri*, and *S. diebeli* in the phylogeny of the subfamily. For Gullo and Kozur (1991) the genus (as *Budurovignathus*) also includes *Epigondolella ciernensis* Kozur and Mock 1972, *E. mirautae* Kovács and Kozur 1980, and *Metapolygnathus longobardicus* Kovács 1984. Other species that have been ascribed to the genus include *Budurovignathus lipoldi* Ramovš 1995 and *Budurovignathus gabriellae* Kozur, Krainer and Mostler 1994.

Sephardiella (as *Carinella*) was defined with a high free blade, well separated, its basal field with irregularly elliptic ends and a central to terminal pit. The lineage of *Sephardiella* was divided into two main groups based in the development of the platform margin: Budurov (1973) and later March et al. (1990) distinguished between smooth forms (including *S. truempyi*, *S. hungarica*, and *S. japonica*) and denticulated forms (*S. mungoensis*, *S. diebeli*, and *S. mostleri*). The Fassanian range of the smooth taxa is apparently followed by the denticulated ones during the Longobardian. This paper is based on the recognition that the differences between smooth and denticulated forms, in addition to other important differences, are of a substantial nature for their separation at the generic level.

Genus *Guexispathodus* n. gen.

Figure 1A

Type species *Neospathodus shagami* Benjamini and Chepstow-Lusty, 1986

Synonymy:

1986 *Neospathodus shagami* Benjamini & Chepstow-Lusty, plate 1, figs. 10-24

1990 *Pseudofurnishius priscus* Sadeddin, fig. 3.1-5

1992 *Pseudofurnishius siyalaensis* Sadeddin & Kozur, fig. 3 A-D

Derivation of the name: in honor of Professor Jean Guex (Lausanne), for coining the term proteromorphosis in retrograde evolution.

Diagnosis (according to Benjamini and Chepstow-Lusty 1986): segminate pectiniform element with slight marginal bulge at base of denticles, sometimes only on one side, in lateral view appearing as an incipient platform. Basal edge very narrow and blade-like, with narrow, nonflaring posterior basal cavity extending back as a groove but ending approximately beneath third denticle from anterior end. Maybe slightly bowed. Relatively short, lightly striated denticles, 6–13 in number. May or may not have one larger (main) denticle, near posterior

end. Denticles free or partially fused. Marginal ridge and narrow, keel-like basal edge present a distinctly battleship-like (as opposed to gondola-like) appearance.

Apparatus: in Benjamini and Chepstow-Lusty (1986) the P_1 elements of *Guexispathodus shagami* are found together with elements identified as *Cypridodella*, *Ellisonia* (?), and *Ketinella maxicavata* Gedik. It is possible that these are part of the multielement of the *Gu. shagami* apparatus, as found in the section only related to *Gu. shagami* specimens. Neither Sadeddin (1990) nor Sadeddin and Kozur (1992) figure these elements. Thus, if the elements figured in Benjamini and Chepstow-Lusty (1986, plate 1, figs. 1–9) effectively belong to *Gu. shagami*, the apparatus of the genus may include an M or S_{3-4} element (fig. 1), an S_1 or P_2 element (fig. 2), S_2 elements (figs. 3–5), and fragments of a possible S_0 element (figs. 8–9).

Assigned species: *Guexispathodus shagami*, *Guexispathodus siyalaensis*

Range: Upper Anisian – Earliest Ladinian

Occurrence: Jordan and Israel

***Guexispathodus shagami* (Benjamini and Chepstow-Lusty 1986)**

Figure 1A

1986 *Neospathodus shagami* Benjamini and Chepstow-Lusty, plate 1, figs. 10–24

1990 *Pseudofurnishius priscus* Sadeddin, fig. 3.1-5

Diagnosis: according to the description of the genus (modified): slight marginal bulge, narrow basal edge with nonflaring posterior basal cavity, short denticles without free blade.

Remark: *Pseudofurnishius priscus* conforms entirely to *Gu. shagami* and represents a junior synonym. The range of the species apparently starts in the Late Anisian and ends in the Early Ladinian.

Occurrence: fossiliferous limestones member of the Saharonim Formation, Makhtesh Ramon (Israel) (Benjamini and Chepstow-Lusty, 1986), and Mukheiris Formation, Siyala Valley (Jordan) (Sadeddin and Kozur, 1992).

***Guexispathodus siyalaensis* (Sadeddin and Kozur 1992)**

1992 *Pseudofurnishius siyalaensis* Sadeddin and Kozur (1992), fig. 3 A-D

The holotype deposited in the Department of Geology and Environmental Sciences, Yarmouk University, Irbid, Jordan, was collected in Wadi Siyala, 2 km S of Jaldá, sample TJ 17.

Diagnosis (modified): species of *Guexispathodus* n. gen. with smooth, slightly asymmetric platform; both free anterior and posterior blade; slightly sigmoidal posterior keel with pointed posterior end and somewhat forward-shifted basal cavity.

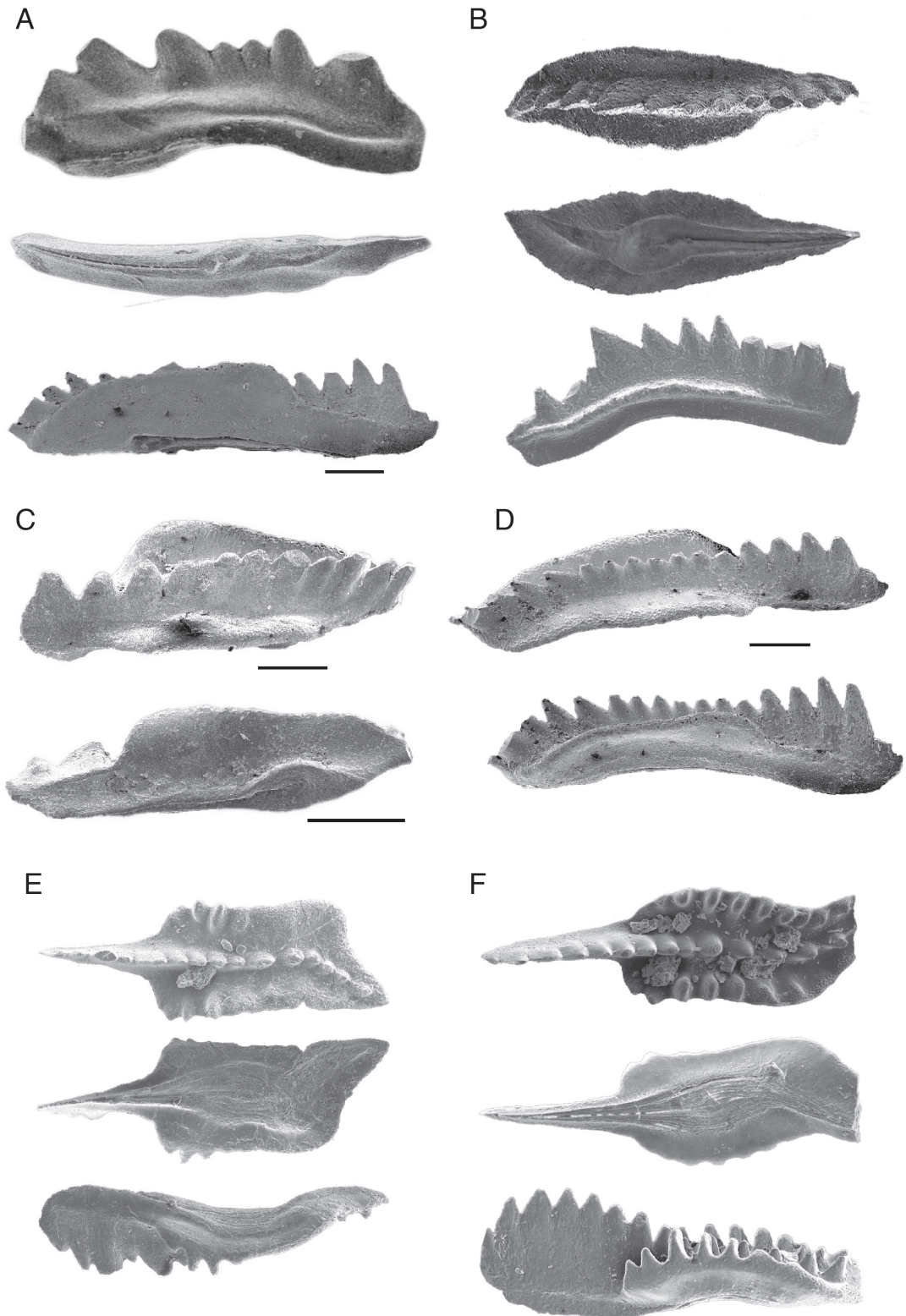


Figure 1. A) *Guexospathodus shagami* (Benjamini and Chepstow-Lusty, 1986), holotype BGU-YF 75/1. YF-75, Saharonim Formation, Har Gevanim, Makhtesh Ramon, Israel (late Illyrian). B) *Marquezella truempyi* (Hirsch, 1971). Right element MGUV-10407. Alós de Balaguer, Spain. C) *Marquezella truempyi denticulata* (Hirsch, 1971). MHNM 0130. Provence, France. D) *Marquezella truempyi denticulata* (Hirsch, 1971). MHNM 0127. Provence, France. E) *Kirilella mungoensis* (Diebel, 1956). Right element. MGUV-10470. Cabo Cope, Murcia, Spain. F) *Kirilella mungoensis* (Diebel, 1956). Right element. MGUV-10420. Calanda, Teruel, Spain.

Occurrence: Mukheiris Formation, Siyala Valley (Jordan).

Genus *Marquezella* n. gen.

Figures 1B–1D

Type species *Gladigondolella truempyi* Hirsch 1971

Synonymy:

1968 *Polygnathus japonicus* n. sp. Hayashi, p. 73, pl. 1a–c

1971 *Gladigondolella truempyi* n. sp. Hirsch, pp. 66–68. pl. 1. figs. 1–10

1972 *Epigondolella hungarica* n. sp. Kozur & Vegh in Kozur & Mock, p. 8. pl. 2. figs. 3–7

1973 *Carinella* n. gen. Budurov

1989 (part) *Sephardiella* n. gen. March, Budurov, Hirsch & Márquez-Aliaga

1989 *Budurovignathus* n. gen. Kozur

Derivation of the name: in honor of Professor Ana Márquez-Aliaga, for her contribution in developing the study of conodonts in the Triassic of the Iberian Peninsula.

Diagnosis: lanceolate platform element, with platform slightly asymmetrical, narrow and with smooth margins, free blade at least in the anterior part. Carina is continuous and of similar height for all the length of the element, with triangular denticles fused in about half of the height of the unit. Basal surface broad, with a narrow basal groove in the anterior half of the unit and wider and elliptical posteriorly; fusiform basal cavity.

Assigned species: *Mar. truempyi*, *Mar. japonica*.

Range: Lower Ladinian (Fassanian).

Occurrence: Muschelkalk of Provence (France) (Hirsch, 1971); Sardinia (Bagnoli et al., 1985); Spanish Pyrenees (Plasencia, 2009); Southern Alps (Muttoni et al., 2004); Briançonnais (Baud et al., 2016); Balaton Plateau (Hungary) (Kovács, 1994); Greece (Balini et al., 2006); Japan (Hayashi, 1968); China (Lehrmann et al., 2015).

Remarks: *Mar. truempyi*, as the type species of the genus, has a straight free blade for up to 1/4 of its length and its carina bears up to 16 denticles. Hirsch (1971) defined two subspecies, *Gladigondolella truempyi truempyi* and *Glad. truempyi denticulata*, that are part of the morphological variability of the species and are not valid.

Mar. japonica (Hayashi 1968) has a lanceolate shape, with smooth margins, but presents a long free blade that extends up to the posterior end. Its narrow profile as well as the smooth margins justify our assignation to *Marquezella* n. gen. Kolar-Jurkovšek et al. (1983) figured an *Epigondolella japonica* of Tuvalian age that presents denticles in the outer margins of platform.

This, together with the wider platform compared with the holotype of Hayashi, suggests that this specimen is not *Mar. japonica*. It seems that *Mar. japonica* had a more restricted distribution than *Mar. truempyi* and that most of the specimens regarded as *Mar. japonica* are really

Mar. truempyi (e.g., Carrillat et al., 1999, pl. 3, figs. 7–15; Krystyn, 1983, taf. 7, figs. 1–7).

A similar situation is found with *E. hungarica*. This species was separated from *Mar. truempyi* based on quantitative differences that are not so clear after the increase in studied material. Contrary to *Mar. japonica*, *E. hungarica* shows no real differences from *Mar. truempyi* and should be regarded as synonym of the former. Carrillat et al. (1999) regarded *Epigondolella hungarica* as a junior synonym of *Carinella truempyi*. Both names have been used for the Triassic of the Monte di Santa Giusta by Bartusch (1985). Finally, Muttoni et al. (2004), in pl. I, figs. 6–8, depict both “B.” *hungaricus* and “B.” *truempyi denticulata* that should be considered in both cases *Mar. truempyi*. This aspect is discussed later in this text.

Chen et al.’s (2016) aff. *Budurovignathus* (in open nomenclature) is a new genus that is different from *Marquezella*. It presents a very prominent cusp above a prominent basal cavity and a rather narrow adult platform, and lacks a sinuous keel. It may have some resemblance to smooth representatives of *Marquezellinae*. However, the relationship awaits a formal description of the new genus.

Apparatus: the apparatus of *Marquezella truempyi* is depicted in Bagnoli et al. (1985), with a quite complete and well-preserved apparatus that includes P₂, M, S₀₋₂, and S₃₋₄ elements.

Range: Early Ladinian (Early Fassanian to Early Longobardian).

Genus *Kirilella* n. gen.

Figures 1E and 1F

Type species *Polygnathus mungoensis* Diebel 1956

Synonymy

1956 *Polygnathus mungoensis* n. sp. Diebel: pl. 1, figs. 1–20; pl. 2, figs. 1–4; pl. 3, fig. 1; pl. 4, fig. 1–5

1966 *Gondolella catalana* Hirsch: Hirsch, p. 80, lám. 1, figs. 1–4

1968 *Epigondolella mungoensis* (Diebel): Mosher, p. 936, lám. 116, figs. 16–19

1971 *Tardogondolella diebeli* n. sp. Kozur & Mostler: pl. 2, figs. 1–3

1972 *Metapolygnathus mungoensis* (Diebel): Kozur, lám. 2, figs. 1–4

1972 *Epigondolella mostleri* n. sp. Kozur: pl. 1, fig. 8

1973 *Carinella* n. gen. Budurov

1983 *Metapolygnathus longobardicus* n. sp. Kovács: pl. 6, figs. 1a–d

1989 (part) *Sephardiella* n. gen. March, Budurov, Hirsch & Márquez-Aliaga

1989 *Budurovignathus* n. gen. Kozur

Derivation of the name: in honor of Kiril Budurov (Sofia) for his contributions to the Triassic conodont taxonomy.

Diagnosis: lanceolate element with a well-separated high anterior free blade. The broad irregular elliptic basal field has a basal groove, narrow in the anterior half of the unit, that widens posteriorly, with a centrally to terminally located fusiform or amygdaloid pit. Adult specimens show a trend towards bifurcation and splitting of the basal cavity. The slightly asymmetrical platform is narrow to broad, depending on the different species, and the platform margins are weakly nodose to strongly denticulated. Carina is continuous and of similar height for all the length of the element, with triangular denticles fused in about half to one-third of the height of the unit.

Apparatus: the multielement apparatus of *Kirilella* n. gen. has been described principally for the most significant member of the genus, *K. mungoensis*. This apparatus has been shown in several papers like those of Orchard (2005) or Plasencia et al. (2007), and it shows a significant difference in the P₂ element, highly modified from *Guexispathodus* n. gen. and *Marquezella* n. gen.

Assigned species: *K. diebeli*, *K. mungoensis*, *K. longobardica*, *K. mostleri*.

Remarks: stratigraphically, the first representative of *Kirilella* n. gen is *K. mungoensis*, and it presents two main evolutionary lineages (Figure 2): one with a tendency to develop more and sharper denticles in the outer margins of the platform, from the nodes of *K. mungoensis* to the numerous denticles of *K. diebeli* and *K. mostleri*, and a second that maintain these nodes, which includes *K. longobardica*.

Range: Early Longobardian-Early Julian.

Occurrence: Worldwide.

Discussion: other possible *Kirilella* species include Kozur's (1993) "*B. cordevolicus*" with a note that its description would appear under Kozur (1993b) in the same *Jahrbuch der Geologischen Bundesanstalt* 136, 4, but that issue does not contain the promised description and we have not been able to locate it in other papers. It has some similarities with specimens of *K. mungoensis* from Rasquera-Benifallet (CCR) figured in Plasencia (2009). For these considerations, and until more information about this species is obtained, we put the species in synonymy with *K. mungoensis*, the closest species with which it shares several characteristics, such as denticulated platform margins and a carina that fuses with the blade in the posterior part of the element.

Metapolygnathus mirautae Kovács and Kozur 1980, a relatively obscure taxon from the Lower Carnian in Csopak (Hungary), originally described as *Metapolygnathus*, was later included in *Budurovignathus* by Gullo and Kozur (1991). The species has a particular morphology; while it shares similarities with *K. mungoensis*, like the bent posterior part of the basal body and the acute end of the element, it also has significant differences, like the lack of a free blade and low height and shape of the fixed blade, with platform margins presenting a reduced nodosity. Such characteristics render the inclusion of this species within *Kirilella* impossible and it could be part of a new genus. While the relationship to *K. mungoensis* still has

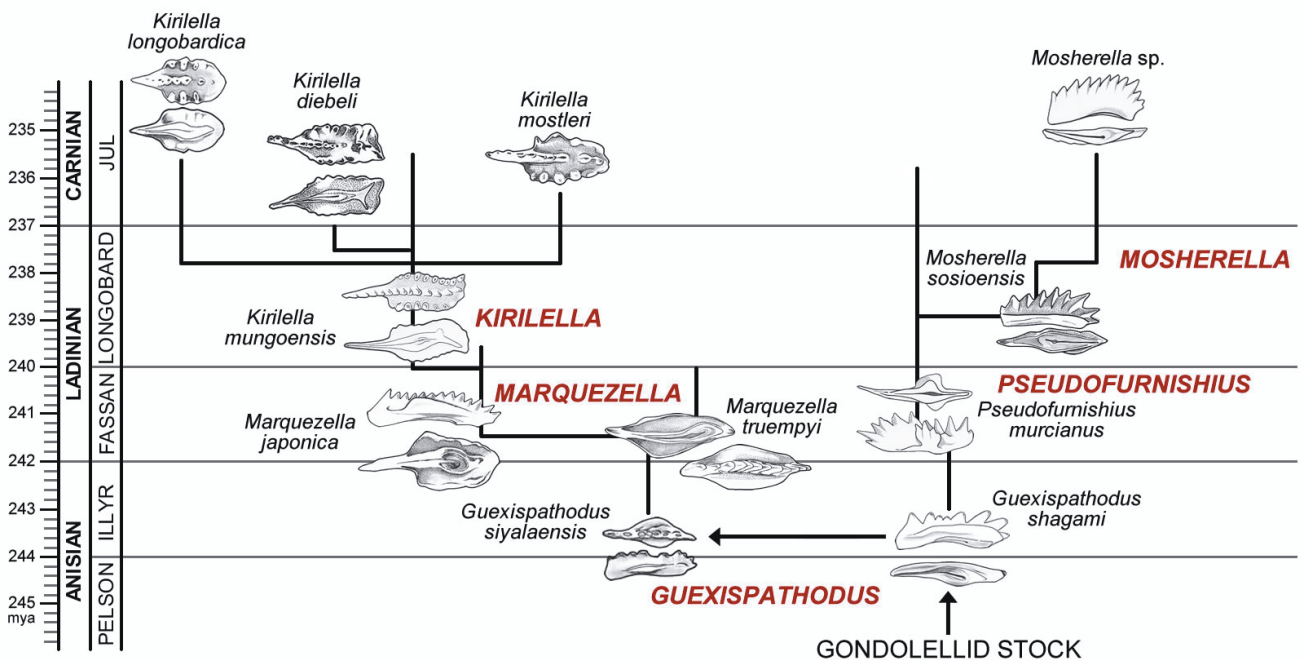


Figure 2. Proposed evolutionary lineage of the subfamily Marquezellinae.

to be discussed, its possible derivation from it cannot be discarded.

Pseudofurnishi van den Boogaard 1966

Pseudofurnishi evolved from *Guexispathodus* with the development of a denticulated platform. Plasencia et al. (2010) showed that this platform and the platforms featured in *Marquezella* n. gen. and *Kirilella* n. gen. may have similar origins and that development of one structure or another (or the complete loss of it) depends on a single change in development expression.

Mosherella Kozur, 1972

The genus is a proteromorph that resulted from the Late Ladinian-Julian environmental stress affecting all lineages of that time. The derivation of *Mosherella sosioensis* (Gullo and Kozur 1989) took place in the Late Longobardian. *Mo. sosioensis* was described as a *Pseudofurnishi* species, but the lack of inner or outer platform justifies the assignment to the genus *Mosherella*, as this genus shares a very similar carina with *Pseudofurnishi*. *Mo. sosioensis* evolved in the last representatives of the subfamily and *Mosherella* probably ends its lineage. There is no known new lineage issued from it.

Neocavitella Sudar and Budurov, 1979 and *Misikella* Kozur and Mock 1974

We reject the assignment of these genera to subfamily Marquezellinae (*Pseudofurnishiinae*) by Chen et al. (2016a). Whereas it is reasonable that both are proteromorphs, they are respectively the result of Tuvalian and Sevastian events. Furthermore, prominent differences of their cusp characteristics contrast with the conspicuous main denticle in *Guexispathodus* n. gen. Given these differences alone, we would refrain from including these genera in the lineage of Marquezellinae.

3. Discussion

A. *Marquezella* n. gen. differs from the other members of subfamily Marquezellinae n. subfam. in three basic aspects:

1) Its narrower shaped platform is symmetrical or slightly asymmetrical, it is entirely smooth or in very few mature forms one or two almost germinal nodes, while *Kirilella* n. gen. is wider, asymmetrical, and at least one marginal node is present even in the earliest stages of development (March et al., 1990; Plasencia, 2009), with two or more high, strongly reticulated nodes in mature forms.

2) Blade, although quite high, is lower in *Marquezella* n. gen. than in *Kirilella* n. gen.; the carina extends continuously along the whole element, with denticles of similar height and directed upwards up to the posterior third, gradually forming a slope; in *Kirilella* n. gen. the blade that occupies the anterior third of the unit is tallest in the anterior part, gradually merging with the platform, usually in the central third of the unit or sometimes

more posterior, leaving at least one discrete and isolated denticle. In more developed adult forms of *Kirilella* n. gen., the platform bears several isolated denticles that continue up to the rear end of the element. Also, in general, but more clearly in senior species of *Kirilella* n. gen., the number of denticles on the blade is reduced. In the earliest representatives of *Kirilella* n. gen., however, this feature is not so clear yet, so this denticle development can be interpreted as an evolutionary tendency.

3) In *Marquezella* n. gen. the amygdaloid pit is usually located in the posterior third of the element, while it is central in *Kirilella* n. gen.

B. *Epigondolella hungarica* (Kozur and Vegh 1972 in Kozur and Mock, 1972): a variation of more elongated specimens of *M. truempyi* that show a narrower and more central pit gave rise to the establishment of *M. hungarica*, described from the Lower Longobardian of the Balaton Plateau (Hungary). According to Kozur and Mock (1972), the variation *hungarica* is intermediary between *Mar. truempyi* and *K. mungoensis*, the main differences being the situation of the basal cavity and the shape of the keel. There is, however, no ground for a specific separation from *Mar. truempyi*, as even Kozur (1974) wrote that the close relation and flowing passage between them make any delimitation difficult. This fact led Carrillat et al. (1999) to regard "*Carinella*" *hungarica* as a junior synonym of "*C. truempyi*."

Bartusch (in Cherchi and Schroeder, 1985) has shown that *Mar. truempyi* and *E. hungarica* overlap considerably and are unsuitable for defining the Fassanian-Longobardian boundary. Further species identified at Monte di Santa Giusta are *Gondolella constricta* Mosher and Clark 1965 and *Carinella japonica*.

C. *Budurovignathus gabriellae* Kozur, Krainer and Mostler 1994: this taxon has widely separated denticles, clearly isolated one from the other (pl. 3, fig. 1), no free blade, platform is very low and the keel is more "comma"-shaped than sigmoidal, all criteria that exclude its inclusion within *Marquezella* n. gen., more likely as another genus, possibly new.

D. "*Budurovignathus*" *lipoldi* (Ramovš 1994/1995): differs from *Mar. truempyi* by a slimmer, lower, and more reduced platform, and a keel of similar width over the entire basal surface, except for the broader portion of the pit. The posterior part of the remaining field is not acuminate as in *Mar. truempyi*. These differences assign this taxon to a different genus of the subfamily Neogondolellinae.

E. "*Budurovignathus*" *ciernensis* (Kozur and Mock 1972), after the locality of Cierna in Slovakia, was originally regarded as a subspecies of *Mar. japonica* and later as an independent species by Kovács and Kozur (1980); the main difference from *Mar. japonica* is that in the former the platform is narrower and with a more acuminate

posterior end. Despite this, these differences fit within the morphological variability of *Mar. japonica*, the reason why we consider *B. ciernensis* a junior synonym of the former.

4. Multielement apparatus comparison

The multielement reconstruction of *Mar. truempyi* (Hirsch, 1971) has been depicted by Bagnoli et al. (1985, plate 1, p. 314; fig. 5) and Plasencia et al. (2007, using the modern nomenclature). The apparatus is basically complete, including a more regular ozarkodiniiform P_2 instead of the pollognathiform element. One of the enantiognathiform elements of Bagnoli et al. (1985, fig. 5.10) may be identified as a diplodelliform S_3 element. Despite these slight discrepancies, it has been emphasized since March et al. (1990) that the apparatuses of Marquiezellinae are widely constant, strengthening the assumption of phylogenetic links that connect *Marquiezella* to *Pseudofurnishius* and *Kirilella*.

While the study of the apparatuses of all studied genera is still incomplete, it seems apparently clear that main differences appear in P_2 elements, with low blade, isolated denticles, as in *Guexispathodus* n. gen. and *Marquiezella* n. gen., and higher blade, fused denticles elements in *Kirilella* and *Pseudofurnishius*.

5. Origin and evolution

Similar evolutionary tendencies seem recurrent in different Triassic lineages (Hirsch, 1994; Kiliç et al. 2016). What we describe here is a full anagenetic lineage between two neospathodiform proteromorphs.

The proteromorph *Guexispathodus* n. gen. first appeared in the Late Anisian of Wadi Siyala (Jordan), sample TJ 17, described under the name *Ps. priscus* Sadeddin (1990), now included in *Guexispathodus* with *Gu. shagami* and *Gu. siyalaensis*. The “neospathodiform” blade structure of *Gu. shagami* is obvious, suggesting a possible ancestry of *Pseudofurnishius*, but *Gu. siyalaensis*, having a well-developed centrally located smooth platform, as well as a more similar forward-shifted basal cavity, bears similarities with immature specimens of *Mar. truempyi*. Consequently, Late Anisian *Gu. siyalaensis* may well be ancestral to the Fassanian *Marquiezella* n. gen., whereas Fassanian *P. murcianus* evolved from *Gu. shagami*, which ranges up to the earliest Fassanian.

As to the ancestry of *Guexispathodus* n. gen., an available contemporaneous *Paragondolella* species may for example be *P. hanbulogi*. The taxon *Paragondolella praehungarica* (generic attribution modified by Budurov and Petrunova, in Muttoni et al., 2000) was proposed by Kovács (1994) as an ancestor of *Marquiezella truempyi*. Not only does this proposed ancestor lack several diagnostic characters of subfamily Marquiezellinae, like a free blade, but it has a moderately wide anterior basal groove.

Moreover, the ontogenetic development figured by Kovács (1994) is different from that of *Marquiezella* n. gen. Despite possible similarities, the phylogeny from *P. praehungarica*, not including the neospathid *Guexispathodus* n. gen., is excluded.

Also, a possible origin in the platform-less *Nicoraella* can be taken in care. While most *Nicoraella* species present short P_1 elements, *Nicoraella microdus* (Mosher, 1968) has an elongated, highly denticulated P_1 element and well could be a forerunner of *Gu. shagami*.

6. Paleogeographic distribution

A. *Guexispathodus* has only been found in the eastern part of the Sephardic province.

B. The paleogeographical extent of *M. truempyi* stretches from the Southern Alpine zone towards the west, where it defines the intermediate realm adjacent to the Sephardic faunal province that fringes the Alpine Tethys (Provence, Sardinia, Pyrenees, and Briançonnais). Towards the east it is found in Balaton, and in South China. *Mar. japonica* is found in Sardinia, Slovakia, and Japan, while *Mar. truempyi* was described first in Provence, southern France (Hirsch, 1971, 1972), and has been found in the Alps (Vrielynck, 1984; Brack and Nicora, 1998; Baud et al., 2016), Sardinia (Bagnoli et al., 1985), and the Pyrenees (Plasencia, 2009; Plasencia et al., 2015), where it is found together with *Ps. murcianus* (Plasencia, 2009). It has been also cited as cf. *truempyi* by Buryi (1997) in the Russian Far East. Most references to *E. hungarica* and *Mar. japonica* are in reality *M. truempyi*: Greece (Krystyn, 1983; Dürkoop et al., 1986; Muttoni et al., 1997), Italy (Brack and Nicora, 1998; Mietto and Fratoni, 1990), Bulgaria (Budurov et al., 1979), Slovenia (Kolar-Jurkovšek and Placer, 1987) Austria (Colins and Nachtmann, 1974), the Himalayas (Agarwal and Singh, 1981), and South China (Lehrmann et al., 2015). *Mar. japonica* occurs in Japan (Hayashi, 1968; Musashino et al., 1980; Koike et al., 1991). Sadeddin and Kozur (1992) alluded to the presence of this species in the Triassic of Jordan without providing a locality or sample number. Its presence in the Germanic faunal province remains undocumented.

C. *Kirilella* n. gen. has a worldwide distribution; the genus was initially geographically limited to the Sephardic province during the Early Longobardian (Huddle, 1970; Eicher and Mosher, 1974; Bandel and Waksmundzki, 1985), becoming cosmopolite in the middle and late Longobardian (Budurov, 1976; Buryi, 1996; Mastandrea et al., 1998; Klets, 2005; Orchard and Balini, 2007; Plasencia et al., 2007; Lehrmann et al., 2015).

D. *Pseudofurnishius murcianus* has a remarkable paleogeographic distribution that is limited to the southern shelf of the Tethys corresponding to the Sephardic faunal

province and stretching from Iberia to Arabia as well as to the Cimmeride land masses as far as Sibumasu from South China to the Malay Peninsula (Plasencia et al., 2015).

7. Conclusions

1. Acuminate Middle-Late Triassic Gondolellidae are characterized by an ellipsoid platform with a central to posterior amygdaloid basal cavity and an octomembrate apparatus of gondolellid affinity.
2. The Marquezellinae n. subfam. starts during the Anisian with the neospathodiform proteromorph *Guexispathodus* n. gen., followed during the Fassanian by the genera *Pseudofurnishius* and *Marquezella* n. gen., and continues in the Longobardian with *Kirilella* n. gen. appearing and ends in the Julian with the neospathodiform proteromorph *Mosherella*.

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3. The anagenetic lineage of the subfamily Marquezellinae n. subfam., characterized by increased complexity of the platform denticulation, represents an important Middle Triassic evolutionary trend.

Nomenclatural acts

This work and the nomenclatural acts it contains have been registered in ZooBank. The ZooBank Life Science Identifier (LSID) for this publication is: <http://zoobank.org/urn:lsid:zoobank.org:pub:10D35ED3-DD6B-492B-A265-E9C0A37A334A>

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