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CONODONTS OF STRATIGRAPHICAL IMPORTANCE FROM THE ANISIAN/LADINIAN BOUNDARY INTERVAL OF THE BALATON HIGHLAND, HUNGARY

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Key-words: Conodonts, Biostratigraphy, Anisian, Ladinian, Triassic, Hungary.

Riassunto. In questo articolo vengono descritti preliminarmente alcuni nuovi taxa di conodonti, significativi per l'intervallo corrispondente al limite Anisico-Ladinico. Sono discussi anche aspetti delle linee evoluti ve cui essi sono attribuiti. Sono inoltre proposti alcuni nuovi taxa. In particolare Gondolella constricta postcor nuta ssp. n., G. fueloepi sp. n. con due nuove sottospecie, G. liebermani Kovács & Krystyn sp. n. e G. i praehungarica sp. n. Due dei nuovi taxa, G. constricta postcornuta e G. ? praehungarica, sono considerati como indici zonali nel Triassico medio delle Balaton Highlands.

Abstract. Stratigraphically important conodonts occurring in the Anisian/Ladinian boundary interval are preliminarily described and their evolutionary lineages discussed. Among them some new taxa are proposed. Gondolella constricta postcornuta ssp. n., G. fueloepi sp. n. with two new subspecies, G. liebermann Kovács & Krystyn sp. n. and G.? praehungarica sp. n. Two of the new ones, G. constricta postcornuta and G.? praehungarica are recognized as zonal index forms in the Balaton Highland Middle Triassic.

Introduction.

The paper presents a brief taxonomic description of the stratigraphically important forms, occurring in the Anisian/Ladinian boundary interval of the Balaton Highland, which have some bearing in defining the boundary (Fig. 1). Zonation, evolutionary events and their significance in the definition of the boundary are discussed in a separate contribution (Kovács, 1993).

A detailed, monographic description of the whole conodont fauna, including the analysis of morphological variation and of the different stages of ontogenetic evolution, as well as the numeric distribution of taxa in the beds investigated, is planned in a forthcoming paper.

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Fig. 1 - Location of the investigated sections in the Balaton Highland. Vertically hatched areas indicate surface occurrences of Middle Triassic rocks.

The specimens illustrated here are reposited in the Museum of the Hungarian Geological Survey, under catalogue numbers T-6447 to T-6487. At the ranges of conodonts the ammonoid zonation is used according to Vörös (1993).

Investigated sections.

Felsöörs.

The upper section on the western slope of Forrás-hegy at Felsöörs exposes the upper member of the Felsöörs Limestone (Trinodosus Zone; Vörös, 1993) and the lower and middle members of the Buchenstein Formation (Reitzi, resp. Curionii Zones). Bed-by-bed sampling at the Felsöörs Limestone and the lower member of the Buchenstein Formation (up to bed No. 111) was carried out in 1978, while that of the middle member in 1986 (samples from 0/86 on) (Fig. 2, 3).

The upper member of the Felsöörs Limestone is built up by alternation of grey, in weathered stage brownish grey, tabular limestone beds and yellowish brown clay beds (beds Nos. 85-99). Ostracods and especially juvenile pelecypod shells are very abundant in these limestone beds.

On the contrary, conodonts occur only in a rather low number. They are mainly represented by juvenile (= "G. constricta" Auct.), medium and adult (= "G.

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Fig. 2 - Distribution of conodonts in the Trinodosus and Reitzi Zones of the Felsöörs section. (Lithostratigraphic column after Vörös, 1993).

Middle Triassic conodonts of Balaton Highland

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cornuta" Auct.), sometimes hyperadult forms of Gondolella constricta cornuta. Besides these, representatives of G. liebermani were also found sometimes. From bed No. 94 to bed No. 99 transitional forms between G. constricta cornuta and G. constricta post-cornuta ssp. n. occur, which are becoming more slender and elongated. However, it should be noted, that such shaped form of G. constricta cornuta (even with an anterior-ward shifted pit) was found already in bed No. 89.

In the yellowish brown, sometimes greenish, siliceous limestone intercalations of the here anomalously thick lower, tuffaceous member of the Buchenstein Formation conodonts are extremely rare, while radiolarians are fairly abundant (Dosztály, 1993). Only a few early juvenile forms of *G. constricta* and three typical specimens of *G. constricta postcornuta* (in beds No. 100* and 110), representing more advanced ontogenetic stages, have been found. In terms of ammonoids, this member includes the *Kellnerites felsoeoersensis, Hyparpadites liepoldti* and *Reitziites reitzi* faunal horizons (see Vörös, 1993).

The tuffaceous member s.s. (exposed in the main, deeper trench) is followed by a transitional "tuff with limestone nodules" (= pyroclastic debris flow with limestone clasts) horizon, exposed in the 3 m long small trench. Its lower boundary at the upper end of the main trench is formed by the bed No. 111 (the last coherent limestone bed upward in the tuffaceous member) and samples from its nodule horizons are numbered as No. 112-116 (beds No. 111/A-H according to Vörös, 1993; according to him they contain ammonoids of the *Halilucites costosus* horizon). In the bed No. 111 single specimens of *G*. aff. *eotrammeri* and *G*. *trammeri* occur, whereas in the nodule horizons representatives of the latter become quite frequent. This small trench is terminated with an about 25 cm thick light yellowish grey, hard, strongly cherty-nodular limestone bed (with brownish grey chert nodules), containing the same conodonts (numbered No. 0/86). *Gladigondolella tethydis* occurs from bed No. 111, in a low number. Further forms are represented by *G. constricta postcornuta* and rarely by *G. alpina szaboi* and *G. alpina alpina*.

After a 3.5 m long covered interval (probably with tuffs) 15-25 cm thick beds of yellowish grey, nodular limestone follow, with red chert nodules (beds No. 1/86 to 18/86), then light red or red-spotted, nodular limestone beds, also with red chert nodules (beds No. 19/86 to 28/86). Above the end of the horizontal, continuously exposed section, scattered outcrops of single beds of light red, nodular, cherty limestone can be seen (beds No. 29/86 to 33/86). Higher up, on the northern slope of the hill and out of the wood, a small cliff is exposed containing three beds of light red, nodular limestone beds with red chert nodules (beds No. 34/86 to 36/86). Though ammonoids have not been found here, in the light the Vászoly sections (see below and in Vörös, 1993) this part corresponds to the *Eoprotrachyceras curionii* zone, while the isolated uppermost outcrop (beds No. 34-36/86) might already correspond to the basal part of the *Protrachyceras gredleri* zone (in sense of Krystyn, 1983).

Gondolella trammeri is predominant and occurs in a great number throughout the section of this middle member, in all beds. Besides this, G. fueloepi (moderately frequent already from the bed No. 1/86 on), G. ? praehungarica (subordinate, but present in many beds; mostly juvenile forms) and rare representatives of G. transita are characteristic for this interval, both from bed No. 3/86 on. G. constricta postcornuta and G. constricta balkanica (?) range up into this member. From bed No. 10/86 upward



Fig. 3 - Schematic distribution of conodonts in the upper part of the Felsöörs section (Curionii Zone + lowermost part (?) of Gredleri Zone).

remarkably elongated gondolelloids related to the *G. bakalovi*-group are common. *Gladigondolella tethydis* is also common throughout the section.

An important evolutionary event can be recognized from bed No. 31/86 on, by the appearance of true metapolygnathoids ("*M.*" *hungaricus*). In the uppermost exposed beds (Nos. 34-36/86) already transitional forms between "*M.*" *hungaricus* and "*M.*" *mungoensis* do occur, indicating the Fassanian/Longobardian boundary interval or the basal part of the latter.

Vászoly, Öreghegy.

Ditch P 11a.

The limestone intercalations of the lower tuffaceous member of the Buchenstein Formation are fairly rich in conodonts (especially the beds No. 1, 5 and 6). This part of the section (up to bed No. 17) was sampled for conodonts by I. Szabó (the results see in Kovács et al., 1990; Fig. 4). Additional sampling was made later by the present author in beds No. 1-6.

Gondolella constricta cornuta is predominating up to bed No. 6 (containing two internal beds, both sampled for conodonts: samples No. 6 and No. 6^{*}), and is present up to bed No. 12, but higher up it disappears. Transitional forms between *G. constricta cornuta* and *G. constricta postcornuta* occur rarely already in bed No. 1 (yellowish, phosphatic limestone layer lying immediately on top of the Megyehegy Dolomite of platform facies) and more frequently in beds No. 3 and 4.

Primitive representatives of G. constricta postcornuta characterize the beds No. 5, 6 and 6*; however, they are still subordinate in number as compared with G. constricta cornuta. Forms that would conceptually correspond to G. pseudolonga also occur in this horizon; however, a detailed study is still needed to decide, whether they fall inside the field of variation of G. constricta cornuta or they represent an independent subspecies of G. constricta. There is a slight shift here in the faunal change concerning conodonts and ammonoids. The latters change with one bed higher only: the bed No. 5 contains still Parakellnerites aff. meriani B, whereas bed No. 6 already Kellnerites sp., indicating the Kellnerites felsoeoersensis horizon (see Vörös, 1993).

Typical forms of *G. constricta postcornuta* occur from bed No. 8 on. In the limestone nodule horizons of the tuffaceous beds No. 8, 9 and 12 they predominate in the conodont association and show already undoubtedly the same morphology (the cusp is fused with the platform end even in juvenile forms without any stronger denticle before it, and the pit is remarkably anteriorward shifted), which characterize the representatives in the *Eoprotrachyceras curionii* ammonoid zone. The *constricta* lineage shows already a typical "Ladinian" evolutionary stage from bed No. 8 on. Also, in these beds *G. constricta cornuta* is already subordinate in number against *G. constricta postcornuta*. Ammonoids from bed No. 9 indicate the *Hyparpadites liepoldti* horizon (Vörös, 1993). *G. liebermani* is common in all these beds (from No. 1 to 12), whereas *G. excelsa* is represented only by a few specimens.



Fig. 4 - Distribution of conodonts in the Vászoly P 11a section. (Lithostratigraphical column after Vörös 1993).

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The tuff beds (No. 13 to 15) have not been sampled for conodonts (see Kovács et al., 1990). Subsequently Vörös (1993, and in Vörös & Pálfy, 1989) has found specimens of *Reitziites reitzi* in bed No. 14.

Also, at the time of the sampling for conodonts, the reddish, ammonoid-bearing limestone beds No. 16A (reconstructed from isolated blocks in the wall of the trench; see Vörös & Pálfy, 1989, fig. 2) and No. 16 were not yet distinguished (see Kovács et al., 1990, fig. 5). These yielded a rich ammonoid fauna belonging to the *Halilucites costosus* horizon (Vörös, 1993) and the latter the same conodonts, as the purplish red crinoidal limestone beds of the Mencshely section (beds No. -6 to -1; see below), with the exception of *G. trammeri*. For this reason, the Anisian/Ladinian boundary was proposed here between beds No. 16 and 17 by Kovács et al. (1990), at the base of its first appearance in bed No. 17.

Higher up in the section, in the white, thick bedded micritic limestone (Vászoly Limestone Member) G. trammeri predominates, in associaton with G. fueloepi, G. constricta balkanica? and Gladigondolella tethydis. This part of the section, according to a nearby found specimen of Eoprotrachyceras curionii (Vörös, 1993), should already belong to the Curionii Zone.

Ditch P2.

Two samples from the lower tuffaceous member of the Buchenstein Formation (No. 1/78 and 2/78 in Kovács et al., 1990; fig. 6) yielded a poor conodont fauna, including Gondolella constricta cornuta, G. constricta postcornuta, G. excelsa and G. mesotriassica (s.s.). Interestingly, Gladigondolella tethydis already appears in the purplish limestone bed of sample No. 1/78.

This is the only section, in which a few determinable conodonts have been found in the ammonoid nodules of the *Reitziites reitzi* horizon (the tuff bed No. 4 according to the numbering of Vörös, 1993). These include *G. constricta postcornuta, G. constricta* juv., *G. alpina alpina, G. excelsa* and *G. aff. eotrammeri* (1-2 specimens from each). The *Halilucites costosus* ammonoid horizon is missing in this section (a probable hyatus?).

On the other hand, the first bed (No. II/3 in Kovács et al., 1990; fig. 6 and No. 1 in Vörös, 1993) of the overlying white, thick-bedded micritic limestone (Vászoly Limestone Formation) yielded a specimen of *Eoprotrachyceras curionii* (Vörös, 1993). Unfortunately, the sample dissolved from this bed was very poor in conodonts.

Higher up in the section G. trammeri predominates in the conodont association, but Gladigondolella is also common, indicating a full pelagic connection. G.? praehungarica, characteristic of the Nemesvámos Limestone Member of the Felsöörs section, is not present in the Vászoly Limestone. On the other hand, rare specimens of G. transita have been found and in bed II/6 forms belonging to the G. bakalovi-group are frequent. (For distribution of conodonts see Kovács et al., 1990; fig. 6).

Mencshely.

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The section has been excavated on Cser-tetö Hill, and exposes the uppermost bed of the Felsöörs Limestone and the lower tuffaceous member of the Buchenstein Formation, overlain by purplish red crinoidal limestone (Fig. 5).



Fig. 5 - Distribution of conodonts in the Mencshely section. (Lithostratigraphical column after Vörös, 1993).

The topmost bed of Felsöörs Limestone (No. -22) contains rare specimens of the same conodont association as the topmost bed (No. 99) of the same formation in the Felsöörs section, with transitional forms between *Gondolella constricta cornuta* and *G. constricta postcornuta*.

The brownish yellow or grey coloured, siliceous limestone intercalations (beds No. -18 to -12) of the lower, tuffaceous member of the Buchenstein Formation (comprising the *Kellnerites felsoeoersensis* and *Hyparpadites liepoldti* ammonoid horizons; Vörös, 1993) contain subspecies of *G. constricta* in a low number, among them *G. constricta postcornuta*.

The few ammonoid fragments dissolved from the tuff beds of the *Reitziites reitzi* horizon (Vörös, 1993) yielded only a few *Gondolella* fragments and ramiform elements.

The overlying purplish red crinoidal limestone beds (No. -6 to -1) represent the *Halilucites costosus* ammonoid horizon (Vörös, 1993). In the first bed (No. -6) G. aff. eotrammeri and G. trammeri jointly occur, but higher up the former is missing, whereas the latter is quite frequent. Typical forms of G. constricta postcornuta are also frequent, but representatives of G. constricta cornuta are already missing. This facies was favourable for the szaboi lineage: G. alpina szaboi (morphologically closely resembling G. bulgarica, that became extinct at the end of the Pelsonian) and G. alpina alpina are common in it. On the excelsa lineage G. fueloepi occurs already in this horizon. So do Gladigondolella tethydis, indicating that full pelagic conditions had been established by this time.

After a fault, the same lithology is repeated, with ammonoids of the same age (beds No. +1 to +5). This part of the section has not been investigated for conodonts.

Taxonomy

Genus Gondolella Stauffer & Plummer, 1932

Remarks. Supraspecific taxononomic subdivision of gondolelloid conodonts has been widely discussed in the last quarter of century. A group of conodont workers (especially in North America) preferred to preserve the name "Gondolella" s.s. only for a Late Carboniferous evolutionary lineage of gondolelloids (for a summary see Clark et al., 1981). On the other hand, Kozur (1989) proposed numerous new genera, practically for all gondolelloid stocks from the Late Carboniferous to the Late Triassic.

In fact, however, both taxonomic concepts face certain controversies. If one stock is separated as "Gondolella" s.s. in the Late Carboniferous, the inclusion of all other stocks from the Late Carboniferous to the Late Triassic into a single genus, "Neogondolella" Bender & Stoppel, 1965 (with its type-species "Neogondolella" mombergensis Tatge, 1956) is certainly inconsequent. On the other hand, if compared with the taxonomic subdivision of Paleozoic polygnathoid conodonts, which are almost all included into one genus ranging from the Late Siegenian to the Early Visean (Ziegler, 1973, 1975, 1977), with a number of morphologically different evolutionary lineages, separation of almost all gondolelloid stocks as independent genera is merely an increase of arbitrary taxa and is just an unnecessary increase of names, without practical usefulness. Therefore the present author is inclined to use only the genus "Gondolella" for all Late Carboniferous to Late Triassic gondolelloid conodonts.

As ramiform elements of the Middle-Late Triassic gondolelloid apparatuses are considerably underrepresented against Pa-elements, only the latters are considered in the present contribution.

G. constricta lineage

Gondolella constricta Mosher & Clark, 1965

Gondolella constricta cornuta (Budurov & Stefanov, 1972)

Pl. 1, fig. 1-3; Pl. 2, fig. 1

- 1984 Gondolella constricta "cornuta" morphotype Nicora & Kovács, p. 147, pl. 7, fig. 6; pl. 8, fig. 1,2; pl. 9, fig. 1-5; pl. 10, fig. 1 (cum. syn.).
- 1984 "Gondolella" cornuta -- Farabegoli et al., fig. 5, a1-a3, c1-c3.
- 1986 Gondolella constricta "cornuta" morphotype γ -- Kovács, pl. 5, fig. ? 6a-d, 7a-c; pl. 6, fig. ?3a, b, 5a, b; pl. 10, fig. 4a-c.
- 1986 Gondolella constricta -- Kovács, pl. 4, fig. ?4a-d; pl. 5, fig. ?5a-d, ?8.
- 1986 Neogondolella constricta -- Sudar, pl. 6, fig. 10-13; pl. 7, fig. 9-11.

1986 Neogondolella cornuta -- Sudar, pl. 6, fig. 1-9.

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1990 Gondolella constricta morphotype & Kovács et al., p. 187, pl. 3, fig. 6a, b.

1990 Gondolella constricta morphotype γ Kovács et al., only pl. 1, fig. 4a-c.

Remarks. Nicora & Kovács (1984) recognized that Gondolella constricta Mosher & Clark, 1965 and Neogondolella cornuta Budurov & Stefanov, 1972 represent different ontogenetic stages of the same species. In fact, the constricta-group includes several forms with certain morphological differences, which are hard to distinguish in early juvenile and adult (especially hyperadult) ontogenetic stages. For this reason Kovács et al. (1990) considered part of them as morphotypes of the same species, similarly to the Middle Devonian Polygnathus linguiformis Hinde, in which numerous morphotypes and a few subspecies are distinguished (Ziegler, 1977).

In the present contribution the closely related Gondolella constricta α , β and γ morphotypes (Kovács et al., 1990) are distinguished at subspecific level (e.g. as "cornuta", "balcanica" and "postcornuta"), because they have some stratigraphic importance and allow the recognition of zones in the Balaton Highland Middle Triassic (e.g. G. constricta cornuta and G. constricta postcornuta zones in Kovács, 1993). For this reason we retain the name Gondolella constricta cornuta (Budurov & Stefanov) for G. constricta morphotype α (in sense of Kovács et al., 1990). However, a detailed comparison of the Nevadian and Balkanide populations is unavoidably necessary.

G. constricta cornuta evolved from G. bifurcata bifurcata, as proven by transitional forms (Nicora, in Kovács et al., 1990, pl. 1, fig. 3a-c) and gave rise to G. constricta postcornuta (= G. constricta morphotype γ according to Kovács et al., 1990; see below).

The evolution and taxonomic subdivision of the G. constricta lineage will be discussed in details in a separate contribution. For this reason, the stratigraphically less important G. constricta "morphotype β " (in sense of Kovács et al., 1990, probably equivalent to Neogondolella balkanica Budurov & Stefanov, 1975) is not dealt with here.

Gondolella constricta postcornuta ssp. n.

Pl. 1, fig. 4, 5; Pl. 2, fig. 2-5; Pl. 6, fig. 4

1980 Gondolella longa - Szabó et al., pl. 59, fig. 8, 11. ? 1982 Gondolella mesotriassica Kozur & Mostler, only pl. 1, fig. 3a, b. 1990 Gondolella constricta morphotype Y - Kovács et al., p. 188, pl. 3, fig. 5; ?non pl. 1, fig. 4a-c.

Derivatio nominis. Because its derivation from Gondolella constricta cornuta (Budurov & Stefanov, 1972)

Holotype. Pl. 1, fig. 4 a-d; T 6451.

Locus typicus. Road-side section at Öskü, Balaton Highland, Hungary.

Stratum typicum. Vászoly Limestone Member of the Buchenstein Fm., sample No. 4 (Kovács et al., 1990, fig. 10).

Diagnosis. Elongated, slender gondolelloids, with a posteriorly inclined main denticle completely fused with the posterior platform end in all ontogenetic stages. Anteriorly of it, no distinct, larger denticle is present on the low carina. The unit is slightly arched in lateral view, with a similarly slightly arched upper edge of the carina, which is gradually decreasing in height posteriorly. The basal pit is small, with protruding margin and with an usually considerably extended loop behind it.

Remarks. The main difference of *G. constricta postcornuta* against *G. constricta cornuta* can be seen in late juvenile, medium and subadult ontogenetic stages. In the latter, in these ontogenetic stages, the next to the last denticle of the carina is clearly distinct and is the largest one. In *G. constricta postcornuta* instead, no distinct, larger denticle is present anteriorly of the last one, which is completely fused with the platform end. On the other hand, in early juvenile stage in which a distinct main denticle is already completely fused with the last denticle, thus having the characteristic, "horn"like appearance as the holotype of "Gondolella cornuta" in Budurov & Stefanov, 1972, pl. 3, fig. 20-22) they are practically indistinguishable from each other. For this reason, in the present paper these ontogenetic stages are not shown (see Pl. 1, 2).

During the following studies it has been found that the most important morphological changes in the evolution of the *G. constricta* lineage around the Anisian/Ladinian boundary interval, are as follows:

1) slendering and elongation of the unit,

2) anteriorward shifting of the basal pit, resulting in the posteriorward extension of the loop,

3) disappearance of the larger denticle, recognizable only in the late juvenile, medium and subadult ontogenetic stages, situated immediately before the main one completely fused with the platform end.

The first two morphological changes can be recognized already on forms occurring in the *meriani* B ammonoid horizon or even in the Trinodosus Zone (section Felsöörs), but still showing the posterior end of the carina typical for *G. constricta cornuta*. Therefore the third phenomen, recognizable from the *felsoeoersensis* ammonoid horizon upward, is considered by the present author as the most diagnostic for taxonomic classification. All the three phenomena are well observable jointly on specimens of *G. constricta postcornuta* from the *liepoldti* ammonoid horizon onward (see section Vászoly P 11a), showing already a typical "Ladinian" character in the evolution of the *constricta* lineage.

Kovács et al. (1980) differentiated Gondolella pseudolonga sp. n. from "Neogondolella" cornuta Budurov & Stefanov, 1972 and considered as main difference between the two the shape of the platform. It is more elongated and slender in the former, resembling "Neogondolella" longa Budurov & Stefanov, 1973. The position of the basal pit is also more anteriorward shifted in *G. pseudolonga*. Younger ontogenetic stages corresponding to *Gondolella constricta* Mosher & Clark, 1965, and hyperadult ones were not considered in that paper.

Three of the specimens from the Southern Alps figured by Kovács et al. (1980) show the first two characters described above, but their posterior end of carina is typical for *G. constricta cornuta*. Instead the fourth one (Kovács et al., 1980, fig. 3a, b) seems to fall entirely within the variability field of *G. constricta cornuta*. However forms resembling the very slender, elongated ones illustrated by Mietto in Kovács et al. (1980) (except fig. 3a, b) occur in the material of Balaton Highlands not within the range of *G. constricta postcornuta*, but above. This point will be further discussed within the "*G. bakalovi*" group.

Relations. G. constricta postcornuta ssp. n. evolved from G. constricta cornuta with a fairly gradual transition. Transitional forms between them characterize the *meriani* B ammonoid horizon (see section Felsöörs). The first primitive representatives of the subspecies occur in the uppermost bed of the *meriani* B horizon in the Vászoly P11 section, whereas typical ones, in great number, are yielded from the *liepoldti* horizon on.

Forms, morphologically related to the *G. bakalovi*-group, evolved from *G. constricta postcornuta* through transitional forms in the higher part of the Curionii Zone. They occur first (and in a large number) in bed No. Vöh-II/6 in the Vászoly P2 section (see Kovács et al., 1990, fig. 6, assigned as "*G. "pseudolonga*" gr.") and in bed No. 10/86 in the upper part of the Felsöörs section. In constrast to the rise of *G. constricta postcornuta* from *G. constricta cornuta*, that of the *G. bakalovi*-group from *G. constricta postcornuta* suggests a rapid evolutionary change, because typical forms of the two taxa do not occur together. The rarely occurring Gondolella transita Kozur & Mostler, 1971 also evolved from G. constricta postcornuta through transitional forms at the base of the Curionii Zone (see section Felsöörs, upper part).

The Balkanide Gondolella tardocornuta (Budurov & Stefanov, 1984) (resulting from the revision of "Neogondolella" balcanica Budurov & Stefanov, 1975) is distinguished from the slender G. constricta postcornuta first of all by its broad, massive platform, which is broadest in the middle (see Budurov & Stefanov, 1984, pl. 1, fig. 15-20). This thick, "fat" form, along with G. subodolica (Budurov & Stefanov, 1973) of similar platform outline seems to be a typical Balkanide element. In the studied area such forms do not occur and were also not found in other investigated Tethyan areas (for example in NE Hungary; Kovács, unpubl.) and in the eupelagic Epidauros section of Greece (Krystyn, 1983). If G. tardocornuta should be considered at subspecific level or as an independent species of the G. constricta group, it cannot be decided at present, as no details about its ontogenetic stages and morphological variations have been published. Nevertheless, it certainly belongs to a different, Balkanide branch of the G. constricta lineage, though also to evolve from G. constricta cornuta (cf. Budurov & Stefanov, 1984, p. 607).

Range. From the uppermost part of the *merianii* B horizon to the lower Curionii Zone.

Occurrence. Forms that can certainly be assigned to *G. constricta postcornuta* are known so far only from the Balaton Highland. Most probably they occur also in the Southern Alps. On the other hand, this subspecies of the *G. constricta* lineage is missing in the eupelagic Triassic of Northeastern Hungary (Kovács, unpubl.).

Gondolella mesotriassica Kozur & Mostler, 1982

Remarks. Kozur & Mostler (1982, pl. 1, fig. 2a, b, 3a, b, 4a-c) figured three specimens as "G. mesotriassica", which are not conspecific. The holotype (pl. 1, fig. 4a-c) has a remarkably high carina (the highest in the G. constricta group); such forms occur rarely in our material from the Reitzi Zone. The form figured by them on pl. 1, fig. 2a, b seems to correspond to "G. pseudolonga" Kovács, Kozur & Mietto (which also needs a throughful revision), whereas the one figured on pl. 1, fig. 3a, b may probably correspond to G. constricta postcornuta described herein (though it is certainly not a typical form).

Gondolella transita Kozur & Mostler, 1971

Pl. 3, fig. 1-3

1971 Gondolella transita Kozur & Mostler, p. 13, pl. 2, fig. 12 a-c. 1980 Gondolella transita - Kovács & Kozur, pl. 4, fig. 14a, b; pl. 5, fig. 7a-c. ? 1980 Gondolella transita - Kozur & Mirauta, pl. 1, fig. 1a-d.

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Remarks. Typical forms of this rarely occurring species are characterized by a slightly sigmoidally bent shape in upper view and a rather flat platform with thick margins. These features, as well as the low carina and the anteriorward shifted basal pit with a posteriorly extended asymmetrical loop, make these forms as "the most gladigondolelloid-type Triassic gondolelloids". This similarity concerns the Pa-elements only, the other elements of the apparatus being different.

However, in the material of the Felsöörs section, not only asymmetric, but also symmetric forms occur. These forms have a similarly flat platform and anteriorly shifted basal pit, but their carina is straigth, without asimmetrically bent posterior end. Also, their loop is symmetric. Thus, the asymmetric (or "excentric") posterior end is not exclusive for this species.

Relations. G. transita, as shown by transitional forms, evolved from G. constricta postcornuta. The first, rather symmetric forms, that can be attributed to it, occur in bed No. 3/86 in the Felsöörs section (Fig. 3). Transitional forms can be found until the end of the range of the latter.

G. transita represents a side-branch of the G. constricta lineage. No immediate phylogenetic relationship exists with the G. aff. bakalovi-group, which occurs higher up in the Felsöörs section and represents the direct continuation of the G. constricta lineage (see below).

Kozur (1972 and 1980) supposed an evolutionary lineage G. transita \rightarrow "M." truempyi \rightarrow "M." hungaricus, which has been disproven by our investigations in the Felsöörs section (see below).

The Balkanide G. excentrica (Budurov & Stefanov, 1972) probably represents a homeomorphic evolutionary line, independent from the Tethyan G. transita. It should be noted, however, that the "excentric" lateral bending of the posterior end of the carina (together with or without the platform end) and of the loop on the lower surface does not represent a sufficient diagnostic taxonomic feature (see also the case of G. transita). Such forms may occur in most of the Triassic gondolelloids. Therefore the so far published determinations from the Tethyan Triassic as "G. excentrica", based solely on the "excentric" or asymmetric posterior end, should be revised. A detailed comparative study of populations of G. excentrica and G. transita from their type areas, however, would be necessary.

Range. Curionii Zone; whether it ranges up to the top of the zone, it cannot be decided in the discontinuously exposed upper part of the Felsöörs section, where also the ammonoid control is lacking. It can only be proven that the ranges of *G. transita* and "*M.*" *hungaricus* partly overlap.

Occurrence. Sure occurrence has been recorded up to now only in the Balaton Highland, Hungary.

"Gondolella bakalovi-group"

Pl. 2, fig. 6

Remarks. G. constricta postcornuta ssp. n. in the Curionii Zone of the Balaton Highland gave rise to forms resembling the Balkanide Gondolella bakalovi (Budurov & Stefanov, 1975). As other forms of the Balkanide conodont province (Budurov & Stefanov, 1975; Budurov et al., 1983) like G. huckriedei Budurov & Stefanov, G. lindstroemi Budurov & Stefanov, G. subodolica Budurov & Stefanov and even G. mombergensis longa Budurov & Stefanov, also G. bakalovi do not occur in Tethyan pelagic facies. They are attributed to that Balkanide species only in open taxonomy. Most probably they represent a homeomorphic stage of a separate Tethyan lineage. The rise of "G. bakalovi-group" from G. constricta postcornuta can be recorded from bed No. 10/86 in the upper part of the Felsöörs section and from bed Vöh-II/6 above the Vászoly P2 section. Specimens deriving from this last section have been attributed in Kovács et al. (1990, fig. 6), to "G. pseudolonga". A similar form was figured by Krystyn (1983, pl. 5, fig. 3a, b) from the eupelagic Epidauros section as G. cf. constricta. Kozur & Mirauta (1980, pl. 1, fig. 2a-d; pl. 2, fig. 1a-d) figured specimens which still await for detailed comparative studies with the Balkanide species. The form figured as "G. cf. bakalovi" by Krystyn (1983, pl. 5, fig. 4a-c) from the eupelagic Epidaurus section seems to be an aberrant G. trammeri, as suggested by the shape of the carina and platform.

These forms are characterized by a peculiarly shaped posterior end of the unit: slender, but strongly built posterior extension of the platform end with 1-4 denticles. The last denticle is usually stronger. The beginning of this posterior extension is usually marked by some constriction. On their lower surface, the loop is considerably extended posteriorly behind the small, narrow pit with protruding margin.

Range. Higher part of Curionii Zone.

Occurrence. These pelagic forms resembling the group of the Balkanide G. bakalovi are reported so far from the Balaton Highland, Hungary and from the Apuseni Mts. in Romania (Kozur & Mirauta, 1980). "G. pseudolonga" described from the Southern Alps by Kovács et al. (1980) probably also belongs to this group, exception made for pl. 1, fig. 3a, b, which could be related to G. constricta cornuta, according to the previously discussed interpretation.

G. szaboi-trammeri lineage

Gondolella alpina alpina Kozur & Mostler, 1982

Pl. 4, fig. 4; Pl. 5, fig. 1-3

1982 Gondolella alpina Kozur & Mostler, p. 292, pl.1, fig. 1a, b; pl. 2, fig. 4a-c, 5a, b. ? 1983 Gondolella cf. alpina Krystyn, pl. 3, fig. 1a-c.

Remarks. Forms related to G. alpina Kozur & Mostler, 1982 and to G. szaboi Kovács, 1983 are quite characteristic for the costosus horizon in the investigated area. Besides their different ranges, the main morphological difference between them can be seen in the different length of the platform. Whereas in typical forms of G. alpina it ends abruptly, leaving the anterior third of the carina free (as free-blade), in those of *G. szaboi* it extends until the anterior end of the unit, leaving practically no free-blade. Furthermore, in typical forms of the former the basal pit is larger, with thick margin (closely resembling that of *G. trammeri*), whereas in those of the latter it is smaller, with a posteriorly extended loop behind it. However, because of the wide field of transition between them, it seems reasonable to separate them at subspecific level.

Relations. G. alpina alpina is closely related to G. alpina szaboi and to G. trammeri. It is interpreted to represent a side-branch of the G. szaboi-G.trammeri lineage.

Range. Frequent in the costosus horizon, but was found also in the reitzi horizon (section Vászoly P2). Kozur & Mostler (1982) described it from a bed "with Parakellnerites sp." However, this long-ranging ammonoid genus occurs from the meriani B to the costosus horizons (Vörös, 1993).

Occurrence. Its sure occurrence has been proven so far only in the Fellbach Limestone of the Gailtal Alps (Kozur & Mostler, 1982) and in the Buchenstein Formation of the Balaton Highland. It seems to characterize open intrashelf basin environments. On the other hand, in the eupelagic facies of NE Hungary it was not found (Kovács, unpubl.) and its occurrence in the Epidauros section of the Inner Hellenides is also uncertain (Krystyn, 1983).

Gondolella alpina szaboi Kovács, 1983

Pl. 4, fig. 1-3

1983 Gondolella szaboi Kovács, p. 114, pl. 4, fig. 1-4.

Remarks. For the reasons discussed above, this form is separated here only at subspecific level from *G. alpina* Kozur & Mostler, 1982.

Relations. The rise of the G. szaboi - G. trammeri lineage from Gondolella bulgarica (Budurov & Stefanov, 1975) took place in the latest Pelsonian through G. praeszaboi (with two subspecies described in detail by Kovács, Papsová & Perri). This early evolution of the lineage can be recorded in NE Hungary and SE Slovakia. The Illyrian evolution in NE Hungary may be similar, through rare forms representing a link between G. praeszaboi and G. alpina szaboi (Kovács, Papsová & Perri, 1993; Kovács, unpubl.). In the Balaton Highland area, however, only the late stage of its evolution can be studied.

The evolution and taxonomy of the G. szaboi-G. trammeri lineage will be analysed in details in a separate work. For the main differences against G. alpina alpina see above.

Range. *Trinodosus* Zone to the top of the Reitzi Zone, *costosus* horizon in sense of Vörös (1993). It seems to characterize the slope facies (crinoidal wackestones to packstones).

In the Balaton Highland the occurrence of the *G. szaboi-G. trammeri* lineage was facies controlled; no representatives have been found below the *reitzi* horizon (except *G.* aff. *eotrammeri*, a few representatives of which have been found also in the *liepoldti*

AMMONOID		CONODONTS
ZONES	horizons	Gondolella llebermanl Gondolella constricta cornuta Transitional forms between G. c. cornuta and G. c. postcornuta Gondolella constricta postcornuta Gondolella aff. eoirammeri Gondolella alpina alpina Gondolella trammeri Gondolella tramsita Gondolella transita Gondolella transita Gondolella Pakalovi-Group "Metapolygnathus" hungaricus Gladigondolella tethydis
v	recubariense (?)	
	Curionii	
REITZI	costosus	
	reitzi	
	liepoldti	
	felsoeoersensis	
م	meriani B	
μ	camunum	

Fig. 6 - Ranges of the stratigraphically most important conodonts in the Anisian/Ladinian boundary interval of the Balaton Highland, according to the ammonoid chronology by Vörös (1993). T trinodosus; P - polymorphus; C - curionii.

horizon of the section Vászoly P 11a) (Fig. 6). Its appearance in the Balaton Highland Buchenstein basin was evidently connected to the establishment of full pelagic conditions, best indicated by the appearance of gladigondolelloids. *G. alpina szaboi* (along with *G. alpina alpina*) is frequent here in the *costosus* horizon and disappears at the base of the Curionii Zone. The holotype and the paratypes (figured by Kovács, 1983; samples collected by I. Szabó) derive from the Öreghegy Hill between Vászoly and Pécsely, from shaft No. 17 (see Kovács et al., 1990, fig. 8), from purplish red calcarenites (with "*Protrachyceras reitzi*"; Szabó, in Kovács, 1983 and Kovács et al., 1990) similar to those characterizing the *costosus* horizon at the top of the Mencshely section. The ammonoids from older collections still await for revision in the light of Vörös's new, bed-by-bed investigations. Consequently in the present paper only the occurrences within the described sections are considered. Occurrence. Balaton Highland, in the *reitzi*? and the *costosus* horizons; NE Hungary (Kovács, unpubl.); Reifling Limestone of the Northern Calcareous Alps (Krystyn, in Kovács, 1983) and the West Carpathians (Papsová, pers. comm.). Typical forms in the upper part of Trinodosus Zone are certainly present (Krystyn, in Kovács, 1983), while the attribution of those forms occurring in the lower part of the Trinodosus Zone (e.g. in NE Hungary; Kovács, unpubl.) is still uncertain.

Gondolella aff. eotrammeri Krystyn, 1983

1990 Gondolella aff. eotrammeri - Kovács et al., p.188, pl. 2, fig. 1-3.

Remarks. The forms interpreted as the forerunner of *G. trammeri* in the studied area are referred to this open taxonomic category. However, their affiliation to *G. eotrammeri*, described from the eupelagic Epidauros section of the Inner Hellenides by Krystyn (1983) is uncertain (see Kovács et al., 1990, p. 188). This problem will be analysed in more details in a separate contribution with Dr. Alda Nicora (Milano).

Range. In the Balaton Highland it occurs in the *liepoldti* (rare), *reitzi* (rare; found only in the Vászoly P2 section) and in the basal part of the *costosus* (more frequent) ammonoid horizons (Fig. 6). Its last occurrence and the first occurrence of *G. trammeri* coincide in the basal part of the *costosus* horizon. However, its first occurrence in the Balaton Highland is most probably facies controlled, because representatives of the *G. szaboi-G. trammeri* lineage are not known below the *liepoldti* horizon. Instead, in NE Hungary and SE Slovakia they appear earlier (Kovács, Papsová & Perri, in press).

Occurrence. So far known only from the lowermost Buchenstein Formation of the Balaton Highland, Hungary and of the Southern Alps, Italy.

Gondolella trammeri Kozur, 1972

Remarks. G. trammeri is the most common Ladinian conodont in the area studied and also in Hallstatt Limestone-type eupelagic sequences (Krystyn, 1983; Kovács et al., 1990). It differs from its forerunner, G. aff. eotrammeri by its straight upper edge of the carina (except the anterior third) which is arched in the latter.

This species is represented mostly by earlier ontogenetic stages in the areas investigated up to now; mature stages are rare.

Range. From the base (?) of the *costosus* horizon to the Archelaus Zone (except its uppermost part ?).

¹⁹⁷² Gondolella haslachensis trammeri Kozur in Kozur & Mock, p. 13, pl. 1, fig. 1, 3, 4, 7 (non 2, 5, 6).

¹⁹⁷⁹ Gondolella trammeri - Mietto & Petroni, pl. 1, fig. 6; pl. 2, fig. 2, 3-5.

¹⁹⁸⁰ Gondolella trammeri - Kovács & Kozur, pl. 6, fig. 6a-c, 7a-c, 8.

¹⁹⁸² Gondolella trammeri praetrammeri Kozur & Mostler, pp. 294-295, only pl. 1, fig. 5a, b.

¹⁹⁸³ Gondolella trammeri - Krystyn, p. 239, pl. 1, fig. 5, 6; pl. 2, fig. 3, 4.

¹⁹⁹⁰ Gondolella trammeri - Kovács et al., pl. 2, fig 4-6.

Occurrence. Very common in Tethyan eupelagic basin and open intrashelf basin facies. More important recorded occurrences: Balaton Highland, Hungary (very frequent); Southern Alps (frequent; Mietto & Petroni, 1979; Nicora, in Kovács et al., 1990); NE Hungary (less frequent; Kovács, 1986 and unpubl.); Inner Hellenides, section Epidauros (frequent, Krystyn, 1983).

G. excelsa lineage

Gondolella liebermani Kovács & Krystyn sp. n.

Pl. 6, fig. 1-3

1983 Gondolella cf. szaboi Krystyn, p. 236, pl. 1, fig. 1, 4, 5.

1990 Gondolella aff. szaboi Kovács et al., fig. 5, 7, 9, 13, 14 (its presence is indicated only on the stratigraphic columns).

Derivatio nominis. In honour of Dr. Henry M. Lieberman (presently in Houston, USA) for his contribution to the stratigraphy of the Carnian Raibl Group of the Southern Alps.

Holotype. Pl. 6, fig. 1a-d; T 6469.

Locus typicus. Vászoly, Öreghegy Hill, Balaton Highland, Hungary.

Stratum typicum. Section P 11a, bed No. 5.

Diagnosis. Unit moderately arched in lateral view. Carina fairly high, practically of the same height all along its length, except the posterior 1/4, where it decreases gradually. However, due to arching, it is highest in the middle. Denticles are completely fused, except their tips. Lateral surface of the carina smooth, without prominent striation. Platform subparallel, with moderately thick, slightly upturned margins and rounded posterior end. It extends almost all along the length of the unit, leaving free only the first 1-2 denticles, or no free blade at all, and tapers gradually in its anterior third. Keel fairly wide, with a posteriorly located, flaring pit and rounded loop.

Remark. This new species is introduced here in co-authorship with Dr. L. Krystyn (Vienna), as its independency was recognized jointly when discussing his material published in 1983.

Relations. G. liebermani sp. n. is a characteristic representative of the G. excelsagroup. G. excelsa Mosher, 1968 s.s. (see Pl. 7, fig. 1a-d in the present paper) is distinguished by its very wide, nearly semicircular, flat platform, which is widest at the beginning of the posterior third. Also, its carina shows a semicircular outline in lateral view, being highest in the middle.

The oldest representatives of *G. fueloepi* sp. n., occurring in the *costosus* horizon of the Reitzi Zone, are distinguished from the latest forms of *G. liebermani* sp. n. by the downward-stepping tendency of the platform margins at the anterior third of the unit. Furthermore, at this point they are more strongly upward turned.

G. szaboi Kovács, 1983 shows some homeomorphic feature. However, it belongs to a different evolutionary lineage (to the G. szaboi-G. trammeri lineage), and not to

the G. excelsa-group. It is distinguished from G. liebermani sp. n. first of all by its narrow platform with strongly upturned margins and its similarly narrow keel with a small pit. Furthermore, the lateral surface of its carina is not smooth, but shows a characteristic striation.

Range. Trinodosus Zone to the liepoldti horizon of the Reitzi Zone.

Occurrence. So far known from the Balaton Highland, from NE Hungary (Kovács, unpubl.) and from the Epidauros section of Greece (Krystyn, 1983). It seems to have been characteristic for Tethyan eupelagic basin and open intrashelf basin environments.

Gondolella fueloepi sp. n.

1973 Gondolella polygnathiformis - Krystyn, pl. 2, fig. 1.
1981 Gondolella n. sp. D Balogh & Kovács, pp. 48, 56.
1983 Gondolella inclinata Krystyn, pl. 3, fig. 5a-c only.
1986 Gondolella n. sp. D nom. dub. Kovács, pl. 4, fig. 8a-c; pl. 6, fig. 7a-d, 8a-c.
1989 Gondolella n. sp. D Kovács et al., p. 49, fig. 4a.

Derivatio nominis. In honour of Academician Dr. József Fülöp, who supported the present author's conodont investigations in Hungary for many years.

Diagnosis. Carina fairly high, highest in the middle, becoming less pronounced in advanced stages (both ontogenetic and phylogenetic) against the massive platform. Denticles are completely fused, except their tips, in advanced stages form a low ridge in the posterior part of the carina. Lateral surface of the carina is smooth, without striation. Platform wide, with typically thickened and massive margins, which tend to bend stepwise downward at their anterior third. Keel very wide, with an extensive loop behind the pit, which is larger on the phylogenetically older representatives and becomes small on younger ones.

Remarks. Two closely related subspecies bound by a wide field of transition are included into this species. These are especially frequent in the Nádaska Limestone Formation of slope facies in NE Hungary, marking an important local zone (Kovács et al., 1989). They are formally introduced here, because of some stratigraphic importance, and will be analysed in details in separate contributions on the *excelsa* lineage and on the conodont biostratigraphy of the Nádaska Limestone Formation.

Gondolella fueloepi fueloepi ssp. n.

Pl. 7, fig. 2, 3; Pl. 8, fig. 4

Derivatio nominis. See the nominative species. Holotype. Pl. 8, fig. 4a-d; T 6478. Locus typicus. Hidvégardó, Szentjános Hill, NE Hungary. Stratum typicum. Szentjánoshegy Limestone Formation, section in the southern neighbourhood of the quarry, sample H-17 (Kovács, 1986, fig. 11).

S. Kovács

Diagnosis. Carina high, highest in the middle, with arched upper edge in lateral view. Platform fairly wide, with thickened, slightly upturned margins, tending to be subparallel in the posterior two-third and, in lateral view, downward stepping at the anterior third of the unit. Platform end mostly rounded, less frequently blunted. Keel wide, with a rounded loop around the pit, which is larger in earlier phylogenetic stages and becomes smaller in later ones.

Remarks. The platform margins become strongly thickened and massive from the medium ontogenetic stage on. Also, from this stage on, the downward stepping at the anterior third of the unit becomes more pronounced.

Relations. G. fueloepi fueloepi ssp. n. evolved from G. excelsa Mosher, 1968 (s.s.) through the slight upward turning and downward stepping of the platform margins, as seen in lateral view. Typical specimens of G. excelsa s.s. (Pl. 7, fig. 1a-d) are characterized by a very high, in lateral view nearly semicircular carina and a very wide, flat platform, which is widest in the middle. For differences against G. fueloepi pseudobifurcata ssp. n. see below.

During the preparation of the manuscript of this paper, and after the closure of the other article by Kovács (1993, in print), a Xerox-copy of a paper by Budurov & Sudar (1989) has been available for the present author by the courtesy of Dr. Alda Nicora, Milano. It contains the description of a new species, *Paragondolella postexcelsa* sp. n., which shows close morphological similarity to *G. fueloepi fueloepi* ssp. n. described herein. On the picture of its holotype (Budurov & Sudar, op. cit., pl. 1, fig. 12, 13) only one remarkable difference can be seen: the downward stepping of the platform margin is missing. This is especially characteristic in *G. fueloepi pseudobifurcata* ssp. n., thus showing an homeomorphic feature to the Carnian *G. polygnathiformis. G. postexcelsa* seems therefore to belong to another evolutionary lineage of the excelsastock and probably represents a transitional phylogenetic stage between *G. excelsa* Mosher, 1968 (or even *G. liebermani* sp. n.?, described above) and *G. foliata inclinata* Kovács, 1983.

This form is very common in the Ladinian basinal formations of the Aggtelek-Rudabánya Mts., NE Hungary, where a local conodont zone may be distinguished (Balogh & Kovács, 1981; Kovács et al., 1989). Consequently the holotypes of both subspecies, representing typical, highly evolved forms, are choosen from that area.

Range. Ladinian, from the *costosus* horizon of the Reitzi Zone to the higher part of the Archelaus Zone (Kovács et al., 1989).

Occurrence. It seems to characterize the Tethyan eupelagic ("Hallstatt") facies; so far known from the Balaton Highland and from NE Hungary (especially frequent in the Nádaska Limestone Formation, where it can be used as a local zonal index form; Kovács et al., 1989), as well as from Hallstatt-type limestones of Austria (Krystyn, 1973) and Greece (Krystyn, 1983).

Gondolella fueloepi pseudobifurcata ssp. n.

Pl. 8, fig. 1, 3

Derivatio nominis. Because of the frequent bifurcation of the posterior end of the carina, resembling *G. bifurcata bifurcata* (Budurov & Stefanov, 1972).

Holotype. Pl. 8, fig. 3a-c; T 6477.

Locus typicus. Tornanádaska, eastern end of Alsóhegy Karstplateau, Szölösardó Unit, Silice Nappe, NE Hungary.

Stratum typicum. Section Alsóhegy-I (type-section of the Nádaska Limestone; Kovács, 1979) bed No. 39.

Diagnosis. Platform wide, very thick and massive in advanced ontogenetic stages, subparallel or widest at the usually blunted or squared off posterior end. Platform margins at the anterior third of the unit are characteristically downward stepping. Behind this point, the carina in adult and hyperadult ontogenetic stages tends to be of the same height, as the thickened platform margins. Adcarinal troughs are deep and very narrow. Posterior end of the carina is usually bifurcated. Keel very wide, with squared off or slightly bifurcated loop behind the fairly small pit.

Relations. The downward stepping platform margin of *G. fueloepi pseudobifurcata* shows (in lateral view) homeomorphic feature to the Carnian *G. polygnathiformis* (Budurov & Stefanov, 1965, emend Mosher, 1973). This homeomorphic feature, however, does not imply a phylogenetic relationship between them, as *G. polygnathiformis* evolved from the different lineage, from *G. foliata inclinata* (Kovács, 1983 and Kovács et al., 1989, fig. 4a).

G. fueloepi pseudobifurcata ssp. n. evolved from G. fueloepi fueloepi ssp. n., as indicated by a wide field of transition between them. Typical forms of the two subspecies are distinguished by several morphological features, which characterize G. fueloepi pseudobifurcata as follows:

- width of the platform margins: the very thick, flat margins extend laterally almost until the carina, leaving only narrow, but deep adcarinal troughs on both sides;

- shape of the platform end: usually blunted or squared-off;

- shape of the carina: nearly of the same height as the thickened part of the platform margins, with a nearly straight upper edge and mostly bifurcated posterior end;

- shape of the loop on the lower surface: usually squared-off or blunted.

Range. Costosus horizon of the Reitzi Zone to the Archelaus Zone (except its uppermost part).

Occurrence. This form seems to characterize Tethyan eupelagic basin and slope facies, where metapolygnathoids are usually underrepresented. So far it is known from the Balaton Highland and especially from NE Hungary (Balogh & Kovács, 1981; Kovács, 1986; Kovács et al., 1989 and Kovács unpubl.), from the Hallstatt limestones of the Northern Calcareous Alps (Krystyn, 1973) and of the Inner Hellenides (Epidauros section, courtesy of Dr. L. Krystyn, Vienna).

"Metapolygnatus" hungaricus lineage

Gondolella ? praehungarica sp. n.

Pl. 5, fig. 4; Pl. 9, fig. 1-5; Pl. 10, fig. 1-3

1979 Neogondolella mombergensis - Mietto & Petroni, pl. 1, fig. 1a, b.

? 1979 Neogondolella excentrica - Mietto & Petroni, pl. 1, fig. 5a-c.

? 1979 Neogondolella subodolica - Mietto e Petroni, pl. 2, fig. 7 a-c.

Derivatio nominis. Because of phylogenetic relationship to "Metapolygnathus" hungaricus (Kozur & Végh), being interpreted as the forerunner of that.

Holotype. Pl. 10, fig. 1a-g; T 6485.

Locus typicus. Felsöörs, Balaton Highland, Hungary.

Stratum typicum. Lower part of the Nemesvámos Limestone Member of the Buchenstein Formation, uppermost part of the section at Forráshegy, bed. No. 29/86.

Diagnosis. Unit nearly straight in upper view, the posterior end may be slightly laterally bent. Platform extends along the whole length of it, leaving no free blade. It builds asymmetrically in younger ontogenetic stages and tends to be parallel in more adult stages. The platform is broadest in the middle or at the posterior two-third and tapers gradually towards both ends. Platform margins are moderately upturned and not thickened. Posterior platform end pointed. Carina consists of partly separated, moderately high denticles, fused only in their lower half to two-third. The second or third denticle before the posterior end is the largest and represents the cusp; the one or two denticles behind it are much smaller than the others. Keel narrow to moderately wide, with a slightly anteriorly shifted small pit, having no protruding margin.

Relations. G. ? praehungarica sp. n. is represented mostly by juvenile forms in the Felsöörs section, showing close relationship to those of G. trammeri, which is likewise represented by earlier ontogenetic stages. They are distinguished from the latters, as seen in light microscope, mainly by the presence of one or two addditional small denticles behind the cusp. Other differences (slightly anteriorly shifted pit and posteriorly extended, pointed loop behind it) can rather be seen only by scanning electron microscope. The close morphological relationship clearly indicates a phylogenetic relationship between them. Development of G. ? praehungarica from G. trammeri could be detected from bed No. 3/86 upward in the upper part of the Felsöörs section.

On the other hand, this new species represents the forerunner of "Metapolygnathus" hungaricus, as shown by transitional forms between them (e.g. Pl. 10, fig. 2, 3)."M." hungaricus is distinguished, in more advanced ontogenetic stages, by the shape of the platform. It is abruptly tapering at its anterior third, leaving some free blade, and having a considerably laterally bent posterior end and the more anteriorly shifted cusp and basal pit. Further studies, based on a richer collection than our present one, may reveal if "primitive" (e.g. Pl. 9, fig. 2,5) and "more evolved" (e.g. Pl. 10, fig. 2, 3) forms could be separated at subspecific level. Our material, however, does not permit it. The "primitive" morphotypes were found also to the range top of the new species.

The "more evolved" morphotypes have an asymmetrically built platform (as the beginning of the "metapolygnathoid" platform building), which resembles in upper view *G. transita*. However, building of the basal structures (pit and loop) unambiguously indicate, that *G. transita* belongs to a different lineage (to the *G. constricta* lineage): its margin of pit is strongly protruding (Pl. 3, fig. 1e), whereas in the new species it is

smooth (Pl. 10, fig. 1g). A further difference can be seen in the denticles of carina, which are short, thick and fairly separated in the posterior third of *G. transita*.

Range. Lower part of the Curionii Zone; recorded in the Felsöörs section from bed No. 3/86 to 29/86. Its first occurrence and the same of "M." hungaricus allow to define a local conodont zone. However, G. trammeri is predominating throughout this zone.

Occurrence. So far known only from the cherty, nodular Nemesvámos Limestone Member of the Felsöörs section, Balaton Highland, Hungary.

Mietto & Petroni (1979) figured three specimens from the Southern Alps which are closely related to G. ? praehungarica: the first specimen, shown on their pl. 1, fig. 1a, b as "Neogondolella mombergensis" seems to be a juvenile, "primitive" form of this new species, still related also to G. trammeri. The second one, shown on pl. 1, fig. 5a-c as "Neogondolella excentrica" is probably an adult stage of G. ? praehungarica, whereas the third specimen, shown on pl. 2, fig. 7a-c as "Neogondolella subodolica" seems to represent an adult transitional form between G. ? praehungarica and "M." hungaricus.

On the problem of the "Metapolygnathus" truempyi and "Metapolygnathus" hungaricus lineages.

Kozur (1972, 1980) and Kozur & Mock (1972) postulated an evolutionary lineage Gondolella transita \rightarrow "Metapolygnathus" truempyi \rightarrow "Metapolygnathus" hungaricus, based on the supposed gradual anteriorward shifting of the basal pit and the increasing asymmetry of the posterior part of the unit. Our subsequent, bed-by bed investigations in the Felsöörs section, from where both Gondolella transita Kozur & Mostler, 1971 and "Metapolygnathus" hungaricus (Kozur & Végh, 1972) have been first described, however, disprove this postulated lineage. In fact, it was found, that "M." hungaricus evolved from the G. szaboi \rightarrow G. transmeri lineage through G. ? praehungarica sp. n. The rise of this lineage leading from G. transita is a typical representative of the G. anteriorward shifting of the basal pit. G. transita is a typical representative of the G. s, fig. 1e). On the other hand, the basal pit of G. ? praehungarica has no protruding margin (see Pl. 10, fig. 1g).

Kozur, in Kozur & Mock (1972, p. 9) and Kozur (1972, pl. 1) considered as the main difference between "M." truempyi and "M." hungaricus the position of the basal pit and the width of the keel around it. Accordingly, "M." truempyi was considered as having a pit almost terminally located on the keel, while "M." hungaricus has a considerably anteriorly shifted pit, with only a slight widening of the keel around it. However, in this way the postulated evolution from G. transita through "M." truempyi to "M." hungaricus is somewhat inconsequent, because it would implie a back-stepping in the evolutionary trend. The pit was already fairly well anteriorward shifted in G. transita.

On the other hand, Bagnoli et al. (1985, pl. 1, fig. 1-4; pl. 2, fig. 1-4) figured several forms of "M." truempyi from Sardinia, with considerably anteriorward shifted basal pit, which would correspond to "M." hungaricus accordingly to the differences between the two species given by Kozur (see above). The present author in 1987 had the opportunity to study the whole collection from the courtesy of Dr. Cristina Perri (Bologna), which is gratefully acknowledged here. It contains specimens both with less and more anteriorward shifted basal pit. In general, however, this fauna from Sardinia is characterized by a more anteriorward shifted position of the basal pit, than the forms figured by Hirsch (1971, 1972) from Provence. Probably Hirsch's material represents an earlier phylogenetic stage. It is, however, clear, that the main difference between "M." truempyi and "M." hungaricus is not ment by the position of the basal pit, which is more or less anteriorward shifted in both, but by the shape of the platform. In "M." hungaricus its margins are flat in lateral view without abrupt downward inclining, whereas in "M." truempyi they are upturned, leaving deep adcarinal throughs, and in lateral view are abruptly downward stepping at the anterior third of the unit, like in the Carnian Gondolella polygnathiformis. (Unpublished discussion between the present author and Dr. C. Perri, 1987).

From the facts, that "M." truempyi does not occur in the Felsöörs section (e.g. it could not be the forerunner of "M." hungaricus) and the otherwise close morphological similarity (except the platform margins) between it and "M." hungaricus, it follows, that these two forms may represent homeomorphic stages on different evolutionary lineages. It raises also the problem of the possible biphyletic origin of "M." mungoensis (Diebel, 1956). Is the "Sephardic" "M. mungoensis" really conspecific with the "Alpine" (or Neotethyan) "M." mungoensis ? The latter, in agreement with Kozur's former proposal, certainly developed from M. hungaricus, as proven by transitional forms occurring in the top part of the Felsöörs section. This so far unpublished idea about the biphyletic origin arose jointly with Dr. L. Krystyn, when he kindly showed me his, unfortunately, not yet published, material from Southern Turkey.

To clear up the morphological relationships between "M." truempyi and "M." hungaricus (especially in the light of Perri's above mentioned material from Sardinia) it is unavoidably necessary to carry out a detailed comparative study of the topotypic materials from Provence and the Balaton Highland. The abrupt downward stepping platform margin of "M." truempyi at the anterior third of the unit seems to be a satisfactory base to distinguish the two species. In the opposite case, however, "Epigon-dolella" hungarica Kozur & Végh, 1972 would be a junior synonym of "Gladigon-dolella" truempyi Hirsch, 1971 and Gondolella ? praehungarica sp. n. might also be that of "Gladigondolella" truempyi denticulata Hirsch, 1971.

The bed-by-bed study of the upper part of the Felsöörs section has not only disproven the postulated evolutionary lineage G. transita \rightarrow "M." truempyi \rightarrow "M." hungaricus, but even the occurrence of "M." truempyi described from the Sephardic domain (Hirsch, 1971, 1972) was not confirmed. This fact raises up the question: how could this section be declared as the type-section of the "M." truempyi zone ? (Kozur, 1980, p. 111, and Kozur & Mirauta, 1980, p. 230).

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PLATE 1

- Fig. 1a-c Gondolella constricta cornuta (Budurov & Stefanov). Late juvenile ontogenetic stage. Spec. No. 2/84. Section Felsöörs, bed No. 89; Trinodosus Zone. (a) Lateral view; b) upper-lateral view; c) platform end, lateral view; (a, b, 66 x; c, 200 x). T-6447.
- Fig. 2a, b- Gondolella constricta cornuta (Budurov & Stefanov). Juvenile ontogenetic stage. Section Felsöörs, bed No. 100^{*}; Reitzi Zone, *felsoeoersensis* horizon. a) Lateral view (73 x); b) platform end, lateral view; (200 x). T-6448.
- Fig. 3a-d- Gondolella constricta cornuta (Budurov & Stefanov). Medium ontogenetic stage. Spec. No. 11/84. Section Felsöörs, bed No. 98, meriani B horizon. a) Lateral view; b) upper-lateral view; c) lower view; d) platform end, lateral view; (a, b, c, 66 x; d, 200 x). T-6449.
- Fig. 4a-d- Gondolella constricta postcornuta ssp. n. Holotype. Medium ontogenetic stage. Spec. No. 8/84. Section Öskü, sample No. 4 (see in Kovács et al., 1990, fig. 10); lower Curionii Zone. a) Slightly oblique lateral view; b) upper-lateral view; c) upper view; d) platform end, upper-lateral view; (a, b, c, 66 x; d, 200 x). T-6451.
- Fig. 5a-d- Gondolella constricta postcornuta ssp. n. Late medium ontogenetic stage. Spec. No. 1/93. Section Mencshely, bed No. (-3); costosus horizon. a) Lateral view; b) upper-lateral view; c) platform end, upper-lateral view; d) upper view; (a, b, d, 50 x; c, 133 x). T-6452.

PLATE 2

- Fig. 1a-c Gondolella constricta cornuta (Budurov & Stefanov). Medium ontogenetic stage. Spec. No. 4/84. Section Felsöörs, bed No. 93; Uppermost part of Trinodosus Zone. a) Lateral view; b) upper lateral view; c) lower view; (52 x). T-6450.
- Fig. 2a-e Gondolella constricta postcornuta ssp. n. Submedium ontogenetic stage. Spec. No. 13/84. Section Öskü/Sóly, tuffaceous horizon of the "Anisian/Ladinian boundary bed" (see in Kovács et al., 1990, fig. 10); Reitzi Zone, reitzi ? or costosus ? horizon. a) Lateral view; b) upper-lateral view; c) upper view; d) platform end, upper-lateral view; e) platform end, lower-lateral view; (a, b, c, 66 x; d, e, 200 x). T-6453.
- Fig. 3a, b- Gondolella constricta postcornuta ssp. n. Submedium ontogenetic stage. Section Mencshely, bed No. (-18); Reitzi Zone, felsoeoersensis horizon. a) Lateral view; b) upper-lateral view; (66 x). T-6454.
- Fig. 4 Gondolella constricta postcornuta ssp. n. Late juvenile ontogenetic stage. Spec. No. 7/84. Section Öskü, sample No. 4 (see Kovács et al., 1990, fig. 10); lower Curionii Zone. Lateral view; (48 x). T-6455.
- Fig. 5a-d- Gondolella constricta postcornuta ssp. n. Medium ontogenetic stage. Spec. No. 2/93. Section Mencshely, bed No. (-3); Reitzi Zone, costosus horizon. a) Upper-lateral view; b) lateral-upper view; c) upper view; d) lower view; (50 x). T-6456.
- Fig. 6a-d- Gondolella sp. aff. bakalovi (Budurov & Stefanov). Spec. No. 3/84. Section Vászoly-Öreghegy II (P2) bed No. 6 (see in Kovács et al., 1990, fig. 6); Curionii Zone. a) Lateral view; b) upper-lateral view; c) upper view; d) lower view; (a, d, 66 x; b, 68 x; c, 63 x). T-6458.

PLATE 3

- Fig. 1a-e- Gondolella transita Kozur & Mostler. Medium ontogenetic stage. Section Felsöörs, bed No. 10/86; Curionii Zone. a) Upper-lateral view; b) lateral-upper view; c) upper view; d) lower view; e) platform end, lower-lateral view, showing the conspicuously protruding margin of the basal pit, characteristic of the constricta lineage; (a, b, c, d, 66 x; e, 160 x). T-6459.
- Fig. 2a-d Gondolella transita Kozur & Mostler. Adult ontogenetic stage, nearly symmetric form. Spec. No. 2/78. Section Felsöörs, bed No. 130/78 (equivalent to 10/86); Curionii Zone. a) Lateral view; b) upper-lateral view; c) upper view; d) lower view; (66 x). T-6460.
- Fig. 3a-c Gondolella transita Kozur & Mostler. Adult ontogenetic stage. Spec. No. 1/78. Section Felsöörs, bed No. 155/78 (equivalent to 30/86), higher Curionii Zone. a) Upper-lateral view; b) lower view; c) upper view; (66 x). T-6461.

- Fig. 1a-e- Gondolella alpina szaboi Kovács. Typical form. Spec. No. 8/93. Section Mencshely, bed No. (-3); Reitzi Zone, costosus horizon. a) Lateral view; b) upper-lateral view; c) lateral-upper view; d) upper view; e) lower view; (66 x). T-6462.
- Fig. 2a, b- Gondolella alpina szaboi Kovács. Spec. No. 7/93. Section Mencshely, bed No. (-3); Reitzi Zone, costosus horizon. a) Lateral view; b) lateral-upper view; (50 x). T-6463.
- Fig. 3a-d- Gondolella alpina szaboi Kovács. Spec. No. 9/93. Section Mencshely, bed No. (-4); Reitzi Zone, costosus horizon. a) Lateral view; b) upper-lateral view; c) upper view; d) lower view; (66 x). T-6464.
- Fig. 4a-d- Gondolella alpina alpina Kozur & Mostler. Spec. No. 1/93. Section Mencshely, bed No. (-3); Reitzi Zone, costosus horizon. a) Lateral view; b) lateral-upper view; c) upper view; d) lower view; (66 x). T-6465.

PLATE 5

- Fig. 1a-d- Gondolella alpina Alpina Kozur & Mostler. Spec. No. 2/93. Section Mencshely, bed No. (-4); Reitzi Zone, costosus horizon. a) Lateral view; b) upper-lateral view; c) upper view; d) lower view; (66 x). T-6466.
- Fig. 2a-d- Gondolella alpina alpina Kozur & Mostler. Late juvenile ontogenetic stage. Spec. No. 4/93. Section Mencshely, bed No. (-4); Reitzi Zone, costosus horizon. a) Lateral view; b) upper-lateral view; c) upper view; d) lateral-lower view; (66 x). T-6467.
- Fig. 3a, b- Gondolella alpina alpina Kozur & Mostler. Spec. No. 3/93. Section Mencshely, bed No. (-4); Reitzi Zone, costosus horizon. a) Lateral view; b) lateral-upper view; (66 x). T-6468.
- Fig. 4a-d- Gondolella ? praehungarica sp. n. Medium ontogenetic stage. Spec. No. 3/93. Section Felsöörs, bed No. 154/78 (bed next below No. 30/86); upper Curionii Zone. a) Lateral view; b) lower-lateral view; c) upper-lateral view; d) upper view; (66 x). T-6479.

PLATE 6

- Fig. 1a-d- Gondolella liebermani Kovács & Krystyn sp. n. Holotype. Adult ontogenetic stage. Section Vászoly P 11a, bed No. 5; uppermost part of meriani B horizon. a) Lateral view; b) upper-lateral view; c) upper view; d) lower view; (66 x). T-6469.
- Fig. 2a-d- Gondolella liebermani Kovács & Krystyn sp. n. Medium ontogenetic stage. Section Vászoly P 11a, bed No. 5; uppermost part of meriani B horizon. a) Lateral view; b) upper-lateral view; c) upper view; d) lower view; (66 x). T-6470.
- Fig. 3a-d- Gondolella liebermani Kovács & Krystyn sp. n. Adult ontogenetic stage. Section Vászoly P 11a, bed No. 6; Reitzi Zone, basal part of *felsoeoersensis* horizon. a) Lateral view; b) upper-lateral view; c) upper view; d) lower view; (50 x). T-6471.
- Fig. 4a-d- Gondolella constricta postcornuta ssp. n. Medium ontogenetic stage. Section Vászoly P 11a, bed No. 8; Reitzi Zone, liepoldti horizon. a) Lateral view; b) upper-lateral view; c) lateral-upper view; d) lower view; (50 x). T-6457.

PLATE 7

- Fig. 1a-d- Gondolella excelsa Mosher. Typical, adult form. Section Vászoly P2, bed No. II/8 (see in Kovács et al., 1990, fig. 6); Curionii Zone. a) Lateral view; b) lateral-upper view; c) upper view; d) lower view; (66 x). T-6472.
- Fig. 2a-d- Gondolella fueloepi fueloepi ssp. n. Adult ontogenetic stage, earliest evolutionary stage. Section Vászoly P 11a, bed No. I/2; lower Curionii Zone. a) Lateral view; b) lateral-upper view; c) upper view; d) lower view; (50 x). T-6473.
- Fig. 3a-d- Gondolella fueloepi fueloepi ssp. n. Adult ontogenetic stage. Section Felsöörs, bed No. 13/85; Curionii Zone. a) Lateral view; b) upper-lateral view; c) upper view; d) lower view; (66 x). T-6474.

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PLATE 8

- Fig. 1a-d Gondolella fueloepi pseudobifurcata ssp. n. Hyperadult ontogenetic stage, earliest evolutionary stage. Spec. No. 3/93. Section Mencshely, bed No. (-3); Reitzi Zone, costosus horizon. a) Lateral view; b) upper-lateral view; c) upper view; d) lower view; (33 x). T-6475.
- Fig. 2a-d Transitional form between Gondolella fueloepi fueloepi ssp. n. and G. fueloepi pseudobifureata ssp. n. Adult ontogenetic stage. Spec. No. 4/93. Section Mencshely, bed No. (-3); Reitzi Zone, costosus horizon. a) Lateral view; b) lateral-upper view; c) upper view; d) lower view; (50 x). T-6476.
- Fig. 3a-c Gondolella fueloepi pseudobifurcata ssp. n. Holotype. Highly evolved form, hyperadult ontogenetic stage. Constriction near to the posterior end and serration on the anterior platform margin mean some pathological features, without taxonomic importance. Spec. No. 3/84. Section Alsóhegy-I, Szölösardó Unit, Silice Nappe, NE Hungary, stratotype of the Nádaska Limestone Formation (see Kovács, 1979; details are in Kovács, 1987, in press), bed No. 39; Longobardian. a) Lateral-upper view; b) upper view; c) lower view; (32 x). T-6477.
- Fig. 4a-d Gondolella fueloepi sep. n. Holotype. Highly evolved form, adult ontogenetic stage. Locality Hidvégardó, Szentjános-hegy (Torna Nappe), section in the southern neighbourhood of the quarry, sample H-17 (see Kovács, 1986, fig. 11); Lower Longobardian (together with Gondolella foliata inclinata Kovács). a) Lateral view; b) upper-lateral view; c) upper view; d) lower view; (36 x). T-6478.

PLATE 9

- Fig. 1a-c Gondolella ? praehungarica sp. n. Early juvenile ontogenetic stage. Spec. No. 4/93. Section Felsöörs, bed No. 13/86; Curionii Zone. a) Lateral view; b) upper view; c) lower view; (66 x). T-6480.
- Fig. 2a-d- Gondolella ? praehungarica sp. n. Juvenile ontogenetic stage. Spec. No. 3/93. Section Felsöörs, bed No. 18/86; Curionii Zone. a) Lateral view; b) lower-lateral view; c) lower view; d) upper view; (66 x). T-6481.
- Fig. 3a-d- Gondolella ? praehungarica sp. n. Juvenile ontogenetic stage. Spec. No. 7/93. Section Felsöörs, bed No. 19/86; Curionii Zone. a) Lateral view; b) upper-lateral view; c) upper view; d) lower view; (66 x). T-6482.
- Fig. 4a-c- Gondolella ? praehungarica sp. n. Late juvenile ontogenetic stage. Spec. No. 8/93. Section Felsöörs, bed No. 19/86; Curionii Zone. a) Upper-lateral view; b) lateral view; c) upper view; (66 x). T-6483.
- Fig. 5a-d- Gondolella ? praehungarica sp. n. Medium ontogenetic stage. Spec. No. 11/93. Section Felsöörs, bed No. 154/78 (bed next below 30/86); upper Curionii Zone. a) Lateral view; b) upper view; c) lateral-lower view; d) lower view; (66 x). T-6484.

PLATE 10

- Fig. 1a-g- Gondolella ? praehungarica sp. n. Holotype. Adult ontogenetic stage. Spec. No. 12/93. Section Felsöörs, bed No. 29/86; upper Curionii Zone. a) Lateral view; b) upper-lateral view; c) upper view; d) lower view; e) platform end, upper-lateral view; f) platform end, lateral-lower view; g) platform end, lateral-lower view; (a, b, c, d, 66 x; e, f, g, 133 x). T-6485.
- Fig. 2a-e- Gondolella ? praehungarica sp. n. Adult ontogenetic stage, transitional form to "Metapolygnathus" hungaricus Kozur & Végh. Spec. No. 13/86. Section Felsöörs, bed No. 29/86; upper Curionii Zone. a) Lateral view; b) upper-lateral view; c) lower-lateral view; d) lower view; e) upper view; (66 x). T-6486.
- Fig. 3a-d- Gondolella ? praehungarica sp. n. Medium ontogenetic stage, highly evolved form. Spec. No. 6/93. Section Felsöörs, bed No. 19/86. Curionii Zone. a) Lateral view; b) upper-lateral view; c) upper view; d) lower view; (66 x). T-6487.

504



1.1



1.18















1.14

