The Permian - Triassic evolution of platform conodonts (Gondolellidae) consists mainly in developing the carina and the platform. During the sublethal environmental stress conditions subsequent to the Permian - Triassic extinction, the Wuchiapingian - Griesbachian Clarkina lineage is replaced by the primitive looking platform-lacking Dienerian - Aegean Neospathodus kummeli - Kashmirella timorensis lineage.

Moreover, above Jinogondolella denticulata, end of the Capitanian Jinogondolella lineage, "Neospathodus" arcucristatus, an atavistic blade-like homeomorph that lacks a platform, underlies Protoclarkina crofti, of the base of the anagenetic Clarkina lineage.

These primitive-looking forms are derived from their immediate ancestors by retrograde evolution, a phenomenon that has been described as proteromorphosis. Such events suggest that proteromorphosis occurs during periods of crisis, with sudden reappearance of homeomorphic forms that are atavistic representatives of the clade. The phenomenon is further substantiated by several additional retrogradations that pace the Triassic, a period prone to such events.

Résumé

L'évolution du Permien au Trias des conodontes à plate-forme (Gondolellidae) consiste principalement en développant la carène et la plate-forme. Pendant la période de stress sous-létal de l'environnement qui suit l'extinction Permo - Triasique, la lignée de Clarkina Wuchiapingien - Griesbachien est
remplacée des la base du Dienerien par la forme primitive démunie de plateforme de Neospathodus kummeli et d'une suite qui termine par Kashmirella timorensis.

Plus est, au-dessus de Jinogondolella denticulata, fin de lignée de Jinogondolella du Capitanien apparaît "Neospathodus" arcucristatus, forme atavique à lame démunie de plate-forme, sous-jacente à Protoclarkina crofti à la base de la lignée de Clarkina.

Ces formes d'aspect primitif sont dérivées de leurs ancêtres immédiats par évolution rétrograde, un phénomène décrit comme protéromorphose. Ces événements suggèrent que la proteromorphose apparaît en période de crise, avec réapparition soudaine d'homéomorphes ataviques de la clade. Le phénomène est d'ailleurs corroboré par plusieurs rétrogradations supplémentaires qui rythment le Trias, une période sujette à de tels événements.
Proteromorphosis of *Neospathodus* (conodonta) during the Permian - Triassic crisis

Évolution rétrograde de *Neospathodus* au cours de la crise Permo - Triasique

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Abstract

The Permian - Triassic evolution of platform conodonts (Gondolellidae) consists mainly in developing the carina and the platform. During the sublethal environmental stress conditions subsequent to the Permian - Triassic extinction, the Wuchiapingian - Griesbachian *Clarkina* lineage is replaced by the primitive looking platform-lacking Dienerian - Aegean *Neospathodus kummeli* - *Kashmirella timorensis* lineage.

Moreover, above *Jinogondolella denticulata*, end of the Capitanian *Jinogondolella* lineage, "*Neospathodus*" *arcucristatus*, an atavistic blade-like homeomorph that lacks a platform, underlies *Protoclarkina crofti*, of the base of the anagenetic *Clarkina* lineage.

These primitive-looking forms are derived from their immediate ancestors by retrograde evolution, a phenomenon that has been described as proteromorphosis. Such events suggest that proteromorphosis occurs during periods of crisis, with sudden reappearance of homeomorphic forms that are atavistic representatives of the clade. The phenomenon is further substantiated by several additional retrogradations that pace the Triassic, a period prone to such events.

Key words: Triassic; Conodonts; Phylogeny; Evolution; Proteromorphosis.
Résumé

L’évolution du Permien au Trias des conodontes à plate-forme (Gondolellidae) consiste principalement en développant la carène et la plate-forme. Pendant la période de stress sous-létal de l’environnement qui suivit l’extinction Permo - Triasique, la lignée de Clarkina Wuchiapingien - Griesbachien est remplacée des la base du Dienerien par la forme primitive démunie de plateforme de Neospathodus kummeli et d’une suite qui termine par Kashmirella timorensis.

Plus est, au-dessus de Jinogondolella denticulata, fin de lignée de Jinogondolella du Capitanien apparaît "Neospathodus" arcucrístatus, forme atavique à lame démunie de plate-forme, sous-jacente à Protoclarkina crofti à la base de la lignée de Clarkina.

Ces formes d’aspect primitif sont dérivées de leurs ancêtres immédiats par évolution rétrograde, un phénomène décrit comme protéromorphose. Ces événements suggèrent que la protéromorphose apparaît en période de crise, avec réapparition soudaine d’homéomorphes ataviques de la clade. Le phénomène est d’ailleurs corroboré par plusieurs rétrogradations supplémentaires qui rythment le Trias, une période sujette à de tels événements.

Mots clés: Trias; Conodontes; Phylogénese; Evolution; Protéromorphose.

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1. Introduction

Hirsch (1994b) following Gould (1977) interpreted evolutionary "simplifications" in terms of heterochrony such as paedomorphism, progenesis and neoteny. The term paedomorphosis is when the descendant species is underdeveloped relatively to the ancestor, smaller in size and simpler in shape, resembling juvenile ancestors; peramorphosis is when the descendant species transcends its ancestor in terms of size and shape; and a neotenous descendant is of the same size as the adult ancestor but is underdeveloped (simpler) in terms of shape (Lieberman, 2011: p. 35).

In their cladogram of gondolellid taxa, Henderson and Mei (2007) consider “the evolution of bifid S₃ elements as the transition of *Mesogondolella* to *Jinogondolella*; the changes in ontogenetic developmental timing, including lack of a platform or its reduction to a narrow rib in juvenile specimens within the development of *Clarkina* (*Neoclarkina*); the paedomorphic loss of platform in entire ontogenetic series (*Neospathodus*); and the peramorphic platform-development in later parts of the ontogenetic series”. Thus *Neospathodus* went through a process wherein the entire ontogenetic series lacks a platform. Reinitialization in *Borinella, Paragondolella, Pridaella* and *Neogondolella*, evolving from *Neospathodus*, consisted in a peramorphic process in which the lineage was restored and additional evolutive features, including the platform were developed.

In the present study, neospathid genera such as *Neospathodus* are seen as the result of proteromorphic retrogradation in the sense of Guex (2001). Atavistic homeomorph forms appear during sublethal stress events, often separated by several millions of years. Hypothetically the simple and economic architecture as potential source of renewed phylogenetic development explains such sudden appearances (Guex et al., 2014).

The gondolelloid record is summarised in the diagram of the faunal record (Figure 1).

Evolution in Lopingian - Induan (Late Permian- Early Triassic) anagenetic gondolellid lineages consists in the development of the carina and the platform. Loss of platform in
homeomorph “Neospathodus” arcucristatus (Late Capitanian) and the Neospathodus kummeli - Kashmirella timorensis lineage (Dienerian - Aegean) took place within the Jinogondolella - Protoclarkina and Clarkina - Paragondolella intervals. Additional side branches of these lineages include that starting with Lopingian Jinogondolella postserata (Wardlaw & Shilong), those of Smithian Borinella and of Anisian Pridaella. Proteromorphic retrogradations occur during periods of crisis, with the sudden appearance of homeomorphic forms that are atavistic representatives of the clade. These primitive-looking forms are derived from their immediate ancestors by retrograde evolution, a phenomenon which has been described as proteromorphosis (Guex, 2001; Guex & al., 2014).

Conodont phylogeny under the sublethal environmental stress conditions following the Permian - Triassic extinction, was paced by proteromorphosis (reappearance of ancestral morphs). Thom’s (1972) cusp catastrophe diagram illustrates this catastrophic event (Fig. 2).

The Permian - Triassic boundary is particularly interesting as conodonts have not been affected too much as they briskly flitted through the extinction event at 252.6 Ma. This is the case for both the rather shallow marine Clarkina and presumably deeper marine Hindeodus conodont lineages, although such attributions may not be hermetic, many taxa may extend to more than one habitat and Hindeodus can possibly also be a shelf dweller (Hirsch, 1994a). For example at Meishan, the contact between limestone bed 24e and volcanic clay bed 25, this event falls within the Clarkina taylorae Zone (Jiang et al., 2007). Above the 8 cm thick volcanic clay (bed 25) follow a black mudstone (bed 26), a calcareous mudstone (bed 27) and a second volcanic clay (bed 28), dated at 252.5 Ma. The base Triassic GSSP golden spike was driven in the middle of the 16 cm thick bed 27, where the conodont Hindeodus parvus appears, a rather incomprehensible choice, if based on faunal criteria alone, thought bed 24e is marked by the onset of a sharp reduction in average size (from 0.63–0.69 to 0.54 mm) as well as deviation to juvenile or dwarfed size of Clarkina (Yin et al. 2001). The genus Hindeodus became extinct during the Griesbachian. In the course of the Late Induan, shortly before the extinction of Clarkina, the appearance of
Neospathodus coincides with the Dienerian carbon excursion and sea level highstand. As an iterative development in gondolellid conodonts, platform reduction leading to blade-like neospathid forms occurred at several occasions, as with Pseudoclarkina bitteri and Neospathodus divergens in the Gerster Formation of the Confusion Range, Utah (Wardlaw & Collinson, 1986).

2. Lineages

Late Permian Gondolellidae (Clarkina) persisted into the earliest Triassic, followed by Smithian and Anisian reinitialisation (Fig. 3).

The Latest Permian - Induan apparently shallow marine lineage of Clarkina consists of Clarkina yini, C. meishansensis, C carinata, C. taylorae, C. planata, C. krystyni. Regarding the origin of the Clarkina lineage, the earliest Wuchiapingian Protoclarkina crofii (Kozur & Lucas 1996), standing for Neogondolella sp. (Croft, 1978, p. 51-52, pl. 5, figs. 1-10; and Wardlaw & Mei, 1998 p. 40-41, Plate 7 Figs. 1-4, 7-20) has a reduced platform representing the initial peramorphic Clarkina trend. It may be preceded by the end Guadalupian “Neospathodus” arcucristatus (Clark & Behnken 1971) [in Ratterman, 1976], without a platform, homeomorph of the genus Neospathodus which is characterized by the absence of a platform (Kozur & Spencer, 1996). The succession of “Neospathodus” arcucristatus - Protoclarkina crofii - Clarkina suggests a complete Lopingian peramorphic trend. Protoclarkina crofii dwelled in the deep-water pelagic uppermost Lamar Limestone of the Delaware Basin (West Texas). Neospathodus divergens is a late Guadalupian or younger species found in the uppermost Gerster Formation of the northeastern Great Basin (NE Nevada and NW Utah) (Bissell, 1973). These early forms of Neospathodus wait for revision.

The Neospathodus kummeli - Kashmirella timorensis succession is an anagenetic lineage that passed into Paragondolella regale. Budurov et al. (1988) held the lineage of Neospathodus cristagalli - N. dieneri - N. pakistanensis - N. waageni - N. discretus - N. conservativus - N.
zarnikovi - N. bransoni - N. triangularis - N. homeri for a lineage, parallel to that of the genus
Kashmirella, comprising K. kummeli - K. novaehollandiae - K. nepalensis - K. albertii - K. zaksi -
K. spathi - K. gondolelloides - K. timorensis, from which the genus Paragondolella emerged.

A strong homeomorphism of the Early Anisian gondolellids is well at the core of taxonomic
and phylogenetic uncertainty, as another branch may be classified under Pridaella. According to
Budurov (1998), Budurov and Petrunova (1998) and Budurov and Petrunova (in Muttoni et al.,
2000, p. 233), the generic name for Gondolella is Paragondolella in the case of P. regale, P.
excelsa, P. inclinata, P. praehungarica, P. fueloepi, P. bulgarica, P. hanbulogi, P. praeszaboi, P.
hystrickyi; and Pridaella in the case of P. trammeri, P. cornuta, P. bakalovi, P. longa, P. transita, P.
bifurcata; the name for Chiosella is Kashmirella and for Budurovignathus it is Sephardiella.

Budurov and Petrunova (1998) also wrote that “in the coastal waters of the Peri-Tethys, the start of
Pridaella constricta marked the beginning of the development of the typical Peri-Tethyan genus
Pridaella (with type species Gondolella constricta), the genus comprising P. shoshonensis, P.
cornuta, P. longa and P. bakalovi.

Given the variations of width of the basal cavity and ornamentation of the carina, several
additional subfamilies and genera were introduced to classify homeomorph blades in addition to the
genus Neospathodus Mosher, 1968 (Subfamily Neogondolellinae Hirsch, 1994b). These include
Novispathodus waageni, N. triangularis, Sweetognathodus kummeli, Triassospathodus homeri that
were illustrated (Maekawa and Igo, 2014; in Shigeta et al., 2014).

Following the large variety of Smithian - Spathian genera and species that belong in the
radiation of the Dienerian genus Neospathodus, reinitialization of a peramorphic trend took place in
the Aegean (Early Anisian).
3. Trends in Evolution

The evolution of the genera in subfamily Neogondolellinae consists in a number of reiterating trends: (i) displacement of the basal cavity from its posterior position toward the middle, accompanied by the modification of its shape from loop-like to amygdaloid; (ii) reduction of the platform, that in most Early and Middle Triassic genera of the family borders the entire unit of adult specimens, by the formation of a free blade; (iii) splitting of the monolobate basal groove into a bilobate, forked platform. The evolutionary trends are paced by recurring proteromorphic neospathid morphs followed by accelerated rates of speciation, such as the Smithian radiation of *Scythogondolella milleri*, *Borinella sibiriensis*, *B. nepalensis*, *B. jubata*.

In the Middle Triassic the lineage of *Paragondolella* that derived from *Kashmirella* prevails in the more open marine scene. The quasi homeomorphic *Pridaella* and *Neogondolella* that radiated from Pelsonian-Illyrian neospathid *Nicoraella* dwelled apparently in shallower environments until their Late Ladinian extinction. Out of *Pseudofurnishius priscus* the Fassanian - Julian Sephardiellinae developed. Budurov and Sudar (1988) proposed the genus *Pridaella* for the lineage starting with *Pridaella constricta*, branching into a normal marine *trammeri* lineage (Peri-Tethyan) on one side, its other offshoot being the restricted marine lineage of *Neogondolella mombergensis* (Germanic facies area). Dzik and Trammer (1980) observed the gradual evolutionary increase in the latter’s morphologically juvenile stages of *N. haslachensis* - *N. watznaueri* in the Fassanian of the Mid-European epicontinental environment (Trammer, 1974).

Narkiewicz and Szulc (2004), discussing the adaptive evolution of *Neogondolella mombergensis* and the emergence of the *mombergensis* - *media* - *haslachensis* - *watznaueri* lineage, noted that Trammer (1971) and Zawidzka (1975) had held *N. media* (Kozur, 1968) as the juvenile stage of a “constricta”-type, and that Budurov and Petrunova (1998) suggested *N. media* to be the delicate early form of *N. constricta*. Consequently, if *N. haslachensis* was a descendant of *N. constricta*, its origin was related to a Tethyan lineage, while having suitable conditions for
development almost exclusively in the Germanic Basin. Assuming, after Trammer (1974), that the
evolution of *mombergensis* lineage was of adaptive character, it may be supposed that rapid
evolution of *N. haslachensis* was controlled by continuous environmental changes in the entire
Germanic Basin under conditions of restricted marine connections with the Tethys. In a pelagic
bedded-chert unit of the Chichibu Belt (South-West Japan), Ishida (1981: p. 116, Plate 2, figs. 2a-c)
identified as *Neogondolella cf. haslachensis haslachensis*, a form resembling *N. cf. haslachensis*
that had been reported from the Early Anisian of the Kocaeli Peninsula (Gedik, 1975). Ishida (1984:
p. 21) re-interpreted this form as *Neogondolella shoshonensis*, moreover précising that in Japan,
this *N. shoshonensis* occurs within the latest Bithynian to Early Pelsonian upper range of
*Paragondolella bulgarica*, preceding *Pridaella. cf. cornuta* and *Paragondolella aff. excelsa*. The
real *Neogondolella haslachensis* is characteristic in the late Fassanian of the Germanic Basin (Dzik
and Trammer, 1980). *Neogondolella haslachensis, N. constricta, N. cornuta, N. pridaensis* and *N.*
mombergensis are signaled in the Russian Far East region of Sikhote-Alin (Buryi, 1996, 1997).

A so far unidentified event during the Early Anisian has precipitated the appearance of the
forms *Kamuellerella - Ketinella - Gedikella*, in the central part of the North Tethys. These small
size ramiform units, found in the Turkish Istanbul Zone (Gedik, 1975; Kılıç, 2004) may suggest
some extraordinary local warming event.

Iterations of the neospațhīd homeomorph *Nicoraella* derived from *Paragondolella
bulgarica* in the Bithynian and radiated into the lineage of *Pridaella*. Later appeared the Pelsonian
narrow bladed *Pseudofurnishius priscus, P. siyalaensis* and the Illyrian *P. shagami* (Benjamini and
Chepstow-Lusty, 1986), out of which emerged the Fassanian *Pseudofurnishius murcianus*. This
taxon is found in stratigraphic sequence, immediately above *P. shagami*, from the very base of the
Fassanian curionii Zone. The Fassanian - Early Julian *Sephardiella* lineage of *S. truempyi - S.
hungarica - S. japonica - S. mungoensis - S. diebeli - S. mostleri* comprises, starting from adult
forms of *Sephardiella mungoensis*, the trend of a slight splitting of its relatively central amygdaloid
basal groove. A link between this provincial Sephardic *Pseudofurnishius* lineage *shagami*-
murcianus- ?sosioensis and the Late Ladinian and Early Carnian neospathid iterations of Mosherella microdus and M. newpassensis, proposed by Sadeddin and Kozur (1992), should be considered as (Plasencia et al., 2015).

The main evolutionary trends during the Ladinian - Carnian interval is the emergence of Metapolygnathus from Paragondolella by (a) the reduction of the platform and development of a free blade (Metapolygnathus tadpole) and (b) the trend of splitting the basal groove (Budurov, 1977).

4. Causes for Atavism in Conodont Evolution

Korte et al. (2010) invoked strong activity of the Siberian Trap terminating at the end of the Griesbachian. Hermann et al. (2011) report recurrent environmental changes triggering Early Triassic ecosystem instabilities, such as the Middle Smithian spore spike concurring with a negative $\delta^{13}$C anomaly, preceding a Late Smithian marine extinction event. The major phylogenetic developments in Triassic conodonts seem also to coincide with severe sea level changes (Hirsch, 1994b), possibly related to anoxic events. Correspondingly, chemical stress and high temperatures may cause resurgences of atavistic structures. Anoxic events, such as an Early Dienerian shelf event on the northern Gondwanian margin correlates in time with similar paleo-oceanographic changes on the equatorial North American margin and the southern Tethys, indicating that discrete, short anoxic events were part of the Early Triassic biotic recovery (Ware et al., 2011).

The conodont record of anagenetic developments and atavistic reversals (Fig. 4A) matches Trotter et al. (2015)’s oxygen isotope records derived from conodont apatite. These show phases of low $\delta^{18}$O of warming associated with humid intervals in the Early Triassic (W1), Middle Anisian, Latest Ladinian, Mid-Carnian (W2) and Sevatian (W3). These events caused retrogradation
triggering existential stress. Cooler intervals were favourable for the Early Anisian, Early Carnian, and Lacian - Alaunian and Rhaetian peramorphosis or anagenesis.

5. Dynamics

The Conodont faunas from uppermost Permian until the End - Triassic listed in the database of Plasencia (2008) and Plasencia et al. (2013) and other available literature suggest biological, evolitional and paleo-diversity dynamics (Fig. 4B). Based on these, our present analysis of the evolutionary trends and strategies of conodonts across the Permian - Triassic crisis, illustrates the environmental stress, caused by the end Permian mass extinction, climatic changes, sea level rise and other cyclic changes of the Permian - Triassic period.

Neospathid genera are possibly the result of proteromorph retrogradation in the sense of Guex (2001). Atavistic homeomorph forms appear during sublethal stress events, often separated by several millions of years. Hypothetically the simple and economic architecture as potential source of renewed phylogenetic development explains such sudden appearances (Guex et al., 2014).

6. Conclusions

1. Conodont phylogeny under the sublethal environmental stress conditions following the Permian - Triassic extinction, was paced by proteromorphosis (reappearance of ancestral morphs). In its aftermath, reinitialization of fully developed peramorphic lineages took place.

2. The major causes of stress that affected evolutionary trends in Triassic conodont lineages are environmental, such as marine regressions, anoxic episodes, and thermal or trophic (nutritional)
stress (Hallam, 1978; Mancini, 1978; Valentine et al., 1994). In comparison with Cope’s rule, these constraints cause decreasing sizes and morphological complexity, which have sometimes been explained by elimination of the more complex forms during extinction events (Saunders et al., 1999). While the larger forms are more vulnerable to extinction (r-selection), more and more decreasing small forms with short life span and rapid proliferation are favoured during stressful episodes.

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Dear Prof. Danelian,

Enclosing herewith is a manuscript for publication in Revue de Micropaléontologie, under the title:

**Proteromorphosis of Neospathodus (Conodonta) During the Permian - Triassic Crisis**
Évolution rétrograde de *Neospathodus* au cours de la crise Permo - Triasique

The corresponding author is Ali Murat KILIÇ and the co-authors are Pablo PLASENCIA, Keisuke ISHIDA, Jean GUEX, and Francis HIRSCH.

I would like to emphasise that this work is an Original Article that is the result of all authors’ research over a timespan of several years. The authors have all directly participated in its planning, analysis and final writing and have read and approved the final version that is submitted here. The present manuscript contains the full text and additional elements from different sources, put for the first time together for the full paper. My University’s representative is fully aware of this submission.

Date: June 23, 2015

Signed Dr. Ali Murat KILIÇ, corresponding author, on behalf of all authors

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Figure 2

The diagram illustrates the relationship between state, time, stress, and peramorphic trend. The vertical axis represents the state, ranging from primitive to advanced. The horizontal axis represents time, ranging from low to high. The stress axis is horizontal as well, ranging from low to high. A peramorphic trend line is depicted, showing the progression from state A to state A' through time and stress. The diagram also includes labeled points B, C, D, and E, indicating different stages of the peramorphic trend. Proteromorphosis is indicated by the curved path from A to A'.
Figure 1. Distribution of Late Permian - Early Triassic conodont lineages through time. Horizontal lines represent atavistic reversals (towards the left), curves symbolise Darwinian anagenesis (after Metcalfe and Isozaki, 2009; Lambert et al., 2007; Wardlaw and Mei, 1998; Wignall and Twitschett, 2002; “Neospathodus” arcucristatus Clark and Behnken, 1971 from Ratterman, 1976).
PROTEROMORPHOSIS OF *NEOSPATHODUS* (CONODONTA) DURING THE PERMIAN - TRIASSIC CRISIS

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Figure 2. The cusp catastrophe of Thom (1972) is a diagrammatic representation of a punctuated anagenesis. Peramorphic trend: Anagenetic lineage of (A) “Neospathodus” arcucristatus, (B) Protoclarkina crofti, (C) Clarkina bitteri, (D) C. meishanensis, (E) C. krystyni; Proteromorphosis: Catastrophic reappearance of atavistic Neospathodus and stasis of (A’) Neospathodus kummeli - Kashmirella timorensis, and re-diversification in (B’) Paragondolella regale - (C’) P. excelsa. The catastrophic event that prompted proteromorphosis coincides with the Dienerian negative carbon excursion and sea-level high-stand. The *Clarkina* peramorphic trend started after the Late Guadalupian atavistic “Neospathodus” arcucristatus Clark and Behnken, 1971 (Ratterman, 1976), with Protoclarkina crofti, Kozur and Lucas 1996 (Wardlaw and Mei, 1998, p. 40-41, Plate 7 Figs. 1-4, 7-2) showing a reduced platform that passes into Clarkina postbitteri Wardlaw and Mei (1994), the oldest species of the *Clarkina* lineage.
PROTEROMORPHOSIS OF *NEOSPATHODUS* (CONODONTA) DURING THE PERMIAN - TRIASSIC CRISIS

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Figure 3. Early - Middle Triassic conodont lineages (252-237 Ma). The Scythian - Dinarian* Gondolelloidean Lineages are represented in function of time (Ma) and increasing pelagic habitat. "Neogondolella" consists of the Lopingian - Induan *Clarkina* that retrogrades into the Dienerian *Neospathodus kummeli* (Fig. 1); Olenekian “Neogondolella” (*Borinella-Scythogondolella*) radiated out of *Novispathodus waageni*. It is unlikely that Anisian *Neogondolella* anchors in the Smithian - Spathian *Borinella* lineage as it rather evolved from Spathian - Aegean *Kashmirella* stock. The *Neospathodus - Kashmirella* lineage initiates a 45 Ma long succession of reinitialization-radiation that ranges until the last Rhaetian *Misikella*. Within the range of the Scythian - Dinarian 15 Ma timespan, *Paragondolella regale* originates from *Kashmirella timorensis*. Thom’s fallback symbols indicate the appearances of isolated proteromorphic taxa, at the origin of new lineages such as Anisian- Ladinian *Nicoraella - Pridaela* and Anisian - Early Julian *Pseudofurnishius - Mosherella*. Most pelagic is the Tethyan equatorial Late Spathian - Julian family Gladigondolelliidae and possibly the exceptional Early Anisian North-Tethyan *Kamuellerella - Ketinella - Gedikella* (KKG) group. The taxa in this interval are arranged according to their increasingly pelagic habitat.

Figure 4. Distribution Scheme of Triassic Conodont Lineages and Number of Taxa through Time: A. Key after Guex (2001); B. Taxa compilation based on Martinez-Perez et al. (2013):
A: Neospathodus; A₁: Kashmirella; A₂-3: Nicoraella; A₄: Pseudofurnishius; A₅: Mosherella; A₆: Neocavitella; A₇: Misikella; N: Neogondolellinae: N₁: Clarkina; N₂: Scythogondolella; N₃: Borinella; N₄: Pridaella; N₅: Neogondolella; N₆: Norigondolella; N₇: Parvigondolella; P: Paragondolella; M₁: Metapolygnathus; M₂: Mazzaella; M₃: Hayashiella; M₄: Carneipigondolella; M₅: Ancyrogondolella; S: Sephardiellinae; E: Epigondolellinae: E₁: Acuminatella; E₂: Mockina