

Elsevier Editorial System(tm) for Revue de Micropaléontologie  
Manuscript Draft

Manuscript Number:

Title: Proteromorphosis of Neospathodus (conodonts) during the Permian - Triassic crisis Évolution rétrograde de Neospathodus au cours de la crise Permo - Triasique

Article Type: Original paper / Article original

Section/Category: Numéro courant

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

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

Corresponding Author: Dr. Ali Murat KILIC, Ph.D.

Corresponding Author's Institution: Bailkesir University

First Author: Ali Murat KILIC, Ph.D.

Order of Authors: Ali Murat KILIC, Ph.D.; Pablo PLASENCIA, Ph.D.; Keisuke ISHIDA, Full Professor; Jean GUEX, Full Professor; Francis HIRSCH, Retired Professor

Abstract: 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.

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 apparait "*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 apparait 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.

1 **Proteromorphosis of *Neospathodus* (conodonta) during the Permian - Triassic**  
2 **crisis**

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

4  
5 Ali Murat KILIÇ<sup>a\*</sup>, Pablo PLASENCIA<sup>b</sup>, Keisuke ISHIDA<sup>c</sup>, Jean GUEX<sup>d</sup>, and Francis HIRSCH<sup>e</sup>

6 <sup>a</sup>Department of Geology, Balikesir University, 10145, Balikesir, Turkey / alimurat@balikesir.edu.tr

7 <sup>b</sup>Department of Geology and ICBIBE, University of Valencia, Dr. Moliner, 50. 46100, Burjassot, Spain / pablo.plasencia@uv.es

8 <sup>c</sup>Laboratory of Geology, Faculty of Sciences, Tokushima University, Tokushima, 770-8502, Japan / ishidak@ias.tokushima-u.ac.jp

9 <sup>d</sup>Dept. of Geology, University of Lausanne, BFSH-2, Lausanne, Switzerland / Jean.Guex@igp.unil.ch

10 <sup>e</sup>Laboratory of Geology, Faculty of Sciences, Naruto University, Naruto, 772-8502, Japan / francishirsch@gmail.com

11

12 **Abstract**

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

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

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

26

27 *Key words:* Triassic; Conodonts; Phylogeny; Evolution; Proteromorphosis.

28

29 **Résumé**

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

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

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

43

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

45

46

47 \*Corresponding author: alimurat@balikesir.edu.tr (Ali Murat KILIÇ)

48

49 E-mail addresses: pablo.plasencia@uv.es (P. Plasencia), ishidak@tokushima-u.ac.jp (K. Ishida), jean.guex@unil.ch (J. Guex)  
50 francishirsch@gmail.com (F. Hirsch)

51

52

53

54

55

56 **1. Introduction**

57

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

64 In their cladogram of gondolellid taxa, Henderson and Mei (2007) consider "the evolution of  
65 bifid S<sub>3</sub> elements as the transition of *Mesogondolella* to *Jinogondolella*; the changes in ontogenetic  
66 developmental timing, including lack of a platform or its reduction to a narrow rib in juvenile  
67 specimens within the development of *Clarkina* (*Neoclarkina*); the paedomorphic loss of platform in  
68 entire ontogenetic series (*Neospathodus*); and the peramorphic platform-development in later parts  
69 of the ontogenetic series". Thus *Neospathodus* went through a process wherein the entire  
70 ontogenetic series lacks a platform. Reinitialization in *Borinella*, *Paragondolella*, *Pridaella* and  
71 *Neogondolella*, evolving from *Neospathodus*, consisted in a peramorphic process in which the  
72 lineage was restored and additional evolutive features, including the platform were developed.

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

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

79 Evolution in Lopingian - Induan (Late Permian- Early Triassic) anagenetic gondolellid  
80 lineages consists in the development of the carina and the platform. Loss of platform in

81 homeomorph "*Neospathodus*" *arcucristatus* (Late Capitanian) and the *Neospathodus kummeli* -  
82 *Kashmirella timorensis* lineage (Dienerian - Aegean) took place within the *Jinogondolella* -  
83 *Protoclarkina* and *Clarkina* - *Paragondolella* intervals. Additional side branches of these lineages  
84 include that starting with Lopingian *Jinogondolella postserata* (Wardlaw & Shilong), those of  
85 Smithian *Borinella* and of Anisian *Pridaella*. Proteromorphic retrogradations occur during periods  
86 of crisis, with the sudden appearance of homeomorphic forms that are atavistic representatives of  
87 the clade. These primitive-looking forms are derived from their immediate ancestors by retrograde  
88 evolution, a phenomenon which has been described as proteromorphosis (Guex, 2001; Guex & al.,  
89 2014).

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

93 The Permian - Triassic boundary is particularly interesting as conodonts have not been  
94 affected too much as they briskly flitted through the extinction event at 252.6 Ma. This is the case  
95 for both the rather shallow marine *Clarkina* and presumably deeper marine *Hindeodus* conodont  
96 lineages, although such attributions may not be hermetic, many taxa may extend to more than one  
97 habitat and *Hindeodus* can possibly also be a shelf dweller (Hirsch, 1994a). For example at  
98 Meishan, the contact between limestone bed 24e and volcanic clay bed 25, this event falls within  
99 the *Clarkina taylorae* Zone (Jiang et al., 2007). Above the 8 cm thick volcanic clay (bed 25) follow  
100 a black mudstone (bed 26), a calcareous mudstone (bed 27) and a second volcanic clay (bed 28),  
101 dated at 252.5 Ma. The base Triassic GSSP golden spike was driven in the middle of the 16 cm  
102 thick bed 27, where the conodont *Hindeodus parvus* appears, a rather incomprehensible choice, if  
103 based on faunal criteria alone, though bed 24e is marked by the onset of a sharp reduction in  
104 average size (from 0.63–0.69 to 0.54 mm) as well as deviation to juvenile or dwarfed size of  
105 *Clarkina* (Yin et al. 2001). The genus *Hindeodus* became extinct during the Griesbachian. In the  
106 course of the Late Induan, shortly before the extinction of *Clarkina*, the appearance of

107 *Neospathodus* coincides with the Dienerian carbon excursion and sea level highstand. As an  
108 iterative development in gondolellid conodonts, platform reduction leading to blade-like neospathid  
109 forms occurred at several occasions, as with *Pseudoclarkina bitteri* and *Neospathodus divergens* in  
110 the Gerster Formation of the Confusion Range, Utah (Wardlaw & Collinson, 1986).

111

112

## 113 **2. Lineages**

114

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

117 The Latest Permian - Induan apparently shallow marine lineage of *Clarkina* consists of  
118 *Clarkina yini*, *C. meishansensis*, *C. carinata*, *C. taylorae*, *C. planata*, *C. krystyni*. Regarding the  
119 origin of the *Clarkina* lineage, the earliest Wuchiapingian *Protoclarkina crofti* (Kozur & Lucas  
120 1996), standing for *Neogondolella* sp. (Croft, 1978, p. 51-52, pl. 5, figs. 1-10; and Wardlaw & Mei,  
121 1998 p. 40-41, Plate 7 Figs. 1-4, 7-20) has a reduced platform representing the initial peramorphic  
122 *Clarkina* trend. It may be preceded by the end Guadalupian “*Neospathodus*” *arcucristatus* (Clark &  
123 Behnken 1971) [in Ratterman, 1976], without a platform, homeomorph of the genus *Neospathodus*  
124 which is characterized by the absence of a platform (Kozur & Spencer, 1996). The succession of  
125 “*Neospathodus*” *arcucristatus* - *Protoclarkina crofti* - *Clarkina* suggests a complete Lopingian  
126 peramorphic trend. *Protoclarkina crofti* dwelled in the deep-water pelagic uppermost Lamar  
127 Limestone of the Delaware Basin (West Texas). *Neospathodus divergens* is a late Guadalupian or  
128 younger species found in the uppermost Gerster Formation of the northeastern Great Basin (NE  
129 Nevada and NW Utah) (Bissell, 1973). These early forms of *Neospathodus* wait for revision.

130 The *Neospathodus kummeli* - *Kashmirella timorensis* succession is an anagenetic lineage  
131 that passed into *Paragondolella regale*. Budurov et al. (1988) held the lineage of *Neospathodus*  
132 *cristagalli* - *N. dieneri* - *N. pakistanensis* - *N. waageni* - *N. discretus* - *N. conservativus* - *N.*

133 *zarnikovi* - *N. bransoni* - *N. triangularis* - *N. homeri* for a lineage, parallel to that of the genus  
134 *Kashmirella*, comprising *K. kummeli* - *K. novaehollandiae* - *K. nepalensis* - *K. albertii* - *K. zaksi* -  
135 *K. spathi* - *K. gondolelloides* - *K. timorensis*, from which the genus *Paragondolella* emerged.

136 A strong homeomorphism of the Early Anisian gondolellids is well at the core of taxonomic  
137 and phylogenetic uncertainty, as another branch may be classified under *Pridaella*. According to  
138 Budurov (1998), Budurov and Petrunova (1998) and Budurov and Petrunova (in Muttoni et al.,  
139 2000, p. 233), the generic name for *Gondolella* is *Paragondolella* in the case of *P. regale*, *P.*  
140 *excelsa*, *P. inclinata*, *P. praehungarica*, *P. fueloepi*, *P. bulgarica*, *P. hanbulogi*, *P. praezsaboi*, *P.*  
141 *bystrickyi*; and *Pridaella* in the case of *P. trammeri*, *P. cornuta*, *P. bakalovi*, *P. longa*, *P. transita*, *P.*  
142 *bifurcata*; the name for *Chiosella* is *Kashmirella* and for *Budurovignathus* it is *Sephardiella*.  
143 Budurov and Petrunova (1998) also wrote that “in the coastal waters of the Peri-Tethys, the start of  
144 *Pridaella constricta* marked the beginning of the development of the typical Peri-Tethyan genus  
145 *Pridaella* (with type species *Gondolella constricta*), the genus comprising *P. shoshonensis*, *P.*  
146 *cornuta*, *P. longa* and *P. bakalovi*.

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

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

155

156

157

158



159 **3. Trends in Evolution**

160

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

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

179 Narkiewicz and Szulc (2004), discussing the adaptive evolution of *Neogondolella*  
180 *mombergensis* and the emergence of the *mombergensis* - *media* - *haslachensis*- *watznaueri* lineage,  
181 noted that Trammer (1971) and Zawidzka (1975) had held *N. media* (Kozur, 1968) as the juvenile  
182 stage of a “*constricta*”-type, and that Budurov and Petrunova (1998) suggested *N. media* to be the  
183 delicate early form of *N. constricta*. Consequently, if *N. haslachensis* was a descendant of *N.*  
184 *constricta*, its origin was related to a Tethyan lineage, while having suitable conditions for

185 development almost exclusively in the Germanic Basin. Assuming, after Trammer (1974), that the  
186 evolution of *mombergensis* lineage was of adaptive character, it may be supposed that rapid  
187 evolution of *N. haslachensis* was controlled by continuous environmental changes in the entire  
188 Germanic Basin under conditions of restricted marine connections with the Tethys. In a pelagic  
189 bedded-chert unit of the Chichibu Belt (South-West Japan), Ishida (1981: p. 116, Plate 2, figs. 2a-c)  
190 identified as *Neogondolella cf. haslachensis haslachensis*, a form resembling *N. cf. haslachensis*  
191 that had been reported from the Early Anisian of the Kocaeli Peninsula (Gedik, 1975). Ishida (1984:  
192 p. 21) re-interpreted this form as *Neogondolella shoshonensis*, moreover precisizing that in Japan,  
193 this *N. shoshonensis* occurs within the latest Bithynian to Early Pelsonian upper range of  
194 *Paragondolella bulgarica*, preceding *Pridaella. cf. cornuta* and *Paragondolella aff. excelsa*. The  
195 real *Neogondolella haslachensis* is characteristic in the late Fassanian of the Germanic Basin (Dzik  
196 and Trammer, 1980). *Neogondolella haslachensis*, *N. constricta*, *N. cornuta*, *N. pridaensis* and *N.*  
197 *mombergensis* are signaled in the Russian Far East region of Sikhote-Alin (Buryi, 1996, 1997).

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

202 Iterations of the neospathid homeomorph *Nicoraella* derived from *Paragondolella*  
203 *bulgarica* in the Bithynian and radiated into the lineage of *Pridaella*. Later appeared the Pelsonian  
204 narrow bladed *Pseudofurnishius priscus*, *P. siyalaensis* and the Illyrian *P. shagami* (Benjamini and  
205 Chepstow-Lusty, 1986), out of which emerged the Fassanian *Pseudofurnishius murcianus*. This  
206 taxon is found in stratigraphic sequence, immediately above *P. shagami*, from the very base of the  
207 Fassanian *curionii* Zone. The Fassanian - Early Julian *Sephardiella* lineage of *S. truempyi* - *S.*  
208 *hungarica* - *S. japonica* - *S. mungoensis* - *S. diebeli* - *S. mostleri* comprises, starting from adult  
209 forms of *Sephardiella mungoensis*, the trend of a slight splitting of its relatively central amygdaloid  
210 basal groove. A link between this provincial Sephardic *Pseudofurnishius* lineage *shagami* -

211 *murcianus*- *?sosoensis* and the Late Ladinian and Early Carnian neospathid iterations of  
212 *Mosherella microdus* and *M. newpassensis*, proposed by Sadeddin and Kozur (1992), should be  
213 considered as (Plasencia et al., 2015).

214 The main evolutionary trends during the Ladinian - Carnian interval is the emergence of  
215 *Metapolygnathus* from *Paragondolella* by (a) the reduction of the platform and development of a  
216 free blade (*Metapolygnathus tadpole*) and (b) the trend of splitting the basal groove (Budurov,  
217 1977).

218

219

#### 220 **4. Causes for Atavism in Conodont Evolution**

221

222 Korte et al. (2010) invoked strong activity of the Siberian Trap terminating at the end of the  
223 Griesbachian. Hermann et al. (2011) report recurrent environmental changes triggering Early  
224 Triassic ecosystem instabilities, such as the Middle Smithian spore spike concurring with a negative  
225  $\delta^{13}\text{C}$  anomaly, preceding a Late Smithian marine extinction event. The major phylogenetic  
226 developments in Triassic conodonts seem also to coincide with severe sea level changes (Hirsch,  
227 1994b), possibly related to anoxic events. Correspondingly, chemical stress and high temperatures  
228 may cause resurgences of atavistic structures. Anoxic events, such as an Early Dienerian shelf event  
229 on the northern Gondwanian margin correlates in time with similar paleo-oceanographic changes on  
230 the equatorial North American margin and the southern Tethys, indicating that discrete, short anoxic  
231 events were part of the Early Triassic biotic recovery (Ware et al., 2011).

232 The conodont record of anagenetic developments and atavistic reversals (Fig. 4A) matches  
233 Trotter et al. (2015)'s oxygen isotope records derived from conodont apatite. These show phases of  
234 low  $\delta^{18}\text{O}$  of warming associated with humid intervals in the Early Triassic (W1), Middle Anisian,  
235 Latest Ladinian, Mid-Carnian (W2) and Sevatian (W3). These events caused retrogradation

236 triggering existential stress. Cooler intervals were favourable for the Early Anisian, Early Carnian,  
237 and Lacinian - Alaiunian and Rhaetian peramorphosis or anagenesis.

238

239

## 240 **5. Dynamics**

241

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

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

252

253

## 254 **6. Conclusions**

255

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

259

260 **2.** The major causes of stress that affected evolutionary trends in Triassic conodont lineages are  
261 environmental, such as marine regressions, anoxic episodes, and thermal or trophic (nutritional)

262 stress (Hallam, 1978; Mancini, 1978; Valentine et al., 1994). In comparison with Cope's rule, these  
263 constraints cause decreasing sizes and morphological complexity, which have sometimes been  
264 explained by elimination of the more complex forms during extinction events (Saunders et al.,  
265 1999). While the larger forms are more vulnerable to extinction (r-selection), more and more  
266 decreasing small forms with short life span and rapid proliferation are favoured during stressful  
267 episodes.

268

269

## 270 **References**

271 Benjamini, C., Chepstow-Lusty, A. 1986. Neospathodus and other Conodonta from the Saharonim  
272 Formation (Anisian-Ladinian) at Makhtesh Ramon. *Journal of Micropalaeontology* 5(1), 67-  
273 75.

274 Bissell, H. J., 1973, Oil and gas possibilities in southern Nevada: Brigham Young University  
275 Geology Studies, v. 20, no. 1, p. 65-77.

276 Budurov, K., 1977. Revision of the Late Triassic Platform Conodonts. *Geologica Balcanica* 7(3),  
277 31-48.

278 Budurov, K.J. & Sudar, M.N., 1998, New Conodont Taxa from the Middle Triassic. *Geology of*  
279 *Himalayas - Paleontology, Stratigraphy and Structure (Contribution to Himalayan*  
280 *Geology)*, 4: 250-254.

281 Budurov, K.J., Sudar, M.N. and Gupta, V.J., (1988), *Kashmirella*, A new Triassic Conodont genus.  
282 *Bull. Indian Geol. Assoc.*, 21: 107-112.

283 Budurov, K. J., Sudar, M. N., 1990. Late Triassic Conodont Stratigraphy. 1st International  
284 Senckenberg Conference and 5th European Conodont Symposium (ECOS V) Contributions  
285 IV Willi Ziegler (ed.): *Papers on Conodonts and Ordovician to Triassic Conodont*  
286 *Stratigraphy*. Courier Forschungsinstitut Senckenberg 118, 203-240.

- 287 Budurov, K., Petrunova, L., 1998. Muschelkalk Conodonts as Components of the Peri-Tethyan  
288 Conodont Fauna, Epicontinental Triassic International Symposium. Hallesches Jahrbuch für  
289 Geowissenschaften, Reihe B, Beiheft 5, Halle, 28–29.
- 290 Budurov K. J., Buryi G. I., Sudar M. N. 1988. *Smithodus* n. gen. (Conodonts) from the Smithian  
291 Stage of the Lower Triassic. *Mitteilungen der Österreichischen Geologischen Bergbaustud*  
292 *34/35*,:295–299.
- 293 Buryi, G. I., 1996. Triassic conodonts from the cherts of the Nanhua Range, north-east China.  
294 *Acta Micropalaeontologica Sinica* 13, 207-214 (in Russian).
- 295 Buryi, G.I. 1997. Evolution of the platform elements of the conodont genus *Metapolygnathus* and  
296 their distribution in the Upper Triassic of Sikhote-Alin, p. 193-197. In: J.M. Dickins (Ed.),  
297 *Late Palaeozoic and Early Mesozoic Circum-Pacific Events and Their Global Correlation*.  
298 Cambridge University Press, *World and Regional Geology* 10, 193-197.
- 299 Croft, J. S., 1978. Upper Permian Conodont and other Microfossils from the Rustler formation,  
300 West Texas. Ohio State University Ma Thesis, Part II, 103-144.
- 301 Dzik, J., Trammer, J., 1980. Gradual evolution of conodontophorids in the Polish Triassic. *Acta*  
302 *Palaeontologica Polonica* 25, 55-89.
- 303 Gedik, I., 1975. Die Conodonten der Trias auf der Kocaeli-Halbinsel (Turkei). *Palaeontographica*,  
304 Abteilung A 150, 99-160.
- 305 Gould, J. S., 1977. *Ontogeny and Phylogeny*. Belknap, Harvard University Press, Cambridge, Mass.  
306 490 p.
- 307 Guex, J., 2001. Environmental stress and atavism in ammonoid evolution. *Eclogae Geologicae*  
308 *Helvetiae* 94, 321–328.
- 309 Guex, J., Caridroit, M., Kuwahara, K., O'Dogherty, L., 2014. Retrograde evolution of *Albaillella*  
310 during the Permian-Triassic crisis. *Revue de Micropaléontologie* 57, 39-43.
- 311 Hallam, A., 1978. How rare is phyletic gradualism and what is its evolutionary significance?  
312 Evidence from Jurassic bivalves. *Palaeobiology* 4, 16-25.

- 313 Henderson, C., & Mei, S., (2007), Geographical clines in Permian and lower Triassic gondolellids  
314 and its role in taxonomy *Palaeoworld* 16 (2007) 190–201
- 315 Hermann, R., Hochuli, P. A., Bucher, H., Bruhwiler, T., Hatmann, M., Ware, D., Roohi, G., 2011.  
316 Terrestrial ecosystems on North Gondwana following the end-Permian extinction.  
317 *Gondwana Research* GR597, doi: 10.1016/j.gr.2011.01.008.
- 318 Hirsch, F., 1994a. Triassic conodont multielements versus Eustatic cycles. Lausanne (1991)  
319 *Mémoires de Géologie, Lausanne* 22, 35-52.
- 320 Hirsch, F., 1994b. Triassic conodonts as ecological and eustatic sensors. In: Embry, A. F.,  
321 Beauchamp, B., Glass, D.J. (Eds.), *Pangea: global environments and resources: Memoir of*  
322 *the Canadian Society of Petroleum Geologists* 17, 949–959.
- 323 Ishida, K., 1981. Fine stratigraphy and conodont biostratigraphy of a bedded-chert member of the  
324 Nakagawa Group. *Journal of Science College of General Education, University of*  
325 *Tokushima* 14, 107-137, (in Japanese with English abstract)
- 326 Ishida, K., 1984. The order of appearance of radiolarians in Anisian Bedded-chert bodies in the  
327 South Zone of the Chichibu Belt, Eastern Shikoku. *Journal of Science College of General*  
328 *Education, University of Tokushima* 17, 15-29, (in Japanese with English abstract).
- 329 Jiang, H., Lai, X., Luo, G., Aldridge, R., Zhang, K., and Wignall, P., 2007, Restudy of conodont  
330 zonation and evolution across the P/T boundary at Meishan section, Changxing, Zhejiang,  
331 China: *Global and Planetary Change*, v. 55, p. 39–55.
- 332 Kılıç, A. M., 2004. Multielement taxonomy of the Triassic conodonts of the Kocaeli region. PhD  
333 Thesis, Cumhuriyet University, Sivas, Turkey, 132 p. (in Turkish with English abstract,  
334 unpublished).
- 335 Kılıç, A. M., Plasencia, P., Ishida, K., Hirsch, F., 2015. The Case of the Carnian (Triassic)  
336 Conodont Genus *Metapolygnathus* Hayashi. *Journal of Earth Science* 26 (2), 219-223.
- 337 Kılıç, A. M., Plasencia, P., Ishida, K., Guex, J., Hirsch, F. Conodonts versus Triassic Climatic and  
338 Eustatic changes. *WMESS Prag*, 2015.

- 339 Korte, C., Kozur, H. W., 2010. Carbon isotope stratigraphy across the Permian – Triassic boundary:  
340 A review. *Journal of Asian Earth Sciences* 39, 215–235.
- 341 Kozur, H., Lucas, S. G., 1996. A new conodont from the uppermost Lamar Limestone of the  
342 Delaware Basin of West Texas. *Texas Journal of Science* 48.
- 343 Lambert, L. L., Wardlaw, B.R., Henderson, C.M., 2007, *Mesogondolella* and *Jinogondolella*  
344 (Conodonta): Multielement definition of the taxa that bracket the basal Guadalupian (Middle  
345 Permian Series) *GSSP Palaeoworld* 16 (2007) 208–221
- 346 Lieberman, D. E., 2011. The evolution of the human head. The Belknap Press of Harvard  
347 University Press, ISBN-13: 978-0674046368 ISBN-10. xii + 756 pp.
- 348 Lucas (2012) \ Lucas, S., 2013. New Triassic Time Scale. In: Tanner, L.H., Spielmann, J.A., Lucas,  
349 S.G. (Eds.), *The Triassic System*. New Mexico Museum of Natural History and Science  
350 Bulletin 61, 366-374.
- 351 Mancini, E. A., 1978. Origin of micromorph faunas in the geologic record. *Journal of Paleontology*  
352 52, 311-322.
- 353 Martinez-Perez, C., Plasencia, P., Cascales-Minana, B., Mazza, M., Botella, H., 2013. New insights  
354 into the diversity dynamics of Triassic conodonts. *Historical Biology*.
- 355 Maekawa, T. & Igo, I., 2014, Conodonts [in Shigeta, Y., Komatsu, T., Maekawa, T. & Tran, H.D.,  
356 editors]. *Olenekian (Early Triassic) Stratigraphy and Fossil Assemblages in Northeastern*  
357 *Vietnam.*, National Museum of Nature and Science Monograph 45, Tokyo March 2014, pp.  
358 190-272.
- 359 Metcalfe, I. & Isozaki, Y. 2009, Current perspectives on the Permian–Triassic boundary and end-  
360 Permian mass extinction: Preface *Journal of Asian Earth Sciences* 36 (2009) 407–412 .
- 361 Mosher, L. C., 1968. Evolution of Triassic Platform Conodonts. *Journal of Paleontology* 42(4),  
362 895- 946.
- 363 Muttoni, G., Gaetani, M., Budurov, K., Zagorchev, I., Trifonova, E., Ivanova, D., Petrounova, L.,  
364 Lowrie, W., 2000. Middle Triassic paleomagnetic data from northern Bulgaria: constraints



365 on Tethyan magnetostratigraphy and paleogeography. *Palaeogeography, Palaeoclimatology,*  
366 *Palaeoecology* 160, 223–237

367 Narkiewicz, K., Szulc, J., 2004. Controls on migration of conodont fauna in peripheral oceanic  
368 areas. An example from the Middle Triassic of the Northern Peri-Tethys. *Geobios* 37, 425-  
369 436.

370 Plasencia, P., 2008. Bioestratigrafía y paleobiología de conodontos del Triásico Medio del Sector  
371 Oriental de la Península Ibérica, PhD Thesis, Universitat de Valencia, 404 pp.  
372 <http://www.tdx.cat/handle/10803/9951>.

373 Plasencia, P., Márquez-Aliaga, A., Sha, J., 2013. A database of Triassic conodonts from a  
374 comprehensive revision of literature. *Spanish Journal of Palaeontology* 28 (2), 215-226.

375 Plasencia, P., Hirsch, F., Sha, J., Márquez-Aliaga, A., 2015. Taxonomy and evolution of the  
376 Triassic conodont *Pseudofurnishius*. *Acta Palaeontologica Polonica*. DOI:  
377 [//dx.doi.org/10.4202/app.2012.0048](http://dx.doi.org/10.4202/app.2012.0048)

378 Ratterman, N.G., 1976, *Conodont Biostratigraphy of the Upper Phosphoria Formation (Upper*  
379 *Permian)*. Ohio State University, 66 pages

380 Rutherford, S. L., Lindquist, S., 1998. Hsp90 as a capacitor for morphological evolution. *Nature*  
381 396, 336-342.

382 Sadeddin, W., Kozur, H., 1992. *Pseudofurnishius siyalensis* n.sp. (Conodonta) from the Lower  
383 Ladinian of Wadi Siyala (Jordan). *Neues Jahrbuch für Geologie und Paläontologie und*  
384 *Monatshefte* 6, 356-368.

385 Saunders, W. B., Work, D. M., Nikolaeva, S. V., 1999. Evolution of complexity in Paleozoic  
386 Ammonoid Sutures. *Science* 286, 760-763.

387 Thom, R., 1972. *Stabilité structurelle et morphogénèse*. W.A. Benjamin Inc., Reading Mass. New  
388 York.

389 Trammer, J., 1971. Middle Triassic (Muschelkalk) conodonts from the SW margins of the Holy  
390 Cross Mts. *Acta Geologica Polonica* 21(3), 379-386.

- 391 Trammer, J., 1974. Evolutionary trends and patterns of extinction of Triassic conodonts. *Acta*  
392 *Palaeontologica Polonica* 19 (2), 251-264.
- 393 Trotter, J. A., Williams, I. S., Nicora, A., Mazza, M. Rigo, M., 2015. Long-term cycles of Triassic  
394 climate change: a new  $\delta^{18}\text{O}$  record from conodont apatite. *Earth and Planetary Science*  
395 *Letters* 415 (2015) 165–174.
- 396 Valentine, J. W., Collins, A. G., Meyer, C. P., 1994. Morphological complexity increase in  
397 metazoans. *Palaeobiology* 20, 131-142.
- 398 Wardlaw, B. R., Collinson, J. W., 1986. Paleontology and deposition of the Phosphoria Formation.  
399 *Contributions to Geology, University of Wyoming* 24(2), 107-142.
- 400 Wardlaw, B.R., (1994) Guadalupian conodont biostratigraphy of the Glass and Del Norte mountains,  
401 In: Wardlaw B.R., Grant R.E. and Rohr D.M., *The Guadalupian Symposium: Smithsonian*  
402 *contributions to Paleobiology*, chapter 3.
- 403 Wardlaw, B. R., Mei, S., 1998. A Discussion of the early reported species of *Clarkina* (Permian  
404 conodonts) and the possible Origin of the Genus. In: Jin et al. (Eds.), *Permian Stratigraphy,*  
405 *Environments and Resources*, v.2, *Palaeoworld* 9, 33-52.
- 406 Ware, D., Jenks, J.F., Hautman, M., Bucher, H., (2011), Dienerian (Early Triassic) ammonoids from  
407 the Candelaria Hills (Nevada, USA) and their significance for palaeobiogeography and  
408 palaeoceanography, *Swiss J Geosci* (2011) 104:161–181 DOI 10.1007/s00015-011-0055-3
- 409 Wignall, P.B., and Twitschett, R.J. (2002), Extent, duration, and nature of the Permian-Triassic  
410 super-anoxic event, *Geological Society of America Special Paper* 356
- 411 Yin, H. F., Zhang, K. X., Tong, J. N., Yang, Z. Y., Wu, S.B., 2001. The global stratotype section  
412 and point (GSSP) of the Permian–Triassic boundary. *Episodes* 24, 102-114.
- 413 Zawidzka, K., 1975. Conodont stratigraphy and sedimentary environment of the Muschelkalk in  
414 Upper Silesia. *Acta Geologica Polonica* 25, 217-256.

COVER LETTER to the Editor of Revue de Micropaléontologie

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

Address: Balikesir University Department of Geological Engineering Balikesir TURKEY

E-mail: [alimurat@balikesir.edu.tr](mailto:alimurat@balikesir.edu.tr) \ [dr.alimurat@hotmail.com](mailto:dr.alimurat@hotmail.com)

Phone (mobil): +905335454425

Phone (office): +906121294 ext. 5401

Fax: +902666121257

Figure 1

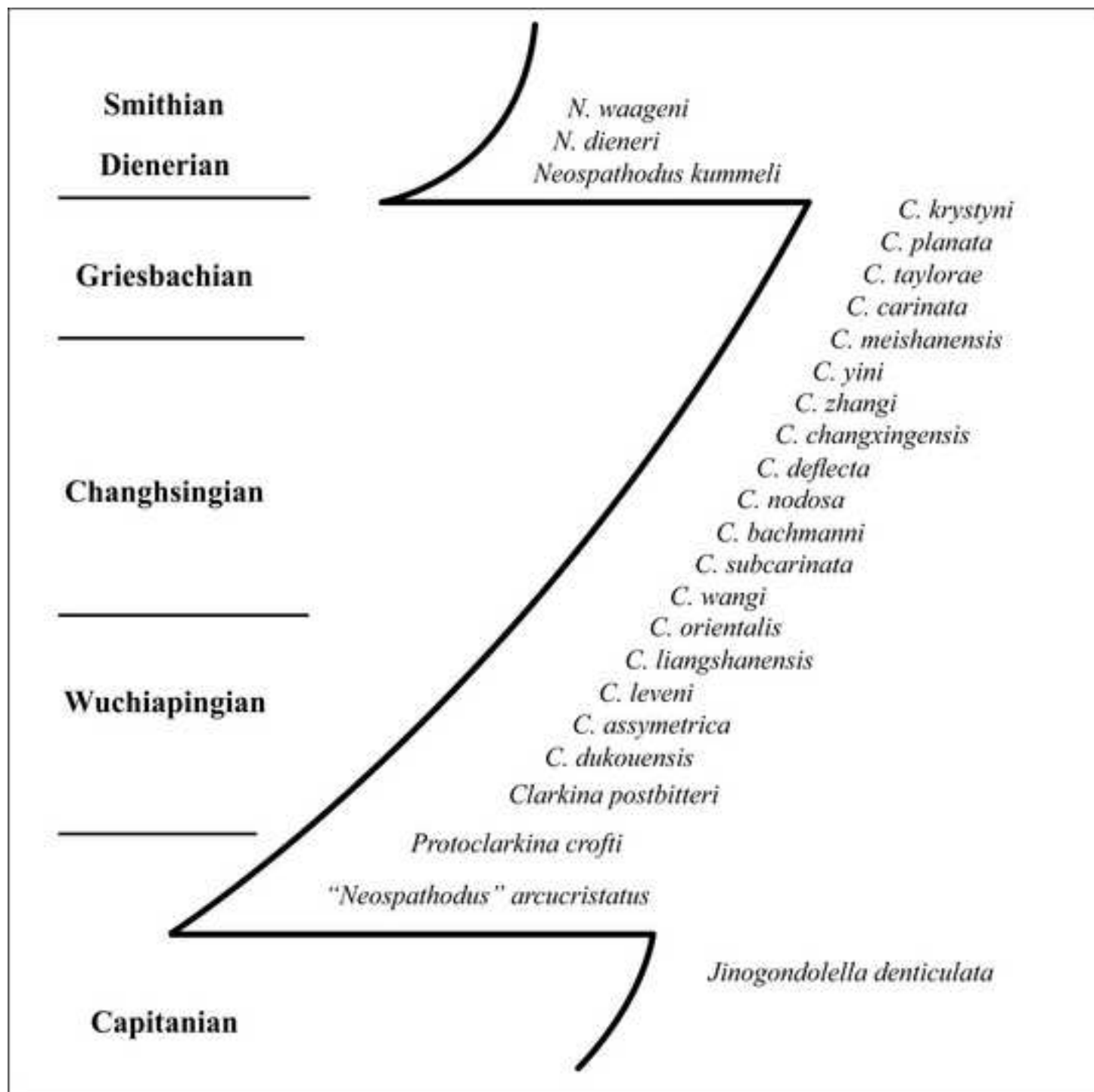


Figure2

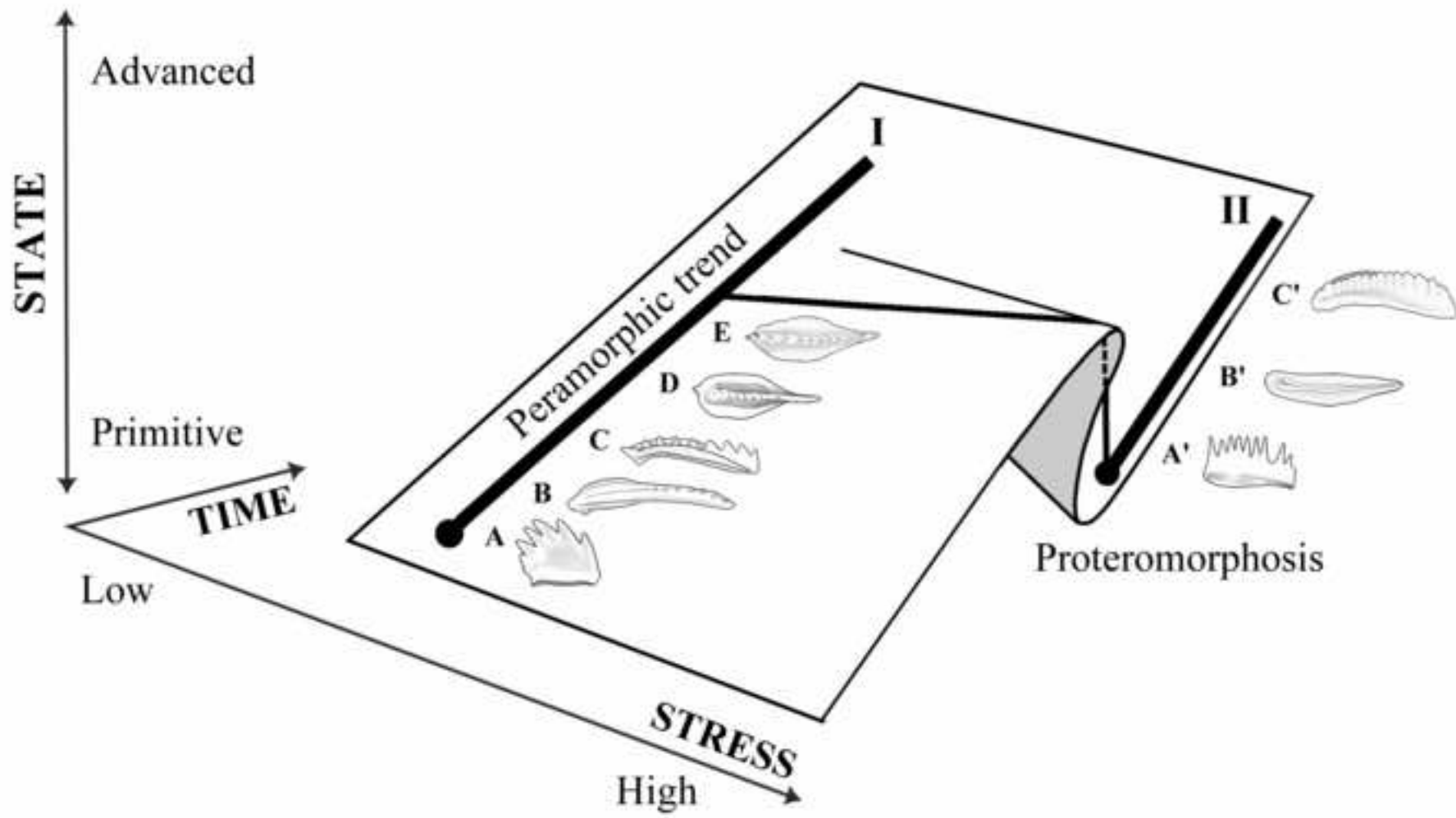


Figure3

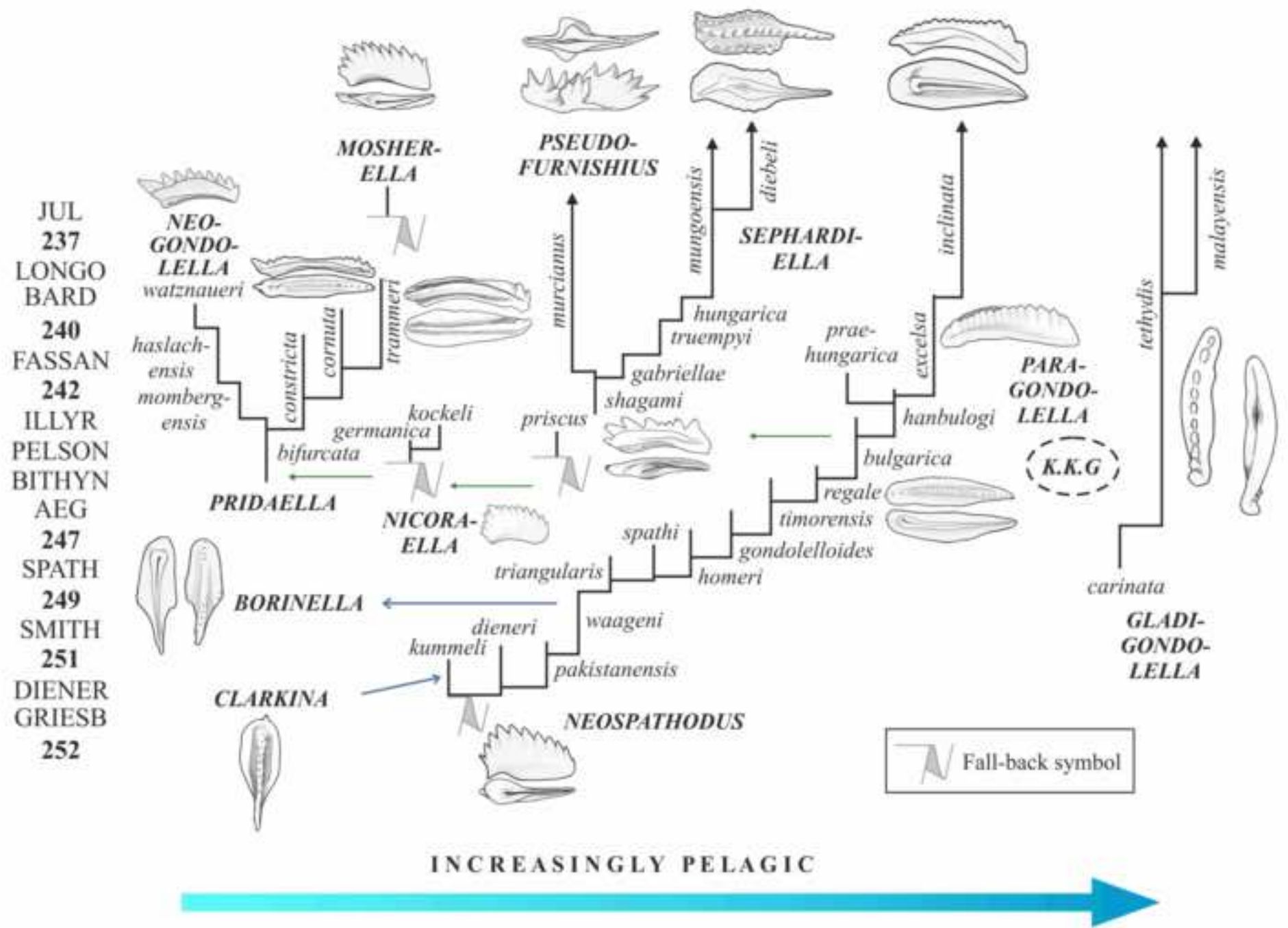
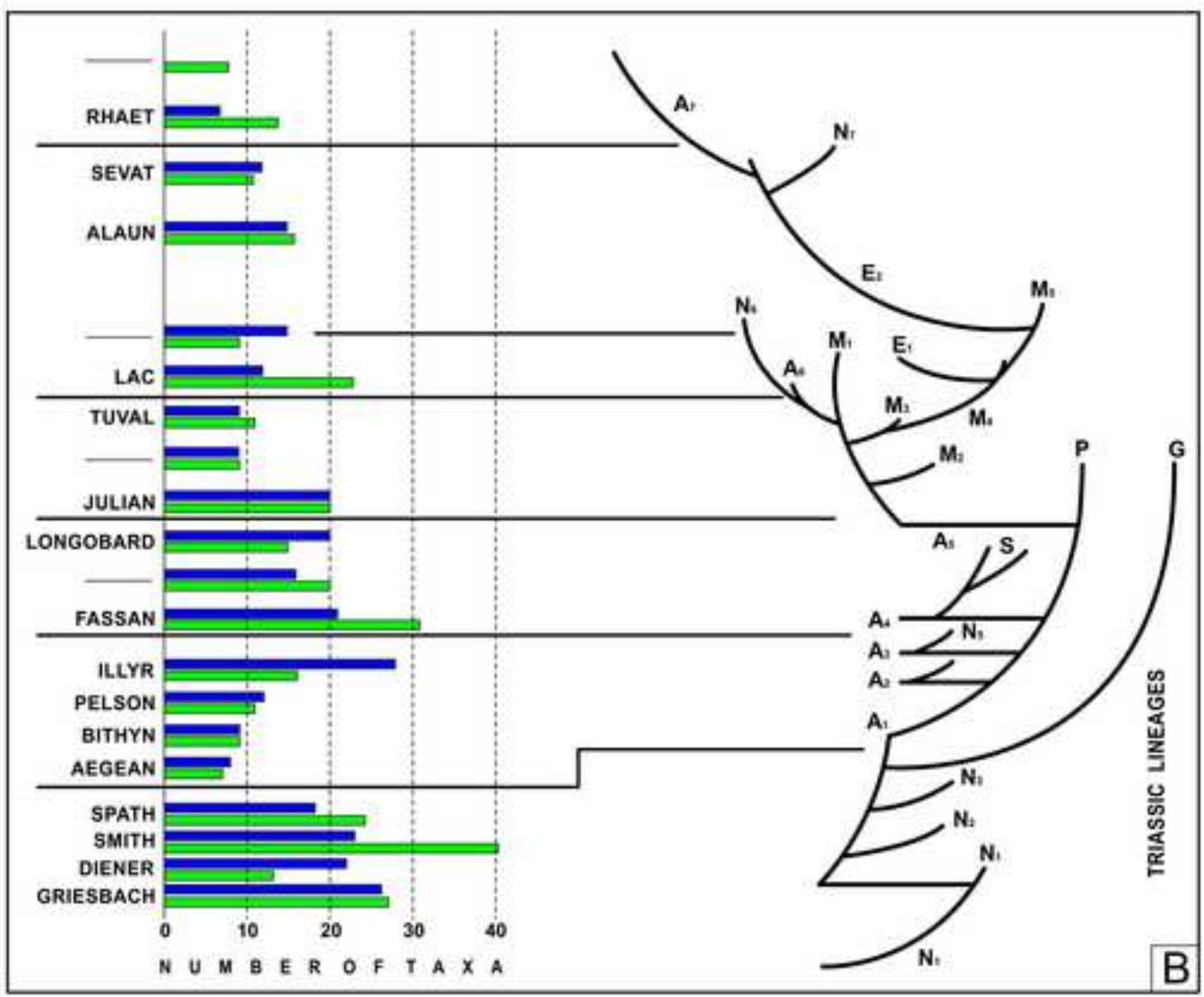
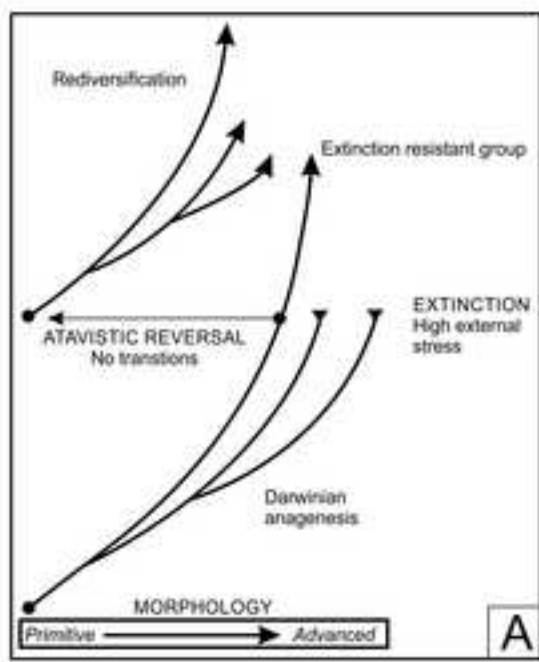


Figure 4



PROTEROMORPHOSIS OF *NEOSPATHODUS* (CONODONTA) DURING THE PERMIAN - TRIASSIC CRISIS

Ali Murat KILIÇ, Pablo PLASENCIA, Keisuke ISHIDA, Jean GUEX, and Francis HIRSCH

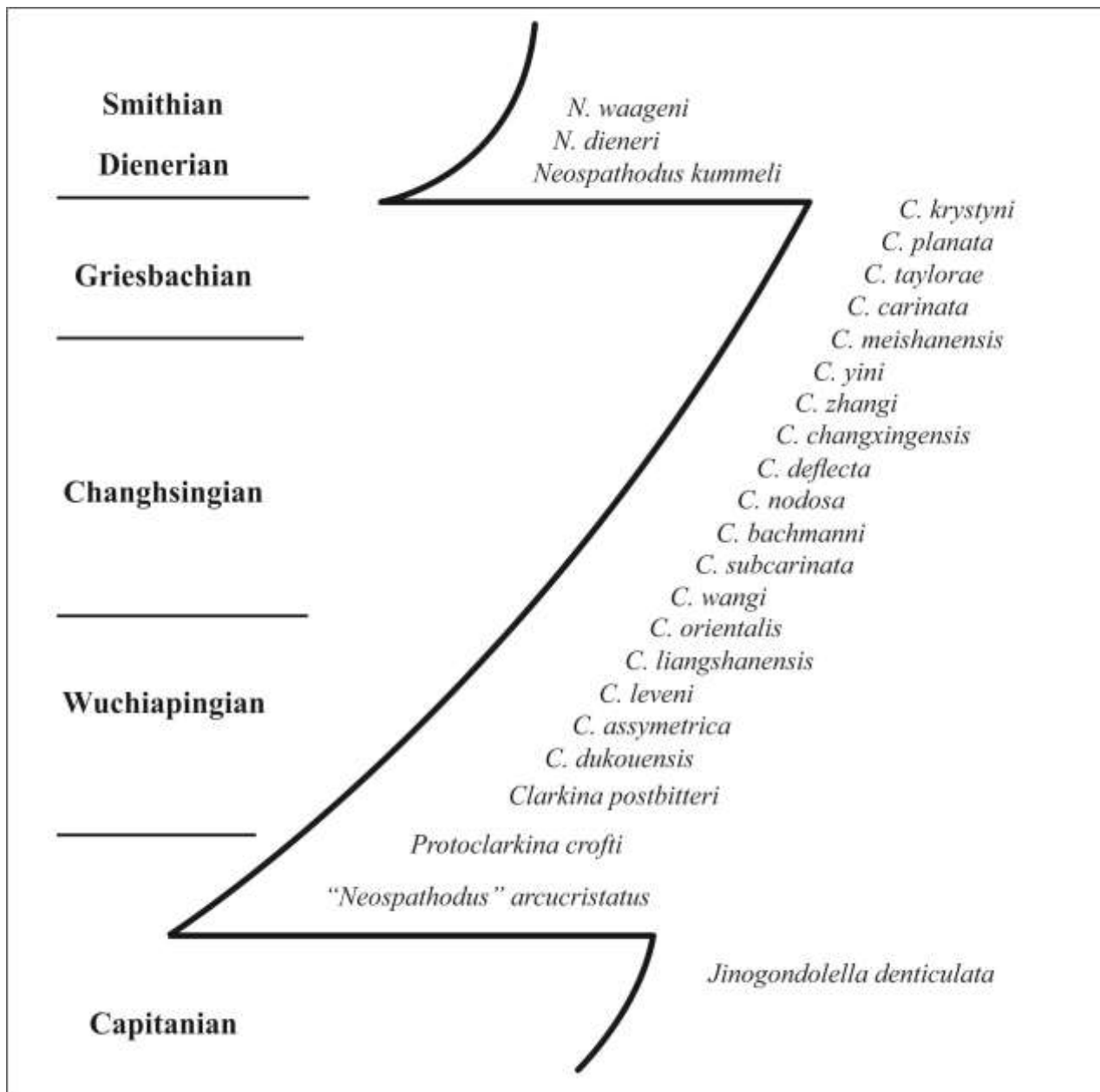


Figure 1. Distribution of Late Permian - Early Triassic conodont lineages through time. Horizontal lines represent atavistic reversals (towards the left), curves symbolise Darwinian anagenesis (after Metcalfe and Isozaki, 2009; Lambert et al., 2007; Wardlaw and Mei, 1998; Wignall and Twitschett, 2002; "*Neospathodus*" *arcucristatus* Clark and Behnken, 1971 from Ratterman, 1976).



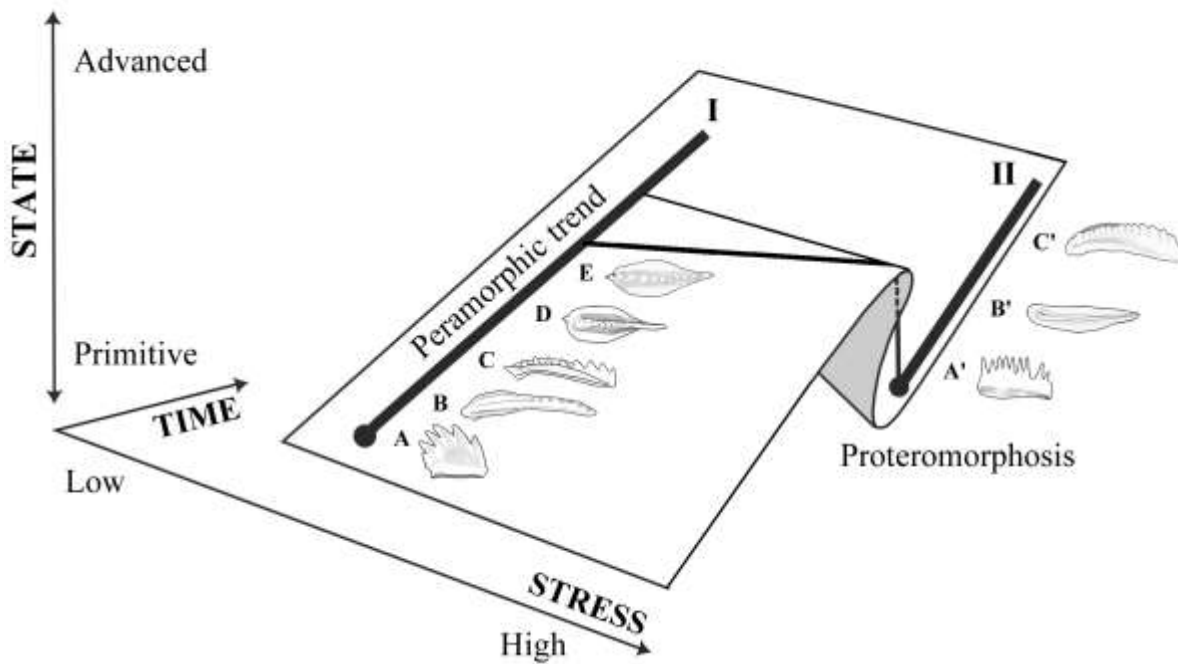


Figure 2. The cusp catastrophe of Thom (1972) is a diagrammatic representation of a punctuated anagenesis. Peramorphic trend: Anagenetic lineage of (A) "*Neospathodus*" *arcucristatus*, (B) *Protoclarkina crofti*, (C) *Clarkina bitteri*, (D) *C. meishanensis*, (E) *C. krystyni*; Proteromorphosis: Catastrophic 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.

Ali Murat KILIÇ, Pablo PLASENCIA, Keisuke ISHIDA, Jean GUEX, and Francis HIRSCH

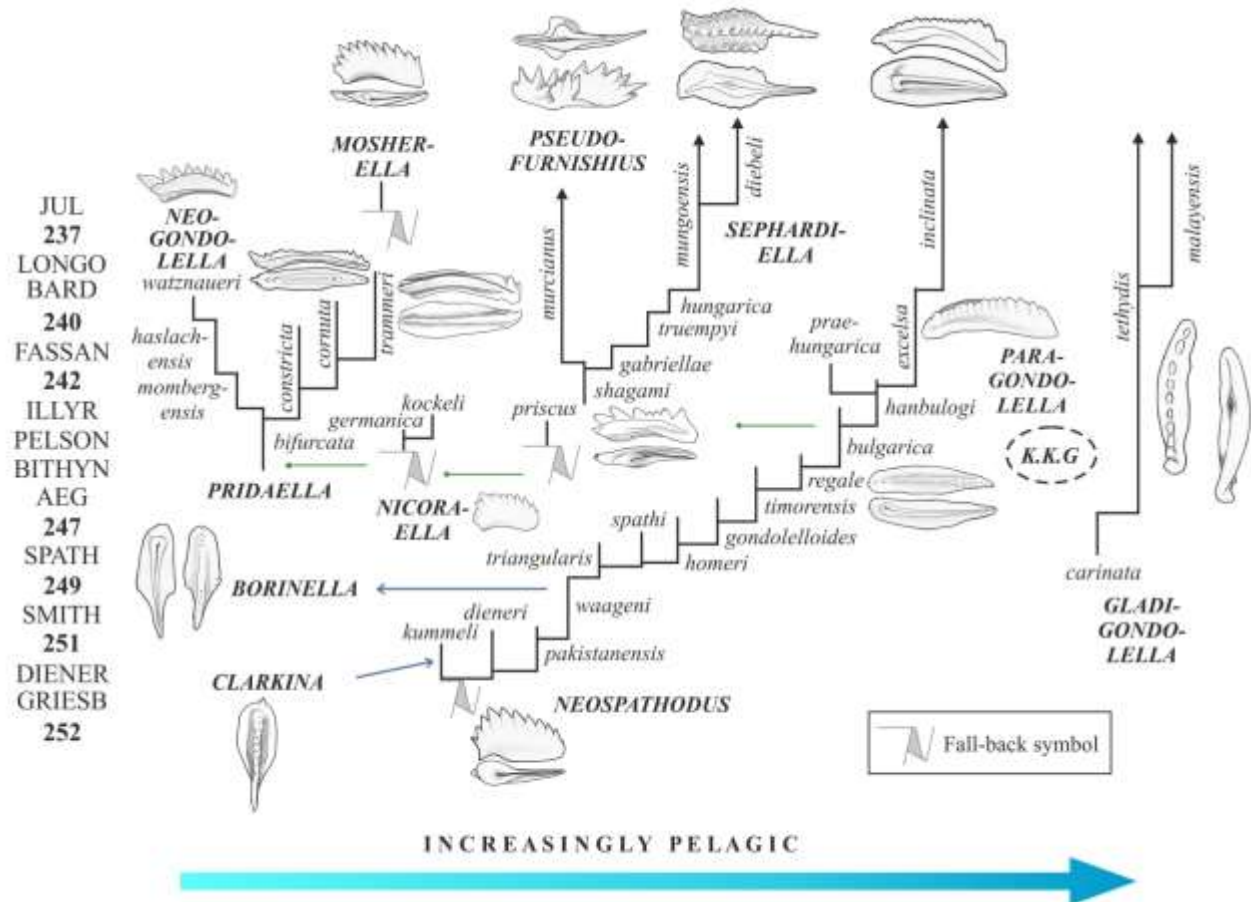


Figure 3. Early - Middle Triassic conodont lineages (252- 237 Ma). The Scythian - Dinarian\* Gondolelloidean Lineages are represented in function of time (Ma) and increasing pelagic habitat. “*Neogondolella*” consists of the Lopingian - Induan *Clarkina* that retrogrades into the Dienerian *Neospathodus 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 proteromorph taxa, at the origin of new lineages such as Anisian- Ladinian *Nicoraella* - *Pridaella* and Anisian - Early Julian *Pseudofurnishius* - *Mosherella*. Most pelagic is the Tethyan equatorial Late Spathian - Julian family *Gladigondolellidae* 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.

(\*) Lucas (2012) coined Dinarian in replacement of Middle Triassic (Anisian - Ladinian stages).

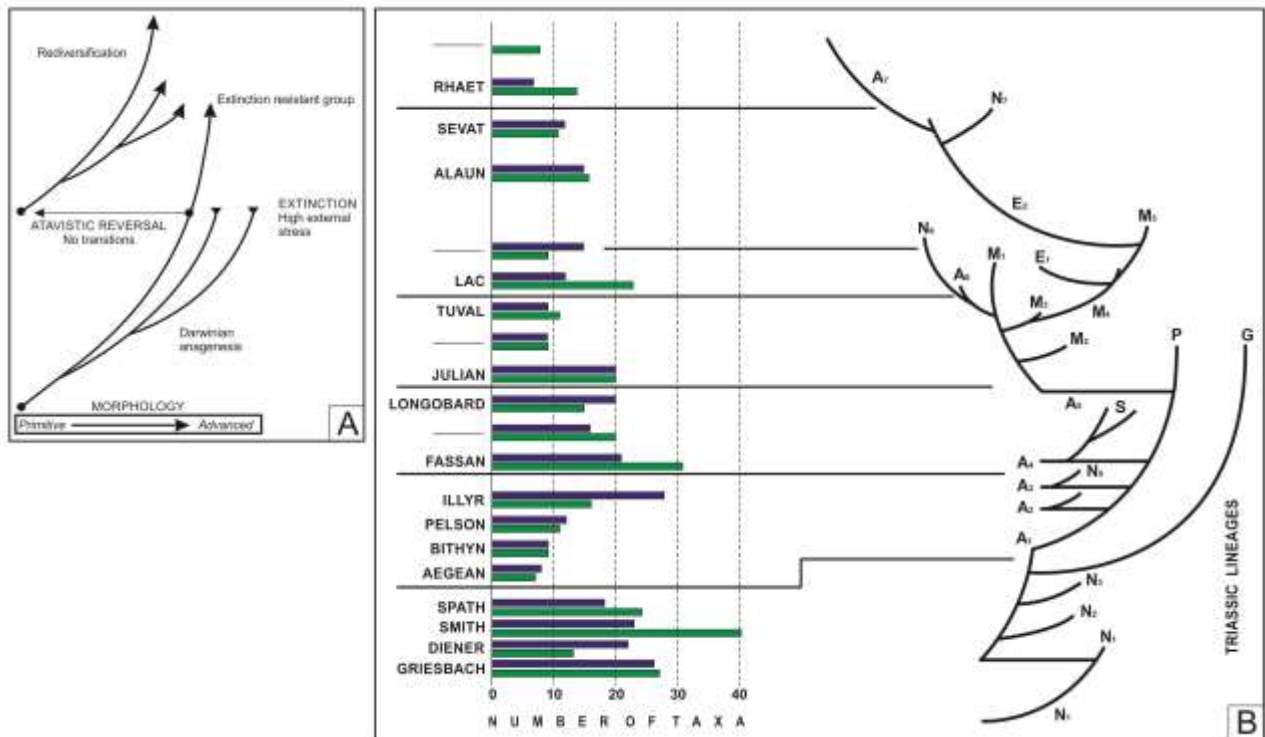


Figure 4. Distribution Scheme of Triassic Conodont Lineages and Number of Taxa through Time: **A**. Key after Guex (2001); **B**. Taxa compilation based on Martinez-Perez et al. (2013):

A: *Neospathodus*; A<sub>1</sub>: *Kashmirella*; A<sub>2-3</sub>: *Nicoraella*; A<sub>4</sub>: *Pseudofurnishius*; A<sub>5</sub>: *Mosherella*; A<sub>6</sub>: *Neocavitella*; A<sub>7</sub>: *Misikella*; N: *Neogondolellinae*: N<sub>1</sub>: *Clarkina*; N<sub>2</sub>: *Scythogondolella*; N<sub>3</sub>: *Borinella*; N<sub>4</sub>: *Pridaella*; N<sub>5</sub>: *Neogondolella*; N<sub>6</sub>: *Norigondolella*; N<sub>7</sub>: *Parvigondolella*; P: *Paragondolella*; M<sub>1</sub>: *Metapolygnathus*; M<sub>2</sub>: *Mazzaella*; M<sub>3</sub>: *Hayashiella*; M<sub>4</sub>: *Carnepigondolella*; M<sub>5</sub>: *Ancyrogondolella*; S: *Sephardiellinae*; E: *Epigondolellinae*: E<sub>1</sub>: *Acuminatella*; E<sub>2</sub>: *Mockina*