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Source: Acta Palaeontologica Polonica, 60(2) : 385-394

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2012.0048

Taxonomy and evolution of the Triassic conodont *Pseudofurnishius*

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Plasencia, P., Hirsch, F., Sha, J., and Márquez-Aliaga, A. 2015. Taxonomy and evolution of the Triassic conodont *Pseudofurnishius*. *Acta Palaeontologica Polonica* 60 (2): 385–394.

Pseudofurnishius is a late Anisian (Pelsonian)–early Carnian (Cordevolian) conodont genus of gondolellid stock, characteristic for the Sephardic Province and restricted to the "Southern Tethys" region of the northern margin of Gondwana. Its most commonly found species, *Pseudofurnishius murcianus*, appears at the base of the Ladinian (Fassanian). The Ladinian material of Spain reveals its ontogeny characterised by initial lateral protrusions from the carina that may develop first mono-platform and later bi-platform units, finally evolving into elaborated multi-denticulated forms. The late Anisian–early Carnian phylogenesis of *Pseudofurnishius priscus* → *P. shagami* → *P. murcianus* is proposed. At the end of the Ladinian, *Pseudofurnishius* expanded to the entire "Southern Tethys" shelf and into Cimmerian terranes that drifted away from northern Gondwana, now accreted to Eurasia, such as the Sibumasu terrane (Southwest China–Malayan Peninsula).

Key words: Conodonta, *Pseudofurnishius*, taxonomy, evolution, Triassic, Sephardic Province.

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Received 19 March 2012, accepted 17 December 2013, available online 10 January 2014.

Introduction

Most Middle to Late Triassic conodonts represent a single clade classified in the family Gondolellidae. The gondolelids inherited their apparatus structure after the Late Devonian prioniodinid *Branmehla* (Dzik 2006) and preserved its fifteen-element composition without significant change until their extinction near the end of the Triassic (von Bitter and Merrill 1998; Orchard and Rieber 1999). The most unusual aspect of the Triassic gondolellids of the *Neogondolella* clade was the detached medial process of the S_0 element (Orchard and Rieber 1999). Most of the gondolellids develop a regular platform in their P_1 elements but in the lineage of *Pseudofurnishius* a peculiar asymmetry and variability developed, including the irregularly distribution of a few high denticles.

This lineage presumably originated and evolved along the northwestern shore of Gondwana, for which the term "Sephardic Province" was proposed by Hirsch (1972), primarily based on the Ladinian distribution of *Pseudofurnishius murcianus* Van den Boogaard, 1966, later corroborated by bivalves (Márquez-Aliaga 1985) and ammonoids (Parnes et al. 1985; Pérez-Valera 2005; Pérez-Valera et al. 2011).

Pseudofurnishius remains restricted to the "Sephardic Province" during the late Anisian and most of the Ladinian. During the latest Ladinian and early Carnian, *P. murcianus* spread out along the northwestern margin of the nascent Meso-Tethys ocean into the Southern Alps, Dinarids and Taurids. Also Gondwana derived fragments of Apulia/Adria in Hungary (Kozur 1993) yield *P. murcianus* and some other species have been found as far as SW China (Yang et al. 2001) and the Malayan Peninsula (Nogami 1968; Hirsch et al. 2007; Ishida and Hirsch 2011) (Fig. 1). The latter two localities are part of the Sibumasu terrane (sensu Metcalfe 2006) that amalgamated to the Asian continent along the Lancangjiang–Bentong-Raub sutures at the end of the Triassic.

Above all, criteria such as the amygdaloid morphology of the basal cavity in the P_1 element and the morphological variability of the P_2 element led Plasencia et al. (2007) to classify the genus *Pseudofurnishius* in the middle–early Late Triassic lineage of the subfamily Sephardiellinae. The latter was originally believed to possess an apparatus including only seven element types, without a diplododellid bifid anterior process bearing S_3 element, but an eight-element type has been recognised more recently (Ishida and Hirsch 2011).

Pseudofurnishius is the only conodont present in many localities of the Middle Triassic in the Sephardic Province and often the only fossil available for biostratigraphic control. However, despite improved knowledge of element morphology, the biostratigraphic position of each of its species has long remained the subject of debate (Gullo and Kozur 1991; Hirsch 1997; Plasencia et al. 2007; Plasencia 2009). The objective of this work is to discuss new evidence in taxonomy, biostratigraphic correlation, geological age, and evolutionary relationships of the genus in general and *P. murcianus*, in particular.

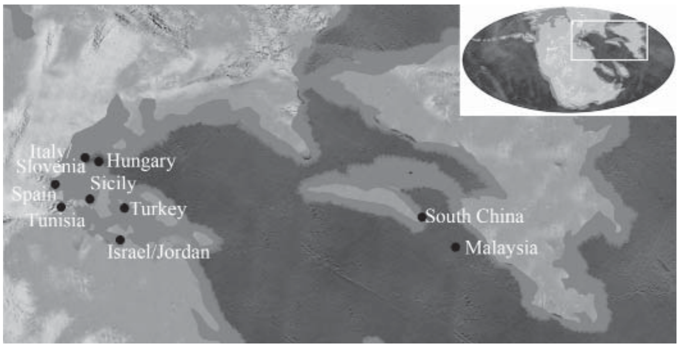


Fig. 1. Paleogeographic distribution of *Pseudofurnishius* occurrences ranging from the Pelsonian to Early Carnian. *Pseudofurnishius murcianus* occurs in all localities; *P. priscus*, *P. shagami*, and *P. siyalaensis* occur in Israel and Jordan; *P. sosioensis* occurs in Sicily and South China. Modified from Plasencia (2009).

Material and methods

The material of *Pseudofurnishius murcianus* (Fig. 2D), the most common species of the genus, consists of several thousand specimens from mostly Sephardic localities (Fig. 1). This study is based on specimens from 24 Ladinian sections in the eastern part of the Iberian Peninsula that spreads, from N to S, from the Pyrenees and Catalonian Coastal Ranges in the north-east to the Iberian Range in the centre-east and the Betic Cordilleras in the south-east (Plasencia et al. 2010). In many horizons, samples with *P. murcianus* are monospecific. Most representative, from a biostratigraphic point of view, is the section of Calasparra, which encompasses a continuous early Fassanian to middle Longobardian sequence (Plasencia and Márquez-Aliaga 2011).

The materials of the other species of the genus are much scarcer: (i) *Pseudofurnishius shagami* (Fig. 2A) 50 specimens from the late Illyrian to early Ladinian of Har Gevanim (Israel; Benjamini and Chepstow-Lusty 1986); (ii) *Pseudofurnishius priscus* (Fig. 2B) and *P. siyalaensis* (Fig. 2C) 7 and 1 specimens, respectively from the late Pelsonian of Wadi Siyala (Jordan; Sadeddin 1990 and Sadeddin and Kozur 1992); (iii) *Pseudofurnishius sosioensis* (Fig. 2E) 23 specimens from the Sosio Valley (Sicily, Italy; Gullo and Kozur 1989).

Institutional abbreviations.—BGU, Department of Geology, Ben Gurion University, Bersheeba, Israel; DGES, Department of Geology and Environment Sciences, Yarmouk University, Irbid, Jordan; MGUV, Museu de Geologia de la Universitat de València, Spain; DGG, Dipartimento di Geologia e Geodesia, Palermo, Italy.

Systematic palaeontology

For the nomenclature of the taxon *Pseudofurnishius* we follow that proposed by Purnell et al. (2000) and the reorientation of the element proposed by Plasencia (2009) (Fig. 3).

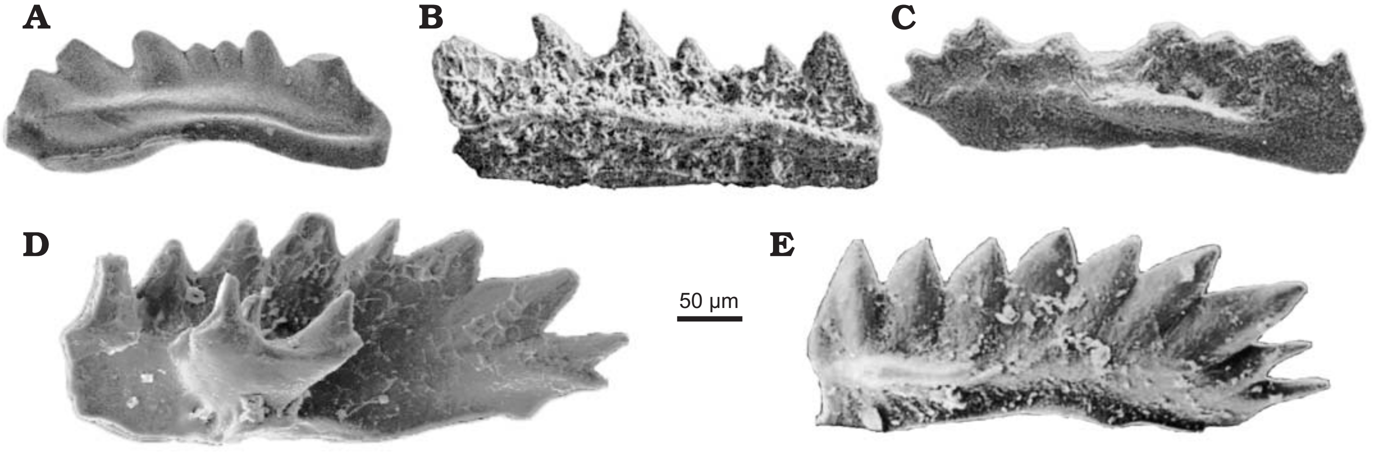


Fig. 2. P_1 element of the Triassic gondolellid conodonts. **A**. *Pseudofurnishius shagami* (Benjamini and Chepstow-Lusty, 1986), holotype, BGU-YF 75/1. YF-75; Saharomin Formation, Har Gevanim, Makhtesh Ramon, late Ilyrian (from Benjamini and Chepstow-Lusty 1986). **B**. *Pseudofurnishius priscus* Sadeddin, 1990, holotype, DGES WII/9/90, TJ 17; Mukheiris Formation, Wadi Siyala, Jalda area, Pelsonian (from Sadeddin 1990). **C**. *Pseudofurnishius siyalaensis* Sadeddin and Kozur, 1992, holotype, DGES S3/1/88, TJ 17; Mukheiris Formation, Wadi Siyala, Jalda area, Pelsonian (from Sadeddin and Kozur 1992). **D**. *Pseudofurnishius murcianus* Van den Boogaard, 1966, MGUV-19891; Cañete Formation, Libros, Iberian Range, Longobardian. **E**. *Pseudofurnishius sosioensis* Gullo and Kozur, 1989, holotype, DGG CK/VIII-2, sample 638; Lercara Formation, Torrente San Calogero, Sosio Valley, Longobardian (from Gullo and Kozur 1989).

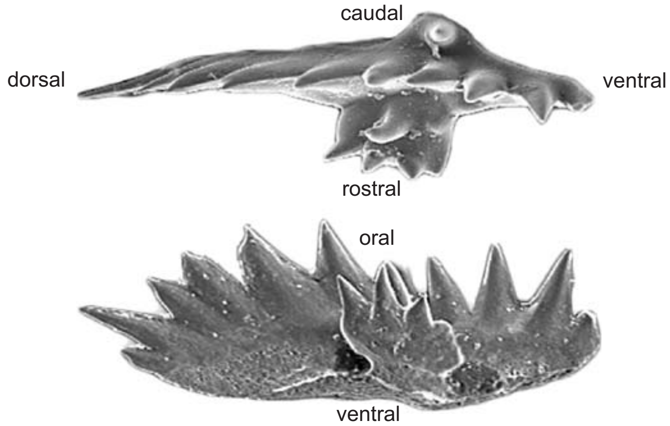


Fig. 3. Descriptive terminology used for the P_1 elements of *Pseudofurnishius murcianus* Van den Boogaard, 1966 (specimen illustrated also in Fig. 5B).

Phylum Chordata Bateson, 1886

Subphylum Vertebrata Linnaeus, 1758

Class Conodonta Eichenberg, 1930

Order Ozarkodinida Dzik, 1976

Superfamily Gondolelloidea Lindström, 1970

Family Gondolellidae Lindström, 1970

Subfamily Sephardiellinae Plasencia, Hirsch, and Márquez-Aliaga, 2007

Genus *Pseudofurnishius* Van den Boogaard, 1966

Type species: *Pseudofurnishius murcianus* Van den Boogaard, 1966; Fuente Aledo, (Sierra de Carrascoy, Murcia, Spain), Post-Carboniferous.

Species included: The following species of the genus are considered valid: *Pseudofurnishius murcianus* Van den Boogaard, 1966, *P. shagami* (Benjamini and Chepstow-Lusty, 1986), *P. priscus* Sadeddin, 1990, and *P. siyalaensis* Sadeddin and Kozur, 1992. The morphology of *P. sosioensis* Gullo and Kozur, 1989, suggests that of a juvenile early Ladinian Sephardiellinae taxon. The species *P. huddlei* Van den Boogaard and Simon, 1973 and *P. regularis* Budurov and Pantić, 1973 are regarded as synonyms of *P. murcianus* (Bandel and Waksmundzki 1985 and Ramovš 1978, respectively).

Emended diagnosis.—A gondolellid with the P_1 element tending to be slightly asymmetric, straight or slightly curved, with at least an inner lateral platform covered with a cluster of prominent irregular denticles, located anterior to mid-length with a relatively short anterior blade with erect denticles. The posterior blade is longer and the denticles posteriorly reclined. Some specimens may have a prominent denticle on the outer lateral margin and others have a nodose platform developed around the margins of the anterior blade. The basal cavity is "cavital (neospathodid)", gradually narrowing towards both ends of the element. An amygdaloid basal pit is located in the central third of the unit. Platform-less species related to the type species are also included in the genus.

Remarks.—The emended diagnosis is proposed because the concept of the genus has changed substantially since the taxon was established by Van den Boogaard (1966). First Ramovš (1977) pointed out the presence of an outer platform and added a more detailed description of the aboral side. Later Gullo and Kozur (1991), considering the smooth species of *Pseudofurnishius*, re-formulated the diagnosis, introducing evolutionary observations and morphological aspects that we consider invalid.

Stratigraphic and geographic range.—Late Pelsonian (late Anisian) to early Cordevolian (early Carnian); "Sephardic Province" during late Anisian to early Ladinian; spread to Southern Alps, Dinarids, Taurids, and Cimerian terranes (Malayan Peninsula, SW China) during late Ladinian–early Carnian. The occurrence of the late Anisian *Pseudofurnishius* species in the area of the "Sephardic Province" suggests that the origin of the genus took place in that realm.

Review of the species included within *Pseudofurnishius*

Anisian

The following three Anisian species of *Pseudofurnishius* are considered valid:

***Pseudofurnishius shagami* (Benjamini and Chepstow-Lusty, 1986)** (Fig. 2A).—The species, characterised by a blade-shaped neospathodid P_1 element, occurs in the lower member of the Saharonim Formation, Makhtesh Ramon, Israel. A late Illyrian to the early Fassanian age is attributed to this interval on the base of the ammonoids: *Gevanites inflatus* Parnes, 1975, *G. altecarinatus* Parnes, 1975, *Israelites ramonensis* Parnes, 1962, and *Eoprotrachyceras curionii ramonensis* (Parnes, 1986) (Benjamini et al. 2005). Its evolutionary relation with *Pseudofurnishius* is inferred from the shape of the basal cavity (Fig. 4A) and the slight curvature of the P_1 element (Plasencia et al. 2007).

***Pseudofurnishius priscus* (Sadeddin, 1990)** (Fig. 2B).—The smooth, reduced platform with sigmoidal bending, and the denticles, less inclined than in any younger species of *Pseudofurnishius*, make *P. priscus* the most primitive species of the genus. The holotype (Sadeddin 1990: 374, fig. 3.1) is reported from level TJ17, Wadi Siyala (Jordan), and a juvenile specimen (Sadeddin 1990: 375, fig. 3.4) from a "Lower Longobardian" level Ab8, Wadi Naur (Jordan). Sadeddin and Kozur (1992: 361, fig. 2) modified the age of sample TJ17 to Fassanian (lower Ladinian). However, the correlation of Triassic across the Dead Sea Rift (Hirsch 1997; Benjamini et al. 2005) suggests that the Wadi Siyala section is coeval with the lower part of the Gevanim Formation of Pelsonian age in Har Arif (Israel) and that level Ab8 at Wadi Naur appears to be equivalent to the late Anisian–early Ladinian lower part of the Saharonim Formation, from where Benjamini and Chepstow-Lusty (1986) described *N. shagami*, in the Ramon section (Israel).

***Pseudofurnishius siyalaensis* Sadeddin and Kozur, 1992** (Fig. 2C).—The material was recovered from level TJ17 of the Wadi Siyala section in Jordan, the same level from where Sadeddin (1990) described *P. priscus*. Diagnostic for *P. siyalaensis* are a broad, smooth and slightly asymmetric platform, a free ventral and dorsal blade, and a sigmoidal keel. These morphological characters differentiate *P. siyalaensis* from other *Pseudofurnishius* species, especially from *P. priscus* and *P. shagami*. The suggestion by Sadeddin and Kozur (1992) that the Fassanian *Neogondolella mostleri* (Kozur, 1980) was the ancestor of *P. siyalaensis*, based on common short asymmetric platforms, is untenable in view of the Pelsonian age of the level, in which *P. siyalaensis* occurs. The attribution of a late Ladinian P_1 element to *P. siyalaensis* (Rigo et al. 2007: fig. 4.3b) is unlikely, as it is shorter, having a rounded anterior basal cavity, a more anterior pit and fewer posteriorly inclined denticles than the Pelsonian holotype of *P. siyalaensis*.

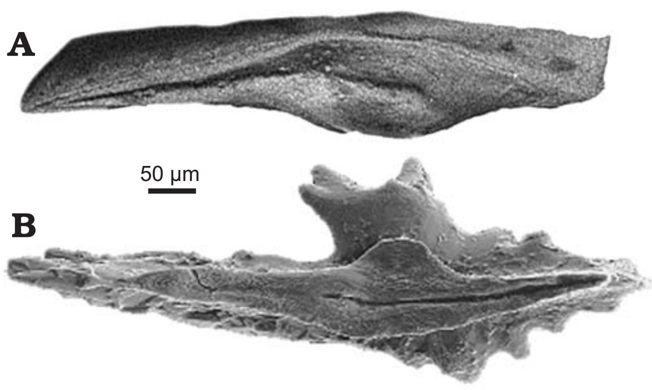


Fig. 4. Comparison of the basal cavities of gondolellid conodonts *Pseudofurnishius shagami* (Benjamini and Chepstow-Lusty, 1986), Har Gevanim, Saharonim Formation, Negev, Israel, Anisian–Ladinian (**A**) and *Pseudofurnishius murcianus* Van den Boogaard, 1966, Arroyo Hurtado, Murcia, Spain, Ladinian (**B**).

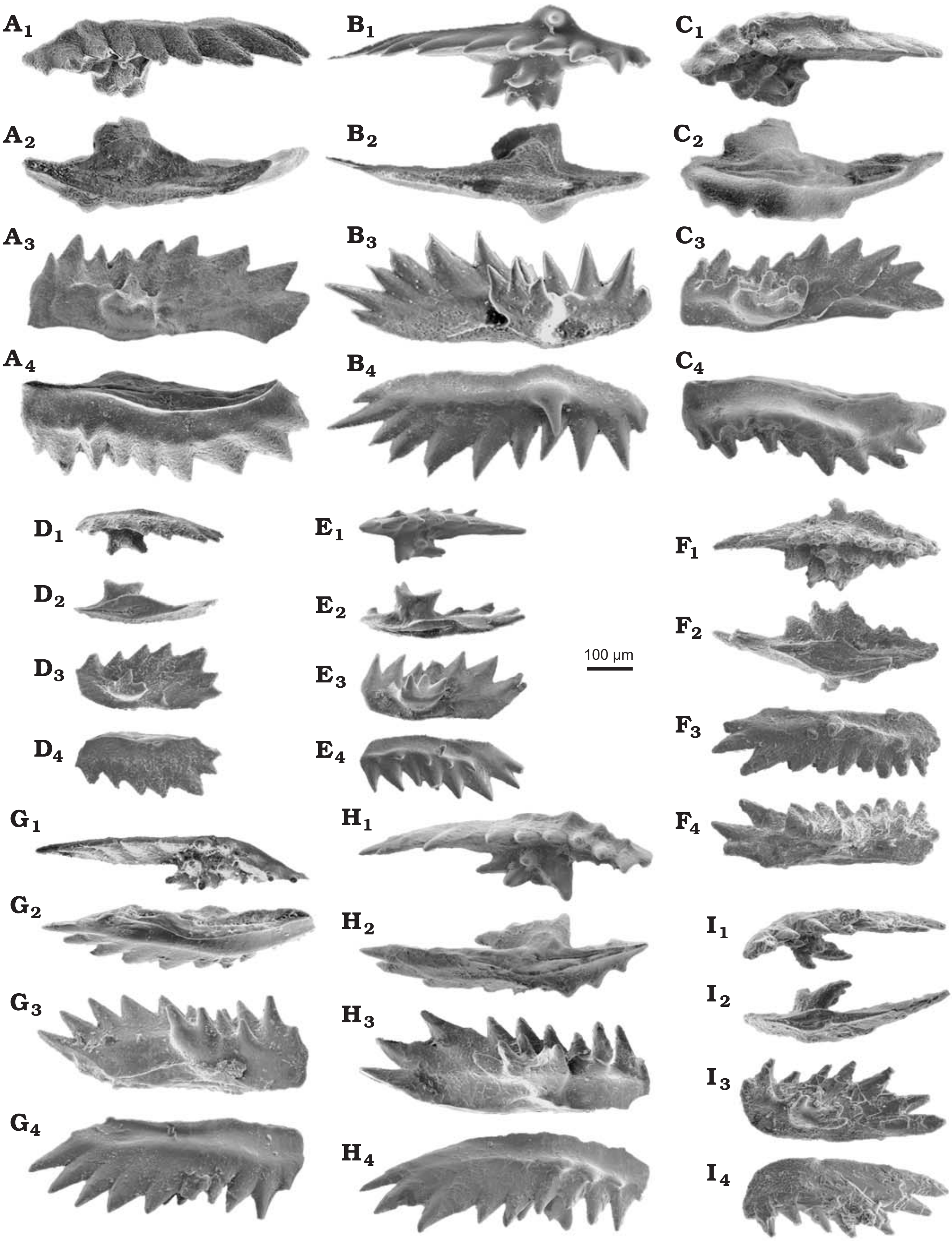
Early Ladinian–early Carnian

Apart from *Pseudofurnishius murcianus* Van den Boogaard, 1966 (Fig. 2D), the type species, several other species, and subspecies have been described: *Pseudofurnishius regularis* Budurov and Pantić, 1973 (figs. 1, 16–18); *Pseudofurnishius huddlei* Van den Boogaard and Simon, 1973 (fig. 2i); *Pseudofurnishius murcianus murcianus* Van den Boogaard, 1966 (in Gullo and Kozur 1991: pl. 5: 6); *Pseudofurnishius murcianus praecursor* Gullo and Kozur, 1991 (Kovács and Kozur 1980: pl. 2.6); *Pseudofurnishius murcianus* subsp. B of Gullo and Kozur (1991: fig. 3f); and *Pseudofurnishius sosioensis* Gullo and Kozur, 1989 (Fig. 2E). The taxonomic status of these taxa is discussed below.

***Pseudofurnishius murcianus* Van den Boogaard, 1966** (Fig. 2D).—To date, specimens of *P. murcianus* were recovered from Ladinian sediments of Spain (Van den Boogaard 1966; Van den Boogaard and Simon 1973; March Benlloch 1986, 1991; Plasencia 2009), Tunisia (Rakus 1981), Egypt and Israel (Huddle 1970; Hirsch 1972; Eicher and Mosher 1974), Jordan (Bandel and Waksmundzki 1985), Slovenia (Ramovš 1977, 1978; Krivic and Stojanovic 1978; Kolar-Jurkovšek 1990), Croatia (Jelaska et al. 2003; Balini et al. 2006), Serbia (Budurov and Pantić 1973), Turkey (Nicora 1981), and Sicily (Catalano et al. 1990; Gullo and Kozur 1991). Late Ladinian to early Carnian occurrences of the species are known from the Southern Alps of Italy (Mastandrea et al. 1998; Balini et al. 2000; Jadoul et al. 2002), Dinarides (Kolar-Jurkovšek et al. 2006, Buser et al. 2008) as well as displaced terranes in Hungary (Kozur 1993) and the Cimmerian terrane of Sibumasu from South-West China (Yang et al. 2001) and Malayan Peninsula (Nogami 1968; Hirsch et al. 2007; Ishida and Hirsch 2011) (Fig. 2).

In the Betic Ranges of Murcia (Spain) the section of Calasparra, one of the most complete Ladinian localities in the Iberian Peninsula, has delivered ammonoids of early and late Ladinian ages (Pérez-Valera et al. 2011). In this section, Plasencia and Márquez-Aliaga (2011) have found *P. murcianus* from the very base of the Fassanian, ranging upwards through the Ladinian. Earlier, the first appearance of *P. murcianus* in the Fassanian was suggested in Israel (Hirsch 1972; Hirsch and Gerry 1974), based on ammonoids at Makhtesh Ramon (Parnes 1962, 1975, 1986; Parnes et al. 1985).The section of Calasparra is not far from that of Fuente Aledo (Sierra de Carrascoy, Murcia, Spain) from where the holotypes of *P. murcianus* and *P. huddlei* originated (Van den Boogaard and Simon 1973). The basal unit of the Calasparra section contains the *Eoprotrachyceras curionii* and *Gevanites awadi* subzones of the *E. curionii* Zone. Both subzones yield specimens of *P. murcianus* with one and two lateral platforms (Fig. 2H, I). Brack et al. (2005) established the Ladinian GSSP at the first appearance datum of *E. curionii.* That raises the Anisian–Ladinian boundary upwards, with the result that the first appearance datum (FAD) of *P. murcianus* occurs at the very base of the Fassanian. The type locality of *P. murcianus* (and *P. huddlei*) once dated as Longobardian by Kozur and Simon (1972), using ostracods, also yields the above men-

Fig. 5. Morphological variability within the P_1 element of the gondolellid conodont *Pseudofurnishius murcianus* Van den Boogaard, 1966. Elements of monoplatform (C, E, G, I), monoplatform with outer denticles (B, H), and biplatform (A, D, F) forms in occlusal (A_1–I_1), basal (A_2–I_2), caudal (A_3–I_3), and rostral (A_4–I_4) views (modified from Plasencia 2009). **A**. Right element, MGUV-10109, sample Ceab-6, Grey Limestones Unit, Alós de Balager, Pyrenees, Ladinian (Fassanian). **B**. Left element, MGUV-10123, sample CLD-24, Cañete Formation, Calanda, Ladinian (Longobardian). **C**. Right element, MGUV-1035, sample He-20, Cañete Formation, Henarejos, Iberian Range, Ladinian (Longobardian). **D**. Right element, MGUV-10157, sample He-14, Cañete Formation, Henarejos, Iberian Range, Ladinian (Longobardian). **E**. Right element, MGUV-10207, sample He-18, Cañete Formation, Henarejos, Iberian Range, Ladinian (Longobardian). **F**. Left element, MGUV-19866, sample Li-8, Cañete Formation, Libros, Iberian Range, Ladinian (Longobardian). **G**. Left element, MGUV-10399, sample Bu-pl, Cañete Formation, Bugarra, Iberian Range, Ladinian (Longobardian). **H**. Left element, MGUV-10251, sample CLP-6, Majanillos Formation, Calasparra, Betic Cordillera, Ladinian (Fassanian). **I**. Right element, MGUV-10255, sample CLP-6, Majanillos Formation, Calasparra, Betic Cordillera, Ladinian (Fassanian). →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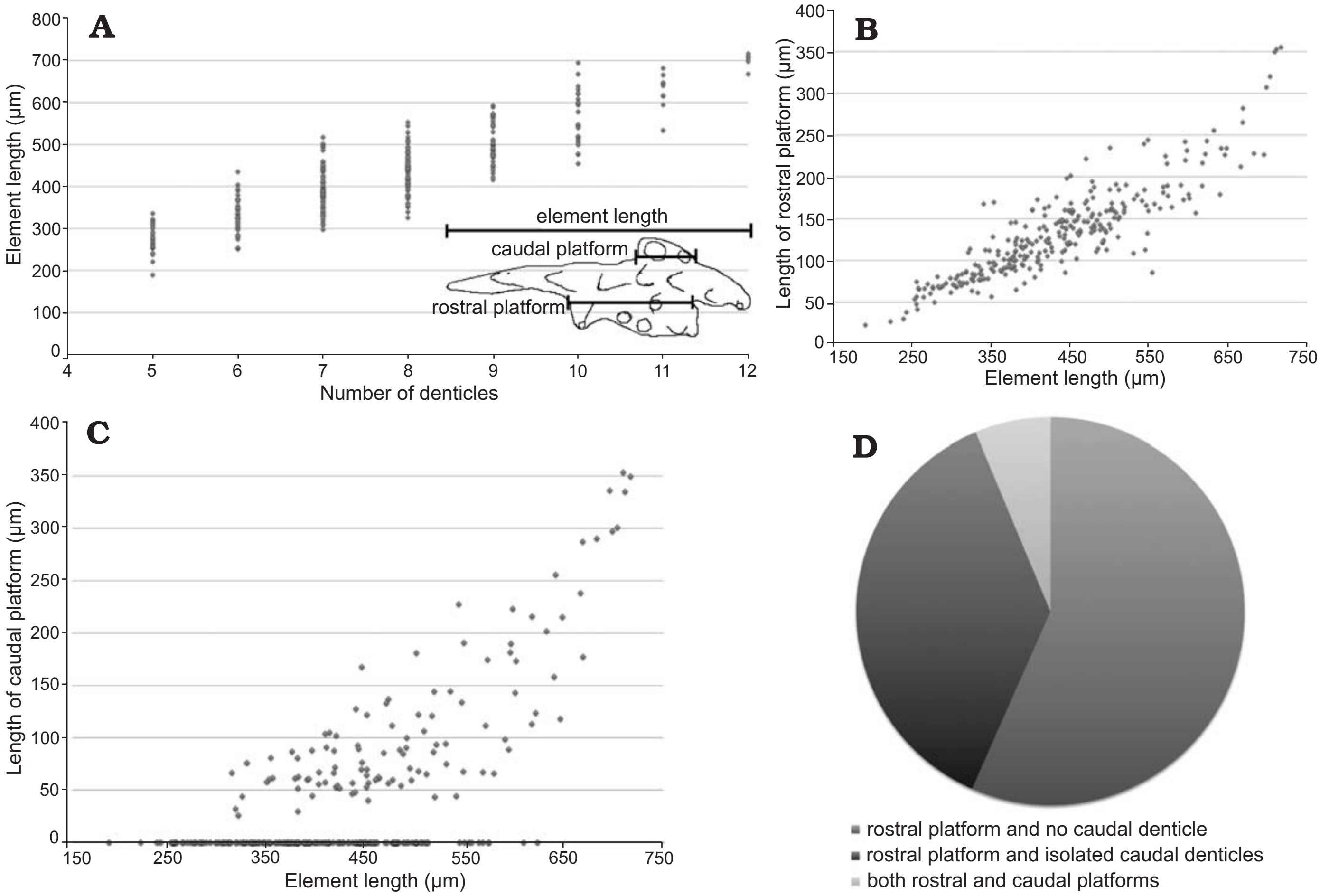


Fig. 6. Morphological variability of gondolellid conodont *Pseudofurnishius murcianus* Van den Boogaard, 1966 in a single population, sample Bu-1-26, Bugarra, Iberian Range, Spain. **A**. Number of the denticles on the blade. **B**. Ratio between rostral platform length and element length. **C**. Ratio between caudal platform length and element length. **D**. Ratio between elements having: rostral platform and no caudal denticles, rostral platform and isolated caudal denticles, both rostral and caudal platforms.

tioned Fassanian ammonites (Sanz de Galdeano 1997; Pérez-López and Pérez-Valera 2007).

The characteristic morphology of *Pseudofurnishius murcianus* consists in the variability of ornamentation of the generally larger rostral platform and occasional smaller caudal platform. Additionally, the complexity in distribution of the denticles that cover the rostral platform, directed both inward and orally, and the presence of denticles on the caudal side, frequently isolated and rarely developed as a platform create the wide morphological variability of this often asymmetrical species (Fig. 5A–I).

Taxonomic status of *Pseudofurnishius huddlei*.—Rich samples in the early Fassanian at Calasparra and Alós de Balager (Spain), Har Gevanim (Israel) and Wadi Naur (Jordan), as well as in the Longobardian at Henarejos (Spain) and Har Gevanim (Israel) contain both “mono-” and “bi-platform” specimens of *Pseudofurnishius murcianus* that appear without any sequential discrimination as a single taxon.

The variability in the irregular pattern of distribution of denticles on both platforms is observable during growth (Fig. 5A–I). The number of blade denticles varies between five and fifteen, among which three to six on its ventral side and two to ten on its dorsal side. Starting with the cusp, located above the basal cavity tip, the denticles of the dorsal blade are large and triangular in shape with a progressively increasing dorsal inclination. The platform typically consists of only a short inner-lateral expansion with short rounded denticles pointing both inwardly and orally. Some specimens may in addition have one or more denticles located on the caudal margin. These characteristics show that *P. huddlei* is actually the mature *P. murcianus*.

Taxonomic status of subspecies within *Pseudofurnishius murcianus* lineage.—In their attempt to unravel variability in *P. murcianus*, Gullo and Kozur (1991) established several subspecies based on material from Sosio Valley (Sicily, Italy) that comprise (in chronological order): *Pseudofurnishius murcianus praecursor* Gullo and Kozur, 1991, that has a rostral and caudal platform, often reduced to one to four denticles or a narrow ridge; *P. murcianus murcianus* Van den Boogaard, 1966, without any denticle on the caudal side of the blade and *P. murcianus* subsp. B, with a very small platform comprising a single large denticle and occasionally one or two small additional denticles. These authors interpret this succession as the “phylo-morphogenetic” lineage of the genus *Pseudofurnishius* that is believed to consist in the generic evolutionary trend of reducing the extension of the platform, starting from the denticulated bi-platform species *P. huddlei* and ending-up in a single inner-lateral platform species *P. murcianus* subsp. B.

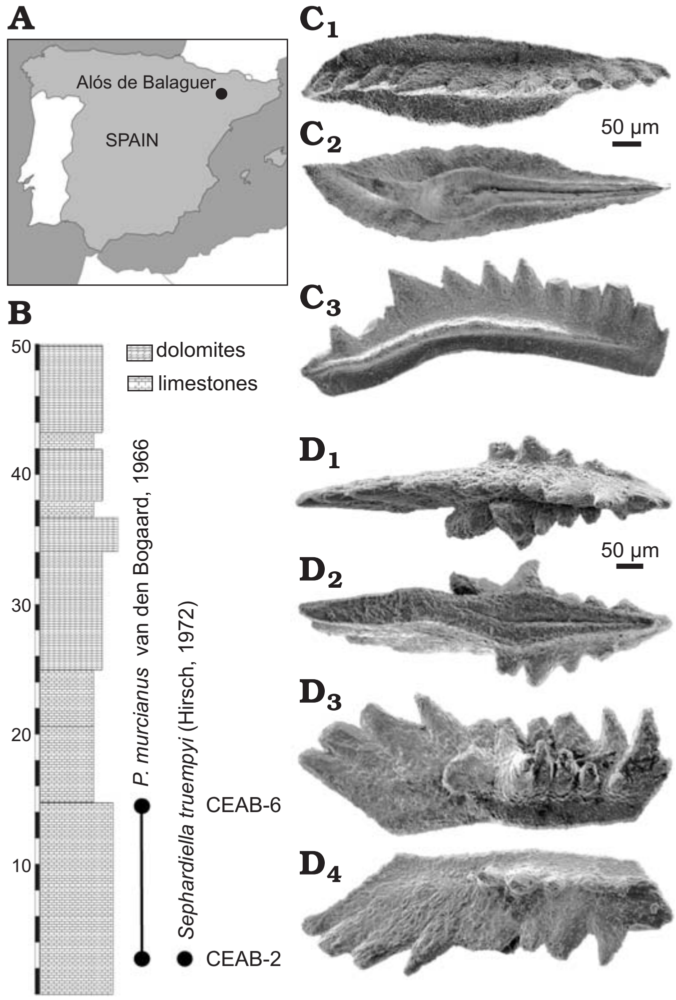
In the first place, we must stress that the establishment of subspecies, as in biology, is valid only in case of geographical isolation and incompatible with the occurrence in the same sample of several subspecies, as it is the case of the subspecies proposed by Gullo and Kozur (1991). See also Dzik and Trammer (1980).

At Bugarra (Iberian Range, Spain), Plasencia et al. (2010) found sample Bu-1-26 to contain 283 well preserved P_1 elements of several different ontogenetic stages of *P. murcianus* showing the morphological variability within a population of that species.

The comparison of total length of the element/number of blade denticles (Fig. 6A); caudal platform length; rostral platform length between points of union with the blade (Fig. 6B), and caudal platform length between points of connection with the blade (Fig. 6C), clearly evidences the continuous variability of *P. murcianus* throughout the entire population. These measurements show a correlation between development, size and number of denticles on each unit. A majority of specimens (185 specimens or 65.3%) have seven to nine denticles on the blade, three or four denticles on the triangularly shaped rostral platform (Fig. 5D, I). This scheme represents the most common morphology. When more denticles are present, the rostral platform shows a very wide variability, as denticles are added in a very irregular pattern (Fig. 5A–C, E, F). This mono-platform morphology would correspond to the type of *P. murcianus murcianus* (Gullo and Kozur 1991), while specimens with eight or nine denticles on the blade and presenting a reduced rostral platform with only one or two denticles would correspond to the morphology described as *P. murcianus* subsp. B of Gullo and Kozur (1991). Although the caudal side of most specimens is a smooth surface devoid of any kind of clearly defined structures, it however, occurs relatively frequently that one or more isolated denticles develop on this side of the blade, from almost germinal to well developed. The presence of at least one of these caudal denticles, which is the main characteristic defining *P. murcianus praecursor*, is quite common in the sample, amounting to 105 specimens or 37.1% (Fig. 5B, E, H) with between one to four denticles. Finally, 14 specimens display a well-developed caudal platform, similar in size to the rostral one, a morphology regarded typical of the species *P. huddlei* (Fig. 5C, F). Furthermore, rare elements with bilateral platforms have been found at Henarejos (Fig. 5C; Longobardian), Wadi Naur, Jordan (middle Longobardian), the Sosio Valley, Sicily (middle–late Longobardian) and at Alós de Balager (Fig. 7; Pyrenees, Fassanian), where accompanied by *Sephardiella truempyi* (Hirsch, 1971).

According to Bandel and Waksmundzki (1985), differences in development of the platform seem to correspond to different ontogenetic stages, and have little to do with the evolution. Consequently, the alleged subspecies in Gullo and Kozur (1991), as well as the species *P. huddlei* Van den Boogaard and Simon, 1973 and *P. regularis* Budurov and Pantic, 1973 correspond merely to ontogenetically more advanced forms, as also pointed out by Ramovs (1977), Bandel and Waksmundzki (1985), and Plasencia (2009).

Summing up, the analysis of the different morphologies present in sample Bu-1-26 shows the same range of morphological variability that has been observed within any normal population of *P. murcianus*, and that all the subspecies of *P.*



E

	CEAB-2	CEAB-6
Pseudofurnishius murcianus (mono-patform)	2	2
Pseudofurnishius murcianus (bi-patform)	4	1
Sephardiella truempyi	2	
Sample weight (g)	1008	3002

Fig. 7. **A**. Geographic location of Alós de Balaguer. **B**. Stratigraphic position of gondolellid conodonts in the Ladinian (Fassanian), Grey Limestone Unit, Pyrenees. **C**. *Sephardiella truempyi* (Hirsch, 1972), right element, MGUV-10407, sample CEAB-2, in occlusal (C_1), basal (C_2), and caudal (C_3) views. **D**. *Pseudofurnishius murcianus* Van den Boogaard, 1966, right element, MGUV-10105, sample CEAB-2, in occlusal (D1)), basal (D_2), caudal (D_3), and rostral (D_4) views. **E**. Conodont distribution at Alós de Balaguer.

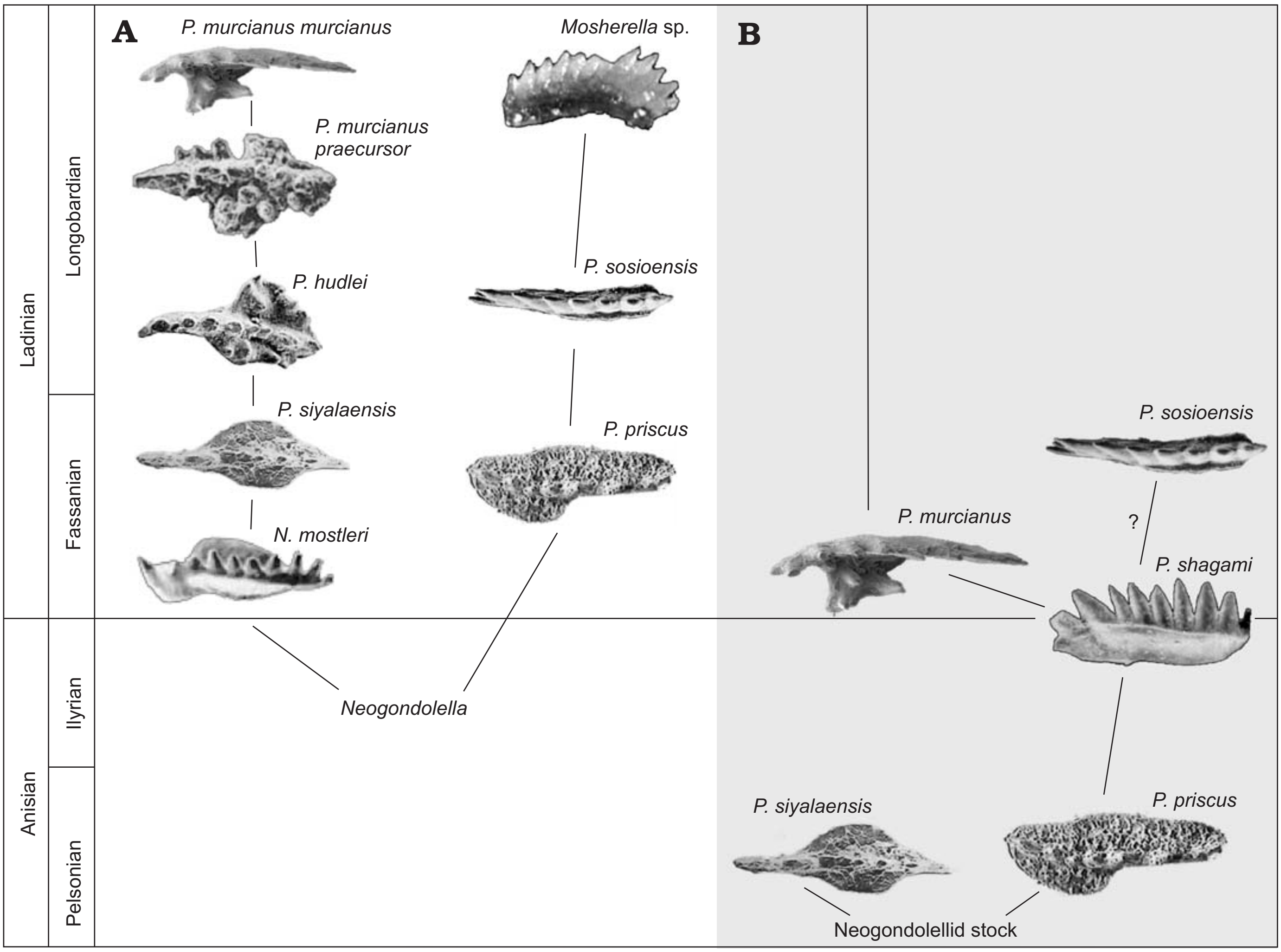


Fig. 8. Evolutionary scenarios for the genus *Pseudofurnishius* after Sadeddin and Kozur (1992) (**A**) and present study (**B**).

murcianus (and also *P. huddlei*) proposed by Gullo and Kozur (1991) can be identified in the same sample. These cannot be understood as stages in an evolutionary lineage according to modal values of their variability (not in typological terms) but they are parts of the ontogeny of the same species. Other populations, as those studied by Ramovs (1977), Bandel and Waksmundzki (1985), and Plasencia (2009) seem to be consistent with this conclusion.

As a second objection to the "Sosio" model of Gullo and Kozur (1991), besides the absence of a coherent description of the section with the position of the samples as evidence in support of their interpretation, the stratigraphic ranges of the successive subspecies, overlapping each other over a short "middle–late Longobardian" time span, strongly contrast with the late Anisian–early Ladinian evolution of the successive species of *Pseudofurnishius* and long Fassanian–Early Cordevolian range of the species *P. murcianus* in particular.

Pseudofurnishius sosioensis **Gullo and Kozur, 1989** (Fig. 2E).—Gullo and Kozur (1989) have erected *P. sosioensis*, characterised by a smooth and small platform on both sides of the element, in the lower part of Torrente San Calogero section (Pietra di Salomone, Sosio Valley, Sicily), followed by bi-platform specimens of *P. murcianus*, which they identified as *P. huddlei,* and mono-platform specimens of *P. murcianus,* higher up in the section. Gullo and Kozur (1991) interpreted as complete "phylomorphogenetic" evolutionary lineage of the genus *Pseudofurnishius,* the succession of *P. priscus* (absent in Sosio) → *P. sosioensis* → *P. huddlei* → *P. murcianus praecursor* → *P. murcianus murcianus* → *P. murcianus* subsp. B, shortly later split in two branches (Sadeddin and Kozur 1992) (Fig. 8A), suggesting *P. sosioensis* as the successor of *P. priscus*. The latter, based on ammonoid evidence, together with *Pseudofurnishius siyalaensis* are Pelsonian (Hirsch 1997) and can consequently not have derived from the Fassanian *Neogondolella mostleri*. The stratigraphic range of *P. sosioensis* from Late Fassanian to Early Longobardian may well be in continuation of the apparently closely related late Anisian–early Ladinian *P. shagami,* and the two are also very similar to each other, sharing the same morphological characteristics of basal cavity and denticulation. Although having rudimentary double platforms, such morphs may also represent a juvenile stage in another taxon of Sephardiellinae taxon. Lack of material however, impeaches a more accurate taxonomic attribution, here.

Evolution of *Pseudofurnishius*

Alternatively to that of Sadeddin and Kozur (1992), we recognise a well age-constrained upper Pelsonian to lower Carnian *Pseudofurnishius* lineage (Fig. 8B). Starting in the late Pelsonian–earliest Illyrian shallow Southern Tethys environments during the initial development of the "Sephardic Province", are both *P. siyalaensis* and *P. priscus* sharing characters that fit in a possible ancestry of *P. shagami* and *P. murcianus*.

Pseudofurnishius priscus and *P. shagami* are so similar to each other that they may well be conspecific (Plasencia et al. 2007). The morphology of the basal cavity of *P. shagami* and *P. murcianus* (Fig. 4) suggests a close evolutionary relationship between both species. As the most successful species of the genus, *P. murcianus* persisted during the whole Ladinian, until its extinction at the beginning of the Carnian.

Mosherella may have originated from *Pseudofurnishius*, as proposed by Kozur (1972), based on the similarities of the blade shape and the basal field in both genera that from the point of view of morphological resemblance is plausible. We must, however, bear in mind that neospathodid morphs originated recurrently as a result of paedomorphosis, presumably in connection to sea level changes (Dzik and Trammer 1980; Hirsch 1994). *Mosherella*, may thus be a neospathodid that resulted from paedomorphosis, a phenomenon recurring with *Neocavitella* (Sudar and Budurov 1979).

Conclusions

- *Pseudofurnishius* is a late Anisian–early Carnian conodont genus characteristic for its occurrence in the "Sephardic Province" and restricted to the Southern Tethys.
- *Pseudofurnishius murcianus* appears in the early Fassanian; it ranges from the Fassanian to the Longobardian characterised by the presence of both "mono-" and "bi-platform" specimens, invalidating the species *P. huddlei*.
- The same morphological varieties found in large Fassanian and Longobardian *P. murcianus* populations are ontogenetical stages of one and the same species. They cannot be understood as stages in an evolutionary lineage.
- Derived from an unknown gondolellid ancestor, the lineage *Pseudofurnishius priscus* → *P. shagami* →*P. murcianus* is proposed.
- During the late Ladinian, *Pseudofurnishius* expanded beyond the "Sephardic Province", spilling over to the Southern Alps and to the Cimmerian terranes as they drifted away from Gondwana.

Acknowledgements

The authors want to express their gratitude to the journal referees, Jerzy Dzik (Instytut Paleobiologii PAN, Warsaw, Poland), Michele Mazza (Università degli Studi di Milano, Italy), and Robert S. Nicoll (Geoscience Australia, Canberra, Australia) for their unaccountable help and constructive remarks. This work has been supported by the Chinese Academy of Sciences (Project "XDB03010000" and Young International Scientist Grant "2010Y2ZA02"), Ministry of Science and Innovation (Project "CGL2011-24408") and by the "Agencia Española de Cooperación Internacional para el Desarrollo" of the Ministry of Foreign Affairs and Cooperation of Spain (MAEC-AECID).

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