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PROTOGNATHODUS (CONODONTA) AND ITS POTENTIAL AS A TOOL FOR DEFINING THE DEVONIAN/CARBONIFEROUS BOUNDARY

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Abstract. The current definition of the Devonian/Carboniferous boundary is the first occurrence of the conodont *Siphonodella sulcata*. Due to difficulties in identification of the early siphonodellids, such as *S. praesulcata* and *S. sulcata*, investigation of *Protognathodus* which enters in the latest Devonian and extends into the Mississippian, was undertaken to determine use as a better indicator of the base of the Carboniferous. During the D/C boundary interval, *Protognathus* is represented by four species: *Pr. meischneri*, *Pr. collinsoni*, *Pr. kockeli* and *Pr. kuehni*.

Although *Pr. kockeli* can be abundant in boundary interval sections, none of the four *Protognathodus* species has a high potential as a tool for redefining the D/C boundary, based on regional variation in first occurrence data, restricted stratigraphic ranges and global distribution, poorly understood facies occurrences, as well as general rarity of the taxa.

Riassunto. La base del Carbonifero è definita dalla prima comparsa del conodonte *Siphonodella sulcata* nella linea evolutiva *Si. praesulcata-Si. sulcata*. Poiché la identificazione dei primi siphonodellidi, quali *S. praesulcata* e *S. sulcata*, presenta difficoltà, è stato esaminato il genere *Protognathodus*, la cui distribuzione stratigrafica si estende dalla parte più alta del Devoniano al Mississippiano, al fine di valutare se fosse un indicatore migliore per la definizione del limite basale del Carbonifero. Durante l'intervallo di tempo comprendente il limite Devoniano/Carbonifero il genere è rappresentato da quattro specie: *Pr. meischneri*, *Pr. collinsoni*, *Pr. kockeli* and *Pr. kuehni*. Benché *Pr. kockeli* sia a volte abbondante in alcune sezioni che comprendono il limite, nessuna delle quattro specie di *Protognathodus* presenta elevate potenzialità per la ridefinizione del limite stesso, a causa della variabilità regionale dei dati di comparsa, di ridotte distribuzioni stratigrafiche e geografiche a livello globale, imputabili forse ad una dipendenza dalle facies non ancora ben chiarita, e, soprattutto, ad una generale rarità delle specie.

Introduction

The base of the Carboniferous System is defined by the First Appearance Datum (FAD) of the conodont species *Siphonodella sulcata*, within the *S. praesulcata-S. sulcata* lineage (Paproth et al. 1991). The Global Stratotype Section and Point (GSSP) is located in the La Serre Trench E' section, Montagne Noire, France. Flajs & Feist (1988) published a biometric study of *S. praesulcata* and *S. sulcata* based on the La Serre faunas, demonstrating that transitional forms are very common. Despite these taxonomic uncertainties, the FAD of *S. sulcata* was chosen to define the base of the Tournaisian. Further studies on the stratotype section have revealed a series of problems, such as lack of other important stratigraphic guides and the existence of reworking (e.g., Flajs & Feist 1988; Ziegler & Sandberg 1996; Casier et al. 2002; Kaiser 2009). Additionally, difficulties in discriminating *S. praesulcata* from *S. sulcata* arose quite immediately (e.g., Ji 1987a; Flajs & Feist 1988; Wang & Yin 1988). A redefinition of the Devonian/Carboniferous boundary (DCB) was reputed nec-

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essary, and in 2008 the International Commission on Stratigraphy established a working group with the goal to propose a new criterion for defining the boundary and finding a new GSSP. A taxonomic overview and revision of the early siphonodellids is in progress (Kaiser & Corradini 2011), but also other conodont genera should be considered for evaluating their potential for identifying the DCB.

This paper addresses the genus *Protognathodus*, a taxon with stratigraphic potential around the DCB and well known since Ziegler (1969) introduced the "*Protognathodus* fauna" to define the youngest Devonian strata, between the "*costatus*" and the "*S. sulcata-P. kockeli*" zones. Later, Ziegler & Sandberg (1984) defined the base of the Upper *praesulcata* Zone by the entry of *Pr. kockeli*.

Four species of *Protognathodus* are known in the time frame across the DCB: *Pr. meischneri* Ziegler, *Pr. collinsoni* Ziegler, *Pr. kockeli* (Bischoff) and *Pr. kuehni* Ziegler & Leuteritz. The goal of this study is to summarize the current knowledge of these species, and take in to account their original taxonomic diagnosis and definitions, precise biostratigraphic ranges, and geographic distributions, in order to evaluate the possible use of one of these taxa to define the base of the Carboniferous.

Phylogeny and stratigraphy of the early *Protognathodus*

Genus *Protognathodus* comprises six species*: Pr. meischneri* Ziegler, *Pr. collinsoni* Ziegler, *Pr. kockeli* (Bischoff), *Pr. kuehni* Ziegler & Leuteritz, *Pr. praedelicatus* Lane et al. and *Pr. cordiformis* Lane et al.

Morphological features and stratigraphic distribution of these forms allow discrimination of two groups: an early group, including *Pr. meischneri*, *Pr. collinsoni*, *Pr. kockeli* and *Pr. kuehni*, occur in the uppermost Famennian and lower Tournaisian; in these species the anterior margins of the cup are opposed. A late group, ranging in upper Tournaisian, includes *Pr. praedelicatus* and *Pr. cordiformis*, which have larger cups that have slightly offset anterior terminations. Lane et al. (1980) suggested that *Pr. praedelicatus is* derived from *Pr. kockeli*, but there is a short stratigraphic gap between the two groups, corresponding to part of the Lower *crenulata* Zone.

The appearance and evolution of the genus *Protognathodus* is easy to follow in the latest Devonian (Fig. 1) as documented by Ziegler (1973). *Protognathodus meischneri*, the oldest species of the genus, evolved from *Bispathodus stabilis* (Ziegler, 1969) by a variation in the position and shape of the basal cavity (cup). In *Protognathodus* the basal cavity extends to the posterior end of the element and is more rounded and inflated; *Pr. meischneri* has an almost symmetrical and unornamented cup. This happened during the late Famennian, contemporaneous to the first occurrence of representatives of the genus *Siphonodella* or slightly before, as suggested by the occurrence of a single specimen of *Pr. meischneri* in the Upper *expansa* Zone in Sardinia (Corradini et al. 2003: tab. 2).

In the very early part of its range *Pr. meischneri* gave rise to *Pr. collinsoni*, characterized by the occurrence of scattered nodes on the upper surface of the slightly asymmetrical cup. Both of these species range to within the Upper *duplicata* Zone (Over 1992).

Protognathodus kockeli, characterized by an asymmetrical cup covered by at least one longitudinal row of nodes, evolved from *Pr. collinsoni* just after the

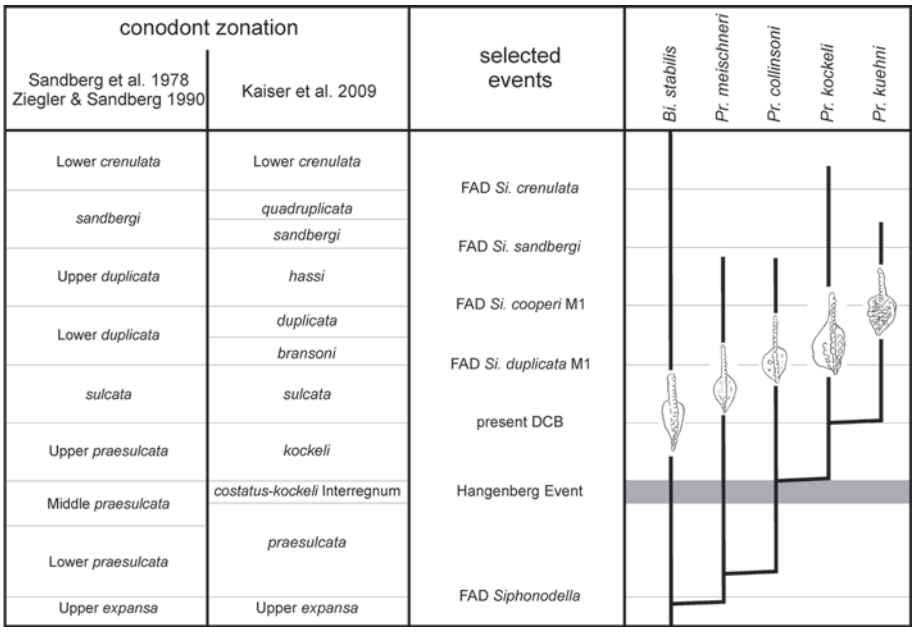


Fig. 1 - Phylogeny and stratigraphic distribution of early representatives of genus *Protognathodus* across the D/C boundary plotted against selected events and aligned to the biozonation schemes after Sandberg et al. (1978), Ziegler & Sandberg (1990) and Kaiser et al. (2009). Sketches are based on the holotypes figured in Ziegler (1973).

Hangenberg Event. It ranges up to the lower part of the Lower *crenulata* Zone in North America (Sandberg et al. 1978), whereas elsewhere it is limited to the *sandbergi* Zone.

Protognathodus kuehni is distinguished by robust transverse ridges on the upper surface of the cup running radially from the margins to the carina, that can be suppressed. It evolved from *Pr. kockeli* and ranges from around the present DCB to the *sandbergi* Zone (Lane et al. 1980).

Repository of the figured specimens. DSTC: Dipartimento di Scienze della Terra, Università di Cagliari; IC: Dipartimento di Scienze della Terra e Geologico Ambientali, Università di Bologna, Alma Mater Studiorum; IPUM: Museo di Paleontologia, Università di Modena e Reggio Emilia; SMNS: Staatliches Museum für Naturkunde Stuttgart.

Systematic palaeontology

Protognathodus synonymy lists herein only include figured specimens that could be clearly assessed. For suprageneric classification, the scheme proposed by Sweet (1988) is followed. The four species considered are discussed in stratigraphic and evolutionary order: *Pr. meischneri*, *Pr. collinsoni*, *Pr. kockeli* and *Pr. kuehni*. Taxonomy is focused only on P1 elements, as the multielement apparatuses of the different species are unknown. Translation of the original diagnosis in German was provided by Sandra Kaiser; it is essentially in agreement with the previous translation by Ziegler (1973).

Class **Conodonti** Branson, 1938

Order **Ozarkodinida** Dzik, 1976

Family Idiognathodontidae Harris & Hollingsworth, 1933

Genus *Protognathodus* Ziegler, 1969

Type species: *Gnathodus kockeli* Bischoff, 1957

Remarks. The apparatus of *Protognathodus* was tentatively reconstructed as seximembrate by Chauffe & Nichols (1995). However, no distinction between members of the apparatuses of the various species was provided and the authors described P2, M, S0, S1 and S2 elements as "vicarious elements of *Protognathodus collinsoni*, *Pr. kockeli* and *Pr. meischneri.*"

Protognathodus meischneri Ziegler, 1969

Pl. 1, figs 1-3

1969 *Protognathodus meischneri* n.sp. Ziegler, p.353, Pl. 1, figs 1-13.

1973 *Protognathodus meischneri* Ziegler – Ziegler (in Ziegler), p. 421-422, *Schmidtognathus* Pl. 2, fig. 3.

1973 *Protognathodus meischneri* Ziegler – Szulczewski, p. 43, Pl. 2, fig. 8.

1976 *Protognathodus meischneri* Ziegler – Dreesen et al., Pl. 2, fig. 10.

1982 *Protognathodus meischneri* Ziegler – Higgins & Wagner-Gentis, Pl. 34, fig. 10.

1984 *Protognathodus meischneri* Ziegler – Hou et al., Pl. 4, fig. 9.

1984 *Protognathodus meischneri* Ziegler – Wang & Yin, Pl. 3, fig. 17.

1985 *Protognathodus meischneri* Ziegler – Austin et al., Pl. 4.9, fig. 14.

1987b *Protognathodus meischneri* Ziegler – Ji, Pl. 1, figs 1-2.

1988 *Protognathodus meischneri* Ziegler – Garcia Alcalde & Menendez-Alvarez, Pl. 1, fig. 8.

1988 *Protognathodus meischneri* Ziegler – Schönlaub et al., Pl. 4, figs 4.

1988 *Protognathodus meischneri* Ziegler – Wang & Yin, Pl. 22, figs 1-2 (only).

1990 *Protognathodus meischneri* Ziegler – Gagiev & Kononova, Pl. 3, figs 27-28.

1992 *Protognathodus meischneri* Ziegler – Over, fig.7.14.

1993 *Protognathodus meischneri* Ziegler – Nemirovskaya et al., Pl. 2, fig. 13.

1995 *Protognathodus meischneri* Ziegler – Chauffe & Nichols, Pl. 2, figs 27-28, 33, 36.

non 1997 *Protognathodus meischneri* Ziegler – Caridroit et al., Pl. 1, fig. 4.

1997 *Protognathodus kockeli* (Bischoff) – Dzik, fig. 8 C.

1999 *Protognathodus meischneri* Ziegler – Sanz Lopez et al., Pl. 1, fig. 15.

2003 *Protognathodus meischneri* Ziegler – Corradini et al., p. 235, pl. 4, fig. 4.

non 2004 *Prothognathodus meischneri* Ziegler – Bardasheva et al., Pl. 13, fig. 44.

Original diagnosis (Ziegler 1969 - German): A species of the genus *Protognathodus* with a generally symmetrical platform, whose surface has no ornamentation.

Remarks. *Pr. meischneri* differs from its ancestor *Bispathodus stabilis* for the more posterior position and greater expansion of the basal cavity; it is distinguished from all other species of *Protognathodus* by the absence of ornamentation on the upper surface of the cup.

Stratigraphic range. According to Ziegler & Sandberg (1984) *Pr. meischneri* first occurs at or near the base of the Lower *praesulcata* Zone; however, a single specimen (Pl. 1, fig. 2) have been found from the Upper *expansa* Zone in Sardinia (Corradini et al. 2003: tab. 2). The last occurrence is within the Upper *duplicata* Zone (Sandberg et al. 1978; Kaiser et al. 2009).

Protognathodus collinsoni Ziegler, 1969

Pl. 1, figs 4-8

1969 *Protognathodus collinsoni* n. sp. Ziegler, p. 353, Pl. 1, figs 14-18.

1973 *Protognathodus collinsoni* Ziegler – Ziegler (in Ziegler), p. 415-416, *Schmidtognathus* Pl. 2, fig. 4.

1973 *Protognathodus collinsoni* Ziegler – Szulczewski, p. 42, Pl. 2, figs 9-10.

1974 G*nathodus kockeli* Bischoff – Gedik, Pl. 7, fig. 6.

1980 *Protognathodus collinsoni* Ziegler – Ebner, Pl. 16, figs 3, 5.

1983 *Protognathodus collinsoni* Ziegler – Wang & Ziegler, Pl. 8, fig. 16.

1984 *Protognathodus collinsoni* Ziegler – Hou et al., Pl. 4, fig. 12.

1984 *Protognathodus meischneri* Ziegler – Wang & Yin, Pl. 3, fig. 16.

1984 *Protognathodus kockeli* (Bischoff) – Luppold et al., Pl. 4, fig. 1.

1985 *Protognathodus collinsoni* Ziegler –Austin et al., Pl. 4.8, fig. 20.

1987 *Protognathodus collinsoni* Ziegler – Kalvoda & Kukal, Pl. 4, fig. 4 (only).

1988 *Protognathodus collinsoni* Ziegler – Wang & Yin, Pl. 22, figs 5-6 (only).

1988 *Protognathodus kockeli* (Bischoff) – Wang & Yin, Pl. 22, figs 9, 13, 17.

1988 *Protognathodus collinsoni* Ziegler – Flajs & Feist, Pl. 9, fig. 6 (only).

1989 *Protognathodus collinsoni* Ziegler – Ji et al., p. 90-91, Pl. 18, fig. 8-9 (only).

1990 *Protognathodus kockeli* (Bischoff) – Gagiev & Kononova, Pl. 3, figs 29-30.

1990 *Protognathodus collinsoni* Ziegler – Gagiev & Kononova, Pl. 4, fig. 4.

1992 *Protognathodus collinsoni* Ziegler – Over, fig.7.15.

1992 *Protognathodus collinsoni* Ziegler – Ji & Ziegler, Pl. 3, fig. 22.

1993 *Protognathodus meischneri* Ziegler – Nemirovskaya et al., Pl. 2, fig. 20.

1995 *Protognathodus* cf. *collinsoni* Ziegler – Chauffe & Nichols, Pl. 2, figs 30, 31-32, 38.

1995 *Protognathodus kockeli* (Bischoff) – Chauffe & Nichols, Pl. 2, figs 35, 37.

1998 *Protognathodus collinsoni* Ziegler – Kalvoda & Kukal, Pl. 4, fig. 4.

2001 *Protognathodus collinsoni* Ziegler – Perri & Spalletta, Pl. 1, fig.4

2003 *Protognathodus collinsoni* Ziegler – Corradini et al., p. 235, Pl. 4, fig. 3.

2009 *Protognathodus collinsoni* Ziegler – Kaiser, Pl. 1, figs 1, 3.

Original diagnosis (Ziegler 1969 - German): A species of the genus *Protognathodus* with a weakly asymmetrical platform, which has single nodes on the surface. The nodes can be both on the right side and left side (outside or inside) of the carina.

Remarks. *Pr. collinsoni* is characterized by one or more nodes scattered on the cup, that can occur on one or both sides of the carina. A few specimens with the cup covered by nodes, identified as *Pr. kockeli*, should be referred to *Pr. collinsoni*, as the nodes are not arranged in a distinct row diagnostic of *Pr. kockeli*.

Stratigraphic range. From the lower part of the Lower *praesulcata* Zone (Ziegler & Sandberg 1984) to at least into the Upper *duplicata* Zone (Over 1992).

Protognathodus kockeli (Bischoff, 1957)

Pl. 1, figs 9-19

1957 *Gnathodus kockeli* n.sp. Bischoff, p. 25, Pl. 3, figs 27-32.

1959 G*nathodus kockeli* Bischoff - Voges, Pl. 33, p. 281-282, fig. 27 (only).

1967 *Gnathodus kockeli* Bischoff – van Adrichem Boogaert, p. 179, Pl. 2, figs 17-18.

non 1968 *Gnathodus kockeli* Bischoff – Manzoni, p. 659-660, Pl. 62, fig.2

1969 *Gnathodus kockeli* Bischoff – Ziegler, p.354, Pl. 1, figs.19-25; Pl. 2, figs 1-5.

1969 *Gnathodus kockeli* Bischoff – Schönlaub, p.330, Pl. 1, figs1-2.

1970 *Gnathodus kockeli* Bischoff – Ziegler & Leuteritz (in Koch et al.), Pl. 8, figs 1-3, 5.

1970 *Gnathodus kuehni* n. sp. – Ziegler & Leuteritz (in Koch et al.), Pl. 8, fig. 4.

1973 *Protognathodus kockeli* (Bischoff) – Ziegler (in Ziegler), p. 417-418, *Schmidtognathus* Pl. 2, fig. 5.

1973 *Protognathodus kockeli* (Bischoff) – Szulczewski, p. 44, Pl. 2, figs 11-13.

1974 *Gnathodus kockeli* Bischoff – Gedik, p. 13, Pl. 7, fig.5.

1980 *Protognathodus kockeli* (Bischoff) – Ebner, p. 16, figs 4, 6.

1980 *Protognathodus kockeli* (Bischoff) – Lane et al., pl. 3, fig. 1.

1984 *Protognathodus kockeli* (Bischoff) – Hou et al., Pl. 4, figs 10.

1984 *Protognathodus kockeli* (Bischoff) – Luppold et al., Pl. 4, fig. 2; Pl.6, fig. 4 (only).

1984 *Protognathodus kockeli* (Bischoff) – Wang & Yin, Pl. 3, fig. 15 (only).

1985 *Protognathodus kockeli* (Bischoff) – Austin et al., Pl. 4.9, figs 13.

1987 *Protognathodus kockeli* (Bischoff) – Kalvoda & Kukal, pl. 4, figs 2-3 (only).

1988 *Protognathodus kockeli* (Bischoff) – Garcia-Alcalde & Menendez-Alvarez, Pl. 1, fig. 7.

1988 *Protognathodus kockeli* (Bischoff) – Flajs & Feist, Pl. 9, figs 8-10.

1988 *Protognathodus collinsoni* Ziegler – Flajs & Feist, Pl. 9, fig. 7.

1988 *Protognathodus kockeli* (Bischoff) – Schönlaub et al., Pl. 4, figs 1-2, 5.

1988 *Protognathodus praedelicatus* Lane et al. – Schönlaub et al., Pl. 4, fig. 10.

1988 *Protognathodus kockeli* (Bischoff) – Weyant., Pl. 2, fig. 10.

1988 *Protognathodus kockeli* (Bischoff) – Wang & Yin, Pl. 22, figs 8, 10-11, 14-15 (only).

1988 *Protognathodus kuehni* Ziegler & Leuteritz – Wang & Yin, Pl. 22, fig. 19.

1989 *Protognathodus kockeli* (Bischoff) – Ji et al., p. 91, Pl. 18, figs 3-5 (only).

1989 *Protognathodus collinsoni* Ziegler – Ji et al., Pl. 18, fig. 7.

1989a *Protognathodus kockeli* (Bischoff) – Clausen et al., Pl. 5, figs 3, 5.

1990 *Protognathodus kockeli* (Bischoff) – Gagiev & Kononova, Pl. 4, figs 5-6.

1993 *Protognathodus kockeli* (Bischoff) – Nemirovskaya et al., Pl. 2, figs 15-16 (only).

1993 *Protognathodus kuehni* Ziegler & Leuteritz – Nemirovskaya et al., Pl. 2, fig. 19.

1992 *Protognathodus kockeli* (Bischoff) – Over, fig.7.16.

1994 *Protognathodus kockeli* (Bischoff) – Korn et al., Pl. 5, figs. 4-11; Pl. 7, figs 8, 10 (only).

? 1995 *Protognathodus kockeli* (Bischoff) – Chauffe & Nichols, Pl. 2, figs 29, 34.

1997 *Protognathodus kockeli* (Bischoff) – Chauffe & Guzman, Pl. 2, figs 7, 15.

1997 *Protognathodus kockeli* (Bischoff) – Dzik, fig. 8 A-B.

1999 *Protognathodus* cf. *kockeli* (Bischoff) – Sanz Lopez et al., Pl. 2, fig. 1.

2001 *Protognathodus kockeli* (Bischoff) – Perri & Spalletta, Pl. 1, fig. 5.

non 2000 *Protognathodus kockeli* (Bischoff) – Wang et al., Pl. 1, fig. 11.

2002 *Protognathodus kockeli* (Bischoff) – Buggisch & Michl, Pl. 4, fig. 125 (only).

2003 *Protognathodus kockeli* (Bischoff) – Corradini et al., p. 235, pl. 4, figs 1-2.

non 2006 *Protognathodus kockeli* (Bischoff) – Dzik, figs 116 M-N.

2008 *Protognathodus kockeli* (Bischoff) – Habibi et al., p. 772, figs 4.6.

2007 *Protognathodus kockeli-Prothognathodus kuehni* – Kaiser, Pl. 2, figs. 3, 5-6.

2009 *Protognathodus kockeli* (Bischoff) – Kaiser et al., Pl. 1, figs 10-11; Pl. 2, fig. 16.

2009 *Protognathodus kuehni* Ziegler & Leuteritz – Kaiser et al., Pl. 1, figs 8-9.

2009 *Protognathodus kockeli* (Bischoff) – Kaiser, Pl. 1, fig. 2.

Original diagnosis (Bischoff 1957 - German): A species of the genus *Gnathodus* [*Protognathodus*] with the following features: approximately a hemispherical platform with one or two lines of coarse nodes on the inner and outer side of the platform. The lines run parallel to the blade.

Emended diagnosis: A species of *Protognathodus* with a row of coarse nodes parallel to the carina on one or both sides of the cup.

Remarks. The coarse, nodose, ornamentation and the presence of at least one row of nodes parallel to the carina on one half of the cup characterizes *Pr. kockeli*; scattered unarranged nodes may occur on the other side of the cup. Some large specimens bear one row of nodes on both sides of the cup, sometimes together with other scattered nodes. Some specimens that bear unarranged coarse nodes on the cup have been referred to this species; however, these should be referred to *Pr. collinsoni*.

Transitional forms between *Pr. kockeli* and *Pr. kuehni* are well known (i.e.: Bischoff 1957: pl. 3, fig. 31; Voges 1959: pl. 33, fig. 26; Higgins et al. 1964: pl. 5, fig. 27; Kaiser 2007: pl. 2, fig. 4); these specimens have a more rounded cup than typical *Pr. kockeli* and bear nodes, sometimes transversally elongated.

Protognathodus kockeli is by far the most abundant and most widely documented species of *Protognathodus*. It has a wide geographic distribution, although in some regions only co-occurs with Lower Carboniferous faunas (see discussion in the next chapter).

Stratigraphic range. The species first appears in the latest Famennian and is the marker for the base of the Upper *praesulcata* Zone (Ziegler & Sandberg 1984). *Protognathodus kockeli* ranges at least up to the *sandbergi* Zone in Europe (Kaiser et al. 2009) and into the Lower *crenulata* Zone in North America (Sandberg et al. 1978).

Protognathodus kuehni Ziegler & Leuteritz, 1970

Pl. 1, figs 20-22

1962 *Gnathodus* n. sp. B Collinson et al., text-fig. 3.

1969 *Protognathodus* n. sp. A Ziegler p.355, Pl. 1, fig. 26.

1970 *Protognathodus kuehni* n.sp. Ziegler & Leuteritz (in Koch et al.), p.715, Pl. 8, figs 6-16.

non 1970 *Protognathodus kuehni* n.sp. Ziegler & Leuteritz (in Koch et al.), p.715, Pl. 8, fig. 4.

1973 *Protognathodus kuehni* Ziegler & Leuteritz – Ziegler (in Ziegler), p. 419-420, *Schmidtognathus* Pl. 2, fig. 6.

1984 *Protognathodus kuehni* Ziegler & Leuteritz – Wang & Yin, Pl. 3, fig. 13.

1984 *Protognathodus kockeli* → *kuehni* – Luppold et al., Pl. 4, fig. 3

1987 *Protognathodus kuehni* Ziegler & Leuteritz – Feist & Flajs, Pl. 2, fig. 1.

1988 *Protognathodus kuehni* Ziegler & Leuteritz – Flajs & Feist, Pl. 9, figs 11-12.

1988 *Protognathodus kuehni* Ziegler & Leuteritz – Schönlaub et al., Pl. 4, figs 3, 7.

1988 *Protognathodus kockeli-Prothognathodus kuehni* – Schönlaub et al., Pl. 4, fig. 6.

1988 *Protognathodus praedelicatus* Lane et al. – Schönlaub et al., Pl. 4, figs 8-9.

1990 *Protognathodus kuehni* Ziegler & Leuteritz – Gagiev & Kononova, Pl. 4, fig. 7.

1994 *Protognathodus kockeli* (Bischoff) – Korn et al., Pl. 7, fig. 9.

non 2000 *Protognathodus kuehni* Ziegler & Leuteritz – Wang et al., Pl. 1, fig. 10.

2007 *Protognathodus kuehni* Ziegler & Leuteritz – Kaiser, Pl. 2, figs 2, 7.

2009 *Protognathodus kuehni* Ziegler & Leuteritz – Kaiser et al., Pl. 2, fig. 15 (only).

Original diagnosis (Ziegler & Leuteritz in Koch et al. 1970 - German): A new species of the genus *Protognathodus* Ziegler [...] with a weak asymmetrical platform, whose surface has robust transverse ridges. These ridges run unordered from the edge radial to the carina. The carina can be, as some specimens reveal, suppressed.

Remarks. The occurrence of transverse ridges on the cup characterizes *Pr. kuehni* and distinguish it from other representatives of the genus. Transitional forms from *Pr. kockeli* are known: they bear both transverse ridges and nodes and have a more asymmetrical cup than *Pr. kuehni*.

In lateral view the carina does not rise above the ornamentation and in some specimens can be suppressed in the posterior part of the cup.

Protognathodus kuehni has a wide geographic distribution, documented in Europe, South China, Siberia and the central USA; however, outside Europe, it is very rare (see discussion in the next chapter).

Stratigraphic range. From the base of the *sulcata* Zone (Kaiser et al. 2009) or just below (Ziegler 1973) to within the *sandbergi* Zone (Lane et al. 1980).

Stratigraphic and geographic distribution

Representatives of genus *Protognathodus* are relatively widely distributed in uppermost Devonian-lowermost Carboniferous rocks around the world (Figs 2-3; Tab. 1). However, their abundance is often associated with peculiar environmental conditions. In deeper-water sediments the occurrence is very irregular and often the different species first occur together, or not in stratigraphic order. In several localities they have been reported only from a higher part of their stratigraphic range (see below for examples and discussion).

In North America "the major habitat of the *Protognathodus* fauna was in nearshore or lagoonal settings where non-argillaceous microbial or algal micrite was deposited" (C. Sandberg, pers. comm. March 30, 2010), and thus *Protognathodus* was regarded as a shallow-water genus. In the Woodford Shale in Oklahoma, occurs in association with offshore taxa. In southern Europe *Protognathodus* is thought to reflect depositional settings at the continental rise and lower slope due to the microfacies characteristics (Kaiser 2005) . More data from different palaeogeographic settings, however, are needed for a more complete evaluation. The standard biofacies model favored by Sandberg (1976) and Ziegler & Sandberg (1984), especially the assessment of the protognathodid biofacies as an indicator of a shallowing, has to be reconsidered (see discussions in Kaiser et al. 2008). More likely, the occurrence of the *Protognathodus* fauna can be related to biotic opportunism during a rise in sea level in the latest Devonian, as evidenced in many sections in the Rheinisches Schiefergebirge.

In the base of the Carboniferous GSSP at La Serre Trench E', representatives of the genus *Protognathodus* are rare in boundary beds and their presence is not regular throughout the section. *Protognathodus kuehni* is reported only in the topmost part of the section (Flajs & Feist 1988; Kaiser 2005, 2009) where the *Protognathodus* fauna is abundant. In the same region, but in a different tectonic unit, in the Puech de la Suque section (Kaiser et al. 2009), *Pr. kockeli* enters just above the Hangenberg Shale equivalent, slightly before the joint first occurrence of *Pr. meischneri* and *Pr. collinsoni*. A single specimen of *Pr. kuehni* has been found higher in the section, together with *Si. quadruplicata* (Kaiser et al. 2009: tab. 6).

Similar late first occurrences of *Pr. kuehni*, and often also of *Pr. kockeli*, are well documented in various geographic areas: Poland (Szulczewski 1973; Dzik 1997), Cantabrian Mountains (Higgins & Wagner-Gentis 1982; Garcia-Alcalde & Menendez-Alvarez 1988), Sardinia (Corradini et al. 2003; Corradini 2008) and Algeria (Weyant 1988); in the western United States no protognathodids have been found in the Devonian (C. Sandberg, pers. comm.).

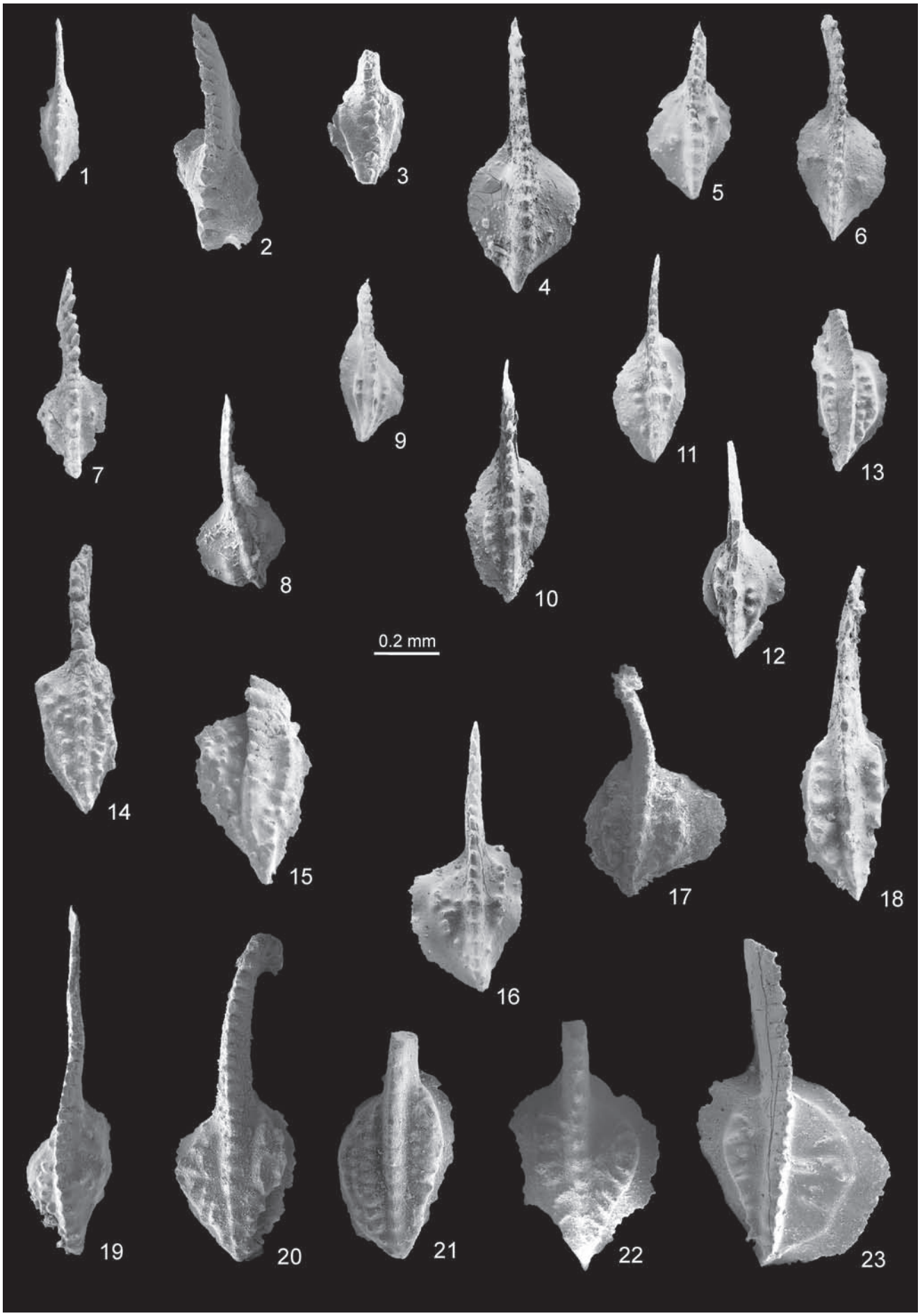
PLATE 1

Figs 1-3 *Protognathodus meischneri* Ziegler, 1969
1) IC P139 966502; Sentiero per Cresta Verde section, Carnic Alps, sample SCV 4;
2) DSTC 30116; Monte Taccu North B section, Sardinia, sample MT Z;
3) IPUM 27648; Monte Taccu North B section, Sardinia sample MT 2A.

Figs. 4-8 *Protognathodus collinsoni* Ziegler, 1969
4) IC P149 966564; Plan di Zermula C section, Carnic Alps, sample PZC 1;
5) IC P149 966569; Plan di Zermula C section, Carnic Alps, sample PZC 1;
6) IC P149 966565; Chiarsò area, Carnic Alps, sample CHRB;
7) IPUM 27647; Monte Taccu North A section, Sardinia sample MT X;
8) SMNS 67400; La Serre Trench E' section, Montagne Noire, sample 70.

Figs 9-21 *Protognathodus kockeli* (Bischoff, 1957)
9) IC P150 966570; Plan di Zermula C section, Carnic Alps, sample PZC 4;
10) IC P190 212112; Plan di Zermula A section, Carnic Alps, sample PZA 2aI;
11) IC P149 966567; Plan di Zermula C section, Carnic Alps, sample PZC 4;
12) IC P174 967133; Passo di Monte Croce Carnico section, Carnic Alps, sample PMC 1;
13) IC P139 966503; Sentiero per Cresta Verde section, Carnic Alps, sample SCV 4;
14) IPUM 27646; Monte Taccu North B section, Sardinia sample MT 1A;
15) IPUM 27645; Monte Taccu North A section, Sardinia sample MT X;
16) IC P149 966568; Chiarsò area, Carnic Alps, sample CHRB;
17) SMNS 67375; Trolp section, Graz Palaeozoic, sample 16;
18) IC P149 966566; Plan di Zermula C section, Carnic Alps, sample PZC 1;
19) DSTC 30117; Monte Taccu North A section, Sardinia sample MT X;
20) SMNS 67374; Trolp section, Graz Palaeozoic, sample 16;
21) SMNS 67401; Puech de la Suque section, Montagne Noire, sample PS 16.

Figs 22-23 *Protognathodus kuehni* Ziegler & Leuteritz, 1970
22) SMNS 67400a; Milles section, French Pyrenees, sample Mi 9 top.
23) SMNS 67710; Grüne Schneid section, Carnic Alps, sample GS 6c2.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In the French Pyrenees, at Milles (Cygan & Perret 1998; Kaiser et al. 2009) abundant protognathodids (mainly *Pr. kockeli*) enter at the base of bed 9, just above a siliciclastic bed interpreted as an equivalent of the Hangenberg Black Shale (Kaiser et al. 2009). Here two specimens of *Pr. kuehni* occur only in the upper part of this bed (Kaiser et al. 2009: tab. 7), representing less than 1% of the whole association. In other sections in the same area (e.g., Pont de Saubette and Moustarde) *Pr. meischneri*, *Pr. collinsoni* and *Pr. kockeli* have their first occurrence all together, and *Pr. kuehni* is not reported (Perret 1988); finally, in the Garcet section (Perret Mirouse & Majesté-Menjoulas 1998), where the DCB is located in a continuous calcareous section with a good recording of *Siphonodella*, no *Protognathodus* have been found across the boundary.

In the Carnic Alps, the Grüne Schneid section exposes a continuous condensed calcareous sequence across the boundary (Schönlaub et al. 1988, 1992; Kaiser et al. 2006). *Protognathodus meischneri* and *Pr. collinsoni* enter in association and are followed, in sequence, by *Pr. kockeli* and *Pr. kuehni* (Kaiser 2007). The latter species is documented only by two certain and five questionable specimens from four samples collected in a 15 cm thick interval and represents about 1% of the association (Kaiser 2005: 118), while *Pr. kockeli*, *Pr. meischneri* and *Pr. collinsoni* are quite abundant in some beds.

In the Kronhofgraben (Schönlaub et al. 1992; Kaiser 2005) and Plan di Zermula A sections (Perri & Spalletta 2001; Kaiser 2005; Kaiser et al. 2009), where the equivalents of the Hangenberg Black Shale, corresponding to the Middle *praesulcata* Zone, are present, no protognathodids were recorded below the shales and *Pr. kuehni* is very rare in only one level, a few centimetres below the first occurrence of *Si. duplicata*. In both sections *Pr. kockeli* enters just above the equivalents of the Hangenberg Black Shale, together with *Si. sulcata*.

In the Rheinisches Schiefergebirge, the type area of the *Protognathodus* fauna of Ziegler (1969), several sections spanning the DCB have been studied and documented (i.e. Clausen et al. 1987, 1989b; Korn et al. 1984; Kaiser 2005 and references therein). Protognathodids are always present, but in many sections they are very rare and their occurrence is limited to a few beds. The only sections in which protognathodids are abundant (e.g., Seiler- Schurf III and Schurf 0, Clausen et al. 1989b) are characterized by much more shaley sedimentation. This is even more evident if we consider the occurrences and abundance of *Pr. kuehni*, which in most sections is represented only by one or two specimens from samples slightly below the entry of *Si. duplicata*, whereas it is abundant only in the Seiler-Schurf III section (Clausen et al. 1989b).

In the Nanbiancun II section, Guangxi, South China (Ji et al. 1989; Wang 1995; Wang & Yin 1988) *Pr. kockeli* first occurs in bed 52 (*sulcata* Zone after Ji

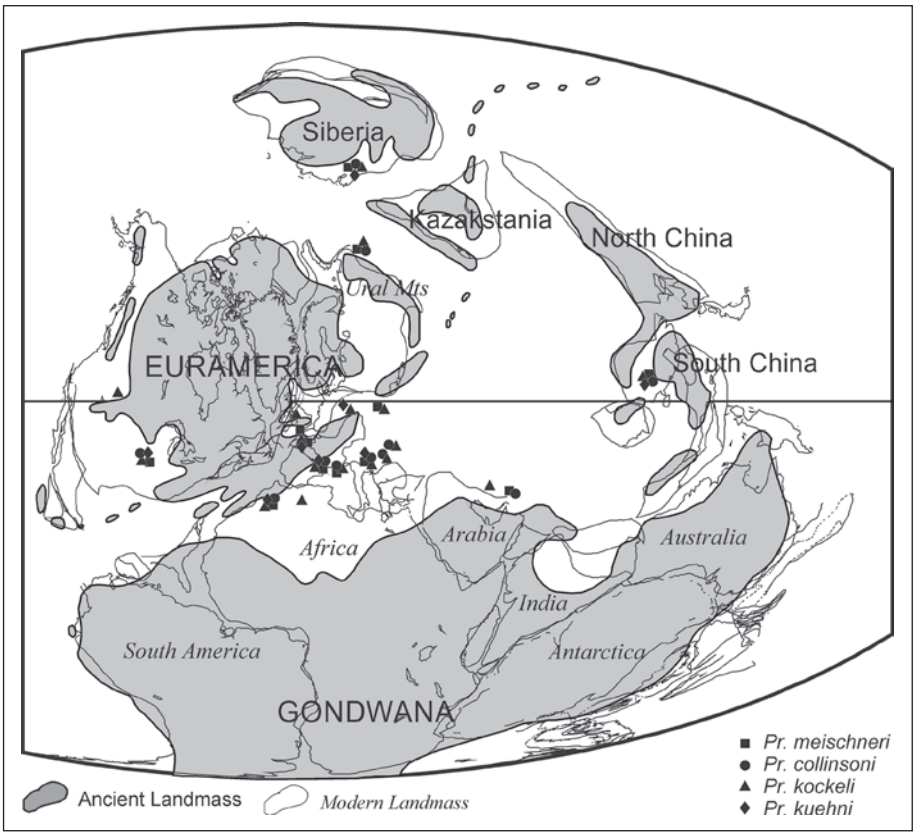

Fig. 2 - Geographic distribution of *Protognathodus* species. Palaeogeographic map redrawn after Scotese (2001).

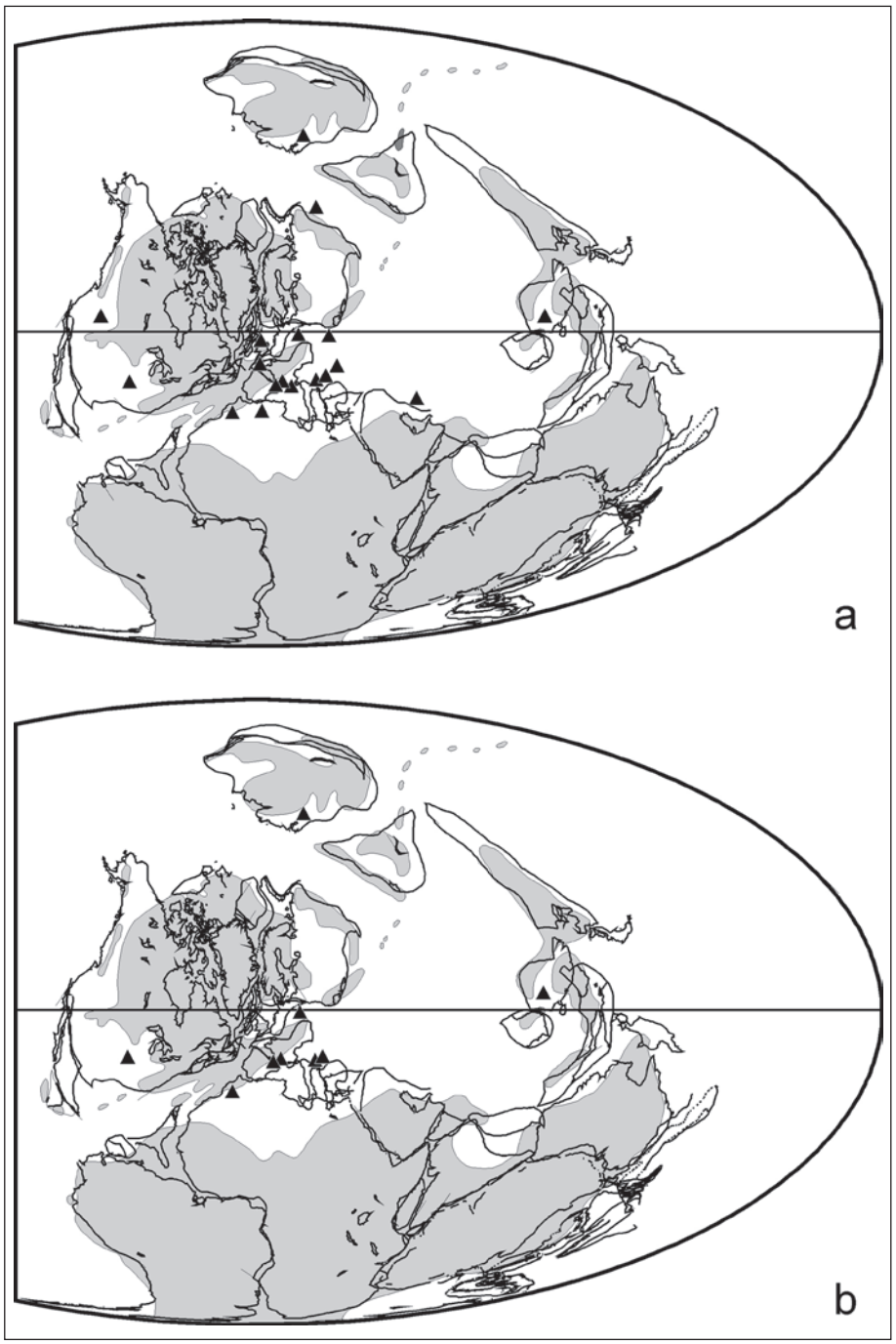

Fig. 3 - Geographic distribution of *Pr. kockeli*. a) Carboniferous occurrences; b) Devonian occurrences.

et al. 1989; Upper *praesulcata* Zone after Wang 1995), whereas *Pr. meischneri* only enters in bed 54 (Lower *duplicata* Zone after Ji et al. 1989; Upper *praesulcata* Zone after Wang 1995). *Protognathodus kuehni* has a single occurrence in bed 56 (Lower *duplicata* Zone after Ji et al. 1989; basal *sulcata* Zone after Wang 1995), but this finding should be confirmed, since the only specimen figured as *Pr. kuehni* actually belongs to *Pr. kockeli*. In levels across the DCB in the Nanbiancun II section, protognathodids are uncommon, representing only 3-7% of the fauna (Wang & Yin 1988: 109), and from the seven sections spanning the boundary in the Nanbiancun area, *Pr. kuehni* is reported only from Nanbiancun II.

In the Muhua section, Guizhou, South China, all four species of *Protognathodus* have been found together in a "grey dense limestone" lens (Wang & Yin 1984: 233), immediately below the first occurrence of *Si. sulcata*. According to Ji et al. (1989), the species occur in different levels: *Pr. meischneri* first occurs in level 21-1 (Middle *praesulcata* Zone), *Pr. collinsoni* in level 21-2 (Upper *praesulcata* Zone), *Pr. kockeli* in level 22-1 (Upper *praesulcata* Zone), and *Pr. kuehni* in level Bed 22-2 (Upper *praesulcata* Zone).

In Dapoushang section, Guizhou, South China (Ji et al. 1989) protognathodids occur in limestone beds from the Lower *praesulcata* Zone to the Lower *duplicata* Zone, but it is difficult to consider these data

		FIGURED				NOT FIGURED			
		Pr. meischneri	*Pr. collinsoni*	*Pr. kockeli*	*Pr. kuehni*	*Pr. meischneri*	*Pr. collinsoni*	*Pr. kockeli*	*Pr. kuehni*
North Gondwana									
Bechar – Algeria (Famennian–Tournaisian)	(Weyant 1988)			T					
Cantabrian Mt – Spain (Famennian–Tournaisian)	(van Adrichem Boogaert 1967)			T					
Cantabrian Mt – Spain (Famennian–Tournaisian)	(Garcia Alcalde & Menendez Alvarez 1988)	T		T					
Cantabrian Mt – Spain (Tournaisian)	(Higgins & Wagner Gentis 1982)	T						T	T
Cantabrian Mt – Spain (Famennian–Tournaisian)	(Sanz Lopez et al. 1999)	F		F		T	F		
Czech Republic (Famennian–Tournaisian)	(Kalvoda & Kukal 1987)		T	T		F	F	F	F–T
Graz – Austria (Famennian–Tournaisian)	(Ebner 1980)		F	F		F–T	T	T	
Iran - Alborz Mts. (Famennian–Tournaisian)	(Habibi et al. 2008)			T					
Iran -Tabas (Famennian–Tournaisian)	(Bahrami et al. in prep. - pers. com.)	T	T						
Montagne Noire - France (Famennian–Tournaisian)	(Feist & Flajs 1987)				T	F–T	F–T	T	
Montagne Noire - France (Famennian–Tournaisian)	(Flajs & Feist 1988)		T	T	T	F	F	F	
Montagne Noire - France (Famennian–Tournaisian)	(Kaiser et al. 2009)	F–T		T	T		F	F	
Pyrenees - France (Famennian–Tournaisian)	(Perret 1988)					F	F–T	F–T	
Sardinia (Famennian–Tournaisian)	(Corradini et al. 2003)	F–T		T	T	T			
Southern Alps (Famennian–Tournaisian)	(Gedik 1974)			T					
Southern Alps (Famennian–Tournaisian)	(Kaiser 2007)			F–T	T	F–T	T		
Southern Alps (Famennian–Tournaisian)	(Perri & Spalletta 2001)		T	T		T			
Southern Alps (Famennian–Tournaisian)	(Schönlaub 1969)			T		? T			
Southern Alps (Famennian–Tournaisian)	(Schönlaub et al. 1988)	F		F–T	F				
Laurussia									
Ardennes – Belgium (Famennian)	(Dreesen et al. 1976)	F				F		F	
Germany (Tournaisian)	(Buggisch & Michl 2002)			T		T		T	
Germany (Famennian–Tournaisian)	(Clausen et al. 1989a)			F				T	T
Germany (Famennian–Tournaisian)	(Clausen et al. 1989b)					F–T		F–T	T
Germany (Famennian–Tournaisian)	(Kaiser et al. 2009)			T	T	F-T	F-T	F	
Germany (Famennian–Tournaisian)	(Korn et al. 1994)			F–T					
Germany (Famennian–Tournaisian)	(Luppold et al. 1984)		T	T	T	T			
Germany (Tournaisian–Visean)	(Voges 1959)			T					
Germany (Famennian)	(Ziegler 1969)	F	F	F	F				
Germany (Famennian–Tournaisian)	(Ziegler & Leuteritz in Koch et al. 1970)			X	T	F–T	F–T	F–T	
Great Britain (Famennian)	(Austin et al. 1985)	F	F	F					
Holy Cross Mt. – Polonia (Famennian–Tournaisian)	(Szulczewski 1973)	X	X	X					
Polonia (Tournaisian)	(Dzik 1997)		T	T					
Polar Ural Russia (Famennian–Tournaisian)	(Nemiroskaya et al. 1993)	T	T	T		F		F	
USA – Illinois (Tournaisian)	(Collinson et al. 1962)				T				
USA – Midcontinent (Famennian)	(Chauffe & Nichols 1995)	F	F	F					
USA – Missouri and Illinois (Tournaisian)	(Chauffe & Guzman 1997)			T					
USA – Oklahoma (Famennian–Tournaisian)	(Over 1992)	T	T	F		F	F	T	
USA – Wyoming (Tournaisian)	(Lane et al 1980)			T					
Omolon Block Far East Russia									
NE Siberia (Famennian–Tournaisian)	(Gagiev & Kononova 1990)	F	F–T	T	T	T		F	
Tajikistan									
Tajikistan (Tournaisian)	(Bardasheva et al. 2004)						T	T	
South China									
Guangxi - China (Famennian)	(Wang & Ziegler 1983)	F	F						
Guilin – China (Famennian–Tournaisian)	(Wang & Yin 1988)	F	F	F–T					
Guizhou - China (Famennian–Tournaisian)	(Hou et al. 1984)		T	T		T	F	F	
Guizhou - China (Famennian–Tournaisian)	(Ji et al. 1989)	F	F–T	F		F			F
Guizhou - China (Famennian–Tournaisian)	(Wang & Yin 1984)	T	F	F	F				
Jianghua – China (Tournaisian)	(Ji 1987b)	T							

Tab. 1 - Localities and relevant literature for reports of Late Devonian/Early Carboniferous protognathodids. Data are grouped in two lists concerning figured and not figured elements. F: Famennian, T: Tournaisian; X: finding in neptunian dykes.

because of inconsistence between text and figures (i.e. page 31-34, 90-91; text figs 6-7; pl. 18). The protognathodids are relatively abundant in the limestone beds just above the equivalent of the Hangenberg Black Shale (Bed E), but the abundance drastically decreases at the base of the *sulcata* Zone (Ji et al. 1989: fig. 7)

No protognathodids have so far been found in Australia (J.A. Talent, pers. comm.).

Conclusion

1. The original diagnoses (in German) of the four early species of *Protognathodus* are clear. A translation in English was provided very soon after they were established (Ziegler 1973). The great majority of the specimens of *Protognathodus* can be easily assigned and only a few transitional specimens are known,

mainly in the upper part of the lineage (*Pr. kockeli-Pr. kuehni*). The diagnosis of *Pr. kockeli* is slightly amended to include specimens, actually rare in collections, with one single row of nodes on only one side of the cup. Some authors seem to have applied a very personal taxonomic approach in the attribution of specimens to the four species, often made on the basis of criteria clearly in contrast with the diagnoses (cf.: Wang & Yin 1988; Chauffe & Nichols 1995).

2. In North America *Protognathodus* is often abundant in shallow water environments. In southern Europe the occurrence of *Protognathodus* is thought to reflect depositional settings at the continental rise and lower slope related to biotic opportunisms. More data from different palaeogeographic settings, however, are needed for a more complete evaluation; the standard biofacies model needs to be assessed.

3. Protognathodids are rare in the great majority of Devonian/Carboniferous boundary sections where they comprise a minor component of the conodont association; while *Pr. kuehni* is very rare (often <1%), *Pr. kockeli* is relatively abundant. Only in a few sections, mainly in the type area, *Protognathodus* species have a local range corresponding to their known global stratigraphic distribution, whereas often they have a very restricted stratigraphic distribution. in some sections, the different species of the genus have a coincident first occurrence, or evolutionary younger forms enter below their evolutionary ancestors.

4. Outside central-southern Europe *Protognathodus* is quite rare, and in some geographic areas such as in Australia, completely absent, or enters only in the Carboniferous, often together with *Si. duplicata* (i.e.: western USA).

5. *Pr. kockeli* is the most abundant and widely documented species of *Protognathodus*, used as the marker of the Upper *praesulcata* Zone (= *kockeli* Zone after Kaiser et al. 2009, the last Devonian biozone). It has a wide geographic distribution, but in many regions it occurs only in the Carboniferous (Fig. 3).

6. *Protognathodus kuehni* is, in general, an extremely rare taxon, with a restricted range in many sections, and, outside the type area, it often occurs only in higher stratigraphic levels. As pointed out by Alberti et al. (1974: 272) recoveries are irregular, even in the type area: "whether the *Pr. kuehni* is found depends on sample quantity and some luck: sample 1008-330 yielded one specimen of each of the four species of *Protognathodus*, while in sample 1008-294 [same bed] among 170 *Protognathodus* specimens no *Pr. kuehni* was found."

In conclusion, *Protognathodus* can be of help in stratigraphic works across the Devonian/Carboniferous boundary, but its potential as a tool for defining the DCB is low, and a decision should consider the rarity, at least of *Pr. kuehni*, *Pr. collinsoni* and *Pr. meischneri*, and the restricted stratigraphic ranges of the taxa.

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