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 Sphenodella sulcata. Due to difficulties in identification of the early siphonodellids, such as S. prae sulcata 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, Protognathodus 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.

Introduction

The base of the Carboniferous System is defined by the First Appearance Datum (FAD) of the conodont species Sphenodella sulcata, within the S. prae sulcata-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. prae sulcata 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. prae sulcata from S. sulcata arose quite immediately (e.g., Ji 1987a; Flajs & Feist 1988; Wang & Yin 1988). A redefineation of the Devonian/Carboniferous boundary (DCB) was reputed nec-

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Phylogeny and stratigraphy of the early Protognathodus

Genus Protognathodus comprises six species: Pr. meischneri Ziegler, Pr. collinsoni Ziegler, Pr. kockeli (Bischoff), Pr. kuebni 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. kuebni, occur in the uppermost Famennian and lower Tournaissian; in these species the anterior margins of the cup are opposed. A late group, ranging in upper Tournaissian, 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
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 kuebni* 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. kuebni*. 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 semembrane by Chauffe & Nichols (1998). 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


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, fig. 14.


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


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


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.

2004 *Protognathodus 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


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


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, fig. 20.

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

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


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 kockeli* (Bischoff) – Chaufte & Nichols, Pl. 2, figs 35, 37.

1998 *Protognathodus collinsoni* Ziegler – Kalvoda & Kulak, 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 *Gnathodus kockeli* Bischoff – Voges, Pl. 33, p. 281-282, fig. 27 (only).


1968 *Gnathodus kockeli* Bischoff – Manzoni, p. 659-662, Pl. 62, fig.2

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


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.


1992 *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).


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).
Protognathodus (Conodonta) and its potential as a tool for defining the Devonian/Carboniferous boundary

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 Gnatobodus n. sp. B Collinson et al., text-fig. 3.
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.
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 kockeli-Protognathodus kuehni – Schönlaub et al., Pl. 4, fig. 6.
1988 Protognathodus praedelaticus 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.
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 [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 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 protognathodids 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 kuebni* 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 Puch 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. kuebni* has been found higher in the section, together with *St. quadruplicata* (Kaiser et al. 2009: tab. 6).

Similar late first occurrences of *Pr. kuebni*, 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.).

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**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 966565; Plan di Zermula C section, Carnic Alps, sample PZC 1;
6) IC P149 966566; Chiaro 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 2a;
11) IC P149 966567; Plan di Zermula C section, Carnic Alps, sample PZC 4;
12) IC P1/74 967133; Passo di Monte Croce Carnico section, Carnic Alps, sample PMC 1;
13) IC P139 966523; Sentiero per Cresta Verde section, Carnic Alps, sample SCV 4;
14) IPUM 27646; Monte Taccu North B section, Sardinia sample MT 1A;
15) IPUM 27648; Monte Taccu North A section, Sardinia sample MT X;
16) IC P149 966568; Chiaro area, Carnic Alps, sample CHRB;
17) SMNS 67375; Trolp section, Graiz 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, Graiz Palaeozoic, sample 16;
21) SMNS 67451; Puech de la Suque section, Montagne Noire, sample PS 16.

Figs 22-23 *Protognathodus kuebni* Ziegler & Leuteritz, 1970

22) SMNS 6740a; Milles section, French Pyrenees, sample Mi 9 top;
23) SMNS 67170; Grüne Schneid section, Carnic Alps, sample GS 6c2.
Protognathodus (Conodonta) and its potential as a tool for defining the Devonian/Carboniferous boundary
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. kuebni* 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. kuebni* 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. kuebni* (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. kuebni* 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. kuebni*, 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

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**Fig. 2** - Geographic distribution of *Protognathodus* species. Palaeogeographic map redrawn after Scotese (2001).
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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...
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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 *Prognathodus* are clear. A translation in English was provided very soon after they were established (Ziegler 1973). The great majority of the specimens of *Prognathodus* 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 opportunism. 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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