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TAXONOMY AND EVOLUTIONARY SIGNIFICANCE OF SOME *GNATHODUS* SPECIES (CONODONTS) FROM THE MISSISSIPPIAN OF THE NORTHERN IBERIAN PENINSULA

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Abstract

A new species of *Gnathodus*, *G. joseramoni*, is defined and *Gnathodus cantabricus* Belka & Lehmann is revised from the study of some new conodont associations and analysis of previous data from the Cantabrian Mountains and the Pyrenees, North Iberian Peninsula. *G. cantabricus* is regarded as a junior synonym of *Gnathodus kiensis* Pazukhin from the Urals. Other occasional European findings of both taxa are indicated and stratigraphic middle Viséan to Arnsbergian ranges are established. Finally, the phylogenetic relations with other *Gnathodus* species are also outlined.

Key words: Conodont, Systematic Palaeontology, Mississippian, Cantabrian Mountains, Pyrenees.

Resumen

Se define una especie nueva de *Gnathodus*, *G. joseramoni*, y se revisa a *Gnathodus cantabricus* Belka & Lehmann, a partir de nuevas asociaciones de conodontos y el análisis de los datos previos en la Cordillera Cantábrica y los Pirineos, Norte de la Península Ibérica. *G. cantabricus* se considera un taxón sinónimo más moderno que *Gnathodus kiensis* Pazukhin de los Urales. Se indican otros hallazgos ocasionales en Europa de ambas especies y se establece su distribución estratigráfica entre el Vísense medio y el Arnsbergiense. Finalmente, se trazan las relaciones filogenéticas con otras especies de *Gnathodus*.

Palabras clave: Conodonto, Paleontología sistemática, Misisípico, Cordillera Cantábrica, Pirineos.

INTRODUCTION

Gnathodus species are widely distributed in deep-water successions of the Mississippian age. Many species of this genus are used as indicators of the early Carboniferous standard conodont zones and, consequently, many papers focus on *Gnathodus*. Important studies on this genus have been carried out in the Cantabrian Mountains (Budinger, 1965; Adrichem Boogaert, 1967; Higgins & Wagner-Gentis, 1982; Park, 1983; Menéndez-Álvarez, 1991, unpublished) and the Pyrenees (Perret, 1993; Sanz-López, 1995, unpublished), in the northern part of the Iberian Peninsula.

Recently, *Gnathodus cantabricus* Belka & Lehmann (1998) was proposed as an upper Viséan species from the Cantabrian Mountains (Spain) and Styria (Austria). It was a minor component in studied conodont samples (less than five per cent of the total elements). Previously, Pazukhin, (in Kulagina *et al.* 1992) described a Serpukhovian species (*Gnathodus kiensis*) from the South Urals that is very close to *G. cantabricus*. Other materials recently assigned to *G. cantabricus* from the middle Viséan of the Cantabrian Mountains and the eastern Catalonian Pyrenees (García-López & Sanz-López, 2002b; Sanz-López, 1995, 2002) are also of interest because they constitute between twenty and forty per cent of total elements collected. Study and comparison of this Spanish material can play an important role providing a new background for discussing the status, biostratigraphic significance, and phylogenetic relationships of "*Gnathodus cantabricus*".

GEOLOGICAL SETTING

The Cantabrian Zone and the Pyrenees are included in the south-western part of the European Variscan orogen. Both areas constitute foreland thrust and fold belts; the first is situated in the north of the Iberian Massif, and the latter lies outside this massif and is surrounded by Mesozoic and Tertiary cover (Fig. 1). A sedimentary high or block, the Cantabro-Ebroian massif (Carls, 1983), was located between the Cantabrian Zone and the Pyrenees in the Devonian, although marine rocks covered the massif from the uppermost Devonian up to the Carboniferous.

In the Cantabrian Zone, nodular cephalopod limestones of the Alba Formation (Comte, 1959) were deposited from upper Tournaisian to Serpukhovian. The Alba Fm. is 20-30 m thick and has yielded rich and diverse conodont associations. Most of the samples studied here (Fig. 1, Tabl. 1) come from the Fold and Nappe province (Julivert, 1971) of the Cantabrian Zone and were collected in the middle part of the Alba Fm. (Carranques, Millaró, Fig. 2, and Olleros de Alba sections, in García-López & Sanz-López, 2002a, b). Additional samples studied in this paper belong to the Dr. Menéndez-Álvarez's collection, deposited in the Department of Geology of the University of Oviedo (samples J-13 and J-5, from the

Entrago section; J-53 and J-54, from the El Portillín section.). Two other samples come from the Picos de Europa unit (Julivert, 1971): CPE-13, from the Cares River section (Blanco-Ferrera *et al*., in press); and CPE-30, collected south of the Sotres village, in the River Duje valley (Blanco-Ferrera, 2002).

Rocks similar in facies, thickness and age to the Alba Fm. are known as the Aspe-Brousset Formation in the Pyrenees (Perret, 1993). A sample studied here, Co42, comes from the eastern Pyrenees and was collected at the comes de Das section, in the Cadí Alpine nappe (Sanz-López, 1995; 2002).

REFERENCES TO *GNATHODUS CANTABRICUS* IN THE CANTABRIAN MOUNTAINS

Higgins (1962) and Budinger (1965) studied middle Viséan conodont associations containing *Gnathodus bilineatus* (Roundy), together with forms that these authors assigned to the Tournaisian species *G. delicatus* Branson and Mehl. Adrichem Boogaert (1967) continued to find these young occurrences of *G. delicatus* and included these Cantabrian associations in his *G. bilineatus*-*G. delicatus* s.l. Zone. However, Higgins (1974) considered those "*G. delicatus*" elements as a new subspecies of *G. bilineatus* (not described), which according to this author would range from the *G. bilineatus* Zone to his lower "unit" of the *L. nodosa* Zone (middle-upper Viséan). Higgins & Wagner-Gentis (1982) chose to include these forms in the variability of *G. bilineatus bilineatus*.

Menéndez-Alvarez (1991, unpublished) collected these "*G. delicatus*" elements from several Cantabrian sections and considered these forms (together with a younger morphotype) to belong to a new species. Earlier, Park (1983) described *Gnathodus* sp. A from the Santa Olaja de la Varga section. This potential new species was based on elements that only correspond to part of the variation included in the Menéndez-Alvarez's species. Belka & Lehmann (1998), from the upper Viséan to Serpukhovian strata of the Santa Olaja de la Varga section, formally described Park's morphotype as *Gnathodus cantabricus*.

SYSTEMATIC PALAEONTOLOGY

The systematic study is only based upon Pa elements, in spite of the multielement reconstruction preferred by conodont taxonomy. A great deal of information is contained in Pa elements at the specific level and the traditional practice is always based on them, while Pb, M and other elements are used for genera or subgenera assignment, which is not the aim of this paper. The terminology applied is shown in Fig. 3. The conodonts referred to are stored in the collections of the Department of Geology of the University of Oviedo.

Genus *Gnathodus* Pander, 1856

Polygnathus bilineatus Roundy, 1926

Gnathodus joseramoni n. sp.
(Pl. 1, Figs. 3-16; Pl. 2, figs. 5-12; Text-Fig. 4.5-4.14)

± 1959 *Gnathodus delicatus* Branson & Mehl.- Voges, p. 283, Pl. 33, Fig. 33 (only).
1962 *Gnathodus bilineatus* (Roundy).- Higgins, Pl. 3, Fig. 32.
1965 *G. delicatus* Branson & Mehl.- Budinger, Pl. 2, Fig. 11 (only).
1967 *G. delicatus* Branson & Mehl.- Adrichem Boogaert, Pl. 2, Fig. 15 (only).
1970 *G. bilineatus* (Roundy).- Marks & Wensink, p. 258, Pl. 2, Figs. 9a, b, 11a and b (only).
1974 *Gnathodus* sp. indet.- Mathews & Thomas, p. 384, Pl. 51, Figs. 1-3, 18? and 19.
± 1977 *Gnathodus* sp. A.- Ebner, p. 471, Pl. 2, Figs. 5 and 7, 8-10? and 13?.
1982 *G. bilineatus bilineatus* (Roundy).- Higgins & Wagner-Gentis, pp. 328-329, Pl. 34, Fig. 3 (only).
1983 *Gnathodus semiglaber* Bischoff.- Park, Pl. 2, Fig. 13 (only).
1983 *Gnathodus* n. sp. A Ebner, 1977.- Park, pp. 84-85, Pl. 3, Figs. 1, 2, 3?, 4 and 5.
1991 *Gnathodus cantabricus* n. sp.- Menéndez Álvarez, pp. 169-171 (part).
1993 Intermediate form between *G. semiglaber* and *G. praebilineatus*.- Perret, Pl. CX, Fig. 3 (only; also illustrated by Perret *et al.*, 1994, Pl. 3, Fig. 18).
1993 *G. b. bilineatus* (Roundy) – (early representatives).- Schönlaub & Kreutzer, Pl. 6, Fig. 14 (only; non Fig. 13= *G. praebilineatus*).
1993 *Gnathodus praebilineatus* Belka .- Schönlaub & Kreutzer, p. 256, Pl. 6, Figs. 7-11.
1993 *G. semiglaber* Bischoff.- Schönlaub & Kreutzer, Pl. 5, Fig. 17 (only).
v 1995 *G. praebilineatus* Belka.- Sanz-López, Pl. 57, Fig. 12 (only).
v 1995 *G. cantabricus* Menéndez Álvarez.- Sanz-López, Pl. 57, Fig. 13.
1996 *G. bilineatus* (Roundy).- Rodríguez Cañero & Guerra-Merchán, p. 244, Pl. 1, figs. 3-4 and 8 (only).
1999 *G. delicatus* Branson & Mehl transitional to *G. praebilineatus* Belka.- Meischner & Nemyrovska, Pl. 1, Fig. 11 (only).
v 2002b *G. cantabricus* Belka.- García-López & Sanz-López, pp. 182-183, Pl. 4, Fig. 10.
v 2002 *G. cantabricus* Belka & Lehmann.- Sanz-López, Tabl. 2.
2003 *G. bilineatus* (Roundy).- Groves, Larghi, Nicora & Rettori, Fig. 3, 2a-c? and 4a-c (only).

Holotype.-A Pa element DPO 15.010 (Pl. 2, Fig. 8, illustrated previously as *Gnathodus cantabricus* Belka by García-López & Sanz-López, 2002b, Pl. 4, Fig. 10); paratypes DPO 15011-DPO 15014.

Type bed.-Bed of sample MILL-5, upper part of the *G. praebilineatus* Zone (Viséan), in the Canalón Member of the Alba Formation in the Millaró section (Fig. 2), Bernesga Valley, León province.

Material.-About 400 Pa elements, 60 elements from the eastern Pyrenees, sample Co42 (DPO 15.030-DPO 15.035) and the others from the Cantabrian Mountains: 25 elements from sample MILL-4 (DPO 15.004-DPO 15.007, Millaró section), about 200 elements from sample MILL-5 (DPO 15.010-DPO 15.015, Millaró section), 115 elements (many immature elements) from sample CPE-30 (Duje River, DPO 15.020-DPO 15.028), 1 element from the sample J-13 and 12 elements from sample J-53 (Menéndez-Álvarez's collection).

Derivation of name.-From Dr. José Ramón Menéndez-Álvarez, who studied and described elements of the new species in his unpublished Ph.D. thesis.

Diagnosis.-Pa elements with a short and often distally convex inner anterior parapet. The parapet can take up two thirds of the inner cup length, although its posterior part is composed of low nodes. Teeth from the posterior blade are only enlarged in mature elements. The cup is very asymmetrical, with the outer half wider at the anterior margin. The outer platform bears nodes that in many elements are arranged in roughly distinct concentric rows.

Description.-The specimens on hand have a short inner parapet that can take up two thirds of the inner cup length. The inner parapet is wider and higher at the anterior part and continues backwards through several low nodes near the carina. The anterior outline of the distal margin of the parapet is concave or straight, and afterwards convex (see elements from samples MILL-5 and CPE-30, Pl.1, Fig. 8; Pl. 2, Figs. 6 and 8, 10-12). The parapet is shorter in the earliest forms; these forms do not have isolated nodes behind the anterior high parapet. This is the case of a few elements of samples Co42 (Pl. 1, Figs. 15-16), MILL-4 (Pl. 1, Figs. 3-4) and MILL-5, where the parapet is located in the middle of the inner cup, the maximum width of the cup developing before that. The smaller elements have a few nodes (four or five) in the anterior part of the inner cup, the second of them being highest (Pl. 1, Fig. 6).

The posterior blade is composed of simple teeth, although the bigger (or mature) elements, from samples Co42, CPE-30, MILL-4 and MILL-5, show some expanded teeth at the posterior carina (Pl. 1, Figs. 14 and 16; PL. 2, Figs. 6, 8, 9 and 11).

The outer half of the cup is wider than the inner one, becoming more than three times wider in the mature elements, in which the widest point is located at the anterior margin. The anterior margin forms a right angle with the carina in the mature elements. In fact, such specimens have a triangular basal cavity. The asymmetry is less conspicuous in the small elements in which the outer anterior margin makes an acute angle with the blade.

The outer cup bears nodes that are usually arranged in distinct concentric rows. The elements from MILL-4 show poor development of the ornamentation (Pl. 1, figs. 3-4) and it is lacking altogether in an element from sample Co42. Concentric rows of nodes are better developed in young samples (MILL-5, Fig. 4.9). Some rare elements have an irregular pattern of ornamentation made of small, low nodes with a smooth

posterior (or post-lateral) part of the outer cup (Pl. 1, Fig. 15; Pl. 2, Figs. 6 and 8). The immature specimens from samples Co42 and CPE-30 show a trend towards one or two rows of nodes (Pl. 1, Figs. 5-6 and 11).

Remarks.-Some elements show morphologies close to the *G. semiglaber* Bischoff, 1957. However, the short inner parapets in *G. joseramoni* n. sp. are slightly longer than in *G. semiglaber*. Furthermore, the small and medium-sized elements do not have the enlarged posterior teeth of the carina, a characteristic of *G. semiglaber*, and the big elements show moderate development of expanded teeth. In *G. joseramoni* the platform outline is less oval and more triangular than in *G. semiglaber* (Pl.1, Figs. 1-2), with a tendency to the *G. bilineatus* outline. The same tendency is observable for the ornamentation of the outer cup. There was a progressive increase in the distinguishable concentric alignment of the nodes, similar to *G. bilineatus*. However, a strong similarity can be still observed between *G. semiglaber* and some particularly large elements of *G. joseramoni*. The element illustrated as *G. semiglaber* by Park (1983, Pl. 2, Fig. 13, sample KANTV-5) is included in the range of variability of the new taxon. It is an element where the ornamentation of the outer cup is poorly developed.

Gnathodus sp. A of Ebner (1977, Pl. 2, figs. 5 and 7) corresponds to immature elements of *G. joseramoni* n. sp. We are doubtful as to the inclusion of too many small elements from Ebner (1977, Pl. 2, Figs. 8-10 and 13) in the new species.

Some previously figured elements from the Rheinisches Schiefergebirge have morphologies very close to *G. joseramoni* n. sp. This is the case of the element from Sauerlandes illustrated by Voges (1959, Pl. 33, Fig. 33). It shows a convex inner parapet, which does not reach the posterior tip of the carina. Park (1983) considered an element from Velberter Sattel as *Gnathodus* n. sp. A Ebner (1977), but in our opinion this also belongs to *G. joseramoni* n. sp. Another element probably belonging to *G. joseramoni* is the specimen named as "*G. delicatus* transitional to *G. praebilineatus* Belka" by Meischner & Nemyrovska (1999, Pl. 1, Fig. 11). Unfortunately, in this specimen the outer cup is damaged and the inner parapet seems to have been blunted, thus hampering a comparison with our material.

Elements of *Gnathodus* sp. indet., figured by Mathews & Thomas (1974) from Devonshire (England), are sometimes identical to *G. joseramoni* n. sp. (see Mathews & Thomas, 1974, Pl. 51, Fig. 3), while other show long, high anterior parapets and narrow outer platforms (Pl. 51, Figs. 1-2, 18 and 19). In our opinion, they seem to be slender elements belonging to *G. joseramoni*.

Elements from the Carnic Alps identified as "*G. praebilineatus*" by Schönlaub & Kreutzer (1993) show a posterior carina with nodes that are wider than in the Spanish elements and with an outer cup which is less enlarged (Fig. 4.5) than in the specimens described here. However, we think it is reasonable to include the Schönlaub & Kreutzer's material in *G. joseramoni* n. sp., due to the characteristics of the inner parapet and outer ornamentation, as well as to the general architecture, which greatly resembles that of our species. In

contrast, *G. praebilineatus* (Pl. 2, figs. 1-4) has a long inner parapet formed by a row of nodes or cross ridges extending to, or near to, the posterior tip of the blade (Belka, 1985).

Other elements, considered by Schönlaub & Kreutzer (1993, Pl. 6, Fig. 14)) as early representatives of *G. b. bilineatus*, are similar to some rare elements from the samples Co42 and CPE-30 (Pl. 1, Figs. 13 and 14). Both the Spanish and the Carnic specimens have a shorter parapet than that of *G. praebilineatus* Belka but longer than the typical parapet of *G. joseramoni*, and an outer cup with a more triangular shape. However, in spite of all these differences, we are inclined to think that they should be considered co-specific with *G. joseramoni* n. sp., since they also have the anterior outer margin of the cup at an angle of 120 degrees to the carina (as is the case of *G. joseramoni*). Unfortunately, we have only collected a few elements in the associations studied.

Finally, we also include in *G. joseramoni* n. sp. certain elements assigned to *G. bilineatus* by Rodríguez Cañero & Guerra Merchán (1996). These authors described them as small specimens showing shorter parapets than in the typical *G. bilineatus*.

Occurrence.-The oldest specimens of *G. joseramoni* n. sp. are from the Cantabrian Mountains (samples MILL-4 and CPE-30, Tabl. 1), the western Pyrenees (illustrated by Marks & Wensink, 1970; and Perret, 1993) and the eastern Pyrenees (sample Co42, Tabl. 1), and were found in the *G. praebilineatus* Zone (Figs. 1 and 2). Elements from the sample 1093 of Higgins (1962, basal part of the Alba Fm. at the Santa Olaja de la Varga section) may be of a similar age (middle Viséan?). The element figured by Budinger (1965, sample Gr2 at the Gildar-Montó) was collected in beds containing *Goniatites* cf. *stenumbilicatus* and was considered to belong to the Go α-β ammonoid unit. The samples from the Cima di Plotta section (Carnic Alps, Italy) studied by Schönlaub & Kreutzer (1993) are probably of a similar age. Finally, the elements of *Gnathodus* sp. A of Ebner (1977), considered here to be a synonym of *G. joseramoni*, were found in his *Gnathodus* sp. A Zone, from Styria (Austria), prior to the first appearance of *G. bilineatus bilineatus*.

Findings of *G. joseramoni* n. sp. in rocks of the *G. bilineatus* Zone are various: Adrichem Boogaert (1967, sample Tr4', Triollo section); Higgins & Wagner-Gentís (1982, sample 2902, Villabellaco section); Park (1983, -sample ES-8- Santa Olaja de la Varga section, -sample KANTV-5- Cervera de Pisuerga, and Velberter Sattels, Germany); Menéndez-Álvarez (1991, sample J-13 from the Entrago section and sample J-53 from the El Portillín section); and Rodríguez Cañero & Guerra-Merchán (1996, Betic Cordillera). Elements figured by Mathews & Thomas (1974) were found immediately below the *G. crenistria* Bed in reworked faunas with *G. bilineatus* from Devonshire (England). Another finding assigned to this age by Grooves *et al.* (2003) is located in the Greek island Chios.

Gnathodus kiensis Pazukhin, 1992

(Pl. 2, Figs. 13-14; Text-Fig. 4.15-4.26)

1962 *Gnathodus delicatus* Branson & Mehl.- Higgins, Pl. 2, Fig. 23, 24?, Pl. 3, Fig. 33?.

1965 *G. delicatus* Branson & Mehl.- Budinger, Pl. 2, Figs. 9, 10, and 12 (only).

1973 *Gnathodus bilineatus* (Roundy).- Durdanović, Pl. 4, Figs. 16a-b.

1981 *G. bilineatus* Roundy.- Metcalfe, Pl. 3, Figs. 4a-d (only).

1983 *Gnathodus* n. sp. A.- Park, pp. 86-87, Pl. 3, Figs. 18-21.

1991 *Gnathodus cantabricus* n. sp.- Menéndez Álvarez, pp. 169-171 (partly), Pl. 23, Figs. 9, 12-13.

* 1992 *Gnathodus kiensis* n. sp.- Pazukhin (in Kulagina *et al.* 1992), p. 87, Pl. 28, Figs. 1-3.

1993 *G. bilineatus* (Roundy).- Perret, pp. 329-333, Figs. 113 B, J, K and L (only).

1993 *G. bilineatus* cf. *bollandensis* Higgins & Bouckaert.- Perret, lám. CX, Figs. 18-19.

1993 *Gnathodus b. bollandensis* Higgins & Bouckaert.- Perret, lám. CX, Fig. 28 (only).

1996 *G. bilineatus* (Roundy).- Rodríguez Cañero & Guerra-Merchán, p. 244, Pl. 1, Fig. 5 (only).

1998 *G. cantabricus* sp. n.- Belka & Lehmann, pp. 37-38, Pl. 2, Figs. 1-3.

v 2002a *G. cantabricus* Belka.- García-López & Sanz-López, p. 152, Pl. 2, Fig. 20.

v 2002 *G. cantabricus* Belka & Lehmann.- Blanco-Ferrera, p. 28, Pl. 1, Fig. 20, Pl. 2, Fig. 1.

Material.-All samples were collected in the Cantabrian Mountains: 23 elements from sample MILL-7 (DPO 15017-DPO 15019, Millaró section), CQ-21 (Carranques section), 2 elements from sample OLL-8 (Olleros de Alba section), 16 elements from sample CPE-13 (Cares River); 59 elements from samples J-5, J-13 and J-54 in the Menéndez-Álvarez's collection.

Revised diagnosis.-In the original diagnosis of the species, Pazukhin (in Kulagina *et al.*, 1992) wrote in Russian: "the platform is wide and asymmetric with nodular and ribbed half-concentric ornamentation on the inner and outer sides of the element, and with a flat, low parapet". In addition, we feel the inner platform being widest at its mid-length, and, in particular, the parapet turning distally (outwards) at the posterior part, are important diagnostic features.

Description.-The spade-shaped platform is wide and asymmetric. The outer cup is wider than inner one, and is ornamented by rows of nodes, sometimes with a half-concentric arrangement, although other elements show nodes distributed at random. The inner cup has a triangular outline and displays a parapet of variable length, but always finishing before the posterior tip of the carina. The parapet is low and is not attached to the carina. It decreases in height towards the back, showing ramp morphology (Menéndez-Álvarez, 1991, Pl. 23, Fig. 9). At the same time, the parapet diverges from the carina. The big elements show a parapet margin with a convex-concave-convex trajectory. The space between parapet and carina is occupied by oblique rows of discrete low nodes. In medium-sized and immature elements, the parapet is parallel or convex with respect to the carina, and is followed backwards by isolated posterior nodes. Posterior concurrence with the

carina is present when these nodes form an oblique row. Divergence between the posterior parapet and the carina is minimized in small elements.

The carina is composed of simple teeth, which are only slightly expanded in the biggest elements. The free blade is 1/2 to 2/5 of the total length of element. The anterior margins of the platform are in approximately opposing locations.

Remarks.-The original material of *Gnathodus kiensis* shows wide ornamented platforms, with the parapet becoming lower and nearly disappearing in adult specimens (Pazukhin in Kulagina *et al.*, 1992). The small forms have smaller ornamented platforms and more separated rows of nodes. They are located towards the limit of the specific variability that we accept now for *Gnathodus kiensis*. An element exactly like the holotype is not present in our samples, which display a too wide platform, a very low parapet, and maximum divergence between the carina and the posterior parapet. However, some elements from sample MILL-7 (Fig. 4.22-23) are similar to the medium-sized specimens of Pazukhin (in Kulagina *et al.*, 1992). Elements described by Park (1983) and Belka & Lehmann (1998) have a weak ornamentation on the outer cup made of randomly distributed nodes (Fig. 4.18), although concentric rows are visible in the holotype of *G. cantabricus* (see Belka & Lehmann, 1998, Pl. 2, fig.1) (Fig. 4.17). We agree with Menéndez-Álvarez (1991), in that poorly ornamented cups are found together with elements where rows of nodes clearly occur, and together with intermediate elements. Blanco-Ferrera *et al*. (in press, Fig. 6.15) illustrated a young morph of *G. kiensis* with a short inner parapet composed of separated nodes isolated backwards (Fig. 4, 19), and in which the outer cup only bears rare nodes.

Elements identical to the holotype of *G. cantabricus* Belka & Lehmann (1998) were found in sample J-54 from Menéndez-Álvarez (1991, lower part of the *L. nodosa* Zone). They are strongly ornamented elements with a high anterior parapet composed by ridges decreasing in height progressively towards the back.

G. joseramoni n. sp. has a shorter inner parapet than *G. kiensis*, and a different platform outline. The first species has a more enlarged triangular outer half of the cup, and the second a more oval outline, which is widest in the central platform. The parapet is convex in *G. joseramoni*, and shorter than in *G. kiensis*, and it is turned distally at the posterior part of the parapet in the second species.

Occurrence.-The oldest findings of *G. kiensis* are recorded in the *G. bilineatus* Zone of the Cantabrian Zone (sample J-13, Entrago section, Menéndez-Álvarez, 1991) and the Betic Cordillera (specimen illustrated by Rodríguez Cañero & Guerra-Merchán, 1996). *G. kiensis* seems to be rare in this biozone.

In contrast, there are far more abundant records in the overlying *L. nodosa* Zone. In the Cantabrian Zone, *G. kiensis* occurs in strata belonging to this biozone at the Matallana section (Higgins, 1962), Gildar-Montó and Panes-Potes sections (Budinger, 1965), Santa Olaja de la Varga (Park, 1983; Belka & Lehmann, 1998), El Portillín, Entrago, Olleros de Alba and Río Nevandi sections (Menéndez-Álvarez,

1991), Olleros de Alba and Millaró sections (García-López & Sanz-López, 2002b) (Fig. 2) and in the Cares River valley (Blanco-Ferrera *et al.*, in press). *G. kiensis* occurs together with *L. multinodosa* (Higgins) and *L. cruciformis* (Clarke), from beds of the Serpukhovian (Pendleian) age at the Santa Olaja de la Varga section (Belka & Lehmann, 1998) and the Carranques section, (García-López & Sanz-López, 2002a). Finally, *G. kiensis* coincides with the entry of *G. bilineatus bollandensis* Higgins at the Puente de Alba section after Menéndez-Álvarez (1991), in strata belonging to the Arnsbergian. However, Higgins & Wagner-Gentis (1982) maintained the lack of *G. b. bollandensis* in the Cantabrian Mountains.

Pyrenean elements considered *G. kiensis*, and illustrated by Perret (1993), were collected at the La Estiva/Chinipro section (Fig. 1) in samples (Chin 13 and Chin13a JD) from the *L. nodosa* Zone. *G. kiensis* has also been reported from Dvor na Uni (Serbia, Durdanović, 1973), England (Metcalfe, 1981) and Styria (Austria, Belka & Lehmann, 1998). It must be noted that the original material of *G. kiensis* comes from the *G. b. bollandensis* Zone, Protvian Horizon (Nm_1b_2-Nm_1c_1, upper Pendleian to lower Arnsbergian, Serpukhovian) of the South Urals (Kulagina *et al.*, 1992). This material seems to correspond to the youngest finding so far known.

CONODONT DISTRIBUTION AND EVOLUTIONARY CONSIDERATIONS

Elements identified here, as *Gnathodus joseramoni* n. sp. and *G. kiensis* were known long ago in the Cantabrian Mountains, but they have only occasionally been described, and the second species display a low abundance. Our relatively incomplete knowledge of these taxa hinders the understanding of their phylogeny, and of their relationships with other *Gnathodus* species. However, taking into account all the materials now available, we think that it is possible to trace some evolutionary trends based on the morphologic change observed in associations from the middle Viséan to the Serpukhovian (Fig. 4).

Older populations of *G. joseramoni* n. sp. from the Iberian Peninsula seems to be part of an innovative radiation episode of the *Gnathodus* species that took place at the *G. praebilineatus* Zone (Fig. 4). This conodont radiation replaced lower Viséan faunas dominated by species of the *G. punctatus* group of Lane *et al*. (1980). The conodont record of this radiation is known for a biozonal interval classically named as the "*anchoralis-bilineatus* Interregnum" (Voges, 1960) in Southern Europe, and frequently corresponding to an episode of chert deposition (Lavandera and Louron members in North Spain) together with the corresponding carbonate sedimentation (Fig. 2).

Belka (1985) proposed *G. praebilineatus* as ancestral species of *G. bilineatus*, and appearing at the base of his *G. austini* Zone. Menéndez-Álvarez (1991) defined the *G. praebilineatus* Zone between the occurrences of *G. praebilineatus* and *G. bilineatus* in the Cantabrian Mountains. After Belka (1985) and Belka & Korn (1994), *G. praebilineatus* was considered to originate from *G. semiglaber* Bischoff (a

species of the *G. punctatus* group) through the development of the inner parapet and the reduction of the expanded posterior blade to the point of becoming a simple one (compare Pl. 1, Figs. 1-2 with Pl. 2, Figs. 2-4). According to Meischner & Nemyrovska (1999) in the Rheinisches Schiefergebirge, *G. praebilineatus* appeared below the *Entogonites nasutus* ammonoid Zone (lower Asbian), before other species of the *G. bilineatus* group such as *G. romulus* and *G. remus* (*E. grimmeri* Zone) and *G. b. bilineatus* (*Goniatites crenistria* Zone, upper Asbian).

Immature specimens of *G. praebilineatus* show low inner parapets that do not extend to the posterior tip of the blade, and an almost unornamented outer cup (Pl. 2, Fig. 1). Belka (1985) considered this morphology as probable for the forerunners or the earliest phylogenetic forms of *G. praebilineatus* in a heterochronic process, and it may correspond to the elements described as *Gnathodus* sp. A from Styria (Ebner, 1977) or from the Cantabrian Mountains (Park, 1983). We consider that most of these elements correspond to *G. joseramoni* n. sp. In contrast, early *G. praebilineatus* are probably the elements described by Belka & Korn (1994, Pl. 2, Figs. 11, Cantabrian Mountains) and Spalletta and Perri (1998, Pl. 3.1.1., Fig. 3, Carnic Alps). These two elements have three 3 rows of nodes in the small outer cup, and the inner parapet is long, although it does not reach to the posterior tip of the carina. Finally, we feel that after Meischner & Nemyrovska (1999), none of these elements should be attributed to *G. praebilineatus*, since they possess a short parapet. These authors indicated which transitional forms between *G. delicatus* and *G. praebilineatus* occur just below and together with *G. praebilineatus*. However, the observation of the phylogenetic link between both species is hindered by the existence of conodont gap between the strata yielding those "transitional" morphs, and older Tournaisian strata containing *G. delicatus*. In our opinion, most of the elements illustrated by Meischner & Nemyrovska (1999, Pl. 1, Figs. 6, 12 and 15; Pl. 2, Fig. 9) could correspond to immature *G. praebilineatus* specimens, since they are small in size and show poorly developed ornamentation on the outer cup.

G. joseramoni n. sp. seems to evolve from *G. semiglaber*. The typical material (Bischoff, 1957) of the ancestral species, *G. semiglaber*, shows nodes behind the high convex anterior inner parapet (Fig. 4.2, holotype); these nodes increase both in number and size in *G. joseramoni* n. sp. to give rise to a longer inner parapet (Fig. 4.5-4.7). They are early growing in the development of immature elements of *G. joseramoni* n. sp. (compare Figs. 4.1 and 4.8). The young elements of *G. joseramoni* have a morphology akin to that of the big *G. semiglaber* elements (peramorphic heterocrony), with the exception of the expanded teeth of the posterior carina. Big elements of *G. joseramoni* n. sp. are similar to *G. semiglaber* because show fused ridges in the high convex parapet and, furthermore, an enlarged posterior carina (Figs. 4.5 and 4.11). Consequently, the expansion of the teeth was delayed during the growing of the element Pa of *G. joseramoni* n. sp., as a paedomorphic morphology (post-displacement process, McNamara, 2001). Supporting evidence also comes from certain Viséan elements considered a morph in the variation of *G.*

semiglaber, and which could give rise to *G. joseramoni* n. sp. This morph (PL. 1, Fig. 1) coexists with typical *G. semiglaber* (Pl. 1, Fig. 2) in the Pyrenees and Millaró sections, and Schönlaub & Kreutzer (1993) illustrated a wide variability of similar elements from the Carnic Alps and classified them as "*G. punctatus*" (Pl. 4, figs. 10-15, 18-22). This morph of *G. semiglaber* shows nodes on the whole surface of the outer cup, and a few nodes behind the high inner parapet, characteristics not found in the typical morph of *G. semiglaber* but present in *G. joseramoni* n. sp. However, the morph is still differentiated from *G. joseramoni* by having the nodes homogeneously distributed on the outer cup, shorter inner parapets, and a more oval platform outline (Figs. 4.3 and 4.4).

As innovative characteristics, *G. joseramoni* n. sp. developed an asymmetric platform, with an increasing width on the anterior outer cup, and a half-concentric arrangement of the rows of nodes (Figs. 4.5 to 4.11). Both characteristics were also independently developed in another lineage, from *G. praebilineatus* to the cosmopolitan *G. bilineatus*. The morphologic resemblance between *G. joseramoni* and *G. praebilineatus* is notorious for small elements, which hinders their easy assignation. We find elements with a short parapet, considered as probably immature *G. joseramoni* (Pl. 1, figs. 5-6 and 11); elements with a long parapet, but without meeting the posterior tip of the blade, considered as probably immature *G. praebilineatus* (Pl. 2, Fig. 1); and elements with intermediate type of parapet.

With respect to *G. kiensis*, Pazukhin (in Kulagina *et al.*, 1992), and later Belka & Lehmann (1998), mentioned the presence of transitional elements between this species and *G. bilineatus*, and interpreted this fact as an indication of a possible derivation of the first species from the second. However, the elements of *G. kiensis* from the *G. bilineatus* Zone studied here can hardly be distinguished from elements of *G. joseramoni*. These modern elements (sample J-53) of the last species have a longer parapet than that of typical elements (sample J-53, Figs. 4.12-4.14), and the anterior ridges of the parapet are higher and sometimes wider than the posterior ridges, as in *G. kiensis*. However, these elements of *G. joseramoni* do not display the divergence between the posterior parapet and the carina. Immature elements have a more convex parapet outline than big elements, parapet that is almost as long as the inner platform, indicating its early development during the growth of the element. Furthermore, the triangular morphology of the outer cup is accentuated during the growth (compare Figs. 4.12 and 4.14). Divergence and a decrease in height of the posterior inner parapet, together with a more rounded platform, are typical characteristics found in *G. kiensis*. They are present in some big elements from the *G. bilineatus* Zone (sample J-13), where, in addition, higher nodes are located at the parapet margin and a deep adcarinal trough lies right next to the carina (Fig. 4.16). The diverging inner parapet is not visible in immature elements of the same associations (Fig. 4.15).

In the same sense, small elements of younger associations of *G. kiensis* have not developed the spade-shaped platform, and the parapet has a convex morphology without the marked posterior carina-parapet

divergence. Consequently, small elements of *G. kiensis* (Fig. 4.20) and some elements of *G. joseramoni* n. sp. (Fig. 4.9) exhibit very similar morphology. In accordance with what has been stated above, we consider that *G. kiensis* originated from *G. joseramoni*, although the speciation from a *G. bilineatus* ancestor should also be analyzed. Undoubtedly, many findings are necessary in order to prove any derivation, particularly those coming from the *G. bilineatus* Zone.

Early elements of *G. kiensis*, from the *L. nodosa* Zone, have a strong ornamentation and long parapet (sample J-54 and Fig. 4.17). They have a high anterior part, and a low wide posterior part of the parapet. The height of the parapet decreases in the younger associations, a feature already described in ontogenetic variation by Pazukhin (in Kulagina *et al.*, 1992). Distal outward deflection of the inner parapet also shows an accentuated development in the younger associations (Figs. 4.22 to 4.26).

So far *G. kiensis* has been only found in the Carboniferous western Palaeo-Tethys Ocean (Iberian Peninsula, Austria, England, Serbia and South Urals). Conodont provincialism during late Viséan (*L. nodosa* Zone) has been pointed out by Higgins (1981), who differentiated two "provinces", Eurasian and Midcontinental. In this scheme, *G. kiensis* can be seen as a component of the deep-water faunas from the Eurasian province. With respect to the middle Viséan, species with restricted palaeogeographic distribution, such as that *G. joseramoni*, *G. praebilineatus*, *G. remus* and *G. romulus*, have so far only been found in the Eurasian province (see occurrences of the three last taxa in Meischer & Nemyrovska, 1999), which suggests certain endemicity in the distribution of the middle Viséan *Gnathodus* species, although the recognition of palaeobiogeographic units based on that distribution will be the object of future studies.

CONCLUSIONS

The study of new material from the Iberian Peninsula, as well as comparison with material previously described by different authors (and included in different species), allows us to describe the new species *Gnathodus joseramoni* n. sp. So far, the new species is known from cephalopod nodular limestones of the *G. praebilineatus* to the *G. bilineatus* zones (middle Viséan) in the Iberian Peninsula, Carnic Alps, England, Styria and Greece. Certain elements probably related to *Gnathodus joseramoni* were illustrated by several authors in the German Rheinisches Schiefergebirge. The taxon evolved from *G. semiglaber*, probably after the origin of *G. praebilineatus*.

Gnathodus cantabricus Belka & Lehmann is regarded as a junior synonym of *G. kiensis* Pazukhin. This species could have evolved from *Gnathodus joseramoni* n. sp., in the *G. bilineatus* Zone, although a derivation from *G. bilineatus* is also possible. The species is easily recognized and occurs frequently, although not abundantly, in the *L. nodosa* Zone, upper Viséan to lower Serpukhovian (Pendleian) in the

Iberian Peninsula. Other occasional findings come from Austria, England, Serbia, and particularly the South Urals, where the species is known in strata as young as the upper Serpukhovian.

According to current data, *Gnathodus joseramoni* n. sp. and *G. kiensis* are endemic species with a geographic distribution restricted to areas included in the upper Viséan Eurasian conodont province of Higgins (1981).

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FIGURE CAPTIONS

Figure 1. Geological sketch with the situation of the localities from the Cantabrian Mountains and the Pyrenees, with conodonts studied (black stars) and referred to in the text (grey stars).

Figure 2. The lithostratigraphic units of the Alba Formation (except for the basal Gorguera Member and the uppermost part of the formation) are indicated in the Millaró stratigraphic section. The section included a sequence of samples that yielded much of the material discussed in this paper, as well as important conodont species.

Figure 3. Terminology used for different morphologic parts on the oral surface of the Pa element of *Gnathodus* (P1 after the notation of Purnell *et al*., 2000). Conventional orientation is accompanied by the biological orientation, surrounded by quotation marks, proposed in Purnell *et al*. (2000).

Figure 4. Diagram showing the morphologic change on the oral surface of different Pa elements from the ancestral species *G. semiglaber* Bischoff to *G. joseramoni* n. sp. and *G. kiensis* Pazukhin. The vertical axis indicates age, series, stages and conodont zones. Magnifications are x 25.

1-4, *Gnathodus semiglaber* Bischoff. *1*, Immature element from sample Co39 (comes de Das section). *2*, Holotype from Bischoff (1957, Pl. 3, Fig. 1). *3*, Ornamented element from sample 1044 A (Cima di Plota section, "*G. punctatus* Cooper" after Schönlaub & Kreutzer, 1993, Pl. 4, Fig. 18). *4*, Element with the anterior outer cup bearing rows of poorly developed nodes, from sample 1045 (Cima di Plota section, "*G. punctatus* Cooper" after Schönlaub & Kreutzer, 1993, Pl. 4, Fig. 15).

5-14, *G. joseramoni* n. sp. *5*, Element with an increment on the number of nodes in the inner posterior cup in relation to *G. semiglaber*, and a concentric arrangement of nodes in the outer cup (sample 1047, Cima di Plota section, *G. praebilineatus* after Schönlaub & Kreutzer, 1993, Pl. 6, Fig. 7). *6-7*, Immature element and mature element with a triangular outline of the outer cup (sample MILL-4, Millaró section). *8-11*, Elements from sample MILL-5 (Millaró section); (*8*) immature element; (*9*) mature element where a slight distal divergence of the inner parapet with respect to the carina is perceptible; (*10*), mature elements with asymmetric cup and half-concentric rows on the outer side; (*11)* holotype of the species. *12-14*, Elements with different sizes and with a long inner parapet (sample J-53, El Portillín section).

15-26, *G. kiensis* Pazukhin. *15-16*, Elements from sample J-13 (Entrago section); (*15*) immature element; (*16*) mature broken element with a spade-shaped platform where the parapet turns outward and the outer cup area decreases. *17*, Holotype of *G. cantabricus* Belka & Lehmann (1998, Pl. 2, Fig. 1, from

sample 16, Santa Olaja de la Varga section), where the inner parapet has anterior high ridges and posterior parapet shows low discrete nodes. *18*, Medium-sized element from Belka & Lehmann (1998, Pl. 2, Fig. 2, sample 18, Santa Olaja de la Varga section). *19*, Immature element from sample CPE-13 (Cares River, Blanco-Ferrera *et al.*, in press). *20-21*, Immature element and holotype of *G. cantabricus* Ménendez-Álvarez (1991, Pl. 23, Fig. 9 and 12 respectively) from sample J-5 (Entrago section). *22-23*, Elements with oblique rows of nodes between the turned inner parapet and the carina from sample MILL-7 (Millaró section). *24-26*, Elements and holotype of *G. kiensis* (*26*) from sample 12 at the Kiya River (Pazukhin in Kulagina *et al.*, 1992, Pl. 28, figs. 1-3).

Plate 1. Oral views of different Pa elements; graphic scale is 200 μm. *1-2*, *Gnathodus semiglaber* Bischoff, 1957, from samples MILL-2 and MILL-5 respectively (specimens DPO 15.002 and DPO 15.008, Millaró section); *1* illustrated previously by García-López & Sanz-López, 2002b, Pl. 4, Fig. 5.

3-16, *Gnathodus joseramoni* n. sp.; *3-4*, specimens DPO 15.005 and DPO 15.006 from sample MILL-4 (Millaró section); *5-11* and *13*, specimens DPO 15.020 to DPO 15.027 from sample CPE-30 (Duje River); *12* and *14-16*, specimens DPO 15.031 to DPO 15.034 from sample Co42 (comes de Das section).

Plate 2. Oral views of different Pa elements; graphic scale is 200 μm. *1-4*, *Gnathodus praebilineatus* Belka, 1985; *1*, specimen DPO 15.029 from sample CPE-30 (Duje River); *2-4*, specimens DPO 15.036-DPO 15.038 from sample Co42 (comes de Das section).

5-12, *Gnathodus joseramoni* n. sp.; *5*, specimen DPO 15.035 from sample Co42 (comes de Das section). *6*, specimen DPO 15.028 from sample CPE-30 (Duje River); *7-12*, specimens from sample MILL-5 (Millaró section), *8*, holotype DPO 15.009 illustrated previously by García-López & Sanz-López, 2002b, Pl. 4, Fig. 10; *7*, *9-12*, paratypes DPO 15.010 to DPO 15.014 respectively.

13-14, *Gnathodus kiensis* Pazukhin, 1992, specimens DPO 15.018 and DPO 15.019 from sample MILL-7 (Millaró section).

Table 1. Conodonts from samples of the Millaró section (1), Olleros de Alba section (2), Carranques section (3), Duje River (4), Cares Rives (5), and the comes de Das section (6).

Localities	1			2	3	4	5	6
Conodonts ↓ samples →	MILL-4	MILL-5	MILL-7	OLL-8	CQ-21	CPE-30	CPE-13	Co42
Gnathodus joseramoni n. sp.	+	+				+		+
G. praebilineatus Belka	+	+				+	+	+
G. cf. *meischneri* Austin & Husri						+		
G. pseudosemiglaber (Thompson & Fellows)	+					cf.		
Geniculatus sp.						+		
Lochriea commutata (Branson & Mehl)	+	+	+	+	+	+	+	+
Pseudognathodus homopunctatus (Ziegler)	+		+			+		+
Ps. symmutatus Rhodes, Austin & Druce	+							+
Vogelnathus campbelli Rexroad	+					+		+
Gnathodus semiglaber Bischoff	cf.	+						
G. romulus Meischner & Nemyrovska		+						+
Gnathodus kiensis Pazukhin			+	+	+		+	
Gnathodus bilineatus (Roundy)			+	+	+		+	
Lochriea nodosa (Bischoff)			+	+			+	
L. mononodosa Rhodes, Austin & Druce			+	+			+	
L. ziegleri Nemyrov., Perret & Meischner			+		+		+	
L. cruciformis (Clarke)			cf.		+			
L. senckenbergica Nemy., Perret & Meischner				+				

Figure 1

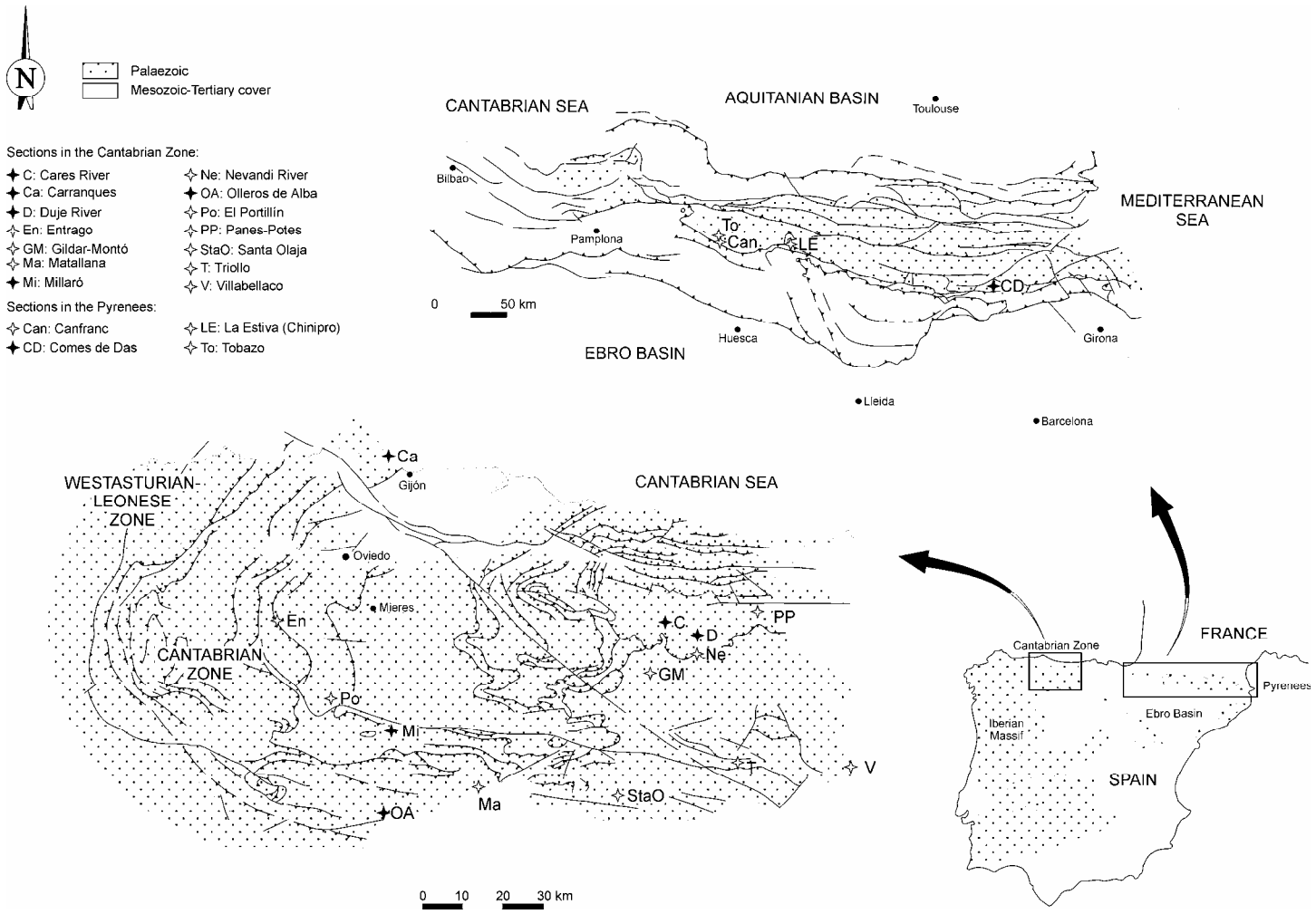

N
Palaezoic
Mesozoic-Tertiary cover
Sections in the Cantabrian Zone:
C: Cares River
Ca: Carranques
D: Duje River
En: Entrago
GM: Gildar-Montó
Ma: Matallana
Mi: Millaró
Ne: Nevandi River
OA: Olleros de Alba
Po: El Portillín
PP: Panes-Potes
StaO: Santa Olaja
T: Triollo
V: Villabellaco
Sections in the Pyrenees:
Can: Canfranc
CD: Comes de Das
LE: La Estiva (Chinipro)
To: Tobazo
CANTABRIAN SEA
AQUITANIAN BASIN
Toulouse
Bilbao
Pamplona
To
Can.
LE
CD
MEDITERRANEAN SEA
0
50 km
Huesca
Girona
EBRO BASIN
Lleida
Barcelona
Ca
Gijón
WESTASTURIAN-LEONESE ZONE
CANTABRIAN SEA
Oviedo
Mieres
En
C
D
PP
Ne
GM
CANTABRIAN ZONE
Po
Mi
V
Ma
StaO
OA
0
10
20
30 km
FRANCE
Cantabrian Zone
Pyrenees
Ebro Basin
Iberian Massif
SPAIN

Figure 2

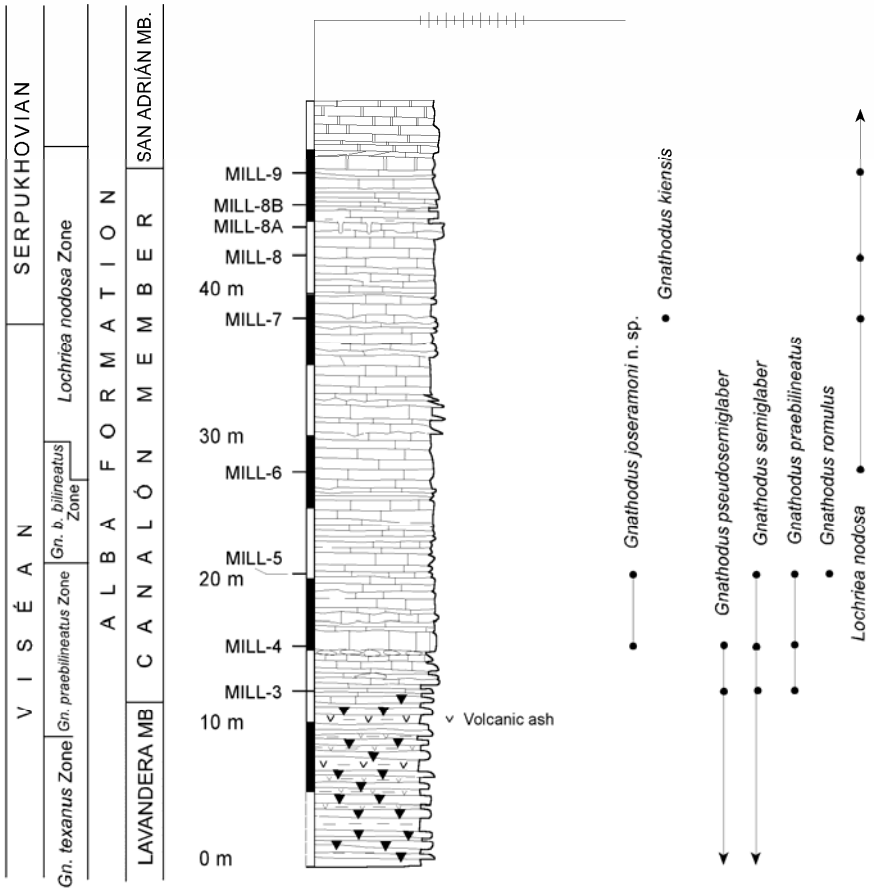


Figure 3

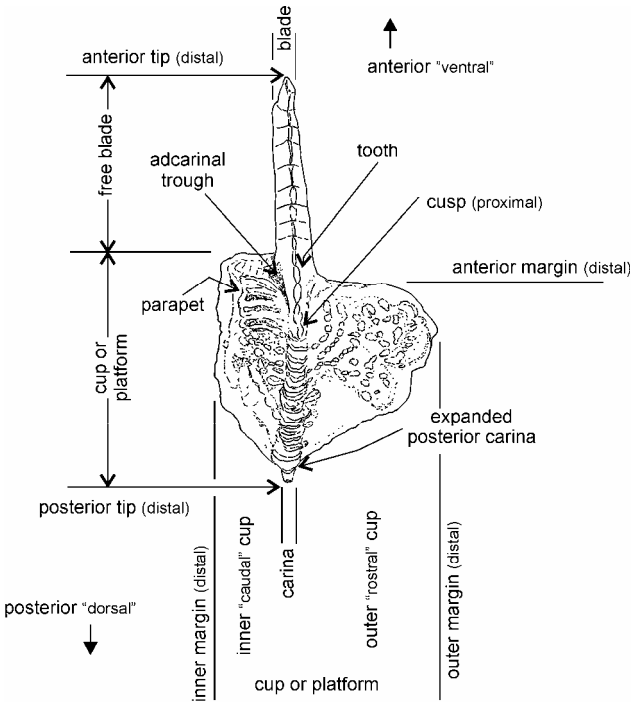
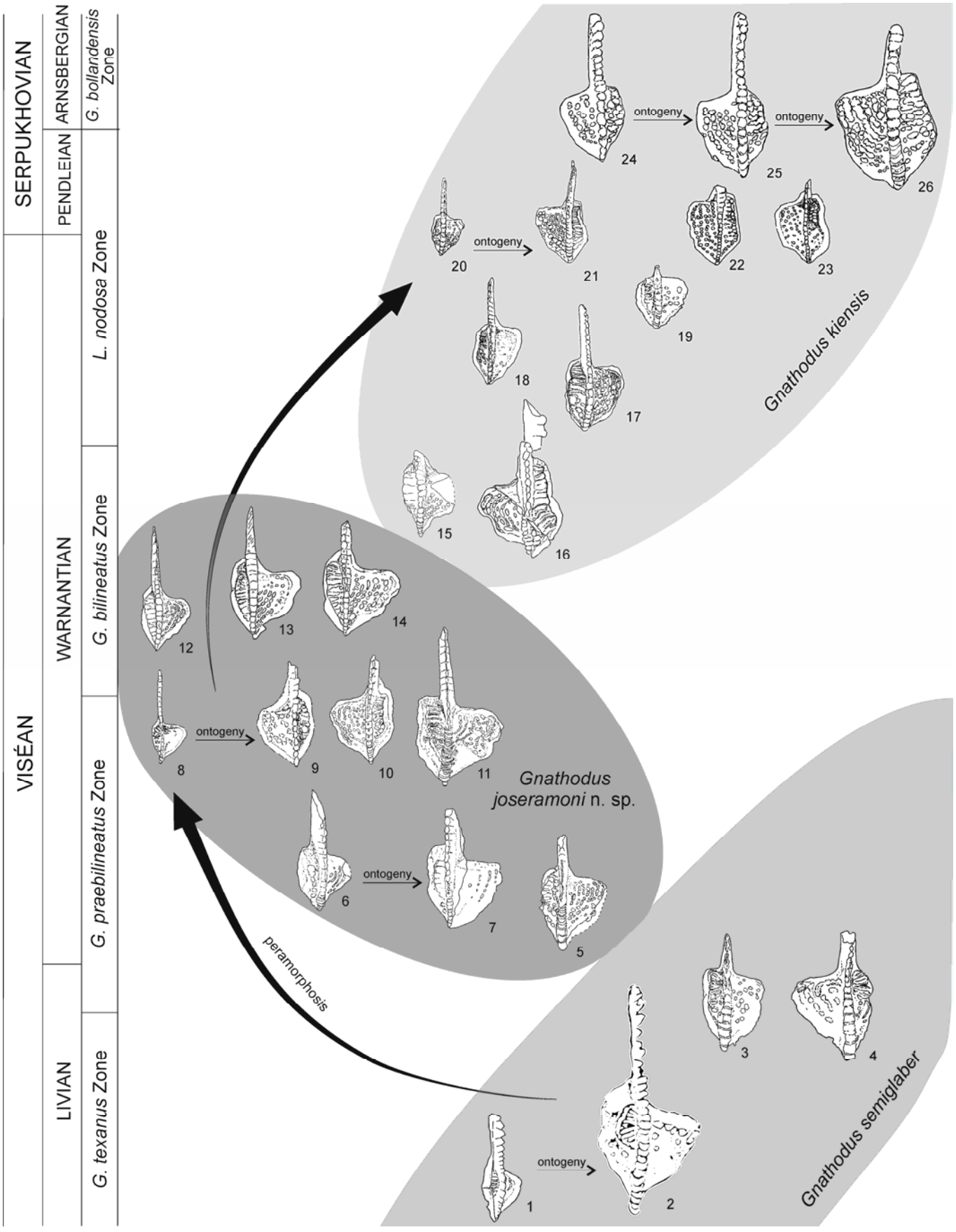


Figure 4


VISÉAN
SERPUKHOVIAN
PENDLEIAN
ARNSBERGIAN
G. bollandensis Zone
WARNANTIAN
L. nodosa Zone
G. bilineatus Zone
G. praebilineatus Zone
LIVIAN
G. texanus Zone
Gnathodus kiensis
Gnathodus joseramoni n. sp.
Gnathodus semiglaber
ontogeny
peramorphosis
1
2
3
4
5
6
7
8
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26

Plate 1

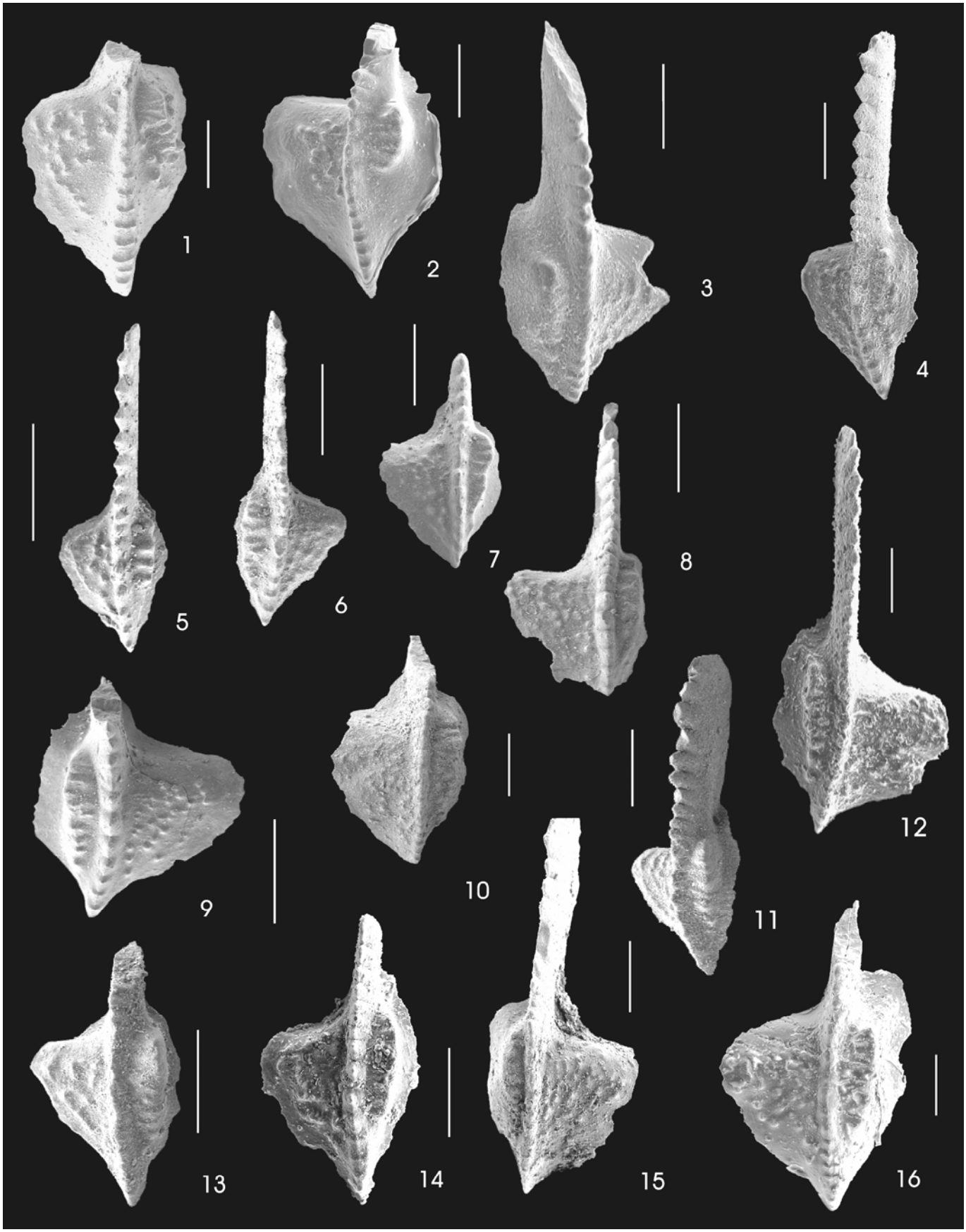
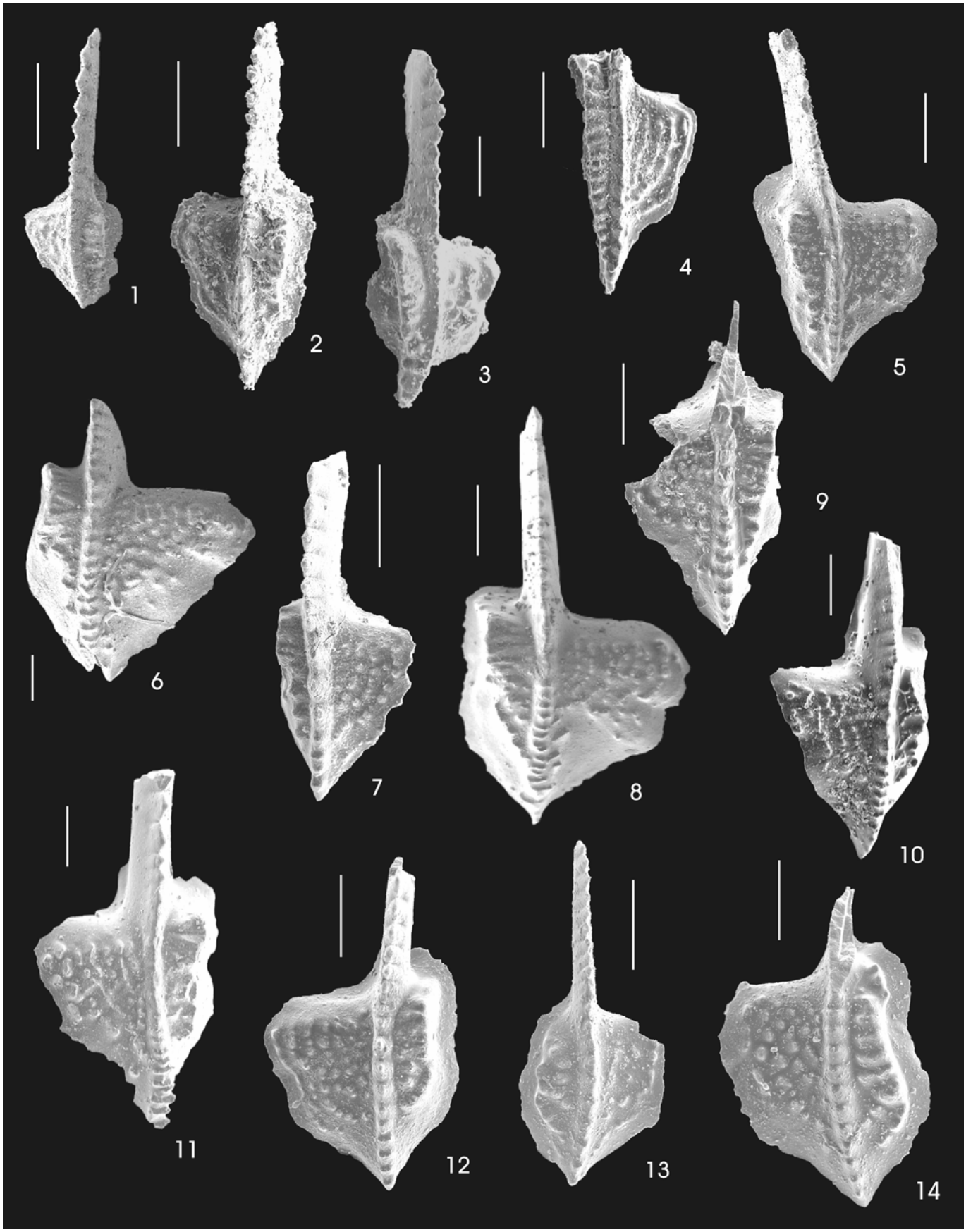
Plate 2