

Late Viséan/early Serpukhovian conodont succession from the Triollo section, Palencia (Cantabrian Mountains, Spain)

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Keywords — conodonts, Carboniferous, Viséan, Cantabrian Mountains, biostratigraphy, palaeoecology. The present study reports upon the conodont faunas of the uppermost lower Viséan (Carrión unit) through the lower Serpukhovian (Peña unit) deep water Triollo section, Cantabrian Mountains, Palencia, Spain. The condensed succession of grey, laminate, nodular and cherty limestones with marl intercalations contains abundant and diverse conodont faunas. Three new species of *Vogelgnathus*, *V. cantabricus*, *V. palentinus* and *V. triolloensis*, as well as one new species and one new subspecies of *Gnathodus*, *Gn. boogaardi* and *Gnathodus girtyi pyrenaicus* Nemyrovska & Perret subsp. nov., are described. All stratigraphically important taxa for the studied interval are described. Four conodont zones are distinguished, three in the Viséan, *Gnathodus praebilineatus*, *Gn. bilineatus* and *Lochriea nodosa* Zones, and one in the lower Serpukhovian, *L. ziegleri* Zone. It is proposed to identify the Viséan/Serpukhovian boundary at the first appearance of *L. ziegleri*. The Triollo carbonate succession (Carrión and Peña units) is compared by conodonts with coeval deposits in other areas. The conodonts are divided into eight palaeoecological groups, their occurrences are analysed and diagrammatically illustrated. Four peaks representing invasions of the *Vogelgnathus*-dominated faunas may correspond to the four flooding events during late Viséan and early Serpukhovian times. Investigations of the conodont biofacies together with sedimentological studies of the Triollo sections indicate deep water, basinal depositional conditions.

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Introduction

The boundary between the Viséan and Serpukhovian Stages has been traditionally defined on goniatites and placed at the base of the *Cravenoceras leion* (now *Emstites leion*)

goniatite Zone. Korn (1996) proposed *Edmooroceras pseudocoronula* Bisat, which is geographically less restricted, as a better alternative. However, although the Mississippian goniatites provide high-resolution regional subdivisions, their endemic character prevents their effective use for interregional and intercontinental correlation. The conodonts are regarded as a more promising and more reliable group for correlation since they generally show fewer geographical restrictions, occur in more varied lithologies of marine rocks and were less dependent on the palaeoenvironments than other faunas. That is why the conodonts from the Viséan/Serpukhovian boundary beds in England, Ireland, Germany, Poland, Russia, Ukraine and France have been proposed for the identification of the Viséan/Serpukhovian boundary (Skompski *et al.*, 1995).

The *Lochriea* lineage has been selected for this purpose. Two species of strongly ornamented advanced *Lochriea* competed for the position of the species-marker for the boundary, *L. cruciformis* (Clarke) and *L. zieglerei* Nemyrovskaya, Perret & Meischner. They occur almost together and near to the boundary, but some discrepancies still exist concerning their first appearances. *Lochriea cruciformis* appears earlier than *L. zieglerei* in Germany, but much later in England and Spain (Cantabrian Mountains, Esla area). Such a deeper water section as at Triollo was supposed to resolve this discrepancy.

The primary objective of the present research was to study the conodonts and describe the new *Vogelgnathus* species distinguished by van den Boogaard, as well as the stratigraphically important species found for the first time in the Cantabrian Mountains, but formerly known only outside Europe, as well as the stratigraphically important taxa in general. The second objective was to analyse the distribution of conodonts throughout the Triollo section and to provide the biostratigraphy (conodont zonation) of the succession. The third task was to analyse with a greater number of closely spaced samples at the Triollo section to test the idea, advanced by van den Boogaard (1992), that the invasions of *Vogelgnathus* fauna were sudden, short-lived and linked to the four most prominent late Viséan-early Serpukhovian eustatic sea level rises (Ramsbottom, 1973, 1977; Ross & Ross, 1988). The fourth objective was to compare the palaeoecological implications of conodonts of the Triollo succession with those based on the microfacial analysis of the rocks.

A section in northeast Triollo, the type section for the "Carrión Formation" to be described by Drs R.H. Wagner & C.F. Winkler Prins, was measured and sampled bed-by-bed (samples 8435-8499) for conodonts by them. Rich in conodonts, it showed characteristic recurrences of *Vogelgnathus campbelli* (van den Boogaard, 1992). At the request of Dr. M. van den Boogaard, some portions of the section, which showed extreme variations in the *Vogelgnathus* content, were additionally sampled (8720-8723, 8750-8757, 8784-8794). Dr. van den Boogaard dissolved with formic acid most of the numerous samples studied, picked out the conodonts and designated the new *Vogelgnathus* species. He also suggested that the dominance of certain groups of species throughout the section could be shown so as to understand better the link between the *Vogelgnathus*-dominated fauna and sea-level rise. All the studied platform conodonts were registered and their number was counted.

After van den Boogaard's retirement, he and Cor Winkler Prins asked the author to continue his work, to analyse the conodont distribution, to describe the new species and to illustrate the periodic recurrence of *Vogelgnathus*-dominated faunas. Although van den Boogaard had already done a great deal of work, he declined to be a co-author. As

we understand the conodonts and their stratigraphical significance in the same way, I continued this work.

Additional samples were processed. The abundant collection of conodonts from the Triollo section was re-examined, some minor revisions were made concerning the identifications of species, the distribution of conodonts was analysed, several conodont zones were distinguished and compared with other areas, the position of the Viséan/Serpukhovian boundary was determined, the most important species of conodonts were illustrated and described, and their palaeoecology determined. The sedimentological work relating to this paper is included in an appendix by Dr Samanakkassou.

Geological setting

The Triollo section is located on the eastern slope of the Carrión Valley, 1 km north of Triollo village, in northern Palencia (Fig. 1). Viséan and lower Serpukhovian deposits are widespread all over the Cantabrian Mountains, and are represented by condensed sequences of the Genicera (or Alba) and Barcaliente formations (Wagner *et al.*, 1971). These are also known as "Griotte Limestone" and the lower part of the "caliza de montaña", respectively. In the province of Palencia, these formations are recognized mainly south of the Ruesga Fault, an important fracture zone where the northern branch of the Cantabric-Asturian arcuate fold belt overrides the southern branch (Wagner & Winkler Prins, in prep.). A series of southward verging thrust slices accompanies the Ruesga Fault in northern Palencia. North of the Ruesga Fault, the Genicera and Barcaliente formations have only been identified in the first thrust slice. The Genicera Formation, consisting of characteristic red and grey nodular limestones with an intervening chert member, ranges from the upper Tournaisian to lower Serpukhovian to the south of the Ruesga Fault. It has a more limited stratigraphic range in the first thrust slice north of this fault. In successive thrust slices the Genicera and Barcaliente formations are replaced by the other stratigraphic units developed in the area the north of the Ruesga Fault, i.e., in the Palentian domain. In the seventh thrust slice nodular limestones and cherts of the Genicera Formation are replaced by light grey limestones with some nodular intervals and cherts of the informal Carrión unit (to be described by Wagner & Winkler Prins, in prep.). Black laminated micritic limestones of the Barcaliente Formation are replaced here by grey more shallow water limestones with some shale intervals of the Peña unit (Wagner & Winkler Prins, in prep.).

In northern Palencia the basal part of the Carrión unit is dated as late early Viséan. It overlies the siltstone unit, which is undated, but which overlies black shales of the Vegamián Formation (uppermost Tournaisian?). The Carrión unit is conformably overlain by the Peña unit (Wagner & Winkler Prins, in prep.).

The present paper addresses the lower part of the carbonate succession north of the Ruesga Fault in the Palentian domain. The whole succession, 42 m thick, spans the interval from mid-Viséan through lower Serpukhovian. The section studied occurs in a small syncline with a faulted core. Two limbs of this syncline are well exposed, and are shown in this paper as Section 1 and Section 2 (Figs. 2, 3, respectively). The third section is a part of a successive anticline and is shown in this paper as Section 3 (Fig. 4). In Section 1 the number of samples goes in ascending order from 8435 to 8478 and includes a

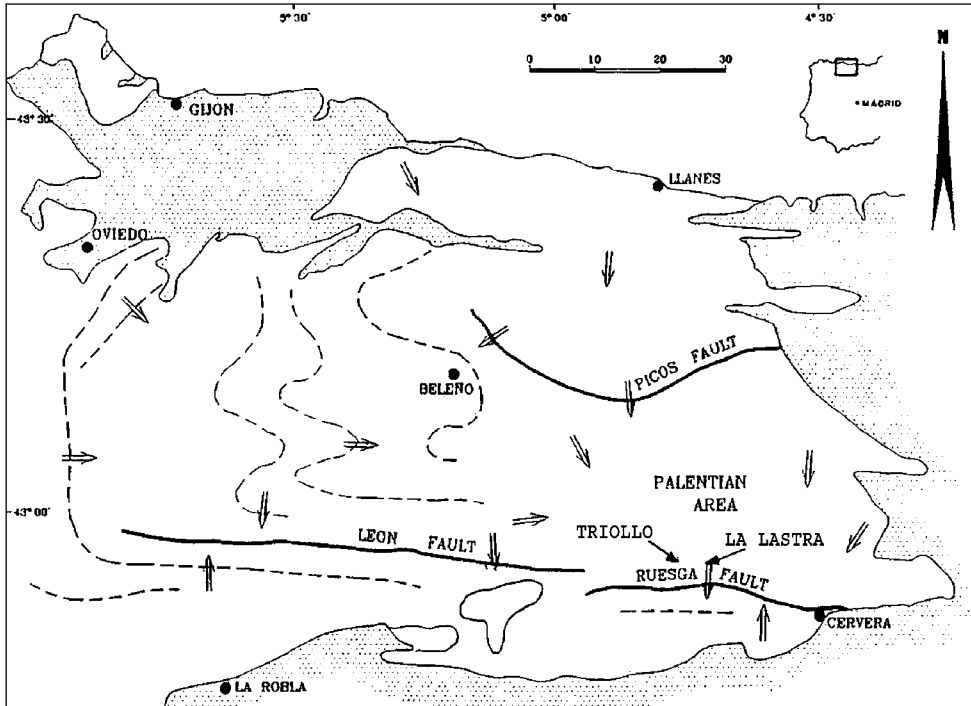


Fig. 1. General map showing the location of the studied section, Triollo village (from Wagner & Winkler Prins, 2000; arrows show the turnaround of vergencies). Supra-Carboniferous cover stippled.

number of additional samples (8720-8723, 8750-8757, 8784-8792). Section 2 was not sampled as closely as Section 1; it contains samples 8494 to 8479 (descending order) with two additional samples 8793 and 8794. Section 3 yielded just a few samples (8495-8499).

Section 1 is characterized by a condensed succession of grey, finely laminated limestones with marly intervals, mottled interlayers, and bands of nodular limestones and a chert member in its lower part (Wagner & Winkler Prins, in prep.). It contains abundant, predominantly pelagic faunas consisting of conodonts, entomozoan ostracodes (mostly in the lower part of the section) and fish remains. Radiolarians occur in the proximity of the chert member and in the limestone layers with cherty nodules. Poorly preserved, mostly juvenile ammonoids were observed in places, mostly in the lower part of the section. The rocks and fauna indicate open, fairly deep marine environments.

Previous studies

The Genicera and Barcaliente formations were studied by Winkler Prins (1968), Wagner *et al.* (1971) and Reuther (1977) in northern León. Winkler Prins (1968) was the first to subdivide the Genicera Formation into three members and "Caliza de Montana" into two; the Vegacerbera Micrite and Valdeteja Biosparite members. The first was later renamed the Barcaliente Formation (Wagner *et al.*, 1971). At the same time, the three

members of the Genicera Formation were given names from a single type locality and previous Carboniferous studies in the Cantabrian Mountains were summarised. From the 1960s onwards the main fossil groups have been studied, such as ammonoids (Kullmann, 1961, 1962, 1963; Wagner-Gentis, 1963; Korn, 1993; mentioned by Wagner, 1957), brachiopods (Winkler Prins, 1968), trilobites (Gandl, 1977) and ostracodes (Becker, 1976, 1982; Sánchez de Posada, 1976, 1987).

The first conodont studies of the Alba (= Genicera) Formation were by Higgins (1962), Budinger & Kullmann (1964), Budinger (1965) and van Adrichem Boogaert (1967). Later, Higgins & Wagner-Gentis (1982) presented additional information on the conodonts and ammonoids. Boersma (1973), studying conodonts from the Spanish Pyrénées, compared them to those of the Palenian basin. Conodonts of the lower part of the Genicera Formation (anchoralis-latus and texanus Zones) were studied by Lane *et al.* (1980) and included in their work on the general post-Siphonodella conodont zonation. These oldest conodonts of the Genicera Formation were also studied partly by Raven (1983).

Only van Adrichem Boogaert (1967) presented a full conodont succession of the Alba (= Genicera) Formation. In his Ph.D. on the Carboniferous conodonts of the Rheinisches Schiefergebirge and Cantabrian Mountains, Park (1983) also provided a detailed analysis of the conodonts of the Genicera and Barcaliente formations of the Cantabrian Mountains from a series of sections including Olleros de Alba, Esla, Resoba and Valdoré south and north of the Ruesga Fault. Unfortunately, this thesis was not published, although this very informative work was widely distributed among conodont workers. At the same time, Menéndez-Álvarez and Méndez started to study the Carboniferous conodonts of the Cantabrian Mountains. A rich collection of conodonts from the Genicera and Barcaliente formations was only partly published in several papers (Menéndez-Álvarez, 1978; Méndez & Menéndez-Álvarez, 1985; Sánchez de Posada *et al.*, 1993).

Since the 1990s, detailed conodont studies of the Viséan and Lower Serpukhovian were carried out by van den Boogaard, who was working on the Palaeozoic conodonts of Spain and Portugal for a long time. He re-investigated the conodonts of van Adrichem Boogaert from the Alba Formation and studied in detail the conodonts from the sections north of the Ruesga Fault sampled by Wagner and Winkler Prins (van den Boogaard, 1992). The Tournaisian and Viséan conodonts of the Cantabrian Mountains and the Spanish Pyrénées were studied by Sanz-López (1995), García-López & Sanz-López (2002a, b) and Sanz-López *et al.* (2004).

Belka & Korn (1994) and Belka & Lehmann (1998) also worked on the Viséan and early Serpukhovian conodonts of the Cantabrian Mountains. The Early Viséan conodonts and ammonoids from the Esla area were presented by Belka & Korn (1994). The Late Viséan and Early Namurian conodonts from this area were published by Belka & Lehmann (1998). The conodont associations from the section at Santa Olaja de la Varga are similar to those from the Triollo section, but differ in abundance of conodonts per 1 kg of rocks and by the virtual absence in Santa Olaja of the *Vogelgnathus* conodont fauna. In the adjacent region of the French Pyrénées, where the Mississippian conodonts have been studied for many years by Perret (1977, 1993), the conodont assemblages are more similar to those studied by Menéndez-Álvarez and Belka from the Alba and Barcaliente formations than to those from the Carrión and Peña units of the Palenian Basin. Probably, the Triollo section represents a deeper water facies than those in the Esla area and the French Pyrénées.

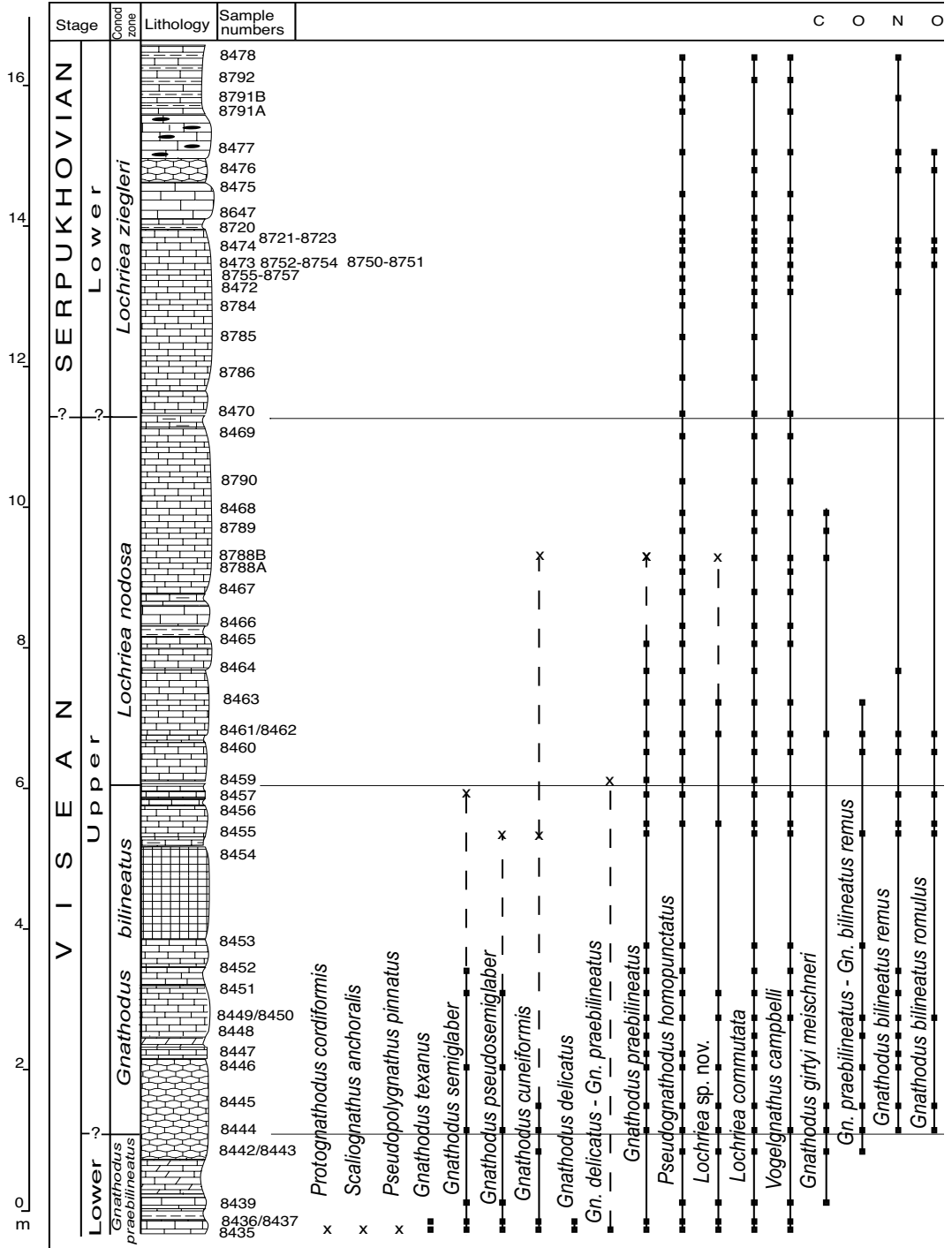
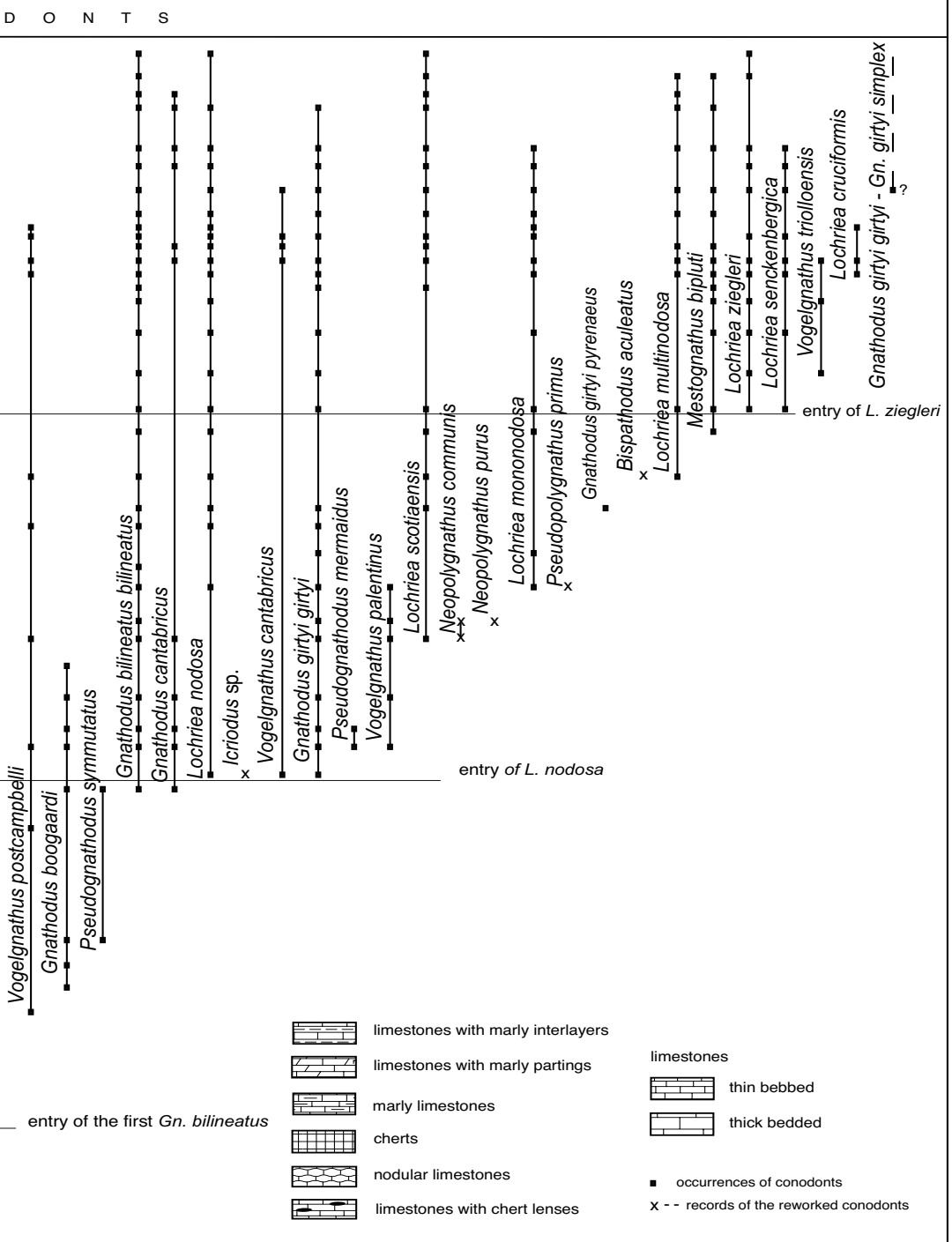


Fig. 2. Distribution chart of the latest early Viséan through early Serpukhovian conodonts at Triollo Section 1



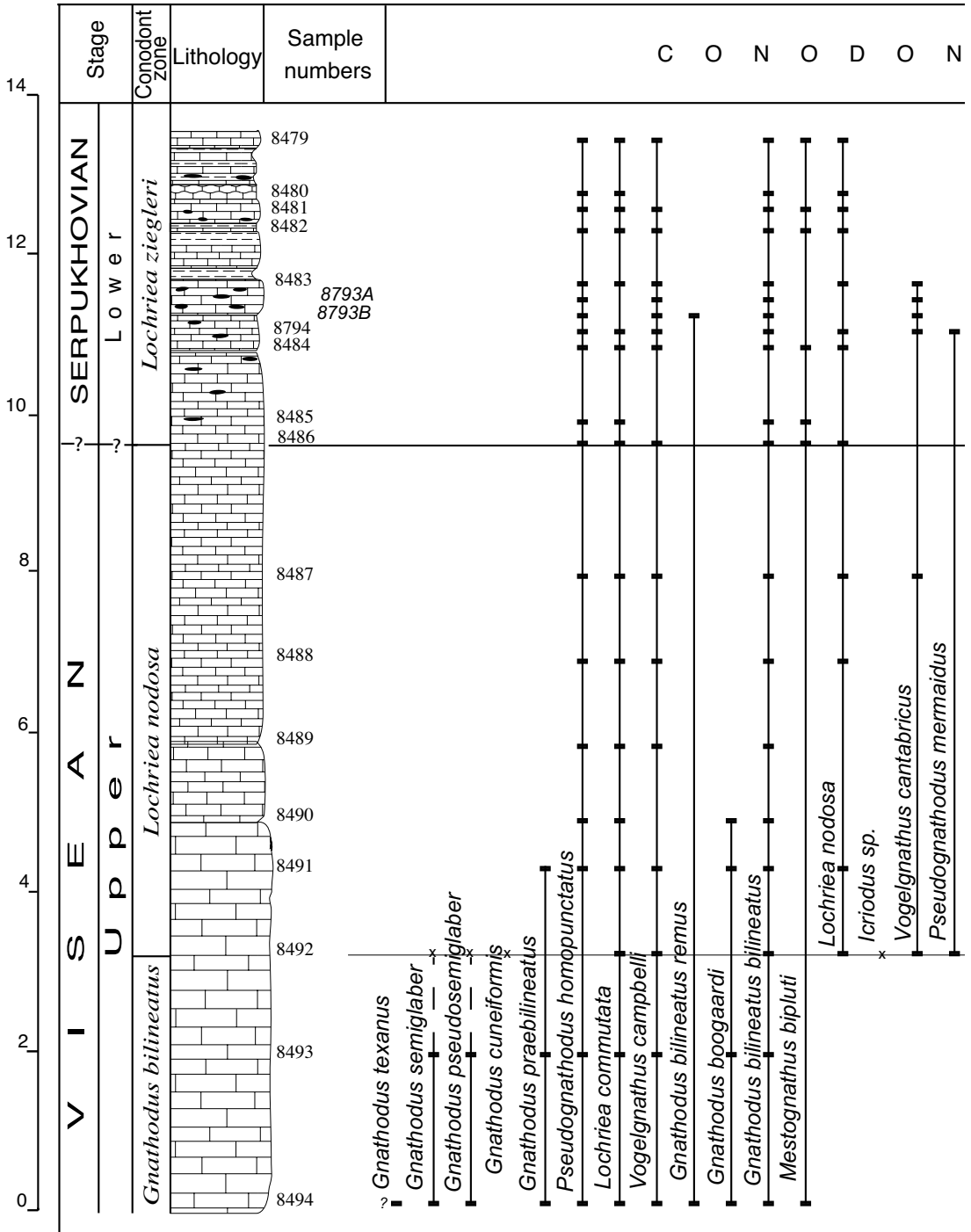
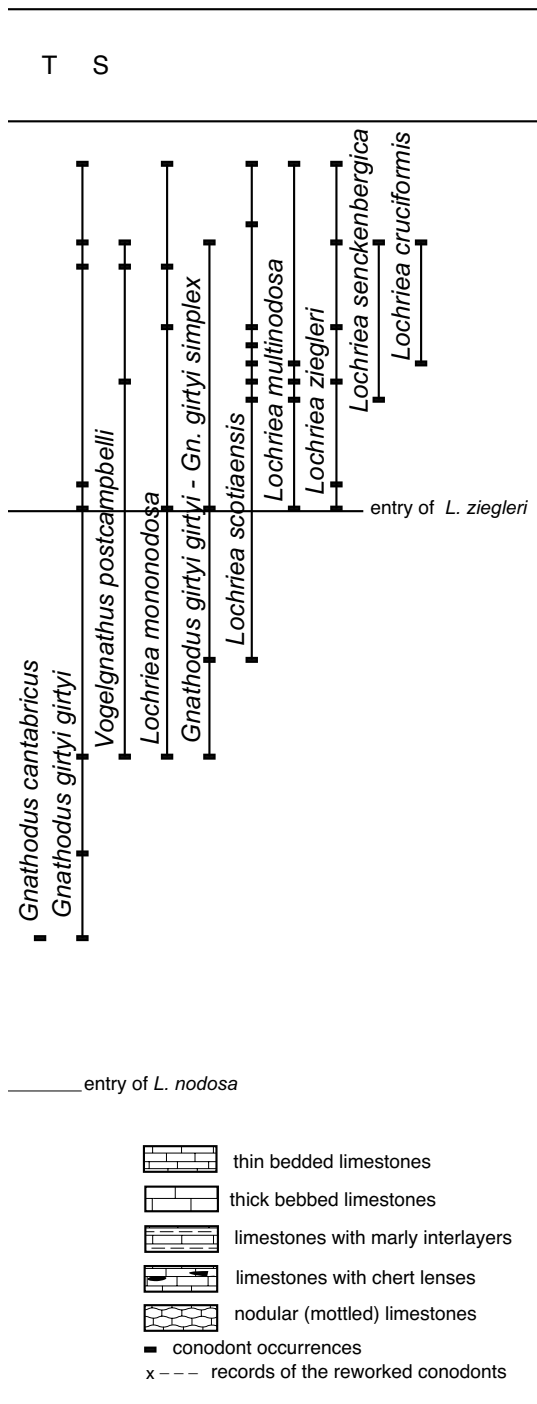


Fig. 3. Distribution chart of the late Viséan through early Serpukhovian conodonts at Triollo Section 2.



Conodont fauna

Ninety-eight samples, each about 1 to 3 kg, were treated with formic acid followed by separation with sodium polytungstate. Each sample was productive except for a number in the lower part of the section, which could not be dissolved. Seventy four thousand five hundred and thirty seven mostly well-preserved platform conodont elements, including a large number of juveniles, were extracted. Conodont frequency is rather high due to a low sedimentation rate and pelagic environments. On the average it is in excess of 100-300 platform elements per 1 kg, and it exceeds 1000 specimens per 1 kg at certain levels (Figs. 5-7; samples 8465, 8467, 8482, 8492, 8752, 8794).

The pectiniform (platform) elements outnumber the ramiform ones. Work concentrated entirely on the platform elements and only these elements have been classified in the present paper.

The conodonts of the Triollo section include all known conodont genera characteristic of the deep water late Viséan-early Serpukhovian successions. These are the *Gnathodus bilineatus* and *Gn. girtyi* groups of species, and the genera *Pseudognathodus*, *Lochriea* and *Vogelgnathus*, which are all represented by species known elsewhere. *Mestognathus bipluti* Higgins, which is supposed to be a more shallow water species, is also present in small numbers around the Viséan/Serpukhovian boundary. Among the ramiform elements the representatives of the genus *Kladognathus* were also found occasionally. However, in general, ecologically mixed conodont assemblages were not found in the Triollo section. Only the lowermost beds contain a number of late and latest Tournaisian and early Viséan species like *Gn. cuneiformis* Mehl & Thomas, *Gn. semiglaber* Bischoff, *Gn. pseudosemiglaber* Thompson & Fellows and *Scaliognathus anchoralis* Branson & Mehl. The latter is re-

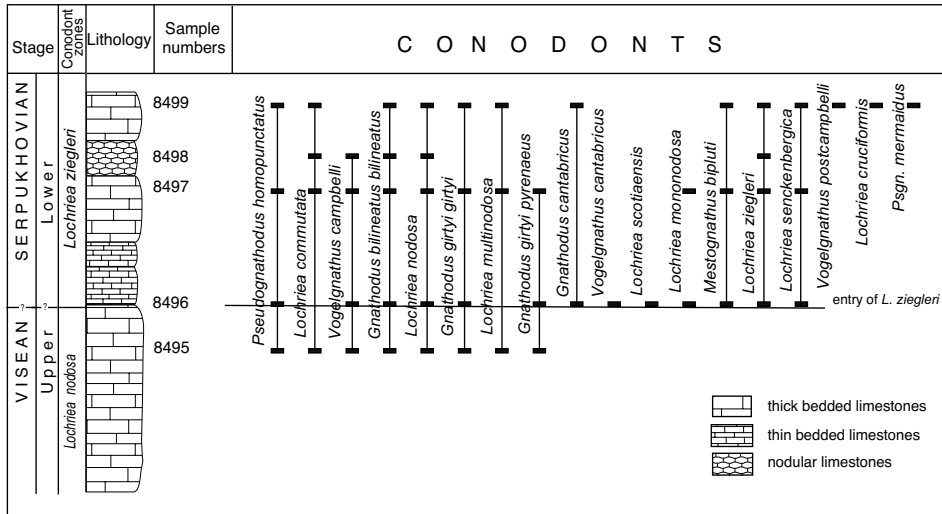


Fig. 4. Distribution chart of the latest Viséan-early Serpukhovian conodonts at Triollo Section 3.

worked. The range of the other above-mentioned species can overlap the range of *Gn. praebilineatus* Belka and *Gn. bilineatus* (Roundy). There are several levels with reworked Devonian and Tournaisian species represented by single specimens.

Simple statistical analysis of the platform conodont assemblages in the Triollo section (Fig. 8) shows that in general conodont fauna here, as elsewhere in the Cantabrian Mountains, is dominated by the *Gnathodus bilineatus* group including *Gn. praebilineatus* Belka, *Gn. bilineatus remus* Meischner & Nemyrovska, *Gn. bilineatus romulus* Meischner & Nemyrovska, *Gn. bilineatus bilineatus* (Roundy) and all transitional forms between them, as well as *Gn. cantabricus* Belka & Lehmann. There are a great number of juveniles, which could not be identified at species level. *Gnathodus bilineatus bilineatus* is the major element of this group (Figs. 5-7).

The next abundant group of conodonts (Fig. 8) includes the *Vogelgnathus* species with *V. campbelli* (Rexroad) being most numerous. *Vogelgnathus postcampbelli* (Austin & Husri), as well as the other three new species, are less common.

The distribution of conodonts throughout the section shows that the assemblage consisting of the *Gn. bilineatus* group of species is persistently dominant except where it is replaced by the *Vogelgnathus* fauna. Where the *bilineatus* group is abundant, the *Vogelgnathus* species play a subordinate role. On the other hand, thousands of tiny specimens of *Vogelgnathus*, mainly *V. campbelli*, dominate *Gn. bilineatus* and the other conodont faunas at several levels throughout the section (Figs. 9-13).

Van den Boogaard (1992, p. 2) pointed out that the sequence of faunas dominated by the *Gnathodus bilineatus* group is "briefly interrupted by faunas in which *V. campbelli* dominates." He examined the conodonts of the other sections in the Cantabrian Mountains to understand whether this drastic change in faunal composition was a local phenomenon of the Triollo section or not. His analysis showed that this scenario is common also in other places of the Cantabrian Mountains. Van den Boogaard regarded the invasions of *V. campbelli* to reflect the periods of maximum sea-level rise.

<i>Protognathodus cordiformis</i>	1	<i>Gn. cantabricus</i>	99
<i>Scaliognathus anchoralis anchoralis</i>	1	<i>L. nodosa</i>	944
<i>Pseudopolygnathus pinnatus</i>	1	<i>Vog. cantabricus</i>	214
<i>Gnathodus texanus</i>	156	<i>Icriodus</i> sp.	3
<i>Gn. semiglaber</i>	177	<i>Gn. girtyi girtyi</i>	1188
<i>Gn. pseudosemiglaber</i>	4401	<i>Ps. mermaidus</i>	74
<i>Gn. cuneiformis</i>	227	<i>Gn. girtyi meischneri</i>	32
<i>Gn. delicatus</i> - <i>Gn. praebilineatus</i>	38	<i>Vog. palentinus</i>	120
<i>Gn. praebilineatus</i>	1552	<i>L. scotiaensis</i>	536
<i>Pseudognathodus homopunctatus</i>	10424	<i>Neopolygnathus communis communis</i>	2
<i>Lochriea</i> sp. nov.	105	<i>Neopolygnathus purus</i>	1
<i>L. commutata</i>	5531	<i>L. mononodosa</i>	137
<i>Vogelgnathus campbelli</i>	19413	<i>Pseudopolygnathus primus</i>	1
<i>Gn. aff. girtyi meischneri</i>	30	<i>Bispathodus aculeatus</i>	1
<i>Gn. praebilineatus</i> - <i>Gn. bilineatus remus</i>	467	<i>Mestognathus bipluti</i>	119
<i>Gn. ex gr praebilineatus</i> - <i>bilineatus juv.</i>	4682	<i>L. multinodosa</i>	695
<i>Gn. bilineatus remus</i>	722	<i>L. zieglerei</i>	924
<i>Mestognathus</i> sp.	2	<i>L. senckenbergica</i>	522
<i>Gn. bilineatus romulus</i>	312	<i>Vog. triolloensis</i>	36
<i>Vog. postcampbelli</i>	264	<i>L. cruciformis</i>	31
<i>Gn. boogaardi</i>	95	<i>Gn. girtyi girtyi</i> - <i>Gn. girtyi simplex</i>	41
<i>Ps. symmutatus</i>	13	<i>Gn. girtyi pyrenaicus</i>	19
<i>Gn. bilineatus bilineatus</i>	20182	Total	74537

Fig. 5. Total number of Pa elements in Triollo sections 1-3.

The third abundant group of conodonts contains the *Pseudognathodus* species, the most numerous being *Ps. homopunctatus* (Ziegler), with less than 100 specimens of *Ps. mermaidus* Austin & Husri throughout the section and very rare *Ps. symmutatus* (Rhodes, Austin & Druce).

The fourth place in abundance of conodonts is occupied by the *Lochriea* group of species. Like in other sections all over the world, *L. commutata* (Branson & Mehl) is much more numerous than the other species of *Lochriea*. At the levels where *Vogelgnathus* dominates (Fig. 8), simple unornamented *Lochriea* species (*L. commutata* (Branson & Mehl), *L. scotiaensis* (Globensky), and *Lochriea* sp. nov.) are represented by a much smaller number of specimens. The same is true to some extent for the ornamented *Lochriea* (*L. nodosa* (Bischoff), *L. mononodosa* (Rhodes, Austin & Druce), *L. zieglerei* Nemirovskaya, Perret & Meischner, *L. senckenbergica* Nemirovskaya, Perret & Meischner, *L. multinodosa* (Wirth) and *L. cruciformis* (Clarke)). Ornamented *Lochriea* species are generally less abundant than the simple ones.

Least abundant is the *Gn. girtyi* group, which, besides rather common *Gn. girtyi girtyi* Hass, includes the forms transitional between *Gn. girtyi girtyi* and an American species, *Gn. girtyi simplex* Dunn, previously unknown from Europe (Nemirovskaya & Nigmatganov, 1994), but recorded from the Bechar Basin, Sahara (collection of M. Weyant). There are forms similar to *Gn. girtyi rhodesi* Higgins, but somewhat different; they could not be certainly identified because of their small size. A small number of the other *girtyi*-related forms, which I have seen before only in the collection of M.-F. Perret (upper Viséan/lower Serpukhovian of the Pyrénées), were also found in the coeval rocks of the

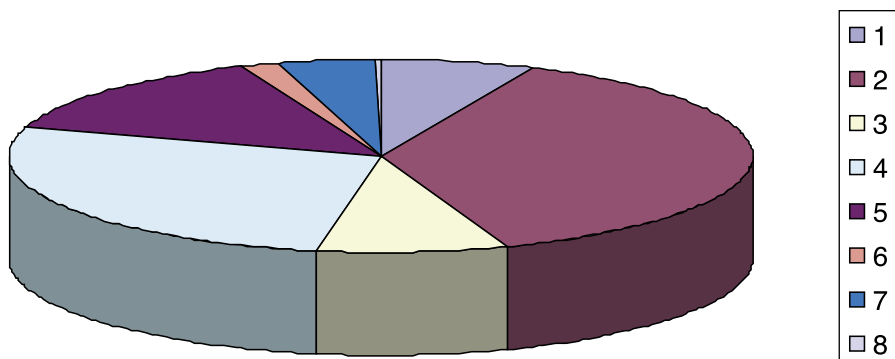


Fig. 6. General statistical characteristics of the latest early Viséan through the early Serpukhovian conodont assemblages in the Triollo sections, showing average contents of the main ecological groups. These groups (1-8) are further referred to in Figs. 7-11.

- 1 *Gnathodus texanus*, *Gn. semiglaber*, *Gn. pseudosemiglaber*, *Gn. cuneiformis*, *Gn. delicatus* and transitional forms between *Gn. delicatus* and *Gn. praebilineatus*;
- 2 *Gnathodus bilineatus* group of species (including *Gn. cantabricus*, *Gn. praebilineatus* and *Gn. boogaardi*);
- 3 Simple *Lochria*: *L. commutata*, *L. sp. nov.* and *L. scotiaensis*;
- 4 *Vogelgnathus* group of species;
- 5 *Pseudognathodus* group of species;
- 6 *Gnathodus girtyi* group of subspecies;
- 7 Ornamented *Lochria*: *L. nodosa*, *L. mononodosa*, *L. multinodosa*, *L. ziegleri*, *L. senkenbergica* and *L. cruciformis*; and
- 8 *Mestognathus*.

Triollo section. These forms are described and named here as *Gn. girtyi pyrenaicus* subsp. nov. (Figs. 2, 4; Pl. 7, figs. 6, 8-12). Rarity of *Gn. girtyi* and *girtyi*-related forms is characteristic for the Cantabrian Mountains (Higgins & Wagner-Gentis, 1982; Park, 1983; van den Boogaard, 1992; Belka & Lehman, 1998). Higgins & Wagner-Gentis (1982) suggested that the reason could be a partial geographic isolation of this region. This may find support by the occurrence of several conodont species of *Vogelgnathus*, *Gnathodus* and *Lochria* unknown from other areas of Laurussia.

Mestognathus bipluti Higgins, known mostly from shallow water deposits, occurs in a number of samples of the Viséan/Serpukhovian boundary interval in the Triollo section. It might have been periodically transported into the investigated basin from more near shore areas. Its quantity is so small, often less than 1% (only in sample 8647 is it 2%), so its contribution is hardly seen in Figure 9.

The *Gn. bilineatus* lineage starts from its ancestor *Gn. praebilineatus*, followed by the first representatives of the *bilineatus* group, *Gn. bilineatus remus* and *Gn. bilineatus romulus*, which gave rise to *Gn. bilineatus bilineatus* and probably to *Gn. cantabricus*. There are forms in the upper part of the section which show the features of more advanced *bilineatus*, but they still cannot be assigned to *Gn. bilineatus bollandensis*. There is another species, *Gn. boogaardi* sp. nov., whose entry was registered within the lowermost part of the *Gn. bilineatus* Zone, but its simple primitive structure with very weakly

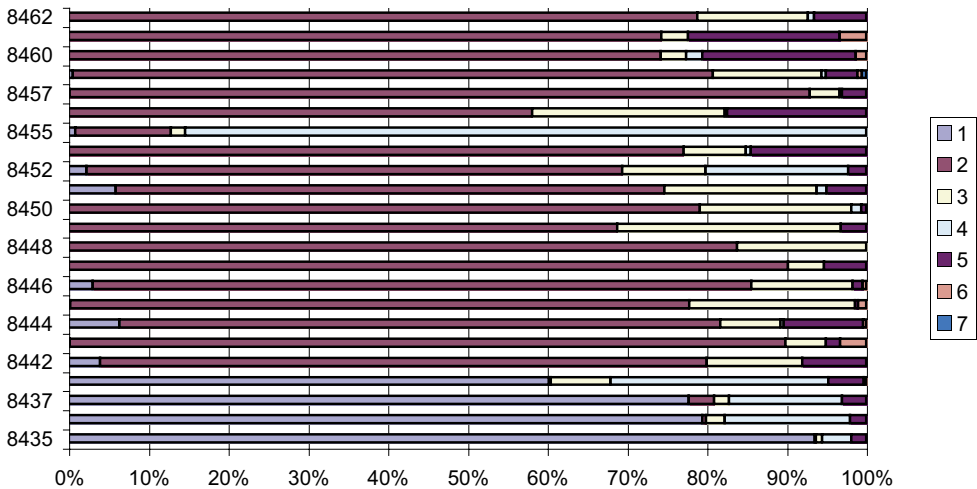


Fig. 7. Statistical characteristics of the latest early Viséan and late Viséan main ecological groups of conodonts in Triollo Section 1, *Gn. praebilineatus* through *L. nodosa* zones, samples 8435-8463.

developed parapet and very weak ornamentation might indicate that it could have originated earlier.

The *Lochriea* lineage is well represented by all known species recorded in the interval of the upper Viséan-lower Serpukhovian elsewhere. *Lochriea* sp. nov. Nemyrovska *et al.* (in press), one of the oldest species of *Lochriea*, which probably appeared at the beginning of the Viséan, is common in the lower part of the Triollo section. It is also known from the lower/upper Viséan boundary beds in other areas (in the Rheinisches Schiefergebirge, Germany – Meischner & Nemyrovska, 1999; in the lower Viséan of the Saoura Valley, Algeria – Nemyrovska *et al.*, in press; in the Arundian of the south Wales – Stone, 1991). The early Viséan species *L. cracoviensis* Belka, 1985, was not found in the Triollo area. The occurrence of *L. scotiaensis* Globensky in the Triollo section is the first record of this species in Europe, although recently I saw it in the collection of M.-F. Perret from the Pyrénées. It was distinguished and so far known only from the upper Viséan of Nova Scotia (Globensky, 1967). The entry of this simple, unornamented *Lochriea* is within the *L. nodosa* Zone. It reaches the Serpukhovian. It is common, but not as abundant as *L. commutata* throughout the section (none of the *Lochriea* species is as abundant as *L. commutata* as a rule). It is most numerous in the lower Serpukhovian beds (Figs. 5-7).

It is suggested that all strongly ornamented *Lochriea* derived from *L. nodosa* (Nemyrovskaya *et al.*, 1994; Skompski *et al.*, 1995). The vertical succession of the strongly ornamented *Lochriea* in Triollo, as well as in the Esla area (Belka & Lehmann, 1998), is almost the same as in other areas. However, it differs a little from that in the Rheinisches Schiefergebirge and the Lublin Basin by the earlier appearance of *L. cruciformis* than *L. ziegleri* and *L. senkenbergica*. *Lochriea mononodosa* is regarded to be an ancestor of *L. nodosa*. That means that its first appearance should be earlier than that of *L. nodosa*. However, in Triollo and Esla the entry of *L. mononodosa* is after the first occurrence of *L. nodosa*. In

both sections *L. mononodosa* is rather rare. Belka explained the later appearance of this species by the small size of his samples, but here in Triollo this explanation would not work, since the conodont faunas are abundant. The forms illustrated as *L. mononodosa* from the Viséan/Serpukhovian boundary beds (Skompski, 1996; Skompski *et al.*, 1995) show a more advanced sculpture than those which could fit the lineage *L. commutata* to *L. mononodosa* to *L. nodosa*. These specimens have only one big node or ridge on one side of the platform, but this node is too big to regard these forms as ancestors of *L. nodosa*. On the other hand *L. mononodosa* is everywhere rather rare, so it is difficult to define its exact entry. In many areas *L. nodosa* and *L. mononodosa* appear simultaneously; the first co-occurrence often coincides with a major increase in conodont diversity and abundance (Somerville & Somerville, 1999).

The same problem occurs with *L. cruciformis*. *Lochriea zieglerei* and *L. senkenbergica* are always found in much greater numbers than *L. cruciformis*. This could be why we cannot get it in the same succession of the *Lochriea* species in different areas. That is why the Viséan/Serpukhovian boundary is easier to define by *L. zieglerei*, which occurs everywhere and with much larger number of specimens.

Conodont biostratigraphy

At least two groups of conodonts have a great potential for subdivision of the upper Viséan and lower Serpukhovian, and intercontinental correlation. These are the *Gnathodus bilineatus* and *Lochriea* groups. Both are well represented and abundant in the Triollo section (Figs. 2-4). The *Gn. bilineatus* group displays the lineage from *Gn. praebilineatus* through *Gn. bilineatus remus* and/or *Gn. bilineatus romulus* to *Gn. bilineatus bilineatus* with a great number of transitional species. *Gnathodus cantabricus* is a form related to *Gn. bilineatus s.l.* although its origin is not clear. The *Gnathodus girtyi* group is important in Viséan sections elsewhere, but not in the Cantabrian Mountains, where it is poorly represented.

The *Lochriea* group of species starts with *L. saharae* and/or *L. commutata*, which gave rise to ornamented *Lochriea* from *L. mononodosa* and *L. nodosa* to *L. zieglerei*, *L. multinodosa*, *L. senkenbergica* and *L. cruciformis*. The *Lochriea* lineage and relationships between its species have been well studied and documented in other areas, more so than those of the *Gn. bilineatus* group. Although *Gn. bilineatus* species are common around the world and are more abundant than *Lochriea* species, the relationships between its numerous morphotypes, species and subspecies are not very clear especially in the lower Serpukhovian. On the other hand, the well-documented lineage of *Lochriea* is valid only for Eurasia, as in North America the strongly ornamented *Lochriea* have not yet been found.

Taking into account the importance of the *Gn. bilineatus* group for the subdivision of the Viséan and worldwide correlations on one hand, and great significance of the *Lochriea* group for the definition of the Viséan/Serpukhovian boundary in Eurasia on the other (Skompski *et al.*, 1995), the following conodont zonation is based on the distribution of these two species groups. It is not a monogeneric zonation, but is good enough for worldwide correlations. Four conodont zones are distinguished in the Triollo section; *Gnathodus praebilineatus*, *Gn. bilineatus* and *Lochriea nodosa* zones in the Viséan, and *Lochriea zieglerei* Zone in the lower Serpukhovian.

Gnathodus praebilineatus Zone — The zone covers the lowermost part of the section, from sample 8435 to 8443, and is represented by marly limestones with sideritic nodules and the lower part of the nodular limestone member. The conodont assemblage consists of numerous *Gn. praebilineatus* and *Pseudognathodus homopunctatus*, common *L. commutata* and *L. saharae*, abundant *V. campbelli* and large numbers of *Gn. pseudosemiglaber*. Basal layers include numerous *Gn. pseudosemiglaber*, *Gn. semiglaber*, *Gn. cuneiformis* and *Gn. texanus*, as well as some transitional forms between *Gn. delicatus* and *Gn. praebilineatus*. Single specimens of reworked, very late Tournaisian forms, *Scaliognathus anchoralis anchoralis*, *Protognathodus cordiformis* and *Pseudopolygnathus pinnatus*, were found in the basal bed (sample 8435). Several specimens of *Gn. girtyi meischneri* occurred in this zone. The upper part of this zone is characterized by the occurrence of numerous transitional forms between *Gn. praebilineatus* and *Gn. bilineatus s.l.*

The lower boundary of the zone is not clear as the section starts with the *Gn. praebilineatus* Zone. Its upper boundary coincides with the lower boundary of the next zone, which is defined by the entry of *Gn. bilineatus*.

Gnathodus bilineatus s.l. Zone — The lower boundary of this zone is defined by the entry of the *Gn. bilineatus remus* and *Gn. bilineatus romulus* (sample 8444), which represent the earliest subspecies of *Gn. bilineatus s.l.* Its upper boundary coincides with the entry of *L. nodosa* and *Gn. cantabricus* (samples 8457-8459).

This zone embraces the interval of the section between sample 8444 and 8457. The main characteristic conodonts are *Gn. bilineatus remus* and *Gn. bilineatus romulus*, with *Gn. praebilineatus*, *L. commutata* and *L. sp. nov.* still being present. *Vogelgnathus campbelli* is abundant only in the upper beds, where *V. postcampbelli* joins this species. In the middle of the zone a species with very simple, primitive ornamentation, *Gn. boogaardi sp. nov.*, occurs. Its first appearance could be much earlier. A great number of juveniles, probably transitional between *Gn. praebilineatus* and *Gn. ex gr. bilineatus*, were recorded in every sample. Single specimens of *Gn. bilineatus bilineatus* and *Gn. cantabricus* occurred in the uppermost bed.

Lochriea nodosa Zone — The lower boundary of this zone is defined by the first appearance of *L. nodosa* (sample 8459); its upper boundary coincides with the entry of more ornamented *Lochriea (L. ziegleri)*. This zone embraces the interval between samples 8459 and 8469 (Section 1). The entry of *L. nodosa* is an important stage of evolution of the *Lochriea* species, which can be traced all over Eurasia.

The most characteristic species of this zone are *L. nodosa*, *Gn. bilineatus bilineatus*, *Gn. cantabricus*, *V. campbelli*, *V. palentinus*, *Ps. homopunctatus*, *L. commutata* and *Gn. girtyi girtyi*, although the last one is not numerous. *Gnathodus praebilineatus*, *Gn. girtyi meischneri* and *L. saharae* are rather scarce, but still present. *Vogelgnathus cantabricus*, *L. mononodosa* and *L. scotiaensis* made their debut in this zone. None of these three species is numerous, but *L. scotiaensis* is much more common than *L. mononodosa*.

Lochriea ziegleri Zone — Only the lower boundary of this zone can be defined in the Triollo section, as the core of the syncline is hidden in the deformed zone. So, the youngest conodonts of this section belong to the *L. ziegleri* Zone. The lower boundary of this zone is defined by the first appearance of *L. ziegleri*, which may be regarded the

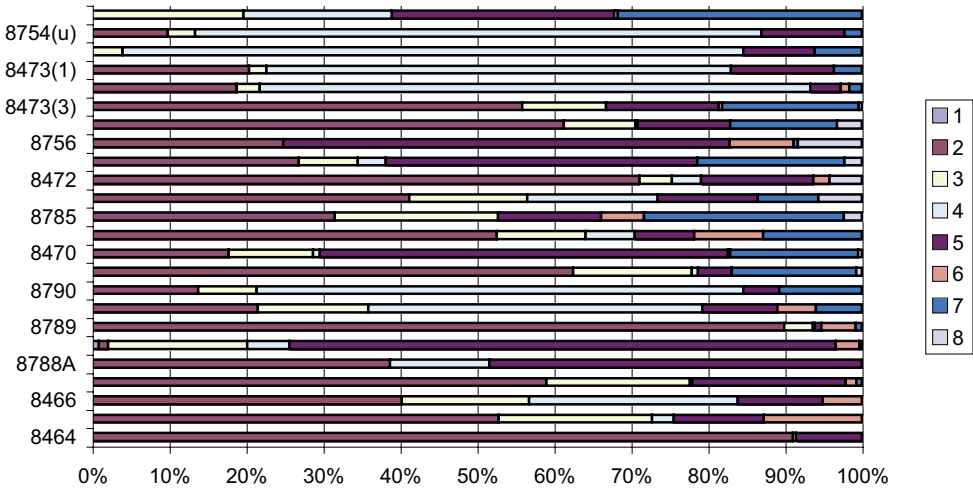


Fig. 8. Statistical characteristics of the late Viséan-early Serpukhovian main ecological groups of conodonts in Triollo Section 1, *L. nodosa* through *L. ziegleri* zones, samples 8464-8753.

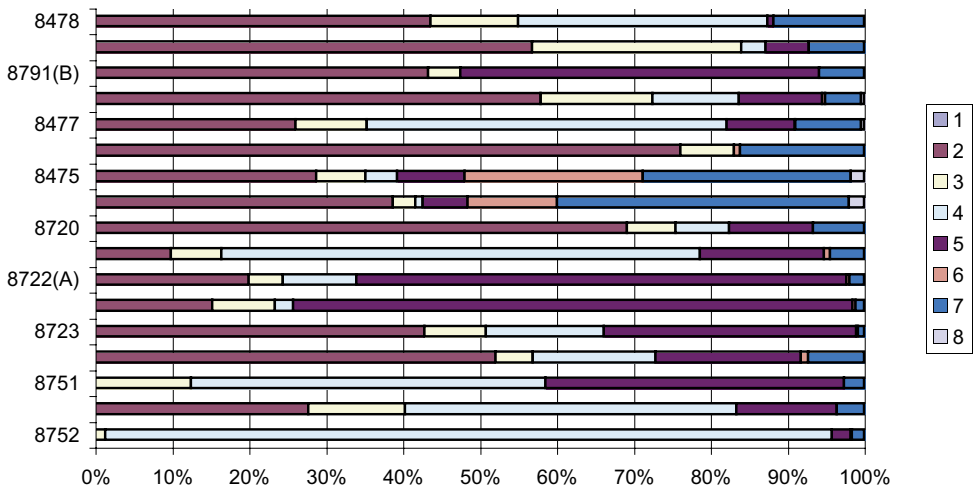


Fig. 9. Statistical characteristics of the early Serpukhovian main ecological groups of conodonts in Triollo Section 1, *L. ziegleri* Zone, samples 8752-8478.

best marker for the Viséan/Serpukhovian boundary. Another advanced (strongly ornamented) *Lochriea multinodosa* appears a little earlier; it is known only from the Cantabrian Mountains, Pyrénées, Graz and Serbia, and its first appearance was never controlled by goniatites. Therefore, I use *L. ziegleri* as the zonal index and draw the lower boundary of this zone at the *L. ziegleri* entry. The following species are characteristic of this zone; *L. ziegleri*, *L. senkenbergica*, *L. multinodosa*, *L. cruciformis*, *Gn. bilineatus bilineatus*, *L. nodosa*, *L. scotiaensis*, *Gn. cantabricus* and *Gn. girtyi girtyi*, *V. campbelli*, *V. postcampbelli* and *V. triolloensis*, *L. commutata* and *Psg. homopunctatus*.

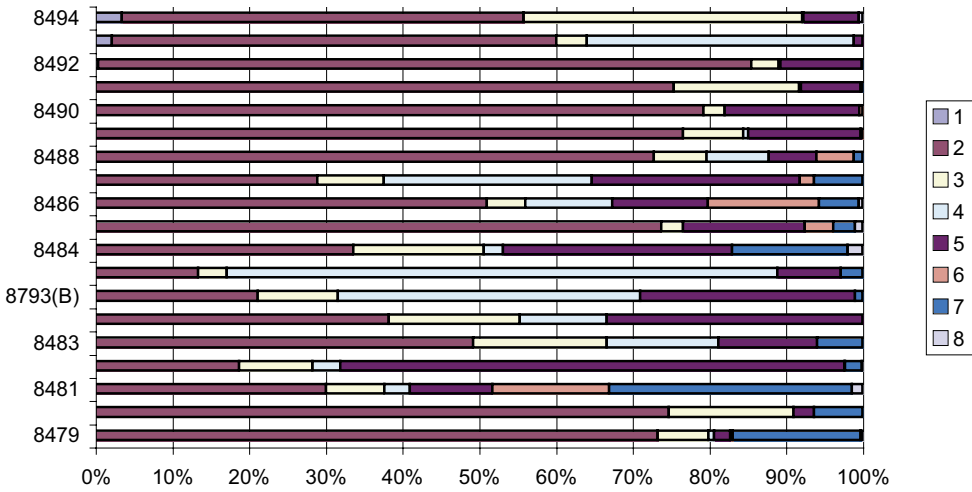


Fig. 10. Statistical characteristics of the late Viséan-early Serpukhovian main ecological groups of conodonts, *Gn. bilineatus* through *L. ziegleri* zones, samples 8494-8479.

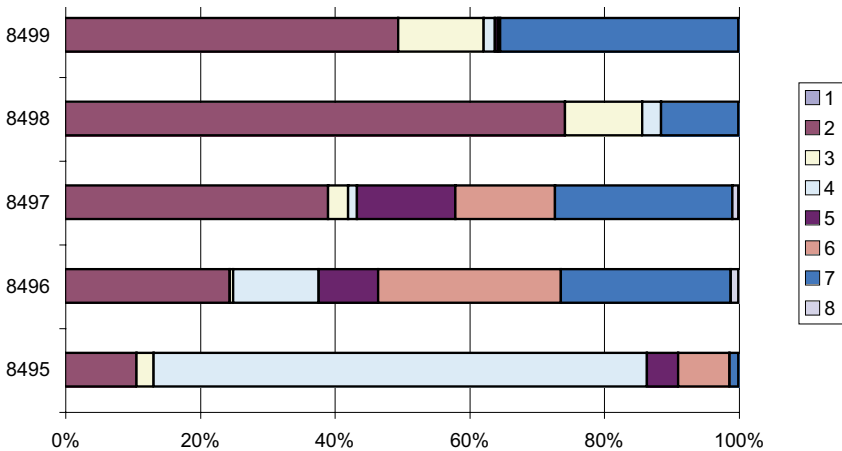


Fig. 11. Statistical characteristics of the latest Viséan-early Serpukhovian main ecological groups of conodonts, late *L. nodosa* through *L. ziegleri* zones, samples 8495-8499.

In Section 2, which represents another limb of the syncline, the forms transitional between *Gn. girtyi girtyi* and *Gn. girtyi simplex* were found (Fig. 3; Pl. 7, figs. 16-20). The latter species was not previously known from Europe. It is widely distributed in North America and is the index-species of the latest Mississippian zone. It is also known from the Bechar Basin, Sahara (collection of M. Weyant). The occurrence of transitional forms between *Gn. girtyi girtyi* and *Gn. girtyi simplex* suggests the latest Viséan-early Serpukhovian. Anita Harris supposed these transitional forms to come in at the very beginning of the Serpukhovian (pers. comm., March, 2002). These forms are rather rare in

the studied area (*Gn. girtyi* group in general in the Cantabrian Mountains is rather rare) and probably that is the reason for their different occurrence in two sections; in Section 1 within the *L. zieglerei* Zone, but in Section 2 below the entry of *L. zieglerei*. Probably the samples including these transitional forms were represented by slightly different facies in both sections (Figs. 2, 3).

Correlation

The majority of conodont species from the Triollo section occur in other areas of Eurasia and North America. In Eurasia, correlation between a number of sections represented by relatively deep-water facies with Triollo is rather easy; even in shallow water sections there are a large number of species in common with it. However, late Mississippian conodont faunas of North America differ greatly, since they are represented mostly by shallow-water taxa and also because some stratigraphically very important Eurasian species have not been yet found there.

Abundant and taxonomically diverse conodont faunas in the Triollo sections enable the correlation of the Carrión unit and the lower part of the Peña unit to the coeval deposits of other areas. Two levels are the most reliable for correlation by conodonts within the studied interval; the entry of *Gn. bilineatus s.l.* and the first occurrence of strongly ornamented *Lochriea*, particularly *L. zieglerei*.

The first appearance of *Gnathodus bilineatus* is controlled by ammonoids in Germany and England. In the Rheinisches Schiefergebirge the first appearance of *Gn. bilineatus romulus* Meischner & Nemyrovskaya, the earliest representative of the *Gn. bilineatus* group, was recorded within the latest *Entogonites nasutus* Ammonoid Zone (still *Pericyclus*-Stufe of the German goniatite zonation), a little below the first occurrence of the *Entogonites grimmeri* (*Goniatites*-Stufe) (Meischner & Nemyrovskaya, 1999). In England, *Gn. bilineatus* is known to come in the middle of the Asbian (Metcalf, 1981; Varker & Sevastopulo, 1985). In North America, *Gn. bilineatus* appears at the base of the Chesterian (Lane & Straka, 1974; A. Harris, pers. comm., 2002). In the Moscow Basin it appears in the Alexinian Horizon (Makhlina *et al.*, 1993), in Urals in the Tulian (Pazukhin *et al.*, 2002), in the Donets Basin in the upper part of the Donetskian Horizon (Kozitskaya *et al.*, 1978).

The entry of strongly ornamented *Lochriea* is also controlled by ammonoids in Germany. Their first occurrence is very close to the base of the first Namurian ammonoid zone; *Emstites pseudocoronula* and *Cravenoceras leion* (Meischner & Nemyrovskaya, 1999).

Thus, the lowermost part of the Triollo section (lowermost part of the Carrión unit, samples 8435-8443, Section 1), below the entry of *Gn. bilineatus romulus* and *Gn. bilineatus remus*, belongs to the older *Gnathodus praebilineatus* Zone. This zone is represented in the Triollo sections only by its upper part and can be compared with the late *Gn. austini* Zone of Poland, which contains *Gn. praebilineatus*, but not *bilineatus* (Belka, 1985), and also to the part of the *Gn. praebilineatus* Zone of the Rheinisches Schiefergebirge (uppermost "Kulm-Kieselkalk" or upper part of the lower Viséan), Germany (Meischner & Nemyrovskaya, 1999). It seems to correspond to the late *Gn. praebilineatus* Zone of the Carnic Alps, Italy and Austria (Perri & Spaletta, 1998; Schönlaub & Kreutzer, 1993), and Pyrénées (Perret, 1993; Sanz López, 2002). The upper part of the *Gnathodus praebilineatus* Zone in Triollo can also be compared to the lower Asbian and maybe Holkerian of

England, and partly to the Tulian Horizon (*Gnathodus austini* Zone) of the Viséan of the Urals, Russia (Nikolaeva *et al.*, 2002). The overlap of *Gn. semiglaber*, *Gn. pseudosemiglaber* and *Gn. praebilineatus* is observed in the late Meramecian and earliest Chesterian in North America as well (A. Harris, pers. comm., March 2002).

The appearance of *Gnathodus bilineatus s.l.* represents an important stage in the evolution of Mississippian conodonts. This species is widely distributed in Eurasia and North America. Its first occurrence can be traced all over the Northern Hemisphere, and therefore it can serve as a good marker for intra- and intercontinental correlation. The interval of the Triollo section, which is characterized by the *Gnathodus bilineatus* Zone (samples 8444–8457 in Section 1 and samples 8494–8492 in Section 2), can be correlated to middle part of the Genicera (or Alba) Formation of the Cantabrian Mountains (van Adrichem Boogaert, 1967; Menéndez-Alvarez, 1978; Higgins & Wagner-Gentis, 1982; Park, 1983; van den Boogaard, 1992; Belka & Lehmann, 1998), to the uppermost part of the lower Viséan – lower part of the upper Viséan (lower part of the “Kulm-Plattenkalk”) of the Rheinisches Schiefergebirge (Meischner & Nemyrovskaya, 1999), and to the late Asbian of England (Metcalf, 1981; Varker & Sevastopulo, 1985). The same conodont assemblage was registered in the lower part of the upper Viséan of the Pyrénées (Marks & Wensink, 1970; Buchroithner, 1979; Perret, 1993; García-López & Sanz-López, 2002a), in the V3b of Belgium (Groessens, 1975), in the Alexinian and Mikhailovian horizons of the Russian Platform and the Urals (Barskov *et al.*, 1984; Makhlina *et al.*, 1993; Pazukhin *et al.*, 2002), and in the upper Meramecian/lower Chesterian (Upper Mississippian) of North America (Webster, 1969; Lane & Straka, 1974; Lane *et al.*, 1980; Krumhardt *et al.*, 1996; A. Harris pers. comm., 2002).

The *Lochriea nodosa* Zone, the latest Viséan zone, is widely recognized in Eurasia both in shallow and deep-water biofacies. In the Triollo section it corresponds to the interval between samples 8459 and 8469 (Section 1), and between samples 8492 and 8586 (Section 2). This part of the section can be compared to the upper beds of the Alba (= Genicera) Formation of the Cantabrian Mountains (van Adrichem Boogaert, 1967; Menéndez-Alvarez, 1978; Higgins & Wagner-Gentis, 1982; Park, 1983; van den Boogaard, 1992; Belka & Lehmann, 1998) and to the uppermost Viséan of the Pyrénées (Boersma, 1973; Buchroithner, 1979; Perret, 1993; Sanz-López, 2002). This zone is recognized in Britain (Varker & Sevastopulo, 1985), Ireland (Somerville & Somerville, 1999), Belgium (Groessens, 1975) and Poland (Belka, 1985; Skompski, 1996). In eastern Europe and Asia the *Lochriea nodosa* Zone was determined in the uppermost Viséan Venevian Horizon of the Moscow Syncline and South Urals (Makhlina *et al.*, 1991, 1993; Pazukhin, in Nikolaeva *et al.*, 2002), and the Tatangian Formation (uppermost Viséan) in China (Wang Zhi-hao & Qi Yu-ping, 2003).

The *Lochriea zieglerei* Zone is the earliest Serpukhovian conodont zone, easily distinguished in Eurasia. Its lower boundary represents the most reliable correlative level in Eurasia and coincides with the Viséan/Serpukhovian boundary. Unfortunately, *Lochriea zieglerei*, as well as all the other strongly ornamented *Lochriea*, has not been found in North America. The upper beds of the Triollo section can be correlated with the lowermost Serpukhovian of the French Pyrénées, England, Poland and Germany (Skompski *et al.*, 1997), Uzbekistan (Nigmatganov, pers. comm, 1999), Moscow Syncline and Urals (Nikolaeva *et al.*, 2002), the Lvov-Volhyn and the Donets Basin, Ukraine (Nemirovskaya, 1982; Nemirovskaya, 1985; Nemyrovskaya, 1999), and China (Wang Zhi-hao & Qi Yu-ping,

2003). In the Cantabrian Mountains and the Pyrénées the *Lochriea multinodosa* Zone was distinguished close to the Viséan/Serpukhovian boundary interval (Marks & Wensink, 1970; Higgins & Wagner-Gentis, 1982; Park, 1983; Perret, 1993). In the Triollo section *L. multinodosa* appears a little earlier than *L. zieglerei*. The presence (and abundance) of *Psg. homopunctatus*, *Gn. girty girtyi* and *L. scotiaensis*, known generally from the Viséan and lowermost Serpukhovian deposits, and the absence of advanced *Gn. bilineatus* (*Gn. bollandensis?*), suggests that the upper part of the Triollo section, characterized by the *L. zieglerei* Zone, is no younger than early Serpukhovian.

Thus, the Viséan/Serpukhovian boundary is easily recognizable in the Triollo section by the entry of *L. zieglerei*, *L. senckenbergica* and *L. cruciformis*. As mentioned above, the first appearance of *L. zieglerei* is preferable for a boundary marker as it is much more numerous elsewhere than *L. cruciformis* (Nemyrovska, 1999; Nikolaeva *et al.*, 2002; Wang Zhi-hao & Qi Yu-ping, 2003).

Main stratigraphic results

The record of abundant and diverse late Viséan and early Serpukhovian conodonts of the Triollo sections confirms the range of the included conodont zones and refines their boundaries. The presence in the Triollo sections of almost all of the known Viséan and Early Serpukhovian conodont species enables a reliable correlation with other areas.

Four conodont zones are distinguished in the studied sections. The material available permits the alternative subdivisions based either on the *Gnathodus bilineatus* group of species or the *Lochriea* lineage. Both could be worked out on a phylogenetical basis. However, since no characteristic species could be found within the *Gn. bilineatus* group in order to define the Viséan/Serpukhovian boundary, and coarsely ornamented *Lochriea* seems to give a good correlative level, a combined zonation was used; the oldest two zones are based on the *Gn. bilineatus* lineage and the two youngest on the *Lochriea* lineage.

It is proposed herein to use *L. zieglerei* as an index fossil to identify the Viséan/Serpukhovian boundary. The lineage *L. nodosa*-*L. zieglerei* can be traced in many Eurasian sections. *Lochriea zieglerei* is widespread, easily recognisable and much more numerous than the other strongly ornamented *Lochriea*. Its appearance is close to the Viséan/Serpukhovian boundary as defined by ammonoids. Its entry may serve as a reliable marker for the base of the Serpukhovian.

The high frequency and great diversity of conodonts in the Triollo sections as well as detailed sampling bed-by-bed has confirmed the idea of van den Boogaard (1992, p. 25) that "quick rather short-lived invasions" of *Vogelgnathus*-dominated fauna "were linked to rapid rises in sea level, may be during the periods of maximum flooding of the late Asbian to early Namurian transgressive-regressive cycles caused by eustatism." Four invasions of *Vogelgnathus* took place during the time span of the Triollo section (late Viséan-early Serpukhovian); one during the late *Gn. bilineatus* Zone, the second and third in the latest Viséan (late *L. nodosa* Zone), and the fourth in the early Serpukhovian (*L. zieglerei* Zone, not in the earliest *L. zieglerei*) (Figs. 7-11). Van den Boogaard noted that these invasions of *Vogelgnathus* linked to the sea-level rise could represent global events.

Systematic palaeontology

Genus *Gnathodus* Pander, 1856

Type species — *Polygnathus bilineatus* Roundy, 1926

Remarks — Because the types of *Gnathodus mosquensis* Pander, 1926, were lost and their type locality was uncertain, *Gn. bilineatus* (Roundy) was designated as the type species of *Gnathodus* (Tubbs, 1986).

Gnathodus bilineatus remus Meischner & Nemyrovskaya, 1999

Pl. 5, figs. 1, 8, 10, 12, 14.

1999 *Gnathodus bilineatus remus* Meischner & Nemyrovskaya, p. 435, pl. 3, figs. 13, 14, 17, 19.

Remarks — Studied specimens differ from *Gn. bilineatus bilineatus* by a wider triangular platform and more asymmetrical anterior margin, and by the convex anterior parapet, which goes outward of, and fuses posteriorly with, the carina. They are very similar to those of the Rheinisches Schiefergebirge, but differ from the German specimens by a less asymmetrical platform, better developed ridges of the parapet and a more strongly ornamented outer platform with more regular subconcentric rows of nodes, as well as by less extended simple carina beyond the posterior end of the platform. Some of them trend towards *Gnathodus cantabricus* (Pl. 5, fig. 7) and others to *Gn. bilineatus bilineatus* (Pl. 5, fig. 12; also Pl. 5, fig. 14, with expanded carina in the posterior half of the platform, the latter is transitional to *Gn. bilineatus bilineatus*). *Gnathodus bilineatus remus* differs from *Gn. cantabricus* Belka & Lehmann by much better developed parapet and less rounded platform shape. It differs from *Gn. bilineatus romulus* mostly by a more asymmetrical and more strongly ornamented platform.

Range — Mid-Viséan boundary beds of Germany (*Entogonites grimmeri* to *Goniatites crenistria* Zones) and upper Viséan through the lowest Serpukhovian of Spain.

Occurrence — Samples 8444-8478 (Section 1) and sample 8793 B (Section 2); upper Viséan – lowest Serpukhovian; *Gn. bilineatus* through *L. ziegleri* zones.

Material — Seven hundred and twenty two specimens.

Gnathodus bilineatus romulus Meischner & Nemyrovskaya, 1999

Pl. 5, figs. 9, 13; pl. 7, fig. 13.

1999 *Gnathodus bilineatus romulus* Meischner & Nemyrovskaya, p. 436, pl. 3, figs. 11, 12, 15, 16, 22.

Remarks — This subspecies differs from *Gn. bilineatus bilineatus* by its more asymmetrical, less ornamented platform and simple carina. It differs from *Gn. bilineatus remus* by having a less well ornamented platform. The parapet of *Gn. bilineatus romulus* does not go much outward of the carina as in *Gn. bilineatus romulus*.

Range — Mid-Viséan boundary beds and lower part of the upper Viséan of Germany (uppermost *Entogonites nasutus* into *Goniatites crenistria* zones), and upper Viséan through the lowest Serpukhovian of Spain.

Occurrence — Samples 8444-8477 (Section 1); mid-Viséan-lower Serpukhovian; *Gn. bilineatus* through *L. ziegleri* zones.

Material — Three hundred and twelve specimens.

***Gnathodus boogaardi* sp. nov.**

Pl. 4, figs. 3, 5, 6, 9.

Holotype — RGM 415195 (Pl. 4, fig. 5).

Paratypes — RGM 416019 (Pl. 4, fig. 6); 416020 (Pl. 4, fig. 9); 416018 (Pl. 4, fig. 3).

Type locality — Triollo section, Palencia, Cantabrian Mountains, Spain.

Type horizon — Sample 8493, Carriòn unit, *Gn. bilineatus* Zone.

Derivation of name — The species is named after Dr. Marinus van den Boogaard, who was the first to study the conodonts of this section, in recognition of his notable contribution to the Carboniferous conodont biostratigraphy of Europe.

Diagnosis — Carminiscaphate Pa element with wide, subtriangular, swollen, smooth or weakly ornamented platform, very poorly developed inner parapet and a simple carina.

Description — Large, subtriangular, asymmetrical platform takes a little more than half of the element length. Outer side wider than the inner one. Widest point of platform in its anterior quarter. Inner side bears poorly developed, short, weak parapet consisting of several fused small nodes and limited at the anterior part of platform. The parapet is positioned very close to carina in most anterior part. Outer side covered in places by randomly scattered, very small nodes, sometimes arranged in longitudinal rows.

Carina simple, consists of discrete denticle-nodes in its anterior and middle parts and fused nodes posteriorly. Carina straight, but slightly incurved in middle part. Laterally, element slightly arched.

Basal cavity wide, deep, and asymmetrical.

Remarks — Only Pa elements (left and right) of this species are known. This species differs from the other species of *Protognathodus* and *Gnathodus* by very poor ornamentation of the platform, an almost smooth platform surface and a very short, indistinct parapet consisting only of several fused nodes or very short ridges. The shape of parapet is reminiscent of *Protognathodus praedelicatus*, but the platform shape resembles more advanced early Viséan species of *Gnathodus*.

Occurrence — Samples 8451-8464 (Section 1) and 8490-8494 (Section 2). Upper Viséan; *Gn. bilineatus* through *L. nodosa* zones.

Because of the rather primitive structure of this species, its entry would be expected to be earlier than the early *Gn. bilineatus* Zone. Sanz-Lopéz noticed similar forms within the *Gn. praebilineatus* Zone in the Spanish Pyrénées (pers. comm., November 2003).

Material — Fifteen specimens.

***Gnathodus cantabricus* Belka & Lehmann, 1998**

Pl. 5, figs. 2, 4, 5, 7, 11.

1983 *Gnathodus* n. sp. A: Park, p. 86, 87, pl. 3, figs. 18-21.

1993 *Gnathodus bilineatus bollandensis* Higgins & Bouckaert: Perret, pl. 10, fig. 28 (only).

1998 *Gnathodus cantabricus* Belka & Lehmann, pp. 37, 38, pl. 2, figs. 1, 2 (only).

1999 *Gnathodus* sp. A Park: Bošič, pp. 175, 176, pl. 2, fig. 160.

2004 *Gnathodus kiensis* Pazukhin: Sanz-López *et al.*, p. 222, pl. 2, fig. 14 (only).

Remarks — Pa elements with broad, asymmetrical platform subcircular in outline. The outer side is semicircular in shape and ornamented by randomly scattered nodes, arranged either in sub-concentric rows of small nodes or rows of nodes parallel to carina. The inner side has a weak parapet, which consists of transverse ridges in its anterior part and nodes posteriorly. It does not join the carina posteriorly, but turns outwards. The carina is simple. By its simple carina, weak ornamentation of the outer side of the platform and not very well developed parapet this species resembles *Gn. praebilineatus*, but differs from it by the parapet construction and spade-shaped platform. *Gnathodus cantabricus* differs from most of the *Gn. bilineatus* s.l. forms, which have a strong, high, well developed ridged parapet, by the shape and ornamentation of the very weak parapet directed outwards of carina, and the spade-shaped platform. Some later forms of *Gn. bilineatus* with the parapet posteriorly directed outwards differ from *Gn. cantabricus* by the platform shape, stronger ornamentation of the outer side and a strong, high, well developed parapet with regular transverse ridges. By the platform shape, *Gn. cantabricus* resembles *Gn. kiensis* Pazukhin (*in* Kulagina *et al.*, 1992), but differs from the latter by the ornamentation of the platform; *Gn. kiensis* has very regular, subconcentric to concentric rows of distinct or fused nodes, which cover both sides of the platform. If *Gn. kiensis* does have a parapet (which is hardly seen on Kulagina *et al.*, 1992, pl. 28, figs. 1-3), it is noded, but not ridged. Probably one of Belka's specimens (Belka & Lehmann, 1998, pl. 2, fig. 3), as well as a specimen illustrated by Sanz-López *et al.* (2004, pl. 2, fig. 13) belong to *Gn. kiensis*. Although the above-mentioned species resemble each other by platform shape and the inner side of the platform, the character of the weak parapet and ornamentation of the platform are different. I would not refer some forms assigned to *Gn. kiensis* by Sanz-López *et al.* (2004) either to *Gn. kiensis* or to *Gn. cantabricus* (i.e., forms illustrated by Perret, 1993, pl. 110, figs. 18, 19). Additional studies are needed to sort out the problem of *Gn. cantabricus* and *Gn. kinesis*. Their ranges are slightly different.

Range — Upper Viséan-lowermost Serpukhovian of Spain (Cantabrian Mountains and eastern Catalanian Pyrénées), France (Pyrénées) and Austria (Styria).

Occurrence — Samples 8460 (8457)-8475 (Section 1), 8490 (Section 2), and 8496 and 8499 (Section 3). Upper part of the upper Viséan-lower Serpukhovian; *Lochriea nodosa* through *L. ziegléri* zones.

Material — Ninety nine specimens.

Gnathodus girtyi Hass, 1953 *sensu lato*

Remarks — This group of species or subspecies is characterized by Pa elements with two marginal parapets of different height and length. The prominent carina can be simple or expanded posteriorly and ridged, extending beyond the posterior end of the platform or taking a lower position than the parapets, which overlap the posterior tip of the platform, and consisting of discrete circular nodes. Although Higgins (1975) sorted out the subspecies of *Gn. girtyi*, there are different conceptions of some taxa, as well as different ideas of the origin of *Gn. girtyi s.l.* The majority of the *Gn. girtyi* group of subspecies (species?) are distinguished by the length and shape of the parapets. These are *Gn. girtyi girtyi* Hass, *Gn. girtyi rhodesi* Higgins, *Gn. girtyi meischneri* Austin & Husri and *Gn. girtyi collinsoni* Rhodes, Austin & Druce. *Gnathodus girtyi intermedius* Globensky differs from the above-mentioned taxa by the nonmerging of the carina with the nodes of the parapets at the posterior end of the element. There are two more taxa with additional nodes on the platform such as *Gn. girtyi soniae* Rhodes, Austin & Druce (another form with the parapets overlapping the posterior tip of the platform like in *Gn. girtyi intermedius*), and with one parapet reduced to several nodes, *Gn. girtyi simplex* Dunn. Skompski (1996) made a short analysis of the subspecies of *Gn. girtyi s.l.* and documented their range.

The *Gnathodus girtyi* group of species is not abundant in the Triollo section, where it is represented by *Gn. girtyi girtyi* Hass, *Gn. girtyi meischneri* Austin & Husri and transitional forms between *Gn. girtyi girtyi* and *Gn. girtyi simplex* Dunn, as well as other forms that display the main feature of *Gn. girtyi girtyi*. These show two long, well developed parapets with shapes different to those in *Gn. girtyi girtyi*. They are short-ranging and occur in the Viséan/Serpukhovian boundary beds in the Triollo sections. Such forms were also registered approximately at the same level in the French Pyrénées. They were incorrectly included in the scope of *Gn. girtyi intermedius* by Perret (1993). This identification was revised and a status of subspecies was given to these forms (*Gn. girtyi pyrenaicus*). *Gnathodus girtyi intermedius* Globensky and *Gn. girtyi soniae* Rhodes *et al.* were not found in the Triollo sections. I could not distinguish *Gn. girtyi collinsoni* here and could not clearly distinguish *Gn. girtyi meischneri* from *Gn. girtyi rhodesi* due to lack of adult specimens. A general revision of the *Gn. girtyi* group of subspecies (or species) is required.

Gnathodus girtyi girtyi Hass

Pl. 7, fig. 15.

Selected synonymy —

1953 *Gnathodus girtyi* Hass, p. 80, pl. 14, figs. 22-24.

1975 *Gnathodus girtyi girtyi*: Higgins, p. 11, pl. 10, figs. 5, 6 (cum. syn.).

1996 *Gnathodus girtyi girtyi*: Skompski, pl. 1, figs. 8, 9.

Remarks — Herein I refer to *Gn. girtyi girtyi* the Pa elements with a prominent carina that continues to the posterior end of the element or extends a little beyond the platform posteriorly, and two high, well developed marginal parapets, regularly ridged anteriorly and noded posteriorly, terminating close to the posterior end of the platform. The transverse ridges of the inner parapet are less developed.

Range — Upper Viséan-lowermost Serpukhovian of Europe and Upper Mississippian of North America.

Occurrences — Samples 8459-8477, 8791A (Section 1), 8479-8490 (Section 2) and 8495-8499 (Section 3); upper Viséan through lower Serpukhovian, *Lochria nodosa* through *L. zieglerei* zones.

Material — One thousand, one hundred and eighty eight specimens.

***Gnathodus girtyi* Hass, 1953 *sensu lato* transition to *Gn. girtyi simplex* Dunn, 1966**
Pl. 7, figs. 16-20.

Remarks — Pa elements with straight to slightly inward-curved carina and two unequal parapets. None of the parapets reaches the posterior end of the element. The inner parapet is a little longer than half the platform length. Its anterior largest portion is ridged and continues to the posterior end of the element as isolated nodes. The outer parapet is strongly reduced down to several nodes. Cup is elongate, asymmetrical, widest anteriorly and pointed posteriorly. The subspecies shows the merging of carina and reduced outer parapet, and resembles *Gn. girtyi simplex*. However, the outer reduced parapet has more nodes than *Gn. girtyi simplex* and sometimes these are located outside the carina, not being merged with the latter.

Occurrence — Sample 8750 (Section 1) and samples 8481, 8486-8488 (Section 2); lower Serpukhovian, *Lochria zieglerei* Zone.

Material — Forty one specimen.

***Gnathodus girtyi meischneri* Austin & Husri, 1974**
Pl. 7, figs. 4, 5, 7, 14.

Selected synonymy —

pars 1974 *Gnathodus girtyi meischneri* Austin & Husri, pp. 53, 54, pl. 2, figs. 1-3, pl. 16, fig. 7 (only) (cum syn.).

1993 *Gnathodus girtyi meischneri*: Perret, p. 334, pl. 105, figs. 28, 35.

pars 1996 *Gnathodus girtyi meischneri*: Skompski, pp. 199, 200, pl. 1, figs. 1, 4, pl. 2, fig. 1 (only).

1999 *Gnathodus girtyi meischneri*: Meischner & Nemyrovskaya, pl. 3, figs. 4-8.

Remarks — Pa elements with a prominent carina, and two parapets of different length and height. The outer parapet is usually developed as a ridge that is significantly lower and shorter than the inner parapet, and directed somewhat outwards of carina in its middle part. Inner parapet is as high as carina, straight and ridged. *Gnathodus girtyi*

meischneri differs from *Gn. girtyi girtyi* by the form and height of outer parapet, which is much better developed in the latter. The inner parapet is the same as in *Gn. girtyi girtyi*. *Gnathodus girtyi collinsoni* Rhodes *et al.* and *Gn. girtyi rhodesi* Higgins also have the outer parapet much lower and shorter than the inner one, but it is much less developed than in *Gn. girtyi meischneri*. Besides, it is more centrally positioned and extended outwards of carina in its middle part. It differs from *Gn. girtyi pyrenaicus* subsp. nov. Morphotype 1 by the shape of the outer parapet, which is flatter and more triangular in shape, and is directed outwards more anteriorly than in *Gn. girtyi meischneri*. The inner parapet is also generally more flattened in *Gn. girtyi pyrenaicus* than in *Gn. girtyi meischneri*.

Range — Upper Viséan of Poland, Ireland, England, Germany, France and Spain.

Occurrences — Samples 8439 to 8468 (Section 1); uppermost lower-upper Viséan; *Gnathodus praebilineatus* Zone through *L. nodosa* Zone.

Material — Thirty two specimens.

***Gnathodus girtyi pyrenaicus* Nemyrovska & Perret subsp. nov.**

Pl. 7, figs. 6, 8-12.

1970 *Gnathodus girtyi*: Marks & Wensink, pl. 3, fig. 12.

1979 *Gnathodus girtyi*: Buchroithner, pl. 2, figs. 7, 8 (only).

1993 *Gnathodus girtyi intermedius*: Perret, p. 335, pl. 105, figs. 27, 29, 31, 33, 38 (only).

1993 *Gnathodus girtyi meischneri*: Perret, p. 334, pl. 105, fig. 28 (only).

1993 *Gnathodus bilineatus bollandensis*: Perret, p. 329, pl. 105, fig. 37 (only).

1999 *Gnathodus girtyi*: Bošič, pl. 3, fig. 3.

Holotype — RGM 416038 (Pl. 7, fig. 12).

Paratype — RGM 416037 (Pl. 7, fig. 11).

Type locality — Triollo section 1, Palencia, Mountains Cantabrian, Spain.

Type horizon — Sample 8468, Carrión unit, late *L. nodosa* Zone.

Derivation of name — The species is named after the Pyrénées where it has been found for the first time.

Diagnosis — Pa elements with a prominent carina that extends a little beyond the platform posteriorly, and two long parapets almost of the same length. The inner parapet is higher, well developed and ridged, but the outer parapet is smooth or covered by small nodes; it is always lower and flatter than the inner one and has a triangular shape with the greater width close to its anterior end. When smooth it shows a tendency to develop the nodes at its angular anterior part or along almost a whole margin.

Description — Pa elements with prominent denticulated carina, which can expand slightly below the posterior end of the element. Carina simple at posterior end. Den-

ticles fused in anterior part, but discrete and prominent posteriorly. Two parapets well developed, both long, reaching the posterior end of the element. Inner parapet generally high, consisting of regular transverse ridges, best developed in its middle part. Adult specimens show the tendency to be wider and flatter in the middle part (Pl. 7, fig. 12). Outer parapet is mostly smooth, margin decorated by very short ridges (mainly in its posterior half) (Pl. 7, fig. 11) or nodes; it is lower and shorter anteriorly than the inner one. Outer parapet generally has a triangular shape with an angular anterior third. In juveniles its margin is distinct and upturned. In adults the outer parapet can be flatter either only in its anterior third or along the whole length. In its anterior third it can be broken into small nodes so its margin becomes less distinct.

In some specimens from the Pyrénées both parapets are flatter and wider. Outer parapet flat with indistinct margin along a whole its length. Small, irregularly arranged nodes often cover not only its angular margin, but also a whole parapet (Pl. 7, figs. 6, 8). Even juveniles have very flat and often triangular outer parapet (Pl. 7, fig. 9). These forms represent another morphotype. The basal cavity is large and asymmetrical.

Discussion — Two morphotypes can be recognized by the character of the outer parapet ornamentation. The forms which have a smooth parapet with the triangular anterior part split into small nodes along its angular anterior margin are assigned to the Morphotype 1 (Pl. 7, figs. 11, 12). These forms were found in both the Triollo section, and the Spanish Pyrénées (Marks & Wensink, 1970, pl. 3, fig. 12) and Graz (Bošič, 1999, pl. 3, fig. 3). Morphotype 2 represents the forms with a smooth, flat, wide outer parapet, which is covered by small irregularly arranged nodes (Pl. 7, figs. 6, 8). Anterior part of the outer parapet is also angular as in Morphotype 1. The outer parapet can be much lower than the inner, and its lateral margin is indistinct and almost flat. There are forms with a smooth outer parapet, but with random small nodes located along its margin (Pl. 7, fig. 10). Both parapets of the Morphotype 2 are wider and flatter than those in Morphotype 1. These forms were found in the French Pyrénées.

Remarks — *Gnathodus girtyi pyrenaicus* subsp. nov. Morphotype 1 is similar to *Gn. girtyi meischneri*, but differs from it by its longer, angular outer parapet in the anterior third; its margin can be broken into several tiny nodes, which makes this indistinct. In *Gn. girtyi meischneri* the outer parapet is shorter, takes a more central position, and its margin is always upraised and distinct. *Gnathodus girtyi pyrenaicus* Morphotype 1 differs from *Gn. girtyi girtyi* by its wider and flatter outer parapet, and its triangular shape. It differs from the other *Gn. girtyi* subspecies by its long and flattened, triangular anteriorly outer parapet. *Gnathodus girtyi pyrenaicus* Morphotype 2 differs from all of the *Gn. girtyi* subspecies by having the flattened outer parapet covered by randomly arranged small nodes.

Range — Uppermost Viséan-lowermost Serpukhovian of the Cantabrian Mountains, Pyrénées, Spain and France; and Upper Sanzenkogel Formation of Graz (uppermost Viséan), Austria.

Occurrence — Samples 8468 (Section 1), 8495-8497 (Section 3); upper part of the upper Viséan-lower Serpukhovian; *Lochriea nodosa* Zone through *L. zieglerei* Zone of the

Triollo section, Palencia, Spain and Pyrénées, France (sections Col des Tantes, Fort du Portalet, Pont de Sebers and Port de la Chourique).

***Gnathodus praebilineatus* Belka, 1985**

Pl. 4, figs. 1, 7, 11; Pl. 5, figs. 3, 6.

- 1985 *Gnathodus praebilineatus* Belka, p. 39, pl. 7, figs. 4-8.
 1993 *Gnathodus bilineatus* (Roundy): Schönlaub & Kreutzer, pl. 6, figs. 12-14.
 1993 *Gnathodus praebilineatus*: Perret, p. 327, pl. 110, figs. 4-6, 10, 13.
 1994 *Gnathodus praebilineatus*: Belka & Korn, pl. 2, fig. 12 (only).
 1998 *Gnathodus praebilineatus*: Belka & Lehmann, pl. 2, figs. 4, 5 (only).
 1998 *Gnathodus praebilineatus*: Perri & Spaletta, pl. 2, figs. 8, 9.
 1999 *Gnathodus praebilineatus*: Meischner & Nemyrovská, pl. 1, figs. 2, 3, 5, 7, 9, 10, 14, 17; pl. 2, figs. 5, 7, 11, 16; pl. 3, figs. 20, 21.
 1999 *Gnathodus praebilineatus*: Bošič, pp. 174, 175, pl. 1, figs. 1-10.
 2004 *Gnathodus praebilineatus*: Sanz-López *et al.*, pl. 2, figs. 1, 2, 4 (only).

Remarks — The species differs from *Gnathodus bilineatus* mainly by its narrower, not fully developed parapet with irregular ridges, and its simple carina and much shallower groove between carina and parapet. Some specimens (Pl. 4, fig. 11; Pl. 5, figs. 3, 6) were assigned to *Gn. praebilineatus* even though the parapets are wide because of the irregular transverse ridges, thus preventing attribution to *Gn. bilineatus*. The specimen on Plate 5, fig. 6 (sample 8439, *Gn. praebilineatus* Zone) is similar to that from the Alba (Genicera) Formation (Early Viséan) of the Esla area, Cantabrian Mountains, Spain, illustrated by Belka and Korn (1994, pl. 2, figs. 11, 12) and especially to the specimen from the lower Viséan of Carnic Alps, Italy (Perri & Spaletta, 1998, pl. 2, fig. 9). All the above mentioned specimens display the transition from *Gn. semiglaber* (Pl. 6, figs. 7, 10). The other specimens of *Gn. praebilineatus* from Triollo show the trend from *Gn. delicatus*.

Range — According to Belka (1985), *Gn. praebilineatus* is known from the base of the *Gn. austini* Zone into the lower part of the *Gn. bilineatus* Zone of Poland, and in the lower Viséan and lower part of the upper Viséan of Spain (Belka & Korn, 1994; Belka & Lehmann, 1998); uppermost lower Viséan of the Rheinisches Sciefergebirge, Germany (Meischner & Nemyrovská, 1999) and mid-Viséan (Asbian) of England (Riley, pers. comm., 1997); lower Viséan of Carnic Alps, Italy and Austria (Perri & Spaletta, 1998; Spaletta & Perri, 1998; Schönlaub & Kreutzer, 1993); lower Viséan of Middle Asia, Uzbekistan (Nigmadganov, pers. comm., 1997) and lower Viséan of the French Pyrénées (Perret, 1993).

Occurrence — Samples 8435-8465 (Section 1). Upper part of the lower and lower part of the upper Viséan; *Gnathodus praebilineatus* through *Gn. bilineatus* and early *L. nodosa* zones.

Material — Three hundred and forty five specimens.

Genus *Lochriea* Scott, 1942

Type species — *Spathognathodus commutatus* Branson & Mehl, 1941 (Pa element); *Lochriea montanaensis* Scott, 1942 (M element).

Remarks — Pa elements of *Lochriea* consist of a subrectangular blade and carina, and a low subcircular to subquadrate, slightly asymmetrical cup, positioned in most species at the posterior end of the element. All known species of *Lochriea*, except of *L. cracoviensis* Belka, were found in the studied section. The species portray the change from simple unornamented platforms (cups) to sculptured platforms bearing nodes or ridges. The distinction between species is generally based upon the shape and ornamentation of the cup-platform. The earliest species, *Lochriea* sp. nov. Nemyrovskaya *et al.* (Pl. 8, figs. 1, 3), *L. commutata* (Branson & Mehl), *L. cracoviensis* (Belka) and *L. scotiaensis* (Globensky), all have a simple unornamented platform. The cup-platform of *L. sp. nov.* and *L. cracoviensis* is not yet positioned at the posterior end of the platform, but shifted anteriorly. In *L. commutata* (Pl. 8, figs. 2, 7) and the younger species the platform is located at the posterior end of the element. The later species, *L. mononodosa* (Rhodes *et al.*), *L. monocostata* Pazukhin & Nemyrovskaya, *L. nodosa* (Bischoff) and *L. costata* (Pazukhin & Nemyrovskaya), are characterized by either one node or ridge on one side of the cup or two nodes or ridges on each side. At the end of the Viséan and/or at the beginning of the Serpukhovian, species appeared with a series of nodes or ridges on each side of the cup-platform. These were *L. senkenbergica* Nemyrovskaya *et al.*, *L. ziegleri* Nemyrovskaya *et al.*, *L. multinodosa* (Wirth) and *L. cruciformis* (Clarke). The species of *Lochriea* are common in the Triollo section, except for rare *L. mononodosa* and *L. cruciformis*. The significance of the above mentioned evolutionary features of the *Lochriea* species for the correlation of the Viséan and Serpukhovian deposits was stated for the first time by Meischner (1970) and Higgins (1975), and recently was analysed in many sections in Europe and discussed in respect to the position of the Viséan/Serpukhovian boundary by Skompski *et al.* (1995).

Short descriptions and remarks on the stratigraphically important species for the Viséan/Serpukhovian boundary are given below. *Lochriea* sp. nov. was mentioned already from the mid-Viséan of the Rheinisches Schiefergebirges (Meischner & Nemyrovskaya, 1999) and from the upper part of the lower Viséan of Sahara (Nemyrovskaya *et al.*, 2002); it is named and described in Nemyrovskaya *et al.* (in press).

Lochriea cruciformis (Clarke, 1960)

Pl. 8, fig. 9.

1960 *Gnathodus cruciformis* Clarke, pp. 25, 26, pl. 4, figs. 10-12.

1967 *Gnathodus commutatus nodosus*: Wirth, fig. 9b-d.

1975 *Paragnathodus cruciformis*: Higgins, p. 71, pl. 7, fig. 10.

1979 *Gnathodus cruciformis*: Buchroitner, pl. 2, fig. 3.

1983 *Paragnathodus nodosus*: Park, pl. 4, figs. 13-15 (only).

1993 *Lochriea cruciformis*: Perret, p. 288, pl. 109, figs. 12, 13 (only).

1995 *Lochriea cruciformis*: Skompski *et al.*, pl. 2, fig. 8; pl. 3, fig. 10; pl. 4, fig. 16.

1996 *Lochriea cruciformis*: Skompski, pl. 3, figs. 6, 7.

1998 *Lochriea cruciformis*: Belka & Lehmann, pl. 4, fig. 4.

2002 *Lochriea cruciformis*: Pazukhin in Pazukhin *et al.*, pl. 1, fig. 8.

Remarks — Pa elements of this species have a platform ornamented with one thin, high ridge on each side. These ridges are connected to carina. That is the most important feature to distinguish this species from the other ornamented species of *Lochriea*. The illustrated specimen (Pl. 8, fig. 9) shows a transitional trend from *L. nodosa*.

Range — Serpukhovian of Eurasia; uppermost Viséan-lowermost Serpukhovian of the Rheinisches Schiefergebirge, Germany.

Occurrence — Samples 8755-8753 (Section 1), 8793B, 8481 (Section 2) and sample 8499 (Section 3); lower Serpukhovian; *Lochriea zieglerei* Zone.

Material — Thirty one specimens.

***Lochriea multinodosa* (Wirth, 1967)**

Pl. 8, fig. 13.

1962 *Gnathodus commutatus* var. *multinodosus* Higgins, p. 8, pl. 2, figs. 13-16 (only).

1967 *Gnathodus commutatus multinodosus*: Wirth, p. 208, pl. 19, figs. 19, 20.

1982 *Paragnathodus multinodosus*: Higgins & Wagner-Gentis, p. 335, pl. 34, fig. 13 (only).

1983 *Paragnathodus multinodosus*: Park, pp.125-127, pl. 4, figs. 20, 22 (only).

1985 *Paragnathodus multinodosus*: Weyant, pl. 6, fig. 27.

1993 *Paragnathodus multinodosus*: Perret, pl. 109, figs. 20, 27, 28 (only).

1994 *Lochriea multinodosa*: Nemirovskaya *et al.*, pl. 1, figs. 9, 10.

1995 *Lochriea multinodosa*: Stojanović-Kuzenko *et al.*, pl. 16, fig. 3, pl. 19, figs. 10, 11.

1995 *Lochriea multinodosa*: Skompski *et al.*, pl. 2, figs. 9, 11, 12.

1998 *Lochriea multinodosa*: Belka & Lehmann, pl. 3, figs. 1-4.

Remarks — Pa elements of the *Lochriea* with large, wide, semi-circular cup (platform), both sides of which are ornamented by numerous small, irregularly arranged nodes.

Range — Uppermost Viséan-lower Serpukhovian of the Pyrénées, the Cantabrian Mountains, Bechar Basin (Sahara, Algeria) and Serbia.

Occurrence — Samples 8790-8792 (Section 1), 8479-8486 (Section 2) and 8495-8499 (Section 3) at Triollo; uppermost Viséan-lower Serpukhovian; latest *L. nodosa* through *L. zieglerei* zones.

Material — Six hundred and ninety five specimens.

***Lochriea nodosa* (Bischoff, 1957)**

Pl. 8, figs. 10, 15, 17.

1957 *Gnathodus commutatus nodosus* Bischoff, pp. 23, 24, pl. 4, figs. 12, 13.

1983 *Paragnathodus nodosus*: Park, pp. 127, 128, pl. 4, figs. 12, 17 (only; cum. syn.).

- 1993 *Paragnathodus nodosus*: Perret, p. 288, pl. 109, fig. 11.
 1994 *Lochriea nodosa*: Nemyrovskaya *et al.*, pl. 1, fig. 8.
 1995 *Lochriea nodosa*: Skompski *et al.*, pl. 1, figs. 3, 4; pl. 2, fig. 4; pl. 3, figs. 1, 3, 6, 7, 9; pl. 4, fig. 4.
 1995 *Lochriea nodosa*: Stojanović-Kuzenko *et al.*, pl. 17, fig. 4 (only).
 1996 *Lochriea nodosa*: Skompski, pl. 3, figs. 8, 9.

Remarks — Pa elements of *Lochriea* with two small to medium-sized nodes on each side of the platform.

Range — Upper part of the upper Viséan through Serpukhovian everywhere in the Northern Hemisphere except for North America.

Occurrence — Samples 8459-8478 (Section 1), 8479-8492 (Section 2) and 8495-8499 (Section 3) at Triollo; upper part of the upper Viséan-lower Serpukhovian; *Lochriea nodosa* through *L. ziegleri* zones.

Material — Nine hundred and forty four specimens.

***Lochriea* sp. nov. in Nemyrovskaya, Perret & Weyant, in press**

Pl. 8, figs. 1, 3.

- 1991 *Lochriea commutata*: Stone, pl. 4, figs. 6, 9.
 1999 *Bispathodus stabilis* (Branson & Mehl) transitional to *Lochriea commutata*: Meischner & Nemyrovskaya, pl. 4, fig. 4.
 2002 *Lochriea saharae nomen nudum*: Nemyrovskaya *et al.*, p. 47.

Remarks — In general outline this species with an unornamented cup resembles *L. commutata* (Branson & Mehl) and *Bispathodus stabilis* (Branson & Mehl). It differs from the former by its more anterior position of the basal cavity, and from the latter by more posterior position of more asymmetrical basal cavity and the shape of the anteriormost part of the blade. It differs from *L. cracoviensis* Belka by simple denticles of the carina-blade.

Range — Viséan of the Rheinisches Schiefergebirge (Germany), Pyrénées (France) and Saoura Valley (Algeria).

Occurrence — Samples 8435-8465 (Section 1), *Gn. praebilineatus* through early *L. nodosa* zones, Viséan.

Material — One hundred and five specimens.

***Lochriea scotiaensis* (Globensky, 1967)**

Pl. 8, figs. 4-6, 8.

- 1967 *Gnathodus scotiaensis* Globensky, p. 441, pl. 58, figs. 2-7, 10, 12.
 1982 *Gnathodus scotiaensis*: von Bitter & Plint-Geberl, p. 202, pl. 6, figs. 13-15, 20.

1992 *Lochriea scotiaensis*: Purnell, p. 36, pl. 6, fig. 12a, b.

1993 *Lochriea commutata*: Perret, pl. 109, fig. 4 (only).

Description — Pa elements with unornamented, inflated, oval to lanceolate elongated platform, which occupies more than a half of the element. Both sides of the platform are convex; its inner side is more convex, and may extend more inwards and anteriorly than the outer side. Orally the specimens often have a twisted appearance. Carina is straight to slightly curved inwards. In lateral view the element is slightly bowed posteriorly.

Remarks — *Lochriea scotiaensis* differs from *L. commutata* (Branson & Mehl), from which it was probably derived, by the shape and size of the platform (it is much more elongate and larger than in *L. commutata*), and by its bowed posterior part in lateral view. It also differs from *L. commutata* and all the other unornamented *Lochriea* (*L. sp. nov.*, *L. cracoviensis*) by asymmetrically inflated sides of the platform, which gives it sometimes a twisted oral appearance.

Range — Upper Viséan (Windsor Group) of Nova Scotia, Canada; Dinantian of England, and upper part of the upper Viséan-lowermost Serpukhovian of the Pyrénées, France, and the Cantabrian Mountains, Palencia, Spain.

Occurrence — Samples 8465-8478 (Section 1), 8479-8487 (Section 2) and sample 8496 (Section 3) at Triollo; uppermost Viséan-lowermost Serpukhovian; late *L. nodosa*- early *L. zieglerei* zones.

Material — Five hundred and thirty six specimens.

***Lochriea senkenbergica* Nemirovskaya, Perret & Meischner, 1994**

Pl. 8, fig. 12.

1994 *Lochriea senkenbergica* Nemirovskaya *et al.*, p. 313, pl. 1, fig. 5; pl. 2, figs. 7-10, 12.

1995 *Lochriea senkenbergica*: Skompski *et al.*, pl. 2, figs. 1-3, 5, 6; pl. 3, fig. 13; pl. 4, figs. 8, 10-12.

1998 *Lochriea senkenbergica*: Belka & Lehmann, pl. 4, figs. 3-5.

Remarks — Pa elements of *Lochriea* ornamented with two large, high nodes or bars located on the both sides of the central part of the platform. Inner bar is always higher than the outer one.

Range — Lower Serpukhovian of Eurasia; the uppermost Viséan through the lower Serpukhovian of the Rheinisches Schiefergebirge (Germany).

Occurrence — Samples 8470-8477 (Section 1), 8481 and 8484 (Section 3), 8496-8499 (Section 3) at Triollo; lower Serpukhovian; *Lochriea zieglerei* Zone.

Material — Five hundred and twenty two specimens.

***Lochriea zieglerei* Nemirovskaya, Perret & Meischner, 1994**

Pl. 8, figs. 11, 14, 16.

- 1962 *Gnathodus commutatus* var. *multinodosus* Higgins, pl. 2, figs. 17, 18 (only).
 1967 *Gnathodus commutatus nodosus*: Wirth, pl. 19, figs. 14, 17.
 1969 *Gnathodus nodosus*: Rhodes *et al.*, pl. 19, figs. 16, 19 (only).
 1975 *Paragnathodus cruciformis*: Higgins, pl. 7, fig. 10 (only).
 1977 *Gnathodus commutatus multinodosus*: Perret, pl. 51, fig. 23.
 1982 *Paragnathodus multinodosus*: Higgins & Wagner-Gentis, pl. 32, figs. 12, 15 (only).
 1983 *Paragnathodus* sp. 1: Nemirovskaya, pl. 1, figs. 15, 19.
 1983 *Paragnathodus nodosus*: Park, pl. 4, figs. 18, 24 (only).
 1983 *Paragnathodus nodosus*: Riley *et al.*, pl. 2, figs. 10, 14.
 1987 *Paragnathodus multinodosus*: Barskov *et al.*, pl. 16, figs. 23-25 (only).
 1990 *Paragnathodus nodosus*: Nemirovskaya *et al.*, pl. 3, fig. 3 (only).
 1992 *Paragnathodus cruciformis*: Pazukhin in Kulagina *et al.*, pl. 29, fig. 14 (only).
 1993 *Paragnathodus cruciformis*: Perret, pl. 109, fig. 14 (only).
 1994 *Lochriea zieglerei* Nemirovskaya *et al.*, pp. 312, 313, pl. 1, figs. 1-4, 6, 7, 11, 12; pl. 2, figs. 2, 11.
 1995 *Lochriea zieglerei*: Skompski *et al.*, pl. 1, figs. 5, 7-9, 11, 12; pl. 2, figs. 7, 10; pl. 3, figs. 2, 4, 5, 11, 14; pl. 4, figs. 6, 7, 9, 13, 15.
 1995 *Lochriea nodosa*: Stojanović-Kuzenko *et al.*, pl. 17, figs. 5, 7; pl. 19, fig. 12.
 1996 *Lochriea zieglerei*: Skompski, pl. 3, figs. 1-3.
 1998 *Lochriea zieglerei*: Belka & Lehmann, pl. 4, figs. 6, 7.
 2002 *Lochriea zieglerei*: Pazukhin in Pazukhin *et al.*, pl. 1, fig. 6.

Remarks — Pa elements of *Lochriea* with the platform ornamented with large, discrete nodes located on ridge-like elevations or long thick ridges on both sides of the cup close to its posterior margin. They generally follow the shape of the posterior margin of the platform.

Range — Lower Serpukhovian of Europe and China; the uppermost Viséan through the lower Serpukhovian of the Rheinisches Schiefergebirge (Germany).

Occurrence — Samples 8470-8478 (Section 1), 8479-8486 (Section 2) and 8496-8499 (Section 3) at Triolo; lower Serpukhovian; *Lochriea zieglerei* Zone.

Material — Nine hundred and twenty four specimens.

Genus *Pseudognathodus* Park, 1983

Type species — *Pseudognathodus homopunctatus* (Ziegler, 1960).

***Pseudognathodus homopunctatus* (Ziegler, 1960)**

Pl. 7, figs. 2, 3.

- 1957 *Gnathodus commutatus punctatus* Bischoff, p. 24, pl. 4, figs. 7-11, 14.
 1960 *Gnathodus homopunctatus* Ziegler, p. 39, pl. 4, fig. 3.
 1983 *Pseudognathodus homopunctatus*: Park, pp. 132-135, pl. 4, figs. 27-33 (cum. syn.).
 1986 *Gnathodus homopunctatus*: Belka & Groessens, pl. 7, figs. 11-15.
 1991 *Gnathodus s.l. homopunctatus*: Stone, pp. 28-29, pl. 3, figs. 1-4.
 1993 *Pseudognathodus homopunctatus*: Perret, p. 349, pl. 5, figs. 21-26.

Remarks — Pa elements of this species are characterized by oval, symmetrical, flattened or a little swollen cup ornamented by one longitudinal row of small nodes on each side. It differs from *Ps. symmutatus* (Rhodes *et al.*) by its ornamented wider cup (in *Ps. symmutatus* it is smooth, much narrower and lower positioned) and from *Ps. mermaidus* Austin & Husri (Pl. 7, fig. 1) by smaller nodes on both sides of the cup.

Range — Viséan through the lower part of the Serpukhovian of Eurasia and North Africa (Bechar Basin, Algeria).

Occurrence — This species occurs in almost every sample at the Triollo sections, being the second most abundant species after *V. campbelli*; uppermost lower Viséan-lower Serpukhovian; *Gn. prae bilineatus* through *L. zieglerei* zones.

Material — Ten thousand four hundred and twenty four specimens.

Genus *Vogelgnathus* Norby & Rexroad, 1985

1985 *Vogelgnathus* Norby & Rexroad, pp. 2, 3.

1992 *Vogelgnathus*: Purnell & von Bitter, pp. 316, 317.

Type species — *Spathognathodus campbelli* Rexroad, 1957.

Vogelgnathus campbelli Rexroad, 1957

Pl. 1, figs. 1, 2, 4, 5, 9.

1957 *Spathognathodus campbelli* Rexroad: p. 37, pl. 3, figs. 13-15.

1965 *Spathognathodus weneri* Ziegler: Budinger, p. 82, pl. 5, figs. 14-18, text-fig. 26.

1965 *Spathognathodus campbelli*: Budinger, p. 80, pl. 5, figs. 9-13, text-fig. 26.

1985 *Vogelgnathus campbelli* Norby & Rexroad, pp. 3-11, pl. 1, figs. 1, 2 (assemblage); pl. 2, figs. 3-10 (Pa elements); pl. 2, figs. 1, 2; pl. 3, figs. 5, 9, 10 (Pb elements); pl. 3, figs. 1-4 (M elements); pl. 3, fig. 6 (Sa elements); pl. 3, figs. 7, 8 (Sb elements); pl. 3, figs. 11, 12 (Sc elements).

1990 *Vogelgnathus campbelli*: Rexroad & Horowitz, pp. 511, 512, pl. 2, figs. 3-8 (cum. syn.).

1990 *Vogelgnathus campbelli*: Ramovš, p. 97.

1992 *Vogelgnathus campbelli*: van den Boogaard, pl. 1, figs. a-e, pl. 2, fig. c, pl. 3, figs. a-d.

1992 *Vogelgnathus campbelli*: Purnell & von Bitter, p. 317, 318, figs. 4.1-4.4.

1999 *Vogelgnathus campbelli*: Meischner & Nemyrovska, pl. 4, fig. 15.

Diagnosis — Pa elements carminiscaphate, elongated, denticulate, the denticles, with about 20 subequal denticles, mature elements twice as long as height. Main cusp moderately prominent, but slightly larger than other denticles. Highest point laterally is in the middle of the element. Lateral line present on anterior blade. Basal cavity one half to one third of element, extending to posterior end.

Range — Upper Mississippian (Chesterian) of the United States, Viséan and lower Serpukhovian of Eurasia.

Occurrence — Viséan and lower Serpukhovian, in almost every sample throughout the Triollo section.

Material — Sixteen thousand nine hundred and twenty six specimens.

***Vogelgnathus cantabricus* sp. nov.**

Pl. 2, figs. 1, 2, 4-7; Pl. 3, figs. 1-3.

Holotype — RGM 415444 (Pl. 3, figs. 1a-d).

Paratype — RGM 416012 (Pl. 3, figs. 2a-c).

Type locality — Peña Santa Lucia section, Palencia, Cantabrian Mountains, Spain.

Type horizon — Sample 6935, Peña unit, uppermost Viséan-lowermost Serpukhovian.

Derivation of name — After the Cantabrian Mountains.

Diagnosis — Spathognathodontan Pa element moderately short, longer than high. Straight anteriorly, but posteriorly strongly flexed. Cusp wider, but not much taller, than the adjacent anterior process denticles. Upper margin of posterior process laterally concave. Tiny denticles 3-7 can occur. Basal cavity very large, flat and subcircular to pear-like, extending beyond the low posterior end of element and occupying a half to two thirds of the element length.

Description — Only the spathognathodontan Pa elements are known. Lefts and rights are mirror images. The element is short and almost straight, the posteriormost part is strongly flexed. The length is more than twice the height. The anterior process is about 80% of the element length, and has 11-15 denticles of subequal width and height. The posterior denticles are thinner and often fused. The denticles of the anterior half of the anterior blade can be discrete. The cusp is twice as wide and just slightly higher than the adjacent anterior denticles. In general, the cusp is not prominent. Its posterior slope is abrupt. Posterior process is low, short and laterally with a concave upper margin. It can be smooth, but more commonly bears 3-7 tiny denticles. They do not reach the posteriormost part of the unit, which is occupied by a basal cavity, which is extended beyond the posterior process. The basal cavity is large, very wide, asymmetrical and subcircular to pyriform. It occupies a half to two thirds of the element length. Its outer side is wider posteriorly. Laterally the anterior blade is rectangular with slightly oblique anterior end. Posterior process concave. The lower margin of the posteriormost part of the element is somewhat turned-up.

Remarks — *Vogelgnathus cantabricus* differs from *V. campbelli* and *V. postcampbelli* by its concave upper margin of the posterior process, and the much larger and wider basal cavity extended beyond the posteriormost part of the posterior process. It differs from *V. palentinus* and *V. angustus* Jenkins in being much shorter, and having a much wider basal cavity without constrictions. Laterally, it differs from the two above mentioned species by the shape of the posterior process and having no shelf-like lowering of the posterior process, but having a concave smooth or tiny denticulated posterior blade, which does not reach the posteriormost end of the element. *Vogelgnathus cantabricus*

differs from all the abovementioned species by extension of the basal cavity beyond the posteriormost tip of the posterior blade and by a turned-up lower margin of the posteriormost part of the element. It differs from *V. triolloensis* sp. nov. by its much larger basal cavity, and much smaller cusp and partly fused denticles.

Occurrence — Samples 8459-8475 (Section 1), 8483-8492 (Section 2) and sample 8496 (Section 3) at Triollo; sample 6935 at Peña Santa Lucia section, uppermost Viséan-lowermost Serpukhovian; *L. nodosa* through *L. zieglerei* zones.

Material — One hundred and eighty one specimen.

***Vogelgnathus palentinus* sp. nov.**

Pl. 2, figs. 10, 11; Pl. 3, figs. 5, 6.

Holotype — RGM 416011 (Pl. 2, fig. 11a, b).

Paratypes — RGM 416010 (Pl. 2, fig. 10a, b).

Type locality — Triollo Section 1, Palencia, Cantabrian Mountains, northwest Spain.

Type horizon — Sample 8463, Carrión unit, *Lochriea nodosa* Zone.

Derivation of name — After the province of Palencia (northwest Spain).

Diagnosis — Pa element long, slender and almost straight, but for the posteriormost part, which is flexed. Length is much greater than height. Cusp larger than the next several anterior denticles, but almost equal in size with the other denticles of the anterior process. Posterior process much lower, step-like, bears five to seven tiny denticles. Long basal cavity takes half to two thirds of the element length and has a constriction at the inner side somewhat anterior to the cusp.

Description — Only the spathognathodontan Pa elements are known. Lefts and rights are mirror images. The element is long and almost straight; its posteriormost part is flexed. The unit is bowed. Anterior process takes about 80% of the unit length and has discrete or partly fused denticles of subequal size. The first five to seven denticles located anteriorly to the cusp are slightly shorter and thinner. The anteriormost denticles are shorter than the others. The number of denticles of the anterior process varies from 17 to 21, but on average they are about 20 to 21. The posterior-most of this row of denticles, i.e., cusp, is twice as wide and high as the others. Posterior process much lower than the anterior, and has 5-7 tiny and commonly fused denticles. Laterally, the lower margin of the unit is straight; the upper margin is slightly convex. Shelf-like posterior process is short (17-20% of the element length) and decreases abruptly to the posterior end. The basal cavity is long, rather narrow. The shape of flares follows the flexed posterior part of the unit. The basal cavity occupies one half to two thirds of the element length. Its inner side has a constriction near its mid-length. Both anterior and posterior parts of the inner flare are almost of the same length, but the anterior part is about twice as wide as the posterior one.

Remarks — This species differs from *V. campbelli* and *V. postcampbelli* by the characteristics of the posterior process (shelf-like and much lower in *V. palentinus*), by its flexed posterior part and long narrow basal cavity with a constriction. It differs from *V. cantabricus* and *V. triolloensis* by its longer anterior process, slightly convex upper margin, more elongated and narrower basal cavity with a constriction, and straight, but not turned-up, lower posteriormost margin.

Vogelgnathus palentinus resembles *V. angustus* Jenkins (in Jenkins *et al.*, 1983) very much. However, T.B.H. Jenkins pointed out the following differences (written comm., July, 1995) to van den Boogaard: *V. angustus* has a smaller basal cavity, just half the length of the element, whereas in *V. palentinus* it is often two thirds of the unit length; *V. palentinus* is more strongly bowed; the inner flare is about twice as wide anterior to the constriction than the posterior one, whereas in *V. angustus* both anterior and posterior parts of inner flare are about the same width each side of medial constriction; the cusp is taller and wider than the adjacent anterior denticles in *V. palentinus*, whereas in *V. angustus* it is almost subequal with the adjacent denticles; and tiny denticles of the posterior process are always present in *V. palentinus*, but only a minority of specimens of *V. angustus* has them.

Occurrence — Samples 8460-8467 (Section 1) at Triollo; lower half of the upper Viséan, Carrión Formation, *L. nodosa* Zone. Sample LL1 at the La Lastra section, upper Viséan.

Material — One hundred and fifty five specimens.

***Vogelgnathus postcampbelli* (Austin & Husri, 1974)**

Pl. 1, figs. 3, 7, 10.

1974 *Spathognathodus postcampbelli* Austin and Husri, p. 57, pl. 5, figs. 1, 3, 4 (Pa elements).

1985 new genus n. sp.: Rexroad and Merrill, pl. 1, figs. 3, 5, 6 (Pa elements), fig. 4 (Sa elements).

1985 *Vogelgnathus* n. sp.: Norby & Rexroad, p. 11, pl. 1, figs. 3-5 (Pa elements).

1986 *Vogelgnathus* n. sp. Norby & Rexroad: Mapes & Rexroad, pl. 1, figs. 16-18 (Pa elements).

1992 *Vogelgnathus campbelli*: van den Boogaard, pl. 2, figs. a, b, d.

1992 *Vogelgnathus postcampbelli*: Purnell & von Bitter, p. 327, figs. 13-1 – 13-4.

1996 *Vogelgnathus postcampbelli*: Krumhardt *et al.*, pp. 49, 50, pl. 3, figs. 28-31.

Remarks — *Vogelgnathus postcampbelli* resembles *V. campbelli*, but differs by having much smaller denticles of the posterior process which form a lower level or step in the element laterally. The main cusp looks more prominent, although it is not higher than the denticles of the anterior process. Besides, Pa elements of *V. postcampbelli* are generally longer than those of *V. campbelli*.

Range — Upper Viséan-lower Serpukhovian of Europe, Upper Mississippian (late Chesterian, *Cavusgnathus monocerus* (= *Adetognathus unicornis*) Zone of North America.

Occurrence — Samples 8450-8474 and 8720-8723 (Section 1), 8484-8488 (Section 2) and 8498 (Section 3) at Triollo; upper Viséan-lower Serpukhovian, *Gnathodus bilineatus* through *Lochria ziegleri* zones.

Material — Two hundred and ninety specimens.

***Vogelgnathus triolloensis* Nemyrovskaya sp. nov.**

Pl. 2, figs. 3, 8, 9; Pl. 3, figs. 4.

Holotype — RGM 384700 (Pl. 2, fig. 3).

Paratype — RGM 416009 (Pl. 2, figs. 9).

Type locality — Triollo Section 1, Palencia, Cantabrian Mountains, northwest Spain.

Type horizon — Sample 8786, basal Serpukhovian, Carrión unit, *Lochriea zieglerei* Zone.

Derivation of name — After the village of Triollo, Palencia.

Diagnosis — Spathognathodontan Pa element short, at least twice as long as high. Unit almost straight, posteriorly slightly flexed. Denticles of anterior and posterior processes are mostly discrete. Anterior process has seven to ten denticles. Cusp larger and taller than adjacent anterior denticles. Posterior process oblique, low and denticulate. Basal cavity small, occupies up to half the element length. Lower posterior-most part turned-up.

Description — Only spathognathodontan elements are known. Lefts and right individuals are mirror images. The unit is short and almost straight, posteriorly flexed. The anterior blade is about two thirds of the element length and bears seven to ten discrete denticles of subequal size. Anterior blade decreases abruptly anteriorly. The cusp is twice as wide as and higher than the adjacent anterior denticles. Posterior slope of the cusp is oblique. The posterior process is commonly one third of the element length and decreases gradually posteriorly. It is much lower than the anterior blade. It bears three to seven tiny discrete denticles. The basal cavity is very broad, but rather small and occupies one third to a half of the element length. It usually does not extend far anteriorly behind the cusp. The posterior lower surface is turned-up.

Remarks — *Vogelgnathus triolloensis* is similar to *V. cantabricus* by its gross morphology, wide basal cavity and turned-up posteriormost part, but differs in the ratio of the length of the anterior/posterior, its posterior process being longer than in *V. cantabricus*. It further differs from *V. cantabricus* by its larger cusp and shorter basal cavity that does not expand beyond the posteriormost tip of the posterior blade. For the differences between the other species of *Vogelgnathus*, see *V. cantabricus*, above.

Occurrence — Samples 8784-8786 (Section 1) at Triollo; basal Serpukhovian, the lowermost part of the *L. zieglerei* Zone.

Material — Thirty six specimens.

Palaeoecological implications of conodonts

A nodular limestone succession (Genicera Formation) similar in age to the Triollo section (Carrión unit) was regarded by previous workers to represent palaeoenvironments from a submarine platform, rather a deep water one, well below wave base (Higgins, 1981) to deeper than 200 m, either a slope or outer shelf (Seibert, 1988; Belka, 1990; van den Boogaard, 1992; Perret, pers. comm., 2004). The Triollo succession was developed mostly in mudstone facies with marly partings, chert lenses and nodules, which is typical for deep-water environments in slope or even basinal settings. The conodont assemblages are broadly similar to coeval successions in the Cantabrian Mountains and Pyrénées; diverse conodont faunas with a great number of *Gn. bilineatus* group of species, *Pseudognathodus homopuctatus*, common *Lochriea* and very rare *Gn. girtyi*. However, the large variety of conodonts and abundance of the *Vogelgnathus* fauna distinguishes the Triollo succession from all the other sections in the Cantabrian Mountains and Pyrénées. Even the *Gn. girtyi* group, which is extremely rare or absent in the other parts of the Cantabrian Mountains, is represented in the Triollo section by several species. The *Vogelgnathus* fauna consists mostly of two widespread (cosmopolitan) species, *V. campbelli* and *V. postcampbelli*, as well as three new species unknown so far in the other areas. Single elements, which might be related to *Vogelgnathus* and illustrated herein as 'unidentified elements' (Pl. 1, figs. 6, 8, 11), occur occasionally throughout the section. The abundance of *Vogelgnathus* allowed van den Boogaard to recognize the periodical invasion of this fauna where *Vogelgnathus* dominates to the extent of reaching 80% of all of the Pa elements in a particular sample. Van den Boogaard investigated the conodonts from other sections in the Cantabrian Mountains specifically to understand whether this phenomenon was common over a wider area (van den Boogaard, 1992). His study showed that in the other sections, too, the *Gnathodus*-dominated sequences were briefly interrupted by abundant *Vogelgnathus*. He wanted to understand if these short invasions of deeper *Vogelgnathus* fauna were connected to the periods of maximum flooding of the transgressive-regressive cycles (Ross & Ross, 1988). When all the available conodonts from the other sections were studied he concluded that the Triollo section was the best to link this phenomenon with the global rises in sea level. Wagner and Winkler Prins sampled the Triollo section again, bed-by-bed, and with very closely spaced samples, and van den Boogaard received more data. It was his idea to show the distribution of the main palaeoecological groups of conodonts in diagrams. Continuing his work, I studied the conodonts, slightly revising his identifications and slightly modifying the content of his palaeoecological conodont groups.

The conodont associations of the Triollo succession were divided into eight palaeoecological groups: 1 – late Tournaisian and early Viséan *Gnathodus* species; 2 – *Gnathodus bilineatus* group of species; 3 – simple *Lochriea* species; 4 – *Vogelgnathus* group; 5 – *Pseudognathodus* group; 6 – *Gnathodus girtyi* group; 7 – ornamented *Lochriea* species; and 8 – *Mestognathus* species (Figs. 5-10).

The late Tournaisian/early Viséan *Gnathodus* group of species (1) includes *Gn. texanus*, *Gn. semiglaber*, *Gn. pseudosemiglaber*, *Gn. cuneiformis*, *Gn. delicatus*, and transitional forms between *Gn. delicatus* and *Gn. praebilineatus*.

The *Gnathodus bilineatus* group (2) consists of *Gn. bilineatus remus*, *Gn. bilineatus romulus*, *Gn. bilineatus bilineatus* and all transitional forms between them. *Gnathodus*

praebilineatus, *Gn. cantabricus* and *Gn. boogaardi* were also included in this group, although more detailed microfacial analysis is required to confirm this assignment. *Gnathodus bilineatus bilineatus* is the most abundant taxon.

The simple *Lochriea* group of species (3) includes *L. commutata*, *L. sp. nov.* and *L. scotiensis*. *Lochriea commutata* is the most common throughout the sequence.

The *Vogelgnathus* group (4) consists of *V. campbelli*, *V. postcampbelli*, *V. cantabricus*, *V. palentinus* and *V. triolloensis*. *Vogelgnathus campbelli* is dominant.

The *Pseudognathodus* group of species (5) consists mostly of abundant *Ps. homopunctatus*. *Pseudognathodus symmutatus* and *Ps. mermaidus* are both very rare.

The *Gnathodus girtyi* group of species (6) includes *Gn. girtyi girtyi*, *Gn. girtyi meischneri*, *Gn. girtyi pyrenaicus*, and transitional forms between *Gn. girtyi girtyi* and *Gn. girtyi simplex*.

The ornamented *Lochriea* group (7) includes *L. nodosa*, *L. mononodosa*, *L. multinodosa*, *L. zieglerei*, *L. senkenbergica* and *L. cruciformis*.

Mestognathus (8) is represented by *M. bipluti*. It is included only in the general diagrams; it is ignored for those reflecting sample contents since it is barely present (Tables 1-3, Fig. 5).

Generalised statistical characteristics of the whole conodont assemblage in the Triollo succession show that the *Gnathodus bilineatus* group dominates (38%), the *Vogelgnathus* group takes the second place (27%) and *Pseudognathodus homopunctatus* occurs in almost every sample, being dominant at several levels; its average content in the succession is rather high (14%). Among the other groups, the late Tournaisian/early Viséan *Gnathodus* species are rather numerous (7%), but only in the lowest samples. Simple *Lochriea* species are common and persistent throughout the succession (8%). The *Gnathodus girtyi* group and ornamented *Lochriea* are not abundant. The *Gnathodus girtyi* group is very rare in the Cantabrian Mountains and, where it occurs, is represented only by a small number of specimens.

The numerical distribution of conodonts belonging to the above mentioned groups is shown in Tables 1-3. The average contents are shown in Figures 6-10. There are several levels extremely rich in *Vogelgnathus campbelli*. The present study of the Triollo sections, with additional sampling, has shown very rapid changes from *Vogelgnathus*-dominated to the more common *Gnathodus/Lochriea*-dominated assemblages. Detailed sampling and studies distinguished four peaks (80% or more) of *Vogelgnathus* dominance. The first peak occurs in the late *Gn. bilineatus* Zone (sample 8455 in Section 1), the second at the beginning of second half of the *Lochriea nodosa* Zone (sample 8788B in Section 1), the third in the late *Lochriea nodosa* Zone (samples 8790 in the Section 1 and 8495 in the Section 3), and the fourth in the early *Lochriea zieglerei* Zone, but not at the beginning (samples 8473(2), 8754(1), 8752 up to 8721 in Section 1 and sample 8794 in Section 2). Close sampling in Section 1 has yielded the most detailed results. The fauna in the other beds are dominated by *Gn. bilineatus*, and contain minor quantities of *Pseudognathodus*, *Lochriea* and even smaller amounts of *Gn. girtyi*. In the Upper Viséan, the beds with numerous *Gn. bilineatus s.l.* contain much smaller amount of *Ps. homopunctatus*. Where *Ps. homopunctatus* is abundant, the *Gn. bilineatus* group of species plays a subordinate role. It seems that *Lochriea* could share the settings together with *Ps. homopunctatus*. Van den Boogaard (1992) supposed that later in the Serpukhovian, when *Ps. homopunctatus* became extinct, *Lochriea* probably took its place (Figs. 6-10). Higgins (1981, p. 43)

regarded the environment in northern Spain (Genicera Formation) occupied by *Gn. bilineatus*, *Ps. homopunctatus* and the *Lochriea* species as a submarine platform at a considerable depth, well below the wave base, but probably less than 200 m.

According to Seibert (1988), who considered the deposition of the siliceous deposits at a depth of about 200 m (open marine environments), the Genicera Formation was deposited at depths between 100 and 300 m. Sandberg and Gutschik (1984) supposed that *Gnathodus* was a nectobenthic slope dweller (c. 200 m up to 50 m). Van den Boogaard (1992) correctly concluded that, if shallowing caused the disappearance of *Gn. bilineatus*, it should have been replaced by a *Mestognathus* and *Hindeodus* fauna. These are, however, extremely rare in the Triollo section despite the abundance of conodonts and the *Vogelgnathus*-dominated fauna replaces the *Gn. bilineatus* assemblage. Belka (1990) mentioned that *Lochriea* and *Vogelgnathus* are commonly found in beds deposited on the slope, but van den Boogaard (1992) considered that *Vogelgnathus* belonged to the basinal faunas and took the place of the Tournaisian spathognathodids, which probably migrated basinwards after the Tournaisian/Viséan extinction event.

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Table 1. Numerical distribution of latest early Viséan through early Serpukhovian conodonts at Triollo Section 1.

Conodonts \ Samples	8435	8436	8437	8439	8442	8443	8444	8445	8446	8447	8448	8449
<i>Protognathodus cordiformis</i>	1											
<i>Scaliognathus anchoralis anchoralis</i>	1											
<i>Pseudopolygnathus pinnatus</i>	1											
<i>Gnathodus texanus</i>	134	7	14									
<i>Gn. semiglaber</i>	c. 100	6	4	6			16		5			
<i>Gn. pseudosemiglaber</i>	c. 1960	1108	706	549			29		16			
<i>Gn. cuneiformis</i>	c. 150	12	50		1	1	6	2				
<i>Gn. delicatus</i> - <i>Gn. praebilineatus</i>	c. 30	2										
<i>Gn. praebilineatus</i>	4	6	32	2	18	291	c. 250	12	78	80	3	16
<i>Pseudognathodus homopunctatus</i>	47	29	30	41	2	10	c. 80	3	9	7		3
<i>Lochriea sp. nov.</i>	8	12	5	16	1	7	10	21	1			4
<i>L. commutata</i>	c. 12	22	14	53	2	21	50	c. 160	88	6	6	22
<i>Vogelgnathus campbelli</i>	93	224	141	c. 251			3					
<i>Gn. aff. girtyi meischneri</i>				1		17	2	7	3			
<i>Gn. praebilineatus</i> - <i>Gn. bilineatus remus</i>					1	5	c. 200	20	120		10	13
<i>Gn. ex gr praebilineatus</i> - <i>bilineatus juv.</i>						c. 200		c. 572	c. 370		10	5
<i>Gn. bilineatus remus</i>							c. 150	c. 50	c. 10	40	8	30
<i>Mestognathus sp.</i>								1				
<i>Gn. bilineatus romulus</i>							2	20				
<i>Vog. postcampbelli</i>												
<i>Gn. boogaardi</i>												
<i>Ps. symmutatus</i>												
<i>Gn. bilineatus bilineatus</i>												
<i>Gn. cantabricus</i>												
<i>L. nodosa</i>												
<i>Vog. cantabricus</i>												
<i>Icriodus sp.</i>												
<i>Gn. girtyi girtyi</i>												
<i>Ps. mermaidus</i>												
<i>Gn. girtyi meischneri</i>				2		1	1	2				
<i>Vog. palentinus</i>												
<i>L. scotiaensis</i>												
<i>Neopolygnathus communis communis</i>												
<i>Neopolygnathus purus</i>												
<i>L. mononodosa</i>												
<i>Pseudopolygnathus primus</i>												
<i>Bispathodus aculeatus</i>												
<i>Mestognathus bipluti</i>												
<i>L. multinodosa</i>												
<i>L. zieglerei</i>												
<i>L. senckenbergica</i>												
<i>Vog. triolloensis</i>												
<i>L. cruciformis</i>												
<i>Gn. girtyi girtyi</i> - <i>Gn. girtyi simplex</i>												
<i>Gn. girtyi pyrenaicus</i>												
Total	c. 2541	1428	996	c. 921	25	c. 553	c. 799	c. 870	c. 612	133	37	93
Number of Pa elements per 1 kg	617	775	383	1338	10	865	785	539	375	70	38	78

Conodonts \ Samples	8450	8451	8452	8453	8455	8456	8457	8459	8460	8461	8462	8463
<i>Protognathodus cordiformis</i>												
<i>Scaliognathus anchoralis anchoralis</i>												
<i>Pseudopolygnathus pinnatus</i>												
<i>Gnathodus texanus</i>												
<i>Gn. semiglaber</i>		16	2				1					
<i>Gn. pseudosemiglaber</i>		1			5							
<i>Gn. cuneiformis</i>					1							
<i>Gn. delicatus</i> - <i>Gn. praebilineatus</i>		2	1					2				
<i>Gn. praebilineatus</i>	6	c. 80	c. 20	5	20	c. 100	25	c. 300	c. 100	30	18	10
<i>Pseudognathodus homopunctatus</i>	2	16	3	12		57	23	15	390	26	9	9
<i>Lochriea sp. nov.</i>	2	1				1					3	3
<i>L. commutata</i>	58	60	14	25	13	78	30	51	70	5	16	34
<i>Vogelgnathus campbelli</i>	3	4	24	1	c. 580	1	3		20		1	94
<i>Gn. aff. girtyi meischneri</i>												
<i>Gn. praebilineatus</i> - <i>Gn. bilineatus remus</i>	15			c. 20	30				3	c. 10		c. 20
<i>Gn. ex gr praebilineatus</i> - <i>bilineatus juv.</i>	228		c. 30	c. 100	27	c. 50	c. 710		c. 1000	c. 50	25	173
<i>Gn. bilineatus remus</i>		c. 80	c. 30		2	c. 20	1		c. 200	3		
<i>Mestognathus sp.</i>												
<i>Gn. bilineatus romulus</i>	2				5	c. 20	2		c. 200	5		
<i>Vog. postcampbelli</i>	1				c. 20				5			
<i>Gn. boogaardi</i>		c. 60	10	3			3		4		2	2
<i>Ps. symmutatus</i>				12			1					
<i>Gn. bilineatus bilineatus</i>							1		c. 100	12	60	27
<i>Gn. cantabricus</i>							1		7		3	1
<i>L. nodosa</i>								2				
<i>Vog. cantabricus</i>								2				
<i>Icriodus sp.</i>								1				
<i>Gn. girtyi girtyi</i>								2	29	3		3
<i>Ps. mermaidus</i>									28	2		
<i>Gn. girtyi meischneri</i>										2		
<i>Vog. palentinus</i>									18			74
<i>L. scotiaensis</i>												
<i>Neopolygnathus communis communis</i>												
<i>Neopolygnathus purus</i>												
<i>L. mononodosa</i>												
<i>Pseudopolygnathus primus</i>												
<i>Bispathodus aculeatus</i>												
<i>Mestognathus bipluti</i>												
<i>L. multinodosa</i>												
<i>L. zieglerei</i>												
<i>L. senckenbergica</i>												
<i>Vog. triolloensis</i>												
<i>L. cruciformis</i>												
<i>Gn. girtyi girtyi</i> - <i>Gn. girtyi simplex</i>												
<i>Gn. girtyi pyrenaeus</i>												
Total	317	c. 320	c. 134	c. 178	c. 703	c. 327	c. 800	c. 375	c. 2174	c. 148	137	c. 423
Number of Pa elements per 1 kg	256	202	132	77	376	177	736	731	950	58	29	485

Conodonts \ Samples	8464	8465	8466	8467	8788A	8788B	8789	8468	8790	8469	8470	8786
<i>Protognathodus cordiformis</i>												
<i>Scaliognathus anchoralis anchoralis</i>												
<i>Pseudopolygnathus pinnatus</i>												
<i>Gnathodus texanus</i>												
<i>Gn. semiglaber</i>												
<i>Gn. pseudosemiglaber</i>												
<i>Gn. cuneiformis</i>						3						
<i>Gn. delicatus</i> - <i>Gn. praebilineatus</i>												
<i>Gn. praebilineatus</i>	9	6				4						
<i>Pseudognathodus homopunctatus</i>	3	202	59	c. 1000	15	233	11	51	22	6	304	6
<i>Lochriea sp. nov.</i>						7						
<i>L. commutata</i>	6	339	88	935		52	43	101	7	17	60	9
<i>Vogelgnathus campbelli</i>		30	124	14	4	18		335	121	1	5	
<i>Gn. aff. girtyi meischneri</i>												
<i>Gn. praebilineatus</i> - <i>Gn. bilineatus remus</i>												
<i>Gn. ex gr praebilineatus</i> - <i>bilineatus juv.</i>	10	c. 340	14	168			52	125		20	c. 40	
<i>Gn. bilineatus remus</i>	12											
<i>Mestognathus sp.</i>										1		
<i>Gn. bilineatus romulus</i>												
<i>Vog. postcampbelli</i>		12					3		3			
<i>Gn. boogaardi</i>	1											
<i>Ps. symmutatus</i>												
<i>Gn. bilineatus bilineatus</i>		c. 550	c. 200	c. 2800	12		c. 1000	11	27	65	c. 62	41
<i>Gn. cantabricus</i>		10										
<i>L. nodosa</i>				26			9	46	18	19	42	9
<i>Vog. cantabricus</i>												
<i>Icriodus sp.</i>												
<i>Gn. girtyi girtyi</i>		218	27	72		8	42	30			2	7
<i>Ps. mermaidus</i>												
<i>Gn. girtyi meischneri</i>						c. 10	c. 10	4				
<i>Vog. palentinus</i>		6	20	2								
<i>L. scotiaensis</i>		3						10	8	4	3	
<i>Neopolygnathus communis communis</i>		1	1									
<i>Neopolygnathus purus</i>			1									
<i>L. mononodosa</i>				9		1				3	12	
<i>Pseudopolygnathus primus</i>				1								
<i>Bispathodus aculeatus</i>									1			
<i>Mestognathus bipluti</i>											3	
<i>L. multinodosa</i>									3		12	
<i>L. zieglerei</i>											13	1
<i>L. senckenbergica</i>											16	
<i>Vog. triolloensis</i>												5
<i>L. cruciformis</i>												
<i>Gn. girtyi girtyi</i> - <i>Gn. girtyi simplex</i>												
<i>Gn. girtyi pyrenaicus</i>								5				
Total	41	c. 1717	c. 534	c. 5027	31	c. 336	c. 1170	718	210	136	c. 574	78
Number of Pa elements per 1 kg	c.62	1509	625	1438	31	592	1450	298	368	44	363	78

Conodonts \ Samples	8785	8784	8472	8757	8756	8755	8473(3)	8473(2)	8473(1)	8754(l)	8754(u)	8753
<i>Protognathodus cordiformis</i>												
<i>Scaliognathus anchoralis anchoralis</i>												
<i>Pseudopolygnathus pinnatus</i>												
<i>Gnathodus texanus</i>												
<i>Gn. semiglaber</i>												
<i>Gn. pseudosemiglaber</i>												
<i>Gn. cuneiformis</i>												
<i>Gn. delicatus</i> - <i>Gn. praebilineatus</i>												
<i>Gn. praebilineatus</i>												
<i>Pseudognathodus homopunctatus</i>	17	23	7	89	7	101	66	128	55	266	63	60
<i>Lochriea</i> sp. nov.												
<i>L. commutata</i>	10	27	1	17		78	45	92	9	112	17	10
<i>Vogelgnathus campbelli</i>			4	8		2		2295	244	2302	423	36
<i>Gn. aff. girtyi meischneri</i>												
<i>Gn. praebilineatus</i> - <i>Gn. bilineatus remus</i>												
<i>Gn. ex gr praebilineatus</i> - <i>bilineatus juv.</i>		20	6	11		c. 116	c. 50	c. 100	c. 50			
<i>Gn. bilineatus remus</i>			3				1	1				
<i>Mestognathus</i> sp.												
<i>Gn. bilineatus romulus</i>							1	1				
<i>Vog. postcampbelli</i>						1						
<i>Gn. boogaardi</i>												
<i>Ps. symmutatus</i>												
<i>Gn. bilineatus bilineatus</i>	c.40	53	25	48	3	c. 400	c. 200	c. 500	34		57	
<i>Gn. cantabricus</i>												
<i>L. nodosa</i>	16	11		39	1	7	16	23	8	c. 50	9	c. 25
<i>Vog. cantabricus</i>								1	4	3	4	3
<i>Icriodus</i> sp.												
<i>Gn. girtyi girtyi</i>	7		1		1		2	34				1
<i>Ps. mermaidus</i>												
<i>Gn. girtyi meischneri</i>												
<i>Vog. palentinus</i>												
<i>L. scotiaensis</i>			1				4	5			4	5
<i>Neopolygnathus communis communis</i>												
<i>Neopolygnathus purus</i>												
<i>L. mononodosa</i>	4					3	9	10		c. 10	1	5
<i>Pseudopolygnathus primus</i>												
<i>Bispathodus aculeatus</i>												
<i>Mestognathus dipluti</i>	3	10	2	5	1	27	2					
<i>L. multinodosa</i>					3	c. 20	c. 25	c. 20	4	c. 30	3	c. 28
<i>L. zieglerei</i>	2	3		2		c. 57				c. 40		
<i>L. senckenbergica</i>	1			1		c. 30	c. 30	c. 20	3	c. 40		
<i>Vog. triolloensis</i>		30										1
<i>L. cruciformis</i>						1?			5			8
<i>Gn. girtyi girtyi</i> - <i>Gn. girtyi simplex</i>												
<i>Gn. girtyi pyrenaicus</i>												
Total	c. 100	177	50	220	16	c. 844	c. 451	c. 3230	c. 411	c. 2858	c. 581	c. 182
Number of Pa elements per 1 kg	90	52	37	602	83	872	601	4313	992	3777	830	334

Conodonts \ Samples	8752	8474	8751	8750	8723	8722(B)	8722(A)	8721	8720	8647	8475	8476
<i>Protognathodus cordiformis</i>												
<i>Scaliognathus anchoralis anchoralis</i>												
<i>Pseudopolygnathus pinnatus</i>												
<i>Gnathodus texanus</i>												
<i>Gn. semiglaber</i>												
<i>Gn. pseudosemiglaber</i>												
<i>Gn. cuneiformis</i>												
<i>Gn. delicatus</i> - <i>Gn. praebilineatus</i>												
<i>Gn. praebilineatus</i>												
<i>Pseudognathodus homopunctatus</i>	108	168	59	78	259	333	274	227	33	24	45	
<i>Lochriea</i> sp. nov.		2										
<i>L. commutata</i>	c. 45	c.140	7	c. 15	54	30	14	92	19	12	25	20
<i>Vogelgnathus campbelli</i>	4185	463	64	57		7	9	793		4	20	
<i>Gn. aff. girtyi meischneri</i>												
<i>Gn. praebilineatus</i> - <i>Gn. bilineatus remus</i>												
<i>Gn. ex gr praebilineatus</i> - <i>bilineatus juv.</i>												
<i>Gn. bilineatus remus</i>		3						c. 20				8
<i>Mestognathus</i> sp.												
<i>Gn. bilineatus romulus</i>		10						c. 20				12
<i>Vog. postcampbelli</i>	2				67	4	32	86	2			
<i>Gn. boogaardi</i>												
<i>Ps. symmutatus</i>												
<i>Gn. bilineatus bilineatus</i>		c. 340		209	338	70	86	c. 100	209	160	148	73
<i>Gn. cantabricus</i>	3	5		6								6
<i>L. nodosa</i>	c. 15	19		c. 10		1	1		10	c. 80	c. 30	3
<i>Vog. cantabricus</i>	2	94	6	9			1				1	
<i>Icriodus</i> sp.												
<i>Gn. girtyi girtyi</i>	? 9 juv.			4	2	2	2	12		48	c. 100	1
<i>Ps. mermaidus</i>												
<i>Gn. girtyi meischneri</i>												
<i>Vog. palentinus</i>												
<i>L. scotiaensis</i>	c. 15	c. 20	4	5	9	7	5				8	9
<i>Neopolygnathus communis communis</i>												
<i>Neopolygnathus purus</i>												
<i>L. mononodosa</i>	2			4				2	3	7	7	3
<i>Pseudopolygnathus primus</i>												
<i>Bispathodus aculeatus</i>												
<i>Mestognathus bipluti</i>										8	9	
<i>L. multinodosa</i>	c. 12	c. 12	4	5						c. 70	c. 20	
<i>L. zieglerei</i>	c. 25	c. 15		c. 15	6			c. 30			54	12
<i>L. senckenbergica</i>	c. 15			6		4	7	c. 30			28	4
<i>Vog. triolloensis</i>												
<i>L. cruciformis</i>									7			
<i>Gn. girtyi girtyi</i> - <i>Gn. girtyi simplex</i>												? 19
<i>Gn. girtyi pyrenaicus</i>												
Total	c. 4438	c. 1291	144	c. 423	735	458	431	1412	283	c. 413	c. 514	151
Number of conodonts per 1 kg	4454	700	260	297	635	773	862	1012	314	178	224	82

Conodonts\Samples	8477	8791(A)	8791(B)	8792	8478
<i>Protognathodus cordiformis</i>					
<i>Scaliognathus anchoralis anchoralis</i>					
<i>Pseudopolygnathus pinnatus</i>					
<i>Gnathodus texanus</i>					
<i>Gn. semiglaber</i>					
<i>Gn. pseudosemiglaber</i>					
<i>Gn. cuneiformis</i>					
<i>Gn. delicatus</i> - <i>Gn. praebilineatus</i>					
<i>Gn. praebilineatus</i>					
<i>Pseudognathodus homopunctatus</i>	104	30	10	56	12
<i>Lochriea sp. nov.</i>					
<i>L. commutata</i>	c. 80			28	c. 150
<i>Vogelgnathus campbelli</i>	556	31		31	483
<i>Gn. aff. girtyi meischneri</i>					
<i>Gn. praebilineatus</i> - <i>Gn. bilineatus remus</i>					
<i>Gn. ex gr praebilineatus</i> - <i>bilineatus juv.</i>					
<i>Gn. bilineatus remus</i>	c. 20		4		c. 10
<i>Mestognathus sp.</i>					
<i>Gn. bilineatus romulus</i>	c. 12				
<i>Vog. postcampbelli</i>					
<i>Gn. boogaardi</i>					
<i>Ps. symmutatus</i>					
<i>Gn. bilineatus bilineatus</i>	272	c. 140	c. 40	563	c. 640
<i>Gn. cantabricus</i>	6	c. 20	8		
<i>L. nodosa</i>	c. 20	5			c. 25
<i>Vog. cantabricus</i>					
<i>Icriodus sp.</i>					
<i>Gn. girtyi girtyi</i>	1	1			
<i>Ps. mermaidus</i>					
<i>Gn. girtyi meischneri</i>					
<i>Vog. palentinus</i>					
<i>L. scotiaensis</i>	c. 30	40	5	c. 120	20
<i>Neopolygnathus communis communis</i>					
<i>Neopolygnathus purus</i>					
<i>L. mononodosa</i>	6				
<i>Pseudopolygnathus primus</i>					
<i>Bispathodus aculeatus</i>					
<i>Mestognathus bipluti</i>	5	1			
<i>L. multinodosa</i>	c. 20	8	7	62	
<i>L. zieglerei</i>	c. 30			8	c. 80
<i>L. senckenbergica</i>	c. 25			1	c. 70
<i>Vog. triolloensis</i>					
<i>L. cruciformis</i>					
<i>Gn. girtyi girtyi</i> - <i>Gn. girtyi simplex</i>					
<i>Gn. girtyi pyrenaicus</i>					
Total	c. 1187	c. 276	c. 74	c. 869	c. 1490
Number of Pa elements per 1 kg	496	305	85	366	1568

Table 2. Numerical distribution of late Viséan through early Serpukhovian conodonts at Triollo Section 2.

Conodonts \ Samples	8479	8480	8481	8482	8483	8793(A)	8793(B)	8794	8484	8485	8486	8487
<i>Protognathodus cordiformis</i>												
<i>Scaliognathus anchoralis anchoralis</i>												
<i>Pseudopolygnathus pinnatus</i>												
<i>Gnathodus texanus</i>												
<i>Gn. semiglaber</i>												
<i>Gn. pseudosemiglaber</i>												
<i>Gn. cuneiformis</i>												
<i>Gn. delicatus</i> - <i>Gn. praebilineatus</i>												
<i>Gn. praebilineatus</i>												
<i>Pseudognathodus homopunctatus</i>	32	3	38	3204	173	88	112	c. 400	107	17	44	43
<i>Lochria sp. nov.</i>												
<i>L. commutata</i>	c. 80	11	c. 20	465	c. 200			c. 180	c. 50	3	18	17
<i>Vogelgnathus campbelli</i>	11		11	165	195	30	141	3814	9		50	42
<i>Gn. aff. girtyi meischneri</i>												
<i>Gn. praebilineatus</i> - <i>Gn. bilineatus remus</i>												
<i>Gn. ex gr praebilineatus</i> - <i>bilineatus juv.</i>												
<i>Gn. bilineatus remus</i>								c. 15				
<i>Mestognathus sp.</i>												
<i>Gn. bilineatus romulus</i>												
<i>Vog. postcampbelli</i>			? 1	10				3				
<i>Gn. boogaardi</i>												
<i>Ps. symmutatus</i>												
<i>Gn. bilineatus bilineatus</i>	1095	83	107	916	661	101	c. 85	717	123	77	225	46
<i>Gn. cantabricus</i>												
<i>L. nodosa</i>	c. 30	7	c. 20	c. 100	c. 21			c. 40	c. 10		c. 10	10
<i>Vog. cantabricus</i>					12	5	17	9				1
<i>Icriodus sp.</i>												
<i>Gn. girtyi girtyi</i>	5		c. 50	2						4	c. 60	
<i>Ps. mermaidus</i>								c. 40				
<i>Gn. girtyi meischneri</i>												
<i>Vog. palentinus</i>												
<i>L. scotiaensis</i>	c. 18	7	7		34	45	42	c. 20	c. 12			4
<i>Neopolygnathus communis communis</i>												
<i>Neopolygnathus purus</i>												
<i>L. mononodosa</i>	8			c. 8	3						2	
<i>Pseudopolygnathus primus</i>												
<i>Bispathodus aculeatus</i>												
<i>Mestognathus bipluti</i>	4		5	4					7	1	2	
<i>L. multinodosa</i>	c. 80						3	c. 100	c. 15		4	
<i>L. zieglerei</i>	c. 130		c. 58	c. 50				c. 10		3	7	
<i>L. senckenbergica</i>			c. 30						c. 30			
<i>Vog. triolloensis</i>												
<i>L. cruciformis</i>			c. 8				? 1					
<i>Gn. girtyi girtyi</i> - <i>Gn. girtyi simplex</i>			5								4	3
<i>Gn. girtyi pyrenaicus</i>												
Total	c. 1493	111	c. 360	c. 4874	c. 1349	269	c. 416	c. 5333	c. 363	101	c. 426	166
Number of Pa elements per 1 kg	946	115	218	1942	527	363	525	1840	175	65	258	110

Conodonts \ Samples	8488	8489	8490	8491	8492	8493	8494
<i>Protognathodus cordiformis</i>							
<i>Scaliognathus anchoralis anchoralis</i>							
<i>Pseudopolygnathus pinnatus</i>							
<i>Gnathodus texanus</i>							1
<i>Gn. semiglaber</i>					2	c. 10	c. 10
<i>Gn. pseudosemiglaber</i>					7	c. 10	c. 10
<i>Gn. cuneiformis</i>					1		
<i>Gn. delicatus</i> - <i>Gn. praebilineatus</i>					1		
<i>Gn. praebilineatus</i>				c. 12		c. 10	5
<i>Pseudognathodus homopunctatus</i>	102	113	44	58	244	10	45
<i>Lochria sp. nov.</i>			1				
<i>L. commutata</i>	113	60	6	125	82	36	227
<i>Vogelgnathus campbelli</i>	131	5		2	5	321	1
<i>Gn. aff. girtyi meischneri</i>							
<i>Gn. praebilineatus</i> - <i>Gn. bilineatus remus</i>							
<i>Gn. ex gr praebilineatus</i> - <i>bilineatus juv.</i>							c.10
<i>Gn. bilineatus remus</i>							1
<i>Mestognathus sp.</i>							
<i>Gn. bilineatus romulus</i>							
<i>Vog. postcampbelli</i>	2						
<i>Gn. boogaardi</i>			1	4	2	2	1
<i>Ps. symmutatus</i>							
<i>Gn. bilineatus bilineatus</i>	1196	591	195	c. 560	1980	522	301
<i>Gn. cantabricus</i>			3				
<i>L. nodosa</i>	14			2	2		
<i>Vog. cantabricus</i>					1		
<i>Icriodus sp.</i>					1		
<i>Gn. girtyi girtyi</i>	c. 70	2	1				
<i>Ps. mermaidus</i>					2		
<i>Gn. girtyi meischneri</i>							
<i>Vog. palentinus</i>							
<i>L. scotiaensis</i>							
<i>Neopolygnathus communis communis</i>							
<i>Neopolygnathus purus</i>							
<i>L. mononodosa</i>	4						
<i>Pseudopolygnathus primus</i>							
<i>Bispathodus aculeatus</i>							
<i>Mestognathus bipluti</i>							3
<i>L. multinodosa</i>							
<i>L. zieglerei</i>							
<i>L. senckenbergica</i>							
<i>Vog. triolloensis</i>							
<i>L. cruciformis</i>							
<i>Gn. girtyi girtyi</i> - <i>Gn. girtyi simplex</i>	c. 10						
<i>Gn. girtyi pyrenaeus</i>							
Total	c. 1642	771	251	c. 763	2330	c. 921	c. 615
Number of conodonts per 1 kg	843	543	109	454	1029	453	271

Table 3. Numerical distribution of the latest Viséan-early Serpukhovian conodonts at Triollo Section 3.

Conodonts \ Samples	8495	8496	8497	8498	8499
<i>Protognathodus cordiformis</i>					
<i>Scaliognathus anchoralis anchoralis</i>					
<i>Pseudopolygnathus pinnatus</i>					
<i>Gnathodus texanus</i>					
<i>Gn. semiglaber</i>					
<i>Gn. pseudosemiglaber</i>					
<i>Gn. cuneiformis</i>					
<i>Gn. delicatus</i> - <i>Gn. praebilineatus</i>					
<i>Gn. praebilineatus</i>					
<i>Pseudognathodus homopunctatus</i>	20	54	35		1
<i>Lochriea sp. nov.</i>					
<i>L. commutata</i>	11		27	8	76
<i>Vogelgnathus campbelli</i>	317	37	12	2	
<i>Gn. aff. girtyi meischneri</i>					
<i>Gn. praebilineatus</i> - <i>Gn. bilineatus remus</i>					
<i>Gn. ex gr praebilineatus</i> - <i>bilineatus juv.</i>					
<i>Gn. bilineatus remus</i>					
<i>Mestognathus sp.</i>					
<i>Gn. bilineatus romulus</i>					
<i>Vog. postcampbelli</i>					10
<i>Gn. boogaardi</i>					
<i>Ps. symmutatus</i>					
<i>Gn. bilineatus bilineatus</i>	46	140	360	52	287
<i>Gn. cantabricus</i>		c. 10			c. 10
<i>L. nodosa</i>	3	c. 20	c. 25	5	c. 30
<i>Vog. cantabricus</i>		39			
<i>Icriodus sp.</i>					
<i>Gn. girtyi girtyi</i>	30	161	c. 130		2
<i>Ps. mermaidus</i>					2
<i>Gn. girtyi meischneri</i>					
<i>Vog. palentinus</i>					
<i>L. scotiaensis</i>		3			
<i>Neopolygnathus communis communis</i>					
<i>Neopolygnathus purus</i>					
<i>L. mononodosa</i>		4	7		
<i>Pseudopolygnathus primus</i>					
<i>Bispathodus aculeatus</i>					
<i>Mestognathus bipluti</i>		7	8		2
<i>L. multinodosa</i>	5		c. 40		c. 80
<i>L. zieglerei</i>		c. 70	c. 100	3	c. 100
<i>L. senckenbergica</i>		c. 60	c. 70		1
<i>Vog. triolloensis</i>					
<i>L. cruciformis</i>					
<i>Gn. girtyi girtyi</i> - <i>Gn. girtyi simplex</i>					
<i>Gn. girtyi pyrenaicus</i>	3	5	6		
Total	432	c. 613	c. 814	70	c. 601
Number of Pa elements per 1 kg	289	507	408	61	462

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Appendix: Sedimentology

Description

Section 1 is 16.60 m thick and can be subdivided into the following sub-layers:

- A ferruginous mottled layer of mudstone and wackestone. Mottling may have resulted from the common intraclasts. This layer is fossil-rich, and includes crinoids, bivalves, rare ammonoids, trilobites and bioclasts.
- Above the ferruginous layer follows a 1.3 m-thick, reddish nodular limestone consisting of mudstone and wackestone. The fossil content includes ammonoids, thin-shelled ostracodes, fragments of solitary corals (Pl. 9, fig. 1), crinoids and radiolarians.
- A light grey limestone overlies the nodular limestone. It is characterized by mudstone, with a few radiolarians, and marly partings.
- A 1.3 m-thick cherty limestone follows, consisting of radiolarian wackestone and, rarely, packstone. Microlamination occurs in two thin sections. Dolomitization occurs rarely.
- Above the cherty layer is a thick sequence of thin-bedded limestones with marly intervals. A threefold series of thick-bedded, nodular and cherty limestones, followed by marly limestone, occur in the uppermost part of the section. This series is dominated by wackestone in its basal part and mudstone to wackestone, rarely packstone, in its upper part. Radiolarians are common, along with ammonoids (Pl. 9, figs. 2, 3), crinoids, ostracodes (basically thin-shelled forms) and bivalves. The uppermost part is commonly recrystallized.

Section 2 represents another limb of the fold. The lower part is composed of thick-bedded, laminated limestones, whereas the middle part is thin bedded. The upper part is heterogeneous, consisting of thin-bedded limestone, thick bedded cherty limestone with marl intercalations, and nodular limestone (Pl. 9).

The thick-bedded limestone is composed of mudstone and wackestone. Fossils include radiolarians, ammonoids, crinoids and rare ostracodes. Quartz grains occur in one of the thin sections (#8492). The thin-bedded middle part consists of mudstone with rare radiolarians (Pl. 9, fig. 4) and a few ostracodes. Peloids occur in one thin section. The uppermost part is similar to that of the top of section 1 and is commonly recrystallized.

Section 3 is shorter and composed of, from bottom to top, thick-bedded limestone, including mudstones with rare radiolarians; thin-bedded limestone, consisting of wackestone with radiolarians, ammonoids and ostracodes; thick-bedded, commonly recrystallized limestone; nodular limestone consisting of mudstone and wackestone, including radiolarians and peloids (Pl. 9, fig. 5); and thick-bedded limestone, mostly recrystallized and including crinoids.

Palaeoecological interpretation of the sedimentary data

From the 58 thin sections analyzed, 52.6% consist of mudstone and 42.2% of wackestone (mudstone to wackestone transitions, representing 12%, were added to half to mudstone and wackestone, respectively). The remaining 5.2% of the thin sections are

composed of wackestone to packstone. This composition points to an environment well below wave base, but above the CCD (considering the preserved calcitic components). Fossils consist predominantly of pelagic biota of ammonoids, radiolarians, thin-shelled bivalves and ostracodes. Further rare fossils include trilobites, fragments of corals and isolated fragments of crinoid ossicles, basically limited to the lower part of Section 1. The fossil association points to a deep-water, pelagic environment, with minor shedding of elements (such as corals and rare quartz grains) possibly originating from shallower environments. Peloids within cemented areas (Pl. 9, fig. 5) indicate early cementation at the sea floor. Lamination in a few samples points to absence of burrowing organisms.

Basinal limestone with cherty and marly interlayers are widespread in the Palaeozoic rocks, particularly in Devonian and Carboniferous sequences of the Cantabrian Mountain (Spain), the Pyrénées (Spain and France), Rheinisches Schiefergebirge (Germany) and the Carnic Alps (Austria), among others (see Tucker, 1974). The depositional environment deduced from the facies analysis fits the results obtained by the conodont associations.

Explanations of plates

All illustrated specimens are from the Triollo section except of two specimens illustrated in figures 5 and 6 of Plate 3, which are from the La Lastra section (3 km to the southeast of the Triollo section). All illustrated specimens are housed in the Nationaal Natuurhistorisch Museum, Leiden, The Netherlands.

Plate 1

Figs. 1, 4. *Vogelgnathus campbelli* (Rexroad, 1957).

Fig. 1. RGM 414377, SEM 0602, sample 8435.

Fig. 4. RGM 415058, SEM 0603, sample 8483.

Figs. 2, 5, 9. *Vogelgnathus campbelli* (Rexroad, 1957) transitional to *V. postcampbelli* (Austin & Husri, 1974).

Fig. 2. RGM 414639, SEM 0692, sample 8463.

Fig. 5. RGM 283397, SEM 0576, sample 8790.

Fig. 9. RGM 416000, SEM 0575, sample 8790.

Figs. 3, 7, 10. *Vogelgnathus postcampbelli* (Austin & Husri, 1974).

Fig. 3. RGM 416001, SEM 0577, sample 8790.

Fig. 7. RGM 416002, SEM 0575, sample 8790.

Fig. 10. RGM 416003, SEM 0573, sample 8790.

Fig. 6, 8, 11. Unidentified elements which might be related to *Vogelgnathus*.

Fig. 6. RGM 384786, SEM 0663, sample 8754.

Fig. 8. RGM 416004, SEM 0697, sample 8445, $\times 80$.

Fig. 11. RGM 416005, SEM 0698, sample 8445.

Magnification $\times 120$, unless otherwise indicated.

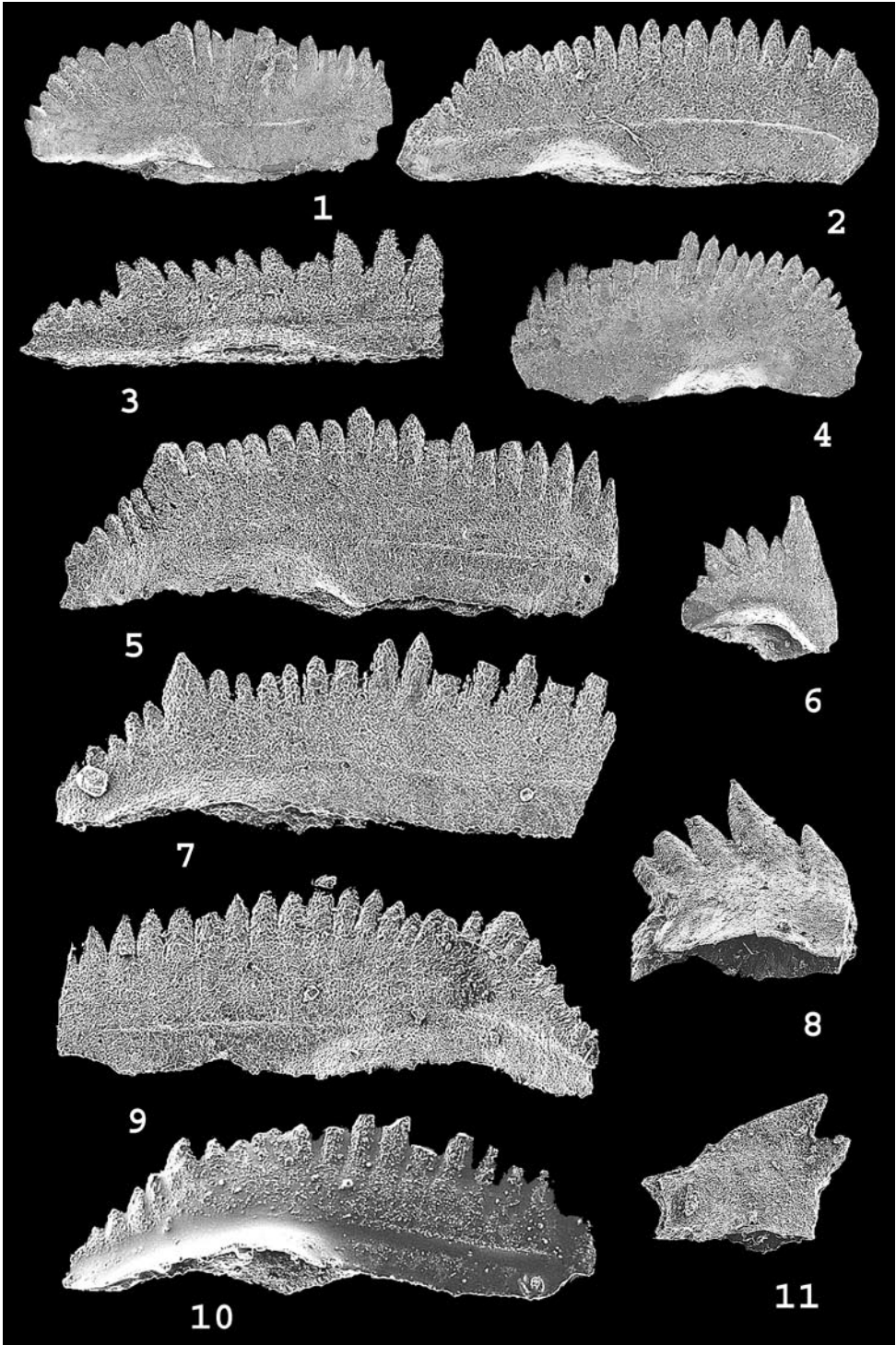


Plate 2

Figs. 1, 2, 4 -7. *Vogelgnathus cantabricus* sp. nov.

Fig. 1. RGM 414591, SEM 0581 sample 8459.

Fig. 2. RGM 416006, SEM 0582, sample 8459.

Fig. 4. RGM 384815, SEM 0579, sample 8752.

Fig. 5. RGM 414870, sample 8473. a, SEM 0585. b, SEM 0586.

Fig. 6. RGM 416008, SEM 0584, sample 8473.

Fig. 7. RGM 416007, sample 8459. a, SEM 2005. b, SEM 0583.

Figs. 3, 8, 9. *Vogelgnathus triolloensis* sp. nov.

Fig. 3. RGM 384700, holotype, sample 8786. a, SEM 0592. b, SEM 0591. c, SEM 2004.

Fig. 9. RGM 416009, sample 8786. a, SEM 2003. b, SEM 0588.

Fig. 8. RGM 415060, SEM 0605, sample 8483.

Figs. 10, 11. *Vogelgnathus palentinus* sp. nov.

Fig. 10. RGM 416010, sample 8463. a, SEM 2001. b, SEM 0689.

Fig. 11. RGM 416011, holotype, sample 8463. a, SEM 2002. b, SEM 0690.

Magnification $\times 120$.

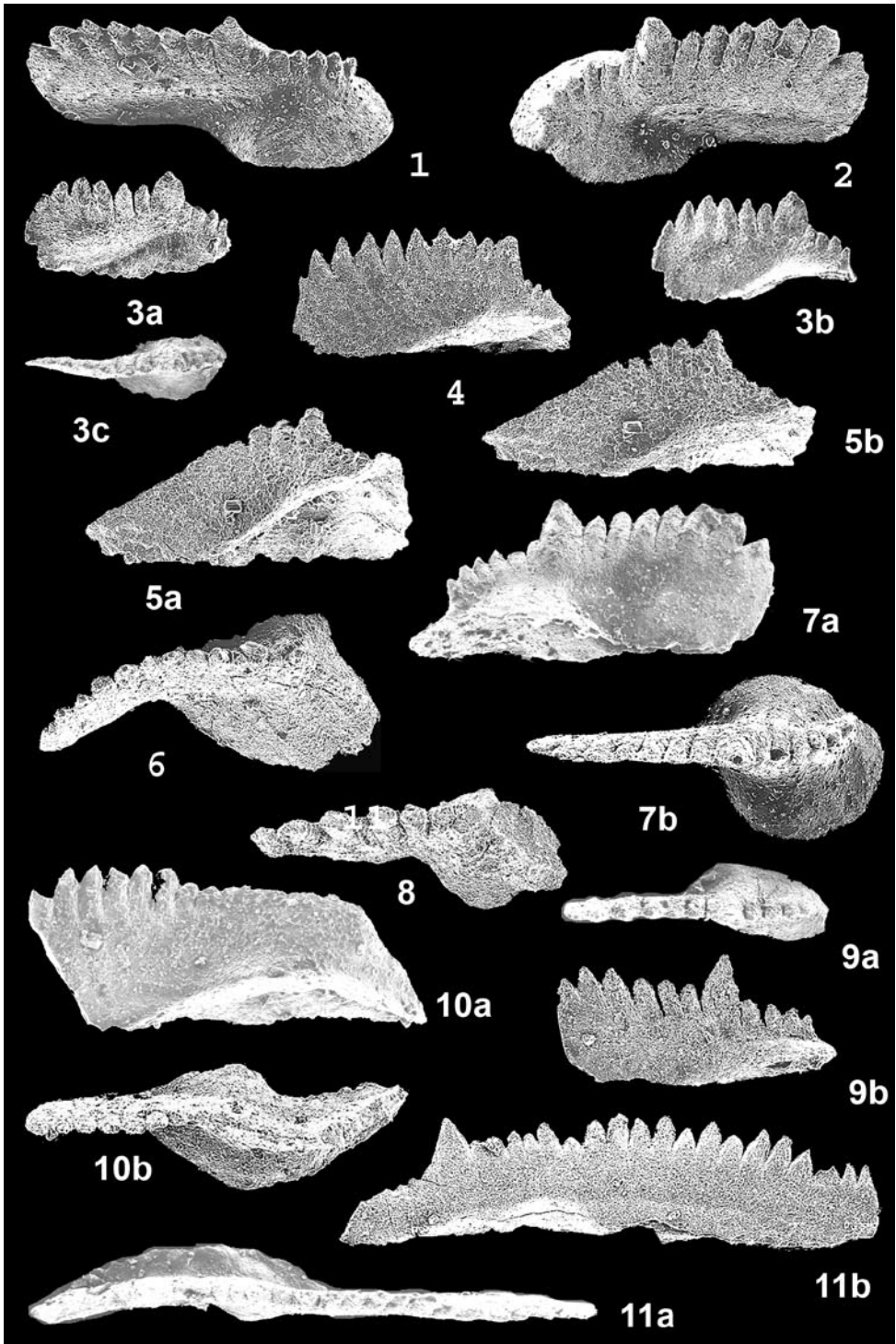


Plate 3

Figs. 1-3. *Vogelgnathus cantabricus* sp. nov.

Fig. 1. RGM 415443, holotype, sample WP6935. a, SEM 0001. b, SEM 0125-01. c, SEM 0127. d, SEM 0129.

Fig. 2. RGM 416012, sample WP6935. a, SEM 0124-01. b, SEM 0123. c, SEM 0125-02.

Fig. 3. RGM 416013, SEM 959, sample 8474.

Fig. 4. *Vogelgnathus triolloensis* sp. nov.

Fig. 4. RGM 416014, sample 8473. a, SEM 0220. b, SEM 0221.

Figs. 5, 6. *Vogelgnathus palentinus* sp. nov.

Fig. 5. RGM 416015, sample LL1, section La Lastra, latest Viséan-earliest Serpukhovian. a, SEM 959205. b, SEM 959204.

Fig. 6. RGM 416016, same sample. a, SEM 959206. b, SEM 959207.

All illustrated specimens are from the Triollo and La Lastra sections unless otherwise indicated, × 120.

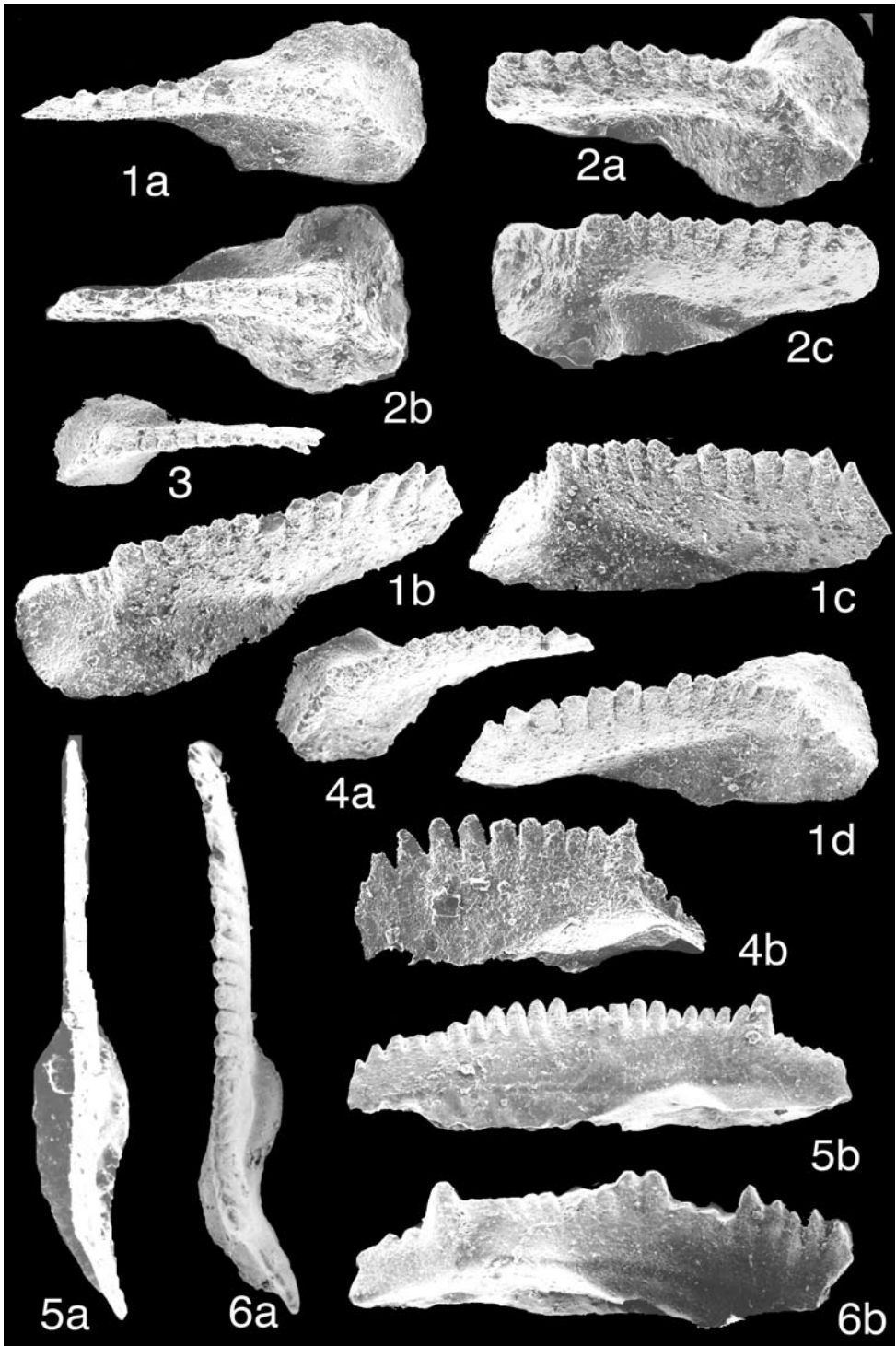


Plate 4

Figs. 1, 7, 11. *Gnathodus praebilineatus* Belka, 1985.

Fig. 1. RGM 414580, SEM 0645, sample 8459.

Fig. 7. RGM 414499, SEM 0643, sample 8447.

Fig. 11. RGM 414597, SEM 0641, sample 8460.

Figs. 2, 4, 8, 12. *Gnathodus delicatus* (Branson & Mehl, 1938) transitional to *Gn. praebilineatus* Belka, 1985.

Fig. 2. RGM 414521, SEM 0612, sample 8451.

Fig. 4. RGM 414530, SEM 0611, sample 8452.

Fig. 8. RGM 416017, SEM 0648, sample 8451.

Fig. 12. RGM 415160, SEM 0636, sample 8492.

Figs. 3, 5, 6, 9. *Gnathodus boogaardi* sp. nov.

Fig. 3. RGM 416018, SEM 0613, sample 8452.

Fig. 5. RGM 415195, SEM 0609, sample 8493.

Fig. 6. RGM 416019, SEM 0608, sample 8493.

Fig. 9. RGM 416020, SEM 0610, sample 8493.

Fig. 10. *Gnathodus joseramoni* Sanz-López, Blanco-Ferrera & Carcía-López, 2004; RGM 414427, SEM 0651, sample 8447.

Magnification $\times 60$.



Plate 5

Figs. 1, 8, 10, 12, 14. *Gnathodus bilineatus remus* Meischner & Nemyrovská, 1999.

Fig. 1. RGM 415271, SEM 0634, sample 8499.

Fig. 8. RGM 416021, SEM 0619, sample 8460.

Fig. 10. RGM 414933, SEM 0647, sample 8478.

Fig. 12. RGM 384799, SEM 0644, sample 8753, specimen showing trend to *Gn. bilineatus bilineatus* (Roundy).

Fig. 14. RGM 416051, SEM 0635, sample 8478.

Figs. 2, 4, 5, 7, 11. *Gnathodus cantabricus* Belka & Lehmann, 1998.

Fig. 2. RGM 416022, SEM 0617, sample 8460.

Fig. 4. RGM 414648, SEM 0642, sample 8465.

Fig. 5. RGM 416025, SEM 0638, sample 8460.

Fig. 7. RGM 416026, SEM 0615, sample 8460, specimen showing trend from *Gn. bilineatus remus*.

Fig. 11. RGM 384872, SEM 0614, sample 8750.

Figs. 3, 6. *Gnathodus praebilineatus* Belka, 1985.

Fig. 3. RGM 416027, SEM 0642, sample 8465.

Fig. 6. RGM 416028, SEM 0650, sample 8439, specimen showing trend from *Gn. semiglaber*.

Figs. 9, 13. *Gnathodus bilineatus romulus* Meischner & Nemyrovská, 1999.

Fig. 9. RGM 414460, SEM 0694, sample 8444, specimen showing trend to *Gn. bilineatus bilineatus* (Roundy).

Fig. 13. RGM 414557, SEM 0649, sample 8456, specimen showing trend to *Gn. bilineatus bilineatus* (Roundy).

Magnification $\times 60$.

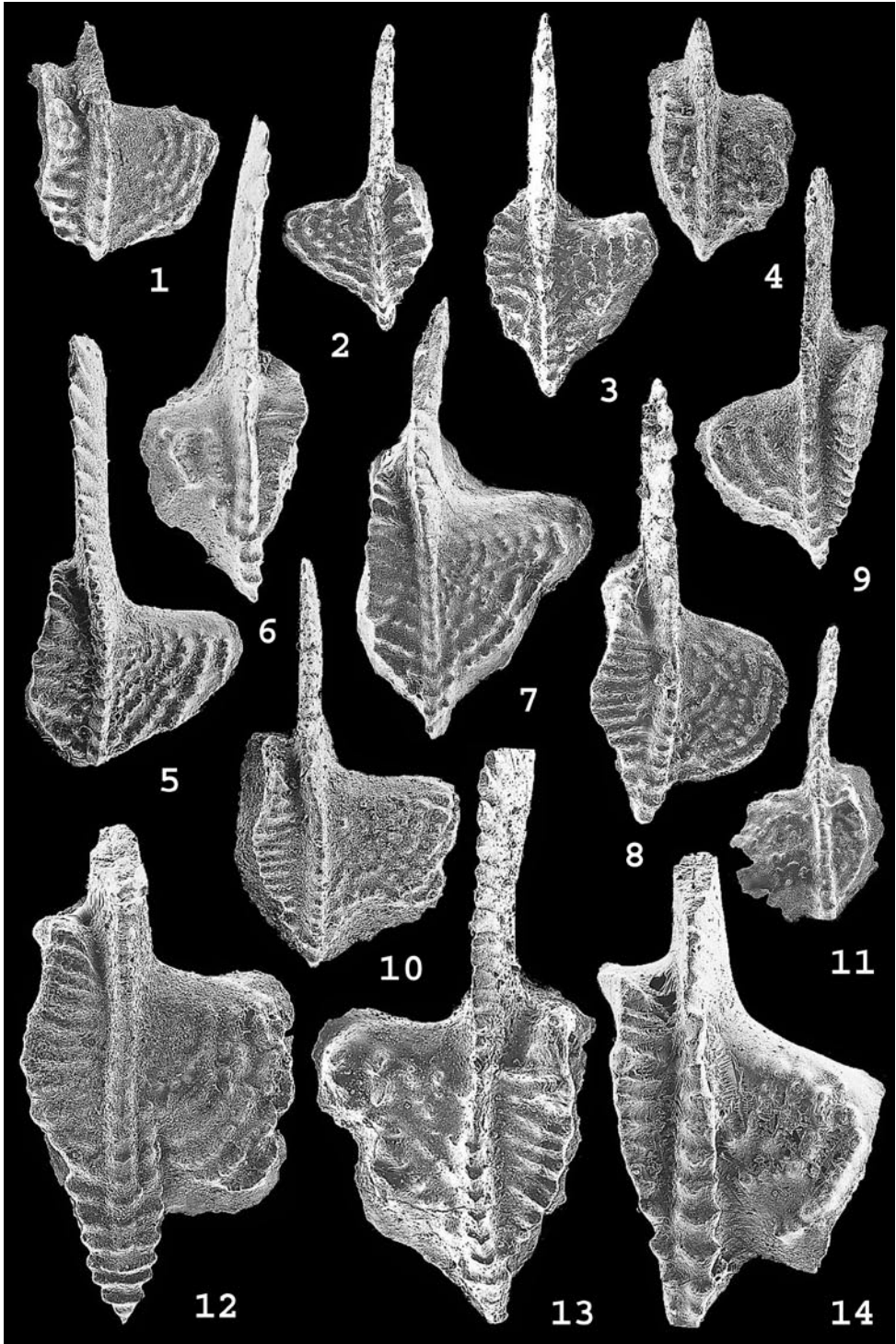


Plate 6

Figs. 1, 9, 12. *Gnathodus pseudosemiglaber* Thompson & Fellows, 1970.

Fig. 1. RGM 414544, SEM 0626, sample 8455.

Fig. 9. RGM 416029, SEM 0629, sample 8455.

Fig. 12. RGM 414425, SEM 0646, sample 8436.

Figs. 2, 3, 5, 6, 8. *Gnathodus pseudosemiglaber* Thompson & Fellows, 1970, transitional to *Gn. girtyi meischneri* (Austin & Husri, 1974).

Fig. 2. RGM 414892, SEM 0625, sample 8475.

Fig. 3. RGM 416030, SEM 0624, sample 8475.

Fig. 5. RGM 414360, SEM 0623, sample 8435.

Fig. 6. RGM 416031, SEM 0622, sample 8435.

Fig. 8. RGM 416032, SEM 0621, sample 8435.

Figs. 4, 11. *Gnathodus cuneiformis* Mehl & Thomas, 1947.

Fig. 4. RGM 414437, SEM 0652, sample 8439.

Fig. 11. RGM 414356, SEM 0653, sample 8435.

Figs. 7, 10. *Gnathodus semiglaber* Bischoff, 1957.

Fig. 7. RGM 414475, SEM 0655, sample 8445, × 40.

Fig. 10. RGM 416033, SEM 0656, sample 8445.

All illustrated specimens are × 60 unless otherwise indicated.

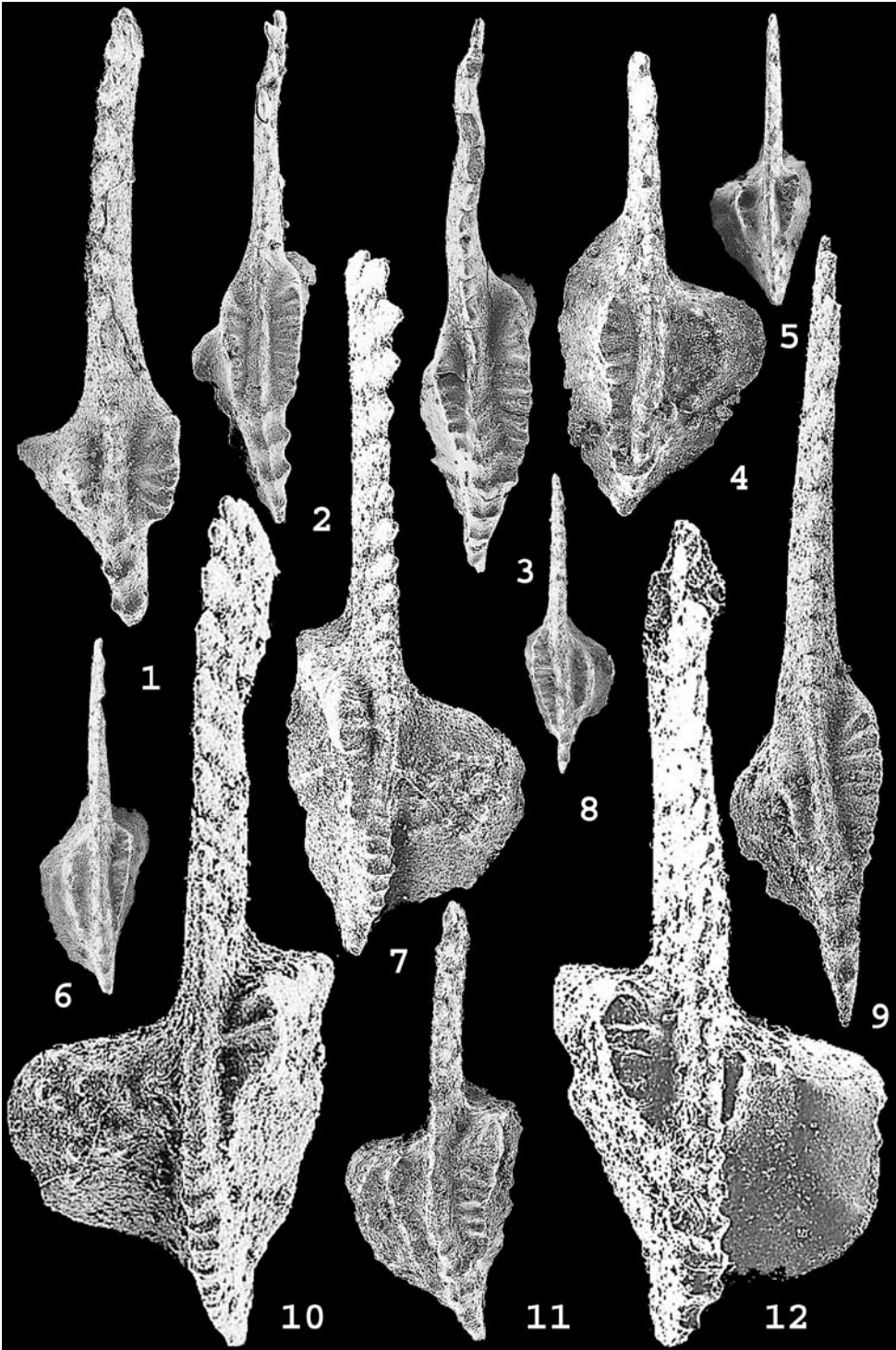


Plate 7

Fig. 1. *Pseudognathodus mermaidus* (Austin & Husri, 1974); RGM 238398, SEM 0673, sample 8794.

Figs. 2, 3. *Pseudognathodus homopunctatus* (Ziegler, 1960).

Fig. 2. RGM 384918, SEM 0668, sample 8721.

Fig. 3. RGM 416034, SEM 0666, sample 8794.

Figs. 4, 5, 7, 14. *Gnathodus girtyi meischneri* (Austin & Husri, 1974).

Fig. 4. RGM 414743, SEM 0687, sample 8468.

Fig. 5. RGM 416035, SEM 0688, sample 8468.

Fig. 7. RGM 416036, SEM 0684, sample 8790.

Fig. 14. RGM 384664, SEM 0661, sample 8788, showing trend to *Gn. girtyi pyrenaicus* Nemyrovskaya & Perret sp. nov.

Figs. 6, 8-12. *Gnathodus girtyi pyrenaicus* Nemyrovskaya & Perret, subsp. nov.; Figs. 6, 8-10: French Pyrénées:

Fig. 6. FR-6, sample Por 20, section Fort du Portalet (Perret, 1993, pl. 105, fig. 9);

Figs. 8, 10. FR-7 and FR-8 sample Tan 29, section Col de Tantes, uppermost Viséan (Perret, 1993, pl. 105, figs. 38, 39);

Fig. 9. FR-9, sample Ach 17 p, section Port de la Chourique, lower Serpukhovian (fig. 28, pl. 105, from Perret, 1993).

Figs. 11, 12. Palencia:

Fig. 11. RGM 416037, SEM 0685, sample 8468.

Fig. 12. RGM 416038 (holotype), SEM 0686, sample 8468.

Fig. 13. *Gnathodus bilineatus romulus* Meischner & Nemyrovskaya, 1999; RGM 416041, SEM 0693, sample 8444.

Fig. 15. *Gnathodus girtyi girtyi* Hass, 1953; RGM 414656, SEM 0630, sample 8465.

Figs. 16-20. *Gnathodus girtyi* Hass, 1953 s.l. transitional to *Gn. girtyi simplex* Dunn, 1966.

Fig. 16. RGM 415114, SEM 0633, sample 8488.

Fig. 17. RGM 416039, SEM 0658, sample 8488.

Fig. 19. RGM 416040, SEM 0657, sample 8488.

Fig. 18. RGM 414981, SEM 0631, sample 8481.

Fig. 20. RGM 384874, SEM 0659, sample 8750.

Magnification $\times 60$.

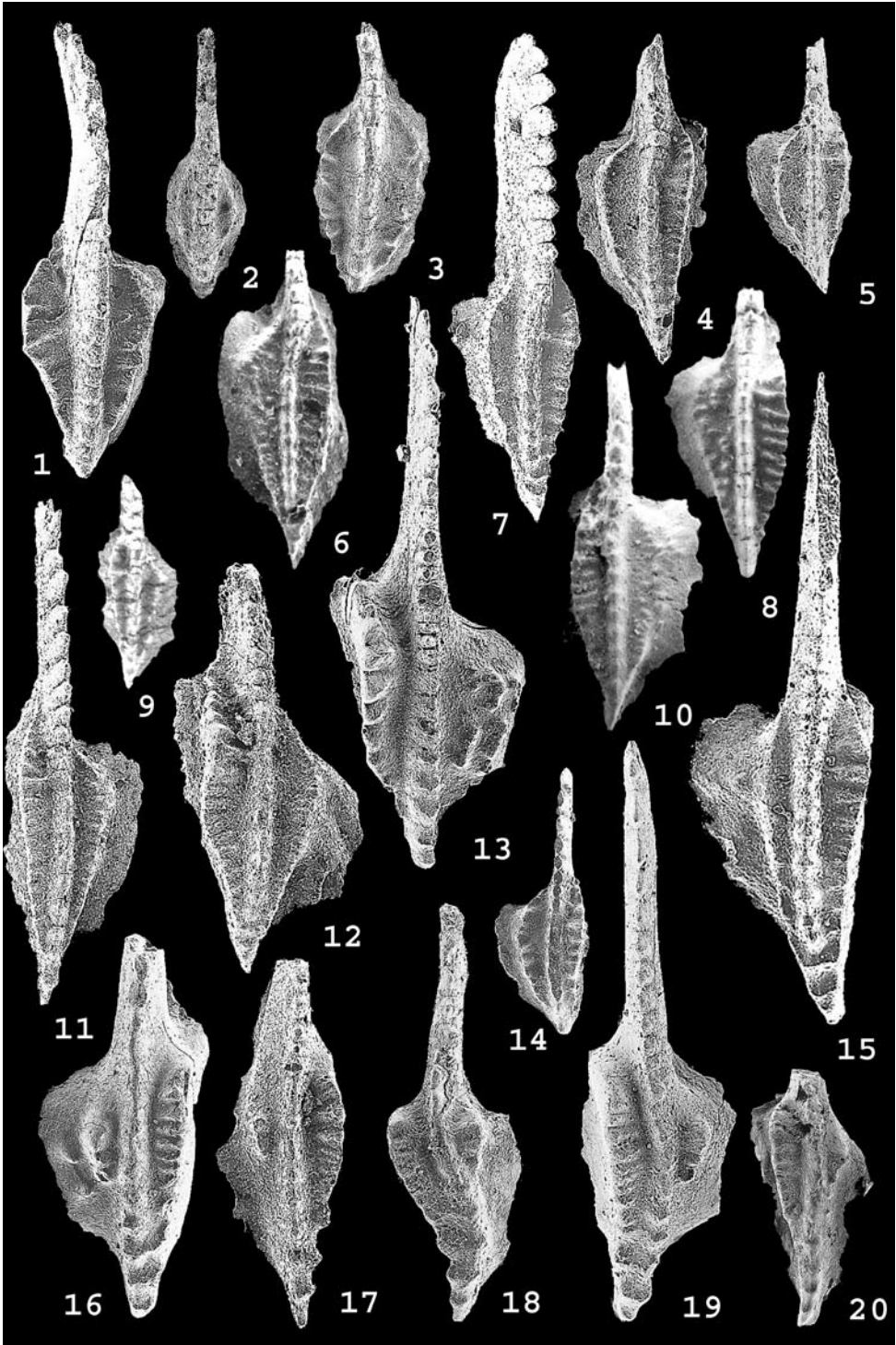


Plate 8

Figs. 1, 3. *Lochriea* sp. nov. Nemyrovská *et al.*, in press.

Fig. 1. RGM 414485, SEM 0699, sample 8445.

Fig. 3. RGM 414403, SEM 0695, sample 8436.

Figs. 2, 7. *Lochriea commutata* (Branson & Mehl, 1941).

Fig. 2. RGM 416042, SEM 0696, sample 8436.

Fig. 7. RGM 416043, SEM 0679, sample 8790.

Figs. 4-6, 8. *Lochriea scotiaensis* (Globensky, 1967).

Fig. 4. RGM 414894, SEM 0672, sample 8475.

Fig. 5. RGM 414965, SEM 0669, sample 8479.

Fig. 6. RGM 416044, SEM 0671, sample 8479.

Fig. 8. RGM 416045, SEM 0670, sample 8479.

Fig. 9. *Lochriea* cf. *cruciformis* (Clarke, 1960).

Fig. 9. RGM 416046, SEM 0683, sample 8790, showing trend from *L. nodosa* (Bischoff, 1957).

Figs. 10, 15, 17. *Lochriea nodosa* (Bischoff, 1957).

Fig. 10. RGM 414593, SEM 0675, sample 8459.

Fig. 15. RGM 416047, SEM 0680, sample 8790, the specimen showing trend to *L. senckenbergica* Nemyrovská *et al.*, 1994 or *L. multinodosa* (Wirth, 1967), lateral margins are partly broken.

Fig. 17. RGM 416048, SEM 0682, sample 8790.

Figs. 11, 14, 16. *Lochriea ziegleri* Nemyrovská *et al.*, 1994.

Fig. 11. RGM 384875, SEM 0677, sample 8750.

Fig. 14. RGM 416050, SEM 0676, sample 8750.

Fig. 16. RGM 384949, SEM 0674, sample 8720.

Fig. 12. *Lochriea senckenbergica* Nemyrovská *et al.*, 1994; RGM 415809, SEM 0667, sample 8794.

Fig. 13. *Lochriea multinodosa* (Wirth, 1967); RGM 416049, SEM 0678, sample 8790.

Magnification $\times 80$.

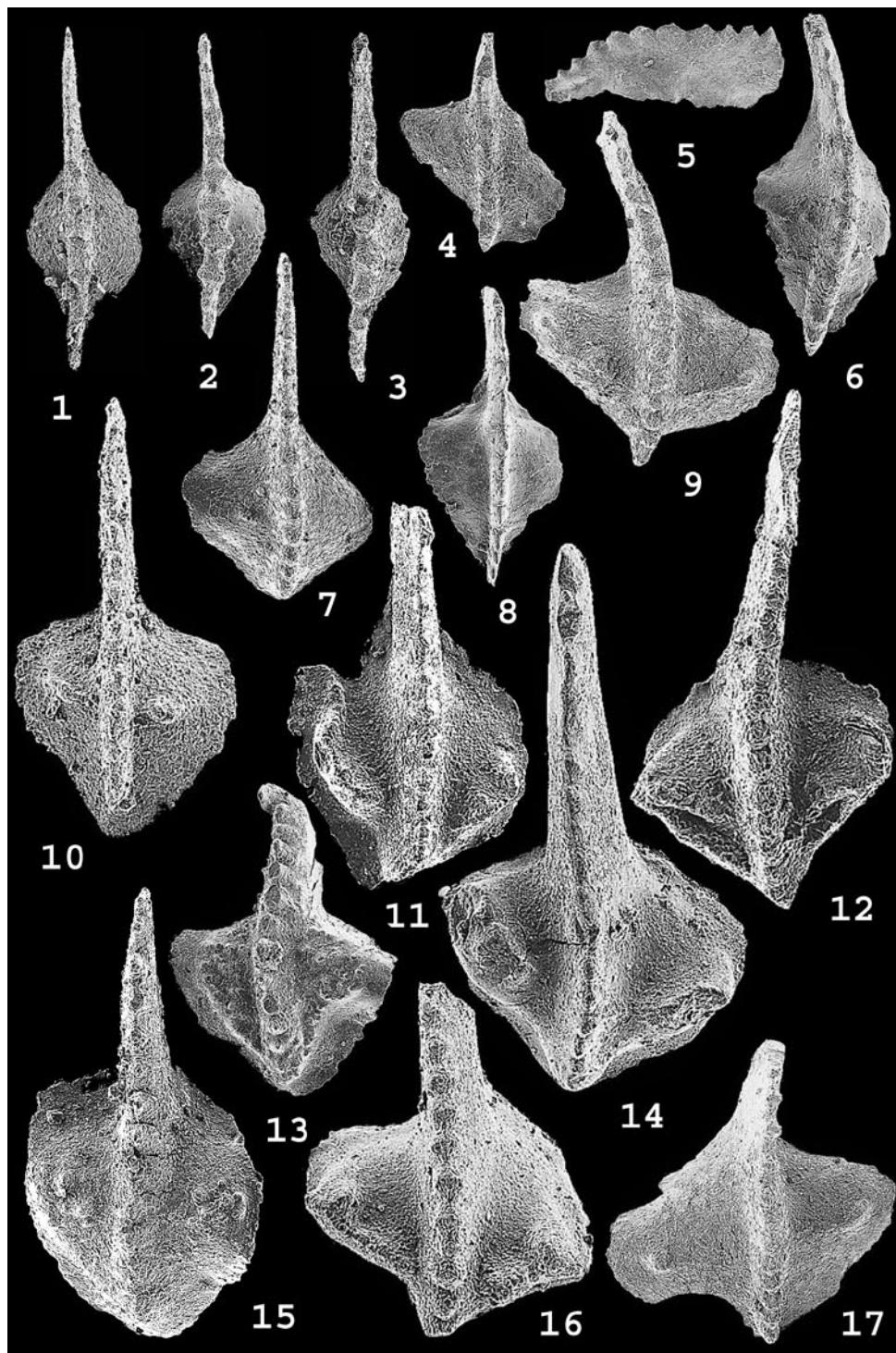


Plate 9

Fig. 1. Wackestone including fragments of solitary rugose corals and a few shells in the matrix. Note the mottled structures and the abundance of residual material (dark). Scale bar is 2 mm long. Section 1, sample 8447.

Fig. 2. Wackestone-packstone rich in ammonoids. The matrix includes ostracodes, bivalves and shell fragments. Scale bar is 1 mm long. Section 1, sample 8494.

Fig. 3. Wackestone rich in radiolarians with rare ammonoids. Scale bar is 1 mm long. Section 1, sample 8496.

Fig. 4. Details of radiolarian wackestone. Scale bar is 0.1 mm long. Section 1, sample 8484.

Fig. 5. Detail of peloid-rich areas. Scale bar is 0.5 mm long. Section 1, sample 8498.

