The recurrence of *Vogelgnathus campbelli*-dominated conodont faunas in the Viséan and early Namurian of the Cantabrian Mts (Spain): a reflection of sea-level fluctuations?

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The conodont faunas from the Viséan and lower Namurian limestone succession in the Cantabrian Mts are mainly characterised by abundant *Gnathodus* spp. and minor amounts of *Lochriea* spp. However, *Gnathodus* and *Lochriea* are four times largely or almost completely replaced by *Vogelgnathus campbelli*, every time during a relatively short interval. Apart from being present in moderate quantities in basal Viséan faunas, *V. campbelli* is lacking in most of the *Gnathodus*-dominated faunas from the Cantabrian Mts. These invasions by *V. campbelli* are supposed to have occurred during a rise of sea level enabling this – presumably more offshore – species to enter the region while at the same time the habitat of *Gnathodus* c.s. was partly or almost completely drowned. These sea level rises are thought to represent the periods of maximum flooding of the transgressive-regressive cycles envisaged by Ross & Ross (1988). In this particular case, the ones during the late Asbian, the early and the late Brigantian and the early Namurian, and may be an earlier one during the late Chadian. Reference is made to comparable, possibly contemporaneous, invasions by *V. campbelli* in the Pyrenees and in Japan.

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Introduction

During the study of conodont faunas from an upper Viséan to lower Namurian section from Triollo in the Cantabrian Mountains (Spain) it appeared that in a short interval of the rock sequence the composition of the fauna changed drastically from the normal *Gnathodus bilineatus*-dominated fauna to a fauna in which almost 80% of the Pa elements belong to *Vogelgnathus campbelli* (Rexroad, 1957). To investigate whether this is only a local phenomenon or of more regional significance, faunas from several other sections in the Cantabrian Mts were examined. From this examination appears that in other sections too the sequence of faunas dominated by *Gnathodus bilineatus* (Roundy, 1926) is briefly interrupted – and in some sections more than once – by faunas in which *V. campbelli* dominates or is a rather important constituent. This phenomenon is even more conspicuous because in most *Gnathodus*-dominated faunas in this region *V. campbelli* is absent to rare.

The distribution of *V. campbelli* in sections studied by Budinger (1965), van Adrichem Boogaert (1967) and Higgins (in Higgins & Wagner-Gentis, 1982) has been checked. Comparison with the data provided by Higgins is somewhat hindered by the fact that he apparently investigated only the coarser sieve fractions. For instance he reported as the highest yield per kilogramme of samples from the Entrago section a total of 165 conodonts, whereas in my samples from the Entrago section the highest total yield per kg amounts to more than 3000 Pa elements. Probably because I counted all conodonts not able to pass the sieve with a 0.053 mm opening. Because the Pa elements of *V. campbelli* are slender and relatively small the species is underrepresented in the coarser fraction (see Table 1). Therefore one has to assume that the real percentage of *V. campbelli* in his faunas may be higher than appears in his data. Considering the data provided by Budinger (1965) one notes that the number of specimens per sample is relatively small. Whether this is due to small rock samples or the result of studying coarser fractions only, cannot be determined from his published data. In his distribution charts (Budinger, 1965, tables 3, 5 and 6) numbers are given for *Spatho-*

Table 1. Numbers of Pa elements in the coarse and fine fractions of sample WP 1990 91E from Triollo.

	Gnathodus bilineatus	*Gnathodus homopunctatus*	*Gnathodus girtyi*	*Lochriea commutata*	*Vogelgnathus campbelli*
Fraction not passing a 0.25 mm sieve-opening	16	2	1	2	8
Fraction between 0.25 and 0.053 mm sieve-opening	68	9	1	29	494
Total of both fractions	84	11	2	31	502

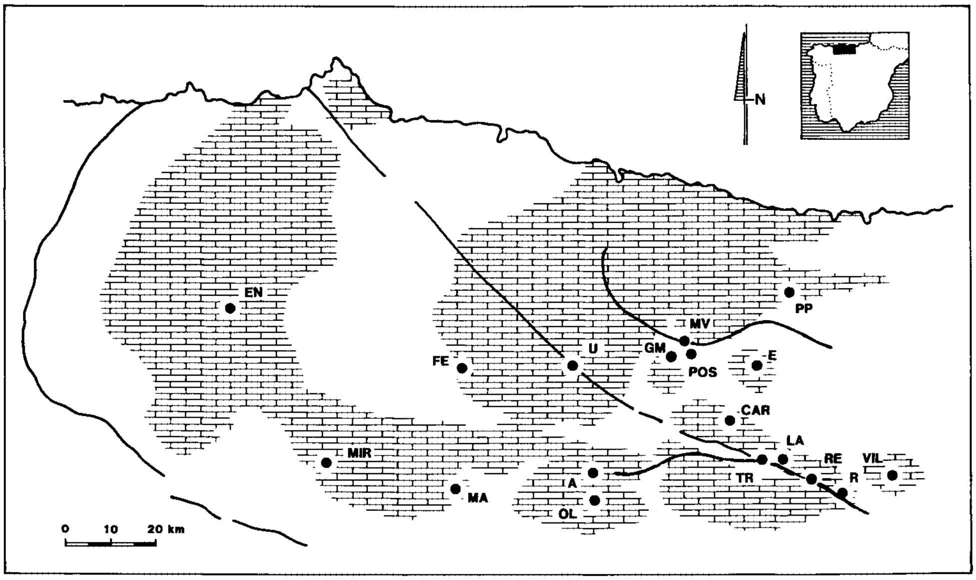

Fig. 1. Approximate maximum extent of the carbonate platform in the Cantabrian area during the Viséan and Lower Namurian (slightly adapted version of figs. 31E-H of Seibert, 1988).
Localities mentioned in the text: A = Aguasalio; CAR = Cardaño de Arriba; E = Enterrias; EN = Entrago de Teverga; FE = Felechosa; GM = Gildar-Montó; LA = La Lastra; MA = Matallana; MIR = Mirantes de Luna; MV = Sta. Marina de Valdeón; OL = Sta. Olaja de la Varga; POS = Posada de Valdeón; PP = section between Panes and Potes; R = Ruesga Dam; RE = Resoba; TR = Triollo; U = La Uña; VIL = Villabellaco.

gnathodus campbelli and *Spathognathodus werneri* Ziegler, 1962. The specimens he assigned to *S. werneri* are – in my opinion – not *S. werneri* but specimens of *V. campbelli*. Arguments for this re-assignment will be presented below in the section 'Remarks upon *Vogelgnathus campbelli*'. In the use of Budinger's data *S. werneri* is included in the totals for *V. campbelli*.

All studied sections (see Fig. 1) were taken from the Genicera Formation (commonly referred to as Alba Fm., see Wagner et al., 1971). The Genicera Formation is transgressive over a large part of the Cantabrian Mts. It lies disconformably over other formations. In most of the area the basal layer contains late Tournaisian, *pseudosemiglaber* Zone conodont faunas (e.g. at Entrago, Aguasalio and Villabellaco; see Raven, 1983, p. 300), whereas in other parts of the area the faunas of the basal layer are indicative of the middle Viséan *bilineatus* Zone (e.g. at Cardaño and Posada de Valdeón (see van der Ark, 1982).

According to Higgins & Wagner-Gentis (1982), early and middle Viséan times were characterised in the Cantabrian Mountains by local non-deposition followed by a short period of widespread sedimentation, followed in turn by a period of widespread non-deposition into the *bilineatus* Zone. From then on, into the Namurian E_1-E_2, deposition seems to have been continuous.

Acknowledgements

I am indebted to Drs R.H. Wagner (Jardín Botánico de Córdoba) and C.F. Winkler Prins (NNM, Leiden), who critically read an earlier draft of this paper and made suggestions that have improved the final version. I wish to express my gratitude to Dr H.A. van Adrichem Boogaert for putting a sample from Triollo at my disposal and I thank Mr J.J. Timmers for drawing the figures and combining the SEM micrographs into plates and Mr J.B. Jonkers for typing the manuscript.

Conodont distribution in the various sections examined

TRIOLLO

Conodonts from this section were investigated by van Adrichem Boogaert (1967). Since the numbers of specimens obtained have not been entered in his distribution chart (van Adrichem Boogaert, 1967, enclosure 4), the present author has reinvestigated these faunas as well as an additional limestone sample (62TR4) taken by van Adrichem Boogaert in 1962 but not used for his study. The numbers of conodont Pa elements are given in Table 2A. The position of the samples and the corresponding percentage of the sum of the species of *Gnathodus* and the percentage of *Vogelgnathus campbelli* are shown in Fig. 2. From this Fig. 2 and Table 2A it appears that except for sample 62TR4 all faunas are dominated by *Gnathodus bilineatus*. Sample 62TR4, taken directly above the chert bed, contains more than 80% of *V. campbelli*. This sample is within the *bilineatus* Zone. The base of the *nodosa* Zone may be somewhere below sample 62TR11 in which *Lochriea nodosa* (Bischoff, 1951) appears for the first time.

Winkler Prins sampled a parallel section at Triollo and conodont data are given in Table 2B and Fig. 3. Here also the fauna from a sample taken directly above the chert bed (1990 91E) is dominated by *V. campbelli* (c. 80%). In sample TR2 at the base of this part of the section – with a fauna belonging to the *texanus* Zone (see Table 2B) – the number of Pa elements of *V. campbelli* amounts to about 7.5%.

The data on the faunas from the two Triollo sections thus show a significant percentage of *V. campbelli* in the *texanus* Zone and a very high percentage in the *bilineatus* Zone, well below the appearance of *Lochriea nodosa*.

RESOBA

Figure 4 shows the position of samples and percentages of Pa elements of *Gnathodus* and *V. campbelli* from part of a section near Resoba made available by Winkler Prins and Wagner.The numbers of specimens of the different species are given in Table 3. No data are available from the lower part of this section between samples 1990 6831 and 071 RE3 because the samples 1980 RE 3A and 1980 RE 3B could not be disintegrated by means of formic acid because of their high silica content.

Samples 1981 10C, 71G 6833 and 071 RE3A taken from the lower 50 cm of the limestone above the chert show a dominance of *V. campbelli* (up to 93% in sample

Table 2. Numbers of Pa elements in samples from Triollo and Entrago de Teverga.

	Gnathodus sp.	*Gnathodus bilineatus*	*Gnathodus homopunctatus*	*Gnathodus girtyi*	*Lochriea commutata*	*Lochriea nodosa*	*Lochriea multinodosa*	*Vogelgnathus campbelli*	Number of Pa elements/kg
A) Triollo, coll. Van Adrichem Boogaert									
62 TR 5	—	31	3	—	4	3	—	—	?
62 TR 11	1[a]	10	2	—	1	1	—	—	?
62 TR 4a	—	54	4	—	3	—	—	—	?
62 TR 4'	—	1557	52	4	82	—	—	138	?
62 TR 4	—	84	9	3	23	—	—	604	750
62 TR 3	—	168	1	7	10	—	—	1	?
B) Triollo, coll. Winkler Prins									
1984 TR 3H	—	26	—	—	13	9	12	3	60
1984 TR 3G	135[a]	690	28	101	229	—	—	8	1490
1984 TR 3F	2[a]	41	6	—	4	—	—	—	80
1990 91E	—	84	11	2	31	—	—	502	670
1984 TR 3D	—	52	1	—	12	—	—	—	100
1984 TR 3C	3[a]	34	1	—	12	—	—	—	47
1984 TR 3B	2[a]	34	—	—	3	—	—	—	77
1984 TR 3A	—	68	2	4	12	—	—	—	106
1984 TR 2	574[b]	—	17	—	—	—	—	48	695
C) Entrago de Teverga									
060 E9	—	48	—	—	6	4	—	1	148
060 E8	—	514	—	2	134	13	38	—	1190
060 E7	20[a]	65	12	2	—	—	—	162	266
060 E6	62[a]	364	20	2	43	14	—	1065	2300
060 E5	18[c]	2196	85	10	101	—	—	691	1846

[a] Specimens of *Gnathodus symmutatus*.

[b] Ten specimens of *Protognathodus praedelicatus*, 105 of *Gnathodus delicatus*, 85 of *G. pseudosemiglaber*, 110 of *G. cuneiformis*, 38 of *G. texanus*, 102 of *G. typicus*, 17 of *G. semiglaber*, 13 of *G. punctatus*, 18 of *G. symmutatus*, and 76 *G.* sp. indet.

[c] Seven specimens of *G. semiglaber*, and 11 of *G. symmutatus*.

71G 6833). These samples are from a bed relatively high in the *nodosa* Zone, as follows from sample 1990 6831 (a brecciated limestone which proved to be a mixture of upper Tournaisian / lower Viséan and upper Viséan limestones) which yielded a few specimens of *Lochriea nodosa*. Higher in the Resoba section (sample 1980 RE4C) specimens of *V. campbelli* reach an amount of up to 16%. This part of the section is

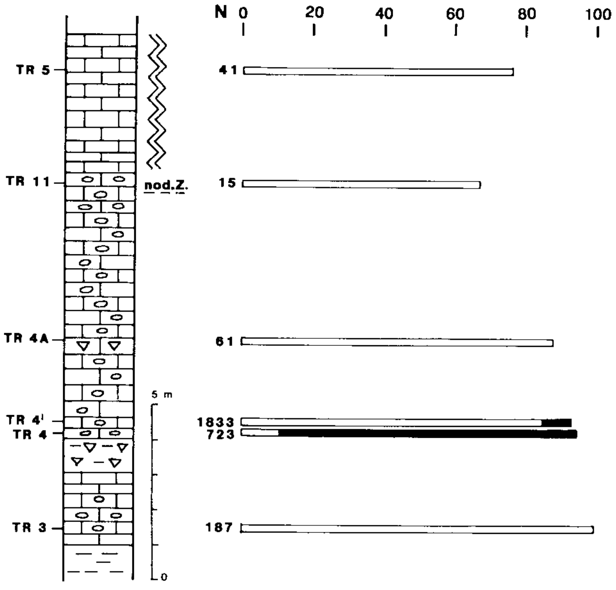

Fig. 2. Section near Triollo (redrawn from van Adrichem Boogaert, 1967, fig. 47)

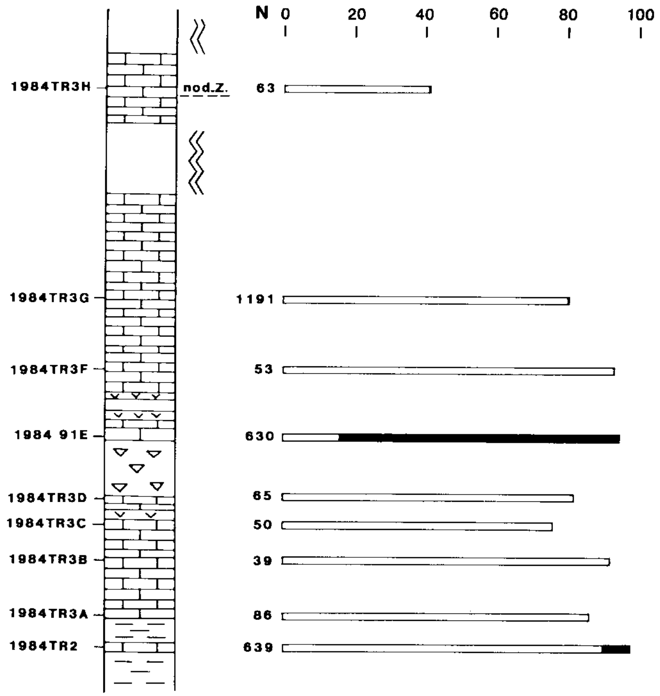

Fig. 3. Section near Triollo sampled by C.F. Winkler Prins.

Legend of Figs. 2-14 (all drawn to the same scale). Numbers in vertical column headed by N represent numbers of Pa elements in the faunas. Open bar = percentage of *Gnathodus* spp.; solid bar = percentage of *Vogelgnathus campbelli*; remaining percentage is that of *Lochriea* spp.

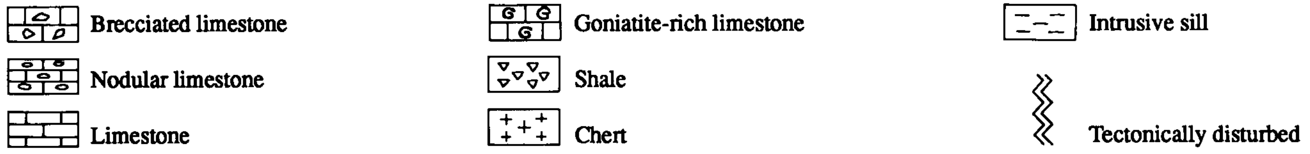

Table 3. Numbers of Pa elements in samples from Resoba.

	Gnathodus semiglaber	*Gnathodus bilineatus*	*Gnathodus symmutatus*	*Gnathodus homopunctatus*	*Gnathodus girtyi*	*Lochriea commutata*	*Lochriea nodosa*	*Vogelgnathus campbelli*	Number of Pa elements/kg
1980 RE4E	—	5	—	—	—	—	—	—	2
71H 6834	—	1884	77	93	7[a]	127	—	1	2000
1980 RE4C	—	40	1	10	—	16	—	13	64
1980 RE4B	—	6	—	—	—	3	—	—	25
1980 RE4A'	—	73	3	—	—	2	—	2	48
1980 RE4A	3	40	1	—	3	7	—	1	32
071 RE3A	—	178	30	28	—	38	—	198	470
71G 6833	—	3	—	—	2	—	1	75	60
1981 10C	—	98	—	43	—	34	—	137	380
1980 RE3C	—	3	2	—	—	1	1	1	30
71F 6832	—	16	—	3	—	5	—	—	66
071 RE3	—	9	—	—	—	—	—	—	11
1990 6831	—	3096[b]	—	148	—	633[c]	15	91	766
71E 6831	170[d]	7	9	4	1	4	—	1	280

[a] I.a. some specimens of *Gnathodus girtyi rhodesi*.

[b] Total of *Gnathodus bilineatus*, *G. semiglaber*, *G. pseudosemiglaber*, and *G. girtyi*, which were not counted separately because of the large number of juveniles.

[c] Total of *Lochriea commutata* and *Gnathodus symmutatus* which were not counted separately because of the large number of juveniles.

[d] Total of *G. semiglaber* and the juveniles of the other species of *Gnathodus*.

considered to belong still to the upper Viséan because of the occurrence of some specimens of *Gnathodus girtyi rhodesi* Higgins, 1975 in sample 71H 6834 a little higher in the section. The part of the section above sample 1980 RE4E possibly consists of lower Namurian sediments because of the occurrence of *Gnathodus girtyi simplex* Dunn, 1965.

The data from the Resoba section thus show a *V. campbelli*-dominated fauna rather high in the *nodosa* Zone. Higher in the section, maybe near the top of the Viséan, a not inconsiderable percentage of that species occurs.

ENTRAGO DE TEVERGA

Conodont faunas from this section (Fig. 5 and Table 2C) have been studied by Menéndez-Alvarez (1978) and Higgins (in Higgins & Wagner-Gentis, 1982). Gandl (1977) studied the trilobite faunas as well as some conodont faunas from part of the section. He could not sample the lower part of the Genicera Formation because that

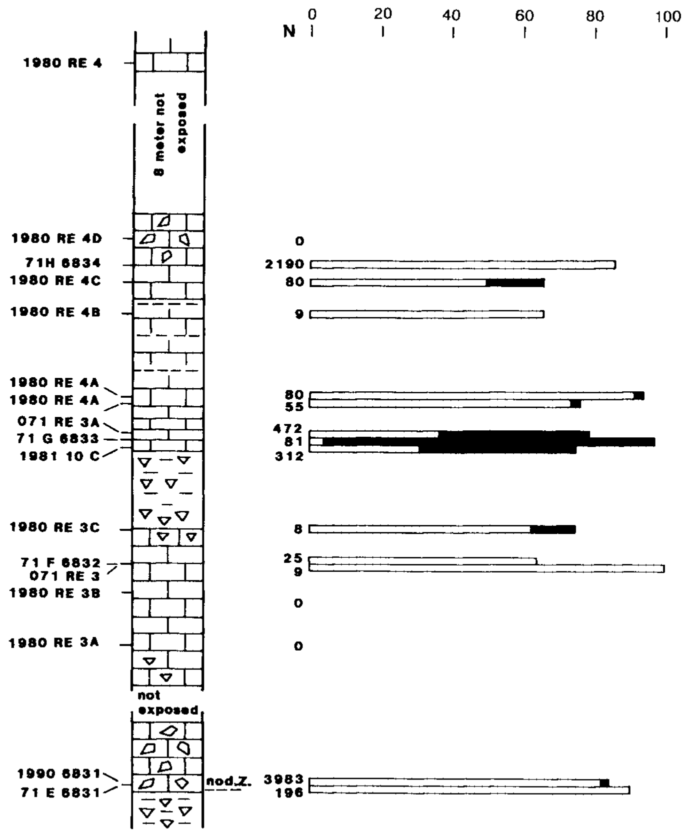

Fig. 4. Section near Resoba sampled by C.F. Winkler Prins.

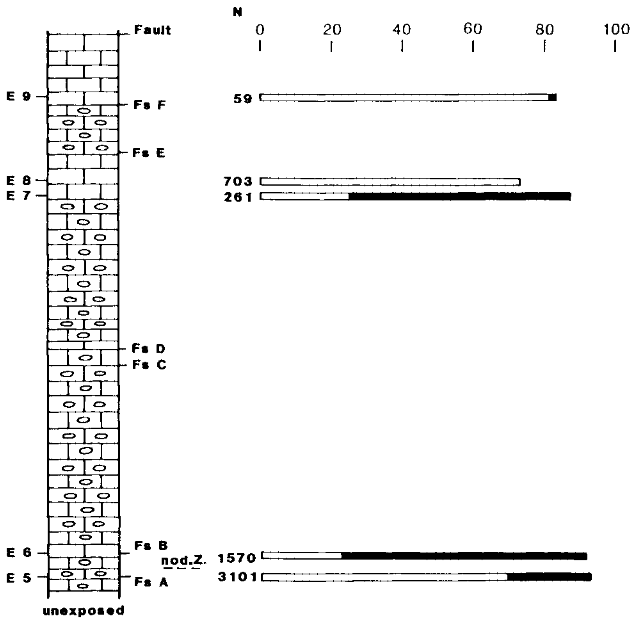

Fig. 5. Section near Entrago de Teverga, modified and redrawn from Gandl (1977) and Menéndez-Alvarez (1978). E5-E9 indicate approximate position of the samples taken by C.F. Winkler Prins.

was not exposed at the time. The stratigraphically lowest beds sampled by Gandl yielded trilobites of Go?ß age. Conodonts from beds lying immediately above his samples Fs A and Fs B (see Fig. 5) belong to the *bilineatus* Zone and *nodosa* Zone, respectively. Gandl did not report the occurrence of *V. campbelli* because he only mentioned the stratigraphically important species. Samples taken by Winkler Prins in 1977 – 060 E5 and 060 E6 (with c. 70% *V. campbelli*) – probably were obtained from the same beds, since they also yielded a *bilineatus* Zone fauna and a *nodosa* Zone fauna respectively. Winkler Prins took the samples 060 E7 (with c. 60% *V. campbelli*) and E8 higher in the section, somewhat below level Fs E of Gandl. These samples are of Namurian age because the stratigraphically lower level Fs D of Gandl already yielded Namurian trilobites. Winkler Prins did not sample the beds between samples 060 E6 and 060 E7. I have therefore no data on the faunal contents of these beds. However, Menéndez-Alvarez (1978) and Higgins (in Higgins & Wagner-Gentis, 1982) studied samples from this part of the section and do not report the occurrence of *Vogelgnathus campbelli*. Menéndez-Alvarez encountered *V. campbelli* in a sample from the top of the *bilineatus* Zone and Higgins reports *V. campbelli* from beds directly above the fault. These beds may according to Gandl (1977) be a repetition of the upper part of the section below the fault.

The available data on the Entrago de Teverga section thus show two levels extremely rich in *Vogelgnathus campbelli* – one just above or at the base of the *nodosa* Zone and one in the lower Namurian.

LA LASTRA (FIG. 6 AND TABLE 4A)

Two samples (1984 LL1 and WP 90) taken from a dark grey limestone outcrop 1500 m E of La Lastra – rich in goniatites as described by Wagner-Gentis (1980) and indicating the basal E1 Zone – yielded conodont faunas in which *Vogelgnathus campbelli* counts for 19% and 22%, respectively. Sample 1984 LL 1A taken directly below the goniatite-rich bed has a *V. campbelli* content of only 1.9%.

In this locality there thus occurred a rather sudden, considerable increase in the percentage of *V. campbelli* in earliest Namurian times.

CARDAÑO DE ARRIBA

This section was studied by van Adrichem Boogaert (1967). Since he did not provide the numbers of specimens encountered, I have reinvestigated his faunas. The data are shown in Table 4B and Fig. 7 of which the stratigraphic column is a simplified version of fig. 46 of van Adrichem Boogaert (1967). The basal sample CAR 9, directly above the transgressive contact, already contains *L. nodosa*. It is an open question whether the deposition of this bed took place near the base of the *nodosa* Zone or somewhat later. In the fauna from sample CAR 11 c. 75% of the Pa elements belongs to *V. campbelli*. The shales above sample CAR 13 already are of Namurian age. The Cardaño section thus shows a *V. campbelli* invasion high in the *nodosa* Zone.

SANTA OLAJA DE LA VARGA

Table 4. Numbers of Pa elements in samples from La Lastra, Cardaño de Arriba, Santa Olaja de la Varga, La Uña and Posada de Valdeón.

	Gnathodus bilineatus	*Gnathodus homopunctatus*	*Gnathodus girtyi*	*Lochriea commutata*	*Lochriea nodosa*	*Lochriea multinodosa*	*Lochriea mononodosa*	*Lochriea cruciformis*	*Vogelgnathus campbelli*	*Mestognathus* sp.	*Hindeodus* sp.	*Geniculatus claviger*
A) La Lastra												
WP 90	1150	—	—	219	114	3	14	—	429	1	7	—
WP84 LL1	724	—	—	135	44	2	10	—	221	—	2	—
WP84 LL1A	2641	—	12	449	137	5	18	5	68	1	—	—
B) Cardaño de Arriba II												
64 Car 13	21	3	—	10	14	—	1	—	5	—	—	—
64 Car 11	243	13	5	34	25	—	3	—	979	—	—	—
64 Car 10	22	1	—	2	—	—	—	—	—	—	—	—
64 Car 9	12	—	—	—	1	—	—	—	—	—	—	—
C) Santa Olaja de la Varga												
OL 11	42	—	—	20	3	—	—	—	—	—	—	—
OL 10	547	—	—	211	35	—	12	5	1	—	—	—
OL 9	399	—	1	36	26	—	—	—	—	2	—	—
OL 8	201	13	—	25	—	—	—	—	—	—	—	—
OL 7	1045	52	7	56	—	—	—	—	242	—	—	—
OL 6	9	—	—	2	—	—	—	—	—	—	—	—
D) La Uña												
U 12	—	—	—	1	—	—	—	—	—	2	—	—
U 11	72	—	1	10	8	35	—	—	—	—	—	2
U 10	92	18	—	11	5	7	—	—	45	—	—	—
E) Posada de Valdeón												
64 Pos 4	15	13	—	2	10	—	—	—	—	2	—	—
64 Pos 3	550	156	7	91	—	—	—	—	20	—	—	—
64 Pos 2	1360	56	2	28	2	—	—	—	117	—	—	—
64 Pos 1	179	10	14	12	—	—	—	—	—	—	—	—

The faunas of this section, as studied by van Adrichem Boogaert (1967), have been reinvestigated. The data are shown in Fig. 8 and Table 4C. The stratigraphic column in Fig. 8 is a somewhat simplified version of fig. 12 of van Adrichem Boogaert (1967), just to indicate the relative position of his samples. They were taken widely apart and conclusions concerning the detailed distribution of conodont species in the successive beds can therefore not be given. One only notes that in sample OL 7 *V. campbelli* is

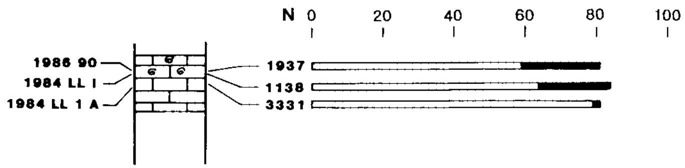

Fig. 6. Outcrop near La Lastra. Samples taken by C.F. Winkler Prins.

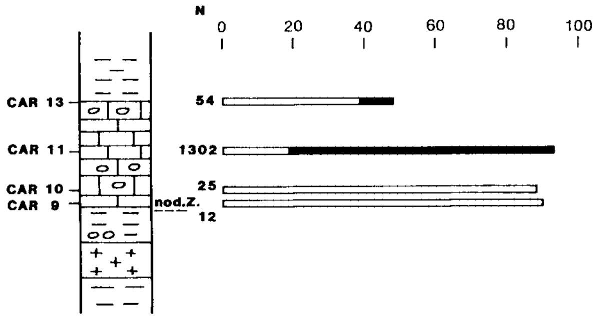

Fig. 7. Section near Cardaño de Arriba (redrawn from van Adrichem Boogaert, 1967, fig. 46).

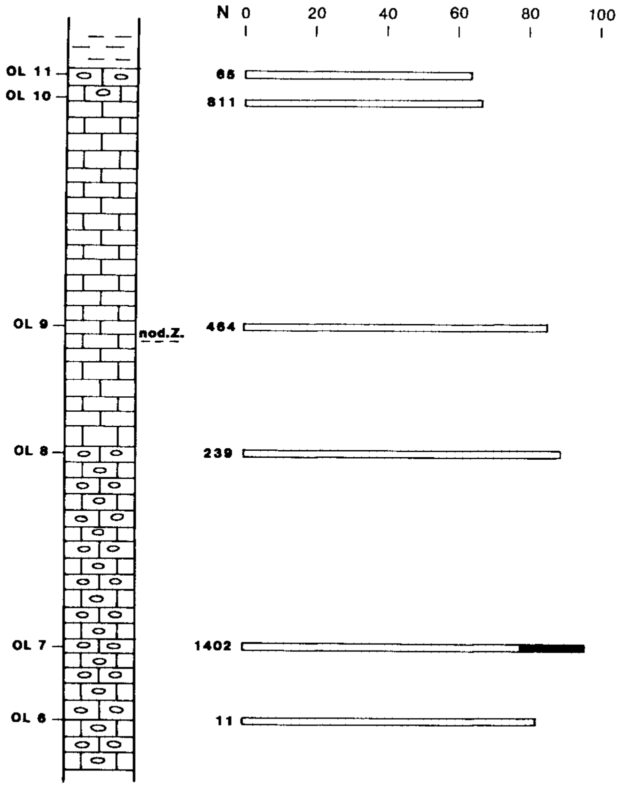

Fig. 8. Section near Santa Olaja de la Varga (redrawn from van Adrichem Boogaert, 1967, fig. 12).

relatively abundant (c. 17%). Maybe this sample marks the onset of an invasion by *V. campbelli*, but this remains speculative. Close sampling might provide the answer. If this bed does indicate the approximate position of an invasion by *V. campbelli*, then this would be in the *bilineatus* Zone.

LA UÑA

See Figure 9 and Table 4D. The stratigraphic column of Fig. 9 has been drawn after fig. 19 of van Adrichem Boogaert (1967). The samples from this section are also widely spaced. The only thing we can conclude from this Fig. 9 is that sample U 10, taken at the base or a level closely above the base of the *nodosa* Zone contains a fair amount of *V. campbelli* (c. 25%). The top of the nodular limestone above sample U 13 marks the top of the Viséan. This figure thus gives the impression that there may have been an invasion by *V. campbelli* near the base of the *nodosa* Zone.

POSADA DE VALDEÓN

This section (see Fig. 10 and Table 4E) has also been studied by van Adrichem Boogaert (1967, fig. 30). Samples were also widely spaced but in this case too the fauna at the base of the *nodosa* Zone, or slightly above it, contains some *V. campbelli*.

VILLABELLACO

Higgins (in Higgins & Wagner-Gentis, 1982) investigated several sections from the lower Carboniferous of the Cantabrian Mts. As mentioned in the introduction, *V. campbelli* may be underrepresented in his data because it appears that only the coarser sieve fractions were used.

However, the data concerning the Villabellaco section seem sufficient for comparison (see Fig. 11 and for numbers of specimens Higgins & Wagner-Gentis, 1982, table 3). Fig. 11 shows a high percentage of *V. campbelli* in a sample from the *bilineatus* Zone and a clear dominance, high in the *nodosa* Zone.

MATALLANA

In a section near Matallana Higgins (in Higgins & Wagner-Gentis, 1982, table 2 and text-fig. 8) found two faunas with *V. campbelli*, one in the *bilineatus* Zone (8%) and one at the base of the *nodosa* Zone (5.5%). In all other faunas from this part of the section *Gnathodus bilineatus* is the dominant species and *V. campbelli* is absent.

THE PANES-POTES AND AGUASALIO SECTIONS

Two of the sections studied by Budinger (1965), one between Panes and Potes and another one near Aguasalio yielded faunas rich in *V. campbelli* rather closely above the base of the *nodosa* Zone (See Figs. 12 and 13 and Table 5). Although his faunas are small there can be no doubt about the temporary abundance of *V. campbelli*. As

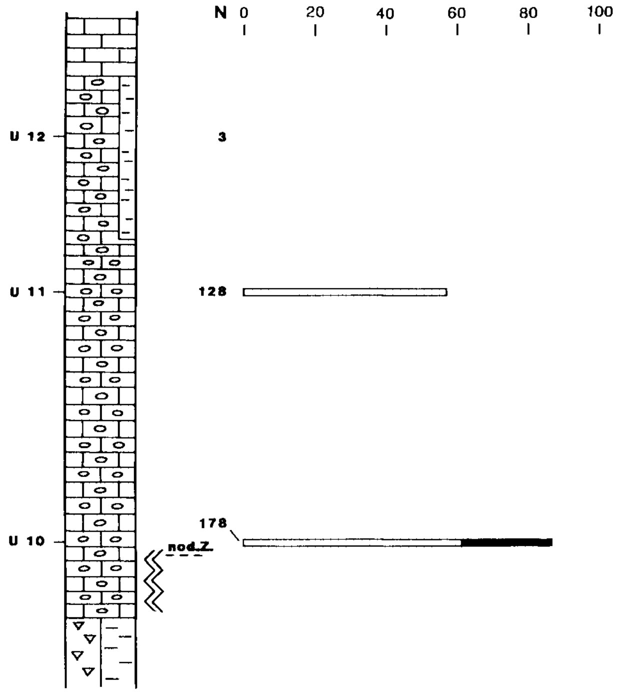

Fig. 9. Section near La Uña (redrawn from van Adrichem Boogaert, 1967, fig. 19).

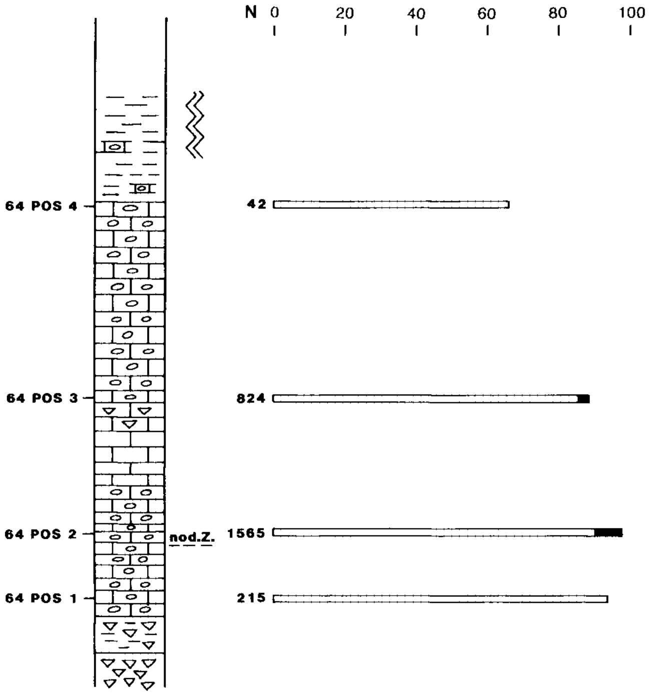

Fig. 10. Section near Posada de Valdeón (redrawn from van Adrichem Boogaert, 1967, fig. 30).

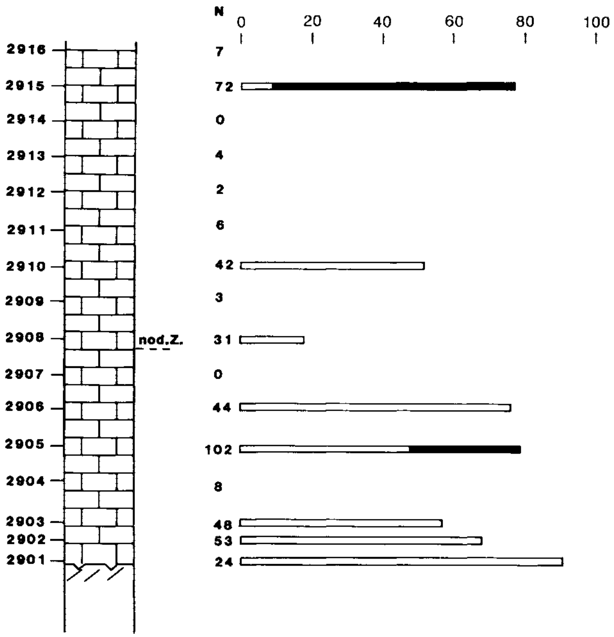

Fig. 11. Section near Villabellaco (redrawn from Higgins & Wagner-Gentis, 1982, text-fig. 4).

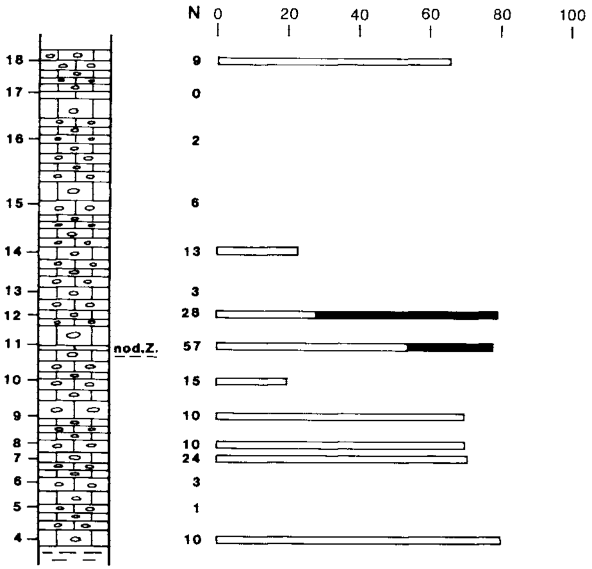

Fig. 12. A section between Panes and Potes (redrawn from Budinger, 1965, fig. 5).

already mentioned in the introduction, the number of specimens of *V. campbelli* in Table 5 is the sum of *Spathognathodus campbelli* and *S. werneri* of Budinger's distribution charts (Budinger, 1965, tables 5-6).

THE GILDAR-MONTO AREA

Budinger (1965, table 3, fig. 4) obtained small faunas from this section (see Table 5). Nevertheless, if we use only his faunas of 10 specimens or more to calculate percentages we get the picture of Fig. 14 showing a high percentage of *V. campbelli* in three different places. One occurs some 2.5 m above the base of the *nodosa* Zone, one lies high in the *nodosa* Zone and one in what Budinger in his table 3 considers to be lower Namurian.

DATA FROM SOME OTHER LOCALITIES

In the 15 years following the study of van Adrichem Boogaert (1967) several other Leiden geologists have sampled limestones from the Genicera Formation. Their samples, however, were generally taken so widely spaced, sometimes up to 10 m apart, that hitting a sample with a fauna dominated by *V. campbelli* must have been pure luck. From the more than 50 sections studied – the faunas of which are stored in the Nationaal Natuurhistorisch Museum – only five samples show a high percentage of *V. campbelli*. At Felechosa 40%, near Mirantes de Luna 39%, near the Ruesga Dam 26%, near Santa Marina de Valdeón 29%, and near Enterrias 54%. All five samples are from the *nodosa* Zone, the next sample in the respective sections was however, taken so many metres lower down that one does not know from which part of the *nodosa* Zone this fauna derives. I mention this to show that probably at more localities in the Cantabrian Mts sec-

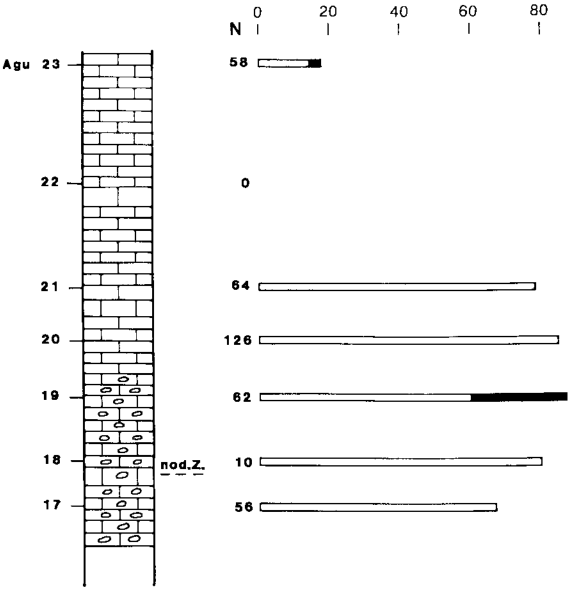

Fig. 13. Section near Aguasalio (redrawn from Budinger, 1965, fig. 6).

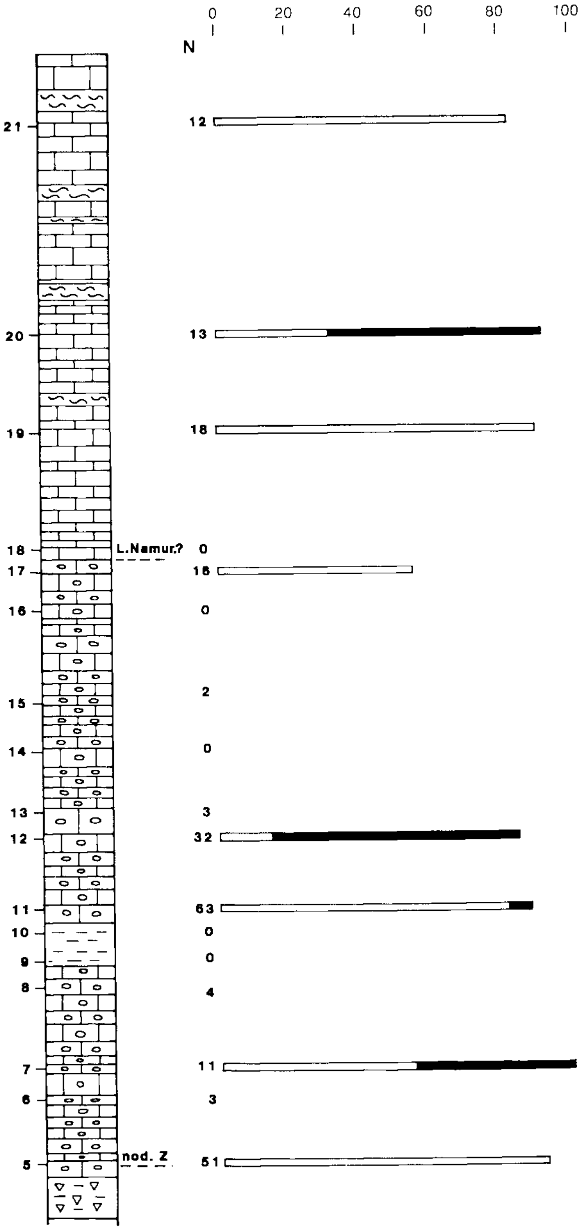

Fig. 14. Section in the Gildar-Montó area (redrawn from Budinger, 1965, fig. 4).

Table 5. Numbers of Pa elements in samples taken by Budinger (1965, tables 3, 5 and 6).

	Gnathodus bilineatus	*Gnathodus delicatus*	*Gnathodus girtyi*	*Gnathodus semiglaber*	*Gnathodus texanus*	*Lochriea commutata*	*Gnathodus homopunctatus*	*Lochriea nodosa*	*Lochriea crusiformis*	*Vogelgnathus campbelli*	*Geniculatus claviger*	*Mestognathus beckmanni*
Gildar-Montó area												
Budinger fauna 21	10	—	—	—	—	2	—	—	—	—	—	—
20	1	—	1	—	—	—	2	1	—	8	—	—
19	15	—	1	—	—	—	—	1	1	—	—	—
17	9	—	—	—	—	—	—	3	4	—	—	—
15	—	—	—	—	—	—	1	1	—	—	—	—
13	—	—	—	—	—	—	1	1	—	1	—	—
12	5	—	—	—	—	—	—	5	—	22	—	—
11	35	2	—	—	—	7	15	1	—	3	—	—
8	4	—	—	—	—	—	—	—	—	—	—	—
7	3	2	—	—	1	—	—	—	—	5	—	—
6	1	—	—	—	—	2	—	—	—	—	—	—
5	30	4	1	1	4	2	8	1	—	—	—	—
Panes-Potes section												
Budinger fauna 18	4	2	—	—	—	2	—	1	—	—	—	—
16	2	—	—	—	—	—	—	—	—	—	—	—
15	3	—	—	—	—	3	—	—	—	—	—	—
14	3	—	—	—	—	6	—	2	1	—	—	1
13	2	—	—	—	—	1	—	—	—	—	—	—
12	3	—	1	—	—	4	4	1	1	14	—	—
11	30	—	—	—	—	6	1	6	—	14	—	—
10	3	—	—	—	—	6	6	—	—	—	—	—
9	7	—	—	—	—	3	—	—	—	—	—	—
8	7	—	—	—	—	2	1	—	—	—	—	—
7	15	2	—	—	—	4	—	—	—	3	—	—
6	—	1	—	—	—	1	—	—	—	1	—	—
5	1	—	—	—	—	—	—	—	—	—	—	—
4	7	1	—	—	1	—	—	—	1	—	—	—
Aguasalio section												
Budinger fauna 23	8	—	—	—	—	45	—	1	2	2	—	—
21	40	—	—	—	—	13	10	1	—	—	—	—
20	100	—	—	—	—	20	6	—	—	—	—	—
19	32	—	1	—	—	8	4	1	—	16	2	—
18	2	—	3	—	1	—	2	2	—	—	—	—
17	30	—	2	—	—	20	4	—	—	—	—	—

tions can be found containing levels with faunas dominated by *V. campbelli* and in case this can be demonstrated it proves that samples should be taken more closely spaced if one really wants to learn the history of the site.

Discussion

As shown in the preceding chapter, the succession of Viséan and lower Namurian strata in the Cantabrian Mountains contains at several localities one or more levels which are extremely rich in *Vogelgnathus campbelli*. One also observes that these invasions by *V. campbelli* have been of relatively short duration, for beds closely above and below often show low percentages or are even devoid of this species (e.g. TR 4' only 50 cm above TR 4, van Adrichem Boogaert, pers. commun.). In some sections the percentage reached by *V. campbelli* is less high, only some 10-20%. Considering the rather wide spacing of the samples taken from these sections it is possible that in those cases not the bed with the highest *V. campbelli* content was investigated but an adjacent layer. Of course it is also possible that *V. campbelli* was never very abundant in this particular part of the section. More closely spaced samples are required to answer this question.

It appears that in the upper Viséan and lower Namurian succession *V. campbelli* more than once became the dominant form (Fig. 15). The first clear peak (up to 80% of *V. campbelli* at Triollo) occurs in the middle of the *bilineatus* Zone. *V. campbelli* became the dominant form for the second time at or slightly above the base of the *nodosa* Zone (i.e. at Entrago up to 67%). In some sections, e.g. also at Entrago, *V. campbelli* started to increase in number somewhat below the base of this zone. *V. campbelli* became dominant for a third time high in the *nodosa* Zone (e.g. at Resoba over 90%). A fourth time *V. campbelli* reached a high percentage, up to 60% (at Entrago), in the lower Namurian.

The faunas in the other beds of the sections are dominated by *Gnathodus bilineatus* and contain generally minor amounts of *G. symmutatus* Rhodes, Austin & Druce, 1969, *G. homopunctatus* Ziegler, 1960, *G. girtyi* Hass, 1953, and species of *Lochriea*. The question therefore arises why the *Gnathodus*-dominated fauna temporarily disappeared to be replaced by a *Vogelgnathus*-dominated fauna? Let us consider first of all the disappearance of *G. bilineatus* and allied forms.

According to Higgins (1981, p. 43), the environment in northern Spain occupied by *G. bilineatus*, *G. homopunctatus* and several species of *Lochriea* was a submarine platform at a considerable depth of water, less than 200 m but well below wave base. According to Seibert (1988) the deposition of the middle through upper Viséan sediments of the Genicera Formation took place at a depth between 100 and 300 m. He considered the siliceous sediments to be deposits of an open marine deeper pelagic environment, probably at a depth of around 200 m. According to Sandberg & Gutschick (1984) *Gnathodus* was a nektobenthic slope dweller, whose habitat bottomed out seaward against the dysaerobic zone (depth c. 200 m) and reached upwards to the top of the dysphotic zone (depth c. 50 m). These opinions all basically agree.

If the change of environment causing *G. bilineatus* to disappear was towards a

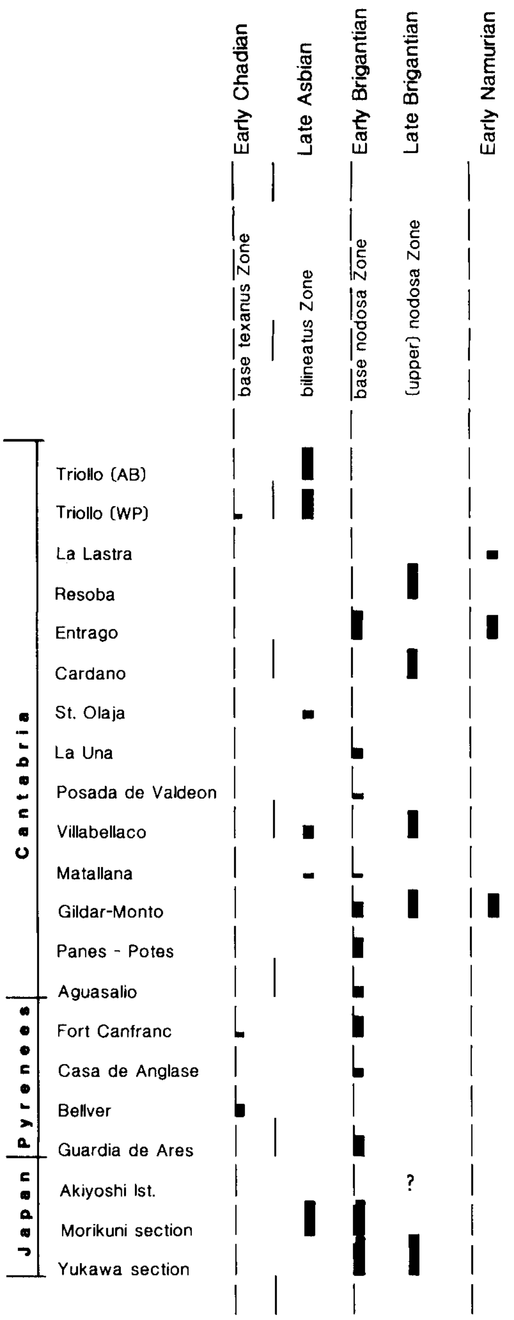

Fig. 15. Approximate stratigraphic position of samples with a comparatively high percentage of *Vogelgnathus campbelli* in the section from the Cantabrian Mountains, the Pyrenees and SW Japan. Height of the solid bars is roughly proportional to the percentage of *V. campbelli* in the faunas. For an idea of the scale: the bar of the La Lastra sample represents c. 20%, the bar in the upper *nodosa* Zone of the Yukawa section represents 100%.

decrease of water depth then the fauna would have become enriched in *Hindeodus* and *Mestognathus* (Sandberg & Gutschick, 1984, p. 151). In the biofacies model of Higgins (1981) the fauna of the shallower inner shelf is almost identical to that of the deeper water. In both environments *Gnathodus bilineatus*, *G. girtyi* and *Lochriea nodosa* flourished and *G. homopunctatus*, *L. commutata* (Branson & Mehl, 1941), *Mestognathus* and *Cavusgnathus* occurred in smaller quantities. The faunas of the red nodular limestones of the pelagic platform contain abundant *G. bilineatus*, *L. nodosa* and smaller quantities of *G. homopunctatus*, *L. commutata* and *Mestognathus*. The shallower lagoonal environment is characterised by *Mestognathus* (relatively abundant), *L. commutata* and *G. homopunctatus*. Shallowing of the environment apparently has not been the case, for *Mestognathus* and *Hindeodus* are extremely rare, and I also did not encounter faunas consisting of *L. commutata* and *G. homopunctatus* without *G. bilineatus*. Therefore I assume that the environment changed towards an increased water-depth. Sandberg & Gutschick (1984) designed a biofacies model of the *anchoralis-latus* Zone providing data which can be partly applied to the Late Viséan case of the Cantabrian Mts. Basinwards of the gnathodid biofacies in the Sandberg & Gutschick model (1984, fig. 14) *Polygnathus communis communis* Branson & Mehl, 1934 occurs and even more offshore *Bispathodus utahensis* Sandberg & Gutschick, 1984. Both species are ubiquitous, euryhaline dwellers of the euphotic zone (Sandberg & Gutschick, 1984). *Polygnathus communis communis* constitutes the bulk of the faunas in most biofacies except in the most offshore biofacies where *Bispathodus utahensis* predominates. However, this latter species also occurs everywhere in the euphotic zone. *Polygnathus communis communis* dominates in a large number of the late Tournaisian faunas from the Cantabrian Mountains. *Bispathodus utahensis* has not been recorded from that area. The Pa element of *Vogelgnathus campbelli* superficially resembles the Pa element of *B. utahensis*. Both have a slender form and their basal cavities seem more or less alike. However, *B. utahensis* differs in not showing the horizontal ridge beneath which the blade thins, which is characteristic of *V. campbelli*. *V. campbelli* is not ubiquitous in the Cantabrian Mts. It is often absent or rare in the gnathodid fauna. Therefore I suppose that *V. campbelli* was part of the plankton (or nekton) not in the shallow zone above the carbonate platform but more offshore, in a more basinal setting. Maybe *V. campbelli* was one of those marine animals that needed a high column of water for their daily vertical movement, maybe they or their prey shunned the light, like so many other marine animals, nowadays. Its habitat could overlap with the deeper part of the habitat of *Gnathodus* and *Lochriea*. Thus *V. campbelli* could co-exist with these species in deeper environments, but be absent in shallower ones. The assumption of the *V. campbelli* facies overlapping the deepest part of the gnathodid biofacies is supported by the observations of Ramovš (1990) on Carboniferous faunas from the Central-Karawanken. Ramovš found *V. campbelli* in all his faunas together with *G. bilineatus* and/or species of *Lochriea*. He stated that his faunas were poor, possibly originating from a rather deeply basinal environment.

According to Belka (1991) 'representatives of the Gnathodontidae and Bactrognathidae and of *Lochriea*, *Vogelgnathus* and *Pseudopolygnathus* are commonly found in strata deposited on the slope and outer shelf. Importantly, conodonts recovered from the deepest basinal sediments all represent long-ranging and conservative stocks. The peculiarity of the late Tournaisian extinction, first of all, lies in the fact that all conservative stocks of Spathognathodontidae disappeared after being continuously present in the basinal realm since the beginning of the Devonian..... A consequence of the elimination of basinal spathognathodids was the attempt of some forms that originally occupied the slope and shelf margin to change their habitat by migrating basinwards in the Viséan'. In my opinion *Vogelgnathus campbelli* has taken the place of the spathognathodids in the basinal faunas.

So, if in the Cantabrian Mts sea level rose, parts of the region may have become too deep for *Gnathodus* and *Lochriea* to survive and their place was taken by *V. campbelli*. But, in other less deep areas of the carbonate platform, relative rise of sea level may not have been sufficient to make *Gnathodus* c.s. disappear, but enough to enable *V. campbelli* to live there too.

Of course it may not have been necessary that *V. campbelli* depended on the presence of a considerable column of water for an eventual daily vertical movement. As pointed out by Nicoll (1984) conodont distribution will be related to changes in the physical conditions of the total water column. Nicoll sums up a number of factors: temperature, turbidity, energy levels, salinity, nutrient levels, plant and animal communities that would have provided habitats, predator pressure. Most if not all of these parameters will change if sea level rises considerably.

If indeed a rise in sea level created the conditions for the temporarily establishment of the *Vogelgnathus* dominated fauna, then one might expect – if the deepening was not caused by local tectonic movements but as a result of eustatism – to find indications of these events in other sections. As has been recorded in the previous chapter a number of sections show beds dominated by *Vogelgnathus* inserted between the gnathodid dominated beds. Their approximate stratigraphic position is indicated in Fig. 15. Approximate, because it is difficult to know what, for instance, will be the exact position of the *Vogelgnathus* peak within the *bilineatus* Zone. Especially so, because many of the sections are condensed and possibly contain one or more stratigraphic breaks. One has to keep that in mind when looking at Fig. 15 which shows that sites, at present rather widely apart (Entrago - Gildar Montó are c. 100 km apart, see Fig. 1), had a peak in the distribution of *Vogelgnathus* at approximately the same time. Figure 15 shows that one *Vogelgnathus* level is near the middle of the *bilineatus* Zone, late Asbian. Another level near the base of the *nodosa* Zone, early (?)[1] Brigantian, a third level high in the *nodosa* Zone (late Brigantian) and a fourth one in the early Namurian.

It is very tempting to assume that we are dealing with four events of regional or may be even supraregional extent. Ross & Ross (1988, fig. 6) indicated that the early Carboniferous saw a number of worldwide transgressive-regressive cycles – related to eustatic movements – amongst others one in the late Asbian, two in the Brigantian and one in the early Namurian. So it would appear that the levels with a *Vogelgnathus* peak correlate with eustatic sea level rises. The data of Ross & Ross (1988) are partly

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[1] Early (?) Brigantian, because if indeed the second *V. campbelli* dominated level is a result of the eustatic rise of sea level, than it should be the early Brigantian one, and consequently the base of the *nodosa* Zone in the Cantabrian Mts would be early or late early Brigantian.

based on papers by Ramsbottom. Ramsbottom (1977) indicates in his figure 10 depicting mesothemic cycles in British Dinantian and Namurian rocks that onlap over the shelf edge occurred in the late Chadian, in the Holkerian,in the late Asbian, in the early and the late Brigantian, in the Pendleian and the early Arnsbergian.

He suggested (Ramsbottom, 1973 and 1977) that these mesothems had an eustatic origin. Concerning the cyclothemic units in the Asbian and Brigantian Ramsbottom (1979) supposed that each cycle lasted about 500 ka.

Ramsbottom (1981) calculated the eustatic rise in sea level needed for deposition of a thickness of rocks and concluded to a maximum rise in sea level of 26.5 m in the Late Asbian, of 32.5 m in the Early Brigantian, of 34.0 m in the Late Brigantian and 50.9 m in the Pendleian. This of course are mean figures for the length of the duration of the cycles. Sea level may have been higher during part of the time. These data therefore give little information about how much the sea level had to rise to make the *Gnathodus* fauna almost disappear and to enable *Vogelgnathus* to take over. Because the eustatic events would influence the distribution of faunas worldwide, sections outside the Cantabrian Mts should also be investigated to look for changes in faunal composition like the ones recorded in NW Spain.

For such an investigation the samples will have to be very closely spaced, because, as stressed above, the parts of the sections with the *Vogelgnathus* invasions are thin and easily missed. The relatively small thickness of the bed(s) with *Vogelgnathus campbelli* indicates that the invasion was of rather short duration. Normal conditions with *Gnathodus* and *Lochriea* were quickly resumed. According to Schlager (1981, p. 209) the drowning process, in order to succeed, had to be rapid and short, probably between 100 ka and 1 Ma. Because of the subdued relief on carbonate platforms they were drowned at once. Earlier in his paper Schlager (1981, p. 204) stated that at a rate of 1 to 10 mm/yr it would take sea level only 10 to 100 ka to rise a hundred metres.

DATA FROM OUTSIDE THE CANTABRIAN MOUNTAINS

A literature search for comparative data does not yield much information.

Marks & Wensink (1970) provided data about two sections situated north of Canfranc Railway Station in the Aragón Valley (western Pyrenees). The section at Fort Canfranc ranges from the *Scaliognathus anchoralis* Zone into the Namurian (Marks & Wensink, 1970, table I). The top sample from the *anchoralis* Zone and a sample about half a metre above the base of the *texanus* Zone have a modest content of *V. campbelli*, 5 and 9% respectively. Several samples from the overlying part of the section are dominated by *Gnathodus* spp. and devoid of *V. campbelli*. The next sample with *V. campbelli* and than with 51% was found at the base of the *nodosa* Zone. Apart from one sample c. 5 m higher in the section with about 4.5% *V. campbelli*, all other samples from this section into the lower Namurian are devoid of this species and dominated by *Gnathodus bilineatus*. The second section, near Casa de Anglase (Marks & Wensink, 1970, table II), ranges from the *bilineatus* Zone into the lower Namurian. A sample at or slightly above the base of the *nodosa* Zone contains 21.5% of *V. campbelli* and 50% of *G. bilineatus*. One sample c. 8.5 m higher in the section has a *V.*

campbelli content of c. 7%. The other faunas from this section do not contain any *Vogelgnathus*.

Although in both sections the samples are relatively widely spaced, c. 1.5 m and 3.5 m respectively, the peak in the distribution of *V. campbelli* at, or slightly above, the base of the *nodosa* Zone is apparent.

Boersma (1973) described some sections from the Central Spanish Pyrenees. In a section north of Bellver some beds of the Compte Formation contain conodonts of the *texanus* Zone and about 30% of *Vogelgnathus campbelli* (Boersma, 1973, table 6 and fig. 14, and pers. observ.). These beds lie c. 1.20 m above beds of the *costatus* Zone and 3 m below a chert layer with phosphatic nodules indicating, according to Boersma, a transgression of minor extent which created an environment suddenly favourable to radiolaria. In beds higher in this section *Gnathodus* dominates the fauna.

From a section near La Guardia de Arés, some 45 km WSW of Bellver, beds at c. 3.5 m above the upper chert layer yielded small conodont faunas, consisting only of large specimens, belonging to the lower part of the *nodosa* Zone with a *V. campbelli* content of about 50% (Boersma, 1973, fig. 8, table 2, and pers. observ.). A sample 1.5 m above the chert, also consisting of large conodonts only, contains c. 11% of *V. campbelli*. At the time of deposition of these beds the sea was strongly transgressing (Boersma, 1973, p. 341). In beds lower in this section, below the chert layers, *Gnathodus* is the dominant form and *V. campbelli* is not present.

These data from the Pyrenees suggest that a rise in sea level during the transgressive phase enabled *V. campbelli* to flourish in this area, once near the base of the Viséan and once in the *nodosa* Zone. Whether this species may have reached higher percentages and more than twice, cannot be determined. Boersma's faunas generally are small and contain often only large specimens. Smaller specimens are generally missing, probably because many specimens are fragmented by tectonic pressure and also because the finer sieve fractions may have been discarded.

Ramovš (1990) – already referred to earlier in this paper – reports that *V. campbelli* occurs in almost all of the very sparse faunas from Jezersko (Central- Karawanken, Slovenia) belonging to the *bilineatus* and *nodosa* Zones. These faunas have been encountered in autochthonous limestones intercalated between flysch sediments deposited in a basinal environment.

Hisaharu Igo (1973) described a section from the Akiyoshi Limestone Group of SW Japan. In a conodont-bearing limestone situated immediately above a reddish tuffaceous shale *G. bilineatus* and *V. campbelli* are particularly abundant. This bed is at least some 40 m above the lowest bed with *Lochriea nodosa*, consequently this abundance of *Vogelgnathus* is high in the *nodosa* Zone. Igo described another fauna from a sample he assumed to be the uppermost conodont assemblage in the Ohkubo area. In this fauna *V. campbelli* was extremely abundant.

From the distribution charts of Koike (1967) it appears that *V. campbelli* occurs in almost all samples of assemblage zones NI and NII of the Nagoe Formation from the Iwamoto, Niiyabara, Yukawa and Morikuni sections in the Atetsu Limestone of SW Japan. Some samples from these sections show a high percentage of *V. campbelli*. Near the top of the NI of the Morikuni section there is a sample with conodonts of the *bilineatus* Zone, containing a *V. campbelli* content of 88% (Koike, 1967, table 2b, sample 10). According to this table sample 10 contains 97 specimens of *V. campbelli* per kg of rock sample. Actually I think it should read sample 9 for in Koike's table 1 sample 9 of the Morikuni section has a conodont content of more than 80 per kg, whereas sample 10 only has 11-20 per kg. Sample 9 is from a limestone with chert layers, some 11 m below the first sample with *Lochriea nodosa*. Somewhat higher in this section sample 11 of the NII zone (in my opinion erroneously stated as 11a in table 2) contains 9 specimens of *V. campbelli* and one of *L. commutata*. This sample occurs above the base of the *nodosa* Zone.

In the Yukawa section the Nagoe NII assemblage zone (Koike, 1967, table 2b) contains two samples – 110 and 114 – which consist of *V. campbelli* only, respectively 10 and 14 specimens per kg, both in the *nodosa* Zone.

So, although *V. campbelli* occurs in most samples, it seems to be very abundant up to strongly dominant in some samples. Thus, I wonder if also in Japan we see the same phenomenon of invasions by *V. campbelli* at rising sea levels as occurs in the Cantabrian Mts. According to Koike the carbonates of the Nagoe Formation accumulated in relatively shallow and calm water. Considering that most of the conodont faunas of the Nagoe Formation of the Atetsu Limestone contain *Gnathodus bilineatus*, which is generally considered to be a conodont of deeper water, I wonder if, indeed, all of the Nagoe Formation was deposited in a shallow water environment. Maybe part of the deposition of the Nagoe Formation took place in a deeper environment, an environment that also occasionally became still deeper by an eustatic rise of sea level enabling *V. campbelli* to become an important constituent of the fauna.

Metcalfe (1981) published a number of distribution charts of conodonts from Carboniferous strata of the Craven Lowlands of northern England. *Vogelgnathus campbelli* occurs in several samples, but the numbers of specimens are small and do not allow any conclusions concerning its habitat.

Austin & Husri (1974) published distribution charts of conodonts from Lower Carboniferous sections of Ireland. *Vogelgnathus campbelli* occurs in some of the samples in small numbers not allowing any conclusion to be drawn about its way of life.

Rexroad & Horowitz (1990) provided data concerning the conodont distribution in faunas from a large number of sections from the Chesterian Beaver Bend Limestone in Indiana. The Beaver Bend Limestone was deposited on a continental shelf of shallow tropical water open to circulation from the open sea with fairly normal ranges of salinity (Rexroad & Horowitz, 1990). *Gnathodus bilineatus modocensis* Rexroad, 1957 occurs in most of the faunas, *Vogelgnathus campbelli* in only half of the samples and generally in minor amounts. However, it reaches percentages of 50 to 70% in sample 3R of loc. 6, sample 7R of loc. 8, sample 4 of loc. 10 and samples 3R and 3 of loc. 11. Evidently at these levels there was a change in facies enabling *V. campbelli* to become temporarily dominant. Whether these levels represent one event or several is not clear as they are situated in different parts of the respective sections.

Remarks upon *Vogelgnathus campbelli*

Norby & Rexroad (1985) presented an extensive list of synonyms of the Pa element.

Not included were:

1965 *Spathognathodus campbelli* Rexroad, 1957 — Budinger, p. 80, pl. 5, figs. 9-13; textfig. 26.
1965 *Spathognathodus werneri* Ziegler, 1962 — Budinger, p. 82, pl. 5, figs. 14-18; textfig. 26.

A late reference is:

1990 *Vogelgnathus campbelli* (Rexroad, 1957) — Ramovš, p. 97.

As already pointed out by several authors, i.e. Wirtz (1967), Koike (1967) and Ramovš (1990) the species is rather variable and some specimens do show some resemblance to *Spathognathodus werneri* in that the denticles posterior of the main denticle are much smaller than those in front of the main denticle (see Pl. 2: b, d and Pl. 3: a). However, *S. werneri* does not show the lateral ridge, and the anterior process has a different denticulation.

These specimens with shorter denticles in the posterior part show some resemblance to *V. postcampbelli* (Austin & Husri, 1974). However, they are within the range of variation of *V. campbelli,* because the faunas contain various intermediate forms. Also *V. postcampbelli* is shorter and possesses c. 16 denticles, whereas the specimens in the faunas used for this study all have more than 20 denticles.

The holotype and about 50% of the other specimens described by Norby & Rexroad (1985) do show small nodes on the lower left-hand side of the anterior part of the blade. I did not observe such nodes on any of my specimens and neither did other authors report on it.

Norby and Rexroad observed that specimens of *V. campbelli* show a tendency to be shorter in younger strata. I did not observe real differences between the oldest fauna (early Viséan, Plate 1), that of the late Viséan (Plate 2) and the youngest fauna (early Namurian, Plate 3).

Other elements of the apparatus are absent to extremely rare.

Conclusions

The data concerning the distribution of *Vogelgnathus campbelli* in the sections from the Cantabrian Mts presented in this paper show that rather sudden facies changes occurred which brought about drastic changes in the composition of the conodont faunas. It is suggested that these sudden, rather short-lived invasions by *Vogelgnathus* were linked to rapid rises in sea level, maybe during the periods of maximum flooding of the late Asbian to early Namurian transgressive-regressive cycles caused by eustatism. It looks as if effects of these events were felt also in Japan (and Indiana?) considering the occurrence of levels with extremely abundant *V. campbelli.* Whether or not *V. campbelli* was able to reach such high percentages would depend on the original configuration of the site and consequently we must not expect these witnesses of eustatic rise in all Lower Carboniferous marine sequences. Nevertheless, investigation of closely spaced samples may reveal that more sections are hiding this phenomenon and thus possibly can be correlated in great detail. The samples do not only need to be closely spaced, but also the finer fractions of their insoluble residues have to be investigated because *Vogelgnathus campbelli* is a rather slender conodont which easily passes the sieve and, consequently, is often underrepresented in the coarser fraction.

The modest amount (7.5%) of *V. campbelli* in a sample from the *texanus* Zone (lower Viséan) at Triollo and the c. 30% in a sample taken near Bellver (Pyrenees) and the modest percentage at Canfranc suggest that in earliest Viséan times the sea level may have risen too. This rise might correspond to the late Chadian transgressive-regressive cycle indicated in fig. 6 of Ross & Ross (1988). According to Webster & Groessens (1991, fig. 2) the base of the *texanus* Zone, is basal Viséan, and approximates the base of the late Chadian.

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Plate 1

Pa elements of *Vogelgnathus campbelli* (Rexroad, 1957) from Triollo; *texanus* Zone, early Viséan, sample 1984 TR2. Length of bar 100 µm.

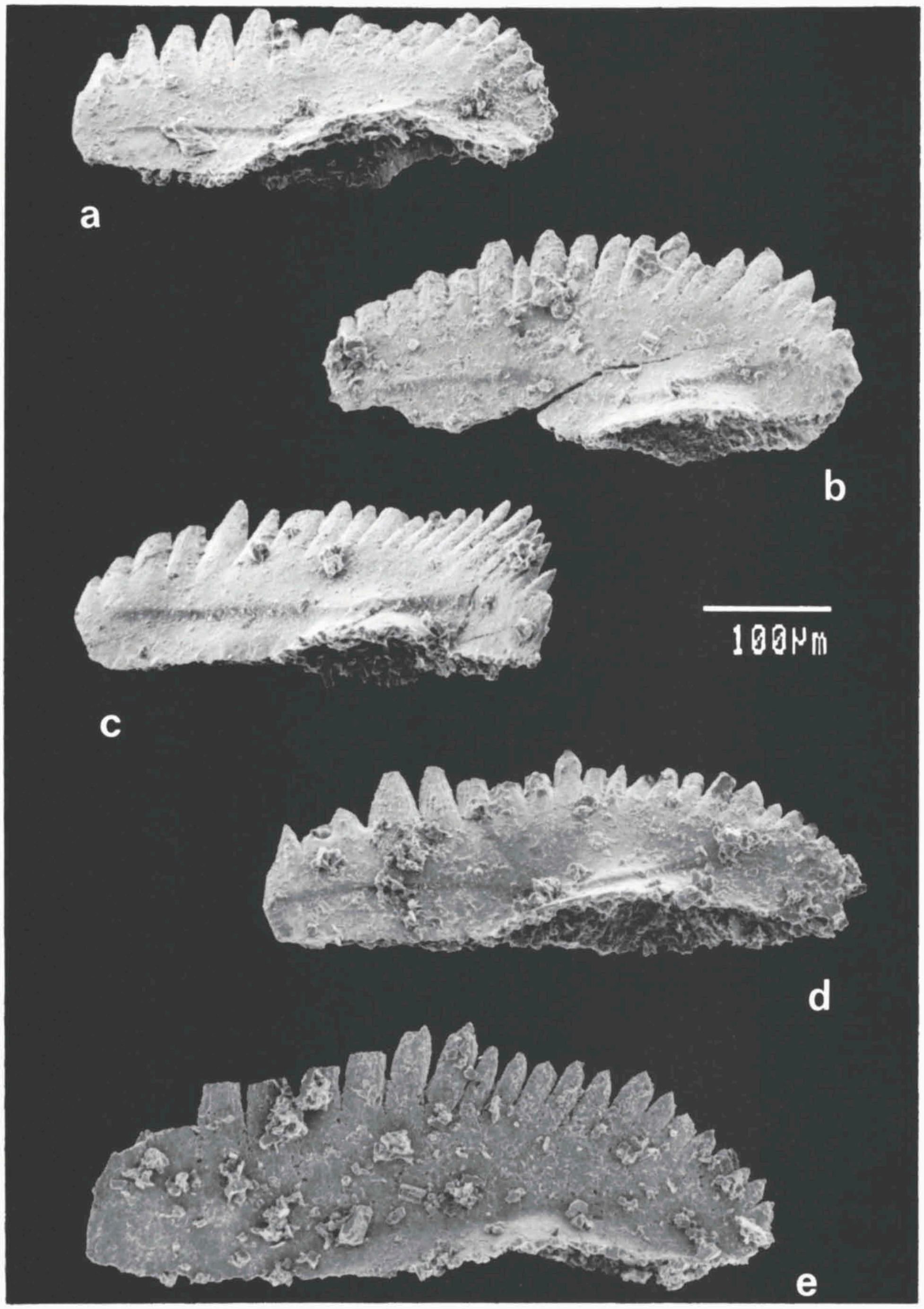

a
b
c
100μm
d
e

Plate 2

Pa elements of *Vogelgnathus campbelli* (Rexroad, 1957) from Santa Olaja de la Varga; *bilineatus* Zone, sample OL 7. Length of bar 100 μm.

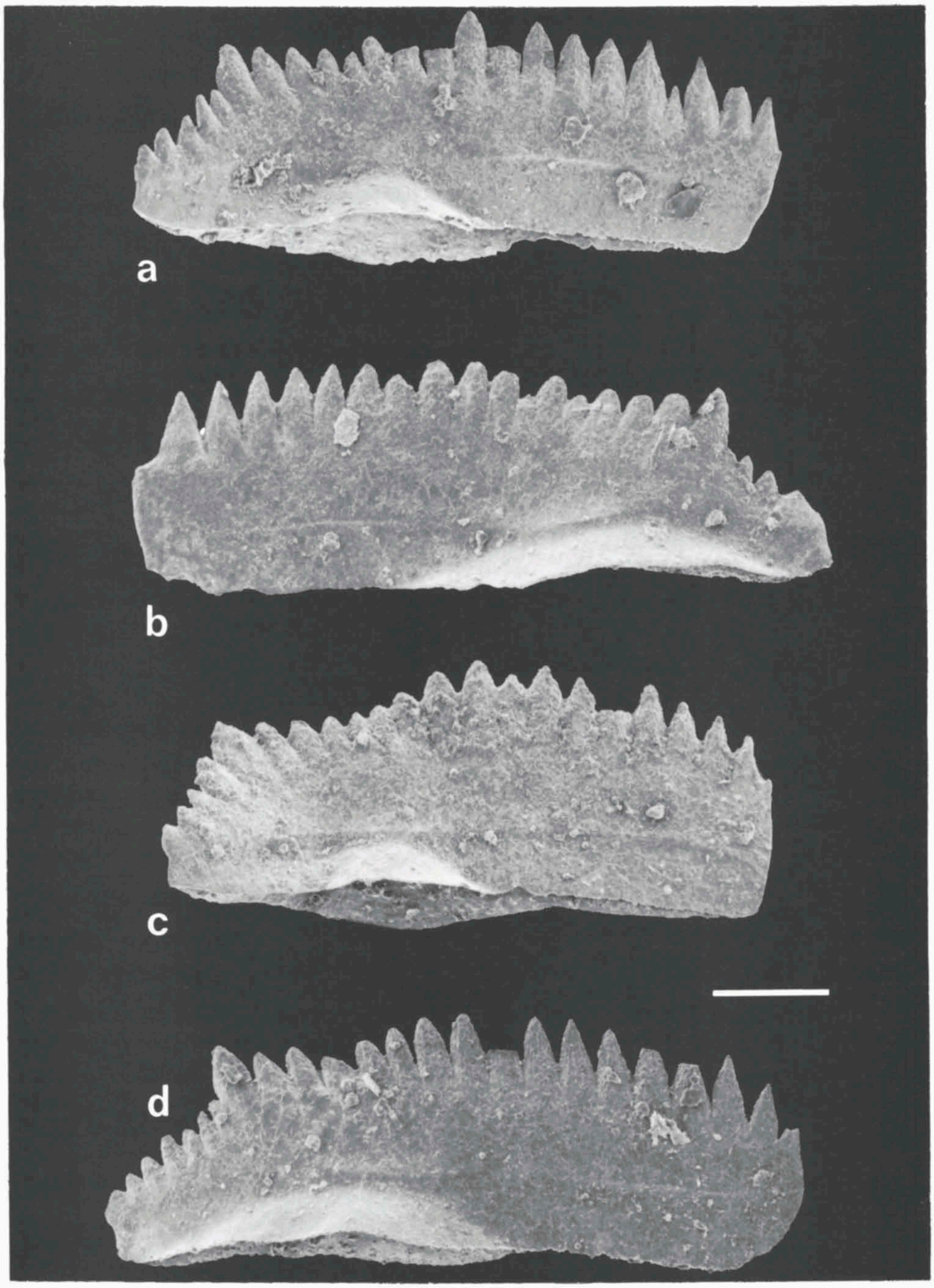
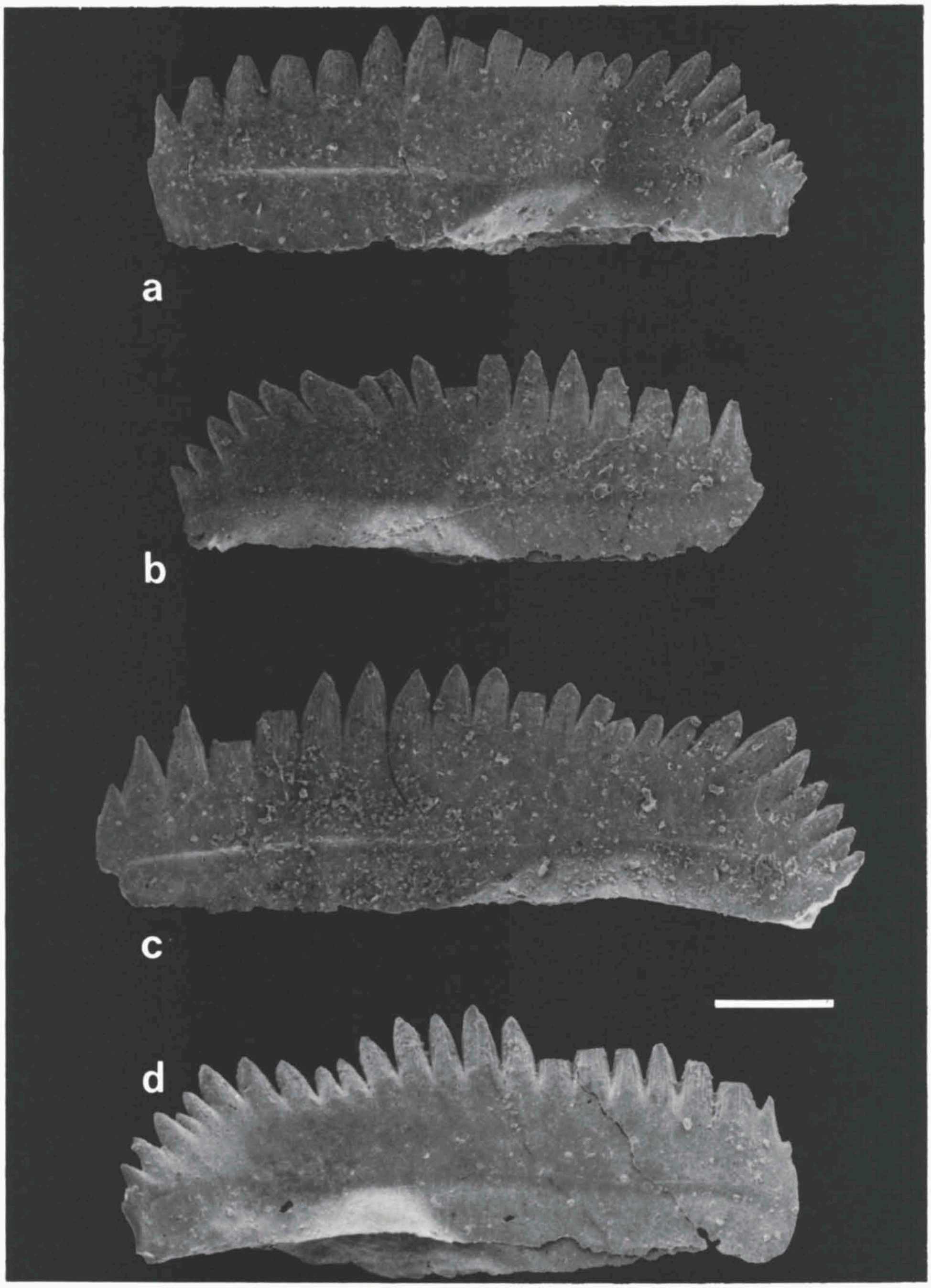

a
b
c
d

Plate 3

Pa elements of *Vogelgnathus campbelli* (Rexroad, 1957) from La Lastra; Early Namurian, sample WP 90. Length of bar 100 µm.


a
b
c
d