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Late Viséan/early Namurian conodont succession from the Esla area of the Cantabrian Mountains, Spain

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ABSTRACT:

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Conodont fauna recovered from pelagic nodular limestone sequence exposed near Santa Olaja de la Varga precisely dates the upper part of the Alba Formation in the Esla area of the Cantabrian Mountains. In terms of goniatite stratigraphy, the formation ranges into the early Namurian E2 interval which has been identified by the occurrence of the conodont *Gnathodus bollandensis*. The investigated conodont fauna includes exclusively deep-water forms and is dominated by species of *Gnathodus* and *Lochriea*. The former genus is represented primarily by the *bilineatus* lineage, in which a new species *Gnathodus cantabricus* sp. nov. has been recognized and is described herein. Representatives of the another gnathodontid *girtyi* lineage, generally present in the late Viséan/early Namurian deep-water faunas, are extremely rare. The vertical succession of *Lochriea* species is closely comparable to those recognized in Northern England, Poland and Ukraine. The Viséan/Namurian boundary is thus placed at the first occurrence of *Lochriea cruciformis*, 4.7 m below the top of the Alba Formation.

INTRODUCTION

The base of the Namurian is defined by the entry of the goniatite *Cravenoceras leion* [now *Emstites leion* (BISAT, 1930)], following the concept of BISAT (1930, 1950), which was adopted by the Carboniferous Congress at Heerlen in 1958. In practice, however, it appears that the identification of this limit outside England is hardly possible, primarily, because the species *Emstites leion* seems to be restricted in its geographic distribution to Northern England (KORN 1996). It is important to recognize general problems in stratigraphical correlation using goniatites because goniatite species as a rule have an endemic character in the Early Carboniferous. Goniatite faunas do, however, produce short-ranging forms suitable to achieve a very high-resolution in regional subdivisions. In contrast to ammonoids, most of conodont species do not exhibit any biogeographic restriction in the late Viséan/early Namurian time and thus are suitable even for intercontinental correlations. The only disadvantage is that conodont evolution during this time is characterized by a low diversity episode dominated by long-ranging taxa (ZIEGLER & LANE, 1987, SWEET 1988, BELKA 1990).

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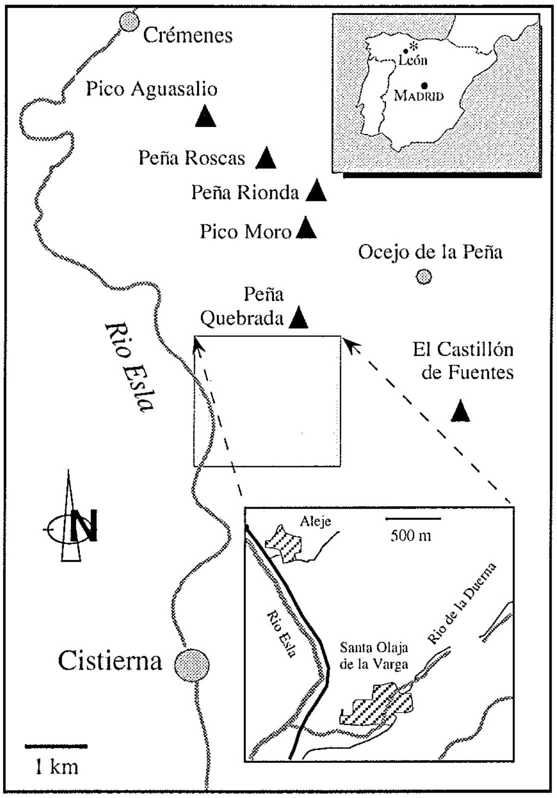

Fig. 1. Geographical location of the study area; asterisk marks the location of the sampled section at Santa Olaja de la Varga

An attempt to integrate the British ammonoid scheme with the conodont stratigraphy was made by HIGGINS (1975). He presented the vertical distribution of conodont species in the late Viséan - early Westphalian strata of Northern England and showed small changes in the conodont faunas at the Viséan/Namurian boundary. The use of subspecies of *Gnathodus girtyi* for correlation purposes in the late Viséan/early Namurian interval as proposed by HIGGINS (1975) cannot, however, be recommended because of taxonomic problems (*e.g.* TYNAN 1980; GRAYSON & *al.* 1990). Recently, SKOMPSKI & *al.* (1995) evaluated the biostratigraphic utility of *Lochriea* species in this interval. They showed that in various regions of Europe, from the Moscow Basin in Russia to the Pyrenees, there are three species of *Lochriea* (*L. cruciformis*, *L. ziegleri*, *L. senckenbergica*) occurring close to the Viséan/Namurian boundary. The species *L. cruciformis*, in particular, seems to be of great stratigraphic importance as its first occurrence coincides with the boundary in England, Poland, and the Ukraine. Because these records are from relatively shallow-water environments, conodont data from a deep-water, basinal realm are needed to evaluate the stratigraphical significance of *L. cruciformis*.

In this report, we provide a detailed information on the conodont succession from the late Viséan/early Namurian interval of the Alba Formation in the southern part of the Cantabrian Mountains. The investigated section is located in the vicinity of Santa Olaja de la Varga, a small village in the Esla valley (Text-fig. 1). The exposure is a small abandoned quarry, about 1 km northeast of the village directly next to the road, on the northern side of Rio de la Duerna (Text-fig. 2). In terms of conodont ecology and stratigraphy, the Alba Formation in the Cantabrian Mountains is of particular interest in that it comprises exclusively pelagic sediments in which no significant facies changes can be observed in the late Viséan/early Namurian interval (Text-fig. 3).

GEOLOGICAL SETTING

The section at Santa Olaja de la Varga represents a small fragment of the Devonian-Carboniferous sequence of the western flank of the Aguasalio Syncline. This fold structure builds the centre of the Esla nappe (RUPKE 1965) which is the uppermost nappe unit within the Cantabrian zone, the outer fold belt of the Iberian Variscides. Due to the structural position on the top of the Cantabrian nappe stack, the rocks of the Esla nappe were never subjected to high temperatures and remained unmetamorphosed. The Carboniferous sequence starts with shallow-water clastics and carbonates of the Ermita Formation. Conodont data indicate that these sediments were deposited after the late Famennian transgression (Lower *expansa* Zone) and during the Early Carboniferous (RAVEN 1983). The top of the formation has an erosional character. In the Esla area, the Ermita Formation ranges up to the Tournaisian *cuneiformis* Zone (BELKA & KORN 1994). Overlying is a carbonate, about 17-18 m thick unit composed predominantly of red and grey nodular limestones. It has been renamed several times, but most commonly the name Alba Formation was used. The basal beds of the Alba include conodont fauna of the *texanus* Zone (early Viséan). Thus, between the Ermita and Alba formations there is a stratigraphic gap comprising the Tournaisian *anchoralis* Zone and probably also the lowest part

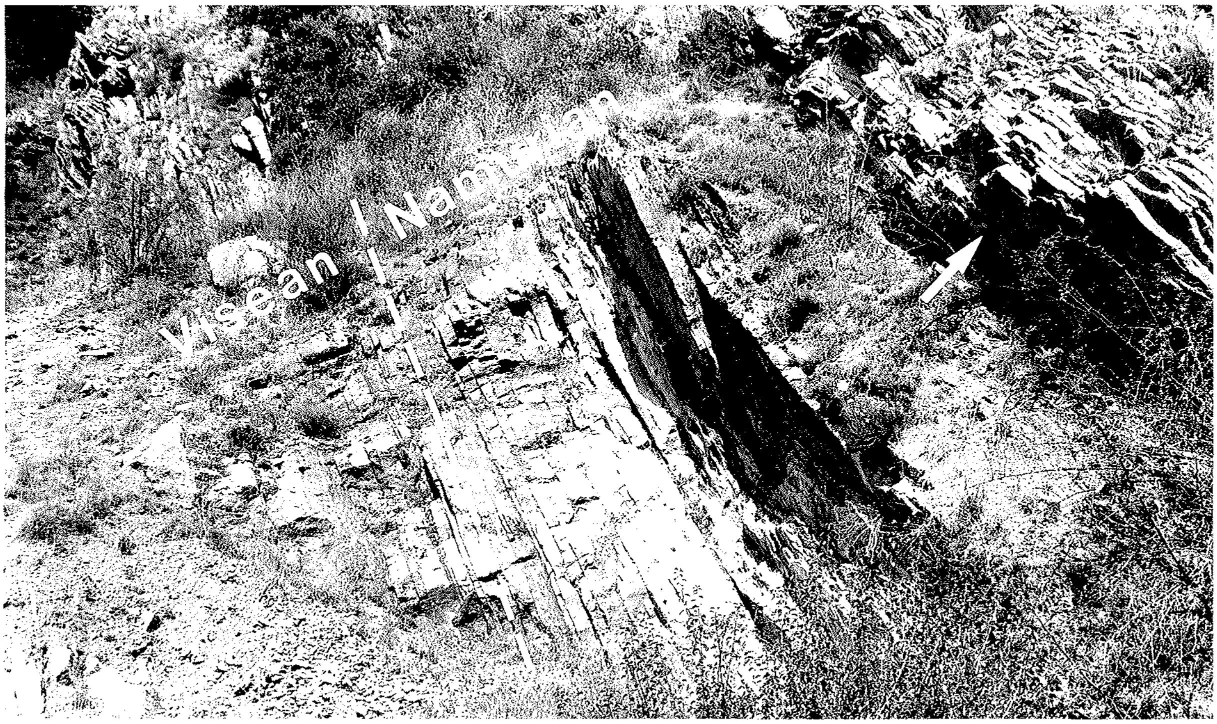

Fig. 2. Exposure of Alba Formation at Santa Olaja de la Varga section; basal beds of the overlying Barcaliente Formation are arrowed

Fig. 3. Late Viséan/early Namurian interval of the Alba Formation at Santa Olaja de la Varga section with the position of the Viséan/Namurian boundary; hammer at centre for scale

of the Viséan (BELKA & KORN 1994). The top of Alba has not yet been precisely dated. The ammonoid fauna collected from loose, carbonate debris in the upper portion of the unit contained forms indicative of the early Namurian E2 goniatite interval (WAGNER-GENTIS 1963). The Alba Formation is followed by some 500 metres of allodapic limestones of the Barcaliente Formation which ranges in age up to the lower Reticuloceras (R1) goniatite interval (KULLMANN 1979).

The contact between Ermita and Alba formations represents a distinct lithological break and change in facies from a regressive to a transgressive sequence. In its basal metre the Alba Formation exhibits a sequence of rock textures ranging from sandstones and grainstones to mudstones and a succession of biotic components, both of which reflect a rapid change from shallow water neritic to much deeper pelagic sedimentation (BELKA & KORN 1994). Upwards, the sequence consists of monotonous mudstones with some bioclastic wackestone intercalations. The fauna in the mudstones includes radiolarians, conodonts, and encrusting foraminifers, whereas the wackestones bear a very diverse biota dominated by benthic elements. The lithology and fauna point to open marine pelagic environment within the photic zone (KORN 1993). RAVEN (1983) considered deposition at depths between 10 and 50 m in well-oxygenated seawater for the red nodular limestones of the Alba Formation.

PREVIOUS STUDIES

The section at Santa Olaja de la Varga is a classic locality of stratigraphical and palaeontological studies in the Cantabrian Mountains. The first reports provided descriptions of goniatites collected primarily from loose debris in the exposure (WAGNER 1957, KULLMANN 1961, WAGNER-GENTIS 1963). Beside ammonoids, a very rich fauna of pelagic entomozoan ostracods and trilobites has been found in the section (BECKER & *al.* 1975, BECKER 1976, GANDL 1977). Although, the conodonts have been the subject of numerous investigations, analysis was generally restricted to the content of a few isolated samples (HIGGINS 1962; LANE & *al.* 1980; HIGGINS & WAGNER-GENTIS 1982). It was VAN ADRICHEM BOOGAERT (1967), who for the first time presented the conodont succession of the Alba Formation. Later on, this fauna was reinvestigated by VAN DEN BOOGAARD (1992). The most comprehensive conodont data, based on seventeen samples, is provided by PARK (1983), but his report remained unpublished, unfortunately. All these studies, although partially solving some stratigraphic problems, contained no precise information on the position of the Viséan/Namurian boundary in the section. Even a detailed lithological column of the Alba Formation at Santa Olaja de le Varga was not published before SEIBERT (1988) made the first detailed description of facies and lithology. More recently, LEHMANN (1995) sampled bed-by-bed the upper part of the section, and subsequently analysed microfacies and biota.

LITHOLOGY

The section investigated for the present paper comprises the upper part of the Alba Formation is situated in the Rio de la Duerna valley. The lithology, microfacies and fauna have been described in detail by LEHMANN (1995) and consequently only a brief summary will be given here. The sequence begins almost exactly in the middle of this unit and extends to the basal beds of the overlying Barcaliente Formation (Text-figs 2 and 4). The main part of the section (beds 1 to 32) is composed of well-bedded, uniform mudstones intercalated with some wackestone layers (Text-fig. 4). In fact only beds No. 17 and 24 display the characteristic griotte texture (Text-fig. 3). The mudstones contain predominantly pelagic fauna of radiolarians, conodonts and ammonoids. Benthic organisms are present more frequently in the wackestones. Among these are crinoids, gastropods, trilobites, ostracods, and encrusting foraminifers. The overlying *ca.* 80 cm thick package (beds 33 to 43) consists of alternation of thin mudstone and marl layers, in which trilobites, entomozoan ostracods, and ammonoids occur abundantly. The only exception is a 10 cm thick carbonate breccia layer. This clast-supported breccia is poorly sorted and includes micritic lithoclasts, crinoids, and small rugose corals. The random distribution of allochems suggests a gravity-flow deposition. The topmost part of the Alba Formation (beds 44 to 52) is developed as marls described by WAGNER (1971) as the Olaja beds. In some horizons a rich fauna of entomozoan ostracods can be observed (BECKER & *al.* 1975; BECKER 1976). This 1.6 m thick only unit attains more than 20 m thickness in other places of the Cantabrian Mountains. These marls represent the

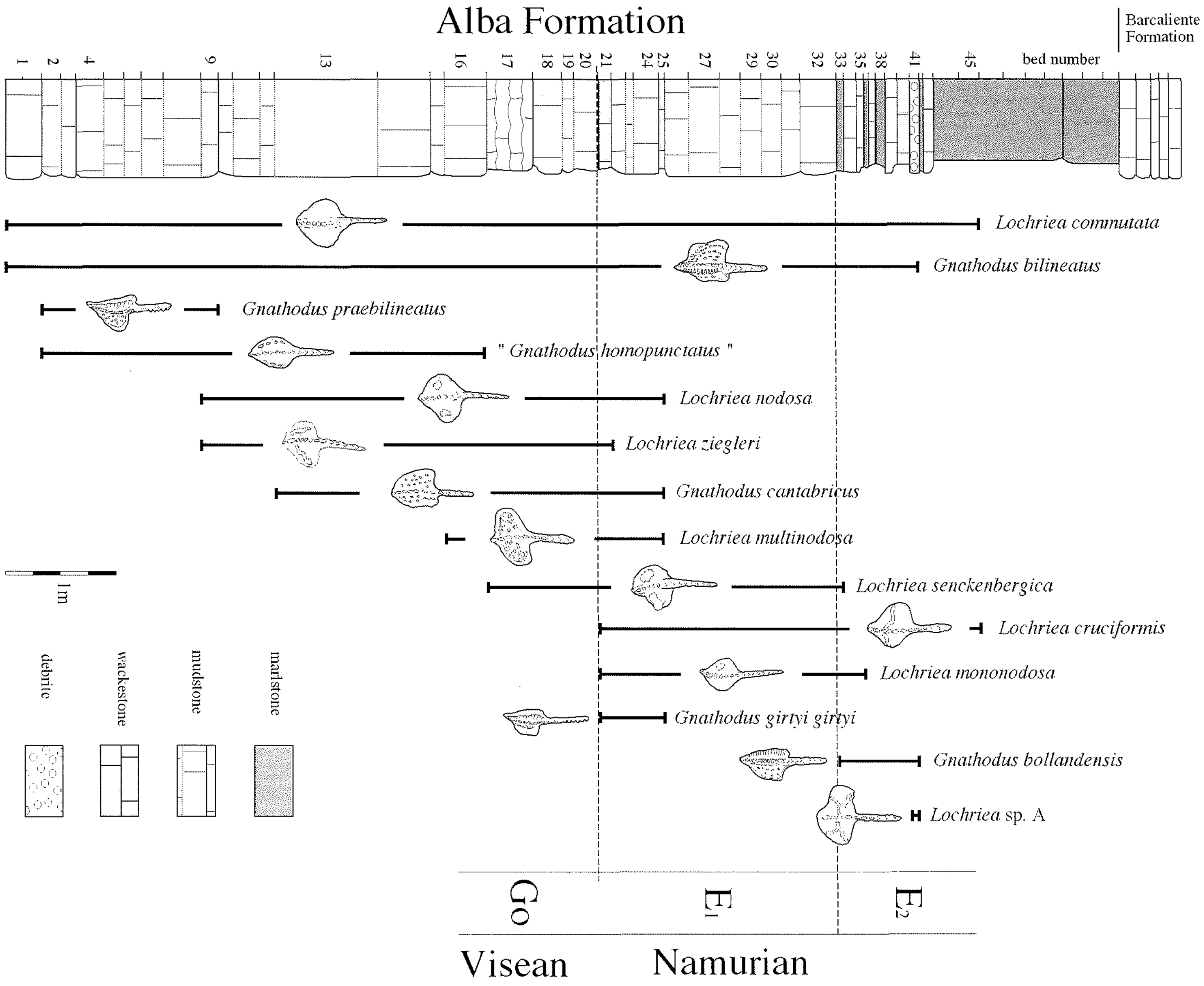

Fig. 4. Lithological column and stratigraphical ranges of selected conodont species in the upper part of the Alba Formation at Santa Olaja de la Varga; the productive samples are indicated by bed numbers.

deepest basinal environment in the entire pelagic sequence of the Alba Formation.

CONODONT FAUNA

Twenty-seven samples, each about 1-1.5 kg, were collected from the Santa Olaja de la Varga section. With exception of four samples taken from the uppermost marls of the Alba and basal beds of the Barcaliente Formation, all samples were productive and contained conodonts (APPENDIX and Pls 1-5). Some of them also yielded encrusting foraminifers and poorly preserved radiolarians. Conodont frequency, in average below 50 specimens per kilogram of rock, was rather low considering the pelagic conditions during sedimentation and a low sedimentation rate. In some layers, however, conodonts appear to be extremely rich. PARK (1983) demonstrated a conodont sample with almost 2000 platform elements, but he did not provide any information as to sample weight. The taxonomic content of this assemblage and its position in the schematic lithological column presented by PARK suggest that this sample must have been collected approximately from the interval between beds 14 and 17 (Text-fig. 4).

In the investigated conodont fauna the platform elements distinctly outnumber the ramiform ones. The fauna is dominated by representatives of *Gnathodus* and *Lochriea*, which belong to typical and usually common forms in the open-marine and deep-water environments during the late Viséan/early Namurian time. No species of genera known predominantly from the shallow-water settings, such as *Mestognathus* or *Cavusgnathus*, were recovered. There is, however, an anomaly in the composition of the deep-water conodont assemblage from the Santa Olaja de la Varga section. In contrast to other deep-water faunas known from Europe and North America (*e.g.* HASS 1953, DUNN 1965, MEISCHNER 1970, HIGGINS 1975), which generally include both Viséan gnathodontid lineages *bilineatus* and *girtyi*, representatives of the latter group are extremely rare here. Only three Pa elements of G. *girtyi* were found (*see* Appendix). In addition, there is no record of other taxa of the *girtyi* lineage at all. The rarity of *G. girtyi* and the absence of *girtyi*-related forms (for list and description *see* HIGGINS 1975) are characteristic features of the late Viséan/early Namurian conodont faunas in the Cantabrian Mountains (HIGGINS & WAGNER-GENTIS 1982, PARK 1983, VAN DEN BOOGAARD 1992). HIGGINS & WAGNER-GENTIS (1982) postulated a partial geographic isolation of this region in order to explain this fact.

The gnathodontid *bilineatus* lineage is represented by *G. bilineatus* (*see* Pl. 1), its ancestor *G. praebilineatus* (*see* Pl. 2, Figs 4-6), and by two species which evolved from *G. bilineatus*. These are *G. bollandensis*, found for the first time in the Namurian of the Esla area, and *G. cantabricus* sp. nov. which is described herein (*see* Pl. 2, Figs 1-3 and Pl. 3, Fig. 10). From the two other important Early Carboniferous lineages *Lochriea* and *Vogelgnathus*, only representatives of the former were recovered. We did not detect any horizons characterized by large quantities of *Vogelgnathus campbelli*. Two such samples were reported by PARK (1983) from the section. These invasions by *V. campbelli* interpreted to reflect the periods of maximum sea-level rise (VAN DEN BOOGAARD 1992) occur in the Early Carboniferous of the Cantabrian Mountains in very different stratigraphical positions. The *Lochriea* lineage is well represented by all species of the genus known to live during late Viséan/early Namurian time (*L. commutata*, *L. nodosa*, *L. mononodosa*, *L. ziegleri*, *L. senckenbergica*, *L. multinodosa*, and *L. cruciformis*) (*see* Pls 3-5). The stratigraphic sequence of *Lochriea* species is not known in all details (*see* SKOMPSKI & *al.* 1995). Because the oldest forms, *L. cracoviensis* and *L. commutata*, have a smooth cup, an evolutionary trend of increasing complexity in platform ornamentation can be easy postulate for the development of Pa elements within this genus. Transitional forms observed in the examined fauna allow to infer a phylogenetic sequence from *L. nodosa* to *L. ziegleri*, and further to *L. senckenbergica*, and to *L. cruciformis*. Small specimens of *L. multinodosa* bear cup ornamentation (Pl. 3, Figs 1-3) which suggests that this species presumably also derived from *L. nodosa*. The species *L. mononodosa* makes its debut in the examined fauna very late. This is probably due to relatively small rock samples we processed, because PARK (1983) found *L. mononodosa* starting as low as *L. nodosa* in the Santa Olaja de la Varga section.

The conodont elements examined during this study yield a colour alteration index (CAI) values of 2-2.5. The same level of thermal maturity reported BELKA & KORN (1994) from other exposure of Alba Formation in the Esla area. It reflects heating temperatures not higher than 100° C (EPSTEIN & *al.* 1977), assuming that the heating resulted from burial during Late Carboniferous time.

STRATIGRAPHIC IMPLICATIONS

The conodont sequence rcognized at the Santa Olaja de la Varga section indicates that the Alba Formation ranges here into the lower Namurian (Text-figs 2-4). Although the top of the formation cannot be directly dated, these data are in good agreement with the results presented by HIGGINS & WAGNER-GENTIS (1982) from other localities in the Cantabrian Mountains, where the formation reaches into the early Namurian E2b goniatite interval. In terms of conodont stratigraphy, this interval can be identified by the occurrence of *Gnathodus bollandensis* (HIGGINS 1975; SKOMPSKI & *al.* 1995). We can thus infer that the E2 goniatite fauna reported by WAGNER-GENTIS (1963) certainly derived from the top of Alba carbonates, between beds 33 and 43. It is therefore evident that the marls at the top of the Alba Formation, the Olaja beds sensu WAGNER (1971), do not correspond to the E1 goniatite interval as some workers previously supposed (REUTHER 1977, BECKER 1982). They represent the E2 interval.

The vertical succession of *Lochriea* species is closely comparable to those recognized in northern England, Poland, and the Ukraine (SKOMPSKI & *al.* 1995; SKOMPSKI 1996). In our interpretation, it is therefore justified to trace tentatively the base of the Namurian at bed No. 21, at the first occurrence of *Lochriea cruciformis* (Text-figs 3-4). This is in obvious conflict with data provided by MEISCHNER (*in* SKOMPSKI & *al.* 1995) from the Rhenohercynian belt, where this species is supposed to have its first occurrence already during the late Viséan. However, some controversy existed in the Rheinisches Schiefergebirge concerning the position of the Viséan/Namurian boundary when the conodont data were assembled. In terms of goniatite stratigraphy, the boundary has recently been revised and placed at the first appearance of *Edmooroceras pseudocoronula* (KORN 1996, KORN & HORN 1997). The relationship of the goniatite succession to the conodont occurrences cannot be evaluated and thus remains questionable since information on the positions of the critical conodont samples in the sections was not published.

We hope that this contribution may stimulate further work in the Rhenohercynian Zone and elsewhere to clarify the relation of conodont lineages to records of other fossils, and in particular of ammonoids.

SYSTEMATIC PALAEONTOLOGY

Figured specimens are reposited at the University of Tübingen (GPIT).

Genus *Gnathodus* PANDER, 1856

Type species: *Polygnathus bilineatus* ROUNDY, 1926

Gnathodus cantabricus sp.n.

(Pl. 2, Figs 1-3)

1983. *Gnathodus* n.sp. A; S.-I. PARK, pp. 86-87, Pl. 3, Figs 18-21.

1993. *Gnathodus bilineatus bollandensis* HIGGINS & BOUCKAERT; M.-F. PERRET, Pl. 10, Fig. 28 (only).

1994. *Gnathodus* sp. A PARK; R. BOSIC, pp. 106-108, Pl. 5, Figs 1-3.

HOLOTYPE: The specimen illustrated in Pl. 2, Fig. 2.
TYPE LOCALITY: Santa Olaja de la Varga section, Cantabrian Mountains, Spain.
TYPE HORIZON: Bed No. 16, Alba Formation (4.9 m below the top of formation).
DERIVATION OF NAME: From the Cantabrian Mountains in Spain, where the species was first discovered.
DIAGNOSIS: Carminiscaphate Pa element characterized by a broad, spade-shaped cup with asymmetrical halves; the outer side of the cup is wider than the inner side and only weakly ornamented by randomly scattered nodes.

MATERIAL: Twenty Pa elements.

DESCRIPTION: Cup of Pa elements with a distinct asymmetry in the width, shape and ornamentation of halves, represents about a half of the unit length; broad outer cup commonly widest in anterior third, its margin forms convex curve, characteristically meeting posterior tip without sinus in margin; inner side narrower, with the widest point in the midlength of inner margin; inner margin variable, slightly convex; outer side weakly ornamented by randomly scattered small nodes in most specimens, but arranged in rows parallelling cup margin in some instances; inner side bears a weak parapet composed of nodular rows or indistinct ridges; parapet typically does not reach carina and terminates posterior to the widest place of inner cup; carina is fused and slightly incurved in posterior part; basal cavity deep, wide and asymmetrical; free blade straight, with denticles of equal high.

REMARKS: Except for Pa elements, no other elements of *Gnathodus cantabricus* are known. The apparatus included one set of paired asymmetric Pa elements, since left and right elements of these pairs may be distinguished. It is likely that the apparatus of *G. cantabricus* in architecture and organisation was similar to the well-known apparatus *of Gnathodus bilineatus* (*see* Pl. 1 and NORBY 1976), from which *G. cantabricus* evolved. Pa elements of *G. bilineatus* differ from those of *G. cantabricus* by having well-developed, long parapet on the narrow inner cup and characteristic quadrate-shaped, flat outer cup. Cup of *G. bilineatus* is thus different in outline (more asymmetrical) and, in addition, stronger ornamented.

The Pa element of *Gnathodus cantabricus* is similar to that of species *G. praebilineatus*. It can be distinguished, however, by the character of the inner side and a more circular outline of the cup in *G. cantabricus*. Specimens of *G. praebilineatus* have a cup that is distinctly triangular in outline.

OCCURRENCE: Pa elements of *Gnathodus cantabricus* sp.n. are known to occur in the Cantabrian Mountains, Spanish Pyrenees, and Styria (Austria).

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APPENDIX: Numerical distribution of conodont elements in the Santa Olaja de la Varga section; Conodont sample numbers are bed numbers

APPENDIX

Bed No's		1	2	4	9	13B	13T	16	17	18	19	20	21	24	25	27	29	30	32	33	35	38	41	45
Lochriea commutata	Pa	1	2	-	1	-	-	9	9	1	-	-	31	3	18	1	-	2	-	5	8	4	4	1
	Pb	-	-	-	-	-	-	-	3	-	-	-	2	-	1	-	-	-	-	-	-	-	1	-
	M	-	1	-	4	-	-	1	3	-	-	-	17	-	9	-	-	-	-	1	3	-	1	1
	S	-	-	-	-	-	-	1	2	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Gnathodus bilineatus	Pa	1	1	-	3	2	2	42	43	6	-	-	167	2	169	4	5	16	2	7	3	1	1	-
	Pb	-	-	-	-	-	-	1	1	-	-	-	6	-	4	-	-	-	-	-	-	1	-	-
	M	-	-	-	-	-	-	-	-	-	-	-	4	-	1	1	-	-	-	-	-	-	-	-
	S	-	-	-	-	-	-	3	-	-	-	-	7	-	2	-	-	-	-	-	-	1	-	-
Gnathodus praebilineatus	Pa	-	3	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
"Gnathodus" homopunctatus	Pa	-	2	-	4	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
"Gnathodus" symmutatus	Pa	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lochriea nodosa	Pa	-	-	-	3	-	-	4	3	-	-	-	13	2	2	-	-	-	-	-	-	-	-	-
	Pb	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	-	-	-	-	-	-	-
Lochriea ziegleri	Pa	-	-	-	2	-	2	1	2	-	1	-	8	-	-	-	-	-	-	-	-	-	-	-
Gnathodus cantabricus	Pa	-	-	-	-	1	-	2	1	1	-	-	12	1	2	-	-	-	-	-	-	-	-	-
Lochriea multinodosa	Pa	-	-	-	-	-	-	1	-	4	-	4	10	-	1	-	-	-	-	-	-	-	-	-
Lochriea senckenbergica	Pa	-	-	-	-	-	-	-	5	-	-	-	10	-	3	-	-	-	-	1	-	-	-	-
Gnathodus girtyi girtyi	Pa	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	-	-	-	-	-	-	-
Lochriea cruciformis	Pa	-	-	-	-	-	-	-	-	-	-	-	3	-	3	-	-	-	-	2	-	-	-	1
Lochriea mononodosa	Pa	-	-	-	-	-	-	-	-	-	-	-	2	-	3	-	-	-	-	6	1	-	-	-
Gnathodus bollandensis	Pa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	2	2	-
Lochriea sp. A	Pa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Lochriea spp.	Pa	-	-	-	1	2	3	6	2	-	-	2	8	-	13	-	-	-	-	-	-	-	2	-
	Pb	-	1	-	-	-	-	1	2	-	-	-	12	-	2	-	-	-	-	1	-	1	1	-
Gnathodus spp.	Pa	-	6	1	3	6	4	28	50	9	-	2	77	1	47	3	-	15	4	8	4	1	14	2
	Pb	-	2	-	-	-	-	2	1	1	-	-	12	-	2	-	-	1	-	-	-	3	-	-
	M	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	S	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Idioprioniodus spp.		-	-	-	1	1	2	2	6	1	-	1	16	1	4	-	1	-	-	2	-	-	1	-
Kladognathus spp.		-	-	-	-	-	-	3	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unassigned ramiform elements		-	3	-	15	-	2	13	11	-	-	-	46	-	39	2	1	2	-	24	6	8	6	1
Total counted conodonts		3	21	1	45	12	15	121	151	23	1	9	467	11	327	11	7	36	6	58	25	22	34	6

PLATE 1

Gnathodus bilineatus (ROUNDY, 1926)

1 – Pa element, upper view, sample 16, × 65
2 – Pa element, upper view, sample 16, × 80
3 – Pa element, upper view, sample 21, × 50
4 – Pa element, upper view, sample 25, × 80
5 – Pa element, upper view, sample 9, × 85
6 – M element, lateral view, sample 27, × 150
7 – Sc2 element, lateral view, sample 38, × 65
8 – Sc1 element, lateral view, sample 21, × 110
9 – Pb element, lateral view, sample 16, × 80
10 – Pb element, lateral view, sample 38, × 65

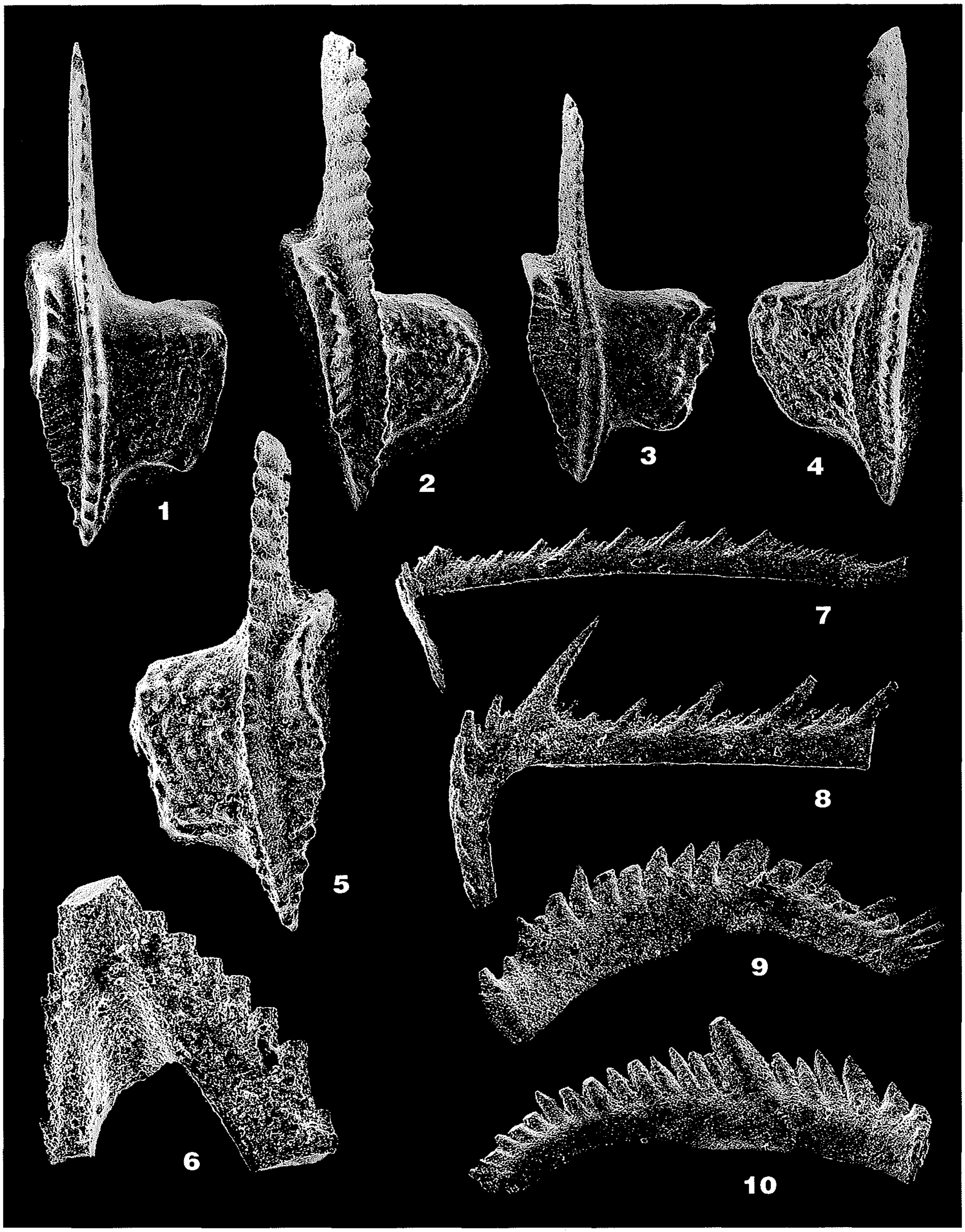
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PLATE 2

1-3 – *Gnathodus cantabricus* sp.n.
1 – Pa element, holotype, sample 16, × 90
2 – Pa element, sample 18, × 90
3 – Pa element, sample 21, × 75

4-6 – *Gnathodus praebilineatus* BELKA, 1985
4 – Pa element, sample 2, × 90
5 – Pa element, sample 9, × 110
6 – Pa element, specimen showing transition to *G. bilineatus*, sample 2, × 75

7-8 – "*Gnathodus*" *homopunctatus* ZIEGLER, 1960
7 – Pa element, sample 2, × 90
8 – Pa element, sample 9, × 110

All upper views

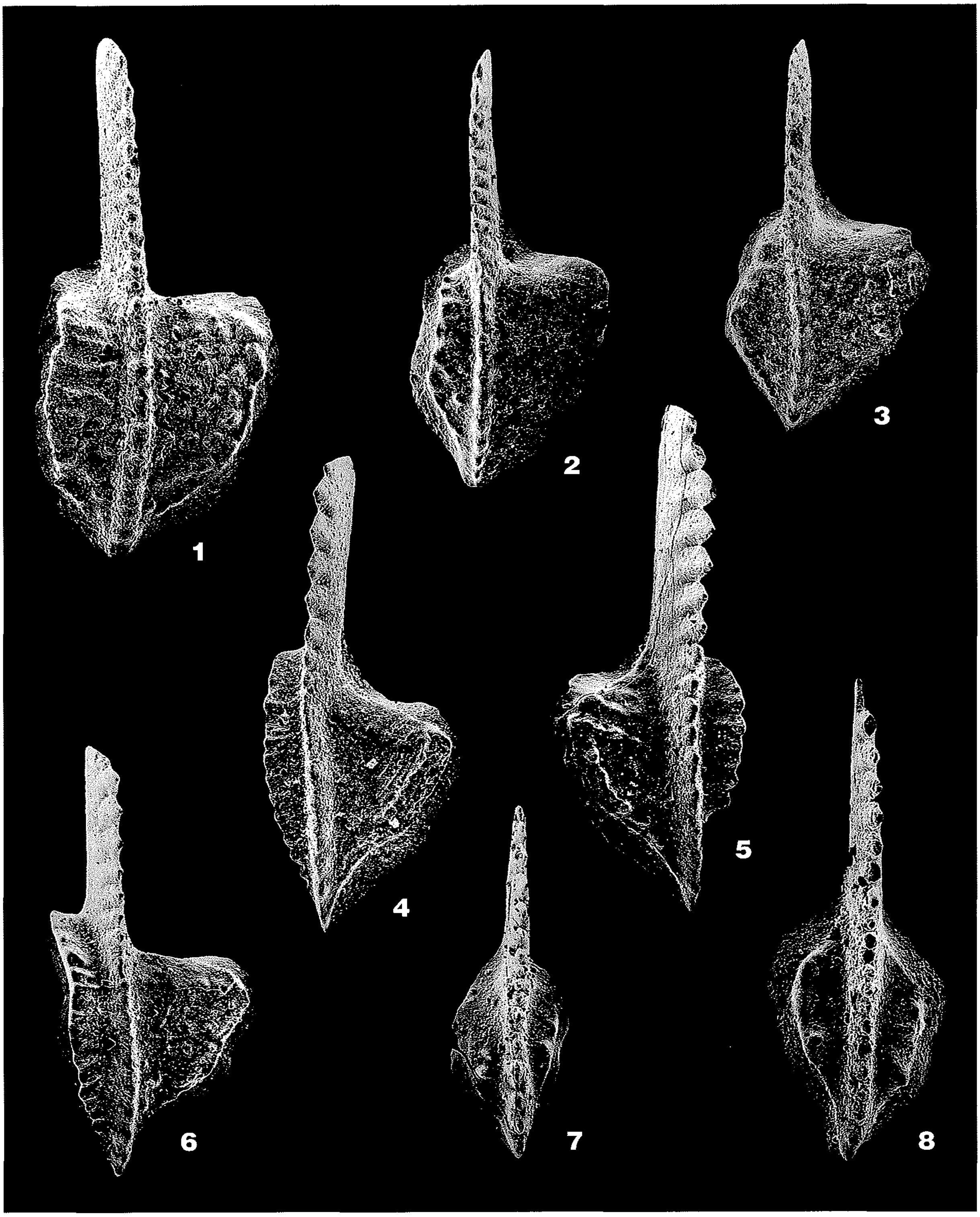
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PLATE 3

1-4 – *Lochriea multinodosa* (WIRTH, 1967)
1 – Pa element, sample 20, × 90
2 – Pa element, sample 20, × 90
3 – Pa element, sample 18, × 90
4 – Pa element, sample 21, × 100

5-8 – *Lochriea commutata* (BRANSON & MEHL, 1941)
5 – Pa element, sample 2, × 90
6 – Pa element, sample 25, × 90
7 – M element, lateral view, sample 21, × 80
8 – M element, lateral view, sample 21, × 90

9 – *Lochriea* spp., Pb element, lateral view, sample 38, × 120

10 – ?*Gnathodus bollandensis* HIGGINS & BOUCKAERT, 1968,
Pb element, lateral view, sample 38, × 110

Unless otherwise stated, all figures are upper views

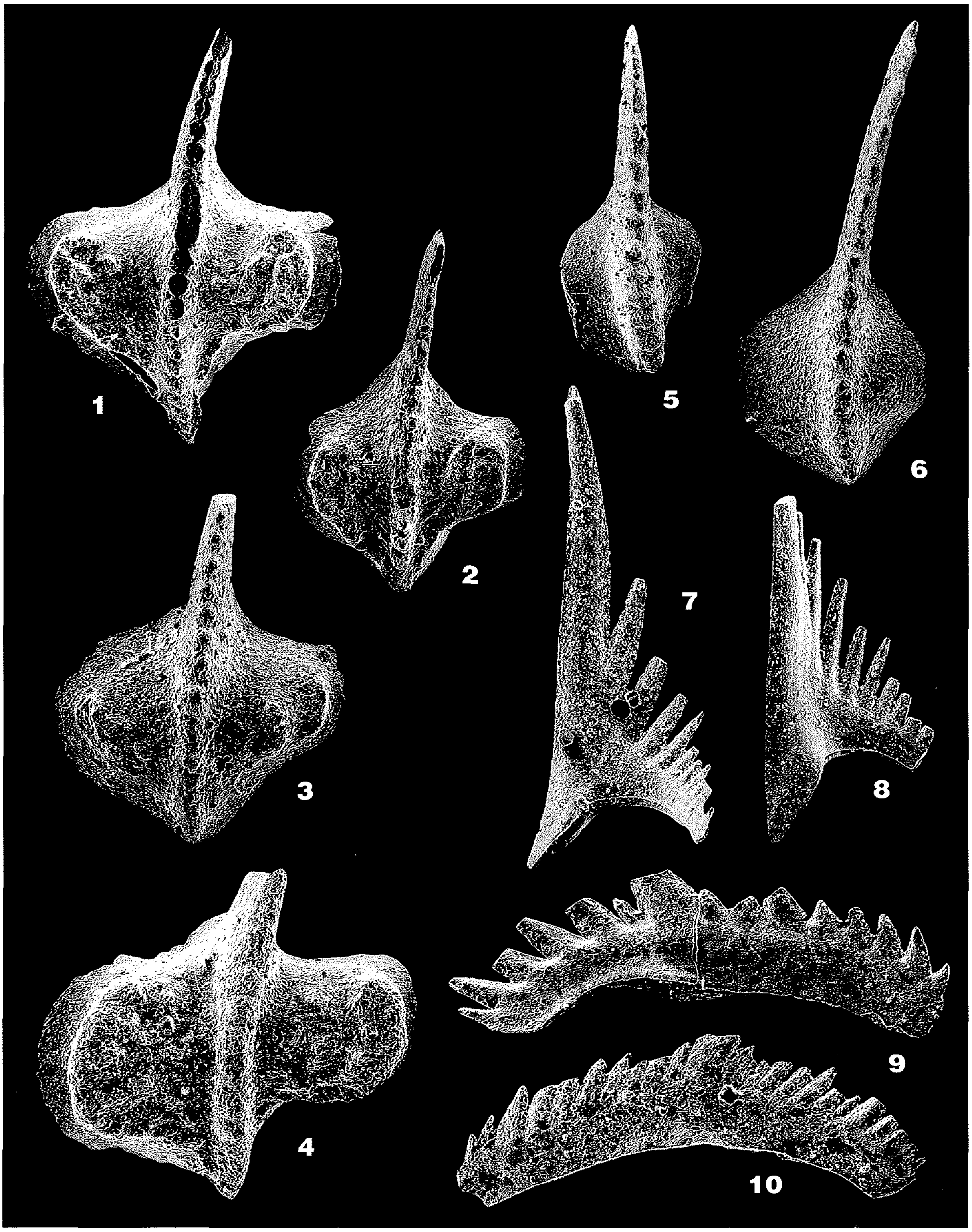
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PLATE 4

1-2 – *Lochriea nodosa* (BISCHOFF, 1957)
1 – Pa element, transitional form to *L. ziegleri*, sample 16, × 120
2 – Pa element, transitional form to *L. ziegleri*, sample 9, × 90

3, 5 – *Lochriea senckenbergica* NEMIROVSKAYA, PERRET & MEISCHNER, 1994
3 – Pa element, sample 21, × 95
5 – Pa element, sample 21, × 95

4 – *Lochriea cruciformis* (CLARKE, 1960); Pa element, sample 25, × 90

6-7 – *Lochriea ziegleri* NEMIROVSKAYA, PERRET & MEISCHNER, 1994
6 – Pa element, sample 17, × 120
7 – Pa element, sample 16, × 85

8 – *Lochriea* sp. A, Pa element, sample 41, × 60

All figures are upper views

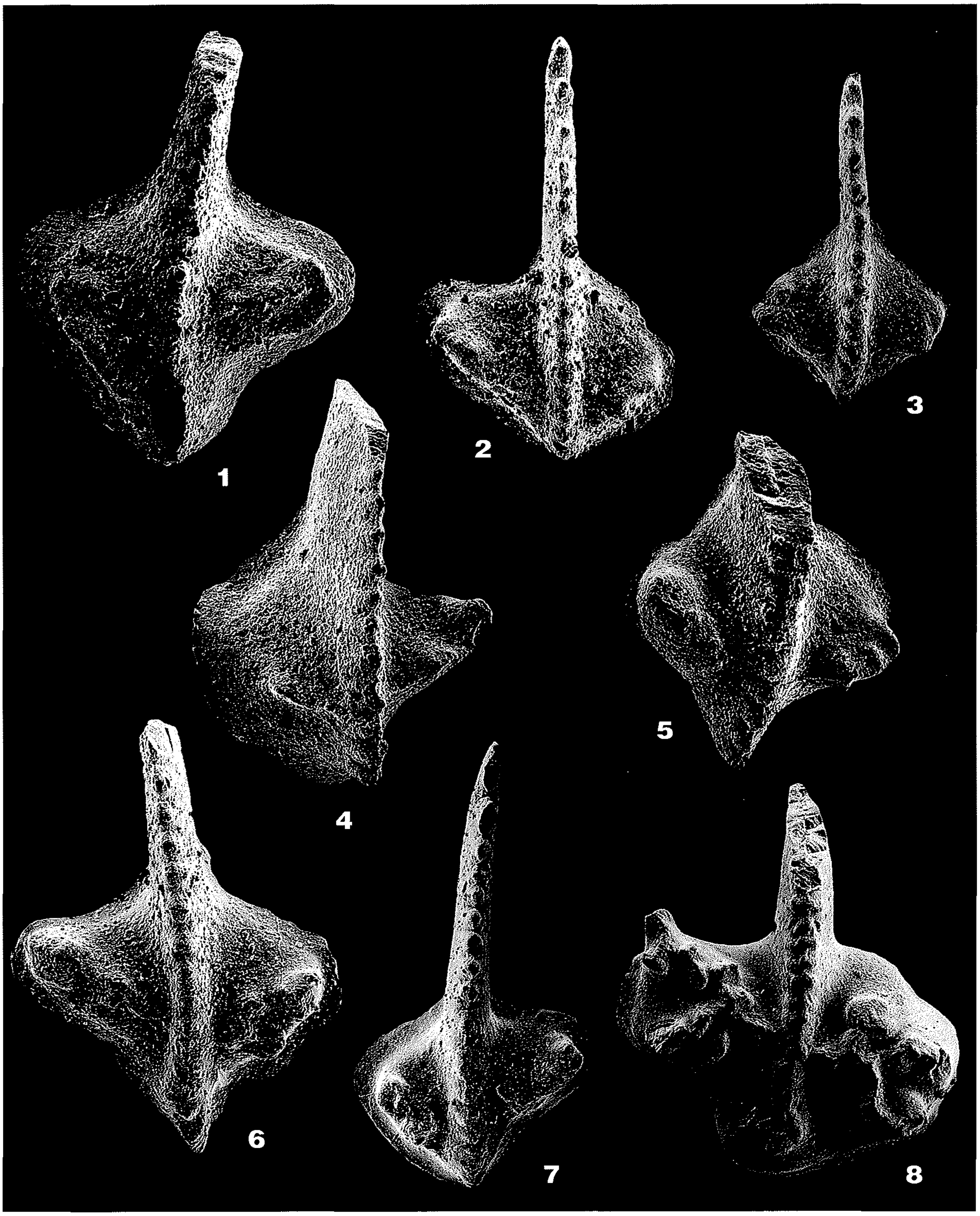
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PLATE 5

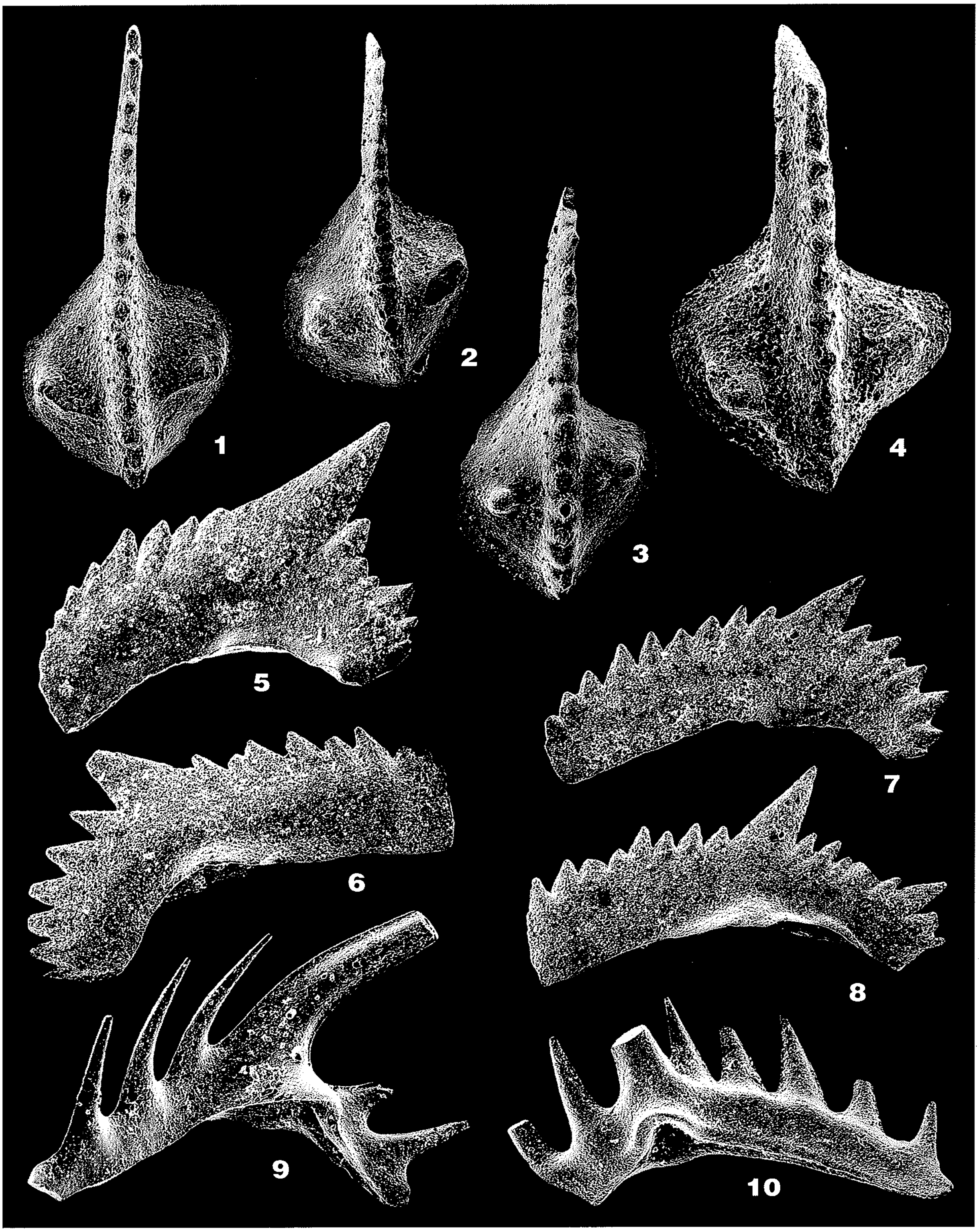
1-4 – *Lochriea nodosa* (BISCHOFF, 1957)
  1 – Pa element, upper view, sample 25, × 110
  2 – Pa element, upper view, sample 21, × 65
  3 – Pa element, upper view, sample 21, × 95
  4 – Pa element (juv.), upper view, sample 9, × 140

5 – *Lochriea* spp., Pb element, lateral view, sample 21, × 120

6-8 – ?*Lochriea nodosa* (BISCHOFF, 1957)
  6 – Pb element, lateral view, sample 25, × 120
  7 – Pb element, lateral view, sample 21, × 90
  8 – Pb element, lateral view, sample 21, × 90

9 – *Idioprioniodus* sp., Sb element, lateral view, sample 9, × 120

10 – *Idioprioniodus healdi* (ROUNDY, 1926), Pb element, lateral view, sample 25, × 90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