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Origin of *Gnathodus bilineatus* (Roundy, 1926) related to goniatite zonation in Rheinisches Schiefergebirge, Germany

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ABSTRACT – A gap in our knowledge of conodont zonation is closed by faunas from a limestone turbidite series in Rheinisches Schiefergebirge, Germany. *Gnathodus bilineatus* (Roundy, 1926) sensu lato originates with two morphotypes high in the Pericyclus-Stufe, cu II, Lower Carboniferous. *Gn. bilineatus romulus* n.ssp. enters still in the uppermost Entogonites nasutus Zone. *Gn. bilineatus remus* n.ssp. follows suite in the E. grimmeri Zone. *Gn. bilineatus bilineatus* appears in the Goniatites crenistria Zone. *Gn. girtyi* Hass, 1952 precedes *Gn. bilineatus romulus* n.ssp. by just a few beds and therefore starts within the Entogonites nasutus Zone. The ancestry of *Gn. praebilineatus* Belka, 1985, most likely the ancestor of *Gn. bilineatus*, remains uncertain. It is recommended to set the base of the *Gnathodus bilineatus* Zone with the first appearance of *Gnathodus bilineatus romulus* n.ssp.

RIASSUNTO – [L'origine di *Gnathodus bilineatus* (Roundy, 1926) in relazione alla zonazione a goniatiti nel Rheinisches Schiefergebirge, Germania] – Le fauna a conodonti ritrovate in torbiditi calcaree nella regione del Rheinisches Schiefergebirge, Germania, consente di risolvere i problemi relativi alla biozonatura del Carbonifero inferiore. *Gnathodus bilineatus* (Roundy, 1926) sensu lato si origina, con due morfotipi, nella parte alta del Pericyclus-Stufe, cu II, Carbonifero inferiore. *Gnathodus bilineatus romulus* n.ssp. compare nella parte alta della Entogonites nasutus Zone. *Gn. bilineatus remus* n.ssp. appare poco dopo, nella E. grimmeri Zone. *Gn. bilineatus bilineatus* compare nella Goniatites crenistria Zone. *Gn. girtyi* Hass, 1952 precede *Gn. bilineatus romulus* n.ssp. di alcuni strati e quindi inizia durante la Entogonites nasutus Zone. Il progenitore di *Gn. praebilineatus* Belka, 1985, da cui probabilmente si è originato *Gn. bilineatus*, rimane indefinito. La base della *Gnathodus bilineatus* Zone viene indicata dalla comparsa di *Gnathodus bilineatus romulus* n.ssp.

INTRODUCTION

Gnathodus bilineatus embraces a large group of morphotypes with bilineate ornamentation on their platforms. They span the interval from the latest early Viséan through the Serpukhovian. The group displays high specific and intraspecific diversity and a number of variations as described and figured by many conodont workers (Lane & Straka, 1974; Higgins, 1975; Metcalfe, 1981; Higgins & Wagner-Gentis, 1982; Park, 1983; Belka, 1985; Schönlaub & Kreutzer, 1993; Perret, 1993; Nemirovskaya & Nigmatganov, 1993; Belka & Korn, 1994; Krumhardt *et al.*, 1996; Spalletta & Perri, 1998).

The *Gnathodus bilineatus* group is significant in the stratigraphy of the Carboniferous. Three conodont zones are named after its members. These are the late Viséan *Gn. bilineatus*-Zone and two Serpukhovian zones: *Gn. bilineatus bollandensis* and *Gn. postbilineatus*, respectively. The world-wide distribution of the taxa of the *bilineatus* group and their apparent diagnostic features make them reliable tools for long-ranging correlation.

ORIGIN OF *GN. BILINEATUS* IN TERMS OF AMMONOID STRATIGRAPHY

Bischoff (1957) gave a first account of Lower Carboniferous conodonts from the Rheinisches Schiefergebirge, followed by Voges (1959, 1960). Neither of them established a formal *Gnathodus bilineatus*-Zone. Voges (1959, tab. 1, pp. 270, 283; 1960, p. 26) defined an 'anchoralis – bilineatus Interregnum' as the time-interval between the termination of *Scaliognathus anchoralis* and the appearance of *Gnathodus bilineatus* which he (Voges, 1960, tab. 5, p. 29) dated as within the Pericyclus-Stufe, Entogonites nasutus Zone (cu II 8). This datum was confirmed by Meischner (1970, fig. 2, p. 1171) who also, on the basis of more conodont faunas, emended a *Gnathodus bilineatus bilineatus* Zone from the one originally termed 'bilineatus Zone' by Böger (1962, p. 152). Meischner (1970, fig. 2) speculated that *Gn. bilineatus* may derive from either *Gn. semiglaber* or *Gn. delicatus*, - the latter he figured as overlapping with *Gn. bilineatus* in the ammonoid Zone cu II 8. Weyer (1972) reported *Gn. bilineatus* from the Pericyclus-Stufe of the Harz

Mountains.

This early origin of *Gn. bilineatus* was generally accepted that time by authors dealing with conodont/ammonoid-correlation in Europe (Bender *et al.*, 1971; Paproth *et al.*, 1983; Conil *et al.*, 1990; Riley, 1990a, 1993). Later in Belgium the first appearance of *Gn. bilineatus* was dated as V2b or Warnantian (Groessens, 1974; Belka & Groessens, 1986), and in England as the base of late Asbian (Varker & Sevastopulo, 1985; Riley, 1993).

When Belka (1985) described *Gn. praebilineatus* as a Viséan homeomorph of the Tournaisian species *Gn. delicatus*, the exact position of the origin of *Gn. bilineatus* in terms of the ammonoid zonation became uncertain as it was not clear where in the supposed lineage *Gn. praebilineatus*–*bilineatus* the specimens of Voges (1959), Weyer (1972) and those ascribed to *Gn. delicatus* (and partly *Gn. cf. cuneiformis*) by Meischner (1970) had to be placed. The material on which Meischner (1970, fig. 2) had based his schematic phylogeny of the *Gnathodus* species was therefore revised during a sabbatical of Tamara Nemyrovska in Göttingen, 1996.

Some of the uncertainty about the origin of *Gn. bilineatus* may be due to unsatisfactory correlation of goniatite zones between Germany and other regions (Riley, 1990a, 1990b, 1993; Korn, 1996). The German zonation around the critical boundary as established by Nicolaus (1963) was recently revised by Korn (1996). The lower boundary of the *Goniatites*-Stufe (cu III) was shifted from the base of the *Entogonites grimmeri* Zone to the beginning of *Goniatites hudsoni* (= *Goniatites schmidtianus* syn.). It coincides now with the base of a prominent marker-horizon in the Rheinisches Schiefergebirge, the “grimmeri-Bank” (Text-fig. 3).

Nicolaus (1963)	Korn (1996)
<i>Goniatites</i> -Stufe, cu III	<i>Goniatites</i> -Stufe, cu III
<i>Goniatites cren. crenistria</i>	<i>Goniatites crenistria</i>
	<i>Goniatites globostriatus</i>
<i>Goniatites cren. schmidtianus</i>	— <i>Goniatites hudsoni</i>
— <i>Entogonites grimmeri</i>	<i>Entogonites grimmeri</i>
<i>Entogonites nasutus</i>	<i>Entogonites nasutus</i>
<i>Pericyclus</i> -Stufe, cu II	<i>Pericyclus</i> -Stufe, cu II

GEOLOGICAL SETTING, NATURE OF THE RECORD

The Lower Carboniferous sediments in the Rheinisches Schiefergebirge originated in the foreland of the Variscan (= Hercynian) Orogen (Text-fig. 1). Deep-water Kulm facies was bordered in the northwest by a calcareous shelf on which Carboniferous Limestone and detrital limestones were deposited (Text-fig. 2). The earlier part of the sequence was controlled by extensional tectonics during which little clastic

material entered the basin. During the Tournaisian and lower Viséan this is expressed in reduced thickness of shales, alum-shales and cherts in basal positions, condensed sequences on top of drowned Devonian reefs, and tholeiitic basaltic volcanism in the southeast.

In the *Scaliognathus anchoralis* Zone some of the former reefs were revived and started to shed limestone turbidites into the adjacent depressions (Meischner 1971, p. 18, fig. 6). These beds are intercalated with the younger part of the chert series to form what is regionally called ‘Kulm-Kieselkalk’ (cherty limestones). Simultaneously the volcanic activity changed to explosive keratophyre type the frequent, cm-thin ashes of which are intercalated with the cherty limestones and cherts.

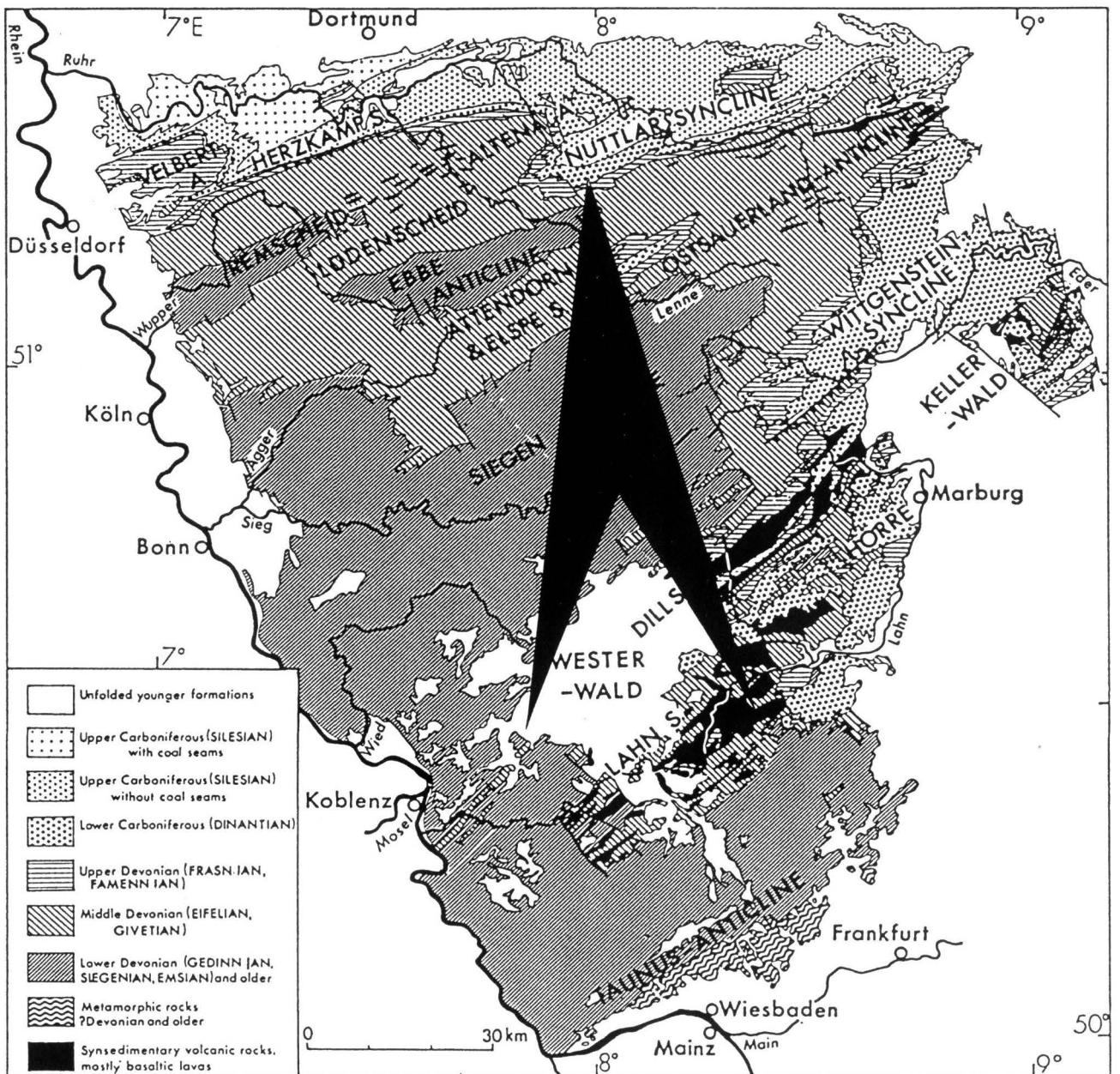
The former shelf was subsequently drowned and delivered limestone turbidites of the “Kulm-Plattenkalk” during the upper Viséan (*Goniatites*-Stufe), before the whole area was covered by the prograding flysch and molasse deposits of the newly forming Variscan mountains in the younger part of the upper Viséan and in the Namurian.

Despite the marked contrasts between the facies of the alum shales, cherts and cherty limestones, the reduced sequences, and the limestone turbidites within the Rheinisches Schiefergebirge, the basal sequence is remarkably persistent, laterally. Individual beds with specific fauna and cm-thin tuffs can be traced over major parts of the basin (Nicolaus, 1963; Meischner, 1962, 1971). The general sequence of black shales and cherts followed by lighter-coloured, variegated, calcareous cherts, then dark shales and siltstones, can be followed over greater parts of the external pre-Variscan basins of Europe, Asia Minor and Central Asia, the major facies changes being synchronous at least in the Harz Mountains, southern England, Montagne Noire and South Portugal (Engel *et al.*, 1983).

In the area south of Arnsberg in Westphalia, limestone turbidite activity persisted from the *Sc. anchoralis*- into the *Gn. bilineatus* Zone (Text-fig. 2). A continuous section from the Kulm-Kieselkalk into the shales and limestones of the Kulm-Plattenkalk was sampled at Ober-Röhre by Meischner in 1967. The conodonts were used for the construction of the stratigraphic chart in Meischner (1970, fig. 2), but were never published in detail.

The section in the former limestone quarry of Ober-Röhre, which is now part of the waterworks of the town of Sundern, consists of thinly bedded shales, cherts and acidic tuffs intercalated with limestone turbidites (Text-fig. 3). The critical interval extends over 20 m from the upper *Entogonites nasutus* to the *Goniatites crenistria* Zone, i.e. by definition: across the *Pericyclus*/*Goniatites* (cu II/cu III) boundary. It contains the typical goniatites at reasonable frequencies (Nicolaus, 1963).

The boundary between the *Pericyclus*- and *Goniatites*-Stufen in the sense of Korn (1996) is drawn at the base of the “grimmeri-Bank” just above the

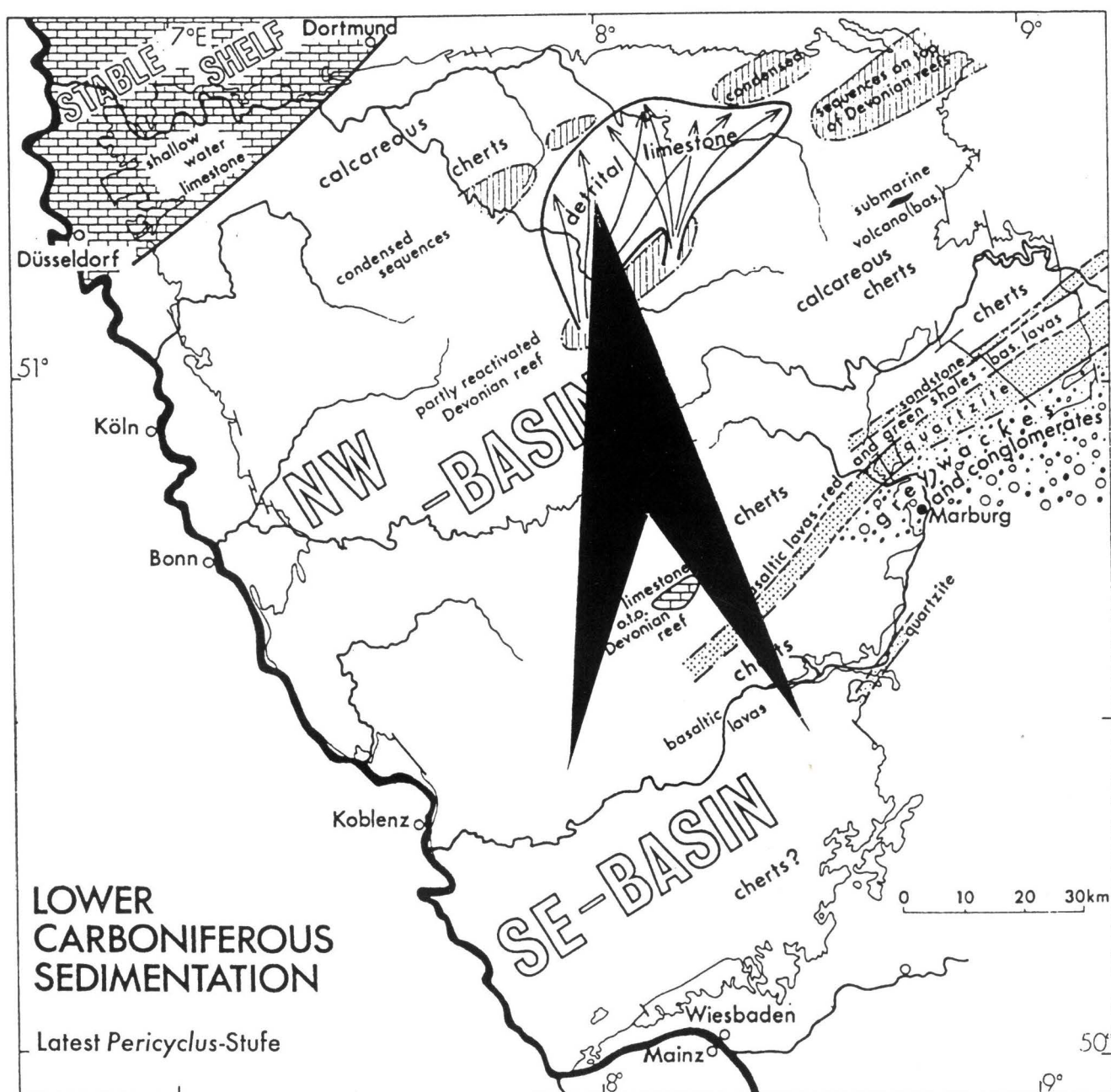


Text-fig. 1 - Geological sketchmap of Rheinisches Schiefergebirge east of the river Rhein, locality Ober-Röhre indicated by arrow. (From Meischner, 1971, fig. 3, modified).

limestone bed of conodont sample No. 8. *E. grimmeri* occurs frequently together with *Goniatites hudsoni* in this bed. Single specimens of *E. grimmeri* are found lower down in the sequence, the lowest ones ca. 4 m lower or halfway between conodont sample Nos. 11 and 12, where they mark the base of the *E. grimmeri* Zone. The uppermost *E. nasutus* was found in this outcrop by Helmkamp (1969, Taf. 1) 7 m below the

"grimmeri-Bank", i.e.: 3 m below the base of the *E. grimmeri* Zone or between conodont samples 12 and 13.

As an old quarry wall in a now protected water supply area, the section is still accessible, and may even be resampled, with the permission of the owners, Stadtwerke Sundern, Schwemker Ring 1, 59846 Sundern, Sauerland.



Text-fig. 2 - Sedimentation in the upper *Pericyclus*-Stufe (upper cu II) in Rheinisches Schiefergebirge east of the river Rhein, locality Ober-Röhre indicated by arrow. (From Meischner, 1971, fig. 6, modified).

CONODONTS

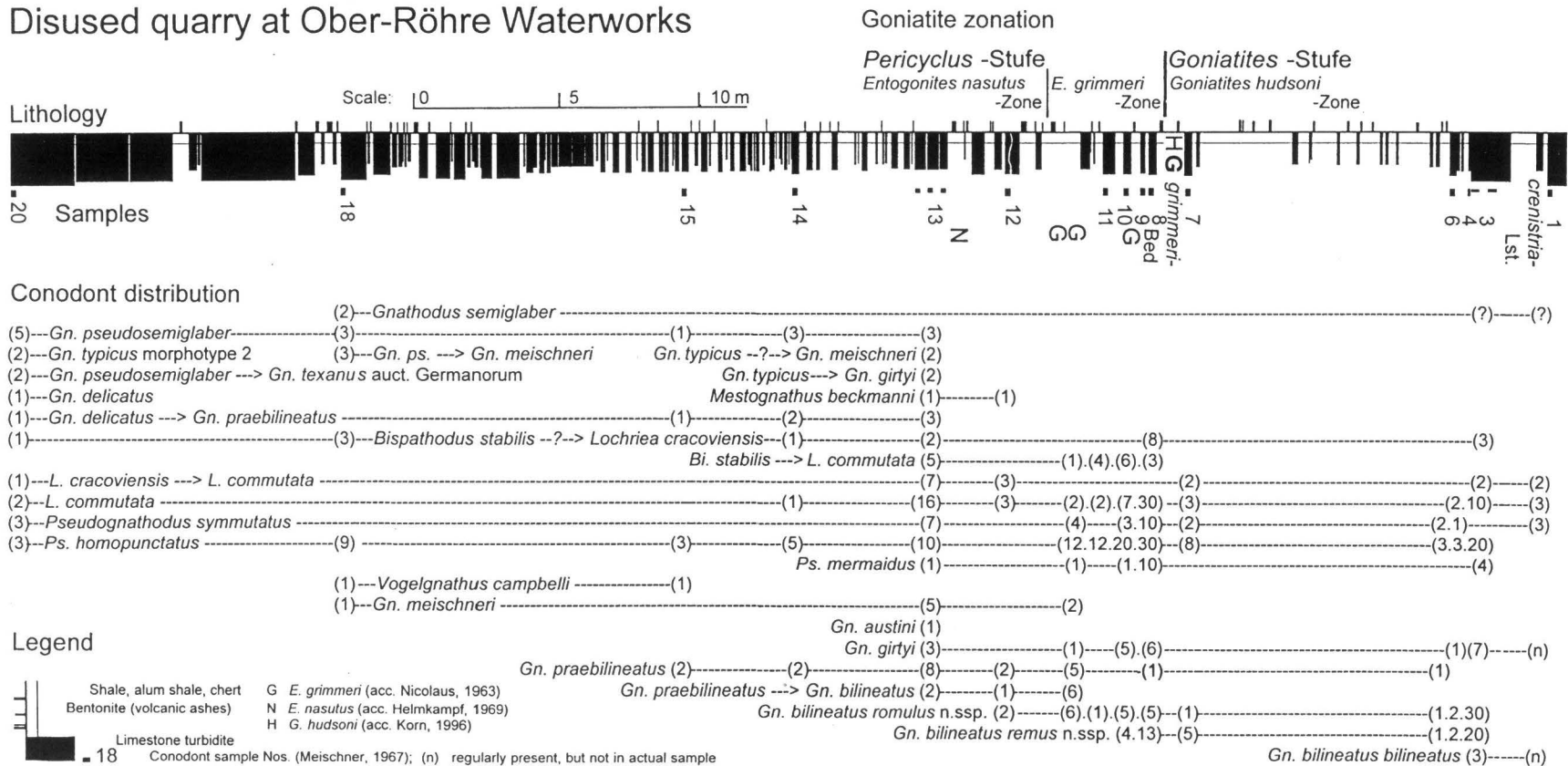
The nature of the host-rocks suggests that all the conodonts are reworked and incorporated in turbidity currents that travelled from intra-basinal carbonate shoals to deep bottoms. Older conodont species that were already extinct at the time of the final deposition of their elements may therefore be admixed with the coeval faunas. This is obvious in the case of Upper

Devonian or Tournaisian species, but may go unnoticed with younger, Viséan taxa. A certain control is available by the occurrence of characteristic species of the underlying *Siphonodella*- and *Scaliognathus anchoralis* zones. Such reworked elements are rare throughout the sequence.

Species of different contemporaneous, neritic and pelagic facies may still occur mixed in the turbidites. However, shallow water species are rare in the samples

Text-fig. 3 - Distribution chart of conodonts from the section of Ober-Röhre. Section after surveys by Helmkauf (1969, cu II) and Nicolaus (1963, cu III), modified. Lithology simplified to enhance limestone turbidite beds. The youngest sample (No. 1) from the very coarse base of a thicker turbidite is atypical. Regularly conodonts are frequent at this level, especially so *Gn. bilineatus* and *Gn. girtyi*.

Rheinisches Schiefergebirge, Germany Disused quarry at Ober-Röhre Waterworks



from isolated limestones on top of the shoals. Thus the turbidites should regularly contain pelagic conodont faunas at their actual evolutionary level admixed with a few shallow-water and slightly older elements.

All suitable limestone beds were sampled and yielded reasonable conodont faunas. 326 specimens of platform conodonts of the genera *Gnathodus*, *Pseudognathodus* and *Lochriea*, and a number of ramiform elements were recovered from 20 samples, 1.5 kg each. Most abundant are *Pseudognathodus homopunctatus*, *Lochriea commutata*, *Gnathodus bilineatus* and *Ps. symmutatus*. In the lower part of the section *Gn. pseudosemiglaber* and forms transitional between *Gn. delicatus* and *Gn. praebilineatus* occur. A few older species of *Gnathodus* were found in the lowermost sample, some of them likely to be reworked. The middle and upper parts of the section contain a number of *Gn. praebilineatus* and *Gn. bilineatus* as well as forms transitional between them.

In this section we recognise not only the lineage *Gn. praebilineatus* — *Gn. bilineatus*, but also transitional forms and relationships between other species of *Gnathodus* such as the *Gn. girtyi* group, and also between the genera *Bispathodus* and *Lochriea* (Text-fig. 3).

Gnathodus girtyi is represented by the earliest species of this group, *Gn. meischneri* and a single specimen of *Gn. austini* in the lower part of the section, and higher up by *Gn. girtyi* proper (aff. *Gn. girtyi girtyi*). The latter appears slightly earlier than *Gn. bilineatus*. The specimen assigned to *Gn. austini* has two very short and poorly developed parapets, the inner one very prominent anteriorly, and a much expanded, posteriorly high carina. In *Gn. meischneri* two parapets are developed, though unequally, and the carina is simple or just a little expanded. In contrast, *Gn. girtyi* has two well developed, long parapets and a simple carina.

The genus *Pseudognathodus* includes here all of its known three species: *Ps. symmutatus*, *Ps. homopunctatus* and *Ps. mermaidus* the latter appearing slightly later than the first two species. *Ps. homopunctatus* is most abundant (Text-fig. 3).

Lochriea is represented by *L. commutata* which is common throughout the sequence. There are also specimens with rather thick carinae which resemble *L. cracoviensis*. However, the author of that species, Belka (1985), did not confirm our provisional identification (personal communication, 1996, 1997).

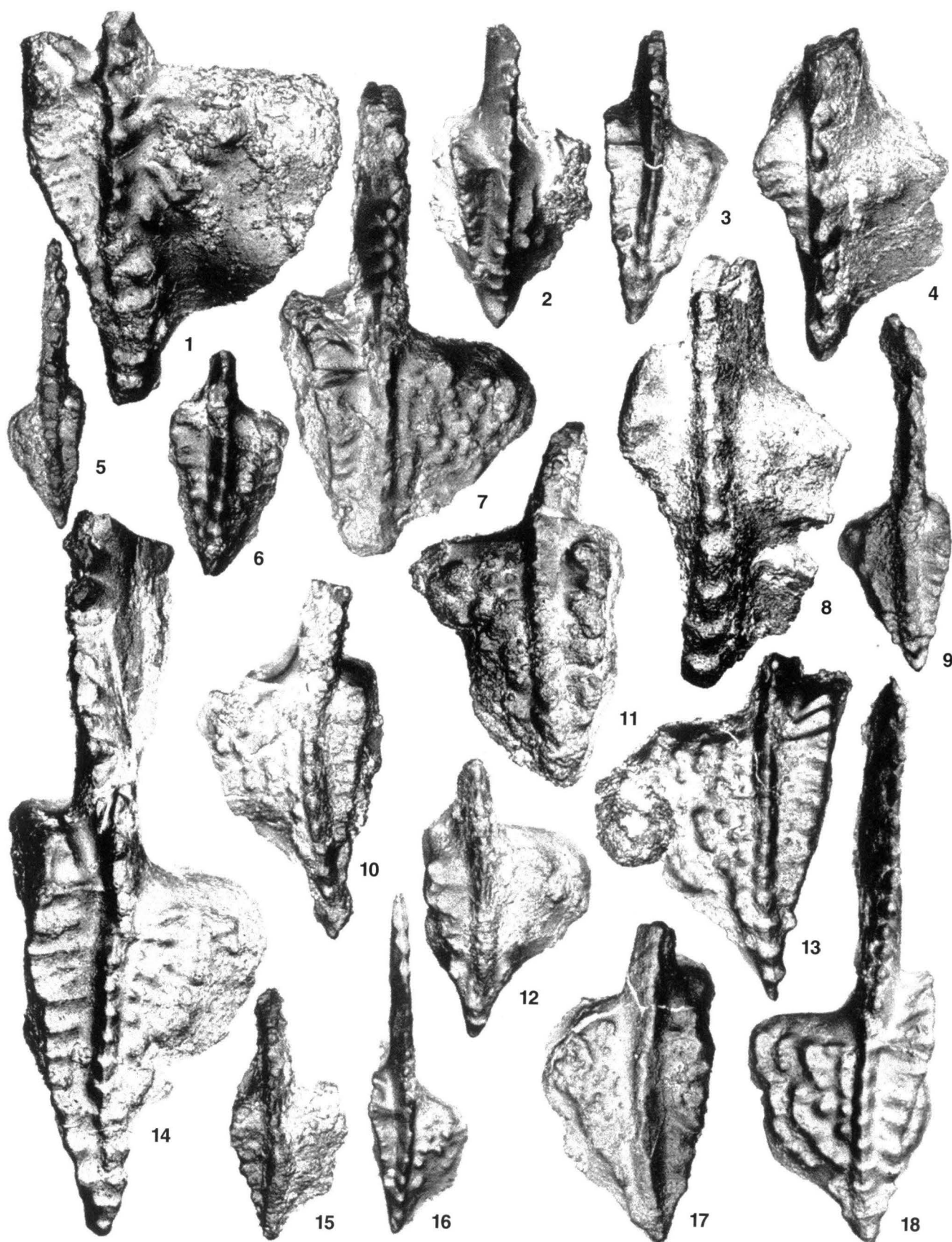
There are some forms with features transitional between *Bispathodus stabilis* and *L. commutata*. They are very similar orally to the *Lochriea* species, but the basal cavity is not yet posteriorly located as it should be in *Lochriea*. They resemble *Bi. stabilis* Morphotype 2 of Ziegler, Sandberg & Austin (1974, p. 104, pl. 3, fig. 2 and pl. 3, fig. 1). The upper limit of the range of *Bi. stabilis* was shown by Lane, Sandberg & Ziegler (1980) as high as mid-Texas Zone. *Bi. stabilis* Morphotype 2 and also Morphotype 1 by illustration (Pl. 3, fig. 1) have an expanded, posteriorly shifted basal cavity. Otherwise, their forms are orally more close to *Bi. stabilis* than ours which bear some progressive features, for example: the almost rectangular lateral profile and a more convex cup, both characteristic of *Lochriea*. Only the basal cavity is not located at the posterior end of the element. As the position of the basal cavity is an essential generic feature, and *Lochriea* probably derives from *Bispathodus stabilis*, we are most likely dealing with forms transitional between the latest *Bispathodus* and the earliest *Lochriea*. Such forms were registered already in the lower Viséan deposits of the Bechar Basin, Sahara, and in the Pyrénées, France, by M.-F. Perret and the second author of this paper and will be described jointly with Marcel Weyant (in preparation). In the distribution chart we separated the transitional forms between *Bi. stabilis* and *L. commutata* with a narrow carina, and the forms transitional between *Bi. stabilis* and *Lochriea*, with a wider carina (*L. cracoviensis*?).

Sufficient numbers of *Gn. praebilineatus* and *Gn. bilineatus* as well as transitional forms allow to distinguish these species according to the development of the parapet, its length, width and height, the character of the carina, characteristics of the outer platform, depth and width of the groove between the parapet and carina, and the character of the posterior

EXPLANATION OF PLATE 1

All illustrated specimens are housed in Institut und Museum für Geologie und Paläontologie, Göttingen, Germany. Only Pa elements are illustrated. Magnification: x80.

- Fig. 1 - *Gnathodus* aff. *pseudosemiglaber* Thompson & Fellows. Sample No. 13.
 Figs. 2-3, 5, 7, 9-10, 14, 17 - *Gnathodus praebilineatus* Belka.
 2, 5) Sample No. 15; 3, 10, 14, 17) Sample No. 13; 7, 9) Sample No. 14.
 Figs. 4, 8 - *Gnathodus pseudosemiglaber* Thompson & Fellows. Sample No. 13.
 Figs. 6, 11-12, 15 - *Gnathodus delicatus* Branson & Mehl transitional to *Gnathodus praebilineatus* Belka.
 6) Sample No. 15; 11) Sample No. 13; 12, 15) Sample No. 14.
 Figs. 13, 16, 18 - *Gnathodus praebilineatus* Belka transitional to *Gnathodus bilineatus* (Roundy).
 13, 18) Sample No. 13; 16) Sample No. 11.



tip of the element. The specimens of *Gn. praebilineatus* from Ober Röhre correspond to those described by Belka (1985). They have a long, rather narrow, not well developed parapet, a shallow groove between the parapet and a long, simple, posteriorly positioned carina.

Meischner (1970, fig. 2) listed these forms partly as *Gn. delicatus* which, according to Belka (1985), is an older, Tournaisian, homeomorph of *Gn. praebilineatus*, partly as *Gn. cf. cuneiformis*. The newly described subspecies of *Gn. bilineatus* he regarded as transitional between these species and *Gn. bilineatus*.

There are also specimens which resemble forms from the Cima di Plotta Formation of the Carnic Alps (Schoenlaub & Kreutzer, 1993) and from the Viséan sections of Slovenia and Serbia (Stojanovich-Kuzenko, 1996), and the specimen illustrated by Weyer (1972, Abb. 13) from the *E. nasutus* Zone of Germany.

The relation of *Gn. delicatus* and *Gn. praebilineatus* remains uncertain. In the *E. nasutus* Zone there occur a few specimens transitional between the two species together with the characteristic forms of *Gn. praebilineatus*. However, there remains a gap of 20 m in section between the last true *Gn. delicatus* and the first true *Gn. praebilineatus*. A relatively rich fauna (No. 18) in this gap has neither of the species.

Gnathodus bilineatus includes a number of variations. Some of them are characterised by a very broad triangular platform with a highly asymmetrical anterior margin, a high and wide, well developed parapet, coarse ornamentation of the outer platform, and very long and strong, expanded parapet which extends posteriorly beyond the posterior margin of cup. Others are more symmetrical with a well developed, wide parapet, gently rounded outer platform and poor ornamentation on the outer platform. Still other forms correspond to a more common conception of the subspecies *Gn. bilineatus bilineatus*, with an almost rectangular outer platform with subconcentrically arranged rows of nodes, a well developed, moderately wide parapet, a shallow groove between the parapet

and the carina which is expanded posteriorly to some degree, and a row of small denticles on the outer side of the posterior part of the carina, parallel to the latter. The shape of the parapet of the earliest asymmetrical *Gn. bilineatus* forms resembles to some extent the parapet shape of the latest *Gn. bilineatus* from the Serpukhovian of South Tien Shan (Nigmadganov & Nemirovskaya, 1992) and the Pyrenees (Buchroitter, 1979; Perret, 1993). Descriptions of *Gn. praebilineatus* and two new subspecies of *Gn. bilineatus* are given below.

The new forms are introduced as formal subspecies. There is not much sense in Open Nomenclature in a case like this when two clearly identifiable, equally frequent forms are represented among about 100 specimens.

SYSTEMATIC PALAEONTOLOGY

Genus GNATHODUS Pander, 1856

Type species – *Polygnathus bilineatus* Roundy, 1926 (Tubbs, 1986).

GNATHODUS BILINEATUS BILINEATUS (Roundy, 1926) Pl. 3, fig. 18

The type subspecies is well known and easily identified (see Krumhardt *et al.*, 1996, for synonymy).

GNATHODUS BILINEATUS REMUS n.ssp. Pl. 3, figs. 13-14, 17, 19

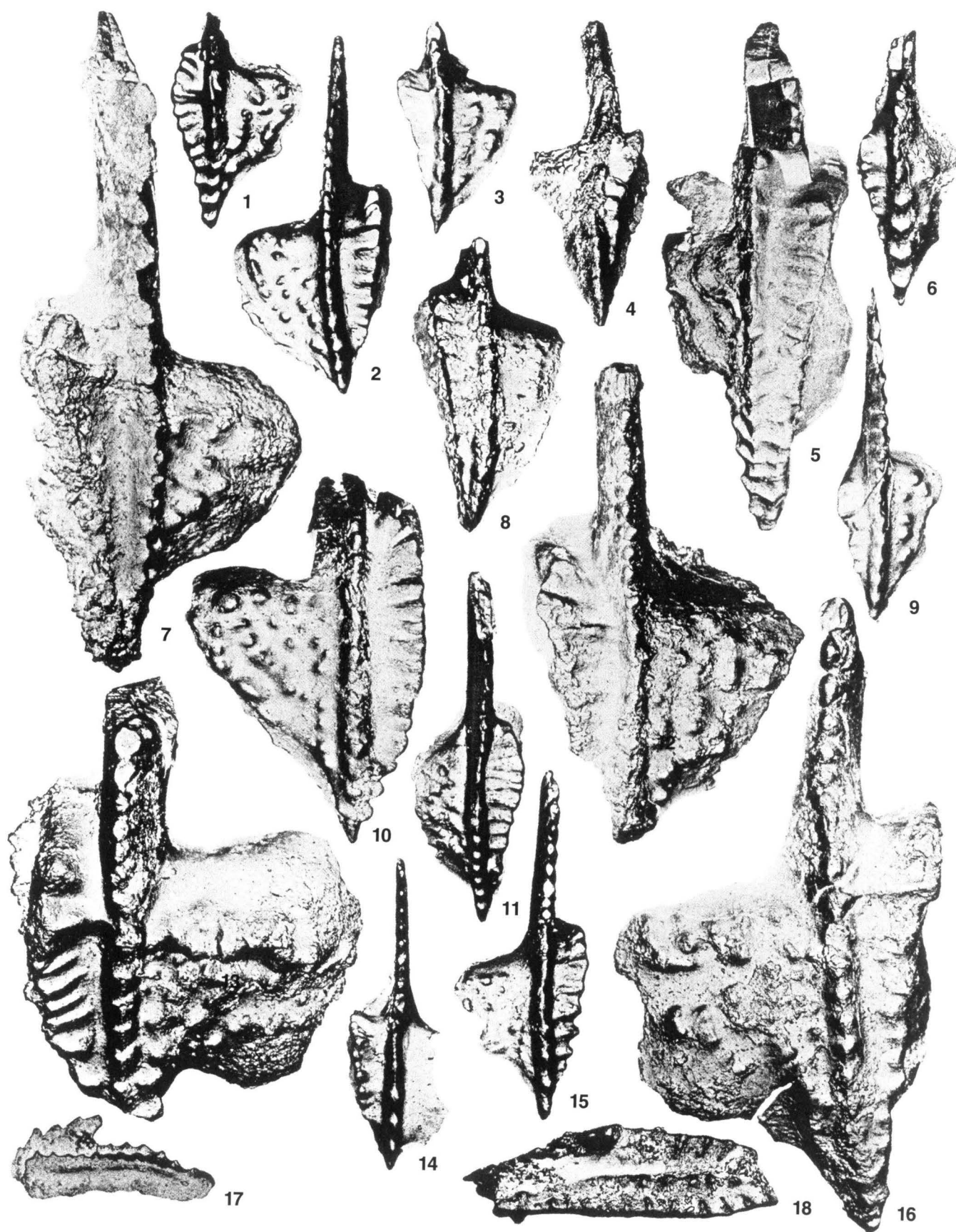
Holotype – Pl. 3, fig. 14.

Locus typicus – Abandoned quarry at Ober-Röhre waterworks, town of Sundern, district of Arnsberg, Westphalia, Sample No. 8, *Pericyclus*-Stufe (cu II),

EXPLANATION OF PLATE 2

All illustrated specimens are housed in Institut und Museum für Geologie und Paläontologie, Göttingen, Germany. Only Pa elements are illustrated. Magnification: x80.

- | | |
|-----------------------|---|
| Figs. 1-3 | - <i>Gnathodus praebilineatus</i> Belka transitional to <i>Gnathodus bilineatus</i> (Roundy). Sample No. 11. |
| Fig. 4 | - <i>Gnathodus austini</i> Belka. Sample No. 13. |
| Figs. 5, 7, 10-13, 16 | - <i>Gnathodus praebilineatus</i> Belka. |
| | 5, 11) Sample No. 11; 10) Sample No. 8; 7, 12, 13, 16) Sample No. 13. |
| Fig. 6 | - <i>Gnathodus pseudosemiglaber</i> Thompson & Fellows. Sample No. 13. |
| Fig. 8 | - <i>Gnathodus aff. subbilineatus</i> Lane, Sandberg & Ziegler. Sample No. 3. |
| Fig. 9 | - <i>Gnathodus delicatus</i> Branson & Mehl transitional to <i>Gnathodus praebilineatus</i> Belka. Sample No. 20. |
| Fig. 14 | - <i>Gnathodus praebilineatus</i> Belka transitional to <i>Gnathodus bilineatus romulus</i> n.ssp. Sample No. 11. |
| Fig. 15 | - <i>Gnathodus praebilineatus</i> Belka transitional to <i>Gnathodus bilineatus remus</i> n.ssp. Sample No. 11. |
| Figs. 17-18 | - <i>Mestognathus beckmanni</i> Bischoff. |
| | 17) Sample No. 12; 18) Sample No. 13. |



uppermost *Entogonites grimmeri*-Zone, 0.5 m below *E. grimmeri*-Bed.

Derivatio nominis – After Remus, legendary co-founder of Rome, twin brother of Romulus.

Material – 45 specimens.

Description – Pa element with very wide, triangular, asymmetrical platform. The well developed parapet extends anteriorly far beyond the anterior margin of the platform, which is therefore extremely asymmetrical. Parapet high and wide, arched in lateral view, consisting of up to 12-14 transverse ridges, steeply dropping into the wide, deep trough between carina and parapet. Outer margin convex anteriorly and here higher than the carina. The parapet ends posteriorly by merging with the carina.

Outer platform wing-shaped, triangular, very wide in its most anterior part, anterior margin oblique, posterior one rounded, moderately convex and covered by discrete, medium-sized nodes arranged parallel to the lateral-posterior margin of the platform, i.e. at an angle of 45-80° to the carina. Gerontic specimens show almost subconcentric rows of nodes.

Carina well developed, long, extending posteriorly beyond the platform and consisting of fused denticles or nodes which are coarser posteriorly.

Juveniles show almost all the features characteristic of this subspecies: strong asymmetry, triangular shape of the platform, long expanded carina and nodose ornamentation on the outer platform.

Remarks – *Gn. bilineatus remus* differs from the other known taxa of *Gn. bilineatus* by its triangular shape, the highly asymmetrical anterior margin, and the long, expanded carina, which extends far beyond the posterior end of the platform. The platform is considerably more strongly ornamented than in *Gn. bilineatus romulus*.

Occurrence – Samples 3, 4, 6, 7, 8, 9, *Entogonites grimmeri*- into *Goniatites crenistria*-Zones.

GNATHODUS BILINEATUS ROMULUS n.ssp.
Pl. 3, figs. 1-12, 15-16

Holotype – Pl. 3, fig. 15.

Locus typicus – Abandoned quarry at Ober-Röhre waterworks, town of Sundern, district of Arnsberg, Westphalia, Sample No. 8. *Pericyclus*-Stufe (cu II), *Entogonites grimmeri*-Zone, 0.5 m below *E. grimmeri*-Bed.

Derivatio nominis – After Romulus, legendary founder of Rome, twin brother of Remus.

Material – 52 specimens.

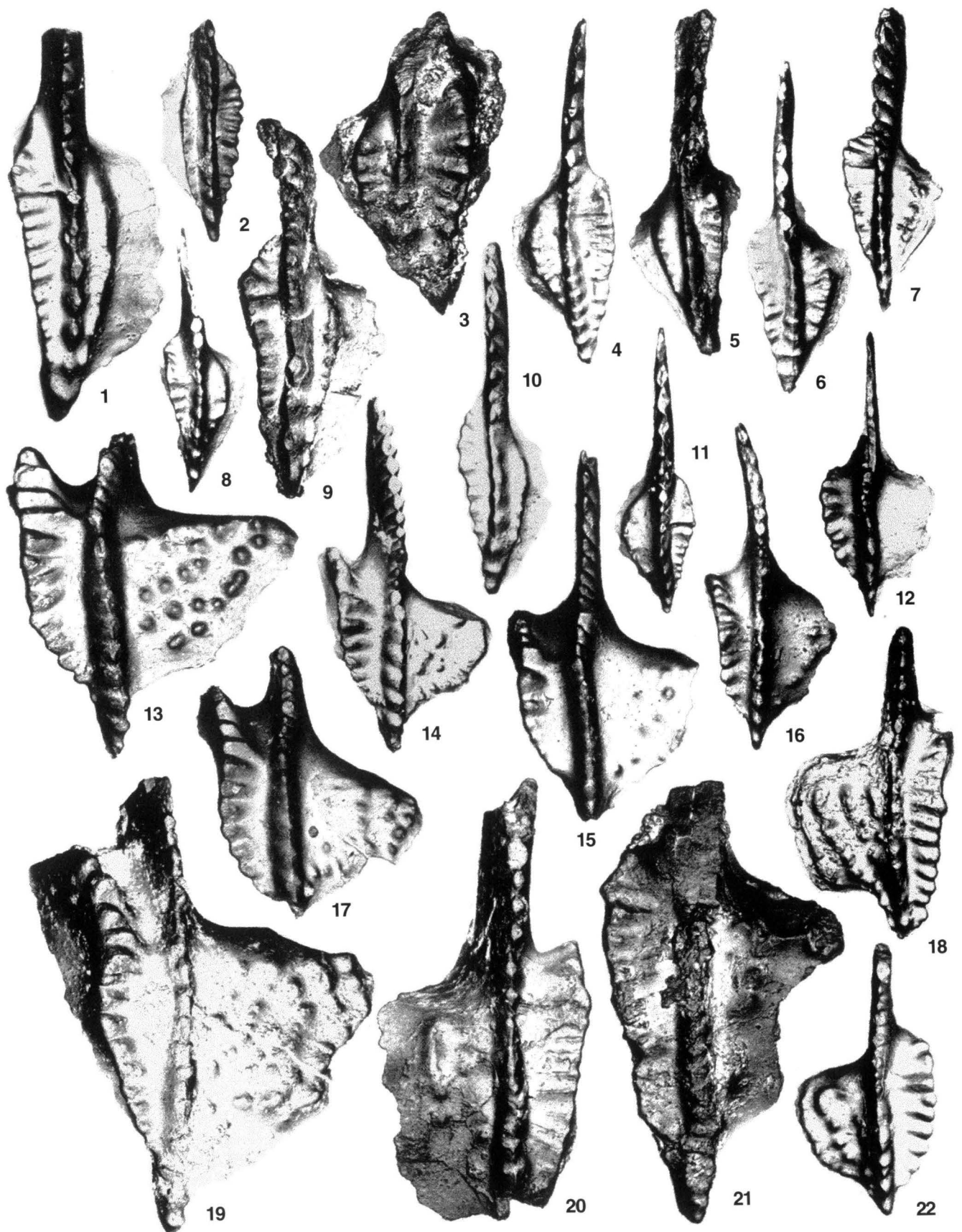
Description – Pa element with moderately wide, asymmetrical platform, inner parapet well developed, long, rather wide and high, consisting of transverse ridges, ending before the posterior tip of the element by merging with the carina close to its posterior end. Long, posteriorly slightly expanded carina, extending little beyond the posterior margin of the platform. Groove between parapet and carina moderately wide and deep. The third anterior transverse ridge of the parapet usually crosses the groove and reaches the carina. This feature is present on all morphotypes of *Gn. bilineatus*, *Gn. praebilineatus* and *Gn. girtyi* from the type section. Outer platform wide and rounded, mostly flat or slightly convex, rarely subquadrate to semirounded, ornamented with one or two rows of nodes paralleling the outer margin. In juvenile specimens the nodes are scattered randomly and occupy preferentially the marginal part of the outer platform. There are also juveniles with a smooth and flat outer platform, but the parapet is always well developed.

Remarks – This subspecies differs from *Gn. bilineatus bilineatus* by its semirounded, poorly ornamented outer platform, the narrow carina, the wide and high parapet, and the deep, wide trough between parapet and carina. It differs from *Gn. bilineatus remus* n.ssp. by the less asymmetrical shape, a more slender carina, which does

EXPLANATION OF PLATE 3

All illustrated specimens are housed in Institut und Museum für Geologie und Paläontologie, Göttingen, Germany. Only Pa elements are illustrated. Magnification: x80 (except Fig. 18).

- Figs. 1-2, 9-10 – *Gnathodus girtyi* Hass.
1, 2) Sample No. 8; 9) Sample No. 13; 10) Sample No. 11.
- Fig. 3 – *Gnathodus* cf. *meischneri* Austin & Husri. Sample No. 13.
- Figs. 4-8 – *Gnathodus meischneri* Austin & Husri. Sample No. 13.
- Figs. 11-12, 15-16 – *Gnathodus bilineatus romulus* n.ssp.
11, 12, 16) Sample No. 11; 15) Holotype, sample No. 8.
- Figs. 13-14, 17, 19 – *Gnathodus bilineatus remus* n.ssp. Sample No. 8; Fig. 14 = Holotype.
- Fig. 18 – *Gnathodus bilineatus bilineatus* (Roundy). Sample No. 3, x 70.
- Figs. 20-21 – *Gnathodus praebilineatus* Belka. Sample No. 12.
- Fig. 22 – *Gnathodus bilineatus romulus* n.ssp. transitional to *Gnathodus bilineatus bilineatus* (Roundy). Sample No. 4.



not extend posteriorly much beyond the platform, and by the poorly ornamented outer platform.

Occurrence – Samples 3, 4, 6, 7, 8, 9, 10, 11, 12, uppermost *E. nasutus*- into *Go. crenistria*-Zones.

GNATHODUS PRAEBILINEATUS Belka 1985

Pl. 1, figs 2-3, 5, 7, 9-10, 14, 17; Pl. 2, figs 5, 7, 11, 16; Pl. 3, figs. 20-21

- 1985 *Gnathodus praebilineatus* - BELKA, p. 39, pl. 7, figs. 4-8.
 1993 *Gnathodus bilineatus* Belka - SCHÖNLAUB & KREUTZER, pl. 6, figs. 12-14.
 1993 *Gnathodus praebilineatus* Belka - PERRET, p. 327, pl. CX, figs. 4-6, 10, 13.
 1994 *Gnathodus praebilineatus* Belka - BELKA & KORN, , pl. 2, fig. 12 (only).
 1998 *Gnathodus praebilineatus* Belka - BELKA & LEHMANN, pl. 2, figs. 4,5 (only).
 1998 *Gnathodus praebilineatus* Belka - PERRI & SPALLETTA, pl. 2, fig. 8 (only).

Remarks – It has become common practice to refer to *Gn. praebilineatus* specimens which do not fit well the description and first illustrations of *Gn. praebilineatus* by Belka (1985) just because they occur below the entry of *Gn. bilineatus* proper, are similar to *bilineatus*, but still have no well developed parapet and a very shallow and narrow groove between parapet and carina. Some of these forms have a short parapet and an expanded carina which distinguishes them from *Gn. praebilineatus*. All of our specimens have a broad triangular platform with a long though not well developed parapet, formed mostly by transverse ridges which are better developed anteriorly. The third ridge usually crosses the shallow groove between parapet and carina and joins the carina. The parapet reaches the posterior end of the element. Here it consists, instead of ridges, of a row of nodes that can be fused to the posterior tip of the carina. The carina is simple and

long. The platform is ornamented by randomly spaced, irregularly scattered nodes. In some specimens they can be arranged in rows, the innermost ones parallel to the carina, the others longitudinal or following the shape of the cup.

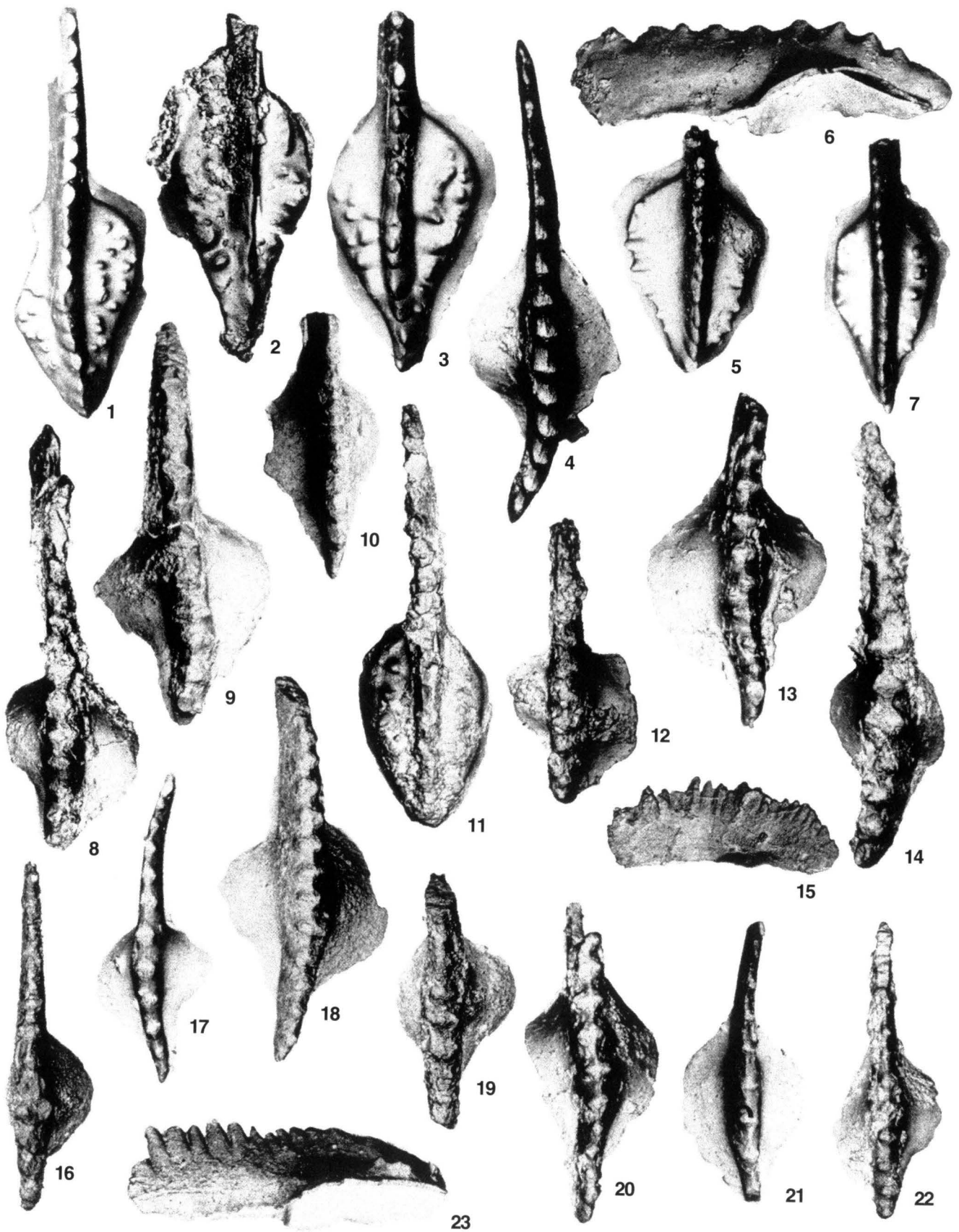
The main differences between *Gn. praebilineatus* and the first *Gn. bilineatus* in Ober Röhre are as follows: (1) in *Gn. praebilineatus* the inner parapet is not completely developed, it is longer and narrower than in *Gn. bilineatus*, its transverse ridges are irregular, and the posterior ones can be replaced by nodes; (2) the carina is simple in *Gn. praebilineatus* whereas in *Gn. bilineatus* it is expanded posteriorly to various degrees, and extends posteriorly beyond the platform; (3) the groove between the parapet and carina is narrower and shallower in *Gn. praebilineatus*; (4) the outer platform is ornamented by subconcentric rows of nodes in *Gn. bilineatus* whereas in *Gn. praebilineatus* the nodes are irregularly arranged and randomly spaced. There occur a number of transitional forms between *Gn. praebilineatus* and *Gn. bilineatus* (Pl. 1, figs. 13, 16, 18; Pl. 2, Figs. 11, 3), and also forms transitional between *Gn. delicatus* and *Gn. praebilineatus* (Pl. 1, Figs. 6, 11-12, 15, Pl. 2, fig. 9), but no transitionals between *Gn. semiglaber* and *Gn. praebilineatus*. One of our specimens (Pl. 1, fig. 14) resembles the one of Weyer (1972, Abb. 13) from the *E. nasutus* Zone, but none of them the specimens of Voges (1959).

We did not include in the synonymy *Gn. sp. A* of Ebner (1977, p. 471, pl. 2, figs. 5, 7-10, 13) because these specimens have a very short parapet ("ein kurzes und niedriges Parapet"). We also did not include in the synonymy the specimen illustrated by Spalletta & Perri (1998, pl. 3.1.1, fig. 3) from the Dolina section, Carnic Alps which is closer to *Gn. semiglaber* in our opinion as it possesses a short, rounded parapet and an expanded carina. Likewise, we did not include the specimens illustrated as *Gn. praebilineatus* by Schönlaub & Kreutzer (1993, pl. 6, figs. 7-11), as they have short,

EXPLANATION OF PLATE 4

All illustrated specimens are housed in Institut und Museum für Geologie und Paläontologie, Göttingen, Germany. Only Pa elements are illustrated. Magnification: x80.

- Figs. 1-3 - *Pseudognathodus mermaidus* Austin & Husri.
 1, 3) Sample No. 8; 2) Sample No. 13.
 Fig. 4 - *Bispathodus stabilis* (Branson & Mehl) transitional to *Lochriea commutata* (Branson & Mehl). Sample No. 11.
 Figs. 5, 7, 11, 23 - *Pseudognathodus homopunctatus* Ziegler.
 5) Sample No. 11; 7) Sample No. 9; 11) Sample No. 15; 23) lateral view, Sample No. 9.
 Fig. 6 - *Pseudopolygnathus symmutatus* (Rhodes, Austin & Druce), lateral view. Sample No. 8.
 Figs. 8-9, 12 - *Lochriea cracoviensis* Belka transitional to *L. commutata* (Branson & Mehl).
 8, 9) Sample No. 13; 12) Sample No. 12.
 Figs. 10, 18 - *Bispathodus stabilis* (Branson & Mehl).
 10) Sample No. 13; 18) Sample No. 11.
 Figs. 14, 16, 19 - *Bispathodus stabilis* transitional to *Lochriea cracoviensis* Belka. Sample No. 18.
 Fig. 15 - *Vogelgnathus campbelli* (Rexroad). Sample No. 18.
 Figs. 17, 20-22 - *Lochriea commutata* (Branson & Mehl).
 17, 21) Sample No. 11; 20) Sample No. 13; 22) Sample No. 14.



round *semiglaber*-type parapets and a thick and posteriorly much expanded carina. We include, however, in *praebilineatus* their early representatives of *Gn. bilineatus*. The specimens of von Bitter & Plint-Geberl (1982, pl. 6, figs. 9-11) from Canada look very similar to *Gn. praebilineatus*, whereas forms illustrated by Austin & Husri (1974, pl. 3, figs. 4-5), which Belka regarded as *Gn. praebilineatus*, in our opinion look more similar to true *Gn. bilineatus*. This demonstrates the wide range in the understanding of *Gn. praebilineatus* which is partly due to the reasons mentioned above. Belka himself in his last papers (Belka & Korn, 1994; Belka & Lehmann, 1998) demonstrated that his conception of *Gn. praebilineatus* is wider now than it has been in his original description of the species (Belka, 1985).

Range – From the base of the *Gn. austini*-Zone into the lower part of the *Gn. bilineatus*-Zone (Belka, 1985). Lower part of upper Visean of Spain, lower part of the Alba Formation (Belka & Korn, 1994, Belka & Lehmann, 1998). Early Upper Visean of England (Asbian; it enters before *E. grimmeri* and extends into the *Goniaticites globostriatus*-Zone, Riley, personal communication, March, 1997). Lower Visean of the Carnic Alps (Italy, section Dolina, Spalletta & Perri, 1998. Austria, Cima di Plotta fm, Schoenlaub & Kreutzer, 1993). Lower Visean of Middle Asia, Middle Tien Shan (Nigmatganov, personal communication, March, 1997).

Occurrences in the studied section – Sample Nos. 6, 11, 12, 13, 14, 15, *Pericyclus*-Stufe (cu II), *Entogonites nasutus*- to *E. grimmeri* Zone, and a single specimen in sample No. 6, *Goniaticites crenistria*-Zone (reworked?).

CONCLUSIONS

The first appearance of *Gnathodus bilineatus romulus* n.ssp. is recorded in conodont sample No. 12 a little below the first occurrence of *Entogonites grimmeri* in the section, which, by definition, means: within the uppermost *Entogonites nasutus*-Zone, *Pericyclus*-Stufe, of the German goniatite zonation.

The present study explains the statements of Voges (1959, 1960) and Weyer (1972) about the first appearance of *Gn. bilineatus* in the *E. nasutus*-Zone since their illustrated specimens are evolutionary older than *Gn. bilineatus bilineatus*.

Gn. praebilineatus may be considered the immediate ancestor of *Gn. bilineatus*. Forms transitional between the two species occur in the uppermost *Pericyclus*-Stufe, but not higher in the section. The relation of *Gn. delicatus* and *Gn. praebilineatus* remains unsolved in the studied section. Transitional forms occur together with *Gn. praebilineatus*. However, these are not very frequent, and the last and only true *Gn. delicatus* was

found in the lowermost sample of the section thus still allowing for a time gap between the two species. No forms transitional between *Gn. semiglaber* and *Gn. praebilineatus* (like in the Carnic Alps and Cantabrian Mountains) or between *Gn. pseudosemiglaber* and *Gn. praebilineatus* were found in the Ober Röhre section.

We recommend that the lower boundary of the *Gnathodus bilineatus*-Zone should be set at the first appearance of *Gnathodus bilineatus romulus* in the uppermost *E. nasutus*-Zone, close to the beginning of the *E. grimmeri*-Zone.

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Dr. Zdzislaw Belka commented on some questionable specimens of his species *Gn. praebilineatus* and contributed useful discussions. Dr. Dieter Korn, Dr. Nick Riley and Dr. Dieter Weyer supplied important detail concerning the ammonoid zonation. Dieter Korn was especially helpful with information on the section at Ober-Röhre. Dr. George Sevastopulo vetted the MS linguistically. Our sincere thanks are due to all of them. The Stadtwerke Sundern, Herr Wortmann, are thanked for their kind co-operation.

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APPENDIX

LIST OF CONODONT NAMES

Genus *Bispathodus* Müller, 1962

- Bispathodus stabilis* (Branson & Mehl, 1934)
- Bispathodus stabilis* Morphotypes 1, 2 Lane, Sandberg & Austin, 1974

Genus *Gnathodus* Pander, 1856

- Gnathodus austini* Belka, 1985
- Gnathodus bilineatus bilineatus* (Roundy, 1226)
- Gnathodus bilineatus bollandensis* Higgins & Bouckaert, 1968
- Gnathodus bilineatus remus* n.ssp.
- Gnathodus bilineatus romulus* n.ssp.
- Gnathodus cuneiformis* Mehl & Thomas, 1947
- Gnathodus delicatus* Branson & Mehl, 1938
- Gnathodus girtyi* Hass, 1959
- Gnathodus meischneri* Austin & Husri, 1974
- Gnathodus mermaidus* Austin & Husri, 1974
- Gnathodus postbilineatus* Nigmatganov & Nemirowskaya, 1992
- Gnathodus praebilineatus* Belka, 1985
- Gnathodus pseudosemiglaber* Thompson & Fellows, 1970
- Gnathodus semiglaber* Bischoff, 1957
- Gnathodus subbilineatus* Lane, Sandberg & Ziegler, 1980
- Gnathodus texanus* auct. Germanorum Meischner, 1970
- Gnathodus typicus* Cooper, 1939
- Gnathodus* sp. A Ebner, 1977

Genus *Lochriea* Scott, 1942

- Lochriea commutata* (Branson & Mehl, 1941)
- Lochriea cracoviensis* Belka, 1985

Genus *Mestognathus* Bischoff, 1957

- Mestognathus beckmanni* Bischoff, 1957

Genus *Pseudognathodus* Soo-in-Park, 1983

- Pseudognathodus homopunctatus* (Ziegler, 1960)

Pseudognathodus symmutatus (Rhodes, Austin & Druce, 1969)
Pseudognathodus mermaidus (Austin & Husri, 1974)

Genus *Scaliognathus* Branson & Mehl, 1941
Scaliognathus anchoralis Branson & Mehl, 1941

Genus *Vogelgnathus* Norby & Rexroad, 1985
Vogelgnathus campbelli (Rexroad, 1957)

LIST OF GONIATITES

Genus *Entogonites* Kittl, 1904
Entogonites grimmeri Kittl, 1904
Entogonites nasutus (Schmidt, 1941)

Genus *Goniatites* de Haan, 1825
Goniatites crenistria crenistria Phillips, 1836
Goniatites crenistria schmidtianus Nicolaus, 1963
Goniatites globostriatus (Schmidt, 1925)
Goniatites hudsoni Bisat, 1934

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