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by Otto WALLISER † & Pierre BULTYNCK

WALLISER, O. & BULTYNCK, P., 2011 – Extinctions, survival and innovations of conodont species during the Kačák Episode (Eifelian-Givetian) in south-eastern Morocco. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **81**: 5-25, 4 figs, 4 pls, Brussels, November 30, 2011 – ISSN 0374-6291.

Abstract

For the first time the complete conodont fauna from the GSSP for the base of the Givetian at Jebel Mech Irdane in the Tafilalt (SE Morocco) is described. The conodont faunas described by BULTYNCK in 1987 from the Bou Tchrafine ridge in the same area and from the Jebel Ou Driss (Mader, SE Morocco) in 1989 are updated. Many new morphotypes of *Polygnathus linguiformis* and other conodont species are described. *Polygnathus amphora, P. pseudoeiflius* and *Icriodus hollardi* are established as new species.

Keywords: Conodonts, Kačák, Eifelian-Givetian, Morocco.

Résumé

L'entière faune à conodontes trouvée au GSSP pour la base du Givetien et localisée dans le Jebel Mech Irdane du Tafilalt (Sud-Est du Maroc) est décrite pour la première fois. Les identifications des faunes à conodontes du Bou Tchrafine dans la même région décrites par BULTYNCK (1987) ainsi que celles du Jebel Ou Driss dans le Mader (Sud-Est du Maroc) décrite en 1989 sont mises à jour. Des nouveaux morphotypes de *Polygnathus linguiformis* et d'autres espèces de conodontes sont décrits. *Polygnathus amphora, P. pseudoeiflius* et *Icriodus hollardi* sont décrits comme nouvelles espèces.

Mots-clefs: Conodontes, Kačák, Eifelien-Givetien, Maroc.

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† Otto WALLISER passed away late December 2010. The present paper is dedicated to his memory. He was a brilliant geologist-palaeontologist. The last two years we worked together on the conodont faunas described herein.

Introduction

The Global Stratotype Section and Point (GSSP) for the base of the Givetian is located in the Jebel Mech Irdane in the Tafilalt of SE Morocco. The position of the boundary was designated by the Subcommission on Devonian Stratigraphy (SDS) and is based on the first occurrence of the conodont species *Polygnathus hemiansatus* considered to be a direct descendant of *Polygnathus pseudofoliatus*. The boundary level is within the Kačák Episode (WALLISER *et al.*, 1995). Many samples from the Mech Irdane section contain abundant and very diverse conodont faunas, hundreds of specimens per kilogramme. At the time of the discussion of the GSSP for the base of the Givetian the study of the conodont faunas was limited to the evolutionary lineage *P. pseudofoliatus – P. hemiansatus,* as well as *Polygnathus ensensis*, the species considered important for the boundary definition. These species groups were figured in the guide-book for the field meeting of the SDS in the Tafilalt-Mader area in 1991 (WALLISER, *ed.*, 1991).

The conodont faunas are not only rich by the number of specimens but the species also demonstrate a large variability. This allows recognition of different morphotypes in known species or new species that are useful for establishing lineages and for biostratigraphy. The description of these morphotypes and new species is the main purpose of the present paper. The study of the Mech Irdane conodonts is combined with an update of earlier described conodonts from the same time interval in the same region: the Bou Tchrafine section in the N Tafilalt (BULTYNCK, 1987) and the Ou Driss section in the Mader (BULTYNCK, 1989). The position of the three studied sections is shown in Fig. 1.

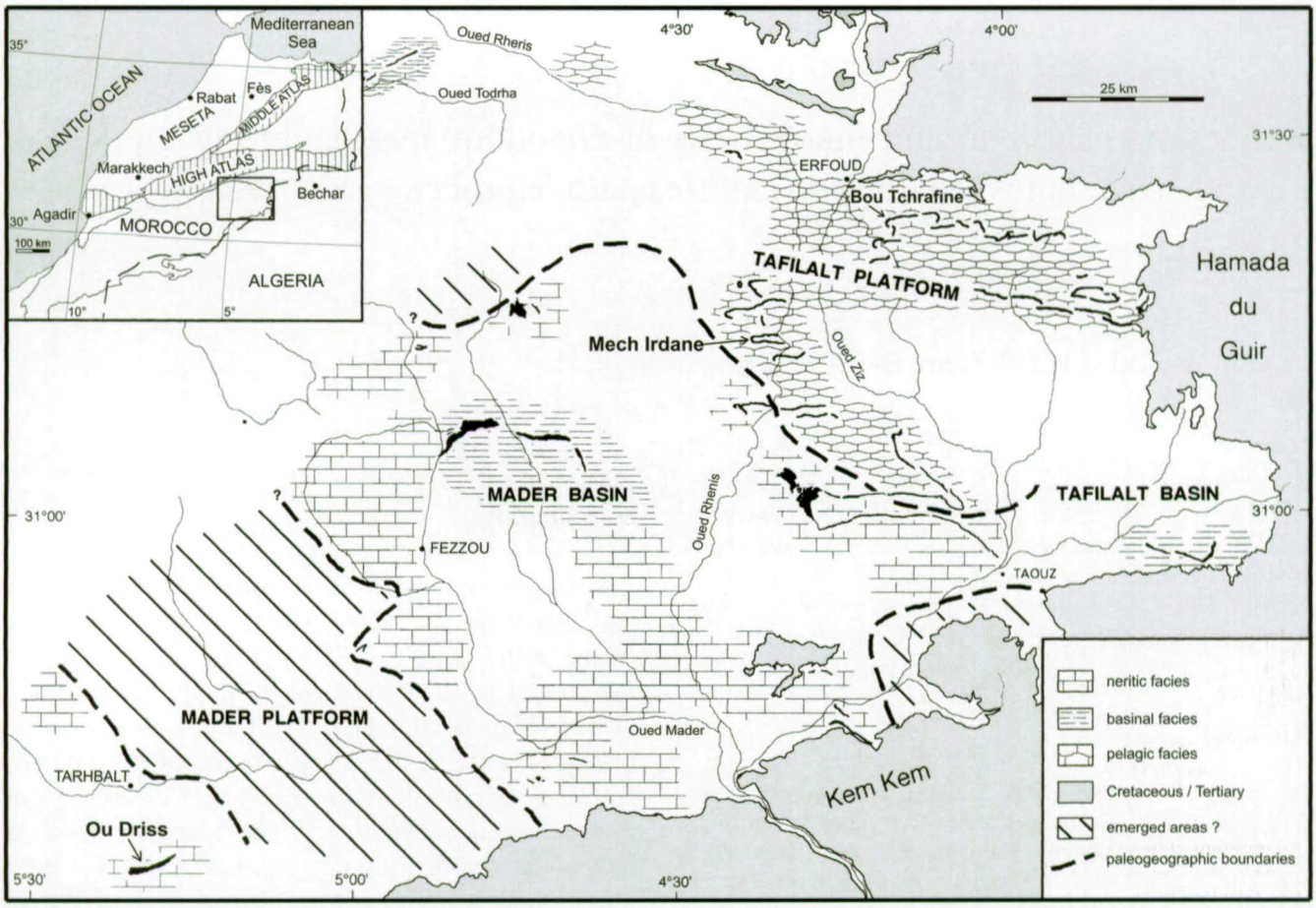

Fig. 1 – Map of the Tafilalt and Mader region with indication of paleogeography during the late Eifelian and early Givetian. The three studied sections, Jebel Mech Irdane, Bou Tchrafine and Jebel Ou Driss East are indicated with arrows.

The Late Eifelian Events (Kačák Episode)

The GSSP for the base of the Givetian is placed in a stratigraphic succession showing a sharp facies change due to an hypoxic perturbation (WALLISER *et al.*, 1995). The terminology for this hypoxic interval caused some confusion in earlier literature. HOUSE (1985) introduced the name Kačák Event, after the Kačák Member or Shale in the Bohemian Massif. It is a black and calcareous shale in which the index tentaculite *Nowakia otomari* occurs. In the uppermost part of the Choteč Limestone just below the Kačák Member the index conodont *Tortodus kockelianus* occurs (CHLUPAC *et al.*, 2000). At the same time WALLISER (1985) proposed the *otomari* Event based on the onset of the dacryoconarid lineage of the species *Nowakia otomari*. Some authors considered that the Kačák Event and the *otomari* Event covered the same period and were synonymous. It was also demonstrated that the Kačák Event was not instantaneous but represents a polyphased biotic crisis (GARCIA-ALCALDE *et al.*, 1990). In order to solve this confusing situation WALLISER (2000) proposed a Kačák Episode with the Late Eifelian 1 Event and the Late Eifelian 2 Event.

In the Mech Irdane section (Fig. 2) the base of the Late Eifelian 1 Event corresponds with the sudden onset of dark shales and can be assigned to the *otomari* Event. During the late Eifelian 2 Event the dark shales become progressively lighter and contain marly and nodular limestones. The Kačák Episode is 0.50 m thick.

In the Bou Tchrafine section (Fig. 3) the base of the Late Eifelian 1 is drawn at a level showing a changeover from light brown shales to gray shales with nodules and two thin limestone beds at the base, samples 15 and 15a. In these limestones occur dark spots with organic matter and concentrations of dacryoconarids, including *Nowakia otomari*. In the Late Eifelian 2 Event the shales and limestone nodules as well as bed 15b show brownish spots due to the presence of hematite and also yield a hematitic fauna. The Kačák Episode is represented by about 2 m of strata.

The Jebel Ou Driss Eastern section (Fig. 4) shows more neritic influences than the two other sections. The base of the Late Eifelian 1 Event can be recognized

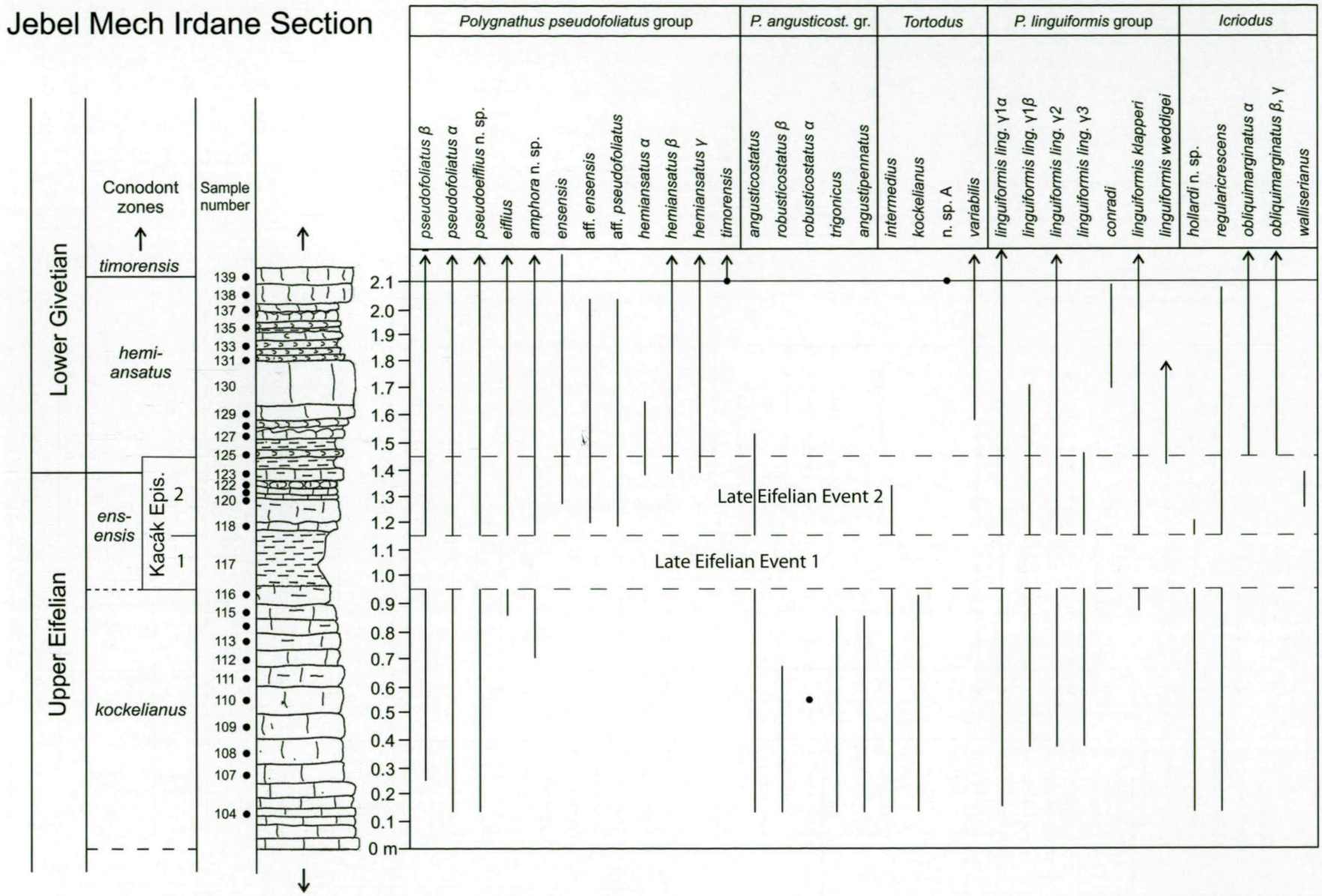

Fig. 2 – Table showing the ranges of conodont species and their morphotypes in the Jebel Mech Irdane section, from the *kockelianus* Zone to the base of the *timorensis* Zone. No conodonts recovered from the interval between samples116 and 118.

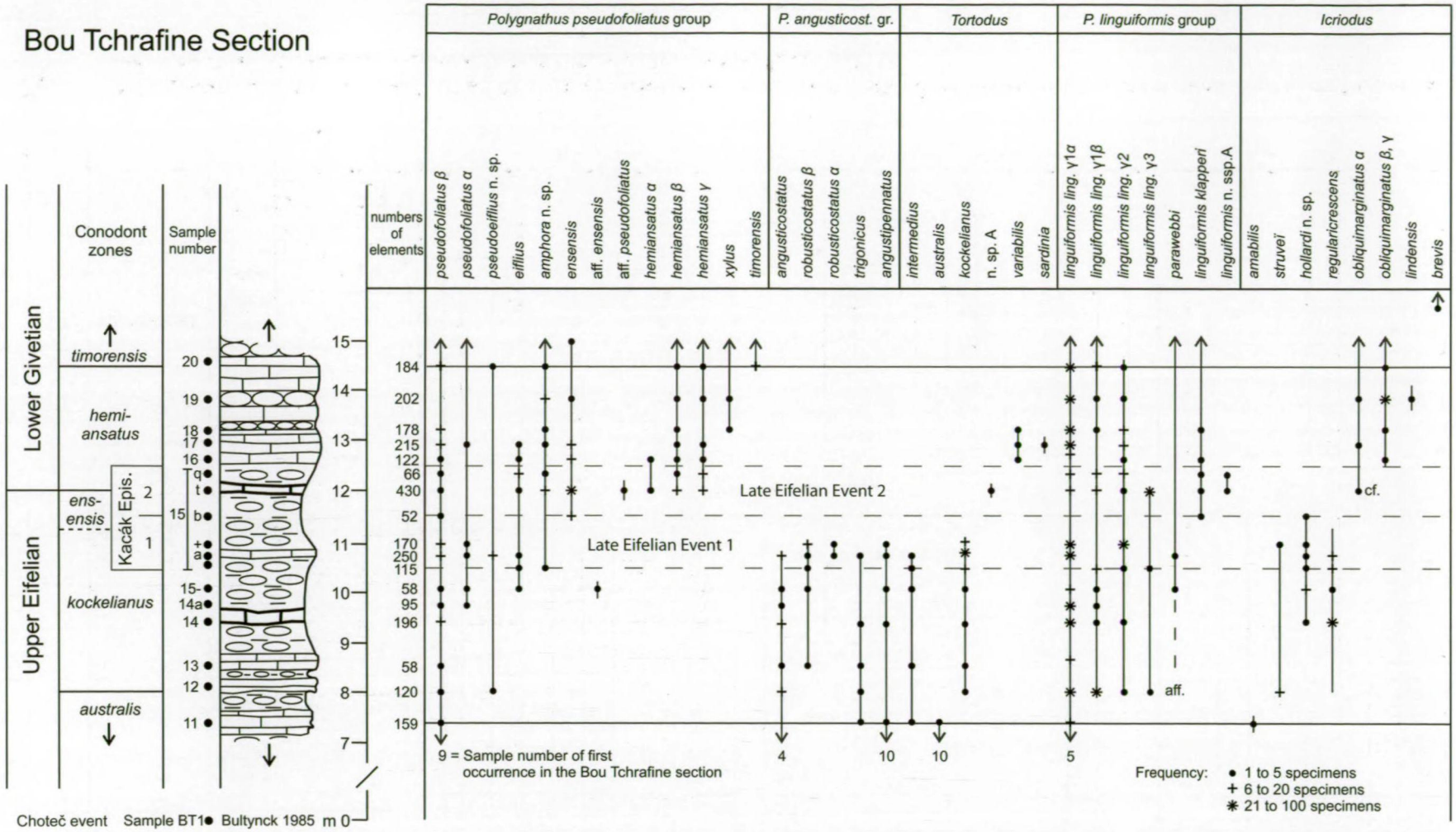

Fig. 3 – Table showing the ranges and frequency of conodont species and their morphotypes in the Bou Tchrafine section from the top of the *australis* Zone to the base of the *timorensis* Zone.

by the sudden colour change of brown-reddish marls to dark gray shales and limestones at the level of bed ODE-8-19 and continuing upward to bed ODE-7-1. Just above occurs a level with four compact limestone beds that forms a characteristic ridge in the Jebel Ou Driss and that is considered to represent the Late Eifelian 2 Event. The total Episode is represented by 2.50 m of strata.

In the three sections the Late Eifelian 1 Event and the lower part of the Late Eifelian 2 Event are assigned, in part or entirely, to the *ensensis* Zone. The uppermost part of the Late Eifelian 2 Event belongs to the *hemiansatus* Zone. The onset of the Kačák Episode may be related to the basal sea level rise of cycle If of JOHNSON *et al.* (1985) that also belongs to the *ensensis* Zone.

Extinction levels

The species of the *Polygnathus angusticostatus* group show a more or less simultaneous extinction level in the three sections (Figs 2-4). However, in the Mech Irdane section and in the Ou Driss E section the extinction level is below the Kačák Episode. In the Bou Tchrafine section it is slightly above the base of the Kačák Episode and also more simultaneous for the different species than in the two other sections. The discrepancy between the Mech Irdane section and the Bou Tchrafine section can be explained by the presence of the interval with dark shales without a conodont record at the base of the Kačák Episode in the former section.

One should also consider that the changeover to dark shales is less pronounced in the Bou Tchrafine section than in the two other sections.

Most *Icriodus* species of the common Eifelian *Icriodus* type (the *I. corniger-struvei* group) that have a rather broad spindle and a rather short posterior extension of the median row denticles behind the spindle, disappear below the Kačák Episode. The last representative, *Icriodus struvei*, disappears slightly below the Kačák Episode after probably giving rise to the *Icriodus arkonensis* group in the Kačák Episode (WEDDIGE, 1977); *Icriodus walliserianus* is the earliest representative. The innovative *Icriodus regularicrescens*, first occurs in the *costatus* Zone and ranges into the Kačák Episode and above, is ancestral to the *Icriodus obliquimarginatus* group in which we recognize three morphotypes α, β and γ. The α morphotype seems to be restricted to the pelagic-hemipelagic facies, the β and γ morphotypes occur also in the neritic facies.

Survival and innovations

The Polygnathus pseudofoliatus group

In the *kockelianus* Zone, below the Kačák Episode, the P. *pseudofoliatus* group is represented in the three sections by *P. pseudofoliatus, P. pseudoeiflius* n. sp., *P. eiflius* and *P. amphora* n. sp. The last mentioned species also occurs in the Plum Brook Shale of Ohio (US), described by SPARLING (1995) as *P. pseudofoliatus* subsp. A. The Plum Brook Shale was assigned by SPARLING to the upper part of the *ensensis* Zone.

The most characteristic innovation in the *P. pseudofoliatus* group took place during the Late Eifelian Event 2 by the initiation of the *Polygnathus hemiansatus* lineage, characterized by the modification of the anterior trough margins. In the earlier species of the *P. pseudofoliatus* group the anterior trough margins are steep and relatively symmetric on the inner and outer side. In the *hemiansatus* lineage the anterior trough margins become strongly asymmetric. The outer anterior through margin is characterized by the development of an outward bowing spoon-like structure and a pointed or linear constriction in the outer platform margin just posterior to the geniculation point. The inner anterior trough margin is only slightly outward bowing and is steep.

In the Mech Irdane section the platform surface of *P. hemiansatus* is strongly ribbed in the interval from bed 123 to bed 129. From bed 131 on, the surface of the platform can be also punctuated and becomes more elongated.

The Polygnathus linguiformis group

Three new morphotypes of *Polygnathus linguiformis linguiformis*, γ_1, γ_2 and γ_3, appear in the upper part of the *kockelianus Zone.* The γ_3 morphotype has a short stratigraphic range and disappears slightly above the Kačák Episode and does not reach the top of the *hemiansatus* Zone. Notable is the presence of *Polygnathus conradi* in the upper part of the *hemiansatus* Zone in the Mech Irdane section. It was decribed by CHATTERTON (1978) from the Eifelian-Givetian boundary interval from a section in the Canadian Northwest Territories. Until now it was not recognized outside this area.

Systematic Paleontology

The different species, based on P_1 elements, are described or discussed in the same order as in the three range charts (Figs 2-4). We distinguish a *Polygnathus*

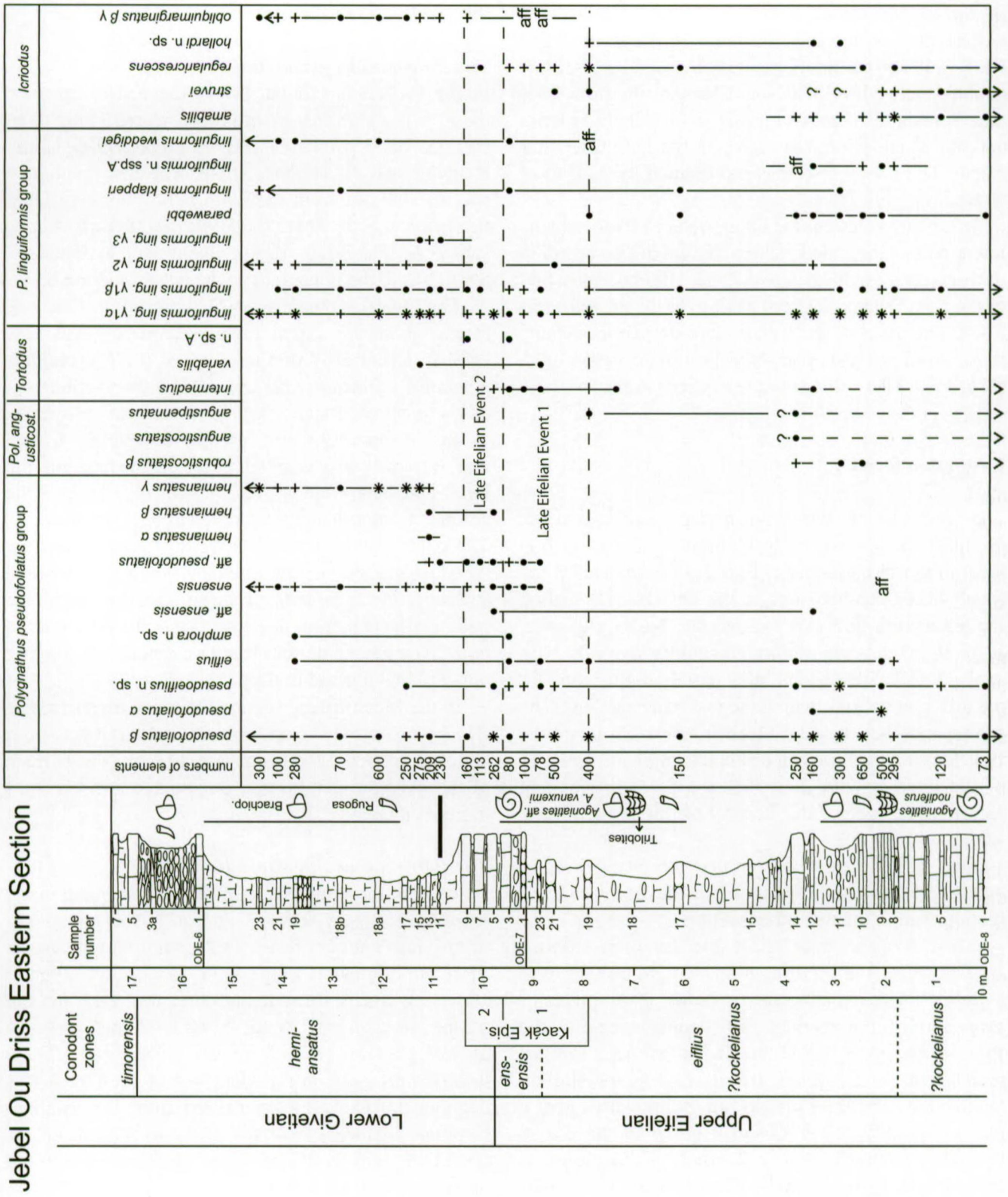

Fig. 4 – Table showing the ranges and frequency of conodont species and their morphotypes in the Jebel Ou Driss Eastern section from the ? *kockelianus* Zone to the base of the *timorensis* Zone. See Fig. 3 for the meaning of the frequency symbols.

pseudofoliatus group, a *Polygnathus angusticostatus* group, the genus *Tortodus*, the *Polygnathus linguiformis* group and the genus *Icriodus*. Synonymy lists are only established for a few taxa. The reader is cautioned that except otherwise mentioned, the stratigraphic ranges of the described species are only based on the data from the Moroccan sections described herein.

Polygnathus pseudofoliatus group

Polygnathus pseudofoliatus WITTEKINDT, 1966

Pl. 1, Figs 1-2

Description

Two morphotypes are recognized. The morphotype α conforms perfectly to the holotype of the species. The P_1 element of the β morphotype is more elongated.

Alpha morphotype. - The slightly asymmetric platform is relatively flat, broad oval-shaped and the anterior termination is narrow. The anterior part of the platform shows a weak rostrum. Posterior of the rostrum the platform margins widen gradually on both sides, the outer margin distinctly more than the inner, and describes a convex curve to the posterior end of the platform. The carina is slightly curved and reaches the posterior end of the platform. Except for the anterior trough margins, the platform is covered with nodes and irregular ribs and the adcarinal troughs are narrow. The inner side of the anterior trough margins shows a few short ribs and the anterior margins decline steeply downward.

Beta morphotype. - The platform of the beta morphotype is more slender and the rostrum more distinct than in the alpha morphotype. The adcarinal troughs are more developed than in the alpha morphotype and ribs predominate in the platform ornamentation.

Range

The α morphotype occurs from within the *kockelianus* Zone to the *ansatus* Zone. The β morphotype first occurs at the base of the *australis* Zone and ranges into the *ansatus* Zone.

Polygnathus pseudoeiflius n.sp.

Pl. 1, Figs 3-5

1971 — *Polygnathus* aff. *eiflius* BISCHOFF & ZIEGLER - KLAPPER, pl. 2, figs 14, 15, 20.

1987 — *Polygnathus eiflius*, BISCHOFF & ZIEGLER, 1957 - BULTYNCK, pl. 8, only figs 16, 18.

Derivatio nominis

The name refers to the species' similarity with *Polygnathus eiflius.*

Holotype

Geoscience Center, Göttingen University, specimen n° 1601-487-Y113-89, figured on Pl. 1, Fig. 5.

Paratypes

Geoscience Center, Göttingen University, specimens n° 1601-487-Y108-10 and n° 1601-487-Y115-12, figured on Pl. 1, Figs 3 and 4.

Locus typicus

Jebel Mech Irdane section.

Stratum typicum

Bed 113.

Diagnosis

The new species is characterized by a short rostrum with parallel margins and representing about one third or less of the total platform length. The outer margin forms a strong nearly half-circular expansion and the inner margin a weakly convex curve. The outer margin of the rostrum can be slightly diagonal and for that reason these forms were mostly assigned to or compared with *P. eiflius*.

Range

The species occurs from within the *kockelianus* Zone to within the *timorensis* Zone.

Polygnathus eiflius BISCHOFF & ZIEGLER, 1957

Pl. 1, Fig. 6

non 1980 — *Polygnathus eiflius* BISCHOFF & ZIEGLER, 1957 - BULTYNCK & HOLLARD, p. 45, pl. 5, fig. 15; pl. 6, fig. 5 (= *Polygnathus amphora* n. sp.).

non 1987 — *Polygnathus eiflius* BISCHOFF & ZIEGLER, 1957 - BULTYNCK, pl 8, figs. 15 – 18 (figs. 15, 17 = *P. amphora* n. sp.; figs 16, 18 = *P. pseudoeiflius* n. sp.).

Description

Platform typically with short anterior symmetric rostrum. The main part of platform is asymmetric and widest at mid-length. Outer platform–half is wider than inner and its margin is moderately to strongly convex. The surface is covered with fine nodes or irregular ribs. The margins of the anterior rostrum are relatively high and mostly serrated. They continue as a diagonal ridge or row of nodes on the main part of

the platform, in the direction of the carina or ± parallel to the carina.

Range
The species is less common than *P. pseudofoliatus*. It appears also slightly later (within *kockelianus* Zone) and disappears in the lower part of the *timorensis* Zone.

Polygnathus amphora n.sp.
Pl. 1, Figs 18-20

1980 — *Polygnathus eiflius* BISCHOFF & ZIEGLER, 1957 - BULTYNCK & HOLLARD, pl. 5, fig. 15; pl. 6, fig.5.
1987 — *Polygnathus eiflius* BISCHOFF & ZIEGLER, 1957 - BULTYNCK, pl. 8, figs 15, 17.
1995 — *Polygnathus pseudofoliatus*, WITTEKINDT subsp. A - SPARLING, pl. 3, figs 10-22.

Derivatio nominis
The outline of the platform is similar to a Greek vase with the name amphora.

Holotype
Geoscience Center, Göttingen University, specimen n° 1601-487-Y131-49, figured on Pl. 1, Fig. 19.

Paratype
IRScNB n°b1968, figured in Bultynck 1987, pl. 8, fig. 15.

Locus typicus
Jebel Mech Irdane section.

Stratum typicum
Bed 131.

Diagnosis
The new species can be easily distinguished from the α and β morphotypes of *P. pseudofoliatus* by the long rostrum with parallel margins and representing one third to half of the total platform.

Remarks
The specimen figured on Pl.1, Fig. 18 is a transitional form between *P.* aff. *P. pseudofoliatus* to *P. amphora.*

Range
The species has been recognized from the upper part of the *kockelianus* Zone to the lower part of the *timorensis* Zone, based on data from Morocco and N. America (SPARLING, 1995, *Polygnathus pseudofaliatus* subsp. A)

Polygnathus ensensis ZIEGLER & KLAPPER, 1976
Pl. 1, Figs 21-22

Remarks
According to the holotype and paratypes of the species, typical *ensensis* specimens should have a slightly constricted anterior platform with denticulated/serrated margins. The posterior part of the platform shows convex platform margins, especially on the outer side. Some of the specimens do not show clearly these characteristics and their identification is indicated with "?". It is stressed herein that the outer platform margin can be distinctly convex in the posterior half. This is also the case in the holotype and one paratype of the species (ZIEGLER & KLAPPER in ZIEGLER *et al.*, 1976, pl. 3, figs 4, 8). It is also noted that the geniculation points are not always opposite (ibidem, pl. 3, fig. 8; BULTYNCK & HOLLEVOET 1999, pl. 1, fig. 4; UYENO 1998, pl. 14, fig. 23).

Range
P. ensensis ranges from the base of the *ensensis* Zone into the major part of the *timorensis* Zone.

Polygnathus aff. ***P. pseudofoliatus***
WITTEKINDT, 1966
Pl. 1, Figs 7-10

Diagnosis
Strongly ribbed platform, with typically ± parallel platform borders. Anteriorly there may be a weak to more strong constriction on the outer side. The anterior adcarinal trough margins are steep.

May include transitional forms to *Polygnathus hemiansatus*.

Polygnathus hemiansatus BULTYNCK, 1987
Pl. 1, Figs 11-17

Description
The main characteristics of *Polygnathus hemiansatus* are the constriction in the outer platform margin just posterior to the geniculation point and the strongly outwards bowing of the outer anterior trough margin forming a spoon-like structure. The degree of development of these two characteristics allows to distinguish three morphotypes.

In the α morphotype the platform posterior to the geniculation points is rounded and short and mostly showing strong ribs.

In the β morphotype the platform is elongated and the constriction in the outer platform margin rises to a distinct point in the margin and the spoon-like structure is short.

In the γ morphotype the platform is elongated and the constriction in the outer platform margin forms a high shoulder-like structure. The spoon-like structure is well developed.

Range

The α morphotype is restricted to the lower part of the *hemiansatus* Zone and the β and γ morphotypes range into the *ansatus* Zone.

Polygnathus angusticostatus group

Polygnathus angusticostatus WITTEKINDT, 1966

Pl. 2, Figs 3-4

Diagnosis

Relatively long oval-shaped to triangular platform with wide, shallow adcarinal troughs. Short, conspicuous ribs at margin of platform. Carina low, slightly extending behind platform.

Range

First occurrence in *costatus* Zone (BULTYNCK, 1985, pl. 7, fig. 21) and may range into the *hemiansatus* Zone.

Polygnathus angustipennatus

BISCHOFF & ZIEGLER, 1957

Pl. 2, Figs 5a-5b

Diagnosis

Short platform, with deep adcarinal troughs, high upturned, denticulated platform margins. Blade long with numerous slender denticles, high in the anterior part. High carina, clearly longer than platform with wider denticles than denticles of the blade, and ± triangular in lateral view. Large pit.

Range

From *australis* Zone to *ensensis* Zone.

Polygnathus robusticostatus

BISCHOFF & ZIEGLER, 1957

Pl. 2, Figs 1-2

Diagnosis

Anterior half of platform rounded to oval-shaped with strong ribs and narrow adcarinal troughs. Posterior part of platform triangular with pointed end (α morphotype). Some specimens are more elongated with a weak constriction or rostrum in the anteriormost part of the platform (= β morphotype). The latter is somewhat similar to *P. angusticosatus*, but the platform of the β morphotype of *P. robusticostatus* is more flat with narrow, shallow adcarinal troughs. The α morphotype corresponds to the holotype.

Range

The species has been recorded from the *costatus* Zone to the top of the *kockelianus* Zone.

Polygnathus trigonicus

BISCHOFF & ZIEGLER, 1957

Pl. 2, Fig. 6

Diagnosis

Platform triangular, slightly narrowing in the anteriormost part, covered with nodes or short ridges. Anterior platform margins ± straight. The anterior part of the platform is characterized by an inner and outer row of nodes diverging in the anterior direction and delimiting a triangular surface on the platform without ornamentation. Free blade short with denticles of nearly equal size. Platform surface clearly arched, and pit located on anteriormost part of lower surface.

Range

The species was only found from the *australis* Zone to the *ensensis* Zone.

Genus *Tortodus* WEDDIGE, 1977

Tortodus? intermedius (BULTYNCK, 1966)

Pl. 2, Figs 11-12

Diagnosis

The slender denticles of the anterior half of the P_1 element, contrast with the wider, ± triangular in lateral view, denticles of the posterior half. There is a lateral thickening ("wulst") in the posterior half, but no platform. In lateral view the lower margin is straight in the anterior half, concave in the posterior part. Conspicuous pit with oval to drop-like outline and with small lips, located in the anterior half of the element. The assignment to the genus *Tortodus* is questioned because the posterior end is not twisted.

Range
From *australis* Zone to *ensensis* Zone.

Tortodus sardinia (MAWSON & TALENT, 1989)
Pl. 2, Fig. 15

Remarks
Numerous, tightly packed, rather slender denticles. In lateral view the lower margin is straight in the anterior half, concave in the posterior half. No platform development. Oval shaped pit, approximately at midlength of the P_1 element. The figured specimen is very similar to the specimens figured by MAWSON & TALENT 1989, pl. 7, figs 5 and 6.

Range
Was only found in *hemiansatus* Zone.

Tortodus variabilis (BISCHOFF AND ZIEGLER, 1957)
Pl. 2, Figs 13-14

Description
In lateral view the outline of the upper margin, formed by the tips of the denticles, is typically undulating, culminating in the anterior third and posterior 2/3 of the P_1 element. Conspicuous platform development or thick " wulst" with nodes or irregular ribs in posterior 2/3 of the element. Posterior part curved or twisted.

Range
Was found from *ensensis* Zone to *timorensis* Zone.

Tortodus n. sp. A
Pl. 2, Fig. 10

Remarks
In *Tortodus* n. sp. A the outline of the denticles are more uniform than in *Tortodus*? *intermedius* in which the denticles of the anterior half contrast with those of the posterior half; in *T.* n. sp. A the posterior part of the P_1 element is slightly twisted which is not the case in *Tortodus*? *intermedius*.

Range
Was found in *ensensis* and *hemiansatus* Zones.

Polygnathus linguiformis group
Polygnathus linguiformis linguiformis
HINDE, 1879

Remarks
ZIEGLER and KLAPPER 1976 regarded the *Polygnathus linguiformis* γ morphotype (BULTYNCK, 1970) as identical with the holotype of that species and consequently indicated the γ morphotype as *P. linguiformis linguiformis*. A new analysis of P_1 elements of the *P. linguiformis* material from Morocco, mainly from the Mech Irdane, Ou Driss and Bou Tchrafine sections allows recognition of minor and more important differences in the morphology of P_1 elements that were previously assigned to *P. linguiformis linguiformis*. More important differences permit recognition of three major morphotypes: γ1, γ2 and γ3. On the basis of minor differences the γ1 morphotype is subdivided into γ1a and γ1b. These new morphotypes can be recognized in figured material from different geographical areas in Europe, N. America and Australia and are useful in biostratigraphy. According to NARKIEWICZ & BULTYNCK (2010) the last occurrence of *P. linguiformis* is at the top of the *hermanni* Zone. It should be stressed that the holotype of *Polygnathus linguiformis linguiformis* is from the "Conodont bed" of HINDE 1879 with many reworked conodonts, especially *P. linguiformis linguiformis* and *Latericriodus latericrescens latericrescens* (HUDDLE, 1981). Some authors extend the range of *P. linguiformis linguiformis* into the top of the Givetian or the base of the Frasnian (e.g. ORR & KLAPPER, 1968 and SANDBERG *et al.*, 1994) but in the sections they describe there are discontinuity surfaces and there can be reworking. UYENO (1998) reported it in the Middle *varcus* (*ansatus*) Zone in the Northwest Territories (Canada).

Polygnathus linguiformis linguiformis
HINDE, 1879 γ1 morphotype
Pl. 3, Figs 1-2

Description
The tongue represents about one-third of the total platform-length and its surface is crossed by strong, continuous transversal ridges. The margin of the outer platform, anterior to the tongue (further indicated as "platform") is high, flange-like and its rim is nearly rectilinear. The adcarinal trough is deep and wide. The margin of the narrower inner platform is only slightly

raised and can be straight or slightly concave or convex. The inner platform is ornamented with nodes and/or straight or irregular ribs.

In the γ1a morphotype (Pl. 3, Fig. 1) the width of the tongue decreases progressively from the end of the anterior platform to the end of the tongue. In the Bou Tchrafine section it occurs from the *costatus* Zone to the top of the *hermanni* Zone. It is the dominant and longest ranging morphotype of the species.

In the γ1b morphotype (Pl. 3, Fig. 2) there is a pronounced constriction in the outer platform margin, just anterior of the onset of the narrow tongue. This morphotype is most common in the *kockelianus* and *ensensis* Zones, but less than morphotype γ1a; it becomes more rare from the *hemiansatus* Zone on and it is nearly absent in the *timorensis* and the *ansatus* Zones.

Polygnathus linguiformis linguiformis
HINDE, 1879 γ2 morphotype
Pl. 3, Fig. 3

Description
In the γ2 morphotype the outer platform is characterized at about mid-length by a pronounced widening and by the development of a high flange, especially in the posterior part of the platform.

Range
This morphotype occurs in the studied Moroccan sections from the *kockelianus* Zone to the base of the *ansatus* Zone.

Polygnathus linguiformis linguiformis
HINDE, 1879 γ3 morphotype
Pl. 3, Figs 4-6

Description
The general outline of the γ3 morphotype is slender. In comparison with the γ1 and γ2 morphotypes the relative length of the tongue is clearly longer and may represent about the half-length of the P_1 element. The inner and outer margins of the platform are upturned, both at the same level and are parallel in the anteriormost part. In upper view, the transition from the outer platform-margin to the tongue describes a curve. The tongue is pointed. This morphotype is somewhat similar to *Polygnathus linguiformis bultyncki* WEDDIGE, 1977. However, the latter subspecies is more robust and the transition from the outer platform margin to the tongue does not describe a regular curve.

Range
In the Moroccan sections it occurs mainly from the *kockelianus* Zone to the *hemiansatus* Zone, it becomes rare in the *timorensis* Zone and the youngest occurrence is in the lowest part of the *ansatus* Zone.

Polygnathus linguiformis klapperi
CLAUSEN, LEUTERITZ & ZIEGLER, 1979
Pl. 3, Figs 7-8

Description
The relatively flat anterior platform with strong ridges and sometimes nodes on the inner platform, the curved transition from the outer platform margin to the well developed tongue with many strong transversal ribs and clearly bent downward are the main characteristics of the subspecies.

In *Polygnathus linguiformis pinguis* WEDDIGE, 1977 the tongue is less developed, less bent downward and the inner platform margin is slightly convex in front of the tongue.

Range
In the Moroccan sections the subspecies ranges from within the *kockelianus* Zone to the *semialternans* / *latifossatus* Zone.

Polygnathus linguiformis subsp. A
UYENO & BULTYNCK, 1993
Pl. 3, Fig. 9

Description
The platform is rather short and squat. The anterior platform is more or less square shaped. The inner and outer platform halves are separated from the carina by an adcarinal trough, the outer one being wider than the inner. The outer platform margin is much higher than the inner and serrated, but without development of a prominent flange. The transition from the outer platform margin to the tongue is rounded and the tongue is deflected inward and downward, moderately long with strong to weaker transverse ridges that can be slightly interrupted by the carina.

Range
In the Morrocan sections the subspecies occurs from the *ensensis* Zone to the *hemiansatus* Zone.

Polygnathus linguiformis weddigei
CLAUSEN, LEUTERITZ & ZIEGLER, 1979
Pl. 3, Figs 10-11

Description
The surface of the platform is flat, the posterior half is turned inward and bent slightly downward. The carina is curved and can be mostly recognized until the pointed posterior end. The posterior part of the platform is characterized by the presence of weak ± transversal ribs. According to the holoype the outer platform margin is regularly curved over the total length. The ribs on the outer platform show a radial pattern.

Range
In the Morrocan sections the species occurs from the *hemiansatus* Zone to the *ansatus* Zone.

Polygnathus conradi CHATTERTON, 1978
Pl. 3, Figs 12-14

Remarks
The main characteristic of this species is the twisted tongue-like posterior end of the platform with strong transversal ribs that can be continuous or interrupted by the carina. The species shows similarities with *Polygnathus linguiformis* theta morphotype in JOHNSON, KLAPPER & TROJAN, 1980 (pl. 4, fig. 35) that in Nevada occurs in the *costatus* Zone.

Range
The Moroccan specimens occur in the *hemiansatus* Zone. CHATTERTON (1978) mentions that the species occurs slightly below and above the Eiflian-Givetian boundary in the Canadian Northwest Territories.

Polygnathus parawebbi CHATTERTON, 1974
Pl. 3, Figs 15-16

Remarks
The outline of the platform of *Polygnathus parawebbi* is similar to the platform outline of *Polygnathus linguiformis linguiformis* γ1a morphotype as described herein. However, in *P. parawebbi* the ribs on the tongue are interrupted by the carina, reaching the posterior end of the platform.

Range
In the Moroccan sections the species ranges from the *kockelianus* Zone to the *timorensis* Zone. However, in other areas the species occurs from the *australis* Zone to the *ansatus* Zone.

Genus *Icriodus* BRANSON & MEHL, 1938
Icriodus hollardi n. sp.
Pl. 4, Figs 1-6

V 1987 — *Icriodus platyobliquimarginatus* n. sp. BULTYNCK, pl. 5, figs 8-9 only.
V 1987 — ? *Icriodus struvei* WEDDIGE, 1977- BULTYNCK, pl. 5, fig. 10 only.

Derivatio nominis
In honour of Henri Hollard for his tremendous work on the Devonian of the Anti-Atlas (Morocco).

Holotype
IRScNB n° b6372, figured on Pl. 4, Fig. 2.

Paratypes
IRScNB n° b6371, b6373, b6374, figured on Pl. 4, Figs 1, 3, 4; Göttingen specimens n°s 1601-487-J-109-5 (Pl. 4, Fig. 5) and 1601-487-J-104-5 (Pl. 4, Fig. 6).

Locus typicus
Jebel Ou Driss, eastern section.

Stratum typicum
Taboumakhlouf Formation, sample ODE-8-19.

Diagnosis
Spindle concavo-convex to slightly biconvex, pointed, elongated anterior part, with a typically individualized middle denticle row; two to three last middle row denticles on the spindle are higher than lateral row denticles; posterior extension of middle row with mostly three to four denticles, typically slightly higher, can however be at same level of last MR (middle row) denticles on spindle. About five denticles in inner and outer lateral denticle row with rounded sections. Posterior expansion of cavity relatively broad, asymmetric, more expanded on outer side.

Remarks
The new species partly corresponds to *Icriodus struvei* in BULTYNCK, 1987 (pl. V, fig. 10 only) and *I. platyobliquimarginatus* ibidem (pl. V, figs 8-9 only). The spindle of *Icriodus struvei* is more elongated and curved and the denticles of the posterior extension of the middle denticle row are more slender. In *Icriodus platyobliquimarginatus* the posterior extension of the

middle row is longer and the last denticle is strongly reclined.

Range
In the Moroccan sections the species occurs in the *kockelianus* and in the *ensensis* Zones.

Icriodus obliquimarginatus
BISCHOFF & ZIEGLER, 1957
Pl. 4, Figs 16-19

Description
Three main morphotypes are recognized.

The *α morphotype* (Figs 17-19) corresponds to the holotype. The spindle is narrow, and even more narrowing to its posterior end and showing an irregular denticulation pattern. The posterior middle row extension is long (minimum five to six denticles) and is slightly curved in upper view. In lateral view the outline of the upper margin of the posterior MR extension is slightly convex, the highest point being close to the posterior end. In lateral view the posterior margin is moderately to strongly reclined. The outer margin of the basal cavity widens progressively from the anterior to the posterior end.

The *β morphotype* (Fig. 16) differs from the α morphotype by the regular denticulation pattern. The MR denticles are slightly anterior to the corresponding lateral row denticles or alternate.

The *γ morphotype* (See BULTYNCK, 1987, pl. 4, fig. 16). Nearly straight longitudinal axis. Very regular denticulation pattern, middle row and lateral row denticles alternating or middle row denticles slightly anterior to corresponding lateral row denticles. The denticles of the posterior extension of the middle row are ± of equal size. The cusp is not much higher than the neighboring denticles and in lateral view the posterior margin is straight.

Remarks
Typical transitional specimens between *Icriodus regularicrescens* and *I. obliquimarginatus* (Pl. 4, Fig. 20 a-b) are characterized by a long spindle showing a regular denticulation pattern and by a middle denticle-row posterior extension with at least 4 denticles. The spindle is widest at about mid-length.

Range
In the Moroccan sections transitional specimens between *I. regularicrescens* and *I. obliquimarginatus* first occur in the upper part of the *kockelianus* Zone. The β and γ morphotypes appear at the base or slightly above the base of the *hemiansatus* Zone. The α morphotype appears in the upper half of the *hemiansatus* Zone. The different morphotypes occur to the top of the *timorensis* Zone.

Icriodus struvei WEDDIGE, 1977
Pl. 4, Figs 9-10

Diagnosis
The anterior half of the spindle is narrow and elongated and its outline is triangular. The middle row and lateral row denticles slightly alternate. The short posterior extension of the medial-row denticles is slightly curved.

Range
In the Moroccan sections the species was found from the lower part of the *costatus* Zone to the base of the *ensensis* Zone.

Conclusions

The Kačák Episode cannot be considered as an event. In the SE Moroccan Tafilalt and Mader it may start in the uppermost part of the *kockelianus* Zone, occupies the entire *ensensis* Zone and ends in the lower part of the *hemiansatus* Zone. It is best qualified as an hypoxic interval. Extinctions are limited to five species/morphotypes of the *Polygnathus angusticostatus* group in the Bou Tchrafine section and to 4 in the Mech Irdane section. The Episode is better characterized as an innovation period of the *Polygnathus pseudofoliatus* group with the appearance of *Polygnathus amphora* n.sp., *P. ensensis* and *P. hemiansatus*. The outline of the anterior trough margins of *P. hemiansatus* represents an innovation in comparison with earlier *Polygnathus* species, e.g. *P. costatus*, *P. pseudofoliatus* and *P. eiflius*. These species have rather steep anterior through margins. In *P. hemiansatus*, on the other hand, the outer anterior through margin develops to an expanding spoon-like structure. Also the morphology of the P_1 element of the *Icriodus obliquimarginatus* group changes drastically in comparison with the earlier species of the *corniger-struvei* group. It should also be mentioned that the base of the *timorensis* Zone shown in BULTYNCK, 1987 is moved upward, from bed BT18 to BT20. The *Polygnathus timorensis* specimen from bed 18, figured on pl. 7, fig. 11 of the 1987 paper is no longer considered as a good *P.*

timorensis representative because the platform margins are not nodose as mentioned in the original diagnosis of KLAPPER, PHILIP & JACKSON, 1970.

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Explanation of plates

Most figured specimens are from the Mech Irdane (MI) section. They are deposited in the collections of the Museum of the Geoscience Center, Goettingen University (GZG). They bear a tripartite registration number e.g. 1601-487-Y104-7. The number 1601 is the collection number, 487 is the locality number of the Mech Irdane section and Y104-7 is the number of a figured specimen, 104 is the sample number and 7 refers to the specimen. Other figured specimens are from the Bou Tchrafine section (BT) and from the eastern part of the Jebel Ou Driss (ODE). They are deposited in the micropaleontological collections of the Department of Palaeontology of the Royal Belgian Institute of Natural Sciences (IRScNB n° b6305-b6381) Magnifications are x50 unless otherwise noted. The figured specimens are upper views of P_1 elements except where otherwise stated.

Plate 1

Fig. 1 — *Polygnathus pseudofoliatus* Wittekindt, 1966, alpha morphotype, n. 1601-487-Y104-7.
Fig. 2 — *Polygnathus pseudofoliatus* Wittekindt, 1966, beta morphotype, n. 1601-487-Y107-3.
Figs 3-5 — *Polygnathus pseudoeiflius* n. sp., holotype and two paratypes, n°s 1601-487-Y108-10, 115-12 and 113-39; Fig. x60.
Fig. 6 — *Polygnathus eiflius* Bischoff & Ziegler, 1957, n° 1601-487-Y115-5.
Figs 7-10 — *Polygnathus* aff. *P. pseudofoliatus* Wittekindt, 1966, transitional forms to *Polygnathus hemiansatus* Bultynck, 1987, n°s 1601-487, Y122-3, Y122-15 and 16, Y122-6; Fig. 10 x60.
Fig. 11 — *Polygnathus hemiansatus* Bultynck, 1987, alpha morphotype, n° 1601-487-Y123-7; x60.
Figs 12-15 — *Polygnathus hemiansatus* Bultynck, 1987, gamma morphotype, n°s 1601-487-Y123-15, Y-123-2, Y-125-17, Y127-6; Figs 12, 14, 15 x60.
Fig. 16 — *Polygnathus hemiansatus* Bultynck, 1987, beta morphotype, n° 1601-487-Y131-42.
Fig. 17 — *Polygnathus hemiansatus* Bultynck, 1987, gamma morphotype, n° 1601-487-Y132-5; x60.
Fig. 18 — *Polygnathus* aff. *P. pseudofoliatus* Wittekindt, 1966, transitional form to *Polygnathus amphora* n. sp., n° 1601-487-Y118-28; x60.
Figs 19-20 — *Polygnathus amphora* n. sp., holotype and a juvenile form, n°s 1601-487-Y131-49, Y118-7.
Figs 21-22 — *Polygnathus ensensis* Ziegler & Klapper, 1976, n°s 1601-487-Y123-19 and Y123-14, oblique-lateral view.

Plate 2

Figs 1-2 — *Polygnathus robusticostatus* Bischoff & Ziegler, 1957, n°s 1601-487-X109-2 and X108-5.
Figs 3-4 — *Polygnathus angusticostatus* Wittekindt, 1966, n°s 1601-487-X112-3 and X104-3.
Fig. 5a,b — *Polygnathus angustipennatus* Bischoff & Ziegler, 1957, n°s 1601-487-X104-29; fig. 5b is an oblique lateral view.
Fig. 6 — *Polygnathus trigonicus* Bischoff & Ziegler, 1957, n° 1601-487-X104-22.
Fig. 7 — *Polygnathus hemiansatus* Bultynck, 1987, beta morphotype, sample ODE 7-5, n° IRSNB b6305.
Fig. 8a-b — *Polygnathus timorensis* Klapper, Philip & Jackson, 1970, sample BT20, n°s IRSNB b6366; 8b is an outer lateral view.
Fig. 9a-b — *Polygnathus timorensis* Klapper, Philip & Jackson, 1970, sample BT20, n°s IRSNB b6367; 9b is an outer lateral view.
Fig. 10 — *Tortodus* n. sp. A, n° 1601-487-139-X, inner lateral view; x60.
Figs 11-12 — *Tortodus* ? *intermedius* (Bultynck, 1966), n°s 1601-487-X104-12 and X104-13; fig. 12 is an inner lateral view.
Figs 13-14$_{a-b}$ — *Tortodus variabilis* (Bischoff & Ziegler, 1957), n° 1601-487-X157-X and ODE-8-21; fig. 14b is an outer lateral view; the anterior part is broken; Fig. 14 a, b x60.
Fig. 15 — *Tortodus sardinia* Mawson & Talent, 1989, n° 1601-487-X128-19, inner lateral view.
Figs 16-17 — *Polygnathus timorensis* Klapper, Philip & Jackson, 1970, n°s 1601-487-X139-1 and X139-6; Fig. 17 is an inner lateral view.

PLATE 3

Fig. 1 — *Polygnathus linguiformis linguiformis* HINDE, 1879, γ1a morphotype, n° 1601-487-L108-2.
Fig. 2 — *Polygnathus linguiformis linguiformis* HINDE, 1879, γ1b morphotype, n° 1601-487-L107-2, inner oblique lateral view.
Fig. 3 — *Polygnathus linguiformis linguiformis* HINDE, 1879, γ2 morphotype, n° 1601-487-L108-1.
Figs 4-6 — *Polygnathus linguiformis linguiformis* HINDE, 1879, γ3 morphotype, n°s 1601-487-L122-13, L122-8 and L122-7.
Figs 7-8 — *Polygnathus linguiformis klapperi* CLAUSEN, LEUTERITZ & ZIEGLER, 1979, n°s 1601-487-L123-54 and L118-1; Fig. 8 is an oblique inner lateral view.
Fig. 9 — *Polygnathus linguiformis* sp. A UYENO & BULTYNCK, 1993, n° ODE-8-10, n° IRScNB b6368; x60.
Figs 10-11 — *Polygnathus linguiformis weddigei* CLAUSEN, LEUTERITZ & ZIEGLER, 1979, n°s 1601-487-L141-21 and
— L130-ob-4.
Figs 12-14 — *Polygnathus conradi* CHATTERTON, 1978, n°s 1601-487-X123-1, X127-1 and L141-31.
Figs 15-16 — *Polygnathus parawebbi* CHATTERTON, 1974, n°s 1601-487-L104-13 and L103-2; oblique inner lateral views, Fig. 15 x60.

PLATE 4

Magnification x45, except where otherwise stated.

Figs 1-4 — *Icriodus hollardi* n. sp., holotype and three paratypes, 1, 2 sample ODE-8-19 and 3, 4 sample BT-15, n°s IRScNB b6369, b6370, b6371 and b6372; Fig. 4 is an inner lateral view.
Figs 5-6 — *Icriodus hollardi* n. sp., two paratypes n°s 1601-487-J109-5 and J104-5.
Figs 7_{a-b}-8 — *Icriodus amabilis* BULTYNCK & HOLLARD, 1980, sample ODE-8-9, n° IRScNB b6373, Fig. 7b is a lower view and 8 is an outer lateral view.
Figs $9\text{-}10_{a-b}$ — *Icriodus struvei* WEDDIGE, 1977, sample ODE-8-9 and ODE-8-21, n° IRScNB b6374 and b6375; Fig. 10b is an inner lateral view.
Figs 11-12 — *Icriodus walliserianus* WEDDIGE, 1988, n°s 1601-487-J219-2 and J123-52.
Figs 13-15 — *Icriodus regularicrescens* BULTYNCK, 1970, samples ODE-8-23, ODE-8-19, ODE-X-X, n°s IRScNB b6376, b6377 and b6378; Fig. 15 is a transitional form to *Icriodus obliquimarginatus* BISCHOFF & ZIEGLER, 1957.
Fig. 16_{a-b} — *Icriodus obliquimarginatus* BISCHOFF & ZIEGLER, 1957, beta morphotype, sample ODE-7-11, n° IRScNB b6379 ; Fig. 16b is an inner lateral view of the same specimen; x62.
Figs 17-19 — *Icriodus obliquimarginatus* BISCHOFF & ZIEGLER, 1957, alpha morphotype n°s 1601-487-J125-9, J125-7 and J129-20.
Fig. 20_{a-b} — *Icriodus regularicrescens* BULTYNCK, 1970, transitional form to *Icriodus obliquimarginatus*, n° 1601-487-J104-2; Fig. 2b is an inner lateral view.

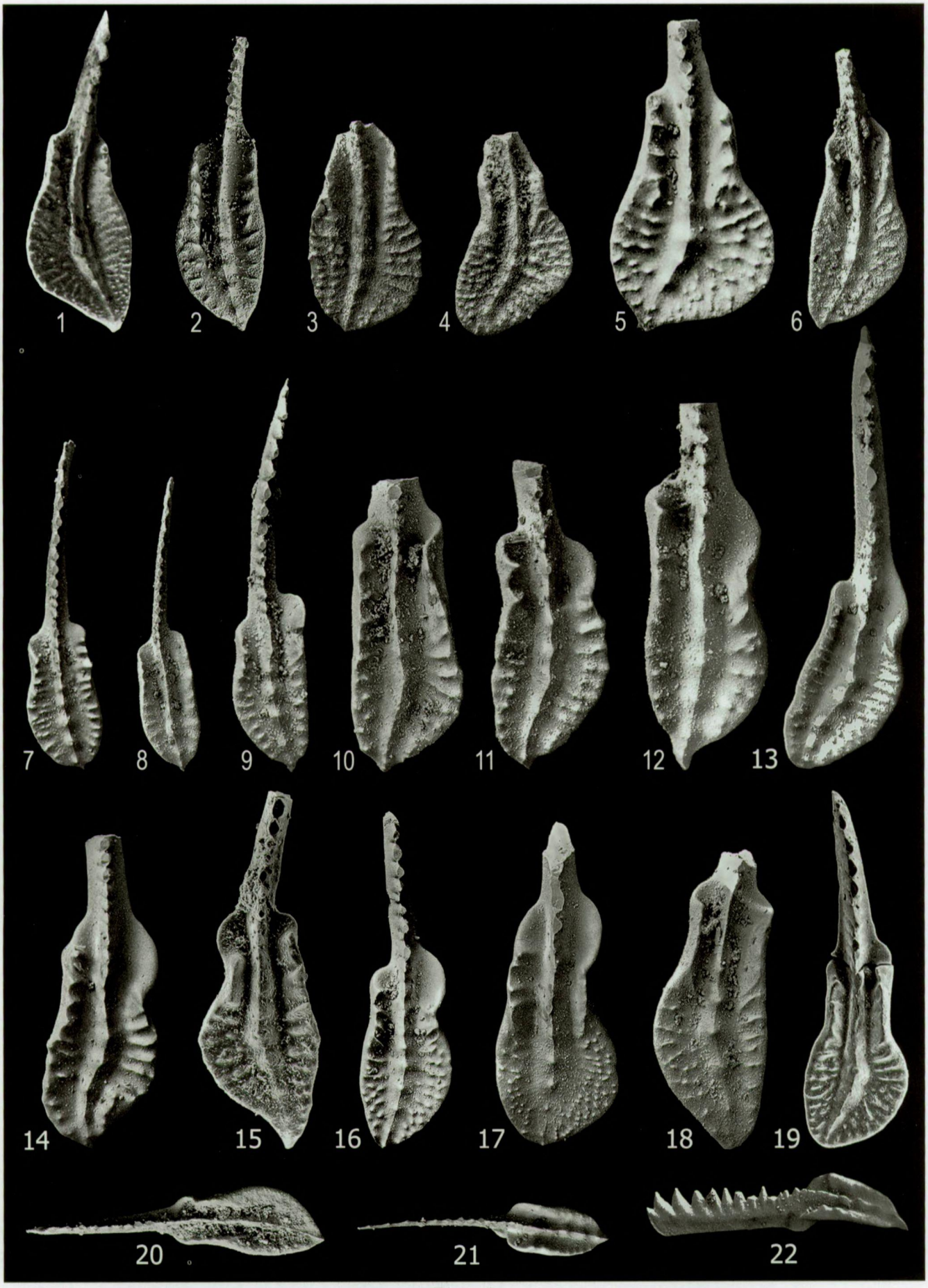

PLATE 1

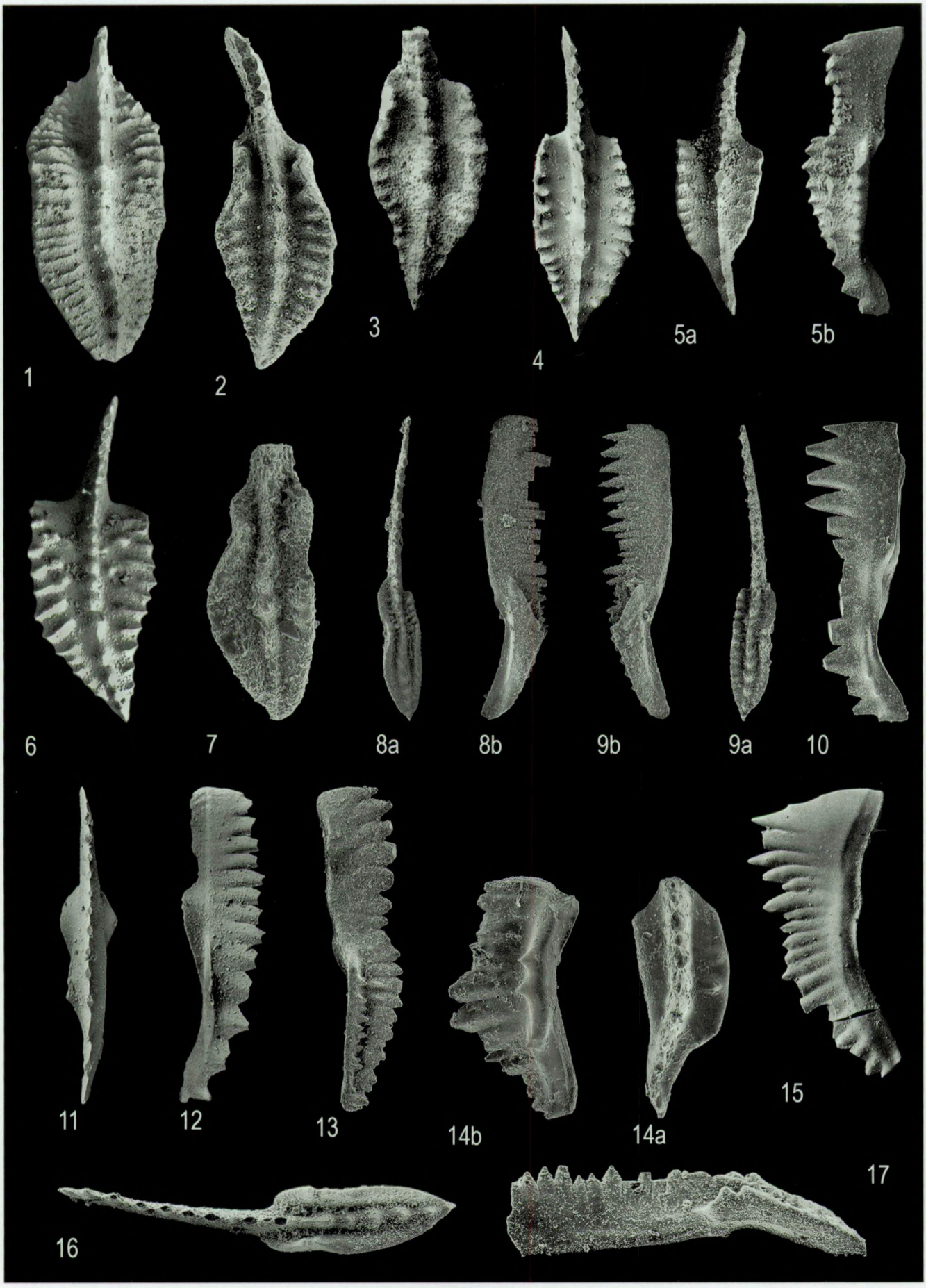

PLATE 2

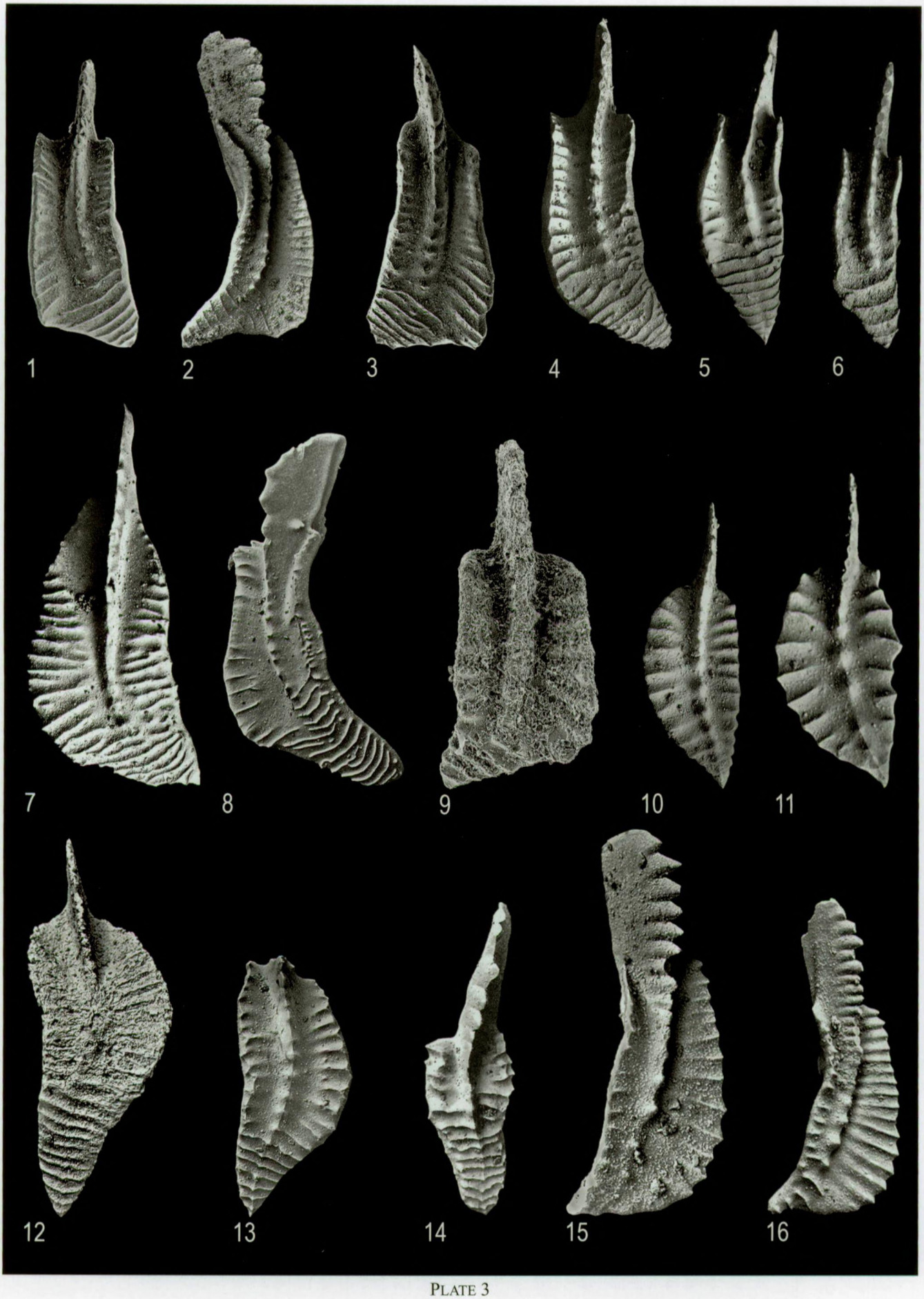

PLATE 3

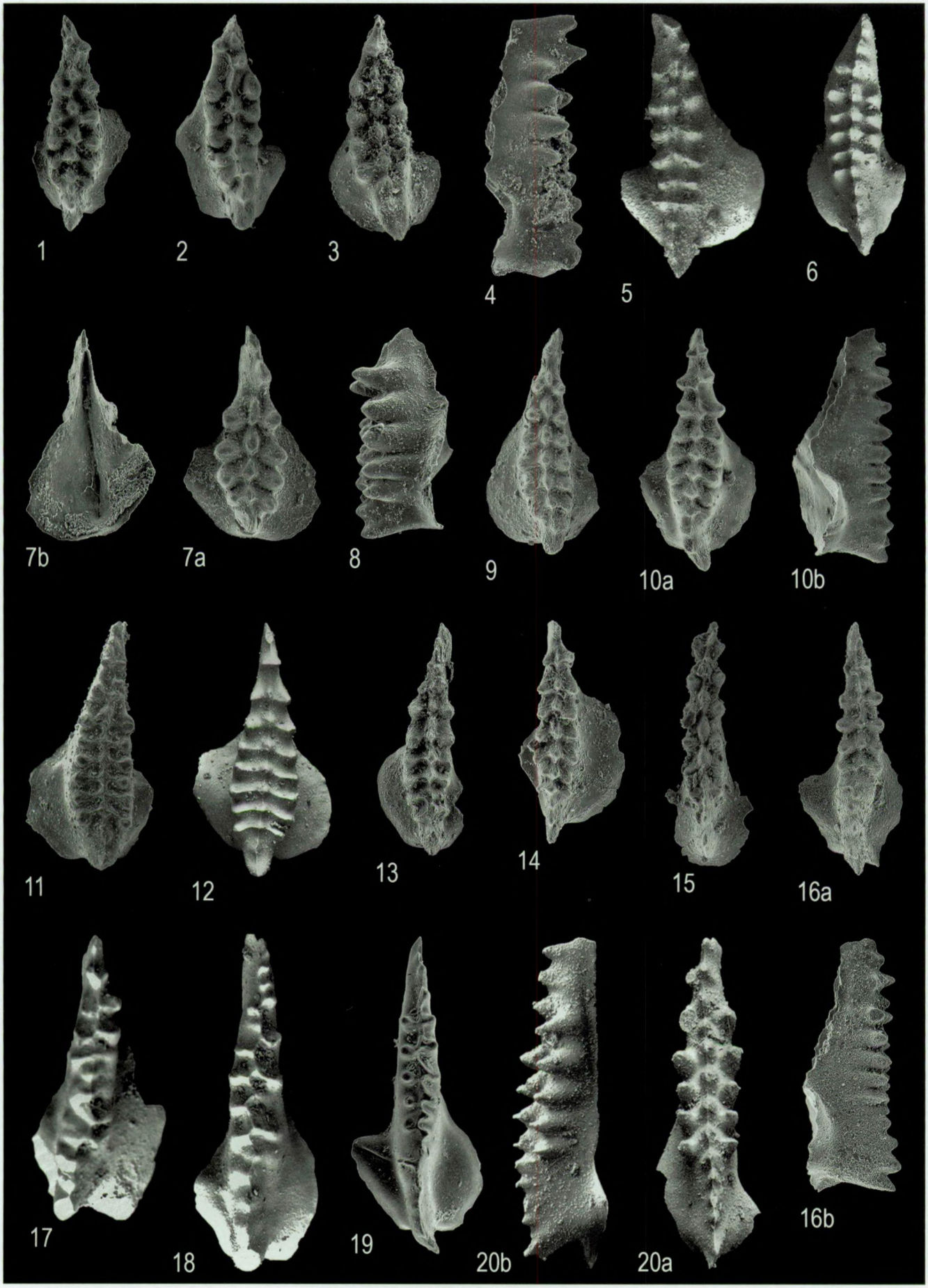

PLATE 4