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New upper Givetian to basal Frasnian conodont faunas from the Tafilalt (Anti-Atlas, Southern Morocco)

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Conodont faunas, mostly from previously unsampled sections of the Tafilalt (eastern Anti-Atlas, Morocco) and spanning the upper Givetian to basal Frasnian, include first records of species for the region and NW Gondwana as well as new taxa: *"Ozarkodina" maroccanica* n. sp., *Polygnathus aequidivisus* n. sp., *Po. dengleri sagitta* n. ssp., *Po. jorfensis* n. sp., *Po. saevus* n. sp., *Po. tafilensis* n. sp., and *Schmidtognathus longicavus* n. sp. The morphology of *Tortodus subsymmetricus* n. sp. suggests relationships of *Tortodus* with Frasnian ancyrognathids. Other taxa are described in open nomenclature: *Po. cristatus* n. ssp., *Icriodus* aff. *I. symmetricus*, *Skeletognathus* aff. *Sk. norrisi*, and enigmatic supposed Pb elements (Gen. et sp. indet.). *Ctenopolygnathus lanei* Kuzmin (1995) is emended and distinctive morphotypes are recognized in *Ct. angustidiscus* and *Po. collieri*. *Mesotaxis falsiovalis* Sandberg *et al*. (1989) is a subjective junior synonym of the widely overlooked *M. guanwushanensis* (Tian, 1988). The revised regional lithostratigraphy and conodont sequences allow to refine the upper Givetian zonation. The former Upper *disparilis* Zone is subdivided into successive *Po. dengleri sagitta* and *Po. dengleri dengleri* subzones. The basalmost Frasnian *Ancyrodella rotundiloba pristina* Zone (= MN 1 Zone) is preserved as a thin, condensed limestone just at one locality (Bine Jebilet). The overlying Frasnes Event Beds (Lower Styliolinites) seem to fall in the subsequent *Ad. rotundiloba soluta* Zone (MN 2 Zone). Records of rare taxa, such as *Po. paradecorosus*, *Po. pollocki* Morphotype 1, oldest *Po. webbi*, *Ct. angustidiscus*, and *Ct. lanei* may be helpful for correlation into distant areas or shallower facies.

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INTRODUCTION

Upper Givetian to lower Frasnian conodont faunas from the Tafilalt of the eastern Anti-Atlas (SE Morocco) have been described in a series of now classical papers by P. Bultynck and co-authors (e.g., Bultynck and Hollard 1980; Bultynck and Jacobs 1981; Bensaid *et al*., 1985; Bultynck 1986, 1987; Gouwy and Bultynck, 2002). Earlier, Bensaid (1974) published the first few upper Givetian conodont lists from Hassi Nebech. Some additional data were provided by Ebert (1993; no conodont illustrations) and, based on a single sample from the Ouidane Chebbi area, by Belka *et al*. (1999). Detailed data, based on rigorous bed-by-bed collecting and complete identifications of faunas, including taxonomic documentation, are only available for the famous Bou Tchrafine section of the Tafilalt Platform. The faunas from other sections around the Middle/Upper Devonian boundary that were briefly discussed by Bensaid *et al*. (1985) were never fully published. Aboussalam (2003), with preliminary data in Aboussalam and Becker (2001, 2002), investigated platform and basinal sections around the latest middle Givetian Taghanic Crisis, revised the conodont zonation (*ansatus* to *cristatus ectypus* zones) of the middle/upper Givetian transition, and described some new and rare species of *Polygnathus* and *Tortodus*. Field work continued subsequently and focussed on the upper Givetian and basal Frasnian, originally stimulated by the aim to improve the conodont-ammonoid correlation of the *Pharciceras* Stufe (preliminary data in Aboussalam and Becker, 2004, 2005). The new conodont faunas include several first regional records of taxa, additional new species of *Polygnathus, Schmidtognathus*, and *Tortodus*, extend the known range of some forms, and contribute to the refinement of the zonation. Various other forms cannot be assigned to known species and are identified in open nomenclature. Several regionally rare species seem helpful for correlation into more shallow, neritic facies or into distant regions. The conodont ranges in the topmost Givetian *Petteroceras* Beds and in the basal Frasnian are important for a better understanding of the evolutionary impact of the global Frasnes Event, a still poorly studied, polyphase (Becker and Aboussalam, 2004; Aboussalam and Becker, 2004) sequence of transgressive and widespread hypoxic phases around the middle/upper Devonian boundary.

Conodont genera are abbreviated as follows: "*Ozarkodina*" = *Oz.*, *Icriodus* = *I.*, *Bipennatus* = *Bi.*, *Tortodus* = *T.*, *Polygnathus* = *Po.*, *Linguipolygnathus* = *L.*, *Ctenopolygnathus* = *Ct., Schmidtognathus* = *S.*, *Klapperina* = *Kl.*, *Elsonella* = *El.*, *Mesotaxis* = *M.*, *Ancyrodella* = *Ad.*, *Belodella* = *B.*, *Skeletognathus* = *Sk.*

GEOLOGICAL SETTING AND STUDIED LOCALITIES

The Givetian of the Tafilalt is mostly characterized by condensed pelagic limestones that contain rich faunas of ammonoids, nautiloids, tentaculitoids and ostracods, as well as a restricted low diversity benthic community, consisting of proetid and phacopid trilobites, crinoid remains, small solitary rugose corals, rare tabulate corals (thamnoporids and cladochonids), brachiopods (rhynchonellids and lingulids), bivalves (e.g., the large-sized genus *Panenka*), and gastropods. Coral biostromes with *Phillipsastrea*, other hermatypic Rugosa, alveolitids, branching Tabulata and some stromatoporoids are only developed in the southern Tafilalt Amessoui Syncline (Massa, 1965; Aboussalam, 2003) and document a transition to shallower, neritic facies. This suggests that the Tafilalt Platform was gently dipping northwards but increased thicknesses and more complete sedimentation also characterize the Ouidane Chebbi area in the eastern Tafilalt. The easternmost Tafilalt at Mkarig is, again, more condensed and incomplete. The grading into argillaceous and hypoxic facies with pyritic (secondarily goethitic to haematitic) faunas of the Hassi Nebech area in the SE Tafilalt documents a transition to the Tafilalt Basin (Wendt *et al.*, 1984). Goniatite shales have also been found to intercalate and overlie the upper middle Givetian coral patch reefs at El Atrous N (Aboussalam, 2003), Oum el Jerane, and Jebel Ouaoufilal in the southern Tafilalt. The palaeobathymetric difference between pelagic carbonate platform, small-sized elevations with more neritic facies and hypoxic shale basins was probably low and goniatite shales were deposited in depression areas that were sheltered from strong bottom currents. This palaeobathymetric interpretation is perhaps supported by conodont biofacies data. Supposed shallow-water conodonts (*Belodella*, relative high percentages of *Icriodus*) occur in limestones that are intercalated with goniatite shales at Hassi Nebech and Oum el Jerane.

Sections of the central and northern Tafilalt Platform feature various unconformities that developed in the course of the interplay between eustatic sea level change, regression controlled submarine erosion, and local subsidence variation. Sections in the western and northern Tafilalt (Mdoura-East, Jebel Amelane, Mounkara) lack parts of the upper part of the upper Givetian and the lower Frasnian black styliolinites may wedge out over short distances. At the northwestern edge of the platform (Ras-el-Kebber) the middle Givetian and lower part of the upper Givetian are missing. At Jebel Mech Irdane (Ebert, 1993), above the basal Givetian GSSP, and at the neighbouring Jebel Ihrs, the upper Givetian and lower Frasnian have been subsequently reworked and completely removed. Disconformities on the central platform have been documented by Aboussalam (2003, Seheb el Rhassal) and Ebert (1993, Hamar Laghdad; confirmed by our restudy). At Jebel Erfoud middle Frasnian (pre-Kellwasser) erosion has very locally truncated underlying beds down to the early Eifelian. But a few tens of metres laterally, the Givetian is present, contains filled neptunian dykes, and the upper Frasnian Kellwasser facies is only preserved as reworked clasts or in veins within basal middle Famennian massive limestones. This illustrates the fast changing and small-scale palaeotopography of some platform parts. The most complete successions were found in the western part of the Seheb el Rhassal ridge (Section 3), at Bou Tchrafine, Ouidane Chebbi, and Hassi Nebech. The basalmost Frasnian can only be recognized in a single section at Bine Jebilet.

Bensaid *et al.* (1985), Bultynck (1987), and later Wendt and Belka (1991) recognized that the base of the lower Frasnian styliolinites is not isochronous throughout the Tafilalt. Their observation is confirmed by our re-sampling. In some sections (e.g., Mdoura-East) the first black limestones fall in the upper part of the lower Frasnian (*transitans* Zone = MN 4 Zone) and the main part of the substage is missing in a sedimentary gap. The styliolinites clearly belong to two distinctive transgressive pulses of consistently different age in the lower Frasnian; only the older unit (Lower Styliolinites) that mostly lacks ancyrodellids and goniatites is considered in this study.

New conodont samples come from the following sections (Figs. 1, 2, Tables 1–5):

Bine Jebilet (BJ; Table 1 and Fig. 2), northern Tafilalt Platform, SE of Jorf, along the track *ca*. 300 m off the main road to Erfoud, x = 601.2, y = 495.3; lower extension of Famennian succession illustrated in Becker (1993). Heavy quarrying has destroyed much of the outcrop in the last five years.

Ras-el-Kebber (ReK; Table 2), northwestern edge of Tafilalt Platform, isolated Devonian hill *ca*. 12 km SSE of Jorf, x = 586.9, y = 490.0; single sample from irregularly bedded, laterally fast changing, red, bioclastic crinoidal limestone, deposited as platform margin debris and mass flows; with many gastropods, trilobites and ammonoids of the *Taouzites taouzensis* Zone (upper MD III-D).

Mdoura-East (Md-E; Table 3 and Fig. 2), western Tafilalt Platform, second hill coming from the main road to Msissi, *ca*. 10.5 km W of Rissani, x = 597.0, y = 478.2; lower extension of Famennian section described in Becker (1993).

Jebel Amelane (JA; Table 2), Jebel Ighace on 1:50 000 topographic map, western Tafilalt Platform, *ca*. 8 km W of Rissani, x = 600.3, y = 476.4. Previous descriptions of the higher Givetian were given in Becker and House (2000*b*) and Aboussalam (2003) but the published data require significant revision. For example, it turned out that the Lower and Upper Marker Beds were misidentified; the latter is not developed in the western Tafilalt and only the massive Upper *Sellagoniatites* and Lower Marker Beds are present (Fig. 2).

Seheb el Rhassal (SeR-1 to 3), continuation of Bou Tchrafine ridge W of the Oued Amerbouh, see Aboussalam (2003); Section 1 lies at x = 618.0, y = 481.3, lateral Section 2

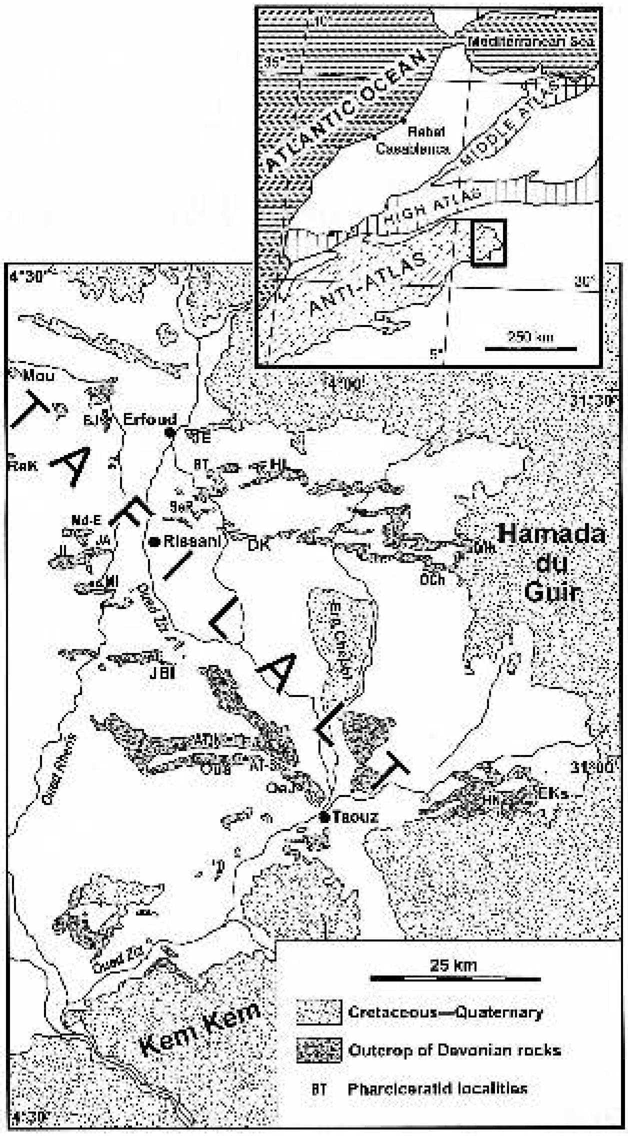


Fig. 1. Overview of Devonian outcrops of the Tafilalt, showing the location of investigated (sampled or measured) sections

AT-N — El Atrous North; BJ — Bine Jebilet; BT — Bou Tchrafine; DK — Dar Kaoua; EKs — Erg Kseir; ET-S — El Atrous South; HL — Hamar Laghdad; HN — Hassi Nebech Sections 1, 2; JA — Jebel Amelane; JBI — Jebel Bou Ifarherioun; JE — Jebel Erfoud; JI — Jebel Ihrs; Md-E — Mdoura-East; MI — Jebel Mech Irdane; Mk — Mkarig; Mou — Mounkara; OCh — Ouidane Chebbi; OeJ — Oum el Jerane; Oua — Jebel Ouaoufilal; ReK — Ras-el-Kebber; SeR — Seheb-el-Rhassal Sections 1–3

ca. 80 m westwards, lateral Section 3, which is more complete in the upper Givetian than the others (Fig. 2), lies *ca.* 500 m further westwards.

Bou Tchrafine (BT; Table 4 and Fig. 2), central Tafilalt Platform, *ca.* 8 km S of Erfoud, x = 616.8, y = 487.8. The upper Givetian to basal Frasnian was previously studied by Bultynck and Hollard (1980), Bultynck and Jacobs (1981), Ziegler and Klapper (1982), Bensaid *et al.* (1985), Bultynck (1986, 1987), Ebert (1993), Becker and House (2000*a*) and Aboussalam (2003).

Dar Kaoua (DK; Table 2 and Fig. 2), central Tafilalt Platform, *ca.* 22 km SE of Erfoud, x = 627.3, y = 478.6; downward continuation of Frasnian/Famennian section studied by Becker (1993). A single sample was taken from the locally very solid Lower Marker Bed that yielded an important and very well preserved goniatite fauna.

Ouidane Chebbi (OCh; Table 5 and Fig. 2), *ca.* 44 km E of Erfoud, eastern Tafilalt Platform, slightly transitional to Tafilalt Basin, x = 651.1, y = 472.2; previously illustrated in Aboussalam (2003). Extensive quarrying has destroyed almost all Upper Givetian sections along several kilometres of lateral outcrop. This is probably one of the reasons why Belka *et al* (1999) illustrated the *Pharciceras* Stufe only in a very rough way and with just one conodont sample taken from its top.

Oum el Jerane (OeJ), *ca.* 16 km NW of Taouz, southern Tafilalt Platform, x = 620.25, y = 444.0, downward continuation of Famennian succession sampled by Korn *et al.* (2000) and Hartenfels and Becker (2006), *ca.* = section El Atrous II in Bensaid *et al.* (1985); single sample with few conodonts from solid turbiditic limestone overlying goniatite shale with goethitic *Lunupharciceras*, other pharciceratids, and several undescribed tornoceratids.

Hassi Nebech (HN), Tafilalt Basin, *ca.* 20 km ENE of Taouz, Section 1 at x = 656.2, y = 438.6, Section 2 lies 2 km eastwards; previously illustrated in Bensaid *et al.* (1985) and Aboussalam (2003). Both sections have become famous for incredibly rich goethitic or haematitic pharciceratid faunas that are collected by berber boys from the adjacent Begaa village and partly sold to rock shops in Erfoud and elsewhere. Further to the east, just W of the Erg Kseir, the argillaceous upper Givetian becomes very unfossiliferous and, therefore, has not been sampled.

In the interest of a complete conodont record, reference is also given to former samples from Bou Tchrafine, Hamar Laghdad, El Atrous North and South, and Seheb el Rhassal, Sections 1, 2. Previous to the current investigations, a set of samples collected jointly by the second author and the late M. R. House at Bou Tchrafine and Bine Jebilet was sent to G. Klapper, who kindly provided lists of identifications.

TAFILALT LITHOSTRATIGRAPHY AND CONODONT FAUNAS

The upper Givetian and basal Frasnian of the Tafilalt can be easily subdivided into a succession of thick, solid and massive or more nodular and recessive marker units (see Bultynck and Walliser, 2000), each with a distinctive ammonoid and conodont fauna (Fig. 2). Once the general sequence is understood, orientation in the field becomes easy, even when new outcrops are examined. However, the mentioned unconformities need to be recognized and lithological correlation into the more shallow or more basinal southern Tafilalt areas is not straight forward. Most coral-stromatoporoid biostromes of the Amessoui Syncline were drowned in the course of the transgressive pulses of the Taghanic Events but at Oum el Jerane small patches of biostromes with alveolitids, other Tabulata, and some *Phillipsastrea* may be intercalated between upper Givetian shales with goniatites and

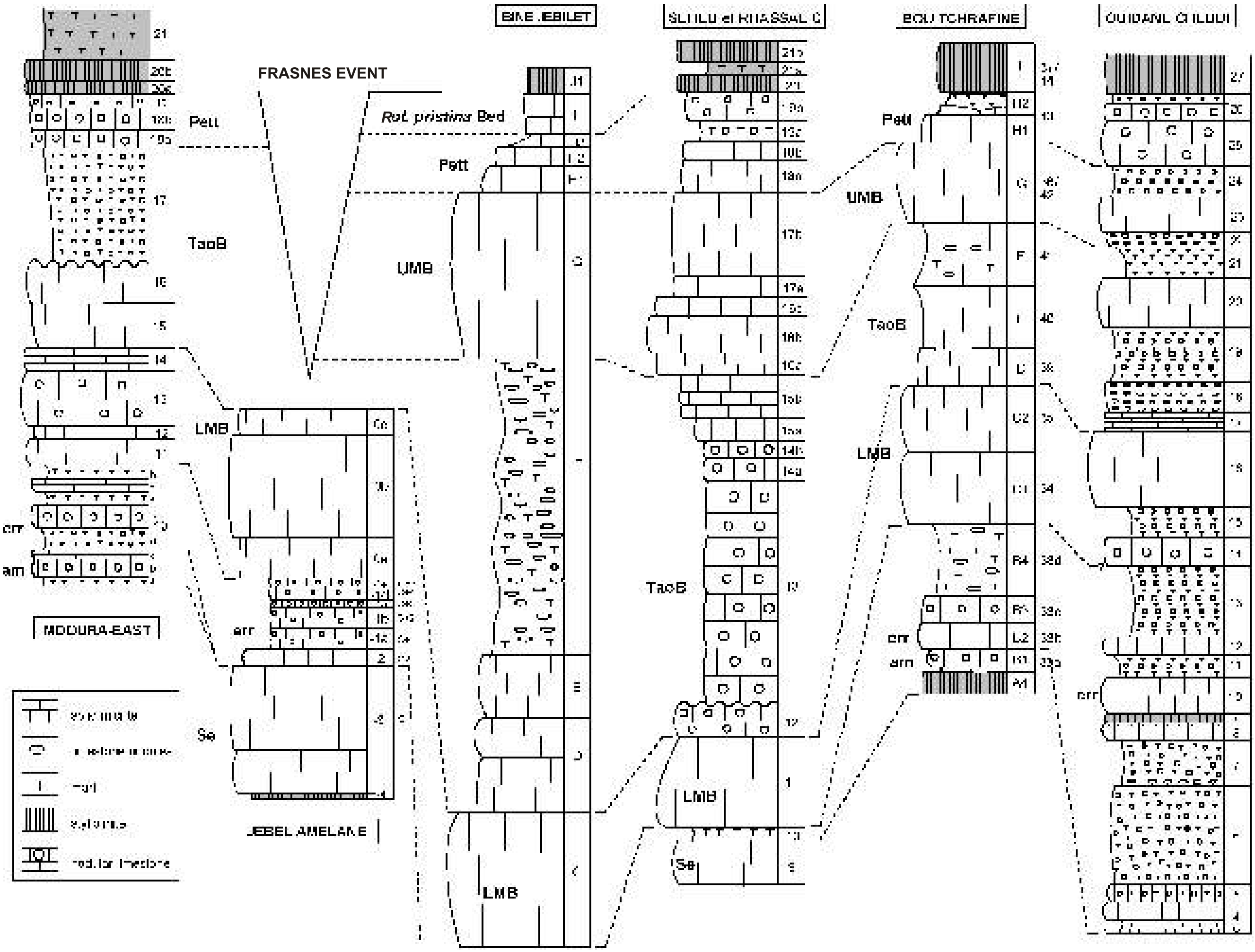


Fig. 2. Litho- and biostratigraphical correlation of upper Givetian to basal Frasnian sections of the northern to central Tafilalt in a rough W–E transect (vertical scale: 6 mm = 10 cm)

Pett — *Petteroceras* Beds, UMB — Upper Marker Bed, TaoB — *Taouzites* Beds, LMB — Lower Marker Bed, err — *erraticus* Beds, am — *Pharciceras* aff. *P. amplexum* Bed, Se — Upper *Sellagoniatites* Bed; shaded units — dark grey to black, organic-rich lithology

turbiditic limestones. In the more basinal Hassi Nebech areas some of the marker units still can be identified, others are lost in a thick argillaceous succession. The regional sequence of pharciceratid-bearing beds within the upper Givetian to basal Frasnian of the Bouia Formation (Unit K, Bultynck and Walliser, 2000), starting just above the *Pharciceras* aff. *P. amplexum* Bed of the Upper Tully Event Interval (topmost middle Givetian; Becker, 2007), is as follows (from base to top, conodonts illustrated in Figs. 3–9):

MZERREBITES ERRATICUS BEDS

Greenish-grey, thin-bedded to somewhat nodular limestones, alternating with marls or thin crinoidal beds; often rich in phacopids (Aboussalam, 2003; Stegemann, 2006) and commonly with the compressed, name-giving goniatite and close relatives, but with only rare *Pharciceras*. These beds represent regionally the early post-Taghanic phase. They have been sampled at Md-E (bed 10e), JA (top of bed C2 = top bed 11), BT (beds B2, 3 = 33b, c), SeR-2 (beds E2a, b), OCh (beds 3c–8), EA-S (bed 10), HN-1 (beds 10e–i), and HN-2 (bed 10d).

Conodonts can be abundant and diverse. The number of recorded species (ß-diversity) significantly exceeds faunas from the underlying *Pharciceras* aff. *P. amplexum* Bed. A wide range of species can be common and documents the significant post-Taghanic bloom in several conodont genera: *Po. varcus, Po. xylus* (Aboussalam, 2003, pl. 16, figs. 4, 6), *Po. ovatinodosus* (Aboussalam, 2003, pl. 15, fig. 16), *Po. limitaris* (variability illustrated by Aboussalam, 2003, pl. 18), *Po. dubius, I. difficilis, S. hermanni, S. wittekindti, S. pietzneri* and *S. latifossatus.* The previously dominant *L. linguiformis* disappears suddenly and completely from almost all faunas but, surprisingly, remains very common in the supposedly more basinal Hassi Nebech area (Aboussalam, 2003, pl. 17, fig. 3). Taxa that are moderately frequently encountered are *Po. ansatus, Oz. semialternans* and *Oz. sannemanni proxima*. Many other forms constitute only a minor part of available assemblages: *Po. timorensis, Po. pennatus, Po. housei* (only at

Table 1

Upper Givetian and basal Frasnian conodont record at Bine Jebilet

Bine Jebilet					
Conodont zones	*dengleri*	*norrisi*		*pristina*	*soluta*
bed and sample no.	top G	H1-2	H3	I	base J
Oz. sann. sannemanni	1				
Po. ordinatus	2	11			
Po. xylus	4	32	13	34	2
Po. ovatinodosus	2	17	4	26	1
Po. dengleri dengleri	13	51	11	25	3
T. subsymmetricus n. sp.		13			
Oz. plana		1			
Po. limitaris		2			
Sk. norrisi		1Pb	*	*	3
Po. cf. *Po. xylus*		2			
Po. saevus n. sp.		5			
S. wittekindti		1			
S. longicavus n. sp.		1			
Oz. sannemanni proxima		2	1		
Oz. sannemanni adventa		5	2	*	1
Kl. disparalvea		1	1		
I. difficilis		18	*	*	35
Po. varcus		44	10	2	2
Po. dubius		16	6	38	14
I. symmetricus		2	*	*	4
Po. pennatus		13	*	51	15
Po. dengleri sagitta n. ssp.		54	7	10	
Po. webbi		1	*	1	
Po. pollocki M1		2	*	1	
Po. tafilensis n. sp.		8	*	15	
Po. aequidivisus n. sp.		1			
Po. paradecorosus		6	*	*	3
Po. collieri M2				2	
Po. angustidiscus				1	
Po. cristatus n. ssp.				1	
Po. cristatus cristatus				1	3
Ad. rotundiloba binodosa				2	
Ad. rotundiloba pristina				12	
Po. jorfensis n. sp.				3	
Po. cf. *Po. uyenoi*				1	
Po. alatus				8	5
Po. lanei				6	2
I. subterminus					5
M. guanwushanensis					2
total conodonts	22	310	55	239	100
species diversity	5	26		20	16

SeR-2, Aboussalam, 2003, pl. 18, figs. 3–5), *Po. acrinodosus* (only at SeR-2, Aboussalam, 2003, pl. 18, figs. 1–2), *Po. hemipennatus* (only at SeR-2, Aboussalam, 2003, pl. 18, figs. 6, 7), *I. expansus, I. brevis brevis* (Aboussalam, 2003, pl. 23, figs. 3, 4), *T. bultyncki* (only at HN-2), *Tortodus* n. sp. *sensu* Aboussalam (2003, only at JA), *Oz. sannemanni sannemanni, Oz. sannemanni proxima* (Aboussalam, 2003, pl. 24, figs. 11, 12), *Oz. plana*, *Oz. maroccanica* n. sp. (only at SeR-2, see Aboussalam, 2003), *S. gracilis, S.* aff. *S. hermanni* (only at BT, Aboussalam, 2003, pl. 21, figs. 14, 15), *S.* aff. *S. wittekindti* (only at SeR-2), *El. rhenana*, and *Prioniodina* sp. *L. mucronatus* (only at SeR-2) and *Po. pseudofoliatus* (only at OCh, Aboussalam, 2003, pl. 28, fig. 5) are rare relict species in single sections. Large Pb elements resembling *Bryantodus* cf. *B. nitidus* (Aboussalam, 2003, pl. 22, fig. 13) may belong to the apparatus of a large-sized *Tortodus*.

RED *LUNUPHARCICERAS* BEDS

Reddish-grey, haematite-enriched, nodular or thin-bedded limestones with poor macrofauna that include the oldest *Lunupharciceras*. This level correlates with a restricted occurrence of hypoxic goniatite shales with many *Mzerrebites* and early *Lunupharciceras*, but still without *Synpharciceras*, at Oum el Jerane, which is overlain by turbiditic limestones and, laterally, by the last patches of coral biostromes. Available conodont samples are from Md-E (bed 10g), JA (bed C+1) BT (bed B4 = 33d or 33), SeR-1 (bed E2), SeR-2 (bed E2c), OeJ (bed 8), and EA-N (beds 11–13). Ebert (1993) recorded contemporaneous conodonts from HL.

The conodont content varies significantly from section to section but the yield can be extremely low (e.g., at Md-E). Together with the rarity of macrofauna, this suggests a phase of very oligotrophic conditions; the lack of organic carbon improved the preservation of oxidized iron. A range of species can occur rather commonly and this documents faunal similarity with the underlying unit: *Po. ansatus, Po. xylus, Po. varcus, Po. ovatinodosus, Po. limitaris, Po. dubius* (Aboussalam, 2003, pl. 19, figs. 2, 3), and *S. wittekindti*. *S. hermanni, S. latifossatus*, and *S. pietzneri* can be moderately common. This unit contains regionally the last known *Po. timorensis* (at SeR-1) and *L. mucronatus* (at JA). Taxa that form minor parts of assemblages are *Po. cristatus ectypus, Po. pennatus* (only at JA), *Oz. semialternans, Oz. maroccanica* n. sp. (only at SeR-1), *Oz. sannemanni sannemanni, S.* aff. *S. hermanni* (only at BT, Aboussalam, 2003), *I. brevis latecarinatus* (only at BT), *I. difficilis* (only at SeR-1) and *E. rhenana* (only at SeR-1).

LOWER MARKER BED

The widespread but heavily quarried, massive Lower Marker Bed of Becker and House (1994) was specially studied by Ebert (1993), who named it as “Unterer *Pharciceras*-Horizont”. It represents a shallowing upwards cycle, with the development of a hardground at the top. However, the unit can be subdivided into two parts, which contain different faunas and both subunits seem to belong to two different sedimentary phases. In the more basinal Hassi Nebech area, the massive limestone has changed into fossiliferous grey nodular limestone with *Synpharciceras* and other pharciceratids. In the Amessoui Syncline (Jebel Ouaoufilal) small goethitic goniatite faunas prove that the Lower Marker Bed is replaced by a poorly exposed, hypoxic goniatite shale.

The lower subunit has been sampled at Md-E (beds 11, 12), BT (bed C1 = 34, also literature data), HN-1b (bed 11b), and

Table 2

Conodont record of samples from Jebel Amelane, Dar Kaoua and Ras-el-Kebber

Jebel Amelane		
Conodont zones	*hermanni*	*ectypus*
bed and sample no.	C2	C+1
Po. varcus	18	54
L. linguiformis	5	
L. mucronatus	*	2
I. difficilis	14	
Po. ansatus	3	46
Po. ovatinodosus	39	12
Tortodus sp.	1	
Po. timorensis	2	
I. brevis eslaensis	2	
Po. xylus	58	131
Oz. sann. proxima	1	
Oz. semialternans	2	5
Po. limitaris	24	31
S. wittekindti	24	27
S. pietzneri	25	19
S. hermanni	2	
Po. pennatus	2	3
Po. dubius	57	36
Prioniodina sp.	2	
Oz. sann. sannemanni	2	1
Oz. plana	1	
Oz. sann. adventa	3	
Ozarkodina sp.	2	
S. latifossatus		2
Po. cristatus ectypus		2
Palmatolepis sp.*		1
total conodonts	289	402
species diversity	22	15

Palmatolepis sp.* — sampling admixture from higher bed

Dar Kaoua	
Conodont zones	*disparilis*
bed and sample no.	LMB
Po. varcus	4
Po. xylus	3
I. difficilis	1
S. wittekindti	1
S. pietzneri	1
Po. limitaris	1
Po. dubius	7
Kl. disparilis	1juv
Kl. cf. *Kl. disparilis*	1
Tortodus sp.	1
total conodonts	21
species diversity	10

Ras-el-Kebber	
Conodont zones	*sagitta*
bed and sample no.	III-B
S. wittekindti	1
Po. dubius	10
Po. cristatus ectypus	3
S. peracutus	2
Po. pennatus	1
Kl. disparata	3
Kl. disparilis	8
Kl. disparalvea	1
Kl. vysotzkii	1
Po. dengleri sagitta	2
total conodonts	32
species diversity	10

HN-2 (bed 10f). Unrevised data for HL were published by Ebert (1993). Available collections are not very large and, in absolute numbers, no conodont is really common. The following species list does not differ much from the underlying unit: *Po. varcus, Po. xylus, Po. ansatus, Po. ovatinodosus, Po. dubius* (only at Md-E), *Po. pennatus, Po. cristatus ectypus, Po. limitaris, Oz. semialternans* (only at BT), *Oz. sannemanni sannemanni* (only at Md-E), *Tortodus* sp., *I. difficilis* (only at Md-E), *I. brevis brevis, S. hermanni, S. latifossatus* (only at BT), *S. pietzneri, S. wittekindti, S. peracutus* and *E. rhenana* (only at HN).

Richer faunas are available from the upper subunit, which was sampled at Md-E (beds 13, 14), BT (bed C2 = 35 and literature data), DK, BJ (identification list provided by Klapper), and HL (Ebert, 1993). By contrast to the lower subunit, *Po. ovatinodosus* is the most common species, followed by *S. pietzneri* and *Po. dubius*. Moderately common are *Po. xylus, Po. cristatus ectypus, Po. dubius, Po. pennatus*, *S. hermanni,* and *S. wittekindti*. Minor faunal components are *Po. varcus, Po. ansatus* (only at Md-E), *Oz. semialternans* (only at Md-E), a different "*Ozarkodina*" (from BJ), *Tortodus* sp., *T.* aff. *T. weddigei* (only at Md-E), *I. brevis latecarinatus, I. difficilis, I. arkonensis arkonensis* (only at Md-E, Fig. 8A, B), *I. symmetricus* (only at Md-E), *S. latifossatus, S. peracutus, E. rhenana* (only at BJ), *Kl. vysotzkii* (Fig. 9A, B)*, Kl. disparilis*, and *Kl. disparata*. Section Md-E yielded rare conodonts that may represent Pb elements (Gen. et sp. indet., Fig. 8G–I).

TAOUZITES BEDS

The Lower Marker Bed is overlain by a recessive succession of nodular and thin-bedded limestones that include rich ammonoid levels, especially just above the Lower Marker Bed or at the top of the sequence (OCh, bed 21, red nodule layer at Md-E = bed 17). The oxyconic and sometimes very large-sized *Taouzites taouzensis* and the small-sized *Pseudoprobeloceras pernai* are most characteristic. Corresponding goniatite shales of the Tafilalt Basin produced a flood of pharciceratids and *Taouzites*. The level has not been recognized in the southern Tafilalt where outcrop conditions of the topmost Givetian are very poor. It is possible to subdivide the *Taouzites* Beds in all sampled sections but so far no differences in conodont faunas from the lower or upper part are apparent. Samples are available from Md-E (beds 15–17), BT (beds 39–41), OCh (beds 21, 22), and HL (Ebert, 1993).

By comparison with the underlying unit the faunal composition has changed. *Po. ovatinodosus* is not very common any more and *Schmidtognathus* species are also less abundant. Instead, faunas are dominated by *Po. dengleri sagitta* n. ssp. (Fig. 6A), *Po. dubius, Kl. disparilis* (Fig. 9E), and locally (e.g., OCh), by a resurge of *Po. xylus* and *Po. varcus*. Moderately common conodonts are *Po. cristatus ectypus* and *S. wittekindti.* Minor faunal elements are represented by *Po. ovatinodosus, Po. aequidivisus* n. sp. (only at BT), *Po. pennatus, Po. limitaris, Po. ordinatus, I. difficilis* (only at BT), *I. symmetricus* (only at BT, Fig. 8C), *Tortodus* sp. (only at OCh), *T.* aff. *T. weddigei* (only at Md-E), *S. peracutus* (Fig. 7K)*, S. pietzneri* (only at HL), *Kl. vysotzkii, Kl. disparalvea*,

Table 3

Upper Givetian conodont record at Mdoura-East

Mdoura-East												
Conodont zones	*hermanni*		?	*ectypus*	*disparilis*		*sagitta*			*norrisi*		
bed and sample no.	10e	10g	11	12	13	14	15	16	17	18a	18b	19
Oz. semialternans	2	*	*	*	*	1						
S. hermanni	7	*	5	*	9	*	*	*	*	1		
Po. limitaris	3	*	*	*	5	*	*	2	*	1		
S. pietzneri	3	*	*	*	20	1						
Po. dubius	3	1	3	3	22	19	34	67	*	48	37	1
Po. pennatus	2	*	1	*	11	2	*	*	*	10	12	4
S. wittekindti		1	1	1	14	3	1	3	*	1		
Oz. sann. sannemanni			2	*	*	*	*	*	*	7	3	
Po. ansatus			2	*	6	4						
Po. xylus			2	4	17	*	3	9	*	140	155	8
I. difficilis			5	5	17	6	*	*	*	10	7	
Po. ovatinodosus			3	1	5	1	*	1	*	24	13	
Po. cristatus ectypus				1	1	14	4	9	1	1		
S. peracutus				2	*	6	4	2	*	1	4	3
Po. varcus				4	4	*	*	7	*	17	45	1
S. latifossatus					3							
Kl. vysotzkii					2	*	9	1	*	1		
I. arkonensis arkonensis					2							
I. symmetricus					3	*	*	*	*	*	2	
T. aff. *T. weddigei*						3	1					
Gen. et. sp. indet						3	3					
Kl. disparilis							25	14				
Po. dengleri sagitta n. ssp.							14	20	1	4	1	
Kl. disparalvea								3	*	1	4	
Po. dengleri dengleri										26	15	19
Oz. sann. adventa										21	1	
Po. aequidivisus n. sp.										2		
Kl. disparata											1	
Po. ordinatus											3	
Tortodus sp.											1	
Po. tafilensis n. sp.											1	9
S. gracilis												1
I. aff. *I. symmetricus*												1
total conodonts	20	2	24	21	141	63	98	138	2	316	305	47
species diversity	12			8	20		14			25		

and *Kl. disparata* (only at OCh, Fig. 9C, D). Again there are questionable Pb elements (Gen. et sp. indet.), both from Md-E and OCh (Fig. 8J–L). The episodic rarity of *Icriodus*, "*Ozarkodina*" and *Tortodus* are an interesting palaeoecological aspect that perhaps can be explained by a deepening and changes in trophic conditions.

UPPER MARKER BED

This widespread, heavily quarried, solid and massive marker unit of Becker and House (1994, 2000*a*) was named by Ebert (1993) as "Oberer *Pharciceras*-Horizont" and also represents a shallowing upwards cycle. In several sections prominent subunits can be recognized and the hardground and unconformity at the top contains many corroded goniatites and large breviconic nautiloids. In the western Tafilalt (Md-E, JA, JI, JMI) this regressive event caused erosion down to the *Taouzites* Beds whilst a thin nodular level is preserved just above it at Ouidane Chebbi in the eastern Tafilalt. The correlation into the Tafilalt Basin at Hassi Nebech is rather unclear although some beds of grey nodular limestone (bed 40 of Bensaid *et al.*, 1985) overlie the main pharciceratid level.

Table 4

Topmost middle Givetian to basal Frasnian conodont record at Bou Tchrafine, including former records of P. Bultynck and co-authors (B) or of Ebert (1993: E)

	Bou Tchrafine									
Conodont zones	*hermanni*		*ectypus*		*disparilis*		*sagitta*		*dengleri*	*norrisi*
bed and sample no.	B2	B3	B4	C1	C2	D	E	F	G	H1-2
bed and sample no.	33b-c		33d	34	35	39	40	41	42	43
Po. timorensis	3									
Po. ovatinodosus	8	8	1	B	B	*	*	3	9	B
Tortodus sp.	2	1	1	*	*	*	*	*	B	
Oz. semialternans	2	*	1	B						
Po. varcus	13	11	*	B	B	*	*	*	3	B
Po. ansatus	8	*	1							
Po. xylus	3	6	4	*	B	*	*	2	35	
I. difficilis	8	*	*	*	*	*	*	2	3	
Oz. sannemanni proxima	3	*	*	*		*	*	*	1	
Oz. sann. sannemanni	1	*	*	*	*	*	*	*	B	B
S. hermanni	27	11	2	B						
S. wittekindti	6	6	1	B	B	*	*	1	2	
S. pietzneri	1	3	*	B	B					
Po. limitaris	1	7	1	E	*	1	*	*	B	(B)
Po. dubius	1	*	*	*	*	*	1	*	1	B
El. rhenana		1								
S. aff. *hermanni*		2	1							
S. latifossatus		1	*	B	B					
Po. cristatus ectypus			? B	B	B	*	1	11	B	
S. peracutus				E	*	*	*	1	B	B
I. latecarinatus					B					
Kl. disparilis					B	*	*	1	2	
Po. dengleri sagitta n. ssp.							1	2	3	
Po. aequidivisus n. sp.							2	*	3	B
I. symmetricus								2		
Kl. disparalvea								1	B	B
Kl. vysotzkii								4		
Po. pennatus								1	4	
Po. dengleri dengleri									7	B
Oz. plana									1	
S. wittekindti									4	
Po. ?uyenoi									1	
Po. webbi									1	
S. gracilis									2	
Ct. angustidiscus									1	
Po. tafilensis n. sp.									2	
I. expansus									B	B
Po. collieri									B	B
Po. ordinatus										B
M. guanwushanensis										B
Mehlina gradata										B
total conodonts	87	57	13			1	5	31	85	
species diversity	18		14		10		14		27	14

Conodont data come from ReK, BJ (top bed G, faunal list of Klapper and new sample), BT (bed 36 = 42, including a new sample), SeR-3 (beds 16c and 17b), OCh (bed 23), and HL (Ebert, 1993).

As in the Lower Marker Bed, *Po. ovatinodosus* is relative common, as are *Po. varcus* (especially at BT), *Po. xylus, Po. dubius, Po. aequidivisus* n. sp. (Fig. 6N–Q; perhaps included in *Po. pollocki* in Bultynck, 1986), and *S. peracutus*. Moderately common are *Kl. disparilis*, *Kl. disparalvea*, *Po. dengleri sagitta* n. ssp. (Fig. 6B), and *Po. dengleri dengleri*. Many other species, including several taxa that enter new, form a small to minor part of faunas: *Po. pennatus, Po. ordinatus*, *Po. limitaris, Po. cristatus ectypus, Po. collieri* (BT record of Bultynck, 1986), *Po. webbi* (Fig. 5U)*, Ct. angustidiscus* (only at BT), *Po. tafilensis* n. sp. (only at BT), *I. expansus* (only at BT), *I. brevis brevis* (only at BT), *I. brevis eslaensis* (only at OCh), *I. difficilis*, *I. symmetricus, Oz. sannemanni sannemanni, Oz. sannemanni proxima* (only at BT, Fig. 8P), *Oz. sannemanni adventa* (only at Md-E), *Oz. plana*, *Prioniodina* sp., *T. caelatus, S. wittekindti, S. gracilis* (only at BT), *Kl. disparata*, and *Kl. vysotzkii* (ReK). As in older beds, there are *Bryantodus*-type Pb elements that may belong to a *Tortodus* apparatus. There is also a transitional specimen between *Po. ovatinodosus* and *Po. uyenoi* (Fig. 7I).

PETTEROCERAS BEDS

The *Petteroceras* Beds consist of one to three, mostly reddish and iron-rich micritic limestones that are encrusted on the Upper Marker Bed or separated by very thin argillaceous interbeds. Various species of the multilobed and (sub)oxyconic *Petteroceras* and first *Ponticeras* are very characteristic. None of the topmost Givetian goniatites regionally survived into the Frasnian (Becker and Aboussalam, 2004). This is also true for the last species of the large bivalve *Panenka* and for the phacopids. In order to elucidate the extinction around the Middle/Upper Devonian boundary with the highest possible precision, lower and upper parts of the *Petteroceras* Beds were sampled separately.

From the lower part, new samples are available from Md-E (beds 18a, b), BJ (bed H1, 2), BT, and OCh (bed 25). *Po. ovatinodosus* continues to be relative common, which is

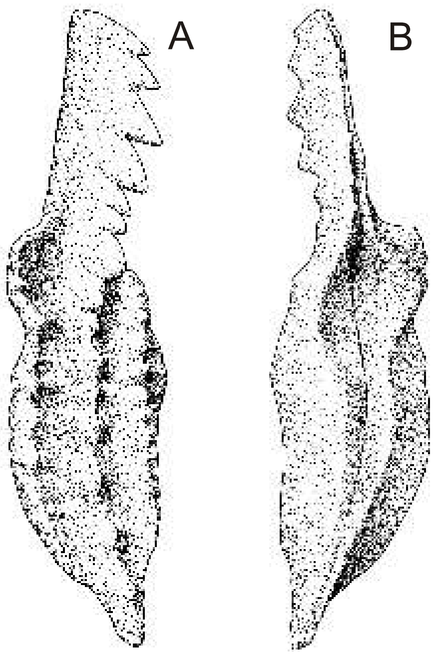


Fig. 3. Idealized drawing of *Schmidtognathus longicavus* n. sp., based on holotype B9A.1-28, upper (A) and lower (B) views, × 150

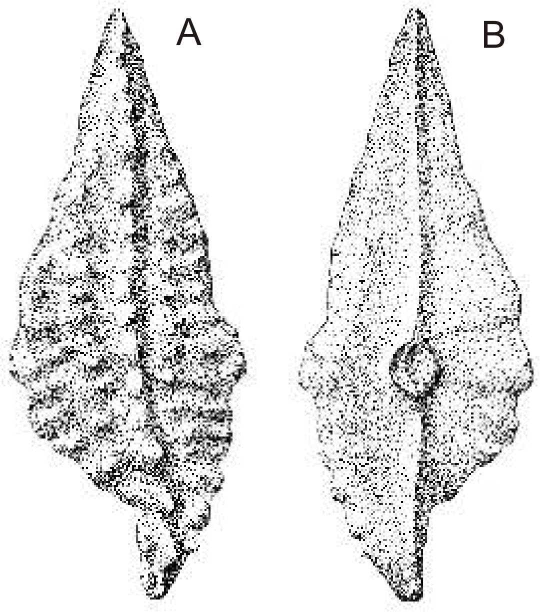


Fig. 4. Idealized morphology of *Tortodus subsymmetricus* n. sp., based on holotype B9A.1-52, upper (A) and lower (B) views, × 50

also true for *Po. varcus*, *Po. xylus* (Fig. 5I–K), *Po. dengleri sagitta* n. ssp., *Po. dengleri dengleri* (Fig. 6E, F), and *Po. dubius*. *I. difficilis, Oz. sannemanni adventa* (Fig. 8R), *Po. ordinatus* (Aboussalam, 2003, pl. 19, fig. 5), *Po. pennatus* and *Po. tafilensis* n. sp. (Fig. 5P, R) can be moderately common. A characteristic new species from BJ is *T. subsymmetricus* n. sp. (Fig. 8N, O). Minor faunal constituents are *Po. limitaris, Po. cristatus ectypus* (only at Md-E), *Po. paradecorosus, Po. webbi* (only at BJ), *Po. aequidivisus* n. sp. (Fig. 6R), *Po. saevus* n. sp. (only at BJ, Fig. 5L–O), *I. symmetricus, Oz. sannemanni sannemanni* (Fig. 8 Q), *Oz. sannemanni proxima* (only at BJ), *Oz. plana* (only at BJ), *I. expansus* (only at BT), *Tortodus* sp., *T. bultyncki* (Aboussalam 2003, pl. 25, figs. 1–3), *S. hermanni* (only at Md-E), *S. peracutus* (Fig. 7L), *S. wittekindti, S. longicavus* n. sp. (only at BJ, Fig. 7A, B), *Mehlina gradata* (BT record of Bultynck, 1986), *Kl. vysotzkii* (only at Md-E), *Kl. disparilis* (Ebert, 1993), *Kl. disparalvea* (Aboussalam, 2003, pl. 20, figs. 1, 2), *Kl. disparata* (only at Md-E), *Sk. norrisi* (only Pb Element at BJ, Fig. 8S), *Sk.* aff. *Sk. norrisi* (only at OCh, Fig. 7G, H), and *M. guanwushanensis* (*M. falsiovalis* record at BT of Bultynck and Walliser, 2000).

The topmost Givetian thin or nodular limestones of the upper *Petteroceras* Beds were sampled at three localities (Md-E, bed 19, BJ, bed H3, OCh, bed 26) and, together with literature data, produced a similar fauna to the lower *Petteroceras* Beds but slight differences can be recognized. *Polygnathus varcus* can be very common and *Po. xylus* (various morphotypes, perhaps including *Po. pseudoxylus*, Fig. 5C–H), *Po. dubius, Po. dengleri sagitta* n. ssp., and *Po. dengleri dengleri* (Fig. 6C, D) are also abundant. Moderately frequently encountered are *Po. ovatinodosus, Po. ordinatus, Po. tafilensis* n. sp. (at Md-E), and *S. peracutus*. "*Po. rugosus sensu* Ziegler, 1965" in Bultynck (1986) may be conspecific with somewhat older, irregularly ornamented morphotypes of *Po. limitaris* that were figured by Aboussalam (2003). Minor faunal elements are *Po. pennatus, Po. aequidivisus* n. sp., *Po. alatus* (only at OCh), *Po. collieri* (BT record of Bultynck, 1986), *I. expansus* (only at BT), *I. difficilis* (only at OCh), *I.* aff. *I. symmetricus* (only at Md-E, Fig. 8D, E), *Oz. sannemanni sannemanni* (only at BT), *Oz. sannemanni proxima, Oz. sannemanni adventa, S. gracilis* (only at Md-E, Fig. 7Q, R), *Kl. disparalvea*, and *M. guanwushanensis* (*M. falsiovalis* record from OCh of Belka *et al*., 1999). There are no *Tortodus* or *Skeletognathus*.

ROTUNDILOBA PRISTINA BED

A thin, solid, red and micritic limestone that lacks any macrofauna is developed at BJ between the last *Petteroceras* Bed and the first black styliolinites of the Frasnes Event Interval. During the search for a Middle/Upper Devonian stratotype, a range of Tafilalt sections was investigated by Bensaid *et al*. (1985) but a regressive phase right at series boundary caused a widespread unconformity that made the region unsuitable for the GSSP selection. The local preservation of a basalmost Frasnian limestone at BJ may indicate a small palaeotopographic depression but the overlying lower Styliolinites are not very thick. It is possible that the basalmost Frasnian is preserved in the shaly successions of the Tafilalt Basin and of the Amessoui Syncline (Bultynck, 1982; Bensaid *et al*., 1985).

A first sample of bed I at BJ was given to G. Klapper and the bed was re-sampled subsequently. It produced a rather diverse fauna with relative common early *Ancyrodella*, including *Ad. rotundiloba pristina* (simple morphotypes, Fig. 9K, L, O, P, and more advanced morphotypes, Fig. 9Q, R, all = early

Table 5

Topmost middle Givetian to basal Frasnian conodont record at Ouidane Chebbi

Ouidane Chebbi													
Conodont zones	*hermanni*						*sagitta*		*deng.*	*norrisi*			*soluta*
bed and sample no.	3c	4	5	6	7	8	18	21	23	25	26a	26b	28
Po. xylus	19	*	*	*	*	*	47	*	16	2	13	39	
L. linguiformis	3	1	*	*	*	1							
Po. ovatinodosus	153	17	12	1	2	*	3	1	*	*	*	15	
I. difficilis	46	7	2	*	*	*	*	*	*	*	*	1	1
Po. varcus	8	7	2	*	*	*	40	*	9	*	3	1	
Po. ansatus	10												
I. expansus	3												
Palmatolepis sp.*	1*												
S. pietzneri	8												
Po. timorensis	6	1											
S. gracilis	9	1											
Oz. semialternans	2	1											
S. latifossatus	18	1											
Oz. sannemanni proxima	2	*	*	*	*	*	*	*	*	*	*	1	
Po. pennatus	3	*	*	*	2	*	*	*	*	2	*	2	22
S. hermanni	1	*	1										
Po. limitaris	1	*	*	*	2								
S. wittekindti	4	1	*	*	2	*	9	1	2				
Po. dubius	60	*	*	*	*	*	50	1	9	*	13	13	4
S. cf. *S. pietzneri*		1											
I. brevis brevis		1											
Po. pseudofoliatus			1										
Tortodus sp.							1						
S. peracutus							1						
Kl. disparata							6						
Kl. vysotzkii							6						
Gen. et sp. indet.							3						
Po. dengleri sagitta							18	*	9	*	3		
Po. crist. ectypus							13	1	6				
Po. ordinatus							1	*	*	1	5	7	
Kl. disparilis							30	*	2				
I. brevis eslaensis									2				
Po. webbi									1				
Po. dengleri dengleri									1	1	16	29	
Kl. disparalvea									1	*	1		
Sk. aff. *Sk. norrisi*										1			
Po. alatus												2	
Oz. sannemanni adventa												1	
Sk. norrisi													1
Po. collieri													2
total conodonts	357	39	18	1	8	1	228	4	58	7	54	111	30
species diversity	22						14		11	14			5

Palmatolepis sp.* — sampling admixture from higher bed

morphotype of *Ad. rotundiloba sensu* Klapper, 1989), and, less common, *Ad. rotundiloba binodosa* (simple and advanced morphotypes, Fig. 9I, J, M, N). Other abundant conodonts are *Po. xylus* (including forms that may be assigned to *Po. pseudoxylus*), *Po. ovatinodosus, Po. tafilensis* n. sp., *Po. dubius, Po. pennatus* and *Po. dengleri dengleri*. *Po. dengleri sagitta* n. ssp., and *Po. alatus* (Fig. 7O, P) are moderately common. The faunal list of the rather distinctive assemblage is completed by rare *Po. collieri* Morphotype 2 (only at BJ)*, Po. paradecorosus* (Fig. 6G–I)*, Po. pollocki* Morphotype 1 (Fig. 6S)*, Po. webbi, Po. cristatus cristatus* (Fig. 9H)*, Po. cristatus* n. ssp. (Fig. 9F, G), *Po. jorfensis* n. sp. (Fig. 7C–F), *Po.* cf. *Po.*

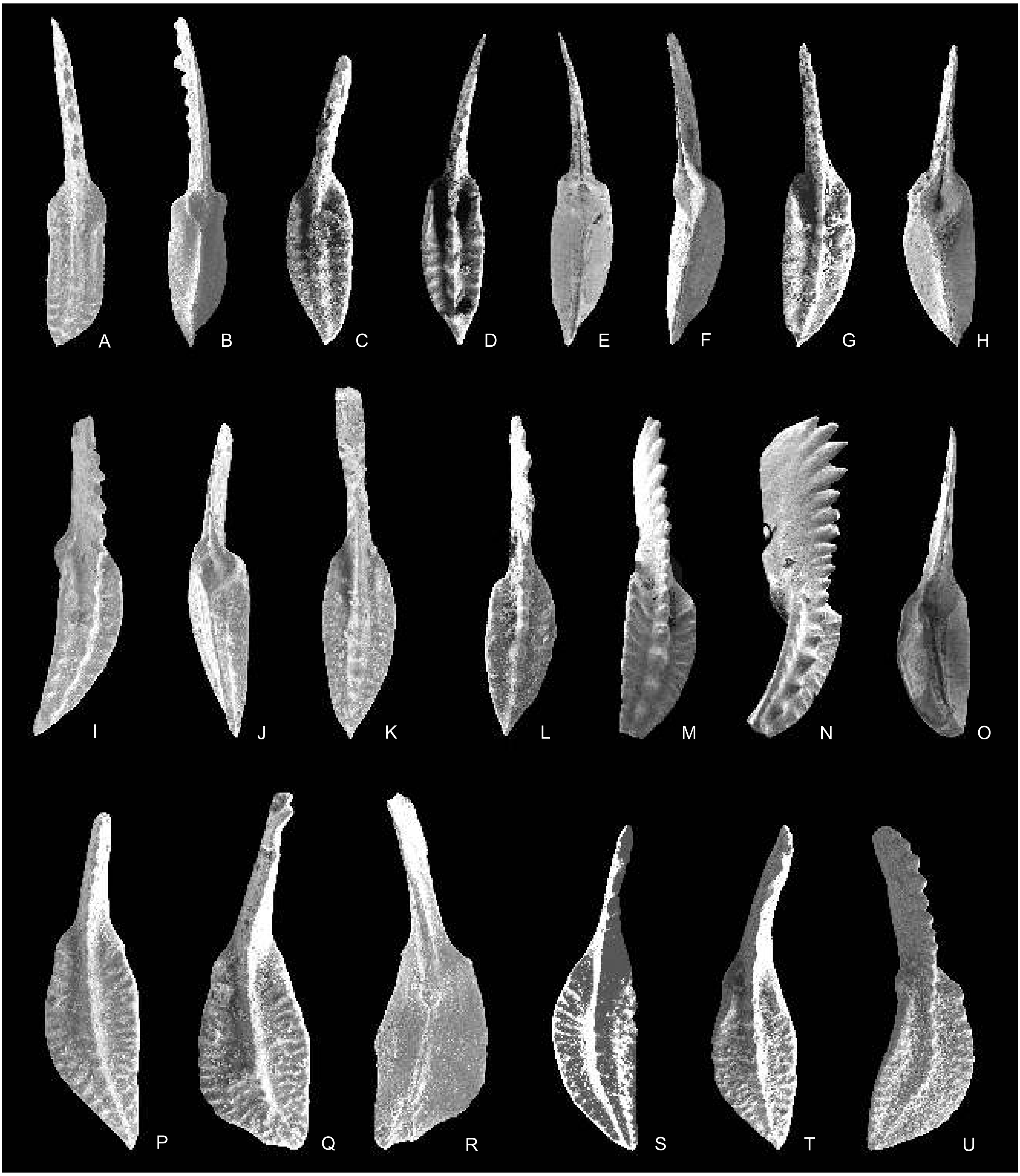


Fig. 5. Givetian polygnathids from the Tafilalt

A, **B** — *Po. xylus*, B9A.1-1, BT, bed A2 (*ansatus* Zone), typical morphotype, × 50; **C** — *Po. xylus*, B9A.1-2, OCh, bed 26b (topmost *norrisi* Zone), small-sized morphotype with relative flat platforms, × 75; **D**–**F** — *Po. xylus*, B9A.1-3, OCh, bed 26b (*norrisi* Zone), morphotype with transverse ribs and anteriorly positioned basal pit, × 75; **G**, **H** — *Po. xylus*, B9A.1-4, OCh, bed 26b (*norrisi* Zone), morphotype with flat platform and basal pit under anterior platform, × 75; **I**, **J** — *Po. xylus*, B9A.1-5, BJ, bed H1, 2 (lower *norrisi* Zone), strongly curved morphotype, × 75; **K** — *Po. xylus*, B9A.1-6, BJ, bed H1, 2 (lower *norrisi* Zone), subsymmetric morphotype with low blade, × 65; **L** — *Po. saevus* n. sp., paratype B9A.1-7, BJ, bed H1, 2 (lower *norrisi* Zone), × 75; **M**–**O** — *Po. saevus* n. sp., holotype B9A.1-8, BJ, Bed H1, 2 (lower *norrisi* Zone), × 75; **P** — *Po. tafilensis* n. sp., paratype B9A.1-9, BJ, bed H1, 2 (lower *norrisi* Zone), × 50; **Q, R** — *Po. tafilensis* n. sp., holotype B9A.1-10, BJ, bed H1, 2 (lower *norrisi* Zone), × 50; **S**, **T** — *Po. tafilensis* n. sp., paratypes B9A.1-11 and A.1-12, Md-E, bed 19 (upper *norrisi* Zone), × 40; **U** — *Po. webbi*, B9A.1-67, BT, bed 42 (*dengleri dengleri* Subzone), × 40

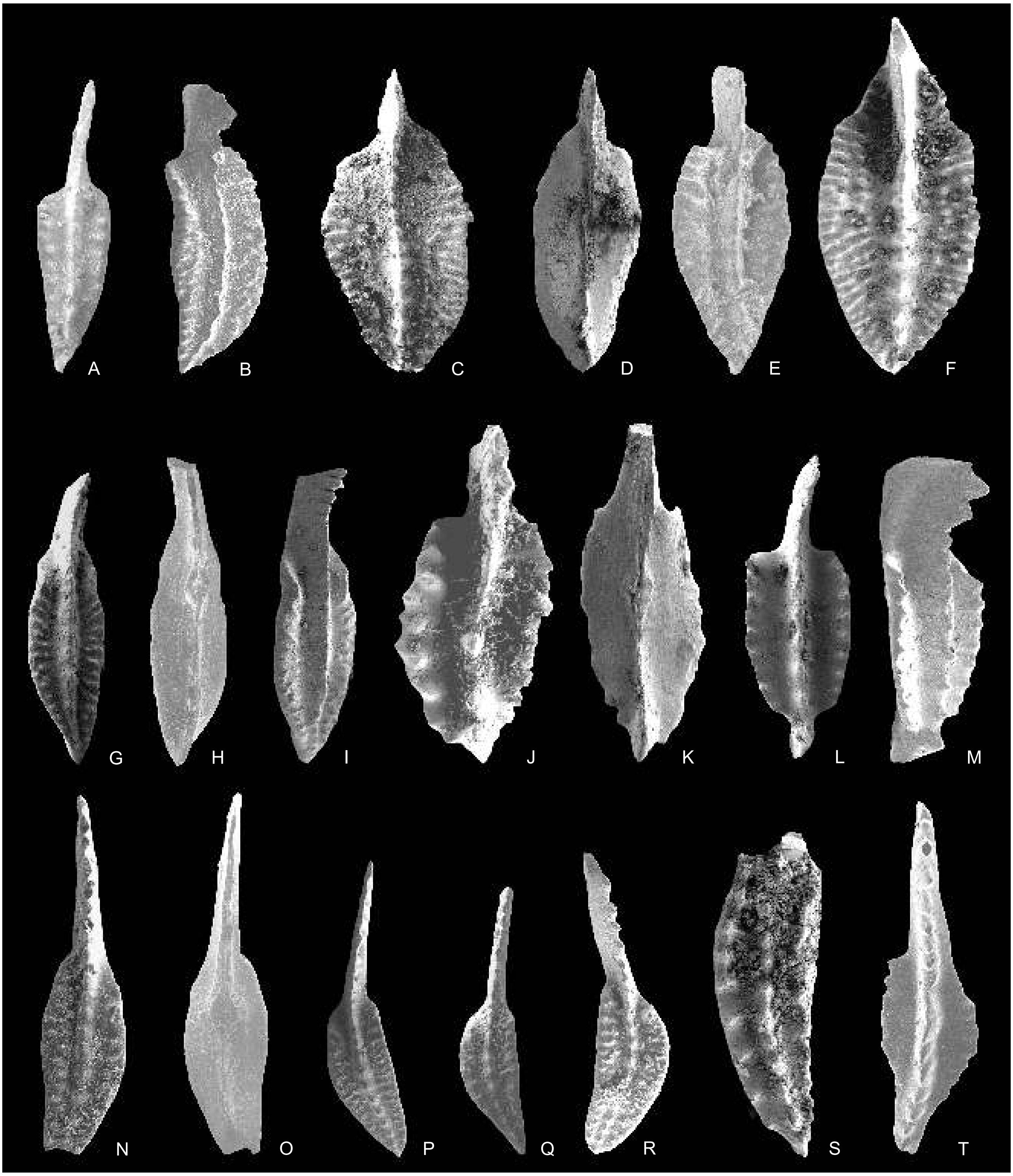


Fig. 6. Upper Givetian to basal Frasnian polygnathids of the Tafilalt

A — *Po. dengleri sagitta* n. ssp., holotype B9A.1-13, narrow morphotype, Md-E. bed 16 (*dengleri sagitta* Subzone), × 50; **B** — *Po. dengleri sagitta* n. ssp., paratype B9A.1-14, moderately wide, slightly asymmetric morphotype, BT, bed 42 (*dengleri dengleri* Subzone), × 40; **C**, **D** — *Po. dengleri dengleri*, B9A.1-15, OCh, bed 26b (upper *norrisi* Zone), × 40; **E** — *Po. dengleri dengleri*, B9A.1-16, Md-E, bed 18 (lower *norrisi* Zone), × 50; **F** — *Po. dengleri dengleri*, B9A.1-17, BJ, bed H1, 2 (lower *norrisi* Zone), × 40; **G**, **H** — *Po. paradecorosus*, B9A.1-18, BJ, bed I (*rotundiloba pristina* Zone), × 50; **I** — *Po. paradecorosus*, B9A.1-19, OCh, bed 28 (*rotundiloba soluta* Zone), × 50; **J, K** — *Po. collieri* Morphotype 2, B9A.1-20, BJ, bed I (*rotundiloba pristina* Zone), × 50; **L**, **M** — *Ct. lanei*, B9A.1-21, BJ, bed I (*rotundiloba pristina* Zone), × 75; **N–O** — *Po. aequidivisus* n. sp., paratype B9A.1-22, BT/bed 42 (*dengleri dengleri* Subzone), × 65; **P** — *Po. aequidivisus* n. sp., holotype B9A.1-23, BT, bed 42 (*dengleri dengleri* Zone), × 50; **Q** — *Po. aequidivisus* n. sp., paratype B9A.1-24, BT, bed 42 (*dengleri dengleri* Zone), × 65; **R** — *Po. aequidivisus* n. sp., paratype B9A.1-25, slightly transitional to *Po. tafilensis* n. sp., BJ, bed H1, 2 (lower *norrisi* Zone), × 50; **S** — *Po. pollocki* Morphotype 1, B9A.1-26, BJ, bed I (*rotundiloba pristina* Zone), × 75; **T** — *Ct. angustidiscus*, B9A.1-27, BT, bed 42 (*dengleri dengleri* Subzone), × 50

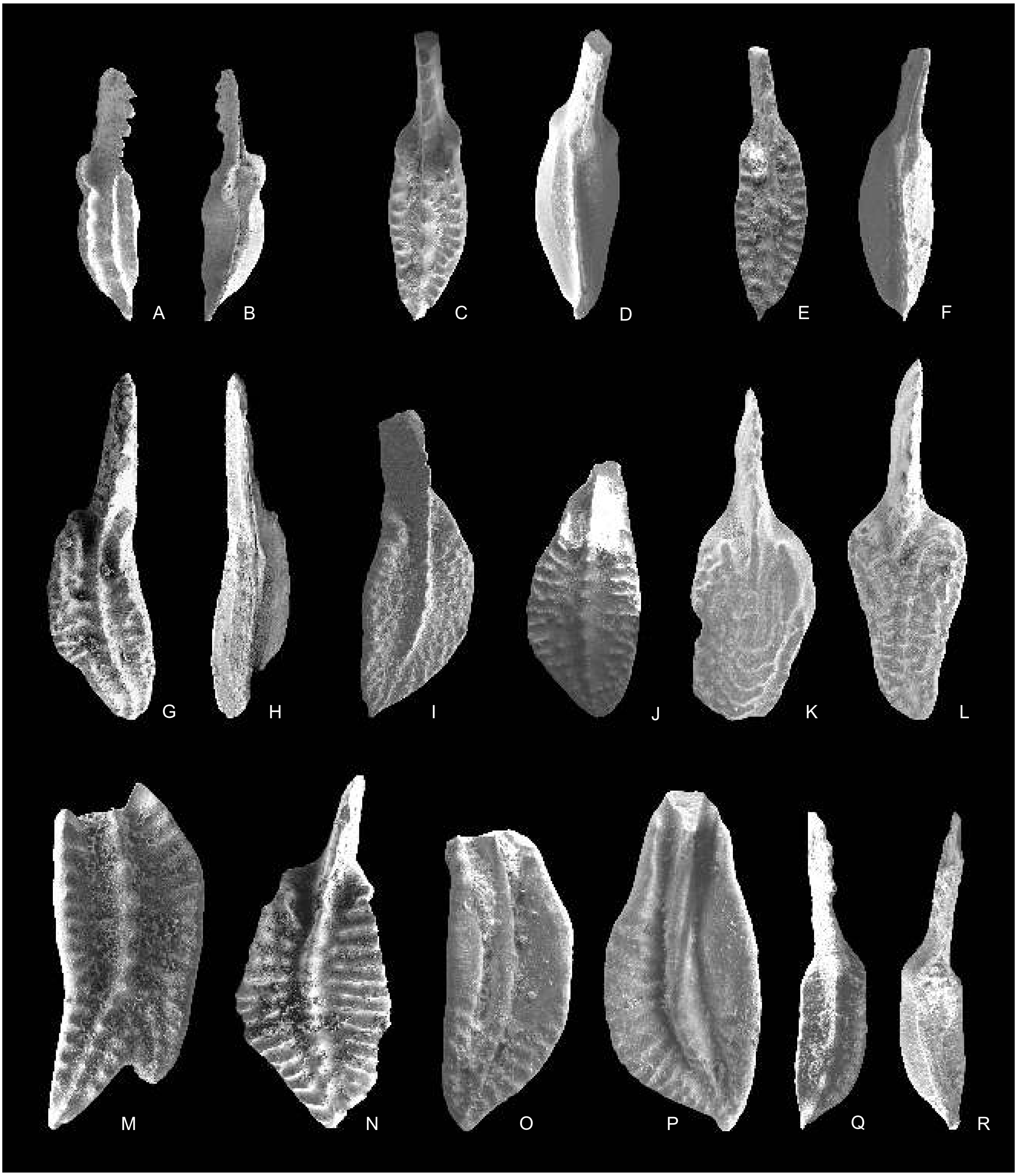


Fig. 7. *Polygnathus, Schmidtognathus* and *Skeletognathus* from the highest Givetian and basal Frasnian of the Tafilalt

A, **B** — *S. longicavus* n. sp., holotype B9A.1-28, BJ, bed H1, 2 (lower *norrisi* Zone), × 75; **C**, **D** — *Po. jorfensis* n. sp., paratype B9A.1-29, BJ, bed I (*rotundiloba pristina* Zone), × 65; **E**, **F** — *Po. jorfensis* n. sp., holotype B9A.1-30, BJ, bed I (*rotundiloba pristina* Zone), × 65; **G**, **H** — *Sk.* aff. *Sk. norrisi*, B9A.1-31, OCh, bed 25 (lower *norrisi* Zone), × 50; **I** — *Po. ovatinodosus*, transitional to *Po. uyenoi*, B9A.1-32, BT, bed 42 (*dengleri dengleri* Subzone), × 50; **J** — *Po.* cf. *Po. uyenoi*, specimen with smooth rostrum, B9A.1-33, BJ, bed I (*rotundiloba pristina* Zone), × 50; **K** — *S. peracutus*, morphotype with subconcentric ridges, B9A.1-34, OCh, bed 18 (lower *dengleri sagitta* Subzone), × 30; **L** — *S. peracutus*, B9A.1-35, Md-E, bed 18b (lower *norrisi* Zone), × 30; **M** — *Po. pennatus*, pathological specimen with secondary platform lobe, B9A.1-36, BJ, bed H1, 2 (lower *norrisi* Zone), × 65; **N** — *Po. pennatus*, transitional to forms previously identified as *Po. rugosus*, B9A.1-37, OCh, bed 28 (*rotundiloba soluta* Zone), × 40; **O**, **P** — *Po. alatus*, B9A.1-38 and 1-39, BJ, bed I (*rotundiloba pristina* Zone), both × 65; **Q**, **R** — *S. gracilis*, B9A.1-40, Md-E, bed 19 (upper *norrisi* Zone), × 75

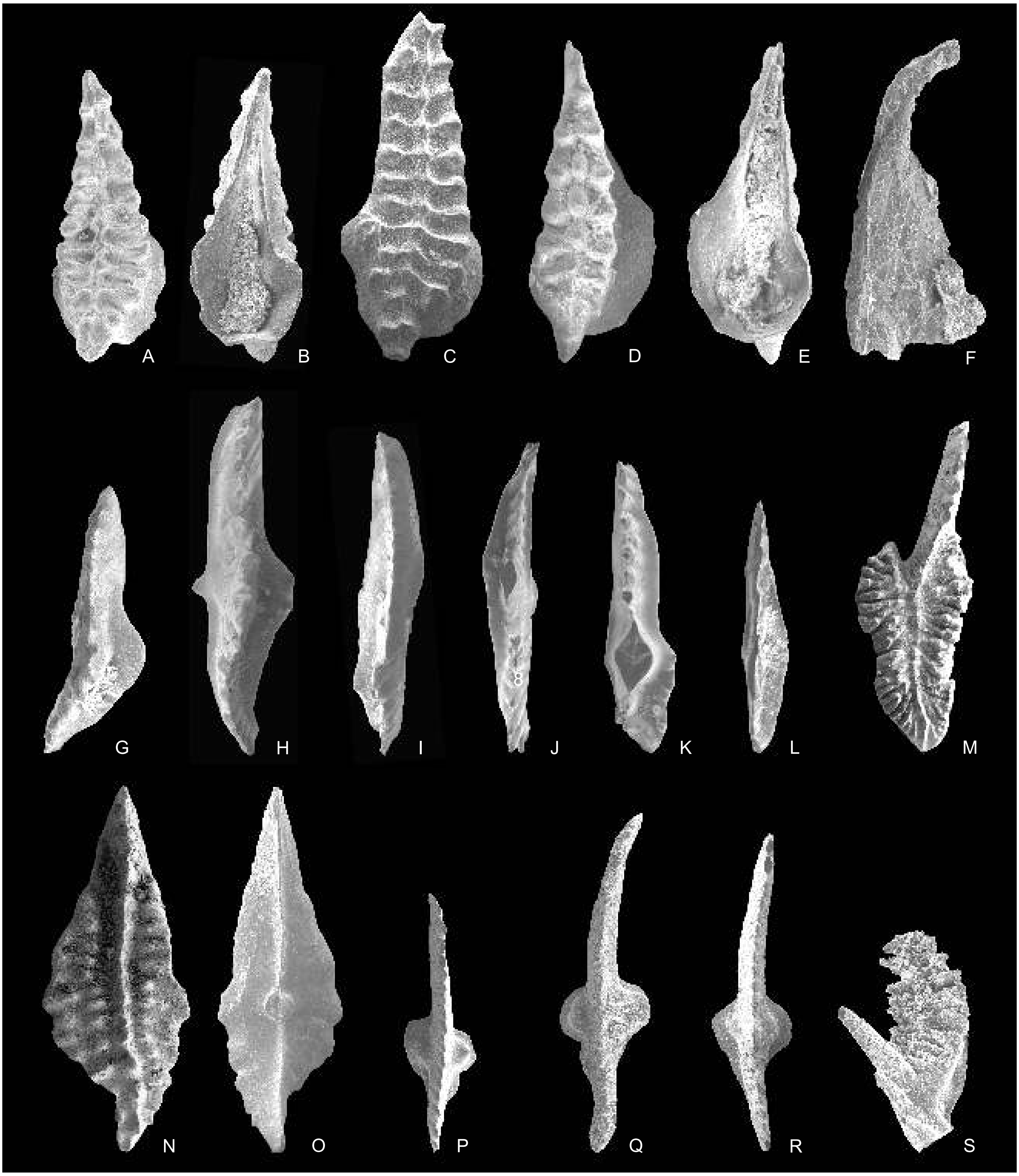


Fig. 8. Various conodonts from the upper Givetian and lower Frasnian of the Tafilalt

A, **B** — *I. arkonensis arkonensis*, B9A.1-41, Md-E, bed 13 (*disparilis* Zone), × 50; **C** — *I. symmetricus*, morphotype with relative strong transverse ridges between nodes, in this respect resembling *I. arkonensis*, B9A.1-42, BT, bed 41 (upper *dengleri sagitta* Subzone), × 50; **D, E** — *I.* aff. *I. symmetricus* (*sensu* Bultynck and Jacobs, 1982), B9A.1-43, Md-E, bed 19 (upper *norrisi* Zone), × 75; **F** — *B. resima*, B9A.1-44, Md-E, bed 20 (Upper Styliolinite), × 75; **G, I** — Gen. et sp. indet., three different morphotypes, B9A.1-45 to 1-47, Md-E, bed 14 (upper *disparilis* Zone), all × 50; **J–L** — Gen. et sp. indet., three different morphotypes, B9A.1-48 to 1-50, OCh, bed 18 (lower *dengleri sagitta* Subzone), all × 50; **M** — *Sk. norrisi*, Pa element, B9A.1-51, OCh, bed 27b (*rotundiloba soluta* Zone), × 50; **N, O** — *T. subsymmetricus* n. sp., holotype B9A.1-52, BJ, bed H1, 2 (lower *norrisi* Zone), × 40; **P** — *Oz. sannemanni proxima*, B9A.1-53, BT, bed 42 (*dengleri dengleri* Subzone), × 50; **Q** — *Oz. sannemanni sannemanni*, B9A.1-54, Md-E, bed 18a (lower *norrisi* Zone), × 50; **R** — *Oz. sannemanni adventa*, B9A.1-55, BJ, bed H1, 2 (lower *norrisi* Zone), × 50; **S** — *Sk. norrisi*, Pb element, B9A.1-56, BJ, bed H1, 2 (lower *norrisi* Zone), × 55

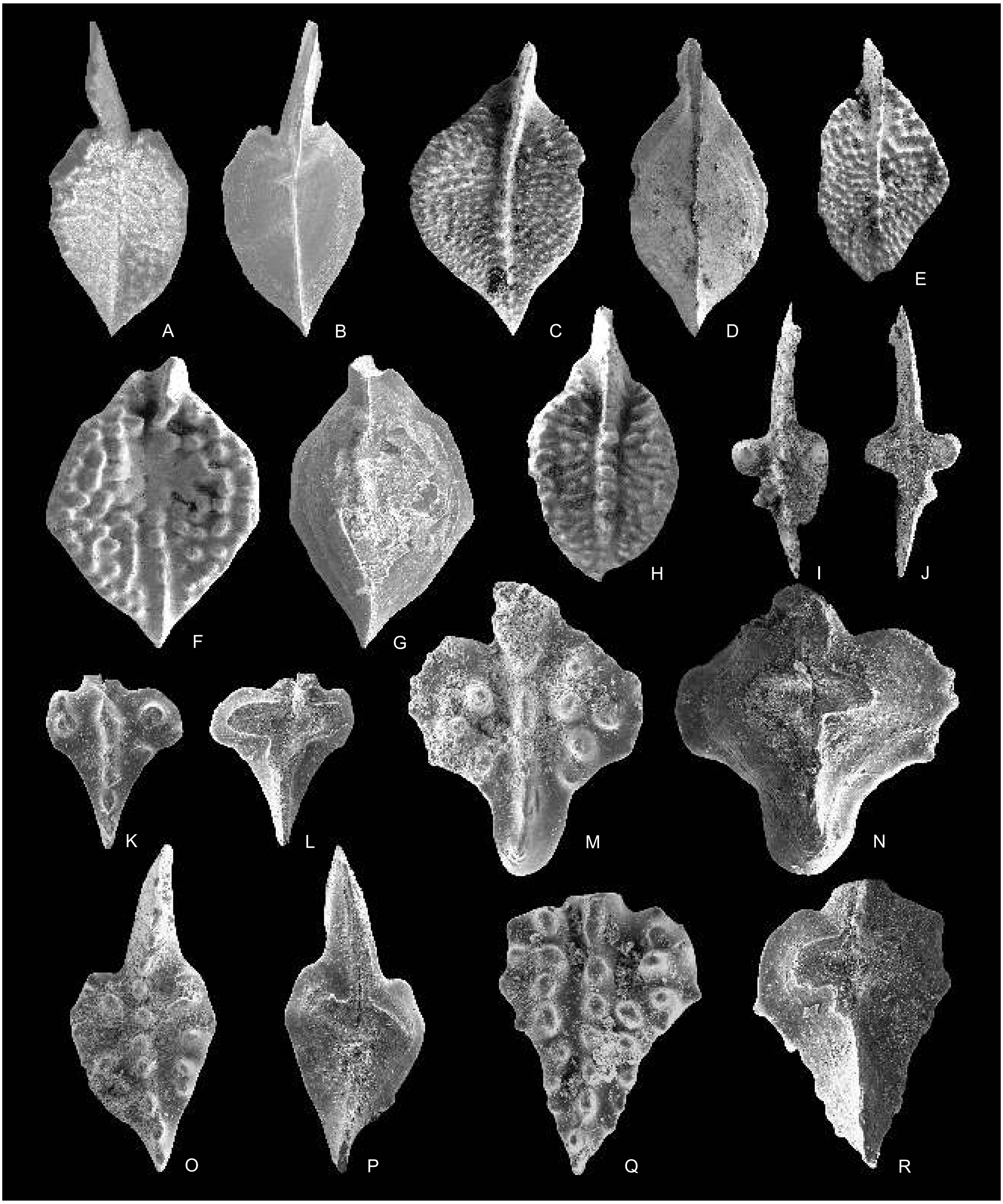


Fig. 9. ***Klapperina, Po. cristatus*** **and** ***Ancyrodella*** **from the upper Givetian and basal Frasnian of the Tafilalt**

A, **B** — *Kl. vysotzkii*, B9A.1-57, Md-E, bed 13 (*disparilis* Zone), × 35; **C**, **D** — *Kl. disparata*, B9A.1-58, Och, bed 18 (*dengleri sagitta* Subzone), × 35; **E** — *Kl. disparilis*, B9A.1-59, OCh, bed 18 (*dengleri sagitta* Subzone), × 35; **F**, **G** — *Po. cristatus* n. ssp., B9A.1-60, BJ, bed I (*rotundiloba pristina* Zone), × 35; **H** — *Po. cristatus cristatus*, B9A.1-61, BJ, bed I (*rotundiloba pristina* Zone), × 35; **I**, **J** — *Ad. rotundiloba binodosa*, simple morphotype with small platform lobes and few nodes, B9A.1-62, BJ, bed I (*rotundiloba pristina* Zone), × 50; **K**, **L** — *Ad. rotundiloba pristina*, simple morphotype with very few nodes, B9A.1-63, BJ, bed I (*rotundiloba pristina* Zone), × 50; **M**, **N** — *Ad. rotundiloba binodosa*, advanced morphotype with additional nodes and large, rounded platform lobes, B9A.1-64, bed I (*rotundiloba pristina* Zone), × 50; **O**, **P** — *Ad. rotundiloba pristina*, simple morphotype with few nodes, B9A.1-65, BJ, bed I (*rotundiloba pristina* Zone), × 50; **Q**, **R** — *Ad. rotundiloba pristina*, advanced morphotype with numerous nodes, B9A.1-66, BJ, bed I (*rotundiloba pristina* Zone), × 50 *uyenoi* (possibly pathological, Fig. 7J), *Po. incompletus* (record of G. Klapper), *Ct. angustidiscus, Ct. lanei* (Fig. 6L, M), *Belodella* sp., and *I. subterminus* (record of G. Klapper).

FRASNES EVENT STYLIOLINITES (LOWER STYLIOLINITES)

The widespread, black, often marly, lower Frasnian styliolinites have been investigated in detail at BT by Bensaid *et al*. (1985) and Bultynck (1986). The onset of styliolinites marks the boundary between units K and L within the Bouia Formation (Bultynck and Walliser, 2000). Wendt and Belka (1991) applied the misleading term "Lower Kellwasser Member" to the succession but correlation with the Frasnes Event Interval was recognized by Belka *et al*. (1999). A basal, moderately solid or concretionary limestone and subsequent rather argillaceous beds mostly lack ancyrodellids and, therefore, were difficult to date. The BT conodont record has been confirmed by re-sampling, also at BJ and OCh, but there are slight differences of faunal composition from locality to locality. Only the Lower Styliolinites represent the true Frasnes Event Interval whilst the younger subunit (Upper Styliolinites) with several *Ancyrodella* species, more abundant ammonoids (*Manticoceras*), bivalves and brachiopods seems to correlate with the latest lower Frasnian Timan Event (Becker and House, 1997). The Frasnes Event Interval can be recognized in the Tafilalt Basin, but not so far in the Amessoui Syncline of the southern Tafilalt.

The total number of recorded species is rather high but many forms are represented by few specimens. *Polygnathus pennatus* can be dominant (Fig. 7N) and small *Ct. lanei* are abundant at BJ. Locally (BJ) even more abundant *I. difficilis* and other icriodids appear to be in conflict with the interpretation of the styliolinites as having formed during deepening and transgression. As at the Frasnian–Famennian boundary, it is possible that palaeoecological factors other than bathymetric changes influenced the icriodid distribution. This was also recently postulated for *Icriodus* blooms around the lower/middle Frasnian boundary of Poland (Sobstel *et al*., 2006). It is remarkable that the shallow-water genus *Belodella* (Fig. 8F) may occur in lower Frasnian styliolinites, too (as it does in the argillaceous Tafilalt Basin at Hassi Nebech, Bensaid, 1974; Aboussalam, 2003) but a belodellid spike was also observed in the Holy Cross Mountains. The extreme rarity of *Ancyrodella* and the presence of *Mesotaxis* in the Lower Styliolinites is in accord with a deepening (Sobstel *et al*., 2006).

Moderately common species of the Lower Styliolinites are *Po. varcus, Po. dubius,* and *Sk. norrisi* (Fig. 8M). *Po. xylus*, *Po. ovatinodosus* (only at BT), *Po. aequidivisus* n. sp., *Po. collieri* Morphotype 2 (Fig. 6J, K), *Po. paradecorosus, Po. webbi, Po. cristatus cristatus*, *Po. alatus* (only at BJ), *Ct. lanei* (only at BJ), *I. brevis brevis* (only at BT), *I. brevis latecarinatus* (only at BT), *I. symmetricus* (only at BJ), *I. subterminus, I.* aff. *I. arkonensis* (only at BJ), *I.* aff. *I. expansus* (only at BJ), *Oz. sannemanni sannemanni* (only at BT), *Oz. sannemanni adventa* (Only at BJ), *Oz. semialternans?* (BT record of Klapper), *Ad. rotundiloba soluta* (BT record of Bultynck and Walliser, 2000), *Ad. rotundiloba rotundiloba* (BT record of Bultynck and Walliser, 2000), *M. guanwushanensis* (new specimens from BJ), and *M. ?asymmetrica* (BT record of Bultynck, 1986) are rare.

CONODONT ZONATION

Aboussalam (2003) has revised the conodont zonation for the lower part of the *Pharciceras* Stufe and the new data are in full agreement with the recognition of successive *Oz. semialternans* (*Pharciceras* aff. *P. amplexum* Bed), *S. hermanni* (*Mzerrebites erraticus* Beds) and *Po. cristatus ectypus* (Red *Lunupharciceras* Beds) Zones (Table 3). The extended regional data show that the zonal assignment of individual faunas is partly hampered by the unfortunate fact that zonal markers may locally enter as subordinate faunal elements. This is true for the *cristatus ectypus* Zone, *disparilis* Zone, and especially for the *norrisi* and *rotundiloba soluta* zones. Alternative zonal markers are even less common. Without the context of regional litho- and ammonoid biostratigraphy this has led in the past to some wrong age assignments. The zonal characteristics can be briefly summarized as follows (Table 6):

S. HERMANNI ZONE

Defined by the entry of the name-giving or of various other *Schmidtognathus* species, especially of *S. wittekindti* and *S. pietzneri. Po. limitaris, Po. dubius* and first *Po. pennatus* are important alternative zonal markers. Rare forms that are restricted to the zone are *Po. housei, Po. acrinodosus*, and *Po. hemipennatus.* There are also first rare *S. gracilis*, which confirms the rather early record of the species from the neighbouring Maider region by Bultynck and Jacobs (1981). *S. hermanni* includes a morphotype or possible new subspecies with very large basal cavity that may extend beyond the platform, forming an incipient side-lobe.

PO. CRISTATUS ECTYPUS ZONE

Defined by the entry of the name-giving subspecies. There are no other zonal markers in the nodules below the Lower Marker Bed. *S. peracutus* enters as an important additional zonal index above the zonal base in the lower part of the latter.

KL. DISPARILIS ZONE

Entry of the name-giving or of any other *Klapperina* species, such as *Kl. vysotzkii* (identified as transitional forms between *Po. cristatus* and *Klapperina* by Ziegler and Klapper, 1982), *Kl. disparalvea*, or *Kl. disparata*, in the upper subunit of the Lower Marker Bed. Bultynck and Jacobs (1981) did not find *Klapperina* at this level at Bou Tchrafine but the genus was first recorded by Ebert (1993) and our sampling at BT, DK, Md-E, JA, and BJ confirmed this. The *disparilis* Zone (= former Lower *disparilis* Zone) is a rather condensed interval throughout the Tafilalt. It features the youngest *Po. ansatus* at Md-E, which conforms to the rare youngest global records

(Aboussalam, 2003). The same section has the youngest known *I. arkonensis arkonensis* (Fig. 8A, B), which extends its range upwards from the *cristatus ectypus* Zone of Northern Spain (Garcia-Lopez, 1987), and the oldest *I. symmetricus*. The composite of Klapper (1997) gives a much higher entry of the latter species but relatives are already known from the *cristatus ectypus* Zone (Garcia-Lopez, 1987). Upper Givetian forms close to *I. symmetricus* need further detailed revision.

PO. DENGLERI SAGITTA SUBZONE

Entry of the name-giving and relative common new subspecies at the base of the *Taouzites* Beds. The Tafilalt samples suggest that *Po. ordinatus* can be regionally used as an alternative marker species. In other regions (Aboussalam, 2003), the species ranges downwards into the *hermanni* Zone. *Po. aequidivisus* n. sp. enters as a rare form and continues in later topmost Givetian zones.

The new subzone forms the lower part of the previous (Klapper and Johnson, 1990) Upper *disparilis* Zone or the lower part of the *dengleri* Zone *sensu* Bultynck and Jacobs (1981). Based on the age of illustrated specimens, it seems that it can also be recognized at least in North Cornwall (Kirchgasser, 1970) and the Holy Cross Mountains of Poland (Racki and Bultynck, 1993). It needs to be emphasized that it does not correlate with the Lower *dengleri* Subzone of Klapper and Johnson (1980), which was defined by the entry of *Kl. disparilis* and which included the whole interval from the base of the *disparilis* to the top of the (new) *dengleri dengleri* Subzone. Feist and Klapper (1985) noted early relatives of *Po. dengleri* in the upper part of the Lower *disparilis* of the Montagne Noire.

PO. DENGLERI DENGLERI SUBZONE

Entry of the nominate subspecies of *Po. dengleri* near the base of the Upper Marker Bed. This subzone is an important level since a number of other polygnathids enter, which are rare in the Tafilalt but which occur elsewhere and in different settings. These are *Po. webbi, Po. collieri* and *Ct. angustidiscus.* According to the composite range of Klapper (1997), *Po. webbi* enters at the base of the Frasnian (CS 96.9) but Uyeno (1974) and Norris and Uyeno (1983) previously published records from the topmost Givetian *insita* Fauna of NE and Central Alberta. The new Moroccan material confirms and extends the range down into the highest Givetian. *Ct. angustidiscus* enters in the shallow-water Upper *subterminus* Fauna of Iowa, Alberta and Manitoba (e.g., Witzke *et al*., 1989; Rogers, 1998) but it was found below *Po. dengleri* in Nevada (Johnson *et al*., 1980) and Central Asia (Bardashev, 1992). In the Pyrenees, a morphotype with curved, long posterior appendix of the carina was found just below *Sk. norrisi* and together with *Po. dengleri*, which suggests the *dengleri dengleri* Subzone (Liao *et al*., 2001). Klapper (1997) gives a composite range of *Po. collieri* that begins slightly above the lower range of *Sk. norrisi*, but the Bultynck (1986) record requires a downwards range extension, probably at least for Morphotype 2. *Polygnathus tafilensis* n. sp. enters as a rare form in the *dengleri dengleri* Subzone and continues into the Frasnian. The transitional specimen between *Po. ovatinodusus* and *Po. uyenoi* from BT is slightly younger than the two types of the rare species from the *disparilis* Zone of Central Asia (Bardashev, 1992) and NW Canada (Uyeno, 1978).

The new *dengleri dengleri* Subzone does not correlate with the former Upper *dengleri* Subzone of Klapper and Johnson (1980), which was defined by the entry of *Sk. norrisi*. It represents an upper subdivision of the former Lower *dengleri* Zone and of the Upper *disparilis* Zone (Klapper and Johnson, 1990). Based on *Ct. angustidiscus*, it may correlate with the Upper *subterminus* Fauna of North America (see discussion in Rogers, 1998).

SKELETOGNATHUS NORRISI ZONE

Entry of the name-giving species, which also can be recognized (at BJ) based on its characteristic (e.g., Sandberg *et al*., 1989; Kirchgasser, 1994) Pb element. *M. guanwushanensis* (= *falsiovalis*) can serve as a good alternative marker, but both taxa are very rare in the *Petteroceras* Beds of the region. Bultynck (1986) recorded *Mehlina gradata* from the latter at BT but in North America (e.g., Norris *et al*., 1982, Witzke *et al*., 1989) the species may enter before *Sk. norrisi*, as a marker of the underlying Upper *subterminus* Fauna. *T. subsymmetricus* n. sp. from BJ is a good local marker species for the *norrisi* Zone. *Po. saevus* n. sp., *S. longicavus* n. sp., and *Sk.* aff. *Sk. norrisi* are rare species that are restricted to the *norrisi* Zone in the Tafilalt. The first species may continue in the Canadian Frasnian (Uyeno, 1974). The *norrisi* Zone is the type-level of *T. bultyncki*, not the lower Taghanic Event Interval, as reported by mistake in Aboussalam (2003); but the species is more typical for older strata.

Several other polygnathids enter in the topmost limestone layers of the Tafilalt Givetian that may be useful for correlation into shallower facies: *Po. alatus, Po. paradecorosus, Po. pollocki* Morphotype 1, and some *Po. xylus* morphotypes. Klapper (1997) gives a composite range of *Po. alatus* that only just pre-dates the base of the Frasnian and this is confirmed by the new Tafilalt record. Uyeno and Wendte (2005) listed *Po. alatus* from low in the *norrisi* Zone of the Archie well of Alberta, Racki and Bultynck (1993) illustrated it from the *norrisi* Zone of the Holy Cross Mountains (Poland). All these rather consistent data do not resolve the enigmatic, much older (upper part of *ansatus* Zones, middle Givetian) records from New York (Huddle, 1981) and Nevada (Johnson *et al*., 1980). *Po. pseudoxylus*, described from the lower Frasnian of the central Russian Platform (Kononova *et al*., 1996), is very close to *Po. xylus* and its total range is not yet well established. In a later review (Ziegler *et al*., 2000), the species was also listed from the late lower Frasnian of the Rhenish Massive and of the Volga-Ural Province. The Tafilalt topmost Givetian populations of *Po. xylus* consist of a range of morphotypes (Fig. 5C–K), which may include *Po. pseudoxylus*, but small specimens of both species currently cannot be distinguished. The rather early entry of *Po. pollocki* Morphotype 1 at BJ seems in accord with the previous record of the species from OCh in Belka *et al*. (1999) but their material was not figured. *Po. pollocki* is more typical for the Frasnian

(Druce, 1976), where it includes smooth forms (Morphotype 2, Zhuravlev, 1999, probably a separate taxon), gave rise to derived species, and it (Morphotype 2) is used as a zonal index of shallow-water Russian Platform deposits (Kozlova, 2002; Zhuravlev *et al*., 2006). *Po. paradecorosus* (e.p. = *Polygnathus* nov. sp. Dzik, 2002) was documented by Ji and Ziegler (1993) from the lower Frasnian (MN zones 2–4) of South China, but without illustrations, they also claim an older occurrence in the *disparilis* Zone. The Moroccan specimen confirms a range of the distinctive species at least from the *norrisi* Zone. In Germany and Russia it is also common in the middle Frasnian (*Po. decorosus* in Ziegler *et al*., 2000) and later it gave rise to *Avignathus* (see Dzik, 2002).

The base of the topmost Givetian *norrisi* Zone correlates with the base of the former Lowermost *asymmetricus* Zone (Ziegler, 1971), with the base of the former Upper *dengleri* Subzone (Klapper and Johnson, 1980), with the base of the Lower *falsiovalis* Zone of Sandberg *et al*., (1989), and with the base of the shallow-water *Pandorinellina insita* Zone (e.g., Uyeno, 1978; Norris and Uyeno, 1983; Witzke *et al*., 1989; Bultynck, 2007).

A significant extinction event at the top of the *Petteroceras* Beds affected the genera *Schmidtognathus* and *Klapperina*, as well as some long-ranging species, such as *Po. limitaris, Oz. plana*, and regionally, *I. expansus*.

ANCYRODELLA ROTUNDILOBA PRISTINA ZONE
(MN 1 ZONE)

Entry of the name-giving subspecies (= early *rotundiloba* morphotype of Klapper, 1985), which also defines MN Zone 1 of Klapper (1989) and the base of the Upper Devonian in the Montagne Noire GSSP. *Ad. rotundiloba binodosa* does not precede *Ad. rotundiloba pristina* (Becker and Aboussalam, 2004) but is a contemporaneous sister subspecies; both seem to have their roots in *Oz. sannemanni*, which is widespread in the topmost Givetian. Some rare forms may be useful for the recognition of the Frasnian elsewhere: *Po. cristatus* n. ssp., *Po. incompletus* and *Ct. lanei. Po. incompletus* was originally (Uyeno, 1974) described from the basal Frasnian of Alberta, which was confirmed by McLean and Klapper (1998, p. 527) in the southern District of Mackenzie (lower Hay River Formation) and by Uyeno and Wendte (2005) for a borehole in central Alberta. *Po. cristatus* n. ssp. also occurs in the basal Frasnian of the Rhenish Massive (new record). *Po. cristatus cristatus* enters at BJ at the base of the Frasnian (Fig. 9F) but very similar forms were illustrated as *Po. cristatus?* from the Upper *disparilis* Zone of the Montagne Noire (Klapper, 1989) and from the *norrisi* Zone (Lodi Limestone) of New York (Kirchgasser, 1994). *Ct. lanei* was first described as *Po*. aff. *Po. angustidiscus* from higher parts of the lower Frasnian of New York (West River Shale, Huddle, 1981). The Canadian specimens of Klapper and Lane (1985) are from even higher, middle Frasnian strata. On the Russian Platform, *Ct. lanei* enters in the Upper Timan Formation (Timan) and Snetnaya Gora Beds (Main Devonian Field), levels which were thought to fall in the basal Frasnian (Kuzmin, 1995; Zhuravlev *et al*., 1997, 2006). This interpretation is supported here.

Po. jorfensis n. sp. is currently restricted to the *rotundiloba pristina* Zone of the Tafilalt. A somewhat similar form was illustrated by Bai *et al*. (1982) from the basalmost Frasnian of Guangxi, South China, as *Polygnathus* sp. C.

ANCYRODELLA ROTUNDILOBA SOLUTA ZONE
(MN 2 ZONE)

Entry of the name-giving subspecies or of late *rotundiloba* morphotypes *sensu* Klapper (1985), which also defines MN Zone 2 of Klapper (1989). *Ancyrodella* is exceedingly rare in the Lower Styliolinites of the Tafilalt and the index form and the nominate subspecies were only noted by Bultynck and Walliser (2000). *M. asymmetrica* was questionably listed by Bultynck (1986); his illustrated specimen, however, is from the younger top of the lower Frasnian (Upper Styliolinites) at BT. Our samples include no additional material. The facies-controlled lack of ancyrodellids and the presence of both *Sk. norrisi* and *M. guanwushanensis* (= *falsiovalis*) previously led to a dating as *norrisi* Zone (see discussion in Bultynck, 1986), but the rich basal Frasnian fauna from underlying limestone at BJ and the sparse *Ancyrodella* record of Bultynck and Walliser (2000) place all black styliolinites unequivocally in the lower Frasnian. In the Tafilalt, the entry of stout morphotypes of *I. subterminus* with abruptly increasing height of the denticles of the posterior middle row extension (Bultynck and Hollard, 1980; Bultynck, 1986; new collections) is a good ecostratigraphical marker for the *rotundiloba soluta* Zone, but other morphotypes of the species extend down into the upper Givetian (latest review in Bultynck, 2007). There are even middle Givetian records, which are obviously based on confusion with similar species, such as *I. lilliputensis, I. obesus* or *I. excavatus* (see Bultynck, 1987, 2007). *I. uyenoi* Savage (1992) is not kept as an upper Frasnian subspecies of *I. subterminus* but granted full species status. Rare specimens from BJ assigned to *I.* aff. *I. expansus* have alternating nodes of the median and lateral rows and the posterior extension of the first consists only of a single large node. *I.* aff. *I. arkonensis* from BJ has fewer nodes in all rows than in the older, typical *I. arkonensis*. These two icriodids need further study and may be characteristic for the lower Frasnian.

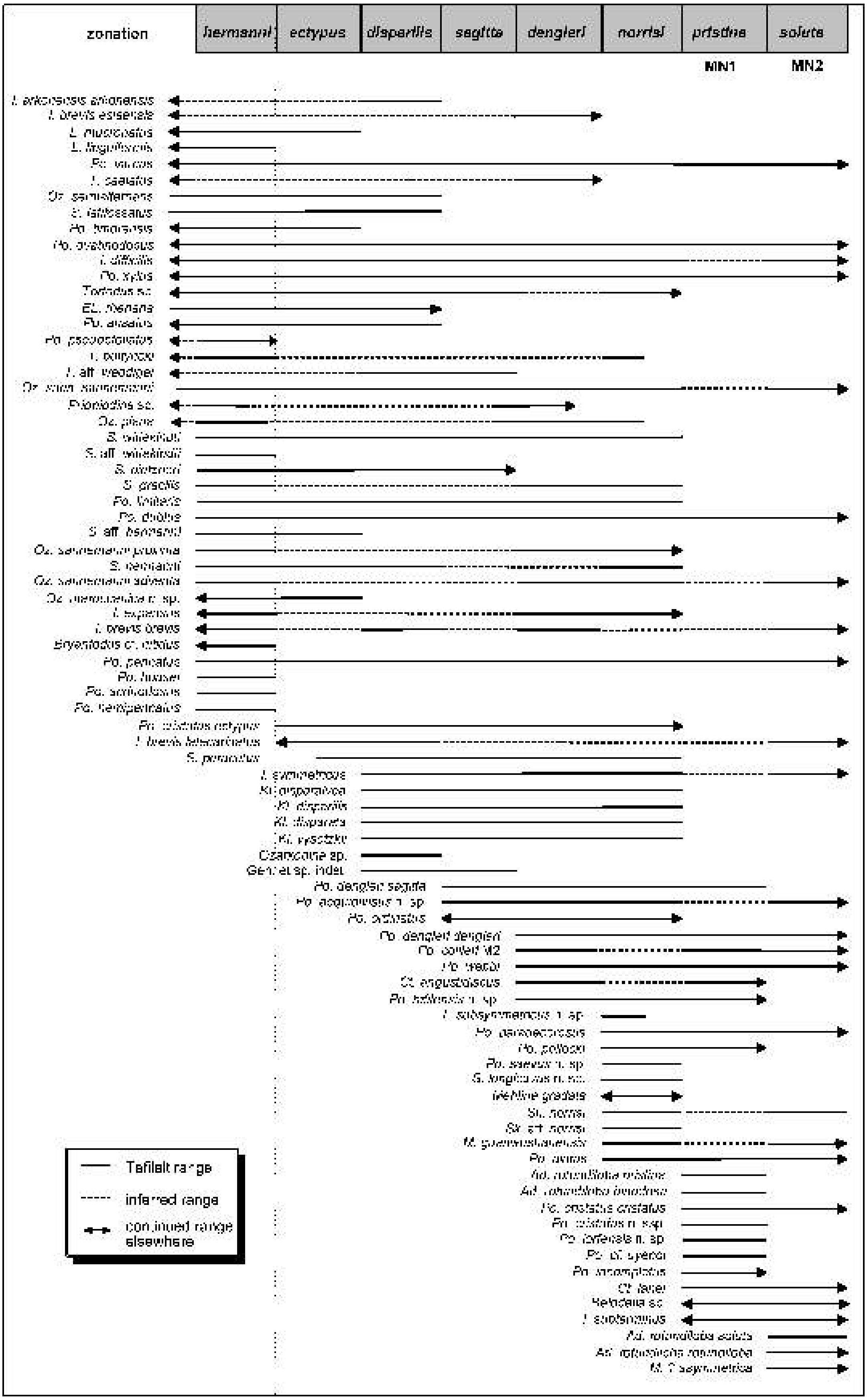
Klapper and Johnson (1990) noted that *Sk. norrisi* ranges up into the MN Zone 2 and this was confirmed in the compilation of composite ranges by Klapper (1997) and by Uyeno and Wendte (2005). It suggests that the Lower Styliolinites are not younger than the MN 2 Zone. The precise age of organic-rich styliolinite intervals is of considerable economic interest since these are potential source rocks that continue in Algeria (Lüning *et al*., 2004).

TAXONOMY

In recent years it became clear that most species-rich Devonian conodont genera include different and parallel, short- or long-ranging phylogenetical lineages that should be recognized at the generic level. This taxonomic revision should incorporate data on apparatus composition, as in the Frasnian polygnathids *Avignathus* and *Uyenognathus*. But the mor-

Table 6

Ranges of all Tafilalt upper Givetian to basal Frasnian conodont taxa



Interrupted lines indicate record gaps, arrows indicate a range continuation outside the Tafilalt or in higher beds phology of the Pa elements is also an important feature. Therefore, and despite older or younger iterative trends, we accept the generic separation of *Linguipolygnathus* and *Ctenopolygnathus*. The remaining Givetian to basal Frasnian polygnathids still have to be assigned to well defined different lineages. This task is beyond the scope of this paper. Dzik (2002) and Murphy *et al*. (2004) have argued that the true *Ozarkodina* is a Silurian to basal Devonian genus but did not propose a new generic assignment for the majority of Givetian and Frasnian species. *Nicollidina* Dzik (2002) embraces only the *Oz. brevis* Group. Until taxonomic progress is achieved, we refer all other species to "*Ozarkodina*".

The Moroccan samples show that many well established species can be rare or represented just by single specimens. Rarity is not a reason to disregard taxa, especially when data shall become useful for palaeodiversity and palaeoecological analysis or for the establishment of full time ranges. Rare species are a biological normality in present day ecosystems. Their naming requires a careful comparison with more common species whose intraspecific variability is established. We have encountered two examples (in *Tortodus* sp. and *Po. pennatus*, Fig. 7M) where bizarre morphologies, such as the development of secondary platform branches, are a pathological feature (compare pathological *Polygnathus* illustrated by Szulczewski, 1971). Deformation (pathological or diagenetic) and stratigraphical misplacing (reworking, leaks from higher beds) are an obstacle for the taxonomy of rare taxa but this can be overcome by careful comparisons with the wealth of literature data on variations and ranges.

All material, including designated types, is housed in the museum of the GPI, Münster (collection number GPIM B9A.1, figured specimens numbered as A.1-1 to A.1-67).

Ancyrodella rotundiloba pristina
Khalymbadzha and Chernysheva, 1970
Fig. 9K, L, O–R

* 1970, *Ancyrodella pristina* Khalymbadzha and Chernysheva; 89–90, pl. 1, figs. 3–8;

* 1970, *Ancyrodella prima* Khalymbadzha and Chernysheva; 88–89, pl. 1, figs. 1, 2;

e.p. 1974, *Ancyrodella rotundiloba binodosa* Uyeno; 24, 25, pl. 1, figs. 2A, B, ?6A, B;

e.p. 1974, *Ancyrodella rotundiloba* subsp. A Uyeno; 25, 26, pl. 2, fig. 6A, B;

e.p. 1985, *Ancyrodella rotundiloba*, early morphotype Klapper; 24, 26, 27, pl. 1, figs. 1–6, 9–18 [only], pl. 2, figs. 5–8, 11, 12 [only], pl. 3, figs. 5–11;

e.p. 1989, *Ancyrodella pristina* Sandberg *et al*.; 210, 211, text-fig. 2.2–2.4, 7, pl. 1, figs. 3, 4, 13, 14 [non figs. 9, 10 = *rotundiloba soluta*];

e.p. 1989, *Ancyrodella soluta* Sandberg *et al*., 211, 212, text-fig. 2.5, 2.7 [only].

Type. — Original of Khalymbadzha and Chernysheva, 1970; pl. 1, figs. 5–7.

Discussion. — The taxonomy of early ancyrodellids has been the subjective of an extensive and contrary discussion in the last two decades. There is significant variation concerning platform shape and ornamentation, the size of the basal cavity, and the presence/absence and course of keels and swellings on the underside. Based on the succession of morphologically variable populations, it is possible to distinguish subspecies in *Ad. rotundiloba* that are very important for lower Frasnian biostratigraphy. However, identification and zonal recognition requires median sized to mature specimens since juveniles of all subspecies are similar. Our concept of *Ad. rotundiloba pristina* mostly follows the definition of the early morphotype of *Ad. rotundiloba sensu* Klapper (1985). Most critical are the subtriangular outline of the platform and the size of the basal cavity, which amounts to or exceeds 50% platform width. The Bine Jebilet population includes simple morphotypes or ontogenetic stages with rather lanceolate outline and very few marginal secondary nodes (Fig. 9K, L), slightly more advanced morphotypes with more secondary nodes (up to 10) and with rounded anterior platform, partly only on one side (Fig. 9O, P; = *Ad. pristina* Morphotype 3 of Sandberg *et al*., 1989), or advanced morphotypes with even more secondary nodes (up to 20), including a few on the platform between the two main (primary) nodes and small marginal nodes (Fig. 9Q, R; part of *Ad. soluta* Morphotype 3 Sandberg *et al*., 1989).

Ad. rotundiloba binodosa differs in its distinctively rounded two platform lobes that may bear just two or a few additional nodes. The morphotype figured in Figure 9M, N is somewhat unusual and very advanced since it features a few additional nodes on the platform, not at its margins. It is clear from the literature that there are many transitional forms between *Ad. rotundiloba binodosa* and *Ad. rotundiloba pristina*. With respect to the juvenile holotype of *Ad. rotundiloba binodosa* and the morphological intergradation, the separation of *binodosa* and *pristina*, even as subspecies, can be questioned.

Our concept of *Ad. rotundiloba soluta* follows the distinction of late morphotypes of *Ad. rotundiloba* by Klapper (1985) and is centered on its type and closely related forms. This subspecies defines MN Zone 2 (Klapper, 1989) and has a smaller basal cavity (*ca*. 20–45% platform width at maturity) than *Ad. rotundiloba pristina* and more (20–30) platform nodes. Its outline can vary (Sandberg *et al*., 1989; Kralick, 1994) and small keels may develop as a lateral extension of the basal cavity in advanced specimens. There are described transitional morphotypes between *pristina* and *soluta* but none of the Bine Jebilet specimens falls in *Ad. rotundiloba soluta* if defined by the basal cavity, not by the surface nodation. Our distinction of *Ad. rotundiloba pristina* and *soluta* differs from Sandberg *et al*. (1989) but follows a population approach and allows zonal assignments, correlating with Klapper´s (1989) MN 1 and 2 zones. *Ad. rotundiloba rotundiloba* has a more densely noded platform and a small basal pit (up to *ca*. 20% platform width), mostly ending in short keels, and, typically, swellings of the underside adjacent to the free blade. The succession of *Ad. rotundiloba soluta* and *Ad. rotundiloba rotundiloba*, both included in the late morphotype of *Ad. rotundiloba* by Klapper (1985), may allow to subdivide MN Zone 2, but not in the Tafilalt, where ancyrodellids are too rare in the Lower Styliolinite.

Occurrence. — Only in the *rotundiloba pristina* Bed of BJ.

Ctenopolygnathus lanei (Kuzmin, 1995) (emend.)

Fig. 6L, M

1981, *Polygnathus* aff. *Po. angustidiscus* Huddle; B25, pl. 17, figs. 1–9;
?e.p. 1985, *Polygnathus* aff. *Po. angustidiscus* Klapper and Lane; 932, fig. 16.5–6 [figs. 16.2–4 = transitional to *Po. brevilamiformis* Ovnatanova 1986];
non 1992, *Polygnathus* aff. *Po. angustidiscus* Bardashev; pl. 9, figs. 19, 26, 28, 29;
non 1992, *Polygnathus* aff. *Po. angustidiscus* Norris *et al.*; 76, pl. 14, figs. 19–21;
* 1995, *Polygnathus lanei* Kuzmin; 305, pl. I, fig. 7;
1995, *Polygnathus* aff. *Mesotaxis ? dengleri* Hüneke; pl. 1, fig. 22;
1997, *Polygnathus lanei* Zhuravlev *et al.*; tabs. 1–4, pl. 1, fig. 8;
1999*a*, *Polygnathus lanei* Ovnatanova *et al.*; 282, 283;
1999*b*, *Polygnathus* aff. *Po. angustidiscus* Ovnatanova *et al.*; 352, text-fig. 2;
2000, *Polygnathus lanei* Zhuravlev; 720;
non 2001, *Polygnathus* aff. *Po. angustidiscus* Liao *et al.*; 23, pl. 4, figs. 29, 30;
2002, *Polygnathus lanei* Kozlova; 174, 175, figs. 1, 2;
2002, *Ctenopolygnathus angustidiscus* Dzik; 588, fig. 17A–E;
2006, *Polygnathus lanei* Zhuravlev *et al.*; 752, 753, fig. 6.

Types. — Lectotype, designated here, PIN 4551/5 (Kuzmin, 1995, pl. I, fig. 7).

Type locality and level. — Southern Timan, Ukhta River, Outcrop 13A, Timan Formation, Upper Member, sample 3.

Diagnosis. — Platform subrectangular (typical specimens) or somewhat irregular, not reaching posterior tip, with moderately deep and wide adcarinal furrows; upturned margins slightly serrated or with short transverse ribs. Free blade short, with two or three dominant teeth near anterior end, grading into a straight or slightly curved carina that consists of fused teeth and that extends with one or two, sometimes accentuated teeth posterior of the platform. Basal pit small, positioned under anterior platform half.

Discussion. — The Moroccan material has a much longer platform and much shorter free anterior blade and free posterior carina than in *Ct. angustidiscus*. Ornamented platform margins also occur in the latter (Fig. 6S, T). There is some variation concerning the platform widths but a rectangular shape is typical. Only early juveniles may be subtriangular, resembling *Po. brevilamiformis*. Similar specimens were assigned by Huddle (1981) and Klapper and Lane (1985) to *Po.* aff. *Po. angustidiscus*. Kuzmin (1995) introduced the name *Po. lanei* and figured a specimen from the Timan. But since he provided no diagnosis and type designation, the validity of his species remained questionable. Despite this, it has been used by subsequent Russian authors (e.g., Zhuravlev *et al.*, 1997, 2006; Zhuravlev, 2000; Kozlova, 2002), even as a lower Frasnian zonal marker of a *Po. lanei* Subfacies. Article 13.1.2. of the International Zoological Code requires for species that were introduced between 1930 and 1999 only a reference to a description, which allows a clear species distinction. The short reference in Kuzmin (1985) to the morphological characterization in Klapper and Lane (1985, p. 932) fulfils this requirement. Hence, *Ct. lanei* is valid but type designation and diagnosis are added here. With respect to its wide distribution, stratigraphical and biofacies significance, we think it is useful to recognize *Ct. lanei.*

There was perhaps considerable variability within the upper Givetian/lower Frasnian *angustidiscus-lanei-brevilamiformis* Group (Zhuravlev, 2000; Dzik, 2002), as it has been repeatedly reported for the supposed descendent *Ct. brevilaminus*, but this needs further documentation. Forms that lie outside the characteristics of the three named taxa were illustrated by Uyeno (1974: pl. 5, fig. 4A, C, latest Givetian form, assigned to *Po. brevilaminus*, with very narrow adcarinal furrows and high platform borders, here named the “Firebag Morphotype” of *Ct. angustidiscus*; pl. 5, fig. 5A–C, late lower Frasnian form assigned to *Po. brevilaminus* with very high free blade; pl. 4, fig. 2A, C, twisted late lower Frasnian specimen with short platform and very high free blade assigned to *Po.* cf. *Po. decorosus*) Norris *et al.* (1982, “Firebag Morphotype” from the upper Givetian Lower *subterminus* Fauna); Norris and Uyeno (1983, “Firebag Morphotype” from the upper Givetian Slave Point Formation); Bardashev (1992, lower Frasnian specimens with fully developed platform); Rogers (1998, upper Givetian “Firebag Morphotype” from Iowa) and Liao *et al* (2001, upper Givetian *Po.* aff. *Po. angustidiscus* with very long, twisted, posterior carina extension). The “Firebag Morphotype” may warrant taxonomic separation and may have stratigraphic significance as an upper Givetian taxon. The upper Frasnian *Ct. aspelundi* (Savage and Funai, 1980) also has narrower, smoother platforms with high borders but only an incipient free posterior carina. The small-sized basal Famennian *Ct. nanus* (Savage, 1992) closely resembles the older *Ct. lanei* apart from a characteristic carina flexure on the posterior platform. The upper Frasnian *Ct. dutroi* (Savage, 1992) is very similar to the triangularly shaped *Ct. brevilamiformis* but smooth.

Myshkina and Zhuravlev (2005) proposed the multi-element genus *Youngquistognathus* for Frasnian species around *Po. rossicus* Zhuravlev (2000) and *Po. sinuosus* Szulczewski (1971), but it is a subjective junior synonym of *Uyenognathus* Savage (2004), with the type species *Po. sinuosus wadleighensis* Savage (1987). Typical are a torsion of the Pa element as in *Tortodus* and massive, strongly curved Pb elements that differ from the Pb in *Polygnathus*. The genus is somewhat homoemorphic to *Tortodus* but the Pa has smaller basal pits that are positioned under the anterior platform, not under the centre. It may also include the poorly known *Po. persulcatus* Youngquist *et al.* (1948) and *Polygnathus* sp. A Kuzmin (1995). It ranges into the early Famennian (“*Polygnathus*” n. sp. E Orchard, 1989, *Po.* aff. *Po. sinuosus* Bultynck and Martin, 1995). If the hardly twisted *Po. angustidiscus* is included in *Youngquistognathus* (=

Uyenognathus), as proposed by Myshkina and Zhuravlev (2005), the genus becomes a subjective junior synonym of *Ctenopolygnathus* Müller and Müller (1957). But the Pb elements of the apparatus reconstructed for *Ct. angustidiscus* (= *Ctenopolygnathus* sp. A in Dzik, 2002), close relatives (the "Firebag Morphotype", Norris *et al*., 1982), and *Ct. brevilaminus*, as a probable descendent, are typical for *Polygnathus* (Norris and Uyeno, 1983; Schülke, 1999). *Po. lanei* has not been included in *Youngquistognathus* by the original authors and does not show torsion. It falls in *Ctenopolygnathus*, which is defined by its posteriorly free carina. This genus should not include homoemorphic Emsian to middle Givetian species, as suggested by Bardashev *et al*. (2002), but probably represents a lineage with secondarily reduced platform (Dzik, 2002).

Occurrence. — Lower Frasnian (beds I, J, *rotundiloba pristina* and *rotundiloba soluta* zones) at BJ (B9A.1-21). Closely similar specimens have previously been recorded from the lower and middle Frasnian of New York State (Huddle, 1981), the north-west Territories of Canada (Klapper and Lane, 1985), the Harz Mts. (Germany, Hüneke, 1995), the Timan (NW Russia, Kuzmin, 1995; Ovnatanova *et al*., 1999*a*, *b*) and other parts of the Russian Platform (Zhuravlev *et al*., 1997, 2006; Kozlova, 2002).

Gen. et sp. indet.

Fig. 8G–L

Description. — Carina almost straight (Fig. 8I–L) and very slightly twisted to curved and more strongly torted (Fig. 8G, H), especially at the posterior end; with numerous (*ca*. 15–18) small, fused denticles and with a dominant main cusp *ca*. at midlength or slightly posterior to that position. An elongated, narrow to slightly lobed, mostly smooth platform is restricted over the total length to the outer side. Small nodes may occur in the vicinity of the main cusp. Only one specimen has a very short, minor platform remnant on the inner side (Fig. 8H).

Discussion. — The development of a central main cusp, the torsion, and the elongated, very asymmetric platform development resemble nothognathellan Pb elements but these have their platform on the inner side. There are few similarities with *Tortodus* species but in *T. bultyncki*, *T. weddigei* and *T. beckeri* narrow platforms are present alternating both on the inner and outer side. The restricted range of the currently enigmatic forms rules out that they belong to the apparatus of a long-ranging genus. The rather high variability could express species differences. It needs to be mentioned that the *Klapperina* apparatus is still unknown and that the genus enters in the same beds as the supposed Pb elements. The Pa element homoemorphy between *Klapperina* and *Palmatolepis* could well be associated with a slight homoemorphy (platform development) in Pb elements, creating an apparatus with a comparable functional morphology.

Occurrence. — *disparilis* Zone (Md-E, bed 14) to *dengleri sagitta* Zone (Md-E, bed 15; OCh, bed 18).

Icriodus aff. *I. symmetricus*

Fig. 8D, E

1982, *Icriodus* aff. *I. symmetricus* Bultynck and Jacobs; 38, pl. III, fig. 36.

Discussion. — A single specimen (B9A.1-43) differs from *I. symmetricus* in a median row of denticles that is not higher but only equally high as the side rows.

Occurrence. — Restricted to the *norrisi* Zone of Md-E (bed 19). The same form occurs in Belgium in the lower Frasnian (Bultynck and Jacobs, 1982).

Mesotaxis guanwushanensis (Tian, 1988)

1957, *Polygnathus dubia dubia* Bischoff and Ziegler; pl. 16, figs. 18, 19, pl. 21, figs. 1, 2;
1958, *Polygnathus dubia dubia* Ziegler, 1958; 57, 58, pl. 1, fig. 3a, b [only, holotype of *falsiovalis*];
1981, *Polygnathus asymmetricus ovalis* Bultynck and Jacobs; pl. VII, fig. 12a, b [specimen with relative large basal cavity, still transitional to *Po. dengleri dengleri*];
1982, *Polygnathus asymmetricus* Bultynck; fig. 3;
1982, *Polygnathus asymmetricus* n. subsp. Ziegler and Klapper, 1982, 471, pl. 1, fig. 6 [re-illustrated holotype of *falsiovalis*];
* 1988, *Polygnathus guanwushanensis* Tian (in Hou); 329, pl. 129, figs. 4, 7, 8;
* 1989, *Mesotaxis falsiovalis* Sandberg *et al*.; 213;
1992, *Mesotaxis falsiovalis* Yatskov and Kuzmin; 87, tab. 1, pl. 2, fig. 10a, b;
1999, *Mesotaxis falsiovalis* Belka *et al*.; fig. 8, tab. 2;
2000, *Mesotaxis falsiovalis* Bultynck and Walliser; 14;
2000, *Mesotaxis falsiovalis* Ding *et al*.; 201, 202, pl. I, figs. 3, 4 [slightly intermediate to *Po. dengleri dengleri*];

Lectotype. — Here designated as the specimen figured by Tian (in Hou, 1988) on pl. 129, fig. 4a, b.

Discussion. — When Sandberg *et al*. (1989) named the former *Po. asymmetricus* n. subsp. of Ziegler and Klapper (1982) as *M. falsiovalis*, they were obviously not aware of the fact that Tian (in Hou, 1988) had just previously named the same species as *Po. guanwushanensis*, based on material from the lower Frasnian of Longmenshan, Sichuan. Consequently, *M. falsiovalis* is a subjective junior synonym of the Chinese species and cannot serve as the base for a zonal name. It is intriguing that even other Chinese conodont workers (e.g., Ji and Ziegler, 1993; Bai *et al*., 1994; Wang, 1994; Ding *et al*., 2000) did not refer to the *Mesotaxis* species that had been named (still as *Polygnathus*) by Xiong (in Xian *et al*., 1980) and Tian (in Hou, 1988).

The holotype of *M. falsiovalis* has an extremely small basal pit. It is similar, very narrow, but slightly elongated in the type material of *M. guanwushanensis*, still resembling to some extent the basal pit in the ancestral *Po. dengleri dengleri*. As emphasized by the authors of *M. falsiovalis* (Sandberg *et al*., 1989, p. 213), there are many transitional specimens between *Po. dengleri dengleri* and *M. falsiovalis*, and, therefore, the mentioned difference of the basal pit morphology is not sufficient to keep *M. falsiovalis* and *M. guanwushanensis* as separate species. For example, the basal pit of specimens illustrated by Bischoff and Ziegler (1957, pl. 21, fig. 1) and Yatskov and Kuzmin (1992) agree with the *M. guanwushanensis* holotype. The latter lacks the adcarinal troughs and ridges of *Po. dengleri dengleri*.

Klapper and Johnson (1990) questioned whether *M. falsiovalis* can be kept separate from the somewhat younger *M. asymmetrica* but our unpublished collections from the topmost Givetian (*norrisi* Zone) of the Montagne Noire suggest that both forms not only have slightly different Pa but also different Pb elements. *M. guanwushanensis*, therefore, is not a subjective junior synonym of *M. asymmetrica*. In the also mostly overlooked *M. trachyta* (Tian, 1988), the basal pit is slightly widened and it sits at the anterior end of the platform. In "*M.*" *tiandengensis* (Xiong in Xian *et al*., 1980), the basal pit is very large, as in "*M.*" *unilabia*, but it is positioned under the posterior half of the platform. In "*M.*" *orchardi* (Tian, 1988), the basal pit is even larger than in "*M.*" *unilabia*. The "*unilabia* Group" with their large, often L-shaped basal cavity seems to represent a taxon that is homoeomorphic to *Klapperina* and which evolution started in the lower Frasnian from "*M.*" *ovalis*. It also includes *M. keithi* Uyeno and Wendte (2005) and, perhaps, *Palmatolepis baheensis* Xiong in Xian *et al*. (1980), *Pa. paradisparilis* Uyeno and Wendte (2005), and the closely related *Pseudopolygnathus* sp. nov. A Druce (1976).

Occurrence. — All new material is from the Lower Styliolinite (*rotundiloba soluta* Zone) at BJ. Bultynck (1982, 1986), Belka *et al.* (1999), and Bultynck and Walliser (2000) recorded the species from the *Petteroceras* Beds (*norrisi* Zone) of BT and OCh.

"Ozarkodina" maroccanica n. sp.

2003, *Ozarkodina* n. sp. Aboussalam; 171, 172, tab. 7, 16;

* 2003, *Ozarkodina maroccanica* Aboussalam; pl. 24, figs. 13–16 [nom. nud.].

Derivation of name. — Named after Morocco.

Type locality and level. — Seheb el Rhassal, Section 2, bed E2a, *hermanni* Zone.

Types. — Holotype MB.Ct.604 (Museum für Naturkunde, Berlin; Aboussalam 2003, pl. 24, figs. 13, 14), paratype Mb.Ct.605 from Pic de Bissous (Montagne Noire), bed 26e6 (*semialternans* Zone; Aboussalam, 2003, pl. 24, figs. 15, 16), three more paratypes from Pic de Bissous (Aboussalam, 2003, tab. 16), one paratype from Seheb el Rhassal, Section 1 (Aboussalam, 2003, tab. 7).

Diagnosis. — Blade slightly curved, twisted and bent downwards, with 15–19 mostly broad, strongly fused teeth that are highest in the anterior part and above the moderately small, round basal cavity, which is positioned *ca*. 1/3 of total length before the posterior end. Denticles of the posterior half are somewhat oblique and sit above a weakly developed shoulder.

Discussion. — Aboussalam (2003) described this new species from the Tafilalt and the Montagne Noire but preferred to keep it in open nomenclature. By mistake, the originally planned species name was kept on the plate explanations, producing a nomen nudum. Continued sampling in the Tafilalt did not produce new material but we prefer to validate the proposed name. *Oz. maroccanica* n. sp. differs from *Oz. semialternans* and *Oz. intermedia* by broader teeth and a rather straight base of the Pa element, especially in the posterior half. The basal cavity is rather different from that in Pb elements of prioniodinid species that are also more torted. All subspecies of *Oz. sannemanni* have small platforms around the basal cavity. The latter is smaller and oval in *Oz. plana*, which also has more, narrower and strongly oblique posterior teeth. There is some homoeomorphy with the Eifelian *Oz. obliqua*, which has a more centrally located small basal cavity, incurved anterior end, and regularly some very narrow teeth that are sandwiched between wide ones in the anterior half or middle of the blade. *Oz. maroccanica* n. sp. may posses some narrow teeth behind the basal cavity (e.g., in the holotype).

Occurrence. — *ansatus* to *semialternans* Zone of the Montagne Noire (Pic de Bissous) and *hermanni* to *cristatus ectypus* Zone of the Tafilalt (Seheb el Rhassal).

Polygnathus aequidivisus n. sp.

Fig. 6N–R

e.p. 1982, *Polygnathus* aff. *Po. dubius* Bultynck and Jacobs; 39, pl. III, figs. 15, 16;

e.p.1993, *Polygnathus pollocki* Racki and Bultynck; pl. 4, fig. 5;

? 1993, *Polygnathus aequalis* Racki and Bultynck; pl. 4, fig. 6.

Derivation of name. — According to the *ca*. equal length of free blade and platform.

Types. — Holotype B9A.1-23 (Fig. 6P), two paratypes (B9A.1-22 and 1-24) from BT (Fig. 6N, O, Q), two more topotypic paratypes, one paratype (B9A.1-25) from BJ (Fig. 6R), two paratypes from Md-E.

Type locality and level. — Upper Marker Bed (bed 42, *dengleri dengleri* Subzone) of Bou Tchrafine.

Diagnosis. — Platform slender, curved, with markedly convex outer margin, flat, as long as or only slightly longer than free blade, ornamented by fine transverse ridges and some, often fused nodes; carina narrow, bordered by rather shallow furrows, reaches the posterior tip and consists of small, low nodes. Basal pit moderately large, positioned near the centre of the anterior platform half. Free blade straight, with 9–10 low, fused denticles.

Discussion. — The new species shows some variability concerning platform widths, curvature and ornamentation. *Po. paradecorosus* has also short, slender, curved platforms with transverse ridges but a slightly constricted anterior platform with a small rostrum, deeper adcarinal groves, and a more dominant carina with enlarged, fused nodes (see Fig. 6G–I or Ji and Ziegler, 1993). In the Frasnian *Po. decorosus* s.

str. (*sensu* its lectotype, Klapper *et al*., 1970), the platform is even smaller, ornamented by isolated nodes, lacks a short rostrum, and the carina is dissolved into nodes towards the posterior end (for typical specimens see also Ji and Ziegler, 1993, pl. 40). *Po. pollocki* Morphotype 1 has an even narrower and much longer platform (*ca*. 2/3 of total lengths), deep adcarinal furrows (see Fig. 6S), high platform borders, and more distinctive denticles of the free blade (see holotype of Druce, 1976). *Po. tafilensis* n. sp. seems to be related but has longer and wider platforms and mostly also a slight anterior platform constriction.

Occurrence. — *dengleri sagitta* Subzone of BT, *dengleri dengleri* Subzone of BT, and *norrisi* Zone of BJ, ?BT and Md-E. The species seems to continue in the lower Frasnian of the Ardennes (Bultynck and Jacobs, 1982) and of the Holy Cross Mountains (Racki and Bultynck, 1993).

Polygnathus collieri Huddle, 1981

Fig. 6J, K

*e.p. 1981, *Polygnathus collieri* Huddle; 27, 28, pl. 9, figs. 20–25, pl. 10, fig. 22 [= Morphotype 3], pl. 11, figs. 1–4, pl. 13, fig. 11 [= Morphotype 2), pl. 12, figs. 1–3 [= Morphotype 1];

1981, *Polygnathus* aff. *Po. collieri* Huddle; pl. 17, figs. 32–34 [= Morphotype 2];

1986, *Polygnathus collieri* Bultynck; pl. I, fig. 6 [= Morphotype 2].

Discussion. — When Huddle (1981) established *Po. collieri*, he based the species on forms from different stratigraphical levels that may represent different taxa and these are here recognized as distinctive morphotypes. The holotype from the Genundewa Limestone is a rather unique, slightly twisted specimen with relative broad and deep adcarinal depressions. As discussed by Huddle (1981), it shows some similarities with *T. caelatus*, especially with forms with short free blade (e.g., Huddle, 1981, pl. 13, figs. 7 and 8) that Aboussalam (2003) assigned to *T.* aff. *T. caelatus*. The central position of the basal pit would be in accord with a placing of the species in *Tortodus* but the pit is relatively small. Other figured specimens from the North Evans Limestone and Genundewa Limestone, here assigned to Morphotype 2, are not torted, have very deep and narrow adcarinal furrows, strong, irregular folds of the upturned platform margins, and a furrow of the underside (Huddle, 1981, pl. 11, fig. 3, pl. 17, fig. 34; Fig. 6K) that runs in the free blade. Morphotype 3 from the West River Shale is perhaps not conspecific, has two or three rows of rather regular nodes along the high platform margins, and a basal pit that lies in the anterior part of the platform. Our Moroccan specimens all conform to Morphotype 2. The Chinese *S. xianliensis* Xiong (in Xian *et al*., 1980) resembles Morphotype 2 but has a longer free blade. It resembles *Polygnathus* n. sp. Orr (1964) from the Alto Formation (*cristatus ectypus* Zone) of southern Illinois. A specimen figured by Szulczewski (1971) from the Frasnian of the Holy Cross Mountains as *T.* aff. *T. caelatus* is not torted and may be a relative of Morphotype 3 but the basal pit lies under the platform centre.

Occurrrence. — Upper Marker Bed (BT I, bed 42, *dengleri dengleri* Subzone, Bultynck, 1986), *Petteroceras* Beds (BT II, bed 11, *norrisi* Zone, Bultynck, 1986), *rotundiloba prista* Zone (MN 1 Zone) of BJ (bed I), and Lower Styliolinites (*rotundiloba soluta* Zone, MN 2 Zone) of OCh (bed 28) and BT (Bultynck, 1986).

Polygnathus cristatus n. ssp.

Fig. 9F, G

Description. — Large, wide and very thick, bowl-shaped platform with a central depression, ornamented by numerous, coarse, partly fused nodes that show strong wear in the central part. The free blade is mostly broken off and continues as a more or less straight carina, which consists of worn nodes in the central part and of a ridge in the posterior part.

Discussion. — This new subspecies of *Po. cristatus* is characterized by its very robust and wide Pa element, which is not flat as in the other subspecies, but centrally concave. *Po. cristatus ectypus* Huddle, 1981 has thinner Pa elements and smaller, isolated nodes. In *Po. cristatus cristatus*, the nodes of the moderately wide platform are partly merged to form transverse ridges (Fig. 9H). The robust morphology and strong wear of central nodes suggest that the new form had adapted to a rather solid diet that strongly stressed the Pa elements. Since the same morphotypes occur contemporaneously in Morocco and Germany, and not earlier in the middle Givetian, it is suggested that they represent an adaptive and evolutionary novelty, not just an ecomorphotype. Naming will await the documentation of German material.

Occurrence. — A single specimen (B9A.1-60) from the basalmost Frasnian (bed I) of BJ.

Polygnathus dengleri sagitta n. ssp.

Fig. 6A, B

e.p. 1957, *Polygnathus dengleri* Bischoff and Ziegler; 87, 88, pl. 15, fig. 19, pl. 16, figs. 1, 4 [only];

e.p. 1959, *Polygnathus dengleri* Krebs; pl. 1, fig. 9 [only];

e.p. 1970, *Polygnathus dengleri* Kirchgasser; 348–349, text-fig. 4, pl. 64, fig. 4, pl. 66, fig. 2 [only];

1978, *Mesotaxis* cf. *M. dengleri* Uyeno; 247, pl. II, fig. 22;

non 1980, *Polygnathus* aff. *P. dengleri* Savage and Funai; 811, pl. 1, figs. 20–27 [fide Savage 1992 = *Po. unicornis*];

e.p. 1981, *Polygnathus dengleri* Bultynck and Jacobs; 19, pl. VII, figs. 1–3 [only; figs. 6–9 = *Po. dengleri dengleri*];

e.p. 1982, *Polygnathus dengleri* Bai *et al*.; pl. X, figs. 3–6 [only];

1986, *Polygnathus dengleri* Ji *et al*.; pl. II, fig. 14;

e.p. 1989, *Polygnathus dengleri* Kuang *et al*.; pl. 39, fig. 19 [only];

e.p. 1992, *Polygnathus dengleri* Bardashev; pl. 8, figs. 25, 29–31 [only];

e.p. 1993, *Polygnathus (?) dengleri* Racki and Bultynck; pl. 4, fig. 13, pl. 5, figs. 3, ?4, 7;

e.p. 1993, *Mesotaxis ? dengleri* Ji and Ziegler; pl. 33, fig. 7 [only];

e.p. 1994, *Polygnathus dengleri* Kirchgasser; pl. 3, fig. H;

e.p. 1994, *Polygnathus dengleri* Weary and Harris; pl. 1, figs. 16, 17 [only];

e.p. 2001, *Polygnathus dengleri* Liao *et al*.; 26, pl. 4, figs. 7, 8 [only].

Derivation of name. — According to the arrow-shaped, subtriangular platform outline.

Types. — Holotype B9A.1-13 (narrow morphotype, Fig. 6A), paratype B9A.1-14 (moderately wide morphotype, Fig. 6B), 39 additional topotypic paratypes, 6 paratypes from BT, 71 paratypes from BJ, 30 paratypes from OCh, and 2 paratypes from ReK.

Type locality and level. — Md-E, bed 16 (middle *Taouzites* Bed, *dengleri sagitta* Subzone).

Diagnosis. — Platform elongated, narrow to moderately wide, more or less symmetrical, markedly subtriangular, flat, with shallow adcarinal depressions, ornamented by transversal ridges and small fused nodes. Free blade short, consisting of few fused, high denticles that grade into a straight carina that is formed by low nodes and that reaches the pointed posterior tip of the platform. Basal pit small, slightly elongate and positioned in the middle of the anterior platform half.

Discussion. — The type series of *Po. dengleri* of Bischoff and Ziegler (1957) consists mostly of specimens with oval, leaf-like, wide platform and rather coarse ornament but the new subspecies was figured as one of the variants. Uyeno (1978) identified a narrow, subtriangular specimen from Canada as *M.* cf. *M. dengleri*, which is here included in the new subspecies. Johnson *et al.* (1980) separated two morphotypes of *Po. dengleri*, an older ("Lower *dengleri* Zone") with coarse ornament, and a younger ("Upper *dengleri*" = *norrisi* Zone) with finer ornament. Both, excluding an extreme variant, have the platform outline of *Po. dengleri dengleri*. Bultynck and Jacobs (1981) distinguished three morphotypes (α, ß, γ) in Moroccan material. The new subspecies includes Morphotype α and some specimens of Morphotype ß.

The lower range than in typical *dengleri*, supported by the ages of figured specimens in Bultynck and Jacobs (1981), allows to recognize *Po. dengleri sagitta* n. ssp. as a stratigraphically significant chronosubspecies. It overlaps higher up with *Po. dengleri dengleri* in the topmost Givetian and basalmost Frasnian, where the nominate subspecies gradually starts to dominate. At this level, there are some intermediate narrow specimens but it is possible to assign individuals to the two subspecies in populations where both forms co-occur (e.g., in BT, bed 43; see figured material of Bultynck and Jacobs, 1981). Because of the stratigraphic significance, since different "early" and "late" morphotype designations have been used in previous literature, and following an old suggestion of Mouravieff (1980), we propose a formal subspecies terminology.

Since there is no evidence for nothognathellan Pb elements in *Po. dengleri*, the species should not be included in *Mesotaxis*. The extreme *Po. dengleri* variant of Johnson *et al*. (1980, pl. 4, fig. 30) falls outside the range of variation of Moroccan populations and is here excluded from the species.

Occurrence. — *dengleri sagitta* Subzone (*Taouzites* Beds) of BT, OCh, and Md-E, *dengleri dengleri* Subzone (Upper Marker Bed) of BT, ReK, OCh, and BJ, *norrisi* Zone (*Petteroceras* Beds) of BT, Md-E, OCh, and BJ, and *rotundiloba pristina* Zone (MN 1 Zone) of BJ. Based on illustrated specimens, the new subspecies has previously been recorded from the latest Givetian and Frasnian (up to MN Zone 3) of Germany (Bischoff and Ziegler, 1957), SW England (Kirchgasser, 1970), the Pyrenees (Liao *et al.*, 2001), Poland (Racki and Bultynck, 1993), New York State (Kirchgasser, 1994), West Virginia (Weary and Harris, 1994), NW Canada (Uyeno, 1978), Central Asia (Bardashev, 1992), and Guangxi, South China (Bai *et al*., 1982; Ji *et al*., 1986; Kuang *et al*., 1989; Ji and Ziegler, 1993).

Polygnathus jorfensis n. sp.

Fig. 7C–F

? 1982, *Polygnathus* sp. C. Bai *et al*.; pl. IX, fig. 5.

Derivation of name. — Named after Jorf, the village N of the type locality.

Types. — Holotype B9A.1-30 (Fig. 7E, F), paratype B9A.1-29 (Fig. 7C, D), one more unfigured paratype.

Type locality and level. — Basalmost Frasnian (bed I, *rotundiloba pristina* Zone) of BJ.

Diagnosis. — Platform narrow, elongated, flat, with shallow adcarinal furrows, only slightly curved (subsymmetric), with small, short anterior rostrum, and with regular, short, strong transverse ribs. Carina composed of a low to moderately high denticle row, reaching the posterior end. Basal pit moderately large, shallow, positioned near anterior platform end.

Discussion. — The new species resembles the basal Frasnian *Polygnathus* sp. C. of Bai *et al*. (1982), which lower surface, unfortunately, has not been figured. *Po. paradecorosus* is strongly asymmetric, has weaker ornament, deeper adcarinal groves, and fused carina nodes. *Po. ovatinodosus* has wider platforms, deeper adcarinal furrows, and is also more asymmetric. The latter feature, finer ornament, and a different position of the basal pit serve to distinguish *Po. aequidivisus* n. sp. Narrow morphotypes of *Po. pennatus* have much deeper adcarinal furrows and upturned platform margins; the basal pit lies much more posteriorly under the platform. However, there is a slight resemblance to a specimen figured as *Po.* cf. *Po. pennatus* by Garcia-Lopez (1987) from the *cristatus ectypus* Zone of Northern Spain. This unique specimen does not have the flat platform of *Po. jorfensis* n. sp. and is not regarded as conspecific.

Occurrence. — Only known from the type locality and level.

Polygnathus saevus n. sp.
Fig. 5L–O

e.p. 1974, *Polygnathus* cf. *P. decorosus* Uyeno; 38, 39, pl. 4, fig. 7A–C [only];

Derivation of name. — Following the lat. *saevus* = angry; due to the pronounced, spiny free blade.

Types. — Holotype B9A.1-8 (Fig. 5M–O), paratype B9A.1-7 (Fig. 5L), three more topotypes/paratypes.

Type locality and level. — Lower *Petteroceras* Beds (bed H1, 2, *norrisi* Zone) at BJ.

Diagnosis. — Platform narrow, inclined, slightly asymmetric and bent downwards, with moderately deep adcarinal groves and characteristic, relative fine transversal ridges; slightly shorter as the free blade, which consists of 10 to 11 well-defined denticles that increase considerably in height towards the anterior end. On the platform the blade grades into a row of isolated nodes. Lower surface with a relative large basal pit under the joint of blade and platform and with a curved ridge that reaches the posterior tip.

Discussion. — The new, rare species seems to be a relative of *Po. xylus* but differs (especially from typical morphotypes, Fig. 5A, B) in the high, prominent free blade, the more isolated nodes of the carina, and in wider adcarinal depressions, especially in the anterior platform part. No similar morphotypes have been seen in large *Po. xylus* material from the middle Givetian of Morocco or from elsewhere. Late *xylus* morphotypes may be more transitional (Fig. 5C–H, K) and ancestral but have a free blade with short teeth. *Po. pseudoxylus* Kononova *et al.* (1996) shares the position of the basal pit at maturity but also has a different free blade with lower denticles, narrow adcarinal groves, and merged carina denticles. A high free blade is developed in various Frasnian polygnathids but most of these have longer platforms. *Po. saevus* n. sp. shows close similarities with a specimen figured by Uyeno (1974) from the late lower Frasnian of Alberta as *P.* cf. *P. decorosus*. A lower Frasnian polygnathid figured by Uyeno and Wendte (2005, pl. 2, fig. 23) is also similar but has strongly fused carina nodes. *Po. klugi* Rogers (1998) is more asymmetric, has deeper adcarinal groves, higher platform margins, a shorter free blade with fewer (*ca.* 8) teeth, and a basal pit that is located posteriorly, well under the platform. *Po. siratchoicus* Ovnatanova and Kuzmin (in Menner *et al.*, 1992) has also fewer (7 to 8) but even higher free blade teeth, a platform that is not bent downwards, and a rather regular platform ornament with broad transverse ribs.

Occurrence. — Only at type locality and level.

Polygnathus tafilensis n. sp.
Fig. 5P–T

e.p. 1982, *Polygnathus dubius* Bultynck and Jacobs; 39, pl. III, figs. 9–11 [only];

? 1999, *Polygnathus decorosus* Belka *et al.*; tab. 2, pl. 3, fig. 8.

Derivation of name. — Named after the Tafilalt region.

Types. — Holotype B9A.1-10 (Fig. 5Q, R), paratype B9A.1-9 (Fig. 5P), paratypes B9A.1-11 and 1-12 (Fig. 5S, T) from Md-E, 21 more topotypic paratypes, two paratypes from BT, eight more paratypes from Md-E.

Type locality and level. — Lower *Petteroceras* Beds (bed H1, 2; *norrisi* Zone) at BJ.

Diagnosis. — Platform moderately wide, flat, strongly asymmetric, with very small anterior constrictions and curved outer posterior margin, ornamented by fine nodes and transverse ridges. Free blade shorter than platform, consisting of low, strongly fused teeth; carina narrow, low, reaching the pointed posterior tip, consisting of strongly fused denticles. Basal pit small, positioned under the anterior platform half.

Discussion. — The new species slightly resembles *Po. ovatinodosus* but has a flatter platform, shallower adcarinal furrows and, especially, a different, flat anterior joint of platform and carina, lacking the well developed short rostrum of the latter. It may have been derived from the latter, which co-occurs in the Tafilalt. The ornament of the new species is somewhat intermediate between *Po. ovatinodosus* and *Po. pennatus*, which has much stronger ribs (Fig. 7N). *Po. webbi* (Fig. 5U) and *Po. denisbricae* differ in their asymmetrically raised platform margins. *Po. dubius* has a well developed anterior rostrum with high, parallel platform margins and much deeper adcarinal furrows. There are rare transitional specimens to *Po. aequidivisus* n. sp. (Fig 6R). *Po. paradecorosus*, including *Polygnathus* sp. F figured from OCh by Belka *et al.* (1999; non Klapper and Lane, 1985), has inclined steeper platform margins, deep adcarinal troughs, a narrower platform, and stronger transverse ribs.

Occurrence. — In the Upper Marker Bed of BT (bed 42; *dengleri* Subzone), in the *Petteroceras* Beds (*norrisi* Zone) of BJ (bed H1, 2) and Md-E (beds 18b and 19), and in the *rotundiloba pristina* Zone (bed I) of BJ. Specimens figured by Bultynck and Jacobs (1982) are from the *norrisi* Zone of the Ardennes (Nismes). A much younger, middle Frasnian, OCh specimen assigned by Belka *et al.* (1999) to *Po. decorosus* may be related to *Po. tafilensis* n. sp. but has isolated carina nodes on the posterior platform and is less asymmetric.

Schmidtognathus longicavus n. sp.
Figs. 3, 7A, B

Derivation of name. — According to the long extension of the basal cavity.

Types. — Only the holotype (B9A.1-28).

Type locality and level. — Lower *Petteroceras* Bed (bed H1, 2; *norrisi* Zone) at BJ.

Diagnosis. — Small sized, platform asymmetric, almost smooth, not reaching the pointed, posterior tip; with well-devoped short rostrum at outer anterior end, with deep and wide adcarinal depressions, and with high, slightly crenulated margins. Free blade short (*ca.* 1/3 total length), consisting of six fused, low teeth, grading into a ridge-like, moderately high carina. Basal pit large, shallow, positioned under the anterior platform end, continuing as a narrow inversion almost until the posterior end.

Discussion. — The new species combines a *Po. timorensis*-type platform with the wide, elongated and partially inverted basal cavity as found in *S. latifossatus* and in many *S. gracilis* (Fig. 7R). Its spoon-like anterior rostrum allows easy distinction from all described representatives of both. All three species form a natural group that differs from the main *Schmidtognathus* with their moderately large cavity that runs posteriorly into a thin carina. However, there are specimens with intermediate lower surface morphology, e.g. in *S. gracilis* (see discussion in Johnson *et al*., 1980). *S. longicavus* is the youngest species of the genus but co-existed with *S. gracilis* and with last *S. peracutus*.

Occurrence. — Only in the type locality and level.

Skeletognathus aff. *Sk. norrisi*

Figs. 7G, H

Discussion. — The asymmetric curvature and position of the carina and free blade, the platform outline and irregular ornamentation strongly resemble *Sk. norrisi* but the secondary platform overgrowths has not yet really started. The specimen appears to be transitional between a polygnathid and *Skeletognathus* and hence, an aff. identification is given.

Occurrence. — One specimen (B9A.1-31) from the lower *Petteroceras* Bed (bed 25) at OCh (*norrisi* Zone).

Tortodus subsymmetricus n. sp.

Figs. 4, 8N, O

Derivation of name. — According to the weakly twisted, almost symmetrical platform.

Types. — Holotype B9A.1-52 (Fig. 8N, O) and 12 topotypic paratypes.

Type locality and level. — BJ, lower *Petteroceras* Bed (bed H1, 2; *norrisi* Zone).

Diagnosis. — Platform at maturity wide, flat, asymmetric, gently curved and only very slightly torted, extending over the whole length, converging to the anterior and posterior ends, with transverse ridges or rows of elongated nodes; carina very low, consisting of strongly merged denticles that slightly rise in height at the anterior end. Basal cavity symmetric, relative small at maturity, positioned under posterior half of the platform, with thick lips continuing as almost straight ridge towards the anterior and posterior end.

Description. — The types include a complete ontogenetic series from early juveniles of *ca*. 0.3 mm length to mature forms, such as the holotype, that reach more than 1.5 mm lengths. In earliest stages the blade/carina is still dominant and the short platform is restricted to the central area, as in *T. variabilis*. In subsequent early stages the platform remains narrow but extends towards the anterior and posterior ends and a variable amount of nodes develops. At median size the platform becomes wider but the size of the basal cavity does not increase with growths. A very slight torsion is only introduced at maturity, if at all; the ornament varies between distinctive nodes as in the holotype and more irregular low ridges in paratypes. Only the first three anterior denticles of the carina may rise above the platform ornament but are never high. The almost straight carina of the underside remains a very stable feature throughout ontogeny.

Discussion. — The new species is related to *T. caelatus* (= *beckmanni*, ? = *asperus*) but is distinguished by its much less torted platform and the characteristic straight carina of the aboral side. The holotype is also more regularly ornamented but some paratypes show irregular transverse ridges. The large intraspecific variation of *T. caelatus* has been documented by Huddle (1981) and Aboussalam (2003). Close relatives with anteriorly restricted platform seem to reach the upper Frasnian (*Po.? rugicosta* Miller and Youngquist, 1947). The variability within the BJ population mostly concerns the ornament, not the subsymmetric platform shape. Therefore, there is no morphological overlap with *T. caelatus* from lower Tafilalt strata or with illustrated North American populations. The previously overlooked middle Givetian *T. mirabilis* Ji (in Hou *et al*., 1986) displays a short, free blade, coarser, nodose ornament, and a spinose posterior appendix of the carina that extends beyond the platform. This Chinese species shows some similarity with *T.* n. sp. aff. *T. caelatus* (= *Prioniodina macrodenta* Huddle, 1981, pl. 19, figs. 1, 2). All other species of *Tortodus* have at maturity smaller platforms than *T. subsymmetricus* n. sp. or free blades.

Shape and ornament of *T. subsymmetricus* n. sp. resemble species of *Ancyrognathus*, especially of early Famennian forms that lack a side-lobe. However, it is more likely that poorly ornamented species of *Tortodus*, such as *T. tedi* (Uyeno and Wendte, 2005), are phylogenetically close to *An. ancyrognathoideus*, the unlobed ancestral species of the genus. We suppose that *Tortodus* gave rise to *Ancyrognathus*, although this needs to be supported by topmost Givetian and lower Frasnian apparatus reconstructions. Especially the assumption that widespread *Bryantodus*-type and rather large Pb elements of the Givetian, which strongly resemble Pb elements of *Ancyrognathus* (e.g., Klapper, 1990), belong to *Tortodus* species, needs to be substantiated.

Occurrence. — Only in the type locality and level.

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