



Veliger morphs in *Pristiograptus*, a robust graptoloid from the Ludlow series (Silurian) of Morocco

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The velum of veliger morphs is a rare, impersistent, delicate structure developed on the thecal apertures of some graptolites, and which may become stabilised in evolutionary descendants, thereby producing a new morphotype. This paper describes their discovery for the first time in the genus *Pristiograptus*.

Urbanek (1970) was the first to recognise and define veliger morphs, in graptolites of Ludlow age. He described veliger morphs in species of *Bohemograptus*, *Monoclimacis*, *Neolobograptus*, and *Neocucullograptus*; they comprise those forms in which some specimens exhibit microfusellar additions to the apertural regions of earlier-completed thecae. That is, the normal thecal shape and profile for the species was completed much earlier than the velum additions which were secreted in presumed old age of the colony. In some species (*Monoclimacis micropoma* Jackel, 1889) the velum additions can be quasi-proximal introductions (i.e. they occur more pronouncedly on proximal thecal apertures but cannot be proved to spread along the rhabdosome either during astogeny or during evolutionary lineages). In other species (*Bohemograptus bohemicus* (Barrande, 1850)) they are restricted to the proximal thecae; whilst on others (*B. praecornutus* Urbanek, 1970) they also occur on medial and distal thecae as well as in association with the sicula.

Furthermore, in some lineages such as *B. praecornutus* to *B. cornutus* Urbanek (Urbanek 1970: pl. 8) the microfusellar additions eventually become stabilised as specific characters present when the thecae are completed; there is no pause before 'postmatural' additions and those with the new structure in *B. cornutus* would not then be considered veliger morphs in the strictest sense.

The microfusellar tissue of the velum structures is not simple. Urbanek (1970: pp. 195–197) distinguished two kinds; microfusellar tissue and pseudomicrofusellar tissue. The former consist of strongly-pigmented, possibly multilayer, narrow, fuselli, lacking discontinuities between them. The pseudomicrofusellae consist of rather wider bands, sometimes of half the width of normal fuselli and irregularly distributed.

Veliger morphs have now been discovered in *Pristiograptus* (below) primarily in a species from Tazzarine, in the eastern Anti-Atlas of Morocco (for geology see Destombes *et al.* 1985).

In summary, a veliger morph is a species polymorph that exhibits microfusellar or pseudomicrofusellar additions (velum) to the 'normal' thecal apertures. The other polymorph lacks velum structures.

Veliger morphs in *Pristiograptus ?kosoviensis* (Bouček, 1931)

In the Moroccan specimens (Fig. 1) it is not too certain which form of microfusellar tissue is present, although there is a suggestion of pseudomicrofusellar tissue in two specimens (Fig. 1G, H). Velum additions occur throughout the length of the colony but are sometimes more pronounced on the proximal thecae. They may be much more extensive than shown here because

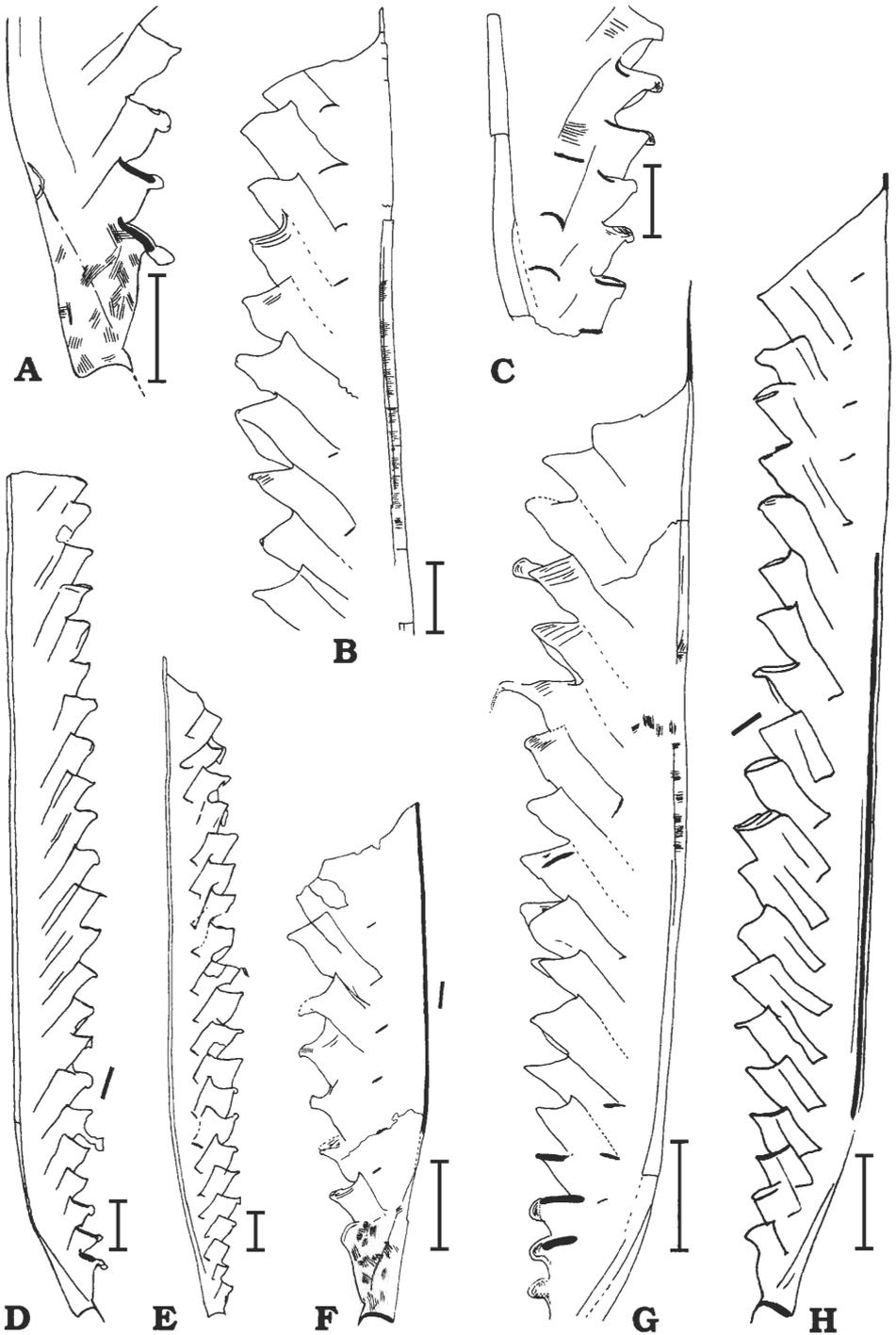


Fig. 1. A–H. *Pristiograptus* ?*kosoviensis* (Bouček, 1931) from author's locality JW10, *incipiens* Biozone, eastern Anti-Atlas of Tazzarine, Morocco, respectively. A. SM X.28486 showing cortical bandages, thickened apertural lips (black) and outlines of microfusellar additions to first three thecae. B. SM X.28487 distal →

they project outwards normal to the bedding plane. They do not occur on all specimens in the collection, perhaps on about 50% of them, although preservation does not enable one to be sure of the proportions.

A peculiar feature of this material is that even in relatively early growth stages with six or seven thecae developed, not only is the periderm exceptionally thick (with cortical bandages clearly visible in places: Fig. 1A, F), but velum structures are present. This suggests that in this species velum additions are not late astogenetic developments; unless, of course, colony growth has been retarded at some stage. Perhaps in support of this last possibility is the exceptionally thick periderm of relatively early growth stages. Many of the specimens have thickened apertural lips, depicted in heavy black on the figures, to which the velum has been added.

Pristiograptus ?kosoviensis occurs at about the *incipiens* Biozone level in the Moroccan sequence, and is associated with *Saetograptus chimaera* (Barrande, 1850) and *Saetograptus* sp. There are no pristiograptid-like species at higher levels in the sequence so one cannot test the possibility of these microfusellar additions becoming stabilised in the lineage. I have found, in addition to the Moroccan species, a specimen of *P. dubius* (Suess, 1851) (SM X.28494) from the Ludlow of Sarn, Shropshire, UK which also displays microfusellar additions to the completed, simple, tubular thecae, suggesting that veliger morphs may also occur in this species.

The form of the microfusellar additions in *P. ?kosoviensis* is not altogether clear in this flattened, in-the-rock material, but they may be very similar to some examples figured by Urbanek (1970: pls. 21, 22, and fig. 15) each termed a 'velum' in *Bohemograptus bohemicus tenuis* (Bouček, 1936). Certainly in the Moroccan specimens the additions appear to be either platform-like around the thickened apertural lip, or rounded lappets attached to the lip (or sometimes dependant from it).

It can be concluded, therefore, that *P. ?kosoviensis* has microfusellar additions which appear relatively early in the growth of the colony, are present on all thecae to varying degrees, but that they do not as far as is presently known, become stabilised in the evolutionary lineage to which *P. ?kosoviensis* belongs. Nor do they occur on all specimens in this collection of *P. ?kosoviensis*.

The timing of the stabilisation of the veliger morphs in Urbanek's (1970) original cases is interesting. Although present in the lineages in the unstabilised state for about one graptolitic biozone (?0.5 million years) they then became a fixture in possibly as little as half this time, as in the *B. praecornutus* to *B. cornutus* lineages and, later, in the *Neocucullograptus auriculatus* to *N. inexpectatus* lineage. It follows, therefore, that if the geological record happens to be rather poor at a crucial level, then new, established morphotypes might seem to appear quite suddenly in the record. Clearly graptolithologists will need to beware of this possibility.

A final problem concerns the stratigraphic occurrence of veliger morphs. Urbanek (1970) has clearly demonstrated that new morphotypes result from the stabilisation process. But why only in the early to middle Ludlow?

thecae showing virgula and cortical bandages crossing the dorsal wall of the rhabdosome. C. SM X.28488 broken part of a medium growth stage showing bases of interthecal septae, thickened, some thickening of the lip on th1, th4 and th5, fuselli in places, and microfusellar additions to the ventral lip area of all thecae. D. SM X.28489 more mature rhabdosome with irregular microfusellar tissue attached to th 6, more normal additives to other thecae, and thickened apertural lips on several thecae. E. SM X.282490 typical rhabdosome showing thecal overlap. F. SM X.28491 fairly early growth stage with robust virgula, characteristic proximal flexure, bandages, bases of interthecal septae, and microfusellar additions to thecal apertures. G. SM X.228492 mature specimen with spike-like virgula, thickened thecal apertures and microfusellar thecal additions. H. SM X. 28493 specimen showing position of sicula, sicular aperture, interthecal septae, and microfusellar thecal additions; short, heavy bar indicate cleavage/bedding intersection where visible: it seems to have little effect on the dimensions of the rhabdosomes. Scale bars 1 mm.

Descriptions

Class Graptolithina Bronn, 1849

Genus *Pristiograptus* Jaekel, 1889

Pristiograptus ?*kosoviensis* (Bouček, 1931)

Fig. 1A–H.

?*Monograptus kosoviensis* sp. nov.; Bouček 1931: p. 2, text figs. 1c–d.

?*Pristiograptus kosoviensis* (Bouček, 1931); Přibyl 1943: pp. 26–27, pl. 3: 14–15.

Material. — A large number of specimens from Tazzarine, in the eastern Anti-Atlas, Morocco, all flattened in black shale, with slight tectonic deformation caused by a single cleavage at a high angle to the bedding. All the specimens are deposited in the Sedgwick Museum Cambridge, UK (abbreviated SM); figured specimens numbers X.28486–28493; other specimens X.28500–28549.

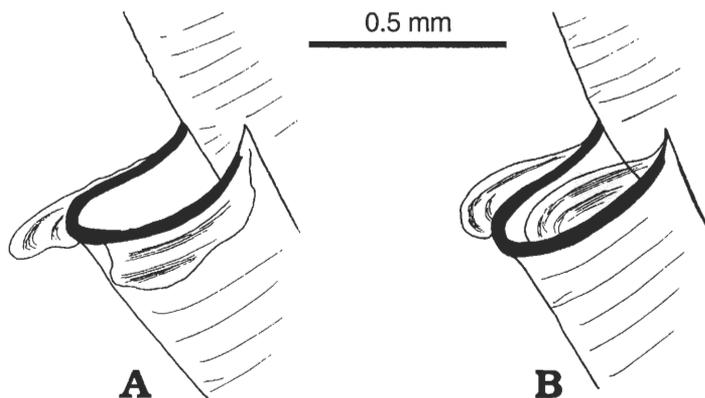


Fig. 2. Suggested form of the velum structure on the thecal apertures of *Pristiograptus* ?*kosoviensis*. **A.** Plate-like growths of microfusellar tissue (*sensu lato*). **B.** Lateral elevations of microfusellar tissue (*sensu lato*).

Diagnosis. — Robust pristiograptid of the *P. tumescens/dubius* group, up to 2 mm long, with a maximum dorsoventral width of 2.40 mm (proximally 1.00–1.30 mm); proximal thecal spacing 12–14 in 10 mm; distal thecal spacing 10–12 in 10 mm; angle of thecal inclination 43–50°; thecal length proximally ca. 1 mm; distal thecal length ca. 2 mm; thecal overlap 1/2 throughout, after first few thecae where it is less; thecal apertures almost normal length of thecal tube; base of interthecal septum heavily thickened; thecal apertural lips often heavily thickened; fuselli on distal thecae 14–17 per mm; cortical bandages possibly ca. 1 mm long, width up to 0.20 mm exhibiting longitudinal fibrils; bandages arranged in criss-cross pattern except over dorsal surface where they are normal to length of colony; ‘velum’ structures of thinner periderm, with microfusellar tissue, possibly some pseudomicrofusellar tissue, in the form of smaller plate-like or lappet-like additions to the thickened thecal apertures present in a high proportion of the specimens; sicula 2.00–2.20 mm, apex reaching level of second thecal aperture or above; sicular aperture 0.50 mm, with short, spike-like virgella; Σ value = 1.30 mm; virgella robust, projecting distally only 1–2 mm; proximal end with striking ventral curvature, dorsal wall sharply recurved at th3–th4.

Remarks. — *P. ?kosoviensis* is an unusual species for a robust pristiograptid in having a high thecal spacing (10–14 in 10 mm) and a long sicula. Most robust forms have a thecal spacing of

8–12 in 10 mm, such as *P. dubius* (except that in the late Ludlow higher thecal spacing do occur: see Rickards & Wright 1999 and Urbanek 1992). The proximal end flexure is similar to that seen in *P. tumescens* (Wood), which occurs at the same horizon, but *P. tumescens* is a less robust species, with a lower thecal spacing and a shorter sicula.

The robust pristiograptids have recently been reviewed by Rickards and Wright (in press). Of those species with similar overall dimensions *P. kolednikensis* Příbyl (1940) has a lower thecal spacing and S value. *P. fragmentalis* (Bouček, 1936) has a similarly robust rhabdosome and S value, but the thecal spacing is lower and the proximal end is straighter, lacking the sharp ventral recurvature of *P. ?kosoviensis*. The two forms are possibly closely related, *P. fragmentalis* being late in time (*kozlowskii/caudatus* or *formosus/spineus* biozones). The original material of *P. kosoviensis* described by Bouček (1931) and redescribed by Příbyl (1943) is not well-constrained by modern standards, but the species certainly has the right dimensions and thecal spacing and the known horizon is about the same as the Moroccan material.

Another not dissimilar species is *Pseudomonoclimacis latilobus* (Tsegelnuk, 1976; see Urbanek 1997), in that it has undulating thecal apertural rims which are heavily thickened and rounded. However, this species has a sicula with a pronounced dorsal tongue, a proximal end that has a well-exposed sicula and is slimly curved, and a very high thecal spacing of 18–19 in 10 mm proximally (compared with 10–14 in 10 mm)

Pristiograptus dubius labiatus Urbanek (1997) is also rather similar to *P. ?kosoviensis* but is a less robust form. The thecal spacing proximally, at 15 in 10 mm, is only slightly higher than in *P. ?kosoviensis*, but the sicula has a very strong dorsal process.

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