

Silica bodies in the Early Cretaceous *Programinis laminatus* (Angiospermae: Poales)

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Abstract

Silica bodies in short cell epidermal leaf cells of the Early Cretaceous *Programinis laminatus* (Poales) in Burmese amber are characterized. The great majority are rondels and elongated quadrates aligned horizontally in relation to the leaf axis. Rondel types include circular, elliptical, oblong, long and short forms. Quadrate types include short and long rectangles, trapezoids and pentagons. A comparison of *P. laminatus* silica bodies with those in extant epidermal leaf cells of the Poales aligns the fossil with the family Poaceae and representatives of the subfamily Pooideae.

Key Words: Cretaceous phytoliths, Burmese amber, *Programinis laminatus*, Grass silica bodies.

Zusammenfassung

Silikatkörper in kurzen Zellen der epidermalen Blattzellen werden für die unterkreidezeitliche Süßgrasartige *Programinis laminatus* (Poales) aus dem Burma Bernstein beschrieben. Die Mehrzahl sind Rondelle und horizontal verlängerte Quader. Die Rondell-Typen beinhalten kreisförmige, elliptische, längliche, lange und kurze Formen. Die Quader-Typen beinhalten kurze und lange Rechtecke, Trapezoide und Fünfecke. Eine Vergleich der Silikatkörper von *P. laminatus* mit solchen in rezenten epidermalen Blattzellen der Poales ist im Einklang mit einer Zuordnung zur Familie Poaceae und Vertretern der Unterfamilie Pooideae

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1. Introduction

Early Cretaceous Burmese amber contains a series of interesting angiosperm flowers, including those with affinities to the Momimiaceae (POINAR & CHAMBERS, 2005), Cornaceae (POINAR et al. 2007a), rosids (POINAR et al. 2008) and Cunoniaceae (CHAMBERS, et al. 2010). A leaf portion of an Early Cretaceous grass-like monocot from these deposits was previously described as *Programinis laminatus* Poinar and placed in the Poales (POINAR 2004). In that study, while silica bodies were noted in epidermal cells, they were not studied in detail. The present study characterizes short cell silica bodies in the leaf epidermis of *P. laminatus*. The fossil silica bodies are compared with short cell phytoliths reported from the leaf epidermis of other families in the Poales as well as representatives of subfamilies of the Poaceae in attempts to determine the systematic position of *P. laminatus*.

Acknowledgements

The author thanks Kenton Chambers for providing literature on silica bodies, Günter Bechly for supplying the German abstract and Emmet Judziewicz and Roberta Poinar for reading over earlier versions of the manuscript.

2. Materials and methods

The original accession number (B-P-3B) of *P. laminatus* referred to a single piece of amber. However, this piece was subsequently divided into two separate pieces, both containing leaf portions of *P. laminatus*. Both pieces of amber were first trimmed and re-

shaped with a thin-bladed diamond saw, then sanded and polished on a rotary wheel with different grades of sandpaper and finally re-shaped with a soft buffing disc to remove surface blemishes. Amber piece 1 is trapezoidal in shape, measuring 13 mm in greatest dimension (Fig. 1). The leaf fragment in piece 1 is 5 mm in length and 3 mm in width. Amber piece 2 is triangular in shape, measuring 18 mm in greatest length (Fig. 2). The leaf fragment in piece 2 is 7 mm in length and 3 mm in width. The new accession numbers are B-P-3B1 for amber piece 1 and B-P-3B2 for amber piece 2. Both specimens are deposited in the Poinar amber collection maintained at Oregon State University, Corvallis OR 97331. Terminology follows that presented in PIPERNO (2006).

The amber originated from a mine first excavated in 2001, in the Hukawng Valley, southwest of Maingkhwan in Kachin State (268200 N, 968360 E) in Burma (Myanmar). This new amber site, named the Noije Bum 2001 Summit Site, was assigned to the Early Cretaceous, Upper Albian, on the basis of paleontological evidence (CRUICKSHANK & KO, 2003), placing the age at 97–110 mya. Nuclear magnetic resonance spectra and the presence of araucaroid wood fibers in amber samples from the Noije Bum 2001 Summit site indicate an araucarian (possibly *Agathis*) tree source for the amber (POINAR et al. 2007b). Observations, drawings and photographs were made with a Nikon SMZ-10 R stereoscopic microscope and Nikon Optiphot compound microscope with magnifications up to 800 X.

3. Results

In the present work, silica bodies are treated as phytoliths that form inside grass silica cells, as defined by MULHOLLAND & RAPP (1992). The epidermal cells of *P. laminatus* are

arranged in 1-8 columns along the leaf margin and in 1-6 columns between rows of stomata. Based on the slight curvature of the leaf portion, the abaxial surface was exposed and all observations relate to that surface. In both leaf portions of *P. laminatus*, (Figs. 1, 2), silica bodies were distributed between the veins (intercostal) and over the veins (costal) in short epidermal cells (Figs. 3, 4). Intercostal silica bodies were examined in the present study because of their clarity in the fossilized leaf. The bodies were examined in their natural orientation in the leaf fragments. The shapes described here and shown in the figures are the outlines of the base as seen in planar view. It is highly questionable if silica bodies could be liberated from the epidermal cells using available laboratory techniques and the leaves would probably be destroyed in the process.

The majority of the silica bodies of *P. laminatus* fall in two general unspecialized groups (Table 1, Fig. 5). The first comprises rondels with smooth, mostly curved outlines. These included circular (Figs. 3A; 4A; 5A), elliptical (Fig. 5B), oblong (Figs. 3B; 4B; 5C), long (Fig. 3D; 4D; 5D) and short rondels (Fig. 4C; 5E). The second group consisted of horizontally elongated quadrates. These included short rectangles (Figs. 5F) and long rectangles (Figs. 3C; 5H). Other less common shapes of horizontally elongated quadrates were pentagons (Figs. 3E; 5G) and trapezoids (Fig. 5I). Many of the silica bodies had double outlines and ranged from 8-23 μm in greatest dimension (Table 1). None of the silica bodies contained granules.

4. Discussion

Phytoliths in leaf epidermal cells of clades in the Poales are quite variable, however they do not occur in all clades (PRYCHID et al. 2004). They are completely absent in the Anarthriaceae, Eriocaulaceae, Hydatellaceae, Mayacaceae, Typhaceae, Prioniaceae and Xyridaceae and lacking in the leaf epidermal cells of the Ecdeiocoleaceae, Juncaceae and Flagellariaceae. Phytoliths are represented by silica sand or spherical and spinulose bodies in the Bromeliaceae, while members of the Centrolepidaceae have irregular rectangular phytoliths, particles or sand. In the Cyperaceae, phytoliths are mostly conical (rarely nodular), often with small spines (satellites) around the base. Members of the Joinvilleaceae have irregular nodular or smooth, cubical phytoliths. In the Rapateaceae, epidermal phytoliths are usually small with several to many per cell. Phytoliths are usually absent in the Restionaceae but are spherical when present. Those of the Thurniaceae are nodular or in the form of sand with several per cell (PRYCHID et al. 2004; OLLENDORF 1992). None of the phytoliths in the above clades are similar to the silica bodies from *P. laminatus*.

Silica bodies from the epidermal short cells of *P. laminatus* are relatively unspecialized, however circular to oval silica bodies are well-established diagnostic features in a wide variety of extant grasses (BROWN 1984; TWISS 1992; MULHOLLAND & RAPP 1992; PIPERNO & PEARSALL 1998; PIPERNO 2006; RAPP & MULHOLLAND 1992).

METCALFE (1960) listed 20 types of short cell grass leaf silica bodies. His round types, recovered from the pooidids *Briza erecta* Lam. and *Elymus canadensis* (L.) overlap in shape and size with the round types from *P. laminatus*. Brown's oblong types in *Brachypodium pinnatum* Beauv. (Pooideae) and *Aristida ciliata* Desf. (= *Stipagrostis ciliata* (Desf.) De Winter (Arundinoideae) are similar in size and shape to those of *P. laminatus*. Also the horizontally elongated (elongated- smooth) silica bodies as found in *Bromus*

coloratus Steud. (Pooideae) and *Anthochloa lepidula* Nees & Meyen (Pooideae) also resemble those of the fossil.

In the classification of grass phytoliths by TWISS et al. (1969), 26 types of silica bodies grouped in four classes were presented. Their Pooideae (=Festucoideae) class contains 8 types of geometrically simple silica bodies. Their circular, rectangular, elliptical, and oblong types fall within the shape and size range of those in *P. laminatus*.

ELLIS (1979) separated grass silica bodies into three main categories based on the surface or planar view: vertically elongated, equidimensional and horizontally elongated. Under equidimensional were placed cuboid, slightly rectangular and round. In the category of horizontally elongated silica bodies were included oblong and elongate with smooth outline. All of the above shapes are represented in *P. laminatus*.

In their study of the anatomy of East African grasses, PALMER & TUCKER (1983) described elliptical (19 μm in length) and oblong (17 μ in length) silica bodies from *Festuca abyssinica* A. Richard (Pooideae) that resembled those from *P. laminatus*. Square and circular silica bodies were also present. Rectangular (25 μm in length), oblong and elongated smooth silica bodies occurred in *Vulpia bromoides* (L.) Gray (Pooideae). Oblong elliptical smooth silica bodies (28 μm in length) occurred in *Pseudobromus sylvaticus* Schumann (Pooideae) and oblong silica bodies (14 μm in length) occurred in *Secale africanum* Stapf (Pooideae) (PALMER & TUCKER 1983).

BROWN (1984) listed 8 major classes of leaf epidermal silica bodies in grasses from North America. Of all the silica bodies presented in his table 1 and depicted in his figure 1, those that resembled the fossils were in his "double outline class". It is interesting that Brown was one of the few authors that noted a double outline at the base of grass silica

bodies. This double rim appears to be associated with the silica body itself rather than representing the inner wall of the silica cell closely appressed to the silica body. A double outline occurs in many of the silica bodies of *P. laminatus*, although the inner outline is often faint. The silica body types noted by BROWN (1984) that resemble those of *P. laminatus* are irregular oval to circular double rim types as found in *Oryzopsis hymenoides* (Roem. & Schult.) Ricker ex Piper (Pooideae) (Brown's III A3)(14-18 μm in greatest length), short, non-sinuuous forms with round ends (also with double outline) as found in *Elymus canadensis* (L.)(Pooideae) (Brown's V B 2b1)(28 μm in greatest length), *Bromus inermis* Leys. (Pooideae) (Brown's V B2b2)(25 μm in greatest length), *Agropyron spicatum* (Pursh.) Scribn. & J. G. Sm. (= *Pseudoroegneria spicata* (Pursh.) A. Löve (Pooideae) [Brown's V B2b3 (23 μm in greatest length) and V B2b4(18 μm in greatest length)] and with irregular ends as occurs in *A. spicatum* (Brown's V B2d1) (20 μm in greatest length). These closely resemble the size and shape of silica bodies in *P. laminatus*.

In their key to the major shape types of grass silica bodies, MULHOLLAND & RAPP (1992) recognized eight common shapes in three geometric classes. These shapes are portrayed by the outline of the base as viewed from the top (top or planer view). Restricting the definition of silica body as phytoliths that form inside grass silica cells, they defined the base as the relatively flat, broad side of the body. The authors also introduced the term "rondel" for oval to circular and short trapezoidal silica bodies. Of the 8 shapes described by MULHOLLAND & RAPP (1992), those in the rondel and rectangle category fall within the shape range of silica bodies in *P. laminatus*. MULHOLLAND & RAPP (1992) noted that their geometric classes of silica bodies are actually idealized groupings since a wide variation in basal outline, face concavity and general configuration occurs. Most faces were not

completely flat and most shapes were not strictly rectangular, pyramidal or conical and could not be assigned to any other defined geometric figure.

Silica body morphotypes have been used to determine the systematic placement of their producers (METCALFE 1960; BROWN 1984; PRYCHID et al. 2004). Circular to oval rondel types of silica bodies as well as short and long rectangles are well-established diagnostic features of grass leaf epidermal cells (METCALFE 1960; TWISS et al. 1969; PALMER & TUCKER, 1983; BROWN 1984; TWISS 1992; MULHOLLAND & RAPP 1992; RAPP & MULHOLLAND 1992; PIPERNO & PEARSALL 1998; PIPERNO 2006). Based on the shape of silica bodies in short celled leaf epidermal cells of *P. laminatus*, the fossil falls within the Poaceae. There are no types of silica bodies that would eliminate *P. laminatus* from the Poaceae. The typical shapes found in *P. laminatus* (circular, elliptical, oblong and rectangular) are most closely associated with members of the Pooideae, but also occur in the leaf epidermal cells of some Arundinoideae, Chloridoideae Panicoideae and Bambusoideae (PRAT 1936; METCALFE 1960; MULHOLLAND 1989).

Early Cretaceous grasses are not unexpected. Grass phytoliths have been recovered from soil, paleosol, sediment and rock environments dating back to the Early Tertiary (TWISS 1992; STRÖMBERG 2004) and more recently, phytoliths from dinosaur coprolites in India showed that at least five taxa of extant grass subclades were present by the Late Cretaceous (PRASAD et al. 2005). Since the Burmese amber mines are on the Burma Plate (MITCHELL 1993), which is part of Laurasia, *P. laminatus* is an Old World clade. Based on past climatic reconstructions, *P. laminatus* inhabited tropical-subtropical forested areas in southern Asia some 100 million years ago (BOUCOT et al. 2011).

5. References

- BOUCOT, A. J., CHEN XU & SCOTese, C. R. (2011): Preliminary compilation of Cambrian through Miocene climatically sensitive deposits. - *Memoirs of the Society of Economic Paleontologists and Mineralogists* (In press).
- BROWN, D. A. (1984): Prospects and limits of a phytolith key for grasses in the Central United States. - *Journal of Archaeological Science*, **11**: 345-368.
- CHAMBERS, K. L. (2010): *Tropidogyne*, a new genus of Early Cretaceous Eudicots (Angiospermae) from Burmese amber. - *Novon*, **20**: 23-29.
- CRUICKSHANK, R. D. & KO, K. (2003): Geology of an amber locality in the Hukawng Valley, northern Myanmar. - *Journal of Asian Earth Science*, **21**: 441-455.
- ELLIS, R. P. (1979): A procedure for standardizing comparative leaf anatomy in the Poaceae. II. The epidermis as seen in surface view. - *Bothalia*, **12**: 641-671.
- METCALFE, C. R. (1960): *Anatomy of the Monocotyledons. I. Gramineae*. 794 pp.; Oxford (Clarendon Press).
- MITCHELL, A. H. G. (1993): Cretaceous-Cenozoic tectonic events in the western Myanmar (Burma) -Assam region. - *Journal of the Geological Society, London*, **150**: 1089-1102.
- MULHOLLAND, S. C. (1989): Phytolith shape frequencies in North Dakota grasses: a comparison to general patterns. - *Journal of Archaeological Science*, **16**: 489-511.
- MULHOLLAND, S. C. & RAPP, JR., G. (1992): A morphological classification of grass silica-bodies. - In: RAPP, JR., G. & MULHOLLAND, S. C. (eds): *Phytolith Systematics: Emerging Issues*: 65-89; New York (Plenum Press).

- OLLENDORF, A. L. (1992): Toward a classification scheme of sedge (Cyperaceae) phytoliths.
 In: RAPP, JR., G. & MULHOLLAND, S. C. (eds): Phytolith Systematics: Emerging
 Issues: 91-106; New York (Plenum Press).
- PALMER, P. G. & TUCKER, A. E. (1983): A scanning electron microscope survey of the
 epidermis of East African Grasses, II. - Smithsonian contributions to Botany,
53:1-72.
- PIPERNO, D. R. (2006): Phytoliths, a comprehensive guide for Archaeologists and
 Paleoecologists. 238 pp.; New York, N. Y (Altamira Press).
- PIPERNO, D. R. & PEARSALL, D. M. (1998): The silica bodies of tropical American
 grasses: morphology, taxonomy, and implications for grass systematics and fossil
 phytolith identification. - Smithsonian Contributions to Botany, **85**: 1-40.
- POINAR, JR., G. O. (2004): *Programinis burmitis* gen. et sp. nov., and *P. laminatus* sp.
 nov., Early Cretaceous grass-like monocots in Burmese amber. -Australian
 Systematic Botany, **17**: 497-504.
- POINAR, JR., G. O. & CHAMBERS, K. L. (2005): *Palaeoanthella huangii* gen. and sp,
 nov., an Early Cretaceous flower (Angiospermae) in Burmese amber. –Sida, **21**:
 2087-2092.
- POINAR, JR., G. O. CHAMBERS, K. L. & BUCKLEY, R. (2007a): *Eoëpigynia burmensis*
 gen. and sp. nov., an Early Cretaceous eudicot flower (Angiospermae) in Burmese
 amber. -Journal of the Botanical Research Institute of Texas, **1**: 91–96.
- POINAR, JR., G. O. LAMBERT, J. B. & WU, Y. (2007b): Araucarian source of fossiliferous
 Burmese amber: spectroscopic and anatomical evidence. -Journal of the Botanical
 Research Institute of Texas, **1**: 449- 455.

- POINAR, JR., G. O., CHAMBERS, K. L. & BUCKLEY, R. (2008): An Early Cretaceous angiosperm fossil of possible significance in rosid floral diversification. -Journal of the Botanical Research Institute of Texas, **2**:1183–1192.
- PRASAD, V., STRÖMBERG, C. A. E., ALIMOHAMMADIAN, H. & SAHNI, A. (2005): Dinosaur coprolites and the Early Evolution of Grasses and Grazers. –Science, **310**: 1177-1180.
- PRAT, H. (1936): La Systematique des Graminees. -Annales des sciences naturelles Botanique, Paris, X, **18**: 165-258.
- PRYCHID, C. J., RUDALL, P. J. & GREGORY, M.(2004): Systematics and Biology of silica bodies in Monocotyledons. -The Botanical Review, **69**: 377-440.
- RAPP, JR., G. & MULHOLLAND, S. C. (1992): Phytolith Systematics: Emerging Issues, 350 pp.; New York (Plenum Press).
- STRÖMBERG, C. A. E. (2004): Using phytolith assemblages to reconstruct the origin and spread of grass-dominated habitats in the Great Plains during the Late Eocene to Early Miocene. -Palaeogeography, Palaeoclimatology, Palaeoecology, **207**: 239-275.
- TWISS, P. C. (1992): Predicted world distribution of C3 and C4 grass phytoliths. - In: RAPP, JR., G. & MULHOLLAND, S. C. (eds): Phytolith Systematics: Emerging Issues: 113-128; New York (Plenum Press).
- TWISS, P. C., SUESS, E. & SMITH, R. M. (1969): Morphological Classification of Grass Phytoliths. -Proceedings of the Soil Science Society of America, **33**: 109-115.

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Figure captions

Fig. 1. Portion of *Programinis laminatus* leaf in amber piece 1. Bar = 0.7 mm.

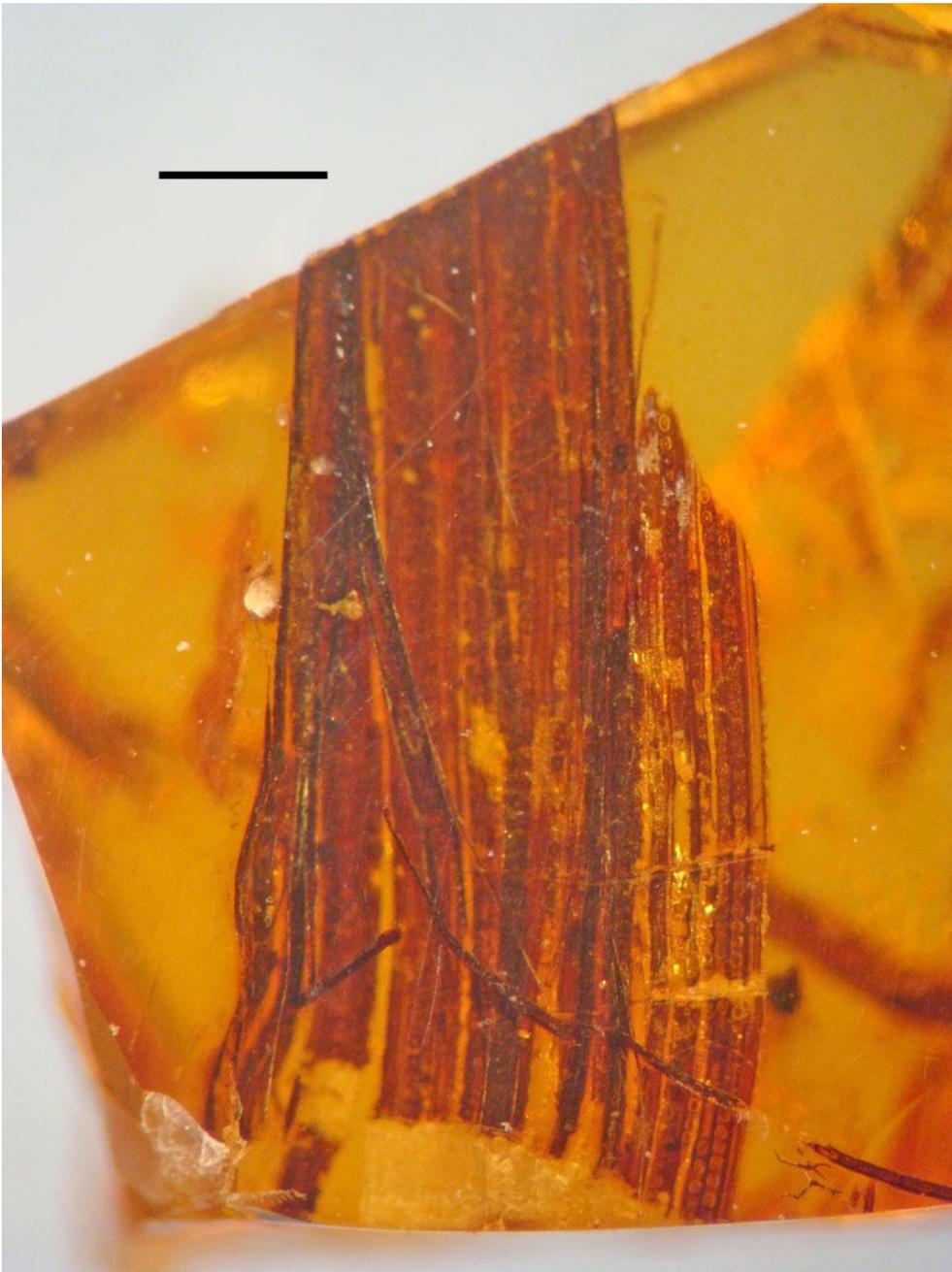


Fig. 2. Portion of *Programinis laminatus* leaf in amber piece 2. Bar = 0.8 mm.

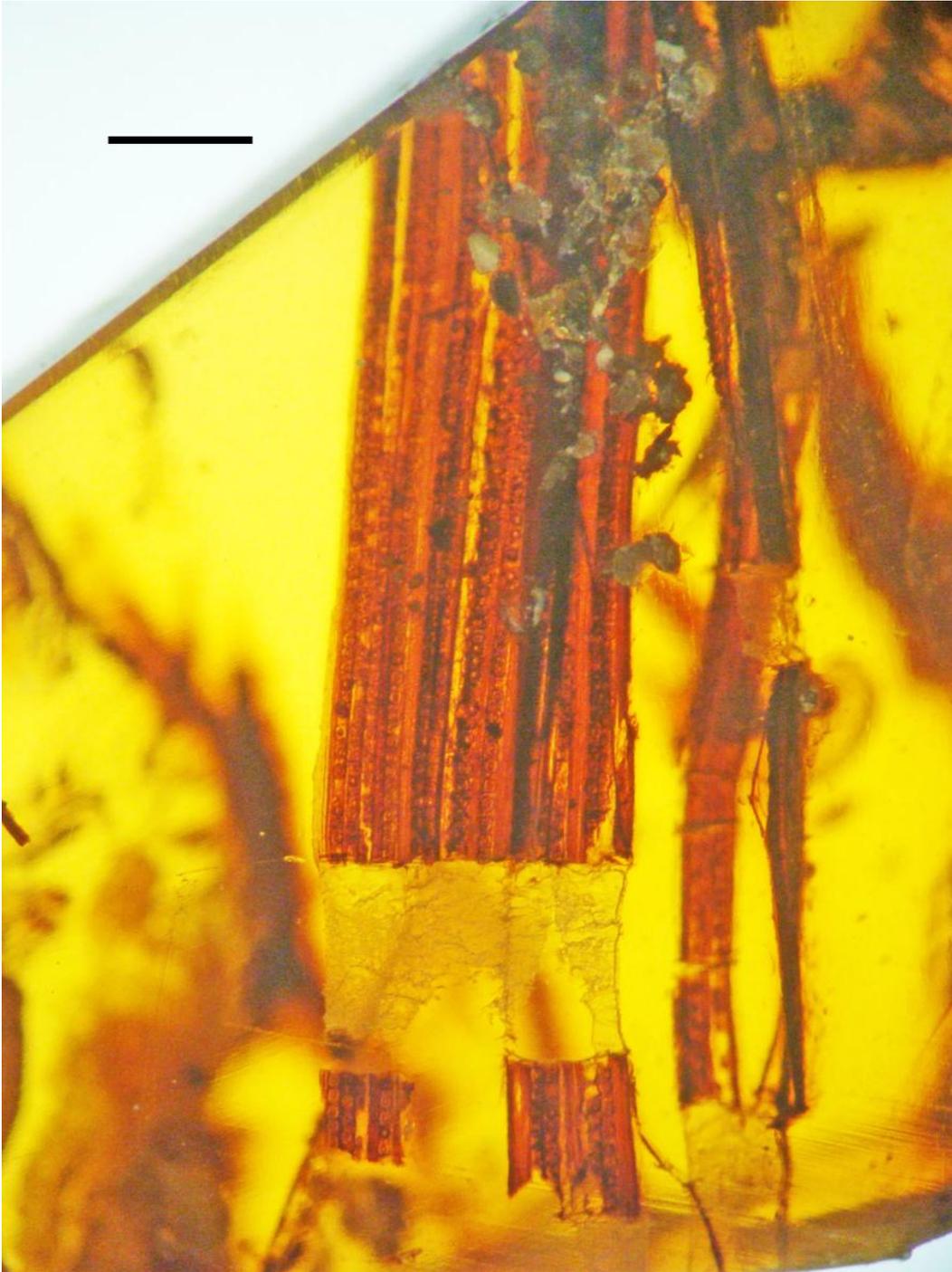


Fig. 3. Silica body types in leaf epithelial cells of *Programinis laminatus* in amber piece
1. A = circular (entire) rondel; B = oblong rondel; C = short rectangles; D = long rondel;
E= pentagon. Bar = 28 μ m.

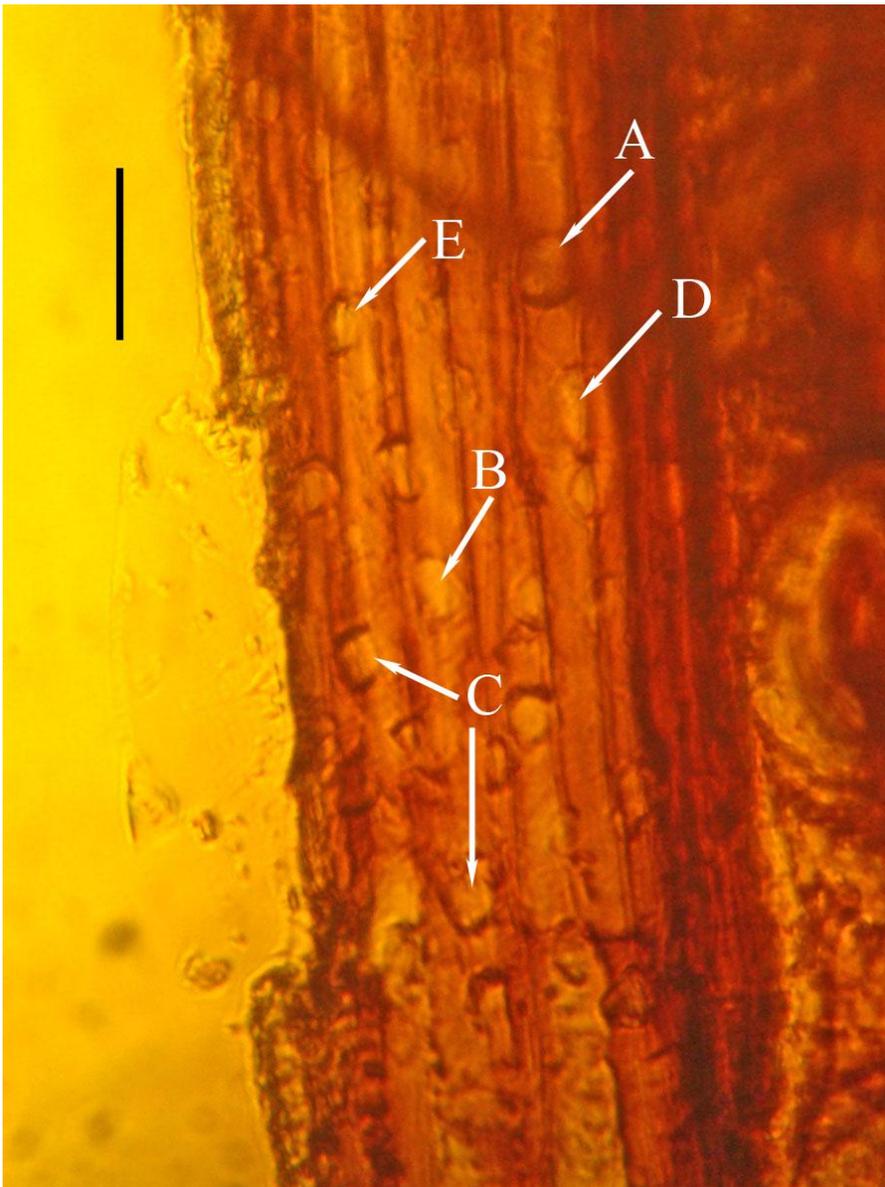


Fig. 4. Silica bodies types in leaf epithelial cells of *Programinis laminatus* in amber piece
2. A = circular (entire) rondel; B = oblong rondel; C = short rondel; D = long rondel. Bar
= 40 μm .

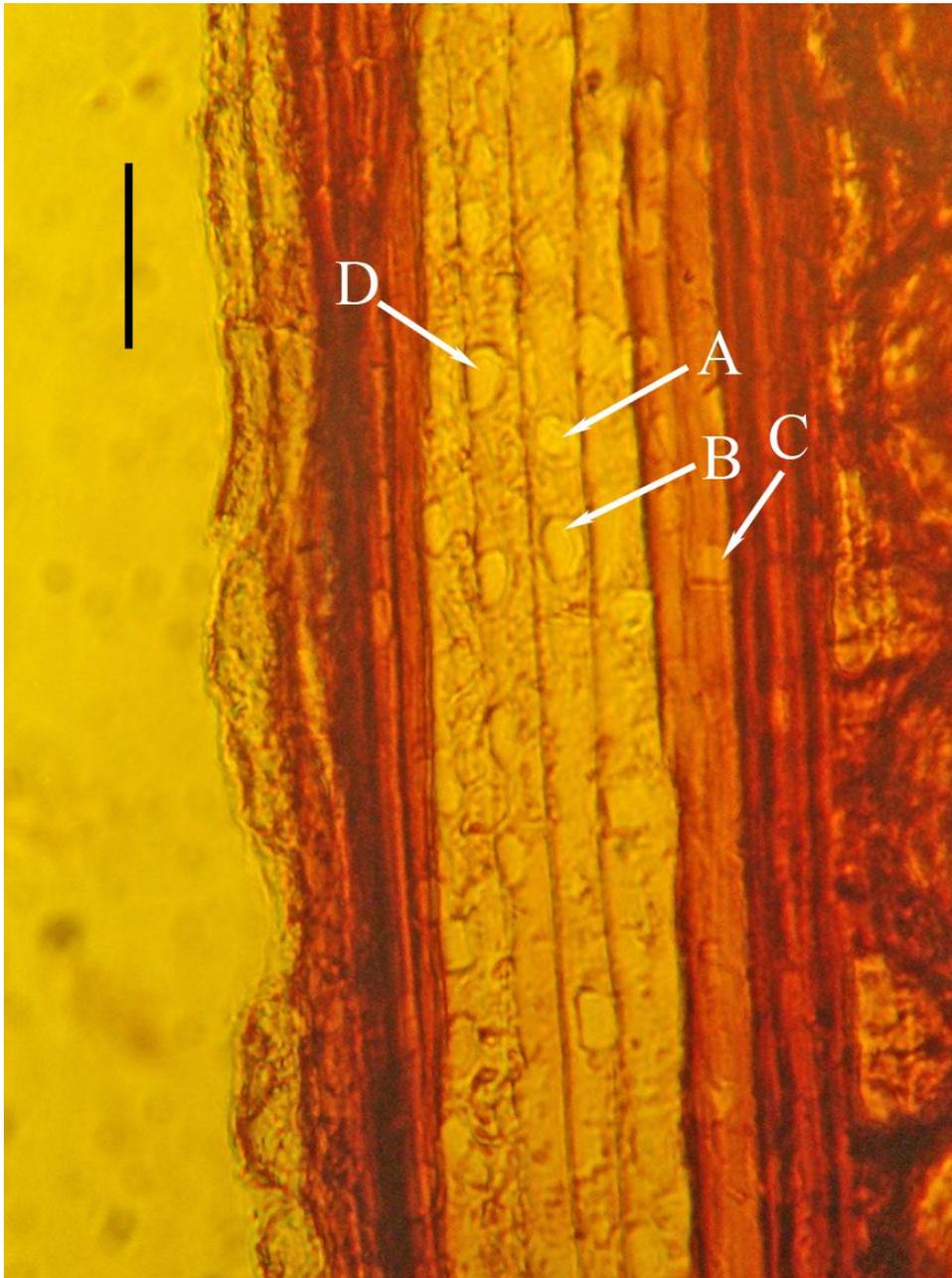
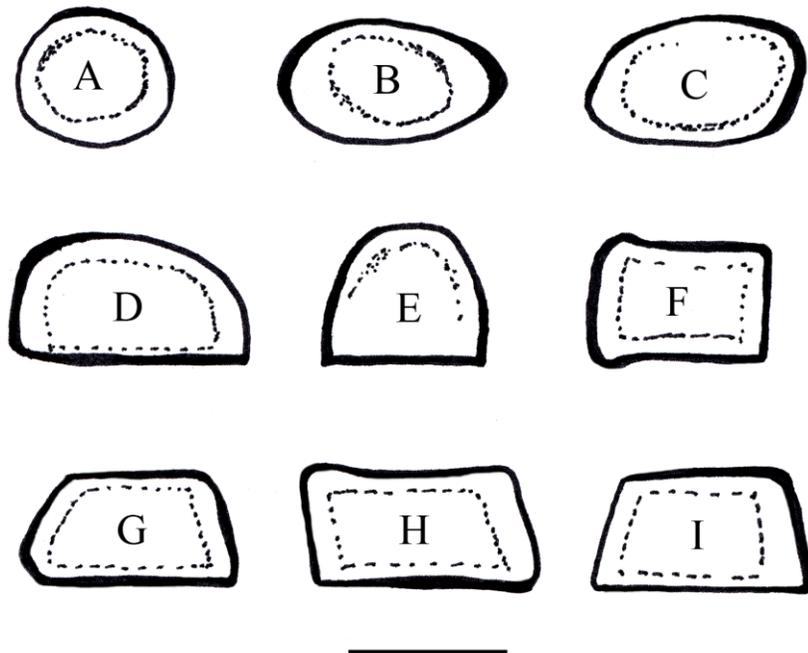


Fig. 5. Planar view of basic types of silica bodies in epidermal leaf cells of *Programinis laminatus*. A = circular (entire) rondel; B = elliptical rondel; C = oblong rondel; D = long rondel; E = short (flat) rondel; F = short rectangle; G = pentagon; H = long rectangle; I = trapezoid. Bar = 17 μ m.



6. Table 1. Types, shapes and sizes of epidermal cell leaf silica bodies in *Programinis laminatus* (all measurements in microns)(See **Fig. 5** for corresponding shapes).

Type	Shape	part measured	average size	size range
A	Circular rondel	diameter	10	8-13
B	Elliptical rondel	greatest diameter	15	12-20
C	Oblong rondel	greatest diameter	14	9-20
D	Long rondel	diameter	16	12- 20
E	Short rondel	base	12	8- 14
F	Short rectangle	base	12	9-15
G	Pentagon	base	13	11-15
H	Long rectangle	base	15	13-23
I	Trapezoid	base	15	12--17

