

On *Montsechia*, an angiospermoid plant from the Lower Cretaceous of Las Hoyas, Spain: new data and interpretations

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Received 13 June 2011; accepted for publication 20 October 2011

ABSTRACT. *Montsechia* from the Las Hoyas Locality, Cuenca, Spain, previously described as a floating plant with whorled leaves is re-interpreted as having a dimorphic long shoot – short shoot branching system with heterophyllous elongate and scaly leaves. The stomata and trichomes are observed in the scaly leaves. The growth habit is interpreted as heloxerophytic over the coastal marshland habitats. The ovulate cupules are terminal on the reproductive short shoots and contain a solitary ovule. Pollen grains are occasionally found on the nucellus betraying a gymnospermous pollination mode. The pollen tube morphology is like in gnetophytes and angiosperms. Some seed-like structures on scale leaves and bud cataphylls contain larval remains and are interpreted as nematode galls. The taxonomic affinities of *Montsechia* are with the helophytic proangiosperms, in particular the Baisiales. The *Montsechia* – *Montsechites* (“*Ranunculus*”) assemblage of Montsec and La Hoyas is comparable to the mid-Cretaceous proangiosperm assemblages of Transbaikalia, Mongolia and eastern China.

KEYWORDS: *Montsechia*, early angiosperm, proangiosperms, nematode galls, Cretaceous, Las Hoyas locality, Spain

INTRODUCTION

The pre-Albian angiosperm records are of great interest bearing on the problem of angiosperm origin and the rates of initial angiosperm evolution. *Montsechia vidalii* (Zeiller 1902) Teixeira 1954 from the supposed Barremian deposits of Spain ranks among the earliest angiosperm-like fossils supposedly indicating a long pre-Albian history of the group (Daviero-Gomez et al. 2006, Gomez et al. 2006). However, since angiosperm characters are reported in diverse non-angiospermous (proangiospermous) Cretaceous and even pre-Cretaceous plants (reviewed in Krassilov 1997, 2009), a cautious revision of such finds is necessary before evolutionary implications are discussed.

Both the interpretation of *Montsechia* as angiosperm (Gomez et al. 2006) and my preliminary conclusion on gnetophytic affinities of this plant (Krassilov 2006) were presented at the 7th European Paleobotanical and Palynological Conference, Prague, 2006, and the issue

has remained controversial ever since. This paper reports on my further results concerning growth form and reproductive structures, as well as the seed-like bodies interpreted as nematode galls. As in the present day wheat nematodes, the galls seem to have been quite similar to the seeds. A designation “seed-like body” is here applied to uncertain cases.

My results based on a limited material must be considered as preliminary step toward understanding *Montsechia* and its significance for the problem of angiosperm origins.

MATERIAL AND METHODS

Montsechia is abundant in laminated carbonates at Las Hoyas outcrop of Iberian Basin, from which I obtained 30 specimens courtesy of Alexander Bannikov and Tatyana Kodrul who visited this locality during post-congressional field trips in 2005 and 2008. A larger slab about 20 × 15 cm presents several shoot

fragments and several dozens detached scale leaves and bract compressions bearing seed-like bodies. The material was studied on the rock surface as well as on film transfers and in bulk maceration residues. Altogether, 70 seed-like bodies were cleared for light microscopy and mounted for SEM. The microphotographs were obtained with the stereomicroscope Leica 300, dissecting light microscope Nikon Eclipse and scanning electron microscope FE1 Quanta 200.

The material is stored in the palaeobotanical depository of the Institute of Evolution, University of Haifa, No. SLH 1 – 70.

VEGETATIVE MORPHOLOGY

The traditional interpretation of *Montsechia* as having successive leaf whorls on monomorphic shoot axes is incorrect. Gomez et al. (2006) have discerned two growth forms, with long decussate leaves and scaly spiral leaves, but failed to recognize dimorphic shoot systems and heterophylly in both the long-leafed and short-leafed varieties. The leaves are decussate rather than whorled, the apparent whorls consisting of adjacent leafy short shoots at the last order branching nodes.

The material at hand represents leafy shoots of three orders of branching. The first order axes about 1.5 mm thick give off distichous lateral branches that are opposite at the regularly spaced branching nodes. The lateral branches are slender, upcurved, of unequal length, with decussate leaves, subtending axillary short shoots that can be missing from the axils of a few apical leaf pairs (Pl. 1, fig. A).

Both long and short shoots are heterophyllous, foliated with elongate and scaly leaves. One or another leaf shape prevails distinguishing the “leafy” and “scaly” forms (Pl. 1, figs A–C). In the leafy form (Fig. 1), the prevailing leaf shapes are linear, falcate, sessile, bluntly pointed, thick and apparently succulent, with strong fibers transpiring through the epidermis (Pl. 2, figs A–C; Pl. 3, fig. B). The leaf apices are minutely serrate with microscopic teeth (Pl. 3, fig. B). Their axillary short shoots are distichous, opposite at the branching nodes, developing as small knobs and varying from hemispherical to club-shaped when fully developed. The short shoot leaves are heteromorphic, with a few scale leaves at the base followed by a tuft of overlapping transitional and elongate leaves. Two intermingling leaf tufts of the opposite short shoots produce an apparent “leaf whorl” of the node.



Fig. 1. *Montsechia vidalii* (Zeiler) Teixeira, long-leafed branching shoot

The scaly form is also heterophyllous (Fig. 2), but the elongate leaves are mostly shed leaving raised leaf cushions that protrude between the

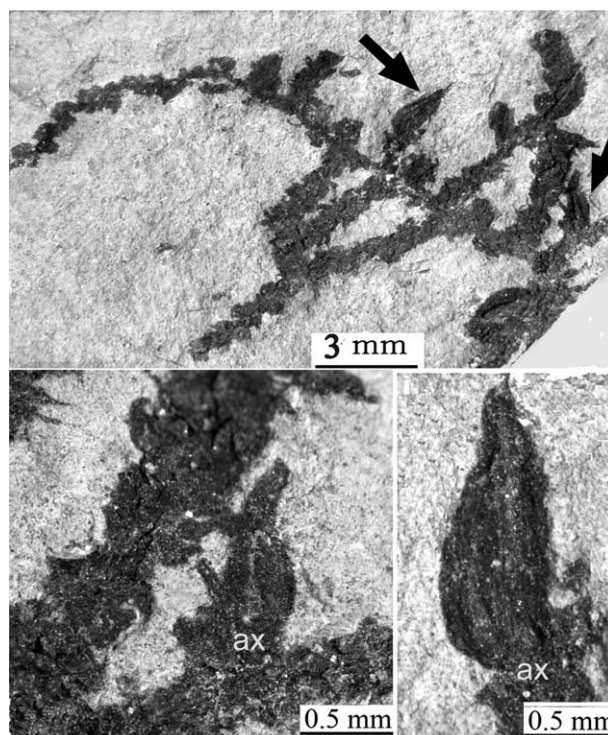


Fig. 2. *Montsechia vidalii* (Zeiler) Teixeira, branching scale-leaved shoot with two buds (arrows) and the buds magnified; ax, shoot axis sprouting from between the cataphylls

scales. A few welting leaves may persist (Pl. 1, fig. B). The short shoots vary from hemispherical to shortly cylindrical, uniformly covered with scale leaves that are shortly triangular, acute, imbricate, decurrent, with the free part slightly spreading.

The scale leaf cuticle is moderately thick, papillate, with a fringe of transversely elongate cells and with a few stomata in the central part of their adaxial face (Pl. 3, figs A, B). The stomata are irregularly scattered on the densely trichomate leaf surface, with sunken guard cells and irregular subsidiary cells that are smaller than the pavement cells.

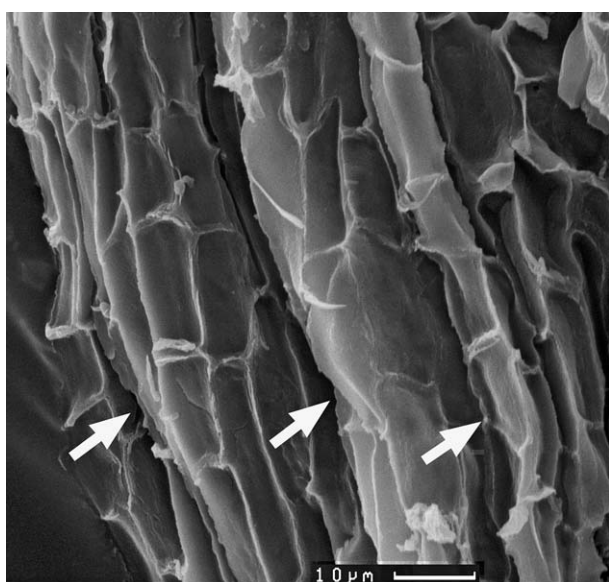


Fig. 3. *Montsechia vidalii* (Zeiler) Teixeira conducting tissue of a shoot axis (Pl. 2, fig. C), arrows on the bundles of spiral tracheids or tracheid fibers surrounded with metatracheal parenchyma

A few anatomical features are discernible in cleared shoot axes. The conducting tissue is organized in a few parallel bundles showing spiral tracheids or tracheary fibers surrounded with tabloid cells of metatracheal parenchyma (Fig. 3).

REPRODUCTIVE STRUCTURES

Attached to *Montsechia* shoots are the bladder-like thick walled, but feebly cutinized structures investing a solitary inner body which is well cutinized and detachable by maceration, but actually never found dispersed (therefore not assignable to *Spermatites* Miner 1935, a form genus for dispersed seed-like bodies probably comprising also bryophyte

sporogonia). In both the leafy and scaly varieties, these structures are borne terminally on the short shoots developing in the leaf axils of penultimate branches, but in the leafy variety they are solitary and scattered (Pl. 4, fig. B), whereas as they are more frequent and aggregated on reproductive shoots. In Fig. 2, the scale-leaved branching system bears two conical buds (arrows) with the shoot axis sprouting between the overlapping cataphylls. A few cataphylls persist on the axis of the sprouting long shoots (Pl. 5, figs C, D) that produce several pairs of fertile short shoots (Pl. 5, figs A, B).

A leafy shoot in Pl. 4 fig. B produces distichous short shoots only one of which is fertile (arrow). The opposite short shoot bears a terminal tuft of elongate leaves topologically equivalent to the ovulate structure the external coat of which is formed of incompletely connate leaves adhering to the inner body. In the scale-leaved reproductive shoot system, the fertile short shoots produce one to several pairs of small falcate leaves before the terminal ovulate structure. Slender scale leaves spread sideways from the elongate terminal body (Pl. 5, fig. B) that is notched at the apex and shows a median split between the constituent bracts. This structure was left intact for documentation, but an analogous if but acuminate and slightly falcate structure in Pl. 5, fig. A was macerated yielding a cutinized inner body Pl. 5, fig. E).

These observations seem congruous with interpretation of the external seed coat as a cupule formed of bracteate appendages, with the foliage leaves down the axis partly involved in fusion. Their shapes vary from ovate, shortly apiculate, broadly truncate at base to elongate-elliptic, cuneate or slightly cordate at base, apically acuminate or pungent, about 1.5–3.0 mm long. The cupule walls are thick compressions with indistinct longitudinal folds or ribs, fibrous, showing longitudinal cell files. Irregular pits on the walls apparently represent hair bases. They contain a solitary ovule that is epitropous (curved up toward the apex), elongate or elliptic, straight or slightly curved, keeled, about 1.0–1.5 mm long. The chalazal end is smoothly rounded; the micropylar end is bluntly pointed or shortly mucronate.

Cleared ovules show a slender inner integument one cell layer thick, extending up to 2/3 of the nucellus length (Pl. 6, fig. C; Pl. 7, fig. C),

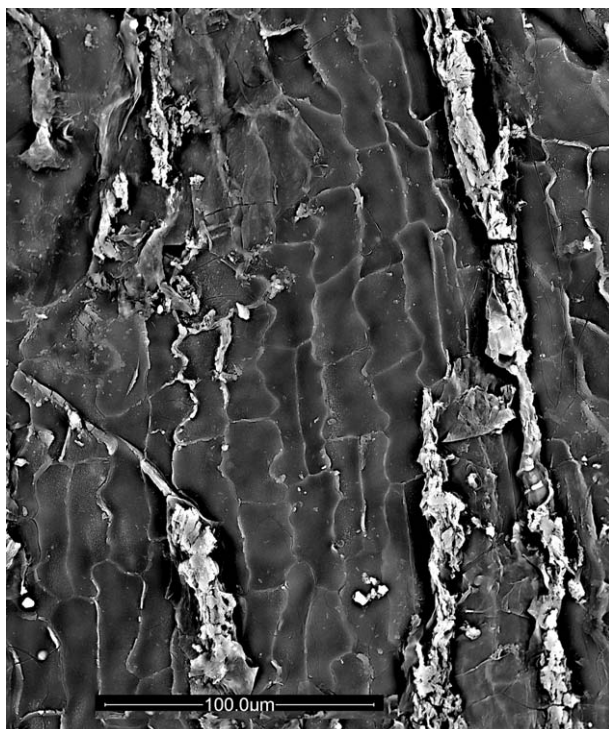


Fig. 4. *Montsechia vidalii* (Zeiler) Teixeira, nucellar cuticle showing sinuous cell walls

but mostly lost in development. The nucellus is relatively massive, free and strongly cutinized (Pl. 6, fig. A), showing longitudinal files of elongate thin-walled cells with sinuous anticlinal walls (Fig. 4). The nucellar features remain unchanged in the fewer apotropous (curved down toward the base ovules). A distinct chalazal cap (hypostase) is formed at the hilum that is typically shifted short distance toward the micropyle (Pl. 6, fig. B). The nucellar apex is transformed into the likewise prominent epistase extending as a short nucellar beak. The hypostase is discoid to hemispherical, thicker and darker stained than the rest of the nucellus, with epidermal cell rows of chalazal region converging toward it. The epistase is a hood-like strongly papillate structure of sinuously contorted cells, fairly distinct, yet not sharply delimited from the rest of the nucellar body (Pl. 7, fig. C).

Pollen chamber is scarcely discernible, but a few pollen grains are found attached to the epistase region. Their preservation precludes detailed description, but the outlines are broadly elliptic, about 20 μm over the longer axis, with a depressed median sulcus extending the whole length of the apertural face and bordered by arcuate lateral folds apparently delimiting a bilobed saccus (Pl. 8, fig. C). A single grain considerably larger than the

rest shows a tube 5 μm wide emerging from between the narrow saccus lobes and turning down the nucellus (Pl. 8, fig. B). The tube is non-septate, thereby distinct from fungal hyphae present on the nucellus. If this is an instant of germination then the larger size of the grain can be explained by swelling at gametophyte development, while the tube propagation is intercellular without damaging the nucellar cells.

Dispersed pollen grains of this type were found in the maceration residue to be described elsewhere. A few dispersed seeds and stamen-like structures are found among the *Montsechia* debris, but their attribution to this plant is uncertain. The seed in Fig. 5B is elongate-elliptical 0.7 mm long, traversed by a median ridge, tapered to both ends, with a slender stalk-like extension at the base and a relatively long micropylar tube. The seed body is surrounded by a feebly imprinted fringe probably representing cupular lobes inflated in the median plane. Prominent pits on the surface of the seed appear to be hair bases or scars of shed bristles.

The stamen-like structure in Fig. 5A has a stout stalk that is distally expanded bearing what appears to be an elongate synangium. A small scale persists at the base of the stalk. The synangium is longer than the stalk, slightly curved, attached by the broad base and

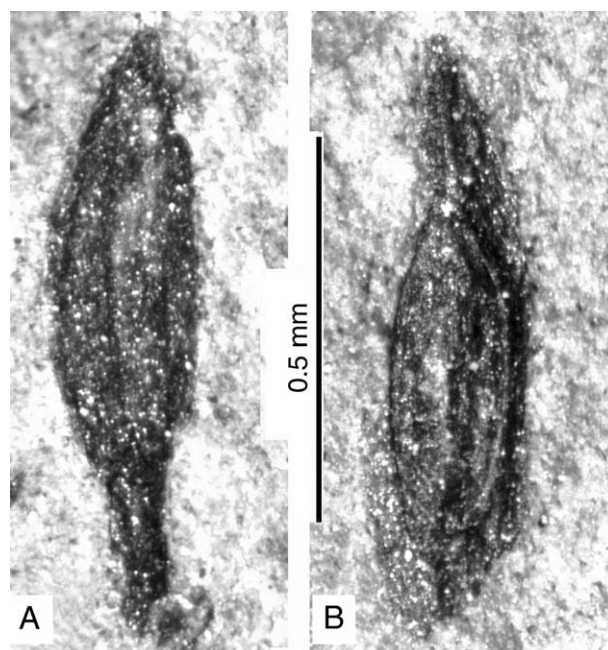


Fig. 5. Reproductive structures found among the small debris of *Montsechia vidalii* (Zeiler) Teixeira. **A**, Microspotophyll; **B**, Seed

tapered to the apex. It is traversed with three prominent longitudinal grooves apparently representing suture lines of four linear sporangia coherent for their entire length. Their bases are expanded protruding as minute thickenings or auriculae over the point of stalk attachment. Since this is the only specimen no attempts at maceration were made.

NEMATODE GALLS

Seed-like bodies on scale leaves and cataphylls, although similar to the cupulate ovules, are here interpreted as galls on account of larval remains found in some of them (morphology and development of nematode galls are reviewed in Zuckerman & Rhode 1981, Meyer & Maresquelle 1983). The gall bodies are solid easily detachable capsules symmetrically constricted and thickened at both ends or at the pointed end alone. They are most frequently found on detached cataphylls that are usually preserved their concave face up exposing the gall.

An attached seed-like body in Pl. 4, fig. A is nearly spherical with a short tube-like outgrowth pointing down the shoot. The tube is filled with a resistant dark matter. A transversely ridged coiled body at the base of the tube (arrow) is interpreted as a nematode larva of an early developmental stage, while the smaller rounded bodies marked with arrowheads can be unhatched eggs, but they are either poorly preserved or overmacerated.

Plate 7, fig. A shows a small conical body macerated from a cataphyll. It is shortly pointed at the dome-like apex and slightly constricted toward the base, with a prominent circular hole short distance above the base opening an exit from the gall cavity. A ruptured tissue projecting from the exit hole can be a crumpled larval exuvium. The gall surface is corrugate and longitudinally fissured. A thick coiled body emerging sideways through a crevice in the wall (Fig. 6) supposedly represents a more advanced stage of larval development.

DISCUSSION

Montsechia still remains a poorly studied fossil plant. Its age assignment, morphological interpretation, palaeoecology, taxonomic

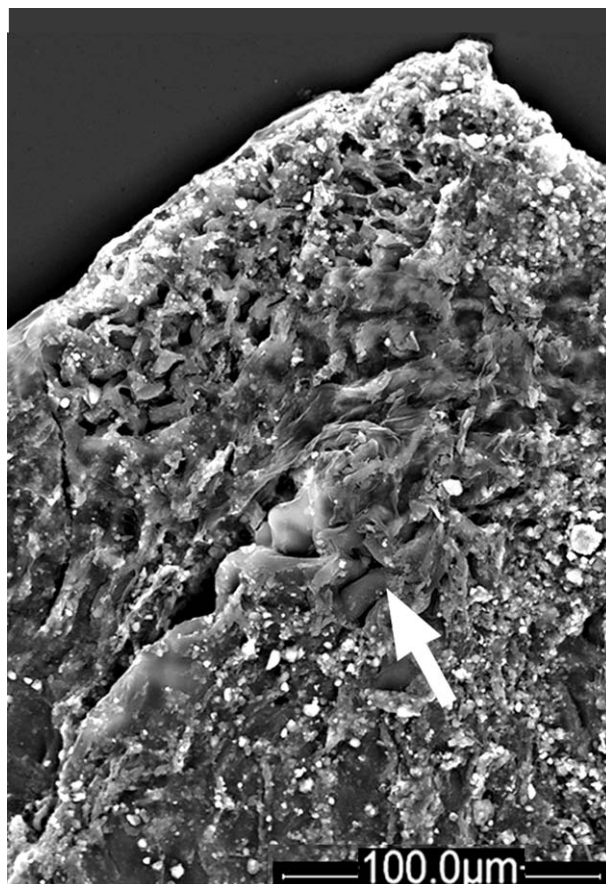


Fig. 6. Gall on *Montsechia vidalii* (Zeiler) Teixeira, annulate larva seen through crevice in the wall, magnified from Pl. 8, fig. A

affinities and significance for angiosperm evolution are the matters of discussion briefly considered below.

AGE ASSIGNMENT

For lacustrine carbonates that are the major source of pre-Albian angiosperm-like fossils, age assignments are problematic, because their associated faunistic assemblages, although rich and of high preservation quality, are poorly correlated with chronostratigraphic scales. *Montsechia vidalii* and the related if not conspecific plant *Montsechites (Ranunculus) ferreri* (Teixeira 1954, Blanc-Louvel 1964) has been first described as *Pseudoasterophyllites vidali* Zeiller 1902 from lithographic limestones of the Montsec Range, Pyrenees (El Montsec de Rubiès, Lleida Province, northeastern Spain), then considered to be Late Jurassic (Kimmeridgian), but later re-assigned to Neocomian (Barale et al. 1984). The same species was found as a dominant plant macrofossil in the famous Las Hoyas Locality of Eastern Iberian Basin, Cuenca Province, central – eastern

Spain, the geological age being given as Late Hauterivian based on charophyte and gastropod assemblages (Sanz et al. 1988) to be changed to Late Barremian (Gomez et al. 2006, Soriano & Decl ns 2006, Fregenal-Martinez et al. 2007, Buscalioni & Fregenal-Martinez 2010), although the lacustrine fauna scarcely provides a substage resolution. The recently found leaf fragments with areolate venation typical of dicotyledonous angiosperms (Barral-Cuesta & Gomez 2009) indicate a possibility of still younger age, because this type venation first appeared in the Aptian (?) – Albian.

Stratigraphic correlation of the comparable Wealden assemblages of Western Europe is based on marine intercalations indicating the age range from Berriasian to Albian (Allen & Wimbledon 1991). In Transbaikalia, the closely comparable invertebrate and plant assemblages from lacustrine carbonates are dated as Aptian (Vakhrameev & Kotova 1977), although palynological correlation suggests even younger ages up to the Albian (Nichols et al. 2006). The plant assemblages contain diverse gnetophytes (Krassilov & Bugdaeva 1999 and elsewhere), but authentic angiosperms are wanting or extremely rare and uncertain. It has to be taken into consideration that a pre-Albian age of angiosperm mesofossil from Portugal is presently debated (Heimhofer et al. 2007).

GROWTH HABIT

The laminated carbonates of Las Hoyas and similar fossiliferous deposits worldwide contain autochthonous remains of lacustrine biota as well as allochthonous material from surrounding wetlands. Fine lamination and cyclic structure are characteristic features of such sedimentary sequences. Well-preserved organic remains indicate water column stratification of a meromictic lake. Relative abundance of autochthonous and allochthonous material depends on the influx of terrestrial material varying with orbital cycles and on minor scale with seasonality. *Montsechia* is commonly considered to be a floating plant and therefore autochthonous or nearly so. However, under bulk maceration the fossiliferous carbonate lamellae reveal a widely variable content of silt and clay, ranging from clayey limestones to marls or calcareous mudstones. *Montsechia* is associated with the clayey varieties indicating

a transport of plant debris with the terrestrial runoff.

While the “holistic analysis” of lacustrine ecosystem of Las Hoyas is very preliminary so far (Buscalioni & Fregenal-Martinez 2010), the better studied lacustrine carbonates and their fossils from the Lower Cretaceous of Transbaikalia indicate stable oligotrophic conditions of low saprobity sustained by the balance of primary production and turnover rates (Sinichenkova & Zherikhin 1995), whereas floating macrophytes are abundant in eutrophic water bodies, in their turn enhancing eutrophication. Therefore floating vegetation is an unlikely source of abundant fossils, such as *Montsechia*, in the laminated lacustrine carbonates.

The traditional interpretation of *Montsechia* as having successive leaf whorls on monomorphic shoot axes is incorrect. Gomez et al. (2006) have discerned two growth forms, with long decussate leaves and short spiral leaves, but failed to recognize dimorphic shoot systems and heterophylly in both the long-leaved and short-leaved varieties, the latter of a more obvious xeromorphic habit. The raised leaf cushions and occasional wilted long leaves on scaly shoots suggest that such leaves were deciduous, probably shed under drier conditions. The plant is here interpreted as heloxerophytic, growing in water-logged periodically desiccated coastal marshes and sprouting leafy shoots with the rise of lake level. Ovulate cupules might have been produced in dry season as in the present day scale-leaved podostems of a similar growth habit (Graham & Wood 1975).

The seed-like galls are abundant on the scaly variety of *Montsechia*, in which the internodes of leafy shoots are much shortened resulting in a denser scale-leaf cover. The elongate foliage leaves are shed or wilt, while the infested scale leaves are hypertrophically expanded and transformed into (deciduous?) gall-bearing bracts. Since shortening of internodes, xeromorphism, wilting and hypertrophy are the well-known morphological effects associated with nematode gall production (Meyer & Maresquelle 1983), the scaly variety of *Montsechia vidalii* is here interpreted as resulting from a heavy nematode infestation.

Nematodes commonly produce root galls, but some ascend to aboveground organs. The wheat nematode *Anguina tritici* attacks aboveground organs at the second larval stage, deforming leaves and replacing seeds by seed-like galls

containing thousands of slender larvae (Nyvall 1999). The crop infesting galls prefer sandy/silty soil being sensitive to pH and soil temperature. In fact, bulk maceration of limestone lamellae with scaly shoots and gall-bearing bracts of *Montsechia vidalii* reveals a considerable content of clay and silt betraying an impact of terrestrial runoff. The abundance of gall-bearing bracts may suggest transport sorting of plant debris from a marshy plant growth on alluvial soil of a river delta intruding the lake.

Optimum conditions for nematode reproduction are warm (near 25°C) moist soil, pH near 7, and the presence of turf grass roots, which tells something of *Montsechia* growth habit and habitat.

INTERPRETATION OF REPRODUCTIVE STRUCTURES

Whether *Montsechia* was an angiosperm depends on interpretation of ovulate structures in the first place. If interpreted as solitary carpels developing into achene-like fruits (Gomez et al. 2006) these structures find no analogues among conventional angiosperms, but are comparable to proangiosperm cupules, such as *Baisia* (Krassilov & Bugdaeva 1982). They are borne in the position of terminal leaf tufts on the leafy short shoots with subtending leaves adhering to the walls. The cupule was thus formed by extension of leaf fusion down the shoot axis. The ovules with a massive nucellus, slender inner integument and a reduced pollen chamber are like in *Caytonia* (Krassilov 1977) and *Baisia*, with pollen grains landing on the top of the nucellus (Krassilov & Bugdaeva 1982). The associated microsporophyll resembles an angiosperm stamen except that the synangium appears radially symmetrical as in *Caytonanthus*. Thus, the combination of characters is altogether proangiospermous.

A critical distinction between angiosperms and proangiosperms, revealing parallel tendencies of morphological evolution is germination of pollen grains on the nucellus, which in *Montsechia* is poorly documented. Yet pollen grains certainly reached to the ovules, and in one case at least germination on the nucellus is a possibility. The intercellular pollen tube propagation occurs in both gymnosperms and angiosperms, although unbranched haustorial

tubes are more typical of gnetophytes and some angiosperms (reviewed in Friedman 1995).

PROBABLE PHYLOGENETIC AFFINITIES

Scaly habit with dimorphic shoots has few analogs among angiosperms (e.g. in the Podostemaceae: Imaichi et al. 1999), but is typical of extinct cheirolepids, the scale-leaved plants of supposedly heloxerophytic habit having their ovules enclosed in the winged cone scales, the wing lobes resembling scale leaves and perhaps derived by leaf fusion like the bracteate cupules of *Montsechia*.

The vegetative morphology is unknown in the Baisiales, the Early Cretaceous marsh plants of bennettitalean – gnetophytic affinities, producing abundant supposedly airborne one-seeded indehiscent cupules on a hairy receptacle persistent in disseminule (Krassilov & Bugdaeva 1982, Krassilov 2009). Notwithstanding their phylogenetic relationships, *Baisia* represents the same morphological trend as *Montsechia*.

Up the geological scale, *Gerofittia* group from the Late Cretaceous (Turonian) of the Negev Desert produced plagiotropous shoots from creeping stems or directly from flattened roots. The shoots were heterophyllous with linear and scaly leaves. The lacerate one-seeded cupules with bristle-like basal appendages were borne terminally on the copiously branched reproductive shoots. Despite its rather advanced geological age, the group is interpreted as probably proangiospermous, related to gnetophytes, but also comparable with the extant Podostemaceae in its growth habit (Krassilov et al. 2005).

The Podostemaceae is a peculiar family of riverweeds allegedly related to the Crassulaceae on account of embryological similarities and molecular data. Whatever its phylogenetic position, the Podostemaceae is unique among angiosperms in having tetranucleate embryo sac and lacking double fertilization (reviewed in Murguía-Sánchez et al. 2002). Some podostems are comparable to *Gerofittia* in their root-borne plagiotropous shoots and to both *Gerofittia* and *Montsechia* in heterophylly of their scaly and linear leaves and in the cupule formed of connate leaves or ramuli (Jäger-Zürn et al. 2002). The nucellar apex may protrude beyond the inner integument forming an endostomium, a feature worth mentioning in relation to

the stigma-like epistase of *Montsechia* (the comparison does not imply direct phylogenetic relationships between *Montsechia* and Podostemaceae).

CONCLUSION

Montsechia is characterized by shoot dimorphism and heterophyly. Slender shoots with decussate long leaves produced knobby axillar short shoots bearing both scaly and elongate leaves. In the “scaly” form, both long and short shoots are foliated with scale leaves that are cutinized and trichomate, with sunken stomata. Scaly shoots and small debris, including gall infested leaves and bud scales are amassed in the clayey varieties of carbonate lamellae deposited under a stronger impact of terrestrial runoff and transport sorting. Thus both morphology and taphonomy indicate a heloxerophytic growth habit.

The ovulate structures of *Montsechia* are comparable with *Baisia* (Krassilov & Bugdaeva 1982) and other proangiospermous cupulate ovules (Krassilov 1997) with pollen grains alighting on the nucellus. Pollination in *Montsechia* is insufficiently studied, but there is evidence of pollen grains settling on the nucellus and germinating there, whereas in angiosperms the ovules are immature at anthesis and the pollen reception/germination functions are delegated to the extraovular stigmatic structures..

Before and for a short period after the appearance of conventional angiosperms, there were peculiar Mesozoic plant communities of small rhizomatous proangiosperms of gnetophytic alliance producing abundant cupulate disseminules. The *Montsechia vidalii* – *Montsechites ferreri* association of El Montsec and Las Hoyas evidently belonged to this type “angiosperm cradle communities” (Krassilov & Bugdaeva 1999).

The nematode galls on *Montsechia* suggest that plant – parasite interactions might have contributed to morphological evolution by inflicting a stunted xeromorphic habit and related dissemination strategies.

ACKNOWLEDGEMENTS

I am grateful to Alexander Bannikov (Palaeontological Institute, Russian Academy of Sciences, Moscow) and Tatyana Kodrul (Geological Institute, Russian

Academy of Sciences, Moscow) for providing the fossil plant material from the Las Hoyas locality. I acknowledge the instructive comments to manuscript of this paper by Maria Barbacka and the other reviewers. I thank Alex Berner, Technion, Haifa for his help in SEM studies.

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PLATES

Plate 1

Montsechia vidalii (Zeiler) Teixeira, shoot dimorphism

- A. Long shoot bearing distichous long-leafed short shoots at branching nodes
- B. Scale-leafed shoot with leaf cushions of shed long leaves (arrows), accompanied by a falcate long leaf (left) and a bract (right)
- C. Scale-leafed branch bearing short shoots of unequal length
- D. Scaly short shoots in the axils of decussate long leaves; arrow on a short shoot with a seed-like structure (gall?) on a scale leaf

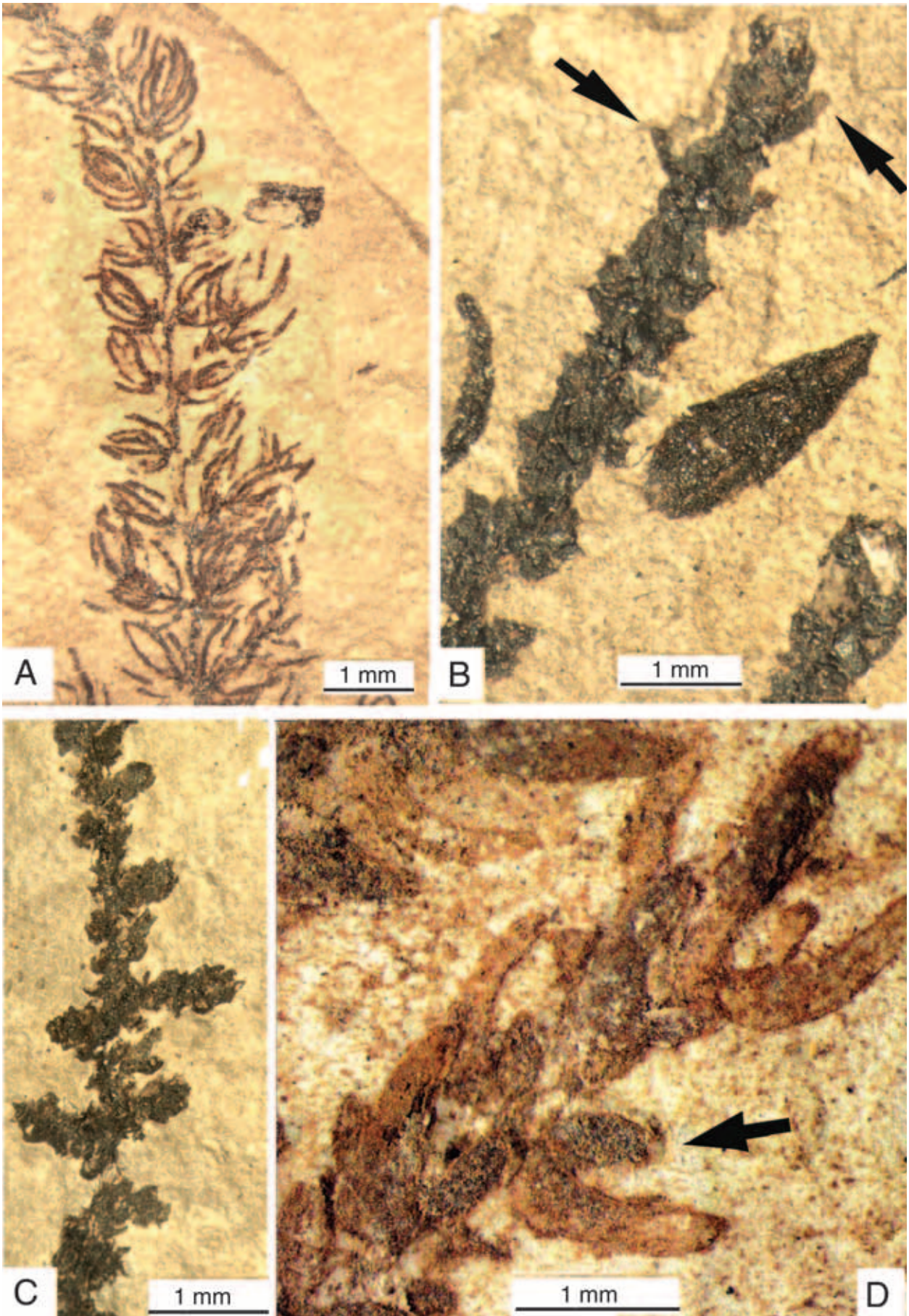


Plate 2

Montsechia vidalii (Zeiler) Teixeira, heterophylly of the short shoots, SEM

A-C. Heterophyllous short shoots foliated with elongate and scaly leaves

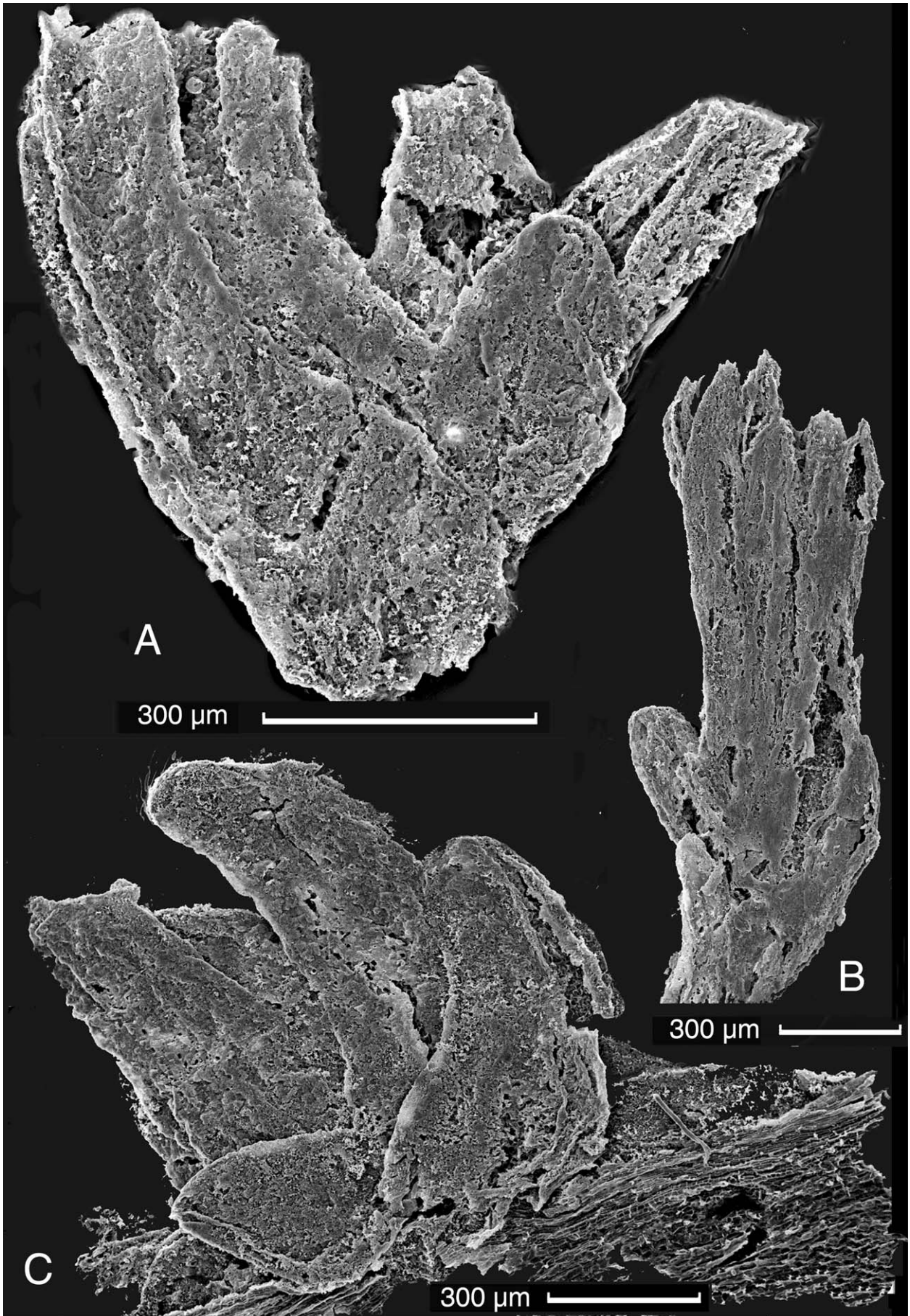


Plate 3

Montsechia vidalii (Zeiler) Teixeira, leaf micromorpology, SEM

- A. Scale leaf, adaxial cuticle with stomatal pits and hair bases
- B. Middle part of (A) magnified; **hb**, hair basis, **st**, stoma
- C. Microserrate tips of fibrous elongate leaves, **fb**, fibres

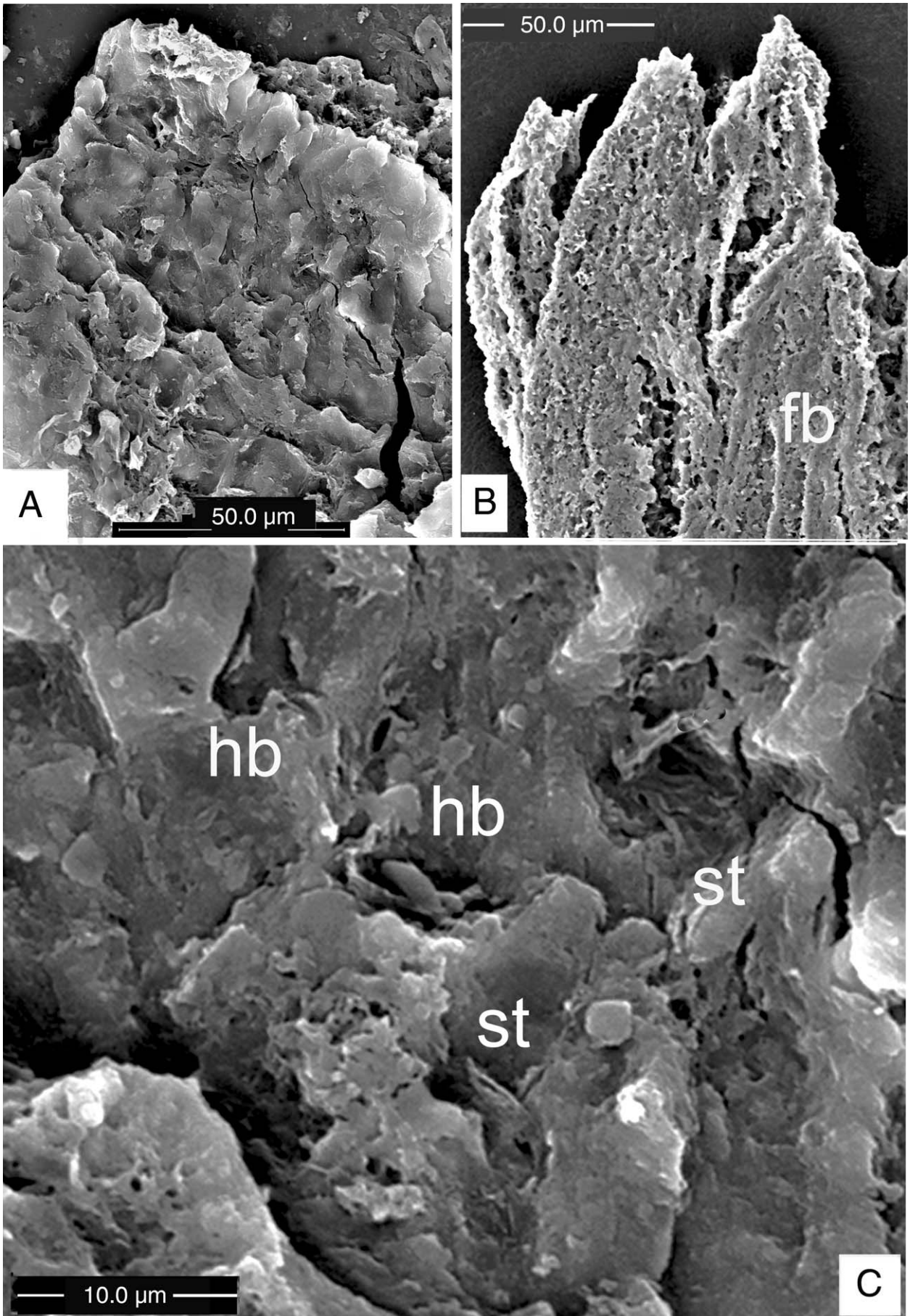


Plate 4

Montsechia vidalii (Zeiler) Teixeira, seed-like structures on long-leafed shoots

- A. Long-leafed shoot with a seed-like nematode gall (arrow) and the cleared gall inserted
- B. Long-leafed shoot bearing a cupulate ovule terminal on a short shoot (arrow) opposite a vegetative short shoot with a tuft of elongate leaves; cleared ovule inserted
- C. Gall from (A) showing a coiled annulate larva (arrow) and small rounded bodies (arrowheads), probably nematode eggs

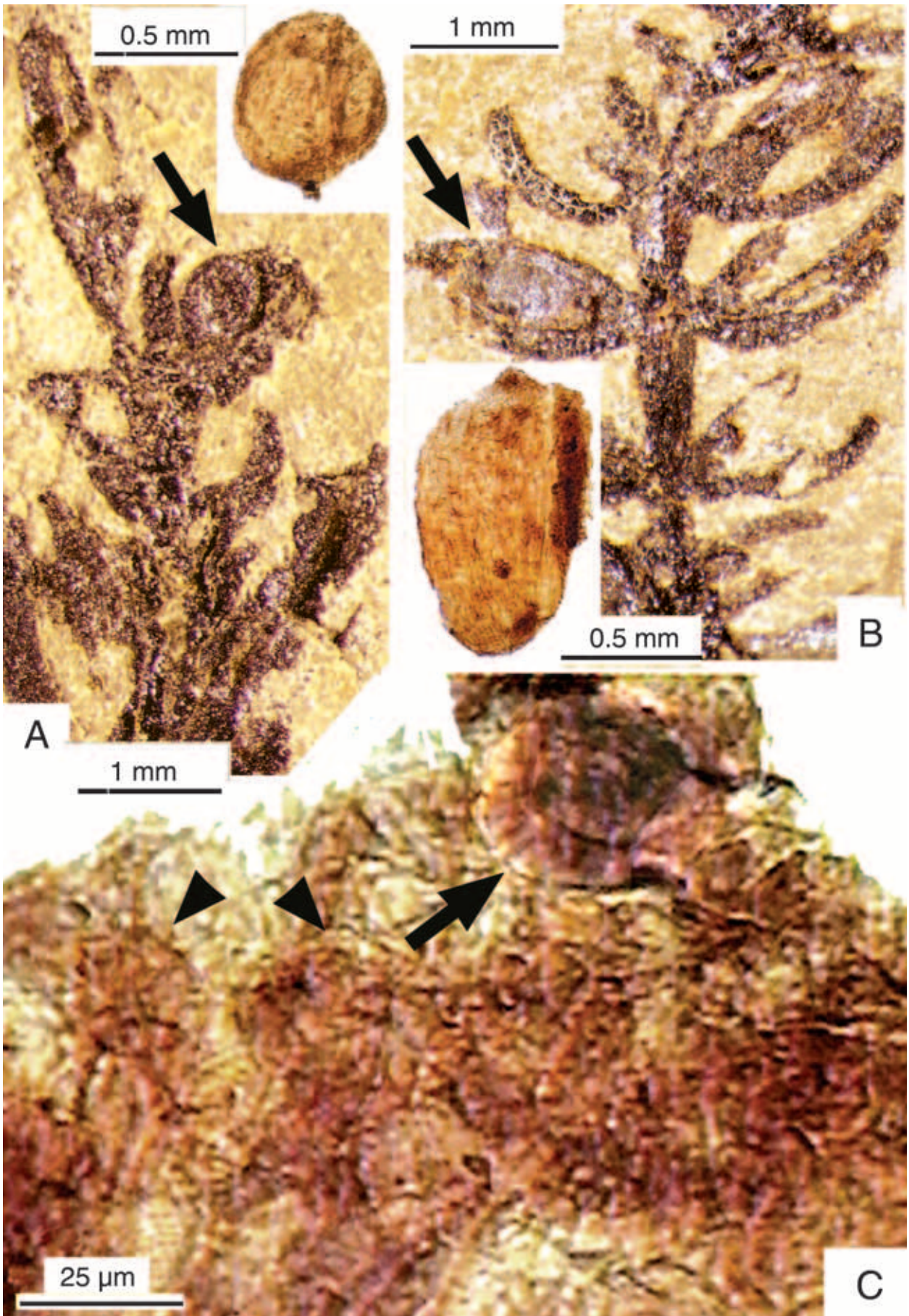


Plate 5

Montsechia vidalii (Zeiler) Teixeira, seed-like bodies on scaly shoots

- A. Fertile short shoot with a pair of falcate scale leaves beneath the terminal ovulate cupule
- B. Fertile short shoot with several pairs of scale leaves beneath the terminal ovulate cupule showing a median split between connate bracts of the wall
- C, D. Reproductive long shoots bearing fertile short shoots with bracteate cupules (arrow on cupule enlarged in fig. A)
- E. Cleared ovule from the cupule shown in fig. A.

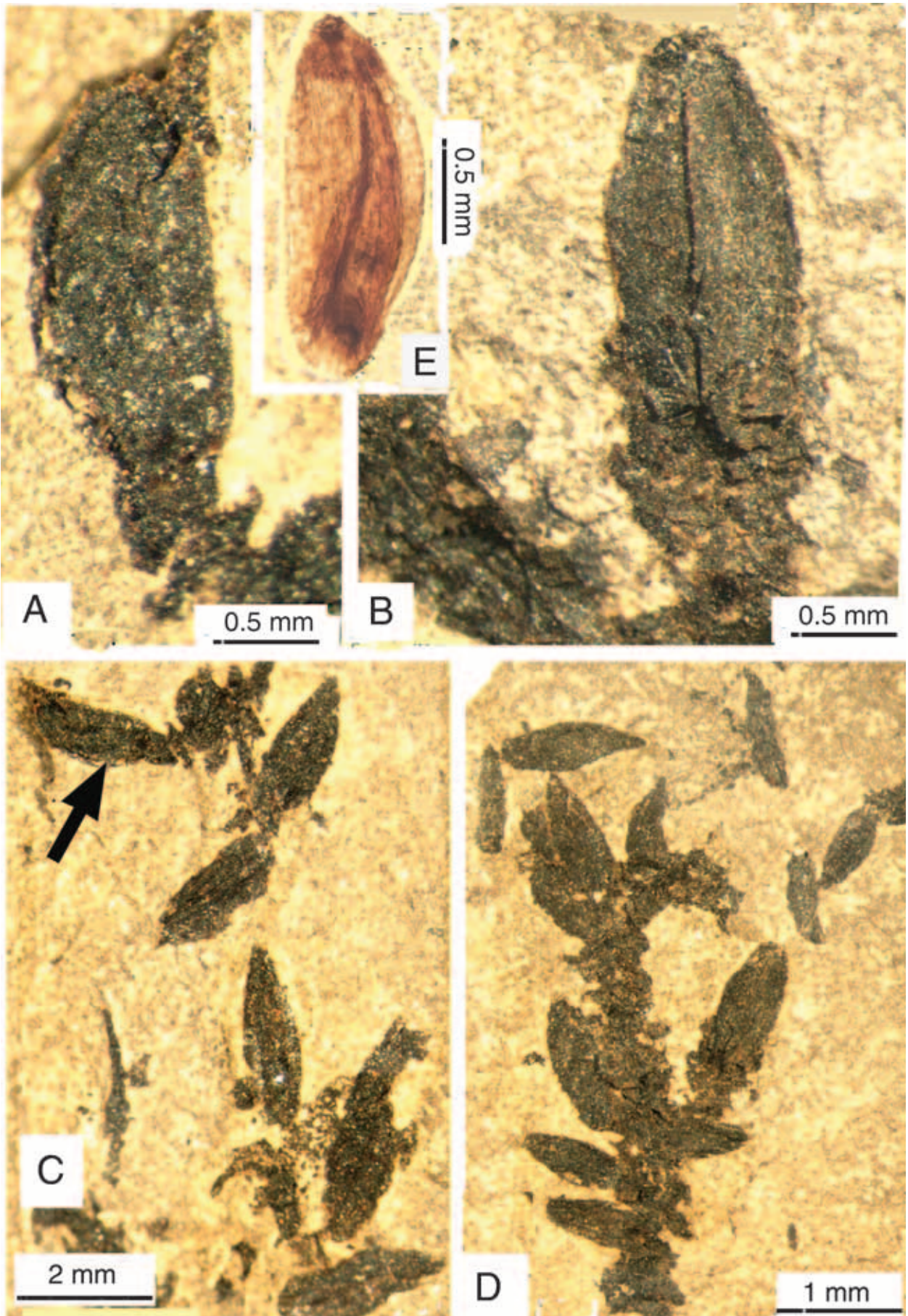


Plate 6

Montsechia vidalii (Zeiler) Teixeira, ovule morphology

- A. Nucellus with a well-developed papillate apical cap (epistase); the hilum scar is on the back face
- B. Hemispheric prominence (hypostase) over the hilum that is shifted up from the chalaza
- C. Ovule showing funiculus and with inner integument (ii) partly preserved

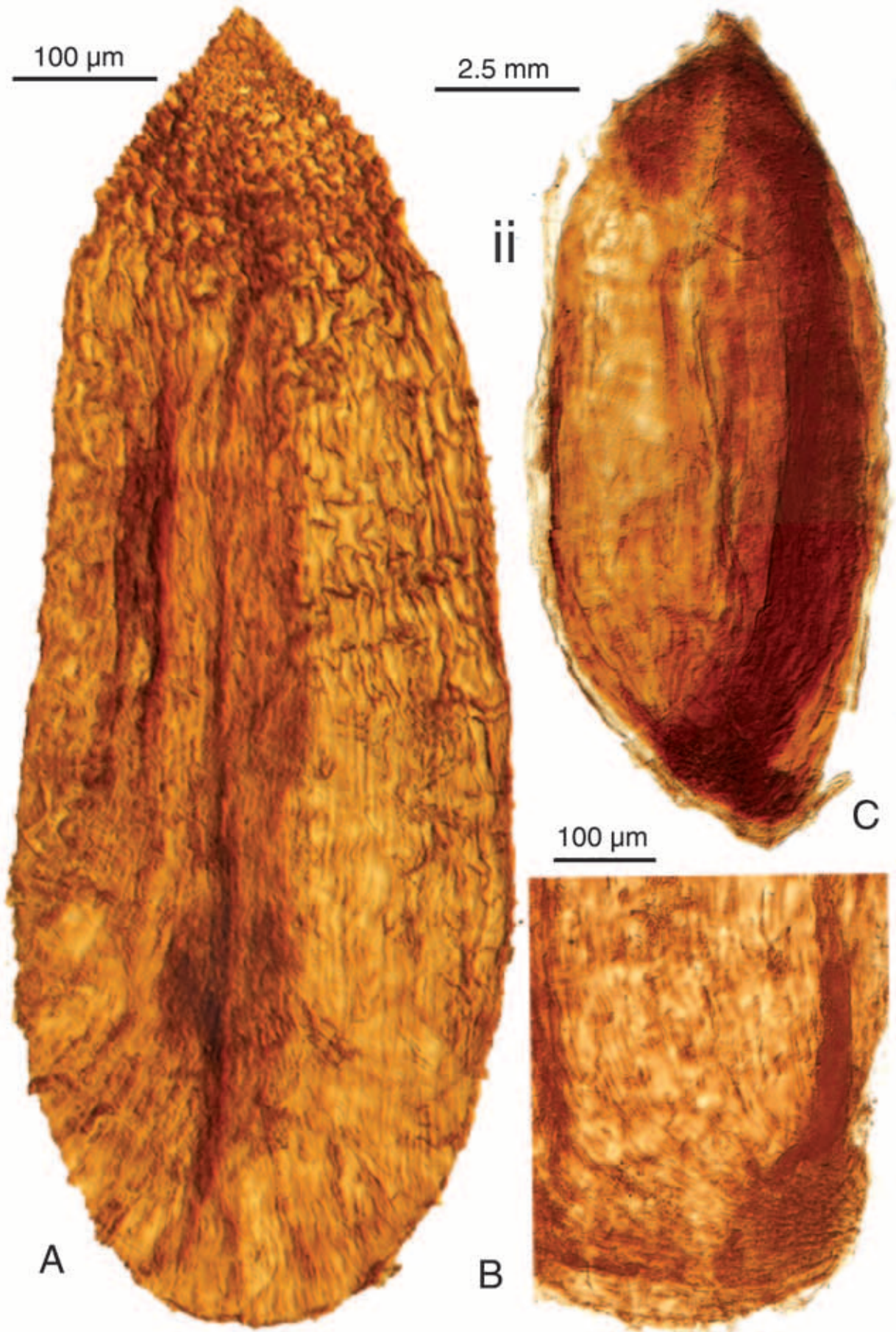


Plate 7

Montsechia vidalii (Zeiler) Teixeira, pollen grains on the nucellus

- A. Location of germinate pollen grain on the nucellus (arrow)
- B. Swollen pollen grain with a pollen tube emerging between the saccus lobes
- C. Smaller pollen grain of the same type stuck between cuticular folds in the middle part of the nucellus

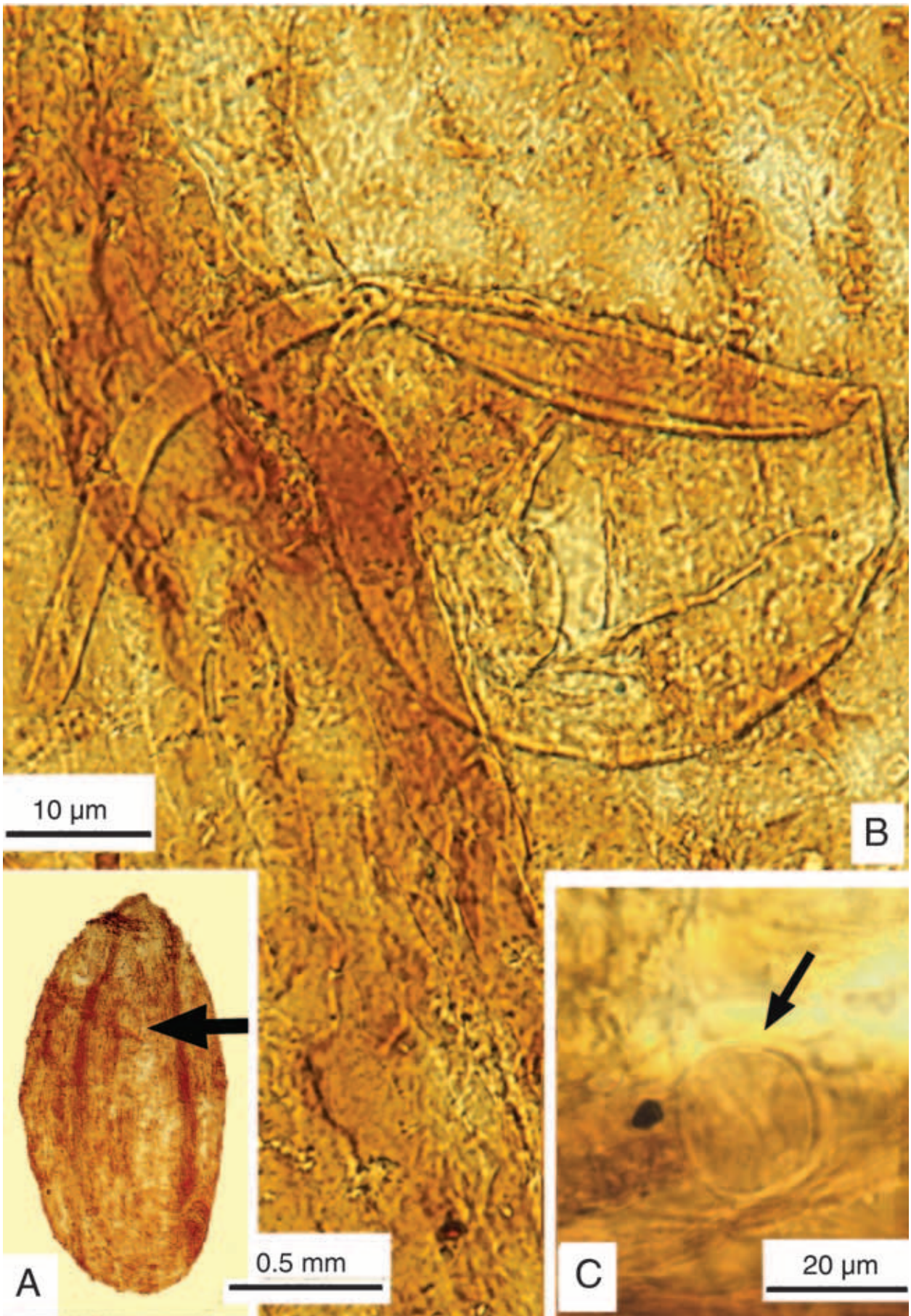


Plate 8

Montsechia vidalii (Zeiler) Teixeira, morphological details of a gall and ovule, SEM

- A. Gall capsule with an exit hole near the base, arrow indicates the position of a larva shown on Fig. 6 in the text
- B. Exit hole magnified
- C. Ovule with inner integument of transverse cells partly preserved

