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Unveiling the anatomy of *Balanophora latisepala* (Balanophoraceae): an astonishing achlorophyllous root-holoparasitic plant

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Abstract. *Balanophora latisepala* (Tiegh.) Lecomte (Balanophoraceae), a dioecious root-holoparasitic plant from Thailand, exhibits sophisticated adaptations for parasitism. We investigated the anatomical characteristics of fresh specimens collected from Saraburi and Chiang Mai provinces using light microscopy and histological techniques, including paraffin sectioning and counterstain with safranin and fast green. Our examination revealed a complex tuber vascular system comprising composite bundles of host and parasite tissues and specialised transfer cells. The achlorophyllous leaves showed reduced anatomical features, lacking stomata and possessing compact mesophyll without intercellular spaces. Male inflorescences developed synandria with 8–11 anthers and conducting strands supporting pollen production and nectar secretion, whilst female inflorescences produced numerous reduced pistils with J- or U-shaped embryo sacs. Post-fertilisation, the fruits developed sclerenchymatous pericarps protecting the few-celled embryo and endosperm during dry seasons. These anatomical characteristics demonstrate efficient nutrient acquisition strategies of *B. latisepala*, reproductive specialisation and environmental stress tolerance. Further investigations using transmission electron microscopy could provide deeper insights into nutrient transfer mechanisms and fungal interactions within this successful holoparasitic species.

Keywords: Balanophoroideae, composite bundle, parasitism, synandrium, transfer cell

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INTRODUCTION

Balanophora J.R. Forst. & G. Forst. is a genus of herbaceous root-holoparasitic plants in the family Balanophoraceae. This genus comprises approximately 25 species distributed throughout Asia and Australia (POWO, 2024), with eight species reported in Thailand (Hansen, 1972a; Chaiwerawattana *et al*., 2022; Sakdapipanich *et al*., 2024). *Balanophora latisepala* (Tiegh.) Lecomte was first described as *Balaniella latisepala* Tiegh. in 1907, then treated as *Balanophora latisepala* in 1915. The species typically grows on small host roots, such as those of *Tetrastigma* sp. and *Ficus religiosa* L., in many types of forests at 0–1,600 m elevation (Hansen, 1972b). Regarding its morphology, *B. latisepala* is characterised by a dioecious whitish-yellow plant reaching 10–25 cm in height, an underground tuber with stellate warts, distichous phyllotaxis, synandria on male florets, and numerous pistils and claviform spadicles on a female inflorescence (Hansen, 1972b, 1976).

Regarding the developmental progression of *Balanophora*, the embryo initially creates a nodule of parenchyma and penetrates the host root. Subsequently, composite vascular bundles comprising parasite and host tissues are constructed along with tuber strand formation, accompanying tuber enlargement and lobe formation while the inflorescences develop. Finally, the inflorescences emerge from the tuber and bloom (Shivamurthy *et al*., 1981a, 1981b; Gedalovich-Shedletzky & Kuijt, 1990; Hsiao *et al*., 1995; Kuijt & Hansen, 2015).

Although the anatomy of several species of this genus has been studied, *e.g. B. abbreviata* Blume, *B. fungosa* J.R. Forst. & G. Forst. (Arekal & Shivamurthy, 1978, as cited in Sato & Gonzalez, 2016; Shivamurthy *et al*., 1981a, 1981b; Gedalovich-Shedletzky & Kuijt, 1990), *B. spicata* Hayata and *B. tobiracola* Makino (Hsiao *et al*., 1995), the anatomical attributes of *B. latisepala* remain unexamined. A detailed examination of its anatomical adaptations will enhance our understanding of its nutrient acquisition mechanisms and reproductive specialisations. Such knowledge will not only expand our comprehension of holoparasitic plant biology and evolution, but also contribute valuable insights to broader ecological and conservation research. This study therefore presents a comprehensive anatomical investigation of *B. latisepala* to understand its functional adaptations and environmental role.

MATERIALS AND METHODS

Fresh specimens of *B. latisepala* were collected from two populations located in temple areas in Saraburi and Chiang Mai provinces, Thailand. The collected specimens were identified based on morphological characteristics following Hansen (1972b) and dried specimens were deposited in the Department of Botany, Chulalongkorn University (BCU).

For anatomical examination, male and female plants from each population were sampled. Each part of the plants from two populations (two individuals per population), including tubers, leaves, and male and female inflorescences, was cut into approximately 1 × 1 cm pieces, then dehydrated using ethanol series, infiltrated with paraffin liquid (KemAus™) and embedded in surgiplast paraplast (Leica). Tissue blocks were sectioned into 7–20 µm thick slices (depending on structure) using a rotary microtome (Leica RM2125). The sections were stained with safranin O and counterstained with fast green, respectively (Johansen, 1940). Slides were permanently mounted using coverquick 2000 mounting medium (Q Path®). Leaf peeling was performed using a razor blade, and photographs were taken without staining. All anatomical features were examined under an upright light microscope (ZEISS Axio Lab. A1) and images were captured using a ZEISS Axiocam 208 color camera.

Results

The anatomical investigation of *B. latisepala* revealed significant insights into its vegetative and reproductive structures. The results are presented using four main aspects: tuber structure, leaf characteristics, male inflorescence anatomy and female reproductive structures.

1. Anatomical structure of tubers

The tubers of *B. latisepala* primarily comprise a parenchyma matrix with distributed vascular tissues (Figs. 2A–B). Composite bundles radiate outward from the host root towards the periphery (Fig. 2A), branching dichotomously along their path (Figs. 2D & 3C). Each consists of two components: a vascular core comprising both host and parasite cells, and a composite bundle sheath composed entirely of parasite cells (Fig. 2E). Within the vascular core, massive transfer cells intersperse among host vasculatures, establishing direct contact with host xylem and phloem (Figs. 2C–E & 3A–B). Additionally, elaioplasts (confirmed by Sudan III staining) are observed in tuber cells of fresh material (Fig. 2F).

At the apex of the composite bundle, a meristem is presented, parasite meristematic cells, characterised by large nuclei, likely develop into sheath parenchyma and transfer cells, whilst host meristematic cells with small nuclei appear to develop into the xylem, phloem, and pericycle-like parenchyma (Fig. 2E). The composite bundle sheath enclosing the vascular core consists of 2–5 cell layers of parenchyma, with most cells containing raphides or druse crystals readily detected in fresh specimens (Fig. 2G). The innermost layer of the sheath occasionally includes transfer cells nearly identical in size to adjacent sheath parenchyma cells.

Tuber bundles, composed entirely of parasite cells, emerge from composite bundle sheath, occasionally ramifying in a bifurcated manner, and partially enter the inflorescence peduncle (Fig. 3C). Some tuber bundle cells differentiate into vessel members with annular to scalariform thickening (Figs. 3A–B).

The tuber matrix consists of polygonal to oblong-polygonal parenchyma cells measuring 15–125 × 45–210 µm with minimal to no intercellular spaces. The outer surface of the tuber comprises a single layer of epidermal cells lacking trichomes, with the outer half of each cell reinforced by a secondary cell wall (Fig. 3D). Dark brown septate fungal hyphae, approximately 2.7 µm in width, were observed intracellularly without causing apparent symptoms. While fungal conidia were absent, microsclerotia were present (Fig. 3E). Additionally, smaller intracellular hyaline hyphae (1.3–2.1 µm in width) were observed, staining with fast green (Fig. 3E). These endophytic fungi were localised near the tuber surface. Notably, pycnidia, asexual fungal fruiting bodies containing numerous conidia, were observed within the tuber surface. The plant cells surrounding these pycnidia appeared damaged (Fig. 3F).

2. Leaves morphology and anatomy

The leaves of *B. latisepala* are achlorophyllous with palmately parallel venation (Fig. 4A). In the transverse section, isobilateral leaves comprise tightly packed mesophyll cells without intercellular spaces (Fig. 4B). Leaf epidermal peels reveal diverse cell shapes, ranging from oblong-rectangular to elliptic forms. Notably, both leaf surfaces lack stomata, suggesting a reduced requirement for gas exchange (Figs. 4C–D).

3. Male inflorescences anatomy

Male inflorescences develop as racemes arising from a tuber (Fig. 1A). Each floret comprises a synandrium with 8–11 anthers surrounded by 4–5 tepals (Fig. 5F).

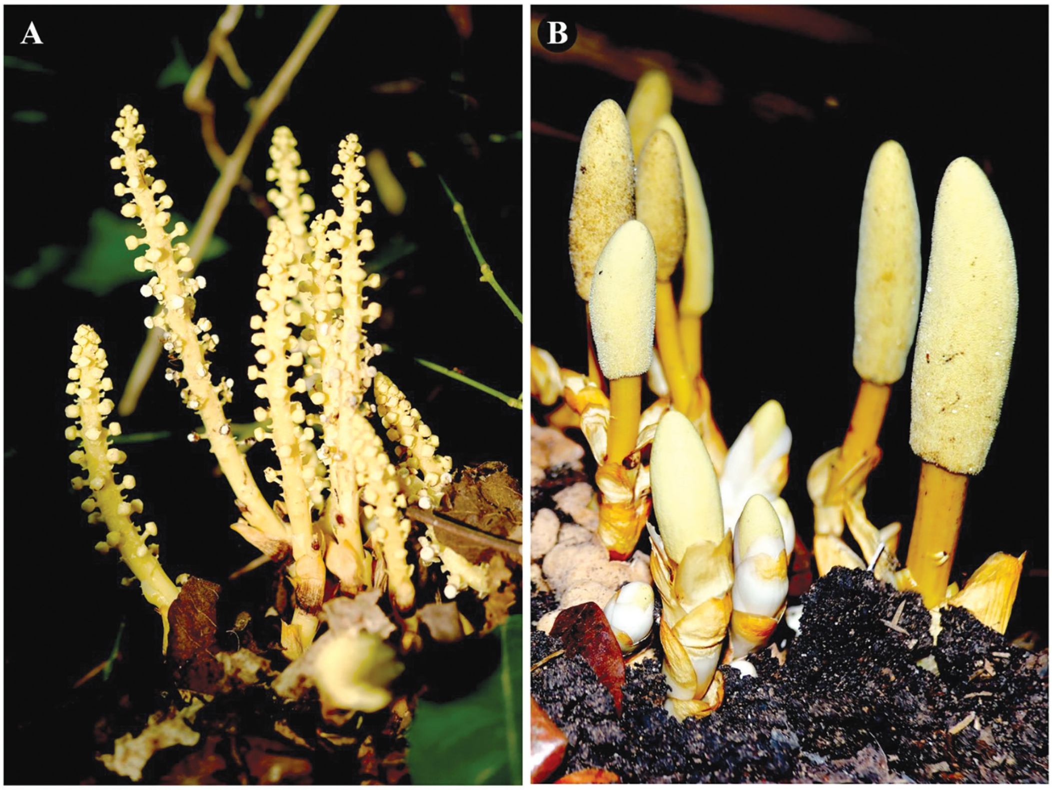

FIGURE 1. *Balanophora latisepala* in natural habitat: A. male inflorescences; B. female inflorescences. Photos by J. Sangrattanaprasert.

Microspores and pollen grains develop within anthers of young florets (Fig. 5C). The tepals exhibit valvate aestivation, with short cells connecting adjacent tepal edges (Figs. 5A–B). Composite conducting strands extend from the tuber throughout the peduncle and the inflorescence (Figs. 3C & 5A, E–F). Xylem lacunae typically form after conducting strand maturation in male and female inflorescences (Figs. 5G–H & 6B–C). Longitudinal sections reveal conducting strands terminating at the bases of male floret pedicels (Figs. 5A, D).

4. Female inflorescences, embryo sac and fruits anatomy

Female inflorescences emerge from tubers similarly to male inflorescences (Fig. 1B). Transverse sections show composite conducting strands distributed throughout the peduncles and inflorescences (Fig. 6A). Each reduced female floret consists solely of a pistil, developing perpendicularly to the main axes of the female inflorescences (Fig. 7A) and at the base of claviform spadicles (Fig. 7B).

The pistil exhibits an archegonium-like shape with a filiform style and ovate to elliptic ovary. As the genus lacks an ovule, the embryo sac develops from a single initial cell at the ovary centre (Fig. 7C). This initial cell undergoes several divisions, developing into a J- or U-shaped embryo sac (Figs. 7D–F). Post-fertilisation, the few-celled embryo, lacking cotyledons, is surrounded by large endosperm cells. The ovary wall cells redifferentiate into sclereid (Figs. 7G–H).

DISCUSSION

1. Tuber structure and host-parasite interaction

The presence of host and *B. latisepala* tissues within the host root boundary aligns with established developmental patterns of *Balanophora* tubers. When the embryo forms a nodule and penetrates the host root, it triggers host tissue meristematic activity around the primary haustorium. Subsequently, stelar parenchyma differentiates into tracheary elements, whilst cortical cells undergo extensive division, leading to rapid tuber enlargement. During tuber lobe formation, the secondary haustorial meristem, comprising both host and parasite cells, initiates composite bundle development towards the periphery, branching to support the tuber lobes thoroughly (Shivamurthy *et al*., 1981a; Kuijt & Hansen, 2015).

Consequently, *B. latisepala* tubers encase the host root with composite bundles extending outward. The tuber bundles (or tuber strands) emerging from the composite bundles sides disperse throughout the tuber and enter the inflorescence, indicating efficient vascular supply to both tuber and inflorescence. This organisation explains the presence of tuber-strand-like vascular tissues within the inflorescence.

Within composite bundles, transfer cells are arranged in series extending from vascular cores to composite bundle sheaths. This arrangement facilitates direct nutrient transport from the host vascular tissue to the parasite (Hsiao *et al*., 1995). Previous studies of at least two *Balanophora* species reported

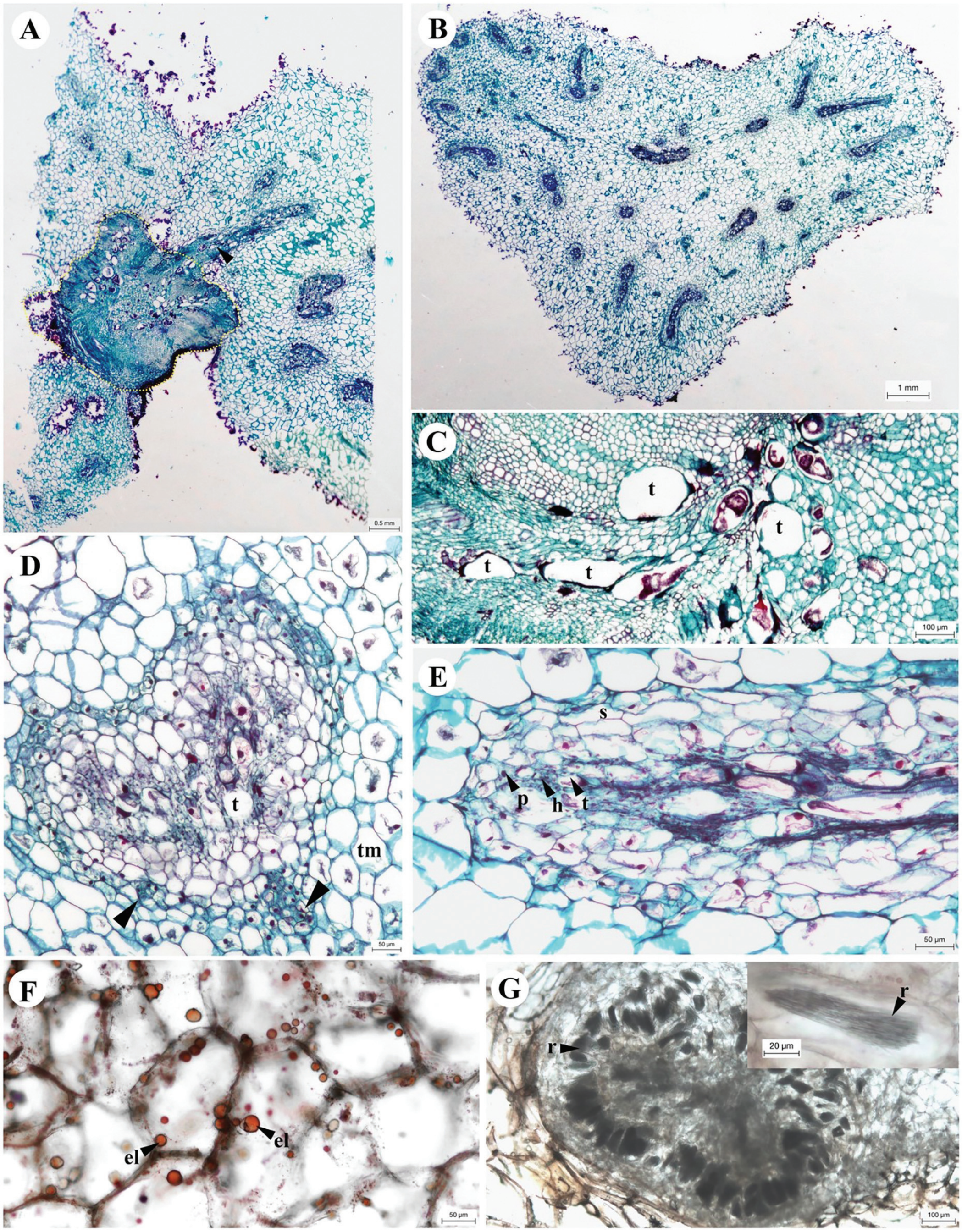

FIGURE 2. Tuber sections of *Balanophora latisepala*: A. host root (centre) surrounded by tuber tissue (bounded by yellow dotted line) showing emergent composite bundle (arrow); B. tuber section; C. composite tissue between host and parasite within-host root, showing transfer cells (t); D. tuber bundles (arrows) extending from composite bundle with transfer cells (t) into tuber matrix (tm); E. longitudinal section of composite bundle apex showing parasite meristematic cells (p), host meristem (h), and developing transfer cells (t), with composite bundle sheath (s) delineating the meristems; F. elaioplasts (el) stained with Sudan III; G. raphides (r) within composite bundle sheath cells.

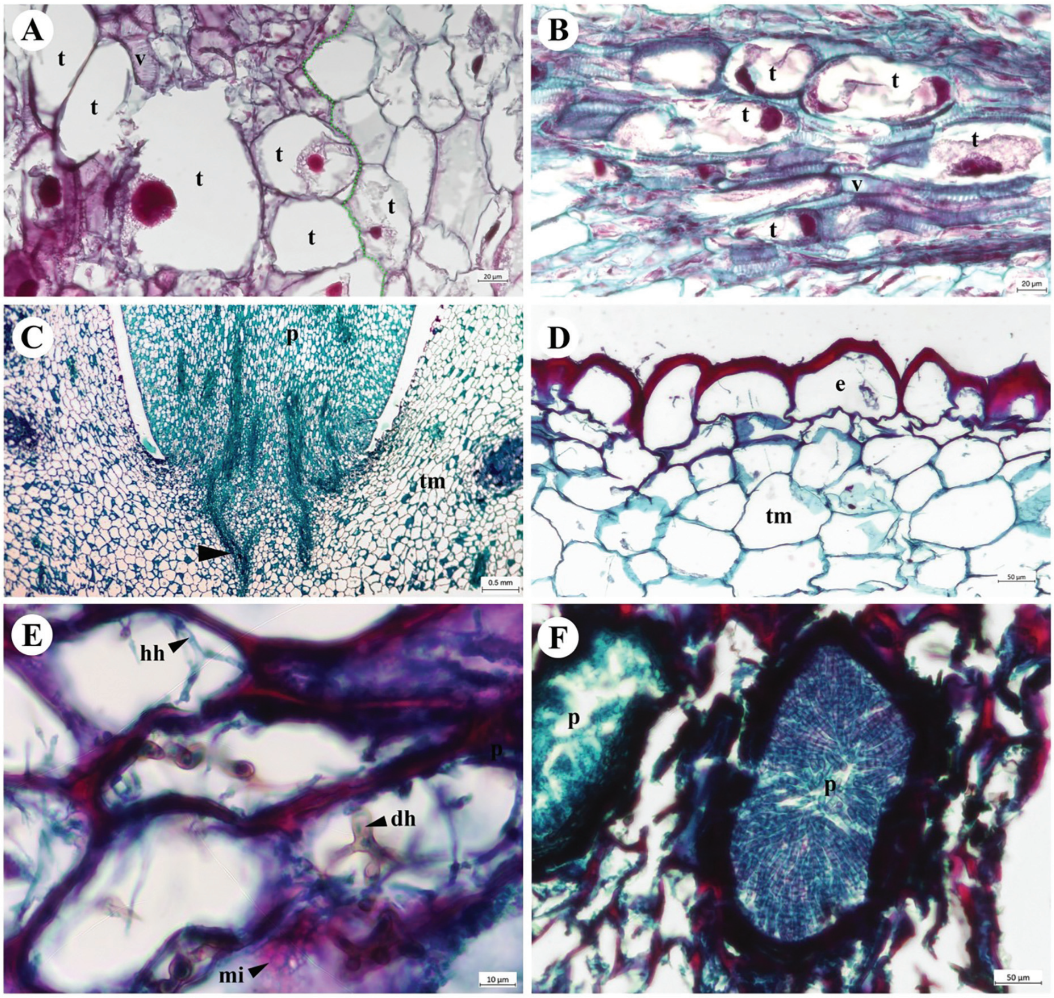

FIGURE 3. Additional tuber sections of *Balanophora latisepala*: A. composite bundle section showing vessel elements (v) and transfer cells (t) arranged serially from vascular core (left of green dotted line) to composite bundle sheath (right of green dotted line); B. longitudinal section of composite bundle revealing transfer cells (t) and vessel elements (v); C. longitudinal section of intermediate zone between tuber matrix (tm) and inflorescence peduncle (p) showing composite bundle with dichotomous branching (arrowhead); D. epidermal cells (e) with secondary wall and compact parenchyma in tuber matrix (tm); E. intracellular fungal endophytes showing asymptomatic dark brown septate hyphae (dh), hyaline hyphae (hh) and microsclerotia (mi); F. pycnidia (p) embedded within infected tuber tissues.

labyrinthine cell walls in transfer cells adjacent to host tracheary elements, whilst walls adjoining other transfer cells remain thinner (Hsiao *et al.*, 1995). However, the present study cannot definitively confirm the presence of the labyrinthine wall, suggesting the need for transmission electron microscopy investigation.

Dark septate fungal endophytes, previously reported in various plant groups including angiosperms, gymnosperms and pteridophytes, belong to the phylum Ascomycota (Peterson *et al.*, 2008). These fungi typically colonise plant roots, enhancing plant growth and fitness, often functioning as mycorrhizal fungi (He *et al.*, 2019). The observed cellular damage surrounding pycnidia suggests the presence of plant-pathogenic fungi, potentially contributing to localised parasite cell deterioration.

2. Leaf adaptations

The thick, leathery, achlorophyllous leaves of *B. latisepala* typically occur on the lower portion of peduncles, contrasting with leafless Balanophoraceae genera such as *Corynaea* Hook. f., *Ditepalanthus* Fagerl and *Helosis* Rich. (Kuijt & Hansen, 2015). Vascular bundle arrangement varies within the family: *B. latisepala* exhibits approximately eight bundles, whilst *Langsdorffia hypogaea* Mart. and *Lophophytum mirabile* Schott & Endl. possess three, and *Scybalium fungiforme* Schott & Endl. shows only one (Kuijt & Hansen, 2015).

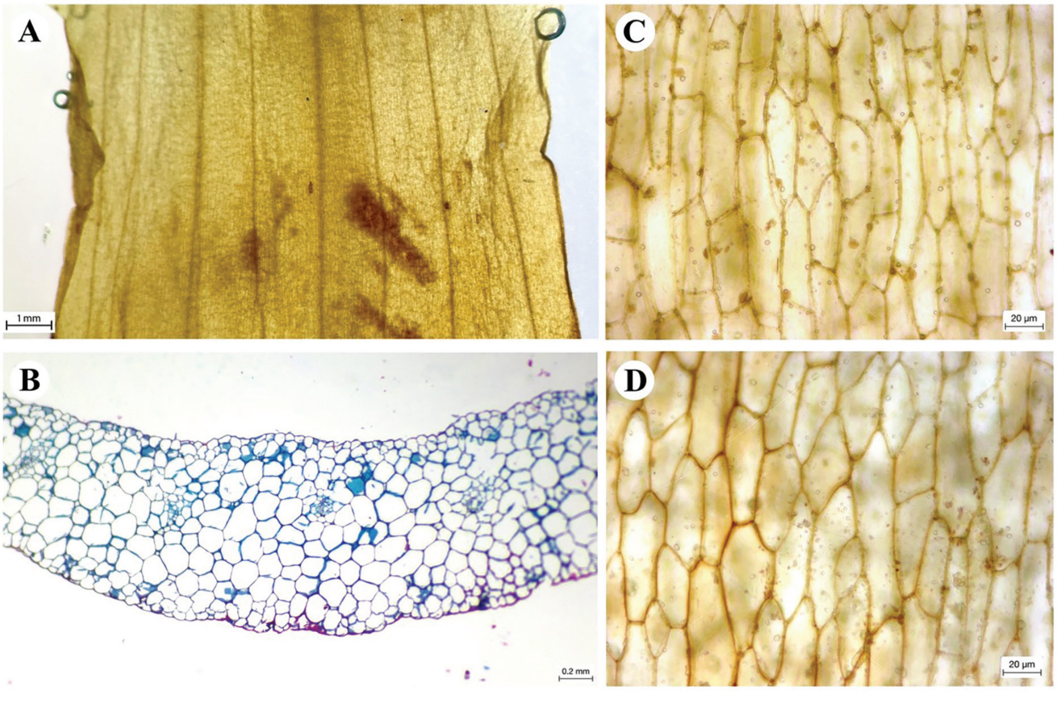

FIGURE 4. Leaf characteristics of *Balanophora latisepala*: A. achlorophyllous leaf showing parallel venation; B. transverse section showing compact mesophyll and horizontal vascular bundles; C.–D. leaf epidermal peels showing oblong-rectangular and elliptic cells: C. adaxial surface, D. abaxial surface.

Like other achlorophyllous Balanophoraceae genera (including *Hachettea* Baill., *Langsdorffia* Mart., *Lophophytum* Schott & Endl., *Scybalium* Schott & Endl. and *Thonningia* Vahl), *B. latisepala* leaves lack stomata, reflecting their obligate holoparasitic lifestyle. The compact, intercellular-space-free mesophyll further indicates reduced reliance on stomatal gas exchange. Whilst respiration likely utilises host-derived organic substrates, stomatal absence may restrict gas exchange, potentially contributing to slower parasitic growth rates (Kuijt & Dong, 1990).

3. Male inflorescences

Balanophora latisepala exhibits dioecy, with male and female plants often occurring nearby. The subfamily Balanophoroideae is characterised by synandria which are structures formed by anther fusion within each male floret (Kuijt & Hansen, 2015). Our observations reveal 8–11 anthers per synandrium in *B. latisepala*. Studies of *B. elongata* Blume synandrium development demonstrate its origin from a 'synandrium primordium', a meristematic cell cluster that differentiates into numerous pollen-sac lobes (Eberwein *et al*., 2009). This developmental pattern supports the hypothesis that the high number of pollen sacs in *Balanophora* results from longitudinal septation during synandrium development (Endress & Stumpf, 1990).

The synandrium structure facilitates abundant pollen production. During anthesis, exposed pollen grains increase potential contact with pollinators visiting the inflorescences. Additionally, *B. latisepala* male florets feature extrafloral nectaries at the pedicel base. This secreted nectar accumulates as droplets on subtending bracteoles, similar to observations in *B. kuroiwai* Makino and *B. tobiracola* (Kawakita & Kato, 2002). Conducting strands extending from the rachis to pedicel bases suggest their role in transporting host-derived substances for nectar secretion.

4. Female inflorescences and fruits

Female inflorescences comprise thousands of reduced carpellate florets, each retaining only a single-carpelled pistil, alongside claviform spadicles. Rather than typical ovules, a nucellar structure ('mamelon') occupies the central ovary region, containing megaspores that develop into the embryo sac (Holzapfel, 2001). The U- or J-shaped embryo sac in *Balanophora* resembles that of *Lophophytum*, contrasting with the straight embryo sacs of *Corynaea*, *Helosis* and *Rhopalocnemis* Jungh. (Sato & Gonzalez, 2016). Within Balanophoraceae *s.s.*, embryo sac inversion orients the egg apparatus towards the ovary apex, facilitating pollination (Arekal & Shivamurthy, 1978, as cited in Sato & Gonzalez, 2016). This pattern reflects convergent evolutionary adaptations to parasitism, distinct from varied egg apparatus positions in other Santalales families (Sato & Gonzalez, 2016).

The claviform spadicles, likely represent lateral structures derived from the primary inflorescence axis (Eberwein *et al*., 2009). This interpretation, supported by researchers including Griffith (1846) and

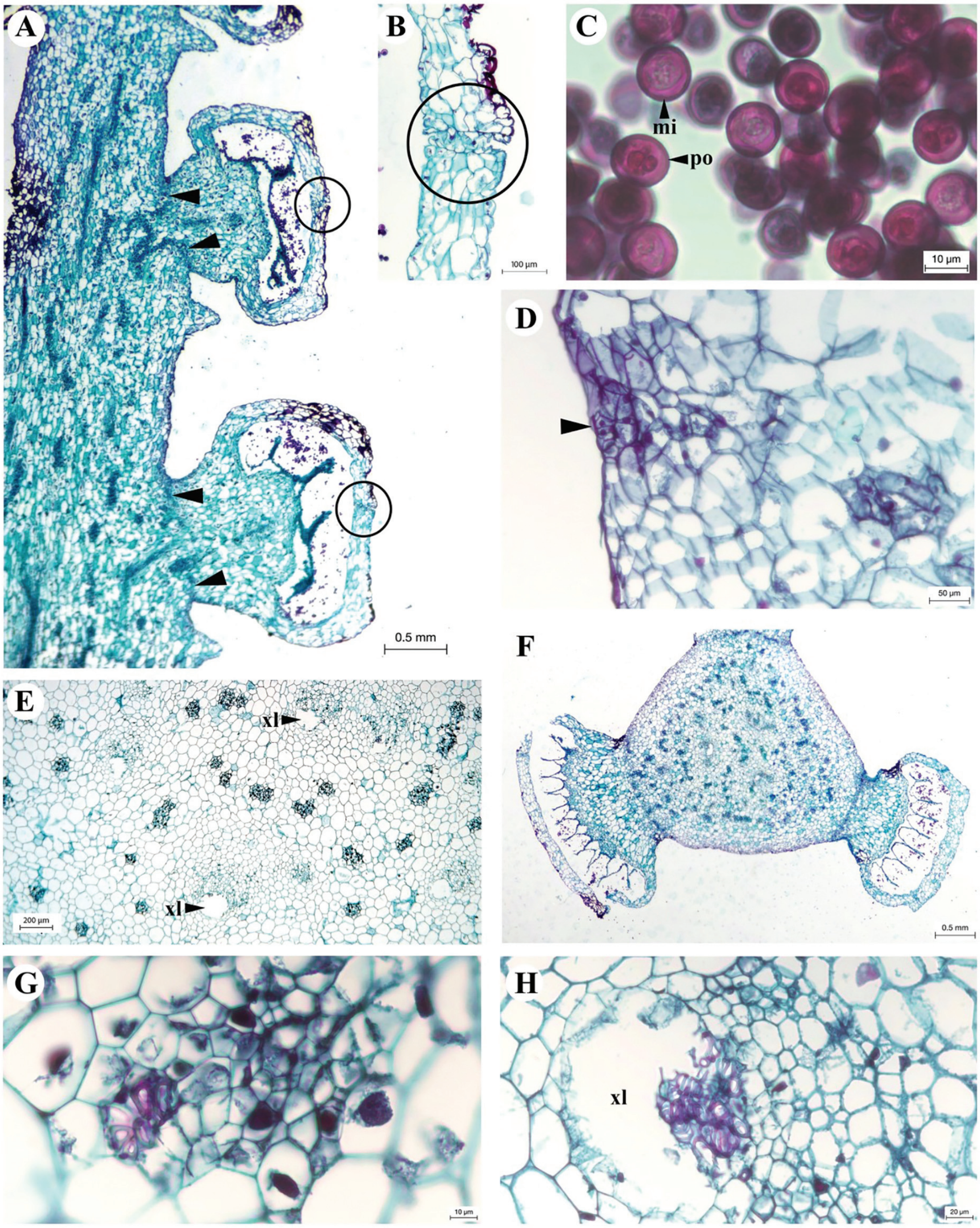

FIGURE 5. Male inflorescence anatomy: A. longitudinal section showing young male florets with short cells between adjacent tepal margins (circle) and conducting strands throughout inflorescence, extending to pedicel bases (arrowhead); B. high-magnification view of tepal edges showing short cells; C. developing microspores (mi) and pollen grains (po); D. developing conducting strands at pedicel bases (arrowhead); E. peduncle in transverse section showing diffuse conducting strands with xylem lacunae (xl); F. young inflorescence in transverse section showing florets with 8–11 anthers; G.–H. conducting strand development: G. young stage, H. mature stage with xylem lacuna (xl).

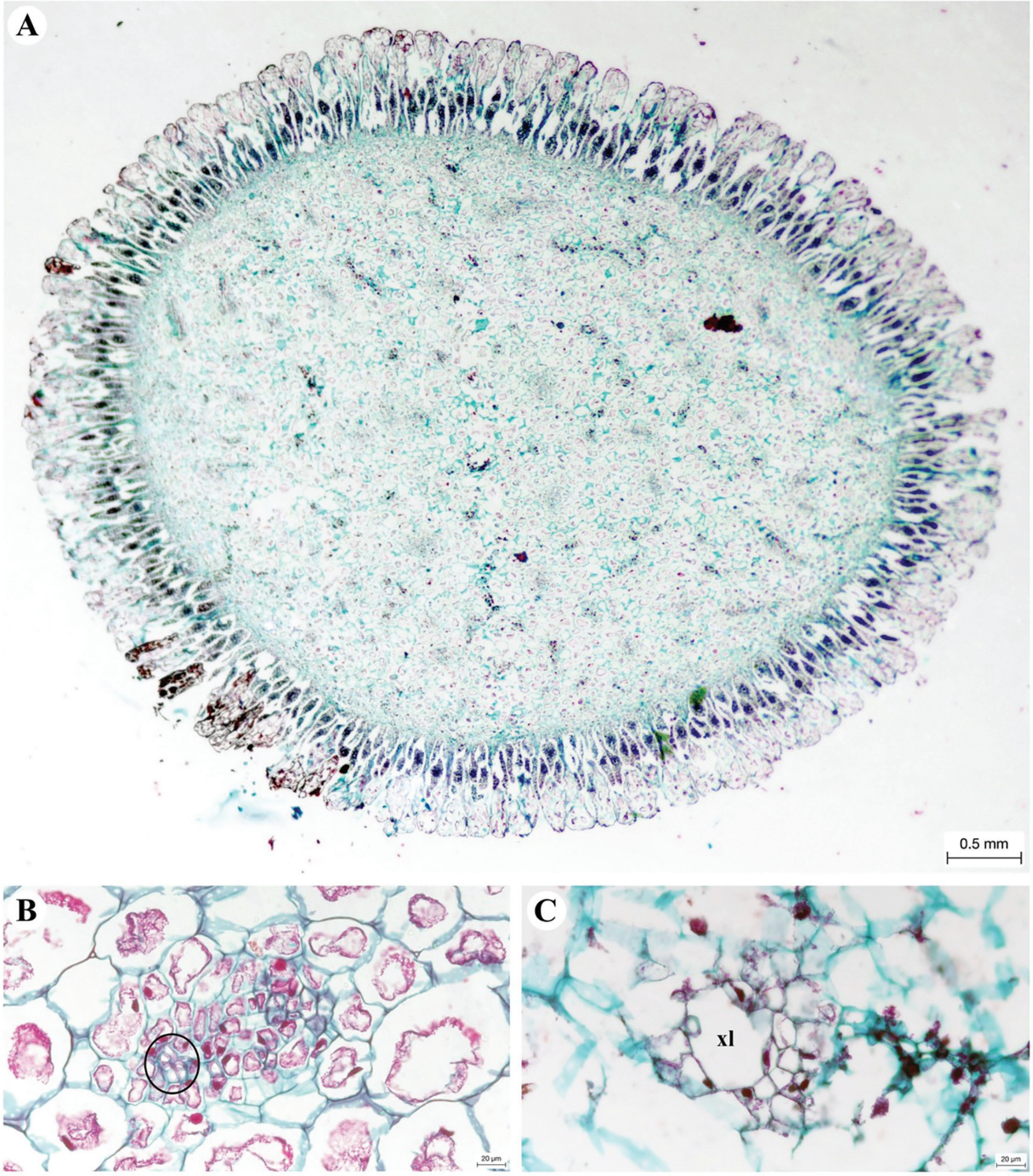

Figure 6. Female inflorescence anatomy: A. transverse section of female inflorescence; B.–C. conducting strand development: B. young stage showing protoxylem (circle), C. mature stage with xylem lacuna (xl).

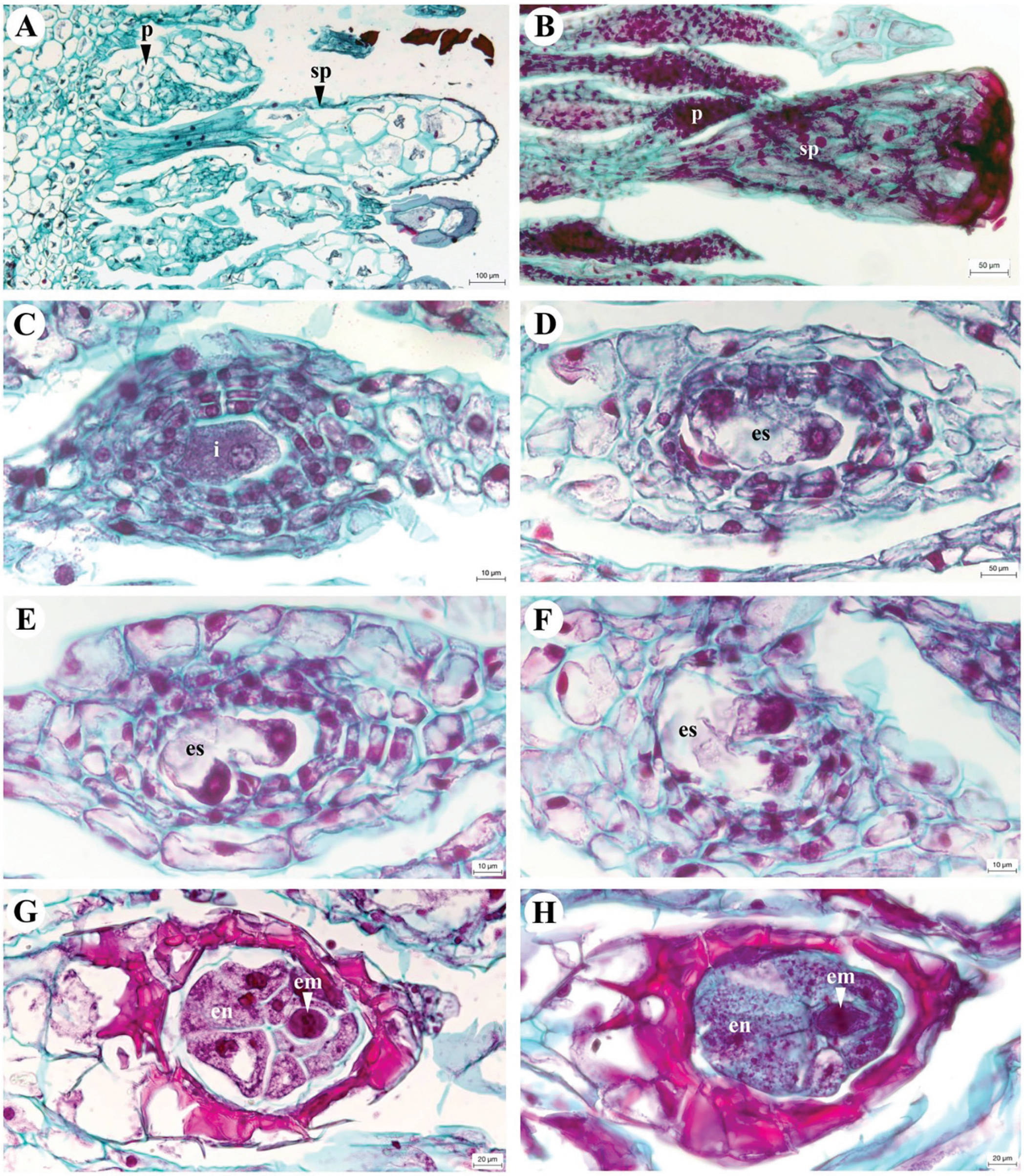

FIGURE 7. Female reproductive structures of *Balanophora latisepala*: A.–B. pistil (p) positioning: A. on main axis adjacent to spadicle (sp), B. at spadicle base; C.–F. embryo sac development: C. initial cell (i) within ovary, D. binucleate embryo sac (es), E. J-shaped binucleate embryo sac, F. U-shaped binucleate embryo sac; G.–H. few-celled embryo (em) surrounded by endosperm cells (en), enclosed by sclerenchymatous pericarp.

Weddell (1850), contrasts with alternative views suggesting they function as bracts. Evidence from *B. wilderi* Setch. shows transitional forms between male-flower bracts and claviform structures. These structures may serve secretory functions, producing either nectar for pollination or protective hydration for carpellate flowers (Eberwein *et al.*, 2009).

Balanophora latisepala fruits typically develop during the dry season, September to October(–May) (Hansen, 1972b). The stone cell layers protect the embryo from environmental stresses, particularly high temperature and drought. The fruits' size and weight resemble orchid seeds, suggesting wind dispersal potential. Their rough-textured walls might facilitate insect attachment, though this remains unobserved. Rainwater may also aid dispersal. In contrast, South American species produce larger fruits that do not fit wind dispersal, potentially relying on herbivores attracted to their high starch content for distribution (Kuijt & Hansen, 2015).

CONCLUSION

This anatomical investigation of *B. latisepala* from Thailand demonstrates sophisticated adaptations supporting its holoparasitic lifestyle. The intricate tuber vascular system facilitates efficient nutrient acquisition from host roots, whilst reduced reproductive structures and simplified embryo sac development reflect evolutionary adaptations minimising resource requirements. The unique leaf characteristics, including stomatal absence and dense mesophyll, align with its achlorophyllous nature, whilst the sclerenchymatous pericarp provides embryo and endosperm protection during dry seasons. These findings enhance our understanding of the structural and functional adaptations enabling *B. latisepala*'s success as a holoparasite.

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