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Anatomical and histochemical studies of foetid-odor emission osmophores on the labella of two *Orchidantha* (Lowiaceae) species

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ABSTRACT: *Orchidantha* (Lowiaceae) flowers exhibit a fascinating pollination strategy, employing foul scents to attract pollinators specifically to the prominent median petal, known as the labellum. In Thailand, two distinct *Orchidantha* species, *O. foetida* and *O. siamensis*, exhibit divergent floral morphologies. This variation includes differences in the structure of the labellum, the overall form and coloration of the flowers, and their geographic distribution. This study investigates the secrets hidden within their foul-odored labella, revealing the intricate structures and chemical compositions of their scent-producing glands, known as osmophores. Employing a combination of microscopic techniques, we uncovered crucial differences in the labella anatomy of these two species. Only adaxial labellum of *O. foetida* functions as osmophores with papillate and non-papillate cells, while labellum of *O. siamensis* exhibits osmophoric activity on both the adaxial and abaxial surfaces with a similar cellular pattern of papillate and non-papillate cells. Interestingly, *O. foetida* alone harbors osseous aerenchyma within its labella, potentially aiding in the metabolic processes fueling scent production. Histochemical analysis identified scent-related compounds accumulating within the osmophoric cells of both species including alkaloids, carbohydrates, lipids, mucilage, phenolic, and terpenes. These findings shed light on the diverse traits of labellum of *Orchidantha* species employ in their pollination strategy. The subtle variations in osmophore morphology and chemistry between *O. foetida* and *O. siamensis* may well reflect adaptations to distinct pollinator preferences.

KEY WORDS: foetid-scent, lip, *Orchidantha foetida*, *Orchidantha siamensis*, papillose, pollination, scent secretory structure.

INTRODUCTION

Orchidantha N. E. Brown, comprising only 32 species, is a single genus in the family Lowiaceae of the order Zingiberales. It strictly distributes from Southern China, mainland Southeast Asia including Laos, Thailand, Vietnam, Malay Peninsula to Borneo (Niissalo *et al.*, 2022). A strongly emitted odor from flowers is one of notable characters of most *Orchidantha* species. Their odors, described as smells of bugs and coconut oil (Holttum, 1970), formic acid and butyric acid (Pedersen, 2001), foetid smell (Jenjittikul and Larsen, 2002), fungal smell (Johansen, 2005), carrion or decaying fruit (Cui *et al.*, 2015), dung–like (Nagamasu and Sakai, 1999; Sakai and Inoue, 1999; Trần and Leong-Škorničková, 2010; Vislobokov *et al.*, 2017), scent of decomposed mushrooms (Leong-Škorničková, 2014a), dead rotten animal (Leong-Škorničková *et al.*, 2014b), pungent smell (Poulsen and Leong-Škorničková, 2017), dead fish (Zou *et al.*,2017), and blue cheese (Trần *et al.*, 2020), play a critical role in pollinator attraction (Van der Niet *et al.*, 2014; Vislobokov *et al.*, 2017, Niissalo *et al.*, 2022).

Plants from various families emit strong foetid scents from their flowers e.g. Araceae Juss. (Sivadasan and Sabu, 1989; Beath, 1996; Gibernau *et al.*, 1999; Maia *et al.*, 2010; Prieto and Crascante-Marín, 2017), Hydnoraceae C. Agardh (Burger *et al.*, 1988; Bolin *et al.*, 2009), Orchidaceae Juss. (Peter and Johnson, 2006; Sugiura *et al.*, 2021), Lowiaceae Ridl. (Sakai and Inoue, 1999; Vislobokov *et al.*, 2017), Rafflesiaceae Dumort. (Davis and Lantoh, 1996) were reported to be visited or pollinated by beetles. In *Orchidantha*, Sakai and Inoue (1999) first discovered a deceptive pollination of *O. inouei* Nagam. & S. Sakai in Malaysia and that the flowers were visited and pollinated by dung beetles, but did not provide rewards for them. In agreement with the report by Vislobokov and colleagues (2017), the Vietnamese *O. virosa* neither offers rewards nor a mating site for its pollinator, the carrion–beetle.

Histochemistry, a chemical testing approach using chemical test to analyze putative substances from plant secretory structures (Demarco, 2017), is one of the evidences for plant taxonomy and interpretations of plant and animal interactions (Teixeira *et al.*, 2004; Naczk *et al.*, 2018; Stpiczyńska *et al.*, 2018; Plachno *et al.*, 2019; Wiśniewska *et al.*, 2021). Lipids in osmophores on adaxial lip surface of *Bullophyllum* Thouars are a product of the pollination mechanism that attracts flies with volatile oils (Teixeita *et al.*, 2004). Volatile secretions in osmophores on fertile stamens and staminodes of *Philodendron adamantinum* Mart. ex Schott (Araceae) act as signals for its pollinator, nocturnal *Cyclocephalini* beetles as well (Gonçalves-Souza *et al.*, 2017). Secreted residues from osmophores on spur surfaces of food–deceptive orchids, *Bulbophyllum* Thouars species, imply residence time of pollinators on labella spurs (Naczk *et*

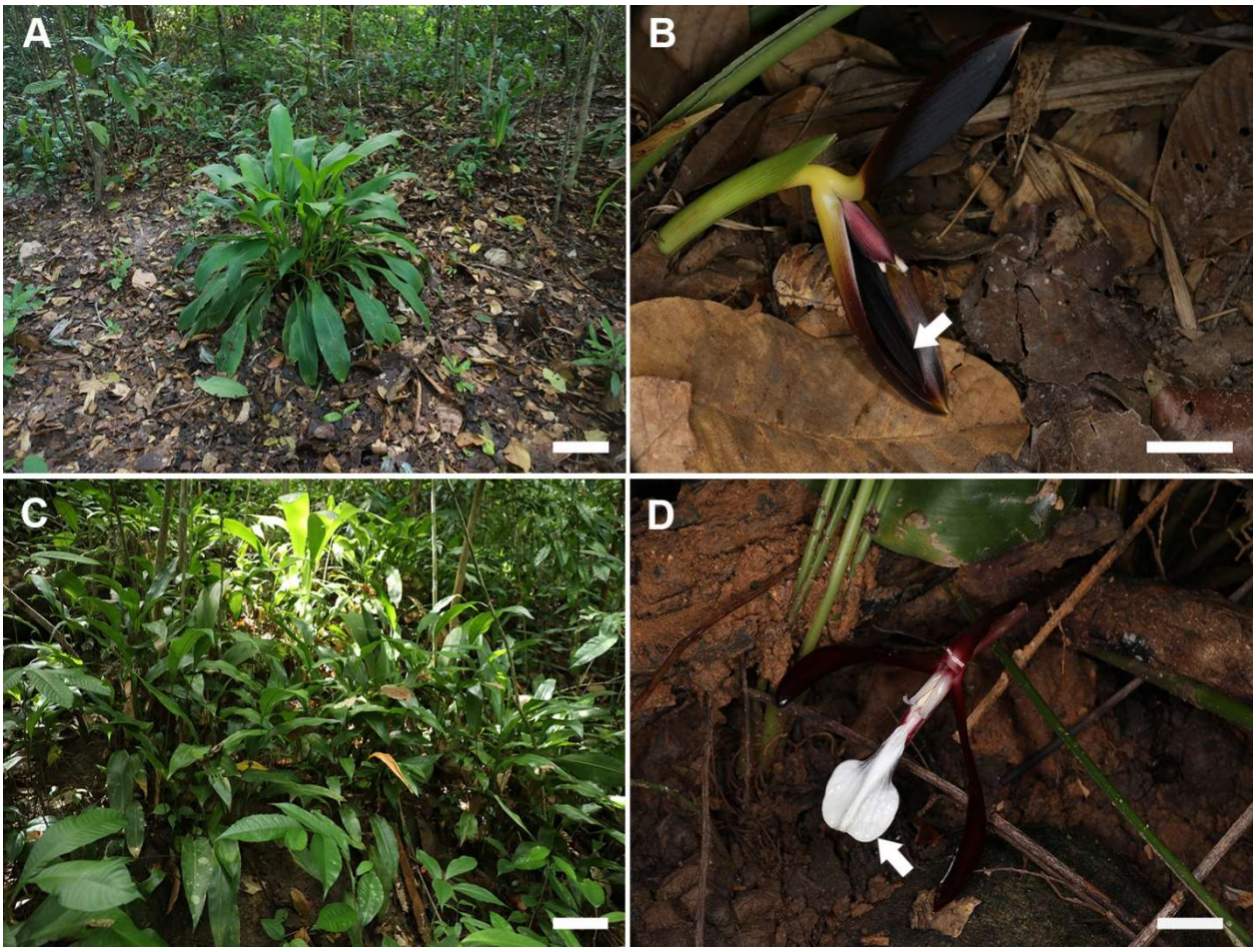

Fig. 1. Morphology of ***Orchidantha foetida*** Jenjitt. & K.Larsen and ***O. siamensis*** K. Larsen in natural habitats (A–D). **A:** Habit of *O. foetida*. **B:** Flower with dark labellum (arrowheads) of *O. foetida*. **C:** Habit of *O. siamensis*. **D:** Flower with white labellum (arrowheads) of *O. siamensis*. (Photographed by Possathorn Nopun). Scale bar: A = 50 cm; B = 2 cm; C = 30 cm; D = 2 cm.

al., 2018). In unpollinated flowers of *Epipactis helleborine* (L.) Crantz (Orchidaceae), heterogeneous secretion including carbohydrates, lipids, and phenolic compounds remains detectable on the surface of the lip until the end of anthesis. The fact was referred to as the enhancement of scent perception of pollinators (Kowalkowska *et al.*, 2018). Relation between plants and insects in fly-pollinated species in the subfamily Asclepiadoideae (Apocynaceae), *Echidnopsis cereiformis* Hook. f. and *Stapelia scitula* L.C.Leach, were confirmed by the presences of secretions on petals (Wiśniewska *et al.*, 2021). The protein–rich secretion species, *E. cereiformis*, probably attracted protein–deprived flies, while *S. scitila*, lipid–rich secretion species, normally allured flies to transfer pollinia by scent mimicry or acted as visitor guide (Wiśniewska *et al.*, 2021).

In Thailand, two species of *Orchidantha*, *O. foetida* Jenjitt. & K.Larsen and *O. siamensis* K. Larsen, are reported and found in different regions with highly distinct in floral morphology. *Orchidantha foetida*, an endemic species distributed in the Eastern region, possesses an unusual flower resembling orchid's flowers with two lateral sepals supporting one remarkable dark labellum called claw type flower (Jenjittikul and Larsen, 2002; Niissalo *et al.*, 2022) (Fig. 1A–1B). Meanwhile, *O. siamensis*, distributed specifically in southernmost region, contains noticeable white labellum without the support from lateral sepals. This floral type is called propeller (Niissalo *et al.*, 2022) (Fig. 1C–1D).

Labellum (also known as lip), an outstanding floral character, is a modified petal which, as previous studies on deceit pollination system of *Orchidantha* revealed, may produce very stinky scents involved in pollinator attraction (Sakai and Inoue, 1999; Vislobokov *et al.*, 2017). However, anatomy and histochemistry of the *Orchidantha* labellum in relation to the pollination syndrome has not been investigated. This study aimed to investigate the potential pollinator-attracting compounds emitted by different floral types within the two *Orchidantha* species, *O. foetida* and *O. siamensis*. To achieve this, we conducted a detailed anatomical and histological analyses of the labellum, a floral part known for its role in odor emission.

Table 1. Histochemical tests for plant secretory structures.

Detections	Chemicals	Positive Results	References
alkaloids	Wagner's reagent	red, brown	Dermaco (2017)
carbohydrates	Periodic acid and Schiff reagent (PAS reaction)	magenta	
lipids	0.5% (w/v) ethanolic Sudan black B solution	black	
mucilage	0.1% (w/v) aqueous ruthenium red solution	magenta, red	
phenolic compounds	10% (w/v) aqueous ferric chloride solution	black, brown	
terpenes	NADI reagent	blue, red, violet	
Osmophores activity	0.1% (w/v) neutral red	red	Stern *et al.* (1987)

MATERIAL AND METHODS

Plant materials

Three populations of *O. foetida* were sampled and individuals collected during June and July 2018 from Eastern part of Thailand; Kantharalak District, Sisaket Province (lat. 14°37'21.036"N, long. 104°43'6.456"E), Nam Yuen District, Ubon Ratchathani (lat. 14°27'41.58"N, long. 105°6'15.4764"E) and Si Mueang Mai District, Ubon Ratchathani Province (lat. 15°25'22.3392"N, long. 105°14'20.2776"E). Populations of *O. foetida* exhibit a restricted distribution, primarily inhabiting lowland evergreen forests and areas adjacent to paddy fields. Only one population of *O. siamensis* were sampled and individuals collected during October 2019 from Southern part of Thailand; Chana District, Narathiwat Province (6°16'19.344"N, 101°38'24.396"E). Population of *O. siamensis* is found in tropical rainforest environments, specifically along hillsides near waterfalls. All collected plant specimens were cultivated in a greenhouse at Mahidol University's Salaya Campus, located in Nakhon Pathom Province, Thailand, for 1 month prior to the commencement of experiments. Labella from three individual plants per species were collected from the flowers at anthesis stage. They were immediately fixed in a 1:1 mixture of 50% formaldehyde–acetic acid–ethanol (FAA) and water. After overnight fixation, the samples were transferred to pure FAA for further anatomical analysis.

Anatomical and histochemical investigations

Anatomy of previously fixed labella was studied using modified paraffin methods (Johansen, 1940; Kermanee, 2008). Samples were placed in closed container with vacuum pump to remove air, washed three times in 50% ethanol and then slightly dehydrated using a graded tertiary butyl alcohol (TBA) series, pure TBA, and and a mixture of pure TBA with paraffin oil (1:1), respectively. The dehydrated samples were infiltrated with melted paraplast at 60ºC for three times in an oven and embedded to form blocks. Next, the samples were serially sectioned in a transverse plane at 30 µm using a rotary microtome. The sections were then mounted onto microscopic slides using a solution of 3% formalin and Haupt's adhesive. To ensure adherence, the slides were warmed on a hot plate (40–50°C) until the sections were completely dry. Finally, the slides were stored at room temperature until the staining process. Finally, the slides were stored at room temperature (25°C) until the staining process. Finally, paraplast were removed from the sectioned samples, dehydrated and rehydrated gradually using ethanol series, and stained with Safranin–O and Fast Green for anatomical observations using a light microscope (Olympus BX50, Japan). The images were captured by cellSens Imaging Software (Olympus).

The histochemical tests were performed on free-hand sections at 80–100 µm of fresh labella following the modified protocols of Stern *et al.* (1987) and Dermaco (2017) to investigate osmophores location and detect any putative substances in cells. Fresh lips of both species were sectioned by the free hand method and placed into reagents to detect the presence of specific compound as shown in Table 1. The Wagner's reagent (potassium iodide in distilled water with iodine) was used to identify the presence of alkaloids by applied sections with Wagner's reagent (20 minutes). The PAS reaction (Periodic acid–Schiff reaction) was used for carbohydrates detection by immersed sections in 1% sodium tetraborate solution (30 minutes), then transferred to 1% periodic acid (10 minutes), and rinsed gently in distilled water. Next, the sections were immersed in Schiff's reagent (5 minutes) in the dark and washed by sodium metabisulfite (10 minutes). Finally, they were rinsed in tap water (10 minutes). A 0.5% (w/v) ethanoic solution of Sudan Black B (Sigma–Aldrich™) were used to test for lipids by stained the sections for 20 miniutes, washed briefly in 70% EtOH, and rinsed in distilled water. A 0.1% (w/v) aqueous ruthenium red solution (Loba Chemie™) was applied directly to the sections (5 minutes) and washed twice in distilled water to test for mucilage. A 10% (w/v) aqueous ferric chloride solution (Ajax–Finechem™) was applied directly to the sections (30 minutes) and washed them twice in distilled water for surplus stain removing to confirm the presence of phenolic compounds. The NADI reaction (naphtol and diamine reaction) were used to test for terpenes by applied NADI reagent to the sections (1 hour) in the dark and washed in 0.1 M sodium phosphate buffer (pH 7.2) (2 minutes). A 0.1% (w/v) neutral red (KemAus™) was used to localize osmophores area by stained the section for 20 minutes and rinsed briefly in distilled water. All examinations were observed under a light microscope (Olympus BX50, Japan) and compared with unstained samples for result interpretation.

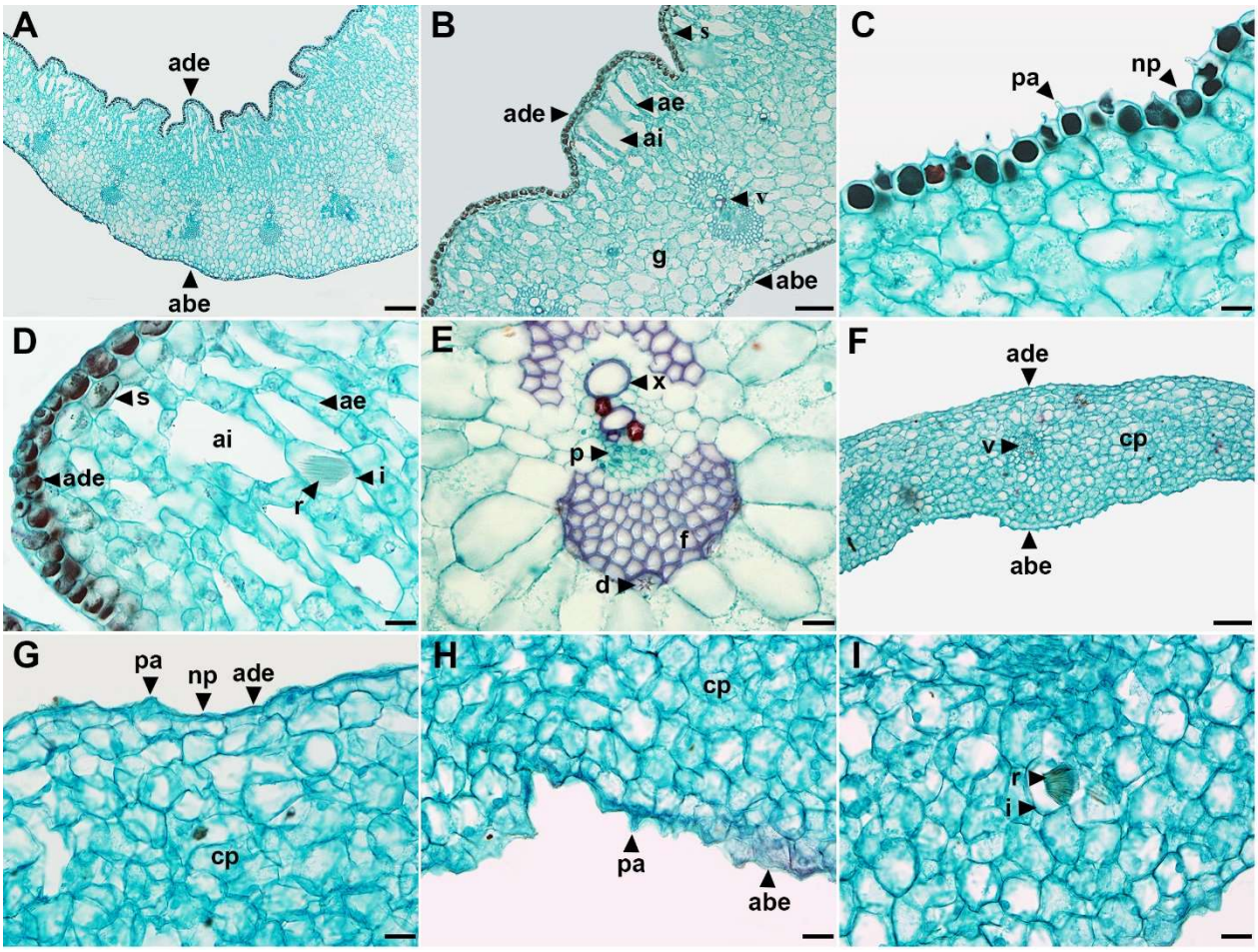

Fig. 2. Labella anatomy of ***Orchidantha foetida*** (A–E). **A:** Labella transverse section presents deeply sulcate at adaxial epidermis. **B:** Labella anatomical layer comprises of adaxial epidermis, single subjacent cell, aerenchyma layer with air spaces, ground parenchyma with vascular bundle, and abaxial epidermis. **C:** Papillate cells (protuberance of periclinal surface) and non-papillate cells densely stained in cytoplasm at adaxial surface. **D:** Adaxial side of labellum reveals non-protuberance epidermal cells, single subjacent cell layer, reticulated aerenchyma cells with large air spaces, and idioblast with raphide crystals. **E:** Vascular bundle and presence of druse crystal in outermost layer of fiber cells. Labella anatomy of ***O. siamensis*** (F–I). **F:** Labella anatomical layer comprises of adaxial epidermis, compacted parenchyma with vascular bundle, and abaxial epidermis. **G:** Adaxial epidermis with small papillate and non-papillate cells. **H:** Abaxial epidermis with papillate cells. **I:** Idioblast with raphide crystals in ground parenchyma. Abbreviations: abe, abaxial epidermis; ade, adaxial epidermis; ae, aerenchyma; ai, air space; cp, compacted parenchyma; d, druse crystal; f, fiber; g, ground parenchyma; i, idioblast; np, non-papillate cell; p, phloem; pa, papillate cell; r, raphide crystals; s, subjacent cell layer; v, vascular bundle; x, xylem. Scale bar: A = 200 μm; B = 100 μm; A = 200 μm; B = 100 μm; C–E = 20 μm; F = 200 μm; G–I = 20 μm.

RESULTS

Labella anatomical characters (Fig. 2)

In labella transverse section, the adaxial side of *O. foetida* labella exhibited a significantly grooved or sulcate surface, especially on the lateral regions flanking the central area, while, the abaxial surface displayed minimal furrowing or appeared entirely smooth across the entire section. However, the adaxial surface of *O. siamensis* labella showed a relatively straight profile with minor undulations and the abaxial surface presented a concavity that coincided with the location of the vascular bundles. The adaxial epidermal cell shape of *O. foetida* were various from isodiametric to rectangle with densely stained cytoplasm. On this surface, we can distinguish two main types of epidermal cells. The first type featured protusion called papillae. These papillate cells were generally distributed along the lateral regions of the labellum. The second type consisted of non-papillate cells. These cells were primarily found in the central part of the labellum, but were also interspersed with the papillate cells. The epidermal cells of *O. siamensis* revealed rather different traits from *O. foetida*. The axial epidermal cells were typically rectangular and exhibited a smooth periclinal surface without densely stained cytoplasm. Interestingly, a small number of cells possessed very minor protuberances on their periclinal surface. However, these papillate cells were infrequent, and their distribution was inconsistent. There was a single subjacent cell layer at the adaxial side of *O. foetida* labella

Table 2. Histochemical detections in the epidermal cells of the labellar transverse sections of ***Orchidantha foetida*** and ***O. siamensis***.

Detections	*O. foetida*	*O. siamensis*	
	Labellar adaxial epidermal cells[1]	Labellar adaxial epidermal cells	Labellar abaxial epidermal cells
Alkaloids	+, c, *	+, c	+, c
Carbohydrates	+, c	+, cl	+, cl
Lipids	+, c, *	–, p	+, c
Mucilage	+, c	+, cl	+, cl
Phenolic compounds	+, c	+, c	+, c
Terpenes	+, c, *	+, c	+, c
Osmophore activity	+, c	+, c	+, c

[1] The histochemical detection in the abaxial epidermis was omitted due to its non–osmophoric activity (see text for details). '+' = positive result at the targeted cells; '–' = negative result at the targeted cells; 'c' = substances were detected in the cytoplasmic contents of the cells; 'cl' = substances were detected in cuticular layer of the targeted cells; 'p' = substances were detected in the other cells, for example, subjacent cells, aerenchyma and parenchyma; '*' = minute droplets of the putative substances can be detected in the other cells.

comprised of rectangular parenchyma along the epidermis. Moreover, the aerenchyma layer and ground parenchyma occurred next to the subjacent layer. The aerenchyma was composed of rectangular cells that was loosely arranged in a reticulated pattern enclosing large air spaces. This layer occurred throughout the labella transverse section of *O. foetida*, but in some regions, for example at the lateral and marginal parts of the labellum, this layer was absent, and parenchyma replaces it instead. However, labella of *O. siamensis* revealed compacted of parenchyma on both adaxial and abaxial sides without air spaces. Idioblast cells, characterized by the presence of raphide crystals, were observed in both species, though their cellular localization differed between *O. foetida* and *O. siamensis*. In the former, they were predominantly found in the aerenchyma, while in the latter, they were concentrated in the ground parenchyma. Vascular bundles in labella of *O. foetida* present in the ground parenchyma were arranged in a regular manner along labella sections, and were covered by phloem fibers, especially on the abaxial side. In addition, druse crystals were found at the outermost layer of fibers. In *O. siamensis*, vascular bundles had less fibers and were located at central layer of parenchyma throughout the section. Epidermal cells on the abaxial surface of *O. foetida* exhibited heterogeneity. Most cells were rectangular and displayed a smooth periclinal wall, with some cells showing dense staining. However, a small population of papillate cells were also observed. The infrequent presence of papillate cells introduced inconsistency to the overall epidermal patterning. Examination of the abaxial epidermis of *O. siamensis* revealed isodiametric epidermal cells with protuberances on periclinal walls without densely stained cytoplasm. These papillate cells were distributed throughout the tissue section. Neither species exhibited stomata on either surface of their labellum.

Histochemical investigations on labella

The putative substances on labella transverse sections of *O. foetida* and *O. siamensis* revealed by histochemical tests were volatiles osmophores location and main chemical compositions in detected epidermal cells (Table 2). The cytoplasmic contents of both papillate and non-papillate cells of *O. foetida* labella at the adaxial side stained dark red in neutral red, indicating osmophoric activity, whereas only the cell walls of abaxial epidermal cells stained red confirming the non-osmophoric activity at abaxial side. Because of this outcome, another histochemical tests on labella of *O. foetida* were focused only on adaxial side. Ruthenium Red staining revealed the presence of mucilage within the cytoplasm of both adaxial epidermal cell types. This was evident by the intense dark red coloration observed in these cells. The PAS reaction indicated carbohydrate accumulation in the cytoplasm of both adaxial epidermal cell types by magenta stained. Even though other cells were also stained, high accumulation of carbohydrates was found in the epidermal cells. Sudan Black B staining revealed a distinct accumulation of lipids within the cytoplasm of adaxial papillate and non-papillate cells. This observation was further supported by the presence of lipid droplets in both subjacent cells and aerenchyma cells. The ferric chloride test provided evidence for the presence of phenolic compounds. This was indicated by the dense black staining observed in the cytoplasm of both adaxial epidermal cell types. Reddish brown staining of the cytoplasm of adaxial papillate and non-papillate cells by Wagner's reagent confirmed the presence of alkaloids. Moreover, minute droplets of alkaloids were detected in subjacent cells, aerenchyma cells, and parenchyma cells. The presence of terpenes were detected by the NADI reaction was clearly visible in dark blue staining of the cytoplasm of both adaxial epidermal cell types, with the presence of minute droplets in other cells. Neutral red staining resulted in intense and uniform cytoplasmic uptake throughout the adaxial and abaxial epidermal cells of the *O. siamensis* labella. This observation provides strong confirmatory evidence for the presence of osmophores on both surfaces of the labellum. Our investigation centered on the adaxial surface, where histochemical analyses consistently revealed the presence of putative substances within the cytoplasm of adaxial epidermal cells. These included phenolic compounds

(staining brown with ferric chloride), alkaloids (staining brown with Wagner's reagent), and terpenes (staining violet with the NADI reaction). Conversely, analyses revealed the presence of mucilage and carbohydrates primarily on the cuticular layer of adaxial epidermal cells. This observation suggests that the accumulation of these substances occurred extracellularly, rather than within the cytoplasmic compartment of the cells. Notably, the lipid test yielded negative results within the adaxial epidermal cells. This is likely due to the minimal intracellular lipid accumulation observed in this cell type. Conversely, the ground parenchyma cells exhibited strong cytoplasmic staining, appearing positive black under the test. On the abaxial side, abaxial epidermal cells were positively stained at cytoplasmic contents in almost all histochemical tests, including lipids (staining black with Sudan Black B), phenolic compounds (staining brown with ferric chloride), alkaloids (staining brown with Wagner's reagent), and terpenes (staining violet with the NADI reaction). Analyses of mucilage and carbohydrates on the abaxial surface yielded results consistent with those observed on the adaxial surface. In both locations, mucilage and carbohydrates were exclusively detected at the cuticular layer of the abaxial epidermal cells, with no evidence of their presence within the cytoplasm. Histochemical analyses of *O. siamensis* labella failed to detect minute droplets, a feature previously observed in *O. foetida*.

DISCUSSION

Labella anatomy in *Orchidantha*

Our research on the Lowiaceae family has revealed that *O. siamensis* possesses osmophores on both the adaxial and abaxial surfaces of its labellum, a unique finding within this species. In contrast, *O. foetida* only exhibits osmophores on the adaxial surface. These findings suggest a possible correlation between the observed phenomenon and the floral morphology and orientation of these species during anthesis. During the flowering, the lateral sepals of *O. siamensis* spread outward, failing to provide support for the labellum. As a result, the white labellum is positioned above the ground. The presence of both side osmophores on labellum of *O. siamensis* could potentially enhance the intensity of the foul scent, thereby attracting pollinators to both sides of the labellum. In *O. foetida* flower, prior to anthesis, it exhibits a downward-facing floral orientation to the ground. During flowering, the dorsal sepal assumes an arched position above the labellum, while the lateral sepals remain closed and provide continuous support until the flower fully opens. As described by Niissalo *et al.* (2022), this floral form is characterized as the 'claw type', wherein the labellum is exclusively presented in an adaxial orientation during anthesis, while the abaxial surface remains concealed by the lateral sepals. The exclusive localization of osmophores to the adaxial surface of the *O. foetida* labellum may be correlated with its strategic position as a pollinator landing platform. By emitting scents from these osmophores, the labellum can effectively attract pollinators, thereby facilitating successful pollination. In 2015, Cui *et al.* studied osmophores on the labellum of *O. chinensis* var. *longisepala* (D. Fang) T. L. Wu and reported that osmophores were found only on the adaxial side as presented in labellum of *O. foetida* form this studied. Moreover, results from transmission electron microscope (TEM) confirmed osmophore cells presenting only at adaxial side which contains several mitochondria, plastids, and endoplasmic reticulum indicating high cell metabolism (Cui *et al.*, 2015).

Labellum (inner petal) is a remarkable floral part in Lowiaceae that is diverse in shape and color and essential for pollinator attraction (Vislobokov *et al.*, 2017; Niissalo *et al.*, 2022). In this present study, there are two different anatomical patterns in the transverse section of the labella from two *Orchidantha* species. Some species in Orchidaceae have papillate and non-papillate cells osmophores on the labellum, e.g., *Cohniella cepula* (Hoffmanns.) Carnevali & G. A. Romero and *C. jonesiana* (Rchb. f.) Christenson (Kettler *et al.*, 2019). In Lowiaceae, this is the first report of osmophores with papillate and non-papillate cells on the labellum. Adaxial epidermal cells are densely stained in the cytoplasm because some pigments accumulate in the cells (anthocyanin, flavonoids, tannin, etc.) (Adachi and Machado, 2020; Kermanee, 2020). Based on floral morphology, *O. foetida* possesses the only dark color labellum among the studied species, which corresponds with anatomical results. Aerenchyma with several air spaces is found at the adaxial side of the labellum of *O. foetida*. This arrangement in the labellum was reported in some species of Orchidaceae (Stpiczyńska *et al.*, 2018; Arévalo-Rodrigues *et al.*, 2022). Labella transverse sections of *Bulbophyllum longiflorum* Thouars (Orchidaceae; section Cirrhopetalum) exhibited dense protoplast epidermal cells subtended by several subjacent layers and irregular-shape aerenchyma with many air spaces at the adaxial side (Stpiczyńska *et al.*, 2018). Some species of *Anathallis* Barb. Rodr., such as *A. sclerophylla* (Lindl.) Pridgeon & M. W. Chase (Orchidacae), presented large air spaces with aerenchyma at abaxial side of the labellum (Arévalo-Rodrigues *et al.*, 2022). Aeration is a mechanism to form aerenchyma with air spaces, which is commonly present in plants under waterlogging, flooding, drought conditions or in wetland or aquatic habitats (Suralta and Yamauchi, 2008; Yuan *et al.*, 2021). Aerenchyma formation promotes large air spaces in tissue, which retards diffusion and facilitate sufficient internal oxygen (O_2) for cellular respiration (Jackson and Armstrong, 1999; Colmer, 2003; Suralta *et al.*, 2010). Stpiczyńska *et al.* (2018) hypothesized that the

presence of aerenchyma within the labellum of *Bulbophyllum* flowers (Orchidaceae) is correlated with their highly mobile and hinged labellum. Furthermore, they suggested that this anatomical feature represents an adaptation facilitating pollination in *Bulbophyllum*. Despite the immobile nature and exclusively adaxial presentation of the *O. foetida* labellum, the presence of aerenchyma within this structure could potentially contribute to two distinct functions. One possible function of aerenchyma in the *O. foetida* labellum could be to facilitate the internal supply of oxygen (O_2) for cellular respiration, particularly within the osmophores, which are known to exhibit high metabolic demands. Another potential role of aerenchyma and air spaces within the labellum could be to facilitate the gradual release and diffusion of the foul scent emitted to attract pollinators. The distribution of aerenchyma on the adaxial side of the labellum in *O. foetida* correlates with the exclusive localization of osmophores to the same surface, suggesting a functional association between these structures. In contrast, the absence of aerenchyma in the labellum of *O. siamensis* indicates a different morphological and potentially functional arrangement. The protuberance of epidermal cells, known as papillae, is an important characteristic of the labellum, serving as pollinator attraction, guiding, tactile stimulation on the pollinator's body, and protection flower against desiccation (Faria *et al.*, 2020). Our examination of the labella anatomy revealed the presence of both papillate and non-papillate cell types within the two species under investigation. Pansarin *et al.* (2014) proposed that osmophores containing papillate cells were associated with a wider range of floral scent compounds compared to those lacking papillate cells. In addition, the appearance of papillate cells on the labellum also causes an increase in secretion surface (Arévalo-Rodrigues *et al.*, 2022). Therefore, species with the presence of papillate cells may have an effective scent-emitting capacity in a wider range than species that do not have papillate cells. Idioblasts, raphide crystals containing cells, are found in the labella transverse sections. Raphide crystals are calcium oxalate crystals which are the product of the calcium ion and oxalic acid reaction (Franceschi and Nakata, 2005; Kermanee, 2020). The presence and accumulation of raphide crystals within the labellum function as a crucial component of the plant's physical defense mechanisms, deterring herbivory and safeguarding the scent-producing structures (Coté and Gilbernau, 2012; Reposi *et al.*, 2021).

In addition to the distinct locations of osmophores and the presence of aerenchyma on the labellum, another conspicuous morphological characteristic differentiating *O. foetida* and *O. siamensis* is their variation in color of the labellum. Niissalo *et al.* (2022) classified *Orchidantha* flowers into three categories based on the coloration of labellum: dark, white, and puce types. Moreover, phylogenetic reconstruction and character evolution studies within the Lowiaceae suggested that the ancestral traits were characterized by a claw-type flower, a dark-colored labellum, and a scent reminiscent of feces or decomposition. In contrast, the derived traits exhibited a propeller-type flower, a puce or white labellum, and a mushroom-like scent (Niissalo *et al.*, 2022). The flower of *O. foetida* is the claw-type with dark labellum which is defined as ancestral characters within family, while the flower *O. siamensis* is the propeller-type with white labellum which is the derived characters. Based on the comparative anatomy of the labellum, the presences of osmophores and aerenchyma at adaxial surface of labellum are the unique traits in *O. foetida* flower. In contrast, the presence of osmophores on both sides of labellum and the absence of aerenchyma are unique in *O. siamensis* flower. Therefore, the anatomical characteristics observed in this study provide compelling evidence supporting the differentiation between ancestral and derived morphological traits (including the flower type and the color of labellum) within the Lowiaceae family. Moreover, the variation in labella color among *Orchidantha* species is likely to attract the difference groups of visitors and pollinators visiting the flowers. Vislobokov *et al.* (2017) entirely summarized data of labella coloration and type of pollinators within the genus *Orchidantha*. They reported that species with puce or dark labella were visited by diurnal dung beetles (Scarabaeidae) or nocturnal carrion beetles (Hybosoridae), whereas species with white labella were usually visited by fruit beetles (Nitidulidae) (Vislobokov *et al.*, 2017). In 2021, Leong-Škorničková and colleagues (Leong-Škorničková *et al.*, 2021) also reported that *O. jiewhoei* Škorničk. & A. Lamb., white-labellum species, was visited by sap beetle (Nitidulidar sp.). Therefore, the variation of labella color in *O. foetida* and *O. siamensis* affect in attraction the difference types of visiting pollinators. The pollination ecology of the Lowiaceae family remains poorly studied, with available information primarily focused on species with dark-colored labellum. Previous studies have demonstrated that dung beetles and carrion beetles are effective pollinators of Lowiaceae species with a fetid odor, a pollination mechanism known as coprocantharophily (Sakai and Inoue, 1999; Vislobokov *et al.*, 2017; Niissalo *et al.*, 2022). However, the pollination ecology of *O. foetida* and *O. siamensis* remains unexplored. Consequently, further investigations into the pollination biology of these species are warranted.

Labella histochemistry in *Orchidantha*

Histochemical analyses are widely applied for osmophoric location and accumulation of essential compounds in osmophores (Davies *et al*, 2014; Kowalkowska *et al.*, 2015; Wiśniewska *et al.*, 2019; Adachi and Machado, 2020). While neutral red staining is a valuable tool for initial localization of osmophores, it

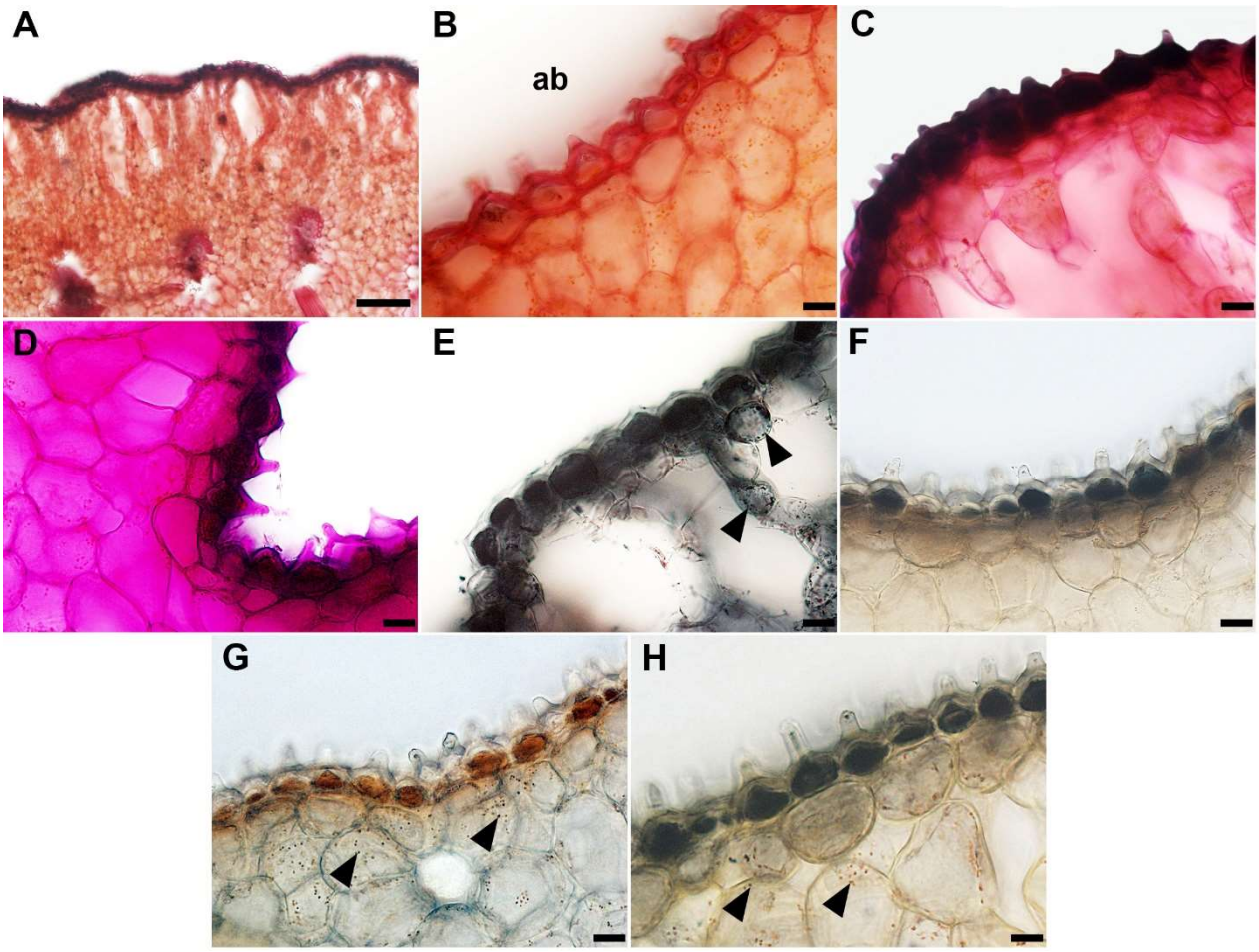

Fig. 3. Histochemical examinations of ***Orchidantha foetida*** on adaxial labella transverse sections (A, C–H). **A.** Osmophores location on epidermis of adaxial labellum surface by neutral red. **B.** Abaxial epidermal cells of labellum stained red at cell wall by neutral red. **C–H:** Detection of putative substances on adaxial epidermal cells. **C.** Mucilage by Ruthenium Red. **D.** Carbohydrates PAS reaction. **E.** Lipids by Sudan Black B with presence of minute droplets (arrowheads). **F.** Phenolic compounds examination to ferric chloride. **G.** Alkaloids examination to Wagner's reagent with presence of minute droplets (arrowheads). **H.** Terpenes examination to NADI reaction with presence of minute droplets (arrowheads). Abbreviation: ab, abaxial side. Scale bar: A = 100 μm; B–H = 20 μm.

is crucial to complement this technique with anatomical and additional histochemical tests for definitive confirmation of osmophore identity (Silva-Batista *et al.*, 2021).

Mucilage was detected in the cytoplasmic contents of labella epidermal cells of *O. foetida* (only adaxial) and only in the cuticular layer of *O. siamensis* labellum (both sides) (Fig. 3C, 4C–D). Mucilage is a complex of polymeric polysaccharides including D–galactose, D–xylose, L–arabinose, L–rhamnose, and galacturonic acid, which is generally found in several plants, e.g., *Aloe vera* L., *Moringa oleifera* Lam., etc. (Tosif *et al*., 2021). The detection of the mucilage can be done with ruthenium red (Jia *et al.*, 2015; Dermaco, 2017). This dye will selectively bind with the carboxyl oxygen of galacturonic acid and change to magenta or red (Vigneswaran *et al.*, 2014). In 2022, Arévalo-Rodrigues *et al.* reported mucilage production and secretion from the floral glands of several species from the subtribe Pleurothallidinae (Orchidaceae). Mucilage secretion plays a dual role in floral biology. Firstly, it acts as a protective barrier for floral organs against microbial attack. Secondly, it facilitates successful pollination by enhancing pollinator-plant interactions (Arévalo-Rodrigues *et al.*, 2022). The labellum of the two *Orchidantha* species is covered with sticky mucilaginous exudation during floral development until flowering. Therefore, the presence of the mucilage in the osmophore cells is not only a secondary metabolite from osmophoric activity but also functions as a lubricant during floral development and is involved in pollination mechanisms.

Our investigation using the PAS reaction reveals positive staining for carbohydrates within the cytoplasm of the labella epidermal cells in *O. foetida* (restricted to the adaxial surface) and the cuticular layer on both sides of the labellum in *O. siamensis* (Fig. 3D, 4E–F). Because of the high metabolic activity of the osmophores, the accumulation of carbohydrates as resources for energy consumption is commonly presented (Wiśniewska *et al.*,

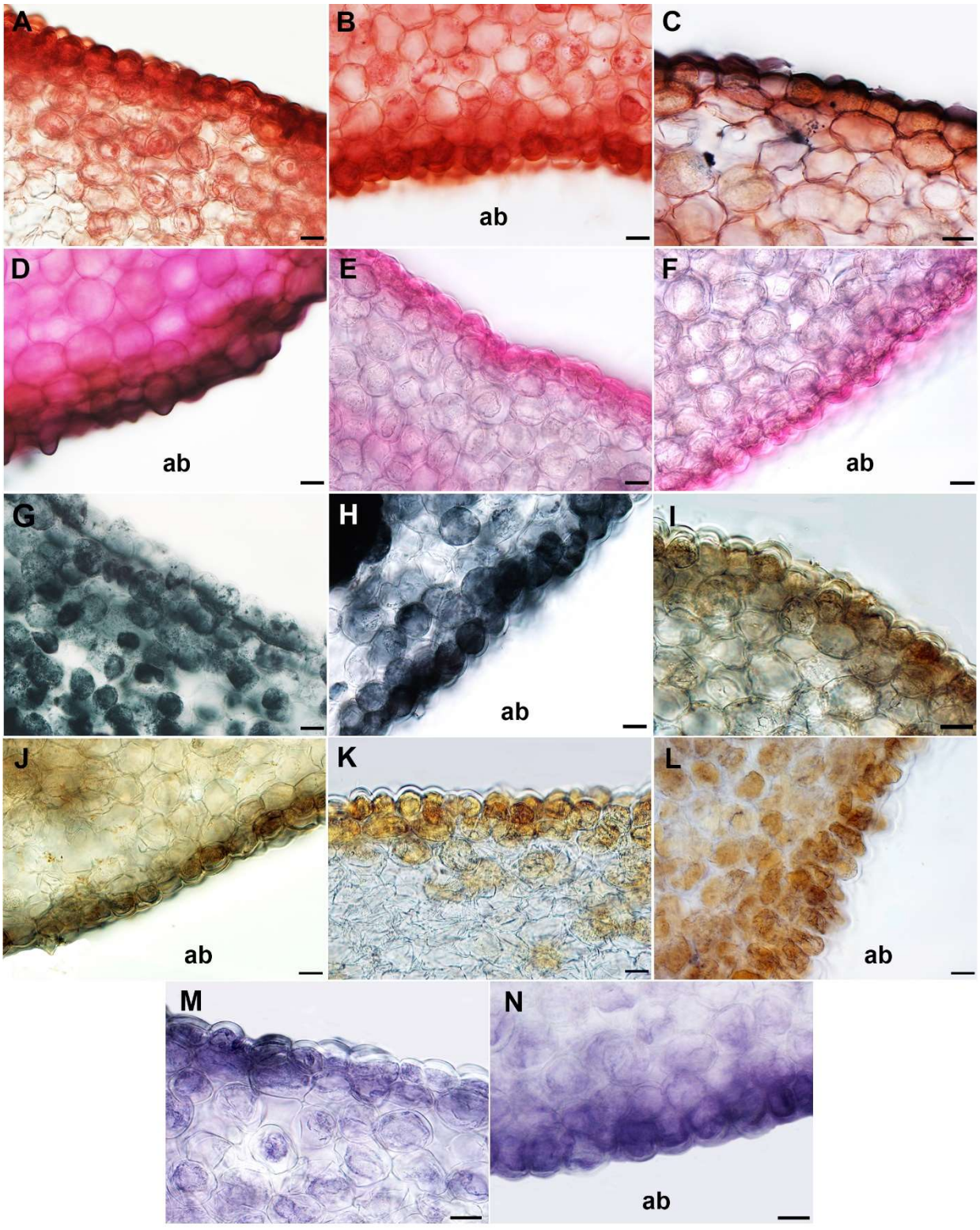

Fig. 4. Histochemical examinations of ***Orchidantha siamensis*** on adaxial (A, C, E, G, I, K, and M) and abaxial (B, D, F, H, J, L, and N) labella transverse sections. **A–B:** Osmophores location and activity of adaxial and abaxial epidermal cells by neutral red. **C–D:** Detection of mucilage on adaxial (C) and abaxial (D) epidermal cells by Ruthenium Red. **E–F:** Detection of carbohydrates on adaxial (E) and abaxial (F) epidermal cells PAS reaction. **G–H:** Detection of lipids on adaxial (G) and abaxial (H) epidermal cells by Sudan Black B. **I–J:** Detection of phenolic compounds on adaxial (I) and abaxial (J) epidermal cells by ferric chloride. **K–L:** Detection of alkaloids on adaxial (K) and abaxial (L) epidermal cells by Wagner's reagent. **M–N:** Detection of terpenes on adaxial (M) and abaxial (N) epidermal cells by NADI reaction. Abbreviation: ab, abaxial side. Scale bar: A–N = 20 µm.

2019). The principle of the PAS reaction is an oxidation of diol in carbohydrates by periodic acid to form aldehyde, which finally reacts with Schiff's reagent and causes magenta coloring (Jensen, 1962). The osmophores in several orchid species were reported to accumulate carbohydrates in the cells revealed by the PAS reaction, e.g., *Bulbophyllum echinolabium* J. J. Sm. (Wiśniewska *et al.*, 2019), *Acianthera saurocephala* (Lodd.) Pridgeon & M. W. Chase (Arévalo-Rodrigues *et al.*, 2022), etc. The carbohydrates are only detected at cell wall of the adaxial and abaxial epidermal cells of *O. siamensis*. Since carbohydrates are one of components of primary cell wall (Kermanee, 2020), labella epidermal cells of *O. foetida* may have a low accumulation of carbohydrates or a depletion of accumulated carbohydrates (Kermanee, 2020).

Sudan Black B serves as a common stain for visualizing lipids within plant cells. This occurs through its selective partitioning into triacylglyceride-rich regions, resulting in the characteristic black coloration (Dudareva and Pichersky, 2006). The cytoplasm of the adaxial epidermal cells of *O. foetida* stained black indicating high aggregation of lipids. Moreover, many minute lipid droplets are also found at aerenchyma (Fig. 3E). These droplets may be produced by any cells and transported to the epidermis for emission. Lipids are detected on both sides of *O. siamensis* labellum, especially at the abaxial side, where the cytoplasm is densely stained black while the parenchyma is stained on the adaxial side (Fig. 4G–H). This result may indicate that the depletion of lipids in the adaxial epidermal cells and the parenchyma can lead to the production and accumulation of lipids, which are finally transported *via* lipid droplets to epidermal cells. The gradient of lipids accumulation between cells were also observed in labellum of *Brasiliorchis schunkeana* (Campacci and Kautsky) R. B. Singer, S. Koehler & Carnevali (Orchidaceae) with substantial deposit lipids in the epidermis, sub-epidermis, and some parenchyma cells (Lipińska *et al.*, 2022). Arévalo-Rodrigues *et al.* (2022) reported the lipid droplets in osmophores of species from subtribe Pleurothallidinae (Orchidaceae) (*Pleurothallis ruscifolia* (Jacq.) R. Br. in W. T. Aiton and *Octomeria gracilis* Lodd. ex Lindl.). They commented that the presence of lipid droplets in osmophores which related to the emission of lipophilic volatile compounds, which are essential for floral fragrance assembly.

Phenolic compounds were detected in the epidermal cells of the two *Orchidantha* species as brown color (Fig. 3F, 4I–J). Phenolic compounds are plant secondary metabolites involved in plant development and defense mechanisms. The phenolic compounds can be detected in the osmophores. The detection of phenolic compounds utilizes a ferric chloride ($FeCl_3$) test which reacts to phenol leading to the precipitation of iron in black or brown colors (Dermaco, 2017). Skubatz *et al.* (1996) examined the presence of phenolic compounds in osmophores of *Sauromatum guttatum* Schott (Araceae) which related to the presence of phenol-volatile compounds in floral odor; phenol, *m*–cresol, and *p*–cresol. As reported by Jürgens *et al*. (2006), the phenolic compounds were present in the osmophores of many *Ceropegia* L. spp. (Apocynaceae) which conformed to scent profiles with a high average relative amount of phenolic-volatiles (31% of *p*–cresol from *Apteranthes joannis* (Maire) Plowes and 58% of *p*–cresol from *Orbea semota* (N. E. Br.) L. C. Leach). Even if the phenolic compounds were commonly found in the osmophores, they were sometimes reabsorbed and metabolized by plant tissue instead of releasing scent. In 2018, Marinho *et al.* investigated the terpenes and phenolic compounds accumulated in the floral osmophores of *Bauhinia rufa* Steud., *Hymenaea courbaril* L., and *Caesalpinia pulcherrima* (L.) Sw. (Fabaceae). However, GC-MS analys of the floral fragrance constituents revealed only terpenoids. The phenolic compounds were metabolized by other plant tissue, so they were not involved in the scent profiles of three species (Marinho *et al.*, 2018).

The labella epidermis of the two *Orchidantha* species contains alkaloids, with several alkaloid droplets stained densely brown inside the cells (Fig. 3G, 4K–L). Alkaloids are plant nitrogen-containing secondary metabolites serving in defense against abiotic and biotic stresses (Bhambhani *et al.*, 2021). To test the alkaloids, Wagner's reagent (potassium iodide with iodine) is applied to plant tissues, where potassium cation binds with nitrogen by covalent bonding, resulting in the precipitation of potassium-alkaloid as red or brown colors (Parbuntari *et al.*, 2018).

The terpenes were detected in the labella epidermis of the two *Orchidantha* species. It may be explained that the accumulated terpenes in the epidermis are depleted by osmophoric activity, and the terpenoid droplets produced by the other cells are transported to the osmophores (Kermanee, 2020). The terpenes are widely detected by the NADI (naphthol and diamine) reaction. The couple of naphthol and diamine will bind with various terpenes and cause blue color (monoterpenes and sesquiterpenes), red color (diterpenes, triterpenes, irregular terpenes), and blue color (mixtures of monoterpenes and sesquiterpenes with their derivatives) (Dermaco, 2017). The NADI reaction is usually paired with neutral red staining to assure the location of the osmophores (Reposi *et al.*, 2021). There are many studies reporting the presence of terpenes in osmophores, for example the osmophores on staminate and pistillate flowers of *Catasetum fimbriatum* Rchb. f. (Orchidaceae) (Reposi *et al.*, 2021), the osmophores on the sepal of *Anathallis obovata* (Lindl.) Pridgeon & M. W. Chase (Orchidaceae) (Arévalo-Rodrigues *et al*., 2021). Since terpenes are one of the major scent volatile compounds, the detection of them in the osmophores on labella of the two *Orchidantha* species directly involved in floral scent emission.

CONCLUSION

This comparative investigation unveiled novel insights into the intriguing labella structures and chemical variation of two Thai *Orchidantha* species, *O. foetida* and *O. siamensis*. Both species possess osmophores, specialized scent glands dedicated to their pollination strategy. However, key anatomical and histochemical differences were observed. *Orchidantha foetida* displayed a more complex architecture, featuring papillate and non-papillate epidermal cells adorned with a sulcate adaxial surface. This surface harbors osseous aerenchyma, potentially facilitating oxygen supply for enhanced scent production. Histochemical analysis revealed the accumulation of scent-related compounds (mucilage, carbohydrates, lipids, terpenes, phenolics, and alkaloids) only in the adaxial epidermal cells of labellum. In contrast, *O. siamensis* exhibits a simpler osmophore structure, with non-papillate adaxial and papillate abaxial epidermal layers with compacted parenchyma in labella anatomy. Similar to *O. foetida*, histochemical analysis pinpointed scent-related compounds accumulating in both epidermal layers and certain parenchyma cells. This suggests multifaceted roles for these tissues in scent production and storage. These contrasting labella anatomy and histochemical profiles might reflect adaptations to distinct pollinator interactions in each species. Further research on pollinator observation could exactly validate pollination biology on *Orchidantha.* By elucidating the intricate interplay between labella anatomy and histochemistry, this work paves the way for further exploration of floral adaptations and their ecological significance in *Orchidantha* and beyond.

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