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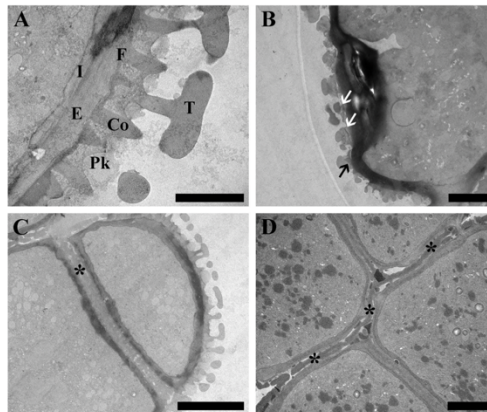


Figure 6. Transmission electron microscopy (TEM) micrographs of *Xyris complanata* pollen (A–D). A. Pollen wall ultrastructure. B. The apertural area of pollen grain showing shorter columellae found in the operculum. C. The fusion of tectum elements of two adjacent pollen grains within the tetrad. D. The cross-linking of tectal elements of two neighbouring pollen grains between tetrads. A, B. Cross-section. C, D. The longitudinal-section. Arrows indicate short columellae. Asterisks indicate the fusion of tectal elements. Abbreviations: T, tectum; Co, columella; F, foot layer; Pk, pollenkitt; E, exine; I, intine. Scale bars = 2 μm (A), 5 μm (B, D), 10 μm (C).

tural area, probably by folding inwards during desiccation (Figures 3D, 4G) as also found in pollen from *Crocosmia* × *crocosmiflora* (Blackmore & Barnes 1986).

Our findings of *Xyris complanata* exine ornamentation, reticulate (LAM) and heterobrochate microreticulate to perforate (SEM), is similar to the SEM results of Phonsena (2012) but different from the LM study by Jones and Pearce (2015), which

1970, 1972; Kral 1998; Phonsena 2012; Luz et al. 2015). Even though the description of the exine ornamentation of *Xyris* pollen varies depending on palynologists as well as types and magnification of microscopy used, this character was used as a key character in many studies. Phonsena (2012) further categorised pollen from Thai and southeast Asian *Xyris* species into subgroups based on microreticulate and microreticulate-granulate sculpturings,

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2000). It is also interesting that the widest layer on the exine of this plant taxon is the columella layer and the inter-columellar space tends to be filled with pollenkitt. The presence of pollenkitt on the pollen wall of *X. complanata* was also confirmed by both LM and SEM studies (Figures 3E, 4I, J). Even though the function of the columellae is certainly complex, this structure would enhance the space within the outer layer of exine for depositing coating material, including pollenkitt (Hesse 1981; Ferguson & Skvarla 1982). Among 20 functions of pollenkitt proposed by Pacini and Hesse (2005), possible roles for this plant species might be associated with various pollination strategies, starting from pollen donor flowers to stigmas. However, as shown in Figure 1B–D, a number of polyads were found on the *Apis* bee's body, pollenkitt would play an important role in enabling adhesion of aggregated pollen to pollinators as well as gathering pollen grains together during transport. Wall et al. (2002), Boyd et al. (2011), and Freitas and Szalma (2006) pointed out that *Xyris* flowers are normally pollinated by Hymenoptera and syrphids.

In general, aggregated pollen can be divided into two types due to the continuity of their exine envelope, viz. calymmate and acalymmate (Van Campo & Guinet 1961; Hesse et al. 2009; Halbritter et al. 2018). The individual pollen grain within these units is bound by two means, i.e. simple cohesion (fusion of the tectum) and crosswall cohesion (extensinous bridge) (Skvarla et al. 1976; Takahashi & Sohma 1984). Based on our LM and TEM results, a discontinuous exine envelope at the attachment area of the adjacent monads was observed. It was also found that the tight junction between neighbouring pollen grains within the tetrad appears to be involved with the fusion of tectal elements, while the looser one could be found between those of contiguous tetrads, which is associated with partial fusion of the tectum. The latter can cause dis-aggregation of the polyad that could also be found in our experiment. The tectal linkage is also adapted in many plant taxa to aggregate their pollen and the cohesion between tetrads can be achieved by means

## Conclusions

*Xyris complanata* pollen differs from those of other *Xyris* taxa in two morphological characteristics. The polyad together with its ulcerate apertural type are useful tools for taxonomic delimitation of this *Xyris*. The tetrads are connected by the fusion of the tectum of neighbouring tetrads. The dispersal unit feature as well as the presence of pollenkitt are mechanisms facilitating the entomophily of this plant species. However, studies on the ultrastructure, molecular phylogenetics, reproductive biology, and pollination ecology are still crucial in order to answer the question why the pollen of *X. complanata* is so different from those of other *Xyris* species.

## Acknowledgements

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## Disclosure statement

No potential conflict of interest was reported by the authors.

PowerPoint interface showing a presentation slide with a microscopic image of cells. The slide is titled "Click to add notes". The interface includes a menu bar (File, Edit, View, Insert, Format, Arrange, Tools, Slide Show, Window, Help) and a ribbon with tabs (Home, Insert, Draw, Design, Transitions, Animations, Slide Show, Review, View). The slide content area displays a microscopic image of cells, likely yeast or fungi, showing internal structures and yellowish granules. The status bar at the bottom indicates "Slide 5 of 9", "English (Thailand)", and "Accessibility: Investigate".

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PowerPoint interface showing a presentation slide with a microscopic image of cells. The interface includes the menu bar (File, Edit, View, Insert, Format, Arrange, Tools, Slide Show, Window, Help), the ribbon (Home, Insert, Draw, Design, Transitions, Animations, Slide Show, Review, View), and the status bar (Slide 5 of 9, English (Thailand), Accessibility: Investigate, Notes, Comments, 107%). A video feed of a person is visible in the top right corner.

The main slide displays a microscopic image of several cells, likely yeast or fungi, showing internal structures and yellowish contents. The slide is part of a presentation with 9 slides, with slide 5 currently selected. The left sidebar shows thumbnails of the other slides, including a slide with a red box around a cell image.

The status bar at the bottom indicates the current slide is 5 of 9, the language is English (Thailand), and the accessibility tool is Investigate. The zoom level is 107%.