

The Origin and Identity of the Calyculus in Loranthaceae: Inferred From the Floral Organogenesis of *Loranthus tanakae* Franch. & Sav.

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Abstract: The flowers of the hemiparasitic family Loranthaceae are always subtended by a rimmed structure known as the calyculus. The origin and identity of the calyculus have been disputed for more than a century. Various hypotheses have been proposed, for example, an outgrowth of the axis, a reduced calyx, and a bracteolar (prophyllar) origin, but controversies remain. To obtain a plausible explanation of the origin of the calyculus, we investigated the flowers of *Loranthus tanakae* using scanning electron microscopy and light microscopy to observe the entire developmental process of the floral parts. Our results show that bracts are not present in *L. tanakae*. The calyculus, which lacks serving vascular bundles, initiates as a semicircular primordium and then develops into a circular structure by an adnation at both sides. The flower primordium usually cleaves into six petals from its centre along a whorled pattern in two series with three petals each, before or after the calyculus closed. Isomerous stamen primordia probably follow the same initiation pattern as petals do. Several carpels of different sizes initiate simultaneously as a united primordium. We support the hypotheses that the calyculus is of bract or bracteole origin due to its independent initiation from the inflorescence rachis, its similar morphology and positioning as the bract or bracteole, and that having no developmental relationship with the petals. We suggest keeping the usage of the term “calyculus”. *Loranthus* flowers should be considered monochlamydeous with three whorls of floral parts, namely petal, androecium, and gynoecium.

Keywords: Monochlamydeous; bract; calyculus; initiation; whorled pattern

1 Introduction

The hemiparasitic family Loranthaceae, in the sandalwood order Santalales, is a monophyletic group with ca. 76 genera and more than 1,000 species [1]. The flowers vary greatly in morphology and remain largely unexplored with several questions of homology unanswered [2]. The morphological diversity in the flowers of Loranthaceae is embodied in several aspects: there is a variety of inflorescence types in a basic form of dichasia and dichasial-derived partial inflorescences through Loranthaceae and other Santalalean families [3]; the great majority of flowers are bisexual while a few are unisexual; many showy members of this family possess colourful corolla with a specific banded pattern of a contrasting colour or colours [4]; the number of the undifferentiated perianth varies from four to eight; and both choripetalous and gamopetalous flowers are represented. Choripetalous flowers are usually actinomorphic while the symmetry of gamopetalous flowers is either actinomorphic or zygomorphic. Despite the various morphologies, the basic floral pattern is conserved in this family. Besides the outermost foliar structures, such as the bract, bracteoles, cupular pedicel, loranthaceous flowers are always subtended by a circular rim, known as a calyculus, positioned outside the petals. Inside the two whorls composed of the calyculus and petals are the stamen and carpels. Stamens are equal in number to the petals. The peculiar structure, the calyculus, is also found in other santalalean taxa, but controversies remain for its exact origin and identity.

Various hypotheses have been proposed to explain the calyculus. The earliest controversies can be traced back to the nineteenth century. Some taxonomists considered it to be an outgrowth of the floral axis without relation to the perianth [5-9]. Others, however, considered the calyculus to be equivalent to the calyx [10-15]. Endress [16], Nickrent and collaborators [4,17], Kuijit [18], and Suaza-Gaviria et al. [19] agreed with this view, interpreting the calyculus as a reduced calyx or as homologous with the calyx. By investigating the morphoanatomy of some neotropical species, Suaza-Gaviria et al. [19] suggested that the calyculus is an irregular calyx developed from an independent ring primordium. They further advocated that the use of the term calyculus should be abandoned, following Eichler [6,20].

Venkata Rao [21] conducted a comparative study on the inflorescences of Proteaceae and Loranthaceae, suggesting that the calyculus was a vestigial whorl of bracts in consequence of a reduction of lateral branch inflorescences from a highly branched ancestor. Wanntorp and Ronse De Craene [2] support the bracteolar origin of the calyculus differently: their conclusion relies on organogenesis evidence. They investigated the floral development in species of Loranthaceae, Santalaceae, Opiliaceae, and Olacaceae, which have been recognized as closely related in Santalales by molecular phylogenetic studies [22], and discussed the origin and evolution of the perianth in detail. Based on their observations of two species of American genera (*Struthanthus* and *Phthirusa*), the calyculus, initiating from two lateral primordia, is of bracteolate origin and has replaced the calyx.

In the present study, we examined an Asian species of *Loranthus*, *Loranthus tanakae* with standard light microscopy (LM) and scanning electron microscopy (SEM) methods. *Loranthus* consists of ca. 10 species mainly distributed in temperate and subtropical regions of Asia and Europe with six species in China [23]. It is a genus of glabrous shrubs with axillary or terminal spikes. The flowers are mostly bisexual, choripetalous with five or six petals, green, yellow, or white in colour, and are much smaller than their showy gamopetalous relatives. Flowers have isomerous stamens and an ovary with one locule. *L. tanakae* is mainly distributed in East Asia including China, Japan, and Korea, and has a relatively wide range of hosts. With a combination of previous studies, the developmental processes of its floral parts can complement the morphological and ontogenetic data in clarifying the origin and identity of the calyculus and other floral organs in Loranthaceae.

2 Material and Methods

2.1 Material Collection

The reproductive buds and inflorescences of *L. tanakae* were collected from natural forests of oak trees in Fengxian County, Shaanxi Province, China, every five days from March to May and from August to November in 2012 and 2013. Vouchers (FX12050001, ~03, ~05, ~11) of *L. tanakae* were deposited in the Herbarium of the Research Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry (CAF), Beijing, China.

2.2 SEM Observation

Fresh materials were fixed and stored in formalin-acetic-alcohol (FAA, 50% ethanol: acetic acid: formaldehyde = 89:6:5). The floral buds and inflorescences were dissected in 70% or 95% ethanol. For SEM investigation, materials were dehydrated through a graded series of ethanol:isoamyl acetate (1:0, 3:1, 1:1, 1:3, and 0:1) for 30 min each, critical-point dried in carbon dioxide using a Hitachi HCP-2, coated with gold palladium with a Hitachi E-1010 at 15 mA, and finally viewed and photographed with a Hitachi S-4800 SEM at 10.0 kV.

2.3 LM Observation

Fixed materials, firstly centrifuged with an Eppendorf Concentrator Plus, were dehydrated through a series of ethanol and xylene for 2 hours each time, then infiltrated and embedded in paraplast (40-60°C) for approximately 3-4 days prior to sectioning. Embedded materials were serially sectioned at 0.4 μm with a Kede KD-3358 microtome and mounted onto slides. Sections were stained in fast green and the

counterstain safranin, and finally viewed and photographed with a Zeiss Axio Imager. A1 fitted with a Zeiss AxioCam MRc5 digital camera.

3 Results

3.1 Development of the Calyculus and the Petals

Initiation of the inflorescences of *L. tanakae* in buds begins in August and lasts until the flowering season of the following year. Each spike bears 10-20 flowers (Fig. 1(A)) and blooms from May to June. A flower usually has five or six (occasionally four) petals, isomerous stamens, and an ovary with one locule (Fig. 1(B)). Characteristically, the flower is subtended by a persistent calyculus (Fig. 1(C)), as well as other species of *Loranthus* (Figs. 1(D)-1(F)).

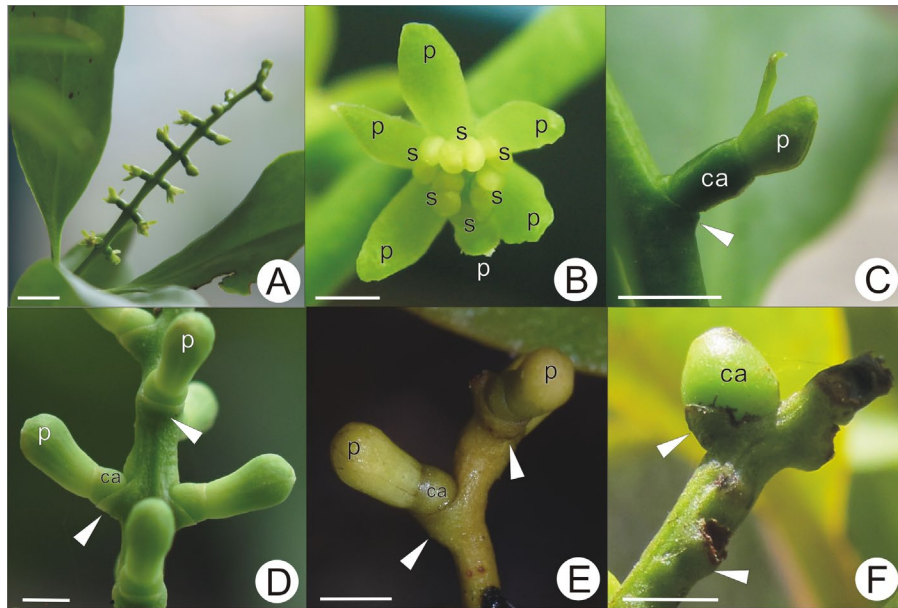


Figure 1: Inflorescences and infructescence of four species in *Loranthus*. (A) Flowering inflorescence of *L. tanakae*; (B) Top view of a mature flower of *L. tanakae*; (C) Lateral view of a bud of *L. tanakae* about to bloom; (D) Inflorescence of *L. guizhouensis*; (E) Inflorescence of *L. pseudo-odoratus*; (F) Infructescence of *L. delavayi*. Abbreviations: ca, calyculus; p, petal; s, stamen. Scale bars: 1 cm in A and F, and 2 mm in B-E

The semicircular calyculus primordium independently arises from the inflorescence rachis as a pioneer (Fig. 2(A)), followed by the initiation of a hemisphere flower primordium in its axil (Figs. 2(A)-2(B)). The calyculus soon extends laterally towards the axis (Figs. 2(C)-2(E)) with both sides eventually adnating toward each other on the adaxial side, forming a circular structure enclosing the young flower (Fig. 2(F)). Meanwhile, the flower primordium cleaves from the centre of its surface (Fig. 2(D)) before (Figs. 2(D)-2(F)) or after (Fig. 2(G)) the calyculus closed. Six petal primordia form along a whorled pattern in two series with three petals each (Figs. 2(D)-2(G)): the first series includes a top-adaxial petal and two latero-abaxial petals; the second series consists of the other three alternate petals (indicated by the series numbers in Figs. 2(D), 2(F), and 2(G)). Most often, five petals (Figs. 2(H)-2(I)) also cleave from the centre of the flower primordium before (Fig. 2(H)) or after (indicated by the solid arrow in Fig. 2(I)) the calyculus closed. Four-petaled flowers are occasionally observed (Fig. 2(J)). During later bud development, the calyculus continues growing upwards to become a cylinder (Figs. 1(C), 4(F)).

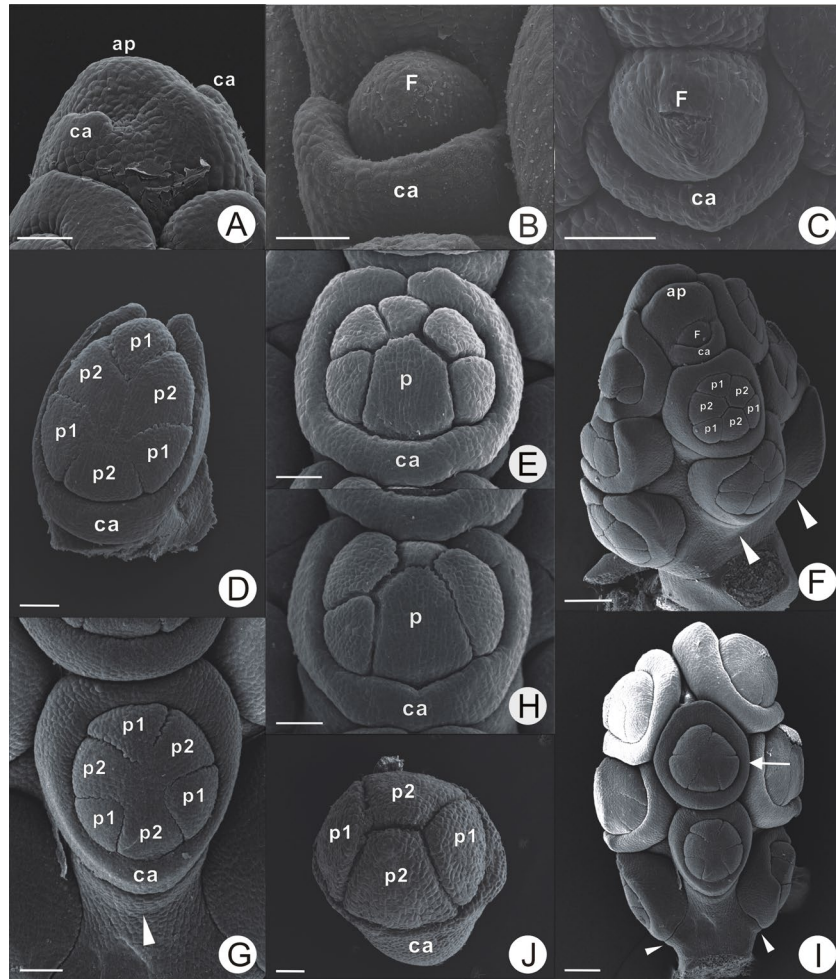


Figure 2: Initiation and development of the calyculus and the petals of *Loranthus tanakae*. (a) An apex of a young inflorescence with two calyculus primordia initiating from the rachis; (B) Lateral view of a flower primordium surrounded by a calyculus primordium; (C) Top view of a calyculus encircling the flower primordium; (D) Petal primordia cleaving from the flower centre before the calyculus closes; (E) Two sides of the calyculus about to join; (F) A young inflorescence with several flowers of different ages, showing the circular calyculus and completely separated petals inside; (G) Petals cleaving after the calyculus closed, showing a whorled pattern of the six petals in two series; (H) A flower with five separated petals and the encircling calyculus; (I) Flowers with six or five petals clustered in one inflorescence, showing the cleavage of the petals after the calyculus closed; (J) A flower with four petals. Abbreviations: ap, inflorescence apex; ca, calyculus; F, flower primordium; p, petal, numbers show initiation sequence of the two series of the petals. Scale bars: 100 µm in A-E, G, H and 200 µm in F, I-J

3.2 Development of the Androecium and the Gynoecium

Stamen primordia, the number equalling the petals, are initiated opposite to the petals (Figs. 3(A)-3(B)) and then differentiate into anthers and filaments (Figs. 3(C)-3(D)). An anther possesses two thecae, each bearing one anther sac (Figs. 3(C), 4(D)-4(E)). Each stamen is connected to a petal at the bottom of the filament (Figs. 3(D), 4(F)). A gynoecium primordium emerges in the centre of the flower, consisting of several carpels of unequal size (Fig. 3(E)). The circle of united carpels grows upwards, forming an angled hollow cylinder (Figs. 3(F), 4(C)). The rimose top of the gynoecium is soon closed in a later developmental stage (Fig. 3(G)). A mature style is angled with several concave dips on the stigma (Figs. 3(H)-3(I)).

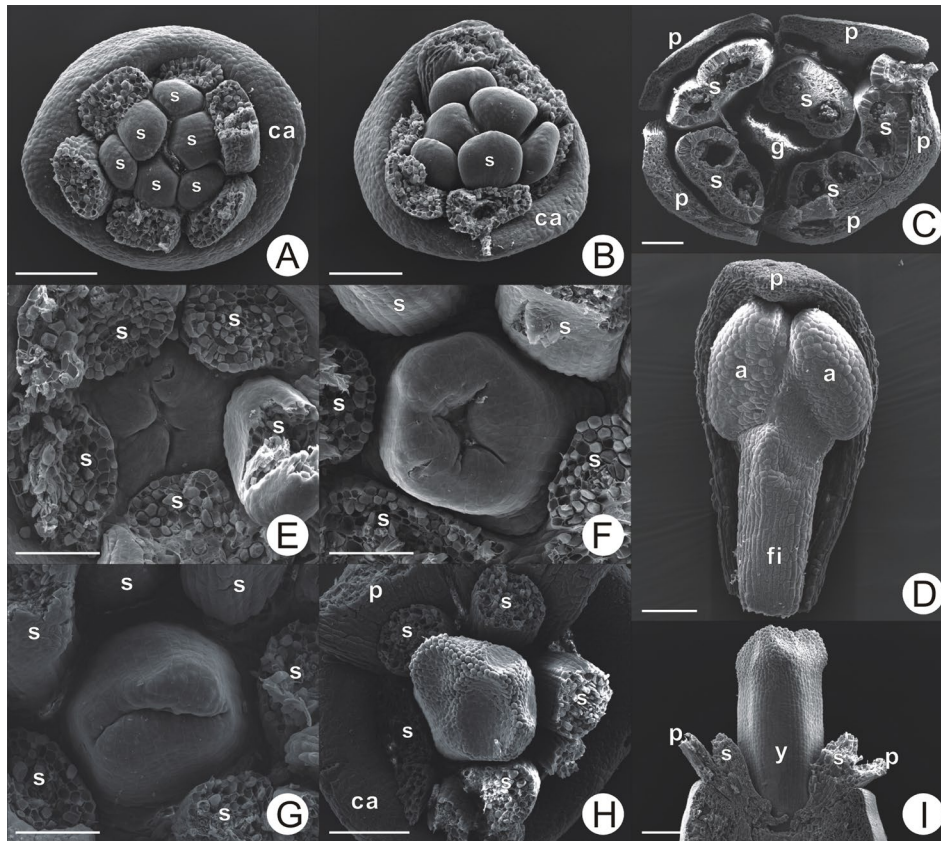


Figure 3: Initiation and development of the androecium and the gynoecium of *Loranthus tanakae*. (A) Six stamen primordia are initiated opposite the petals; (B) Elongating stamens in a later stage; (C) Transverse section through a flower bud, showing the two thecae of each stamen and one anther sac of each thecae; (D) Lateral view of a stamen covered by a petal, showing the anther and the filament; (E) Initiation of a gynoecium with several carpel primordia; (F) Elongating gynoecium; (G) The rimose top of the gynoecium is closing; (H) Top view of the stigma; (I) Lateral view of the angled style. Abbreviations: a, theca; ca, calyx; fi, filament; p, petal; s, stamen; y, style. Scale bars: 100 μm in E-G and 200 μm in A-D, H-I

3.3 Floral Vascular Bundles

The calyx is formed by an epidermal layer and a mesophyll with several layers of parenchymatous cells at the base (Figs. 4(A)-4(B)). No vascular bundles were observed in the calyx (Figs. 4(A)-4(B), 4(F)). Six (or five in five-petaled flowers) vascular bundles enter the common base of the petals and filaments (Figs. 4(A)), and then split into two traces: the outer traces enter the upper part of the petals and the inner traces to the stamens (Figs. 4(C)-4(E)). Occasionally, some petals are served by two vascular bundles (indicated by triangles in Fig. 4(C)). Several vascular bundles serve the gynoecium at its base but the number is uncertain (Figs. 4(A)-4(C), 4(F)).

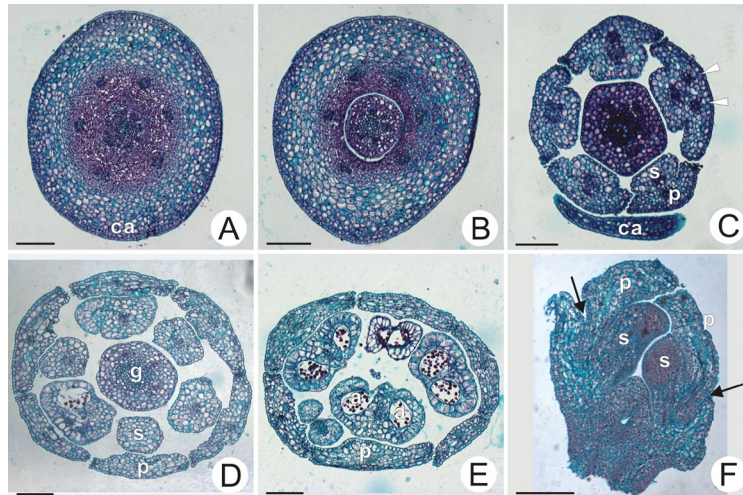


Figure 4: Floral anatomy of *Loranthus tanakae*. (A) Transverse section of the flower base; (B) An upper part of a flower bud with the split between the gynoecium and other floral whorls; (C) Transverse section of the middle part of a flower, showing the common base of the petal and filament, and the pentagonal base of the style; (D-E) Transverse sections of mature flowers with two thecae of each stamen; (F) Longitudinal section of a young flower; arrowheads indicate the boundaries between the calyculus and stamens. Abbreviations: ca, calyculus; g, gynoecium; p, petal; s, stamen. Scale bars: 200 μ m

4 Discussion

4.1 Bract

The existence of bracts and bracteoles is common in Loranthaceae, and most species have an inconspicuous and small bract while a few species, such as *Tolypanthus* and *Elytranthe* have large and showy bracts. The number of bracts and bracteoles varies and sometimes are used as diagnostic characters in distinguishing taxa (e.g., the tribe *Elytrantheae* and the tribe *Lorantheae*: the former was characterized by one bract and two bracteoles, and the latter by only one bract). The flower of *Loranthus* is usually considered to be subtended by a bract that is described as ovate, concave, ca. 1 mm [23]. In the present study, however, no bract primordium is initiated in the young inflorescences or observed in later developmental stages of *L. tanakae*. The pedicel is extremely short, like a protuberance outside the young flower on the abaxial side where a “bract” is thought to be located (identified by triangles in Figs. 2(F), 2(G), 2(I)), and then the pedicel becomes concave at the base of the mature flower (indicated by the triangle in Fig. 1(C)). Therefore, the structure previously known as a “bract” is merely a part of the pedicel rather than a separate organ. None of the other foliar structures, such as perophyll, prophyll, or cupular pedicel, were observed in *L. tanakae*. Among other species of *Loranthus*, that the protuberances of pedicel are more evident and slightly vary in shapes (indicated by the triangles in Figs. 1(D)-1(F)) might be the reason that they used to be regarded as a bract.

4.2 The Calyculus

The calyculus is present in all lorantheaceous flowers and other santalalean taxa such as in several genera of Olacaceae s.l., Schoepfiaceae, Opiliaceae, and Santalaceae s.l. [17], but its origin and identity are contentious. Three main views have been proposed to define the origin of the calyculus: an outgrowth of the floral axis; a calyx or being homologous with the calyx; and a bracteolar (prophyllar) origin. The view that the calyculus was an outgrowth of the floral axis was presented by some early researchers [6-9] but has been abandoned since the mid-20th century.

Most modern researchers believe that the calyculus has a close relationship with the calyx. Narayana [14] regarded the calyculus as a true calyx because his anatomical studies on *Nuytsia floribunda* showed

that the calyculus was supplied with vascular bundles. Maheswari et al. [13], who studied the floral morphology and embryology of the Lorantheoideae, and Agarwal [24] and Patil and Pai [25] who studied *Ola*, also held this view. Endress [16], Kuijt [18,26,27], and Nickrent and collaborators [4,17] interpreted the calyculus as a reduced calyx, following “a rule of thumb” in angiosperms that it is usually homologous with a calyx if only one series of perianth is present. Using LM and SEM methods, Suaza-Gaviria et al. [19] examined eight species from six genera, all native to the Colombian Andes. According to the positional and structural criteria of homology, they support Kuijt’s [18] view that neither cupule (= cupular pedicel) nor calyculus is foliar in origin so the terms of “cupule” and “calyculus” should be abandoned in Lorantheaceae, which is in agreement with Eichler [6,20].

A few authors support an alternative view of the bracteolar origin of the calyculus. Although Venkata Rao [21] raised this hypothesis, he mistakenly took Proteaceae and Lorantheaceae as relatives and made comparative morphological studies to draw this conclusion. In the context of a phylogenetic framework, Wanntorp and Ronse De Craene [2] investigated flowers in Santalales, providing floral ontogenetic evidence on two species of Lorantheaceae (*Struthanthus* and *Phthirusa*), which revealed that the calyculus initiated from two lateral primordia that extended laterally and rapidly connected on the adaxial side to form a continuous rim around the flower. The calyculus primordia were in the position of prophylls and did not follow the general development of a calyx. Therefore, Wanntorp and Ronse De Craene demonstrated that a calyculus, of bracteolate origin, has replaced the calyx.

Based on our newly presented evidence, we agree with Wanntorp and Ronse De Craene [2] that the calyculus should not be considered a calyx. Generally, the developmental processes of the calyculus are absolutely independent from other floral organs. First, the calyculus directly arises from the inflorescence rachis rather than from a floral primordium. It is outside the flower without being a part of it. The flower primordium initiates in the axil of the calyculus and then differentiate floral organs such as petals. The calyculus has similar morphology and is located in the same position as a bract or a bracteole. Secondly, the calyculus arises as a single primordium and then forms a rim structure by an adnation of both sides on the adaxial side, independent of whether or not the petals have cleaved. In other words, there are no quantitative, spatial, and temporal relations between the calyculus and the petals, indicating that the calyculus is probably of bract or bracteole origin. Moreover, the calyculus is poorly vascularised while other floral parts are served by well developed vascular bundles, consistent with the results for neotropical taxa [19].

Suaza-Gaviria et al. [19] examined eight loranthaceous species of neotropical taxa, and gained the results for floral organogenesis for six species, with only one species, *Gaiadendron punctatum* exhibiting the initiation and completely developmental processes of the calyculus. The calyculus was described as a ring meristem in all the flowers they examined, yet some of their SEM photographs clearly showed that the calyculus initiate as a semicircular primordium, positioning outside of the floral primordium, and then expand to become a ring meristem in a later stage (see *G. punctatum* in their Figs. 6(A) and 6(B), and *Passovia pedunculata* Kuijt in Fig. 9(D)). The developmental processes of the calyculus in *G. punctatum* and *P. pedunculata* resemble what we have observed in *L. tanakae*. Similar situations were also observed by Wanntorp and Ronse De Craene [2] (see their Figs. 4(C)-4(D), 5(B), 5(C), and 5(E)). Now that scholars have not reached a consensus on the origin of the calyculus, though no substantive disagreement exists between different studies, the authors recommend that follow this term, calyculus, until new evidence from different disciplines than morphology or anatomy could be obtained.

4.3 Petals

The stamens of *Loranthus* are numerically equal to the petals and likely follow the same initiation pattern as two series with three stamens in each because of their triangular arrangement and different sizes (Figs. 3(A)-3(B)). Wanntorp and Ronse De Craene [2] indicated that the stamens form two trimerous whorls of distinct sizes in *Struthanthus* sp. and *Passovia pyrifolia* (\equiv *Phthirusa pyrifolia*). Suaza-Gaviria et al. [19] also described the unequal stamens with three long stamens alternate to three short stamens in early developmental stages in *Psittacanthus acinarius*, *Oryctanthus callicarpus*, *Passovia pedunculata*,

and *P. pyrifolia*. Being uniform in size was considered to be plesiomorphic for stamens in Loranthaceae. However, it seems that the stamen primordia do not initiate simultaneously or follow an exactly one-whorled initiation pattern, rather shifting back to equal sizes by anthesis. Both petals and stamens suggest that possible merosity in *Loranthus* and other six-petaled loranthaceous flowers is trimerous. The carpels of six-petaled loranthaceous flowers are usually interpreted as three, in accordance with the trimerous petals and stamens. In the present study, however, the number of carpels is indeterminate, served by several vascular bundles which are also indeterminate (Figs. 4(A)-4(D)). Several carpels of different sizes initiate simultaneously as a ring-shaped primordium with two to five lobes inward (Figs. 3(E)-3(F)). The hollow of the circle is eventually closed to form a stigma with several depressions on its surface (Fig. 3(H)). Therefore the number of carpels is not necessarily three but indeterminate.

5 Conclusions

Our observations indicate that bracts are not present in *L. tanakae* and the structure previously known as a “bract” is the extremely short pedicel. We support the hypotheses that the calyculus is of bract or bracteole origin, and suggest the trimerous whorled initiation pattern of petals and stamens. Therefore, the flower of *Loranthus* should be considered monochlamydeous with three whorls of floral parts, namely, petal, androecium, and gynoecium.

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