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CONNATE OVARIES AND MULTIPLE FRUITS IN RUBIACEAE, WITH REDUCTION OF *CONJUGATOVARIUM* TO SYNONYMY WITH *MITCHELLA* (RUBIACEAE – MITCHELLEAE)

E. Robbrecht* & B. Verstraete

Multiple fruits are rare in Rubiaceae, occurring in only 14 genera. They have evolved in different ways in phylogenetically distant clades. We present a survey of all known occurrences of multiple fruits in the family. Leaving aside the poorly known genus *Pagameopsis*, we distinguish four types: (i) double or multiple drupes resulting from fusion of neighbouring ovaries (Prismatomerideae, Mitchelleae and Morindeae), (ii) dry fruits resulting from partial fusion of a flower pair (*Calanda* in Knoxieae), (iii) dry multiple fruits dehiscing by an operculum (Anthospermeae – Operculariinae), and (iv) massive fleshy, woody or fibrous globose multiple fruits formed by expansion of the inflorescence tissue embedding numerous ovaries (Naucleeae). Based on this framework, we evaluated the systematic position of the Taiwanese genus *Conjugatovarium*, characterised by paired flowers with connate ovaries. Comparison of the characters excludes affinity with most lineages possessing multiple fruits due to major differences in habit, floral and fruit morphology, and biogeography. However, *Conjugatovarium lalashanianum* matches *Mitchella undulata* in all morphological characters, and both taxa co-occur in northern Taiwan. We formally place *Conjugatovarium* in synonymy with *Mitchella* and treat *C. lalashanianum* as *M. undulata*.

Keywords. *Calanda*, Morindeae, Naucleeae, Operculariinae, *Pagameopsis*, Prismatomerideae, Schradereae, syncarps, Taiwan, taxonomy.
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Introduction

Generic delimitation within Rubiaceae has been a subject of taxonomic scrutiny due to the family's morphological diversity and complex evolutionary history. Recent efforts to compile and evaluate all generic names in Rubiaceae (Verstraete *et al.*, 2025) revealed several taxa that warrant closer attention because of uncertain affinities or insufficient documentation. Earlier contributions resulting from this work have clarified the taxonomic history and nomenclature of *Anthospermum* (Robbrecht & Verstraete, 2025) and *Caelospermum* (Verstraete & Robbrecht, 2025).

In continuation of this series, we investigate *Conjugatovarium* S.S.Ying, a monospecific genus described from Taiwan (*C. lalashanianum* S.S.Ying) and currently treated as endemic to that island (Ying, 2023). The genus was established solely on morphological grounds with only a brief comparison, stating that it is "somewhat like the genus *Damnacanthus* C.F.Gaertner" but differs by being "a minute smooth herb" (Ying, 2023). In our earlier

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overview (Verstraete *et al.*, 2025), we tentatively placed *Conjugatovarium* in the tribe Mitchelleae, following the implied affinity with *Damnacanthus* C.F.Gaertn., although this placement was made with reservation due to limited evidence and lack of a comparative analysis.

A remarkable feature of *Conjugatovarium* is reflected in its name: the ovaries of the two terminal flowers are fused (Latin *conjugo*, 'to unite', and *ovarium*, 'ovary'). Such connate ovaries are known to occur in Rubiaceae (Robbrecht, 1988) but are extremely rare. It has been recorded in only scattered and phylogenetically unrelated lineages. Despite the potential diagnostic relevance of this character, Ying (2023) did not compare *Conjugatovarium* with other Rubiaceae exhibiting similar connate ovaries, leaving its actual affinity unresolved.

To clarify the position of *Conjugatovarium* within Rubiaceae, we therefore undertake a survey of connate ovaries and multiple fruits across the family. By comparing this particular feature in *Conjugatovarium* with similar occurrences elsewhere in Rubiaceae, we aimed to reassess its tribal placement and evaluate whether its recognition as a distinct genus is justified.

Terminology

Roth (1977) defined "collective or multiple fruits" as fruits composed of several to many flowers and originating from an inflorescence. Souza (2022) followed this definition of "multiple fruits"; it aligns with the cases of Rubiaceae presented in the present article, and we therefore adopt this term.

In Rubiaceae literature, multiple fruits have traditionally been referred to as "syncarps" (e.g. Ridsdale, 1978; Johansson & Wong, 1988; Robbrecht, 1988; Mouly & Fleurot, 2021; Ntore & Lachenaud, 2022). Razafimandimbison *et al.* (2009) used "syncarps or multiple fruits", whereas Razafimandimbison *et al.* (2012) and Löfstrand *et al.* (2014) used the term "multiple fruits". The term 'syncarp' is potentially misleading in this context. In floral morphology, syncarpy (= coenocarpy) refers to the fusion of carpels within a single flower (Leins & Erbar, 2010), a condition that is universal in Rubiaceae. Therefore, strictly speaking, syncarpy describes a situation within a single flower, and the term would be more accurate as 'syncarpelly'.

Materials and methods

We surveyed the occurrence of connate ovaries and multiple fruits in Rubiaceae, based on published literature (e.g. Robbrecht, 1988) and unpublished morphological observations by the authors (E.R.). All taxa reported to possess these characters were compiled, and their tribal placement was indicated on a simplified phylogenetic tree of Rubiaceae based on Razafimandimbison & Rydin (2024). This allowed us to assess the phylogenetic distribution of these characters across the family. The resulting data were then compared with the morphological and biogeographical information provided in the protologue of *Conjugatovarium* (Ying, 2023) in order to infer its possible affinity. Herbarium material of *Conjugatovarium* was not available for study, and observations were therefore restricted to the original description and the accompanying illustrations (Ying, 2023).

Conjugatovarium lalashanianum is known only from the holotype collected at Lala Shan in northern Taiwan (Ying, 2023). Because no coordinates were provided in the protologue, we used the approximate locality of the collection site, corresponding to the Lala Shan National Forest Recreation Area (24°42'41"N, 121°25'60"E). Georeferenced occurrence records were obtained from GBIF for *Mitchella undulata* Siebold & Zucc. (GBIF.org, 2025). The maps were generated in R v.4.4.2 with ggplot2 v.3.5.1 (Wickham, 2016), using vector tiles provided by Stadia Maps (https://stadiamaps.com) and OpenMapTiles (https://openmaptiles.org), and geodata by OpenStreetMap (https://www.openstreetmap.org).

Results and discussion

Connate ovaries and multiple fruits in Rubiaceae

Multiple fruits are rare in Rubiaceae, occurring in only 14 out of approximately 620 currently accepted genera. Aggregate fruits (derived from a single flower; Roth, 1977) are absent from Rubiaceae.

The scattered distribution of multiple fruits across the family (**Figure 1**) indicates multiple and different independent origins, but there is notable concentration within two major lineages of subfamily Rubioideae: the Psychotrieae and Spermacoceae alliances (*sensu* Razafimandimbison & Rydin, 2024). In subfamily Dialypetalanthoideae, multiple fruits occur only in four genera of tribe Naucleeae. Within the Psychotrieae alliance, they are confined to the clade (Schradereae (Prismatomerideae (Morindeae, Mitchelleae))), hereafter referred to as the SPMM clade, which contains seven genera with connate ovaries and multiple fruits. In the Spermacoceae alliance, the feature is even rarer and found only in the genus *Calanda* K.Schum. (tribe Knoxieae) and in two genera of subtribe Operculariinae of tribe Anthospermeae. Connate ovaries are also reported for *Pagameopsis* Steyerm. (Piesschaert *et al.*, 2001; Taylor, 2025), a genus of uncertain position (Razafimandimbison & Rydin, 2024). Mapping these occurrences onto the phylogenetic tree of Razafimandimbison & Rydin (2024) indicates that multiple fruits have evolved independently within the family at least four times (**Figure 1**). Note that multiple fruits were not considered in analyses of fruit evolution in Rubiaceae (Eriksson & Bremer, 1991; Bremer & Eriksson, 1992). Occasional fusion of neighbouring ovaries in an otherwise normal inflorescence has been reported for *Psychotria* L. (Piesschaert *et al.*, 2001); however, such teratological cases probably occur in many genera, so the phenomenon is not considered in this paper.

Figure 1. Simplified phylogenetic tree of Rubiaceae (after Razafimandimbison & Rydin, 2024), showing (in bold) the tribal placement of 13 genera with connate ovaries and multiple fruits. A 14th taxon, *Pagameopsis* (*incertae sedis*) is not shown.

Prismatomerideae. Tribe Prismatomerideae comprises only two genera, *Rennellia* Korth. and *Prismatomeris* Thwaites, both woody taxa distributed in tropical Asia (Razafimandimbison *et al.*, 2021). Their morphology and anatomy were thoroughly examined by Igersheim & Robbrecht (1993), who documented the occurrence of connate ovaries in both genera. In many species, the ovaries of neighbouring flowers are completely or at least partially connate, with clusters of 2 to c.10 flowers united in this way (**Figure 2**A). This fusion results in the development of multiple drupes.

Mitchelleae. Tribe Mitchelleae consists of two genera, *Mitchella* L. and *Damnacanthus* C.F.Gaertn., which were placed far apart in earlier classifications of Rubiaceae. Their

Figure 2. Connate ovaries and multiple fruits in Rubiaceae: A, *Rennellia elliptica* Korth., cluster of three flowers with connate ovaries; B, *Mitchella undulata*, connate ovaries with calyces; C, *Mitchella undulata*, double drupe with remnants of two calyces; D, *Morinda citrifolia*, multiple drupe; E, *Calanda* (*Pentanisia rubricaulis*), infructescences; F, *Pomax umbellata* (Gaertn.) Sol. ex A.Rich., pseudo-umbel with multiple fruits topped with an operculum; G, *Nauclea pobeguinii* (Pobég.) Merr., globose multiple fruit with a corolla remnant; H, *Schradera morindoides* C.M.Taylor, congested inflorescence with non-connate buds. Photographs reproduced with permission: A by Lars Mannzen; B from Robbrecht *et al.* (1991: figure 6G); C by esdena; D by juju98; E by Rogerio Ferreira; F by Timothy Duncan; G by Patricia Barberá; H by John L. Clark.

close relationship was first demonstrated by Robbrecht *et al.* (1991), through a detailed morpho-anatomical study, and later confirmed by molecular phylogenetic analysis of subfamily Rubioideae (Andersson & Rova, 1999). Finally, tribe Mitchelleae was described to accommodate the two genera (Razafimandimbison *et al.*, 2008).

The genus *Mitchella* comprises two species of creeping herbs: *M. repens* L. from North and Central America, and *M. undulata* from East Asia – a remarkable disjunction discussed by Huang *et al.* (2013). In *Mitchella*, pairs of 2-locular ovaries are connate, forming a 4-carpellate fused structure in which the two calyces remain distinct (**Figure 2B**; Robbrecht *et al.*, 1991: figure 6G). The fruit is a double drupe, crowned by two persistent calyces and containing two groups of four pyrenes (**Figure 2C**). In this way, *Mitchella* shares similarities with some species of *Lonicera* L. (Caprifoliaceae), in which after the loss of the central flower of a triplet, partial or complete fusion of the ovaries of the remaining flower pair takes place (Srivastav *et al.*, 2023). Robbrecht *et al.* (1991) also postulated that in *Mitchella* the paired flowers result from the loss of the central flower of a 3-flowered cyme. This hypothesis is supported by the occasional occurrence of a minute remnant of an axis between the two flowers, only observable in a very young stage of development.

Damnacanthus differs in being a small evergreen shrub with heterophyllous leaves and, in many species, paired thorns (Robbrecht *et al.*, 1991: figure 2A). Its floral morphology closely resembles that of *Mitchella*; however, the ovaries are not connate. The frequent occurrence of flowers in pairs suggests a structural resemblance with *Mitchella*, indicating that the connate flower pairs in *Mitchella* and the non-connate but paired condition in *Damnacanthus* may be considered as homologous.

Morindeae. Tribe Morindeae is pantropical and comprises five genera: *Appunia* Hook.f., *Caelospermum* Blume, *Gynochthodes* Blume, *Morinda* L. and *Siphonandrium* K.Schum. (Razafimandimbison *et al.*, 2009). Connate ovaries and multiple fruits are widespread in the tribe, except in *Appunia* and *Siphonandrium*. Fusion may involve only two ovaries or as many as 50, forming prominent multiple drupes, most conspicuously in *Morinda citrifolia* L. (vernacular name noni) (**Figure 2D**). The generic name *Morinda* alludes to this structure (Latin *morum*, vernacular name 'mulberry') (Verstraete *et al.*, 2025).

Razafimandimbison *et al.* (2012) provided a detailed analysis of the evolution of multiple fruits in Morindeae, examining 61 species in total; 90% of these bear multiple fruits. They also reported reversals from multiple to simple fruits, apparently linked to shifts in dispersers – multiple fruits for larger animals, and simple fruits for birds.

Schradereae. Tribe Schradereae is monogeneric, containing only *Schradera* Vahl, a genus of shrubs with a disjunct distribution in tropical America and Malesia (Puff *et al.*, 1998). Puff *et al.* (1993) documented its distinct morpho-anatomy: species bear compact pseudanthia of numerous small, sessile flowers within an involucre, superficially resembling the multiple heads of *Morinda* (**Figure 2H**). However, the ovaries remain entirely free, each developing into a single berry. Schradereae is included here because its highly congested inflorescences may represent an evolutionary precursor to connate ovaries. Its position as sister to the remainder of the SPMM clade (**Figure 1**) supports this hypothesis. It is also in line with the observation that the degree of ovary fusion prior to fruit development varies greatly from only a basal fusion of the ovaries to completely fused ovaries. Basal fusion followed by further fusion during fruit development was reported for *Breonia* A.Rich. (Razafimandimbison, 2002) and *Gynochthodes* and *Morinda* (Razafimandimbison *et al.*, 2012).

Calanda (Knoxieae). Within the morphologically diverse tribe Knoxieae, connate ovaries are known only from the monospecific Angolan genus *Calanda* K.Schum. (Puff & Robbrecht, 1989), synonymised with *Pentanisia* Harv. as *P. rubricaulis* (K.Schum.) Kårehed & B.Bremer (Kårehed & Bremer, 2007). This perennial subshrub shows a striking deviation from the typical floral structure that characterises the uniovulate Knoxieae (Puff & Robbrecht, 1989). In Knoxieae, flowers are often paired, but the pairs are not homologous to the terminal flower pairs of *Mitchella*. Here, they are in a lateral position and helicoidally arranged on inflorescence axes. This results from unequal promotion of lateral elements of the basically thyrso-paniculate inflorescence, as documented for *Otiophora* Zucc. (Puff, 1983).

The paired flowers of *Calanda* possess bilocular ovaries in which one locule is reduced and sterile, and the calyx lobes are reduced, except for one enlarged lobe crowning the sterile locule. The strongly congested inflorescences consist of numerous flower pairs fused by inflorescence tissue and their sterile locules. This connate structure can erroneously be interpreted as a bilobed bract. The two fertile ovary locules sit on the 'bract' but remain free from one another. The whole structure develops into a double dry fruit, composed of the 'bract' and two free mericarps each with one seed. The inflorescences and infructescences are so strongly congested that the arrangement of the flower pairs can no longer be deduced. The fertile locules are hidden on the adaxial side of the 'bracts'; an outside observation (**Figure 2E**) shows only the 'bracts'. For detailed morpho-anatomical documentation, see Puff & Robbrecht (1989), in particular their figures 1d–f, 16 and 17.

Anthospermeae – Operculariainae. Within tribe Anthospermeae, the Australian subtribe Operculariainae comprises three genera: *Opercularia* Gaertn., *Pomax* Sol. ex DC. and *Eleuthranthes* F.Muell. ex Benth. (Puff, 1982). *Opercularia* and *Pomax* are perennial herbs or subshrubs characterised by partial inflorescences – arranged in pseudo-umbels in *Pomax* – that are composed of three or more flowers with connate ovaries. These produce dry multiple fruits that open through the abscission of an apical operculum, which is formed by the fused apical portions of the individual fruits and sheds as a single unit (**Figure 2F**). The third genus, *Eleuthranthes*, is poorly known and lacks evidence of connate ovaries. A more detailed morpho-anatomical investigation of Operculariainae is needed. A recent paper describing a new species of *Pomax* (Ngugi, 2022) contains a vague carpological description wrongly naming the multiple fruit a 'pome' or an 'operculate capsule'.

Naucleeae. The cosmopolitan tribe Naucleeae comprises woody taxa, including the tallest trees in Rubiaceae, such as *Nauclea diderrichii* (Laurent) Merr. (vernacular name opepe), valued for its high-quality timber (Robbrecht, 1994). The tribe is typically characterised by dense, globose heads bearing countless numbers of flowers on a common receptacle (Ridsdale, 1978). In the past, the remarkable inflorescences and fruits of Naucleeae were used to justify its segregation as a separate family, Naucleaceae, but this view is no longer accepted (Robbrecht, 1993).

In most genera, the ovaries remain free, and the heads mature into a cluster of free fruitlets (e.g. *Ludekia* Ridsdale). However, in nearly all species of the two genera *Breonia* (subtribe Breoniinae) and *Nauclea* L. (subtribe Naucleinae), the heads develop into massive, fleshy globose multiple fruits (**Figure 2G**) and the ovaries are embedded in expanded inflorescence tissue, as in pineapples (*Ananas comosus* (L.) Merr.) or members of Moraceae. Two genera of subtribe Adininae, *Myrmeconauclea* Merr. and *Ochreinauclea* Ridsdale & Bakh.f., were described as producing "pseudosyncarps" (Ridsdale, 1978) or "pseudomultiple fruits" (Löfstrand *et al.*, 2014; Razafimandimbison & Bremer, 2002; Razafimandimbison *et al.*, 2005), in which the tissues of the upper part of the ovary and the lower part of the calyx are fused. During maturation, the connecting tissue extends between the ovaries and becomes fibrous or only slightly woody, leaving the individual cocci still distinguishable. These fruits still meet the morphological definition of multiple fruits, and the distinction between pseudo- and true multiple fruits seems unnecessary in a Rubiaceae context.

Pagameopsis. The genus *Pagameopsis* contains only two species restricted to the Guiana Shield (POWO, 2025). Although it belongs to Rubiaceae, its placement within the family is *incertae sedis* (Razafimandimbison & Rydin, 2024; Verstraete *et al.*, 2025). The ovaries of adjacent flowers are mostly fused, forming clusters of two or three flowers (Piesschaert *et al.*, 2001). Figures 8 and 12 in the latter publication show a weak fusion of the outer layers of the ovaries, with the later endocarps clearly delineated. The fruits are dry and indehiscent. Piesschaert *et al.* (2001) had no fully mature fruits available and gave no information on the degree of fusion in the fruiting stage. Taylor *et al.* (2004) describes the fruits as drupaceous, "sometimes fused to the other fruits". Whether the fruits are fleshy or dry is not entirely clear (Taylor, 2025).

Comparison of Conjugatovarium *with Rubiaceae having connate ovaries*

The survey provides a comparative framework for assessing the systematic position of *Conjugatovarium* among Rubiaceae with multiple fruits. Most genera can be excluded as potential close relatives based on clear discrepancies in life form or fruit morphology (Table). In addition, many taxa with multiple fruits occur in regions that are biogeographically incompatible with the distribution of *Conjugatovarium*, which is endemic to Taiwan. Only *Mitchella*, and in particular the East Asian species *M. undulata*, shares several characters with *Conjugatovarium*, including paired flowers, connate ovaries forming double fruits, and a similar general habit. We therefore consider *Mitchella undulata* as the sole plausible candidate for a close relationship with *Conjugatovarium*.

The descriptions and illustrations in the protologue of *Conjugatovarium lalashanianum* correspond in all characters to those of *Mitchella undulata* as documented by Robbrecht *et al.* (1991) and in the *Flora of Taiwan* (Liu & Yang, 1998) and the *Flora of China* (Chen & Taylor, 2011). A direct comparison of the characters reveals no consistent morphological differences between the two taxa. The quantitative characters all overlap. The descriptions in the Floras and the protologues also share important qualitative characters, such as

Table. Morphological and biogeographical similarities (bold) and differences between *Conjugatovarium* and Rubiaceae with connate ovaries and multiple fruits

Taxon (genera with connate ovaries/total no. of genera)	Morphological and biogeographical characters
Conjugatovarium	Creeping herb
	Paired flowers with connate ovaries, double drupes
	Endemic to Taiwan
Prismatomerideae (2/2)	Woody plants
	Multiple drupes resulting from the fusion of 2–10 ovaries
	Tropical Asia
Mitchella (Mitchelleae 1/2)	**Creeping herbs**
	Paired flowers with connate ovaries, double drupes
	***M. undulata* reported from Taiwan**
Morindeae (4/5)	Woody plants (trees, lianas, shrubs and geofrutices)
	Multiple drupes resulting from the fusion of a high numbers of ovaries
	Pantropical
Calanda (Knoxieae 1/17)	Perennial subshrub
	Double dry fruit composed of a bract-like fusion of 2 sterile carpels bearing 2 free mericarps
	Endemic to Angola
Anthospermeae – Opercularinae (2/3)	Perennial herbs or subshrubs
	Dry multiple fruits, composed of 3 or more ovaries, opening with an operculum
	Endemic to Australia
Naucleeae (4/18)	Tall woody plants, some of them even dominant rain forest trees
	Globose multiple fruits composed of numerous free or partly connate ovaries embedded in expanded inflorescence tissue
	Cosmopolitan
Pagameopsis	Small shrubs
	2 or 3 ovaries connate; dry, indehiscent fruits
	Endemic to the Guiana Shield

the shape of the leaf blades and their bases, which is truncate to slightly cordate, and the 4-merous flowers with lobes villous inside. In addition, the occurrence of *Mitchella undulata* in Taiwan is confirmed in the *Flora of Taiwan* (Liu & Yang, 1998), and the species is recorded from localities near the type locality of *Conjugatovarium lalashanianum* (Figure 3). All available evidence indicates that *Conjugatovarium lalashanianum* should be synonymised with *Mitchella undulata*.

Conclusion

Our survey shows that multiple fruits are phylogenetically scattered in Rubiaceae and morphologically diverse; they are not homologous and result from fusion of ovaries or

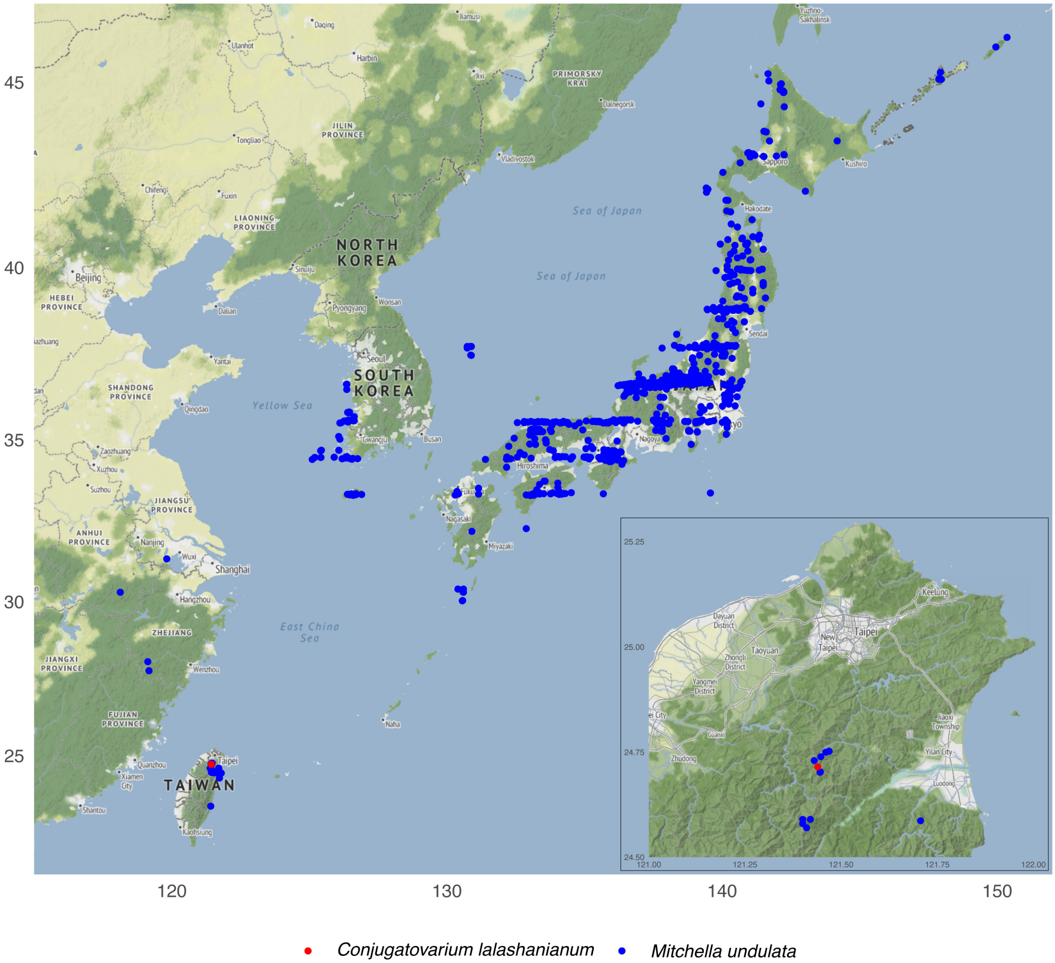

Figure 3. Distribution of *Mitchella undulata* (blue dots). The red dot indicates the type locality of *Conjugatovarium lalashanianum*. Inset: northern Taiwan.

inflorescence tissues, or a combination of both. Within this framework, the supposed distinct genus *Conjugatovarium* falls well within the morphological variation of *Mitchella*. Detailed comparison reveals that *Conjugatovarium lalashanianum* is indistinguishable from *Mitchella undulata* in habit and floral and fruit morphology, and both taxa occur sympatrically in northern Taiwan. We therefore place *Conjugatovarium* in synonymy with *Mitchella* and treat *C. lalashanianum* as *M. undulata*.

Taxonomic treatment

Tribe Mitchelleae Razafim. & B.Bremer

Mitchella L., Sp. Pl. 1: 111 (1753)
Conjugatovarium S.S.Ying, New Taxa & New Names 6: 1 (2023), **syn. nov.**

Mitchella undulata Siebold & Zucc., Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 4(3): 175 (1846). – Type: Japan, In Japonia, *s.d.*, *Bürger H s.n.* (lectotype M [M0154188], designated by Akiyama *et al.*, 2017: 138).
Conjugatovarium lalashanianum S.S.Ying, New Taxa & New Names 6: 3 (2023), **syn. nov.** – Type: Taiwan, Taoyuan City, Fuhsin District, Lalashan, 2150 m, 3 vi 2023, *Ying S.S. s.n.* (holotype NTUF).

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