EDINBURGH JOURNAL OF BOTANY 82, Article 2028:
1–9 (2025). https://doi.org/10.24823/EJB.2025.2028

Published by the Royal Botanic Garden Edinburgh
ISSN (online): 1474-0036, ISSN (print): 0960-4286

# *BOURNEA* IS NOT SUPPORTED AS SEPARATE FROM *OREOCHARIS* (GESNERIACEAE)

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The genus *Bournea* Oliv., established in 1893 and comprising two morphologically very similar species with actinomorphic flowers, was included in *Oreocharis* Benth. in 2011, essentially based on molecular data. However, a recent publication has suggested that *Bournea* should be maintained as a genus distinct from *Oreocharis*, based on morphological, palynological and DNA sequence data. By contrast, in another recent publication also based on DNA sequences, *Bournea* is placed within *Oreocharis*. The morphological, palynological and published molecular phylogenetic data are discussed here. The conclusion is that the overall evidence available is insufficient to support an independent genus, *Bournea*.

*Keywords*. *Bournea*, China, molecular phylogeny, morphology, *Oreocharis*, phylogeny, synonymy, taxonomy.
Received 5 February 2024 Accepted 4 December 2024 Published 25 March 2025

## Introduction

The small Chinese genus *Bournea* Oliv. has had an eventful history. The genus was described on the basis of a single species, *Bournea sinensis* Oliv. (Oliver, 1893), and it took almost 100 years before a second species, *Bournea leiophylla* (W.T.Wang) W.T.Wang & K.Y.Pan, originally described as *Chirita leiophylla* W.T.Wang, was included in the genus (Wang *et al.*, 1990). Both species are small rosette plants and are remarkable for having actinomorphic, 4- or 5-merous white flowers.

The first to question the monophyly and justification of the genus were Wang *et al.* (2010) in a molecular phylogenetic study of Old World Gesneriaceae with actinomorphic flowers. Based on an analysis of *trn*L–F and ITS sequences, they found that *Bournea sinensis* was sister to species of *Ancylostemon* Craib (the genus is now in *Oreocharis* Benth.; Möller *et al.*, 2011a) and that *B. leiophylla* was nested within a group of *Oreocharis* species. In a later study focusing on *Oreocharis* and using the same markers and the same sequences for *Bournea leiophylla*, Möller *et al.* (2011a) came to the same conclusions and synonymised *Bournea* (together with nine other Chinese genera) under *Oreocharis*.

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Recently, Chen *et al.* (2020) carried out a new molecular analysis, using six chloroplast regions and the nuclear ribosomal ITS region. These authors presented palynological data in (putative) support of their morphological and molecular data. Their results were in disagreement with the results obtained by Wang *et al.* (2010) and Möller *et al.* (2011a): the two *Bournea* species were sister to each other and formed a sister clade to the remaining species of *Oreocharis* included in their study. In consequence, the authors advocated for the re-establishment of *Bournea*. However, Kong *et al.* (2022) published a phylogeny, based on multiple nuclear genes, in which the two *Bournea* species were again firmly placed within *Oreocharis*, supporting the taxonomic decision of Möller *et al.* (2011a).

In the present paper, the results of the studies mentioned above are discussed and the case is made for not supporting *Bournea* as a separate genus.

## The case for inclusion of *Bournea* in *Oreocharis*

### *Morphology*

The two species of *Bournea* are perennial acaulescent plants with long-petiolate ovate or elliptic leaves, long-stalked (scapose) umbelliform to spherical pair-flowered cymes, long bracteoles, and actinomorphic (regular, rotate) flowers that are white. The lobes of the corolla are scarcely longer than the calyx lobes and are fused in the lower part. Their position is almost upright erect, thus forming a rather narrow funnel. The stamens are long exserted and bear a small anther at the tip. *Bournea sinensis* usually has 4-merous flowers and *B. leiophylla* 5-merous flowers, but there is much variation and overlap. The number of corolla lobes is always paralleled by the number of calyx lobes and stamens, the flowers consequently being genuinely actinomorphic. There is now a consensus that in Gesneriaceae, taxa with actinomorphic flowers have developed repeatedly and independently from ancestors with zygomorphic flowers (Burtt, 1970; Wang *et al.*, 2010; Möller *et al.*, 2011a, 2011b).

The inclusion of *Bournea* in *Oreocharis* (Möller *et al.*, 2011a) rests primarily on molecular data, supported by a shared vegetative and fruit morphology (rosette plants with spirally arranged leaves, and loculicidal, bivalved capsules, usually long and cylindrical, occasionally ovoid). The actinomorphic flowers with “dissected corollas” in *Bournea* are very similar in *Thamnocharis esquirolii* (Lévl.) W.T.Wang (Chen *et al.*, 2020), which is nested deep in *Oreocharis* (as *Oreocharis esquirolii* Lévl. in Möller *et al.*, 2011a). Apart from the character of actinomorphic flowers, which has been shown to have evolved several times from ancestors with zygomorphic flowers (Wang *et al.*, 2010; Möller *et al.*, 2011b) and does not necessarily support distinct lineages, vegetative and floral characteristics do not separate *Bournea* from *Oreocharis*.

## *Molecular data*

Wang *et al.* (2010) and Möller *et al.* (2011a) generated data for two DNA sequences (*trn*L–F and ITS of, respectively, 9 and 39 out of 157 accepted *Oreocharis* species [GRC, 2024]) and, based on their analyses, reached the same conclusion: the two *Bournea* species were not closely related and were separately nested in *Oreocharis* (although referred to by Wang *et al.*, 2010, as *Ancylostemon*, a genus synonymised into *Oreocharis* by Möller *et al.*, 2011a). Kong *et al.* (2022) used 574 nuclear orthologous genes to reconstruct a phylogeny of 111 *Oreocharis* species and found them to be sister to each other but also nesting within *Oreocharis*. Only the analysis by Chen *et al.* (2020) of 40 species, based on six chloroplast regions and the nuclear ribosomal ITS region, has found the two *Bournea* to be sister species and sister to *Oreocharis*. They used ITS data retrieved from GenBank, and combined these with data for six loci excised from newly acquired entire chloroplast genomes (*atp*B–*rbc*L, *ndh*H–*rps*15–*ycf*1, *rpl*32 – erroneously named *rpl*132, *trn*C–*trn*D, *trn*L–F, *trn*T–L). They then performed Bayesian inference and maximum likelihood analyses. As detailed below, there are several problematic issues with the molecular data and the analyses.

*Is* Bournea *monophyletic or not?* Scrutiny of the *Bournea* data indicated that the *trn*L–F data acquired for *B. leiophylla* by Chen *et al.* (2020), Q1208 and Q1215 (vouchers: Y.M.Shui *et al.* B2015-255 [KUN] and Y.M.Shui *et al.* B2015-272 [KUN], respectively), and those from GenBank for the same species (GU350676; voucher: ZXR-05-01, Fujian, China [PE]), have different phylogenetic positions, the former basal in Chen *et al.* (2020: figure 2) and the latter identical to Chen's *Oreocharis auricula* (S.Moore) C.B.Clarke (Q1207) sequence. Thus, it seems that the data available for *Bournea leiophylla* on GenBank are from misidentified or mixed-up material, probably including *Oreocharis auricula* or a closely related species (see also Guo *et al.*, 2018). This has probably resulted in the sister relationship of *Oreocharis auricula* and *Bournea leiophylla* reported in the original publication of the data by Wang *et al.* (2010), where the non-monophyly of *Bournea* was first proposed. Thus, the non-monophyly of the two *Bournea* species is probably attributable to an artefact.

The same *Oreocharis* datasets for ITS and *trn*L–F were repeatedly used in consecutive publications (e.g. Möller *et al.*, 2011a; Chen *et al.*, 2014; Guo *et al.*, 2018; Yang *et al.*, 2020, Ling *et al.*, 2022; Lv *et al.*, 2022; Hu *et al.*, 2023), usually with the addition of new species samples, thus perpetuating a possible illusion of a non-monophyly of *Bournea*.

*Sample combination and phylogenetic signal swamping*. In Chen *et al.* (2020), the situation is complicated because the authors combined chloroplast and nuclear data from different accessions for both *Bournea* species. In other words, they combined probably erroneous ITS data from GenBank and presumably genuine *trn*L–F data acquired themselves for *Bournea leiophylla*.

The reason why the *Bournea* samples resolved as sister to *Oreocharis* in the combined chloroplast and nuclear analysis in Chen *et al.* (2020: figure 3) could be that the phylogenetic signal from the six chloroplast regions (making up around 7400 base pairs with 418 parsimony-informative characters) swamped the signal from the single nuclear ITS region (with 684 base pairs with 210 parsimony-informative characters). This is supported by the tree based on chloroplast data alone, showing the same sister relationship of *Bournea* to *Oreocharis* (Chen *et al.*, 2020: figure 2).

*Chloroplast–nuclear incongruence*. The different positions of *Bournea* in the chloroplast (Chen *et al.*, 2020) and nuclear analyses (Kong *et al.*, 2022) could be due to a genuinely incongruent phylogenetic signal for the two genomes. Kong *et al.* (2022) generated a maximum-likelihood phylogeny of 111 *Oreocharis* species, based on 574 transcriptome-based nuclear markers (with 829,926 base pairs and 186,601 parsimony-informative characters). The two *Bournea* species were found to be sister to each other and nested within *Oreocharis* with maximum node support (Kong *et al.*, 2022: figure 2a). This work supports the finding that the earliest *Bournea leiophylla* data used by Wang *et al.* (2010) are indeed erroneous, because these do not place the species as sister to *B. sinensis*, and it also means that the two *Bournea* species may indeed be closely related.

Regarding the position of *Bournea*, however, there remains a conflict between the phylogenies in Chen *et al.* (2020) and Kong *et al.* (2022). This may be due to differences in sampling depth, because Chen *et al.* (2020) sampled only 40 species. Nevertheless, when the tree topologies from the two studies are compared, strongly supported incongruencies become apparent in the placement of some species in different major clades, quite apart from the *Bournea* species. For example, *Oreocharis farreri* (Craib) Mich.Möller & A.Weber and *Oreocharis pinfaensis* (H.Lév.) Mich.Möller & W.H.Chen are sister to each other with maximum node support in Chen *et al.* (2020) but are placed in two separate major clades in Kong *et al.* (2022). Other cases involve *Oreocharis baolianis* (Q.W.Lin) Li H.Yang & M.Kang and *Oreocharis guileana* (B.L.Burtt) Li H.Yang & F.Wen, sister to each other in Chen *et al.* (2020) but separated into different subclades in a different major clade in Kong *et al.* (2022); and *Oreocharis chienii* (Chun) Mich.Möller & A.Weber, *Oreocharis cotinifolia* (W.T.Wang) Mich.Möller & A.Weber and *Oreocharis acaulis* (Merr.) Mich.Möller & A.Weber showing incongruence placements between the two studies.

These instances may either be due to errors (misidentifications or mix-ups) resulting from the sampling differences between the studies (~35% of the taxa are shared between the studies by Chen *et al.*, 2020, and Kong *et al.*, 2022), or they may represent cases of chloroplast capture, perhaps after hybridisation. This is not an unknown phenomenon in plants more generally (Möller *et al.*, 2020; Morales-Briones *et al.*, 2021; Qin *et al.*, 2023), in Gesneriaceae in particular (de Villiers *et al.*, 2013) or even in *Oreocharis* specifically (Puglisi *et al.*, 2011). Moreover, discordances between large next-generation sequencing–based chloroplast and nuclear datasets are now frequently reported (e.g. Stubbs *et al.*, 2020), and their consequences are far from fully understood (e.g. Morales-Briones *et al.*, 2021).

*Omission of critical species*. A further limiting aspect of the studies by Chen *et al.* (2020) and Kong *et al.* (2022) is the omission of critical species such as *Oreocharis primuloides* (Miq.) C.B.Clarke. In previous publications (Möller *et al.*, 2011a; Chen *et al.*, 2014; Guo *et al.*, 2018; Lv *et al.*, 2022; Hu *et al.*, 2023), this species was found to be in a basal polytomy with *Bournea sinensis* or formed a basal lineage in *Oreocharis*. In consequence, inclusion of this species in future analyses, along with a coherent sampling strategy using verified plant material, is needed to properly ascertain the phylogenetic placement of the two species of the erstwhile '*Bournea*'.

## *Palynology*

In addition to the molecular data, Chen *et al.* (2020) also presented palynological data, which they claimed provided evidence for the separation of *Bournea* and *Oreocharis*. Based on scanning electron microscopy (SEM) micrographs, the authors concluded that the two species of *Bournea* shared the same pollen characteristics, and they described the pollen as "single-grained, isopolar, radial symmetry, prolate, amb circular, tricolporate, aperture membrane granulum, exine verrucate, tectum verrucate, supratectal elements granulum…" Of particular importance is the exine, which is described as "verrucate", and is said to be diagnostic for the two *Bournea* species. Referring to an M.Sc. thesis (Zhang, 2018), the authors also stated that the pollen of *Oreocharis* is more heterogeneous than previously thought. However, this point was not elaborated in detail.

We disagree with Chen *et al.* (2020) in several respects. First, the pollen grains of the two *Bournea* species are shown at different levels of hydration, making comparisons of shape, the ratio of the length of the polar axis to the equatorial diameter, ornamentation and measurements difficult. Second, the pollen is described as tricolporate, which is in conflict with the descriptions by Wang *et al.* (1995) and Zhang (2018), who classified the pollen grains as tricolpate and provided evidence through light microscopy and SEM images (according to Luegmayr, 1993, Palee *et al.*, 2004, and Wang *et al.*, 1995, tricolporate pollen does occur but is rare in Asian Gesneriaceae). Third, following the terminology of Hesse *et al.* (2009) and Halbritter *et al.* (2018), the exine of both *Bournea* species is microreticulate or microreticulate-perforate rather than verrucate. The former is a common exine type in both New and Old World Gesneriaceae. The description of the exine by Chen *et al.* (2020) as "verrucate" is incorrect and misleading. The microreticulate pattern of the two *Bournea* species does not contrast with patterns found in *Oreocharis* (Zhang, 2018) and cannot be used to separate the two genera.

Following our re-evaluation of the data provided by Chen *et al.* (2020) and Zhang (2018), we present revised descriptions of the two *Bournea* species (without size measurements, for the reasons noted above): *B. sinensis* – dry pollen isodiametric, isopolar, prolate, outline elliptic, tricolpate, apertures infolded (membrane ornamentation not visible), exine microreticulate to perforate, with nanoechinate suprasculpture; *B. leiophylla* – hydrated pollen isopolar, isodiametric to oblate, spheroidal, tricolpate, with ornamented aperture membrane (microverrucae, microechinae, and microrugulae), exine microreticulate to perforate, with nanoechinate-nanostriate suprasculpture.

Our revised pollen descriptions do not include new features for *Oreocharis* or other Gesneriaceae (see Luegmayr, 1993; Palee *et al.*, 2004; Zhang, 2018). The pollen of *Oreocharis* is well documented: the grains are small, spheroidal, and tricolpate, with exine ornamentation ranging from microreticulate to reticulate-foveolate. The significant exine variation does not allow *Oreocharis* to be characterised on the basis of pollen characters (Palee *et al.*, 2004; Liu *et al.*, 2012; Chen *et al.*, 2013; Zhang, 2018).

Regarding the suprasculpture, the pattern described for *Bournea* is also found in many *Oreocharis* species (see the SEM images in Zhang, 2018). For instance, the nanoechinate-nanostriate suprasculpture of *Bournea leiophylla* resembles that of *Oreocharis maximowiczii* C.B.Clarke, and the nanostriate suprasculpture in *B. sinensis* resembles that of *O. bodinieri* H.Lév. Overall, there is no convincing palynological evidence to separate *Bournea* from *Oreocharis*.

## Conclusions

It is almost certain that the strong morphological similarity between the two species previously placed in *Bournea*, particularly in terms of the actinomorphic flower, is due to a close evolutionary relationship, as was found in the studies that used the highest number of molecular markers (Chen *et al.*, 2020; Kong *et al.*, 2022). However, there is a discrepancy regarding the placement of the species, which is due to the plastid data suggesting they are not nested in *Oreocharis* whereas the nuclear data suggest that they are. The study by Chen *et al.* (2020), as discussed above, has too many shortcomings (particularly the omission of critical species) to conclude that an independent genus *Bournea* can be supported.

We also disagree with the conclusions of Chen *et al.* (2020), who suggested that palynological data can distinguish *Bournea* from *Oreocharis*. Using their own data, we reach different conclusions with respect to terminology, methodology and the distribution of similar pollen types. We see no evidence that palynological characters support the recognition of *Bournea* as distinct from *Oreocharis*.

Our final assessment is that the morphological and palynological overlap between the two genera does not justify their separation, regardless of whether the molecular data resolves *Bournea* as sister to *Oreocharis* or places the species as nested within it. Thus, until new and more robust data become available, *Bournea* should remain a synonym of *Oreocharis*, as has already been accepted by other authors (e.g. Li *et al.*, 2023: 216).

## Acknowledgements

The Royal Botanic Garden Edinburgh (RBGE) is supported by the Scottish Government's Rural and Environmental Science and Analytical Services Division. RBGE is thanked for providing general support and facilitating the research of M.M. and D.J.M. We would also like to thank Dr Yu-Min Shui for discussions on *Bournea*. Lastly, we are grateful to two anonymous reviewers for their critical comments on the manuscript.

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