Not so ancient: Misclassification of alpine plants biases the dating of the evolution of alpine biota in the Himalaya-Tibet Orogen

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One Sentence Summary: The evolution of alpine plant species in the Himalaya-Tibet Orogen is much younger than proposed by Ding et al. and started not until before the Miocene.

Abstract: Ding *et al.* (Science 2020) proposed that the extant lineages of the alpine flora of the Tibet Himalaya Hengduan region emerged by the early Oligocene. We argue that these results are based on misclassifying high montane taxa as alpine and that their data support alpine habitats only at about 7.5 mio years before present.

Main Text: The reconstruction of the surface uplift history in the Himalaya-Tibet Orogen (HTO) is a consequential but contentious question in the geosciences, paleoclimatology, paleoecology, and evolutionary ecology. There is controversial discourse regarding the spatial extend, event sequence, and timing of uplift. Bioscientists have joined the debate using fossil evidence (*1*–*3*) and dated phylogenies (*4*–*6*) to inform biome constituency, i.e. the timing of life being exposed to montane or alpine climates. Fossil deposits from the Eocene to Pliocene eras have been investigated in several parts of the HTO, but no fossils that are strictly bound to the alpine zone have been found. Therefore, dated phylogenies are the most promising bioscientific contribution which, however, is bound to a fundamental cladistic principle, namely the monophyly of clades that corroborate synapomorphic traits – in this case being strictly bounded to the alpine habitat.

Ding *et al.* (*7*) used phylogenetic reconstructions of biome and geographic range evolution to investigate the evolution of alpine flora in the HTO. They reported that the extant lineages of HTO alpine flora had emerged by the early Oligocene, which also places the geographic uplift into alpine elevations to at least that time and led them to conclude that the flora of the Hengduan Mountains on eastern margin of the Tibetan Plateau is the world's longest continuously existing alpine flora. However, we challenge their classification of plants that are denoted to be strictly alpine and claim that

substantial misclassification led to false modeling results. Consequently, the early timing of the Tibetan uplift to alpine habitats does not stand. Clear support for an uplift only exists for ~7.5 Mio years based on the presented data, with a maximum range of uncertainty up to ~15 Mio years before present. In either case, the timing is decidedly later than the proposed Oligocene.

Since Ding et al. (*7*) presented no species-specific arguments for classifying taxa into the categories alpine or non-alpine, we could not re-examine the authors' evidence here. Furthermore, the authors assumed that biome occupancy was the same across the geographic ranges of species. This assumption is misleading due to extended Holocene forest clearings and the expansion of treeless pastures with alpine species into elevations naturally suitable for tree growth in some areas of the HTO which results in current geographic ranges being widely a pattern of the pastoral economy (*8*). We reclassified the status of the plant taxa of the Saxifragaceae and the Delphinieae (see suppl. 1) as the evolutionary histories of these taxa are the main argument for the early Oligocene alpine emergence in the HTO region (*7*). We followed the widely accepted definition of alpine that refers to treelessness due to temperature limitations (*9*) that also Ding and coworkers claimed to have employed. We exclusively focused on taxa that Ding *et al.* denoted to be strictly alpine. We used publicly available descriptions of habitat and elevation distributions in regional floras, online databases, and individual scientific publications (*8*, *10–12*) to determine whether current distribution is limited only to arctic-alpine environments, or whether they currently also occur in forest or forest edge environments. Out of the 29 Delphinieae and 137 Saxifragaceae species originally classified as strictly alpine by Ding *et al.,* we only assigned 10 and 55 respectively, to the alpine category (Fig. 1). Of the remaining 19 and 82 species respectively, 10 and 22 are explicitly noted in the literature to occur in forested areas, and the final 9 and 60 species inhabit elevation ranges that clearly include lower- to upper-montane elevations. Note that when in doubt, we scored species as strictly alpine so that our argument is only based on instances wherein Ding *et al.* clearly misclassified the species.

More importantly, the strictly arctic-alpine species form a monophyletic clade in only four cases in the Saxifragaceae (Fig. 1), and never in the Delphinieae. Thus, only four strictly arctic-alpine crown groups support the idea that cladogenesis took place within an arctic-alpine environment, while the evolutionary age of the stem groups bear no information regarding a synapomorphic trait, e.g. "alpine" in this case. Considering that the presented dataset claims to encompass all extant species of these monophyla, the age of the oldest known alpine crown group dates to about 7.5 Ma before present (Fig. 1 Cladogenetic event 1). For the Delphinieae, the lack of monophyletic alpine clades means the phylogeny does not support any certain date for the evolution of alpine flora. Furthermore, the fact that more than half of the taxa from the Delphinieae and Saxifragaceae presented in this study occur both in alpine and non-alpine elevations indicates recent expansion to the alpine zone rather than alpine species radiation. Instead, most speciation events probably occurred in open habitats of the high montane zone such as rock faces and scree slopes, suggesting there were pre-adapted lineages that evolved into the present day "alpine" flora. This presumption is strongly supported

by multiple observations of warm to cold temperate Oligocene to Miocene fossil floras from different parts of the HTO (*13*–*15*).

Finally, while we appreciate the great effort towards characterizing the evolution of the alpine flora of the HTO, we think that a clear and transparent assessment of what qualifies species and higher clades to be strictly adapted to the alpine environment is necessary. Additionally, there should be a comprehensive inclusion of all related lower elevation taxa of the investigated species groups, which we cannot discuss in detail here. In conclusion, neither the early Oligocene nor the claim of the longest permanently existing alpine flora are supported by the data presented in Ding et al. (*7*).

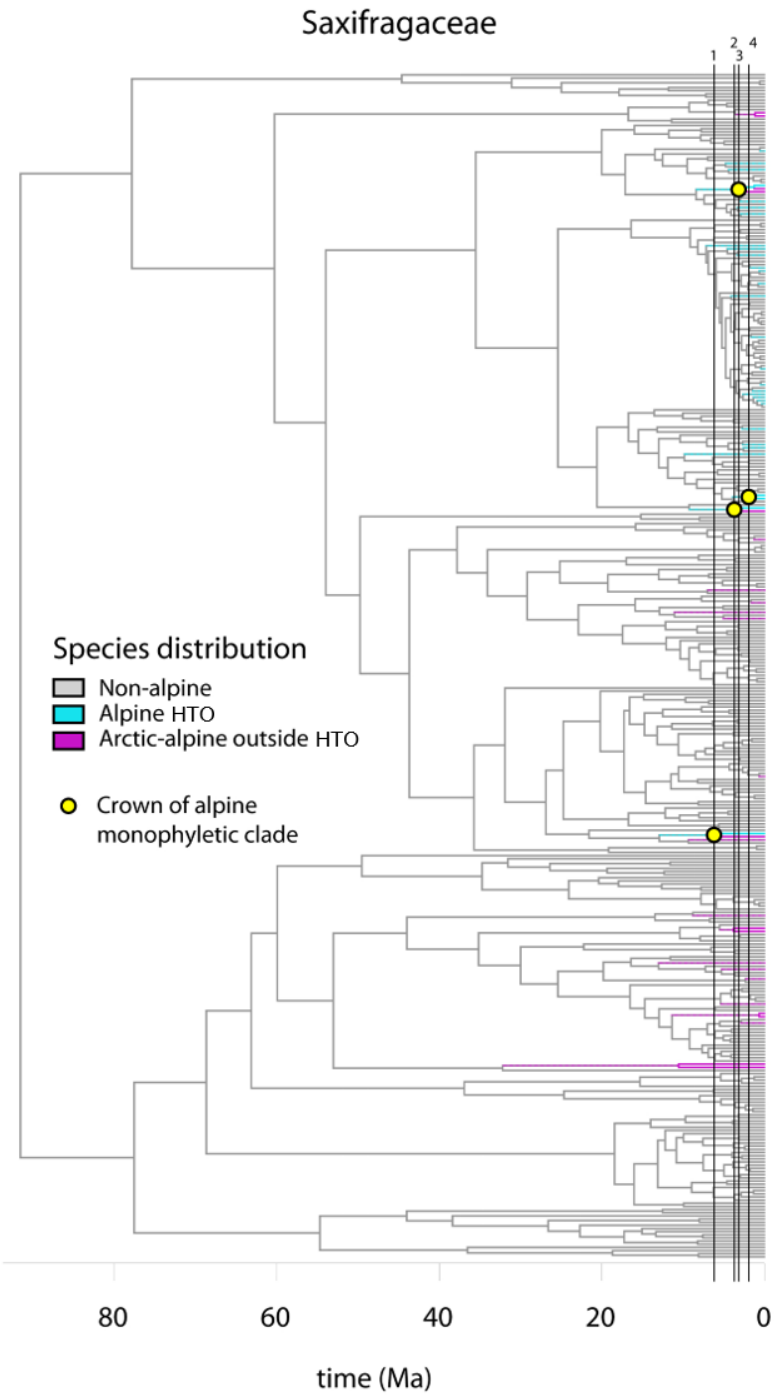

Fig. 1. Marginal maximum a posteriori reconstruction of the joint history of geographic range and biome evolution on the maximum clade credibility of tree of Saxifragaceae using RevBayes from Ding *et al*. The phylogenetic tree has been recolored based on a reclassification of the taxa regarding their current alpine distributions with all taxa that (co-)occur in non-arctic-alpine habitats are grey, while all taxa strictly occurring in arctic-alpine bioms are colored, with blue taxa occurring in the target region and purple taxa occurring outside the target region. The four yellow circles indicate crowns of arctic-alpine monophyletic clades supporting speciation in an alpine habitat; the vertical bars give the indication of the timing of the respective splits.

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