Section ONE

Boswellia taxonomy, nomenclature and evolution

The majority of global conventions and conservation practices deal with the conservation and sustainable use at the species level, and the vast majority of conservation assessments are made at this level also. As such, it is critically important that species can be distinguished from each other to ensure that like is being compared with like. To achieve this, an assessment of how robust the species level taxonomy is for a particular group and the provision of tools to distinguish among species are necessary. In fact, the development of identification tools can be a useful methodology for testing species level taxonomy. Identification at the species level relies upon sound taxonomy with characters that can distinguish among each species, and as the description of each species is based upon a diagnosis accompanied by a "type" voucher specimen that displays those characters it is not possible to describe species based upon chemical or molecular markers alone.

In the case of *Boswellia*, there is a long history of taxonomic study that has been covered and summarized elsewhere (see Thulin, 2020). *Boswellia* also benefits from having a recently published taxonomic monograph including an identification key (see Thulin, 2020). The author Prof. Mats Thulin is a professional (albeit now retired) taxonomist with many years' experience of working on *Boswellia* and significant field experience in many range States coupled with detailed examination of over 700 herbarium specimens. As such, he is regarded as the foremost *Boswellia* taxonomist globally, and in his own words most species of *Boswellia* are relatively straightforward to identify in the field.

However, *Boswellia* is not without its controversial taxonomy, and new species have been described relatively recently – albeit these are usually very local in distribution and have generally been separated from more widespread taxa or found in obscure and difficult to reach localities. It therefore becomes important to have an updatable resource on *Boswellia* as future taxonomic change or novelties are quite likely.

There are several situations in *Boswellia* where taxonomic complexity is prevalent.

The first of these is on the Soqotra Archipelago where there are currently eleven recognised taxa as well as unconfirmed reports of hybrids. These taxa appear to be part of a recently arrived and actively diversifying group (Forrest *et al*, unpub.). At present, as the island is small and most species have a small number of mature individuals recorded, there is little trade affecting Soqotra although this could change very rapidly should trade in Soqotran frankincense be actively marketed and subsequently increase.

The second situation involves two species in east Africa, namely *B. microphylla* and *B. neglecta*. The former was formerly treated within the latter until it became apparent that there were some characters that could be used to distinguish two taxa. However, *B. microphylla* was never formally described as a subspecies of *B. neglecta*, and this means that a number of studies – especially those dealing with resin chemistry and distribution – likely contain samples labelled as *B. neglecta* which in fact represent *B. microphylla*. As *B. neglecta* especially is increasingly coming into trade it is necessary to unequivocally determine if these represent distinct species or not and to recognise that in past and future studies.

The third situation involves Arabian *B. sacra* and Somali *B. carteri*. Both these names are used extensively in trade, even though Thulin (2020) recognised that *B. carteri* is a superfluous and illegitimate name under the International Code of Botanical Nomenclature. Some authors have claimed evidence from both morphology and from resin chemistry that two distinct species occur on the two continents but again Thulin (2020) adequately dismissed those assertions and concluded a single taxon was involved. Given the levels of trade in this species however further detailed taxonomic research is warranted.

The fourth situation involves whether additional taxa await discovery. The most obvious example of this is *B. papyriefra* "Kebtele" which was highlighted as having a unique and distinct resin chemistry by Melese (2007). While resin chemistry cannot be used to describe a new species, it may unveil morphological differences previously uncollected or overlooked, as was the case when *B. occulta* was described in 2019 (Thulin *et al*, 2019). In that case, a specimen previously identified as *B. frereana* (Glover & Gilliland 719, K) was re-determined as *B. occulta* once the characters for the new species were formally described.

In this section, we report on taxonomic investigations into scenarios two and three and conclude that there is no taxonomic evidence to separate *B. sacra* into two separate taxa, and that *B. microphylla* and *B. neglecta* are two distinct taxa.

Section 1.1

Boswellia sacra – one species or two?

The argument as to whether there are one or two species in Arabia and northeast Africa – *B. sacra* and *B. carteri* respectively – has been raging for decades. The taxonomic history of this is covered in detail elsewhere (Thulin, 2020). However, even Thulin has highlighted that at times he considered that there may be two species involved but has finally stated that this is not the case, in that resin chemistry cannot be used to describe a novel taxon and that the chemical characters cited have little utility in terms of identification and diagnostic characters in either the field or the herbarium, and also that the morphological characters cited do not differentiate two taxa when taking into account variation across the range of the species.

In order to finally put an end to these differences of opinion, a study was undertaken to measure a wide range of characters from specimens across the distribution range of *B. sacra* including Oman, Somalia and Yemen. The detailed results are presented in Gibson (2023) and are currently being prepared for publication in an open access journal (see Appendix 1.1). The results are summarized here.

A total of 37 characters were considered and measured, including both key characters used by Thulin (2020) when attempting to distinguish between the taxa and also several novel characters not examined directly by Thulin (2020). No characters could be found that can be used to distinguish between *B. sacra* occurring in Arabia from that occurring in Somalia. As such, if presented with any specimens for which no prevenance was available, it would not be possible to identify whether the specimen came from which area, but the specimen could be identified as *B. sacra*.

However, it was noted that a small number of characters when analysed via plots could be viewed as overlapping but showing a non-random distribution. While not affecting a decision to maintain a single species, it was noted that it is not unexpected that populations separated by the Gulf of Aden may show some differentiation due to a significant barrier to gene flow. However, this should be tempered by the fact that both this study and Thulin (2020) note that there is variation of characters within Somalia that is greater than variation between Somalia and Arabia – suggesting that other potential barriers to gene flow exist. It would be of academic interest to undertake research into genetic differentiation across the range of *B. sacra*, alongside detailed morphological studies based on voucher specimens as well as linked resin chemistry analyses, but these are very unlikely to reveal characters that can be used to distinguish two species taxonomically. It is reiterated here that while some studies show resin chemistry differences between Arabian and Somali populations, these cannot be used to distinguish new species and were based upon very few samples without vouchers.

It should also be noted that many collections in herbaria are sterile or nearly so, and that flower and fruit characters were among those displaying variation. As such, detailed floral studies would be of value, and further encouragement for the collection of flowering and fruiting samples deposited in accessible global herbaria.

Section 1.2

Boswellia microphylla and *Boswellia neglecta*

Although *B. microphylla* was published as a new species more than 100 years ago, it has long been considered as the same species as *B. neglecta* and has been treated as such by many authors in recent studies. This in part explains why there are no studies at all on the resin chemistry of *B. microphylla* – the only species in the genus outside Soqotra for which this is the case. This has implications for any assessment or study using the name *B. neglecta* as these may contain samples or distribution points that in fact represent a different species.

A total of 43 characters were considered and measured, including both key characters used by Thulin (2020) to distinguish between the taxa and also several novel characters not examined directly by Thulin (2020). Several characters were located that either singly or in combination can be used to distinguish between specimens representing two distinct taxa, and plots of character pairs show a non-random distribution that can visually distinguish two clusters. As such it is considered that two species are involved, and that this is suggestive of a significant barrier to gene flow even though much of the range of these two species overlaps in eastern Africa. As a result, further investigation of the potential environmental differences segregating these species via Species Distribution Modelling would be of interest, as would a more detailed molecular study focusing on differentiation between these two species and *B. rivae* as these three taxa are largely overlapping and also share the character that cutting the bark does not readily increase the amount of resin exuded and subsequently collected and sold. This has been highlighted by some as a potentially naturally sustainable harvesting system that could benefit local communities (DeCarlo *et al* 2023), and as such more detailed resin chemistry studies may lead the way to an increase in trade through resin chemistry profiles that facilitate marketing.

Section 1.3

Nomenclature

As well as being able to distinguish between different species, it is also desirable to use their correct names. This ensures that in comparative studies, the identification and naming of individuals can be compared "like for like" and avoids confusion if more than one name is used for the same species. Further, the International Code of Botanical Nomenclature requires that a species is described according to its unique morphological characters which are represented on a "type" specimen (or specimens) meaning that the name is linked directly to the identity of that species.

All recorded names in *Boswellia* have been checked against their original publications. Where any case of nomenclatural complexity was uncovered, this was checked with experts at the International Plant Names Index (IPNI) and changes made and incorporated where necessary. The majority of global databases take their cue from IPNI and as such these changes will eventually filter down to other global and thematic repositories.

All names and authors have been uploaded to the Frankincense Resource Portal where they can also be viewed species by species and updated as necessary. This has included uploading 65 names, of which 24 are currently accepted.

In the case of *B. carteri* – a name which has been extensively used taxonomically in the past and as such is widely used in commerce today to refer to plants and their resins occurring in or collected from Somali - it has been demonstrated that the name *B. carteri* is superfluous and illegitimate. Arguments to maintain *B. carteri* as a separate taxon have been shown here and elsewhere to be inaccurate. There is no valid precedent to adopt the name *B. carteri* based on commercial use and were such a name proposed for conservation such a proposal would very likely be rejected. There are, as noted, no valid taxonomic characters that can be used to

separate *B. carteri* from *B. sacra*. The question therefore remains as to how to deal with the extensive use of the name *B. carteri* in commerce.

There are several options. The first is to promote the fact that no such species of *Boswellia* exists and encourage all stakeholders to use the name *B. sacra*, and eventually the name will disappear from popular use. If for some reason commercial users are not willing to take such a step because the name is fundamental to their business and relies on the connection to Somalia, then the name could be highlighted as a commercial name and cited as *Boswellia sacra* "carteri" – although in reality if the connection to Somalia is important it would make more sense to cite that directly.

Section 1.4

Phylogeny and Evolution

In order to ascertain the relationships between and the evolutionary history of *Boswellia* species, a plastid molecular phylogeny was constructed allowing the following conclusions.

Figure 1.1 shows a phylogeny reconstructed using sequences from plastid *rpl32-ndhF-trnL*, *atpH-atpI* and *rps16-rps8*. This clearly shows that *Boswellia* is monophyletic and can be classified into three distinct clades. The first represents the Indian species *B. ovalifoliolata* and *B. serrata* which makes sense geographically as the sister genus *Garuga* (not shown in Figure 1.1) is restricted to south and southeastern Asia. The second clade includes all other species of *Boswellia*, and the third includes all species endemic to Soqotra. Informal molecular dating suggests that the radiation on Soqotra may have occurred as recently as <2 million years ago but this requires empirical confirmation. Few species can be distinguished from each other based on the hypervariable plastid loci used in this study, with no differentiation between Arabian and African *B. sacra*. Further, standard plastid DNA barcodes (*matK* and *rbcL*) show no differentiation among species of *Boswellia* (A. Forrest, unpub.). While the endemic Soqotran taxa form a distinct clade, it is not possible to state from which species or region this clade originated as resolution is as yet not high enough.

Several accessions have been added to this phylogeny and await formal analyses and molecular dating prior to publication.

Section 1.5

Conclusion

This study has resolved taxonomic complexity in the species pairs *B. sacra* and *B.* "carteri" and also *B. microphylla* and *B. neglecta*, demonstrating that there are no characters in the former example that differentiate between accessions from Arabia and Africa. In the latter case two species can clearly be distinguished.

Boswellia nomenclature has been thoroughly revised and updated on the International Plant Names Index as well as added to the Frankincense Resource Portal

Phylogenetic studies differentiate three geographical clades in *Boswellia* but hypervariable plastid loci cannot distinguish among the majority of species.

Section 1.6

Outputs

Taxonomic and phylogenetic studies outlined above are in preparation for publication in the Edinburgh Journal of Botany, a gold standard open access journal.

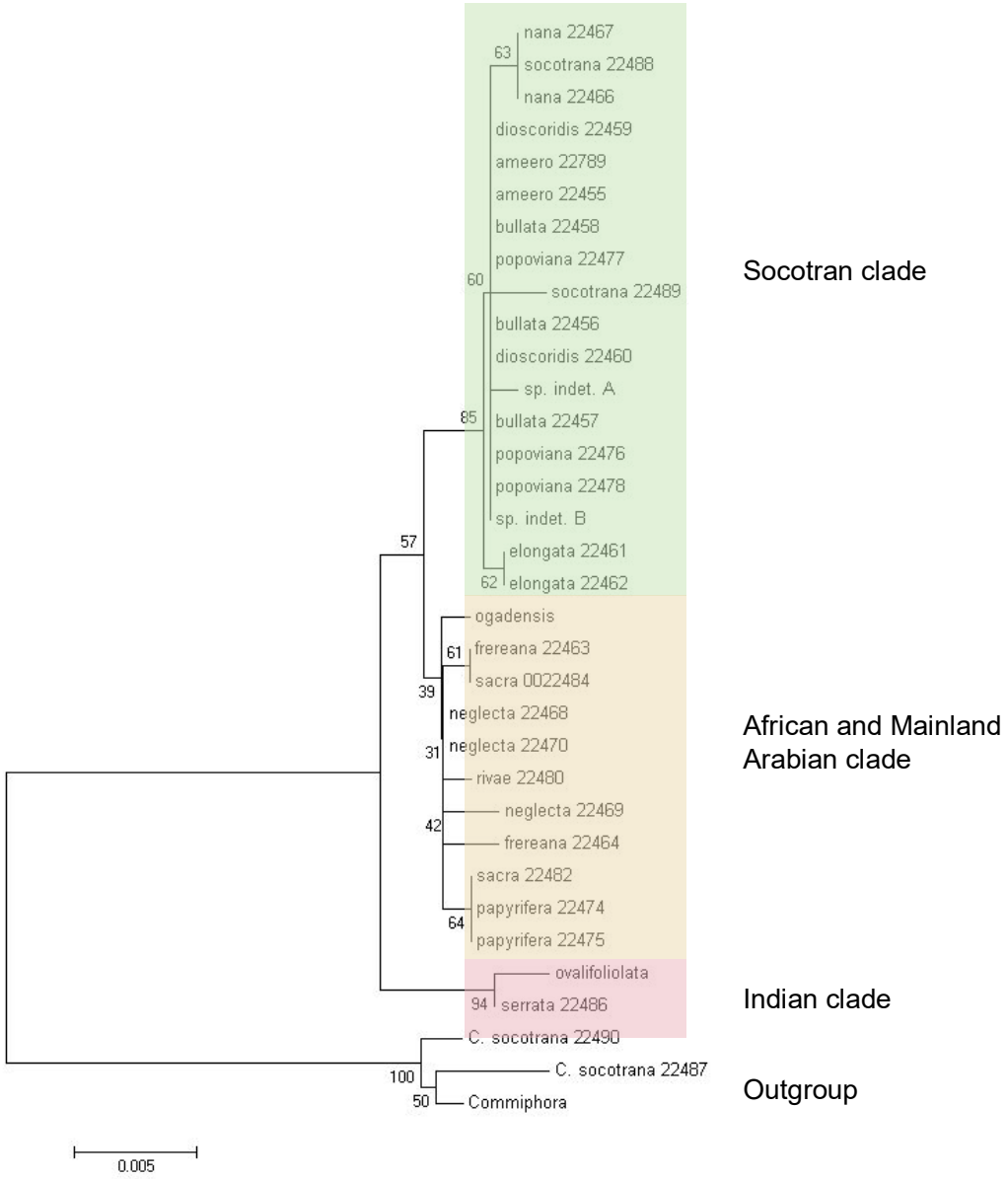

Figure 1.1. Phylogeny of *Boswellia* based upon three plastid loci. Three major clades are indicated.

Section 1.7

References

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