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Introduction

The genus *Noronhia* Stadtm. ex Thouars (Oleaceae), formerly circumscribed to be endemic to Madagascar and the Comoro Islands, has recently been expanded to include species from the Mascarenes and continental Africa (HONG-WA & BESNARD, 2013, 2014). *Noronhia* was first recognized by Jean-Frédéric Stadtmann (1762-1807) based on *Olea emarginata* Lam. (≡ *Noronhia emarginata* (Lam.) Stadtm. ex Thouars), but only validly published as a monotypic genus by DU PETIT-THOUARS (1806). Four additional species were described between 1890 and 1920, and a total of 41 species were included in the only taxonomic treatment of the genus (PERRIER DE LA BÂTHIE, 1949), which was later revised for the “Flore de Madagascar et des Comores” volume (PERRIER DE LA BÂTHIE, 1952). Four other species have been described since (BOSSET, 1973; LABAT et al., 1999; CALLMANDER et al., 2009). As currently circumscribed, *Noronhia* thus comprises these 45 species as well as species formerly recognized under *Chionanthus* L., namely those from Madagascar, the Comoros, the Mascarenes, and continental Africa (HONG-WA & BESNARD, 2013; HONG-WA et al., 2014). Two major clades can be distinguished within this broadly circumscribed *Noronhia*, one composed of species from continental Africa, the African clade, and another that includes species from the Malagasy Floristic Region, i.e. Madagascar, the Comoros and Mascarenes, and surrounding islands (TAKHTAJAN, 1986), referred to hereafter as the MFR clade. *Noronhia*, as currently circumscribed, is monophyletic and is sister to a clade composed of other members of the tribe Oleeae (HONG-WA & BESNARD, 2013, 2014; ZEDANE et al., 2016).

In this paper, I present a taxonomic revision of the members of the MFR clade, specifically the species from Madagascar and the Comoro Islands. *Noronhia* has traditionally been divided into three sections based on the presence or absence of a corona and on the length of the corolla tube (PERRIER DE LA BÂTHIE, 1952). Sections *Linociera* and *Noronhiae*, the latter referred to using the superfluous name *Genuinae* by PERRIER DE LA BÂTHIE (1952), are characterized by the presence of a corona but differ in the length of the corolla tube, which is longer than the corolla lobes in *Noronhiae* but shorter in *Linociera*, whereas section *Ecoronulatae* lacks a corona. The recent phylogenetic study of the group (HONG-WA & BESNARD, 2014) has shown, however, that none of these sections is monophyletic, limiting the usefulness of this infrageneric classification. Moreover, nine of the species treated by PERRIER DE LA BÂTHIE (1949, 1952) lacked descriptions of floral characters, rendering this classification even less useful. Thus, not only did this focus on a few floral features make it difficult to distinguish between sections using only leaf and/or fruit features or other floral characters, it also made the identification of specimens quite a challenge when flowers are missing. Indeed, PERRIER DE LA BÂTHIE (1949, 1952) first provided a key separating the sections based solely on the length and shape of the corolla and the presence or absence of a corona, and then within each section, a key to the species, again mostly based on floral features.

Apart from these issues, species delimitation in these earlier treatments was also unclear. PERRIER DE LA BÂTHIE (1949, 1952) recognized species based mainly on the shape and size of flowers, the length of the corolla tube, the presence or absence of a corona, the shape of the corona lobe, the shape of the anthers as well as some vegetative features such as leaf arrangement, shape, size and apex. However, variation in

these features sometimes overlaps, blurring the limits between different species. In other instances, members of the same species are distinct enough to be recognized only as single entities. Therefore, to assess patterns of variation and species boundaries within *Noronhia*, an integrative approach, using molecular and morphological data, was applied (HONG-WA & BESNARD, 2014). A variety of qualitative features (e.g. plant habit, presence of indumentum, color of bark, leaf, flower and fruit, texture of leaf and fruit, leaf venation pattern, flower arrangement, inflorescence structure, and fruit shape, ornamentation and apex) was used to sort available specimens into narrowly defined groups considered as “species hypotheses” (HONG-WA & BESNARD, 2014), referred to hereafter simply as “entities”. Plastid (trnL-F, trnT-L, trnS-G, trnK-matK) and nuclear (ITS) DNA sequences obtained from 68 of the 87 entities recognized, many of which were represented by multiple individuals, were used to build a species-level phylogeny. Despite a number of unresolved relationships, especially at basal nodes, more than half of the analyzed entities were recovered as being reciprocally monophyletic, suggesting distinct evolutionary lineages (HONG-WA & BESNARD, 2014). Concomitant with the phylogenetic analyses, morphological characters from c. 1,000 specimens representing the 87 entities were analyzed using principal component and discriminant analyses. Quantitative measurements (e.g. length, width, and thickness) were obtained from leaves, flowers and fruits and included only continuous variables (HONG-WA & BESNARD, 2014).

Overall, three datasets were used to recognize species: the qualitative features to sort specimens into groups, the molecular data to identify monophyletic entities, and the quantitative morphological variables to assess patterns of morphological variation. Results from the quantitative analyses (molecular and morphological) were used in an integration-by-cumulation approach (PADIAL et al., 2010) to test the species hypotheses. This approach considers the additive value of each line of evidence in distinguishing species since these are taken to be separately evolving lineages that can be recognized based on multiple lines of evidence under the general lineage concept of species (DE QUEIROZ, 2007). A single form of evidence can be sufficient in any one case, however, given that each line of evidence, resulting from evolutionary processes affecting lineage splitting and divergence, may or may not appear at the same time in all the entities (DE QUEIROZ, 2007 ; PADIAL & DE LA RIVA, 2010). The integration-by-cumulation approach is more appropriate when diversification has occurred recently and/or over a relatively short period of time, which can be considered to be the case for *Noronhia* (HONG-WA & BESNARD, 2013, 2014; ZEDANE et al., 2016). Entities whose members formed a monophyletic and/or morphologically coherent group were considered as robust hypotheses of species and thus provided the basis for this treatment.

While at the time the analyses were being performed, some of these entities were known from only one or two specimens, additional material from Madagascar became available afterwards that confirmed their circumscription and/or expanded their known range. Similarly, although most specimens could be assigned to one of the 87 entities during initial sorting, some were difficult to place because of their incompleteness (e.g. being sterile) or their intermediate morphology (e.g. fitting the description of two or more entities). The additional material made it possible to characterize some of these

specimens and to assign them to one of the initially recognized entities or to consider them as new entities altogether. Lastly, newly available specimens also included entirely distinct novelties, which are described here.

The present treatment places 98% of the c. 1,800 examined specimens of *Noronhia* from Madagascar and the Comoro Islands in 87 species, of which 82 are endemic to Madagascar; three occur only in the Comoros; one is shared between Madagascar and the Comoros; and one between the Comoros and the Mascarenes. *Noronhia* is the largest member of the olive family in Madagascar, where only three other genera (*Jasminum* L., *Olea* L., and *Schrebera* Roxb.) are found since species formerly placed in *Chionanthus* are now included in *Noronhia* (HONG-WA & BESNARD, 2013) and *Comoranthus* Knobl. is being subsumed under *Schrebera* (G.E. Schatz, pers. comm.). *Noronhia* appears to have colonized Madagascar c. 23 million years ago from an African ancestor and subsequently dispersed to other surrounding small islands (HONG-WA & BESNARD, 2013; but see also ZEDANE et al., 2016). The bulk of its diversification started c. 15 million years ago (HONG-WA & BESNARD, 2013) and seems to have involved mechanisms related to adaptation to novel environments (HONG-WA & BESNARD, 2014). Natural hybridization, as suggested by material exhibiting intermediate morphologies between some species and incongruence patterns between plastid and nuclear-based phylogenies, may also have been an important mechanism of diversification for this genus. Polyploidy within *Noronhia*, though suspected (HONG-WA & BESNARD, 2013, 2014), remains to be documented as chromosome counts are still unavailable.

Madagascar is the current center of diversification of *Noronhia*. Species on this island have colonized a wide diversity of habitats from sea level to > 2000 m elevation. They commonly occupy dense forests of the humid east or the dry west as well as woodlands of the central high-plateau or scrublands of the south (cf. MOAT & SMITH, 2007). They occasionally occur in open habitats. Variation in substrate preference is equally significant, with species growing on diverse substrates such as lava, limestone, metamorphic rocks, quartzite, sandstone, and white sand. The distribution of the genus covers the entire island, although many species have narrow ranges. Areas with the highest species richness correspond to topographically complex regions of the north and the south (HONG-WA, 2012). Undersampled areas in the north, from the Manongarivo massif to the Makira region, as well as much of the western domain, where endemism is also high, may harbor a higher diversity of *Noronhia* than is currently estimated based on available collections. Increased efforts to collect material from these areas would provide a fuller picture of species diversity and diversification of *Noronhia* in Madagascar. Comprehensive studies in continental Africa are also needed to document its diversity there. Furthermore, some species from West Malesia, currently placed in *Chionanthus*, present morphological affinities with *Noronhia* and may also belong to the genus, thus potentially extending its geographic range.

The updated treatment presented here, although far from being exhaustive, represents a first step to understanding species diversity within *Noronhia*. It also provides a framework for advancing studies on the systematics, biogeography, ecology and evolutionary biology of the genus as well as for promoting the conservation of its species in

Madagascar. Thus, in an effort to provide the best available information about *Noronhia* in Madagascar and the Comoros, this treatment includes an identification key, species descriptions, nomenclatural notes, an etymological section when relevant, distributional, habitat and phenological information, a list of selected specimens, a preliminary assessment of conservation status, illustrations, photos of living plants, and distribution maps. The terminology used in the species description generally follows that of STEARN (2004). Information on phenology and habitat obtained from herbarium specimens has been supplemented by personal observations. Phenological information may not accurately portray the reproductive season of each species due to a lack of all-year-round sampling. A delay in and/or shortening of reproductive season has also been observed and reported by local populations. Distribution maps use the five simplified bioclimatic zones of Madagascar (SCHATZ, 2000; after CORNET, 1974) as a basemap and include locality data that represent the known range of each species as of early 2015. A list of representative specimens observed includes detailed locality data, with geo-coordinates placed in brackets when assigned post-facto using maps and the MISSOURI BOTANICAL GARDEN'S GAZETTEER TO MALAGASY BOTANICAL COLLECTING LOCALITIES (2016). For each species, comprehensive specimen records along with photos of living plants taken in the field are available on the MADAGASCAR CATALOGUE (2016). Furthermore, high-resolution images of type specimens are available from MO (TROPICOS, 2016) and P (SONNERAT, 2016) as well as from JSTOR Plant Science [<http://plants.jstor.org>]. Herbaria are abbreviated according to INDEX HERBARIORUM (2016). CNARP is the acronym used for the herbarium of the Centre National d'Application de la Recherche Pharmaceutique in Antananarivo (Madagascar); and Daraina is used for the herbarium of the village of Daraina in Loky-Manambato region, west of Vohémar in northern Madagascar. In addition, the following abbreviations are also used: AP = Aire Protégée, FC = Forêt Classée, PN = Parc National, RNI = Réserve Naturelle Intégrale, RS = Réserve Spéciale, STF = Station Forestière.

Of the 87 species of *Noronhia* recognized in Madagascar and the Comoro Islands, 36 are new and three others are elevated from an infraspecific rank, thus requiring new combinations. In addition, three other species were recognized as new based on vegetative morphology and molecular data (HONG-WA & BESNARD, 2014) but are excluded from this treatment. Formal description of these novelties will await better material with flowers and/or fruits. In his treatments, PERRIER DE LA BÂTHIE (1949, 1952) rarely designated a holotype specimen. Therefore, a lectotype has been chosen among the syntypes based on various criteria as indicated in the "Notes" section wherever relevant. In total, 17 lectotypifications are made here. Moreover, the phylogenetic study of *Noronhia* and its relatives showed that *Chionanthus* species from Africa and the Madagascar Floristic Region (MFR) formed a monophyletic group, with *Chionanthus* from the latter region all embedded within *Noronhia* (HONG-WA & BESNARD, 2013). To accommodate this phylogeny, all species of *Chionanthus* from Africa and the MFR were systematically transferred to *Noronhia*, making new combinations regardless of their taxonomy (HONG-WA & BESNARD, 2013). The necessary taxonomic evaluation of the Malagasy taxa is done in this treatment, thus making yet other new combinations or establishing synonymies when needed.