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Journal of Plant Taxonomy and Geography (*Webbia*) is a peer-reviewed journal on Plant Taxonomy, Nomenclature, Phylogeny, Phytogeography and Palaeobotany of the Vascular Plants.

The journal aims to allow research in botanical topics such as taxonomy, systematics, nomenclature, molecular phylogeny, conservation, biogeography, and history of botany, and botanical collections.

It was founded in **1905** in Florence by **Ugolino Martelli** (1860-1934), a botanist well known for his studies of and contributions to the systematics of the tropical genus *Pandanus* and on the Flora of Sardinia.

In the 19th century Florence represented one of the most important European centres in Plant Taxonomy and Phytogeography with several notable Italian botanists worth mentioning such as Filippo Parlatore, Teodoro Caruel, Eugenio Baroni, Stefano Sommier, Odoardo Beccari and Ugolino Martelli himself. In 1842 **Filippo Parlatore** (1817-1877) founded in Florence the *Herbarium Centrale Italicum (FI)*, which soon became one of the most important herbaria in the world. Most of the specimens described and/or cited in *Webbia* are still kept in it.

In 1905, and as a consequence of this multitude of activities in Plant Systematics and Phytogeography, Ugolino Martelli established the journal *Webbia-Raccolta di Scritti Botanici*, firstly published annually in a single issue, and later twice a year. Webbia also began to be a place of publication of contributions from Tropical Botany, especially after the Royal Colonial Herbarium founded in 1904 in Rome was moved to Florence in 1914, currently named Tropical Herbarium Study Center (Centro Studi Erbario Tropicale - Herbarium FT) belonging to the Department of Biology of the University of Florence.

Webbia had been created in honor of **Philip Barker Webb** (1793-1845), a close friend of Filippo Parlatore, who before passing away entrusted his personal herbarium and a library rich of old botanical books and publications to the then Botanical Museum in Florence.

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Opinion

Is the demise of plant taxonomy in sight? Maybe yes, maybe no…

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> *Taxonomy – the scientific discipline that explores, discovers, interprets, represents, names, and organizes organic beings – is an integral component of biogeography, evolutionary biology, ecology, conservation and other biodiversity studies* (Ebach et al. 2011: 550).

The wide and significant spectrum of taxonomy in our society is clearly stated in the above quote by Ebach et al. (2011). As taxonomists who have embraced the amalgamation of traditional and modern research techniques, we have witnessed dramatic changes and the gradual disappearance of one of the oldest disciplines in biological science, that is, taxonomy and the associated application of nomenclature. In this note we address some of the causes and effects behind reductionism and the ensuing curricular changes affecting research, education and training in taxonomy in major academic institutions.

Over the last few years scientific specialization has had an unprecedent impact in society enabling biological research progress primarily due to the implementation of technological innovation, raising employment and economic development. As a result, the resolutions in scientific and educational institutions have been adjusted accordingly. The field of botany, in particular, has undergone significant changes. Botany has been influenced by shifts in the approach to the scientific method, to the extent that this traditional field of studies has been increasingly replaced in universities and research institutes by broader meaning labels, such as of "Plant Biology" and "Integrative Biology." In fact, several claims regarding the vanishing of taxonomic research have been made, from the lack of funding (Ebach and Holdrege 2005; Guerra García et al. 2008), training of new personnel (Drew 2011; Britz et al. 2020), denying recognition (Dar et al. 2012; Wheeler 2014), and reductionism (Crisci 2008; Crisci et al. 2020).

According to Dar et al. (2012), taxonomic impediment in education is based in part on the deficiency in institutional and financial support, lack of appreciation, job opportunities, turn-around in research output, and relative lower impact factor for taxonomic journals, among other causes. Furthermore, in an era of genomics and applied science, the taxonomist has become an endangered species (Ali et al. 2014). All these adverse factors are overwhelming and difficult to overcome by the community of taxonomists, to the extent that potential new positions emerging from retirement of senior taxonomists are being modified in scope or lost from the academic program.

Among the previous indicators, reductionism has impacted taxonomy in programs and institutions throughout the world. The changes are evident in numerous major universities that used to have old traditional and prestigious botany and zoology departments and graduate programs with strong taxonomic training but are now integrated into more widely contemporary named departments and units dominated by non-organismal professionals (Woodland 2007). These changes have enabled modern approaches intersecting evolutionary biology and technological applications putting aside a curriculum embracing aspects of classical taxonomy. The increasing practice of reductionism with concomitant decrease of organismal biology is directed to applied sciences and more profitable programs that have driven the way for the neglect of taxonomy (Dar et al. 2012).

In a recent provocative and somewhat alarmist commentary entitled the "*End of Botany*," Crisci et al. (2020, but see also Crisci 2006, 2008), reflected on the modern meaning of botany in light of the influence of methodological reductionism. It is clear, even to the most distracted researcher, that over the last three decades or so there has been an erosion in the conceptual perception of botany as a typical multidimensional discipline. This decline is associated to the use of new, more inclusive techniques that often disconnect our understanding and objectivity from the surrounding natural world. Within this context, plant taxonomy and nomenclature, two core components in the botanical and zoological sciences, have been directly and adversely affected by reductionism, an ongoing issue for most teachers responsible for the training in plant taxonomy (Crisci et al. 2019, 2020). The limited training has produced numerous plant biologists lacking basic training, hence unable to morphologically recognize some of the most common plant species, i.e., the loss of the operational and predictive value of botany. This problem has also been addressed in a paper discussing the "*One-dimensional Systematist*," (Crisci 2006), a topic worthwhile exploring in conjunction with the aspects addressed below, which may be needed to understand this discussion.

THE EFFECT OF REDUCTIONISM ON PLANT TAXONOMY

Reductionism encompasses a set of ontology-based, epistemic, and methodological opinions about the relations between different scientific domains (Brigandt and Love 2019). In science, reductionism leads to marketable inventions that may have detrimental effect on the outcomes of quality and planning in order to attain a fabricated metric evaluation dictated by corporations and personal needs (Muller 2018). For instance, Crisci et al. (2020: 1173) stated: "*…molecular biology cannot dispense with the reference systems of biology as a whole provided by Botany, among other disciplines..., it is impossible to complete a biological project at any level of hierarchy in nature without any scientific names associated with the observations or experimentations.*" Thus, because of their multidimensional approach, the research core components of botany and plant taxonomy cannot be reduced to a few modules of investigation (Crisci 2006; Crisci et al. 2020). Reductionism alone cannot express the complexity of nature. Taxonomy, as opposed to reductionism, is based on critical and practical analyses with several layers and contextual factors leading to specific outcomes (Mingers 2014, reviewed in Fox and Alptekin 2018).

CLASSIFICATION AND IDENTIFICATION AS MULTIDIMENSIONAL METHODOLOGICAL PROCESSES

In the broad sense, classification and identification are intimately connected and are cognitive and basic aspects of botany. Their dissemination synthesis is reflected in a correct and stable procedure of scientific names according to the nomenclatural rules established by the International Code of Nomenclature (Turland et al. 2018). Because of classification and identification are complex processes based on a multidimensional knowledge, they cannot be the result of a single method focused solely on one source of information. For instance, identification cannot be based only on DNA barcodes (Hebert et al. 2002), a method that is not easy to access or that cannot replace morphology (Will and Rubinoff 2004; Will et al. 2005) and presents either promises or serious pitfalls (cf. Moritz and Cicero 2004).

On the other hand, it is likely that a good number of sequencing DNA accessions with misidentified (or lacking vouchers) has been deposited in DNA sequencing data repositories. Therefore, the reconstruction of a phylogenetic hypothesis based only on molecular information extracted from a GeneBank source without supporting reliable herbarium vouchers and accurate morphological identification of the species investigated (taxonomic sampling), is not admissible. In addition, issues of hybridization and lineage sorting are not easily resolved in a single-gene phylogeny and multiple datasets from different genomic regions are desirable to generate a more accurate phylogenetic scheme. According to Rouhan and Gaudeul (2021) molecular taxonomy is at disadvantage because of the potential lack of genetic divergence in sister-species sharing recent origins, i.e., they will share alleles due to recent ancestry. Thus, the amalgamation of different datasets, e.g., morphology and molecular, is desirable to more accurately infer evolutionary process (Hillis 1987; Humphries 1988; Patterson et al. 1993; Pennington 1996; Scotland et al. 2003; Martynov 2012; Zanini et al. 2018). In addition, the conflict emerging from combining the data sets should be considered in the outcomes (Bremer 1996; Petersen and Seberg 1998; Wiens 2004).

NAMING TAXA AND THE TYPIFICATION PROTOCOL AT A TURNING POINT

In addition to the excessive reductionism exemplified by the exclusion of formal classification and identification practices based on morphology, another aspect that seriously threatens botany is the superficial approach to botanical nomenclature including the limited knowledge and application of the rules included in the International Code of Nomenclature (Turland et al. 2018). Typification is the merging point between two basic components of botany: taxonomy and nomenclature (Witteveen 2014; Rao 2017; Thompson et al. 2018). Typification is, in fact, a very delicate and often complex process at the base of which lies the stability of scientific names, their application not only in taxonomy, but also in the evaluation of biological diversity and numerous conservation efforts (Thompson et al. 2018; O'Connell et al. 2020).

Type specimens and their names are often formalized automatically. A major responsibility in terms of issues of synonymy and faulty described species falls on journals that easily accept papers with taxonomic mistakes due to superficial and somewhat poorly researched nomenclatural decisions. Behind this issue often lies the lack of a strict peer review evaluation of original voucher materials supporting the typification and nomenclatural content. Nowadays, new species descriptions rely on digital images available on the Internet. Digitalization and natural history virtual collections are certainly important in research and classroom (Cota-Sánchez 2020a), but publishers and authors should be aware about published online digital images with unverified data and/or erroneous information that can be misleading and unrelated to the biological entity in discussion.

Naming of species, as epistemological process, is a basic step in any scientific discipline (Valdecasas et al. 2014; Holstein and Luebert 2017). In biology, and botany in particular, seven characteristics can be associated to formal scientific names including: individuation, hypothesis of relationship, retrieval information, explanatory power, testable predictions, conceptual power, and language (Valdecasas et al. 2014). All these attributes support the stability of each scientific name through the correct process of typification that permits to reproduce and scientifically verify the application of each name.

The process of naming plant species includes uniform and internationally acceptable principles (Haider 2018), but it is often considered a superfluous exercise and a sort of aristocratic waste of time because it can be a tedious and prolonged process (Riedel et al. 2013). Linking a name to an organism (a plant for example), is not a specious exercise but implies an epistemological process that makes any name verifiable anytime allowing to standardize the assessment of biodiversity. Taxonomic plant checklists, floras and monographs are produced with verified names and associated vouchers supporting species' identity by experts in the field (Grace et al. 2021). In other words, taxonomy (and nomenclature) are key components of biology (Costello 2020) and species are the currency of biodiversity (Sigwart et al. 2018), which and in conjunction with monographs disseminate scientific information to accelerate research (Grace et al. 2021).

It is often the case that in numerous university courses when students are asked what the "name" or the components of a scientific name in a plant or animal means, an extensive unawareness about taxonomy and nomenclature is revealed. We believe that students in natural sciences cannot leave university after graduation without mastering the basic principles of scientific names and communication as universal language on which the natural order of the biological knowledge is founded. Furthermore, an integration between descriptive general morphology, ecological and molecular data in the diagnostic and analytical description of a new taxon must be embraced, appreciated and improved (Tautz et al. 2003; Hassemer et al. 2020; Hütter et al. 2020). Training in taxonomy and nomenclature should encompass a holistic equilibrium between morphology and molecular data and other information available (Dunn 2003).

NATURAL COLLECTIONS AND THEIR DESTINY

The decline and reduction of botany is not only due to the extreme effect of scientific reductionism. For years, herbaria, including natural history museums with their vast richness of historical artifacts and natural biological collections, which constitute the foundation of the knowledge of biological diversity, have been gradually losing institutional and governmental support for funding, infrastructure, and professional and technical personnel. In fact, many institutions remain active thanks to various forms of volunteering and citizen science programs. In many cases, these facilities are in a serious danger of permanent shutdown. Problems due to the lack of funding including basic house-keeping budget, potential employment of new taxonomists, and bureaucracy in the processing of collecting permits are well discussed by Britz et al. (2020), whereas planning, usage, datamining and organization future specimen collections is found in Krell and Wheeler (2014).

It is unfortunate that in a world in which the loss of biodiversity has increased to alarming levels with limited mitigation proactive efforts, the value of biological collections has also been underestimated and their scientific meaning for understanding biodiversity undermined (Meineke et al. 2018). However, several endeavors have been focused on the management, use and exploitation of the vast data stored in biological collections (Baldini and Guglielmone 2012; Rønsted et al. 2020), including preserved specimens in herbaria and living material in botanical gardens, with ensuing digitalization and big data captured in online cyber portals and databases available on the Internet (Heberling and Isaac 2017; Soltis 2017; James et al. 2018; Alba et al. 2020; Miralles et al. 2020; Paton et al. 2020).

CAN JOURNAL METRICS BE USED TO EVALUATE PLANT TAXONOMY?

The journal metric evaluation, based on the number of bibliographic citations of a research article by a journal or a researcher, influences the quality and often the originality and value of a scientific production, including botany (cf. Alberts 2013; Crisci 2006; Muller 2018; Crisci and Katinas 2020). Nowadays all aspects that establish the scientific production are often related to economic profit, in which social and human interactions are pure marketing relationships. Thus, we question is whether this metric assessment is a trustworthy parameter to assess the value of botany-related publications. Furthermore, the rigid metrics and impact factor method to taxonomic research are inapplicable as stated by Krell (2000: 507) "*… is impossible to classify taxonomic or ecology journals as more or less important. They can only be classified as of high or low quality, which does not affect the number of citations.*"

Taxonomy, as one of the oldest biological disciplines, cannot be evaluated as other subjects, such as molecular genetics, bacteriology, virology, neuroscience or cancer research. The fact that these other fields have more practical applications in technology explains how impact factors adversely affect taxonomic research with a decrease in funding opportunities, number of taxonomists and limited appreciation (Ebach et al. 2011; Britz et al. 2020).

As indicated, Crisci et al. (2020), affirm that in recent times the term "botany" has been increasingly replaced with "plant sciences," as if it had a derailing connotation. The authors add that this practice should be avoided, stating that "*Part of this image problem is based on misconceptions of how some botanical subdisciplines work*" (Crisci et al. 2020: 1174). The view that plant taxonomy and nomenclature are purely formal aspects of plant knowledge based solely on description and its nominal understanding, is an evident misunderstanding and adverse notion of these foundational scientific concepts. We agree with Crisci et al. (2020: 1174) that plant taxonomy must be considered a scientific discipline that requires "*theoretical, empirical and epistemological rigor, a hypothesis-driven approach, and field and lab expertise.*" As such, emphasis must be made to reinstate this discipline in major biological academic programs throughout the world, especially in tropical countries where the largest spots with plant animal diversity remain.

A DECLINE OF INTEREST AND SUPPORT IN TAXONOMY OR SOMETHING ELSE?

In this regard, it is important to reflect how we, as botanists, place ourselves with respect to the study of plants. While we admit and welcome the impressive impact of new research technologies for human development, we advocate that plant taxonomy should be maintained at the center of the imminent destiny of the biosphere. With an evolving economy and strong trend towards applied science, the debate is still open and challenging (Wheeler and Meier 2000; Schuh 2003; Will et al. 2005; Garnet and Christidis 2017; Funk et al. 2017), but most importantly, it is worth considering that botany deserves the right of citizenship as a multidisciplinary science rather than a downgraded subject as part of reductionism.

It is also essential to recognize that botany, in particular plant taxonomy, has an integral role as discipline in the understanding of reality. The excessive reductionism prevailing in contemporary educational systems may disregard and ultimately eliminate its cognitive centrality needed to understand nature. A good starting point towards the resurgence of organismal taxonomy is found in a recent stimulating and promising paper by Wheeler (2020). However, as stated by Tancoigne and Dubois (2013), it is not a matter of declining but of inertia that affects taxonomy. We argue that the existing crisis of "*inertia*" in taxonomy requires rapid action by the community of taxonomists around the world. As pointed out in Wheeler (2014) and Bebber et al. (2014), a sensitive aspect can be also traced in the relationship between the increase quantity of new species described and number of authors involved in the designation. This practice seems to reflect changes in the scientific practice rather than taxonomic expertise, quality and capacity in plant taxonomy. Increased number of authors in the species description of a new species doesn't necessary mean more taxonomic training and equal understanding of typification, taxonomic and nomenclatural rules among investigators.

A last, but not of lesser importance, in addition to reductionism, an issue for deliberation regarding the future of taxonomy is how the COVID-19 pandemic has been affecting the teaching and training of the future generations of plant taxonomists (Cota-Sánchez 2020a) and the world's botanical community (Baldini 2020; Cota-Sánchez 2020b). Current academic programs for instruction in plant systematics and training in taxonomy and nomenclature around the world involve remote teaching models in conjunction with numerous digital botanical archives and supporting digital and social media platform for plant identification. Nonetheless, current experiences by the authors of this commentary indicate while training in taxonomy may be successful, the effectiveness of the delivery and grasping and accurate use of terminology is hampered by the lack of direct face-to-face contact and live specimens for demonstration and training.

As a result of the challenges imposed by remote teaching, which was new for many, several organizations have made significant contributions to online instruction during the COVID-19 crisis. Worth mentioning is the dedication of the Education Committee of the Botanical Society of America (BSA). This organization has been offering remote peer support sessions for teaching, a great forum to share teaching ideas and resources and to discuss techniques that work well and those not working for the instructor and students. The BSA also has a fabulous resource section (https://cms.botany.org/home/resources/online_resources.html) with links to diverse and interesting creative teaching exercises that can be adapted for online undergraduate courses in biological sciences, including botany (BSA, 2021). We feel that all these resources, and many others available in the public domain, will be very handy for students and instructors to become more confident in the remote teaching world. Therefore, it should not be difficult for botany instructors to find creative and innovative ways to approach teaching and training in plant taxonomy and keep this basic discipline alive rather than extinguishing.

In summary, we should be mindful that in the light of climate change and unparalleled anthropogenic changes, the current biodiversity crisis needs urgent attention to classify, name, and identify the remaining biological diversity in order to cover with intellectual competence knowledge gaps, especially in plant taxonomy (Aedo et al. 2017). It is only with coordinated efforts among plant and animal taxonomists, academic institutions, industries and governments that this traditional but essential scientific field will reemerge as an ultimate resource, including the rediscovery of the value of botanical monographies (Grace et al. 2021), to catalogue those unknown species waiting to be described in the lingering pristine terrestrial and marine ecosystems of the Earth.

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The taxonomic circumscription of *Aconitum* subgenus *Aconitum* (Ranunculaceae) in Europe

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Abstract. In this article, we present a revised taxonomic circumscription of *Aconitum* subg. *Aconitum* (Ranunculaceae) in Europe. In total, the subgenus contains some 250 species with the major center of diversity in Eastern Asia. Altogether 94 taxa (species and infraspecific taxa, including hybrids) occur in Europe. Among them, 22 are native species, and 28 are nothospecies (including hybrid formulae). The research is based on former (since Linnaeus) and recent species diagnoses integrating herbarium and field studies carried out in the Alps, Carpathians, Balkans, Spanish Sierra Nevada, Sudetes, and Corsica. The subgenus includes three sections in Europe: the diploid sect. *Cammarum*, the tetraploid sect. *Aconitum*, and the monospecific, allopolyploid sect. *Angustifolium*. Additionally, a triploid, hybridogenous nothosection *Acomarum* (sect. *Aconitum* × sect. *Cammarum*) is presented. For each species, type citation, a concise morphological description, including infraspecific variation and hybridization, geographical distribution, and iconography sources are given. Also, a key to the determination of all taxa is presented. The proposed system scrutinizes former and recent species concepts and gives a base for further studies on the genus' phylogeny and biotechnology.

Keywords: *Aconitum,* geographical distribution, Europe, hybrids, Linnaean taxonomy, nomenclature, species concept.

INTRODUCTION

The genus *Aconitum* L. (monkshood) comprises ca. 300–400 species distributed in temperate regions of the northern hemisphere, with a center of diversity in the eastern Himalaya, southwestern China, and Japan (Kadota 1987; Li and Kadota 2001; Luo et al. 2005). From a total number of ca. 250 species belonging to the subgenus *Aconitum*, 22 species may be found in Europe, with eight species occurring exclusively in the Carpathian and Balkans Mts (Boroń et al. 2020). The subgenus includes both the "temperate" forest (diploid) and "cold" high-mountain (tetraploid) species, which are differentiated both morphologically (Starmühler 1998; Mitka 2003; Novikoff and Mitka 2011) and cytogenetically (Ilnicki and Mitka 2009, 2011).

Genera *Aconitum* L., *Delphinium* L., *Consolida* (DC.) S.F Gray, *Aconitella* Spach, and *Staphisagria* J. Hill form the monophyletic tribe Delphinieae Schröd., subtribe Delphiniinae Benth. & Hook. f. (Tamura 1993; Keener et al. 1999; Turland and Barrie 2001; Jabbour and Renner 2011a, b). Zygomorphic flowers and the presence of diterpene alkaloids turned out to be the synapomorphies to this taxonomic group (Johansson 1995; Jabbour et al. 2009, 2014). Genus *Aconitum* consists of the following monophyletic subgenera: subg. *Aconitum*, subg. *Fletcherum* (Tamura) Y.Hong & Q.E.Yang, subg. *Galeata* (Rapaics) Y.Hong & Q.E.Yang, and subg. *Lycoctonum* (DC.) Peterm. (Kita et al. 2000; Utelli and Ito 2000; Luo et al. 2005; Jabbour and Renner 2011b; Hong et al. 2017). The monophyly and taxonomic rank of subg. *Anthora* (Rapaics) Peterm. is unclear and deserves further studies (Novikoff and Mitka 2015). The endemic of the Qinghai–Tibetan Plateau *A. gymnandrum* Maximowicz has been recently transferred from the monotypic *Aconitum* subg. *Gymnaconitum* (Stapf) Rapaics to an independent genus *Gymnaconitum* (Stapf) Wei Wang & Z.D.Chen based on molecular data (Wang et al. 2013).

Aconitum subg. *Aconitum* is known for its remarkable morphological plasticity and notorious hybridization, leading to difficulties in the circumscription of taxa (Kadota 1981; Tutin et al. 1993; Sutkowska et al. 2013, 2017a, b). To clarify the sectional treatment of the subgenus, we used both cytogenetic and morphological criteria (Starmühler 1996b, 2000; Ilnicki and Mitka 2009, 2011; Joachimiak et al. 1999; Mitka and Starmühler 2000; Novikoff and Mitka 2011).

The subgenus *Aconitum* in Europe has basic (monoploid, i.e., in a single complete set of chromosomes) number $x = 8$ and ploidy levels $2x$, $3x$, $4x$, and $6x$. It consists of the diploid sect. *Cammarum* DC. (2n ($2x$) = 16), the triploid nothosection *Acomarum* Starm. (2n ($3x$) = 24), the tetraploid sect. *Aconitum* (2n ($4x$) = 32), and the monospecific hexaploid sect. *Angustifolium* (Seitz) Rottensteiner, represented by the allopolyploid *A. angustifolium* Rchb. (2n ($6x$) = 48) (Seitz 1969; Zieliński 1982a, b; Simon et al. 2001; Ilnicki and Mitka 2009, 2011).

Section *Aconitum* includes high-mountain species that inhabit open sites in the subalpine and alpine zones. Section *Cammarum* is represented by forest species, which usually are distributed in montane (up to ca. 1150–1200 m above sea level), foreland and lowland/upland areas (Mitka 2000, 2002; Novikoff and Mitka 2011). Intersectional hybrids (*Aconitum* sect. *Aconitum* × *Aconitum* sect. *Cammarum*) are circumscribed within nothosect. *Acomarum* Starm. (Wacławska-Ćwiertnia and Mitka 2016; Starmühler 2001).

We also include to the list *A. carmichaelii* from the section *Euchylodea* with 2n ($4x$) = 32, 2n ($6x$) = 48 or, often, 2n ($8x$) = 64 (Yang 1996; Li and Kadota 2001). In Europe, *A. carmichaelii* is used as an ornamental plant, while in China (native area) it is mostly cultivated for medicinal purposes (Yu et al. 2016; Zhao et al. 2017).

In the present article, we propose an annotated Linnaean taxonomic system of *Aconitum* subg. *Aconitum* in Europe. It is based on the classical works by Reichenbach (1819, 1821, 1827, 1840), Gáyer (1906, 1909, 1911, 1912), Götz (1967), Seitz (1969), Skalický (1982), and Flora Europaea (Tutin et al. 1993), supplemented by our recent systematic studies carried out in the Alps, Carpathians, Sudetes, and Balkans.

We adopt the following taxonomic treatment of *Aconitum* subgenus *Aconitum* in Europe (see also Appendix):

Aconitum L. subg. *Aconitum*
1. Sect. *Aconitum*
    1A. Subsect. *Aconitum* [syn. sect. *Napellus* Wolf (DC.) subsect. *Napellus* (Wolf) Rapaics]
        1a. Ser. *Aconitum*
        1b. Ser. *Castellana* Rottensteiner, **ser. nov.**
        1c. Ser. *Taurica* Mucher ex Starm.
        1d. Nothoser. *Acorica* Mucher ex Starm. (ser. *Aconitum × ser. Taurica*)
    1B. Subsect. *Burnatii* Rottensteiner
2. Sect. *Cammarum* DC.
    2A. Subsect. *Cammarum* (DC.) Rapaics
        2a. Ser. *Variegata* Steinberg ex Starm.
        2b. Ser. *Toxica* (Rchb.) Mucher
        2c. Nothoser. *Toxigata* Starm. (ser. *Toxica* × ser. *Variegata*)
3. Nothosect. *Acomarum* Starm. (sect. *Aconitum* × sect. *Cammarum*)
4. Sect. *Angustifolium* (Seitz) Rottensteiner, **stat. nov.**
5. Sect. *Euchylodea* Rchb.
    5a. Ser. *Japonica* (Nakai) Kadota

MATERIAL AND METHODS

We have evaluated all recognized taxa from the *Aconitum* subg. *Aconitum* distributed in Europe based on our experience of many years of field investigations, morphological and biogeographical studies, as well as analysis of herbarium material. For each taxon, we provided comprehensive data on its distribution and morphological characteristics. We reviewed all available sources for taxon synonymy and type citations. Basing on morphological data, a binary key for the identification of the representatives of the subgenus *Aconitum* has been developed.

The chromosome numbers were investigated in the Carpathians and Sudetes Mts (Joachimiak et al. 1999; Ilnicki and Mitka 2009, 2011; Mitka et al. 2007) or taken from the on-line DCDB database (http://hdl.handle.net/2445/95875; Bosch et al. 2016).

RESULTS

Key to the taxa of Aconitum *subgenus* Aconitum *in Europe*

1\. Root napiform; stem ± stiff upright, rarely ± flexuous (*A.* sect. *Burnatii*); cauline leaves usually without reticulate venation; seeds smooth to transverse wrinkled or with transverse lamellae on one side, the uppermost segment of the leaf lobe with two, rarely with 4–6 teeth 2

1.* Root globose; stem upright to bent to overhanging or spreading-climbing, flexuous; cauline leaves with reticulate venation; seeds always with transverse lamellae on one side, the uppermost segment of the leaf lobe, located in its middle, with 4–12 teeth....................sect. *Cammarum* ….35

2\. Carpels sterile……………………………nothosect. *Acomarum* (*A.* sect. *Aconitum* × *A.* sect. *Cammarum*)............3

2.* Carpels fertile ………..14

3\. Hood outside glabrous (or with just some single hairs) ………...4

3.* Hood outside hairy 11

4\. Cauline leaves net-veined...... *A. superbum* × *A. variegatum*

4.* Cauline leaves not net-veined...5

5\. Pedicel glabrous or with just some single hairs at the top; filaments glabrous or just sparsely pilose............................6

5.* Pedicel hairy at least above the bracteoles; filaments ± densely pilose..7

6\. Carpels mostly completely glabrous ……………..................... ....*A. ×acutum* (*A. tauricum* × *A. variegatum*)

6.* Carpels pilose on the suture.. ....*A. ×berdaui* nothosubsp. *berdaui* (*A. firmum* subsp. *firmum* × *A. variegatum* subsp. *variegatum*)

7\. Pedicels with glandular hairs...8

7.* Pedicels without glandular hairs 9

8\. Pedicel pilose with strict glandular hairs ………....……… .... *A. ×mielichhoferi* (*A. degenii* × *A. tauricum*)

8.* Pedicel pilose with curved and s-formed glandular hairs..... ....*A. pilipes* × *A. tauricum*

9\. Pedicels above the bracteoles with curved, crisped and strict hairs ... *A. ×cammarum* (*A. napellus* × *A. variegatum*)

- a. Tepals with monotonic deep blue color .... fo. *cammarum*
- a.* Tepals white and blue strips............................. fo. *bicolor*

9.* Pedicels above the bracteoles only with curved and crisped hairs 10

10\. Bracteoles triangular to linear, 2–5 mm long........................ ....*A. ×exaltatum* (*A. plicatum* × *A. variegatum* subsp. *variegatum*)

10.* Bracteoles lanceolate to spathulate, 5–7 mm long............... .... *A. ×schneebergense* (*A. napellus* × *A. variegatum*)

11\. Cauline leaves net-veined........*A. superbum* × *A. vitosanum*

11.* Cauline leaves not net-veined 12

12\. Tepals outside with only eglandular hairs............................. ....…. *A. ×berdaui* nothosubsp. *walasii* (*A. firmum* subsp. *moravicum* × *A. variegatum* subsp. *variegatum*)

12.* Tepals outside with eglandular and glandular hairs........13

13\. Tepals outside with curved eglandular hairs and s-formed glandular hairs..................................*A. napellus* × *A. pilipes*

13.* Tepals outside with curved eglandular hairs and strict glandular hairs. *A. ×acuminatum* (*A. degenii* × *A. napellus*)

14\. Cauline leaves with uppermost leaf segments only 1–3 (–4) mm broad; tepals light blue to whitish; hood ± triangular; seeds with transverse lamellae.. .... sect. *Angustifolium*…*A. angustifolium*

- a. Pedicels and tepals outside glabrous.......fo. *angustifolium*
- a.* Pedicels and tepals outside ± pubescent..fo. *carniolicum*

14.* Cauline leaves mostly with broader leaf segments; tepals mostly blue to violet; hood ± hemispherical; seeds smooth to transverse wrinkled ....sect. *Aconitum*…15

15\. Stem at least in the inflorescence region flexuous (zigzag); inflorescence axis, pedicels and tepals outside glandular pilose...subsect. *Burnatii*…16

15.* Stem stiff, upright; inflorescence axis, pedicels and tepals outside with a different pubescence ....subsect. *Aconitum*…19

16\. Hood about as broad as high...........................*A. maninense*

16.* Hood distinctly broader than high...................................17

17\. Stem in the lower third glabrous; cauline leaves almost glabrous; nectary spur globose ....*A. pentheri*

17.* Stem in the lower third pubescent or pilose; cauline leaves densely pilose; nectary spur hooky 18

18. Stem in the lower third pubescent; cauline leaves with narrow segments; pedicels straight; filaments glabrous or pilose .... *A. burnatii*

18.* Stem in the lower third pilose; cauline leaves with broad segments; pedicels bent; filaments always pilose .... *A. nevadense*

19. Nectary spur elongated and bent backward .... ser. *Castellana* … *A. castellanum*

19.* Nectary spur not elongated and not bent backward 20

20. Nectary spur distinctly globose; tepals outside glabrous to densely pubescent .... ser. *Aconitum*…21

20.* Nectary acephalous; tepals outside glabrous or only sparsely pubescent .... ser. *Taurica*…32

21. Nectary claw erect or only slightly curved at the top .... *A. corsicum*

21.* Nectary claw distinctly curved 22

22. Cauline leaves net-veined 23

22.* Cauline leaves not net-veined 30

23. Tepals outside densely curved and crisped eglandular pubescent, plant above 2 m high .... *A. superbum*

23.* Tepals outside with a different pubescence or glabrous 24

24. Tepals outside densely curved and crisped eglandular pubescent and glandular pilose, bracteoles divided .... *A. firmum* subsp. *skerisorae*

24.* Tepals outside glabrous or hairy 25

25. Tepals outside and pedicels glabrous .... *A. firmum*

a. Bracteoles all similar, undivided, lanceolate....subsp. *fissurae*

a.* Bracteoles of lower flowers bigger and divided .... b

b. Bracteoles of lower flowers in ± deeply divided .... subsp. *firmum*

b.* Bracteoles of lower flowers only bigger or just little divided ....nothosubsp. *fussianum* (subsp. *firmum* × subsp. *fissurae*)

25.* Tepals outside and pedicels eglandular pubescent hairy ....

a. Pedicels eglandular pubescent .... *A. firmum* subsp. *moravicum*

a.* Pedicels below the bracteoles glabrous .... *A. firmum* subsp. *moravicum* × *A. variegatum* subsp. *variegatum*

25.** Tepals outside glabrous or hairy, pedicels glandular or glandular/eglandular pubescent 26

26. Pedicels glandular pilose only above bracteoles ....*A.* ×*mariae* nothosubsp. *mariae* (*A. firmum* subsp. *firmum* × *A. maninense*)

26.* Pedicel with a different pubescence 27

27. Pedicels curved and crisped eglandular and glandular pubescent, mainly above the bracteoles, tepals outside glabrous .... *A.* ×*nanum* (*A. bucovinense* × *A. firmum*)

27.* Pedicels with a different pubescence 28

28. Pedicels sparsely glandular pubescent only above the bracteoles .... *A.* ×*czarnohorense* (*A. firmum* × *A.* ×*nanum*)

28.* Pedicels with a different pubescence 29

29. Pedicels and tepals outside curved and crisped eglandular pubescent and glandular pilose ......*A.* ×*mariae* nothosubsp. *paxii* (*A. firmum* subsp. *moravicum* × *A. maninense*)

29.* Pedicels only sparsely curved and crisped eglandular pubescent and glandular pilose, mainly just above the bracteoles, tepals outside glabrous .... *A.* ×*zapalowiczii* (*A. firmum* × *A.* ×*mariae* nothosubsp. *paxii*)

30. Pedicels densely curved and crisped eglandular and glandular pubescent .... *A. bucovinense*

a. Carpels glabrous or rarely pilose on the ventral side .... fo. *bucovinense*

a.* Carpels pubescent .... fo. *orthotricha*

30.* Pedicels eglandular hairy 31

31. Cauline leaves with linear to narrow lanceolate segments, the uppermost 2–4 mm broad, longly acuminated; flowers mauve to mauvish-blue; hood 18–20 mm high from base .... *A. anglicum*

31.* Cauline leaves with mostly broader segments, which are shortly acuminated; flowers dark blue to violet; hood 13–18 (–20) mm high from the base .... *A. napellus*

a. Carpels densely pubescent; often with bulbils in the lower leaves .... subsp. *lobelii*

a.* Carpels glabrous or just sparsely pubescent on the backside; never with bulbils .... b

b. Carpels sparsely pubescent on the backside c

b.* Carpels glabrous .... d

c. Bracteoles 2–3 (–4) mm long ..... nothosubsp. *polatschekii* (subsp. *formosum* × subsp. *lobelii*)

c.* Bracteoles (3–) 5–8 (–20) mm long ... nothosubsp. *seitzii* (subsp. *lobelii* × subsp. *napellus*)

d. Filaments of stamens toothed .... subsp. *lusitanicum*

d.* Filaments of stamens not toothed.................................. e

e. Bracteoles (3–) 5–8 (–20) mm long; carpels 3 (–4).......... .... subsp. *napellus*

e.* Bracteoles shorter; carpels 2–3 ....f

f. Bracteoles 1–2 (–3) mm long; carpels 2–3 .... subsp. *formosum*

f.* Bracteoles (2–) 3 (–4) mm long; carpels (2–) 3 .... nothosubsp. *hinterhuberi* (subsp. *formosum* × subsp. *napellus*)

32. Tepals outside always glabrous .... ser. *Taurica*

A. Stem rigid, bracteoles linear to lanceolate 2–5 (–7) mm, carpels 3; tepals outsides always glabrous .. *A. tauricum*

a. Pedicels with strict and crisped, glandular or eglandular hairs above the bracteoles; carpels often sparsely pubescent on the suture .... subsp. *latemarense*

a.* Pedicels with only few hairs on the top or glabrous; carpels mostly glabrous ....b

b. Pedicels with solitary hairs at the top; carpels mostly glabrous .... nothosubsp. *hayekianum* (subsp. *latemarense* × subsp. *tauricum*)

b.* Pedicels glabrous; carpels glabrous....subsp. *tauricum*

I. Inflorescence with many, ± long side racemes ....var. *eustachyum*

I.* Inflorescence without or only with few short side racemes .... var. *tauricum*

i. Nectaries and filaments glabrous....fo. *tauricum*

i.* Nectaries and filaments ± densely pilose ....fo. *taurericum*

A.* Stem weekly ramificated, bracteoles triangular to linear, 1–2 (–3) mm long; carpels 2 (–3) ....*A. clusianum*

32.* Tepals outside sparsely hairy... 33

33. Bracteoles triangular to linear, 1–2 (–3) mm long; carpels 2 (–3) .... *A. plicatum*

a. Pedicels eglandular pubescent, carpels glabrous...................... .... subsp. *plicatum*

a.* Pedicels eglandular and/or glandular pilose; carpels pubescent... subsp. *sudeticum*

33.* Bracteoles linear, lanceolate or spathulate, 3–5 (–8) mm long; carpels 2–3... 34

34. Bracteoles situated always shortly below the flower at the top of the pedicel; carpels (2–) 3.. .... *A. ×teppneri* (*A. napellus* × *A. tauricum*)

a. Carpels glabrous..b

a.* Carpels sparsely pubescent on the backside c

b. Pedicels sparsely curved and crisped eglandular pubescent...nothosubsp. *teppneri* (*A. napellus* subsp. *napellus* × *A. tauricum* subsp. *tauricum*)

b.*Pedicels glandular and eglandular curved and crisped pubescent and pilose....................... nothosubsp. *kerneri* (*A. napellus* subsp. *napellus* × *A. tauricum* subsp. *latemarense*)

c. Pedicels sparsely curved and crisped eglandular pubescent..nothosubsp. *goetzii* (*A. napellus* subsp. *lobelii* × *A. tauricum* subsp. *tauricum*)

c.* Pedicels glandular and eglandular curved and crisped pubescent and pilose................ nothosubsp. *haderlappii* (*A. napellus* subsp. *lobelii* × *A. tauricum* subsp. *latemarense*)

34.* Bracteoles situated distant from the flower, below to or in the middle of the pedicel; carpels 2–3................................... ....*A. ×bavaricum* (*A. napellus* × *A. plicatum*)

a. Carpels glabrous....... nothosubsp. *bavaricum* (*A. napellus* subsp. *napellus* × *A. plicatum*)

a.* Carpels sparsely pubescent on the backside ....nothosubsp. *lusenense* (*A. napellus* subsp. *lobelii* × *A. plicatum*)

35. Pedicels and tepals outside glabrous or eglandular pubescent...ser. *Variegata*…36

35.* Pedicels and tepals outside glandular pilose or very rarely glabrous (*A. degenii* subsp. *rhaeticum*, *A. toxicum* subsp. *bucegiense*)..39

36. Pedicels eglandular curved pubescent; carpels glabrous or pubescent on the backside

a. bracteoles at the middle of pedicel or below..................... ....sect. *Euchylodea*…*A. carmichaelli*

a.* bracteoles in the upper part below flower....................37

36.*Pedicels mostly glabrous; tepals outside always glabrous; carpels glabrous or pilose on the suture............................38

37. Pedicels and tepals outside eglandular curved pubescent; carpels mostly pubescent on the backside ...... *A. vitosanum*

37.*Pedicels sparsely eglandular curved pubescent; tepals outside glabrous; carpels mostly glabrous ....*A. ×aquilonare* (*A. variegatum* × *A. vitosanum*)

38. Hood not much higher than broad; claws of the nectaries strongly curved; spurs of the nectaries mostly reaching the top of the hood; carpels 3, glabrous .... *A. vivantii*

38.* Hood distinctly higher than broad; claws of the nectaries upright; spurs of the nectaries not reaching the top of the hood; carpels 3–5, glabrous or pilose on the suture............. ....*A. variegatum*

a. Carpels 3, glabrous.................................... subsp. *nasutum*

a.* Carpels 3–5, pilose at least on the suture......................b

b. Carpels 3, only sparsely pilose on the top of the suture .. .. nothosubsp. *podobnikianum* (subsp. *nasutum* × subsp. *variegatum*)

b.* Carpels 3–5, densely pilose on the suture .... subsp. *variegatum*

c. Bracteoles 2–3 (–5) mm long, linear to narrow lanceolate; carpels always 3.....................................var. *carniolicum*

c.* Bracteoles (4) 5–8 (–25) mm long, spathulate, ovate or leaflike; carpels (3–) 5...d

d. Leaf sheaths underside pubescent; pedicels sparsely pubescent below the bracteoles; carpels pilose on the suture and often also on the backside ....var. *stiriacum*

d.* Leaf sheaths underside glabrous; pedicels glabrous; carpels only pilose on the suture.......................var. *variegatum*

39. Tepals outside densely glandular pilose or very rarely glabrous ....(*A. degenii* subsp. *rhaeticum*, *A. toxicum* subsp. *bucegiense*)…ser. *Toxica*…40

39.* Tepals outside totally or almost glabrous .... nothoser. *Toxigata*…46

40. Hood distinctly higher than broad; nectary claw upright; nectary spur not reaching the top of the hood 41

40.* Hood about as high as broad or broader than high; nectary claw curved; nectary spur always reaching the top of the hood 42

41. Pedicels and tepals outside with curved and s-formed glandular hairs.. *A. pilipes*

41.* Pedicels and tepals outside with straight glandular hairs.... .... *A. lasiocarpum*

a. The whole pedicel glandular pilose.....subsp. *lasiocarpum*

a.* Pedicel only above the bracteoles glandular pilose, below the bracteoles glabrous or curved or crisped eglandular pubescent ....subsp. *kotulae*

42. Bracteoles broad ovate, with reticulate venation.... *A. toxicum*

a. Tepals outside glabrous or almost glabrous....................b

a.* Tepals outside curved or straight glandular pilose c

b. Pedicels glabrous.................................... subsp. *bucegiense*

b.*Pedicels just sparsely straight glandular pilose, mainly above the bracteoles..........nothosubsp. *ungarianum* (subsp. *bucegiense* × subsp. *toxicum*)

c. Pedicels and tepals outside only with straight glandular hairs ....subsp. *toxicum*

c.*Pedicels and tepals outside also or only with curved glandular hairs..d

d. Pedicels and tepals outside with curved and straight glandular hairs............... nothosubsp. *nyaradyanum* (subsp. *crispulum* × subsp. *toxicum*)

d.* Pedicels and tepals outside only with curved glandular hairs .... subsp. *crispulum*

42.* Bracteoles linear to narrow ovate 43

43. Pedicels and tepals outside with straight, curved and s-formed glandular hairs ....*A. ×pilosiusculum* (*A. degenii* × *A. pilipes*)

43.* Pedicels and tepals outside only with straight glandular hairs 44

44. Bracteoles narrow ovate or spathulate, with branching veins .... *A. ×dragulescuanum* (*A. degenii* × *A. toxicum*)

a. Pedicels, bracteoles and tepals outside only with straight glandular hairs......nothosubsp. *dragulescuanum* (*A. degenii* subsp. *degenii* × *A toxicum* subsp. *toxicum*)

a.* Pedicels, bracteoles and tepals outside with curved and straight glandular hairs........nothosubsp. *grintescuanum* (*A. degenii* subsp. *degenii* × *A toxicum* subsp. *crispulum*)

44.* Bracteoles linear to lanceolate, without branching veins..... 45

45. Nectary claw distinctly curved; nectary spur capitate or slightly recurved... *A. degenii*

a. Tepals outside glabrous ....b

a.* Tepals outside glandular pilose....................................... c

b. Pedicels glabrous..................................... subsp. *rhaeticum*

b.* Pedicels sparsely glandular pilose, mainly above the bracteoles..........................nothosubsp. *lippertianum* (subsp. *paniculatum* × subsp. *rhaeticum*)

c. Bracteoles linear, situated about in the middle of the pedicel..subsp. *paniculatum*

I. Nectaries and filaments glabrous.........var. *laxiflorum*

I.* Nectaries glabrous or pilose; filaments ± densely pubescent ....var. *turrachense*

c.* Bracteoles lanceolate to spathulate, situated at the top of the pedicel .... e

e. Carpels 5, densely pilose ....subsp. *valesiacum*

e.* Carpels 3–5, mostly glabrous..f

f. Pedicels below the bracteoles almost glabrous; carpels 3–5, mostly glabrous............ nothosubsp. *gandogeri* (subsp. *paniculatum* × subsp. *valesiacum*) f.* Pedicels below the bracteoles sparsely to densely glandular pilose; carpels 3, glabrous .... subsp. *degenii*

II. Pedicels below the bracteoles only sparsely glandular pilose .... var. *intermedium*

II.* Pedicels below the bracteoles densely glandular pilose.. .... var. *degenii*

i. Hood ± hemispheric ....fo. *degenii*

i.* Hood cymbiform, spur of nectaries capitate.............. .... fo. *craciunelense*

45.* Nectary claw almost upright and only very slightly curved; nectary spur elongated and half or almost totally recurved................*A.* ×*gayeri* (*A. degenii* × *A. lasiocarpum*)

46. Hood distinctly higher than broad; nectary claw upright; nectary spur not reaching the top of the hood 47

46.* Hood about as high as broad or slightly higher; nectary claw curved; nectary spur always reaching the top of the hood 48

47. Pedicels sparsely crisped and s-formed glandular pilose, mainly above the bracteoles; carpels (3–) 5 mostly ± densely pilose .... *A.* ×*austriacum* (*A. pilipes* × *A. variegatum*)

47.* Pedicels sparsely straight glandular pilose, mainly above the bracteoles; carpels 3–5, pilose only on the suture......... .... *A.* ×*pawlowskii* (*A. lasiocarpum* × *A. variegatum*)

48. Bracteoles narrow, without reticulate veination............... 49

48.* Bracteoles broad spathulate to narrow ovate, with reticulate venation.. 50

49. Tepals outside sparsely glandular pilose; carpels 3–5........... .... *A.* ×*hebegynum* (*A. degenii* × *A. variegatum*)

49.* Tepals outside glandular pilose and eglandular pubescent; carpels 3.........*A.* ×*tuscheticum* (*A. degenii* × *A. vitosanum*)

50. Carpels glabrous or pilose on the suture................................ ....*A.* ×*bartokianum* (*A. toxicum* × *A. variegatum*)

a. Pedicels and tepals outside curved glandular pilose; carpels glabrous ....nothosubsp. *rapaicsianum* (*A. toxicum* subsp. *crispulum* × *A. variegatum* subsp. *nasutum*)

a.* Pedicels and tepals outside straight glandular pubescent ....b

b. Carpels glabrous............ …nothosubsp. *bartokianum* (*A. toxicum* subsp. *toxicum* × *A. variegatum* subsp. *nasutum*)

b.* Carpels pilose on the suture... ....nothosubsp. *sooanum* (*A. toxicum* subsp. *toxicum* × *A. variegatum* subsp. *variegatum*)

50.* Carpels entirely pubescent.....*A. lasiocarpum* × *A. toxicum*

TAXONOMIC TREATMENT

Aconitum L. sect. *Aconitum* subsect. *Aconitum* ser. *Aconitum* in Europe is represented by six species, four nothospecies, and one hybrid formula; ser. *Castellana* Rottensteiner – by single species; ser. *Taurica* Mucher ex Starm. – by two species; nothoser. *Acorica* Starm. (ser. *Aconitum* × ser. *Taurica*) – by one species and two nothospecies (Mitka et al. 2017).

Aconitum sect. *Aconitum* subsect. *Burnatii* Rottensteiner consists of four endemic species distributed in the Sierra Nevada, Maritime Alps, French Massif Central, Balkans, and Western Carpathians (Rottensteiner 2018).

Aconitum sect. *Cammarum* DC. ser. *Variegata* Steinberg ex Starm. in Europe comprises three species and one nothospecies; ser. *Toxica* (Rchb.) Mucher is represented by four species, three nothospecies, and one hybrid formula; nser. *Toxigata* Starm. (ser. *Toxica* × ser. *Variegata*) – by five nothospecies.

Aconitum sect. *Angustifolium* Rottensteiner consists of one species (Seitz 1969).

Aconitum nothosect. *Acomarum* Starm. (*Aconitum* sect. *Aconitum* × *Aconitum* sect. *Cammarum*) consists of seven nothospecies and four hybrid formulae (Starmühler 2001; Wacławska-Ćwiertnia and Mitka 2016).

1. – Sect. ***Aconitum***

1A. – Subsect. ***Aconitum***

Description

Hood falciform, hemispherical, i.e., above rostrum wide-convex, or rounded-conic, 1–1.5 times higher than wide; claws of the nectaries bent and reaching the top of the hood, spurs of the nectaries acephalous, capitate or slightly bent, reaching the top of hoods; carpels 2–3, inflorescence axis, pedicels and tepals outside eglandular, glandular/eglandular pubescent/pilose or glabrous; leaves divided into 3 or 5 (–7) lobes and dissected to the base, the uppermost leaf segment linear to ovate, sometimes with 1–2 teeth; nectary spur capitate; seeds without membranous lamellae or rugulose, black to black-brown, with one or three longitudinal wings, then one wing more developed than the other two; root fusiform.

1a. – Ser. ***Aconitum***

Type species: *A. napellus* L.

Diagnostic characters: nectary spur distinctly globose; tepals outside glabrous to densely pubescent.

Aconitum anglicum Stapf, Curtis's Bot. Mag. 151: tab. 9088. 1926

Iconotype: Stapf, Curtis's Bot. Mag. 151: tab. 9088, 1926.
Synonyms: *A. napellus* auct., *A. napellus* L. subsp. *napellus* (sensu Seitz 1969)
Distribution: Southwest and West England and East Wales.

Diagnostic characters: tubers up to 9 cm, by 3 cm at the top; stem with fine curled hairs; leaves 5- to 3-partite, deeply laciniate with lobes linear to narrowly linear-lanceolate and acuminate, the uppermost 2–4 mm wide, almost glabrous; pedicels (1–) 2 (–3) cm long, quite erect; flowers mauve to mauvish-blue, minutely downy, curved eglandular pubescent; hood 18–20 mm high from the base; lower tepals strongly deflexed; lateral tepals 12–17 mm; claws of the nectaries curved almost horizontal, with a capitate spur; filaments hairy; carpels 3, glabrous.

Iconography: Stapf (1926); Ross-Craig (1948); Clapham et al. (1957).
Literature: Seitz (1969); Starmühler (1998).
Hybrids: unknown.

Aconitum bucovinense Zapał., Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 89–90. 1908a, *pro hybr*. [reprinted in Zapałowicz 1908b].

Type citation: "In montanis et subalpinis Bucovinae australis: Jakobeny, Pojana niegri prope Dorna Kandreny (*Rehman*)".
Typus: lectotype or, perhaps, holotype: KRAM 132396! (Wacławska-Ćwiertnia and Mitka 2016).
Synonyms: *A. callibotryon* Rchb. subsp. *bucovinense* (Zapał.) Grinţ., *A. callibotryon* Rchb. subsp. *rigidum* (Rchb.) Grinţ., *A. firmum* Rchb. subsp. *bucovinense* (Zapał.) Aschers. & Graebn.
Distribution: Eastern Carpathians, Southern Carpathians.

Diagnostic characters: the uppermost leaf segment 3–5 mm wide; hood and pedicels densely curved and crisped eglandular pubescent and often glandular pilose; claws of the nectaries curved, glabrous or pilose; bracteoles linear to obovate-lanceolate; filaments and stamens pilose; carpels glabrous or, rarely, pilose on the dorsal side (fo. *bucovinense*) or pubescent (fo. *orthotricha*).

Iconography: Mitka (2003: 179, fig. 12A-C); Novikoff and Mitka (2011: 49, fig. 5F,G).
Literature: Starmühler (1998); Starmühler (2000); Mitka (2003); Starmühler (2010); Wacławska-Ćwiertnia and Mitka (2016).

Lower taxa:

a) fo. ***bucovinense***

Diagnostic characters: carpels glabrous or, rarely, pilose on the dorsal side.

b) fo. ***orthotricha*** Gáyer, Magyar Bot. Lap. 9: 168. 1909

Type citation: did not provided by the author.
Typus: not designated.
Synonyms: none.

Diagnostic characters: carpels pubescent.

Hybrids:
a) ***Aconitum ×nanum*** (Baumg.) Simonk., Enum. Fl. Transsilv.: 64. 1887

Type citation: "In mtb. Csibesz et Arszuluj".
Typus: lectotype, (Romania) in m. Arszuluj (1812) – CL-Baumgarten 4745!
Synonyms: *A. napellus* L. var. *nanum* Baumg., *A. tauricum* Wulfen subsp. *nanum* (Baumg.) Gáyer, *A. tauricum* Wulfen subsp. *nanum* (Baumg.) Grinţ.
Hybrid origin: *A. bucovinense* × *A. firmum*.

Diagnostic characters: hoods glabrous, pedicels eglandular and glandular pubescent.

b) ***Aconitum ×czarnohorense*** (Zapał.) Mitka, The genus *Aconitum* in Poland and adjacent countries: 77. 2003

Type citation: "W Górach Pokucko-Marmaroskich, szczególnie na Czarnej Horze i w Alpach Rodneńskich w krainie kosodrzewu często, najwyżej tam 2010–2030 m; liczne okazy z Czarnej Hory i z Pietrosu w Alpach Rodneńskich".
Typus: lectotype, Góry Pokucko-Marmaroskie, Pietrosz, 8.08.1880, leg. et det. *H. Zapałowicz, KRAM 246853*! (Wacławska-Ćwiertnia and Mitka 2016).
Synonyms: *A. napellus* L. em Skalický var. *czarnohorense* Zapał. fo. *czarnohorense, A. napellus* L. var. *czarnohorense* Zapał. fo. *amoenum* Zapał., *A. napellus* L. var. *czarnohorense* Zapał. fo. *glabratum* Zapał., *A. napellus* L. var. *czarnohorense* Zapał. fo. *hoverlanum* Zapał., *A. napellus* L. var. *czarnohorense* Zapał. fo. *nanum* Zapał. non Baumg., *A. napellus* L. em Skalický var. *czarnohorense* Zapał. fo. *rodnense* Zapał., *A. napellus* L. var. *czarnohorense* Zapał. fo. *tenuisectum* Zapał., *A. napellus* L. em Skalický var. *czarnohorense* Zapał. fo. *turkulense* Zapał.
Hybrid origin: *A. bucovinense* × *A. ×nanum.*

Diagnostic characters: hoods glabrous, pedicels below bracteoles glandular pilose or glabrous.

Iconography: (Mitka 2003: 179, fig. 12E); Novikoff and Mitka 2011: 49. fig. 5K).

Aconitum corsicum Gáyer, Magyar Bot. Lap. 8: 181. 1909

Type citation: "Corsica: M. Coscione (*Kralik* – W; *Reverchon* – D)".
Typus: paratypus, WU 0034394.
Synonyms: *A. lobelianum* Rouy-Fouc., *A. napellus* L. var. *compac-*

tum Rapaics., *A. napellus* L. subsp. *corsicum* (Gáyer) W. Seitz, *A. pyramidale* Mill. var. *corsicum* (Gáyer) P.Fourn.
Distribution: Corsica.

Diagnostic characters: hood and pedicels densely pubescent, inflorescence rigid, in lower part ramified; claws of the nectaries erected, at theirs top slightly bent, spur of the nectaries capitate or acephalous, reaching the top of the hoods; filaments pilose; bracteoles linear to linear-lanceolate 3–5 mm; carpels glabrous; the uppermost leaf segment 2–4 mm wide.

Iconography: Jeanmonod and Gamisans (2007).
Literature: Gáyer (1909); Starmühler (1998).
Hybrids: unknown.

Aconitum firmum Rchb., Uebers. Aconitum: 20. 1819

Type citation: "in Carpathorum tractu *Townson*!, *Genersich*!, *Kitaibel*!, *Wahlenberg*!, *Sadler*! in Transylvania *Baumgarten*! in Carinth. Alp. *Fladnitz*. v. *Vest*!"
Typus: iconotype, "Rchb., Mon. Acon.: 85, Tab. XIV, fig. 1, 1821" (Skalicky 1990).
Synonyms: *A. flerovii* Steinb. in Komarov, *A. palmatifidum* Rchb., *p.p.*, *A. romanicum* Wołoszczak, *A. tatrae* Borb., *A. koelleanum* Rchb. var. *firmum* (Rchb.) Rchb., *A. napellus* L. var. *firmum* (Rchb.) Pawł., *A. napellus* L. var. *babiogorense* Zapał. fo. *babiogorense, A. napellus* L. var. *babiogorense* Zapał. fo. *subfissum* Zapał., *A. napellus* L. var. *carpaticum* Zapał. fo. *carpaticum*, *A. napellus* L. var. *subtatrense* Zapał. fo. *subtatrense, A. napellus* L. var. *subtatrense* Zapał. fo. *abnorme* Zapał., *A. napellus* L. var. *subtatrense* Zapał. fo. *latisectum* Zapał., *A. napellus* L. var. *tatrense* Zapał., *A. skerisorae* auct., non Gáyer, *A. tauricum* auct. Fl. Carpathorum, non Wulfen.
Distribution: Carpathian Mts, Apuseni Mts, Balkans, Central Russian Highlands.

Diagnostic characters: bracteoles (2.5–) 3–17 mm long, at least those of the lowest flowers in terminal raceme divided or at least toothed; pedicels and tepals outside glabrous (subsp. *firmum,* subsp. *fissurae*, and nothosubsp. *fussianum*), curved and crisped eglandular pubescent and glandular pilose (subsp. *skerisorae*), or eglandular pubescent (subsp. *moravicum*); bracteoles 2–5 (–7) mm long, wether toothed nor divided; stamens glabrous (subsp. *firmum*) or villose (subsp. *fissurae* and nothosubsp. *fussianum*).

Iconography: Bauhin (1671: 183); Reichenbach (1821: t. xiv, fig. 1); Mitka (2003: 178); Novikoff and Mitka (2011: 49).
Literature: Skalický (1990); Starmühler (1998); Starmühler (2000); Starmühler and Mitka (2001); Mitka (2003); Starmühler (2010); Novikoff and Mitka (2011); Mitka et al. (2017).

Lower taxa:

a) subsp. ***firmum***

Diagnostic characters: pedicels and tepals outside glabrous; bracteoles ± deeply divided; stamens glabrous.

b) subsp. ***fissurae*** Nyár., Enum. Pl. Cheia Turzii: 132. 1939

Type citation: "[Romania] Transsilvania, Cheia Turzii, Repezieul caprelor; Nr. 435214; 06.09.1936; leg. *E.I. Nyárády* (CL)" (Starmühler and Mitka 2001).
Typus: lectotype, CL 435214.
Synonyms: *A. romanicum* Wołoszczak, *A. flerovii* Steinberg in Komarov.

Diagnostic characters: pedicels and tepals outside glabrous; bracteoles entire or slightly toothed; stamens villose.

c) subsp. ***skerisorae*** (Gáyer) Starm., Siebenbürg. Arch. 36: 18. 2000

Type citation: "Plantae Hungariae exsiccatae, Comit. Kolozs, in lapidosis fl. Melegszamos ad pag. Melegszamos, Nr. 60705; 17.07.1904 leg. *Z. Zsák* (BP); *A. skerisorae* Gáy., rev. Gáyer 1910" (Starmühler 2000).
Typus: neotype, BP 60705.
Synonyms: *A. skerisorae* Gáyer, *A. tatrae* Borbás var. *skerisorae* Soó, *A. napellus* Rchb. subsp. *skerisorae* Seitz non Gáyer (Soó 1972).

Diagnostic characters: pedicels and tepals outside eglandular pubescent and glandular pilose; bracteoles from lanceolate to divided; stamens villose or rarely glabrous.

d) subsp. ***moravicum*** Skalický, Preslia 54 (2): 115 1982

Type citation: "[Czech Republic] Beskydy, u cesty na západ, svahu Smrku, 1025 m, Nr. 322; 27.07.1943; leg. *R. Kurka* (PCR) " (Starmühler and Mitka 2001)
Typus: holotype, PCR 322.
Synonyms: *A. napellus* L. subsp. *firmum* (Rchb.) Gáyer var. *carpaticum* Maloch.

Diagnostic characters: pedicels and tepals outside eglandular pubescent; bracteoles at least those of the lowest flowers divided or at least toothed, rarely undivided; stamens mostly pilose.

e) nothosubsp. ***fussianum*** Starm. (*A. firmum* subsp. *firmum* × *A. firmum* subsp. *fissurae*) – see hybrids of *A. firmum*.

Hybrids:

a) ***Aconitum firmum*** nothosubsp. ***fussianum*** Starm., Siebenbürg. Arch. 36: 17. 2000

Type citation: “Transilvania (Siebenbürgen, Erdély), Muntii Apuseni (Siebenbürgisches Westgebirge, Nyugati-havasok), Muntii Vladeasa (Vlegyásza-hegyseg), W Huedin (Bánffyhunyad), im Valea Draganului (Nagysobos) beim Dorf Lunca, 735 m”.
Typus: holotype, GZU 000225133.
Synonyms: none.
Hybrid origin: *A. firmum* subsp. *firmum* × *A. firmum* subsp. *fissurae.*

Diagnostic characters: tepals outside glabrous; bracteoles toothed or lobed; stamens villose.

b) ***Aconitum*** ×***nanum*** (Baumg.) Simonk. (*A. bucovinense* × *A. firmum*) – see *A. bucovinense.*

c) ***Aconitum*** ×***czarnohorense*** (Zapał.) Mitka (*A. firmum* × *A.* ×*nanum*)– see *A. bucovinense.*

d) ***Aconitum*** ×***mariae*** Rottensteiner, Mitka & Novikov, **nothospec. (hybr.). nov.**

Typus: [Slovakia] Hungaria, comitatus Szepes, Montes Bélaenses, in valle Drechslerhäuschen sub monte Stirnberg, alt. cca. 1400–1500 m, solo calc.; 01.09.1907; leg. *E.G. Nyárády* (holotype, SIB).

Diagnosis

A. ×*mariae* differs from *A. firmum* by glandular pilose pedicels and differs from *A. maninense* by glabrous tepals.

Description

Inflorescence axis glabrous, pedicels glandular pubescent and pilose, often only above the bracteoles, bracteoles linear, lanceolate, spathulate or even divided, situated in the upper half of the pedicel, tepals outside glabrous, filaments of the stamens glabrous or sparsely pilose, carpels glabrous or sparsely pilose on the backside.

Hybrid origin: *A. firmum* s.str. × *A. maninense.*

Eponymy

This new *Aconitum* hybrid is named after a distinguished botanist, our friend and colleague from the Institute of Botany of the Jagiellonian University in Kraków, Professor Maria Zając (1955–2018).

e) ***Aconitum*** ×***mariae*** Rottensteiner, Mitka & Novikov nothosubsp. ***paxii*** (Starm.) Mitka, **comb. nov.**

Basionym: *A. firmum* Rchb. nothosubsp. *paxii* Starm. in Starmühler & Mitka, Thaiszia 10 (2): 127, 2001.
Type citation: “Polen, Galizien, Nord-Karpaten, Hohe Tatra (Tatry Wysokie), S-Ufer vom Großen Fischsee (Morskie Oko), N 49°11.64’, E 20°04.12’, 1395 m alt.; Hochstaudenflur; 13.08.1997; leg. *U. et W. Starmühler*” (Starmühler and Mitka 2001).
Typus: holotype, GZU 000232750.
Synonyms: *A. palmatifidum* Rchb. fo. *piliferum* Gáyer.
Hybrid origin: *A. firmum* subsp. *moravicum* × *A. maninense.*

Diagnostic characters: pedicels curved and crisped eglandular pubescent and glandular pilose.

Iconography: Mitka (2003: 178, fig. 11E).

f) ***Aconitum*** ×***zapalowiczii*** (Starm.) Mitka, Studia Universitatis Babeş-Bolyai, Biologia, 62: 166. 2017

Basionym: *A. firmum* Rchb. nothosubsp. *zapalowiczii* Starm. in Starmühler & Mitka, Thaiszia 10 (2): 128, 2001.
Type citation: “Polen, Galizien, Nord-Karpaten, Hohe Tatra (Tatry Wysokie), S-Ufer vom Großen Fischsee (Morskie Oko), N 49°11.64’, E 20°04.12’, 1395 m alt.; Hochstaudenflur; 13.08.1997; leg. *U. et W. Starmühler*” (Starmühler and Mitka 2001).
Typus: holotype, GZU 000232751.
Synonyms: none.
Hybrid origin: *A. firmum* × *A.* ×*mariae* nothosubsp. *paxii.*

Diagnostic characters: pedicels only sparsely curved and crisped eglandular pubescent and glandular pilose, mainly just above the bracteoles.

Iconography: Mitka (2003: 178, fig. 11F).

Aconitum napellus L., Sp. Pl. ed. 1, 1: 352. 1753

Type citation: “in Helvetia, Bavaria, Gallia”.
Typus: lectotype in Herb. Clifford: 214, A. 3, sheet A, BM 000628795 (Seitz 1969).
Synonyms: *A. autumnale* Clus. ex Rchb., *A. bernhardianum* Rchb., *p.p.*, *A. compactum* Rchb., *A. eminens* Koch. ex Rchb., *A. laxum* Rchb., *A. linnaeanum* Gáyer, *A. lobelianum* Rchb., *A. meyeri* Rchb., *A. neomontanum* Wulfen, *A. neubergense* Clus. ex Rchb., *A. pyramidale* Mill. ex Rchb., *A. strictum* Bernh., *A. vulgare* DC., *Delphinium napellus* (L.) Baill.
Distribution: Alps, Pyrenees, Iberian Peninsula, Bohemian Massif.

Diagnostic characters: inflorescence axis, pedicels and hoods outside pubescent; filaments not toothed; nectaries bent horizontal, spur of nectaries capitate; inflorescence rigid or loose/ramified; bracteoles (3–) 5–8 (–20) mm long and carpels (2–) 3, densely pubescent (subsp. *lobelii*) or carpels sparsely pubescent on the backside only (nothosubsp. *seitzii*); carpels glabrous, bracteoles linear to lanceolate, rarely spathulate (4–) 5–8 (–15) mm (subsp. *napellus*), 1–2 (–3) mm long (subsp. *formosum*); or nectaries hardly bent; filaments ± toothed, carpels 2–3 (subsp. *lusitanicum*); bracteoles (2–) 3 (–4) mm long and carpels (2–) 3 glabrous (nothosubsp. *hinterhuberi*) or carpels sparsely pubescent on the backside (nothosubsp. *polatschekii*).

Iconography: Matt., New Kreuterb.: 472, fig. D, 1563; Clus. Rar. Pl. Hist. 2: 96 *pro Aconit. Lycoct. vi. Napellus vulgar.*, 1601; Jacq. Fl. Austr. v. 4, t. 381, 1776.
Literature: Cappelletti and Poldini (1984); Molero and Blanché (1986); Mucher (1991a); Starmühler (1999); Starmühler (2001); Starmühler (2002).

Lower taxa:
a) subsp. ***napellus***

Diagnostic characters: carpels 3 (–4), glabrous; bracteoles linear to lanceolate, rarely spathulate (4–) 5–8 (–15) mm; filaments not toothed.

b) subsp. ***lobelii*** Mucher, Phyton (Horn) 31(1): 130. 1991

Type citation: "Ostalpen, Steiermark, Salzkammergut, Totes Gebirge, Loser, Panoramastraße, Hochstaudenflur, 1020 m, 9.8.1989, leg *W. Mucher*, GZU" (Mucher 1991c).
Typus: holotype, GZU 000274111. Isotypes, GJO, GZU 000274112 – GZU 000274117, W, WU.
Synonyms: *A. lobelianum* Host, *p.p.*, non Rchb., *A. lobelianum* (Rchb.) Host. in Gáyer, *p.p.*

Diagnostic characters: carpels (2–) 3, densely pubescent; bracteoles linear to lanceolate, (3–) 5–8 (–20) mm; filaments not toothed, pilose.

c) subsp. ***formosum*** (Rchb.) Gáyer in Hegi, Fl. Mitteleur. 3: 498. 1912

Type citation: "Salzburger Alpen (Untersberg, Schafberg)" (Gáyer 1912: 498)
Typus: iconotype, "Reichenbach 1825, Ill. Spec. Acon. Gen., icon. 65" (Starmühler 1997b).
Synonyms: *A. formosum* Rchb., *A. napellus* L. [var.] *formosum* (Rchb.) Koch, *A. napellus* [var.] β *hemisphaericum* fo. *formosum* (Rchb.) Beck.
Iconography: Gáyer (1912: 499, fig. 655 a–c).

Diagnostic characters: carpels 2–3, glabrous; bracteoles linear to lanceolate, only 1–2 (–3) mm long; filaments not toothed.

d) subsp. ***lusitanicum*** Rouy, Le Naturaliste 6: 405. 1884

Type citation: "Prov. de *Tras-os-montes*: environ de Bracança, à San Martin ho d'Augueira. – Sept. 1854. – leg. *E. Schmitz*" (Rouy 1884).
Typus: not designated.
Synonyms: none.

Diagnostic characters: carpels 2–3, glabrous; filaments toothed.

e) nothosubsp. ***hinterhuberi*** (*A. napellus* subsp. *formosum* × *A. napellus* subsp. *napellus*) – see hybrids of *A. napellus.*

f) nothosubsp. ***polatschekii*** (*A. napellus* subsp. *formosum* × *A. napellus* subsp. *lobelii*) – see hybrids of *A. napellus.*

Hybrids:

a) ***Aconitum napellus*** L. nothosubsp. ***hinterhuberi*** Starm., Fritschiana 18: 12. 1999

Type citation: "*Aconitum brauneanum*, Untersberg, 1825, leg. *Hinterhuber* (WU-Keck). Dieser Beleg wurde bereits von Seitz 1966 als "*A. napellus* ssp. *hians* gegen ssp. *neomontanum*" revidiert" (Starmühler 1999).
Typus: holotype, WU-Keck.
Synonyms: none.
Hybrid origin: *A. napellus* subsp. *formosum* × *A. napellus* subsp. *napellus.*

Diagnostic characters: carpels (2–) 3, glabrous; bracteoles (2–) 3 (–4) mm long; filaments of stamens not toothed.

b) ***Aconitum napellus*** L. nothosubsp. ***polatschekii*** Mucher ex Starm., Fritschiana 18: 13. 1999

Type citation: "Ostalpen, Steiermark, Mariazellerland, Südufer des Hubertussees an der niederösterreichischen Grenze, feuchte Wiese, 840 m; 04.08. 1989; leg. *W. Mucher*" (Starmühler 1999).
Typus: holotype, GZU 000274119. Isotype, W.
Synonyms: none.
Hybrid origin: *A. napellus* subsp. *formosum* × *A. napellus* subsp. *lobelii.*

Diagnostic characters: carpels (2–) 3 sparsely pubescent on the backside; bracteoles (2–) 3 (–4) mm long.

c) ***Aconitum napellus*** L. nothosubsp. ***seitzii*** Mucher ex Starm., Fritschiana 18: 14. 1999

Type citation: "Ostalpen, Steiermark, Mariazellerland, in der Walster, Bachufer beim Kaiser Franz Josef Denkmal 810 m; 04.08.1989; leg. *W. Mucher*" (Starmühler 1999).
Typus: holotype, GZU 000274118. Isotype, W.
Synonyms: none.
Hybrid origin: *A. napellus* subsp. *lobelii* × *A. napellus* subsp. *napellus.*

Diagnostic characters: carpels (2–) 3 sparsely pubescent on the backside; bracteoles (3–) 5–8 (–20) mm long.

Aconitum superbum Fritsch, Verh. K.K. Zool.-Bot. Ges. Wien 45: 370. 1895

Type citation: "Mala Vrata unweit vom Berge Koprivnica zwis-

chen Bugojno und Kupres/Bosnien (Sostarič, Aug. 1895)".
Typus: holotype, WU 2540.
Synonyms: *A. adriaticum* Gáyer, *A. sostaricianum* Fritsch, *A. napellus* L. subsp. *superbum* (Fritsch) W. Seitz
Distribution: Western and Central Balkans.

Diagnostic characters: plant 200–300 cm high; inflorescence axis, pedicels and hoods outside eglandular pubescent; leaves on the lower side with distinct reticulate venation, the uppermost leaf segment ovate; filaments pilose; carpels 2 (–3) glabrous.

Iconography: Seitz (1969: 16).
Literature: Fritsch (1895); Gáyer (1909).
Hybrids:

a) ***A. superbum*** × ***A. variegatum*** – more studies required.
b) ***A. superbum*** × ***A. vitosanum*** – more studies required.

1b. – Ser. ***Castellana*** Rottensteiner, **series nova**

Type species: *A. castellanum* (Molero & Blanché) Rottensteiner.

Diagnosis

Spurs of nectaries are elongated and backward bent.

Description

Monotypical series with only one species, separated from the other series of subsection *Aconitum* by the unique character of the elongated and backward bent spur of the nectaries.

Aconitum castellanum (Molero & Blanché) Rottensteiner, **stat. nov.**

Basionym: *A. napellus* L. subsp. *castellanum* Molero and Blanché, Anal. Jardin Bot. Madrid 41: 213. 1984.
Type citation: "Laguna del Marquesado, 30S XK1349, loco humido umbraoque – in populeto – ad 1400 m, *J. Molero et A. Rovira* die 20-VIII-1983 legerunt".
Typus: holotype, BCF 71554.
Distribution: Iberian Peninsula.

Diagnostic characters: stem and leaves glabrous or glabrescent; inflorescence ramified, curved eglandular pubescent; hood hemispheric-falciform; nectaries hardly curved, spur of the nectaries elongated and bent backward; filaments not dentate, pilose; carpels 3–5, glabrous.

Iconography: Molero and Blanché (1986: 238).
Literature: Molero and Blanché (1984), Molero and Puig (1990).
Hybrids: unknown.

1c. – Ser. ***Taurica*** Mucher ex Starm.

Type species: *A. tauricum* Wulfen

Diagnostic characters: inflorescence simple or shortly ramose; bracteoles triangle to linear, glabrous or at margins ciliate; hood and pedicels glabrous; nectary spur acephalous or hardly capitate.

Aconitum clusianum Rchb., Mon. Aconit.: 91. 1821

Type citation: "Bohemian Sudetes: Aupagrund".
Typus: iconotype: Reichenbach, Mon. Aconit. Tab. III, 1. 1821
Distribution: Sudetes, Bohemian Massif.

Diagnostic characters: plant 30–150 cm high, inflorescence weakly ramified, hood falciform or rounded-conic, pedicels glabrous; carpels 2 (–3) glabrous; spur of nectaries acephalous or capitate; bracteoles triangle to linear 1–2 (–3) mm long; filaments pilose; the uppermost leaf segment ovate or lanceolate-ovate 3–5 mm wide.

Iconography: Reichenbach (1821: tab. XIII, fig. 1); Mitka (2003, 177: fig. 10D).
Literature: Mitka (2003).
Hybrids: unknown.

Aconitum tauricum Wulfen in Koelle, Spicil. Observ. Acon.: 15. 1788

Type citation: "Frequentissimum in apricis Taureri Malnizesis, Radstadienis, etc."
Typus: iconotype, "Typus gesehen von Gáyer, Magyar Bot. Lap. P. 146 (1909): (W) – ist vernichtet; Abbildung bei Reichenbach, illustr. Aconit. T. 63 (1827)" (Seitz 1969).
Synonyms: *A. dolomiticum* A.Kern.; *A. hayekianum* Gáyer; *A. koelleanum* Rchb., *p.p.*; *A. napellus* L. subsp. *koelleanum* (Rchb.) Mucher; *A. parviflorum* Host.; *A. taurericum* Rchb.; *A. trichocarpum* Rchb., *A. napellus* L. subsp. *tauricum* (Wulfen) Gáyer in Hegi, *A. napellus* L. var. *tauricum* (Wulfen) Sér., *A. napellus* fo. *koelleanum* (Rchb.) Gürke in Richter-Gürke.
Distribution: Alps.

Diagnostic characters: plant 60–80 cm high; inflorescence rigid; hoods falciform or hemispherical; inflorescence axis and tepals outside glabrous, pedicels glabrous (subsp. *tauricum*), with solitary hairs at the top (nothosubsp. *hayekianum*) or pilose above bracteoles (subsp. *latemarense*); inflorescence with a lot of long side racemes (var. *eustachyum*) or without or only a few short side racemes (var. *tauricum*), filaments glabrous (fo. *tauricum*) or pilose (fo. *taurericum*); spur of nectaries acephalous or hardly capitate; the uppermost leaf segments 1–3 mm wide.

Iconography: Clusii Histor. Rarior. Plant p. XCV, n. IV, 1601; Reichenbach (1827: t. 63).
Literature: Mucher (1993a); Starmühler (2001).

Lower taxa:

a) subsp. ***tauricum*** var. ***tauricum*** fo. ***tauricum***

Diagnostic characters: inflorescence compact, without or with only a few short side racemes; pedicels, carpels, nectaries and filaments glabrous.

b) subsp. ***tauricum*** var. ***tauricum*** fo. ***taurericum*** (Rchb.) Gáyer, Magyar Bot. Lap. 8: 145. 1909

Type citation: none.
Typus: not designated, probably iconotype is Rchb., Monogr. Acon.: 87, tab. 12, figs. 2, 3, 1820.
Synonyms: *A. taurericum* Rchb., *A. tauricum* Wulfen in Koelle subsp. *taurericum* (Rchb.) Grinţ.

Diagnostic characters: inflorescence compact, without or with only a few short side racemes; pedicels, carpels, nectaries and filaments pilose.

c) subsp. ***tauricum*** var. ***eustachyum*** (Rchb.) Starm., Hladnikia 6: 42. 1996

Type citation: none.
Typus: not designated, probably iconotype is Monogr. Aconit.: 96, tab. 15, fig. 3, 1820.
Synonyms: *A. eustachyum* Rchb., *A. napellus* L. subsp. *eustachyum* (Rchb.) Gáyer in Hegi, *A. napellus* L. [var.] γ *eustachyum* (Rchb.) Fiori.

Diagnostic characters: inflorescence ramified; pedicels with solitary hairs or glabrous; carpels mostly glabrous.

d) subsp. ***latemarense*** (Degen & Gáyer) Starm. in W.Maurer, Fl. Steiermark 1: 84. 1996

Type citation: "Tirol: in lapidosis subalpinis ad pedem montis Latemar prope Karersee, alt. ca.1600–1800 m, 30.VIII.1906, *Degen*".
Typus: not designated.
Synonyms: *A. latemarense* Degen & Gáyer, *A. tauricum* Wulfen in Koelle var. *latemarense* (Degen & Gáyer) Mucher.

Diagnostic characters: pedicels with mixed glandular and eglandular pubescence; carpels often sparsely pubescent on the suture.

e) nothosubsp. ***hayekianum*** (*A. tauricum* subsp. *latemarense* × *A. tauricum* subsp. *tauricum*) – see hybrids of *A. tauricum*.

Hybrids:

a) ***Aconitum*** **×*acutum*** Rchb. (*A. tauricum* × *A. variegatum*) – see nsect. *Acomarum*.
b) ***Aconitum*** **×*mielichhoferi*** Rchb. (*A. degenii* × *A. tauricum*) – see nsect. *Acomarum*.
c) ***Aconitum tauricum*** Wulfen in Koelle nothosubsp. ***hayekianum*** (Gáyer) Grinţ. in Savulescu, Flora Reipublicii Populare Române, 2: 475. 1953

Type citation: "Sanntaler Alpen" (Gáyer 1911)
Type specimens: not designated.
Synonyms: *A. dolomiticum* Hayek, *p.p., A. ranunculifolium* Rchb. var. *dolomiticum* Evers, *p.p.*
Hybrid origin: *A. tauricum* subsp. *latemarense* × *A. tauricum* subsp. *tauricum.*

Diagnostic characters: pedicels with solitary hairs at the top; carpels mostly glabrous.

d) ***Aconitum pilipes*** **×** ***A. tauricum*** – see nothosect. *Acomarum.*

1d. – Nothoser. ***Acorica*** Mucher ex Starm. **(*Aconitum*** ser. ***Aconitum*** × ***Aconitum*** ser. ***Taurica*)**

Type species: *A. plicatum* Rchb., designated here.

Diagnostic characters: spur of nectaries acephalous or hardly capitate, hoods pilose.

Aconitum plicatum Köhler ex Rchb., Uebers. Aconitum: 29. 1819

Type citation: "In Sudetis *Koehler*!".
Typus: iconotype in Reichenbach, Icon. Fl. Germ. Helv., Vol. 4: Icon. T. 98, Nr. 4708d. 1840 (Starmühler 1997a).
Synonyms: *A. amoenum* Rchb., *A. bernhardianum* Rchb., *p.p.*, *A. callibotryon* Rchb., *A. hians* Rchb., *A. koehleri* Rchb., *A. laetum* Rchb., *A. multifidum* Koch ex Rchb., *A. rigidum* Rchb.
Distribution: Sudetes, Bohemian Massif, Bavarian Alps.

Diagnostic characters: plant 30–150 cm high, inflorescence weakly ramified, hood falciform or rounded-conic, carpels glabrous, pedicels eglandular pubescent (subsp. *plicatum*) or glandular/eglandular pilose (subsp. *sudeticum*); carpels 2 (–3) glabrous; spur of nectaries acephalous or capitate; bracteoles triangle to linear 1–2 (–3) mm long; filaments pilose; uppermost leaf segment ovate or lanceolate-ovate 3–5 mm wide.

Iconography: Mattioli (1563: 472, fig. D); Clusius (1601: 96, *pro Aconit. Lycoct. vi. Napellus vulgar.*); Jacquin (1776: t. 381); Reichenbach (1840: 48, fig. 4708 d); Mitka (2003: 177).
Literature: Cappelletti and Poldini (1984); Molero and Blanché

(1986); Mucher (1991a); Starmühler (1999); Starmühler (2001); Starmühler (2002); Mitka (2003).

Lower taxa:

a) subsp. ***plicatum***

Diagnostic characters: pedicels eglandular pubescent; carpels glabrous.

b) subsp. ***sudeticum*** Mitka, The genus *Aconitum* in Poland and adjacent countries: 76. 2003.

Type citation: "Sudety Wschodnie, Masyw Śnieżnika, nad potokiem Czarna, 960 m, pod Dzikim Stokiem, 10.8.1988, leg. *Z. Szeląg*" (Mitka 2003).
Typus: holotype, KRAM. Isotypes, KRAM. Paratypus, KRA.
Synonyms: none.

Diagnostic characters: pedicels eglandular and/or glandular pilose; carpels pubescent.

Hybrids:

a) ***Aconitum*** **×*bavaricum*** Starm., Ber. Bayer. Bot. Ges. 71: 105. 2001, nothosubsp. ***bavaricum***

Type citation: "Aconita rarissima selecta (2001), Deutschland, Bayern, Bayerischer Wald, NNE Bodenmais, Großer Arber, E-Hang unter dem Gipfel, über der Bodenmais-Mulde, N 49°06.66', E 13°08.08', 1435 m alt.; 31.08.2000; leg. *W. Starmühler* (GZU)" (Starmühler 2001).
Typus: holotype, GZU 000232791. Isotype, M, Herb. STARMÜHLER.
Synonyms: none.
Hybrid origin: *A. napellus* subsp. *napellus* × *A. plicatum*.

Diagnostic characters: bracteoles situated distant from the flower, carpels glabrous.

b) ***Aconitum*** **×*bavaricum*** Starm. nothosubsp. ***lusenense*** Starm., Ber. Bayer. Bot. Ges. 71: 105. 2001

Type citation: "Ranunculaceae subtrib. Delphiniinae exsiccatae, Fasc. 5 (2001), Deutschland, Bayern, Bayerischer Wald, NE Grafenau, Lusen, am Weg vom Teufelsjoch zur Böhm-Hütte, 1045 m alt.; Quellufer; 29.08.2000; leg. *W. Starmühler* (GZU)" (Starmühler 2001).
Typus: holotype, GZU 000232817. Isotype, GJO, JACA, KRA, LE, LG, LI, M, MEL, NY, PE, Herb. STARMÜHLER, TBI, TNS, W, Z.
Synonyms: none.
Hybrid origin: *A. napellus* subsp. *lobelii* × *A. plicatum*.

Diagnostic characters: carpels sparsely pubescent on the backside.

c) ***Aconitum*** **×*teppneri*** Mucher ex Starm., Ber. Bayer. Bot. Ges. 71: 107. 2001, nothosubsp. ***teppneri***

Type citation: "Ostalpen, Steiermark, Hochschwab, Schönleiten, Latschengebüsch, 1680 m, 22.8.1989, leg. *W. Mucher* (GZU) (Starmühler 2001).
Typus: holotype, GZU 000274190. Isotypes, GZU 000274195, GZU 000274196, W, WU.
Synonyms: none.
Hybrid origin: *A. napellus* subsp. *napellus* × *A. tauricum* subsp. *tauricum.*

Diagnostic characters: pedicels sparsely curved and crisped eglandular pubescent, carpels glabrous.

d) ***Aconitum*** **×*teppneri*** Mucher ex Starm. nothosubsp. ***goetzii*** Mucher ex Starm., Ber. Bayer. Bot. Ges. 71: 108. 2001

Type citation: "Österreich, Steiermark, Totes Gebirge, Pühringer Hütte – Salzofen, 21.8.1934, leg. *W. Möschl* (GZU)" (Starmühler 2001).
Typus: holotype, GZU 000274189.
Synonyms: none.
Hybrid origin: *A. napellus* subsp. *lobelii* × *A. tauricum* subsp. *tauricum.*

Diagnostic characters: pedicels sparsely curved and crisped eglandular pubescent; carpels sparsely pubescent on the backside.

e) ***Aconitum*** **×*teppneri*** Mucher ex Starm. nothosubsp**.** ***haderlappii*** Starm., Fritschiana 30: 14. 2002

Type citation: "Slowenien, Kranjska (Krain), Kamniške Alpe (Steiner Alpen), N Kamnik (Stein), bei der Cojzova koča (Zois-Hütte) auf dem Kokrsko sedlo (Kanker-Sattel), 1790 m alt.; Hochstaudenflur; 20.08.1991; leg. *W. Mucher* (GZU)" (Starmühler 2002).
Typus: holotype, GZU 000232745.
Synonyms: none.
Hybrid origin: *A. napellus* subsp. *lobelii* × *A. tauricum* subsp. *latemarense.*

Diagnostic characters: pedicels glandular and eglandular curved and crisped pubescent and pilose, carpels sparsely pubescent on the backside.

f) ***Aconitum*** **×*teppneri*** Mucher ex Starm. nothosubsp. ***kerneri*** Starm., Fritschiana 30: 15. 2002

Type citation: "*Aconitum dolomiticum* A. Kerner ex Hayek, Flora stiriaca exsiccata Nr. 845, Stiria inferior [Slovenija, Štajerska], in uliginosis prope refugium Kocbekhütte in monte Molička planina in Alpibus Lithopolitanis (Sanntaler-sive Steineralpen), solo calcareo, 1760–1800 m s.m.; 08.1905 et 1907; leg. *A. Hayek et L. Derganc* (GZU)" (Starmühler 2002).

Typus: holotype, GZU. Isotypes, GZU 000274195, GZU 000274196, LJU, WU.
Synonyms: *A. dolomiticum* Hayek, *p.p., A. ranunculifolium* Rchb. var. *dolomiticum* Evers, *p.p.*
Hybrid origin: *A. napellus* subsp. *napellus* × *A. tauricum* subsp. *latemarense.*

Diagnostic characters: pedicels glandular and eglandular curved and crisped pubescent and pilose, carpels glabrous.

1B. – Subsect. ***Burnatii*** Rottensteiner

Type species: *A. burnatii* Gáyer.

Description

Differs from subsection *Aconitum* (series *Aconitum*) by the flexuous zigzag stem (at least in the region of the inflorescence) and by glandular pilose inflorescence.

Aconitum burnatii Gáyer, Magyar Bot. Lap. 8: 141. 1909

Type citation: "Alpes Maritimae. Italia, au Col de la Madonna d. Fenestre (*Bourgeau* pl. alp. mar. n. 13 – W)".
Typus: not designated.
Synonyms: *A. divergens* Pančić subsp. *burnatii* (Gáyer) W. Seitz, *A. delphinense* Gáyer, *A. napellus* L. subsp. *burnatii* (Gáyer) J.-M. Tison.
Distribution: Maritime Alps, France (Massif Central).

Diagnostic characters: stem in the lower third pubescent; leaves densely pubescent; the uppermost leaf segment (2–) 3–4 mm; pedicels straight; bracteoles linear 2–3 mm long; hood broader than high, falciform; spur of nectaries elongate capitate, filaments sparsely pilose or glabrous; carpels glabrous or pubescent.

Iconography: Molero and Blanché (1986: 238).
Literature: Seitz (1969); Seitz (1970); Rottensteiner (2018).
Hybrids: unknown.

Aconitum maninense (Skalický) Mitka, Studia Universitatis Babeş-Bolyai, Biologia, 62, Sp. Iss. 2017

Basionym: *A. firmum* Rchb. subsp. *moravicum* Skalický var. *maninense* Skalický, Preslia 57: 136, 1985.
Type citation: "Proles localis (natio) angustiarum Maninska úžina et Kostelecká úžina inter Považská Bystrica et Súl'ov."
Typus: holotype, PRC 725!
Distribution: Western Carpathians.

Diagnostic characters: stem in the lower third glabrous; leaves sparsely pubescent, the uppermost leaf segment 4–6 mm wide; pedicels straight to bent; bracteoles linear to obovate-lanceolate and then divided; hood as broad as high, rounded-conic or hemispherical; spur of nectaries hooked; filaments glabrous or sparsely pilose; carpels glabrous or pubescent.

Iconography: Mitka (2003: 178).
Literature: Starmühler and Mitka (2001); Mitka (2003); Mitka et al. (2017).

Hybrids:

a) ***Aconitum*** ×***mariae*** Rottensteiner, Mitka & Novikov (**nothospec. nov**.) nothosubsp. ***mariae*** (*A. firmum* subsp. *firmum* × *A. maninense*) – see *A. firmum*.

b) ***Aconitum*** ×***mariae*** Rottensteiner, Mitka & Novikov nothosubsp. ***paxii*** (Starm.) Mitka **comb. nov**. (*A. firmum* subsp. *moravicum* × *A. maninense*) – see *A. firmum*.

Aconitum nevadense Uechtr. ex Gáyer, Magyar Bot. Lap. 8: 180. 1909

Type citation: "Sierra Nevada. (*Willkomm* n. 321 – W), Aleazaba (*M. Jimenes* – K)".
Typus: not designated.
Distribution: Sierra Nevada, Pyrenees.
Synonym: *A. occidentale* Timb. Lagr. f. ex Gáyer

Diagnostic characters: stem in the lower third pilose; leaves densely pubescent, uppermost leaf segment (2–) 3–4 mm wide; pedicels bent; bracteoles triangle or linear 1–3 (–4) mm long; hood broader than high, falciform to hemispherical; spur of nectaries capitate; filaments pilose; carpels glabrous or pilose.

Iconography: Molero and Blanché (1986: 236).
Literature: Gáyer (1909); Rottensteiner (2018).
Hybrids: unknown.

Aconitum pentheri Hayek, Ann. Nat. Hofmus. 31: 68. 1917

Type citation: "In monte Žlep prope Ipek, 1800 m.s.m., leg. *A. Penther*".
Typus: iconotype in Hayek, Ann. Nat. Hofmus. 31: Taf. 1, 1917.
Synonym: *A. divergens* Pančić *nom. illeg. p.p., A. burnatii* Gáyer subsp. *pentheri* (Hayek) Jalas.
Distribution: Balkans.

Diagnostic characters: stem in the lower third glabrous; leaves ± glabrous, the uppermost leaf segment 3–5 mm wide; pedicels bent; bracteoles linear-lanceolate 1–3 mm long; hood broader than high, falciform; spur of nectaries globose; filaments pilose; carpels glabrous.

Iconography: Hayek (1917).

Literature: Seitz (1969).
Hybrids: unknown.

2. – Sect. ***Cammarum*** DC.

2A. – Subsect. ***Cammarum*** (DC.) Rapaics

Description

Leaves divided into 3 or 5 lobes and dissected to the base, uppermost leaf segment ovate or linear with more than two teeth; hoods conical, i.e., above rostrum distinctly elongated, 1.6–2.5 times higher than wider, rarely hemispherical, i.e., above rostrum wide-convex; claws of the nectaries erect or slightly bent, mostly not reaching the top of the hood; spurs of nectaries backward bent or semi-spiral coiled, do not reach the top of hoods; carpels 3 or 5; seeds with membraneous 4–6 lamellae and with one conspicuously winged edge, goldish to light brown; root globose.

2a. – Ser. ***Variegata*** Steinberg ex Starm.

Type species: *A. variegatum* L.

Diagnostic characters: indumendum glabrous or eglandular pubescent.

Aconitum variegatum L., Sp. Pl. ed. 1: 532. 1753

Type citation: "In Italiae, Bohemiae montibus".
Typus: lectotype, Herb. Linn. No. 695.8, LINN (Götz 1967).
Synonyms: *A. cammarum* Jacq., *A. bernhardianum* Wallr., *A. dominii* Sill., *A. gracile* Rchb., *p.p.*, *A. judenbergense* Rchb. (Gáyer), *A. macranthum* Rchb., *A. rostratum* Bernh.
Distribution: Montane and submontane areas of Europe (Alps, Balkans, Sudetes, Transilvania), descending to the lowlands. In Central Europe, it attains the eastern limit of the geographical distribution in the West Carpathians.

Diagnostic characters: inflorescence axis and tepals outside glabrous; hoods conical; filaments glabrous or sparsely pilose; stalks of nectaries erect, glabrous or sparsely pilose; carpels glabrous (subsp. *nasutum*), pilose on the suture (subsp. *variegatum*) or only sparsely pilose on the top of the suture (nothosubsp. *podobnikianum*), pedicel glabrous and bracteoles spathulate to incised (var. *variegatum*) or bracteoles filiform to narrow lanceolate (var. *carniolicum*), or pedicel at least under the bracteoles sparsely pubescent (var. *stiriacum*).

Iconography: Clusius (1601: 98, *pro Aconit. Lycoct.* × *Thora Italica*); Reichenbach (1827: t. 34; 1840: t. 82 fig. 4682); Novikoff and Mitka (2011: 44).

Literature: Cappelletti and Poldini (1984); Mucher (1991b, 1992); Starmühler (1997a); Mitka and Starmühler (2000); Mitka (2003); Novikoff and Mitka (2011).

Lower taxa:

a) subsp. ***variegatum*** var. ***variegatum***

Diagnostic characters: bracteoles (4) 5–8 (25) mm long, spathulate, ovate or leaflike; carpels 3–5, densely pilose only along the suture; pedicels glabrous.

b) subsp. ***variegatum*** var. ***carniolicum*** Starm., Fritschiana 10: 1. 1997

Type citation: "Slowenien, Krain, ENE Laibach (Ljubljana), etwa 3 km NW Sagor (Zagorje), im Tal vom Kotredesch-Bach (Kotredeščica) E der Ruine Gallenberg (Gamberk), 460 m alt., GF 9855/2; Gebüsch; 31.08.1996; leg. *A. Podobnik*; det. W. Starmühler (LJU)" (Starmühler 1997a).
Typus: holotype, LJU. Isotypes, CL, GJO, GZU, IBF, JACA, KL, KRA, LE, LI, LG, LJM, M, MEL, NY, OSC, PE, Herb. PODOBNIK, SIB, Herb. STARMÜHLER, TBI, TNS, TK, W, WU, Z.
Synonyms: none.

Diagnostic characters: bracteoles short, only 2–3 (5) mm long, linear to narrow lanceolate; carpels always only 3, densely pilose along the suture.

c) subsp. ***variegatum*** var. ***stiriacum*** Mucher, Verh. Zool.-Bot. Ges. Österreich 129: 144. 1992

Type citation: "Österreich, Steiermark, Koralpe, Seekar, Hochstauden-flur, 1915 m, 11.9.1991, leg. *W. Mucher*, GZU" (Mucher 1992)
Typus: holotype, GZU 000206408. Isotypes, GZU 000206409 – GZU 000206420, KL, KRA, W, WU, Herb. MUCHER.
Synonyms: none.

Diagnostic characters: bracteoles (4) 5–8 (25) mm long, spathulate, ovate or leaflike; pedicels sparsely pubescent below the bracteoles; carpels (3–) 5, pilose on the suture and often also on the backside.

Iconography: Mucher (1992: 145, fig. 1).

d) subsp. ***nasutum*** (Fischer ex Rchb. em. Rupr.) Götz, Feddes Repert. 76 (1–2): 36. 1967

Type citation: "Saxonia metalifera" (Reichenbach 1823: tab. IX, fig. 2).
Typus: not designated, probably iconotype is Rchb. Illustr. Spec. Aconit., tab. IX, fig. 2, and tab. X, 1823.
Synonyms: *A. nasutum* Fischer ex Rchb., *p.p.*

Diagnostic characters: carpels 3, glabrous.

e) nothosubsp. ***podobnikianum*** – see hybrids of *A. variegatum*.

Hybrids:

a) ***Aconitum*** **×*austriacum*** Mucher. (*A. pilipes* × *A. variegatum*) – see nothoser. *Toxigata*.

b) ***Aconitum*** **×*aquilonare*** A. Kerner ex Gáyer, Magyar Bot. Lapok 10: 201. 1911

Type citation: "Croatia – Fužine. *Borbás* – HUW" (Gáyer, 1911).
Typus: lectotype, WU-Kerner 0034380.
Synonym: *A. variegatum* L. fo. *aquilonare* (Gáyer) M. Niketić.
Hybrid origin: *A. variegatum* × *A. vitosanum*.

Diagnostic characters: pedicels sparsely eglandular curved pubescent; tepals outside glabrous; carpels mostly glabrous.

c) ***Aconitum*** **×*hebegynum*** DC. (*A. degenii* × *A. variegatum*) – see nothoser. *Toxigata*.

d) ***Aconitum*** **×*pawlowskii*** Mitka & Starm. (*A. lasiocarpum* × *A. variegatum*) – see nothoser. *Toxigata*.

e) ***Aconitum variegatum*** L. nothosubsp. ***podobnikianum*** Mucher, Carinthia II 183/103 (2): 522. 1993

Type citation: "*Aconitum variegatum* L. subsp. *variegatum*, Slovenija, Nanos, ad orientem a refugio alpino Vojkova koca dicto, ad margines silvarum, 1240 m s.m., 0250/1, Nr. 117683(1), 4. 10. 1987, leg. *A. Podobnik*, LJU. Isotypes: GZU, LJU" (Mucher 1993).
Typus: holotype, LJU 117683(1). Isotypes, GZU 000274191, LJU.
Synonyms: none.
Hybrid origin: *A. variegatum* subsp. *nasutum* × *A. variegatum* subsp. *variegatum*.

Diagnostic characters: pedicels glabrous or sparsely pubescent only below bracteoles; stamens glabrous; carpels 3, only sparsely pilose on the top of the suture.

Aconitum vitosanum Gáyer, Magyar Bot. Lap. 8: 203. 1909

Type citation: "Bulgaria: Vitoša, inter saxa i. monte medio, *Keck* et *Pichler* Pl. Bulg. 1890".
Typus: holotype, W (?). Isotypes, WU-Halácsy-Europ. 0034442, WU 0034443, WU 0034444.
Synonyms: *A. variegatum* L. var. *diffusum* (Rchb.) Penev & Simeon. (*nom. nud.*).
Distribution: Balkans, Northern Italy.

Diagnostic characters: Inflorescence axis and pedicels pubescent; petals outside curved eglandular pubescent; hoods hemispherical or rounded-conic; filaments glabrous; stalks of nectaries glabrous; carpels glabrous or pubescent on the backside.

Iconography: Penev and Simeonovski (1970: 63).
Literature: Starmühler (1996c).
Hybrids: *A.* ×*aquilonare* A.Kern. ex Gáyer *(A. variegatum* × A. *vitosanum*) – see *A. variegatum*.

Aconitum vivantii Rottensteiner, **nom. nov.**

Basionym: *A. variegatum* subsp. *pyrenaicum* Vivant & Delay, Bull. Soc. Bot. France, Lettres Bot. 127: 501, 1981. There is a new name necessary in the rank of a species because the name *A. pyrenaicum* is already occupied by a taxon from the subgenus *Lycoctonum*.
Type citation: "haute vallée d'Aspe (Pyr.-Atl.) en amont du hameau des Forges d'Abel. … vers 1700 m d'altitude au-dessus de la hetraie-sapinére d'Esplungére ...".
Typus: not designated.
Synonyms: none.
Distribution: Pyrenees: Navarra, Guipúzcoa (Spain).

Diagnostic characters: inflorescence axis and tepals outside glabrous; pedicels almost always glabrous or very rarely sparsely pubescent just below flowers; hoods hemispherical or rounded-conic; filaments glabrous; nectaries strongly bent, mostly reaching the top of the hood, glabrous; carpels 3, glabrous.

Iconography: Molero and Blanche (1986: 240).
Hybrids: most probably with *A. napellus*.

2b. – Ser. ***Toxica*** (Rchb.) Mucher

Type species: *A. toxicum* Rchb.

Diagnostic characters: indumendum glandular pilose.

Aconitum degenii Gáyer, Magyar Bot. Lap. 5: 123. 1906

Type citation: "Comit. Besztercze-Naszód: in lapidosis, umbrosis ad cacumen montis calcarei Craciunel prope Rodnam; in lapidosis graminosis montis calc. Galarin; secus rivulos montanos ad Rodna-Borberek; Comit. Csik: in montibus calcareis Ócsém et Nagy-Hagymás; Comit. Máramaros: Oberhalb der Luhyer Klause Hoverla im Fichtenwalde; Comit. Torda-Aranyos: in valle Csepilor sub alpe Nagy-Bihar; Comit. Kolozs: ad margines silvarum prope Rogozsely sub tractu Vlegyászae".
Typus: lectotype, CL-Soó!
Synonyms: *A. hebegynum* auct. Fl. Carpathorum non DC., *A. molle* Rchb., *A. paniculatum* Lam., *p.p.* (*nom. inval.*).
Distribution: Alps, Carpathians, Balkans.

Diagnostic characters: hood rounded-conic; carpels (3–) 5 pubescent (subsp. *valesiacum*) or glabrous, pedicels and petals glandular pilose, bracteoles in the middle of pedicels (subsp. *paniculatum*), filaments glabrous (var. *laxiflorum*) or pubescent (var. *turrachense*), pedicels and petals glabrous (subsp. *rhaeticum*); bracteoles in the upper part of the pedicels or just below flower (subsp. *degenii*), spur of nectaries semi-spiral coiled (fo. *degenii*) or capitate (fo. *craciunelense*); pedicels below bracteoles and hood ± glabrous (var. *intermedium*).

Iconography: Mucher (1993a: 55); Novikoff and Mitka (2011: 46).
Literature: Mucher (1993a); Starmühler (1996d, 1996e); Ilnicki and Mitka (2011); Novikoff and Mitka (2011); Ziman et al. (2015).

Lower taxa:

a) subsp. ***degenii*** var. ***degenii*** fo. ***degenii***

Diagnostic characters: bracteoles lanceolate to spathulate, in the upper part of pedicel; pedicels below the bracteoles densely glandular pilose; tepals outside glandular pilose; hood ± hemispheric; carpels 3, glabrous.

b) subsp. ***degenii*** var. ***degenii*** fo. ***craciunelense*** Gáyer, Magyar Bot. Lap. 5: 126. 1906

Type citation: "Comit. Besztercze-Naszód: ad cacumen montis Craciunel. (*Degen*, H.D.)".
Type specimens: not designated.
Synonyms: none.

Diagnostic characters: bracteoles lanceolate to spathulate, in the upper part of pedicel; pedicels below the bracteoles densely glandular pilose; tepals outside glandular pilose; hood cymbiform; carpels 3, glabrous.

c) subsp. ***degenii*** var. ***intermedium*** (Zapał.) Mitka, Caryologia 64(4): 449. 2011

Type citation: "Płaj między Mołodą a Jajcem nad Łomnicą, Tomnatek w Polenicy Popowiczowskiej, Jabłonica na Przesmyku Tatarskim (*Wołoszczak*), Jawornik koło Mikuliczyna (*Rehman*), Bystrzec pod Czarną Horą (*Śleńdziński*)" (Zapałowicz 1908b: 221).
Typus: lectotype, KRAM 132196 (Mitka 2003).
Synonyms: *A. hebegynum* auct. Fl. Carpathorum, non DC., *A. paniculatum* Lam. var. *prutense* Zapał., *A. paniculatum* fo. *latiusculum* Zapał.

Diagnostic characters: bracteoles lanceolate to spathulate, in the upper part of pedicel; pedicels below the bracteoles only sparsely glandular pilose; tepals outside glandular pilose; carpels 3, glabrous.

d) subsp. ***paniculatum*** (Arcang.) Mucher var. ***turrachense*** (Mucher) Mucher, Phyton (Horn) 33 (1): 63. 1993

Type citation: "Ostalpen, Steiermark, Gurktaler Alpen, 2 km südlich von Predlitz, Gebüschsaum, 1020 m, 26.8.1989, leg. *W. Mucher* (GZU)" (Mucher 1993a).
Typus: holotype, GZU 000274182. Isotypes, GJO, GZU 000274183, GZU 000274185 – GZU 000274188, W. Paratype, GZU 000274184.
Synonyms: *A. paniculatum* Lam. subsp. *paniculatum* var. *turrachense* Mucher.

Diagnostic characters: bracteoles linear, in the middle of the pedicel; tepals outside glandular pilose; nectaries glabrous or pilose; filaments ± densely pubescent.
Iconography: Mucher (1990).

e) subsp. ***paniculatum*** (Arcang.) Mucher var. ***laxiflorum*** (Rchb.) Mucher, Phyton (Horn) 33 (1): 60. 1993

Typus: lectotype, see Mucher (1993a) for details.
Synonyms: *A. cernuum* Rchb. non Wulfen [var.] α *laxiflorum* Rchb., *A. paniculatum* subsp. *paniculatum* var. *paniculatum* (*nom. inval.*).

Diagnostic characters: bracteoles linear, in the middle of the pedicel; tepals outside glandular pilose; nectaries and filaments glabrous.

Iconography: Mucher (1993a).

f) subsp. ***rhaeticum*** Starm., Fritschiana 7: 2. 1996

Type citation: "Schweiz, Graubünden, Oberhalbstein S Tiefencastel, Abhang zum rechten Ufer des Adont N Präsanz (Personz), 1360–1375 m alt., GF 9423/2; *Alnus incana–Prunus padus*-Wald; 14.08.1995; leg./det. *W. Starmühler* (GZU)" (Starmühler 1996d).
Typus: holotype, GZU 000212973. Isotypes: LE, M, NY, PE, TI, W, Z, Herb. STARMÜHLER.
Synonyms: none.

Diagnostic characters: tepals outside, pedicels and nectaries glabrous.

Iconography: Starmühler (1996d).

g) subsp. ***valesiacum*** (Gáyer) Mucher, Phyton (Horn) 33(1): 64. 1993

Type citation: "Mauvoisin, vallee de Bagnes [Suisse, Valais] (BP, Götz 1967)" (Mucher 1993a).
Typus: holotype, BP.
Synonyms: *A. valesiacum* Gáyer, *A. variegatum* L. subsp. *valesiacum* (Gáyer) Greuter & Burdet.

Diagnostic characters: bracteoles lanceolate to spathulate, situated at the pedicel's top; pedicels above the bracteoles densely glandular pilose, below the bracteoles – sparsely pilose or glabrous; tepals outside glandular pilose; carpels 5, densely pilose; nectaries and filaments glabrous.

Iconography: Götz (1967), Mucher (1993a).

h) nothosubsp. ***gandogeri*** Mucher (*A. degenii* subsp. *paniculatum* × *A. degenii* subsp. *valesiacum*) – see hybrids *of A. degenii*.

i) nothosubsp. ***lippertianum*** Starm. (*A. degenii* subsp. *paniculatum* × *A. degenii* subsp. *rhaeticum*) – see hybrids *of A. degenii*.

Hybrids:

a) ***Aconitum degenii*** Gáyer nothosubsp. ***gandogeri*** Mucher, Phyton (Horn) 33 (1): 65, 1993

Type citation: "Suisse, Vaud, Pays d'Enhaut, Vallee de Gerignoz, LaMontagnette, alt. 1445 m, cs. 579/143; 17.8.1952; leg. *A. Maillefer*, LAU (as *A. paniculatum* Lam.)" (Mucher 1993).
Typus: holotype, LAU.
Synonyms: none.
Hybrid origin: *A. degenii* subsp. *paniculatum* × *A. degenii* subsp. *valesiacum.*

Diagnostic characters: the filaments of the hybrid are in most cases pilose, although both parents have glabrous filaments; pedicels below the bracteoles almost glabrous; carpels mostly glabrous; tepals outside glandular pilose.

b) ***Aconitum degenii*** Gáyer nothosubsp. ***lippertianum*** Starm., Fritschiana 7: 11. 1996

Type citation: "Schweiz, Kt. Graubünden, Oberhalbstein S Tiefencastel, Abhang zum rechten Ufer des Adont N Präsanz (Personz), 1325 m alt., GF 9423/2; *Alnus incana*-Wald mit *Corylus avellana, Sorbus aucuparia, Berberis vulgaris* etc.; 14.08.1995; leg./det. *W. Starmühler* (GZU)" (Starmühler 1996e).
Typus: holotype, GZU 000212947. Isotypes, LE, M, PE, Herb. STARMÜHLER, Z.
Synonyms: none.
Hybrid origin: *A. degenii* subsp. *paniculatum* × *A. degenii* subsp. *rhaeticum.*

Diagnostic characters: pedicels sparsely glandular pilose above the bracteoles; tepals glabrous.

c) ***Aconitum ×dragulescuanum*** Mucher (*A. degenii* subsp. *degenii* × *A. toxicum* subsp. *toxicum*) – see *A. toxicum*.

d) ***Aconitum ×gayeri*** Starm., Stapfia 45: 41. 1996

Type citation: "Tanssilvania, Rodna – Borberek [= Valea Vinului], Nr. 135419; 28.8.1897; *L. Walz* (CL)" (Starmühler, 1996b).
Typus: holotype, CL 135419! Isotype, Detto, Nr. 135418 (CL).
Synonyms: none.
Hybrid origin: *A. degenii* × *A. lasiocarpum.*

Diagnostic characters: hood rounded-conic or conic, petals outside pilose, carpels pilose, spur of nectaries reaching the top of the hood, pedicels above bracteoles densely glandular pilose, below bracteoles sparsely pilose, bracteoles linear to lanceolate.

e) ***Aconitum ×hebegynum*** DC. (*A. degenii* × *A. variegatum*) – see nothoser. *Toxigata*

f) ***Aconitum ×mielichhoferi*** Rchb. (*A. degenii* × *A. tauricum*) – see nsect. *Acomarum*

g) ***Aconitum ×pilosiusculum*** (Ser.) Gáyer, Magyar Bot. Lapok 10: 200. 1911

Type citation: "Neotype: Patura-ge de Lavaraz, Alpes de Bex, 26.9.1879, *Jaccard* (ZT)" (Starmühler 1996a).
Typus: neotype, ZT.
Synonyms: *A. variegatum* L. var. *pilosiusculum* Ser., *A. rostratum* Bernh. ex DC. var. *pilosiusculum* Ser.
Hybrid origin: *A. degenii* × *A. pilipes.*

Diagnostic characters: hood rounded-conic, bracteoles lanceolate to spathulate, tepals outside pilose, carpels pilose, pedicels glandular pilose and eglandular pubescent.

Aconitum lasiocarpum Rchb., Uebers. Aconitum: 55. 1819

Type citation: "in Hungar Comit. Marmarosch. *Sadler*!".
Typus: neotype, "An schattigen Stellen in der Voralpenregion auf dem Gebirge Craciunel bei Alt Rodna, 1.8.1882, leg. *Porcius*" – WU-Kerner" (Mitka 2003).
Synonyms: *A. cammarum* L. var. *beskidene* Zapał., *A. dasycarpum* Schur.
Distribution: Western and Eastern Carpathians, Podilya (Ukraine).

Diagnostic characters: inflorescence axis and tepals outside glandular pilose, hood conical; pedicels glandular pilose (subsp. *lasiocarpum*) or below bracteoles glabrous or sparsely eglandular pilose and curved and crisped eglandular pubescent (subsp. *kotulae*); bracteoles linear or lanceolate, rarely spathulate, (2.5–) 3–6 (–12) mm; carpels glandular pilose.

Iconography: Reichenbach (1827: t. 9); Mitka (2003: 175); Novikoff and Mitka (2011: 44).
Literature: Gáyer (1911); Starmühler (1993, 1996a); Joachimiak et al. (1999); Mitka and Starmühler (2000); Mitka (2003).

Lower taxa:

a) subsp. ***lasiocarpum***

Diagnostic characters: pedicels entirely glandular pilose.

b) subsp. ***kotulae*** (Pawł.) Starm. & Mitka, Acta Soc. Bot. Polon. 69 (2): 150. 2000

Type citation: "Tatry Wysokie [High Tatras]: dol. Koprowa – skraj lasu. ok. 1300 m: 19.8.1925; leg. *B. Pawłowski* (KRAM-Pawłowski 320228 – Neotype)" (Mitka and Starmühler 2000).
Typus: neotype, KRAM-Pawłowski 320228. Paratype, KRAM 132168.
Synonyms: *A. variegatum* L. subsp. *kotulae* Pawł., *A. variegatum* fo. *kotulae* (Pawł.) Skalický, *A. paniculatum* Lam. var. *podolicum* Zapał. fo. *podolicum*, *A. paniculatum* Lam. var. *podolicum* Zapał. fo. *latilobum* Zapał., *A. podolicum* (Zapał.) Voroshylov, *A. hebegynum* auct., *p.p.*, *A. beskidense* (Zapał.) Gáyer, *A. cammarum* Jacq. var. *koscieliskanum* Zapał., *p.p.*, *A. cammarum* Jacq. var. *beskidense* Zapał., *A. gracile* Rchb. subsp. *grosserratum* (Gáyer) Grinţ. fo. *beskidense* Zapał.

Diagnostic characters: pedicels below bracteoles glabrous or sparsely eglandular pilose and curved and crisped eglandular pubescent.

Hybrids:

a) ***Aconitum* ×*gayeri*** Starm. (*A. degenii* × *A. lasiocarpum*) – see *A. degenii.*

b) ***Aconitum lasiocarpum* × *A. toxicum*** – hood rounded-conic, bracteoles linear-ovate with reticulate venation, pedicels glandular pilose, carpels pilose.

c) ***Aconitum* ×*pawlowskii*** Mitka & Starm. (*A. lasiocarpum* × *A. variegatum*) – see nothoser. *Toxigata.*

Aconitum pilipes (Rchb.) Gáyer, Magyar Bot. Lap. 10: 200. 1911

Basionym: *A. cammarum* L. var. *pilipes* Rchb., Fl. Germ. Exurs. 738, 1832.
Type citation: "Salvesental bei Imst".
Typus: neotype, WU-Kerner.
Distribution: Western and Eastern Alps.

Diagnostic characters: hood conical, outside glandular pilose; pedicels curved and s-formed glandular pilose and eglandular pubescent; bracteoles spatulate 3–6 mm, situated just below the flower; filaments pilose; carpels 5, entirely pubescent.

Iconography: Starmühler (1996b: 171).
Literature: Starmühler (1996b, 2001).

Hybrids:

a) ***Aconitum* ×*austriacum*** Mucher, Carinthia II 183/103(2): 524. 1993

Type citation: "Österreich, Salzburg, Hohe Tauern, Habachtal, Weg von der Moar-Alm zum Noitroi-Steig, Hochstaudenflur, 1540 m, 30. 8. 1991, leg. *W. Mucher*, GZU" (Mucher 1993b).
Typus: holotype, GZU 000206194. Isotypes: GJO, GZU 000206195, KL, KRA,W, WU 0034381, Herb. MUCHER.
Synonyms: none.
Hybrid origin: *A. pilipes* × *A. variegatum.*

Diagnostic characters: carpels sparsely pubescent or pubescent at the suture.

b) ***Aconitum* ×*pilosiusculum*** (Ser.) Gáyer (*A. degenii* × *A. pilipes*) – see *A. degenii.*

c) ***Aconitum napellus* × *A. pilipes*** – see nothosect. *Acomarum*

d) ***Aconitum pilipes* × *A. tauricum*** – see nothosect. *Acomarum*

Aconitum toxicum Rchb., Uebers. Aconitum: 43. 1819

Type citation: "Hab. in Transylvaniae alpibus. *Baumgarten!*".
Typus: lectotype, "Transsylv., in graminosis alpestris, [1]827, leg. *Baumgarten* (as *A. neomontanum*, rev. E. Götz 1966 as *A. toxicum* Rchb.)", W (Mucher 1993).
Synonyms: *A. bosniacum* Beck, *A. diabolicum* Gáyer, *A. neomontanum* auct. non Koelle, *A. schurii* Beck., *A. schurii* fo. *retyezatense* Gáyer, *A. toxicum* Rchb. *bosniacum* (Beck) Hayek, *A. toxicum* Rchb. fo. *diabolicum* (Gáyer) Grint., *A. toxicum* [var.] β *schurii* Beck.
Distribution: Transilvania, Eastern Carpathians (Ceahlau Mts), Southern Carpathians, Balkans.

Diagnostic characters: pedicels glandular pilose (subsp. *toxicum*), glandular/eglandular pubescent (subsp. *crispulum* and nothosubsp. *nyaradyanum*), sparsely straight glandular pilose (nothosubsp. *ungarianum*), or glabrous (subsp. *bucegiense*); hood outside glandular pilose (subsp. *toxicum*), glandular/eglandular pubescent (subsp. *crispulum* and nothosubsp. *nyaradyanum*), or glabrous (subsp. *bucegiense* and nothosubsp. *ungarianum*); filaments in the upper part, pilose; hood rounded-conic or conical; carpels glabrous; bracteoles ovate, sometimes divided, with reticulate venation.

Iconography: Reichenbach (1827: t. 37).
Literature: Mucher (1993a, 1993b); Mitka (2000); Starmühler (2000).

Lower taxa:

a) subsp. ***toxicum***

Diagnostic characters: pedicels and tepals outside with straight glandular trichomes.

b) subsp. ***crispulum*** (Nyár.) Mucher, Phyton (Horn) 33(1): 70. 1993

Type citation: "Transsilvania, distr. Brasov, ad rivum Gr. Weidenbachsub mtbus Bucegi prope pagum Rasnov, alt. cca. 720 m s.m., 12.8.1929, leg. *E.I. Nyárády* (SIB-Nyárády)" (Mucher 1993a).
Typus: lectotype, SIB-Nyárády. Paratype, SIB-Nyárády.
Synonyms: *A. toxicum* Rchb. var. *crispulum* Nyárády in Borza.

Diagnostic characters: pedicels and tepals outside with curved glandular trichomes.

Iconography: Mucher (1993a).

c) subsp. ***bucegiense*** (Nyár.) Mucher, Phyton (Horn) 33(1): 68. 1993

Type citation: "Transsilvania, distr. Brasov, ad pedem montium Bucegi, prope Valea Toplitei, versus pagum Rasnov, in quercetis, una cum typo, alt. cca 700 m s.m., Nr. 601109, 22.9.1940, leg. *P. Cretzoiu*, det. E.I. Nyárády (CL)" (Mucher 1993a).
Typus: holotype, CL. Isotypes, CL, SIB.
Synonyms: *A. toxicum* Rchb. var. *bucegiense* Nyár.

Diagnostic characters: pedicels glabrous.

Iconography: Mucher (1993a).

d) nothosubsp. ***nyaradyanum*** Mucher – see hybrids of *A. toxicum.*

e) nothosubsp. ***ungarianum*** Starm. – see hybrids of *A. toxicum.*

Hybrids:

a) ***Aconitum* ×*dragulescuanum*** Mucher, Phyton (Horn) 33(1): 72. 1993 nothosubsp. ***dragulescuanum***

Type citation: "Transsilvania, in praeruptis et graminosis rupium calc. Mt. Hagimasul Mare, supra rivum Nagyàg, alt. 1500–1740 m s.m., distr. Ciuc; 19.8.1948; *J.E. Nyárády* (SIB-Nyárády)" (Mucher 1993).
Typus: holotype, SIB-Nyárády.
Synonyms: none.
Hybrid origin: *A. degenii* subsp. *degenii* × *A. toxicum* subsp. *toxicum.*

Diagnostic characters: pedicels, bracteoles and tepals outside with straight glandular trichomes only.

b) ***Aconitum* ×*dragulescuanum*** Mucher nothosubsp. ***grintescuanum*** Starm., Siebenbürg. Arch. 36: 16. 2000

Type citation: "Rumänien, Siebenbürgen (Transilvania, Erdély), Süd-Karpaten (Carpatii Meridionali, Déli Kárpátok), Retezat-Gebirge (Muntii Retezatului, Retyezát-havasok) S Hotzing (Hateg, Hátszeg), Nationalpark Retezat, am Weg von der Gura Zlata-Hütte zum Retezat, am Bach Dobrun, 1470 m"
Typus: holotype, GZU 000232748.
Synonyms: none.
Hybrid origin: *A. degenii* subsp. *degenii* × *A toxicum* subsp. *crispulum.*

Diagnostic characters: pedicels, bracteoles and tepals outside with curved and straight glandular trichomes.

c) ***Aconitum lasiocarpum*** × ***A. toxicum*** – bracteoles spathulate or linear-ovate with reticulate venation, hood slightly conical or round-conic, carpels pilose.

d) ***Aconitum toxicum*** Rchb. nothosubsp. ***nyaradyanum*** Mucher, Phyton (Horn) 33(1): 71. 1993

Type citation: "Transsilvania, distr. Brasov, ad rivum Gr. Weidenbach sub mtibus Bucegi prope pagum Rasnov, alt. cca. 720 m s.m., Nr. 195107; 12.8.1929; leg. *E.I. Nyárády* (CL)" (Mucher 1993a).
Typus: holotype, CL 195107.
Synonyms: none.
Hybrid origin: *A. toxicum* subsp. *crispulum* × *A. toxicum* subsp. *toxicum.*

Diagnostic characters: pedicels and tepals outside glandular/eglandular pubescent.

e) ***Aconitum toxicum*** Rchb. nothosubsp. ***ungarianum*** Starm., Siebenbürg. Arch. 36: 21. 2000

Type citation: "Siebenbürgen (Transilvania, Erdély), Burzenländer Senke (Depresiunea Birsei, Barcasági-medence) SW Kronstadt (Brasov, Brassó), S Rosenau (Risnov, Barcarozsnyó), am rechten Ufer vom Grossen Weidenbach (Ghimbasel), 720 m."
Typus: holotype, GZU 000232749.
Synonyms: none.
Hybrid origin: *A. toxicum* subsp. *bucegiense* × *A. toxicum* subsp. *toxicum.*

Diagnostic characters: tepals outside glabrous or almost glabrous; pedicels sparsely glandular pilose, mainly above the bracteoles.

2c. – Nothoser. ***Toxigata*** Starm. (ser. ***Variegata*** × ser. ***Toxica***)

Type species: *A.* ×*hebegynum* DC., designated here.

Diagnostic characters: indumentum glandular and eglandular pubescent.

Aconitum* ×*austriacum Mucher, Carinthia II 183/103(2): 524. 1993

Type citation: "Österreich, Salzburg, Hohe Tauern, Habachtal, Weg von der Moar-Alm zum Noitroi-Steig, Hochstaudenflur, 1540 m, 30. 8. 1991, leg. *W. Mucher*" (Mucher, 1993b).
Typus: holotype, GZU 000206194. Isotypes, GZU 000206195, WU 0034381, GJO, KL, KRA, W, Herb. MUCHER.
Synonyms: none.
Hybrid origin: *A. pilipes* × *A. variegatum*.

Diagnostic characters: Pedicels sparsely crisped to s-formed glandular pilose, mainly above the bracteoles; tepals outside glabrous; hood higher than broad; nectaries claw upright; nectaries spur curved backward, not reaching the top of the hood; carpels (3) 5, mostly +/- densely pilose.

Iconography: Mucher (1993b).
Literature: Starmühler (1996a).

Aconitum* ×*bartokianum Starm., Siebenbürg. Arch. 36: 10. 2000

Type citation: "Aconita rarissima selecta (1999), Rumänien, Transilvania (Siebenburgen, Erdély), Süd Karpaten, Munţii Retezatului […]; 14.08.1992; leg. *W. Mucher et U. Starmühler* (GZU)".
Typus: holotype, GZU 000225135. Isotypes, CL, GJO, Herb. STARMÜHLER, TNS.
Synonyms: none.
Hybrid origin: *A. toxicum* × *A. variegatum*.
Distribution: Transilvania, Southern Carpathians.

Diagnostic characters: hood conical; bracteoles spathulate or linear-ovate with reticulate venation; nectaries reaching the top of the hood; filaments glabrous or sparsely pilose. Pedicel and tepals outside straight glandular pilose; carpels glabrous – nothosubsp. *bartokianum*. Pedicel and tepals outside curved glandular pilose; carpels glabrous – nothosubsp. *rapaicsianum*. Pedicel and tepals outside straight glandular pilose; carpels pilose on the suture – nothosubsp. *sooanum*.

Iconography: Starmühler (2000: 11).
Literature: Starmühler (2000).

Lower taxa/hybrids:

a) nothosubsp. ***bartokianum***

Hybrid origin: *A. toxicum* subsp. *toxicum* × *A. variegatum* subsp. *nasutum.*

Diagnostic characters: pedicel and tepals outside straight glandular pilose; carpels glabrous.

b) nothosubsp. ***rapaicsianum*** Starm., Siebenbürg. Arch. 36: 14. 2000

Type citation: "Aconita rarissima selecta (1999), Rumänien, Transilvania (Siebenbürgen, Erdely), Süd-Karpaten, Muntii Retezatului (Retezat-Gebirge, Retyezát-havasok), Nationalpark Retezat, S-Hang des Retezat, 1980 m alt.; Hochstaudenflur mit *Achillea distans, Adenostyles alliariae, Angelica sylvestris, Carduus personata, Deschampsia cespitosa, Rumex alpinus, Seriecio ovatus, Senecio cacaliaster* etc.; 14.08.1992; leg. *W. Mucher et U. Starmühler* (GZU)" (Starmühler 2000).
Typus: holotype, GZU 000225136. Isotypes, CL, GJO, Herb. STARMÜHLER, TNS.
Synonyms: none.
Hybrid origin: *A. toxicum* subsp. *crispulum* × *A. variegatum* subsp. *nasutum.*

Diagnostic characters: pedicel and tepals outside curved glandular pilose; carpels glabrous.

Iconography: Starmühler (2000: 11).

c) nothosubsp. ***sooanum*** Starm., Siebenbürg. Arch. 36: 15. 2000

Type citation: "Hungaria media, Alpes Biharienses, ad balnea "Biharfüred"; 13.07.1914; leg. *L.T. Haisz* (CL-Soó)" (Starmühler 2000).
Typus: holotype, CL-Soó.
Synonyms: none.
Hybrid origin: *A toxicum* subsp. *toxicum* × *A. variegatum* subsp. *variegatum.*

Diagnostic characters: pedicel and tepals outside straight glandular pilose; carpels pilose along the suture.

Iconography: Starmühler (2000: 11).

Aconitum* ×*hebegynum DC., Regn. Veg. Syst. Nat.: 376. 1817, **pro spec.**

Type citation: "Hab. in dumetis Alpium Vallesiae, Austriae (*Jacq.*) et in Carpathorum convallibus (*Wahlenb.*)".
Typus: neotype, "(Schweiz) cultivé, provenant d'un pied vivant récolté ä la Gemmi – G-DC" (Starmühler 1997b).
Synonyms: none.
Hybrid origin: *A. degenii* × *A. variegatum.*
Distribution: Alps, Balkans.

Diagnostic characters: Hood about as high as broad or slightly higher; nectary claw curved; nectary spur backward bent always reaching the top of the hood; bracteoles linear-lanceolate, rarely spathulate 4–6 (–8) mm long, mostly glandular pilose. Pedicels and tepals outside sparsely glandular pilose; carpels 3–5 glabrous or sparsely glandular pubescent.

Iconography: Mucher (1993b: 519–527).
Literature: Gáyer (1906).

Aconitum ×pawlowskii Mitka & Starm., Acta Soc. Bot. Pol. 69: 151. 2000

Type citation: "(Tatra Mts.) Tatry, pod Raptawickimi Turniami (dol. Kościeliska) od półn., ok. 1300 m, piargi wapienne, 3.9.1932, leg. *B. Pawłowski*".
Typus: holotype, KRAM-Pawłowski 320221.
Synonyms: none.
Hybrid origin: *A. lasiocarpum* × *A. variegatum.*
Distribution: West Carpathians.

Diagnostic characters: Hood conical; nectary claw curved; nectary spur backward bent not reaching the top of the hood; bracteoles linear-lanceolate, lanceolate, glabrous or ciliate 2.5–6 (–12) mm long. Pedicels above bracteoles straight glandular pilose, below bracteoles sparsely straight glandular pilose or appressed curved pubescent; carpels 3–5 on the suture pilose.

Iconography: Mitka and Starmühler (2000: 151); Mitka (2003: 173).
Literature: Mitka and Starmühler (2000); Mitka (2003).

Aconitum ×tuscheticum (N.Busch) N.Busch, Opred. Rast. Kryma i Kavkaza 30. 1919

Basionym: *A. caucasicum* N.Busch subsp. *pubiceps* (Rupr.) N.Busch var. *tuscheticum* N.Busch, Tr. Jur'jev. Bot. Sada 1: 3, 1900.
Type citation: "Dzhvari-Vozeli. 13.VII.[18]76. *Radde*" (LE).
Typus: holotype, LE (?).
Synonyms: *A. caucasicum* N.Busch subsp. *pubiceps* (Rupr.) N. Busch var. *tuscheticum* N.Busch, *A. nasutum* Rchb. subsp. *tuscheticum* (N.Busch) A.N.Luferov, *A. pubiceps* Rupr. var. *tuscheticum* (N.Busch) Grossh.
Hybrid origin: *A. degenii* × *A. vitosanum.*
Distribution: Caucasus, Slovenia.

Diagnostic characters: plant 50–100 cm high; inflorescence axis, pedicels and tepals outside glandular and eglandular pubescent.

Iconography: none.
Literature: Luferov (2000); Starmühler (1996c).

3. – Nothosect. ***Acomarum*** Starm. (= nothosect. ***Acopellus*** Starm.)

Type species: *A. ×cammarum* L. em. Fries, designated here.

Diagnosis

Carpels totally or partially sterile.

Description

Leaves divided into 3 or 5 lobes and dissected to the base; hoods hemispherical or conical, 1.2–2.0 (–2.5) times higher than wider; claws of the nectaries erect or slightly bent, reaching or not the top of the hood; spurs of nectaries backward bent or semi-spiral coiled; carpels 3 or 5; seeds with membraneous 4–6 lamellae and with one conspicuously winged edge; inflorescence ramose or rarely dense ramified; root elongated.

Aconitum ×acuminatum Rchb., Uebers. Aconitum 46. 1819

Type citation: "Hab. in monte Baldo *Heineken*! Hb. *Mertens*".
Typus: not designated.
Synonym: *A. lobelianum* Host. in Gáyer fo. *brachytrichum* Gáyer.
Hybrid origin: *A. degenii* × *A. napellus.*
Distribution: Alps.

Diagnostic characters: hood glandular pilose and eglandular pubescent, pedicels above bracteoles glandular pilose and below eglandular pubescent, carpels 3, glabrous or overall pubescent.

Iconography: Reichenbach (1827: t. 68).
Literature: Starmühler (2001).

Aconitum ×acutum Rchb., Uebers. Acon. 21. 1819

Type citation: "Hab. in valle Kalstahl Tyrol. *Sieber*! in Alp. Seethal supra Judenburg v. *Vest*!".
Typus: not designated.
Synonym: *A. ×zahlbruckneri* Gáyer.
Hybrid origin: *A. tauricum* × *A. variegatum.*
Distribution: Eastern and Southeastern Alps.

Diagnostic characters: hood glabrous, hemispherical; pedicels glabrous or eglandular pubescent; filaments glabrous or sparsely pilose, stalks of nectaries glabrous or pubescent; carpels mostly glabrous.

Iconography: Reichenbach (1821: Tab. 12, 2 *pro species*).
Literature: Starmühler (2001).

Aconitum* ×*berdaui Zapał., Rozpr. Wydz. Mat.-Przyr. Akad. Umiej., Dział B. Nauki Biol. 48: 88. 1908a, pro hybr. [reprinted in Zapałowicz, 1908b].

Type citation: "In regione subalpina Tatrorum: in valle Kościeliska et altero loco non indicato (*Berdau*), Podspady ad Jaworzynka".
Typus: lectotype, "Dol. Kościeliska, ?.08.1855, leg. *Berdau*, det. *Zapałowicz* (16.02.1908), KRAM 133482!" (Wacławska-Ćwiertnia and Mitka 2016).
Synonyms: *A. lengyeli* Gáyer, *A. odotandrum* Wissjul.
Hybrid origin: *A. firmum* × *A. variegatum*.
Distribution: Europe: Sudetes, Transilvania and the Balkans.

Diagnostic characters: inflorescence axis, pedicels and tepals outside pilose (nothosubsp. *walasii*) or glabrous (nothosubsp. *berdaui*); hoods conical; filaments glabrous or sparsely pilose, spur of the nectaries semi-spiral coiled; carpels pilose on the suture.

Iconography: Mitka (2003: 173); Novikoff and Mitka (2011: 44.
Literature: Wissjulina (1939); Starmühler and Mitka (2001); Mitka (2003), Novikoff and Mitka (2011), Wacławska-Ćwiertnia and Mitka (2016).

Lower taxa/hybrids:

a) nothosubsp. ***berdaui***

Hybrid origin: *A. firmum* subsp. *firmum* × *A. variegatum* subsp. *variegatum*.

Diagnostic characters: inflorescence axis, pedicels and tepals outside glabrous.

Iconography: (Mitka 2003: 173, fig. 6D).

b) nothosubsp. ***walasii*** (Mitka) Mitka, The genus *Aconitum* in Poland and adjacent countries: 56. 2003

Type citation: "Poland, Western Carpathians, Pogórze Spisko-Gubałowskie Foothills), Podhale, Wzn. Gubałowskie, Roztoki, żwirowiska nad Czarnym Dunajcem, 22.8.1957, leg. *E. Pancer*" (Mitka 2003).
Typus: holotype, KRA 003852.
Synonyms: *A.* ×*lengyelii* Gáyer nothosubsp. *walasii* Mitka.
Hybrid origin: *A. firmum* subsp. *moravicum* × *A. variegatum* subsp. *variegatum*.

Diagnostic characters: inflorescence axis, pedicels and tepals outside pilose.

Iconography: Mitka (2003: 176, fig. 9E).

Aconitum* ×*cammarum L. em. Fries, Sp. Pl. 1 (ed. 2): 751. 1762 *em*. Nov. Flor. Suec. (ed. 2): 171. 1828

Type citation: "Austria, Styria".
Typus: not designated. Conflict of original material has been revealed (The Linnaean Plant Name Typification Project, 2006).
Synonyms: *A. intermedium* DC., *A. stoerkianum* Rchb.
Hybrid origin: *A.* sect. *A.* (*A. napellus* ?) × *A. variegatum*.
Distribution: Europe (garden plant, sometimes naturalized).

Diagnostic characters: hood glabrous; tepals deep blue (fo. *cammarum*) or with white strips (fo. *bicolor*); pedicels above bracteoles sparsely curved pubescent, below bracteoles glabrescent; carpels glabrous; filaments pilose.

Iconography: Reichenbach (1827: t. 71, *A. stoerkianum*); Mitka (2003: 173, fig. 6F), Novikoff and Mitka (2011: 44).
Literature: Mitka (2003).

Lower taxa:

a) var. ***cammarum*** fo. ***cammarum***

Diagnostic characters: tepals with monotonic, usually deep blue, color.

b) var. ***cammarum*** fo. ***bicolor*** (Schult) DC., Syst. Nat. [Candolle] 1: 372. 1817

Type citation: none.
Typus: not designated.
Synonyms: none.

Diagnostic characters: tepals variegate, with white and blue stripes.

Aconitum* ×*exaltatum Bernh. ex Rchb., Ill. Spec. Acon.: Tab. LXXII. 1827

Type citation: "In montium Sudetorum Aupagrund, *Funk*!".
Type specimens: not designated, probably BM 000613639.
Synonyms: *A. exaltatum* var. *hamatum* Rchb. [= *A. hamatum* (Rchb.) Gáyer], *A. speciosum* Otto ex Rchb.
Hybrid origin: *A. plicatum* × *A. variegatum*.
Distribution: Sudetes, Bohemian Massif, Bavarian Alps.

Diagnostic characters: inflorescence axis and hoods outside glabrous; hoods rounded-conic or slightly elongated; pedicels glabrous or eglandular curved and crisped pubescent, stamens pilose, spur of nectaries backward bent or capitate; carpels mostly entirely sterile.

Iconography: Mitka (2003: 177, fig. 10F).
Literature: Mitka (2003).

Aconitum* ×*mielichhoferi Rchb., Uebers. Acon.: 29. 1819

Type citation: "Hab. in Alp. Carinth. Salisb. (in quodam certi harum regionum loco) *Mielichhofer*!".

Typus: not designated.
Synonym: *A.* ×*ronnigeri* Gáyer.
Hybrid origin: *A. degenii* × *A. tauricum*.
Distribution: Eastern and Southeastern Alps.

Diagnostic characters: pedicels at least above the bracteoles densely glandular pilose; bracteoles filiform to spathulate; tepals outside sparsely to densely glandular pilose; hood about as broad as high; nectaries always pilose, their stalks distinctly bent, their spur capitate, always reaching the top of the hood; carpels 3, glabrous to densely hairy.

Literature: Starmühler (2001).

Aconitum **×*schneebergense*** Gáyer, Magyar Bot. Lapok 8: 189. 1909

Type citation: "Hab. in Schneeberg Austriae Inf. (*Portenschlag* – W, duo exempla: unum cum nota: *A. neomontanum,* Schneeberg, alterum: Austria Inf.)".
Typus: not designated.
Synonyms: *A.* ×*algoviense* Gáyer, *A. laxum* Gáyer, *A.* ×*virgatum* Rchb. ex Gáyer.
Hybrid origin: *A. napellus* × *A. variegatum*.
Distribution: Alps.

Diagnostic characters: pedicels above the bracteoles ± densely crisped eglandular pubescent, below the bracteoles ± glabrescent; tepals outside glabrous; hood about as high as broad; nectaries mostly glabrous, hardly curved, with a capitate to hooked spur, always reaching the top of the hood; filaments always hairy; carpels 3–4, glabrous or pilose on the suture.

Literature: Starmühler (2001).

Hybrid formulae:

Aconitum napellus × ***A. pilipes*** – hood rounded, pedicels above bracteoles glandular pubescent and below bracteoles eglandular pubescent; spur of nectaries backward bent or capitate, carpels glabrous or entirely pubescent, sterile.

Aconitum pilipes × ***A. tauricum*** – hood rounded; pedicels glandular pubescent, spur of nectaries capitates; carpels glabrous or slightly pubescent.

Aconitum superbum × ***A. variegatum*** – more studies are required.

Aconitum superbum × ***A. vitosanum*** – more studies are required.

4. – Sect. ***Angustifolium*** (Seitz) Rottensteiner, **stat. nov.**

Basionym: *A.* subsect. *Angustifolium* Seitz, Feddes Repert. 80 (1): 60. 1969
Type species: *A. angustifolium* Bernh. ex Rchb.

Diagnosis characters: seeds tricorn, pyramidal, membraneous 6–8 lamellae, root napiform.

Description: stem up to 60 cm, glabrous; leaves with 5-7 lobes, narrowly dissected; leaf segments linear to lanceolate, up to 4 (–6) mm wide; inflorescence compact, pyramidal or slightly ramified; pedicels firm, with tri-lobed or entire linear bracteoles; flowers violet; hood from crescent-shape to hemispherical, glabrous or sparsely pubescent; nectaries hardly bent with ± capitate spurs, always reaching the top of the hood; filaments glabrous; carpels 2–3, glabrous or pilose on the dorsal or ventral side.

Aconitum angustifolium Bernh. ex Rchb., Mon. Aconit.: 95, t. 15, fig. 2. 1821

Type citation: "In Styriae valle Wochinensi: *Bernhardi*! (ibid.) circa lacum, in altitude circiter 2000 pendum: *de Vest*! In Sibiria: *Pallas!*".
Typus: iconotype: Reichenbach (1820): Monogr. Aconit.: 24 (Seitz 1969).
Synonyms: *A. albicans* Host, *A. napellus* subsp. *angustifolium* (Bernh. ex Rchb.) Gáyer, *A. tenuifolium* Host.
Distribution: Julian Alps and Prealps in Italy and Slovenia.

Diagnostic characters: uppermost leaf segment 1–3 (–4) mm wide; flowers light blue to whitish; hood often ± triangular, about as high as broad; inflorescence axis, pedicels and tepals outside glabrous (fo. *angustifolium*) or ± pubescent (fo. *carniolicum*); nectaries hardly bent, their spur ± capitate, always reaching the top of the hood; filaments glabrous; carpels 2–3, glabrous or pilose on the dorsal or ventral side.

Iconography: Reichenbach (1821: t. 15, fig. 2).
Literature: Gáyer (1909); Seitz (1969); Nikolić (1994); Martinčič (1999); Aeschimann et al. (2004).
Hybrids: unknown.

Lower taxa:

a) fo. ***angustifolium***

Diagnostic characters: inflorescence axis, pedicels and tepals outside glabrous.

b) fo. ***carniolicum*** Gáyer, Magyar. Bot. Lap. 8: 184. 1909

Type citation: "Krain, Küstenland, Steiermark. Auf der Zhaun u. Krushza (*Fleischmann* – W); Stiria, Auen a. d. Mur (*Maly* – W. loco ergo incerto)" (Gáyer 1909).
Typus: not designated.
Synonyms: none.

Diagnostic characters: inflorescence axis, pedicels and tepals outside ± pubescent.

5. – Sect. ***Euchylodea*** Rchb.

Type species: *A. kusnezoffii* Rchb.

Diagnostic characters: nectary lobes inflated; spurs thick, long and hamate curved or short saccate; stipes slightly incurved or nearly erect.

Description: root obconical or elongated, 2–5 cm; stem up to 200–300 cm long, usually intensively branched on the level of inflorescence; cauline leaves with 5 lobes with narrow lanceolate segments; pedicel densely pubescent; bracteoles acute ovate; tepals lilac-blue, outside pubescent; hood hemispherical to slightly elongated; carpels 5, mostly glabrous.

5A. – Ser. ***Japonica*** (Nakai) Kadota

Type species: *A. japonicum* Thunb.

Diagnostic characters: leaf blades pentagonal to roundish pentagonal, sometimes roundish reniform; lateral lobes shallowly to medially 2-parted or sometimes deeply incised.

Aconitum carmichaelii Debeaux, Actes Soc. linn. Bordeaux 33: 87. 1879

Type citation: "La region montagneuse du Tché-foû, près de Bamboû Temple (très-probablement la Pagode neuve) ou il a été découvert par le Dr. *Carmichael* en 1875".
Typus: not designated.
Synonyms: *A. bodinieri* H. Lév. & Vaniot, *A. chinense* Paxton, *A. fischeri* auct., *A. lushanense* Migo, *A. wilsonii* Stapf ex Veitch.
Distribution: China, Vietnam; neophyte in Europe: Scotland, France, Germany, Austria.

Diagnostic characters: Root obconical, 2–4 cm long, 1–1.6 cm broad; stem rigid, upright, 200–300 cm; cauline leaves pentagonal, ± pubescent on the lower surface; inflorescence with many side inflorescences; pedicel densely pubescent; bracteoles acute ovate; tepals lilac-blue, outside pubescent; hood about as high as broad; nectaries glabrous, with an upright claw and a recurved spur; filaments dentate, glabrous; carpels 5, mostly glabrous.
Iconography: Wang et al. (2003).
Literature: Li and Kadota (2001); Lin et al. (2017).
Hybrids: unknown.

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APPENDIX

CHECKLIST OF *ACONITUM* SUBG. *ACONITUM* IN EUROPE

A. ×acuminatum Rchb. [*A. degenii* × *A. napellus*]
A. ×acutum Rchb. [*A. tauricum* × *A. variegatum*]
A. adriaticum Gáyer = **A. superbum** Fritsch
A. albicans Host = **A. angustifolium** Bernh. ex Rchb.
A. ×algoviense Gáyer = **A. ×schneebergense** Gáyer [*A. napellus* × *A. variegatum*]
A. amoenum Rchb. = **A. plicatum** Köhler ex Rchb.
A. anglicum Stapf
A. angustifolium Bernh. ex Rchb.
  fo. **angustifolium**
  fo. **carniolicum** Gáyer
A. ×aquilonare A.Kern. ex Gáyer [*A. variegatum* × *A. vitosanum*]
A. ×austriacum Starm. [*A. pilipes* × *A. variegatum*]
A. autumnale Clus. ex Rchb. = **A. napellus** L.
A. adriaticum Gáyer = **A. superbum** Fritsch
A. ×bartokianum Starm. [*A. toxicum* × *A. variegatum*]
  nothosubsp. **bartokianum** Starm. [*A. toxicum* subsp. *toxicum* × *A. variegatum* subsp. *nasutum*]
  nothosubsp. **rapaicsianum** Starm. [*A. toxicum* subsp. *crispulum* × *A. variegatum* subsp. *nasutum*]
  nothosubsp. **sooanum** Starm. [*A. toxicum* subsp. *toxicum* × *A. variegatum* subsp. *variegatum*]
A. ×bavaricum Starm. [*A. napellus* × *A. plicatum*]
  nothosubsp. **bavaricum** [*A. napellus* subsp. *napellus* × *A. plicatum*]
  nothosubsp. **lusenense** Starm. [*A. napellus* subsp. *lobelii* × *A. plicatum*]
A. ×berdaui Zapał. [*A. firmum* × *A. variegatum*]
  nothosubsp. **berdaui** [*A. firmum* subsp. *firmum* × *A. variegatum* subsp. *variegatum*]
  nothosubsp. **walasii** (Mitka) Mitka [*A. firmum* subsp. *moravicum* × *A. variegatum* subsp. *variegatum*]
A. bernhardianum Rchb., *p.p.* = **A. napellus** L.
A. bernhardianum Rchb., *p.p.* = **A. plicatum** Köhler ex Rchb.
A. beskidense (Zapał.) Gáyer = **A. lasiocarpum** Rchb. subsp. **kotulae** (Pawł.) Starm. & Mitka
A. bodinieri H.Lév. & Vaniot = **A. carmichaelii** Debeaux
A. bosniacum Beck = **A. toxicum** Rchb.
A. bucovinense Zapał.

      fo. **bucovinense**
      fo. **orthotricha** Gáyer
A. burnatii Gáyer
  subsp. *pentheri* (Hayek) Jalas = **A. pentheri** Hayek
A. callibotryon Rchb. = **A. plicatum** Köhler ex Rchb.
A. ×cammarum L. em. Fries [*A. napellus* × *A. variegatum*]
    var. *beskidene* Zapał. = **A. lasiocarpum** Rchb.
    var. **cammarum**
      fo. **cammarum**
      fo. **bicolor** (Schult) DC.
    var. *pilipes* Rchb. = **A. pilipes** (Rchb.) Gáyer
A. cammarum Jacq.
    var. *beskidense* Zapał. = **A. lasiocarpum** Rchb. subsp. **kotulae** (Pawł.) Starm. & Mitka
    var. *koscieliskanum* Zapał., *p.p.* = **A. lasiocarpum** Rchb. subsp. **kotulae** (Pawł.) Starm. & Mitka
A. carmichaelii Debeaux
A. castellanum (Molero & Blanché) Rottensteiner
A. caucasicum N.Busch
  subsp. *pubiceps* (Rupr.) N.Busch
    var. *tuscheticum* N.Busch = **A. ×tuscheticum** (N.Busch) N.Busch [*A. degenii* × *A. vitosanum*]
A. cernuum Rchb., non Wulfen
[var.] *α laxiflorum* Rchb. = **A. degenii** Gáyer subsp. **paniculatum** (Arcang.) Mucher var. **laxiflorum** (Rchb.) Mucher
A. chinense Paxton = **A. carmichaelii** Debeaux
A. compactum Rchb. = **A. napellus** L.
A. clusianum Rchb.
A. corsicum Gáyer
A. ×czarnohorense (Zapał.) Mitka [*A. bucovinense* × *A. ×nanum*]
A. dasycarpum Schur = **A. lasiocarpum** Rchb.
A. degenii Gáyer
  subsp. **degenii**
    var. **degenii**
      fo. **degenii**
      fo. **craciunelense** Gáyer
    var. **intermedium** (Zapał.) Mitka
  nothosubsp. **gandogeri** Mucher [*A. degenii* subsp. *paniculatum* × *A. degenii* subsp. *valesiacum*]
  nothosubsp. **lippertianum** Starm. [*A. degenii* subsp. *paniculatum* × *A. degenii* subsp. *rhaeticum*]
  subsp. **paniculatum** (Arcang.) Mucher
    var. **laxiflorum** (Rchb.) Mucher
    var. **turrachense** (Mucher) Mucher
  subsp. **rhaeticum** Starm.
  subsp. **valesiacum** (Gáyer) Mucher
A. delphinense Gáyer = **A. burnatii** Gáyer
A. diabolicum Gáyer = **A. toxicum** Rchb.
A. divergens Pančić *nom. illeg.*, *p.p.* = **A. pentheri** Hayek
  subsp. *burnatii* (Gáyer) W.Seitz = **A. burnatii** Gáyer
A. dolomiticum A.Kern. = **A. tauricum** Wulfen in Koelle
A. dolomiticum Hayek, *p.p.* = **A. tauricum** Wulfen in Koelle nothosubsp. **hayekianum** (Gáyer) Grinţ. in Savulescu [*A. tauricum* subsp. *latemarense* × *A. tauricum* subsp. *tauricum*]
A. dolomiticum Hayek, *p.p.* = **A. ×teppneri** Mucher ex Starm. nothosubsp. **kerneri** Starm. [*A. napellus* subsp. *napellus* × *A. tauricum* subsp. *latemarense*]
A. ×dragulescuanum Mucher [*A. degenii* × *A. toxicum*]
  nothosubsp. **dragulescuanum** [*A. degenii* subsp. *degenii* × *A. toxicum* subsp. *toxicum*]
  nothosubsp. **grintescuanum** Starm. [*A. degenii* subsp. *degenii* × *A. toxicum* subsp. *crispulum*]
A. eminens Koch ex Rchb. = **A. napellus** L.
A. ×exaltatum Bernh. ex Rchb. [*A. plicatum* × *A. variegatum*]
  var. hamatum Rchb. = **A. ×exaltatum** Bernh. ex Rchb. [*A. plicatum* × *A. variegatum*]
A. eustachyum Rchb. = **A. tauricum** Wulfen subsp. **tauricum** var. **eustachyum** (Rchb.) Starm.
A. firmum Rchb.
  subsp. **firmum**
  subsp. **fissurae** Nyár.
  nothosubsp. **fussianum** Starm. [*A. firmum* subsp. *firmum* × *A. firmum* subsp. *fissurae*]
  subsp. *maninense* (Skalický) Starm. = **A. maninense** (Skalický) Mitka
  subsp. **moravicum** Skalický
    var. *maninense* Skalický = **A. maninense** (Skalický) Mitka
  nothosubsp. *paxii* Starm. in Starmühler & Mitka = **A. ×mariae** Rottensteiner, Mitka & Novikov nothosubsp. **paxii** (Starm.) Mitka, **comb. nov.** [*A. firmum* subsp. *moravicum* × *A. maninense*]
  subsp. **skerisorae** (Gáyer) Starm.
  nothosubsp. *zapalowiczii* Starm. = **A. ×zapalowiczii** (Starm.) Mitka [*A. firmum* × *A. ×mariae* nothosubsp. *paxii*]
A. firmum Rchb. subsp. **firmum** × **A. firmum** Rchb. subsp. **moravicum** Skalický
A. firmum Rchb. subsp. *firmum* × *A. maninense* (Skalický) Mitka = **A. ×mariae** Rottensteiner, Mitka & Novikov nothospec. (hybr.) nov. [*A. firmum* s.str. × *A. maninense*]
A. fischeri Auct. = **A. carmichaelii** Debeaux
A. flerovii Steinberg in Komarov = **A. firmum** Rchb. subsp. **fissurae** Nyár.
A. formosum Rchb. = **A. napellus** L. subsp. **formosum** (Rchb.) Gáyer in Hegi
A. ×gayeri Starm. [*A. degenii* × *A. lasiocarpum*]
A. gracile Rchb., *p.p.* = **A. variegatum** L. subsp. **variegatum**

subsp. *grosserratum* (Gáyer) Grinţ.
fo. *beskidense* Zapał.= **A. lasiocarpum** Rchb. subsp. **kotulae** (Pawł.) Starm. & Mitka
A. hamatum (Rchb.) Gáyer = **A. ×exaltatum** Bernh. ex Rchb. [*A. plicatum* × *A. variegatum*]
A. hayekianum Gáyer = **A. tauricum** Wulfen in Koelle
A. ×hebegynum DC. [*A. degenii* × *A. variegatum*]
A. ×hebegynum Auct. Fl. Carpathorum, non DC. = **A. degenii** Gáyer subsp. **degenii** var. **intermedium** (Zapał.) Mitka
A. hebegynum Auct., *p.p.* = **A. lasiocarpum** Rchb. subsp. **kotulae** (Pawł.) Starm. & Mitka
A. hians Rchb. = **A. plicatum** Köhler ex Rchb.
A. intermedium DC. = **A. ×cammarum** L. em. Fries [*A. napellus* × *A. variegatum*]
A. koehleri Rchb. = **A. plicatum** Köhler ex Rchb.
A. koelleanum Rchb., *p.p.* = **A. tauricum** Wulfen in Koelle
var. *firmum* (Rchb.) Rchb. = **A. firmum** Rchb.
A. laetum Rchb. = **A. plicatum** Köhler ex Rchb.
A. lasiocarpum (Rchb.) Gáyer
subsp. **kotulae** (Pawł.) Starm. & Mitka
subsp. **lasiocarpum**
A. lasiocarpum (Rchb.) Gáyer × **A. toxicum** Rchb.
A. latemarense Degen & Gáyer = **A. tauricum** Wulfen subsp. **latemarense** (Degen & Gáyer) Starm. in W.Maurer
A. laxum Gáyer = **A. ×schneebergense** Gáyer [*A. napellus* × *A. variegatum*]
A. laxum Rchb. = **A. napellus** L.
A. ×lengyelii Gáyer = **A. ×berdaui** Zapał. [*A. firmum* × *A. variegatum*]
nothosubsp. walasii Mitka. = **A. ×berdaui** Zapał.
nothosubsp. **walasii** (Mitka) Mitka [*A. firmum* subsp. *moravicum* × *A. variegatum*]
A. linnaeanum Gáyer = **A. napellus** L.
A. lobelianum Host., non Rchb., *p.p.* = **A. napellus** L. subsp. **lobelii** Mucher
fo. *brachytrichum* Gáyer. = **A. ×acuminatum** Rchb. [*A. degenii* × *A. napellus*]
A. lobelianum Rchb. = **A. napellus** L.
A. lobelianum (Rchb.) Host. in Gáyer, *p.p.* = **A. napellus** L. subsp. **lobelii** Mucher
fo. *brachytrichum* Gáyer. = **A. ×acuminatum** Rchb. [*A. degenii* × *A. napellus*]
A. lobelianum Rouy-Fouc. = **A. corsicum** Gáyer
A. lushanense Migo = **A. carmichaelii** Debeaux
A. maninense (Skalický) Mitka
A. ×mariae Rottensteiner, Mitka & Novikov [*A. firmum* s.str. × *A. maninense*]
nothosubsp. **mariae** [*A. firmum* subsp. *firmum* × *A. maninense*]
nothosubsp. **paxii** (Starm.) Mitka, **comb. nov.** [*A. firmum* subsp. *moravicum* × *A. maninense*]
A. meyeri Rchb. = **A. napellus** L.
A. ×mielichhoferi Rchb. [*A. degenii* × *A. tauricum*]
A. molle Rchb. = **A. degenii** Gáyer
A. multifidum Koch ex Rchb. = **A. plicatum** Köhler ex Rchb, *A. multifidum* Auct. Fl. Carpathorum, non Koch = **A. bucovinense** Zapał.
A. ×nanum (Baumg.) Simonk. [*A. bucovinense* × *A. firmum*]
A. napellus L.
subsp. *angustifolium* (Bernh. ex Rchb.) Gáyer = **A. angustifolium** Bernh. ex Rchb.
subsp. *burnatii* (Gáyer) J.-M. Tison. = **A. burnatii** Gáyer
subsp. *castellanum* Molero and Blanché = **A. castellanum** (Molero & Blanché) Rottenst.
subsp. *corsicum* (Gáyer) W. Seitz = **A. corsicum** Gáyer
subsp. *eustachyum* (Rchb.) Gayer in Hegi = **A. tauricum** Wulfen subsp. **tauricum** var. **eustachyum** (Rchb.) Starm.
subsp. *firmum* (Rchb.) Gáyer, *p.p.* = **A. firmum** Rchb.
subsp. **firmum**
var. *carpaticum* Maloch = **A. firmum** Rchb. subsp. **moravicum** Skalický
subsp. **formosum** (Rchb.) Gáyer
subsp. *hians* (Rchb.) Gáyer = **A. plicatum** Köhler ex Rchb.
nothosubsp. **hinterhuberi** Starm. [*A. napellus* subsp. *formosum* × *A. napellus* subsp. *napellus*]
subsp. *koelleanum* (Rchb.) Mucher = **A. tauricum** Wulfen in Koelle
subsp. **lobelii** Mucher
subsp. **lusitanicum** Rouy
subsp. **napellus**
var. *babiogorense* Zapał.
fo. *babiogorense* = **A. firmum** Rchb.
fo. *subfissum* Zapał. = **A. firmum** Rchb.
var. *carpaticum* Zapał.
fo. *carpaticum* = **A. firmum** Rchb.
var. *compactum* Rapaics. = **A. corsicum** Gáyer
var. *czarnohorense* Zapał. = **A. ×czarnohorense** (Zapał.) Mitka [*A. bucovinense* × *A. ×nanum*]
fo. *amoenum* Zapał. = **A. ×czarnohorense** (Zapał.) Mitka [*A. bucovinense* × *A. ×nanum*]
fo. *czarnohorense* Zapał. = **A. ×czarnohorense** (Zapał.) Mitka [*A. bucovinense* × *A. ×nanum*]
fo. *glabratum* Zapał. = **A. ×czarnohorense** (Zapał.) Mitka [*A. bucovinense* × *A. ×nanum*]
fo. *hoverlanum* Zapał. = **A. ×czarnohorense** (Zapał.) Mitka [*A. bucovinense* × *A. ×nanum*]

- fo. *nanum* Zapał., non Baumg. = **A. ×czarnohorense** (Zapał.) Mitka [*A. bucovinense* × *A. ×nanum*]
- fo. *rodnense* Zapał. = **A. ×czarnohorense** (Zapał.) Mitka [*A. bucovinense* × *A. ×nanum*]
- fo. *tenuisectum* Zapał. = **A. ×czarnohorense** (Zapał.) Mitka [*A. bucovinense* × *A. ×nanum*]
- fo. *turkulense* Zapał. = **A. ×czarnohorense** (Zapał.) Mitka [*A. bucovinense* × *A. ×nanum*]

    - [var.] *γ eustachyum* (Rchb.) Fiori = **A. tauricum** Wulfen subsp. **tauricum** var. **eustachyum** (Rchb.) Starm.
    - var. *firmum* (Rchb.) Pawł. = **A. firmum** Rchb.
    - [var.] *formosum* (Rchb.) Koch. = **A. napellus** L. subsp. **formosum** (Rchb.) Gáyer in Hegi
    - [var.] *β hemisphaericum* Form
      - fo. *formosum* (Rchb.) Beck. = **A. napellus** L. subsp. **formosum** (Rchb.) Gáyer in Hegi
    - var. *nanum* Baumg. = **A. ×nanum** (Baumg.) Simonk. [*A. bucovinense* × *A. firmum*]
    - var. *napellus*
      - fo. *koelleanum* (Rchb.) Gürke in Richter-Gürke = **A. tauricum** Wulfen in Koelle
    - var. *subtatrense* Zapał.
      - fo. *abnorme* Zapał. = **A. firmum** Rchb.
      - fo. *latisectum* Zapał. = **A. firmum** Rchb.
      - fo. *subtatrense* = **A. firmum** Rchb.
    - var. *tatrense* Zapał. = **A. firmum** Rchb.
    - var. *tauricum* (Wulfen) Sér. = **A. tauricum** Wulfen in Koelle
  - subsp. *napellus* sensu Seitz, 1969 = **A. anglicum** Stapf nothosubsp. **polatschekii** Mucher ex Starm. [*A. napellus* subsp. *formosum* × *A. napellus* subsp. *lobelii*]
  - nothosubsp. **seitzii** Mucher ex Starm. [*A. napellus* subsp. *lobelii* × *A. napellus* subsp. *napellus*]
  - subsp. *skerisorae* Seitz, non Gáyer = **A. firmum** Rchb. subsp. **skerisorae** (Gáyer) Starm.
  - subsp. *superbum* (Fritsch) W.Seitz = **A. superbum** Fritsch
  - subsp. *tauricum* (Wulfen) Gáyer in Hegi = **A. tauricum** Wulfen in Koelle
- **A. napellus** L. × **A. pilipes** (Rchb.) Gáyer
- *A. nasutum* Fischer ex Rchb., *p.p.* = **A. variegatum** L. subsp. **nasutum** (Fischer ex Rchb. em. Rupr.) Götz
  - subsp. *tuscheticum* (N.Busch) A.N.Luferov = **A. ×tuscheticum** (N.Busch) N.Busch [*A. degenii* × *A. vitosanum*]
- *A. neomontanum* Wulfen = **A. napellus** L.
- *A. neomontanum* Auct., non Koelle = **A. toxicum** Rchb.
- *A. neubergense* Clus. ex Rchb. = **A. napellus** L.
- **A. nevadense** Uechtr. ex Gáyer
- *A. occidentale* Timb. Lagr. f. ex Gáyer = **A. nevadense** Uechtr. ex Gáyer
- *A. odotandrum* Wissjul. = **A. ×berdaui** Zapał. [*A. firmum* × *A. variegatum*]
- *A. palmatifidum* Rchb., *p.p.* = **A. firmum** Rchb.
      - fo. *piliferum* Gáyer = **Aconitum ×mariae** Rottensteiner, Mitka & Novikov nothosubsp. **paxii** (Starm.) Mitka, **comb. nov.** [*A. firmum* subsp. *moravicum* × *A. maninense*]
- *A. paniculatum* Lam., *p.p.* (*nom. inval.*) = **A. degenii** Gáyer subsp. **degenii**
  - subsp. *lasiocarpum* (Rchb.) Soó = **A. lasiocarpum** (Rchb.) Gáyer
  - subsp. *paniculatum*
    - var. *paniculatum* (*nom. inval.*) = **A. degenii** Gáyer subsp. **paniculatum** (Arcang.) Mucher var. **laxiflorum** (Rchb.) Mucher
    - var. *podolicum* Zapał.
      - fo. *latilobum* Zapał. = **A. lasiocarpum** (Rchb.) Gáyer subsp. **kotulae** (Pawł.) Starm. & Mitka
      - fo. *latiusculum* Zapał. = **A. degenii** var. **intermedium** (Zapał.) Mitka
    - var. *prutense* Zapał. = **A. degenii** var. **intermedium** (Zapał.) Mitka
    - var. *turrachense* Mucher = **A. degenii** Gáyer subsp. **paniculatum** (Arcang.) Mucher var. **turrachense** (Mucher) Mucher
- *A. parviflorum* Host. = **A. tauricum** Wulfen in Koelle
- **A. ×pawlowskii** Mitka & Starm. [*A. lasiocarpum* × *A. variegatum*]
- *A. ×paxii* (Starm.) Mitka = **A. ×mariae** Rottensteiner, Mitka & Novikov nothosubsp. **paxii** (Starm.) Mitka, **comb. nov.** [*A. firmum* subsp. *moravicum* × *A. maninense*]
- **A. pentheri** Hayek
- **A. pilipes** (Rchb.) Gáyer
- **A. pilipes** (Rchb.) Gáyer × **A. tauricum** Wulfen
- **A. ×pilosiusculum** (Seringe) Gáyer [*A. degenii* × *A. pilipes*]
- **A. plicatum** Köhler ex Rchb.
  - subsp. **plicatum**
    - var. *clusianum* (Rchb.) Mitka & Starm. = **A. clusianum** Rchb.
  - subsp. **sudeticum** Mitka
- *A. podolicum* (Zapał.) Voroshylov = **A. lasiocarpum** (Rchb.) Gáyer subsp. **kotulae** (Pawł.) Starm. & Mitka
- *A. pubiceps* Rupr.
    - var. *tuscheticum* (N.Busch) Grossh. = **A. ×tuscheticum** (N.Busch) N.Busch [*A. degenii* × *A. vitosanum*]
- *A. pyramidale* Mill. ex Rchb. = **A. napellus** L.
- *A. ranunculifolium* Rchb.
    - var. *dolomiticum* Evers, *p.p.* = **A. tauricum** Wulfen in Koelle nothosubsp. **hayekianum**

    - (Gáyer) Grinţ. in Savulescu [*A. tauricum* subsp. *latemarense* × *A. tauricum* subsp. *tauricum*]
    - var. *dolomiticum* Evers, *p.p.* = **A. ×teppneri** Mucher ex Starm. nothosubsp. **kerneri** Starm. [*A. napellus* subsp. *napellus* × *A. tauricum* subsp. *latemarense*]
- *A. rigidum* Rchb. = **A. plicatum** Köhler ex Rchb.
- *A. romanicum* Wołoszczak = **A. firmum** Rchb. subsp. **fissurae** Nyár.
- *A. ×ronnigeri* Gáyer = **A. ×mielichhoferi** Rchb. [*A. tauricum* subsp. *latemarense* × *A. tauricum* subsp. *tauricum*]
- **A. ×schneebergense** Gáyer [*A. napellus* × *A. variegatum*]
- *A. schurii* Beck. = **A. toxicum** Rchb.
      - fo. *retyezatense* Gáyer = **A. toxicum** Rchb.
- *A. skerisorae* Auct., non Gáyer = **A. firmum** Rchb.
- *A. skerisorae* Gáyer = **A. firmum** Rchb. subsp. **skerisorae** (Gáyer) Starm.
- *A. speciosum* Otto ex Rchb. = **A. ×exaltatum** Bernh. ex Rchb. [*A. plicatum* × *A. variegatum*]
- *A. sostaricianum* Fritsch = **A. superbum** Fritsch
- *A. stoerkianum* Rchb. = **A. ×cammarum** L. em. Fries [*A. napellus* × *A. variegatum*]
- *A. strictum* Bernh. = **A. napellus** L.
- **A. superbum** Fritsch
- **A. superbum** Fritsch × **A. variegatum** L.
- **A. superbum** Fritsch × **A. vitosanum** Gáyer
- *A. tatrae* Borb. = **A. firmum** Rchb.
    - var. *skerisorae* Soó = **A. firmum** Rchb. subsp. **skerisorae** (Gáyer) Starm.
- *A. taurericum* Rchb. = **A. tauricum** Wulfen in Koelle subsp. **tauricum** var. **tauricum** fo. **taurericum** (Rchb.) Gáyer
- *A. tauricum* Auct. = **A. firmum** Rchb.
- **A. tauricum** Wulfen in Koelle
  - nothosubsp. **hayekianum** Gáyer (Gáyer) Grinţ. in Savulescu [*A. tauricum* subsp. *latemarense* × *A. tauricum* subsp. *tauricum*]
  - subsp. **latemarense** (Degen and Gáyer) Starm.
  - subsp. *nanum* Auct. fl. Carpat. Orient., non (Baumg.) Grinţ. = **A. bucovinense** Zapał.
  - subsp. *nanum* (Baumg.) Grinţ. = **A. ×nanum** (Baumg.) Simonk. [*A. bucovinense* × *A. firmum*]
  - subsp. *nanum* (Baumg.) Gáyer = **A. ×nanum** (Baumg.) Simonk. [*A. bucovinense* × *A. firmum*]
  - subsp. *taureticum* (Rchb.) Grinţ. = **A. tauricum** Wulfen in Koelle subsp. **tauricum** var. **tauricum** fo. **taurericum** (Rchb.) Gáyer
  - subsp. **tauricum**
    - var. **eustachyum** (Rchb.) Starm.
    - var. *latemarense* (Degen & Gáyer) Mucher = **A. tauricum** Wulfen in Koelle subsp. subsp. **latemarense** (Degen & Gáyer) Starm. in W.Maurer
    - var. **tauricum**
      - fo. **tauricum**
      - fo. **taurericum** (Rchb.) Gáyer
- *A. tenuifolium* Host. = **A. angustifolium** Bernh. ex Rchb.
- **A. ×teppneri** Mucher ex Starm. [*A. napellus* × *A. tauricum*]
  - nothosubsp. **goetzii** Mucher ex Starm. [*A. napellus* subsp. *lobelii* × *A. tauricum* subsp. *tauricum*]
  - nothosubsp. **haderlappii** Starm. [*A. napellus* subsp. *lobelii* × *A. tauricum* subsp. *latemarense*]
  - nothosubsp. **kerneri** Starm. [*A. napellus* subsp. *napellus* × *A. tauricum* subsp. *latemarense*]
  - nothosubsp. **teppneri** [*A. napellus* subsp. *napellus* × *A. tauricum* subsp. *tauricum*]
- **A. toxicum** Rchb.
  - subsp. **bucegiense** (Nyár.) Mucher
  - subsp. **crispulum** (Nyár.) Mucher
  - nothosubsp. **nyaradyanum** Mucher [*A. toxicum* subsp. *crispulum* × *A. toxicum* subsp. *toxicum*]
  - subsp. **toxicum**
    - [var.] *bosniacum* (Beck) Hayek = **A. toxicum** Rchb.
    - var. *bucegiense* Nyár. = **A. toxicum** Rchb. subsp. **bucegiense** (Nyár.) Mucher
    - var. *crispulum* Nyárády in Borza = **A. toxicum** Rchb. subsp. **crispulum** (Nyár.) Mucher
    - [var.] *β schurii* Beck = **A. toxicum** Rchb.
    - var. *toxicum*
      - fo. *diabolicum* (Gáyer) Grint. = **A. toxicum** Rchb.
  - nothosubsp. **ungarianum** Starm. [*A. toxicum* subsp. *bucegiense* × *A. toxicum* subsp. *toxicum*]
- *A. trichocarpum* Rchb. = **A. tauricum** Wulfen in Koelle
- **A. ×tuscheticum** (N.Busch) N.Busch [*A. degenii* × *A. vitosanum*]
- *A. valesiacum* Gáyer = **A. degenii** Gáyer subsp. **valesiacum** (Gáyer) Mucher
- **A. variegatum** L.
  - subsp. *kotulae* Pawł. = **A. lasiocarpum** (Rchb.) Gáyer
  - subsp. **kotulae** (Pawł.) Starm. & Mitka
  - subsp. **nasutum** (Fischer ex Rchb. em. Rupr.) Götz
  - nothosubsp. **podobnikianum** Mucher [*A. variegatum* subsp. *nasutum* × *A. variegatum* subsp. *variegatum*]
  - subsp. *pyrenaicum* Vivant & Delay = **A. vivantii** Rottensteiner.
  - subsp. *valesiacum* (Gáyer) Greuter & Burdet = **A. degenii** Gáyer subsp. **valesiacum** (Gáyer) Mucher
  - subsp. **variegatum**
    - var. **carniolicum** Starm.
    - var. *diffusum* (Rchb.) Penev & Simeon. = **A. vitosanum** Gáyer
    - var. **stiriacum** Mucher

  var. **variegatum**
    fo. *aquilonare* (Gáyer) M.Niketić = **A. ×***aquilonare* A.Kern. ex Gáyer [*A. variegatum* × *A. vitosanum*]
    fo. *kotulae* (Pawł.) Skalický = **A. lasiocarpum** (Rchb.) Gáyer subsp. **kotulae** (Pawł.) Starm. & Mitka
A. ×*virgatum* Rchb. ex Gáyer = **A. ×schneebergense** Gáyer [*A. napellus* × *A. variegatum*]
A. vitosanum Gáyer
A. vivantii Rottensteiner, **nom. nov.**
A. vulgare DC. = **A. napellus** L.
A. wilsonii Stapf ex Veitch. = **A. carmichaelii** Debeaux
A. ×*zahlbruckneri* Gáyer = **A.** ×**acutum** Rchb. [*A. tauricum* × *A. variegatum*]
A. ×**zapalowiczii** (Starm.) Mitka [*A. firmum* × *A.* ×*mariae* nothosubsp. *paxii*]

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Argostemma quarantena (Rubiaceae, Ruboideae), a new species from southern Western Ghats, India

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Abstract. *Argostemma quarantena*, a new rubiaceous species from Vagamon Hills of southern Western Ghats, India is described and illustrated here. The species shows similarities with two south Indian endemics, *A. anupama* and *A. courtallense*, but differs in many qualitative attributes. The present status of genus *Argostemma* in India is briefly discussed. An artificial key for the identification of *Argostemma* in Western Ghats is also provided.

Keywords: Argostemmateae, Epilithic, Kottayam, Vagamon Hills.

INTRODUCTION

Argostemma Wall., is a genus of small perennial herbs, widely distributed in tropical and sub-tropical Asia, except for two African species namely, *A. africanum* K.Schum. and *A. pumilum* Benn. (Sridith 1999; Sridith and Puff 2000). It is one of the four genera of the tribe Argostemmateae of subfamily Ruboideae (Rydin et al. 2009). Wallich (in Roxburgh 1824) described the genus *Argostemma* based on the species *A. sarmentosum* from the former British India. He also described three more species in the same publication, viz., *A. rostratum* & *A. verticillatum* from subtropical Himalaya and *A. pictum* from Malaya. In the ensuing years, many new species were added to the genus and presently *Argostemma* comprises 100 to 200 species (100: Mabberley 2017; 165: The Plant List 2013; 175: WCSP 2020; 220: Bremer 1989; Bremer and Manen 2000) with highest concentration in South East Asia. A dozen of new species have been added to the genus from S.E. Asia over the last 10 years (Sridith 2012; Choudhary et al. 2013; Lanorsavanh and Chantaranothai 2016; Nuraliev et al. 2017; Quang et al. 2019; Hsu et al. 2020; Lanorsavanh et al. 2020; Van Do et al. 2020).

The species of *Argostemma* are frequently lithophytic, or occasionally epiphytic inhabiting moist to wet places with high humidity, on wet rock faces by waterfalls, or on large boulders in or along streams (Sridith and Puff 2000). Flowers of *Argostemma* are either star-shaped or bell-shaped with free stamens or stamens of which the anthers may be coherent into a cone-like structure (Sridith and Puff 2001; Sridith 2007). *Argostemma diversifolium* Ridl. and *A. separatum* Aranas, H.W.C. Hsu, & Alejandro are the only known species in the genus with free stamens in star-shaped corolla (Sridith 2007; Hsu et al. 2020).

Argostemma is one of the least studied rubiaceous genus in India. After Hooker (1880), no one attempted a comprehensive systematic treatment of the genus in India. Hooker included 17 species of *Argostemma* in the Flora of British India which covers the areas of present day India, Pakistan, Afghanistan, Nepal, Tibet, Bangladesh, Burma (Myanmar), Ceylon (Sri Lanka) and Malayan Peninsula, out of which 7 species were described from the present day political boundaries of India, viz., *A. courtallense* Arn., *A. humile* Benn., *A. khasianum* C.B.Clarke, *A. pumilum* Benn., *A. rostratum* Wall., *A. sarmentosum* Wall. *and A. verticillatum* Wall. Later, *A. neurocalyx* Miq., *A. tavoyanum* Wall. ex Benn. and *A. timorense* Benn. from Andaman & Nicobar Islands and *A. Anupama* Sivar. From the Western Ghats were added to the Indian flora (Vasudeva Rao 1986; Pandey and Diwakar 2008; Sivarajan, 1984; Jayanthi et al. 2013).

In the Western Ghats, the genus is represented by four species, namely, *A. anupama*, *A. courtallense*, *A. rostratum* and *A. verticillatum* (Nayar et al. 2014). Deb and Basu (1990) reduced *A. anupama* and *A. tavoyanum* as synonyms to *A. courtallense*. Later, Sridith (1999) reinstated the status of *A. tavoyanum* and Sivarajan and Pradeep (1993) did the same for *A. anupama*. Thus, the genus *Argostemma* in India is presently represented by 11 species, chiefly distributed in North East India and Western Ghats. During a floristic exploration in the Vagamon Hills in southern Western Ghats, India, the authors encountered an interesting species of *Argostemma*, notable due to its densely hairy, strongly anisophyllous leaves and much short, congested umbels. Detailed study of the literature (Hooker 1880; Gamble 1921; Ridley 1923 and 1927; Bremer 1989; Sridith 1999; Chen et al. 2011) and comparison of type specimens of Indian species in major herbaria in India (CAL, CALI, MH) and abroad (BM, K, etc.) revealed that the unknown taxon is morphologically similar to *A. anupama* and *A. courtallense*, but shows distinct differences as shown in table 1. Hence, it is described and illustrated here as a new species from India.

Argostemma quarantena Balan & Robi, **sp. nov**. (Figures 1 and 2)

Type: INDIA, Kerala, Kottayam district, Vagamon Hills, ± 1000 m, 12 July 2020, *A.J.Robi & Anoop P.B. 15561* (holotype, MH!; isotypes, MBGH!, MH!).

Diagnosis

The new species is closely similar to *A. anupama*, but differs in it stem (suberect, terete stem vs erect, quadrangular stem), stipules (1.5–2.0 mm long, deltate stipules vs c. 1 mm long, ovate stipules), leaves (obovate-oblanceolate, densely strigose lamina with 6–10 pairs veins vs ovate-lanceolate, scabrous lamina with 4–6 pairs veins), length and form of umbel (c. 1.5 cm long, congested umbel vs 2.5–3.5 cm long, lax umbel), pedicels (2–3 mm long, stout, hirsute pedicels vs 8–10 mm, slender, pubescent pedicels), calyx lobes (2.5 mm long vs 4.0 mm long), corolla lobes (4.5 mm long, triangular vs 5.5–6.0 mm long, lanceolate) and anther filaments (not twisted vs twisted). It also shows similarities with *A. courtallense*, but differs mainly by its stipules (1.5–2.0 mm long, deltate stipules vs 7–8 mm long, ovate stipules), shape and indumentum of leaves (anisophyllous leaves with obovate-oblanceolate and densely strigose lamina vs isophyllous leaves with ovate-orbicular and sparsely pubescent lamina), number of lateral veins (6–10 pairs vs 4–7 pairs lateral veins), umbel (c. 2 cm long, congested umbel vs 4–8 cm long, lax umbel), corolla lobes (4–4.5 mm long vs 7–8 mm long) and anthers (ca 1.5 mm long, white anthers vs ca 3 mm long, yellow anthers). (Table 1).

Description

Epilithic, perennial herb, 3–7 cm tall; attached to the substrate with dense, much-branched matted roots. Tuber 4–5 × 3–4 mm, ovoid. Stem suberect, unbranched, terete, 1.5–4 cm long, glabrous, succulent. Stipule deltate, 1.5–2 × 1.5–2 mm, hairy along margins, deciduous. Leaves opposite, 2–3 pairs, upper 4 pseudoverticillate, strongly anisophyllous, mostly subfalcate; petiole 3–4 mm long, hairy; large leaf blade narrowly obovate-oblanceolate or elliptic, 5–9 × 1.2–2.5 cm, small leaf blade ovate-elliptic, 1.5–4.5 × 0.6–1.5 cm, membraneous, acute to shortly acuminate at apex, cuneate at base, inequilateral, densely strigose above, so below along the veins; venation brochidodromous, veins 6–10 pairs, raised below. Inflorescence solitary, terminal, 6 to 10-flowered, much congested, pedunculate umbel; peduncle 0.5–1.3 cm long, much shorter than leaf, unbranched, glabrous. Flowers 4-merous, actinomorphic; bracts 4–6, of unequal size, fused basally and forming a cup-like involucrum, each bract ovate, 4–5

Figure 1. (a) *Argostemma courtallense*. (b) *A. rostratum*. (c) *A. verticillatum*. (d, e) *A. quarantena* sp. nov., Habitat. (f, g) Habit. (h) Inflorescence. (i) Tuber. (j) Stipule. (k) Calyx with pistil. (l) Corolla and stamens. (m) Seeds.

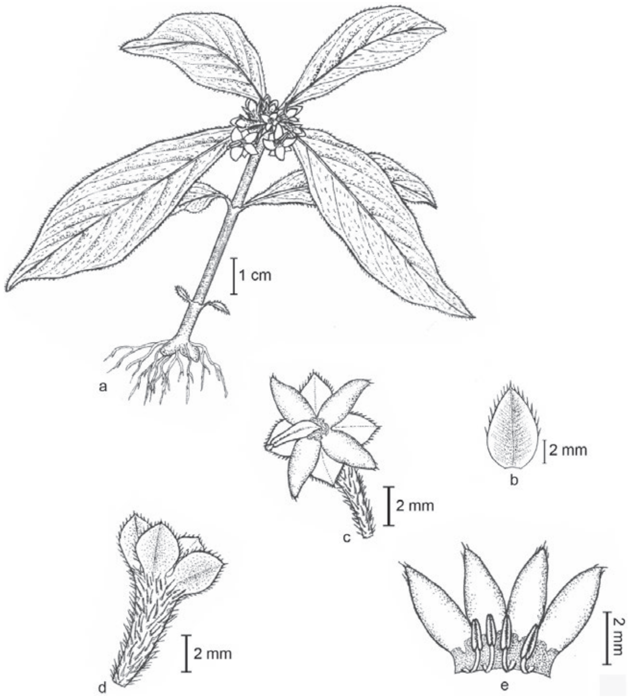

Figure 2. *Argostemma quarantena*. sp. nov. (a) Habit. (b) Bract. (c) Flower. (d) Calyx. (e) Split opened corolla. Drawn by Anoop P. Balan.

× 4–5 mm, acute at apex, hairy along margins, green; pedicels 2–3 mm long, stout, dilated above, densely hirsute. Calyx campanulate, tube short, densely hirsute; lobes 4, ovate, 2.5 × 2.5 mm, acute at apex, hairy along margins, spreading, enlarged in fruit, venation inconspicuous. Corolla white with green blotches at base of the tube, star-shaped; corolla tube 0.6–0.8 mm long; corolla lobes triangular-lanceolate, 4–4.5 × 2–2.5 mm, spreading, with a tuft of hairs at back towards apex. Stamens 4, filaments free, inserted at the base of the corolla tube, ca 1.5 mm long, bent at the middle, white; anthers connivent in a cone around the stigma, oblong, as long as filament, opening by apical pores, white. Ovary inferior, 2–locular, many-ovuled; style slightly exserted from the stamens, ca 3 mm long, stout, glabrous; stigma clavate. Fruit capsular, opening by an apical operculum, subglobose, 3–4 × 3–4 mm, densely hairy, crowned by persistent calyx. Seeds many, 0.3–0.4 × 0.2–0.3 mm, angled and minutely tuberculate, pale brown.

Etymology

The specific epithet *quarantena* indicates the outbreak of COVID-19 corona virus across the world in 2020. The term *quarantena* was used in 14th–15th century Venetian language for a forty-day isolation period. The

Table 1. Comparison of *Argostemma quarantena* sp. nov. with *A. anupama* and *A. courtallense.*

Attributes	*A. quarantena*	*A. anupama*	*A. courtallense*
Stem	Suberect, terete, glabrous, 3–7 cm tall.	Erect, quandrangular, puberulous, 2–6 cm tall.	Erect, terete, pubescent, 8–20 cm tall.
Stipule	Deltate, 1.5–2 × 1.5–2 mm.	Ovate, c. 1 × 0.5 mm, minute	Ovate, 7–8 × 1–2 mm.
Leaves	2–3 pairs, strongly anisophyllous; lamina narrowly obovate-oblanceolate or elliptic, 1.5–10 × 0.6–2.5 cm, cuneate and unequal at base, acute to shortly acuminate at apex, densely strigose on both surfaces, pale grey-glaucous below.	2–3 pairs, anisophyllous; lamina ovate-lanceolate, 2–9 × 1–1.8 cm, cuneate and unequal at base, acute at apex, scabrous on both surfaces, white-glaucous below.	2-pairs, isophyllous; lamina ovate-orbicular, 8–12 × 5–8 cm, subacute or rounded and equal at base, acute at apex, sparsely pubescent on both surfaces, white-glaucous below.
Petiole	3–4 mm long.	5–6 mm long	0–2 cm long.
Venation	6–10 pairs.	4–6 pairs	4–7 pairs.
Bract	4–6, ovate, 4–5 × 4–5 mm.	4–5, ovate, 3–4 × 1.5–2.5 mm.	4, ovate, 4.0 × 2.5 mm.
Inflorescence	6 –10 flowered, much congested; peduncle 0.5–1.3 cm long.	6–8 flowered, lax; peduncle 2.0–3.5 cm long.	3–many flowered, lax; peduncle 3–6 cm long.
Pedicel	2–3 mm long, stout, densely hirsute.	8–10 mm long, slender, pubescent.	8–10 mm long, slender, pubescent.
Flower	4-merous.	4–5- merous	4-merous.
Calyx	Lobes 4, ovate, 2.5 × 2.5 mm, with rounded sinuses.	Lobes 4–5, ovate, 4 × 3 mm, with rounded sinuses	Lobes 4, ovate, 3 × 2 mm, with acute sinuses.
Corolla	Lobes 4, triangular lanceolate, 4–4.5 × 2–2.5 mm	Lobes 4–5, elliptic-lanceolate, 5.5–6 × 2–2.5 mm.	Lobes 4, ovate, 7–8 × 2–2.5 mm.
Stamens	4, filaments ca 1.5 mm long, free, bent at middle; anthers white, oblong, ca 1.5 mm long.	4-5, filaments ca 2 mm long, free, twisted; anthers white, oblong, ca 2 mm long.	4, filaments 3 mm long, free, bent at middle; anthers yellow, lanceolate, ca 3 mm long.

new species was described during the 2020 quarantine period imposed to curb the spread of the COVID-19 virus. This species is a dedication to the lakhs of people including eminent botanists and scientists who have lost their lives due to the COVID-19 virus in the year 2020.

Phenology

July to September

Distribution and ecology

Argostemma quarantena is known only from its type locality at Vagamon Hills, South India. Vagamon hills are traversed by numerous perennial fast flowing streams which originated from evergreen forest patches and pseudosholas at 1000–1400 m elevations asl. This species is thriving on boulders beside such streams and shaded areas, growing with mosses and ferns.

Conservation status

Argostemma quarantena is so far known only from the type locality, Vagamon Hills of Western Ghats, with an extent of occurrence estimated to be less than 10 km^2. The authors located 5 groups of fewer than 100 plants along the streams. *Argostemma spp.* are normally found in wet, shady, undisturbed habitats and are very sensitive to microclimatic changes (Sridith & Puff, 2000). The type locality of *A. quarantena* is outside of protected forest areas and is under threat due to habitat loss as a result of human encroachment. Extensive field surveys are needed to assign appropriate threatened category of IUCN (2012), therefore it is classified as Data Deficient (DD) according to IUCN standards.

Paratype

INDIA: Kerala, Kottayam district, Vagamon Hills, ± 1000 m, 30 July 2020, *Anoop P.B. & A.J.Robi & 15562* (MBGH!, MH!).

Key to the identification of Argostemma *in the Western Ghats*

1a. Umbels branched; flowers 5-merous 2

1b. Umbels unbranched; flowers 4-merous (except *A. anupama*) 3

2a. Leaves 2 pairs; peduncle much shorter than the leaves .... ***A. verticillatum***

2b. Leaves 3 pairs; peduncle as long as the leaves ***A. rostratum***

3a. Leaves 2–3 pairs, anisophyllous; anthers white 4

3b. Leaves 2 pairs, isophyllous; anthers yellow ***A. courtallense***

4a. Stem terete; lamina densely strigose with 6–10 pairs veins; pedicels <5 mm long .... ***A. quarantena***

4b. Stem quadrangular; lamina scabrous with 4–6 pairs veins; pedicels >8 mm long .... ***A. anupama***

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A new *Pisonia* (Nyctaginaceae) from Jamaica, with an updated list of species in the genus and a key to the West Indian taxa

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Abstract. Here we describe a new species of *Pisonia* (Caryophyllales: Nyctaginaceae) from Jamaica, named *P. jamaicensis* Proctor ex Caraballo, K.Campbell, & S.Cross, restricted to limestone hills in the central and western part of the island. The species description is complemented with an illustration, pictures, a distribution map, and notes on its biology and conservation, including an IUCN evaluation. We also present a list of the 27 currently accepted species of *Pisonia* with their general distributions, and a key to separate the 16 taxa reported for the West Indies.

Keywords: Caribbean islands, Caryophyllales, Dioecious trees, Island endemic trees, Karst endemics, West Indies.

INTRODUCTION

The genus *Pisonia* L. (Caryophyllales: Nyctaginaceae) is widely distributed in tropical regions around the globe, although its diversity certainly lies within the American continent (Stevens 2001 onwards). Recent studies have reexamined the circumscription of the genus and transferred a number of species to other genera within tribe Pisonieae (Rossetto et al. 2019; Chagas and Costa-Lima 2020; Rossetto and Caraballo-Ortiz 2020). As a result, the number of currently accepted species in *Pisonia* has been estimated to be around 25 (The Plant List 2013 onwards; Ulloa Ulloa et al. 2018 onwards).

In the West Indies, the genus is represented by approximately 15 species, most of them endemic to the region (Acevedo-Rodríguez and Strong 2012). During current studies on the diversity of *Pisonia*, Caraballo-Ortiz found collections from Jamaica that did not match any of the previously published congeners. After morphological comparisons with all known species for the West Indies, we concluded that this taxon represents an undescribed species.

This finding concords with the view of George R. Proctor, who labeled a series of specimens from the Institute of Jamaica Herbarium as "*Pisonia jamaicensis* Proctor" during the early 2000's, although he did not provide a description and effectuate its publication. In this work, we decided to adopt Proctor's proposed name and formally describe the species as *P. jamaicensis* Proctor ex Caraballo, K.Campbell, & S.Cross.

Pisonia jamaicensis is a tree restricted to wooded summits and upper cliffs of limestone hills in central and western Jamaica. We complement the species' description with an illustration, pictures, a distribution map, and notes on its biology. We also discuss how to separate this species from the other congener in Jamaica, and present a preliminary conservation assessment following the IUCN criteria. A table summarizing the currently accepted *Pisonia* worldwide with their general distributions is also included, along with a dichotomous key to separate the taxa reported for the West Indies.

MATERIALS AND METHODS

We studied all the collections identified as *Guapira* Aubl., *Pisonia*, and *Neea* Ruiz & Pav. from Jamaica deposited in 18 herbaria (CAYM, F, FLAS, FTG, HACC, IJ, JBSD, K, MAPR, MO, NY, P, SJ, UC, UPR, UPRRP, US, and UCWI). Measurements presented in the description were taken from dried plants using physical or virtual specimens (including types, accessible through the JSTOR Global Plants website [https://plants.jstor.org/]), while notes on colors of fresh structures for the new species were taken from plants in the field.

The estimated area of occupancy (AOO) and extent of occurrence (EOO) were calculated using GeoCat (Bachman et al. 2011) by plotting estimated points of all known localities based on herbarium specimens and field explorations. The AOO and EOO were complemented with information on number of known populations, demographic profile and trends, and known threats to conduct an IUCN evaluation based on criteria B and D. The categories and criteria obtained were verified with the Species Information Services (SIS) tool from IUCN (2020) using the same input information as in GeoCat. The SIS tool generated a draft assessment for *P. jamaicensis* which will be submitted to IUCN and updated as more information on the species became available in the future.

To prepare the updated list of *Pisonia*, first we retrieved all currently accepted species from the Vascular Plants of the Americas website (Ulloa Ulloa et al. 2018 onwards). Then, we compiled all *Pisonia* species included in recent regional floras across the American continent and evaluated any discrepancies. For *Pisonia* species from the West Indies, we conducted a deeper study by examining types and protologues of all published taxa reported for the region. We found that most species presented in Ulloa Ulloa et al. (2018 onwards) matched with the ones we found as accepted in regional studies.

One of the species listed in Ulloa Ulloa et al. (2018 onwards) and Acevedo-Rodríguez and Strong (2012) for the West Indies, *P. suborbiculata* Hemsl., was excluded from the final list because it was transferred to *Guapira* by Lundell (1968) as *G. suborbiculata* (Hemsley) Lundell (Graveson 2012; The Plant List 2013 onwards). Conversely, we added the species *P. clarensis* (Borhidi) M.A.Díaz because it was transferred to *Pisonia* by Díaz Dumas (1991), and *P. proctorii* Lundell, which was accepted in a regional study (Balick et al. 2000). Following Acevedo-Rodríguez and Strong (2012) and Ulloa Ulloa et al. (2018 onwards), we recognized *P. macranthocarpa* (Donn. Sm.) Donn. Sm., although some floristic treatments have merged this taxon under the widespread *P. aculeata* L. (Jørgensen and León-Yánez 1999).

Recently, many species of *Pisonia* from the Indian and Pacific Oceans were transferred to *Ceodes* J.R.Forst. & G.Forst. and *Rockia* Heimerl (Rossetto and Caraballo-Ortiz 2020), and species from Brazil were transferred to *Guapira* (Chagas and Costa-Lima 2020), and therefore, were excluded from this assessment. Our final list contained 27 species of *Pisonia* (including the one described in this study), of which 16 taxa – representing 15 species and one subspecies – are present in the West Indies (Table 1).

TAXONOMIC TREATMENT

Pisonia jamaicensis Proctor ex Caraballo, K.Campbell, & S.Cross **sp. nov.** (Figures 1 & 2)

Pisonia subcordata sensu Adams, Fl. Pl. Jamaica 262. 1972, not Swartz, Prodr. 60. 1788. Pro parte (specimen *Proctor 28854*).

Type: Jamaica, St. Catherine Parish, along road between Ewarton and Worthy Park, woodland over limestone, 1500–1700 ft [457–518 m], 5 July 1968 [♀, fr], *Proctor 28854* (holotype, FTG! (barcode № 00038146).

Diagnosis

Pisonia jamaicensis is distinguished from its only other known congener in Jamaica, *P. aculeata*, by a combination of the following characteristics: tree with unarmed branches (vs. scandent shrubs or treelets with

Table 1. List of all currently accepted species of *Pisonia* (Nyctaginaceae), with their major and minor distributions and selected reference studies where each taxon has been recognized.

No.	Scientific name	Major distribution	Minor distribution	References
1	*Pisonia aculeata* L.	Pantropical	Africa, America, Asia, Australia, India, Malagasy, Mauritius, Myanmar, Seychelles, Sri Lanka	Acevedo-Rodríguez and Strong (2012); Pramanick et al. (2016)
2	*Pisonia albida* (Heimerl) Britton ex Standl.	West Indies	Hispaniola, Puerto Rico	Acevedo-Rodríguez and Strong (2012)
3	*Pisonia ambigua* Heimerl	South America	Argentina, Bolivia, Brasil, Paraguay, Perú	Furlan and Giulietti (2014); Nee (2014)
4	*Pisonia byrsonimifolia* Heimerl & Ekman	West Indies	Cuba	Díaz Dumas (1991); Acevedo-Rodríguez and Strong (2012)
5	*Pisonia calafia* León de la Luz & R.A.Levin	Central America	Mexico	León de la Luz and Levin (2012); Villaseñor (2016)
6	*Pisonia capitata* (S.Watson) Standl.	North America	Mexico, United States of America (AZ)	Clement and Spellenberg (2003); Villaseñor (2016)
7	*Pisonia clarensis* (Borhidi) M.A. Díaz	West Indies	Cuba	Díaz Dumas (1991)
8	*Pisonia donnellsmithii* Heimerl ex Standl.	Central America	El Salvador, Guatemala, Mexico	González-Martínez and Cruz Durán (2016); Villaseñor (2016)
9	*Pisonia costata* (Bojer ex Bouton) Choisy	Indian Ocean	Mascarenes	Philcox and Coode (1994)
10	*Pisonia ekmanii* Heimerl	West Indies	Cuba	Díaz Dumas (1991); Acevedo-Rodríguez and Strong (2012)
11	*Pisonia flavescens* Standl.	North America	Mexico	González-Martínez and Cruz Durán (2016); Villaseñor (2016)
12	*Pisonia floribunda* Hook. f.	Pacific Ocean	Galapagos	Jørgensen and León-Yánez (1999)
13	*Pisonia grandis* R.Br.	Asia, scattered islands from western Indian Ocean to eastern Pacific Ocean	Australia, China, India, Laccadive, Malagasy, Maldives Islands, Malaysia, New Caledonia, Pakistan, Polynesia, Sri Lanka	Airy-Shaw (1952); Pramanick et al. (2016)
14	*Pisonia horneae* Caraballo & Trejo	West Indies	Puerto Rico	Caraballo-Ortiz and Trejo-Torres (2017)
15	*Pisonia indecora* Heimerl	South America	Bolivia	Nee (2014)
16	*Pisonia jamaicensis* Proctor ex Caraballo, K.Campbell, & S.Cross	West Indies	Jamaica	This study
17	*Pisonia macranthocarpa* (Donn. Sm.) Donn. Sm.	West Indies, Central America, South America	Cuba, Mexico, Central America, South America	González (2007); Acevedo-Rodríguez and Strong (2012)
18	*Pisonia margaretiae* Proctor	West Indies	Grand Cayman Island	Acevedo-Rodríguez and Strong (2012); Proctor (2012)
19	*Pisonia ochracea* Heimerl	West Indies	Hispaniola	Acevedo-Rodríguez and Strong (2012)
20	*Pisonia petiolaris* Heimerl & Ekman	West Indies	Cuba	Díaz Dumas (1991); Acevedo-Rodríguez and Strong (2012)
21	*Pisonia proctorii* Lundell	Central America	Belize	Balick et al. (2000)
22	*Pisonia roqueae* Trejo & Caraballo	West Indies	Puerto Rico	Caraballo-Ortiz and Trejo-Torres (2017)
23a	*Pisonia rotundata* Griseb. subsp. *acutiuscula* (Heimerl) M.A.Diaz & Esquivel	West Indies	Cuba	Díaz Dumas (1991); Acevedo-Rodríguez and Strong (2012)
23b	*Pisonia rotundata* Griseb. subsp. *rotundata*	West Indies, North America	Bahamas, Cuba, Hispaniola, and United States of America (FL)	Díaz Dumas (1991); Acevedo-Rodríguez and Strong (2012)
24	*Pisonia silvatica* Standl.	Central America	Costa Rica, Panama	González (2007)
25	*Pisonia subcordata* Sw.	West Indies	Puerto Rico, Lesser Antilles, Virgin Islands	Acevedo-Rodríguez and Strong (2012)
26	*Pisonia taina* Trejo	West Indies	Puerto Rico	Trejo-Torres (2005)
27	*Pisonia zapallo* Griseb.	South America	Argentina, Bolivia, Brazil, Paraguay	Furlan and Giulietti (2014); Nee (2014)

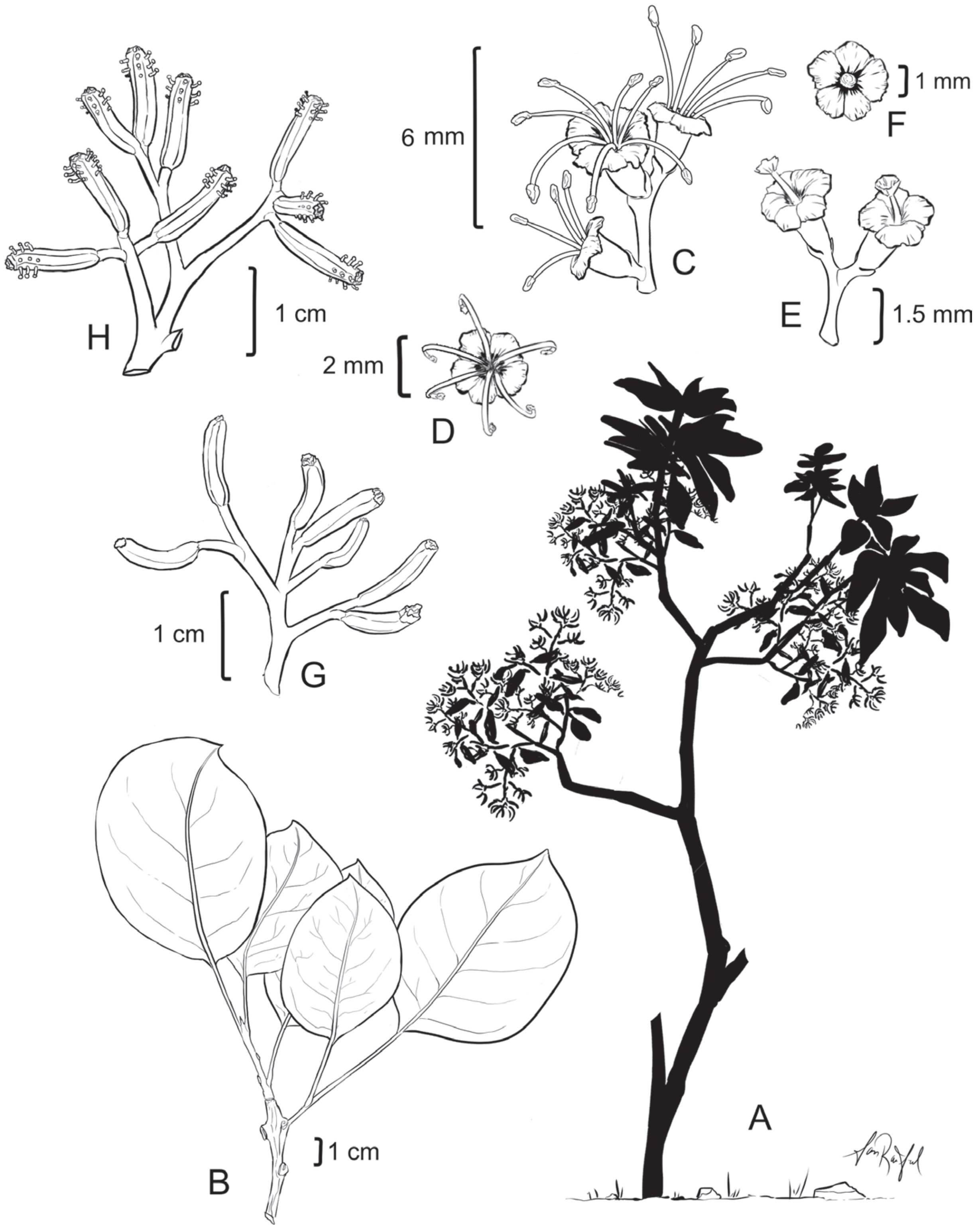

Figure 1. *Pisonia jamaicensis*. A. Silhouette of a tree showing its habit and branches with leaves and infructescences. B. Branch with leaves. C. Partial inflorescence with staminate flowers. D. Top view of a staminate flower. E. Partial inflorescence with pistillate flowers. F. Top view of a pistillate flower. G. Partial infructescence with unripe anthocarps (fruits). H. Partial infructescence with ripe anthocarps. Note the sticky glands present at the distal portion of the anthocarp. Reference specimens: *Cross & Campbell 151* (panels A, E–H); *Proctor 28854* (panel B); *Cross & Campbell 150* (panels C–D). Illustration credit: Ramos Sepúlveda.

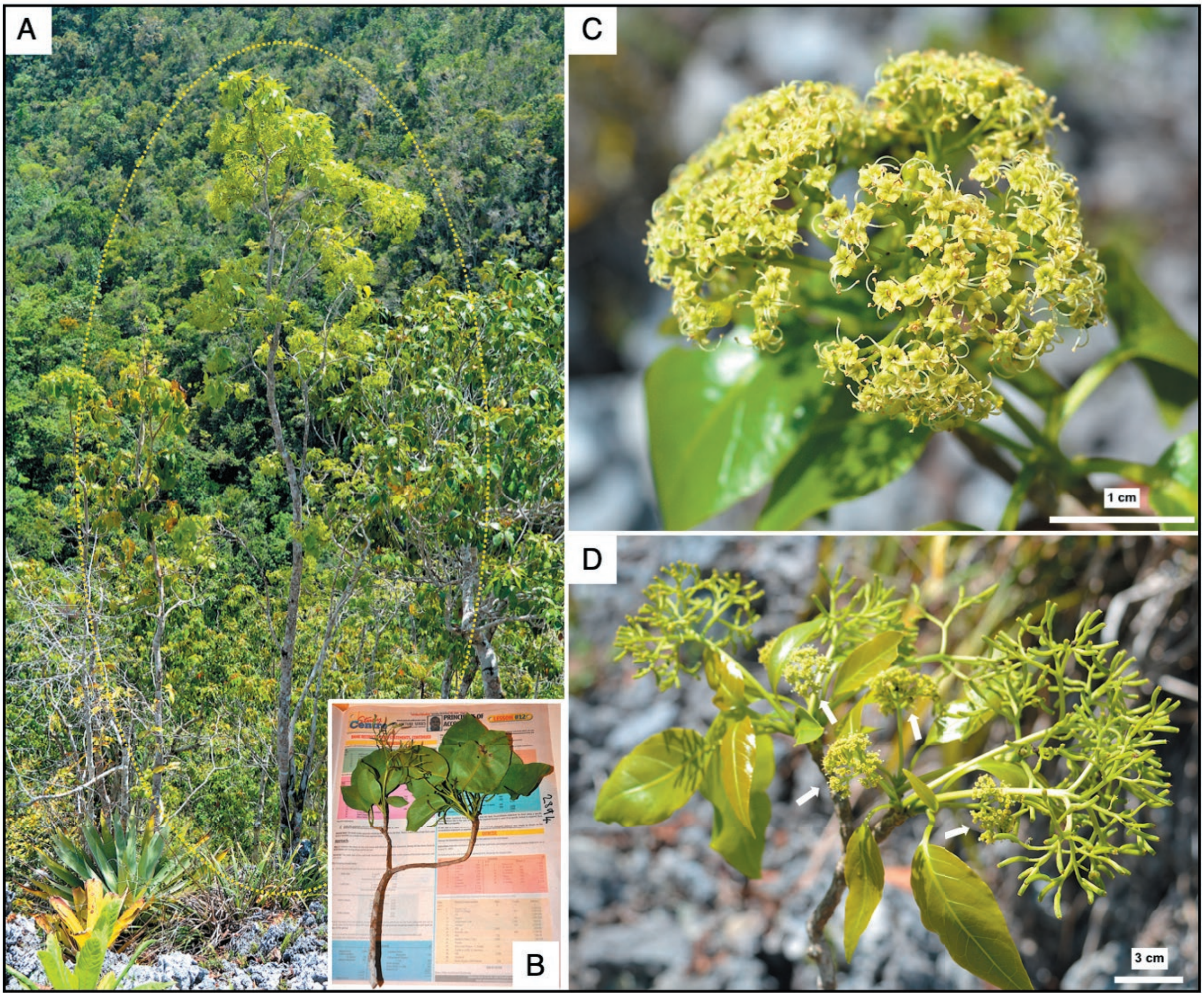

Figure 2. *Pisonia jamaicensis*. A. Mature tree in a rocky limestone slope. B. Branch with developed leaves and ripe fruits. C. Inflorescence with staminate flowers in anthesis. D. Inflorescences with pistillate flowers in anthesis (white arrows) and infructescences with unripe fruits. Note the young leaves (panels A, C–D), which were produced after the first massive flowering in late March when the tree was completely leafless. Reference specimens: *Cross & Campbell 151* (panels A, D); *Abdo et al. 2894* (panel B); *Cross & Campbell 150* (panel C). Photo credits: K.C.S.E.C (A, C & D) and Courtney Lyn (B).

branches armed with spines), leaves ovate and shiny when fresh (vs. leaves elliptic and dull when fresh), and anthocarps narrowly elliptic or oblong, slightly curved when unripe, with viscid glands restricted to the distal 1/3 portion (vs. anthocarps clavate or obovate, straight, with viscid glands along their whole length). *Pisonia jamaicensis* is endemic to Jamaica whereas *P. aculeata* has a pantropical distribution.

Description

Trees dioecious 6–8 m high. *Bark* vertically striated, grayish. *Twigs* slightly ancipitous, greenish, and puberulent when young, especially at leaf nodes; terete, glabrous, and grayish when old; prominent vertical lenticels 2–4 x 1 mm, brown. *Leaves* deciduous, clustered towards distal portion of branches; opposite or subopposite, decussate; young leaves at apical tip brown, resiniferous; petioles 2–7 (–11) cm long, green; blade ovate, rarely elliptic, the blade sometimes asymmetric, 7–12 (–22) x 4–8 (–16) cm, apex acute, rarely rounded, slightly plicate and unequal at the tip, base acute to rounded, rarely oblique or truncate, slightly cuneate at connection with petiole; margin entire; adaxial side glabrous or slightly puberulous, glossy; abaxial side puberulent, pubescent along veins and at the base of the blade, semi-glossy; blade slightly thick when fresh, drying chartaceous or soft coriaceous and brittle; abaxial and adaxial sides light green when fresh, turning greenish or brown when dry; veins pinnate, reticulate, adaxially glabrous, not raised, abaxially puberulent or pubescent; main vein yellowish-greenish on fresh leaves, drying black; secondary veins arcuate, positioned about 45° from the midvein, up to ten pairs, opposite or subopposite, drying blackish or dark brown; tertiary veins not raised, inconspicuous. *Inflorescences* mostly terminal, sometimes axillary, dendroid, 5–9 cm long, pale green when fresh, drying brownish, puberulent; crown expanded, semi-rounded; bracts and bracteoles subulate, subtending each flower, sometimes present at the base of two flowers. *Flowers* sessile or with a short pedicel ca. 1 mm long, puberulent, tube greenish with five dark longitudinal ridges bearing slightly visible glands, lobes cream-whitish; staminate flowers campanulate at anthesis, 3–4 mm long, with five exserted stamens, filaments 1–3 mm long, filiform; pistillate flowers campanulate at anthesis, 2.5–3 mm long, style exserted ca. 1 mm, with two arcuate lobes, penicillate. *Infructescences* dendroid, 5–9 cm long, green when fresh, drying brown; peduncle terete at base, slightly ancipitous distally; crown lax, branches forked or pseudo-dichotomous. *Fruits* anthocarps (achenes), narrowly elliptic to oblong, 12–15 x 1 mm, light green, ripening black, straight or slightly curved, crowned with five calix lobes, stigma persistent, exserted ca. 0.8 mm; husk softly ligneous, pubescent, about 0.2 mm thick, with 5 longitudinal ridges, viscid glands over the ridges restricted to the distal 1/3, glands capitate, about 1 mm long, stalk pubescent, tip resinous. *Seeds* narrowly elliptic, 1 mm long, light brown.

Etymology

We named the species after the island of Jamaica, where the species is endemic.

Phenology

Pisonia jamaicensis has been recorded flowering from March to April and fruiting from April to July. Trees shed leaves before flowering, and produce new leaves during or just after the flowering stage. Apparently, adult trees do not shed their leaves if they are not reproductive on a given year. The vast majority of *Pisonia* species seems to follow the same synchronized phenological pattern to shed leaves between February and March and produce a mast flowering during March and April. This behaviour might help facilitate cross pollination events in this mainly dioecious genus.

Some reproductive individuals of *P. jamaicensis* were observed bearing a few inflorescences of the opposite sex (i.e., subandroecious or subgynoecious). This situation can be interpreted as an uncommon adaptation in *Pisonia* to ensure fruit set in small populations or when first colonizing an island, and has been previously reported in three other species from the Caribbean (Proctor 2012; Caraballo-Ortiz and Trejo-Torres 2017).

Distribution

Pisonia jamaicensis is restricted to karstic limestone hills in central and western Jamaica (Figure 3) at elevations between 350–700 m. The 22 known collections for the species span the parishes of Hanover, Manchester, St. Catherine, St. James and Trelawny (Figure 3). The estimated AOO and EOO for its current distribution were 48 km^2 and 1,934 km^2, respectively. Although not reported yet from the parishes of Clarendon, St. Ann, St. Elizabeth, and Westmoreland, it is probable that *P. jamaicensis* is also present there.

Ecology

Pisonia jamaicensis is apparently restricted to woodlands on exposed or semi-exposed hilltops and hillsides in dog-toothed moist limestone with loose rocks. We currently lack information on many ecological aspects for the species including suitable habitat and substrate, floral visitors, seed dispersers, and germination rates.

Associated species (ranked by family) include: *Comocladia* sp. (Anacardiaceae), *Plumeria* sp. (Apocynaceae), *Syngonium* sp. (Araceae), *Dendropanax* sp. (Araliaceae), *Agave* sp. (Asparagaceae), *Asplenium* sp. (Aspleniaceae), *Tournefortia staminea* Griseb. (Boraginaceae), *Hohenbergia* sp. (Bromeliaceae), *Pitcairnia bromeliifolia* L'Hér. (Bromeliaceae), *Bursera aromatica* Proctor, (Burseraceae), *Clusia* sp. (Clusiaceae), *Euphorbia punicea* Sw. (Euphorbiaceae), *Jatropha* sp. (Euphorbiaceae), *Pithecellobium alexandri* (Urb.) Urb. var. *alexandri* (Fabaceae), *Lisianthius* sp. (Gentianaceae), *Miconia fadyenii* (Hook.) Judd & Skean (Melastomataceae), Myrtaceae spp., *Peperomia* sp. (Piperaceae), *Phyllanthus* sp. (Phyllanthaceae), *Adianthum* sp. (Pteridaceae), *Spathelia* sp. (Rutaceae), *Sapindus* sp. (Sapindaceae), and *Lagetta lagetto* (Sw.) Nash (Thymelaeaceae).

Demography and conservation notes

Detailed demographic profiles for *P. jamaicensis* have not been developed yet. However, preliminary field observations suggest that the estimated total number of individuals is greater than 250, distributed across five to seven subpopulations (Figure 3). At the St. James population (*Abdo et al. 2894*; *Cross & Campbell 150*; *Cross & Campbell 151*), over 50 mature and immature plants were observed. Here, the ratio between observed pistil-

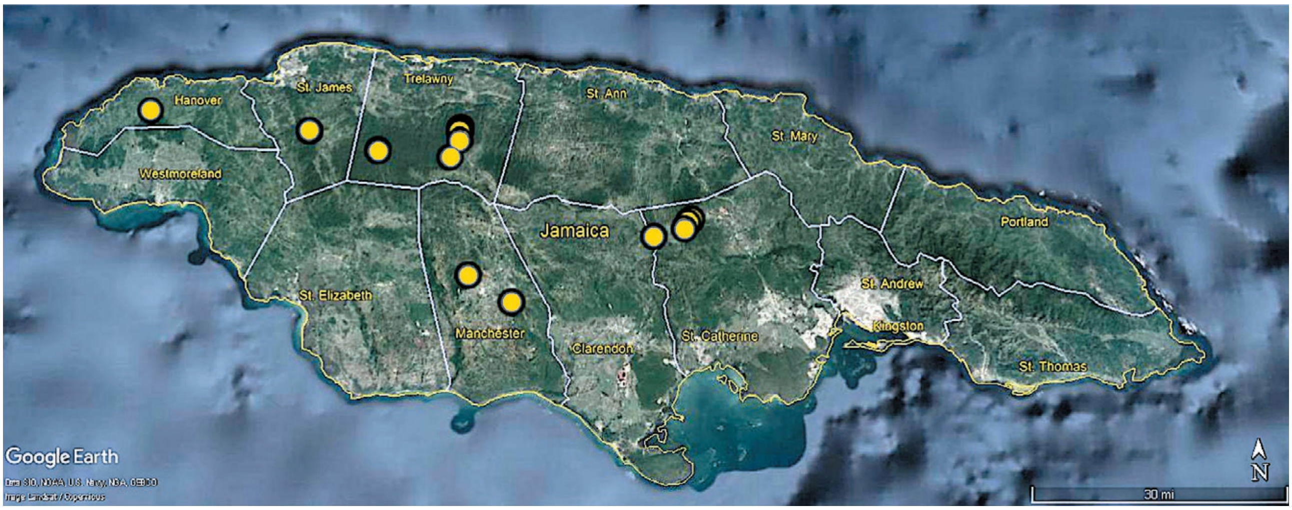

Figure 3. Map of Jamaica showing the distribution of *Pisonia jamaicensis*. The localities where the species has been reported are indicated with yellow circles. Map credit: Google Earth.

late (female) and staminate (male) trees was estimated to be approximately 3:2.

Pisonia jamaicensis does not seem to be directly threatened by targeted harvesting or collection, and we are not aware of any commercial or traditional use for the species. Given its restricted distribution to tops and upper slopes of limestone hills, the species can be threatened by local farming and associated activities such as slash and burn, development, mining (especially for bauxite), and the impact of climate change such as intense droughts, fires, and hurricanes.

Most (82%) of the known specimens for the species were collected over 20 years ago and we currently have little knowledge about their current status. This is especially relevant for half of the localities, which were found more than 40 years ago. It is likely that some of the sites where *P. jamaicensis* was reported have been altered, especially the ones outside protected areas. Fortunately, approximately 70% of the known localities are within areas with some level of legal protection such as the Cockpit County and Dolphin Head forest reserves. In addition, the rugged terrain where the species grows might offer certain degree of protection from forest clearing for agricultural purposes.

The relatively widespread distribution of *P. jamaicensis* across the rugged terrain from central and western Jamaica, the low levels of direct threats, and the estimated AOO and EOO estimated indicate that the species should be classified as Vulnerable, under the specific IUCN criteria B2ab(i,iii,iv);D1 (IUCN 2020). However, some subpopulations in unprotected lands might be at high risk of disappearing. We thus recommend conducting surveys to assess the current status of all known populations to refine this first evaluation and focus conservation efforts where most needed.

Additional specimens examined (paratypes)

JAMAICA: Hanover Parish: Dolphin Head Mountain, NE side of mountain, top of Dolphin Head Mountain, on hillside, 544 m, 7 Sep 2001 [sterile], *P. Acevedo-Rdgz. et al. 11987* (IJ [barcode № 000015910]; US [barcode № 01012906]). Manchester Parish: 1.5 mi due SE of Mandeville, wooded limestone hillside, ca. 2100 ft [640 m], 30 Mar 1974 [sterile], *G.R. Proctor 33759* (IJ [barcode № 000015899]); Marshalls Pen, about 2.25 mi due NW of Mandeville, wooded rocky limestone hillside, ca. 2100 ft [640 m], 5 Mar 1980 [sterile], *G.R. Proctor 38632* (IJ [barcode № 000015917]). St. Catherine Parish: Charlton to Worthy Park, in woodland on limestone, 1700 ft [518 m], 3 Mar 1963 [sterile], *C.D. Adams 12313* (UCWI [accession № 28290, two sheets]); Dodds Valley district, about 2 mi W of Lluidas Vale, wooded limestone hillside, ca. 1500 ft [457 m], 24 Apr 1965 [♀, fl], *G.R. Proctor 26393* (IJ [barcode № 000015922]); Halfway between Ewarton and Worthy Park, on exposed limestone near quarry and in woodland, 1500 ft [457 m], 17 Aug 1967 [sterile], *C.D. Adams 13009* (UCWI [accession № 27980]). St. James Parish: Jericho, N ca. 2 km past last settlement on an overgrown track towards Crownlands, NW atop steep hill (surrounded by boulders), Plummer's Mountain, 580–600 m, 15 Jun 2011 [♀, fr], *M. Abdo, K. Campbell, et al. 2894* (FTG [barcode № 00148023]); Henny Mountains, Jericho, exposed craggy limestone hilltop, 540 m, 18°20'14.58"N, 77°51'47.24"W [WGS84], 3 April

2019 [♂, fl], *S. Cross & K. Campbell 150* (IJ [two sheets]); Henny Mountains, Jericho, exposed craggy limestone hilltop, 540 m, 18°20'14.58"N, 77°51'47.24"W [WGS84], 3 April 2019 [♀, fl, fr], *S. Cross & K. Campbell 151* (IJ [three sheets]). Trelawny Parish: Wilson Valley district, 1.5 mi N of Warsop, Island View Hill, wooded limestone hilltop, 2000–2200 ft [610–671 m], 10 Apr 1961 [♂, fl], *G.R. Proctor 22188* (IJ [barcode № 000015905]); Wilson Valley district, 1.5 mi N of Warsop, Island View Hill, wooded limestone hilltop, 2000–2200 ft [610–671 m], 10 Apr 1961 [sterile], *G.R. Proctor 22189* (IJ [barcode № 000015896]); Belmore Castle area, N of Quick Step, wooded rocky limestone hillside, ca. 1500 ft [457 m], 12 Jun 1976 [♀, fr], *G.R. Proctor 36294* (MO [barcode № MO-653339]); Belmore Castle district, about 2 mi N of Quick Step, moist forest on limestone, ca. 1500 ft [457 m], 12 Jun 1976 [♀, fr], *R. F. Thorne & G. R. Proctor 48233* (MO [barcode № MO-2062567]); Along road N of Burnt Hill, wooded rocky limestone hillside, ca. 1700 ft [518 m], 23 Feb 1980 [sterile], *G.R. Proctor 38599* (IJ [barcode № 000015897]); Cockpit Country, vicinity of Ramgoat Cave, wooded rocky limestone hillside, ca. 1500 ft [457 m], 20 Apr 2000 [♂, fl], *G.R. Proctor 51686* (IJ [barcode № 000015920]); Cockpit Country, vicinity of Ramgoat Cave, wooded brink of limestone cliff, ca. 1500 ft [457 m], 23 Apr 2000 [♀, fl], *G.R. Proctor 51690* (IJ [barcode № 000015886; 000015908]); Cockpit Country, vicinity of Ramgoat Cave, wooded brink of limestone cliff, ca. 1500 ft [457 m], 23 Apr 2000 [♂, fl], *G.R. Proctor 51692* (IJ [barcode № 000015918]); Ram Goat Cave, 450 m, 18°20'07"N, 77°33'29"W, 9 Dec 2000 [sterile], *T. Parker 3513* (IJ [barcode № 000015921]); Cockpit Country, vicinity of Ramgoat Cave, brink of limestone cliff, ca. 400 m, 28 Jun 2007 [sterile], *G.R. Proctor 52602* (IJ [barcode № 000015930]); Cockpit Country, Ramgoat Cave, near brink of limestone cliff, ca. 1200 ft [366 m], 6 May 2000 [♀, fr], *G.R. Proctor 51698* (IJ [barcode № 000015909]); Cockpit Country, vicinity of Ramgoat Cave, wooded brink of limestone cliff, ca. 1500 ft [457 m], 10 Jun 2000 [sterile], *G.R. Proctor 51720* (IJ [barcode № 000015894]).

Dichotomous key to separate species of Pisonia *from the West Indies*

The following dichotomous artificial key contain the 16 taxa of *Pisonia* that, based on our assessment, are currently accepted for the West Indies. Most members in this genus have short flowering and fruiting periods, and therefore, many collections in herbaria are sterile. In consequence, the characters used to build this key are mostly vegetative, complemented with geographic locations and reproductive features. Certain taxa appear more than once to cover variations in their morphology. Some entries have been modified from Trejo-Torres (2005) and Caraballo-Ortiz and Trejo-Torres (2017).

The key to separate the nine genera within Pisonieae presented in Rossetto and Caraballo-Ortiz (2020) should help users verify that their specimens are actually *Pisonia* and not *Guapira* or *Neea*, which are the only other genera from this tribe present in the West Indies.

1 a. Twigs armed with spines 2

b. Twigs unarmed 3

2 a. Scandent shrubs, or treelets; leaves glabrous or with sparse trichomes; twigs pubescent, drying grayish .... ***P. aculeata***

b. Shrubs or trees; leaves with dense trichomes along mid-vein; twigs smooth, drying blackish .... ***P. macranthocarpa***

3 a. Leaves mainly > 10 cm long and > 10 cm wide 4

b. Leaves mainly ≤ 10 cm long and ≤ 10 cm wide 5

4 a. Fresh leaves dull green on both sides; leaf apex mostly rounded; flowers > 5 mm long; fruits 5-ribbed; Grand Cayman .... ***P. margaretiae***

b. Fresh leaves shiny green on both sides; leaf apex mostly acute; flowers ≤ 5 mm long; fruits 10-ribbed; Puerto Rico .... ***P. horneae***

5 a. Leaves with apex acute 6

b. Leaves with apex rounded, obtuse, or emarginate 11

6 a. Leaves with base acuminate to attenuate; fruits with viscid glands distributed along the whole length .... ***P. macranthocarpa***

b. Leaves with base rounded to oblique; fruits with viscid glands restricted to the distal half 7

7 a. Leaf veins at abaxial side raised to the finer ramifications .... ***P. taina***

b. Leaf veins at abaxial side not raised to the finer ramifications 8

8 a. Leaves > 3 cm wide; Jamaica and Puerto Rico to Lesser Antilles 9

b. Leaves ≤ 3 cm wide; Cuba 10

9 a. Leaves ovate, chartaceous; staminate inflorescence an expanded, non-flabellate crown; Jamaica .... ***P. jamaicensis***

b. Leaves broadly elliptic or rounded, coriaceous; staminate inflorescence with flabellate crown; Puerto Rico to Lesser Antilles .... ***P. subcordata***

10 a. Leaves elliptic with revolute margins ....***P. rotundata*** subsp**.** ***acutiuscula***

b. Leaves ovate with flat margins .... ***P. clarensis***

11 a. Leaf veins at abaxial side raised to the finer ramifications .... ***P. taina***

b. Leaf veins at abaxial side not raised to the finer ramifications...12

12 a. Leaves with base acuminate to attenuate; fruits with viscid glands distributed along the whole length ....***P. macranthocarpa***

b. Leaves with base rounded to oblique; fruits with viscid glands restricted to the distal half.......................................13

13 a. Leaves elliptic or oblong...14

b. Leaves rounded or obovate 18

14 a. Petioles 5 (–7) mm long 15

b. Petioles > 7 mm long..16

15 a. Leaves oblong; twigs densely covered with yellowish indumenta; Hispaniola ....***P. ochracea***

b. Leaves elliptic; twigs densely covered with dark brown or blackish indumenta; Cuba.. ....***P. rotundata*** subsp**.** ***rotundata***

16 a. Leaves > 4 cm wide; twigs and leaves drying grayish; Hispaniola and Puerto Rico.................................... ***P. albida***

b. Leaves ≤ 4 cm wide; twigs and leaves drying brownish or greenish; Cuba 17

17 a. Leaves elliptic, drying brownish; apex rounded or obtuse ***P. petiolaris***

b. Leaves oblong, drying greenish; apex emarginate or obcordate..***P. ekmanii***

18 a. Leaf blade ≤ 5 cm long × 3 cm wide ....***P. petiolaris***

b. Leaf blade > 5 cm long × 3 cm wide 19

19 a. Leaves drying shiny yellow on adaxial side and dull light brown on abaxial side; blade margins slightly revolute; petioles 0.9–1.7 cm long; Cuba ....***P. byrsonimifolia***

b. Leaves drying dull black on adaxial side and dull dark brown on abaxial side; blade margins flat; petioles 1.7–4 cm long; Puerto Rico 20

20 a. Leaves puberulent, especially on the abaxial side and along veins; staminate inflorescences with a globose crown ....***P. roqueae***

b. Leaves glabrous, sometimes slightly puberulent on the abaxial side at base of main vein; staminate inflorescences with a flabellate crown..................................... ***P. subcordata***

DISCUSSION

The addition of *P. jamaicensis* increases to 27 the number accepted species of *Pisonia* and brings in a second species – the first endemic – of this genus to the flora of Jamaica. The rest of the Greater Antilles and Grand Cayman also have endemic *Pisonia*, making the West Indies a hotspot for the genus. In fact, more than half (16 taxa; 59%) of its diversity is found in the Caribbean, of which 88% are restricted to the region and 69% are single-island endemics (Table 1). Cuba is the most diverse island with seven taxa (six species and one subspecies), of which 71% are endemics. The second most diverse island is Puerto Rico holding six species with half of them endemics, followed by Hispaniola with three species and 33% endemism. All other islands or archipelagos (i.e., Bahamas, Cayman Islands, Jamaica and the Lesser Antilles) have two species of *Pisonia*, with the only endemics in Grand Cayman and Jamaica.

The records of *P. subcordata* from Jamaica reported by Adams (1972) and Acevedo-Rodríguez and Strong (2012) are in part based on the misidentification of *Guapira rotundifolia* (Heimerl) Proctor (e.g., *Adams 12610* [UCWI], *13010* [UCWI]; *Goodfriend & Tanner 2281* [UCWI]; *Harris 10958* [US], *10985* [B, K, NY, UCWI, US], *11183* [US]; *Proctor 27530* [US], *32481* [MO, US], *34371* [MO]) or *Neea nigricans* Fawc. & Rendle (*Proctor 21346* [NY]), as clarified by Proctor (1982). However, some specimens originally labeled as *P. subcordata* were, in fact, the species here described. When sterile, *G. rotundata* can be separated from *P. jamaicensis* based on mature leaves, which are elliptic or obovate, stiffly leathery, and dry yellowish brown with secondary veins brown, thin and inconspicuous. These characters contrast with the leaves of *P. jamaicensis*, which are ovate (rarely broadly elliptic or rounded), chartaceous or soft leathery, and dry brown with secondary veins black, corky and conspicuous.

After clarifying that *P. subcordata* is not present in Jamaica, this island now contains two species of *Pisonia*: *P. aculeata* and the newly described *P. jamaicensis*. The former can be separated from the latter by having a scandent habit with twigs bearing spines, and broadly elliptic fruits with viscid glands distributed along the whole length (vs. tree habit with unarmed twigs, and narrowly elliptic fruits with viscid glands restricted to the upper third portion in *P. jamaicensis*). Regarding the distribution of *P. subcordata*, this species is now restricted to coastal habitats in northern and eastern Puerto Rico, Virgin Islands and the Lesser Antilles, extending to Martinique (Acevedo-Rodríguez and Strong 2012; Caraballo-Ortiz and Trejo-Torres 2017).

Our estimate of 27 accepted species in *Pisonia* is still in need of more investigation as some taxa are poorly known and it is difficult to assess their validity. For example, *P. proctorii*, a spineless liana from Belize, could be a variation of *P. aculeata*. Moreover, *P. indecora* Heimerl might represent a species of *Guapira*, possibly *G. boliviana* (Britton ex Rusby) Lundell (E.F.S. Rossetto, pers. comm.). Therefore, further work on *Pisonia* is needed to help refine its taxonomy and reach a more precise estimation of accepted species.

Although no comprehensive phylogenetic or biogeographic study of *Pisonia* have been published to date, a recent study of tribe Pisonieae by Rossetto et al. (2019) found an intriguing relationship between *P. grandis* and the taxa from the West Indies. However, *P. grandis* – renowned as the Birdcatcher tree – has a native range covering myriads of islands across the Indian and Pacific Oceans but does not reach the American continent. Further systematic studies on the genus might shed light on this finding and help reconstruct the evolutionary relationship among species to resolve taxonomic uncertainties, especially within the *P. aculeata* complex, whose members have a shrubby-scandent habit and are often armed with stout spines.

AUTHOR CONTRIBUTIONS

MACO prepared a first draft of the manuscript, revised herbaria, prepared the species description, compiled the list of accepted Pisonia, and built the dichotomous key. KCSEC and SJC collected the species, revised herbaria, prepared the distribution map, and performed the IUCN evaluation. All authors contributed to the manuscript and approved the final version.

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A new *Muscarella* (Orchidaceae: Pleurothallidinae) from Tapantí National Park, Costa Rica

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Abstract. A new species of *Muscarella* from Costa Rica, is described and illustrated. Muscarella tapantiensis most resembles *M. coeloglossa* but differs in the longer pedicels (3-5 vs. 1-2 mm), the shorter (2.5-2.8 vs. 3.75 mm), connate (vs. free) lateral sepals, and the lip with triangular (vs. broadly rounded) lower lateral lobes. *Muscarella xanthella* also resembles *M. tapantiensis*; however, it differs in the successively flowered raceme with alternate pedicels, the deeply fimbriate petals and the thick, rounded lip with densely verrucose lateral lobes. We provide illustrations, etymology, notes on ecology, pictures of the plants and habitat, and a distribution map of the new species. We discuss the inclusion of this species in the genus *Muscarella*.

Keywords: floristics, *Muscarella coeloglossa*, *Muscarella xanthella*, Neotropics, orchid taxonomy, *Specklinia*.

INTRODUCTION

A fundamental principle of any study aimed at understanding the specific relationships among different organisms is to identify them correctly. This simple rule becomes critical and unpractical when the research is carried out in a tropical, biologically-rich region (Higgins and Ruokolainen 2004). Biologists esteem that, in the tropics, only about 86% of life diversity has been apprehended by science, and the degree of the average knowledge may vary among living groups (Mora et al. 2011).

With over 50,000 ha, Tapantí-Macizo de la Muerte National Park (TNP) is one of the largest protected areas in Costa Rica (Sánchez 2002; Bernard et al. 2009) and one of the species-rich spots for orchids in the country (Pupulin 2003; Pupulin and Bogarín 2012; Crain and Fernández 2020). Because of this high diversity and the ease to reach the park within less than two hours from the capital city of San José, ongoing floristic, ecological and biogeographical projects have been carried out by Lankester Botanical Garden and scientific partners for almost two decades (Pupulin 2001; 2003, Pupulin et al. 2009; Pupulin and Bogarín 2012). In 2015, a long-term research project led by Dr. Jyotsna Sharma from Texas Tech University was initiated to understand if mycorrhizal fungi distribution and specificity influence the distribution of epiphytic orchid species in a community. The massive numbers of co-occurring species there (Figure 1) offer a unique opportunity to test the limits of the species co-existence hypothesis. As part of required taxonomic identification of the epiphytic orchid species subjected to fungal analyses in the study site, a species of *Muscarella* Luer proved impossible to match with any previously described taxon.

Muscarella is a Neotropical genus of the Pleurothallidinae with around 50 species ranging from Mexico to Brazil and the Antilles (Luer 2006; Pessoa et al. 2014). The genus is distinguished by the cespitose plants with loose racemes, flowers with long-tailed sepals and fringed, fimbriate or denticulate petals, and a thick, fleshy lip that is somehow ciliate (Luer 2006). Most species bear longitudinal calli, and the column-foot is variously concave (Luer 2006). The species of *Muscarella* were initially treated under *Pleurothallis* R.Br. and later into a broad concept of *Specklinia* Lindl. (Pridgeon et al. 2001). Lindley (1830) described *Specklinia* to include minute, herbaceous plants with flowers of gibbose sepals, free petals and a labellum a third length of the sepals, and membranaceous, winged columns. However, Garay (1974) transferred it to the subgeneric level under *Pleurothallis*. Then, Luer (1986) built ten sections within *Pleurothallis* to group species with similar floral features, including a section of minute flowers with thick, fringed or verrucose, lobed lips, which he named *Pleurothallis* section Muscariae Luer (1986). Later, Pridgeon et al. (2001) proposed a broad concept of *Specklinia*, sister to the *Platystele-Scaphosepalum* clade, for small plants with an abbreviated stem with an annulus, flowers with sepals connate to different degrees, a lip hinged to the column foot, and a column provided with a toothed apex and ventral anther and stigma. They based their findings on initial molecular phylogenies of the subtribe. The concept included species of *Pleurothallis* sections *Hymenodanthae* Barbosa Rodrigues (1882), *Muscariae* Luer, and *Tribuloides* Luer (1986) and species from *Acostaea* Schltr. (Schlechter 1923), *Empusella* Luer (Luer 2004) and *Pseudoctomeria* Kraenzl. (Kraenzlin 1925).

Finally, Luer (2006) considered the new circumscription of *Specklinia* as a polyphyletic aggregation of many taxa; thus, he proposed the transfer of section *Muscariae* (Luer 1986) to genus *Muscarella*. The genus is a monophyletic and morphologically discernible group from the rest of *Specklinia*, and it is supported by the most recent molecular phylogenetic studies in the Pleurothallidinae (Karremans et al. 2015; Pérez-Escobar et al. 2017)

Figure 1. Landscape at Tapantí National Park, along Rio Grande de Orosi, Cartago, Costa Rica, the type locality of M. tapantiensis. Photographs by F. Pupulin.

Muscarella comprises 11 species in Costa Rica, including the species proposed here as new (Luer 2006; Ossenbach et al. 2007). We describe it hereafter.

MATERIALS AND METHODS

We collected living specimens at TNP, Cartago, Costa Rica, and cultivated them in the collections at Lankester Botanical Garden (JBL), University of Costa Rica. Living plants were documented with sketches using a Leica® MZ9.5 stereo-microscope with a drawing tube. The sketches were digitalized, and the images were used for diagramming a draft composite template in Adobe Photoshop® CC. Photographs were taken with a Nikon D7100, Nikon Bellows PB-6 extension, and a Nikon AF-D 50 mm f/1.8 lens. Descriptions were prepared from both living specimens and herbarium material deposited at JBL. Locality data were obtained with a Garmin eTrex Vista GPS and supporting maps and recorded along with phenology observations in a computerized database at JBL. Ecological zones follow the Holdridge Life Zone System (Holdridge 1967, Holdridge 1987). Distribution maps were made using the geographic information system software ArcView GIS 3.3 (ESRI, California, USA). Specimens were preserved in formaldehyde: acetic acid: ethanol [FAA (53% ethanol, 37% water, 5% formaldehyde, and 5% glycerol)].

RESULTS

Muscarella tapantiensis Mel.Fernández & Bogarín, **sp. nov.** (Figure 2.).

Type: COSTA RICA, Cartago: Paraíso, Orosi, Tapantí, Parque Nacional Tapantí, bajando por el sendero Oropéndola, epífitas a lo largo del borde del río Grande de Orosi, 9°44'10.15"N 83°46' 54.80"W, 1330 m, bosque pluvial premontano, 25 setiembre 2015, *M. Fernández 1080, L. Oses and A. Orellana* (holotype JBL-spirit, J0159).

Diagnosis

Muscarella tapantiensis most resembles *M. coeloglossa* (Luer and Hirtz) Luer but differs from it by the longer pedicels (3-5 mm in *M. tapantiensis* vs. 1-2 mm), the shorter (2.5-2.8 vs. 3.75 mm), connate (vs. free) lateral sepals, and the lip with triangular (vs. broadly rounded) lower lateral lobes.

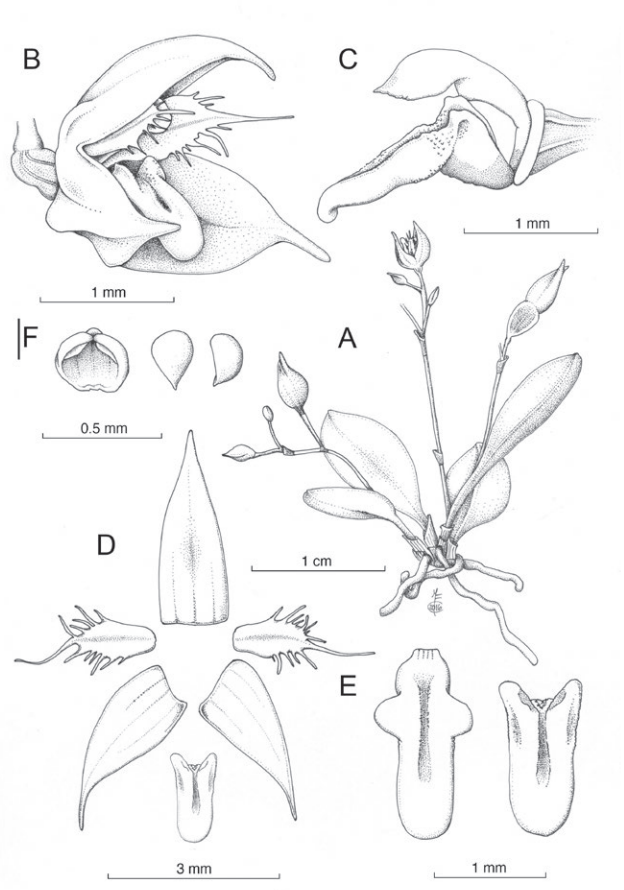

Figure 2. Illustration of *Muscarella tapantiensis*: A. Habit. B. Flower. C. Column and lip, lateral view. D. Dissected perianth. E. Lip, flattened, and natural position. F. Anther cap and pollinia. Drawn by M. Fernández based on *M. Fernández 1080* (holotype).

Description

Plant epiphytic, caespitose, erect or subpendent, very small, up to 1.8 cm tall. Roots slender, flexuous, 0.5 mm in diameter. Ramicauls slender, erect, 1.8–4.0 mm long, enclosed by 2 thin, tubular sheaths becoming papyraceous with age. Leaves erect, oblong-elliptic, subacute to obtuse, thick, coriaceous, conduplicate, abaxially cuneate, 0.5–1.3 × 0.3–0.5 cm, the base narrowing into a petiole 3-5 mm long. Inflorescence an erect, loose, flexuous, successively flowered raceme producing up to 6 flowers, to 3.5 cm long, as long as or exceeding the leaves, developed laterally from the ramicaul, peduncle filiform, to 1.7 cm long, rachis to 2.3 cm long, floral bracts tubular, acute, to 0.5 mm. Pedicel slender, persistent, to 3-5 mm long. Ovary terete, widened apically, 0.5 mm long. Flowers inconspicuous, less than 3 mm in diameter, sepals and petals translucent yellow-greenish to pinkish, hyaline, the petals with a longitudinal light pink midvein, the yellow lip turning to light green apically, basally stained with purple-red. Dorsal sepal elliptic, acute to acuminate, conduplicate, concave, entire, carinate beneath, briefly connate to the lateral sepals, 2.2–2.5 ×

0.8–1.0 cm. Lateral sepals ovate, slightly acuminate-subfalcate, concave, entire, carinate beneath, briefly connate at the base, 2.5–2.8 × 1.0-1.2 mm. Petals elliptic-ovate, fimbriate, aristate, 1.7–2.0 × 0.6–0.8 mm. Lip oblong, rounded, 3-lobed, 1.5 × 1.0 mm when spread, verrucose and papillose mostly at base, the lateral lobes triangular, acute, minutely erose, erect in natural position, shorter than the midlobe, the midlobe 0.5 mm wide, rounded, with a longitudinal sulcate callus with two paralell light keels, the apex slightly revolute, hinged to the column foot. Column greenish, terete, widened apically, with two small wings, arcuate, footed, the foot apex concave with two verrucose, lateral thickenings, 1.2–1.3 × 0.4 mm. Anther and rostellum subapical, the stigma ventral. Pollinarium with two pyriform pollinia, hooked towards the base, 0.2 mm, lacking accessory structures. Capsule globose, 6-ridged, ridges prominent, green, purple between ridges, 3.5–4.0 × 3.0 mm. (Figure 2).

Etymology

After Tapantí National Park, the place where plants of this species were first collected.

Distribution and habitat

Only known from Costa Rica, growing on mossy twigs, mostly of *Saurauia montana* (Actinidiaceae), in open areas along or close to riparian premontane wet and rain forests of the Caribbean watershed of the Talamanca mountain range (Figure 3).

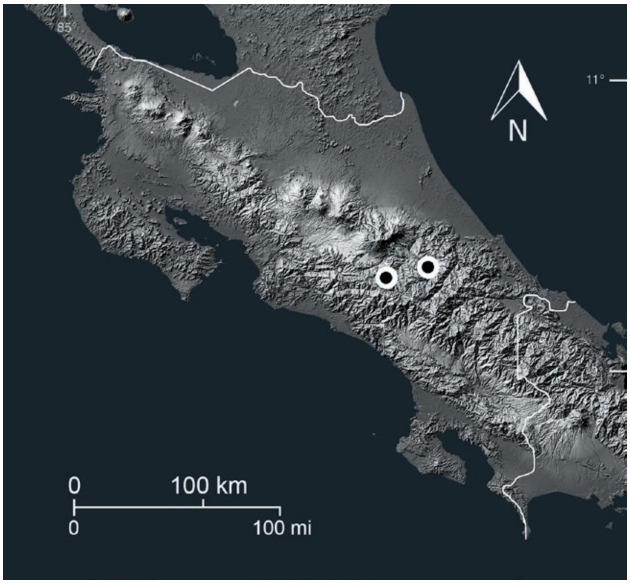

Figure 3. Distribution of *Muscarella tapantiensis* in Costa Rica (Central America), based on M. Fernández 1080 (holotype), *D. Bogarín 9362* & *A. Karremans 4934* (paratypes). Only two marks are shown since the holotype and one paratype were collected in the same area.

Flowering time

Plants were seen in flower in the wild from October to April. At TNP, a flowering peak occurs between November and January.

Additional specimens examined (paratypes)

COSTA RICA. Cartago: Paraíso, Orosi, Tapantí, Parque Nacional Tapantí, Sendero Oropéndola, orillas del Río Grande de Orosi, 9°44’37.86”N 83°47’04.28”W, 1296 m, epífitas en árbol de Saurauia sp. (Actinidiaceae) a orillas del río, bosque pluvial premontano, 30 octubre 2011, *D. Bogarín 9362 and M. Bonilla* (JBL-spirit, D4865) (Figure 4). Cartago: Turrialba, Tayutic, Platanillo, siguiendo el camino paralelo al río Platanillo, que va hacia el origen de este, unos 3.5 km del centro de Platanillo, sobre árboles solitarios en potreros, 9º47’52.90”N 83º33’44.51”W, 1049 m, 4 febrero 2012, *A. Karremans 4934* (JBL-spirit, D5464).

DISCUSSION

The new species is recognized by the small, less than 3 mm in diameter, translucent yellow-greenish to pinkish flowers with concave sepals, fimbriate and aristate petals, and a lip with two short lateral lobes, characters that agree with the concept of *Muscarella*. The new species most resembles the Ecuadorian *Muscarella coeloglossa* (Luer & Hirtz) Luer, but differs from it by the longer pedicels (3-5 mm in *M. tapantiensis* vs. 1-2 mm), the shorter (2.5-2.8 vs. 3.75 mm), connate (vs. free), apically acuminate (vs. rounded) lateral sepals, and the lip with triangular (vs. broadly rounded) lower lateral lobes. The Ecuadorian *Muscarella xanthella* (Luer) Luer also resembles *M. tapantiensis*, mostly because of the more or less elliptic leaves and the small pinkish flowers with concave, translucid sepals. Nevertheless, *Muscarella xanthella* produces a fasciculous-like inflorescence with pedicels congested at the apex of the peduncle, different from the successively flowered raceme with alternate pedicels of *M. tapantiensis*. When looking closer to the flower, the lacerate petals of *Muscarella xanthella* differ from the deeply fimbriate ones of *M. tapantiensis*, and the lip is thick, rounded with densely verrucose lateral lobes. In contrast, *Muscarella tapantiensis* bears thinner, triangular lobes at the base and is papillose mostly at the base.

Figure 4. Flowers of *Muscarella tapantiensis* from Tapantí National Park showing two variations of sepal color: A. Variation with reddish sepals, from the holotype (*M. Fernández 1080*). B. Variation with yellow sepals, based on *D. Bogarín 9362*.

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Memecylon viswanathanii, a new species of Melastomataceae from Kalakkad-Mundanthurai Tiger Reserve (KMTR), India

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Abstract. *Memecylon viswanathanii* R.Rajesh, P.Sakthidhasan & C.Rajasekar, a new species of Melastomataceae, is described and illustrated from the Kalakkad-Mundanthurai Tiger Reserve (KMTR) in the southern Western Ghats of India. *M. viswanathanii* is close to *M. parvifolium* Thwaites and *M. varians* Thwaites but differs by several vegetative and floral characters. The species is assessed here as Critically endangered as per IUCN Red List.

Keywords: Southern Western Ghats, Critically endangered, *M. parvifolium*, *M. varians.*

INTRODUCTION

The genus *Memecylon* L. belonging to the family of Melastomataceae (The Angiosperm Phylogeny Group IV 2016) has 357 species (Renner et al. 2007 onwards) or around 379 (Michelangeli et al. 2020). It is reported that there are 55 species distributed in India wherein 22 species are endemic to the Western Ghats (Viswanathan and Manikandan 2001; Sivu et al. 2012, 2018; Prabhu and Murugan 2017; Das et al. 2018; Radh and Nampy 2019; Vadhyar et al. 2020). During an inventory in 2017, plant specimens were collected from the Kalakkad-Mundanthurai Tiger Reserve (KMTR) in the southern Western Ghats of Tamil Nadu in India. A critical assessment of pertinent literature (Clarke 1879; Gamble 1919; Bremer 1979, 1987; Viswanathan 2001) revealed that specimens of *Memecylon* collected from Vaniyangal podavu at an elevation of c. 1405 m MSL in the KMTR were hitherto unknown to science and turned out to be a new species. It is described here with a diagnosis, comparison with closely related species, detailed description, illustrations, phenology and other related details.

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Memecylon viswanathanii R.Rajesh, P.Sakthidhasan & C.Rajasekar, **sp. nov.** (Figures 1 & 2)

Type: INDIA, Tamil Nadu, Tenkasi district, Kadayam Forest Range, Vaniyangal podavu, ±1405 m, 01 March 2017, *R. Rajesh, P. Sakthidhasan & C. Rajasekar 1494* (holotype, MH!; isotypes, K!; Herbarium, Department of Botany, Bharathidasan University, Tiruchirappalli!).

Diagnosis

Closely related to *M. parvifolium* Thwaites and *M. varians* Thwaites by branches and greyish bark, coria-

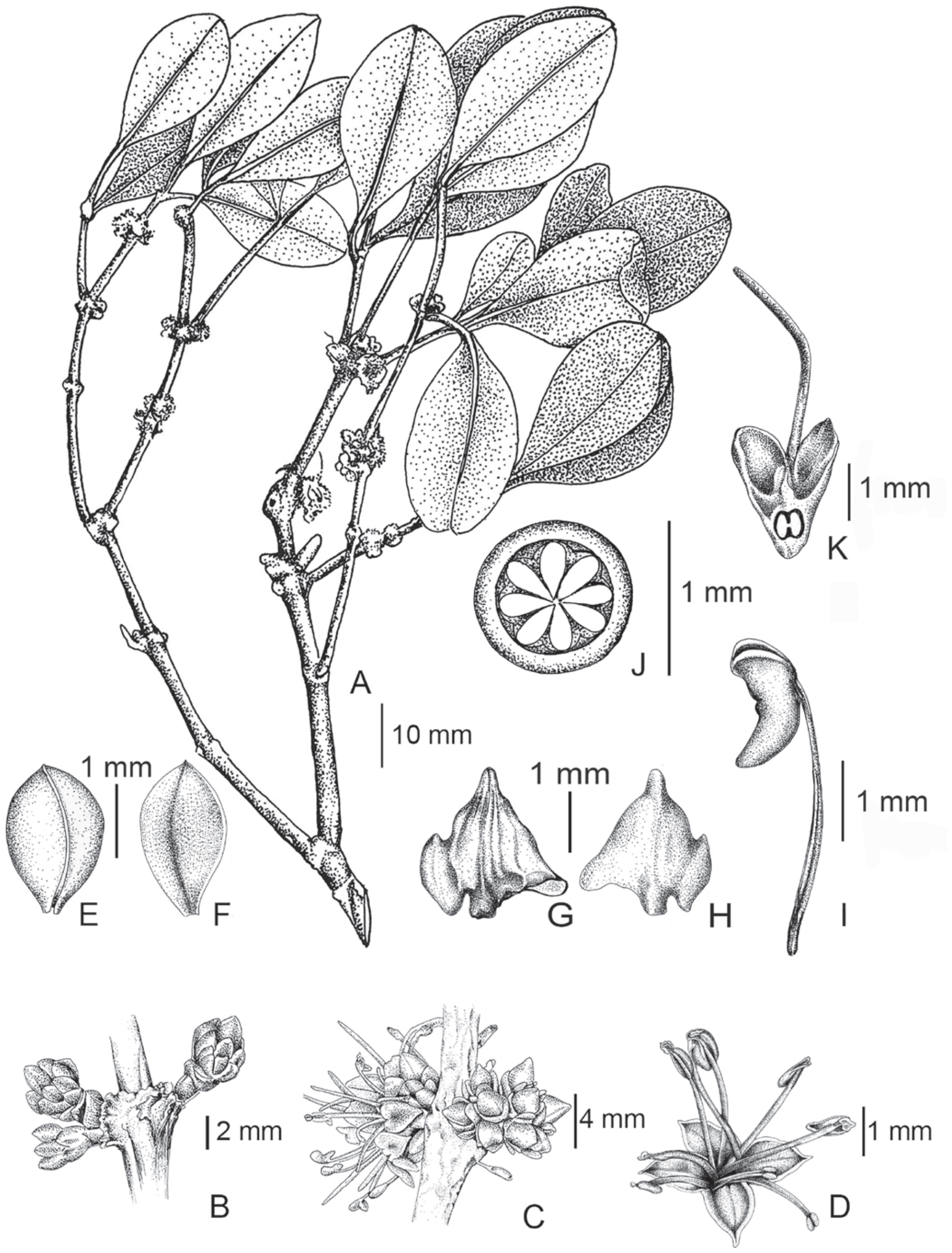

Figure 1. *Memecylon viswanathanii* R.Rajesh, P.Sakthidhasan & C.Rajasekar, A, flowering branch; B, floral buds; C, opened and unopened flowers; D, flower; E, bracteole – abaxial surface; F, bracteole – adaxial surface; G, petal - abaxial view; H, petal – adaxial view; I, stamen; J, cross section of ovary; K, longitudinal section of ovary with two calyx lobes removed.

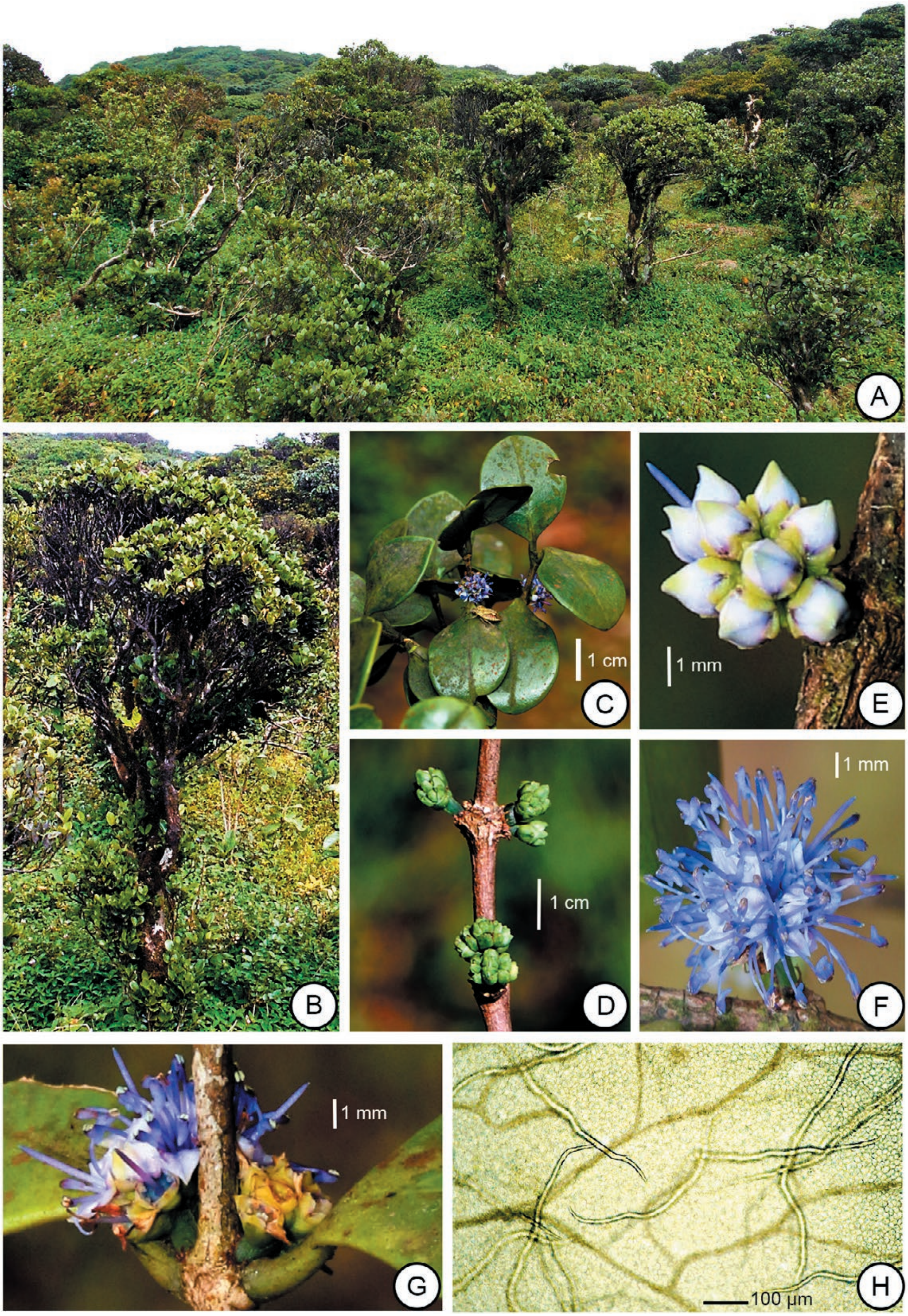

Figure 2. *Memecylon viswanathani* R.Rajesh, P.Sakthidhasan & C.Rajasekar, sp. nov. A, trees in the southern Tropical wet evergreen forest; B, tree; C, flowering twig; D, immature floral buds with bracteoles; E, unopened flowers; F, fully opened flowers; G, flowers after fertilization; H, a portion of cleared leaf showing narrowly filiform unbranched sclereids.

Table 1. Comparison of *M. viswanathanii* with *M. parvifolium* and *M. varians*.

Character	*M. parvifolium*	*M. varians*	*M. viswanathanii*
Leaves	elliptic to elliptic-obovate, cuneate at base, obtuse to rounded or notched or sometimes acute or occasionally shortly and indistinctly caudate at apex, more or less shining above, drying dark green, 1–3.5 × 0.5–2.5 cm	elliptic, cuneate at base, acute to acuminate or caudate and subacute to obtuse at the very apex, more or less dull on both sides, drying yellowish green, 3–9 × 1.5–3 cm	broadly elliptic, obtuse or obtusely cuneate at base, obtusely rounded, retuse or emarginate at apex, more or less shining above, drying yellowish green, 1.5–3.2 × 1–2 cm
Leaf margins	often revolute	not revolute	revolute
Petiole length	1-2 mm	2-3 mm	3–4 mm
Foliar sclereids	Aggregated to sclerocysts around the veins or vein-endings	irregularly elongated to filiform, often branched	narrowly filiform, unbranched
Peduncle length	0 mm	1-6 mm	2–4 mm
Pedicels	shorter than or about the same length as the calyx	0 or shorter than the calyx	0
Receptacle	smooth	± papillose	warty
Calyx	smooth or shallowly striate inside	smooth or shallowly striate inside	smooth inside
Petals	white	blue	whitish pale blue
Disc	smooth or shallowly striate	smooth or shallowly striate	smooth
Connectives	without a gland	without or with a gland	with a gland

ceous leaves with indistinct intramarginal and lateral veins and inflorescence in axillary fascicles but differing in having broadly elliptic leaves with petioles up to 4 mm long, narrowly unbranched filiform sclereids, absence of pedicels and whitish pale blue flowers from *M. parvifolium* and *M. varians*, up to 4 mm long peduncles, warty receptacle and connective bearing gland from *M. parvifolium* and smaller leaves with revolute margin and shorter peduncles from *M. varians* (Table 1).

Description

Trees, c. 4 m high; branches and branchlets subquadrangular; bark ashy grey mixed with brown; nodes annular; internodes abbreviated, 0.4–2.5 × 0.2–0.6 cm. Leaves decussate – opposite, coriaceous, broadly elliptic, obtuse or obtusely cuneate at base, revolute at margin, obtusely rounded, retuse or emarginate at apex, 1.5–3.2 × 1.0–2.0 cm, green with pale yellow above, yellowish green beneath when dry, yellow with age, glabrous; midrib prominent, sulcate adaxially, raised abaxially; intramarginal and lateral veins indistinct, rarely basal 2 to 3 pairs faintly distinct up to half way adaxially; petioles grooved adaxially, 3–4 × 0.4–0.5 mm. Foliar sclereids monomorphic, narrowly filiform, unbranched. Flowers in axillary fascicles, either at leaf axils or leafless nodes, 6–12 pairs in each fascicle, either at one side or both sides of a node, 4-merous, bisexual with an epigynous disc, 1–1.5 × 1.5–2 mm; fascicles each c. 8 mm across; open flowers including hypanthium and expanded petals 5–6 × 2.5–3 mm; bracteoles many, in clusters, at the base of the flowers, elliptic, green, denticulate at margin, c. 0.5 × 1 mm; peduncles 2–4 × 1–2 mm; pedicels 0. Receptacles pale blue, campanulate-cyathiform, prolonged above ovary, continuous with calyx, warty outside. Calyx shallowly 4-lobed; cup warty outside, pale blue outside, c. 1 × 1.2 mm; lobes deltoid or triangular in outline, warty outside, smooth inside, pale blue with pink tinge outside, c. 0.5 × 1 mm. Petals 4, imbricate in bud, whitish pale blue, orbicular, deltoid in outline, slightly undulate at margin, subacuminate at apex, 2.5–3 × 1.5–2 mm. Disc dark blue, smooth. Stamens 8, equal; filaments bluish white, whitish dark blue, incurved in bud, straight, 4–5 × c. 0.2 mm; anthers dithecous, pale brown, opening by slits, c. 0.2 × 0.3 mm; connectives blue, attached ventrally with anthers, nearly axe-shaped, obtuse – rounded at base, 0.8–1 × 0.2–0.3 mm; gland disc-shaped, at dorsal middle of the surface, pinkish brown. Ovary 1-celled; ovules 8, attached to central placenta; style blue to pinkish blue after fertilization, 4–5 × 0.2-0.3 mm. Fruit not collected.

Etymology

The specific epithet is in honor of Prof. M.B. Viswanathan, Department of Botany, Bharathidasan University, for his contribution to the field of Plant Taxonomy in India.

Phenology

Flowering: February to April.

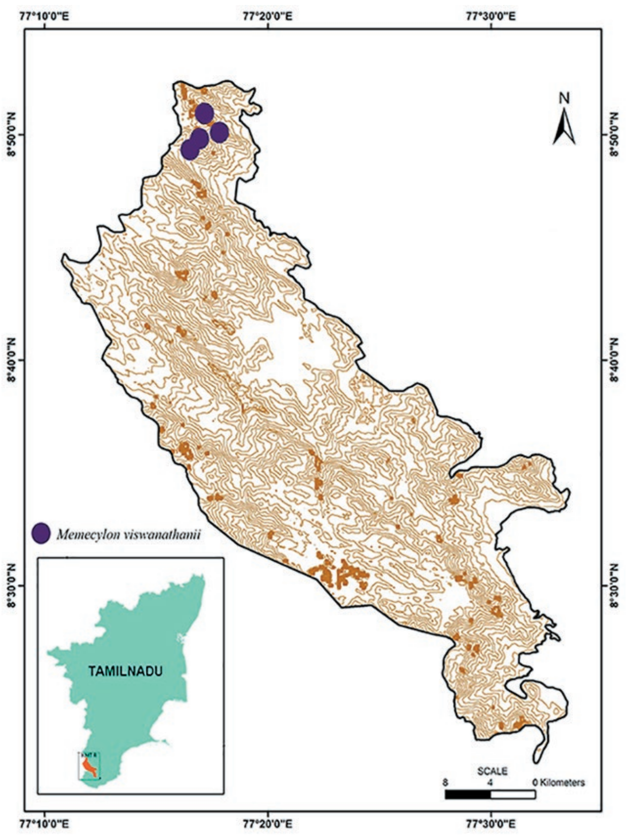

Figure 3. Distribution of *Memecylon viswanathanii* R.Rajesh, P.Sakthidhasan & C.Rajasekar (purple circles) in the Kalakkad-Mundanthurai Tiger Reserve (KMTR).

Distribution

Endemic to the Kadayam Forest Range of the Tenkasi district in the KMTR of India.

Habitat

Southern Tropical wet evergreen forest with trees of *Mappia nimmoniana* (J.Graham) Byng & Stull and *Monosis travancorica* (Hook.f.) H.Rob. & Skvarla, shrubs of *Psychotria bisulcata* Wight & Arn., undershrubs of *Hedyotis ramarowii* (Gamble) R.S.Rao & Hemadri and herbs of *Acmella paniculata* (Wall. ex DC.) R.K.Jansen, *Eriocaulon ensiforme* C.E.C.Fischer, *Impatiens tanyae* R.Kr.Singh, Arigela & Kabeer, *Peperomia dindygulensis* Miq., *Rostellularia simplex* Wight, *Sonerila travancorica* Bedd., *Utricularia reticulata* Sm. and *Zenkeria sebastinei* A.N.Henry & Chandrab. Populations are restricted to elevations above 1400 m in the northern part of the KMTR.

Conservation Status

This species comprises 252 mature individuals in 4 populations. We recommend a conservation status of critically endangered (CR) based on IUCN Red List Guidelines and Criteria (IUCN, 2019), on the basis of B1. Extent of occurrence (EOO) – 6.51 km^2 and B2 and Area of occupancy (AOO) – 0.203 km^2 (Figure 3).

Taxonomic affinity

Comparison of *M. parvifolium*, *M. varians* and *M. viswanathanii* is given in Table 1.

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Studies of the Homalomeneae (Araceae) of Peninsular Malaysia VIII: *Homalomena joanneae* [Chamaecladon Clade], a new locally endemic limestone-obligated species

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Abstract. *Homalomena joanneae* is described and illustrated as a new species of the Chamaecladon Clade restricted to the industrially threatened limestone of Gunung Kanthan, Kuala Kangsar, Perak, and compared with its probable nearest congener, *H. hendersonii* from Kelantan.

Keywords: *Homalomena* Chamaecladon Clade, taxonomy, Perak, Gunung Kanthan, Silurian-Devonian limestone.

INTRODUCTION

Homalomena remains the least well studied large genus of Asian Araceae, and of which the species of the Chamaecladon clade (*sensu* Wong et al. 2013) are perhaps the least well understood. This is partly because species of the Chamaecladon clade tend to be outwardly rather similar in appearance, especially as preserved specimens, and partly because along with producing some of the smallest blooms in the family, much of the key diagnostic data present in the usually tiny spadix is lost in herbarium specimens; thus, historical Types are for the most part uninformative.

The earliest accounts of *Homalomena* for Peninsular Malaysia are those of Hooker (1893), and Ridley (1907, 1925). These are now taxonomically unreliable as well as decidedly incomplete. Furtado (1939) attempted to untangle the taxonomy of *Homalomena* in the Indo-Malaysian region but, as has been noted in previous papers (e.g., Ng et al., 2011), succeeded only in further confusing an already difficult situation, especially so for the Chamaecladon clade. Following Furtado, no critical work was attempted until the early 2000s when a series of papers began to lay a tentative ground-work for tackling the taxonomy of Peninsular *Homalomena*: Baharuddin and Boyce 2005, 2010, 2011, Boyce and Wong 2017; Zulhazman et al. 2011, 2012. Ng et al. (2011) suggested an informal framework of higher classification and Mashhor et al. (2011) proposed a decidedly tentative checklist building upon that of Hay et al. (1995).

The current situation in Peninsular Malaysia is that for the most part species of the Chamaecladon clade are difficult to name to species with any degree of confidence, largely owing to the reasons noted above. Nevertheless, there are very clearly new species that warrant description ahead of a full revision. The latter, while obviously desirable, is for the present impracticable since time is not available to revisit all of the Type localities in order to establish the circumscription of the pre-existing species.

Here we describe one such species from the Silurian-Devonian limestone of Gunung Kanthan that initially was thought to be *Homalomena hendersonii* Furtado from the limestone of Kuala Betis, Kelantan, some 80km to the east, but which on flowering proved to neither match *H. hendersonii* nor to be applicable to any pre-existing species.

Geological formations in this paper are verified with Tate et al. (2008).

Homalomena joanneae S.Y. Wong & P.C. Boyce, **sp. nov.** (Figures 1 & 2A)

Type: Cultivated at Forest Research Institute Malaysia, 5 Oct. 2020, *Ong Poh Teck FRI 96468* (original collection Malaysia, Perak, Kuala Kangsar District, Chemor, Gunung Kanthan, Area D, 04°45’73”N, 101°07’25”E, 217m asl, *Joanne Tan Pei Chih s.n.*) (holotype KEP!; isotype KEP – spirit SC11647). (Figures 1 and 2A).

Diagnosis

Homalomena joanneae is overall most similar to *H. hendersonii*, but readily differentiated by the rather few, large, pale green pistilate florets with an obliquely inserted style/sigma (vs pistillate florets numerous, white with a symmetrically inserted style/stigma), a stigma scarcely wider than the style (vs stigma noticeably wider than the style), and an ascending (vs orthotropic) style, and subglobose pale creamy staminodes (vs staminodes teardrop-shaped, white). *Homalomena joanneae* also differs from *H. hendersonii* by pale cream somewhat lax staminate florets equalling the height of the pistillate florets (vs smaller, more numerous congested white stamens that are shorter than the pistillate florets).

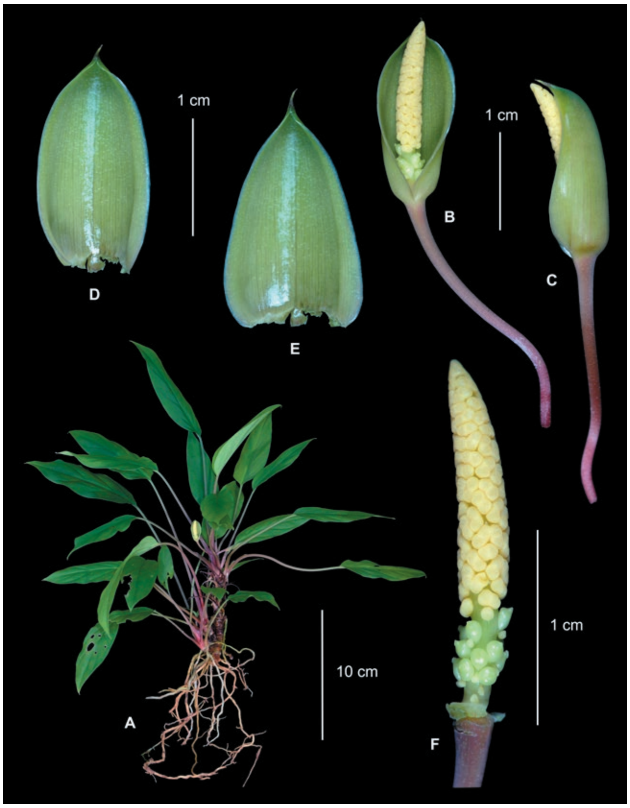

Figure 1. *Homalomena joanneae* (A) Cultivated flowering habit. (B) Bloom at pistillate anthesis. (C) Bloom at pistillate anthesis. (D) Spathe, artificially removed, natural form. (E) Spathe limb, slightly spread out. (F) Spadix at pistillate anthesis, spathe artificially removed. All from *Ong Poh Teck FRI 96468*.

Description

Small aromatic (terpenoids) herbs to c. 20 cm tall, although usually rather less. Stem epigeal, erect, older portions medium brown, partially clothed by the netted-fibrous remnants of old petiole bases, rooting from the nodes and from though the petiole bases; roots c. 1–2 mm diameter, tough, flexuous, whitish to pale brown, somewhat velvety. Leaves numerous, petioles erect, the older ones slightly spreading with the blades held more or less parallel to the ground; petiole 4–13 cm long, c. 2 mm diameter midway, dorsally narrowly channelled, pale green heavily suffused with pale maroon, especially in the lower half, microscopically velutinous; petiolar sheath 1.5–3 cm long, extending c. one-fifth length of the petiole, clasping at the base, width between both margins c. 1 mm, wings persistent; leaf blade lanceolate to elliptic oblong to ovate, 6–9.5 cm long, 3–4 cm wide, thinly coriaceous, microscopically scintillating-velutinous dark green adaxially, paler green abaxially, base cuneate, apex acute with a brief (c. 1.5 mm long)

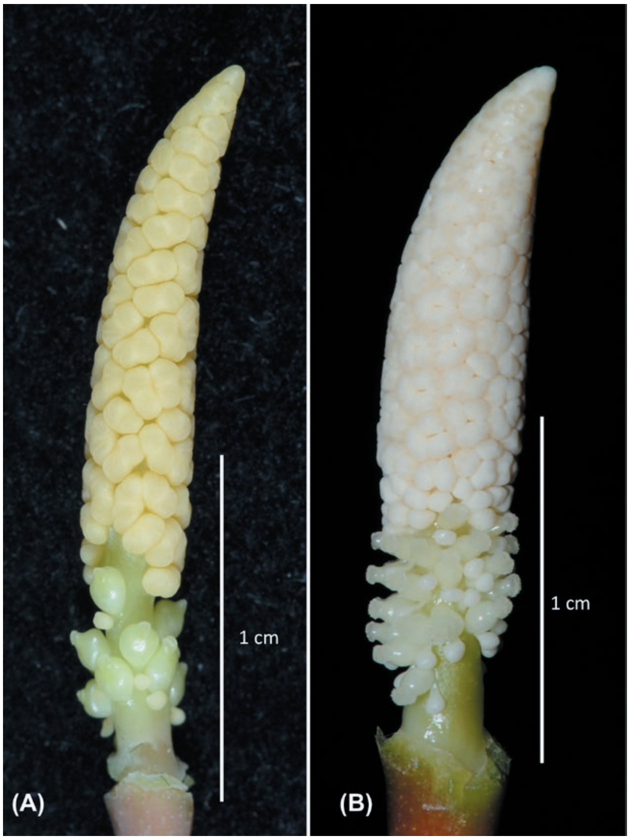

Figure 2. Spadix comparisons (A) *Homalomena joanneae* and (B) *Homalomena hendersonii.*

Figure 3. *Homalomena hendersonii. M.R.Henderson SFN29663* [SING] – HOLOTYPE. Image © Singapore Herbarium, used with permission.

tubule, margins smooth or slightly sinuous; midrib adaxially rather impressed, abaxially slightly prominent; primary lateral veins c. 4 on each side of midrib, adaxially impressed, abaxially slightly prominent, alternating with very much fainter regularly interspersed broken interprimaries, diverging at c. 35–60° from the midrib; secondary venation obscure, pellucid-striate; tertiary venation forming a faint darker tessellate reticulum most clearly visible adaxially; all veins running into a slightly thickened intramarginal vein. Blooms paired (always?), produced sequentially in a simple synflorescence; peduncle terete, slender, 2–3 cm long, c. 3 m diameter, green flushed pale maroon; spathe narrowly ellipsoid, not constricted, opening wide at anthesis, c. 2 cm long, 8 mm wide, with a terminal short mucro to c. 2 mm long, spathe gaping wide at anthesis with the margins spreading but seemingly not recurving, and opening far enough to expose the pistillate florets, then closing post staminate anthesis and persisting until basal dehiscence at fruit dispersal, exterior medium matte green with very faint longitudinal veins and minute scattered white speckles, interior similarly coloured but glossy, the margins hyaline. Spadix equalling spathe limb at opening and then extending to very slightly exceed spathe, c. 2 cm long, c. 3.5 mm diameter at mid-point, short stipitate, stipe c. 2 mm long, smooth, pale green; pistillate floret zone c. 5 mm long; pistils lax, broadly compressed ovoid, c. 1 mm tall × 0.8–0.9 mm diameter, pale greenish, style obliquely inserted on the upper surface (relative to the spadix axis), stigma capitate, hardly wider than the style, 0.3–0.4 mm diameter; each pistil with a single staminode situated on ventral side of the floret relative to the base of the spadix; interpistillar staminodes subglobose, c. 0.2 mm long pale creamy; staminate flower zone c. 1.3 cm long, tapering cylindrical, apex acute; staminate florets well-defined, somewhat lax, each consisting of two stamens, stamens rounded, c. 0.5 mm tall, 1–1.5 mm long × 0.5–0.8 mm wide, creamy white with the thecae tips very slightly transparent. Infructescence, fruit and seed not observed.

Eponymy

Named for Joanne Tan Pei Chih, formerly a research officer at the Forest Biodiversity Division, Forest Research Institute Malaysia (FRIM) from 2008 to 2020. Her expertise includes plant taxonomy in which she was actively involved with the flora survey in Gunung Kanthan, Perak. Joanne is also a horticulturist, previously maintaining a collection of rare and endangered plants at FRIM, in particular soft herbs such as *Begonia* that are difficult to maintain in cultivation.

Distribution and ecology

So far known only from the Gunung Kanthan where it occurs lithophytically on shaded Silurian-Devonian limestone at low altitudes.

Notes

Homalomena joanneae is associated with the Silurian-Devonian karst of the Kinta Valley (Ros and Ibrahim 2003), while *H. hendersonii* (Fig. 2B, 3) occurs under 80km distant at Kuala Betis, Kelantan, on the edge of the Gua Musang Formation of the Permo-Triassic Gua Musang Group (Kamal et al. 2016). Such distributions are typically representative of the incidences of highly localized floral endemism that is such a striking feature of the flora of Peninsular Malaysia.

Murray Ross Henderson (1899–1982) was among the first to draw particular attention to the limestone flora of Peninsular Malaysia (Henderson 1939). Later, a series of papers by Chin (1977, 1979, 1982) resulting from his Masters research under Ben Stone (1933–1994) presented the first comprehensive checklist for the Peninsular limestone flora, including the Araceae (Chin 1982: 176–183), and Kiew (2014) produced a checklist for the Batu Caves in Selangor, from where recently a taxonomically novel endemic *Schismatoglottis* was described (Wong and Boyce 2020).

For Gunug Kanthan, Tan et al. (2014) published three endemics [*Gymnostachyum kanthanense* Kiew (Acanthaceae), *Meiogyne kanthanensis* Ummul-Nazrah & J.P.C. Tan (Annonaceae) and *Vatica kanthanensis* Saw (Dipterocarpaceae)]. The highly precarious future of many of the most important limestone karst towers including for Gunung Kanthan was summarized most recently in Kiew et al. (2013). The mining operations for cement at Gunung Kanthan have already impacted very considerably on the hill (Figures 4 & 5).

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Figure 4. Drone photograph of Gunung Kanthan showing the still pristine southern flanks.

Figure 5. Drone photograph of Gunung Kanthan showing mining operation on the northern half.

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Studies on Homalomeneae (Araceae) of Borneo XXVII: A new *Homalomena* [Chamaecladon Clade] endemic to the Santubong Peninsula

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Abstract. A new species of *Homalomena* Chamaecladon Clade is described from the Santubong Peninsula, Kuching Division, Sarawak, to where it is endemic, and compared with *H. paucinervia* from the nearby Matang Massif, and with *H. atrox* from Sri Aman, the two other most similar described species from NW Borneo. All three species are illustrated from living plants, and keyed-out.

Keywords: Araceae, *Homalomena*, Chamaecladon clade, Sarawak, Borneo, Paleogene sandstones.

INTRODUCTION

Homalomena is one of the largest genera of aroids occurring on Borneo, with 64 accepted species, and with at least twice that number yet to be described (Boyce & Croat 2011). Species of the *Homalomena* Chamaecladon clade (*sensu* Wong et al. 2013) are distinctive by the spathe lacking a constriction and by having pistillate florets wherein the staminode is much shorter than the pistil. Currently the clade consists about 140 published names, of which about 40 are of unresolved status and 19 are confirmed synonyms. The clade occurs from Sumatera though to New Guinea, and as far north as southern Indochina. The principle areas of species' richness and diversity are Peninsular Malaysia and, especially, Sumatera wherein the diversity of form, especially epidermis ornamentation reaches extraordinary extremes (Wong et al. 2020). It is puzzling that Borneo, an island with a staggeringly rich aroid flora, appears to be much less provided for in species and with much lower diversity when it comes to the Chamaecladon clade.

Species of the *Homalomena* Chamaecladon clade (*sensu* Wong et al. 2013) occurring in NW Borneo pose taxonomic problems in part owing to misapplication of West Malaysian species' names to undescribed Bornean species and in part because species' boundaries remain poorly understood. The first species for the clade described from NW Borneo was *H. paucinervia* Ridl. (Ridley 1905), described from riverside rocks of the Matang Massif near Kuching. After that, save Furtado's stumbling attempt to clarify the taxonomy for *Homalomena* (Furtado 1939), no further taxonomic progress was made until the publication of *H. atrox* P.C.Boyce et al. (Boyce et al. 2010) for a facultative rheophyte from Batang Ai, Sri Aman Division, Sarawak.

Work began in earnest with Wong & Boyce (2020) describing two species, *Homalomena acuminata* (Ridl.) S.Y.Wong & P.C. Boyce and *H. ridleyi* S.Y.Wong & P.C.Boyce for plants long-confused with Peninsular Malaysian *H. griffithii* (Schott) Hook.f. [Chamaecladon clade]. Here we continue with a new species from the Santubong peninsular hitherto assigned to Ridley's *H. paucinervia* from Matang

As has been noted in previous papers (e.g., Hay 1998, Boyce and Wong 2015, Kartini et al. 2015; Wong and Boyce 2020) the extraordinarily complex surface geology of the island of Borneo is enormously important in the separation of species in aroid genera such as *Homalomena*, *Schismatoglottis*, and *Alocasia*, among others. Geology in this paper is specified based on Hutchinson (1989, 2005) and Tate (2001).

1. *Homalomena santubognensis* S.Y.Wong & P.C.Boyce, sp. nov.

Type: Malaysian Borneo. Sarawak, Kuching, Santubong N.P., Jungle Trail, Waterfall F1, 1°44'35.1"N 110°19'23.9"E, 175 m asl., 19 Sep 2020, *Wong Sin Yeng & P.C.Boyce AR-2438* (holotype SAR!; isotype SAR - spirit!). (Figure 1 and 2A).

Diagnosis

Homalomena santubognensis is most similar to *H. paucinervia* but readily distinguished by the overall stouter spadix (spadix width × length 4 mm × 1.9 cm [1:4.5] vs 3 mm × 1.95 mm [1:6.5]), by a stigma about half as wide as the ovary (vs equaling the ovary in width), by pistillate florets each with an oblong staminode (vs pistillate florets lacking staminodes), by petioles entirely green not stained deep red in the lower half, and by leaf blades abaxially semi-glossy pale green (not slightly glaucous). From *H. atrox*, the only other species in NW Borneo with lanceolate leaf blades, *H. santubongensis* is immediately distinct in being entirely glossy-glabrous (not microscopically pubescent), and by the smooth (not corrugated petiolar sheath).

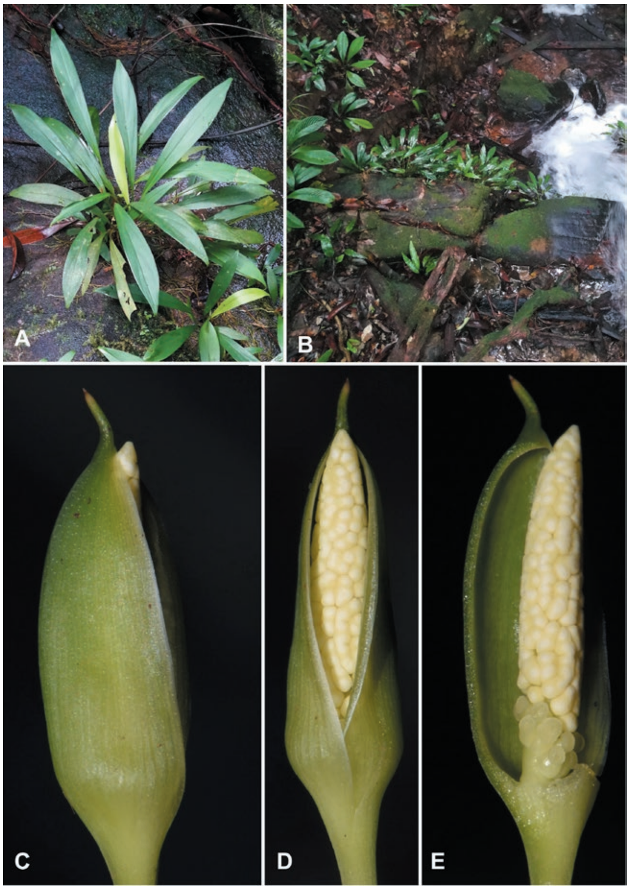

Figure 1. *Homalomena santubongensis* (A) Plant in habitat. (B) Habitat. (C & D) Bloom at pistillate anthesis. (E) Bloom at late pistillate anthesis, nearside of spathe artificially removed. A, C–E from *AR-2438*.

Description

Small strongly aromatic (terpenoids) Steensian rheophytes (Boyce and Wong 2019: 505 et seq.) up to c. 13 cm tall. Stem epigeal, erect and congested, in older plants occasionally becoming somewhat elongated and decumbent with the active tip ascending, rooting from the lower-most nodes and through the petiole bases; roots c. 1–3 mm diam., tough, flexuous, pale brown, slightly velvety, highly adhesive to substrate. Leaves up to c. 15 together per shoot, petioles erect to spreading; petiole 4–10 cm long, c. 2 mm diam. midway, dorsally very narrowly channelled, bright medium green, glossy glabrous; petiolar sheath 1.5–3 cm long, extending c. 1/4 length of the petiole, clasping at the base, width between both margins c. 1 mm, wings persistent; leaf blade narrowly elliptic to oblong-lanceolate, 6–12 cm long by 2–3 cm wide, thinly coriaceous, glossy, glabrous, medium green adaxially, abaxially paler green with the higher order veins darker-

Figure 2. Spadix comparisons (A) *Homalomena santubongensis* and (B) *Homalomena paucinervia.*

translucent, base cuneate, apex acute to acuminate with a brief (c. 1.5 mm long) tubular mucro, margins smooth; midrib adaxially slightly impressed, abaxially prominent; primary lateral veins 4–6 on each side of midrib, adaxially slightly impressed, abaxially alternating with much fainter much more numerous interprimaries, diverging at c. 40°–60° from the midrib; secondary and tertiary venation obscure; all veins running into a very slightly thickened intramarginal vein. Blooms up to 5 together, produced sequentially in a simple synflorescence; peduncle terete, slender, 2–5 cm long by c. 1 mm diam., coloured as for petiole; spathe ellipsoid, not constricted, at anthesis 2.2 cm long by 5–8 mm wide, with a terminal short mucro to 1–2 mm long, exterior glossy dark green with faint paler speckling, interior glossy medium green, spathe gaping at anthesis with the margins recurving and opening to expose the pistillate florets, closing post staminate anthesis and persisting until basal dehiscence at fruit dispersal. Spadix slightly exceeding spathe limb opening at anthesis, c. 1.9 cm long by c. 5 mm diam., shortly stipitate, stipe stout, c. 3 mm diam.; pistillate florets in two or three (incomplete) spirals, ovaries oblong-globose; stigmas about half as wide as ovary, ca. 0.3 mm diam., disc-like, sessile; associated staminodes oblong, sessile, cream, about tall as the ovary; staminate zone c. 1.5 cm long, apex acute; staminate florets each consisting of two stamens, anthers rounded, c. 0.5 mm tall, 1–1.5 mm long by 0.5–0.8 mm wide, dirty white with the tips pale; post anthesis blooms pendulous by bending of the peduncle. Infructescence ripening within the persistent spathe, exposed by the spathe shedding; fruit rather squat with the tops flattened by pressing on the spathe interior during development and the stigma impressed, whitish green with the stigma remnants brown, crushed fruits smelling faintly of overripe fruit/butyric acid; seed, very small, c. 1 mm long, oblong-ellipsoid, testa longitudinally ribbed.

Etymology

The species epithet is derived from the name of the type locality, plus the Latin suffix *-ensis*, indicating 'originating from'.

Distribution

Known only from the Santubong Peninsular where it is locally abundant.

Ecology

Rheophytic in the flood zone of relatively exposed Paleogene sandstone waterfalls and streambanks under humid lowland between 40–240 m asl.

Notes

With the addition of *Homalomena santubongensis* the described species of lanceolate-leaved *Homalomena* Chamaecladon clade now number three for NW Borneo. Although *Homalomena paucinervia* (Figure 3) is highly similar in overall appearance it is separated not only by the characteristics described here but also geographically and to an extent ecologically, with *H. santubongensis* restricted to the more open and somewhat drier Paleogene sandstones of the Santubong Peninsula, while *H. paucinervia* occurs on the much wetter Cretaceous sandstones of the Matang Massif. *Homalomena atrox* (Figure 4), from riverine shales on the Batang Ai drainages is distinct by the microscopically pubescent leaves and petioles.

The three species may be keyed out as follows:

1. Leaf blades and petioles microscopically pubescent; petiolar sheaths corrugated. Batang Ai drainage on shales........ ....***Homalomena atrox***

Figure 3. *Homalomena paucinervia* (A) Plant in habitat. (B) Habitat. (C & D) Bloom at pistillate anthesis. (E) Bloom at late pistillate anthesis, nearside of spathe artificially removed. A, C–E from *AR-2121*.

Leaf blades and petioles not microscopically pubescent; petiolar sheaths smooth **2**

2. Spathe opening wide to reveal the pistillate florets; spadix 4 mm × 1.9 cm [1:4.5]; stigma about half as wide as the ovary; pistillate florets each with an oblong staminode, petioles entirely green; leaf blades abaxially semi-glossy pale green. Paleogene sandstones. Santubong .... ***Homalomena santubongensis***

Spathe not opening wide enough to reveal the pistillate florets Spadix 3 mm × 1.95 mm [1:6.5]), stigma equaling the ovary in width, pistillate florets lacking staminodes, petioles stained deep red in the lower half, leaf blades abaxially slightly glaucous. Cretaceous sandstones. Matang Massif .... ***Homalomena paucinervia***

Additional specimen examined (paratypes)

MALAYSIA: Sarawak, Kuching, Santubong N.P,. Summit Trail, Waterfall F5, 1°44’34.8”N 110°19’19.9”E, 120 m asl., 22 Jul 2007 *P.C.Boyce, Wong Sin Yeng & S.Maclean AR-2104* (SAR).

Figure 4. *Homalomena atrox* (A) Bloom at late pistillate anthesis, nearside of spathe artificially removed. (B). Flowering plant. All from *AR-2375*.

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Typification and synonymy of the Atlantic Forest endemic species *Napeanthus primulifolius* (Gesneriaceae)

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Abstract. During the nomenclatural revision of Acanthaceae names described by Friar J.M.C. Vellozo in his *Florae fluminensis*, we realized that *Pedicularis acaulis* Vell. was conspecific with *Napeanthus primulifolius* (Gesneriaceae), a Brazilian Atlantic Forest endemic species. This study presents the complete and updated synonymy of *N. primulifolius*, including two new synonyms: *Pedicularis acaulis* and *Oreocharis notha* C.B.Clarke. We also propose a lectotype for *N. primulifolius* based on G.Raddi's specimens and *P. acaulis* based on Vellozo's original plate.

Keywords: *Florae fluminensis*, Giuseppe Raddi, historical plant collections, Vellozo.

INTRODUCTION

Napeanthus Gardner is a Neotropical genus of Gesneriaceae comprising 20 species (and possibly another ten undescribed ones) occurring in tropical rainforests of Central and South America (Leeuwenberg 1958; Weber 2004; Wiehler 1983). The genus shows a conspicuous number of species confined to the Andean foothills (Bolivia, Colombia, Peru, and Venezuela) and the Guiana Shield (Suriname, Guyana, French Guiana, and northern Brazil), besides two disjunct species in the Atlantic Forest of eastern Brazil (based on Leeuwenberg 1958; 1971; Skog 1974; Feuillet and Skog 2002). *Napeanthus* had already been previously pointed out by Leeuwenberg (1958) as a unique genus among New World Gesneriaceae, later allocated by Wiehler (1983) in its own tribe, Napeantheae Wiehler. Recently molecular phylogenetic studies support this monogeneric tribe as the first diverging lineage in the subfamily Gesnerioideae Burnett, recovered as sister to clade consisting of tribes Beslerieae Bartling & Wendl.f. + Titanotricheae Yamaz. ex W.T.Wang (Smith 2000; Möller and Clark 2013; Luna et al. 2019; Ogutcen et al. 2021). Species of *Napeanthus* are distinguished from other New World Gesneriaceae by being rosette herbs, generally acaulescent, with grouped stomata (in islands), calyx generally accrescent in fruit, stamens typically 4 (plus a staminodium), nectary absent, and dry capsules with loculicidal or septicidal dehiscence (Leeuwenberg 1958; Wiehler 1983; Weber 2004).

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Napeanthus was described by Gardner (1843) to accommodate a peculiar species from the Atlantic Forest of Serra dos Órgãos, in the State of Rio de Janeiro, Brazil, named *N. brasiliensis* Gardner. Nonetheless, an obscure species described in Oxalidaceae ca. 20 years before *Napeanthus* by Raddi (1820), *Oxalis primulifolia* Raddi [as "primulaefolia"], was pointed out by Sandwith (1956) as conspecific with *N. brasiliensis*, being the accepted and correct name for this species. Alongside *N. reitzii* (L.B.Sm.) Burtt ex Leeuwenb., they are the only known species of *Napeanthus* distributed in the Brazilian Atlantic Forest (Leeuwenberg 1958; Chautems 1991; Chautems 2003; Hinoshita et al. 2018).

During the preparation of the nomenclatural revision of Acanthaceae names described by Vellozo (1829, 1831) in his "*Florae fluminensis*," we detected that one of the names under *Pedicularis* L. (genus in which Vellozo described some Acanthaceae, following the Linnean arrangement "Didynamia, Angiospermia") did not match any taxa of this family known to Brazil. This intriguing species (i.e., *Pedicularis acaulis* Vell.) represented a species of *Napeanthus* (i.e., *N. primulifolius*, Gesneriaceae) based on the habit, leaves arrangement, leaf-blade morphology, indumentum color in the young leaves and other vegetative structures, and inflorescence and calyx morphology described and depicted by Vellozo (1829, 1831). In this study, we discuss the similarities between both names and justify the inclusion of *P. acaulis* as a synonym of de *N. primulifolius*. Additionally, when investigating the identity of *N. primulifolius*, we also found another synonym (i.e., *Oreocharis notha* C.B.Clarke) for this name, with the type specimen erroneously cited as being from the Philippines.

TAXONOMIC TREATMENT

Napeanthus primulifolius (Raddi) Sandwith, Webbia 12(1): 332. 1956

Type: Brazil, [Rio de Janeiro]: [Mun. Magé], "[...] nei Boschi di Mandiocca vicino ai torrenti" [woods of Fazenda Mandiocca, close to streams], [1817–1818], *G. Raddi s.n.* (lectotype, first-step designated by Leeuwenberg (1958, p. 347) as "holotype" and "isotype," second-step designated here PI barcode PI006250! = K negative No. 2697; isolectotypes: FI barcode FI005344!, FI barcode FI005345!, PI barcode PI006251! = K negative No. 2696). Figures. 1, 2A.

(≡) *Oxalis primulifolia* Raddi [as "*primulaefolia*"], Mem. Mat. Fis. Soc. Ital. Sci. Modena, Pt. Mem. Fis. 18: 400. 1820

(≡) *Acetosella primulifolia* (Raddi) Kuntze, Revis. Gen. Pl. 1: 93. 1891

(=) *Pedicularis acaulis* Vell., Fl. Flumin.: 270. 1829 [1825, publ. 7 Sep–28 Nov 1829]; Fl. Flumin. Icon. 6: t. 107. 1831 [1827, publ. 29 Oct 1831], *nom. illeg.* non *Pedicularis acaulis* Scop. (1771), **syn. nov.**

Type: Brazil, [Rio de Janeiro], [Mun. Paraty], "[…] silvis maritimis Pharmacopolitanis," [1782–1790], [preserved specimen presumably not extant] (lectotype [icon] original parchment plate of *Florae fluminensis* in the Manuscript Section of the Biblioteca Nacional, digital object cat. No. mss1198655_111; later published in Vellozo, Fl. Flumin. Icon. 6: tab. 107, 1831). Fig. 2B.

(=) *Napeanthus brasiliensis* Gardner, London J. Bot. 2: 14. 1843

Type: [Brazil] Brasiliæ, [Rio de Janeiro] Provinciæ Rio de Janeiro, "in sylvis densis primævis in montibus vulgo Serra dos Organos," February 1838, *G. Gardner 581* (lectotype designated by Leeuwenberg (1958, p. 348) as "holotype" K barcode K000601592 ex herb. Hook.!; isolectotypes BM barcode BM000992330 ex herb. Gardner!, BM barcode BM000992331 ex herb. Gardner!, CGE [cited by Leeuwenberg (1958)], E barcode E00155094!, FI barcode FI009832 ex herb. Webbianum!, G barcode G00365564!, G barcode G00365565 ex herb. Moric.! = F negative No. 26253!, K barcode K000601593 ex herb. Benth.! [annotated by Leeuwenberg (1958) as "isotype"], NY barcode NY00312996 ex herb. Meisner, comm. Schuttlenworth!, NY barcode NY00312997 ex herb. British Museum!, P barcode P00606336 ex herb. E. Drake!, W [cited by Leeuwenberg (1958)]).

(=) *Oreocharis notha* C.B.Clarke, Monogr. Phan. 5: 64. 1883, **syn. nov.**

Type: Brazil, [probably Rio de Janeiro] Manille? [on the original label, referring to Manila, Philippines], S.loc. indicato, s.d., [probably *A. Saint-Hilaire s.n.*] (holotype P barcode P04060096 ex herb. Bory! = E photo barcode E00155095!).

Description

Terrestrial perennial herbs, 10–25 cm high. *Stems* short, 3–15 mm long, cylindrical, glabrous, rhizomatous. Leaves rosulate, grouped at the apex of the stem; leaf blade sessile, 5.0–23.0 × 1.5–6.5 cm, oblong-spathulate or oblanceolate, apex acute, base subcordate, margin slightly crenate-serrate, sinuate, glabrous adaxially, sparsely

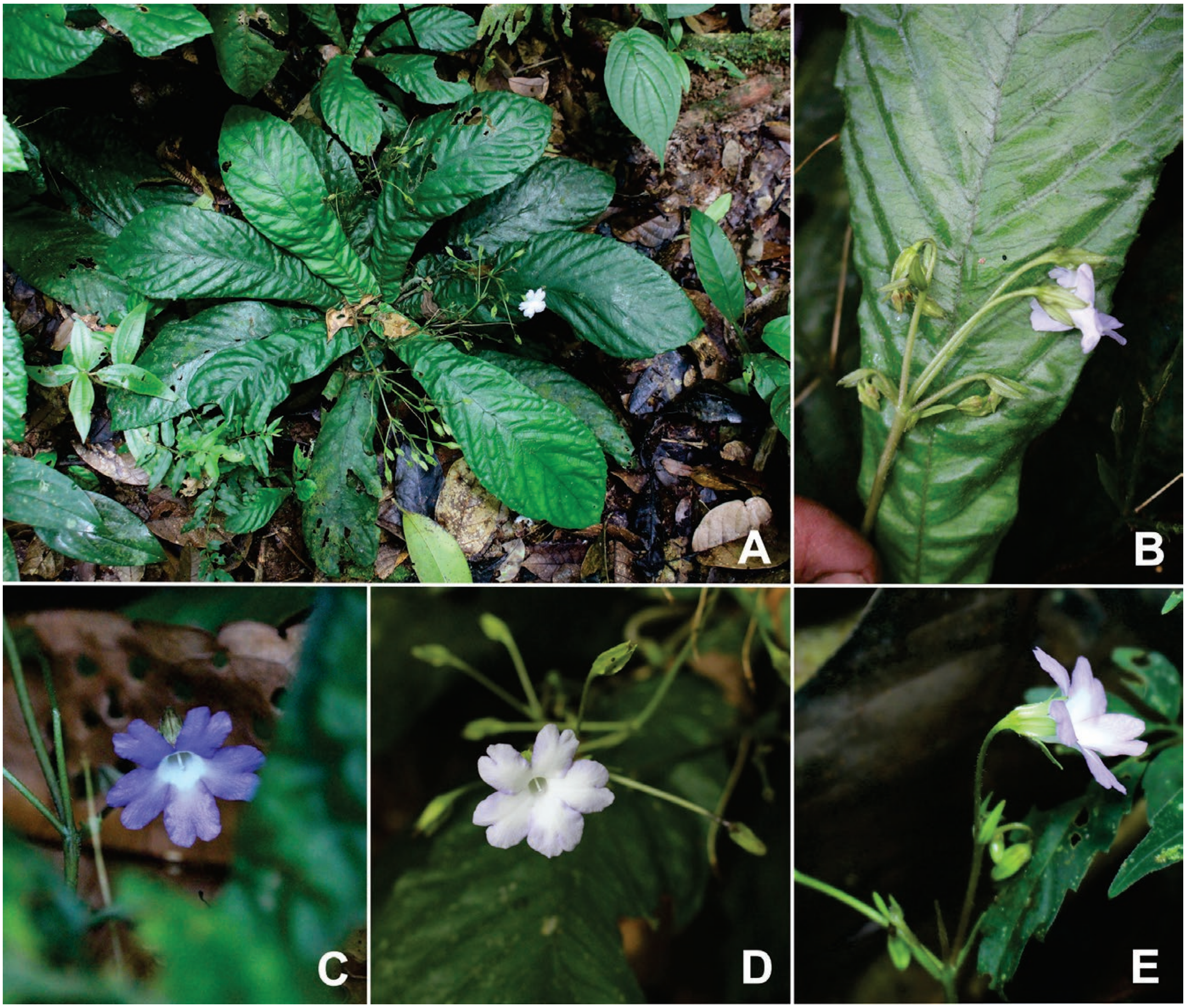

Figure 1. *Napeanthus primulifolius* (Raddi) Sandwith. A. Habit. B. Inflorescence detail. C. Flower at full anthesis. D. Older flower. E. Flower, lateral view showing the calyx lobes. Photographs taken by Nicco L. Faria.

pilose abaxially, trichomes concentrated on the veins, crass (papyraceous when dry); enervation with 6–9 pairs of secondary veins. Inflorescences simple, 4(–6)-flowered, or compound, with at least one of the lateral flowers replaced by a new peduncle; peduncles (or peduncles segments on compound inflorescences) 0.4–1.4 cm long, glabrescent; bracts 2, 3.0–12.0 × 1.0–4.0 mm, linear, oblong or lanceolate, apex acute or acuminate, puberulous on both surfaces, green; pedicels 1.5–6.0 cm long, slender, glabrescent. Calyx campanulate, green; lobes 5, 7.0–15.0 × 3.0–5.0 mm, equal, connate for ⅓ to ½ of their length, oblong, elliptic or lanceolate, spreading, inconspicuously veined, apex acuminate, margin entire, glabrous adaxially, puberulous abaxially, slightly fleshy, chartaceous when fresh, membranaceous when dry. Corolla early caducous, tubular, 10.0–15.0 × 5.0–6.0 mm, glabrous on both surfaces; tube 6.0–8.0 mm long, whitish; limb zygomorphic, spreading, lobes 5, 5.0–7.0 × 4.0–6.0 mm, unequal, obovate, apex 2-lobate, margin slightly crenate-serrate, sinuate, bluish or pale lilac, whitish at age. Stamens 4, included, didynamous; filaments 3.0–3.5 mm long, glabrous; anthers oblong-reniform, ca. 0.75 mm long; staminode 1, 0.8–1.0 mm long, glabrous. Ovary ovoid, glabrous; style 3.8–5.0 mm long, erect, glabrous; stigma obscurely 2-lobed; disk absent. Capsule 4.0–6.0 mm long, apiculate, 2-valved, loculicidal; valves glabrous; accrescent calyx erect, enlarged, becoming thicker, conspicuously veined. Seeds ellipsoid, brown, shining.

Figure 2. *Napeanthus primulifolius* (Raddi) Sandwith and its synonym *Pedicularis acaulis* Vell. A. The lectotype of *Oxalis primulifolia* Raddi, the basionym of *N. primulifolius*, at PI (barcode PI006250). Photograph courtesy of the Herbarium Horti Botanici Pisani (PI), Università di Pisa, reproduced with permission. B. The lectotype of *Pedicularis acaulis* from Biblioteca Nacional.

Iconography

Vellozo (1831, vol. 6: tab. 107), as *Pedicularis acaulis* Vell.; Hoehne (1970: tab. 189 and tab. 190), as *Napeanthus brasiliensis* Gardner; Chautems (2003: figure J, plate 1); Hinoshita et al. (2018: figure 1d–h).

Distribution and habitat

Napeanthus primulifolius is endemic to eastern Brazilian Atlantic Forest understories, especially on steep banks near streams where plants are rooted in earth among rocks. It was recorded in southern Bahia and in Serra do Mar Mountain Range (from Rio de Janeiro to northeastern Paraná).

Specimens examined

BRAZIL: **Bahia**: Mun. Arataca, Serra das Lontras, 12 February 2005 (fl, fr), *J.G. Jardim et al. 4375* (CEPEC, NY, RB); ibidem, RPPN Caminho das Pedras, 22 July 2005 (fr), *J.G.Jardim et al. 4726* (CEPEC); ibidem, Serra do Peito de Moça, 12 October 2005 (fr), *A.M.A.Amorim et al. 5283* (CEPEC); ibidem, Serra do Peito de Moça, 14 April 2006 (fr), *A.M.A.Amorim et al. 5781* (CEPEC); ibidem, Serra das Lontras, 29 April 2006 (fl, fr), *A.M.A.Amorim et al. 5978* (CEPEC); ibidem, 21 January 2007 (fl, fr), *R.A.X. Borges et al. 596* (CEPEC, NY); Mun. Buerarema, rod. São José da Vitória – Una, 12 May 1999 (fr), *A.M.A.Amorim et al. 3065* (CEPEC, NY); Mun. Camacã, 21 January 1971 (fl, fr), *T.S.Santos 1384* (CEPEC, US); ibidem, RPPN Serra Bonita, 2 February 2005 (fr), *A.M.A. Amorim et al. 4770* (CEPEC, NY); ibidem, 29 October 2005 (fr), *A.M.A.Amorim et al. 5427* (CEPEC); ibidem, 4 December 2007 (fl), *M.M.M.Lopes et al. 1557* (CEPEC); Mun. Santa Luzia [= Mun. Camacã], Serra da Onça, 21 November 1996 (fl, fr), *W.W.Thomas et al. 11382* (CEPEC); Mun. Una, Serra dos Quatis, 21 February 1986 (fr), *T.S.Santos & E.J.Judziewicz 4103* (CEPEC); ibidem, Serra Javi, 10 March 1986 (fr), *T.S.Santos et al. 4226* (CEPEC, US). **Paraná:** Mun. Guaraqueçaba, Rio do Costa, 4 February 1971 (fr), *G.Hatschbach 26267* (MBM, MO); ibidem, Salto Morato, 15 November 1993 (fl), *G.Hatschbach & J.M. Silva 59775* (MBM); ibidem, Morro do Bronze, 12 February 2002 (fl), *J. Carneiro 1309* (MBM). **Rio de Janeiro:** S. loc. indicato, s.d. (fl), *Glaziou 1075* (P); S.loc. indicato, 1821 (fl), *Langsdorff s.n.* (P barcode P03509121 ex herb. Richard); [Mun. Duque de Caxias], estrada Rio – Petropolis, 5 May 1972 (fl), *D.Sucre & T.Soderstron 9095* (RB); ibidem, Xerém, 22 March 1950 (fl, fr), *Brade & A.P. Duarte 20252* (RB); [Mun. Engenheiro Paulo de Frontin], Palmeiras, 13 January 1877 (fl), *Glaziou 8835* (P – 2 sheets); Mun. Guapimirim, Granja Monte Olivete, 18 January 1995 (fl, fr), *J.M.A.Braga et al. 1709* (RB), ibidem, Estrada das Andorinhas, 20 December 1995 (fr), *J.A.LiraNeto et al. 189* (RB); Mun. Lídice, estrada Angra dos Reis – Lídice, 16 March 1978 (fr), *V.F. Ferreira et al. 326* (RB); [Mun. Magé], [Fazenda] Madiocca, s.d., *Riedel s.n.* (LE, NY); ibidem, [...] prés Mandioca, 1816–1821 (fl), *A.Saint-Hilaire s.n.* (P barcode P03509114); ibidem, Serra dos Órgãos, 16 July 2017 (fr), *J.M.A.Braga 17-042* (RB); Mun. Mangaratiba, Reserva Ecológica Rio das Pedras, 30 November 1996 (fl, fr), *M.G.Bovini et al. 1104* (RB); ibidem, 9 December 1997 (fl, fr), *R.C.Lopes et al. 86* (RB); ibidem, 16 March 2001 (fr), *T.C.C.Lopes et al. 11* (RB); [Mun. Nova Friburgo], [Macaé de Cima] Alto Macahé, 15 June 1891 (fl), *Glaziou 18412* (P, R); ibidem, 30 November 1891 (fl), *Glaziou 19745* (P); [Mun. Nova Iguaçu], Serra do Tinguá, 11 February 1943 (fl, fr), *F.Guerra s.n.* (RB 47949); ibidem, Reserva Biológica do Tinguá, 17 January 2002 (fl), *M.G.Bovini et al. 2143* (RB); ibidem, 22 October 2002 (fl), *L.C.Giordano et al. 2585* (RB); Mun. Paraty, estrada Paraty – Cunha, 19 June 1978 (fr), *G.Martinelli 4652* (RB); ibidem, Fazenda São Roque, 2 August 1988 (fr), *M.C. Marques 72* (RB); ibidem, divisa dos estados Rio de Janeiro – São Paulo, 12 April 1991 (fr), *L.S.Sarahyba et al. 812* (RB); ibidem, Patrimônio, 7 July 1992 (fr), *L.C. Giordano et al. 1478* (RB); ibidem, Laranjeiras, 8 December 1993 (fr), *T.Konno et al. 388* (RB); ibidem, Morro do Corisco, 8 March 1994 (fr), *C.Duarte 21* (RB); ibidem, Apa-Cairuçú, 12 February 2003 (fr), *M.G.Bovini & M.Nadruz 2259* (RB); Mun. Petrópolis, Serra da Estrella, 16 June 1937 (st), *J.G.Kuhlmann 123* (RB); Mun. São Fidélis, Poço Parado, 11 May 2012 (fr), *M.Perret et al. 73* (VIES); [Mun. Teresópolis], Serra dos Órgãos, 10 December 1948 (fl), *A.P.Duarte & E.Pereira s.n.* (RB 65302). **São Paulo:** Mun. Cunha, Parati – Cunha, 1 March 1984 (fl, fr), *A.Chautems & G.Martinelli 123* (US); Mun. Peruíbe, Estação Ecológica Juréia-Itatins, 29 May 1996 (fr), *L.P.Queiroz & R.Belinello 4526* (HUEFS, SP); [Mun.] Santos, May 1875 (fr), *Mosén 3789* (P ex herb. Glaz.); Mun. São Miguel Arcanjo, Parque Estadual Carlos Botelho, 20 April 2002 (fr), *S.Bortoleto et al. 49* (ESA); ibidem, 8 December 2004 (st), *A.O. Araujo 470* (ESA); Mun. São Sebastião, Parque Estadual da Serra do Mar, 20 April 2000 (fr), *J.P.Souza et al. 3312* (ESA, MBM, SPF, UEC); Mun. Sete Barras, Parque Estadual de Carlos Botelho, 21 April 2002 (fr), *R.Farias et al. 655B* (ESA); Mun. Ubatuba, 1987 (fr), *Edna (SUDELPA) s.n.* (SPF 67679); ibidem, Parque Estadual da Serra do Mar, 15 January 1990 (fl), *F.C.P.Garcia et al. 549* (ESA, IAC); ibidem, Picinguaba, 13 November 1990 (fl, fr), *R.Maquete et al. 287* (IBGE, HRB, RB); ibidem, 2 December 1993 (fl), *L.Rossi & G.L.Esteves 1373* (SP, PMSP); ibidem, Estação Experimental do IAC, 17 November 1997 (fl), *C.Kameyama et al. 113* (SPF); ibidem, Parque Estadual da Serra do Mar, 21 January 2001 (fl), *P.Fiaschi & A.Lobão 583* (SPF); ibidem, Picinguaba, 29 May 2014 (fl, fr), *G.Colletta et al. 1707* (ESA); 29 May 2014 (fl), *G.Colletta et al. 1708* (ESA); ibidem, 29 May 2014 (fl), *G.Colletta et al. 1719* (ESA).

Taxonomic and nomenclatural notes

Vellozo (1829) described four species under *Pedicularis* L. (currently placed in Orobanchaceae) in his "*Florae fluminensis*" following the Linnaean arrangement "Didynamia, Angiospermia." Three of them corresponded to species of Acanthaceae, and one of them, *Pedicularis acaulis* Vell., which was annotated by Vellozo (1829) as of doubtful placement and possibly belonging to a different genus, does not. *Pedicularis acaulis* Vell. is a later homonym of *P. acaulis* Scop., an accepted name in Orobanchaceae for an alpine species from the Italian Alps to the northwestern mountains of the Balkan Peninsula (Mayer 1972). Since the description of *P. acaulis* Vell., this name has never been mentioned in any taxonomic treatment for Brazilian Lamiales and remained forgotten until this moment (pers. observ.). However, when we analyzed the original description (Vellozo 1829) and the later published original plate (Vellozo 1830) hosted at Biblioteca Nacional [National Library of Brazil] (Fig. 1B), we realized that some morphological characters, i.e., rosette habit, acaulescent stems, sessile leaves, cymose inflorescence simple or compound (with at least one of the lateral flowers replaced by a new peduncle), and the calyx lobes overlapping in the margin, matched those from the small gesneriad genus *Napeanthus*. Of the only two *Napeanthus* species in eastern Brazil, i.e., *N. primulifolius*, which occurs from Bahia to northeastern Paraná, and *Napeanthus reitzii* (L.B.Sm.) B.L.Burtt ex Leeuwenb.,

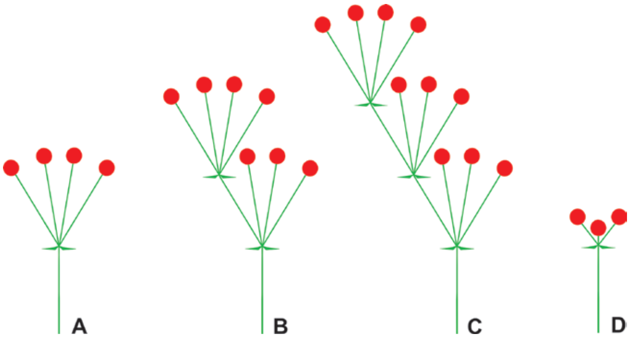

Figure 3. Inflorescences schemes of the two species of *Napeanthus* Gardner from Eastern Brazil. A–C. *Napeanthus primulifolius* (Raddi) Sandwith. D. *Napeanthis reitzii* (L.B.Sm.) Burtt ex Leeuwenb.

from Paraná and Santa Catarina], *P. acaulis* Vell. is conspecific with *N. primulifolius*, due to their rosette habit, acaulescent, pseudoverticillate leaves grouped at the stem apex, cymose inflorescences simple (often 4-flowered) or compound (with at least one of the lateral flowers replaced by a new peduncle) (Fig. 3A–C), flowers with long pedicels, and calyx lobes elliptical. *Napeanthus reitzii* is a herb with elongated stems, leaves distributed along the stem (with relatively short internodes), inflorescence cymose simple, 3-flowered (dichasium) (Fig. 3D), flowers with short pedicels, and calyx lobes trullate. Based on these morphological characters and geographic distribution, we propose the synonymy of *P. acaulis* Vell. under *N. primulifolius*. Furthermore, because there are no preserved specimens of Vellozo's names published in "*Florae fluminensis*" (see Lima 1995) and the illustrations (i.e., Vellozo 1831) were published after the protologue (i.e., Vellozo 1829) and are not considered part of the author's original material, in accordance with the Art. 9.4 and related of the International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) – ICN (Turland et al. 2018), we chose Vellozo's original plate as the lectotype.

Leeuwenberg (1958) referred to G. Raddi's specimens deposited at PI herbarium only as a "holotype" and "isotype," without any reference to the herbarium catalog number or even without any explicit indication in the sheets. Thus, we chose one of these specimens as a second-step lectotype, according to Art. 8.1 and 9.17 of the ICN (Turland et al. 2018).

When Clarke (1883) described *Oreocharis notha*, he was unsure of where this specimen was collected (possibly from Manila, Philippines) and the generic placement of this species, indicated in the protologue with a question mark. This author also pointed out that the long calyx and ovoid ovary in this species were different from other *Oreocharis* Benth. In fact, the calyx with long lobes accrescent in fruit is not found in any known species of *Oreocharis* s.str., not even in genera recently synonymized by Möller et al. (2011), which had calyx lobes shorter than the corolla. On the label of the specimen studied by Clarke (1883), housed at P herbarium, there is the following handwriting, possibly written after this author: "*Napeanthus, ex h. Bory, A.S.-H.* [August Saint-Hilaire], *Brasilia!*." It is likely to be a duplicate of a gathering of A. Saint-Hilaire incorporated into Bory's collection for being an endemic species to eastern Brazil and unlikely cultivated as ornamental in the Philippines. Also, the *Napeanthus* specimen in the Saint-Hilaire collection and the type of *Oreocharis notha* in Bory's collection, both at P, show inscriptions with the same handwriting.

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A numerical approach to the taxonomy of some species of the Subtribe Cassiinae in Nigeria

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Abstract. Twelve morphological parameters from the leaves, fruits, and pedicel of fifteen (15) species of the subtribe Cassiinae were studied using the methods of numerical taxonomy. Characters such as leaflet length, leaflet width, and leaflet length/width ratio contributed significantly in the delimitation of the species studied. While *C. italica* and *Ch. mimosoides* are the most closely related taxa, *C. fistula* and *C. singueana* appear to be the most distantly related as reflected by the cluster coefficients. Further illustrations as revealed by the dendrogram and scatter plot generated placed the 15 studied species into three groups. While we acknowledge the relevance of phylogenetic analysis in taxonomic studies as it is in recent times, we strongly support the application of numerical taxonomy to compliment findings.

Keywords: Custer analysis, fruits, Cassiinae, leaves, PCA, Numerical taxonomy.

INTRODUCTION

Cassia Linn. is a very large genus in the subtribe Cassiinae, which is comprised of about 500 to 600 species (Airy-Shaw 1973; Saheed and Illoh 2010). It is the largest genera in the sub family Caesalpinioideae, and ranks among the 25 largest genera of the dicotyledons as reported by Irwin and Turner (1960). In West Africa, it consists of about 22 species aside from the introduced or cultivated species (Hutchinson and Dalziel 1958; Saheed and Illoh, 2010; Kolawole 2017). The genus includes trees, shrubs, and herbs and has a pantropical distribution, but very few in Asia (Irwin and Barneby 1981). It is characterized by the possession of evenly-pinnate leaves with stipules of various types; flowers slightly irregular, solitary, racemose or paniculate; stamens 5 or 10, frequently unequal; fruits sessile or stalked, terete or flattened and often partitioned crosswise (Irwin and Barneby 1982; Larsen et al. 1984). Bentham (1871) in his revision of the genus indicated that it is comprised of three distinct groups. Three separate genera, i.e. *Cassia sensu* *stricto*, *Chamaecrista* Moench, and *Senna* Mill. were recognized based on characters of filaments and the presence or absence of bracteoles (Irwin and Barneby 1981, 1982; Lock 1988; Larsen 1993; Hou et al. 1996; Mabberley 1997; Singh 2001). These three genera belong to the tribe Cassieae and subtribe Cassiinae of the Leguminosae-Caesalpinioideae.

Numerical taxonomy or taximetrics refers to the application of various mathematical procedures to numerically encoded character state data for plant species under study. This approach results in a classification based on a greater number of characters from sets of data (multivariate) to develop an entirely phenetic classification of maximum predictivity as put by Pandey and Misra (2009).

Morphometric techniques have long been established as valuable tools for exploring the development, population differentiation, and systematics of plants (Bookstein et al. 1985; Wiens 2000; Forey and MacLeod 2002; Jensen 2003; Bateman and Rudall 2006). Authors have also applied this techniques in the study of *Ficus* species (Sonibare et al. 2004), *Acalypha* species (Soladoye et al. 2008), *Indigofera* species (Soladoye et al. 2010a), *Jatropha* species (Kolawole et al. 2016), *Berlinia* species (Chukwuma et al. 2016), accessions of *Senna didymobotrya* (Jeruto et al. 2017) etc. In morphometric studies however, diagnostic characters are essential. These characters are constant within a group but vary between groups and could be used to identify natural plant groups from several others of similar ranking (Davis and Heywood 1963; Kent and Coke 1992; Jeruto et al. 2017). Morphological characters are helpful in the identification and delimitation of taxa and genera into tribes and subfamilies (Yousuf et al. 2008), and these characters have been recognized as basic criteria for identification and authentication of plants (Sultana et al. 2011).

Boonkerd et al. (2005) investigated some species of *Cassia* L. that were difficult to determine due to morphological complexes. In order to investigate the taxonomic status of this genus, morphological characters from 508 specimens of 18 taxa were analyzed using numerical cluster analysis and canonical discriminate analysis. A total of 32 vegetative and reproductive morphological characters were focused on in this analyzes. As a result of numerical cluster analysis, they suggested *Cassia* s.l. can be separated into four groups, *viz. Chamaecrista, Senna alata, Senna,* and *Cassia* s.str. with an average taxonomic distance of 1.30. His result was supported by Irwin and Barneby's (1981) classification. Moreover, the filament length, fruit length, and ovary stalk are useful quantitative characters for discriminating the three genera and further grouping.

Many members of the subtribe Cassiinae are economically important. *Senna* species could be stimulant laxatives and used for the treatment of constipation (Bradley 1992). Significant inhibitory activity of *Senna* species against leukemia has also been documented in mice as reported by Jimoh et al. (2013). In Nigeria, the plants are used for treating eczema and other skin defects caused by fungal infections (Akinremi et al. 2000). The leaves are also prepared into vegetable soup for smallpox and measles. The leaves of *Senna podocarpa* (Guill. and Per.) Lock. are extensively known for their anti-gonorrhoeal and purgative properties as well as being a guinea worm and sore-healing remedy among the Igbos in Nigeria. A concoction of the fresh leaves is used in the treatment of syphilis (Gomes et al. 1997), herpes, and swine fever (Silva et al. 1997) and as purgative and for repelling or killing insects such as termites, bed bugs and mosquitoes (Elujoba et al. 1999).

Taking into consideration the close affinities existing between members of the sub-tribe Cassiinae, the present study aimed at using numerical methods to examine the differences and similarities in the morphological characters used to delimit some species of this legume group. The chief goal of our study is to determine the traits that would contribute strongly to the delimitation of the taxa based on their similarities.

MATERIALS AND METHODS

Selection of species

Fifteen species of the subtribe Cassiinae were selected based on availability, and employed in this study. These include *Cassia fistula* L., *Cassia italica* Mill., *Cassia sieberiana* DC., *Cassia singueana* (Del.) Lock., *Chamaecrista mimosoides* (L.) Greene, *Chamaecrista rotundifolia* (Pers.) Greene, *Senna alata* (L.) Roxb, *Senna biflora* L., *Senna hirsuta* (L.) Irwin & Barneby, *Senna obtusifolia* (L.) Irwin & Barneby, *Senna occidentalis* (L.) Link., *Senna podocarpa* (Guill. & Per.) Lock, *Senna siamea* (Lam.) Irwin & Barneby, *Senna sophera* (L.) Roxb. and *Senna spectabilis* (DC.) Irwin & Barneby.

Plant collection, preparation and authentication of herbarium specimens

Field trips were undertaken to different ecological zones of Nigeria for the collection of available species of Cassiinae (Table 1). Fresh specimens for the study were collected from a variety of sources such as open vegetation, roadsides, private gardens, and bushy areas. Upon

Table 1. Voucher specimens prepared for the Cassinae species studied.

S/N	Species	Places of Collection/Locality	Voucher number	Latitude (N)	Longitude (E)
1	*Cassia fistula* Linn.	Beside Block 10, UNILORIN main Campus, Ilorin	FHI 109792	8.496642	4.542143
2	*Cassia italica* Mill.	GSU campus, Gombe Metropolis, Gombe State	FHI 109966	10.306208	11.164688
3	*Cassia sieberiana* DC.	Beside Sports Centre, OAU Campus, Ile Ife, Osun State.	FHI 109967	7.116667	3.616667
4	*Cassia singueana* (Del.) Lock.	Along Kashere –Alhaleri road, Kashere, Gombe State.	FHI 109965	9.9	11.016667
5	*Chamaecrista mimosoides* (L.) Greene	Ori Eru Village, Asa LGA, Kwara State.	FHI 109868	8.422145	4.44047
6	*Chamaecrista rotundifolia* (Pers.) Greene	Tunfure Cattle village, Along Airport Road, Gombe.	FHI 109788	10.619407	13.075471
7	*Senna alata* (L.) Roxb	Sekona village, Ede South LGA, Ede	FHI 109787	7.65824	4.457619
8	*Senna biflora* Linn.	Infront of Olu of Akoda Palace, Akoda, Ede, Osun State	FHI 109867	7.31443	4.263754
9	*Senna hirsuta* (L.) Irwin & Barneby	In front of FUOYE main gate, Oye Ekiti, Ekiti State	FHI 109869	7.79976	5.320353
10	*Senna obtusifolia* (L.) Irwin & Barneby	Along Pindinga- Kashere road, Akko LGA, Gombe State	FHI 109790	9.813505	10.92536
11	*Senna occidentalis* (L.) Link.	Gaa Imam Area, Along Ajase-Ipo Road, Ilorin, Kwara State	FHI 109866	8.5	5
12	*Senna podocarpa* (Guill. & Per.) Lock	U I Botanical Nursery, Dept. of Botany, U I, Ibadan.	FHI 109870	7.4477245	3.8967116
13	*Senna siamea* (Lam.) Irwin & Barneby	Behind Federal High Court, GRA, Gombe State.	FHI 110012	10.719038	13.356643
14	*Senna sophera* (L.) Roxb.	Along Agah Ganmo Road, Ifelodun LGA, Kwara State	FHI 109785	8.546826	5.090122
15	*Senna spectabilis* (DC.) Irwin & Barneby	In front of LAUTECH Senate Building, Ogbomoso, Oyo State.	FHI 109965	8.1700515	4.2664348

collection of fresh plants, voucher specimens were prepared according to established protocols (Soladoye et al. 2010a,b; Kolawole et al. 2016; Chukwuma et al. 2016), and authenticated at the Forest Herbarium Ibadan (FHI) while the duplicates were deposited at Ilorin University Herbarium. FHI is listed in Holmgren et al. (1990).

MORPHOMETRIC ANALYSIS

This was based on morphological measurements from fresh and previously deposited herbarium specimens representing 15 species within the tribe Cassinae. Field observations were made from individual species of several populations across the country. Representative photographs of individual plant species were taken using a 16.0 megapixels Sony digital camera. Specifically, twenty-five accessions of each species were examined for their morphological characteristics. Some traits which were difficult to assess accurately or were unsuitable for rapid and accurate scoring were eliminated. Quantitative morphological data such as leaflet length, leaflet width, petiole width, petiole length, pedicel length, pedicel width, fruit length, fruit width, etc., were taken using thread, a standard metre rule and an electronic digital calliper (Titan 3105) graduated in millimetres (later converted to centimetres). These measurements were compiled for each Operational Taxonomic Unit (OTU) and the corresponding mean values of the recorded characters were carefully calculated and keyed into a Microsoft Excel spreadsheet. They were thereafter subjected to Principal Components Analysis (PCA) and Cluster Analysis using Paleontological Statistics (PAST) and SPSS 20.0 statistical software.

RESULTS

Species distribution

Cassinae species exhibit a wide distribution accros all geo-ecological zones of Nigeria but appears to be

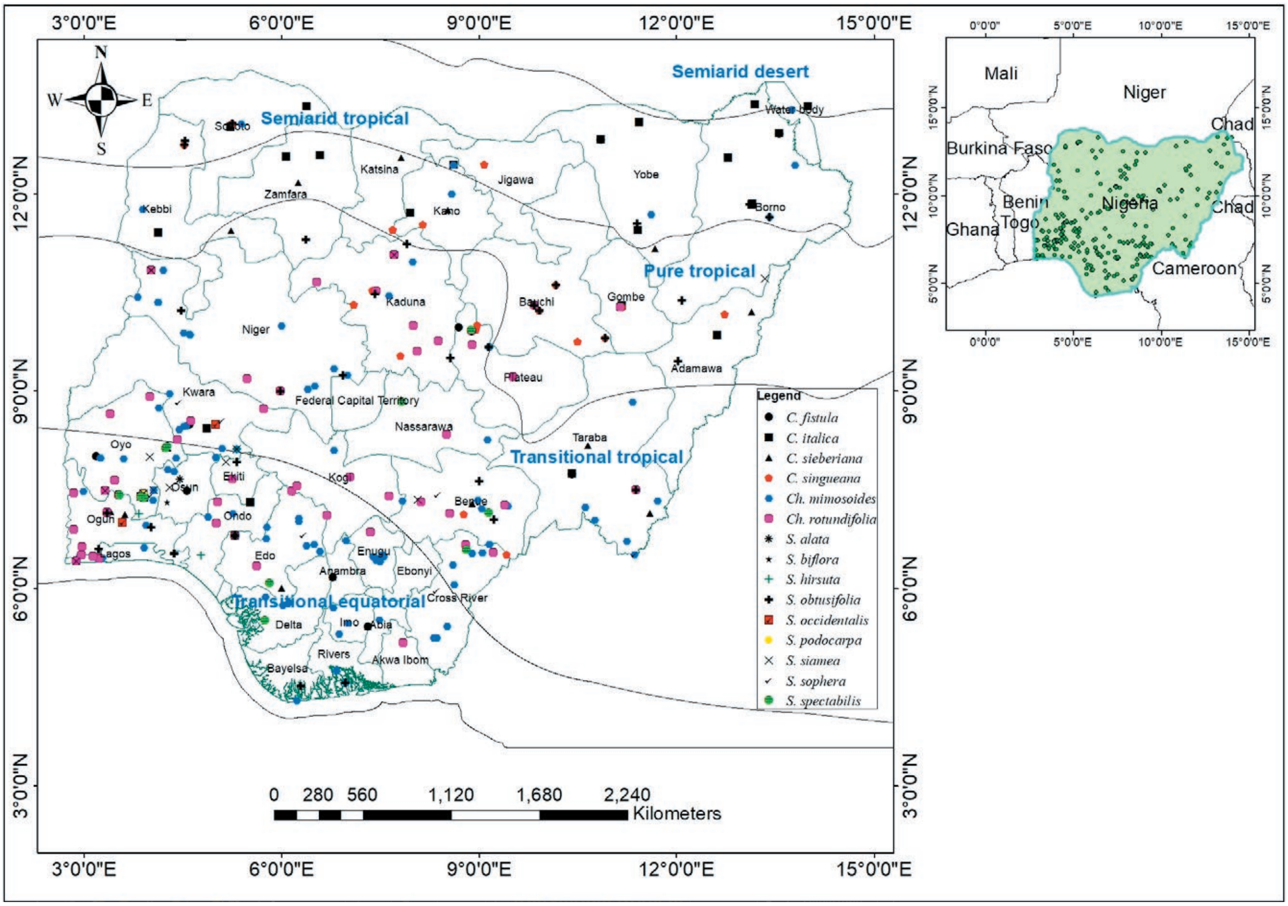

Figure 1. Distribution of the subtribe Cassinae in Nigeria.

more abundant in southern Nigeria which is characterised by a transitioal equatorial climatic zone (Figure 1). This area recieves more rainfall that other zones, and may profer a more suitable habitat for the growth of the species studied.

Quantitative traits of the species

The morphological appearance of each representative species is shown in Figure 2, while the quantitative features are listed in Table 2. The highest leaflet length was observed in *Senna alata* (12.73 ± 3.29 cm) while the lowest was recorded in *Chamaecrista rotundifolia* (1.62 ± 0.13 cm). The least leaflet width was recorded in *Chamaecrista mimosoides* (0.59±0.02 cm) while the highest was observed in *Cassia fistula* (6.69 ± 0.51 cm). Leaflet length/width ratio measured the highest in *Chamaecrista mimosoides,* with a mean value of 6.95 ± 1.33 cm while the least mean value of 1.02 ± 0.09 cm was observed in *Chamaecrista rotundifolia*.

The longest petiole was observed in *Senna podocarpa* (9.1 ± 0.75cm) while the shortest was obtained in *Senna siamea* (0.24 ± 0.05 cm). The highest and the least petiole width was obtained in *Cassia italica* (2.66 ± 0.44 cm) and *Senna siamea* (0.09 ± 0.01cm) respectively. The least ratio of petiole length and width was obtained in *Cassia italica* (0.89 ± 0.19 cm) the highest is recorded in *Senna sophera* (27.45 ± 2.13 cm).

Furthermore, *Cassia sieberiana* had the longest fruit (53.19 ± 3.12 cm) while the shortest was observed in *Chamaecrista rotundifolia* (2.92 ± 0.22 cm). Conversly, the highest fruit width was recorded in *Cassia sieberiana* (1.44 ± 0.09 cm) and the least was in *Chamaecrista rotundifolia* (0.34 ± 0.02 cm). The highest and least ratio of the fruit length and width were recorded in *Senna obtusifolia* (38.96 ± 0.02 cm) and *Senna biflora* (4.54±0.39 cm) respectively.

The longest pedicel was observed in *Cassia sieberiana* (3.97 ± 1.96 cm) while the shortest was in *Senna biflora* (0.28 ± 0.35 cm). The highest pedicel width was recorded in *Senna occidentalis* (0.27 ± 0.14 cm) and the

Figure 2: Morphology of the species of the subtribe Cassinae studied. **A**- *Cassia fistula,* **B**- *Cassia italica,* **C**- *Cassia sieberiana,* **D**- *Cassia singueana,* **E**- *Senna alata,* **F**- *Senna biflora,* **G**- *Senna hirsuta,* **H**- *Senna obtusifolia.*

least was in both *Cassia fistula* and *Senna spectabilis* with 0.02 ± 0.04 and 0.02 ± 0.01 respectively. The highest pedicel length/width ratio was observed in *Cassia singueana* (83.04 ± 7.31 cm), while the least wasin *Senna biflora* (2.29 ± 0.52 cm) (Table 2).

Cluster analysis of the studied species of subtribe Cassiinae using morphological characters

Similarity indices for the studied species of the subtribe Cassiinae based on euclidean distance for the morphological traits is presented in Table 3. The least coefficient was observed between *C. italica* and *Ch. mimosoides* (11.52), followed by *S. alata* and *S. occidentalis* (11.96), while the highest were observed between *C. singueana* and *S. biflora* (82.85). The species are divided into three (3) clusters (Figure 3, Table 4). The first cluster comprises 11 species, while the second and third clusters are represented by 2 species each. The result of the agglomeration schedule (Table 4) showed that the most closely related taxa are *C. italica* and *Ch. mimosoides* with a coefficient of 132.743 while the most distantly related are *C. fistula* and *C. singueana* with a coefficient of 4225.493. The variance in the observed morphological traits using principal component analysis is also presented in Table 5. As revealed, only four (4) components contributed 80.5% of the total variance, while the remaining eight (8) were uninformative and contributed insignificantly to the delimitation of the taxa studied.

The first component is most highly correlated with leaflet length, the second is most correlated with petiole width, the third with pedicel length/pedicel width ratio while the fourth component is most highly correlated with fruit length (Table 6a). When components are rotated, the first is still most highly correlated with leaflet length. The second is most highly correlated with fruit length/fruit width ration, the third with pedicel

Figure 2 cont'd. **I**-*Senna occidentalis,* **J** -*Senna podocarpa,* **K**-*Senna siamea,* **L**-*Senna sophera.* **M**-*Senna spectabilis,* **N**-*Chamaecrista mimosoides,* **O**-*Chamaecrista rotundifolia.*

length and the fourth is most highly correlated with pedicel with (Table 6b).

Correlation coefficients for the morphological traits

The correlation coefficients for the morphological characters in the species studied are presented in Table 7. The results clearly showed that leaflet length is significantly positively correlated at $p < 0.01$ with leaflet width (r = 0.941), petiole length (r = 0.798), ratio of petiole length and width (r = 0.394), fruit length (r = 0.580), fruit width (r = 0.761), ratio of fruit length and width (r = 0.290) and pedicel width (r = 0.208). Similarly, the results showed that leaflet length is significantly negatively correlated at $P < 0.01$ with the ratio of leaflet length and width (r = -0.449) and the ratio of pedicel length and width (r = -0.263). Negative but non-significant correlation exists between leaflet length and petiole width (r =-0.127), pedicel length (r =-0.111).

Significantly positive correlation at $p < 0.01$ also exists between leaflet width and petiole length (r = 0.848), ratio of petiole length and width (r = 0.332), fruit length (r = 0.532), fruit width (r = 0.692), ratio of fruit length and width (r = 0.283) and pedicel width (r = 0.240). The results show that leaflet width is significantly negatively correlated at $P < 0.01$ with ratio of leaflet length and width (r = -0.526) and ratio of pedicel length and width (r = -0.186). Negative correlation exists between leaflet width and pedicel length (r = -0.070); also positive correlation exists between leaflet width and petiole width (r = 0.017).

Significantly negative correlation at $P < 0.01$ exists between ratio of leaflet length and width and petiole length (r = -0.497), petiole width (r = -0.352), ratio of petiole length and width (r = -0.341), fruit length (r =-0.2950), ratio of fruit length and width (r = -0.366) and pedicel length (r = -0.497). Also, significantly negative correlation at $P < 0.05$ exists between ratio of leaflet

Table 2. Quantitative morphological characteristics of the species of Cassiinae studied (mean ± standard error).

Species	Leaflet length	Leaflet width	Leaflet length/width	Petiole length	Petiole width	Petiole length/width	Fruit length	Fruit width	Fruit length/ width	Pedicel length	Pedicel width	Pedicel leng/ width
C. fistula	11.89±0.82^{i}	6.69±0.51^{k}	1.78±0.10^{a}	5.87±0.83^{h}	0.44±0.04^{de}	13.34±0.19^{bcd}	49.00±3.43^{e}	1.44±0.22^{f}	34.27±4.03^{g}	0.69±0.88^{ab}	0.02±0.04^{a}	32.91±2.25^{f}
C. italica	2.62±0.51^{bc}	1.51±0.38^{d}	1.77±0.18^{a}	2.32±0.38^{c}	2.66±0.44^{h}	0.89±0.19^{a}	8.58±1.43^{b}	0.86±0.07^{c}	9.94±1.15^{bcd}	3.15±0.34^{i}	0.19±0.15^{efg}	16.73±3.74^{cde}
C. sieberiana	8.38±1.10^{h}	3.34±0.35^{g}	2.52±0.32^{abcd}	4.32±0.52^{f}	0.27±0.04^{bcde}	16.46±2.14^{de}	53.19±3.12^{f}	1.44±0.09^{f}	37.01±5.40^{gh}	3.97±1.96^{j}	0.21±0.30^{fgh}	19.28±1.31^{de}
C. singueana	3.83±0.11^{cd}	1.88±0.12^{de}	2.04±0.11^{abc}	3.53±0.41^{e}	0.46±0.61^{de}	11.75±3.90^{bcd}	9.60±1.05^{b}	0.81±0.05^{c}	11.78±0.62^{cd}	2.39±2.07^{fgh}	0.03±0.04^{ab}	83.04±7.31^{h}
Ch. mimosoides	4.10±0.80^{d}	0.59±0.02^{b}	6.95±1.33^{e}	0.32±0.02^{ab}	0.04±0.00^{ab}	9.01±1.71^{bc}	4.63±0.15^{a}	0.39±0.09^{a}	11.95±0.23^{cd}	1.21±1.40^{cd}	0.07±0.12^{c}	18.29±4.59^{de}
Ch. rotundifolia	1.62±0.13^{b}	1.02±0.09^{c}	1.59±0.09^{a}	0.58±0.04^{b}	0.04±0.01^{ab}	14.13±2.59^{cd}	2.92±0.22^{a}	0.34±0.02^{a}	8.70±0.96^{bc}	2.84±1.35^{hi}	0.05±0.46^{bc}	60.4±2.86^{g}
S. alata	12.73±3.29^{i}	5.51±0.95^{i}	2.3±0.28^{abc}	5.77±0.87^{h}	0.71±0.06^{f}	8.21±1.29^{b}	20.88±4.32^{d}	1.71±0.21^{g}	12.14±1.35^{cd}	0.86±1.00^{bc}	0.18±0.27^{ef}	4.73±0.58^{ab}
S. biflora	0.32±0.03^{a}	0.03±0.01^{a}	11.27±3.40^{f}	NC	NC	NC	3.65±0.22^{a}	0.81±0.80^{c}	4.54±0.39^{a}	0.28±0.35^{a}	0.13±0.37^{d}	2.29±0.52^{a}
S. hirsuta	7.57±2.20^{gh}	3.37±0.66^{g}	2.22±0.31^{abc}	5.06±0.51^{g}	0.25±0.18^{bcd}	27.45±2.13^{f}	14.49±0.93^{c}	0.56±0.12^{b}	27.04±2.74^{f}	2.05±1.38^{efg}	0.14±0.19^{efg}	10.63±7.74^{abcd}
S. obtusifolia	3.88±0.32^{cd}	2.33±0.09^{f}	1.66±0.10^{a}	3.68±0.75^{e}	2.24±0.23^{g}	1.66±0.38^{a}	16.22±1.32^{c}	0.42±0.32^{a}	38.96±5.26^{h}	1.95±2.98^{ef}	0.22±0.25^{h}	8.96±1.69^{abcd}
S. occidentalis	7.66±1.50^{gh}	4.15±0.52^{h}	1.84±0.30^{ab}	4.87±0.50^{g}	0.45±0.09^{de}	11.23±2.20^{bc}	10.85±1.13^{b}	0.84±0.37^{c}	12.85±1.04^{d}	1.68±1.31^{de}	0.27±0.14^{i}	6.36±0.65^{abc}
S. podocarpa	11.79±0.73^{i}	6.22±0.32^{j}	1.9±0.11^{ab}	9.1±0.75^{i}	0.49±0.14^{ef}	20.03±5.24^{e}	10.58±0.46^{b}	1.35±0.12^{f}	7.90±0.33^{ab}	2.48±1.54^{gh}	0.25±0.29^{i}	10.12±1.44^{abcd}
S. siamea	5.9±0.51^{ef}	2.09±0.20^{ef}	2.83±0.22^{bcd}	0.24±0.05^{ab}	0.09±0.01^{abc}	2.82±0.67^{a}	22.23±2.42^{d}	1.22±0.07^{e}	18.21±1.96^{e}	2.83±24.75^{hi}	0.21±0.06^{gh}	13.25±0.57^{bcde}
S. sophera	4.92±0.51^{de}	1.65±0.29^{d}	3.02±0.30^{cd}	5.05±0.59^{g}	0.28±0.21^{cde}	25.28±1.68^{f}	10.57±1.37^{b}	0.55±0.11^{b}	20.21±3.59^{e}	2.39±2.03^{fgh}	0.18±0.58^{e}	22.45±3.80^{ef}
S. spectabilis	6.4±0.83^{fg}	1.86±0.17^{de}	3.44±0.31^{d}	2.95±0.51^{d}	0.24±0.02^{bcd}	12.27±2.41^{bcd}	22.92±1.73^{d}	1.11±0.10^{d}	20.75±1.47^{e}	0.35±0.18^{b}	0.02±0.01^{a}	21.77±1.54^{e}

NC- Not computed. Mean values with the same letters within the same column are not significantly different at $P < 0.05$.

Table 3. Dissimilarity Indices for the species of Cassiinae based on their morphological traits.

	C. fistula	*C. italica*	*C. sieberiana*	*C. singueana*	*Ch. mimosoides*	*Ch. rotundifolia*	*S. alata*	*S. biflora*	*S. hirsuta*	*S. obtusifolia*	*S. occidentalis*	*S. podocarpa*	*S. siamea*	*S. sophera*	*S. spectabilis*
C. fistula	0.00														
C. italica	52.72	0.00													
C. sieberiana	16.06	54.95	0.00												
C. singueana	68.34	67.29	81.55	0.00											
Ch. mimosoides	53.44	11.52	55.79	65.29	0.00										
Ch. rotundifolia	60.87	46.12	71.37	24.24	43.02	0.00									
S. alata	45.86	22.22	44.47	79.83	24.51	60.38	0.00								
S. biflora	66.03	19.52	65.22	82.85	20.68	60.81	26.97	0.00							
S. hirsuta	44.41	33.36	42.41	75.93	28.09	56.45	26.50	40.27	0.00						
S. obtusifolia	43.59	31.10	41.56	79.85	32.45	62.58	30.00	39.01	28.88	0.00					
S. occidentalis	51.48	16.55	50.78	76.84	16.11	55.46	11.96	21.20	22.29	28.83	0.00				
S. podocarpa	52.44	24.00	52.96	74.27	20.89	53.17	17.56	29.46	21.91	38.04	12.50	0.00			
S. siamea	39.58	17.14	39.50	71.89	20.94	53.26	15.30	27.81	27.94	22.58	17.54	26.07	0.00		
S. sophera	44.77	27.46	46.95	62.68	20.59	42.28	29.24	38.17	14.75	33.60	22.89	20.41	27.39	0.00	
S. spectabilis	32.45	22.56	35.02	63.45	21.50	45.61	21.18	35.70	21.86	25.89	21.49	24.62	13.53	18.21	0.00

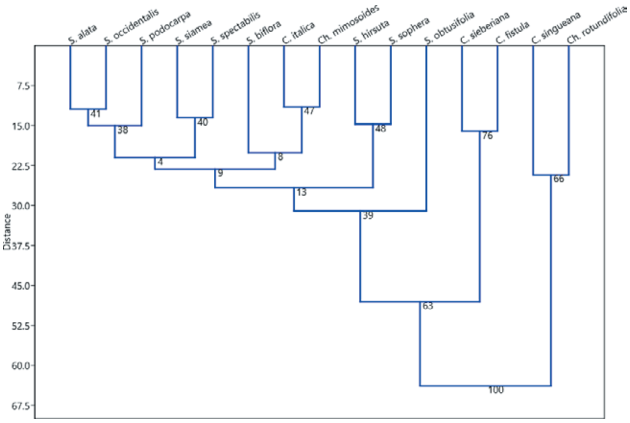

Figure 3. Dendrogram of *Cassinae* species studied based on Unweighted Pair Group Method with Arithmetic Mean (UPGMA).

Table 4. Agglomeration schedule of the studied species of subtribe Cassiinae as viewed from the perspective of clusters on morphological characters.

Stage	Cluster Combined		Coefficients
	Cluster 1	Cluster 2	
1	2	5	132.743
2	7	11	142.963
3	13	15	183.061
4	9	14	217.529
5	7	12	232.285
6	1	3	257.891
7	2	8	404.332
8	7	13	456.309
9	2	7	562.417
10	4	6	587.472
11	2	9	748.365
12	2	10	986.341
13	1	2	2375.399
14	1	4	4225.493

1- *C. fistula,* **2**- *C. italica,* **3**- *C. sieberiana,* **4**- *C. singueana,* **5**- *Ch. mimosoides*, **6**- *Ch. rotundifolia* , **7**- *S. alata,* **8**- *S. biflora,* **9**- *S. hirsute,* **10**- *S. obtusifolia,* **11**- *S. occidentalis,* **12**- *S. podocarpa,* **13**- *S. siamea,* **14**- *S. sophera,* **15**- *S. spectabilis*

length and width and fruit width ($r = -0.180$) and ratio of pedicel length and width ($r = -0.279$). Pedicel length is significantly positively correlated with pedicel width ($r = 0.414$) and ratio of pedicel length and width ($r = 0.237$) at $P < 0.01$. Fruit length is significantly positively correlated with fruit width ($r = 0.654$) and ratio of fruit length and width ($r = 0.743$) at $P < 0.05$.

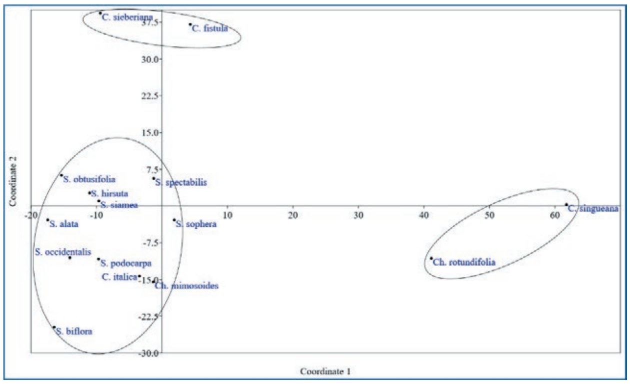

Figure 4. Scatter plot of species of Cassiinae studied based on the quantitative morphological characters after the first and second principal coordinate analyses (PCoA).

Table 5. Variance in the observed morphological traits using Principal Component Analysis.

Components	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	4.428	36.901	36.901	4.428	36.901	36.901
2	1.948	16.232	53.133	1.948	16.232	53.133
3	1.903	15.859	68.992	1.903	15.859	68.992
4	1.387	11.558	80.550	1.387	11.558	80.550
5	.995	8.294	88.843			
6	.822	6.847	95.690			
7	.234	1.952	97.642			
8	.153	1.277	98.920			
9	.076	.635	99.555			
10	.034	.284	99.839			
11	.013	.111	99.949			
12	.006	.051	100.000			

DISCUSSION AND CONCLUSIONS

Morphometrics adds to species descriptions using quantitative elements, allowing more rigorous comparisons within a genus (Kolawole et al. 2016), and it has extensively been employed in many studies (Soladoye et al. 2010b; Deshmukh 2011; Rahman et al. 2013; Zhigila et al. 2015). In the present study, we employed numerical methods in understanding the relationship between members of the tribe Cassinae in Nigeria. Our Findings revealed marked differences in the vegetative and reproductive characters, and were important in the delimitation of the studied taxa.

Table 6a Component Matrix of examined characters.

	Component			
	1	2	3	4
Leaflet length	**.931**	-.212	-.181	-.108
Leaflet width	.928	-.106	-.121	-.115
Leaflet length/width	-.613	-.324	-.581	.026
Petiole length	.854	.015	.042	-.369
Petiole width	.048	**.793**	-.012	.244
Petiole length/width	.436	-.329	.488	-.488
Fruit length	.698	-.167	.040	.627
Fruit width	.710	-.185	-.378	.177
Fruit length/width	.498	.118	.234	**.618**
Pedicel length	.130	.574	.589	-.071
Pedicel width	.319	.733	-.330	-.330
Pedicel length/width	-.216	-.326	**.789**	.086

Extraction Method: Principal Component Analysis.
4 components extracted.$_{a}$

Table 6b. Rotated Component Matrix of examined characters.

	Component			
	1	2	3	4
Leaflet length	**.905**	.343	-.095	.108
Leaflet width	.876	.333	.019	.143
Leaflet length/width	-.426	-.272	-.746	.078
Petiole length	.892	.076	.227	.113
Petiole width	-.260	.210	.498	.575
Petiole length/width	.648	-.198	.262	-.496
Fruit length	.344	.887	-.017	-.060
Fruit width	.589	.483	-.287	.225
Fruit length/width	.099	**.782**	.277	-.018
Pedicel length	-.025	-.002	**.835**	.026
Pedicel width	.268	-.178	.331	**.802**
Pedicel length/width	-.189	.012	.311	-.806

Extraction Method: Principal Component Analysis.
Rotation Method: Varimax with Kaiser Normalization.
Rotation converged in 9 iterations.$_{a}$

The species exhibited significant morphological variations. Leaflet length was highest in *S. alata* and least in *Ch. mimosoides*, while the width was highest in *C. fistula* and least in *Ch. mimosoides*. Interestingly, the highest and smallest leaflet length/width ratios were observed in the twin-taxa - *Ch. mimosoides* and *Ch. rotundifolia* respectively. While petiole was longest in *S. podocarpa* (9.1 cm), it was shortest in *S. siamea* (0.24 cm). Generally, the fruits were considerably long (≥10 cm long) except in *C. italica, S. singueana, Ch. mimosoides, Ch.*

Table 7. Correlation matrix based on quantitative traits of the studied species of subtribe Cassiinae.

	Leaflet length	Leaflet width	Leaflet length/width	Petiole length	Petiole width	Petiole length/width	Fruit length	Fruit width	Fruit leng/ width	Pedicel length	Pedicel width	Pedicel length/width
Leaflet length	1.000											
Leaflet width	**.941****	1.000										
Leaflet length/width	-.449**	-.526**	1.000									
Petiole length	**.798****	**.848****	-.530**	1.000								
Petiole width	-.127	.017	-.352**	.105	1.000							
Petiole length/width	.394**	.332**	-.341**	.574**	-.433*	1.000						
Fruit length	.580**	.532**	-.295**	.316**	-.069	.138	1.000					
Fruit width	.761**	.692**	-.180*	.465**	-.087	-.040	.654**	1.000				
Fruit leng/width	.290**	.283**	-.366**	.247*	.186*	.196**	.743**	.104	1.000			
Pedicel length	-.111	-.070	-.497**	.047	.223**	.199*	.107	-.078	.144*	1.000		
Pedicel width	.208**	.240**	-.176*	.329**	.325**	-.055	-.038	.162	.034	.414**	1.000	
Pedicel length/width	-.263**	-.186*	-.279*	-.148*	-.160*	.156*	-.063	-.223**	-.104	.237**	-.641*	1.000

* represents significantly different at $P < 0.05$; ** represents significantly different at $P < 0$

rotundifolia, and *S. biflora* where they were shorter (<10 cm). The fruit size and pedicel length are dependent on the age of plants as earlier noted by other reports (Irvine 1961; Burkill 1995; Kolawole et al. 2016). Leaf shape and size also varies within the same plant stand. Nwachuwu and Mbagwu (2006) thought that such variations observed may be due to environmental as well as genetic factors and the interaction among them. Nevertheless, previous studies suggested that light intensity may affect the carbohydrate balance, which could affect the length of the cells in the direction of the long axis, thereby leading to differences in the length, shapes, and width of the leaves (Soladoye et al. 2010a; Kolawole et al. 2016).

In our study, leaflet length was significantly positively correlated at $P < 0.01$ with characters such as leaflet width, petiole length, ratio of petiole length and width, fruit length, fruit width, ratio of fruit length and width, and pedicel width. Similarly, leaflet width showed high positive correlations with petiole length, fruit length, and fruit width respectively. Nevertheless, there exist negative correlations between leaflet length and leaflet length/width ratio, leaflet length and petiole width, leaflet length and pedicel length, leaflet width and leaflet length/width ratio, petiole length and pedicel length/with ratio. Previous related studies on the genus *Ficus* had shown highly significant positive correlations between leaf length and leaf width, leaf length and lamina length, leaf length and petiole length, lamina length and lamina width; and negative correlations between leaf width and leaf length/width ratio, petiole length and fruit length/petiole length ratio Sonibare et al. (2004). Jeruto et al. (2017) in their study on *Senna didymobotrya* also reported high positive correlations between plant height and stem height, pod length and pod width, leaf number and leaflet number, leaflet length and leaflet width, inflorescence length and inflorescence length of the basal stalk (peduncle). These amongst others, are supporting evidences for the application and relevance of morphometrics in taxonomic studies.

Results from the PCA analysis showed that only four components accounted for 80.5% of the total variance. The first component contributed 36.9%, the second contributed 16.2%, the third had 15.8% while the fourth had 11.6%. However, the other 8 components collectively accounted for the remaining 19.5% and produced insignificant contributions to the delimitation of the taxa studied. In furtherance, cluster analysis from our findings revealed the infra-specific relationship between the 15 species of Cassiinae studied, based on the quantitative morphological traits evaluated. There is a greater affinity between *C. italica* and *Ch. mimosoides*. These two species seem not to be easily separated as shown in the dendrogram and further supported by the distance measure (coefficients of cluster) revealed through the agglomeration schedule. This trend also follows for *S. alata* and *S. occidentalis, S. alata* and *S. podocarpa, S. siamea* and *S. spectabilis*, *S. hirsuta* and *S. sophera,* and likewise *C. fistula* and *C. sieberiana*. While *S. singueana* and *Ch. rotundifolia* occupy an isolated position towards the bottom of the scatter plot, *C. fistula* and *C. sieberiana* also co-exist in the upper left of the plot, and others are clustered together in a more central position; hence dividing the studied taxa into three clusters. Observations also showed less dissimilarity coefficients between *Ch. mimosoides* and *C. italica*, *S. alata* and *S. occidentalis, S. occidentalis* and *S. podocarpa, S. alata* and *S. podocarpa*, *S. siamea* and *S. spectabilis, S. hirsuta* and *S. sophera, S. fistula* and *S. sieberianna,* thus reflecting their morphological similarities.

It is noteworthy that the affinity between *S. alata* and *S. podocarpa* as evidenced in this study, supports the folklore claims in south-western Nigeria that they are closely related. According to this belief, *S. alata* is the foreign species while *S. podocarpa* is regarded a native species to Nigeria. Also, a similar result had been observed in the pollen morphological studies of these two species as their pollens are not easily separated by light microscope (Kolawole 2017). A close association of the species of the genus *Senna* in the first cluster is in agreement with the previous findings of Saheed and Illoh (2011), Ogundipe et al. (2009) and Rahman et al. (2013) who reported that they are taxonomically related. Ecologically, the species studies are sympatric in distribution, extending from the southern part of Nigeria to the drier areas in the north, but more abundant across the transitional equatorial region which receives more rainfall than other regions within the study area.

However, with the continuous human induced anthropogenic activities in the area, there is a high tendency of further reduction in the distribution of the species in the near future if conservation strategies are not rapidly developed and implemented. Such strategies would also checkmate the gradual but eventual loss of our endangered and threatened species, especially the overexploited.

The present study has added to the understanding of Cassiinae species in Nigeria, through the application of numerical taxonomy. Findings showed that despite the overlapping nature of the quantitative morphological traits examined, the species can still be distinguished from each other using certain characters. Our study also further supports the creation of *Chamaecrista* and *Senna* from the old *Cassia*. Nevertheless, while the relevance of molecular characters has been witnessed in recent taxonomic studies, we strongly suggest that the use of morphological characters should not be ignored as it formed the basis for traditional taxonomy, and as evidenced in most of the classification systems used up to this date.

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Pollen morphology and variability of species from the genus *Rubus* L. (Rosaceae) alien and invasive in Poland

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Abstract: *Rubus* L. is one of the most species-rich and most taxonomically challenging genera in the family Rosaceae. The aim of this study was to investigate pollen morphology and the ranges of inter- and intraspecific variability of the studied *Rubus* alien species, as well as verify the taxonomic usefulness of these traits in distinguishing studied taxa from this genus. We analysed six quantitative pollen characteristics and the following qualitative ones: exine ornamentation, pollen outline and shape. The study was conducted on 24 samples of six alien *Rubus* species found in Poland. 720 pollen grains were measured in total. The most important pollen features included exine ornamentation and length of the polar axis (P). In the conducted studies there were no features of pollen indicating "invasiveness". The results of our research fill the gap in knowledge on pollen structure in Rubus species alien to Poland and Europe. They may constitute a foundation for further research on the reproduction of these species (e.g. pollen viability and fertility), thus facilitating identification of features determining their expansive character.

Keywords: pollen morphology, interspecific variability, intraspecific variability, *Rubus*, alien and invasive brambles.

INTRODUCTION

Many bramble species are found outside their natural distribution area as a result of their use in horticulture, while some have been introduced accidentally (Király 2018). Alien brambles can become established very far from their original range and some of them became invasive (Evans and Weber 2003; Henderson 2007; Bennett et al. 2011; Clark et al. 2013). The identification of the taxa in the secondary range is difficult, especially in the case of apomictic species of Eurasian origin, with misidentifications, even using molecular methods, being relatively frequent (Alice et al. 2014; Bruckart et al. 2017). Király (2018) expressed an opinion that alien species from the genus *Rubus* generate significant ecological and nature conservational threats worldwide; however, the European flora and vegetation are not seriously affected by their impacts.

Lambdon et al. (2008) reported that in Europe 35 *Rubus* species are 'aliens in Europe', 10 species are 'aliens of European origin' and 21 species – 'aliens to Europe'. According to DAISIE (2009), in Europe 34 alien *Rubus* taxa are found, including all the studied species. Kurtto et al. (2010) reported in Europe 10 "non-native" *Rubus* species, and about 20 native species with secondary occurrences outside the original range. In turn, Tokarska-Guzik et al. (2012) showed for Poland the occurrence of six alien bramble species.

Rubus is one of the most taxonomically challenging genera in the family Rosaceae. Difficulties arise from the large number of species with similar morphological characteristics and often small, local ranges of natural occurrence, as well as polyploid hybridisation and apparently frequent facultative apomixis (Weber 1996; Alice and Campbell 1999). Therefore, among brambles, pollen of only 48 European species had been characterised until 2019 (Erdtman et al. 1961; Reitsma 1966; Teppner 1966; Eide 1981a, 1981b; Gonzalez Romano and Candau 1989; Monasterio-Huelin and Pardo 1995; Tomlik-Wyremblewska 1995; Wrońska-Pilarek et al. 2012, 2016; Kosiński et al. 2018). These data have been supplemented by the latest comprehensive palynological study by Lechowicz et al. (2020), who described pollen grains of 58 Polish and European *Rubus* species, and by Xiong et al. (2019), who examined 155 species and 13 varieties representing all the 12 subgenera of this genus.

The most important features of bramble pollen grains include exine ornamentation (ornamentation type, width and orientation of striae and grooves), length of colpori, type of the bridge, costae colpi and the number and size of perforations (Reitsma 1966; Naruhashi and Takano 1980; Eide 1981a, 1981b; Kosenko et al. 1982; Gonzalez Romano and Candau 1989; Hebda and Chinnappa 1990, 1994; Ueda 1992; Monasterio-Huelin and Pardo 1995; Tomlik-Wyremblewska 1995, 2000; Li et al. 2001; Tomlik-Wyremblewska et al. 2004; Wrońska-Pilarek et al. 2006, 2012; Wang et al. 2007; Kasalkheh et al. 2017; Gupta and Dash 2018; Xiong et al. 2019; Lechowicz et al. 2020). In the opinion of Tomlik-Wyremblewska (1995, 2000), pollen size and shape prove to be poor criteria in species identification.

The aim of this study was to describe and analysed pollen morphology and the inter- and intraspecific variability of all six alien *Rubus* species (on the basis of 24 pollen samples) found in Poland, based on all pollen features. All of the studied bramble species, are distributed throughout Europe as aliens. We also investigated if pollen grains of the invasive and expansive bramble species differ in structure from pollen of other species, and whether any differences may affect their invasive properties.

MATERIALS AND METHODS

Pollen morphology

The plant material was collected in the herbarium of the Institute of Dendrology, Polish Academy of Sciences in Kórnik (KOR) and stored in the herbarium of the Department of Forest Botany, the Poznań University of Life Sciences (PZNF), which did not require any permits to conduct research.

The study was conducted on 24 samples of six alien *Rubus* species (*R. allegheniensis* Porter, *R. armeniacus* Focke, *R. canadensis* L., *R. laciniatus* Willd., *R. odoratus* L. and *R. xanthocarpus* Bureau & Franch) found in Poland, the Czech Republic, Ukraine, Germany and France. A list of the species analysed with their affiliation to series is shown in Table 1.

In this paper the taxonomic classification of the studied taxa from the genus *Rubus* was adopted after Zieliński (2004), with further modifications (Kosiński et al. 2018). The verification of the taxa was made by Prof. Jerzy Zieliński (Institute of Dendrology, Polish Academy of Sciences in Kórnik), a batologist - taxonomist specialising in the genus *Rubus*.

Several, randomly selected inflorescences (flowers) were collected from 24 localities representing invasive Rubus species in five European countries (Table 2). Pollen grains were acetolysed according to the method of Erdtman (1960). The pollen grain samples were then mixed with 96% alcohol and centrifuged 4 times, with processed grains subsequently divided into two groups. One half of the processed sample was immersed in an alcohol-based solution of glycerin for LM, while the other was placed in 96% ethyl alcohol in preparation for scanning electron microscopy (SEM). The SEM observations were carried out using a Zeiss Evo 40 microscope,

Table 1. The taxonomic classification of the *Rubus* species studied.

No	Species	Subgenus	Section	Subsection	Series
1	*R. xanthocarpus*	*Chamaerubus*	-	-	*Xanthocarpi*
2	*R. odoratus*	*Anoplobatus*	-	-	-
3	*R. canadensis*	*Rubus*	*Rubus*	*Rubus*	*Canadenses*
4	*R. allegheniensis*	*Rubus*	*Rubus*	*Rubus*	*Alleghenieses*
5	*R. armeniacus*	*Rubus*	*Rubus*	*Hiemales*	*Discolores*
6	*R. laciniatus*	*Rubus*	*Rubus*	*Hiemales*	*Rhamnifolii*

while LM measurements of acetolysed pollen grains were conducted at a 400× magnification using a Levenhuk D870T microscope equipped with a camera and software enabling accurate grain measurement. The exine sculptural elements were measured when taking SEM photos on an area of 25 μm^2 according to the methods of Ueda and Tomita (1989). SEM pictures were taken from samples numbered 1–5 (see: Table 2). Measurements taken from 30 mature, randomly selected, properly developed pollen grains were made using the light microscopy (LM), with 720 pollen grains measured in total.

The pollen grains were analysed for six quantitative characters: length of the polar axis (P) and equatorial diameter (E), length of the ectoaperture (Le), distance between apices of two ectocolpi (d), and the P/E, and Le/P ratios (Figure 1). The pollen shape classes (P/E ratio) were adopted according to the classification proposed by Erdtman (1952): oblate-spheroidal (0.89–0.99), spheroidal (1.00), prolate-spheroidal (1.01–1.14), subprolate (1.15–1.33) and prolate (1.34–2.00). In addition, the following qualitative characters were also determined: outline, shape, operculum structure and exine ornamentation.

Exine ornamentation types were identified based on the classification proposed by Ueda (1992). The types and subtypes of the striate exine ornamentation were characterised by the height and width of grooves, width of striae, and the number and diameter of perforations.

The descriptive palynological terminology followed Punt et al. (2007) and Halbritter et al. (2018).

Statistical analysis

The normality of distributions for the studied traits (P, Le, d, E, P/E and Le/P) was tested using Shapiro-Wilk's normality test (Shapiro and Wilk 1965). Multivariate analysis of variance (MANOVA) was performed on the basis of the following model using a MANOVA procedure in the GenStat 18th edition: $\mathbf{Y}=\mathbf{XT}+\mathbf{E}$, where: $\mathbf{Y}$ is the $(n\times p)$-dimensional matrix of observations, n is the number of all observations, p is the number of traits (in this study $p=6$), $\mathbf{X}$ is the $(n\times k)$-dimensional matrix of design, k is the number of species (in this study $k=24$), $\mathbf{T}$ is the $(k\times p)$-dimensional matrix of unknown effects, and $\mathbf{E}$ – is the $(n\times p)$-dimensional matrix of residuals. Next, one-way analysis of variance (one-way ANOVA)

Table 2. List of localities of the *Rubus* species studied.

No	Species	Localities	Geographical coordinates	Collector, herbarium
1	*R. allegheniensis* 1	Czech Republic, Fryšták	49°16’04,6”N, 17°40’01,5”E	Zieliński; KOR
2	*R. allegheniensis* 2	Czech Republic, Lukov	49°17’24,4”N, 17°43’45,8”E	Zieliński; KOR
3	*R. allegheniensis* 3	Poland, Janowo	54°02’18,2”N, 14°58’09,3”E	Zieliński; KOR
4	*R. allegheniensis* 4	Poland, Łukęcin	54°02’34,9”N, 14°52’23,8”E	Zieliński; KOR
5	*R. armeniacus* 1	Poland, Resko	53°46’24,2”N, 15°24’20,2”E	Boratyńska, Dolatowska, Zieliński; KOR
6	*R. armeniacus* 2	Poland, Golędzinów	51°16’07,6”N, 16°55’25,5”E	Zieliński; KOR
7	*R. armeniacus* 3	Poland, Dziwnów	54°01’30,3”N, 14°45’09,5”E	Boratyńska, Dolatowska, Zieliński; KOR
8	*R. armeniacus* 4	Poland, Trzebiatów	54°03’45,7”N, 15°15’56,6”E	Tomlik; KOR
9	*R. armeniacus* 5	Poland, Cichowo	51°59’39,2”N, 16°58’45,9”E	Boratyńska; KOR
10	*R. canadensis* 1	Poland, Międzygórze	50°13’40,6”N, 16°46’00,1”E	Kosiński; KOR
11	*R. canadensis* 2	Poland, Stronie Śląskie	50°17’29,9”N, 16°52’25,3”E	Kosiński, Zieliński; KOR
12	*R. canadensis* 3	Germany, Pulsnitz	51°10’57,3”N, 14°00’50,3”E	Hans-Werner; KOR
13	*R. canadensis* 4	Poland, Nowa Morawa	50°14’11,9”N, 16°53’28,1”E	Illegible name; KOR
14	*R. laciniatus* 1	Poland, Rzeszów	50°02’14,8”N, 22°00’16,9”E	Wróblewski; KOR
15	*R. laciniatus* 2	Poland, Glinna	53°17’12,6”N, 14°43’11,9”E	Celiński; KOR
16	*R. laciniatus* 3	Poland, Poznań	52°27’14,0”N, 16°50’54,9”E	Krysztofiak; KOR
17	*R. laciniatus* 4	Poland, Małolesie	53°17’50,9”N, 14°42’33,5”E	Wróblewski; KOR
18	*R. laciniatus* 5	France, Paris	48°50’35,6”N, 02°21’34,2”E	Wróblewski; KOR
19	*R. odoratus* 1	Poland, Mościenica	52°15’01,5”N, 17°03’47,4”E	Bugała; KOR
20	*R. odoratus* 2	Poland, Niedrzwica Duża	51°06’51,3”N, 22°23’16,2”E	Illegible name; KOR
21	*R. odoratus* 3	Poland, Kórnik	52°14’28,4”N, 17°05’34,5”E	Zieliński; KOR
22	*R. odoratus* 4	Ukraine, Rudki	49°38’30,2”N, 23°29’27,5”E	Wróblewski; KOR
23	*R. odoratus* 5	Poland, Rzeszów	50°02’14,8”N, 22°00’16,9”E	Wróblewski; KOR
24	*R. xanthocarpus* 1	Poland, Miedzianka	50°50’22,5”N, 20°22’03,3”E	Maciejczak, Bróż, Zieliński; KOR

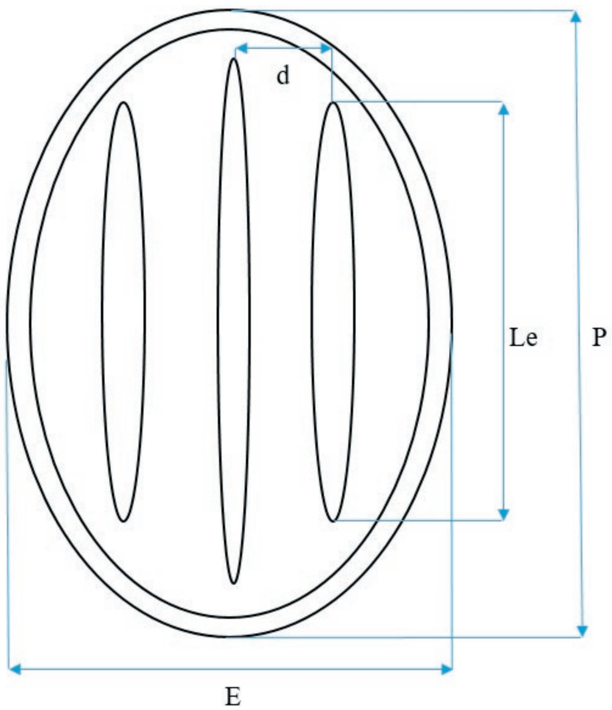

Figure 1. Scheme of the investigated quantitative characters (P, E, Le and d).

was carried out to determine the effects of *Rubus* samples on variability of P, Le, d, E, P/E and Le/P. The minimal, maximal and mean values as well as standard deviations of traits were calculated. Fisher's least significant differences (LSDs) were calculated for individual traits and on this basis homogeneous groups were established. The relationships between observed traits were assessed on the basis of Pearson's correlation. Relationships of six observed traits were presented in a heatmap. Results were also analysed using multivariate methods. The canonical variate analysis was applied in order to present multitrait assessment of similarity of tested samples in a lower number of dimensions with the least possible loss of information (Rencher 1992). This makes it possible to illustrate variation in species in terms of all observed traits in the graphic form. The Mahalanobis distance (Mahalanobis 1936) was suggested as a measure of "polytrait" species similarity (Seidler-Łożykowska and Bocianowski 2012), which significance was verified by means of critical value D_α called "the least significant distance" (Camussi et al. 1985). Mahalanobis distances were calculated for all species samples. The differences between the analysed species were verified by cluster analysis using the nearest neighbour method and Euclidean distances. All the analyses were conducted using the GenStat 18th edition statistical software package.

RESULTS

General morphological description of pollen

A description of pollen grain morphology of the *Rubus* species studied is given below and illustrated in SEM photographs (Figures 2 and 3). Morphological observations for the other quantitative characters of pollen grains are shown in Tables 3 and 4.

Pollen grains of the *Rubus* species studied were tricolporate, isopolar monads (Figure 2). According to the pollen size classification by Erdtman (1952) based on the length of the polar axis, analysed pollen grains were small (10–25 µm; 54.5%) or medium-sized (25.1–50 µm; 45.5%). Pollen grains had a small range of average values for trait P, ranging from 20.57 to 27.82 µm.

The average length of the polar axis (P) was 24.75 (15.16–33.65) µm (Table 3). The smallest mean P was found for pollen of *R. xanthocarpus* (20.57 µm), while the largest – for *R. armeniacus* (27.82 µm) (Table 3). In the *R. xanthocarpus* sample all measured pollen grains were small at a narrow range of polar axis length (18–24

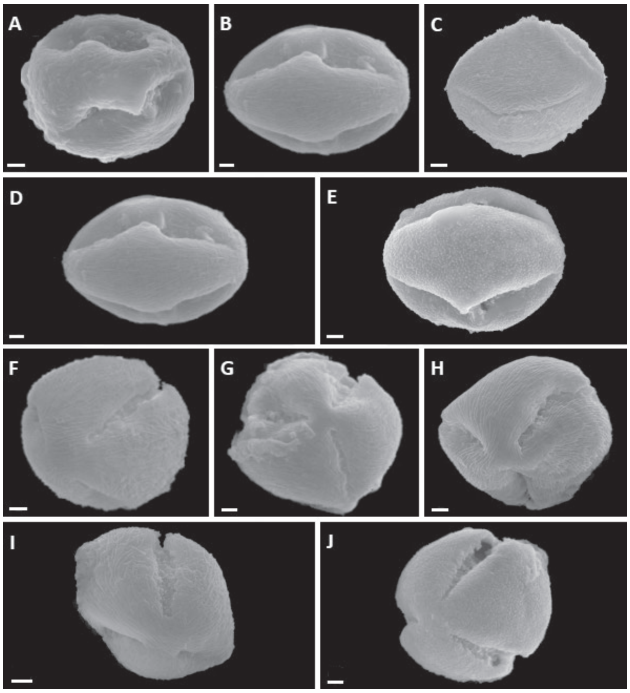

Figure 2. Equatorial and polar views of pollen grains under a scanning electron microscope (SEM) (A-E). (A) *R. allegheniensis,* (B) *R. armeniacus,* (C) *R. canadensis,* (D) *R. laciniatus,* (E) *R. odoratus* – pollen grains in equatorial view, two colpori and exine ornamentation visible. (F-J) (F) *R. allegheniensis,* (G) *R. armeniacus,* (H) *R. canadensis,* (I) *R. laciniatus,* (J) *R. odoratus* - pollen in polar view, three colpori and exine ornamentation visible. Scale bars = 2 µm.

Table 3. Minimal, maximal and mean values as well as standard deviations (s.d.) for P, Le and d.

Trait *Rubus*	P					Le					d				
	Mean		Min	Max	s.d.	Mean		Min	Max	s.d.	Mean		Min	Max	s.d.
R. allegheniensis 1	27.01	ab[#]	23.00	33.65	2.35	21.81	abcde	16.63	29.27	2.82	6.40	a	3.46	9.23	1.53
R. allegheniensis 2	26.55	abc	22.05	30.17	2.44	20.89	cdefg	16.68	23.9	2.04	5.83	a	3.15	9.17	1.68
R. allegheniensis 3	25.24	cdef	22.52	30.26	1.90	20.86	cdefg	17.01	24.88	1.71	4.79	b	3.21	6.16	0.81
R. allegheniensis 4	24.47	efgh	22.00	28.00	1.72	20.80	cdefg	16.00	24.00	1.63	4.27	bcdef	2.00	8.00	1.36
R. armeniacus 1	27.02	ab	22.74	31.45	2.11	22.25	abc	19.56	26.06	1.78	3.96	bcdefg	2.60	5.59	0.76
R. armeniacus 2	27.41	a	23.13	29.62	1.65	22.31	abc	17.15	26.73	2.12	4.45	bc	2.96	6.15	0.75
R. armeniacus 3	27.01	ab	23.44	30.18	1.79	22.85	ab	17.81	26.74	2.16	3.95	bcdefg	2.00	5.16	0.90
R. armeniacus 4	27.13	ab	22.19	29.81	1.47	21.86	abcde	16.79	25.38	1.63	3.92	cdefg	2.32	6.00	0.86
R. armeniacus 5	27.82	a	22.98	30.80	2.00	23.16	a	18.27	26.21	2.05	4.06	bcdefg	2.42	6.45	0.89
R. canadensis 1	21.98	jkl	19.88	24.80	1.19	18.79	ijk	15.75	21.6	1.30	2.31	k	1.67	4.38	0.59
R. canadensis 2	23.03	hijk	20.27	27.80	1.93	19.64	ghij	17.06	24.32	1.80	2.58	jk	1.62	6.23	0.88
R. canadensis 3	25.71	bcde	20.37	29.02	1.98	21.20	cdef	16.16	24.78	1.98	4.33	bcd	2.00	7.28	1.32
R. canadensis 4	21.27	l	20.00	24.00	1.23	18.13	jk	14.00	20.00	1.57	2.60	ijk	2.00	4.00	0.86
R. laciniatus 1	26.46	abc	23.22	29.31	1.37	21.91	abcd	18.81	25.13	1.64	3.53	defgh	2.00	6.17	1.01
R. laciniatus 2	24.84	defg	21.29	30.16	2.68	20.34	efgh	17.11	26.28	2.38	3.45	fghi	1.93	4.88	0.79
R. laciniatus 3	26.36	abcd	22.63	28.82	1.63	21.48	bcde	16.23	25.05	1.75	3.27	ghij	1.76	5.32	1.01
R. laciniatus 4	24.61	efg	15.16	27.48	2.53	20.66	defg	16.00	23.76	1.70	2.96	hijk	1.15	6.37	1.06
R. laciniatus 5	24.44	efgh	21.96	26.52	1.08	19.89	fghi	16.61	22.74	1.50	4.43	bc	3.04	5.82	0.83
R. odoratus 1	23.85	fghi	21.49	26.71	1.31	19.92	fghi	16.14	22.44	1.64	3.69	cdefgh	2.36	5.23	0.72
R. odoratus 2	22.86	ijk	20.62	25.70	1.35	18.71	ijk	15.02	21.84	1.71	3.86	cdefg	2.12	5.32	0.84
R. odoratus 3	23.38	ghij	20.81	25.78	1.32	18.95	hijk	15.80	22.60	1.65	4.30	bcde	2.51	6.28	0.90
R. odoratus 4	21.66	kl	18.71	23.95	1.35	17.64	kl	14.67	20.34	1.40	3.45	efgh	2.67	5.12	0.72
R. odoratus 5	21.78	kl	19.37	23.43	0.94	17.90	k	15.60	19.70	1.14	3.51	defgh	2.00	5.46	0.90
R. xanthocarpus 1	20.57	l	18.00	24.00	1.43	16.23	l	14.00	18.00	1.31	3.87	cdefg	2.00	6.00	1.07
LSD$_{0.001}$	1.5					1.54					0.85				
ANOVA *F*			47.35***					29.89***					26.10***		

[#] a, b, ... – values with different letters in columns are significantly different (P<0.001).

µm). On the other hand, the longest pollen grains were found in *R. armeniacus* (22.19–31.45 µm).

The mean equatorial diameter (E) was 17.49 (14–28.23) µm. The shortest mean equatorial diameter was recorded in pollen of *R. xanthocarpus* (17.60 µm), and the longest was found in *R. allegheniensis* (24.19 µm; Table 4).

The outline in the polar view was mostly circular with obtuse apices, less often elliptic, whereas in the equatorial view the outline was mostly elliptic, rarely circular (Figure 2).

The mean P/E ratio was 1.16, ranging from 0.66 in *R. laciniatus* to 2.00 in *R. armeniacus* (Table 4). On average the P/E ratio values were always above 1.00, ranging from 1.10 in *R. odoratus* to 1.24 in *R. laciniatus*. Pollen grains of the examined species were most frequently subprolate (48.8% – 351 pollen grains) or prolate-spheroidal (42.9% – 309), rarely prolate (5% – 36) and very rarely oblate-spheroidal (1.9% – 14).

The polar area index (PAI) or the apocolpium index, in other words the d/E ratio, averaged 0.18 (0.05–0.41). The lowest mean value of this ratio (0.05) was recorded in *R. laciniatus*, while the highest (0.41) – in *R. allegheniensis*.

Rubus pollen grains usually have three apertures colpori. The colpori were arranged meridionally, regularly, more or less evenly spaced and were usually long, with a mean length of 20.34 (14.00–29.27) µm (Table 3). On average, the shortest colpori were found in *R. xanthocarpus* and *R. canadensis* (14.00 µm), while the longest was recorded in *R. armeniacus* (19.56 µm). On average, the length of the colporus (Le) constituted 82% of the polar axis length (P) and ranged from 67 to 97%. The colpori were narrow, linear or fusiform in outline. Their width varied and was usually greatest in the equatorial region. Sculpturing of ectocolpus membranes approached rugulate, rarely partly psilate (Figure 3). Colpus margins frequently had small undulations (Figure 3). In all the studied species a bridge was observed,

Table 4. Minimal, maximal and mean values as well as standard deviations (s.d.) for E, P/E and Le/P.

Trait *Rubus*	E					P/E					Le/P				
	Mean		Min	Max	s.d.	Mean		Min	Max	s.d.	Mean		Min	Max	s.d.
R. allegheniensis 1	24.19	a$^{\#}$	19.07	27.23	1.93	1.12	cde	0.96	1.37	0.10	0.81	def	0.68	0.90	0.07
R. allegheniensis 2	23.33	abc	16.87	27.06	2.63	1.14	cde	1.01	1.37	0,09	0.79	f	0.67	0,91	0.05
R. allegheniensis 3	22.09	cdef	20.06	24.50	0.99	1.14	cde	1.02	1.35	0,08	0.83	abcde	0.68	0,94	0.06
R. allegheniensis 4	21.20	efgh	18.00	24.00	1.45	1.16	abcde	1.00	1.40	0,10	0.85	ab	0.73	0,92	0.06
R. armeniacus 1	22.79	abcd	19.86	25.04	1.33	1.19	abc	1.08	1.45	0,08	0.83	abcdef	0.69	0,94	0.05
R. armeniacus 2	23.30	abc	20.20	25.82	1.46	1.18	abcde	1.08	1.30	0,06	0.81	bcdef	0.68	0,90	0.05
R. armeniacus 3	23.54	abc	20.42	27.76	2.02	1.15	bcde	1.02	1.29	0,08	0.85	abcd	0.75	0,94	0.04
R. armeniacus 4	24.09	a	20.93	28.23	1.51	1.13	cde	0.99	1.28	0,06	0.81	def	0.74	0,87	0.03
R. armeniacus 5	23.82	ab	15.14	27.27	2.45	1.18	abcde	0.94	2.00	0,18	0.83	abcd	0.76	0,90	0.04
R. canadensis 1	19.07	hi	16.26	22.48	1.42	1.16	bcde	1.01	1.28	0,07	0.85	a	0.72	0,93	0.04
R. canadensis 2	19.75	hgh	16.76	23.58	1.66	1.17	abcde	0.96	1.40	0,08	0.85	ab	0.75	0,90	0.03
R. canadensis 3	23.40	abc	17.83	27.24	2.42	1.10	de	0.99	1.36	0,09	0.83	abcdef	0.71	0,92	0.05
R. canadensis 4	18.47	hi	14.00	20.00	1.46	1.16	bcde	1.00	1.43	0,10	0.85	ab	0.70	0,91	0.05
R. laciniatus 1	22.47	bcde	18.83	26.55	1.84	1.18	abcd	1.04	1.38	0,09	0.83	abcde	0.75	0,91	0.04
R. laciniatus 2	21.30	defg	17.31	26.78	2.45	1.17	abcde	0.97	1.37	0,10	0.82	abcdef	0.74	0,89	0.03
R. laciniatus 3	22.52	bcde	16.47	27.84	2.33	1.18	abcde	0.99	1.60	0,14	0.81	bcdef	0.72	0,88	0.04
R. laciniatus 4	21.46	def	16.88	26.12	2.20	1.16	bcde	0.66	1.52	0,14	0.85	abc	0.76	1,45	0.12
R. laciniatus 5	19.78	ghgh	17.88	21.76	0.95	1.24	a	1.10	1.38	0,08	0.81	bcdef	0.70	0,88	0.04
R. odoratus 1	19.51	gh	15.60	22.60	1.63	1.23	ab	1.06	1.38	0,08	0.84	abcd	0.72	0,91	0.05
R. odoratus 2	19.44	gh	16.25	21.82	1.54	1.18	abcde	1.06	1.46	0,08	0.82	abcdef	0.71	0,89	0.04
R. odoratus 3	20.73	fghg	17.96	23.37	1.35	1.13	cde	1.01	1.35	0,08	0.81	cdef	0.71	0,89	0.04
R. odoratus 4	19.76	hgh	16.43	22.41	1.76	1.10	e	0.94	1.34	0,10	0.81	bcdef	0.74	0,88	0.03
R. odoratus 5	18.93	hi	14.79	21.82	1.98	1.16	abcde	1.02	1.49	0,12	0.82	abcdef	0.71	0,91	0.05
R. xanthocarpus 1	17.60	i	16.00	22.00	1.55	1.18	abcde	1.00	1.50	0.11	0.79	ef	0.64	0.90	0.06
LSD$_{0.001}$	1.55					0.08					0.04				
ANOVA *F*			36.27***					3.30***					4.06***		

\# a, b, ... – values with different letters in columns are significantly different (P<0.001).

crossing the colpus at the equator and dividing it into two parts, formed by two bulges of the ectexine that meet in the middle (Figure 3). These equatorial extensions were of the same or unequal length.

Exine ornamentation in all species was striate-perforate, with the exception of *R. odoratus*, which had a verrucate ornamentation with small perforations (Figure 3). Exine ornamentation elements were highly variable (Figure 3). Striae and grooves usually ran parallel to colpori and the polar axis, but frequently they also formed fingerprint-like twists. Striae were straight or forked and of varying length, width and height.

The investigated pollen of individual *Rubus* species was classified according to the striate exine ornamentation classification proposed by Ueda (1992). The cited author distinguished six types (I-VI) and six subtypes (I-III, each A and B). In our study only subtypes IIA and IIIA were found (Figure 3). Subtype IIA had prominent perforations between ridges and with short intervals of ridges. Subtype IIIA had more distinct ridges due to their steep slope; the ridges had small diameter (0.15~0.30 μm). Four species (*R. allegheniensis, R. armeniacus, R. xanthocarpus, R. laciniatus*) belonged to the IIA subtype, which was characterised by distinct striae, narrow grooves and frequently by prominent, numerous perforations. Subtype IIIA was represented by only one species (*R. canadensis*) with higher (i.e. more conspicuous than in subtype IIA), fairly narrow striae in comparison with subtype IIA. Striate-verrucate exine ornamentation with flattened and wavy muri and small, few perforations was found only in *R. odoratus*.

Interspecific variability of pollen grains

Results of MANOVA indicated that the all the *Rubus* samples were significantly different when investigated in terms of all the six quantitative traits jointly

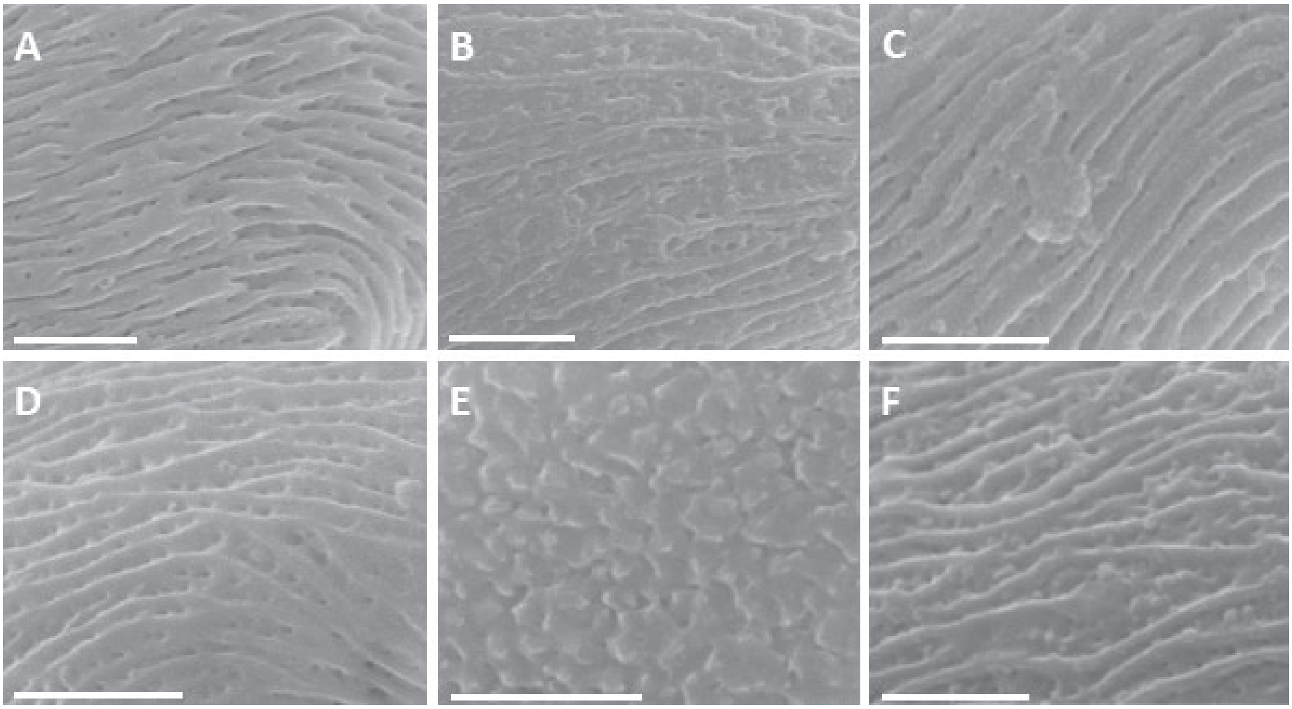

Figure 3. Types and subtypes of striate exine ornamentation. (A) *R. allegheniensis* (subtype-IIA), (B) *R. armeniacus* (IIA), (C) *R. canadensis* (IIIA), (D) *R. laciniatus* (IIA), (E) *R. odoratus* (verrucate ornamentation), (F) *R. xanthocarpus* (IIA). Scale bars = 2 μm.

(Wilk's l=0.1495; $F_{23;696}$=11.27; P<0.0001). The analysis of variance for the six biometric traits [P ($F_{23;696}$=47.25), Le ($F_{23;696}$=29.89), d ($F_{23;696}$=26.10), E ($F_{23;696}$=36.27), P/E ($F_{23;696}$=3.30) and Le/P ($F_{23;696}$=4.06)] confirmed variability of the tested species at a significance level α=0.001 (Tables 3 and 4). The mean values and standard deviations for the observed traits indicated a high variability among the tested samples, for which significant differences were found in terms of all the analysed morphological traits (Tables 3 and 4). The density plots of P and P/E by *Rubus* species samples are presented in Figures 4 and 5, respectively. Variability of the observed traits across all *Rubus* species on the basis of *F*-statistics ranked as follows: P>E>Le>d>Le/P>P/E. The ranking of variability in the *Rubus* species calculated as a sum of coefficients of variations for the six observed traits is: *R. allegheniensis* (sample 1), > *R. laciniatus* (4) > *R. allegheniensis* (2) > *R. canadensis* (3) > *R. laciniatus* (3) > *R. canadensis* (2) > *R. canadensis* (4) > *R. laciniatus* (2) > *R. allegheniensis* (4) > *R. armeniacus* (5) > *R. xanthocarpus* > *R. odoratus* (5) > *R. laciniatus* (1) > *R. armeniacus* (3) > *R. odoratus* (2) > *R. odoratus* (4) > *R. canadensis* (1) > *R. odoratus* (3) > *R. armeniacus* (1) > *R. odoratus* (1) > *R. allegheniensis* (3) > *R. armeniacus* (4) > *R. armeniacus* (2) > *R. laciniatus* (5).

The performed correlation analysis indicated statistically significant correlation coefficients for six out of 15 coefficients (Figure 6). Trait P was significantly correlated with Le (r=0.969), d (0.508) and E (0.955). Additionally, E was correlated with Le (0.915) and d (0.551). A negative significant correlation was observed between d and Le/P (-0.615).

In the presented dendrogram, as a result of the nearest neighbour grouping using the Euclidean distances method, the *Rubus* samples were divided into two groups (Figure 7). The first group comprised 14 samples, while the other was composed of the other 10 samples. In the dendrogram (Figure 7) a trend towards clustering of samples of individual species is observed, indicating similar traits of their pollen grains. The first group comprised almost all samples of *R. laciniatus* (samples 1-4), *R. armeniacus* (samples 1-5), and *R. allegheniensis* (samples 1-4), while the other group was composed of samples of *R. canadensis* and *R. odoratus* (Figure 7).

Individual traits vary in terms of their importance and share in the joint multivariate variation. A study on the multivariate variation for *Rubus* species samples includes also identification of the most important traits in the multivariate variation of species. Analysis of canonical variables is a statistical tool making it possible to solve the problem of multivariate relationships (Seidler-Łożykowska et al. 2013, Lahuta et al. 2018, Wrońska-Pilarek et al. 2018, Bocianowski and Majchrzak 2019). Figure 8 shows vari-

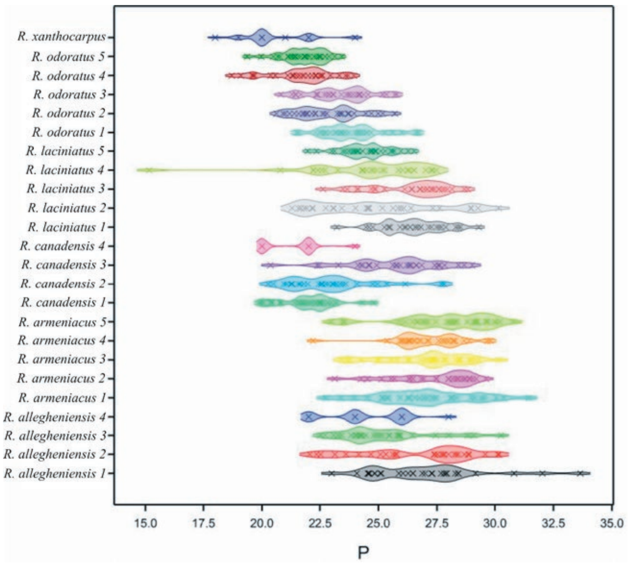

Figure 4. The density plot of P for individual *Rubus* species. The point "x" denotes trait observation for particular species. The points are plotted along a line, with a kernel density smooth on either side to indicate the density of points along the line.

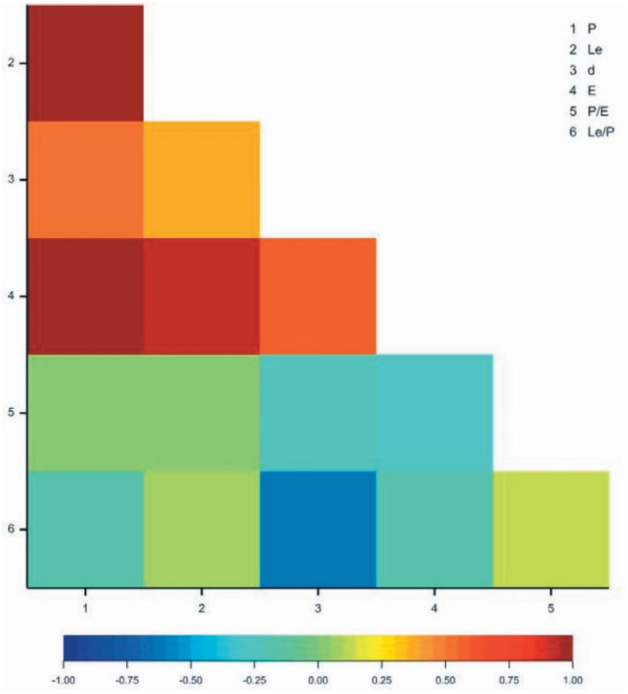

Figure 6. Heatmap for linear Pearson' correlation coefficients between observed traits (r_{cr}=0.406). The heatmap provides a graphical representation of a correlation matrix between pairs of the observed traits. Each element of the correlation matrix is represented by a shaded rectangle indicating the value at that location, using a different colour or shading density.

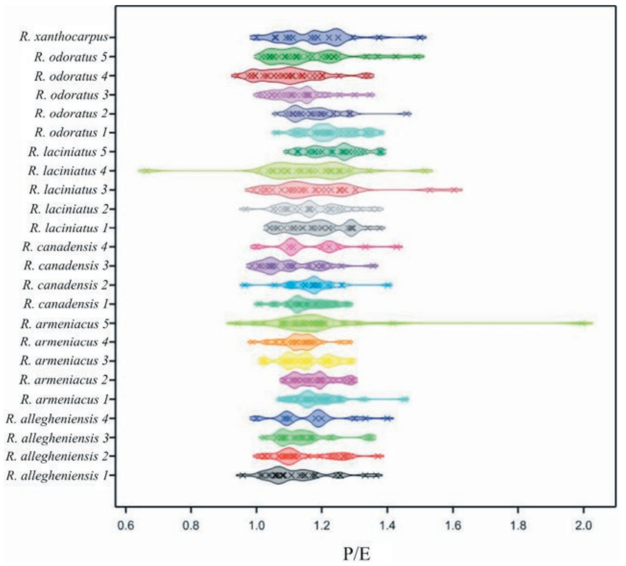

Figure 5. The density plot of P/E for individual *Rubus* species. The point "x" denotes trait observation for particular species. The points are plotted along a line, with a kernel density smooth on either side to indicate the density of points along the line.

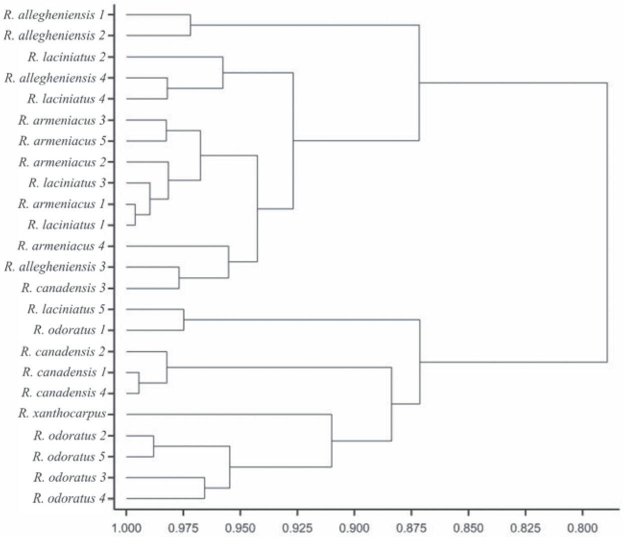

Figure 7. Dendrogram of the nearest neighbour cluster grouping of *Rubus* species on the basis of six traits. The length of the lines denotes similarity/distance between two species or between two groups of species and determined hierarchical clusters.

ability of the six pollen grain traits in 24 studied *Rubus* samples in terms of the first two canonical variables. In the graph the coordinates of the point for particular species are the values for the first and second canonical variables, respectively. The first two canonical variables

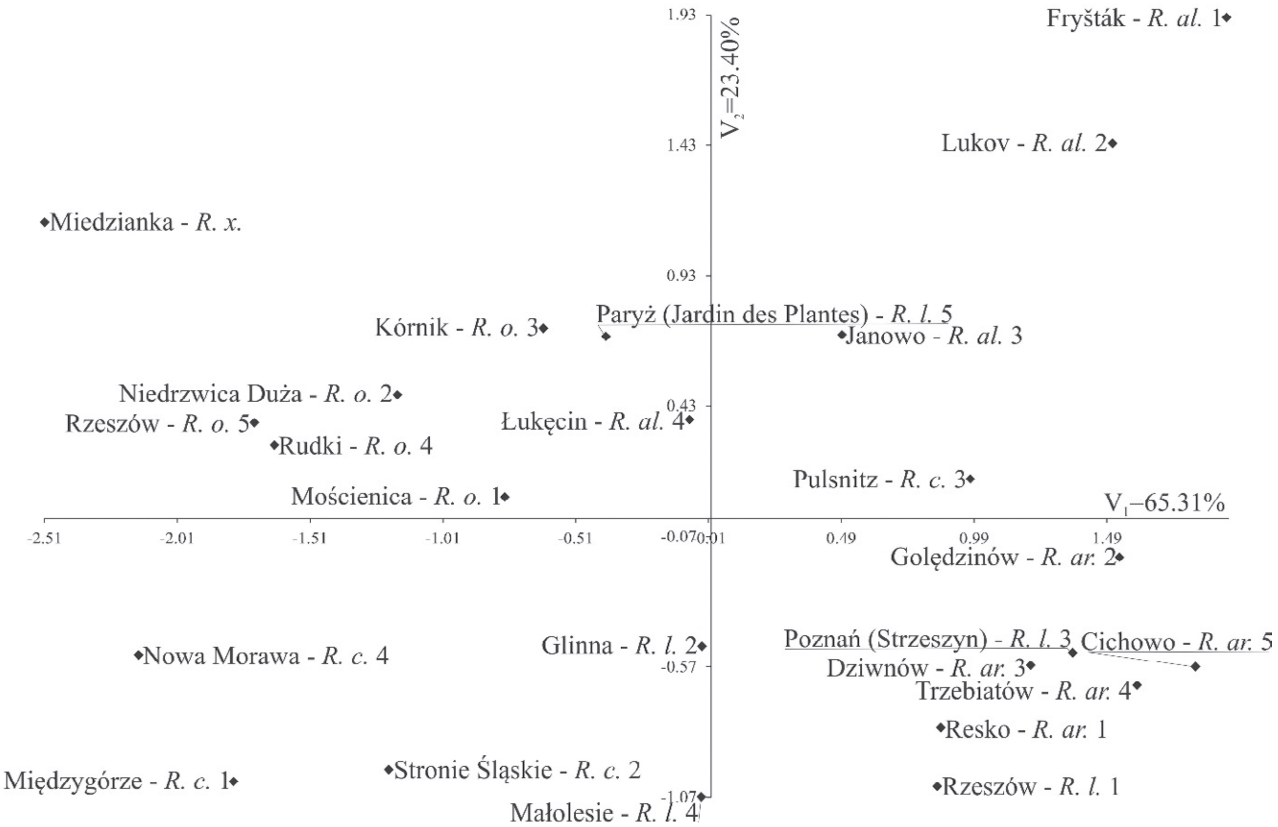

Figure 8. Distribution of 24 *Rubus* species in the space of the first two canonical variables.

accounted for 88.71% of the total multivariate variability among the individual species samples (Table 5, Figure 8). The most significant, positive, linear relationship between the first canonical variables was found for P, Le, d and E (Table 5). The second canonical variable was significantly positively correlated with d and negatively correlated with Le/P (Table 5). The greatest variation in terms of all the traits jointly (measured Mahalanobis distances) was found for *R. allegheniensis* (sample 2) and *R. canadensis* (sample 4), with the Mahalanobis distance between them amounting to 4.78 (Table 6). The greatest similarity (0.56) was found for *R. armeniacus* (sample 1) and *R. armeniacus* (sample 4). The Mahalanobis distance is unitless and scale-invariant, and takes into account the correlations of the data set. On the basis of Mahalanobis distances we identified samples showing greatest similarity for all observed traits jointly.

Table 5. Correlation coefficients between the first two canonical variables and original traits.

Trait	First canonical variable	Second canonical variable
P	0.989***	-0.102
Le	0.942***	-0.256
d	0.595**	0.802***
E	0.982***	-0.035
P/E	-0.116	-0.195
Le/P	-0.216	-0.623**
Percentage variation	65.31%	23.40%

** P<0.01; *** P<0.001

DISCUSSION

In the lists of alien species of Europe (Lambdon et al. 2008; DAISIE 2009; Kurtto et al. 2010), the studied *Rubus* species have the status of 'aliens in Europe' and naturalised within the continent (*R. allegheniensis, R. armeniacus, R. canadensis, R odoratus, R. xanthocarpus*) or 'aliens of European origin' - naturalised and neophytes within the continent (*R. laciniatus*). We studied all the six bramble species considered by Tokarska-Guzik et al. (2012) to be alien for Poland. All these species are domesticated kenophytes in Poland, occur-

Table 6. Mahalanobis' distances between studied *Rubus* species.

Rubus species		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
R. allegheniensis 2	2	1.03																						
R. allegheniensis 3	3	1.96	1.52																					
R. allegheniensis 4	4	2.61	2.25	0.78																				
R. armeniacus 1	5	2.76	2.20	1.56	1.81																			
R. armeniacus 2	6	2.29	1.78	1.47	1.92	0.56																		
R. armeniacus 3	7	2.59	2.37	1.67	1.81	1.09	1.09																	
R. armeniacus 4	8	2.72	2.17	2.02	2.38	1.19	1.10	1.25																
R. armeniacus 5	9	2.57	2.29	2.04	2.30	1.25	1.12	0.79	1.02															
R. canadensis 1	10	4.76	4.17	2.88	2.28	3.11	3.51	3.29	3.51	3.73														
R. canadensis 2	11	4.29	3.72	2.40	1.82	2.53	2.93	2.69	2.98	3.13	0.63													
R. canadensis 3	12	2.11	1.77	1.31	1.60	1.66	1.52	1.23	1.28	1.38	3.13	2.63												
R. canadensis 4	13	4.78	4.21	2.94	2.33	3.45	3.79	3.61	3.85	4.05	0.62	1.08	3.31											
R. laciniatus 1	14	3.00	2.46	1.65	1.70	0.69	1.03	0.92	1.12	1.14	2.72	2.12	1.42	3.09										
R. laciniatus 2	15	3.18	2.54	1.45	1.28	1.38	1.68	1.66	1.74	1.98	1.91	1.36	1.54	2.20	0.99									
R. laciniatus 3	16	3.25	2.63	2.04	2.10	1.16	1.41	1.34	0.99	1.28	2.77	2.22	1.50	3.16	0.63	1.12								
R. laciniatus 4	17	3.64	2.98	2.03	1.79	1.71	2.10	1.99	1.89	2.18	1.87	1.41	1.85	2.25	1.32	0.99	1.23							
R. laciniatus 5	18	2.88	2.31	1.32	1.14	2.15	2.23	2.47	2.78	2.73	2.44	2.06	2.20	2.38	2.08	1.51	2.36	2.17						
R. odoratus 1	19	3.40	2.86	1.65	1.11	2.24	2.46	2.42	2.81	2.76	1.73	1.34	2.22	1.72	1.96	1.24	2.18	1.75	0.82					
R. odoratus 2	20	3.49	2.95	1.78	1.34	2.66	2.83	2.83	3.11	3.23	1.68	1.48	2.41	1.50	2.41	1.52	2.59	2.11	1.07	0.80				
R. odoratus 3	21	2.88	2.38	1.25	1.08	2.37	2.42	2.47	2.68	2.89	2.14	1.85	1.89	2.05	2.19	1.41	2.40	2.08	1.17	1.23	0.78			
R. odoratus 4	22	4.01	3.50	2.36	1.96	3.19	3.38	3.25	3.41	3.71	1.50	1.56	2.71	1.26	2.87	1.93	2.95	2.34	2.04	1.67	1.02	1.19		
R. odoratus 5	23	4.00	3.47	2.36	1.88	3.22	3.41	3.31	3.53	3.69	1.47	1.53	2.78	1.11	2.88	1.94	2.96	2.31	1.71	1.28	0.72	1.27	0.75	
R. xanthocarpus 1	24	4.60	4.11	3.19	2.82	4.19	4.32	4.33	4.52	4.71	2.41	2.60	3.75	1.92	3.92	2.99	4.01	3.48	2.38	2.23	1.57	2.02	1.46	1.23

$D_{0.05}=2.73$

ring naturally in North America and Asia; except for *R. laciniatus* – native to Eurasia, which in Poland is an invasive anthropophyte (www.iop.krakow.pl). In turn, *R. xanthocarpus* colonise anthropogenic plant communities, *R. armeniacus* – anthropogenic and seminatural ones, while the other four species are found in anthropogenic, seminatural as well as natural communities (Zieliński 1991; Bróż and Zieliński 1993; Weber 1993; Tokarska-Guzik et al. 2012).

All palynologists agree that the most important pollen features for the species in the genus *Rubus* are the width, number and course of grooves (muri) and the width of the striae, as well as the number and diameter of perforations (Ueda and Tomita 1989; Ueda and Okada 1994; Tomlik-Wyremblewska 1995, 2000; Li et al. 2001; Wrońska-Pilarek et al. 2006, 2012, Xiong et al. 2019; Lechowicz et al. 2020). Some authors considered pollen size and shape as potentially important features in the diagnosis of the analysed *Rubus* species (Candau and Romanos 1987; Monasterio-Huelin and Pardo 1995; Wrońska-Pilarek et al. 2012; Ghosh and Saha 2017), while others claimed that they have no diagnostic significance (e.g. Li et al. 2001; Tomlik-Wyremblewska et al. 2004). Based on Candau and Romanos (1987); Monasterio-Huelin and Pardo (1995); Wrońska-Pilarek et al. (2012) or Ghosh and Saha (2017) and our results, we partially agree with they former opinion, because the length of the polar axis (P) has been an important feature.

According to current palynological studies, European native bramble species are less variable in terms of exine ornamentation than Asian ones. Comprehensive palynological studies by Li et al. (2001), Xiong et al. (2019) and Lechowicz et al. (2020) confirmed this thesis. Li *et al.* (2001) examined 103 *Rubus* species from China, which belonged to four types and 11 subtypes, and Xiong et al. (2019) divided pollen grains of 168 taxa into six types and three subtypes of exine ornamentation. However, in the study of Lechowicz et al. (2020) in the examined 58 European *Rubus* species only two types of exine ornamentation were found (striate and striate-verrucate with microgranules). Other European palynologists distinguished in brambles mainly striate or striate-perforate exine ornamentation (Reitsma 1966; Eide 1981a, 1981b; Monasterio-Huelin and Pardo 1995; Tomlik-Wyremblewska 1995, 2000; Wrońska-Pilarek et al. 2006, 2012; Polyakova and Gataulina 2008; Ghosh and Saha 2017; Kasalkheh et al. 2017). Ueda and Tomita (1989) and Ueda (1992) distinguished six types and six subtypes of striate exine ornamentation in species from the genus *Rosa* and the family Rosaceae, including the genus *Rubus*. Hebda and Chinnappa (1990) divided Canadian rosaceous pollen types into two broad categories based on sculpturing. In the current study the analysed *Rubus* pollen grains were classified into two sculpturing subtypes (II A, III A), which were most frequently represented among the European native bramble pollen (e.g. Reitsma 1966; Eide 1981a, 1981b; Wrońska-Pilarek et al. 2012; Kasalkheh et al. 2017; Lechowicz et al. 2020).

Authors of many palynological studies (e.g. Tomlik-Wyremblewska 1995, 2000; Li et al. 2001; Wrońska-Pilarek et al. 2012) reported that the bridges are located in most of the studied *Rubus* species. In a study by Lechowicz et al. (2020) and in our study, bridges were observed in all the analysed species. This structure was not used as a basis for the identification of species, because they were very similar in all species.

In the opinion of Li et al. (2001), pollen shape in *Rubus* varied from spheroidal, subspheroidal, prolate and perpolate, to occasionally rhomboid and hexagonal in the equatorial view. In turn, Monasterio-Huelin and Pardo (1995) stated that they were only prolate or spheroidal, while other authors distinguished several pollen shape types - subprolate, prolate spheroidal, prolate or perprolate (Tomlik-Wyremblewska 1995, 2000; Wrońska-Pilarek et al. 2006, 2012; Ghosh and Saha 2017; Kasalkheh et al. 2017). Xiong et al. (2019) showed that pollen shape varies from suboblate, spheroidal, subprolate and prolate to perprolate, while Lechowicz et al. (2020) distinguished the greatest number, i.e. six types of pollen shape (subprolate**,** prolate-spheroidal, prolate, spheroidal, oblate-spheroidal and perprolate). We agree with the opinions by Tomlik-Wyremblewska (1995, 2000) and Lechowicz et al. (2020) that pollen shape turned out to be a poor criterion in identifying bramble species, because most pollen grains (ca. 90%) are similar in shape – either subprolate or prolate-spheroidal.

So far, morphological features of pollen grains have not been analysed in terms of their impact on the invasive character of the alien bramble species. Our results showed no differences in the pollen structure of the invasive *R. laciniatus* compared to the other five studied alien bramble species (Figures 7 and 8), but also with dozens of *Rubus* species native to Poland and Europe described by our team in another paper (Lechowicz et al. 2020). It may be stated that pollen morphology does not determine expansion of the studied species. Pollen viability and germination may have a greater impact on the expansive properties of such bramble species as *R. laciniatus*. The arrangement of the investigated samples on the dendrogram (Figure 7) showed that samples of the same species (e.g. *R. allegheniensis, R. armeniacus, R. odoratus*) often form clusters, except for *R. laciniatus*. This means that *R. laciniatus* pollen grains were more similar to those of other species than to one another.

CONCLUSIONS

- Interspecific variability of pollen features was found with but the highest and the lowest variability observed for pollen of the same bramble species (e.g. *R. allegheniensis* - samples 1 and 3, *R. laciniatus* - samples 4 and 5 or *R. armeniacus* - samples 5 and 2) (Figure7).
- In the case of the invasive anthropophyte (*R. laciniatus*), the greatest intraspecific variability was found, as individuals of this species differed the most from each other (Figure 7), while no interspecies variation with other non-invasive bramble species was found. Thus so it may be assumed that pollen morphology probably does not affect invasive traits of this species.
- Results of our studies fill the gap in knowledge on pollen structure of species from the genus *Rubus* alien for Poland and Europe. They may be used in further studies on reproduction of these species (e.g. pollen viability and fertility), facilitating identification of traits determining their expansive character.

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Additions to the lichen genus *Rhizocarpon* in Pakistan and their comparative analysis

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Abstract. As part of a comprehensive study of lichen diversity of northern areas of Pakistan using molecular and morphological approaches, we found four species of the genus *Rhizocarpon*. The analysis revealed two new species in the lichen biota of Pakistan namely, *Rhizocarpon lavatum* and *Rhizocarpon petraeum*, while the other two, *Rhizocarpon disporum* and *Rhizocarpon geminatum* are reported for the second time, from new localities. In comparison to literature information and GenBank sequences of the same taxa, variation in the morpho-anatomical features and nucleotide differences in the ITS marker of nrDNA have been documented. Descriptions and phylogenetic analysis of the taxa are given, along with information on ecology and distribution.

Keywords: Khyber Pakhtunkhwa, Lichens, Rhizocarpaceae, Taxonomy.

INTRODUCTION

Rhizocarpon Ramond ex DC. (Rhizocarpaceae, lichenized Ascomycota) is a large genus of lichenized or lichenicolous fungi, comprising approximately 200 currently accepted species (Davydov and Yakovchenko 2017). The members of the genus are usually recognized by a crustose thallus, a distinct prothallus, black lecideine apothecia, Rhizocarpon-type asci, and hyaline to brown, halonate ascospores that can be transversely septate or submuriform to muriform (Fletcher et al.2009; McCarthy and Elix 2014). The genus has a wide distribution throughout temperate to polar and alpine regions (Feuerer and Timdal 2004; Ihlen 2004; Kirk et al. 2008), occurring on siliceous or calcareous rocks (Moniri et al. 2009).

Ihlen and Ekman (2002) proposed a variety of infrageneric arrangement in *Rhizocarpon*. Previously suggested infrageneric arrangements based on presence or absence of the yellow substance rhizocarpic acid in the thallus or the septation of the ascospores are unnatural. Some species with grey or brown thallus may have evolved from a yellow ancestor. They have also justified that during the course of evolution, spore septation and colour, amyloidity of the thalline medulla, and the presence of stictic acid complex and rhizocarpic acid are changed multiple times (Ihlen and Ekman, 2002). The most widely-used classification is the one proposed by Thomson (1967), who divided the genus into taxa with a yellow thallus containing the pigment rhizocarpic acid (subgenus *Rhizocarpon*), and taxa with white, grey or brown thalli lacking rhizocarpic acid (subgenus *Phaeothallus*) (Ihlen 2004).

Only four species of this genus were so far known to occur in Pakistan, i.e., *R. disporum* (Nägeli ex Hepp) Müll.Arg., *R. geminatum* Körb. *R. geographicum* (L.) DC. (Ahmad 1965; Poelt 1961) and *R. viridiatrum* (Wulfen) Körb. (Ahmad 1965; Singh and Sinha 2010; Aptroot and Iqbal 2012). This study adds two more to the list of *Rhizocarpon* species of Pakistan.

MATERIALS AND METHODS

Morphological and chemical studies

The collections were made during a lichen survey of different sites of Azad Jammu and Kashmir, Pakistan, in 2019. Morphological characters were observed under a stereomicroscope (Meiji Techno, EMZ-5TR, Japan). Standard microscopy and spot tests (Hale 1979) were used for further identification. Measurements were made from free hand sections of apothecia mounted in water on glass slides. The sections were observed with a compound microscope (MX4300H, Meiji Techno, Japan).

DNA extraction and PCR amplification

We extracted fungal DNA from the thallus using a 2% CTAB protocol (Gardes and Bruns 1993). Molecular data were generated for the internal transcribed spacer (ITS) region. The primer pair ITS1F (Gardes and Bruns 1993) and ITS4 (White et al.1990) was used to amplify the ITS region under the PCR conditions used by Khan et al. (2018). PCR products were visualized in a 1 % agarose gel (Sambrook and Russell 2001) and sent to BGI Hong Kong, for sequencing.

Phylogenetic analysis

The ITS locus was amplified and sequenced for all specimens yielded fragments of about 700-800 bp each. The BioEdit sequence alignment editor was used to reassemble forward and reverse sequences (Hall 2005). The nucleotide sequence comparison was performed using the Basic Local Alignment Search Tool (BLAST) of the National Centre for Biotechnology Information (NCBI) (Altschul et al. 1990). The multiple sequence alignment was performed using MAFFT v.7 with all parameters set to default values (Katoh and Standley 2013). The phylogenetic tree was executed using software MEGA 10.0 (Kumar et al. 2018) with ML method based on Tamura 3-parameter model. Nodal support was evaluated using the "rapid bootstrapping" option with 1,000 replicates. For rooting purpose of the tree, *Catolechia wahlenbergii* (Ach.) Körb. (HQ650649) was selected as an out-group.

Phylogeny

Closest matching sequences were downloaded from GenBank for subsequent phylogenetic analysis. A total of 47 ITS rDNA sequences were analysed. The data matrix had 523 unambiguously aligned nucleotide positions among which 246 were constant, 271 variable, 213 parsimony-informative and 57 were singleton variants.

The Pakistani collections clustered in well supported groups (Figure 5). The sequence of Pakistani *R. geminatum* clustered with sequences from Norway (KY266908, AF483614), Svalbard (KP314320) and China (MK629880) of the same taxon. The affinity of these to the sister branch including *R. bolanderi* (Tuck.) Herre and *R. disporum* group which also contain the sequence of *R. disporum* from Pakistan. The Pakistani *R. petraeum* sequence clustered with *R. petraeum* (HQ605942) from Turkey to which the same taxon from Norway (AF483609) appeared as sister. The fourth sequence of Pakistani specimens clustered with *R. lavatum* reported from the same countries as those of *R. petraeum*.

TAXONOMIC TREATMENT

Rhizocarpon disporum (Nägeli ex Hepp) Müll. Arg., Revue mycol., Toulouse 1(4): 170. 1879 (Figure 1)

Thallus: Crustose-areolate, epilithic, effuse, dull, 13–14 cm across, pruinose. Areoles: immarginate, smooth, plane to convex, irregular, inflated, 0.3–1 mm in diameter. Colour: dark brown to greyish-black. Prothallus: distinct, black, prominent at margins or in between the areoles. Cortex: brown upper side, hyaline inside, paraplectenchymatous, 12–20 µm thick, with epinecral layer 10–20 µm thick, cells isodiametric, 8–10 µm in diameter. Medulla: 200–300 µm thick, hyphae white, 2–4 µm wide. Algal layer: 85–125 µm thick, uneven, algae dispersed, mostly confined to upper portion of medulla, cells chlorococcoid, sphaerical to subsphaerical, 12–20 µm in diameter.

Apothecia: frequent, present among or at the sides of areoles; Disc: black, adnate, pruinose, strongly con-

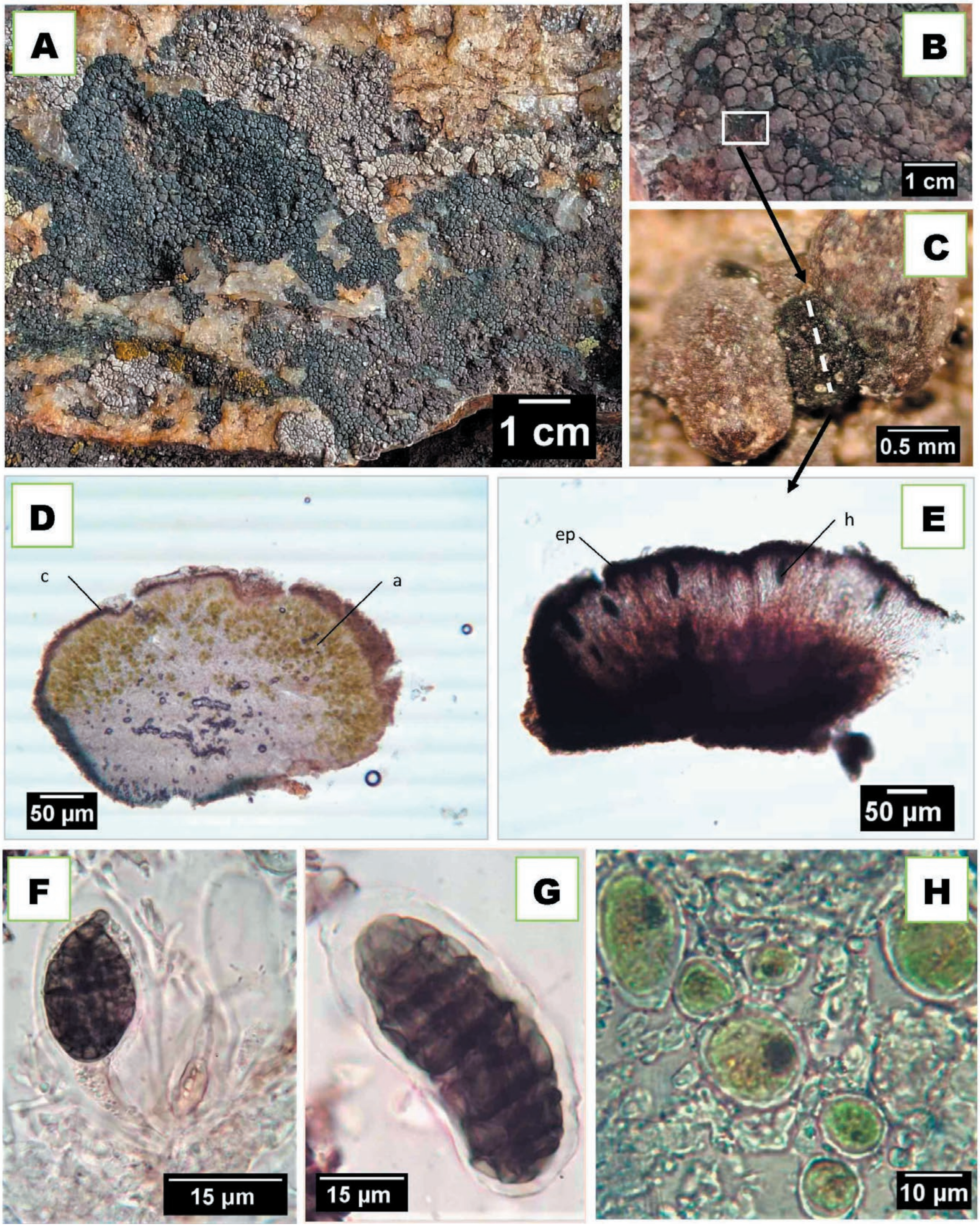


Figure 1. (A-H): ***Rhizocarpon disporum.*** **A:** Thallus; **B:** Areoles; **C:** Apothecium; **D:** Cross section of thallus (c: cortex; a: algal layer); **E:** Cross section of an apothecium (h: hymenium; ep: epihymenium); **F:** 1-spored asci; **G:** Ascospore; **H:** Chlorococcoid photobiont.

vex, 0.3–0.8 mm in diameter. Margins: indistinct. Exciple: thick, distinct, black, 40–50 µm wide. Paraphyses: hyaline, septate, brown capitate, apex swollen, 3–4 µm wide. Epihymenium: blackish brown, 12–18 µm tall. Hymenium: hyaline, 80–125 µm tall. Hypothecium: dark brown, 40–60 µm tall. Asci: hyaline, clavate, 1-spored, 60–75 µm × 30–35 µm. Ascospores: initially olive green becoming dark brown or blackish when mature, halonate, 3–5 µm thick, slightly curved, often tapered, muriform, broadly to narrowly ellipsoid, 40–55 µm × 20–28 µm.

Chemistry: K–, C–, KC–: According to literature, it contains stictic acid and/or norstictic acid (Timdal & Holtan-Hartwig 1988; Feuerer & Timdal 2004; Galloway 2007) or to lack lichen substances (Timdal & Holtan-Hartwig 1988).

Material Examined

PAKISTAN. Naran: Babusar top, 35°14’N, 74°04’E; 4,173 m; moist temperate forest, on rock; July 21, 2019, *A.N. Khalid & K.Habib,* (BAB-107), (LAH36713).

Substrate and Ecology

It was found in temperate climate at an altitude of 4,173 m.a.s.l., growing on rocks exposed to sun and rain. The region has hilly topography having maximum and minimum temperature of 35^{o}C and -8C, respectively, and receive heavy snowfall in winter.

Distribution

It is known from Europe (Austria, Switzerland, Czech Republic, Estonia, France, Germany, Norway, Sweden, Spain) (Timdal & Holtan-Hartwig 1988; Feuerer 1991; Golubkov and Matwiejuk 2009; https://www.gbif.org/); North America (Greenland, Canada, Mexico, US) (Feuerer & Timdal 2004); Australia, New Zealand (McCarthy and Elix 2014; Galloway 2007), Antarctica (Øvstedal and Lewis Smith 2001) and Asia (Iran, Turkey, Pakistan) (Abbas et al. 2001; https://www.gbif.org/; Aptroot & Iqbal 2012).

Comments

Rhizocarpon disporum is characterized by having grey to greyish black, or brown thallus, flat to convex or almost globose areoles, brown ascospores, and monosporous asci (Smith et al. 2009; Nash et al. 2004). The ITS sequence of Pakistani *R. disporum* is exactly similar to the same taxon from Siberia (MK629883, KY680774) indicating they are all the same species. The sequence of *R. disporum* from China (MK629882, MH979407, MH979408), Russia (KY680783) and USA (HQ650708) formed slightly separate branch from the Pakistani and Siberian *R. disporum.* Previously it has been reported from Gilgit-Baltistan, Pakistan (Poelt 1961). Our finding from Babusar Top is the second report of this taxon from Pakistan also represents a new record to Khyber Pakhtunkhwa.

Rhizocarpon geminatum Körb., Syst. lich. germ. (Breslau): 259. 1855 (Figure 2)

Thallus: crustose, epilithic, verrucose, areolate, determinate, 6 cm across, smooth, somewhat glossy, pruinose. Areoles: rounded to irregular, bullate, subglobose to rarely plane, 0.2–1 mm in diameter. Colour: dark brown to black when dry, dark reddish brown when wet. Prothallus: black, present among the areoles. Cortex: blackish, paraplectenchymatous, 12–25 µm thick, with an epinecral layer of 5–10 µm thick, cells rounded, 10–16 µm in diameter. Medulla: hyphae white, 3–4 µm wide. Algal layer: algae evenly distributed throughout thallus, cells chlorococcoid, sphaerical to subsphaerical, 15–20 µm in diameter.

Apothecia: frequent, present between or at the side of areole. Disc: black, smooth, plane to strongly convex, glossy, pruinose, 0.2–0.6 mm in diameter. Margins: indistinct. Exciple: thick, distinct, peripherally black, grey to brown inside, prosoplectenchymatous, 40–55 µm wide. Paraphyses: hyaline, septate, apex swollen, 3–4 µm in width. Epihymenium: dark brown, 12–20 µm tall. Hymenium: hyaline, 130–200 µm tall. Hypothecium: brown, 75–96 µm tall. Asci: hyaline, 2-spored, 55–65 µm × 14–25 µm. Ascospores: pale green initially, becoming dark brown, broadly to narrowly ellipsoid, halonate, muriform, 35–50 µm × 24–32 µm.

Chemistry: K–, C–, KC–: Stictic acid and norstictic acid has been reported or to lack lichen substances according to literature, not examined in the present material (Feuerer 1991; Timdal & Holtan-Hartwig 1988; Øvstedal & Lewis Smith 2001; Feuerer & Timdal 2004; Fletcher et al. 2009; Galloway 2007). McCarthy & Elix (2014) have observed a new chemotype containing only bourgeanic acid as well as the chemotypes with stictic acid and its satellite compounds (constictic, cryptostictic and peristictic acids) or norstictic acid, ±accessory bourgeanic acid.

Material Examined

PAKISTAN. Kaghan Valley: 34°90’N, 73°65’E; 2,409 m; temperate climate, on rocks; July 21, 2019, A.*N. Khalid & K. Habib*, (BAB-108), (LAH36714).

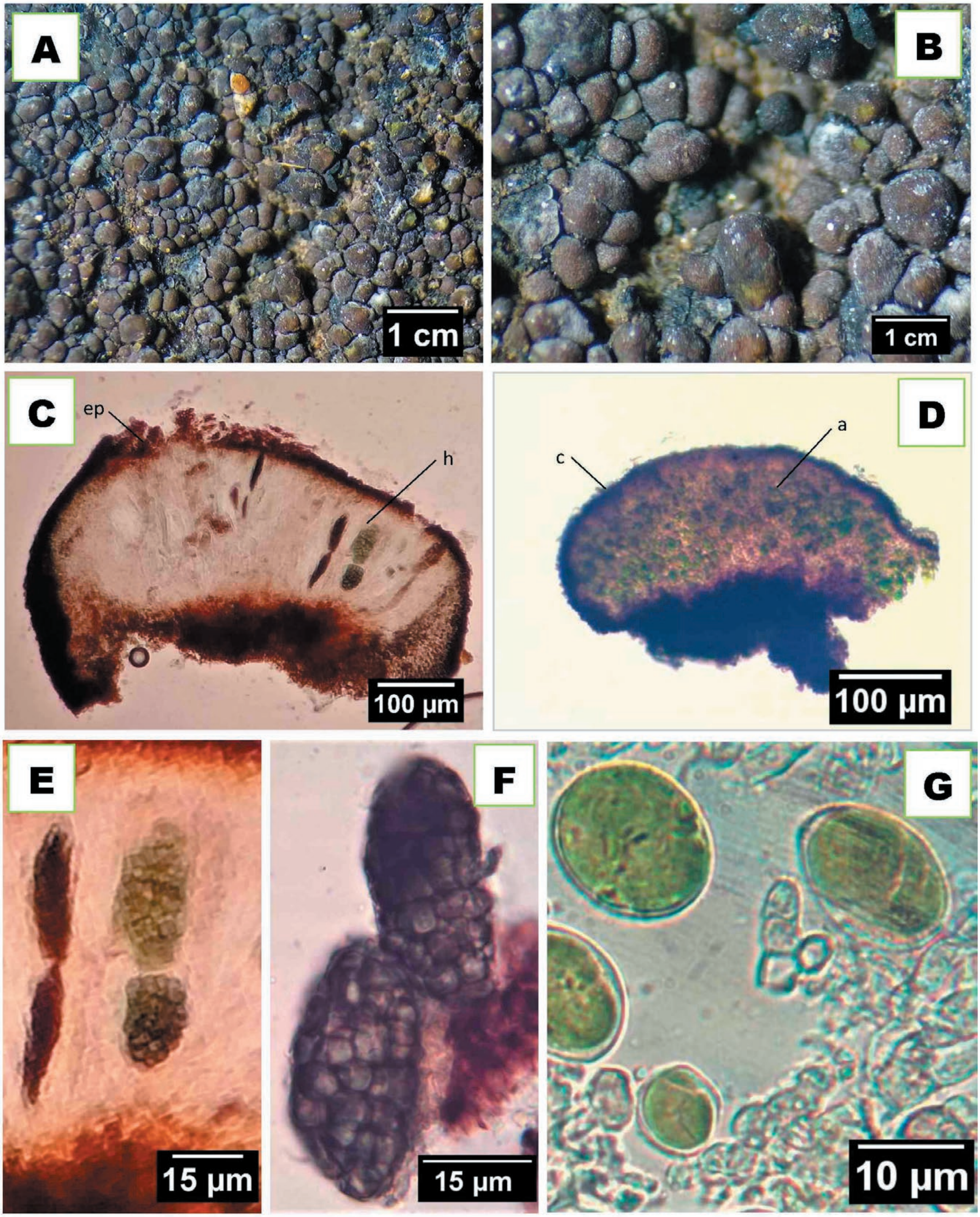


Figure 2. (A-G): *Rhizocarpon geminatum*. A&B: showing verrucose thallus; **C:** Cross section of an apothecium (h: hymenium; ep: epihymenium); **D:** Cross section of thallus (c: cortex; a: algal layer); **E:** Two spores per ascus; **F:** Ascospores; **G:** Chlorococcoid photobiont.

Substrate and Ecology

It was found at an altitude of 2,509 m.a.s.l., growing on sun and rain exposed rocks in partially forested area. The region has hilly topography with mean maximum and minimum temperature: 21.5°C and -2°**C** respectively, and receive heavy snowfall in winter.

Distribution

The species is known from North America, (Nash et al. 2004), Europe (Clauzade and Roux 1985, Timdal and Holtan-Hartwig 1988, Feuerer 1991, Feuerer and Timdal 2004; Fletcher et al. 2009), Antarctica (Øvstedal and Smith 2001), Australia (McCarthy and Elix 2014) and Asia (Ahmad 1965, https://www.gbif.org/).

Comments

Rhizocarpon geminatum is characterized by its dark grey convex-areolate thallus, a non-amyloid medulla, innate apothecia, moderately large ascospores, 2-spored asci and a variable chemistry (McCarthy and Elix 2014). Morphologically, it is close to *R. grande* but that species has 8-spored asci, smaller ascospores, and a thallus containing gyrophoric acid (C+ red) (Smith et al. 2009).

Phylogenetically, there are four nucleotide difference at site 77, 82, 124 and 504 between Pakistani *R. geminatum* and *R. geminatum* (KP314320, MK629880, KY266908) from Svalbard, China and Norway respectively, but similar at the same position for *R. geminatum* reported from Norway (AF483614). Previously, it has been reported from Swat, Pakistan (Ahmad 1965). Our finding from Naran represents a new record for this region and also represents its wide distribution in Pakistan.

Rhizocarpon lavatum (Fr.) Hazsl., Magyar Birodalom Zuzmó-Flórájá: 206. 1884 (Figure 3)

Thallus: crustose, epilithic, rimose–areolate, deeply cracked, 8 cm across, dull. Areoles: smooth, epruinose to slightly pruinose, polygonal to elongated, flat to weakly convex, initially contiguous becoming discrete, 0.4–1.2 mm in diameter, 0.2–0.7 mm thick, replicating by division. Colour: rusty brown to dark brown when dry, pale reddish brown when wet. Prothallus: absent. Cortex: two layered, upper layer blackish, lower layer hyaline, paraplectenchymatous, 25–33 µm thick, with isodiametric cortical cells, 12–15 µm in diameter. Medulla: hyphae white, 3–4 µm wide; Algal layer: 74–93 µm thick, continuous, even, corresponding with areole size, photobiont chlorococcoid, cells globose to subglobose, 10–20 µm in diameter.

Apothecia: frequent, appear between areoles. Disc: brown to black, flat to convex, rounded, rarely irregular, up to 1.2 mm in diameter, dull, slight pruinose. Margins: concolorous to disc, persistent, distinct, continuous, slight glossy, more prominent in younger ones. Exciple: peripherally blackish brown, inside hyaline, poorly differentiated from hypothecium. Paraphyses: hyaline, septate, apex swollen, 2–3 µm wide. Epihymenium: reddish brown, 30–40 µm high. Hymenium: hyaline, 130–155 µm tall. Hypothecium: dark brown, 25–35 µm tall. Asci: hyaline, 8-spored, 70–95 µm × 15–22 µm. Ascospores: narrowly ellipsoid to ellipsoid, halonate, hyaline, eumuriform, 8–17cells in optical view, 24–32 µm × 8–12 µm.

Chemistry: K–, C–, KC–: According to literature, this species lacks lichen substances (Feuerer 1991; Ihlen 2004; Galloway 2007; Fletcher et al. 2009; Joshi et al. 2010; Timdal and Holtan-Hartwig 1988).

Material Examined

PAKISTAN. Azad Jammu & Kashmir: Neelam Valley; Kel, 34° 50’ N, 74° 22’ E; 2,097 m; on rock; July 12, 2019, *A.N. Khalid & K. Habib*, (KL-01), (LAH36711).

Substrate and Ecology

It was found in Himalayan temperate forest, growing on sun and rain exposed rocks at an altitude of 2,097 m.a.s.l. The mean maximum and minimum temperature of the area is 28°C and -2°C, respectively, and receive an average annual rainfall of 749 mm. The dominant tree species around were *Cedrus deodara* (Roxb. ex Lambert) G.Don, *Pinus wallichiana* A.B. Jacks., *Picea smithiana* Boiss., *Abies pindrow* Royle.

Distribution

The species is reported from North and South America (Feuerer & Timdal 2004; Nash et al. 2004), Europe (Clauzade and Roux 1985; Fletcher et al. 2009), Australia, New Zealand (Galloway 2007; McCarthy and Elix 2014), Antarctica (Øvstedal and Smith 2001), and Asia (https://www.gbif.org/; Ahmad 1965).

Comments

Rhizocarpon lavatum is recognized by its large apothecia with thick margin, long narrow ascospores with many cells (15–24), and rimose thin thallus lacking secondary substances (Ihlen, 2004; Wang et al. 2015). Morphologically, *R. lavatum* is close to *Rhizocarpon timdalii* but the later can be distinguished by strongly convex areoles and apothecia. *Rhizocarpon reductum* is another most similar species to *R. lavatum*, but the presence of stictic acid makes it distinct. Apart from that charac-

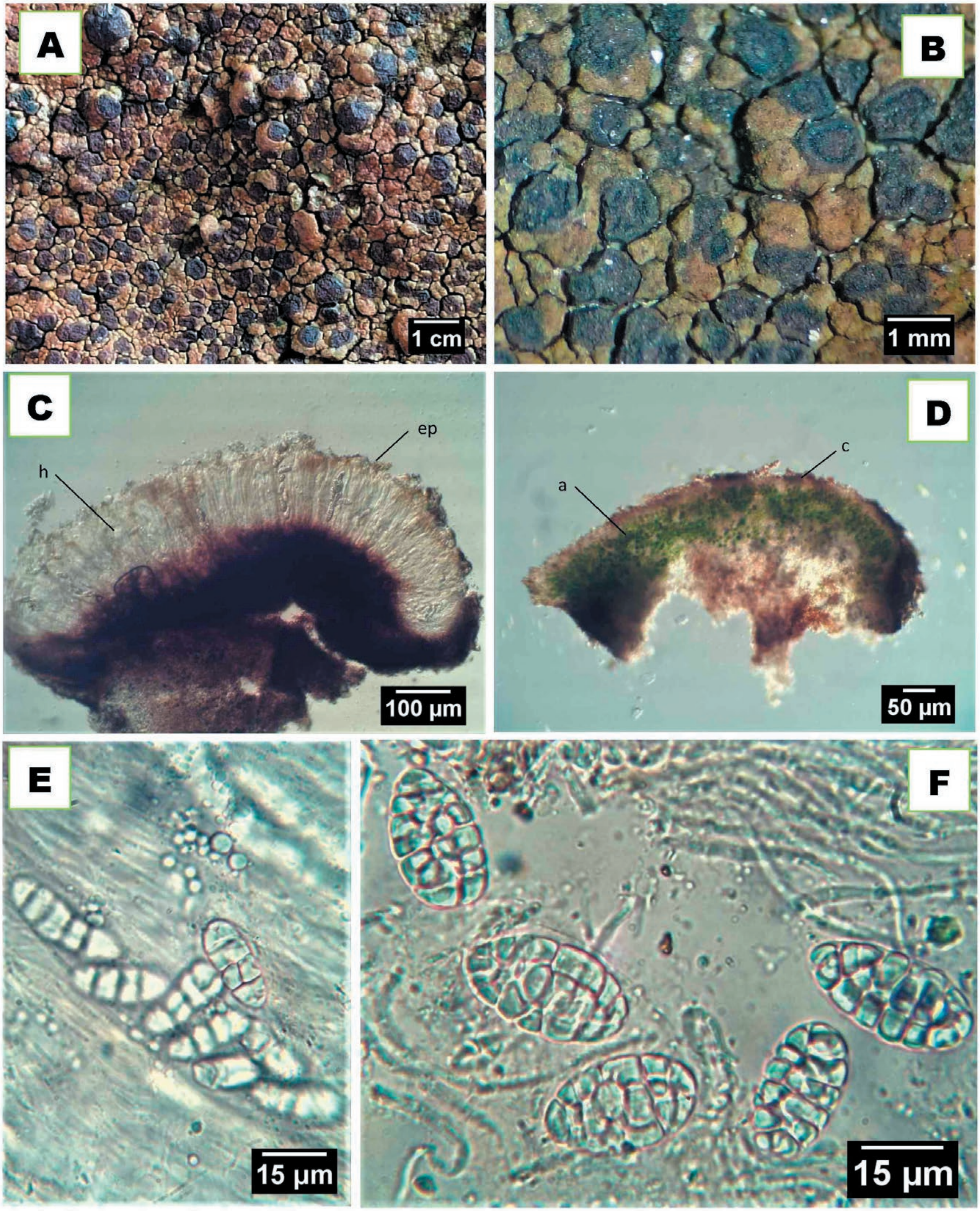


Figure 3. (A-F): ***Rhizocarpon lavatum.*** **A:** showing crustose areolate thallus; **B:** Apothecia; **C:** Cross section of an apothecium (h: hymenium; ep: epihymenium); **D:** Cross section of thallus (c: cortex; a: algal layer); **E:** Eight-spored ascus; **F:** Ascospores.

ter, *R. reductum* is distinct from *R. lavatum* in having more areoles, a thinner apothecial margin, and a taller hymenium (Ihlen 2004). Another similar species, *R. sublavatum*, but it can be separated from *R. lavatum*, by its darker thallus, usually with more areoles, smaller apothecia with a much thinner margin (Ihlen 2004). This study adds *R. lavatum* as a new record to the lichen biota of Pakistan.

Rhizocarpon petraeum (Wulfen) A.Massal., Ric. auton. lich. crost. (Verona): 102. 1852 (Figure 4)

Thallus: crustose, epilithic, areolate, 3–5 cm across, dull, effuse. Areoles: smooth, epruinose to slightly pruinose, polygonal to irregular, 0.2–1.2 mm wide, 0.2–0.6 mm thick, plane to weakly convex, discrete to rarely contiguous, replicating by division, thin towards thallus margins. Colour: dark grey when dry, no change when wet. Prothallus: absent. Cortex: two layered, upper layer dark brown, lower layer hyaline, paraplectenchymatous, 30–45 µm thick, cells isodiametric, 15–25 µm in diameter. Medulla: hyphae white, 3–4 µm wide; Algal layer: 60–95 µm thick, continuous, photobiont chlorococcoid, cells globose 11–15 µm.

Apothecia: innate, frequent, Disc: black, epruinose to slightly pruinose, smooth, somewhat shiny, fissured, mostly flat to weakly convex when old, often irregular to rounded, up to 0.6 mm in diameter. Margins: indistinct, thin. Exciple: dark brown at rim, inside hyaline. Paraphyses: hyaline, septate, branched, anastomosing, apical cells swollen, 2–3 µm wide. Epihymenium: dark brown, 10–25 µm tall. Hymenium: hyaline, 120–160 µm tall. Hypothecium: dark brown, 35–87 µm tall. Asci: hyaline, 8-spored, *Rhizocarpon*-type, 90–115 µm × 20–35 µm. Ascospores: narrowly ellipsoid to ellipsoid, sometimes slightly ovoid, halonate, hyaline, becoming dark when over mature, eumuriform, 8–15 cells in optical view, 20–28 µm × 8–12 µm.

Chemistry: K+ (yellowish), C–; Secondary metabolite Stictic acid is reported according to literature (Ihlen 2004), not examined in the present material.

Material Examined

PAKISTAN. Azad Jammu & Kashmir: Neelam Valley; Kel, 34°50’N, 74°22’E; 2,097 m a.s.l.; moist temperate forest, on rock; July 12, 2019, *A.N. Khalid & K. Habib*, (KL-02), (LAH36712).

Substrate and Ecology

It was found in temperate climate at an altitude of 2,097 m.a.s.l., growing on base-rich rocks. The mean maximum and minimum temperature of the area is 28°C and -2°C, respectively, and receive an average annual rainfall of 749 mm. The dominant tree species around were *Cedrus deodara* (Roxb. ex Lambert) G.Don, *Pinus wallichiana* A.B. Jacks., *Picea smithiana* Boiss., *Abies pindrow* Royle.

Distribution

The species been reported from Europe (Czech Republic, Estonia, France, Germany, Netherland, Norway, Spain, Sweden, UK, Poland) (Ihlen 2004; Fletcher et al. 2009; Golubkov and Matwiejuk 2009), North America (Canada, US) (https://www.gbif.org/), Australia and Asia (Zhao et al. 2013).

Comments

In our phylogenetic analysis, *R. petraeum* and *R. reductum* were found to be strongly supported sister taxa (Figure 5). Morphologically, *R. petraeum* is also very close to *R. reductum,* as both contain stictic acid and usually have the same insoluble lichen pigments in the ascomata, but *R. petraeum* is distinct in having broader apothecia, and larger ascospores containing more cells.

There were two nucleotide differences found in comparison to the sequence of *R. petraeum* (HQ605942) reported from Turkey. This study reports it as a new record to the lichen biota of Pakistan.

COMPARATIVE ANALYSIS AND CONCLUSIONS

Our study on four *Rhizocarpon* species (Table 1) revealed some deviations in the areole size, presence or absence of pruina, height and pigmentation of hymenium and number of cells per ascospore) with in the same taxa published descriptions (Ihlen 2004; Wang et al. 2015).

Rhizocarpon lavatum shows great morphological variation having a wide ecological amplitude (Ihlen 2004) The areole size, pruinose disc of apothecia and lesser number of cells per ascospore of the Pakistani material were found to be in disagreement with the published descriptions (Ihlen 2004; Wang et al. 2015). The areole size was a big difference found between Chinese and Pakistani *R. lavatum* i.e., 0.4–1.2 mm (vs. 0.2-0.4 mm). The height and pigmentation of hymenium in Pakistani material was almost identical to Chinese specimen as compared to Nordic collection in which the height of hymenium was larger (Table 1).

In Pakistani *R. petraeum* we found thickness of areoles, presence and absence of pruina, height and pigmentation of hymenium and number of cells per ascospore in disagreement with the published descrip-

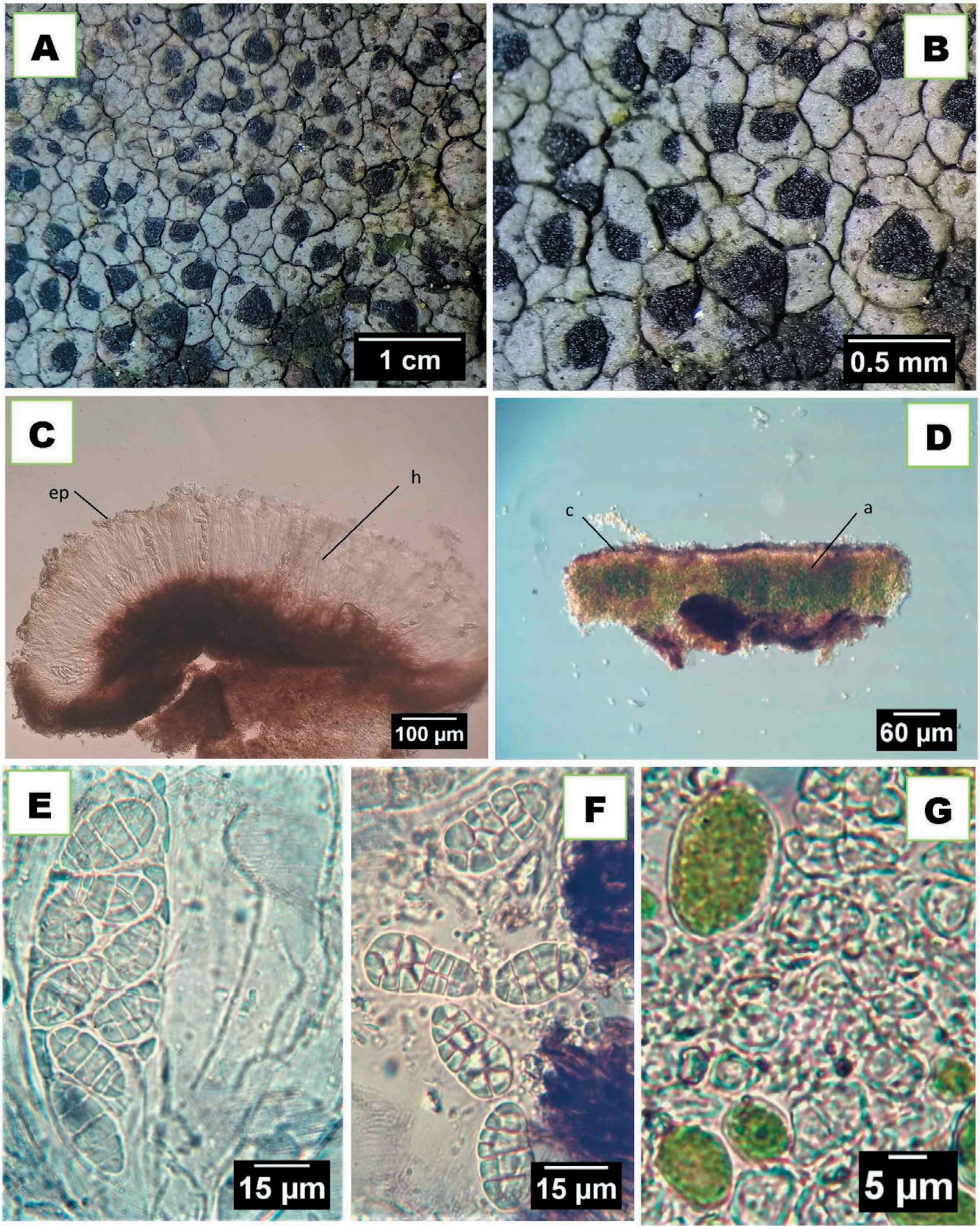


Figure 4. (A-G): ***Rhizocarpon petraeum.*** **A:** showing crustose areolate thallus; **B:** Apothecia; **C:** Cross section of an apothecium (h: hymenium; ep: epihymenium); **D:** Cross section of thallus (c: cortex; a: algal layer); **E:** Eight-spored ascus; **F:** Ascospores; **G:** Chlorococcoid photobiont.

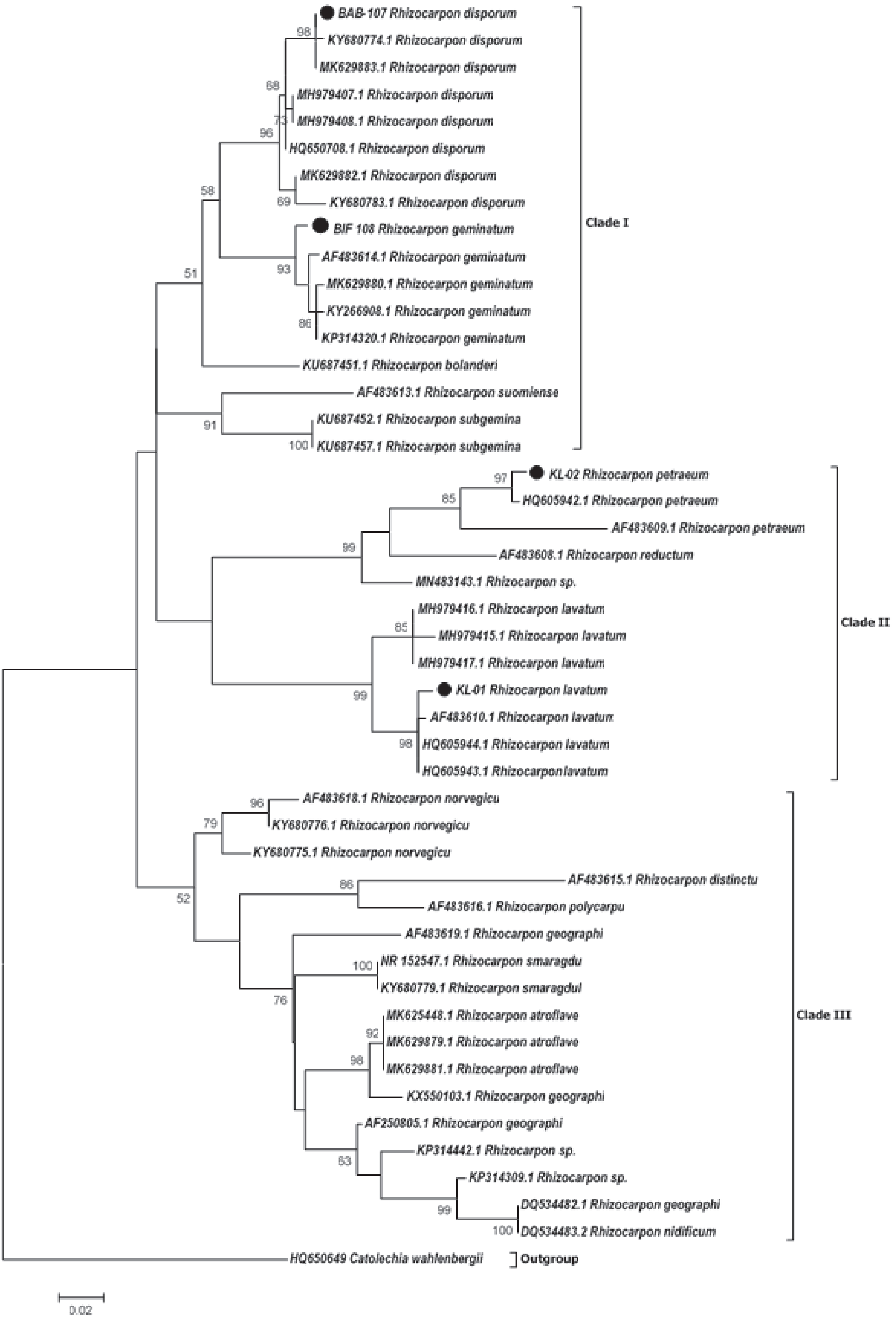
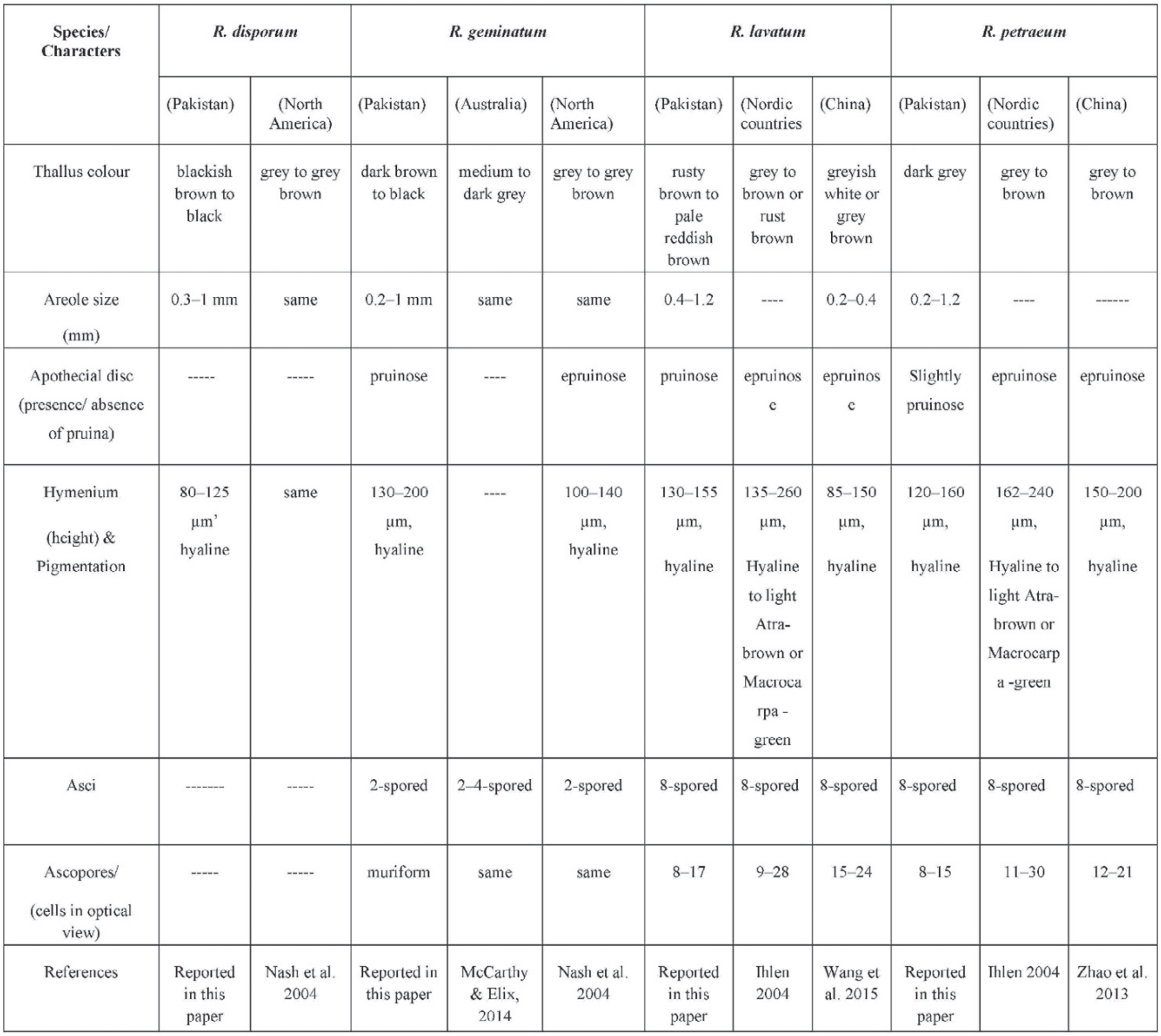


Figure. 5 ITS-based phylogenetic analysis of *Rhizocarpon* species inferred by using Maximum Likelihood method based on Tamura 3 parameter model. The sequences generated from Pakistan are marked with ●.

Table 1. A brief comparison of morpho-anatomical heterogeneity of Pakistani *Rhizocarpon* species with different countries.



Species/ Characters	*R. disporum*		*R. geminatum*			*R. lavatum*			*R. petraeum*		
	(Pakistan)	(North America)	(Pakistan)	(Australia)	(North America)	(Pakistan)	(Nordic countries	(China)	(Pakistan)	(Nordic countries)	(China)
Thallus colour	blackish brown to black	grey to grey brown	dark brown to black	medium to dark grey	grey to grey brown	rusty brown to pale reddish brown	grey to brown or rust brown	greyish white or grey brown	dark grey	grey to brown	grey to brown
Areole size (mm)	0.3–1 mm	same	0.2–1 mm	same	same	0.4–1.2	----	0.2–0.4	0.2–1.2	----	------
Apothecial disc (presence/ absence of pruina)	-----	-----	pruinose	----	epruinose	pruinose	epruinose	epruinose	Slightly pruinose	epruinose	epruinose
Hymenium (height) & Pigmentation	80–125 µm’ hyaline	same	130–200 µm, hyaline	----	100–140 µm, hyaline	130–155 µm, hyaline	135–260 µm, Hyaline to light Atra-brown or Macrocarpa - green	85–150 µm, hyaline	120–160 µm, hyaline	162–240 µm, Hyaline to light Atra-brown or Macrocarpa -green	150–200 µm, hyaline
Asci	-------	-----	2-spored	2–4-spored	2-spored	8-spored	8-spored	8-spored	8-spored	8-spored	8-spored
Ascopores/ (cells in optical view)	-----	-----	muriform	same	same	8–17	9–28	15–24	8–15	11–30	12–21
References	Reported in this paper	Nash et al. 2004	Reported in this paper	McCarthy & Elix, 2014	Nash et al. 2004	Reported in this paper	Ihlen 2004	Wang et al. 2015	Reported in this paper	Ihlen 2004	Zhao et al. 2013

tions of Chinese and Nordic (Ihlen 2004; Zhao et al. 2013). The number of cells per ascospore were less in Pakistani specimen than the Nordic countries and Chinese taxa i.e., 8–15 (vs. 13–21) and (vs. 12–21), respectively. The areole thickness of Pakistani specimen was greater as compared to the Chinese taxon i.e., 0.2–0.6 mm (vs. 0.14–0.2 mm), while the hymenium pigmentation was largely in agreement with the Chinese description (Zhao et al. 2013), whereas the height and pigmentation of hymenium is not similar to the description of Ihlen (2004).

The description of Pakistani *Rhizocarpon disporum* is very close to North American samples, which however differs by its colour of thallus, blackish brown to black (vs. grey to grey brown), taller epinecral layer 10-20 µm (vs. 10 µm) and slightly curved ascospores (vs. not curved) (Nash et al. 2004).

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Strelitzia nicolaii Regel & Körn. (Strelitziaceae), a casual alien plant new to Northern Hemisphere

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Abstract. The ongoing naturalization of the blue giant paradise bird tree, *Strelitzia nicolaii*, is here reported for the first time for NW Sicily (Italy). Native to SE Africa, this ornamental plant was locally introduced around mid XIX century. During last two decades the first cases of pollination and dispersal have been recorded, and within last 10 years several individuals were able to establish in abandoned Citrus orchards or in private gardens subject to moderate soil management.

Keywords: subtropical ornamental plants, Mediterranean, naturalization, urban areas, dispersal, pollination.

INTRODUCTION

Sicily is home of around 400 fully naturalized or causal alien plants (Galasso et al., 2018). During last decades, their number experienced a dramatic increase. Additionally, the island often represents the first or the only Italian – or even European – region where the naturalization of many tropical and subtropical woody plants occurred (e.g. Raimondo and Fici 1991; Villari and Zaccone 1999; Raimondo and Domina 2007; Pasta et al. 2012, 2014, 2016, 2017; Badalamenti and La Mantia 2018).

Although the International Plant Names Index (IPNI) lists as much as 34 binomial epithets referred to the genus *Strelitzia*, nowadays just five taxa are recognized at species rank (Argent 2011; Cron et al. 2012; Baijnath and McCracken 2019). Among them, *Strelitzia alba* (L. f.) Skeels, *S. caudata* R.A. Dye and *S. nicolaii* Regel & Körn. share the same caulescent/tree-like habit, reaching heights of up to 15 m (Moore and Hyypio 1970). These three species may be distinguished by petal color (white in *S. alba*, blue in the other two), inflorescence structure (compound with 2-5 spathes in *S. nicolaii*, simple in the other two) and ecology/distribution range (Wright 1913; Dyer 1945; van der Venter et al. 1975; Goldblatt and Manning 2000; Archer 2003).

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This last species, the one concerned in the present paper, was dedicated by Regel and Körnickie (1858) to Nikolai Nikolaevic, mentor of the Russian Imperial Society of Horticulture of Saint Petersburg. As already pointed out by Speciale and Domina (2016) and according to art. 60.8 of the Shenzen Code (Turland et al. 2018), the correct specific epithet for this species is '*nicolaii*' (or '*nikolaii*'), and not '*nicolai*', as originally (mis)spelled in the protologue and currently reported on many papers concerning the genus *Strelitzia* (e.g., Cron et al. 2012). In fact, the whole protologue was written in German and the authors did not explicitly adopt the latinized form of the granduke's name.

Within its original distribution range, *S. nicolaii* prefers rich and moist soils with good drainage in full sun to part shade. Its native habitat are the evergreen coastal forests and thicket communities of the coastal dune environments of eastern South Africa, S Mozambique, E Botswana, KwaZulu-Natal and E Zimbabwe. During last years, the so-called giant blue bird of paradise has been recorded as fully naturalized in New South Wales in Australia (Duretto et al. 2017). It was not possible to confirm a record (https://en.wikipedia.org/wiki/Strelitzia_nicolai) on its naturalization near Veracruz, eastern Mexico. As far as we know, up to now the species only occurs there under cultivation (P. Díaz Jiménez, *pers. comm.*).

The first report of cultivation of *S. nicolaii* in Italy dates back to the first half of the XIX century (Manetti 1845; Tenore 1845). The plant was for long time erroneously reported by many European scholars with the misused binomial *S. augusta*, although the true *S. augusta* Thunb. is an illegitimate synonym of *S. alba* (Archer, 2003). As for Sicily, Ostinelli (1910) states that '*S. augusta*' was already cultivated in Palermo around 1865, and in 1884 it grew in the Botanical Garden of Palermo (Todaro 1885). However, most of – if not all – the previous records of *S. augusta* and all the available specimens of tree-like *Strelitzia* observed and studied in Sicily belong to *S. nicolaii* (Speciale and Domina 2016). Due to its highly appreciated ornamental value, shortly after its introduction in Sicily *S. nicolaii* was widely diffused in local public and private gardens, where some phenological observations were reported by Buscalioni and Trinchieri (1906).

Figure 1. Information on the current distribution of *Strelitzia nicolaii*. Empty closed line: original distribution range in SE Africa; full dot: naturalization site in SE Australia; full square: location of the nuclei of NW Sicily (Italy) mentioned in this study.

Here we provide some details on the first case of naturalization of *S. nicolaii* for Europe, the Mediterranean area and the whole northern hemisphere.

RESULTS AND DISCUSSION

The first naturalized individuals of *S. nicolaii* were observed in three different sites (Figure 1). The plants of the first two sites grow in two private gardens close one another located in the plain of Palermo. Both were part of a wide Citrus orchard named 'Fondo Anfossi', almost destroyed due to urban sprawl in the 1960s. A parcel (coordinates: 38°10'47" N, 13°19'36" E, 33 m a.s.l.) was still cultivated until 1990s, when the previous intensive agricultural practices (application of fertilizer and pesticides, annual soil tilling by means of a motor hoe) have ceased. Since then, weed eradication is only done by means of a grass trimmer and instead of massive summer irrigation, some water supply is provided to the plant by means of an automatized system. After the death of most of the Citrus trees, many other fruit trees and/or ornamental plants have been introduced, such as *Annona cherimolia* Mill., *Araujia sericifera* Brot., *Asparagus setaceus* (Kunth) Jessop, *Cycas revoluta* Thunb., *Dolichandra unguis-cati* (L.) L.G. Lohmann, *Lantana camara* L., *Melia azedarach* L., *Parthenocissus* spp., *Phoenix canariensis* Chabaud, *Pittosporum tobira* (Thunb.) W.T. Aiton, *Robinia pseudoacacia* L., *Solanum pseudocapsicum* L., *Solanum torvum* Swartz, *Trachycarpus fortunei* (Hook.) H.Wendl., *Washingtonia* spp. and *Wisteria sinensis* (Sims) Sweet, and subsequently many of these species escaped from cultivation. As for *S. nicolaii*, it was introduced in the garden in 1989; the first ripen fruits (Figure 2) were observed in 2005, and the first seedlings started to grow around 30 m far from the nearest mother plants just one year after, 2006. Currently four new plants have been observed, i.e. 3 reproductive adults born between 2009 and 2010 and one young

Figure 2. Open fruit of *S. nicolaii* (photo credit: G. Collesano).

Figure 3. Young plant of *S. nicolaii* born in a private garden in the Plain of Palermo (photo credit: G. Collesano).

plant born in 2014 (Figure 3), located some 15-20 m far from them. Another single plantlet, probably three years old, growing in an abandoned orchard some 300 m apart from the first nucleus (coordinates: 38°10'15" N, 13°19'44" E), has been observed in early April 2019.

No detailed data are available on the spread of the casual plants forming the third nucleus, located within the "Bioparco di Sicilia" (Carini, Palermo province, coordinates: 38°10'04" N, 13°10'38" E), a large private park (about 60,000 m^2) including a zoological garden and several exhibitions promoting nature conservation and environmental education. Here naturalization processes have started less than 10 years ago. The first 50 individuals of *S. nicolaii* were introduced in the 'dinosaur area' at the same time the park was founded (1998), and subsequently more blue giant paradise bird trees have been planted in the other sectors of the park. Most of them started to flower around 2011–2012, and the first evidences of seed dispersal, mostly concentrated along the paths of the zoo, were noticed around 2014. Considering that numerous isolated seedlings and saplings currently grow some dozens meters far from the adult ones, it sounds highly probable that they represent the offspring of reproductive individuals dispersed by local birds and established during last 5 years. Surprisingly, some of local individuals of *S. nicolaii* have recently been predated by the alien palm weevil, *Rhynchophorus ferrugineus* (Olivier 1790) (Fiorello et al. 2015).

Figure 4. Bee visiting the inflorescence of *S. nicolaii* (photo credit: G. Collesano).

S. nicolaii produces very low amounts of viable seeds through self-pollination (Yamburov et al., 2016), while subtropical frugivorous passerine perching birds (Cronk and Ojeda 2008), attracted by its sugar-rich nectar and the intense blue color of the petals, play a major role in their pollination. Sunbirds are known to pollinate the blue giant paradise bird trees (Frost and Frost, 1981): they have been observed sitting on the portion of the blue petals enclosing the anthers in contact with the sticky pollen (Nichols 2007). In order to perform sexual reproduction in the Mediterranean biome, *S. nicolaii* must have managed to overcome the lack of native pollinators. Under local conditions, the species is in bloom all the year, with a peak activity during spring and summer. Due to the abundant production of sweet nectar, its inflorescence attracts bees (Figure 4) and probably also other insects like daily or nocturnal moths, and even lizards.

As *S. nicolaii* may flower during winter, like loquat (Merino and Nogueiras 2003), it may represent a key source of nectar for the few active Hymenopterans (namely bumblebees), and small birds (Cecere et al. 2010; Da Silva et al. 2014). Throughout the area of the municipality of Palermo, whose bird fauna is still quite rich (Lo Valvo et al. 1985), the flowers of many ornamental and cultivated plants such as *Aloe* ssp. and *Eriobotrya japonica* Lindl. are visited by chiffchaffs, *Phylloscopus* spp. (La Mantia and R. da Silveira Bueno, *pers. comm.*), but in order to confirm and quantify their role we should analyze the pollination rate comparing visited vs. non-visited inflorescences.

When mature, the capsular fruits of strelitzias break open to reveal arils whose bright orange color is due to bilirubin, a compound previously known only in animals (Pirone et al. 2009, 2010). This permanent color likely contributes to the long-lasting attraction of avian frugivores (Frost and Frost, 1981; Nichols, 2007) and perhaps to rats. Its appeal for seed dispersers is also due to the high lipid content of the arils (up to 67% of the dry mass in *S. nicolaii* according to Frost and Frost 1981). Recent experiments on captive birds (Downs et al. 2015) underlined that some frugivorous birds may have a very high assimilative efficiency, exploiting almost entirely the high lipid content of the arils of *S. nicolaii*, and to release their seeds in less than half an hour.

CONCLUSIONS

The bio-ecological traits and the geographic origin of alien plants play a major role in their ability to become invasive out of their original range (Gosper et al. 2010; Marco et al. 2010). Many introduced subtropical and tropical plants escape from backyards many decades after being introduced, and now thrive within semi-natural plant communities (Badalamenti et al. 2013) and are able to invade harsh environments (Badalamenti et al. 2018). In order to set up an appropriate management plan for *S. nicolaii*, more information on its ecology in S Africa should be collected. Furthermore, the speed of local naturalization processes should be monitored, taking into account that in Australia, i.e. under similar Mediterranean-type climatic conditions, *S. nicolaii* is able to colonize semi-natural environments (Duretto et al. 2017).

Ad hoc investigations, especially focused on ornamental plant nurseries, where individuals of giant blue paradise bird tree may be far more numerous, should be carried out in order to verify if the casual or full naturalization of *S. nicolaii* already occurred, yet unrecorded, elsewhere in Sicily, S Italy and in the whole Mediterranean area. Any additional information could improve the assessment of the potential behavior of *S. nicolaii* as a real threat for local plant communities and habitats and help decision-makers in order to plan its eradication if needed (Rejmánek and Pitcairn 2002).

Experimental investigations should be carried out in order to verify to which extent the lack of mechanical soil tillage affects the establishment rate of the seedlings.

It could be interesting to carry out more systematic studies in order to verify which is (or are) the main vectors of pollination and dispersal. A cost-effective strategy could be to put a fix color and infrared camera in order to film not only the diurnal but also the nocturnal visitors of the inflorescences.

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