Typification and nomenclature of the western Indian Ocean islands ferns and lycophytes described in Linnaeus filius's Supplementum plantarum

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Abstract

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Carl Linnaeus filius (1741–1783) published 16 new species names of ferns and lycophytes in *Supplementum plantarum* in 1782. Nine of these new taxa originated from the western Indian Ocean islands and were based on collections cited as "Sonnerat per Thouin" or "Thouin" in their protologues. Correspondence between André Thouin (1747–1824) and the younger Linnaeus indicates that those new names were based on a set of 50 collections that Thouin shipped to Linnaeus f. in 1779 and were in reality collected by Philibert Commerson (1727–1773) and not Pierre Sonnerat (1748–1814). Original material has been located in Linnaeus filius's herbarium (now in LINN-HS) and duplicates have been located in the Thouin herbarium (now MPU) and in G, P, P-LA and SBT. We formally designate lectotypes for five fern and two lycophyte names described by the younger Linnaeus in *Supplementum plantarum: Acrostichum punctatum* L. f., *Acrostichum viviparum* L. f., *Adiantum furcatum* L. f., *Adiantum repens* L. f., *Lycopodium gnidioides* L. f., *Lycopodium verticillatum* L. f., and *Polypodium pica* L. f. A lectotype is additionally designated for *Asplenium daucifolium* Lam., the currently accepted name for *Acrostichum viviparum*.

Keywords

LYCOPHYTA – PTERIDOPHYTA – Madagascar – Mauritius – Réunion – Carl Linnaeus filius – André Thouin – Philibert Commerson – Pierre Sonnerat – Nomenclature

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Introduction

Carl Linnaeus filius (1741–1783) published in April 1782 his most significant publication: *Supplementum plantarum*. This work was intended to supplement his father's *Systema vegetabilium* (Linnaeus, 1774). Linnaeus f. (1782) described 16 new fern and lycophyte species in this work, 13 are basionyms or even still taxonomically accepted species. Eight of these new taxa originated from the western Indian Ocean islands and were based on collections cited as "Sonnerat per Thouin" and one as "Thouin" in their protologues.

André Thouin (1747–1824) was the Chief Gardener and subsequently Head horticulturalist of the Jardin du Roi in Paris for 60 years (1764–1824) (now the Jardin des Plantes, main site of the Muséum national d'Histoire naturelle [MNHN]), a member of the Académie Royale des Sciences in Paris (from 1786) and first Professor of the MNHN in charge of teaching the cultivation and naturalization of foreign plants from 1793 (Cuvier, 1825). Thouin finally became Director of the MNHN between 1814 and 1817. Thouin was part of the network of naturalists and botanists of his time and maintained a rich correspondence (Letouzey, 1989). Both Carl Linnaeus the elder (1707–1778) and his son were among his correspondents (Bertemes, 1935). The Bibliothèque centrale of the MNHN holds 32 letters spanning from 1774 to 1782 (BC: MS 2081) that were transcribed by Bertemes (1935). In a letter sent to the younger Linnaeus dated 15 December 1779, Thouin announced that he had shipped 50 dried plants to him and added in a note that the shipment included collections from the Sonnerat herbarium along with 180 species of seeds in March 1779 (Bertemes, 1935: 103). Linnaeus f. replied in a letter dated 20 February 1780 to Thouin with a critical list of names associated with Thouin's numbering (five numbers were missing) (see Bertemes, 1935: 107–108) (Fig. 1). This list was entitled "Plantae missae Sonneratii" and included seven new fern and two lycophyte species from the western Indian Ocean islands described by Linnaeus f. two years later: *Acrostichum australe* L. f. [with Thouin's numbering 31], *A. punctatum* L. f. [28], *A. spicatum* L. f. [33], *A. viviparum* L. f. [26], *Adiantum furcatum* L. f. [40], *A. repens* L. f. [37], *Lycopodium gnidioides* L. f. [13], *L. verticillatum* L. f. [12] and *Polypodium pica* L. f. [43].

After his death at the age of 42, Linnaeus filius's herbarium, along with that of his father, were sold to Sir James Edward Smith (Jarvis, 2007). Specimens attributed to the younger Linnaeus are held in Herbarium Linnaeus (LINN) and Herbarium Smith (LINN-HS). Thouin's herbarium was bought by Jacques Cambessèdes (1799–1863). This significant herbarium was then left by his widow to the Faculté des Sciences de Montpellier (MPU) (Planchon, 1863).

Original material seen and annotated by the younger Linnaeus of the nine names listed above has been found in his own herbarium in LINN-HS. All specimens bear an original label in Thouin's hand with a number corresponding to the manuscript list sent by Linnaeus f. to Thouin in 1780 (Fig. 1–2). Linnaeus f. added in his hand the epithets of the names of the taxa he published in *Supplementum plantarum* two years later. Duplicate specimens have been located in G, MPU, SBT, P and P-LA.

Thouin did not himself travel to the western Indian Ocean but incorporated in his herbarium collections from there made by several naturalists of his time including both Philibert Commerson (1727–1773) and Pierre Sonnerat (1748–1814). Sonnerat was a naturalist, explorer and colonial administrator (Dorr, 1997). He travelled to the western Indian Ocean during 1770 and 1771 where he visited Mauritius ("île de France"), Réunion ("île Bourbon") and Madagascar (Morel, 2019a). Sonnerat met the famous French naturalist Commerson in Mauritius in October 1770 and they were in the southeast of Madagascar (Fort-Dauphin) at the same time in November 1770 (Morel, 2019b). Very few botanical collections made by Sonnerat are known from the time he spent in the western Indian Ocean (e.g. in P-LA) but several are known from the Cape region where he travelled from Mauritius in March-April 1771 (Morel, 2019a). It is conceivable that some of the Sonnerat collections made during his journey in the western Indian Ocean islands were incorporated "originally in the Commerson herbaria" (Stafleu & Cowan, 1985: 744) but no mention or trace of Sonnerat has been found on material studied in G, LINN-HS, MPU, P, P-LA, P-JU and SBT. On the other hand, Commerson is present in a ubiquitous manner among all those collections (see above). Thouin "was particularly generous in giving specimens to the younger Linnaeus" (Savage, 1963: ix), shipping another 1,200 collections to the younger Linnaeus after a visit to Paris in 1782 (BC: MS 2081). Thouin wrote in a note that: "la majeure partie des Plantes que j'ai donné à M. le Linné sont du Voyage de Commerson" [the vast majority of plants that I gave to Linnaeus originate from Commerson's travel] (BC: MS 2081; see Bertemes, 1935: 119–120). Knowing that the younger "Linnaeus was not particularly careful in recording collectors' names" (Savage, 1963: ix), we can assume that the fern and lycophyte specimens from the western Indian ocean islands sent by Thouin to the younger Linnaeus were collected by Commerson and not Sonnerat. Further evidence can be seen among Thouin's duplicates where the abbreviation "C^{on}" for Commerson in Thouin's hand is visible on the labels (Fig. 2).

Thouin was particularly careful in the collections he gave to Linnaeus f. He numbered all those collections and wrote "ceux qui me sont restés sont accompagnés de Lin. n° qui signifie donné à M. Linné sous le n°" [those that I kept are accompanied by Lin. n° which means given to Mr. Linné under n°] (BC: MS 2081). Thouin would then be able to follow the new determinations and names with which Linnaeus f. had promised to provide him.

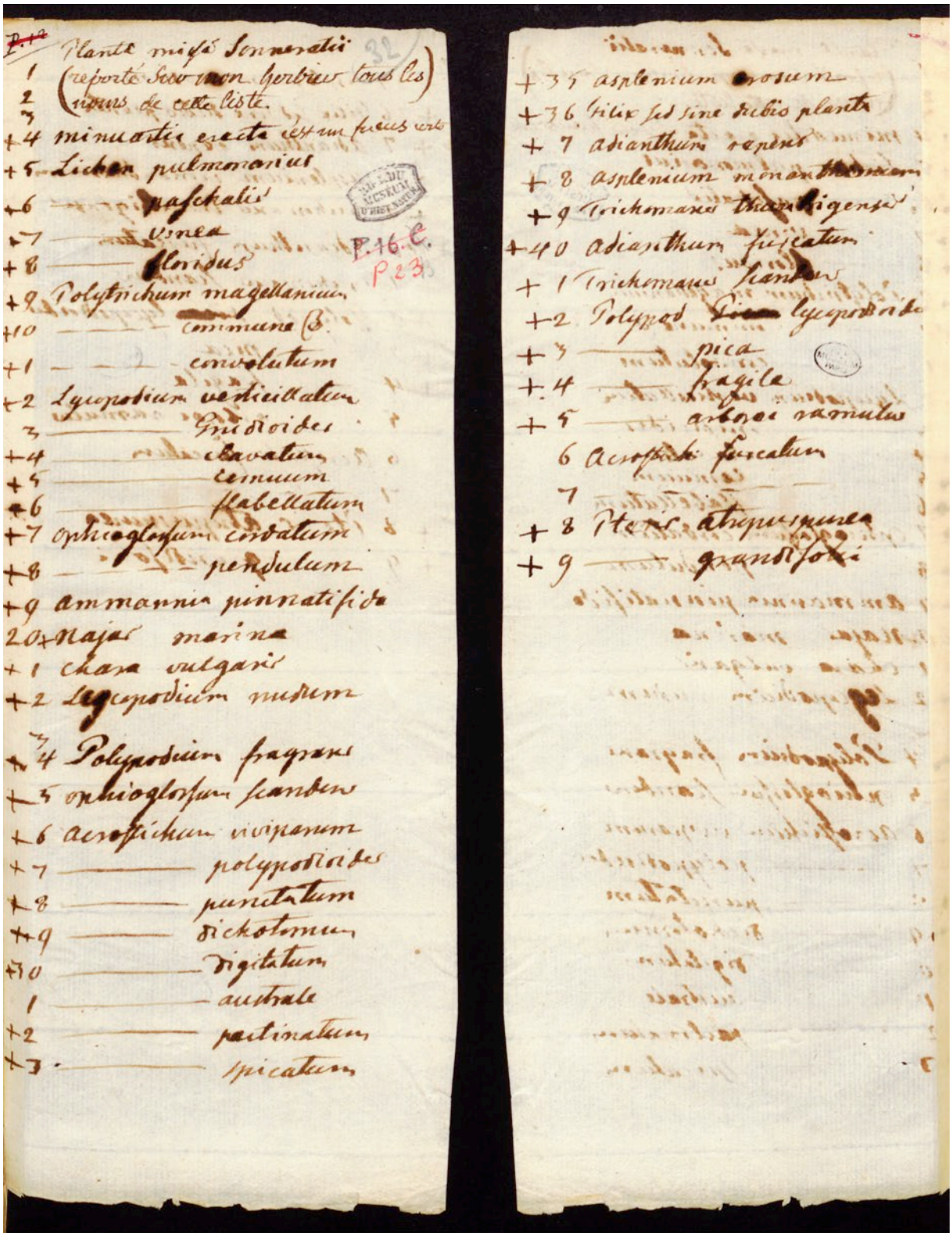


Fig. 1. – Manuscript list in Linnaeus filius's hand dated 20 February 1780 associated with Thouin's numbering entitled "Plantae missae Sonneratii" including the seven new fern and two lycophyte species from the western Indian Ocean islands described by Linnaeus f. in *Supplementum plantarum*.
[MS 2081, p. 23 front and back; © Muséum national d'Histoire naturelle, Bibliothèque centrale, Paris]

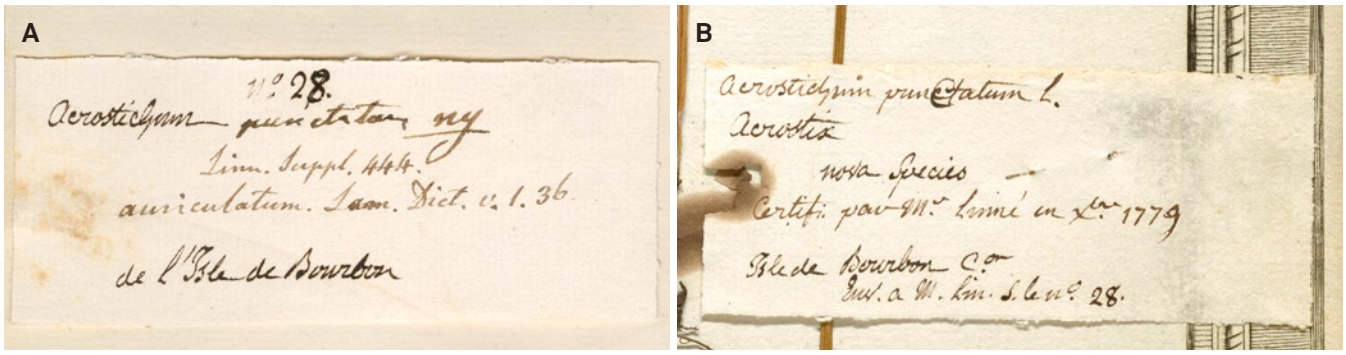


Fig. 2. – Labels of original material of *Acrostichum punctatum* L. f. **A.** Lectotype in LINN-HS bearing in Thouin's hand the number "28" to which Linnaeus f. has added the epithet "punctatum" and "ny" (="new"); **B.** Isolectotype in MPU originating from Thouin's herbarium with, in Thouin's hand: "Con" for Commerson as collector and "Env. a m. Linn. S. le nº 28" [sent to Linnaeus under nº 28].
[**A:** LINN-HS nº 1622.27; © Linnean Society of London; **B:** MPU1054971; © Université de Montpellier – Herbier MPU (SPH)]

Commerson's collections (over 30,000) reached Paris in 1774 and were incorporated in the P herbarium only in 1793 (Stafleu & Cowan, 1976). In the meantime, Antoine-Laurent de Jussieu (1748–1836) was given "the custody of all Commerson collection on 11 January 1776" (Stafleu & Cowan, 1976: 532). Several collections went to his own herbarium (now P-JU), but also for example to Jean-Baptiste de Lamarck (1744–1829) (now P-LA), Charles Louis L'Héritier de Brutelle (now G) (1746–1800) and Thouin (now MPU). This explains why the Commerson labels vary and are different in each of these herbaria. We accept as original material only specimens associated with Commerson's labels with the mention in Thouin's hand of the number corresponding to the manuscript list (see above) or "Env. a Linn. S. le nº" [sent to Linnaeus under nº] for duplicates of original material (Fig. 2–4, 6). Due to the multifarious history of Commerson's labels and frequent historical errors in identifying true Thouin original material and duplicates, we prefer to designate lectotypes instead of considering LINN-HS collections as holotypes. LINN-HS collections can be found on the Linnean collections (2019) website. MPU and P collections can be found on the E-recolnat (2019) website and G collections on the CHG (2019) website.

Typification

Acrostichum australe L. f., Suppl. Pl.: 444. 1782.

≡ ***Actiniopteris australis*** (L. f.) Link, Fil. Sp.: 80. 1841. *(Pteridaceae)*

Lectotypus (designated by Pichi-Sermolli, 1962: 27): **Mascarenes**: "31. Acrostichum des Isles de France & de Bourbon", s.d., *Commerson s.n.* (LINN-HS nº 1622.51 image seen; isolecto-: MPU [MPU1071909]!, SBT nº 1.2.1.28 image seen) (Fig. 3).

Notes. – A single specimen of original material is extant in LINN-HS [LINN-HS nº 1622.51]. This specimen bears a label in Thouin's handwriting including the number "31" to which Linnaeus f. added in his hand "australe ny" ("ny" indicating 'new'). The LINN-HS specimen was cited as holotype by Pichi-Sermolli (1962) and this use is here treated as an error to be corrected to lectotype (Turland et al., 2018: Art. 9.10). Duplicates of this original material have been located in MPU [MPU1071909] and SBT [SBT nº 1.2.1.28]. The identity of the lectotype material corresponds with the current usage of the name.

The type locality is either Mauritius from the "montagne des 3 mamelles et celle du rampart" or "St. Paul" in Réunion as written by Thouin on the MPU specimen (Fig. 3).

Actiniopteris australis is endemic to Mauritius and Réunion in the Mascarenes archipelago (Badré & Lorence, 2008).

Acrostichum punctatum L. f., Suppl. Pl.: 444. 1782 [nom. illeg.] [non L., 1763].

≡ ***Bolbitis auriculata*** (Lam.) Alston in J. Bot. 72, Suppl.: 3. 1934. ≡ *Acrostichum auriculatum* Lam., Encycl. 1: 36. 1783 [nom. nov.]. *(Dryopteridaceae)*

Lectotypus (designated here): **Réunion**: "nº 28. Acrostichum de l'île de Bourbon", s.d., *Commerson s.n.* (LINN-HS nº 1622.27 image seen; isolecto-: MPU [MPU1054971, MPU1054973]!, P [P01427005]!) (Fig. 2, 4).

Notes. – A single specimen of original material is extant in LINN-HS [LINN-HS nº 1622.27]. This specimen bears a label in Thouin's hand to which Linnaeus f. has added the words "punctatum ny" (Fig. 2, 4). This specimen bears the number "28". Two collections representing duplicates of the original material have been located in MPU [MPU1054971, MPU1054973] and are considered as isolectotypes. A third duplicate of this original material has been located in P [P01427005]. This specimen is the only known duplicate



Fig. 3. – Isolectotype of *Acrostichum australe* L. f. in MPU.
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Fig. 4. – Lectotype of *Acrostichum punctatum* L. f. in LINN-HS.
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originating from the herbarium of Dr. Baron J.-A. Barbier (1767–1846), bequeathed to the MNHN and incorporated within the collection in 1847. The identity of the lectotype material corresponds with the current usage of the name.

The specimens cited as type by Mickel (2002), Lorence & Rouhan (2008) and Roux (2009) at C [C10001539], S [S-P-2197] and P [P01426989, P01427003] are Commerson collections without any Thouin annotation and are not considered here as original material. Another Commerson collection is extent in G [G00341870]. Unusually for Commerson collections, G00341870, P01426989 and P01427003 bear a precise collection locality and date: "des bords de la rivière des Calebasses en février 1773".

Bolbitis auriculata is distributed in Tropical Africa, the Comoro islands, Mauritius, Réunion and Madagascar (Lorence & Rouhan, 2008).

Acrostichum spicatum L. f., Suppl. Pl.: 444. 1782.

≡ ***Lepisorus spicatus*** (L. f.) Li Wang in Bot. J. Linn. Soc. 162: 35. 2010. *(Polypodiaceae)*

Lectotypus (designated by Mazumdar, 2016: 218): **Mauritius**: "33. Acrostichum de l'Isle de France", s.d., *Commerson s.n.* (LINN-HS nº 1642.1 image seen; isolecto-: MPU [MPU1238477, MPU1238486]!).

Notes. – A single specimen of original material is extant in LINN-HS [LINN-HS nº 1642.1]. This specimen bears a label in Thouin's hand to which Linnaeus f. added the epithet "spicatum". This specimen bears the number "33" and was designated by Mazumdar (2016: 218) as lectotype. Two collections representing duplicates of original material have been located in MPU [MPU1238477, MPU1238486] and are considered as isolectotypes. Those two specimens bear the number "32" which is an error for "33" (see Fig. 1). Other Commerson collections are extent in G [G00348187], P [P00482674], and P-JU [P00674763]. The identity of the lectotype material corresponds with the current usage of the name.

Lepisorus spicatus is known from continental Africa (Ivory Coast, Cameroun, and Gabon), São Tomé and Príncipe, the Comoro islands, Mauritius, Réunion, the Seychelles islands and Madagascar (Badré, 2002a).

Acrostichum viviparum L. f., Suppl. Pl.: 444. 1782.

≡ *Asplenium viviparum* (L. f.) C. Presl, Tent. Pterid.: 109, tab. 3, fig. 20. 1836 [nom. illeg.] [non Blume, 1828].

Lectotypus (designated here): **Mascarenes**: "nº 26. Acrostix prolifera seu vivipara des isle[s] de France et de Bourbon", s.d., *Commerson s.n.* (LINN-HS nº 1629.13 image seen; isolecto-: MPU [MPU1036711]!, G [G00341868, G00341869]!).

= ***Asplenium daucifolium*** Lam., Encycl. 2: 310. 1786. **Lectotypus** (designated here): **Mauritius**: "Isle de France", s.d., *Commerson s.n.* (MPU [MPU1034656]!) (Fig. 5). *(Aspleniaceae)*

Notes. – A single specimen of original material is extant in LINN-HS [LINN-HS nº 1629.23]. This specimen bears a label in Thouin's hand to which Linnaeus f. added the epithet "vivipara". This specimen bears the number "26" and is here designated as lectotype. Three duplicates of original material have been located in MPU [MPU1036711] and in G [G00341868, G00341869]. The G duplicates originate from the herbarium of Augustin-Pyramus de Candolle (1778–1841).

The combination of *Acrostichum viviparum* in the genus *Asplenium* L. proposed by Presl (1836) is illegitimate as it is a later homonym of *Asplenium viviparum* published by Blume (1828). The correct name is *A. daucifolium* Lam. published in 1786. Lamarck (1786: 310) cited in the protologue: "M. Commerson a trouvé cette plante à l'Isle de France. (v.s. in h. D. Thouin)". The original material has been located in Thouin's herbarium in MPU. It bears in Lamarck's hand: "daucifolium lam. dict." (Fig. 5). The type was mistakenly believed to be in P by Morton (1963). A collection in P-LA [P00564950] cited by Tardieu-Blot (2002) as a possible isotype is not considered as original material as it was determined as "Darea" by Lamarck with no direct reference to *A. daucifolium* except the locality "isle de France".

Asplenium daucifolium is endemic to Mauritius, Réunion, and Madagascar (Tardieu-Blot, 2002).

Adiantum furcatum L. f., Suppl. Pl.: 447. 1782.

Lectotypus (designated here): **Réunion**: "40. de l'Isle de Bourbon", s.d., *Commerson s.n.* (LINN-HS nº 1629.15 image seen; isolecto-: G [G00341871]!, MPU [MPU018221]!) (Fig. 6).

= ***Asplenium rutifolium*** (Berg.) Kunze in Linnaea 10: 521 (1836). ≡ *Caenopteris rutifolium* Berg. in Acta Petropol. 1782: 249. 1786. *(Aspleniaceae)*

Notes. – The protologue of *Adiantum furcatum* included references to Plukenet (1700: 83, tab. 350, fig. 4) and to two specimens as "Thunberg. Thouin" with the mention "Habitat in Cape. Bonae Spei & Insula Helenae". Two specimens of original material are extant in LINN-HS: a specimen collected by Carl Peter Thunberg (1743–1828) in the Cape region [LINN-HS nº 1629.16] with duplicates in SBT [SBT10616] and UPS [UPS-THUNB nº 24774], and a specimen from Réunion originating from Thouin's shipment in 1780 (see above) [LINN-HS nº 1629.15]. Swartz (1801, 1806) excluded the reference to "Filicula corniculata Insulae Sanctae Helenae" of Plukenet (1700) which refers to a species of *Elaphoglossum* Schott ex J. Sm., *E. bifurcatum* (Jacq.) Sw., a fern endemic to



Fig. 5. – Lectotype of *Asplenium daucifolium* Lam. in MPU.
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Fig. 6. – Lectotype of *Adiantum furcatum* L. f. in LINN-HS).
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St. Helena. Christ's (1899) transfer of *Adiantum furcatum* to *Elaphoglossum* (as *E. furcatum* (L. f.) Christ) is a nom. illeg. currently treated as a synonym of *E. bifurcatum* (Jacq.) Sw. (Roux, 2009; Vasco et al., 2009).

The two specimens of original material extant in LINN-HS where Linnaeus f. added "Adianthum furcatum" are identifiable as a species of the genus *Asplenium* L. The combination of *Adiantum furcatum* in the genus *Asplenium* would be illegitimate, as it is preoccupied by *Asplenium furcatum* Thunb. (= *A. aethiopicum* (Burm. f.) Bech.). Linnaeus f.'s name should be treated as a synonym of *Asplenium rutifolium* (Tardieu-Blot, 1958), the first available name in the genus. Its basionym, *Caenopteris rutifolium*, was described by Peter Jonas Bergius (1730–1790) based on a Thunberg collection in SBT [SBT10616], a duplicate of original material (isosyntype) of *Adiantum furcatum*.

The *Commerson s.n.* collection [LINN-HS nº 1629.15] (bearing the number "40" corresponding to the younger Linnaeus manuscript list sent to Thouin) is here designated as lectotype. It is chosen over the Thunberg collection as Linnaeus f. added to the label "Adianthum furcatum ny". Duplicates of original material are extant in G [G00341871] and MPU [MPU018221].

Asplenium rutifolium is distributed in Mauritius, Réunion, Madagascar, the Comoro islands and the Cape region to Malawi and Yemen in Continental Africa (Tardieu-Blot, 2002).

Adiantum repens L. f., Suppl. Pl.: 446. 1782.

≡ ***Davallia repens*** (L. f.) Kuhn, Fil. Deck.: 27. 1867 [nom. cons.]. *(Davalliaceae)*

Lectotypus (designated here): **Mauritius**: "37. Adianthum de l'Isle de France" (LINN-HS nº 1635.21 image seen; isolecto-: G [G00341867]!, MPU [MPU1063796]!).

Notes. – While proposing the conservation of *Davallia repens* (L. f.) Kuhn against *Davallia repens* (Bory) Desv., Lindsay & Middleton (2003) correctly identified original material of *Adiantum repens* L. f. in LINN-H, but did not formally designate the specimen as lectotype. We formally designate here the LINN-HS [LINN-HS nº 1635.21] material as lectotype. Duplicates of original material have been located in G [G00341867] and MPU [MPU1063796]. The identity of the lectotype material corresponds with the current usage of the name.

Davallia repens is a widespread species growing from tropical West Africa to Queensland in Australia (Noteboom, 1994).

Lycopodium gnidioides L. f., Suppl. Pl.: 448. 1782.

≡ ***Phlegmariurus gnidioides*** (L. f.) A.R. Field & Bostock in PhytoKeys 20: 40. 2013. *(Lycopodiaceae)*

Lectotypus (designated here): **Mauritius:** "nº 13. Lycopodium de l'Isle de France", s.d., *Commerson s.n.* (LINN-HS nº 1649.38 image seen; possible isolecto-: MPU [MPU1066139, MPU1066140]!).

Notes. – A single specimen of original material seen by Linnaeus f. is preserved in LINN-HS. Thouin's handwritten label with the number "13" is complemented by Linnaeus f.'s annotation "gnidioides". This collection is here designated as lectotype and its identity corresponds with the current usage of the name.

Two collections originating from Thouin's herbarium and collected by Commerson in Mauritius are extant in MPU [MPU1066139, MPU1066140]. None bears Thouin's numbering but "Isle de France Con" is present in Thouin's hand. Both are very likely duplicates of original material and considered here as possible isolectotypes.

Roux (2009) mentioned a specimen collected by Commerson from Mauritius at P [P00677322] as a possible isotype ("?iso.") which is not considered as original material here (see above).

Lycopodium gnidioides has been classically accepted in the genus *Huperzia* Bernh. (Bardé, 2002b; Roux, 2009; Rakotondrainibe, 2015). A recent molecular phylogeny focusing on Madagascar showed that Malagasy *Huperzia* species should now be accepted in the Southern Hemisphere genus *Phlegmariurus* (Herter) Holub. (Bauret et al., 2018).

Phlegmariurus gnidioides is known in continental Africa from South Africa to Malawi, São Tomé and Príncipe, the Comoro islands, Réunion, Mauritius and Madagascar (Badré, 2002b).

Lycopodium verticillatum L. f., Suppl. Pl.: 448. 1782.

≡ ***Phlegmariurus verticillatus*** (L. f.) A.R. Field & Testo in Molec. Phylogenet. Evol. 94: 645 (2015). *(Lycopodiaceae)*

Lectotypus (designated here): **Réunion:** "nº 12. Lycos des Bois de l'Isle de Bourbon", s.d., *Commerson s.n.* (LINN-HS nº 1649.12.1 image seen; isolecto-: MPU [MPU1054548]!, SBT nº 1.2.2.94 image seen).

Notes. – Tardieu-Blot (1971) mentioned the type as "Maurice. Sonnerat in Herb. Thouin". This cannot be accepted as an effective lectotypification as both the locality and collector are wrongly cited. Badré (2002b), Verdcourt (2005), Roux (2009) and Roux & Cooper-Driver (2016) cited this specimen at SBT as holotype but failed to indicate the term "lectotype". Thus, none can be accepted as an effective

lectotypification (Turland et al., 2018: Art. 9.23). The original material carrying the epithet in Linnaeus f.'s hand "verticillatum" is in LINN-HS [LINN-HS nº 1649.12.1] and designated here as lectotype. Its identity agrees with the current usage of the name.

Two duplicates of this original material are extant in MPU [MPU1054548] and SBT [SBT nº 1.2.2.94].

Phlegmariurus verticillatus is known in continental Africa from South Africa to Zambia and in Cameroun and São Tomé and Príncipe, the Comoro islands, Réunion, and Madagascar (Badré, 2002b).

Polypodium pica L. f., Suppl. Pl.: 446. 1782.

≡ ***Tectaria pica*** (L. f.) C. Chr. in Dansk Bot. Ark. 7: 65. 1932. *(Tectariaceae)*

Lectotypus (designated here): **Madagascar:** "43. Polypodium de l'Isle de Madagascar", s.d., *Commerson s.n.* (LINN-HS nº 1622.112 image seen; isolecto-: MPU [MPU1061079]!, P-LA [P00564805] image seen; possible isolecto-: MPU [MPU1061080]!).

Notes. – A single specimen of original material seen by Linnaeus f. is preserved in LINN-HS. Thouin's handwritten label with the number "43" is completed by Linnaeus f.'s annotation "pica ny". This collection is here designated as lectotype. Duplicates of this original material are extant in P-LA [P00564805] and MPU [MPU1061079]. A second collection in MPU is missing the number "43" but seems likely to be a duplicate of the original material and is considered here as a possible isolectotype.

Tectaria pica is endemic to Mauritius, Réunion, and Madagascar (Badré et al., 2002).

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