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Taxonomy, distribution and nomenclature of three confused broad-leaved *Potamogeton* species occurring in Africa and on surrounding islands

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A taxonomic revision of broad-leaved *Potamogeton* species ascribed to the '*P. schweinfurthii–thunbergii* complex' occurring in Africa and on surrounding islands is presented. Three species, *P. nodosus*, *P. richardii* and *P. schweinfurthii*, are recognized in the African mainland. The widespread species *P. nodosus* has been widely overlooked in sub-Saharan Africa. It is recorded here for the first time from eight countries of tropical and southern Africa and from six surrounding islands. The distribution of *P. richardii* is critically revised and the species is recorded for the first time from Cameroon, Swaziland and Madagascar. *P. schweinfurthii* is recorded for the first time from Algeria, Tunisia, Burkina Faso and Niger. The nomenclature of all three species is revised. Lectotypes are designated for six names. All original material of the name *P. thunbergii* Cham. et Schltdl. actually belongs to *P. nodosus* Poir. The correct name for the East and southern African species called '*P. thunbergii*' is *P. richardii* Solms. The lectotype of *P. schweinfurthii* designated by Dandy proved to be *P. nodosus*. A new type is therefore proposed for the species generally named *P. schweinfurthii* and the name itself is proposed for conservation. The morphology and stem anatomy of *P. nodosus*, *P. richardii* and *P. schweinfurthii* are described. In spite of some overlaps in the morphological variation in their vegetative characters, a detailed analysis of the variation patterns and instructions for reliable identification are given. The distributions of all three species are described, based solely on reliably identified specimens, many of which were also examined anatomically. Distribution maps are provided.

ADDITIONAL KEYWORDS: anatomy – determination – morphology – new records – revision – typification – variation.

INTRODUCTION

In spite of the fact that the diversity of *Potamogeton* in Africa, compared with other continents, is relatively low (cf. Wiegleb, 1988), the taxonomy of the African species was obscure for a long time and some taxonomic questions remain unanswered. A century ago, Bennett, besides creating many correct records, also erroneously introduced a few species that have actually never been collected in Africa, such as *P. alpinus* Balb. (Bennett, 1895, 1897, 1901), *P. friesii* Rupr. (Bennett, 1897) and *P. filiformis* Pers. (Bennett, 1895, 1901). The voucher specimens that relate to these records are *P. schweinfurthii* A. Benn., *P. pusillus* L. *s.s.* and *P. pectinatus* L., respectively. A few other names were proposed by Bennett (1901) as new: *P. livingstonei* A. Benn., which is a robust and broad-leaved form of *P. pectinatus* L.; *P. preussii* A. Benn., a name based on several syntypes, each of which belongs to either *P. octandrus* Poir. or *P. pusillus s.s.*; and *P. schweinfurthii* A. Benn., the only name today adopted for a distinct African species. In his later papers (Bennett, 1904, 1910, 1924) he added *P. venosus* A. Benn. (a morphotype of *P. schweinfurthii* without floating leaves), and from the islands adjacent to the eastern coast of Africa *P. semicoloratus* A. Benn., *P. chamissoi* A. Benn. and *P. *vaginans* Bojer ex A. Benn. Graebner (1907) in his monograph reported

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altogether 20 species from Africa and surrounding islands.

All these taxa are recognized in the worldwide treatment of *Potamogeton* by Hagström (1916), who also added eight new species from Africa and surrounding islands. Altogether (approximately) 31 species were recorded from this continent in the late 1920s. This is much higher than the 14–15 species today confirmed from Africa and surrounding islands (cf. Wiegleb & Kaplan, 1998). The number of *Potamogeton* taxa recorded from Africa was much reduced in three important taxonomic works covering three major parts of Africa: northern Africa was reviewed by Maire (1952), tropical Africa by Dandy (1937) and southern Africa by Obermeyer (1966).

The most difficult group of broad-leaved *Potamogeton* species was critically investigated by Symoens, van de Velden & Büscher (1979). They presented a pilot study of the *P. thunbergii–nodosus* complex in Africa. They proved that *P. nodosus* and '*P. thunbergii*' *sensu* Obermeyer non Cham. et Schltdl. (in this paper called *P. richardii*) really represent two distinct evolutionary entities, with different stem anatomies and chromosome numbers, in spite of very weak morphological differentiation. In contrast, they found no reason for distinguishing southern African populations of '*P. thunbergii*' from East African *P. richardii*. They provisionally outlined the distribution of *P. nodosus* and '*P. thunbergii*' in Africa based on the material available to them at that time, and concluded that there is no overlap in the distributional ranges of the two species as there was no country where both the species occur. *P. nodosus* was reported mainly from northern and western Africa, south to Angola, whereas '*P. thunbergii*' was identified in southern and eastern Africa. Subsequent examination of additional specimens from southern Africa revealed the scattered occurrence of *P. nodosus* in Namibia, Botswana and South Africa (Schoeters, 1980).

In the course of his studies on Potamogetonaceae for the Species Plantarum – Flora of the World, Z. Kaplan examined herbarium material of this group from Africa (more than 1300 specimens of the *P. nodosus–schweinfurthii–thunbergii* complex preserved in 34 herbaria). A careful examination of the morphology and stem anatomy of some suspect specimens from southern Africa revealed much southern and south-eastern occurrence of *P. nodosus*. New localities for taxa extremely rare in Africa were also found. These observations revealed a need to re-evaluate some taxonomic and nomenclatural assumptions and critically review plant material from the whole of Africa and surrounding islands. In addition to other findings, it has also been found that confusion and misinterpretation also affected the type material, and its detailed evaluation showed that at least one of the generally accepted names belongs to a different species.

The dataset collected by Z. Kaplan was combined with an updated list of specimens studied by J. J. Symoens, including the records collected mainly for Flora Zambesiaca and for Flora of Tropical East Africa. The aim of the present paper is to define three similar broad-leaved species occurring in Africa in terms of variation in morphology and stem anatomy, revise the distributions of these species and provide a critically checked nomenclature.

MATERIAL AND METHODS

Specimens of the following herbaria were studied: ALF, B, BCF, BM, BOL, BP, BR, BRNM, BRNU, BRVU, C, CGE, COI, EA, ETH, FI, FT, G, GENT, GOET, K, KRA, L, LD, LE, LG, LISU, LIV, LY, M, MHU, MPU, NAI, NH, P, POZG, PR, PRA, PRC, PRE, S, TUB, U, UPS, W, WAG, WRSL, WU, YA, Z and ZT, and additional selected collections from ASW, JE, HAL and HBG were seen. Only reliably identified specimens, many of which were examined anatomically, were used to construct the distribution maps. Only well-preserved and often flowering or fruiting specimens were selected for the list of representative specimens of each species, usually listing several of them for each country. All specimens cited in the text were seen unless otherwise indicated.

Lists of representative specimens were arranged according to the World Geographical Scheme for Recording Plant Distributions (Brummitt, 2001). Outline maps of this standard were used for drawing maps of species distributions.

J. J. Symoens studied live plants of *P. richardii* and *P. schweinfurthii* in the field in the Democratic Republic of the Congo (1956–72), Zimbabwe (1973) and Kenya (1993–97). Selected samples of *P. richardii* ('*P. thunbergii*') from Burundi and South Africa were cultivated in 1977–78 at the Vrije Universiteit, Brussels. Additional samples of *P. schweinfurthii* and *P. nodosus* were cultivated by Z. Kaplan in the Experimental Garden at the Institute of Botany, Průhonice, Czech Republic. Many populations of *P. nodosus* were studied by both authors in many countries of Europe, Africa and western Asia. Personal collections of the authors are preserved in PRA and BRVU, respectively, and duplicates distributed to several other herbaria.

Descriptions of submerged leaves refer to the membraneous leaves on the submerged part of the stem that are morphologically different from the coriaceous upper leaves usually floating on the water surface. This definition does not include the coriaceous leaves that are secondarily submerged by a sudden rise in water level. Lengths of fruit given in the text include the beak.

For the investigation of stem anatomy, short pieces of stem were cut from the internode of a main stem, soaked for 1 to several days in a solution of water, alcohol and glycerol at a ratio of 1 : 1 : 1. Thin slices of stem were either cut transversely by hand with a razor blade under a stereomicroscope and then stained in a drop of water with toluidine blue (Z. Kaplan) or cut to a thickness of 5 μm using a microtome from stem segments embedded in paraffin and then stained with ammoniacal fuchsine and astra blue (J.-J. Symoens). After 1–3 min, depending on stainability, the samples were washed in distilled water and studied under a microscope using transmitted light, either directly (Z. Kaplan) or after mounting in Canada balsam or Entelan New (Merck) (J.-J. Symoens). Observations were made at a magnification of 20–60× (for general anatomical pattern) or 150–400× (for thickening of endodermal cells, occurrence of interlacunar and subepidermal bundles, development of pseudohypodermis).

RESULTS

Evaluation of type material of *Potamogeton thunbergii* Cham. et Schltdl.

Chamisso & Schlechtendal (1827) based their species on two elements from the vicinity of Cape Town, South Africa: the record '*Potamogeton natans* Thunb. Fl. Cap.' and the collection 'in Promontorio bonae spei ad Hartebeestkraal prope Brackrivier mense Januario Mundt et Maire lecta'. The material from Hartebeeskraal, Western Cape, South Africa, collected by Mundt & Maire, was reported by Bennett (1905) from B. However, this specimen was destroyed during World War II and our search through the specimens of B proved unsuccessful. However, two duplicates survive: one in Schlechtendal's herbarium in HAL and one in Chamisso's herbarium kept in LE. A single shoot is preserved on the sheet in HAL. The plant is in flower, with five floating and two submerged leaves. The floating leaves have an elliptical lamina, of green-brownish colour, show no indication of a discoloured section at the upper end of the petiole at the junction with the lamina, and are broadly cuneate at the base. The submerged leaves are well preserved, with the lamina oblong to narrowly oblong, on long petioles. Stem anatomy shows the stele to be of trio type, the endodermis of O-type and no bast bundles in the cortex. The plant clearly belongs to the species now called *P. nodosus*. The herbarium sheet preserved in LE bears one shoot. The plant has a spike with young fruits and six leaves concentrated on the upper part of the stem. One of the leaves is submerged, with a petiole 16 cm long and a narrowly oblong lamina; the rest are floating leaves, with a similar shape and colour to those of the HAL duplicate. The LE specimen also belongs to *P. nodosus*.

The specimen '*P. natans sensu* Thunberg, Fl. Cap.', which refers to the citation 'In fluvio Zeekorivier, et Verkeerde valley' in Thunberg's (1823) Flora Capensis, is preserved in Thunberg's herbarium at UPS under number 3843. There is no indication of the origin of the plant on the sheet but this is the only specimen in Thunberg's herbarium identified by him as '*P. natans*' (see also Juel, 1918). This specimen consists of two flowering shoots, each with several elliptical floating leaves, one also with three remnants of petiolate submerged leaves. The stem anatomy is fully consistent with that of *P. nodosus* but clearly excludes identity with the African species now called '*P. thunbergii*': stele of proto type, endodermis of O-type, interlacunar and subepidermal bundles absent, pseudohypodermis absent. Thus, like the HAL and LE specimens, this syntype also belongs to *P. nodosus*.

As the Mundt & Maire's specimens are the only ones undoubtedly seen by Chamisso & Schlechtendal, we selected a lectotype from among the plants in this collection. We selected the duplicate in the Schlechtendal's herbarium in HAL for designation as it is better preserved:

Potamogeton thunbergii Cham. et Schltdl., Linnaea 2(2): 221, t. 6, f. 21. 1827. ('Thunbergii')
Type: 'Potamogeton Thunbergii Nb., P. natans Thbg., Cap., *Mundt et Maire*' (lectotype: HAL, lectotype designated here); 'Potamogeton Thunbergii N., P. natans Thunb., fluitanti affinis, Hartebeestkraal pr. Brakrivier, C[ap]. B[onae]. Sp[ei]., Jan. [18]19, *Mundt et Maire*, Hb. Cham.' [= Hartebeeskraal, Western Cape, South Africa] (isolectotype: LE).

The name '*P. thunbergii*' therefore cannot now be used for the African species with big tricarinate fruits, U-endodermis, and well-developed interlacunar and subepidermal bundles. However, another name, *P. richardii* Solms, is available for this species (see below). This name has commonly been used for this species, particularly in East Africa.

Evaluation of type material of *Potamogeton schweinfurthii* A. Benn.

When Bennett (1901) published this name, he cited three collections (syntypes): 'Nile Land. Abyssinia: Begemeder; in Lake Tana, *Schimper 1359* ! British East Africa: at the mouth of the Bahr el Arab, *Schweinfurth 1223* ! in the Bahr el Ghazal, near the Nuer Villages, *Schweinfurth 1165* !'. We found at least one of these collections in BM, CGE, E, K, LD, NH, P and PRE. However, only the *Schimper 1359* in BM and K, *Schweinfurth 1223* in K, and *Schweinfurth 1165* in K

are the duplicates seen by Bennett and upon which he based his description of *P. schweinfurthii*.

There are two sheets of *Schimper 1359* in BM and a single sheet in K, each bearing several plant fragments, with many submerged leaves and a few floating leaves. The submerged leaves are sessile or with a petiole of up to 2.8 cm, and a lamina up to 21 cm long and 6–13 mm wide. The stem has a stele of trio to oblong type, endodermis of U type, interlacunar bundles present as scattered in one circle, subepidermal bundles absent and a pseudohypodermis of one continuous layer. These plants are what is now called *P. schweinfurthii*.

Two sheets of *Schweinfurth 1223* are preserved in K. These sheets bear a tightly pressed mass of plant shoots with many submerged leaves and a few floating leaves. The submerged leaves have petioles 4–10 cm long and laminas *c*. 8–11.5 cm long and 5–11.4 mm wide. The stem has a stele of trio type, endodermis of O-type, lacks both interlacunar and subepidermal bundles, and pseudohypodermis is present in one incomplete layer. This collection clearly belongs to *P. nodosus*.

The single sheet of *Schweinfurth 1165* in K bears a plant with two submerged, one transitional and four floating leaves. The submerged leaves have petioles 4.0–4.3 cm long, and laminas 8.3–8.9 cm long and 4.5–11 mm wide. The floating leaves have petioles 3–4 cm long, and laminas 3.9–4.7 cm long and 10–19 mm wide. The stem has a stele of trio type, endodermis of O-type, cortex without bundles and no subepidermal bundles or pseudohypodermis. This plant is taxonomically identical with *P. nodosus*.

When working on a revision of the genus *Potamogeton* in tropical Africa, Dandy (1937) designated the specimens on one of the sheets *Schweinfurth 1223* preserved in K as a lectotype of the name *P. schweinfurthii* A. Benn. The full records of the type material follow:

'Reise nach Central-Africa im Auftrage der Humboldt Stiftung, Mündung des Bahr el Arab, am Gazellen-Fluss [= mouth of Bahr al 'Arab (river) into Bahr al Ghazal (river), Sudan], 28 Fbr. [18]69, *G. Schweinfurth 1223*' (lectotype: K, designated by Dandy, 1937; photo: BM, PRA; isolectotypes: B†, E *n. v.*, K, LD, NH *n. v.*, P, PRE); 'Reise nach Central-Africa im Auftrage der Humboldt Stiftung, bei den Nuer-Dörfern [= Nur, Sudan], am Gazellen-Fluss, 15 Fbr. [18]69, *G. Schweinfurth 1165*' (syntype: B†, K); 'Plantæ Abyssinicæ, Im Zana [sic!] See [= Lake Tíana, Ethiopia] (in offenem Wasser, nah am Ufer) bei Angasha, 9 Novbr. [18]63, *Schimper 1359*' (syntype: B†, BM, CGE, E *n. v.*, K, W†).

Unfortunately, as described above, the lectotype of the name *P. schweinfurthii* actually belongs to *P. nodosus* and not to the species today widely known under the former name. On the basis of Dandy's typification, our recent examination of the lectotype and the strict application of the nomenclatural rules of the ICBN (Greuter *et al*., 2000), the name *P. schweinfurthii* would become a synonym of *P. nodosus* and a different name would have to be used for the African species under concern. There are several names at the rank of species available for this taxon, the three oldest of them being of equal priority: *P. repens* Hagstr., *P. promontoricus* Hagstr. and *P. capensis* Scheele ex Hagstr. However, each of these names was only used by its author in the original protologue but not adopted by any other researcher. Using any of these names would be a typical example of resurrection of a long-forgotten name for purely nomenclatural reasons. In contrast, the name *P. schweinfurthii* was in consistent use for more than 100 years.

The use of the name *P. schweinfurthii* in a new sense would constitute an undesirable change contrary to Art. 57.1 of ICBN. This widely used name would be replaced by one of its synonyms and itself would become a synonym of another name, which could cause confusion of literature records. As the lectotypification by Dandy was formally correct, it cannot be superseded without a conservational proposal. To avoid the disadvantageous change and ensure nomenclatural stability, we propose to conserve the name *P. schweinfurthii* A. Benn. with one element of the original material of Bennett, the specimen *Schimper 1359* preserved in K, as its conserved type (Kaplan & Symoens, 2004).

DESCRIPTIONS, NOMENCLATURE AND DISTRIBUTIONS

Only brief descriptions, consisting exclusively of diagnostic characters, are given. Besides *P. nodosus*, the two species most frequently confused with it in tropical and southern Africa are described, namely *P. schweinfurthii* and *P. richardii*. All features and character values are described exclusively from material of African origin.

The complete nomenclature is provided for *P. richardii* and *P. schweinfurthii*. Because of the extensive synonymy of *P. nodosus* (see also Wiegleb & Kaplan, 1998), only the more important synonyms are cited here, especially those most frequently used and based on material from Africa or adjacent territories.

The revised distributions of all three species in Africa and on surrounding islands are given. The identity of all collections of *P. nodosus* from tropical and southern Africa given in the list of specimens and in the map was confirmed by stem anatomy. The distribution of *P. richardii* is based either on well-developed fruiting specimens or on anatomically studied herbarium collections and purged of misidentified specimens of *P. nodosus* and morphotypes of

P. schweinfurthii with floating leaves. Only selected representative specimens are listed for each species. However, the maps are more or less up to date and all reliably identified specimens seen by us were included. A detailed distribution of *P. schweinfurthii* for many countries is also available (Obermeyer, 1966; Lisowski *et al*., 1978; Jafri, 1984; Symoens, 1984; Wiegleb, 1995). The literature is relatively reliable as it generally refers to the easily recognizable phenotype of this species with only submerged leaves developed. The literature on *P. richardii* is less reliable because of the confusion with *P. nodosus*, which was not previously recognized in the greater part of Africa.

Potamogeton nodosus Poir. in Lam., Encycl. Méth. Bot., Suppl. 4: 535. 1816. ('nodosum')
Type: [Canary Islands:] 'Potamogeton nodosum (n), *Brouss*[*onet*], Canar., herb. Poiret' (lectotype: P, lectotype designated here; isolectotype: FI-W).

= *P. canariensis* Link in Buch, Phys. Beschr. Canar. Ins. 138. 1825.
Type: [Canary Islands:] 'Canarische Inseln', *Buch* (holotype: B†).

= *P. leschenaultii* Cham. et Schltdl., Linnaea 2(2): 223, t. 6. fig. 23. 1827. ('Leschenaultii')
Type: [Canary Islands:] 'Potamogeton Leschenaultii, *Leschnenaultio* in insula Teneriffa lecta, Ex herb. Kunth, Ex Museo Paris, 1821' (syntype: BM, fragment from and illustration of the B collection, which itself was destroyed during World War II; no duplicate has recently been found in P, B or other herbaria).

= *P. mascarensis* Cham. et Schltdl., Linnaea 2(2): 228. 1827.
  ≡ *P. fluitans* proles *mascarensis* (Cham. et Schltdl.) Graebn. in Engl., Pflanzenr. 31 (IV.11): 60. 1907.
  ≡ *P. americanus* ssp. *mascarensis* (Cham. et Schltdl.) A. Benn., J. Bot. 46: 160. 1908.
Type: [Mascarene Islands:] 'isle de france' [= Mauritius] (lectotype: P, lectotype designated here).

= *P. syriacus* Cham. et Schltdl., Linnaea 2(2): 227. 1827.
  ≡ *P. fluitans* proles *syriacus* (Cham. et Schltdl.) Graebn. in Engl., Pflanzenr. 31 (IV.11): 60. 1907.
Type: 'Potamogeton syriacus N., Beiruti, Syria, majo, *Ehremberg* [sic!, = *G. Ch. Ehrenberg*], Hb. Cham.' (lectotype: LE, lectotype designated here); 'Museum botanicum Berolinense, *G. Ch. Ehrenberg*: Iter orientale, Potamogeton fluitans L., Syria: Berut, 18.v.1824' (isolectotype: B†, BRVU, illustration: BM).

= *P. thunbergii* Cham. et Schltdl., Linnaea 2(2): 221, t. 6, f. 21. 1827. ('Thunbergii')
  ≡ *P. natans* var. *angustatus* (b) *capensis* Kunth, Enum. Pl. 3: 128. 1841.
  ≡ *P. natans* var. *capensis* T. Durand et Schinz, Consp. Fl. Afric. 5: 494. 1894.
  ≡ *P. americanus* var. *thunbergii* (Cham. et Schltdl.) A. Benn. in Dyer, Fl. Capens. 7: 46. 1897. ('Thunbergii')
  ≡ *P. fluitans* proles *thunbergii* (Cham. et Schltdl.) Graebn. in Engl., Pflanzenr. 31 (IV.11): 61. 1907.
Type: for lectotypification see page 331.

= *P. semicoloratus* A. Benn., J. Bot. 48: 150. 1910.
Type: [Arabian Peninsula:] 'Unio itiner, 1857, In rivulis vallis Fatme prope Unsert Arab. d. 29. Febr [18]36, leg. *W. Schimper 893*' (lectotype: BM, lectotype designated here, photo: PRA; isolectotypes: BREM, LE, P, PRC, TUB, W); 'Hab. In rivulis palmetorum vallis Fatme, Flor. Febr, *S. Fischer 100*' (syntype: CGE, K, LE, M); 'Island of Socotra. East of Somali Land. E. Africa, leg. Prof. *B. Balfour*, 1880' (syntype: BM, LE, P, S).

= *P. stagnorum* Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55/5: 159. 1916 [1 November]; Hagstr. in R. E. Fr., Wiss. Erg. Schwed. Rhod.-Kongo-Exp. 1911–1912, 1(2): 187. 1916 [December].
Type: [Zambia:] 'Exped. Suecica in reg. Central.-Africanis 1911–12, Potamogeton stagnorum J. O. Hagstr. n. sp., Rhodesia bor. orient. in rivulo Chimona ad Bangweolo, 20 IX 1911, leg. *R. E. Fries 691*' (holotype: UPS).

Floating leaves usually present, always in flowering or fruiting adult plants (sometimes absent in adult fertile plants growing in strongly flowing water, but we have not seen such specimens from Africa); lamina coriaceous, light green, opaque, often with a reddish tinge, sometimes brownish or rarely secondarily blackish (when dried slowly), narrowly oblong to broadly elliptical, mostly narrowly to broadly cuneate and narrowed towards the petiole, but sometimes even rounded at base, particularly in standing water; petiole often narrowly winged towards the lamina, never with a discoloured section.

Submerged leaves usually present, well developed and preserved in running water, but sometimes decaying in shallow standing water, petiolate; lamina membraneous, narrowly oblong to oblanceolate-oblong, never reduced to phyllodes, light green to reddish brown, usually 11–15-veined in fully developed upper leaves, lower leaves with fewer veins, gradually narrowed towards a narrowly obtuse or subacute apex, often broadly obtuse in leaves from the basal parts of the stem, never mucronate; petiole mostly more than

3 cm long, often even longer than 10 cm in running water, but can sometimes be very short in standing water, 0.2–2 times as long as the lamina.

Stipules widest near the base and gradually narrowing to their apex, often quickly decaying and gradually disappearing. Peduncles as thick as or sometimes slightly thicker than the stem. Fruits 3.0–3.9(–4.0) mm long, reddish brown or sometimes reddish green, with ± obtuse and low dorsal keel.

Stem anatomy: stele of trio or sometimes proto type, endodermis of O-type, interlacunar bundles absent, rarely a few present, subepidermal bundles absent, rarely a few present, pseudohypodermis absent or present as one, often incomplete layer.

Representative herbarium specimens (see also Figs 1, 2).

Macaronesia: AZORES: Santa Maria, 28.vi.1896, *W. Trelease 969a* (BM, K); *W. Trelease 969b* (BM, C, K); *W. Trelease 969c* (BM); vi.1899, *Carreiro 862* (BM), 1953, *B. F. C. Sennitt s. n.* (BM); Santa Maria, Santana, 9.viii.1969, *D. T. Pombo s. n.* (BM). CANARY IS. Teneriffa [= Tenerife], Bufadero Valley, v.1846, *E. Bourgeau 533* (BM, CGE, G, LE, P, PRA, PRC); 9.viii.1889, *O. Simony s. n.* (Z); Teneriffa [= Tenerife], Tejina, *c*. 100 m, 13.vi.1901, *J. Bornmüller 2864* (BR, G, K, LD, LE, P, PR, PRC, S, WU, Z); Tenerife, Igueste de San Andrés, 9 V 1933, *E. Asplund 1181* (G, S); *E. Asplund 1182* (G, S); Tenerife, Igueste [= Igueste de San Andrés], *c*. 700 m, 15.iv.1908, *C. Schröter s. n.* (ZT); Tenerife, St. Croix, 1848, *L. H. Boivin 247* (P); Tenerife, Las Palmas, 13.iv.1908, *C. Schröter s. n.* (ZT); Gomera, Fragoso, iii.1906, *C. J. Pitard 685* (B, BM, BRVU, G, P, S); Gran Canaria, Virgen, iv.1882, *W. Hillebrand s. n.* (Z); Gran Canaria, Azuaje, 26.iv.1891, *O. Gelert s. n.* (C, KRA); Gran Canaria, St. Felipe, 2.v.1897, *O. Gelert s. n.* (C). MADEIRA: Machico, in river, 30.viii.1858, *R. T. Lowe 289* (BM, G, K, LE); 11.viii.1858, *R. T. Lowe 289* (BM, K, P); 30.v.1859, *R. T. Lowe 289* (BM); 26.vi.1865, *G. Mandon 232* (BM, BREM, BRVU, C, G, GOET, K, LE, LY, P, PRC, S, Z); 12.vii.1866, *F. M. Norman* (CGE).

Northern Africa: ALGERIA: Alger [= Algiers], viii.1837, *Bové s. n.* (BM, G, LE, P); Oued Harrach [= El Harrach], 3.viii.1856, *G.-L. Durando s. n.* (BRVU, CGE, MPU); Maison Carrée [= El Harrach], 3.viii.1857, *G.-L. Durando s. n.* (LIV); Baba Ali, 8.ix.1878, *J. A. Battandier s. n.* (BRVU, MPU); Sig, 6.vi.1850, *G. L. Durando 150* (G, MPU, P); Prov. Oran, Sidi-bel-abbés [= Sidi Bel Abbès], Sarno River, 15.vi.1872, *A. Warion s. n.* (G); La Calle [= El Kala], 24.vi.1841, *M. C. Durieu de Maisonneuve s. n.* (P); Prov. Constantine, Setif, 21.vi.1840, *M. C. Durieu de Maisonneuve s. n.* (P); Constantine, Roumel [= Chelghoum el Aïd], 3.ix.1878, *V. Reboud 2263* (BRNM, G, K, P, Z); Department Constantine, Biskra, Oase Vieux Biskra, 30.vii.1954, *Doppelbaur s. n.* (M); Prov. Oran, Aïn Sefra, Tiout, *c*. 1050 m, 31.v.1901, *B. P. G. Hochreutiner 551* (G, Z); Prov. Oran, Colomb Bichar [= Béchar], 2.iv.1910, *C. Schröter s. n.* (ZT). EGYPT: [Al Buhayrah], Alexandria, Kefr El-Douar, xi.1880, *A. Letourneux 322* (BRVU, G, K, P, PRC, Z); [Al Buhayrah], Qussus el Bahani N of Resetta, 7.vi.1925, *N. D. Simpson 3449* (K); [Al Buhayrah], Nile Delta, Etai El Baroud [= Ityāy al Bārūd], 22.ix.1971, *M. Mahdi s. n.* (M); [Ash Sharqīyah], Bilbeis [= Bilbays], 8.ix.1922, *N. D. Simpson 1584* (K); 11.viii.1927, *N. D. Simpson 5223* (K); 21.vi.1929, *A. Khattab s. n.* (S); [Al Jizah], El Kanka, 7.ii.1929, *N. D. Simpson 6482* (K); [Al Jizah], Cairo region, Giza, Mansurya canal, 24.v.1986, *L. Triest et al. 507* (BRVU); El Faiyun [= Al Fayyûm], Sennuris [= Sinnûris], 15.vii.1960, *L. Boulos s. n.* (BRVU, U); [= Al Fayyûm], Medinet El Faiyum [= Al Fayyûm], 29.ix.1967, *V. Täckholm et al. s. n.* (LD, S, U); [Ash Sharqīyah], Uadi Tumilat [= Wadi Tumilat], 3.v.1880, *G. Schweinfurth 411* (C, G-Boiss); [Ash Sharqīyah], Kafr Hauwan near Fagus [= Fāqūs], 11.v.1880, *G. Schweinfurth 413* (G-Boiss, K). LIBYA: Between Zlitan [= Zlitan] and Homs [= Al Khums], Wady Kâm [= Ki'am], 22.iv.1939, *N. Y. Sandwith 2736 & N. D. Simpson 39680* (BM, K, S); Tripoli, 18.iii.1887, *P. Taubert 71* (BM, G, K, P); el-Gubba [= Al Qubbah] – Ain Mara [= 'Ayn Marrah], 28.iv.1934, *R. Pampanini & R. Pichi-Sermolli 159* (G, FI); Wadi Derna, 200 m, 24.v.1887, *P. Taubert 660* (G); 20 11967, *L. Boulos 1264* (S); 31.iii.1970, *Davis 50360* (K); Western Fezzan, Gat [= Ghāt], 700 m, 5.iii.1934, *R. Corti 1272* (FI); Western Fezzan, Sérdeles [= Al 'Uwaynāt], 650 m, 20.iii.1934, *R. Corti 1277* (FI). MOROCCO: Distr. Ouazzane, Oued Elbiad River *c*. 5 km S of Ouazzane (= Wazzan), *c*. 130 m, 2.vi.2002, *Z. Kaplan et al. 02/97* (PRA); Distr. Tétouan, detached river arm of Oued Laou River 7 km SW of Tleta-Oued-Laou, 4.vi.2002, *c*. 5 m, *Z. Kaplan et al. 02/98* (PRA); Distr. Tanger (= Tangier), stream below water reservoir near Regaia, *c*. 5 m, 7.vi.2002, *Z. Kaplan et al. 02/107* (PRA); Kenitra, *c*. 23 km from Ouazzane on road to Chefchaouen, 105 m, 23.vi.1992, *G. Stark 1759* (LIV); Zeluan [= Selouane], Moulin, 5.vi.1932, *Sennen & Mauricio 8531* (BC, BCF, BM, BRNU, G, GE, MPU); *c*. 10 km SSE of Rabat, valley of Oued Akrech, 22.v.1961, *J. J. F. E. de Wilde et al.* (*Pl. Marocc. Exs. 2370*) (BM, WAG); Camp Boulhaut [= Ben Slimane], 15.v.1912, *C.-J. Pitard 1433* (G, K, MPU, P); Moyen Atlas, Guigou, Skoura, 1300 m, 24.vi.1980, *J. Lewalle 9587* (BM, BR); Prov. Er Rachidia, Meski, 26 km SE of Er Rachidia, 2.iv.1943, *D. Podlech 50792* (M); *D. Podlech 50794* (M); Near Marrakech, Guéliz, 465 m, 21.v.1926, *H. Lindberg*

Figure 1. A well-preserved specimen of *Potamogeton nodosus* from Tanzania (*E. Milne-Redhead & P. Taylor 10908*, BM). Stem anatomy of this plant is: stele of trio type, endodermis of O-type, interlacunar absent, subepidermal bundles absent, pseudohypodermis absent.

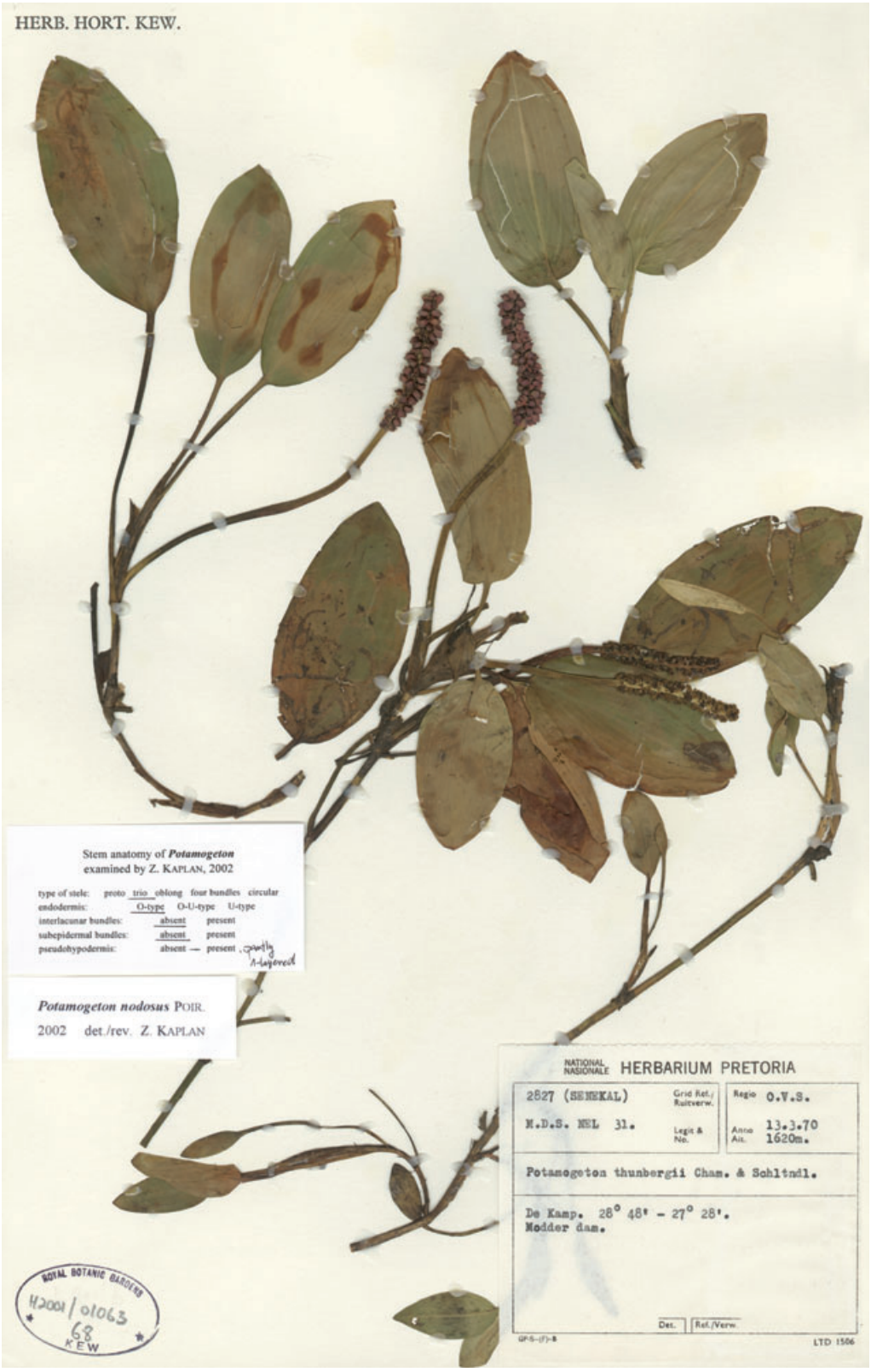

Figure 2. Plants of *Potamogeton nodosus* with only floating coriaceous leaves, which mimics *P. richardii* superficially (*M. D. S. Nel 31*, K). Stem anatomy (endodermis of O-type, both interlacunar and subepidermal bundles absent) identifies this collection as *P. nodosus*. The plants also have the reddish brown fruit typical of this species.

2986 (B, C, K); Ouarzazate, 10.v.1932, *R. Maire s. n.* (P); Asif Tamrhart, *c*. 7 km N of Agadir, 27.iv.1961, *J. J. F. E. de Wilde et al*. (*Pl. Marocc. Exs. 1889*) (BM, WAG). TUNISIA: Oued Chila, E of Menzel Bou-Zelfa [= Manzil Bu Zalafah], 23.v.1883, *E. Cosson et al*. *s. n.* (P); Oued Zargua, vi.1881, *Roux s. n.* (MPU); Bargou, 2.vi.1887, *A. Letourneux s. n.* (P); Degache, 30.iv.1887, *A. Letourneux s. n.* (P).

West Tropical Africa: MAURITANIA: Adrar, Hij, 9.v.1934, *T. Monod 384* (P). MAURITANIA/ SENEGAL: 'Région du fleuve Sénégal [= Senegal River Valley]: Saint-Louis – Richard-Toll, Podor, Matam Gandiole, Makana, Rosso', 1950–1951, *P. J. Berhaut s. n.* (P). SENEGAL: Dakar, Mt. Rolland near Thiès, 22.vii.1948, *J. G. Adam 1621* (P). NIGER: Tinnia, 11.x.1967, *B. Peyre de Fabrégues 2563* (P); Aïr Mtns, Mt. Bagluzcus, Jiabel-Allen, *A. Chevalier 43410* (P); Aïr Mtns, Oued Iferouāne, 2700 ft, x.1961, *D. N. Hall s. n.* (K); Aïr Mtns, Tamgak Wadi, 730 m, 25.iii.1970, *P. N. Bradley 101* (K).

West-Central Tropical Africa: GULF OF GUINEA IS. Fernando Po [= Bioko], Lagoa Biao, 5700 ft, 14.ix.1959, *F. Melville 488* (BM, K); Bioko, Luba [= Ciudad de Luba, Equatorial Guinea], Moseete River, 2 m, 15.iii.1990, *Carvalho 4299* (G, K, P).

North-east Tropical Africa: CHAD: Tibesti Mtns, Yebbi-Bou, 1300 m, 17.iii.1931, *Dalloni s. n.* (BRNU, LD, P); Ennedi Mtns, Aouei [= Aoué], 2900 ft, 30.x.1957, *P. C. Hutchison 131* (BM); Ennedi Mtns, Aoué, 24.xii.1966, *T. Monod 13768* (BRVU, P); Hadjer el Hamis, delta of Chari River, x.1964, *Bard s. n.* (P). ETHIOPIA: Harer [= Hārer], 1889, *Robecchi-Brichetti 38* (FT). SOCOTRA: [without locality], 1880, *B. Balfour s. n.* (BM, LE, P, S). SUDAN: Jebel Marra [= Jabal Marrah Mtns], Nyertete, 3800 ft, 20.i.1964, *G. E. Wickens 1020* (K); 20.iv.1965, *G. E. Wickens 2914* (K); Jebel Marra Mtns [= Jabal Marrah], Nyertete, *c*. 120 km E of Zalingei, *c*. 1400 m, 26.i.1965, *W. J. J. O. de Wilde et al*. (*Pl. Afr. Centr. Exs. 5604*) (K, P); Darfur, Jawa, 3.xii.1954, *J. K. Jackson 3285* (K); Gezira [= Al Jazirah], Abu Sin canal, 23.i.1936, *F. W. Andrews A142* (BR, K, P); Gezira [= Al Jazirah], Wad Medani [= Wad Madani], 10.ii.1965, *W. J. J. O. de Wilde et al*. (*Pl. Afr. Centr. Exs. 5711*) (BR, K, WAG); Gezira [= Al Jazirah], Hag Abdulla [= Hajj 'Abd Allah], Bolein canal, 10.ii.1950, *K. W. Jones J58A* (BM); 29.iii.1950, *K. W. Jones J58* (BM); Gezira [= Al Jazirah], Hag Abdulla [= Hajj 'Abd Allah], Masala canal, 17.i.1950, *K. W. Jones J60* (BM); Lake No, near the Suddite Factory, 17.vi.1929, *N. D. Simpson 7204a* (BM, K); Ghabat el Arab [= Wang Kai], Bahr el Arab [= Bahr al 'Arab River], vii.1929, *N. D. Simpson 7204b* (BM); Ghabat el Arab [= Wang Kai], Bahr el Ghazal [= Bahr al Ghazal], 10.iii.1930, *N. D. Simpson 7665* (K, W).

East Tropical Africa: TANZANIA: Malagarasi Swamps, 29.viii.1952, *Lowe s. n.* (BM, EA, K); Songea Distr., Likonde River, 750 m, 26.vi.1956, *E. Milne-Redhead & P. Taylor 10908* (B, BM, BR, EA, K).

South Tropical Africa: ANGOLA: Sa da Bandeira [= Lubango], *F. Welwitsch 249* (BM, K, P). ZAMBIA: Abercorn [= Mbala], Uningi Pans, 5500 ft, 10.iv.1964, *L. D. E. F. Vesey-FitzGerald 4266* (K); Luapula Distr., near S part of Lake Bangweulu, Mboyalubambe Island, 10 km S of Lake Chale, 1062 m, 6.iii.1996, *S. A. Renvoize 5752* (K); Serenje Distr., Bangweulu flats, Lulimala River, 30.vii.1959, *W. C. Verboom 2622* (K); Mankoya Distr. [= Kaoma], Luena River, 20.xi.1959, *R. B. Drummond & A. J. Cookson 6639* (BM, K); Mumbwa Distr., Mumbwa Dam, 19.ix.1947, *J. P. M. Brenan & P. J. Greenway 7884* (EA, K). ZIMBABWE: Victoria Falls, Zambezi River, ix.1905, *L. S. Gibbs 146* (BM); Distr. Wankie [= Hwange], Kazuma Range, Katsatetsi River, 1000 m, 10.v.1972, *G. E. Gibbs Russell 1950* (WAG); Distr. Binga, Sinamwenda River, Elephant Island, 28.ix.1970, *D. S. Mitchell 1272* (K); Distr. Marandellas [= Marondera], Chiota Tribal Trust Land, Chikokorana Pan, 1200 m, 29.iv.1972, *G. E. Gibbs Russell 1985* (B, BR, M) [The herbarium sheet with this label preserved in PRE bears broad-leaved plants of *P. schweinfurthii* (the identity confirmed with stem anatomy). They seem to belong to the collection *G. E. Gibbs Russell 1984* from the same site (see page 351) but are incorrectly labelled as *G. E. Gibbs Russell 1985*]; Mrs Strickland's farm Charity, [*collector unknown*, label partly burned] (BM).

Southern Africa: BOTSWANA: Distr. Northern, near the Okavango River, 22.ii.1984, *P. A. Smith 4372* (BR, K); Distr. Ngamiland, Okavango River downstream from Red Cliffs, 1030 m, 30.iv.1975, *G. E. Gibbs Russell 2874* (WAG); Distr. Northern, Okavango delta, lower Boro River, 31.xii.1974, *H. Hiemstra 204* (BR, K); Distr. Northern, Okavango Swamp, Kwai River upstream from Txatxanika Camp, 1000 m, 1.iii.1972, *G. E. Gibbs Russell & H. M. Biegel 1479* (BR, K, PRE); Okavango, outlet of Xaxanika lagoon, 8.iv.1984, *W. Ellery 32* (PRE); Distr. Northern, Thamalakane River upstream from Crocodile Camp, 1000 m, 22.i.1972, *G. E. Gibbs Russell & H. M. Biegel 1370* (B, BR, K, M, P, WAG); Distr. Northern, Thamalakane River at Maun, 1000 m, 22.i.1972, 13.iii.1961, *H. M. Richards 14692* (BR, K); *G. E. Gibbs Russell & H. M. Biegel 1374* (B, BR, K, WAG); Distr. Northern, Xahajo, Thaoge River, 23.ix.1974, *P. A. Smith 1118* (K); Maun, Maunachira River *c*. 100 m downstream Godikweisland, 6.ii.1985, *Ellery 279* (M); Distr. Northern, along Lake [Ngami]

beach and in Nghabe river above Lake mouth, 22.ii.1977, *P. A. Smith 1922* (BR, K). LESOTHO: Distr. Léribé, Hlotse, 1911, *Dieterlen & Dieterlen 831*. (BM, BRVU, K, P); Sehlabathebe National Park, Tsoelikana River valley, *c*. 2275 m, 4–14.i.1973, *J. Guillarmod et al*. *99* (K); 10.i.1979, *F. K. Hoener 2139* (K, PRE, S, WAG). NAMIBIA: Runtu [= Rundu], Okavango River, 9.v.1939, *O. H. Volk 1882* (BR, M, PRE); Distr. Grootfontein, Runtu [= Rundu], Okavango River, 6.iii.1958, *H. Merxmüller & W. Giess 1889* (BR, M, PRE); Niangana [= Nyangana], Okawango [= Okavango River], v.1934, *Dinter 7738* (B); Distr. Grootfontein, Blockfontein, Omuramba Omatako River, vii.1939, *Müller-Stoll 184* (M); Distr. Maltahöhe, Alt Zaris, 20.x.1939, *O. H. Volk 755* (M); Distr. Caprivi Strip, Singalamwe, *c*. 3300 ft, 1.i.1959, *D. J. B. Killick & O. A. Leistner 3229* (K, M). SOUTH AFRICA: Western Cape Province, Hartebeeskraal, Brakrivier, i.1819, *Mundt & Maire s. n.* (HAL, LE); Western Cape Province, Cape Town, Zeekoeivlei River, *Thunberg 3843* (UPS, Herb. Thunberg); Western Cape Province, Knysna Distr., 4.xi.1931, *A. V. Duthie 1173* (BOL); Eastern Cape Province, Distr. Alexandria, on road Salem – Alexandria, Farm 'The Lomonds' of G. I. Suttie at Skiet Rug, Bushmans River, 8.i.1960, *D. M. Comins 1846* (K); Eastern Cape Province, Vlaktefonteinplaas, 16 km of Sterkspruit, 1440 m, 12.ii.1970, *M. D. S. Nel 18* (K, PRE); Free State, Steynsrus, Turffontein Plaas, Springbokkampdam, 9.i.1993, *P. Van Eeden 15* (PRE); Free State, De Kamp, Modder dam, 1620 m, 13.iii.1970, *M. D. S. Nel 31* (K, PRE); Gauteng, Distr. Pretoria, 4 mi. E. of Hammanskraal, Kaalllaagte, farm of Mr Botha, 4500 ft, 19.iii.1963, *Mauve & Schlieben 9597* (B, BM, EA, G, K, M, PRE, S, Z); Gauteng, Witwatersrand, Roodepoort Distr., Florida Lake, near Johannesburg, 1550 m, 17.x.1925, *V. A. Wager s. n.* (PRE); 30.iii.1926, *C. E. Moss 12007* (BM, M); 4.ii.1929, *C. E. Moss 17345* (BM); Northern Province, Naboomspruit, Mosdene Farm, Vlei pool and Nyl River, 27.ii.1974, *G. Germishuizen 8* (K, PRE); KwaZulu-Natal, Distr. Bergville, Rustenburg Road from Bergville, 4000 ft, 17.xii.1958, *D. Edwards 2408* (G, K, M, Z); KwaZulu-Natal, Distr. Estcourt, 3.5 mi. Mooi River on Rietvlei road, 4600 ft, 23.iv.1963, *D. Edwards 3119* (PRE); KwaZulu-Natal, Nyalazi State Forest, Pan S of Kentron airstrip, 24.ix.1985, *G. F. van Wyk 593* (NH); KwaZulu-Natal, Gingindhlovu, xi.1932, *J. Gerstner s. n.* (NH); KwaZulu-Natal, Durban Distr., Wentworth, Happy Valley, 40–45 ft, 15.iii.1966, *C. J. Ward 5423* (K, WAG); KwaZulu-Natal, Distr. Durban, Bluff, Happy Valley Swamp, 26.xii.1962, *B. J. Huntley 135* (PRE); KwaZulu-Natal, Dumisa [near Umzinto], 800 m, 27.ix.1912, *H. Rudatis 1691* (G, PR, W, WAG).

Western Indian Ocean: COMOROS: Mayotte, Grande Terre, Ouangani, Coconi, Valarano-Coconi, 19.viii.2002, *F. Barthelat et al*. *993* (P). MAURITIUS: 'isle de france' [without locality], [1769–1773], *P. Commerson s. n.* (P); [without locality], 1846–1848, *Boivin s. n.* (W); Beaux-Songes, x.1849, *Boivin s. n.* (P). MADAGASCAR: Prov. Diego-Suarez [= Antseranana], on road Joffreville [= Ambohitra] – Mt. Ambre [= Ambohitra], x.1944, *A.-M. Homolle 16* (P); Between Vohémar [= Iharana] and Ambilobé, 28.vii.1939, *R. Decary 14634* (K, P); Analanantsoa, Ambodisakoana, Manongarivo River, 40 m, 21.xi.1994, *P. Derleth 173* (G, K, P); Marovoay, x.1907, *H. Perrier de la Bathie 7164* (P); Prov. Majunga, Bedilo [= Bediloha], v.1912, *K. Afzelius s. n.* (LD, S); Andranoboka, 20.vi.1938, *R. Decary 13453* (P); *R. Decary 13462* (P); 3 km of Besalampy, 12.x.1968, *J.-L. Guillaumet 2253* (P); Andreba, Alaotra Lake, 1200–1300 m, 12.xi.1946, *G. Cours 3092* (P); Nossi-Vé Lake [near Toamasina], 15.ix.1882, *Humblot 324* (K, P); Andranomalaza, *c*. 20 m, 9.x.1970, *Bogner 314* (K, M); Tsarasaotra, i.1898, *H. Perrier de la Bathie 456* (P); Sahafitahana, 5 km S of Moramanga on road to Anosibé, *c*. 800 m, 7.ii.2002, *A. Raynal-Roques & J. Jérémie 24971* (P); Befandriana-Sud [= Befandriana Atsimo], 5.viii.1963, *P. O. Appert 127* (Z); Distr. Morombeau [= Morombe], SW of Befandriana [= Befandriana Atsimo], *c*. 150 m, 6.iv.1955, *H. Humbert 29745* (P, PRA); Ranozaza [near Toleara], *H. Poisson 332* (P); Toliara [= Toleara], near Beza Mahafaly Reserve W of Betioky, Valley of Ehazoara River, 175 m, 11.xii.1988, *P. B. Phillipson 2856* (BR, C, G, K, P, S, WAG) [The sheet of this collection preserved in BR bears two detached spikes of *P. nodosus* and one vegetative shoot of *P. schweinfurthii*. The latter species is not known to occur in this part of Madagascar and the vegetative fragment was probably mixed in this collection during specimen processing.]; Androy, Beteny, 22.xi.1931, *R. Decary 9364* (P); Fort-Dauphin [= Taolagnaro], Ianakoty, 4.iv.1966, *M. Peltier 5953* (P). RÉUNION: 'Bourbon' [without precise locality], 1846–1852, *Boivin s. n.* (G, fragments in BM and BRVU); *Richard s. n.* (K); Bernica, Saint-Paul, 5.ix.1962, *T. Cadet 241* (K). SEYCHELLES: Mahé, Anse Royale, 50–100 ft, 1908, *J. S. Gardiner s. n.* (K); 12.vii.1936, *C. Osborne-Day 53* (BM); 21.ii.1962, *C. Jeffrey & M. Zelia 1169* (K).

Subantarctic Islands: MARION-PRINCE EDWARD IS.: Marion Island, Albatros Lake, 10 m, 25.ix.1965, *B. J. Huntley 2058* (K, P, PRE).

Potamogeton nodosus in the strict sense is usually considered to be a species of warm-temperate and subtropical regions of the northern Hemisphere. However, it penetrates into the tropics and in some areas even further south into the warm-temperate regions of the southern Hemisphere. In America, besides its range on the North American mainland, it is quite frequent

in the Caribbean (from Cuba across the chain of islands south-east to the Windward Islands and Trinidad) and reaches Venezuela and the Brazilian state of Pará on the South American mainland. Wiegleb (1990a, 2002) recently confirmed the occurrence of *P. nodosus* in Indo-China (Andaman Islands, Burma, Thailand, Vietnam), Malesia (Jawa, Lesser Sunda Islands, Philippines, Sulawesi, Sumatera), Papua New Guinea, Australia (Northern Territory, Western Australia) and the south-western Pacific (New Caledonia, Vanuatu). In fact, *P. nodosus* occurs as far south as the southern border of the range of *Potamogeton* as it occurs on the Marion Islands at latitude 46°20′S (see list of representative specimens). Even more southerly sites are occupied by *P. ochreatus* Raoul on the Antipodean Islands south of New Zealand (46°40′S) and in South America by *P. linguatus* Hagstr. on Navarino Island, Magallanes, Chile (54°50′S). Now, the presence of *P. nodosus* is confirmed on the African mainland right down to its southernmost tip.

In Africa, *P. nodosus* most often occurs in rivers and standing water in lowlands along the coast, particularly along the Mediterranean and South African coasts (Fig. 3). It is also often found in large inland

Figure 3. Distribution of *Potamogeton nodosus* in Africa and on surrounding islands based on examined herbarium specimens. Only collections confirmed by stem anatomy are illustrated in tropical and southern Africa.

river deltas, such as that of the Okavango river. In its entire range, *P. nodosus* often behaves as 'island species', as more than any other *Potamogeton* species it is recorded from islands. Also around Africa, *P. nodosus* was collected on most islands with suitable aquatic habitats. On the African mainland, this species is absent in tropical rain forests. There are no *Potamogeton* species in this habitat. This is probably because of a combination of acidic and nutrient-poor water and high temperatures. Similarly, species of *Potamogeton* do not occur in Amazonia.

Potamogeton nodosus is here reported for the first time from Gulf of Guinea Islands, Ethiopia, Tanzania, Zambia, Zimbabwe, Namibia, Botswana, South Africa, Lesotho, Seychelles, Comoros, Mauritius, Réunion and Marion-Prince Edward Islands.

Altitudinally, most of the localities occur at or near sea level or up to altitudes of 300 m a.s.l. However, particularly on plateaux, *P. nodosus* reaches altitudes of 1000–1500 m a.s.l. It has only exceptionally been collected at higher altitudes.

Potamogeton richardii Solms in Schweinf., Beitr. Fl. Aethiop. 194. 1867. ('Richardi')

= *P. americanus* var. *richardii* (Solms) Solms ex Schweinf., Bull. Herb. Boissier 2, App. 2: 8. 1894. ('Richardi')

Type: [Ethiopia:] 'Schimperi iter Abyssinicum, Sectio prima: plantae Adoënses, In rivis et aquis stagnantibus prope Adoam [= Adwa], U[nio]. i[tiner]. 1840, d. 11. Juni 1837, leg. *W. Schimper 135*' (lectotype: K, lectotype designated here, photo: PRA; isolectotypes: BM, BR, BRVU, CGE, FI-W, G, GOET, HBG, K, L, LE, LG, M, MPU, P, S, TUB, U, ZT); [Ethiopia:] 'Herbarium Richard, Potamogeton natans L., Chiré [= Shirē], Legerunt *Quartin-Dillon et Petit*' (syntype: P); [Ethiopia:] 'Abyssinie: Chiré: plaine de Beless, Févr.-Mars 1841, *Quartin-Dillon, 3^{e} envoi, 2^{e} centurie, n^{o} 86*' (syntype: P).

= *P. fibrosus* Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55(5): 160. 1916.

Type: [label 1:] '[*C. L. P. Zeyher*] *91.*' [label 2:] '. . . Pot. fibrosus, 13/8. [19]07. O. Hagström' [original locality not given in the herbarium label but supposed by Hagström (l. c.) to originate from South Africa] (holotype: S).

Floating leaves always present on adult plants, which never flower and fruit in the absence of floating leaves; lamina coriaceous, light green to deep green or sometimes olive green, occasionally slightly shiny, sometimes brownish or secondarily blackish (when dried slowly), oblong to broadly elliptical, mostly rounded or sometimes broadly cuneate at base; petiole sometimes narrowly winged towards the lamina, often with a discoloured section on its upper end at the junction with the lamina, though sometimes only on some leaves or not very apparent. Intermediate leaves, similar in shape to floating leaves, sometimes develop just below the water surface.

Submerged leaves decaying early, generally not present on adult plants, rarely one or two are present at the fruiting stage, often partly rotten, short to long petiolate; lamina membraneous, narrowly oblong to linear-lanceolate, sometimes almost reduced to phyllodes, mid green to blackish, 5–9(–15)-veined, gradually narrowed towards a narrowly obtuse apex, never mucronate; petiole often narrowly winged towards the lamina, mostly 5–15 cm long, exceptionally up to 23 cm long, 0.3–2 times as long as the lamina.

Stipules robust, widest near the base and gradually narrowing towards the apex, persistent grey fibres remain after they decay. Peduncle as thick as or sometimes even thinner than the robust stem. Fruits (3.7–)3.9–5.2(–5.5) mm long, ochre brown to pale brown or seldom dark blackish brown or greenish brown, rarely with reddish-brown tinge, with acute and high distinct dorsal keel and often with a pair of low lateral keels or ridges.

Stem anatomy: stele of trio type, endodermis of U-type, interlacunar bundles present in (1–)2–3 circles, subepidermal bundles mostly present, pseudohypodermis present, one-layered.

Representative herbarium specimens (see also Figs 4, 5).

West-Central Tropical Africa: BURUNDI: Bujumbura, Ijenda, 2000 m, 2.i.1966, *J. Lewalle 186* (BR, K); Bururi, Tora, 2100 m, 7.ii.1971, *J. Lewalle 5149* (BR, G); Bujumbura, Gakara, Bastnesite, 1900 m, 4.i.1970, *J. Lewalle 4297* (BR); Prov. Muramwya, Nyakirwa, Mubarazi, 2150 m, 21.i.1977, *M. Reekmans 5679* (BR, BRVU, K); Muzenga, Sikuvyaye River, 22.ix.1974, *J. Rammeloo 4759* (B, BR, BRVU, U, WAG, Z); Prov. Ruyigi, Kigamba, 1600 m, *M. Reekmans 6000* (BR, BRVU, C, K, PRE, UPS, WAG); Prov. Ruyigi, Giharo Moso, 1300 m, 1.ii.1976, *M. Reekmans 4766* (BR, WAG); Prov. Ruyigi, Nkanka Mosao, Kinwa, 1300 m, 26.ii.1977, *M. Reekmans 5745* (BR, BRVU, C, K, PRE, WAG); Between Mugeni and Vigeni, 1.iii.1926, *A. Peter* (*in herb. W. Lemke 10237*) (JE). CAMEROON: West Cameroon, Division Boyo, approach to Mbi Crater by short cut from Belo-Afua, 9.xii.1998, *M. Cheek 9884* (K, PRA); Division Bamenda, Oku, 2000 m, 17.ii.1958, *F. N. Hepper 2840* (K); West Cameroon, Prov. South West, Bakossi Mtns, Mount Kupe Forest, Manenguba, Lake Edip, 1200 m, 20.xi.1998, *W. G. Gosline 186* (K). RWANDA: Volcans National Park, Gahinga, 2380 m, 14.ii.1972, *P. Van der Veken 9371* (BR, BRVU); Pref. Kibungo, Akagera National Park,

Figure 4. A robust form of *Potamogeton richardii* with big pale brown tricarinate fruits and petioles of floating leaves with discoloured sections (*J. Pawek 13230*, K).

Figure 5. An adult plant of *Potamogeton richardii* with remnants of submerged leaves (*F. G. Meyer 7827*, K).

near Lake Ihema, 1300 m, 21.ix.1969, *G. Bouxin & M. Radoux* (*INRS 946*) (BR, GENT, LG); Pref. Kibungo, Rusumo, on road to Kibungo, River Kagogo, 1380 m, 27.vi.1978, *J. Raynal 20746* (G, P); Pref. Cyangugu, Nyungwe Forest, on road Butare – Cyangugu, km 100, 2000 m, 21.viii.1969, *G. Bouxin & M. Radoux* (*INRS 741*) (BR, GENT, LG); Astrida [= Butare], Tshyahinda, on road to Kasave, *c*. 1900 m, 11.vi.1957, *P. Deuse 1023* (K); 'Terr. Astrida' [= Pref. Butare], 2000 m, 24.iii.1956, *R. Christiaensen 1568* (BR, BRVU, PRA). DEMOCRATIC REPUBLIC OF THE CONGO: On road Nioka – Mahagi, Beelen, *c*. 1700 m, 18.viii.1949, *A. Taton 893* (BR); Nioka, Korda, 15.v.1952, *Liben 285* (BR, BRVU); Albert National Park [= Virunga National Park], Mushumangabo, 2075 m, viii.1937, *J. Lebrun 7114* (BR, K, P); Albert National Park [= Virunga National Park], between Mikeno & Nyamuragira, Mushumangabo, 1950 m, 21.viii.1937, *J. Louis 5472* (BR); Kapanga, xi.1932, *Overlaet 42* (BR, BRVU); xi.1932, *Overlaet 491* (BR); Kapanga, Tshibaba, Lupana River, ix.1933, *Overlaet 832* (BR, BRVU); Katanga, Marungu Plateau, on road Pepa – Luonde, Sonse, Kansimba River, 1930 m, 28.vi.1957, *J.-J. Symoens 4729* (BRVU, PRA); Katanga, Manika Plateau, 3 km E of Kaziki, 2000 m, 12.vi.1969, *S. Lisowski et al. 6153* (BR, BRVU, PRA); Katanga, Manika Plateau, Kisote, 1500 m, 5.iv.1969, *S. Lisowski et al. 4187* (BR, BRVU, K).

North-east Tropical Africa: ERITREA: Scimenzana, Guna-Guna, 21.ix.1902, *A. Pappi 723* (BR); Amasen, Baratanti, 17.i.1902, *A. Pappi 3531* (EA, FT, G, L, P, S, U); Saganeiti [= Segeneyti], Gorge de Degerra, 2200 m, 10.iii.1892, *G. Schweinfurth & D. Riva 891* (BM, BR, BRVU, G, K, LE, P, S, Z); Somomo Lake 2–3 km N of Adi Kwala along the road to Mendefera, *c*. 2000 m, 18.xi.1988, *O. Ryding et al. 1587* (K, UPS). ETHIOPIA: Adi Abun, 6000 ft, 20.iii.1863, *W. Schimper 958* (BM, Z); Nura, Gors, 'Amba Sea', 11.iii.1856, *W. Schimper 571* (K, P); 11.iii.1856, *W. Schimper 1594* (BR, P); Adoa [= Adwa], 11.vi.1837, *W. Schimper 135* (BM, BR, BRVU, CGE, FI-W, G, GOET, HBG, K, L, LE, LG, K, M, MPU, P, S, TUB, U, ZT); Tigray Region, 14 km E of Wukro [= Wik'ro], at small stream on the Azbi Plateau, 2600 m, 11.x.1995, *I. Friis et al. 6696* (BR, C, K); Semién [= Simén Mts.?], Addeschiè [= Adi Sighe?], 6.iv.1937, *R. Pichi-Sermolli 2712* (BM, K); Harar Prov., NE end of Lake Alemaya (Haramala), *c*. 15 km NW of Harar [= Harer], *c*. 2000 m, 25.vii.1961, *W. Burger 401* (C, K); Haramaia, 6600 ft, 13.iii.1933, *J. B. Gillett 5471* (BM, K); Idli valley, *c*. 42 km along the road Harrar [= Harer] to Jijiga, 1400 m, 26.x.1969, *J. J. F. E. De Wilde 5863* (BR, K, WAG); About 100 km N of Addis Ababa, Blue Nile road, between Fitche [= Fiche] and Debra Libanos [= Debre Libanos], near Portuguese Bridge, *c*. 2000 m, 25.iv.1966, *W. J. J. O. de Wilde et B. E. E. de Wilde-Duyfjes* (*Pl. Aethiop. Exs. 10873*) (B, BR, C, EA, K, P, PRE, UPS, WAG); Prov. Shoa, 60 km NNE of Addis Abeba, Bole Valley below Mulu Farm, 1650 m, 23.x.1971, *M. G. Gilbert 2211* (EA, K); Prov. Shoa, Entoto ridge, northern Addis Ababa, *c*. 2600 m, 21.iii.1976, *J. W. Ash 3490* (BR, K, UPS, WAG); About 5 km NE of Addis Ababa, *c*. 2400 m, 26.iv.1965, *W. J. J. O. de Wilde et B. E. E. de Wilde-Duyfjes* (*Pl. Aethiop. Exs. 6438*) (B, BR, C, K, WAG); About 15 km ENE of Addis Ababa, near road to Asmara, *c*. 2200 m, 31.iii.1965, *W. J. J. O. de Wilde et al. 6051* (WAG); Prov. Shoa, Addis Ababa, Entotto Mt. beyond Italian Embassy, 2800 m, 6.xii.1961, *F. G. Meyer 7621* (K); Prof. Kaffa, 7 km E of Jimma, 1750 m, 26.xii.1961, *F. G. Meyer 7827* (K); Prof. Kaffa, Jimma, 1830 m, 12.viii.1961, *K. Brehme* (*in herb. H. F. Mooney 9087*) (K); Prof. Kaffa, about 5 km E of Jimma, at the road to Addis Ababa, Kochi, 1740 m, 9.xii.1970, *I. Friis et al. 607* (BR, C, K, WAG); Prof. Kaffa, about 4 km N of Bonga, along the road to Jimma, 1750 m, 12.i.1973, *I. Friis et al. 2225* (BR, C, K, WAG); Prov. Shoa, 263 km SW of Addis-Ababa, 64 km along the Hosanna [= Hosa'ina] road at Wokite, lake at Dilla village, 2800 m, 4.xi.1972, *J. W. Ash 1760* (K, UPS, WAG); About 30 km S of Shashamane [= Shashemenē], E of Lake Awasa, *c*. 1500 m, 14.vi.1965, *W. J. J. O. de Wilde et B. E. E. de Wilde-Duyfjes* (*Pl. Aethiop. Exs. 7067*) (BR, K, WAG); Kunnama, 15.iii.1958, *H. Smeds 1359* (K); Prov. Sidamo, 22 km N of Kebre Mengist [= Kibre Mengist] on the road to Agere Selam, 2100 m, 5.xi.1972, *I. Friis et al. 1086* (C).

East Tropical Africa: KENYA: Distr. Turkana, Moruassigar, 7000 ft, 18.ii.1965, *J. B. Newbould 7277* (EA, K); Briakfield near Kitale, 6000 ft, ix.1969, *Tweedie 3696* (K, P); 20 miles ENE of Kitale, 6500 ft, 9.xi.1961, *A. Bogdan 5317* (EA, K); Prov. Rift Valley, SW slopes of Mt. Elgon, 6500 ft, 30.xii.1952, *R. Ross 1346* (BM, BR, LD, S); Prov. Rift Valley, SW of Mt. Elgon, 8000 ft, 31.xii.1952, *R. Ross 1366* (BM, BR, LD); Distr. Ravine, Lake Narasha, 2750 m, 16.x.1953, *R. B. Drummond & J. H. Hemsley 4803* (BM, EA, K, S); Distr. Kisii, Gucha River, near Magombo market, 11.iii.1975, *D. Vuyk 520* (PRA, WAG); 5 mi. W of Thomsons Falls [= Nyahururu Falls], 8000 ft, 20.i.1959, *A. Bogdan 4758* (EA, K, LE); Aberdare Mtns, Kinangop, 8800–8900 ft, iv.1938, *P. Chandler 2269* (B, BR, K, P); Naro Moru River Lodge, 1920 m, 19.x.1985, *Beentje 2482* (K); Meru Distr., Lake Ellis, 3450 m, 19.i.1985, *C. C. Townsend 2279* (K); Kiambu Distr., Ruira River, 6000 ft, 21.x.1934, *G. Taylor 1022* (BM); Meru, 21.ii.1922, *R. E. Fries & T. C. E. Fries 1800* (BR, K, UPS); Aberdare Range, near the W part of the Nyeri track, 2900 m, 11.vii.1948, *O. Hedberg 1509* (BM); Nairobi, Karura forest, 21.iii.1953, *Verdcourt & Steele 913* (BM, K); Mt.

Aberdare, *c*. 3300 m, 20.iii.1922, *R. E. Fries & T. C. E. Fries 2611* (UPS); Nairobi Distr., Nairobi River, 100 yards from Ainsworth bridge, 5500 ft, 10.iii.1967, *O. M. Mwangangi 22* (K); 15 miles NW of Kitale, Mr Buchholz's farm, 6200 ft, 22.iii.1961, *Y. G. Buchholz AB 5118* (EA, FT, K); Narok Distr., Nasampolai Valley on the road to Narok, 11.iii.1972, *P. J. Greenway & Kanuri 14993* (EA, K, M, PRE). TANZANIA: Bukoba Distr., Kishanda, x.1931, *c*. 4500 ft, *A. E. Haarer 2337* (BR, EA, G, K); Uha, Kassulo [= Kasulu], 1380 m, 24.ii.1920, *Baschant* (B); Ufipa Distr., Malonje Plateau, Sumbawanga Road, 1650 m, 16.iii.1959, *H. M. Richards 12169* (BR, K); Iringa Distr., Mufindi, Luisenga Lake, 5700 ft, 15.iii.1962, *R. Polhill & S. Paulo 1767* (B, BR, EA, K, PRE); Rungwe Distr., near Mwakaleli, Kandete, Mwatesi River, 8.v.1975, *F. N. Hepper et al*. *5418* (K, WAG); Njombe Distr., between Njombe and Kipengere, *c*. 1500 m, 27.ix.1970, *M. Thulin & B. Mhoro 1218* (EA, K, UPS); Kyimbila Distr., N of Lake Nyasa [= Lake Malawi], *A. Stolz 2462* (BM, BR, C, K, P, PRE, UPS, Z). UGANDA: Kyadondo, Magigye, 6000 ft, v.1915, *R. A. Dümmer 2473* (BM, BOL, K); Kampal [= Kampala], King's Lake, 3900 ft, i.1936, *G. L. Hancock & P. C. Chandler 135* (BM, BR, K); Entebbe, 3900 ft, ix.1905, *Brown 333* (K); Masaka Road, mile 13, 3850–3900 ft, vi.1937, *P. Chandler 1662* (B, BM, K); Toro Distr., Fort Portal, 7.iv.1932, *C. Hazel 226* (K); Kiagwe, Namanve, 3730 ft, viii.1932, *W. J. Eggeling 503* (K); Distr. Eastern Ankole, Kashari County, Rukanja swamp, 1550 m, 9.x.1993, *P. K. Rwaburindore 3628* (BR, UPS); Western Prov., Kigezi Distr., Virunga Mtns, swamp at NW end of Lake Bunyonyi, *c*. 1950 m, 27.xi.1934, *G. Taylor 2174* (BM); Kigezi Distr., Kachwekano Farm, 6400 ft, vi.1951, *J. W. Purseglove P.3636* (K).

South Tropical Africa: MALAWI: Northern Prov., Mzimba Distr., Mzuzu, Marymount, 4500 ft, 24.x.1973, *J. Pawek 7442* (BR, LG, PRE, WAG); Northern Prov., Nkhata Bay Distr., Vipya Plateau, 36 mi. SW of Mzuzu, 1670 m, 12.xi.1977, *J. Pawek 13230* (BR, PRE, K, WAG); Northern Prov., Nkhata Bay Distr., 3 mi. SSE of Chikangawa, 5700 ft, 12.xi.1977, *E. Phillips 3056* (K, WAG, Z); Southern Prov., Zomba, Zomba Plateau, Chagwa Dam, 1690 m, 14.iv.1989, *S. T. Iversen & K. Martinsson 89235* (UPS). ZAMBIA: Abercorn [= Mbala] Distr., Abercorn [= Mbala], 1500 m, 5.ii.1964, *H. M. Richards 18927* (B, BRVU, K); Abercorn [= Mbala] Distr., Chipululu Dam, Mibole River, 1500 m, 6.i.1965, *H. M. Richards 19424* (K); Distr. Fort Rosebery [= Mansa], Chinwa Sheba, near Lake Bangweulu, stream *c*. 1 mi below Chinwa Sheba lakelet, 12.ii.1959, *R. Watmough 246* (BM); Shiwangandu [= Shiwa Ngandu], 5.ii.1955, *D. B. Fanshawe 1993* (BM, BR, K). ZIMBABWE: Distr. Salisbury [= Harare], Cleveland Dam, 5000 ft, *F. Eyles 659* (BM, K); 7 km ENE of Inyanga, Troutbeck, 2020 m, 31.xii.1973, *P. Bamps et al*. *481* (BR, WAG); 4.5 km ENE of Rugare, Little Connemara, 2250 m, 1.i.1974, *P. Bamps et al*. *526* (BR); Distr. Inyanga, *c*. 3 km W of Mt. Inyangani, *c*. 2000 m, 8.xii.1930, *T. C. E. Fries et al*. *3632* (BM, LD, LG); Distr. Inyanga, Lake Moodie, 29.ix.1974, *W. B. Cleghorn 2979* (B, K); Distr. Inyanga, *c*. 4 mi from Inyanga Village along Troutbeck road, *c*. 6300 ft, 26.iv.1967, *J. E. Rushworth 746* (BR); Division Umtali [= Mutare], Distr. Manica, Odzani River Valley, *A. J. Teague 571* (BOL, K, PRE); Distr. Matobo, Farm Besna Kobila, *c*. 4800 ft, i.1956, *O. B. Miller 3239* (PRE).

Southern Africa: SOUTH AFRICA: Free State, North, Viljoenskroon area (E), Kromdraai Farm 238, 1365 m, 18.xi.1991, *C. J. Ward & J. D. Ward 170* (PRE); Free State, Pretoria, Zeekoegat, 6.iii.1937, *J. E. Repton 982* (NH, P); Gauteng, Pretoria, pond at Birchleigh, 18.iv.1925, *C. E. Moss 11012* (BM); Gauteng, Rooikop, Bushveld, Elands River, 5.xii.1935, *J. C. Smuts & M. C. Gillett 3002* (PRE); Mpumalanga, between Breyten and Chrissiesmeer, Oostekant van pad, 5.i.1971, *G. K. Theron 2477* (PRE); Mpumalanga, Bethal distr., Vlakpan N of Kinross, on road to Grootpan, 8.iii.1984, *C. Reid 737* (PRE); Mpumalanga, Standarton [= Standerton], Hooge Veld, *A. Rehmann 6801* (BM, K, Z); Northern Province, Letaba, pond above provincial secondary road bridge across the Ramadiepa River, 12.i.1960, *J. C. Scheepers 849* (B, BM, G, K, M, P, W); Eastern Cape Province, Division Humansdorp, Hankey [= Hankey, Eastern Cape, South Africa], 5.x.1927, *H. G. Fourcade 3312* (BOL, K); Eastern Cape Province, Grahamstown, 'Inniskilling' BK Webber, 19.ii.1975, *P. J. Coetzee 12* (PRE); Eastern Cape Province, 5 km from Peddie on road to Grahamstown, 19.i.1979, *T. Arnold 1102* (PRE); Western Cape Province, Knysna Distr., Portland, ii.1925, *A. V. Duthie 981* (BOL); Kwazulu-Natal, Distr. Umwoti, Umwoti Road. bridge on Greytown – Maritzburg [= Pietermaritzburg] road, 3200 ft, 10.iv.1962, *D. Edwards 2752* (K); Kwazulu-Natal, between Pietermaritzburg & Greytown, xi.1883, *F. Wilms 2371* (BM, K); Kwazulu-Natal, Distr. Lions River, [Howick:] Umgeni [River] above Midmar [dam], 3600 ft, 13.x.1964, *E. J. Moll 1248* (K); Kwazulu-Natal, Distr. Umzinto, Umgayi, *c*. 1250 ft, 20.iii.1966, *C. J. Ward 5453* (K, PRE, WAG). SWAZILAND: Tonkwane Estates, 4 mi. SW of Mbabane, 3400 ft, 5.xii.1979, *J. Culverwell 1332* (PRE).

Western Indian Ocean: MADAGASCAR: Fianarantsoa, Ambatofinandrahana, Itremo, small valley W of Itremo Mtns, 1680 m, 26.xi.1993, *J.-N. Labat et al*. *2430* (BR, K, P); Distr. Ambatondrazaka, Ampilaona [= Ampilahoana] – Amparafaravola, 750 m, 20.xi.1938, *G. Cours 259* (P).

The submerged leaves of *P. richardii* do not persist on the plants but decay early during the development of a plant, usually when the floating leaves develop. Herbarium specimens rarely have submerged leaves (Fig. 4). Of the approximately 350 herbarium specimens examined in this study, only 13 had remnants of submerged leaves and were in this respect complete, which is less than 4%. The following collections contain specimens that have the best preserved submerged leaves (see also Fig. 5): *J. Lewalle 5149* (BR, G), *Overlaet 832* (BR, BRVU), *R. Christiaensen 1567* (BRVU) and *F. G. Meyer 7827* (K). Care must be taken to distinguish submerged leaves, which are membraneous and narrowly oblong to linear-lanceolate, from floating coriaceous leaves of elliptical shape that are beneath the water surface because of a sudden rise in water level.

Potamogeton richardii is a strictly African (incl. Madagascar) species (Fig. 6), growing mainly in regions with a high rainfall (1500 mm or more per year). It occurs mostly at elevated altitudes up to 3450 m a.s.l. The species is mainly distributed in the Afromontane region (archipelago-like regional centre of endemism, according to White, 1983). It occurs from

Figure 6. Distribution of *Potamogeton richardii* in Africa and on surrounding islands based on fruiting material and/or anatomically examined herbarium specimens.

Eritrea to the southernmost part of Africa, including the eastern half of the Zambezian Domain, and is here reported for the first time from Cameroon, Swaziland and Madagascar.

The recent discovery of *P. richardii* in Cameroon adds one more species to the list of the species with a disjunctive distribution occurring in the Cameroon mountains and in the Ethiopian and East African mountains. Engler (1892) emphasized the high number of species common to the Cameroon highlands and the mountains of eastern Africa, in spite of the great distance separating them (*c*. 3000 km). Similar patterns of distribution on the African mainland have been found for taxa of very different families, e.g. *Rapanea melanophloeos* (L.) Mez of the Myrsinaceae (see distribution map no. 685 in Taton, 1980), *Hypericum revolutum* Vahl of the Guttiferae (map no. 72 in Bamps, 1971) and *Aframomum zambesiacum* (Baker) K. Schum. ssp. *zambesiacum* of the Zingiberaceae (map no. 438 in Lock, 1978).

Because of the frequent misidentification of *P. nodosus* in southern Africa, *P. richardii* was (generally under the name *P. thunbergii*) erroneously reported from Namibia (Obermeyer, 1966; Podlech, 1966; Lisowski *et al*., 1978; Clarke & Klaassen, 2001), Botswana (Lisowski *et al*., 1978; Grignon & Johnsen, 1986), Lesotho (Obermeyer, 1966), Seychelles (Robertson, 1989), and Mauritius and Réunion (Scott, 1984). Note also that all the specimens we studied from the Okavango watershed, referred to *P. richardii* (as '*P. thunbergii*'), proved to belong to *P. nodosus*, whereas true *P. richardii*, often reported from there, is absent from this region (see Fig. 6).

Although this study revealed that *P. nodosus* and *P. richardii* may occur close to each other in some countries, their ranges are nearly mutually exclusive. The main areas of distribution of these two species in Africa are different: *P. richardii* is common in a strip *c*. 500–1000 km wide from Eritrea along the Great Rift Valley down to eastern South Africa but is rare elsewhere (Fig. 6), whereas *P. nodosus* occurs mainly in northern and southern Africa and on surrounding islands and is absent from the equatorial tropical areas (Fig. 3). The only part of Africa where both species occur close to each other is eastern South Africa.

Potamogeton schweinfurthii A. Benn. in Dyer, Fl. Trop. Afr. 8: 220. 1901, nomen propositum ad conservationem. ('Schweinfurthii')

Type: 'Plantæ Abyssinicæ, Im Zana [sic!] See [= Lake T'ana, Ethiopia] (in offenem Wasser, nah am Ufer) bei Angasha, 9 Novbr. [18]63, *Schimper 1359*' (proposed conserved type: K, see Kaplan & Symoens, 2004; duplicates: B†, BM, CGE, E *n. v.*, W†).

– *P. capensis* Scheele ex A. Benn., Ann. K. K. Naturhist. Hofmus. Wien 7: 287. 1892, nom. nud.

Authentic specimens: 'Im flüsse Zwartkopsrivier (Distr. Uitenhage) [= Zwartkops River, by Uitenhage, Eastern Cape, South Africa], Januar 1830, *Zeyher 919*' (BREM, CGE, K, W†).

– *P. lucens* var. *azoricus* A. Benn., J. Bot. 42: 71. 1904, nom. nud. ('azorica')

– *P. azoricus* A. Benn. ex Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55(5): 198 et 265. 1916, nom. nud.

Authentic specimens: 'Island of St. Michael, Azores, 1848, *T. C. Hunt*' (BM, CGE, K); 'Azores, San Miguel, 26.viii.1894, *Wm. Trelease 962*' (BM, K).

= *P. repens* Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55(5): 170. 1916 [1 November]; Hagstr. in R. E. Fr., Wiss. Erg. Schwed. Rhod.-Kongo-Exp. 1911–1912, 1(2): 185. 1916 [December].

Type: [Zambia:] 'Exped. Suecica in reg. Central.-Africanis 1911–12, Potamogeton repens J. O. Hagstr. n. sp., Rhodesia bor. orient in lacu Bangweolo ad Kasomo, 19.ix.1911, leg. *R. E. Fries 655*' (holotype: UPS, photo: BM, PRA; isotype: Z).

= *P. nodosus* var. *billotii* f. *angustissimus* Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55/5: 188. 1916 [1 November]; Hagstr. in R. E. Fr., Wiss. Erg. Schwed. Rhod.-Kongo-Ex. 1911–1912, 1(2): 186. 1916 [December].

Type: [Zambia/Zimbabwe border:] 'Exped. Suecica in reg. Central.-Africanis 1911–12, Potamogeton nodosus Poir. var. Billotii (F. Schultz) f. angustissimus J. O. Hagstr. n. sp., Rhodesia: in flumine Zambesi ad Victoria Falls, vii.1911, leg. *R. E. Fries 137*' (holotype: UPS, photo: PRA).

= *P. promontoricus* Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55(5): 182. 1916.

Type: [Western Cape, South Africa:] [label 1:] 'Potamogeton no. 5. E. Z., 2. 7.' [label 2:] 'Cap. bon. spei [= Cape of Good Hope], *Drege*' [label 3:] 'Potamogeton promontoricus mihi ad int., 8.iii.1906. Determ. O. Hagström.' (holotype: UPS, photo: BM, PRA).

= *P. capensis* Scheele ex Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55(5): 203. 1916.

Type: [label 1:] 'Im flüsse Zwartkopsrivier (Distr. Uitenhage) [= Zwartkops River, by Uitenhage, Eastern Cape, South Africa], Januar 1830 [*C. L. P. Zeyher*] *919*' [label 2:] Pot. capensis Scheele, determ. O. Hagström, 07' (lectotype: S, lectotype designated here; isolectotypes: BREM, LD); '18/12 [18]29, Zwartkopsrivier, meter 100' [*Drege*] *8799*' (syntypes: G, P, S); [Phoenix, KwaZulu-Natal, South Africa:] 'Plantæ Africæ australis, Reg. Natal, Umschlangwe River, 660 m, 19.viii.1893. leg. *R.*

Schlechter 3120' (syntypes: BM, G, K, LD, LE, LY, PRC, S, W, Z); [Mozambique:] 'Herbarium Normale Austro-Africanum, Regio Orientalis, Mathibis Kom in provincia Delagoa, In aquosis, alt. 500 ped., August 1886, legit *H. Bolus 1393*' (syntypes: BM, BOL, G, K, P, UPS, W, Z).

= *P. venosus* A. Benn., Trans. & Proc. Bot. Soc. Edinburgh 29(1): 52. 1924.

Type: [South Africa:] 'Natal [= KwaZulu-Natal], In a pool Umhlonqwe, April 18th. 1884, *J. M. Wood 3015*' [The locality is hardly legible in the herbarium label and was incorrectly cited as 'Umplmzue' by Bennett in the protologue. We follow the wording given by Obermeyer (1966):66.] (holotype: K; isotypes: BM, BOL, NH).

= ?*P. bunyonyiensis* Denny et Lye, Kew Bull. 28: 120. 1973.

Type: 'Uganda, Rubanda county, District Kigezi U2, near Kifuka Resthouse, Lake Bunyoni [sic!], Latitude: 1°17′ South, Longitude: 29°55′ East, Altitude: 1950 meters, Grid: RJ-23-58, Habitat: in 1–2 m deep water at lake-shore, 22/41970, Leg. *K. A. Lye, A. B. Katende & P. Denny 5216*' (holotype: K).

Floating leaves absent or present; lamina coriaceous, light green, opaque, often with a reddish or brownish tinge, narrowly oblong to elliptical, mostly narrowly cuneate at base; petiole sometimes narrowly winged towards the lamina, never with a discoloured section.

Submerged leaves almost always present, sessile, subsessile to petiolate; lamina membraneous, narrowly lanceolate to oblong-elliptical, sometimes the lowest leaves reduced to phyllodes, green-brownish or reddish, seldom fresh green, generally 7(–9)-veined, rarely up to 13-veined, lower leaves sometimes only 5-veined, with acute to mucronate apex; petiole mostly 0–3 cm long, rarely that of the uppermost leaves up to 7 cm long, mostly 0–0.2 times as long as the lamina, rarely that of the uppermost leaves up to as long as the lamina.

Stipules persistent, relatively long and narrow throughout their length, acute. Peduncles thicker than the stem, at least towards the spike. Fruits 2.9–3.9(–4.1) mm long, greyish green or dark green to yellowish green or sometimes yellow-brown, with ± obtuse and low dorsal keel.

Stem anatomy: stele of trio type, rarely of proto or oblong type, endodermis of U-type, interlacunar bundles present, in one circle (rarely in two circles of which one is incomplete), subepidermal bundles absent or scattered ones present, pseudohypodermis present, one-layered.

Representative herbarium specimens (see also Figs 7, 8)

Macaronesia: AZORES: São Miguel, 1845, *T. C. Hunt s. n.* (FI-W) 1848, *T. C. Hunt s. n.* (BM, CGE, K); 26.viii.1894, *W. Trelease 962* (BM, K); São Miguel, Furnas Lake, *c*. 280 m, viii.1898, *K. Bohlin s. n.* (LD, S); 27.vii.1968, *B. Goncalves 2414* (BM); 6.viii.1970, *J. Dolman 415* (BM); 1.ix.1970, *A. Hansen s. n.* (C); 7.ix.1978, *C. Simon 78–81* (PRA); 6.vii.1979, *C. Simon 79-482* (PRA).

Northern Africa: ALGERIA: Wilaya Ouargla, Tassili n'Ajjer, Iherir, 1070 m, 31.iii.1982, *D. Podlech 36968* (G, M). EGYPT: [Ash Sharqīyah], Iushar, Bilbeis [= Bilbays] road, 10.i.1927, *N. D. Simpson 4341* (K); 10.i.1927, *N. D. Simpson 4341* (G, K); [Ash Sharqīyah], *c*. 4 km from Bilbeis [= Bilbays] on the Iushar el Raml road, 7.xi.1926, *E. Agroudi 4136* (G); [As Suways], Suez, canal, 31.iii.1924, *N. D. Simpson 2847* (K); 23.iv.1880, *G. Schweinfurth 412* (C, G, G-Boiss, K, PR); ii.1877, *A. Letourneux s. n.* (P); xi.1879, *A. Letourneux s. n.* (G, P); Upper Egypt, Lake Nasser, Khor Kalabsha, 60 km S of Aswan, 7–12.v.2001, *M. M. Ali s. n.* (ASW, PRA). LIBYA: Tassili n'Ajjer, Ghat, El Barkat [= Al Birkah], 700 m, 29.iii.1949, *Leredde 95* (BM); Gebel Akhdar [= Al Jabal al Akhdar], *c.* midway between Derna and Susa along the coastal road, Wadi Lathrun, 19.i.1967, *L. Boulos 1212* (S). TUNISIA: Gafsa, iii.1908, *C. J. Pitard 507* (G, K, LY, ZT); Gafsa, 31.i.1908, *S. Murbeck* (LD); Tozeur [= Tawzar], iv.1909, *C. J. Pitard 1415* (G).

West Tropical Africa: BURKINA FASO: Tengréla, 19.i.1985, *J. Lejoly 85/030* (BR); between Banfora and Tiafora [= Tiéfora], 4.iv.1966, *L. Aké Assi 8617* (G, K). MALI: Région Nord (Désert et Sahel), river N of Lake Faguibine, 1932, *A. Leclerq* (*in herb. A. Chevalier 42568*) (P); Gourma-Malina, Lake Niangaye, 15.ii.1934, *Mission d'études de la Biologie des Acridiens 492* (P); Bamba, [Niger River], 4.iii.1932, *A. Chevalier 43808* (P); Gao, Niger, 4.iii.1936, *M. de Wailly 4976* (BR, K, P); 19.ii.37, *M. de Wailly 4827* (BR, K, P). NIGERIA: Prov. Bornu, Distr. Chad, Mallam Fatori, *G. Jackson 2587* (K). NIGER: Lac Tchad [= Lake Chad], 'Niger non loin du Tchad', 17.ii.1968, *J. Léonard 4518* (BR); Lake Chad, Tchingoa Island, 18.ii.1968, *J. Léonard 4530* (BR, BRVU). SENEGAL: [without locality], 1820, *C. H. Bacle* (G); 1830, *Leprieur s. n.* (G, P, W); Lake Paniéfoul [= Lake Guier], i.1826, *Leprieur s. n.* (BM, G, K, L, P); vii.1993, *A. Thiam s. n.* (BR); Delta of Sénégal River, Thieng Island, 2 m, 1999, *F. Malaisse et J. Matera 307* (BR, K).

West-Central Tropical Africa: BURUNDI: Prov. Bubanza, Cibitoke, 17.iv.1984, *A. Caljon 3010* (B, GENT, WAG); Kiringi, 5 mi N of Tanganyika, 800 m, 16.v.1982, *M. Reekmans 11228* (BR, BRVU, K, S, UPS); Bujumbura, 780 m, 19.x.1968, *L. Niyongere 40*

Figure 7. An ordinary form of *Potamogeton schweinfurthii* with only submerged leaves (*M. M. Ali s. n.*, PRA).

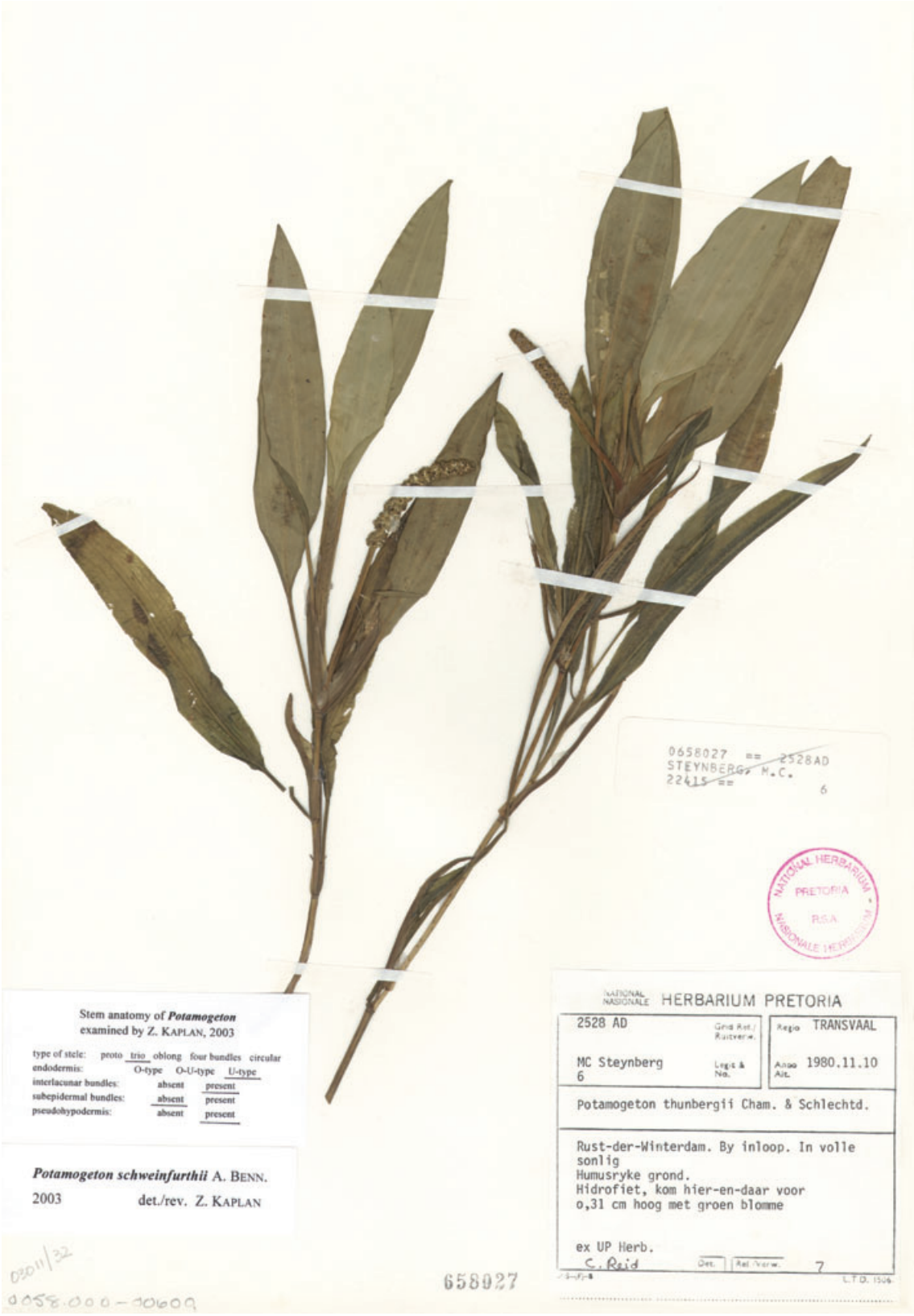

Figure 8. A specimen of *Potamogeton schweinfurthii* with well-developed coriaceous floating leaves (*M. C. Steynberg 6*, PRE).

(BR, K); Bujumbura, delta of Rusizi River, 780 m, 17.xi.1971, *J. Lewalle 6302* (G). CAMEROON: Préf. Buea, Ekona, 350 m, 17.iii.1970, *Meurillon* (*C.N.A.D. 1855*) (K, P, WAG). RWANDA: Préf. Ruhengeri, Bugarama-mines, 30.vii.1974, *P. Van der Veken 10445* (B, BR, BRVU, GENT, WAG); On road Butare – Cyangugu, km 68, Rwasenkoko, 25.viii.1974, *P. Van der Veken 11051 bis* (GENT, WAG); Préf. Gikongoro, Nyungwe Forest Reserve, Rwasenkoko, 1900 m, 30.x.1982, *G. Troupin 16324* (BR, K, WAG). DEMOCRATIC REPUBLIC OF THE CONGO: Albertville [= Kalemie], Lake Tanganyika, 23.i.1927, *D. H. Linder 1922* (K, P); Upemba National Park, Lake Upemba, Benito Island, 30.xi.1948, *G. F. de Witte 4740* (BR, U); Katanga, Lubumbashi, *c*. 1200 m, 11.xi.1963, *J.-J. Symoens 10609* (BR, BRVU, K, M, PRA); 27.v.1976, *F. Malaisse 9091* (BR, BRVU); Katanga, Lubumbashi, on road to Kipushi, 1170 m, 18.x.1964, *J.-J. Symoens 11027* (BR, BRVU, K); 9.xi.1964, *J.-J. Symoens 11041a* (BR, BRVU, K, M, PRA); Katanga, Lubumbashi River 12 km NE of Elisabethville, 25.iv.1962, *A. Schmitz 7692* (BR); Katanga, Kapeya, Kalongo River, 1125 m, 4.vi.1969, *F. Malaisse 7037* (BR, BRVU, K); Kafubu, Kafubu River, 13.xi.1987, *R. D'hose 177* (BR, WAG).

North-east Tropical Africa: CHAD: Lake Moyló N of Lake Chad, 7.i.1968, *J. Léonard 4278* (BR); Lake Yuorsoula N of Lake Chad, 6.i.1968, *J. Léonard 4264* (BR, G); Lake Chad near Bol, 26.xi.1969, *F. N. Hepper 3997* (BR, K, P, WAG); Lake Chad 10 km N of Hadjer el Hamis, 13.xii.1969, *F. N. Hepper 4181* (BR, K, WAG); Southern side of Lake Chad near Hadjer el Hamis, 28.xi.1969, *F. N. Hepper 4047* (K, P); About 80 km N of Fort Lamy [= N'Djamena], Lake Chad near Hadjer el Hamis, *c*. 250 m, 5.i.1965, *W. J. J. O. de Wilde et al*. (*Pl. Afr. Centr. Exs. 5219*) (BR, K, P, WAG); 5.i.1965, *W. J. J. O. de Wilde et al*. (*Pl. Afr. Centr. Exs. 5223*) (WAG); Lake Chad, Kika Island, 13.ii.1968, *J. Léonard 4500* (BR, BRVU); Lake Chad, Ngueiemiran Island, 15.ii.1968, *J. Léonard 4505* (BR, BRVU); Hadjer el Hamis, delta of Chari River, x.1964, *Bard s. n.* (P); Yoursoula, 6.i.1968, *J. Maley 175* (P). ERITREA: Amasen, Taclesan [= Ādī Tekelezan], *Terracciano & Pappi 420* (FT); Asmara, Adi Nefas [= Ādī Nifas], Mai-Belà, 26.iv.1909, *E. Chiovenda 139* (FT); Amasen, near Amba-Deró, along the Mai-Mascialà, 22.ii.1902, *A. Pappi 3808* (FT). ETHIOPIA: Prov. Shoa, in the upper part of the Mugher river system about 50 km N of Addis Ababa, Bole Gorge, *c*. 2300 m, 13.xi.1972, *I. Friis et al*. *1160* (BR, C, K); About 100 km N of Addis Ababa, Blue Nile road, between Fitche [= Fiche] and Debra Libanos [= Debre Libanos], near Portuguese Bridge, *c*. 2000 m, 25.iv.1966, *W. J. J. O. de Wilde et B. E. E. de Wilde-Duyfjes* (*Pl. Aethiop. Exs. 10882*) (B, BR, C, K, P, UPS); In shallow water along lake Awasa, about 20 km SW of Shashamane [= Shashemenē], *c*. 1500 m [correctly 1680 m], 14.vi.1965, *W. J. J. O. de Wilde et B. E. E. de Wilde-Duyfjes* (*Pl. Aethiop. Exs. 7015*) (B, BR, C, K, P, UPS, WAG); Sidamo, shore of Lake Awasa by Awasa Hotel, 22.vi.1979, *M. Tadesse 547* (UPS). SOMALIA: Erigavo Distr., Medishe [= Midhisho, near Erigavo], 28.i.1945, *P. E. Glover & H. B. Gilliland 593* (BM, EA, K); Baia d'Obbia [= Hobyo], 1890, *Brichetti s.n.* (FT). SUDAN: Jebel Marra [= Jabal Marrah Mtns], Mortagello, 4600 ft, 4.v.1964, *G. E. Wickens 1554* (K); Jebel Marra [= Jabal Marrah Mtns], Nyertete, 3800 ft, 20.iv.1965, *G. E. Wickens 2916* (BRVU, FI, K); Jebel Marra Mtns [= Jabal Marrah], *c*. 120 km E of Zalingei, *c*. 10 km W of Golol, *c*. 1350 m, 21.i.1965, *W. J. J. O. de Wilde et al*. (*Pl. Afr. Centr. Exs. 5474*) (BR, K, P, WAG); Jonglei [= Junqalī] Prov., *c*. 40 km ENE of Shambe, Kobeck, in Nile Swamps, 405 m, 1.ii.1983, *J. M. Lock 83/11* (K); Jonglei [= Junqalī] Prov., 85 km N of Bor, 3 km NE of Jonglei [= Junqalī], Fakadit, 440 m, 27.i.1982, *J. M. Lock 82/5* (K); 30 km N of Bor, Bur Akok, E side of White Nile, 15.iv.1978, *J. Green 48* (K).

East Tropical Africa: KENYA: Kisumu, Lake Victoria, 5.xii.1952, *R. Ross 1301* (BM, BR, LD); Lake Naivasha, 1890 m, iv.1935, *P. Chandler 2271* (B, BR, K, P); 18.vi.1970, *I. Friis 75* (C, WAG); Kenya Prov., Kiambu Distr., Ngong Forest, Karen Pond, 5900 ft., 4.xi.1934, *G. Taylor 1594* (BM). TANZANIA: Bukoba, Victoria Nyanza [= Lake Victoria], 21.iv.1905, *W. A. Cunnington 56* (BM); Mwanza, Lake Victoria, ix.1910, *H. J. P. Winkler 4100* (WRSL); Western Prov., Kigoma, Lake Tanganyika, 31.i.1953, *R. Ross 1471* (BM, BR, LD); Masai Distr., NE side of Ngorongere Crater floor, Gaitokitok Springs, 25.xi.1956, *P. J. Greenway 9062* (B, EA, K); Arusha Distr., Arusha National Park, Lake Matheo, Kawange, 5000 ft, 4.xi.1969, *M. Richards 24581* (K, M, P); Arusha Distr., Chini, Moshi, 2400 ft, 3.ix.1964, *J. S. S. Beesley 3* (BR, K); West Usambara Mtns, km 1 of Shume – Lushoto Road, 2000 m, 19.xi.1975, *A. J. M. Leeuwenberg 10816* (EA, WAG); West Usambara Mtns, Lushoto Distr., 4 miles NE of Lushoto, Mkuzi, 1600 m, 22.iv.1953, *R. B. Drummond & J. H. Hemsley 2193* (BM, EA, K, S); Singida Distr., 23 mi from Singida, Ikungi, 5150 ft, 26.iv.1962, *R. Polhill & S. Paulo 2193* (BR); Manyoni Distr., Kazikazi, 31.vii.1931, *B. D. Burtt 3345* (BR, EA, K); Ufipa Distr., Lake Kwela, *c*. 1500 m, 18.iii.1950, *A. A. Bullock 2652* (BM, K); 5.vii.1950, *A. A. Bullock 2980* (BM, K); 10.iii.1959, *H. M. Richards 11119* (BR, K); 15.iii.1959, *H. M. Richards 12158* (B, BR, K, S). UGANDA: Distr. Kigezi, Rubanda county, Lake Bunyonyi, Habukara Island, 1950 m, 22.iv.1970, *K. A. Lye 5215* (BR, EA, K, P, UPS); Distr. Kigezi, Lake Bunyonyi, Sharp's Island, 6500 ft., 7.ix.1952, *E. M. Norman 160* (K); Bufundi, Lake Bunyonyi, 5.iv.1927, *D. H. Linder 2590* (K);

Busoga Distr., Butembe Bunya county, Lake Victoria, Macdonald Bay S of Mukobe Hill, 3720 ft, 14.i.1953, *G. H. S. Wood 574* (BM, BR, EA, K); [Lake Victoria], Sese [= Sese Islands], Fumwe [= Fumwe Island], 3800 ft, 3.ii.1934, *A. S. Thomas 1226* (K); Entebbe, edge of Lake Victoria, 3700–3750 ft, i.1938, *P. Chandler 2089* (B, BM, BR, EA, K, P); *P. Chandler 2090* (B, BM, BR, K); Jinja, at the shore of Lake Victoria, 1135 m, 12.iii.1948, *O. Hedberg 324* (EA, K, S, UPS); Jinja Distr., Jinja, Napoleon Gulf, 3700 m, 11.iv.1955, *P. J. Greenway & D. Roberts 8829* (BM, EA, K).

South Tropical Africa: MALAWI: Lake Malawi, Likoma Island, iii.1988, *C. Kasselmann 136* (B, M); Lake Nyansa [= Lake Malawi], Kota Kota [= Nkhotakota], 20.vi.1904, *W. A. Cunnington 8* (BM); Distr. Mangochi, Lake Malawi, Monkey Bay, 1625 ft, 2.ix.1956, *E. I. Newman & T. C. Whitmore 651* (BM, WAG); 16.vii.1972, *G. E. Gibbs Russell 2102* (B, BR, K, M, PRE); Distr. Mangochi, Shire River, 3 mi. S of ferry, 8.vii.1975, *J. H. Seyani 272* (BR). MOZAMBIQUE: Inhacoro [= Tambara], [1926] *J. Surcouf s. n.* (P); Distr. Manica and Sofala, Búzi, Inhafenga, River Mababa, 13.viii.1967, *M. F. de Carvalho 912* (BR); Distr. Manica and Sofala, below Spungabera [= Espungabera], ix.1961, *J. A. Whellan 1866* (BM); Inhambane, Massinga, Rio das Pedras, 8.vii.1981, *J. de Koning & F. Hiemstra 8932* (BR, K); Prov. Delagoa, Mathibis Kom, 500 ft, viii.1886, *H. Bolus 1393* (BM, BOL, G, K, P, UPS, W, Z). ZAMBIA: S of Lake Tanganyika, viii.1986, *C. Kasselmann 104* (B, M); Walamba, 22.v.1954, *D. B. Fanshawe 1228* (K); Mazambuka Distr., Kafue River, Pontoon Crossing, 3.ix.1947, *P. J. Greenway & J. P. M. Brenan 8043* (BM, BR, K, PRE); Mapanza West, River Munyeke, 3500 ft, 5.ix.1953, *E. A. Robinson 308* (BM, BR, K); 4.x.1953, *E. A. Robinson 336* (BM, K). ZIMBABWE: Sinoia Cave, Lomagundi, 3900 ft, 12.vii.1921, *F. Eyles 3161* (BOL, K); Distr. Salisbury, Darwendale, Hunyani River, 8.i.1973, *G. E. Gibbs Russell 2526* (WAG); Distr. Salisbury, Hunyani River at confluence with Gwebi River, 5.i.1973, *G. E. Gibbs Russell 2500* (BR); Distr. Marandellas [= Marondera], Chiota Tribal Trust Land, Chikokorana Pan, 1200 m, 29.iv.1972, *G. E. Gibbs Russell 1984* (B, BR, K, M, P, PRE, WAG); Distr. Matobo, Matopos Dam, 14.i.1958, *J. M. Rattray s. n.* (BM, K); Distr. Chipinga [= Chipinge], Lower Rupembe, Sabi River, 1290 ft., 24.i.1957, *J. B. Phipps 148* (K).

Southern Africa: BOTSWANA: Kachikau, Simati, Linyanti River swamps W of Shaile, 950 m, 17.iv.1975, *D. Edwards 04348* (K); Distr. Northern, Boteti River, 3.xii.1978, *P. A. Smith 2547* (K). NAMIBIA: Distr. Otjiwarongo, Uitkomst, 27.ii.1939, *O. H. Volk 1511* (M); Distr. Grootfontein, Otavifontein, 3.ii.1959, *B. de Winter & W. Giess 6787* (M); 3.ii.1969, *Giess & Smook 10621* (M, WAG); 10.iii.1973, *W. Giess 12539* (M); 12.iii.1974, *H. Merxmüller & W. Giess 30229* (K, M, WAG); Distr. Grootfontein, Otavi, x.1909, *Dinter 724* (P); 29.xii.1924, *Dinter 5254* (B, BOL, G, Z); 21.vi.1936, *Dinter 7647* (B, K); Von Bach Dam [by Okahandja], 16.xi.1994, *E. le Roux 1* (PRE); Distr. Grootfontein, Rietfontein, 30.xii.1939, *Rehm s. n.* (M); Tsams-Ost, 14.ii.1979, *M. Müller 1013* (M, WAG). SOUTH AFRICA: Northern Cape Province, Daniels Kuil [= Daniëlskuil], ii.1924, *M. Wilman s. n.* (K). Western Cape Province, Brandvlei, Worcester, 1875–1880, *A. Rehmann 2415* (K); Western Cape Province, 'Cap de B[onne] Esp[érance]' [= Cape of Good Hope Peninsula], [1844–1846] *Verreaux* (G, P); Western Cape Province, 'Cap bon[ae] spei' [= Cape of Good Hope], *Drege 2.7* (UPS). Eastern Cape Province, Regio Port St. Johns, Intafufu River, 12.x.1968, *V. A. Wager 4* (K, NH); Eastern Cape Province, Distr. Uitenhage, Zwartkopsrivier [= Zwartkops River], 100 m, i.1830, [*C. L. P. Zeyher*] *919* (S); xi [1829], [*C. L. P. Zeyher*] *4327* (W); 18.xii [18]29, *Drege 8799* (G, P, S); Eastern Cape Province, Distr. Uitenhage, Uitenhage, xi [1829], *Zeyher 640* (BM, BOL, K). Gauteng, Distr. Pretoria, Piennars River dam [near Pretoria], 12.vi.1964, *Vahrmeyer 4306* (K, M, WAG); Gauteng, Bronkhorstspruit, xii.1883, *F. Wilms 1652* (BM, G, K); Gauteng, Vereeniging, Kookfontein, Klip River, 25.xii.1919, *J. Burtt-Davy 18175* (K); 25.xii.1919, *J. Burtt-Davy 18176* (CGE, K); Gauteng, Vereeniging, Vaal River, 4.ix.1926, *C. E. Moss 13372* (BM). Mpumalanga, Badplaas, 6.x.1975, *R. Crawford 240* (K). Northern Province, Tzaneen, the Plains Farm between Letsitele and Island, 15.vii.1975, *Balsinhas & Craw 02736* (K, WAG); Northern Province, Distr. Kruger National Park, Red Rocks, 2.vi.1961, *H. P. van der Schiff 5679* (K, M, W); Northern Province, Rust-der-Winterdam [by Rust de Winter], 10.xii.1980, *M. C. Steynberg 6* (PRE). North-West Province, Potchefstrom Distr., Potchefstroom, ii.1945, *E. Schelpe 1006* (NH). KwaZulu-Natal, Shihadla, Maputa [= Lusutfu River], 10.ix.1971, *R. G. Strey 10450* (K, LISU); KwaZulu-Natal, Kosi system, sea level, 1.viii.1974, *C. J. Ward 8507* (K, NH); KwaZulu-Natal, Kosi system, Kosi Bay, Nhlange Lake [= Kosimeer Lake], 1 m, 29.xi.1984, *M. C. Ward 872* (NH); KwaZulu-Natal, Lake Sibayi, Banda Band Bay, *c*. 1.5–2 m, 27.x.1976, *C. F. Musil 429* (BR, K, NH, Z); KwaZulu-Natal, Lake Sibaya, Dunyeni Bay, *c*. 20 m, 6.vi.1983, *M. C. Ward 452* (NH); KwaZulu-Natal, Mkuze, Mkuze dam, 28.ix.1976, *C. F. Musil 418* (BR, C, K, WAG, Z); KwaZulu-Natal, Regio Hlabisa, Hluhluwe Game Reserve, 350 ft, 3.v.1955, *C. J. Ward 2577* (K, NH, S); KwaZulu-Natal, Richards Bay, Umsingazi lake, 25.vi.1976, *C. F. Musil 300* (NH); KwaZulu-Natal, Richards Bay, Msuingazi canal,

c. 2 m, 7.i.1975, *C. J. Ward 8750* (K); KwaZulu-Natal, Richards Bay, S of harbour entrance, 16.iii.1980, *C. J. Ward 9317* (K, NH); KwaZulu-Natal, Richards Bay, fresh water lake, 20.v.1952, *V. A. Wager s. n.* (NH); KwaZulu-Natal, Regio Lions River, Medmar Dam [by Howick], 2000 ft, 4.iii.1968, *E. J. Moll 4037* (NH); KwaZulu-Natal, Umschlangwe River [by Phoenix], 660 m, 19.viii.1893, *R. Schlechter 3120* (BM, G, K, LD, LE, LY, PRC, S, W, Z); KwaZulu-Natal, Port Natal [= Durban], 1847, *W. Gueinzius 462* (G, S); KwaZulu-Natal, Umtamvuna Nature Reserve [W of Port Edward], Turtle Pools, 11.xi.1984, *A. Abbott 2197* (NH *81856*).

Western Indian Ocean: MADAGASCAR: Ivondro, 1830, *Goudot s. n.* (G, P); East, Lake Nossi-Vé [near Toamasina], 27.ix.1882, *Humblot 352* (K, P); East, Vatomandry, 18.ii.1904, *J. Guillot 95* (G, P); x.1921, *H. Perrier de la Bathie 14203* (P); xi.1921, *H. Perrier de la Bathie 14085 bis* (P); Prov. Manonjary [= Mananjary], coastal zone, iii–iv.1909, *F. Geay 7907* (P); Centre, Antsirabe, Lake Andraikiba, 2.iv.1895, *C.-J. Forsyth-Major s. n.* (G); i.1927, *H. Perrier de la Bathie 17893* (P); xi.1955, *J. Bosser 8707* (P); 19.xi.1995, *M. Desfayes 951119.08* (herb. M. Desfayes); East, S of estuary of Mangoro River [near Ambodiharina], x.1921, *H. Perrier de la Bathie 14201* (P).

Potamogeton schweinfurthii occurs in most of Africa, but is particularly rare in the north-western part (Fig. 9). It is relatively frequent in large lakes and locally also in other aquatic habitats especially in eastern and southern Africa. Besides the African mainland, the species has been collected in the Azores and in Madagascar. It is here reported for the first time from Algeria, Tunisia, Burkina Faso and Niger.

DISCUSSION

Distinguishing the three similar broad-leaved species that occur in tropical and southern Africa, *P. nodosus*, *P. schweinfurthii* and *P. richardii*, is sometimes difficult, especially when only incomplete or inadequately preserved material is available. Although each of these species produces a 'typical' or specific phenotype, which is easy to recognize, they may mimic morphology similar to one or both of the other species. The wide morphological variation in *Potamogeton* taxa, in particular their phenotypic plasticity (cf. Kaplan, 2002), makes these phenotypes morphologically indistinguishable when specimens lack other important features, such as fruits or well-preserved submerged leaves. The range in variation of some characters shows considerable overlap between species.

In attempts to identify southern- and eastern-African broad leaved *Potamogeton* species we must accept that there are no simple morphological characters for the easy determination of all specimens. This also means that the characters given below are generally not exclusive: if the specimen has a particular character, the species is identified, but if it does not, the species is not excluded from consideration. This is the main reason why it is impossible to construct a simple key using only external vegetative morphology.

The determination of African specimens of the *P. nodosus–richardii–schweinfurthii* complex usually starts with well-developed and preserved specimens or morphotypes specific for one of the species. The process of identification may follow the following steps. If a plant has several to many well-preserved submerged leaves that are all sessile or only shortly petiolate (up to 2 cm), the specimen is *P. schweinfurthii*. The occurrence of submerged leaves with the lamina reduced to phyllodes in addition to well-preserved laminar leaves, whether these are sessile or petiolate, also indicates *P. schweinfurthii*. Another important feature of this species is the sharply mucronate apex of submerged leaves. Freely flowering or fruiting plants without floating leaves also should be *P. schweinfurthii*. Plants with fruits that are distinctly and sharply three-keeled (on the dorsal side and laterally) and more than 4.0 mm long belong to *P. richardii*. A clear discoloured section at the upper end of the petiole (at the junction with the lamina) of floating leaves is present in eastern and southern African *Potamogeton* species only in *P. richardii*. Well-developed and preserved submerged leaves with a narrowly obtuse to subacute but not sharply mucronate apex and long petioles indicate that the plant belongs to *P. nodosus*.

Alternatively, identification can be made by means of successive exclusion of the eligible species. For example, more than two well-preserved submerged leaves on the main stem of an adult plant exclude *P. richardii*. This species also does not have deeply reddish fruits. Completely sessile or subsessile submerged leaves exclude *P. nodosus*. Submerged leaves obtuse at their apices exclude *P. schweinfurthii*. The diagnostic characters of these three species are summarized in Table 1, which can be also used as a multi-access key to the taxa.

If a determination based on the above characters fails, which often means that the specimen is insufficiently developed or inadequately preserved, details of stem anatomy are needed for a reliable identification. The importance of stem anatomy for *Potamogeton* systematics was revealed by Raunkiaer (1896, 1903) and later repeatedly utilized to resolve taxonomic difficulties in various studies, e.g. by Fischer (1904, 1905, 1907), Hagström (1916), Ogden (1943, 1974a, b),

Figure 9. Distribution of *Potamogeton schweinfurthii* in Africa and on surrounding islands based on examined herbarium specimens.

Symoens *et al*. (1979), Tur (1982), Wiegleb (1990a, b), Kaplan (2001) and Kaplan & Wolff (2004). A detailed review is provided by Wiegleb (1990c). Descriptive terms used in stem anatomy are explained by Wiegleb & Kaplan (1998), and Symoens *et al*. (1979) give line drawings and Kaplan (2001) colour photographs of the important anatomical structures (interlacunar and subepidermal bundles, pseudohypodermis).

At this stage of the identification process the specimen may belong to any of the three species. If the anatomical study shows that the endodermis is of O-type and there are no bast bundles in the cortex (or rarely one or a few) the specimen is *P. nodosus*. Identification of this species based on stem anatomy is generally successful if the stem tissue is well prepared. In contrast, distinguishing between *P. schweinfurthii* and *P. richardii* is more difficult because these species share many anatomical features: endodermis consists of U-cells and at least one circle of interlacunar bundles is present. However, *P. richardii* usually has two or three circles of well-developed interlacunar bundles, whereas in *P. schweinfurthii* they are mostly confined to a single circle, or rarely two circles of which one is incomplete. Subepidermal bundles are usually numer-

Table 1. Synoptical survey of the most important diagnostic characters of *Potamogeton nodosus*, *P. schweinfurthii* and *P. richardii*

	P. nodosus	*P. schweinfurthii*	*P. richardii*
Presence of floating leaves on adult fertile plants	always present	absent or present	always present
Presence of a discoloured section at the upper end of the petiole of floating leaves	always absent	always absent	often present
Presence of submerged leaves on adult fertile plants	usually present, particularly in running water, sometimes decaying in shallow standing water	almost always present	decaying early, rarely one or two present
Shape of apex of submerged leaves	narrowly obtuse to subacute, never mucronate	acute to mucronate	narrowly obtuse to subacute
Length of petiole of submerged leaves	mostly more than 3 cm, often even longer than 10 cm in running water	mostly 0–3 cm, rarely that of the uppermost leaves up to 7 cm	mostly 5–15 cm, exceptionally up to 23 cm
Occurrence of phyllodial leaves	absent	often present near the stem base	sometimes present (but mostly not preserved on adult plants)
Fruit length (with rare extremes in parentheses)	3.0–3.9(–4.0)	2.9–3.9(–4.1)	(3.7–)3.9–5.2(–5.5)
Colour of dry ripe fruit	reddish brown	greyish green to yellowish green	ochre brown to pale brown
Shape of thickening of endodermal cells in stem	O-type	U-type	U-type
Presence of interlacunar bundles in the cortex of stem	absent, rarely a few present	present, usually in one circle, rarely in two circles of which one is incomplete	present in (1–)2–3 circles

ous in *P. richardii* but absent or only scattered in *P. schweinfurthii*. Before the final determination, the anatomical data should be compared with the morphology of the plant. In most cases, these two species are relatively easily distinguishable. By contrast, plants of *P. schweinfurthii* with well-developed floating leaves may sometimes be very similar to diminutive phenotypes of *P. richardii*. The occurrence of well-preserved submerged leaves, and relatively small (up to 3.9 mm long), greyish green to yellowish green fruits with or without indistinct lateral keels only indicate *P. schweinfurthii*. By contrast, large (often more than 4 mm long) and distinctly tricarinate fruits of ochre brown to pale brown colour are typical of *P. richardii*.

An investigation of stem anatomy is usually necessary for the identification of landforms. Care must be taken not to section the lower part of the stem as it often has an abnormal anatomy. Thanks to its unique stem anatomy, *P. nodosus* is often easily recognizable in well-prepared specimens. Yet the reliable identification of landform of *P. schweinfurthii* and *P. richardii* is often impossible. It is unlikely that any of the badly prepared or fragmentary herbarium specimen will be identified. This shows the importance of collecting rich and well-developed voucher collections whenever possible and their careful preparation.

The majority (86%) of the specimens of *P. nodosus* from Africa in herbaria were designated with incorrect names (particularly *P. natans*, '*P. thunbergii*' or '*P. fluitans*') or were unidentified. However, the extent and pattern of confusion vary greatly between the regions of Africa. Identification of the material from Africa north of the Sahara, inspired by European Floras, resulted in 26% correctly identified. The most often misapplied name is that of the northern temperate species *P. natans* L. (33%), followed by the generally misinterpreted name '*P. fluitans*' (18%). By contrast, most of the collections of *P. nodosus* from north-east tropical Africa were named *P. schweinfurthii* (35%) or *P. richardii* (13%), whereas those from southern Africa were mostly called *P. thunbergii* (64%) or *P. schweinfurthii* (10%). Only two collections (4%) of *P. nodosus* from southern Africa were correctly identified, and none from south tropical Africa, which are most frequently identified as *P. richardii* (33%) or *P. thunbergii* (25%). Rare confusions include, for example, *P. lucens* (4%), *P. parmatus* (1%) or *P. octandrus* (1%). Nineteen per cent of the col-

lections of *P. nodosus* from Africa south of the Sahara in herbaria were unidentified.

Similarly, *P. nodosus* was widely confused with other species, and many records of *P. richardii* are incorrect. The vast majority of adult plants with preserved submerged leaves identified in herbaria as *P. thunbergii* or *P. richardii* actually belong to *P. nodosus* (83%) or *P. schweinfurthii* with floating leaves (11%) and only 6% were identified correctly. This may also have affected the descriptions of *P. richardii* given in local floras.

The misidentification of *P. nodosus* as *P. richardii* in the southern part of Africa is easily understood as they have similar above-water parts. In addition, the floating-leaved morphotypes of *P. schweinfurthii* (Fig. 8) are often incorrectly determined as *P. richardii*, even though they mostly have also submerged leaves. The reason is that *P. schweinfurthii* is sometimes described as a totally or predominantly submerged species, whereas the plants with floating leaves are usually assigned to *P. richardii* regardless of their other characters. *P. schweinfurthii* is able to flower and fruit freely with all its leaves submerged. On the other hand, this species shows high variation (and perhaps also plasticity) in its capacity to produce floating leaves. Some populations even consist of mature individuals with abundant well-developed coriaceous floating leaves, if the water is not too deep. This fact is sometimes neglected. The following herbarium vouchers are representative specimens of the phenotype of *P. schweinfurthii* with floating leaves: *J. Burtt-Davy 18176* (K), *J. Léonard 4530* (BR, BRVU), *E. le Roux 1* (PRE), *A. Rehmann 2415* (K), *A. Rehmann 6578* (K), *M. C. Steynberg 6* (PRE), *C. J. Ward 8750* (K), *F. Wilms 1652* (BM, K).

In fact, the occurrence of floating leaves varies greatly not only in *P. schweinfurthii* but also in some related species, both at the taxonomic level and within populations, as is illustrated by the following examples. The variation in the production of floating leaves in *P. schweinfurthii* is analogous to that in some other species of the *P. lucens* group (*sensu* Wiegleb, 1988) such as *P. illinoensis* Morong, *P. gramineus* L., *P. wrightii* Morong and of the unrelated *P. alpinus* Biv. These taxa also exhibit within-species variation in this character as both populations with abundant floating leaves or entirely submerged leaves and all kinds of intermediate states occur. The fact that it was a river-form (phenotype) with narrow floating leaves that was originally described as *P. schweinfurthii* led to superfluous descriptions of the more usual or '*lucens*-like' forms as separate species by Hagström (1916) and Bennett (1924). Similarly, the eastern Asian species, *P. wrightii*, was initially defined as having only submerged leaves (Morong, 1886) and the floating-leaved forms were later repeatedly described as *P. hindostanicus* Hagstr., *P. malainoides* Miki and *P. jeholensis* Kitagawa (see Wiegleb, 1990b). In addition, the range of variation of the American *P. illinoensis* was not appreciated for a long time. It was first described by Morong in 1880, but still St. John (1925) considered it 'a very local species, restricted to a part of the Mississippi valley in western Illinois, eastern Iowa, and Minnesota' and the majority of the specimens of *P. illinoensis* were called either '*P. lucens*', '*P. angustifolius*' or '*P. Zizii*'. Several new names were proposed for this species mainly for specimens from Central and South America (e.g. *P. *brasiliensis* A. Benn., *P. ziziiformis* Hagstr., *P. macrophylloides* Hagstr., *P. pulchelliformis* Hagstr., *P. pedersenii* Tur) before it was recognized that all these forms belong to a single variable species (Wiegleb & Kaplan, 1998). Therefore, the presence vs. absence of floating leaves in a specimen cannot be taken as a diagnostic character in the identification of many species pairs, including the couple *P. richardii* and *P. schweinfurthii*. However, we are aware that experimental confirmation of the variation and plasticity in the capacity of *P. schweinfurthii* to produce floating leaves is desirable.

It was a heterophyllous plant that was described by Denny & Lye (1973) under the name *P. bunyonyiensis*, and thought to be a hybrid between *P. schweinfurthii* and *P. richardii* (as '*P. thunbergii*'). We have studied the type *K. A. Lye et al. 5216* (K) and 11 other collections of broad-leaved *Potamogeton* from Lake Bunyonyi. The type specimen is a terminal flowering part of a stem, with both floating and submerged leaves, which have lanceolate-oblong lamina, acute to markedly mucronate at apex, and petioles without any trace of a discoloured section. This plant clearly shows the features of *P. schweinfurthii* but no sign of unequivocal influence of *P. richardii*. We are unable to distinguish *P. bunyonyiensis* from other specimens of *P. schweinfurthii* with floating leaves. The stem anatomy is also within the variation range of that of *P. schweinfurthii*. Until there is more convincing evidence, the existence of an hybrid between *P. schweinfurthii* and *P. richardii* is doubtful.

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