Multivariate morphometric analysis of the *Potamogeton compressus* group (Potamogetonaceae)

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The *Potamogeton compressus* group is a complex of three to five closely related species with a circumpolar distribution in the Northern Hemisphere. Multivariate morphometric analyses (principal component analysis, cluster analysis, canonical and classificatory discriminant analyses) were used to elucidate the patterns of variation within this group and to test the morphological differentiation of the species recognized in the current literature. From the entire distribution range, 156 specimens of the group were included in the numerical methods. Results from morphological comparison are discussed in relation to molecular data, reproductive behaviour and geographical distribution. Morphometric analyses provided evidence that this complex can be clearly divided into three groups, one of which was subdivided mainly on the basis of allopatric occurrence and genetic differentiation. These groups correspond to four species accepted here: *P. acutifolius* (temperate regions of Europe), *P. compressus* (boreal and temperate regions of Europe and Asia), *P. manchuriensis* (northeastern China and Russian Far East) and *P. zosteriformis* (boreal and temperate regions of North America). Two species, *P. acutifolius* and *P. compressus*, are partly sympatric, but clearly differentiated morphologically and genetically, and effectively isolated reproductively. Endemic *P. manchuriensis* is characterized by a unique combination of characters and an occurrence in a limited geographical area. Allopatric *P. zosteriformis* is weakly differentiated morphologically from *P. compressus*, but differs markedly in molecular markers correlated with geographical differentiation. It may represent a cryptic species. In contrast, a recently suggested concept of southern Siberian *P. henningii* was not supported by our analyses. Plants so named are considered here as slender phenotypes of the widespread and variable *P. compressus*. © 2012 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2012, **170**, 112–130.

ADDITIONAL KEYWORDS: aquatic plants – differentiation – numerical taxonomy – species complex – species delimitation – variation.

INTRODUCTION

Potamogeton L. is one of the most diverse and taxonomically difficult genera of aquatic plants (Wiegleb & Kaplan, 1998; Kaplan, 2002a). The main sources of taxonomic complexity include the reduced morphology, which limits the number of taxonomic characters that can be used to separate species (Preston & Croft, 1997; Kaplan & Štěpánek, 2003; Kaplan, Fehrer & Hellquist, 2009), extensive phenotypic plasticity (Kaplan, 2002b), partitioning of genetic variation between rather than within populations (Hettiarachchi & Triest, 1991; Kaplan & Štěpánek, 2003) and the occurrence of many hybrids (e.g. Preston, 1995; Wiegleb & Kaplan, 1998; Kaplan & Fehrer, 2007; Kaplan *et al*., 2009; Kaplan, 2010a). The highest species and hybrid diversity is in temperate regions of the Northern Hemisphere. The genus contains several taxonomically intricate groups with a complicated classification and identification (Wiegleb, 1988; Wiegleb & Kaplan, 1998).

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Recent studies on *Potamogeton* taxonomy have concentrated mainly on the occurrence and diversity of hybrids (e.g. Preston, Bailey & Hollingsworth, 1998; Kaplan, 2001a, 2005a, 2007; Kaplan *et al.*, 2002, 2009; Fant, Kamau & Preston, 2003; Kaplan & Fehrer, 2004, 2006, 2009, 2011; Kaplan & Wolff, 2004; Kaplan & Zalewska-Gałosz, 2004; Zalewska-Gałosz, Ronikier & Kaplan, 2009, 2010; Kaplan, Fehrer & Hellquist, 2011; Kaplan & Uotila, 2011). Only a few studies have recently dealt with the morphological delimitation of species (e.g. Wiegleb, 1990a,b; Preston, 1995; Kaplan & Štěpánek, 2003; Kaplan & Symoens, 2005; Kaplan, 2005b; Les, Murray & Tippery, 2009). Although molecular data are now available for most *Potamogeton* spp. and species-specific markers have been used for the molecular delimitation of species in studies of hybridization (see the references above), detailed morphometric studies are missing, even for taxonomically intricate groups, and multivariate morphometric analyses have never been employed for the precise delimitation of *Potamogeton* spp.

The *Potamogeton compressus* aggregate is a well-defined group of linear-leaved species with markedly compressed stems and leaves with sclerenchymatous strands in addition to true vascular veins (which make them appear many-veined, see Fig. 1). It has a circumpolar distribution in the Northern Hemisphere. Its delimitation in this study corresponds to *Potamogeton* subsection *Compressi* Hagström (Hagström, 1916). The number of species included varies between authors and regions. Linnaeus (1753) described only one species within this group, *P. compressus* L., with five-veined leaves (finer sclerenchymatous strands not included), long peduncles and cylindrical spikes. However, this Linnean name was commonly misapplied by other researchers. For example, Oeder (1765), Fieber (1838) and Reichenbach (1845) adopted this name for the species known today as *P. friesii* Rupr., Roth (1788) and Presl & Presl (1819) for a species described later as *P. obtusifolius* Mert. et W.D.J.Koch and Lamarck & de Candolle (1805) for what is now called *P. acutifolius* Link. This was the main reason why *P. compressus* was repeatedly redescribed by different authors. Schumacher (1801) proposed for this species the name *P. zosterifolius* Schumach., Willdenow (1809) *P. complanatus* Willd. and Wahlenberg (1824) *P. laticaulis* Wahlenb.

Another species of this group was recognized by Link and published in Roemer & Schultes (1818) as *P. acutifolius* Link. This name applies to plants that have leaves with three vascular veins, short spikes and short peduncles. In contrast with *P. compressus*, this species often also differs by its shorter, narrower and more acute leaves. Plants similar in a vegetative stage to the European *P. acutifolius* were collected by
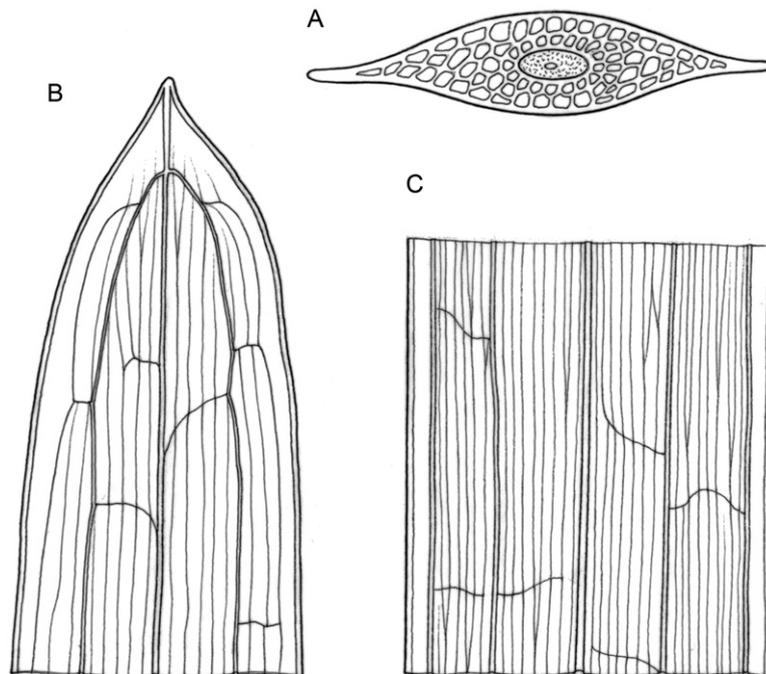
Figure 1. Details of morphology of *Potamogeton compressus* illustrating characteristic features of the *Potamogeton compressus* group: A, compressed stem (shown in cross-section); B, C, apex and middle section of a leaf with stronger vascular veins and numerous finer sclerenchymatous strands (drawn by Eva Smrčinová).

Litvinov and Desoulavy on expeditions to Manchuria in 1902–1903. These specimens were sent for identification to the British expert Bennett, who described them as *P. acutifolius* ssp. *manchuriensis* A.Benn. (Bennett, 1904). Later, apparently influenced by Hagström's comment 'Manchurian plants referred to *P. acutifolius* surely are something else' (Hagström, 1916: 72), Bennett (1924) elevated this taxon to species level. Neglecting this change of rank, an isonym was later proposed by Fernald (1932).

In one of his numerous papers on the taxonomy and nomenclature of *Potamogeton*, Bennett (1910) described another species, resembling weak forms of *P. compressus*, as *P. henningii* A.Benn. He incorrectly interpreted the origin of the specimen as being from the Caucasus, whereas it actually originates from the lowland of the Don River in Russia (see also Tzvelev, 1986).

Fernald (1932) compared North American material with a few European collections of *P. compressus* and, based on rather small differences in fruit characters, leaf venation and the texture of stipules, separated American populations of *P. compressus* under a new name *P. zosteriformis* Fern. A close resemblance of both species was occasionally commented on by later researchers (Reveal, 1977; Wiegleb & Kaplan, 1998; Brayshaw, 2000), but the variation in the species has never been studied in detail across the entire range.

Although the name *P. henningii* occasionally appeared in Russian floras (Yuzepchuk, 1934; Mäemets, 1979), it has only exceptionally been adopted for new collections. However, the name was recently resurrected by Volobaev (1993) and applied to narrow-leaved plants of the *P. compressus* group from southern Siberia. Volobaev's refined concept was then accepted by other authors who had adopted the Komarovian narrow species concept (e.g. Papchenkov & Garin, 2000).

Our field and herbarium experience indicates that plants of some of these taxa can be consistently 'identified' only on the basis of the origin of the sample. Some are possibly based on extreme forms of variation, but these are connected by all intermediate forms and their delimitation is difficult. The role of phenotypic plasticity (Kaplan, 2002b) is also greatly underestimated when species concepts which are too narrow are adopted. We therefore subjected a representative collection of plants covering all recognized species from the entire range of the complex to multivariate morphometric analysis. The aims of this paper were: (1) to elucidate patterns in morphological variation in the *P. compressus* group; (2) to test whether the species recognized in the literature can really be reliably identified by morphological characters; (3) to reveal the level of their morphological differentiation; and (4) to find the most reliable morphological features for the identification of distinguishable taxa.

MATERIAL AND METHODS

PLANT MATERIAL

Data for multivariate morphometric analyses were collected from specimens in the herbaria BM, BP, BRNM, BRNU, C, E, FR, G, GH, K, LD, LE, M, MSB, P, PRA, S, U, W, WU, Z and ZT (acronyms follow Thiers, 2011). In addition, the morphology and distribution of these species were studied during an examination of numerous herbaria for a monograph of Potamogetonaceae within the framework of the Species Plantarum Project – Flora of the World (for the complete list of studied herbaria, see Kaplan, 2008, 2010a,c). An attempt was made to collect data from specimens representing the range of distribution of the complex. Only well-preserved specimens bearing both well-developed leaves and mature fruits were considered in the analyses. The total number of plants included in the analysis was 156. Each plant was tentatively ascribed to one of five groups, corresponding to five species adopted in the contemporary literature. These were defined as follows:

1. *P. acutifolius*: European plants with short peduncles and short, almost globose, spikes with only a few flower whorls;
2. *P. compressus*: Eurasian plants with long peduncles and long, cylindrical spikes with several flower whorls;
3. *P. henningii*: narrow-leaved plants from eastern European Russia and southwestern and southern Siberia, very similar to *P. compressus*; since the discrimination between *P. henningii* and narrow-leaved forms of *P. compressus* was obscure to us, we tentatively adopted the identifications of these specimens made by the leading protagonists of this concept (P. Volobaev, V. Papchenkov);
4. *P. manchuriensis*: syntype specimens of the name *P. acutifolius* ssp. *manchuriensis* and similar narrow-leaved plants from northeastern China and the Russian Far East, with cylindrical spikes and long peduncles; and
5. *P. zosteriformis*: North American plants very similar to Eurasian *P. compressus*.

A list of specimens included in the morphometric study, with basic data on their origin, is given in Table 1.

Although mostly only one or a few shoots were available from each site, this had little if any negative influence on the representativeness with respect to intrapopulational variation. The plants studied are

Table 1. A list of specimens included in the morphometric study

Taxon	Reference code	Country of origin	Voucher collection records
P. acutifolius	A01	Great Britain	30.viii.1953, *D. A. Cadbury* (BM)
	A02	Great Britain	*A. Bennett 4375* (G)
	A03	Great Britain	*E. C. Wallace 4032* (K)
	A04	Great Britain	*G. C. Druce 2505* (K)
	A05	Great Britain	*G. C. Hillman 98* (BM)
	A06	Great Britain	*N. D. Simpson 45.468* (BM)
	A07	Sweden	2.viii.1935, *H. Fries* (G)
	A08	Sweden	30.viii.1899, *C. B. v. Porat* (C)
	A09	Sweden	*E. Asplund (in G. Samuelsson, Pl. Suec. Exs. 76)* (K)
	A10	Sweden	*E. Th. Fries & H. Fries (in G. Tiselius, Potam. Suec. Exs., fasc. 2: 98)* (K)
	A11	Sweden	ix.1882, *G. Gustafsson* (P)
	A12	Sweden	ix.1895, *C. G. H. Thedenius* (C)
	A13	Denmark	15.viii.1869, *P. Nielsen* (C)
	A14	Denmark	21.viii.1904, *I. Pedersen* (C)
	A15	Denmark	4.viii.1899, *I. Baagøe* (C)
	A16	Denmark	8.ix.1894, *A. E. Andersen* (C)
	A17	France	22.vii.1878, *Guyon* (BM)
	A18	France	*A. Boullu (in C. Billot, Fl, Gall. Germ. Exs. 1067)* (G)
	A19	France	*A. Le Grand (in F. Schultz, Herb. Norm. 620)* (G)
	A20	France	*E. Bonnet 3065* (K)
	A21	France	*E. Jeanpert 210* (G)
	A22	France	*H. Bouby 1829* (P)
	A23	France	*H. Bouby 1829* (P)
	A24	France	vii.1878, *Ch. Magnier* (K)
	A25	Belgium	15.vii.1926, *E.-M. Bernays* (P)
	A26	Belgium	*G. C. Van Haesendonck (in A. Thielens & A. Devos, Kickxia Belg. 176)* (P)
	A27	Netherlands	*J. Wttewaall (in Reichenbach, Fl. Germ. Exsicc. 1104)* (P)
	A28	Switzerland	25.vii.1905, *E. Baumann* (ZT)
	A29	Switzerland	26.vi.1943, *E. Berger* (ZT)
	A31	Germany	7.ix.1922, *W. Koch & G. Kummer* (ZT)
	A32	Germany	*H. Hofmann (in Pl. Crit. Sax. 280)* (G)
	A33	Germany	vi.1902, *G. Fischer* (C)
	A34	Germany	*W. Lobin 986* (FR)
	A35	Czech Republic	25.vi.1964, *K. Fiala* (BRNU)
	A36	Czech Republic	26.vii.1905, *F. Čouka* (BRNU)
	A37	Czech Republic	*Velenovský (in Fl. Exs. Austro-Hung. 2688)* (P)
	A38	Czech Republic	*Z. Kaplan 03/147* (PRA)
	A39	Czech Republic	*Z. Kaplan 91/443* (PRA)
	A40	Czech Republic	*Z. Kaplan 92/447* (PRA)
	A41	Czech Republic	*Z. Kaplan 98/205* (PRA)
	A42	Poland	13.vi.2004, *J. Zalewska-Gałosz* (PRA)
	A43	Slovakia	2.vi.1927, *A. Margittai* (BP)
	A44	Slovakia	6.vii.1982, *Š. Husák* (PRA)
	A45	Slovakia	*Z. Kaplan 95/450* (PRA)
	A46	Hungary	25.vii.1931, *Z. Kárpáti* (BP)
	A47	Hungary	25.viii.1926, *A. Boros* (BP)
	A48	Romania	2.vii.1913, *I. Prodan* (BP)
	A49	Romania	*E. I. Nyárády (in Fl. Roman. Exs. 215)* (K)
	A50	Lithuania	8.vii.1897, *H. Kuehn* (C)
	A51	Russia	*W. D. Andrejew 288* (BP, K)

Table 1. *Continued*

Taxon	Reference code	Country of origin	Voucher collection records
P. compressus	C01	Great Britain	1.viii.1942, *R. B. Abell* (BM)
	C02	Great Britain	4.viii.1935, *J. E. Lousley* (BM)
	C03	Great Britain	*Ch. Bailey 1233* (BM)
	C04	Great Britain	*E. S. Edees 7297* (BM)
	C05	Sweden	11.vii.1943, *E. Almquist* (S)
	C06	Sweden	18.vii.1920, *G. Samuelsson* (LD)
	C07	Sweden	18.vii.1920, *G. Samuelsson* (S)
	C08	Sweden	22.vii.1921, *E. Almquist* (S)
	C09	Sweden	*E. P. Vrang (in G. Tiselius, Potam. Suec. Exs, fasc. 2: 96)* (K)
	C10	Sweden	*G. A. Ringselle (in I. Dörfler, Herb. Norm. 4594)* (P)
	C11	Sweden	*G. Lohammar (in G. Samuelsson, Pl. Suec. Exs. 75)* (K)
	C12	Sweden	vii.1869, *C. A. Ringenson* (LD)
	C13	Sweden	viii.1901, *A. Fries* (S)
	C14	Sweden	viii.1904, *C. Kurck* (LD)
	C15	Denmark	12.vii.1857, *H. Mortensen* (C)
	C16	Denmark	19.vii.1903, *I. Baagøe* (C)
	C17	Denmark	24.vi.1897, *J. Baagöe* (S)
	C18	Denmark	24.viii.1893, *I. Baagøe* (C)
	C19	Denmark	25.vi.1901, *J. Baagöe* (G)
	C20	Denmark	28.vii.1969, *E. Worsøe* (C)
	C21	Denmark	29.vii.1896, *J. Baagöe* (G)
	C22	Finland	19.viii.1982, *T. Ulvinen & M. Tihtarinen* (C)
	C23	Finland	31.vii.1888, *O. Collin* (LD)
	C24	Finland	*A. Kurtto 4515* (BRNM)
	C25	Finland	*A. Kurtto 4515 (in Soc. Éch. Pl. Vasc. Eur. Bass. Méd. 12731)* (MSB)
	C26	Finland	*C. Cedercreutz & G. Åberg (in Pl. Finl. Exs. 1028)* (P)
	C27	Belgium	*G. C. Van Haesendonck (in A. Thielens & A. Devos, Kickxia Belg. 175)* (P)
	C28	Belgium	vii.1868, *A. Thielens* (P)
	C29	Switzerland	30.viii.1878, *Lerch* (G)
	C30	Switzerland	7.viii.1869, *F. Tripet* (K)
	C31	Germany	10.vii.1896, *R. Ruthe* (P)
	C32	Germany	19.vii.1905, *G. Fischer* (M *26816*)
	C33	Germany	21.viii.1906, *W. Niebler* (M *25903*)
	C34	Germany	*W. Niebler (in Fl. Exs. Bav. 1092)* (G)
	C35	Czech Republic	23 VI 1873, *E. Fiek* (PR)
	C36	Czech Republic	VII 1900, *Rohlena* (PR)
	C37	Poland	13.vii.1871, *C. Baenitz* (BP)
	C38	Poland	13.vii.1871, *C. Baenitz* (BP)
	C39	Poland	*Schwarz (in A. Callier, Fl. Siles. Exs. 94)* (G)
	C40	Belarus	7.viii.1892, *J. Paczoski* (G)
	C41	Lithuania	23.vi.1925, *W. Koch* (PRA)
	C42	Russia	11.vii.1862, *F. Heidenreich* (WU)
	C43	Russia	27.vii.1896, *J. E. Aro* (BP)
	C44	Russia	vii.1880, *H. F. Olsoni* (LD)
	C45	Russia	vii.1880, *J. V. Johnsson* (BP)
	C46	Russia	*W. D. Andrejew (in Herb. Fl. Ross. 1636)* (BP)
	C47	Russia	*A. K. Skvortsov 10169* (BM)
	C48	Russia	13.viii.1914, *S. J. Enander* (LD)
	C49	Russia	*S. Rosbach & V. Mozer 14840* (PRA)
P. henningii	H01	Russia	10.vii.1995, *V. Papchenkov & O. Kozlovskaya* (PRA)
	H02	Russia	14.viii.1959, *V. M. Katanskaja* (LE)
	H03	Russia	15.viii.1959, *V. M. Katanskaja* (LE)
	H04	Russia	16.vii.1959, *V. M. Katanskaja* (LE)
	H05	Russia	22.viii.1989, *P. Volobaev* (LE)
	H06	Russia	*N. Schipczinsky (in Sukaczew 487)* (LE)
	H07	Russia	*N. Šipčinskij 487* (LE)

Table 1. *Continued*

Taxon	Reference code	Country of origin	Voucher collection records
P. manchuriensis	M01	Russia	14.vii.1891, *S. Koržinskij* (LE)
	M02	Russia	8.viii.1926, *G. Melvil* (LE)
	M03	Russia	*D. P. Vorob'ev 410* (LE)
	M04	Russia	*I. K. Schischkin 537* (LE)
	M05	Russia	*N. Desoulavy 1904* (LE)
	M06	Russia	*V. Komarov 615* (LE) [I]
	M07	Russia	*V. Komarov 615* (LE) [II]
	M08	Russia	*V. Komarov 685* (LE)
	M09	China	10.vi.1925, *B. V. Skvortzov* (GH)
	M10	China	20.vii.1930, *B. V. Skvortzov* (GH)
	M11	China	*A. Baranov 1147* (LE)
	M12	China	*B. Skvorcov 10* (LE)
	M13	China	*B. Skvorcov 25* (LE)
	M14	China	*D. Litvinov' 2338* (LE)
	M15	China	*D. Litvinov' 2463* (LE)
	M16	China	*N. Desoulavy 495* (LE)
	M17	China	12.vii.1895, *V. L. Komarow* (LE)
	M18	China	*Fuh Pei-Yun 2553* (LE)
P. zosteriformis	Z01	Canada	2.viii.1882, *J. Fowler* (E)
	Z02	Canada	*C. H. Ostenfeld 555* (C)
	Z03	Canada	*W. K. W. Baldwin & A. J. Breitung 3730* (K)
	Z04	Canada	16.viii.1886, *J. R. Churchill* (BM)
	Z05	Canada	*F. Marie-Victorin et al. 33864* (P)
	Z06	Canada	*Rolland 13043* (BM)
	Z07	USA	*Bogaers & Farjon 645* (U)
	Z08	USA	*E. Hall 491* (G)
	Z09	USA	*Clawson 362* (U)
	Z10	USA	*F. Warnock 115* (W)
	Z11	USA	*Johnson 59* (U)
	Z12	USA	*Z. Kaplan C1728* (PRA)
	Z13	USA	*Z. Kaplan & C. B. Hellquist 05/442* (PRA)
	Z14	USA	*Z. Kaplan & C. B. Hellquist 05/451* (PRA)
	Z15	USA	*Z. Kaplan C1591* (PRA)
	Z16	USA	*Z. Kaplan & C. B. Hellquist 05/339* (PRA)
	Z17	USA	*Z. Kaplan & C. B. Hellquist 05/349* (PRA)
	Z18	USA	12.vii.1893, *C. A. Davis* (K)
	Z19	USA	25.vi.1893, *C. F. Wheeler* (M)
	Z20	USA	29.viii.1895, *O. A. Farwell* (M)
	Z21	USA	31.viii.1904, *C. K. Dodge* (E)
	Z22	USA	vii.1892, *B. C. Taylor* (G)
	Z23	USA	viii.1897, *J. E. Campbell* (M)
	Z24	USA	*W. Kiener 20994* (BM)
	Z25	USA	*O. A. Stevens 559* (G)
	Z26	USA	*Z. Kaplan C1612* (PRA)
	Z27	USA	*Z. Kaplan C1661* (PRA)
	Z28	USA	*Z. Kaplan & C. B. Hellquist 05/353* (PRA)
	Z29	USA	*Z. Kaplan & C. B. Hellquist 05/357* (PRA)
	Z30	USA	*Z. Kaplan & C. B. Hellquist 05/391* (PRA)
	Z31	USA	*Z. Kaplan & C. B. Hellquist 05/395* (PRA)
	Z32	USA	*F. G. Meyer 653* (BM)

predominantly self-pollinated or persist at their sites vegetatively, and genetic variation within populations is generally low or absent in contrast with that between populations (Hettiarachchi & Triest, 1991; Kaplan & Štěpánek, 2003). This is why populations are usually fairly uniform morphologically and a random herbarium sample represents most of the variation of the entire population.

CHARACTERS SCORED

Ten morphological characters were scored for each plant. The selection of characters was made to include particularly those commonly used in the relevant literature, with additions of those that were identified as important during our field and herbarium experience. The quantitative characters scored are listed in Table 2.

For all characters, values are the mean of up to five measurements scored on each plant. Exceptions to this rule were caused by the lack of sufficient numbers of the organ involved [e.g. for peduncle length (PeduncLength) and length of fruiting spikes (SpikeLength) in specimens with fewer inflorescences].

The morphological distinction between the true vascular veins and the additional sclerenchymatous strands in leaves (Fig. 1B, C) was sometimes obscure, which particularly applied to the outer pair of veins in the leaves of species with five vascular veins (see also Discussion). The difference could best be observed in old leaves that had lost the green pigment and become yellowish or brownish. However, these old, senescent leaves were not always available. To facilitate consistent and unambiguous scoring of these characters, the numbers of vascular veins and sclerenchymatous strands were scored on well-preserved green leaves as a single character: the total number of 'veins' (NoVeins). However, these two sorts of 'veins' are distinguished correctly from the viewpoint of the morphological terminology in further descriptions and in the taxonomic treatment, which will be presented as the second part of this study.

The stem width (StemWidth) was measured along the longer axis of the cross-section of the compressed stem (Fig. 1A), and in the middle of the length of the broadest internode in the upper part of the stem, below the flowering region. The characters length of the middle stem leaves (LengthLeaves), stipule length (StipuleLength), PeduncLength and Spike-Length were measured directly using a ruler without magnification. The characters width of the middle stem leaves (WidthLeaves), NoVeins, width of stem in its upper part (StemWidth), number of flower whorls (NoFlowerWhorls), number of carpels per flower that develop to mature fruits (NoCarpels) and length of fruit including beak (FruitLength) were measured or counted under a stereomicroscope.

MULTIVARIATE MORPHOMETRIC ANALYSES

In the morphometric analyses of the specimens, we used a combination of clustering and ordination methods and discriminant analyses (Marhold, 2011).

First, correlation coefficients among characters for each tentatively recognized species (see section on Plant Material) were computed in order to reveal highly correlated characters that may potentially distort the results of some analyses. At the same time, potential departures of the character distribution from a normal distribution were tested using the Shapiro–Wilk statistic for each character for all characters and species.

As the second step, cluster analyses were applied to the matrix of all material in order to obtain information about the grouping of specimens on the basis of overall morphological similarity. From the clustering methods, Ward's method (minimization of the increase of the error sum of squares) and UPGMA (unweighted pair-group method using arithmetic averages), based on Euclidean distances and data standardized by standard deviation, were employed (Everitt, 1986). As a complement, two principal component analyses, based on complete and reduced datasets, were performed (Podani, 1994) to find the phenetic relationships among specimens in an ordination space.

On the basis of the results of cluster and ordination analyses and of predefined groups of specimens

Table 2. Characters used in the morphometric study

Character acronym	Detailed definition of the character
LengthLeaves	Length of the middle stem leaves (mm)
WidthLeaves	Width of the middle stem leaves (mm)
NoVeins	Total number of 'veins' of the middle stem leaves (vascular veins plus additional sclerenchymatous strands)
StemWidth	Width of stem in its upper part (mm)
StipuleLength	Stipule length (mm)
PeduncLength	Peduncle length (mm)
SpikeLength	Length of fruiting spikes (mm)
NoFlowerWhorls	Number of flower whorls (verticills)
NoCarpels	Number of carpels per flower that develop to mature fruits
FruitLength	Length of fruit incl. beak (mm)

(tentatively recognized species), we performed several canonical and classificatory discriminant analyses (Klecka, 1980; Marhold, 2011). In the case of analyses based entirely on predefined groups of specimens, this could involve circular argumentation, but, as they gave negative results, this argument is not really relevant here.

As the last step, basic statistical parameters (mean values, minimum and maximum values, standard deviations and 5th and 95th percentiles) were calculated for each group of specimens resulting from the previous analyses.

The discriminant and principal component analyses were performed using SAS 9.1.3 software (SAS Institute Inc., 2007). For the cluster analyses, SYN-TAX 2000 (Podani, 2001) software was used.

RESULTS

The distribution of the measured characters departed from the normal distribution, and therefore the Spearman nonparametric correlation coefficient and k nearest-neighbour nonparametric classificatory discriminant analyses (Klecka, 1980) were subsequently used. The correlation coefficients did not exceed 0.90 for any character pair, and thus all of the measured characters were retained for further analyses. The highest correlation coefficients, 0.88292 and 0.82572, were found between the characters LengthLeaves vs. PeduncLength and FruitLength vs. StemWidth, respectively, in the group of *P. henningii* specimens (see Table 2 for character explanations).

Ward's cluster analysis of all specimens (Fig. 2) resulted in a dendrogram that divided specimens into two main clusters: the first comprised groups of *P. acutifolius* and *P. manchuriensis* specimens, and the second comprised *P. compressus*, *P. zosteriformis* and *P. henningii*. *Potamogeton acutifolius* and *P. manchuriensis* formed two separated subclusters in the first cluster, but specimens of the three other groups were intermingled in subclusters of the second cluster. UPGMA cluster analysis (diagram not shown) gave similar results, but a few specimens from the group of *P. acutifolius* were separated from the rest of the specimens into a separate cluster.

The ordination diagram from the principal component analysis based on the complete set of data (Fig. 3) shows a pattern similar to the results of the cluster analyses. Specimens of *P. acutifolius* and of *P. manchuriensis* were separated from the rest of the material along the first axis, and were separated from each other along the second axis. The remaining groups of specimens appeared to be intermingled, forming one cloud in the ordination diagram. All characters, except NoCarpels and FruitLength, almost equally contributed to the division of specimens along

the first component axis. Most prominent among them were SpikeLength, NoFlowerWhorls and LengthLeaves. The second axis was most strongly correlated with the characters WidthLeaves and StemWidth. When the specimens of the group of *P. acutifolius* were excluded from the principal component analysis (Fig. 4), specimens of *P. manchuriensis* (except one specimen) were separated along the first axis from the rest of the material, with two specimens of *P. henningii* in between them. No structure appeared along the second axis. Morphological characters most strongly correlated with the first axis were WidthLeaves, Stem-Width, SpikeLength and NoVeins.

Ordination of the other restricted dataset of specimens of *P. compressus*, *P. zosteriformis* and *P. henningii* did not show any grouping of specimens (diagram not shown); specimens of the first two groups were spread almost across the ordination diagram, whereas those of *P. henningii* appeared in its centre, intermingled with specimens of the other groups.

In the subsequent step, several canonical and classificatory discriminant analyses were performed with the aim of finding the most important characters separating the predefined groups and testing the potential success of such separation. This also included groups resulting from the cluster and principal component analyses.

The first canonical discriminant analysis was based on two groups of specimens, *P. acutifolius* vs. the rest of the analysed material. The histogram of the canonical analysis showed two clearly separated peaks (Fig. 5). The most important characters correlated with the canonical axis were NoFlowerWhorls, SpikeLength, PeduncLength and LengthLeaves. In accordance with this, the results of the k nearest-neighbour nonparametric classificatory discriminant analysis (with $k = 2$) indicated complete success of separation without any misidentified specimens.

The canonical discriminant analyses of specimens of *P. manchuriensis* as one group and specimens of *P. compressus*, *P. zosteriformis* and *P. henningii* as the second again showed complete separation of *P. manchuriensis* from the rest of the material (Fig. 6). The most important characters correlated with the axis separating these two groups were WidthLeaves, NoVeins, StemWidth and NoFlowerWhorls. The nonparametric classificatory discriminant analysis (with $k = 6$) showed all specimens of *P. manchuriensis* to be correctly identified, but 1.27% of the other specimens were incorrectly classified into this species.

Like the results of the principal component analysis, canonical discriminant analysis of specimens of the groups of *P. compressus*, *P. henningii* and *P. zosteriformis* showed rather poor separation of these taxa (Fig. 7). Success of classification of these three
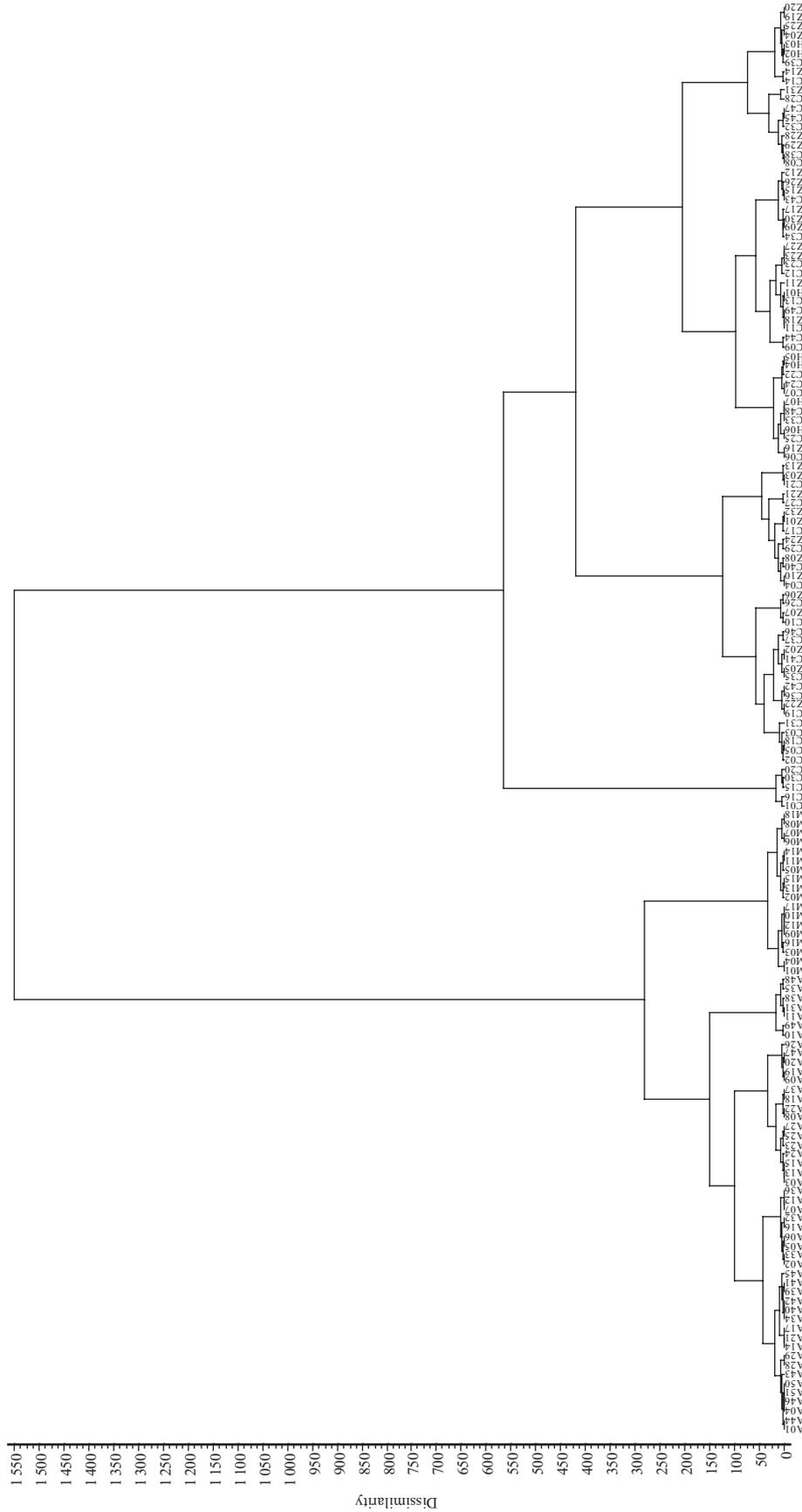
Figure 2. Ward's cluster analysis of the whole set of specimens of the *Potamogeton compressus* group. Groups of specimens: A, *P. acutifolius*; C, *P. compressus*; H, *P. henningii*; M, *P. manchuriensis*; Z, *P. zosteriformis*. For the numbers of specimens, see Table 1.
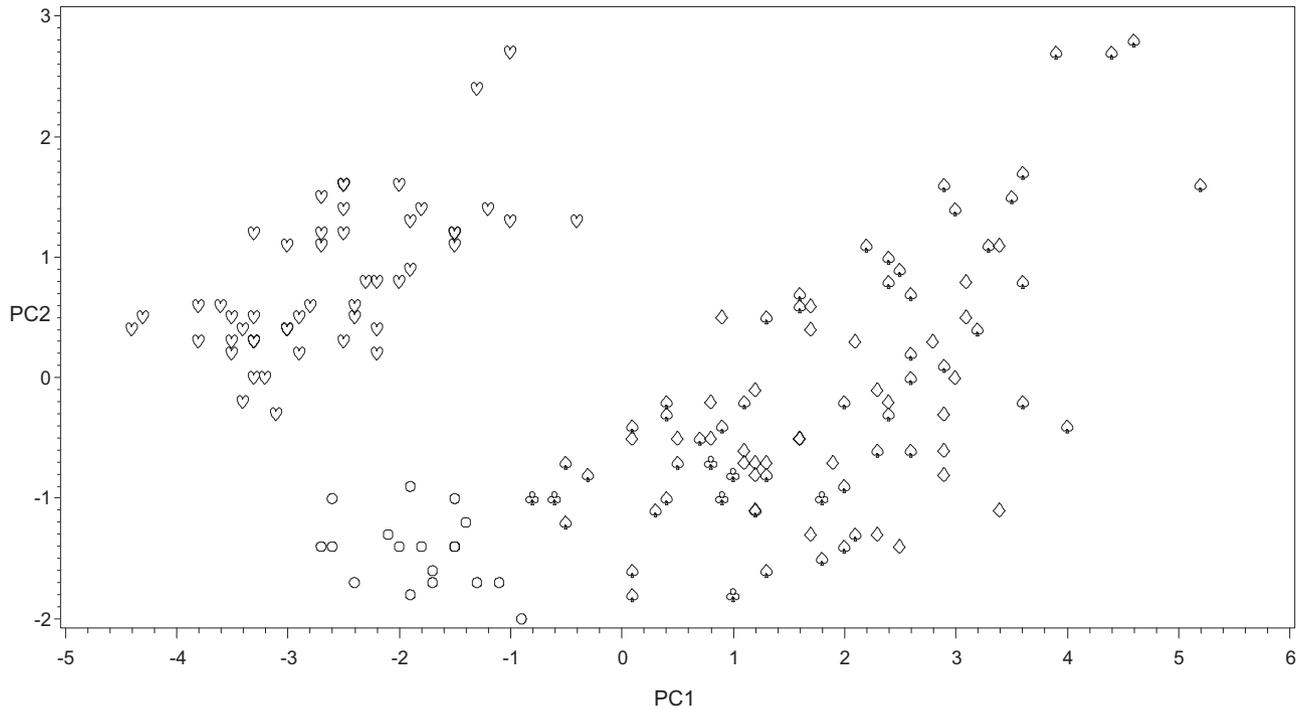
Figure 3. Principal component analysis of the *Potamogeton compressus* group based on ten morphological characters and the complete set of data. Heart, *P. acutifolius*; spade, *P. compressus*; club, *P. henningii*; circle, *P. manchuriensis*; diamond, *P. zosteriformis* (see also Table 3: PCA1). The first two axes explain 57.1% and 11.6% of the variation, respectively.

Table 3. Results of the principal component analyses of the *Potamogeton compressus* group based on ten morphological characters

Character	PCA1 (Fig. 3)		PCA2 (Fig. 4)	
	PC1	PC2	PC1	PC2
LengthLeaves	**0.354**	−0.135	0.297	−0.056
WidthLeaves	0.309	**0.493**	**0.404**	0.040
NoVeins	**0.346**	0.160	**0.365**	0.004
StemWidth	0.309	**0.467**	**0.384**	−0.067
StipuleLength	0.311	0.052	0.291	−0.101
PeduncLength	**0.332**	−0.329	0.220	**0.476**
SpikeLength	**0.377**	−0.277	**0.379**	0.063
NoFlowerWhorls	**0.358**	−0.367	0.324	−0.269
NoCarpels	0.189	0.366	0.207	**0.613**
FruitLength	0.227	−0.195	0.208	**−0.550**

PCA1, analysis based on the complete set of data (Fig. 3). PCA2, analysis with the exclusion of the group of *P. acutifolius* (PCA2, Fig. 4).
PC1, PC2, eigenvector values for the first and second principal components. Higher values are shown in bold type.
For an explanation of the character acronyms, see Table 2.

groups of specimens was rather low, being 36.73%, 57.14% and 78.13%, respectively (with $k = 2$). The same was true for the separation of *P. compressus* and *P. henningii* (i.e. the Eurasian material) from *P. zosteriformis* (i.e. the North American material), in either canonical discriminant analysis (Fig. 8) or classificatory discriminant analysis (67.86% and 81.25% correct classification rate for the groups, respectively, with $k = 14$). Characters strongly correlated with the canonical axis in the latter case were NoFlowerWhorls and NoCarpels.

Canonical discriminant analysis of specimens of *P. compressus* as one group vs. those of *P. henningii*, *P. manchuriensis* and *P. zosteriformis* as the other did not give meaningful results (Fig. 9). The success of the classificatory discriminant analysis was low (69.39% for *P. compressus* and 77.19% for the rest of the material, with $k = 13$).

There was only some shift among the groups of specimens of *P. compressus* and *P. henningii* in canonical discriminant analyses (Fig. 10), caused mainly by the characters LengthLeaves, WidthLeaves and StemWidth, which were strongly correlated with the canonical axis. Results of the classificatory discriminant analysis in this case were 63.27% and 100% for the groups, respectively (with $k = 16$).

Basic statistical parameters (mean values, minimum and maximum values, standard deviations and
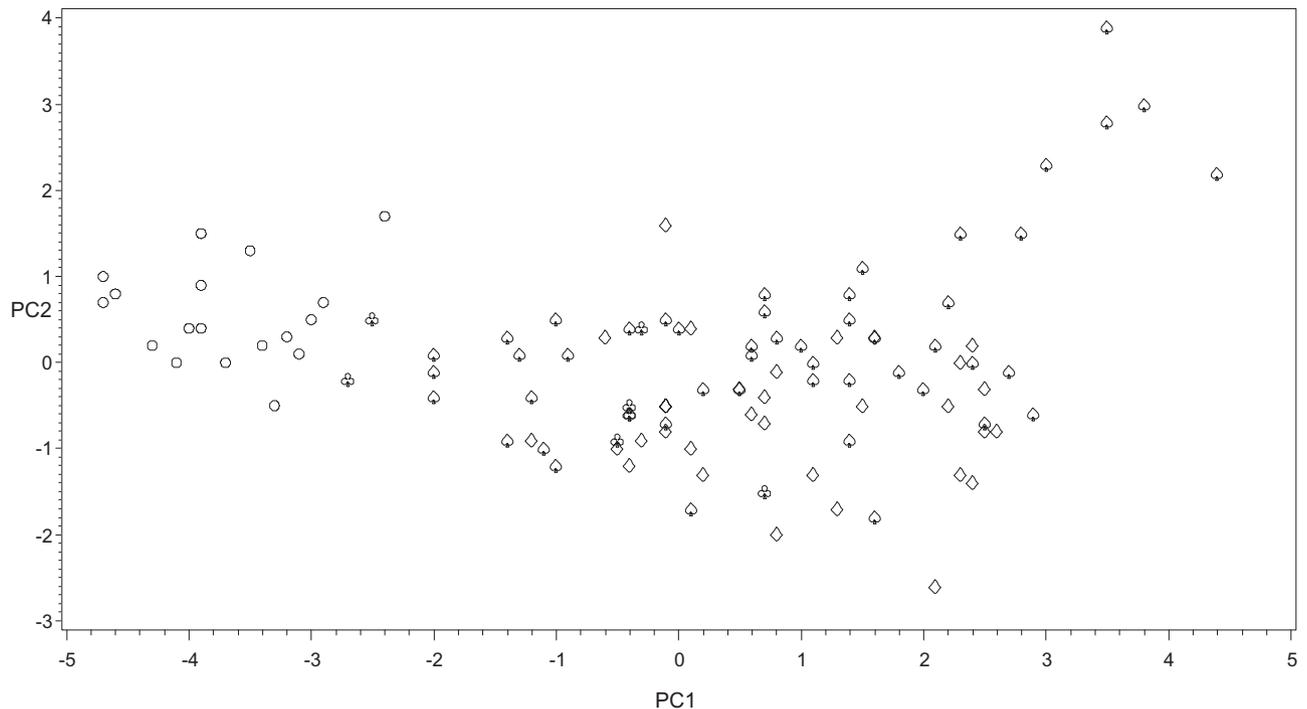
Figure 4. Principal component analysis of the *Potamogeton compressus* group based on ten morphological characters and the set of data with the exclusion of the group of *P. acutifolius*. Spade, *P. compressus*; club, *P. henningii*; circle, *P. manchuriensis*; diamond, *P. zosteriformis* (see also Table 3: PCA2). The first two axes explain 47.8% and 10.6% of the variation, respectively.

Table 4. Results of the canonical discriminant analyses of the *Potamogeton compressus* group based on ten morphological characters

Character	CDA1 (Fig. 5) CAN1	CDA2 (Fig. 6) CAN1	CDA3 (Fig. 7) CAN1	CAN2	CDA4 (Fig. 8) CAN1	CDA5 (Fig. 9) CAN1	CDA6 (Fig. 10) CAN1
LengthLeaves	**0.756**	0.506	0.124	**0.619**	−0.031	**0.604**	**0.666**
WidthLeaves	0.265	**0.828**	0.356	**0.663**	0.183	**0.692**	**0.706**
NoVeins	0.527	**0.811**	0.129	0.083	0.105	0.525	0.120
StemWidth	0.321	**0.774**	0.285	**0.562**	0.139	**0.648**	**0.621**
StipuleLength	0.520	0.463	0.029	−0.004	0.030	0.293	0.005
PeduncLength	**0.823**	0.396	−0.180	0.206	−0.225	0.485	0.152
SpikeLength	**0.926**	0.668	0.291	0.342	0.198	0.473	0.425
NoFlowerWhorls	**0.966**	**0.716**	**0.702**	0.160	**0.641**	0.220	0.447
NoCarpels	0.220	0.209	−0.465	**0.566**	−0.589	**0.772**	0.367
FruitLength	0.399	0.691	0.116	−0.312	0.189	0.259	−0.295

The groups in the discriminant analyses are defined as: CDA1, the group of *P. acutifolius* vs. the rest of the material (Fig. 5); CDA2, the group of *P. manchuriensis* vs. the rest of the material (Fig. 6); CDA3, the groups of *P. compressus, P. henningii* and *P. zosteriformis* (Fig. 7); CDA4, the Eurasian (i.e. the groups of *P. compressus* and *P. henningii*) vs. North American material (i.e. the group of *P. zosteriformis*) (Fig. 8); CDA5, the group of *P. compressus* vs. merged groups of *P. henningii, P. manchuriensis* and *P. zosteriformis* (Fig. 9); CDA6, the groups of *P. compressus* and *P. henningii* (Fig. 10). CAN1, CAN2, the total canonical structure (expressing correlations of characters with the first and second canonical axes). Higher values are shown in bold type. For an explanation of the character acronyms, see Table 2.

FREQUENCY
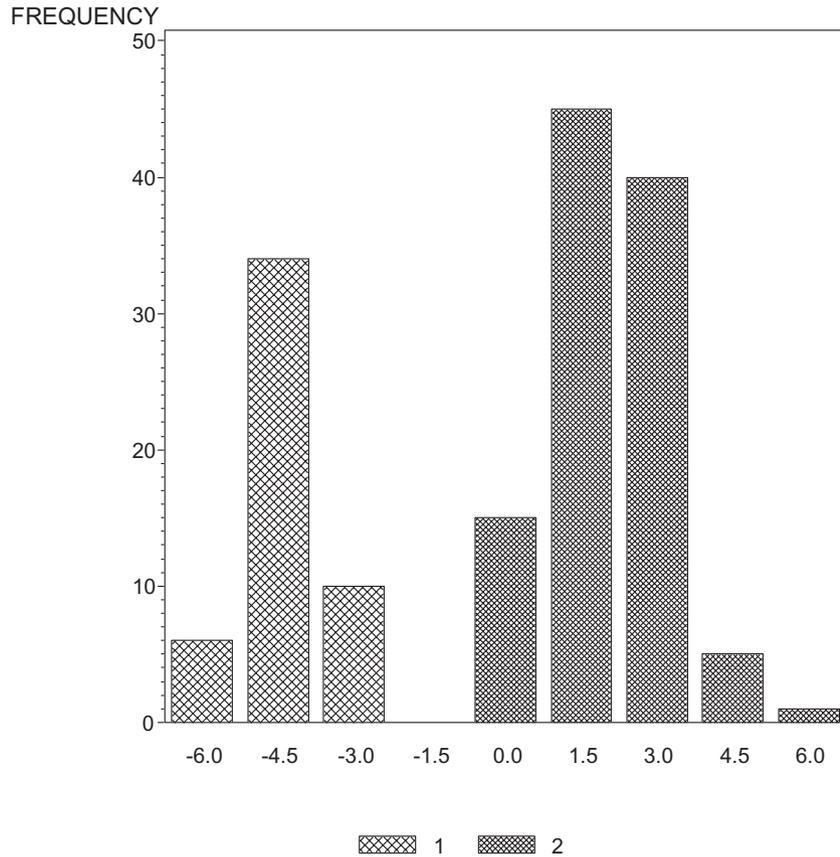
Figure 5. Canonical discriminant analyses of the *Potamogeton compressus* group based on ten morphological characters and the groups defined as: 1, the group of *P. acutifolius*; 2, rest of the material (see also Table 4: CDA1). The numbers on the *x* axis represent values of the discriminant function.

5th and 95th percentiles) calculated for each group of specimens resulting from the previous analyses are given in Table 5.

DISCUSSION

The results of the morphometric study show that the plant material of the *P. compressus* complex can be clearly divided across its range into three well-differentiated groups, corresponding to *P. acutifolius*, *P. manchuriensis* and the rest of the complex.

As expected, *P. acutifolius* was identified as the most distinct member in this complex. Within its range (temperate regions of Europe), it is partly sympatric with *P. compressus*. Morphological differentiation of these two species was revealed as straightforward, in accordance with empirical observations from the field and herbaria. Since their description almost two centuries ago, they have always been considered as separate species in innumerable European floras and floristic reports. They differ by a suite of characters, and fully fruiting specimens are easy to distinguish. Morphological characters, resolved in our

analyses as diagnostic, mostly corresponded to those reported by previous researchers (e.g. Hagström, 1916; Dandy, 1980; Preston, 1995; Wiegleb & Kaplan, 1998; Kaplan 2001b, 2010b). The number of flower whorls and the length of the fruiting spikes show distinct gaps between their variation ranges and there is only a small overlap in variation in peduncle length. However, identification in the vegetative state can be uncertain and misleading (Wiegleb, 1988; Wiegleb & Kaplan, 1998; Kaplan, 2001b, 2002b), although *P. compressus* is usually more robust than *P. acutifolius* and has longer and broader leaves.

Recent molecular studies confirmed the occurrence of interspecific hybrids between these two species, which are often difficult to identify unequivocally solely with morphological characters (Zalewska-Gałosz & Ronikier, 2010; Z. Kaplan & J. Fehrer, unpubl. data). In addition to morphology, the parental species are also well differentiated genetically (Lindqvist *et al.*, 2006; Zalewska-Gałosz & Ronikier, 2010; Fehrer & Kaplan, 2011), which may be the reason why their hybrids are completely sterile or, rarely, have only one or a few fruits in a spike. The
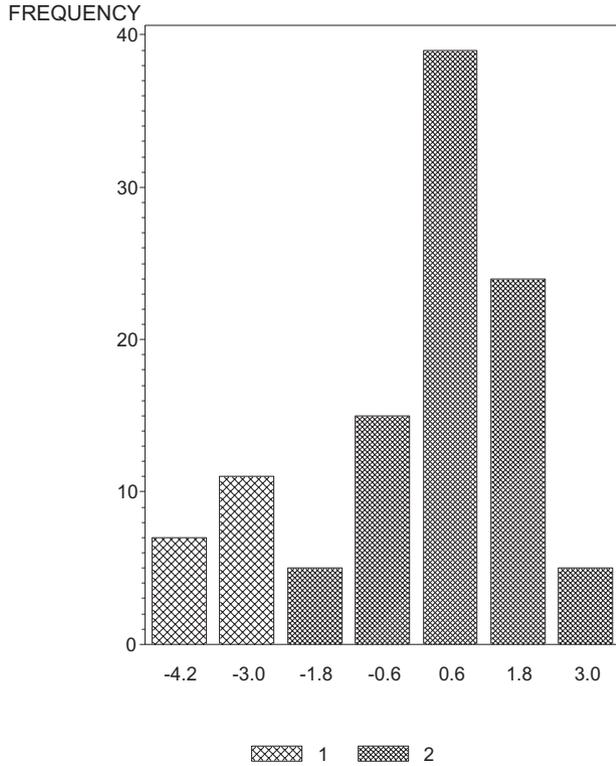
Figure 6. Canonical discriminant analyses of the *Potamogeton compressus* group based on ten morphological characters and the groups defined as: 1, the group of *P. manchuriensis*; 2, rest of the material (see also Table 4: CDA2). The numbers on the *x* axis represent values of the discriminant function.

hybrids are thus unlikely to have been included in our study that was based exclusively on fully fertile specimens. Both clear morphological and genetic differentiation, coupled with predominant sterility of interspecific hybrids, support the view that *P. acutifolius* and *P. compressus*, although similar in vegetative parts, are two separate species.

In addition to the diagnostic characters in generative organs, *P. acutifolius* also differs from all other species of the *P. compressus* group by having leaves with only three vascular veins (a midrib plus one pair of lateral veins), as opposed to five vascular veins in the others. However, this simple diagnostic character is not always easy to score on a specimen. The vascular veins can best be observed in old leaves that have lost the green pigment and have become yellowish or brownish. In these leaves, the sclerenchymatous strands are suppressed and often become entirely invisible. In contrast, the sclerenchymatous strands are best seen in younger fresh green leaves. In these leaves, however, the distinction between the strands and the veins is least apparent. The best way to score the number of sclerenchymatous strands

Table 5. Basic statistical parameters (minimum and maximum values, mean values, standard deviations, 5th and 95th percentiles) calculated for each group of specimens resulting from the morphometric analyses. For an explanation of the character acronyms, see Table 2

Taxon	Parameter	Length-Leaves	Width-Leaves	NoVeins	StemWidth	Stipule-Length	Pedunc-Length	Spike-Length	NoFlower-Whorls	NoCarpels	FruitLength
P. acutifolius, n = 50	Min–max	34–113	1.8–4.3	13–25	0.9–2.4	9–23	3–23	4–9	1.2–3.7	1.0–1.1	2.9–4.1
	Mean/stdev	64.94/16.860	2.854/0.590	17.72/2.483	1.582/0.306	14.84/3.899	7.84/3.334	5.68/1.151	2.26/0.500	1.002/0.014	3.55/0.314
	5%–95%	42–108	2.1–3.9	15–21	1.2–2.2	10–22	4.0–12.0	4.0–8.0	1.7–3.0	1.0–1.0	3.0–4.0
P. compressus, n = 56	Min–max	67–192	2.2–4.8	17–35	1.2–3.0	12–32	23–112	12–26	5.0–8.5	1.0–1.8	3.4–4.6
	Mean/stdev	125.27/26.193	3.495/0.718	24.61/4.062	1.991/0.409	21.46/4.906	46.93/16.144	17.91/2.919	6.60/0.714	1.11/0.186	3.88/0.244
	5%–95%	85–171	2.40–4.60	19–33	1.40–2.60	12.0–30.0	28.0–77.0	13–23	5.8–7.5	1.0–1.6	3.5–4.2
P. manchuriensis, n = 18	Min–max	59–127	1.6–2.3	9–19	0.9–1.5	10–24	18–55	10–22	5.0–6.0	1/0	3.1–3.8
	Mean/stdev	93.27/20.204	1.983/0.189	15.44/2.229	1.189/0.153	16.17/3.666	31.39/9.684	12.94/2.940	5.22/0.428		3.43/0.181
	5%–95%	59–127	1.6–2.3	9–19	0.9–1.5	10–24	18–55	10–22	5.0–6.0	1.0–1.0	3.1–3.8
P. zosteriformis, n = 32	Min–max	70–182	2.8–4.8	19–33	1.4–2.8	13–32	19–86	12–24	5.0–9.0	1.0–1.1	3.5–4.6
	Mean/stdev	124.38/25.898	3.625/0.485	25.06/3.715	2.05/0.336	21.62/4.989	43/14.969	18.53/2.652	7.20/0.919	1.00/0.018	3.93/0.269
	5%–95%	83–176	2.8–4.4	19–33	1.6–2.6	14–30	26–77	15–23	6.0–8.5	1.0–1.0	3.5–4.4
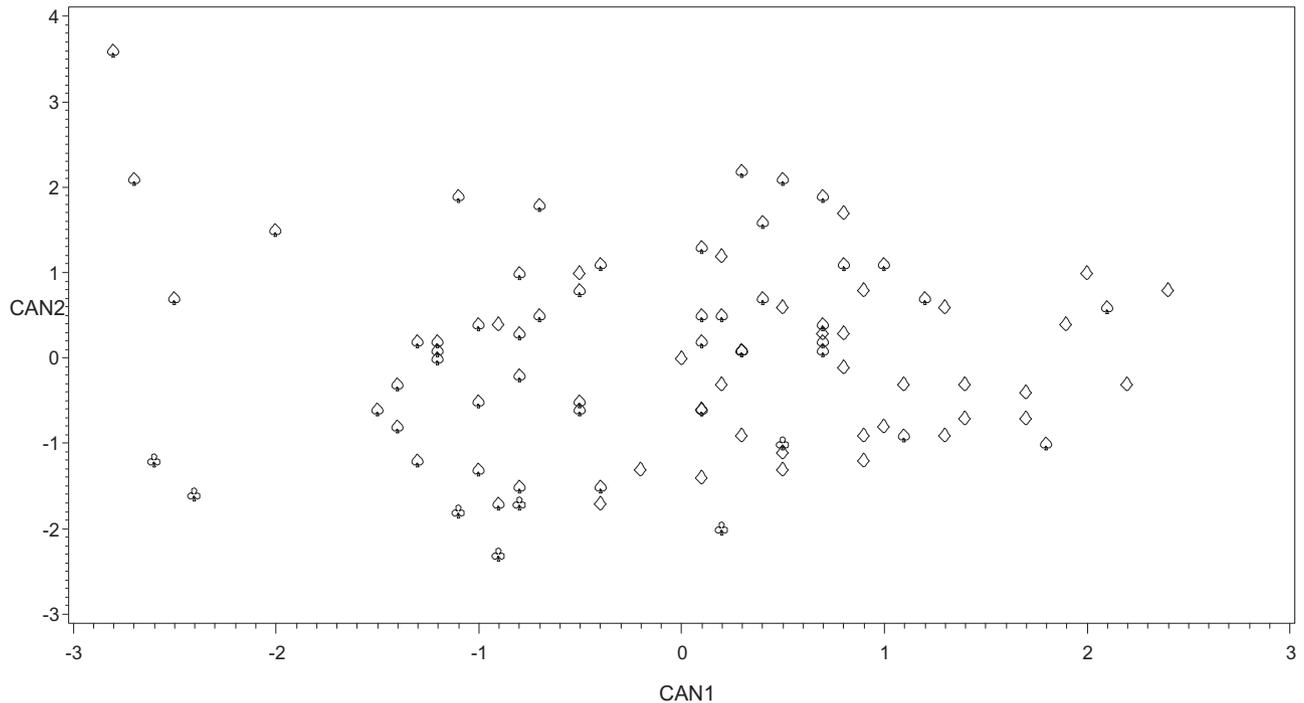
Figure 7. Canonical discriminant analyses of the *Potamogeton compressus* group based on ten morphological characters and the groups defined as: spade, the group of *P. compressus*; club, the group of *P. henningii;* diamond, the group of *P. zosteriformis* (see also Table 4: CDA3). The first two axes explain 55.7% and 8.0% of the variation among the groups, respectively. The numbers on the axes represent values of the discriminant function.

alone is therefore to count all longitudinal 'veins' in the green leaves and to subtract the number of vascular veins counted in the old leaves.

Plants somewhat similar to European *P. acutifolius*, but sampled in northeastern China and the Russian Far East, which were tentatively designated as *P. manchuriensis* here, proved to be morphologically clearly differentiated from both *P. acutifolius* and the rest of the complex. They resemble *P. acutifolius* in vegetative characters, such as the width of the leaves, number of observable 'veins' and width of the stem, but differ markedly in generative characters, such as the number of flower whorls and lengths of spikes and peduncles. This species is rarely represented in accessible herbaria, is still poorly understood and is rarely described in the available modern literature (notable exceptions being Tzvelev, 1987; Wiegleb & Kaplan, 1998; Guo *et al.*, 2010). No collection was available to the monographer Hagström, and that is why the description of this species was missing in his influential worldwide taxonomic study (Hagström, 1916). In spite of the clear morphological separation, *P. manchuriensis* is still sometimes incorrectly called '*P. acutifolius*' in the Chinese literature (e.g. Guo & Li, 1992). Although fresh material for molecular confirmation is not available, a unique combination of characters and clear morphological

differentiation lead us to consider *P. manchuriensis* as a separate species.

The North American vicariant form of the Eurasian *P. compressus* was distinguished by Fernald (1932) as a separate species under the name *P. zosteriformis*. He stated that his new species differed by a narrower stem, fewer lateral veins in leaves, less persistent stipules and larger, more quadrate fruits. However, the present study did not confirm consistent differences in the investigated characters of stem width, number of veins and fruit length. In contrast, the previously unrecorded characters number of flower whorls and number of carpels were strongly correlated with the canonical axis in the classificatory discriminant analysis.

The fruit shape used by Fernald was not included in the morphometric analyses because complex characters like this are difficult to score. However, our observations made on more than 200 herbarium collections indicate that no clear-cut differentiation between Eurasian and North American populations exists. Both extreme forms reported by Fernald (obliquely obovate vs. quadrately suborbicular) occur on both continents and are connected by all sorts of intermediates. As already pointed out by Wiegleb (1988), Fernald underestimated variation in fruit shape; nevertheless, his own plates show that fruit
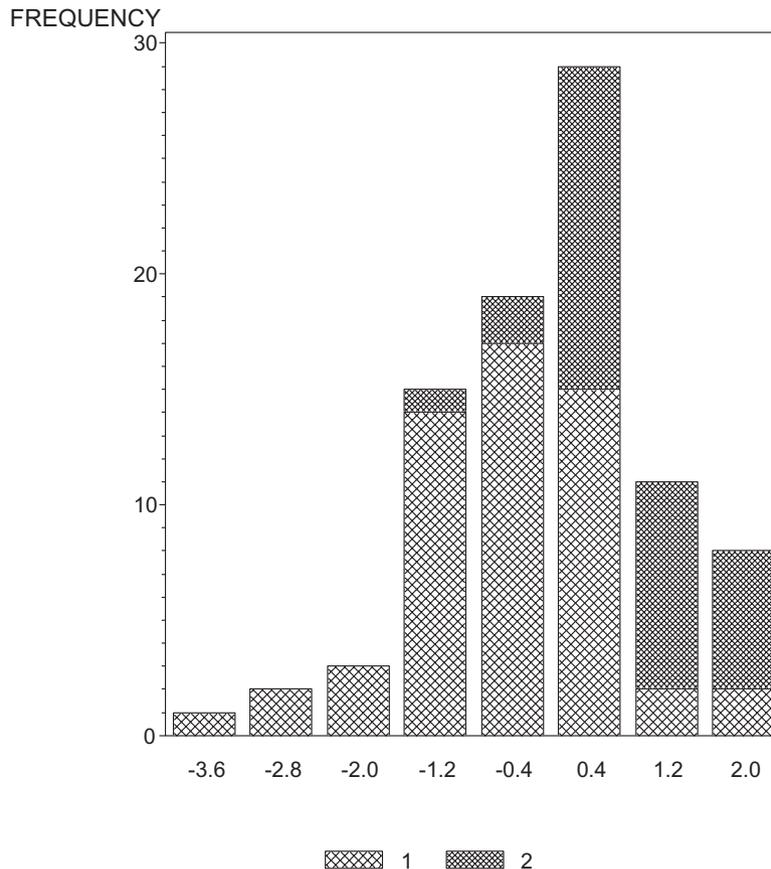
Figure 8. Canonical discriminant analyses of the *Potamogeton compressus* group based on ten morphological characters and the groups defined as: 1, Eurasian material (i.e. the groups of *P. compressus* and *P. henningii*); 2, North American material (i.e. the group of *P. zosteriformis*) (see also Table 4: CDA4). The numbers on the *x* axis represent values of the discriminant function.

shape and size display a great variation. Considerable variation in the shape of the fruit and in the position of the beak can occasionally be observed even within a single specimen. Similarly, no essential differences were observed in the persistence and texture of stipules. Their disintegration is a gradual process associated with their age and the growth of the stem, and is partly under environmental control.

In general, the morphological differentiation between *P. compressus* and *P. zosteriformis* is weak. Most morphological characters studied show considerable variation and extensive overlap. Only some tendencies in selected characters and differences in average values can be found; for example, *P. zosteriformis* has, on average, more whorls in a spike, and *P. compressus* tends to produce more frequently two fruits per flower, whereas *P. zosteriformis* has almost always only one (for similar observations for the consistently reduced carpel number in *P. zosteriformis*, see Posluszny, 1981). In general, it is difficult or impossible to assign a specimen to one or other species without a knowledge of its origin.

If these two forms occurred sympatrically and were genetically indistinguishable, we would not assign any taxonomic status to them, because they could not be readily distinguished. However, in our case, there is obvious differentiation at the molecular level associated with geographical differentiation. The studied samples of Eurasian *P. compressus* and North American *P. zosteriformis* consistently differ in sequences of several nuclear and plastid markers (Lindqvist *et al.*, 2006; Fehrer & Kaplan, 2011). The level of divergence in internal transcribed spacer (ITS) sequences between *P. compressus* and *P. zosteriformis* is comparable with that between other *Potamogeton* spp. (J. Fehrer & Z. Kaplan, unpubl. data).

This species pair may well represent a cryptic species complex. Neither form can be consistently distinguished morphologically, but, taking into account their genetic differentiation, which is perfectly correlated with geographical allopatry, it may be reasonable to follow their current treatment as separate species. Their allopatric ranges facilitate their identification, and that is why this concept does
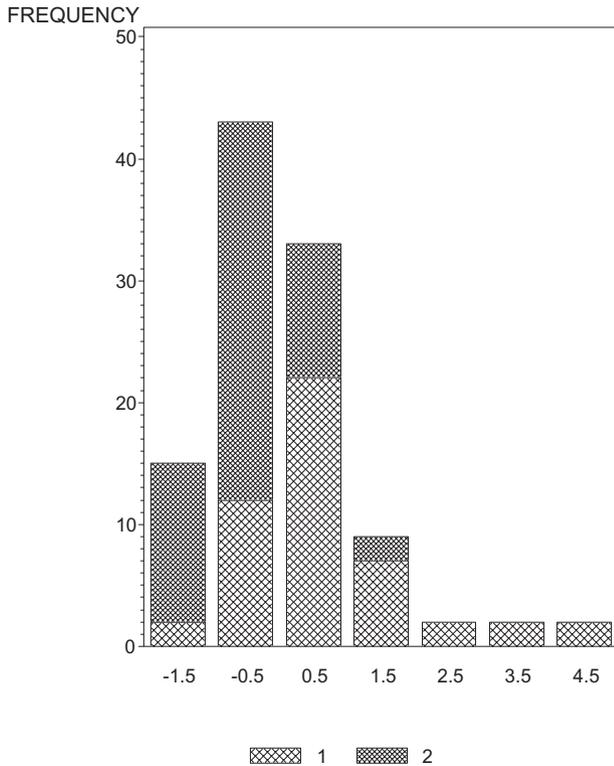
Figure 9. Canonical discriminant analyses of the *Potamogeton compressus* group based on ten morphological characters and the groups defined as: 1, the group of *P. compressus*; 2, merged groups of *P. henningii*, *P. manchuriensis* and *P. zosteriformis* (see also Table 4: CDA5). The numbers on the *x* axis represent values of the discriminant function.

Figure 10. Canonical discriminant analyses of the *Potamogeton compressus* group based on ten morphological characters and the groups defined as: 1, the group of *P. compressus*; 2, the group of *P. henningii* (see also Table 4: CDA6). The numbers on the *x* axis represent values of the discriminant function.

not threaten the practical aspect of systematics. Another advantage of this taxonomic solution is that the North American populations may maintain the currently well-established and frequently used name *P. zosteriformis* (e.g. Reveal, 1977; Hellquist & Crow, 1980, 1986; Hellquist & Hilton, 1983; Wiegleb, 1988; Wiegleb & Kaplan, 1998; Brayshaw, 2000; Haynes & Hellquist, 2000; Ceska, 2001).

At the moment, because of the vague morphological delimitation between *P. compressus* and *P. zosteriformis*, the exact border between their distribution ranges is uncertain, and a possible zone of geographical overlap should be considered. Genetic differentiation may well follow the separation between the continents, but this should be tested in future studies. More extensive sampling, particularly in eastern Siberia, the Russian Far East, Japan and Alaska, and detailed molecular and morphometric analyses, are necessary to identify the exact morphological and geographical delimitations of these species.

The last studied group was based on recent specimens identified as *P. henningii*. This is an obscure

taxon now distinguished by only a few Russian botanists. It had been almost forgotten for a long time before the name was resurrected by Volobaev (1993) and applied to slender plants of the *P. compressus* group from southern Siberia. It most resembles narrow-leaved forms of *P. compressus*. The morphological distinction between *P. compressus* and *P. henningii*, reported by Volobaev (1993), was not confirmed in our analysis. All characters showed perfect overlap, with variation ranges in *P. henningii* being narrower and placed within that of *P. compressus*.

Although these Siberian plants have a somewhat different appearance (particularly smaller leaves and slender stem) than the usual robust European plants of *P. compressus*, these differences are substantially blurred when all European material of this species is considered. Variation in Eurasian material of

P. compresus (incl. *P. henningii*) appears to be continuous and does not allow any clear separation of subgroups.

Plants recognized as *P. henningii* seem to be just slender phenotypes of *P. compressus*, being products of phenotypic plasticity, extreme forms of normal clinal variation or simultaneous results of both factors. The exact background of this morphological pattern remains to be resolved. In any case, phenotypes similar to *P. henningii* also occur occasionally in Europe, particularly in northern regions (Scandinavia, the Baltic region and northern European Russia), with similar habitats and climate, and they can be obtained in cultivation from typical broad-leaved plants of *P. compressus*. Similarly, the slender Siberian plants cultivated under the same conditions at the Experimental Garden in Průhonice, Czech Republic, produced phenotypes comparable in size and shape of leaves to some of the European plants. This indicates that at least part of the observed difference may be attributed to phenotypic plasticity. Field observation in Siberia and herbarium studies have revealed that several other *Potamogeton* spp. (mainly *P. friesii* Rupr., *P. alpinus* Balb. and *P. perfoliatus* L.) tend to produce slender and rather narrow-leaved forms in the Siberian environment in comparison with plants of the same species growing in temperate Europe with nutrient-rich and relatively warm water bodies.

Last, but not least, differentiation at the molecular level comparable with that revealed between *P. compressus* and *P. zosteriformis* was not found when European *P. compressus* was compared with a Siberian population corresponding to *P. henningii* (J. Fehrer & Z. Kaplan, unpubl. data). Because these Siberian populations cannot be consistently separated from narrow-leaved European populations, recorded morphological characters are under environmental control, the contrasting phenotypes have a largely sympatric distribution and no genetic differentiation was found in markers that usually show species-specific differences, we do not adopt the view that *P. henningii* is a separate species, and consider it to be a part of the variation of the widespread and variable *P. compressus*.

ACKNOWLEDGEMENTS

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