Distribution and synonymy of *Plagiochila punctata* (Taylor) Taylor, with hypotheses on the evolutionary history of *Plagiochila* sect. *Arrectae* (Plagiochilaceae, Hepaticae)

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Abstract. For a long time, *Plagiochila* (sect. *Arrectae*) *punctata* (Taylor) Taylor has been treated as an endemic of Atlantic Europe. Studies of larger specimen sets demonstrated that the species is widespread in mountainous regions of the Neotropics where it is known under several names including *P. stolonifera* Lindenb. & Gottsche, *P. choachina* Gottsche and *P. patzschkei* Steph. In tropical Africa *P. punctata* is established as *Plagiochila subalpina* Steph., nom. illeg. The sporophyte of *P. punctata* is described for the first time, based on material from Costa Rica. A maximum likelihood analysis of a nrITS sequence alignment with sequences of *P.* sects. *Fuscoluteae* (outgroup), *Arrectae*, and *Rutilantes* as well as of *P. rubescens* (Lehm. & Lindenb.) Lindenb. results in a tree with well bootstrap supported *Arrectae* and *Rutilantes* clades. ITS sequences of *Plagiochila punctata* from the Comoros and Zaire are placed in an unsupported monophyletic lineage together with *P. punctata* sequences from the British Isles and Ecuador. The species is nested in a robust clade with *P. spinulosa* (Dicks.) Dumort. and *P. stricta* Lindenb. The weak genetic separation of these three species indicates a recent diversification; the disjunct ranges may be the result of long range dispersal events. *Plagiochila rubescens* from southern South America is placed sister to *P.* sect. *Arrectae*. The latter section possibly originated from southern South American ancestors, diversified in tropical America after the uplift of the Andes and reached the Holarctics and tropical Africa by long range dispersal of diaspores.

Key words: Africa, biogeography, Europe, neotropics, *Plagiochila* sect. *Arrectae*, Plagiochilaceae.

Nowadays, bryophyte species are generally assigned to large ranges that often span several continents (e.g. Schofield and Crum 1972, Tan and Pócs 2000). This approach is based on the limited morphological variation of bryophyte populations from different regions which gives no reason for a division into taxa. However, homogeneous morphology has not always been an obstacle to splitting populations into different binomials. Especially in the second half of the nineteenth, and the first decades of the twentieth century, numerous names were proposed because of the exotic origin of a specimen rather than morphological differences.

Contrary to the trend, the so called "geographical species concept" was in use for *Plagiochila* until recently. The tradition of

describing *Plagiochila* taxa with small ranges and at best minor morphological differences (e.g. Inoue 1987) may be explained by the poorness of stable morphological characters within the genus and study of only limited numbers of specimens. Study of larger numbers of specimens usually makes a good case for application of wider species concepts and often results in range extensions of assumed endemics (e.g. Heinrichs et al. 2000, Heinrichs 2002).

Originally, *Plagiochila* sect. *Arrectae* Carl (Carl 1931) was set up for a somewhat heterogeneous neotropical species group [*Plagiochila subviminea* Steph. is now known as *Adelanthus lindenbergianus* (Lehm.) Mitt., see Grolle (1972)]. Carl (1931) characterised the section as having laterally appressed small-celled leaves and teeth usually restricted to leaf apex and ventral margin. Recent morphological, phytochemical and molecular investigations demonstrated that the majority of binomina accepted by Carl (1931) should be placed in the synonymy of a few broadly defined species (e.g. Heinrichs et al. 1998, 2004a). The new synonymies led also to range extensions of originally Neotropical *Arrectae* species to Atlantic Europe [*P. bifaria* (Sw.) Lindenb., *P. papillifolia* Steph., *P. retrorsa* Gottsche, *P. stricta* Lindenb., overview in Groth et al. (2003)]. *Plagiochila stricta* is now also known from tropical Africa (Lindner et al. 2004); *P. retrorsa* from the Appalachian Mountains of the United States (Rycroft et al. 2001). Hence *P. spinulosa* (Dicks.) Dumort. and *P. punctata* (Taylor) Taylor remain the only members of *P.* sect. *Arrectae* that are restricted to Europe (e.g. Paton 1999, Damsholt 2002).

Initially, *P. punctata* was the only European member of the Neotropical *P.* sect. *Choachinae* Carl (1931), a group treated as a synonym of *P.* sect. *Arrectae* by Heinrichs (2002). Carl (1931) already discussed similarities between *P. punctata* and *P. choachina* Gottsche from tropical America. Jones (1962) drew attention to similar phenotypes in tropical Africa; Pócs (1993: 110) emphasised that

this species group "badly needs a revision". Here we present the results of a morphological and molecular investigation of *P. punctata* and related taxa from tropical Africa and America.

Materials and methods

Morphological investigation. The morphological investigation is based on more than 300 specimens of *Plagiochila* sect. *Arrectae* from the herbaria BOL, EGR, F, FLAS, G, GOET, JE, INB, LPB, MO, NY, RB, S, STR, U, W as well as identified and unidentified African *Plagiochila* materials from EGR, GOET and the private herbaria of Eberhard Fischer and Volker Buchbender (Koblenz, Germany).

Molecular investigation. Upper parts of a few shoots of the specimens *Holz & Franzaring CH-00-45*, *Pócs et al. 9270/J & 7193* and *Rycroft 020723-6* (Table 1) were isolated. Genomic DNA was extracted using a modified CTAB method with Quiagen tip 20 columns, following Hellwig et al. (1999; specimen *Holz & Franzaring CH-00-45*) or with Invisorb Spin Plant Mini Kit (Invitec, Berlin, Germany; other specimens). PCR-amplification and sequencing followed the protocols described in Heinrichs et al. (2002b; specimen *Holz & Franzaring CH-00-45*) or Heinrichs et al. (2004b; other specimens).

The new nrITS sequences were compared with GenBank sequences using the BLASTN program (Altschul et al. 1997) and put into a large alignment of Plagiochilaceae ITS sequences. In all cases sequences of members of *Plagiochila* sect. *Arrectae* Carl were identified as most similar to the new sequences (data not shown). Based on these results, representatives of *Plagiochila* sect. *Arrectae* and its previously established sister section, *P.* sect. *Rutilantes* Carl (e.g. Groth et al. 2002, 2003; Heinrichs 2002a), were sampled. *Plagiochila aerea* Taylor and *P. fuscolutea* Taylor (*P.* sect. *Fuscoluteae* Carl) were chosen as outgroup, according to the results of Groth et al. (2003).

Thirty two ITS1-, 5.8S-, and ITS2 sequences from Heinrichs (2002), Heinrichs et al. (2002a, 2004a, 2004b), Groth et al. (2002, 2004a), Lindner et al. (2004), one *P. stricta* sequence from GenBank (AY438586) and the new sequences (Table 1) were aligned manually in BioEdit version 5.0.9 (Hall 1999), resulting in an alignment including 761 putatively homologous sites (alignment available

Table 1. Geographic origins, vouchers (collector and collection number), and GenBank/EMBL accession numbers of the taxa investigated. Vouchers are deposited at GOET unless indicated otherwise

Taxon	Origin	Voucher	Accession number
P. aerea Taylor	Costa Rica	*Heinrichs et al. 4321*	AJ422028
P. bidens Gottsche	Brazil	*Gradstein 5378* (G)	AF539458
P. bifaria (Sw.) Lindenb.	Tenerife	*Drehwald 3922*	AJ413173
P. bifaria (Sw.) Lindenb	British Isles	*Rycroft 01014*	AY453387
P. bifaria (Sw.) Lindenb.	Brazil	*Costa & Gradstein 3805*	AY453388
P. bifaria (Sw.) Lindenb.	Costa Rica	*Heinrichs et al. 4394*	AY453389
P. bifaria (Sw.) Lindenb.	Ecuador	*Holz EC-01-113*	AJ422011
P. bifaria (Sw.) Lindenb.	Ecuador	*Holz EC-01-416*	AJ422010
P. bifaria (Sw.) Lindenb.	Bolivia	*Heinrichs et al. 4402*	AY453390
P. bifaria (Sw.) Lindenb.	Bolivia	*Heinrichs et al. 4069*	AJ620673
P. bifaria (Sw.) Lindenb.	Bolivia	*Heinrichs et al. 4076*	AJ620674
P. bifaria var. *rosea* (R.M.Schust.) J. Heinrichs	Venezuela	*Pócs et al. 9714/K*	AJ620672
P. cuneata Lindenb. & Gottsche	Bolivia	*Heinrichs et al. 4093*	AF539460
P. deflexa Mont. & Gottsche	Costa Rica	*Heinrichs & al. 4160*	AJ416083
P. exigua (Taylor) Taylor	Ireland	*Hakelier s.n.*	AF539461
P. fuscolutea Taylor	Costa Rica	*Heinrichs & al. 4400*	AJ416086
P. gymnocalycina (Lehm. & Lindenb.) Mont.	Bolivia	*Drehwald & Drehwald 4729*	AY390531
P. punctata (Taylor) Taylor	British Isles	*Rycroft 01013*	AJ413174
P. punctata (Taylor) Taylor	Ecuador	*Holz EC-01-389*	AJ422018
P. punctata (Taylor) Taylor	Comoros	*Pócs et al. 9270/J*	AJ781749
P. punctata (Taylor) Taylor	Zaire	*Pócs et al. 7193*	AJ781750
P. retrorsa Gottsche	Costa Rica	*Heinrichs & al. 4154*	AJ422021
P. rubescens (Lehm. & Lindenb.) Lindenb.	Chile	*Holz & Franzaring CH-00-45*	AJ781751
P. rubescens (Lehm. & Lindenb.) Lindenb.	Chile	*Rycroft 020723-6*	AJ 781752
P. rutilans Lindenb. var. *moritziana* (Hampe) J. Heinrichs	Ecuador	*Holz EC-01-404*	AJ416080
P. rutilans Lindenb.	Bolivia	*Groth 101*	AJ416081
P. rutilans Lindenb. var. *standleyi* (Carl) J. Heinrichs & D.S. Rycroft	Ecuador	*Holz EC-01-499*	AJ416079
P. spinulosa (Dicks.) Dumort.	British Isles	*Rycroft 01012*	AJ413175
P. spinulosa (Dicks.) Dumort.	Belgium	*Dauphin et al. 3811*	AY275173
P. steyermarkii H.Rob.	Venezuela	*Steyermark et al. 112531*	AF539465
P. stricta Lindenb.	Costa Rica	*Heinrichs et al. 4401*	AJ416646
P. stricta Lindenb.	Ecuador	*Holz EC-01-478*	AJ416647
P. stricta Lindenb.	Madagascar	*Pócs et al. 9868/AF*	AJ633128
P. stricta Lindenb.	Madeira	*Sim Sim s.n.* (LISU)	AY438586
P. stricta Lindenb.	Tenerife	*Drehwald 3920*	AJ416649
P. stricta Lindenb.	Tenerife	*Rycroft 01071*	AJ416648
P. trichostoma Gottsche	Costa Rica	*Heinrichs et al. 4324*	AJ416028

from JH). The parts lacking of some sequences were coded as missing.

Phylogenetic trees were inferred using maximum likelihood (ML) criteria as implemented in PAUP* version 4.0b10 (Swofford 2000). To decide on the nucleotide substitution model with the smallest number of parameters that best fits the data, the program Modeltest 3.06 (Posada and

Crandall 1998) was used. Based on the results of the tests, the model selected by the hierarchical LRT was the HKY85 model (Hasegawa et al. 1985) with gamma shape parameter (G) for among site variation calculated from the data set (HKY85 + G). A ML analysis (with the HKY85 + G model) was implemented as heuristic search with 10 random-addition sequence replicates. The confidence of branching was assessed using 200 bootstrap resamplings in ML-analysis (Felsenstein 1985, Hillis and Bull 1993).

Results

The ML analyses resulted in two optimal topologies (−ln = 4375.2833) which differed only minutely in branch length. Hence, only one topology is depicted in Fig. 1. The ingroup is resolved into two robust clades assignable to *P*. sects. *Arrectae* and *Rutilantes*. A well supported clade of two accessions of *P. rubescens* from Chile is placed sister to *P.* sect. *Arrectae* in a robust sister relationship. Branches within the *Rutilantes* clade are longer than within the *Arrectae* clade. The *Arrectae* species form a largely polytomous topology. Ten accessions of *P. bifaria* are placed in a well supported monophyletic lineage and are sister to a robust clade with accessions of *P. spinulosa*, *P. stricta* and *P. punctata* s. l.; the sister relationship is not supported. The genetic distances between *P. spinulosa*, *P. stricta* and *P. punctata* s.l. are very small. The monophyly of *P. spinulosa* achieves good bootstrap support. *Plagiochila stricta* accessions from Costa Rica, Ecuador, Madagascar, Madeira, and Tenerife form a polytomous clade with robust Neotropical and Macaronesian subclades. A *Plagiochila punctata* accession from the British Isles is placed in an unsupported monophyletic lineage with an accession from Ecuador (previously determined as *Plagiochila patzschkei* Steph.) and accessions from the Comoros and Zaire (assigned to *P. subalpina* Steph., nom. illeg.). A sister relationship of the accessions from Zaire and Ecuador achieves good support.

The weak molecular separation of the above taxa supports a broader circumscription of *P. punctata* and leads to the following synonymy:

Plagiochila punctata (Taylor) Taylor, London J. Bot. 5: 261. 1846. *Jungermannia punctata* Taylor, Trans. Bot. Soc. Edinburgh 1: 179. "1844" 1843. Type: Ireland (not seen).

= *Plagiochila stolonifera* Lindenb. & Gottsche, in Gottsche, Lindenb. & Nees, Syn. Hep.: 655. 1847. Type: Mexico, Sempoaltepec, *Liebmann 195* (lectotype, here designated, W hb. Lindenb. 921).

= *Plagiochila choachina* Gottsche, in Triana & Planchon, Ann. Sci. Nat., Bot. (ser. 5) 1: 95. 1864. Type: Colombia, Bogotá, Choachi, 2600 m, 1860, *Lindig 1725* p.p. (isotype, G [ster., Lindig s.n., hb. Stephani "Bescherelle ex Museo Paris"]).

= *Plagiochila subalpina* Steph., Hedwigia 30: 268. 1891, nom. illeg. [Art. 64.1 ICBN], non *P. subalpina* (Nees ex Lindenb.) Mont. & Nees. Type: Tanzania, Kilimandscharo, 1889, 3000 m, *Meyer "429"* (holotype, G 003776 [ster.]).

= *Plagiochila denudata* Steph., Spec. Hep. 2: 549. 1905. Type: Brazil, Apiahy, *Puiggari 2093* (lectotype, here designated, G [male, soc. *Plagiochila bifaria* (Sw.) Lindenb.]); ibid., *Puiggari 769b* (paralectotype, G [ster.]).

= *Plagiochila jaapii* Steph., in Herzog, Biblioth. Bot. 87 (2): 201. 1916: Type: Bolivia, Comarapa, *Herzog 4256* (holotype, G [ster.]).

= *Plagiochila lacouturei* Steph., in Herzog, Biblioth. Bot. 87 (2): 203. 1916: Type: Bolivia, Comarapa, *Herzog 4201* (holotype, G [ster.]).

= *Plagiochila patzschkei* Steph., in Herzog, Biblioth. Bot. 87 (2): 207. 1916: Type: Bolivia, Comarapa, *Herzog 4246* (holotype, G [ster.]; isotype, JE [ster.]).

Plants in mats or intermingled with other bryophytes, to ca. 5(7) cm long with leafy shoots to ca. 3 mm wide. Leafy stems dorsoventrally flattened, to ca. 400 μm in diameter, with a 1–5 cells thick cortex and a 3–14 cells
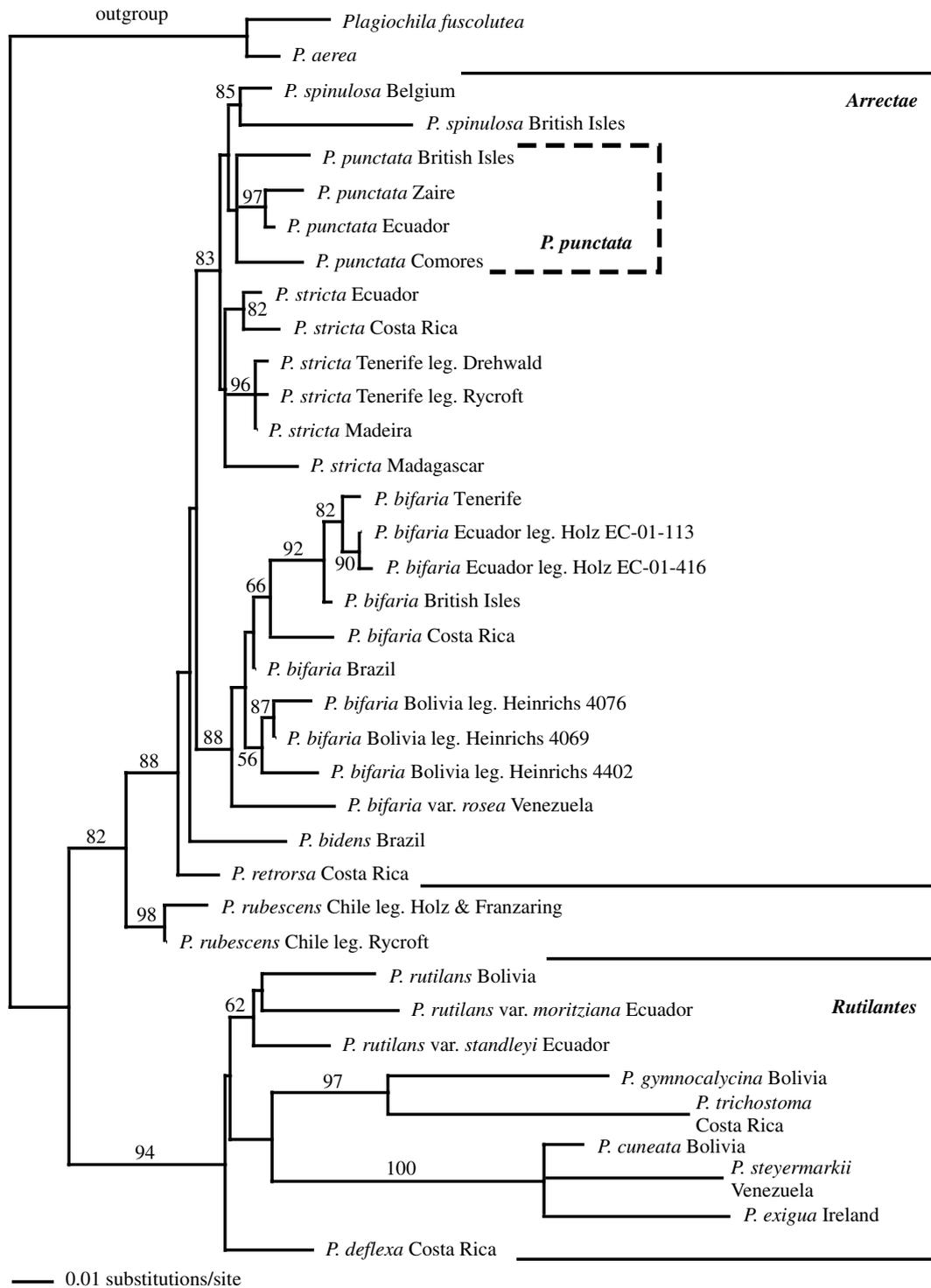
Fig. 1. Molecular phylogeny of *Plagiochila* species based on nrDNA ITS1-5.8S-ITS2 sequence comparisons using 761 aligned positions. The rooted tree ($-\ln = 4375.2833$) resulted from a maximum likelihood analysis of 37 sequences (including the outgroup sequences), using the HKY + G model with estimated gamma shape (G = 0.53), calculated as the best model by Modeltest 3.06 (Posada and Crandall 1998); bootstrap percentage values (> 50%) were determined for maximum likelihood
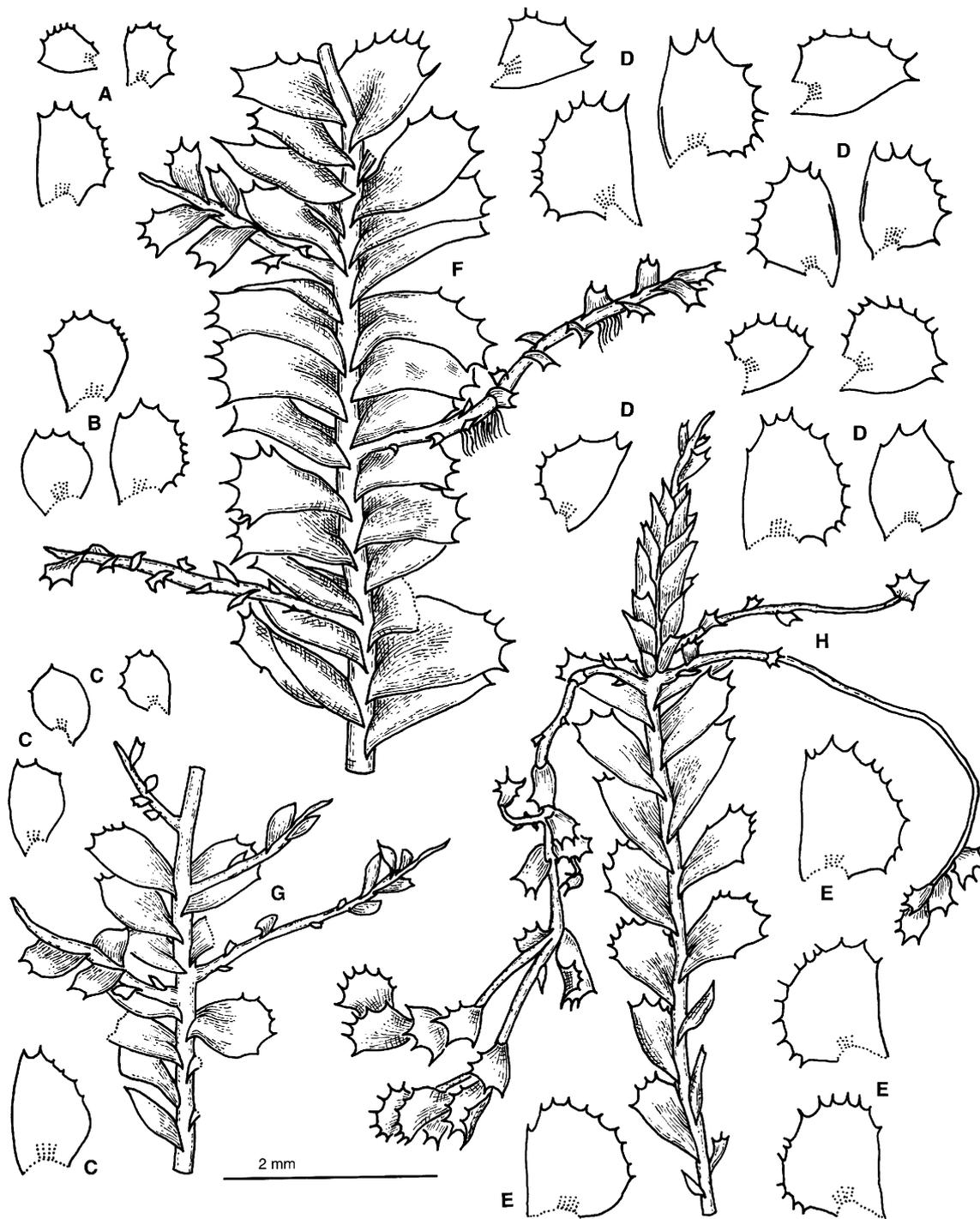
Fig. 2. *Plagiochila punctata* (Taylor) Taylor. **A-E**, leaves; **F**, **G**, parts of shoots, dorsal view; **H**, part of male shoot with androecium, dorsal view [**A** from isotype of *P. choachina* Gottsche (G), **B** from Zaire, *Pócs* et al. 7193 (EGR), **C**, **G** from Comoro Archipelago, *Pócs* et al. *9270/J* (EGR), **D**, **F** from British Isles, *Rycroft 01013* (GOET)], **H** from lectoype of *P. denudata* Steph.]
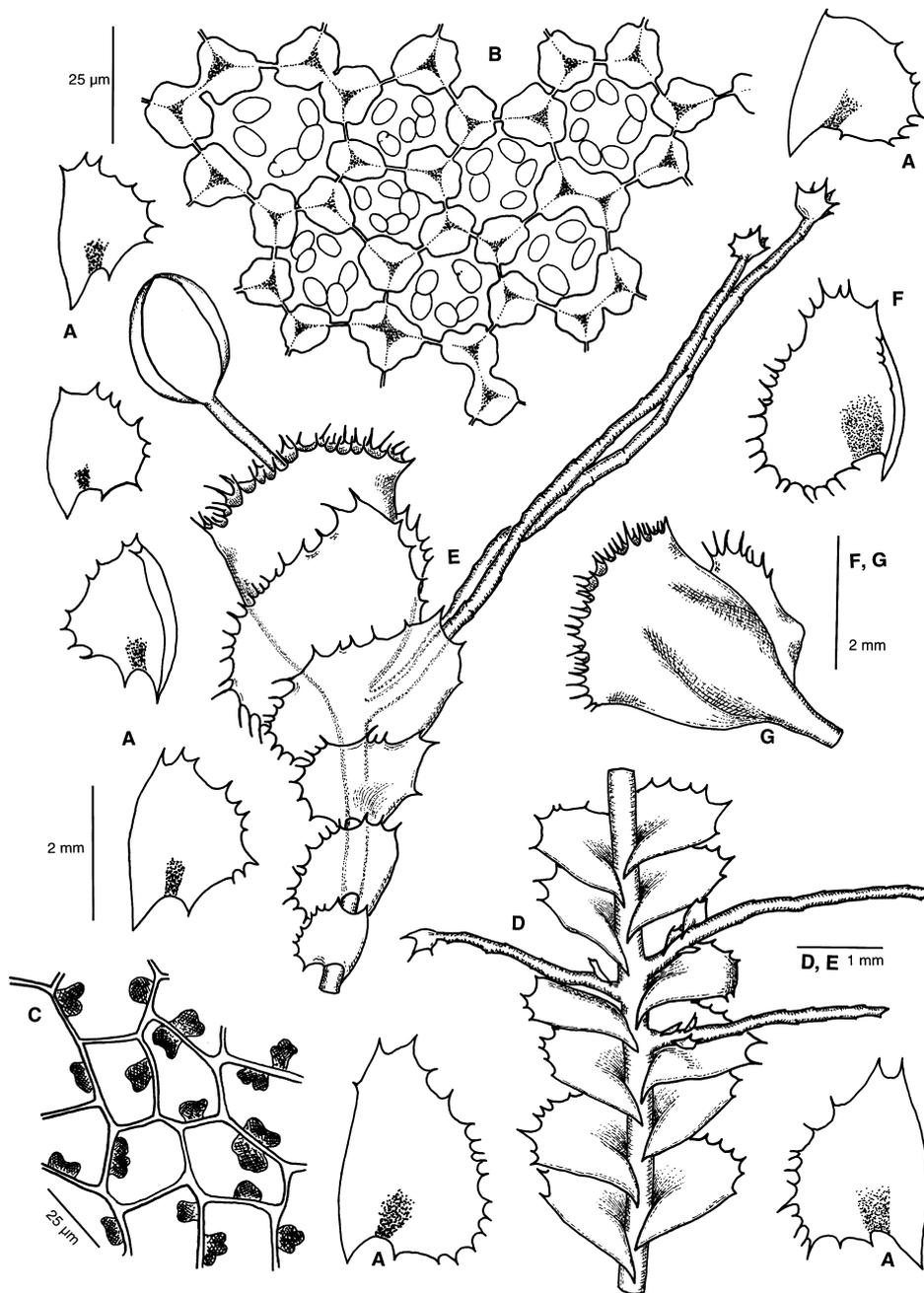
Fig. 3. *Plagiochila punctata* (Taylor) Taylor. **A** leaves, **B** leaf cells with oil bodies; **C** cells from capsule wall epidermis, surface view; **D** part of shoot, dorsal view; **E** top of shoot with sporophyte, lateral view; **F** female bract; **G** perianth with dorsal wing [all from *Heinrichs* et al. *4174* (GOET)]

thick medulla. Branches of the lateral-intercalary type, often flagelliform, moderately to frequently present, sometimes very numerous, giving the plant a feather like habit, occasionally only flagelliferous shoots present. Leaves remote to imbricate, partly caducous (especially on branches), leaving parts of stem bare; erecto-patent to obliquely or widely spreading,

both dorsally and ventrally at most shortly decurrent, variable in shape, broadly and asymmetrically ovate, obovate or suborbicular, with broadly rounded to subtruncate apex, ca. (0.7−)0.9–1.2(−1.4) times as long as wide, dorsal leaf margin entire or with a single tooth, apex and ventral margin with 2–16 triangular to ciliate, straight or curved teeth, apical teeth sometimes coarser than teeth from ventral margin, broadly triangular to elongate triangular. Leaf cells slightly broader than long to moderately elongate with diameters of ca. 18–32(−40) μm, leaf base usually with a short, ill-defined vitta; trigones usually large, nodulose, often confluent; cuticle smooth to indistinctly papillose, especially at leaf margins. Oil bodies 3–8 in ± isodiametric cells, homogeneous to indistinctly coarsely segmented. Underleaves vestigial, consisting of a few cells only. Androecia on main shoots and on branches, simple, becoming intercalary, bracts in 5–12 pairs, opposite bracts not or only weakly overlapping dorsally. Gynoecia terminal, often with 1–2 innovations, bracts larger than the subtending leaves, with a more prominent, broader vitta, often toothed all around. Perianths campanulate to broadly cylindrical, to ca. 3 mm long, mouth arched upwards, densely toothed by elongate triangular to ciliate teeth, often with a toothed dorsal wing. Capsule (described from *Heinrichs et al. 4174*) short-exserted, subglobose, valves ca. 1.3–1.8 × 0.6–0.9 mm, brown, not twisted; epidermal cells in surface view shorter than broad to moderately elongate, towards base of valve more elongate, with 1(−2) large nodulose, in surface view often somewhat branched thickenings on many walls; innermost cells in surface view elongate, irregular, with thickenings on the longitudinal and a few transverse walls, opposite thickenings of longitudinal walls sometimes connected by ± slender coalescences on the radial walls or thickenings nodulose to cone-like, discrete; valves in cross section ca. 70–90 μm thick, 6–8-stratose, epidermal cells slightly larger than inner ones, ca. 16–25(−30) μm thick, inner cells ca. 6–16 μm thick. Spores ca. 21–27 μm, globose, 1-cellular, sporoderm baculate. Elaters ca. 8–10 μm thick, unispiral, covered by granulae.

Selected specimens examined:

AFRICA – COMORO ARCHIPELAGO. NGAZIDJA ISLAND: Karthala volcano, 1860 m, 1992, *Pócs et al. 9270/J* (EGR, GOET). **MADAGASCAR.** Mt. Andrianavibe, 5 km ESE of Andasibe, 950–1050 m, 1994, *Szabo 9487/BW* (EGR). **TANZANIA.** KILIMANJARO: way Marangu to Mandara Hut, 2200 m, 1971, *Jones & Pócs 6365/N* (G 210155). **UGANDA.** RUWENZORI: 4200 m, 1932, *Hauman 898* (G 003777). **ZAIRE.** KIVU: Mt. Biega, 2700 m, 1991, *Pócs 7193* (G 434466). **AMERICA – COSTA RICA.** CARTAGO: 1500 m, 1900, *Werckle s.n.*, Bryotheca Levier 6275 (G). **DOMINICAN REPUBLIC.** LA VEGA: Arroyo Prieto, 1100 m, 2003, *Pócs 03171/O* (EGR, GOET). **VENEZUELA.** MÉRIDA: P.N. de Sierra Nevada, 2600 m, 1995, *Kelly et al. 10860c* (GOET). **ECUADOR.** ZAMORA-CHINCHIPE: San Francisco research station, 1800-1850 m, 2001, *Holz EC-01-389* (GOET). **BOLIVIA.** CHUQUISACA: Hernando Siles, 1170 m, 1984, *Lewis 84-919* (F, GOET, LPB). **EUROPE – BRITISH ISLES.** SCOTLAND: West Perth, The Trossachs, 205 m, 2001, *Rycroft 01013* (GOET). **SPAIN:** TENERIFE: Montañas de Anaga, 900 m, 1999, *Drehwald 990357* (GOET).

Throughout the tropics, *P. punctata* is restricted to mountainous regions. In Europe, the species occurs from the lowlands to ca. 1000 m. Plants with a feather-like habit are more common in the tropics than in Europe. The leaves of some African phenotypes are in all slightly smaller than those typically found in *P. punctata*. *Plagiochila punctata* is morphologically close to *P. spinulosa*, *P. stricta*, and *P. pseudo-attenuata* S. Arnell. However, *P. spinulosa* (Paton 1977) and *P. pseudo-attenuata* (type BOL!, Arnell 1962) differ by the partly long decurrent ventral leaf base; *P. stricta* has more triangular leaves and is usually distinctly papillose (Rycroft et al. 2002).
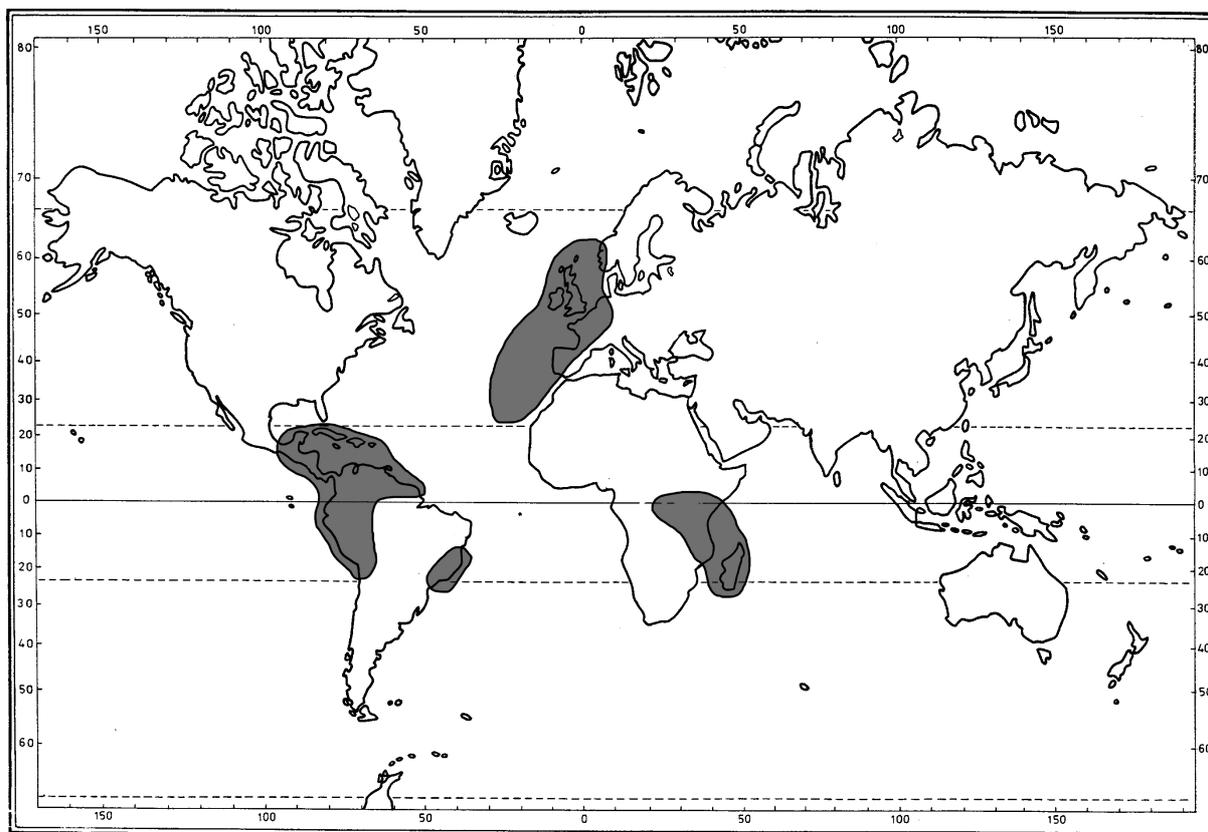
Fig. 4. Distribution of *Plagiochila punctata* (Taylor) Taylor

Discussion

Homogeneous morphology does not necessarily mean genetic congruence. Several studies of fast evolving molecular markers of bryophyte morphospecies with broad geographic ranges revealed phylogenetic structure at species level (e.g. *Bryum argenteum*, Longton and Hedderson 2000; *Claopodium whippleanum*, *Dicranoweisia cirrata*, *Scleropodium touretii*, Shaw et al. 2003; *Hylocomium splendens*, Chiang and Schaal 1999; *Pyrrhobryum mnioides*, McDaniel and Shaw 2003; *Symphyogyna hymenophyllum*, *S. podophylla*, Schaumann et al. 2003, *Plagiochila* div. spec., Heinrichs et al. 2003, 2004b; Renker et al. 2002; Rycroft et al. 2002). Several morphospecies actually proved to be poly- or paraphyletic in molecular trees (e.g. *Mielichhoferia mielichhoferiana*, Shaw 2000, *Fontinalis* div. spec., Shaw and Allen 2000, *Hygrohypnum smithii*, Stech and Frahm 2001; *Hygroamblystegium tenax*, Van-

derpoorten et al. 2001, 2003). These findings indicate the necessity to test morphological species concepts with molecular markers. However, maximum likelihood analyses of *Plagiochila* ITS datasets supported hypotheses based on morphological analyses (e.g. Groth et al. 2003). Furthermore in this case, a morphological phenotype continuum forms a monophyletic lineage in an ITS topology, leading to a range extension (Fig. 4) and broad synonymy of an originally European species, *Plagiochila punctata*. However, it must be said that the monophyly of *P. punctata* depends on the taxon sampling and that the species concept presented here is also the result of a morphological investigation. Earlier ML analyses of ITS variation utilising only the European and the Ecuadorian *P. punctata* sequences resolved a monophyletic lineage (Heinrichs 2002, Groth et al. 2004a, Heinrichs et al. 2004b) or lead to a paraphyletic topology

(Heinrichs et al. 2004a). Obviously *Plagiochila punctata*, *P. spinulosa* and *P. stricta* are the result of a recent radiation and the variation of the ITS region does not provide enough signal to separate the species clearly.

Plagiochila punctata belongs to the largest natural species group of *Plagiochila* in Europe, *P.* sect. *Arrectae* (e.g. Groth et al. 2003). Neotropical-Atlantic European disjunctions seem to be typical for representatives of this group. Their occurrence in tropical Africa has recently been demonstrated by the detection of the Neotropical-Atlantic European *Plagiochila stricta* on Madagascar (Lindner et al. 2004). Accordingly, *Plagiochila punctata* is the second species of *P.* sect. *Arrectae* which occurs both in tropical America and Africa as well as in atlantic Europe. A third *Plagiochila* species with a tropical American-African range is *Plagiochila boryana* Steph. of *P.* sect. *Hylacoetes* Carl (Heinrichs 2002, Groth et al. 2003).

The very similar ITS sequences of disjunct *Arrectae* specimens (Rycroft et al. 2002, Heinrichs et al. 2004a) can best be explained by relatively recent divergence subsequent to continental drift. However, although the *Arrectae* are obviously able to build up disjunct ranges by long range dispersal of diaspores, they seem to be restricted to tropical America, Africa, and the Holarctics. Morphologically similar species groups from southern South America and New Zealand (*P.* sect. *Durae* Carl) or from Asia and western North America (*P.* sect. *Peculiares* Schiffn.) form separate clades in analyses of cp *rps*4 and nrITS datasets (Groth and Heinrichs 2003, Groth et al. 2004b).

Surprisingly, *Plagiochila rubescens*, a species from southern South America with unclear sectional affiliation, is placed sister to *P.* sect. *Arrectae*. Leaves and oil bodies of *P. rubescens* are more similar to those of *P. cristata* (Sw.) Lindenb. of *P.* sect. *Adiantoideae* Lindenb. (Heinrichs 2002) than to those of members of sect. *Arrectae*; the sporophyte as well as the secondary metabolite pattern are still unknown. Accordingly, incorporation of

P. rubescens in sect. *Arrectae* seems premature. However, the molecular topology provides some indication on the origin of *P.* sect. *Arrectae*: the sister relationship of *P.* sect. *Arrectae* and *P. rubescens* points at a possible derivation of *Arrectae* species from Southern South American ancestors. The highest diversity of *P.* sect. *Arrectae* is found in tropical America, where the group is restricted to mountainous regions. Prior to the late Miocene uplift of the Andes this region was presumably dry (Parrish 1990) whereas southern South America was colonised by moist forests and surely settled by *Plagiochila* species. Tropical Africa and the Holarctics with their less diverse *Arrectae* spectrum were possibly colonised by long range dispersal events originating from Neotropical populations. This dispersion scenario is displayed in Fig. 5.

The *Arrectae* and *Rutilantes* topologies in the molecular tree differ considerably. The well resolved *Rutilantes* clade may be explained by a gradual accumulation of diversity. In contrast, the *Arrectae* species branch off from a largely polytomous clade, indicating a rapid diversification which could be correlated with the rise of the Andes. Sudden diversifications
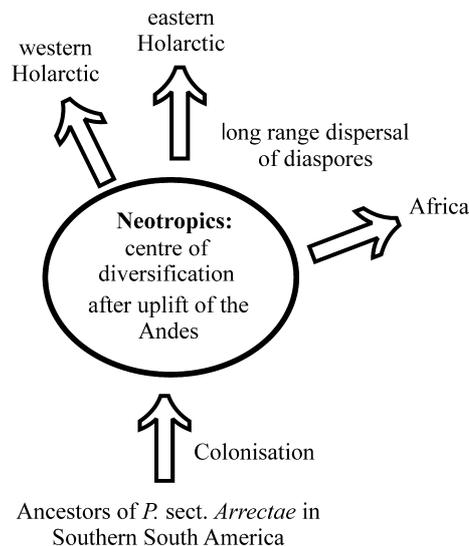

Fig. 5. Possible dispersal scenario of *Plagiochila* sect. *Arrectae* Carl

of Neotropical groups have also been proven for cormophytes, e.g. for the genus *Inga* (Richardson et al. 2001).

About 30 years ago, Inoue (1976: 16) stated that "many species of *Plagiochila* are highly local endemics". Recent research has usually disproved this dictum. Local endemics are actually rather the exception within this largest genus of hepatics.

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