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Article

Gymnostomiella (Pottiaceae, Bryophyta) revisited: new insights revealed by a morphometric analysis

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With 4 figures, 3 tables and 1 appendix

Abstract: A morphometric analysis of the five accepted species of the moss genus *Gymnostomiella* is presented, including *G. orcutii* and *G. tanganyikae*, which were previously considered synonymous of *G. vernicosa* and *G. erosula* respectively. The PCA analysis includes *G. monodii*, *G. orcutii*, and the two described varieties of *G. vernicosa* (var. *vernicosa* and var. *tenerum*) in the same group, whereas *G. erosula, G. longinervis* and *G. tuberculosa* are clearly differentiated. *G. tanganyikae* is also included in other group, together with *G. erosula*. Our results indicate that there are no morphological reasons to separate *G. monodii* and *G. vernicosa* into different species. The morphometric distances obtained between *G. orcutii*, *G. vernicosa* var. *tenerum*, and *G. monodii* are similar, and lower than those obtained between these taxa and *G. erosula*, *G. longinervis* and *G. tuberculosa*. Therefore *G. monodii* and *G. vernicosa* var. *tenerum* are synonymised with *G. vernicosa* var. *vernicosa*.

Key words: *Gymnostomiella*, morphometric analysis, Pottiaceae, taxonomic revision.

Introduction

Gymnostomiella M. Fleisch. is a predominantly pantropical genus of the Pottiaceae (Zander 1993), which also occurs in subtropical areas (Arts 1998, Frey & Stech 2009). This genus was revised by Arts (1996, 1998) and Arts & Sollman (2002), together with *Splachnobryum* Müll.Hal., which is an ecological and morphological apparently similar genus. One of the characteristics of *Gymnostomiella* is the low number of species and localities known for most taxa. Among the six species of *Gymnostomiella* recognised by the Index Muscorum (Wijk et al. 1962), only five were accepted by Arts (1998): *G. burmensis* E. B. Bartram*, G. erosula* (Müll. Hal. ex Dusén) Arts, *G. longinervis* Broth.*, G. monodii* P. de la Varde and *G. vernicosa* (Hook. ex Harv.) M. Fleisch. In the same study, *G. tenerum* (Müll. Hal. ex Dusén) Arts was considered to be a variety of *G. vernicosa,* whereas *G. orcutii* E. B. Bartram was synonymised with *G. vernicosa* var. *vernicosa*,

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as proposed by Readfearn (1991). Additionally, *G. tanganyikae* De Sloover was reduced by Readfearn (l.c.) to synonymy with *G. erosula*. Similarly, *G. burmensis* was synonymised with *Pottia tuberculosa* Renauld & Paris and later on combined as *G. tuberculosa* (Renauld & Paris) Arts & P. Sollman (Arts & Sollman 2002).

The genus *Gymnostomiella* is referred to the Pottiaceae mainly due the papillose cells, and the obovate or spathulate leaves (Arts 1996, 1998; Zander 1993). The two genera, *Gymnostomiella* and *Splachnobryum*, have similar leaves, costas and cells areolation, and neither of them have paraphyses in the perichaetium or perigonium. The genus *Splachnobryum* is distinguished from *Gymnostomiella* by its smooth cells, clavate axillary hairs, naked archegonia, anacrogynous condition, conical operculum and haplolepideous peristome (Allen & Pursell 2000). Morpho-phylogenetic analyses support the inclusion of *Gymnostomiella* in the Pottiaceae due to its relationship with *Barbula* Hedw. and relatives (Zander 1993). Molecular phylogenetic analyses support the inclusion of both *Gymnostomiella* and *Splachnobryum* in the Pottiaceae (Werner et al. 2004), together with *Hyophila* Brid. as the closest relative to *Gymnostomiella*, although additional data are still necessary to establish their definite phylogenetic relationship within the Pottiaceae.

Gymnostomiella species were formerly separated morphologically by leaf size and shape, leaf apex morphology, costa length, cell papillosity, presence or absence of an apiculate apex, and length/width ratio of leaves (Arts 1998). Arts (l.c.) agreed with Eddy (1990) that the value of these presumably discriminating characters is debatable. Some of the selected characters, such as leaf shape, are highly variable in the accepted species, especially in *G. vernicosa* (Arts 1998). Additionally, some of the discriminating characters considered, might not to be of high taxonomic value. As an example, leaf papillosity has been considered an important character for separating species and varieties within *Gymnostomiella* (Arts 1998, Zander 1993). Accordingly, Zander (1993) retained *G. orcuttii* (from America) and *G. vernicosa* (initially considered restricted to Asia) as separated species, on the basis of differences in leaf cell papillosity, although Readfearn (1991) had previously synonymised them. However, leaf cell papillosity is not always a convenient character to separate species within the Pottiaceae, as was evidenced in *Barbula indica* (Hook.) Spreng. (Werner et al. 2003).

When we tried to identify specimens of *Gymnostomiella* from different microhabitats collected at the type locality of *G. monodii* (El Berbara, Mauritania), we found a continuum of morphological variability that made it very difficult to allocate the specimens as *G. monodii* or *G. vernicosa*. This raised us doubts about the validity of the characters currently used to distinguish these species. Within *Gymnostomiella*, *G. vernicosa* is the species with the widest geographical distribution, also showing the greatest variations regarding its described morphological characters (Arts 1998). On the contrary, only two more localities (in Oman and Yemen) are known for *G. monodii* (Kürschner 2000), in addition to the type locality (El Berbara, Mauritania).

Unfortunately, the restricted geographical range of most of the *Gymnostomiella* species, especially of G. *monodii* and *G. tuberculosa*, as well as the fragmented patterns of their respective distributions, prevented us from obtaining enough fresh specimens of each species to perform molecular analyses. Therefore, the central aim of the present work was to carry out statistical morphometric analyses. For these, we surveyed specimens of all the recognized species of the genus and also from *G. orcuttii* and *G. tanganyikae*. In addition, one collection of *Splachnobryum obtusum* (Brid.) Müll. Hal. was included in the survey.

Specifically we addressed two questions:

1. Does the occurrence of morphological discontinuity support the recognition of *G. monodii* as a different species?
2. Are the characters currently used to distinguish the accepted *Gymnostomiella* species furthermore useful?

Material and methods

Plant material. A total of 583 plants belonging to eight taxa of 60 collections of *Gymnostomiella* (see Appendix) were studied. Within these samples, type specimens were included whenever possible. Some of the studied specimens were collected by the authors in Mauritania (in nine different microhabitats from the type locality of *G. monodii*), and Cape Verde (Santo Antão). These collections are housed in TFC herbarium of La Laguna University. Other studied material was loaned from ALTA, BR, E, FH, H, HBG, JE, L, MUB, O and US herbaria.

Morphological characterization. In total, 24 descriptive morphological characters were used. From these, 21 are quantitative (see Table 1 for the 16 quantitative characters considered, excluding cells sizes). In addition, we also considered 3 qualitative characters previously used by Arts (1998), which were scored as semiquantitative characters (apiculus presence, papillosity range and KOH reaction). Since sporophytes are only known for one of the studied species (*G. vernicosa*; Arts 1998), only vegetative characters (essentially those from the leaves) were included in the analyses. Finally, although gemmae are present in some of the species, they do not always occur, as it is the case in *G. monodii*. For this reason gemmae were also excluded from the analyses. Preference was given to the characters that Arts (1998) considered important for taxa separation within the genus (i.e., maximum leaf length and maximum leaf width, apiculus presence, costa length and cell papillosity). Although the criteria were mainly related to leaf shape (expressed through different measures and ratios) and cell papillosity, cellular characters were also initially considered and measured (length and width of the marginal apical cells, as well as of the cells in three different leaf areas: upper, median and basal). However, cellular characters and KOH reaction were finally excluded from the analyses due to the high degree of overlapping among species, and the lack of significant differences (results not shown). Finally, some characters were taken into consideration as ratios, such as maximum leaf length/maximum leaf width ratio; maximum width of leaf/ leaf base width ratio; and costa length/ maximum leaf length (see Table 1), in order to avoid size effects and to provide additional information on the leaf characters (Frampton & Ward 1990).

If possible, at least ten plants were measured from each collection referred in the appendix, a number that is considered to be sufficient for recording the morphological range of a species (Rico & Bachman 2006).

Table 1. Characters measured and abbreviations (median leaf).

Abbreviation	Morphological character
BNV	Costa width at the leaf base
DLFB-MW	Distance between leaf base and the maximum width line
L	Maximum leaf length
L/MW	Maximum length/maximum width ratio
LNV	Costa length
LNV/L	Costa length/maximum leaf length
MW	Maximum leaf width
NCA-N	Number of cells between the apex and the costa
WB	Leaf base width
WB/MW	Maximum width of leaf/ leaf base width ratio
Pap0	Number of cells in the leaf apex with zero papillae (%)
Pap1	Number of cells in the leaf apex with one papillae (%)
Pap2	Number of cells in the leaf apex with two papillae (%)
Pap3	Number of cells in the leaf apex with three papillae (%)
Pap> 3	Number of cells in the leaf apex with more than three papillae (%)
APIC	Number of leaves with an apiculate apex (%)

The characters related to the cells were not included in the table.

Each character was measured in one leaf of each of these ten gametophytes. Thus, one measurement was made for each character in one leaf of the 583 plants studied. Exceptions were cell sizes (length and width) and papillae number per cell, for which we attempted to measure 50 cells per each leaf area considered (upper, median and basal parts). The apical marginal cell was also measured. Each measurement was taken from a randomly chosen leaf situated in the central segment of the stem (median leaf). The basic data matrix constructed contains 583 leaves in which the above-mentioned characters were measured. Then, we calculated the mean values of each leaf character from each collection (i.e., the mean of the ten plants). This method was used both with herbarium and own collected specimens. Characters were examined under an optical microscope (Leica CM-U) and parameters were measured with a video camera (Leica EC3 Camera) connected to the optical microscope to transfer the image to a computer. The Leica LAS EZ software (Leica Microsystems Ltd. 2009) was used for image analysis.

Statistical analyses. We performed the analyses in several steps using two data sets. First, we used a global data matrix that contained 23 characters and 583 plants (including all the species and varieties of the genus *Gymnostomiella*, their synonymous types and *Splachnobryum obtusum*). A second matrix was built with the main diagnostic characters (see Arts 1998) of *G. monodii* and *G. vernicosa*, including varieties and synonymies. This second matrix was constructed with the median values obtained from the ten leaves measured from each collection. Different analyses were carried out on each data matrix, but only the results obtained with the second matrix are shown here. All the data were standardised before analysed to avoid the possible influence of variation that would result from various types of characters (Sokal & Rohlf 1997). The symmetry and unimodality of the frequency distributions of the measured character values were verified to assess the possibility of conducting a statistical analysis (Sokal & Rohlf 1997; Zar 1999).

Principal components analysis (PCA; McCune & Grace 2002) was performed using Canoco 4.5 (ter Braak & Šmilauer 2002) based on the second data matrix with all taxa considered and taking the mean values of each character of each collection as operational units (OTU). PCA was used to detect primary patterns among all the OTUs because this method requires no a priori knowledge of the origins of the OTUs and a general tendency between main groups can be traced. PCA was also used for partial analyses with the two varieties of *G. vernicosa,* including also the two synonyms (*G. orcutii* and *G. tanganyikae*) and *G monodii*. The matrix of the standardised characters was plotted along the two component axes. The most discriminatory descriptors were inferred from the length of the vector and its correlation with the respective axes. When discriminatory characters were ratios the use of any correlated descriptor was avoided.

Canonical discriminant analyses (DA; Sneath & Sokal 1973) were implemented to determine whether there was sufficient information in the quantitative and qualitative leaf characters to enable separation of the taxonomic units (i.e., species, varieties) previously recognised by Arts (1998). The analyses were also conducted to search for the best linear combination of variables to discriminate taxa. DA maximises the among-group variation relative to the within-group variation, and it requires an a priori assignment of OTUs to groups (McCune & Grace 2002).

The species, varieties and respective synonymies of the global standardised data matrix were used as a priori in DA. *Gymnostomiella tuberculosa* and *Sphachnobryum obtusum* were excluded from this multivariate analysis because of the scarcity of available specimens. The DA was based on Mahalanobis distances (McCune & Grace 2002), which allow to infer relationships between taxa.

To show the variability of the most important quantitative and qualitative characters within each species in a clear and readily comparable way, graphical tests (box-plot containing medians and percentiles) illustrating the variation in the parameters were plotted. The most discriminatory descriptors were inferred from the partial PCA. Seven of them are quantitative continuous traits and three are ratios. Due to the differences in sample size, Kruskal-Wallis and Mann-Whitney tests for a posterior comparison of each pair of means were made (Zar 1999). All the variables were tested for normality with the Kolmogorov-Smirnov test (Zar 1999). All DA analyses were performed with the aid of the STATISTICA 6.0 package (http://www.statsoft.com).

Results

The absolute data matrix analyses do not differentiate *Gymnostomiella monodii* and *G. vernicosa*, and short distances are obtained for the other taxa. For this reason, these results are not

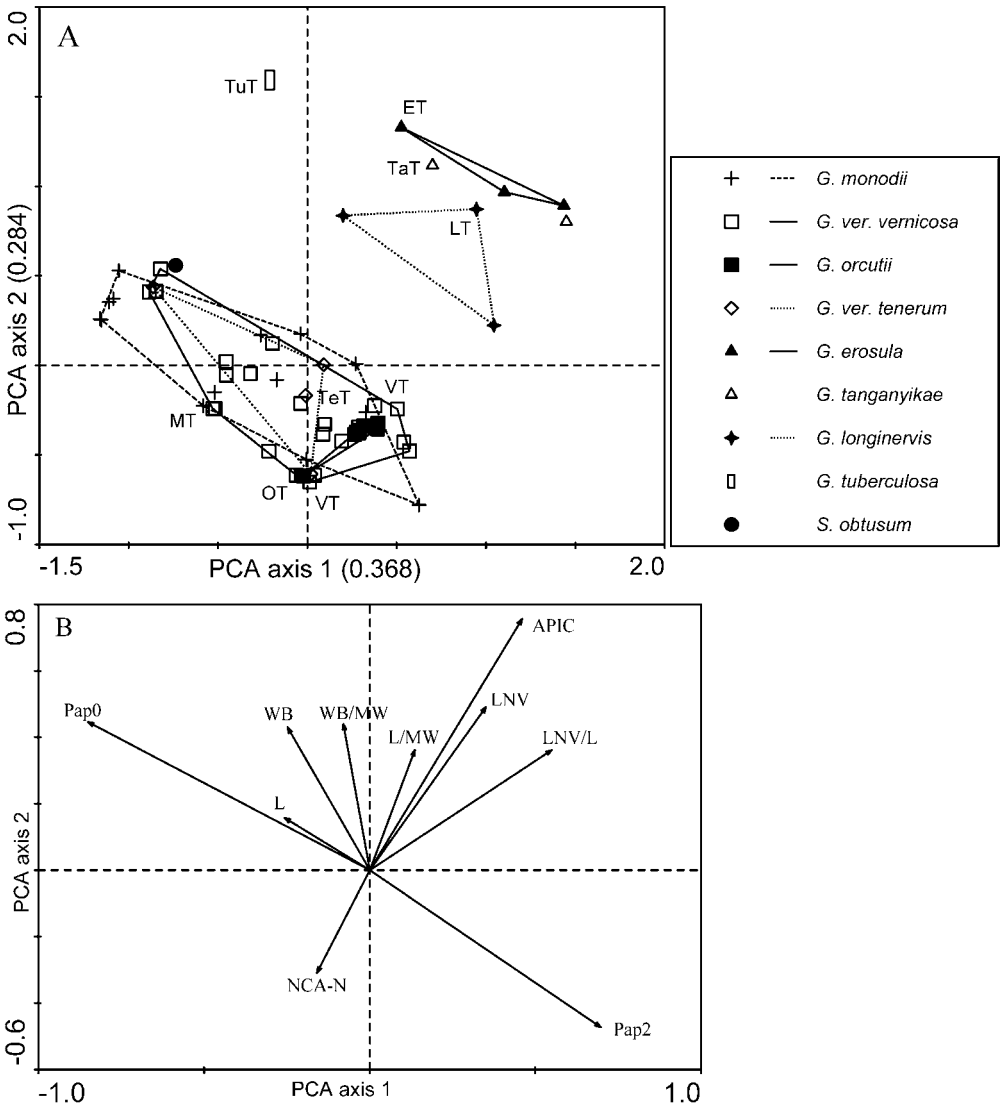

Fig. 1. PCA with all the species and standardized variables. In the variable plot (A) are shown the (ten) most important characters according to the length of their vectors. *G. ver. vernicosa*: *Gymnostomiella vernicosa* var. *vernicosa*; *G. ver. tenerum*: *Gymnostomiella vernicosa* var. *tenerum*. MT : *G. monodii* types; VT : *G. vernicosa* var. *vernicosa* types; TeT : *G. vernicosa* var. *tenerum* types; ET : *G. erosula* types; TaT : *G. tanganyikae* types; TuT : *G. tuberculosa* types.

shown and all the results below are obtained from the analyses of the second data matrix, built with the main diagnostic characters.

Three distinct groups of species are resolved by PCA (Fig. 1A, eigenvalues 0.368 and 0.284). On the lower left area of the graph a first group contains *G. vernicosa* s.l. (including *G. orcutii* and *G. vernicosa* var. *tenerum*) and *G. monodii*. *Splachnobryum obtusum* is positioned at the

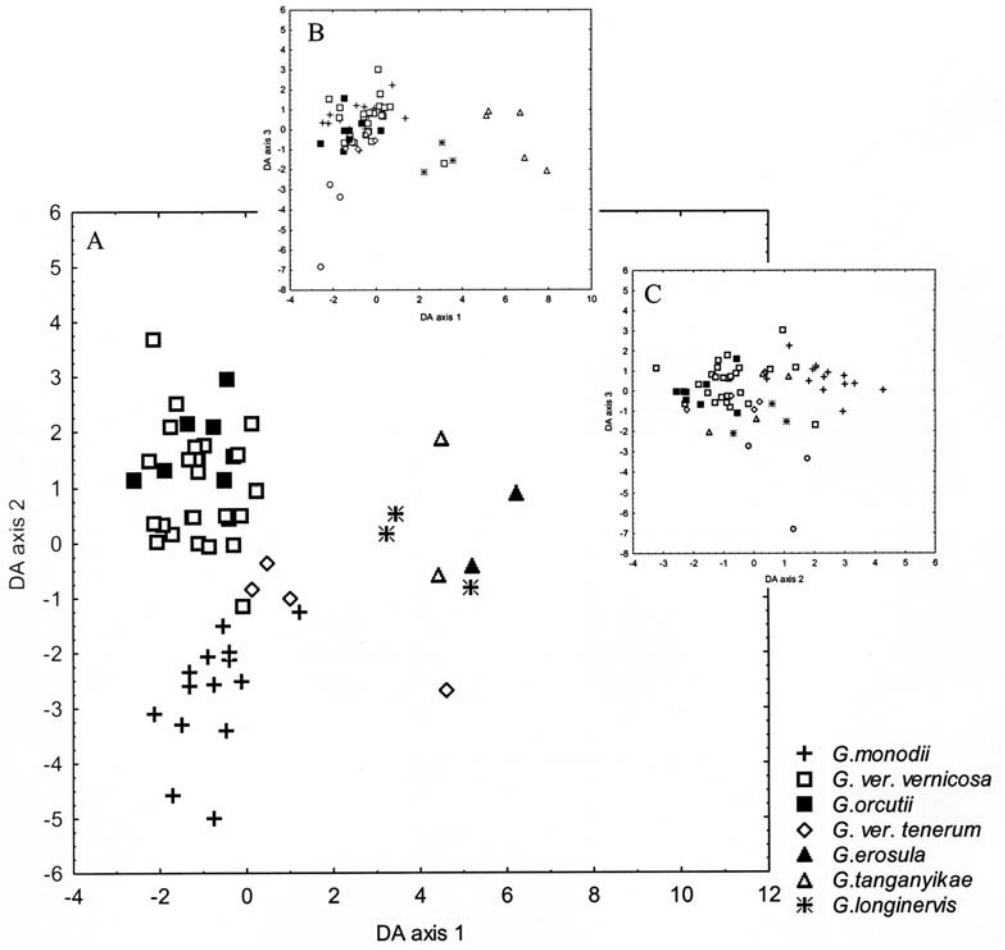

Fig. 2. DA with all the variables and species of *Gymnostomiella*. *Gymnostomiella tuberculosa* and *Splachnobryum obtusum* could not be included due to the low number of specimens. Diagram (A) showing axes 1 and 2; (B) axes 1 and 3; and (C) axes 2 and 3. *G. ver. vernicosa*: *Gymnostomiella vernicosa* var. *vernicosa*; *G. ver. tenerum*: *Gymnostomiella vernicosa* var. *tenerum*.

margin of this group. A second group, on the right top area of the graph, is formed by *G. erosula* and the synonymysed *G. tanganyikae*. Finally, *G. tuberculosa* and *G. longinervis* are situated in separate positions with respect to these two groups. The types of each taxa of the *G. monodii-G. vernicosa* group are positioned at the margin of the polygon of each species.

The differences among the *G. vernicosa* (s.l.)-*G. monodii* group and the separate mentioned species are resolved by ordination (Fig. 1B), especially on the basis of the number of leaves with apiculate apex (APIC), number of cells between the apex and costa (NCA-N), costa length (LNV) and costa length/maximum leaf length ratio (LNV/L). However, the only characters defining the amplitude of the *G. vernicosa* (s.l.)-*G. monodii* group are leaf papillosity and maximum leaf length (L). There is a wider range of variation gradient in *G. monodii* and G. *vernicosa* var. *vernicosa* than in *G. orcutii* and *G. vernicosa* var. *tenerum*, which might be related to the sample size (smaller in the last two taxa). All characters with low weights (e.g. cell sizes) were

Table 2. Discriminant function analysis summary. Variables included in the DA with all the species (see Figure 2). Significant variables are shown in boldface.

	Wilks'	Partial	F-remove	*p*	Toler.	1–Toler.
L	0.004	0.769	1.852	0.115	0.007	0.992
MW	0.003	0.875	0.874	0.522	0.019	0.980
DLFB-MW	0.003	0.937	0.412	0.865	0.095	0.904
WB	**0.004**	**0.688**	**2.790**	**0.024**	**0.018**	**0.981**
LNV	0.004	0.805	1.486	0.209	0.060	0.939
BNV	0.004	0.777	1.760	0.134	0.426	0.573
NCA-N	**0.006**	**0.549**	**5.051**	**0.000**	**0.579**	**0.420**
L/MW	**0.004**	**0.715**	**2.448**	**0.042**	**0.021**	**0.978**
WB/MW	**0.004**	**0.744**	**2.120**	**0.044**	**0.023**	**0.976**
LNV/L	0.004	0.818	1.363	0.255	0.048	0.951
Pap0	**0.004**	**0.800**	**1.536**	**0.046**	**0.241**	**0.758**
Pap1	0.004	0.719	2.403	0.193	0.314	0.685
Pap2	0.004	0.822	1.331	0.268	0.403	0.596
Pap3	0.004	0.822	1.329	0.268	0.362	0.637
Pap> 3	0.003	0.865	0.957	0.467	0.351	0.648
APIC	**0.006**	**0.503**	**6.087**	**0.000**	**0.618**	**0.381**

No. of variables in model: 16; Grouping: Species (7 groups); Wilks' Lambda: 0.003; F (102, 217) = 3.673; $p < .0001$

Table 3. Mahalanobis distances using variables normalized (see Figure 2). Significant distances are shown in boldface.

	G. monodii	*G. ver.* var. *vernicosa*	*G. orcutii*	*G. ver.* var. *tenerum*	*G. erosula*	*G. longinervis*
G. monodii	+++	**22.508**	**19.579**	**15.046**	**79.925**	**65.426**
G. ver. var. *vernicosa*		+++	**29.304**	6.043	**81.941**	**61.263**
G. orcutii			+++	**19.743**	**51.645**	**67.951**
G. ver. var. *tenerum*				+++	**71.101**	**62.974**
G. erosula					+++	**54.078**
G. longinervis						+++

removed from the ordination. *Splachnobryum obtusum* is related to those plants of *G. monodii* and *G. vernicosa* var. *vernicosa* with a high percentage of cells without papillae.

The DA plots performed using all species (with the exception of *G. tuberculosa* and *S. obtusum* due their low number of specimens) also show two groups along axis 1. The first one includes *G. vernicosa* s.l. and *G. monodii*, and the second one contains the rest of species, except one collection of *G. vernicosa* var. *tenerum* (Figure 2A). The axis 2 shows a gradient from *G. monodii* and *G. vernicosa* var. *tenerum* to *G. vernicosa* var. *vernicosa* and *G. orcutii*. A clear separation of *G. longinervis* and *G. erosula* is observed again when axis 2 and 3 are considered (Fig. 2B), although in this case *G. vernicosa* and *G. monodii* do not show any separation, and only some of

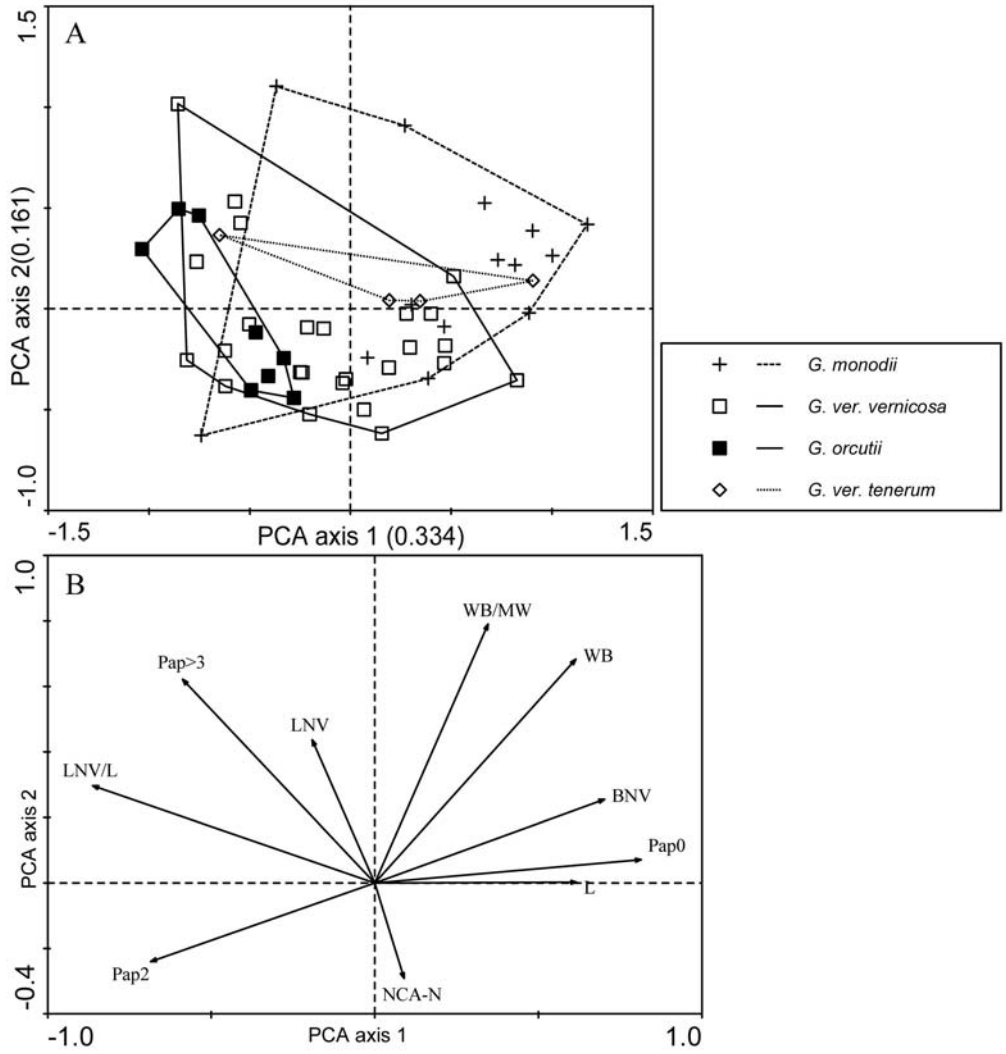

Fig. 3. PCA with all the standardized variables and species and varieties of *Gymnostomiella vernicosa*, and *G. monodii*. In the variable plot (A) are shown the (ten) most important characters according to the length of their vectors. *G. ver. vernicosa*: *Gymnostomiella vernicosa* var. *vernicosa*; *G. ver. tenerum*: *Gymnostomiella vernicosa* var. *tenerum*.

the collections of *G. vernicosa* var. *tenerum*, appear separated in the lower left area of the graph. Axes 1 and 3 again show the distance among some of the collections of *G. vernicosa* var. *tenerum* and the other species; while among the other species there is not a clear separation (Fig. 2C).

Significant variables in the DA (Table 2) are leaf base width (WB), number of cells between the costa and the apex (NCA-N), leaf shape represented by maximum length/maximum width of the leaf ratio (L/MW), maximum width of the leaf/leaf base width ratio (WB/MW), absence of papillae (Pap0) and the number of leaves with an apiculate apex (APIC).

Mahalanobis distances (Table 3) of all the species included in the general DA (Fig. 2) show that distances between *G. monodii* and *G. vernicosa*, and *G. vernicosa* var. *tenerum* and *G. or-*

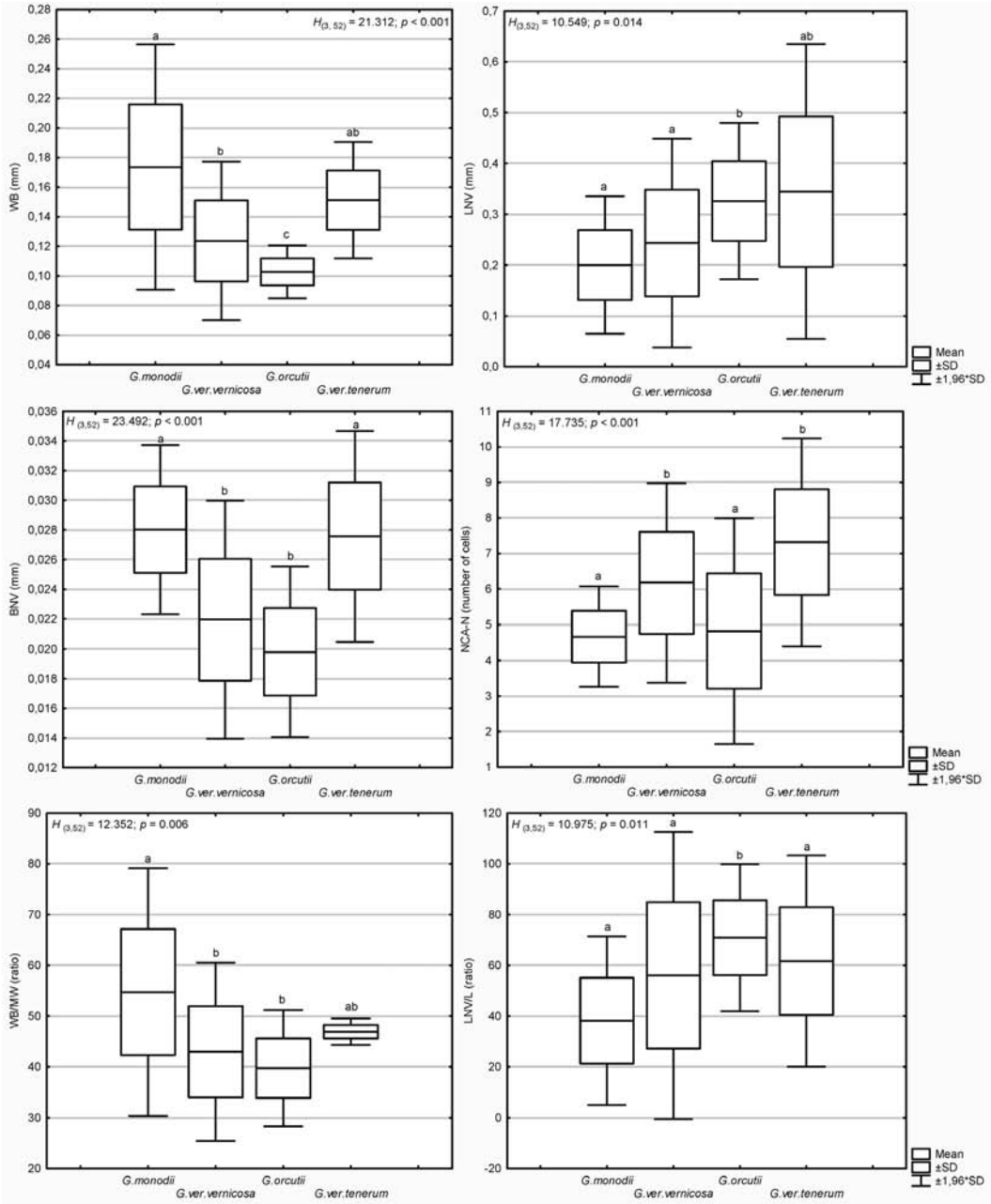

Fig. 4 (continuation next page). Mean values (SD) of the significant variables obtained in the PCA of the varieties related to *G. vernicosa* and *G. monodii* (see Fig. 3). The variable L/MW is not showed because there were no significant differences among taxa ($p > 0.05$). G. ver. *vernicosa*: *Gymnostomiella vernicosa* var. *vernicosa*; G. ver. *tenerum*: *Gymnostomiella vernicosa* var. *tenerum*.

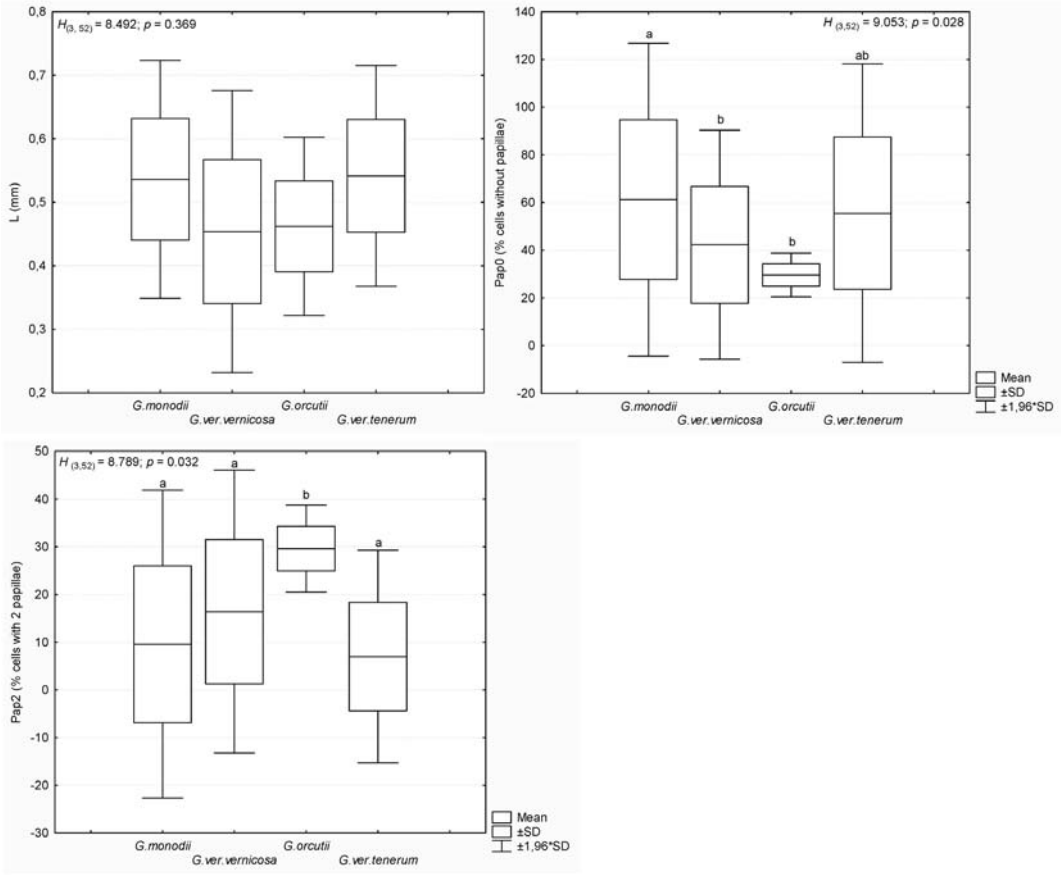

Fig. 4. (**continued**). Mean values (SD) of the significant variables obtained in the PCA of the varieties related to *G. vernicosa* and *G. monodii* (see Fig. 3). The variable L/MW is not showed because there were no significant differences among taxa ($p > 0.05$). *G. ver*. *vernicosa*: *Gymnostomiella vernicosa* var. *vernicosa*; *G. ver*. *tenerum*: *Gymnostomiella vernicosa* var. *tenerum*.

cutii are similar; whereas distances between these varieties, including *G. monodii* and *G. erosula* (including the synonym *G. tanganyikae*) and *G. longinervis* are higher (more than 40 % in all cases). It is remarkable that when *G. vernicosa* var. *vernicosa* and *G. vernicosa* var. *tenerum* are compared, we obtained the only non-significant distance.

When PCA is performed using the taxa of the *G. vernicosa-G. monodii* group (Fig. 3A), all taxa overlap (both varieties of *G. vernicosa*, *G. orcutii* and *G. monodii*). Some of the collections of *G. monodii* (upper right area of the graph) represent an extreme of the variation continuum from these taxa. *G. orcutii* especially overlaps with *G. vernicosa* var. *vernicosa*; while *G. vernicosa* var. *tenerum* is in a middle position between *G. vernicosa* var. *vernicosa* and *G. monodii*. When PCA analysis is performed with the first data matrix with absolute values (not shown) the different taxa, including *G. longinervis* and *G. erosula,* are somewhat differentiated.

In the PCA variable-plot (Fig. 3B) the main variables along axis 1 (eigenvalue 0.334) are the number of papillae, especially the absence of them, and the leaf length (L). The absence of papillae is directly correlated with leaf length. Thus, longer leaves have fewer papillae. Other impor-

tant variables are the costa length/maximum leaf length ratio (LNV/L) and costa width at the leaf base (BNV). The most important variables along axis two (eigenvalue 0.161) are the maximum width of the leaf/leaf base width ratio (WB/MW), leaf base width (WB), number of papillae (Pap > 3) costa length (LNV) and the number of cells between the apex and the costa (NCA-N).

The mean values and standard deviation of the significant variables of the PCA (see Fig. 3) are shown in Fig. 4. There is a high degree of overlapping in each of the characters among the four taxa (*G. monodii,* both varieties of *G. vernicosa* and *G. orcutii*), although with different levels of significance depending on the taxon and the character. *Gymnostomiella monodii* fails to show a significant difference from the total sample mean in any of the considered characters. This species shows significant differences with *G. orcutii* and *G. vernicosa* var. *vernicosa* with respect to the leaf base width (WB), costa width at the leaf base (BNV), maximum width of the leaf/ leaf base width ratio (WB/MW) and proportion of cells in the leaf apex with zero papillae (Pap 0), but for these characters the differences with *G. vernicosa* var. *tenerum* are not significant. However, with this last species, *G. monodii* has significant differences only in number of cells between the apex and the costa (NCA-N). The two varieties of *G. vernicosa* (var. *vernicosa* and var. *tenerum*) show significant differences only with respect to the costa width at the leaf base (BNV).

Discussion

Arts (1998) accepted the consideration of *G. orcutii* as conspecific with *G. vernicosa* var. *vernicosa*, which had been already proposed by Readfearn (1991). Our results also confirm this synonymization, since the distances between these two taxa are not significant. The synonymization of *G. tanganyikae* with *G. erosula* realized by Arts (1998) is also supported by our morphometric analyses. However, our study suggests that the characters used by that author have little value for species delimitation in the case of *G. vernicosa* and *G. monodii.* The specimens of *G. monodii* studied by Arts (1998) always showed a broadly pointed acuminate leaf apex. However, among our specimens of this species, leaves with a rounded apex as in *G. vernicosa* are also present, as well as those with an intermediate leaf apex.

When *G. monodii* was described by Potier de la Varde (1953), the species was distinguished from the other known species at that time (*G. orcutii*, *G. longinervis* and *G. vernicosa*) by the number of papillae per cell (only one). Potier de la Varde (l. c.) also indicated that papillose cells were exclusive to the upper area of the leaves. Other characters considered by Potier de la Varde (1953) involved leaf shape: largely ovate, shortly acuminate, and with apiculus in the case of *G. monodii*, while the leaves of the other three species were considered to be from spathulate to largely round. He also commented the high affinity between *G. monodii* and *G. orcutii,* their differences in the papillae number, and the absence in *G. monodii* of papillae in the lower part of the leaves.

De Sloover (1977) also separated *G. monodii* and *G. tanganyikae* because of the presence of 1 papilla in the upper cells; although this author indicated that sometimes there are also 2–3 papillae per cell in both species. In our study, we found 1–3 papillae in the type specimen of *G. orcutii*, 0–3 papillae in the isotype of *G. vernicosa*, 0–1 papillae in the isotype of *G. vernicosa* var. *tenerum*, 0–2 papillae in the isotype of *G. monodii*, and absence to more than 3 papillae in our collections of fresh material of *G. monodii*. In the analyses carried out with all species (Fig. 1A, B), it was observed that the absence or presence of papillae (at least more than one papillae per cell), is an important character of plant variation, more so than for species variation. In some species of the genus *Tortula* Hedw. sect. *Pottia* (Rchb.) Kindb., such as *Tortula lindbergii* Broth. and *T. pallida* (Lindb.) R. H. Zander, papillae number is frequently variable (Ros & Werner 2006). Additionally, in some *Didymodon* species such as *D. tophaceus* (Brid.) Lisa and *D. sicculus* M. J. Cano et al., the number of papillae per cell is variable (Jiménez 2006, Werner et al. 2009).

We conclude that *G. monodii*, *G. vernicosa* var. *vernicosa*, and *G. vernicosa* var. *tenerum* might represent the extremes of a very variable taxon. However, a morphometric analysis clearly indicates *G. monodii* should not be considered a different species from *G. vernicosa* s.l. The taxon *G. vernicosa* var. *tenerum* should be considered within the same taxonomical category as *G. vernicosa* var. *vernicosa* because the Mahalanobis distances obtained were not significant and the number of papillae (the main character considered by Arts 1998) is a highly variable character that overlaps between these taxa. In addition, the costa width at the leaf base is the only morphological character that shows significant differences between both varieties. The Mahalanobis distances observed between *G. monodii*, *G. vernicosa* var. *tenerum* and *G. vernicosa* var. *vernicosa* were shorter than those obtained between these taxa and *G. erosula* and *G. longinervis* (see Table 3). A PCA analysis with only these taxa shows a high degree of overlapping between them. For these reasons, we propose that *G. monodii* should be considered conspecific with *G. vernicosa*, as well as *G. vernicosa* var. *tenerum* does not deserve recognition at any taxonomical rank, but should be included within the variability of *G. vernicosa* var. *vernicosa*.

In the nineteenth and early twentieth centuries, bryologists preferred to use a geographical or typological species concept where species were defined as largely invariant units (e.g. Heinrichs et al. 2009). Many species were known only from type material (e.g. Stephani 1898–1925, Warnstorf 1911), as occurred with *G. tuberculosa*; others were known in only very few localities, as with most of the *Gymnostomiella* species. More recently, authors have accepted intraspecific morphological variation and lowered numerous local taxa to synonyms of more widespread bryophyte species (Gradstein 1994, Heinrichs et al. 2009). *Gymnostomiella monodii* was initially described from an isolated locality in the Sahara desert (Mauritania) (Potier de la Varde 1953). The key of De Sloover (1977) considered the geographical distribution restricted to Africa and distinguished *G. monodii* and *G. tanganyikae* group from the other species described at that time. However, the last two localities reported for the first species (Kürschner 2000) included *G. monodii* into the distribution range of *G. vernicosa,* because there was no geographical reason to conserve *G. monodii* as a different species, as was suggested by Arts (1998) regarding the varieties of *G. vernicosa*.

Morphological species concepts do not always coincide with phylogenetic species concepts. In bryophytes, evidence is accumulating both for cryptic speciation (e.g. Shaw 2001), as well as for the opposite: morphologically different species that have no consistent phylogenetic separation, as occurs for instance with many aquatic mosses (e.g. Werner et al. 2007). Sometimes only subtle morphological differences distinguish species with a clear phylogenetic separation, as it is the case of *Leucodon treleasei* (Cardot) Paris and *L. canariensis* (Brid.) Schwägr., both endemics from Macaronesian (Stech et al. in press). The morphological characters found in *Gymnostomiella* species (leaf base width, number of cells between the apex and the costa, maximum length/ maximum width of the leaf ratio, maximum width of the leaf/ leaf base width ratio, apiculus presence and proportion of cells without papillae) are rather subtile and difficult to appreciate in some specimens. This is especially true when these characters function better for mean values than for extreme values, and there is a high degree of overlapping. Until the appearance of additional work with molecular data, a small key with the four accepted species is presented here.

Key to distinguish *Gymnostomiella* species

1 Costa percurrent or ending (1)2(3) cells below the apex 2
1' Costa ending (3–4)5–7(8–9) cells below the apex 3
2 Costa percurrent in most leaves, leaf apex acute and apiculate . . . . . *G. tuberculosa*
2' Costa ending 1–2(3) cells below the apex, leaf apex rounded to broadly acute or apiculate . . . . . *G. longinervis*
3 Most leaves 1.5–2.2 times as long as wide and with apiculate apex, costa (0.2)0.3–0.5(0.6) mm long, costa occupying at least 50 % of the leaf length . . . . . *G. erosula*
3' Most leaves 1.2–1.8 times as long as wide, costa (0.05)0.1–0.4(0.5–0.7) mm long, a high proportion of leaves with the costa extending only 25–60 % of the leaf length . . . . . *G. vernicosa*

Taxonomical additions

Gymnostomiella vernicosa (Hook. ex Harv.) M. Fleisch., Musci Buitenzorg 1: 310. 53. 1904.
Type: Burma, Prome, N. Wallich s.n., 1826 (isotypes: E00002193!, E00002193!).
Basionym: *Gymnostomum vernicosum* Hook. ex Harv., Icon. Pl. 1: pl. 17: f. 4. 1836.
Splachnobryum tenerum Müll. Hal. ex Dusén, Kongl. Svenska Vetenskapsakad. Handl. 28(3): 39. 1896. Type: [Liberia] ubi ad Monrovian, in rupibus, P. Dusén s.n., 21 July 1890 (Isotypes: BR 50472–32!, H 3864–014!). *Gymnostomiella tenerum* (Müll. Hal. ex Dusén) Arts, J. Bryol. 19: 76. 1996. *Gymnostomiella vernicosa* var. *tenerum* (Müll. Hal. ex Dusén) Arts, J. Bryol. 20: 424. 1998 **syn. nov.**
Gymnostomiella monodii P. de la Varde, Rev. Bryol. Lichénol. 22: 6. 1. 1953. Type: Mauritania, falaise humide de la source incrustante d'El Berbera Adrar, T. Monod 10961, 22 Oct. 1952 (Isotype: BR50465–25) **syn. nov.**

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Appendix. Plant material studied.

Gymnostomiella erosula: Cameroon, P. Dusén 29/19, H 3864–003, isosyntype; Cape Verde Islands (Santo Antão), J. M. González-Mancebo s.n., TFC 19012, 19013.
Gymnostomiella longinervis: Japan (Oita), A. Noguchi s.n., BR 169410–48; Japan (Oita), A. Noguchi 369, US; Philippines (Tigon river), C. B. Robinson 18053, H 1884–003, isotype.
Gymnostomiella monodii: Mauritania (El Berbara), T. Monod 10961, BR 50465–25, isotype; Mauritania (El Berbara), J. M. González-Mancebo s.n., TFC 19014–19022; Oman (Dhofar), A. G. Miller 7325, E 00164618; Yemen (From Nakhadi to Wasab), A. G. Miller 10114, E 00164617; idem, A. G. Miller 587, E 00164619.
Gymnostomiella orcutii: Ecuador, Galapagos Islands, S. R. Gradstein M84, BR 310309–06; Jamaica, C. R. Orcutt 2786, FH, type; U. S.A., Puerto Rico (South of Arecibo), W. C. Steere 6637, 5047, 5049, 5469, 5054, FH; Cuba (Trinidad), W. H. Welch 9439, FH.
Gymnostomiella tanganyikae: Burundi (Bujumbura-Rumonje), J. L. De Sloover 19210, BR 50466–26, holotype; Burundi (Bujumbura- Rumonje), BR 275156–57.
Gymnostomiella tuberculosa: Madagascar, L 0360187, isotype.
Gymnostomiella vernicosa: Burma, W. H. Harvey s.n., E 00002192, isotype; Burma (Prome), N. Wallich s.n., E 00002193, isotype; China (Peking), D. Vent s.n., JE; Comores (Anjouan), T. Pócs 9168/D, BR 310314–11; India (Jabalpur), G. Topál s.n., ALTA; India (Calcuta) N. C. Gangulee 3082, H; India (Calcuta), N. C. Gangulee 3101, FH; India (Mangalur), J. Pfleiderer 6844, JE; India (Rajasthan), T. Arts In05/01, MUB 8146; India, (Dema Dun), W. Sollan s.n., O; Indonesia (Java), F. K. Schllephacke, Osterfeld & H. Winter s.n., O; Indonesia (Mittle-Java), F. K. Schllephacke, Osterfeld & H. Winter s.n., JE; Malaysia (Selangor), H. Mohamed s.n., H; Oman (Dhofar), A. G. Miller 7308, E 00164618; idem, A. G. Miller 7300a, E 00164620; idem, A. G. Miller 6687, E 00164621; idem, A. G. Miller 7288, E 00164622; idem, A. G. Miller 7286, E 00164623; idem, A. G. Miller 7308, E 00164624;Yemen (Wadi Sara), D. G. Long & A. G. Miller 10144, BR 310311–08.
Gymnostomiella vernicosa var. *vernicosa*: Birmania (Rangoon), H. Möller s.n., HBG 2–312032; Thailand (Chiang Mai), T. Arts Thai 20/01, BR 312250–07; Thailand (Phra Nakhon Si), T. Arts Thai01/01, BR 312248–05.
Gymnostomiella vernicosa var. *tenerum*: Liberia (Monrrovia), collector illegible, H 3864–014, isotype; Liberia (Monrrovia), P. Dusén s.n., BR 50472–32, isotype; Thailand (Phangnga, Insel Khao Ping Gun), A. Schäfer-Verwimp 16173, BR 310313–10; Thailand (Phangnga), A. Schäfer-Verwimp 16175, BR 310312–09.
Splachnobryum obtusum: Mauritania (Oum Lemhart), J. M. González-Mancebo s.n., TFC 19023.