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ON THE TAXONOMIC SIGNIFICANCE OF SECONDARY METABOLITES IN THE LEJEUNEACEAE (HEPATICAE)

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ABSTRACT: Chemical analysis of representatives of about thirty genera of Lejeuneaceae has shown that the terpenoid and flavonoid content of the Lejeuneaceae is basically comparable to that of other Hepaticae and quite diversified. Among the terpenoids detected, some are common throughout the family (elemenenes, germacrenes), others are distributed more restrictedly and are indicative of evolutionary relationships among genera, e.g. borneols (*Nipponolejeunea*), pinguisanines (*Acrolejeunea* complex), striatenes (Ptychanthoideae, *Omphalanthus* complex), calamenanes (*Lopholejeunea*) and labdanes (*Ptychanthus, Tuzibeanthus*). Flavonoids are present in smaller amounts than terpenoids and comprise some compounds unique to bryophytes (lutonarin, kaempferol-3-methylether). The genus *Omphalanthus* stands out by its total inability to biosynthesize flavonoids. At the species level the chemical constitution may vary considerably and in some species evidence for the existence of chemical races was detected.

INTRODUCTION

Considerable progress has been made in the isolation and identification of the secondary metabolites of the bryophytes (this symposium), yet relatively little is known about the taxonomic relevance of these substances. Moreover, most of the taxa which have been investigated chemically are from Japan, Europe and North America, but very little is known about the chemistry of the tropical and southern hemispheric groups. One of the largest tropical bryophyte groups are the Lejeuneaceae, which include about 80–90 genera and hundreds of species (Gradstein 1979). The taxonomy of the Lejeuneaceae is problematical, especially with respect to the genera, and opinions vary as to their correct delimitation by lack of monographs and due to insufficient understanding of the variation of the characters. Also, the taxonomy is somewhat hampered by the lack of "good" morphological characters useful for the delimitation of the taxa.

These considerations have instigated the authors to undertake a joint investigation on the occurrence of secondary metabolites in members of the Lejeuneaceae, with the aim of detecting new characters relevant to the taxonomy of the family. Our study was based on analysis of materials from various parts of the world, especially from South America, New Guinea and Japan, and collected mainly by the first author and his associates. Voucher specimens are kept in the herbarium of the University of

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TABLE 1. The occurrence of terpenoids in the genera of Lejeuneaceae subfamily Ptychanthoideae (Gradstein et al. 1985). Tribal classification according to van Slageren (1985).

	Species checked (total nr. of spp. per genus)	TERPENOIDS		
		Monoterp.	Sesquiterp.	Diterp.
PTYCHANTHEAE				
Acrolejeunea complex				
Acrolejeunea	3 (15)	+	+++++	+
Trocholejeunea	1 (2)	+	+++++	
Frullanoides	2 (7)		+++++	+
Ptychanthus complex				
Schiffneriolejeunea	2 (16)		++	++++
Mastigolejeunea	3 (15)		+++	+++
Thysananthus	4 (10)	+	+++	+++
Ptychanthus	1 (2)	+	++++	++
Tuzibeanthus	1 (1)		++++	++
Archilejeunea complex				
Spruceanthus	1 (5)		+++++	+
Archilejeunea	3 (10)		++++	+
Lopholejeunea complex				
Lopholejeunea	3 (30)		+++++	++
Marchesinia	2 (7)	+	+	+
BRACHIOLEJEUNEAE				
Brachiolejeunea complex				
Brachiolejeunea	1 (5)		+++	+++
Blepharolejeunea	2 (5)		+++	++++
Lindigianthus	1 (1)		++	+
Symbiezidium complex				
Symbiezidium	2 (3)	+	+++++	
Stictolejeunea complex				
Stictolejeunea	2 (2)	+	+++	+++

Utrecht (U). Lipophilic substances were studied by Y. Asakawa and his associates and hydrophilic substances were studied by R. Mues and R. Klein. The present paper briefly reviews the results obtained for two main groups of compounds, the terpenoids and the flavonoids.

TERPENOIDS

About 60 species of Lejeuneaceae in 26 genera have so far been checked for the occurrence of terpenoids (Asakawa et al. 1980, Gradstein et al. 1981, Inoue et al. 1981, Gradstein et al. 1985, Asakawa & Inoue 1987). It appears that most of the taxa elaborate large quantities of sesquiterpenes and/or diterpenes, whereas only few synthesize monoterpenes. Triterpenes are very rare and have thus far been detected only in *Diplasiolejeunea patelligera*, which produces the triterpene hop-22-ol as a minor component. The general terpenoid composition is shown in Table 1 for members of the subfamily Ptychanthoideae.

Among the various terpenoids detected in the Lejeuneaceae, some are of wide distribution in the family such as the elemenes and germacrenes (sesquiterpenes) and seem to be of little taxonomic importance. Other compounds appear to be of more restricted distribution and are suggestive of evolutionary relationships among the various genera. The following chemotaxonomic conclusions can be drawn:

Monoterpenes

Borneols. Borneol and bornyl acetate are odorous substances which have been detected within Lejeuneaceae only in the species (2) of *Nipponolejeunea* (Inoue et al. 1981). *Nipponolejeunea* is a morphologically very peculiar genus, which is nowadays placed in the monotypic subfamily Nipponolejeuneoideae. The unique monoterpenes of *Nipponolejeunea* clearly underline the patristic differences between this genus and other Lejeuneaceae.

Sesquiterpenes

Pinguisanes (Table 2, Figs. 1, 2). Pinguisane-type sesquiterpenes are unique for liverworts and have been found in Aneuraceae and in the Jungermannialean families Ptilidiaceae, Lepidolaenaceae, Porellaceae and Lejeuneaceae (Asakawa 1982). Their

TABLE 2. The occurrence of pinguisane-type sesquiterpenes in the Lejeuneaceae. 1–8: pinguisanines. 1: pinguisenal. 2: pinguisanine. 3: dehydropinguisanine. 4: dehydropinguisenol. 5: pinguisanolide. 6: hydroxypinguisanolide. 7: isopinguisanolide. 8: hydroxyisopinguisanolide. 9–13: pinguisones. 9: pinguisenol. 10: deoxopinguisone. 11: dehydrodeoxopinguisone (=pinguisenene). 12: pinguisone. 13: norpinguisone methyl ester. ++ = major component. + = minor component. The number and quantity of unidentified pinguisane-type compounds is shown in brackets.

	Pinguisanines								Pinguisones					Unidentified
	1	2	3	4	5	6	7	8	9	10	11	12	13	
PTYCHANTHOIDEAE														
Acrolejeunea complex														
Acrolejeunea	++	++	++		++		+		+					(6+)
Trocholejeunea	++	+	++	++	++						+			(2+)
Frullanoides	++	+	+		++	++	+	++						
Ptychanthus complex														
Mastigolejeunea														(7+)
Thysananthus											+			(5+)
Ptychanthus										+	++			(2++)
Tuzibeanthus														(2++)
Archilejeunea complex														
Spruceanthus														(1++)
Archilejeunea														(5+)
Brachiolejeunea complex														
Blepharolejeunea												++		
BRYOPTERIDOIDEAE														
Bryopteris													++	(2+)

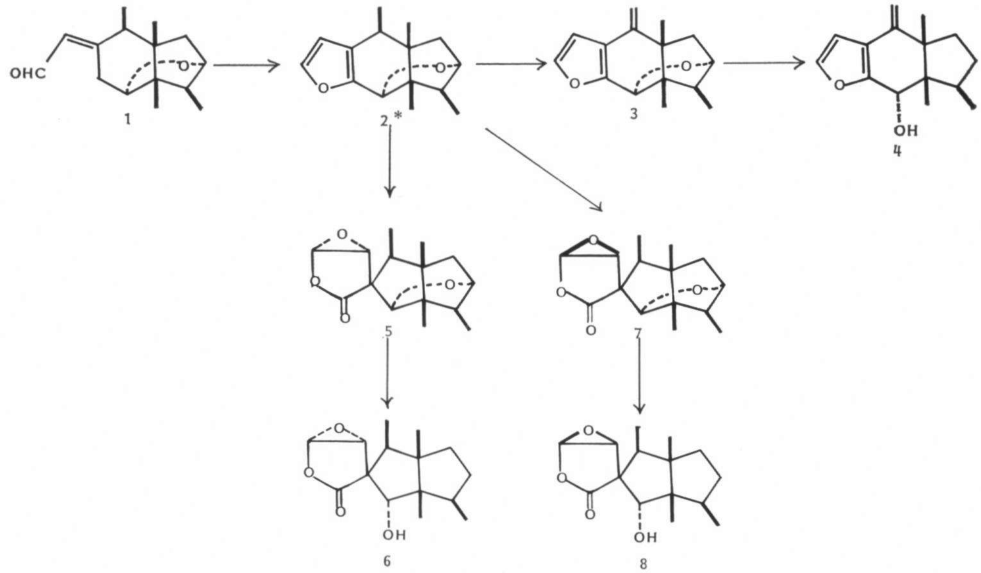

FIG. 1. Possible biogenetic pathways of the pinguisanines detected in the Lejeuneaceae. Compounds are numbered as in Table 2. *: the structure (2) has been revised by ^{1}H NMR.

distribution in the Jungermanniales seems to coincide with the Ptilidiinoid-Porelliinoid and Ptilidiinoid-Lepidolaeniinoid lines of evolution postulated by Schuster (1972) on morphological grounds and supported by flavonoid evidence as well (Mues 1982). Within Lejeuneaceae, pinguisanes have been detected in 10 different genera of Ptychanthoideae and in *Bryopteris* (Bryopteridoideae), but not in other subfamilies. About 25 different compounds were detected and 13 compounds have thus far been isolated and identified. Based on their presumed biogenesis, the known pinguisanes fall into two groups:

1. *Pinguisanines.* Eight compounds belong in this group (Table 2). Their possible biogenetic relationships are shown in Fig. 1. Pinguisanines appear to be chemical markers of the *Acrolejeuna* complex: *Acrolejeunea*, *Trocholejeuna* and *Frullanoides.* They were found in all investigated species (6) of this generic complex and on average 3–4 different pinguisanines were found in each sample (7 in *Frullanoides chinantlana*!), often as major components. Some pinguisanines are also found in the Ptilidiaceae (pinguisenal) or the Porellaceae (pinguisanin and pinguisanolide), but other compounds have not yet been detected in any other group of plants. Clearly, the members of the *Acrolejeunea* complex appear to be excellently characterized by their possession of pinguisanine-type substances.

2. *Pinguisones.* Pinguisone-type substances detected in the Lejeuneaceae include pinguisenol, pinguisenene, pinguisone and norpinguisone methyl ester (Table 2). Their tentative biogenetic relationships are depicted in Fig. 2. Norpinguisone methyl ester is the only norpinguisone so far detected in the Lejeuneaceae and it is perhaps

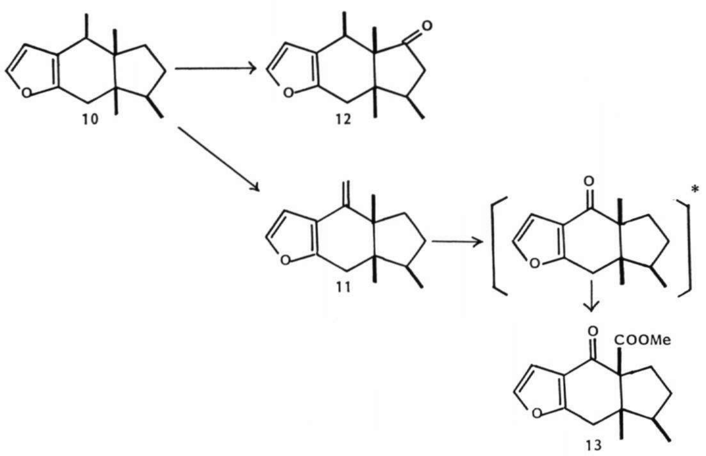

FIG. 2. Possible biogenetic pathways of the pinguisones detected in the Lejeuneaceae. Compounds are numbered as in Table 2. *: this compound (norpinguisone) has been isolated from *Porella vernicosa* and *Trichocoleopsis sacculata*, but not yet from Lejeuneaceae.

taxonomically significant that this substance, which is chemically somewhat less closely related to the detected pinguisones than the three others, was found in the Bryopteridoideae (as major component) but not in the Ptychanthoideae. Norpinguisone methyl ester has also been found in *Porella* and is a very common substance of that genus (Asakawa 1982). Other pinguisones detected as major components in the Lejeuneaceae are pinguisenene (marker of *Ptychanthus*) and pinguisone, which has been detected only in *Blepharolejeunea securifolia* (Gradstein et al. 1981). The scattered distribution pattern of pinguisones in the Lejeuneaceae that has emerged from our study is taxonomically intriguing and needs to be substantiated by further investigations.

Unidentified pinguisanes. Unidentified pinguisanes have been found as major compounds in *Ptychanthus*, *Tuzibeanthus*, and *Spruceanthus* and as minor compounds in several other genera. Of considerable taxonomic significance is the fact that the two unidentified pinguisanes of *Tuzibeanthus* are the same as those found in *Ptychanthus*. These two genera also share the same striatenes and labdanes as major components and are thus chemically very close (see below).

Striatenes. Striatene-type sesquiterpenes (striatene, striatol) were detected in Bryopteridoideae, Ptychanthoideae and in some members of the *Omphalanthus* complex (Lejeuneoideae): *Leucolejeunea*, *Cheilolejeunea* and *Anoplolejeunea*. Although apparently fairly widely distributed within the family, the distribution of the striatenes in the Lejeuneacae seems to coincide with taxonomic groups at the subfamily and genus complex level.

Calamenanes. 5-hydroxycalamenene is elaborated as a major component in all investigated species of *Lopholejeunea*: *L. eulopha*, *L. howei* and *L. subfusca*. Small quantities were detected in *Archilejeunea olivacea* and *Mastigolejeunea undulata*. Apparently, this compound is a chemical marker of *Lopholejeunea*.

Cinnamolide. Cinnamolide is the only drimane-type sesquiterpene thus far detected in the Lejeuneaceae and large amounts of this compound were detected in a sample of *Lejeunea flava* from Japan (Gradstein et al. 1985). The terpenoid content found in *Lejeunea flava* is quite unique among Lejeuneaceae and completely different from that of other investigated species (8) of the genus *Lejeunea*, all which contain diterpenoids as major components but no drimane-type sesquiterpenes.

Diterpenes

In contrast with the sesquiterpenes, very little is known about the absolute configuration of the diterpenes of the Lejeuneaceae. The taxonomic significance of the diterpenes can therefore only be assessed very provisionally. The most significant result thus far seems to be the detection of identical labdane-type diterpenes in the genera *Ptychanthus* and *Tuzibeanthus*. The taxonomic relationships of *Tuzibeanthus*, a monotypic genus from eastern Asia of which the sporophyte remains unknown, has been subject of diverging opinions among taxonomists. Mizutani (1961) placed it near *Ptychanthus*, Schuster (1963) placed it in *Mastigolejeunea* (as *M.* subgenus *Tuzibeanthus*), Gradstein (1975) placed it near *Archilejeunea*, in the *Archilejeunea* complex, and Inoue (1976), finally, reduced it to subgeneric rank under *Ptychanthus*. Though morphologically different from *Ptychanthus* by its very different leaf areolation, the terpenoid make-up of *Tuzibeanthus* is very similar to that of *Ptychanthus*: the two genera share the same pinguisanes (pinguisenene excepted), labdanes and striatenes as major components. Chemical affinities to *Mastigolejeunea* and *Archilejeunea*, however, have not been found. Our data appear to be in support of a very close relationship between *Tuzibeanthus* and *Ptychanthus* and indicate a more remote relationship of these two genera to other Ptychanthoids.

As stated above, species of the genus *Lejeunea* elaborate large quantities of diterpenoids (all still unidentified). In two species of *Cheilolejeunea* investigated, however, we have not detected any diterpenoids but instead found only a few sesquiterpenes, including striatenes. Species of *Lejeunea* and *Cheilolejeunea* have in the past often been confused although it is now generally recognised, on morphological grounds, that the two genera are quite unrelated and belong to different generic complexes. The detected chemical characteristics, although based on analysis of rather few samples only, apparently coincide with these morphological trends.

Flavonoids

A general screening on the presence of flavonoids and related hydrophilic compounds in Lejeuneaceae subfamily Ptychanthoideae was carried out by Kruijt et al. (1986). More recently, selected taxa of Lejeuneaceae were investigated by Mues and Klein (in prep.). In quite a number of genera flavonoids were observed on thin-layer plates (2D-TLC). However, often the flavonoids were present in small amounts only, as opposed to the terpenoids which are normally abundant. Furthermore, when more

TABLE 3. The occurrence of flavonoids in the genera of Lejeuneaceae subfamily Ptychanthoideae and some other genera (Kruijt et al. 1986, Mues unpubl.). + = flavonoids present. — = flavonoids absent. Tribal classification according to van Slageren (1985).

	Species checked (total nr. of spp. per genus)	FLAVONOIDS
PTYCHANTHEAE		
Acrolejeunea complex		
Acrolejeunea	1 (15)	?
Trocholejeunea	1 (2)	+
Frullanoides	1 (7)	+
Ptychanthus complex		
Schiffneriolejeunea	3 (16)	+
Mastigolejeunea	2 (15)	+
Thysananthus	5 (10)	+
Ptychanthus	1 (2)	?
Archilejeunea complex		
Spruceanthus	1 (5)	+
Archilejeunea	3 (10)	±
Lopholejeunea complex		
Lopholejeunea	3 (30)	±
Marchesinia	6 (7)	±
BRACHIOLEJEUNEAE		
Brachiolejeunea complex		
Brachiolejeunea	3 (5)	+
Blepharolejeunea	2 (5)	+
Dicranolejeunea	1 (8)	?
Odontolejeunea	1 (4)	?
Lindigianthus	1 (1)	—
Symbiezidium complex		
Symbiezidium	2 (3)	?
Stictolejeunea complex		
Neurolejeunea	1 (3)	±
Stictolejeunea	1 (2)	+
OTHER GENERA (LEJEUNEOIDEAE)		
Omphalanthus	4 (6)	—
Cheilolejeunea	1 (?)	+
Lejeunea	1 (?)	+

than one sample of a species was available for analysis, considerable variation in flavonoid content was sometimes observed. For instance, in two samples checked for *Brachiolejeunea laxifolia*, *B. phyllorhiza* and *Lopholejeunea evansiana* each, one sample contained flavonoids whereas the other lacked them; in five samples of *Archilejeunea juliformis* checked by us, one contained flavonoids but in the other four samples no trace of flavonoids could be detected. These findings are indicative of the existence of chemical races in certain species of the Lejeuneaceae, as has already been suggested for terpenoids by Gradstein et al. (1985) and for flavonoids by Kruijt et al. (1986).

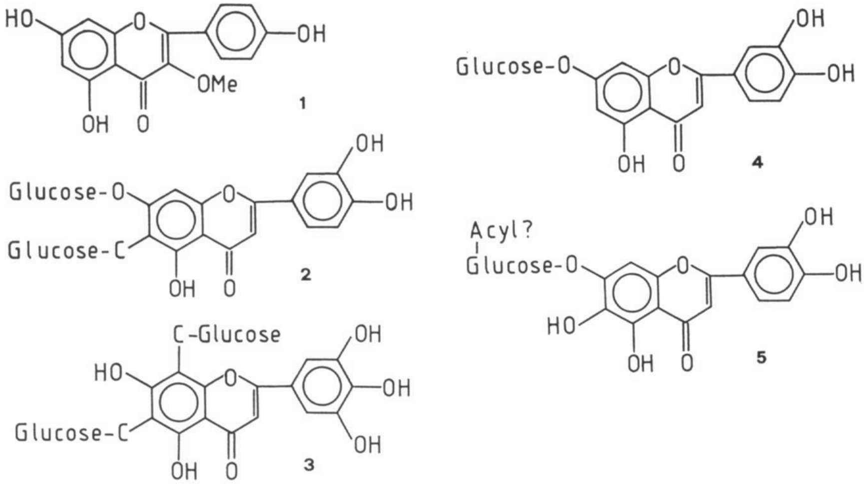

FIG. 3. Flavonoids detected in the Lejeuneaceae. 1. kaempferol-3-methylether. 2. lutonarin. 3. tricetin 6, 8-di-C-β-D-glucopyranoside. 4. luteolin 7-O-glucoside. 5. 6-hydroxyluteolin 7-O-glucoside acylated at the glucose.

Table 3 presents a listing of the Lejeuneaceae genera (mostly Ptychanthoideae) for which flavonoid analysis has been carried out and shows the occurrence of this compound type in the family. In addition to the Ptychanthoideae, which were already investigated (in part) by Kruijt et al. (1986), we have analysed the following species of the subfamily Lejeuneoideae: *Lejeunea cavifolia*, *Cheilolejeunea mimosa*, *Omphalanthus filiformis*, *O. jackii*, *O. ovalis* and *O. paramicola*. The first two species contained flavonoids but in all four species of *Omphalanthus* (2 samples per species checked) we were unable to detect any flavonoids. From six species of Lejeuneaceae flavonoid compounds have thus far been isolated and at least partly identified. In *Marchesinia brachiata* Kruijt et al. (1986) found two luteolin di-C-glycosides and from *Frullanoides densifolia* they isolated kaempferol-3-methylether (Fig. 3: 1), a free flavonol aglycone hitherto unknown in bryophytes. We have recently identified flavonoids from the following species: *Lejeunea cavifolia*, *Stictolejeunea squamata*, *Brachiolejeunea laxifolia* and *B. phyllorhiza*. The compounds were isolated by paper chromatography and their identity was determined by means of UV spectroscopy, hydrolysis and co-chromatography using authentic samples. The specimens were identified by the first author unless otherwise indicated.

1. ***Lejeunea cavifolia.*** Three flavonoid compounds were observed on 2D-TLCs, one of them only in traces. The two main compounds were identified as lutonarin (=iso-orientin 7-O-glucoside) and tricetin 6, 8-di-C-β-D-glucopyranoside (Fig. 3: 2, 3). The latter compound has been found in various liverwort genera, for instance *Metzgeria*, *Radula* and *Plagiochila*, but lutonarin was hitherto unknown in bryophytes.

Material investigated. Switzerland, near Interlaken, *Mues s.n.*, det. R. Mues (2, 95 g extracted).

2. ***Stictolejeunea squamata.*** Two flavonoids were observed on 2D-TLCs, one of them in traces only. The other flavonoid was isolated and identified as tricetin 6, 8-di-C-β-D-glucopyranoside (Fig. 3: 3), which was also detected in *Lejeunea cavifolia* and other bryophytes (see above).

Material investigated: Guyana, *Gradstein 4896* (250 mg), *Gradstein 5048* (170 mg); Suriname, *Lindeman et al. 620* (4 g), *Florschütz 4757* (60 mg); French Guiana, *Gradstein 5890* (250 mg).

3. ***Brachiolejeunea laxifolia.*** Luteolin-7-O-glucoside (Fig. 3: 4) was isolated from this species. Two further flavonoids were observed on a 2D-TLC in traces.

Material investigated: Colombia, *Florschütz 4465*, det. M. W. van Slageren (300 mg); Ecuador, *Gradstein et al. 3389 & 3413* (350 mg); Peru, *Hegewald 9261* (310 mg), *Frahm et al. 796* (900 mg).

4. ***Brachiolejeunea phyllorhiza.*** Four flavonoid compounds were detected on 2D-TLCs and identified as 1) 6-hydroxyluteolin-7-O-glucoside acylated with a still unknown acid at the glucose (Fig. 3: 5), 2) luteolin-7-O-glucoside, also found in *B. laxifolia* (Fig. 3: 4), 3) luteolin 7-O-glucoside acylated with a still unknown acid at the glucose, and 4) luteolin as free aglycone. These four compounds have been detected previously in other liverworts, especially in species of *Frullania* (Mues et al. 1983, Mues et al. 1984, Yuzawa et al. 1987).

Material investigated: Colombia, *Gradstein s.n.*, hb. Utrecht 421169B, det. R. Kruijt (8 g).

The above data on flavonoid occurrence in Lejeuneaceae hardly allow for conclusions on the chemotaxonomy of the family in general. Five different flavonoid structure types were observed, all of which have also been detected in other liverworts: flavonol, flavone di-C-glycoside, flavone C/O-glycoside, flavone O-glycoside, and acylated flavone O-glycoside. Thus, there appears to be no essential difference in flavonoid structure types between Lejeuneaceae and other liverworts, although flavonols have so far been detected in liverworts in a few species only. Some taxa, most notably the neotropical genus *Omphalanthus*, stand out by their apparent inability to biosynthesize flavonoids and in other genera flavonoids are produced only in very small amounts. The two species of *Brachiolejeunea* investigated both synthesize the same kind of flavonoids (luteolins), which may be of taxonomic significance. Further analysis of flavonoids in Lejeuneaceae might throw more light on the existence of correlations between flavonoid chemistry and the taxonomy of the species and genera of this large family of liverworts.

General Conclusion

The terpenoid and flavonoid content of the Lejeuneaceae is quite diversified and the study of this chemical diversity has proven to be a fruitful field of enquiry. The data obtained in the course of our investigations are in general insufficient to assess chemotaxonomy on the species level, due to the limited number of samples investigated and by lack of an understanding of the chemical variation within species. At higher taxonomic levels (genus, generic complex, subfamily), however, the data seem to be taxonomically significant in several instances and seem to lead to relevant conclusions concerning the correlation between morphology and chemistry. Nevertheless, it should be realized that the chemotaxonomic conclusions presented here are still preliminary and that much work needs to be done to substantiate our knowledge of the chemotaxonomy of the Lejeuneaceae.

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