STUDIES ON COLOMBIAN CRYPTOGAMS XIII. OIL BODIES AND TERPENOIDS IN LEJEUNEACEAE AND OTHER SELECTED HEPATICAE

S. ROB GRADSTEIN[1], REIKO MATSUDA[2]
AND YOSHINORI ASAKAWA[2]

In a preceding paper (Gradstein et al. 1977) oil bodies were described in 62 species of leafy Hepaticae from tropical South America. Four main morphological oil body types were distinguished (Fig. I): the *Massula*-type (small, homogeneous oil bodies), the *Bazzania*-type (large, homogeneous oil bodies), the *Jungermannia*-type (finely segmented oil bodies) and the *Calypogeia*-type (coarsely segmented oil bodies).

The present paper reports oil body data from twenty further neotropical species of leafy Hepaticae. In addition to oil body morphology, particular attention is paid to the chemical consituents, especially the terpenoids (mono-, sesqui-, di- and triterpenoids), which are generally assumed to be the chemical components of the liverwort oil bodies (e.g. Asakawa et al. 1980a, Suire & Asakawa 1979). Although the present study (the first of its kind based on tropical American bryophytes) yielded many new substances, most of them are still unidentified because the amount of plant material available was usually too small to permit their isolation.

About two-third of the species treated are members of the large and taxonomically complex, tropical family Lejeuneaceae (e.g. Schuster & Hattori 1954; Gradstein 1980), and all of them are "holostipous". Lejeuneaceae are usually subdivided into a number of subfamilies characterized e.g. by sporophyte characters and by the predominance of species with entire underleaves (holostipous) or divided underleaves (schizostipous). Among the two largest subfamilies Lejeuneoideae and Ptychanthoideae, species of Lejeuneoideae are mainly schizostipous whereas Ptychanthoideae are exclusively holostipous. The holostipous Lejeuneaceae are usually the bigger plants and therefore easier to handle for chemical analysis. Thus far, chemical data have been published for the following holostipous species of Lejeuneaceae (all Ptychanthoideae): *Marchesinia mackaii* from Europe (Asakawa et al. 1980a) and Japanese *Ptychanthus striatus* (e.g. Asakawa et al. 1980d), *Spruceanthus semirepandus* (Asakawa et al. 1980a), *Trocholejeunea sandvicensis* (Asakawa et al. 1980c, d) and *Tuzibeanthus chinensis* (Asakawa et al. 1980d). A large variety of terpenoid compounds was found, many of them still unidentified.

The living material on which our study was based was mainly collected in Colombia by the senior author and his co-workers in the summer of 1980, during the

[1] Institute of Systematic Botany, University of Utrecht, Heidelberglaan 2, Utrecht, The Netherlands.
[2] Institute of Pharmacognosy, Tokushima Bunri University, Yamashiro-cho, Tokushima 77.0 Japan.

third Ecoandes expedition (Aguirre & Van Reenen, 1980). Voucher specimens are kept in the herbaria of the Universities of Bogotá (COL) and Utrecht (U).

The material was purified and examined for oil bodies by the senior author and

TABLE 1. Terpenoids and aromatic compounds in Colombian Hepaticae.

Species	Compounds detected
Adelanthus decipiens (GA* 3688)	β-barbatene, **196 (181)** (aromatic compound), 196 (181), 252 (161), **218 (218)**, 248 (233), 280 (163), 280 (163), 280 (211), 280 (226), 232 (217) (eudesmanolide), **232 (217)** (eudesmanolide), 294 (81), n-C_{28}, 414 (43), 428 (69), 410 (69), 430 (55), campesterol **(8)**, stigmasterol **(9)**, sitosterol **(10)**, 426 (207) (sterol).
Clasmatocolea vermicularis (GA 3689)	β-barbatene, 204 (161), 204 (93), β-chamigrene, 220 (205), 222 (97), 220 (205), 222 (43), 222 (119), 220 (119), 220 (43), 218 (81), 220 (43), 218 (175), 278 (68), 232 (190) (eudesmanolide), **diplophylline (39)**, *oxyfrullanolide* **(40)**, *dihydrooxyfrullanolide* **(41)**, 250 (71), 410 (81), brassicasterol, campesterol, stigmasterol, sitosterol, 424 (55).
Cryptochila grandiflora (GA 3669)	202 (159), 204 (107), 204 (161), *β-barbatene*, γ-maaliene **(42)**, 204 (121), 220 (121), ? (69), ? (43), 220 (43), **220 (95)**, **218 (95)**, **220 (95)**, 248 (96), 220 (106), 262 (106), 278 (68), 278 (81), 278 (81), 278 (41), ? (79), 278 (81), ? (143), 326 (162), 314 (95), 372 (43) (diterpene acetate), 372 (94), 380 (83), 382 (382), 408 (208), brassicasterol, campesterol, stigmasterol, sitosterol, 428 (280), 426 (69).
Gongylanthus granatensis green form (GA 3694)	δ-cuparenol, 278 (68), 278 (81), 278 (81), 282 (107), 4-hydroxy-3′-methoxybibenzyl **(48)**, ? (134), 290 (134), ? (134), 248 (121) (aromatic compound), **3, 4′-dimethoxybibenzyl**, 410 (69), brassicasterol, campesterol. sitosterol, stigmasterol.
Gongylanthus granatensis whitish-blue form (GA 3695)	δ-elemene, 202 (159), β-barbatene, 202 (105), spathulenol **(49)**, ? (41), 220 (93), 220 (178), 272 (109), 278 (68), 298 (93), 272 (149), 234 (150), **276 (43)**, 286 (109), 286 (93), 286 (107), 318 (108) (furanoditerpene), 290 (123), 286 (107), 318 (125), 304 (95), 304 (137), 268 (255), 326 (326), n-C_{29}, campesterol, stigmasterol, diploptene (?),
Herbertus subdentatus (GA 3672)	longifolene **(43)**, 204 (119), 204 (135), cuparene **(44)**, 220 (205), 220 (161), ? (119), **δ-cuparenol (45)**, *iso-cuparenol* **(46)**, 290 (208), 2, 3-dihydroxycuparene **(47)**, 364 (135), 402 (207), 402 (251), 382 (382), ? (95), campesterol, stigmasterol, sitosterol, 426 (69), 424 (207), 426 (342).
Lepicolea pruinosa (GA 3667)	δ-elemene, 202 (159) (calamenene-type), α-elemene, β-selinene **(50)**, *α-selinene* **(51)**, bicyclogermacrene, cuparene, 220 (205), spathulenol, 218 (91), 202 (95), 220 (93), 220 (161), 220 (109), 278 (68), *dihydrofrullanolide* **(52)**, **frullanolide (53)**, 250 (81), 282 (92), n-C_{27}, n-C_{29}, 410 (69), 416 (82), 408 (82), 432 (95), 392 (97), campesterol, stigmasterol, 418 (82), 424 (257), 424 (409).
Syzygiella liberata (GA 3685)	β-barbatene, *trans-β*-farnesene, bicyclogermacrene, ? (93), **? (69)** (sesquiterpene alcohol), ? (109), ? (68), 294 (67), **272 (81)**, **286 (81)**, 288 (81), 336 (81), ? (59), 370 (95), 354 (310), 356 (161), campesterol, stigmasterol, 426 (69) (sterol).

Species	Compounds detected
LEJEUNEACEAE	
Anoplolejeunea conferta (GA 3674b)	124 (109), 122 (57), 122 (57), β-elemene (**1**), *bicyclogermacrene* (**2**), 202 (93), 218 (123), sesquiterpene alc: 220 (41), 220 (43), 220 (207), 234 (81), furanosesquiterpene 234 (108), PS-2 (**3**), PS-3 (**4**), 278 (68), 278 (109), *PS*-4 (**5**), *PS*-5 ,*PS*-6 (**6**), *PS*-7 (**7**), ? (123), ? (153), 336 (alkane), 410 (69), campesterol (**8**), stigmasterol (**9**), sitosterol (**10**).
Archilejeunea viridissima (G 3607)	122 (57), 122 (57), sesquiterpene hydrocarbon: 204 (123), β-elemene, 204 (95), ? (109), *bicyclogermacrene*, sesquiterpene alcohol: 222 (71), 220 (71), ? (137), ? (109), 222 (109), 220 (107). 238 (109), 220 (59), furanosesquiterpene 250 (109), 278 (68), 278 (82), 278 (81), 232 (176), 272 (135), 288 (176), phytol (**11**), 304 (95), 304 (95), 304 (189), 304 (149), 360 (95), 310 (59), n-C_{25}, 418 (81) (acetate), 410 (69), ? (113), 434 (43) (diterpene acetate), ? (113), campesterol, stigmasterol, sitosterol, 404 (319) (diterpene acetate).
Brachiolejeunea chinantlana (GVR 1857)	β-caryophyllene (**16**), *bicyclogermacrene*, sesquiterpene alcohols: 220 (95), 218 (109), 218 (109), 220 (43), pinguisanin (**17**), dehydropinguisanin (**18**), furanosesquiterpenes: 238 (123), 220 (109), 272 (109), 272 (135), *pinguisanolide* (**19**), isopinguisanolide (**20**), 272 (81), 272 (135), *hydroxypinguisanolide* (**21**), *hydroxyisopinguisanolide* (**22**), 236 (109), *pinguisenal* (**23**), 304 (95), 304 (147), 294 (69), ? (83), ? (57), ? (57), 420 (69), n-C_{29}, 430 (147), 394 (394), campesterol, stigmasterol, sitosterol.
Brachiolejeunea laxifolia (GA 3654)	128 (78), sesquiterpene hydrocarbons: bicyclogermacrene, 204 (95), 204 (161), sesquiterpene alcohols: 220 (109), ? (137), 220 (109), bazzanenol (?), 218 (82), γ-eudesmol (**15**), 222 (195), 222 (109), 220 (109), 236 (164), 250 (109), 278 (93), ? (135), 272 (191), 272 (191), 276 (189), 286 (149), 272 (135), ? (79), 298 (218), ? (203), 260 (188), 304 (147), ? (189), n-C_{25}, 410 (69), n-C_{27}, campesterol, stigmasterol, sitosterol, ? (257).
Brachiolejeunea securifolia (GA 3642)	sesquiterpene hydrocarbons: PS-1 (**24**), 204 (161), 204 (123), *bicyclogermacrene*, sesquiterpene alcohols: 220 (205), 222 (137), 220 (119), 220 (95), *pinguisone* (**25**), 260 (159), 260 (109), 278 (124), 272 (95), **244** (**244**), 304 (185), ? (107), 286 (205), 304 (147), 410 (69), campesterol, stigmasterol, sitosterol, 410 (257).
Bryopteris fruticulosa (GVR 1829)	122 (57), 122 (57), δ-elemene (**26**), 204 (161) (cadinane-type), 204 (121), *trans*-β-farnesene (**27**), *bicyclogermacrene*, *bazzanene*, sesquiterpene alcohols: 220 (109), 220 (202), 220 (202), 220 (82), 222 (107), 220 (205), 260 (185), 220 (59), *norpinguisanemethyl ester* (**28**), 272 (135), 278 (68), 278 (81), 278 (81), 294 (69), 306 (246), 322 (108), 326 (79), 326 (81), 326 (277), 360 (95), 360 (147), 360 (288), 362 (55) (diterpene acetate,) 306 (135), 306 (221), 396 (43) (diterpene acetate), 378 (177) (diterpene acetate), 378 (43) (diterpene acetate), 368 (208), 376 (43) (diterpene acetate), 360 (43) (diterpene acetate), 410 (69), ? (208), campesterol, stimgasterol, sitosterol, 476 (135).

Species	Compounds detected
Dicranolejeunea cipaconea (GA 3696)	204 (93), 204 (124), *bicyclogermacrene*, 220 (109), 220 (109), 218 (137), ? (109), 220 (82), 222 (162), 230 (195), 222 (123), 272 (59), 272 (109), 272 (135), 278 (68), 278 (81), 286 (206), 264 (69), 286 (175), 246 (176), 290 (71), 304 (95), 304 (147), 304 (59), 304 (67), 304 (137), 410 (69), 382 (382), 394 (394), campesterol. stigmasterol, sitosterol, 416 (43), (sterol), 410 (55).
Leucolejeunea xanthocarpa (GA 3674a)	thujopsene (**31**), δ-elemene, *β-chamigrene* (**32**), 204 (189), 204 (136), PS-1, 220 (205), 222 (151), 222 (207), 272 (229), 272 (95), 272 (257), 3, 4′-dimethoxybibenzyl (**33**), 276 (155), ? (155), 310 (155), 330 (189), 316: 318 (175), 364: 366 (189), 350: 352 (175: 177), ? (177), 402 (136), 406 (169), campesterol, stigmasterol, sitosterol, 428 (207).
Marchesinia brachiata fertile, dead (GVR 2017)	204 (119), acoradiene (**34**), calamenene (**35**), ? (208), 272 (229), 272 (229), 272 (135), 278 (68), 286 (57), 278 (68), 286 (135), 286 (74), 272 (135), 304 (121), 302 (81), 308 (55), 304 (95), 360 (43), 286 (243), 306 (137), 304 (179), 410 (131), 430 (71), 401 (69), n-C_{29}, campesterol, stigmasterol, sitosterol.
Marchesinia brachiata sterile (VS s.n.)	n-octane, n-nonane, iso-nonane, undecane, isoundecane, 204 (161), 204 (121), 204 (81), δ-elemene, **β-caryophyllene (16)**, *bicyclogermacrene*, dimethyleugenol (**36**), 4-*hydroxy*-3, 5-*dimethoxy allylbenezene* (**37**) or 3-*hydroxy*-4, 5-*dimethoxy allylbenzene* (**37′**), 220 (109), 220 (107), ? (208), 220 (208), 220 (82), 234 (43), 278 (68), 270 (74), ? (99), 294 (67), ? (71), 270 (57), ? (194), ? (208), ? (194), ? (194), 386 (386), ? (194), ? (194), 298 (298), campesterol, stigmasterol, sitosterol.
Omphalanthus paramicola (GA 3674)	204 (161), β-caryophyllene, β-barbatene, *β-chamigrene*, **204 (69)**, 222 (43), **222 (43)**, 220 (220), 220 (220), 272 (205), 272 (135), 272 (135), 272 (121), 272 (137), 274 (124), ? (135), 288 (135), 360 (135), 302 (137), **304 (135)**, 304 (179), 410 (69), 382 (281) campesterol, stigmasterol, sitosterol.
Omphalanthus platycoleus (G 3579)	204 (189), (chamigrene-type), **widdrene (38)**, δ-elemene, **β-chamigrene**, 204 (136), **bazzanene**, 204 (93), 222 (151), 220 (123), 222 (207), **234 (219)** (dihydrosesquiterpene lactone), 344 (124), 416 (151) (bibenzyl), campesterol, stigmasterol, sitosterol.
Symbiezidium barbiflorum (G 3606)	n-octane, n-nonane, n-undecane, PS-1, 204 (107), β-chamigrene, 204 (95), ? (207), 204 (121), **bicyclogermacrene**, ? (137), 220 (43), 238 (97), 222 (107), 252 (193), 282 (109), 282 (43), 282 (109), 266 (97), 276 (276), 278 (68), 268 (81), 278 (81), *?* (190) (acetate), 276 (221), 268 (57), ? (43) (acetate), ? (141), 352 (219), ? (95), ? (57), (alkane), ? (57) (alkane), 410(69), n-C_{29}, campesterol, stigmasterol, sitosterol.

* Collectors are abbreviated as follows (for full collection data see text): G = S.R. Gradstein; GA = S.R. Gradstein & J. Aguirre C.; GVR = S.R. Gradstein & G.B.A. Van Reenen; VS = M.W. Van Slageren.

subsequently analyzed chemically by the junior authors. Air-dried ground material was extracted with ether. The crude extracts were directly analyzed by gaschromatography-mass spectrometry (GC-MS). The mass spectra obtained by GC-MS equipped with a computer were identified by direct comparison with those of authentic specimens and/or published information. The major components were further isolated by preparative thin layer chromatography and their chemical structures were confirmed by spectral evidence. Table I lists the identified and unidentified compounds detected in each species. Known chemical structures are shown in Figs. II–IV. Details of the chemical structure of new compounds will be reported elsewhere.

RESULTS

HERBERTACEAE

Herbertus subdentatus (Steph.) Fulf.

Oil bodies *Jungermannia*-type, numerous per leaf cell, similar to those recorded by Gradstein et al. (1977) for the related *H. limbatus* (= *H. acanthelius*, fide Van Reenen, 1981) (Colombia, Páramo de Guasca, 3150 m, sterile, Gradstein & Aguirre 3672, det. G.B.A. Van Reenen).

Herbertus subdentatus elaborates cuparene (44), δ-cuparenol (45) and isocuparenol (46) as major components. Cuparene and δ-cuparenol are also the major components of *H. aduncus* ssp. *aduncus* and *H. aduncus* ssp. *sakuraii* from Japan (Asakawa et al. 1979b, 1980a) and it thus appears that *H. subdentatus* and *H. aduncus* are chemically rather similar. This supports the view held by Van Reenen (1981) that the Andean *H. subdentatus* is taxonomically very close to *H. aduncus*.

LEPICOLEACEAE

Lepicolea pruinosa (Tayl.) Spruce

Oil bodies *Massula*-type, 5–8 per leaf cell, small, irregularly ellipsoid, 6–8 × 4 μm, homogeneous, masked by the numerous chloroplasts (Colombia, Páramo de Guasca, 3150 m, sterile, Gradstein & Aguirre 3667, det. R. Grolle).

A blueish-green, very slender shade form of this species.

Oil bodies in this specimen are similar to those reported for *Lepicolea scolopendra* from New Zealand (Stewart, 1978).

The chemical constitution of *Lepicolea pruinosa* is of considerable interest because it consists of the two sesquiterpene lactones frullanolide (52) and dihydrofrullanolide (53) as major components. These components are well-known as the characteristic allergenic substances of Frullaniaceae (Asakawa et al. 1976) and their discovery in *Lepicolea* constitutes the first record of these evolved sesquiterpenoids in a group of Jungermanniales considered to be primitive. Another chemical similarity to *Frullania* is the presence of selinene-type sesquiterpene hydrocarbons (50, 51).

ADELANTHACEAE

Adelanthus decipiens (Hook.) Mitt.

Oil bodies *Jungermannia*-type, present in all leaf cells, 5–12 per cell except in the larger leaf-base cells, which have up to 20 oil bodies; globose to subellipsoid, 4–11 × 4–8 μm, finely granulose within a very distinct membrane, brownish-gray (Colombia, Páramo de Guasca, 3150 m, sterile, Gradstein & Aguirre 3688, det. teste R. Grolle).

Oil bodies in this specimen (a weak shade-form with small or reduced teeth at leaf apex, approaching *A. crossii* Spruce) are similar to those illustrated by Schuster (1967) for plants from the West Indies. The gaschromatogram of *A. decipiens* shows an unidentified aromatic compound and an eudesmane-type sesquiterpene lactone as the main chemical components. The second major ones are three unidentified oxygenated sesquiterpenes. Diterpenes appear to be lacking in this species.

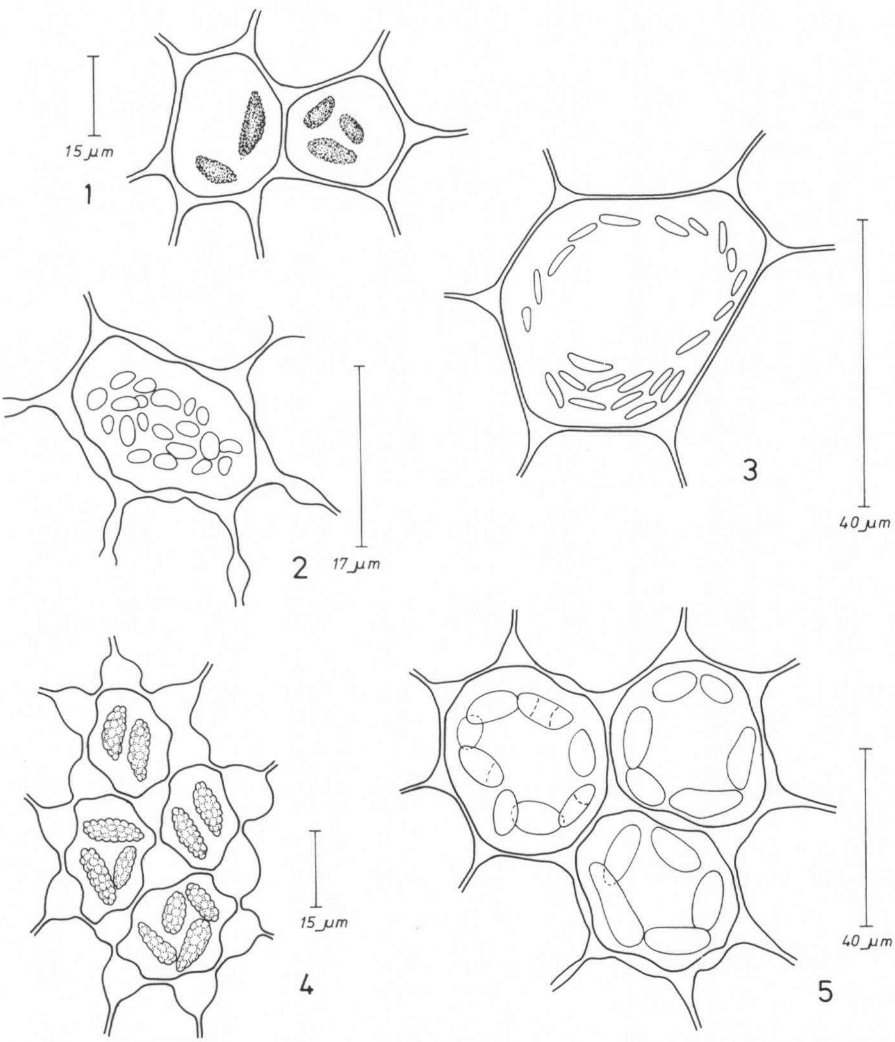

FIG. 1. Oil bodies in Colombian Lejeuneaceae. 1. *Anoplolejeunea conferta* (Meissn.) Evans: *Jungermannia* type. 2. *Archilejeunea viridissima* (Lindenb.) Evans: *Massula* type. 3. *Dicranolejeunea cipaconea* (Gott.) Steph.: *Massula* type. 4. *Omphalanthus paramicolus* (Herz.) Gradst.: *Calypogeia* type (but rather large). 5. *Symbiezidium barbiflorum* (Lindenb. & Gott.) Trev.: *Bazzania* type.

JUNGERMANNIACEAE

Cryptochila grandiflora (Lindenb. & Gott.) Grolle

Oil bodies *Jungermannia*-type, 2–6 per leaf cell, globose to subellipsoid, 5–9×4–5 μm, finely granulose-papillose, becoming almost homogeneous upon degeneration (Colombia, Páramo de Guasca, 3150 m, sterile, Gradstein & Aguirre 3669, det. teste R. Grolle).

Stewart (1978) reported coarsely segmented to homogeneous oil bodies in this species. His observations might have been based in part on degenerating material.

Cryptochila grandiflora produces β-barbatene (13) as major sesquiterpene hydrocarbon, a compound which is widely distributed among the Hepaticae. Other major components are two unidentified sesquiterpene alcohols and diterpene acetates.

ARNELLIACEAE

Gongylanthus granatensis (Gott.) Steph.

Oil bodies *Jungermannia*-type, similar to those reported earted earlier for this species (Gradstein et al. 1977) except for their somewhat smaller number (2–6 per leaf cell) and their larger size 8–14 μm (Colombia, Páramo de Guasca, 3150 m, sterile, Gradstein & Aguirre 3694 & 3695, det. teste R. Grolle).

Gongylanthus granatensis exists in Colombia in two strikingly different colour forms: a dark green form (Gradstein 3694) and a whitish-blue form (Gradstein & Aguirre 3695). Morphologically the two forms seem to be ± identical, apart from their colour, but in chemical respect they are completely different. The green form shows a very simple gaschromatogram, mainly consisting of various aromatic compounds, particularly bibenzyl derivatives (48) as the major components. The whitish-blue form, however, has a much more complicated chemical constitution, consisting of an unidentified sesquiterpene acetate and a furanoditerpenoid (probably) as major components and sesquieterpene hydrocarbons such as δ-elemene (26), β-barbatene (13) and a sesquiterpene alcohol, spathulenol (49) and various unidentified diterpenoids as minor components. Further material, preferably larger quantities, are needed to describe the observed chemical variation in *Gongylanthus granatensis* more adequately.

The two colour forms were found growing together in the field in various shaded as well as exposed habitats. A clear-cut habitat difference has not been observed, although it was noted that the whitish-blue form thrives more vigorously in the shaded locations.

LOPHOCOLEACEAE

Clasmatocolea vermicularis (Lehm.) Grolle

Oil bodies *Jungermannia*-type, 2–3 per leaf cell, identical to those observed earlier in this species (Gradstein et al. 1977) (Colombia, Páramo de Gusca, 3150 m, sterile, Gradstein & Aguirre 3689).

The genus *Clasmatocolea* consists according to Engel (1980) of twenty species belonging to several morphologically distinct subgenera. Oil body structure, however, seems to be very uniform in this genus. *Clasmatocolea vermicularis* elaborates the eudesmane sesquiterpene lactones diplophylline (39) and oxyfrullanolide (40) and its dihydroderivative (41) as main components. Diplophylline has already been isolated from *Chiloscyphus polyanthos* (Asakawa et al. 1979a), which belongs to the same family as *Clasmatocolea*. The presence of oxyfrullanolide is of considerable interest because this component, known as one of the characteristic allergenic substances of *Frullania dilatata* (Knoche et al. 1969; Asakawa et al. 1976), is reported here for the first time from a species outside Frullaniaceae.

PLAGIOCHILACEAE

Syzygiella liberata Inoue

Oil bodies *Jungermannia*-type, present in all leaf cells, highly variable in number, ca 3–12 per cell, globose to irregularly ellipsoid-angular, 4–8×4 μm, finely granulose-papillose, colourless (Colombia, Páramo de Guasca, 3150 m, fertile (female), Gradstein & Aguirre 3685).

Syzygiella liberata belongs in *S.* subg. *Pseudoplagiochila* – habitually very similar to *Plagiochila* – and is thus only known from a few localities in the Colombian Andes (Gradstein & Hekking, 1979). The oil bodies in *S. liberata* appear to be similar to those found in other species of the genus, except for their more variable number.

S. liberata produces a sesquiterpene alcohol and oxygeneated diterpenoids as the major components, but no *ent*-secoaromadendrane-type sesquiterpenes characteristic for *Plagiochila* (Asakawa et al. 1980c).

Thus, *S. liberata* shows no particular chemical affinity to *Plagiochila*.

LEJEUNEACEAE SUBFAM. BRYOPTERIDOIDEAE

Bryopteris fruticulosa Tayl.

Oil bodies *Massula*-type, present in all leaf cells and rather numerous, 15–25 per cell, small, narrowly ellipsoid to globose, (2–)4–5×2 μm, homogeneous (Colombia, Risaralda, Marsella, 1500 m, fertile, Gradstein & Van Reenen 1829)

Our material is autoicous ("*Br. fruticulosa* ssp. *monoica* Stotler") and the oil bodies are similar to those reported earlier for *Bryopteris* (e.g. Stotler & Crandall-Stotler 1974).

The crude extract shows a complex gaschromatogram with the common sesquiterpene hydrocarbons bazzanene (14) (known from various species of *Bazzania*) and bicyclogermacrene (2), and the furanosesquiterpene norpinguisane-methylester (28), known from various *Porella* species (e.g. Asakawa et al. 1978), as the major sesquiterpenoid components.

Bryopteris fruticulosa also elaborates a number of unidentified diterpene acetates.

LEJEUNEACEAE SUBFAM. PTYCHATHOIDEAE

Archilejeunea viridissima (Lindenb.) Evans

Oil bodies (Fig. I.2) *Massula*-type, present in all leaf cells and largely filling up the cell lumen, 15–20 per cell, bluntly ellipsoid, 5–7×2–3 μm, sometimes appearing globose (when seen from the side), ca 2–4 μm, homogeneous (Colombia, Risaralda, Marsella, 1500 m, fertile, Gradstein 3607, det. G. M. C. Buskes).

The presence of homogeneous, *Massula*-type oil bodies in *Archilejeunea viridissima* is of considerable taxonomic interest, because the closely related *Archilejeunea parviflora* and some African *Archilejeunea* species have segmented, *Jungermannia*-type oil bodies (Gradstein, 1975; Geissler & Gradstein, 1981). On the other hand, *Massula*-type oil bodies do occur in *Archilejeunea kiushiana* from Japan and in the very closely related (congeneric?) tropical Asiatic genus *Spruceanthus*.

The observed occurence of segmented and homogeneous oil bodies within a single genus was thus far not yet known from the genera of Ptychanthoideae, but it does occur occasionally in genera of other subfamilies, e.g. in *Lejeunea* and *Taxilejeunea* (Lejeuneoideae) and in *Colura* (Cololejeuneoideae). Normally, however, the different oil body types serve as stable, generic characters in Lejeuneaceae (e.g. Schuster & Hattori, 1954).

The gaschromatogram of *Archilejeunea viridissima* shows a large amount of unidentified sesquiterpene alcohols, furanoditerpenes and a diterpene acetate. The major sesquiterpene hydrocarbon is the common bicyclogermacrene (2).

Brachiolejeunea (Spruce) Schiffn.

Three different species of this common neotropical genus have been studied: two species of the subgenus *Brachiolejeunea* (*Br. laxifolia, Br. securifolia*) and one species of the subgenus *Plicolejeunea* (*Br. chinantlana*).

Brachiolejeunea chinantlana Schiffn.

Oil bodies *Massula*-type, present in all leaf cells, slightly larger/broader and less numerous than in *Br. laxifolia*, 12–20 per cell, broadly ellipsoid, 6–8 × 3–4 μm, often appearing rounded (when seen from the side), ca 3–4 μm, homogeneous (Colombia, Risaralda, Marsella, 1500 m, fertile, Gradstein & Van Reenen 1857).

New to Colombia. This species is closely related to *Brachiolejeunea densifolia* and differes mainly by the paroicous inflorescence.

Brachiolejeunea chinantlana elaborates several pinguisane-type sesquiterpenes, such as pinguisanin (17), pinguisanolide (19) and pinguisenal (23), which are also major components of the related *Trocholejeunea sandvicensis* (Asakawa et al. 1980b) and *Acrolejeunea pusilla* (unpubl. obs.) from Japan. The close taxonomic relationship between *Brachiolejeunea* subg. *Plicolejeunea, Trocholejeunea* and *Acrolejeunea* (Gradstein, 1975) thus seems confirmed by terpenoid chemistry.

Brachiolejeunea laxifolia (Tayl.) Schiffn.

Oil bodies *Massula*-type, homogeneous, similar to those reported for this species by Gradstein et al. (1977) (Colombia, Páramo de Chisaca, 3700 m, fertile, with *Brachiolejeunea securifolia*, Gradstein & Aguirre 3654, det, teste M.W. van Slageren).

The gaschromatogram shows two unidentified sesquiterpene alcohols and three oxygenated sesquiterpenoids as major components. The presence of sesquiterpene and diterpene hydrocarbons is poor.

Brachiolejeunea securifolia (Spruce) Steph.

Oil bodies *Massula*-type (?), ± homogeneous or faintly segmented by 2–8 septations (degeneration?), present in all leaf cells, 10–15 per leaf cell, narrow ellipsoid, 5–8 × 2–2.5 μm or globose, 2–3 μm, colourless (Colombia, Páramo S. Isabel, 3750 m, fertile, Gradstein & Aguirre s.n.; ibid., Páramo de Chisacá, 3700 m, fertile, Gradstein & Aguirre 3642, det, teste M.W. van Slageren).

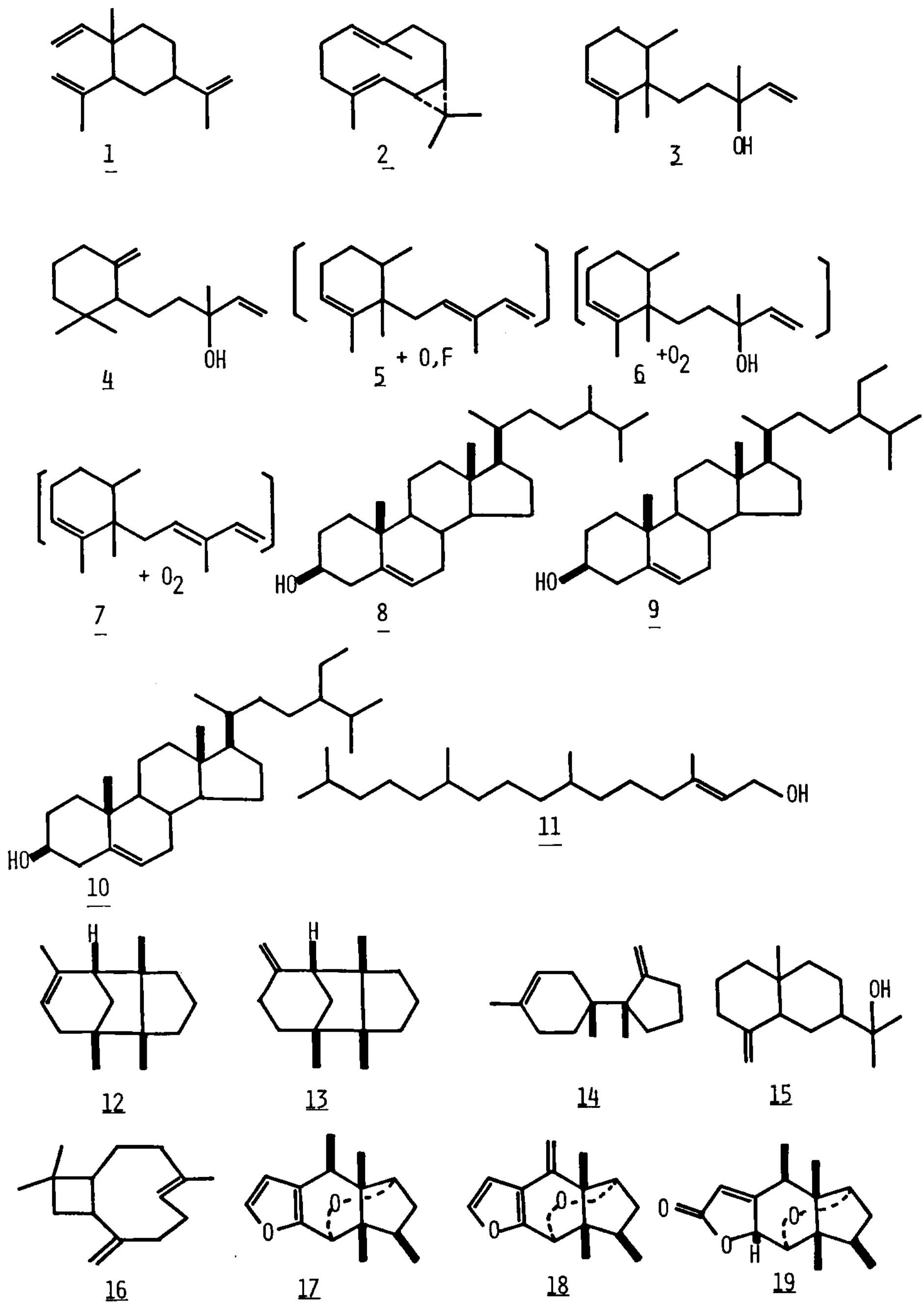

FIG. 2. Some terpenoids and aromatic compounds detected in Colombian Hepaticae.

New to Colombia, where it probably is not uncommon in the higher Andean zones as a heliophilous epiphyte, ranging from the upper subandean forest to the subpáramo (ca 2500–3400 m). Oil bodies in *Brachiolejeunea securifolia* are ± similar to those in the related *Br. nitidiuscula* (Gradstein et al. 1977).

Br. securifolia elaborates the common bicyclogermacrene (2), the furanosesquiterpene pinguisone (25), isolated from *Aneura pinguis* (Benesova et al. 1969), and three other sesquiterpenoids and a diterpene (M^+ 304) as major components. The species shows no particular affinity to *Br. laxifolia*, the type species of *Brachiolejeunea*.

A weak relationship with *Br. chinantlana* is seen since both species biosynthesize the common pinguisane-type sesquiterpenes, like pinguisanin and pinguisone. The production of these sesquiterpenoids is much more diversified, however, in *Br. chinantlana*.

Dicranolejeunea cipaconea (Gott.) Steph.

Dicranolejeunea circinnata (Spruce) Steph. *syn. nov.*

Oil bodies (Fig. I.3) *Massula*-type, present in all leaf cells, 10–15 in median leaf cells, up to 25 in the larger, basal leaf cells, small, narrowly ellipsoid, 5–7×2–2.5 μm, homogeneous (Colombia, Páramo de Guasca, 3150 m, male plants, Gradstein & Aguirre 3696).

A rare, robust high-Andean species, earlier known only by 19th century type collections from Colombia (leg. Lindig, isosyntype of *Lejeunea cipaconea* Gott. in G, fide Dr P. E. Geissler) and Peru (Andes, Tunguragua, leg. Spruce, isotype of *Lejeunea circinnata* Spruce in BM). The observed presence of homogeneous oil bodies in *Dicranolejeunea cipaconea* is remarkable, because other species of *Dicranolejeunea*, including its type species *D. axillaris*, have finely segmented, *Jungermannia*-type oil bodies (Gradstein et al. 1977). See also our remarks under *Archilejeunea viridissima*.

The gaschromatogram of *D. cipaconea* shows many sesqui- and diterpenoids. The major components are two unidentified oxygenated sesquiterpenoids (?) and probably a diterpene hydrocarbon (M^+ 272).

Marchesinia brachiata (Sw.) Schiffn.

Oil bodies *Massula*-type but rather large, tending to the *Bazzania*-type, 7–15 per leaf cell, bluntly ellipsoid to subglobose, 5–9×3–5 μm, homogeneous, rapidly desintegrating (Colombia, Risaralda, above Termales, fertile (female), 2500 m, Gradstein & Van Reenen 2017; Netherlands Antilles, Saba, 800 m, sterile, Van Slageren s.n., 23.VIII. 1980).

Oil body data agree with earlier observations in *Marchesinia brachiata* (Gradstein, 1975). *M. brachiata* is a common, widespread neotropical species, which shows considerable morphological variation (e.g. Evans, 1908). The two collections examined represent quite different forms of the species. The Colombian plants are robust and fertile with forked branching and numerous perianths, imbricated mucronate leaves, large underleaves (six times stem width) and 3-toothed lobules. The plants from Saba are much more slender, sterile and sparingly branched with rather distant, mucronate leaves, smaller underleaves (3–4 times stem width) and 2-toothed lobules.

Chemically only the sterile plants from Saba have been analysed from fresh material. Major components are the sesquiterpene hydrocarbons bicyclogermacrene (2) and β-caryophyllene (16) and some eugenol derivatives including dimethyl eugenol, which has also been found in *Marchesinia mackaii* (Asakawa et al. 1980a). From the robust, fertile Colombian sample only $\pm$ dead plants, slightly attacked by fungi, were available for chemical analysis. The gaschromatogram of this sample is completely different from that obtained from the living plants from Saba, showing neither eugenol compounds nor large amounts of sesquiterpene hydrocarbons but instead much oxygenated diterpenoids together with oxygenated sesquiterpenoids. Although we assume that the observed chemical differences are, at least in part, due to the different conditions of the two samples, some chemical variation might be expected to occur in living populations of this polymorphic species. This deserves further study.

Symbiezidium barbiflorum (Lindenb. & Gott.) Trevis.

Oil bodies (Fig. I.5) *Bazzaina*-type, ca 4–7 per leaf cell, present in all leaf cells, large, ellipsoid, 10–20×4–6 μm, homogeneous or, rarely (degeneration?), with a few (2–5) septations (Colombia, Risaralda, Marsella, 1500 m, fertile, Gradstein 3066).

This is the first report of *Bazzania*-type oil bodies in Lejeuneaceae. *Symbiezidium* oil bodies, previously unknown, are not unlike those in the related genus *Marchesinia*, but the latter often has smaller and more numerous oil bodies, more resembling the *Massula*-type.

Symbiezidium barbiflorum produces much bicyclogermacrene (2), together with various sesquiterpene acetates and what seems to be an oxygenated diterpene (M^+ 352) as major components. It further contains PS-1 (24) and unidentified sesquiterpene alcohols as minor components.

LEJEUNEACEAE SUBFAM. LEJEUNEOIDEAE

Anoplolejeunea conferta (Meissn.) Evans

Oil bodies (Fig. I.1) *Jungermannia*-type, present in all leaf cells, 1–4 per cell, rather large, broadly ellipsoid and often narrowly pointed, or more or less globose, 6–15×4–6 μm, finely granulose-papillose (Colombia, Páramo de Guasaca, 3150 m, fertile, with *Leucolejeunea xanthocarpa* and *Omphalanthus paramicolus*, Gradstein & Aguirre 3674b).

The oil bodies in this sample are similar to those described by Lorscheitter-Baptista (1977) for southern Brazilian *Anoplolejeunea* sp. Earlier reports of numerous small, homogeneous, *Massula*-type oil bodies in *Anoplolejeunea conferta* (Gradstein, 1975; Gradstein et al. 1977) must be erroneous and have probably been obtained from plants with degenerated oil bodies.

Anoplolejeunea conferta elaborates several unique, unidentified sesquiterpenes like (3) and (4), which have also been detected in *Ptychanthus striatus* (Lejeuneaceae subfam. Ptychanthoideae) (Takeda et al. 1980). The main sesquiterpene hydrocarbon is bicyclogermacrene (2), which is widely distributed in the Hepaticae. The major oxygenated sesquiterpene alcohols are PS-series (5–7), whose structure remains to be clarified.

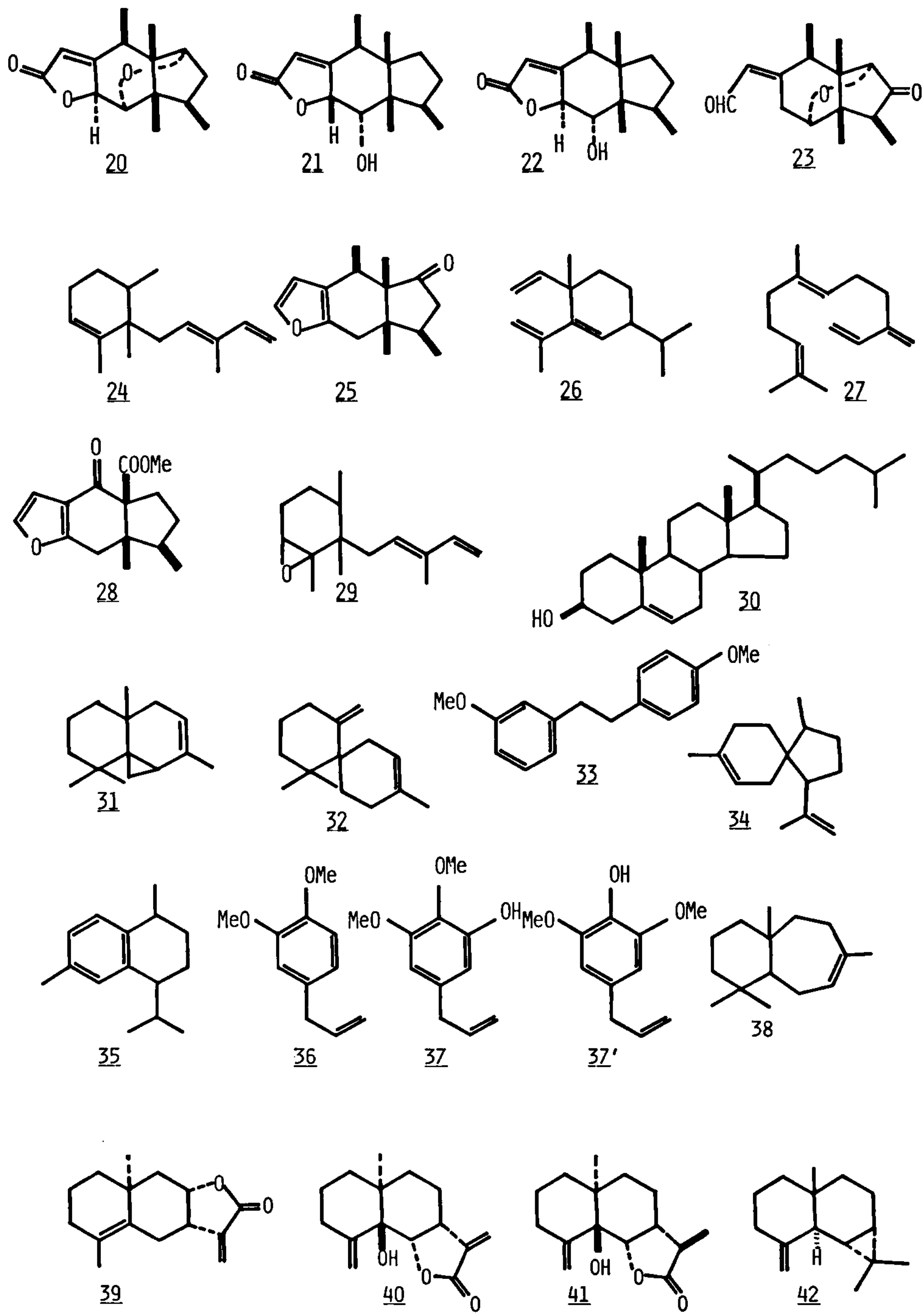

FIG. 3. Some terpenoids and aromatic compounds detected in Colombian Hepaticae.

Leucolejeunea xanthocarpa (Lindenb. & Gott.) Evans

Oil bodies *Calypogeia*-type but very large ("*Leucolejeunea-type*", Schuster, 1966), 1–2 per leaf cell, 14–22×6–10 μm, grayish-brown, rather finely granulose-papillose (less coarsely granulose as in the related genus *Cheilolejeunea*), upon degerneration falling apart into numerous small granules (Colombia, Páramo de Guasca, 3150 m, sterile, with *Anoplolejeunea conferta* and *Omphalanthus paramicolus*, Gradstein & Aguirre 3674a).

Leucolejeunea xanthocarpa elaborates β-chamigrene (32) and probably its epimer as major components. A bibenzylderivative (33) was also detected, as a minor substances.

L. xanthocarpa is chemotaxonomically interesting because of the presence of three components with two pair molecular weight peaks (316: 318; 364: 366; 350: 352), none of which were detected in other members of the family thus far. Two of these components are also among the major substances.

Omphalanthus Nees

The neotropical genus *Omphalanthus* Nees (excl. *O. roccatii* (Gola) Schust. from E. Africa = *Evansiolejeunea*) was long considered to consist of a single common species, *O. filiformis* (Sw.) Nees, characterised by the pendulous growth, rounded leaves, large, undivided underleaves, cell walls with large, knot-like trigones and no intermediate thickenings, bluntly pointed lobules with a distal papilla and the terete-eplicate perianth (Evans, 1908). Recently, the circumscription of the genus was broadened by the description of *O. platycoleus* Herz. from Colombia (Herzog, 1955), which has a flattened, 3-plicate perianth, and by the incorporation in *Omphalanthus* of *Peltolejeunea* (Spruce) Schiffn. (Schuster, 1963), comprising species with narrow, pointed leaves and 5-plicate perianths.

During last year's fieldwork in the Colombian Andes, the first author collected living material of three species of *Omphalanthus*: the common *O. filiformis* and the rare *O. platycoleus* Herz. and *O. paramicola* (Herz.) Gradst. *comb. nov.* (*Brachiolejeunea paramicola* Herzog, Hedwigia 74: 95, fig. 8a-b. 1934). The latter species is a typical *Omphalanthus* (but see below) except for its perianth, which is pluriplicate (2 lateral, 1–2 dorsal and 3–4 ventral folds). The genus as here defined thus embraces species with perianths ranging from eplicate to pluriplicate and inflated to flattened, which examplifies the current trend in Lejeuneaceae taxonomy to attribute less weight to perianth characters for generic delimitation (Schuster, 1963; Gradstein, 1980).

Omphalanthus apparently attains its highest diversity in the tropical Andes, where at least five species occur: *O. filiformis* (Sw.) Nees (? = *O. grandistipulus* Steph.), *O. jackii* (Steph.) Gradst., *O. ovalis* (Lindenb. & Gott.) Gradst. (? = *O. wallisii* (Steph.) Gradst.), *O. platycoleus* Herz. and *O. paramicola* (Herz.) Gradst.[8] Some further binomin in *Omphalanthus* and *Peltolejeunea* exist, but their status is doubtful and in need of revision. A further deviating character of *O. paramicola* is the presence of

[8] A second pluriplicate species of *Omphalanthus* was recently discovered by Dr. A. M. Cleef at 4160 m (!) in the Sierra Nevada de Cocuy, Colombia (Cleef 10373). This species stands out by its highly papillose cuticle and is apparently undescribed.

brownish cell-wall pigmentation, a character lacking in other species of *Omphalanthus* (and most other Lejeuneoideae!) but present in the recently described genus *Aureolejeunea* Schuster (Phytologia **29**: 428–429, 1978). This genus, based on four new species described by Schuster from the paramo's above Merida, Venezuela, seems closely related to *Omphalanthus*. Judging from the original diagnosis (type specimens have not been made available) *Aureolejeunea* seems to differ mainly by the creeping habit, the thinner stems, which have the ventral merophyte only 2–4 cells wide as in *Leucolejeunea* and the smaller overall size of the plants. The genus was compared by its author with *Leucolejeunea*. The above species can be distinguished by the following key:

1. Leaf-lobe apex narrow, (sub)acute to finely acuminate. Perianth inflated, 5-plicate, beak long (8 cells or more). Autoicous 2
1. Leaf-lobe apex broader, rounded to subobtuse. Perianth inflated-eplicate or flattened-plicate, beak short (up to 3 cells long) or wanting, Autoicous or dioicous 3
2. Leaf-apex (sub) acute. Underleaves undivided .... *O. ovalis*
2. Leaf-apex finely acuminate. Underleaves short bifid. .... *O. jackii*
3. Plant reddish-brown to dark brown, autoicous, usually fertile. Perianth flattened, 6–8-plicate, with 2 innovations .... *O. paramicola*
3. Plant yellowish-brown, dioicous (always?), usually sterile. Perianth inflated or flattened, 0–4-plicate, with 1(–2) innovations 4
4. Perianth inflated-eplicate, without beak .... *O. filiformis*
4. Perianth ± flattened, 3–4-plicate, with a short beak .... *O. platycoleus*

Oil bodies have thus far been reported in *O. filiformis*, *O. jackii* and *O. ovalis* (Gradstein et al. 1977). In all of them the oil bodies are large, coarsely segmented, 2–5(–8) per cell and varying from longly and blundly ellipsoid (12–15 × 5–7 μm) to subglobose (4–6 μm). Below, oil bodies and chemical data are reported for the first time in *O. platycoleus* and *O. paramicola*.

Omphalanthus paramicola (Herz.) Gradst.

Oil bodies (Fig. I.4) essentially similar to those in the next species (*O. platycoleus*), 2–4 per leaf cell, bluntly and longly ellipsoid, 10–18 × 5–7 μm, coarsely granulose (Colombia, Páramo de Guasca, 3140 m, fertile, Gradstein & Aguirre 3674).

This interesting species was thus far only known from the type specimen, collected south of Bogotá in the páramo El Bocqueron by C. Troll, nr 2165 (JE holo). New collections have now turned up from Guasca, just north of Bogotà, where it was found on twigs in subpáramo scrub at 3350 m by Dr. Cleef (nr 3450, COL & U) and by the senior author (see above), as well as from Venezuela, dept. Tachira, SE of Santa Ana, 2875 m, on twigs, collected by Steyermark & Dunsterivlle 101005, 16. II. 1968 (NY, U, VEN).

Chemical analysis of *O. paramicola* from Guasca yielded β-chamigrene (32), an unidentified sesquiterpene hydrocarbon and a sesquiterpene aldohol, together with an oxygenated diterpene as major components. No sesquiterpene lactones were detected in this species. The related *Omphalanthus platycoleus* and *Leucolejeunea xanthocarpa* also contain β-chamigrene as major component, but otherwise the three species are chemically different.

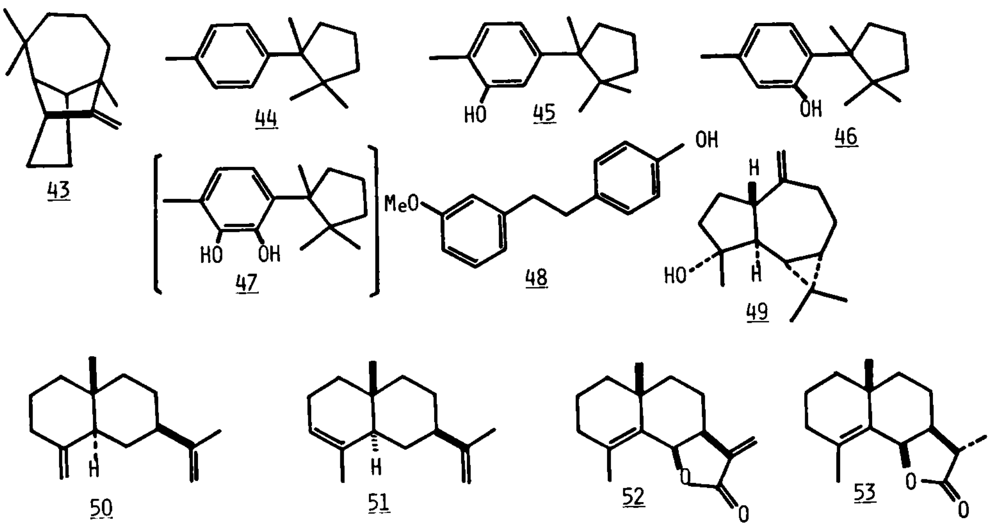

FIG. 4. Some terpenoids and aromatic compounds detected in Colombian Hepaticae.

Omphalanthus platycoleus Herz.

Oil bodies *Calypogeia*-type (but rather large, tending to the "*Leucolejeunea*-type"), present in all leaf cells, consistently 3–4 per cell, large, bluntly and longly ellipsoid, 12–16 × 4–5 μm, coarsely granulose (Colombia, Risaralda, above Termales, 3750 m, fertile (female), Gradstein 3579).

A rare species, thus far known only from the type collection (Colombia, unknown loc., leg. Killip, not seen). While the type specimen is said to posses perianths with a smoothly rounded, broad ventral keel, the ventral perianth keel in our specimen is rather sharply angled at each side.

O. platycoleus elaborates various sesquiterpenoids of which the common β-chamigrene (32), widdrene (38) and bazzanene (14) are the major components. Of particular interest is the presence of a dihydrosesquiterpene lactone (hitherto unidentified). Lactones are characteristic for e.g. Frullaniaceae but hitherto unknown in the Lejeuneaceae.

SUMMARY

Data on structure and chemistry of oil bodies are being provided for twenty species of leafy Hepaticae, most of them belonging to Lejeuneaceae.

Oil bodies are described as new for *Symbiezidium*, which stands out among Lejeuneaceae by its large, *Bazzania*-type oil bodies.

The observed occurence of segmented as well as homogeneous oil bodies in *Archilejeunea* and *Dicranolejeunea* constitutes a further break-down of what was generally considered a stable generic character in Lejeuneaceae.

Detected chemical compounds include a large number of unidentified terpenoids. Sesquiterpene lactones, traditionally considered important chemical markers for Frullaniaceae, were newly detected in *Lepicolea* (Lepicoleaceae), *Clasmatocolea* (Lophocoleaceae) and *Omphalanthus* (Lejeuneaceae). Of particular chemotaxonomic interest is the discovery of large quantities of pinguisane-type sesqui-

terpenes in *Brachiolejeunea* subg. *Plicolejeunea*, *Trocholejeunea* and *Acrolejeunea*, corroborating the close morphological relationship among these three groups, as well as the occurence of two morphologically and chemically distinct races in *Gongylanthus granatensis*. Obeserved intraspecific chemical variation in *Marchesinia brachiata* is considered dubious and possibly related to the different states of preservation of the material.

Further taxonomic notes include new synonymy in *Dicranolejeunea* (*D. cipaconea* (Gott.) Steph. = *D. circinnata* (Spruce) Steph. *syn. nov.*) as well as a key to the five Andean species of *Omphalanthus* Nees. The morphological circumscription of *Omphalanthus* is expanded by the inclusion of *Brachiolejeunea paramicola* Herz. (= *O. paramicola* (Herz.) Gradst. *comb. nov.*), characterised by the pluriplicate perianth.

ACKNOWLEDGEMENTS

We wish to thank Prof. T. Takemoto for his helpful suggestions, Miss G. C. M. Buskes, Dr. E. P. Geissler, Dr. R. Grolle, Drs. G. B. A. van Reenen and Drs. M. W. van Slageren for checking some identifications, and Miss N. Tokunaga and Mr. H. Rypkema for technical assistance.

The senior author is furthermore indebted to Drs. J. Aguirre-C. and other staff members of the Instituto de Ciencias Naturales, Universidad Nacional, Bogotá for fieldwork assistance and to the Netherlands Foundation for the advancement of Tropical Research (WOTRO) for financial support.

REFERENCES

Aguirre, J. & G. B. A. van Reenen. 1980. Ecoandes expedition. The Bryological Times **4**: 6.

Asakawa, Y., J.-C. Muller, G. Ourisson, J. Foussereau & G. Ducombs. 1976. Nouvelles lactones sesquiterpeniques de *Frullania* (Hepaticae). Isolement, structures propriétés allergisantes. Bull. Soc. Chim. France: 1465–1466.

Asakawa, Y., M. Toyota & T. Takemoto. 1978. Sesquiterpenes of *Porella* species. Phytochemistry **17**: 457–460.

Asakawa, Y., M. Toyota, T. Takemoto & C. Suite. 1979a. Pungent sesquiterpene lactones of european liverworts, *Chiloscyphus polyanthus* and *Diplophyllum albicans*. Phytochemistry **18**: 1007–1009.

Asakawa, Y., N. Tokunaga, M. Toyota, T. Takemoto, S. Hattori, M. Mizutani & C. Suire 1979b. Chemosystematics of bryophytes II. The distribution of terpenoids in Hepaticae and Anthocerotae. J. Hattori Bot. Lab. **46**: 67–76.

Asakawa, Y., N. Tokunaga, T. Takemoto, S. Hattori, M. Mizutani & C. Suire. 1980a. Chemosystematics of Bryophytes IV. The distribution of terpenoids and aromatic compounds in Hepaticae and Anthocerotae. J. Hattori Bot. Lab. **47**: 153–164.

Asakawa, Y., M. Toyota, M. Kano & T. Takemoto. 1980b. Dehydropinguisanin, dehydropinguisenol and pinguisenal. Three pinguisane-type sesquiterpenes from *Trocholejeunea sandvicensis*. Phytochemistry **19**: 2651–2654.

Asakawa, Y., H. Inoue, M. Toyota & T. Takemoto. 1980c. Sesquiterpenoids of fourteen *Plagiochila* species. Phytochemistry **19**: 2623–2626.

Asakawa, Y., C. Suire, M. Toyota, N. Tokunaga, T. Takemoto, S. Hattori & M. Mizutani. 1980d. Chemosystematics of bryophytes. V. The distribution of terpenoids and aromatic compounds in European and Japanese Hepaticae. J. Hattori Bot. Lab. **48**: 285–303.

Benesova, V., Z. Samek, V. Herout & F. Sorm. 1969. Isolation and structure of pinguisone from *Aneura pinguis* (L.) Dum. Coll. Czech. Chem. Commun. **34**: 582–592.

Engel, J. J. 1980. A monograph of *Clasmatocolea* (Hepaticae). Fieldiana Bot. n. ser. **3**: 1–229.

Evans, A. W. 1907. Hepaticae of Puerto Rico VIII. *Symbiezidium*, *Marchesinia Mastigolejeunea*, *Caudalejeunea* and *Bryopteris*. Bull. Torrey Bot. Cl. **34**: 533–568.

———. 1908. Hepaticae of Puerto Rico. IX. *Brachiolejeunea, Ptychocoleus, Archilejeunea, Leucolejeunea* and *Anoplolejeunea*. Bull. Torrey Bot. Cl. **35**: 155–179.

Geissler, E. P. & S. R. Gradstein. 1981. On a small collection of living Lejeuneaceae from Peru. Boissiera 32: ... (in press).

Gradstein, S. R. 1975. A taxonomic monograph of the genus *Acrolejeunea* (Hepaticae) with an arrangement of the genera of Ptychanthoideae. Bryophyt. Biblioth. **4**: 1–162.

———. 1980. The genera of the Lejeuneaceae: past and present. In: Bryophyte Systematics (G. C. S. Clarke & J. G. Duckett eds.), p. 83–107. Acad. Press, London and New York.

Gradstein, S. R., A. M. Cleef & M. H. Fulford. 1977. Studies on Colombian Cryptogams II. Hepaticae - Oil body structure and ecological distribution of selected species of tropical Andean Jungermanniales. Proc. Kon. Ned. Akad. Wetensch. ser. c, **80**: 377–420.

Gradstein, S. R. & W. H. A. Hekking. 1979. Studies on Colombian Cryptogams IV. A catalogue of the Hepaticae of Colombia. J. Hattori Bot. Lab. **45**: 93–144.

Herzog, Th. 1955. Hepaticae aus Colombia und Peru. Feddes Rep. **57**: 156–203.

Knoche, H., G. Ourisson, G. W. Perold, J. Foussereau & J. Maleville. 1969. Allergenic component of a liverwort: a sesquiterpene lactone. Science **166**: 239–240.

Lorscheitter-Baptista, M. L. 1977. Flora illustrado do Rio Grande do Sul. Lejeuneaceae. Bol. I.C.B. Proto Alegre 36, **5**: 1–39.

Reenen, G. B. A. van. 1981. Studies on Colombian Cryptogams XII. High Andean species of *Herbertus* S.F. Gray (Hepaticae). Lindbergia **7**: (in press).

Schuster, R. M. 1963. An annotated synopsis of the genera and subgenera of Lejeuneaceae. Beih. Nova Hedwigia **9**: 1–203.

———. 1966. The Hepaticae and Anthocerotae of North America I: i–xvii, 1–802. New York.

———. 1967. On *Adelanthus* Mitten ... Nova Hedwigia **12**: 353–361.

Schuster, R. M. & S. Hattori. 1954. The oil-bodies of the Hepaticae, II. The Lejeuneaceae. J. Hattori Bot. Lab. **11**: 11–86.

Stewart, G. H. 1978. Oil bodies of the New Zealand leafy Hepaticae (Jungermanniales). New Zealand Journ. Bot. **16**: 185–205.

Stotler, R. E. & B. Crandall-Stotler. 1974. A monograph of the genus *Bryopteris*. Bryophyt. Biblioth. **3**: 1–159.

Suire, C. & Y. Asakawa. 1979. Chemotaxonomy of bryophytes: a survey. In: Bryophyte systematics (G. C. S. Clarke & J. G. Duckett eds.), p. 447–477. Acad. Press, London and New York.

Takeda, R., Y. Ohta & Y. Hirose. 1980. Study on the chemical constituents of *Ptychanthus striatus*. 100th Annual Meeting of Pharmaceutical Society of Japan, Tokyo, Symposium papers p. 195.