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Gradsteinia andicola, a remarkable aquatic moss from South America

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Abstract. A new moss genus and species, *Gradsteinia andicola*, is described from the northern Andes of Colombia. It is an aquatic moss known sterile and characterized by 1) oblong or oblong-ovate, concave, cucullate and recurved-apiculate leaves with a very strong and variable costa that is basically single but commonly repeatedly branched and spurred from the base, giving the leaves a polycostate appearance; 2) thick-walled, porose and irregularly uni- to multistratose lamina cells; 3) bicellular axillary hairs; 4) the presence of incomplete limbidia; 5) the absence of paraphyllia, pseudoparaphyllia, central strand and alar cells. Until the sporophyte of *Gradsteinia* becomes known, this very distinct genus is tentatively placed in the family Donrichardsiaceae, based primarily upon the presence of variously multistratose leaf laminae and leaf areolation.

In the course of my examination of aquatic pleurocarpous mosses for my treatment of the Amblystegiaceae for *Flora Neotropica*, I was surprised by a specimen collected at altimontane elevations in Colombia that was unlike any of the known genera of aquatic pleurocarps. I feel confident in proposing a new species and genus for its inception, although the material available is sterile and sexual organs are not observed. For reasons discussed below I tentatively place *Gradsteinia* in the small family Donrichardsiaceae, close to *Donrichardsia* Crum & Anderson, until more material and sporophytes become available. The generic name honours my friend S. Rob Gradstein, the Deputy Director of Cryptogams in the *Flora Neotropica* project, and is a tribute to his contribution to world and in particular neotropical bryology.

Gradsteinia andicola Ochyra, gen. & spec. nov. (Figs. 1-3)

Plantae aquaticae, sat robustae, fragiles, flavo-virides vel fuscae, nitentes. Caulis elongatus, erectus, rigidus, simplex vel parce irregulariter ramificatus, 13 vel plura cm longus, pilis axillaribus bicellularibus, paraphylliis et pseudoparaphylliis nullis, in sectione transversa ovalis vel ellipticus, e cellulis externis 2-3(-4)-stratosis, minoribus, fuscis, parietibus valde incrassatis, internis 4-5-stratosis, magnis, hyalinis, parietibus sat crassis, fasciculo centrali nullo. Folia caulinarum et ramealium similia, sat remote disposita, siccitate erecto-patentia, curvata vel leviter convoluta, madefacta laxe imbricata, carinato-concava,

incurvata, non decurrentia, (1.1-)1.7-2.0 mm longa, (0.4-)0.6-0.8 mm lata, oblonga vel oblongo-ovata, apice rotundata, cucullata minute recurvato-apiculata, marginibus erectis, integris vel minutissime distanter parce serrulata in parte apicali, cellulis laminae irregulariter fluctuante uni-vel multistratosis, pellucidis vel obscuris, elongato-hexagonalibus vel oblongo-rhomboidalibus, supra costas lineari-flexuosis, 50-90 μm longis, 7.5-10.5 μm latis, parietibus crassis, porosis, in parte folii infima fuscescenti-lutescentibus, rhomboidalibus vel breviter rectangularibus, 10-15 μm latis, 15-25 μm longis, parietibus valde incrassatis porosisque, cellulis folii angularibus aliis conformibus, costis validissimis, valde variabilibus, callosis, dorso alatis, cristatis, 1/3-4/5 basi folii occupantibus, bifurcis vel pluripartitis, basi coalitis, ramis dein divergentibus vel parallelis, saepissime iteratim ramificatis et in cellulas laminae inconspicue confluentibus, ultramedio vel prope folii extremitatem evanescentibus exarata, limbis imperfectis, crassis, polystratosis praedita. Inflorescentia ut sporophyta ignota.

Plants moderately robust, in lustrous, dense tufts, typically stiff, fragile and wiry in texture when dry, light to yellowish-green above, brown to blackish-brown and usually incrustated with silt below. Stems up to 13 or more cm long, erect-ascending, sometimes prostrate to suberect, not radiculose, terete and distinctly catenulate when wet, often attenuate, simple or sparsely, freely or sometimes fastigiately branched, usually proliferous because of repeated annual growth from innovations formed below the inactive apical cells and stretching to nearly the same direction as that of the preceding stem, light brown below, green above, in transverse section rounded or elliptic, consisting of 2-3 or, in places, 4-5 rows of small, rounded cortical cells with strongly incrassate, light brown walls surrounding 3-5 rows of large, hyaline, thick-walled medullary cells;

central strand absent; paraphyllia absent; buds scattered along stem or in leaf axils, consisting of a small branch primordium covered with reduced leaves; pseudoparaphyllia none; axillary hairs infrequent, bicellular, brown, short. Stem and branch leaves similar, shrivelled, curved and rolled when dry, rather distant, irregularly erect-spreading to patent, loosely imbricate, navicular and distinctly incurved when wet giving the stem and branches a catenulate appearance, (1.1-)1.7-2.0 mm long, (0.4-)0.6-0.8 mm wide, non decurrent, usually slightly narrowed at base, oblong or oblong-ovate, concave, rounded and cucullate at the apex with most leaves in the upper part of shoots recurved-apiculate, mostly eroded and fimbriate in the older part of the stem and branches; margins entire or distantly minutely serrulate above, plane below, erect to inflexed above, very often with incomplete, multistratose limbidia; lamina cells irregularly uni- to multistratose, with frequent unistratose areas and patches in the upper part, giving the leaf surface an uneven and ragged appearance, smooth or slightly prurulose, thick-walled and porose almost throughout, linear-hexagonal to oblong-rhomboidal, straight to somewhat flexuose, attenuate or oblique at the ends, 50-90 μm long, 7.5-10.5 μm wide, becoming shorter, rhomboidal, 20-40 μm long at the extreme apex and narrower, 5-7 μm wide, at the margins; cells at the insertion uni- to multistratose, short rectangular, 10-15 μm wide, 15-25 μm long, with strongly incrassate and porose walls, yellow to intensively orange-brown on older leaves; alar cells not differentiated, short rectangular to subquadrate; costa very difficult for observation and interpretation, imperceptibly merging into multistratose lamina cells, basically single but more often forked from the large multistratose base occupying 1/3-4/5 the leaf base with 2 main branches, divergent or parallel above, ending in the upper part of the lamina or extending to the apex, forming distinct crests on the

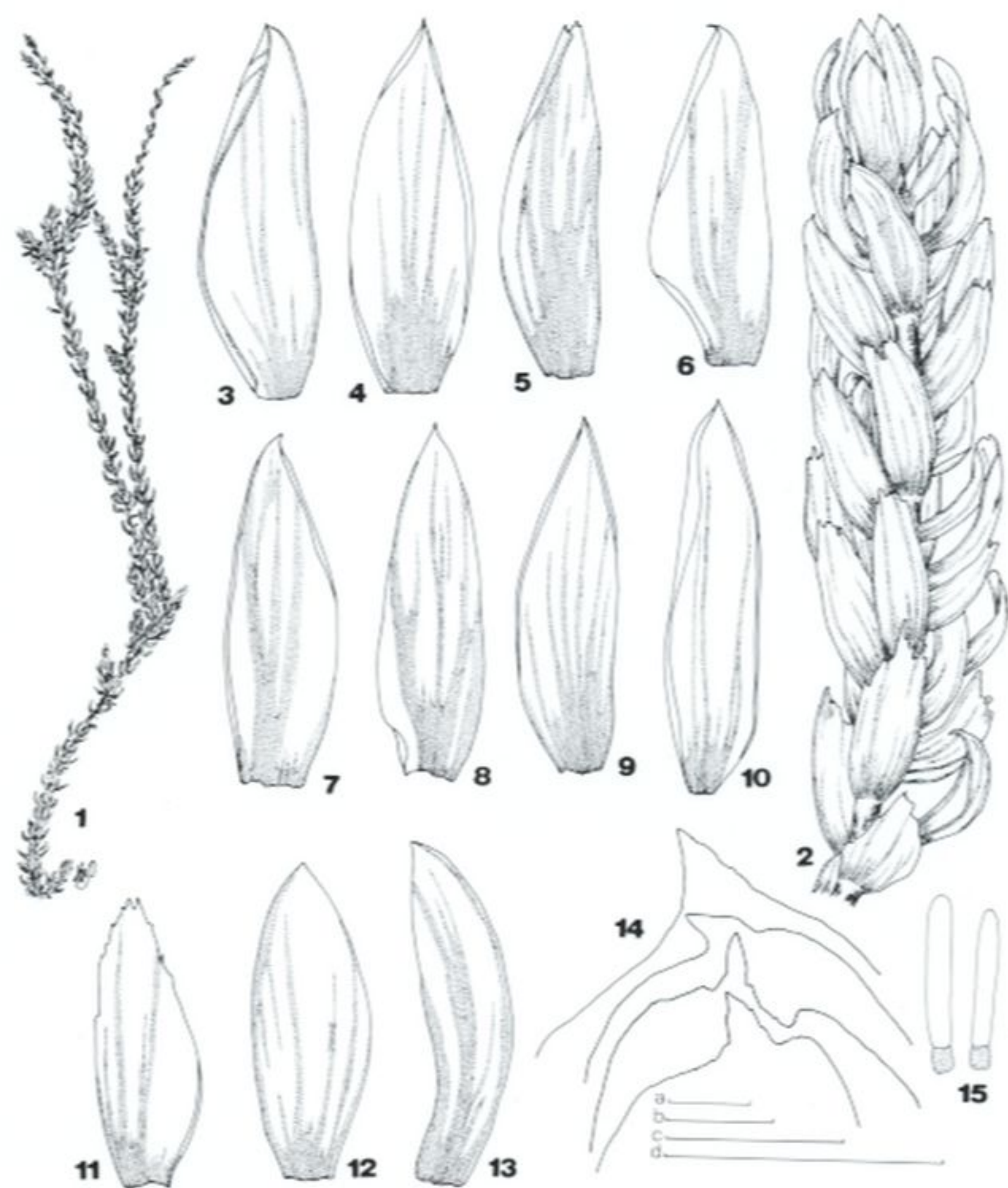


Fig. 1. *Gradsteinia andicola* Ochyra. 1: habit sketch when wet; 2: portion of stem when wet; 3-13: leaves; 14: outlines of leaf apices; 15: axillary hairs (all drawn from the isotype: KRAM). Scale bars: a - 100 μ m (fig. 14), b - 1 cm (fig. 1), c - 1 mm (fig. 2) and 100 μ m (fig. 15), d - 1 mm (fig 3-13).



Fig.2. *Gradsteinia andicola* Ochyra. Spectrum of transverse section of leaves from the base to the apex (all drawn from the isotype - KRAM). Scale bar 100 μm .

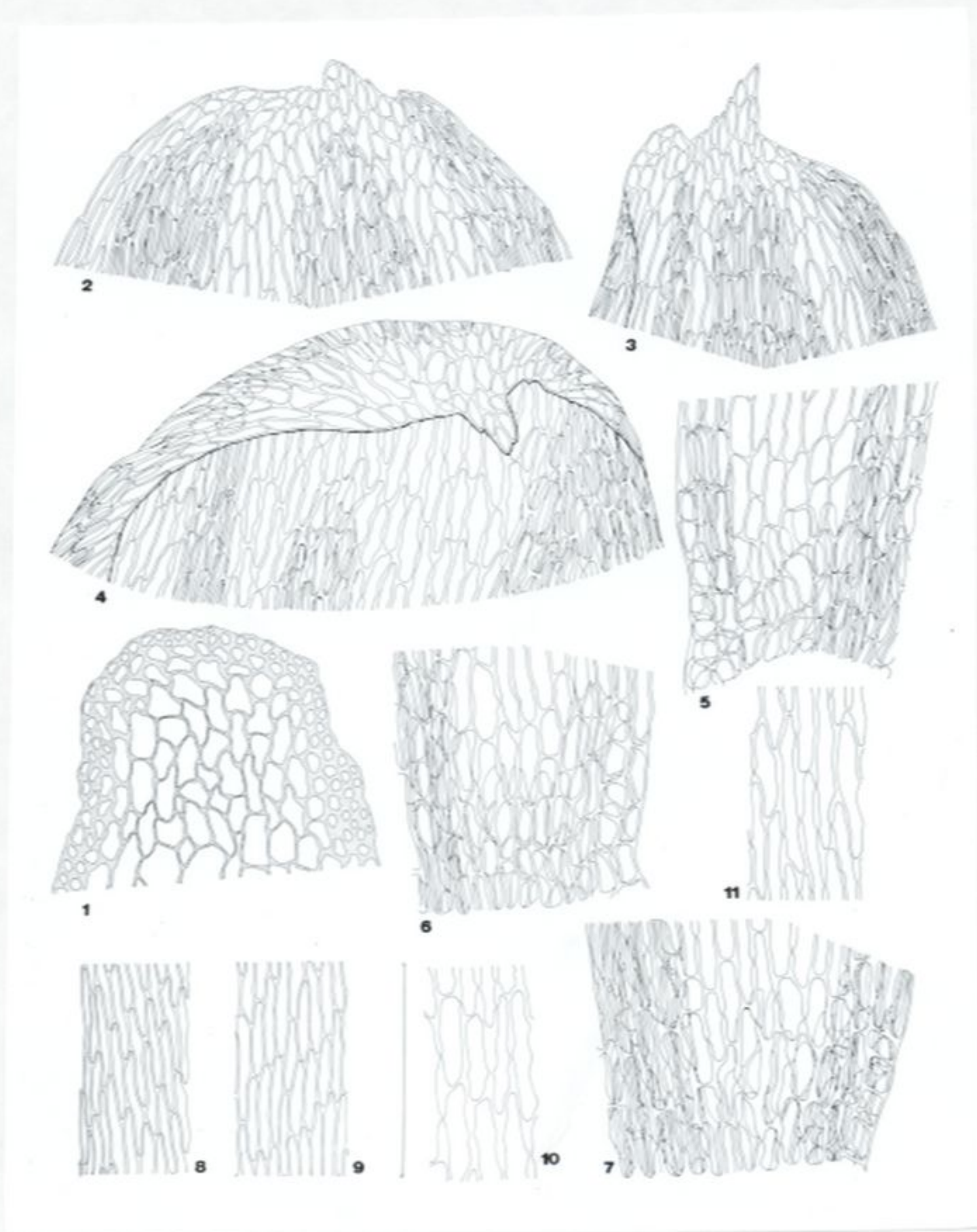


Fig.3. *Gradsteinia andicola* Ochyra. 1: Transverse section of stem; 2-4: leaf apices; 5-7: basal leaf cells; 8: upper marginal cells; 9-11: mid-leaf cells (all drawn from the isotype - KRAM). Scale bar 100 μ m.

dorsal surface of the leaves and numerous lateral spurs and secondary branches usually confluent with each other, sometimes situated at the margins and giving the leaves a limbate appearance, in transverse section composed of small, thick-walled cells of the same shape and size as the adjacent lamina cells. No means of asexual reproduction observed. Inflorescences and sporophytes unknown.

Type: Colombia, Dept. Meta: Páramo de Sumapaz, Hoya Sitiales, lagunita 1 km al E approx. de la Laguna Sitiales, temporalmente seco, con *Myriophyllum elatinoides* y *Ranunculus sp.*, alt. 3650 m, 22 January 1973, A.M. Cleef 8236 (Holotype COL; isotypes BM, F, FLAS, H, KRAM, LPB, MEXU, MO, NY, U).

Discussion

Gradsteinia is a very distinct and unique genus immediately recognizable from all other genera of pleurocarpous mosses by its peculiar leaf structure and costa condition. The leaves are loosely imbricate, concave, boat-shaped and cucullate at the apex when wet; when dry, however, they are curved and inrolled as well as striate owing to numerous irregular strands and crests on their dorsal surface. Young leaves have a short, distinct and mostly recurved apiculus, while the older leaves on the lower part of the stems and branches are without exception fimbriate and incised due to erosion and destruction of their apices, a feature typical of many aquatic and semi-aquatic mosses. However, the most fascinating character of the genus is undoubtedly the state of the lamina cells and the costa.

Basically the lamina is unistratose, especially distally, but there is an extraordinary tendency for multiplication of the number of layers of the lamina cells. In the absence of any logical rule in the stratosity pattern, the laminae have a varying and diversified surface as clearly

visible in transverse section of the leaves (Fig. 2). Practically, it is impossible to find even two leaves that are similar to one another as regards the system of the uni- and multistratose patches and areas in the laminae. As a rule, however, the basal part of the leaves is 2-5-stratose and can be interpreted as the base of a costa that occupies 1/3-4/5 of the leaf insertion. It is readily observed as an intensively yellow- or orange brown, obscure area imperceptibly merging on one or both sides with the very narrow lamina, which is merely 1-2-stratose and visible as a more pellucid, yellow to yellowish-green spot. In addition, limbidia frequently occur along the leaf margins. These are salient, swollen, 3-6-stratose leaf borders of varying width and very irregular shape extending from the leaf insertion to mid-leaf or sometimes as far as the leaf apex, where they coalesce with one another as well as with multistratose streaks radiating from the costa.

The costa itself is difficult to interpret because it is not always clearly delimited, and numerous spurs and secondary branches radiating from the main branches or the basal portion of the costa may considerably obscure its true nature. Despite these difficulties the costa can be interpreted as basically single but forked from the base, as seen in the majority of the leaves. It usually consists of two very strong branches, divergent or rarely becoming above, arising from a polystratose base and clearly visible on most leaves as distinct, sharply delimited, brown crests on their dorsal surface. They cease either freely in the upper part of the lamina or extend to the acroscopic margins and fuse with the limbidia, if present, or continue their course as marginal or inframarginal thickenings connivent at the apex. Very often each main branch is secondarily ramified and spurred, sometimes from the base, suggesting a polycostate state of the leaves. However, these secondary branches and spurs are as a rule weaker and narrower than the main

branches. Because of the frequent reticulate connections, the costal system in *Gradsteinia* is very intricate. Some leaves can in fact may be interpreted as lacking a discrete costa, since it imperceptibly diffuses into multistratose lamina.

The peculiar structure of the leaf lamina and the costa make *Gradsteinia* an almost unmistakable moss and on that basis alone the genus deserves to be recognized. A similar constellation of character states is unknown in any presently recognized genus. The determination of its correct systematic position, however, is hampered by the absence of sporophytes. As gametophytic convergence - i.e. the occurrence of the same structural character states in taxa of remote phylogenetic relationship - is common in aquatic mosses, the evaluation of the affinity of *Gradsteinia* remains speculative.

Although perichaetia have not been found in *Gradsteinia andicola*, the presence of profusely branched stems as well as numerous arrested branch primordia indicate that this moss is pleurocarpous. Therefore, considerations on its systematic position should focus on the diplolepidous mosses, especially the orders Leucodontales, Hookeriales and Hypnales, which are exclusively pleurocarpous (Buck & Vitt 1986).

Gradsteinia seems unrelated to any family or genus of the Leucodontales. This order includes taxa with either thick-walled and isodiametric lamina cells or elongate cells; when elongate, the leaves are uni- or ecostate and in addition, have distinct alar cells. Polystratosity of the lamina is very rarely found in this order, and among aquatic genera of this group it is seen only in species of *Neckeropsis* Reichardt sect. *Pseudoparaphysanthus* (Broth.) Fleisch. (Ochyra & Enroth 1989), *Rhabdodontium* Broth. (Norris & Montalvo 1981), *Muellerobryum* Fleisch. or in the very poorly known Indian moss *Pinnatella limbata* Dixon (Dixon 1921), which most probably represents a separate genus. As well, a tendency for multiplication of the

layers of the lamina cells occurs in some aquatic genera of the Thamnobryaceae, including *Handeliobryum* Broth. (Ochyra 1986a), *Limbella* (C. Muell.) Broth. (Ochyra 1987a) and *Thamnobryum* Nieuwl. (Ochyra 1990). Although this family is considered to be a hypnobryalean taxon (Buck & Vitt 1986), much evidence suggests its closer affinity to isobryalean neckeraceous mosses rather than to any other group of pleurocarps. All of these taxa are characterized by having a single costa and short lamina cells, at least above. Because of its elongate lamina cells and forked costa, *Gradsteinia* could hardly be placed in any family of the Leucodontales. A relationship of *Gradsteinia* to the order Hookeriales has been seriously taken into account in my initial considerations. This large order includes many genera and hundreds of species that are mainly distributed in the tropics and temperate areas in the Southern Hemisphere. Its classification is still debatable and although several systems have recently been proposed (Miller 1971; Crosby 1974; Buck 1987, 1988; Whittemore & Allen 1989), no general consensus has so far been reached as regard the circumscription of families and genera. The main reason of the incongruity of the various classifications of the Hookeriales is the general lack of correlation between gametophytic and sporophytic characters. As a result the concept of family in this order depends on the importance attributed by the autor to characters of either generation *Gradsteinia* displays some characters to support placement in this order, including bicellular axillary hairs, porose and thick-walled lamina cells as well as the lack of pseudoparaphyllia, central strand and differentiated alar cells. The costa condition and variously polystratose lamina of *Gradsteinia*, however, would seem to preclude such placement. Apart from a few ecostate genera such as *Stenodesmus* (Mitt.) Jaeg. and *Phylophyllum* C. Muell., the Hookeriales include either unicastate or bicastate genera. In bicastate taxa the

costa is perfectly double, i.e. consisting of two independent branches arising from the leaf base. In some taxa, however, for instance in certain species of *Callicosta* C. Muell. (Crosby 1969), the costae coalesce below and as a result such leaves can be interpreted as having single, branched or forked costae. Such a situation is not exceptional in mosses and in several other genera with long double costae, for example in *Plagiothecium* B.S.G., one can observe fusion of the basal part of the costae. Whether the costa in *Gradsteinia* should be interpreted as a single costa, which is secondarily forked, or as a double costa which is secondarily fused at the base remains a question for discussion. In many leaves of *G. andicola* the costa consists of two principal branches that are much stronger than the remaining secondary branches and spurs. The two branches are divergent or rarely parallel above and clearly visible as sharply delimited crests on the dorsal surface of the leaves. This situation to some extent resembles that in many hookeriaceous taxa with true double costae.

As far as I know, multistratose laminae have not been described for any hookerioid moss. However, examination of *Diploneuron* Bartr., a genus endemic to the West Indies, revealed that Bartram (1936) and Allen and Crosby (1986) overlooked partial bistratosity of the laminae in *D. connivens* Bartr., the only species of the genus. *Diploneuron* has a double costa with two salient branches that are parallel after diverging near the base and continue from about mid-leaf as limbidia along the acroscopic margins, becoming connivent at the apex. The lamina is usually irregularly bistratose, especially distally, but also in the lower part of the leaf. Partial bistratosity of the lamina cells in *Diploneuron* does not suggest the genus should be considered closely related to *Gradsteinia* but indicates that a tendency for multiplication of the layers of the lamina cells does occur in the Hookeriales. In the sterile state, *Diploneu-*

ron seems rather incongruous in the Hookeriales; by its leaves it resembles very closely some species of the former genus *Sciaromium* (Mitt.) Mitt. (Ochyra 1987b). Therefore, only sporophytic character might definitely refute an assumption on the relationship of *Gradsteinia* with hookeriaceous mosses.

Partial or perfect polystratosity of the laminae is most often found in the Hypnales and it is an important diagnostic character of the Vittaceae (Ochyra 1987c), Hipnobartlettiaceae (Ochyra 1987d) and Donrichardsiaceae (Ochyra 1986b), which are segregates of the large and very heterogeneous family Amblystegiaceae and comprise almost exclusively aquatics. It is interesting to note these are unicostate taxa, multistratose laminae so far being unknown in bi- or ecostate families of the Hypnales including Entodontaceae, Hylocomiaceae, Sematophyllaceae, Plagiotheciaceae and Hypnaceae. It is thus obvious the above three families of the Hypnales, along with the genus *Hygrohypnum* Lindb. (Amblystegiaceae), which includes many species with spurred or bifurcate costae, need a careful assessment when considering the relationship of *Gradsteinia*.

When observing the leaves of *G. andicola* for the first time, I immediately associated this moss with *Ochyraea tatrensis* Vána (Hypnobartlettiaceae), a remarkable aquatic pleurocarp endemic to the Carpathians (Vána 1986). Like the Colombian *Gradsteinia*, the European *Ochyraea* has oblong-ovate to oblong-lanceolate leaves that are concave, entire, rounded at the apex and lack a discrete costa. The internal part of the leaves in *O. tatrensis* is irregularly 2-4-stratose and can be interpreted as a costa. It is ill-defined, occasionally interspersed with unistratose spots, and imperceptibly merges with the narrow, unistratose lamina in the fringes of the leaf. The costa of *Ochyraea* to some extent resembles that of *Gradsteinia*. However, the latter genus lacks paraphyllia, while the *Ochyraea* is

characterized by having numerous filamentous paraphyllia on the surface of the stem and branches. Because the presence and the shape of paraphyllia seem to be very indicative for phylogenetic relationships in mosses, *Gradsteinia* and *Ochyraea* are rather distantly related taxa, despite the striking similarity of the leaves and costa condition. For the same reason it is necessary to exclude any relationship of *Gradsteinia* to other genera of Hypnobartlettiaceae, including *Hypnobartlettia* Ochyra of New Zealand, *Koponenia* Ochyra of Bolivia, *Platylomella* Andrews of eastern North America and *Cratoneuropsis* (Broth.) Fleisch. of Australasia, all having filiform paraphyllia (Ochyra 1987d).

Gradsteinia andicola is also entirely different from *Vittia pachyloma* (Mont.) Ochyra, which is the only species of the monogeneric family Vittiaceae (Ochyra 1987c). This taxon has a single, clearly delimited costa, which is confluent at the apex with the salient limbidia, while the lamina cells are short, rhombic to oblong-rhomboidal, mostly unistratose but in some populations partially to entirely 2-4-stratose. Such a combination of gametophytic characters precludes a relationship of *Vittia* and *Gradsteinia*.

It would be tempting to see a likeness between *G. andicola* and some species of *Hygrohypnum* Lindb. of the Amblystegiaceae. This genus is extremely difficult to define and seems to be a convenient repository for a variety of aquatic pleurocarps with a very variable costa. As presently defined (Jamieson 1976), *Hygrohypnum* consist of about 16 species that are widely distributed but scattered in the mountains throughout the Holarctic. No less than 13 species have been described in or transferred to *Hygrohypnum* in Central and South America (Wijk et al. 1962; Bartram 1965; Sharp 1978; Crum 1985; Nishimura 1985). Having examined all relevant type collections of the neotropical *Hygrohypnum* species, I am confident of

their misplacement in this genus. They are either identical to, or supposedly conspecific with species of *Sematophyllum* Mitt., *Pseudocalliergon* (Limpr.) Loeske, *Rhynchostegium* B.S.G., *Drepanocladus* (C. Muell.) Roth, *Trachyphyllum* Gepp, *Chrysohypnum* Hampe and even *Bryum* Hedw., and bear no resemblance to *G. andicola*, perhaps except for *H. peruvienne* R. S. Williams. The latter species has broadly ovate, acuminate leaves with a strong, broad costa that is basically single but usually forked or repeatedly divided into 3-5 branches. Although it is known only in a sterile state, its gametophyte fits well the *Platyhypnidium-Rhynchostegium* complex of the Brachytheciaceae. Therefore I transferred this species to *Rhynchostegium* as *R. peruvianum* (R. S. Williams) Ochyra (in Schultze-Motel & Menzel 1987).

Until fertile material of *Gradsteinia* is available, the best placement for this genus appears to be in the Donrichardiaceae. Originally this family was established to accommodate the monospecific genus *Donrichardia* Crum & Anderson of eastern North America. Its principal diagnostic characters were a variously multistratose leaf lamina, prorate leaf cells and a very strong and broad costa (Ochyra 1985). Subsequently *Richardsiopsis* Ochyra, *Sciaromiopsis* Broth. and *Sciaromiella* Ochyra have been placed in this family (Ochyra 1986b,c). In the present circumscription the Donrichardiaceae seems to be unnatural and polyphyletic. Unfortunately, the sterile condition of all genera placed in the family impedes an assessment of their true relationships within the Amblystegiaceae-Brachytheciaceae complex.

Gametophytically, *Gradsteinia* is very unlike *Sciaromiella* and *Sciaromiopsis*. Both genera differ from *Gradsteinia* by the presence of very discrete 2-5-stratose limbidia which are confluent with a single costa, as well as ovate-lanceolate and plane leaves. The leaf laminae are irregularly 2-

3-stratose in places because of the frequent spurs radiating from the limbidia and, more rarely, from the costa. As well, the presence of pseudoparaphyllia and non-porose lamina cells seem to preclude a close relationship of these genera with *Gradsteinia*. The genus is also very different gametophytically from *Richardsiopsis lacustris* (Rich. & Herz.) Ochyra of South America, which has narrowly lanceolate and gradually long-acuminate leaves and a very strong and long excurrent costa, which is occasionally slightly spurred below but otherwise very sharply delimited from the lamina cells.

Of all genera currently placed in the Donrichardsiaceae, *Gradsteinia* seems to be closest to *Donrichardsia*. Both genera are similar in habit, leaf shape as well as the strong tendency for multistratosity of leaf laminae and branching costae. However, closer examination reveals many dissimilarities and differences, which preclude congenericity of these taxa. *Donrichardsia* has (1) broadly foliose pseudoparaphyllia (none in *Gradsteinia*); (2) a small central strand in the stem (none); (3) thin-walled and non-porose lamina cells (thick-walled and porose); (4) distinctly prorate cells (smooth or very slightly prorate); (5) leaves plane (deeply concave and cucullate at the apex); (6) leaf margins sharply serrulate to serrate above (entire or minutely and distantly serrulate). The costa in *Donrichardsia* is often laterally spurred but the spurs are generally few and slender. As a consequence, the costa of *Donrichardsia* is very distinct and sharply delimited from the lamina cells contrary to the blurring and unclear costa in *Gradsteinia* which gradually merges into the lamina cells. Likewise, multistratose lamina strands are clearly delimited in *Donrichardsia* and the large patches of multistratose cells characteristic of *Gradsteinia* are totally lacking in the lamina of *Donrichardsia*. The combination of these features seems to be sufficient to support the generic distinctiveness of *Donrichardsia* and *Gradsteinia*.

Crum and Anderson (1979) strongly advocated the relationship of *Donrichardsia* to *Hygrohypnum*, but I feel that suggestion of its alliance with eurhynchoid genera (Crum 1969) should be seriously re-assessed. On the other hand, many species of *Hygrohypnum* seem to have much more in common with some taxa of the *Platyhypnidium-Rhynchostegium* complex of the Brachytheciaceae than with other taxa currently placed in the Amblystegiaceae. Taking into account the aquatic nature of these taxa resulting in a strong tendency for ramification of the costa, *Gradsteinia* would not appear to be anomalous in this group of genera. Therefore its tentative placement in the Donrichardsiaceae, in the proximity of *Donrichardsia*, seems to be acceptable until the interrelationships of some species of *Hygrohypnum*, *Rhynchostegium*, *Eurhynchium*, *Platyhypnidium* and the Donrichardsiaceae is critically evaluated.

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