

ON SCHUSTER'S CONTRIBUTION TO HEPATICOLOGY О ВКЛАДЕ ШУСТЕРА В ГЕПАТИКОЛОГИЮ

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Abstract

Rudolf M. Schuster was one of the leading hepaticologists of the 20th century. His classification of the liverworts has been the standard one for many years and his liverwort manual of eastern North America, in 6 volumes, is the largest and most beautifully illustrated liverwort Flora that has ever been published. He was a great explorer and made immense contributions to our knowledge of the liverwort flora of the Southern Hemisphere, which he considered the cradle of the liverworts. Original phylogenetic thought and new biogeographical interpretations pervade his work. The treatment of the world's liverworts for Engler & Prantl's "*Die natürlichen Pflanzenfamilien*" and the book series "*Austral Hepaticae*" unfortunately remained unfinished.

Abstract

Рудольф М. Шустер был одним из ведущих гепатикологов 20-го века. Его классификация печеночников на протяжении многих десятилетий оставалась наиболее используемой бриологами мира, а его шеститомное издание "Флора печеночников Северной Америки к востоку от 100-ого меридиана" является крупнейшей и наиболее превосходно иллюстрированной флорой печеночников, из числа когда-либо опубликованных. Шустер был величайшим исследователем, внесшим огромный вклад в познание флоры печеночников Южного полушария, которое он считал колыбелью печеночников. Оригинальные филогенетические и биogeографические интерпретации пронизывают все его работы. К сожалению, многие из его работ, в том числе обработка флоры печеночников мира для книги "*Die natürlichen Pflanzenfamilien*" и серия книг "*Austral Hepaticae*" остались незавершенными.

KEYWORDS: liverworts, hornworts, systematics, biodiversity, biogeography, heritage

Rudolf M. Schuster (1921–2012) was one of the leading hepaticologists of the 20th century. His classification of the liverworts has been the standard one for many years and "*The Hepaticae and Anthocerotae of North America East of the Hundredth Meridian*", in six volumes and covering almost 6000 pages (Schuster 1966–1992), is the largest and most beautifully illustrated liverwort flora that has ever been published. The work is more than just a flora; it is an encyclopedia and not exclusively restricted to North America as is evidenced by *Neohodgsonia mirabilis* and *Tylimanthus tenellus*, two species from New Zealand, appearing on the cover of the first volume. The introductory chapters on morphology and anatomy are still the most comprehensive treatments available on the subject and a mine of information. Being of German descent, Rudy Schuster was able to read the 19th century German morphological literature and could amass the rich information kept therein. When the first volume of the flora came out in 1966 – I was still an undergraduate student – I received a free copy from one of my professors on condition that I would review it for the journal

TAXON. I took myself to the task, went to the countryside where I stayed in total seclusion in a monastery for two weeks, read the book from cover to cover, learned an amazing amount about liverworts, and worked hard on the review. The text was accepted and became my first scientific paper in English (Gradstein, 1968).

Schuster's life and work have been well summarized by David Long (Long, 2015). His publications include eight books and about 250 scientific articles, some of them very lengthy, almost book-like. The wealth of new hepaticological data includes descriptions of about 365 new species and more than one hundred new genera (Qiu *et al.*, 2013; Engel *et al.*, 2015). Together with Riclef Grolle (1934–2004), Schuster was the only hepaticologists of this time who knew all the groups. Moreover, he was familiar with most of them in the field, having done fieldwork on all continents (Long, 2015). Those who had the opportunity to join Rudy Schuster into the field will remember them as unforgettable, great learning experiences. Rudy seems to have very much enjoyed his traveling, could talk about his field experiences at length and

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with much enthusiasm, and occasionally hinted about his adventures in his writings, for example in his paper on *Perssoniella* (Schuster, 1965). This unusual endemic liverwort from New Caledonia was long known from limited, gametophytic material and its taxonomic position was puzzling. The plants had been believed to grow by means of an apical cell with only two cutting faces, a rare feature in the leafy liverworts where it was otherwise only known in *Pleurozia*. As Schuster wrote: “...the genus simply did not fit in any of the groups, families or even suborders which I recognized in my most recent classification of the Hepaticae (Schuster 1958). In order to resolve this problem, a collecting expedition to New Caledonia was organized, for March, 1962. M. Luc Chevalier, of the Museum at Noumea, was kind enough to take my wife, Dr. David Bierhorst, and myself to Montagne des Sources, where he had earlier taken Selling, who collected the type of *Perssoniella* there. I do not care to dwell on the harrowing trip up to Montagne des Sources: it involved building a bridge for the Land Rover; crossing boulder-infested streams that threatened to demolish the Land Rover; a fire in the vehicle occasioned by the battery breaking free and shorting out; avoiding washed out sectors of the “road” by riding with two wheels high on steep banks – and finally a dead stop, where large boulders had blocked the overgrown path that we used for a road. Suffice to say, we eventually got there. Although collecting was limited by a typical tropical downpour, and by very limited time available there, numerous collections of *Perssoniella* were made....” (Schuster, 1965, p. 480).

Schuster’s worldwide travels were related to his ambitious aim to write a monographic treatment of the families and genera of liverworts of the world, updating Schiffner’s treatment in Engler & Prantl’s “*Die natürlichen Pflanzenfamilien*” (Schiffner, 1893). He held the strong conviction that such a goal could only be achieved by studying freshly collected material (Schuster, 1988). Although the treatment remained unfinished, a wealth of specimens and precursory publications resulted from the project. His collecting activities yielded about 60,000 specimens, from all continents and countless observations on habitat and morphological variation of the species. Major and surprising new insights emerged from these activities. While in the field in New Caledonia, for example, Schuster discovered that the morphology of the leafy liverwort genus *Pleurozia* had been misinterpreted, and that the ventral and dorsal sides of the plants had been confused. Admittedly, distinguishing between dorsal and ventral in *Pleurozia* can be tricky because the underleaves are absent, rhizoids are usually lacking and plants are often growing erect. It had generally been assumed that the leaf lobule, a characteristic feature of most of the species in the genus, is the ventral leaf lobe. However, when examining material of *P. caledonica* from New Caledonia – a species growing prostrate and producing

rhizoids – Schuster found that the lobule is dorsal in position, not ventral (Schuster, 1965). By the old, erroneous interpretation the plants would be growing upside down!

The fresh collections also allowed for making observations on oil bodies and this yielded important new insights into the taxonomy of the Lejeuneaceae (Schuster & Hattori, 1954; Schuster, 1992), the largest and most difficult group of the liverworts. Thus, he found that the genus *Acrolejeunea* (at the time called “*Ptychocoleus*”) was heterogeneous and contained species with homogeneous or segmented oil bodies. Those with segmented oil bodies, mostly from Africa, were referred to a new genus which he called *Phragmilejeunea* (Schuster, 1961). The novel genus was accepted in a subsequent monograph of *Acrolejeunea* (Gradstein, 1975), but the name *Phragmilejeunea* had to be abandoned, being antedated by the name *Schiffneriolejeunea* Verd.

Producing classifications and formulating concepts on liverwort origin and evolution were Schuster’s main preoccupations (Long, 2015). His ideas about primitive and advanced characters and the course on evolution (e.g., Schuster 1949, 1979b, 1984, 2002), however, were essentially based on “taxonomic instinct” or “*Fingerspitzengefühl*”, as he used to call it, not on rigorous phylogenetic analysis. It would be interesting to check which of his ideas have been confirmed in recent molecular-phylogenetic studies, and which have not. His classification of the liverworts, developed over almost half a century in series of major publications (Schuster, 1953, 1966, 1979b, 1984, 2000), however, has been highly successful and was widely adopted over many years. The backbone of his system was the subdivision of the liverworts into two main groups, Jungermanniidae and Marchantiidae, each with three or four orders and with several suborders (Table 1). Upright growing, \pm isophyllous plants with three rather similar rows of leaves, such as *Haplomitrium*, *Herbertus* and *Lepicolea*, were considered primitive while anisophyllous and thalloid taxa were considered more advanced. This idea had first been proposed by the Austrian botanist Richard Wettstein and had been adopted in the classifications of Alexander W. Evans and Frans Verdoorn (Verdoorn, 1932); the latter two authors had also recognized the two subclasses of liverworts. Schuster’s classification, however, was far more comprehensive than the previous ones which still had a strong holarctic bias. Schuster’s system, in contrast, was the first one that was truly global.

The application of molecular phylogenetics in the last twenty years has led to considerable modification of the classification of liverworts (Crandall-Stotler *et al.*, 2009; Söderström *et al.*, 2016). A comparison of Schuster’s classification and the current system shows an increase in the number of subclasses (from 2 to 5) and orders (from 6-7 to 14) (Table 1). In addition, five major changes have been made:

Table 1. Classification of liverworts according to R. M. Schuster and recent authors.

Schuster (1964-1992)	Crandall-Stotler <i>et al.</i> (2009), Söderström <i>et al.</i> (2016)
CLASS HEPATICAE	DIVISION MARCHANTIOPHYTA
	CLASS HAPLOMITRIOPSIDA
	Order Haplomitriales (= Calobryales)
	Order Treubiales
SUBCLASS JUNGERMANNIIDAE	CLASS JUNGERMANNIOPSISIDA
Order Calobryales	SUBCLASS JUNGERMANNIIDAE
Order Jungermanniales (incl. <i>Pleurozia</i>)	Order Jungermanniales
	Order Porellales
Order Metzgeriales (incl. <i>Blasia</i>)	SUBCLASS METZGERIIDAE
	Order Metzgeriales
	Order Pleuroziales
Order Treubiales	SUBCLASS PELLIIDAE
	Order Fossombroniales
	Order Pallaviciniales
	Order Pelliiales
SUBCLASS MARCHANTIIDAE	CLASS MARCHANTIOPSISIDA
Order Monocleales	SUBCLASS BLASIIDAE
Order Marchantiales (incl. <i>Lunularia</i> and <i>Neohodgonsonia</i>)	Order Blasiales
Order Sphaerocarpaceles	SUBCLASS MARCHANTIIDAE
	Order Marchantiales (incl. <i>Monoclea</i>)
	Order Lunulariales
	Order Neohodgonsoniales
	Order Sphaerocarpaceles

1) A third class Haplomitriopsida, was added, containing *Haplomitrium* (Calobryales) and *Treubia* (Treubiales). Schuster had already noted their similarity but nevertheless kept them apart, even though in an apparent “sister” position (e.g., Schuster, 2002, p. 12).

2) Metzgeriales proved to be paraphyletic and were split into Metzgeriidae and Pelliidae.

3) *Blasia*, generally considered a member of the Metzgeriales, proved to be a member of Marchantiopsida (subclass Blasiidae).

4) *Pleurozia*, considered a member of the leafy liverworts (Jungermanniales), proved to be a member of the thalloid Metzgeriidae (order Pleuroziales).

5) *Monoclea* proved to be a (highly apomorphic) member of the order Marchantiales (family Monocleaceae). Previously, the genus has been placed in an order of its own, Monocleales.

Many further changes have been added at lower taxonomic levels; for a detailed discussion of these changes the paper by Crandall-Stotler *et al.* (2009) should be consulted.

This comparison of classifications would be incomplete without a brief mention of Schuster's contribution to the taxonomy of *Takakia*. This extraordinary genus,

first described in 1958, has attracted much attention of bryologists and its taxonomic placement was long controversial because the plant was long only known from gametophytic material. Schuster took actively part in the discussion and in 1997, after the sporophyte of *Takakia* had been discovered and it appeared that *Takakia* was a moss [as had been suggested first by M. Mizutani based on the stalked archegonia of *Takakia*], he wrote a lengthy review paper summarizing the unusual features and discussing possible phylogenetic relationships of the plant (Schuster, 1997). Although the phylogenetic considerations were narrative and his final conclusion – that *Takakia* should be a separate division between liverworts and mosses with remote similarities to Calobryales and Andreaeopsida – not supported by subsequent molecular evidence, the paper was highly informative and very well balanced. I consider this one of Schuster's finest papers, and the best one written on *Takakia*.

Besides his work on taxonomy and morphology, Schuster made important contributions to the biogeography of liverworts. Work on this subject had long been hampered by the taxonomic chaos that had been created by Stephani's treatment of the liverworts of the world, “*Species Hepaticarum*” (Stephani, 1898–1924), which



Fig. 1. *Ruizanthus venezuelanus* R.M. Schust. (Balantiopsidaceae). Photograph by R. Rico (Mérida).

included descriptions of a huge number of superfluous taxa (the necessary revision of the work is still ongoing). Because of this, possibilities for meaningful analysis of liverwort distributions at world level had long been limited. Schuster's first paper on the subject appeared in 1969 under the title "*Problems on antipodal distribution in lower land plants*", being part a series of lectures on plant systematics, each by a different author, presented at the "Smithsonian Summer Institute in Systematics – 1968" and published in a special volume of *TAXON*. Schuster's contribution dealt with the geographic ranges of selected genera and families of liverworts with main distribution in the Southern Hemisphere, the area which

he had studied in great detail and considered of crucial biogeographic interest. Many important new ideas were contained in the paper and the summary is therefore reproduced here in full:

"The geographical distribution of the more primitive Hepaticae (subclass Jungermanniae) exhibits the same patterns of endemism and disjunction, and highly specific and restricted ranges as found in many groups of vascular plants. The subantarctic region is shown to have an unduly high preponderance of primitive genera present (ca. 50% of all known unspecialized types), of which very many are strictly endemic there. Many of these groups are cold-adapted types which seem to have exhibited only limited dis-

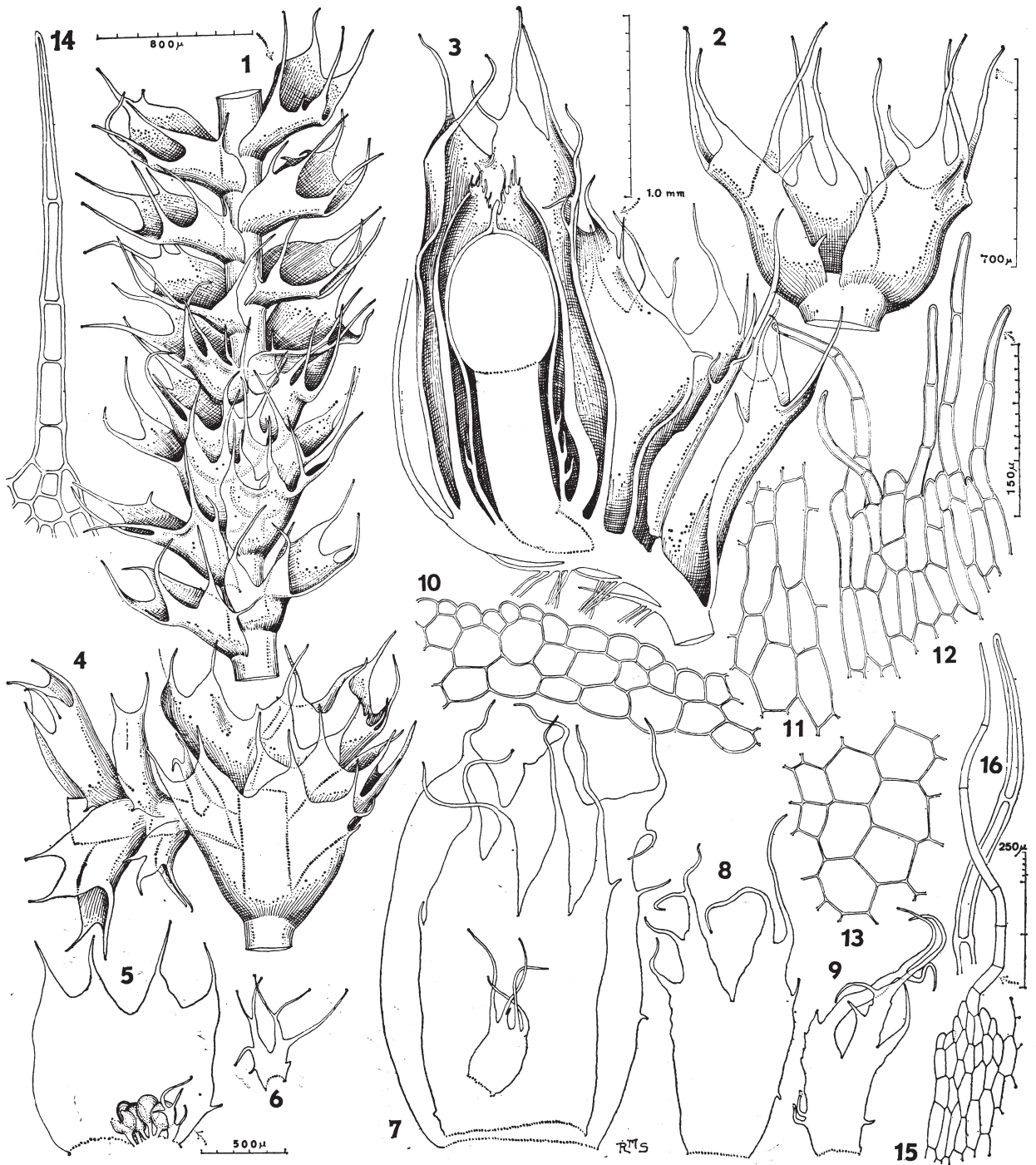


Fig. 2. *Ruizanthus venezuelanus* R.M.Schust., drawn by R.M. Schuster. Reproduced with permission from *New Manual of Bryology*, Vol. 2 (1984).

placement northward as a result of late-Tertiary and Pleistocene deterioration of the climate; others (Blepharostomataceae) have shown some striking dispersal to the cold regions at the opposite side of the globe, but the bulk of taxa remain Antipodal. Other families (Gymnomitriaceae, Scapaniaceae) that seem to lack tolerance for warm climates are today very preponderantly Arctic subarctic (and Alpine subalpine), but the most primitive taxa are still strictly subantarctic, leading to the conclusion that these

largely Holarctic families are originally Panarctic. From the evidence given it is concluded that many but probably not all major groups of the Jungermanniae may have originated in this Panarctica (Gondwanaland). The recent overwhelmingly "in phase" data corroborating the theory of continental drift, plus the relatively late times for separation of the Australian-Tasmanian-New Zealand area from Antarctica (ca. 40-60 m.y. ago; perhaps somewhat earlier in the case of New Zealand) suggest much of the dispersal

(of older, unisexual taxa) may have been overland during late Mesozoic and early Tertiary times. Ranges of some taxa on islands near or on the Mid-Atlantic and Indian-Ocean ridges, islands which vary from 1-20 million years in age, clearly indicate some taxa (especially bisexual ones) may have wider powers of spore-dispersal than sometimes assumed. Present evidence does not, often, allow us to distinguish between ancient "overland" dispersal, and more recent dispersal via spores" (Schuster 1969, p. 46).

The subject was further explored in "*On the persistence and dispersal of transantarctic Hepaticae*" (Schuster, 1979a) and "*Dispersal mechanisms and distribution patterns in Hepaticae and Anthocerotae*" (Schuster, 1983a), and culminated in "*Phytogeography of the Bryophyta*" in the New Manual of Bryology (Schuster, 1983b). The latter work has remained the principal reference on liverwort biogeography, even though it is now partially outdated. A final paper on the subject, "*Origins of the Neotropical Hepaticae*", appeared in 1990, being based on a lecture at the International Botanical Congress in St. Louis. Here, Schuster pointed out that the Neotropics, especially the northern Andes, is the "hottest hotspot" in the world in terms of endemic liverworts. The high endemism was explained by the long-term isolation of the area, exceeding 40 Mio years, and the continuous, strong local tectonic activity, producing ample new ("raw") habitats for speciation and evolution. A large number of endemic species and about 25 genera, were described by Schuster based on his fieldwork in the Neotropics. Among them were several rare monospecific groups, such as *Ruizanthus* (Figs. 1, 2), *Platycaulis*, *Pseudocephaloziella*, *Leptoscyphopsis*, *Nanomarsupella* and *Paramomitrium*, that have not or have only once or twice been collected since. About half the new neotropical genera described by Schuster and many of the new species, however, have now become synonyms and were replaced by older names. One reason for this was Schuster's neglect of the study of types (Long, 2015) and his dislike of the principles of nomenclature: "I continue to sweep under the proverbial rug some nomenclatural problems of which I am fully aware, but which I trust will not become obvious to some of my more adventurous contemporaries..." (Schuster, 1974, p. ix).

Schuster's greatest fascination has been the liverwort flora of the Southern Hemisphere and "*Austral Hepaticae*" (Schuster, 2000, 2002) was to become the grand synthesis of his work in that part of the world. Unfortunately, the book remained unfinished; of the planned five volumes, only three have appeared. A perusal of the three published volumes is suggestive of the wealth of data that would have been contained in the series. Being over 80 years old, work on *Austral Hepaticae* was increasingly becoming a burden as is evident from one of the last letters that I received from him, dated 16 February 2002:

821 W. Calle del Regalo
Green Valley, Ariz. 85614, USA
Feb. 16, 2002

Dear Rob,

I meant to write you last summer, but getting proof read of Volume II of AH took all my time and energy. Olga is overwhelmed with the Ms, as am I.

I have been "fighting" with Plagiochilaceae, for Volume III, and they have worn me down; I am about to call it quits, they need more years that I have left. I keep trying to see patterns in sporophyte microanatomy. The figures of *Szweykowskia* and *Steeerochila* you published (with J. Heinrichs) leave me full of doubts. I would like to get a few plants of each from you, if possible, with a perianth or two. I remain puzzled as to how to interpret branching in *Steeerochila* and would much like to see material. Inoue once sent me 1-2 plants, but they were so bad I gave up on the problem.

Under separate cover (sea mail) I send a copy of recent papers and that of the *Lepidozia* paper; I do not remember when I last sent you reprints; if you let me know what you need, I will try to get you copies. I would appreciate copies of your recent ones, especially Gradstein & Reiner (*Szweykowskia*), Heinrichs et al. (*Glauc-escentes*), H. & G. (*P. longiramea*; sect. *Crispatae*; *P. subplana*); Müller, H. & G. (sect. *Plagiochila*).

Sincerely yours,

Rudy

Schuster's contribution to hepaticology is monumental, his publications are exceptionally rich in detail, and the quality of his illustrations is unsurpassed. His writing is lengthy and the text is typically accompanied by numerous footnotes. Lewis Anderson in a tribute to Rudy Schuster (Anderson, 1988) counted 2384 footnotes in his North American flora and concluded that Schuster had "a passionate love affair with the footnote". As they often contain descriptions of new taxa, new combinations or other crucial new taxonomic information, Schuster's footnotes are an essential part of the text and cannot be ignored.

In the preparation of his manuscripts, Schuster was aided by his wife, Olga, who was a professional editor and took care of the conception and completion of the work, and getting it ready for publication. As a token of his appreciation, Schuster dedicated to her a new genus from Ecuador, *Olgantha* (= *Triandrophyllum*), and a new species from Australia, *Austrolejeunea olgae* (= *Nephelolejeunea nudipes*). Sadly, both names are now considered synonyms.

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