



On the morphology, systematics and phylogeny of *Noteroclada* (Noterocladaceae, Marchantiophyta)

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Abstract: *Noteroclada* Taylor ex Hook. & Wilson has long been recognized as a unique leafy taxon having affinities to the north temperate, simple thalloid liverwort genus, *Pellia* Raddi. Although a suite of diagnostic characters clearly separate it from *Fossombronia* Raddi and other leafy, anacrogynous taxa, considerable confusion regarding its identity exists in historical treatments. There are unresolved questions in regards to the extent and significance of morphological variation within the genus, the number of species that should be recognized, the geographic range that it occupies and its position in liverwort phylogeny. Morphological, experimental and molecular techniques are employed to address these questions. These studies show that there are two forms of perennating tubers, which are geographically partitioned, that plants are always monoicous, that sporophytes are enclosed by a shoot calyptra and *Fossombronia*-like caulocalyx and that sporeling ontogeny is different from that of *Pellia*. Molecular analyses show some genetic variation within *Noteroclada*, but both morphological and molecular data support the recognition of but a single species, *N. confluens* Taylor ex Hook. & Wilson. It is confirmed that there are no reliable specimens of *Noteroclada* from Africa, Australasia or the Kerguelen sector and that the genus has two centers of distribution in Latin America, with disjunct populations in the Falkland Islands, South Georgia, Tristan da Cunha and Gough Island. Significant ontogenetic differences between *Noteroclada* and *Pellia* support their placement in separate monogeneric families of the Pelliales.

Keywords: *atpB-rbcL* spacer, distribution, indels, Latin America, Noterocladaceae, Pelliales, *rbcL*, *rps4*, sporeling ontogeny, *trnT-trnF* spacer, tubers, typification.

Introduction

Noteroclada Taylor ex Hook. & Wilson is a large, fairly common foliose hepatic of moist, montane habitats of the western Cordillera of Latin America, ranging from Mexico down the Andean chain to Fuegia and subantarctic islands, with a second area of distribution in the Atlantic rainforests of southeastern Brazil (Grolle 2002, Gradstein & Costa 2003). It has also been reported from Gough Island in the mid-Atlantic (Grolle & Seppelt 1986, Frey & Stech 2009), as well as southern Africa (Schuster 1992) and Kerguelen's Island (Hooker & Taylor 1844, Taylor & Hooker 1847), but these range extensions are considered dubious and in need of verification (Grolle 2002). It has been traditionally aligned with the North Temperate, simple thalloid genus *Pellia* Raddi in the Pelliaceae, which is currently recognized by most authors as the only family in the Pelliiales of the subclass Pelliidae (He-Nygrén et al. 2006, Crandall-Stotler et al. 2009). Although the relationship between *Noteroclada* and *Pellia* has been rarely questioned, assumptions about the level of that relationship vary from its inclusion in the genus *Pellia* (Austin 1875) to its placement in a separate family (Reimers 1954, Frey & Stech 2005) or even a separate order (Frey & Stech 2008, 2009). Although easily distinguished by their leafy versus thalloid facies, *Noteroclada* and *Pellia* share many important anatomical features, including similar associations with glomeromycotean fungi (Ligrone et al. 2007), dispersed androecia in which antheridia are borne singly in scattered thallus-derived chambers, spheroidal, 4-valved capsules with well-developed basal elaterophores, and precocious, endosporic spore germination. On the other hand, phylogenetic distance between the two genera is suggested by their different apical cell geometries, modes of branch development and gynoeceal organizations (Renzaglia 1982).

Like *Pellia*, populations of *Noteroclada* form extensive, dense mats over constantly moist soil along stream banks, at the edge of lakes or bogs, or over seeps, but never grow submerged. This is in contrast to *Austrofossombronia marionensis* R.M.Schust. and the species of *Fossombronia* Raddi assigned to that genus by Schuster (1994), namely, *F. peruviana* Gottsche & Hampe and *F. australis* Mitt., which occupy similar habitats, but can grow partially submerged and form turfs rather than mats when on soil. These species of *Fossombronia* resemble *Noteroclada* in being large foliose plants with dorsally scattered, naked archegonia, but differ in their scattered, but non-chambered, antheridia and bright purple to violet rhizoids (Goebel 1930). Specimens of *Fossombronia* from submerged habitats, however, are usually sterile and lack these diagnostic rhizoids, making their distinction from *Noteroclada* much less obvious. In fact, it is possible that reports of *Noteroclada* from the Kerguelen sector, which first appeared in Hooker & Taylor (1844), are based on miss-identifications of *F. naumannii* Schiffn. and/or *F. australis*.

Historically, the confusion between *Noteroclada* and *Fossombronia* began with the naming of *Jungermannia porphyrorhiza* Nees (Nees 1833). According to Proskauer (1955), the holotype of *J. porphyrorhiza*, which is from Minas Gerais State, Brazil, contains stems of both *Noteroclada* and *Fossombronia*. A note and annotated drawings by Gottsche, suggesting that the specimen represented a new genus with *Fossombronia*-like females and *Pellia*-like males, are included in the herbarium

packet. Montagne (1839) expanded the description of *J. porphyrorhiza* to include the sporophyte, which he described and illustrated as having a globose, 4-valved capsule. In this treatment, characters of *Fossombronia*, e.g., purple rhizoids, have been clearly mixed with those of *Noteroclada*, e.g., 4-valved capsules. Subsequent to the naming of *Noteroclada confluens* Taylor ex Hook. & Wilson (Hooker & Wilson 1844:166), Nees (1846) erected the genus *Androcryphia* Nees to include *A. porphyrorhiza* (Nees) Nees (= *J. porphyrorhiza*) and *A. confluens* (Taylor ex Hook. & Wilson) Nees (= *Noteroclada confluens* and *J. confluens* Hook. f. & Taylor), a species which according to Hooker & Taylor (1844) was distributed in Cape Horn and Kerguelen's Island as well as Brazil and the Falkland Islands. Male plants with antheridia immersed in a close succession of dorsal thallus tubercles were described in both species, but rhizoid color was indicated only for *A. porphyrorhiza*. In a slightly expanded treatment in 1847, Taylor and Hooker provided more detailed specimen information and suggested that the Gardner plants from Brazil might be different from the Antarctic collections, but nonetheless, Mitten in 1855 reduced all of the above to *Noteroclada porphyrorhiza* (Nees) Mitt. At the same time, he extended the range of *Noteroclada* to include New Zealand, based on collections of Colenso from Titiokura (Hawkes Bay region). Some twenty years later, Colenso described three additional species of *Noteroclada* from New Zealand, *N. perpusilla* Colenso (1884), *N. lacunosa* Colenso (1885) and *N. longiuscula* Colenso (1886). Surprisingly, Stephani (1892, p. 273) reduced four of Colenso's species of *Fossombronia* from New Zealand (*F. gregaria* Colenso, *F. macrophylla* Colenso, *F. nigricaulis* Colenso, and *F. rosulata* Colenso) to *Noteroclada porphyrorhiza* without comment. Upon later studying the original material of *J. porphyrorhiza*, however, Stephani (1900) modified his treatment of *Androcryphia* (= *Noteroclada*), pointing out for the first time that the specimen upon which the name was based actually was a mix of *Fossombronia* and *Androcryphia*. He recognized a single species, *A. confluens*, described the rhizoids as hyaline, listed *A. porphyrorhiza* and *N. leucorhiza* Spruce as synonyms, and restricted the distribution of the genus to Latin America, making no mention of either the Mitten or Colenso taxa. Finally, with the transfer of *J. porphyrorhiza* to *Fossombronia* by Proskauer (1955), *Androcryphia* became a synonym of *Fossombronia*, and *Noteroclada* became the accepted name of the taxon. Today, *Noteroclada* is recognized as clearly distinct from *Fossombronia*, but whether historical reports of *Noteroclada* from Australasia and the Kerguelen sector are due to the inclusion of *Fossombronia* characters in early circumscriptions of the genus remains to be determined.

The morphology and developmental anatomy of *Noteroclada* have been well documented in the fairly comprehensive studies of Leitgeb (1877), Schiffner (1911), Ellwein (1926) and Renzaglia (1982). Fortunately, all of these authors worked on specimens that were truly *Noteroclada*; the source of Leitgeb's specimens is not indicated, but Schiffner (1911) and Ellwein (1926) studied specimens from Brazil, and Renzaglia (1982), specimens from Peru. Although these studies agree in most details of gametophyte shoot and branch development, including tetrahedral apical cell geometry, leaf formation and gametangial ontogeny, they differ somewhat in their interpretations of sexual condition, gynoecial position and the form of post-fertilization structures associated with the sporophyte. It is significant that Schiffner

(1911), who provided the first detailed treatment of sporophyte anatomy and early sporeling ontogeny, described the capsule wall morphology of *Noteroclada* as being most similar to that of *Treubia* K.I.Goebel and quite different from that of *Pellia*. These findings were verified by Ellwein (1926), but have not been cited in recent works.

Although there is a solid foundation of anatomical data on *Noteroclada*, the extent and significance of morphological variation within the genus have never been assessed. Consequently, whether the genus comprises a single species, as generally recognized, or multiple species, as proposed by Spruce (1885, 1890), is equivocal (Proskauer 1955, Gradstein et al. 2001, Gradstein & Costa 2003). To resolve this taxonomic ambiguity and clarify the geographic range and relationships of *Noteroclada*, we have undertaken this comprehensive, systematic revision of the genus. Our treatment includes evaluation of all epithets historically associated with the names *Noteroclada* and *Androcryphia*, with designation of type specimens when appropriate, appraisal of morphological variation in over 500 herbarium specimens, verification of distribution records, review of sporeling ontogeny in axenic cultures of two select populations, assessment of character modulation under common garden conditions, and DNA sequence analysis of six representative populations.

Materials and methods

PLANT MATERIAL: Both recently collected and pertinent historical specimens of *Noteroclada*, including potential nomenclatural types, were obtained on loan from 27 herbaria (see acknowledgements). General morphological features, such as plant width, leaf shape, and sexual condition, were recorded for all collections. Samples were subsequently removed from a few specimens for more detailed anatomical study, using paraffin-sectioning and/or scanning electron microscopy (SEM) methods. These included Bandeira 59 (s), Bresinsky & Garrido 156 (M), Dusén s.n. (H), Dusén 79 (s), Engel 10971 (NY), Gomez 19876 (JE), Halling 5738, 5848 (NY), Hyvönen 2782 (G), Mosén s.n. (G), Schiffner 313, 394, 712, 1173 (w), Wace 657 (BM), and Williams 2729 (NY). Anatomical data were also gleaned from four live specimens of *Noteroclada*, namely, Forrest 566 and Villarreal 1042 (both from field collections) and Costa & Gradstein 3909 and Weiss & Schwerdtfeger s.n. (both from transplants maintained in a glasshouse at the University of Göttingen), and two specimens of *Pellia epiphylla* (L.) Corda, i.e., Zhang 4071 and Stotler 4352; vouchers of these are deposited in (ABSH). Detailed collection data for these are provided in the 'Select Specimens Examined' section of this paper. Taxon sampling for the molecular studies included six accessions of *Noteroclada*, seven accessions, representing four species of *Pellia*, and five outgroup taxa of the Pelliidae; see Table 1 for voucher information and GenBank accession numbers.

MORPHOLOGICAL METHODS: Specimens were prepared for SEM viewing and serial paraffin sectioning according to the procedures outlined in Crandall-Stotler & Stotler (2007). Optical images were captured with either an Olympus SZX12 dissecting microscope equipped with an Optronics digital camera or a Leica CTR 5000 compound microscope with a Q Imaging Retiga 2000R camera. To improve depth of focus, multiple images were stacked in Helicon Focus ver. 3.79. SEM specimens were viewed and digital images captured with a Hitachi S570 SEM.

AXENIC CULTURE METHODS: Transplants of live plants from Brazil, Ecuador, Mexico and Venezuela were placed on vermiculite, moistened with Hatcher's media (1965) in Phytakon culture dishes in an environmental chamber kept @15°C with a 14/10 hr day/night cycle, 1265 lux light intensity. Mature sporophytes, which were subsequently produced in the samples from Brazil and Venezuela, were used to initiate axenic spore cultures, following the procedures of Hatcher (1965). Eight replicate cultures from each sample were randomly placed on the same shelf of an environmental chamber kept @14°C with a 12 hr day/night cycle, 1930 lux light intensity. Spore cultures of *Pellia epiphylla* were established

Table 1. Voucher information and GenBank accession numbers for taxa utilized in this study. All vouchers are deposited in ABSH.

Taxon	Voucher information (Ax = axenic culture)	GenBank Accession Numbers			
		<i>rbcL</i>	<i>rps4</i>	<i>trnL</i> region	<i>atpB-rbcL</i> spacer
Ingroup Taxa					
<i>Noteroclada confluens</i> Hook. & Wilson	Vidal-Russell s.n., Bariloche, Argentina	HM00527	HM005737	HM005750	HM005723
<i>Noteroclada confluens</i> Hook. & Wilson	Long 31768, Ushuaia, Argentina	DQ268977	DQ268990	HM005751	HM005724
<i>Noteroclada confluens</i> Hook. & Wilson	Costa & Gradstein 3909, Rio de Janeiro, Brazil (Ax)	HM005728	HM005738	HM005748	HM005722
<i>Noteroclada confluens</i> Hook. & Wilson	Weiss & Schwerdtfeger s.n., Andes, Ecuador	HM005729	HM005739	HM005748	HM005721
<i>Noteroclada confluens</i> Hook. & Wilson	Villarreal 1042, Puebla, Mexico	HM005730	HM005740	HM005752	HM005725
<i>Noteroclada confluens</i> Hook. & Wilson	Forrest 566, Mérida, Venezuela (Ax)	AY688784	AY688797	HM005747	HM005720
<i>Pellia appalachiana</i> R.M.Schust.	Davison 3579, Ala- bama, U.S.A. (Ax)	AY688785	AY688799	n/a	n/a
<i>Pellia epiphylla</i> (L.) Corda	Forrest & Villarreal 619, North Carolina, U.S.A.	HM005731	HM005741	n/a	n/a
<i>Pellia epiphylla</i> (L.) Corda	Forrest, Forrest & Bry- son 700, Scotland, U.K.	HM005732	HM005742	n/a	n/a
<i>Pellia endiviifolia</i> (Dicks.) Dumort.	Higuchi s.n., Japan [fromSIUC green- house culture]	AY688786	AY688800	n/a	n/a
<i>Pellia endiviifolia</i> (Dicks.) Dumort.	Muth s.n., France	HM005733	HM005743	n/a	n/a
<i>Pellia neesiana</i> (Gottsche) Limpr.	Forrest & Badcock 598, British Columbia, Canada	HM005734	HM005744	n/a	n/a
<i>Pellia neesiana</i> (Gottsche) Limpr.	Wheeler s.n., Oregon, U.S.A.	HM005735	HM005745	n/a	n/a
<i>Pellia neesiana</i> (Gottsche) Limpr.	Long s.n., Utah, U.S.A.	HM005736	HM005746	HM005752	HM005726
Outgroup Taxa					
<i>Allisonia cockaynii</i> (Steph.) R.M.Schust.	Stotler & Crandall-Stot- ler 4470, New Zealand	AY507389	AY507432	n/a	n/a
<i>Calycularia crispula</i> Mitt.	Furuki, s.n., Japan	AY507395	AY507437	n/a	n/a
<i>Fossombronina australis</i> Mitten	Stotler & Crandall- Stotler 4610, New Zealand (Ax)	AY507392	AY507434	n/a	n/a
<i>Makinoya crispata</i> (Steph.) Miyake	Stotler & Crandall- Stotler 4047, China	AY877390	AY877393	n/a	n/a
<i>Phyllohallia nivicola</i> E.A.Hodgs.	Stotler & Crandall- Stotler 4537, New Zealand	AY507418	AY507459	n/a	n/a

in a similar manner. Sporeling ontogeny was monitored at weekly intervals until juvenile shoots were formed. Common garden comparisons were made after plants reached reproductive maturity.

MOLECULAR METHODS: DNA extraction, PCR and DNA sequencing methods follow Forrest & Crandall-Stotler (2004). Two chloroplast coding regions, namely the *rbcL* gene and the *rps4* gene (including its 3' spacer), were sequenced for all taxa, while two predominantly non-coding regions, the *trnT*_{UGU} - *trnL*_{UAA} intergenic spacer region (including the *trnL*_{UAA} gene), and the *atpB-rbcL* spacer region, were sequenced for the *Noteroclada* accessions and one *Pellia* species. Primer sequences for the *atpB-rbcL* region are from Chiang et al. (1998), and those for the *trnT-trnF* region are from Meissner et al. (1998). Primers for *rbcL* and *rps4* are given in Forrest & Crandall-Stotler (2004).

Two separate matrices were compiled. The first included sequences from all four loci, for a subset of the taxa (the five *Noteroclada* accessions and one *Pellia* species for outgroup orientation). Several parts of the non-coding regions were not alignable between *Pellia* and *Noteroclada*. A second matrix comprised the two coding regions *rbcL* and *rps4*, for all sampled taxa. In both cases alignment gaps were treated as missing data. Maximum parsimony (MP) analyses were run in PAUP* (Swofford 2002) under Fitch parsimony, using the Exhaustive algorithm for the first matrix, and an heuristic search algorithm for the second matrix (250 replicates of Tree Bisection and Reconnection, with a limit of 25 trees saved per step). Maximum parsimony bootstrapping of the first matrix was performed using 250 Branch and Bound replicates; MP bootstrapping of the second matrix was performed with 1000 Bootstrap replicates, using 25 Tree Bisection and Reconnection replicates. For the second matrix, jModeltest (Guindon & Gascuel 2003; Posada 2008) was used to establish the model of DNA evolution with the best fit to the data, using a fixed JC tree; Akaike's Information Criterion led to the selection of a General Time Reversible model (Yang 1994). Maximum likelihood (ML) analysis was run in PAUP, with a General Time Reversible model of molecular evolution, estimating all parameters from the data and using the trees found in the MP heuristic search as starting trees. Maximum likelihood bootstrapping was conducted in GARLI 0.951 (Zwickl 2006) with 250 replicates. Lastly, the utility of the universal plant barcoding region of *rbcL*, as selected in Hollingsworth et al. (2009), was tested in this group by selecting the 5' end of *rbcL* up to the position where primer aR (Kress & Erickson 2007) would sit. This corresponded to character 616 in our alignment. We used this locus to generate neighbour-joining trees using both uncorrected p-distances and the General Time Reversible model of molecular evolution.

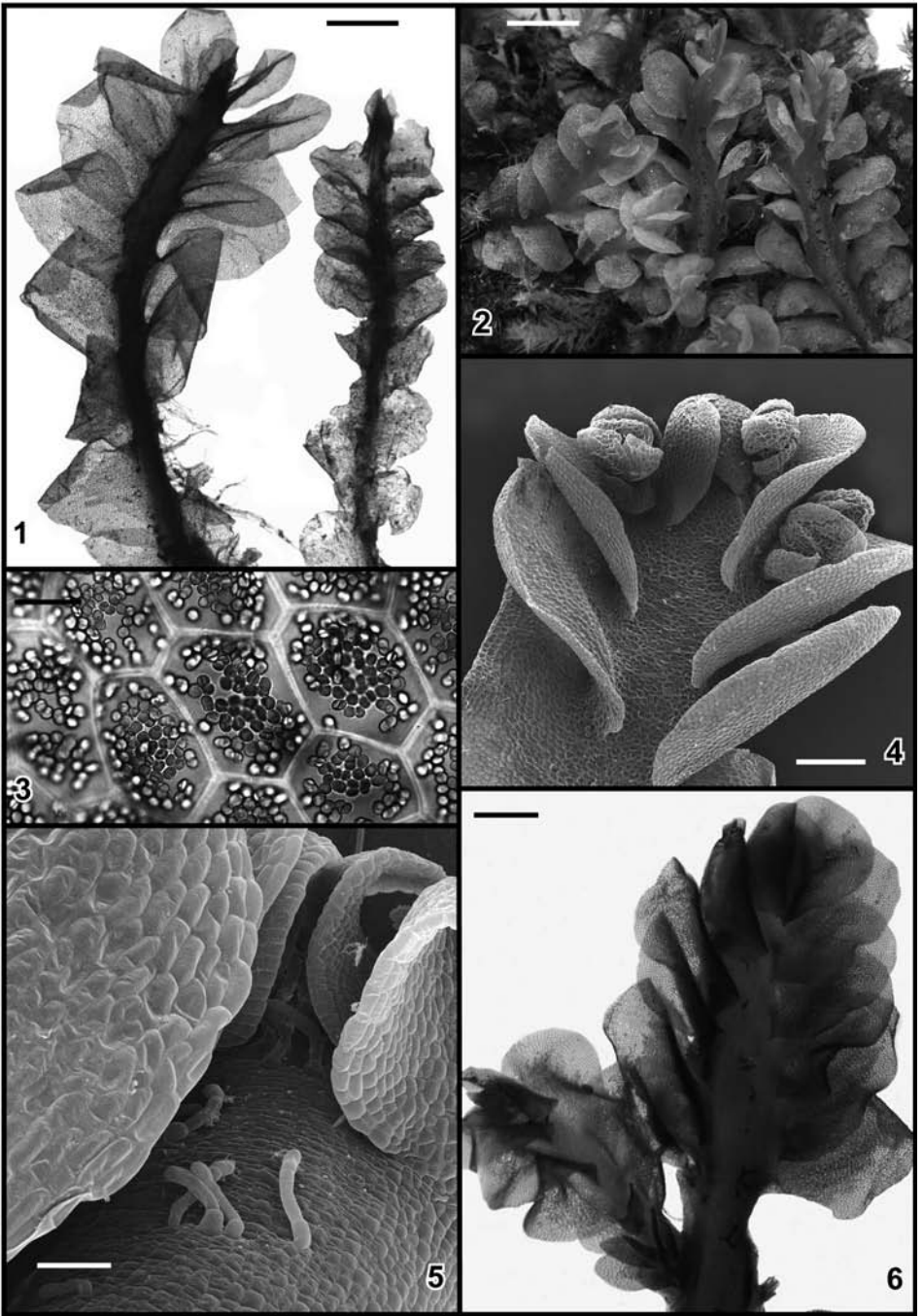
Results

MORPHOLOGICAL STUDIES: In nature, plants of *Noteroclada* are bright grass-green, with the ventral side of the somewhat flattened, fleshy, often reddish stems densely covered with hyaline to pale yellow rhizoids. With drying, as in herbarium collections, the shoots become light to dark brown, and the rhizoids can then appear light tan, but they are never purple like the rhizoids of *Fossombronia*. The rhizoids are long, slender and unbranched, like those of *Pellia*, in contrast to the broader, contorted, often short rhizoids of *Fossombronia*, and are only rarely absent or sparse, as in the type of *N. arrhiza* Spruce. Leaves are suborbicular to elliptical or ovate, 1.1–3.0 mm wide by 1.5–3.8 mm long, with the apices always rounded and the margins entire (Figs 1, 2). Young leaves at the stem apex are inserted in an oblique succubous line, while mature leaves have an almost longitudinal insertion, with almost no insertion onto the dorsal side of the stem (Figs 2, 4). Leaf stance is horizontal, never erect or patent as in many species of *Fossombronia*. There is a central multistratose area, extending from the leaf base to just beyond the leaf middle, that gradates from six cell layers near the insertion line to two cell layers distally (Fig. 1). The distal third to half of the leaf and several cell rows inwards from the leaf margins are unistratose (see also Renzaglia 1982, Fig. 258). Median cells in the unistratose part of the leaf

are usually elongated, 40–54 μm wide by 78–85 μm long, hexagonal in outline and thin-walled with inconspicuous trigones (Fig. 3). In plants with less elongated leaves, median leaf cells are isodiametric, 38–54 μm in diameter, but otherwise similar. Each cell contains up to 20 small, glistening, homogeneous oil bodies that are about the same size as the chloroplasts. This type of oil body morphology was consistent among the four live populations studied, including the population from Brazil, and are at variance with the report of finely segmented oil bodies in Brazilian populations by Gradstein & Costa (2003). Although not usually preserved in herbarium specimens, in live plants uniseriate, hyaline slime hairs, similar to those of *Pellia endiviifolia* (Dicks.) Dumort., are found on the ventral side of the stems at and just below the shoot apex (Fig. 5). Initially, each ventral merophyte produces two hairs, each consisting of 5 cells and a terminal slime papilla, but in older merophytes four hairs may be present, aligned in a transverse row, as also reported by Leitgeb (1877).

Proskauer (1955), noting the small size of Gardner's plants from Brazil, questioned whether differences in plant size might differentiate two species within *Noteroclada*. In fact, there is substantial size difference between the lectotype of *N. confluens* from Brazil, with an average shoot width of 3.2 mm, and those of *N. leucorhiza* and *N. arrhiza* from the Andes, with average shoot width of 6.4 mm (Fig. 1). However, these type specimens represent the extremes. Although there is a tendency for plants to be smaller in the Atlantic rainforests of Brazil than in Andean sites, there is variation across the entire size range in both locales, sometimes even within a single population. It is of note that the leaves of smaller plants, including those in the lectotype of *N. confluens*, have isodiametric leaf cells in contrast to the elongate leaf cells of larger plants. Within a single collection, the smaller plants are either sterile or bear only antheridia, while larger plants, with more elongate leaves bear archegonia or sporophytes in addition to spent antheridia. Our studies suggest that plant size is most likely influenced by a combination of habitat and developmental age and is not a species defining character.

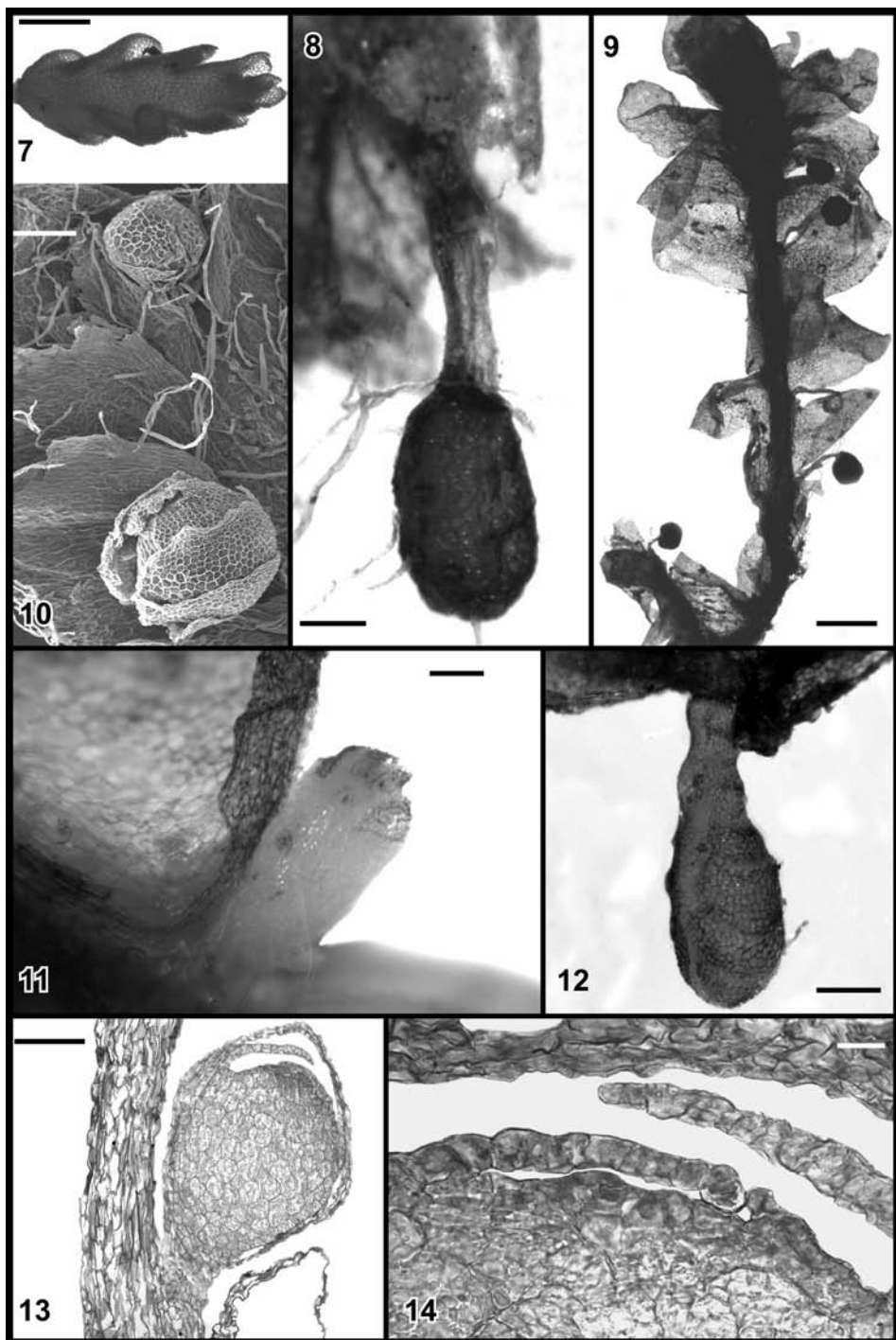
Branching in *Noteroclada* is sparse and always monopodial, never dichotomous or furcate as in *Pellia* and *Fossombronia* (Fig. 6). All branches develop from lateral primordia that lie just ventral to the basiscopic margins of the leaves (Fig. 4). These primordia are differentiated close to the shoot apex, as detailed by Leitgeb (1877, p. 121) and Renzaglia (1982, Fig. 252), but typically remain dormant unless the main apex is damaged, or until they lie some distance below the apex. Consequently, branches typically occur only near the base of older shoots, where they may be obscured by the growth of neighboring plants on top of them. Allsopp & Ilahi (1970a, Fig. 1) showed experimentally that decapitation of the shoot apex in cultured plants results in the formation of regenerant shoots from the branch primordia, as also does the addition of 1% to 4% glucose to the culture medium. We found that similar regenerant branches, or cladia, are also produced in natural populations, occurring in about 6% of the specimens examined. In contrast to normal branches, which are morphologically similar to the main shoot, these cladia are small, 2–3 mm long by 0.3–1.4 mm wide, and possess reduced, concave leaves and thick fleshy stems that are easily detached from the main stem (Fig. 7). They form new shoots with mature morphology only after being separated from the parent plant.



Figs 1-6.

In addition to cladia, branch primordia can also give rise to subterranean tubers (Figs. 8, 9), as we first reported in 2005 (Zhang et al. 2005). In some populations, tubers may also develop from the main shoot apex. It is surprising that the occurrence of such tubers was not noted by previous authors since they are present in 25% of the herbarium specimens we studied, including an isotype and the lectotype of *N. confluens* and *N. leucorhiza*, respectively, as well as several of Schiffner's collections from Brazil [301, 313, 394, 1173 (w)]. Tuber formation is more common in populations with sporophytes, occurring in 40% of these as compared to only 17% of populations that lack sporophytes. There are two distinct tuber morphologies that appear to be non-randomly distributed, an ellipsoidal form (Fig. 8) and a spheroidal form (Fig. 9). The ellipsoidal form is common to populations from the Atlantic rainforests of Brazil and Uruguay, with only four specimens seen from outside this area having tubers of this type, three from Columbia and one from Mexico. Spheroidal tubers occur in all other populations from the western Cordillera, Tierra del Fuego, Falkland Islands, Tristan da Cunha and Gough Island, and are absent from Atlantic rainforest collections. In both types, the tuberous branch consists of a swollen terminal tuber, subtended by a slender, leafless stalk that is up to 4 mm long and is comprised of elongate, thin-walled cells. In both, the incipient tuber branch is fleshy and hyaline, with leaves at its apex, but the spheroidal tuber branch is globose (Fig. 10), while the ellipsoidal tuber branch is twice as long as broad (Fig. 11). In the ellipsoidal tuber type there are at least five series of tightly appressed, scale-like leaves produced (Fig. 12), in contrast to the two series of larger, concave, apically overarching leaves in the spheroidal form (Fig. 13). After leaf formation, the apical cell of the incipient tuber branch is converted to a more or less flattened meristem (Figs 13, 14), which halts further apical growth. As the tubers enlarge, their epidermal cells darken and become thick-walled, and the cells of the interior expand and are packed with starch grains (Fig. 15). The leaves become inconspicuous, appearing as small buttresses on the surface of ellipsoidal tubers (Fig. 16) or as darkly pigmented, membranous scales in spheroidal tubers (Fig. 17). Rhizoids are often present along the ventral surface of the ellipsoidal tubers, but are lacking in the spheroidal ones. In both tuber types, the stalk cells elongate to several times their original length, and the tuber is pushed down into the plant mat and/or soil. In the few examples we have seen of detached, germinating tubers, a new leafy shoot emerges from the axil of a scale leaf at the tuber apex, presumably from a branch primordium. Since the cells of the tuber proper are isodiametric in both ellipsoidal and spheroidal types, it is likely that the difference in shape is due to the ellipsoidal type having more merophytes formed from the apical cell prior to its elimination

Figs 1–6. 1. Shoots from the lectotypes of *N. confluens* (right) and *N. leucorhiza* (left), dorsal view; scale bar = 1.6 mm. 2. Monoicous shoots from a glasshouse population from Ecuador, dorsal view; scale bar = 2.6 mm. 3. Median leaf cells with small, homogeneous oil bodies; scale bar = 30 μ m. 4. Apical portion of a shoot with 3 lateral branches in early stages of development, viewed in SEM; scale bar = 350 μ m. 5. Ventral slime hairs, viewed in SEM; scale bar = 100 μ m. 6. Shoot bearing archegonia and a normal leafy branch, dorsal view; scale bar = 2 mm. [2 from Weiss & Schwerdtfeger s.n. (ABSH); 3 from Forrest 566 (ABSH); 4 from Dusén 79 (s); 5 from Freire 4189a (ABSH); 6 from Bresinsky & Garrido 156 (M).]



Figs 7-14.

than is the case in spheroidal types. The non-random distribution of these morphologies and the fact that there is no intermixing of tuber types on single plants or within populations suggest that this ontogenetic difference is an intrinsic, genetically controlled character.

Although reported to be monoicous, or occasionally dioicous (e.g., Spruce 1885, Gradstein & Costa 2003), our studies confirm that *Noteroclada* is always monoicous and protandrous, with two distinct patterns of gametangial distribution. In some populations, archegonia are formed from young merophytes that are still producing antheridia and are subsequently distributed in two rows just to the inside of the perigonal chambers (Fig. 18). In other populations, however, the two types of gametangia are temporally and spatially separated, with androecia being produced much earlier than gynoecia (e.g., Goebel 1930, Fig. 710), in which case it is possible to find plants that have only androecia, as reported by Schiffner (1911). We have never found populations that have only gynoecia, as one might expect in a dioicous taxon, but we have seen shoots with old archegonia that seem to lack antheridia, intermixed with monoicous shoots. In this perennial taxon, there can be repeated cycles of gametangial production, each cycle beginning with formation of antheridia and their chambers at the shoot apex (see Renzaglia 1982 for details). With continued growth, the maturing perigonal chambers are arranged in two (or four) longitudinal rows on the dorsal surface of the stem (Fig. 19). Mature antheridia are pale yellow, globose, 240–270 μm in diameter, and have untiered jacket cells and 4-celled stalks that are one cell high. The perigonal chambers are apically inclined, with the cells on the posterior side being slightly more elongated than those on the anterior side; a chimney-like neck is formed around the ostiole or mouth of the chamber by elongation of the surrounding cells (Fig. 19). This type of androecium is fundamentally like that of *Pellia*.

In Frey & Stech (2009, p. 42), archegonia are inaccurately described as being "in clusters, surrounded by an involucre." This type of gynoecium is characteristic of *Pellia*, but in *Noteroclada* both nascent and unfertilized archegonia are naked, like those of *Fossombronina* (Figs 18, 19). In natural populations, fertilization occurs when the archegonia are still close to the shoot apex where they are more or less clustered and protected by the young leaves, while in cultured plants archegonia may remain viable for a short distance below the apex. After fertilization, a caulocalyx develops from the stem cells just to the outside of the enlarging calyptra (Figs 20, 21).

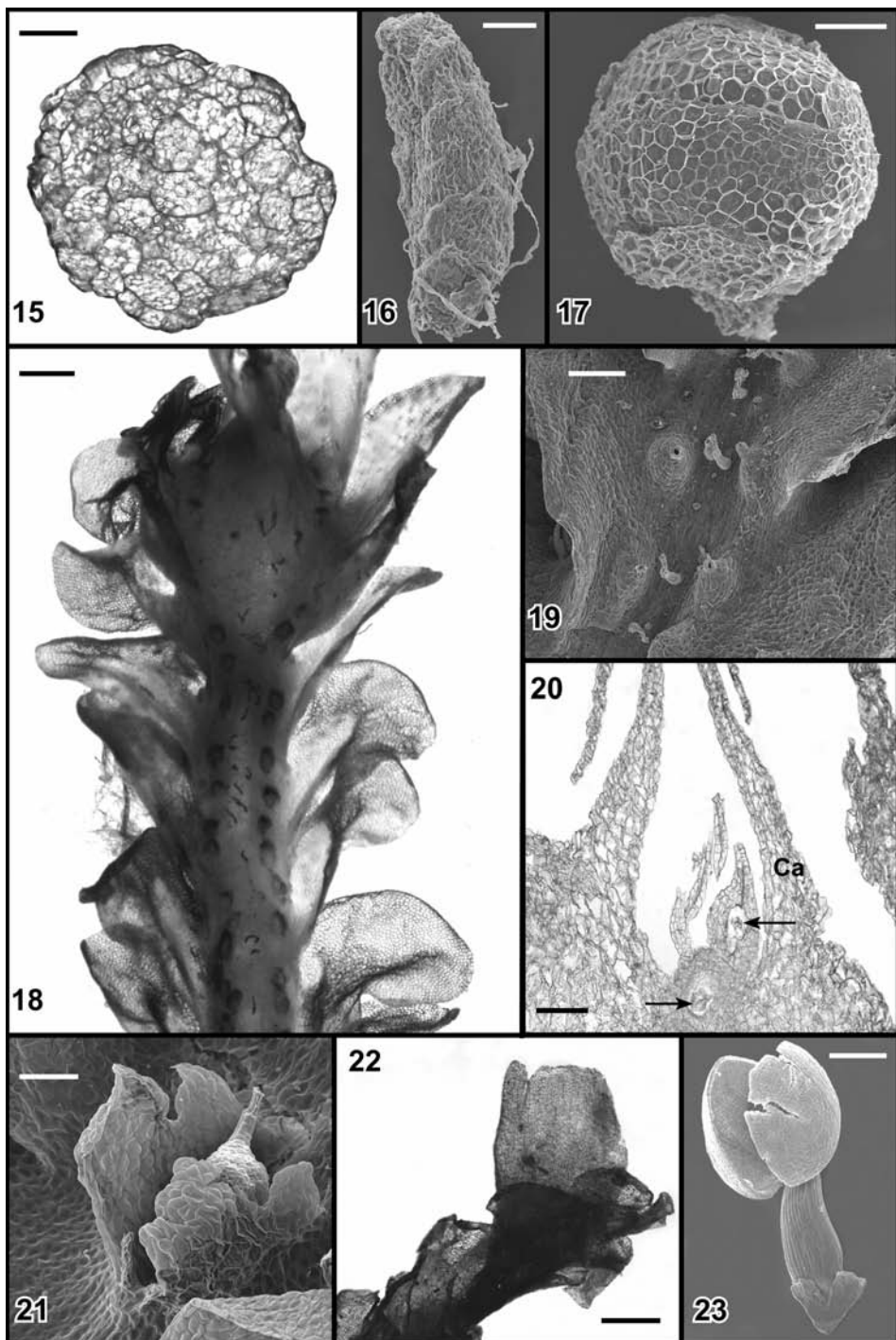
Figs 7–14. 7. Cladium that has detached from the stem, dorsal view; scale bar = 750 μm . 8. Nearly mature ellipsoidal tuber, lateral view; scale bar = 200 μm . 9. Plant with several spheroidal tubers dispersed from just below the developing sporophyte to the base of the shoot, ventral view; scale bar = 1.6 mm. 10. Shoot with developing spheroidal tubers, ventral view in SEM; scale bar = 300 μm . 11. Early stage of ellipsoidal tuber development, ventral view; scale bar = 300 μm . 12. Median stage of ellipsoidal tuber development, showing 5 series of scale-like leaves on the fleshy exterior; scale bar = 200 μm . 13, 14. Longitudinal section of a developing spheroidal tuber, showing the flattened apex and overarching leaves; scale bars = 100 μm (13) and 15 μm (14). [7 from Dusén 79 (s); 8 from Gardner n. 32 (MANCH, isoelectotype of *N. confluens*); 9 from Spruce s.n. (MANCH, lectotype of *N. leucorhiza*); 10, 13, 14 from *Engel 10971* (NY); 11 from King, Guevara & Forero-G. C-844 (us); 12 from Osorio 17.646 (F).]

In early stages of development, the caulocalyx is 2-parted and deeply lobed, with broad openings on both anterior and posterior sides, but as growth continues, it becomes cylindrical and multistratose at the base (Figs 18, 22). The upper half of the caulocalyx is unistratose, with the mouth lobed, somewhat compressed and deeply incised on the anterior side. Since fertilization occurs within the cluster of archegonia at the shoot apex, a single caulocalyx usually encloses several archegonia, more than one of which may be fertilized (Fig. 20). Usually, only a single sporophyte matures within a caulocalyx, but we have, on occasion, observed two sporophytes emerging from the same caulocalyx. Leitgeb (1877) explained the usually terminal position of sporophytes as due to fertilization halting further shoot growth, whereas Renzaglia (1982) contended that an actively dividing shoot apical cell is present even as embryos are developing. We have observed that although developing sporophytes are terminal, old caulocalices with degenerating, dehisced sporophytes occur a short distance below the apex, confirming that *Noteroclada* is truly anacroyous.

Considerable stem growth beneath the fertilized archegonium encloses the sporophyte in a 3- or 4-stratose shoot calyptra inside the caulocalyx. Some of the neighboring archegonia are elevated on the sides of the calyptra and the sporophyte foot is deeply embedded in the stem. According to Schiffner (1911), archegonia may also be elevated on the inner surface of the caulocalyx, but we have only observed them on the basal third of the shoot calyptra.

Our observations of sporophyte anatomy expand upon the descriptions of Schiffner (1911) and Ellwein (1926), with which they mostly agree. As is also true in *Pellia*, the foot is obconoidal, with a very well developed collar or involucellum, the seta is large, 10 to 12 cells in diameter, and the capsule is spheroidal, with a persistent basal elaterophore and 4-valved dehiscence (Figs 23, 24). The description of capsule dehiscence as irregular by Hooker & Taylor (1844), which was then copied by Nees (1846), was likely based on observations of immature capsules, apparently at the spore tetrad stage of development. Spruce (1885), Stephani (1900) and Ellwein (1926, Fig. 142) describe the capsule wall of *Noteroclada* as bistratose, but our

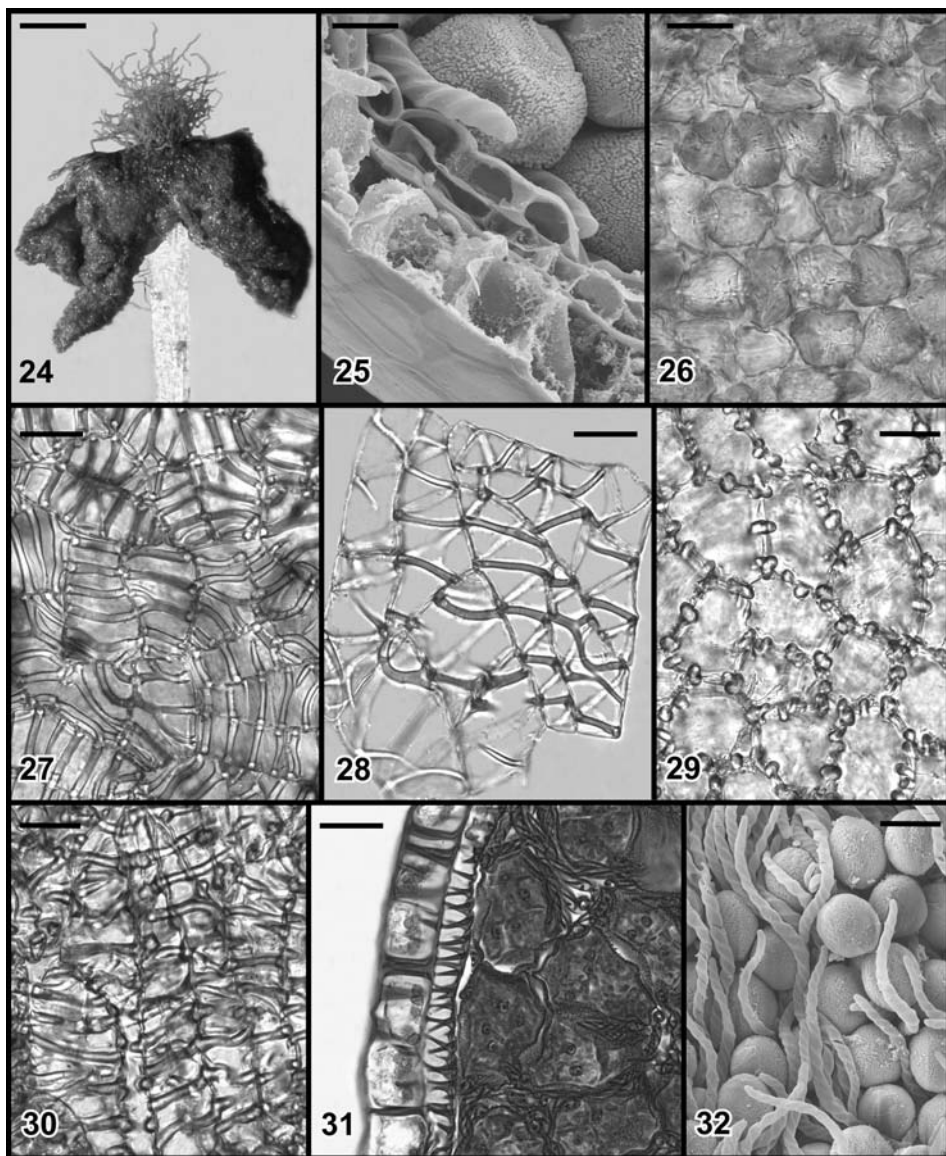
Figs 15–23. 15. Transverse section of an ellipsoidal tuber, showing cells packed with starch; scale bar = 60 μm . 16. Ellipsoidal tuber, lateral view in SEM; the tuber apex is directed towards the top of the image and the point of stalk attachment is towards the bottom; scale bar = 200 μm . 17. Spheroidal tuber, lateral view in SEM; there is a small part of the stalk at the bottom of the image; scale bar = 200 μm . 18. Portion of a fertile stem, with a developing caulocalyx at the apex and 2 rows of perigonal chambers lateral to 2 rows of unfertilized archegonia towards the base; scale bar = 1 mm. 19. Antheridia and archegonia, dorsal view in SEM; scale bar = 260 μm . 20. Longitudinal section of a gynoeccium, shortly after fertilization, showing the developing caulocalyx (Ca) and 2 fertilized archegonia, with embryos (at arrows); scale bar = 100 μm . 21. A fertilized archegonium and caulocalyx in very early stages of development, dorsal view in SEM; scale bar = 100 μm . 22. Caulocalyx after seta elongation and capsule dehiscence; note that the remnants of the old sporophyte were removed prior to imaging; scale bar = 1 mm. 23. Sporophyte, hand-dissected from the shoot calyptra prior to seta elongation; note the conoidal foot and well developed involucellum and the spheroidal capsule that has split along one pair of dehiscence lines; scale bar = 450 μm . [15 from Schiffner 1173 (w); 16 from Schiffner 712 (w); 17, 20 from Engel 10971 (NY); 18 from Freire 4189a (ABSH); 19, 21 from Forrest 566 (ABSH); 22 from Gardner n. 32 (FH, hb. Taylor, lectotype of *N. confluens*); 23 from Mosén s.n. (G).



Figs 15-23.

findings agree with those of Schiffner (1911); i.e., the capsule wall is 3-stratose for most of its length, becoming 4-stratose at the base and occasionally 2-stratose at the apex (Fig. 25). This is also in contrast to capsule structure in *Pellia*, in which the wall is bistratose, except at the 3-stratose base. In surface view, outer capsule wall cells are isodiametric to shortly rectangular, 30–42 µm in diameter, and possess unthickened, bright yellow walls and large, bright yellow triangular trigones (Fig. 26). There are no thickenings other than the trigones on either the radial or tangential walls. In section, the outer layer of cells is 40–45 µm in depth, about the same depth as the combined layers of inner cells (Fig. 25). Cells of the inner layers are elongate and fusiform, 20–30 µm wide by 80–100 µm long; their walls bear one or more yellow spiral thickening bands that appear as transverse bands, 3.0–3.5 µm wide, on the inner tangential wall (Figs 27, 28). In intact capsules the spiral nature of the thickenings is somewhat obscured by the underlying cells, but it is clearly seen when the layers are physically separated from each other (Fig. 28). According to Schiffner (1911), the capsule wall thickening pattern of *Noteroclada* is comparable to that of *Treubia* and is quite different from that found in *Pellia*. Our studies show that the outer capsule wall cells of *Pellia epiphylla* are different, with dispersed rod-like thickenings on all of the radial walls (Figs 29, 31), in contrast to Schuster's illustrations of *Noteroclada*-like outer wall thickenings in other species of *Pellia* (Schuster 1992, Fig. 850). The inner cell wall thickenings of *P. epiphylla* (Fig. 30) have been interpreted as semiannular bands by most authors (e.g., Schiffner 1911, Schuster 1992), but in sectioned capsules it is clear that they are spiral thickenings like those of *Noteroclada* (Fig. 31). Although *Treubia* also possesses spiral thickening bands on the inner capsule wall cells, it has no wall thickenings in the outer cells, and is no more like *Noteroclada* than is *Pellia*.

There are abundant elaters in the capsules, some randomly dispersed throughout the spore mass (Fig. 32) and others associated with the elaterophore. Those near the base of the elaterophore are short and broad, 16–20 µm wide by 85–100 µm long, and have four, yellow to ochre-colored, spiral-thickening bands, but most of the elaters are long and slender, 6.0–8.5 µm wide by 180–350 µm long, and have either two spiral bands throughout or three bands medially, tapering to two bands at the tips. We found no capsules with only very short elaters, as described by Hooker & Taylor (1844). Spores at the post-tetrad, but pre-germination stage, are spheroidal and range from 45–50 µm in diameter (Fig. 33), as compared to those of *Pellia* at the same stage, which are larger and slightly longer than broad, 55–60 µm by 65–70 µm (Fig. 34). Although spores in both genera have been described as warty or granulate (Schiffner 1911, Schuster 1992), the exine ornamentation of the two is actually quite different when seen in SEM. In *Noteroclada* the exospore is densely pilate, with the pila often confluent at their capita, and then appearing as short, irregular ridges (Fig. 33). The pila measure 1.3–1.4 µm high, with the stalks, 0.6–0.7 µm wide and the capita, 1.2–1.4 µm wide. There is a well defined, granulate, circular tetrad scar or laesura, which is bisected by a monolete ridge, or commissure, at the proximal pole; this structure was designated as a 'calotte' or proximal cap by Schiffner (1911, p. 331). Spores of *Pellia* are densely covered with a mixture of small granulae and larger, scattered verrucae, 1.2–1.4 µm high and 1.5–1.6 µm broad, and like *Noteroclada* have a circular laesura at the proximal pole. In both taxa, changes that



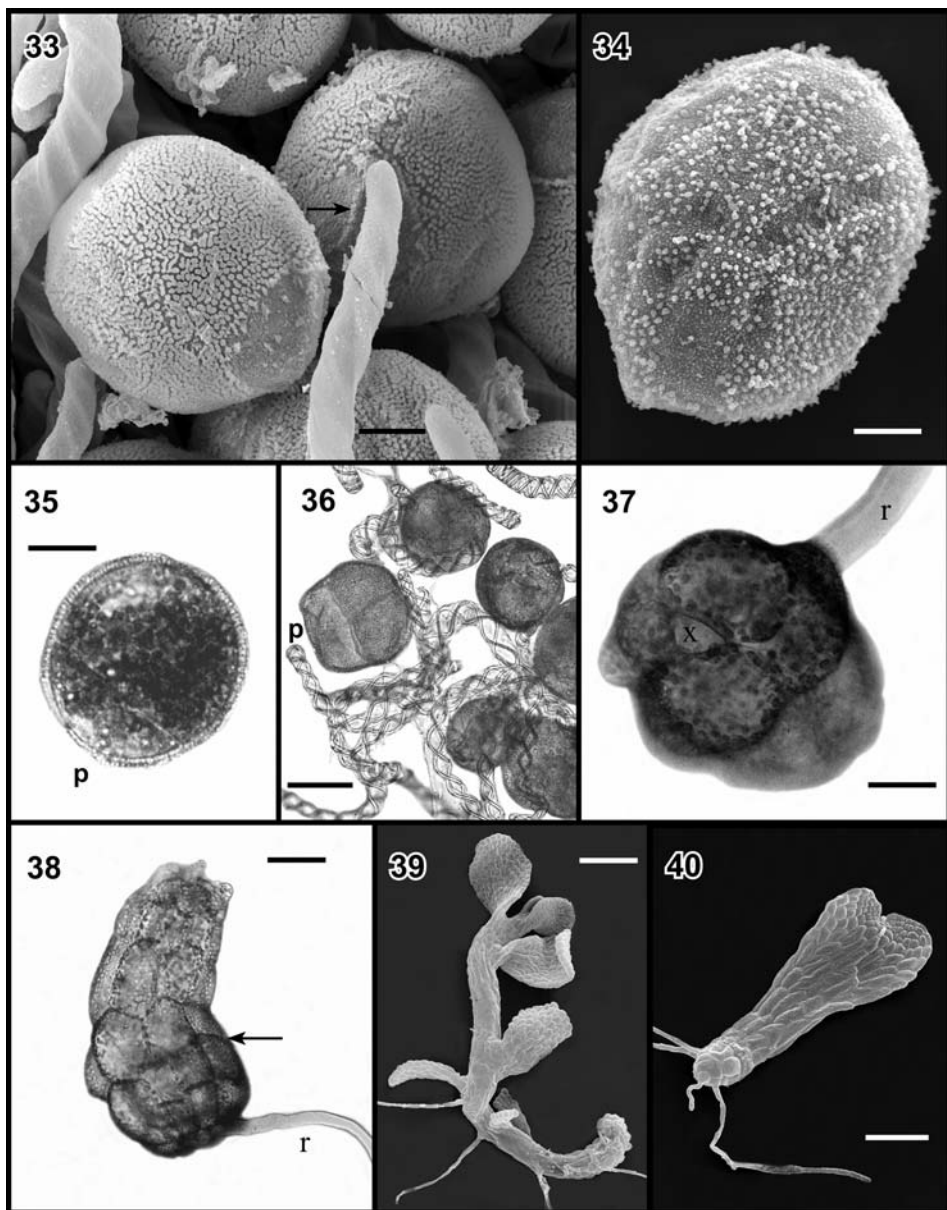
Figs 24–32. 24–28. *Noteroclada confluens*. 24. Dehiscent capsule with persistent, basal elaterophore; scale bar = 600 μ m. 25. Longitudinal section of a capsule wall, viewed in SEM; scale bar = 15 μ m. 26. Outer capsule wall cells in surface view; scale bar = 45 μ m. 27. Innermost layer of capsule wall cells, surface view with all cell layers in place; scale bar = 25 μ m. 28. Innermost layer of capsule wall cells that has been separated from subtending layers, surface view; scale bar = 25 μ m. 29–31. *Pellia epiphylla*. 29. Outer capsule wall cells in surface view; scale bar = 40 μ m. 30. Inner layer of capsule wall in surface view with both layers in place; scale bar = 20 μ m. 31. Longitudinal section of an undehiscent capsule, showing the 2-layered wall and precocious, endosporic protonemata; scale bar = 40 μ m. 32. *N. confluens*, intermixed spores and elaters, prior to spore germination, viewed in SEM; scale bar = 40 μ m. [24, 26, 27 from Dusén s.n (s); 25, 28, 32 from Forrest 566 (ABSH); 29–31 from Zhang 4071 (ABSH).]

occur in the exospore during germination disperse these exine ornamentations (Bartholomew-Began 1996) and obscure the proximal laesura.

Spore germination in *Noteroclada* is precocious and endosporic as in *Pellia*, but sporeling ontogeny differs from that of *Pellia* in several details. First, in *Noteroclada* the germinating spore remains spheroidal and enlarges only slightly prior to cell division, becoming only 70–75 μm in diameter at the 2-celled stage (Fig. 35). The first division wall is transverse and divides the spore into a small, somewhat hyaline proximal cell and much larger, densely chlorophyllose distal cell. The distal cell divides vertically to form two equal-sized cells (Fig. 36), each of which undergoes another vertical division to form a tier of four cells at the distal end of the sporeling, as illustrated by Ellwein (1926, Fig. 147). At the same time, the proximal cell divides by several oblique divisions to form a cluster of smaller cells at the proximal pole. We have never seen the pattern described and illustrated by Schiffner (1911, Fig. 7) in which the first division extends longitudinally through the spore and the four-celled stage includes the proximal cap. At the time of capsule dehiscence, the multicellular "spores" are either at the two-tiered stage or have begun to form a third tier of cells through transverse divisions of the original distal tier cells. It is notable that the "spore" remains spheroidal and does not increase in size during intracapsular cell division.

Soon after release from the capsule, the first rhizoid of the protonema is formed from one of the small proximal cells and breaks through the spore wall at the monoete ridge of the laesura. At this stage, the protonema always consists of three distinct tiers of cells. The cells of the central and distal tiers undergo patterned divisions, comparable to those of *Pellia* protonemata (Bartholomew-Began 1996, Figs 13–22), and then enlarge, stretching the exospore to at least two times its original width. With continued growth, additional rhizoids emerge from the proximal tier and the stretched exospore is ruptured distally, typically within three weeks of spore inoculation. A tetrahedral apical cell is then delineated from one of the distal cells of the somewhat elongate protonema by three oblique divisions (Fig. 37). This juvenile apical cell is isolateral, with the ventral face only half the width of the lateral faces, in contrast to the nearly equilateral apical cell of the adult phase (see Leitgeb 1877, pl. IX; Renzaglia 1982, Fig. 241). A juvenile shoot with two rows of leaves is subsequently produced by regular spiral segmentations of the apical cell (Figs 38, 39). The primary or first-formed leaves of the juvenile plant are very small, consisting of two basal cells and a terminal slime papilla, but larger, more typical leaves are produced after two or three cycles of segmentation. Goebel (1930, Fig. 969) reported that two or three leafy shoots can develop from a single protonema, but we have always found only one leafy shoot per protonema. As Bartholomew-Began has

Figs 33–40. 33. Spores of *Noteroclada confluens* after release from the tetrad, but prior to germination, viewed in SEM; note the circular laesura and monoete ridge or commissure at the arrow; scale bar = 12 μm . 34. Spore of *Pellia epiphylla* after release from the tetrad, but prior to germination, viewed in SEM; scale bar = 7 μm . 35–39. *N. confluens*. 35. Two-celled stage of protonema development, showing the asymmetric first division; p, proximal pole of the spore; scale bar = 25 μm . 36. Later stage of protonema development, showing quadrant formation in the distal cell; p, proximal pole of the spore;



scale bar = 40 μ m. 37. Apical cell (x) formation from a distal cell of a young sporeling, after emergence of the protonema from the spore wall; r, first rhizoid of the sporeling; scale bar = 50 μ m. 38. Young juvenile phase of the sporeling, with primary leaves forming at the shoot apex, viewed in OM; remnants of the exospore extend from the point of rhizoid emergence (r) to the position of the arrow; scale bar = 280 μ m. 39. Juvenile shoot, viewed in SEM; scale bar = 280 μ m. 40. Juvenile thallus of *P. epiphylla*, viewed in SEM; scale bar = 150 μ m. [33, 35–39 from Forrest 566 (ABSH); 34 from Zhang 4071 (ABSH); 40 from Stotler 4352 (ABSH).

illustrated (1996, Fig. 5), in *Pellia* the spore initially undergoes three transverse divisions, the first of which is median, to form an ellipsoidal, four-celled protonema, prior to any vertical division and the protonema consists of 23 or 24 cells when released from the capsule. An apical cell with two cutting faces is delimited from a distal tier cell prior to exospore rupture, and a short, cylindrical juvenile phase precedes the establishment of adult apical cell geometry and thallus formation (Fig. 40). Although the protonemata of both taxa display tiered construction, their tiered patterns are derived differently, and both the ontogeny and form of their juvenile phases are different. These differences suggest that although phylogenetically related, the divergence between the two taxa is ancient.

COMMON GARDEN STUDIES: Specimens from Brazil (Costa & Gradstein 3909) and Venezuela (Forrest 566) that were used to establish common garden experiments were of size classes comparable to the types of *N. confluens* and *N. leucorhiza*, respectively, i.e., the average width of the Brazilian plants was 3.0 mm and the average width of the Venezuelan plants was 6.0 mm. We observed no differences in rates of spore germination, sporeling ontogeny, or gametangial formation between the two sets of cultures, and mature plants showed no differences in plant width, leaf shape or leaf cell morphology. Regardless of locality of spore origin, plants grown from spores, randomly intermixed on the same shelf of an environmental chamber, are 6.1–6.5 mm wide, have leaves somewhat longer than wide, 1.8–2.0 mm wide by 3.0–3.2 mm long, and median leaf cells that are almost twice as long as broad, 42–54 μm wide by 75–100 μm long. Oil bodies number 10 to 12 per cell and are small, shiny and homogeneous. On the other hand, a population of small plants from Brazil, averaging 3.0 mm in width, and large plants from Ecuador, averaging 5.2 mm in width, that were transplanted into adjacent pots in a glasshouse at the University of Göttingen remained distinct, even after four years of greenhouse cultivation. These contrasting results suggest that plant size is likely modulated by differences in gene expression that occur early in ontogeny. Thus, spores, which are totipotent, display similar patterns of gene expression when placed in identical environments, but plants that have already established different gene expression patterns maintain their differences despite being placed in a common environment.

DISTRIBUTION STUDIES: Our studies confirm that *Noteroclada* is predominantly a Latin American taxon. It occurs in the mountains of central Mexico and Costa Rica, and is widely distributed in the Andes Mountains from western Venezuela to Cape Horn, Tierra del Fuego. There is a second center of distribution in the lower elevation, coastal mountains of southeastern Brazil, with extensions into eastern Uruguay and Paraguay. On the Atlantic side of the continent, the range extends from Tierra del Fuego to the Falkland Islands and South Georgia, the latter according to Hässel de Menendez (1977), and further north in the mid-Atlantic, to Gough Island and the islands of Tristan da Cunha. The genus is typically found at elevations above 2000 m in Mexico, Costa Rica and the northern to central Andes, but occurs at much lower elevations in other parts of its range. Except for South Georgia, these distributional data have been verified with specimens, as detailed in the ‘Select Specimens Examined’ section of this paper.

Reports of *Noteroclada* also occurring in South Africa, Kerguelen Island and/or New Zealand are problematic. In 1986 Grolle & Seppelt indicated that *N. confluens*

was widespread in Africa as well as Latin America, South Georgia, Gough Island and Kerguelen Island, without supporting citations. Later, Schuster (1992, p. 434) wrote "A second (?undescribed) species of *Noteroclada* occurs in South Africa (RMS & Shaun Russell) in the Drakensberg area." However, as discussed by Wigginton & Grolle (1996), no description of this Drakensberg taxon has ever been published and there seems to be no reliable evidence of *Noteroclada* occurring in Africa. Still, Gradstein et al. (2001) and Gradstein & Costa (2003) include South Africa in the distribution, based on the Schuster (1992) statement. We have verified that all specimens from Africa, filed as *Noteroclada* or *Androcryphia*, are species of *Fossombronia*, including a specimen from Drakensberg, South Africa [Transvaal, ravine forested sink hole, c. 9 m deep with trickling waterfall, near the Bonnet, Graskop, c. 1675 m, 12.9.1976, Rankin 203 (BM)]. We have not been able to locate the RMS & Shaun Russell specimen, but it also is likely a *Fossombronia*. The Drakensberg plants that we have seen are large, 5.4–6.6 mm wide, and have planate, horizontally inserted, oblong leaves with rounded apices and long, densely matted purple rhizoids; the specimen was annotated by Grolle in 2000 as "not *Noteroclada*," and by Perold, Sept. 2000, "possibly *Austrofossombronia*".

In the Taylor herbarium (FH), a large collection labeled "*Noteroclada confluens* Tayl. mss, Kerguelen's Land, J.D.Hooker 1840," is verified as *Fossombronia* cf. *australis*. Small sub-samples of this original collection also exist in BM, H-SOL, NY, PC and s. Except for one specimen in the Mitten herbarium (NY), they are all referable to *Fossombronia*, as are all other specimens from Kerguelen Island that have been labeled *Noteroclada* or *Androcryphia*. The single, problematic specimen (NY) contains the same *Fossombronia* as other Kerguelen specimens, but also contains *Noteroclada confluens*. This specimen is on the same sheet as another Kerguelen specimen that does contain only *Fossombronia* and four specimens of *Noteroclada* labeled Falkland Is., J.D.Hooker. It is probable that the *Noteroclada* stems in the problematic Kerguelen specimen came from one of the Falkland Island specimens on the same sheet since it contains the same small, woody roots as occur in the Falkland Island collections. We have seen many collections of *Fossombronia australis* from Kerguelen Island, but have no reliable evidence that *Noteroclada* occurs there.

There are two specimens in NY labeled *Androcryphia*, New Zealand that contain *Noteroclada* and there is a specimen of *Noteroclada* in MANCH labeled South Sea Island. One of the New Zealand specimens, labeled Colenso 1184, contains a mix of *Noteroclada* and *Fossombronia*, as also does the South Sea Island specimen. Each specimen contains only a few stems, which were likely extracted from a larger collection, and has only scanty collection information. Having found no specimens of *Noteroclada* that are unquestionably from Australasia, we agree with Grolle (2002) that the genus does not occur in the Pacific sector.

MOLECULAR STUDIES: The four-locus matrix contained a total of 3552 aligned base pairs, of which 396 were variable, but only five were parsimony informative. Of the four regions, the *rbcL* gene was most informative, while the *rps4* regions contained the highest proportion of base changes (see Table 2). However, the two non-coding regions contained several potentially useful indel characters that were not coded for this analysis (Table 3). Two in the *atpB-rbcL* spacer were unique to the Brazilian

Table 2. Distribution of characters by locus for 6 *Noterochlada* and one *Pellia* accession.

LOCUS	Aligned length (bases)	Constant characters, including <i>Pellia</i>	Parsimony uninformative characters, including <i>Pellia</i>	Parsimony informative characters, including <i>Pellia</i>	Constant characters, <i>Noterochlada</i>	Parsimony uninformative characters, <i>Noterochlada</i>	Parsimony informative characters, <i>Noterochlada</i>
<i>atpB-rbcL</i>	754	675 (89.5%)	77 (10.2%)	2 (0.3%)	751 (99.6%)	1 (0.1%)	2 (0.3%)
<i>trnL</i>	726	669 (92.1%)	57 (7.9%)	0 (0.0%)	722 (99.4%)	4 (0.6%)	0 (0.0%)
<i>rbcL</i>	1483	1338 (90.2%)	143 (9.6%)	2 (0.1%)	1476 (99.5%)	5 (0.3%)	2 (0.1%)
<i>rps4</i>	590	474 (80.3%)	116 (19.7%)	0 (0.0%)	583 (98.8%)	7 (1.2%)	0 (0.0%)

Table 3. DNA alignment showing potentially informative indel regions in *Noterochlada* sequences.

Collection	<i>atpB-rbcL</i> spacer	<i>trnL</i> region
Ecuador	GAAG-AAGGATTATATATA--TTTTTTTTTT-----CTCACTCCC	CAAATTAATCAGAAATT
Venezuela	GAAG-AAGGATTATATATA--TTTTTTTTTT-----CTCACTCCC	CAAATTAATCAGAAATT
Mexico	GAAG-AAGGATTATATATA--TTTTTTTTTT-----CTCACTCCC	CAAATTAATCAGAAATT
Brazil	GAAGTAAGGATTATATATAATTTTTTCTCTTTTTTTTCTCACTCCC	CAAATT--CAGAAATT
Argentina	GAAG-AAGGATTATATATA--TTTTTTTTTCTC-TTTTTTTTTTCTCACTCCC	CAAATT--CAGAAATT
Tierra del Fuego	GAAG-AAGGATTATATATA--TTTTTTTTTCTC-TTTTTTTTTTCTCACTCCC	CAAATT--CAGAAATT

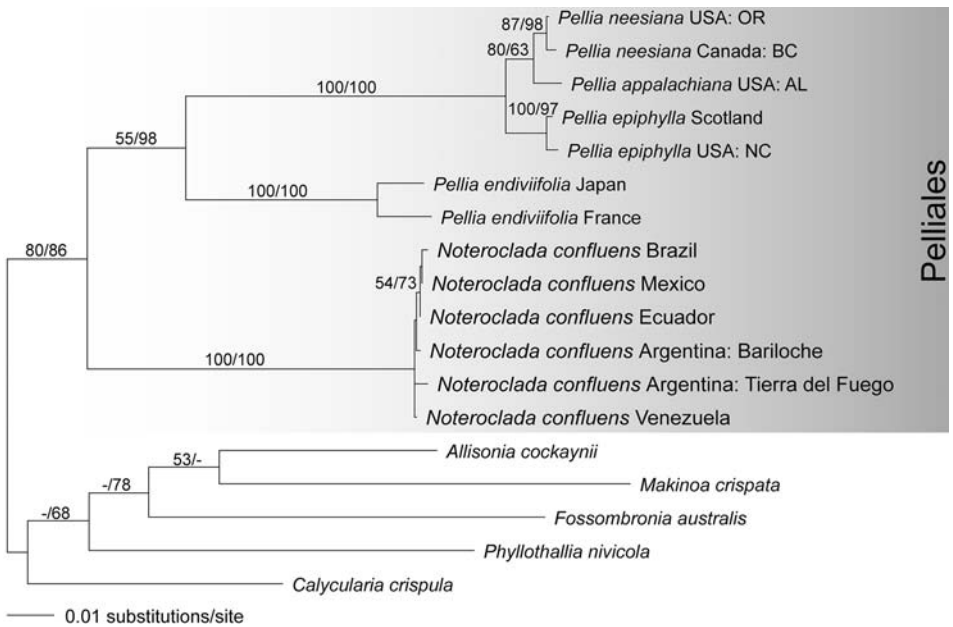


Fig. 41. One of three maximum likelihood phylograms resulting from an heuristic analysis of a concatenated matrix of *rbcL* and *rps4* sequences (-ln 7615.917). Maximum parsimony and maximum likelihood bootstrap values are show above the branches.

Noteroclada (a 1 bp insertion 511 bp into the alignment, and a 2 bp insertion at 530 bp) while one 13 bp gap (at 541 bp) was shared between Venezuela and Ecuador, with a similar 14 bp gap in the Mexican sequence. A further 1 bp gap at 542 bp that is shared by the two Argentine sequences but is absent from the Brazilian sequence may prove informative given greater sampling within the species. In the *trnL* region, a 3 bp gap 551 bp into the alignment was shared by the two Argentinian and the Brazilian sequences. It was not possible to compare the *Noteroclada* sequences with *Pellia* at any of these gap sites, as they were too divergent. Unfortunately the 3' spacer of *rps4*, although apparently highly variable, was not useful in this study due to the presence of both mononucleotide and dinucleotide repeats that proved impossible to read through with Sanger sequencing.

An exhaustive search of the four-locus matrix found 10 most parsimonious trees, of length 403 steps. Internal branches within *Noteroclada* are very short - only one or two steps (data not shown). The only clade recovered in all 10 trees contains the two Argentinian accessions of *Noteroclada*; MP bootstrap analysis gave this clade 66% support.

The two-locus matrix contained 1869 aligned characters, of which 625 were variable, and 443 were parsimony-informative. Parsimony analysis recovered 32 MPTs of length 1184 steps. All of the conflict between these 32 MPTs is within *Noteroclada*,

which again contains some very short branches. Pelliales is supported as monophyletic with respect to the chosen outgroups with 79% MP and 90% ML bootstrap support, while the monophyly of the *Noteroclada* accessions receives 100% support. Within *Noteroclada*, only the clade of the two Argentine accessions is well supported, with 91% ML bootstrap support, while there is very weak support for a clade of the accessions from Ecuador, Mexico and Brazil (54% MP BS). However, given the extremely low number of variable characters within *Noteroclada*, this is only to be expected.

From the likelihood phylogram (Fig. 41), it can be seen that the levels of molecular variation within each of the multi-accessioned *Pellia* species [*P. neesiana* (Gottsche) Limpr., *P. epiphylla* and *P. endiviifolia*] are of a similar order to that within *Noteroclada*. Based on phylogenetic analysis of the four chloroplast regions sequenced for this study there is no molecular evidence that *Noteroclada* comprises more than one species in Latin America. However, the insertions and deletions within the non-coding regions provide evidence of genetic variation within *Noteroclada*. It is likely that further sampling, by providing more informative characters, will allow stronger inferences about the partitioning of its variation.

Discussion

Recognition of *Noteroclada* as a monospecific taxon is supported by morphological, experimental and molecular sequence data. Although there is a tendency for plant size to differ between Andean and Atlantic rainforest populations, common garden experiments demonstrate that adult plant size can be modified by environment during early stages of ontogeny and is not a reliable indicator of genetic divergence. On the other hand, tuber morphologies are, with only few exceptions, geographically partitioned, with small spheroidal forms common in Andean populations and larger, ellipsoidal forms occurring in populations from the Atlantic rainforest. Since both types of tubers have rather hard exteriors, are packed internally with starch, and generally remain attached to their parent shoots, their primary function is probably perennation, rather than reproduction or dispersal. This suggestion is further supported by the observation that tuber formation in axenic cultures occurs only after a culture becomes crowded and the agar begins to dry out, regardless of spore source. Although tuber shape does seem to predict specimen locality, we do not deem it a suitable character to delineate species in the absence of any other evidence of speciation. In fact, indel data suggest a different pattern of partitioning (Table 3) than tuber morphology, with the populations from the northern Andes and Mexico being different from those of the southern Andes and Brazil. Given the broad distribution range of *N. confluens*, both genetic and morphological variation are to be expected, but a more comprehensive sampling of populations is needed to evaluate their significance.

The distribution of *Noteroclada* includes several disjunctions, e.g., the Andes to southeastern Brazil, Tierra del Fuego to the Falkland Islands and South Georgia, and South America to Tristan da Cunha and Gough Island. Despite their closer

proximity to Brazilian populations, plants from Tristan da Cunha and Gough Island are morphologically like those of the Andes and Falkland Islands; i.e., they are large, to 8.2 mm in width, and have oblong leaves and spheroidal tubers. According to Wace (1961), Gough Island owes its vegetation to long distance dispersal by wind, water or animals, and shares several floristic elements with southwest Chile and the Falkland Islands. *Noteroclada* is dispersed primarily through spores, but these are large, thin-walled and actively growing when released from the capsule and are not likely to be dispersed over great distance by wind, as suggested to explain the disjunction of *Herbertus* Gray from South America to Gough Island (Heinrichs et al. 2010). Possible dispersal agents, however, could be migratory seabirds, such as shearwaters and albatrosses that have been known to fly from Tierra del Fuego and the Falkland Islands to the eastern Atlantic. In fact, Tristan da Cunha and Gough Island are primary breeding sites for many such seabirds.

A phylogenetic relationship between *Noteroclada* and *Pellia* is clearly supported by a combination of morphological and molecular data. They are resolved as sister taxa in a monophyletic clade of the Pelliidae and share several morphological characters, including solitary antheridia in perigonial chambers, spheroidal capsules with a basal columella and precocious, endosporic spore germination. Still, intrinsic ontogenetic differences suggest evolutionary distance between them. For example, they differ in early patterns of protonemal division and juvenile plant formation, as well as in shoot apical cell geometry, branch origin and ontogeny, gynoeceal organization and subsequent development of structures associated with the sporophyte. In our view, these significant, ontogenetic differences support the placement of *Noteroclada* and *Pellia* in separate, monogeneric families as proposed by Frey & Stech (2005).

Taxonomy

Controversy over application of the correct generic name for this remarkably distinct genus of hepatics persisted for well over 100 years, with some workers utilizing the name *Noteroclada*, while others preferred the name *Androcryphia* for the same taxon. Proskauer (1955) documented chronologically the use of *Noteroclada* versus *Androcryphia* and solved this dilemma by pointing out that both are validly published, legitimate names and that *Androcryphia* should not be simply regarded as a substitute name for *Noteroclada*, i.e., a nomenclatural synonym. Nees (1846) had proposed the name *Androcryphia* ("hidden males") as a replacement name for *Noteroclada*, explaining in a footnote (Nees 1846, p. 470) that he regarded Taylor's Greek nonsensical. He considered it to be derived from *notos* (Gk. νοτος = the back), and *clados* (Gk. κλάδος = branch). That would render the meaning "dorsal branches," which indeed would be an inapplicable choice. Taylor & Hooker (1847, p. 446), however, pointed out that Taylor's name should not have been superseded since the prefix was instead based upon *noteros* (Gk. νοτερός = moist), referring to "plants of wet places," a perfectly correct and logical choice. Apart from that, Nees (1846) included two species in his genus, *A. porphyrorhiza* and *A. confluens*. More recently, Grolle (1983) selected *A. confluens* as the generitype, which would render

Androcryphia a nomenclatural synonym of *Noteroclada*, but he was apparently unaware that Evans (1949) had earlier designated *A. porphyrorhiza* as the type of *Androcryphia*. Proskauer (1955, p. 195–197) argued, and rightly so, that *Androcryphia* was therefore not a substitute name for *Noteroclada* because when typified with *A. porphyrorhiza* it automatically became a synonym of *Fossombronina*.

Proskauer (1955) also pointed out that both the generic name *Noteroclada* and the binomial *N. confluens* were validly published by Hooker & Wilson (1844, p. 166) in their paper on a list of bryophytes collected by G. Gardner in Brazil. Regardless of the brevity, their statement "similar to *Jungerm. hyalina*, but larger, n. 32" fulfills the requirement of a *descriptio generico-specifica* (McNeill et al. 2006: Article 42.1) for this monotypic genus. In their running list of the bryophytes, the binomial was ascribed to Thomas Taylor, appearing as number "134. *Noteroclada confluens*, Tayl. MSS.". On a later page in the same volume of the London Journal of Botany, Hooker & Taylor (1844, p. 477) presented a paper that treated the same taxon in detail. However, in the introduction to this work they pointed out that several naturalists had proposed the establishment of various new genera, which they did not find entirely acceptable. Rather, they (Hooker & Taylor 1844, p. 367) ". . . steered a middle course, and separated the *Jungermanniae* into sections to which we have given the names of the genera." They did not accept *Noteroclada* as a genus, but instead considered it a section of *Jungermannia*. Geissler & Bischler (1987) included it as "*Jungermannia confluens* Hook.f. & Taylor" in the Index Hepaticarum, but without (Taylor ex Hook. & Wilson) as parenthetical authors of the epithet, which would be the correct citation. And, even though both *N. confluens* and *J. confluens* were published in the same volume, they do not have equal priority since the papers were not issued simultaneously. According to Stafleu & Cowan (1979, p. 297, #3008) each of the seven volumes of the London Journal of Botany consisted of 12 parts, issued monthly, which ran anywhere from a total of 612 to 678 pages. One can argue by extrapolation that the W.J.Hooker and W.Wilson description on page 166 was likely issued by March, whereas the J.D.Hooker and T.Taylor description on page 477 was not issued until July (Stafleu & Cowan 1986, p. 191). In view of the above, the author entries "Tayl. ex Hook. & Tayl." for the genus *Noteroclada* (London J. Bot. 3: 477, 1844) and "(Hook.f. & Tayl.) Spruce" for the binomial *N. confluens* (Trans. Proc. Bot. Soc. Edinburgh 15: 531, 1885) by Willi in Index Hepaticarum (1989, p. 33) are obviously incorrect.

Traditionally, *Pellia* and *Noteroclada* comprise the Pelliaceae, notwithstanding Reimers (1954) who proposed the monogeneric family Noterocladaceae, albeit without a Latin description or diagnosis. Schuster (1991) likewise regarded *Noteroclada* to differ strikingly from *Pellia*, and separated it into the subfamily Noterocladoideae R. M. Schust. More recently, Frey & Stech (2005) validly published Noterocladaceae and then further isolated *Noteroclada* from *Pellia* when they named the order Noterocladales W.Frey & Stech (Frey & Stech 2008). While our data support the placement of *Pellia* and *Noteroclada* into separate families, their resolved relationship in phylogenetic analyses warrants placing them into the same order, Pelliiales.

PELLIALES He-Nygrén, Juslén, Ahonen, Glenny & Piippo, *Cladistics* 22: 27. 2006.

Pelliaceae H.Klinggr., *Höh. Crypt. Pruess.* 13, 1858.

TYPE: *Pellia* Raddi nom. cons., *Jungermanniografia Etrusca*: 38. 1818 [preprint], [= *Memorie Mat. Fis. Soc. Ital. Sci. Modena* 18: 49. 1820]. T: *P. epiphylla* (L.) Corda

Noterocladaceae W.Frey & Stech, *Nova Hedwigia* 81: 67. 2005. [Noterocladaceae Reimers in Melchior & Werdermann, *Engler's Syllabus der Pflanzenfam.*, ed. 12, 1: 226. 1954. (nom. nud.)]

TYPE: *Noteroclada* Taylor ex Hook. & Wilson, *London J. Bot.* 3: 166. 1844. T: *N. confluens* Taylor ex Hook. & Wilson, *London J. Bot.* 3: 166. 1844. (vide Proskauer, 1955: 197)

Jungermannia L., *Sp. Plt.*: 1131. 1753. pro parte, excl. typus.

Pellia Raddi nom. cons., *Jungermanniografia Etrusca*: 38. 1818 [preprint], [= *Memorie Mat. Fis. Soc. Ital. Sci. Modena* 18: 49. 1820]. pro parte, excl. typus.

Androcryphia Nees in Gottsche, Lindenberg & Nees, *Syn. Hepat.*: 470. 1846. pro parte, excl. typus.

Noteroclada confluens Taylor ex Hook. & Wilson, *London J. Bot.* 3: 166. 1844.

TYPE: Brazil, Organ Mountains [Serra dos Órgãos], Gardner n. 32 [134 is the running number in the Hooker and Wilson paper]. Lectotype designated by J.Proskauer, *Bryologist* 58: 194; 197, 1955. (FH - hb. Taylor; isolectotypes: BM (2), E, FH (2), G, MANCH, NY (2))

Jungermannia porphyrorhiza Nees in Martius, *Fl. Bras. Enum. Pl.* 1, 1: 343. 1833. pro parte, excl. typus (planta masculina)

Jungermannia (Noteroclada) confluens (Taylor ex Hook. & Wilson) Hook. f. & Taylor, *London J. Bot.* 3: 478. 1844. [NB: Of the four locations cited by the authors, the original material from Kerguelen is *Fossombronina*, not *Noteroclada*.]

Androcryphia porphyrorhiza (Nees) Nees in Gottsche, Lindenberg & Nees, *Syn. Hepat.*: 470. 1846. pro parte, excl. typus.

Androcryphia confluens (Taylor ex Hook. & Wilson) Nees, *Syn. Hepat.*: 471. 1846.

Noteroclada porphyrorhiza (Nees) Mitt. in J.D.Hooker, *Fl. Antarct. Voy.* 2, *Fl. Nov.-Zel.* II: 163. 1855. pro parte, excl. typus.

Pellia porphyrorhiza (Nees) Austin, *Bull. Torrey Bot. Club* 6: 29-30. 1875. '*porphyrorrhiza*' pro parte, excl. typus.

Pellia phyllobola Austin MSS. [nom. nud.], *Bull. Torrey Bot. Club* 6: 29. 1875. Original material: Chile, leg. Ch. Gay (H-SOL, NY). [In the Austin manuscript of *P. phyllobola* (MANCH) "*Pellia epiphylla*", *Herb. Mus. Paris* in *Herb. Sulliv.*, Hab. Chili, Ch. Gay" was cited. A packet of that was found in the Mitten herbarium (NY), while a specimen labelled in Austin's hand was found in the Lindberg herbarium (H-SOL).]

Noteroclada leucorhiza Spruce, *Trans. Proc. Bot. Soc. Edinburgh* 15: 530. 1885. Type: *Noteroclada leucorhiza* Spr. [Ecuador] Altar. [Spruce s.n.] Lectotype, designated here: (MANCH). [We have studied specimens from several herbaria often designated to be the "type" with printed 'Hepaticae Spruceanae' labels, but with both "Tunguragua et El Altar" hand written as the location. It is problematic if these should be considered isolectotypes since only "in monte Altar" is cited in the protologue while Tunguragua was never mentioned. There is no way to be sure which of the two locations represents the actual origin of each packet.] (?isolectotypes: BM (2), DUKE, E, M, MANCH, MICH, NY (2), US, W)

Noteroclada arrhiza Spruce, *Mem. Torrey Bot. Club* 1: 138. 1890. '*arrhiza*'. Type: Flora South America. Sorata, Bolivia, 10,000 ft., Feb., 1886. Leg. H. H. Rusby 3005 p.p.[in a packet labelled *Marchantia* L.]. Lectotype, designated here: (NY). SYN. NOV.

Excluded Names

The following names, validly published or not, have been wrongly associated with either *Noterochlada* or *Androcryphia*.

Androcryphia longiseta Austin, Proc. Acad. Nat. Sci. Philadelphia (1869) 21: 228. 1869. ≡ *Fossombronia longiseta* (Austin) Austin, Hepat. Bor.-Amer. Exsicc.: 118. 1873. Lectotype designated by Stotler et al., Bryologist 106: 136, 2003. (H-SOL; isolectotypes: CAS, F, FH, H-SOL, MANCH, MICH, NY)

Noterochlada perpusilla Colenso, Trans. & Proc. New Zealand Inst. 17: 260–261. 1884[1885]. ≡ *Fossombronia perpusilla* (Colenso) Steph., Sp. Hepat. 1: 379. 1900. Lectotype designated by Stotler et al., Bryologist 106: 138. 2003. (BM; isolectotype: G)

Noterochlada lacunosa Colenso, Trans. & Proc. New Zealand Inst. 18: 248. 1885[1886]. ≡ *Treubia lacunosa* (Colenso) Prosk., Bryologist 58: 199. 1955. [Proskauer (1955) transferred this species to the genus *Treubia* based upon details of the description, but he was unable to locate any type material. He chose not to provide a neotype, stating that he would leave that for a later bryologist to do if necessary. In their revisionary study of *Treubia*, Schuster & Scott (1966) also chose not to designate a neotype.]

Noterochlada longiuscula Colenso, Trans. & Proc. New Zealand Inst. 19: 299. 1886[1887]. Type: "Hab. Hilly woods at Pohue, north-west from Napier, County of Hawke's Bay; 1885: Mr. A. Hamilton". [No original material was found either at the Museum of New Zealand/Te Papa Tongarewa (WELT), which holds Colenso specimens or the British Museum, Natural History (BM), which holds the Colenso specimens communicated to J. D. Hooker, or in any of the other herbaria that we have searched. From the Colenso description it is clear that this species is neither *Noterochlada* nor *Fossombronia*. A neotype will need to be selected in order to place this taxon.]

Androcryphia dentata Steph. ms., Tasmania, leg. Weymouth, /Levier 513/ [ms. in icones ined. (G), nom nud.] ≡ *Fossombronia dentata* Steph., Sp. Hepat. 1: 394. 1900. Lectotype, designated here: Hb. E. Levier, N° 513, *Fossombr. dentata* Stnsp., Tasmania, on earth, Trevallyn, Launceston (near Bridge), 22 Sept. 1893, legit A. Weymouth, in Herb. F. Stephani (G no. 22166; isolectotype AD).

Androcryphia confluens (Taylor ex Hook. & Wilson) Nees var. *major* Herzog, Biblioth. Bot. 21 (87): 270. 1916. nom. nud. Original material: Am Bachrand beim Abstieg von der Passhöhe (Cerros de Malaga) zum Rio Paracti, ca 3600–3800 m, Juni 1911, Herzog 4388 ≡ *Fossombronia herzogii* K.I. Goebel in Herzog, Biblioth. Bot. 21 (87): 269. 1916. Lectotype designated by Freire & Stotler, Bryologist 110: 820. 2007. (JE; isolectotype: M)

Noterochlada lenta Tayl[or]. MSS, [ms. in herb., nom. nud.] = *Jungermannia gollanii* Steph. Original material: Nepal, Wallich, Sir W.J. Hooker, 1843. (FH; duplicates: BM (2), MANCH, NY)

Androcryphia wallichiana Lehm. [ms. in herb., nom. nud.] = *Jungermannia gollanii* Steph. Original material: Nepalia, Wallich, Herbarium Lehmannianum. (s; duplicate in hb. Lindenberg, w) [This specimen, likely sent to Lehmann by W.J. Hooker, is no doubt part of the same gathering by N. Wallich that T. Taylor labeled as *Noterochlada lenta*.]

SELECT SPECIMENS EXAMINED: *NOTEROCLADA* - MEXICO. MEXICO: Puerto de la Cruzes, 3000 m, Duell 341 (JE); PUEBLA: nr Volcan Iztaccihuatl, 3680 m, Villarreal 1042 (ABSH). COSTA RICA. CARTAGO: San Gerardo, 5 km NW crater Irazú, 2000 m, Gomez 19876 (JE). COLOMBIA. ANTIOQUIA: Medellín, Boqueron, Onraedt 83A10302 (HB. VÁÑA); BOYÁCA: Bosques de Arcabuco, 2700 m, Bischler 1902 (HB. VÁÑA); CUNDINAMARCA: 15 km NNW of Facativá, ca 2330 m, King, Guevara & Forero-G. C-844 (US); NARIÑO: Correg. de El Encano. 2740 m, Ramirez P. 10137 (MO). VENEZUELA. MÉRIDA: Paramo de Mucubaji, over 3500 m, Forrest 566 (ABSH); Laguna Negra, 3500 m, Freire 4189a (ABSH); TACHIRA: Cabeceras del Río Quinimarí, 2500–2800 m, Steyermark & Dunsterville 100808 (F, NY). BRAZIL. MINAS GERAIS: Serra de Caldas, Mosén s.n., as *Androcryphia confluens* (BM, F, FH, G, NY, S, US, W); PARANÁ: Guartelá, 700–800 m, Hatschbach & Barbosa 58220 (C); RIO GRANDE DO SUL: Hamburger Berg, Lindman B.101 (BM, FH, S(2)); RIO DE JANEIRO: Serra de Bocaina,

ca 500 m, Costa & Gradstein 3909 (ABSH); Serra do Itatiaya, Bandeira 59 (s); Teresópolis, ca 800 m, Costa & Amado Filho s.n. (ABSH); SANTA CATARINA: N of Campos Novos, 850 m, Vitt 21132 (JE); SÃO PAULO: nr Cantareira, 800 m, Schiffner 712; Schiffner 1173 (w); nr Alto da Serra, 900 m, Schiffner 394 (w); Apiahy, 1100 m, Schiffner 313 (w). ECUADOR. CARCHI: Páramo de El Angel, 3400 m, Gradstein, Weber & Lanier Gr.3386 (G, NY); COTOPAXI: Cotopaxi National Parc, 3550 m, Gradstein & Frahm 6688 (G); PINCINCHA: 13,000 ft., Bell 117 (BM); TUNGURAHUA: NW slopes of Tungurahua, 8500 ft., Bell 858 (BM); s.l. "Andes 5", harvested from Göttingen Botanical Garden glasshouse, Weiss & Schwerdtfeger s.n. (ABSH). PERU. CAJAMARCA: Quebrada Cavilan, Cerro Huayllacongá, 3150 m, P. & E.Hegewald 6532 (F, JE, MO); LA LIBERTAD: Cerro las Gordas, P. & E.Hegewald 5967 (F (2), JE, MO); LIMA: Kolpayunku, 3660 m, Cerrate, Gómez & Ojeda 4836 (US). BOLIVIA. COCHABAMBA: Carrasco, Serranía Siberia, 2720 m, Churchill, Decker & Mogro 22638 (MO); LA PAZ: Apolo, 4800 ft., Williams 2240, as *Androcryphia confluens* (BM, FH, NY); Pelichuco [sic], 11000 ft., Williams 2729, as *A. confluens* (NY); SANTA CRUZ: Vallegrande, Serranía Altares, Cerro El Centinela, 2300 m, Lewis 85-620 (HB. VÁÑA). CHILE. AISÉN: Puerto Chacabuco, Bresinsky & Garrido 156 (M); [ARAUCANÍA:] Cautín, Parque Nacional Conguillío, 1110 m, Mahú & Harnell 10672 (F, JE, MO); Malleco, W of Purén, Sierra Nahuelbuta, 450 m, Hutchinson 268 (UC); [BIOBÍO:] Ñuble, San Fabián, 450 m, Mahú 11242 (JE); [LOS LAGOS:] Llanquihue, Yervas Buenas, 20 m, Mahú & Tapia 21745 (MO); [LOS RÍOS:] Valdivia, Cerro Tralcan, 380–440 m, Engel 10971 (F, H-SOL, NY); [MAGALLANES AND ANTÁRTICA CHILENA:] Magallanes, Parque Nacional Torres del Paine, Halling 5848 (NY); Patagonian, Punta Arenas, Dusén s.n., as *N. leucorhiza* (H-SOL, S(2)); Isla Navarino, 200 m, Hyvönen 2782 (G, JE); Rio Azopardo, Dusén 79, as *N. leucorhiza* (G, H-SOL(2), S(2), W); JUAN FERNANDEZ ISLANDS: Mas Afuera, ca 1100 m, C. & O. Skottsberg 101 (NY, S); PARAGUAY. CORDILLERA: SE Caacupé, 240 m, Geissler 15135 (G). ARGENTINA. CHUBUT: Rio Calileufu, Kühnemann s.n. (CHR); CÓRDOBA: Supra El Durasno, Hosseus 173, as *Androcryphia confluens* (JE); RIO NEGRO: Bariloche District, Llaol Llaol, Vidal-Russell s.n. (ABSH); SANTA CRUZ: Rio de las Vueltas, ca 450 m, Sleumer 1700 (S); TIERRA DEL FUEGO: Ushuaia, Cordillera Guanaco above Lago Roca, ca 580 m, Long 31768 (ABSH); Parque Nacional Tierra del Fuego, W of Ushuaia, Halling 5738 (F, NY); TUCUMÁN: Camino a Tafi del Valle, Price et al. 1729 (MO). URUGUAY. DURAZNO: Rio Negro, Osorio 17.646 (F); LAVALLEJA: Carretera Pan de Azúcar-Minas, Zorrón 3028, as *A. confluens* (BM, NY, S(2), US, W). FALKLAND ISLANDS. WEST FALKLANDS: Cheeks' Creek, 40 ft., Engel 3480 (F); EAST FALKLANDS: Mullet Creek Stream, 200 ft., Engel 3186 (F). SOUTH GEORGIA. [none of the specimens of *Noterochlada* cited to be in AAS by Hässel (1977) could be located (H.Peat, pers. comm.)]. TRISTAN DA CUNHA. Above Burntwood, 600 m, Christophersen & Mejland 832, as *Fossombronina fernandeziensis* Steph. (O, S). GOUGH ISLAND. Cave above Glen Beach, Wace 657 (BM).

PELLIA - *Pellia appalachiana* R.M.Schust.: U.S.A. ALABAMA: Lawrence County, Bankhead National Forest, 600 ft., Davison 3579 (ABSH). *Pellia endiviifolia*: FRANCE. Salon en Provence, nr Marseille, Muth s.n. (ABSH). JAPAN. TOKYO, from greenhouse, Higuchi s.n. (ABSH). *Pellia epiphylla*: U.S.A. ILLINOIS: Jackson Co., Little Grand Canyon, Li Zhang 4071 (ABSH); Jackson Co., Giant City State Park, Stotler 4352 (ABSH). NORTH CAROLINA, Yancey Co., Blue Ridge Parkway, Forrest & Villarreal 619 (ABSH). SCOTLAND. EAST LOTHIAN: Humber, L.Forrest, S.Forrest & Bryson 700 (ABSH). *Pellia neesiana*: CANADA. VANCOUVER ISLAND, BC: Pacific Rim National Park, Forrest & Badcock 598 (ABSH). U.S.A. OREGON: Bastendorf bog, Wheeler s.n. (ABSH).

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