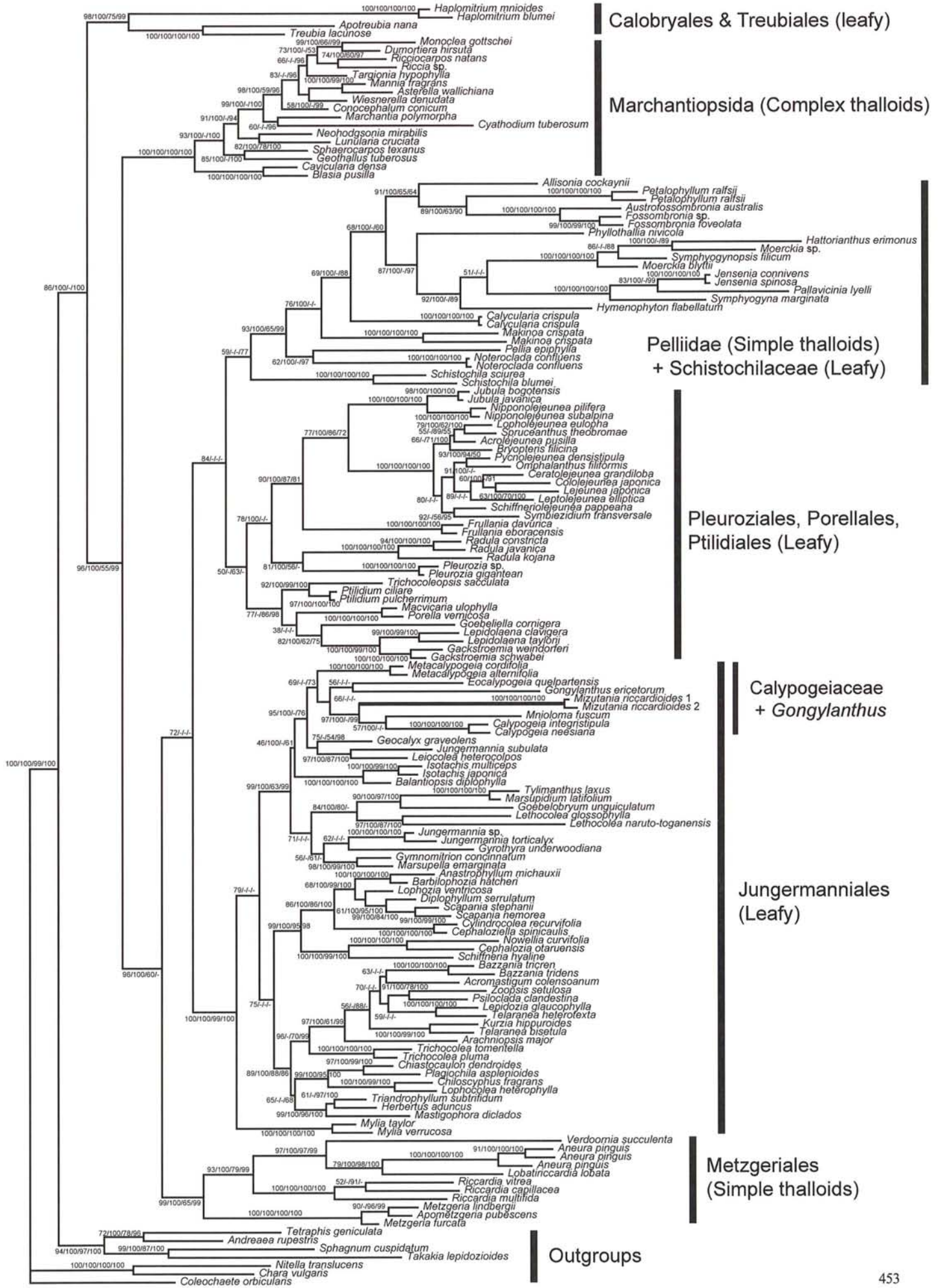
Haplomitrium mnioides
Haplomitrium blumei
Apotreubia nana
Treubia lacunose
Monoclea gottschei
Dumortiera hirsuta
Ricciocarpos natans
Riccia sp.
Targionia hypophylla
Mannia fragrans
Asterella wallichiana
Wiesnerella denudata
Conocephalum conicum
Marchantia polymorpha
Cyathodium tuberosum
Neohodgsonia mirabilis
Lunularia cruciata
Sphaerocarpos texanus
Geothallus tuberosus
Cavicularia densa
Blasia pusilla
Calobryales & Treubiales (leafy)
Marchantiopsida (Complex thalloids)
Allisonia cockaynii
Petalophyllum ralfsii
Petalophyllum ralfsii
Austrofossombronia australis
Fossombronia sp.
Fossombronia foveolata
Phyllothallia nivicola
Hattorianthus erimonus
Moerckia sp.
Symphyogynopsis filicum
Moerckia blyttii
Jensenia connivens
Jensenia spinosa
Pallavicinia lyelli
Symphyogyna marginata
Hymenophyton flabellatum
Calycularia crispula
Calycularia crispula
Makinoa crispata
Makinoa crispata
Pellia epiphylla
Noteroclada confluens
Noteroclada confluens
Schistochila sciurea
Schistochila blumei
Pelliidae (Simple thalloids)
+ Schistochilaceae (Leafy)
Jubula bogotensis
Jubula javanica
Nipponolejeunea pilifera
Nipponolejeunea subalpina
Lopholejeunea eulopha
Spruceanthus theobromae
Acrolejeunea pusilla
Bryopteris filicina
Pycnolejeunea densistipula
Omphalanthus filiformis
Ceratolejeunea grandiloba
Cololejeunea japonica
Lejeunea japonica
Leptolejeunea elliptica
Schiffneriolejeunea pappeana
Symbiezidium transversale
Frullania davurica
Frullania eboracensis
Radula constricta
Radula javanica
Radula kojana
Pleurozia sp.
Pleurozia gigantean
Trichocoleopsis sacculata
Ptilidium ciliare
Ptilidium pulcherrimum
Macvicaria ulophylla
Porella vernicosa
Goebeliella cornigera
Lepidolaena clavigera
Lepidolaena taylori
Gackstroemia weindorferi
Gackstroemia schwabei
Pleuroziales, Porellales,
Ptilidiales (Leafy)
Metacalypogeia cordifolia
Metacalypogeia alternifolia
Eocalypogeia quelpartensis
Gongylanthus ericetorum
Mizutania riccardioides 1
Mizutania riccardioides 2
Mnioloma fuscum
Calypogeia integristipula
Calypogeia neesiana
Calypogeiaceae
+ Gongylanthus
Geocalyx graveolens
Jungermannia subulata
Leiocolea heterocolpos
Isotachis multiceps
Isotachis japonica
Balantiopsis diplophylla
Tylimanthus laxus
Marsupidium latifolium
Goebelobryum unguiculatum
Lethocolea glossophylla
Lethocolea naruto-toganensis
Jungermannia sp.
Jungermannia torticalyx
Gyrothyra underwoodiana
Gymnomitrion concinnatum
Marsupella emarginata
Anastrophyllum michauxii
Barbilophozia hatcheri
Lophozia ventricosa
Diplophyllum serrulatum
Scapania stephanii
Scapania hemorea
Cylindrocolea recurvifolia
Cephaloziella spinicaulis
Nowellia curvifolia
Cephalozia otaruensis
Schiffneria hyaline
Bazzania tricren
Bazzania tridens
Acromastigum colensoanum
Zoopsis setulosa
Psiloclada clandestina
Lepidozia glaucophylla
Telaranea heterotexta
Kurzia hippuroides
Telaranea bisetula
Arachniopsis major
Trichocolea tomentella
Trichocolea pluma
Chiastocaulon dendroides
Plagiochila asplenioides
Chiloscyphus fragrans
Lophocolea heterophylla
Triandrophyllum subtrifidum
Herbertus aduncus
Mastigophora diclados
Mylia taylor
Mylia verrucosa
Jungermanniales
(Leafy)
Verdoornia succulenta
Aneura pinguis
Aneura pinguis
Aneura pinguis
Lobatiriccardia lobata
Riccardia vitrea
Riccardia capillacea
Riccardia multifida
Metzgeria lindbergii
Apometzgeria pubescens
Metzgeria furcata
Metzgeriales
(Simple thalloids)
Tetraphis geniculata
Andreaea rupestris
Sphagnum cuspidatum
Takakia lepidozioides
Nitella translucens
Chara vulgaris
Coleochaete orbicularis
Outgroups

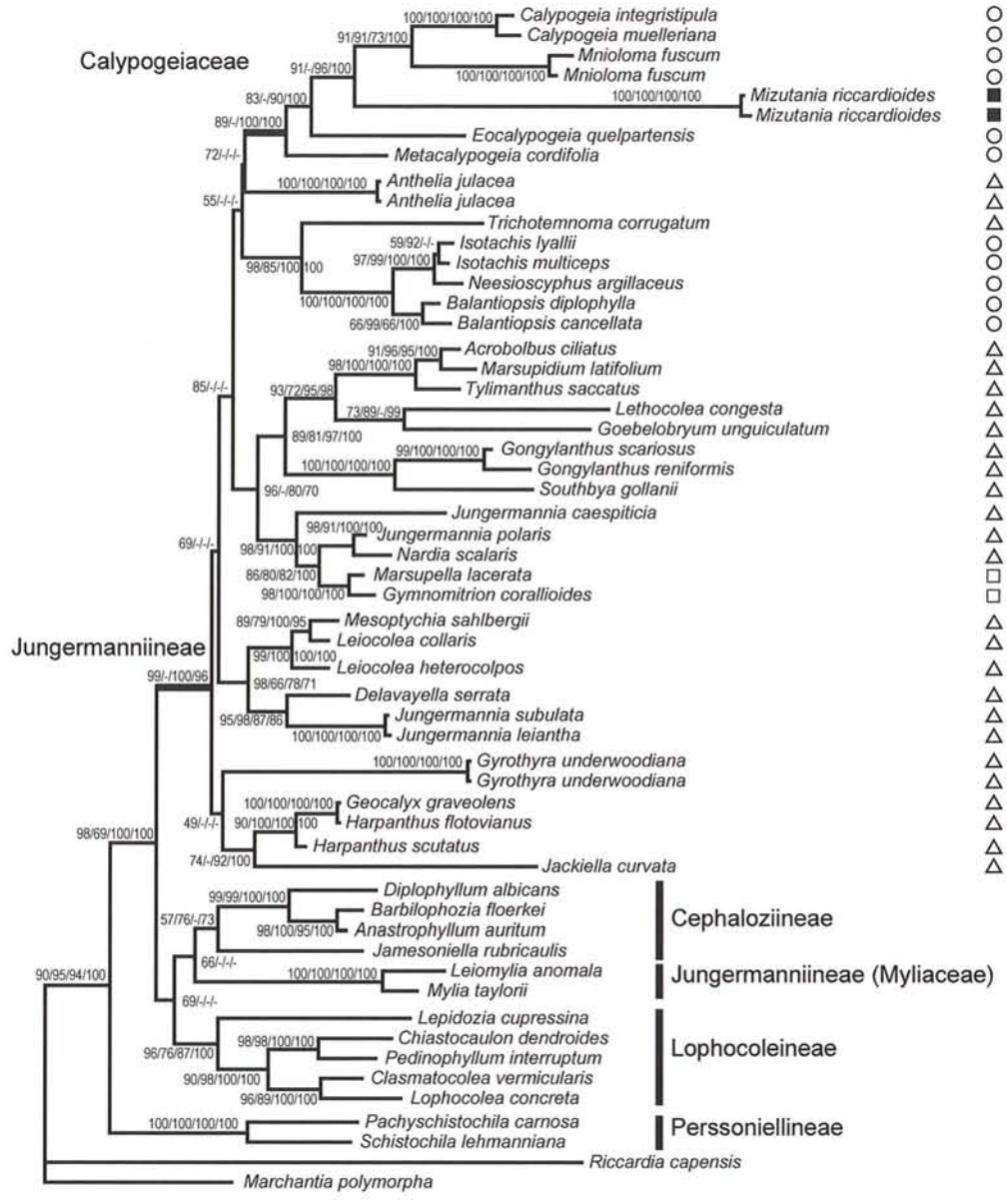

Fig. 5. The ML tree based on the analysis of the *rps4* gene sequences. Numbers above the branches are LBP/BP/PPB/AU; in %. incubous: ○; saccubous: △; transverse: □; thalloid: ■.

in the leafy liverworts by Tsubota & Deguchi (2004) might be ascribed to contamination by gemmae of *Calypogeia*. The analyses, however, were conducted on the basis of the three samples from three different localities (Genting Highlands, Cameron Highlands, Fraser's Hill) in the Malay Peninsula and no trace of fragments of plants including gemmae of Calypogeiaceae were detected in the samples. It is therefore highly improbable that our results are derived from contamination. The present study, also reveals that *Pleurozia* is not a sister to Metzgeriales but to *Radula* (Fig. 4). Although there are gametophytic similarities between *Pleurozia* and Metzgeriales (Crandall-Stotler & al., 2005), morphological differences have been observed in the sporophyte: the capsule cell wall of *Pleurozia* is 9–10-stratose and the valves lack an elaterophore (Schuster, 1984), while in Metzgeriales the capsule wall is bistratose and each valve has an elaterophore. It therefore seems doubtful that Pleuroziales and Metzgeriales are closely related.

Calypogeiaceae (Jungermanniales suborder Jungermanniineae) are a nearly cosmopolitan family comprising four genera: *Calypogeia*, *Eocalypogeia*, *Metacalypogeia*, and *Mnioloma*. Characteristic are the incubous leaves, ventral intercalary or occasionally terminal female branches, and well-developed marsupium. Although the thalloid morphology of *Mizutania* is entirely different from the leafy morphology of other Calypogeiaceae, there are some close morphological similarities: (1) The rudimentary, intercalary sexual branches of *Mizutania* are reminiscent of those of Calypogeiaceae; they are short and of determinate length, and have reduced leaves and 2–3-lobed bracts which are irregularly or indistinctly triseriate. Intercalary sexual branches seem to be a synapomorphy of Calypogeiaceae including *Mizutania*, but excluding *Eocalypogeia*. (2) Oil bodies of *Mizutania* consist of minute granules similar to those of many Calypogeiaceae. (3) The chromosome number of *Mizutania* of $n = 9$ (Inoue & Furuki, 1992) is consistent with

that of 9 or 18 in Calypogeiaceae (Tatuno, 1941). (4) Asexual reproduction by means of 1–3-celled ellipsoidal greenish exogenous gemmae on leaf margins or surface is common in the Calypogeiaceae and *Mizutania* (Calypogeiaceae: Schuster, 1969, fig. 119; *Mizutania*: fig. 1H). (5) The massive cuticle on the thallus surface of *Mizutania* is reminiscent of the cuticle found in several species of *Mnioloma* (*Mizutania*: fig. 1C–F, H and K; *Mnioloma*: Schuster, 2000, figs. 206, 209, 210, 210A).

In the phylogenetic tree based on *rbcL* sequences (Fig. 4), *Calypogeia*, *Metacalypogeia*, *Eocalypogeia*, *Mizutania* (Calypogeiaceae), and *Gongylanthus* (Arnelliaceae) form a single clade. However, in the phylogenetic analysis based on *rps4*, Calypogeiaceae is sister to the Antheliaceae, and Arnelliaceae is closely related to Acrobolbaceae (Fig. 5). Heinrichs & al. (2007) resolved a sister relationship of Calypogeiaceae and Arnelliaceae, while Roo & al. (2007) found a less close relationship between these two families. The presence of marsupium would be a synapomorphy of these two taxa.

Evolution of the flattened form within leafy liverworts lineages. — In the leafy liverworts lineages, species with a flattened form clearly lacking differentiated stem and leaves occur sporadically in isolated genera. Schuster (1984) argued that modifications (adaptations) of the leafy gametophore to the thalloid form occurred repeatedly in Jungermanniidae, and suggested that the flattened gametophyte evolved via several steps in this group: the stem has changed intoa thallus-like structure by flattening and broadening, and leaves became reduced to the vestigial leaf primordia hardly recognizable as leaves. As a result, the plant body obtains a thalloid-like or unquestionably thalloid morphology, as seen in the case of *Enigmella*, *Schiffneria* and *Zoopsis*. The ultimate step, where the thallus becomes entirely unistratose with no indication of a recognizable axis, would be seen in such 'advanced' taxa like *Cololejeunea* and *Radula*. *Mizutania* grows in unstable places in tropical regions as the species do mentioned above. Thalloid plants of *Mizutania* with leafy sexual branches are unistratose, lacking differentiation of leaf and stem, and have an irregular axis as a result of growth by apical and marginal meristems. These morphological modifications of *Mizutania*, indicate a more derivative character state than those of *Pteropsiella* and *Cololejeunea*, where leaves are still recognizable as vestigials, and could be considered a nearly final state of reduction according to the modification theory proposed by Schuster (1984).

Several epiphytic species including *Cololejeunea metzgeriopsis* (Schuster, 1966; Gradstein & al., 2006), *Radula aguirrei* R.M. Schust. (Schuster, 1991) and *Radula yanoella* (Schuster, 1984, 1991) are similar to *Mizutania* in having leafy sexual branches on unistratose thalli, although the similarity might be a result of convergent evolution. The morphological features found in *Cololejeunea metzgeriopsis* and several species of *Radula* have been interpreted as neoteny (Schuster, 1984; Gradstein & al., 2003), because *Cololejeunea* and *Radula* have typical persistent thalloid protonemata in juvenile phase in their ontogeny. Morphological variations observed in Lejeuneaceae seem to have originated by multiple heterochronic events, In the early development of gametophyte of Lejeuneaceae, three developmental stages are recognizable: (1) thalloid protonemal stage, (2) primary stage with no underleaves, (3) juvenile stage characterized by constant phyllotaxis with one underleaf per each lateral leaf. Morphological variations are interpreted as the retention of these stages in the mature gametophyte (Gradstein & al., 2003). Recent molecular phylogenetic study revealed that *Cololejeunea metzgeriopsis* is not phylogenetically isolated from other *Cololejeunea* species (Gradstein & al, 2006; Gradstein & Wilson, 2009). Protonemal neoteny is usually interpreted as an adaption to the growth in short-lived habitats such as on living leaves where rapid maturation and completion of the life cycle are compulsory (Thiers, 1988; Gradstein, 1997; Gradstein & al., 2006). It is not clear yet whether the morphological features of *Mizutania* are also derived from neoteny. Study on the spore germination of Calypogeiaceae is needed to determine whether a free living stage of thalloid protonemata occurs during development. Thus for, only filamentous protonemata have been found in several species of *Calypogeia* (Nehira, 1966).

Several leafy liverworts growing on soil, such as *Enigmella* (Acrobolbaceae), *Pteropsiella* (Lepidoziaceae), *Schiffneria* (Cephaloziaceae) and *Zoopsis* (Lepidoziaceae), also have a thalloid appearance. *Enigmella thallina* G.A.M. Scott. & K.G. Beckm., having a multistratose thallus, has been described as a member of the Acrobolbaceae by Beckmann & Scott (1992). They reported that *Enigmella* and *Lethocolea* were growing in mixed colonies on damp soil and the two genera have a long marsupium with numerous hairs on its whole surfaces. They mentioned that a thalloid habit might be a transient phenotypic response to the environmental conditions as seen in *Radula yanoella* which may remain in its juvenile phase due to environmental pressure. Plants of *Enigmella* might have arisen from an ancestral leafy form by the stem flattening and broadening; and through reduction of leaves as represented by the three species mentioned above. Leafy liverworts such as *Zoopsis* and *Schiffneria*, with no distinctly differentiated stem and leaves, are both also found in the places where *Mizutania* grows. These thalloid Jungermanniidae have shared features in that the leaves are extremely reduced, except on sexual branches. They also have similar habitat preferences: slightly dry habitats, where other species do not grow, or unstable habitats which are disturbed by collapse of the substrate caused by squalls. These selection pressures may have caused morphological convergence in these leafy liverworts towards the flattened form.

Divergence time of Calypogeiaceae based on the fossil record and molecular study was estimated about 50 Ma (Grolle & Meister, 2004; Heinrichs & al., 2007). He-Nygrén (2007) suggested that the long branches of Antheliaceae, Calypogeiaceae and Gyrothyraceae indicate isolation from common jungermannioid ancestor. In our phylogenetic analysis, however, it appears that *Mizutania* is the most isolated taxon (Figs. 4–5).

Morphological diversity within the Jungermanniineae. — The Jungermanniineae are a morphologically highly diverse group as compared with other suborders of Jungermanniales (Hentschel & al., 2006). Variability of characters such as leaf arrangement, sexual branches, underleaves and protective structures around archegonia and embryos, is generally considered to be of taxonomic importance. He-Nygrén (2007)

considered the presence of perigynium to be a synapomorphy for Jungermanniineae, although several taxa lack this character. In leafy liverworts, the perigynium is considered the most recently evolved device protecting the developing sporophyte (Hentschel & al., 2006; He-Nygrén, 2007). Acquisition of new protective structures might open up possibilities for adaptation to new habitats and thus may lead to divergent evolution in this group. Specifically, in the acquisition of a marsupium (a highly specialized perigynium penetrating the substrate), the Calypogeiaceae and other related families might have gained an advantage through facilitation of prostrate growth. Presence of a marsupium would be a character supporting placement of *Mizutania* in the Calypogeiaceae; however, no such structure has yet been discovered. We would predict its occurance in *Mizutania*.

In the Jungermanniineae, all four fundamental leaf insertion patterns of liverworts are observed: incubous, succubous, transverse and thalloid with no differentiation of leaf and stem. The leaf arrangement variation is reflected in the phylogenetic tree (Fig. 5). Taxa with incubous leaves, indicated by open circles, correspond to Calypogeiaceae and Balantiopsidaceae; those with succubous leaves (open triangles) to Acrobolbaceae, Arnelliaceae, Delavayellaceae, Geocalycaceae, Gyrothyraceae, Jackiellaceae, Jungermanniaceae, Mesoptychiaceae and Trichotemnomaceae; those with transversely inserted leaves (open squares) to Gymnomitriaceae; and those with a thalloid structure (solid square) to *Mizutania*. Mapping of leaf insertion types on the phylogenetic tree indicates that the thalloid structure of *Mizutania* might have evolved through modification of a gametophore with incubous leaf insertion. In the Jungermanniineae, the incubous leaf insertion and the thalloid form derived from it might be associated with increasing desiccation tolerance. The incubous leaf insertion is considered to be a more adaptive form for prostrate growth in a dry environment compared with a succubous and transverse leaf insertion pattern (Schuster, 1984; Renzaglia & al., 2000). This is because the shoot apex is always protected from exposure to the air by the large lateral leaves. Massive verrucae on the surface of the thallus of *Mizutania* including the apical cell, seem to enhance desiccation tolerance. We suggest that the occurrence of massive verrucae in several other species of Calypogeiaceae might be a pre-adaptation for evolution to the simple gametophore of *Mizutania*.

■ TAXONOMIC CONCLUSIONS

There are several morphological similarities between Calypogeiaceae and *Mizutania*, including (1) short sexual branches of determinate length with 2–3-lobed, irregularly or indistinctly triseriate, reduced leaves (bracts); (2) oil bodies consisting of minute granules; (3) chromosome number $n = 9$; (4) asexual reproduction by means of 1–3-celled ellipsoidal greenish exogenous gemmae on leaf margins or leaf surface; and (5) a massive cuticle (also in *Mnioloma*). Intercalary sexual branches seem to be synapomorphous characters of Calypogeiaceae (except *Eocalypogeia*) and *Mizutania*. By its morphological features, *Mizutania* may be regarded as the most derived taxon in the Jungermanniineae. Molecular-phylogenetic analyses show, that *Mizutania* is nested within Calypogeiaceae. We therefore propose that Mizutaniaceae be reduced to the synonymy of Calypogeiaceae.

Calypogeiaceae Arnell

= Mizutaniaceae Furuki & Z. Iwats. in J. Hattori Bot. Lab. 67: 291. 1989, **syn. nov.** – Type: *Mizutania* Furuki & Z. Iwats.

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