ON THE PHYLOGENETIC POSITION OF THE GENUS CLAOPODIUM: A REVIVAL OF A 19TH CENTURY IDEA

О ПОЛОЖЕНИИ РОДА CLAOPODIUM В ФИЛОГЕНИИ МХОВ: ВОЗВРАЩЕНИЕ К ИДЕЕ 19 ВЕКА

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Abstract

Molecular phylogenetic analysis of nuclear ITS and plastid rps4–trnS found species of the genus Claopodium in the clade formed by species of Brachytheciaceae and Meteoriaceae, including Trachypodaceae. Claopodium is resolved as sister to Brachytheciaceae, thus we suggest its placement in this family, despite it will be the only taxon of the family with pluripapillose laminal cells. The taxonomic value of the papillose leaf cells in pleurocarpous mosses is discussed.

Резюме

Молекулярно-филогенетический анализ последовательностей ДНК ядерного (ITS) и хлоропластного (rps4–trnS) участков выявляет положение рода Claopodium в кладе, включающей Brachytheciaceae, Meteoriaceae и Trachypodaceae. Большинство анализов показывает сестринское положение Claopodium к Brachytheciaceae, и, соответственно, мы относим его к этому семейству, несмотря на то, что он, таким образом, оказывается единственным родом семейства, в котором клетки листа имеют папиллы, одиночные или множественные. Обсуждается таксономическая значимость признаков папиллозности клеток листа у бокоплодных мхов.

KEYWORDS: Brachytheciaceae, Meteoriaceae, nrITS, rps4–trnS, papillose cells, branch initials

INTRODUCTION

Pleurocarpous mosses of the order Hypnales with 4400 species include more than one third of the current species diversity of bryophytes (Huttunen et al., 2012a). The order forms a terminal clade in moss phylogeny and its lineages were diversified much more rapidly as compared to acrocarpous mosses (Shaw et al., 2003; Laenen et al., 2014). The classification of the order Hypnales at the family level is especially difficult, because peristomial characters used in the Fleischer–Brotherus system of pleurocarps appeared to be highly homoplasious. Molecular phylogenetic data showed that they are largely associated with epiphytism (Huttunen et al., 2004, 2012b; Hedenäs, 2012).

Molecular phylogenetic approach has resulted in changes of the genera affiliation in many families, and these corrections are still continuing for some genera that were least considered in the course of general revisions. The genus Claopodium (Lesq. & James) Renauld & Cardot is one of such ‘hanging’ taxa. Claopodium was originally described as a subgenus of the genus Hypnum, which included at that time a vast majority of pleurocarpous moss species. While “Bryologia Europaea” introduced many narrower conceived genera for European species (Bruch et al., 1836–1855), in the other regions of the world Hypnum sensu lato persisted (Müller, 1851; Mitten, 1859; Dozy & Molkenboer, 1855-1870). Lesquereux & James (1884) followed the latter tradition, accepting Heterocladium, Thuidium, Elymus and other taxa at the subgeneric rank.

In the original description of Hypnum subgen. Claopodium, Lesquereux & James (1884) underlined its similarity with Thuidium due to papillose leaf cells and leaf shape, and also with Eurhynchium in the absence of paraphyllia and in the peristome structure, although they did not explain which details of the latter structure they meant. They also noted that Hypnum subgen. Claopodium differs from both of these genera in the form of capsule and lid. Grout (1928) selected C. whippleanum as a type of the genus.

The presence of papillae was considered to be an important character state in the Fleischer–Brotherus system of bryophytes which dominated in the 20th century. Relying on the importance of papilae, Brotherus (1925)
The genus needs segregation in a separate family. The genus does not relate to these families. Accessed 10 June 2020) despite it was already clear that www.theplantlist.org/tpl/search?q=Claopodium&_csv=on, or Thuidiaceae (e.g. Tropicos, https://www.tropicos.org/ in Leskeaceae (Goffinet et al. 2005; Frey & Stech, 2009), following the revision of the limit between Thuidiaceae and Leskeaceae by Buck & Crum (1990), when many genera of Thuidiaceae were transferred to Leskeaceae.

The genus Claopodium was included in a number of molecular phylogenetic analyses (Gardiner et al., 2005; Ignatov et al., 2007; Huttunen et al., 2012a) and these analyses found it in a position sister to Homalia and even placed in that genus (Olssoon et al., 2010). Alternative suggestion for placement of this species and also a closely related A. attenuatus was suggested by Ignatov et al. (2019), who revived an idea of Limpricht to segregate subgenus Pseudanomodon, which is very close to Homalia and thus obviously belongs to Neckeraceae.

Claopodium is currently accepted in Leskeaceae (Goffinet et al., 2009; Frey & Stech, 2009), following the revision of the limit between Thuidiaceae and Leskeaceae by Buck & Crum (1990), when many genera of Thuidiaceae were transferred to Leskeaceae.

The genus Claopodium was generated in earlier projects are described in Huttunen et al. (2008) and Huttunen & Ignatov (2010). For PCR-amplification of chloroplast region rps4–trnS primers trnS-F and rps5’ from Hernández-Maqueda et al. (2008) were used. Laboratory work for newly sequenced samples was done in the molecular laboratory in the Turku University Herbarium (TUR), University of Turku, and in the molecular laboratory in N.V. Tisitsin Main Botanical Garden, Moscow. DNA was extracted using the Nucleospin Plant II DNA Extraction Kit (Machery-Nagel) following the respective manufacturer’s protocol. Uncleaned PCR products were sent to Macrogen Inc., South Korea (www.macrogen.com) for purification and sequencing. Sequences were edited manually with PhyDE® v0.9971 (Müller et al., 2005). All sequences are deposited in EMBL (European Molecular Biology Laboratory) or NCBI (The National Center for Biotechnology Information) GenBank. The sequencing protocol in the molecular laboratory of the N.V. Tisitsin Main Botanical Garden differed so that amplification products were separated on a 1% agarose gel in 1x TAE with ethidium bromide staining and purified using MinElute® Gel Extraction Kit (Qiagen, Germany). Purified PCR products were sequenced using the ABI PRISM® BigDye™ Terminator v.3. kit (Applied Biosystems) and further analyzed on an ABI PRISM 3730 automated sequencer (Applied Biosystems) at the “Genom” Common Facilities Centre, Moscow, Russia. Data on sequences generated de novo are in Appendix, while for others the Genbank number is shown in trees.

Sequence editing and phylogenetic analyses. Alignment of the sequence data was performed in Bioedit using alignment from Huttunen & Ignatov (2010) as scaffold. Bayesian Analyses were performed in MrBayes 3.2.6 (Ronquist et al., 2012), with 20,000,000 generations, four runs, 25% trees burn-in, and chain temperature 0.02. Convergence of each analysis was evaluated using Trace 1.4.1 (Rambaut & Drummond, 2007). Maximum Likelihood (ML) trees were estimated using RAxML 8.2.12 (Stamatakis, 2014) from 1000 independent searches each starting from distinct random trees. Analyses were performed on the Cipres Science Gateway (http://www.phylo.org/portal2) on XSEDE (Miller et al., 2010).

Myurium was selected as the outgroup for rooting the trees due to its position in the sister clade to Brachytheciaceae and Meteoriaceae in a broader analysis of the pleurocarpous mosses (Huttunen et al., 2012a).
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Fig. 1. Bayesian molecular phylogenetic tree of nrITS region, showing position of Claopodium sister to Brachytheciaceae. Posterior probabilities from Bayesian analysis (PP>70) and ML bootstrap support (BS>50) are shown at branches (continued on page 4).
**Morphological observations.** Material for Laser Confocal Scanning Microscopy was taken from herbarium and studied with preparation similar to ordinary light microscopy material. Shoots without fixation were stained by 0,1mM DAPI and berberin and investigated under Olympus FV-1000, with 405 and 473 nm lasers; series of 5-15 optical obtained with 40x objective lens and up to 6x digital zoom were Z-stacked by the microscope software.

**RESULTS**

Both methods of the analysis reveal the same tree topology (Fig. 1), resolving the terminal clade of *Ctenidium*+*Hyocmitum*+*Meteoriaceae*+*Claoodium*+*Brachytheciaceae* with maximal support (PP=1, BS=100). The clade of *Meteoriaceae*+*Claoodium*+*Brachytheciaceae* is also resolved with maximal support, and contains two subclades: *Meteoriaceae*, with moderate support (PP=0.97, BS=63), and *Claoodium*+*Brachytheciaceae*, with high support (PP=1, BS=91). The only exception was *Claoodium assurgens*, which was resolved in a clade with *Diaphanodon* within *Meteoriaceae*. Hereafter in the text the generic name *Claoodium* will refer to the *Claoodium* clade including *C. bolanderi*, *C. crispifolium*, *C. pellucinerve*, *C. rostratum*, and *C. whippleanum*, and excluding *C. assurgens*.

The *Claoodium*+*Brachytheciaceae* clade is subdivided into *Claoodium*, with moderate support (PP=0.96, BS=67), and *Brachytheciaceae*, with high support (PP=1, BS=94). Within the *Meteoriaceae*, the genus *Meteorium* was resolved as monophyletic, while other genera represented by a single species each formed assemblages similar to previous analyses (Huttunen et al., 2004). *Claoodium assurgens* is clustered with *Diaphanodon blandus* with substantial support (PP=1, BS=94).

Within *Brachytheciaceae*, subfamilies *Eurhynchioideae* and *Heliconioteioidae* are resolved monophyletic with high support: PP=1 & BS=95 and PP=1 & BS=100 respectively, and core *Brachytheciaceae* is also strongly supported (PP=1 & BS=93), excluding genera *Frahmella*.
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and Scleropodium, which subfamilial positions vary between different analyses (Huttunen & Ignatov, 2004). Genera of the Brachytheciaceae are monophyletic in tree in Fig. 1 as well.

The Bayesian tree based of rps4–trnS plastid region (Supplementary materials 1) results in a similar topology, although the clade supports are generally quite low due to overall lower variation than in ITS region, and the genus Claopodium itself is not resolved as monophyletic, as well as e.g. Meteorium.

However the concatenated tree of ITS and rps4–trnS region for a smaller selection showed a slightly higher support for clades as compare with ITS tree: e.g. for Meteoriaceae PP=0.99 & BS=80 vs. PP=0.97 & BS=63, for Claopodium+Brachytheciaceae BS=94 vs. BS=91, for Brachytheciaceae BS=99 vs. BS=94.

Morphological observations. Studies of the proximal branch leaf arrangement around branch primordia in C. whippleanum, C. bolanderi and C. rostratum (Fig. 3) revealed them having the same pattern as in all other Brachytheciaceae and Meteoriaceae.

However, arrangement of proximal branch leaf in Claopodium is not easy to observe. First, the outermost foliose structures around branch primordia are spaced after bud becomes larger, so it is difficult to say which is the outermost (in most Brachytheciaceae the triangular leaves cover next leaves by their basal angle, but this is not the case in Claopodium). The second reason is that outermost structures are quite fragile and easily fall down, although in this case the order of the proximal branch leaves is becoming more apparent (e.g. Fig. 3B). Observation by light microscope often do not help to understand this arrangement, as the stem is slightly flattened in Claopodium and buds are seen only in profile (Fig. 3C), and only in rare lucky cases the position of the outermost leaf is clearly seen with LCSM (Fig. 3G–H). Some of LCSM photos unequivocally show that the arrangement of foliose structures around branch primordia in Claopodium is the same as in Brachytheciaceae and Meteoriaceae (Fig. 3D–F).

Fig. 2 Bayesian molecular phylogenetic tree based on concatenated dataset of nrITS and rps4–trnS, with Posterior probabilities from Bayesian analysis (PP>70) and ML bootstrap support (BS>50) at branches.
Fig. 3. Branch primordia in Cladophora: A, C: *C. rostratum* (Russia, Adygeya, Ignatov, MHA9001806); B, D: *C. bolanderi* (USA, California, Shevock 33066, MHA9060731), E–H: *C. whippleanum* (U.S.A., California, Ignatov, MHA 9060747). Numbering of proximal branch leaves follows Spirina & Igantov (2005): the outermost, pointed downwards leaf is morphologically the third one, while the first and second branch leaves are reduced. In Fig. B third leaf is broken, however its insertion cells show its identity.
DISCUSSION

The overall topology of ITS tree agrees with the previously obtained subdivisions into subfamilies and grouping of genera in the family Brachytheciaceae (Ignatov & Huttunen, 2002; Huttunen & Ignatov, 2004; Huttunen et al., 2007) and, in general, also Meteoriaeae (Huttunen & Quandt, 2007), which ensures that the dataset of ITS is comprehensive for taxonomic conclusions.

Plastid data are less variable, thus the tree based solely on rps4–trnS has a similar topology but lacks significant support (shown in Supplementary Materials only). Concatenated tree based on a smaller subset of taxa with the ITS plus plastid data results in moderate branch support, additionally supporting monogeneous ITS tree. *Claopodium* was found in a sister position to Brachytheciaceae, albeit not in as a clade, but in a grade.

The position of *Claopodium* is not that surprising in light of historical fluctuation in morphological delimitation of the family Brachytheciaceae. In 20th century the family included a number of genera, placed in it because of similar habit, e.g. *Tomentypnum* was placed in the family because of its similarity with *Hom alotheicum* (cf. Corley et al., 1981; Crum & Anderson, 1981), or sometimes was included in *Hom alotheicum* (Robinson, 1962). Another approach was taken by Noguchi (1991), who transferred *Duthiella* from Meteoriaeae to Brachytheciaceae because of the perfect peristome, which he considered as an important key character for differentiation between these two families.

The molecular phylogenetic analysis of Ignatov & Huttunen (2002) and Huttunen & Ignatov (2004) determined the generic content of the family Brachytheciaceae. It has not changed since that with the exception of adding a monospecific South American genus *Stenocarpidopsis*. At the same time, molecular definition of the family made the general morphological circumscription of the family Brachytheciaceae more vague due to inclusion of ecosaceous plants (*Unclejackia*), specialized tropical epiphytes with short seta (*Squamidium, Zelometeypnum*), as well as other epiphytic plants like *Helicodontium* and *Okamuraea*, with so different peristome that they were never placed in Brachytheciaceae in "pre-molecular era".

Fortunately, the specific arrangement of juvenile, proximal branch leaves around branch primordia (Ignatov, 1999), previously called pseudoparaphyllia, helped to distinguish representatives of the Brachytheciaceae and Meteoriaeae from other pleurocarps: in these families the outermost leaf is pointed downwards, covering the most part of bud. Later it was shown that such specific pattern of leaf arrangement can be assumed as the reduction of the first and second branch leaves (Spirina & Ignatov, 2005; Ignatov & Spirina, 2012), thus the third leaf appears to be outermost. This explains its position different from other pleurocarps where the outermost leaves are in lateral, "four o’clock position" (Ignatov & Hedenäs, 2007). Partial reduction of outermost leaves was subsequently found in some other families, but this pattern was either unstable, represented only in some buds, as in Fontinalaceae (Spirina & Ignatov, 2011) and Lembo phyllaceae (Spirina & Ignatov, 2015), while in Leucodonaceae it is stable, but the outermost (morphologically the third) branch leaf is commonly subdivided into narrow lobes (Spirina & Ignatov, 2010). Thus, Brachytheciaceae and Meteoriaeae remain the only families where such pattern is stable and clearly performed. Position of *Claopodium* in a clade with Brachytheciaceae and Meteoriaeae is thus additionally supported by the similar pattern. The remaining question is its familial position, whether it should be placed in the Meteoriaeae, Brachytheciaceae or its own family.

The placement in the Meteoriaeae, though contradicting the results of molecular phylogenetic analysis, may be attractive from the morphological basis: almost all species of Meteoriaeae have papillose cells, while none of the Brachytheciaceae have real papillae, if one does not consider strongly prorate cells ("with papillae in distal cell corners") in some *Brachythecium* segregated formally to the genus *Bryhnia*. The presence of papillae was even considered as the main distinction between Brachytheciaceae and Meteoriaeae (Huttunen & Ignatov, 2004).

However, combination of two characters, structure and arrangement of papillae in leaf laminal cells and cell shape differ between Meteoriaeae and *Claopodium*. Both taxa may have uni- and pluripapillose cells, but in most pluripapillose Meteoriaeae papillae are in row and cells are elongate and narrow, while in pluripapillose *Claopodium* cells are rhombic and simple papillae are scattered over cell lumen. There are some exceptional cases in Meteoriaeae, such as: *Papillaria* s.str. (de Oliveira et al., 2020) with rhombic cells and papillae scattered over cell lumen, but papillae are branching and complex in structure; *Floribundaria walkeri* with scattered simple papillae over cell lumen but elongate cells; and *Duthiella flaccida* with rhombic pluripapillose cells but papillae in row.

*Claopodium assurgens* has unipapillose leaf cells similar to *Diaphanodon blandus* with simple papilla at center of cell lumen. The two species also share irregularly to regularly pinnately branching stems with dimorphic leaves: stem leaves in both species are larger in size, rather abruptly tapering from ovate basal part to acuminate acumen, while branch leaves are smaller, more gradually tapering to acuminate acumen. The anomalous position of *C. assurgens* is also supported by a very different sporophyte structure: its capsule is almost straight vs. curved in other *Claopodium* species; operculum high-conic and attenuate to rostrum vs. low conic; exostome teeth are narrow vs. broad; and endostome basal membrane is low (Fleischer, 1923) vs. high. *Diaphanodon* shares with *C. assurgens* erect capsule, rostrate lid, narrow lanceolate exostome teeth and low endostome basal membrane, while unlike *C. assurgens*, *Diaphanodon* has subglobose to ovoid capsules and several specialized characters in its sporophyte: seta is short, 2 mm, vs. 10–15 mm in *C.
assurgens; endostomial cilia are absent vs. 2 reduced, and spores are large, \(> 30 \mu m \) vs. \(< 20 \mu m\). Although it is likely that \(C.\ assurgens\) can be placed directly to \(Diaphanodon\), we are pending such a taxonomic resolution until a more comprehensive analysis of this group and hopefully addition of few \(ClaoPodium\) taxa that might be closely related to \(C.\ assurgens\), and \(Diaphanodon\) procumbens. The later species has an interesting combination of gametophytic character states that is intermediate between \(D.\ blandus\) and \(C.\ assurgens\). In addition, testing the phylogenetic position of the newly delimited \(Diaphanodon\) would require denser sampling of closely related Meteoriaceae species.

The obtained phylogenetic trees support two possible solutions for taxonomic placement of the \(ClaoPodium\): it can be segregated in a separate monogenic family or included in the Brachytheciaceae. Although the former solution will leave Brachytheciaceae less heterogeneous morphologically, we prefer the latter one. Monogenic families are necessary if taxon lacks obvious close relatives, but close relationship between \(ClaoPodium\) and Brachytheciaceae is well-supported from phylogenetic analyses, present and previous (e.g. Huttunen et al., 2012a). It is also worthy to remember the original description of \(ClaoPodium\), where it was compared not only with Thuidiaceae, but also with \(Eurhynchinum\) (at that time including \(Kindber gia\), \(Eurynchiatrum\), and \(Oxyrhynchinum\)). The combination of short, slightly curved, horizontal and usually dark brown capsules does not look unique among pleurocarpous mosses, but in temperate flora is not common either, being rather different from longer and gradually curved capsules characteristic of Amblystegiaceae and some Thuidiaceae+Leskeaceae, as was outlined by Hedenäs (1989, 1997), calling Pylaisiaceae that time temperate Hypnaceae. These differences were also likely implied by Lesquereux & James (1884), and considered important, albeit not explicitly formulated.

Recent changes in systematics of pleurocarps are mostly related to the earlier overestimation of sporophytic characters (especially peristome modifications), while gametophytic characters (e.g. proximal branch leaves arrangement around branch primordia) appeared to be more conservative and informative in taxonomy. However in the case of \(ClaoPodium\) it is the opposite: papillose leaf laminal cells appeared to be less important for taxonomy than the capsule shape.

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**Appendix**

**Specimen vouchers and EMBL or Genbank accession numbers**

| Species | Isolate | Provenance | Voucher | ITS | rps4-trnS |
|---------|---------|------------|---------|-----|-----------|
| *Aerobryopsis subuligera* | SH178 | China, Hunan | Koponen et al. 51514 (H) | LR861607 | |
| *Chrysoleclum re overrunum* | SH5 | China, Hunan | Koponen et al. 55572 (H) | LR861821 | |
| *Cladopodium assergens* | OK2595 | Australia, Queensland | Streimann 46523 (MHA 9060729) | LR861606 | MT782120 |
| *Cladopodium bolanderi* | OK2593 | USA, California | Shevekov 33066 (MHA9060731) | LR861602 | LR861480 |
| *Cladopodium crispifolium* | OK2596 | USA, California | Norris 76870 (MHA9060736) | LR861605 | LR861481 |
| *Cladopodium crispifolium* | OK2615 | USA, California | Ignatov sn (MHA9080726) | LR861604 | LR861482 |
| *Cladopodium crispifolium* | OK2616 | USA, California | Ignatov sn (MHA9060724) | LR861603 | LR861483 |
| *Cladopodium rostrosum* | OK2614 | USA, Chicago, | Ignatov 13-2028 (MHA9060744) | LR861604 | LR861479 |
| *Diaphanodon blandus* | SH1660 | China, Xizang | G. Miehe & U. Wundisch (TUR114841) | LR861608 | |
| *Diaphanodon blandus* | SH104 | Philippines, Mt. St. Tomas | B.-C. Tan sn 29-30.XI.1986 (H) | LR861599 | |
| *Pseudospiridentopsis hirsuta* | SH11 | China, Hunan | Koponen et al. 55834 (H) | LR861600 | |
| *Toxospora imponderosa* | ABAGAM56 | Ecuador, Quito to Santo Domingo | J-P. Frahm 107 (BONN) | LR861609 | |
| *Trachypodium serrulatum* | SH211 | China, Hunan | Koponen et al. 54101 (H) | LR861601 | |