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Source: American Fern Journal, 97(3) : 127-135

Published By: The American Fern Society

URL: https://doi.org/10.1640/0002-8444(2007)97[127:HIIACP]2.0.CO;2

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American Fern Journal 97(3):127–135 (2007)

Hyalotrichopteris is Indeed a *Campyloneurum* (Polypodiaceae)

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ABSTRACT.—The relationships of the rare Mesoamerican fern *Campyloneurum anetioides* are inferred by comparing sequences of $trnL_{UAA}$-$trnF_{GAA}$ intergenic spacer of the plastid genome. In the past, this taxon was either treated as the single member of the genus *Hyalotrichopteris* or as part of the diverse Neotropical genus *Campyloneurum*. Analyses of the cpDNA give unambiguous support to the taxonomic placement of this species within *Campyloneurum*. The closest relatives within the genus *Campyloneurum* are currently unknown because limited taxon sampling and variation of the cpDNA sequences do not allow to elucidate this question. However, we can conclude that *C. anetioides* is unlikely the derivative of an early separation within *Campyloneurum*.

Relationships of *Hyalotrichopteris anetioides* (H. Christ) W. H. Wagner have been controversial. The species was first described in *Polypodium* by Christ (1909), and placed in its own genus, *Hyalotricha* (*H. anetioides* (H. Christ) Copel.), by Copeland (1953). *Hyalotricha* Copel. is a later homonym of *Hyalotricha* Dennis, and so the former has now been renamed *Hyalotrichopteris* W. H. Wagner (Wagner, 1978). Copeland (1953) indicated possible relationships of *Hyalotricha* to grammitid ferns, Polypodiaceae *s.s.*, Vittariaceae, and to ''Aspidiaceae'' (*Tectaria* Cav. and *Ctenitis* (C. Chr.) C. Chr.), but favored the last suggestion. On the basis of stomatal structure, van Cotthem (1970) suggested an alliance of *Hyalotricha* to Vittariaceae. Crabbe *et al.* (1975) placed *Hyalotricha* in the Grammitidaceae, near *Loxogramme* (Blume) C. Presl, without further comment. Pichi Sermolli (1977) postulated closest affinities of *Hyalotricha* to *Goniophlebium* C. Presl (= *Serpocaulon*; Smith *et al.*, 2006) and a largely American group of polypod genera (his Polypodiaceae *s.s.*) that also included *Campyloneurum* C. Presl. Wagner and Farrar (1976), in the most careful examination of the morphology of *Hyalotricha* to date, accepted its

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generic distinctness, and adduced strong evidence for its inclusion in subfamily Polypodioideae of the Polypodiaceae (rather than with the grammitid ferns, or Vittariaceae, or ''Aspidiaceae''); however, Wagner and Farrar did not speculate on the generic level affinities of *Hyalotricha*, nor did they mention *Campyloneurum* as a possible relative. The later genus includes about 50 species occurring throughout South America, Mesoamerica, the Caribbean, to Florida in the North (Tryon and Tryon, 1982a, b; León, 1992, 1995).

Most recently, American authors have regarded *Hyalotrichopteris anetioides* (= *Campyloneurum anetioides* (H. Christ) R. M. Tryon & A. F. Tryon) either as a member of *Campyloneurum* (Tryon and Tryon, 1982a, b; León, 1992, 1995), or have accepted its generic distinctness as *Hyalotrichopteris* (Wagner, 1978; Lellinger, 1988, 1989). Lellinger (1988, 1989) considered *Hyalotrichopteris* a satellite of *Campyloneurum*, based on characters believed to be rare in the latter genus, namely, the small (not exceeding 10 cm) spathulate leaves, a single excurrent free veinlet in each areole, marginal free veinlets, and multicellular branched hairs *Hyalotrichopteris* (Lellinger, 1988). In her revision of *Campyloneurum*, León (1992, 1995) noted that these supposed unique features in *Hyalotrichopteris* are shared by species of *Campyloneurum*. Relatively small leaves (but still considerably larger than in *Hyalotrichopteris*) are found in *C. chrysopodum* (Klotzsch) Fée and *C. falcoideum* (Kuhn *ex* Hieron.) M. Meyer *ex* Lellinger, whereas branched multicellular hairs occur also in *C. aphanophlebium* (Kunze) T. Moore and *C. repens* (Aubl.) C. Presl. León considered the presence of *Campyloneurum*-like venation in *Hyalotrichopteris anetioides* as a critical character supporting close relationships of this species to *Campyloneurum*. Excurrent free veinlets along the blade margins occur in several species of *Campyloneurum* such as *C. brevifolium* (Lodd. *ex* Link) Link, as well as in juvenile fronds of larger species, and excurrent veinlets within non-costal areoles occur in *C. aphanophlebium* and *C. falcoideum*. Based on the shared morphological features, León (1992) considered *C. aphanophlebium* as the putative closest extant species to *Hyalotrichopteris*/*Campyloneurum anetioides.*

The introduction of DNA sequence data as a further marker to discover relationships has greatly improved our understanding of the phylogeny of polygrammoid ferns, as well as other groups of ferns (Schneider *et al.*, 2004a, b). These studies have resolved many uncertainties about the interpretation of relationships and the underlying morphological evidence. As an example, an extensive study on the grammitids found strong support for several genera that were recently proposed based on morphological evidence, which appears to be remarkable considering the high degree of homoplasy in these ferns (Ranker *et al.*, 2004). Other genera such as *Microsorum* Link and *Polypodium* L. were found to be polyphyletic as currently defined (Schneider *et al.* 2004a, b, 2006a, b; Smith *et al.*, 2006). Using nucleotide sequence variation of the chloroplast genome (cpDNA), relationships of several enigmatic polypod genera have recently been discovered, the Himalayan genus *Gymnogrammitis* Griff. (Schneider *et al.*, 2002), Malesian *Thylacopteris* Kunze *ex* J.Sm. (Schneider

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et al., 2004a), and southern South American *Synammia* C. Presl (Schneider *et al.*, 2006b). cpDNA data (Janssen and Schneider, 2005) have also confirmed the generic concept of *Aglaomorpha* Schott proposed by Roos (1985), who utilized exclusively morphological evidence.

Existing studies on polypod ferns (Polypodiaceae) have included one or more samples of *Campyloneurum*, and almost all other genera in the family, but sequence data has been unavailable for *Hyalotrichopteris anetioides*. In this study, we explore the relationships of this narrowly distributed Costa Rican and Panamanian species using cpDNA data.

Materials and Methods

A sample of the rare *Hyalotrichopteris anetioides* was collected by one of us (A.F.R.A.) in Costa Rica. All samples representing other species of *Campyloneurum* or other genera included were collected either in Botanical Gardens or provided by colleagues. Some sequences were obtained from Genbank (see Table 1 for accession numbers). The sampling strategy follows the phylogenetic hypotheses outlined in previous studies (Schneider *et al.*, 2004a, b, 2006a, b). Besides *H. anetioides*, we collected sequences for eight species of *Campyloneurum*, one species of *Niphidium* (sister genus of *Campyloneurum*) and seven species of *Microgramma*, the sister to the clade comprising *Campyloneurum* and *Niphidium*. *Microgramma* was assigned as the outgroup clade. Table 1 gives information on vouchers and Genbank accession numbers. Sequences of the $trnL_{UAA}$-$trnF_{GAA}$ intergenic spacer (*trnL-F* IGS) region were obtained using primers and protocols described in previous studies (Haufler *et al.*, 2003; Schneider *et al.*, 2004a, b; Janssen and Schneider, 2005). Sequencing was carried out on a MegaBACE 1000 capillary sequencer using DYEnamic ET Primer DNA Sequencing Reagent (Amersham Biosciences, UK). All sequences were assembled and manually aligned using TreV (Staden Package, http://sourceforge.net/projects/staden). The final alignment was adjusted manually in MacClade 4.0 (Maddison and Maddison, 2000). Ambiguously aligned regions were excluded from all analyses. The few scattered indels did not include any phylogenetic information concerning the relationships of *H. anatioides*.

Maximum parsimony (MP) and maximum likelihood (ML) analyses were performed with PAUP* version 4.0b10 (Swofford, 2000). Model and parameters were selected using the hierarchical likelihood ratio test and the Akaike information criterion as implemented in Modeltest (Posada and Crandall, 1998). Selected model and parameters were implemented in PAUP before conducting ML analysis. MP and ML analyses were calculated using the heuristic mode with 1000 (MP) and 100 (ML) random-addition-sequence replicates, TBR branch swapping, and MULTREES on. Bootstrap values were calculated for both (MP and ML) with 1000 bootstrap replicates, each with 10 random-addition-sequence replicates, TBR branch swapping and MULTREES on. ML analyses were also performed using PHYML (Guindon and Gascuel, 2003; Guindon *et al.*, 2005). In addition, we explored the robustness of the

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TABLE 1. Taxon sampling: For each taxon the following information is given: voucher information including herbarium of deposition, accession number in the fern DNA database (http://www.pryerlab.net), and Genbank accession numbers

Campyloneurum C. Presl
Campyloneurum anetioides (H. Christ) R. M. Tryon & A. F. Tryon: Costa Rica; *Rojas 6281* (CR); **EF104510** – *Campyloneurum angustifolium* (Sw.) Fée: Costa Rica; *Chisaki & Carter 1004* (UC 1618523); **AY083647** – *Campyloneurum aphanophlebium* (Kunze) T. Moore: Bolivia; *Acebey 772* (UC 1735546); **EF104511** – *Campyloneurum asplundii* (C. Chr.) Ching: Mexico; *Kessler s.n.* (GOET); **EF104512** – *Campyloneurum brevifolium* (Lodd. *ex* Link) Link: cult. Göttingen, Old Bot. Garden; *Kreier s.n.* (GOET); **EF104513** – *Campyloneurum chlorolepis* Alston: Venezuela; *Smith 1159* (UC 1487590); **AY083648** – *Campyloneurum phyllitidis* (L.) C. Presl: cult. Berlin, Bot. Garden (Acc. 017-59-74-63); *Schuettpelz 612* (GOET); **EF104514** – *Campyloneurum sphenodes* (Kunze *ex* Klotzsch) Fée: Costa Rica; *Horich s.n.* (UC 1617915); **AY083649** – *Campyloneurum xalapense* Fée: (1) cult. Göttingen, Old Bot. Garden; *Kreier s.n.* (GOET); EF104515 & (2) Mexico; *Lautner L02-41* (GOET); **EF104516**.
Niphidium J. Sm.
Niphidium nidulare (Rosenst.) Lellinger: Costa Rica; *Ranker 1831* (COLO); **EF104519**.
Microgramma *C. Presl*
Microgramma bifrons (Hook.) Lellinger: Peru; *van der Werff 18062* (MO); **DQ642224** – *Microgramma latevagans* (Maxon & C. Chr.) Lellinger: Bolivia; *Jimenez 1285* (LPB); **EF104517** – *Microgramma mauritiana* (Willd.) Tardieu:m (1) cult. Zürich Bot. Garden; *Kreier s.n.* (GOET); DQ642225 & (2) cult. Zürich Bot. Garden; *Kreier s.n.* (GOET); **DQ642226** – *Microgramma nitida* (J. Sm.) A. R. Sm.: Mexico; *Krömer 2678* (GOET); **EF104518** – *Microgramma squamulosa* (Kaulf.) de la Sota: cult. Zürich Bot. Garden; *Kreier s.n.* (GOET); **DQ642228** – *Microgramma tecta* (Kaulf.) Alston: cult. RBG Edinburgh (Acc. 19875234); *Schneider s.n.* (E); **DQ642230** – *Microgramma vacciniifolia* (Langsd. & Fisch.) Copel.: cult. Charles Alford; *Kreier s.n.* (GOET); **DQ642231**

results using the neighbor net algorithm as implemented in Splitstree 4 (Huson and Bryant, 2006), using different settings to evaluate the robustness of the analyses (e.g., different distance measures such as LogDets and number of dimensions calculated).

Analyses were performed in two steps. In the first step, we compared the *trnL-F* sequence of *Hyalotrichopteris anetioides* with all currently available sequences of this cpDNA region available in GenBank and with additional available data. This comparison was made using Blastn (Altschul *et al.*, 1990) and by performing maximum parsimony analyses and maximum likelihood analyses with all available data. In the second step, we inferred the relationships of this species with a data set including only *Campyloneurum*, *Microgramma*, and *Niphidium* species. The later dataset was inferred employing MP, ML and neighbor net analyses.

RESULTS

A sequence of 342 base pairs was generated for *H. anetioides*, which was in the range of length variation (ca. 340 to 370 bp) currently known for the *trnL-F* IGS in *Campyloneuron* and relatives. The data set consisted of 230 included characters of which 37 were parsimonious informative and 35 were variable but non-parsimonious informative. The number of informative sites dropped

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to 16 considering only *Campyloneurum* and *H. anetioides*. Both Blastn and the maximum parsimony analyses using all available *trnL-F* IGS sequences of Polypodiaceae indicated *Hyalotrichopteris anetioides* as a member of *Campyloneurum* (results not shown). Phylogenetic reconstructions using maximum parsimony, maximum likelihood, and network approaches found this species embedded in *Campyloneurum* (Figs. 1, 2). The maximum parsimony analysis resulted in 45 most parsimonious trees with a length of 96 steps (consistency index [CI] = 0.7288, homoplasy index [HI] = 0.2712, retention index [RI] = 0.8730, and rescaled consistency index [RC] = 0.7275). *Campyloneurum* was monophyletic in all 45 most parsimonious trees, and *Hyalotrichopteris anetioides* was sister to *Campyloneurum angustifolium* in 89% of 45 most parsimonious trees. A single unambiguous character state change separated *H. anetioides* from *C. angustifolium* and in turn one unambiguous character state change characterized this clade. The *Campyloneurum* clade had a bootstrap value of 98% (Fig. 1) and the clade was characterized by six unambiguous character state changes. Only two well supported clades were found in all most parsimonious trees: a clade comprising the two collections of *C. xalapense* and a clade consisting of *C. asplundii* and *C. chlorolepis*). Maximum likelihood analysis found a single tree (Fig. 1) with -ln = 834.16001, using the TVM model with freqA = 0.3331, freqC = 0.1636, freqG = 0.1842, freqT = 0.3190, R(a) = 1.9602, R(b) = 3.3907, R(c) = 0.0435, R(d) = 1.3489, R(e) = 3.3987, R(f) = 1.000. Based on the hierarchical likelihood ratio test, this model and parameters were best, whereas the Akaike information criterion preferred a slightly different model TVM + I. Analyses with the alternative model found the same topology.

The ML tree was fully resolved, but bootstrap values >75% were found only for clades present in the strict consensus tree of the most parsimonious trees obtained in the maximum parsimony analysis. *Hyalotrichopteris anetioides* was found to be sister to *C. angustifolium* (Fig. 1), but alternative relationships were found in the Splitgraph analysis (Fig. 2).

Discussion

Status of Hyalotrichopteris anetioides.—Our data suggest that *Hyalotrichopteris anetioides* nests within *Campyloneurum*. To separate it generically renders *Campyloneurum* paraphyletic. *Hyalotrichopteris anetioides* shares with species of *Campyloneurum* the principal characters defining the genus, namely areolate venation with costal areoles containing one excurrent free veinlet and non-costal areoles containing (1–)2–5 excurrent free veinlets (León, 1992). Characters used by Lellinger (1988, 1989) to separate *Hyalotrichopteris* are either not restricted to *H. anetioides*, such as the branched multicellular hairs (which also occur in *Campyloneurum aphanophlebium*), or are unreliable, such as frond size and habitat. The unusually large number of marginal excurrent free veinlets, which is uncommon in *Campyloneurum* in general, may correlate with the reduction in leaf size.

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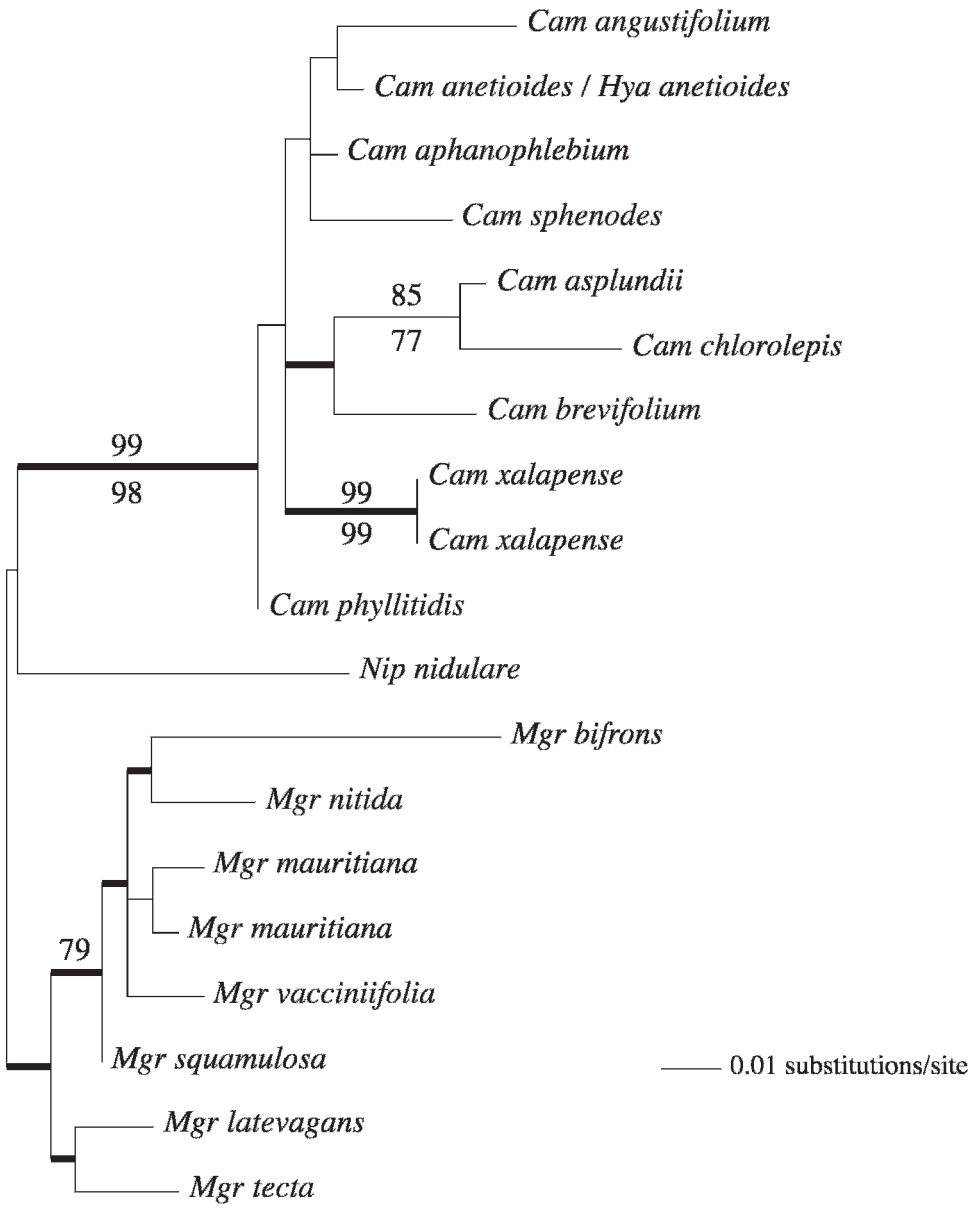


FIG. 1. Phylogram generated in a maximum likelihood analysis of the *trnL-F* IGS data set. Numbers above branches correspond to ML bootstrap values, and numbers below branches correspond to MP bootstrap values. BS values ≥ 75% are given. Thickened lines indicate branches present in the strict consensus of 45 most parsimonious trees. Abbreviations: *Cam* = *Campyloneurum*, *Hya* = *Hyalotrichopteris*, *Mgr* = *Microgramma*, *Nip* = *Niphidium*.

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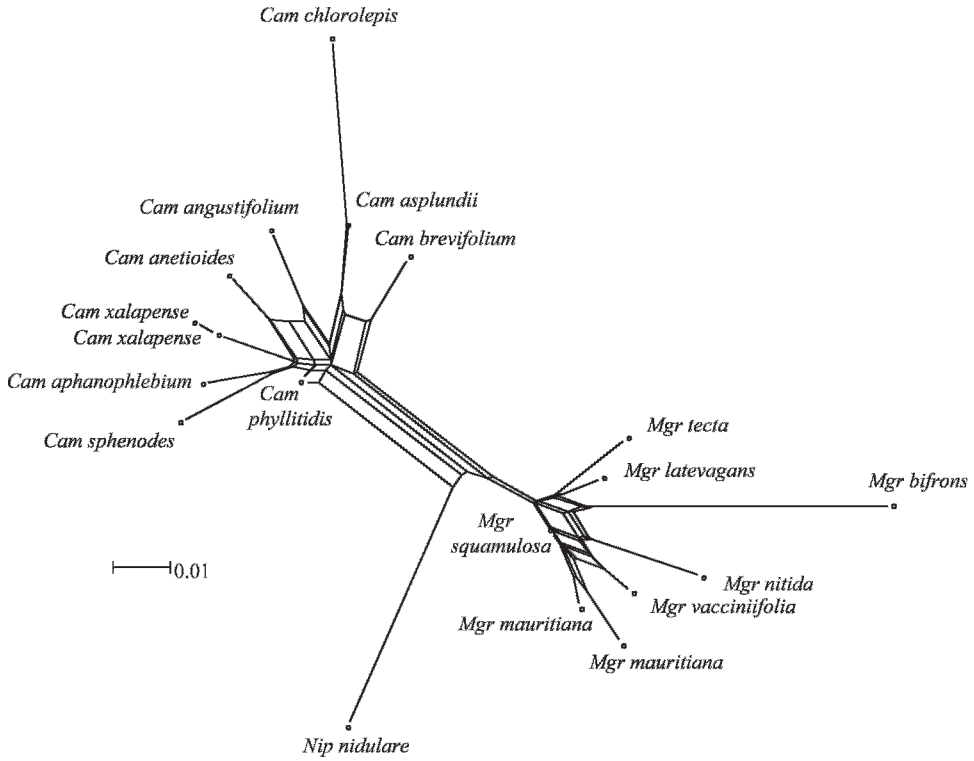


FIG. 2. Splitstree generated with the Neighbornet algorithm and uncorrected P-distances. Settings: weight modified as least squares, and maximum dimensions set to four. Statistics; nsSplits = 45, total weight = 0.40393516. Abbreviations as in Fig. 1.

Relationships within Campyloneurum.—León (1992) tentatively divided *Campyloneurum*, a genus of ca. 50 species, into ten groups, of which six are represented in our study. She placed *C. anetioides* in the *C. aphanophlebium* group, comprising only these two species. This group is characterized by having specialized branched, multicellular hairs. Further shared characteristics are the presence of undivided, primary, non-costal areoles, free veinlets along the margin, and medial sori.

Our results (Fig. 1) suggest that there is some affinity between *Campyloneurum anetioides* and *C. aphanophlebium*, but other species such as *C. angustifolium* may have closer relationships. Our current taxon sampling is insufficient to explore the relationships among species of the genus *Campyloneurum* as demonstrated in the low resolution in our maximum parsimony analyses and the many alternative topologies in neighbor net analyses. We cannot draw any conclusions about the monophyly of some proposed groups within the genus *Campyloneurum* and/or the species delimitation of some putative closely related species in the *C. angustifolium* group. These questions require a much denser taxonomic sampling. This restriction also applies to the position of taxa at the earliest split within the

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genus, although *C. phyllitidis* is not only the sister to the remaining genus but also shows similarities in its morphology with the sister genus *Niphidium* such as prominent costa and veins on the abaxial leaf surface, coriaceous blades, and erect fronds. Our data set contains only 36 parsimony-informative sites from a total of 230 included characters. This low percentage (about 16%) of informative sites may indicate that *Campyloneurum* has diverged and radiated relatively recently. Similar low percentage of informative and/or variable sites were reported in other studies employing the *trnL-F* IGS region to elucidate relationships between closely related species of Polypodiaceae (Haufler *et al.*, 2003; Janssen and Schneider, 2005; Schneider *et al.*, 2006a, b; Smith *et al.*, 2006) and Aspleniaceae (Schneider *et al.*, 2005). In the Aspleniaceae study, divergence times were estimated for a lineage of asplenioid ferns (Schneider *et al.*, 2005) and the results indicated a diversification in the Miocene corresponding to a level of sequence divergence as observed in *Campyloneurum*. The exact timing of this genus diversification is currently unknown but the distribution of the genus suggests putative correlations with geological and climatic changes in the upper Tertiary shaping the extant plant diversity of South and Central America. Future studies require not only denser sampling of species within the genus and but also sampling of more variable markers.

Acknowledgments

This investigation was supported by the German Science Foundation (DFG) grant to HS (SCHN758/2-1 and SCHN758/2-2) as part of the Schwerpunkt program (SPP 1127) ''Radiations – origin of biological diversity''. We thank also two anonymous reviewers for the kind suggestions that helped to improve this publication.

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