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https://doi.org/10.11646/phytotaxa.733.1.8

Filicites, Dorfiella, Hydropteris, or Hydropteridium: The correct name for a group of aquatic ferns from the Late Cretaceous of North America

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There are inconsistencies in the published literature over the appropriate name to apply to a group of plants from the Late Cretaceous (Campanian to Maastrichtian) of western Canada and the western United States variously known as *Filicites knowltonii* (Dorf (1942: 127), *Dorfiella knowltonii* (Dorf) Weber (1976: 3), *Hydropteris pinnata* Rothwell & Stockey (1994: 481), *Hydropteridium pinnatum* (Rothwell & Stockey) Hermsen & Jud (in Hermsen *et al.* 2019: appendix B), and *Dorfiella pinnata* (Rothwell & Stockey) Aulenback (2021: 63). These plants are interpreted as rhizomatous aquatic ferns bearing pinnate fronds with pinnae that have reticulate venation and enigmatic simple appendages that have variously been interpreted as floats, sporocarps (structures enclosing groups of sporangia), or reduced fronds consisting of one pinna each (Weber 1976, Rothwell & Stockey 1994, Aulenback 2009, 2021). They are generally thought to have affinities to heterosporous water ferns in the order Salviniales (e.g., Rothwell & Stockey 1994, Aulenback 2021). In order to fully understand the morphology, diversity, geographical and temporal distributions, and evolutionary connections of this group of ferns, the nomenclatural uncertainty surrounding them requires resolution.

Dorf (1942) described the first such material, from the Lance Formation of Wyoming, USA, and assigned it to *Filicites* Schlotheim (1820: 403) ex Brongniart (1822: 26) as the new species *Filicites knowltonii*. *Filicites* was historically used as a catch-all for varied types of fossil fern material (Weber 1976, Cleal 2012, Doweld 2012), and the genus name *Filicites* was formally rejected in 2016 (Wilson 2016). In 1976, Weber made *F. knowltonii* the type of the new genus *Dorfiella* Weber (1976: 3) as the new combination *Dorfiella knowltonii*, describing a second species, *Dorfiella auriculata* Weber (1976: 5), from the Olmos Formation of Coahuila, Mexico. Later, Rothwell & Stockey (1994) described similar fern material from a locality near Cardston, St. Mary River Formation, Alberta, Canada, as a new genus with the type and sole species *Hydropteris pinnata*. Others (Doweld 2001, Aulenback 2009, 2021, IFPNI International Editorial Board 2014–2025) noted, however, that the name *Hydropteris* Rothwell & Stockey (1994: 481) is an illegitimate homonym, *Hydropteris* having already been used as a genus name for dispersed spores, *Hydropteris* Kondinskaja (1966: 120). To fix this error, Doweld (2001) proposed the replacement genus name *Hydropteridium* Doweld (2001: X), with Hermsen & Jud (in Hermsen *et al.* 2019) subsequently establishing the new combination *Hydropteridium pinnatum*. Aulenback (2009) separately interpreted *Hydropteris pinnata* as a species of *Dorfiella*, later formally transferring it to *Dorfiella* as the new combination *Dorfiella pinnata* (Aulenback 2021), although Aulenback's new combination was not validly published, among other issues (see remarks below for more details).

In effect, the names *Filicites knowltonii* and *Hydropteris pinnata* have been used interchangeably in the literature on these ferns when they occur in the western United States and Canada. The name *F. knowltonii* was simply used in publications predating 1994 (excepting Weber 1976), whereas the name *H. pinnata* has been favored in publications from and postdating 1994, the year of its publication (see references in the occurrence list below). The connection between the species has been recognized by some previous authors. Erwin (1997) highlighted the similarity between Dorf's (1942) *F. knowltonii* material from Wyoming, Rothwell & Stockey's (1994) *H. pinnata* material from Alberta, and undescribed putative *H. pinnata* material from the Kaiparowits Formation of Utah, USA. Johnson identified a specimen (YPM PB 006259, held at the Yale Peabody Museum, New Haven, Connecticut, USA) from the Hell Creek Formation of North Dakota, USA, initially as *F. knowltonii* (Johnson 1989) and later as *H. pinnata* (Johnson 2002). Finally, Wilson *et al.* (2021) synonymized the names, accepting *H. pinnata* and listing *F. knowltonii* as its synonym. Given the history of usage of the names *F. knowltonii* and *H. pinnata*, I here agree that they should be considered the same species.

As noted above, the genus names *Filicites* (rejected) and *Hydropteris* (homonym) cannot be used, leaving *Dorfiella* and *Hydropteridium* as the remaining existing genus names that could be applied to this species of fossil ferns. *Dorfiella knowltonii* (= *Filicites knowltonii*) is the designated type for the genus *Dorfiella* (Weber 1976); *Hydropteridium pinnatum*

(= Hydropteris pinnata) is the type for the genus Hydropteridium because, as a replacement for an illegitimate name, Hydropteridium automatically took on the type of the name it replaced (see Article 7.5 in Turland et al. 2025). When their type species are treated as synonymous, Dorfiella has priority over Hydropteridium because Dorfiella was published first. Thus, the correct name for these ferns is Dorfiella knowltonii. Hydropteris pinnata, Hydropteridium pinnatum, and Dorfiella pinnata, nom. inval., which all share the same type, are here considered heterotypic (taxonomic) synonyms for D. knowltonii.

Dorfiella Weber (1976: 3). Type (designated by Weber 1976: 3):—Dorfiella knowltonii (Dorf) Weber (1976: 3, 'knowltonii') ≡ Filicites knowltonii Dorf (1942: 127, 'knowltoni').

- = Dorfiella Aulenback (2021: 62), nom. illeg., non R.Weber. Type (designated by Aulenback 2021: 62):—Dorfiella auriculata Weber (1976: 5).
- = Hydropteridium Doweld (2001: X). ≡ Hydropteris Rothwell & Stockey (1994: 481), nom. illeg., non Kondinskaja (1966: 120). Type (by monotypy in Rothwell & Stockey 1994: 481):—Hydropteris pinnata Rothwell & Stockey (1994: 481).

Notes:—Although Aulenback's (2021) treatment of *Dorfiella* was presented as an emendation of Weber's (1976) genus, I here argue that Aulenback instead inadvertently created a later homonym, *Dorfiella* Aulenback, *nom. illeg*. This interpretation is based on the following principles outlined in the Madrid *Code*: 1) A genus name that has the same spelling as but a different type than a previously published valid genus name is a homonym (Article 53.1 in Turland *et al.* 2025); and 2) The circumscription of a taxon that "definitely excludes its type" or its syntypes creates a homonym (Article 48 in Turland *et al.* 2025). Aulenback (2021) listed *D. auriculata* (holotype from the Olmos Formation, Coahuila, Mexico) as the type for *Dorfiella*, whereas Weber (1976) had designed *D. knowltonii* (syntypes/cotypes from the Lance Formation, Wyoming, USA) as the type when originally erecting the genus. In addition to *D. auriculata*, Aulenback's (2021) circumscription of *Dorfiella* included material from the St. Mary River and Horseshoe Canyon formations (both of Alberta, Canada) assigned to *D. pinnata*, *nom. inval.*, and *Dorfiella* sp.; the originally designated type species and its syntype material from Wyoming were not discussed. *Dorfiella knowltonii* could thus be considered to be excluded from Aulenback's (2021) concept of *Dorfiella* due to a combination of the designation of *D. auriculata* as the type—supplanting *D. knowltonii*—as well as omission of the correct type and its specimens. Even if Aulenback's (2021) treatment of *Dorfiella* is considered an emendation of Weber's (1976) genus *Dorfiella* that contains errors rather than a later homonym, it has no impact on the conclusions below regarding which are the correct names for the two species of *Dorfiella*.

Dorfiella knowltonii (Dorf) Weber (1976: 3, 'knowltoni') ≡ Filicites knowltonii Dorf (1942: 127, pl. 4, figs. 7, 8, 10, 11. 'knowltoni'). Lectotype (designated here):—USA. Wyoming: US Geological Survey locality 1462, Niobrara County, Upper Cretaceous Lance Formation, USNM 40250a (Dorf 1942, pl. 4, fig. 11). Repository: National Museum of Natural History, Smithsonian Institution, Washington, DC, USA. Remaining syntypes: UCMP 2455 (Dorf 1942, pl. 4, fig. 7), UCMP 2456 (Dorf 1942, pl. 4, fig. 8), USNM 40250 (Dorf 1942, pl. 4, fig. 10).

= Hydropteridium pinnatum (Rothwell & Stockey) Hermsen & Jud (in Hermsen et al. 2019: appendix B) ≡ Hydropteris pinnata Rothwell & Stockey (1994: 481, figs. 1–41) ≡ Dorfiella pinnata (Rothwell & Stockey) Aulenback (2021: 63, figs. 44A–I, 45A, 45B, 48), nom. inval. Holotype (designated by Rothwell & Stockey 1994: 481):—CANADA. Alberta: "Riverbank exposure on the north side of the St. Mary River approx. 50 m below the spillway of the St. Mary Reservoir, east of Cardston" (Rothwell & Stockey: 481), Upper Cretaceous St. Mary River Formation, UAPC-ALTA S36881 (Rothwell & Stockey 1994: figs. 1, 5, 12, 15, 16; Aulenback 2009: figs. 117, 120; Aulenback 2021: fig. 44A, 44C, 44G). Repository: Paleobotanical Collection, University of Alberta, Edmonton, Alberta, Canada.

Notes:—While the name *Dorfiella knowltonii* has been incorporated into some online databases (IFPNI International Editorial Board 2014–2025; Gross 2024a, b), it has been ignored in the published literature subsequent to when Weber (1976) established it as a new combination. To be fair, the title and abstract of Weber's (1976) paper creating the genus *Dorfiella* seem to imply that *D. auriculata* represents both the new genus and species and make no mention of *D. knowltonii*, meaning that it would be easy to miss the key detail that *D. knowltonii* is the type for *Dorfiella* in a standard literature search. Nevertheless, Weber (1976: 3) created the new combination *D. knowltonii* and clearly designated it as the type for *Dorfiella* in the protologue for the genus.

Of eleven total specimens of *D. knowltonii* originally studied by Dorf (1942), four were figured with the original description of *Filicites knowltonii*, two held at the University of California Museum of Paleontology (UCMP) in Berkeley, California, USA, and two held at the National Museum of Natural History (USNM) in Washington, DC, USA. Because Dorf (1942) designated all four specimens as cotypes (syntypes), a lectotype from the syntype series is here designated. Images

of the material held at UCMP (UCMP 2455, 2456) were available online (Gross 2024 a, b), and images of the material held at USNM (USNM 40250, 40250a) were provided to me via email. It should be noted that the number USNM 40250 applies to eight specimens of *D. knowltonii* held by USNM, and the illustrated specimen (Dorf 1942, pl. 4, fig. 10) has an unfigured counterpart (this part-counterpart specimen has been counted as two specimens for the purpose of the preceding discussion). While Dorf (1942) indicated that USNM 40250a is a counterpart, no corresponding part was located among the images examined for this study. All four illustrated specimens are portions of sterile fronds with multiple attached pinnae, and all show the basic frond and pinna structure of the genus and species. The lectotype is designated as USNM 40250a because it appears to be a high-quality specimen, although any of the original syntypes would have been adequate.

The combination *Dorfiella pinnata* (basionym *Hydropteris pinnata*) proposed by Aulenback (2021) was assigned to *Dorfiella* Aulenback, *nom. illeg.*, *non* R. Weber. It was not validly published because the citation of the basionym for the new combination included the full pagination of the paper rather than only the page(s) on which the basionym or protologue was published (see Note 1 under Article 41.5 in Turland *et al.* 2025). Since a new suborder, a new family, and a new genus were also introduced by Rothwell & Stockey (1994) in the same paper in which they described *Hydropteris pinnata*, the entire publication cannot be considered part of the protologue for the species.

Aulenback (2009, 2021) argued that *D. knowltonii* spores figured by Rothwell & Stockey (1994: figs. 18–41) were not *in situ* in the macrofossil remains of *D. knowltonii* on the specimen (UAPC-ALTA S36001B, St. Mary River Formation, Alberta) from which they were macerated, but instead are either similar to or belong to another taxon representing a putatively different plant, *Thromboazolla sweetii* Aulenback (2021: 41). *Thromboazolla sweetii* encompasses three-dimensionally preserved, isolated groups of sori containing *Parazolla* Hall (1969: 1174)-type megaspores and microspore massulae; its type material is from the Horseshoe Canyon Formation, Alberta, Canada (Aulenback 2009, 2021). Since the vegetative organs of *T. sweetii* are not known, however, a more plausible hypothesis is that *T. sweetii*-type soral clusters were produced by the *D. knowltonii* plant.

Occurrence:—This species occurs in western Canada and the western United States, from Alberta in the north to Colorado and Utah in the south. Its temporal range is Campanian–Maastrichtian.

Figured records

- CANADA. Alberta: Edmonton Group: Bell (1949: 41, pl. 1, figs. 1, 3, as *Filicites 'knowltoni'*), Aulenback (2021: 65, fig. 46A–D, as *Dorfiella* sp.).
- CANADA. Alberta: St. Mary River Formation: Bell (1965: pl. 11, figs. 5, 6, as *Filicites 'knowltoni'*), Rothwell & Stockey (1994: 481, figs. 1–41, as *Hydropteris pinnata*), Aulenback (2009: figs. 117–124, 126, as "*Hydropteris pinnata*", quotes in original source), Aulenback (2021: 63, figs. 44A–I, 45A, 45B, 48, as *Dorfiella pinnata*).
- USA. Colorado: Denver Formation: Holian (2025: 168, pl. 25, figs. B, C, as Hydropteris pinnata).
- USA. Montana: Hell Creek Formation: Wilson et al. (2021: 7, fig. 4A, as Hydropteris pinnata).
- USA. North Dakota: Hell Creek Formation: Johnson (1989: 173, pl. 16, fig. 7, as *Filicites knowltonii*), Johnson (2002: pl. 2, fig. 3, as *Hydropteris pinnata*).
- USA. Utah: Kaiparowits Formation: Miller et al. (2013: fig. 7.8B–D, as *Hydropteris* cf. *H. pinnata*), Miller et al. (2013: fig. 7.8A, as *Hydropteris* sp.).
- USA. Wyoming: Lance Formation: Dorf (1942: 127, pl. 4, figs. 7, 8, 10, 11, as Filicites 'knowltoni').

Additional published but unfigured occurrences verified by images posted online

USA. South Dakota: Hell Creek Formation: Stockey *et al.* (2016: 707, as *Hydropteris*, verified by specimens DMNH EPI.30187, EPI.51921–EPI.51926, repository Denver Museum of Nature and Science, Denver, Colorado, USA).

Dorfiella auriculata Weber (1976: 5, pls. 1–3 and fig. 1). ≡ *Dorfiella auriculata* (R.Weber) Aulenback (2021: 62, figs. 47, 49), *nom. illeg. et inval.*, *non* R.Weber. Holotype (designated by Weber 1976: 5):—MEXICO: Coahuila: Nueva Rosita Mine no. 6, Upper Cretaceous Olmos Formation, GIM-PB 412 (Weber, 1976, pl. 3). Repository: Museo de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México, Mexico City, Mexico.

Notes:—While Aulenback (2021) labeled his treatment of *D. auriculata* an emendation, the species was assigned to *Dorfiella* Aulenback *non* R.Weber, so it is here treated as an illegitimate homonym. The combination *D. auriculata* (R.Weber) Aulenback was also invalidly published because Aulenback's (2021) citation of the basionym included the full pagination of Weber's (1976) paper rather than only the page(s) on which the basionym or protologue were published.

Occurrence:—Restricted to the Olmos Formation, Coahuila, Mexico. Weber (1976) gave the age as Maastrichtian.

Acknowledgements

I would like to thank J. Wingerath for providing images of *Filicites knowltonii* from the USNM collections. Images of specimens held at the Denver Museum of Nature and Science are available in the museum's online collections database (https://imu.dmns.org/dmns/paleo.html). The citation for the first valid publication of the genus name *Filicites* follows that listed in *The International Fossil Plant Names Index* (IFPNI International Editorial Board 2014–2025), which differs from the citations in Cleal (2012) and Doweld (2012).

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