×*Abacopterella altifrons* (Thelypteridaceae), a new intergeneric fern hybrid from Australia

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Summary

Almeida, T.E., Smith, A.R., Bostock, P.D., Bloesch, Z. & Field, A.R. (2023). ×***Abacopterella altifrons*** (Thelypteridaceae), a new intergeneric fern hybrid from Australia. ***Austrobaileya* 13: 41–50.** The new nothogenus, ×*Abacopterella* T.E.Almeida & A.R.Field and a new nothospecies, ×*Abacopterella altifrons* T.E.Almeida & A.R.Field (*Abacopteris aspera* (C.Presl) Ching × *Christella queenslandica* (Holttum) A.R.Field & Z.Bloesch, comb. nov.) are described, based on recent phylogenomic evidence identifying the Australian 'Russell River Fern' to be an intergeneric hybrid. A new combination, *Christella queenslandica* (Holttum) A.R.Field & Z.Bloesch, accommodates findings of recent investigations of this species' phylogenetic placement based on phylogenomic data. A description, illustrations, notes, and a conservation status assessment for the nothospecies are presented, as well as an updated list of all Thelypteridaceae occurring in Australia.

Key Words: Thelypteridaceae; ×*Abacopterella*; ×*Abacopterella altifrons*; *Abacopteris*; *Christella*; *Christella queenslandica*; flora of Queensland; flora of Wet Tropics; checklist of species; hybridisation; nothogenus; nothospecies; conservation status

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Introduction

Reticulation is known to be a relevant process in evolution, connecting and promoting genetic exchange in otherwise isolated lineages (Dunning & Christin 2020). Hybridisation (Mallet 2007) and horizontal gene transfer (Dunning & Christin 2020) are the main processes that promote reticulation. In hybridisation, several outcomes are possible, including the formation of single or recurrent F1 hybrids, hybrid swarms or zones that can promote introgression, and the emergence of a new lineage of hybrid origin (Mallet 2007; Schumer *et al.* 2014). Traditional species description based upon alpha-taxonomic species delimitation (as defined by Mayo *et al.* 2008) and in-use hierarchical categorical classification systems both fail to accommodate this evolutionary reality that lineages can reticulate. This is particularly relevant among ferns.

Reproductive barriers in ferns are suggested to evolve more slowly than in flowering plants, with multiple interspecific and intergeneric hybrids recognized (Barrington *et al.* 1989; Rothfels *et al.* 2015; Liu *et al.* 2020). There are currently 32 described nothogenera, of which 12 are validly published and required if adopting the current classification of ferns (Liu *et al.* 2020). Two belong to Thelypteridaceae: ×*Chrismatopteris* Quansah & D.S.Edward (*Christella* H.Lév. × *Pneumatopteris* Nakai) and ×*Chrinephrium* Nakaike (*Christella* H.Lév. × *Pronephrium* C.Presl).

Recently, and for the first time, an intergeneric hybrid in Thelypteridaceae was tested using phasing of genomic data, providing evidence of a hybrid between species of *Abacopteris* Fée and *Christella* (Bloesch *et al.* 2022). Thelypteridaceae is a

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cosmopolitan family with an estimated 1190 species and 37 genera (Fawcett & Smith 2021). The family is monophyletic (Almeida *et al.* 2016; Fawcett *et al.* 2021), with two main lineages, subfamilies Thelypteridoideae C.F.Reed and Phegopteridoideae Salino, A.R.Sm. & T.E.Almeida (PPG I 2016). Eleven genera and 23 species were recorded from Australia (Bostock 1998; Field 2020) with two species, *Amblovenatum queenslandicum* (Holttum) T.E.Almeida & A.R.Field and *Chingia australis* Holttum, considered endemic (Field 2020).

We examined new material of Thelypteridaceae collected since the family was revised for *Flora of Australia* (Bostock 1998) and found two putative hybrids from the Australian tropics. One, named by Bloesch *et al.* (2022) as the 'Russell River Fern' has three recorded populations (**Map 1**; Bloesch *et al.* 2022). The other, named the 'Tully River Fern' (Bloesch *et al.* 2022) is known from a single locality. Using genomic data from nuclear loci, Bloesch *et al.* (2022) were able to confirm the hybrid origin of the two ferns and indicate the putative parents. The 'Russell River Fern' was found to be an F2, or later hybrid involving *Abacopteris aspera* (C.Presl) Ching and *Amblovenatum queenslandicum*, and the 'Tully River Fern' was considered likely to be an F1 hybrid between *Christella subpubescens* (Blume) Holttum and *C. parasitica* (L.) H.Lév.

Evidence from allele ratios of the sampled population indicates that the 'Russell River Fern' is more likely an F2 hybrid or a lineage of hybrid origin than a primary hybrid (Bloesch *et al*. 2022). The 'Russell River Fern' has been collected multiple times and is known from multiple sites; hence, this evidence warrants formal taxonomic recognition. Conversely, further research is needed to resolve the parentage of the 'Tully River Fern' and to review its identification as *Amblovenatum tildeniae* (Holttum) T.E.Almeida & A.R.Field (Field 2020).

Named taxa enable stability of scientific communication and recognition in biodiversity legislation and, in the case of nothotaxa, better reflect the uncertainty around parentage and whether a plant is an F1 hybrid, complex hybrid, or species of hybrid origin. Therefore, we here describe a new nothogenus and nothospecies for the 'Russell River Fern'. Although a nothospecies is often considered to be a primary hybrid, we chose to describe the 'Russell River Fern' as a nothospecies because only one of three populations has thus far been sampled phylogenomically, and whether the three populations are a cohesive lineage or resultant from separate hybridisation events remains unknown.

In addition to providing insights about reticulating evolution, the phylogenetic tree presented by Bloesch *et al.* (2022) provided evidence that *Amblovenatum queenslandicum* is more appropriately placed in *Christella* (Bloesch *et al.* 2022) and a new combination in that genus is also made in this paper. An updated checklist for Australian Thelypteridaceae is presented (**Appendix 1**) following the classification of Fawcett & Smith (2021).

Materials and methods

We examined herbarium materials from the following herbaria: BRI, CNS, UC and US (all specimens cited have been seen), and material collected from wild populations throughout the north-eastern coast and hinterland of the Wet Tropics of Queensland, Australia. Living material was cultivated for four years in a tropical shade house in Cairns, Queensland, Australia, under 80% shade cloth, irrigated on alternating days and liquid fertilized on alternating weeks. Plants were grown in 250 mm diameter black plastic pots in a 1–5 mm 1:1 bark:scoria growing medium and were repotted biennially. Living plants were also examined in the private collection of Nada and Garry Sankowsky, Tolga, Australia. The terminology used to describe general morphology was based on Radford (1986) and Lellinger (2002).

Conservation status was assessed using IUCN Red List Categories and Criteria (IUCN 2018) to calculate the Extent of Occurrence (EOO) and the Area of Occupancy (AOO), using the GeoCAT tool (Bachman *et al.* 2011)

based on the records from the three locations (**Map 1**). A 2 km width grid cell was used for the estimation of AOO.

Taxonomy

Christella queenslandica (Holttum) A.R.Field & Z.Bloesch, **comb. nov.**

Amphineuron queenslandicum Holttum, *Kew Bull.* 41: 518 (1986); *Thelypteris queenslandica* (Holttum) Christenh., *Global Fl.* 4: 36 (2018); *Amblovenatum queenslandicum* (Holttum) T.E.Almeida & A.R.Field, *Aust. Syst. Bot.* 33: 68 (2020). **Type:** Australia: Queensland. Cook District: State Forest Reserve 756, Kaaru Logging Area, Queensland, 4 September 1981, *D.L. Jones 114* (holo: CNS [QRS 65258]; iso: BRI [AQ0411774]).

A species description can be sourced in the *Flora of Australia* account (Bostock 1998: 350).

***Distribution and habitat*:** *Christella queenslandica* is an occasional fern in well-lit rainforest understory, near creeks, and long-term canopy gaps in lowland to lower montane rainforest. It is endemic to the wet tropical rainforests of northeast Queensland. By contrast, sympatric *Christella dentata* (Forssk.) Brownsey & Jermy and *C. parasitica* (L.) Lev. are much more abundant and tend to be pioneers on disturbed rainforest edges. Both *C. dentata* and *C. parasitica* have widespread tropical distributions.

***Notes*:** *Christella queenslandica* (Tully River fern) is placed phylogenetically within the genus *Christella* and not within the genus *Amblovenatum* (Bloesch *et al.* 2022). Holttum (1986) does not discuss why it was placed in the genus *Amphineuron* (≡ *Amblovenatum*). It lacks the spherical yellow glands on the laminae characteristic of *Amblovenatum* and keys to the genus *Christella* in the generic keys of Bostock (1998) and Fawcett & Smith (2021). *Christella queenslandica* has similar fronds and rhizome to those of *C. dentata*, being distinguished in the field by its foliage which has a consistently spicy smell and mildly irritant exudate when crushed, more deeply incised pinna lobes, and a single pair of reflexed basal pinnae (compared to 2–4 pairs of reduced basal pinnae in *C. dentata*). *Christella queenslandica* has similar frond shape and division, spicy smell, and basal pinnae to *C. parasitica*, being distinguished by its erect rhizome (compared to horizontal creeping rhizome in *C. parasitica*).

×Abacopterella T.E.Almeida & A.R.Field, **nothogen. nov.**

A taxon of hybrid origin with parentage originating from species of *Abacopteris* Fée and *Christella* H.Lév.

×Abacopterella altifrons T.E.Almeida & A.R.Field, **nothosp. nov.**

A taxon of hybrid origin originating from *Abacopteris aspera* (C.Presl) Ching × *Christella queenslandica* (Holttum) A.R.Field & Z.Bloesch). It is similar to *Abacopteris aspera* in having anastomosing venation and short-creeping rhizomes. It differs from *Abacopteris aspera* by the larger, 1-pinnate-pinnatifid fronds, with 10–20 pairs of pinnae. It is similar to *Christella queenslandica* in having 1 pinnate-pinnatifid fronds, but differs in having anastomosing veins, broader pinnae, and short creeping rhizomes. **Type:** Australia: Queensland. Cook district: Wooroonooran National Park, Russell River pack Track, 14 February 2018, *A.R. Field 4646 & R. Jago* (holo: BRI [AQ629845, comprising 1 sheet]; iso: BHCB, CNS 146459.1, UC).

Plants terrestrial. **Rhizomes** short-creeping; scales lanceolate, (4)5–12 mm wide, brown, glabrous. **Fronds** monomorphic to slightly dimorphic (fertile pinnae slightly narrower and more incised), 102–140 cm long; stipes 37–69 cm long, stipe bases covered with scales similar to those on the rhizome, abaxially with sparse narrow linear scales, adaxially sulcate with one-celled acicular trichomes. **Laminae** elliptic to ovate, chartaceous, 53–72 × 28–50 cm, 1-pinnate-pinnatifid, apical pinnae pinnatifid, not pinna-like, always widened and lobed towards their base, lateral pinnae 10–20 pairs, 20–26 × 2.6–3.6 cm, perpendicular to ascending, proximal pair slightly deflexed, sessile, narrowly triangular to triangular, apex caudate, base truncate, pinna margins lobed, 1/4–1/3 towards costae; buds absent, aerophores round and slightly

raised, acroscopically at axils of pinnae; rachises abaxially with short, setiform hairs, 0.05–0.2 mm long, and capitate, stalked glandular hairs, 0.01–0.03 mm long, adaxially with acicular hairs, 0.18–0.4 mm long and glandular hairs, 0.01–0.03 mm long; costae abaxially rounded, with setiform hairs to 0.2 mm long, some to 0.5 mm, adaxially sulcate and covered with acicular hairs; costules, veins, and blades abaxially bearing setiform hairs, adaxially glabrous; veins 10–14 pairs per segment, at 60º to costule, mostly anastomosing and forming parallel rows of areoles below (proximal to) the sinuses, the basal-most areoles joining to form excurrent veinlets that join the next row of areoles, veins free on the lobes; segments 4.1–5.1 mm wide, apices rounded. **Sori** round, medial, indusiate; indusia conspicuous, round-reniform, entire, with setiform hairs to 0.2 mm long; sporangia setose. Spores variable, with three observed types: 50–60 µm diameter, spherical, unreduced spores (rare), 30–40 µm long, monolete, winged spores (rare); and 30–40 µm collapsed monolete unwinged spores (predominant type). **Figs. 1 & 2**.

***Additional specimens examined*: Queensland.** Cook District: National Park 226, Bartle Frere, first Combo Russell River pack trail, Jun 1993, *Bostock 1414 & Jago* (BRI, NSW); *ibid*, Sep 1993, *Bostock et al. 1457* (BRI, NSW); *ibid*, ex plant cultivated at Sankowsky living plant collection, Tolga, ex *Bostock 1414 & Jago*, Nov 2015, *Field 3918* (BRI, CNS, UFP). North Kennedy District: Porter's Creek, off Bruce Highway, NW of Ingham, May 1992, *Cumming 11952 & Thomas* (BRI).

***Distribution and habitat*:** ×*Abacopterella altifrons* (Russell River Fern) is endemic to Australia in the Wet Tropics of Queensland. It has been documented from two locations, near the Russell River pack track in the Innisfail region, and Porter's Creek in the Hinchinbrook region and also reported from Melele Creek (*Tng s.n*., Daintree Research Observatory Field Herbarium) and a tributary of Bailey Creek (Nada Sankowsky, pers. comm.) in the Daintree–Bloomfield region.

×*Abacopterella altifrons* is an extremely rare, terrestrial fern that forms small colonies in brightly lit areas on forest edges, tracks, or in long-term canopy gaps in lowland mesic complex mesophyll vineforests. This species tends to form localized multi-plant colonies with each plant bearing three to nine fronds; the plants generally long-lived. New plant establishment has been observed both from rhizome division and apparently from spores, evidenced by plants appearing at sites not connected to established plants. The population near the Russell River pack track has been monitored for over 30 years (R.L. Jago pers. comm.; A.R. Field pers. obs.) and has persisted in the same general area through severe canopy disturbance caused by Tropical Cyclones Winifred (1986), Larry (2006) and Yasi (2011).

***Notes*:** ×*Abacopterella altifrons* occurs sympatrically with *Abacopteris aspera,* from which it differs by the higher number of pinna pairs (10–20 pairs in ×*Abacopterella altifrons vs.* up to eight pairs in *Abacopteris aspera*), the incised lobulate pinna margins (*vs.* entire to crenulate in *Abacopteris aspera*), and the pinnatifid apical pinna (*vs.* conform in *Abacopteris aspera*). Mature plants of ×*Abacopterella altifrons* generally bear numerous fronds and form a larger and localized colony, differing from mature *Abacopteris aspera* which bear few fronds and usually are isolated plants scattered throughout the forest floor. Fronds of ×*Abacopterella altifrons* are more erect and paler green than *Abacopteris aspera*, which has fronds that are more spreading and usually a darker green. These traits were maintained when plants were cultivated side-by-side under uniform conditions.

×*Abacopterella altifrons* also occurs sympatrically with *Christella queenslandica*, from which it differs by its short-creeping rhizomes with a loose cluster of fronds (*vs.* erect with a vase-shaped rosette of fronds in *C. queenslandica*) and anastomosing veins (*vs.* free veins in *C. queenslandica*, except for costal areoles formed by basal veins from adjacent segments uniting and forming an excurrent vein toward the sinus). ×*Abacopterella altifrons* is a brighter yellow-green than *C. queenslandica* and also lacks the spicy aroma and irritating exudate sometimes recorded in *C. queenslandica*.

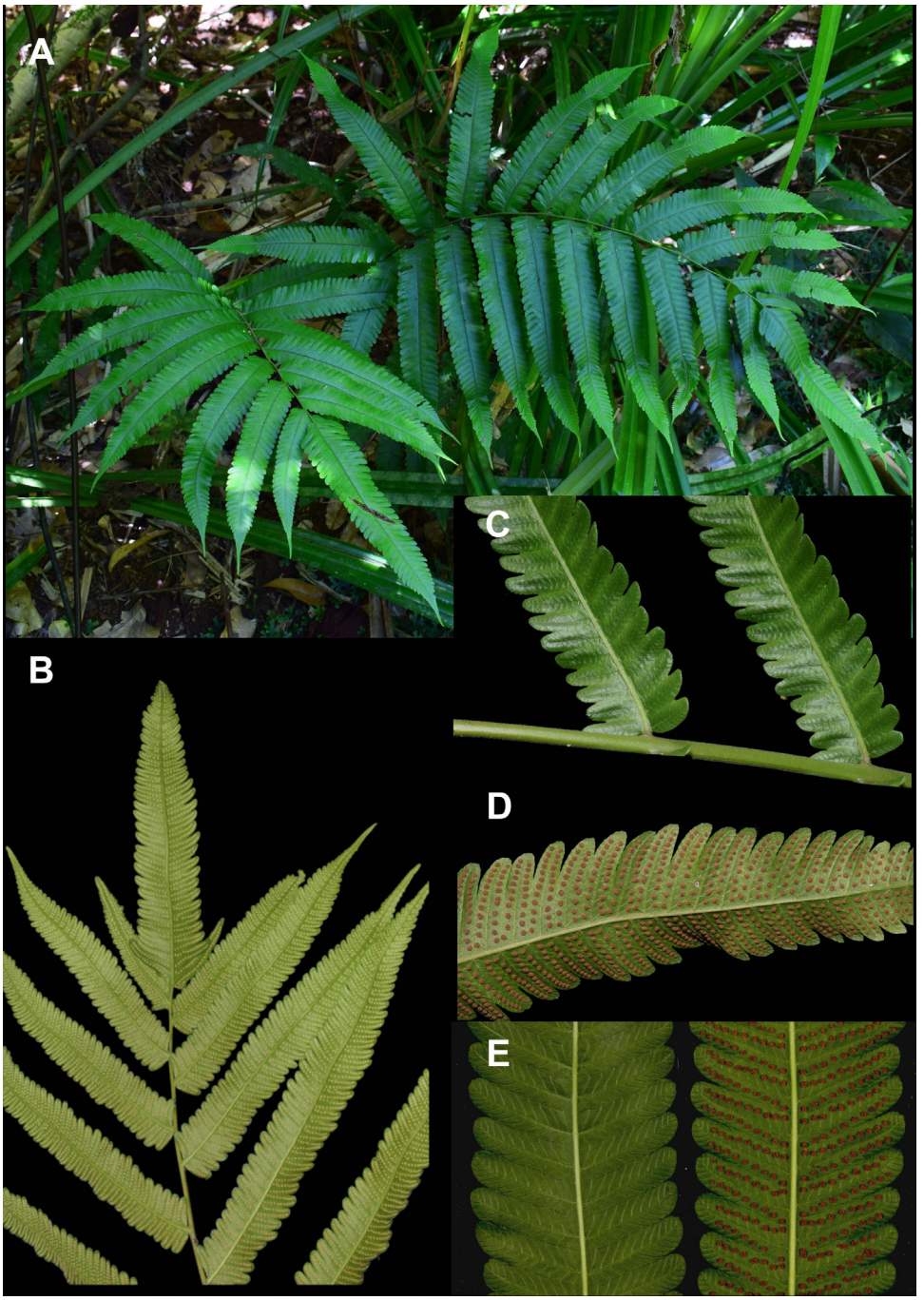

Fig. 1. ×***Abacopterella altifrons***. A. habit. B. abaxial view of a fertile frond, showing non-conform apex. C. adaxial side of pinnae. D. abaxial side of a pinna, showing soral pattern. E. abaxial side of sterile (left) and fertile (right) pinnae, showing venation pattern. A–E taken in habitat at location of *Field 4646* (CNS).

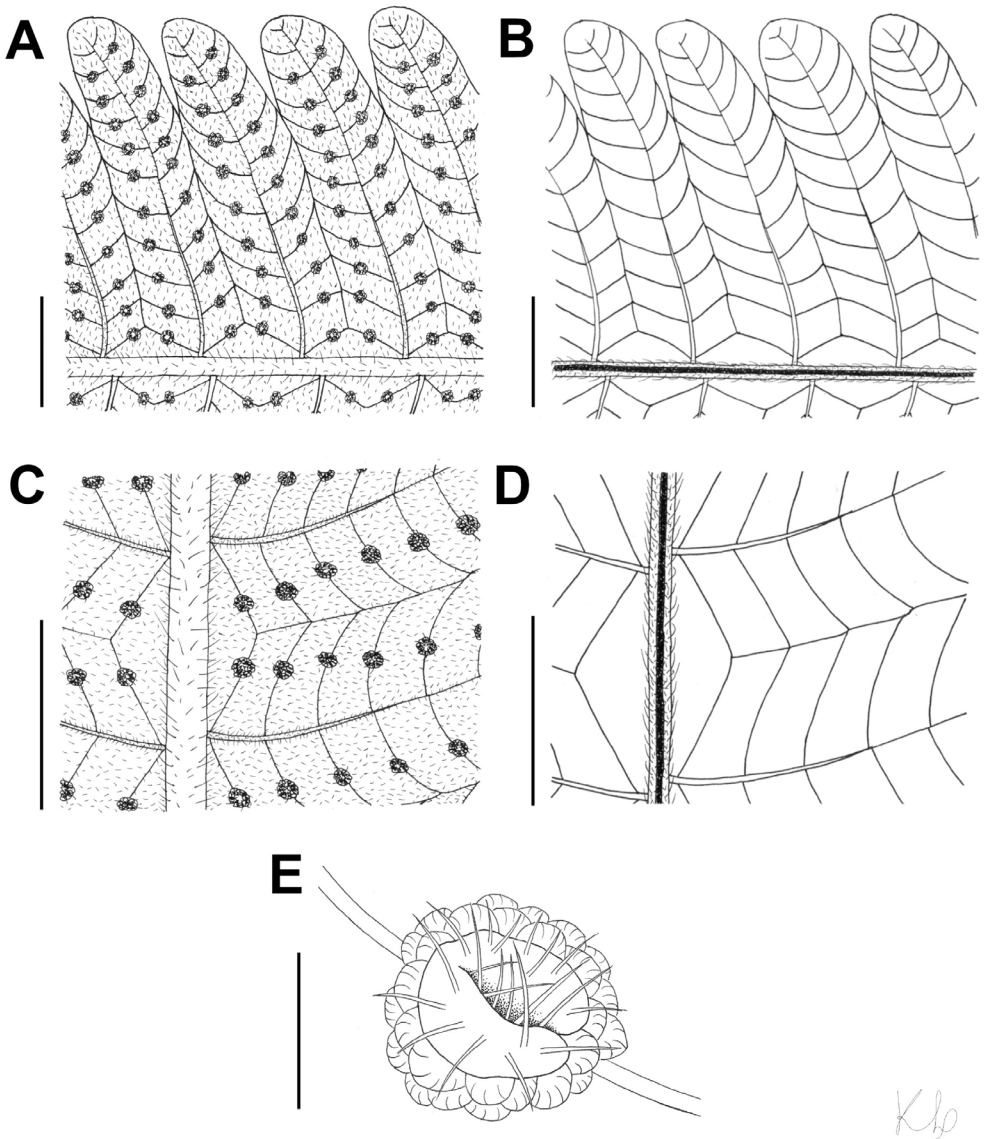

Fig. 2. ×***Abacopterella altifrons***. A & B. abaxial view of a fertile frond, showing overall aspect and details of indument, sori disposition, and venation. C & D. adaxial view of a fertile frond, showing overall aspect and details of indument. E. sori, showing acicular hairs on the indusium. Scale bar: A–D: 0.5 cm. E: 0.5 mm. All from *Field 4646* (BHCB). Del. Keven S. Lima.

Spore production was observed in both wild specimens and cultivated plants. Although we did not test for viability, most spores are malformed and appear inviable. New, apparently spore-grown individuals, have been observed in the wild and once in cultivation (A.R. Field, pers. obs.), but we do not know if these are the result of sexual or apomictic reproduction or are *de novo* hybrids with the same parentage. Both *Abacopteris* and *Christella* have *x*=36 (*n*=72) (Tindale & Roy 2002), and future studies should focus on investigating the ploidy level to clarify if any of the populations are allopolyploid (Bloesch *et al.* 2022). A survey on the genetic structure of known populations of ×*Abacopterella altifrons* is also recommended to assess the genetic divergence and understand its sexual and asexual reproductive processes.

***Etymology*:** ×*Abacopterella altifrons* is named for having tall fronds, in comparison with the species from the parental genera (*Abacopteris* and *Christella*).

Conservation status: Hybrids are not included in IUCN Red Lists (IUCN 2022a) with their presence considered a species stressor (IUCN 2022b); however, this policy does not explicitly cover nothospecies. This policy of not applying IUCN conservation status to hybrid individuals has been criticised for potential conservation decision bias (Bauer *et al*. 2021).

For the purposes of conservation assessment, we here consider that ×*Abacopterella altifrons* is not a primary hybrid (Bloesch *et al*. 2022); hence it is eligible for conservation status assessment.

The species has an EOO of 29,673 km^2 and an AOO of 12.000 km^2, and which respectively meet the CR and EN categories under IUCN criteria (IUCN 2019). Although the species is known from protected areas, populations observed in the field have a very small number of individuals. ×*Abacopterella altifrons* is maintained in four *ex situ* cultivated collections in Australia.

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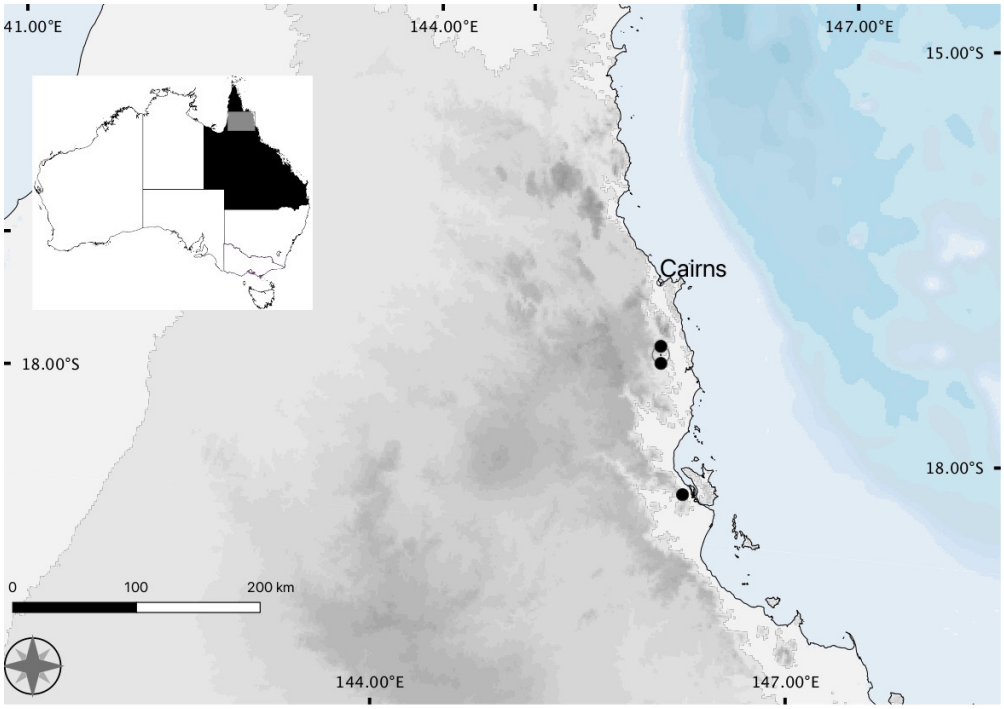

Map 1. Distribution of ×***Abacopterella altifrons***. The Extent of Occurrence (EOO) and the Area of Occupation (AOO) were calculated based on these records.

Appendix 1.

An updated list of Australian Thelypteridaceae according to the classification of Fawcett & Smith (2021). Superseded names listed in Field (2020) are presented in square brackets. * putative hybrid identity based on Bloesch *et al.* (2022).

Subfamily Phegopteridoideae Salino, A.R.Sm. & T.E.Almeida

Macrothelypteris polypodioides (Hook.) Holttum

Macrothelypteris torresiana (Gaudich.) Ching

Subfamily Thelypteridoideae C.F.Reed

×Abacopterella altifrons T.E.Almeida & A.R.Field

Abacopteris aspera (C.Presl) Ching [≡ *Pronephrium asperum* (C.Presl) Holttum]

Amblovenatum immersum (Blume) Parris

Amblovenatum opulentum (Kaulf.) J.P.Roux

Amblovenatum terminans (Hook.) J.P.Roux

***Amblovenatum tildeniae** (Holttum) T.E.Almeida & A.R.Field [? *Christella subpubescens* (Blume) Holttum × *Christella parasitica* (L.) H.Lév]

Ampelopteris prolifera (Retz.) Copel.

Chingia australis Holttum

Christella arida (D.Don) Holttum

Christella dentata (Forssk.) Brownsey & Jermy

Christella hispidula (Decne.) Holttum

Christella parasitica (L.) H.Lév.

Christella queenslandica (Holttum) A.R.Field & Z.Bloesch [≡ *Amblovenatum queenslandicum* (Holttum) T.E.Almeida & A.R.Field]

Christella subpubescens (Blume) Holttum

Cyclosorus interruptus (Willd.) H.Ito

Grypothrix triphylla (Sw.) S.E.Fawc. & A.R.Sm. [≡ *Pronephrium triphyllum* (Sw.) Holttum]

Pakau pennigera (G.Forst.) S.E.Fawc. & A.R.Sm. [≡ *Pneumatopteris pennigera* (G.Forst.] Holttum)

Plesioneuron tuberculatum (Ces.) Holttum

Reholttumia costata (Brack.) S.E.Fawc. & A.R.Sm. [≡ *Pneumatopteris costata* (Brack.) Holttum]

Reholttumia sogerensis (Gepp) S.E.Fawc. & A.R.Sm. [≡ *Pneumatopteris sogerensis* (A.Gepp) Holttum]

Reholttumia truncata (Poir.) S.E.Fawc. & A.R.Sm. [≡ *Pneumatopteris truncata* (Poir.) Holttum]

Sphaerostephanos heterocarpos (Blume) Holttum

Strophocaulon unitum (L.) S.E.Fawc. & A.R.Sm. [≡ *Sphaerostephanos unitus* (L.) Holttum]

Thelypteris confluens (Thunb.) C.V.Morton