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Notes on *Vernonia pratensis* Klatt (Asteraceae: Vernonieae)

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Abstract

Vernonia (Asteraceae: Vernonieae) is monophyletic if circumscribed to include only a North American clade of ca. 20 species. *Vernonia pratensis*, an endemic species of Madagascar, has been placed in the synonymy of *Cyanthillium patulum* or considered a distinct species in *Bothriocline*. In this study we characterise the pollen and cypsela of *Vernonia pratensis*, *Bothriocline longipes,* and *Cyanthillium patulum* with details on morphology and ultra-sculpture. The pollen grains of these species are 3-brevicolporate or 3-porate and echinolophate; in *B. longipes* and *V. pratensis* there is an inconspicuous colpus formed by interlacunar gaps (absent in *C. patulum*). The cypselae of *B. longipes* and *V. pratensis* have prominent ribs, broader or equally as wide as the grooves and that are fused into a shallow, apical rim; the grooves are covered by unicellular trichomes (type 1) with a striate cuticle. By contrast, the cypselae of *C. patulum* have ribs narrower than the grooves and not fused apically; the grooves are covered by infundibular idioblasts, and bilobed glandular trichomes at the base. Based on these morphological findings, *V. pratensis* is here placed in *Bothriocline* and named *B. madagascariensis*. This is the single species that occurs in Madagascar within a genus of ca. 50 species otherwise restricted to Tropical Africa and subtropical Southern Africa. Full palynological descriptions, measurements, and scanning electron microscopy (SEM) and light microscopy (LM) images are provided for the three species (*B. longipes*, *B. madagascariensis,* and *C. patulum*), as well as a full taxonomic description of *B. madagascariensis*, with a preliminary conservation status assessment, nomenclatural notes, and a discussion of possible relationships with other species of *Bothriocline*.

Key words: *Bothriocline*, *Cyanthillium*, Madagascar, pollen, taxonomy

Introduction

Vernonia Schreber (1791: 541), as historically defined, was polyphyletic (Keeley *et al.* 2007, 2021). This led to its current circumscription, with just ca. 20 species from North America (henceforth *Vernonia* sensu stricto; Robinson 1999a, 1999b). Therefore, all other species of *Vernonia* (*Vernonia* sensu lato) must be transferred to other genera (i.e., existing, resurrected, or new genera). During the course of a revisionary study of Vernonieae (Asteraceae) from Madagascar, we noted that *Vernonia pratensis* Klatt (1892: 295) was treated as a species of *Bothriocline* Oliv. ex Bentham (1873: 30) sect. *Bothriocline* by Jeffrey (1988) and later as a synonym of *Cyanthillium patulum* (Aiton 1789: 184) Robinson (1990: 252) by Robinson (1990, 1999a); however, neither author provided an explanation for their decisions.

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Bothriocline and *Cyanthillium* Blume (1826: 889) belong to subtribe Erlangeinae, which is defined by a combination of pollen characteristics (often 3-porate lophate or 3-colporate and non-lophate) and the presence of 5-alkylcoumarins (Keeley & Robinson 2009, Robinson *et al.* 2016). However, a recent molecular phylogeny indicates that this subtribe is polyphyletic and, notably, suggests that *Cyanthillium* and *Bothriocline* belong to distinct subclades (Keeley *et al.* 2021). The current definition of *Bothriocline* relies on cypsela characteristics (Pope 1983, 1992, Jeffrey 1988, Jeffrey & Beentje 2000). *Cyanthillium* was resurrected from synonymy in *Vernonia* by Robinson *et al.* (1980) based on chemical characters (i.e. the presence of types of sesquiterpene lactone that are absent from the American *Vernonia*: elemanolides and vernolide-type germacranolides) and chromosome number ($x = 9, 11, 18$), and later re-circumscribed (Robinson 1990). Both genera have leaves with T-shaped trichomes and caducous pappi, but *Bothriocline* comprises perennial herbs or shrubs (rarely annual) whereas *Cyanthillium* includes annual or short-lived perennial herbs.

The objective of this study is to establish the generic placement of *Vernonia pratensis* in *Bothriocline* or *Cyanthillium* through comparisons of their pollen and cypselae.

Materials and methods

Taxonomic sampling:—Three unopened, mature flower buds and three cypselae of *Bothriocline longipes* (Oliver & Hiern 1877: 266) Brown (1894: 389), *Cyanthillium patulum,* and *Vernonia pratensis* were obtained from six specimens (two duplicates for each species) from K and P herbaria (acronyms following Thiers (2025, continuously updated)). Samples were labelled with an abbreviation of the genus plus the last two numbers of the herbarium voucher (Appendix 1, Tables 1, 2).

Sample preparation and microscopic observations:—Pollen grains were treated with the acetolysis method (Erdtman 1960), following the modifications proposed by Melhem *et al.* (2003). Measurements and light microscopy photomicrographs were performed under a Leica LMD7 Microdissection Microscope and a Leica DFC 7000T video camera supported by LAS software. Permanent slides were deposited in the pollen reference collection of the Bioimaging Lab, Royal Botanic Gardens, Kew, United Kingdom. For scanning electron microscopy (SEM), acetolysed pollen grains were washed and placed on a metal stub with carbon cement and sputter coated with platinum (10 nm) using a quorum-Q150t es Series. Cypselae samples were similarly coated. Samples were imaged under a Hitachi 8230 Scanning Electron Microscope, with a 5 kV electron beam, at the Bioimaging Lab, Royal Botanic Gardens, Kew.

Pollen analysis:—Measurements were taken under Light Microscopy on 25 randomly selected pollen grains from each specimen. The equatorial axis (EA) was measured in equatorial and polar views (EV and PV, respectively) and the polar axis (PA) in equatorial view, excluding spines. Ten measurements of pollen morphometric parameters were also made: length and width of the pori, length and width of the poral lacuna, size of lophae and lacunae, thickness of the nexine and sexine layers (excluding spines, following Kingham 1976) and the spine length measured separately. Exine measurements were made in the mesocolpium region. Lumen and muri of the reticulum were imaged using SEM.

The measurements of polar and equatorial axes were statistically analysed for the arithmetic mean (x), average standard deviation (Sx), sample standard deviation (s), coefficient of variability (V%), and 95% confidence interval (CI) (Vieira 2011, Zar 2010). For exine characters, the arithmetic mean and range were calculated for each pollen grain size class and exine (sexine + nexine). The CI and Sx are present in descriptions in the following order: [EA in EV x PA in EV] x [EA in PV].

Pollen terminology follows Punt *et al.* (2007) and Halbritter *et al.* (2018). Pollen shape classes and amb types follow Erdtman (1952); colpus length categories follow Mark *et al.* (2012); and sculpturing and apertures type specific to Vernonieae follow Robinson *et al.* (2016). The endoaperture classes and sexine/nexine thickness index follow Antonio-Domingues *et al.* (2022). Cypselae and trichomes terminology follows Pope (1983) who proposed a classification of these structures for erlangeoid genera.

Results

Pollen description:—Pollen grains are monads, medium-sized [35.1 (38.1 µm ± 1.5) 41.0 × 32.7 (35.5 µm ± 1.4) 38.2] × [34.0 (37.1 µm ± 1.5) 40.2] (Table 1), radially symmetrical, isopolar, oblate spheroidal (Table 1), amb circular or subcircular, circular to ellipsoidal in equatorial view, angulaperturate, polar area very large. Apertures 3-brevicolporate or 3-zonoporate, pori circular to ellipsoidal, elongated to equator or polar direction, narrow, short, and non-constricted, apices rounded, margo absent, membrane granulate, protruding aperture absent; operculum not observed; poral lacunae elongated along equatorial or polar axis, interlacunar gaps present or absent. Exine 4.1–8.1 µm thick, sexine 1.8–6.6 times thicker than nexine, sculpture echinolophate; spine 1.3–2.1 µm (Table 2), base non-constricted, apices acute; lopha (ridge) 2.8–3.3 µm, continuous (interlacular ridges absent) or discontinuous (interlacular ridges present), nanoreticulate-perforate (0.1–0.3 µm), lacuna (lumina) 8.1–9.4 µm. A summary of the measurements is shown in Tables 1 and 2.

TABLE 1. Dimensions (µm) of pollen grains in equatorial and polar view using light microscopy for *Bothriocline longipes*, *Bothriocline madagascariensis* (=*Vernonia pratensis*), and *Cyanthillium patulum*. Specimens were identified by the species name and the last two numbers of the herbarium voucher (see Specimen analysed). Equatorial View (EV), polar view (PV), Confidence Interval (CI) at 95% of probability of the lowest sample values (IC-) and highest sample values (IC+), arithmetic mean (x), average standard deviation (sx), sample standard deviation (s), coefficient of variability (V%), species *affinis* (^{a}), oblate spheroidal (OS).

Specimen	Equatorial Axis (EV)			Polar Axis (EV)			P/E	Form	Equatorial Axis (PV)		
	CI - ($x \pm sx$) CI +	s	V%	CI - ($x \pm sx$) CI +	s	V%	x		CI - ($x \pm sx$) CI +	s	V%
B. longipes 04	41.5 (42.1 ± 0.3) 42.8	1.5	3.6	38.7 (39.3 ± 0.3) 40.0	1.5	3.8	0.9	OS	40.7 (41.1 ± 0.3) 42.1	1.7	4.0
B. longipes 10	40.0 (41.0 ± 0.3) 41.5	1.4	3.4	37.0 (37.4 ± 0.2) 37.9	1.0	2.8	0.9	OS	39.7 (40.3 ± 0.3) 40.8	1.3	3.3
C. patulum 22	34.7 (35.5 ± 0.3) 35.9	1.4	4.0	33.3 (33.8 ± 0.2) 34.3	1.2	3.7	1.0	OS	34.4 (34.9 ± 0.2) 35.4	1.2	3.6
C. patulum 75	35.0 (35.9 ± 0.3) 36.5	1.5	4.2	31.7 (42.4 ± 0.4) 33.2	1.9	5.8	0.9	OS	34.1 (34.9 ± 0.4) 35.8	2.1	5.9
B. madagascariensis 19	35.2 (35.7 ± 0.2) 36.2	1.2	3.4	33.0 (33.5 ± 0.2) 34.0	1.2	3.6	0.9	OS	33.8 (34.5 ± 0.3) 35.1	1.5	4.4
B. madagascariensis 22	37.8 (38.5 ± 0.3) 39.2	1.7	4.4	35.9 (36.5 ± 0.3) 37.1	1.5	4.0	1.0	OS	36.2 (36.9 ± 0.3) 37.5	1.5	4.1

TABLE 2. Dimensions (µm) pollen grains aperture, spine, reticulum and exine layers in equatorial view using light microscopy. Specimens were identified by the species names and the last two numbers of the herbarium voucher (see Specimen analysed). Length (L), Width (W), Sp (Spine), Lumen (Lu), Ridge (Ri), Lacunae (La), Sexine (S), Sexine/Nexine (S/N), Nexine (N), Exine (E).

Specimen	Pore	Poral lacuna	Muri	Lophae	Exine
	W–L	W–L	Sp–Lu	Ri–La	S (S/N) N–E
B. longipes 04	7.2–4.2	11.7–8.9	1.3–0.1	2.8–9.4	5.2 (4.1) 1.3–6.5
B. longipes 10	6.5–4.1	10.4–8.1	1.9–0.2	3.3–8.8	5.3 (3.6) 1.5–6.8
C. patulum 22	4.8–5.5	9.9–6.9	1.5–0.3	2.8–7.5	4.3 (3.7) 1.1–5.4
C. patulum 75	4.5–5.7	10.4–5.4	2.1–0.2	2.8–7.3	3.6 (2.8) 1.4–5.0
B. madagascariensis 19	4.0–3.1	5.3–9.8	–	2.9–8.1	4.2 (2.3) 1.8–6.0
B. madagascariensis 26	3.9–3.9	6.6–10.3	1.2–0.3	2.9–9.3	4.6 (2.7) 1.7–6.2

Bothriocline longipes (Fig. 1 A–C, 2 A–D)

Pollen grains axes [40.6 (41.5 µm ± 0.4) 42.4 × 37.4 (38.4 µm ± 0.4) 39.3] × [39.9 (40.8 µm ± 0.4) 41.7]; 3-brevicolporate, poral lacunae elongated to equator, interlacunar gaps present, pori ellipsoidal, slightly elongated along polar direction. Exine 6.6 µm thick, sexine 3.8 times thicker than nexine; ridges of the sculpture continuous (interlacunar ridges absent).

Vernonia pratensis (Fig. 1 D–F, 2 E–H)

Pollen grains axes [35.9 (37.1 µm ± 0.5) 38.2 × 33.8 (35.0 µm ± 0.5) 36.1] × [34.5 (35.7 µm ± 0.5) 39.7]; 3-brevicolporate, poral lacunae elongated to equator, interlacunar gaps present, pori ellipsoidal, slightly elongated in polar direction. Exine 6.1 µm thick, sexine 2.5 times thicker than nexine; ridges of the sculpture discontinuous (interlacunar ridges present).

Cyanthillium patulum (Fig. 1 G–I, 2 I–L)

Pollen grains axes [34.7 (35.6 µm ± 0.4) 36.4 × 32.1 (33.1 µm ± 0.4) 34.1] × [33.9 (34.9 µm ± 0.4) 35.9]; 3-porate, poral lacunae elongated along polar direction, interlacunar gaps absent, pori circular. Exine 5.2 µm thick, sexine 3.1 times thicker than nexine; ridges of the sculpture continuous (interlacunar ridges absent).

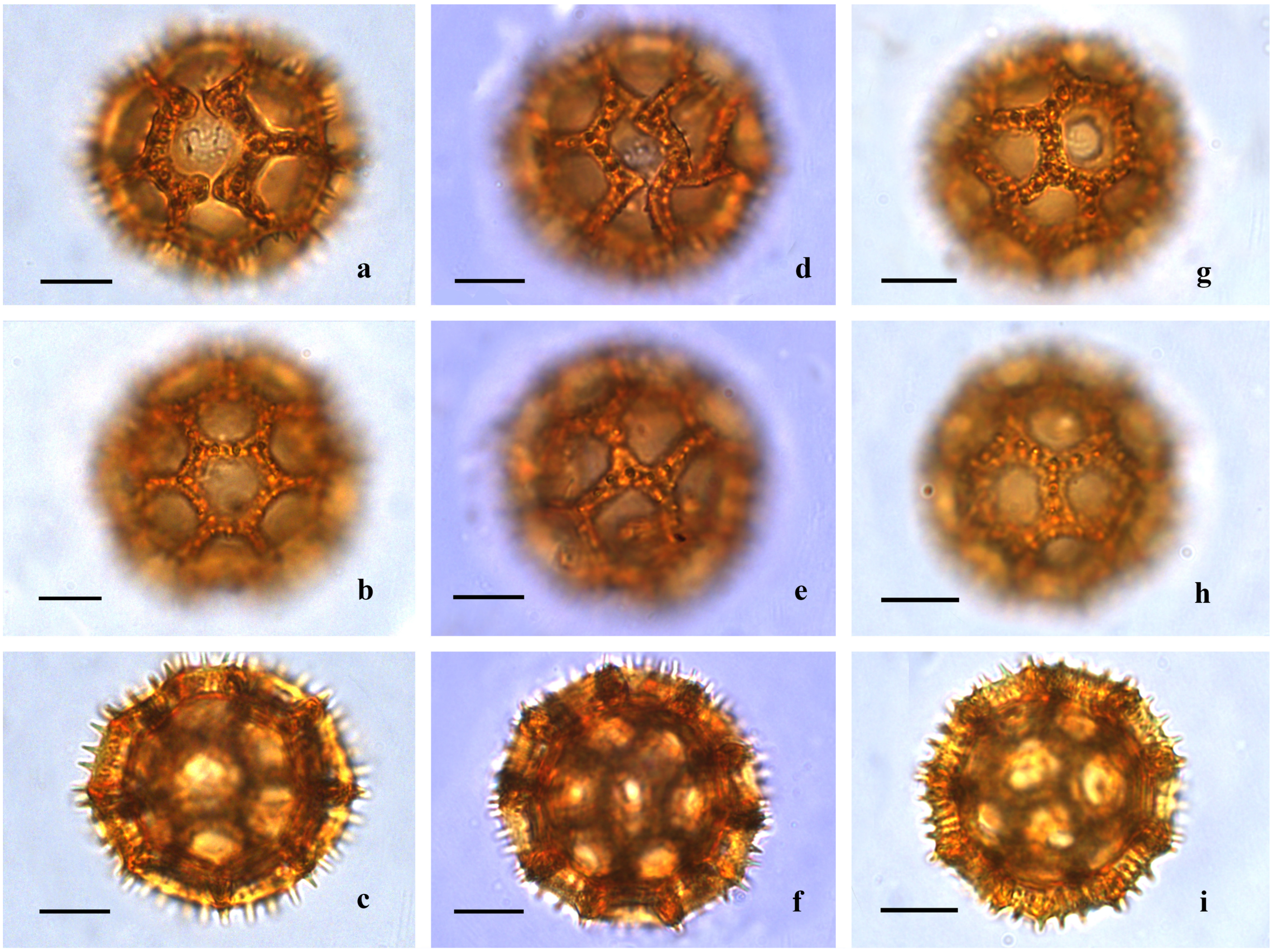

FIGURE 1. Light microscopy of the pollen grains. **A**–**C.** *Bothriocline longipes*. **A.** General view of the porus, porus membrane, and lacunae with interlacunar gaps; equatorial view. **B.** General view of the apocolpium and the continuous ridges; polar view. **C.** Optical section: equatorial view. **D**–**F.** *Bothriocline madagascariensis* (= *Vernonia pratensis*). **D.** General view of the porus, porus membrane, and lacunae with interlacunar gaps; equatorial view. **E.** General view of the apocolpium and the discontinuous ridges; polar view. **F.** Optical section; equatorial view. **G**–**I.** *Cyanthillium patulum*. **G.** General view of the porus, porus membrane, and lacunae without interlacunar gaps; equatorial view. **H.** General view of the apocolpium and the continuous ridges; polar view. **C.** Optical section; equatorial view. Scale bars—10 µm.

Cypselae description:—*Bothriocline longipes* (Fig. 3 A–B, Table 3). Cypselae obovoid, bluntly angled, 1.2–1.8 × 0.6–0.8 mm, 4–5(–8)-ribbed, ribs low and broader than grooves, rounded above with shallow apical rim formed by fusion of the ribs, grooves with unicellular trichomes (type 1) with striate cuticle (cypsela type 3). Pappus setae uniseriate, 1.2–2 mm long, stramineous, setose, barbellate, caducous, straight, apex acute.

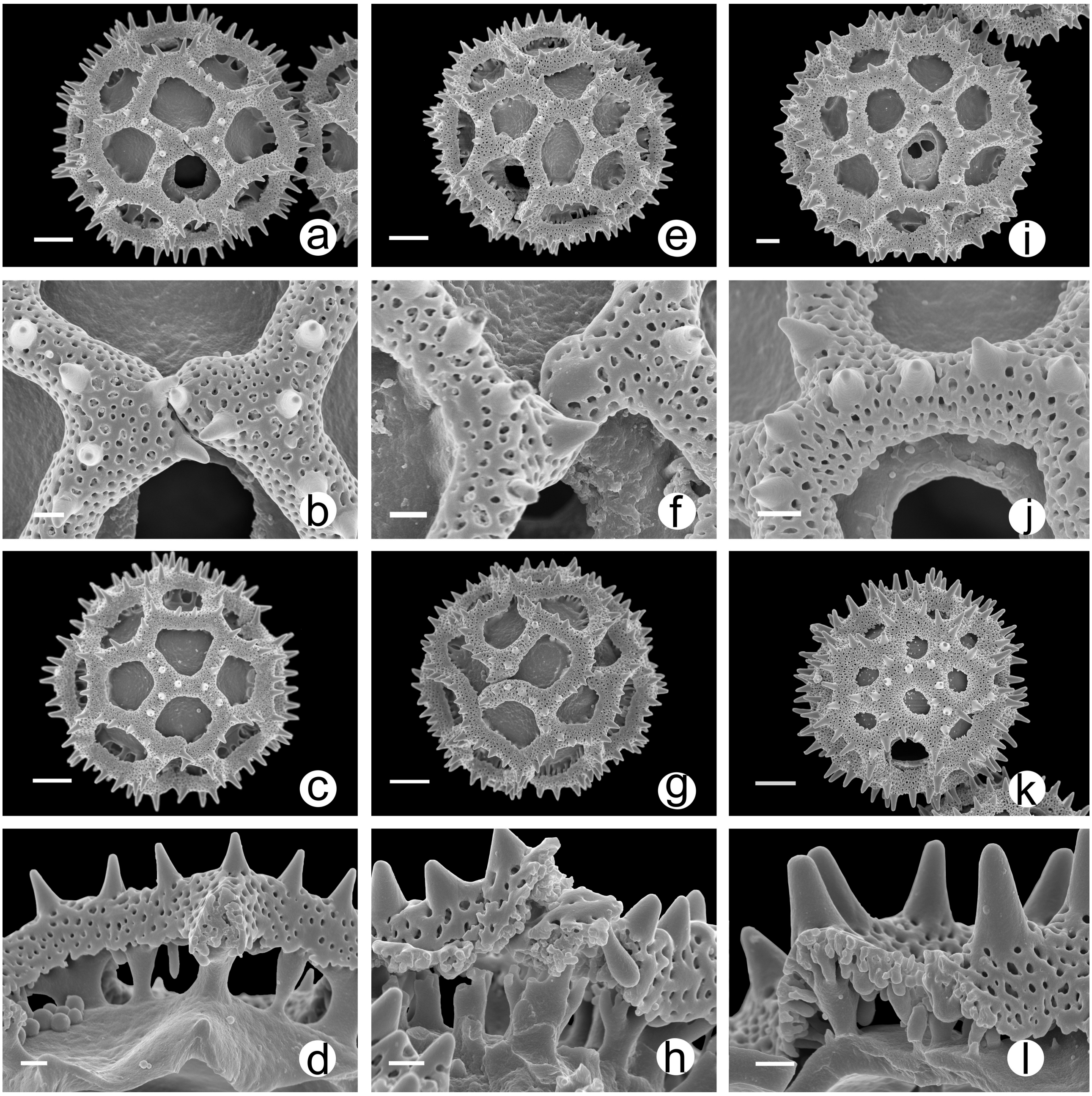

FIGURE 2. Scanning electron microscopy of the pollen grains. **A–D.** *Bothriocline longipes*. **A.** General view of the porus, porus membrane, lacunae with interlacunar gaps, and the continuous ridges; equatorial view. **B.** Detail of lacunae with interlacunar gaps, equatorial view. **C.** General view of apocolpium and the continuous ridges; equatorial view. **D.** Detail of columellae. **E–H.** *Bothriocline madagascariensis* (= *Vernonia pratensis*). **E.** General view of the pori, poral membrane, lacunae with interlacunar gap, and the continuous ridges; oblique equatorial view. **F.** Detail of lacunae with interlacunar gaps; equatorial view. **G.** General view of the apocolpium and the discontinuous ridges, polar view. **H.** Detail of columellae. **I–L.** *Cyanthillium patulum*. **I.** General view of the pori, poral membrane, lacunae without interlacunar gaps; equatorial view. **J.** Detail of lacunae without interlacunar gaps; equatorial view. **K.** General view of apocolpium and the continuous ridges; oblique polar view. **L.** Detail of columellae. Scale bars—**A**, **C**, **E**, **G**, **I**, **K.** = 5 μm; **B**, **D**, **F**, **H**, **J**, **L.** = 5 μm;

Vernonia pratensis (Fig. 3 C–D, Table 3)

Cypselae oblong-obovoid, angled, slightly curved, 1.4–1.7 × 0.5–0.6 mm, 7–8-ribbed, ribs prominent and broader or equalling the grooves, rounded above with shallow apical rim formed by fusion of the ribs, grooves densely covered by unicellular trichomes (type 1) with striate cuticle (cypsela type 3). Pappus setae uniseriate, 1.2–2 mm long, light stramineous, setose, barbellate, caducous, straight, apex acute.

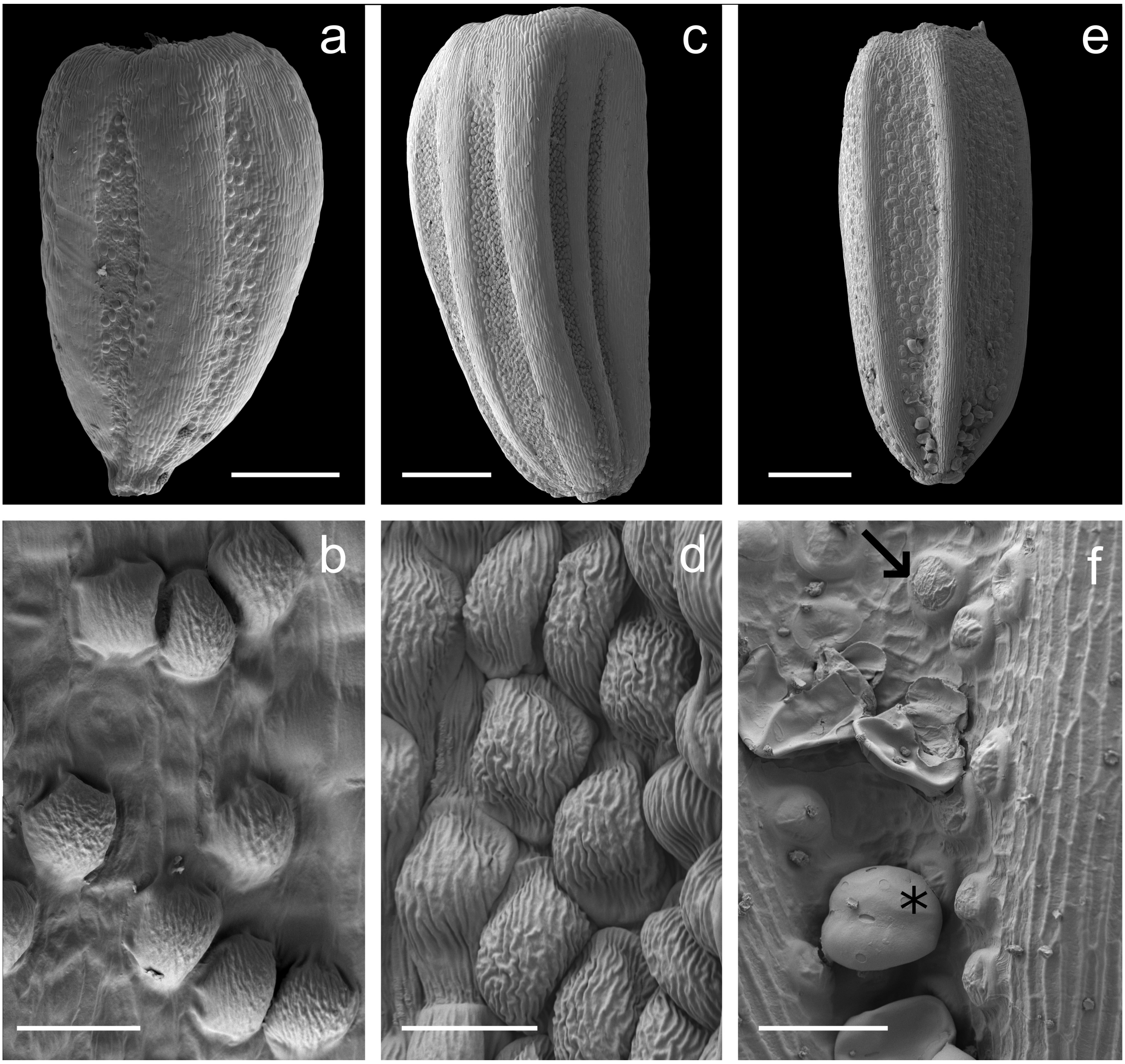

FIGURE 3. Scanning electron microscopy of the cypselae. **A**, **B.** *Bothriocline longipes.* **A.** Cypsela. **B.** Detail of groove with unicellular trichome with striate cuticle. **C.**, **D.** *Bothriocline madagascariensis* (=*Vernonia pratensis*). **C.** Cypsela. **D.** Detail of groove with unicellular trichome with striate cuticle. **E**, **F.** *Cyanthillium patulum.* **E.** Cypsela. **F.** Detail of groove with enlarged and dome-shaped epidermal cells with striate cuticle (infundibular idioblast sensu Redonda-Martínez *et al.* 2017) (arrow) and bilobed glandular trichome (asterisk). Scale bars **A**, **C**, **E.** = 250 µm; **B.** = 25 µm; **D**, **F.** = 20 µm.

Cyanthillium patulum (Fig. 3 E–F, Table 3)

Cypselae narrowly oblong-obovoid, angled, 1–1.5 × 0.5–0.6 mm, 4–6-ribbed, ribs prominent and narrower than grooves, ± truncate above, without distinct apical rim, ribs not fused apically, grooves with some modified, enlarged and dome-shaped epidermal cells with ribbed cuticle (appearing concave in dry cypselae; infundibular idioblast sensu Redonda-Martínez *et al.* 2017), bilobed glandular trichomes (type 2) at the base of the grooves (cypsela type 1). Pappus setae uniseriate, 2–3 mm long, white, setose, serrulate, somewhat twisted, caducous, apex acute.

TABLE 3. Cypselae characteristics and trichomes. Type classification follows Pope (1983).

Character	*Bothriocline longipes*	*Bothriocline madagascariensis*	*Cyanthillium patulum*
Cypsela type	type 3	type 3	type 1
Shape	obovoid	oblong-obovoid	narrowly oblong-obovoid
Apical rim	shallow formed by fusion of ribs	shallow formed by fusion of ribs	indistinct
Relative size of ribs	broader than grooves	broader or equalling grooves	narrower than grooves
Trichome on cypsela	unicellular with striate cuticle (type 1)	unicellular with striate cuticle (type 1)	bilobed glandular (type 2)
Modified epidermal cells on cypsela	absent	absent	infundibular idioblasts
Trichome complement on vegetative parts and type	asymmetric T-shaped (type 8)	flagelliform with uniseriate stalk (type 7) and asymmetric T-shaped (type 8)	symmetric T-shaped (type 9)

Discussion

Vernonia pratensis was first described as *Cyanopis madagascariensis* Candolle (1836: 69), based on a specimen collected by Bojer in Madagascar in 1835. However, *Cyanopis* Blume (1828: 6) is a superfluous name for *Cyanthillium* Blume (Blume 1826: 889), a genus traditionally considered, until the end of the 20th century, a synonym of *Vernonia*. Thus, Klatt (1892) proposed a replacement name, *Vernonia pratensis* Klatt, for *C. madagascariensis* due to *Vernonia madagascariensis* Lessing (1831: 644) (= *Distephanus madagascariensis* (Less.) H.Rob. & V.A.Funk in Funk *et al.* (2012: 452)) taking priority. *Vernonia pratensis* was placed in the genus *Bothriocline* sect. *Bothriocline* by Jeffrey (1988) as *B. madagascariensis* (DC.) Jeffrey (1988: 266). However, Robinson (1990, 1999) considered *V. pratensis* as a synonym of the south-east Asian *Cyanthillium patulum*, which was then taken up by CWG (2024) and POWO (2024).

Despite belonging to different subclades in the most recent molecular phylogenetic study of Vernonieae (Keeley *et al.* 2021), *Bothriocline* (Erlangeinae clade) and *Cyanthillium* (combined Erlangeinae/Centrapalinae clade) share morphological similarities (e.g., leaves with T-shaped trichomes, acuminate to cuspidate phyllaries with pale or reddish margins). However, characters used to set both genera apart have exceptions: species of *Cyanthillium* are annual or rarely short-lived perennial herbs (*C. wollastonii* (Moore 1911: 105) Robinson *et al.* 2016: 67), while species of *Bothriocline* are most commonly perennial herbs or shrubs, but sometimes annual herbs (e.g., *B. emilioides* Jeffrey (1988: 266), *B. laxa* Brown (1894: 388), *B. quercifolia* Jeffrey (1988: 261)). *Cyanthillium* has alternate leaves, whereas *Bothriocline* frequently has leaves arranged opposite, or in whorls of three, but sometimes alternate (e.g., *B. emilioides*, *B. steetziana* Wild & Pope (1977: 319)), or opposite at the base and alternate above (e.g., *B. mbalensis* (Wild & Pope 1977: 318) Jeffrey 1988: 261). Corollas of *Cyanthillium* have apical hairs, a character absent in *Bothriocline* except for *B. pectinata* (Hoffman 1906: 196) Wild & Pope (1977: 320). *Vernonia pratensis* is an annual herb, with alternate leaves and corollas without apical hairs, a combination of characters that does not unambiguously assign this species to either *Bothriocline* or *Cyanthillium*. Pollen and cypsela are more reliable sources of characters to distinguish *Cyanthillium* and *Bothriocline*.

The pollen grains of *Cyanthillium* and *Bothriocline* are 3-aperturate, echinolophate, with irregularly disposed lacunae, notably at the poles. The main difference between the two genera is the presence of an inconspicuous colpus formed by interlacunar gaps, which are present in *Bothriocline* and absent in *Cyanthillium* (Robinson 1990, Robinson *et al.* 2016). This characteristic explains why Kingham (1976) described the pollen grains of *Bothriocline* as tricolporate (group IV). Robinson (1990) and Robinson *et al.* (2016) also cite that the disposition of the columellae is different in both genera: in *Cyanthillium* they are present only at the intersection of the muri, and in *Bothriocline* the columellae invade the submural space. Our pollen analysis of *B. longipes* and *Vernonia pratensis* confirms the presence of interlacunar apertural gaps and the presence of a brevicolporus in both species. However, the disposition of columellae seems more variable than previously described: they are not restricted to intersections of muri in *Cyanthillium patulum*, neither in *C. cinereum* (Antonio-Domingues *et al.* in prep.) and there are no obvious differences among the disposition of columellae in *C. patulum*, *B. longipes,* and *V. pratensis*.

Pope (1983) provided a detailed study of cypselae and trichomes in Erlangeinae, classifying the cypselae into 19 types and the trichomes into 9 types. Species of *Bothriocline* have type 3 cypselae (except *B. pectinata* with type 2 cypselae). Type 3 cypselae have rounded to ± truncate apices with a low apical rim or a distinct apical cup, ribs are low and broader than or equal to the shallow intermediary grooves, which are filled with unicellular trichomes (type 1) with striate cuticle. The pappus is absent or composed of caducous barbellate setae. Type 2 cypselae differ by the absence of type 1 trichomes in the grooves, covered only by infundibular idioblasts (Pope 1983). In our analysis, the cypselae of *B. longipes* are type 3 whereas *Cyanthillium patulum* has type 1 cypselae (ribs narrower than grooves and not fused apically, grooves covered by infundibular idioblasts and bilobed, type 2 trichomes). *Vernonia pratensis* is characterized by cypselae with prominent ribs, broader and/or equal in width to the grooves and rounded above with a shallow apical rim formed by fusion of the ribs and grooves covered by type 1 trichomes (with striate cuticle), similar to type 3 cypselae observed in *Bothriocline* (Table 3).

Additionally, the trichome complement (i.e., range of trichome types present in a taxon) is also frequently informative at different taxonomic levels in Vernonieae (Faust & Jones 1973, Redonda-Martínez *et al.* 2012, Wagner *et al.* 2014). *Cyanthillium* has only T-shaped trichomes (type 9 *sensu* Pope (1983)) (Robinson 1990; Robinson *et al.* 2016) whereas *Bothriocline* have ± asymmetric T-shaped trichomes (type 8 *sensu* Pope (1983)) and/or flagelliform trichomes with uniseriate stalks bearing an erect terminal cell (type 7 *sensu* Pope (1983)). *Vernonia pratensis* has an indumentum composed of type 7 and 8 trichomes on stems, leaves, flowering branches and on outer phyllaries, like in *Bothriocline* (Table 3).

Geographically, *Bothriocline* is distributed in Tropical and subtropical Southern Africa with a centre of diversity in central and eastern Africa (Lisowski 1992, Jeffrey & Beentje 2000). The number of species in the genus is a matter of debate: ca. 30 species (Pope 1992, Jeffrey & Beentje 2000), ca. 50 (Lisowski 1992), or 60–70 (CWG 2024, POWO 2024, WFO 2024), which points to an urgent need for taxonomic revision. On the other side, *Cyanthillium* has 11 species in tropical and subtropical regions of the Eastern Hemisphere with one widespread weed, *C. cinereum* (Linnaeus 1753: 862) Robinson (1990: 352) in tropical regions, including Madagascar (Robinson 1999a, POWO 2024). *Cyanthillium patulum*, one of the species into which *Vernonia pratensis* was placed in synonymy (Robinson 1990, 1999a), occurs in tropical and subtropical Asia and north-western Pacific islands (Ghafoor 2015, Koyama *et al.* 2016). *Vernonia pratensis* is restricted to the Analamanga region in central Madagascar. The only species of *Cyanthillium* in Madagascar is *C. cinereum* (a widespread, weedy species) and, to date, no species of *Bothriocline* have been recorded in Madagascar.

Based on the morphological study presented here, *Vernonia pratensis* belongs to the genus *Bothriocline* due to 3-brevicolporate pollen grains with interlacunar apertural gaps and cypselae with broad ribs apically fused and grooves covered by unicellular trichomes with striate cuticle (type 3 cypsela sensu Pope (1983)). The trichome complement also supports this placement. The combination for *V. pratensis* in *Bothriocline* was already made by Jeffrey (1988) and he placed this species in *B.* sect. *Bothriocline* (based on characteristics of the cypsela and ecology).

Bothriocline madagascariensis (DC.) Jeffrey (1988: 266). *Cyanopis madagascariensis* Candolle (1836: 69). *Vernonia pratensis* Klatt (1892: 295), non Hiern (1898: 523), nom. illeg. [= *Vernonia kandtii* Muschler (1911: 87)]. Type:—MADAGASCAR. 'Croît dans les prairies et les savannes aux bords des forêts à l'île de Madagascar', 1835, *Bojer* s.n. (holotype G-DC-G00464354!; isotypes K00272831!, P00434074!) (Fig. 4).

Annual herb, up to 50 cm tall. Rootstock a short, slender taproot, base of one or a few flowering stems. Stems poorly to moderately branched, greenish, sometimes reddish towards base, sparsely pubescent, indumentum composed of ± asymmetric T-shaped trichomes and flagelliform trichomes with uniseriate stalks bearing an erect terminal cell, somewhat four-angled, sulcate. Leaves simple, alternate, shortly petiolate, petiole 0.15–1.3 cm long; blade narrow to wide ovate, unfrequently elliptic, 2–5.5 × 0.9–2.8 cm, venation eucamptodromous, midrib thick and flattened, furrowed, prominent abaxially, slightly prominent adaxially, secondary veins 6–8 pairs, membranaceous, somewhat discolour, both sides very sparsely pubescent, slightly denser along midribs and secondary veins, indumentum composed of ± asymmetric T-shaped trichomes and flagelliform trichomes with uniseriate stalks bearing an erect terminal cell, adaxial surface green, abaxial surface green-greyish, densely dark reddish glandular punctate, margin serrate, serrulate towards base, apex acute, base cuneate. Inflorescence terminal, capitula organised in lax, irregular corymbs; flowering branch 4.5–17.5 cm long, four-angled, green, frequently slightly reddish, sparsely pubescent,

FIGURE 4. Illustration of *Bothriocline madagascariensis* (= *Vernonia pratensis*) in Drake del Castillo (1900: plate 479). © The Board of Trustees—RBG, Kew.

indumentum composed of ± asymmetric T-shaped trichomes and flagelliform trichomes with uniseriate stalks bearing an erect terminal cell, leaf-like bracts 1–2.6 × 0.4–1.1 cm. Capitula 5–12 per corymb, pedunculate, peduncle 1.4–3.2 cm long, 4-angled, costate, green to reddish, with similar indumentum as branches but denser, subinvolucral bracts 1–4, lanceolate to linear, 1.3–1.6 mm long, apex attenuate, densely pubescent, somewhat deciduous; involucre (2.7–)4–5 mm tall, (1.5–)3–6 mm diam., ovoid; phyllaries weakly imbricate, 4-seriate, upper third vinaceous and diminutively furfuraceous, apex acuminate, margin scarious, outer phyllaries wide ovate to ovate, 1.7–2.1 × 0.7–1.1 mm, glabrate to very slightly pubescent, indument composed of ± asymmetric T-shaped trichomes and flagelliform trichomes with uniseriate stalks bearing a long erect terminal cell, inner phyllaries ovate to lanceolate, 2.8–5 × 0.9–1.5 mm, glabrate; receptacle fimbrillate, fimbria up to 0.1 mm. Florets 12–16 per capitulum; corolla lilac, actinomorphic, corolla tube 2–2.8 × 0.4–0.6 mm, glabrous or stipitate-glandular, corolla lobes 5, 0.6–0.8 mm long, glabrous or sparsely glandular, apex acute; anthers 5, reddish purple, apical anther appendage triangular vitreous, anther base calcarate, rounded; style lacking a basal node, style shaft 2– 2.6 mm long, lilac, glabrous throughout except for pubescence upper ca. 0.2–0.3 mm beneath style-arms, style-arms 0.6–1 mm long. Cypselae oblong-obovoid, angled, slightly curved, 1.4–1.7 × 0.5–0.6 mm, 7–8-ribbed, ribs prominent and broader or equalling the grooves, light stramineous, rounded above with shallow apical rim formed by fusion of the ribs, grooves densely filled with unicellular trichomes (type 1, sensu Pope (1983)) with striate cuticle (type 3 cypsela sensu Pope (1983)), dark green; carpopodium inconspicuous; pappus setae uniseriate, 1.2–2 mm long, light stramineous, setose, barbellate, caducous, apex acute.

Etymology:—The epithet *madagascariensis* means occurring in Madagascar.

Vernacular names:—'Volontany tanety' (*Alleizette* 104), 'Volontamantanety' (Humbert 1923).

Distribution, habitat, and phenology:—The species occurs in grasslands of the Central Highlands of Madagascar, frequently associated with disturbed lands (Humbert 1960). Humbert (1923) mentions *Vernonia pratensis* in his "Liste D" of *Vernonia* spp. restricted to the Central Highlands, between the latitudes of 18°S and 21°S. Flowering between January and July.

Preliminary Conservation status:—*Bothriocline madagascariensis* is an annual herb, endemic to Madagascar. The species is known from eight old collections, one of which has no collection date (*Baron* s.n.) and seven were collected between 1835 (*Bojer* s.n.) and 1913 (*Perrier de la Bâthie* 3168, 3200). According to available data, this species is recorded from Central Madagascar (Imerina or the former province of Antananarivo) at ca. 1,200 m a.s.l. It occurs in grasslands, cultivated fields, and is also known as a ruderal plant. The extent of occurrence (EOO) and area of occupancy (AOO) are estimated to be around 20 km^2 each, both fall within the threshold for Endangered status under IUCN's criterion B. The majority of localities of the species are not precise across the "Imerina or Central Madagascar" which is a large area, except for one specimen known from Nanisana (*Alleizette* 104), where the species is threatened by habitat loss due to intensive urban expansion, which could lead to continuing decline and result in the extirpation of occurrences. However, due to the ambiguity of the delimitation of the "Imerina or Central Madagascar" (a vast area), the lack of precise locality names, and the impact of intensive urbanisation combined with the last collections made a century ago (1913), the extinction risk of the species is uncertain. Therefore, *B. madagascariensis* is assessed as Data Deficient (DD). More research on population size, distribution and trends is recommended for this species.

Additional specimens examined:—MADAGASCAR. s.l., *R. Baron s.n.* (P00588921!); 'Central Madagascar', January 1882, *R. Baron 899* (K002068425!); [Analamanga:] 'Imerina, Pr. Tananarivo', 1880, *J.M. Hildebrandt 4078* (K002068424!, P00588924!, P00588925!); 'Nanisana' [Nandihizana], May 1905, *C. d'Alleizette 104* (P00588920!); 'Imerina, champs', c. 1200 m, July 1912, *J.M.H.A. Perrier de la Bâthie 2869* (P0588919!, TAN); 'Rudérale, Tananarive', April 1913, *J.M.H.A. Perrier de la Bâthie 3168* (K002068426!, P00588922!); 'Prairies, près des habitations, champs, Tananarive', Juin 1913, *J.M.H.A. Perrier de la Bâthie 3200* (P00588923!).

Nomenclatural comments:—IPNI (2024) and WFO (2024) report the name "*Vernonia pratensis* Drake", which would have been 'published' in *Histoire Physique, Naturelle et Politique de Madagascar* (published by Alfred and Guillaume Grandidier), volume 36, tome 6 (Atlas 4), plate 479 (Drake del Castillo 1900) (Fig. 4). However, there is no evidence from the plate that Drake del Castillo intended to publish a new species, as he was aware of the existence of *Vernonia pratensis* Klatt, which he cited one year prior (Drake del Castillo 1899: 243). Therefore, we conclude that it has not been validly published and should be considered as a designation (Art. 6.3).

Taxonomic comments:—Humbert (1923) considered this species morphologically closely related to *Vernonia leopoldi* (Sch.Bip. ex Walpers 1843: 949) Vatke (1875: 478) [= *Orbivestus leopoldi* (Sch.Bip. ex Walp.) Robinson (2009: 490)] and *Vernonia chinensis* Lessing (1831: 105, 674) [= *Cyanthillium patulum*] but differing by the number of phyllaries, their width and pubescence. *Orbivestus* is defined by its divaricately seriate-cymose branching of the inflorescence, a characteristic absent in *Bothriocline madagascariensis*. Its morphological similarities with *C. patulum* are discussed above.

Annual species in *Bothriocline* are found in two different sections: *B.* sect. *Bothriocline* and sect. *Paludosae* Jeffrey (1988: 257). Species belonging to the latter are found in aquatic or semi-aquatic environments (seasonal ponds or swamp margins, etc.) and have narrow leaves. In *B.* sect. *Bothriocline*, *B. madagascariensis* has a similar habit to *B. quercifolia*, they both share an involucre of 3–4 series (only 4 in *B. madagascariensis*) of weakly imbricate phyllaries with their upper-third part vinaceous, but *B. quercifolia* has opposite inferior leaves (vs. alternate), higher number of florets per head (39–49 vs.12–16) and the phyllaries have wider scarious margins. They also have similar ecology, namely high altitude grasslands, and disturbed vegetation (Jeffrey 1988, Lisowski 1992). *Bothriocline quercifolia* occurs in Tanzania, Rwanda, Burundi and D.R. Congo, whereas *B. madagascariensis* is the sole member of the genus in Madagascar.

Two collections (*Baron* 899, *Bojer* s.n.) have leaves with longer petioles (1–1.3 vs. 0.15–0.5 cm long) but no other differences have been observed.

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APPENDIX I. List of specimens investigated in pollen and cypselae analyses

Bothriocline longipes (Oliv. & Hiern) N.E.Br. TANZANIA. Lushoto District, 9 June 1970, *Shabani 567* (K002613510); ibid., 2 September 1960, *C.D. Mgaza 371* (K002613504).

Cyanthillium patulum (Aiton) H. Rob. CHINA. Hong Kong, 19 October 1969, *S.Y. Hu 8300* (K002682375). THAILAND., Ban (?) Wan Mukdahan, 16 June 1932, *M.C. Lakshanakara 948* (K002683622).

Vernonia pratensis Klatt. MADAGASCAR. 'Imerina, champs', July 1912, *J.M.H.A. Perrier de la Bâthie 2869* (P00588919); Antananarivo, 1 April 1913, *J.M.H.A. Perrier de la Bâthie 3168* (K002068426).