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Cercestis blancii (Araceae), a remarkable new species from South Cameroon exhibiting a unique sequential monopodial growth and spiny aerial feeding roots

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ABSTRACT

Cercestis blancii Jeanson (Araceae) is described as a new species presenting unique life traits in the family concerning the repetitive alternation of one cataphyll and one foliage leaf along the monopodial stem. The young, narrow part of the stem is easily damaged by elements falling from the canopy or by other accidents, resulting in the proliferation of unusual branches leading to the colonization of moderate-sized and understory host tree branches. This specific habit is unique in the family Araceae. The freely hanging, narrow, sharply spined feeding roots are also unique in the family. Despite of its reduced species number, the genus *Cercestis* exhibits a high diversification of growth habits. This new species is described while taxonomic work on Araceae in Central Africa is enriched by the recent publication of the Araceae volume for the Flore du Gabon. This discovery confirms that Araceae is a remarkably diverse family not only from a taxonomic point of view but also regarding ecology and life forms.

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The family Araceae is globally poorly diversified in Africa compared to tropical America and Asia, totalling about 150 species, while there are already about 1200 species described for Asia and 2000 species for the Neotropics (Boyce and Croat 2011 onwards). The species number in the genus *Cercestis* is currently estimated to be 10 (Boyce and Croat, loc. cit., POWO, 2025). Most of these species were described more than a century ago (*C. afzelii* Schott, *C. congensis* Engl., *C. dinklagei* Engl., *C. ivorensis* A. Chev., *C. kamerunianus* (Engl.) N.E. Br., *C. sagittatus* Engl.). Only quite recently, two more species have been added, *C. taiensis* Bogner & Knecht (Bogner and Knecht 1995) and *C. hepperi* Jongkind (Jongkind, 2010). In addition to these eight species, Bogner (1986) transferred the genus *Rhektophyllum* with its two species, *R. mirabile* N. E. Br. and the more recently described *R. camerunense* Ntépé (Ntépé, 1981) to the genus *Cercestis*, making the new combinations *C. mirabilis* (N.E. Br.) Bogner and *C. camerunensis* (Ntépé) Bogner. Although this change was not accepted by Ntépé-Nyamè (1988) in her monograph for the Flore du Cameroun, it is the modern circumscription of the genus (e.g. Mayo et al. 1997, POWO 2025) and so it can be said that six *Cercestis* species were recorded in Cameroon by Ntépé-Nyamè (*C. camerunensis, C. congensis, C. dinklagei, C. ivorensis, C. kamerunianus* and *C. mirabilis*). In his treatment of *Cercestis* for the Flore du Gabon, Mayo (2024) suggested that *C. ivorensis* may be a West African species that has been confused with *C. kamerunianus* in Cameroon, thus reducing the *Cercestis* species previously described for Cameroon to five species. Despite of her thorough field studies of Araceae in most areas of Cameroon during many years for her thesis (Missé-Ntépé 1973) and Flore du Cameroun (Ntépé-Nyamè 1988), including the southern coastal forests, it seems that Colette Ntépé did not notice the existence of the new species presently described. A key to the species of *Cercestis* from Cameroon and neighboring countries is proposed at the end of this article.

During the Radeau des Cimes (Canopy Raft) expedition sponsored by ELF Foundation, between September and December 1991 in the forest east of Ebodje village in the Campo area in South Cameroon (Figure 2(A)), Patrick Blanc discovered a species of climbing Araceae which although assignable to the genus *Cercestis* (Figure 2(B)), was immediatly recognisable in the field as new because of two most striking and unique features: the presence of fierce barbed free-hanging roots and the unusual regular alternation of one cataphyll and one foliage leaf along the monopodial vegetative climbing stems.

Although this first collection was satisfactory in many respects, information was still lacking

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concerning its sequential growth habits, and more observations were necessary before describing the plant as a new species. Nothing happened concerning the further study of this new species during 26 years, until March 2017, when Blanc came back to the same area and observed more individuals with the help of Innocent Medjo. In March 2018, Blanc and Marc Jeanson visited the same area again with Medjo and more plants were studied. Finally, in September 2023, Jeanson, Ngansop and Blanc visited the area once more and were thus able to complete the necessary observations *in situ*.

In addition to the morphological and ecological observations made during the successive field trips, we were able to study herbarium specimens from P and YA, as well as collections from K, B and BR, which were sent on loan. Online collections from NL were also studied as well as online information available on GBIF. To better understand morphological characters and growth patterns of other *Cercestis* species, living collections from Muséum national d'Histoire naturelle (Paris, France), Jardin Botanique – Parc de la Tête d'Or (Lyon, France) and Jardin Botanique Jean Marie Pelt (Nancy, France) were also carefully studied, as well as photos from iNaturalist (2025).

The habitat of this species is the littoral forest south of Kribi. This species occurs as dispersed individuals in the more or less disturbed forests close to the ocean between Biyo and Campo, as well as in the well-preserved primary forests east of Ebodje, where the type specimen was collected in 1991. Some individuals have also been observed in partly disturbed forests east of Campo, around Nkol Elon village. All specimens seen since 1991 have thus been observed within an area covering less than 500 km2 (Figure 1).

The annual rainfall in Campo is about 2700 mm, and the climate is a typical four-seasonal equatorial climate (Oslisly, 2006). The forest type is the « forêt littorale » *sensu* Letouzey (1968), characterised by dominant tree species like *Lophira alata* and *Sacoglottis gabonensis*. Among the other common dominant trees reaching the forest canopy at 40 to 45 m above the soil, we can mention *Dialium pachyphyllum, Pycnanthus angolensis, Desbordesia glaucescens, Irvingia grandifolia, Erythrophloeum ivorense* and *Piptadeniastrum africanum* (Blanc, 1992). More global floristic studies of the tree species in the Campo area can be found in Tchouto et al. (2006) and Ngueguim et al. (2017). The abundance of *Lophira alata* is interpreted as originating from ancient human disturbances by Letouzey (1968), but the analysis of the forest limits evolution during Quaternary climatic changes is more congruent with an ancient forest refuge area interpretation for these littoral forests (Maley 1996). The high diversity and endemism of plant species in these South Cameroon littoral forests, extending southwards to Equatorial Guinea and Gabon, is also an argument in favour of ancient forest refuges during the Pleistocene dry periods (Sosef 1994; Maley 1996; Tchouto et al. 2006; Lachenaud 2017).

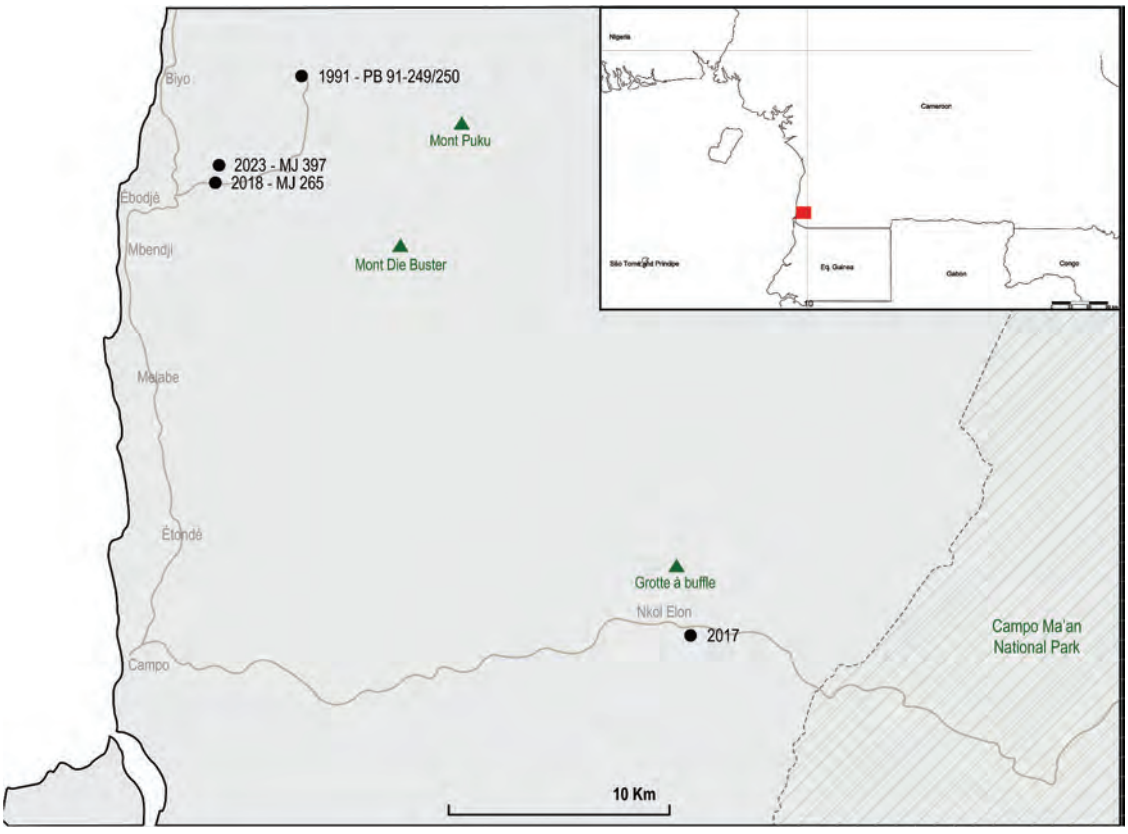

Figure 1. Distribution map of *Cercestis blancii*.

Cercestis blancii Jeanson, sp. nov.

Type: Cameroun. Région du Sud, Département de l'Océan, Arrondissement de Campo, Camp Akok au nord-est d'Ebodjé. Climbing on trees in primary forest, monopodial growth alternating a cataphyll and a foliage leaf, black shiny fierce barbed hanging feeding roots. Radeau des Cimes scientific expedition financed by Fondation ELF. N 2°37'02'"/E 9°54'05"'. 10 December 1991, *Patrick Blanc PB 91–249*, accession numbers P00878114, P00878112, P00878115, P00878113, P00878117, P00878116 (Holotype P! Isotype YA !)

Additional specimens: Cameroun. Région du Sud, Département de l'Océan, Arrondissement de Campo, Camp Akok au nord-est d'Ebodjé, N 2°37'02'"/E 9° 54'05"', 11 December 1991, *Patrick Blanc PB 91–250*, accession numbers P00878118, P00878119 (P!). Cameroun, Région du Sud, Département de l'Océan, Arrondissement de Campo, Est d'Ebodjé N 02.58087/E 009.86366. 10 Mars 2018, *Marc Jeanson, Innocent Medjo and Patrick Blanc MJ 265* (YA !). Cameroun, Région du Sud, Département de l'Océan, Arrondissement de Campo, Est d'Ebodjé, N 02.57062/E 009.86381, 9 September 2023, *Marc Jeanson, Eric Ngansop and Patrick Blanc MJ 397* (YA !).

Diagnosis

High climbing hemiepiphyte differing from all the other Cercestis species by its shiny black free-hanging feeding roots covered with fierce recurved spines, by the regular alternation along the stem of one cataphyll and one foliage leaf produced through a monopodial growth pattern and by the large dissociated brown berries.

Plant a hemiepiphyte, climbing vertically to 6–10 m on host tree trunk and then ± horizontally over host's lateral branches, producing leafy shoots, spiny feeder roots and flagella. **Stem** : stem surface with small, irregularly dispersed, < 1 mm long, spiny rugosities, monopodial with alternation of a long internode ending with a cataphyll and a short internode ending with a foliage leaf; long internodes 20–30 × 0.6–1.0 cm, short internodes 2–3 × 1.2–1.8 cm ; *flagella* up to 10 m long, 0.2–0.3 cm diam., bearing only cataphylls. **Roots**: *anchor roots* horizontally clasping the host, < 5 × 0.2 cm diam., mostly produced on short internode; *feeding roots* ±5–8 per plant, vertically free-hanging, 6–10 m long ×0.3–0.4 cm diam., rigid, shiny black with fierce spines, produced only on short internode. **Leaves** : *Cataphyll* 5–10 cm long, not keeled dorsally, with annular insertion at node, pale green, marcescent and later deciduous, veins parallel. *Foliage leaf*: petiole 40–60 cm long, terete, sheath short, 4–6 cm long, geniculate at base and apex; blade broadly cordate-sagittate, 40–50 cm long overall, 1.5 - 1.8 times longer than wide, widest at or just above petiole junction, midrib and secondary veins mostly impressed adaxially, prominent abaxially with red extrafloral nectaries, finer veins weakly prominent abaxially, margins convex; anterior lobe 30–35 cm long, shortly acuminate; posterior lobes 10–15 cm long, retrorse to slightly introrse, rounded apically; costal secondary veins 2–3 per side; basal secondary veins 5–6 per side, joining into a well developed basal rib with a long basiscopic denudation, innermost vein on each side often free, sinus distinct oblong-parabolic to spathulate. **Inflorescence** : (observed only at pre-anthesis) succeeding foliage leaf, 1 or more and then in condensed sympodium ; *peduncle* shorter than spathe, ±1/3 of spathe length ; *spathe* ± cylindric, lacking constriction, green with a few reddish extrafloral nectaries, 3.5 cm long; *spadix* as long as spathe, almost sessile, female zone ±1/6 of spadix length. **Flowers**: *male flowers*: androecium probably (2-) 3–-4-staminate, stamens densely arranged, free, connective thick, thecae lateral, dehiscing by apical slits; *female flowers* laxly arranged, ovary cylindric, light pink, slightly inclined towards spadix apex, unilocular, ovule solitary, anatropous, placenta basal, style very short, stigma entirely covering ovary apex, lobed by centrifugal furrows and with depressed centre. **Infructescence**: pendent, ovoid, with persistent green spathe enlarging during maturation, male spadix axis persistent; *berries* green near base, narrowing distally, maturing light brown and distinctly separated apically, pericarp 1–2 mm thick, whitish, not fleshy; *seed* elliptic,18–20 mm long, with large white cotyledonary hyperphyll, lacking endosperm.

Cercestis blancii has most often been observed growing on forest understory trees usually less than 15 m tall and with a trunk diameter less than 20 cm (Figure 2(C)). The most frequent host trees belong to different species of *Garcinia* (Clusiaceae), but *C. blancii* also climbs on other small understory trees belonging to Violaceae (*Rinorea spp.*), Myrtaceae, Sapindaceae, Rubiaceae and Ochnaceae for instance. The two large leaved species of *Cercestis* (*C. mirabilis* and *C. camerunensis*) are very easy to spot in the forest because their leaves are clearly visible under the main branches of the host trees while their stems climb vertically along the bare trunks. In contrast, *C. blancii* is usually almost invisible from the forest floor because its leaves unfold among the foliage of their supporting understory trees. For example, the leaves of the numerous plagiotropic branches of *Garcinia* spp. are retained for many years and, together with the leaves of other small surrounding trees, mostly obscure those of *C. blancii*. Once its vertically climbing stem reaches the insertion of the lower branches of these small trees, the *C. blancii* plant usually grows along these more or less horizontal lateral branches, most often between 6 and 10 meters above the forest floor. During its progression along the oblique or horizontal tree branches, the stem of



Figure 2. A - The Radeau des Cimes on the primary forest canopy during the scientific expedition from October to December 1991, Ebodje, Campo; B - Patrick Blanc holding the type specimen of *Cercestis blancii* on 10th December 1991, Ebodje, Campo; C - An adult plant creeping along the base of a bifurcating branch of a tree; D - An adult plant creeping and branching in the lower part of the crown of a small forest tree; E - Patrick Blanc showing the leaf display in a branched adult specimen of *Cercestis blancii*, his pants teared by the spiny hanging feeding roots, March 2017, Nkol Elon, Campo; F - Alternance of short and long internodes with the dry cataphyll and the foliage leaf petiole insertions; G - Brown basal geniculum along the first half of the foliage leaf sheath, the sheath base embracing the growing stem; H - Abaxial and adaxial surfaces of the leaves; I - Median and posterior lobes of the leaf, the median lobe midrib reaching 35 cm; J - Extrafloral nectaries mostly along the midrib and secondary veins; K - Secondary veins and faint network of interprimary and tertiary veins.

C. blancii produces new lateral leafy shoots (Figure 2 (D)). The foliage of the highest individuals is usually impossible to distinguish from the forest floor and they are only detected due to their shiny black fiercely spined free-hanging feeding roots growing vertically downward and reaching the forest floor. These long spiny feeding roots are ultimately the only contact the plant has with the ground since the initial stem progressively decays so that the adult plant becomes a secondary hemiepiphyte, a term deemed controversial by some authors (Zotz et al. 2021).

All the individuals display a regular alternation along the stem of one cataphyll and one foliage leaf but only the large foliage leaves are clearly noticeable on a living plant (Figure 2(E)). The cataphyll is 5 to 10 cm long with mostly identical parallel veins and its base embraces the stem (Figures 2(F),3(E)), an indication of monopodial growth. It is not two-keeled as in the prophylls characteristic of Monocotyledons (Arber 1925) and especially of the quite similar large prophylls of most species of *Philodendron* in which the stems are sympodial (Blanc 1978; Ray 1987b). The cataphyll is pale green but it soon withers and becomes brown and dry (Figure 2(F)) after which it is deciduous once the distal foliage leaf is fully expanded.

The foliage leaf blade is broadly cordate-sagittate, prominently lobed at the base and acuminate at the apex (Figure 2(H)). The texture is membranaceous, slightly fleshy and shiny. The blade reaches globally 40 to 50 cm in total length i.e. 30 to 35 cm for the median lobe and 10 to 15 cm for the posterior lobes (Figure 2 (I)). The midrib and the 3 to 4 primary lateral veins on each side are mostly sunken adaxially and prominently raised on the abaxial surface. The midrib and the major secondary veins have conspicuous shiny glandular spots (extrafloral nectaries) surrounded by a bright red aureole on the abaxial leaf surface (Figure 2(J)), and some smaller glands are scattered over the blade. Similar extrafloral nectaries on the leaves have been observed in other genera of Araceae like *Alocasia* (Belin-Depoux, 1978), *Philodendron* (Keeler et al., 2024; Gonçalves-Souza et al. 2016) and *Culcasia* (Gibernau et al. 2008). The possible presence of lacunar parenchyma and secretory canals would need further anatomical investigations. The interprimary veins, as well as the network of the reticulate tertiary veins, are faint and weakly raised on the abaxial surface (Figure 2 (K)). The basal veins of the posterior lobes merge with the margin of the blade. The petiole is 40 to 60 cm long and is terete and pulvinate with a basal and apical geniculum. The 2 to 3 cm long basal geniculum is yellowish, turning brown due to a multi-layered transversely furrowed drying epidermis; it covers the abaxial surface of the basal half of the shortly sheathing leaf base that embraces the stem (Figure 2(G)). The upper geniculum, connecting the petiole to the blade, is also 2 to 3 cm long but more slender.

The internode is 2 to 3 cm long between the cataphyll and foliage leaf, while the internode length reaches 20 to 30 cm between the foliage leaf and succeeding cataphyll (Figure 3(A,B,E)). Stem diameter differs according to the leaf type sequence (cataphyll or foliage leaf). The stem reaches its maximum diameter (12 to 18 mm) in the short internode between cataphyll and foliage leaf insertion, but just above the latter, it abruptly decreases to 6 to 10 mm in diameter and remains narrow diameter until the emergence of the next cataphyll. The regular alternation of one cataphyll and one foliage leaf is thus easily observed at the growing stem apex. In the older parts of the stem the annular cataphyll scar can be seen below the annular petiole insertion as well as through the abrupt difference in stem diameter between long and short internodes. The stem surface is covered with small, irregularly dispersed spiny rugosities less than one mm long.

The growing apex of the stem emerges from the short foliage leaf sheath, and the internode between foliage leaf and succeeding cataphyll elongates as soon as the stem apex emerges (Figure 3(C)). As the elongation of this narrow internode continues, the stem tip remains enveloped by the next cataphyll (Figure 3(D)), and elongation is almost complete when the cataphyll reveals the young, not yet expanded foliage leaf (Figure 3(E)). The precocious elongation of the long internode before its tissues harden leads to numerous successive traumatisms affecting the young growing stems.

Both cataphyll and foliage leaves possess an axillary bud (Figure 3(F,G)), and this, together with their annular insertion on the stem, is an obvious indication of the monopodial growth habit of the stem before the eventual production of a terminal inflorescence. These axillary buds can produce new stems after traumatisms as the leafy stems climb or creep along the more or less horizontal branches of the supporting tree. These new axillary stems, issued by resting buds, first produce two or three cataphylls with reduced internodes, each of these cataphylls possessing an axillary bud that is also able to produce a new stem, hence, this frequent congested succession of stems (Figure 3(H,I)). Globally, each plant on a tree is thus the result of stem breakage or necrosis of the apical parts followed by new stems issued from the axillary buds of either cataphylls or foliage leaves or both along the main stems but it is also due to the outgrowth of some new axillary buds of the reduced scale leaves of each outgrowing previously dormant axillary buds (Figure 3(H-J)). The foliage of a plant climbing in small trees is thus most often distributed along 5 to 8 stems simultaneously growing horizontally along the tree branches in a more or less centrifugal pattern once the main initial stem has reached the zone of emergence of the lateral branches of the supporting tree (Figure 3(J,K)).



Figure 3. A - Succession of very short and long internodes along the monopodial stems; B - The drying and caducous cataphyll inserted at the base of each short internode and the persisting foliage leaf at its top; C - One stem node with drying basal cataphyll and upper foliage leaf sheathing petiole base, the growing apex emerging from its embracing short sheath; D - The unprotected long internode emerging from the leaf sheath, the new green cataphyll being folded around the next foliage leaf and stem apex; E - Precocious elongation of the fragile internode between the foliage leaf and the next cataphyll; F - The short thick internode with the axillary bud of the shedded cataphyll at its base and the axillary bud of the foliage leaf at the top, still protected by the turned down sheath; G - The short thick internode with the scars of both the lower cataphyll and the upper foliage leaf, each subtending an axillary dormant bud; H - Successive traumatisms in a short stem portion leading to at least four new shoots, two of them on the right being necrosed and the two on the left still growing; I - Multiple stems at the top small portion of an initial stem, these quite congested successive stems being issued from the previously dormant axillary buds of cataphylls, foliage leaves and the scale leaves of the new outgrowing buds; J - Successive clustered stems issued from the axillary buds ; notice the thick geniculum at the base of foliage leaves petioles; K - At least 7 simultaneously growing stems issued from a single initial stem along one meter in length; L - Innocent Medjo holding a long rolled flagellum with very narrow stem and producing only small cataphylls, March

The leafy stem may turn into a flagellum when it loses connection with the supporting branch. These flagelliform shoots are narrow (2 to 3 mm in diameter) and they produce only small cataphylls separated by long internodes, as is usual for other climbing Araceae (Blanc 1980). Once the flagellum reaches the ground, it continues to grow on the forest floor, still producing only cataphylls and some short adventitious roots. The flagellum may grow for a long distance, some flagella reaching about 10 m in length (Figure 3(L)) before it eventually comes into contact with a tree trunk, climbs vertically and produces its first foliage leaves, which are 8 to 10 cm long. Most often, the flagellum encounters a small shrub or a tree sapling, climbs along the narrow host stem and produces only two to three foliage leaves, each separated by a short internode and one or two cataphylls, after which its apex turns back into a flagellum (Figure 3(M)). This process is repetitive and creates a population of small plants climbing on shrubs up to about one meter above the ground, each one producing a rosette of only a few foliage leaves (Figure 3(N)). In more lighted situations, for instance, at the periphery of a treefall gap, the stem climbs at the base of a shrub or a small tree and immediately gives rise to the characteristic monopodial succession of a cataphyll and a foliage leaf separated by either a short or a long internode (Figure 3(O)).

Once it reaches a tree trunk, the stem climbs by adventitious clasping anchor roots, the usual type of stem fixation in climbing Araceae. These clasping roots are mostly initiated along the short internode between cataphyll and foliage leaf (Figure 4(A)), but some also appear along the long internode between foliage leaf and the next cataphyll, especially in juvenile specimens. They are about 2 mm diam. and usually less than 5 cm long when partly encircling horizontally the narrow supporting tree trunk or other support (Figure 4(B)). The characteristic shiny black and spiny feeder roots arise from the short internode and hang free down to the ground from the stems that creep along the tree branches (Figure 4(C,D,I,J)). They are very rigid, only 3 to 4 mm in diameter and usually vary between 6 and 10 meters long. These feeding roots are not numerous, usually totalling only five to eight for a well-developed and much-branched plant and are produced from the younger parts of the obliquely growing shoots. The characteristic emergences are initiated early, just a few centimeters behind the root tip, where the tissue is still soft and green (Figure 4(E)). Their shape is conical at first: the tip then hardens and becomes sharply pointed and oriented either perpendicularly to the root axis or recurved upwards or downwards, thus creating a fierce barbed root structure (Figure 4 (F-H)). These spiny emergences are shiny black, as is the cylindrical root itself. The wounding effect of these barbed free-hanging roots is accentuated by their more or less zigzag shape (Figure 4(J, K)), whence the tearing of clothes that results if a person collides with one of these almost invisible, dreadful, rigid barbed roots (Figure 2(E)). These fierce barbed roots may be a good protection against herbivorous mammals foraging on the forest floor. Once they reach the ground, they creep horizontally just under the leaf litter, their diameter increases and their surface becomes covered by a dense tomentum but they still produce spiny emergences on the upper side (Figure 4 (L)). At this creeping stage, the root produces secondary lateral roots on the lower side, which penetrate the soil (Figure 4(L,M)).

The structure of the inflorescence globally matches that of the other *Cercestis* species. It is terminal and appears just after a foliage leaf, and according to our limited observations, it seems that one or more inflorescences are produced following a condensed sympodial succession (Figure 5(A)). The continuation arises from the axillary bud of the cataphyll preceding the last foliage leaf, the stem then acquiring sympodial growth (Figure 5(A,H)). The continuation shoot produces the regular succession of one cataphyll and one foliage leaf through monopodial growth until a new terminal inflorescence eventually appears, but according to our observations of many adult individuals, the production of inflorescences seems to be a rare event. The spadix is completely enclosed within a green, more-or-less cylindrical, unconstricted spathe on which some reddish glands (extrafloral nectaries) can be seen, at least when young (Figure 5(A)). The inflorescence observed on the type specimen has a total length of 3,5 cm but is probably not fully developed. The spadix stipe is much reduced (Figure 5(B)). The flowers are unisexual. Both female and male flowers are naked and devoid of a perigon. The ovary is generally cylindrical and colored light pink. All the ovaries are somewhat inclined in the direction of the spadix apex. The style is reduced and the stigma completely covers the top surface of the ovary. The stigma is crested due to radial furrows and slightly depressed centrally. The ovary is unilocular with a single basal anatropous ovule (Figure 5(E)). The male flowers are congested on the spadix without any space between

2018, Ebodje, Campo; M - Flagellum creeping on forest floor and producing two foliage leaves then turning back to flagellum state; N - Flagellum climbing at the base of a tree trunk and producing some congested foliage leaves before turning back to flagellum or climbing higher along the trunk; O - Young plant vertically climbing along a narrow tree stem, already exhibiting the characteristic succession of cataphylls and foliage leaves separated by either short or long internodes.



Figure 4. A - Narrow short anchoring roots issued from the short internode and a single thick feeding root at the right; B - Short clasping roots horizontally embracing a small tree branch; C - Two parts of stems alternating long and short internodes, the solitary freely hanging feeding spiny roots always appearing on the short internode; D - Part of a short internode with basal cataphyll scar and upper foliage leaf scar with a solitary freely hanging black feeding root issued from this short internode; E - Apical growing part of a freely hanging feeding root, the spiny emergences precociously initiated along these soft green tissues; F - Part of the narrow fierce barbed feeding root with sharply pointed rigid emergences; G - Narrow black feeding roots with wounding emergences oriented in different directions; H - A 8 meters long barbed feeding root with a constant narrow diameter; I - An adult plant sending the long black feeding roots freely hanging far from the supporting tree trunk; J - Freely hanging shiny black feeding roots zigzaging during growth thus increasing the wounding effect when an animal brushes against it; K - Patrick Blanc holding the freely hanging feeding roots, almost invisible in forest understory due to their black colour and shiny surface reflecting the light; L - Increased diameter of a feeding root reaching the forest floor with spiny emergences and dense tomentum on upper surface while the lower surface produces numerous secondary roots penetrating the soil; M - Distal part of a feeding root showing the much branched secondary roots penetrating the forest soil up to 10 to 15 cm in depth.



Figure 5. A - Young terminal inflorescence emerging from the foliage leaf sheath with basal smaller not yet expanded inflorescences following a condensed sympodial succession ; the spathe is totally enclosing the spadix ; the axillary bud of the last cataphyll will give rise to the continuation vegetative shoot; B - Reduced stipe of the inflorescence, female flowers in basal part of the spadix and male flowers covering its long upper part; C - Spadix fully enclosed in the spathe, female flowers covering one sixth of the spadix length and male flowers the upper five sixth; D - Separate basal naked female flowers with pinkish cylindrical ovary and crested stigma; E - Female flowers with unilocular ovary and a single anatropous ovule; F - Congested male flowers with thick whitish connective, pollen extruded through two slits at the top of thecae; G - Innocent Medjo, Patrick Blanc and Marc Jeanson holding a specimen with an infructescence hanging at the end of a leafy stem, Ebodje, March 2018; H - Infructescence with fully separate brown berries, the continuation sympodial shoot being issued from the last cataphyll just under the last foliage leaf insertion; I - Infructescence base protected by the enlarged persistent lower part of the spathe and narrow stem of the continuation shoot; J - Infructescence with protecting lower part of the spathe, fully dissociate apically narrowed brown berries and upper persistent dry axis of the male portion of spadix; K - Longitudinal section in a mature infructescence, each individual large berry with a 2 mm thick pericarp and a central large white storaging cotyledonary hyperphyll; L - Germination of a large, 2

free stamens, thus obscuring the androecial structure of each male flower. Nevertheless, according to the disposition of the stamens, it appears that each male flower has three or four stamens, or sometimes only two, each characterised by a thick connective and lateral thecae (Figure 5(B,F)). The pollen is extruded through two slits at the top of the thecae (Figure 5(D, F)). The mature infructescence hangs down at the end of a leafy stem (Figure 5(G,H)). The basal part of the spathe is persistent and enlarges during infructescence maturation (Figure 5(I, J)). The infructescence is overall ovoid, and the individual berries are clearly separate from each other (Figure 5(H,J)). They are narrowed toward the tip and colored light brown when ripe, the base remaining green (Figure 5(K)). The male part of the spadix axis persists until maturation of all the individual fruits (Figure 5(J, K)). The pericarp of each fruit is 1 to 2 mm thick, whitish and not fleshy. The seed is 18 to 20 mm long, exalbuminate (without endosperm), and the large white central tissue is the storage cotyledonary hyperphyll (Figure 5(K)).

Seed germination is characterized by the production of a long flagelliform stem which is at first erect (Figure 5(L,M)) before bending down and creeping on the soil surface (Figure 5(N)). This very narrow, 1 mm thick stem, reaches 40 to 50 cm and produces only small cataphylls every 5 to 10 cm before producing the first foliage leaf (Figure 5(O,P)). The first foliage leaf is followed by cataphylls which are again separated from each other by long internodes before one or two foliage leaves are produced. At this stage, the stem issuing from the germinated seed acquires the same growth habit as a flagelliform shoot hanging from a tree originating from an adult stem. The growth habits of the species are summarized in the Figure 6.

DISCUSSION

Following the pioneer work by Irmisch (1874), Engler (1877) focused on the growth habits and especially the succession of cataphylls and foliage leaves along the stems in his comprehensive study of Araceae. Concerning the genus *Cercestis*, he just mentions that the terminal inflorescence follows the production of many foliage leaves in the usual pattern of most Araceae genera that exhibit a sympodial growth. More recent studies of branching patterns in relation to the leaf type (cataphyll or foliage leaf) mostly concern the sympodially articulated stems of *Anthurium* and *Philodendron* species (Ritterbusch, 1971; Blanc, 1978; Ray, 1987a, 1988). It appears that the few comments concerning the growth form in relation with leaf types of the different *Cercestis* species (Engler, 1877; Knecht 1983; Ntépé-Nyamè, 1988; Bogner and Knecht, 1995; Jongkind, 2010) simply suggest that the climbing stems produce a succession of foliage leaves in a monopodial growth pattern until the emergence of a terminal inflorescence, then initiating a sympodial growth pattern of one prophyll, an indeterminate number of foliage leaves and eventually a new terminal inflorescence. However, Knecht (1983) illustrated the intercalation of a cataphyll between groups of foliage leaves in some species like *C. afzelii*, *C. ivorensis* and *C. dinklagei* (as *C. stigmaticus*) but without any regular morphological succession. The drawing in the description of *C. taiensis* (Bogner and Knecht 1995) points to the presence of cataphylls between the foliage leaves, but there is no comment concerning the pattern of succession of leaf types, perhaps due to the short, congested internodes, which render the observation more difficult.

A more unusual situation in *Cercestis* concerns the production of short axillary stems bearing foliage leaves and terminal inflorescences; these stems appear in the axil of a cataphyll of a narrow climbing or creeping stem somewhat similar to a flagellum, as can be deduced from drawings by Engler (1911, Fig. 41) for *C. dinklagei* (as *C. stigmaticus*) as well as by Mayo et al. (1997) also for *C. dinklagei*. According to the drawing by Ntépé-Nyamè (1988), our observations of many living specimens, herbarium collections and digitized specimens of *C. congensis* available on GBIF.org (2025) it appears that axillary short shoots producing foliage leaves and inflorescences are initiated in the axils of the cataphylls of the main narrow flagelliform shoot which either creeps on the forest floor or climbs to only a few meters on small trees. This unusual growth habit seems to be the general rule for *C. congensis* but new observations on living plants in their natural environment are necessary in order to give a general interpretation of this growth habit.

Otherwise, the succession of groups of cataphylls followed by groups of foliage leaves along the stem in Araceae has been interpreted as an adaptation to fluctuations of the environment, to the vegetative propagation or globally to adjust photosynthetic activity (Blanc, 1982). The adaptive consequences of this

cm long seed, the stem being first erect; M - Erect germinating stem, the first two internodes being reduced then progressively elongating, producing only cataphylls; N - Germinating stem issued from the large seed, the roots appearing at the first cataphyll node, the narrow 2 mm thick stem elongating on the forest floor and producing only cataphylls every 5 to 10 cm; O - Elongating germination flagelliform stem creeping at the soil surface, reaching 50 cm in length but still producing only small cataphylls; P - Flagelliform stem issued from germination producing the first foliage leaf just after a last bigger cataphyll then followed by a new flagelliform part of the monopodial axis.

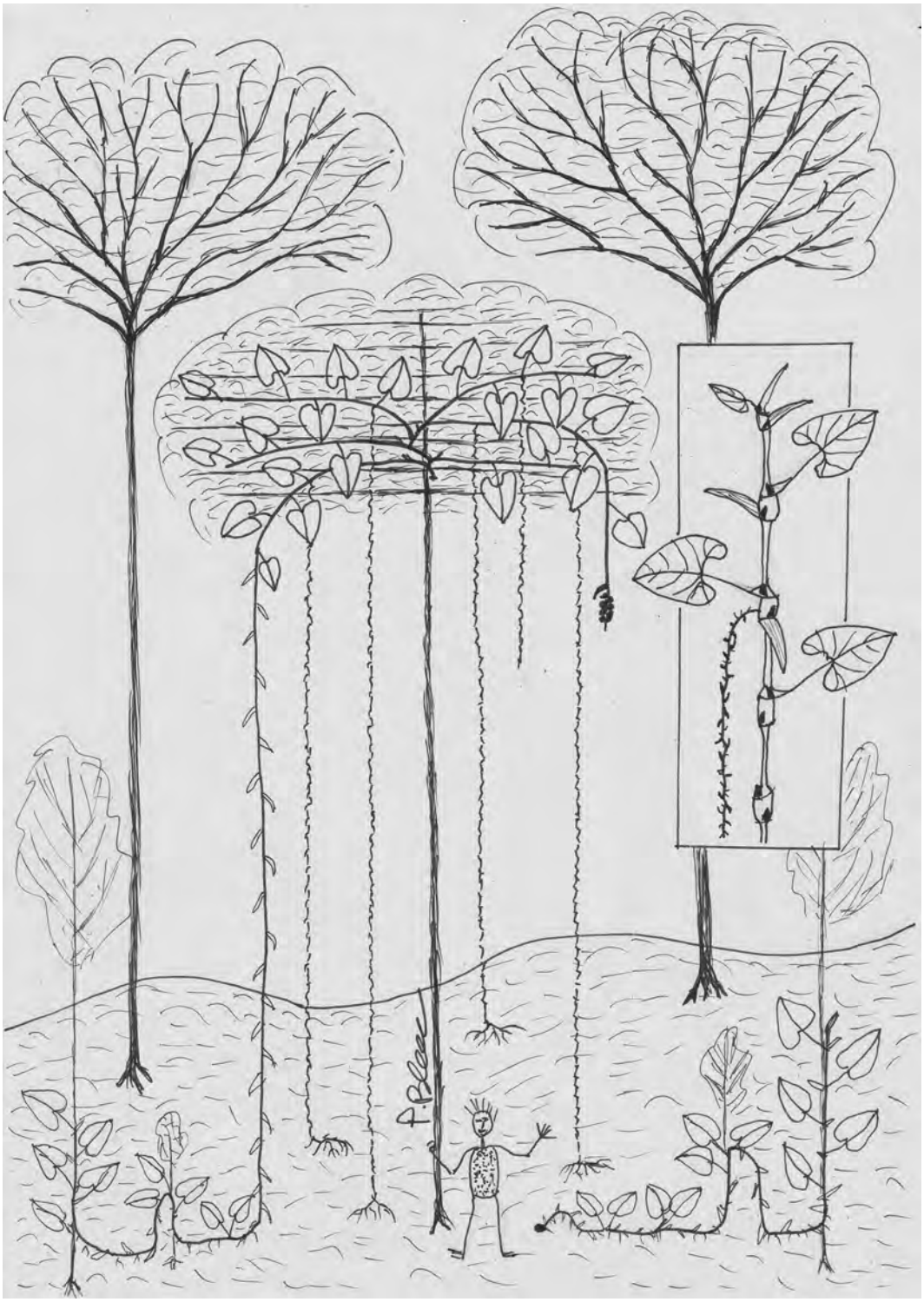

Figure 6. Synthetic representation of the growth habits of *Cercestis blancii*.
Credits: Figure 6 by Patrick Blanc. All photos by Patrick Blanc and Marc Jeanson except 2A by Dany Cleyet-Marrel, 2B by Pascal Héni and 2E by Innocent Medjo.

succession is also described in *Monstera adansonii* var. *klotschiana* (Andrade and Mayo, 1998) as well as in *Philodendron rudgeanum* and *P. fragrantissimum* (Andrade and Mayo, 2000). The succession of groups of cataphylls and groups of foliage leaves in the genus *Cercestis* has been described in relation to the production of terrestrial flagelliform shoots in *C. mirabilis* (as *Rhektophyllum mirabile*) by Blanc (1980), as well as in *C. dinklagei* (as *C. stigmaticus*) and *C. ivorensis* by Knecht (1983). These alternating groups of clustered foliage leaves and dispersed cataphylls along the flagelliform part of the same stem are biologically essential for most *Cercestis* species in the colonisation of the forest floor, the rocky areas and the stems of small

shrubs. This is very effective because new axillary flagella appear in the foliage leaf rosette. They sometimes cover very large areas just as we have observed in *C. camerunensis* and *C. mirabilis* in the same Campo area where *C. blancii* occurs.

As regards the growth of the flagelliform stem emerging at germination, it seems unwise to infer, without more precise observations and experiments, attraction of the apex towards the darkest areas of the surroundings (skototropism) as first proposed by Strong and Ray (1975) and later documented in many other climbing species (Rodriguez-Qintero et al., 2022). In genera of climbing Araceae, the flagelliform seedling stem seems to occur mostly in species producing comparatively large seeds, as Madison (1977) observed in his survey of *Monstera* species. The germination of large-seeded *Pothos* species is characterized by a flagelliform stem (Boyce and Hay, 2001; Tillich, 2003) as well as in different *Heteropsis* species (Balcazar-Vargas et al., 2012). Among those *Cercestis* species for which germination has been observed, the first leaves produced are foliage leaves separated by short internodes, as Knecht (1983) has reported for *C. afzelii* and *C. stigmaticus*. Despite its quite large seeds (12 mm long), *C. camerunensis* also produces foliage leaves at germination (P. Blanc, pers. obs.). Until now, *C. blancii* is thus the only *Cercestis* species to produce a flagellum at germination and is the species with the largest seeds in the genus.

The repetitive alternation along a stem of one or two cataphylls and one foliage leaf has been considered a characteristic growth habit trait of the genera *Anthurium* and *Philodendron* (except subgenus *Pteromischum*) since Irmisch and Engler (loc. cit.) but we now have to add *Cercestis blancii* since it follows the same sequential production of one cataphyll and one foliage leaf. However, *C. blancii* differs fundamentally in this alternating leaf type pattern since in *Anthurium* and *Philodendron* the growth is sympodial, a terminal inflorescence always being produced after the foliage leaf, and an identical continuation segment or module ("article" in Blanc, 1978) originating from the axillary meristem of the cataphyll. In *Cercestis blancii*, the growth is monopodial, the same apical meristem producing one cataphyll, one foliage leaf, one cataphyll and so on. Contrary to most *Anthurium* species in which the two cataphylls are reduced in size, the single cataphyll of *Philodendron* is usually quite large and somewhat similar to that of *C. blancii*. In *Philodendron*, the cataphyll is the prophyll ("Vorblatt") of the new module, which is reduced to this prophyll, one foliage leaf and one terminal inflorescence. This is in accordance with the fact that prophylls of new axes in Angiosperms are usually reduced to a membranous sheathing foliar organ lacking an expanded blade. The situation is quite different in *C. blancii* because growth is monopodial and accordingly, the cataphyll does not have the morphological significance of a prophyll. Moreover, the regular monopodial alternation of these two leaf types is correlated with a regular difference in stem diameter and internode length. Both cataphyll and foliage leaf produce an axillary resting bud in *C. blancii* while only the cataphyll produces a secondary axillary resting bud in *Philodendron*, the foliage leaf being devoid of an axillary bud (Engler 1877; Ritterbusch 1971; Blanc 1978). The physiognomical similarity between leaf type alternation in *Philodendron* and *C. blancii* despite their fundamental difference in growth habit (sympodial *vs* monopodial) could be related to the proximity of the *Philodendron* and Culcasieae (including *Cercestis*) clades, as recently attested by Haigh et al. (2023) even though *Philodendron* is American and Culcasiae are African. The superficial similarity of leaf type alternation in *Philodendron* and *C. blancii* despite deeply different morphogenetic construction seems to be a unique case of convergence (or the existence of a shared common ancestor), at least in the Araceae family.

Monocotyledon leaves are characterized by their sheathing leaf base enclosing and protecting all the younger parts of the stem, thus reducing the impact of external traumatisms and allowing continuous growth of the stem (Arber 1925; Holttum 1955; Corner 1966; Hay 2019). The foliage leaf sheath is short in all *Cercestis* species (except *C. camerunensis*) but in the case of *C. blancii*, the new internode emerging from the short leaf sheath is long and very narrow and it thus lacks protection while its tissues are still immature and tender (Figure 3(C,D)). The cataphyll of each segment soon withers, exposing the distal part of the stem (Figure 3(E)). As a consequence, this apical part of the stem is very fragile. The situation is different in the other *Cercestis* species with short internodes, where the new leaf blade emerges directly from the sheath, and is not subtended by a long, fragile internode. The young apical part of the *C. blancii* stem is thus very vulnerable and can easily be damaged by mechanical trauma as well as herbivorous and pathogen attacks. Recurrent traumatisms could be the main reason explaining the unusually profuse branching of the adult stems in correlation with the presence of a resting bud in the axil of both cataphyll and foliage leaf. We observed that either one or both buds of a same segment can give rise to new axillary shoots (Figure 3(F–L)). This recurrent aerial branching on long shoots associated with traumatisms seems to be exceptional in the Araceae. When comparing *Philodendron* and *C. blancii*, both with regular alternation of one cataphyll and one foliage leaf , it appears that the cataphyll has a protective effect over all the younger parts of the stem in *Philodendron*, thus reducing the external traumatisms whereas in

contrast, the cataphyll of *C. blancii* soon exposes the younger parts of the narrow stem which becomes easily damaged by external attacks.

Recurrent traumatisms in *Cercestis blancii* are thus at the origin of this profuse branching, which differs from the sequential branching along the main monopodial stem in other climbing genera of Araceae producing axillary detached stems as in many *Pothos* and *Rhaphidophora* species (Engler, 1877; Boyce, 1999; Boyce and Hay, 2001). This means that traumatisms can be turned to advantages when colonising host trees, as in the case of *C. blancii*. The role of traumatisms leading to new solutions in colonising a habitat has been shown by Blanc (2002), especially concerning the tropical forest understory species where low light intensity is a limiting factor, and this is noteworthy in the case of broken leaves producing new plants on the forest floor in many families such as Begoniaceae, Gesneriaceae, Melastomataceae, Rubiaceae, Primulaceae, Piperaceae, Urticaceae as well as in the case of recurrent basal emergence of new shoots producing their own new root system leading to potential immortality. In mature tree crowns at the top of forest canopy, directly exposed to high light intensity, strong winds, low air humidity and proliferation of insect and disease attacks, recurrent traumatisms are at the origin of profuse branching, as observed and detailed by Blanc (1992), leading him to propose a new interpretation of the growth habits of mature tree crowns once they reach the forest canopy. This new adaptive architectural interpretation through successive shoot and branch necrosis involves a downward progressive individualisation of the main branches which contradicts the reiteration concept involving upward differentiation of the main branches (Hallé et al. 1978) but it tentatively explains why the global "cauliflower" shape of mature tree crowns is so similar in all tropical forests whatever the species or continent (Blanc 1992; 2012; 2020 and Figure 2(A)). Pruning of the apical parts of the shoot is widely used in horticulture to allow the development of lateral shoots thus creating a much-branched plant, but the importance of natural pruning in the construction and global architecture of plants seems to have been largely overlooked. The morphogenetic patterns governing the succession of cataphylls and foliage leaves along monopodial as well as sympodial stems need new investigations and the genus *Cercestis*, due to its high diversity of growth habits despite the small number of species, would be a good group with which to start progressing towards a better understanding of the dynamics of morphological structures in relation to their adaptive implications.

Key for Cercestis species from Cameroon and neighbouring western central African countries (Gabon, Equatorial Guinea, Nigeria, Central African Republic, Republic of the Congo and Democratic Republic of the Congo)

1 - Adult plant with pinnatisect leaves. 2
- Adult plant with entire, oval, cordate, hastate or sagittate leaves. . .. .

requirements and based on observation of individuals in littoral forests in Cameroon by the authors, we can infer that the extent of occurrence of *Cercestis blancii* may be superior to 93 km2 but inferior to 500 km2, falling within Endangered status under the criterion B2. The littoral forests in which the species has been observed also extend southwards to Equatorial Guinea and Gabon, meaning an even greater EOO, but as no observation or collection has yet been made in these regions, we can only suspect this species to have this wider distribution. If *Cercestis blancii* should be found in these countries, the present conservation status would be revised. *Cercestis blancii* is endemic to Cameroon, where it occurs in the Southern region in the Campo arrondissement. The species is known from four specimens and one observation collected in unprotected forests subjected to selective logging and agro-industry farming. This species is thus known from four specimens and one observation (4 unique occurrences) with precise localization representing three existing subpopulations. These three subpopulations represent a total of three "locations" (sensu IUCN 2012) with respect to the main threat of habitat destruction, agro-industry farming, exceeding the upper limit for Critically Endangered status, but falling within the limit for Endangered status. We estimate that the past loss of its habitat, which will continue, has and will induce a strong continuous decline in habitat quality, number of subpopulations and mature individuals in the next ten years as well as an important decline of its EOO and AOO. *Cercestis blancii* is therefore assigned a status of EN B1ab(i,ii,iii,iv,v) + B2ab(i,ii,iii,iv,v).

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Author contributions

Marc Jeanson contributed to every section and contributed to the mounting and registration of the specimens at P.

Eric Ngansop Tchatchouang contributed to fieldwork and commented the manuscript.

Patrick Blanc contributed to every section.

The data that support the findings of this study are openly available in the virtual herbarium of the Muséum national d'Histoire naturelle in Paris at https://science.mnhn.fr/institution/mnhn/collection/p/item/search/form using the barcode numbers (accession numbers) indicated in the article.

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