Taxonomic and Nomenclatural Notes on Philippine ferns. V.
On the identity of *Asplenium lepturus*, *A. militare*, and *A. nigrescens* (Polypodiales, Aspleniaceae)

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The identity of *Asplenium nigrescens*, *A. lepturus*, and *A. militare* is clarified. Diagnostic characteristics, distribution, and habitat information for each species are provided. *A. nigrescens*, *A. lepturus*, and *A. militare* are distinct species. Key and photos are provided for the identification of the species. The collections by de Vore and Hoover are discussed.

Keywords: endemic, identification key, Malesia, nomenclature, pteridophyte taxonomy

INTRODUCTION

The genus *Asplenium* was described by Linnaeus in “Species Plantarum” (1753). Newman (1840) described the family Aspleniaceae in “A History of British Ferns” – in which he placed *Asplenium*, *Athyrium* (Roth 1800), and *Scolopendrium* (Adanson 1763) based on sorus and indusium characteristics. The work of 19th- and early 20th-century pteridologists concentrated on the description of new species and a delineation of families based on morphological characters. The circumscription of these early families was considered unnatural from the taxonomic and evolutionary point of view by many and remained controversial until recently. This situation resulted in a plethora of classification schemes (cf. Christenhusz and Chase 2014), in which families were created or merged. In the late 20th century, technical and biochemical developments facilitated molecular studies. The use of DNA sequencing has proven to be an extremely helpful tool in increasing our understanding of fern evolution, diversification, and the clarification of species relationships (Schneider et al. 2004a; Schuettelpelz and Pryer 2009; Rothfels et al. 2015; Xu et al. 2018). Greater technical advances and the use of computers allowed statistical studies to analyze the large amount of data being generated.

Recent studies have consistently demonstrated that the Aspleniaceae is a monophyletic family composed of two genera – *Asplenium* and *Hymenasplenium* (Murakami 1995; Schuettelpelz and Pryer 2007; Dong et al. 2012; Rothfels et al. 2012; Ohlsen et al. 2015; Schneider et al. 2017; Xu et al. 2018). About 38 genera have been recognized in the family over time based on morphological data (Xu et al. 2020). Molecular analyses of *Asplenium* species since the 1990s have shown that all the segregated genera should be included in *Asplenium* (Murakami and Schaal 1994; Murakami et al. 1999; Schneider et al. 2004b, 2005; Perrie and Brownsey 2005; Schuettelpelz and Pryer 2007). *Hymenasplenium* was first segregated from *Asplenium* by Hayata (1927) based on the dorsiventral anatomy of its rhizome. Other morphological distinctions that support the separation of *Hymenasplenium* and *Asplenium* (Lin and Viane 2013) have been described since. *Asplenium* has a base chromosome number of x = 36 and *Hymenasplenium* of 39 or 38 (Mitui et al. 1989; Schneider et al. 2017; Xu et al. 2020). Bellefroid et al. (2010) reported four base numbers in Aspleniaceae: x = 39, 38, 36, and 35 due to dysploidy, a rearrangement of chromosome parts that changes the number of...
chromosomes but not the amount of DNA. *Asplenium* is the largest genus in the family with ca. > 700 species and 122 listed hybrids; *Hymenasplenium* is represented by < 30 species (Lin and Viane 2013).

Some recent research has focused on the understanding of reticulate evolution and the species circumscription of some complexes in *Asplenium* (Murakami and Schaal 1994; Perrie and Brownsey 2005; Shepard *et al.* 2008; Chang *et al.* 2018). The number of studies based on the analysis of one gene (Hasebe 1993, 1994; Murakami *et al.* 1999) quickly increased to include several genes and a larger number of species in which *Asplenium* species were included (Pryer and Schuettpelz 2004; Testo and Sundue 2016; Schneider *et al.* 2017; Chang *et al.* 2018; Xu *et al.* 2020).

Salgado (1990) reported 43 species of *Asplenium* in the Philippines. Barcelona (2021) revised and updated this list to 42 species, with an additional three possible species still to be reported. While revising this genus it became obvious that specimens were often misidentified, confusion about the identity of several species was noticed, and some species were in fact complexes or aggregations of similar species (Salgado 1996, 2005, 2017, 2020; Salgado and Fraser-Jenkins 2013). *A. lepturus* C.Presl from Hainan (China), Laos, Philippines, and Vietnam, and *A. nigrescens* Blume from the Sunda Islands to New Guinea, Solomon Islands, and Vanuatu appear to be closely related species, which are confused and often misidentified in herbaria. These species have never been carefully studied. With the existing confusion between *Asplenium lepturus* and *A. contiguum* (Kaulfuss 1824) from Hawaii, it is important that the taxonomy of *A. lepturus* be clarified in Malesia before studies are made to determine its identity in relation to *A. contiguum*. The mysterious *A. militare* Copel. – which has been collected maybe twice on Mt. Apo, Mindanao – has never been evaluated in relation to *A. nigrescens*, which is found in Mindanao and in the adjacent island of Borneo, and whose description seems to match. Mindanao and Borneo share a common geological and botanical history in the Pleistocene when a land bridge occurred between the two islands (Voris 2000). The five collections made by de Vore and Hoover on Mt. Apo have often been misidentified as *A. militare*. These specimens will be studied and compared with *A. militare* and *A. nigrescens*, which they superficially resemble. This study attempts to clarify the species status of *A. lepturus*, *A. militare*, and *A. nigrescens*.

**MATERIALS AND METHODS**

**Institution Visited**
The specimens of *A. lepturus*, *A. nigrescens*, and *A. militare* deposited at Botanischer Garten und Botanisches Museum Berlin, Berlin, Germany (B); Natural History Museum, London, England, United Kingdom (BM); Royal Botanic Garden Edinburgh, Scotland, United Kingdom (E); Royal Botanic Gardens, Kew, England, United Kingdom (K); Naturalis Biodiversity Centre, Leiden, Netherlands (L); The New York Botanical Garden, Bronx, New York, United States (NY); Muséum national d’histoire naturelle, Paris, France (P); Charles University, Prague, Czech Republic (PRC); Swedish Museum of Natural History, Stockholm, Sweden (S); Smithsonian Institution, Washington, DC, United States (US); and Naturhistorisches Museum Wien, Vienna, Austria (W) were examined and verified, as well as their digital images. The Conservatoire et Jardin botaniques de la Ville de Genève, Geneva, Switzerland (G); Miami University, Oxford, OH, United States (MU); Missouri Botanical Garden, Saint Louis, MO, United States (MO); University of Michigan, Ann Arbor, MI, United States (MICH); Harvard University, Cambridge, MA, United States (GH); and University of California, Berkeley, CA, United States (UC) collections were consulted using the herbarium database photos. The herbarium acronyms in the “Index Herbariorum” and the “International Code of Nomenclature for Algae, Fungi, and Plants (Shenzhen Code)” were followed.

**Methodology**
Photos of live specimens posted on Phytoimages.siu.edu (Pelser *et al.* 2011) were consulted. The character states (such as habit, indument type, size, shape, color, length, width, dissection, and production of buds) of morphological features (such as roots, rhizome, fronds, pinnae, and sori) were examined. The identity of the specimens was confirmed. Only specimens whose identity was verified are reported. Notes on the habitat and distribution of the species were taken from herbarium specimen labels. A comparison of the types was made in order to assess their morphological similarities and differences. The collections by de Vore and Hoover (*de Vore and Hoover*) were studied and compared to the three species in this study. The abbreviations of authors follow the “International Plant Names Index.” The designation of holotype follows the “International Code of Botanical Nomenclature.” The Creative Common licenses of the owner’s herbaria for use of images were confirmed by the author. The botanical terminology used in the descriptions is that of Lellinger (2002).

**Herbarium Specimens Examined and Confirmed**

*Asplenium lepturus* C.Presl (Figure 1)

Asplenium lepturus C.Presl., Epimieliae Botanicae: 72 (Presl 1849). Type: Philippines, Luzon; *habitat in insula Luzon; Cuming 211*; holotype PRC!, isotype B [B 20
Figure 1. Asplenium lepturus (isotype K); notice the marginal teeth of the pinnae.
K[K000448221]! • Luzon, Kalinga Prov., (near boundary with Abra Prov.), Balbalan Municipality, Barangay Balbalasang, Balbalasang-Balbalan National Park, Mt. Balit-it; 17º25.76'N, 120º59.99’E; 2026 m; 22 Feb 2003; J.F. Barcelona 1818; US [01516501]! • Luzon, Mountain Prov., Barlig Municipality, Mt. Amuyao, broadleaf forest; 17º 01.609’N, 121º 06.587’E; 2090 m; 21 Feb 2007; Barcelona, J. F. and Losao-na, N. 3068; US [01516417]! • Luzon, Quezon Prov., Lucban Municipality, Mt. Banahaw de Lucban, SLPC botanic garden approach; 14º04.562'N, 121º30.816’E; 1600 – 1650 m; 29 Mar. 2003; Barcelona, J. F. 2022a; US [01516417]! • VIETNAM. Nhatrang Prov., Annani, Mére et l’enfant; récolté sur une grosse roche en forêt, fougère de 0.30 m de haut; 1800 m; 8 Nov 1922; Poilane 5107; P [P01485284]! • Lam Dong, distr. Ninh Son, municipality Phuoc Binh, 34 km to NE from Dalat city, closed primary wet broadleaved forest, on E macroslope of Gia Rinh mountain ridge, epiphyte, common; 12º07’N, 108º42’E; 1700-1800 m; 4 Apr 1997; L.V. Arenyanov et al. VH3603; MO [6255773]!.

**Asplenium militare** Copel. (Figure 2)

*Asplenium militare* Copel., New Philippine Ferns, Philippine Journal of Science 1, Suppl. IV: 254 (Copeland 1906). Type: Philippines, Mindanao [Island], *ad montem Apo*, 1800 m Copeland 1505; holotype MICH [MICH1003422]!, 2 sheets; isotype B [B20 0018893]!, P [P00642962]!, S [S-P-256]!.

*Asplenium nigrescens* Blume (Figures 3 and 4)

*Asplenium nigrescens* Blume, *Enumeratio Plantarum Javae* 2: 180 (Blume 1828). Type: INDONESIA. Moluccas, Tidore Island; *Crescit in Moluccis supra arbores*; Reinwardt 1183; holotype L [L0051021]!, isotype US [US00135105]! • Java; Gunung Slamat, 4 Sep 1898; M. Raciborski s.n. US [01516489]! • Java; Preanger Province, Mt. Gede, vicinity of Tjibodas; 1700 m; 18 Aug 1909; Palmer and O. Bryant 808 (K) • New Guinea., Tohkiri Mts. East, opposite Waumi River, 0º49’15”S, 132º14’50”E, 11 Jul 1961; P. van Royen and H. Sleumer, HO 7282 L[L3979327]! • Sumatra, G. Singgalan, Feb 1912; C.G. Matthew s.n. K[K000451085]! • G. Koerintji, 2100 m, Apr 1920; W. Bunnemeyer 9641 K[K000451087]! • MALAYSIA. Borneo, Sabah, Maraiparai ridge; 6º5’N, 116º31’E; 5000 ft [1524 m]; 23 Nov 1931; Holtum SFN25615; K [K000451083]! • Borneo, Sabah, upper Kinabalu, falls above Lumu, 7000 ft [2134 m], 9 Jun 1932; J. and M.S. Clemens 29972; US [01516487]! • ibid.;
6°3'N, 116°33'E; 9 Jun 1932; J. and M.S. Clemens 29972; Borneo, Sarawak, ridge of Gunong Mulu Nat. Park, Sungei Tapin headwaters, epiphyte on tree trunk, in midmontane forest, rare; 4°2'N, 114°52'E; elev. 1660 m; 24 Jun 1978; B. Parris 6736; K[000451081]!

• Huon Peninsula, Cronwell Mts., Morobe District, Mannasat, 2408 m; 22 Aug 1964; R. D. Hoogland 9669; US [01516674] • Eastern Highlands District, Kainantu Sub-District, Mount Elandora, west side near village of Suwaira, between Omaura and Aiyura; 11 Feb 1965; Plants of New Guinea, A.C. Jermy 5092 L [L3504733]!

• Mt. Lululua; 5°43'0"S, 151°1′59"E; 13 May 1975; Plants of New Guinea, J.F. Veldkamp, Exped. Rijks. Leiden - Lae Div of Botany 6769; L [L3504736]!

• North Solomons Province, Emperor Range, Mt. Balbi Complex, Waknai; 5°55′0"S, 155°0′0"E; 9 May 1988; O.G. Gideon s.n. L [L3504732]! • NEW CALEDONIA. Franc 1445B; US [01518479] Plateau de Dogny, forêt moyenne, elev. 900 m, 31 Jan 1911 • PHILIPPINES. Mindanao Island, Davao Prov., Mt. Apo, Lake Linao, 30 Oct 1946; Unknown s.n.; L [L3504720] • Mindanao [Island], South Cotabato Prov., General Santos [City], Purok 7, Mt. Matutum, Kinilis, Polomok, 6 Apr 1992; F.J.M. Gaerlan, R.E. Fuentes, E.M. Romero PPI 5211; L [L3504719].

**Asplenium** sp. (Figures 5 and 6)

Asplenium sp. de Vore and Hoover 321, Philippines, Mindanao, Mt. Apo district, May 1903 (K [000445832]!, US [01516673]!, P!.

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**Figure 4.** Asplenium nigrescens (not a type L); showing the lobed apical segment.

**Figure 5.** Asplenium sp. (de Vore and Hoover 321, K) collected on Mount Apo; compare with A. nigrescens, A. militare, and A. lepturus.
RESULTS AND TAXONOMIC TREATMENT

Taxonomy
Division Polypodiophyta Cronquist, Takht. and Zimmerm. 1966: 133.
Class Polypodiopsida Cronquist, Takht. and Zimmerm. 1966: 133.
Subclass Polypodiidae Cronquist, Takht. and Zimmerm. 1966: 133.
Suborder Aspleniineae Gaudich. 1826: 311.
Subfamily Asplenioideae Link 1841: 73.
Genus Asplenium L 1753: 1078.

Key to the Species
The following key distinguishes between the species being studied. The measurements for A. militare reported here have been taken from Copeland’s (1960) description due to the lack of complete specimens available in herbaria.

DISCUSSION

Asplenium nigrescens was described by Blume (1828) from a specimen collected in Tidore, Moluccas (Reinwardt 1183). Its holotype is in Leiden (L [L0051021], Figure 3). Presl (1849) described A. lepturus from a collection by Cuming (Cuming 211) in Luzon, Philippines. Its holotype is in Prague (PRC) and isotypes in B, BM, E, GH, K, MICH, P, US, and W. A. lepturus and A. nigrescens have widely spaced long teeth, in the distal half of the pinna margin (Figures 1 and 3). These long teeth and the narrow long caudate pinnae give the flexuous A. lepturus a distinctive feathery appearance. A. nigrescens is a robust plant with thicker stipe and rachis, and its pinnae are wide and straight. It lacks the delicate elegance of the pendulous A. lepturus – with its slenderer, flexible fronds and narrow pinnae. The deep pinna incisions down to the costa in A. nigrescens are not found A. lepturus. A. nigrescens’s frond apical segment with wide rounded lobes in the lower portion of the segment then becoming acuminate apically with blunt teeth (Figure 4) differs from the not lobed, long acuminate with narrow acute teeth frond apical segment of A. lepturus (Figure 1). The stipes of A. nigrescens have translucent hairs with a dark reddish-brown tip in contrast with the glabrous A. lepturus. Both species have small reddish-brown scales with two basal branches, scattered along the veins on the abaxial side of the pinna. A. nigrescens has long wide brown scales along the costa while A. lepturus lacks them.

1a. Fronds up to 150 cm long or possibly more, occasionally proliferous; apical segment shape similar to lateral pinnae but smaller .................. A. militare

1b. Fronds up to 120 cm long, not proliferous; apical segment shape different from lateral pinnae .................. 2

2a. Pinnae oblong-trapezoid, straight, margins parallel not narrowing except close to the apex; pinnae (1.1)1.5-2(2.8) cm wide in the middle region, (9.6)10-12.2(15) cm long; pinna apex acuminate; pinnae often torn with deep incisions all the way to the costa; lamina apex with wide rounded lobes becoming acuminate with blunt teeth ... A. nigrescens

2b. Pinnae linear-trapezoid, falcate, margins not parallel gradually narrowing toward the apex; pinnae (0.6)0.8-1.1(1.2) cm wide in the middle region, (7.2)9-12(15) cm long; pinna apex long acuminate; pinnae not cut with deep incision; lamina apex not lobed, long acuminate with narrow acute teeth ................................ A. lepturus

Figure 6. Asplenium sp. (de Vore and Hoover 321, K); notice the serration of the margin and the basiscopic shape of the pinnae.
sori of mature *A. nigrescens* and *A. lepturus* are straight and oblique to the costa. The spores of the isotypes of *A. nigrescens* and *A. lepturus* have a fenestrate pattern (cf. Lellinger and Taylor 1997) and are identical. Young plants of both species are difficult to distinguish; mature plants are easily identifiable.

The gross morphology of *A. nigrescens* and *A. lepturus* is superficially similar, and the species have often been confused and misidentified. Unfortunately, these species have been rarely used in molecular studies. Xu *et al.* (2020) found in his comprehensive study of the Aspleniaceae, that *A. nigrescens* and *A. lepturus* are not as closely related as their morphology would suggest. This important molecular study of about 420 species was based on six genes. The study supported the monophyly of the family Aspleniaceae, which was resolved into four superclades, and in turn subdivided into clades and subclades. The *Tarachia* clade was found to be composed of five strongly supported subclades. The *A. aethiopicum* subclade containing *A. lepturus* appears as a sister to the other four subclades. The *A. crinicaule* subclade includes *A. nigrescens* and shows *A. nigrescens* as being more closely related to the species in the three other subclades than to the *A. aethiopicum* subclade containing *A. lepturus*. Within the *Tarachia* clade, *A. lepturus* and *A. nigrescens* appear to be more distantly related than expected from their similar morphology. This is an unexpected finding because these two species have a very similar morphology. This is not the first instance in which morphologically similar species have a significant difference in DNA base sequence. Murakami *et al.* (1999) studied the *rbcL* gene of 25 species of *Asplenium* with various morphological characters in a preliminary attempt to understand relationships within the Aspleniaceae. The species resolved in groups of species with similar base sequences. The majority of the species in a group had similar morphologies, but there were some that differ in morphology. Molecular similarities are not always supported by morphology. The molecular evidence presented in this study supports the separation of *A. nigrescens* from *A. lepturus* into different species.

*Asplenium nigrescens* is apparently restricted to the islands of Malesia, New Guinea, Solomon, and Vanuatu. It has been reported from Java (Blume 1828), Borneo (Christensen and Holtum 1934; Parris *et al.* 1992), and the Moluccas (Blume 1828; Christensen 1905). Collections from Sulawesi, Ceram, and Sumatra can be found at L and P. Other collections from various locations in New Guinea, including the island of New Britain in the Bismarck Archipelago (P. F. Stevens and Y. Lelean 58313, L), are deposited in US and L. Osia G. Gideon (O.G. Gideon *et al.* s.n., L) collected it on Mt. Babli, Emperor Range, Wakunai, North Solomon Province, Papua New Guinea. It has been collected (A. F. Braithwaite RSNH 2364, K) on the island of Espiritu Santo in the New Hebrides, now the Republic of Vanuatu. The specimens collected in Camiguin de Mindanao in 1912 (*Flora of the Philippines, Bureau of Science 14794, P*); in Lake Linao, Mt. Apo in 1946 (*PNH 759, L*); on Mt. Kitanglad, Bukidnon Province (V.B. Amoroso and D.N. Karger 746, UC); and on Mt. Mututum, South Cotabato Province in 1992 (*Gaerlan, Fuentes and Romero PPI 5211, L*) belong in *A. nigrescens*. *A. nigrescens* is reported here as a new record for the Philippines. A survey of the literature and herbarium specimens has not yielded any reports of *A. nigrescens* from mainland SE Asia. *A. lepturus* is found in Hainan (China), Laos, Philippines, and Vietnam. There are doubts about its presence in Hawaii. It may be conspecific with *A. contiguum*, but this still has to be clarified. The plants collected on Mt. Quebrada (*Edaño PNH16618, K*) and Mt. Bubonbirit (M. Kato, G. Murata and H.G. Gutierrez 513, L; M. Kato, G. Murata and H.G. Gutierrez 525, L), Ilocos Norte Province, Luzon, mark the northernmost outpost of *A. lepturus* in Malesia. *A. lepturus* and *A. nigrescens* are high elevation mountain ferns, usually collected above 1600 m, and normally epiphytic yet occasionally epilithic in montane cloud forests (Raciborski 1898; Christensen and Holtum 1934; Backer and Posthumus 1939).

Copeland (1906) described *A. militare* (*Copeland 1505*) from a plant he collected at 1800 m on Mt. Apo, Mindanao, in October 1904. It was photographed in March 2010 on Mt. Apo by Leonardo Co (cf. photo by L.L. Co. Phytoimages, DOL34320, Pelser *et al.* 2011). The isotypes of *A. nigrescens* and *A. militare* share the following characteristics: pinna shape, pinna lamina with deep incisions down to the costa, pinna margin with very large wide teeth in turn capped with 2–4 small teeth, and divergent sori (Figures 2 and 3). *A. militare* differs from *A. nigrescens* in having more robust stipes, fronds up to 150 cm long, occasionally proliferous (cf. photo by L.L. Co. Phytoimages, DOL34320, Pelser *et al.* 2011), and longer pinnae. The apical segment of *A. militare* is similar to the pinnae but smaller, while that of *A. nigrescens* is pinnatisect different from the pinnae (Figure 4; cf. photo by L.L. Co. Phytoimages, DOL34320, Pelser *et al.* 2011). The sori of *A. militare* are parallel to the costa and then deflexing towards the margin avoiding overlapping with the adjacent sorus, while those of *A. nigrescens* are oblique to the costa. All herbarium specimens of *A. militare* consist of a single frond on each sheet, the rhizome, and the basal and apical portions of the frond are missing – making it impossible to measure its total length. The author relied on the original description of the species by Copeland (1906) for measurements of the frond and pinnae. A specimen photographed in 2010 by L. Co (cf. photo by L.L. Co. Phytoimages, DOL34320, Pelser *et al.* 2011) shows a plant of *A. militare* producing a plantlet on the frond apex taking the place of the apical segment.
CONCLUSIONS

Asplenium lepturus, A. nigrescens, and A. militare have significant morphological differences between them and they should be considered separate species. Molecular evidence further supports the separation of A. lepturus and A. nigrescens. A. nigrescens is here formally reported from the Philippines; it is found in the islands of Mindanao and Camiguin de Mindanao. The collections by de Vore and Hoover (de Vore and Hoover 321, K, P) are not conspecific with A. militare or A. nigrescens. The specimen de Vore and Hoover 321 deposited in the US National Herbarium (US 01516673) is A. nigrescens.

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REFERENCES


Copeland’s descriptions (1906, 1960) do not mention it being proliferous. A. lepturus is not conspecific with A. militare and A. nigrescens, as shown by the key. To our knowledge, A. militare has not been included in molecular studies so far.

In 1903, de Vore and Hoover made a collection on Mt. Apo (de Vore and Hoover 321) that may represent three different species (Copeland 1906, Figure 5). The pinna margin of the de Vore and Hoover specimens at K and P (de Vore and Hoover 321; Figures 5 and 6) differ from the types of A. militare (Copeland 1505, B, K, MIC, P, S; Figure 2) and A. nigrescens (Reinwardt 1183, L 0051021, US 00135105; Figure 3) in having the pinna margins finely serrate to serrulate toward the apex, while A. militare and A. nigrescens show on the distal half of the margin widely spaced prominent teeth with 2–4 small apical teeth; the apical segment of A. militare is similar to the pinna but smaller, that of de Vore and Hoover 321 consists of a lobed segment different from the shape of a pinna. The basiscopic side of the pinna is curving rather than straight as is in A. militare and A. nigrescens (Figures 2, 3, 5, and 6). The types of A. militare and A. nigrescens, and the specimens of de Vore and Hoover at K and P do not agree, and the species must remain separate. The specimens de Vore and Hoover 321 at K [K000445832] and P represent an undescribed species. US has a collection of de Vore and Hoover 321 [US 01516673] that matches closely A. nigrescens in details of the pinna, and it should be considered a representative of A. nigrescens. It is different from the collections at K and P. Copeland (1960) reports A. militare as a high elevation (> 1800 m) fern, terrestrial in a gorge (cf. label on P specimen P00642962); A. nigrescens is a preferred epiphyte rarely terrestrial.


