An overview of Neurolaeneae

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Neurolaeneae Rydb. (Figure 1) is a tribe in Compositae, originally proposed by Rydberg (1927) in his treatment for the North American Flora comprising two genera: *Neurolaena* R.Br. (Fig. 1E) and *Schistocarpha* Less. (currently Millerieae). Stuessy (1977) placed the group as a subtribe of Heliantheae Cass., but it was reestablished later in 2002 (Panero and Funk 2002). Although Rydberg (1927) originally considered the tribe to be closely related to Senecioneae Cass., molecular data later suggested it is sister to a clade that includes the tribes Bahieae B.G.Baldwin, Chaenactideae B.G. Baldwin, and Tageteae Cass. in the Heliantheae Alliance (Panero and Funk 2002). Panero (2007) established the current circumscription that includes five genera: *Calea* L. (Figure 1C), *Enydra* Lour. (Figure 1A), *Greenmaniela* W.M.Sharp (Figure 1D), *Heptanthus* Griseb. (Fig. 1B), and *Neurolaena*. Using a recent, family-wide phylogenomic dataset, Mandel et al. (2019) confirmed the placement of Neurolaeneae in the so-called "Heliantheae Alliance" and indicate it is sister to a clade that includes Heliantheae and Coreopsideae Lindl..

The tribe is found on most continents, except Antarctica and Europe, and it is present in 72 countries and nine overseas territories and departments (Figure 2). Three genera in Neurolaeneae are widespread: *Calea*, *Enydra* and *Neurolaena* and among these *Enydra* is the only genus naturally found outside the Americas, occurring in Africa (23 countries), Asia (13 countries) and Oceania (one country). *Neurolaena* is restricted to the Americas where it is known from 30 countries and eight territories in the Caribbean and one territory in South America. *Calea* is the third most widespread genus, occurring from Mexico to Argentina (but the genus is not known from Chile), including Jamaica and Trinidad and Tobago from the Caribbean, and *C. urticifolia* DC., introduced in Africa (Lawalrée 1982). *Heptanthus* and *Greenmaniela* are endemic to Cuba and Mexico, respectively.

Neurolaeneae is comprised of 179 species, and most species in the tribe belong to the genus *Calea* (154 species). Each of the other four genera is represented by far less species diversity, with *Neurolaena*, *Heptanthus*, *Enydra,* and *Greenmaniella* containing twelve, seven, five, and one species, respectively. Representatives of Neurolaeneae (Panero 2007) are recognized by a herbaceous to shrubby habit (rarely treelets); leaves commonly linear, ovate or trullate; capitula discoid or radiate arranged on paniculiform or corymbiform cymes (sometimes solitary); receptacle usually paleate (*Heptanthus* is exclusively epaleate, as are some species of *Calea* and *Neurolaena*); ray florets, when present, are pistillate, disc florets are monoclinous or functionally staminate; cypselae are blackish and the pappus is composed of bristles, scales, minute awns, or more rarely absent (in *Enydra*) (Figure 3).

Figure 1. Generic diversity of Neurolaeneae (Compositae). **A.** *Enydra (Enydra fluctuans* Lour.). **B.** *Heptanthus* (*Heptanthus shaferi* Britton). **C.** *Calea* (*Calea uniflora* Less.). **D.** *Greenmaniella* (*Greenmaniella resinosa* W.M. Sharp). **E.** *Neurolaena* (*Neurolaena lobata* R. Br.). Photos: **A**, L. Liao; **B**, J. L. Gomez; **C**, M. Bonifacino; **D**, C. G. Casanova; **E**, J. L. Gomez.

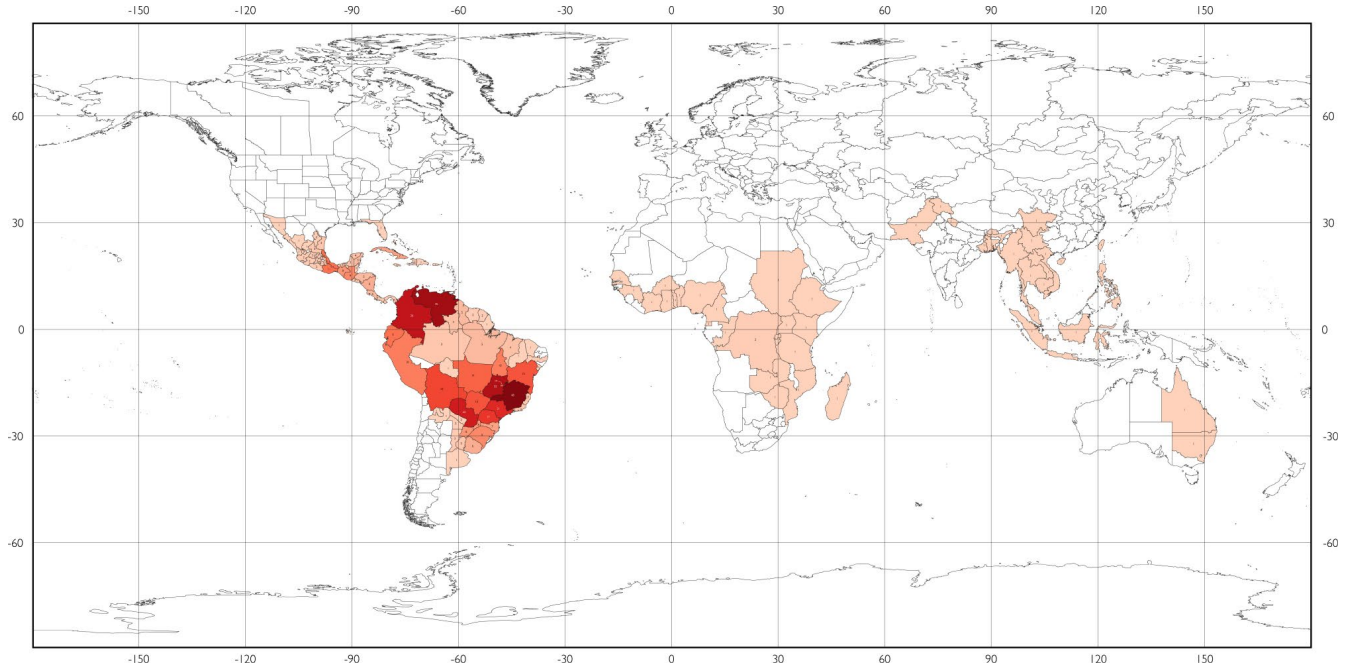

Figure 2. Global distribution and species diversity of the Neurolaeneae. The darker the color the greater the diversity. Notice the two hotspots (SE Brazil and Colombia-Venezuela). Three species of *Enydra* occurs naturally outside the Americas and *Calea urticifolia* was introduced in the Democratic Republic of Congo (Lawalrée 1982).

Enydra and *Heptanthus* are the only genera that are exclusively herbaceous. *Enydra* inhabits aquatic or wet areas, has opposite leaves, solitary sessile capitula, and is mainly characterized by four foliaceous phyllaries which form a cupulate involucre (Snow 1980; Panero 2007) and the epapose nature of its cypselae. *Heptanthus* is distinguished by rosette herbs, solitary, radiate capitula, involucrum with 1-2 series of phyllaries, disc florets functionally staminate and pappus composed of fimbriate scales (Panero 2007). The one species of *Greenmaniella*, *G. resinosa* (S.Watson) W.M.Sharp, is herbaceous or shrubby with alternate leaves, radiate capitula arranged in paniculiform cymes, a 1-2 seriate involucrum, cypselae with small wings in angles, and a pappus with crown of awns (Panero 2007). *Neurolaena* are recognized as herbs, shrubs or treelets, with alternate leaves, usually discoid (rarely radiate) capitula arranged in paniculiform or monochasial cymes, a 2-5 seriate involucrum, and pappus of bristles in 1-2 series (Panero 2007). *Calea* are characterized by being herbs or shrubs with usually opposite (rarely alternate or whorled) leaves, radiate (sometimes discoid) capitula either solitary or arranged in paniculiform or corymbiform cymes, 2-6 seriate involucrum, and pappus of 6-30 scales with entire or erose margins.

Except for a general description of each genus (Panero 2007), there has never been a systematic or phylogenetic study of Neurolaeneae since the tribe was established (Panero et al. 2001). Taxonomic reviews are available for *Enydra* (Snow 1980) and *Neurolaena* (Turner 1982), but no focused study has been carried out in any of the other genera.

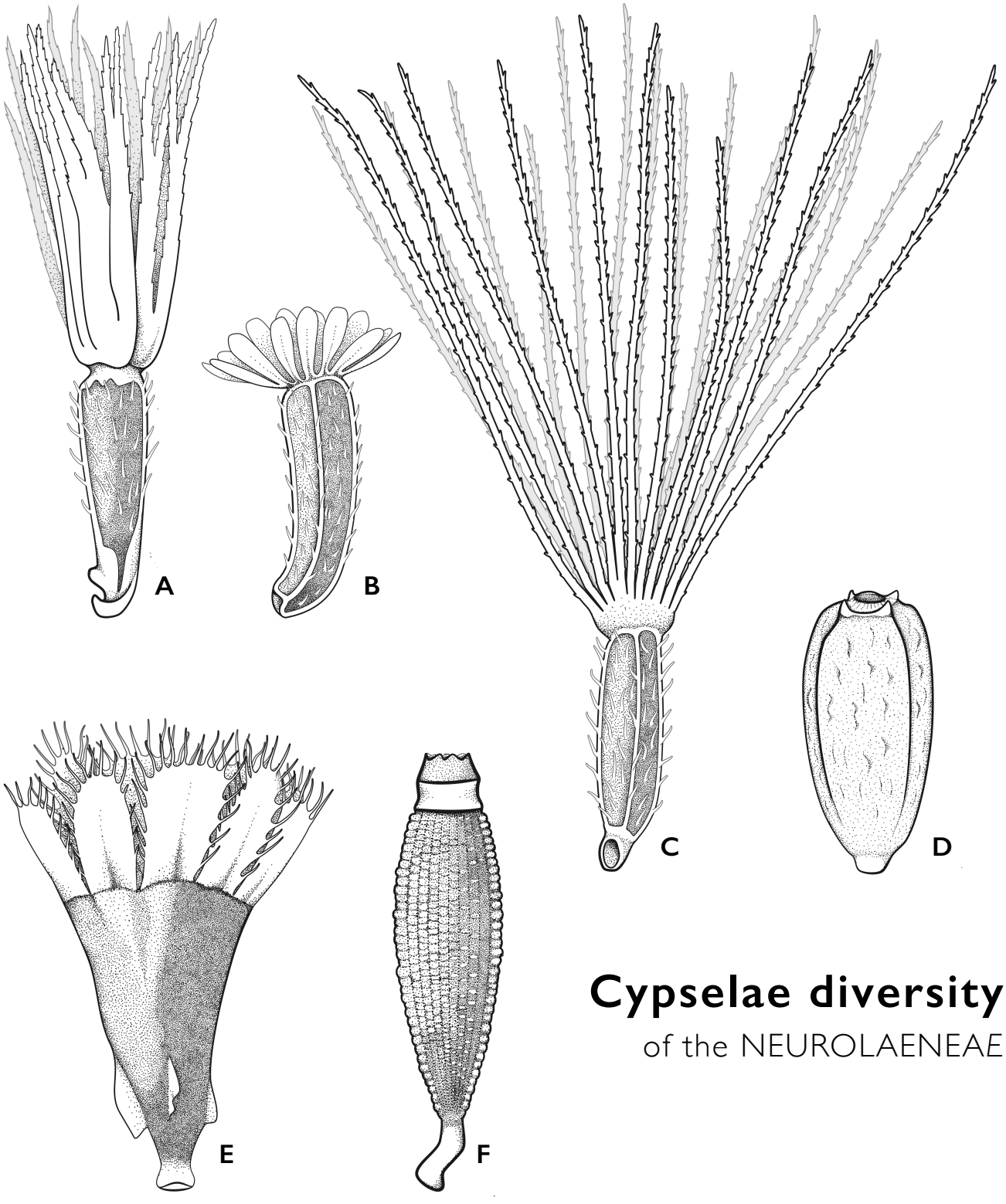

Figure 3. Cypselae diversity in the Neurolaeneae. **A.** *Calea* (*Calea jamaicensis* L.). **B.** *Calea* (*Calea caleoides* (DC.) H.Rob.). **C.** *Neurolaena* (*Neurolaena lobata* R. Br.). **D.** *Greenmaniella* (*Greenmaniella resinosa* W.M. Sharp). **E.** *Heptanthus* (*Heptanthus cochlearfolius* Griseb). **F.** *Enydra* (*Enydra sessilis* DC.). Adapted from Robinson (1981) and Sharp (1935).

NEUROLAENEAE diversity

The size of the circles is proportional to the number of species in each genus.

Calea

Calea L. is the most species-rich genus in the Neurolaeneae. There are 154 species in this genus, corresponding to 87% of the diversity in this tribe, half of which occur in megadiverse Brazil.

Calea clausseniana Baker in Serra da Canastra, Minas Gerais, Brazil.
Photo by J.B.A. Bringel Jr.

Figure 4. Diversity of *Calea,* the most species-rich genus of Neurolaeneae (Compositae). **A.** *Calea* sect. *Calea* (*Calea harlingii* H. Rob.). **B.** *Calea* sect. *Monanthocalea* (*Calea paraguayensis* (Kuntze) Deble). **C.** *Calea* sect. *Haplocalea* (*Calea cymosa* Less.). **D.** *Calea* sect. *Lemmatium* (*Calea fruticosa* (Gardner) Urbatsch, Zlotsky & Pruski). **E.** *Calea* sect. *Meyeria* (*Calea triantha* (Vell.) Pruski). Photos: **A**, A. Cerchiai, ; **B**,G. Heiden; **C**, G. A. Reis-Silva; **D**, H. J. C. Moreira; **E**, P. Schwirkowski.

Key to the Genera of Neurolaeneae

1a. Phyllaries 4; pappus absent ..... **Enydra**

1b. Phyllaries 5 or more; pappus present

2a. Pappus elements scales

3a. Disc florets functionally staminate; pappus elements fimbriate scales ..... **Heptanthus**

3b. Disc florets with functional androecium and gynoecium; pappus elements erose or entire scales ..... **Calea**

2b. Pappus elements bristles or shallow crown with awns

4a. Pappus elements 30-65 bristles 4–7 mm long ..... **Neurolaena**

4b. Pappus shallow crown with 4 awns up to 0.5 mm long ..... **Greenmaniella**

Calea (Figure 4) comprises 87% of species diversity in the tribe. The genus is concentrated in South America, where the highest richness is found in Brazil with 87 species (55 endemics), Venezuela with 33 species (19 endemics), and Colombia with 23 species (11 endemics). Five sections are recognized in *Calea* following Pruski (1998).

Calea sect. *Calea* (Figure 4A) is recognized by umbelliform to cymose capitulescences and pappuses longer than cypselae length (Urbatsch et al. 1986). It contains 52 species that occur across the whole range of the genus. It is the only section that occurs in Central America and the Caribbean, but the center of diversity is Venezuela and Colombia with 39 species - this section and *Calea* sect. *Monanthocalea* (Less.) Pruski (Figure 4B) are the only sections that occur in the Andes. *Calea* sect. *Monanthocalea* (Figure 4B) is characterized by monocephalous or oligocephalous capitulescences on long peduncles, and pappus scales often longer than cypselae (Pruski 1998). It has 33 species with most diversity in Brazil (16 species), but it also reaches the Andes.

Calea sect. *Haplocalea* (Less.) Pruski (Figure 4C) is characterized by whorled leaves, umbelliform capitulescence, and pappus longer than cypselae (Pruski 1998). This section has eight species and has the southernmost distribution. It is more diverse in Brazil and Paraguay, where seven species occur, while the remaining species occurs in Bolivia. *Calea* sect. *Meyeria* (DC.) Benth. & Hook.f. (Figure 4E) is recognized by cymose capitulescences and a smaller pappus, shorter than the cypselae. The highest diversity is in Brazil, where 40 of 49 species occur. *Calea* sect. *Lemmatium* Less. (Figure 4D) is distinguished by congested corymbiform (rarely cymose) capitulescences and pappus scales smaller than cypselae (Urbatsch et al. 1986). It is the most narrowly distributed section with all the twelve species occurring in southern Brazil. This is the only section for which a taxonomic review has been produced (Urbatsch et al. 1986).

Meanwhile, all other studies published on the genus over the past 40 years refer to regional taxonomic descriptions in floras (e.g., Wussow et al. 1985) and new species, such as *Calea funkiana* V.R.Bueno & G.Heiden the most recently described species (Bueno & Heiden 2021).

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