A phylogeny of the Triraphideae including Habrochloa and Nematopoa (Poaceae, Chloridoideae)

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Abstract

To investigate the evolutionary relationships among species of the tribe Triraphideae (including two monotypic genera, Habrochloa and Nematopoa), we generated a phylogeny based on DNA sequences from nuclear ribosomal (ITS) and four plastid markers (rps16-trnK, rps16 intron, rpl32-trnL, and ndhA intron). Habrochloa and Nematopoa form a clade that is sister to Neyraudia and Triraphis. Member of the Triraphideae have paniculate inflorescences, 3-veined, marginally ciliate lemmas, usually with hairy lateral veins, that are apically bifid and awned from between a sinus. A description of the Triraphideae and key to the genera is provided, and the biogeography is discussed, likely originating in Africa.

Keywords

Classification, Habrochloa, molecular phylogenetics, Nematopoa, Neyraudia, Triraphideae, Triraphis

Introduction

Clayton and Renvoize (1986) pointed out that Neyraudia R. Br. was perhaps an ally of Triraphis R. Br. since both genera possess slender microhairs and the two have keeled lemmas that are villous on the lateral veins (Watson and Dallwitz 1992). Based on DNA sequence studies Bouchenak-Khelladi et al. (2008) were first to show strong support for Neyraudia and Triraphis as being sister in the subfamily Chloridoideae Kunth ex Beilschm. Hilu and Alice (2001) and Bouchenak-Khelladi et al.
(2008), using the same \textit{matK} sequence marker placed these two genera in the subtribe Uniolinae Clayton, now a member of tribe Eragrostideae Stapf. Another DNA sequence study supported the placement of the \textit{Neyraudia–Triraphis} clade as being sister to remaining species in the Chloridoideae and, subsequently, the tribe Triraphideae P.M. Peterson [based on subtribe Triraphidinae Stapf (1917)] was erected to include these two genera (Peterson et al. 2010). Using unpublished DNA sequence phylogenies (Peterson and Romaschenko, unpubl.), the monotypic \textit{Habrochloa} C.E. Hubb., was added to the Triraphideae in the classification of all genera within the Poaceae (Soreng et al. 2015, 2017).

Hubbard (1935, 1957a, b) transferred \textit{Triraphis longipes} Stapf & C.E. Hubb. to \textit{Crinipes} Hochst. (Arundinoideae) since it possessed a bearded callus, then later moved it to a new monotypic genus, \textit{Nematopoa} C.E. Hubb. \textit{Nematopoa} was included in the Arundinoideae by Clayton and Renvoize (1986). In more recent classifications (Soreng et al. 2015, 2017), \textit{Nematopoa longipes} (Stapf & C.E. Hubb.) C.E. Hubb. was placed as a synonym of \textit{Triraphis} as originally described. Based on unpublished DNA sequence phylogenies (Peterson and Romaschenko, unpubl.), Soreng et al. (2022) and Gallaher et al. (2022) placed \textit{Nematopoa} in the Triraphideae. Therefore, the current concept of the Triraphideae consists of four genera, \textit{Habrochloa}, \textit{Nematopoa}, \textit{Neyraudia}, and \textit{Triraphis}.

\textit{Habrochloa bullockii} C.E. Hubb. is a small, delicate, African annual (culms 10–25 cm tall) with a fringe of hairs for a ligule and delicate panicles bearing 3–5-flowered spikelets, each including awned, apically bifid, marginally ciliate lemmas that bear trigonous caryopses, whereas \textit{Nematopoa longipes} is a caespitose, southern African perennial (culms 30–80 cm tall) with ciliate, membranous ligules and capillary panicles bearing 4–7-flowered spikelets, each including awned, apically bifid, marginally ciliate lemmas (Clayton et al. 2016). \textit{Neyraudia} consists of four reedlike perennials [culms (0.8–) 1–5 m tall], a cartilaginous ridge with a line of hairs apically for a ligule, and plumose panicles bearing 3–8-flowered spikelets, each including awned, apically bifid lemmas that are ciliate marginally and along lateral veins; three species in tropical and temperate Asia and one species in Africa (Watson et al. 1992; Filgueiras and Zuloaga 1999; Guala 2003; Clayton et al. 2016). \textit{Triraphis} consists of eight annual or perennials (culms 4–140 cm tall) with membranous ligules or a fringe of hairs open or contracted (rarely spiciform) panicles bearing 4–24-flowered spikelets, each including apically 3-lobed and 3-awned lemmas that are ciliate marginally and villous along the lateral veins, and trigonous caryopses; six species in Africa, one in Australasia and one in South America (Watson et al. 1992; Nightingale and Weiller 2005; Clayton et al. 2016).

In the present phylogenetic study, using DNA sequences from nuclear ribosomal (ITS) and four plastid markers (\textit{rps16-trnK}, \textit{rps16} intron, \textit{rpl32-trnL}, and \textit{ndhA} intron), we include for the first time \textit{Habrochloa bullockii}, \textit{Nematopoa longipes}, and \textit{Neyraudia arundinacea} (L.) Henrard with two other species of \textit{Neyraudia} and five species of \textit{Triraphis}. In addition, we include a description of the Triraphideae, key to the genera in the tribe, and hypothesize its biogeographical history.
Materials and methods

Detailed methods for DNA extraction, amplification, and sequencing are given in Romaschenko et al. (2012) and Peterson et al. (2010, 2014a, b, 2015a, b, 2016). We used Geneious Prime 2020 (Kearse et al. 2012) for contig assembly of bidirectional sequences of *ndhA* intron, *rpl32-trnL, rps16* intron, *rps16-trnK* and ITS regions, and implemented in Geneious Muscle algorithm (Edgar 2004) to align the sequences and adjust the final alignment. The maximum likelihood parameters for each region were estimated with GARLI 2.0 (Zwickl 2006) and were used as priors in Bayesian calculations to infer overall phylogeny. The Bayesian tree was constructed using MrBayes v3.2.7 (Huelsenbeck and Ronquist 2001; Ronquist et al. 2012). All compatible branches were saved. The Bayesian analysis was initiated with random starting trees sampling once per 100 generations and continued until the value of the standard deviation of split sequences dropped below 0.01 indicating convergence of the chains. The effective sample size (ESS) value for all the parameters was greater than 200 and the first 25% of the sampled values were discarded. Maximum likelihood bootstrap analyses (Felsenstein 1985) were performed using GARLI with 1000 repetitions. The resulted file containing 1000 trees from the bootstrap analysis was then read into PAUP* v.5.0 (Swofford 2000) to compute the majority rule consensus tree.

Our study was designed to test relationships among species residing in four genera (*Habrochloa, Nematopoa, Neyraudia, and Triraphis*) attributed to the Triraphideae. Representative species from all remaining tribes (Centropodieae P.M. Peterson, N.P. Barker & H.P. Linder, Cynodonteae Dumort., Eragrostideae Stapf, and Zoysieae Benth.) in the Chloridoideae have been included to test the monophyly of the tribe (Peterson et al. 2010). In addition, the phylogeny includes two species from the Danthonioideae, *Danthonia compressa* Austin and *Merxmuellera drakensbergensis* (Schweick.) Conert, and one species from the Panicoideae, *Chasmanthium latifolium* (Michx.) H.O. Yates, which was used as an outgroup.

Results and discussion

Thirty-five new sequences (16%) from five species (nine individuals) are newly reported in GenBank, along with all other sequences for 48 individuals and 41 species included in this study (Table 1). Total aligned characters, numbers of sequences, proportion of invariable sites, and other parameters are noted in Table 2. The resulting plastid and ITS topologies were inspected for conflicting nodes with ≥ 95% posterior probabilities. No supported conflict was found so plastid and ITS sequences were combined.

The Bayesian tree from the combined plastid and ITS regions is well resolved (Fig. 1). Most clades have posterior probabilities equal to 1.00 and additional bootstrap values of 90% or greater. There is strong support for *Habrochloa bullockii + Nematopoa longipes* sister to a monophyletic *Neyraudia* with three individuals of *N. reynaudiana* (Kunth) Keng ex Hitchc. sister to one individual of *N. arundinacea* (type of the genus)
Table 1. Taxon voucher (collector, number, and where the specimen is housed), country of origin, and GenBank accession for DNA sequences of *rps16-trnK*, *rps16* intron, *rps16-trnL*, *ndhA* intron, and ITS regions; **bold** indicates new accession; a dash (–) indicates missing data, an asterisk (*) indicates sequences not generated in our lab.

| Taxon                          | Voucher                        | Country         | *rps16-trnK* | *rps16* intron | *rps16-trnL* | *ndhA* intron | ITS       |
|-------------------------------|--------------------------------|----------------|-------------|---------------|--------------|---------------|-----------|
| 1. Centropodia glauca (Nees) Cope | Davidse 6367 (US)              | South Africa   | JF729075    | –             | JF729175    | JF729164     | JF729164  |
| 2. Centropodia mossamedensis (Rendle) Cope | Schwerkendorf 2250 (US)         | South Africa   | JF729076    | JF729182      | JF729176    | –             | –         |
| 3. Chamaanthium latifolium (Michx.) H.O. Yates | Peterson 22463 (US)            | USA, Maryland   | GU360517    | GU360438      | GU359891    | GU359379     | GU359319  |
| 4. Chloris barbata Sw. | Peterson 22255 & Saarela (US)  | Mexico, Sinaloa | GU360514    | GU360435      | GU359873    | GU359377     | GU359320  |
| 5. Cottus pappophoroides Kunth | Peterson 21463, Soreng, LaTorre & Rojas (US) | Peru, Ancash | GU360060 | GU360456      | GU359842    | GU359363     | GU359237  |
| 6. Damabonia comparsa Austin | Peterson 21986 & Levine (US)  | USA, North Carolina | GU360521    | GU360483      | GU359865    | GU359345     | –         |
| 7. Eleusine indica (L.) Gaertn. | Peterson 21362, Saarela & Flores Villegas (US) | Mexico, Mexico | GU360496    | GU360472      | GU359797    | GU359473     | GU359338  |
| 8. Eleusine poitiana (Chiov.) Chiov. | Burger 2915 (US)               | Ethiopia       | GU360601    | GU360457      | GU359843    | –             | GU359236  |
| 9. Ellisosbha ranger (Pilg.) P.M. Peterson & N.P. Barker | Barker 960 (BOL)               | Namibia        | JF729079    | JF729184      | –             | JF729166     | JF345167  |
| 10. Enneapogon xeler Lehm. | Sachse 008 (MO)                | South Africa, Western Cape | JQ345237    | JQ345279      | JQ345322    | JQ345208     | JQ345168  |
| 11. Entoplocamia aristulata (Hack. & Rendle) Stapf | Seydel 187 (US)               | South Africa   | GU360492    | GU360468      | GU359793    | GU359469     | GU359342  |
| 12. Enneapogon xeler Lehm. | Latz 13486 (MO)                | Australia      | JQ345238    | JQ345281      | JQ345323    | JQ345209     | JQ345169  |
| 13. Enneapogon xeler Lehm. | Peterson 14345, Soreng & Rosenberg (US) | Australia, Western Australia | GU360703    | GU360288      | GU359986    | GU359535     | GU359137  |
| 14. Gouinia virgata var. robusta J.J. Ortiz | Reeder 4714 & Reeder (US)      | Mexico, Zacatecas | KF827775    | KF827710      | KF827639    | KF827584     | KF827521  |
| 15. Gymnopogon granifer Roseng., B.R. Arill. & Izag. | Peterson 16642 & Refolso-Rodriguez (US) | Peru, Apurimac | GU360581    | GU360383      | GU359816    | GU359436     | GU359200  |
| 16. Habrophyla bulbicci C.E. Hubbard | Peterson 23927b, Soreng, Romaschenko & Abaid (US) | Tanzania, Ruwuma | ON012448 | ON012424 | ON012427 | ON012435 | OM980631 |
| 17. Leptocarydion vulpiastrum (De Not.) Stapf | Peterson 24238, Soreng & Romaschenko (US) | Tanzania | KF827792 | KF827725 | KF827660 | KF827595 | KF827539 |
| 18. Leptochloa digitata (R.Br.) Domin | Risker 476 & Kerrigan (MO)        | Australia, Northern Territory | JQ345246 | JQ345289 | JQ345331 | JQ345213 | JQ345178 |
| 19. Muhlenbergia japonica Steud. | Peterson 21986 & Levine (US)   | South Africa   | JF729074    | JF729183      | –             | JF729165     | –         |

**Bold** indicates new accession; a dash (–) indicates missing data, an asterisk (*) indicates sequences not generated in our lab.
| Taxon | Voucher | Country | Accession Numbers |
|-------|---------|---------|-------------------|
| *Nematopoa longipes* (Stapf & C.E. Hubb.) C.E. Hubb. | Simon 2353 | Africa | MF035992* |
| *Neyraudia arundinacea* (L.) Henrard | Peterson 23991, Soreng, Romaschenko & Abeid (US) | Tanzania, Njomba | ON012449 |
| *Neyraudia reynaudiana* (Kunth) Keng ex Hitchc. | Columbus 5302 (RSA) | Tanzania, Region I | KF356392* |
| *Neyraudia reynaudiana* (Kunth) Keng ex Hitchc. | Soreng 5318, Peterson & Sun Hang (US) | China, Yunnan | – |
| *Pappophorum pappiferum* (Lam.) Kuntze | Peterson 21689, Soreng, La Torre & Rojas Fox (US) | Peru, Ancash | GU360700 |
| *Perotis indica* (L.) Kuntze | Peterson 23880, Soreng & Romaschenko (US) | Tanzania, Region I | KF827801 |
| *Psilolemma jaegeri* (Pilg.) S.M. Phillips | Peterson 24247, Soreng & Romaschenko (US) | Tanzania, Region I | KM011122 |
| *Sporobolus virginicus* (L.) Kunth | Peterson 15683 & Soreng (US) | Chile, Region I | GU360610 |
| *Tragus berteronianus* Schult. | FLSP 457 (US) | Peru | GU360616 |
| *Tridens flavus* var. *chapmanii* (Small) Shinners | McColl 4138 (MO) | USA, Missouri | KF827817 |
| *Triplasis americana* P. Beauv. | Kral 12065 (MO) | USA, Georgia | GU827818 |
| *Triraphis andropogonoides* (Steud.) E. Phillips | Mennell s.n. (US) | South Africa, Cape Province | KF827820 |
| *Triraphis mollis* R. Br. | Lazarides 046 & Palmer (US) | Australia, Uluru National Park | KF827821 |
| *Triraphis mollis* R. Br. | Peterson 14344, Soreng & Rosenberg (US) | Australia, Western Australia | GU360669 |
| *Triraphis mollis* R. Br. | Saarela 1608, Peterson, Soreng & Judziewicz (US) | Australia, Northern Territory | ON012450 |
| *Triraphis mollis* R. Br. | Saarela 1615, Peterson, Soreng & Judziewicz (US) | Australia, Northern Territory | ON012451 |
| *Triraphis mollis* R. Br. | Saarela 1648, Peterson, Soreng & Judziewicz (US) | Australia, Northern Territory | ON012452 |
| *Triraphis mollis* R. Br. | Saarela 1656, Peterson, Soreng & Judziewicz (US) | Australia, Northern Territory | ON012453 |
| *Triraphis purpurea* Hack. | Schweickerdt 2115 (US) | Australia, Northern Territory | ON012454 |
| *Triraphis ramosissima* Hack. | Seydel 4278 (US) | Australia, Northern Territory | ON012455 |
| *Zoysia macrantha* subsp. *walshii* M.E. Nightingale | Loch 435 (US) | Australia | GU360640 |

**Phylogeny of the Triraphideae**

24 *Nematobolus langiunculatus* (Nees) P.Ilg., C.E. Hubb., C.E. Hubb.
25 *Nematobolus arundinaceus* (L.) Herrard
26 *Neyraudia ciliata* (Kunth) Keng ex Hitchc.
27 *Neyraudia ciliata* (Kunth) Keng ex Hitchc.
28 *Neyraudia ciliata* (Kunth) Keng ex Hitchc.
29 *Neyraudia ciliata* (Kunth) Keng ex Hitchc.
30 *Neyraudia ciliata* (Kunth) Keng ex Hitchc.
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46 *Neyraudia ciliata* (Kunth) Keng ex Hitchc.
47 *Neyraudia ciliata* (Kunth) Keng ex Hitchc.
48 *Neyraudia ciliata* (Kunth) Keng ex Hitchc.
plus a monophyletic *Triraphis*. The *Triraphis* clade includes six individuals of *T. mollis* R. Br. (type of the genus as treated by Burbidge 1946 and Peterson et al. 2022) sister to *T. schinzii* Hack. and *T. ramosissima* Hack. sister to *T. andropogonoides* (Steud.) E. Philipp + *T. purpurea* Hack. Our molecular data clearly support independent recognition of *Nematopoa* since it is sister to *Habrochloa* and not a member of the *Triraphis* clade.

*Habrochloa bullockii* and *Nematopoa longipes* are clearly aligned within the *Triraphideae*, and together with *Neyraudia* and *Triraphis*, share the following salient morphological features: panicle inflorescences, 3-veined, marginally ciliate lemmas, usually with hairy lateral veins, and lemmas that are apically bifid and awned from between the sinus (Watson and Dallwitz 1992; Watson et al. 1992; Peterson et al. 2010; Clayton et al. 2016). Another probable synapomorphy for these four genera is possession of panicoid-type bicellular microhairs (long, narrow basal and terminal cells; Amarsasinghe and Watson 1988). Watson et al. (1992) verified the presence of panicoid bicellular microhairs for *Habrochloa, Nematopoa*, and *Triraphis* but indicate that they are absent in *Neyraudia arundinacea*. However, Clayton and Renvoize (1986) previously indicated that *Neyraudia* possesses slender microhairs similar to those in *Triraphis*.

Based on a sample containing *Nematopoa*, *Neyraudia*, and *Triraphis*, Gallaher et al. (2022) determined the crown age (10.62 Ma) and stem age (46.76 Ma) of the *Triraphideae*. Although at least three species of *Neyraudia* include tropical and temperate Asia in their distribution, Africa is the most likely area of origin for the *Triraphideae* since all four genera in the tribe include species distributed in Africa. In addition, the *Triraphideae* shares a common ancestor with *Centropodieae*, also from Africa and temperate Asia (Peterson et al. 2011). Because more than half of the genera of Chloridoideae reside in Africa and the larger tribes, i.e., the Eragrostideae

**Table 2.** Characteristics of the five DNA regions (*rps16-trnK, rps16 intron, rpl32-trnL, ndhA and ITS*) and parameters used as priors in Bayesian analyses estimated with GARLI 2.0.

| Characteristic                  | rps16-trnK | rps16 intron | rpl32-trnL | ndhA intron | Combined plastid data | ITS | Overall |
|--------------------------------|------------|--------------|------------|-------------|-----------------------|-----|---------|
| Total aligned characters       | 887        | 1046         | 844        | 1146        | 3923                  | 769 | 4692    |
| Number of sequences            | 45         | 45           | 46         | 42          | 178                   | 41  | 219     |
| Number of new sequences        | 6 (13%)    | 6 (13%)      | 8 (17%)    | 7 (17%)     | 27 (15%)              | 8   | (20%)  |
| Likelihood score (-lnL)         | 3909.0     | 3405.6       | 3778.7     | 4281.4      | 7973.0                | 6   | (16%)  |
| Number of substitution types   | 6          | 6            | 6          |             | 6                     |     |         |
| Model for among-sites rate variation | gamma | Gamma | gamma | gamma | gamma |
| Substitution rates             | 1.2071     | 1.2951       | 1.0625     | 0.9848      | –                     | 1.1422 |        |
| 2.7093                         | 1.2876     | 1.7914       | 2.5216     | –           | 2.6273                |     |        |
| 0.4083                         | 0.3028     | 0.3251       | 0.2912     | 1.7222      | –                     |     |        |
| 1.5405                         | 1.1547     | 1.4401       | 1.9389     | 0.6568      | –                     |     |        |
| 2.9778                         | 2.0746     | 1.5146       | 2.3679     | 4.5253      | –                     |     |        |
| 1.0000                         | 1.0000     | 1.0000       | 1.0000     | 1.0000      | –                     |     |        |
| Character state frequencies    | 0.3088     | 0.3779       | 0.3693     | 0.3669      | –                     | 0.2404 |        |
| 0.1363                         | 0.1226     | 0.1380       | 0.1348     | 0.2374      | –                     | 0.2582 |        |
| 0.1462                         | 0.1743     | 0.1222       | 0.1484     | 0.2641      | –                     | 0.2582 |        |
| 0.4084                         | 0.3251     | 0.3703       | 0.3497     | –           | –                     | 0.2582 |        |
| Proportion of invariable sites | 0.1666     | 0.3154       | 0.0413     | 0.2537      | –                     | 0.2547 |        |
| Gamma shape parameter (α)      | 2.1848     | 1.0833       | 0.9498     | 1.0636      | –                     | 0.9409 |        |
and Zoysieae have centers of diversity there, Hartley and Slater (1960) earlier concluded that the subfamily probably originated on the African continent and spread to other parts of the world (Bouchenak-Khelladi et al. 2008; Peterson et al. 2007, 2010, 2011, 2014c).
Taxonomy

Triraphideae P.M. Peterson, Molec. Phylogen. Evol. 55(2): 591. 2010 ≡ Triraphidinae Stapf, Fl. Trop. Afr. 9: 22. 1917 – Type: Triraphis R. Br., Prodr. 185. 1810.

Description (emendation). Annuals or perennials, sometimes rhizomatous or reed-like (Neyraudia) culms 4–500 cm tall, erect or decumbent; ligules membranous and ciliate or a fringe of hairs; inflorescence a panicle, open to contracted, rarely spiciform; spikelets 2–15 mm long, 3–24-flowered, laterally compressed; glumes usually shorter than the spikelets or upper glume 2 × as long as adjacent lemma (Habrochloa), 0-, 1- or 3-veined, membranous, sometimes hyaline, apex entire to mucronate, rarely awned; lemmas membranous, rarely cartilaginous, 3-veined with ciliate or pilose margins, lateral veins, if present, usually hairy and sometimes extending as awns (Triraphis), apex bifid and awned from between the sinus; paleas 0.5 to as long as lemma, 2-veined; stamens 3; caryopses with adherent pericarp, often trigonous to ellipsoid, sometimes linear.

Included genera. Habrochloa, Nematopoa, Neyraudia, Triraphis.

Key to the genera

1. Lemmas 3-awned, the lateral veins extending into awns................. Triraphis
   – Lemmas 1-awned, the lateral veins never extending into awns .................2

2. Culms (80–) 100–500 cm tall, generally 1–1.5 cm wide at base, often woody; plants perennial, reedlike; ligules cartilaginous at base, apically with a line of hairs; panicles 30–80 cm long, plumose............................................ Neyraudia
   – Culms 10–80 cm tall, ≤ 3 mm wide at base, herbaceous; plants annual not reedlike; ligules membranous with a fringe of hairs, not cartilaginous at base; panicles 2–30 cm long, not plumose.........................................................3

3. Spikelets 2–2.5 mm long; lemmas 1–1.3 mm long, 3-veined, awned, the awns 4–6 mm long; upper glumes 2 × as long as adjacent lemma ............
   ............................................................ Habrochloa
   – Spikelets 6–10 mm long; lemmas 3.5–4.3 mm long, 1-awned, the awns 8–13 mm long; upper glumes 0.5–0.6 × as long as adjacent lemma ....
   .................................................................................................. Nematopoa

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