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Restoring the Generic Rank of Hebanthe Martius (Amaranthaceae)

TH. BORSCH & T.M. PEDERSEN

Abstract:
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It is proposed to re-establish the genus *Hebanthe* (Amaranthaceae, subfam. Gomphrenoideae), described by Martius in 1825, and since then by most authors classified within *Gomphrena* or *Pfaffia* as a section. It is shown that in floral structures, inflorescence architecture, pollen morphology, and vegetative morphology *Hebanthe* is sufficiently distinct to merit segregation at generic level. A synopsis of the 7 species, all lianas, that are recognized by the authors is presented, including *H. occidentalis* (R.E.Fr.) Borsch & Pedersen comb. nov., *H. occidentalis* (R.E.Fr.) Borsch & Pedersen *var. bangii* (R.E.Fr.) Borsch & Pedersen comb. et stat. nov., *H. grandiflora* (Hook.) Borsch & Pedersen comb. nov., *H. reticulata* (Seub.) Borsch & Pedersen comb. nov., and *H. paniculata* Mart. f. *ovatifolia* (Heimerl) Borsch & Pedersen comb. nov. A key to facilitate their identification is provided.

Resumen:
Los autores restablecen el género *Hebanthe* (Amaranthaceae, subfam. Gomphrenoideae), descrito por Martius en 1825, y referido a *Gomphrena* o a *Pfaffia* por la mayoría de los autores posteriores. Consideran que tanto la morfología floral como el porte son en *Hebanthe* suficientemente distintos, por lo que merece ser reconocido a nivel genérico. Dan una sinopsis de las 7 especies aceptadas y una clave para diferenciarlas. Proponen las siguientes nuevas combinaciones: *Hebanthe occidentalis* (R.E.Fr.) Borsch & Pedersen comb. nov., *H. occidentalis* (R.E.Fr.) Borsch & Pedersen *var. bangii* (R.E.Fr.) Borsch & Pedersen comb. et stat. nov., *H. grandiflora* (Hook.) Borsch & Pedersen comb. nov., *H. reticulata* (Seub.) Borsch & Pedersen comb. nov., *H. paniculata* Mart. f. *ovatifolia* (Heimerl) Borsch & Pedersen comb. nov.

Introduction

The genus *Hebanthe* was originally described by Martius in 1825, based on several morphological characters of the flower: Calyx [i.e. bracteoles] faintly coloured, 2-merous, sepals concave. Corolla 5-merous, inner petals swathed in wool. Staminal tube 5-parted, segments 3-fid, middle lobe bearing an elliptical, 1-celled anther, lateral lobes entire. Style scarcely present. Stigma capitate, notched. Utricle indehiscent, 1-seeded (translation by the authors). However, Martius' generic concept has never been used again by later authors, who usually merged *Hebanthe* with other genera, due to single superficial similarities in habit or floral morphology.

On behalf of king Max Joseph I. of Bavaria, Martius went to Brazil from 1817 to 1820 (see

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FÖRTHER 1994). During this journey, he discovered a variety of new plants, among them many new Amaranthaceae. His findings were published in "Nova genera et species plantarum", the three volumes of which appeared in Munich between 1823 and 1832. This monumental work offered Martius the opportunity of a more detailed study of the Amaranthaceae, a family in which Martius had already shown some interest in his earlier work "Plantarum horti academici erlangensis" (1814). In this publication he described the new genus *Pithyranthus* (now referred to *Alternanthera*).

Martius can be considered the first "family specialist" of the Amaranthaceae: In his "Beitrag zur Kenntnis der natürlichen Familie der Amarantaceen" Martius monographically treated all the 28 genera known to science at this time, and also showed their worldwide distribution on a map. This monograph was published in "Nova Acta Leopoldina" in 1826, Vol. 13(1), but according to STAFLEU and COWAN (1981) a preprint already had appeared in 1825. Martius included a lot of plant names into this monograph that he cited as published in "Nova genera et species plantarum" in 1826. Among the generic names also *Hebanthe* is cited.

Until today the best morphological analysis of *Hebanthe* is that of MARTIUS (1825, 1826). *Hebanthe* was covered in detail by the monograph of *Pfaffia* by STÜTZER (1935). However, her study relied largely on the same set of morphological characters that were already used by Martius. Pollen grains of *Pfaffia grandiflora* (= *Hebanthe grandiflora*) were studied by NOWICKE (1975) and those of *Pfaffia laurifolia*, *P. paniculata* and *P. paraguayensis* (all three are synonyms of *Hebanthe paniculata*) by CUADRADO (1988).

New information on morphological, micromorphological and palynological characters of *Hebanthe*, which is presented and discussed in the present paper, suggests that the generic concept of Martius is correct. In comparison with the other taxa in the Gomphrenoideae *Hebanthe* is considered a genus that is clearly defined by a syndrome of characters and that is well distinguished from other genera.

The present paper is the result of a chance encounter between the authors. While working independently, we both arrived at the conclusion that the genus *Hebanthe* was misplaced as a section of *Pfaffia* Mart. and that, in view of its peculiarities in floral structure and biological type, it is better to establish it as an independent genus. As there would be no point in publishing our results separately, we agreed that by pooling our arguments and experience, we would only strengthen our case.

Material and Methods

The present study is mainly based on the analysis of herbarium specimens that were studied during visits of both authors at (abbreviations according to HOLMGREN et al. 1990) BM, C, K, M, P; of T.B. at BR, F, MO, MA, US, VEN, WU and of T.M.P. at G, LIL, S, SI, UPS and Z. The results of extensive field observations in Argentina and Paraguay of the second author have been included.

Pollen grains were treated by acetolysis for 2 minutes as described by ERDTMAN (1960). For scanning electron microscopy acetolyzed pollen grains suspended in water were brought to aluminium stubs previously covered with a thin film of Tempfix. The preparation was then continued after the water had evaporated completely. Pieces of leaves, floral parts, and seeds were mounted on aluminium stubs using doublesided adhesive tape (Tesafix). All specimens were coated with gold (ca. 25 nm) with a Sputter Coater (Balzers Union SCD 040, Balzers GmbH, Wiesbaden) and analyzed in a Cambridge S 200 scanning electron microscope equipped with a LaB_6-cathode for high resolution. The SEM-work has been undertaken in the Botanical Institute of the University of Bonn.

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Historical overview of the classification

Apparently, the only reference in literature concerning the genus *Hebanthe* before the time of Martius is the description of *Iresine erianthos* by POIRET (1813). This name is based on an unpublished description by Vahl of a specimen in Jussieu's herbarium of *Hebanthe paniculata* with deformed flowers. Vahl had placed the species in *Celosia*, but it can be seen from his notes, now in C, that he never dissected a flower and therefore was not aware of the total abscence of the reproductive organs. Apparently, Martius did not associate Poiret's name and description with his new genus.

Martius described *Hebanthe* in "Nova genera et species plantarum" in 1826, comprising four species. Martius defined the genus on the basis of differences to other genera in floral morphology (important characters mentioned are "petalis inferioribus lana stricta cinctis; tubus stamineus quinquepartitus, laciniis trifidis, lacinulis mediis; stigma capitatum aut bilobum"). In the same opus Martius established the genera *Pfaffia*, *Sertuernera* and *Trommsdorffia*. In the "Beitrag zur Kenntnis der natürlichen Familie der Amarantaceen", Martius cites these new taxa as published in "Nova genera et species plantarum", and again gives more or less detailed morphological descriptions. Unfortunately, the "Beitrag" must have appeared earlier (see above). So the date of valid publication is 1825.

Hebanthe was classified within *Gomphrena* as a section by ENDLICHER (1837); judging from his text, he only knew the genus from the description by Martius. The opinion of Endlicher was accepted by MOQUIN-TANDON (1849), who clearly based his opinion on a thorough examination of the available material, and his treatment was in accordance with his generally very wide generic concept. In this concept *Gomphrena* also comprises the genera *Pfaffia* and *Sertuernera*. SEUBERT (1875) built upon the treatment, while a new taxon was added to the genus under this name by HEIMERL (1908).

KUNTZE (1891) transferred *Hebanthe* to *Pfaffia* as a section. Although his change was practically based on no sound arguments or further investigations, probably all later authors of floras and other general works built upon the concept deviced by him. Kuntze also merged the genus *Sertuernera* into *Pfaffia*. SCHINZ (1893, 1934) in his widely known classification of the Amaranthaceae uses the same generic concept of *Pfaffia*, that includes *Sertuernera* and *Hebanthe*. This is accepted by STANDLEY (1917, 1937), FRIES (1920), CHODAT & REHFOUS (1927), SUESSENGUTH (1934), STÜTZER (1935), ELIASSON (1988) and TOWNSEND (1993). New species were added to the genus *Hebanthe* under the generic name *Pfaffia* by FRIES (1920) and CHODAT (1927).

HOOKER (1880) recognized the genus *Hebanthe*, but in a broader sense than in the original circumscription by Martius. Hooker included *Trommsdorffia* together with a group of species at present classified within *Gomphrena*. HEMSLEY (1882) and BAILLON (1887) also recognized *Hebanthe*, again with the inclusion of *Trommsdorffia*. Hemsley added several new species to *Hebanthe*. Many of them are clearly members of the genus *Iresine* and were probably put into *Hebanthe* due to superficial similarities in habit.

DIETRICH (1839) used the concept of Martius without any comment and simply treated *Hebanthe* with the same four species that were described within the genus by MARTIUS (1825, 1826).

Besides, several authors have used the name, describing new taxa, but without reflecting the generic taxonomy of *Hebanthe* (BENTHAM 1844, WATSON 1883, WAWRA v. FERNSEE 1888).

The genus *Hebanthe*
Morphology and palynology

Habit: All species are perennial, woody lianas, mostly leaning or twining, often to a con-

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siderable height. *Hebanthe occidentalis* reaches at least to some 15 m with a trunk 5–10 cm in diameter, as observed by the second author, its mass of inflorescences far away in the tops of trees. Leaves: Opposite; generally with a more or less dense indumentum; hairs multicellular, simple or branched, always roughened by small spinelike excrescences of the cell wall (see Fig. 4). Inflorescence: Flowers basically arranged in racemes, flowers clearly separated from each other and racemes not conspicuously elongating at maturity. Synflorescence (see Fig. 2): A complex branching system with dominating central axis and opposite branches, sometimes with 1–2 accessory branches arising from the same axil. Flowers: Hermaphroditic; tepals 5, unequal, the outer two 3-veined, broadly ovate, rounded, sparsely to richly pubescent with short, simple trichomes, inner narrowly ovate, lateral veins often obsolete , densely wooly on abaxial side, not indurating at maturity (Fig. 3). Androeceum: With 5 stamens, filaments connate for 25–30%, forming a usually shallow cup, with or without 2 lateral appendages, margin always entire, pseudostaminodia 0. Gynoeceum: Ovary sessile, obovoid, stigma sessile or at the end of a very short style, stigma with 2 extremely broad lobes, being in a more or less vertical orientation in the young, and becoming orientated horizontally in mature flowers. Seed: Ovoid, notched at apex, where the funicle is attached, embryo large, cotyledons more or less the length of the radicle, about four times as long as broad, concave; bracteoles falling together with flowers at maturity. Pollen (Fig. 5): Sphaeroidal, pantoporate, 15–22 µm in diameter; pori 34–48, 1.9–2.7 µm in diameter, deeply sunken and mesoporia extremely narrow; parts of the tectum proximal to the apertures interrupted by distinct, elongated perforations, distal part of tectum somewhat undulate or with cylindrical, about 0.4 µm long spinulae.

Generic concept and relations of *Hebanthe*

Table 1 provides a summary of important characters of *Hebanthe* in comparison to morphologically similar and probably more closely related American genera of the Gomphrenoideae. The genus *Iresine* P.Browne has not been included. Its similarities in habit (slender shrubs or lianas) to *Hebanthe* and *Trommsdorffia* sensu Martius are due to convergent or parallel evolution, whereas obvious differences exist in floral structure and pollen morphology (BORSCH 1995). *Hebanthe* is a genus showing a syndrome of characters that is uniformly developed in all species. The character syndrome sets it well apart from other genera of the Gomphrenoideae: The perianth bears conspicuous long and stiff trichomes, arranged in a very specialized way: dorsally only on the inner two tepals and the covered half of the middle tepal (Fig. 3 B); the androeceum consists of entirely glabrous filaments, gradually widening to the base and united into a shallow cup, and with or without two acute lateral appendages varying in size (Fig. 3 D, E); the pollen grains have extremely narrow mesoporia with the tectum laterally reduced, resulting in large perforations close to the aperture (Fig. 5); the stigma consists of two broadly emarginate lobes (Fig. 3 C); the flowers are arranged in a complex, several times branched racemose synflorescence, with the flowers well separated from the beginning of their development, and racemes not elongating at maturity (Fig. 2); the habit is a tall, woody liana.

The specialized arrangement of the long and stiff perianth trichomes, most probably serving dispersal, is a derived character only known from *Hebanthe* in the Gomphrenoideae. It might be interpreted as an adaptation to more humid habitats where the outermost tepals protect the trichomes as long as possible. Most remarkably, a similar arrangement of the indumentum, obviously serving the same purpose, is present in the non related genus *Sericostachys* (Subfam. Amaranthoideae) from tropical Africa. The only species, *Sericostachys scandens*, is also a liana growing in rainforests. The morphology of the androeceum is specialized. A structure that occurs in several species of *Hebanthe*, in which stamen

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appendages and pseudostaminodes are completely lacking, is not known from any other members of the Gomprenoideae; in comparison to species of *Hebanthe* with the appendages present, the filaments with appendages in other genera are generally fused to a much higher degree. The morphology of the pollen grains is distinctly specialized and unique in the Gomphrenoideae. The extremely narrow and distally acute mesoporia are similar to those found in pollen of many of the species of *Gomphrena* (see ELIASSON 1988). In *Gomphrena* the proximal parts of the tectum are completely lacking, with the columellae freely visible, whereas in *Hebanthe* the tectum extends down to the apertures, but it is regularly interrupted by large perforations. The stigma is similar to that of certain species of *Pfaffia*, but the lobes are usually broader in *Hebanthe*. A similar inflorescence morphology (a synflorescence composed of loose racemes with the main axis dominating) occurs in *Froelichia*, a genus very well set apart through a variety of other characters; small lianas occur in *Trommsdorffia* sensu Martius, but this group is also distinguished through a variety of other characters.

This character syndrome clearly defines *Hebanthe* as a distinct evolutionary line within Gomphrenoideae. The genus shows several advanced features, and in the circumscription presented here, it most likely is monophyletic.

A sound hypothesis on the systematic position of *Hebanthe* within the Gomphrenoideae can hardly be given at the moment, as not yet enough is known about the relations between the already established genera. In the Gomphrenoideae a lot of problems arise due to the repeated evolution of similar features, usually based on a rather reduced basic pattern of floral structures. Looking at previous classifications, the idea of *Trommsdorffia* as the closest group (HOOKER 1880) is rather improbable. The superficially similar climbing habit would be the only shared character, a feature easily evolving through parallel evolution and occurring several times in the Gomphrenoideae (also in species of *Alternanthera*, *Iresine* and in *Pseudogomphrena*). Contrary to the treatment of KUNTZE (1891) and subsequent authors, *Hebanthe* is distinct from *Pfaffia*, most strikingly by the indumentum of the perianth, the pollen morphology, the inflorescence architecture, differences of the androeceum, and the habit. Major differences to *Gomphrena*, contrary to the treatment of ENDLICHER (1837) and subsequent authors, are in the indumentum of the perianth, in pollen morphology, in stigma morphology, in inflorescence morphology and, in habit.

Phytogeography

The geographical distribution of the genus *Hebanthe* is not very satisfactorily known, but apparently it reflects the subdivision of the genus proposed by SUESSENGUTH (1934) in subsections *Odontella* and *Anodontella*, the former found in eastern tropical South America, the latter occurring from Mexico and continental Central America along the eastern slopes and foothills of the Andes as far south as the Yungas region of Bolivia and north-western Argentine, reaching into the lowlands of eastern Bolivia and Paraguay, with a single outpost in southern Brazil. *Hebanthe* is apparently absent from the West Indies.

Ecology

The ecology of the genus is unsufficiently known. Most of the species are woodland plants, as is to be expected from their climbing habit. We have generally found them in the outskirts of the tall forest or in secondary woodland and scrub; *H. reticulata* was recorded from the dry Caatinga woodland in north-eastern Brazil.

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Synopsis of the genus *Hebanthe*

Attempts to subdivide the genus *Hebanthe* (or the section *Hebanthe*, respectively, according to most authors) were mostly based on characters of the androeceum, as suggested by FRIES (1920), CHODAT (1927) and formally validated by SUESSENGUTH (1935) as subsections *Odontella* and *Anodontella*. The species with filaments devoid of lateral appendages appear to form a well defined group, probably more closely related to each other than to any species with appendages. However, the relations of these groups need to be further studied.

According to our generic concept *Hebanthe* currently comprises 7 species. In the following synopsis necessary new names are established and a provisional key is presented to provide a possibility to identify the species. We decided to include this key as the critical revision currently underway that will be covering species relationships, species distributions etc., will take some more time to be completed.

Description of the genus:

Hebanthe Mart., Beitr. Amarantac.: 96 (1825) & Nov. Gen. sp. pl. 2: 43, Tab. 140, 142 (1826). Type species: *Hebanthe paniculata* Mart.

The name *Hebanthe* is derived from the greek ηβη (= Behaarung) and ανθος (= flower), according to the wooly flowers.

Hebanthe paniculata Mart., Beitr. Amarantac.: 96. 1825 & Nov. Gen. sp. pl. 2: 43. 1826 ≡ *Iresine paniculata* (Mart.) Spreng., Syst. veg., ed. 16(4), Curae post.: 103. 1827 ≡ *Gomphrena paniculata* (Mart.) Moq. in DC., Prodr. 13(2): 385. 1849 ≡ *Pfaffia paniculata* (Mart.) Kuntze, Revis. gen. pl. 2: 543. 1891. Holotype: Brasil, Prov. Rio de Janeiro, *Martius s.n.* (M!)

= *Iresine erianthos* Poir., Encycl., suppl. 3: 180. 1813 ≡ *Gomphrena eriantha* (Poir.) Moq. in DC., Prodr. 13(2): 386. 1849 ≡ *Pfaffia paniculata* (Mart. Kuntze, Revis. gen. pl. 2: 543. 1891. Type: Vahl s.n., sub *Celosia eriantha* Vahl (P-Juss, not seen). For a consideration on priority and validity of the names see text below.

= *Hebanthe virgata* Mart., Beitr. Amarantac.: 97. 1825 & Nov. Gen. sp. pl. 2: 45. 1826 ≡ *Iresine virgata* (Mart.) Spreng., Syst. veg., ed. 16(4), Curae post.: 103. 1827. Holotype: Brasil, crescit in umbrosis ad fluvium Ypanema, in Provincia S. Pauli, *Martius* (M!)

= *Gomphrena paniculata* (Mart.) Moq. var. *glabrata* Seub. in Mart., Fl. bras. 5(1): 192. 1875 ≡ *Pfaffia paniculata* (Mart.) Kuntze var. *glabrata* (Seub.) Stützer, Repert. Spec. Nov. Regni Veg. Beih. 88: 15. 1935. Lectotype (designated here): Brasil, Rio de Janeiro, 1867, *Glaziou 27* (BR!). As no specimen was designated as holotype a lectotypification is necessary; the specimen chosen as lectotype bears a handwritten label by Seubert.

= *Pfaffia paniculata* (Mart.) Kuntze f. *lanceolata* R.E.Fr., Ark. Bot. 16(12): 6. 1920. Syntypes: [Brasil], Minas Geraes, Caldas, *Regnell I: 452*; [Brasil], Minas Geraes, Lagoa Santa, 12.9.1863, *Warming* (C!); Lagoa Santa, 18.8.1864, *Warming* (C!); Lagoa Santa 24.7.1865, *Warming* (C!); [Brasil], Sao Paulo: Campinas, *Severin 13*; Sao Paulo: Campinas, *Hainer s.n.* Lectotype (designated here): Brasil, ad Lagoa Santa, 18.8.1864, *Warming 324* (C!).

= *Pfaffia paraguayensis* Chodat, Bull. Soc. Bot. Genève 18: 286. 1927. Holotype: Paraguay, Reg. fluminis Yhù, Caaguazu, *Hassler 9459* (G!).

= *Pfaffia laurifolia* Chodat, Bull. Soc. Bot. Genève 18: 287. 1927. Holotype: Paraguay, Amambay, in alta planitie, jul., *Hassler 11280* (G!).

As shown by FRIES (1920), *Iresine erianthos* Poir. and *Hebanthe virgata* Mart. are based on specimens with deformed and sterile flowers. Such specimens are frequently seen in

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herbaria and must also be fairly common in the field. Similar deformities occur in *Hebanthe pulverulenta* Mart. (FRIES 1920, SUESSENGUTH 1934). FRIES (1920) suggested that *I. eriantha* Poir. [= *Pfaffia eriantha* (Poir.) Kuntze] should be withdrawn as a species and better attributed to *Pfaffia paniculata* f. *lanceolata* as a monstrosity. This was accepted by later authors and *I. erianthos* as well as combinations based there upon by MOQUIN-TANDON (1849) and KUNTZE (1891) came out of use. The fact that the deformities occur within different species, that they seem to be invariably sterile, and that it is hard to imagine any form for vegetative reproduction in nature, makes it almost certain that this deformation is due to some external cause, and that as a mere pathological phenomenon it should not be referred to under any name. Some deformed specimens even do not possess any complete flowers, and therefore, their affiliation with a particular species of *Hebanthe* is hardly possible. To accept *I. erianthos* Poir. would cause a disadvantageous disruption of nomenclature, and consequently we have submitted a proposal to formally reject the name for publication in Taxon, as encouraged by the Tokyo Code. In the present paper the existing usage of nomenclature is followed as governed by the Code.

Pfaffia paniculata f. *lanceolata* R.E.Fries comes well within the variability of *Pfaffia paniculata* f. *paniculata* and therefore we consider it worthless. FRIES (1920) argues that the species consists of two forms (f. *lanceolata* and f. *ovatifolia*) varying in their leaf characters. But as Fries does not cite the type Martius used in his description of the species, the concept of his *P. paniculata* f. *lanceolata* does not include the type of *P. paniculata* f. *paniculata*. Consequently, *P. paniculata* f. *lanceolata* has to be treated as a synonym of *P. paniculata* f. *paniculata.*

Pfaffia paraguayensis Chodat and *P. laurifolia* Chodat are based on supposed differences in the texture and indument of the bracteoles, the relative length of the undivided part of the filaments and their appendages, characters which we have found to a large extent depend on the age of the flower; as to the differences in the shape of the leaves, the second author's experience in the field has shown that this is too variable and intergrades to such an extent as to render this character worthless. The same applies to most - if not all - of the infra-specific taxa proposed by STÜTZER (1935), for which reason we disregard them here. The var. ß *pilosiuscula* Moq. in DC. (1849: 382) may have some value, but to appreciate this, a critical revision of the genus will be needed.

SEUBERT (1875) synonymized *Iresine grandiflora* Hook. with his new variety *Gomphrena paniculata* (Mart.) Moq. var. *hookeriana* Seub. (in Mart., Fl. bras. 5(1): 192. 1875). *Iresine grandiflora* Hook. (= *Hebanthe grandiflora* (Hook.) Borsch & Pedersen) is a well defined species that is clearly distinct from *Gomphrena paniculata* (Mart.) Moq. (= *Hebanthe paniculata* Mart.). According to the latin discription by SEUBERT (1875) „filamentorum lobis lateralivbus minutissimis v. deficientibus" the var. *hookeriana* Seubert could be affiliated to *H. paniculata* Mart. as a variety with small or reduced stamen appendages. However, the identity remains doubtful, since no type could be located so far. *Iresine grandiflora* (published by HOOKER in 1837) was probably considered to be a synonym as its stamens completely lack appendages. The later described *Hebanthe hookeriana* Hemsl. is not identical.

Hebanthe paniculata Mart. f. ***ovatifolia*** (Heimerl) Borsch & Pedersen **comb. nov.**

Basionym: *Gomphrena paniculata* (Mart.) Moq. f. *ovatifolia* Heimerl, Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. 79: 230. 1908 ≡ *Pfaffia paniculata* (Mart.) Kuntze f. *ovatifolia* (Heimerl) R.E.Fr., Ark. Bot. 16(12): 6. 1920. Type: [Brasil], prope S. Bernardo in circuitu urbis São Paulo, *Wachsmund s.n.* (W lost). Neotype (designated here): Brasil, *Glaziou 11433* (C!)

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Hebanthe grandiflora (Hook.) Borsch & Pedersen **comb. nov.**
Basionym: *Iresine grandiflora* Hook., Icon. pl. 2: tab. 102. 1837 ≡ *Pfaffia grandiflora* (Hook.) R.E.Fr., Ark. Bot. 16(12): 10. 1920 ≡ *Hebanthe decipiens* Hook.f. in Benth. & Hook., Gen. pl. 3: 41. 1880. Nom. illeg. ≡ *Gossypianthus decipiens* (Hook.f.) O.Kuntze, Revis. gen. pl. 2: 542. 1891. Nom. illeg. Holotype: Peru, Cordillera of Casapi, *Mathews 1419* (K!).

Hebanthe spicata Mart., Beitr. Amarantac.: 97. 1825 & Nov. Gen. sp. pl. 2: 44. 1826 ≡ *Iresine spicata* (Mart.) Spreng., Syst. veg., ed. 16(4), Curae post.: 104. 1827 ≡ *Gomphrena spicata* (Mart.) Moq. in DC., Prodr. 13(2): 387. 1849 ≡ *Pfaffia spicata* (Mart.) Kuntze, Revis. gen. pl. 2: 542. 1891. Holotype: Brasil, in mediterraneis deserti versus luvium S. Francisci in Provincia Minarum, *Martius* (M!).

The variety *Pfaffia spicata* (Mart.) Kuntze var. *pretensis* Suess. was proposed by SUESSENGUTH (1934: 33). It differs only slightly in the morphology of the trichomes and the androeceum. It is doubtful whether these varieties can be separated, but to appreciate this, a critical revision will be needed.

Hebanthe pulverulenta Mart., Beitr. Amarantac.: 97. 1825 & Nov. Gen. sp. pl. 2: 46, Tab. 144, 145. 1826 ≡ *Gomphrena pulverulenta* (Mart.) Moq. in DC., Prodr. 13(2): 386. 1849 ≡ *Pfaffia pulverulenta* (Mart.) Kuntze, Revis. gen. pl. 2: 542. 1891. Holotype: Brasil, in marginibus sylvarum ad Ypanema, Provincia S. Pauli, *Sellow s.n.* (M!; Iso: fragm. ex B in F!)
= *Gomphrena pulverulenta* (Mart.) Moq. var. *rufescens* Moq. in DC., Prodr. 13(29): 386. 1849 ≡ *Pfaffia pulverulenta* (Mart.) Moq. var *rufescens* (Moq.) O.Stützer, Repert Spec. Nov. Regni Veg. Beih. 88: 17. 1935. Holotype: In Brasilia Serra dos Orgaos, *Khotsky 108* (G-DC; Iso: MO!).
= *Pfaffia pulverulenta* (Mart.) Kuntze f. *eriantha* Suess., Repert. Spec. Nov. Regni Veg. 35: 333. 1934. Type: Brasil, Theresopolis, Sierra dos Orgaos, II.1887, *Schenk 2582* (not seen).

Within the species SUESSENGUTH (1934) decribed the three formes *P. pulverulenta* f. *densepilosa* Suess., *P. pulverulenta* f. *glabriuscula* Suess., and *P. pulverulenta* f. monstr. *eriantha* Suess. The first two may turn out to be synonymous with *H. pulverulenta*; the latter is already listed as a synonym because it is a monstrosity that differs only through deformed flowers. STÜTZER (1935) distinguished two varieties (*P. pulverulenta* var. *microdonta* Stützer, *P. pulverulenta* var. *macrodonta* Sützer) on the basis of size differences of the stamen appendages. Their taxonomic value can only be evaluated in the course of a critical revision including a statistical analysis of quantitative data.

Hebanthe reticulata (Seub.) Borsch & Pedersen **comb. nov.**
Basionym: *Gomphrena reticulata* Seub. in Mart.. Fl. bras. 5(1): 194. 1875 ≡ *Pfaffia reticulata* (Seub.) Kuntze, Revis. gen. pl. 2: 543. 1891. Type: ad Chapada et Rio Jequitinhonka prov. Minarum, *Pohl 3255* (W, lost). Lectotype (designated here): Brasil, prov. Minarum, *Pohl 3255* (M!).

Hebanthe hookerina Hemsl., Biol. cent.-amer., Bot. 3: 19. 1882 ≡ *Pfaffia hookeriana* (Hemsl.) Greenm., Publ. Field Mus. Nat. Hist., Bot., Ser.2: 130. 1912 ≡ *Pfaffia grandiflora* (Hook.) R.E.Fr. var. *hookeriana* (Hemsl.) O.Stützer, Repert. Spec. Nov. Regni Veg. Beih.

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88: 17. 1935. Type: *Bourgeau* 1898 (not seen).

STÜTZER (1935) considers this taxon a variety of *Pfaffia* (*Hebanthe*) *grandiflora* (Hook.) R.E.Fr. To form an opinion to this point, a critical revision of the genus will be necessary, which lies beyond the aim of this paper. In order to avoid encumbering the nomenclature of *Hebanthe* with a possibly new combination, we prefer provisionally to retain Hemsley's taxon at specific level. *Gomphrena paniculata* (Mart.) Moq. var. *hookeriana* Seub., described from Brazilian material, most likely is not identical to *Hebanthe hookeriana* Hemsl. (see also under *Hebanthe paniculata* Mart.).

Hebanthe occidentalis (R.E.Fr.) Borsch & Pedersen **comb. nov.**
Basionym: *Pfaffia occidentalis* R.E.Fr., Ark. Bot. 16(12): 8. 1920. Holotype: Argentina, prov. Jujuy, Quinta pr. Laguna de la Brea, ad. Sierre Sta Barbara, in fruticetis marginis silvae, florifera 8.8.1901, *Fries 448* (S!; Iso: UPS!, US!).
= *Pfaffia occidentalis* R.E.Fr. var. *densiflora* R.E.Fr., Ark. Bot. 16(12): 9. 1920. Holotype: Argentina, prov. Jujuy, Quinta pr. Laguna de la Brea, ad. Sierra Sta Barbara, 8.8.1901, *Fries 443* (S!; Iso: US!).
= *Pfaffia brachiata* Chodat, Bull. Soc. Bot. Genève 18: 285. 1927. Type: not seen.
= *Pfaffia brachiata* Chodat var. *grandiflora* O.Stützer, Repert. Spec. Nov. Regni Veg. Beih. 88: 8. 1935. Syntypes: Brasil, Civit. Matto Grosso, Santa Anna du Chapada, floribus instructa 28.7.1902, *Malme II 2133*; Bolivia, Villamontes 1924/25, *Pflanz 4076* (W); Argentina, Prov. Jujuy, Quinta pr. Laguna de la Brea ad Sierra Sta. Barbara florifera VII.1901, *Fries 386* (S!); dito, *Fries 386 a* (S!). Lectotype (designated here): Argentina, Prov. Jujuy, Quinta pr. Laguna de la Brea ad Sierra Sta. Barbara, florifera VII.1901, *Fries 386* (S!).

FRIES (1920) formally validated the combination *Pfaffia grandiflora* (Hook.) R.E.Fr., based on *Mathews 1419* (holotype of *Iresine grandiflora* Hook.), but misapplied the name to specimens belonging to *Hebanthe occidentalis* (R.E.Fr.) Borsch & Pedersen var. *occidentalis*. STÜTZER (1935) adopted the name of Fries and refers to it as basionym but explicitly excludes the type. Consequently, a new name is considered to have been published, and the correct citation has to be *P. brachiata* Chodat var. *grandiflora* O.Stützer and not *P. brachiata* Chodat var. *grandiflora* (R.E.Fr., non Hook.) O.Stützer as published by STÜTZER (1935). A latin description is already present, and a lectotype is designated here from the syntypes.

Hebanthe occidentalis var. ***bangii*** (R.E.Fr.) Borsch & Pedersen **comb.** et **stat nov.**
Basionym: *Pfaffia bangii* R.E.Fr., Ark. Bot. 16(12): 11. 1920. Holotype: Bolivia, Mapiri, VII/VIII.1892, *Bang 1521* (F!; Iso: C!, K!, MO!, S!, UPS!, US!, WU!).

As already observed by SUESSENGUTH (1934) and STÜTZER (1935), the three species *Pfaffia occidentalis*, *P. bangii* and *P. brachiata* intergrade imperceptibly, to which can be added that *P. bangii* itself varies considerably, so much that, as also observed by STÜTZER (1935), even parts of the type collection cannot be referred to that taxon as described by Fries. Granted that the collector, Miguel Bang, was not a trained botanist, there is no reason to attribute these differences merely to gross carelesness on his part. The specimens are most likely from the same population, and may even be different branches of the same plant. *P. brachiata,* according to Stützer, should be intermediate between *P. occidentalis* and *P. bangii*, and her var. *grandiflora* should be intermediate between *P. brachiata* and *P. occidentalis*. When identifying material, the second author has had the greatest difficulties deciding to which of these taxa refer a specimen, and very likely as often as not his determination was a guess at

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hazard. In view of this, we find it impossible to keep *P. occidentalis* and *P. bangii* apart at specific level, but as the extremes are so unlike, they can be considered more or less well defined varieties. With this treatment we can not see any necessity for maintaining *P. brachiata*. *P. brachiata* var. *grandiflora*, based on a misidentification of a specimen by FRIES (1920) has been considered distinct, probably because of its larger, broadly lanceolate, acuminate leaves, as opposed to the supposedly ovate, obtuse or short-acuminate leaves of *H. occidentalis*. However, size and shape of leaves vary within the species to such an extent, that they are quite useless for defining infraspecific taxa.

The following species, described under *Hebanthe*, do not belong here:

- *Hebanthe holosericea* Mart., Flora 21(2): 65. 1838 = *Gomphrena vaga* Mart. (SIQUEIRA 1992).
- *Hebanthe mollis* Hemsl., Biol. cent.-amer., Bot. 3: 20. 1882 = *Iresine calea* (Ibañez) Standl. = *Iresine latifolia* (M.Martens & Galeotti) Hook.f. (STANDLEY 1917).
- *Hebanthe palmeri* S.Wats., Proc. Amer. Acad. Arts 18: 144. 1883 = *Iresine palmeri* (S.Wats.) Standl.
- *Hebanthe parviflora* Benth., Bot. voy. Sulphur.: 156. 1844 = *Iresine benthamiana* Kuntze, from the description a *Trommsdorffia* sensu Martius.
- *Hebanthe philippo-coburgii* Zahlbr., in Wawra, H.: Itin. princ. S. Coburgi 2: 57, Tab. 10, A. 1888 = *Alternanthera philippo-coburgii* (Zahlbr.) Suess.
- *Hebanthe subnuda* Hemsl., l.c. = *Iresine interrupa* Benth. (STANDLEY 1917).

Though as stated above, we do not aim to present a critical revision of the genus *Hebanthe* with this paper, we believe that we have accounted for all the species and a number of infraspecific taxa as yet validly published and known to be referable here. The following artificial key may prove a help to identifying the species treated:

1 Indumentum of stem, leaves and inflorescence axes consisting of branched hairs 2
– Hairs not branched 4
2 Filaments with ± distinct appendages (sometimes not all in one flower); eastern Brazil ***H. pulverulenta***
– Filaments never with appendages; western South America 3
3 Underside of leaves with a ± persistent tomentum of branched hairs ***H. occidentalis*** var. ***bangii***
– Underside of leaves soon glabrous, except for the principal veins ***H. occidentalis*** var. ***occidentalis***
4 Filaments entire; mainly Andean north-western South America, Equatorial and Central Americas 5
– Filaments with 2 appendages; Brasil to Argentina and Paraguay 6
5 Leaves and stem glabrescent; tepals 2–2.5 mm long ***H. grandiflora***
– Leaves and stem persistently hirsute; tepals 2.5–3 mm long ***H. hookeriana***
6 Axis and branches of inflorescences hairy, mostly densely so; leaves thin, not glossy above 7
– Axis and branches of inflorescences glabrous or almost so; leaves ± leathery, secondary veins often prominent, upper surface often glossy ***H. reticulata***
7 Leaves ± persistently hairy on both sides; appendages of filament overtopping apex of filament; north-eastern Brazil ***H. spicata***
– Leaves glabrescent, at least above; appendages of filament shorter than apex of filament; eastern Brazil and Paraguay to extreme north-eastern Argentina 8

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8 Leaves lanceolate, often narrowly so, acute or acuminate; range of the species *H. paniculata* f. *paniculata*

– Leaves ovate, mostly obtuse or short-acuminate; apparently restricted to the states of Rio de Janeiro and São Paulo in Brazil. *H. paniculata* f. *ovatifolia*

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Thomas Borsch, Botanisches Institut und Botanischer Garten, Universität Bonn, Meckenheimer Allee 170, 53115 Bonn und Forschungsinstitut Senckenberg, Senckenberganlage 25, 60325 Frankfurt a.M., Deutschland.
Troels Myndel Pedersen, Estancia Santa Teresa, Casilla de Correo no. 1, RA-3427 Mburucuyá, Provincia de Corrientes, Argentina.

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Fig. 1. *H. paniculata* Mart. Reprint of the illustration of the type species of the genus, from Martius, Nova Genera et Species Plantarum (1826).

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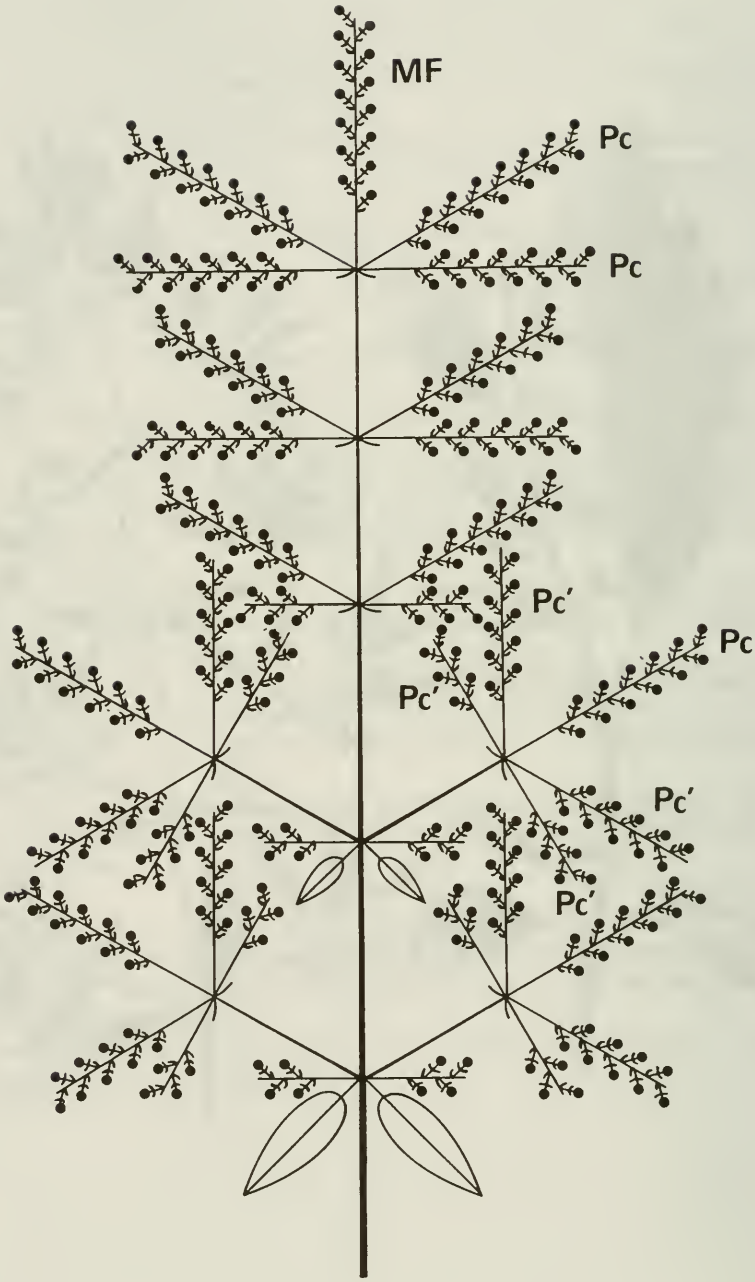

Fig. 2. Inflorescence architecture of *H. paniculata* Mart. Polytelic synflorescence with dominating central axis. MF = main florescence; Pc = paracladium of first order; Pc′ = paracladium of second order.

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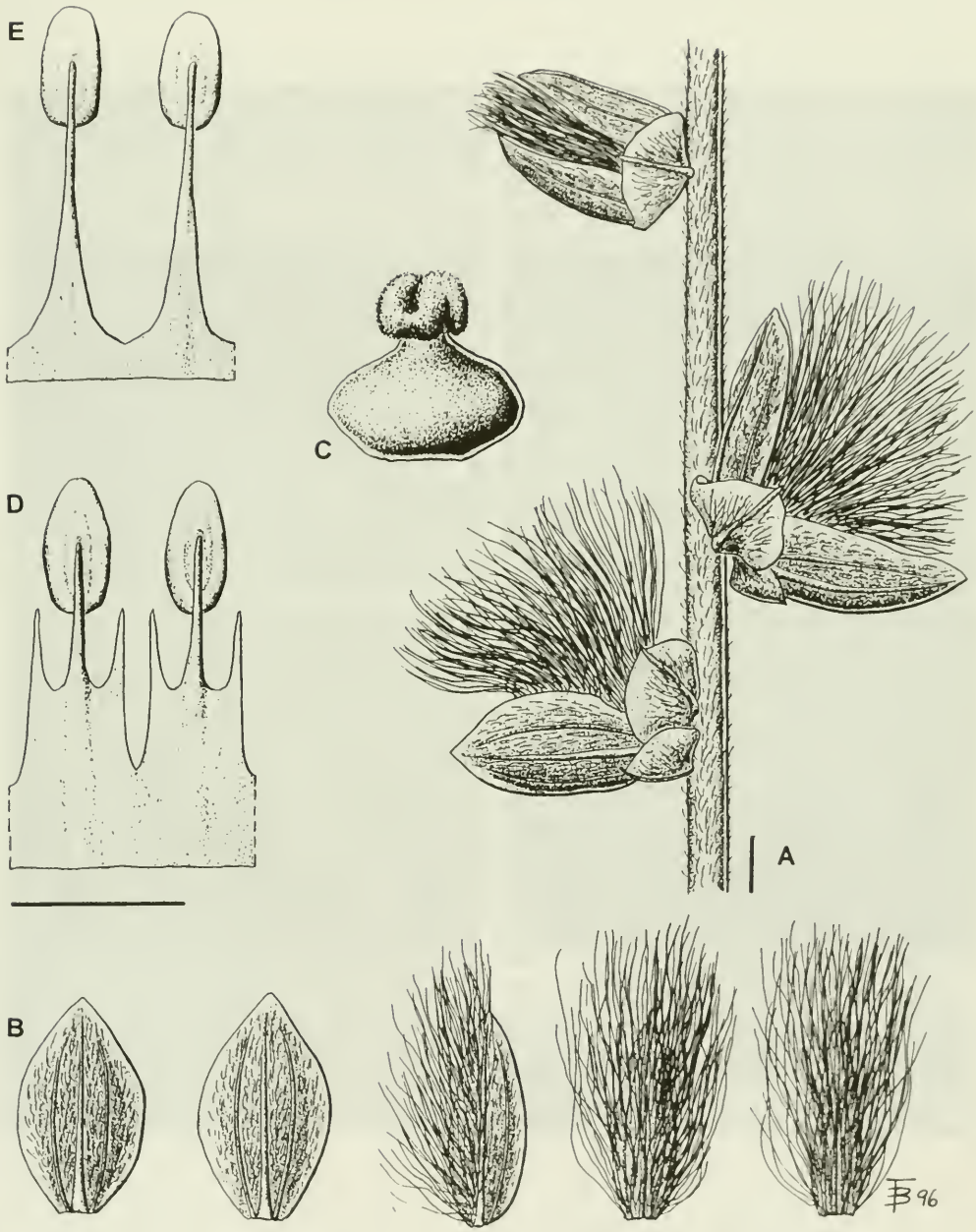

Fig. 3. Floral morphology of *Hebanthe*. A–D: *H. paniculata* Mart. (*Gentry & da Silva 58725*, MO); part of raceme with two flowers at anthesis and one starting to bloom (A); tepals (B); ovary with bilobate stigma (C); part of androeceum with each filament having two appendages, abaxial view (D). E: *H. occidentalis* (R.E.Fr.) Borsch & Pedersen var. *occidentalis* (*Pedersen 13937*, C); part of androeceum, filaments without appendages.

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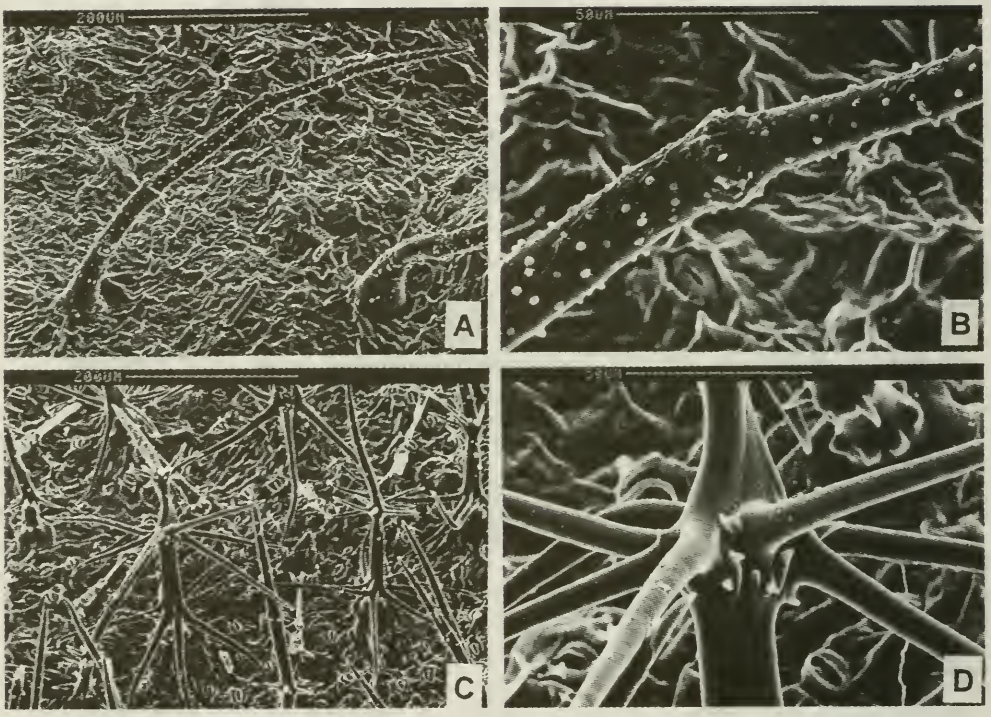

Fig. 4. Scanning electron (SEM) micrographs of hairs from the lower surface of cauline leaves. Unbranched, multicellular hairs in *H. grandiflora* (Hook). Borsch & Pedersen (A,B; *Nee & Taylor 28769*, MO) and branched, multicellular hairs in *H. occidentalis* (R.E.Fr.) Borsch & Pedersen var. *bangii* (R.E.Fr.) Borsch & Pedersen (C, D; *Woytkowski 7464*, MO). Note the occurrence of spinelike excrescences on the outer cell walls.

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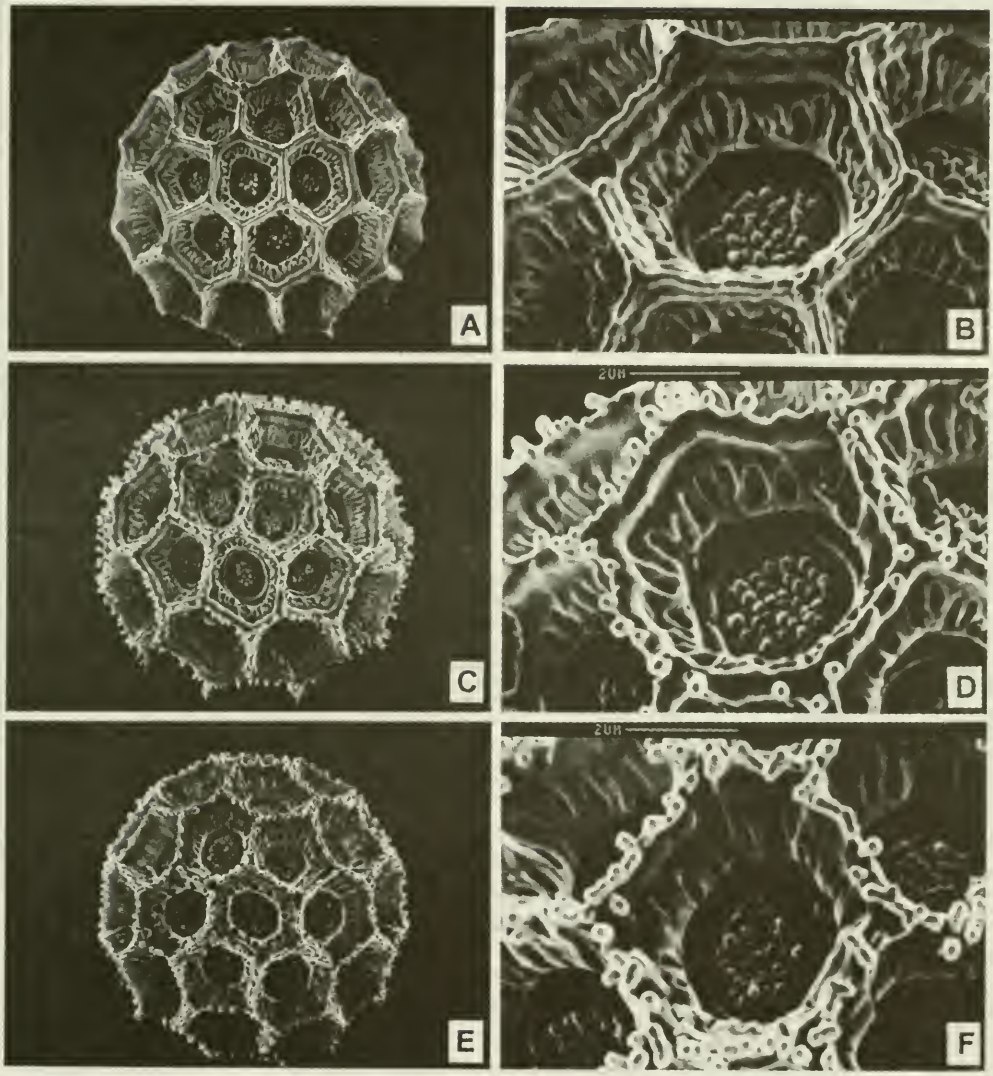

Fig. 5. Scanning electron (SEM) micrographs of acetolyzed pollen grains and apertures of *Hebanthe grandiflora* (Hook.) Borsch & Pedersen (A, B; *Nee & Taylor 28769*, MO); *H. occidentalis* (R.E.Fr.) Borsch & Pedersen var. *occidentalis* (C, D; *Gentry et al. 51786*, MO); and *H. pulverulenta* Martius (E, F; *Dusén 519a*, MO).

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Tab. 1: Summary of morphological and palynological characters of *Hebanthe* in comparison to morphologically similar and probably more closely related American genera of the Gomphrenoideae.

Character	*Froelichia*	*Gomphrena*	*Hebanthe*	*Pfaffia* (*Pfaffia* sensu Mart. & *Sertuernera* Mart.)
Habitus	upright perennial herbs or subshrubs	annual/perennial herbs or subshrubs	woody lianas	upright perennial herbs or subshrubs
Hairs (of leaves and axes)	simple, rough	branched or simple, rough	branched or simple, rough	simple, smooth
Inflorescence	synflorescence of loose racemes, central axis dominating, axillary buds up to 5	solitary, terminal heads or synflorescence of heads with branches dominating	complex synflorescence of loose racemes, central axis dominating, axillary buds up to 3	solitary, terminal heads or synflorescence of heads with branches dominating, axillary buds up to 3
Tepals	connate, unequal	free, subequal	free, unequal	free, subequal
Long and stiff hairs for dispersal	lacking	lacking or equal on all tepals, at base or lower half	dorsally all over on inner 2 tepals, and on covered half of middle tepal	equal on all tepals, at base or lower half, rarely lacking
Androeceum	filaments almost completely fused to a tube, entire; appendages distinct, placed closely together and appearing like pseudostaminodes; pseudostaminodes lacking	filaments basally or ± entirely fused, entire; appendages mostly distinct, rarely obsolete or lacking; pseudostaminodes lacking, rarely present and laciniate	filaments basally fused to a cup, entire; appendages lacking or present; pseudostaminodes lacking	filaments basally fused, ciliate, appendages mostly distinct, rarely obsolete or lacking; pseudostaminodes lacking
Gynoeceum	stigma capitate or pistillate, at the end of a short style	stigma of 2 very narrowly triangular or almost filiform branches, but no papillae on the abaxial side, at the end of a style	stigma broadly emarginate (2 broadly rounded lobes), sessile or at the end of a short style	stigma broadly emarginate (2 broadly or equilaterally triangular lobes), sessile or at the end of a short style
Pollen	mesoporia extremely narrow, distally with a row of spinulae somewhat differing in size, tectum reduced and columellae free	mesoporia extremely narrow, distally with ± elongated or concavespinulae, or rarely smooth; tectum reduced or not	mesoporia extremely narrow, distally undulate or with spinulae, tectum with large perforations close to apertures	mesoporia narrow, distally with konkave, elongated spinulae; tectum complete

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Character	*Pseudogomphrena*	*Quaternella*	*Trommsdorffia* sensu Mart.	*Xerosiphon*
Habitus	leaning or subscandent shrub	upright perennial herbs or subshrubs	scandent shrubs or small lianas	upright perennial herbs
Hairs (of leaves and axes)	simple, smooth	simple, smooth	branched or simple, rough	simple, smooth
Inflorescence	synflorescence of few heads with central axis dominating	synflorescence of heads with branches dominating, axillary buds up to 3	complex synflorescence of heads, central axis dominating, axillary buds up to 3	synflorescence of heads with branches dominating
Tepals	free, subequal	free, subequal	free, subequal	connate, subequal
Long and stiff hairs for dispersal	equal on all tepals, at lower half	equal on all tepals, at base or lower half	equal on all tepals, at base	lacking
Androeceum	filaments almost completely fused to a tube, entire; appendages distinct, placed closely together and appearing like pseudostaminodes; pseudostaminodes lacking.	filaments basally fused, ciliate, appendages mostly obsolete or lacking; pseudostaminodes lacking	filaments basally fused into a cup, entire; appendages lacking; pseudostaminodes rounded triangular or cup's margin only slightly raised	filaments almost completely fused into a tube, entire; appendages distinct; pseudostaminodes lacking
Gynoeceum	stigma of 2 very narrowly triangular branches, at the end of a short style	stigma of 2 almost filiform branches, but no papillae on the abaxial side, at the end of a short style	stigma of 2 equilaterally or narrowly triangular lobes, at the end of a short style	stigma of 2 equilaterally triangular lobes, at the end of a short style
Pollen	mesoporia narrow, distally with elongated concave spinulae; tectum with large perforations close to apertures	mesoporia narrow, distally with concave, elongated spinulae; tectum complete	mesoporia narrow, distally with concave, elongated spinulae, tectum complete	mesoporia extremely narrow, distally with ± elongated or concave spinulae, tectum reduced

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