The anomalous-stemmed species of Heteropterys subsect. Aptychia (Malpighiaceae)

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Amorim, A. M. (Universidade Estadual de Santa Cruz, Departamento de Ciências Biológicas, Ilhéus, 45.650–000, Bahia, Brazil; e-mail: aamorimm@terra.com.br). The anomalous-stemmed species of Heteropterys subsect. Aptychia (Malpighiaceae). Brittonia 55: 127–145. 2003.—Species of the anomalous-stemmed complex of Heteropterys are revised after intensive fieldwork in eastern Brazil. Heteropterys patens (=H. anomalà) is redefined, and three new species are described (H. admirabilis, H. imperata, and H. nordestina). In addition, this treatment provides brief synonymy, lectotypifications, illustrations, and comments for those four species, and a key to all taxa of the complex.

Key words: Malpighiaceae, Heteropterys, Aptychia, Brazil, anomalous-stemmed.

Amorim, A. M. (Universidade Estadual de Santa Cruz, Departamento de Ciências Biológicas, Ilhéus, 45.650–000, Bahia, Brazil; e-mail: aamorimm@terra.com.br). The anomalous-stemmed species of Heteropterys subsect. Aptychia (Malpighiaceae). Brittonia 55: 127–145. 2003.—Espécies do complexo de ramos anômalo de Heteropterys são revisadas com base em coleções atualmente disponíveis e em intensivo trabalho de campo realizado no leste do Brasil. Heteropterys patens (=H. anomalà) é redefinida e três novas espécies são descritas (H. admirabilis, H. imperata, e H. nordestina). Em adição, esse tratamento provê breves sinônimos, lectotipificações, ilustrações e comentários para essas quatro espécies e uma chave analítica para todos os taxas do complexo.

Heteropterys is a large and taxonomically difficult genus of Malpighiaceae. The species of Heteropterys are tremendously diverse in their vegetative and floral morphology but share a noteworthy apomorphy in fruit shape: the dorsal wing of the samara is prominent, thickened on the abaxial edge, and the lateral wings are strongly reduced or absent. All species are found in the Neotropics and just one species is common to both the Old World and New World, occurring in western Africa, Central America, and northern South America (C. Anderson, 2001).

The monophyly of Heteropterys is still unconfirmed, but recent analyses using ITS molecular data from 23 species in this genus showed Heteropterys to be a natural lineage (Amorim, Davis, & Anderson, unpubl. data). Molecular studies (Cameron et al., 2001; Davis et al., 2001) have placed this genus in a clade with other genera in which a lateral wing of the samara is prominent; according to the authors, this clade is poorly supported and more data are needed to improve the results. Ongoing taxonomic studies, especially of the subgenus Heteropterys (Amorim, 2001, 2002; W. Anderson, 1997, 1998, 2001), generally follow the infrageneric classification of Niedenzu (1928) because that is still the most recent study of the genus.

This article is part of my taxonomic revision of the subsection Aptychia, an assemblage of species with sessile pedicels. Specimens of the anomalous-stemmed complex are lianas or rarely small shrubs that occur in coastal Brazil from Rio Grande do Norte to northern São Paulo. They generally have stems conspicuously bearing xylem cylinders that are slightly or deeply dissected but complete. These plants...
show striking variation in leaf form and size, but are easily recognized vegetatively (Fig. 1): the cross-section of the basal part of the stem is generally irregularly sulcate, flattened, or divided into three or more lobes; the petiole bears a pair of glands at base; the lamina is generally very soon glabrescent; and the margins bear many small glands and short cilia, especially in young leaves.

The vegetative and floral variability have long obscured the fact that this complex comprises more than just the two species recognized by Jussieu: *Heteropterys anomala* A. Juss. (the commonly used name) and *H. patens* (Griseb.) A. Juss. (an overlooked name). Two species, *H. bullata* Amorim and *H. oberdanii* Amorim, were recently described, and three new species (*H. admirabilis*, *H. imperata*, and *H. nordestina*) are proposed here on the basis of intensive fieldwork, analyses of herbarium collections, and careful delimitation of the species concepts in this group.

**Key to the anomalous-stemmed species of Heteropterys subsect. Aptychia**

1. Petioles confluent across the node and forming a corky ridge; lamina with lateral veins and reticulum deeply impressed above and prominent below, producing a bullate surface (coastal forests of highest mountains, Bahia) ............................................................................................................ *H. bullata*

1. Petioles not confluent; lamina not bullate, the lateral veins slightly prominent below and reticulum very fine or inconspicuous on both surfaces.

2. Bract 1–2.2 mm long; pedicel 3.5–5 mm wide distally; all petals orange or pale yellow suffused with red; samara usually (38–)46–77 mm long at maturity; nut 8–14 mm diam.

3. Accessory branches of inflorescence evident; pedicel 3.5–7.3 mm long, abruptly thickened distally; lateral petals thickened in center of limb but not carinate; limb of posterior petal triangular; filament of stamen opposite anterior sepal ca. 5.2 mm long, coherent with adjacent filaments and bent inward; connective of anthers distally widened so as to displace the locules laterally and sometimes elongated so as to exceed the locules (coastal forests of highest mountains, Espírito Santo) ............................................................................................................ *H. admirabilis*

3. Accessory branches of inflorescence, if present, very reduced; pedicel 10.4–18 mm long, gradually thickened distally; lateral petals dorsally carinate; limb of posterior petal suborbicular; filament of stamen opposite anterior sepal ca. 3.6 mm long, not coherent with adjacent filaments; connective not widened and equaling the locules (coastal forests of the hills in the state of Rio de Janeiro and restinga forests in northern part of the state of São Paulo) ............................................................................................................ *H. patens*

2. Bract 0.6–1 mm long; pedicel 1.7–2.5(–2.8) mm wide distally; all petals yellow lacking red; samara usually 30–44(–48) mm long at maturity; nut 4–6(–8) mm diam.

4. Cross-section of basal part of stems always cylindrical; leaves appressed; pedicel 3.5–5.7 mm long; flowers borne ultimately in pseudococceae containing 4–20 decussate flowers; samara reddish pink at maturity, borne horizontally (permanently flooded restinga forests, Espírito Santo) ............................................................................................................ *H. oberdanii*

4. Cross-section of basal part of stems cylindrical, irregularly sulcate, flattened, or divided into 3 or more lobes; leaves spreading; pedicel 7–10 mm long, rarely shorter; flowers borne ultimately in 4–6-flowered umbels; samara pale brown at maturity, borne erect when single, obliquely or eventually horizontally when 2 or 3 develop.

5. Inflorescence generally spreading or (in plants from sandy areas) slightly contracted; sepal obtuse or rounded at apex, 1.3–1.5 mm long; lateral petals membranous, slightly thickened in center of limb, or sometimes strongly carinate; limb of lateral petals 3.5–4.2(–4.8) mm long; filaments opposite 2 posterior-lateral petals 2.9–3.5 mm long; styles 2.9–3.3 mm long (tableiro, restinga, semi-deciduous, and moist forests throughout coastal range from Rio Grande do Norte to Espírito Santo) ............................................................................................................ *H. nordestina*

5. Inflorescence often contracted; sepal triangular at apex, 1.8–2.5 mm long; lateral petals strongly carinate; limb of lateral petals 4.5–5.5 mm long; filaments opposite 2 posterior-lateral petals 4–4.3 mm long; styles 4–4.5 mm long (restinga and moist forest in coastal range or dry forests inland, Bahia) ............................................................................................................ *H. imperata*

**Heteropterys admirabilis** Amorim, sp. nov. (Fig. 2)


Liana basi ramis teretibus, sulcatis vel complanatis. Lamina foliorum majorum 8.5–25 cm longa, 6.5–17
cm lata, ovata, oblonga, elliptica, subrotundata, ovato-lanceolata, cordato-orbiculata, oblongo-lanceolata vel late lanceolata, utrinque glabrate; petiolum 16–35 mm longus, basi biglandulifer. Panicula 20–38 cm longa, in ramis deflexis, umbellis congestis 4–6-floris, pedunculo florifero nullo, pedicello 3.5–7.3 mm longo, 1.2–5 mm diametro, abrupte incrassato versus apicem. Petala flava et rubra, in alabastro exposita, patentia, dorso saliter laevia, petala lateralia limbo orbiculato et concavo, petalum posticum limbo triangulato et plano; filamenta heteromorpha, illa petalis postico-lateralibus opposita plerumque longiora crassiora; antherae inaequales, connectivo distaliter dilatato loculos aequaliter vel superantibus et lateralis luxanti; styli postici lyrati, apice dorsaliter apiculati. Samarae 38–50 mm longae, nuce 8–9 mm diametro, lateraliter laevi.

Liana, climbing to 5–20 m; stems at base 2–6 cm diam., the cross-section cylindrical, irregularly sulcate, or rarely slightly flattened, twisted, glabrate, developing small scattered lenticels. Leaves mostly plane, opposite or rarely subopposite on the same stem, spreading; petiolo 16–35 mm long, initially sericeous and soon glabrate, bearing a pair of glands at base, each gland 2–3 mm diam.; stipules present on petiolo, above base, as minute protuberances 0.1–0.3 mm long, apparently absent from old leaves; lamina of larger leaves (8.5–)10.2–23.8(–25) × (6.5–)7–16.8(–17) cm, membranous, ovate, oblong, elliptic, subrotund, ovate-lanceolate, or cordate-orbicular, rarely oblong-lanceolate or widely lanceolate, often asymmetrical, obtuse, rounded or cordate, rarely slightly cuneate at base, acute, cuspidate, retuse to obtuse-rounded, rarely acuminate at apex, the margins bearing toothlike extensions with many small glands or short cilia on borders, especially in young leaves, glabrous or initially sparsely sericeous (with short, appressed, medifixed hairs) and soon glabrescent, the lateral veins slightly prominent below, reticulum very fine and more visible below than above. Inflorescence pa-
niculate, spreading, 20–38 cm long, primary branches 10–22, 0.5–15.5 cm long, secondary branches 6–18 or absent, 0.5–2 cm long, tertiary branches if present ca. 0.5 cm long, accessory branches evident; terminal or axillary, densely and persistently brown-sericeous, pendulous, with the flowers borne ultimately in congested and dense 4–6-flowered umbels; inflorescence bracts like leaves, gradually or
abruptly reduced to 5–6 × ca. 3.6 mm, the margins entire, biglandular at base or eglandular, the glands ca. 1.5 mm diam., bright green; peduncle absent; bracts 1.9–2.2 × 2.4–2.5 mm, broadly ovate, eglandular or bearing 1–2 small glands at base, abaxially densely sericeous, adaxially glabrous; bracteoles like bracts but smaller, eglandular; pedicel (3.5–)4–7.3 × 1.2–5 mm, straight, densely brown-sericeous, abruptly thickened distally. *Sepals* 3–3.5 × 2.5–3 mm, brown, rounded at apex, strongly appressed against filaments in anthesis, abaxially densely sericeous, adaxially glabrous, the anterior sepal eglandular, the lateral 4 biglandular, the glands 3.5–4.7 mm long, elliptic. *Petals* exposed in the enlarging bud, pale yellow suffused with red principally near the claw, glabrous, thickened in center of limb but not carinate; lateral petals spreading, margins proximally strongly erose and revolute in anthesis (principally 2 posterior-lateral petals), claw 3.2–3.5 mm long, limb 4–5 × 4.5–5 mm, orbicular and deeply concave; posterior petal sub-erect, glandular-thickened at margins, claw 3.5–3.7 mm long, limb ca. 3.5 × 4.2 mm, triangular and nearly flat. *Stamens* glabrous; filaments strongly heteromorphic, 3.7–5.2 × 0.3–0.9 mm, connate ½–½ their length, the 2 stamens opposite posterior-lateral petals much thicker than others and straight, ca. 5 mm long, longest stamen opposite anterior sepal coherent with adjacent filaments and bent inward, ca. 5.2 mm long, shortest stamen opposite posterior petal, ca. 3.7 mm long, other stamens 4–4.5 mm long; anthers (1.8–)2–2.5(–2.8) mm long, strongly unequal, reflexed in anthesis, connective distally widened so as to displace the locules laterally and sometimes elongated so as to exceed the locules, the proximal ½–½ dark red, the distal ½–½ pale yellow. *Ovary* 1.5–1.7 mm high, densely sericeous; styles 3.5–4.2 mm long, equalling or slightly exceeding the anthers, glabrous or proximally sericeous, all 3 with a flattened elliptic top and internal stigma; anterior style nearly straight, dorsally strongly apiculate at apex; posterior styles somewhat lyrate, usually dorsally slightly apiculate at apex. *Samara* brown at maturity, (38–)46–50 mm long, borne obliquely, thinly sericeous to glabrate; dorsal wing almost as long as samara, 30–40 × 15–20 mm, the abaxial edge nearly straight; nut 8–9 mm diam., subspheroidal, smooth-sided, without lateral crests or winglets.

*Distribution and habitat.*—In the moist Atlantic coastal forest, between 600 and 900 m in Espírito Santo (Fig. 3). *Heteropterys admirabilis* grows in primary forest and advanced secondary forest, usually along rivers. It can be found in the canopy or below the canopy in shaded areas.

*Etymology.*—The specific epithet refers to the admirable aspect of the flowers, which are very different in size and shape when compared to flowers of other species in this complex.

*Phenology.*—Flowering in January, February, and November; fruiting in March, August, and October.


*Heteropterys admirabilis* closely resembles *H. patens* in leaf shape and the red pigmentation of the petals, but differ in other floral characteristics. *Heteropterys admirabilis* has an inflorescence with evident accessory branches, a distinctly shorter pedicel (3.5–7.3 mm long) that is abruptly thickened distally, petals thickened in the center of the limb but not carinate, and a triangular posterior petal, whereas *H. patens* has an inflorescence with no or very reduced accessory branches, the pedicel long (10.4–18 mm long) and gradually thickened distally, the lateral petals slightly carinate dorsally, and a suborbicular posterior petal. However, the most striking characteristic of *H. admirabilis* is the anthers of which the connective is widened distally so
as to displace the locules laterally and is sometimes elongated so as to exceed the locules. In this respect, *H. admirabilis* differs from all species in this complex. Other differences in size of the floral structures are presented in Table 1.

**Heteropterys imperata** Amorim, sp. nov. (Fig. 4)

**TYPE.** BRAZIL. Bahia: Mun. Uruçuca, 7.3 km na estrada Serra Grande/Itacaré, Fazenda Lagoa do Conjunto Fazenda Santa
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<tr>
<td>petiole—mm long</td>
<td>16–35</td>
<td>(22–)32–48</td>
<td>(10–)15–22</td>
<td>(5–)11–21</td>
<td>6–17</td>
<td>16–45</td>
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<tr>
<td>petiole gland—mm</td>
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<tr>
<td>diameter</td>
<td>2–3</td>
<td>0.8–2.5</td>
<td>1.5–2.2</td>
<td>1.2–1.6</td>
<td>ca. 0.6</td>
<td>1.2–1.6</td>
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<td>lamina—cm</td>
<td>8.5–25 × 6.5–17</td>
<td>7.9–14.2 × 3.2–9.5</td>
<td>6.5–20.3 × 4.3–13</td>
<td>5–15.8(–20.5) × 4–9(–13)</td>
<td>5–11 × 2.4–5</td>
<td>6.5–23 × 4.5–16.5</td>
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<tr>
<td>bract—mm</td>
<td>1.9–2.2 × 2.4–2.5</td>
<td>0.5–1 × 1.3–1.6</td>
<td>0.8–0.9 × 1.5–1.7</td>
<td>0.7–1 × 0.8–1.3</td>
<td>0.6–0.8 × 1.5–1.6</td>
<td>1–1.6 × 2–2.1</td>
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<td>pedicel—mm</td>
<td>3–3.5 × 2.5–3</td>
<td>4.8–6.6 × 1.1–2.6</td>
<td>8.5–10 × 1.5–2.8</td>
<td>(3.5–)5.2–8.5 × 0.9–1.9</td>
<td>3.5–5.7 × 1.6–2.5</td>
<td>1.7–2 × 2.2–2.5</td>
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<tr>
<td>sepal—mm</td>
<td></td>
<td>1.6–1.8 × 1.4–1.6</td>
<td>1.8–2.2 × 1.8–2.4</td>
<td>1.3–1.5 × 1.4–1.8</td>
<td>1.5–2 × 1.6–2</td>
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<td>gland of sepal—mm</td>
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<tr>
<td>long</td>
<td>3.5–4.7</td>
<td>2.4–2.9</td>
<td>1.9–3</td>
<td>1.7–2.4</td>
<td>1.1–2.5</td>
<td>2–2.7</td>
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<tr>
<td>claw of lateral petal—mm long</td>
<td>3.2–3.5</td>
<td>ca. 2.2</td>
<td>2.5–3</td>
<td>2–2.8(–3)</td>
<td>2.7–3.2</td>
<td>1.7–2.2</td>
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<tr>
<td>limb of lateral petal—mm</td>
<td>4–5 × 4.5–5</td>
<td>3.4–3.8 × 2.7–3</td>
<td>4.5–5.5 × 4.5–5</td>
<td>3.5–4.2(–4.8) × 2.1–3.8</td>
<td>3.8–5 × 4.1–5.5</td>
<td>3–3.2 × 3–3.2</td>
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<tr>
<td>claw of posterior petal—mm long</td>
<td>3.5–3.7</td>
<td>ca. 3.7</td>
<td>3–3.3</td>
<td>3–3.7</td>
<td>3.5–4</td>
<td>2.5–3</td>
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<tr>
<td>limb of posterior petal—mm</td>
<td>ca. 3.5 × 4.2</td>
<td>2.5–3 × 2.7–2.9</td>
<td>4.4–5 × 4.2</td>
<td>2.5–3(–4) × (2.4–)3.1–3.3</td>
<td>3.2–3.7 × 4–4.2</td>
<td>ca. 3 × 2.7–3.1</td>
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<tr>
<td>filaments opposite 2 posterior-lateral petals—mm long</td>
<td>ca. 5</td>
<td>ca. 2</td>
<td>4–4.3</td>
<td>2.9–3.5</td>
<td>3.2–3.4</td>
<td>ca. 3.3</td>
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<tr>
<td>filament opposite anterior sepal—mm long</td>
<td>ca. 5.2</td>
<td>ca. 2.8</td>
<td>4–4.2</td>
<td>2.7–3(–3.4)</td>
<td>ca. 2.2</td>
<td>ca. 3.6</td>
</tr>
<tr>
<td>filament opposite posterior petal—mm long</td>
<td>ca. 3.7</td>
<td>ca. 2.6</td>
<td>3–3.2</td>
<td>2–2.5</td>
<td>ca. 2.1</td>
<td>ca. 2.5</td>
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<tr>
<td>anthers—mm long</td>
<td>1.8–2.8</td>
<td>1.4–1.6</td>
<td>1.7–2</td>
<td>1.2–1.8(–2.3)</td>
<td>1.1–1.8</td>
<td>1.5–2.2</td>
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<tr>
<td>ovary—mm high</td>
<td>1.5–1.7</td>
<td>1.2–1.4</td>
<td>1.5–1.8</td>
<td>1.3–1.7</td>
<td>1.2–1.4</td>
<td>1.5–2</td>
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<tr>
<td>styles—mm long</td>
<td>3.5–4.2</td>
<td>3–3.2</td>
<td>4–4.5</td>
<td>2.9–3.3</td>
<td>3–4.3</td>
<td>3.3–3.6</td>
</tr>
<tr>
<td>samara—mm long</td>
<td>(38–)46–50</td>
<td>29–52</td>
<td>45–48</td>
<td>37–43</td>
<td>30–32</td>
<td>(52–)67–77</td>
</tr>
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</table>
Fig. 4. *Heteropterys imperata*. A. Flowering branch with enlarged abaxial view of leaf margin. B. Umbel of flower buds, with one partially removed. C. Flower, from above. D. Lateral petal, abaxial view. E. Androecium, laid out, abaxial view, the stamen second from right opposite the posterior petal, stamen fourth from left opposite the anterior sepal. F. Detail of one anther, adaxial view. G. Gynoecium, anterior style in middle. H. Detail of apex of posterior style. I. Samara. (a–h from the holotype, Carvalho et al. 3559, CEPEC; i from Amorim et al. 397, CEPEC.)

Liana basi ramis teretibus, triangulatis, complanatis vel trilobis. Lamina foliorum majorum 6.5–20.3 cm longa, 4.3–13 cm lata, rotundata, orbiculata, ovata, elliptica, late lanceolata, oblongo-lanceolata interdum oblonga, utrinque glabra; petiolus 10–22 mm longus, basi biglandulifer. Panicula plerunque contracta, 19.5–26 cm longa, erecta vel suberecta, umbellis 4–6-floris interdum 2 floribus proximalibus adjectis, pedunculo florifero nullo, pedicello 8.5–10 longo, 1.5–2.8 mm diametro, gradatim incrassato versus apicem. Petala lucida, in alabastro exposita, patentia, dorsali terina; filamenta inaequalia; styli postici lyrati, apice pedaliformes dorsali terinae. Samarae 45–48 mm longae, nuce laterali terinae.

Liana, climbing to 3–10 m; stems at base 1–3 cm diam., the cross-section cylindrical, triangular, flattened, or deeply divided into 3 lobes, twisted, glabrate, developing small scattered lenticels. Leaves mostly plane, opposite, spreading; petiole (10–)15–22 mm long, initially densely sericeous and soon glabrate, bearing a pair of glands at base, each gland 1.5–2.2 mm diam.; stipules present on petiole, above base, as minute protuberances ca. 0.2 mm long, seldom evident, apparently absent from old leaves; lamina of larger leaves (6.5–)8.2–16.7–20.3) × (4.3–)6.5–13 cm, papery to subcoriaceous, often rounded, orbicular, ovate, elliptic, broadly lanceolate, oblong-lanceolate, or sometimes oblong, obtuse, rounded, cuneate, or slightly cordate at base (sometimes with the petiole partially covered by the base of lamina), rounded, acute, or slightly retuse at apex, the margins bearing many glands and short cilia, especially in young leaves, occasionally with impressed glands scattered below, glabrous or initially sericeous (with short, appressed, medifixed hairs) and soon glabrescent or sometimes thinly sericeous proximally on and near midrib and veins, the lateral veins and reticulum more visible below than above. Inflorescence paniculate, often contracted, 19.5–26 cm long or more, primary branches 4–22, 0.2–13.5 cm long, secondary branches 2–14, 0.1–4 cm long, tertiary branches if present very reduced, accessory branches 0.3–4 cm or absent; terminal or axillary, erect to sub-erect, densely and persistently brown-sericeous, with the flowers borne ultimately in 4–6-flowered umbels, sometimes with another pair of umbels below; inflorescence bracts like leaves and abruptly reduced to 1.7–4.3 × 1.5–2 mm, triangular to lanceolate, the margins entire or sometimes bearing short cilia, biglandular at base, the glands 1.2–1.5 mm diam., bright green; peduncle absent; bracts 0.8–0.9 × 1.5–1.7 mm, rounded, eglandular, abaxially sericeous, adaxially glabrous; bracteoles like bracts but smaller; pedicel 8.5–10 × 1.5–2.5(–2.8) mm, slightly curved upward or sometimes straight in flower, densely brown-sericeous, gradually thickened distally. Sepals 1.8–2.5 × 1.8–2.4 mm, brown, triangular at apex, appressed against filaments in anthesis, abaxially densely sericeous, adaxially glabrous, eglandular or the anterior sepal eglandular and the lateral 4 biglandular, the glands 1.9–3 mm long, elliptic or occasionally orbicular. Petals exposed in the enlarging bud, vivid yellow lacking red, glabrous; lateral petals spreading, margins entire or slightly erosely proximally, claw 2.5–3 mm long, limb 4.5–5.5 × 4.5–5 mm, strongly dorsally carinate with the keel 0.3–1 mm wide, slightly denticate; posterior petal sub-erect, minutely glandular-thickened at margins, claw 3–3.3 mm long, limb 4–4.5 × ca. 4.2 mm, suborbicular, slightly carinate, margins revolute in anthesis. Stamens glabrous; filaments unequal, 3–4.2 × 0.2–0.9 mm, connate ca. ¼ their length, the 2 opposite stamens posterior-lateral petals, 4–4.3 mm long, the longest stamen longest opposite anterior sepal, 4–4.2 mm long, the shortest stamen opposite posterior petal, 3–3.2 mm long, the other stamens 3.5–4 mm long; anthers 1.7–2 mm long, slightly unequal, erect to slightly reflexed in anthesis, connective not widened and equalling the locules, the proximal 2/3–4/5 dark red, the distal ¼–½ pale yellow. Ovary 1.5–1.8 mm high, densely sericeous; styles 4–4.5 mm long, equalling or slightly exceeding the anthers, glabrous, all 3 dorsally apiculate at apex, with a flattened elliptic top and internal stigma; anterior style nearly straight, posterior styles somewhat lyrate. Samara brown at maturity, 45–48 mm long, borne obliquely, thinly seri-
ceous or tomentose to glabrate; dorsal wing 30–38 × 15–17 mm, the abaxial edge straight or curved upward; nut 6–8 mm diam., generally ovoid, smooth-sided, without lateral crests or winglets.

**Distribution and habitat.**—In the restinga, moist forests, and wet forests of the Atlantic coastal range or dry forests inland scattered in the cerrado and campos rupestres in the “Chapada diamantina,” Bahia (Fig. 3). _Heteropterys imperata_ usually reaches into the canopy, along forest borders, in advanced secondary forest or disturbed sites.

**Etymology.**—The specific epithet is derived from the Latin “imperatus” in allusion to its dominant occurrence when found together with _Heteropterys nordestina_ (see comments below) in some places in Bahia.

**Phenology.**—Flowering from June to February and March (immature flowers); fruiting from April to June and August to November.


_Heteropterys imperata_, although collected relatively frequently, has not been recognized for a long time, having been confused previously with _H. anomal a (= _H. patens_). The principal floral difference between the two species is the coloration of petals: all petals of _H. imperata_ are vivid yellow lacking red (vs. all petals orange suffused with red). Furthermore, the petiole of _H. imperata_ is much shorter (10–22 mm long); the inflorescence is often strongly contracted; the flowers are borne ultimately in congested, dense umbels; and the samaras are much smaller, 45–48 mm long (vs. petiole 16–45 mm long, inflorescence spreading, the flowers borne ultimately in lax umbels, and the samaras 52–77 mm long).

I originally intended to describe _Heteropterys imperata_ and the following (_H. nordestina_) as a single, polymorphic, and widespread species. However, during my observations of many populations in north-eastern Brazil, differences in the arrangement of the inflorescence, size of the flowers (see Table 1), and microhabitat were detected for each. _Heteropterys imperata_ usually occurs where sunlight is more abundant and on sandy soils and latisols, whereas _H. nordestina_ occurs preferentially in forest shade and usually on podzols, except for some populations in sandy areas.

Two groups of specimens stand out
among those assigned to this species. In plants from the vicinity of Itacaré and Maruá (Amorim 881, Thomas 9782, T. S. Santos 2882, and T. S. Santos 3545), the petiole is strongly thickened, the leaves are coriaceous with broad laminas (ca. 2 times as long as broad), cordate or partially rounded, concealing the petiole; the secondary veins are usually flat; and the reticulum is inconspicuous. The abaxial edge of the dorsal wing of the samara is curved upward. Another isolated population known only from a small area near the “Chapada diamantina” (the central highlands of Bahia) differs from all other specimens in having a strongly reduced androecium. Specimens from this area are few and incomplete (PCD 764, PCD 943, PCD 956, and Jardim et al. 2530) and more representative collections are necessary to confirm these differences. Further study might show that these specimens represent taxa distinct from Heteropterys imperata, but such a determination will require better collections than are presently available.

Many species of Heteropterys have been recognized as difficult complexes (e.g., *H. oblongifolia* Gleason, *H. pteropetala* A. Juss., *H. syringifolia* Griseb., and *H. trichanthera* A. Juss.). I believe that satisfactory resolution of the taxonomy of these groups requires extensive fieldwork, analyses of specimens, and interpretation of the phenotypic plasticity of some characters. In this case, the differences in floral structure between *H. imperata* and *H. nordestina* warrant the recognition of these taxa at the rank of species. The variation in the size and shape of the flowers is discontinuous, subtle differences in the flowering phenology exist, and, although both species are sympatric in a few places in coastal Bahia, each has a strong preference for distinct microhabitats.

**Heteropterys nordestina** Amorim, sp. nov.  
(Figs. 1, 5)  

**TYPE.** BRAZIL. [Bahia:] In Brasilia circa Bahia, 1839 (fl imm fr), Blanchet 2089 (HOLOTYPE: P, photo MICH; ISOTYPES: BM, G, MICH, photos of isotype at BM, CEPEC, MICH).

Liana basi ramis teretibus, sulcatis, aplanatis vel tri-lobis. Lamina foliorum majorum 5–20.5 cm longa, 4–13 cm lata, elliptica, ovata, obovata, orbiculata, ovato-lanceolata, obovato-oblonga, cuneato-oblonga vel late lanceolata, raro obcordata, utrinque glabra; petiolus 5–21 mm longus, basi biglandulifer. Panicula patenia vel contracta, 15–35 cm longa, in ramis deflexis, umbellis 4–6-floris, pedunculo florifero nullo, pedicello 3.5–8.5 longo, 0.9–1.9 mm diametro, leviter incassato versus apicem. Petala lutea, in alabastro exposita, patentia, dorsifloris carinata, limbo rectangulato vel basi truncato, plano vel concavo; filamenta heteromorpha; styli recti vel lirati, apice dorsifloris apiculati vel truncati. Samarae 37–43 mm longae, nuce lateraliter laevi.

Liana climbing to 1.5–15 m or forming a small shrub when nothing is available to climb on; stems at base 1–2 cm diam., the cross-section cylindrical, irregularly sulcate, flattened, or occasionally divided into 3 or more lobes, twisted, glabrate, developing small scattered lenticels. **Leaves** mostly plane, eventually in inflorescence, opposite, spreading; petiole (5–)11–21 mm long, initially sericeous and soon glabrate, bearing a pair of glands at base, each gland 1.2–1.6 mm diam.; stipules 0.2–0.3 mm long, seldom evident, borne on the base of the petiole, generally absent from old leaves; lamina of larger leaves (5–) 6.1–15.8(–20.5) × (4–)5–9(–13) cm, membranous to subcoriaceous, elliptic, ovate, obovate, orbicular, ovate-lanceolate, obovato-oblong, cuneate-oblong or widely lanceolate, rarely obcordate, obtuse to rounded, rarely acute at base, acute, rounded, shortly cuate or cupidate, rarely refuse at apex, the margins entire or rarely irregularly dentate, bearing many small bordered glands and short cilia, especially in young leaves, glabrous or initially sparsely sericeous (with short, appressed, medifixed hairs) and soon glabrescent or rarely with a persistent sericeous-indument abaxially, the lateral veins slightly prominent below, reticulum very fine and more visible below than above. **Inflorescence** paniculate, spreading or sometimes contracted, 15–35 cm long, terminal or axillary, erect or more frequently pendulous, densely and persistently brown-sericeous, with the flowers borne ultimately in 4–6-flowered umbels; inflorescence bracts like leaves and gradually or abruptly reduced to 1.8–5 × 0.6–1.6 mm, lanceolate or triangular, the margins entire, eglandular or biglandular at base, the
glands 0.6–1.5 mm diam., bright green; peduncle absent; bracts 0.7–1 × 0.8–1.3 mm, ovate or rounded, eglandular or sometimes biglandular, each gland ca. 0.9 mm diam., abaxially sericeous, adaxially glabrous; bracteoles similar to bract but smaller; pedicel (3.5–)5.2–8.5 × 0.9–1.9 mm (ca. 10 × 1.2–2.7 mm in fruit), brown-sericeous, slightly thickened distally, straight or curved. Sepals 1.3–1.5 × 1.4–1.8 mm,
brown, obtuse or rounded at apex, appressed against filaments in anthesis (primarily 2 posterior sepals), abaxially brown-sericeous, adaxially glabrous, eglandular or the anterior sepal eglandular and the lateral 4 biglandular, the glands 1.7–2.4 mm long, elliptic. Petals exposed in the enlarging bud, yellow lacking red, glabrous; lateral petals spreading, margins proximally erose to rarely slightly denticulate, sometimes revolute in anthesis, claw 2–2.8(-3) mm long, limb 3.5–4.2(-4.8) × 2.1–3.8(-4.5) mm, ovate, irregularly rectangular, sometimes truncate at the base, flat to deeply concave, membranous, slightly thickened in center of limb, or sometimes strongly carinate; posterior petal sub-erect, glandular-thickened at margins, claw 3–3.7 mm long, limb 2.5–3(-4) × (2.4–)3.1–3.3 mm, ovate and often truncate at the base, narrowly flat, thickened in center of limb but not carinate. Stamen glabrous; filaments heteromorphic, 2–3.5 × 0.2–0.9 mm, connate ½–⅓ their length, the 2 stamens opposite posterior-lateral petals, 2.9–3.5 mm long, the longest stamen opposite anterior sepal, 2.7–3(–3.4) mm long, the shortest stamen opposite posterior petal, 2.2–2.5 mm long, the other stamens 2.5–3 mm long; anthers 1–1.8(–2.3) mm long, all alike or slightly unequal, reflexed or erect in anthesis, connective with proximal ½–⅔ dark red, the distal ½–⅓ pale yellow. Ovary 1.3–1.7 mm high, sericeous; styles 2.9–3.3 mm long, exceeding the anthers, glabrous, 3 with a slightly flattened-elliptic top, the stigma internal; anterior and posterior styles nearly straight or sometimes somewhat lyrate, dorsally apiculate or truncate at apex, with all 3 facing toward posterior petal. Samara pale brown at maturity, 37–43 mm long, borne erect when single, obliquely or sometimes horizontally when 2 or 3 develop, thinly sericeous to glabrate; dorsal wing 32–38 × 14–18 mm (sometimes much flared distally to produce a flabellate shape), the abaxial edge straight proximally; nut 4–7 mm diam., subseroiroidal, smooth-sided, without lateral crests or winglets.

Distribution and habitat.—Known from northeastern Brazil (Fig. 3) between Rio Grande do Norte to the coast of Espírito Santo, where it occurs widely in all types of restinga (open, flooded, and forest), wet forests (lowland, montane, and tabuleiro), and moist forests (mesophyllous and semi-deciduous) between 5 and 600 m. Heteroperys nordestina is usually a liana growing in the forest canopy, but it is a small shrub in open areas (e.g., in open restinga in Espírito Santo and extreme southern Bahia). In some places in Bahia it can be found in forest remnants near cocoa plantations, whereas in Pernambuco and Alagoas it is found in forest remnants near sugar cane plantations.

Phenology.—Immature flowering specimens have been collected in January and February; flowering occurs primarily from March to July or sometimes until September; fruiting from May to November.

Etymology.—The specific epithet refers to northeastern Brazil, where it is abundant.

H. Melo mulated from Pickel orbicular, or Mun. Lino et al. 07035'S, 20.5°S, 44°15'W, have indument, among collections of specimens from Rio Grande do Norte, Pernambuco, and Alagoas have the strongly carinate lateral petals, the limb irregularly rectangular and deeply concave, and short often glabrate samara; and in some populations from Bahia, the samara shows a flabellate shape (about as wide as long).

The assemblages of populations that show these morphological and ecological traits most clearly could qualify as ecological subspecies, but no reliable characters distinguishing these groups have been observed. Therefore, I choose not to give any of them formal taxonomic status at this time. Furthermore, several collections might represent hybrids between Heteropterys nordestina and possibly the H. oberdanii (in coastal Espírito Santo) or H. imperata (in coastal Bahia).


Liana, climbing to 1.5–4(–10) m; stems at base 1–3 cm diam., the cross-section usually strongly flattened, triangular, or deeply divided into 3 or more lobes, twisted, glabrate, developing small scattered lenticels. Leaves mostly plane, opposite, spreading; petiole 16–39(–45) mm long, initially densely sericeous and soon glabrate, bearing a pair of glands at base, each gland 1.2–
Fig. 6. *Heteropterys patens*. **A.** Flowering branch with enlarged abaxial view of leaf margin. **B.** Flower, from above. **C.** Lateral petal, lateral view. **D.** Androecium, laid out, abaxial view, the stamen second from right opposite the posterior petal, stamen fourth from left opposite the anterior sepal. **E.** Detail of one anther, adaxial view. **F.** Gynoecium, anterior style in middle. **G.** Detail of apex of posterior style. **H.** Samara. (a–g from Amorim & Forzza 3383, SP; h from Silva 378, RBR.)
1.6 mm diam. or rarely eglandular; stipules present on petiole, above base, as minute protuberances ca. 0.3 mm long, seldom evident, apparently absent from old leaves; lamina of larger leaves (6.5–9–19.5–(23) \times (4.5–)6.2–12.5–(16.5) cm, membranous, rounded, subrotund, ovate, elliptic, ovate-lanceolate, or oblong-lanceolate, rounded, obtuse, cuneate or rarely cordate at base, rounded and often apiculate to retuse at apex, the margins bearing many glands and short cilia, especially in young leaves, glabrous or initially sparsely sericeous (with short, appressed, medifixed hairs) and soon glabrescent, the lateral veins slightly prominent below, reticulum very fine and more visible below than above. *Inflorescence* paniculate, spreading, 23–35.5–(47) cm long, primary branches 4–22, 0.8–13 cm long, secondary branches 2–10 or absent, 0.5–2.5 cm long, tertiary and accessory branches if present very reduced; terminal or axillary, pendulous, densely and persistently brown-sericeous, with the flowers borne ultimately in lax 4–6-flowered umbels; inflorescence bracts like leaves, gradually or abruptly reduced to ca. 8 \times 1.1–3 mm, lanceolate to linear-lanceolate, margins entire, eglandular or biglandular at base, the glands 1.8–2.2 mm diam., bright green; peduncle absent; bracts 1.6–2.1 mm, narrowly triangular, eglandular, abaxially sericeous, adaxially glabrous; bracteoles like bracts but smaller; pedicel 10.4–18 \times 1.6–3.5 mm (ca. 11 \times 2–4.5 mm in fruit), slightly curved upward in flower, densely brown-sericeous, gradually thickened distally. *Sepals* 1.7–2 \times 2.2–2.5 mm, brown, obtuse or rounded at apex, pressed against filaments in anthesis, abaxially densely sericeous, adaxially glabrous, the anterior sepal eglandular, the lateral 4 biglandular, the glands 2–2.7 mm long, elliptic or orbicular. *Petals* exposed in the enlarging bud, orange suffused with red, the pigmentation evident in bud, glabrous; lateral petals spreading, margins entire or slightly erose and revolute in anthesis, claw 1.7–2.2 mm long, limb 3–3.2 \times 3–3.2 mm, dorsally slightly carinate with the keel 0.3–0.6 mm wide, slightly decurrent; posterior petal sub-erect, minutely glandular-thickened at margins, claw 2.5–3 mm long, limb ca. 3 \times 2.7–3.1 mm, sub-orbicular, thickened in center but not carinate. *Stamens* glabrous; filaments unequal, 2.5–3.6 \times 0.2–1 mm, connate ca. \( \frac{1}{2} \) their length, the 2 stamens opposite posterior-lateral petals much thicker than others, ca. 3.3 mm long, the longest stamen opposite anterior sepal, ca. 3.6 mm long, not coherent with adjacent filaments, the shortest stamen opposite posterior petal, ca. 2.5 mm long, other stamens 2.8–3.2 mm long; anthers (1.5–)1.8–2.2 mm long, slightly unequal, erect to reflexed in anthesis, connective not widened and equalling the locules, the proximal \( \frac{3}{4}–\frac{1}{2} \) red dark, the distal \( \frac{1}{4}–\frac{1}{2} \) pale yellow or sometimes uniformly dark red. *Ovary* 1.5–2 mm high, densely sericeous; styles 3.3–3.6 mm long, equalling or slightly exceeding the anthers, glabrous, all 3 with a flattened elliptic top, with stigma internal; anterior style nearly straight, dorsally very briefly apiculate at apex; posterior styles somewhat lyrate, dorsally truncate at apex. *Samara* brown at maturity, (52–)67–77 mm long, borne obliquely, thinly sericeous or tomentose to glabrate; dorsal wing 40–63 \times 22–30 mm, the abaxial edge nearly straight; nut 9–14 mm diam., subspherical or ovoid, smooth-sided, without lateral crests or winglets.

**Distribution and habitat.**—Most collections of this species are from the Atlantic coastal forests of the hills in the state of Rio de Janeiro (Fig. 3), principally from the primary forest or forest edges. There are a few collections from the northern part of the state of São Paulo (from nearby the same locality), where it is found in restinga forest.

**Phenology.**—Flowering from February to August, and November (only one collection); fruiting from April to November.

Representative specimens examined. BRAZIL. Unknown locality, s.d. (imm fl), Claussen [probably 2423] (P). **Rio de Janeiro**: Serra dos Órgãos, Nov 1883 (fl), Saldanha s.n. (MICH, R 72295); Mun. Campo Grande, Serra do Mendanha, 4 Apr 1978 (imm fl), Martinelli et al. 4130 (RB); Mun. Macaé, Pico do Frade, 19 Sep 1998 (fr), Giordano et al. 2164 (CEPEC, RB, SP); Mun. Nova Friburgo, Alto Macaé, 15 Jun 1891 (fl), Glaziou 18165 (G, NY, P); Reserva Ecológica de Macaé de Cima, 22°28’S, 42°30’W, 9 Mar 1989 (fl), Lima 3489 (CEPEC, RB); Sítio São Jerônimo, 12 Aug 1995 (fr), Pereira 204 (CEPEC, GU); Mun. Nova Iguaçu, REBIO Tinguá, 10 Feb 1994 (fl), Som-
Heteropterys patens is distinctive in its orange petals suffused with red; the posterior petal is red in the center of the limb and the lateral petals are red near the claw, with the pigment evident in bud. Few species of Heteropterys subsect. Aptychia exhibit this coloration in all the petals (usually all petals have the same color or only the posterior petal has a color different from the lateral petals). This characteristic was noted on some sheets from recent collections from the state of Rio de Janeiro and São Paulo (e.g., Furlan et al. 416; Somner et al. 788), and was confirmed during my fieldwork, and it shows a geographic correlation. Therefore, I am treating some populations from southeastern Brazil (Rio Grande do Norte to coastal Espírito Santo) as distinct species (e.g., H. imperata, H. nordestina, and H. oberdani), because the petals of these plants are always vivid yellow lacking red. Other differences are summarized in the key and Table 1.

Banisteria patens, the earliest name for a species of the anomalous-stemmed complex, was based on a Sellow specimen from São Paulo. When Jussieu described Heteropterys anomala, he had three collections (one from Rio de Janeiro and two others from Bahia, see comments for H. imperata and H. nordestina), and was unaware that the earlier name Banisteria patens applied to his new species. Jussieu (1843) made the combination H. patens, but considered it a probably distinct species, because Sellow's type had an eglandular petiole, only short and oblong-lanceolate leaves, and immature flowers. Grisebach (1858) and Niedenzu (1903) followed Jussieu's taxonomic concepts; Niedenzu (1928) established H. patens var. acuminata (here considered a synonym). Although the occurrence of individuals with eglandular petioles is not common in this group, this character alone is not taxonomically significant. Having studied the types, especially the fragment of H. patens from the Berlin (B), now at NY, and having confirmed through recent collections the high variability in the shape of the leaves, I see no basis for separating H. patens from H. anomala.

Acknowledgments

This study is part of a Ph.D. thesis in preparation under the supervision of Maria Candida H. Mamede at the Universidade de São Paulo. I acknowledge the Centro de Pesquisas do Cacau, Instituto de Botânica de São Paulo, Museu de Biologia Mello Leitão, and The New York Botanical Garden for access to their facilities. The curators of the following herbaria sent loans or gifts for my study: ALCB, CEPEC, CVRD, GUA, HRB, HRCB, HUEFS, HUESC, IAN, JPB, MAC, MBM, MBML, MICH, PEUFR, R, RB, RBR, RFA, SP, SPF, and VIES. Thanks are given to Alain Chautems, André M. de Carvalho, Christiane Anderson, Charles C. Davis, Gardene M. de Sousa, Jomar G. Jardim, José Carlos Oliveira, Ludovic Kollmann, Maria Regina V. Barbosa, Rafaela C. Forzza, Rosangela Lyra-Lemos, Sérgio C. Sant’Ana, and William R. Anderson for all the assistance given in the field or herbarium. A special note of thanks is due to Cristina Bestetti Costa, who encouraged me to write this paper. An early version of the English manuscript was kindly read by Jacquelyn A. Kallunki and Wm. Wayt Thomas, who provided valuable commentary and suggestions for improvement of language and content. The illustrations of the flowering branches and Figure 2b were skillfully drawn by botanical artist Rogério Lupo, who also inked the floral de-
tails in each of the figures. The manuscript was reviewed by W. R. Anderson and K. M. Cameron and edited by T. Zanoni. This work was partially sponsored by The Andrew W. Mellon Foundation through the Graduate Studies Program at The New York Botanical Garden. My visit to European herbaria was partially funded by IAPT Research Grants in Plant Systematics 2001. My research on Heteropterys has been made possible by support from the CAPES/PICDT fellowship at the Universidade Estadual de Santa Cruz.

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The numbers in parentheses refer to the taxa as they appear in the text.

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