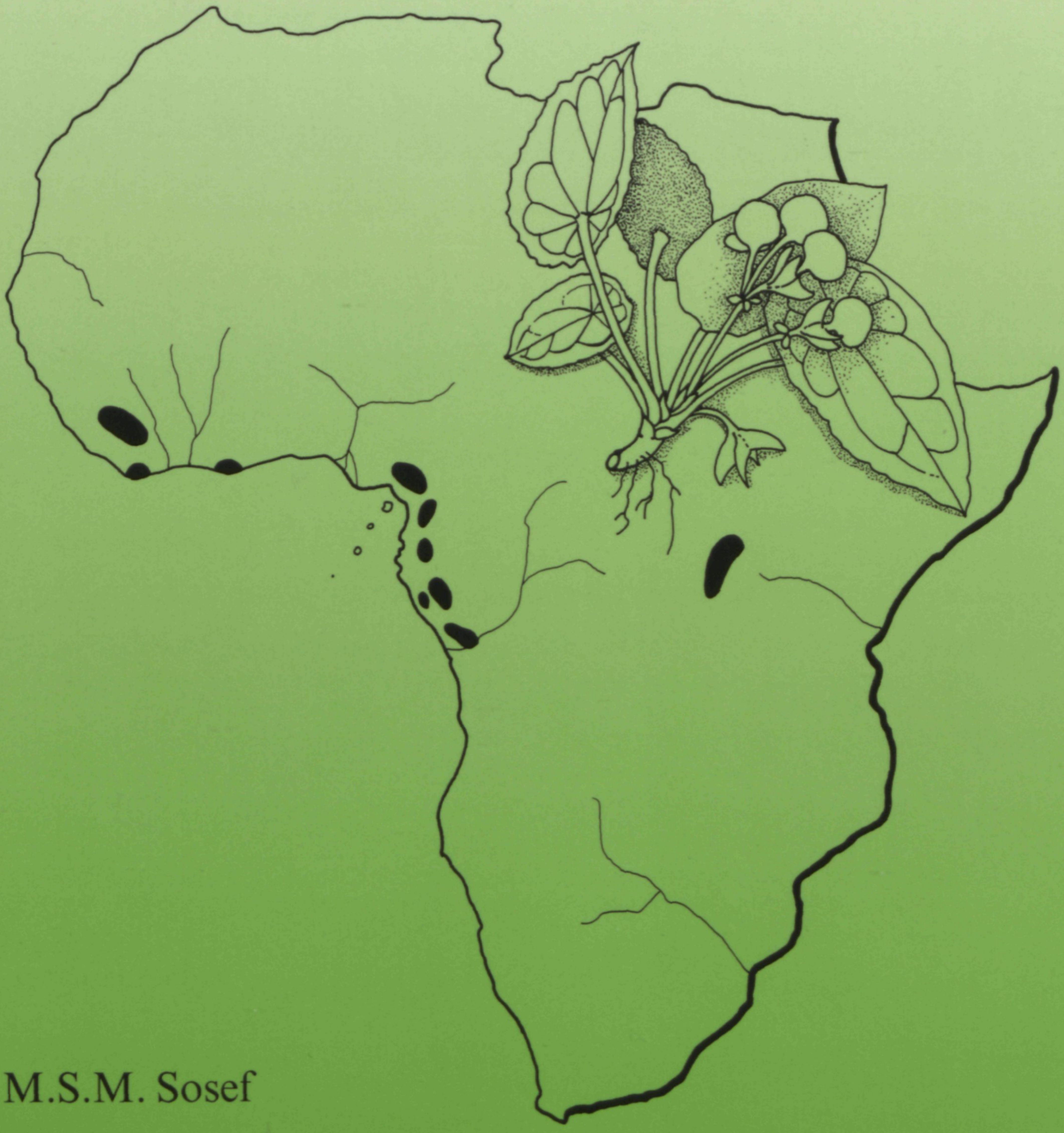
REFUGE BEGONIAS

Taxonomy, phylogeny and historical biogeography of *Begonia* sect. *Loasibegonia* and sect. *Scutobegonia* in relation to glacial rain forest refuges in Africa



M.S.M. Sosef

STELLINGEN

1. Het afraden door Pimentel & Riggins (1987) van het opnemen van continue kwantitatieve kenmerken in een fylogenetische analyse berust op een gedeeltelijk onvermogen van de cladistische methodiek. Aangezien zulke kenmerken wel degelijk fylogenetische informatie bevatten dient er veeleer naar mogelijkheden te worden gezocht deze op een verantwoorde manier te verwerken, opdat ze toch gebruikt kunnen worden.

   Zie paragraaf 12.6 van dit proefschrift.
   Chappill, J.A., 1989. Quantitative characters in phylogenetic analysis. Cladistics 5: 217-234.
   Pimentel, R.A. & R. Riggins, 1987. The nature of cladistic data. Cladistics 3: 201-209.

2. De ideeën van Stuessy (1990) om door middel van het combineren van totaal verschillende manieren van verwantschapsbepaling te komen tot een nieuwe methode, 'The New Phyletics', komen neer op het optellen van appels en koeien en kunnen derhalve niet in de context van de huidige empirische wetenschap worden beschouwd.

   Stuessy, T.F., 1990. Plant taxonomy. The systematic evaluation of comparative data. Columbia University Press, New York. Hoofdstuk 9.

3. Het toepassen van naamgeving volgens de ideeën geformuleerd onder de noemer van fylogenetische taxonomie is in feite een wanhopige poging het Linneaanse binomiale systeem van naamgeving, dat ontworpen is als een praktisch bruikbaar systeem, met geweld te plooien naar een systeem van naamgeving waarin meer direct de fylogenie weerspiegeld is, en is derhalve af te raden.

   Zie paragraaf 11.1 van dit proefschrift.

4. In tropisch Afrika kan een plaatselijke concentratie van soorten uit de secties *Loasibegonia* en *Scutobegonia* worden gezien als een bioindicator voor een voormalig laagland regenbosrefugium.

   Zie Hoofdstuk 12 van dit proefschrift.

5. Zonder taxonomisch onderzoek geen biodiversiteit.

6. Bij confrontatie van de gemiddelde politicus, beleidsmedewerker of universitair bestuurder met de geweldige lacunes die er nog steeds bestaan op het gebied van de meest basale plantensystematische kennis, en daarmee van de biodiversiteit, van de tropen en van tropisch Afrika in het bijzonder, moet deze toegeven dat hij of zij hiervan onvoldoende op de hoogte was én, wat belangrijker is, meent dat de waarde van systematisch onderzoek meer in het algemeen op dit moment te laag wordt ingeschat. Daarom is het de inspanning dubbel en dwars waard om te trachten genoemde personen te informeren.

   BION, 1993. Systematiek: Biodiversiteit en Evolutie. Nationaal Plan voor Systematische Biologie. Den Haag.

7. De vakgroep Plantentaxonomie van de Landbouwuniversiteit Wageningen dient haar naam te wijzigen in 'vakgroep Plantensystematiek', aangezien de eerste naam een te krappe aanduiding is voor het breder georiënteerde onderzoek dat er momenteel plaatsvindt.

   Kalkman, C., 1987. The two sides of a medal. In: P. Hovenkamp et al. (editors). Systematics and evolution: a matter of diversity. Utrecht University. p. 13–21.

   Small, E., 1989. Systematics of biological systematics (or, taxonomy of taxonomy). Taxon 38: 335–356.

8. Een hoogleraar aan een hedendaagse Nederlandse universiteit dient in de eerste plaats te beschikken over onderzoekskwaliteiten, in de tweede plaats over managementskwaliteiten en pas in de derde plaats over didactische kwaliteiten; dit mede als gevolg van het bestaan van een afhankelijkheidsrelatie tussen deze drie eigenschappen.

   Wetenschapsbijlage NRC, 18 november 1993.

9. Religieuze stromingen die het einde van de wereld voorspellen, bespoedigen daarmee slechts de ondergang van zichzelf.

10. Onderzoek naar mogelijkheden honden en vooral katten te fokken die hun behoefte in de tuin van hun 'baas', en niet in die van zijn/haar buren, plegen te doen, zou gefinancierd dienen te worden door het Ministerie van LNV, gelet op de hedendaagse mestproblematiek, en het Ministerie van WVC, in verband met het welzijnsaspect.

Stellingen behorende bij het proefschrift van M.S.M. Sosef: Refuge begonias. Taxonomy, phylogeny and biogeography of *Begonia* sect. *Loasibegonia* and sect. *Scutobegonia* in relation to glacial rain forest refuges in Africa.

Wageningen, 11 maart 1994

REFUGE BEGONIAS

Taxonomy, phylogeny and historical biogeography of *Begonia* sect. *Loasibegonia* and sect. *Scutobegonia* in relation to glacial rain forest refuges in Africa

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REFUGE BEGONIAS

Taxonomy, phylogeny and historical biogeography of *Begonia* sect. *Loasibegonia* and sect. *Scutobegonia* in relation to glacial rain forest refuges in Africa

M.S.M. Sosef

Proefschrift
ter verkrijging van de graad van doctor
in de landbouw- en milieuwetenschappen
op gezag van de rector magnificus,
dr. C.M. Karssen,
in het openbaar te verdedigen
op vrijdag 11 maart 1994
des namiddags te vier uur in de Aula
van de Landbouwuniversiteit te Wageningen.

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Curriculum vitae

Marcus Simon Maria Sosef werd op 4 september 1960 te Delft geboren. In 1978 behaalde hij het VWO diploma aan het St. Stanislascollege aldaar en begon met de studie biologie aan de Rijksuniversiteit Leiden. Het kandidaats-examen werd in 1982 behaald. In de post-kandidaats periode onderzocht hij de oorzaken van de vergrassing van heide-vegetaties en de daaruit resulterende vegetatiepatronen (o.l.v. dr J. Berdowski, Vakgroep Plantenoecologie, Rijksuniversiteit Utrecht) en de plantengeografische positie van Sulawesi (Celebes) in de Maleische archipel (o.l.v. dr M.M.J. van Balgooy, Rijksherbarium, Rijksuniversiteit Leiden). Voor het uitvoeren van deze laatste studie verbleef hij een maand in Bogor, Java. Zijn voornaamste interesse ging uit naar de tropische plantensystematiek. Binnen dit onderzoeksveld voerde hij, in samenwerking met R. de Koning, twee projecten uit, beide aan grassen en begeleid door dr J.F. Veldkamp (Rijksherbarium, Rijksuniversiteit Leiden). De eerste betrof een revisie van de Maleische soorten van het geslacht *Paspalum*. De tweede omvatte een revisie van de geslachten *Heteropholis* en *Thaumastochloa*, inclusief een fylogenetische studie. Ook werd de omgrenzing van de geslachten binnen de groep waartoe deze twee laatste behoren kritisch herzien. Hij studeerde in 1985 cum laude af.

Van september 1985 tot maart 1987 voerde hij een biohistorisch onderzoeksproject uit aan de 17e eeuwse herbaria van de Leidse apotheker Antoni Gaymans. Deze herbaria bevatten planten die destijds in de Leidse Hortus Botanicus aanwezig waren en zij bleken van groot belang bij de reconstructie van de geschiedenis van deze botanische tuin en meer in het bijzonder bij de reconstructie van de oorspronkelijke Clusiustuin.

In de periode van april 1987 tot september 1988 had bij diverse betrekkingen. Hij voerde onder meer een pilot-studie uit naar de mogelijkheden om informatieve kaarten betreffende de voor- of achteruitgang van vegetaties in Nederland te maken d.m.v. het combineren van verspreidingskaarten van afzonderlijke soorten. Hij verwierf een gedegen kennis van de Noord-West Europese flora en was betrokken bij de vertaling en bewerking van twee gidsen voor de planten van dit gebied. Tevens was hij co-auteur van de Flora van Delft en omstreken.

Van september 1988 tot september 1993 was hij aangesteld als OIO bij de stichting NWO (BION). Hij voerde bij de vakgroep Plantentaxonomie van de Landbouwuniversiteit Wageningen een 4-jarig onderzoeks-project uit aan de geografische positie van glaciale regenbos refugia in Afrika. Dit project omvatte taxonomisch, anatomisch, biogeografisch en fylogenetisch onderzoek aan *Begonia* soorten, die als bioindicatoren kunnen fungeren voor de positie van de voormalige refugia. Kennis omtrend die positie is tevens van belang voor natuurbeschermingsdoeleinden. Gedurende dit onderzoek, dat het onderwerp vormde van zijn proefschrift, maakte hij een verzamelreis naar Gabon. In deze periode was hij secretaris van de sectie Plantensystematiek en -geografie van de Koninklijke Nederlandse Botanische Vereniging.

In januari 1992 kreeg hij een part-time aanstelling bij de Landbouwuniversiteit Wageningen in het kader van het internationale PROSEA-project (Plant Resources of South-East Asia). Hij treedt op als associate editor voor botanische aspecten van de hout-leverende bomen, die in 3 boekdelen worden behandeld. Vanaf oktober 1993 werd dit een voltijdse betrekking.

Publikaties:

Koning, R. de, M.S.M. Sosef & J.F. Veldkamp, 1983. A revision of *Heteropholis* and *Thaumastochloa* (Gramineae). Gard. Bull. Sing. 63: 137–162.

Koning, R. de & M.S.M. Sosef, 1985. A revision of the Malesian species of *Paspalum* L. (Gramineae). Blumea 30: 279–318.

Veldkamp, J.F., R. de Koning & M.S.M. Sosef, 1986. Generic delimitations of *Rottboellia* and related genera (Gramineae). Blumea 31: 281–308.

Balgooy, M.M.J. van, R. de Koning & M.S.M. Sosef, 1987. The phytogeographical position of Sulawesi (Celebes). In: P. Hovenkamp (Gen. Ed.). Systematics and evolution: a matter of diversity: 263–270. Faculty of Biology, Utrecht University, Utrecht.

Berdowski, J.J.M., R. Hengeveld & M. Sosef, 1987. Changes in aggregation of a temporal transition of heathland into grassland. In: J.J.M. Berdowski. The catastrophical death of *Calluna vulgaris* in Dutch heathland: 53–62. Elinkwijk BV, Utrecht.

Ham, R. van der & M. Sosef, 1987. Flora van Delft en omstreken. Natuur en Milieucentrum De Papaver, Delft. 106 pp.

Sosef, M.S.M. et al., 1987. A catalogue of the herbaria of Antoni Gaymans (±1630–1680) and a comparison with the collection of the Leiden Hortus Botanicus in 1668. Rijksherbarium, Leiden. 131 pp.

Heniger, J. & M.S.M. Sosef, 1989. Antoni Gaymans (ca 1630–1680) and his herbaria. Arch. Nat. Hist. 16: 147–168.

Sosef, M.S.M. & L. Tjon Sie Fat, 1989. Leidse rozen in een 17e eeuws herbarium. Rozenbulletin 67: 1, 9–10.

Sosef, M.S.M., 1991. Glacial rain forest refuges and speciation in *Begonia* sect. *Loasibegonia*. In: J.H. Seyani (Ed.). The XIIIth AETFAT Congress Zomba, Malawi: Abstracts: 62–63. National Herbarium and Botanic Gardens of Malawi, Zomba.

Sosef, M.S.M., 1991. Glacial rain forest refuges and speciation in *Begonia* sect. *Loasibegonia*. Acta Bot. Neerl. 40: 381.

Sosef, M.S.M., 1992. Novitates Gabonenses 8: Seven new *Begonia* species from Gabon. In: J.J.F.E. de Wilde (Ed.). Studies in Begoniaceae III. Wageningen Agric. Univ. Papers 91-4: 83–116 (ook Belmontia n.s. 24, no 147).

Sosef, M.S.M., 1992. New species of *Begonia* in Africa and their relevance to the study of glacial rain forest refuges. In: J.J.F.E. de Wilde (Ed.). Studies

in Begoniaceae III. Wageningen Agric. Univ. Papers 91-4: 117–151 (ook Belmontia n.s. 24, no 148).

Sosef, M.S.M., 1992. The variable taxon: coding for polytypism within a cladistic analysis. Acta Bot. Neerl. 41: 352.

Sosef, M.S.M., 1993. co-auteur van 16 artikelen in: I. Soerianegara & R.H.M.J. Lemmens (Eds). Plant resources of South-East Asia 5(1). Timber trees: Major commercial timbers. Pudoc, Wageningen.

in druk:

Sosef, M.S.M., 1994. Glacial rain forest refuges in relation to speciation in *Begonia* sect. *Loasibegonia* and sect. *Scutobegonia*. In: J.H. Seyani (Ed.). Proceedings of the XIIIth AETFAT Congress Zomba, Malawi.

Samenvatting

Begonia is een geslacht met ± 1000 soorten en komt in alle tropische streken voor. In Wageningen worden, onder leiding van dr J.J.F.E. de Wilde, de continentaal Afrikaanse begonia's bestudeerd. Continentaal Afrika is met ± 120 soorten, verdeeld over 10 secties, armer aan begonia's dan andere continenten. Een studie aan twee van die secties met in totaal 40 soorten is in dit werk vastgelegd. Er bestond, naast een grote noodzaak tot opheldering van de status van de afzonderlijke soorten, twijfel over de vraag of de twee secties wel te onderscheiden zijn.

Enkele andere belangrijke onderzoeksvragen zijn gerelateerd aan de theorie over regenbosrefugia tijdens de laatste ijstijd.

Het taxonomisch niveau dat de rang van sectie of geslacht krijgt toebedeeld is vrij arbitrair gedefinieerd en wordt verschillend toegepast in het plantenrijk.

Soorten worden in deze studie benaderd volgens het biologisch soortsconcept. Ondersoorten worden gezien als evolutionaire eenheden die in ruimte gescheiden zijn, terwijl variëteiten sympatrisch voorkomen.

Een uitgebreide morfologische studie ligt ten grondslag aan het af- en omgrenzen van de afzonderlijke soorten. De twee secties worden o.a. gekenmerkt door een kruipend rhizoom, een monochasiale bloeiwijze met sterk gereduceerde bloeiwijzeassen, niet-openspringende vruchten en mannelijke en vrouwelijke bloemen met 2 perianth segmenten die vaak helder geel gekleurd zijn. Belangrijke diagnostische kenmerken voor de afzonderlijke soorten zijn te vinden in de vorm van het vruchtbeginsel en de vorm en beharing van de bladeren. Uitsluitend op grond van macromorfologische kenmerken kan geen duidelijk onderscheid tussen de twee secties worden gemaakt (zie echter hieronder).

Eerdere studies toonden een grote verscheidenheid aan bladanatomische kenmerken binnen *Begonia* aan. Er werd een bladanatomische studie aan de hier behandelde soorten uitgevoerd. In de eerste plaats om aanvullende kenmerken voor de verwantschapsanalyse (de fylogenetische analyse) te vinden, om daarmee een veel bredere en steviger basis te verkrijgen. In de tweede plaats om te onderzoeken of er anatomische verschillen tussen de twee secties kunnen worden aangewezen.

De bladanatomie werd bestudeerd m.b.v. electronenmicroscopisch onderzoek en anatomische dwarscoupes en mag succesvol worden genoemd, aangezien beide bovengenoemde doelen werden bereikt. Er blijkt, zelfs binnen deze groep van nauw verwante soorten, een grote variatie aan anatomische kenmerken te bestaan, die in veel gevallen een ondersteuning geeft aan op grond van de macromorfologische studie reeds veronderstelde verwantschappen.

Belangrijke bladanatomische kenmerken zijn:

- het al dan niet aanwezig zijn van een cuticulastructuur op de haren,
- het bezit van korte, worstvormige, vaak geclusterd voorkomende of juist langgerekte, r-vormige, alleenstaande klierharen,
- de aanwezigheid van sclerenchym rond de vasculaire bundels,
- de grootte van de epidermiscellen ten opzichte van de eronder liggende palissade parenchymcellen.

Enkele bladanatomische kenmerken kunnen worden gezien als aanpassingen aan de vaak zeer lichtarme omstandigheden, waaronder de planten in de natuur groeien.

Anatomische kenmerken van de vruchtbeginsels werden onderzocht en eveneens gebruikt voor de fylogenetische analyse. Enkele belangrijke kenmerken zijn de vorm van de placentae, de vorm van de septen en de rangschikking van de ovula.

M.b.v. series preparaten van dwarsdoorsneden werd daarnaast het vaatbundelverloop, de vascularisatie, binnen het vruchtbeginsel geanalyseerd. Eerder onderzoek suggereerde de activiteit van 2 afzonderlijke meristemen bij de vorming van het vruchtbeginsel. Dit werd ook ondersteund door onderzoek uitgevoerd in Wageningen aan de vascularisatie bij soorten van de sectie *Tetraphila*. De vascularisatie van de hier onderzochte soorten steunt deze hypothese echter niet en suggereert een 'normale' opbouw van het vruchtbeginsel uit vruchtbladen.

Ook de anatomische structuur van de papillen op de stijl blijkt variatie te vertonen, die indicatief is voor een gemeenschappelijke afstamming.

Micromorfologische kenmerken van de zaden werden reeds eerder door collega's in Amsterdam onderzocht en blijken bruikbaar voor het onderscheiden van secties binnen het geslacht *Begonia*. Enkele relevante kenmerken werden geselecteerd en toegevoegd aan de datamatrix voor de fylogenetische analyse.

Soorten uit de hier bestudeerde secties zijn in het verleden kunstmatig gekruist, zowel onderling als ook met soorten uit geheel andere secties. Ook werden enkele natuurlijke hybriden waargenomen. In slechts één geval gaat het daarbij mogelijk om een hybride met een soort uit een andere sectie, t.w. de nauw verwante sectie *Filicibegonia*.

De meeste soorten uit de secties *Loasibegonia* en *Scutobegonia* groeien op matig tot sterk beschaduwde plaatsen in vochtig tropisch regenbos. Zij zijn terrestrisch en komen voor op relatief zure, veelal kleiige bodems met een laag Mg-gehalte.

Veel van de soorten zijn moeilijk te cultiveren en vereisen een hoge relatieve vochtigheid, een luchtig, relatief zuur substraat en bescherming tegen direct zonlicht.

De soorten bloeien over het algemeen in duidelijke perioden, meestal 2 per jaar. De bloemen van enkele soorten vertonen slaapbewegingen en zijn gedurende delen van de dag en de nacht gesloten. Het is nog zeer onzeker hoe bestuiving plaatsvindt, hoewel bestuiving via insecten het meest waarschijnlijk is. Het rijpen van de vrucht duurt veelal meerdere maanden. De zaden komen dicht bij de moederplant vrij uit een langzaam desintegrerende vrucht en de zaadverspreiding lijkt derhalve weinig effectief.

Taxonomie streeft naar een stabiel en natuurlijk systeem van classificatie. Een strikte reflectie van de verwantschapsrelaties in de naamgeving strookt echter niet met de stabiliteit ervan. Het accepteren van een bepaalde vorm van parafyletische clada als geslacht biedt een oplossing.

De twee hier bestudeerde secties vormen tesamen zeer waarschijnlijk een monofyletische groep. Als buitengroep komt de sectie *Filicibegonia* als de meest waarschijnlijke in aanmerking.

Op grond van een theoretische vooronderstelling wordt een speciale behandeling van polytypische kenmerken in een fylogenetische analyse voorgesteld.

Een datamatrix voor de 40 soorten en 132 kenmerken werd opgesteld en m.b.v. cladistische methodieken geanalyseerd. Een eerste analyse leverde een zeer instabiel resultaat met een relatief groot aandeel aan 'zwakke' kenmerken. Daarom werd een wegingsmethode opgesteld en toegepast, die de invloed van 'zwakke' kenmerken op de uiteindelijke structuur van de verwantschaps-boom enigzins doet verminderen. Na toepassing van deze methode bleek dat een zevental monofyletische subgroepen kunnen worden onderscheiden. Met twee van die subgroepen werd nog een additionele analyse uitgevoerd, teneinde de binnengroep structuur te achterhalen. Van een vijftal soorten bleef de definitieve positie in de verwantschapsboom onzeker. De uiteindelijk geaccepteerde verwantschapsboom is minder parsimoon dan de initiele.

De belangrijkste conclusie die uit de verwantschaps-relaties mag worden getrokken is, dat de secties *Loasibegonia* en *Scutobegonia* twee monofyletische groepen vertegenwoordigen en dus gehandhaafd dienen te worden. Synapomorfiëen voor de sectie *Loasibegonia* zijn de sappige bladstelen en de korte, worstvormige klierharen. Het bezit van een dunne epidermis, sclerenchym rond de tertiaire nerven, een cuticulastructuur op de cellen van de haren, lange, r-vormige klierharen en een stomp operculum van het zaad zijn karakteristiek voor de sectie *Scutobegonia*.

Tijdens de laatste ijstijd (± 70.000 – 12.000 jaar geleden) was het in tropisch Afrika aanmerkelijk koeler, ± 4°C, en viel er beduidend minder neerslag dan tegenwoordig. Hierdoor zal het areaal laagland regenbos aanzienlijk zijn gekrompen en waarschijnlijk uiteindelijk uiteen zijn gevallen in een aantal refugia, die als eilanden in een gebied met meer droogteresistente vegetatie lagen. Het montane regenbos breidde zich onder deze omstandigheden waarschijnlijk lokaal juist uit. Men dient derhalve, wanneer men spreekt over regenbosrefugia, een duidelijk onderscheid tussen laagland en montaan regenbos te maken.

De hier bestudeerde *Begonia* soorten zijn vrijwel alle strikt gebonden aan beschaduwde, vochtige plaatsen in tropisch laagland regenbos. Zij zullen zich dus tijdens de laatste ijstijd vrijwel uitsluitend in de refugia hebben kunnen handhaven. Aangezien bovendien hun zaadverspreiding weinig effectief lijkt, zal uit hun huidige verspreidingspatronen iets over de ligging van de voormalige refugia kunnen worden afgeleid.

Begonia taxa blijken inderdaad geconcentreerd voor te komen binnen reeds door andere onderzoekers gepostuleerde refugia lokaties, t.w. in Liberia/Ivoorkust, in Kameroen/Gabon en in oost Zaire. Binnen het Kameroen/Gabon gebied zijn een vijf- of zestal kleinere gebieden aan te wijzen met een hoog aantal endemische taxa, die opvallend goed overeenkomen met de gebieden die eerder, op grond van andere gegevens, als mogelijk refugium zijn aangewezen. Deze sterke overeenkomst ondersteunt de gedachte dat de hier bestudeerde begonia's als betrouwbare indicatoren kunnen worden gezien van voormalige refugia. Als zodanig duiden zij op de mogelijkheid dat ook de Mayombe en waarschijnlijk ook de Doudou bergen voormalige refugia voor laagland regenbos zijn geweest.

Het bestaan van geografisch geisoleerde refugia zal een stimulans zijn geweest voor soortvormings-processen. Soorten uit de hier bestudeerde secties moeten in staat worden geacht snel te kunnen evolueren vanwege hun korte levenscyclus en grote plasticiteit in kenmerken. Of dit onder invloed van het ontstaan van de refugia ook is gebeurd, is een belangrijke vraagstelling, die vervolgens bestudeerd wordt m.b.v. een historisch-biogeografische analyse.

Omdat mag worden verondersteld dat de locaties van voormalige refugia ook nu nog gekenmerkt zullen worden door een hoge biodiversiteit, is kennis over hun ligging van groot belang voor natuurbeschermings-activiteiten.

M.b.v. historisch biogeografisch onderzoek wordt geprobeerd de geologische en klimatologische ontwikkelingen te reconstrueren aan de hand van een studie van de fylogenie in combinatie met de verspreidingspatronen van taxa. Tegenwoordig gebeurt dat veelal met cladistische methodieken, waarvan Brook's Parsimonie Analyse theoretisch bezien de meest geschikte is.

Er zijn 25 gebieden van endemisme afgegrensd. Een eerste analyse leidde tot weinig resultaat als gevolg van het relatief grote aandeel van gebieden zonder eigen endemische *Begonia* taxa. Het uitsluiten van deze gebieden leidde tot een beter resultaat, dat echter vanwege de onzekere positie in het areagram van het Doudou gebergte nog niet optimaal is. Uitsluiting van ook dit laatste gebied leidde tenslotte tot een acceptabel resultaat. Het uitsluiten van gebieden lijkt in dit geval goede resultaten te geven, maar de precieze theoretische consequenties ervan dienen nader te worden onderzocht.

In alle analyses is een kerngebied aan te wijzen, bestaande uit een vijftal gebieden in Kameroen en Gabon, dat goed overeenkomt met de regio 'Lower Guinea', die vaak in floristische studies wordt aangehaald.

Omdat uit de analyses blijkt dat zustersoorten slechts zelden in aangrenzende gebieden voorkomen, schijnen er opvallend weinig vicariantiegebeurtenissen te hebben plaatsgevonden. Zo er tijdens de laatste en voorgaande ijstijden vicariantie is opgetreden, is dit mogelijk niet meer aan te tonen vanwege dispersie gebeurtenissen erna. De relaties tussen de gebieden lijken meer een reflectie van floristische similariteit te zijn, dan van een gemeenschappelijke historie.

Er zijn aanwijzingen voor de aanwezigheid van een demarcatielijn langs de Sanaga rivier en een dwars over Equatoriaal Guinea.

Een revisie van de secties *Loasibegonia* en *Scutobegonia*, inclusief een sleutel tot de taxa, wordt gepresenteerd. De taxa gaan vergezeld van uitgebreide beschrijvingen, tekeningen, verspreidingskaarten, oecologische notities en andere relevante gegevens. Recent werden reeds 14 nieuwe soorten gepubliceerd. Daarnaast worden in dit werk de volgende nieuwe taxa beschreven en nieuwe combinaties gepubliceerd:

Begonia letouzeyi Sosef
Begonia prismatocarpa W.J. Hooker subsp. *delobata* Sosef
Begonia prismatocarpa W.J. Hooker subsp. *petraea* (A. Chev.) Sosef
Begonia quadrialata Warb. subsp. *quadrialata* var. *pilosa* Sosef
Begonia quadrialata Warb. subsp. *nimbaensis* Sosef
Begonia quadrialata Warb. subsp. *dusenii* (Warb.) Sosef
Begonia scapigera Hook.f. subsp. *australis* Sosef

De sectie *Loasibegonia* omvat nu 19 soorten, 10 ondersoorten en 2 variëteiten. De sectie *Scutobegonia* heeft 21 soorten en 2 variëteiten.

Contents

1 Summary

Begonia is a genus of ± 1000 species and is represented in all tropical areas. In Wageningen, under the guidance of dr J.J.F.E. de Wilde, the continental African begonias are being studied. Continental Africa has some 120 species, divided over 10 sections, and compared with the amount of species on other continents it is poor. A study on two of those sections with a total of 40 species is recorded in this work. The status of these species was in urgent need of revision, and it was questionable whether the two sections could be upheld.

Some other important research questions are related to the theory on glacial rain forest refuges.

The taxonomic level achieving the rank of section or genus is rather arbitrarily defined and it is being applied differently throughout the plant kingdom.

In this study, species are approached according to the biological species concept. Subspecies are regarded as evolutionary entities separated in space, while varieties occur sympatrically.

An extensive morphological study is the basis for distinguishing the separate species. The two sections are characterized a.o. by a creeping rhizome, a monochasial inflorescence with strongly reduced axes, indehiscent fruits, and male and female flowers with 2 perianth segments that are often bright yellow. Important diagnostic features for the separate species are found in the shape of the ovary and in the shape and the indumentum of the leaves. No clear delimitation between the two sections could be made on the basis of exclusively macromorphological characters (but see below).

Former studies revealed a wide variety of leaf anatomical characters within *Begonia*. A leaf anatomical investigation of the species treated here was performed. Its primary objective was to acquire supplementary characters for the phylogenetic analysis, in order to obtain a more concrete and broader basis. The second objective was to investigate whether anatomical differences between the two sections could be identified.

Leaf anatomy was studied by means of electron microscope research and the analysis of transverse sections. The results are considered to be satisfactory, as both goals mentioned above were reached. It was demonstrated that even within this group of closely related species a wide variety of anatomical characteristics exists, which in many cases support phylogenetic relationships already advanced upon the results of the macromorphological study.

Important leaf anatomical characters are:

- the presence or absence of a cuticula structure on the hairs,

- the presence of short, sausage-shaped, often clustered glandular hairs or of longer, solitary, r-shaped ones,
- the presence of sclerenchyma around the vasculary bundles,
- the size of the epidermal cells in relation to that of the cells of the palisade parenchyma below them.

Some leaf anatomical characters may be regarded as adaptations to the often deeply shaded habitat conditions in which the plants grow naturally.

Anatomical characteristics of the ovary were investigated and also used for the phylogenetic analysis. Some important ones are the shape of the placentae, the shape of the septa and the arrangement of the ovules.

The vascularisation within the ovary was analysed through series of cross sections. Former research suggested the activity of 2 separate meristems in shaping the ovary. This view was supported by research performed at Wageningen on the vascularisation within species of the section *Tetraphila*. The vascularisation of the species studied here does, however, not support this hypothesis and suggests a 'normal' development from carpels.

The anatomical structure of papillae on the style also shows variation which is indicative for common descent.

Micromorphological characters of the seeds were investigated earlier by colleagues in Amsterdam and they proved to be useful in delimiting sections within the genus *Begonia*. Some relevant characters were selected and added to the datamatrix used in the phylogenetic analysis.

Species of the sections studied here have been artificially hybridized in the past, both mutually and with species from quite different sections. Some putative natural hybrids have also been observed. In only one case this possibly concerned hybridization with a species from a different section, viz. the closely related *Filicibegonia*.

Most species of the sections *Loasibegonia* and *Scutobegonia* grow on medium to heavily shaded sites in humid tropical rain forest. They are terrestrial and occur on comparatively acid, often clayey soils with a low Mg-content.

Many of the species are difficult to cultivate and demand a high relative humidity, a light, comparatively acid substrate and protection against direct sunlight.

Generally, the species flower during distinct periods, usually twice a year. The flowers of several species show sleeping movements and are closed during parts of the day and night. It is still quite uncertain how pollination takes place, although insect pollination is the most likely possibility. Maturation of the fruit often takes several months. The seeds are released close to the mother plant from slowly disintegrating fruits and seed dispersal therefore does not seem to be very effective.

Taxonomy strives after a stable and natural system of classification. A strict reflection of genealogical relationships in nomenclature is not compatible with its stability. The acceptance of a certain kind of paraphyletic clades as genera offers a solution.

Most likely the two sections studied here form together a monophyletic group. The section *Filicibegonia* represents the most plausible outgroup.

On account of a theoretical presupposition, a particular treatment of polytypic characters in a phylogenetic analysis is being proposed.

A datamatrix for the 40 species and 132 characters was drawn up and analysed by means of cladistic methods. A first analysis yielded a very instable result with a comparatively large amount of 'weak' characters. That is why a weighting method was developed and applied. It diminishes the influence of 'weak' characters on the final cladogram structure. After application of this method 7 monophyletic subgroups could be identified. In addition, two of those were analysed separately in order to reveal their ingroup structure. The definite position of 5 species remained uncertain. The ultimately accepted phylogenetic tree is less parsimonous than the initial one.

The most important conclusion that may be drawn from the genealogical relations is, that the sections *Loasibegonia* and *Scutobegonia* represent 2 monophyletic groups and therefore they should be upheld. Synapomorphic characters for the section *Loasibegonia* are the juicy petioles and the short, sausage-shaped glandular hairs. The presence of a thin epidermis, sclerenchyma around the tertiary nerves, a cuticula structure on the hairs, long r-shaped glandular hairs and an obtuse operculum of the seed is characteristic for species belonging to the section *Scutobegonia*.

During the last glacial (± 70,000 – 12,000 year B.P.) in tropical Africa it was considerably cooler, ± 4 C, and there was much less precipitation than at present. As a result the area of lowland rain forest presumably shrank considerably and ultimately disintegrated into a number of small refuges, situated as islands within an area occupied by more drought-resistant vegetation. Under these circumstances the area of montane rain forest probably expanded locally. Consequently, when speaking of rain forest refuges, one must make a clear distinction between lowland and montane rain forest.

The *Begonia* species studied here are practically all confined to shaded, humid places in tropical lowland rain forest. During the last glacial, they will have survived almost exclusively in the refuges. Since, moreover, their seed dispersal seems not to be very effective, the location of the former refuges may be deduced from their present-day distribution.

Begonia taxa happen to occur concentrated indeed within the main refuge localities postulated by other researchers, viz. in Liberia/Ivory Coast, in Cameroon/Gabon and in eastern Zaire. Within the Cameroon/Gabon area some 5 or 6 smaller areas with a high number of endemics can be denoted. These coincide remarkably well with the areas earlier indicated as possible refuges on the basis of other data. This strong conformity supports the view that these begonias may be regarded as dependable indicators of former refuges. As such they point to the possibility that also the Mayombe area and possibly the Doudou Mountains represent former lowland rain forest refuges.

The existance of geographically isolated refuges formed a stimulant for speciation processes. Because of their short life cycle and the plasticity of their characters, the present species should be capable to evolve rapidly. Whether this has indeed happened under the influence of the development of refuges is an important question, that is studied next by means of a historical biogeographic analysis.

Because it is plausible that the localities of former refuges will have retained a high degree of biodiversity into our days, knowledge about their location is of prime importance for nature conservation activities.

By means of historical biogeographical research it is attempted to reconstruct the geological and climatological developments, using the phylogeny in combination with the distribution patterns of taxa. Nowadays, cladistic methods are often used, and among these Brooks Parsimony Analysis is considered theoretically the most suitable.

In all, 25 areas of endemism have been demarcated. A first analysis lead to a poor result due to the comparatively large quantity of areas lacking their own endemic *Begonia* taxa. Eliminating these areas from the analysis yielded a better result, which was, however, still not optimal owing to the uncertain position within the areagram of the Doudou Mountains. Disregarding the latter area yielded an acceptable result. Eliminating areas seems to lead to good results in the present case, but the precise theoretical consequences of such actions need to be further investigated.

A core area, composed of some 5 areas in Cameroon and Gabon, can be identified in all analyses that were performed. It coincides comfortably with the 'Lower Guinea' region often cited in floristical studies.

Because the analyses show that sister species rarely occupy adjacent areas, remarkably few vicariance events seem to have occurred. If vicariance did occur during the last and previous glacials, this is perhaps concealed at present because of renewed dispersal after each occasion. The relationships between the areas seem to be more of a reflection of floristic similarity, rather than of a common history.

There are indications for the presence of a demarcation line along the Sanaga River and another one across Equatorial Guinea.

A revision of the sections *Loasibegonia* and *Scutobegonia*, including a key to the taxa, is presented. The taxa are accompanied by extensive descriptions, drawings, distribution maps, ecological notes and other relevant data. Recently, 14 new species have been published. In the present work the following additional new taxa are described and new combinations proposed:

Begonia letouzeyi Sosef
Begonia prismatocarpa W.J. Hooker subsp. *delobata* Sosef
Begonia prismatocarpa W.J. Hooker subsp. *petraea* (A. Chev.) Sosef
Begonia quadrialata Warb. subsp. *quadrialata* var. *pilosa* Sosef

Begonia quadrialata Warb. subsp. *nimbaensis* Sosef
Begonia quadrialata Warb. subsp. *dusenii* (Warb.) Sosef
Begonia scapigera Hook.f. subsp. *australis* Sosef
The section *Loasibegonia* now comprises 19 species, 10 subspecies and 2 varieties. The section *Scutobegonia* has 21 species and 2 varieties.

Keywords: Africa, anatomy, *Begonia*, biodiversity, biogeography, bioindicators, ecology, flora, forest refuges, historical biogeography, palaeoenvironments, phylogeny, rain forest, taxonomy.

2 Introduction

Begonia is a pantropical genus comprising numerous species. Rough estimates of the total number vary between 900 and 1400 species. These numbers continue to increase as newly discovered taxa are being described almost every year. Many *Begonia* species appear to be narrow endemics. These two facts render the larger estimation of the higher total number of species as the more likely one. The genus is divided into many sections (about 80). In continental Africa only 10 sections occur and these are comparatively well delimited as a result of the intensified taxonomic research of the past 15 years. At present the African begonias are comparatively easy to identify, even for non-specialists. The situation in South America, and even more so in South-East Asia, is far less satisfactory. Here a sound framework of sections is lacking or at least largely outdated. Regularly, newly discovered species cannot be attributed to known sections. For non-specialists trying to establish the right name for a begonia from this region is very difficult if not impossible. A first draft of a worldwide key to the sections of *Begonia* (Barkley, 1972a) is available but unfortunately it has been distributed only on a limited scale. A more accessible, but much older work is that by Irmscher (1925). Furthermore, detailed taxonomic study of the African sections has demonstrated that Barkley's key is already outdated by now.

In 1976 taxonomic research on African *Begoniaceae* at Wageningen was initiated by dr J.J.F.E de Wilde. His aim was to continue the work of Irmscher on African begonias and to realize a full taxonomic revision. Nowadays, a total number of some 120 species is recognized in Africa. Irmscher revised the sections *Augustia* Klotzsch and *Rostrobegonia* Warb. (Irmscher, 1961) which collectively comprise 29 species.

While dr de Wilde concentrated on monographing the large section *Tetraphila* A.DC., he guided several eager botanists to the intricacies of the taxononomic difficult genus. That one may easily become entangled in the biosystematic jungle of *Begonia* is well demonstrated by the excellent and exhaustive work of Arends (1992). Although dealing with a rather limited group of 6 species, this author shows that the complicated systematic aspects can be studied through many disciplines. In chronological sequence the following publications were produced by (or with an important contribution of) Wageningen scientists, and show the multidisciplinary approach of the research project: de Wilde & Arends (1979) on *B. loranthoides* Hook.f.; de Wilde & Arends (1980) on section *Squamibegonia* Warb.; Hagman & de Wilde (1984) on two species of the section *Tetraphila* A.DC.; de Wilde (1985a) on the new section *Cristasemen* J.J. de Wilde; Reitsma (1984, 1985) on placentation and the new section *Baccabegonia* Reitsma respectively; van den Berg (1985) on pollen morphology; de Wilde & Arends

(1989) on *B. salaziensis* (Gaud.) Warb.; de Lange & Bouman (1992) on seed micromorphology; Sosef (1992a, 1992b) on new species of the sections *Loasibegonia* A.DC. and *Scutobegonia* Warb.; Arends (1992) on the biosystematics of 6 species of the section *Tetraphila* A.DC. Within the framework of this multidisciplinary approach the present project was formulated (and financed). It incorporates taxonomic, phylogenetic, anatomic, ecologic, biogeographic and historic aspects.

Of the 10 African sections, *Loasibegonia* and *Scutobegonia* were most urgently in need of revision. A full revision had never been published, and before the present study started de Wilde already suspected that these sections might contain many new and undescribed species. This explains misidentifications and general confusion often encountered in literature dealing with these sections. At the same time the sections appeared to present a virtual ideal group to study several aspects of glacial rain forest refuges in Africa (chapters 10 and 12). Their biological aspects promised opportunities to postulate the geographic location of these refuges, using the distribution areas of the taxa involved. A second possibility this group offered was the study of the process of breaking up of a forest area that had been presumably continuous in the past. This process, that supposedly took place during the last glacial, might also have occurred in more ancient glacial periods. The study of these aspects includes phylogenetics followed by cladistic biogeography (chapters 11 and 13).

In the present study cladistic methods were used in order to study the phylogeny of the group (chapter 11). Such methods are to be preferred over others since they base congeniality exclusively on the presence of derived character states. This is the only approach that makes sense in a framework of evolutionary thinking.

Phylogenetic research preferably includes as many characters as possible. In order to increase the number of characters, and as such the reliability of the results, it was decided to perform anatomical studies of leaves and ovaries (chapter 6 and 7) as well. This provided additional characters to those derived from the macromorphological observations (chapter 5). The combined data sets should finally result in a well-founded cladogram (chapter 11).

This study was performed using mainly herbarium material. In addition some 22 species belonging to the two sections studied here are cultivated at Wageningen at present and could be studied in vivo. The plant material was collected in Africa in the course of the past 15 years, mainly by staff of the Department of Plant Taxonomy at Wageningen. Many species could be studied in situ during fieldwork in Gabon in 1991. Additional material for anatomical studies was gathered on that occasion.

In short, the aims of the present study are:

- To realise a full revision of the sections *Loasibegonia* and *Scutobegonia*.
- To study the distribution patterns of the taxa involved in order to reveal their possible indicative value in the light of the geographic location of glacial rain forest refuges.

- To study the phylogeny of the taxa in order to reveal possible vicariance events induced by the breaking apart of the rain forest area during glacial periods with emphasis on the last glacial.

3 History of the sections

The generic name *Begonia* was first published in 1700 by J.P. Tournefort who listed 6 species. They were discovered in the Antilles by C. Plumier who coined the name *Begonia* in honor of M. Bégon, the Intendant of the French Antilles. The first valid publication (as regards botanical nomenclatural rules) of the generic name is that of C. Linné in his Species Plantarum (1753).

Major early contributions to the taxonomy of *Begonia* are those by Klotzsch (1855), who accommodated the 210 species known at that time in 41 genera, and by Alphonse de Candolle (1859), who reduced almost all of Klotzschs' genera to sections of the genus *Begonia*.

The section *Loasibegonia* was described in 1864 by Alphonse de Candolle. It consisted of a single species (indeed the only one known at that time): *B. prismatocarpa* W.J. Hooker. De Candolle coined the name 'Loasibegonia' because the dentate-lobate leaves, the elongated ovary and the yellow colour of the flowers do remind one of those of the genus *Loasa* (*Loasaceae*). Up till then only a few African *Begonia* species had been collected and hence, were known to science. In 1871 J.D. Hooker, in his treatment of the *Begoniaceae* for Oliver's Flora of Tropical Africa, dealt with no less than 26 species, of which the majority was new and based on the extensive West African collections of Gustav Mann. He divided the species into 9 'paragraphs'. His paragraph 2 contains 3 species belonging to the section *Loasibegonia*. The 5th paragraph covers 5 species differing from those in paragraph 2 by forked stigmas and coriaceous fruits with branched placentas. Warburg (1894) coined the name *Scutobegonia* for the latter paragraph, which he gave the rank of section. He interpreted, however, the phrase 'branched placentas' as 'forked placentas', a misunderstanding which has given rise to some confusion. Warburg l.c. distinguished 12 African sections including *Loasibegonia* and *Scutobegonia* that, according to him, differ in having entire and forked placentas respectively. He included in *Scutobegonia* 11 species, among them several which J.D. Hooker had placed in his 6th 'paragraph'. Warburg thus left only a single species in Hookers 6th 'paragraph': the section *Filicibegonia* A.DC.

More species belonging to either one of the sections *Loasibegonia* and *Scutobegonia* were subsequently described by Gilg (1904), Stapf (1906), De Wildeman (1906), Winkler (1906) and Chevalier (1912). Engler's (1921) important account of the African begonias followed the outline of Warburg's treatment with the additional recognition of four series within the section *Scutobegonia*: series *Longicaulis*, *Brevicaules*, *Cordifoliae* and *Euscutatae*. Irmscher described several new species in 1922, while in his treatment of the *Begoniaceae* of the world (Irmscher, 1925) he followed Engler (almost literally) as far as the African species are concerned. It is not until 1954 and 1961 that Irmscher, by then a renowned taxonomist on *Begoniaceae*, described several new species of the section *Scutobegonia*. Unfortunately he was not able to finish his intended monographic treatment of all African begonias.

Subsequently, N. Hallé, intrigued by the numerous species he encountered during his botanical fieldwork in Gabon, took interest in the group (Hallé, 1967 & 1972). In his short account of 1967 he shed doubt on the validity of separating the sections *Loasibegonia* and *Scutobegonia*. He pointed out that in the past several species changed places from one section to the other, while the main distinguishing character – the entire or bifid placentas – seems subject to exceptions. The fact that Wilczek (1969) in his treatment of the *Begoniaceae* of Central Africa accepted the section *Scutobegonia* only is probably inspired by Hallé's remarks.

With the progress of the *Begoniaceae*-project on African begonias at Wageningen, the understanding and correct delimitation of the African sections slowly took shape. Reitsma (1984) discovered that all species of the sections *Loasibegonia* and *Scutobegonia* had undivided placentas. With this observation he discovered that Warburg had wrongly interpreted Hooker's publication. Reitsma (1984: 47) also noted that several species of the section *Scutobegonia* had a slightly aberrant type of ovary. This regards the species which J.D. Hooker grouped together with *B. aspleniifolia* Hook.f. ex A.DC. The latter became the type species of the section *Filicibegonia*. Engler (1921) placed these species in the series *Longicaulis*. This series accommodated the species with an erect stem. In the opinion of de Wilde (1985a: 127) *Begonia* section *Scutobegonia* series *Longicaulis* Engl. should be incorporated in section *Filicibegonia*, a concept endorsed by van den Berg (1985: 71) in his work on the pollen morphology of the group. This transfer was also supported by seed micromorphology (de Lange & Bouman, 1992). *B. thomeana*, up till then accommodated in *Scutobegonia* but clearly differing in several important features, was credited a separate sectional status (de Wilde, 1985a): section *Cristasemen* J.J. de Wilde. As regards section *Filicibegonia* we may conclude that J.D. Hooker, the very first who treated the African begonias, proposed a subdivision that was altered soon but proved to be correct more than a hundred years later. The question remains whether the sections *Loasibegonia* and *Scutobegonia* can be conveniently distinguished (see also de Wilde, 1985a: 125–127). If the placentation type does not provide an unambiguous character, what does? Pollen nor seed characteristics did show sufficient differences, if any at all. The short, almost knob-like stigma of *Loasibegonia* and the forked and twisted one in *Scutobegonia* appear to be inconsistent as a differential character: there are exceptions. Sosef (1992a: 87) left the question pending while describing several new species. A final conclusion is presented in the present publication.

4 Taxonomic concepts

4.1 Genera and sections within *Begoniaceae*

Klotzsch (1855) recognized no less than 41 genera within the family *Begoniaceae*. These were all reduced to sections within the genus *Begonia* by A. de Candolle (1859, 1864). At present the genus incorporates about 80 sections, some with very characteristic features. The desirability of raising at least some sections to the genus level (e.g. section *Casparya* (Klotzsch) Warb., pers. comm. de Lange) remains debatable.

Interspecific relationships are not expressed by a specific epithet. In *Begonia* each species seems to be equally related to the huge amount of other species within the genus. Dividing *Begonia* into genera more or less coinciding with the present-day sections would improve the information content of a name. This profit has to be weighted against the disadvantage of the large number of nomenclatorial changes this would bring about. The problem is that it is often very hard or even arbitrary to define the taxonomic level which is to achieve the genus rank (Kornet, 1988). This has resulted in an inconsistent, often historically determined application throughout the plant kingdom; small genera, encompassing little variation, are generally distinguished in e.g. *Gramineae* (Veldkamp, de Koning & Sosef, 1986) whereas *Begonia* serves as an example of a large genus comprising an overwhelming variation.

In order to achieve nomenclatorial stability, it would be preferable to maintain the large genus *Begonia*. However, I would like to make a strong plea here to always denote the section to which any given species belongs. This addition will certainly improve the information content of a given name. At this moment the lack of a thoroughly revised edition of Barkley's key to the sections of *Begonia* (Barkley, 1972a) and the review of species and sections (Barkley, 1972b; Barkley & Golding, 1974; Baranov & Barkley, 1974) is strongly felt.

A discussion on the genus concept in relation to phylogeny, including the subject of monophyletic and paraphyletic taxa, is presented in paragraph 11.1.

4.2 The species concept

What is a species? It seems ridiculous that this simple question about the nature of the basic unit used by systematists all over the world is very hard to answer in an uncontestable manner. Many different concepts have been formulated (see e.g. Stuessy, 1990) but none of them seems to be satisfactory in all respects. The species concept has gained great interest in philosophic circles (e.g. Ghiselin 1974; Hull, 1976). The most remarkable conclusion being, that the biological species should be looked upon as an 'individual', not as a 'natural kind' (see e.g. Zandee & Geesink, 1987; Geesink & Kornet, 1989). Remarkable, because philosophers have been regarding the biological species as the best example of natural kinds for many decades.

The philosophical ideas have, however, not gained much support from practical taxonomists (or even attention, which is surprising as it concerns the basic unit of their daily routine). Probably mainly because the ideas do not provide simple tools to be used in delimiting or recognizing species. Moreover, some of them cannot be put in the context of practical taxonomy at all. This focuses upon two points.

The first is illustrated in the following example. Suppose population A is identical in all morphological aspects with population A' but there has been no interbreeding for a 'considerable' period of time. Theoretically and philosophically speaking, A and A' now belong to two different evolutionary units each with its own evolutionary fate, because in due time A *will* most likely become different from A' (Wiley, 1981: 25), and they should be regarded as two different 'species'. It must be obvious that this is not at all a practical solution. Fate cannot be determined or predicted. Following this line of reasoning, it can also be argued that, when two populations do not interbreed for some period (several years?), they represent separate species, but the moment they do interbreed again, they become one species again. This cannot be translated into a useful, stable, taxonomic system.

The second point concerns the thought that, when a population of species X becomes isolated and evolves into a new species, not one but two new species have come into existence: the new one *and* the 'old' one. The former species X has ceased to exist because its content has changed. That the acceptance of this idea leads to ridiculous situations in dayly practice, is well formulated by Kornet (1993): "If we accepted every permanent splitting as a speciation event, humankind would be fragmented into two further species by every road-accident in which a couple and its children perish.". Her philosophic approach to the species problem involving the concept of internodons seems promising.

Within this study species are approached according to the biological species concept (Mayr, 1969): 'groups of actually or potentially interbreeding populations which are reproductively isolated from other such groups'. It is obvious that in a study using almost solely herbarium material, this definition cannot be tested. Still, I argue that the morphological species concept has not been applied in the present study because the species have not been approached as such. Morphological *criteria* have been used to delimit what are believed to be biological species.

4.3 Infraspecific taxa

It does not seem surprising that, when a clear definition of a species is hard to give, the circumscription of infraspecific taxa is equally troublesome.

Recently, the problems and even obvious contradictions in the use of infraspecific taxa have received more attention (e.g. Hamilton & Reichard, 1992; Styles, 1986). Three main categories are usually accepted: subspecies, variety and forma.

A forma is generally used to accommodate plants differing from the usual appearance in only a single character and appearing sporadically within populations. Such plants can, in my opinion, be regarded as mutants. Their distinctive character does apparently not spread and hence the forma does not comprise a natural, interbreeding group of organisms. Forma, therefore, does not deserve any taxonomic status and is regarded as a superfluous category.

There is no worldwide consistency in the use of the categories subspecies and variety. They are sometimes even considered equivalent (see Hamilton & Reichard, 1992). I think, however, that a distinction is useful. The subspecies is generally regarded as a category with a stronger geographical component than is the variety (see e.g. Stuessy, 1990: 189). As this is concordant with the use in zoological taxonomy, where, moreover, subspecies is the only accepted infraspecific taxon, this usage is to be strongly recommended. In the present study a subspecies is regarded as a cohesive part of the species differing from other parts in one or more characters and being largely allopatric. Cohesiveness is acquired by interbreeding and the spread of distinctive characters throughout a population via inheritance. A variety is also a cohesive part, but is being largely sympatric.

The inconsistent use of the categories subspecies and variety is made possible because of the insufficient definitions and rules in the International Code of Botanical Nomenclature up to the latest edition (Greuter et al., 1988). I firmly support the plea of Stace (1986) for a uniform system legalized and regulated by its formulation in the Code.

5 Macromorphological features

5.1 General habit

All species of the sections *Loasibegonia* and *Scutobegonia* are rhizomatous herbs usually growing in the soil or sometimes on moss-covered dead trees, wet rocks and rock faces. They may be attached to the base of mossy tree trunks, but they are never true epiphytes. The internode length of the rhizome can vary considerably both within and between species. Long internodes are, however, more frequently encountered within the section *Scutobegonia*. Those of the section *Loasibegonia* are frequently compact with a knotty appearance due to the density of scars left by the fallen leaves. The rhizomes of both sections usually have a more or less zigzag habit. The species in section *Scutobegonia* often show a distinct upright apical part of the rhizome that sometimes even forms a short erect stem. In other species the apical part is horizontally displayed or with the apex ascending at an angle of about 45°.

5.2 Indumentum

Three types of trichomes were observed: non-glandular multicellular hairs, glandular hairs and dentate scales. The non-glandular hairs are usually multiseriate, rarely uniseriate. They may be present on almost any part of the plant except for the inner surface of the perianth segments, the styles and the stamens. On the lower leaf surface they are always associated with the nerves. On the upper surface the hairs are placed as a rule on the intervenial parts. Several species of the section *Scutobegonia* show comb-like structures on their petioles which consist of several hairs situated in a row and with merged bases. Such a comb is observed in other species of *Begonia* as well, for example in *B. goegoensis* N.E. Brown of the Asian section *Reichenheimia* (Klotzsch) A.DC.

Within the sections *Loasibegonia* and *Scutobegonia* three distinct types of glandular hairs were observed. They are always tiny and can only be seen at large magnification (20x). Both glandular and non-glandular hairs will be discussed in more detail in chapter 6.

Two species of section *Loasibegonia*, viz. *B. prismatocarpa* and *B. stellata*, possess dentate scales (see also the notes in the taxonomic treatment of these species). They are similar in structure to those found in the African section *Tetraphila* A.DC. as depicted by Arends (1992: 53). Dentate scales are rare within the family and are found elsewhere only in the African sections *Baccabegonia* Reitsma and *Squamibegonia* Warb. Within the family *Begoniaceae* the latter three sections are regarded as primitive (de Wilde, 1985b; Reitsma, 1984; van den Berg, 1985) and the presence of these scales in 2 species of section *Loasibegonia* might be regarded as a relict. Although this matter is not further pursued in the present publication, it might present a clue to unravel the phylogeny of the African sections of *Begonia*.

5.3 Leaves

The rhizome bears alternate leaves.

Each petiole is accompanied by two stipules which are attached to the very top of the internode and thus are situated just *in front* of the attachment of the petiole (see e.g. fig 17.4). Such stipules are classified as free stipules (Eames, 1961). One stipule of a pair bears a bud in its axil. This bud may produce a lateral branch or an inflorescence.

The petiole is either rather firm and fleshy (section *Scutobegonia*), or weakly succulent and juicy (section *Loasibegonia*). The texture of the petiole proved to be correlated with its anatomical structure. Firm petioles have comparatively small parenchymatous cells (± 0.1 mm in diameter), small epidermal cells and several layers of small cells below the epidermis, whereas juicy petioles have larger parenchymatous and epidermal cells (± 0.2 mm in diameter) and lack layers of small cells below the epidermis. These characteristics are similar to the features of the anatomy of the leaf blade and that of the ovary (chapters 6 and 7 resp.).

The consistency of the petiole proved to be a stable character separating both sections. In herbarium specimens species with succulent petioles are often recognized by their completely flattened and somewhat translucent state. Those with firm petioles become opaque and they are never completely flattened when dry. The colour of the petiole varies between pale bronze-green and dark wine-red. The first condition occurs more often within section *Loasibegonia*, the second is more common in section *Scutobegonia*, but petiole colour proved to be variable within many species.

The petiole continues into the midrib of the blade. The transition is either more or less smooth – without or with only a slight angle – or with a distinct angle. In the latter situation the blade is usually positioned in a horizontal plane. Figures 17.2 and 17.3 serve as good examples of both states.

The texture of the leaf blade is somewhat succulent or fleshy. Texture is probably correlated with leaf thickness.

The shape of the leaf blade varies between circular (e.g. *B. atroglandulosa* and *B. potamophila*) to almost linear (in the odd *B. vittariifolia*). As the leaf blades are often asymmetrical, the measurement of length and width might lead to some controversy. In this publication they are taken as shown in fig. 5.1.

The shape of the leaf blade proved to be very variable within the species dealt with. Not only the length/width ratio of the leaves may vary considerably, but also the occurence of both peltate and non-peltate leaves within a single species is not unusual within the group. (N.B. The term non-peltate is preferred here

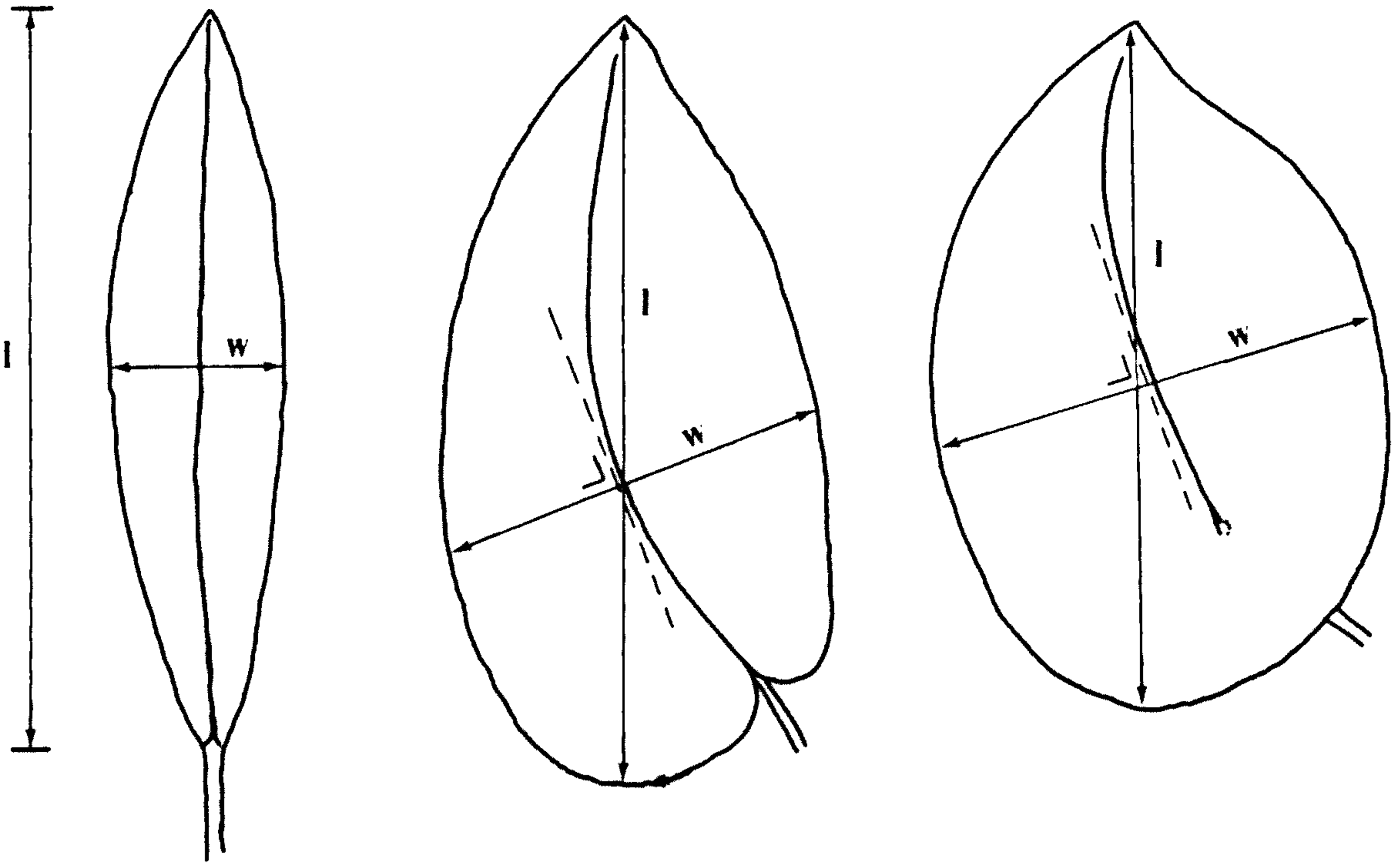

Figure 5.1. Length and width measurements of three different leaf types.

to basifixed because the petiole is often attached more or less oblique to the blade, hence basifixed might be misunderstood.) A particularly illustrative example of the variation in length/width ratio is found within *B. scutifolia* where the ratio ranges from 1.3 to 10. Similar wide ranges were recorded for the African species *B. longipetiolata* Gilg (Arends, 1992: 31). As far as known, the occurrence of both peltate and non-peltate leaf blades within a single species has not been recorded before in *Begoniaceae*. This situation, therefore, deserves some attention. To disclaim possible doubt about the correctness of this observation the following example may serve. Within *B. clypeifolia* a comparison of the collections Arends c.s. 688, Breteler 7687 and Breteler & de Wilde 734, representing peltate-leaved specimens, with Breteler 7712, Reitsma c.s. 3065 and Sita 4128, representing non-peltate-leaved specimens should be convincing as they differ in no other aspects. Smaller specimens of the same species show the same variation, which is demonstrated by comparing the collections A. Louis 1456 (peltate) and A. Louis c.s. 1310 (non-peltate). Later on, the same variation was observed within several other species, viz. *B. hirsutula*, *B. ciliobracteata* and *B. mildbraedii*. Even more convincing evidence is provided by collections with a mixture of peltate and non-peltate leaves, sometimes even within a single plant! Fine examples of such collections are: Andoh 5020, Breteler & de Wilde 343, idem 794. Furthermore, a plant cultivated at WAG showed peltate, semi-peltate and non-peltate leaves (alc. coll. J.J. de Wilde 8786). I could study the phenomenon in the field as well: a plant of *B. hirsutula* having both states occurred within a population of peltate-leaved specimens (coll. J.J. de Wilde & Sosef 10248). It was noted that the petioles of plants from all populations of the latter species continued into the midrib without a distinct angle even though the peltate state is usually correlated with a distinct angle between petiole and midrib.

The nervation of the species of both sections is always basically palmate (actinodromous cf. Hickey, 1979). This state is not always readily distinguished, especially in comparatively narrow leaves where the midrib is often much more prominently present than the other main nerves. In such leaves the other main nerves are few and short but still distinct. On the upper surface the main nerves may be impressed to slightly prominent and they are always glabrous. On the lower surface the nerves are prominent or not. When an indumentum is present this is most crowded on the main nerves. The tertiary nerves are reticulate. This pattern is often conspicuous in herbarium specimens of the section *Scutobegonia* (see also chapter 6.4).

The upper leaf surface is smooth, rugose or bullate. The term rugose is applied to leaves where the main and secondary nerves are impressed on the upper surface (see fig. 17.18). A bulla on the upper surface is often topped with a single hair. The bullae can be simple or compound. A compound bulla, bordered by the reticulate tertiary nerves, has several tops, each of which is often crowned by a hair (see fig. 16.20). The degree of bullateness may be fairly constant within a species (for example within *B. staudtii*) but it may also vary considerably as for example within *B. susaniae* and *B. lacunosa*.

The leaf margin is either smooth, remotely shallowly dentate, sinuate, dentate, denticulate, serrate or crenate. The different character states are depicted in fig. 5.2. In this case as well several states may occur within a single species. The margin may be glabrous but more often it is sparsely or densely ciliate. The cilia are generally placed on top of the teeth. Sometimes (within the section *Scutobegonia*) additional cilia are placed in groups of 2 or 3 together at the base of the teeth. The margin can be either recurved or straight.

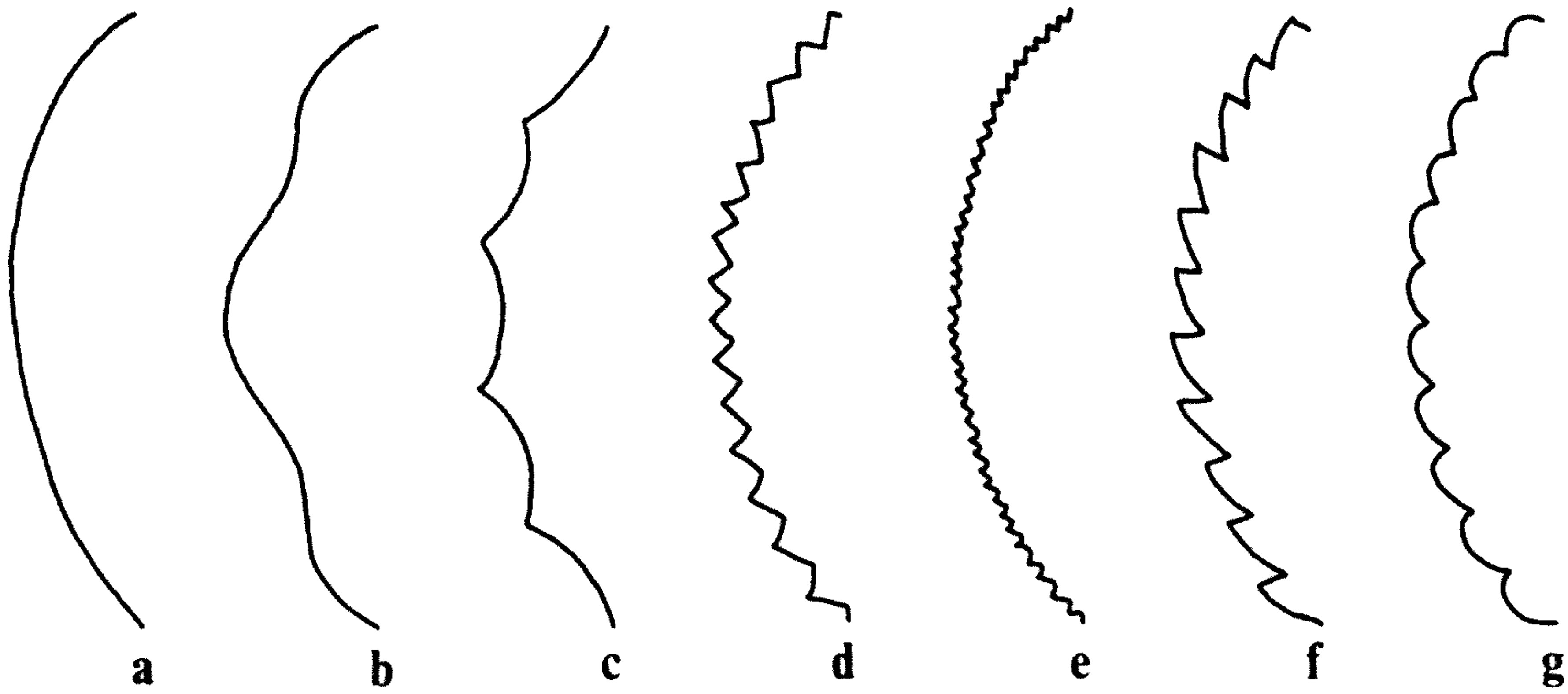

Figure 5.2. Terminology of different leaf margins. a: smooth; b: sinuate; c: remotely shallowly dentate; d: dentate; e: denticulate; f: serrate; g: crenate.

5.4 Inflorescence

The actual inflorescence is borne on the top of a peduncle. This peduncle is usually simple. Dichotomously branched peduncles are present in a few species of the section *Lousibegonia*. When branched, two opposite bracts are present at the forking point. In comparison with the petioles, the peduncle is usually less hairy and paler in colour.

The different types of inflorescence occurring within *Begoniaceae* were thoroughly studied by Irmscher (1914). The dichasium is the basic type of inflorescence and within this basic type a wealth of variation is present. A summary is given by Irmscher (1925).

The sections *Loasibegonia* and *Scutobegonia* possess an identical bisexual type of inflorescence with (1–)2–4(–9) male flowers and (as a rule) a single terminal female flower. Exceptionally two or even three female flowers may be present. The only exception to the bisexual nature is met with in the andro-dioecious *B. schaeferi*.

The inflorescence type is a strongly reduced cincinnal monochasium. The axes of the inflorescence are almost completely reduced and all flowers are inserted very close to each other. Only on closer inspection the zigzag construction characteristic of a cincinnal nature is revealed. The inflorescence of *B. prismatocarpa* was analysed by Irmscher (1914) who already noticed its cincinnal nature. However, he wrongly interpreted the exact position of the bracts. According to Irmscher the *two* lowest bracts of a three-flowered inflorescence are opposite and belong to the first branching point of the inflorescence, consequently the second male flower has no bracts, and the female flower has a single one (his fig. 19b and explanation in the text). The second bract is, however, positioned clearly *above* the attachment of the lowest male flower and thus belongs to the second (male) flower. Consequently every flower has only a single bract. In fig. 5.3 both an actual inflorescence and a schematic representation visualize this conclusion.

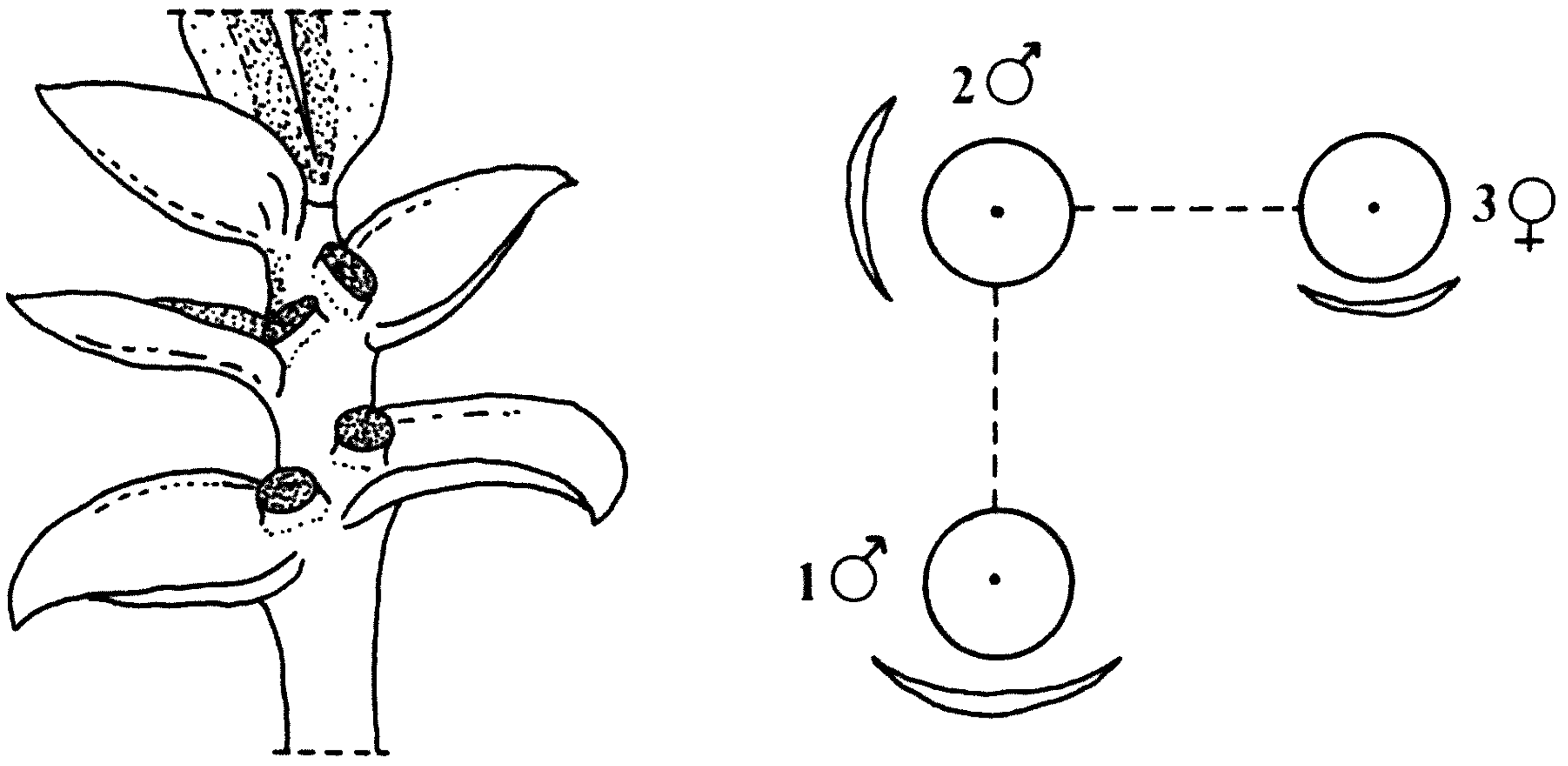

Figure 5.3. Inflorescence structure. Left: 5-flowered inflorescence with cicatrices of 4 male flowers and part of the terminal female flower. Right: flower diagram of 3-flowered inflorescence.

Young inflorescences are more or less rolled in and curved down which gives the impression of a sickle (drepanium). While maturing, the male flowers curve up one by one and eventually reach an erect position or are even curved slightly backwards. The female flower is generally patent to erecto-patent at anthesis. Within the section *Loasibegonia* the female flower improves on this position and the mature fruit is borne erect. In many, but not all, species belonging to the section *Scutobegonia* the female flower recurves towards the substrate after anthesis and eventually the mature fruit is pendulous.

5.5 Flowers

Both male and female flowers of the species treated here have two perianth segments. These are sometimes elliptic but more often more or less circular in outline and rounded or cordate at base. Those of the female flowers are usually slightly larger, especially wider, than those of the male ones. As both segments receive many vascular bundles (see chapter 7.4.2) they can be designated as 'sepals' or 'petaloid sepals'. (See also Arends, 1992: 142; Barabé, 1981: 822; Barabé et al., 1985: 410.) Within the family *Begoniaceae* macromorphologically usually no distinction between sepals and petals can be made, and therefore the term 'tepal' is often applied. The use of the term perianth segment is prefered here because there are indications that this structure may be segregated into a perianth segment and a perianth cylinder (see next paragraph).

At anthesis one of the perianth segments is usually positioned in a vertical plane, the other is more or less horizontally displayed (see for example fig. 16.1). The vertical one is called the upper perianth segment, the horizontal one the lower. The majority of the species of both sections have yellow perianth segments, a minority have white or pinkish ones. The upper segment often has a distinct red spot at its base on the inside which extends into the nerves. The lower segment lacks such a spot. The absence or presence of a red spot may vary within a single species. The outer surface is often orange or reddish, either uniformly so to striate. The orange or red colours are more pronounced on the back of the upper than on that of the lower segment.

The yellow colour of the flowers is only rarely encountered within the family. On the African continent it occurs in *B. thomeana* C.DC. of the monotypic section *Cristasemen* J.J. de Wilde, in *B. flava* Marais, which is very closely related to and maybe even conspecific with the orange-flowering *B. sutherlandii* J.D. Hooker (Irmscher, 1961 and pers. comm. de Wilde), both of the section *Rostrobegonia* Warb., and in *B. iucunda* Irmscher, an odd species, possibly representing a distinct section, probably most closely related to the section *Rostrobegonia*. No yellow flowering begonias are recorded from Asiatic regions. A few species of the mainly Andean section *Huszia* (Klotzsch) A.DC. are the only American representatives with yellow flowers and they were involved in the development of the well-known yellow-flowering tuberous begonias. It has been attempted to transfer the yellow colour, which is often deep and golden, of the species dealt with here into cultivated begonias by means of crossing experiments, but so far without success.

Several species may have either yellow or white flowers. However, during extensive field work of de Wilde and at the occasion of the joint collecting trip with the present author, a population with mixed colours was only encountered once (see note 2 accompanying the description of *B. hirsutula*). The flower colour was generally not found to be correlated with geography; a reason why no taxonomic status was granted to the different states. One exception is *B. atroglandulosa* where such a geographic correlation *is* present and led to the recognition of two distinct subspecies.

5.5.1 Male flowers

The perianth segments of the male flower are inserted on top of a pedicel. In several recent publications on begonias this pedicel has been called the perianth cylinder (de Wilde & Arends, 1980: 380; Arends, 1992: 59). The argument used to interpret this structure as a part of the perianth is that an articulation is absent between the 'segments' and the 'cylinder'. The abscission at the base of the 'pedicel' of the male flower is regarded to be homologous with the abscission present right below the ovary of the female flower. In both publications cited above the outer perianth segments are considered homologous with sepals (Arends, 1992: 142; Charpentier et al., 1989a: 560). The absence of an articulation between sepals and pedicel is quite frequently encountered in the plant kingdom. This would justify to avoid the term perianth cylinder. In my opinion the problem of what to call a true pedicel is raised because the term pedicel is not properly defined in a morphological or anatomical sense. The most accurate description seems to be: 'the ultimate flower stalk' (Rickett, 1954). It is obvious that in different plant groups this might refer to non-homologous organs. It might prove to be worthwile to conduct a profound study towards the nature of the 'pedicel' in different plant families. A dispute whether to use either perianth cylinder or pedicel seems to be quite pointless, since at this stage both may be correct. For practical reasons it is therefore preferred to use the more generally accepted and employed term pedicel.

The number of stamens varies considerably within a single species. Therefore, this character can hardly be used as a diagnostic feature, although there seems to be a tendency among the species to have 'few' or 'many' stamens. A similar kind of wide infraspecific variation was reported by Arends (1992: 73–78). The lowest number found within the group is 6, the highest 48.

The stamens are arranged in a zygomorphic fascicle. The length of the filaments varies within the fascicle, short filaments are arranged on one side, medium sized ones in the middle and long filaments on the other side (fig. 17.5). The filaments are fused for about half of their length forming a short oblique column. The anthers are zygomorphic as well and are always orientated in the same direction: with the two longitudinal slits facing the upper perianth segment. In this way the fascicle reminisces of an amphitheatre (e.g. fig. 16.4). The slits open along the entire length of the anther, not only in the apical part as is the case in several species of the section *Tetraphila* A.DC., which otherwise have a similar androecium (Arends, 1992: 67–72). The apical part of the anther and the extreme ends of the slits are covered by a hood formed by the rear and lateral walls of the anther (see fig. 17.5 and Arends, 1992).

5.5.2 Female flowers

The female flowers are usually shortly pedicellate. The shape of the inferior ovary is an important taxonomic feature within the present group. In absence of female flowers or fruits it is almost impossible for someone not familiar with the group to identify a specimen. In this publication the description of the shape of the ovary (and fruit) always refers to the outline in side view. The general shape varies between narrowly oblong and very shallowly obtriangular. Within the section *Loasibegonia* one subgroup shows narrow ovaries while another has rounded or broadly obovate ones. Those of the section *Scutobegonia* are generally broad, ranging from broadly obovate or circular to very shallowly obtriangular. The only exeption being the odd *B. vittariifolia* with wingless, narrowly spindle-shaped ovaries. Fig. 5.4 demonstrates how the different measurements from the ovary were taken.

Within the section *Loasibegonia* the ovary is often translucent in fresh material. The locules and the often pinkish ovules can be seen right through the ovary wall (see also paragraph 7.3.1). The shape of the locular part is generally correlated with the general outline of the ovary but some variation exists. The best

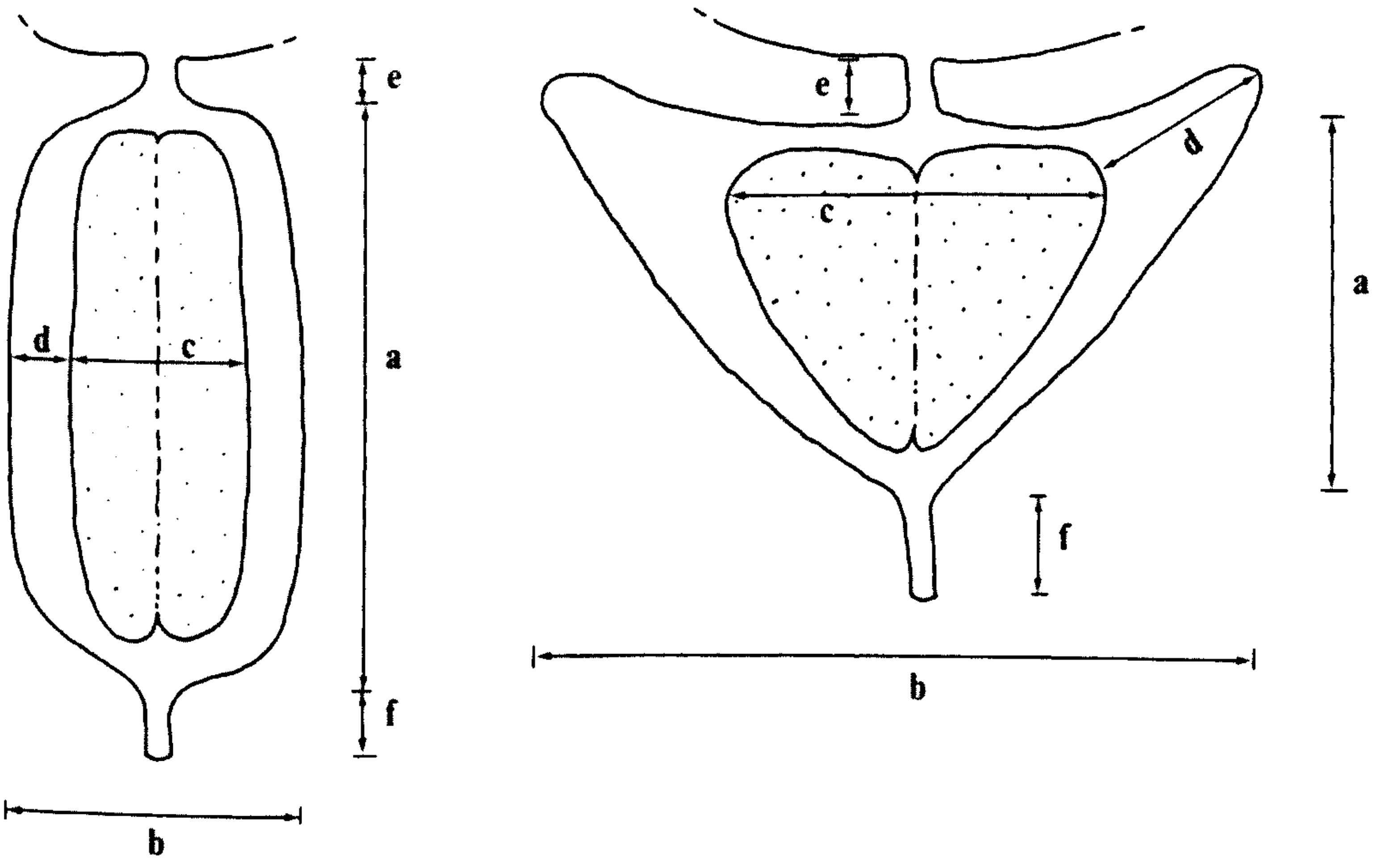

Figure 5.4. Measurements in two different types of ovaries. a: length; b: width; c: width of locular part; d: width of wing; e: beak length; f: pedicel length.

example of an exception is *B. ciliobracteata* with comparatively narrow locules as a component of broad ovaries.

The ovary may bear both glandular and non-glandular hairs. Glandular hairs are always present within the group studied, and hence not useful for species delimitation. The presence of non-glandular hairs on the outer margin of the ovary is not consistent within a species either. However, the presence or absence of such hairs on the locular parts proved to be a most distinctive character.

The shape of the wings on the ovary varies between narrowly ribbon-shaped and very shallowly obtriangular. Sometimes wings are completely absent. The wings may be attached along the entire length of the ovary or only at the apical part. When the ovary is shallowly obtriangular, the wings are sometimes curved upwards.

The apical part of the ovary is usually elongated into a short beak. Often this beak is rather indistinct and can also be considered to be no more than a constriction towards the juncture of the perianth segments. In several species this beak is much more pronounced and quite distinct: e.g. in *B. susaniae* and *B. lacunosa.* Such pronounced beaks are only encountered within the section *Scutobegonia.*

Both sections have a true axile placentation with a single placenta in each locule. It is made plausible by Reitsma (1984) that this single placenta actually consists of two fused ones. The nature of the placentation within the ovary of *Begonia* in general has been subject to much discussion. It will be dealt with in more detail in chapter 7.

The species studied have either three- or four-locular ovaries. Very rarely a two-locular state was observed. Within a single species and even on an individual plant both three- and four-locular ovaries may be found. Plants bearing flowers with variable numbers of locules were also recorded by others, e.g. by Barabé (1980: 820). In general, other *Begonia* species seem to be more constant with regard to this character. A geographical correlation of the number of locules was noted within *B. clypeifolia* and *B. hirsutula.* In the Crystal Mountains plants of the first species have four-locular ovaries, those of the second are three-locular. Outside this area these states do not seem to be fixed. The number of locules is equal to the number of styles. Conform to Arends' findings (1992: 94, fig. 6-12), several abnormal ovaries with a combination of three locules and four styles or with the reversed situation were observed but these are regarded here as anomalies.

The styles are always fused in the basal part. In the apical part they are split and are covered by a papillate stigmatic band. Within section *Loasibegonia* the two arms are usually short and bear a broad, reniform or semicircular stigmatic band which is not or, when semicircular, only slightly coiled. Species belonging to the section *Scutobegonia* often have comparatively long style arms covered by a stigmatic band with a single coil, but exceptions (such as *B. dewildei*) do exist. The stigmatic tissue consists of bottle-shaped papillae and will be discussed in more detail in paragraph 7.3.2.

5.6 Fruits

The fruits in both sections are only slightly enlarged in comparison to the ovary. Only those of *B. ciliobracteata* are markedly larger than the ovary; especially the wings become much broader. The shapes of ovary and fruit are practical identical and hence no separate identification keys for flowering and fruiting material are necessary. In contrast to many other *Begonia* species, the fruits are indehiscent. Wilczek (1969) erroneously classified all species of the sections *Loasibegonia* and *Scutobegonia* among those with dehiscent fruits. The fruits remain on the plants for a considerable length of time, often several months, and they will disintegrate ultimately. More or less erect fruits are found within the section *Loasibegonia* and in a few species of section *Scutobegonia*. The majority of the species of the latter section show a remarkable characteristic, unique within *Begoniaceae*. After anthesis the fruits recurve towards the substrate and, when disintegrating, shed their seeds at the base of the parent plant. More details about this phenomenon and observations on the ripening of the fruits are reported in chapter 10.

The seeds of the two sections are amongst the smallest within the family. They have several characteristic features which are microscopic: see chapter 8.

6 Leaf anatomy

6.1 Introduction

The basis for research on the anatomy of *Begonia* leaves has been established by the profound study of Fellerer (1892). His aim was to reveal the taxonomic affinities of the family. In this he did not fully succeed and even at present the position of the family is unclear (see e.g. Ronse Decraene & Smets, 1990). On the other hand he successfully demonstrated the wealth of anatomical variation and he discovered many different types of trichomes, glandular, non-glandular and scale-like. He described the stomata, which are sometimes arranged in distinct groups, the often multilayered epidermis, cystolyths and different types of crystals, although others had discovered the peculiar twin-cystolyths (and even triads and quartets) earlier (Hildebrand, 1859; Radlkofer, 1890: 115 f(f)). With Fellerer's study it became obvious that the variation within the family was overwhelming and worth further attention, especially because many of the anatomical characters proved to be of systematic value. Unfortunately, he studied but few African species. After Fellerer it was Solereder (1899) who presented a summary of earlier knowledge which was of course mainly based on Fellerer's work.

The well-known German anatomist Haberlandt (1888, 1904, 1916) studied the anatomy of *Begonia* and stressed its functional importance. He pointed to the connection between the generally heavily shaded habitats of begonias and light perception through the lens-shaped epidermal cells. This idea was elaborated upon by Seybold (1955) and Lee (1983), who also presented a fine introduction into the literature and knowledge up till then. Anatomical features similar to those described by Haberlandt (1916) and Lee (1983) were encountered within the species studied here and they are discussed in paragraph 6.4.

More recently, a number of studies on the stomatal arrangements within the family were published (e.g. Boghdan & Barkley, 1972; Hoover, 1986, 1988; Inamdar et al., 1973; Neubauer & Beissler, 1971). In the same period the taxonomic importance of anatomical features within *Begoniaceae* was stressed again by Barkley & Hozid (1971). It was not until almost a century after Fellerer, that another thorough anatomical study wàs performed (Cuerrier et al. 1990, 1991a & 1991b). It was shown that (a combination of) anatomical features are (is) often very distinctive at the sectional level and the authors plead for more attention of begonia taxonomists to anatomical attributes. The present study stresses that anatomy is indeed a very useful tool to study both sectional delimitation and phylogeny and I gladly endorse their plea.

This leaf anatomical study is primarily aimed to characterize the group studied as a whole but also to try to solve the question whether the sections *Loasibegonia* and *Scutobegonia* should be united or not. Furthermore, anatomical characteristics present a welcome additional set of characters to be used in a cladistic analysis. Both these applications are related because it is desirable that any sectional delimitation is corroborated by the results of a phylogenetic analysis.

6.2 Materials and methods

The leaf anatomy of the different species was studied with scanning electron microscopy (SEM) for surface features and with light microscopy for the study of transverse sections. Of most species only a single collection could be studied. Of a few others several collections were available, enabling to study at least some intraspecific variation. This is a far from ideal situation, especially in this group where intraspecific variability is high. However, proper anatomical observations on the juicy leaves of begonia species can only be performed by using material gathered from living plants or alcohol collections, and these are unfortunately scarce. Surface scanning of herbarium material is possible but is far from ideal as often only a limited number of characters can be properly observed. Anatomical observation of transverse sectioned herbarium material is not possible.

A list of taxa and specimens studied is presented below. Several taxa belonging to other sections were studied as well, as they belong to possible outgroups. Codes refer to living collections present at WAG. Voucher specimens of these collections are given between brackets and are present at WAG unless otherwise indicated. When either alcohol material or herbarium material is used this is indicated by 'alc.' and 'herb.' respectively. Several (mainly herbarium) collections were used for SEM observations only. These carry the addition 'SEM only'. Further information on the origin of each collection is given in the paragraph 'Specimens examined' following each species description in the chapters 16 and 17.

section *Loasibegonia*:

(*Begonia*)
adpressa: herb. W.J. de Wilde & de Wilde-Duyfjes 2325, SEM only.
atroglandulosa subsp. *atroglandulosa*: 83PTGA717 (van Veldhuizen 1097); 91PTGA014 (J.J. de Wilde & Sosef 10475), SEM only.
duncan-thomasii: 89PTGB074 (Thomas 5492, K).
gentilii: herb. Gentil s.n. (BR), SEM only.
heterochroma: alc. J.J. de Wilde c.s. 10194.
letouzeyi: 90PTGA027 (J.J. de Wilde c.s. 10080).
microsperma: 86PTCB434 (van Veldhuizen 446, idem 1312).
minuta: herb. Villiers 895 (P), SEM only.
potamophila: 88PTGA017 (van Veldhuizen 1397).

prismatocarpa subsp. *prismatocarpa*: 86PTCB433 (van Veldhuizen 447).
pseudoviola: alc. J.J. de Wilde 8662.
pulcherrima: herb. Bouxin 1207 (BR), SEM only.
quadrialata subsp. *quadrialata* var. *quadrialata*: 82PTGA481 (van Veldhuizen 1299).
salisburyana: herb. Brenan 8531 (K), SEM only.
scapigera subsp. *australis*: 85PTGA519 (van Veldhuizen 1395), SEM only.
scapigera subsp. *scapigera*: 89PTGB073 (van Veldhuizen 1398).
schaeferi: herb. Ledermann 1761 (B), SEM only.
scutifolia: 85PTGA197 (van Veldhuizen 1234, idem 1311); 85PTGA437 (van Veldhuizen 1316), SEM only.
staudtii: alc. van Veldhuizen 445.
stellata: herb. D. Thomas c.s. 7437, SEM only.

section *Scutobegonia*:

(*Begonia*)
aggeloptera: alc. J.J. de Wilde c.s. 10147.
anisosepala: alc. J.J. de Wilde & Sosef 10278.
ciliobracteata: 89PTGB075 = 80PTCM623 (van Veldhuizen 876; plant lost at WAG, new cutting of same collection received from K given the first number).
clypeifolia: 81PTGA297 (Breteler 7687); 83PTGA706 (van Veldhuizen 1099); 90PTGA026 (J.J. de Wilde c.s. 10042).
dewildei: 84PTGA191 (Arends c.s. 700; van Veldhuizen 1348).
erectocaulis: alc. J.J. de Wilde 8791.
erectotricha: alc. J.J. de Wilde c.s. 10189.
ferramica: 85PTGA198 (van Veldhuizen 1313).
hirsutula: 85PTGA182 (van Veldhuizen 1396).
lacunosa: 83PTGA708 (van Veldhuizen 1093).
laporteifolia: herb. Letouzey 13736 (P), SEM only.
mbangaensis: herb. Letouzey 9460 (P), SEM only.
mildbraedii: 90PTGA074 (Breteler c.s. 9985).
peperomioides: herb. Breteler & de Wilde 369, SEM only
scutulum: alc. J.J. de Wilde c.s. 10224.
susaniae: alc. J.J. de Wilde c.s. 10260.
vankerckhovenii: 84PTGA193 (Arends c.s. 699).
vittariifolia: alc. J.J. de Wilde c.s. 10237.
wilksii: alc. J.J. de Wilde & Sosef 10325.
zairensis var. *zairensis*: herb. Léonard 3936 (BR), SEM only.
zenkeriana: herb. Bos 3425, SEM only.

section *Cristasemen*:

(*Begonia*)
thomeana: 80PTST107 (J.J. de Wilde c.s. 141).

section *Filicibegonia*:

(*Begonia*)
elatostemmoides: 82PTGA493 (A. Louis 108).
macrocarpa: 90PTGA193 (Wieringa 938).
sciaphila: 84PTGA146 (Arends c.s. 334).

From each specimen small parts of a single full-grown leaf were taken. The positions of these parts are indicated in fig. 6.1.

The material from living plants was fixed in FAA (5% formalin 36%, 5% acetic acid 96%, 60% ethanol 96% and 30% water) for 12 hours and aspirated in vacuum to remove any air from the tissue, and to let the fixative penetrate the tissue well. Material from living plants as well as that from alcohol collections was then dehydrated through a graded series of increasing concentration of ethanol (up to 96%). The material for microtome sectioning was then passed during a full day through a series of increasing concentration of Kulzer's Technovit 7100 and finally embedded in the same. From this material sections were cut at a thickness of 10μm and stained with 0.5% Toluidine blue in 1 N HCl. The sections were mounted in DPX mountant (80% xylene). Herbarium material, used for SEM observations only, was boiled in water for 30 seconds, cleaned by ultrasonic vibration and dehydrated in a series of increasing concentration of ethanol (up to 96%). Further, all material for SEM observations, immersed in 100% ethanol, was dried using a Balzers Union CPD 020 critical point dryer and subsequently sputter-coated with platina for 3 minutes using a Polaron Sputter Coating Unit E5100. Observation were made with a JEOL JSM-5200 scanning electron microscope while pictures were taken with a Konica FT-1

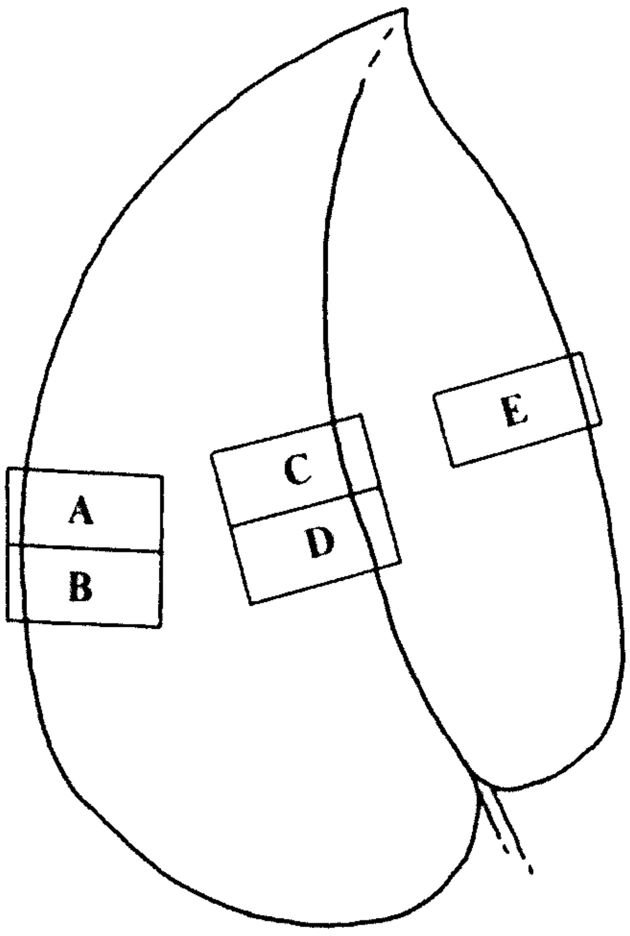

Figure 6.1. Leaf parts taken for anatomical examination. A, C: SEM, upper surface; B: SEM lower surface; D, E: cross sectioning.

camera using a Kodak 5052 TMX film.

Many of the specimens studied by surface scanning carried a dust-like crystalline deposit which, after elimination of other possibilities, was probably caused by the fixation medium. Afterwards a Craf-3 medium was tried and gave good results. FAA performed well when applied to specimens used for transverse sectioning.

6.3 Observations and discussion

In this paragraph a general account of the observed leaf anatomical structures is given and discussed. More specific information is processed in table 6.1, while photographs showing the various anatomical aspects are presented in figures 6.3 and 6.4. A general leaf anatomical description of both sections of *Begonia* presently studied is given in chapter 14.

In the following paragraphs notes relating to the taxonomic relevance of some characters inevitably anticipate on the results of the phylogenetic analyses (chapter 11).

6.3.1 SEM observations

The adaxial epidermal cells form a more or less regular honeycomb-like pattern. The variation in the diameter of these cells among the species studied is enormous and ranges from 10 to 310 μm. Comparatively large epidermal cells are found in section *Loasibegonia*, while smaller ones generally occur in section *Scutobegonia*. The outer surface of each cell is often convex or strongly so (see also paragraph 6.4). The most distinct examples of such strongly convex surfaces are encountered within section *Loasibegonia*. Otherwise, the outer surface of the epidermal cells is smooth, with one exception: that of *B. dewildei* has a beautiful cuticular structure. Different types of cuticular ornamentation have been observed within the family (Metcalf & Chalk, 1979; Cuerrier et al., 1991a). The cuticular ornamentation of *B. dewildei* can be described as irregularly shortly striate with more or less parallel or sometimes interlocked striae (see fig. 6.3.k & l).

The abaxial epidermal cells are usually somewhat smaller than the adaxial ones and more irregular in shape. The stomata are more or less regularly distributed on the lower surface and do not occur in groups as was observed in many other *Begonia* species (see e.g. Cuerrier et al., 1991a, fig. 8). Some specimens were comparatively densely provided with stomata, while in others they occurred more dispersed. Whether or not this variation is caused by environmental factors, and therefore might be variable within a species, is something that needs further study. The stomata are always of the helicocytic type (Payne, 1970), which is most common in the family. The neighbour cells usually have smooth anticlinal walls but undulate walls are sometimes present (e.g. in *B. ferramica* and *B. wilksii*). Several species have stomata that are slightly but distinctly elevated above the surface.

Table 6.1. Leaf anatomical properties of species of *Begonia* sect. *Loasibegonia*, sect. *Scutobegonia* and of several related species.

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legend: - = absent, no; ± = slightly developed, few etc.; + = present, well developed, yes; ? = state unknown, not relevant

1. Total leaf thickness (μm).
2. Thickness of adaxial epidermis (μm).
3. Width of adaxial epidermal cells in surface view (μm).
4. Cuticular ornamentation on epidermis.
5. Anticlinal walls of epidermal layer zigzag in cross section.
6. Degree of convexity of adaxial epidermal cells (1 = 0–12%, 2 = 13–25%, 3 = >25%; see fig. 6.2).
7. Thickness of palisade layer (μm).
8. Shape of palisade cells (r = ± broadly rectangular with rounded abaxial apex, t = triangular).
9. Chloroplast type (l = large ((17–)19–27 μm), s = small (6–15 μm) and light coloured, d = small and dark coloured).
10. Prismatic crystals.
11. Chloroplasts in spongy mesophyll (- = very few, ± = few, + = many).
12. Number of layers of spongy mesophyll.
13. Prominence of midrib on abaxial surface.
14. Prominence of tertiary nerves on abaxial surface.
15. Prominence of midrib on adaxial surface (± = slightly prominent, - = not prominent, s = sunken).
16. Number of vascular bundles in midrib.
17. Vascular bundle in midrib on adaxial surface.
18. Adaxial sclerenchyma on vascular bundles in midrib.
19. Abaxial sclerenchyma on vascular bundles in midrib.
20. Sclerenchyma around tertiary nerves.
21. Type of hairs (m = multiseriate, um = uniseriate with multiseriate base, u = uniseriate).
22. Cells of hairs with distal tips protruding.
23. Cuticular ornamentation on cells of hairs.
24. Type of glandular hairs (s = sausage-shaped, r = r-shaped, g = globuliferous, x = otherwise).
25. Glandular hairs situated in depression.
26. Arrangement of glandular hairs (s = single, g = in groups).
27. Number of glandular hairs or hair groups on 320 x 420 μm (= SEM screen area at magnification of 350x).
28. Hydathodes.
29. Density of stomata (s = scattered ('normal' situation), d = dense).
30. Stomata raised.
31. Neighbour cells of stomata with undulate anticlinal walls.

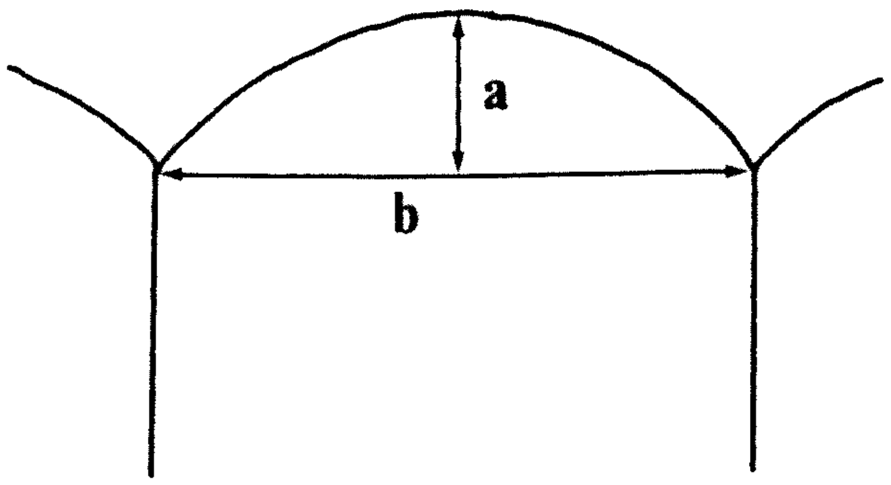

Figure 6.2. Measurement of convexness of epidermal cell, convexness = a ÷ b %.

	1	2	3	4	5	6	7	8	9	10	11	12
Begonia												
sect. *Loasibegonia*												
1. *adpressa*	?	?	30-60	–	?	?	?	r	?	?	?	?
2. *atrogland.* ssp. *atrogland.*	435-460	100-125	70-120	–	+	2	60-90	r	s	+	–	2-3
3. *duncan-thomasii*	205-235	40-60	35-60	–	+	1	75-90	r	l	–	–	1-2
4. *gentilii*	?	?	50-80	–	?	?	?	r	?	?	?	?
5. *heterochroma*	145-210	40-65	50-70	–	±	3	35-55	r	s	–	+	2-3
6. *letouzeyi*	200-230	90-95	50-70	–	+	1	105-115	r	d	+	+	2-3
7. *microsperma*	300-380	115-140	120-160	–	+	1	40-60	t	d	–	+	1-2
8. *minuta*	?	?	60-100	–	?	?	?	r	?	?	?	?
9. *potamophila*	355-390	90-105	130-260	–	±	2	110-130	r	l	–	+	2-3
10. *prismatocarpa* ssp. *prismat.*	215-240	25-40	50-70	–	+	1	70-90	r	l	–	–	2
11. *pseudoviola*	210-220	45-60	120-130	–	–	3	45-70	r	d	–	±	2
12. *pulcherrima*	?	?	50-65	–	?	?	?	?	?	?	?	?
13. *quadrial.* ssp. & var. *quadr.*	700-785	75-115	100-160	–	+	2	160-195	r	l	–	+	5-6
14. *salisburyana*	?	?	50-70	–	?	?	?	r	?	?	?	?
15. *scapigera* ssp. *scapigera*	330-345	65-75	50-90	–	+	3	75-95	r	d	–	+	4
16. *scapigera* ssp. *australis*	?	?	?	–	?	3	?	?	?	?	?	?
17. *schaeferi*	?	?	65-85	–	?	?	?	r	?	?	?	?
18. *scutifolia*	375-415	45-60	60-100	–	+	2	125-135	r	l	–	+	5
19. *staudtii*	145-205	55-70	35-60	–	–	3	20-30	t	d	+	–	2
20. *stellata*	?	?	60-70	–	?	?	?	?	?	?	?	?
sect. *Scutobegonia*												
21. *aggeloptera*	265-300	10-25	25-50	–	–	1	60-80	r	d	+	–	4
22. *anisosepala*	205-235	25-35	35-60	–	–	3	70-95	r	s	+	–	2-3
23. *ciliobracteata*	275-295	17-30	30-50	–	–	1	45-65	r	d	–	+	4-5
24. *clypeifolia*	175-250	15-30	35-60	–	–	1	17-35	t	d	+	+	1-3
25. *dewildei*	555-625	35-40	50-70	+	–	1	105-145	r	s	–	–	5-6
26. *erectocaulis*	370-420	17-30	30-40	–	–	2	60-75	r	d	+	+	7
27. *erectotricha*	175-200	17-30	40-60	–	–	1	30-40	r	d	–	±	5
28. *ferramica*	145-200	45-60	90-130	–	±	1	25-35	t	d	–	–	2
29. *hirsutula*	300-320	15-20	50-70	–	–	1	30-45	r	d	+	±	4-5
30. *lacunosa*	110-130	30-35	30-50	–	±	2	17-30	t	d	+	+	3
31. *laporteifolia*	?	?	25-35	–	?	?	?	?	?	?	?	?
32. *mbangaensis*	?	?	35-60	–	?	?	?	?	?	?	?	?
33. *mildbraedii*	205-270	30-40	50-60	–	–	2	70-110	r	l	+	–	2-3
34. *peperomioides*	?	?	25-45	–	?	?	?	r	?	?	?	?
35. *scutulum*	265-310	5-15	25-30	–	–	1	35-55	r	d	–	–	6-7
36. *susaniae*	115-130	5-10	50-70	–	–	1	40-60	r	d	–	±	3
37. *vankerckhovenii*	335-385	20-30	35-60	–	–	1	80-110	r	s	–	+	4-5
38. *vittariifolia*	335-375	8-17	25-40	–	–	1	65-80	r	d	–	–	5
39. *wilksii*	55-65	15-17	25-35	–	±	1	5-8	t	d	+	±	1-2
40. *zairensis* var. *zairensis*	?	?	25-45	–	?	?	?	?	?	?	?	?
41. *zenkeriana*	?	?	40-55	–	?	?	?	?	?	?	?	?
others												
42. *elatostemmoides*	115-145	45-60	60-70	–	–	2	5-10	t	d	+	–	2-3
43. *macrocarpa*	150-165	45-60	50-70	–	–	1	20-30	r	d	+	–	3
44. *sciaphila*	135-160	27-30	30-45	–	–	1	15-25	r	d	–	–	3
45. *thomeana*	130-160	10-17	30-50	–	±	1	27-35	r	d	+	–	4-5

1	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
1.	–	?	?	?	?	?	m	–	–	s	?	g	(1-)2-3	+	s	?	–
2.	–	1	–	–	–	–	m	+	–	s/g	+	g	0-1	+	s	–	–
3.	s	3	–	–	–	–	m	+	–	s	+	g	1(-2)	+	s	–	–
4.	?	?	?	?	?	?	m	–	–	s	?	g	(1-)2(-3)	+	s	?	?
5.	–	3	–	+	–	–	m	–	–	s	–	s	0-1	+	d	+	–
6.	–	3	+	+	–	–	m	–	–	s	+	s	0-1	+	s	+	–
7.	s	3	+	±	±	–	m	–	–	s	+	g	1	+	d	+	–
8.	–	1	–	–	–	–	m	?	?	s/g	+	g	1	?	s	–	–
9.	–	3	+	+	–	–	m	–	–	s	–	g	0-1	+	s	–	–
10.	–	1	–	–	–	–	m	–	–	s	+	g	2-3	+	s	–	–
11.	–	1	–	±	–	–	m	+	–	s	+	g	(1-)2-3	+	s	–	–
12.	s	3	?	?	?	?	m	–	–	s	+	g	1(-2)	+	s	–	–
13.	–	1	–	–	–	–	m	–	–	s	–	s	(0-)1(-2)	+	s	–	–
14.	–	1	–	?	?	?	m	–	–	s	–	g	0-1	+	s	–	–
15.	–	5	–	+	±	–	m	–	–	s	–	g	2-3	+	s	–	–
16.	?	?	?	?	?	?	m	–	–	s	–	g	2	+	s	–	–
17.	–	3	–	+	–	?	m	–	–	s	+	g	0-1	+	s	–	–
18.	–	1	–	–	–	–	m	–	–	s	–	g	2(-3)	+	s	–	–
19.	s	3	–	+	–	+	m	+	–	s	+	g	1-3	+	d	+	–
20.	?	?	?	?	?	?	m	?	?	s	?	g	0-1	?	s	?	?
21.	–	3	–	+	+	+	m	–	+	r	+	s	3	+	s	–	–
22.	–	3	–	+	–	±	m	–	+	r	–	s	3	+	s	–	–
23.	s	5-7	+	+	–	+	m	+	–	r	–	s	6-9	+	s	–	–
24.	–	5-7	–	+	+	+	m	+	+	r	–	s	6-14	+	s	–	–
25.	–	3	–	–	–	±	um	–	+	r	+	g	0-1	+	d	–	–
26.	s	5-7	–	+	–	+	m	+	+	r	–	s	2(-3)	+	d	–	+
27.	±	5	+	+	–	+	m	+	+	r	–	s	4-5	+	s	–	–
28.	±	3	–	–	–	+	u	?	+	r	–	s	0-1	+	s	–	+
29.	–	3	–	+	–	+	m	+	+	r	–	s	4-5	+	s	–	–
30.	s	3	–	+	+	+	m	–	+	s	+	s	(3-)4	–	s	+	–
31.	s	3	–	?	?	?	um	+	+	r	?	s	4-5	+	d	?	?
32.	–	3	–	?	?	?	m	–	+	r	–	s	4-6	+	d	+	–
33.	–	3	–	–	–	±	m	+	+	r	+	s	4-6	+	s	–	–
34.	–	5	–	?	?	?	m	+	+	r	–	s	2-3	+	s	–	–
35.	–	3	–	–	–	–	m	–	+	s	–	s	12-15	+	d	–	–
36.	s	3	–	+	–	+	m	–	+	r	+	s	2	+	s	–	–
37.	–	1	–	+	±	±	um	–	+	r	–	s	2-3	+	d	–	–
38.	s	3	–	+	–	+	m	–	+	r	–	s	2-4	+	d	–	–
39.	s	3	–	+	+	+	m	–	+	s	–	s	4	–	s	–	+
40.	–	3	–	?	?	?	m	+	+	r	–	s	(3-)4-5	+	d	–	–
41.	s	5	–	+	?	?	m/u	–	–	r	+	s	2-3	+	s	–	–
42.	±	3	+	–	–	–	m	–	–	x	+	s	(1-)2	+	s	–	–
43.	±	5-6	+	–	–	–	m	–	–	x	+	s	2-3	+	d	–	–
44.	±	7	+	–	–	–	m	–	–	x	+	s	3(-4)	+	d	+	–
45.	±	1	+	?	?	?	m	–	+	x	+	s	0-1	+	s	–	–

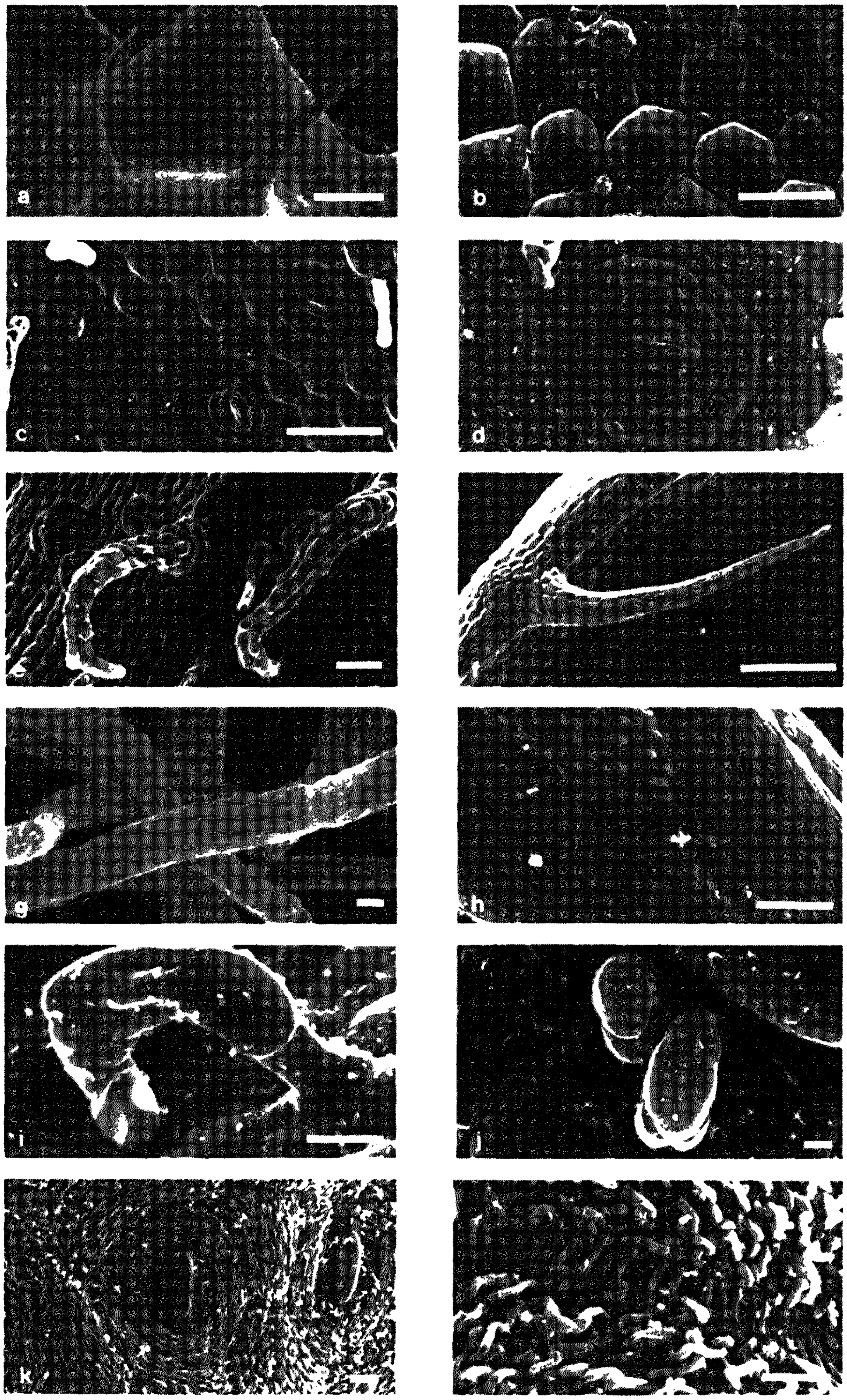
a
b
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Figure 6.3. Leaf anatomy, SEM. **a**: *B. susaniae*, bullate upper leaf surface with minute glandular hairs in depressions (bar = 500 μm); **b**: *B. scapigera* ssp. *scapigera*, strongly convex epidermal cells on upper leaf surface (bar = 50 μm); **c**: *B. hirsutula*, stomata on lower leaf surface (bar = 50 μm); **d**: *B. vankerckhovenii*, stoma (bar = 10 μm); **e**: *B. hirsutula*, midrib lower leaf surface, cells of multiseriate hairs with protruding apex (bar = 50 μm); **f**: *B. microsperma*, hair on leaf margin, small arrow pointing to a hydathode (bar = 500 μm); **g**: *B. ferramica*, uniseriate hairs with cuticula structure (bar = 10 μm); **h**: *B. lacunosa*, cuticula structure on mutiseriate hair (bar = 10 μm); **i**: *B. vankerckhovenii*, r-shaped glandular hair (bar = 10 μm); **j**: *B. potamophila*, sausage-shaped glandular hairs (bar = 10 μm); **k, l**: *B. dewildei*, cuticula structure on lower leaf surface (bars 10 μm and 5 μm resp.); **m**: *B. duncan-thomasii*: hydathode on leaf margin (bar = 10μm).

Hydathodes were observed in almost every species. They occur on the upper surface near the margin and are always associated with a marginal dent. All hydathodes encountered are of a similar structure: a giant stoma or water pore surrounded by a characteristic regular ring of epidermal cells (fig. 6.3.m). Hydathodes were not found in the two closely related species *B. lacunosa* and *B. wilksii*, which confirms the conclusion of Brouillet et al. (1987) that hydathodes might prove useful in taxonomic and phylogenetic studies of *Begoniaceae* (see also paragraph 6.3.2.)

The observations on non-glandular hairs showed that those of the adaxial surface, abaxial surface and margin are all similar in structure. The most commonly encountered type of hair is multicellular and multiseriate (fig. 6.3.e & f). A different type of hair was observed in the two closely related species *B. dewildei* and *B. vankerckhovenii* and in *B. laporteifolia*, all three members of the section *Scutobegonia*. It has a short multiseriate base and a comparatively long uniseriate distal part, giving the petioles of the first two species their characteristic woolly appearance. In *B. laporteifolia* hairs of this type are intermixed with 'normal' ones. An uniseriate type of non- glandular hairs was found in *B. ferramica* and *B. zenkeriana*. In the former species these hairs are very long and they are responsible for the arachnoid appearance of the indumentum. In *B. zenkeriana* the uniseriate hairs are much shorter and intermixed with more numerous 'normal' hairs. The cuticle of the cells of non-glandular hairs is either smooth or has a quite prominently striate ornamentation (fig. 6.3.g & h). The ornamentation is usually most pronounced at the base of the hair and is sometimes even practically absent on the distal part. Smooth hairs are found within the section *Loasibegonia*, while those with an ornamentation are present in the section *Scutobegonia* with only two exceptions, viz. the two closely related species *B. ciliobracteata* and *B. zenkeriana*. The presence or absence of a cuticular ornamentation therefore proved to be a useful character in delimiting the two sections. The cells of the multiseriate hairs can be broadened and slightly protruding outwards at their tips (fig. 6.3.e). Such protuberances were encountered throughout the two sections treated here. More prominent examples of such hairs in other species are depicted by Cuerrier et al. (1991a, fig. 1b). Surprisingly, these authors found protruding tips within *B. quadrialata*, while quite straight cells were observed by me. As in a number of specimens of other species some variation in the amount of protruberance was observed, this character is apparently not very reliable for taxonomic purposes.

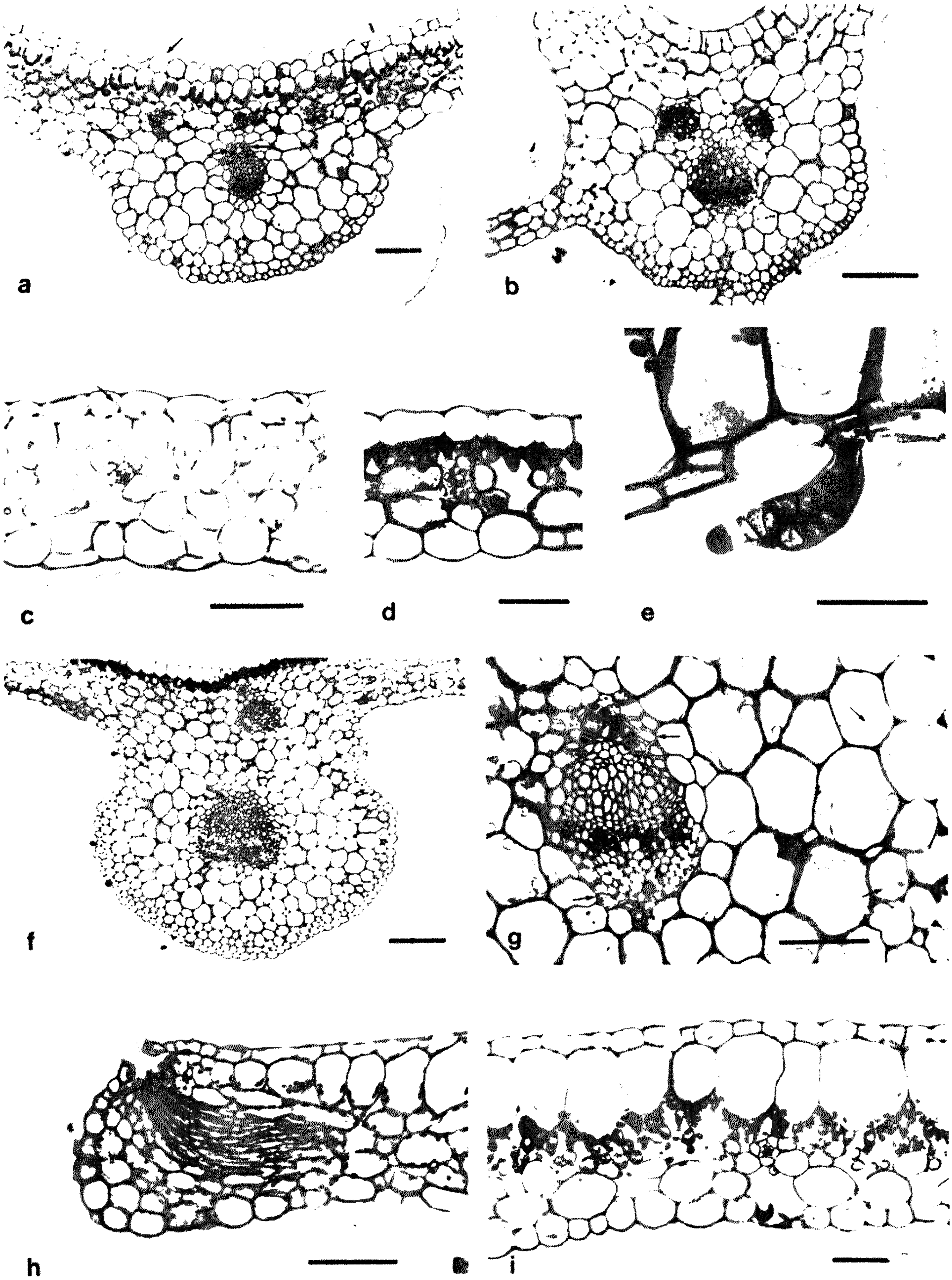
Glandular hairs are present in all species studied and they are usually found on all parts of the plant except for the stamens and the inner surface of the perianth segments. Within section *Scutobegonia* the highest densities are generally present on the ovary. Two types of curved glands and one 'normal' type could be denoted. Within the section *Loasibegonia* and a group of mutually related species belonging to section *Scutobegonia* short sausage-shaped glandular hairs are found which usually occur in groups of two or three together (fig. 6.3.j). They have a very short stalk and a thick, elliptic head placed asymmetrically on the stalk. Most of the species of section *Scutobegonia* possess a type of glandular hair similar to the sausage-shaped one but it has an appreciably longer stalk and a more slender and elongate head giving it the appearance of a walking stick. Such glands generally occur solitary. A third type of glandular hair with a short stipe and a globose head occurs jointly with glands of the first type in a few species of section *Loasibegonia*. In dried material these are coloured dark brown or black and become rather distinct. They are comparatively common throughout the family (see Cuerrier et al., 1991a, table 1). The type of glandular hair proved to be an important character in the phylogenetic analyses. Curved glandular hairs were already observed by Fellerer (1892, plate I, fig. 28 & 29) in *B. carolinaefolia* Regel of the section *Gireoudea* Klotzsch. They are also depicted by Cuerrier et al. (1991a, fig. 4F) who, additionally, noted their presence in *B. froebelii* A.DC., a member of the American section *Huszia* (Klotzsch) A.DC. and in both American and Asian members of the section *Knesebeckia* (Klotzsch) A.DC. On the other hand they do not confirm their presence in *B. carolinaefolia* where Fellerer discovered them. One wonders whether a wrong identification might be involved. The simultaneous occurrence of this type of glandular hair in the sections *Huszia*, *Loasibegonia*, and in a part of *Scutobegonia*, is intriguing as all three sections contain yellow-flowered species, a rare colour within the family. Although this seems to indicate phylogenetic affinity between the section *Huszia* and the sections dealt with here, the individual species are very dissimilar and I do not see any other synapomorphies pointing to a recent common ancestry. The coincidence of parallel developments seems more plausible. Cuerrier et al. (1991a) also note the presence of curved glands in *B. macrocarpa* of the section *Filicibegonia*, which is considered to represent a possible sister-group. In the present study, however, I can not confirm this. In the species belonging to the section *Filicibegonia* a different type of glandular hair was observed. It is hammer-shaped with a symmetrical and rather contracted head. The curved glandular hairs may or may not occur on the upper leaf surface in a distinct depression. On the leaves of *B. thomeana*, belonging to the monotypic section *Cristasemen*, curved glandular hairs were also observed. They differ, however, from the two types observed and described above: the stalk consists of about 5 distinctly flattened cells and the head is much more 'inflated'. Cuerrier et al. (1991a) treat all curved glandular hairs as a single type (their character 12 on page 305) but now it seems that at least three different types have to be distinguished.

6.3.2 Transverse sections

The thickness of the leaves of different species can vary considerably (from 55 to 785 μm). Three species with extremely thin leaves appear to be closely related (*B. lacunosa*, *B. susaniae* and *B. wilksii*, fig. 6.4d).

All species, including those studied from the sections *Filicibegonia* and *Cristasemen*, possess a single-layered epiderm on both surfaces. A hypodermis is absent with one exception: two out of three collections studied (90PTGA026 and 83PTGA706) of *B. clypeifolia* had a hypodermis consisting of one layer of cells on the adaxial and 1-4 layers on the abaxial surface (fig. 6.4i). In the third collection (81PTGA297) a hypodermis was lacking. *B. clypeifolia* is indeed a very variable species and the latter collection was somewhat aberrant from the other two: the fruits are shiny and green and the leaves appear more fleshy, are more elongate and shiny, and they bear tooth-like outgrowths on the leaf margin. Such outgrowths are also observed in specimens of *B. hirsutula* and are regarded as a monstrosity. The anatomy of the leaf of this collection is, however, so distinct from the other two that the possibility of the existence of two separate species was considered. However, after thorough examination, no other distinguishing characters could be found. Other herbarium specimens of 'true' *B. clypeifolia* with elongated leaves are available, while green fruits are sometimes noted on the labels, and the delimitation of the species was not altered. Field observations might cause reconsideration of specific boundaries in the future.

The adaxial epidermal cells are usually convex, as was observed by SEM. Transverse sections allow more accurate observations. Extremely convex (or papillose epidermal cells as Solereder (1899) and Metcalfe & Chalk (1979) call them) occur fairly frequently within the family and, according to the latter authors, they do not seem to be of much taxonomic significance. However, the degree of convexity among the species studied here does not only differ considerably, but it seems to occur in a more pronounced state in several related species. Therefore, despite the fact that Solereder l.c. described the character as variable even within a single species, it was decided to include the character in the phylogenetic analysis. The convexity of the cells was measured according to the method depicted in fig. 6.2. The anticlinal walls of the epidermal cells are not seldom zigzag shaped in the median part (fig. 6.4c). This occurs more often in the section *Loasibegonia* than in the section *Scutobegonia*. Solereder (1899) mentions the occurrence of harmonica-shaped anticlinal walls in the palisade tissue but he does not report them for the epidermal cells. It might be regarded as


a
b
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e
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i

part of a mechanism to store excess water (volume changes) without the risk of collapse in less humid periods.

The palisade tissue is always composed of a single layer but with considerable variation in dimension of the cells. Such variation is also present when their size is taken in relation to the size of the epidermal cells. Up to eight palisade cells may be present below a single epidermal cell, while in other cases this ratio may be 1:1. The ratio is not always correlated with the actual size of the epidermal cells. Large epidermal cells may rest either upon a single or on a number of palisade cells. The palisade layer is often thin in the section *Scutobegonia* and thick in the section *Loasibegonia*, but several exceptions occur. Some of these exceptions appear to be of phylogenetic significance. Note for example (in table 6.1) the aberrant situation in *B. dewildei*, *B. mildbraedii* and *B. vankerckhovenii*, three comparatively primitive species of the section *Scutobegonia*. There is a distinct variation in the shape of the palisade cells as well. They may be more or less broadly rectangular or triangular (see for example fig. 6.4a & d).

The chloroplasts within the palisade cells are arranged along the abaxial walls. The possible function of this position is discussed in more detail in paragraph 6.4. Chloroplasts are of three types: large and light-coloured, small and light-coloured, and small and dark-coloured (see fig. 6.4c & h). The large and small chloroplasts are (17–)19–27 μm and 6–15 μm in diameter respectively. The distribution of the chloroplast types among the species is considered to be of phylogenetic importance since most species of section *Scutobegonia* have small and often dark-coloured ones while large chloroplasts are confined to section *Loasibegonia*. The only exception is *B. mildbraedii* that shows several additional intermediate character states.

The spongy mesophyll is lacunar. Chloroplasts in this tissue are less numerous than in the palisade layer, and their distribution is random. Within the spongy mesophyll solitary prismatic crystals are sometimes present (fig. 6.4g). Their occurrence may be very sparse, and often several transverse sections must be checked to make sure whether they are present at all. They are usually more frequent near to the (main) vascular bundles.

The midrib contains either a single vascular bundle, or a number of them:

Figure 6.4. Leaf anatomy, transverse sections. **a**: *B. potamophila*, midrib with sclerenchyma on adaxial side of vascular bundles only (arrows), strongly convex epidermal cells (arrow) and distinct arrangement of chloroplasts in palisade parenchyma cells (bar = 0.2 mm); **b**: *B. duncan-thomasii*, midrib without sclerenchyma around vascular bundles (bar = 0.2 mm); **c**: *B. letouzeyi*, anticlinal wall of epidermal cells zigzag (arrows), large and light coloured chloroplasts and tertiary nerve without sclerenchyma (bar = 0.2 mm); **d**: *B. wilksii*, very thin leaf, small triangular palisade cells and tertiary nerve with sclerenchyma all around (bar = 0.05 mm); **e**: *B. susaniae*, glandular hair with exudate (bar = 0.05 mm); **f**: *B. lacunosa*, midrib with vascular bundles with sclerenchymatous cap on adaxial and abaxial side, and dark-coloured palisade parenchyma cells (bar = 0.2 mm); **g**: *B. clypeifolia*, detail of vascular bundle in midrib with sclerenchymatous tissue on adaxial and abaxial side (arrows), and prismatic crystals (bar = 0.1 mm); **h**: *B. susaniae*, hydathode on leaf edge (bar = 0.1 mm); **i**: *B. clypeifolia*, leaf with hypodermal layer below and underneath small palisade cells (bar = 0.2 mm).

a compound vascular system. Midribs with a compound vascular system were already reported for the family by Gonçalves Costa (1970, p. 124, fig. 7; 1971, p. 217, fig. 25) and Dunn de Araujo & Gonçalves Costa (1972, fig. 29) and they seem to be quite common. This is supported by the phylogenetic analysis (chapter 11) in which midribs with a simple, non-compound bundle occur in several derived species of the section *Loasibegonia* and the compound situation is interpreted as the primitive condition. The separate bundles are usually arranged in a semi-circle on the abaxial side, and an additional single small bundle may be present on the adaxial side, opposite to this semi-circle. Such a bundle was observed in all species examined of the possible outgroups (sections *Filicibegonia* and *Cristasemen*) and in several species of the sections treated here (see table 6.1 and fig. 6.4a). The latter, however, do not seem to be closely related. Sclerenchymatous tissue may be absent or present around the different bundles of the midrib. When present, this tissue was generally encountered either as a cap surrounding the adaxial or the abaxial side of a bundle or sheating the whole bundle (see fig. 6.4). In some cases only few sclerenchymatous strands (or sclerides) were present around each bundle. The amount of sclerenchymatous strands around the tertiary nerves may vary as well. Similar sclerenchymatous tissue in *Begonia* spp. are depicted and described by Cutler (1978, fig 4.23C). According to Metcalfe & Chalk (1979) this feature is rare in *Begoniaceae* but the findings of Cuerrier et al. (1991a) contradict this remark; these authors regularly observed both short and long sclerides. Lee (1974) also observed similar sclerenchymatous 'caps' in begonia stems (his types 4 and 5 in table II).

The prominence of the main and smaller nerves can be described more accurately by using transverse sections than by examination of herbarium or even of living material.

A cross section of a hydathode in the leaf of *B. susaniae* (fig. 6.4h) showed that it is similar to those encountered by Arends (1992) and Brouillet et al. (1987). The latter made a thorough study of hydathodes within the family and classified them as passive (i.e. connected to the vascular system) and with an epithem.

6.4 Light absorption

The majority, if not all, of the species treated in this study occur in more or less heavily shaded habitats in the understorey of tropical rain forests. Several conspicuous anatomical characteristics were observed which may be regarded as adaptations to such deep shade conditions. These adaptations have been the subject of study by several plant anatomists and physiologists. I was intrigued by the subject, known as physiological plant anatomy (Haberlandt, 1896), as it is related to the subject of glacial rain forest refuges (see chapter 12).

First of all the possession of bullate leaves is generally regarded as an adaptation to low light intensities. Much of the incoming light is blocked or shattered by the canopy leaves. The cone-like leaf protuberances of several species studied here are ideal structures to capture shattered light coming in from many different angles. A second advantage of bullateness might be that the prominent parts of the leaf blade drain easier after rainfall and hence light is not reflected by water lying on the leaf surface. Several other adaptations to these shade conditions have been reported. These are (1) leaf variegation, (2) a red or purple abaxial leaf surface, (3) a glistening or satiny adaxial leaf surface and (4) a blue iridescence (Lee, 1986). No blue iridescence was observed in any of the species presently studied, but examples of all three other adaptations were met with. Multicoloured surfaces are found in e.g. *B. lacunosa* and *B. susaniae*, red-coloured lower leaf surfaces in many species, e.g. *B. heterochroma, B. hirsutula* and *B. erectocaulis*, while a glistening upper leaf surface is often seen in species of the section *Loasibegonia* (e.g. *B. prismatocarpa, B. quadrialata, B. potamophila* and *B. letouzeyi*). An anthocyanin-containing layer reflects photosynthetically useful light and is thus advantageous (Lee & Stone, 1979), because the light passes the chloroplast layer twice and each ray has more chance of hitting a chloroplast. In sciaphilous plants the anthocyanin layer is generally found just below the palisade layer where often virtually all chloroplasts are located. This situation, which increases the profit of such a layer, is also met with in the *Begonia* species studied here. It was also observed by Lee & Stone (1979) a.o. in *Begonia pavonina* Ridley. Leaves having a red undersurface absorb 90% of the PPFD (photosynthetic photon flux density) while green ones absorb only 82% (Lee & Graham, 1986). The latter authors show that although the spectral range of light falling on the forest floor is different from that reaching the canopy, there is no difference in the spectral absorption of light between sun and shade plants. They noted a significant difference in the invested energy, expressed in dry weight per unit area of leaf surface. Shade plants generally have much thinner leaves and thus invest less energy in photosynthetic tissue.

It has been stated that the possession of extremely convex or even papillate epidermal cells will act as lenses to the incoming light. The assumed optical function of the epidermal surface was studied already early in this century by e.g. Haberlandt (1904, 1916), Kniep (1907) and Sperlich (1907) and more recently by Bone et al. (1985). A lens will not increase the amount of light reaching the leaf but only concentrates it on a smaller portion below the epidermal layer. To function optimally, this adaptation requires a correlated specific chloroplast distribution (Lee, 1986: 116). There is a distinct advantage for shade plants to have a discrete and dense layer of chloroplasts at an even distance below the leaf surface. It means that practically all light is captured for photosynthetic activity. The *Begonia* species studied here all show such a distinct pattern of distribution of the chloroplasts: they are arranged along the walls of the abaxial part of the palisade cell (fig. 6.4). These palisade cells are sometimes triangular in transverse section with the tip pointing towards the abaxial side or they are at least rounded abaxially. This causes the formation of a kind of cup or funnel in which the light can be captured. As the chloroplasts are also arranged in only a single layer, none of them blocks the incoming light for another. A similar arrangement of chloroplasts was found in *Triolena hirsuta* Triana (*Melastomataceae*; Lee, 1986: fig. 4.4b). Quite commonly species with more than one (up to

8) palisade cells below a single epidermal cell were observed. This implies that a lens-shaped epidermal cell can benefit several palisade cells.

Additionally, Bone et al. (1985) measured a decrease in reflection from leaf surfaces which were positioned at oblique angles to the incoming light. They suggest that the papillate shape of the epidermal cells might well be the cause of this decrease. A cone-shaped epidermal surface (bullate leaves) would therefore be ideal for reducing such reflection but on the other hand less so to focus incoming light. Shade plants might therefore respond to two kinds of selection pressures: one for optimizing light-focusing properties and one for minimizing reflection. The leaves of several of the *Begonia* species treated here are displayed vertically and, hence, might reflect less light coming in at oblique angles than those which are borne horizontally. These species seem to have responded to the second kind of selection pressure mentioned.

6.5 Conclusions

The cause of the dust-like cristalline deposit present on the specimens observed by SEM is to be further investigated.

Although within the studied group no anatomical features new for the family were observed, many anatomical characters appear to be of taxonomic importance, both at sections level and below that, which is also emphasized by the results of the phylogenetic analysis given in chapter 11. It is recommended that leaf anatomy is incorporated in future research, both on taxonomy and phylogeny, of *Begonia* species.

The range of infraspecific anatomical variation needs further study, seen the data on several collections of *B. clypeifolia* and some incongruities with the observations of Cuerrier et al. (1991a).

The species studied show several features that can be interpreted as adaptations to heavily shaded conditions. More research (biophysical, physiological and anatomical) on general characteristics of shade-adapted plant species is needed to detect the exact advantages of certain conditions observed.

7 Anatomy of the ovary, style and stigma

7.1 Introduction

Earlier taxonomists already considered the anatomy and especially the type of placentation of the inferior ovary of *Begonia* as important taxonomic characters (e.g. Warburg, 1894, Engler, 1921 and Irmscher, 1925 & 1961). These features are used mainly to delimit taxa above the rank of species, viz. sections and subsections (or 'paragraphs'). One of the objectives of the present study is to solve the taxonomic question whether the species concerned belong either to a single or to two separate sections. Consequently, a thorough study of the ovaries of the different species could not have been left out. An important goal was to identify characters valuable for incorporation into the cladistic analyses (chapter 11). Since recent investigations have demonstrated that the nature of the ovary in *Begoniaceae* is rather complicated, the present author felt obliged not to restrict the implementation of his results to their usefulness and meaning for a phylogenetic study, but to place them into a broader context. A short introduction to the problem and a historical review is given below. Those interested in the subject are referred to the detailed investigations of Arends (1992: 85–91, chapter 7) and other works referred to below.

Saunders (1925), Bugnon (1926) and Gauthier (1950) discussed the nature of the ovary in *Begoniaceae*. Saunders and Gauthier state that the ovary wall is of a foliar nature. This implies that it is formed by appendicular organs, i.e. composed of carpels which are congenitally united with the floral tube. This view is supported in more recent studies by Barabé (1981), Barabé & Chrétien (1983) and Barabé et al. (1985). Because a congenital fusion cannot be verified, not even by ontogenetic studies, Sattler (1974) argued that it is pointless to discuss it. According to him it leads to 'pseudo-science' where no one can prove he is right. Sattler l.c. demonstrated that in flowering plants next to carpellate ovaries also various kinds of acarpellate ones exist, to which rationally the carpel concept cannot be applied. Therefore, he favours a more general terminology for the various parts of the ovary.

Reitsma (1984) studied the placentation of many African species of *Begonia*. He interpreted the observation of a constriction in a septum as the more or less explicite demarcation between carpellary and placental tissue. The ability to distinguish between the two types of tissue is refuted by both Charpentier et al. (1989a) and Arends (1992: 99–100), as anatomically no difference can be observed. Reitsma's study, however, is very valuable in the light of the present work as he studied a number of species from the group treated here. Moreover, he distinguished several morphological subtypes within this group.

Within the *Begoniaceae* both axile and parietal placentation is encountered.

The axile situation is quite common. Reitsma (1984) showed that species which were believed to possess a parietal placentation actually were parietal only in the upper part of the ovary and *axile* in the lower part. The ontogenetic studies of Charpentier et al. (1989a, 1989b) on *B. horticola* Irmscher and *Hillebrandia sandwichensis* Oliver led them to the conclusion that in the development of the ovary of such species two meristem systems are involved. An axillary system, originating from the floral apex and reaching only about halfway up the ovarial cavity, and a second system consisting of four parietal meristems situated on the ovary wall. The two meristem systems are linked by a transition zone. In the lower part of the ovary the septa consist exclusively of axillary tissue, while at the apex they are of parietal origin. In the central part of the ovary the septa contain cells originating from both meristem systems (see fig. 7.1). Placentae and ovules are produced by both meristem systems. Thus the ovary is not entirely of appendicular origin as was suggested by previous authors. Charpentier et al. (1989b) also studied *Begonia dregei* Otto & Dietr. which has an entirely axile placentation. Here they distinguished the same two meristem systems, analogous to the former situation. According to them the parietal meristem system of *B. dregei* is of very limited importance and is confined to the very apex of the ovary. The axis including the septa and the placentae is almost entirely of axillary origin. In this case I am not convinced by their interpretations. This is further discussed in paragraph 7.5.

Arends (1992), who investigated species with a partly axile and partly parietal placentation within one ovary, showed that his observations on the vascularisation support the idea of the presence of two different meristem systems. The vascular bundles in the axillary tissue at the base of ovaries studied by him either all peter out about halfway up the ovary or feed the placentae. This led him to the conclusion that the ventral vascular traces, which are situated near the margin of a carpel, are not located in the axillary part of the ovary but in the septa or even in the ovary wall (his figs 7-2, 7-7 and 7-11), where they are either single or fused with the lateral traces. The species studied here all show an axile placentation. The nature of this condition is further discussed in paragraph 7.5.

Anatomical observations on styles and stigmas of *Begoniaceae* in general are very scarce. This is rather remarkable since there is a wealth of forms that seem to be of taxonomic significance. A preliminary study of the stigmatic surfaces was made by Baranov (1977), who recognized several types. The present study is only superficial and, in respect to the promising results, a more detailed study is recommended. Arends (1992) described the structure of the stigmatic papillae for several species of the section *Tetraphila*. So far, these seem to be the only investigations into this matter ever conducted. It is hoped that the present study, which once more stresses the taxonomic importance of anatomical characters of the style and especially the stigma, may encourage others to fully appreciate their value.

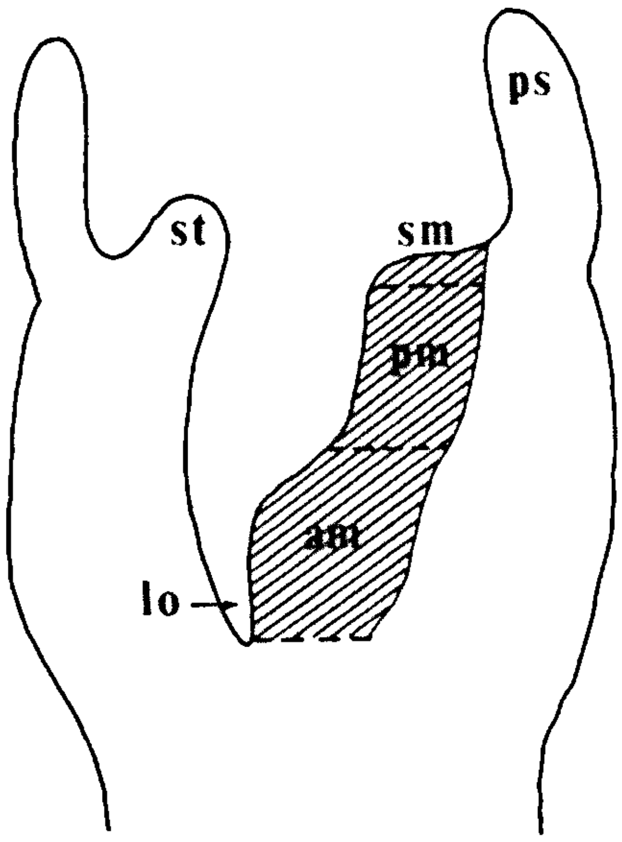

Figure 7.1. Schematic longitudinal section of primordium of female flower. st: style primordium; lo: locule cavity; am: apical meristem; pm: parietal meristem; sm: stylar meristem; ps: perianth segment. Redrawn from Charpentier et al. (1989b).

7.2 Materials and methods

Female flowers were gathered from cultivated material preferably on the first or second day of anthesis. When no living material was available, female flowers were obtained from alcohol collections with a preference for young flowers. From *B. scutulum* only young fruits were available. Fortunately they provided most, though not all, of the features to be scored. In general, herbarium material is not suitable for a detailed study of the anatomy of the female flower as only few features can be observed properly. Therefore, herbarium material was studied only in order to add more information to the datamatrix used for the cladistic analysis. It is in general not considered for the discussion in this chapter. Fixation of living material as well as that from alcohol collections was effected according to the procedure described in paragraph 6.2.1. A number of the broadly winged ovaries were too wide to fit into the trays with the embedding medium. In such cases one or two wings were removed. All sections were stained with a solution of 0.5% Toluidine blue in 1 N HCl and mounted in DPX mountant (80% xylene). Complete series of 10 μm thick sections of a female flower of 21 species were cut in order to be able to study the exact vascularisation patterns. Of flowers belonging to 9 other species every 5th section was mounted.

The pertinent taxa are listed with the investigated material. Several taxa accommodated in two other sections were studied as well as they may serve as possible outgroups to be used in the phylogenetic analysis. Accession numbers of the living collections present at WAG are given. Herbarium vouchers of these collections are added between brackets and are conserved at WAG unless otherwise indicated. When alcohol material is used this is indicated by 'alc.'. When only herbarium material could be studied the indication 'herb. only' is added.

Further information on the origin of each collection is given in the paragraph 'Specimens examined' accompanying each species description in chapter 16 and 17.

section *Loasibegonia*:

(*Begonia*)
adpressa: W.J. de Wilde c.s. 2325, herb. only.
atroglandulosa subsp. *atroglandulosa*: alc. J.J. de Wilde c.s. (WALK-B) 518.
duncan-thomasii: 89PTGB074 (Thomas 5492, K).
heterochroma: alc. J.J. de Wilde c.s. 10194.
letouzeyi: 90PTGA027 (J.J. de Wilde c.s. 10080).
microsperma: 86PTCB434 (van Veldhuizen 446, idem 1312).
minuta: Villiers 895 (P), herb. only.
potamophila: 88PTGA017 (van Veldhuizen 1397).
prismatocarpa subsp. *prismatocarpa*: 86PTCB433 (van Veldhuizen 447).
pseudoviola: alc. J.J. de Wilde 8662.
pulcherrima: Bouxin 267 (BR), herb. only.
quadrialata subsp. *nimbaensis*: 86PTCB097 (van Veldhuizen 504).
quadrialata subsp. *quadrialata* var. *quadrialata*: 82PTGA481 (van Veldhuizen 1299).
salisburyana: Brenan 8432 (K), herb. only.
scapigera subsp. *scapigera*: 89PTGB073 (van Veldhuizen 1398).
schaeferi: Satabié 163 (P), herb. only.
scutifolia: 85PTGA197 (van Veldhuizen 1234, idem 1311).
staudtii: 64PT00400 (van Veldhuizen 445).

section *Scutobegonia*:

(*Begonia*)
aggeloptera: alc. J.J. de Wilde c.s. 10147.
anisosepala: Mann 1647 (K), herb. only.
clypeifolia: alc. Breteler & de Wilde 262.
dewildei: 84PTGA191 (Arends c.s. 700; van Veldhuizen 1348).
erectocaulis: alc. J.J. de Wilde 8791.
erectotricha: alc. J.J. de Wilde c.s. 10189.
ferramica: 85PTGA198 (van Veldhuizen 1313).
hirsutula: alc. J.J. de Wilde c.s. (WALK-B) 64.
lacunosa: 83PTGA708 (van Veldhuizen 1093).
laporteifolia: D.W. Thomas & McLeod 5330, herb. only.
mbangaensis: Bates 297 (K), herb. only.
mildbraedii: 90PTGA074 (Breteler c.s. 9985).
peperomioides: alc. Breteler & de Wilde 369.
scutulum: alc. Breteler & de Wilde 272.
susaniae: alc. Breteler & de Wilde 41.

vankerckhovenii: 84PTGA193 (Arends c.s. 699).
vittariifolia: alc. J.J. de Wilde c.s. 10237.
wilksii: alc. J.J. de Wilde & Sosef 10325.
zairensis var. *zairensis*: Cambridge Congo Exp. 355 (LISC), herb. only.
zenkeriana: Bos 3425, herb. only.

section *Cristasemen*:

(*Begonia*)
thomeana: 80PTST107 (J.J. de Wilde c.s. 141).

section *Filicibegonia*:

(*Begonia*)
elatostemmoides: 82PTGA493 (A. Louis 108).
macrocarpa: 90PTGA 193 (Wieringa 938).
sciaphila: 84PTGA146 (Arends c.s. 334).

All characters not directly related to the vascularisation were scored from a section of the ovary where the placentae are at their widest. The protocol for the measurements is presented in fig. 7.2. As in the leaf anatomical study, only a single collection of each species could be studied, and conclusions about infraspecific variation could not be deducted.

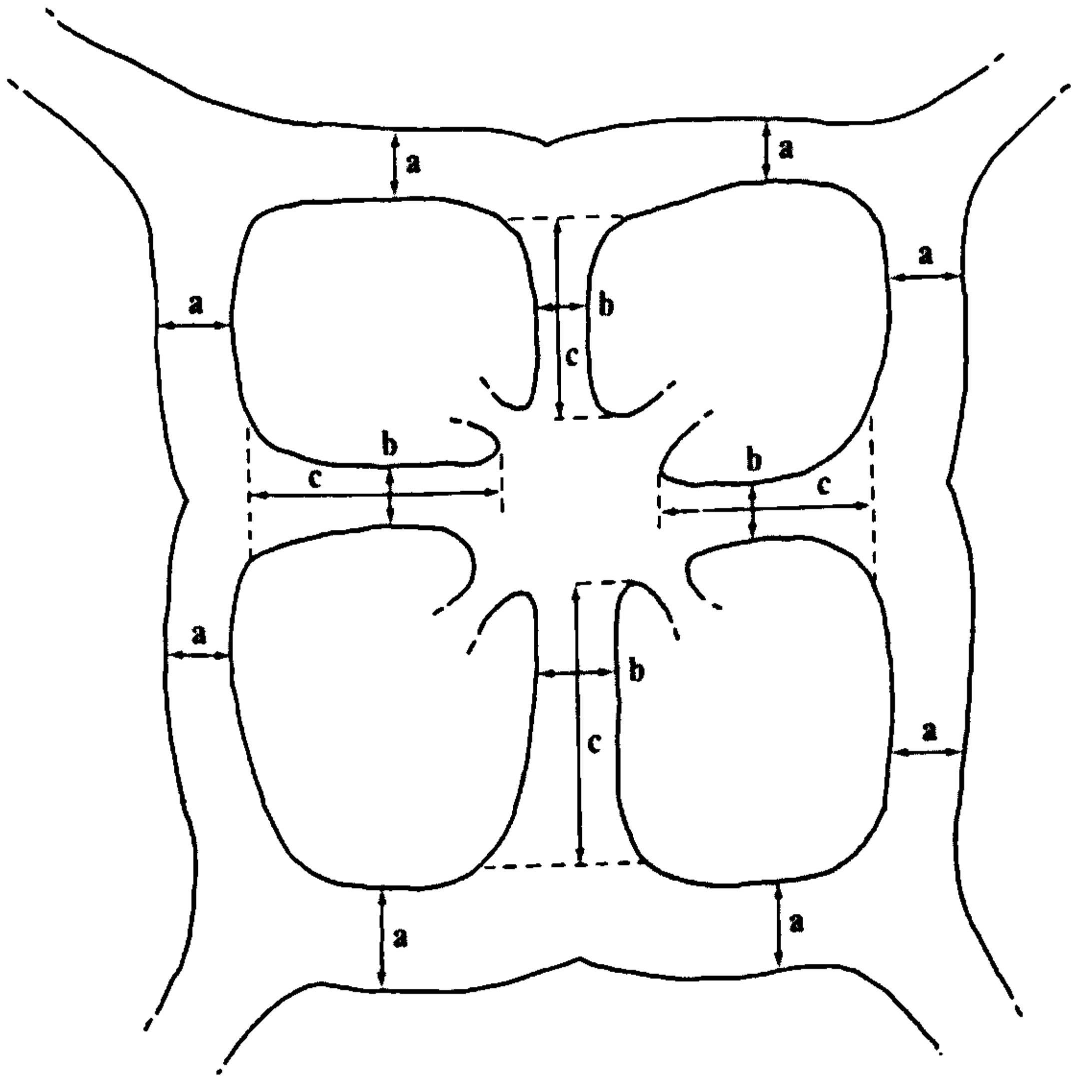

Figure 7.2. Explanation of measurements taken from a cross section of the ovary. a: width ovary wall; b: width septum; c: length septum.

7.3 Results

The observations on the cross-sections are presented in table 7.1. Measurements taken from herbarium material are often not accurate or otherwise not comparable with the data obtained from fresh or alcohol material and are therefore not presented as such in the table. However, in order to be used for the phylogenetic analysis all characters observed have to be divided into classes (see table 11.1, page 89–95). For some of the characters it proved possible to denote the *class* to which a species belongs, despite the fact that no precise measurements could be taken. In such a case this class is presented in table 7.1 followed by an exclamation mark.

7.3.1 General anatomical characteristics of the ovary

A general account of the anatomy of the ovary within the sections *Loasibegonia* and *Scutobegonia* is given. Several ovaries will be discussed in more detail.

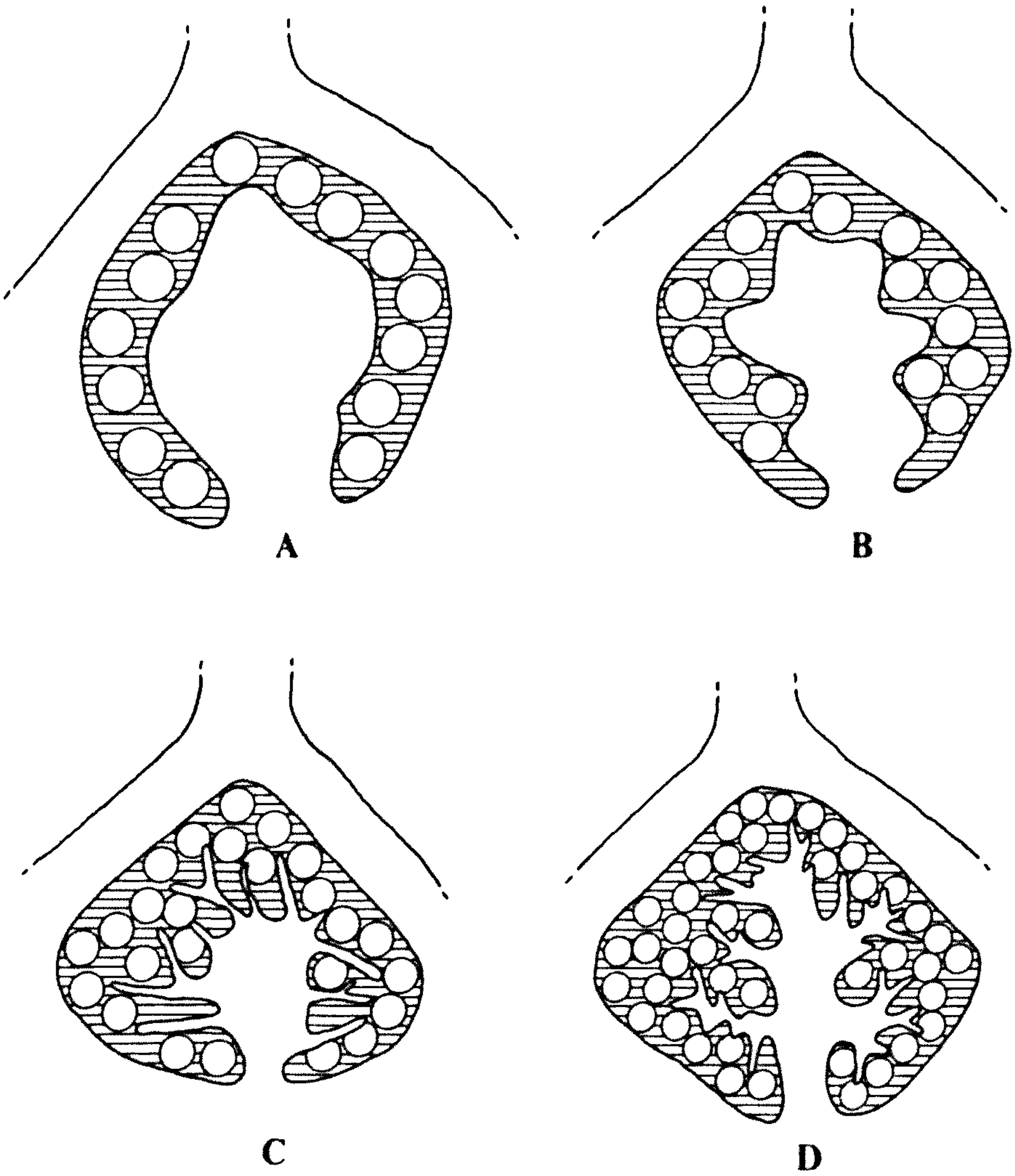

Figure 7.3. Different shapes of the placenta (schematic) and terminology. A: strongly thickened, not or weakly lobed; B: thickened and lobed; C: mushroom-shaped with long funiculae; D: branched, tree-like.

Photographs depicting important characters mentioned in the text are presented in fig. 7.4.

Fig. 7.4 reveals the amazingly wide variation present within this group of closely related species. From a first impression it is obvious that the primary goal of this part of the research, viz. to gain more characters for a cladistic analysis, could probably be easily reached. No less than 12 different characters with a total of 32 different character states have been extracted (see chapter 11). All characters other than those concerning the vascularization (nos 109–116, see table 11.1) proved to be important in phylogenetical sense, since their retention index is invariably high.

The variation in thickness of the ovary wall of the species studied is strikingly wide and ranges from 105 to 520 μm. The thicker walls are generally found within the section *Scutobegonia*, except for *B. aggeloptera*, *B. microsperma* and *B. letouzeyi*, both members of the section *Loasibegonia*, which have comparatively thick ovary walls. The number of cell layers in the ovary wall varies among the species from 5 to 13. Epidermal cells of species of the section *Scutobegonia* are generally much smaller than the cells of the layer right below (fig. 7.4c).

Table 7.1. Anatomical properties of ovaries and stigmas of species of *Begonia* sect. *Loasibegonia*, sect. *Scutobegonia* and of several related species.

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legend: (– = absent, no; ± = few, slightly etc.; + = present, yes; ? = state unknown or not relevant).

1. Ovary wall thickness (μm).
2. Number of cell layers in ovary wall.
3. Number of cell layers in transition zone bordering the locule cavity.
4. Ratio of thickness epidermis layer and outer mesophyll layer (l = less than 0.5, m = more than 0.5).
5. Length/width ratio of septa.
6. Shape of the placentae (st = strongly thickened and not or weakly lobed, lo = thickened and lobed, mu = ± mushroom shaped with long funiculae, tr = branched and ± tree-like, see also fig. 7.3).
7. Number of ovules per locule (counted in a single section; * = estimated because of depauperate ovules).
8. Number of ovule layers (m = 3 or more).
9. Degree of fusion of ventral vascular bundles in the central part of the ovary (n = not fused, s = some fused, a = all fused).
10. Number of internal lateral bundles produced at the base of the ovary.
11. Placentary vascular bundles forming distinct vertical bundles apart from the ventrals.
12. Position of the distinct placentary bundles when present (v = in between the ventrals, b = at the base of the placentae, p = in the placentae).
13. Total length of stigmatic papillae (μm; see fig. 7.5).
14. Width of stigmatic papillae (μm; see fig. 7.5).
15. Length of basal part of stigmatic papillae (μm; see fig. 7.5).
16. Stigmatic papillae with thickened extremity.
17. Stigmatic papillae ribbed.
18. Cuticular structure on epidermal cells of style.

		1	2	3	4	5	6
Begonia							
	sect. *Loasibegonia*						
1.	*adpressa*	?	?	?	?	1!	tr
2.	*atrogland.* ssp. *atrogland.*	210-270	8-9	(1-)2	m	3.1-3.8	mu
3.	*duncan-thomasii*	285-330	9-10	1(-2)	m	5.6-14.0	tr
4.	*heterochroma*	245-295	8(-9)	1-2	m	5.6	lo
5.	*letouzeyi*	385-485	9-10	(1-)2	m	5.5-8.4	lo
6.	*microsperma*	375-405	9-10(-11)	1-2	m	2.5-3.7	st
7.	*minuta*	?	?	?	?	2!	lo
8.	*potamophila*	250-335	6-(7-8)	1(-2)	m	3.0-3.8	lo
9.	*prismatocarpa* ssp. *prismat.*	105-130	7-8	(1-)2	m	3.0-5.0	lo
10.	*pseudoviola*	140-175	(6-)7-8	2-3	m	2.8-3.3	lo
11.	*pulcherrima*	?	?	?	?	1!	tr
12.	*quadrial.* ssp. *nimbaensis*	195-230	7-8	(1-)2	m	1.9-2.6	lo
13.	*quadrial.* ssp. & var. *quadr.*	235-295	6-7	1(-2)	m	2.1-3.2	lo
14.	*salisburyana*	?	?	?	?	2!	lo
15.	*scapigera* ssp. *scapigera*	235-300	8-10	(1-)2	m	1.9	st
16.	*schaeferi*	?	?	?	?	1!	tr
17.	*scutifolia*	160-280	7-9	2-3	m	0.6-1.5	st
18.	*staudtii*	270-300	7-8	(1-)2	m	3.1-4.2	lo
	sect. *Scutobegonia*						
19.	*aggeloptera*	145-165	9(-10)	(2-)3	l	2.1-2.8	tr
20.	*anisosepala*	?	?	?	?	1!	tr
21.	*ciliobracteata*	3!	?	?	?	2!	tr
22.	*clypeifolia*	320-390	10-12	2-3	l	7.5-11.3	tr
23.	*dewildei*	165-210	6-7	1(-2)	m	6.4-7.9	mu
24.	*erectocaulis*	375-475	10-13	2-3	l	5.6-10.0	tr
25.	*erectotricha*	300-345	11	2(-3)	l	4.1-5.6	tr
26.	*ferramica*	205-285	9-10(-11)	1(-2)	m	7.3-7.7	tr
27.	*hirsutula*	205-300	9-12	(2-)3	l	3.1-5.0	tr
28.	*lacunosa*	250-320	11-13	2(-3)	l	6.3-6.6	tr
29.	*laporteifolia*	?	?	?	?	1!	tr
30.	*mbangaensis*	?	?	?	?	1!	tr
31.	*mildbraedii*	185-245	7-8	(1-)2(-3)	l	5.0-8.2	tr
32.	*peperomioides*	380-500	11-13	2-3	l	1!	tr
33.	*scutulum*	480-520	11-13	5	l	28.5-32.5	tr
34.	*susaniae*	235-280	8-9	2(-3)	l	3.0-5.8	tr
35.	*vankerckhovenii*	185-230	(6-)7-8	(1-)2	m	11.1-16.3	tr
36.	*vittariifolia*	215-250	9-10(-11)	2-3	l	3.3-4.5	tr
37.	*wilksii*	165-210	7-8	2(-3)	l	9.6-12.5	tr
38.	*zairensis* var. *zairensis*	?	?	?	?	2!	lo
39.	*zenkeriana*	?	?	?	?	1!	?
	others						
40.	*elatostemmoides*	75-115	5-6	3-4	m	16.7-20	mu
41.	*macrocarpa*	1!	?	3!	m	1!	mu
42.	*sciaphila*	240-320	9(-10)	3-4	m	10.0-16.0	mu
43.	*thomeana*	3!	8-9	3-4	l	± 10	lo

9	10	11	12	13	14	15	16	17	18
s	?	–	?	?	?	?	?	?	?
n	1(-2)	+	v	150-210	25-27	40-60	+	–	–
n	2	–	?	205-220	17	30-35	+	–	+
a	0	+	b	250-295	17-20	25-30	+	+	+
n	0	+	b	170-195	17-20	25-30	–	–	–
n	0(-1)	+	b	140-160	15-17	40-60	–	–	–
?	?	?	?	?	?	?	?	?	?
s	1	+	b	185-220	17-20	30	+	–	+
n	0(-1)	+	v	160-185	15-17	40-55	+	–	–
a	1	+	b	150-200	10-17	35-40	+	–	+
?	?	?	?	?	?	?	?	?	?
s	1	+	v	230-270	17-20	40	+	–	+
s	1	+	v	280-355	20-25	40-65	+	–	+
?	?	?	?	?	?	?	?	?	?
n	0	+	b	135-165	15-17	30-35	+	–	–
n	?	?	?	?	?	?	?	–	–
s	1	+	b	145-160	17-20	35-40	+	?	?
s	1	+	b	200-215	15-17	30-35	+	–	–
n	1	+	b	95-150	8-10	10-17	+	±	–
?	?	?	?	?	?	?	?	?	?
n	?	?	?	?	?	?	?	?	?
n	2	+	b	115-130	8-17	25	+	+	–
n	0(-1)	–	?	140-170	15-27	30	+	–	+
n	2	+	b	140-160	10-15	25-30	+	+	–
n	2	+	b	130-150	8-10	17	+	+	+
n	1	+	v	115-125	17-20	25-30	+	–	+
a	2	+	b	140-165	8-10	17-30	+	+	–
n	2	–	?	250-295	20-27	35	+	–	+
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?
s	1	–	?	220-295	17-20	30-40	+	–	+
n	?	?	?	130-140	10	30	+	+	–
n	2	+	b	215-240	17-25	30	+	–	+
n	2	+	b	270-305	10-17	30	+	+	+
n	0(-1)	+	v	195-205	15-17	30-35	+	–	+
s	0	+	b	265-305	17-25	25-30	+	±	+
n	1	–	?	115-165	10-15	25	+	±	–
?	?	?	?	?	?	?	?	?	?
?	?	?	?	?	?	?	?	?	?
s	2	+	p	220-285	15-17	45-55	+	–	–
?	?	+	p	?	?	?	+	–	?
n	2	+	p	110-130	15	25-30	+	–	+
n	?	+	p	105-125	10-17	20	+	–	?

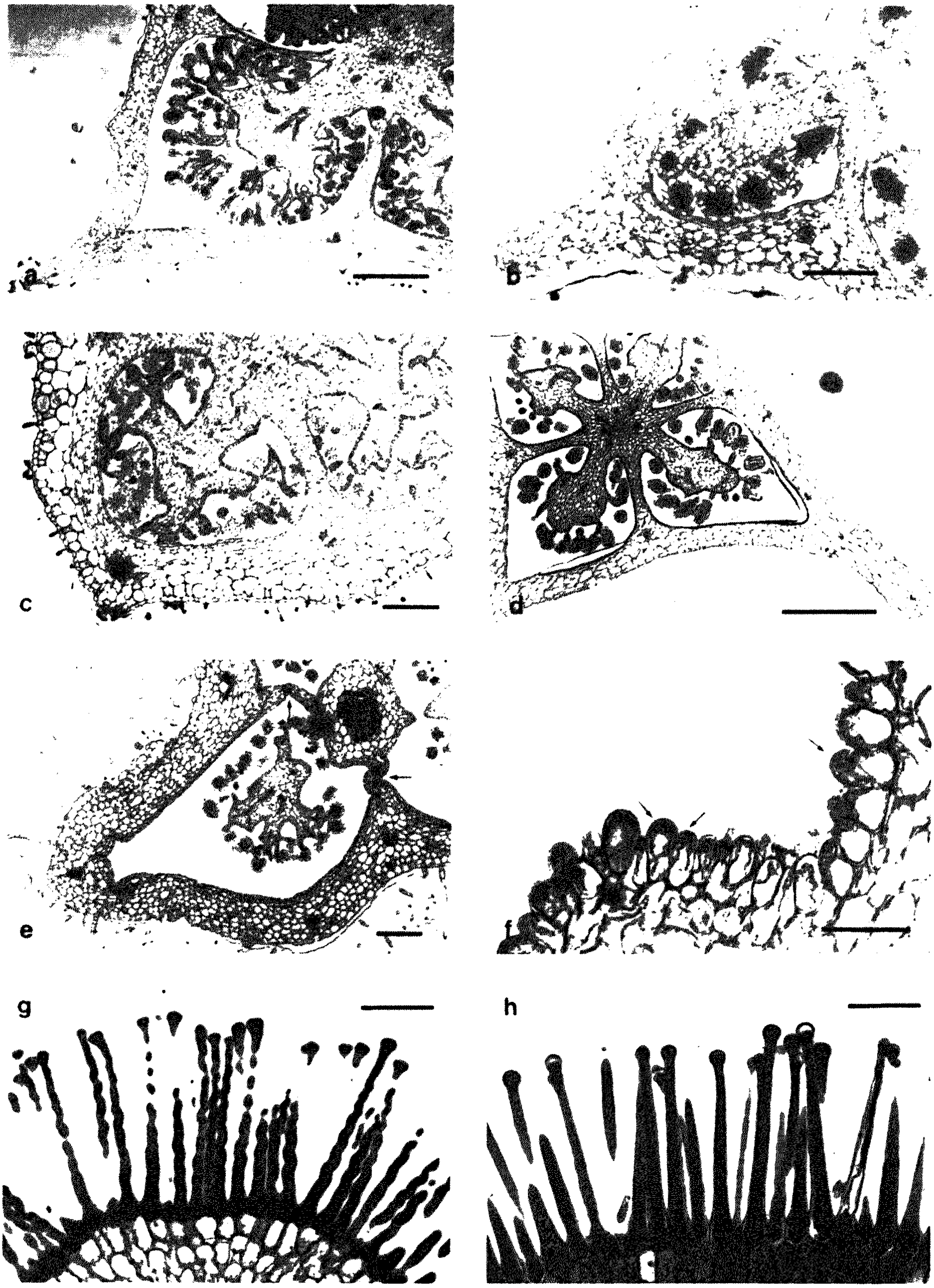

Figure 7.4. Anatomy of the ovary and style. **a**: *B. duncan-thomasii*, locule with branched and tree-shaped placenta (bar = 0.5 mm); **b**: *B. pseudoviola*, locule with thickened and lobed placenta (bar = 0.2 mm); **c**: *B. vittariifolia*, locules with branched and tree-shaped placentae (bar = 0.2 mm); **d**: *B. dewildei*, ovary with mushroom-shaped placentae with long funiculae running towards the ovules (bar = 0.5 mm); **e**: *B. ferramica*, ovary with folded septa (arrows) possibly an effect of greenhouse conditions (bar = 0.2 mm); **f**: *B. susaniae*, cuticula structure on epidermal cells of the style (arrows; bar = 0.05 mm); **g**: *B. susaniae*, ribbed papillae of the style (bar = 0.1 mm); **h**: *B. quadrialata*, smooth papillae of the style (bar = 0.1 mm).

In *Loasibegonia* they are generally about as large as, or only slightly smaller than the cells right below, as was also encountered in the leaf anatomical study (chapter 6). Hence, this character is of taxonomic significance. Some collections showed the same kind of strongly convex epidermal cells as were found in the leaves and discussed earlier. It seemed appropriate to take into account a second character concerning the thickness of the epidermis. Apart from measuring the thickness of this layer, which was used as a character in the leaf anatomical part of this study, the ratio between this thickness and that of the first mesophyll layer might even be a more characteristic feature.

A zone composed of 1 to 4 layers of markedly smaller cells bordering the locule cavity can be distinguished (see e.g. fig. 7.4c). In this respect the ovary wall of *B. scutulum* is exceptional: the outermost layer of this zone is composed of cells with sclerified walls. It must be noted that from this species no young female flower was available and the sections were prepared from a young fruit. The question arises whether in the fruiting stage induration of the walls of cells in this layer is a common phenomenon, at least within the section *Scutubegonia* where the fruits are generally tough. In that case one would expect, however, to find at least the initiation of such thickening in other collections. Nothing of this kind was observed and therefore it is probable that the induration is linked with the fact that the fruits of *B. scutulum* remain on the plants for an exceptionally long period (more than 6 months, see chapter 10). It might give the developing seeds some kind of added protection during this period.

There seems to be a strong correlation between the presence of comparatively large epidermal cells in combination with few layers of smaller cells bordering the locular cavity and a translucent ovary wall.

The shape of the septa is another feature co-determining the general shape of the ovary in cross section. Generally (disregarding several exceptions) the septa found within the section *Scutobegonia* are elongated whereas those of the section *Loasibegonia* are short and thick. Septa of several species belonging to the section *Scutobegonia* were even folded as if they were too long to fit in the ovary (fig. 7.4e). Such a situation was always encountered in ovaries from plants cultivated in the greenhouse at Wageningen and therefore they might be interpreted as anomalities caused by greenhouse conditions.

When subdividing his type B2, Reitsma (1984) used the shape of the placentae as one of the distinctive characteristics, next to the arrangement of the ovules. The present study shows that the shape of the placentae is indeed an important feature in phylogenetic considerations (see chapter 11). Strongly thickened and unbranched placentae are encountered within the section *Loasibegonia* while branched types usually occur in the section *Scutobegonia*. Yet another type of placenta is presently distinguished and apparently overlooked by Reitsma (1984). It can be circumscribed as mushroom-shaped bearing comparatively long funicles, as illustrated in fig. 7.3c and fig. 7.4d. It is characteristic for the section *Filicibegonia* and the species *B. dewildei* and *B. atroglandulosa*. As the latter two are placed in two different sections, the occurrence of this type of placenta is not considered to be of taxonomic value within the group treated here. Reitsma's type B2-d consists of two species belonging to the section *Scutobegonia*: viz. *B. clypeifolia* and *B. ciliobracteata* (as *B. dielsiana*). It seems obvious from his drawings (his figs 10E and 10F) that he observed ovaries with imperfect ovules. Maybe this led him to the recognition of a separate type because the present study does not reveal any structural differences with e.g. *B. lacunosa*, which Reitsma classified as belonging to a different type.

There is considerable variation both in the number of ovules per cross section and in the number of layers in which the ovules are arranged. Comparatively few ovules per locule, arranged in a single layer, are often found in a distinct group of species of the section *Loasibegonia*, and this is regarded as the derived state (see chapter 11).

7.3.2 Styles and stigmas

Close observation of the outer wall of the epidermal cells of the styles showed that it is either smooth or beset with a cuticular ornamentation (fig. 7.4f). Because no SEM observations of the styles were made, the exact nature of this ornamentation could not be revealed. As far as can be judged from the light microscopical observations, it is likely to be similar to the ornamentation found on the epidermal walls of non-glandular hairs (see fig. 6.3.h), hence be striate.

The stigmatic surface consists of bottle-shaped, capitate papillae (fig. 7.4g & h), similar to those reported by Arends (1992: fig. 6-9a). Several parts can be distinguished: a more or less rectangular 'foot', an elongated stalk and a globose head (fig. 7.5). The size of the foot in relation to the total length of

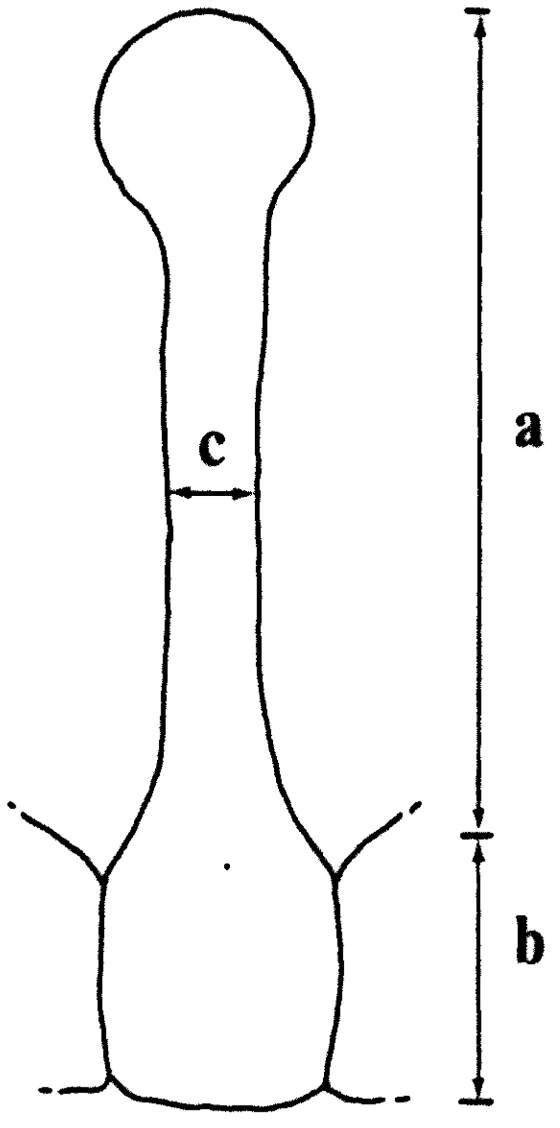

Figure 7.5. Stylar papilla and measurements taken from it. a: length free part; b: length basal part; c: width.

the papilla varies considerably. Also the shape of the stalk varies between species from long and slender to short and thick. The most striking feature encountered was the ribbed stalk (fig. 7.4g), which is only present in long and slender stalks. The presence of ribbed stalks is of taxonomic importance since it is linked to a subgroup of the section *Scutobegonia*. It might be that the ribs are in fact caused by a spiral nature of the stalk. Here again SEM observations could reveal more details and in general a more detailed (SEM) study is highly desirable. Short and thick papillae are found almost exclusively within the section *Loasibegonia* that accommodates elongated ones as well. Within the section *Scutobegonia* elongated ones, either smooth or ribbed, are found.

The taxonomic value of features of the stigmatic tissue was already noted by Baranov (1977, 1981) but little attention has been given to it since. As the present observations indicate a fairly strict correlation with the phylogeny of the group, it is hoped that botanists will pay more attention to this useful structure in the future.

7.4 Vascularisation

7.4.1 Introduction

Authors like Gauthier (1959), Barabé (1981) and Barabé & Chrétien (1983) tried to unravel the true nature of the inferior ovary of *Begonia* by means of a meticulous study of the vascularisation. This was based on the concept that the ovary is made up of carpels, in which vascular bundles can be traced and denoted. Sattler (1974), however, argued that the parts of which the ovary is composed are not always foliar in origin. He stated that accepting this point diminishes considerably the possibility to derive the nature of an ovary from its vascularisation.

Nevertheless, it was decided to study and map out the vascularisation of a number of species to investigate whether recent new views on the subject by Charpentier et al. (1989a, 1989b) would lead to new insights in the vascularisation of the group studied here. Such novel opinions were obtained by Arends (1992) who reconsidered his observations in the light of the conclusions of Charpentier et al. l.c. This subsequently led him to alternative conclusions. Secondly, the occurrence of differences in the vascularisation pattern of distinct species would, again, be a welcome addition of characters for the phylogenetic analysis.

The vascularisation patterns of two species (one of each section and revealing interesting characteristics) are discussed in detail below. Throughout the text observations on other species studied, and particular remarks on general aspects encountered in the majority of them, are given as well. In order to study the exact vascularisation, complete series of transverse sections should be studied. More general aspects of the vascularisation of ovaries may be studied by considering every 5th section, as was done in this study with 9 out of 30 ovaries.

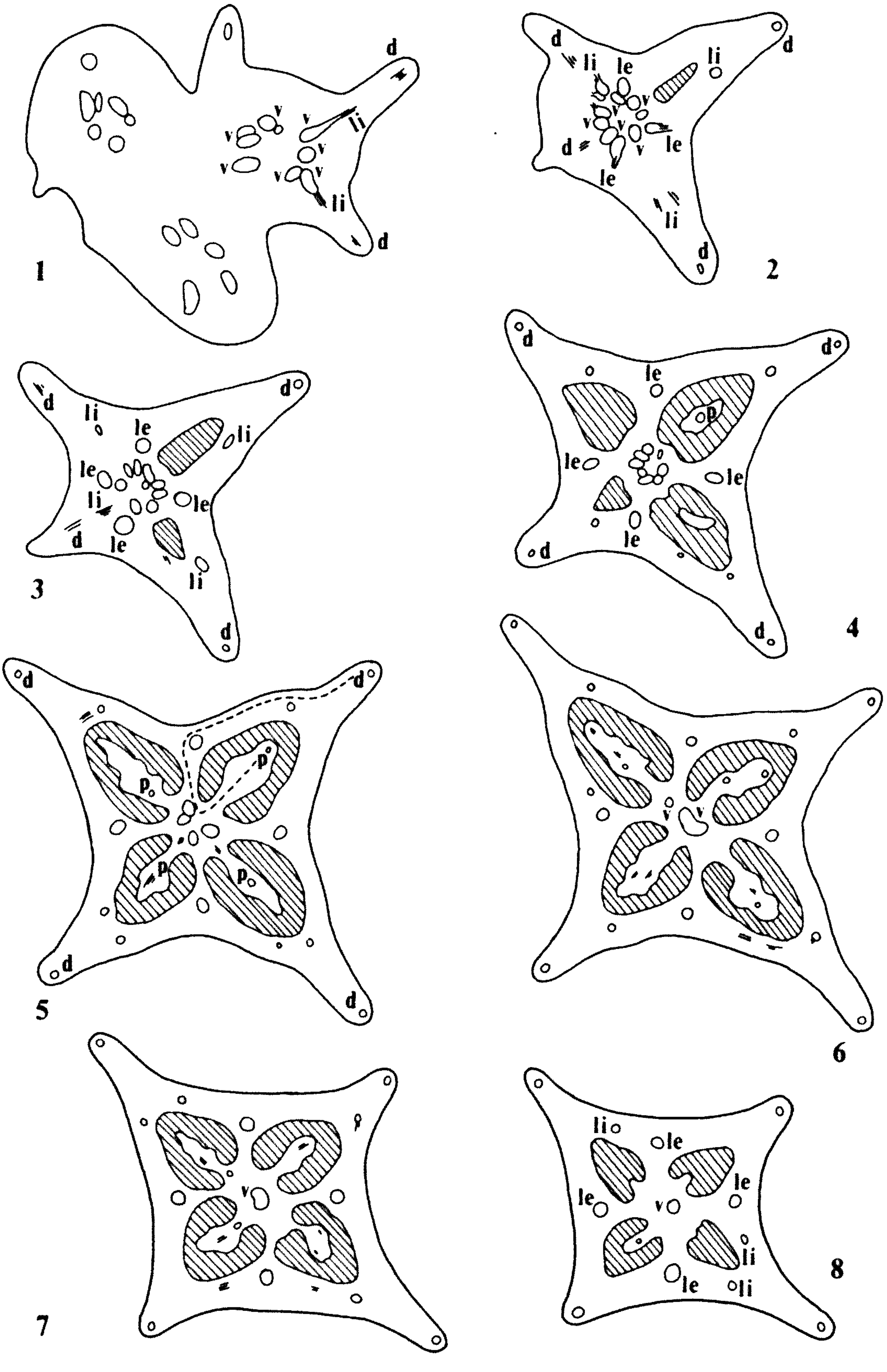

Figure 7.6. Transverse sections of the ovary of *B. pseudoviola*. **1**: basal zone of the ovary (on the right) which is still attached to the pedicels of two male flowers (on the left); **2**, **3**: formation of dorsal and lateral bundles spreading out from the centre; **4**: all bundles have taken their position; **5–8**: zone with placentae, fusion of the ventral bundles.

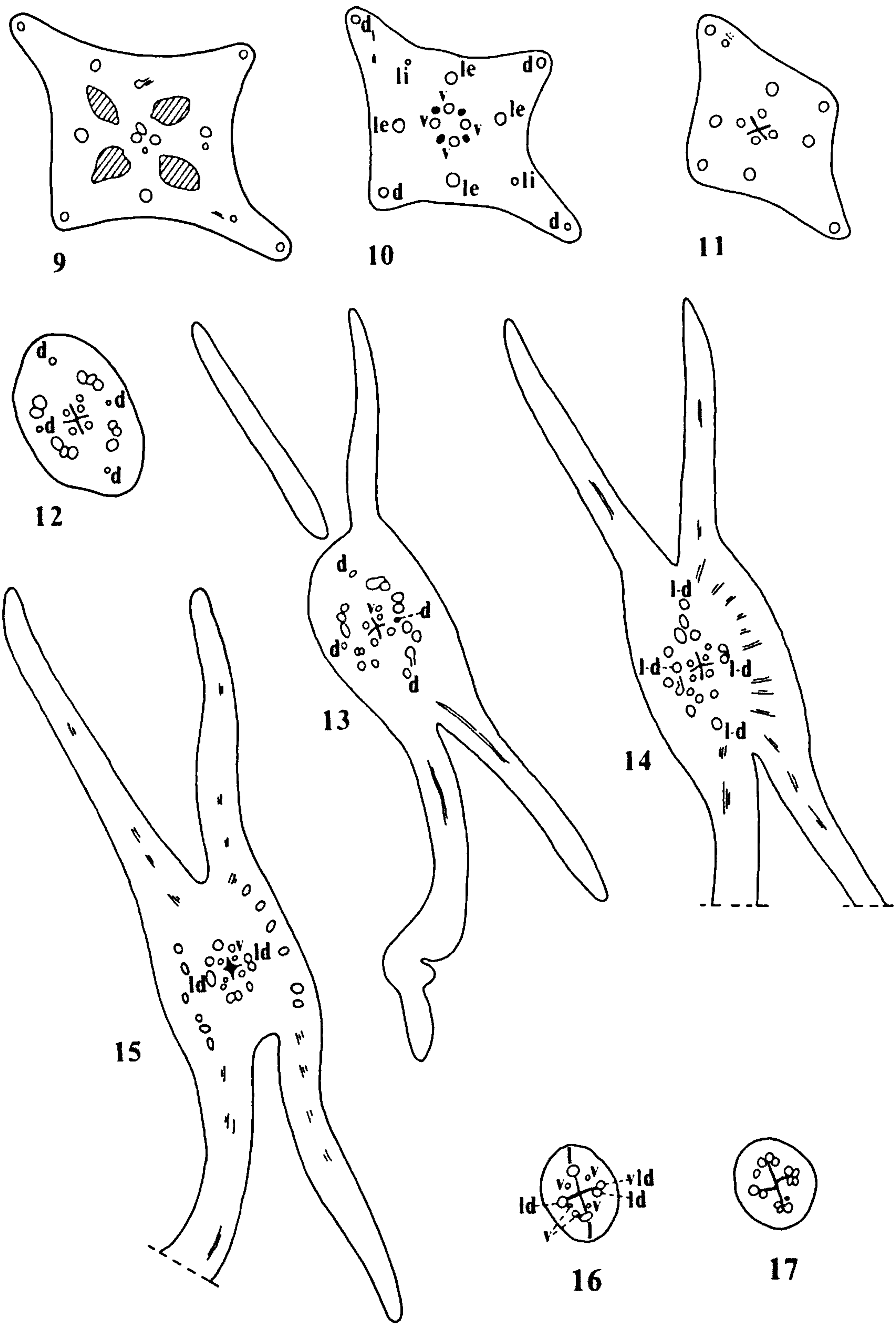

Figure 7.6 (continued). **9**: upper zone of the ovary, separation of the fused ventrals; **10**: stylar channels present in between the ventrals; **11**, **12**: two dorsal bundles situated further away from the centre, two others moving towards the centre, external laterals splitting up, one ventral has split up in its two original components; **13–15**: formation of an outer and inner ring of vascular bundles, fusion of dorsals with external laterals; **16**, **17**: base of the style, formation of four groups of vascular bundles. Further explanation see text.

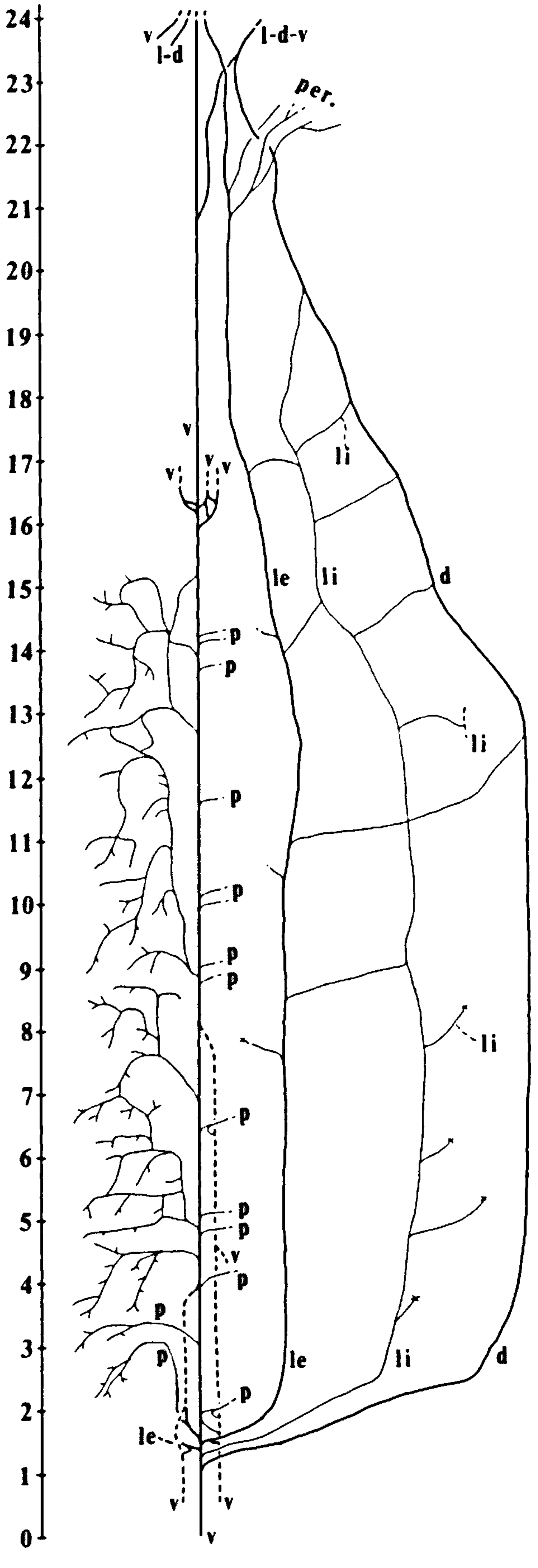

Figure 7.7. Vascularisation pattern of the ovary of *B. pseudoviola*; **per.** denotes vascular bundles feeding a perianth segment, further explanation see text.

7.4.2 The ovary of *Begonia pseudoviola* – section *Loasibegonia*

The ovary studied had four locules. The vascularisation pattern is clarified by means of a series of schematic drawings (fig. 7.6) made from 17 cross sections at more or less regular intervals. In fig. 7.7 the vascularisation pattern of a part of the ovary is given in a reconstructed vertical section along the plane denoted by the dashed line in fig. 7.6.5.

At the very base of the ovary, in the transition zone between pedicel and ovary, a ring of vascular bundles can be observed. After several splitting events the bundles seem to assume a definite position and several bundles branch off and shift towards the perimeter. Some anastomosis occurs. Closer observation shows that this anastomosis is not random; a distinct pattern can be denoted. This pattern perfectly fits the theory that the ovary is built up of carpels. In fig. 7.10 a simplified scheme of the distribution of the main vascular bundles encountered in the ovaries of the sections *Loasibegonia* and *Scutobegonia* is presented. It shows that, interpreting this pattern in line with the carpel theory, the centre of the ovary contains four ventral bundles (**v**). Each of these consists of two fused ventrals of adjacent carpels. Similarly each lateral bundle consists of two fused laterals, one originating from each of two adjacent carpels. The ring of vascular bundles splits up at the base of the ovary into several bundles which can be denoted as ventral, lateral and dorsal bundles. The splitting follows a distinct pattern. In many of the species studied the dorsal bundle is the first one to branch of. It originates from two ventral bundles belonging to the same carpel. The ventrals of adjacent carpels are generally fused below this point but when the dorsal branches of they often become single again over a short distance. Similarly, the lateral bundles originate from two ventrals from adjacent, not the same, carpels as could be predicted (fig. 7.7, level 1.5). The external lateral bundles mentioned above will be denoted **le**. They remain fused throughout the length of the ovary of every species studied here. Bundles which are often present in between the dorsal (**d**) and the external lateral will be denoted as internal laterals (**li**). In the ovary of *B. pseudoviola* three of the four locules receive a single **li** while one locule receives two of them at the bottom of the ovary, that is, below the base of the locule cavity. These **li**'s take their position at the base of the wing. At a higher level the **d** bundle sometimes splits of a second **li** which takes a position opposite to the first **li** in the same locule (see for example fig. 7.6.5.).

Going upwards in the ovary, the placentary vascular bundles (**p**) branch off from the **v** bundles. These enter the placentae in order to feed the ovules. Here again, a **p** sometimes originates from two different ventrals, in agreement with what one would expect from a fused carpel construction (fig. 7.7, level 2 and 6.5). On the other hand in this region the **v** bundles are generally, that is in most of the species studied, situated at the base of, and therefore opposite to the placentae. This is not what one would expect following the carpel theory strictly, but this situation changes in the apical part of the ovary (see below). It should be noted that initially the placentary bundles follow an upward direction but then level out and turn downward towards the ovules. Still higher up in the ovary of *B. pseudoviola* the four ventrals fuse completely (fig. 7.6.6. and 7.7 at level 8) and a single central bundle remains. This situation continues up to level 16 in fig. 7.7.

The upper part of the ovary, that is above the placental region, accommodates several very interesting regions. When a fusion of ventrals (complete or partly) has taken place on a lower level in the ovary, as happens in *B. pseudoviola*, they split up into four equal bundles again (fig. 7.6.9). Each of these is still assumed to consist of two fused ventral bundles from adjacent carpels. Each **v** is now no longer positioned opposite to a placenta but has moved to a position facing a septum. The stylar channel enters the locules at more or less the same level. In the ovary of *B. pseudoviola* this entry takes place at the very top of the locular cavity. In other species studied the entry is generally situated at a slightly lower level, often directly above the attachment point of the placentae. This opening generally extends slightly downward and lateral to this attachment point, which results in a kidney- or moon-shaped opening.

Further up, the ovary narrows into the part which is denoted as the beak. In the ovary of *B. pseudoviola* it can be readily observed that the **le** bundles are the largest ones, the **v** bundles are of medium size while the **d** bundles are only small and apparently of little importance to the supply of organs situated higher up. In many of the species studied here, most of the ventrals bifurcate at this level (fig. 7.7, level 21). One of the pair retains the central position while the other shifts slightly outwards (fig. 7.6.12 and 7.8.13). Sometimes the forked ventrals fuse to split up again higher up. More or less at the same level the large **le** bundles divide, often in threes (fig. 7.6.12). The two dorsals which are situated right below the two perianth segments curve towards the central axis. They fuse at some level – this level can differ considerably even within the same flower – with a product of **le**. The two **d** bundles which are situated in a position in between the two perianth segements remain somewhat further away from the centre. They fork and one of the two resulting bundles fuses with a product of **le** as well and it also moves towards the central part. All such resulting **l-d** bundles positioned towards the centre of the ovary ultimately end up in the styles. Four products of the **le** bundles, each situated more or less opposite to the ventral bundle in the centre, now shift towards the centre as well. All the above mentioned splitting and relocating events result in a situation where two rings of vascular bundles can be distinguished (fig. 7.6.15). The outer ring will feed the perianth segments while the inner one enters the styles. A very interesting aspect is that each of the two products of a single **v** in the centre of the flower eventually turns up in two different styles (fig. 7.6.16 & 17). Hence a style receives two ventral bundles that originate initially from its own carpel. This is in line with the observation that each style is positioned on top of a locule, not in between two of them. Each style in the ovary of *B. pseudoviola* thus receives four bundles: two **v** products, one product of **le** and the above mentioned **l-d** bundle.

Because the perianth segments are supported by numerous vascular bundles, they can be denoted as sepals (see also Esau, 1965: 544 and Arends, 1992: 142).

7.4.3 The ovary of *Begonia clypeifolia* – section *Scutobegonia*

The general aspects of the vascularisation pattern of the ovary of *B. clypeifolia*, as depicted in fig. 7.8 and 7.9 do not differ fundamentally from that of *B. pseudoviola* and will not be repeated here. However, several differences occur, some of which lead to new or supplementary ideas about the nature of the ovary. These will be discussed below.

The **d** and **le** bundles split off at the base of the ovary in a way similar to that found in *B. pseudoviola*. However, at this level the **v** bundles do not separate into simple bundles as was described in the latter species. They remain fused throughout this basal section and one might consider the fusion of the ventrals to be more intimate than that of *B. pseudoviola*. In several of the other species studied, the neat pattern of splitting and refusion of the **v** bundles was rather variable, even among different parts of the same ovary. In contrast to the ovary of *B. pseudoviola* each locule of the ovary of *B. clypeifolia* receives two **li** bundles at the very base. They pass under the locular cavities. Observations on the **li**'s in other ovaries suggests that the number of **li** bundles is related to the width of the ovary. When the ovary is comparatively wide more **li** bundles appear. It seems likely that one of their functions is to reinforce the ovary.

In the middle part of the ovary no fusion of **v** bundles takes place. The **p** bundles arise from the **v** bundles in only a small section of the ovary (fig. 7.9, level (4–)5–7). From the same figure it appears that once a **p** has been split off, it remains an important and large bundle continuing upwards through the 'trunk' of the placenta. Several major strands connect this 'primary placental bundle' with the ovules. Similar to the situation in the ovary of *B. pseudoviola*, the traces which feed the ovules usually curve down in their distal part.

It is obvious from fig. 7.9 that many **li**-like bundles occur along the broad wall of the locule and in the wing of the ovary. The **d** bundles run all the way along the outer margin of the wings and return towards the centre of the ovary along its upper rim. Here the most astonishing observation is, that such a **d** bundle keeps on running towards the centre of the ovary, and eventually merges with a **v** after a short downward curve (fig. 7.9, level 11). This **d** passes straight over the locule and between two **le** bundles. In other species such a connection between **d** and **v** was observed as well, although often the **d** itself does not fuse but is connected with the **v** by a **li** bundle which is split of from the main **d**. This **li** often passes the **le** very closely without connecting to it (fig. 7.8.8). The same kind of observation was made by Arends (1992: 124, f. 7-7-e & -f). When this contact proves to be the general pattern encountered within the ovary of *Begonia*, the interpretation of the bundle **p** in Arends' l.c. figures 7-10-16 through 7-10-19 is erroneous and should be denoted as ventral traces. One of the other **d** bundles fuses with a **v** (fig. 7.8.10, another **d** fuses with an **le**, while the fourth one seems to peter out (fig. 7.8.9–11). The role of the latter in the styles is taken over by a product of an **le**.

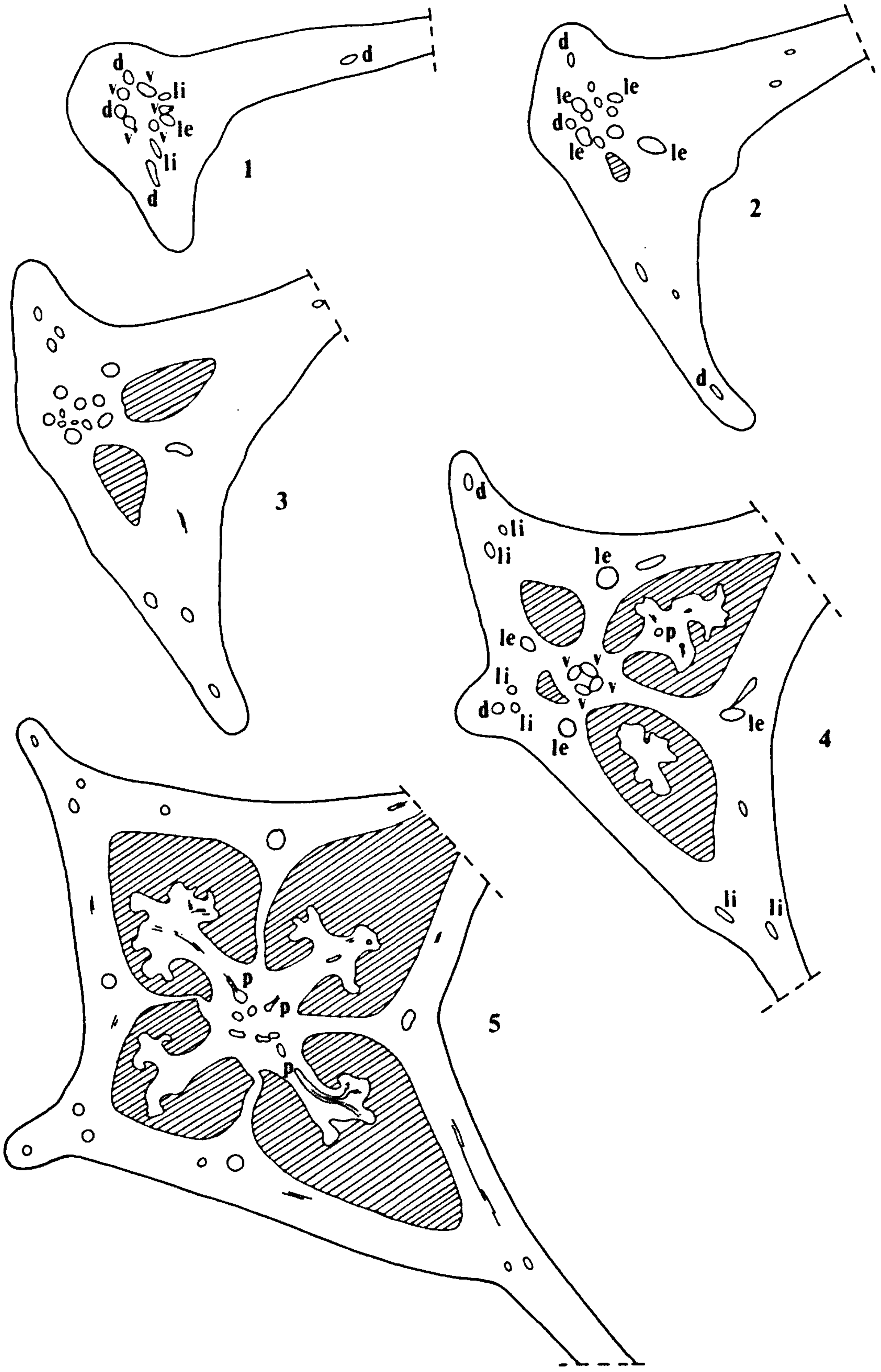

Figure 7.8. Transverse sections of the ovary of *B. clypeifolia*; sections were cut in a way slightly oblique to the central axis. **1, 2**: formation of dorsal and lateral bundles spreading out from the centre; **3, 4**: all main bundles take their positions; **5**: placentae have entered the locules, placentary bundles feed the ovules.

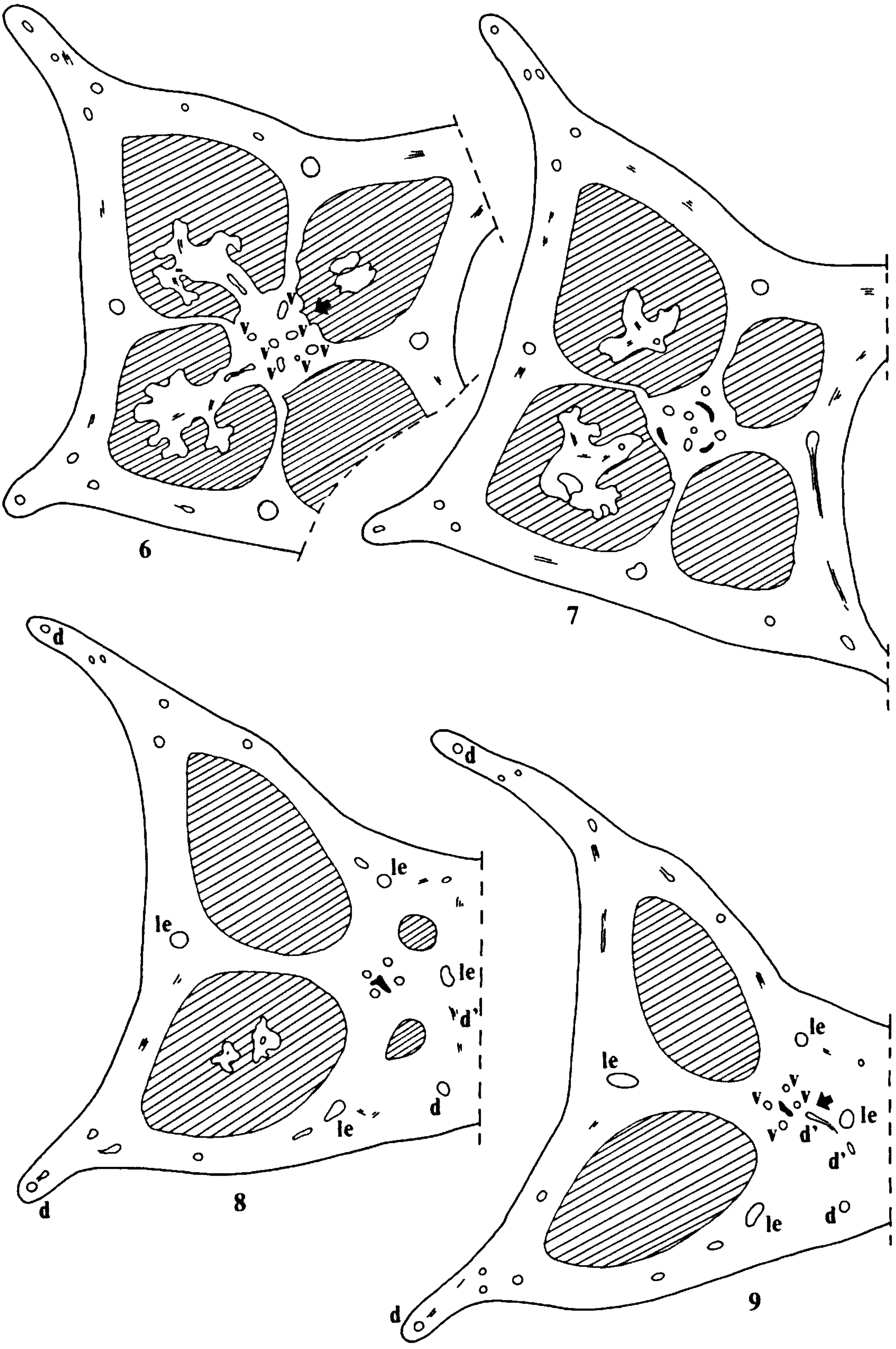

Figure 7.8 (continued), **6**: ventral bundles do not fuse, arrow indicates the entrance of a stylar channel into one of the locules; **7**, **8**: apical part of the locules, stylar channels fuse in the centre (black areas); **9**: arrow indicating the fusion between a ventral bundle and a product of a dorsal one.

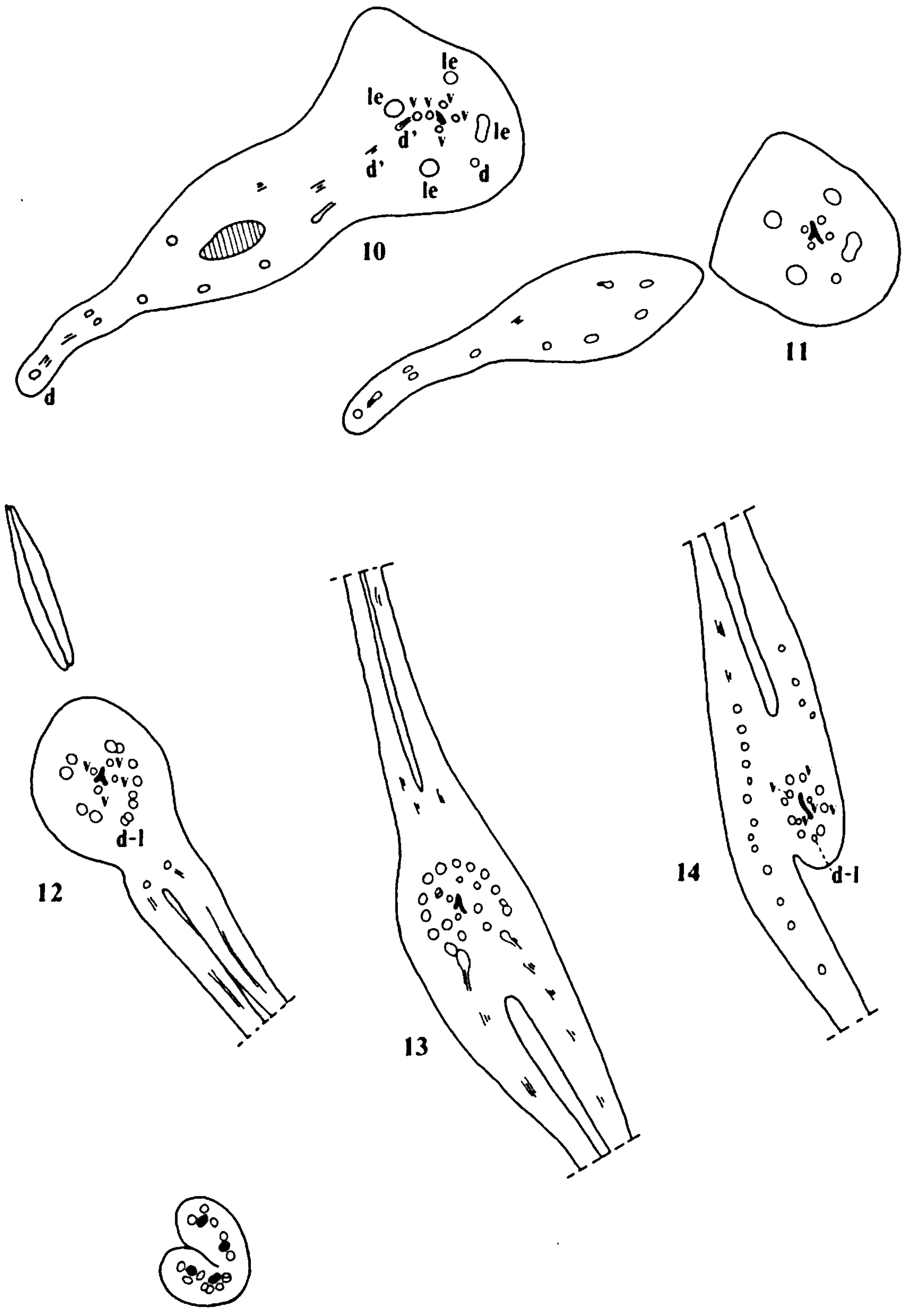

Figure 7.8 (continued), **10**: another fusion between a ventral bundle and a dorsal one; **11**: one dorsal seems to have petered out, another has fused with an external lateral bundle; **12**: last remaining dorsal bundle has fused with a product of a lateral one, all bundles not labeled are products of lateral bundles; **13–14**: formation of an outer and inner ring of vascular bundles, the outer feeding the perianth segments; **15**: division of the style into four arms, each with a stylar channel (black areas). Further explanation see text.

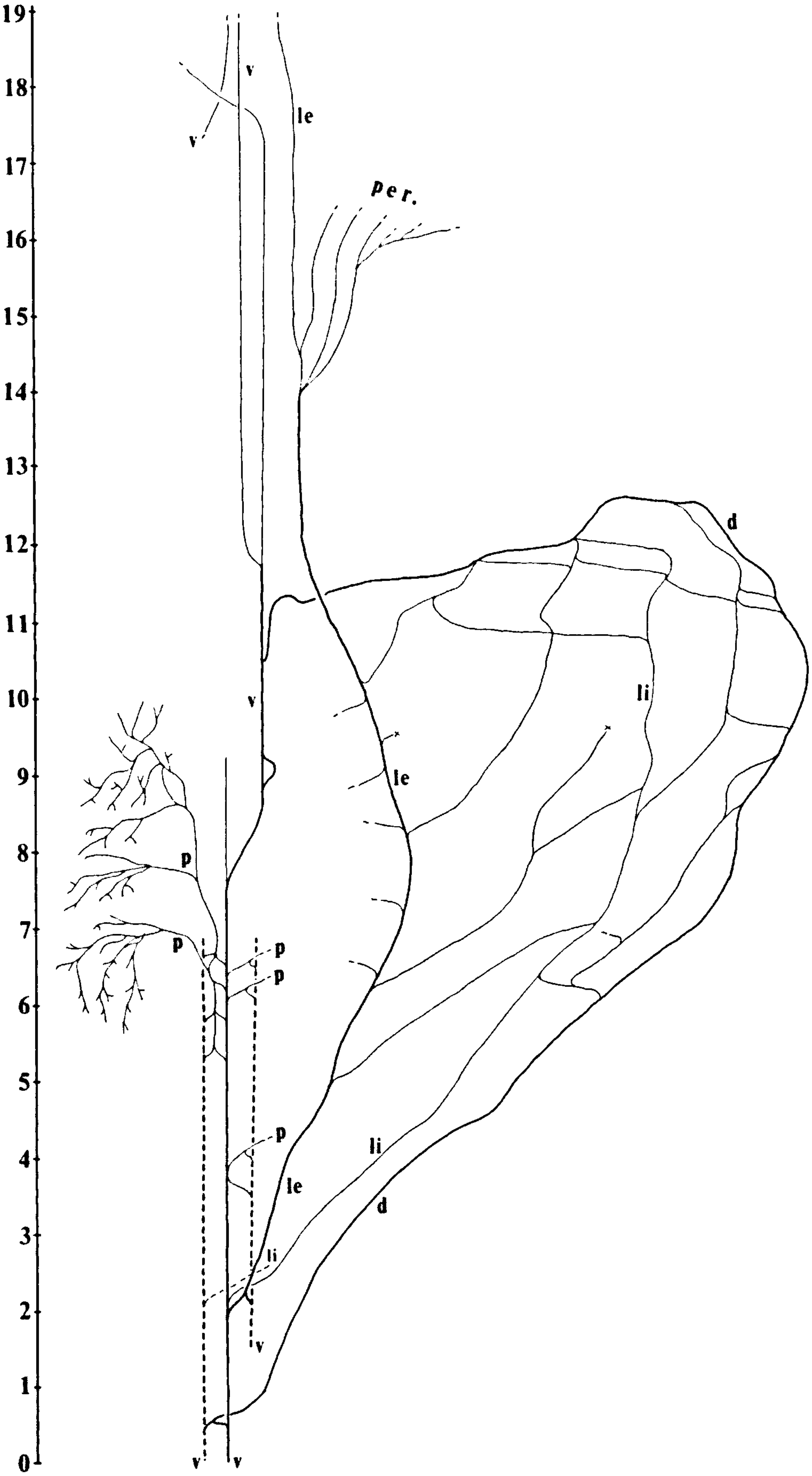

Figure 7.9. Vascularisation pattern of the ovary of *B. clypeifolia*; **per.** denotes vascular bundles feeding a perianth segment, further explanation see text.

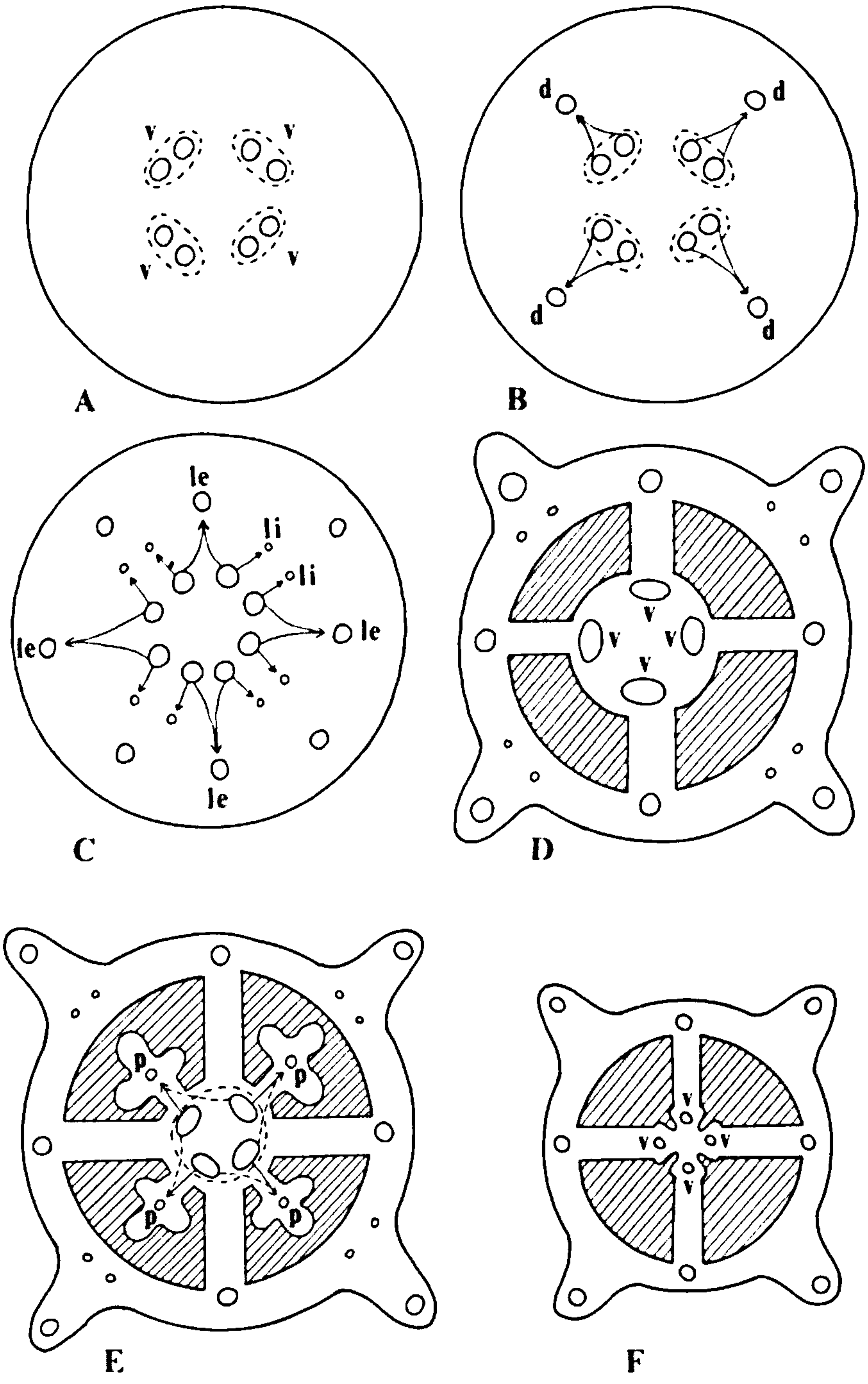

Figure 7.10. Schematic presentation of the vascularisation within the ovary of species of the sections *Loasibegonia* and *Scutobegonia*. Explanation see text.

7.4.4 A general vascularisation pattern

The vascularization in the ovaries of 21 species was studied. It does not seem appropiate to deal with all of them separately here. It was tried, however, to conceive a general vascularisation pattern that fits all species of the two sections studied. This general pattern is presented in fig. 7.10 using a four-locular situation as that of a three-locular ovary is in general not as symmetrical and clear

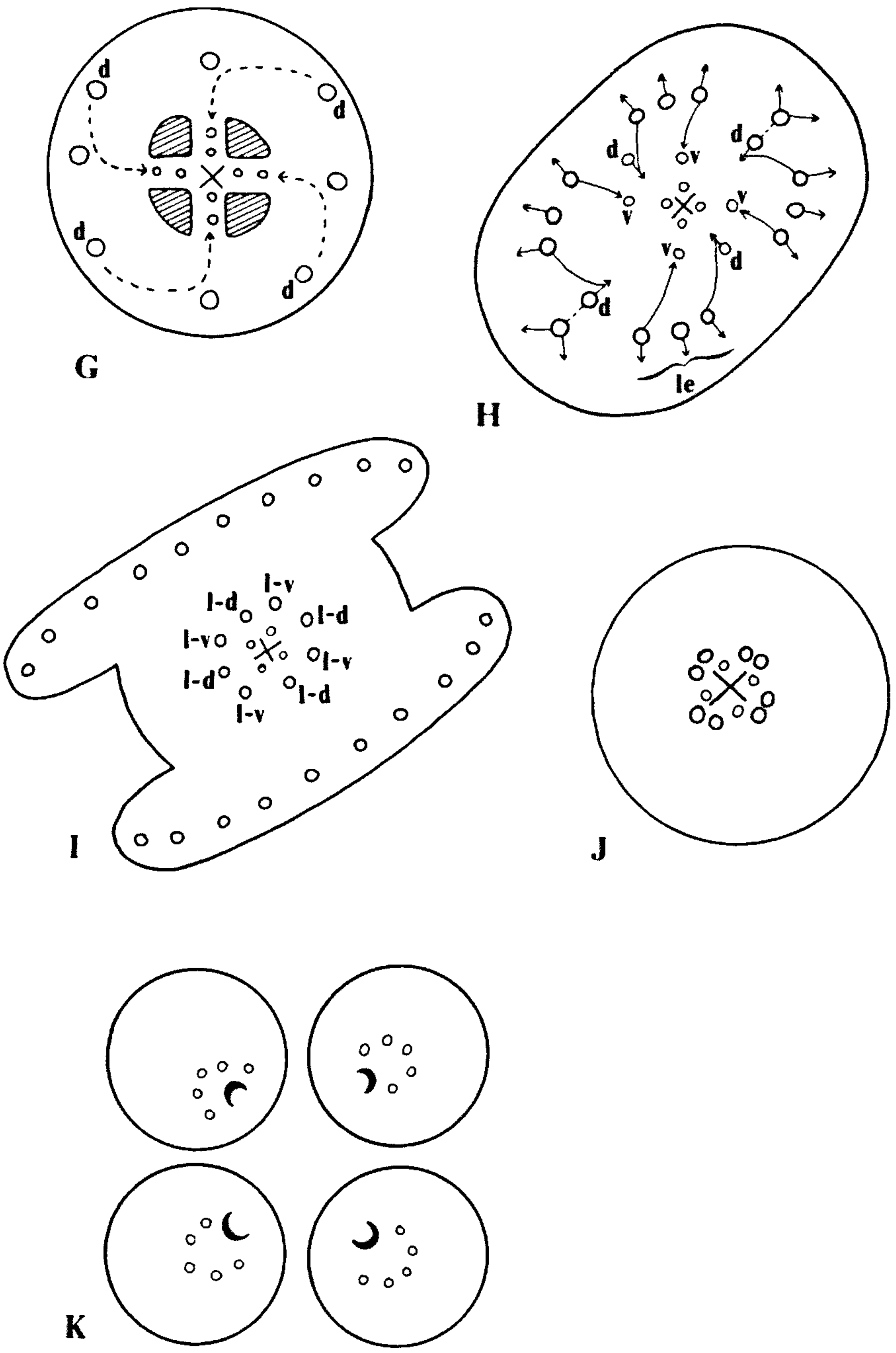

Figure 7.10. (continued).

as that in a four-locular one, particularly in the apical part. The separate cross-sections depicted in figure 7.10 are schematical. Section A represents the stage at the bottom of the ovary with 8 ventrals, which are sometimes fused in pairs. In section B the pairs of ventrals from the same carpel produce a bundle **d** which moves towards the perimeter. Section C shows the **li** bundles which are produced by ventrals. At more or less the same level the **le** bundles often are produced from a pair of ventrals belonging to adjacent carpels. In section D the locules are met with and four main **v** bundles are located in the centre. Section E shows that the placentae are entered by placental traces each sometimes produced by two adjacent **v** bundles, implying that the placenta and ovules are ultimately fed by ventrals from the same carpel. In section F the fused carpel margins give way and the stylar channel is connected to the locule cavity. This gives the *impres-*

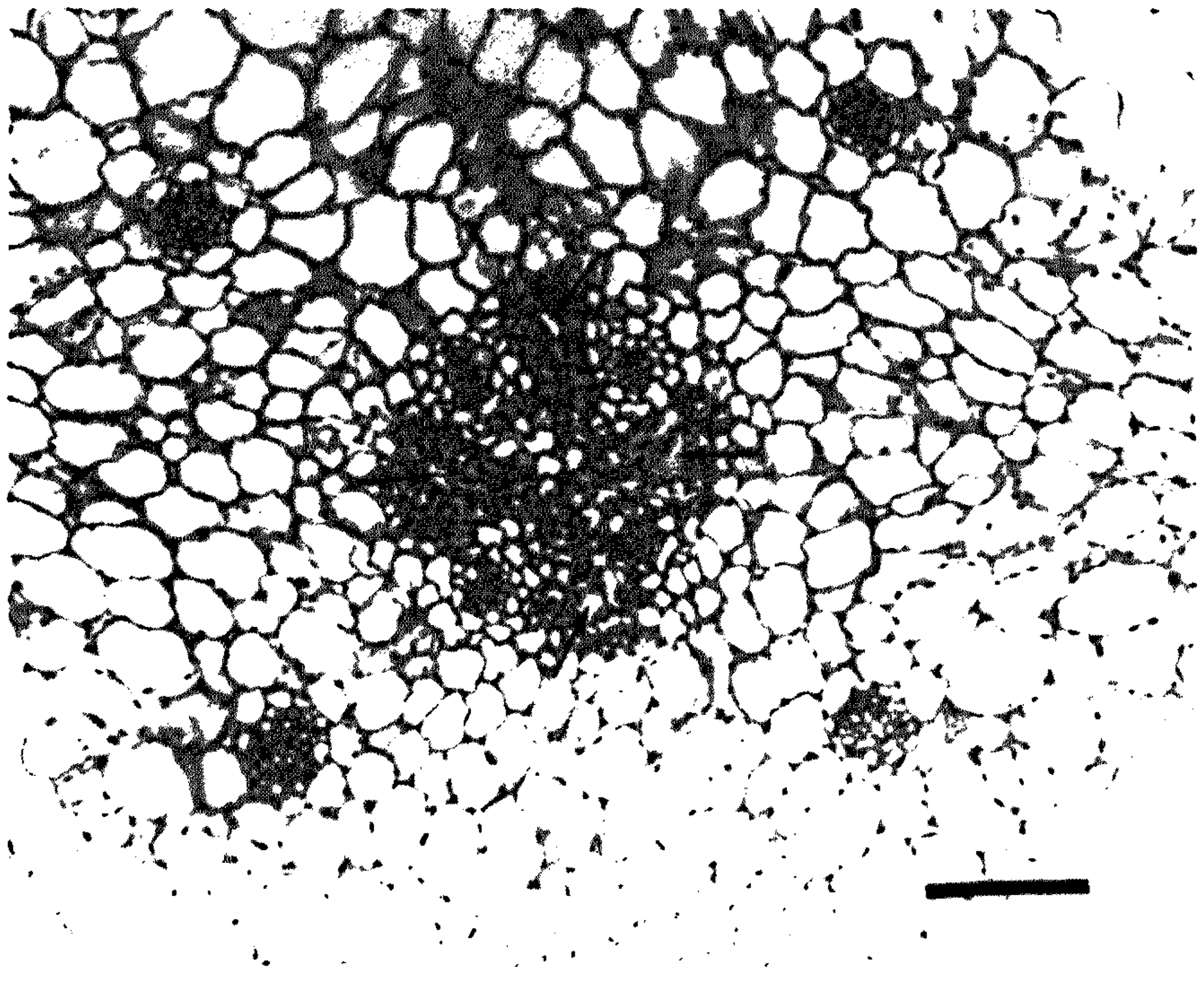

Figure 7.11. *B. pseudoviola*, situation in the apical part of the ovary with entrance of the stylar channel leading to a seemingly parietal situation; arrows pointing to the very apexes of the locular cavities with ventral bundles in between and lateral bundles situated further away (bar = 0.1 mm).

sion of a parietal situation (see also paragraph 7.5). Then, at section G, the **d** bundles connect up with the v's. Section H is more complicated and shows in the first place that the **v** bundles have split up in two, and as such each of them has become singular again. Two of the **d** bundles shift towards the centre while two others split in two. One product of the latter runs towards the centre as well, while the other is involved in 'feeding' the perianth segments. At this level the **le** bundles are generally large and divide into three and later on even more products. Often one of these products fuses with the split products of the two **d**'s while another runs towards the centre and often fuses with a **v**. In some ovaries it was not this **le**-product but the **d** which fused with the **v**. This splitting and fusing pattern is not always as clear and strict as has been sketched in this schematic presentation. The bundles emerging ultimately after this complex level are depicted in section I. Sections J and K show the subsequent constellation of these bundles. Note that the **v** bundles, which have been situated up to this level at the very centre, now move slightly outward, each to be joined in a style with a **l-v**. Each style obtains its v-components from two different **v**'s. Hence the two **v** bundles originally belonging to the same carpel, ultimately enter the same style. Section K shows the bundles continuing to divide higher up in the style.

7.5 Discussion

Considering the many promising anatomical characters provided by the ovary, the primary goal of this part of the study was easily reached. Several of the anatomical features of the ovary proved to be very valuable in the phylogenetic analyses (chapter 11). Future taxonomic studies, especially those concerned with the delimitation of supraspecific taxa or with phylogenetic aspects, may find very useful tools in the anatomy of the ovary.

The secondary objective, viz. further investigation of the true nature of the ovary, is far more complex and much more time consuming to reach. The observations are perfectly matching the hypothesis that the ovary of *Begoniaceae* consists of carpels. In conclusion no other definite statements can be made yet. Being of only secondary interest for the present study it was decided not to pursue matters concerning the nature of the ovary exhaustively. The discussion below will hopefully ultimately add to a thorough understanding of the ovary of *Begonia* in general.

I would like to comment on the observation made by Charpentier (1989b) and by Gauthier (1950) that at the very apex of the locules of the ovary of *B. dregei*, which otherwise has an axillary placentation, a parietal situation exists. This observation is also discussed by Arends (1992: 86 & 89). A similar situation can be observed in the figures of several other *Begonia* species given by Gauthier l.c. and it is encountered in many of the ovaries from the sections studied here (see 7.10F), though not always as obviously. Charpentier et al. l.c. regarded this observation as evidence that in the ovary of *B. dregei* the parietal meristem system is only of limited importance. In their view the very small parietal zone in the top of the ovary is the single product of this meristem system, while most of the ovary axis has been shaped by the axial meristem. However, my interpretation is a different one. I interpret the small 'parietal' zone as the inevitable result of the entrance of the stylar channel, as shown in fig. 7.11. I do not see how this stylar channel should otherwise be connected with the locule cavity *without* creating a parietal situation. A stylar channel passing in between the adjacent carpels would lead to the outer ovary wall and hence be useless. Continuing this line of thought, Gauthier's (1950: 21) conclusion, that apparently 'the margin of each carpel is fused with that of the adjacent carpel more intimately than with the other margin of the same carpel' must be considered false. The stylar channel would have to pass right through the carpel wall in order to create a different situation. This is not very likely.

The interpretation of the vascularisation patterns encountered in the present study does not support the theory on the existence of two different meristem systems as did the pattern described by Arends (1992). The main observation disagreeing with this theory is that the ventral vascular bundles in the central axis of the ovary continue from the bottom all the way up into the styles (see figs 7.7 and 7.9). The fact that at the base of the ovary the **li** bundles split of from those called ventrals, and *not* from those denoted as **le**, is regarded as evidence that the interpretation presented here is the correct one. Evidence that these ventrals are homologous with those called ventrals in Arends' l.c. study is found in the peculiar contact in the apical zone between **d** and **v** *passing* the **le** (see also paragraph 7.4.3 and fig. 7.10G). When indeed two separate meristem systems were involved, one would expect the ventrals to either peter out in the apical zone or perhaps shift towards the ovary wall. My own conclusions based on the observations of Charpentier et al. (1989b) but now taking into account the above mentioned vascularisation patterns, are that only a single meristem is involved. Thus, the two meristem systems denoted by Charpentier et al., connected by a wide transition zone, should be interpreted as a single, elongated meristem system. Moreover, the evidence for a separate axial meristem in young flowers of *B. dregei* should in my opinion have to be provided by the presence of at least an elevation at the base of the ovarial cavity. Their fig. 13 shows, however, a smooth and concave bottom.

8 Micromorphology of the seeds

8.1 Introduction

Detailed studies on the micromorphology of the seeds of *Begonia* have been carried out by Bouman & de Lange (1982, 1983), Keraudren-Aymonin (1983) and de Lange & Bouman (1985, 1986, 1992), which are supplementary to the light microscopic study of Seitner (1972). The studies performed by Bouman and de Lange clearly demonstrate that the micromorphological structure of the seed coat shows characters that are often characteristic at the sectional level and sometimes below that. As in the present study one of the major questions is whether or not to maintain the two sections, it seems unavoidable to take micromorphological seed characters into account while trying to solve this question. The study of de Lange & Bouman l.c. concerned the seeds of 70 collections belonging to no less than 39 different taxa of the sections *Loasibegonia* and *Scutobegonia* and was exhaustive. No new observations were made in the course of the present study. Despite of this fact the micromorphology of the seeds is presented here to complete the 'state of the art' of the taxonomy of the two sections. Their most important conclusion, as regards the present work, was that on the basis of seed micromorphological characters no distinction between the two sections can be made. Still, there remain several questions related to infraspecific variation and to the subgroups they distinguish within the two sections as a whole. These will be discussed below. Further, general characteristics and remarks on infraspecific variation are included.

8.2 General characteristics

Begonia seeds are unique in the plant kingdom because of the presence of a ring of collar cells in between an operculum and the remainder of the testa (fig. 8.1). In germination, the entire operculum is severed from the rest of the seed by the growing radicle. At the same time the walls between the collar cells split open due to the pressure of the expanding radicle (Bouman & de Lange, 1983).

On the African continent the seeds show a large variation in size, shape and cuticular ornamentation. This variation is larger than on other continents (de Lange & Bouman, 1992: 71), which is congruent with the observation that in Africa the species of *Begonia* are much more diverse than on other continents, despite their comparatively limited number.

The seeds of the species of the sections *Loasibegonia* and *Scutobegonia* are very similar. They are among the smallest found on the African continent and

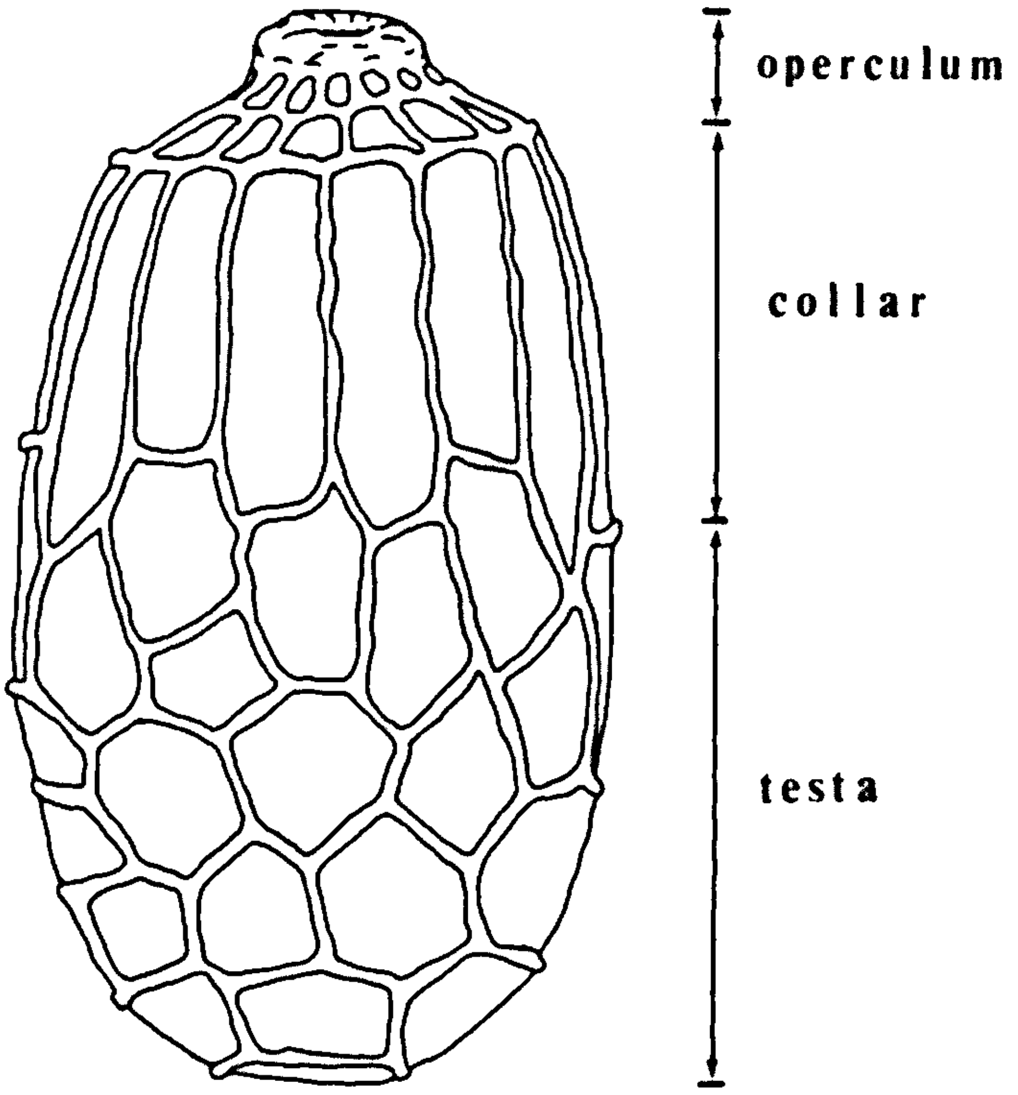

Figure 8.1. Different parts of a begonia seed (redrawn after Seitner, 1972).

even in the world. Their length varies between 270 and 420 µm. Only those of the section *Filicibegonia* and of *B. iucunda* Irmscher are slightly smaller. The collar cells are large compared to the total length of the seed. The seeds are characterized more in particular by the presence of a thick, pronounced cuticular ornamentation. This ornamentation is identical on the collar and testa cells or it may differ slightly. The normal cuticular ornamentation seems to be one with dense, short striae. Sometimes star-shaped or zigzag structures are elevated slightly above the striate layer. In some species much more pronounced star-shaped elevations occur, which leads to the presence of a truly double ornamentation. This occurs in *B. adpressa* and several other species among which there are two that are closely related to the first (*B. pulcherrima* and *B. schaeferi* (as *B. ramosa* in de Lange & Bouman, 1992). In several species of the section *Scutobegonia* the cuticular ornamentation is very dense, giving the seeds a woolly appearance.

The operculum is nipple-shaped to obtuse, and the hilum is situated apically on this operculum, not sunken as in most species of the section *Mezierea* (Gaud.) Warb. (see de Lange & Bouman l.c. plate 17F, 17G & 18). The border between the operculum and the collar is often sunken but it sometimes consists of a flat rim. In the same way the anticlinal boundaries may be sunken or not. In the latter case these may be broad and flat. Anticlinal boundaries may be either straight or undulate. Two species of the section *Scutobegonia*, viz. *B. aggeloptera* and *B. susaniae*, appear to have seeds with papillate cells. A curious feature which to date has not been encountered elsewhere in the family.

8.3 Discussion and conclusions

De Lange & Bouman (1992) group 61 specimens that belong to the sections *Loasibegonia* and *Scutobegonia* into 6 subgroups. Another 9 specimens could not be incorporated in any of those subgroups and were dealt with as 'remaining species'. They also state that recognizing subgroups was difficult, because the character states seemed to show a reticulate pattern. They could trace none or very few correlated character states. Moreover, they sometimes had to assign different specimens of the same species to different subgroups. They mention 5 species where this occurred. I assisted in the identification of all specimens but at the date of their publication my final conclusions were not available yet. Now, after correcting some of these identifications, this number has even increased. Three more species appeared to have samples in different subgroups or at least with markedly different seed characters. It concerns in the first place *B. hirsutula*, which is found in the 'raynaliorum-group' (as *B. subfalcata*) and in the 'hirsutula-group'. A second species is *B. microsperma*, seed samples of which were assigned to the 'vankerckhovenii-group' and to the 'quadrialata-group' (as *B. ficicola*). The third discrepancy concerns *B. susaniae*. One collection was found to possess the strange papillate cells mentioned earlier. But a second collection of this species (Annet 233) showed affinities with the seed structure of *B. hirsutula* and does *not* show the papillate cells. It must be admitted that also the macromorphological features of the latter plant are somewhat deviating from those of the 'typical' *B. susaniae* (see also the notes accompanying the species description elsewhere in this publication) and this collection might represent a distinct taxon. Still, the large degree of presumably infraspecific variation, especially in contrast to the generally limited variation encountered within species of other sections, is weird and remains unexplained.

In consultation with de Lange and Bouman, 7 characters were selected that were applicable in a cladistic analysis. The results of this study (see chapter 11) showed that 3 of these have a comparatively high retention-index, hence were indicative for common ancestry. The shape of the operculum proved to be the most indicative character. Obtuse operculae are generally encountered within the section *Scutobegonia*. The cuticula structure has partly been discussed above and it proved to be another comparatively indicative, but not truly constant character. The third one is the presence of a sunken border between the operculum and the collar. This state is generally present in a subgroup of the section *Scutobegonia* although exceptions occur. The results of the cladistic analysis more or less confirm the existence of a rather reticulate pattern in the seed micromorphological characters which was already mentioned.

In conclusion: although seed characters are highly informative and indicative for the group *Loasibegonia-Scutobegonia* as a whole, they are of much less value for classification purposes and phylogenetic studies at a lower taxonomic level.

9 Hybridisation

9.1 Natural hybrids

9.1.1 Field observations

During a field trip to Gabon in 1991 together with de Wilde a comparatively large hybrid population (several hundred plants) of *B. susaniae x vittariifolia* (coll. J.J. de Wilde c.s. 10238) was encountered in the Crystal Mountains. Both parent species occurred quite abundantly in the direct vicinity of the hybrid population which occupied an area of approximately 15 x 3 m on a vertical rock face. The hybrid plants showed characters that are intermediate between those of the two parent species. The plants of true *B. susaniae* (coll. J.J. de Wilde c.s. 10227) in the vicinity of the hybrid population had broadly elliptic to broadly ovate or circular leaf blades with solitary bullae topped by a red hair and shallowly to very shallowly obtriangular wings on the ovary. Those of *B. vittariifolia* (coll. J.J. de Wilde c.s. 10237) had, as usual, virtually linear leaf blades without any hairs on the upper surface and spindle-shaped, wingless ovaries. The plants of the hybrid population showed a wide variety of leaf blade shapes ranging from narrowly elliptic to ovate, occasionally with red hairs on the upper surface and they had narrowly winged ovaries with obovate wings. The styles and anthers seemed quite normally developed. The plants had just started to flower and observations on seed setting could not be made. I assume that the large hybrid population was not the direct result of a single crossing event. The comparatively large amount of variation within the hybrid population suggested that it contained at least F2 generation plants. Introgression might have occurred but because the hybrid population was spatially separate from the two parent species, I judge this as less likely.

In the course of the same field trip in 1991 a single sterile plant, most likely representing the hybrid *B. clypeifolia x lacunosa*, was found in the Chaillu Massif (coll. J.J. de Wilde c.s. 10382). It grew along an exploitation track where both parent species were quite common. The leaf blades of *B. clypeifolia* (coll. J.J. de Wilde c.s. 10381) were large (± 15-20 cm long), with a distinctly acuminate apex and a unicolourous, glabrous and smooth upper surface. The petioles were long, about 20 cm, and had no or very few long hairs. The leaf blades of *B. lacunosa* (coll. J.J. de Wilde c.s. 10380) were much smaller (± 5-9 cm long), with an acute to slightly acuminate apex and a bullate, hairy upper surface with a distinct dark spot in the centre. The petioles were densely hirsute and short in young leaves, about 5-10 cm, but much longer, up to 25 cm, in over-mature ones which were prostrate. The putative hybrid plant had large leaf blades (± 15 cm long) with acuminate apexes, a brown-red spot in the centre and a bullate and hairy upper surface. The bullateness was however much less pronounced and the hirsuteness less dense than that on the leaves of true *B. lacunosa*. The petioles were approximately 15 cm long and densely hirsute.

9.1.2 Herbarium collections

The field observations are indicative for the incidence of natural interspecific hybrids. This supports the view that several herbarium specimens that do not fit the description of any species known so far, and moreover show more or less intermediate characters, might well represent natural hybrids.

The collection J.J. de Wilde c.s. 9642B probably represents the hybrid discussed above: *B. clypeifolia x lacunosa*. It was collected in the same area (possibly even in the same spot) as the collection mentioned above, and both parent plants were collected in the direct vicinity (coll. J.J. de Wilde c.s. 9642A and 9641 respectively). It shows the same characteristic moderate bullateness, large leaf blades with a dark spot in the centre, and hirsute, long petioles.

In the Chaillu Massif aberrant specimens were collected (Breteler c.s. 8070), which I suppose are *B. lacunosa x B. scutulum*, although neither of the two putative parent species was collected along with the supposed hybrid. The field notes state that the leaves were bullate, although this character has been lost almost completely during the drying process. Bullateness is characteristic for *B. lacunosa*, the only bullate-leaved species in this area. The ovary is hirsute and unwinged, characters which both point to either of the two proposed parent species. The leaves are broadly elliptic to circular with a distinctly rounded to blunt apex, a dentate margin and no hairs on the upper surface. The leaf blades of *B. lacunosa* are sometimes as round as these, but never glabrous above. Also the more coarsely dentate, not denticulate, margin points to affinity with, and not to true, *B. lacunosa*. The only species occurring in the area likely to be the other parent is *B. scutulum*, because this species has blunt to acute leaf blade apices (at least in the Chaillu Massif, see note below the species treatment).

So far only hybrids between species belonging to the section *Scutobegonia* have been mentioned here. Indeed no presumed natural hybrids between two species of the section *Loasibegonia* were detected in herbarium collections (but artificial hybrids do exist, see next paragraph). However, two presumed intersectional hybrids, i.e. between a species of the section *Scutobegonia* and one of the section *Loasibegonia*, were located. The first one concerns a hybrid, possibly *B. mildbraedii x scutifolia*, from the Bélinga area in Gabon. The specimens (Breteler & de Wilde 584A) show leaf blades with the shape of those of broad-leaved forms of *B. scutifolia* but with a more prominent tertiary nervation, which is characteristic for the section *Scutobegonia*. Moreover, the ovary is obovate and has obovate wings which also points to that section as it is not at all characteristic for *B. scutifolia*. Both assumed parents do sometimes grow closely together in the Bélinga area (pers. comm. J. Wieringa) and judging from the characters mentioned, the only likely second candidate occurring in the area is *B. mildbraedii*.

A second presumed intersectional hybrid has been collected in Nigeria (coll.

Olorunfemi c.s. FHI 76333). It has both peltate and non-peltate leaves, a large broadly obtriangular fruit, and a female flower which looks like that of *B. ciliobracteata*. However, the label notes yellow flowers and, moreover, the tertiary nervation is very weak or even not visible while the consistence of the petiole seems to be juicy. True *B. ciliobracteata* should have white flowers, distinct tertiary nerves and firm petioles. Therefore, a second parent from the section *Loasibegonia* is suggested. Of the few representatives occurring in the area *B. quadrialata* seems the most likely one.

In the greenhouse at Wageningen we grow a plant which was collected in the Crystal Mountains, Gabon. It probably represents an intersectional hybrid between a species of the section *Loasibegonia* and one of the closely related section *Filicibegonia*. The aspect of the plant is hairy, pointing to *B. elatostemmoides* of the latter section and which is fairly common in the region. The plant has flowers with pale yellow perianth segments while the female flowers have the structure of those occurring in the section *Filicibegonia*. They drop early and, although selfing was tried often, never set seed. The second parent for this apparently sterile hybrid may possibly be *B. quadrialata*.

9.2 Artificial hybrids

Many species of the two sections dealt with here have beautiful yellow flowers. The yellow colour is often deep golden and has attracted the attention of plant breeders. At the Department of Horticulture and at the Department of Plant Taxonomy, both in Wageningen, many serious attempts have been made to incorporate this yellow colour in other begonias but up till now all of them have failed (pers. comm. prof. Doorenbos and de Wilde). Hybridisation with species from other sections has been successful in several instances but generally such hybrids have white or pink flowers. Only once a hybrid has been produced with a quite unrelated species which yielded orange flowers (*Begonia* 'Mary Deane', see below). The yellow flower colour seems to be of recessive nature.

There are seven reported hybrids of which at least one parent originated from the section *Loasibegonia*. No artificial hybrids have been recorded involving a species from the section *Scutobegonia*, presumably because they are rarely encountered in cultivation. All cultivars are registered by the official registration office linked to the American Begonia Society and they were assigned a number and an official cultivar name.

No 393: *Begonia* 'Ona-Mae' (*B. violaefolia* A.DC. x *B. prismatocarpa* W.J. Hooker), The Begonian 41: 74 (1974).

No 451: *Begonia* 'Buttercup' (*B. prismatocarpa* W.J. Hooker x *B. ficicola* Irmscher), The Begonian 42: 220 (1975).

No 456: *Begonia* 'Pink Lemonade' (*B.* 'Pearlii' x *B. staudtii* Gilg var. *dispersipilosa* Irmscher), The Begonian 42: 221 (1975).

No 457: *Begonia* 'Frosty Knight' (*B.* 'Pearlii' x *B. staudtii* Gilg), The Begonian 42: 221 (1975).

No 523: *Begonia* 'Gold Coast' (*B. prismatocarpa* W.J. Hooker x *B. staudtii* Gilg var. *dispersipilosa* Irmscher), The Begonian 43: 169 (1976).

No 704: *Begonia* 'Pink Chaser' ((*B. solananthera* A.DC. x *B. prismatocarpa* W.J. Hooker) x *B. socotrana* Hook.f.), The Begonian 46: 20 (1979).

No 848: *Begonia* 'Mary Deane' (*B. ficicola* Irmscher x *B. crispula* Yü ex Irmscher), The Begonian 49: 158 (1982).

B. 'Buttercup' and *B.* 'Gold Coast' are very similar and they were compared in detail by Seitner (1978). The same author published an extensive description and fine drawings of the latter hybrid (Seitner, 1977b).

At the Department of Plant Taxonomy at Wageningen the hybrid *B. microsperma* Warb. x *staudtii* Gilg (both of the section *Loasibegonia*) was produced. Ten female flowers of *B. microsperma* were pollinated with pollen of *B. staudtii*. Only one of them developed into a mature fruit. It yielded only 4 viable seeds which all germinated after 36 days. The resulting hybrid plants were quite uniform and intermediate between the two parent plants in having narrowly winged ovaries and leaf blades with intermediate bullateness and hirsuteness. Selfing of these plants, which flowered excessively, led to abundant production of seeds. The second generation plants flowered abundantly and were also markedly uniform and identical to plants of the first generation. We would have expected them to show a range of intermediate states between the two original parent plants.

10 Ecology, cultivation and floral biology

10.1 Ecology

Most of the 40 species of the sections *Loasibegonia* and *Scutobegonia* inhabit primary and old secondary rain forest of the wetter type of the Guineo-Congolian lowland rain forest (White, 1983). In general the species thrive in a climate with an annual precipitation of (1000–)1500–3500(–6000) mm and a dry period of 0–4(–5) months. Some species that are more tolerant to a somewhat drier condition, like *B. quadrialata*, also occur in the drier types of this vegetation in several western African countries. Few taxa, viz. *B. pulcherrima*, *B. schaeferi*, *B. zairensis* var. *montana* and *B. quadrialata* subsp. *nimbaensis*, grow in Afromontane forest. In general, most of the species occur in the areas with the highest amounts of rainfall in tropical Africa. Two areas can be mentioned in particular. The first is the western Cameroon mountain region with an annual precipitation of 2000–3000 mm and up to 6000 mm and more on the slopes of Mount Cameroon (van der Zon, 1992). In this region 15 species are found. A second area is the Crystal Mountains, the most humid region of Gabon with an annual precipitation of 1800–3000 mm (Barret, 1983), which harbours 16 species. A conspicuous number of species grows on hills. These are usually more humid than the surrounding lowland, because of the prevailing clouds, and orographic precipitation.

Beside their preference for moist habitats, the species are always encountered in shaded habitats, often even in deep shade. Measurements of the light intensity in several *Begonia* populations in Gabon showed PFD (Photon Flux Density) values of 5–15 μmol $m^{-2}s^{-1}$. These values are comparable to those measured in a forest in Costa Rica and they comprise only around 0.5% of the light reaching the canopy (Lee, 1983). Many species are strongly hydrophilous and may be found along small streams with fast running water or near waterfalls. Although the habitat of such plants is shady, the shade is not always very deep as along streams and waterfalls often some indirect sunlight is permitted to enter. Other species favour more or less level, clayey soils in the undergrowth of the forest, e.g. *B. heterochroma* , *B. susaniae* and *B. lacunosa*. This habitat is characterized by very deep shade.

All species concerned are terrestrial, but sometimes plants were encountered at the base of mossy tree trunks (rarely as high as 2 m above the ground level). Analyses of soil samples taken from several localities in Gabon showed pH values of 4.2–4.5 (Kroon, 1991), which is comparatively low. The Mg-content of the soil, which is clayey in appearance, is very low and varies between 31 and 170 mg/kg dry matter (Kroon, 1991).

During a field trip to Gabon in 1991, it was observed that often several *Begonia* species grow together on the same site. Not seldom one or more species of the section *Filicibegonia* were present besides those of the sections dealt with at present. Several herbarium labels accompanying specimens from Zaire corroborate this co-occurrence. The sympatric occurrence of several species was also mentioned by Arends (1992: 172–173). In his case it even concerned closely related species. In our case sister species were generally not found to grow side by side (see also chapter 13). In Gabon a comparatively large number of *Acanthaceae* often grew in the vicinity of the species treated here. In the Crystal Mountains this often concerned *Physacanthus nematosiphon* (Lindau) Rendle & Britton. Among other *Acanthaceae* which co-occur with the *Begonia* species are to be mentioned: *Dischistocalyx strobilinus* C.B. Clarke, *Justicia laxa* T. Anderson, *Physacanthus batanganus* (G. Braun & Schumann) Lindau, *Staurogyne letestuana* Benoist and *Stenandriopsis talbotii* (S. Moore) Heine. Species of the genus *Dorstenia* (*Moraceae*) are also often found associated with terrestrial begonias (pers. comm. J. Wieringa).

10.1.1 Cultivation

The conditions of the natural environment generally supplies important indications about how to cultivate the species. It the greenhouse of the Department of Plant Taxonomy, Wageningen, the species treated in this study are placed in glass enclosures to ensure permanent humid conditions. Extra screening to prevent sunburn of the leaves is essential during sunny weather in summer. The potting medium proved to be an important element for successful cultivation of the plants. Ordinary 'Begonia-soil' leads to bleaching of the leaves, probably because the pH is too high. At Wageningen good results were obtained with a composition of 30% river clay, 30% peat dust, 30% black peat and 10% Swedish Sphagnum, without the addition of any chalk or fertilizer. The plants can also be grown indoors in a simple, small plastic container. More tips for the cultivation of several species are to be found in various issues of The Begonian. Several important contributions are cited below relevant species in the taxonomic treatment (chapters 16 & 17). In general, American begonia growers use a higher percentage of *Sphagnum*.

10.2 Floral biology

10.2.1 Flowering

Individual populations of the species treated here flower during distinct periods. J. Wieringa studied 7 populations belonging to 6 species of the section *Scutobegonia* (Wieringa, 1991) in the Crystal Mountains during a period of 5 months (15 December – 15 May). He noted flowering periods of 3 to 4 or more months. After flowering the plants bear fruits and on 2 occasions he observed a second flowering about 1.5 months later. This second flowering was, however, much less intense and comprised only a few individuals in each population. Most species seem to flower during the wet season. In western Central Africa this season covers roughly the period between mid-September and December, after which flowering usually ceases during a brief slightly drier period, and starts again in February through May. Generally, the species flower twice a year.

Observations in the greenhouse of the Department of Plant Taxonomy, Wageningen, revealed that the flowers of several species show sleeping movements. They open and close on specific times of the day. At night the flowers are generally closed. The same observation was made by Wieringa (1991) in wild populations. He noted that this phenomenon occurred only within species of the section *Scutobegonia*, not in those of the sections *Filicibegonia* and *Tetraphila*, where flowers remain open. During very cloudy days with rain in the morning the flowers even remained closed throughout the day. In 'normal' weather the flowers of *B. clypeifolia*, *B. erectocaulis* and *B. hirsutula* closed about noon. Those of *B. susaniae* generally stayed open until late in the afternoon.

A single inflorescence generally consists of 2-4 male flowers and a terminal female one. Starting with the male flowers, they subsequently reach anthesis with intervals of several days. Each individual flower lasts for about 5-10 days, depending on the species (observations made by de Wilde and myself in the greenhouse at Wageningen).

10.2.2 Pollination

Very few observations on the pollination of *Begonia* flowers have been made. The most comprehensive reports are those of Seitner (1976 & 1977a). Without exception he describes pollination of *Begonia* flowers by insects but the observations are almost all made in unnatural habitats. As virtually no *Begonia* species produces nectar, the pollinating insects are probably attracted by the nutrition offered by the pollen itself. How pollination takes place in species of the sections *Loasibegonia* and *Scutobegonia* is not easy to establish. Several features point to insect pollination. First of all the existence of sleeping movements mentioned above would hinder wind pollination during parts of the day and the night and does not seem very functional in that case. Secondly, many species have a distinct red spot at the base of the upper perianth segment which might well attract insects. Also the fact that the flowers of about half of the species are situated at the base of the plants, below the leaf blades, does not seem to be a character favouring wind pollination. In that case one would expect the flowers to be well elevated above the plant in order to catch some wind. Doubts about the presence of wind in the sheltered habitat of the forest floor may be expressed but on the other hand, a single gale wind or storm would suffice. Such winds are not rare in the areas where most of the species thrive. Also the shape and the bearing of the androecium, with all the anther slits directed upwards, towards the upper perianth segment, is a feature in favour of the insect pollination theory. A final argument in favour of this theory is that in general the pollen is not released easily by fresh anthers. Wind will probably not be effective in dislodging pollen while insects probably are. On the other hand, shriveled male flowers often remain attached to the plant, also in natural conditions. These release their pollen much easier and at this stage wind might still be the vector for pollen transport.

The main problem is that hard evidence, undisputable field observations, are generally lacking. During his field work in Gabon, J. Wieringa spent, with commendable patience, many hours beside populations of several species of the section *Scutobegonia* in order to detect their pollinators. He observed several times the hasty call of a hoverfly (*Syrphidae*) but no real visits. The same behaviour was noted for a small bee (*Apoidae*). On the other hand he did observe on several occasions a leaf beetle (*Chrysomelidea, Altinae*) on the plants and also on the flowers. It was eating from the anthers and sometimes from styles. Another leaf beetle (*Chrysomelidea, Galerucinae*) was collected by de Wilde, also while eating from the anthers of a member of the section *Scutobegonia*. These beetles are known to be pollen collectors but they are not very specific as they were observed on flowering grasses as well. It still remains doubtful whether these beetles are really responsible for pollination in this group of *Begonia* species because they were observed very infrequently and, moreover, they damage the anthers considerably. In herbarium collections such damage was encountered only exceptionally, once more pointing to infrequent visits. The beetle collected by de Wilde was checked on adhering pollen but none was found. Finally, the fact that most of the fruits of herbarium specimens contain viable seed would require frequent visits.

Bees as vectors for pollination of *B. longipetiolata* Gilg (sect. *Tetraphila*) were observed by de Wilde and myself in Gabon (Arends, 1992: 170).

In conclusion, the observations discussed above seem to point to insect pollination of species of the sections *Loasibegonia* and *Scutobegonia*, possibly by leafbeetles, but unambiguous observations are still wanting.

Self-pollination of plants in the greenhouse at the Department of Plant Taxonomy, Wageningen, usually does not lead to the production of mature fruits and viable seeds. The young fruits drop early. I therefore suppose that a self-incompatibility system is present in the majority of the species. Species with poor seed set after self-pollination are: *B. dewildei*, *B. lacunosa*, *B. microsperma*, *B. prismatocarpa*, *B. quadrialata*, *B. scutifolia*, *B. letouzeyi* and *B. vankerckhovenii*. On the other hand, the result of selfing of a few other species proved to be somewhat more successful. These are: *B. clypeifolia*, *B. ferramica* and *B. staudtii*.

10.2.3 Fruiting and seed dispersal

The ripening process of the non-dehiscent fruits of species from the sections *Loasibegonia* and *Scutobegonia* takes a long time. Observation at Wageningen on the fruits of 3 species of the section *Loasibegonia*, viz. *B. microsperma*, *B. staudtii* and *B. scutifolia*, showed that they remain on the plant for about 3 months. After this period the fruits desiccate from the top downwards in about a week, the wall becoming papery and pale brown. The wall now disintegrates exposing the seeds. The seeds are often held tightly by the dried placenta tissue and are difficult to remove without damaging them. In natural conditions the fruit remains on the plant, disintegrates further, and releases the seeds slowly. In cultivation, the fruits are best gathered when the apex starts to desiccate. The seeds are ripe by then and can still be removed fairly easily from the soft tissue.

Fruits from species of the section *Scutobegonia* do not desiccate but remain more or less juicy and finally disintegrate by rotting of the ovary wall. At Wageningen, the fruits of *B. ferramica* and *B. vankerckhovenii* remained on the plant for about 4 months before disintegration. Field observations made by J. Wieringa (Wieringa, 1991) showed that the fruits of *B. susaniae* do not disintegrate for at least 2.5 months while those of *B. hirsutula* take 3 months to ripen. The fruits of *B. scutulum* hold the record so far. They remained on the plant during the whole observation period of 5 months and still were not ripe then. This species probably flowers and fruits only once a year.

The fruits of species of the section *Loasibegonia* generally remain in an erect position. Their peduncle remains erect or sometimes it slants outwards but it is always straight. The majority of the species of the section *Scutobegonia* have fruits which incline towards the substrate. This is caused by a curving of both the peduncle and the pedicel. The pedicel below the fruits of some species of this section, those with comparatively long peduncles, does not curve. The peduncle, however, does curve and thus pulls the fruit back in between the leaves or presses it against the substrate when the plant grows on a rock face.

From the above it will be clear that the seeds of all species treated here are shattered close to the parent plant. Dispersal over long distances will probably not occur, although seeds might be transported by the water of streams in the neighbourhood of which a number of the species often grow. Despite of the fact that the seeds do not float, they are small enough to be carried along by fast running water. Other possibilities of seed transportation may be through water running along the soil surface after heavy rains, or with mud sticking to the legs or fur of passing animals.

11 Phylogeny

11.1 Phylogeny, natural classification and nomenclature

Taxonomy is basically dealing with the classification of specimens. Specimens are being assigned to species, the basic taxonomic category. Species are grouped into higher categories like sections or genera, etc. Taxonomists strive after a stable system of classification. It is generally believed that the more 'natural' this system is, the more stable it will prove to be, although some moderation should be brought in (see below). Most taxonomists understand by a natural system some kind of genealogical one. Darwin (1859) already called for the development of such a system. In the 19th and first half of the 20th century classical taxonomists were elaborating the classification system by extensive comparison and evaluation of characters trying to find out which characters were more important than others. As the latter aspect is often one of personal preference, the ultimate goal, a single stable system, was seldom reached. Numerical methods (e.g. Sokal & Sneath, 1963) were developed in order to avoid matters of personal preference as much as possible and to elaborate a stable classification system based on phenetic trees resulting from overall similarity calculations. Phenetic trees do not necessarily reflect the evolution of a group, but numerical taxonomists argued that, as evolution can never be completely reconstructed, the stability of a classification can be secured by the application of numerical methods. Numerical methods are, however, applied by some as a method to reconstruct genuine phylogenetic relationships. To date, most pheneticists admit that phylogenetic methods (see below) are better suited for this purpose. However, they stress that, in comparison with phylogenetic methods, phenetic methods are less subjective and lead to a more stable scheme of 'relationships', and hence to a more stable classification. Hennig (1950, 1966) developed a method for phylogenetic reconstruction based on the evolutionary process of inheritance of character states. Only shared apomorphic (advanced) character states are regarded as indicative for phylogenetic relationships. The method was further elaborated and for example Wiley (1981) may be used as a guideline through both principles and methods. Being based directly on the principles of evolution, this method is to be preferred above phenetic ones, when a scheme depicting genealogical relationships is the goal. The stability of the 'natural' classification should be based on such relationships, hence on the results of phylogenetic methods, because it is the only classification with a sound theoretical basis (Mayr, 1964; Kornet, 1988).

The next step is to translate the phylogenetic tree, the cladogram (two terms treated in the present study as full synonyms), into taxa which should be given a formal name. This step is something completely different from phylogenetic research itself. In this phase it is perhaps even more important that not the genealogical system but, above all, nomenclature should be stable. Arguments concerning practical convenience now enter the scene. The need for a convenient and stable nomenclature usually does not tally with the direct transcription of a phylogenetic scheme into nomenclatorial propositions, as is the case in pure phylogenetic taxonomy (Wiley, 1981: 198 ff.). De Queiroz & Gauthier (1992) even show that striving after a 1:1 relation of phylogeny and nomenclature must lead to the introduction of a nomenclature different from the Linnaean system. The major question now seems to be *why* should there be a 1:1 relation and whether the arguments in favour are sufficiently serious to weigh against the enormous changes this acceptance would bring about? I think the arguments in favour are not strong enough. Particularly since the new nomenclature will not lead to a greater stability as the development of the 'phylogenetic tree of life' will be a process still incorporating many controversal opinions. Furthermore, it is argued below that the problem can be solved by the acceptance of slightly less 'natural' taxa.

The solution involves the acceptance that each taxon with a formal name should not necessarily be strictly monophyletic. When the phylogenetic tree given in fig. 11.1 represents the relationships between the species belonging at present to 2 different genera, A and B, the following 2 solutions can be chosen when strict phylogenetic taxonomy is applied. **1.** Next to genus B, 5 other monotypic genera are to be erected in order to accommodate each of the species 1–5 (following the sequencing convention, Wiley, 1981: 206). **2.** The genera A and B are to be merged into a single genus. Both options necessitate many nomenclatorial changes and strict application of phylogenetic taxonomy therefore does not lead to nomenclatorial stability. I am convinced that a certain kind of paraphyletic cladon, one in which a single lineage is lacking, can be granted a separate taxonomic status (as a section, genus etc.). Such paraphyletic taxa are both stable and, within certain limits, natural. So, in the case of fig. 11.1, both genera A and B can simply be upheld, *knowing* that A is paraphyletic due to the lack of a single terminal lineage. Especially when many synapomorphies are present on node x this solution is far more sensible and convenient to those using taxonomy for practical purposes, than either of the other two solutions would be. Up to certain levels, nomenclature should serve practical purposes, not scientific ones. Not accepting such paraphyletic taxa in nomenclature will undoubtedly lead to either a rapidly increasing number of new names or excessive lumping of genera. Neither is to be encouraged because the scientific advantages do not counterbalance the practical loads. Other kinds of paraphyletic taxa and any polyphyletic ones should, however, always be avoided.

Recently Kornet (1993) showed that phylosophic deduction may lead to the conclusion that most species are of a paraphyletic nature. Although they plead for a monophyletic nature of higher taxa, it seems to me that when a species, always regarded as a basic and strictly monophyletic entity, appears to be paraphyletic, it seems unreasonable to cling to the idea of a strictly monophyletic system of nomenclature.

11.2 Monophyly of the sections *Loasibegonia* and *Scutobegonia*

An important question one should adress before starting a phylogenetic analysis concerns the monophyletic nature of the group. Phylogenetic methods necessitate to include all extant descendants of an ancestral species in order to unravel the correct phylogenetic interrelationships. Synapomorphic character states are generally believed to indicate monophyly. These are not directly at hand for both sections studied here. Moreover, their separate monophyletic origin is in doubt (see chapter 2 and 3). On the other hand, the monophyletic nature of the 2 sections as a whole is likely on the basis of the following arguments:

1. All species possess a non-dehiscent fruit. This is quite rare within *Begoniaceae*. Only the African sections *Mezierea* Gaud. and *Squamibegonia* Warb. show this character as well. These sections, however, are very different in many other respects and they are not believed to represent close relatives (Reitsma, 1984; van den Berg, 1985; de Lange & Bouman, 1992).

2. The inflorescence can be considered as a strongly contracted and reduced monochasium. Dichasial inflorescences are the rule within the family. The reduced axes of the inflorescence and the number of bracts (see also paragraph 5.4) can be regarded as a derived complex. This type of inflorescence is present in several other sections of *Begoniaceae*. In Africa it is found in the section *Filicibegonia*, one of the possible sistergroups. This state, therefore, is not a strong indication of monophyly but it does point to the derived nature of the sections.

3. The same accounts for the reduction in the number of perianth segments to 2 in both male and female flowers.

4. The frequent occurrence of yellow-coloured perianth segments, otherwise so rare within the family (see also paragraph 5.5), seems to present a nice synapomorphy. But, as both white- and yellow-flowered species are present within the group studied, this cannot serve as a synapomorphy either.

5. The seeds of most African species were investigated by de Lange & Bouman (1992). These authors show that the 2 sections as a whole are characterized by a distinct seed micromorphology which, at the same time, is quite unique within the family. As such it serves as a synapomorphy.

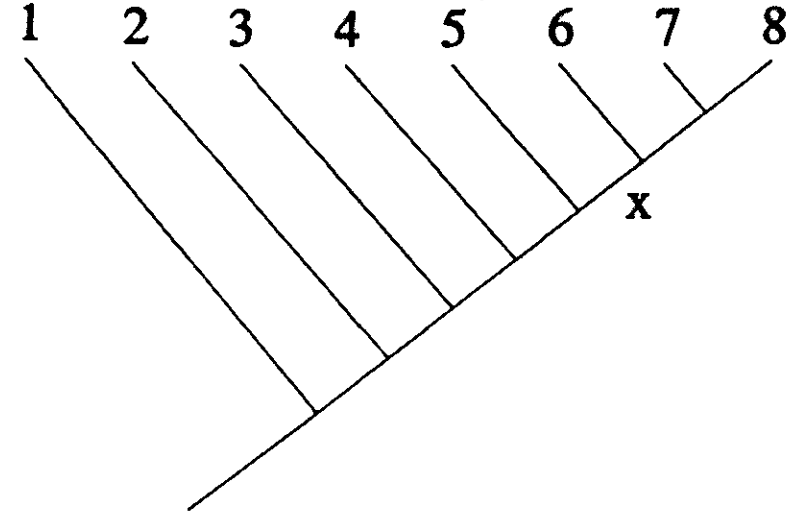

Figure 11.1. Hypothetical cladogram for eight species presently belonging to the genera A and B.

6. Pollen morphology data show that the 2 sections have their own pollen type, at least within the African species of *Begonia* (van den Berg, 1985).

7. Finally, the rhizomatous growth habit is to be mentioned. In Africa only a group of six species around *B. squamulosa* Hook.f. in the section *Tetraphila* are truly rhizomatous, while the strange stems with clinging roots of the monotypic section *Cristasemen* are probably also of rhizomatous origin. Although this state is therefore not truly a uniquely shared one, it does point to the uniformity of the group as a whole. Anticipating on the results of the phylogenetic analyses, which show that the section *Filicibegonia* with erect stems is the most likely direct sistergroup, the rhizomatous nature may be regarded as a synapomorphic feature.

The arguments given above provide sufficient evidence to accept the 2 sections as a monophyletic group.

11.3 Outgroup

The question about monophyly is often followed by the choice of the outgroup. In order to select an outgroup, all sections of *Begonia* were screened using Baranov & Barkley (1974) and Smith et al. (1986). No extra-African sections seemed to represent possible outgroups after this first screening. Of the African ones, the sections *Cristasemen* and *Filicibegonia* appeared to be the two most likely candidates. Both sections have male and female flowers with two perianth segments. The monotypic section *Cristasemen* has in addition yellow flowers and a rhizomatous habit, but the styles and the inflorescence are completely different (see de Wilde, 1985a). The inflorescence of *Filicibegonia* is of the same type as that of the ingroup and the styles are, though not identical, also more or less similar, but the stem is erect. Seed and pollen micromorphological features point to a slight preference for the section *Filicibegonia* as the outgroup, but this preference could not be substantiated directly from anatomical features of the leaves and ovaries. Therefore, a choice is hard to make and the option to take along both possible outgroups in the analyses was preferred. A decision upon which is the closest relative of the ingroup can thus be postponed and be made conditional on the outcomes of the phylogenetic analysis.

Although no phylogenetic analysis has been performed previously, the section *Filicibegonia* does most likely represent a monophyletic group based on the combined occurrence of (in sequence of importance) a unique shape of the stigma, a distinct seed type (de Lange & Bouman, 1992), a zygomorphic androecium, an inflorescence consisting of a contracted cincinnal monochasium, both male and female flowers with two perianth segments and the absence of tubers.

11.4 Polytypism

Polytypism is the occurrence of more than one homologous character state within a taxonomic unit used in a phylogenetic analysis. (It should be noted that the co-occurrence of two different states within a single specimen is not regarded as polytypism in the strict sense. The latter situation generally indicates that the two states are non-homologous and should thus be treated as two distinct characters.) Transforming a polytypic situation into codes in a datamatrix can be done in several ways. The first solution, and the one generally chosen (see e.g. van Welzen, 1989; Adema, 1991), is to create a separate character state to accommodate the polytypic situation. The second solution is to create a separate character for each character state. Both solutions are illustrated in fig. 11.2. The polymorphic state is sometimes coded in the matrix as missing. Nixon & Davis (1991), however, point out that this action leads to incorrect tree topologies and they emphasize that polymorphic terminal taxa should be subdivided into their monomorphic subunits. When a terminal taxon shows polytypism in several characters, their solution leads to a rapid increase of terminal taxa and can be very time consuming. Moreover, when a particular combination of polymorphic states of several characters has not been encountered, this particular subunit is not entered in the data matrix. It might well be that this combination does exist in nature but has not been collected so far. A situation not unlikely, especially when dealing with tropical taxa of which only little material is available, as is the case in the present study. The solution proposed below automatically includes all different combinations of polymorphic character states within an undivided terminal taxon.

The line of reasoning is based on the following presupposition. When there are three taxa, one of which possesses the plesiomorphic, one the apomorphic and one both the plesiomorphic and the apomorphic character state, the most parsimonious explanation for the existence of this situation is, that the taxon possessing the apomorphic state evolved from a population of the polytypic taxon already possessing this apomorphy (see fig. 11.3).

taxon	X	Y	Z
char. state	a	a + b	b

solution 1: create separate state for each polytypic situation
state 1 = a
state 2 = a + b
state 3 = b

solution 2: create separate character for each character state
character 1: state 1 = a present
state 2 = a not present
character 2: state 1 = b present
state 2 = b not present

Figure 11.2. Two solutions to deal with a polytypic situation.

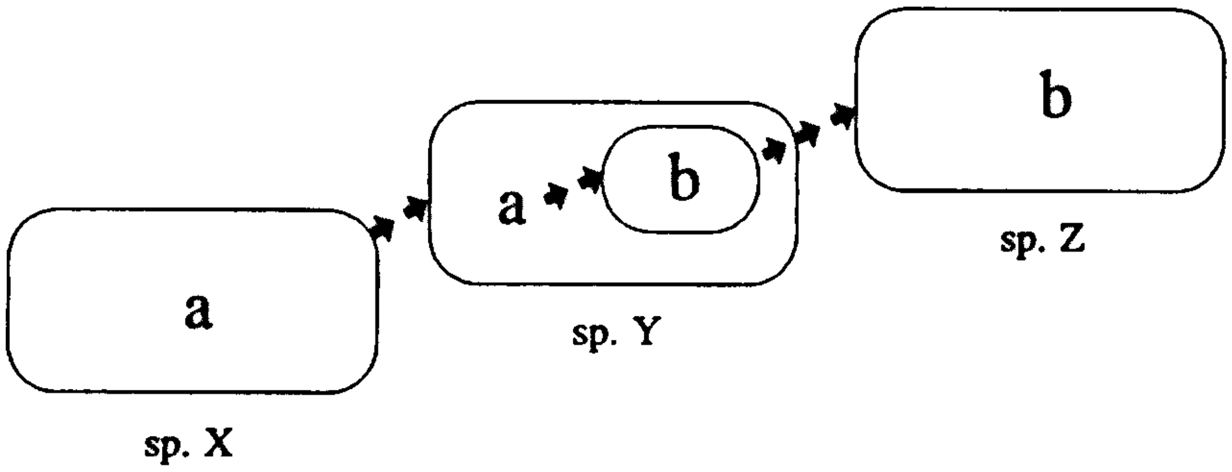

Figure 11.3. Most parsimonous explanation of the phylogeny of three species, one of which is polytypic for a given character.

There is one major disadvantage of the first solution. It does not 'recognize' the synapomorphic state b of the taxa Y and Z in fig. 11.2. This is a serious shortcoming. The different states are disconnected by the delimitation of three separate states. That is, when this character is treated unordered. In the ordered situation the synapomorphy *is* recognized and the solution based on the presupposition above is always the most parsimonious one. The condition that the polytypic state is coded as intermediate between the 2 others must then be met with. When using the second solution for the coding of a polytypic situation, the synapomorphy is recognized as well, without the need to order the character states. But beware, there is a snake in the grass. Both the first solution in the ordered situation and the second solution now need 2 steps to explain the character distribution, where the presupposition only needs one. Unperceivably, a weighting factor of 2 has been attributed to the character. The polytypic character, which is often regarded as not a very 'strong' one, has become twice as important as any other. To adjust for this unwanted situation we can allot the polytypic character a weighting factor of 0.5 or every other character a weighting factor of 2. (N.B.: The programme Hennig86 does not accept fractional numbers!)

Up till now we have discussed only a simple case of polytypism. A slightly more complex situation might occur, for example one as outlined in fig. 11.4. In this situation the first solution, defining intermediate character states and ordering the character, is not possible, at least not within any available MS-DOS computer programme. (The most recent MacIntosh version of PAUP is able to handle these situations.) The second solution, creating different characters for each state, still is. On ethic grounds one might prefer to use the first solution when possible, because here all homologous character states are still accommodated within a single character. This adequately shows the importance of the

taxon	V	W	X	Y	Z
char. state	a	a+d	b	a+b	c

Figure 11.4. A more complicated polytypic situation.

correct use of the concept of homology in defining a character and its states. It is generally stressed that all states within a character should be homologous. This is true, but it is perhaps equally important to incorporate *all* homologous states within a character. If not, unperceivably, a priori weighting might enter the analysis.

The polytypic situations above are still comparatively simple. One can imagine even more complex situations. For example, a variable and widespread taxon might have given rise to several descendant taxa which did not inherit the same character set. When the variability of the widespread taxon is for example geographically correlated, we can presume that one descendant taxon, originating from a vicariance event, receives characters different from those of a second descendant which are again different from those of a third. In such a situation, where a comparatively primitive but highly variable and widespread taxon is involved, the solution of Nixon & Davis (1991) might well prove to be better than the one proposed here. The phylogenetic trees will then probably be slightly better resolved, where the solution proposed here will lead to polytomies sooner. I decided to put up with this weakness and avoid the not only time-consuming but probably also subjective action of subdividing each polytypic taxon. Within the present data polytypic characters are treated as ordered and given a weight of 0.5 when possible. In more complex situations separate characters are created to accommodate each state and these are all given a weight of 0.5.

11.5 Characters and data

The use of quantitative characters in a cladistic analysis poses some problems (Chappill, 1989) and is sometimes even strongly dissuaded (Pimentel & Riggins, 1987). Cladistic methods deal with state changes between discrete character states. Quantitative characters are often more or less continuous and therefore difficult to transform into discrete states. According to those dissuading the use of quantitative characters, subjective elements and 'noisy' or redundant information enter the data when such characters are used. However, the rigorous skipping of all quantitative characters should in its turn be regarded as a highly subjective action dictated by the nature of the method itself, and not by the urge to be objective. Or, to quote Chappill l.c.: 'This would seem to suggest that the discrete characters produced from continuous ones have no basis in reality, a view that is rejected here'. When a quantitative character does seem to indicate phylogenetic relationships, one should somehow try to incorporate it in the cladistic dataset. In the present study histograms were produced for each quantitative character. True gaps or otherwise classes with a frequency distinctly lower than that of the adjacent classes were located and regarded as the boundaries between classes. Chappill's l.c. attributes for an ideal method to transform continuous data into discrete states were applied, especially the third one (the number of states produced should be proportional to the variability of the character), in the final decision about the class sizes and boundaries. The method is thus similar to simple gap-coding (Mickevich & Johnson, 1976). One particular problem is that plants grow. Hence, the height of the plant, length of the petiole or pedicel etc. increases with age or with the process of flowering. To overcome this problem, classes were sometimes circumscribed with an upper limit only, as for example 'pedicel up to 15 mm long'. This approach is also applied by e.g. van Welzen (1989) and Schot (1991) and seems to work well.

The cladistic analyses were performed at the species level because in many cases only a single subspecies of a species could be studied in detail. Living or alcohol material, essential for anatomical observations, was generally available for only one out of two or three subspecies. The characters used in the cladistic analyses are listed in table 11.1. As many characters as possible were selected. The only criterion was the preferably non-polytypic expression of character states within the species and the condition that both character states of a character occur within more than a single species. This resulted in a selection of 132 characters, 76 macromorphological ones, 32 related to the leaf anatomical properties, 17 to those of the anatomy of ovary and style, and 7 seed micromorphological characters. The characters were discussed in the previous chapters. The datamatrix is presented in table 11.2.

11.6 A cladistic analysis

All analyses were performed using the computer program Hennig86 (Farris, 1988). When not indicated otherwise, the commands 'mhennig*' and 'bb*' (tree construction by adding terminals in several different sequences in combination with extensive branch-swapping) were applied to the data and all characters were treated as unordered (except for the polytypic ones, see table 11.1).

11.6.1 Primary analysis

A first analysis was run using the combined sections *Cristasemen* and *Filicibegonia* as the outgroup. The single tree had a length of 1854, a ci (consistency index) of 0.20 and a ri (retention index) of 0.49. The general topology was as given in fig. 11.5. *B. ferramica* is regarded as the most primitive species of the ingroup after which the ingroup is divided into two more or less equal parts which are called here, anticipating on the conclusions, the 'Loasibegonia' tail and 'Scutobegonia' tail.

A second analysis was run using only section *Filicibegonia* as the outgroup. This yielded two trees with length = 1791, ci = 0.21 and ri = 0.50. The general topology being a division at the very base of the ingroup into two groups ('Loasibegonia' and 'Scutobegonia').

A third analysis using only section *Cristasemen* as the outgroup yielded two equally parsimonious trees with length = 1742, ci = 0.21 and ri = 0.49. The

Table 11.1. Characters used in the cladistic analyses. The ordered treatment of a polytypic character in every initial analysis is indicated by 'ord.' whereas an initial weight is indicated by 'w = 0.5' (see text and paragraph 11.4).

Macromorphological characters

1. Rhizome branching
(ord., w = 0.5)
1 = not or infrequently
2 = both 1 and 3
3 = frequently

2. Rhizome type
(ord., w = 0.5)
1 = smooth and elongated
2 = both 1 and 3
3 = compact and often knotted

3. Rhizome width
1 = ≤ 3.5 mm
2 = ≤ 6.5 mm
3 = ≤ 9.5 mm

4. Rhizome apical part
1 = not or slightly ascending
2 = ascending to shortly erect
3 = forming a ± distinct stem of 5 cm or more

5. Stipule length
1 = ≤ 5 mm
2 = ≤ 10 mm
3 = more than 10 mm

6. Stipule apex
1 = blunt to acute
2 = acute to acuminate
3 = acuminate to caudate

7. Petiole length
1 = ≤ 7.5 cm
2 = ≤ 15 cm
3 = ≤ 22.5 cm
4 = up to more than 22.5 cm

8. Petiole hirsuteness
1 = (almost) glabrous
2 = sparsely hirsute
3 = sparsely to densely hirsute
4 = densely hirsute

9. Petiole hairs long and wavy
1 = no
2 = yes

10. Petiole hairs short and curly
1 = no
2 = yes

11. Petiole hairs short and stiff
1 = no
2 = yes

12. Petiole indumentum distribution
(ord., w = 0.5)
1 = ± evenly distributed
2 = both 1 and 3
3 = increasing towards blade

13. Petiole consistency
1 = fleshy and firm (cells ± 0.2 mmø)
2 = succulent-juicy (cells ± 0.1 mmø)

14. Leaf blade type
(ord., w = 0.5)
1 = not peltate
2 = both 1 and 3
3 = peltate

15. Petiole insertion
1 = at ≤ 10 mm
2 = at ≤ 30 mm
3 = at ≤ 50 mm
4 = up to more than 50 mm

16. Petiole attachment to leaf blade
1 = without distinct angle
2 = with distinct angle

17. Leaf blade length
1 = ≤ 8 cm
2 = ≤ 16 cm
3 = ≤ 24 cm

18. Leaf blade mean length/width ratio
1 = ≤ 1.5
2 = 1.6 – 2.5
3 = more than 2.5

19. Leaf blade symmetry
1 = ± symmetric or slightly asymmetric
2 = asymmetric to distinctly so

Table 11.1. (continued).

20. Leaf blade apical part falcate
1 = no
2 = yes

21. Leaf blade largest width
1 = below the middle
2 = ± at the middle
3 = above the middle

22. Leaf blade kidney-shaped or slightly falcate (ord., w = 0.5)
1 = no
2 = sometimes
3 = yes

23. Leaf blade apical part
1 = rounded
2 = blunt to acute
3 = blunt to acuminate
4 = acuminate
5 = long acuminate to caudate

24. Leaf blade margin entire (w = 0.5)
1 = no
2 = yes

25. Leaf blade margin denticulate (w = 0.5)
1 = no
2 = yes

26. Leaf blade margin dentate or serrate (w = 0.5)
1 = no
2 = yes

27. Leaf blade margin crenate (w = 0.5)
1 = no
2 = yes

28. Leaf blade margin remotely dentate in apical part
1 = no
2 = yes

29. Leaf blade margin pilosity
1 = glabrous or very sparsely ciliate
2 = glabrous to ciliate
3 = densely ciliate

30. Leaf blade margin with 2-3 hairs in sinus of teeth
1 = no
2 = yes

31. Leaf blade margin inrolled
1 = no
2 = yes

32. Leaf blade margin colour
1 = concolorous with the blade
2 = red

33. Leaf blade position
1 = horizontal
2 = vertical

34. Leaf blade base (when not peltate)
1 = both sides cuneate
2 = slightly unequal: both sides cordate
3 = unequal: one side cuneate, the other rounded to cordate
4 = one side cuneate or rounded to cordate, the other strongly cordate to auriculate

35. Leaf blade nervation
1 = palmate
2 = palmate-pinnate

36. Number of palmate nerves
1 = 5 or less
2 = 5 - 8 (- 9)
3 = (8 -) 9 - 11

37. Stellate scales
1 = absent
2 = present

38. Upper leaf surface smooth (w = 0.5)
1 = no
2 = yes

39. Upper leaf surface rugose (w = 0.5)
1 = no
2 = yes

40. Upper leaf surface bullate with large solitary bullae (w = 0.5)
1 = no
2 = yes

Table 11.1. (continued).

41. Upper leaf surface bullate with small composite bullae
(w = 0.5)
1 = no
2 = yes

42. Upper leaf surface pilosity
1 = glabrous or sparsely hirsute with long hairs
2 = sparsely hirsute with short stiff hairs
3 = hirsute with long hairs

43. Upper leaf surface unicolourous
1 = yes
2 = no

44. Main nerves lower surface
1 = glabrous or sparsely hirsute
2 = sparsely hirsute to hirsute
3 = hirsute to densely so

45. Main nerves lower surface with appressed hairs
1 = no
2 = yes

46. Smaller secondary nerves lower surface
1 = glabrous to sparsely hirsute
2 = hirsute

47. Colour main nerves lower surface
1 = green
2 = usually red

48. Intercalary areas lower leaf surface pilosity
1 = glabrous
2 = hirsute

49. Lower leaf surface colour
1 = pale to medium green
2 = reddish

50. Peduncle branched
1 = no
2 = yes

51. Fruit position
1 = ± erect
2 = ± erect but on a curved peduncle
3 = pendulous

52. Inflorescence position
(ord., w = 0.5)
1 = ± at the base of the plant or on a short peduncle
2 = both 1 and 2
3 = ± at the same level as the leaf blades on a long peduncle

53. Number of male flowers per inflorescence
1 = ≤ 2 (– 3)
2 = ≤ 4 (– 6)

54. Number of female flowers per inflorescence
1 = 1
2 = 1 – 2

55. Bract shape
1 = elliptic to broadly ovate
2 = broadly elliptic to circular
3 = ± circular

56. Bract length
1 = ≤ 3 mm
2 = ≤ 8 mm
3 = ≤ 13 mm

57. Bract colour
1 = green to pale reddish
2 = bright red (to green)

58. Perianth segment colour
(ord., w = 0.5)
1 = white to pink
2 = both 1 and 3
3 = yellow

59. Upper perianth segment with red spot at base
1 = no
2 = (no or) yes

60. Perianth segment pilosity outer surface
(ord., w = 0.5)
1 = glabrous
2 = glabrous to hirsute
3 = hirsute

61. Perianth segment length
1 = ≤ 16 mm
2 = up to more than 16 mm

Table 11.1. (continued).

62. Number of stamens
1 = ≤ 15
2 = ≤ 30
3 = up to more than 30

63. Pedicel of fruit length
1 = ≤ 3.5 mm
2 = ≤ 9 mm
3 = up to more than 9 mm

64. Ovary translucent
1 = no
2 = yes

65. Ovary shape
1 = narrowly oblong to narrowly elliptic
2 = narrowly elliptic to obovate
3 = obovate to shallowly obtriangular-obovate
4 = shallowly to very shallowly obtriangular

66. Ovary and wings in one colour
1 = no
2 = yes

67. Locular part of ovary colour
1 = whitish or pale green
2 = (pale) green to brown
3 = dark brown to red

68. Locular part of ovary length/width ratio
1 = 3 or more
2 = 2 or less

69. Locular part of ovary hairy
1 = no
2 = yes

70. Wings absent
1 = no
2 = yes

71. Wing shape
1 = linear
2 = linear to obovate
3 = broadly obovate to depressed obovate-obtriangular
4 = shallowly to very shallowly obtriangular

72. Wing attachment
(ord., w = 0.5)
1 = all along ovary
2 = both 1 and 3
3 = in apical part

73. Wings curved upwards
1 = no
2 = yes

74. Beak length
1 = ≤ 2.0 mm
2 = up to more than 2.0 mm

75. Stigmatic band slender, elongated
1 = no
2 = yes

76. Stigmatic band twisted
1 = no or up to 1/2 a turn
2 = yes (± 1 turn)

Leaf anatomical characters

77. Leaf thickness
1 = 80 - 205 μm
2 = 210 - 425 μm
3 = 430 - 750 μm
4 = more than 750 μm

78. Epidermal cells adaxial surface thickness
1 = 10 - 60 μm
2 = 65 - 120 μm
3 = 125 - 230 μm

79. Anticlinal walls of epidermal cells zigzag in cross section
1 = no
2 = slightly
3 = yes

80. Convexity of adaxial epidermal cells
1 = flat to shallowly convex (0 - 12 %)
2 = convex (13 - 25 %)
3 = papillate (more than 25 %)

81. Mean thickness palisade parenchyma
1 = 10 - 70 μm
2 = 75 - 170 μm
3 = 175 - 310 μm

82. Shape of palisade parenchyma cells
1 = broadly rectangular
2 = triangular

83. Chloroplast type
1 = large and light-coloured
2 = small and light-coloured
3 = small and dark-coloured

84. Oxallate crystals present
1 = no
2 = yes

85. Number of layers of spongy parenchyma
1 = 1 – 3
2 = 4 – 7

86. Prominence of midrib lower surface
1 = not prominent
2 = slightly prominent
3 = (distinctly) prominent

87. Prominence of smaller secondary nerves lower surface
1 = not prominent
2 = slightly prominent
3 = distinctly prominent

88. Prominence of midrib upper surface
1 = slightly prominent
2 = not prominent
3 = sunken

89. Vascular bundles in midrib
1 = one central bundle
2 = composite, 3 bundles
3 = composite, 5 or more bundles

90. Vascular bundle in midrib on adaxial side present
1 = no
2 = yes

91. Sclerenchyma sheath on adaxial side of bundles in midrib
1 = absent
2 = weakly developed
3 = continuous

92. Sclerenchyma sheath on abaxial side of bundles in midrib
1 = absent
2 = weakly developed
3 = continuous

93. Sclerenchyma sheath around tertiary nerves
1 = absent
2 = weakly developed
3 = all around

94. Multiseriate hairs present
1 = no
2 = yes

95. Uniseriate hairs with multiseriate base present
1 = no
2 = yes

96. Uniseriate hairs present
1 = no
2 = yes

97. Cells of multiseriate hairs with protruding apex
1 = no
2 = yes

98. Cells of non-glandular hairs with cuticula structure
1 = no
2 = yes

99. Minute glandular hairs shape
1 = short and sausage-shaped
2 = long and r-shaped

100. Minute glandular hairs in groups
1 = no
2 = yes

101. Globuliferous glands present
1 = no
2 = yes

102. Glandular hairs on upper surface in depression
1 = no
2 = yes

103. Density of glandular hairs lower surface
1 = 0 – 1 at 320 x 420 μm
2 = 2 – 3 at 320 x 420 μm
3 = 4 – 6 at 320 x 420 μm
4 = > 6 at 320 x 420 μm

104. Hydathodes present
1 = no
2 = yes

Table 11.1. (continued).

105. Stomata density
  1 = dispersed
  2 = dense

106. Stomata on eminence
  1 = no
  2 = yes

107. Neighbouring cell of stomata with undulate walls
  1 = no
  2 = yes

108. Epidermal cells upper surface width
  1 = 25 - 45 μm
  2 = 45 - 90 μm
  3 = 90 - 120 μm
  4 = more than 120 μm

Characters on anatomy of ovary and styles

109. Ovary wall thickness
  1 = 75 - 175 μm
  2 = 180 - 325 μm
  3 = 330 - 520 μm

110. Ovary wall number of cellular layers
  1 = 5 - 7
  2 = 7 - 10(- 11)
  3 = (9 -) 10 - 13

111. Ovary wall number of cellular layers in transition zone on inner surface
  1 = 1 - 2
  2 = 2 - 3
  3 = 3 - 5

112. Ovary wall epidermal cells relative size
  1 = area 1/5 - 1/2 times as large as cells directly beneath
  2 = 1/2 - 1 times as large as cells directly beneath

113. Septa length/width ratio
  1 = more than 5
  2 = less than 5

114. Placenta shape
  1 = not or weakly lobed, strongly thickened
  2 = lobed, thickened
  3 = ± mushroom shaped with long funiculae
  4 = branched ± tree like

115. Number of ovules per locule
  1 = 8 - 26
  2 = 27 - 108

116. Number of layers of ovules
  1 = 1 - 2
  2 = 3 or more

117. Fusion of ventral vascular bundles
  1 = not fused
  2 = some fused
  3 = all fused

118. Number of internal laterals produced per locule at the base
  1 = 0(- 1)
  2 = 1
  3 = 2

119. Placentary vasc. bundles forming distinct vertical bundles
  1 = no
  2 = yes

120. Position of distinct placentary vasc. bundles
  1 = in between the ventrals
  2 = at base of placentae
  3 = in placentae

121. Stigmatic papillae length/width ratio of free part
  1 = 4.2 - 6.5
  2 = 6.6 or more

122. Stigmatic papillae length base/total length
  1 = 0.09 - 0.20
  2 = 0.20 - 0.37

123. Stigmatic papillae ribbed
  1 = no
  2 = slightly
  3 = yes

124. Stigmatic papillae extremity thickened
  1 = no
  2 = yes

125. Epidermal cells style with cuticula structure
  1 = no
  2 = yes

Table 11.1. (continued).

Seed micromorphological characters

126. Operculum shape
1 = (broadly) nipple-shaped
2 = obtuse

127. Seeds papillate
1 = no
2 = yes

128. Ratio collar to seed length
1 = ≤ 2.0
2 = > 2.0

129. Anticlinal walls collar undulate
1 = no
2 = yes

130. Anticlinal boundaries sunken
1 = no
2 = locally
3 = yes

131. Border operculum – collar sunken
1 = no
2 = yes

132. Cuticular structure
1 = with star-shaped or zigzag elevations
2 = double structure of star-shaped elevations
3 = with short striae
4 = woolly or dense in appearance

general topology does not show an early division into two groups. A Loasibegonia tail and a Scutobegonia tail are segregated after the subsequent splitting off of *B. zairensis*, the *B. wilksii*-group and the *B. ferramica*-group (see paragraph 11.7.2 for the contents of these groups). After analysing more intensively the results of the first and second analysis it proved that the reduction in length was not only due to the removal of section *Cristasemen*. The second analysis yielded an ingroup that was apparently better resolved as well. This is also shown by the slightly higher ri of the second analysis compared to that of the first and third. It was then decided to use only the section *Filicibegonia* as outgroup in subsequent analyses.

The ri and especially the ci indices of these first three analyses are low. The ci of 0.21 indicates that each character state changes on average about 5 times in the tree. It was clear from this figure that the data contained some very 'poor' characters and it was decided to investigate the consequences of successive weighting. Hennig86 uses the rescaled consistency index (scaled multiplication of consistency index and retention index) as a measure of the performance of a character (Farris, 1989). The command 'xsteps w' was applied.

A priori weighting of characters is generally being rejected on the basis of its subjectivity, although the hypothesis-independent weighting method of Sharkey (1989) claims to be objective. A posteriori or hypothesis-dependent weighting is regarded here as a useful tool to further investigate local or overall tree topology. The uncritical use of a posteriori character weighting in the direct construction of cladograms is refuted.

After performing a first weighting iteration on the results of the initial analy-

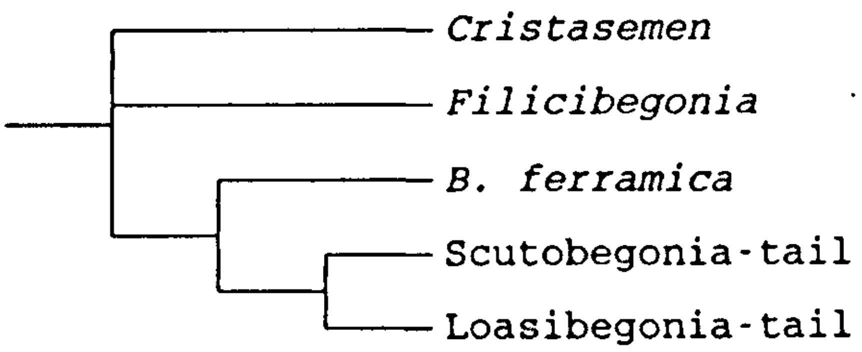

Figure 11.5. Cladogram structure with both sect. *Cristasemen* and sect. *Filicibegonia* denoted as the outgroup.

sis, no less than 77 characters received a weight of zero, hence they were left out of consideration in a second run because of their poor performance in the first. The four trees resulting from this second run had a length of 459, ci of 0.37 and ri of 0.78. The initial division into two major groups, the Loasibegonia tail and Scutobegonia tail, at the base of the ingroup was maintained, but the ingroup topology of these was altered considerably. It now became obvious that a straightforward analysis would not result in a phylogenetic tree with a sound basis. I tried to strengthen this basis using the method described in the next paragraph.

11.6.2 Secondary analyses

Up till now, all non-polytypic characters were treated as unordered. Apart from a priori and a posteriori weighting, discussed above, ordering of character states can be considered. The decision to treat a character as ordered is subjective and may be taken when one has strong indications that the omittance of intermediate character states during the ingroup evolution did not occur or did so rarely. Ordering a character leads to an increase of the weight (importance) of a character change between 2 states not linked directly. Ordering a phylogenetically important character, one with a high ri, will have the least influence on the original cladogram, as the importance of the character is based on its correlation with others that are indicative for the same tree topology. Thus, when character evolution of such a particular and important character did, unexpectedly, not run through the sequence of states proposed in table 11.1 and this character is ordered, the tree topology will probably still be upheld by the other correlated characters.

The influence of taking along an increasing number of ordered characters in an analysis on tree topology was investigated, by means of the following procedure. Using the section *Filicibegonia* as the sole outgroup and no extra characters ordered, an analysis was performed followed by 4 successive weighting iterations (commands 'xsteps w', 'mhennig*' and 'bb*' in sequence; the 5th iteration yielded the same weights for every character as the 4th one). All characters appropriate for ordering (a total of 45, excluding the polytypic ones which were already treated as ordered) were listed and the weights calculated by the 4 subsequent iterations were noted with these. In this way 'strong' and 'poor' characters could be selected. The 45 characters were divided into 5 groups (a more or less arbitrarily chosen number) from 'strong' to 'poor' using the following group criteria:

- group A: every character having a value 4 or higher after the 4th iteration.
- group B: every character having a value of 1 to 3 after the 4th iteration and with at least once a value of 2 after any of the other iterations.
- group C: every character having a value of 1 after every one of the four iterations.
- group D: every character having at least once a value of 1 after any iteration with the rest of the values being zero.
- group E: characters with a value of 0 after every iteration.

The application of these criteria yielded the following 5 groups:

- group A: character 34, 65, 71, 111
- group B: character 67, 89, 93, 110, 114, 120, 123
- group C: character 3, 15, 23, 55, 78, 79, 103
- group D: character 5, 17, 56, 77, 86, 87, 91, 108
- group E: character 4, 6, 7, 8, 21, 29, 36, 44, 62, 63, 80, 81, 83, 88, 92, 108, 109, 117, 130

Subsequent runs were performed each time *adding* one more of the above mentioned groups to the ordered character set. Ordering was always according to the character state sequences provided in table 11.1. For convenience the subsequent runs will be called run-A through run-E. Hence, run-B involves a run using the characters of group A *and* B as ordered (as well as all polytypic ones). All runs resulted in trees with a ci of 0.20, exept for run-E which had a ci of 0.19. The result of run-E was also quite markedly different from those of run-A through -D. This was more or less to be expected as in run-E many characters non- or poorly informative for genealogic relationship were included in the ordered group. Hence, more weight (see above) was applied to them than to any other, non-orderable but often 'stronger', more informative ones. One could argue a priori that the results of such an analysis would be less informative for genealogic relationships than the initial one. It was then decided that the results of run-E were not taken into further consideration. For each of the remaining four runs one successive weighting iteration was performed, the results of which will be used hereafter.

11.7 Towards a conclusive cladogram

After performing the method described in the previous paragraph, the results of 5 separate runs (the primary one plus run-A through -D) were available, together with the results of a successive weighting iteration on each of them, and the outcomes could be compared. It appears that, despite of the low ci and ri values, several obvious similarities between all runs can be denoted. These

Table 11.2. Character states used in the cladistic analysis.

taxon/character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Begonia																																
adpressa	2	3	2	1	2	1	4	3	2	1	1	3	2	3	2	2	2	2	2	1	1	1	4	2	1	1	1	2	1	1	1	1
aggeloptera	1	1	1	3	1	1	1	3	2	1	1	1	1	1	-1	1	1	3	2	1	1	3	2	1	1	2	1	1	2	2	1	2
anisosepala	1	1	2	1	2	1	2	3	2	1	1	1	1	3	2	2	2	2	2	1	2	3	1	1	1	1	2	1	2	2	1	2
atroglandulosa	1	3	1	1	2	2	2	3	2	1	1	1	2	3	2	2	2	1	2	1	1	1	2	2	1	1	1	3	1	1	1	1
ciliobracteata	1	1	2	2	2	1	2	3	2	1	1	3	1	2	-1	1	3	2	2	1	3	2	2	1	1	1	2	1	2	2	1	2
clypeifolia	1	1	3	3	3	1	4	1	1	1	2	1	1	2	3	2	3	2	2	1	1	1	3	2	1	1	1	1	1	1	1	2
dewildei	3	3	1	2	1	1	1	4	1	2	1	1	1	3	1	2	1	3	1	1	3	1	1	2	1	1	1	3	2	1	2	1
duncan-thomasii	2	2	2	1	3	2	3	3	2	1	1	2	2	3	3	2	3	2	1	1	1	1	4	1	2	1	1	3	2	1	1	1
erectocaulis	1	1	3	3	3	1	3	3	2	1	1	2	1	1	-1	1	3	3	2	1	2	1	3	2	1	1	1	1	1	1	1	1
erectotricha	1	1	3	2	2	3	4	3	2	1	1	1	1	3	4	2	3	1	1	1	2	1	4	1	1	1	2	1	2	2	1	1
ferramica	2	1	1	3	1	1	3	4	2	1	1	1	1	3	2	2	2	1	1	1	2	1	1	2	1	1	1	3	1	1	1	1
gentilii	1	1	3	2	2	1	3	2	2	1	1	1	2	3	2	2	2	1	1	1	1	1	4	2	1	1	1	3	2	1	1	-1
heterochroma	1	2	2	2	2	1	3	3	2	1	1	3	2	3	2	2	2	2	2	1	2	3	1	2	1	1	1	1	2	1	1	1
hirsutula	1	1	3	2	2	1	3	3	2	1	1	3	1	2	3	1	3	2	2	1	3	2	3	1	1	2	2	1	2	2	1	1
lacunosa	1	2	2	1	2	3	2	4	2	1	1	3	1	3	2	2	2	2	2	1	1	2	2	1	2	1	1	1	2	1	1	2
laporteifolia	1	1	2	1	2	3	2	4	2	2	1	3	1	3	2	2	3	2	2	1	3	2	2	1	1	1	2	1	2	2	1	1
letouzeyi	2	2	3	1	2	1	4	3	2	1	1	1	2	3	3	2	3	1	2	1	1	1	5	1	2	1	1	2	2	1	1	1
mbangaensis	1	1	2	2	2	1	2	4	2	1	1	1	1	3	2	2	2	1	1	1	2	1	1	1	1	1	2	1	2	2	1	1
microsperma	3	2	2	1	2	1	3	1	2	1	1	2	2	3	3	2	3	2	1	1	1	1	4	1	2	1	1	1	2	1	2	1
mildbraedii	1	2	3	2	2	1	2	3	2	1	1	1	1	3	2	2	2	1	2	1	1	1	2	2	1	1	1	1	2	1	2	2
minuta	3	3	1	1	1	1	1	1	-1	-1	-1	-1	2	3	1	2	1	3	1	1	1	1	5	2	1	1	1	1	1	1	-1	1
peperomioides	1	1	3	3	2	1	3	1	2	1	1	2	1	1	-1	1	2	3	2	1	2	1	4	2	1	1	1	1	1	1	2	2
potamophila	1	2	2	1	2	3	4	4	2	1	1	1	2	3	4	2	3	1	2	1	2	1	4	2	1	1	1	1	3	1	1	1
prismatocarpa	3	3	1	1	1	1	2	3	2	1	1	3	2	1	-1	1	1	1	2	1	1	1	4	1	1	2	1	1	2	1	1	1
pseudoviola	3	3	1	1	1	1	2	3	2	1	1	1	2	1	-1	1	1	1	2	1	1	1	3	2	1	1	1	1	2	1	1	1
pulcherrima	1	1	2	2	3	1	4	2	2	1	1	1	2	3	3	2	2	1	1	1	1	1	4	2	1	1	1	3	2	1	1	1
quadrialata	2	3	2	1	2	1	3	3	2	1	1	1	2	3	2	2	2	1	2	2	2	1	3	2	1	1	1	1	3	1	2	2
salisburyana	1	2	2	1	1	1	3	3	2	1	1	3	2	1	-1	2	2	1	2	1	1	1	4	2	1	1	1	1	3	1	-1	2
scapigera	3	3	3	1	2	2	4	1	2	1	1	-1	2	3	4	2	3	1	1	1	2	1	4	2	1	1	1	3	1	1	2	2
schaeferi	2	2	3	2	2	1	3	3	2	1	1	3	2	3	2	2	2	2	2	1	1	1	5	1	2	1	1	2	2	1	1	1
scutifolia	3	2	1	1	1	2	2	3	2	1	1	2	2	3	1	2	2	2	2	2	1	1	4	2	1	1	1	1	2	1	2	2
scutulum	1	2	3	2	3	3	4	3	2	1	1	2	1	3	3	2	3	1	2	1	2	1	3	2	1	1	1	1	1	1	1	2
staudtii	3	2	3	1	2	1	4	4	2	1	1	1	2	3	3	2	3	1	2	1	2	1	4	2	2	1	1	3	3	1	1	1
stellata	3	3	1	1	1	2	1	1	-1	-1	-1	-1	2	1	-1	1	2	2	1	1	1	1	2	1	1	2	1	1	1	1	1	1
susaniae	1	2	3	1	2	1	2	4	2	1	1	3	1	3	2	2	2	2	2	1	1	1	3	1	2	1	1	1	2	1	1	2
vankerckhovenii	1	2	1	2	1	1	1	4	1	2	1	1	1	3	1	2	2	1	2	1	1	1	1	2	1	1	1	3	2	1	2	1
vittariifolia	3	2	1	2	1	1	1	1	1	1	2	1	1	1	-1	1	3	3	1	1	2	1	2	1	1	2	1	1	2	1	2	2
wilksii	1	2	2	2	2	3	1	4	2	1	1	1	1	3	1	2	2	3	1	1	1	1	2	1	2	1	1	1	2	1	1	1
zairensis	1	2	2	3	2	2	4	3	2	1	1	1	1	3	2	2	2	2	2	1	1	1	3	1	2	1	1	3	2	1	1	-1
zenkeriana	1	1	3	3	3	1	3	2	2	1	1	2	1	1	-1	1	3	2	1	1	3	1	3	2	1	1	1	1	1	1	2	1
thomeana	1	1	1	1	3	2	2	2	2	1	1	1	1	1	-1	2	1	1	1	1	1	1	4	1	1	2	1	1	1	1	1	1
elatostemmoides	-1	-1	-1	-1	3	1	1	4	2	1	1	1	1	1	-1	1	2	2	2	1	1	1	4	1	1	2	1	1	3	1	1	1
macrocarpa	-1	-1	-1	-1	2	1	1	2	2	1	1	1	1	1	-1	1	2	2	2	1	1	1	4	2	1	1	1	1	1	1	1	1
sciaphila	-1	-1	-1	-1	3	1	1	3	2	1	1	1	1	1	-1	1	2	2	2	1	2	1	4	1	1	2	1	1	2	1	1	2

are of a various nature: same topology of a cladon, monophyletic nature of a cladon but with varying topology, and same relative topology of groups of clades. All similarities are discussed in more detail below. Similarities between the separate runs are interpreted as the 'stable' parts of the cladogram, as they are not (or only slightly, see below) affected by ordering of characters. This might be brought about by three situations. First, no ordered characters are involved within or at the root of the 'stable' subgroup and ordering does therefore have no effect. Second, in the unordered run the sequence of changes within the characters treated as ordered in the second run, was already determined by correlation with other characters in a way similar to the ordered situation.

(Table 11.2 continued)

33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69
1	-1	1	3	1	2	1	1	1	1	1	3	2	1	1	1	1	1	1	3	1	1	3	3	2	3	1	1	2	3	1	1	3	2	2	2	2
1	3	1	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	3	1	1	1	1	2	1	3	2	1	1	2	2	1	4	2	2	2	1
1	-1	1	3	1	2	1	1	1	1	1	1	1	1	1	1	2	1	3	1	2	1	1	2	1	1	2	3	1	2	2	1	4	2	2	2	1
1	-1	1	2	1	2	1	1	1	2	1	1	1	1	1	1	1	1	1	3	2	2	1	2	1	2	2	1	1	1	1	2	1	2	2	1	1
2	4	1	2	1	2	1	1	1	1	1	2	1	1	2	1	2	1	3	1	2	1	1	2	2	1	2	3	1	3	2	1	3	2	3	2	1
1	4	1	2	1	2	1	1	1	1	1	1	1	1	2	1	1	1	3	1	2	2	2	2	2	3	2	1	2	3	3	1	4	2	3	2	1
2	-1	2	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	2	3	2	1	1	1	1	1	1	1	1	1	1	1	3	2	1	2	1
1	-1	1	2	1	1	1	2	1	3	1	2	1	1	1	1	1	2	1	3	1	1	3	3	1	3	1	1	2	3	1	1	3	2	2	2	2
2	4	2	2	1	2	1	1	1	1	1	3	1	1	2	2	1	1	3	1	2	2	2	2	2	3	2	3	1	2	2	1	4	2	3	2	2
1	-1	1	3	1	2	1	1	1	3	1	2	1	1	2	1	1	1	3	1	1	1	1	2	1	3	2	3	1	3	2	1	4	2	3	2	1
1	-1	1	2	1	2	1	1	1	3	1	2	1	1	1	2	1	1	3	3	1	1	1	2	1	3	2	3	1	2	3	1	3	-1	2	2	2
1	-1	1	3	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	3	1	1	2	1	-1	3	2	1	1	1	1	-1	2	2	2	2	1
1	-1	1	2	1	2	1	1	1	3	1	2	1	1	2	1	2	1	1	3	2	1	1	2	1	2	2	3	1	2	1	1	3	2	1	2	1
2	4	2	3	1	2	1	1	1	1	1	2	1	1	2	1	2	1	3	1	2	2	1	2	2	3	2	2	1	3	2	1	4	2	3	2	1
1	-1	1	2	1	1	1	2	2	3	2	3	1	1	1	1	1	1	3	1	1	2	2	2	1	2	2	2	2	2	1	1	3	1	2	2	2
1	-1	1	2	1	1	2	1	1	1	1	3	1	2	1	1	1	1	3	1	1	1	2	2	2	1	2	3	2	3	1	1	3	-1	-1	2	2
1	-1	1	3	1	2	1	1	1	3	1	2	1	1	1	1	1	1	1	2	1	1	2	3	1	3	2	2	2	3	2	1	3	2	2	2	2
1	-1	1	2	1	1	2	1	1	3	1	3	2	2	-1	1	1	1	3	1	1	1	2	2	-1	3	2	3	1	2	1	1	3	-1	-1	2	2
1	-1	1	2	1	1	1	2	1	3	1	2	1	1	1	1	1	1	1	3	1	1	2	2	1	3	1	1	2	2	3	1	1	2	2	1	1
1	4	1	2	1	2	1	1	1	1	1	2	1	1	2	1	2	1	2	2	1	2	1	2	1	3	2	2	1	2	2	1	3	2	2	2	1
1	-1	1	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	3	1	1	1	1	1	3	1	1	1	1	1	2	1	2	2	1	1
1	1	2	2	1	2	1	1	1	1	1	1	1	1	2	1	1	1	3	1	2	1	1	2	1	3	2	1	2	3	3	1	4	2	2	2	1
1	-1	1	3	1	2	1	1	1	3	1	3	1	1	1	2	1	1	1	3	2	2	2	2	1	3	2	3	2	3	1	2	2	1	2	1	2
1	2	1	2	2	2	1	1	1	2	1	1	1	1	1	1	1	1	1	3	1	2	1	1	1	3	2	1	1	2	1	2	1	2	2	1	1
1	2	1	2	1	2	1	1	1	3	1	1	1	1	1	1	2	1	1	3	1	1	1	1	1	3	2	2	1	2	1	2	1	2	2	1	1
1	-1	1	3	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	3	1	1	3	3	1	3	1	2	2	3	3	-1	1	2	2	1	1
1	-1	1	3	1	2	1	1	1	1	1	2	1	1	1	1	1	1	1	3	2	2	1	2	1	3	2	2	1	2	1	2	2	2	2	1	1
1	2	1	3	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	3	2	1	1	1	1	3	2	3	1	2	1	-1	2	2	2	1	1
1	-1	1	3	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	3	2	1	2	2	1	3	2	1	2	3	3	2	1	2	2	1	1
1	-1	1	3	1	2	1	1	1	1	1	1	1	1	1	2	1	2	1	3	-1	2	3	3	1	3	1	2	2	3	3	1	3	2	2	2	1
1	-1	1	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	3	1	2	1	1	1	3	2	2	1	2	1	2	1	2	2	1	1
1	-1	1	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	3	1	1	2	1	3	1	3	1	3	2	3	1	1	3	2	3	2	2
1	-1	1	3	1	1	1	1	2	3	1	3	1	1	1	1	1	1	1	3	2	2	2	2	1	3	1	1	2	2	2	2	1	2	2	1	1
1	2	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	-1	3	2	-1	1	1	1	1	-1	1	1	1	-1	-1	-1	-1	-1	-1	-1
1	-1	1	2	1	1	1	2	2	3	2	2	1	1	1	1	2	1	3	1	1	2	1	2	1	3	2	3	2	3	2	1	4	2	2	2	1
1	-1	1	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	2	3	1	1	1	2	1	3	2	2	2	2	1	1	3	2	2	2	2
1	1	-1	1	1	2	1	1	1	1	1	1	1	1	2	1	1	1	3	1	1	1	1	2	1	3	2	2	1	2	2	1	1	-1	2	1	1
1	-1	2	1	1	1	2	1	1	1	1	2	1	1	1	1	1	1	3	3	1	1	1	2	2	1	2	3	1	1	2	1	3	1	2	2	2
1	-1	1	3	1	2	1	1	1	1	1	2	1	1	1	1	1	1	1	3	1	1	2	2	1	3	2	1	2	2	3	1	3	2	2	2	1
2	3	2	2	1	2	1	1	1	1	1	2	1	1	1	1	2	1	3	1	2	1	2	3	2	1	2	3	1	2	1	1	4	2	1	2	2
1	2	1	2	1	2	1	1	1	2	1	1	1	1	1	2	2	2	1	3	2	-1	1	3	1	3	1	1	2	2	3	1	3	2	2	1	1
1	4	2	2	1	2	1	1	1	3	1	3	1	1	1	2	1	1	-1	-1	2	2	1	2	1	1	2	3	1	2	2	1	3	2	2	1	2
1	4	2	2	1	2	1	1	1	1	1	1	1	1	2	1	2	1	-1	-1	2	1	3	3	1	1	2	1	1	2	1	1	3	2	2	1	1
1	4	2	2	1	2	1	1	1	1	1	3	1	1	2	1	1	1	-1	-1	-1	1	1	2	1	1	1	1	1	2	2	1	3	2	2	1	1

Third, the ordering of certain characters can be of minimal influence within a cladon and the structure is being fixed or determined by comparatively many non-ordered ones. The first and third possibilities are becoming less likely when larger amounts of characters are ordered.

The idea now is that by analysing the results of the 5 separate runs, more or less stable subgroups can be identified. These are regarded as the stable elements of the fairly unstable initial cladogram discussed in paragraph 11.6.1. Furthermore, the relative position of the stable elements might be determined with some certainty as well. This may result in a more or less complete cladogram but without certainty about the actual position of several 'unstable' elements.

(Table 11.2 continued)

taxon/character	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Begonia																															
adpressa	1	3	3	1	2	2	1	-1	-1	-1	-1	-1	1	-1	-1	1	2	1	2	-1	-1	-1	-1	-1	2	1	1	1	1	1	2
aggeloptera	1	4	2	2	2	2	2	3	1	1	1	2	1	3	2	2	2	1	2	2	1	3	3	3	2	1	1	1	2	2	1
anisosepala	1	4	2	1	1	1	1	2	1	1	3	2	1	2	2	1	2	1	2	2	1	3	1	2	2	1	1	1	2	2	1
atroglandulosa	1	2	1	1	1	1	1	3	3	3	2	2	1	2	2	1	1	1	2	1	1	1	1	1	2	1	1	2	1	1	2
ciliobracteata	1	3	1	1	1	2	2	3	1	1	1	2	1	3	1	2	3	1	3	3	2	3	1	3	2	1	1	2	1	2	1
clypeifolia	1	4	2	1	1	2	2	2	1	1	1	1	2	3	2	1	3	1	2	3	1	3	3	3	2	1	1	2	2	2	1
dewildei	1	3	1	1	1	1	1	4	1	1	1	3	1	2	1	2	1	1	2	2	1	2	3	2	1	2	1	1	2	2	2
duncan-thomasii	1	3	2	1	1	1	1	2	2	3	1	2	1	1	1	1	3	2	3	2	1	1	1	1	2	1	1	2	1	1	2
erectocaulis	1	4	2	1	1	2	2	3	1	1	2	2	1	3	2	2	3	1	3	3	1	3	1	3	2	1	1	2	2	2	1
erectotricha	1	4	2	1	1	2	2	2	1	1	1	1	1	3	1	2	3	1	1	2	2	3	1	3	2	1	1	2	2	2	1
ferramica	2	-1	-1	-1	1	2	1	2	2	2	1	1	2	3	1	1	2	1	1	2	1	1	1	3	1	1	2	-1	2	2	1
gentilii	1	2	1	1	1	2	1	-1	-1	-1	-1	-1	1	-1	-1	1	2	1	-1	-1	-1	-1	-1	-1	2	1	1	1	1	1	2
heterochroma	1	3	2	1	1	1	1	2	2	2	3	2	1	2	1	1	3	1	2	2	1	3	1	1	2	1	1	1	1	1	1
hirsutula	1	4	2	1	1	2	2	3	1	1	1	1	1	3	2	2	3	1	2	2	1	3	1	3	2	1	1	2	2	2	1
lacunosa	1	3	3	1	2	2	2	1	1	2	2	1	2	3	2	1	3	2	3	2	1	3	3	3	2	1	1	1	2	1	1
laporteifolia	2	-1	-1	-1	2	1	1	-1	1	-1	2	-1	-1	-1	-1	1	3	3	3	2	1	-1	-1	-1	2	2	1	2	2	2	1
letouzeyi	1	3	2	1	2	2	1	2	3	3	1	3	1	3	2	1	2	1	2	2	2	3	1	1	2	1	1	1	1	1	1
mbangaensis	1	4	3	1	2	1	1	-1	1	-1	2	-1	-1	-1	-1	1	3	3	1	2	1	-1	-1	-1	2	1	1	1	2	2	1
microsperma	1	1	1	1	1	1	1	3	3	3	1	2	2	3	1	1	3	2	3	2	2	2	2	1	2	1	1	1	1	1	2
mildbraedii	1	3	2	1	2	1	1	2	1	1	2	2	1	1	2	1	2	1	2	2	1	1	1	2	2	1	1	2	2	2	1
minuta	1	1	1	1	2	1	1	-1	-1	-1	-1	-1	1	-1	-1	-1	1	1	2	1	1	1	1	1	1	1	1	-1	-1	1	2
peperomioides	1	4	2	1	1	2	2	-1	1	-1	-1	-1	1	-1	-1	2	3	1	2	3	1	-1	-1	-1	2	1	1	2	2	2	1
potamophila	1	2	1	1	1	1	1	3	3	2	2	3	1	1	1	1	2	1	2	2	2	3	1	1	2	1	1	1	1	1	2
prismatocarpa	1	1	1	1	1	1	1	2	1	3	1	2	1	1	1	1	1	1	2	1	1	1	1	1	2	1	1	1	1	1	2
pseudoviola	1	1	1	1	2	1	1	2	2	1	3	2	1	3	1	1	1	1	2	1	1	2	1	1	2	1	1	2	1	1	2
pulcherrima	1	1	1	1	2	-1	1	-1	-1	-1	-1	-1	-1	-1	-1	1	2	1	3	2	-1	-1	-1	-1	2	1	1	1	1	1	2
quadrialata	1	2	1	1	1	1	1	4	3	3	2	3	1	1	1	2	1	1	2	1	1	1	1	1	2	1	1	1	1	1	1
salisburyana	1	2	1	1	1	1	1	-1	-1	-1	-1	-1	1	-1	-1	2	1	1	2	1	1	-1	-1	-1	2	1	1	1	1	1	2
scapigera	2	-1	-1	-1	1	1	1	3	2	3	3	2	1	3	1	2	2	1	2	2	1	3	2	1	2	1	1	1	1	1	2
schaeferi	1	3	3	1	2	2	1	-1	-1	-1	-1	-1	1	-1	-1	1	2	1	2	2	1	3	1	-1	2	1	1	1	1	1	2
scutifolia	1	1	1	1	2	1	1	3	2	3	2	3	1	1	1	2	1	1	2	1	1	1	1	1	2	1	1	1	1	1	2
scutulum	1	3	3	1	2	2	2	3	1	1	1	2	1	3	1	2	2	1	2	2	1	1	1	1	2	1	1	1	2	1	1
staudtii	1	1	1	1	1	1	1	2	2	1	3	1	2	3	2	1	3	2	3	2	1	3	1	3	2	1	1	2	1	1	2
stellata	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	1	1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	1	2
susaniae	1	4	2	2	2	2	2	1	1	1	1	2	1	3	1	1	3	2	3	2	1	3	1	3	2	1	1	1	2	2	1
vankerckhovenii	1	3	2	1	1	1	1	3	1	1	1	2	1	2	1	2	1	1	2	1	1	3	2	2	1	2	1	1	2	2	1
vittariifolia	2	-1	-1	-1	2	2	1	3	1	1	1	2	1	3	1	2	3	1	3	2	1	3	1	3	2	1	1	1	2	2	1
wilksii	1	3	3	1	1	2	2	1	1	2	1	1	2	3	2	1	3	1	3	2	1	3	3	3	2	1	1	1	2	1	1
zairensis	1	3	2	2	1	2	2	-1	1	-1	-1	-1	-1	-1	-1	1	2	1	2	2	1	-1	-1	-1	2	1	1	2	2	2	1
zenkeriana	1	4	3	1	1	2	2	-1	1	-1	2	-1	-1	-1	-1	2	3	1	3	3	1	3	-1	-1	2	1	2	1	1	2	1
thomeana	1	3	1	1	1	1	1	2	1	2	1	1	1	3	2	2	2	1	1	1	2	-1	-1	-1	2	1	1	1	2	-1	1
elatostemmoides	1	3	1	1	1	1	1	2	2	1	2	1	2	3	2	1	2	1	1	2	2	1	1	1	2	1	1	1	1	-1	1
macrocarpa	1	3	1	1	1	1	1	2	2	1	1	1	1	3	2	1	2	1	1	3	2	1	1	1	2	1	1	1	1	-1	1
sciaphila	1	3	1	1	1	1	1	2	1	1	1	1	1	3	1	1	3	1	1	3	2	1	1	1	2	1	1	1	1	-1	1

11.7.1 Outgroup structure

In both the primary run and run-A through -D the topology of the outgroup subtree was always as given in fig. 11.6a. After the first weighting procedure on the primary run this topology changed into that shown in fig. 11.6b. After a second weighting procedure on the primary run and after the first weighting procedure on the run-A through -D the topology was as shown in fig. 11.6c. A preference is given here to the topology as presented in fig. 11.6a, as it appears constant in all analyses before weighting, hence is less subjective.

More important is perhaps that an analysis of the character state changes

(Table 11.2 continued)

101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132
1	-1	2	2	1	-1	1	2	-1	-1	-1	1	1	4	2	2	2	-1	1	-1	-1	-1	-1	-1	-1	1	1	1	2	1	1	2
1	2	2	2	1	1	1	1	1	2	2	1	2	4	2	2	1	2	2	2	2	1	2	2	1	2	2	2	1	2	2	1
1	1	2	2	1	1	1	2	-1	-1	-1	-1	1	4	2	2	-1	-1	-1	-1	-1	-1	-1	-1	-1	2	1	2	2	1	2	4
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involved in the determination of the outgroup topology showed that they do not have any influence on the ingroup structure. The preference for one or the other topology is only a matter of ingroup relationships.

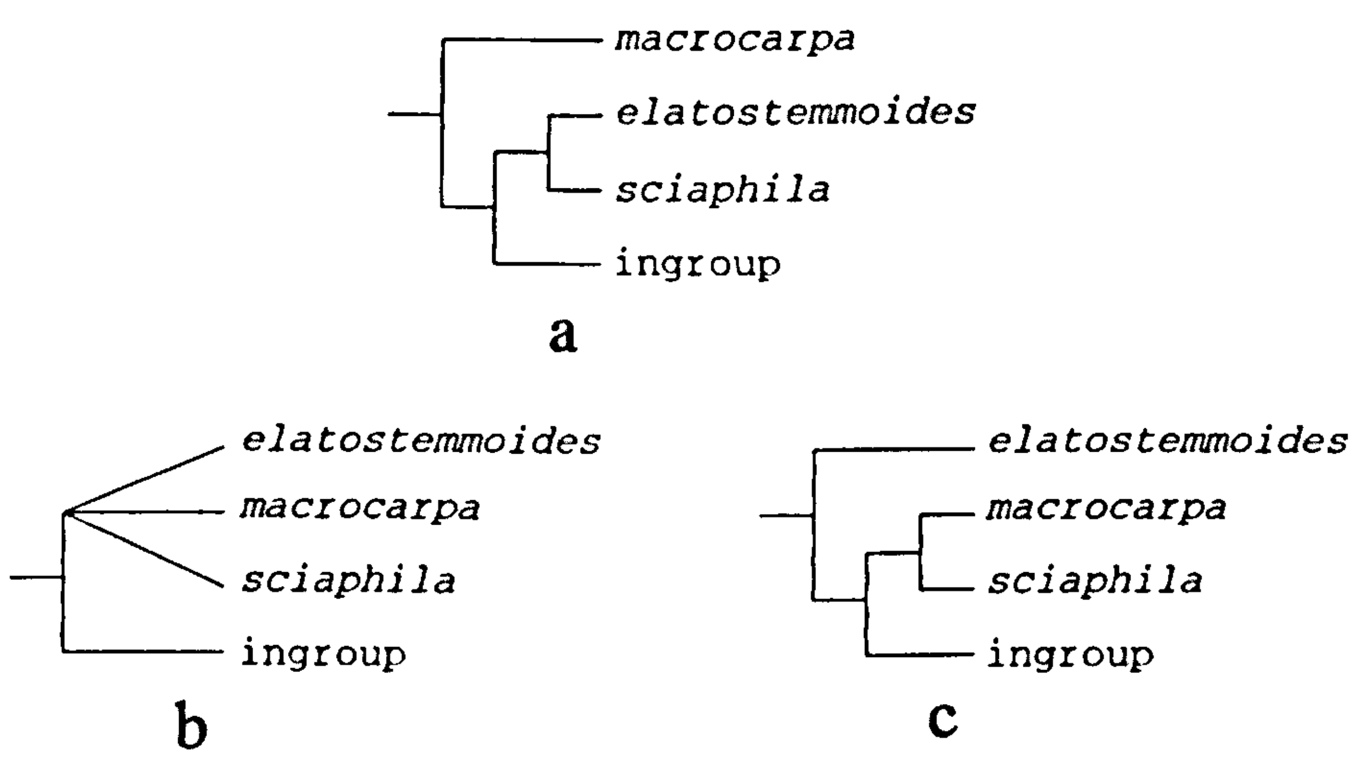


Figure 11.6. Three possible options for the outgroup structure; explanation see text.

11.7.2 Monophyletic subgroups

The *B. scutulum* group

In both the primary run and run-A through -D (all before the weighting procedure) the topology of the *B. scutulum* group, comprising 8 species, was exactly the same. Hence, as it seems to be a very stable element, it is regarded as a monophyletic group and its topology, which is shown in fig. 11.7, is accepted as the correct one. Apomorphic character states for the whole group are e.g. leaf blade up to more than 24 cm long (character 17), ovary dark brown to red (67), number of cell layers in the ovary wall (9–)10–13 (110) and the length/width ratio of the septa in the ovary more than 5 (113). As can be seen from fig. 11.7, *B. scutulum* itself is the most aberrant species within the group, having many autapomorphic character states. Indeed the shape and hirsuteness of the ovary are similar to that found in the *B. wilksii* group (see paragraph 11.7.4), while also several leaf anatomical characteristics differ from those of the rest of the group. Hence, the group must be regarded as a coherent subgroup with *B. scutulum* as a slightly deviating member at its base (see also the discussion in paragraph 11.7.4).

The *B. wilksii* group

In all runs (before the weighting procedure) this group, comprising 4 species, was regarded as monophyletic with a topology as shown in fig. 11.8. The group is accepted as monophyletic and its topology as correct. It shows many synapomorphies e.g. no smooth upper leaf blade surface (38), ovary and wings not concolorous (66), wings attached in the apical part of the ovary only (72), very thin leaf blades (77), sausage-shaped glandular hairs (99), and the border between the operculum and collar of the seed not sunken (131).

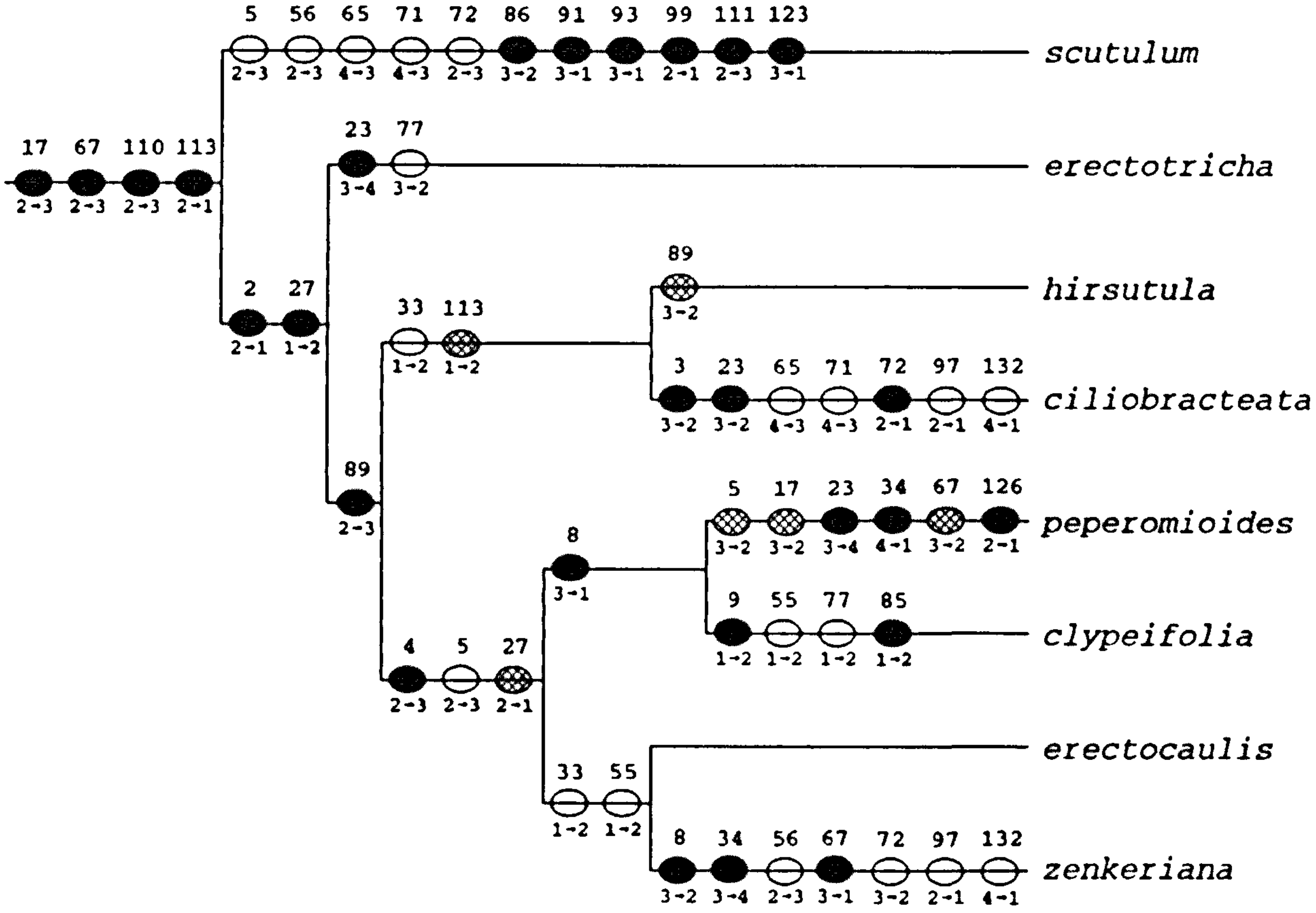


Figure 11.7. Cladogram of the *B. scutulum* group. Only more important characters (those receiving a weight of 1 or more with the 'ccode' command) are depicted; black = apomorphy, open = parallelism, hatched = reversal.

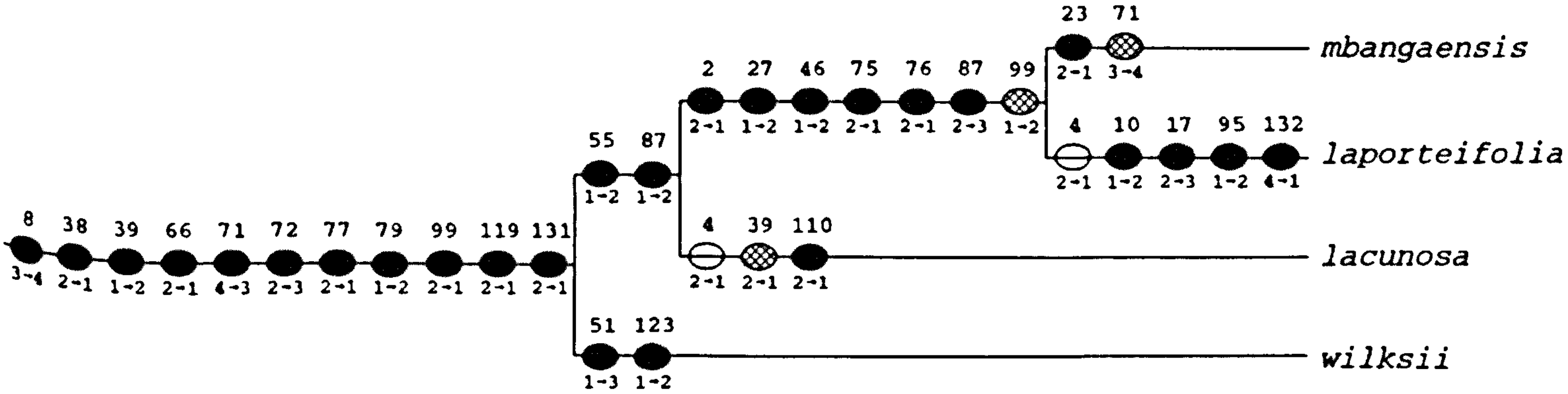


Figure 11.8. Cladogram of the *B. wilksii* group. Only more important characters (those receiving a weight of 1 or more with the 'ccode' command) are depicted; black = apomorphy, open = parallelism, hatched = reversal.

The *B. aggeloptera* group

In all runs, both before and after the weighting procedure, 2 species, *B. aggeloptera* and *B. vittariifolia*, were regarded as direct sister species (fig. 11.9). Synapomorphic characters states for this small group, which is accepted as a mono-

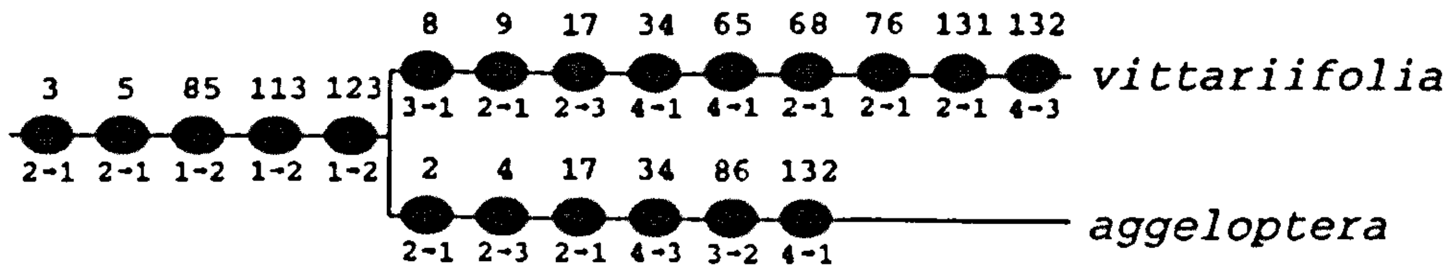


Figure 11.9. Cladogram of the *B. aggeloptera* group. Only more important characters (those receiving a weight of 1 or more with the 'ccode' command) are depicted; black = apomorphy.

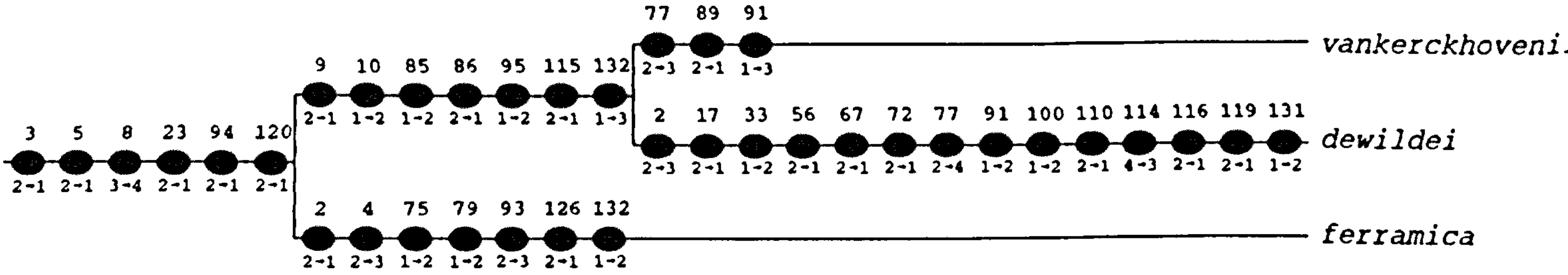


Figure 11.10. Cladogram of the *B. ferramica* group. Only more important characters (those receiving a weight of 1 or more with the 'ccode' command) are depicted; black = apomorphy.

phyletic one, are the very narrow rhizomes and small stipules (3 & 5), the comparatively large number of layers in the spongy parenchyma (85), and the slightly ribbed stigmatic papillae (123).

The *B. ferramica* group

The 3 species of this group were placed together in a monophyletic cladon having the same topology in all runs both before and after the weighting procedure. It is accepted as a monophyletic group and its topology is shown in fig. 11.10. Its synapomorphous character states are a.o. the narrow rhizomes with small stipules (3 & 5), the rounded apex of the leaf blade (23), the absence of multiseriate hairs (94) and the placental vascular bundles which are positioned in between the ventrals (120). All cladogram branches of this subgroup show many state changes. Especially *B. dewildei* is a somewhat aberrant species with many autapomorphic states. *B. ferramica* with its circular leaf blades, unique indumentum of long uniseriate hairs and wingless ovary can even be regarded as a side-slip species within the entire group studied here. The *B. ferramica* group always branches off low in the total cladogram, pointing to primitiveness. This might well explain the many autapomorphic states of each of the three species. They are probably of comparatively ancient origin and did not speciate recently.

The *B. scapigera* group

In all runs both before and after the weighting procedures, the 3 species of the *B. scapigera* group were grouped together with a topology as outlined in fig. 11.11. It is therefore regarded as a monophyletic group with narrowly oblong ovaries with ribbon-shaped wings (65 & 71) and strongly thickened and only weakly lobed placentas (114; with a reversal for *B. staudtii*) as the main synapomorphous character states.

The *B. letouzeyi* group

First of all the position of *B. gentilii* is considered. Many character states of this species, represented only by several voucher specimens of a single collection cultivated at Brussels, could not be scored. In the various analyses it subsequently occupied different positions in the cladograms. In the primary run it showed up at the very base of the section *Loasibegonia*. In run-A through -C it appeared as the sister species of *B. pulcherrima*. In run-D it was positioned right below the *B. scapigera* group. This wandering seems quite strange as *B. gentilii* is not easy to distinguish from *B. pulcherrima*. It is probably caused by the many missing values in its data-line (see table 11.2). The subjective decision was taken to regard this species as the direct sister species of *B. pulcherrima* on the basis of its close morphological resemblance. Furthermore, it was observed that in all analyses (before the weighting procedure) the species *B. adpressa*, *B. duncan-thomasii*, *B. letouzeyi*, *B. pulcherrima* (incl. *B. gentilii*) and *B. schaeferi* were always grouped together to form a monophyletic group, though with a different topology in the various runs. When the weighting procedure was applied, this group often appeared as a paraphyletic subgroup in the cladograms. A second similarity between all results of the runs before weighting could be observed: *B. letouzeyi* was always the most basal species within this group. It was decided to regard this group, comprising 6 species, as a monophyletic subgroup and to run a separate analysis with these 6 species using all data and *B. letouzeyi* as the outgroup species to determine its final topology. This analysis yielded a single tree with length 174, ci = 0.77 and ri = 0.42 which is shown in fig. 11.12. (N.B. In the last analysis *B. gentilii* was not denoted specifically as the sister species of *B. pulcherrima* but turned out to be so.) Tree topology did not change after application of a weighting procedure. It is accepted here as the 'correct' cladogram for this monophyletic subgroup which has large bracts (56) and slender stigmatic bands (75) as the main synapomorphic characters.

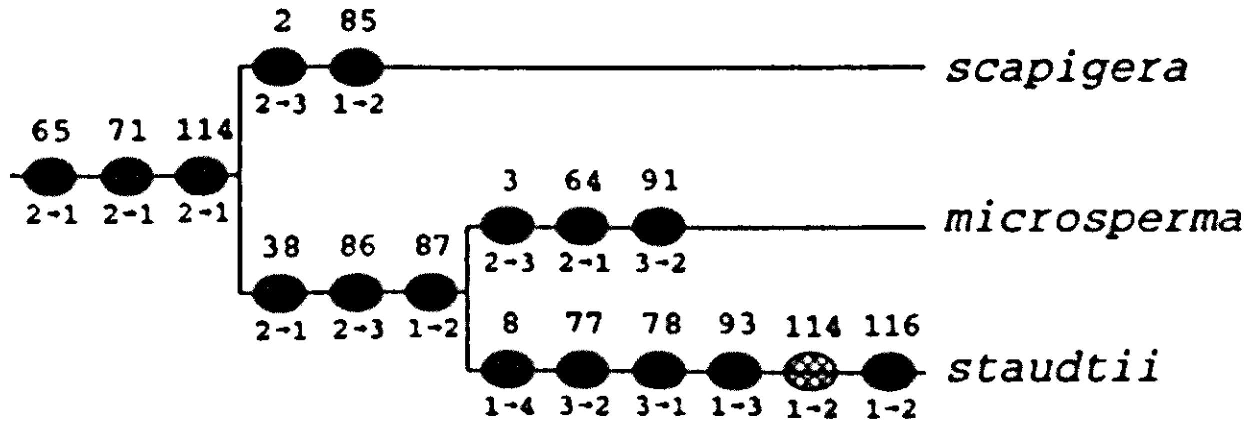


Figure 11.11. Cladogram of the *B. scapigera* group. Only more important characters (those receiving a weight of 1 or more with the 'ccode' command) are depicted; black = apomorphy, hatched = reversal.

The *B. potamophila* group

In all runs before the weighting procedure the following species were always grouped together: *B. atroglandulosa*, *B. minuta*, *B. potamophila*, *B. prismatocarpa*, *B. pseudoviola*, *B. quadrialata*, *B. salisburyana*, *B. scutifolia* and *B. stellata*. The topology of this subgroup did change in the various runs, but *B. potamphila* was always positioned at the very base of this subgroup except in the primary run. After application of the weighting procedure the subgroup was always maintained and again *B. potamophila* turned up at the base of it, now except for run-D where the latter species was placed at the base of the *B. scapigera* group. In 2 other runs the species occurred at the base of the *B. potamophila* group in an unresolved position together with one or more other species of the *B. scapigera* group.

The subgroup of 9 species listed above is accepted as a monophyletic one and, similar to the treatment of the *B. letouzeyi* group, a separate analysis on this subgroup using all data and *B. potamophila* as the outgroup was performed. This yielded a single tree with length = 289, ci = 0.67 and ri = 0.48. The topology of this cladogram, which is given in fig. 11.13, did not change after applying a weighting procedure and is accepted as the 'correct' one. As was expected from the results of the previous runs, *B. potamophila* is a somewhat aberrant species within this subgroup which can be extracted from the many state changes present on the node directly below *B. quadrialata*. The main synapomorphic characters for this subgroup are the narrowly elliptic to obovate ovaries (65) and linear to obovate wings (71).

11.7.3 Relative position of the monophyletic subgroups

In the previous paragraph 7 monophyletic subgroups were denoted. The next

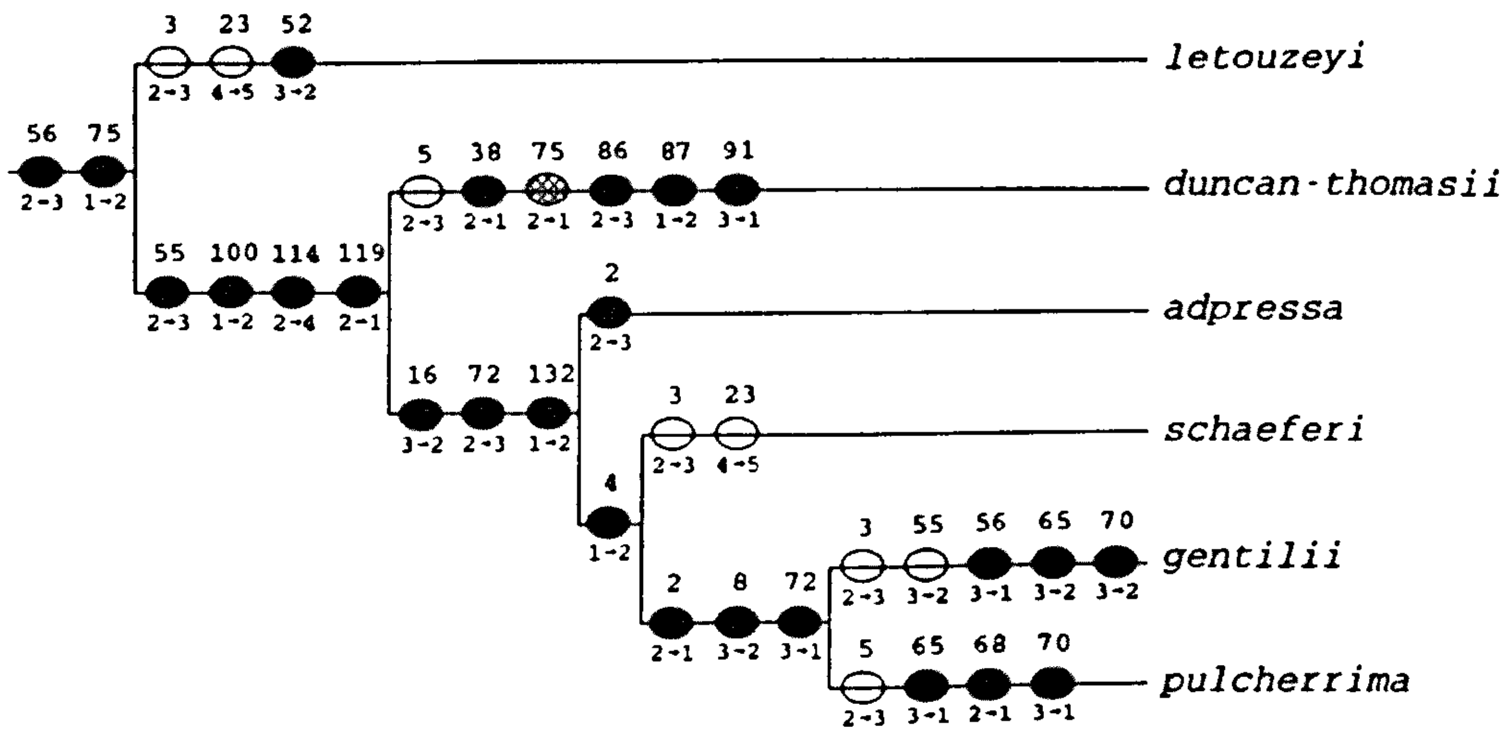


Figure 11.12. Cladogram of the *B. letouzeyi* group. Only more important characters (those receiving a weight of 1 or more with the 'ccode' command) are depicted; black = apomorphy, open = parallelism, hatched = reversal.

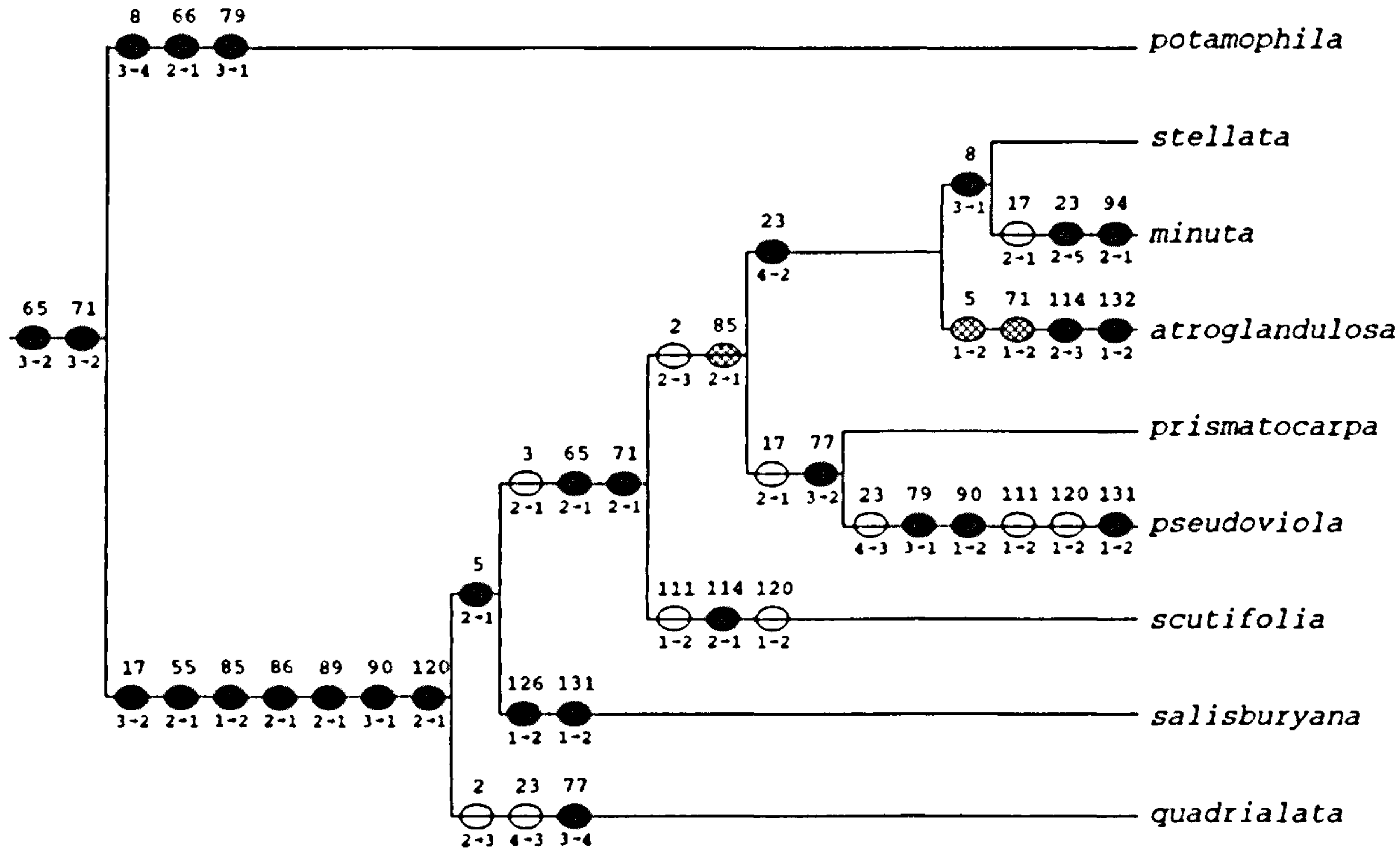


Figure 11.13. Cladogram of the *B. potamophila* group. Only more important characters (those receiving a weight of 1 or more with the 'ccode' command) are depicted: black = apomorphy, open = parallellism, hatched = reversal.

step is to decide on their relative position. The position of 4 of these subgroups, the *B. ferramica* group, the *B. letouzeyi* group, the *B. scapigera* group and the *B. potamophila* group, does not pose any problems. In all runs, both before and after the weighting procedure, their relative position was as given in fig. 11.14.

The relative position of the remaining 3 subgroups varies in the different runs. An overview of their positions in each run is given in fig. 11.15. A weighting procedure applied on the result of run-C and run-D led to a segregation of the species of the *B. wilksii* group. As this subgroup is regarded as a monophyletic one, I assume that the initial topology of the cladogram resulting from run-C and run-D is less stable and less 'correct' than those resulting from the other runs. For this reason the relative position of the 3 subgroups resulting from run-C and -D is rejected. Weighting applied to the results of the primary run led to the recognition of the *B. aggeloptera* group as an ingroup of the *B. scutulum*

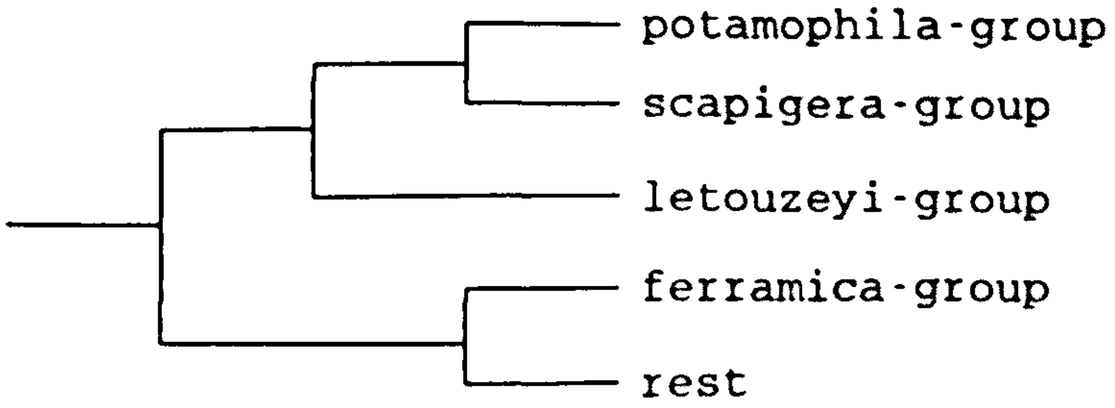


Figure 11.14. Relative position of the subgroups.

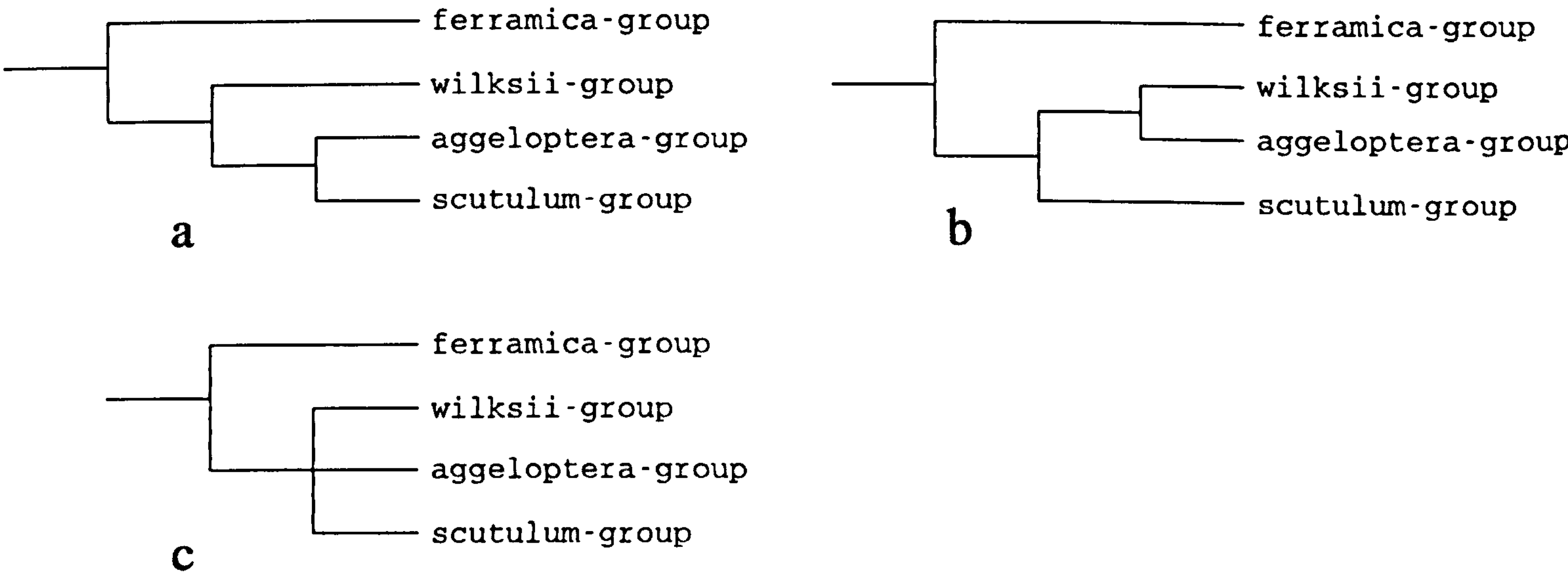


Figure 11.15. Different relative position of the *B. wilksii* group, *B. aggeloptera* group and *B. scutulum* group in the various runs; further explanation see text.

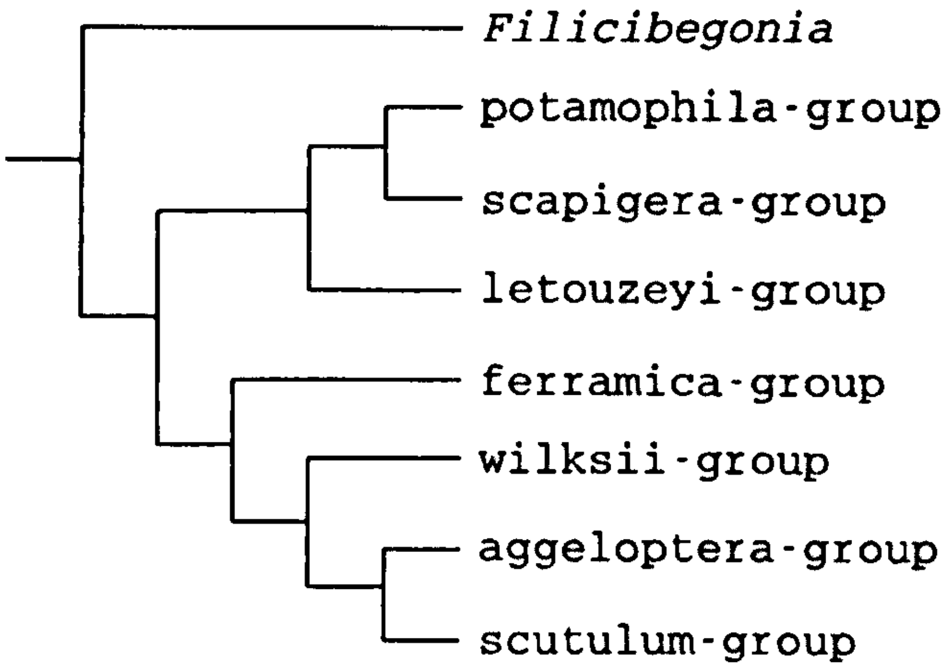


Figure 11.16. Conclusive position of the various subgroups.

group. Weighting applied to the results of run-A and run-B lead to the same relative position as that of the primary run (before weighting; fig. 11.15a). For this reason the relative position of the subgroups as shown in fig. 11.15a is accepted here. This decision results in the acceptance of the cladogram topology given in fig. 11.16.

11.7.4 Position of the remaining species

The position of the remaining 5 species seems dubious as the different runs are dissimilar in their results regarding these species. Still, some congruence can be observed. Below a brief review of the position of each of the 5 species in the subsequent analyses is given together with the ultimate descision taken.

B. anisosepala:

- primary run, run-B: with *B. mildbraedii* as a lineage in between *B. ferramica* group and rest of 'Scutobegonia-tail'
- run-A: with *B. mildbraedii* as a lineage in an unresolved position together with *B. aggeloptera* group and *B. wilksii* group
- weighting procedure on primary run: ingroup position within *B. wilksii* group
- run-C, run-D, weighting procedure on run-A through run-D: separate lineage in between *B. ferramica* group and rest of 'Scutobegonia-tail' but always splitting off after *B. mildbraedii*

Decision: separate lineage in between *B. ferramica* group and rest of 'Scutobegonia-tail' and splitting off after *B. mildbraedii*

B. heterochroma:

- primary run: as most basal lineage of 'Scutobegonia-tail'
- run-A, run-B: as most basal lineage of entire ingroup
- all other analyses, including all results after weighting: as most basal lineage of 'Loasibegonia-tail'

Decision: as most basal lineage of 'Loasibegonia-tail'

B. mildbraedii:

- primary run, run-B: with *B. anisosepala* as a lineage in between *B. ferramica* group and rest of 'Scutobegonia-tail'
- run-A: with *B. anisosepala* in an unresolved position together with *B. aggeloptera* group and *B. wilksii* group
- run-C, run-D, weighting procedure on all runs: separate lineage in between *B. ferramica* group and rest of 'Scutobegonia-tail'

Decision: separate lineage in between *B. ferramica* group and rest of 'Scutobegonia-tail'

B. susaniae:

- primary run: separate lineage in between *B. wilksii* group and *B. aggeloptera* group
- run-A, run-B: unresolved position together with *B. wilksii* group and *B. aggeloptera* group
- run-C, run-D, weighting procedure on run-B and run-C: separate lineage in between *B. aggeloptera* group and *B. scutulum* group
- weighting procedure on primary and run-D: ingroup position within *B. scutulum* group
- weighting procedure on run-A: most basal lineage of *B. aggeloptera* group

Decision: separate lineage in between *B. wilksii* group and *B. aggeloptera* group on account of the presence of this solution in the results of three of the unweighted runs.

B. zairensis:

- primary run: separate lineage in between *B. wilksii* group and *B. aggeloptera* group
- run-A, run-B: unresolved position together with *B. wilksii* group and *B. aggeloptera* group
- all other analyses, including all results after weighting: most basal lineage of 'Scutobegonia-tail'

Decision: most basal lineage of 'Scutobegonia-tail'

Because of the doubt about these decisions being correct, the positions of the 5 species treated above are indicated in the final cladogram by a dashed line.

The question arises whether these species are of hybrid origin, which might explain their wandering nature. In this respect the recent studies of McDade (1990) are of interest. She shows that hybrid taxa have a tendency to show up as a basal lineage to the clade that includes the most derived parental species. Both *B. heterochroma* and *B. zairensis* show characteristics of species represented on the one hand in the 'Loasibegonia-tail' and on the other hand in the 'Scutobegonia-tail'. Both species are generally positioned at the base of either two clades and regarding the results of McDade (1990) might have been evolved from hybridisation between members of the different sections. The wandering nature of *B. susaniae* can be regarded in this light as well, as the species has leaf characters very similar to *B. lacunosa*, a representative of the *B. wilksii* group, while its fruit type is similar to that present in the majority of the species of the *B. scutulum* group. *B. scutulum* itself was described above as a somewhat aberrant species within the *B. scutulum* group as it has a fruit type similar to that present in the *B. wilksii* group. Its position, at the base of the first group, could be regarded in the light of a hybrid origin as well.

11.7.5 The conclusive cladogram

The application of all choices made in the previous paragraphs leads to a conclusive cladogram (fig. 11.17). As discussed above, the position of several species is still uncertain (dashed lines). The cladogram has a length of 1809, a ci of 0.20 and a ri of 0.49. As could be expected, the length is slightly longer and the ci and ri indices are slightly less high than those of the tree resulting from the initial analyses. It is on the other hand tempting to see that application of a weighting procedure on this conclusive cladogram yielded a tree with ci = 0.40 and ri = 0.83, whereas the one yielded from the primary analysis had a ci of 0.37 and an ri of 0.77. This implies that in the conclusive tree preference is given to characters which receive more weight *afterwards*. This could have been predicted, as in the decisions on the relative position of the monophyletic subgroups, but probably even more so in those concerning the 5 remaining species, the topology of the trees resulting from weighting procedures were taken into consideration.

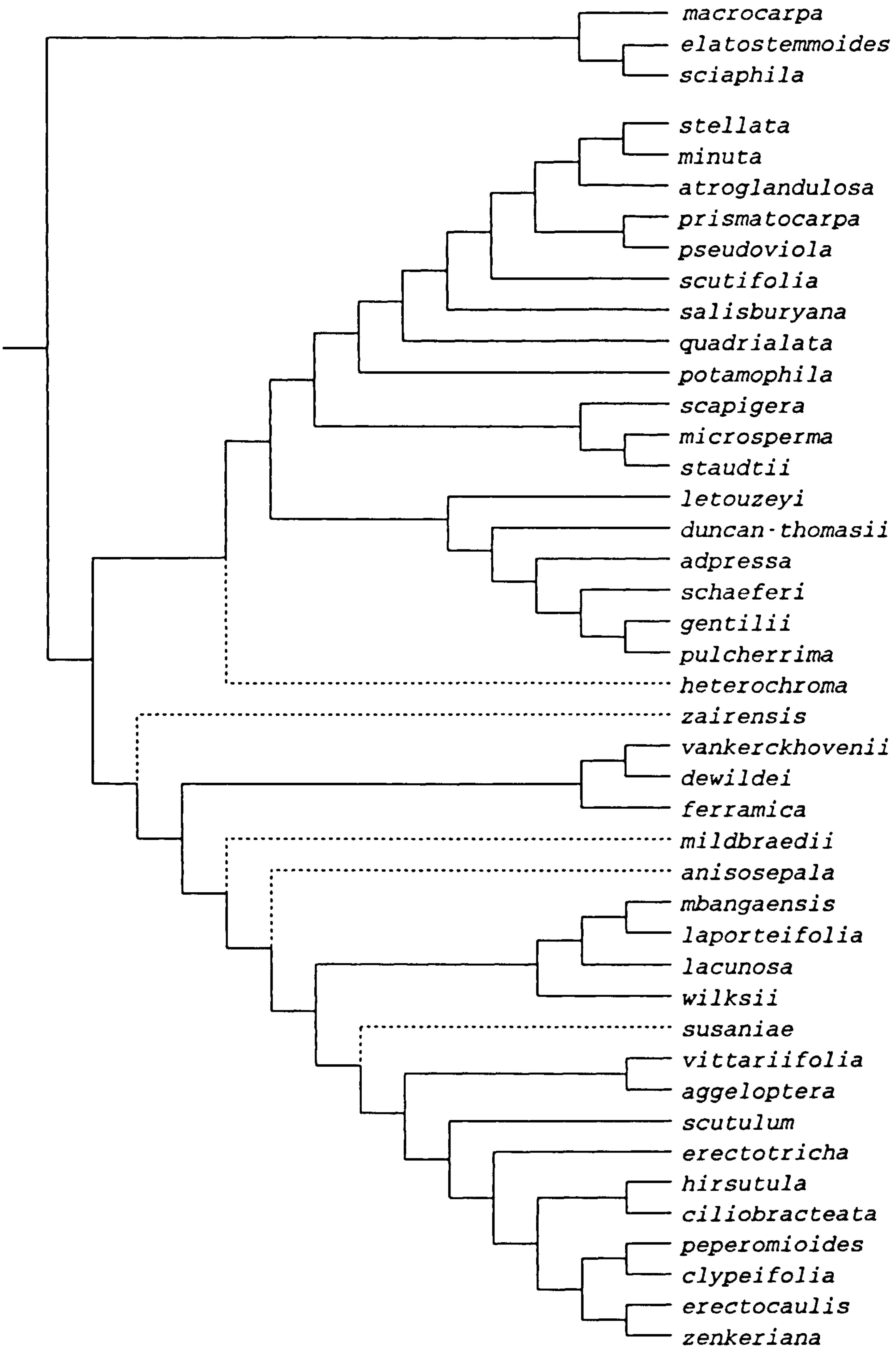


Figure 11.17. Conclusive cladogram of the species of sect. *Loasibegonia* and *Scutobegonia* with three species of sect. *Filicibegonia* denoted as the outgroup; dashed lines indicate more doubtful positions.

11.8 Discussion and conclusions

It is obvious by now that the initial cladogram was rejected in favour of one that is less parsimonious. Still, it is argued here that the presently accepted cladogram is closer to the 'truth' than was the initial one. The structure of the initial one is very feeble. This was already observed when at the very beginning of the process a few minor errors present in the data were corrected, immediately leading to a different tree topology.

The question whether or not the evolutionary process is parsimonious (Nelson & Platnick, 1981: 220 ff.) is applicable to the present situation. As the 'truth' about the evolutionary pathway is not available (in fact, it is what we try to perceive), it is difficult if not impossible to test whether application of the parsimony criterion has led to a 'correct' cladogram. In some cases concurrence with the geographical information present in the cladogram and historical geological evidence may present instruments for verification. As application of parsimony always leads to the *most likely* phylogeny, that is with a minimal amount of ad hoc hypotheses, parsimony seems to be *the only* criterion presently at hand to try and perceive the 'truth'. Less parsimonious cladograms have been accepted by previous authors (Adema, 1991; van Welzen, 1989) in situations similar to the present one.

The most important conclusion that can be drawn from the presented cladogram is that the sections *Loasibegonia* and *Scutobegonia* are most likely of a monophyletic origin. Hence, they are to be upheld as taxonomic units. It is not necessary to apply the concept of paraphyletic taxa as explained in the first paragraph of this chapter. One could argue about the appropriate taxonomic level for the two present taxonomic units. As a choice is largely arbitrary (see also paragraph 4.1), the best solution is to follow the custom within *Begoniaceae*, to consider taxonomic stability and to regard the units as sections.

Important synapomorphic characters for the section *Loasibegonia* are the juicy consistency of the petiole (13) and the presence of short sausage-shaped glands (99). The latter type of gland is, however, also present within several species of the section *Scutobegonia*. Important synapomorphies for the section *Scutobegonia* are the narrow width of the epidermal layer of the leaf blade (78), the presence of (though sometimes weakly developed) sclerenchymatous tissue around the tertiary nerves (93), the presence of a cuticula structure on the cells of the hairs (98), the presence of comparatively long and r-shaped glands (99; see remark above) and an obtuse operculum of the seed (126).

12 Glacial rain forest refuges and begonias

12.1 Pleistocene climate in tropical Africa

The geologic period starting at 2.5 Myr B.P. is characterized by about 9 major and some 12 minor glacials (Hamilton, 1982; Hamilton & Taylor, 1991). In Africa most, but not all, of these glacial periods were drier than the interglacial ones.

The best studied ice-age is the most recent one (±70,000–12,000 yr B.P.). All studies indicate that during this period the environment of tropical Africa was markedly cooler and drier than in our days (Bonnefille et al., 1990). Many data concerning climate and vegetation during the last glacial are available for the east African montane areas (especially Burundi and Uganda), while comparatively very few studies concern the lowlands of central and west Africa (Livingstone, 1975; Hamilton & Taylor, 1991). Fossil pollen records from east African mountains indicate a descent of the vegetation zones of about 1000 m which corresponds with a decrease in temperature of about 6° C (van Zinderen Bakker & Coetzee, 1972; Morrison, 1968; Hamilton, 1982, Bonnefille, 1987). Data from studies on the expansion and retreat of glaciers in this region suggest an even larger decrease of up to 9.5° C (Hamilton & Taylor, 1991). The latter value is probably too high, which is convincingly shown in the comprehensive study of Bonnefille et al. (1990). An estimation of 4 ± 2° C seems closer to the truth.

The coldest period of the last ice-age is dated at (21,000–)20,000 to 14,500(–14,000) yr B.P. (Hamilton, 1982; Hamilton & Taylor, 1991; Maley, 1991). The glacial maximum (driest period with lowest mean temperature) is generally dated around 18,000 yr B.P. From 12,500–12,000 onward climate changed fairly rapidly, becoming moister and warmer, though still colder than today (Giresse & Lanfranchi, 1984; Taylor, 1988). The period between about 9,000 and 4,000(–2,000) yr B.P. was characterised by higher temperatures and more precipitation than today (Hamilton, 1982; Talbot et al., 1984; Lezine, 1988). Other data show a less complex change with gradually warming and moistening from 18,000 yr B.P. onward and a sudden change towards conditions similar to those today at about 9,500 yr B.P. (Maley, 1987 & 1991).

It has been suggested that in western central tropical Africa, due to the influence of cold sea water upwellings, stratiform cloud cover may have been extensive during the glacial maximum, leading to a further reduction in temperature and precipitation, notably in the coastal regions (Maley, 1989). The occurrence of cold upwellings has also been confirmed by a study on variations in marine microfauna (Caratini & Giresse, 1979).

12.2 Pleistocene vegetation changes in tropical Africa

The decrease of temperature and precipitation during the last and also earlier glacial periods must have had a restricting influence on the the area occupied by rain forest vegetation in tropical Africa. Lönnberg (1929) was the first who hypothesized rain forest refuges as a result of these deteriorating conditions. The extent of the rain forest area must have oscillated in accordance with the oscillating climatic factors.

In the course of the study on changing rain forest areas a clear distinction must be made between lowland and montane rain forest vegetations, as their response to the changing climate will have been different and in some aspects even opposite. During a glacial period the area of lowland rain forest will undoubtedly have been diminished fairly drastically. On the other hand, the area of montane rain forest vegetation might well have expanded as a result of the lowering of temperature. Today montane rain forest vegetations are located roughly between 1,000 and 3,000 m altitude. This implies that, taking an average temperature decrease of 4°C, montane rain forest vegetations *could* have descended down to ±350 m a.s.l. (0.6°C per 100 m) as far as the temperature is concerned and consequently have covered a much larger area. It has been suggested that at the time of the last glacial maximum a more or less continuous belt of montane rain forest connected the east African mountain area through Zambia and Angola with the western Cameroon mountains (Hall & Moreau, 1970; Maley, 1991). The presence of montane rain forest, however, also depends on the amount of precipitation and its distribution over the year. The *general* decrease in precipitation during the last glacial period probably will not have allowed for such a vast and continuous extension. Locally, montane rain forest likely will have been present in Zambia and Angola (and possibly also elsewhere, like in parts of southern and western Zaire, western Congo, Gabon and southern Cameroon), in places with sufficient humidity. Relict populations of Afromontane plant species are present in these areas, which constitute the southern rim of the Zaire River catchment (Letouzey, 1968; White, 1981; Maley et al., 1990). In the same area pollen cores also show the former presence of montane rain forest elements (van Zinderen Bakker & Clark, 1962; Caratini & Giresse, 1979; Elenga & Vincens, 1990). Still, in view of the general aridity, it is more plausible that this area carried a (tree) savanna vegetation intermixed with patches of montane rain forest, rather than a continuous belt of this forest type. This idea was also proposed by Colinvaux (1989) for the Amazon region. Such a situation could well explain the considerable floristic similarities between the mountain flora of the west and east African mountains (Hepper, 1965; Hall, 1973), with the patchwork pattern of montane forest serving as a link in the form of 'stepping stones'. In this aspect the study of Lawton (1963) on riverine 'Mushitu'-vegetations in Northern Zambia containing both western African lowland elements and Afromontane ones and that of Meave et al. (1991) on riparian habitats as forest refuges are interesting.

As for lowland rain forest, it is generally agreed that three or four major refuge areas can be designated. The most western one was located in the Sierra Leone/ Liberia area (fig. 12.1, area 1 & a), the second in a central African area comprising south-western Cameroon, Equatorial Guinea and Gabon (fig. 12.1, area 2–5 & c & d), the third and most easterly situated area consists of eastern Zaire (fig. 12.1, area 6) (Aubréville, 1962; Diamond & Hamilton, 1980; Hamilton, 1982; Maley, 1987). There is, however, some disagreement about the exact location of the actual refuges within these areas. Several other authors denote a fourth refuge area along the shore of Tanzania (e.g. Hamilton & Taylor, 1991). Recently evidence for a refuge area located in the Zaire Basin was published (Colyn et al., 1991) and Kingdon (1980) suggested a refuge area around lake Leopold. The latter is refuted by climatic data presented by Moeyersons (1979).

The Sierra Leone/Liberia refuge area is thought to have been situated on the coast (Cape Palmas, fig. 12.1, area a) in propositions of for example Hamilton (1976) and Grubb (1982). Maley (1987, 1989), however, suggested it to be located more inland, due to the influence of the postulated stratiform cloud cover in the coastal zone. Moreau (1969) also positioned this refuge area more inland, based on vertebrate distribution data. Aubréville (1949, 1962), Guillaumet (1967) and Hamilton (1976) proposed two separate refuges in this area, one bordering the coast and one more inland (Mount Nimba and surroundings). On the basis of extensive forest inventory data van Rompaey (1993) concluded that a forest refuge near to the coast is much more likely than one situated inland around Mount Nimba.

Distribution data of both plants and animals point to a small refuge area located at Cape Three Points, in Ghana (fig. 12.1, area b; Aubréville, 1949, 1962; Hamilton, 1976; Diamond & Hamilton, 1980). But Maley (1987), again pointing to the stratiform cloud cover, and Moreau (1969), who did not find any evidence

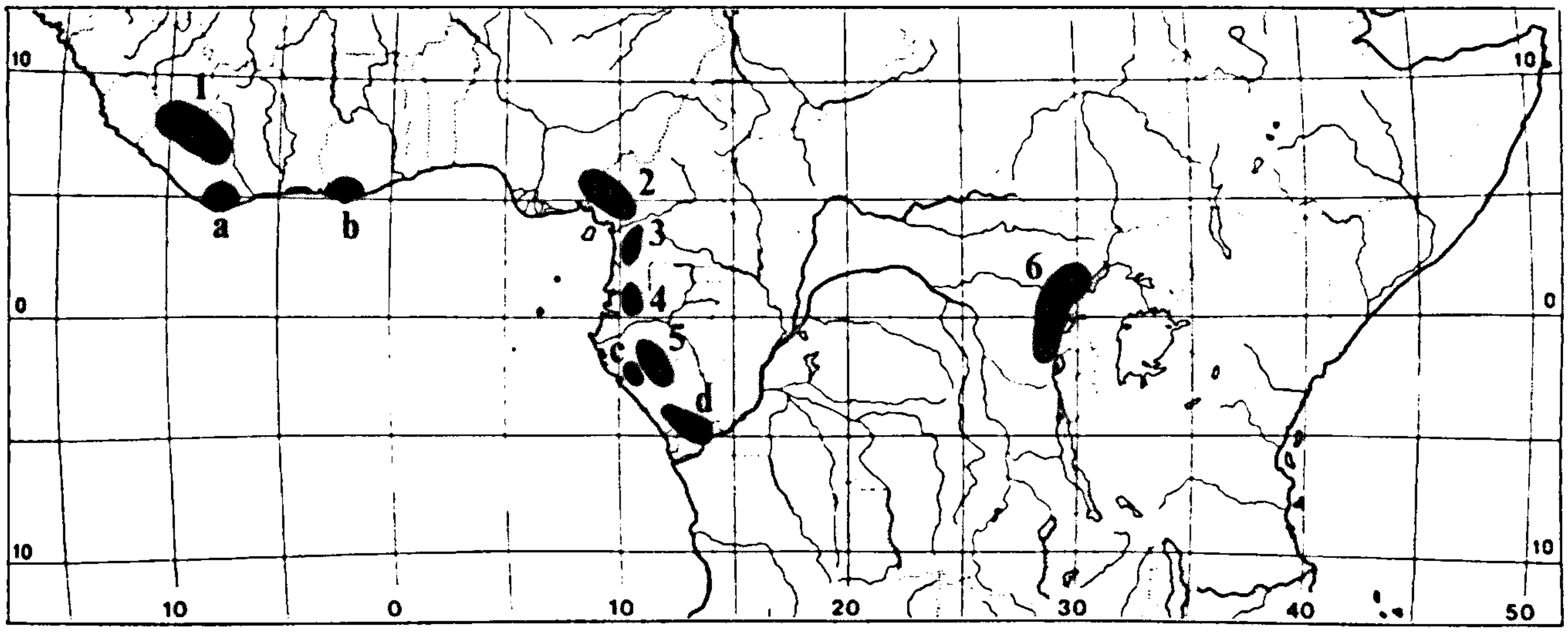


Figure 12.1. Possible glacial lowland rain forest refuge areas in Africa. 1–6: those proposed by Maley (1987); a–d: additional ones indicated by other authors and/or by the distribution patterns of *Begonia* taxa.

in distributional data, both refuted this. Important are the palynological data gathered around lake Botsumtwi (southern Ghana) (Maley, 1987). They show that forest vegetation was replaced by a savanna or savanna-bush vegetation during the coldest phase of the last glacial period.

Analyses of distributional data in order to locate refuge areas were generally performed on a large scale (e.g. Hamilton, 1976; Diamond & Hamilton, 1980; Mayr & O'Hara, 1986; Hamilton, 1988). That is probably why these studies all point to the presence of a single large refuge in the Cameroon/Gabon area. This area coincides with the Lower Guinea phytochorium of White (1979). Maley (1987) suggested that in this region actually four smaller refuges can be denoted (fig. 12.1, areas 2 through 5). His conclusions were based on the postulated stratiform cloud cover during the arid glacial period, as well as on biogeographical observations of Amiet (1987, on frogs), Aubréville (1962, on vegetation), Bernardi (1966, on butterflies), Grubb (1982, on primates), Letouzey (1968, on plants) and Myers (1982, on mammals). Palynological evidence gathered from lake Barombi-Mbo (western Cameroon) indicates the presence of a true lowland forest vegetation with some montane elements during the last glacial period and hence a forest refuge area (Maley & Brenac, 1987).

Most authors agree on the presence of a large refuge area in eastern Zaire (fig. 12.1, area 6). Kingdon (1980) stressed the need to distinguish a montane and a lowland refuge within this area, which is confirmed here.

It is remarkable that many of the proposed refuge areas are located in hill country. The hills might indeed have received more precipitation or were at least more humid due to prevailing clouds than the lower plains. On the other hand it was pointed out earlier that during the last glacial montane rain forest could have descended to fairly low altitudes. This implies that the actual lowland rain forest refuges might well have been smaller than the areas drawn in fig. 12.1 (or indicated in other publications) and that they were confined to the lower altitudinal zones of these areas, as was already suggested by Sosef (1992b). At the same time the upper altitudinal zones of these hilly areas may have been occupied by montane rain forest, which is confirmed by the occurrence of relict populations of montane species (see Maley, 1991: 88 for a review).

12.3 Begonias as bioindicators for former rain forest refuges

12.3.1 Distribution areas

The group of *Begonia* species studied shows several features rendering them quite useful to study glacial forest refuges. They seem to be suitable to serve as bioindicators for the geographic position of former forest refuges for the following reasons:

Most species are narrow endemics and generally inhabit primary rain forest, usually in the lowland but sometimes in the montane zone. They occur in wet to moist habitats and can be classified as strongly hygrophyllous (see chapter 11). Their narrow ecological amplitude and intolerance to changing environmental conditions is also shown by the problematic cultivation of the species under greenhouse conditions. These facts imply that during the last glacial they will not have been able to survive outside a rain forest refuge area. Because of the fact that their seed dispersal mechanism is not very effective in terms of dispersal ability (see paragraph 11.2.3 and Sosef, 1992b: 124), it is assumed that many species have not been able to migrate far away from the refuge areas in the period following the last glacial. This is even strengthened by the frequent presence of a self-incompatability system (see paragraph 11.2.3), which as a consequence requires at least two plants, and thus two seeds beforehand, for successful reproduction. These features imply that the present day distribution areas of the species will, very likely, still largely coincide with the former forest refuge areas.

Fig. 12.2 represents a map with the outlines of the distribution areas of all species and subspecies treated here. The distribution of the two sections as a whole coincides nicely with the areas covered with rain forest (White, 1983). It is supposed that the species with a large area of distribution (e.g. *B. hirsutula*, *B. mildbraedii* and *B. quadrialata*) are not very indicative for the geographic location of a refuge area. I assume that either their ecological preferences are not as strict as those of the other taxa involved, or that they might have a comparatively effective seed dispersal mechanism. As far as can be checked, the latter aspect is not supported by any morphological differences.

From fig. 12.2 we may conclude in general that the distribution patterns of the less widespread taxa very nicely reflect the proposed refuge areas discussed in the previous paragraph. A more detailed discussion follows below.

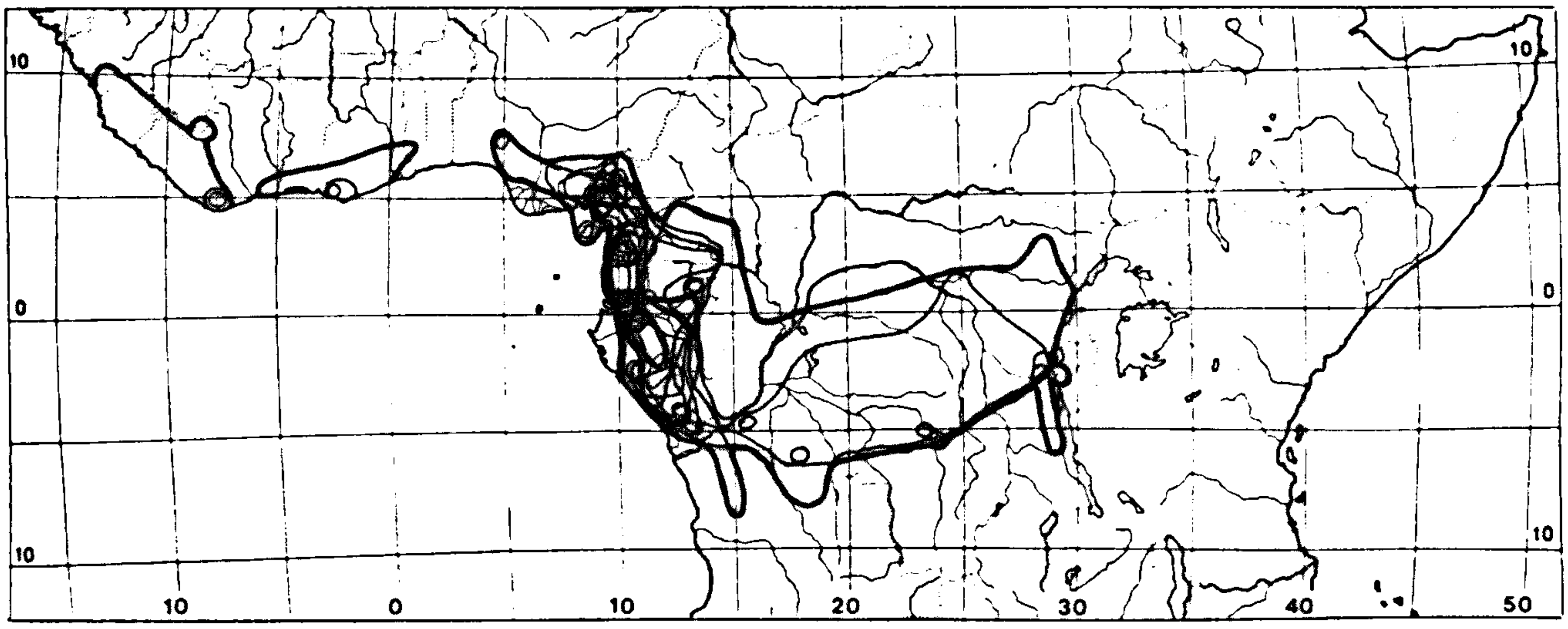


Figure 12.2. Outlines of distribution areas of all species and subspecies of the sections *Loasibegonia* and *Scutobegonia*.

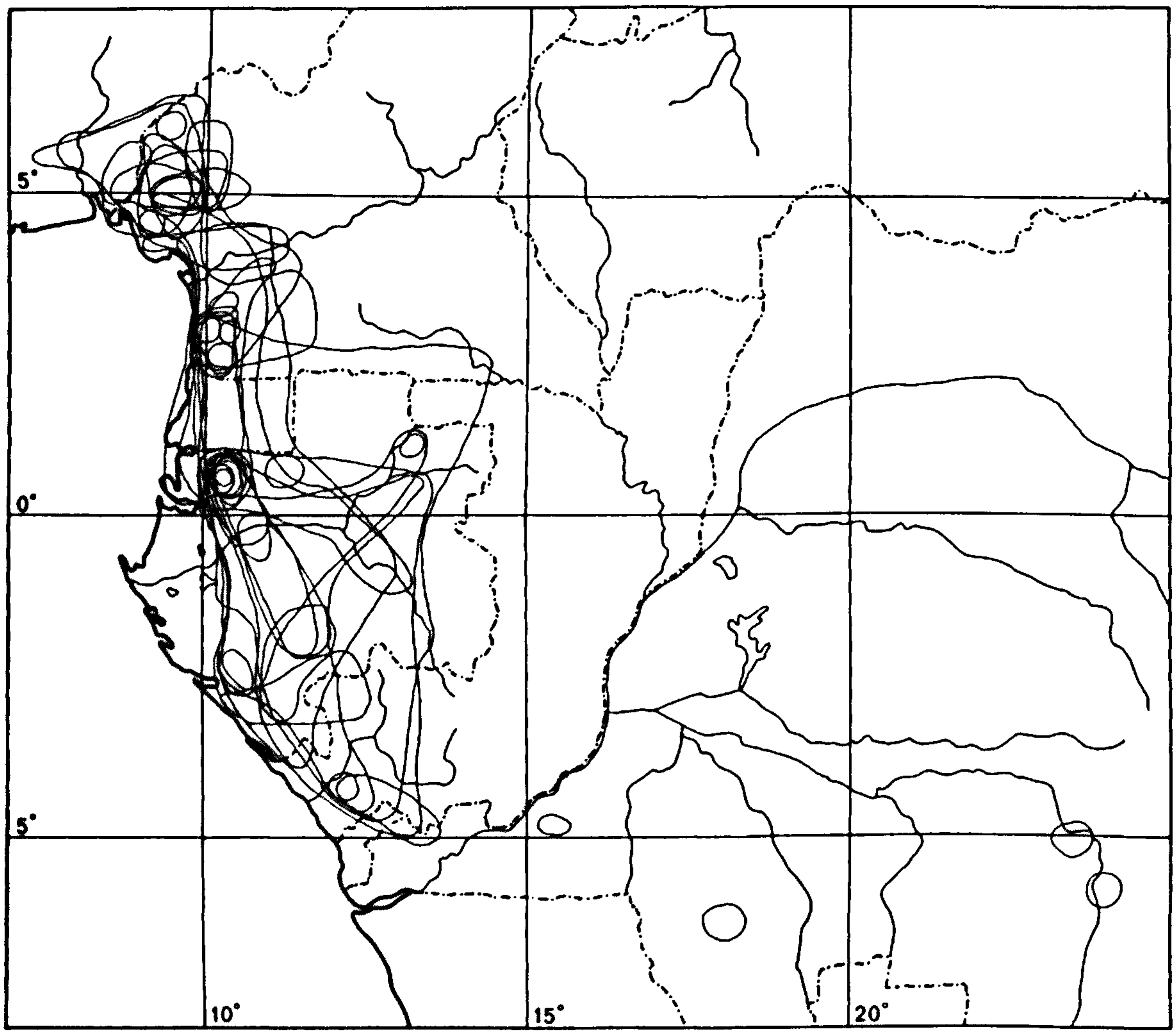


Figure 12.3. As fig. 12.2., but for a restricted area. Note the congruence between the centres with a high biodiversity and the refuge areas 1 through 6 depicted in fig. 12.1.

The Cameroon/Gabon refuge area:

The vast majority of the taxa occurs in this area and as such they strongly confirm that lowland rain forest was present here during the last glacial. A highly interesting observation is that within the Cameroon/Gabon area several subareas with a markedly higher species diversity can be denoted. A more detailed map of the distribution areas of the taxa in this area is presented in fig. 12.3. Comparing the latter figure with the refuges proposed by Maley (fig. 12.1, areas 1 through 6) leads to the conclusion that the distribution areas of the *Begonia* taxa involved strongly confirm the existence of the four smaller refuges within this area proposed by Maley (1987). From north to south these comprise: the western Cameroon mountains (fig. 12.1, area 2), the western part of the South Cameroon Plateau (fig. 12.1, area 3), the Crystal Mountains (fig. 12.1, area 4) and the Chaillu Massif (fig. 12.1, area 5).

Perhaps even more interesting is that, in addition to the four sub-areas mentioned, the distribution areas of the *Begonia* taxa suggest the former existence of several other refuge areas. The Mayombe area, situated in western Congo, Cabinda and western Zaire (fig. 12.1, area d) is one of them. This area has a very rich flora with many endemic species (UICN, 1989; Hecketsweiler, 1991). The second area comprises the Doudou Mountains (south-western Gabon, fig. 12.1 area c), which is occupied by a vegetation that also may be characterized as rich (Wilks, 1990; de Wilde pers. comm.). Besides the endemic species *B. dewildei* no less than 6 other *Begonia* species of the group studied occur here. The occurrence of the endemic species *B. ferramica* in the Bélinga area (north-eastern Gabon, fig. 13.2 area 13) seems to lead to the same conclusion, but as the latter species is somewhat drought-tolerant, I hesitate to suggest a refuge area at this locality as well.

The two suggested refuge areas in western Cameroon are separated by the Sanaga River. This Sanaga River interval has also been observed in the distribution of frogs by Amiet (1987) and that of mammals by Myers (1982).

One should note the absence of any *Begonia* taxon in the coastal area around Port Gentil (extreme west of Gabon). This area is occupied by a forest/savanna vegetation, apparently an unsuitable habitat.

The occurrence of many taxa outside the sub-areas mentioned above, might suggest that lowland forest vegetation did occur here during the last glacial, but perhaps much more patchy (e.g. gallery forest), or was of a somewhat drier type. These suggestions are, however, based on the assumption that practically no dispersal took place after the glacial period, which is probably not true for all taxa involved. On the other hand one wonders why some species dispersed from the proper refuge areas, while others did not: fruit and seed morphology do not indicate striking differences in dispersal potential.

Maley's (1987) concept of several small refuge areas in Cameroon and Gabon now coincides very nicely with the distribution patterns of *Begonia* species derived independently. We might conclude that these taxa can indeed be regarded as bioindicators for the position of glacial rain forest refuges. Here we may, however, end up in circular arguing, as Maley's ideas were also based on data of species distributions and biodiversity. Livingstone (1982) and Sosef (1992b) already warned against such circular reasoning and we should be cautious when formulating statements about former refuge areas based on distributional data. Therefore, the fact that Maley's ideas are at least partly based on paleoclimatological and palynological data is very important, as well as the observations made beforehand that these *Begonia* species have several features (ecology, seed dispersal), which make it plausible that their present day distribution will reflect the former position of those refuges. This is why I have little doubt about the conclusive statement that a concentration of *Begonia* species treated here is indicative of a former refuge area.

The Sierra Leone/Liberia refuge area:

Only few taxa are represented in this area. These seem to confirm the ideas of Aubréville (1949, 1962), Guillaumet (1967) and Hamilton (1976) that two refuge areas existed: one near the coast at Cape Palmas (*B. mildbraedii* and *B. prismatocarpa* subsp. *petraea*; fig. 12.1 area a) and one more inland around the Mount Nimba Massif (*B. quadrialata* subsp. *nimbaensis*; fig. 13.1 area 2), but the evidence is weak.

The Cape Three Points refuge area:

There is a small centre of diversity in this area (fig. 12.1 area b). Disjunct populations of *B. hirsutula* and *B. mildbraedii* occur here and seem to confirm the former presence of a rain forest refuge. However, both of these species are widespread and might well have survived in somewhat less wet and less shaded conditions (e.g. in riverine forest). Therefore, the presence of a true forest refuge in this area remains doubtful.

Populations of *B. salisburyana* and *B. scapigera* subsp. *scapigera* west of the Niger River (fig. 12.2) suggest that some forest remained here during the last glacial.

The eastern Zaire refuge area:

Sosef (1992b) already argued that the position of this refuge as indicated by Maley (1987) might be too northern. The former presence of a slightly more southernly situated refuge area (fig. 13.1 areas 24 and 25) seems to be confirmed by the presence of three taxa, *B. zairensis*, *B. pulcherrima*, and a disjunct population of *B. lacunosa*. As the first two species mentioned occur at medium and high altitudes it is uncertain whether their presence can actually be regarded as an indication for a lowland forest refuge.

A few taxa suggest the presence of isolated forest remnants in the southern part of the Zaire River Basin (*B. gentilii* and *B. vankerckhovenii*; fig. 13.2 area 23). The comparatively wide distribution areas of *B. hirsutula* and *B. mildbraedii* suggest that some lowland forest remained within the Zaire River Basin. Like in the Cameroon/Gabon area discussed above, this might have been distributed patchily (e.g. along rivers, as Meave et al. (1991) suggest for South America) or have been of a somewhat drier type. There are no indications of a major refuge area in the Zaire River Basin as suggested by Kingdon (1980) and Colyn et al. (1991).

12.3.2 Vicariance events

Vicariance is the segregation of an ancestral species into geographically isolated populations leading to speciation. The process of fragmentation of a once more or less continuous lowland rain forest area in tropical Africa during the last glacial period, seems optimal for the occurrence of vicariance events. Because of their short life cycle and the plasticity of their characters, the present species should be capable to evolve rapidly. Several authors plead for more phylogenetic and historical biogeographic research linking speciation with forest refuges (Simpson, 1988; Gentry, 1989). This should be performed on a group of organisms with strong ecological preferences for rain forest vegetation, such as the group of begonias presented here. Some preliminary studies have been published (e.g. Grubb, 1982; Griswold, 1991).

Historical biogeographic research generally tries to present a scenario of the evolution of a certain group, including vicariance, dispersal, extinction and, if possible, an indication of time. Time may well prove to be a very difficult but interesting aspect in the present study. Many glacial periods have prevailed in the Pleistocene (see paragraph 12.1). Most were characterized by lower temperatures and a decreasing precipitation, similar to the last one (Hamilton & Taylor, 1991: 73). We may assume that under these circumstances forest refuges existed during at least several glacial periods and, moreover, probably at more or less the same localities. Speciation events which took place during a comparatively ancient glacial period might well have become blurred by speciation events during more recent ones. This will be a problem when analysing the outcomes of the historical biogeographic research presented in the next chapter. On the other hand, the notion that we might find indications for speciation events from different glacial periods is intriguing.

12.4 Forest refuges, biodiversity and nature conservation

If forest refuges existed, we may expect localities with high degrees of endemism and biodiversity. The refuges constitute the areas from which individual species spread out after climatic conditions turned more favourable for rain forest vegetation. Therefore, knowledge about the exact geographical position of the former refuges is important in the light of nature conservation as was also stressed by Myers (1982). As nature conservation is a matter of great urgence, a method to predict high biodiversity using indicator species and without the need of time-consuming extensive inventories is very valuable.

It should be remarked that the term biodiversity is a rather flexible one. It may be defined as a measurement of species richness, of genetic diversity or a combination of both. When the term is applied for conservation purposes it should at least include some genealogic information, as was recently stressed by Williams, Humphries & Vane-Wright (1991).

13 Historical biogeography

13.1 Introduction

The aim of a historical biogeographical study is to provide a historical scenario explaining present-day distributions of extant organisms leading to a biogeographic history of the areas involved (see also paragraph 12.3.2). The first-order explanation for present day distributions is vicariance (e.g. Nelson & Platnick, 1981; Humphries & Parenti, 1986), which is related to the geological or, as in the present study, the climatological history of the areas involved. Starting point is a cladogram and an area/taxon data matrix in which terminal and sometimes also ancestral taxa are represented. When incorporated, an ancestral taxon is replaced by the sum of the areas of its descendants. These data are converted into a tree, an areagram, showing the possible historical relationships of the areas involved. By comparison of the phylogenies and historical relationships of the areas of several groups of extant organisms, congruencies are traced, which leads to a generalized areagram. While reducing the complexity of the original data by tracing congruencies, an underlying general historical pattern may be discovered. A shared vicariance pattern is interpreted as the result of a shared biogeographic history. Incongruencies are explained by ad hoc hypotheses comprising unique events such as dispersal, extinction, indifference to a speciation opportunity and collecting failure (Brooks, 1990; Humphries et al., 1988; van Welzen, 1992; Wiley, 1988).

13.2 Data

First of all the areas to be used in the analyses have to be defined. They should result from the denotation of the areas of endemism (at least one species confined to the area) supplemented with the remaining areas where the species studied occur (see also Axelius, 1991). This phase is very important and a study on where the borders between the denoted areas had to be drawn was performed using, next to the actual distribution patterns of the *Begonia* taxa involved, the following works: Amiet (1987; the Sanaga River interval), Aubréville (1949; possible refuges in west tropical Africa), Barret (1983; geology and vegetation of Gabon), Colyn et al. (1991; possible refuge in the Zaire bassin), Hamilton (1976, 1982; refuge areas), Hecketsweiler (1991; areas of endemism in Congo), Letouzey (1968; vegetation of Cameroun), Maley (1987, 1991; refuge areas), Ndjelé (1988; centres of endemism in Zaire), Reitsma (1988; vegetation of Gabon), Reitsma et al. (1992; forest refuges in the Crystal Mountains), White (1979, 1983; phytochoria and vegetation of Africa) and Wilks (1990; vegetation of Gabon). This resulted in the recognition of 25 areas as illustrated in fig. 13.1 and 13.2.

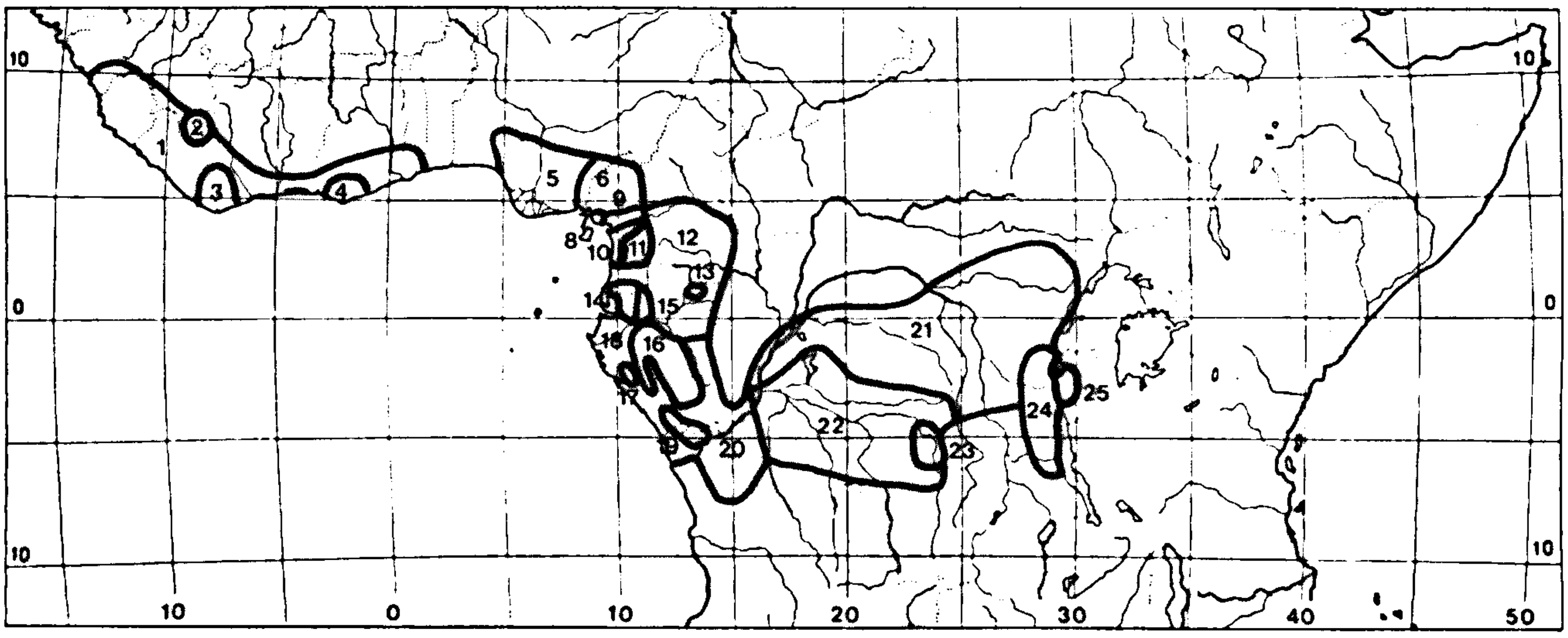


Figure 13.1. Areas of endemism used for the historical biogeographical analysis.

1 = west tropical Africa
2 = Mount Nimba
3 = Cape Palmas
4 = Cape Three Points
5 = S.E. Nigeria
6 = W. Cameroon mountains
7 = Mount Cameroon
8 = Bioko
9 = N. coastal Cameroon
10 = S. coastal Cameroon
11 = Cameroon Plateau
12 = upland Cameroon/Gabon
13 = Bélinga
14 = W. Crystal Mountains
15 = E. Crystal Mountains
16 = Chaillu Massif
17 = Doudou Mountains
18 = coastal Gabon
19 = Mayombe
20 = W. Congo/Zaire
21 = N.C. Zaire
22 = S.C. Zaire
23 = Sankuru
24 = E. Zaire
25 = Rwanda/Burundi

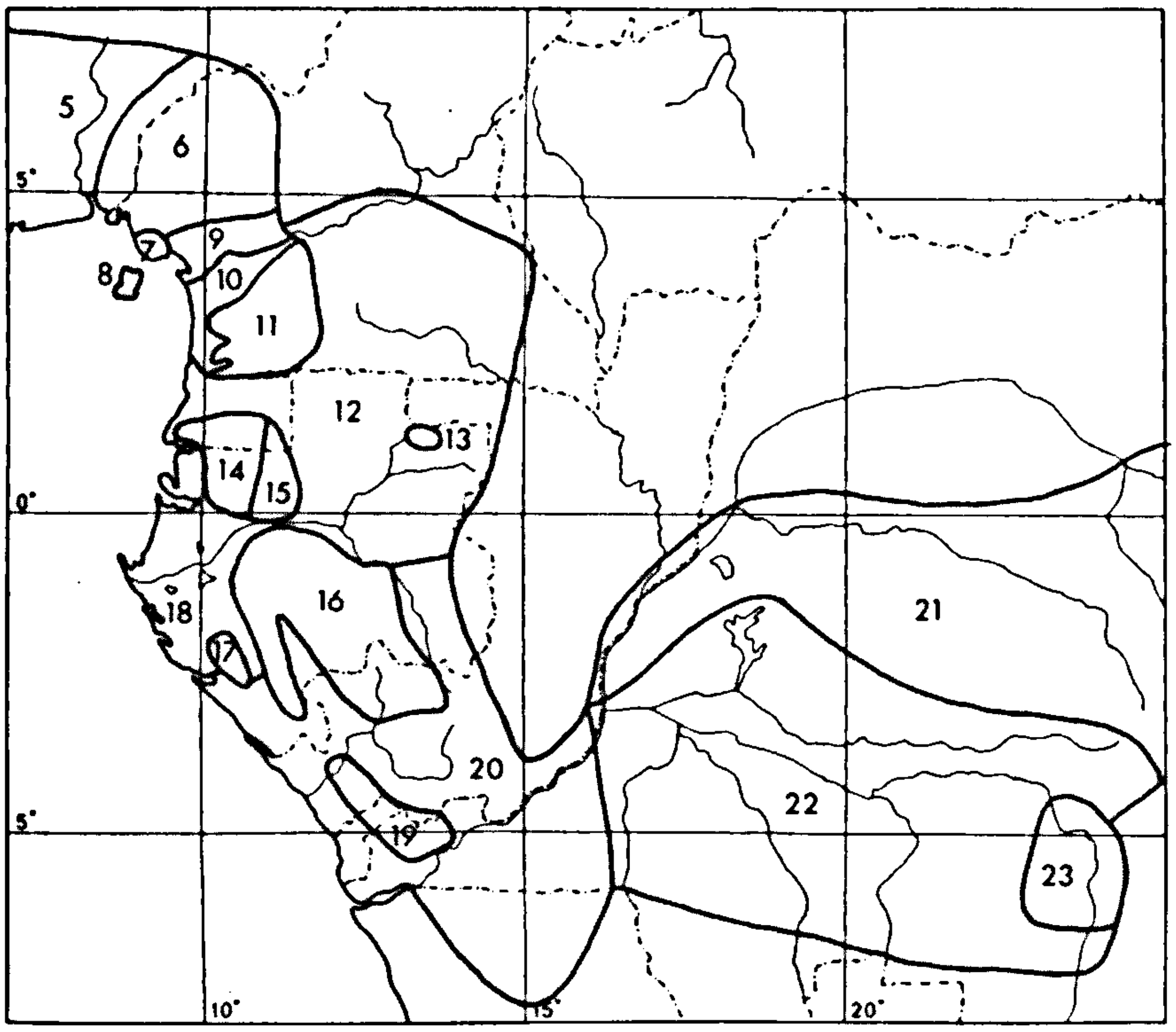


Figure 13.2. As fig. 13.1, but more detailed.

The cladogram of the species has to be transformed into an area/taxon data-matrix. The final cladogram as presented earlier in fig. 11.17 contains several species with doubtful phylogenetic relations (dashed lines) and can thus better not be used to extract the data.

When performing a historical biogeographic analysis it is desirable to analyse the data from two or more different groups of organisms leading to a generalized areagram. I have, despite intensive search and a general appeal (Sosef, 1992b), not been able to locate other suitable groups. In chapter 11 seven distinct monophyletic subgroups have been denoted. Those seven subgroups were used for the historical biogeographical analyses in order to extract generalized patterns. The information on subspecies was added. In the case of three subspecies these were added in an unresolved way to the branch of the species they belong to. Terminal taxa and hypothetical ancestors of all subgroups are shown in fig. 13.3a-g.

When a monophyletic subgroup as a whole is absent from a certain area, one can choose to code this absence as '0' or as 'unknown'. Coding absent or

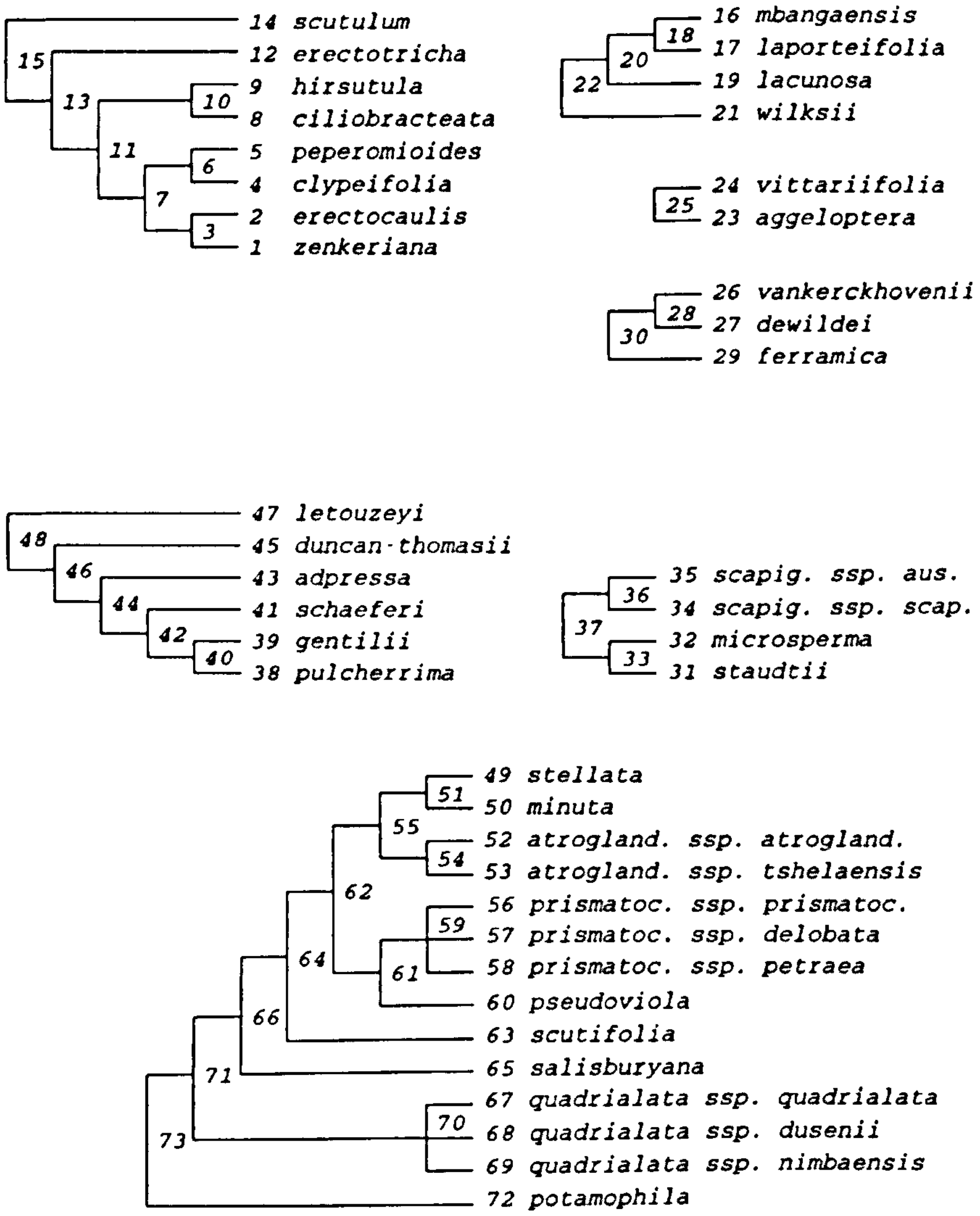


Figure 13.3. Seven monophyletic subgroups used for the historical biogeographical analyses. Numbers of taxa and hypothetical ancestors refer to table 13.1.

missing species as '0' assumes that they are primitively absent from (they nor their ancestors occurred in) the area or have become extinct. The 'unknown' state additionally incorporates the option of collecting failure (it should have been coded as present). Van Welzen (1992: 83) argues that missing species cannot be treated analogous to missing character states. Character states are coded as missing when a species lacks a certain structure. He argues that in that case all absent species should be coded as 'unknown' as all absence may be due to insufficient collecting. Brooks (1990: 21 ff.) is in favour of the use of the 'unknown' state but admits that an a posteriori explanation must be provided. Wiley (1988: 530) explains that coding for 'unknown' may cause problems when there are one or more areas with many missing monophyletic groups. Mainly because indeed many areas lack several of the monophyletic groups used in this analysis, it was decided to code the absence of a species always as '0'. The resulting complete datamatrix is given in table 13.1.

13.3 Methods

Several methods to conduct a historical biogeographical analysis exist. Among them two main groups can be identified: consensus methods (Component Analysis (CA); Page, 1988) and parsimony methods (Component Compatibility Analysis (CCA) and Brooks' Parsimony Analysis (BPA); Zandee & Roos, 1987; Wiley, 1988). The consensus methods need a priori assumptions, the so-called assumptions 1 and 2. They may therefore be regarded as less objective than parsimony methods which do not (van Welzen, 1992). Component Analysis is not suitable for the present data as comparatively many taxa are 'widespread', that is occurring in more than one area of endemism. The interpretation of the results of Component Analysis will then be extremely difficult, at least at present. The method was revised very recently (Page, 1993) but its possible improvements on this point were not yet studied by me. This leaves us with the two parsimony methods.

Biogeographic parsimony methods apply the same quantitative procedures as in phylogenetic parsimony analysis. This is based on the, sometimes questioned, validity of treating areas analogous to taxa and taxa analogous to characters. Synapomorphies represent sister-group relationships of taxa. A reversal respresents an extinction event, whereas a parallelism is interpreted as a dispersal event (Wiley, 1988). Van Welzen (1989: 108–109) has aptly demonstrated that application of BPA might lead to the characterization of a group of areas on the basis of the *absence* of clades, which does not indicate a common historical relationship. Such a relationship should always be based on the presence of clades. Van Welzen (1989: 98) also argues that the major disadvantage of the CCA method in phylogenetic analysis, i.e. the failure to construct the correct cliques in more complicated datasets, decreases when it is applied to historical biogeography. He notes that: 'now the correct cliques will always be formed, due to the fact that the structure of the cladogram has been included'. I, however,

Table 13.1. Distribution data of taxa and hypothetical ancestors (numbers refer to clades in fig. 13.3; an 'a' indicates a hypothetical ancestral taxon; a '*' marks an area with at least one endemic taxon).

	scutulum-group															wilksii-group							aggelopte-ra group			ferramica-group					scapigera-group						
			a			a	a			a	a		a		a			a		a		a			a			a		a			a			a	a
area/taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
West Trop. Afr.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
*Mount Nimba	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
*Cape Palmas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cape Three Pts	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S.E. Nigeria	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	1
*W. Cameroon Mts	0	0	0	0	0	0	0	1	1	1	1	0	1	0	1	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1
*Mount Cameroon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
*Bioko	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
N. Coastal Cam.	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
S. Coastal Cam.	1	0	1	0	0	0	1	1	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
*Cameroon Plateau	1	0	1	0	0	0	1	1	1	1	1	0	1	0	1	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1
Upland Cam./Gab.	0	0	0	1	0	1	1	0	1	1	1	0	1	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
*Belinga	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0
*W. Crystal Mts	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	0	0	1	1	0	1	1	1	1	1	0	1	0	1	0	0	0	0	0	0	0
E. Crystal Mts	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
*Chaillu Massif	0	0	0	1	0	1	1	0	0	0	1	0	1	1	1	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1
*Doudou Mountains	0	0	0	1	0	1	1	0	0	0	1	0	1	0	1	0	0	0	1	1	0	1	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0
Coastal Gabon	0	0	0	1	0	1	1	0	1	1	1	0	1	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
*Mayombe	0	0	0	1	0	1	1	0	1	1	1	0	1	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
W. Coastal Zaire	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0	1	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	1	1	1
N. Central Zaire	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S. Central Zaire	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0
*Sankuru	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0
Eastern Zaire	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
*Rwanda/Burundi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 13.1 (continued)

	letouzeyi-group											potamophila-group																								
			a		a		a		a		a			a			a	a				a		a	a		a		a				a	a		a
area/taxon	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73
West Trop. Afr.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1
*Mount Nimba	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1
*Cape Palmas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	0	1	1	0	0	1	1	0	1
Cape Three Pts	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1
S.E. Nigeria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0	1
*W. Cameroon Mts	0	0	0	1	1	1	1	1	1	0	1	1	0	1	0	0	0	1	0	1	0	1	1	1	1	0	1	1	1	1	0	0	1	1	1	1
*Mount Cameroon	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1
*Bioko	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	1	0	1	0	0	0	0	1	0	1
N. Coastal Cam.	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1
S. Coastal Cam.	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1
*Cameroon Plateau	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	1	1	1	1
Upland Cam./Gab.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	1	1	1	1
*Belinga	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	0	1
*W. Crystal Mts	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	1	1	1	1
E. Crystal Mts	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	1	1	0	1
*Chaillu Massif	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	1	1	1	1
*Doudou Mountains	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coastal Gabon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	0	1
*Mayombe	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	1	1	1	1
W. Coastal Zaire	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	1	1	0	1
N. Central Zaire	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S. Central Zaire	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
*Sankuru	0	1	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eastern Zaire	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
*Rwanda/Burundi	1	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

disagree on this point. When dispersal or extinction events have occurred, CCA will undeniable recognize 'incorrect' monothetic sets. When the 'correct' set is not indicated by any component in the data, the correct clique will still not be found. Therefore, BPA, should be preferred both in phylogenetic and in biogeographical analyses, especially when analysing data likely to contain comparatively many dispersal and extinction events, like the data presently at my disposal. When it appears a posteriori that one or more components of the areagram are based exclusively on the absence of clades, CC can be applicated. In fact, a distinct option should be built into a computer programme like PAUP (Swofford, 1991) in order to eliminate this flaw. The 'irreversable up' option in this program does not provide this neccessity, as it does not allow any reversals, hence extinctions, to occur. For all biogeographical analyses the programm Hennig86 (Farris, 1988) was used. A hypothetical outgroup containing 0's was added.

13.4 Towards a generalized areagram

Before combining the data of the separate monophyletic subgroups, it should be verified whether they indicate more or less the same biogeographic pattern. If not, a generalized pattern will be obscured by the conflicting individual biogeographic patterns when applying BPA (Cracraft, 1988). Separate analyses were performed on the *B. scutulum* group, *B. wilksii* group, *B. scapigera* group, *B. letouzeyi* group and the *B. potamphila* group. The patterns evolving from these groups are indeed more or less similar. Generally, the areas Cameroon Mts, Cameroon Plateau, W. Crystal Mts, Chaillu Massif and Mayombe appear to be closely related. Many areas remain in an unresolved position at the base of the areagram, as they are solely occupied by more widespread species. This situation is dealt with more extensively below.

It can be expected that at least some vicariance events shown in the areagrams of the individual groups are false ones, actually based on dispersal followed by speciation. True vicariance events can only be recognized from congruent patterns, either within an areagram of a single subgroup or in a generalized areagram based on different subgroups. As no congruent vicariance patterns are present among the areagrams of the individual subgroups (and also because of the necessity of a second and third analysis, see below), these results are not presented here.

The data matrix given in table 13.1 was analysed using the commands 'mhennig' and 'bb'. This yielded 74 equally parsimonious trees with length = 158, ci = 0.46 and ri = 0.63. A Nelson consensus tree (Page, 1989) was extracted from these 74 trees and is presented in fig. 13.4. It can be readily concluded from this figure that the tree is not very informative for individual areas. Some very general patterns may, however, be denoted. At the basal part of the areagram the first three splits branch off Rwanda/Burundi and almost all areas situated in western tropical Africa, including Mount Cameroon and Bioko. The next large polytomy seems to segregate several marginal areas in central Africa, leaving in the final large polytomy a 'core' comprising areas in Cameroon, Gabon and western Congo/Zaire, which were proposed as forest refuge areas in the previous chapter. It seems that true vicariance events are smothered by the presence of many so-called 'remnant areas'. These are only occupied by comparatively widespread species (van Welzen, 1992). The tree structure seems to collapse because of dispersal towards and extinction events within these remnant areas. Furthermore, in an areagram a vicariance event can only be shown when an area is occupied by at least one endemic species. If not, its position remains unresolved and the possibility exists that it will be falsely grouped together with other areas on the basis of absent clades (see previous paragraph) due to random extinction. This might be the case in the grouping of N. Coastal Cameroon with W. Coastal Cameroon and also that of E. Crystal Mts with W. Congo/Zaire. To overcome these problems two solutions are available. The first is to enlarge the initial areas of endemism, so that every area is occupied by at least one endemic taxon. The second is to eliminate all such remnant areas from the analysis. When the theory about forest refuges in Africa is correct and when the vast majority of the taxa presently involved did indeed not occur outside of a refuge area during the glacial period, it is permitted to choose the second solution. Areas not occupied by endemic taxa have either been colonized again after the last glacial or are occupied by taxa which remained indifferent. As our primary goal is to investigate whether the occurence of forest refuges has led to speciation, remnant areas can be left out a priori.

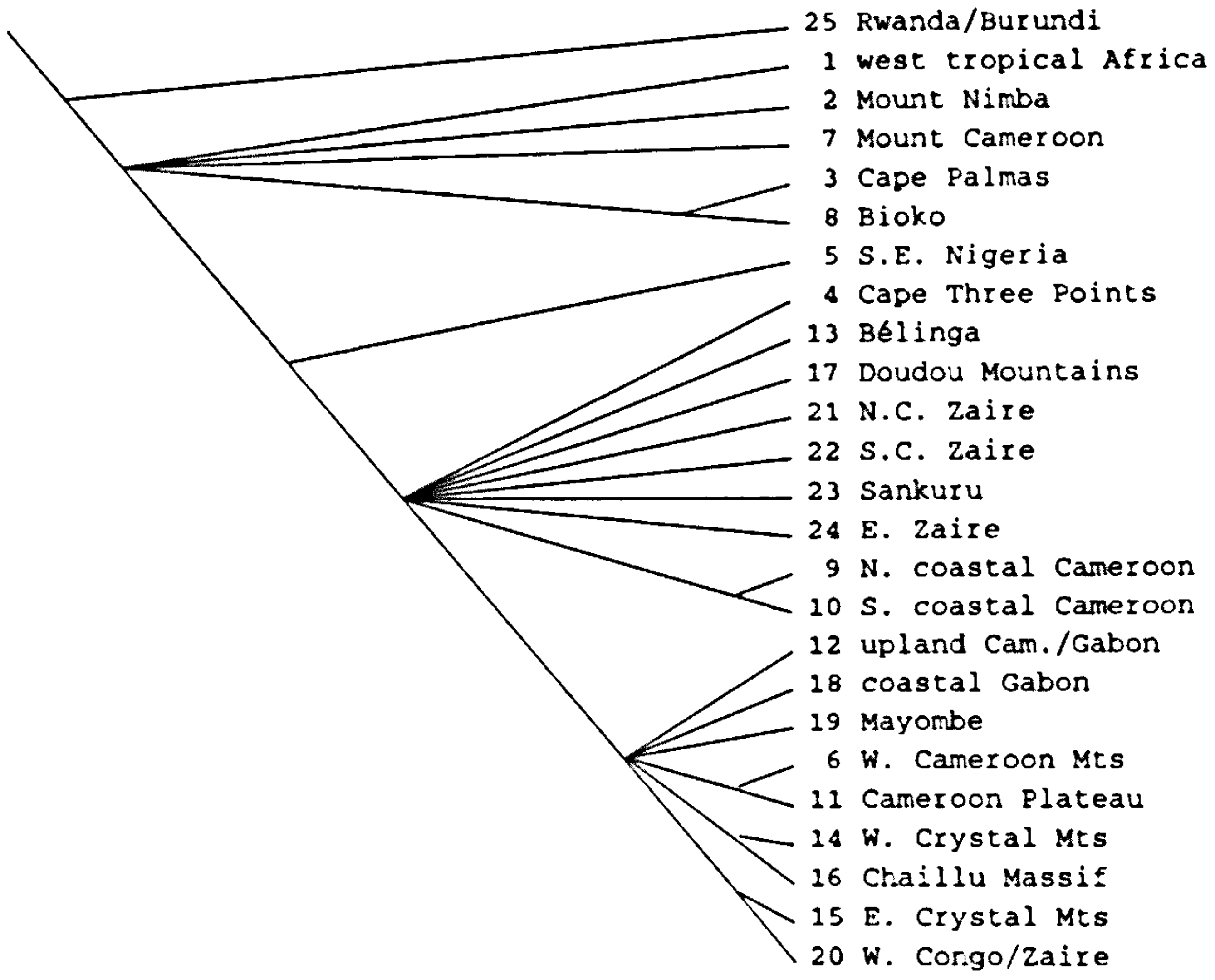


Figure 13.4. Nelson consensus tree of the generalized areagram incorporating all 25 areas.

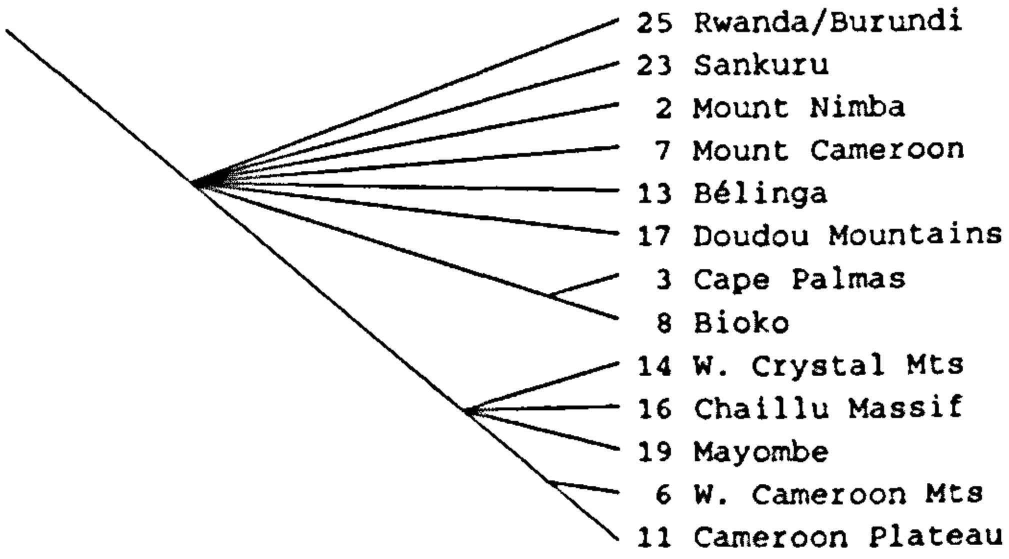


Figure 13.5. Nelson consensus tree of the generalized areagram incorporating the 13 areas denoted with an asterix in table 13.1.

A second analysis was run, this time using the 13 areas denoted with an asterix in table 13.1. The command 'ie' was applied and yielded 26 equally parsimonious trees with length = 120, ci = 0.60 and ri = 0.65. The Nelson consensus tree is presented in fig. 13.5. Due to the large basal polytomy it is still highly uninformative. Like in the first general analysis, a core area comprising areas in Cameroon, Gabon and W. Congo/Zaire is recognized as a distinct entity.

The position of the Doudou Mountains struck me as a bit aberrant. While the presence of species like *B. clypeifolia* and *B. lacunosa* seem to point at a relationship with the core area mentioned above, this does not show from the areagram. Its position seems to be based more on the lack of than on the presence of taxa. Could it be that the Doudou Mountains are still undercollected and that its position is caused by collecting failure? This is not likely as quite a few collectors have visited the area (pers. comm. de Wilde). It might be that its position has become unclear because of severe extinction. Perhaps even more impor-

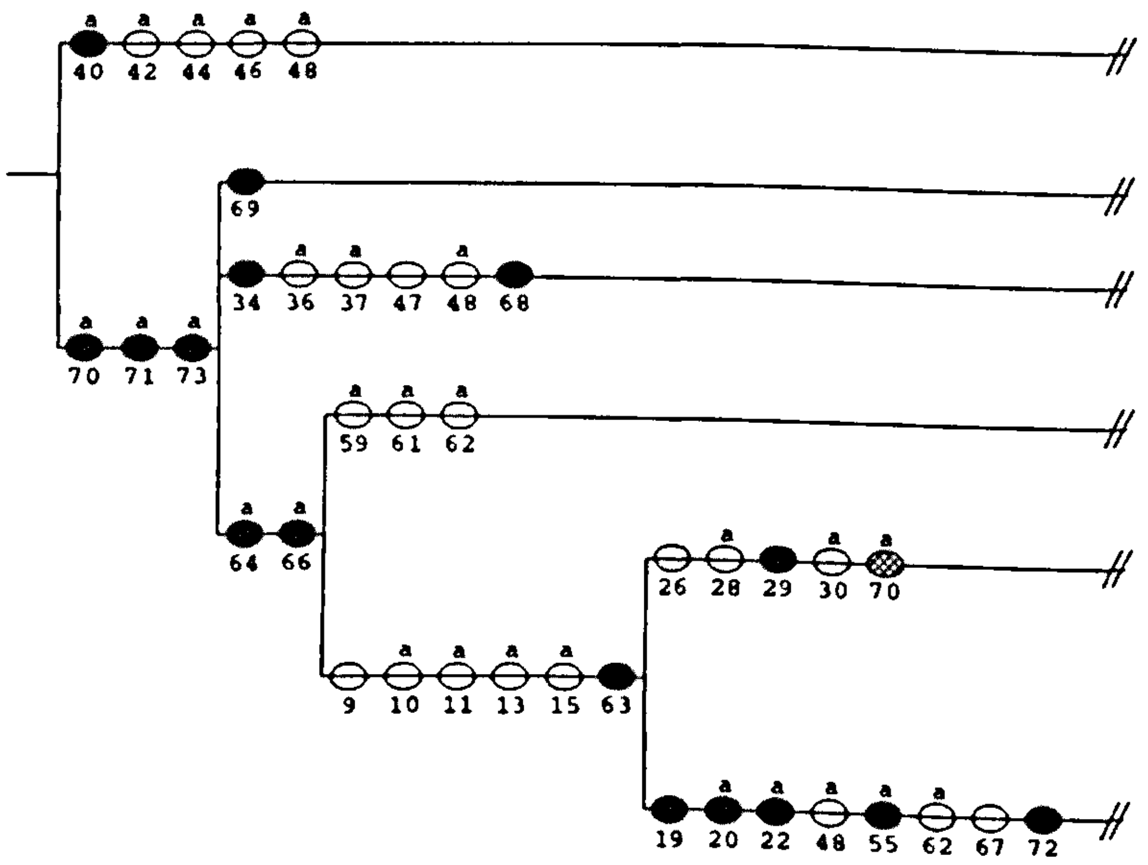


Figure 13.6. One of the three equally parsimonious generalized areagrams resulting from an analysis using the areas denoted with an asterix in table 13.1 but with the omission of the Doudou Mountains; black = apomorphy, open = parallellism (dispersal), hatched = reversal (extinction).

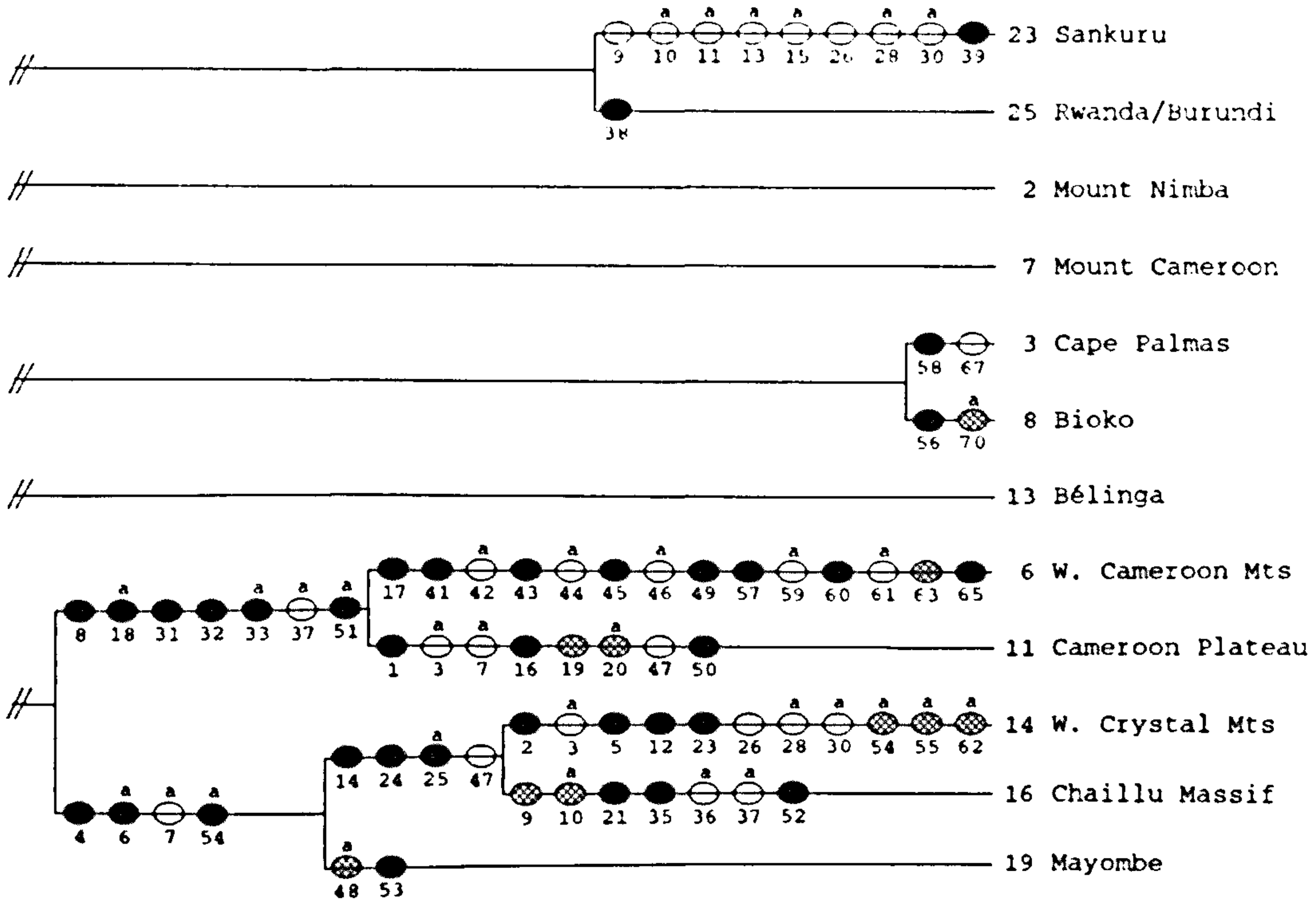
tant is, that analysing each of the 26 individual areagrams showed that the collapse of the trees into the major polytomy in the consensus tree, was mainly caused by the uncertain position of the Doudou Mountains! The obvious choice now is to leave this area out of the analysis as well and see how it influenced the position of the other areas.

A third analysis was performed, using 12 areas (the 13 ones of the previous run but without the Doudou Mountains). The command 'ie' was applied and yielded 3 equally parsimonious trees with length = 109, ci = 0.66 and ri = 0.69. One of these, which is similar to the Nelson consensus tree, is presented in fig. 13.6. The two other trees are given in fig. 13.7. Nowhere does grouping of areas take place solely on the basis of absence of taxa, hence it is allowed to accept the generalized areagrams. The one presented in fig. 13.6 is chosen as the accepted tree, because it is similar to the consensus tree and will therefore not contain any debatable information.

The exclusion of the Doudou Mountains has led to much better resolved trees without the previous large polytomy at the base. The relative position of the individual areas has not changed but apparently the uncertain position of this single area obstructed the obvious relationships of the other ones, like those of the W. Crystal Mts with the Chaillu Massif and of Rwanda/Burundi with Sankuru.

13.5 Discussion and analysis of the results

The generalized areagram presented in fig. 13.6 is regarded as the conclusive result of the historical biogeographical analysis. If the areagram in fig. 13.4,



based on the complete data set, is compared with that of fig. 13.6, it appears that the exclusion of remnant areas from the analysis did not influence the general pattern of relationships shown there. Because there appear to be no serious consequences or strange alterations, the exclusion of remnant areas is so far regarded as a valid action. Possible theoretical drawbacks have, however, not yet been elaborated on.

The splitting off of Rwanda/Burundi together with Sankuru at the very base of the areagram is most likely based on a dispersal event of ancestral taxon 42, which is shown by the parallelism. The early splitting off of these two areas in the areagram suggests that they became separated already comparatively early in geological history. The dispersal event may have taken place at any time, but the hypothetical ancestor of the 2 sections as a whole did probably not occur in these two areas, or at least not in Rwanda/Burundi. Sankuru does accommodate several primitive species, e.g. *B. mildbraedii* (not presented in the data) and *B. vankerckhovenii* (26), but the occurrence of the second species is more parsimoniously explained by dispersal. After the dispersal of ancestral taxon 42 vicariance has apparently occurred, resulting in the species *B. pulcherrima* (38) and *B. gentilii* (39). But, as this vicariance is not based on the occurrence of congruent patterns, a dispersal event with subsequent speciation is equally likely.

The next event is the simultaneous splitting off of Mount Cameroon and Mount Nimba, at least in the accepted tree. Again, the areagram suggests vicariance, in this case of the ancestral taxon 70, the ancestor of the three subspecies of *B. quadrialata*, but no supporting congruent patterns are present. However, we may regard the next segregation involving Bioko and Cape Palmas as a more or less congruent scene. Bioko and Mount Cameroon are situated closely together, separated by a shallow sea that was dry during most glacial periods. Cape Palmas and Mount Nimba are geographically close as well, and represent in fact the forest area in western tropical Africa. When we would slightly enlarge the basic areas of endemism, a congruent pattern would be observed, based on vicariance of the ancestor of *B. quadrialata* (taxon 70) and that of *B. prismatocarpa* (taxon 59). The areagram suggests that the separation of the forest area of western tropical Africa from that situated in central Africa is of comparatively ancient origin. The same is suggested for the combined area comprising Mount Cameroon and Bioko. This appears strange as the split is based on the evolving of two subspecies and we may easily construct a scenario explaining the observed patterns involving the most recent glacial. *B. quadrialata* was probably a comparatively widespread species occurring in western and central tropical Africa. During the last glacial, populations on Mount Nimba and Mount Cameroon became isolated, and vicariance occurred, producing two subspecies. During the following interglacial *B. quadrialata* subsp. *quadrialata* diffused from the refuge areas or from other isolated populations in central Africa and western Africa. In the latter area these refuges possibly comprised at least Cape Palmas, and probably also Cape Three Points (see chapter 12). For *B. prismatocarpa* a similar scenario can be postulated. The species was probably widespread in the period preceding the most recent glacial. Populations in Cape Palmas and Bioko now became isolated, which led to vicariance and the resulting two subspecies. These were, however, not able to diffuse again during the following interglacial. Regarding the two plausible scenarios above, which are, moreover, perfectly in line with the events suggested by the areagram, I conclude that the early secession of the four areas involved is probably caused by the fact that these areas are inhabited by only few taxa and thus closely resemble the hypothetical outgroup area. One could regard this as an artifact, as in fact van Welzen (1992: 76) suggests. On the other hand, this low number of taxa does imply that the areas were invaded from the core region, being separate from it already in an early geological time. Therefore, although the suggested vicariance events may have taken place in a recent geological time, the position in the areagram, showing a more ancient geographical relationship with the core area, might well be correct.

The remaining areas are grouped together because of the occurrence in each of them of two species: *B. hirsutula* (9) and *B. scutifolia* (63). The many parallel events on this branch and on that of Sankuru are in fact based on the dispersal of *B. hirsutula* and *B. vankerckhovenii* (26) to the latter area. This inevitably results in the presence of many ancestral taxa on these branches as well.

The next event is the separation of Bélinga from the core areas. Bélinga accommodates comparatively few species, but it is well sampled. The areagram suggests a possible vicariance event resulting in *B. ferramica* (29), which would imply that *B. vankerckhovenii* (26), an evolutionary more recent species, has dispersed towards this area afterwards. As was already suggested in chapter 11, *B. ferramica* is probably of ancient origin and did therefore not evolve as a result of recent climatological changes.

It should be noted that the remaining core region coincides with the Lower Guinea phytochorium of White (1979). The first division within this region results in Cameroon on one side and Gabon plus Mayombe on the other. Although the individual branches are loaded with clades, it is striking that only very few vicariance events seem to be involved (see below). The ancestral taxon 20 could be spread differently over the tree in an equally parsimonious way, viz. in a parallel situation below the Crystal Mts/Chaillu Massif/Mayombe and below the W. Cameroon Mts respectively. This would imply vicariance of this clade leading to *B. lacunosa* (19) in Gabon/Mayombe and ancestral taxon 18 in Cameroon. It would, however, at the same time assume dispersal of *B. lacunosa* across the Cameroon Plateau towards the W. Cameroon Mts, which is not very likely. Therefore it is presented here including an extinction event, although dispersal is often preferred above extinction, when one has a choice. Because of the very few vicariance events I hold the view that the relationships between the areas involved are caused by floristic affinities rather than by historical ones. Still, it implies that a floristic demarcation line can be drawn between these two sets of areas, situated somewhere across Equatorial Guinea. This demarcation may, however, appear more pronounced in the data because of the low collecting intensity at Equatorial Guinea, and proposing such an interval must be done with some restrictions. These data on *Begonia* species suggest there is a demarcation line, perhaps only a weak one, but it will need confirmation from data, based on other extant organisms.

The separation of Mayombe from the two Gabon areas is attended with vicariance of *B. atroglandulosa* s.l. resulting in the two different subspecies. This requires the extinction of the ancestral taxon 54 in the W. Crystal Mts. It may be defended that, similar to the situation discussed in the previous paragraph, the affinities between the W. Crystal Mts and the Chaillu Massif are a reflection of floristic affinities and not of historical ones. On the branch below these two areas three species and an ancestral taxon are present but none of them shows vicariance.

On the other hand the division of the two areas situated in Cameroon is accompanied by vicariance. Ancestral taxon 51 splits into *B. minuta* (50) in the Cameroon Plateau and *B. stellata* (49) in the western Cameroon mountains. A congruent pattern is encountered for ancestral taxon 18 leading to *B. laporteifolia* (17) in the western Cameroon mountains and *B. mbangaensis* in the Cameroon Plateau (16). These congruent vicariance patterns strongly support the segregation of the south-western Cameroon forest area and the existence of a demarcation line along the Sanaga River, as was already suggested by Amiet (1987). The two sister species *B. laporteifolia* and *B. mbangaensis* are very similar and the vicariance event giving rise to those species might well be of recent origin, possibly due to the existance of forest refuges during the last glacial. The two other sister species involved, *B. stellata* and *B. minuta* are comparatively dissimilar. I am therefore not inclined to believe that vicariance has occurred very recently. It might be the result of a more ancient event, possibly during a more ancient glacial.

The fact that only few vicariance events are traced from the generalized areagram, might be explained by assuming that these are only those of comparatively recent origin, e.g. that they took place during the last glacial (except perhaps for that of ancestral taxon 51, see above). Possible vicariance during previous glacial periods might well have become obscured by renewed dispersal resulting in the display of floristic affinities rather than of vicariance in the data. Others have already pointed to this inability of the present day historical biogeographic methods to reveal such complex historical patterns, especially in continental biotas: "Biogeographic patterns within continental biotas are produced by cycles of vicariance of widespread species, followed by narrow endemism, followed by population dispersion of descendant species to produce more widespread forms, followed by new cycles of vicariance" (Cracraft, 1988: 233). Application of analytical methods, such as BPA, which try to reduce complex data into a single scheme of relationships, does not seem able to reveal the underlying complex 'deep-history' of the biota.

13.6 Conclusions

When conducting a cladistic biogeographic analysis BPA is to be preferred above CCA.

The presence of comparatively many so-called remnant areas in the data poses problems. Skipping these areas from the analysis seems to improve the results, but further attention to theoretical and methodological consequences is required.

It is likely that in the Doudou Mountains comparatively many extinction events have taken place, probably as a result of environmental conditions during glacial periods.

The areagram suggests a biogeographical demarcation line across Equatorial Guinea, but as this area is still insufficiently sampled, no firm statement concerning such a demarcation line can be made.

The data support the presence of a demarcation line along the Sanaga River.

The areagram shows very few vicariance events. Most of the affinities of the areas in the core region are based on floristic similarities, not on historical relationships shown by vicariance. The only more or less likely vicariance events are those resulting in subspecies of *B. atroglandulosa*, *B. prismatocarpa* and *B. quadrialata* and resulting in the species *B. laporteifolia* and *B. mbangaensis* on one occasion and in the species *B. minuta* and *B. stellata* on another. These might be the result of the existence of forest refuges during the last glacial, although the latter two species seem too dissimilar to have evolved from a common ancestor during such a short period. They might be regarded as the sole proof of vicariance during more ancient glacials. Other vicariance events during previous glacial periods may well have become obscured by renewed dispersal. Biogeographical methods presently available are not yet able to reveal complex biogeographic histories.

14 Description of and key to the sections

14.1 Description of the section *Loasibegonia*

section ***Loasibegonia*** A.DC. Prodr. 15,1 (1864) 389; Warb. in Engl. & Prantl, Nat. Pflanzenfam. (ed. 1) 3, 6a (1894) 140; Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3,2 (1921) 618; Irmscher in Engl. & Prantl, Nat. Pflanzenfam. (ed. 2) 21 (1925) 574; Hallé, Adansonia, sér. 2, 7 (1967) 507; Baranov & Barkley, Sections of the genus Begonia (1974) 12; Reitsma, Meded. Landbouwhogeschool Wageningen 83-9 (1984) 23, 43-51; de Lange & Bouman, Acta Bot. Neerl. 34 (1985) 229; Arends, Acta Bot. Neerl. 34 (1985) 230; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 9 ff.; Bouman in de Wilde, Agric. Univ. Wageningen Papers 84-3 (1985) 124; de Wilde, Agric. Univ. Wageningen Papers 84-3 (1985) 125-127; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 13. – TYPE: *B. prismatocarpa* W.J. Hooker, *Mann 563* (K!, holo; B!).

series *Cordifoliae* Engl. in Engl. & Drude l.c. 616; Irmscher in Engl. & Prantl l.c. 574. – TYPE: *B. pseudoviola* Gilg., *Conrau 10* (B!, holo).

series *Euscutatae* Engl. in Engl. & Drude l.c. 617 p.p.; Irmscher in Engl. & Prant l.c. 574 p.p. – LECTOTYPE: *B. quadrialata* Warb., *Preuss 185* (B!; iso B!).

Perennial, terrestrial, rhizomatous monoecious or rarely androdioecious herbs. *Rhizome* with the apical part ascending. *Stipules* generally not persistent, narrowly triangular to very broadly triangular-ovate, herbaceous, with an entire to dentate and ciliate margin. *Leaves* entire, peltate or not; petiole terete, ***generally soft and juicy***; leaf blade slightly to distinctly asymmetrical, sometimes symmetrical, rarely lobed, palmately nerved but the midrib often more pronounced, tertiary nerves in dry condition usually ***not visible***. *Inflorescence* axillary, a contracted cincinnal monochasium consisting of (1–)2–4(–12) male flowers (up to 8 in male inflorescences of androdioecious species) and 1(–3) terminal female flower(s) which are all deflexed in bud; peduncle simple or sometimes branched up to three times; bracts patent, alternating, 1 below each flower, herbaceous, as a rule reducing in size upwards, with a dentate, ciliate margin. *Male flower* erect; pedicel elongated at maturity; perianth segments (sepals) 2, in bud folded together, more or less circular, yellow or less often white, with or without a red spot and nerves at the base, glabrous on the inner side; androecium a zygomorphic fascicle, with the stamens arranged in several distinct rows like in an amphitheatre; filaments fused at base into a central column, those of the inner rows shorter than those of the outer; anthers narrowly elliptic, with a rounded base and often emarginate top, yellow, opening by two unilateral longitudinal slits which run along the whole length of the anther and are facing the upper perianth segment. *Female flower* similar to the male but patent to erecto-patent or rarely erect; perianth segments often slightly larger than those of the male flower; styles 3 or 4, yellow (brown to dark red or purple when dry), fused in the lower part, the top split into two short to very short arms which bear a ***broad, reniform or semicircular*** stigmatic band which is ***not, or when semicircular***

only slightly coiled; ovary shortly beaked, 3–4-locular, 3–4-winged all along or only in the apical half, the wings ***narrow and ribbon-shaped to distinctly broadening upwards***, generally not enlarged in fruit, sometimes absent; the locular part in outline ***oblong to broadly obovate***; placentation axillary, a single placenta per locule, the placenta strongly thickened and not branched to slender, much branched and ± tree-shaped. *Infructescence* often with persistent bracts, its peduncle ***erect or bending outwards*** of the plant but always straight; mature fruit ***erect***, generally juicy at first but finally dry, indehiscent and disintegrating with age, smooth, shortly beaked, usually with a thin wall.

Leaf anatomy:

Surface view – *Non-glandular hairs* multicellular, multiseriate, present or absent on the adaxial surface, present on the nerves on the abaxial surface usually at least on the midrib, rarely absent, ***without cuticular ornamentation***, the cells generally not but sometimes with a slightly protruding tip. *Stellate scales* rarely present. *Curved glandular hairs* present on both surfaces, generally arranged ***in groups of 2–4***, sometimes solitary, situated in depressions or not, small, with a short stalk and short head of about 5–7 cells ('***sausage-shaped***'). *Globuliferous glandular hairs* sometimes present next to the curved ones, with a distinct stalk of 2–3 cells and a globose head of 4–5 cells. *Epidermal cells* polygonal, with straight anticlinal walls; cuticle smooth. *Stomata* regularly dispersed in the abaxial surface, sometimes closely spaced, helicocytic, generally level with the epidermis but sometimes slightly raised; neighbour cells with straight anticlinal walls.

Transverse section – *Lamina* 145–785 μm thick. *Epidermal cells* square to flat rectangular, the outer walls slightly to extremely convex, anticlinal walls generally distinctly ***zigzag*** in the centre, rarely straight; epidermal cells of the adaxial side ***(25–)40–125*** μm thick. *Hypodermis* absent. *Mesophyll*: palisade tissue composed of a single layer, generally of broadly rectangular cells with a rounded abaxial apex, sometimes of triangular cells, chloroplasts arranged along abaxial wall, either large ((17–)19–27 μm) or small (6–15 μm); spongy mesophyll with 1–3(–6) layers. *Midrib* not prominent or sometimes sunken adaxially, not to slightly prominent or sometimes distinctly so on the abaxial surface, with 1–3(–5) discrete vascular bundles arranged in an abaxial arc and sometimes with an additional bundle in the centre on the adaxial side; sclerenchyma sheath on the adaxial side of the vascular bundles absent or present, on the abaxial side of them absent or sometimes slightly developed. *Tertiary nerves* not or slightly prominent on the abaxial side, ***without or rarely accompanied by sclerenchyma tissue***. *Hydathodes* present near dents along the margin, with an epithem. *Crystals* solitary, prismatic, sometimes present and then most abundant near the main nerves.

14.2 Description of the section *Scutobegonia*

section ***Scutobegonia*** Warb. in Engl. & Prantl, Nat. Pflanzenfam. (ed. 1) 3, 6a (1894) 140; Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3,2 (1921) 615; Irmscher in Engl. & Prantl, Nat. Pflanzenfam. (ed. 2) 21 (1925) 574; Hallé, Adansonia, sér. 2, 7 (1967) 507; Wilczek, Fl. Congo, Rwanda et Burundi (1969) 5; Legro & Doorenbos, Neth. J. Agric. Sci. 21 (1973) 168; Baranov & Barkley, Sections of the genus Begonia (1974) 20; Reitsma, Meded. Landbouwhogeschool Wageningen 83-9 (1984) 23, 43–51; de Wilde, Acta Bot. Neerl. 34 (1985) 227; de Lange & Bouman, Acta Bot. Neerl. 34 (1985) 229; Arends, Acta Bot. Neerl. 34 (1985) 230; van den Berg, Agric, Univ. Wageningen Papers 84-3 (1985) 9 ff.; Bouman in de Wilde, Agric. Univ. Wageningen Papers 84-3 (1985) 124; de Wilde, Agric. Univ. Wageningen Papers 84-3 (1985) 125–127; Doorenbos, Begonian 53 (1986) 159; Cuerrier, Bull. Mus. natn. Hist. nat., Paris, 4e sér. 12, sect. B, Adansonia (1990) 323 ff.; idem 339 ff.; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 13; Sosef, Wageningen Agric. Univ. Papers 91-4 (1992) 87 ff.; idem 124 ff. – TYPE: *B. lacunosa* Warb., Preuss 183 (B! holo; B!).

series *Brevicaules* Engl. in Engl. & Drude l.c. 616; Irmscher in Engl. & Prantl l.c. 574. – LECTOTYPE: *B. hirsutula* Hook.f., Mann 1649 (K!; iso P!).

series *Euscutatae* Engl. in Engl. & Drude l.c. 617 p.p.; Irmscher in Engl. & Prantl l.c. 574 p.p.

Perennial, terrestrial, rhizomatous, monoecious herbs. *Rhizome* with the apical part ascending or more often erect to form a short, more or less distinct stem. *Stipules* generally not persistent, narrowly triangular to very broadly triangular-ovate, herbaceous, with an entire to dentate and ciliate margin. *Leaves* entire, peltate or not; petiole terete, generally ***firm and fleshy***; leaf blade slightly to distinctly asymmetrical, sometimes symmetrical, not lobed, palmately nerved but the midrib often more pronounced, tertiary nerves in dry condition usually creating a typical ***reticulate pattern***. *Inflorescence* axillary, a contracted cincinnal monochasium consisting of (1–)2–4(–7) male flowers and 1(–3) terminal female flower(s) which are all deflexed in bud; peduncle simple; bracts patent, alternating, 1 below each flower, herbaceous, as a rule reducing in size upwards, with a dentate, ciliate margin. *Male flower* erect; pedicel elongated at maturity; perianth segments (sepals) 2, in bud folded together, more or less circular, yellow or less often white, often with a red spot and nerves at the base; androecium a zygomorphic fascicle, with the stamens arranged in several distinct rows like in an amphitheatre; filaments fused at base into a central column, those of the inner rows shorter than those of the outer; anthers narrowly elliptic, with a rounded base and often emarginate top, yellow, opening by two unilateral longitudinal slits which run along the whole length of the anther and are facing the upper perianth segment. *Female flower* similar to the male but patent to erecto-patent or rarely erect; perianth segments often slightly larger than those of the male flower; styles 3 or 4, very rarely 2, yellow (brown to dark red or purple when dry), fused in the lower part, the top split into two distinct arms which generally carry a ***narrow and elongated stigmatic band*** which is ***not coiled to coiled*** with a single turn; ovary shortly to distinctly beaked, (2–)3–4-locular, 3–4-winged in the apical half or sometimes all along, the wings usually ***distinctly broadening upwards***, generally not enlarged in fruit, sometimes absent; the locular part in outline often ***obovate to broadly obovate, rarely narrower or ± circular***; placentation axillary, a single placenta per locule, the placenta usually much branched and ± tree-shaped. *Infructescence* often with persistent bracts, its peduncle ***recurved towards the substrate***, rarely curved and pulling the fruit in between the leaves or against the substrate; mature fruit ***pendulous*** on a curved or rarely straight pedicel, generally juicy, indehiscent and disintegrating with age, smooth, shortly to distinctly beaked, usually with a comparatively thick wall.

Leaf anatomy:

Surface view – *Non-glandular hairs* multicellular, multiseriate, sometimes with a multiseriate base and an uniseriate distal part, rarely entirely uniseriate, present or absent on the adaxial surface, on the abaxial one present on the nerves, at least on the midrib, generally ***with but sometimes without cuticular striation***, the cells with or without a slightly protuding tip. *Stellate scales* absent. *Curved glandular hairs* present on both surfaces, generally ***solitary***, situated in depressions or not, small, with an elongated stalk which raises the elongated head distinctly above the epidermal surface ('***r-shaped***') or sometimes with a short stalk and a short ellipsoid head of about 5–7 cells situated just above the epidermal surface ('***sausage-shaped***'). *Globuliferous glands* absent. *Epidermal cells* polygonal, with straight anticlinal walls; cuticle smooth or rarely irregularly shortly striate. *Stomata* regularly dispersed on the abaxial surface, sometimes closely spaced, helicocytic, generally level with the epidermis but sometimes slightly raised; neighbour cells with straight or sometimes undulating anticlinal walls.

Transverse section – *Lamina* 55-625 μm thick. *Epidermal cells* flat rectangular, the outer walls slightly convex, rarely extremely convex; anticlinal walls ***straight or sometimes slightly zigzag*** in the centre; epidermal cells of the adaxial side ***5–60*** μm thick. *Hypodermis* absent or rarely present and consisting of 1 layer on the adaxial and 1–4 layers on the abaxial side. *Mesophyll*: palisade tissue composed of a single layer, generally of broadly rectangular cells with a rounded abaxial apex, sometimes of triangular cells, chloroplasts arranged along the abaxial wall, small (6–15 μm) or rarely large (21–27 μm); spongy mesophyll with 1–3(–6) layers. *Midrib* not prominent or sometimes sunken adaxially, not or slightly prominent or sometimes distinctly so on the abaxial surface, with 1–5(–7) discrete vascular bundles arranged in an abaxial arc and sometimes with an additional bundle in the centre on the adaxial side; sclerenchyma sheath on the adaxial side of the vascular bundles sometimes absent, usually present, on the abaxial side of them absent or present. *Tertiary nerves* not or slightly prominent on the abaxial side, often ***accompanied by sclerenchyma tissue***. *Hydathodes* present near dents along the margin, with an epithem. *Crystals* solitary, prismatic, sometimes present and then most abundant near the main nerves.

14.3 Key to the sections

Among the African begonias the two sections *Loasibegonia* and *Scutobegonia* are characterized as follows:

Plants rhizomatous. Inflorescence a contracted cincinnal monochasium. Both male and female flowers with two perianth segments. Androecium a zygomorphic fascicle with the anthers opening by longitudinal slits and the filaments fused at base. Fruit indehiscent, disintegrating with age.

The short key presented below is meant to be of practical use and is therefore based on characters that can be observed macromorphologically. The delimitation of both sections is supported by several other anatomical and micromorphological characters discussed in previous chapters. When in doubt, these should be taken in consideration.

- Fruit more or less erect; the peduncle straight, sometimes lying almost horizontally on the substrate; petiole comparatively juicy and easily compressible; tertiary nerves without a sclerenchymatous sheath (except in *B. staudtii*), not forming a reticulate pattern in dry condition; ovary/fruit narrowly oblong to very broadly obovate (length/width ratio ± 10 – 0.9) . . . . *Begonia* sect. *Loasibegonia* A.DC.
- Fruit recurved towards the substrate and pendulous, rarely erect but then the peduncle curved and pushing the fruit in between the leaves (except in *B. zairensis*); petiole comparatively fleshy and firm; tertiary nerves with or sometimes with a weakly developed sclerenchymatous sheath, generally forming a prominent reticulate pattern in dry condition; ovary/fruit broadly obovate to very shallowly obtriangular (length/width ratio 1.2 – 0.3), rarely spindle-shaped with acuminate extremities . . *Begonia* sect. *Scutobegonia* Warb.

15 Key to the taxa of *Begonia* sect. *Loasibegonia* and sect. *Scutobegonia*

The description of the shape of the ovary and fruit always refers to the outline in side view. The used terminology of shapes is according to that provided by the Systematic Association Committee for Descriptive Biological Terminology (1962).

prefix to a shape	length : width
narrowly	6:1 – 3:1
no prefix	2:1 – 3:2
broadly	6:5 – 1:1
very broadly/transversely broadly	1:1 – 5:6
depressed/transversely/shallowly	2:3 – 1:2
transversely narrowly/very shallowly	1:3 – 1:6

1 – Leaf blade evidently not peltate 2

– Leaf blade peltate or sometimes sub-peltate 16

2 – Leaf blade narrowly ovate or wider; ovary/fruit narrowly oblong and not acuminate to very shallowly obtriangular with ribbon-shaped to shallowly obtriangular wings 3

– Leaf blade linear; ovary/fruit spindle-shaped, i.e. acuminate at the extremities, wingless . **B.** (*Scutobegonia*) **vittariifolia** N. Hallé (p. 278)

3 – Ovary/fruit narrowly elliptic-oblong to obovate, length/width ratio 1.5 or more; mature fruit erect 4

– Ovary/fruit very broadly obovate to very shallowly obtriangular, length/width ratio less than 1.0; mature fruit pendulous 10

4 – Perianth segments yellow; leaf blade distinctly asymmetrical, the margin entire, sinuate or dentate with acute teeth 5

– Perianth segments pink; leaf blade symmetrical to slightly asymmetrical, the margin dentate with both elongate-rounded and acute teeth . . . . **B.** (*Loasibegonia*) **stellata** Sosef (p. 214)

5 – Leaf blade ovate or broader (Ivory Coast, Nigeria, W. Cameroon or Bioko) 6

– Leaf blade narrowly ovate (S. Cameroon and Gabon) . . . . **B.** (*Loasibegonia*) **scutifolia** Hook.f. (p. 206)

6 – Leaf blade 0.8–7.0 x 0.6–4.3(–5.1) cm, the margin (shallowly) dentate or rarely entire, sparsely ciliate, upper surface hairy or glabrous . . 7

– Leaf blade (2.7–)4.0–11.2 x (2.1–)3.2–8.8 cm, the margin entire, usually distinctly ciliate, upper surface glabrous . . . . **B.** (*Loasibegonia*) **salisburyana** Irmscher (p. 197)

7 – Upper leaf surface glabrous or with up to 1.5 mm long, straight or wavy hairs 8
– Upper leaf surface with 3–7 mm long hairs which are more or less distinctly falcately curved . . . . **B.** (*Loasibegonia*) **pseudoviola** Gilg (p. 180)

8 – Leaf blade unequally (2–)3-lobed (Ivory Coast or Bioko) 9
– Leaf blade not lobed (W.-Cameroon) . . . . **B.** (*Loasibegonia*) **prismatocarpa** W.J. Hooker subsp. **delobata** Sosef (p. 179)

9 – Ovary/fruit elliptic to obovate, 2.9–4.8 mm wide (Ivory Coast) . . . . **B.** (*Loasibegonia*) **prismatocarpa** W.J. Hooker subsp. **petraea** (A. Chev.) Sosef (p. 179)
– Ovary/fruit narrowly ovate to narrowly obovate, 0.8–2.7 mm wide (Bioko) . . . . **B.** (*Loasibegonia*) **prismatocarpa** W.J. Hooker subsp. **prismatocarpa** (p. 175)

10(3) – Locular part of the ovary/fruit usually not hirsute, when hirsute the perianth segments yellow 11
– Locular part of the ovary/fruit densely hirsute; perianth segments white or pale pink . . . . **B.** (*Scutobegonia*) **zenkeriana** Smith & Wasshausen (p. 286)

11 – Lower leaf surface glabrous, at least between the nerves; locular part of the ovary/fruit rarely very sparsely hirsute 12
– Lower leaf surface shortly hirsute all over; locular part of the ovary/fruit generally sparsely hirsute . . . . **B.** (*Scutobegonia*) **erectocaulis** Sosef (p. 234)

12 – Leaf blade distinctly asymmetrical with the petiole attached more or less lateral to the blade, base distinctly cordate on the wider side . 13
– Leaf blade asymmetrical or slightly so with the petiole in line with the longitudinal axis of the blade, base cuneate to rounded on the wider side . . . . . **B.** (*Scutobegonia*) **peperomioides** Hook.f. (p. 264)

13 – Petiole making a distinct, almost right angle with the midrib; leaf blade borne in horizontal position (Gabon and W. Congo) 14
– Petiole continuing into the midrib without a distinct, almost right angle; leaf blade borne in more or less vertical position (widely distributed in tropical Africa) 15

14 – Leaf blade distinctly falcate, the margin crenate or sometimes serrate; petiole hirsute or sparsely so with long hairs. . . . . **B.** (*Scutobegonia*) **aggeloptera** N. Hallé (p. 216)
– Leaf blade not falcate, the margin entire to sinuate-dentate; petiole without or sometimes with very few long hairs . . . . **B.** (*Scutobegonia*) **clypeifolia** Hook.f. (p. 227)

15(13) – Perianth segments white or pale pink, very rarely yellow; mature fruit distinctly enlarged; ovary/fruit and wings usually dark pink, sometimes pinkish green to pale green or whitish . . . . **B.** (*Scutobegonia*) **ciliobracteata** Warb. (p. 222)

– Perianth segments yellow, rarely white; mature fruit not or only slightly enlarged; ovary/fruit and wings dirty dark red to pale red or brownish to olive green . **B.** (*Scutobegonia*) **hirsutula** Hook.f. (p. 242)

16(1) – Plant more or less glabrous or hirsute, but never arachnoid; ovary/fruit usually winged, rarely not winged 17

– Whole plant covered with a white arachnoid indumentum; ovary/fruit not winged . . . . **B.** (*Scutobegonia*) **ferramica** N. Hallé (p. 237)

17 – Petiole densely shortly woolly or felty pilose with curly pinkish red to pale pink hairs; leaf blade 0.9–6.1 x 0.5–3.8 cm 18

– Petiole glabrous or hirsute with long, straight to wavy, white to red hairs, rarely these longer hairs intermixed with short and curly ones; leaf blade often larger, 0.5–26.5 x 0.4–17.0 19

18 – Perianth segments white to pale pink; leaf blade narrowly obovate to narrowly elliptic-obovate, length/width ratio 3 or more . . . . **B.** (*Scutobegonia*) **dewildei** Sosef (p. 232)

– Perianth segments yellow to orange or salmon; leaf blade ovate or elliptic to broadly so or almost circular, length/width ratio 2 or less . . . . **B.** (*Scutobegonia*) **vankerckhovenii** De Wild. (p. 275)

19(17) – All inflorescences bisexual 20

– All or some inflorescences male, containing 4–8 male flowers . . . . **B.** (*Loasibegonia*) **schaeferi** Engl. (p. 203)

20 – Locular part of the ovary/fruit hirsute and in addition with minute glandular hairs, sometimes only sparsely hirsute or only with a fringe of hairs on the suture in between the locules 21

– Locular part of the ovary/fruit not hirsute, often with minute glandular hairs but lacking other hairs, long hairs sometimes present on the edge of the wings 32

21 – Leaf margin usually not entire, ciliate; main and larger secondary nerves sparsely hirsute to hirsute; upper leaf surface not with a reddish sheen in dry condition, glabrous to hirsute 22

– Leaf margin entire or with a few coarse and shallow teeth, glabrous to sparsely ciliate; main and larger secondary nerves not or sparsely hirsute on the lower surface; upper leaf surface often with a reddish sheen in dry condition, glabrous or with few long hairs . . . . **B.** (*Scutobegonia*) **scutulum** Hook.f. (p. 267)

22 – Tertiary nerves of the leaf blade with a sclerenchymatous sheath causing these nerves to be prominent in dry condition, and creating a distinct reticulate pattern 23

– Tertiary nerves of the leaf blade without a sclerenchymatous sheath, sometimes distinct but never prominent in dry condition 28

23 – Leaf blade with a length/width ratio of up to 2.5, upper surface bullate to smooth 24

– Leaf blade with a length/width ratio of 6 or more, upper surface rugose due to the sunken nerves . . **B.** (*Scutobegonia*) **wilksii** Sosef (p. 280)

24 – Perianth segments yellow or rarely white but then the upper leaf surface bullate; petiole and main nerves densely to sparsely hirsute with long and wavy hairs only 25

– Perianth segments white; upper leaf surfae rugose; petiole and main nerves densely hirsute with two types of non-glandular hairs, the first being comparatively long and wavy, the second much shorter, more slender and often curly. **B.** (*Scutobegonia*) **laporteifolia** Warb. (p. 254)

25 – Upper leaf surface smooth 26

– Upper leaf surface bullate . **B.** (*Scutobegonia*) **lacunosa** Warb. (p. 249)

26 – Leaf margin usually denticulate, rarely almost entire; apical 1/4 of the leaf blade usually acute or acuminate (the actual top blunt to acute) 27

– Leaf margin crenate; apical 1/4 of the leaf blade rounded . . . . **B.** (*Scutobegonia*) **mbangaensis** Sosef (p. 259)

27 – Locular part of the ovary/fruit usually without any or rarely with a few long hairs; wings on the ovary/fruit usually very shallowly obtriangular, sometimes to shallowly obtriangular-obovate . . . . **B.** (*Scutobegonia*) **erectotricha** Sosef (p. 237)

– Locular part of the ovary/fruit usually distinctly hirsute, rarely only sparsely so; wings on the ovary/fruit usually depressed obovate to broadly obovate, rarely to shallowly obtriangular . . . . **B.** (*Scutobegonia*) **lacunosa** Warb. (p. 249)

28(22) – Upper leaf surface smooth 29

– Upper leaf surface bullate . . . . **B.** (*Loasibegonia*) **duncan-thomasii** Sosef (p. 156)

29 – Main and larger secondary nerves on the lower surface glabrous or hirsute with patent hairs; upper leaf surface usually densely to sparsely hirsute 30

– Main and larger secondary nerves on the lower surface with adpressed hairs; upper leaf surface not hirsute . . . . **B.** (*Loasibegonia*) **adpressa** Sosef (p. 149)

30 – Locular part of the ovary/fruit sparsely to densely hirsute 31

– Locular part of the ovary/fruit with only a few solitary hairs . . . 46

31 – Leaf blade usually with a few coarse and shallow teeth in the apical half, elliptic to elliptic-ovate or broadly ovate; ovary/fruit circular or broadly obovate to obovate or elliptic . . . . **B.** (*Loasibegonia*) **letouzeyi** Sosef (p. 162)

– Leaf blade without any coarse and shallow teeth in the apical half, circular to broadly elliptic or broadly to very broadly elliptic-ovate, sometimes depressed ovate; ovary/fruit spindle-shaped (with acuminate extremities) or narrowly elliptic to obtriangular-obovate . . . . **B.** (*Loasibegonia*) **potamophila** Gilg (p. 171)

32(20) – Upper leaf surface bullate, sometimes only sparsely so (in dried condition a state with small bullae (of 1–2 mm elevation) is not seldom almost completely lost but can often be deduced from the fact that the hairs on the upper surface have a distinctly widened base, which is actually the very top of the bulla; when in doubt, check with *B.* (*Loasibegonia*) *staudtii* p. 210) 33

– Upper leaf surface smooth 36

33 – Ovary/fruit elliptic to elliptic-oblong or narrower, wings absent or ribbon-shaped 34

– Ovary/fruit broadly obovate to very shallowly obtriangular, wings always present, obovate to very shallowly obtriangular 35

34 – Leaf blade with large and distinct bullae, 1–3(–5) on each 0.25 cm^2 . . . . **B.** (*Loasibegonia*) **microsperma** Warb. (p. 166)

– Leaf blade with small bullae, 10 or more on each 0.25 cm^2 . . . . **B.** (*Loasibegonia*) **staudtii** Gilg (p. 210)

35(33) – Ovary/fruit broadly to very broadly obovate; apical part of the petiole and main and larger secondary nerves in dry condition conspicuously knobby; fruit erect . **B.** (*Loasibegonia*) **duncan-thomasii** Sosef (p. 156)

– Ovary/fruit very broadly triangular-obovate to shallowly obtriangular in side view; petioles and nerves in dry condition smooth; fruit pendulous . . . . **B.** (*Scutobegonia*) **susaniae** Sosef (p. 271)

36(32) – Length/width ratio of the locular part of the ovary/fruit 3 or more; wings absent or ribbon-shaped or becoming slightly wider towards the top; rarely the locular part wider but then wings absent or very narrow ($\leq$ 1 mm); ovary and wings translucent 37

– Length/width ratio of the locular part of the ovary/fruit 2 or less; wings always present, widened towards the top, usually distinctly so; ovary and wings usually not translucent 48

37 – Leaves with long, non-glandular hairs, sometimes only very few, at least on the petiole and/or leaf margin or, if lacking non-glandular hairs then leaf blade more than 5 x 3 cm; leaf blade symmetrical or not 38

– Leaves lacking any long, non-glandular hairs; leaf blade symmetrical, usually broadly caudate in the upper 1/2 or 1/3, 1.2–3.9 x 0.5–1.5 cm . . . . **B.** (*Loasibegonia*) **minuta** Sosef (p. 170)

38 – Plant with 2 kinds of minute glandular hairs, sausage-shaped ones intermixed with shortly stalked ones with a round head, the second in dry condition usually well visible on the peduncle, pedicel and ovary as tiny, black or dark purple spots (both types minute, 20x!); upper leaf surface usually with scattered, short and stiff, non-glandular hairs, at least near the margin 39

– Plant only with minute sausage-shaped glandular hairs which are pale to medium brown in dry condition; upper leaf surface without or with long and wavy, non-glandular hairs 40

39 – Perianth segments white (W. Congo and W. Zaire) . . . . **B.** (*Loasibegonia*) **atroglandulosa** Sosef subsp. **tshelaensis** Sosef (p. 154)

– Perianth segments yellow (S. Gabon) . . . . **B.** (*Loasibegonia*) **atroglandulosa** Sosef subsp. **atroglandulosa** (p. 151)

40(38) – Leaf blade more or less symmetrical, length/width ratio 1.7 or less; both leaf margins shallowly and remotely but distinctly dentate, at least in the apical half; wings on the ovary absent or less than 1 mm wide 41

– Leaf blade slightly to distinctly asymmetrical; leaf margin entire or remotely dentate only on the broader side of the blade; rarely leaf blade more or less symmetrical and remotely dentate on both sides but then length/width ratio 3 or more; wings on the ovary always present, (0.2–)0.5–4.0(–5.5) mm wide 44

41 – Petioles sparsely hirsute; leaf blade ovate to elliptic or broadly elliptic-ovate, the margin concolorous with the blade (E. Zaire, Rwanda, Burundi) 42

– Petioles without or with only a few long hairs; leaf blade broadly elliptic-ovate to almost circular, usually with a distinct pink to dark red margin (S.E. Nigeria, W. Cameroon, Gabon, W. Congo) 43

42 – Wings on the ovary ribbon-shaped; nerves on the lower leaf surface sparsely hirsute; peduncle (3–)8–22 cm long; style of a complex shape (see figs 16.13.4 & 5) . . . **B.** (*Loasibegonia*) **pulcherrima** Sosef (p. 183)

– Wings on the ovary obovate; nerves on the lower leaf surface not hirsute; peduncle 2.5–3 cm long; styles 'normal' (see fig. 16.5.3) . . . . **B.** (*Loasibegonia*) **gentilii** De Wild. (p. 158)

43(41) – Pedicel of the mature fruit 7–27 mm long; ovary/fruit elliptic to circular or broadly obovate (S. Gabon, W. Congo) . . . . **B.** (*Loasibegonia*) **scapigera** Hook.f. subsp. **australis** Sosef (p. 202)

– Pedicel of the mature fruit up to 6 mm long; ovary/fruit linear to narrowly elliptic or rarely elliptic (S.E. Nigeria, W. Cameroon, N. Gabon) . . . . **B.** (*Loasibegonia*) **scapigera** Hook.f. subsp. **scapigera** (p. 199)

44(40) – Wings on the ovary ribbon-shaped or rarely narrowly obovate, 0.2–0.7 mm wide; length/width ratio of the ovary/fruit 5.0 or more 45

– Wings on the ovary usually obovate to obtriangular, rarely ribbon-shaped, (0.2–)0.5–4.0(–5.5) mm wide; length/width ratio of the ovary/fruit 0.9–3.5 46

45 – Leaf blade almost linear to elliptic-ovate, sometimes broadly elliptic or broadly ovate, usually distinctly asymmetrical, at least the elliptic-ovate or broader leaf blades, and gradually tapering towards the top to distinctly acuminate in the apical 1/3 to 1/4 (S.-Cameroon, Gabon, Angola-Cabinda) . . . . **B.** (*Loasibegonia*) **scutifolia** Hook.f. (p. 206)

– Leaf blade elliptic-ovate and gradually but long acuminate in the apical 1/3 to 1/2, only slightly asymmetrical (Mount Cameroon) . . . . . **B.** (*Loasibegonia*) **quadrialata** Warb. subsp. **dusenii** (Warb.) Sosef (p. 194)

46(44) – Leaf blades more or less concolorous, or sometimes with a red margin 47

– Leaf blades with distinct dark green to dark purplish zones around the main and larger secondary nerves (Mount Nimba) . . . .
B. (*Loasibegonia*) **quadrialata** Warb. subsp. **nimbaensis** Sosef (p. 194)

47 – Upper leaf surface glabrous . . . . **B.** (*Loasibegonia*) **quadrialata** Warb. subsp. **quadrialata** var. **quadrialata** (p. 186)

– Upper leaf surface pilose . . . . **B.** (*Loasibegonia*) **quadrialata** Warb. subsp. **quadrialata** var. **pilosa** Sosef (p. 193)

48(36) – Peduncle simple; inflorescences bisexual with (1–)2–4(–5) male and 1(–3) female flowers; bracts usually less than 5 mm long 49

– Peduncle simple or branched; inflorescences either male with 4–8 flowers or bisexual with 1–2 male and 1–2 female flowers; bracts broadly elliptic to circular, 5-9 mm long . . . .
. . . . **B.** (*Loasibegonia*) **schaeferi** Gilg (p. 203)

49 – Upper leaf surface without long hairs or when hirsute the leaf apex acute or acuminate 50

– Upper leaf surface sparsely to densely hirsute with erect red hairs; leaf blade circular to broadly elliptic-ovate or elliptic-obovate, often more or less kidney-shaped, the apical part distinctly rounded . . . .
. . . . **B.** (*Loasibegonia*) **heterochroma** Sosef (p. 160)

50 – Perianth segments yellow, rarely white and leaf blade sometimes with a crenate margin but in both cases the leaf blade borne in more or less vertical position and petiole longer than the blade 51

– Perianth segments white or yellow; leaf blade borne in horizontal position, often with a crenate margin; petiole as long as or shorter than the blade . . . . **B.** (*Scutobegonia*) **anisosepala** Hook.f. (p. 218)

51 – Tertiary nerves without a sclerenchymatous sheath and in dry condition usually not visible, rarely indistinct but never prominent; stigma short, horseshoe-shaped and not twisted, sometimes more elongated and twisted but then the flowers positioned from halfway up the petioles to at about the same level as the leaf blades 52

– Tertiary nerves with a sclerenchymatous sheath and therefore in dry condition visible and often prominent, creating a reticulate pattern; stigma elongated, generally V-shaped and twisted for at least 1/2 a turn; flowers positioned near the base of the petioles 54

52 – Stigma elongated and twisted for at least 1/2 a turn; petiole usually much longer than the leaf blade, the latter pointing with the acute or acuminate apex in a 90° angle with the direction of the rhizome
. . . . 53

– Stigma short, horseshoe-shaped and not twisted; petiole usually shorter or only slightly longer than the leaf blade, the latter pointing with the blunt to acuminate apex parallel to the rhizome . . . .
. . . . **B.** (*Scutobegonia*) **mildbraedii** Gilg (p. 259)

53 – Main and larger secondary nerves on the lower leaf surface distinctly hirsute with patent hairs; smaller secondary nerves sparsely so . . . .
. . . . . **B.** (*Scutobegonia*) **zairensis** Sosef var. **montana** Sosef (p. 285)

– Main and larger secondary nerves only sparsely hirsute with adpressed or patent hairs; smaller secondary nerves without long hairs . . . . **B.** (*Scutobegonia*) **zairensis** Sosef var. **zairensis** (p. 283)

54(51) – Petiole distinctly hirsute with long (± 2–4 mm) and wavy hairs, sometimes only sparsely so; leaf blade borne in horizontal or vertical position 55

– Petiole without any or very sparsely set with short (1–2 mm) and stiff non-glandular hairs; leaf blade borne in horizontal position . . . . **B.** (*Scutobegonia*) **clypeifolia** Hook.f. (p. 227)

55 – Upper leaf surface usually distinctly hirsute; leaf blade borne in horizontal position, usually broadly elliptic or broadly elliptic-ovate to circular and distinctly acuminate; outer side of perianth segments salmon . . . . **B.** (*Scutobegonia*) **erectotricha** Sosef (p. 237)

– Upper leaf surface usually not, but sometimes sparsely hirsute; leaf blade always borne in vertical position, broadly obovate to broadly ovate or obovate to ovate, sometimes narrower, the top blunt to acuminate; outer side of perianth segments yellow to orange or red or with red lines . . . . . . **B.** (*Scutobegonia*) **hirsutula** Hook.f. (p. 242)

16 Descriptions of the species of section *Loasibegonia*

The description of the shape of the ovary and fruit refers to the outline in side view.

Begonia adpressa Sosef **Fig. 16.1, Map 16.1**

Begonia adpressa Sosef, Wageningen Agric. Univ. Papers 91-4 (1992) 126, fig. 2; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 14, pl. 9A. – TYPE: *W.J. de Wilde & de Wilde-Duyfjes 2325* (WAG!, holo; BR!, EA, K!, MO!, P!, PRE, YA!, Z!): 'Cameroun, Bamena, ca 15 km W. of Banganté. Alt. 1200 m, 29-IV-1964'.

Begonia schaeferi auct. non Engl.: van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 39.

Diagnostic characters (for a more detailed description see Sosef l.c.):

Plant 13–28 cm high. **Leaves** peltate; *leaf blade* almost symmetrical to asymmetrical, elliptic-ovate to broadly ovate or broadly elliptic, usually distinctly acuminate in the upper 1/4 to 1/10, (4.7–)7.5–15.5 x (2.7–)4.0–8.5 cm; margin entire or sometimes finely and remotely serrate towards the top, glabrous or sparsely shortly ciliate; *nerves*: the main and larger secondary nerves on the lower surface usually densely hirsute with rather short and antrorsely appressed hairs. **Bracts** very broadly ovate to circular, 6.0–11.0 mm long, red. **Male flower**: *perianth segments* broadly or very broadly ovate, sometimes broadly obovate, with a cuneate to slightly cordate base, (7.2–)9.0–21.0 x (7.0–)10.0–23.0 mm, outside yellow with reddish nerves, inside yellow or light yellow; *androecium* with 26–47 stamens. **Female flower**: *perianth segments* broadly or very broadly ovate to circular, with a rounded to somewhat cordate base, 11.5–27.0 x 13.5–30.0 mm; *styles* 4, 4.5–8.5 mm long; *ovary* broadly obovate or circular to very broadly obtriangular-obovate, 4.0–7.9 x 4.3–6.9 mm, with a comb-like fringe of hairs on the sutures between the locules (sometimes only sparsely so) or densely hirsute all over; wings sometimes absent on one or two sides of the ovary, when present broadly obovate to shallowly obtriangular-obovate, 0–3.6 mm wide. **Infructescence**: *fruit* erect, 5.2–9.1 x 4.9–13.0 mm.

Distribution: CAMEROON: western Cameroon mountains.

Ecology: Terrestrial or on rocks, in shade of moist primary montane forest; at 1000–1750 m altitude.

Notes: 1. Easily distinguished from related species (*Begonia schaeferi* Engl. and others) by the often almost entire leaf-margin and nerves with appressed hairs.

Specimens examined:

CAMEROON: *Etuge & Thomas 494* (BR, MO): South-West Prov., Bangen Subdivision, Mejelet

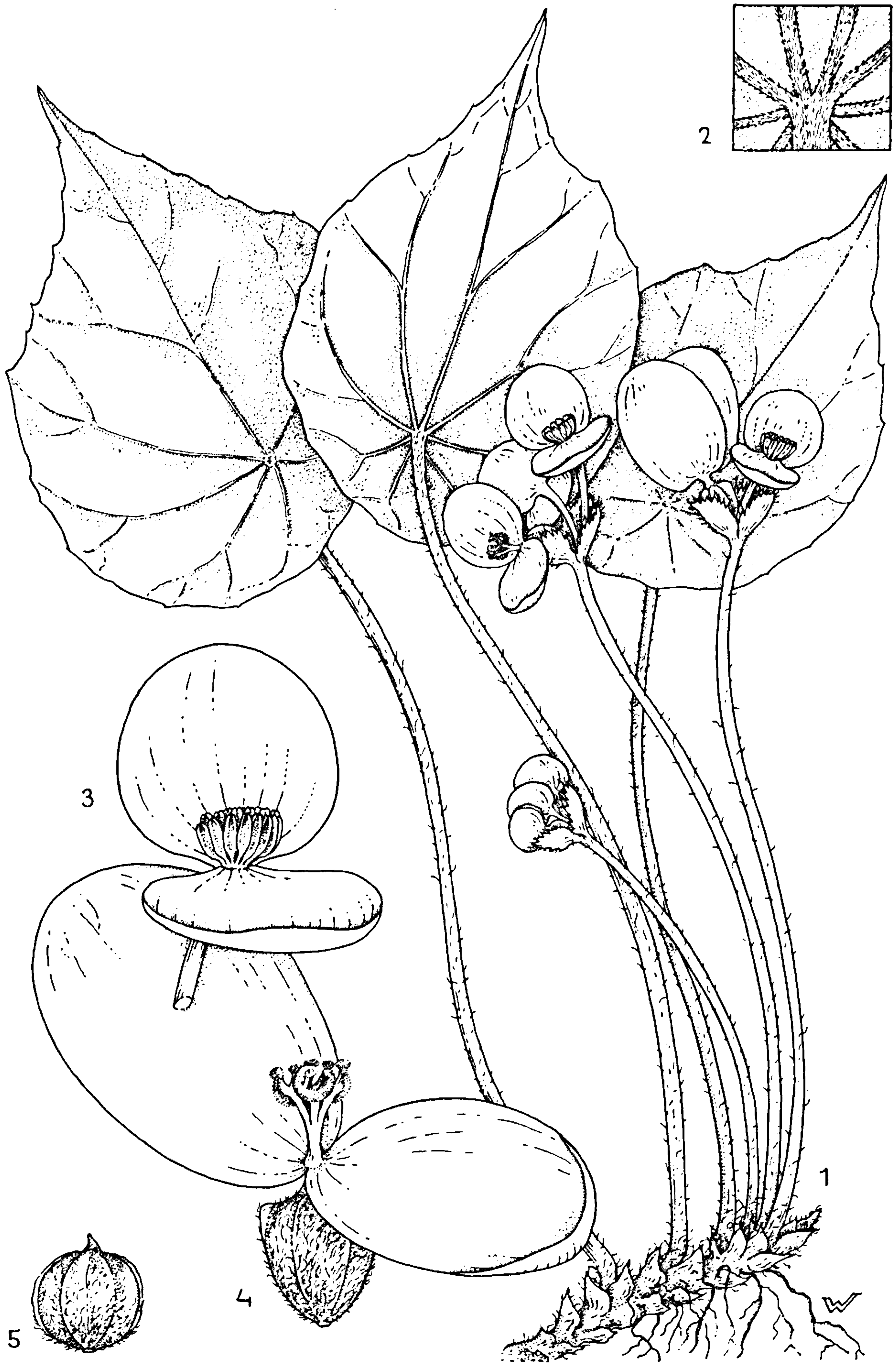
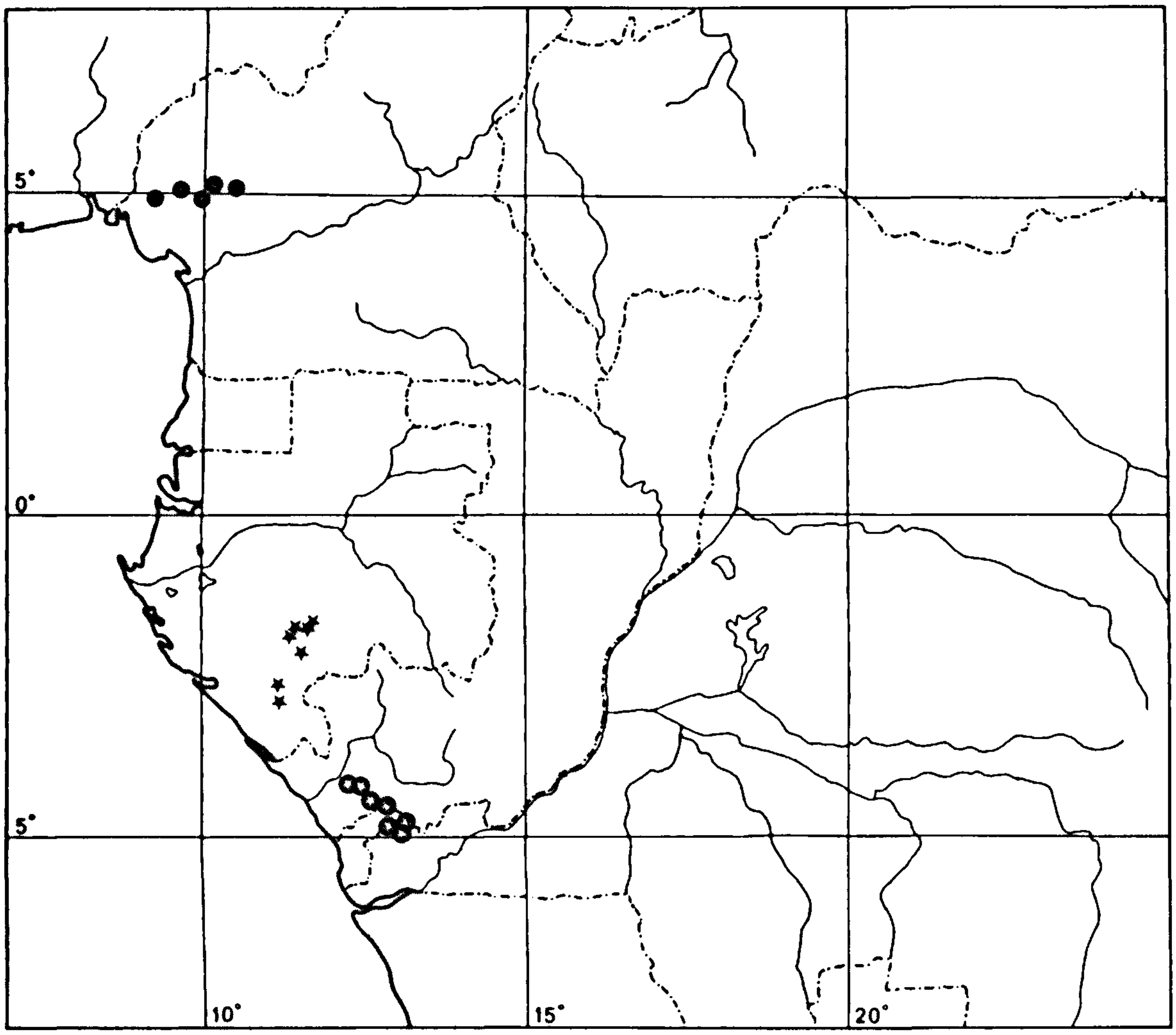


Figure 16.1. *Begonia adpressa* Sosef. – 1: habitus (x$^2/_3$); 2: detail lower leaf surface (x2); 3: male flower (x2); 4: female flower and ovary (x2); 5: fruit (x2). – 1-4: *Satabié 263*; 5: *W.J.J.O. de Wilde & de Wilde-Duyfjes 2325*.



Map 16.1. Distribution of *Begonia adpressa* (dots), *Begonia atroglandulosa* subsp. *atroglandulosa* (solid stars) and subsp. *tshelaensis* (open stars).

Elumseh village, 05°04'N 09°42'E (fl, 02); *Hedin s.n.* (P): Nkong Lon 1, slope of the Lonaco, 04°55'N 09°57'E (fl, fr, 05); *Jacques-Félix 2897* (P): Bafang-Diboum (1st mission), 05°09'N 10°11'E (fl, 01); *Jacques-Félix 2990* (P): Mt Boma, ? (fl, 01); *Satabié 263* (P, YA): summit of Mt Rata, Rumpi Mts, 36 km NW of Kumba, 04°53'N 09°15'E (fl, fr, 03); *Thomas c.s. 5329* (WAG): South-West Prov., forested hillsides in the Bakossi Mts, W of Bangem, 05°05'N 09°42'E (fl, 01); *Villiers 1405* (P, YA): ridge NW of Muekan Aku, 9 km SW of Bangem, 05°02'N 09°43'E (fr, 06); *W.J. de Wilde & de Wilde-Duyfjes 2325* (WAG, holo; B, BR, MO, P, YA, Z): Bamena, c. 15 km W of Bangante, 05°08'N 10°26'E (fl, fr, 04).

Begonia atroglandulosa Sosef **Fig. 16.2, Pl. 5, Map 16.1**

a. subsp. **atroglandulosa**

Begonia atroglandulosa Sosef subsp. *atroglandulosa*, Wageningen Agric. Univ. Papers 91-4 (1992) 88, fig. 1, pl. 1. – TYPE: *Breteler 7727* (WAG!, holo): 'Gabon, 40 km Mimongo-Lebamba, 11 27E, 1 47S, alt. ± 400-500 m, 30-V-1981.'

Diagnostic characters (for a more detailed description see Sosef l.c.):

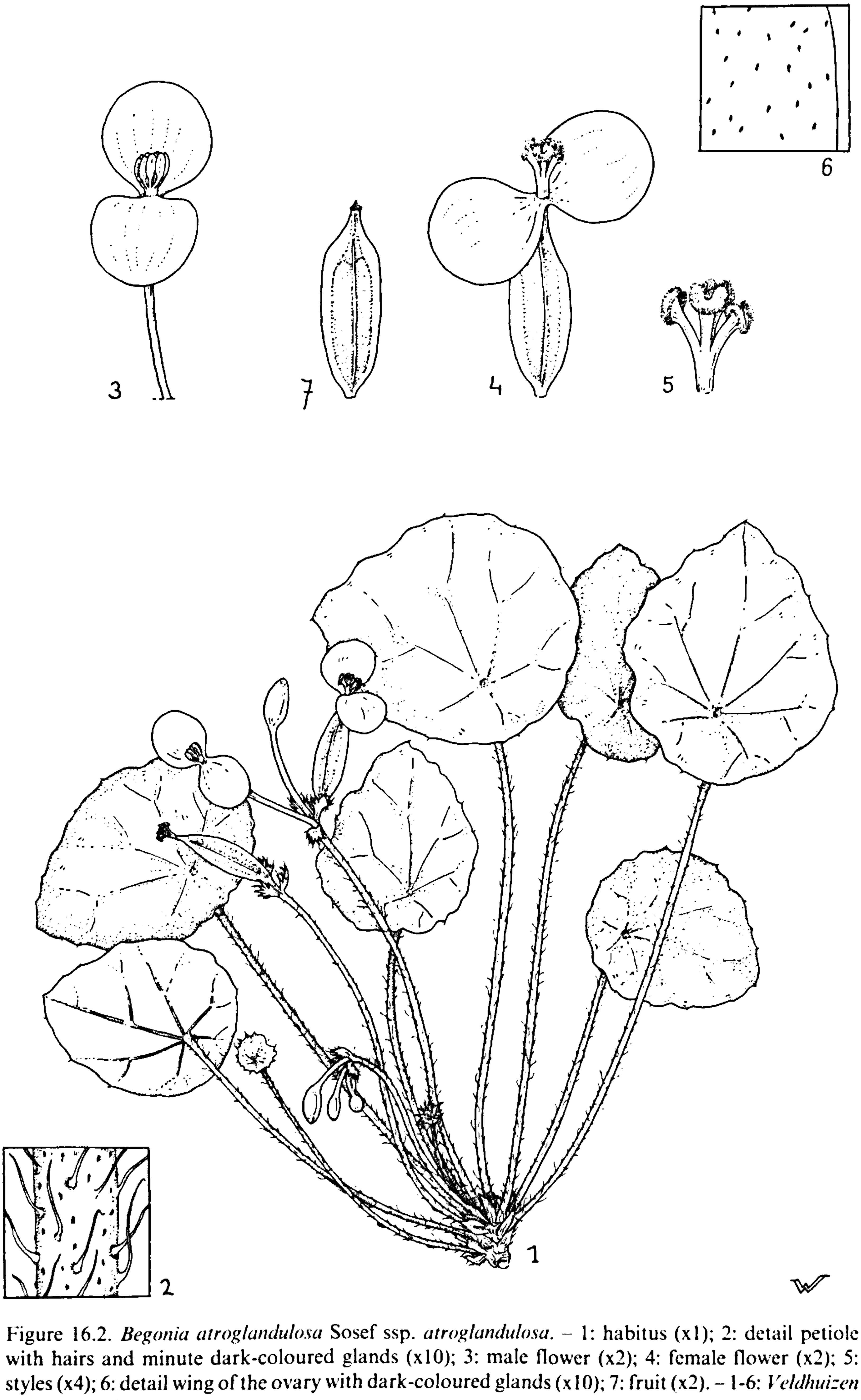


Figure 16.2. *Begonia atroglandulosa* Sosef ssp. *atroglandulosa*. – 1: habitus (x1); 2: detail petiole with hairs and minute dark-coloured glands (x10); 3: male flower (x2); 4: female flower (x2); 5: styles (x4); 6: detail wing of the ovary with dark-coloured glands (x10); 7: fruit (x2). – 1-6: *Veldhuizen 968*; 7: *Breteler 7727*.

Plant up to 11 cm high, scattered with two types of minute glandular hairs one of which turns dark red or dark brown in sicco. **Leaves** peltate; *leaf blade* ovate to circular, not acuminate or rarely indistinctly so in the upper 1/3, 1.4–8.5 x 0.7–7.6 cm; margin entire to irregularly, shallowly sinuate-dentate, glabrous or sparsely ciliate; upper surface glabrous to sparsely hirsute with short hairs in a regular pattern, usually at least near the margin. **Inflorescence** containing 2–5(–9) male flowers and 1(–2) terminal female flower(s); *peduncle* simple or branched once (up to 3 times in glasshouse conditions). **Male flower**: *perianth segments* broadly elliptic to very broadly ovate or transversely broadly elliptic, with a rounded to cuneate base, 3.4–9.5 x 3.2–13.0 mm; the upper segment yellow to orange-yellow or orange-red with red nerves on the outside, the inside yellow with or without a red patch and nerves in the lower half; the lower segment yellow; *androecium* with 6–14 stamens. **Female flower**: *perianth segments* broadly to very broadly ovate, 5.3–10.0 x 6.6–13.5 mm; *ovary* elliptic to narrowly so, 4.1–12.0 x 1.6–5.7 mm, translucent, reddish green; wings oblong to narrowly elliptic-obovate, usually ribbon-shaped, 0.25–1.7 mm wide. **Infructescence**: *fruit* erect, elliptic-oblong or narrowly so to ovate-elliptic, 7.9–13.0 x 2.9–6.9 mm.

Distribution: GABON: Chaillu Massif and Doudou Mountains.

Ecology: Terrestrial on the forest floor or on mossy rock faces and tree trunks in primary or old secondary forest; in shaded moist sites, along banks of streamlets or rivers, sometimes near a waterfall or rapids, often on steep slopes or banks of creeks or vertical rock faces, sometimes in rocky creek beds; at 150–760 m altitude.

Notes: 1. The plants of this and the next subspecies bear two types of minute glandular hairs, one of which dries dark red or dark purple. This type is also encountered in *B. minuta*.

2. Two accessions were studied in vivo at Wageningen. The female flowers of one of these developed abnormally due to the development of stigmatic tissue in the locules of the ovary.

Specimens examined:

GABON: *Breteler 7701* (WAG): about 2 km Lébamba-Mbigou, bed of Biroumdou R., 02°12'S 11°30'E (fl, 05); *Breteler 7722* (WAG): about 20 km Mimongo-Mbigou, Mouyanama upper fall, 01°39'S 11°42'E (fl, 05); *Breteler 7727* (WAG, holo): 40 km Mimongo-Lébamba, 01°47'S 11°27'E (fl, fr, 05); *Le Testu 1306* (BM): Mayombe, Mougniounguibui, Dingouma, 02°55'S 11°12'E (fl, 02); *Le Testu 1334* (BM, P): Mayombe, slope right of Daguégué. Misamou Ibéni, Bamouma, c. 02°50'S 11°10'E (fl, 04); *A. Louis 1443* (LBV, WAG): Ngounié Prov., ± 5 km E of the Mouetse R., behind Mt Ngondo at Mouyanama, c. 01°38'S 11°45'E (fl, 03); *A. Louis 2748* (WAG): Ngounié Prov., road Mimongo-Mbigou, 5 km Ibaga to Mbigou, towards Mt Ngangile, 01°40'S 11°48'E (fl, 02); *Wieringa c.s. 1422* (WAG): Nyanga, 55 km on the road Tchibanga to Ndendé, 02°37'S 11°16'E (fl, fr, 08); *J.J. de Wilde c.s. 10475* (WAG): 18 km along forest exploitation road from Bilengui to Mouila, near bridge crossing the Ogoulou R., 01°55'S 11°20'E (fl, 02); *J.J. de Wilde c.s. (WALK-B) 324* (WAG): Chaillu Massif, missionary station at Mouyanama, about 15 km on the road Mimongo to Mbigou, 60 km along the road from Mbigou, 01°39'S 11°46'E (fl, 02); *J.J. de Wilde c.s. (WALK-B) 325* (WAG): ibid. (fl, 02); *J.J. de Wilde c.s. (WALK-B) 443* (WAG): ibid. (fl, 02); *J.J. de Wilde c.s. (WALK-B) 464* (LBV, WAG): ibid., waterfall at about 20 min. walking distance, 01°39'S 11°46'E (fl, fr, 02); *J.J. de Wilde c.s. (WALK-B) 464A* (WAG): ibid. (fl, 02); *J.J. de Wilde c.s. (WALK-B) 518* (LBV, WAG): Naguila Mountain, about 4 km SE of Missionary station at Mouyanama, about 15 km on the road Mimongo to Mbigou, c. 01°40'S 11°47'E (fl, fr, 02).

CULTIVATED: *van Veldhuizen 967* (WAG): Wageningen, Dept. of Horticulture No 1621 (coll. WALK-B 443, Gabon) (fl, 10); *van Veldhuizen 968* (WAG): Wageningen, Dept. of Horticulture No 1615 (coll. WALK-B 324 and 325, Gabon) (fl, 10); *van Veldhuizen 1089* (WAG): Wageningen, Dept. of Horticulture No 1614 (coll. J.J.F.E. de Wilde et al. (WALK-B) 464, Gabon) (fl, 09); *van Veldhuizen 1094* (WAG): Wageningen, Dept. of Horticulture No 1681 (coll. A. Louis s.n., Gabon) (st, 09); *van Veldhuizen 1097* (WAG): Wageningen, Dept. of Horticulture No 1623 (coll. J.J.F.E. de Wilde et al. (WALK-B) s.n., Gabon, Mimongo) (fl, 09).

b. subsp. **tshelaensis** Sosef **Fig. 16.3, Map 16.1**

Begonia atroglandulosa Sosef subsp. *tshelaensis* Sosef, Wageningen Agric. Univ. Papers 91-4 (1992) 91, fig. 2; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 15, pl. 9F. – TYPE: *F. Hallé 1905* (P!, holo): 'Zaïre, région de Tshela, Mayombe, Congo K., 7 mars 1971.'

Begonia potamophila auct. non Gilg: Wilczek, Fl. Congo, Rwanda et Burundi (1969) 33.

Begonia quadrialata auct. non Warb.: De Wildeman & Durand, Ann. Mus. Congo Bot. sér. II, I,2 (1900) 25; Th. & H. Durand, Syll. Fl. Cong. (1909) 234 p.p.; L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 221.

Differs from the typical subspecies by:
Leaf-blade narrowly elliptic or narrowly ovate to transversely broadly elliptic-ovate, 0.9–9.0 x 0.3–6.2 cm, with 3–7 palmate main nerves. Peduncle up to 14 cm long. Pedicel of the female flower elongated in fruit up to 6 mm; perianth segments 4.7–8.5 x 4.4–8.1 mm, white with red nerves at the base inside; styles 1.7–2.1 mm long; beak up to 3.3 mm long. Fruit 5.3–13.0 x 1.6–4.0 mm.

Distribution: CONGO: Mayombe. ZAIRE: Tshela region.

Ecology: Terrestrial or on rocks in forest; in rocky ravines; on vertical road banks, wet rocks or on very wet vertical face of a cavity in the rock; found in association with *Hymenophyllaceae* and *Begonia lacunosa*; at around 500 m altitude.

Notes: 1. After the publication of this subspecies in 1992 several new collections could be studied. The leaves of these were usually broadly elliptic to circular or even transversely broadly elliptic-ovate. Thus, the only remaining distinct difference between this and the typical subspecies is found in the white instead of yellow flowers. This feature, however, is shown to be variable within several other species (viz. *B. heterochroma*, *B. lacunosa* and *B. anisosepala*). This sheds doubt on the correctness of the recognition of subspecies *tshelaensis*. Although the basis is weak, the situation is at present not altered, since the yellow and white flowering specimens occur in geographically distinct areas separated by a dry savanna zone.

Specimens examined:

CONGO: *Attims 435* (IEC): Mayombe, Mt Bamba pass, 04°18'S 12°28'E (fl, 03); *De Namur 1695* (WAG): Mayombe, Dimonika, 04°14'S 12°27'E (st, 11); *De Namur 2663* (WAG): Mayombe, 5 km past Pounga towards Pointe-Noire, 04°18'S 12°27'E (fl, 07); *De Namur 2687* (WAG): Mayombe, forest of Mt Bamba past M'Vouti, 04°18'S 12°28'E (fl, 07); *De Namur 2777* (WAG): Mayombe, Mt Bamba pass, 04°18'S 12°28'E (fl, 10); *Ecole Superieure de Science 34* (IEC): Mayombe, Dimonika, 04°14'S 12°25'E (fl); *Prévost s.n.* (P): Mayumbe, c. 04°30'S 12°30'E (st, 01); *Sita 1416* (IEC, P): Les Saras, road to M'Vouti, c. 04°14'S 12°31'E (fl, 06); *J.J. de Wilde c.s. 11053* (WAG): Mayombe forest, 4 km on the road Les Saras (Mboulou) to Pointe-Noire, bridge across the Loukénébé R., 04°20'S 12°20'E (fl, 02).

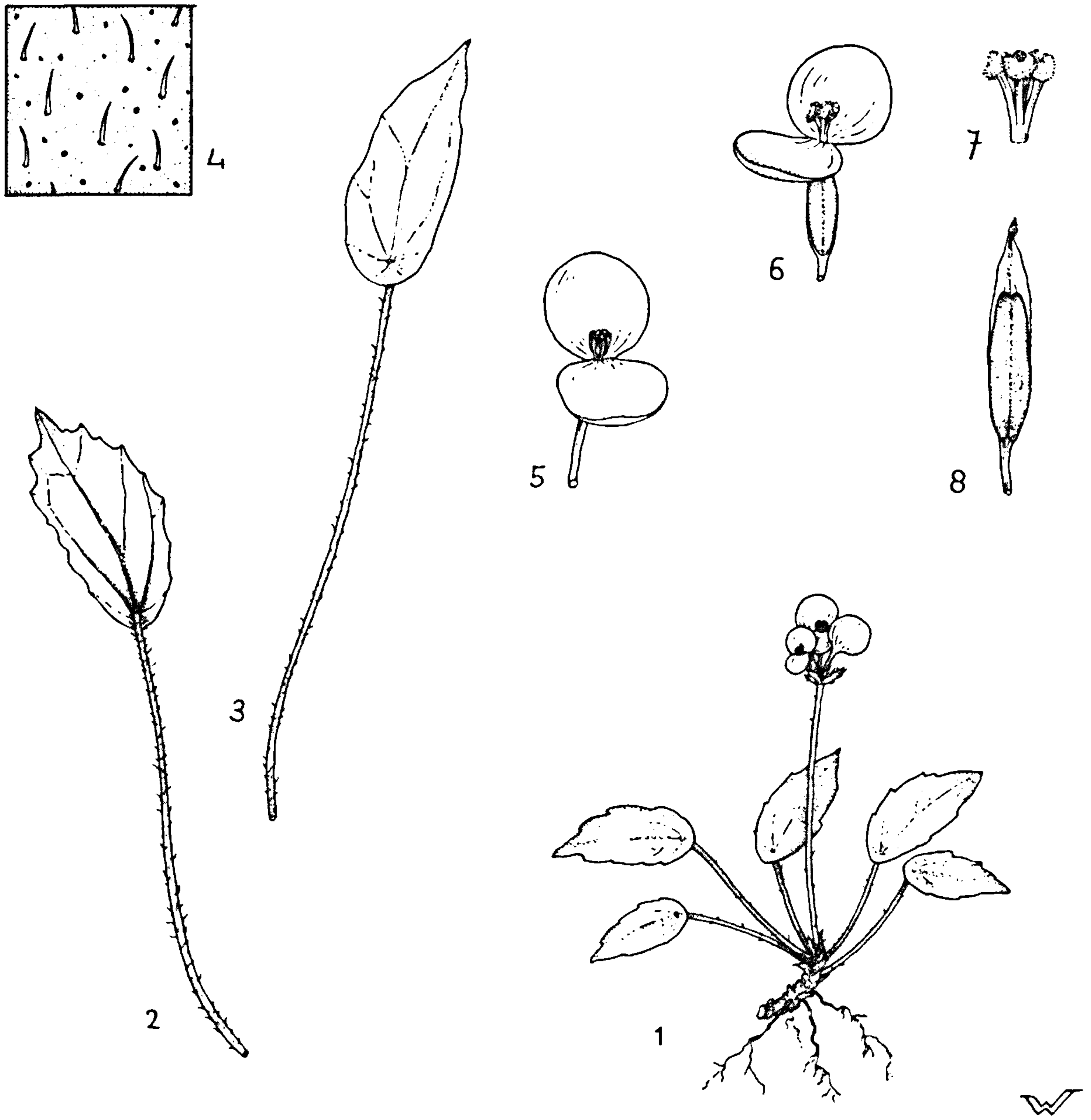


Figure 16.3. *Begonia atroglandulosa* Sosef ssp. *tshelaensis* Sosef. – 1: habitus (x1); 2: lower leaf surface (x^2/$_3$); upper leaf surface (x^2/$_3$); 4: detail upper leaf surface with hairs and dark coloured glands (x4); 5: male flower (x2); 6: female flower (x2); 7: styles (x4); 8: fruit (x2). – 1, 5-7: *N. Hallé 1905*; 2: *Breyne 4509*; 3-4, 8: *Breyne 2644*.

ZAIRE: *Breyne 2644* (BR): Maduda, Tshela region, 04°56'S 13°06'E (fl, fr, 08); *Breyne 4509* (BR): Maduda-Nkai-Mbaku, Tshela region, 04°49'S 13°06'E (fl, fr, 11); *Cabra 39* (BR): between Chindamba and the Lombe, 04°45'S 12°55'E (fl); *F. Hallé 1905* (P, holo): Tshela region, Mayombe, c. 04°30'S 12°30'E (fl, fr, 03); *Tilquin 112* (BR): Lubonga R., on the road to Maduda, Tshela region, 04°46'S 13°06'E (fl, 03); *Tilquin 115* (BR): ibid. (fl, fr, 03); *Tilquin 116* (BR): ibid. (fr, 03).

Begonia duncan-thomasii Sosef **Fig. 16.4, Map 16.2**

Begonia duncan-thomasii Sosef, Wageningen Agric. Univ. Papers 91-4 (1992) 129, fig. 3. – TYPE: *D.W. Thomas & H.L. McLeod 5492* (WAG!, holo; BR!, MO): 'Cameroon, Southwest Province, forest on the west side of Mount Kupé. 4°48'N, 9°42'E, Elev. 1800 m, 1 Feb. 1986.'

Diagnostic characters (for a more detailed description see Sosef l.c.):

Plant up to 25 cm high. **Leaves** peltate; *petiole* in sicco often knobly; *leaf blade* usually slightly asymmetrical, ovate to elliptic-ovate, sometimes narrowly so, acuminate in the apical 1/3 to more or less gradually tapering towards the top, 9.1–20.5 x 4.3–11.5 cm; margin denticulate, often with several larger teeth, ciliate; upper surface rugose-bullate with solitary bullae, each bulla topped with a stiff erect white hair; *nerves*: the main and larger secondary nerves on the lower surface in sicco knobly. **Inflorescence**: *peduncle* usually branched 1 or 2 times, *bracts* more or less enveloping the young flowers, very broadly ovate to ovate or elliptic-ovate, 2.6–11.7 mm long. **Male flower**: *perianth segments* broadly ovate to very broadly so, with a rounded to cordate base, 7.8–16.0 x 6.7–18.0 mm; the upper segment yellow with a large orange-brown-red spot which reaches up to 3/4 of the length of the segment turning more diffusely orange-yellow with age on the outside, the inside yellow, the lower segment light yellow turning yellow with age on the outside, yellow on the inside; *androecium* with 15–32 stamens. **Female flower**: *perianth segments* with a cordate base, 7.1–18.0 x 9.2–19.0 mm; *ovary* very broadly obovate, 2.3–5.3 x 2.9–6.9 mm, sometimes hirsute; wings obovate to broadly obtriangular-obovate, 0.5–2.6 mm wide, the margin entire to shallowly dentate. **Infructescence**: *fruit* erect, very broadly obtriangular-obovate, 9.0 x 7.5 mm.

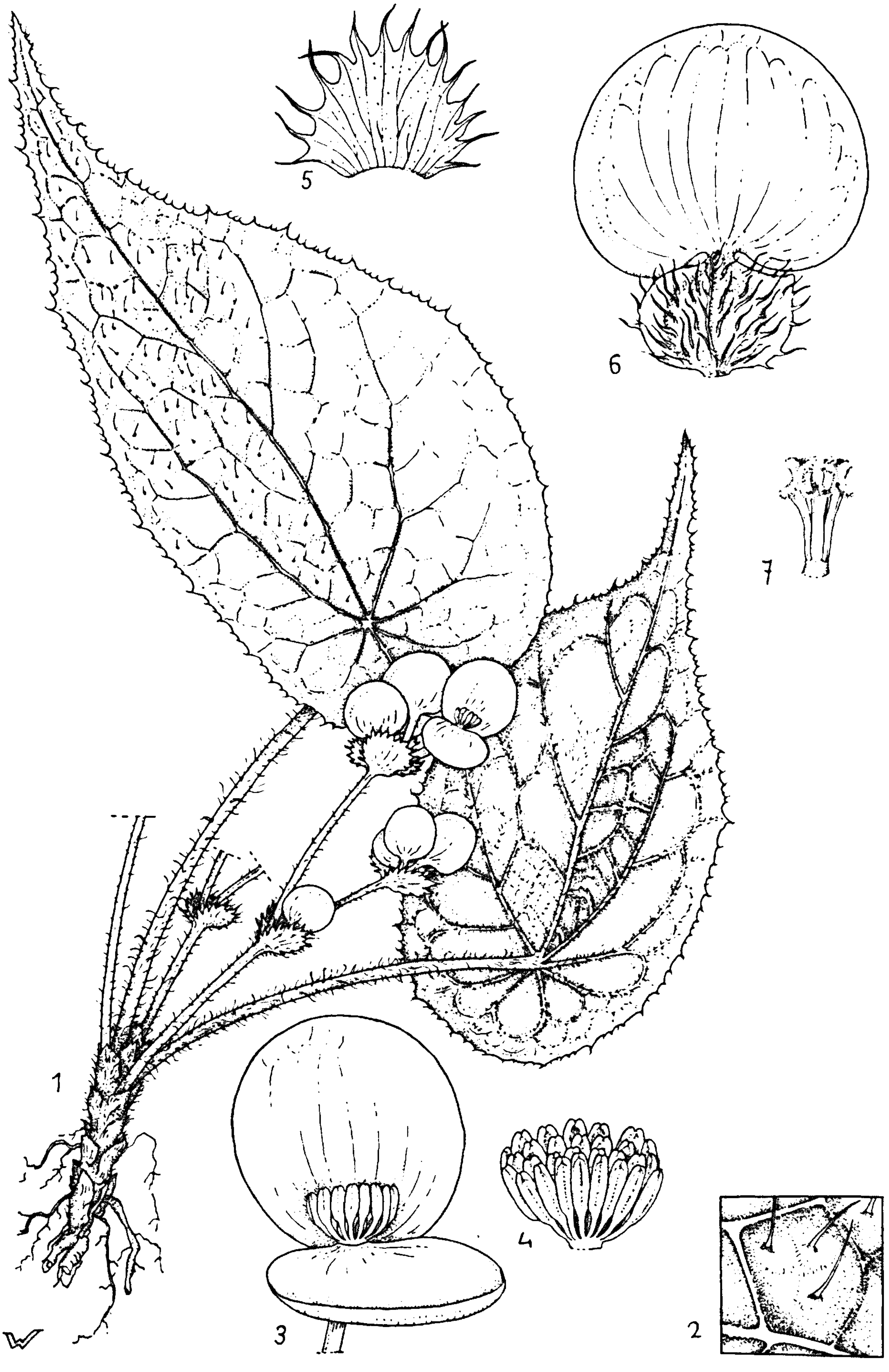
Distribution: CAMEROON: western Cameroon mountains.

Ecology: Terrestrial or on rocks in shaded sites in montane forest; on hillsides; found growing with *Nodonema lineatum* (*Gesneriaceae*); at 1550–2000 m altitude.

Specimens examined:

CAMEROON: *Satabié 259* (P, WAG, YA): eastern slope of Mt Rata, Rumpi Mts, 36 km NW of Kumba, 04°53'N 09°15'E (fl, 05); *Thomas 3164* (MO, YA): South-West Prov., forest on summit of Mt Kupé, 04°47'N 09°43'E (fl, 02); *Thomas c.s. 5294* (WAG): South-West Prov., Bakossi Mts, W of Bangem, 05°05'N 09°42'E (fl, 01); *Thomas c.s. 5492* (WAG, holo; BR): South-West Prov., forest on the west side of Mt Kupé, 04°48'N 09°42'E (fl, 02).

Figure 16.4. *Begonia duncan-thomasii* Sosef. – 1: habitus (x$^2/_3$); 2: detail upper leaf surface (x4); 3: male flower (x2); 4: androecium (x4); 5: bract (x2); 6: female flower and ovary (x2); 7: styles (x2). – 1-7: living plant at WAG, coll. *Thomas & McLeod 5492*.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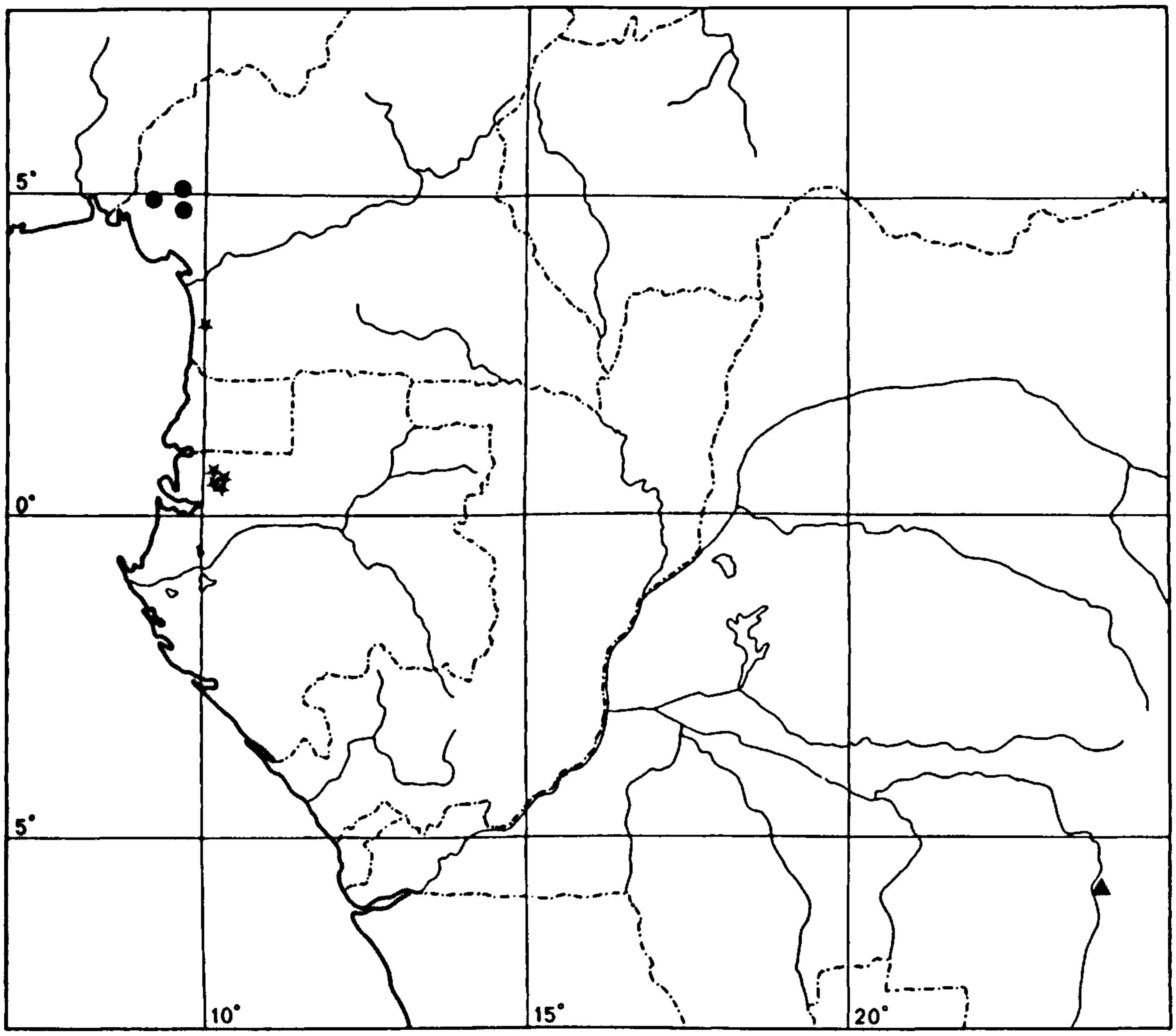


Map 16.2. Distribution of *Begonia duncan-thomasii* (dots), *Begonia gentilii* (triangle) and *Begonia heterochroma* (stars).

Begonia gentilii De Wild. **Fig. 16.5, Map 16.2**

Begonia gentilii De Wild., Ann. Mus. Congo, sér. V, vol. I (1906) 294; T. & H. Durand, Syll. Fl. Congo (1909) 233; Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3,2 (1921) 617; Wilczek, Fl. Congo, Rwanda et Burundi (1969) 35; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39; L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 171, fig. 2.17. – NEOTYPE: *Hort. Brux. s.n.* (BR!, holo): 'J.B.B., juillet 1908'.

Plant up to 21 cm high, scattered with minute glandular hairs, sparsely so on stipules, peduncle, bracts, pedicel of male flower and outside of perianth segments. **Rhizome** rather slender, rather smooth, 3.0–8.5 mm wide, sparsely hirsute with long, wavy, hairs, but more densely so around the leaf axils; the apical part shortly ascending. **Stipules** narrowly ovate to broadly triangular-ovate with a rounded to acute top, 4.4–6.6 mm long; margin entire to dentate, ciliate. **Leaves** peltate; *petioles* making a distinct angle with the midrib, inserted at 1.2–2.5 cm from the nearest margin, 8–21 cm long, juicy, sparsely hirsute with long, wavy, hairs; *leaf blade* in a more or less horizontal position, ± symmetrical, ovate to broadly elliptic-ovate, acuminate at the top, 5.5–10 x 4–8 cm, with 9–10 pal-

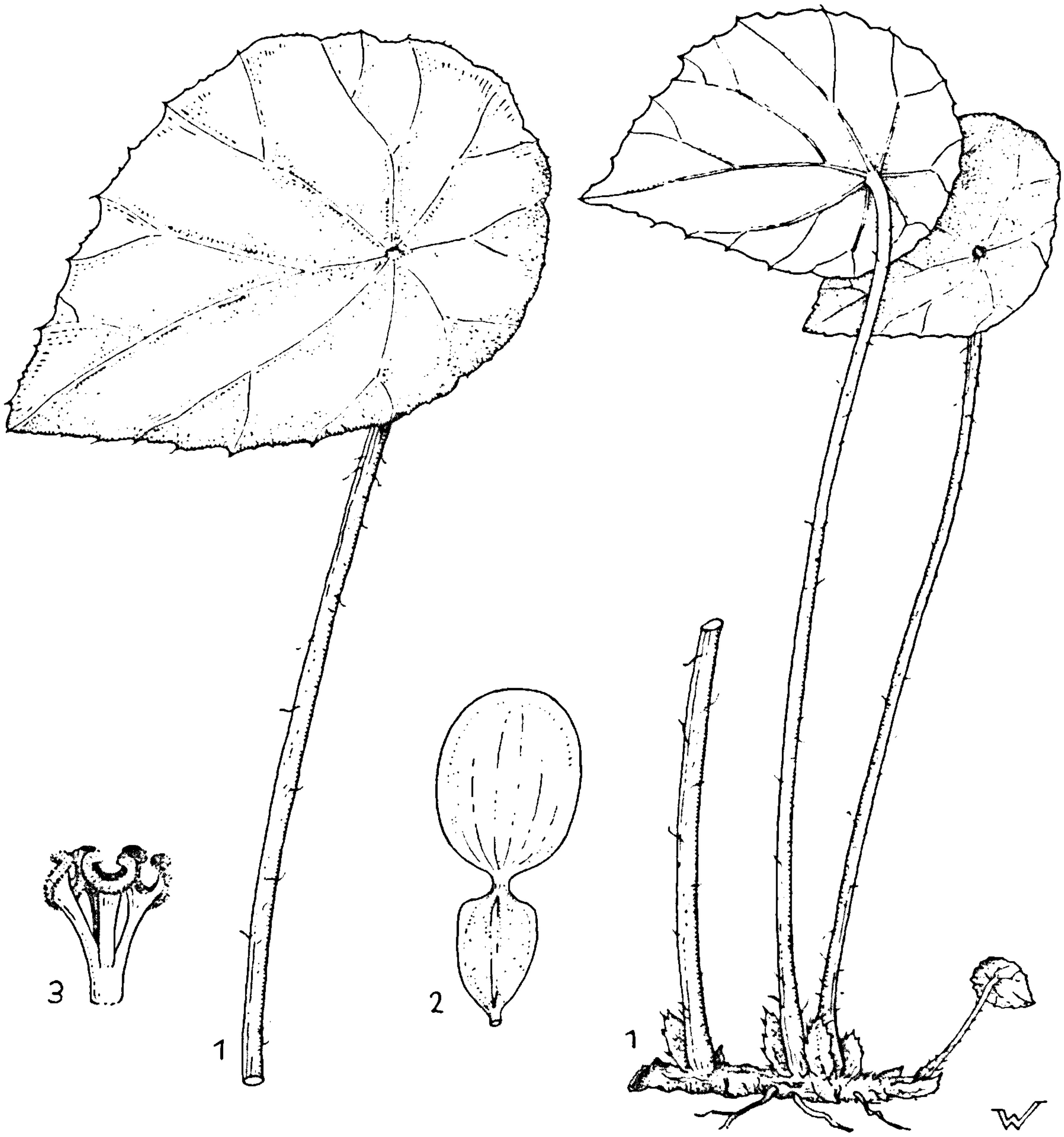


Figure 16.5. *Begonia gentilii* De Wild. – 1: habitus (x$^{2}/_{3}$); 2: female flower (x2); 3: styles (x4). – 1-3: *Hort. Brux. s.n.* (type coll.).

mate main nerves; margin shallowly and remotely dentate in the upper half, sparsely shortly ciliate; base rounded, top acute to blunt; upper surface dull, smooth, glabrous; lower surface paler than the upper, glabrous; *nerves*: the main and larger secondary nerves glabrous and slightly prominent on both surfaces, on the lower slightly contrasting with the interveinal parts, smaller secondary nerves distinct, tertiary nerves indistinct, not prominent. **Inflorescence** containing 3 male flowers and 1 terminal female flower, positioned at the base of the plant; *peduncle* simple, 2.5–3.0 cm long, sparsely hirsute with long, patent hairs; *bracts* 4, broadly elliptic to circular, 1.7–2.5 mm long; margin denticulate, ciliate. **Male flower**: *pedicel* elongated at anthesis up to 25 mm; *perianth segments* broadly elliptic-obovate, with a cuneate base, 9.5–14 x 9–14 mm; the lower segment yellow on both sides, the upper orange-red on the outer and yellow with a red patch and nerves in the basal half on the inside; *androecium* with 11 stamens; column 0.25 mm long; anthers 1.2–1.7 mm long. **Female flower**: similar to the male, sessile or on a very short, 0.65 mm long pedicel; *perianth segments* very broadly ovate with a rounded base, 6–13 x 8.5–15 mm; *styles* 4, ± terete, 3.0–4.2 mm long, fused in the lower 1/4, the tops split into a rounded U-shape, the arms 1.2–1.4 mm long and covered with a slender, stigmatic band which is spirally twisted for ± 1/2 turn; *ovary* obovate-elliptic, 6.5–7.2 x 3.3–4.0 mm, 4-locular, 4-winged in the apical 2/3; the locular part obovate-elliptic, 2.1–3.3 mm wide; beak present, 1.0 mm long; wings elliptic-obovate, 0.25–0.7 mm wide. **Infructescence** not observed.

Distribution: ZAIRE: Kanda-Kanda.

Notes: 1. The species was described in 1906 apparently from a specimen cultivated in the colonial garden at Laeken (Belgium). The 'type-collection' at BR consists of 2 sheats, one bearing a label with 'Hort Brux 7 janvier 1907', the other with 'J.B.B. [=Jardin Botanique Bruxelles] juillet 1908'. Both were thus collected after the species was described and (a part of) the plant was apparently moved to the botanical garden at Bruxelles. The original Gentil collection, according to De Wildeman l.c. collected at 'Route de Lualabourg, Kanda-Kanda' (Lualabourg is a misspelling for Luluabourg), could not be traced and probably does not exist. T. & H. Durand l.c. mention 1902 as the year in which Gentil collected the species. They most likely obtained this date from Gentil himself or from the files of the garden at Laeken. As no herbarium material exists which De Wildeman used for his description, a neotype must be designated. I have chosen the specimen at BR labelled 'J.B.B. 1908' as such, since it is the only existing collection with flowers. The other collection 'from the type plant' at BR and also the ones at K and B should be regarded as important collections but are less desirable to serve as type. (See also the proposal in Taxon (Molloy et al., 1992; Nicolson, 1992).)
2. A sterile specimen collected by E. & M. Laurent might represent this species but its identity is doubtful.

Specimens examined:

CULTIVATED: *Hort. Brux. s.n.* (BR, holo): Hort. Bruxelles (fl, 01); *Hort. Brux. s.n.* (B, BR): J.B.B. (fl, 01); *Hort. Kew s.n.* (K): from Brussels B.G. type plant, 531-08 Brussels, Cult. in Hort. Bot. Reg. Kew. (st); *E. Laurent & M. Laurent s.n.* (BR), identification doubtful: cave at Kondue, 04°58′S 23°16′E (st, 11).

Begonia heterochroma Sosef **Fig. 16.6, Pl. 7b & c, Map 16.2**

Begonia heterochroma Sosef, Wageningen Agric. Univ. Papers 91-4 (1992) 102, fig. 6, pl 3b,c; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 19, pl. 14A. – TYPE: *Bos 5677* (WAG!, holo; BR!, K!, MO, P, YA!): 'Cameroun, 13 km N. of Kribi. Steep slope in high forest, 3 01 N., 9 57 E., 20-XI-1969.'

Diagnostic characters (for a more detailed description see Sosef l.c.):

Plant up to 14 cm high. **Leaves** peltate; *leaf blade* usually distinctly asymmetrical,

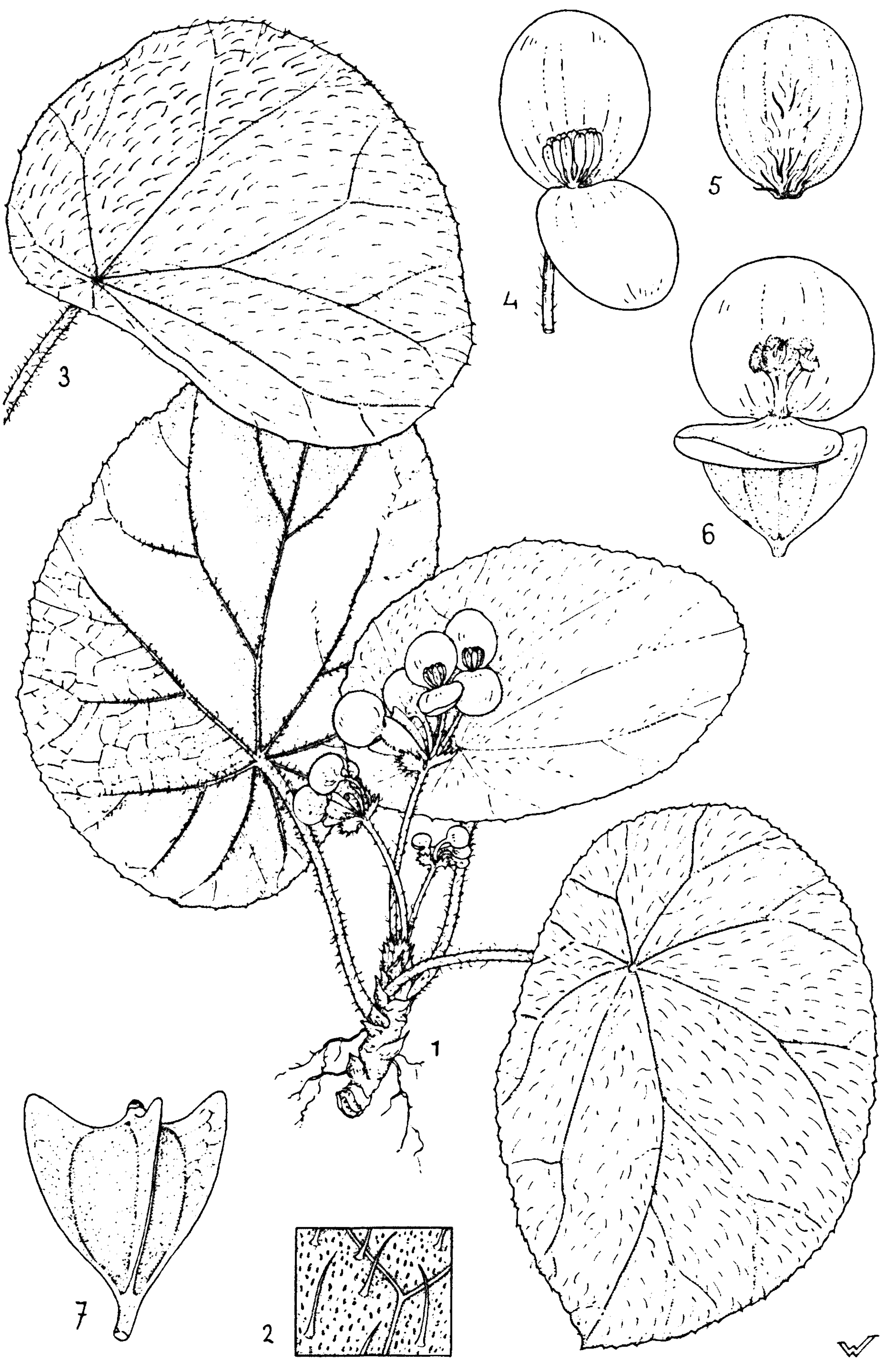


Figure 16.6. *Begonia heterochroma* Sosef. – 1: habitus (x$^{2}/_{3}$); 2: detail upper leaf surface with long hairs and minute glandular hairs (x4); 3: leaf (x$^{2}/_{3}$); 4: male flower (x2); 5: perianth segment of male flower, back (x2); 6: female flower (x2); 7: fruit (x2). – 1-2: *Bos 5677*; 3: *J.J. de Wilde c.s. 8870*; 4-5: *N. Hallé & Villiers 5197*; 6: *J.J. de Wilde c.s. (WALK-B) 161*; 7: *Bos 3834*.

often more or less kidney-shaped, circular to broadly elliptic-ovate or elliptic-obovate, with a rounded apical part, 3.7–13.0 x 2.6–7.7 cm; margin usually more or less entire or sometimes shallowly denticulate, ciliate to very sparsely so; upper surface dark green or bronze-green to violet or reddish, sometimes with a silvery gloss, sparsely to densely hirsute with long red or purple to silvery white, upright hairs. **Male flower**: *perianth segments* elliptic-obovate or broadly elliptic to very broadly elliptic-ovate, with a cuneate to slightly cordate base, 6.5–11.5 x 5.2–10.5 mm, the outside hirsute or sparsely so with white hairs, especially at base or in the basal half; the upper segment yellow to salmon or white with red nerves on the basal half on the outside, the inside yellow or white with a red patch and nerves in the basal half; the lower segment yellow or white on both sides; *androecium* with 15–20 stamens. **Female flower**: *perianth segments* transversely broadly elliptic or very broadly elliptic-ovate to broadly elliptic-ovate, with a rounded to slightly cordate base, 6.2–12.0 x 7.0–14.0 mm; *ovary* broadly obtriangular-obovate to depressed obtriangular-obovate, 3.0–9.7 x 6.0–14.0 mm, pale greenish to dirty dark red, sometimes sparsely hirsute; wings broadly obtriangular to depressed obtriangular-obovate, 1.3–5.1 mm wide, the margin glabrous or with a few hairs. **Infructescence**: *fruit* erect, broadly obtriangular to very broadly obtriangular-obovate, 9.1–11.5 x 8.1–13.0 mm.

Distribution: CAMEROON: north of Kribi. GABON: Crystal Mountains.

Ecology: Terrestrial or on decaying trees in primary or degraded lowland forest; on shaded to very heavily shaded sites, on (steep) clayey slopes and banks, in riverine forest or near streamlets, also on level places; at 80–360 m altitude.

Notes: 1. As the colour of the flower does not show a geographic correlation, and the fact that several other species show either white or yellow flowers within the same species (e.g. *B. lacunosa* and *B. anisosepala*), no taxonomic status was given to these variants.

Specimens examined:

CAMEROON: *Bos 3717* (WAG): 15 km N of Kribi, riverine forest of Mpolongwe R., 03°01′N 09°58′E (fl, 01); *Bos 3834* (BR, P, WAG): about 15 km N of Kribi, 03°01′N 09°58′E (fl, fr, 02); *Bos 5677* (WAG, holo; BR, K, YA): 13 km N of Kribi, 03°01′N 09°57′E (fl, fr, 11).

GABON: *N. Hallé & Villiers 4454* (P): Crystal Mts, Kinguélé falls, Mbé R., 00°29′N 10°20′E (fl, 01); *N. Hallé & Villiers 5176* (P): Crystal Mts, Mt Mvelakéné, 00°36′N 10°10′E (st, 02); *N. Hallé & Villiers 5177* (P): ibid. (fl, 02); *N. Hallé & Villiers 5197* (P): ibid., 5 km W of Méla, 00°36′N 10°13′E (fl, 02); *N. Hallé & Villiers 5329* (P): Crystal Mts, W of Balakabo R., 00°33′N 10°08′E (fl, 02); *N. Hallé & Villiers 5389* (P): Crystal Mts, Kinguélé falls, 00°29′N 10°20′E (fl, 02); *J.J. de Wilde c.s. 8870* (WAG): Kinguélé dam, downstream of hydroelectric power station, bank of Mbé R., 00°26′N 10°16′E (st, 11); *J.J. de Wilde c.s. 10194* (WAG): Crystal Mts, c. 2 km S of Kinguélé, along Mbé R., 00°26′N 10°17′E (fl, 01); *J.J. de Wilde c.s. 10247* (WAG): Crystal Mts, 25 km along road Tchimbélé to Kinguélé, 00°31′N 10°18′E (st, 01); *J.J. de Wilde c.s. (WALK-B) 155* (WAG): Crystal Mts, just E of Mala (Méla) Mytsibé R., an affluent of Zang R., 00°35′N 10°16′E (fl, fr, 01); *J.J. de Wilde c.s. (WALK-B) 161* (WAG): ibid. (fl, 01).

Begonia letouzeyi Sosef **spec. nov.** **Fig 16.7, Map 16.3**

– TYPE: *Letouzey 11080* (P!, holo; P): 'Cameroun, près Esseng, 12 km NNE de Ngambé (feuille IGN 1/200.000 NDikinimeki), 23-I-1972.'

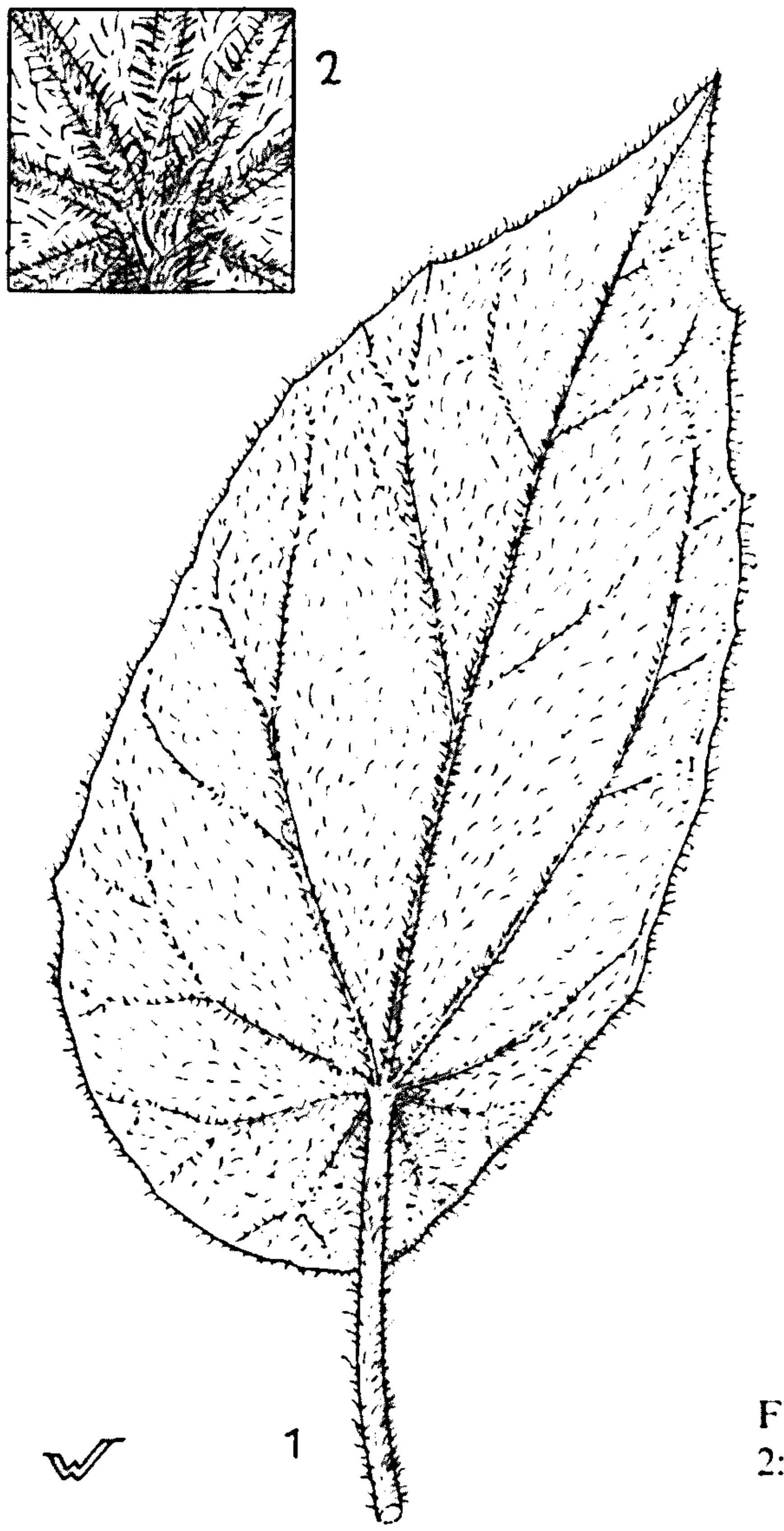


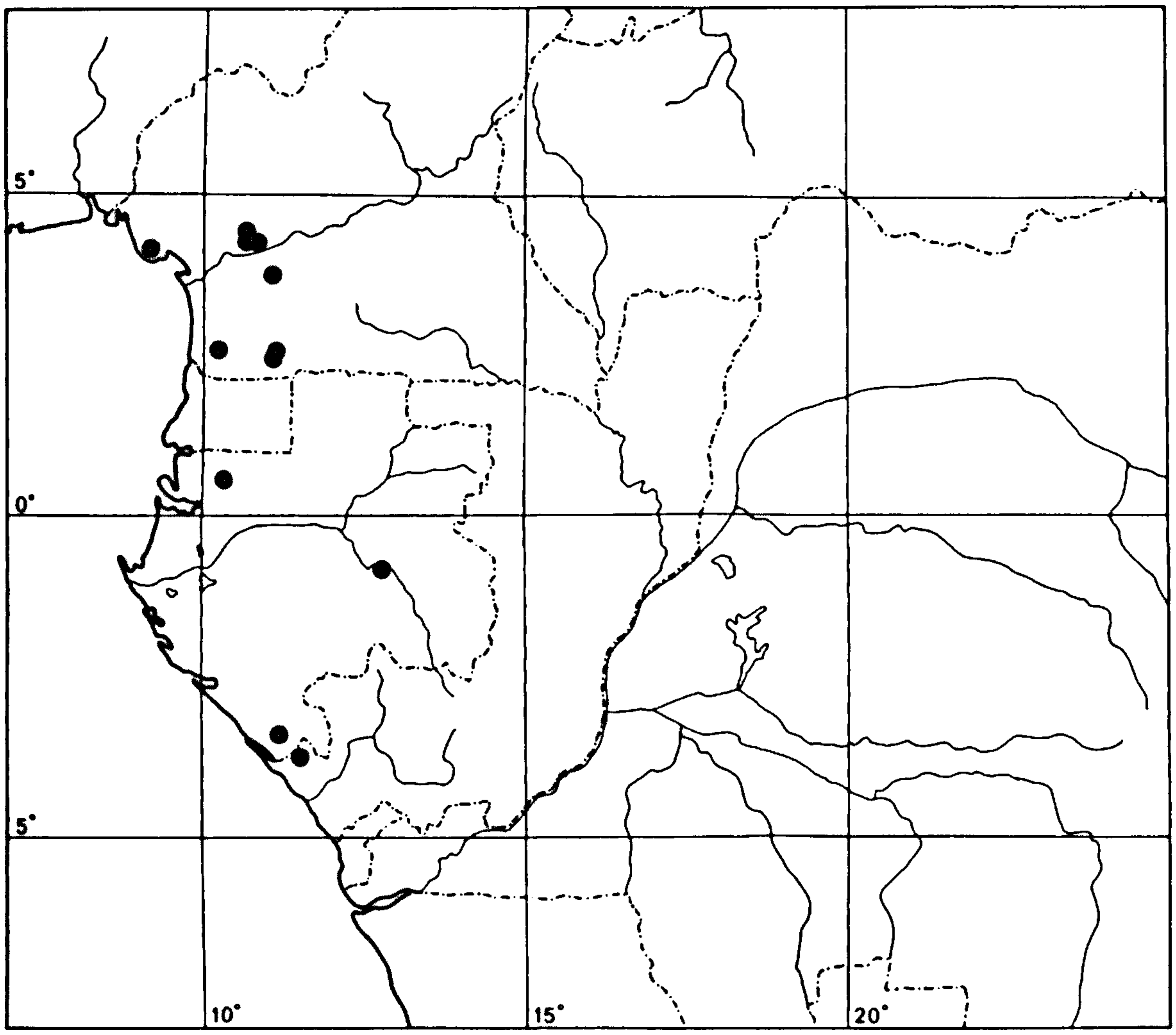
Figure 16.7. *Begonia letouzeyi* Sosef. – 1: leaf (x$^{2}/_{3}$); 2: detail lower leaf surface (x2). – 1-2: *Letouzey 10193*.

Begonia schaeferi auct non Engl., van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 14, 15, 38, 39 p.p.; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 21, pl. 15D.

Diagnosis: *Begonia schaeferi* similis, differt foliis densiter pubescentibus, pedunculis non ramosis et ovaria pilosis.

Plant (3–)10–27 cm high, scattered with minute glandular hairs, sparsely so on stipules and pedicel of male flower, sometimes more dense on bracts. **Rhizome** rather stout and compact to more slender and slightly elongated, (0.8–)1.2–7.8 mm wide, hirsute especially around the leaf axils; the apical part not or slightly ascending. **Stipules** very broadly triangular-ovate to triangular or narrowly ovate, acute to blunt, (1.2–)2.5–7.0(–10.0) mm long, bronze-green to reddish or reddish brown; margin entire to dentate, glabrous to ciliate. **Leaves** peltate; *petioles* continuing into the midrib with a distinct angle, inserted at (3–)7–43 mm from the nearest margin, (2–)10–26 cm long, juicy to slightly fleshy, usually red, sometimes green, hirsute to densely so with long, patent, wavy, white hairs; *leaf blade* in more or less horizontal position, almost symmetrical to asymmetrical, broadly ovate or broadly elliptic-ovate to elliptic-ovate or elliptic, acuminate to caudate in the upper 1/3–1/4 to more or less gradually tapering towards the top, usually with a few coarse shallow teeth in the apical half or sometimes distinctly coarsely dentate in that region, (2.7–)5.0–17.5 x (1.6–)2.5–11.0 cm, juicy, with 8–10 palmate main nerves; margin more or less entire, concolorous with the blade, sparsely to densely shortly ciliate; base rounded, top acute; upper surface light to medium green, dull but glistening in artificial light, smooth, usually densely hirsute with white hairs; lower surface pale green, dull; *nerves*: the main and larger secondary nerves not prominent and concolorous with the blade on the upper surface, on the lower surface not or slightly prominent, green and hirsute with patent hairs, smaller secondary nerves not prominent, distinct to indistinct, sparsely hirsute, tertiary nerves usually not visible, sparsely hirsute. **Inflorescence** containing (1–)2–3 male flowers and 1 terminal female flower, positioned at about halfway up the petioles to at approximately the same level as the leaf blades; *peduncle* simple, 1.5–10.0 cm long, juicy, usually reddish or brown-red, sometimes green, hirsute with long patent white hairs to almost glabrous; *bracts* (2–)3–4(–5), slightly reducing upwards, very broadly ovate or circular to elliptic-ovate, (1.4–)2.5–8.2 mm long, bronze-green to pale red or brown-red; margin dentate, ciliate. **Male flower**: *pedicel* elongated in flower, up to 28 mm long, orange-yellow, glabrous to sparsely hirsute; *perianth segments* very broadly ovate or depressed broadly elliptic to broadly ovate with a rounded to cordate base, (5.5–)8.5–17.5 x (5.5–)8.5–18.0(–28.0) mm, the outside sparsely hirsute with red or white hairs; the upper segment reddish or orange-yellow to yellow with or without red nerves on the outer and yellow to pale yellow with or without a red patch and nerves on the inside; the lower orange-yellow to yellow on the outside and yellow to pale yellow on the inner; *androecium* with 14–39 stamens; column 0.6–2.1 mm long; anthers 0.9–2.1 mm long. **Female flower**: similar to the male one, pedicel usually distinct and elongated in fruit, 0.8–5.0 mm long, glabrous to sparsely hirsute; *perianth segments* very broadly ovate or depressed broadly elliptic to circular, rarely broadly obovate, (6.0–)8.0–22.0 x (6.2–)9.0–20.0(–28.0) mm; *styles* (3–)4, 2.2–6.4 mm long, fused for ca 1/4 to 3/4 of their length, the top horseshoe-shaped, the arms 0.25–2.5 mm long and bearing a usually rather compact stigmatic band which is not twisted or twisted for at most 1/2 a turn; *ovary* circular or broadly obovate to obovate or elliptic, (2.5–)3.9–9.1 x (1.8–)2.2–5.2 mm, brownish green to reddish, not translucent, densely to sparsely hirsute with white or red hairs, sometimes set with a comb-like fringe of hairs in between the locules, (3–)4-locular, (3–)4-winged in the apical part or rarely all along or only (3–)4-angular; the locular part broadly elliptic to obovate or elliptic, as wide as the ovary; beak present, usually short, 0.25–2.6 mm long; wings (when present) patent or sometimes slightly erecto-patent, very broadly obovate to obovate, rarely narrowly elliptic, 0.1–2.2 mm wide, margin usually ciliate; **Infructescence**: its peduncle not recurved towards the substrate; *fruit* erect, circular to elliptic, 4.7–10.0 x 2.7–8.8 mm, dry, with a comparatively thick wall, brown to reddish brown, dull.

Distribution: Western Cameroon, Gabon and western Congo.



Map 16.3. Distribution of *Begonia letouzeyi*.

Ecology: Terrestrial on the forest floor, sometimes on steep slopes or banks, or on bare to mossy rocks, also found on vertical rock faces or epiphytic at the base of mossy tree trunks in primary or degraded lowland or submontane rain forest often near rivers, streams or waterfalls; growing in association with *Aframomum*, *Gilbertiodendron* sp., *Monopetalanthus pellegrinii*, *Dacryodes buettneri* and *Parinari* cf. *gabunensis*; at 350–900 m altitude.

Notes:1. The species is named after the late dr Letouzey, who dedicated his life to the study of the flora of tropical Africa with emphasis on Cameroon. The species is related to *B. schaeferi* and sometimes resembling *B. potamophila* but distinguished from the latter at least by the more broadly shaped ovaries. Notable variation has been observed in the length and shape of the bracts. All specimens from Gabon and Congo and two from Cameroon have smaller and usually narrower bracts. The variation is however gradual and does therefore not lead to any taxonomic consequences.

Specimens examined:

CAMEROON: *Letouzey 9049* (P, YA): 20 km SSE of Zingui (at 50 km SE of Kribi), 02°36'N 10°15'E (fl, 03); *Letouzey 10193* (P, YA): Ongongondje hill, near Akonekye, 15 km NW of Ambam, 02°28′N 11°10′E (fl, 03); *Letouzey 10846* (K, P): near Ndoknabao, 30 km SW of Ndikinimeki, track to Koko, 04°33′N 10°40′E (fl, 12); *Letouzey 11080* (P, holo; YA): near Esseng, 12 km NNE of Ngambé, 04°20′N 10°39′E (fl, 01); *Letouzey 11573* (P, YA): Kombeng ridge, 8 km SSE Matomb, about 50 km WSW of Yaounde, 03°45′N 11°05′E (fr, 07); *Nkongmeneck 579* (WAG, YA): Nkohom ridge at 42 km SSW of Ndiki, 04°22′N 10°48′E (fl, 11); *Satabié 652* (P, WAG, YA): SE slope of Little Mt Cameroon (Etinde), 12 km NW of Limbe (Victoria), 04°06′N 09°09′E (fl, 02); *J.J. de Wilde 8718A* (WAG): Ongongondjé hill, on summit, 02°29′N 11°10′E (fr, 12).

GABON: *Breteler c.s. 9857* (WAG): c. 30 km NE of Lastoursville, right bank of Ogooué, forest exploitation, 00°45′S 12°55′E (fl, fr, 04); *Leroy s.n.* (P): Ogooué, c. 01°30′S 13°30′E (fl); *Thollon 1363* (IEC, P): Mayombe forest, c. 03°30′S 12°00′E (fl, 11); *J.J. de Wilde c.s. 10080* (WAG): Crystal Mts, about halfway Kinguélé-Tchimbélé, 00°33′N 10°21′E (fr, 12); *J.J. de Wilde c.s. 10228* (WAG): Crystal Mts, 23 km along the road Tchimbélé to Kinguélé, 00°33′N 10°18′E (fr, 01); *J.J. de Wilde c.s. 10244* (WAG): Crystal Mts, 25 km along the road Tchimbélé to Kinguélé, 00°31′N 10°18′E (fr, 01).

CONGO: *Attims 409* (BR, IEC, P): Mayombe, summit of the Kouboula Mts, 03°47′S 11°27′E (fl, fr, 02).

Begonia microsperma Warb. **Fig. 16.8, Map 16.4**

Begonia microsperma Warb., Bot. Jahrb. Syst. 22 (1895) 42; Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3,2 (1921) 617; Hutch., Dalz. & Keay, Fl. W. Trop. Afr. (ed. 2) 1,1 (1954) 220; L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 200, fig. 2.6; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 19, pl. 15B. – TYPE: *Dusén 79* (B!, holo; B!): 'Kamerun'.

Begonia ficicola Irmscher, Bot. Jahrb. Syst. 76 (1954) 213; Hutch., Dalz. & Keay l.c. 218; Legro & Doorenbos, Neth. J. Agric. Sci. 19 (1971) 177; Doorenbos, Begonian 47 (1980) 15-16; M. & E. Thompson, Begonias, Compl. Ref. Guide (1981) fig. p. 135, 168; Reitsma, Meded. Landbouwhogeschool Wageningen 83-9 (1984) 45, 47; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 39-40; L.B. Smith et al. l.c. 166, fig. 2.5; Doorenbos, Begonian 53 (1986) 159; Coats, Begonian 56 (1989) 237; Weinberg, Begonian 59 (1992) 181; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 19, pl. 13G. – TYPE: *Dundas FHI 20.351* (K!, holo; COI! (photo)): 'Prov. Cameroons, Distr. Kumba Divn., Loc. Ekumbe Ndene, epiphytic on a Ficus at the base of Ekumbe Ndene waterfall on the River Meme. 6.12.46'.

Plant up to 20 cm high, scattered with minute glandular hairs, sparsely so on rhizome, stipules, petioles, bracts and pedicel of male flower, sometimes sparsely so on peduncle. **Rhizome** rather stout, smooth to somewhat knotted, 1.8–5.9 mm wide, usually glabrous, sometimes with long hairs around the leaf axils; the apical part not directed upwards or sometimes slightly ascending. **Stipules** narrowly triangular to very broadly ovate, slightly acuminate to blunt, 1.8–7.8 mm long, at first dark red-brown but soon loosing its colour and turning light green; margin entire, not ciliate. **Leaves** peltate; *petiole* continuing into the midrib with a distinct angle, inserted at 11–32 mm from the nearest margin, 4.0–20.0 cm long, juicy, light to very pale green, completely glabrous to sparsely hirsute with long, patent, wavy, white hairs; *leaf blade* in a more or less horizontal position, asymmetrical, sometimes only slightly so, elliptic or elliptic-ovate to broadly so, acuminate at the top, 6.1–18.0 x 3.3–12.0 cm, rather firm though slightly succulent, with 6–8(–10) palmate main nerves; margin entire to denticulate, especially in the upper half, sparsely to fairly densely ciliate, concolorous with the blade; base rounded, top acute; upper surface light to dark medium

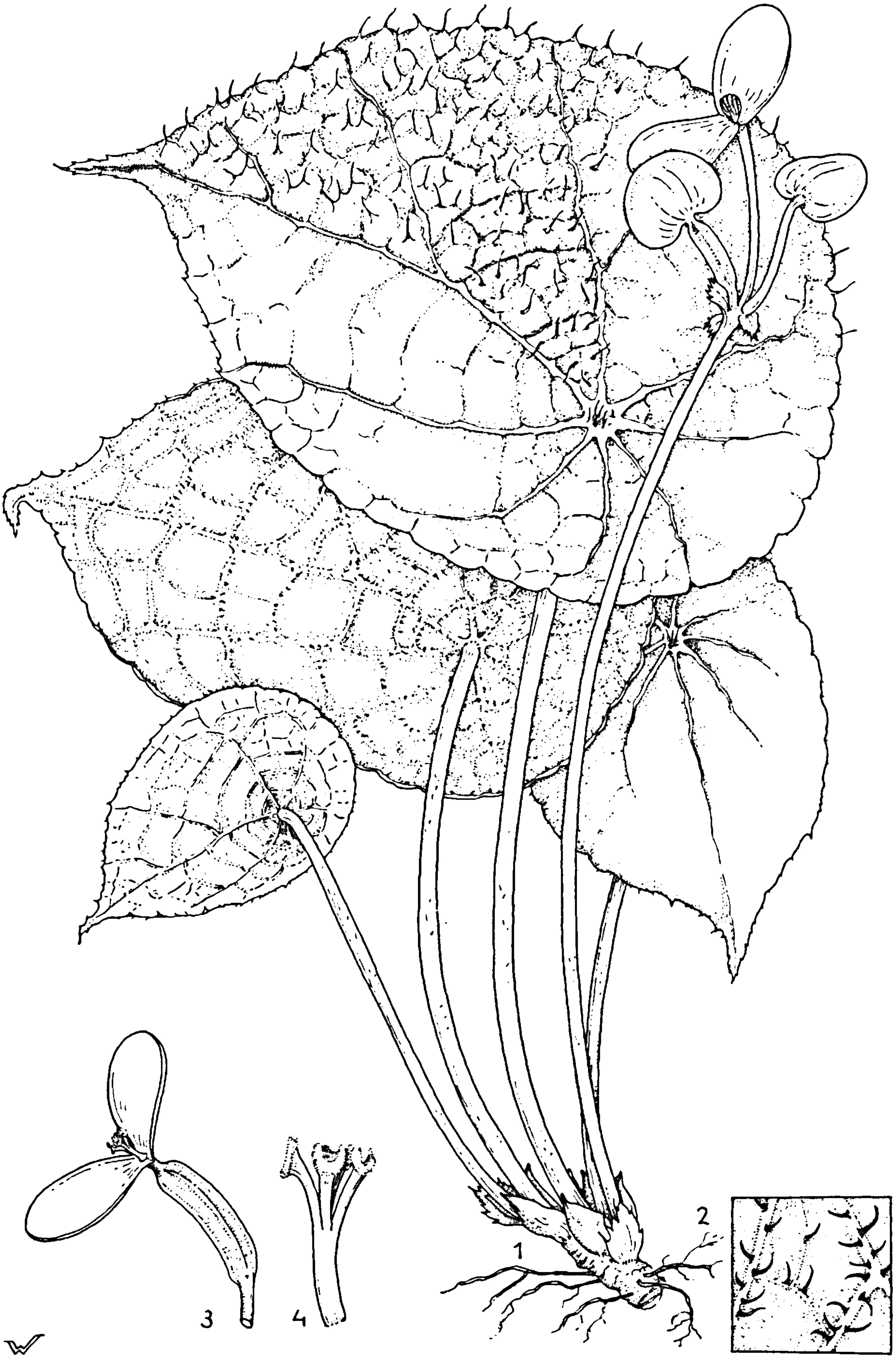


Figure 16.8. *Begonia microsperma* Warb. – 1: habitus (x$^{2}/_{3}$); 2: detail lower leaf surface (x4); 3: female flower (x1); 4: styles (x4). – 1-4: living plant at WAG, voucher *van Veldhuizen 1312*.

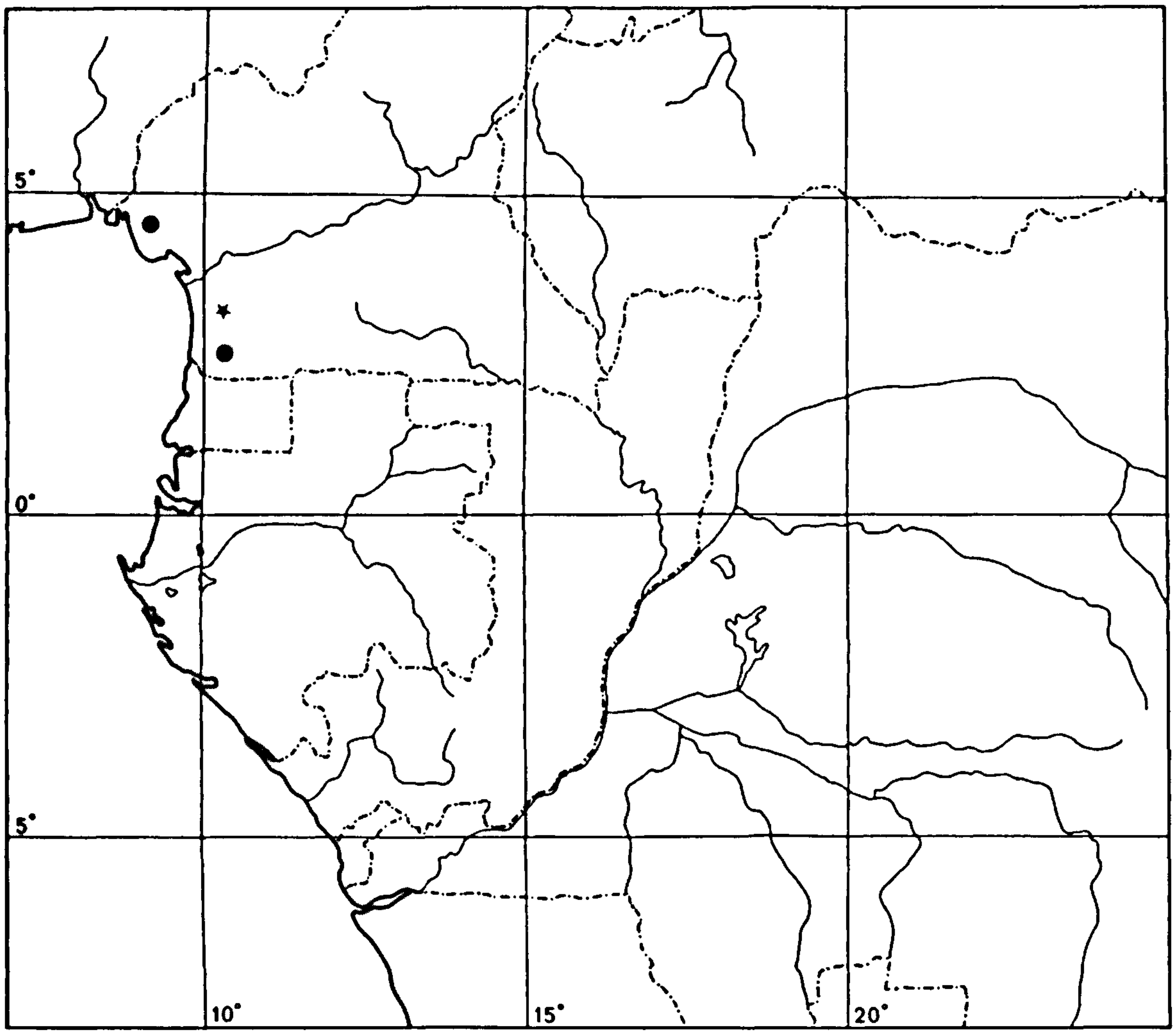
green, shiny, sharply conically bullate, the bullae solitary and topped with a single stiff erect white hair, some hairs at the centre of the blade with a red base; lower surface pale green, dull, without long hairs in between the nerves; *nerves*: the main and larger secondary nerves sunken and with a pale green basal part on the upper surface, on the lower prominent, medium green and hirsute with rather short, patent, stiff hairs which are white with a dark brown-red base, smaller secondary nerves less distinct but still well visible, slightly prominent, sparsely hirsute and creating a reticulated pattern, tertiary nerves indistinct, not prominent. **Inflorescence** containing (1–)2–3 male flowers and 1 terminal female flower, positioned at about the same level as or slightly exserted above the leaves; *peduncle* simple, 6.0–18.0 cm long, light to very pale green, glabrous to sparsely hirsute with white hairs; *bracts* (2–)3–4, circular to ovate, 1.3–5.2 mm long, comparatively dark bronze- or brown-green, the outside with red nerves; the margin dentate, ciliate. **Male flower**: *pedicel* elongated at anthesis up to 34 mm, yellowish green, glabrous to sparsely hirsute; *perianth segments* broadly elliptic-ovate to almost circular or very broadly ovate, with a slightly cuneate to cordate base, 11.5–22.0 x 10.5–22.0 mm, the upper segment turning from orange-red in bud to orange in flower on the outside, the lower yellow or sometimes orange tinged on the outside, the inside of both segments deep yellow with slightly paler tinged nerves; *androecium* with 22–28 stamens; column 0.1–0.5 mm long; anthers 1.6–2.7 mm long. **Female flower**: similar to the male but shortly pedicellate, the pedicel elongated in fruit up to 14.5 mm; *perianth segments* circular to very broadly ovate or very broadly elliptic-ovate, with a rounded to cordate base, 11.0–19.0 x 9.8–24.0 mm; *styles* 4, 2.9–6.5 mm long, fused in the lower 1/2 to only at base, the top split into a short and compact to slender U-shape, the arms 0.5–1.6 mm long and bearing a slender to rather broad, non- or only slightly twisted stigmatic band; *ovary* narrowly elliptic-oblong to narrowly obovate, 9.1–23.0 x 1.6–6.4 mm, medium green, 4-locular, not or very narrowly 4-winged all along; the locular part narrowly elliptic-oblong to narrowly obovate, 1.6–6.0 mm wide; beak absent or short, slightly enlarged in fruit, 0–1.6 mm long; wings (when present) patent, ribbon-shaped or narrowly elliptic-obovate, 0–1.4 mm wide, pale green, the margin entire, glabrous. **Infructescence**: peduncle not recurved towards the substrate though sometimes held almost horizontal; *fruit* erect to erecto-patent, narrowly elliptic-oblong to narrowly elliptic-obovate, 17.0–18.0 x 3.8–4.7 mm, dry, with a thin wall, pale brown.

Distribution: Western Cameroon.

Ecology: Clinging to sheer spray-soaked rock faces or epiphytic (on a *Ficus*) near a waterfall at 100% humidity; in tight groups.

Chromosome number: 2n = 34 + + + + (Legro & Doorenbos l.c.).

Notes: 1. According to Birger (1926) Dusén collected in South-West Cameroon near Mt Cameroon and Buea. The type-specimen of *B. microsperma* (Dusén 79) was therefore probably collected in that area. It is almost certain that it was not collected in the same locality as the type (and a few other collections) of *B. ficicola*, since all plants from that locality have completely glabrous petioles whereas those of Dusén 79 are sparsely hirsute. The specimens collected in the



Map 16.4. Distribution of *Begonia microsperma* (dots) and *Begonia minuta* (star).

extreme south-west of Cameroon have hirsute petioles.
2. Bos 5110 contains double male flowers with up to 9 perianth segments.
3. Notable are the non-ciliate stipules.

Specimens examined:

CAMEROON: *Bos 5110* (P, WAG, YA): W. Camoon, Kumba area, Bai-falls in Meme R., near Ekoumbé, S of Mbonge, Type loc.! 04°28'N 09°09'E (fl, 07); *Dundas FHI 20351* (K, holo): Kumba Distr., Ekumbe Ndene, Ekumbe Ndene waterfall on the R. Meme, 04°28'N 09°09'E (fl, 12); *Dusén 79* (B, holo): ? (see note 1!) (fr); *Hulsewé 1* (WAG): Bai-falls, 25 km from Lobe Estate, 04°28'N 09°09'E (fl, 05); *Keay FHI 37377* (K): Kumba Distr., Ekumbe Ndene waterfalls, Meme R., SE of Mbonge, 04°28'N 09°09'E (fl, 01); *Schultze (in Mildbraed) 6192* (B, HBG): South Cameroon forest area, Kribi-Kampo area, mountains NE of Kampo, Mt Nkolumbembe, between Ebolowa & Kampo, 02°25'N 10°18'E (st, 07); *Schultze (in Mildbraed) 6207* (B): Nkolumbembe, 02°25'N 10°18'E (fl, 07); *Swarbrick 2430* (E, YA): Ekumbe waterfall, Meme R., 04°28'N 09°09'E (fl, 04).

CULTIVATED: *Schwerdtfeger 7475* (B): cult. in Bot. Garten Berlin-Dahlem (fl, 09); *Schwerdtfeger 9431* (B): cult. in Bot. Garten Berlin-Dahlem (fl, 11); *Schwerdtfeger 10596a* (B): cult. in Bot. Garten Berlin-Dahlem (fl, 09); *van Veldhuizen 446* (WAG): Wageningen Agricultural Univ., Dept of Horticult. (coll. Middelburg s.n., 1970, Cameroon) (fl, 03); *van Veldhuizen 1312* (WAG): Wageningen, Bot. Garden 'De Dreijen', cult. no 86PTCB434 (fl, 05).

Begonia minuta Sosef — **Fig. 16.9, Map 16.4**

Begonia minuta Sosef, Wageningen Agric. Univ. Papers 91-4 (1992) 135, fig. 5; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 19, pl. 14B. – TYPE: *Letouzey 12709* (P!, holo, iso; WAG!, YA!): 'Cameroun, colline Nkol Tsia, 488 m (18 km NW Bipindi près Gouap) feuille IGN 1/200.000 Edea.'

Diagnostic characters (for a more detailed description see Sosef l.c.):

Plant up to 6 cm high, practically devoid of long hairs but scattered with two types of minute glandular hairs one of which turns dark purplish in sicco. **Leaves** peltate; *leaf blade* symmetrical to slightly asymmetrical, ovate, sometimes narrowly so, usually broadly caudate in the upper 1/2 to 1/3, sometimes terminating abruptly into a short tail-like appendage or gradually tapering towards the top, 1.2–3.9 x 0.5–1.5 cm; margin usually very shallowly sinuate-dentate, glabrous; *nerves*: the main nerves markedly widening in the marginal zone. **Male flower**: *perianth segments* broadly elliptic to broadly elliptic-ovate, with a rounded to cuneate base, 7.0–8.5 x 5.2–8.2 mm, yellow on both surfaces; *androecium* with 8–14 stamens. **Female flower**: *perianth segments* broadly elliptic to almost circular, 6.8–11.0 x 4.7–6.9 mm; *ovary* narrowly elliptic, 5.9–10.0 x

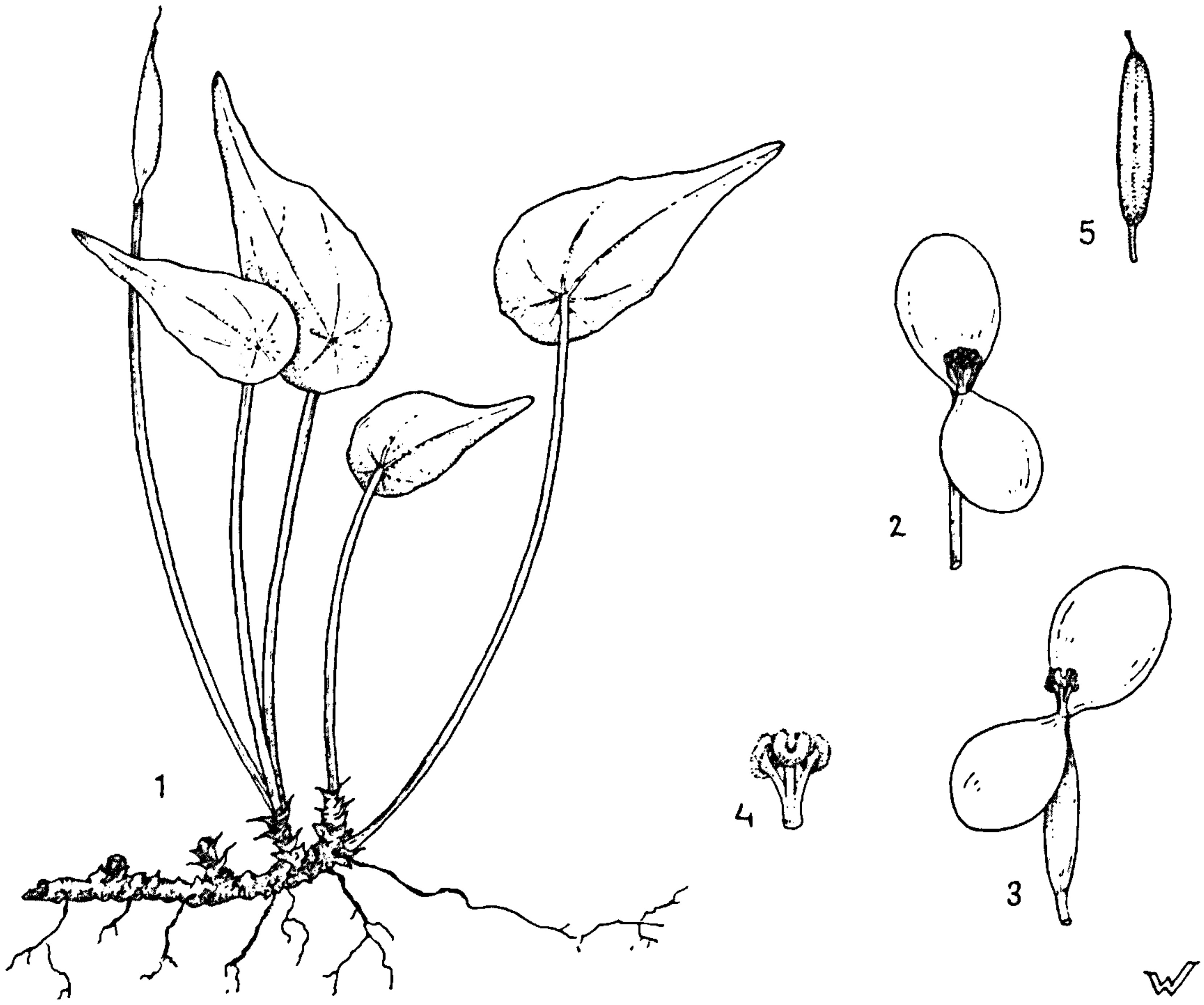


Figure 16.9. *Begonia minuta* Sosef. – 1: habitus (x1); 2: male flower (x2); 3: female flower (x2); 4: styles (x4); 5: fruit (x2). – 1-5: *Letouzey 12709*.

0.8–1.7 mm; wings ribbon-shaped, 0.1–0.4 mm wide. **Infructescence:** *fruit* erect, narrowly elliptic to narrowly obovate, 7.9–13.0 x 1.2–3.0 mm.

Distribution: CAMEROON: Centre-Sud Province.

Ecology: Under trees and bushes; forming a mat on vertical very wet rock faces otherwise covered with mosses; at c. 500 m altitude.

Specimens examined:

CAMEROON: *Letouzey 12709* (P, holo; WAG, YA): Nkol Tsia ridge, 18 km NW of Bipindi near Gouap, 03°10′N 10°16′E (fl, 01); *Villiers 776* (P): ibid. (st, 02); *Villiers 895* (P): ibid. (st, 04); *Villiers 938* (P): Nkol Tsia ridge, 23 km NW of Bipindi, 03°12′N 10°14′E (fl, 06).

Begonia potamophila Gilg

Fig. 16.10, Map 16.5

Begonia potamophila Gilg, Bot. Jahrb. Syst. 34 (1904) 89; Legro & Doorenbos, Neth. J. Agric. Sci. 21 (1973) 168-169; Doorenbos, Begonian 47 (1980) 14-15; Reitsma, Meded. Landbouwhogeschool Wageningen 83-9 (1984) 45, 47, fig. 9D; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39; L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 218; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 14, pl. 8D. – LECTOTYPE: *Zenker 2100* (B!; iso: BM!, E!, G!, K!, LY!, P!, STU!): 'Bipindi, an verrotteten Baüme im Urwald. Höhe ü. d. M. 250. Gelb (chrom.). Juni 99.'

Begonia macropoda Gilg, Bot. Jahrb. Syst. 34 (1904) 90; Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3,2 (1921) 617; Mildbraed, Wiss. Erg. Zweiten Zentral-Afr. Exp. 2, Bot. (1922) 188. – TYPE: *Staudt 116* (B!, holo): 'Lolodorf. Blatt grün, eb..rd. behaart. Blütenfarbe rötlich gelb. Urwald NW. d. Station, 400-450 m. Humus, schattig feucht, 3/III 95.'

Begonia batesii C.DC., Candollea 2 (1925) 228; van den Berg l.c.; L.B. Smith et al. l.c. 142, fig. 2.21 (as *B. potamophila*) & 3.11. – TYPE: *Bates 475* (G!, holo; BR!, K!, L!, P!, Z!): 'NKomo R. 75 miles from Gaboon. Atakama, hill near river. Forest hill. Fls. yellow. May 1896.'

Plant up to 25(–40) cm high, scattered with minute glandular hairs, sparsely so on stipules and outside of perianth segments, sometimes more densely so on petioles. **Rhizome** rather stout and compact to slightly elongated, rather smooth, (1.3–)1.8–5.3 mm wide, densely hirsute to almost glabrous but then at least hirsute around the leaf bases and on the younger parts; the apical part not or slightly ascending. **Stipules** broadly to very broadly triangular-ovate or shallowly triangular, blunt to long attenuate, 1.6–6.5 mm long, light green to light brownish, glabrous to hirsute; margin more or less entire to finely dentate, ciliate. **Leaves** peltate; *petiole* continuing into the midrib with a distinct angle, inserted at (8–)14–55 mm from the nearest margin, 3.5–28.0 cm long, firm but juicy, red to dark red, usually densely hirsute with long, patent, wavy, white to red hairs; *leaf blade* in a more or less horizontal position, slightly asymmetrical to asymmetrical, broadly elliptic to circular or broadly to very broadly elliptic-ovate, sometimes depressed ovate, usually with a distinct and long acuminate top, sometimes almost rounded, (4.6–)6.6–14.5(–20.0) x (4.0–)5.0–11.5(–15.0) cm, juicy or crisp, with 8–10(–11) palmate main nerves; margin usually more or less entire, sometimes serrulate-denticulate or remotely dentate in the apical part, densely ciliate, concolorous with the blade; base rounded, top acuminate or rarely rounded; upper surface light to medium or darker greyish green (brown to somewhat glossy greyish brown when dry), dull, smooth, covered with red

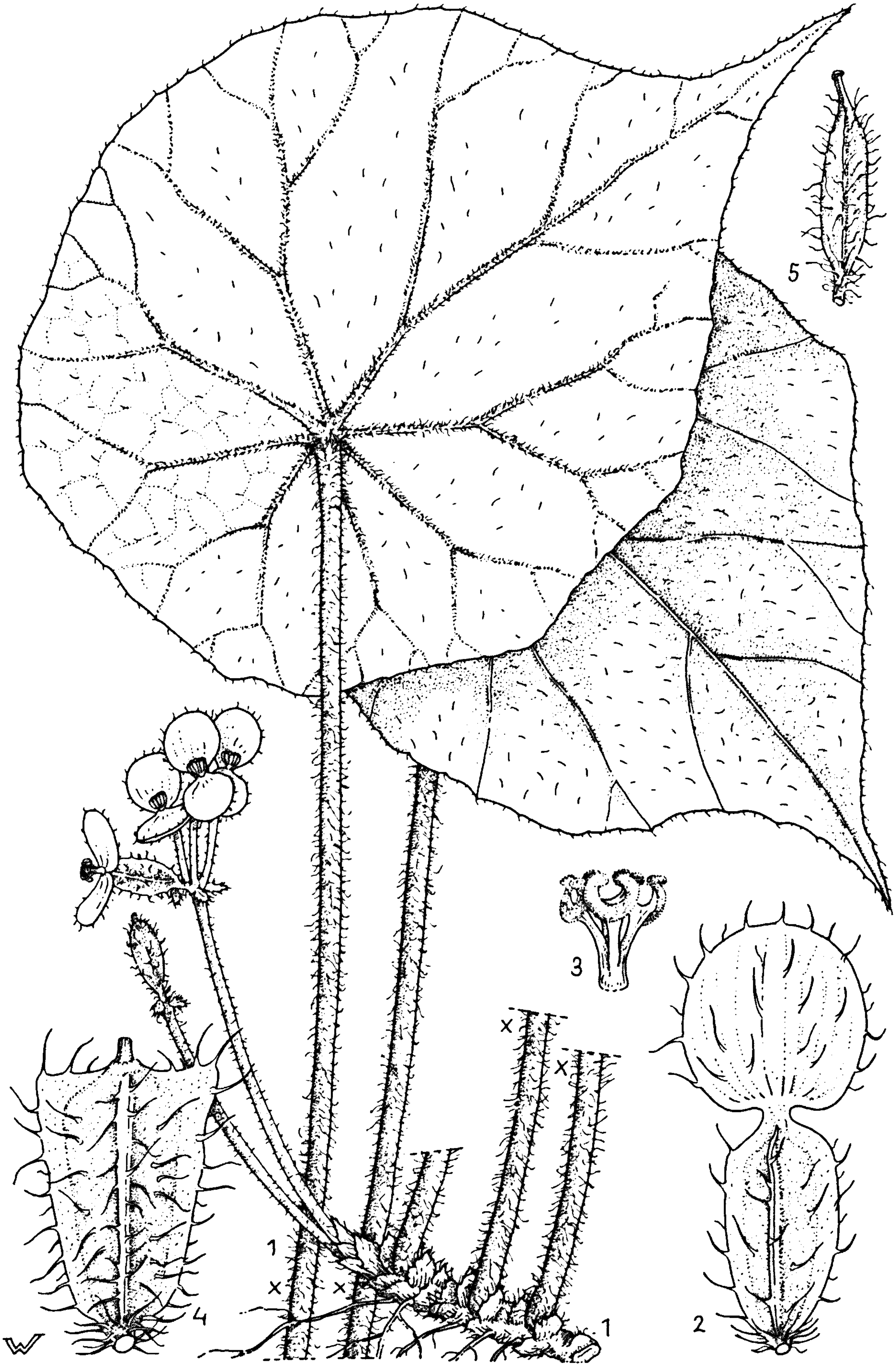
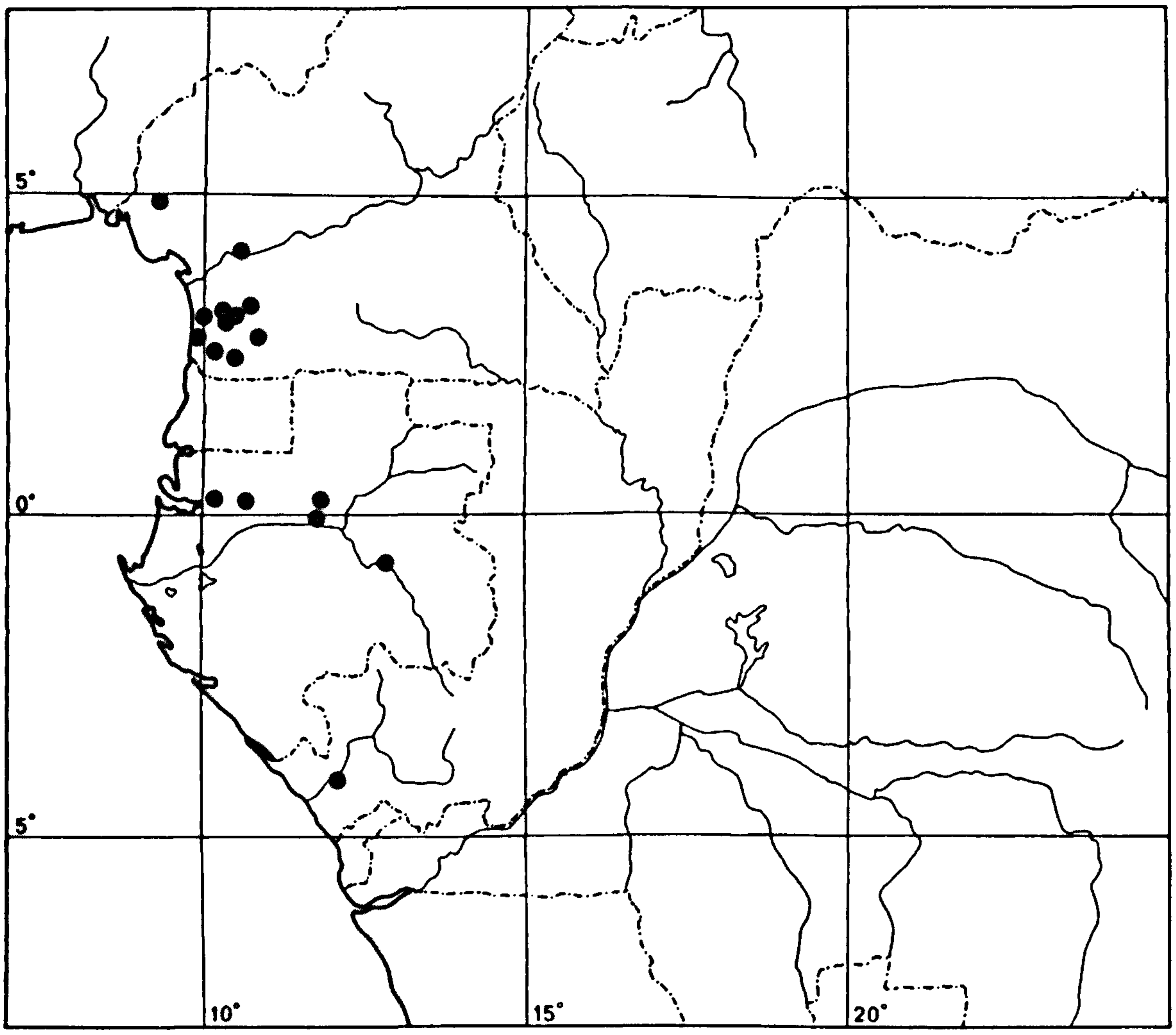


Figure 16.10. *Begonia potamophila* Gilg. – 1: habitus (x$^{2}/_{3}$); 2: female flower (x2); 3: styles (x4); 4: fruit (x2); 5: fruit (x2). – 1: *Breteler c.s. 9892*; 2-4: living plant at WAG, voucher *van Veldhuizen 1288*.

to white soft hairs; lower surface pale green, dull, hirsute in between the main nerves; *nerves*: the main and larger secondary nerves not prominent to slightly sunken on the upper surface, on the lower slightly prominent, medium green to pale green and densely or rarely sparsely hirsute with long to relatively short, patent hairs, smaller secondary nerves distinct, not prominent, tertiary nerves less distinct to indistinct, not prominent. **Inflorescence** containing 2–4 male flowers and 1(–2) terminal female flower(s), positioned halfway up the petioles to more or less at the same level as the leaf blades; *peduncle* simple, (1.0–)2.0–9.5 cm long, pale reddish bronze-green to red, densely hirsute to hirsute with red to white hairs, sometimes sparsely so; *bracts* (3–)4–6(–7), sometimes an additional bract is present on the pedicel of the female flower, ovate to circular, sometimes very broadly ovate, (0.9–)1.3–3.9 mm long, pale green to reddish green; margin dentate, ciliate. **Male flower**: *pedicel* elongated at anthesis up to 35(–47) mm, pale reddish green to red or orange-green, hirsute or rarely glabrous; *perianth segments* broadly ovate to circular, sometimes ovate or broadly elliptic-obovate, with a rounded to slightly cuneate base, (5.1–)6.8–19.0 x (4.7–)6.0–18.0 mm, the outside hirsute with white hairs, especially towards the base and along the margins, rarely glabrous; the upper segment deep yellow to red on the outside, the inside yellow with or without a red patch and nerves in the basal half or the latter sometimes running up to the top; the lower segment pale yellow to deep yellow or pale pinkish yellow on the outside, the inside yellow; *androecium* with 18–32 stamens; column 0.1–0.4 mm long; anthers 0.9–2.0 mm long. **Female flower** similar to the male but almost sessile to shortly pedicellate, the pedicel elongated in fruit up to 3.0(–6.5) mm; *perianth segments* broadly or very broadly ovate to circular or slightly transversely broadly elliptic, sometimes elliptic-ovate, with a rounded to slightly cordate base, (5.7–)7.2–13.5 x (5.2–)5.5–15.0 mm; *styles* 3–4, 2.1–3.9(–5.1) mm long, fused in the lower 1/2 to 1/6, the top split and horseshoe-shaped, the arms 0.8–1.8 mm long and bearing a slender to rather compact stigmatic band which is spirally twisted for up to 1/2 a turn; *ovary* spindle-shaped or narrowly elliptic to obtriangular-obovate, 5.9–13.0 x 1.3–5.3(–8.7) mm, pale to medium green but the pinkish ovules shining through the translucent wall; 3–4-locular, 3–4-winged all along, usually hirsute, sometimes very sparsely so; the locular part narrowly elliptic to elliptic or obovate, 1.0–5.3(–6.2) mm wide; beak practically absent or short, 0–1.3 mm long; wings patent, from very narrow and almost absent to well developed, ribbon-shaped to broadly obtriangular, 0.1–1.4(–5.3) mm wide, green to pale green or turning whitish in fruit, margin ciliate, sometimes sparsely so. **Infructescence**: peduncle not recurved towards the substrate; *fruit* erect to ascending, narrowly elliptic or elliptic to obtriangular-obovate, 7.3–17.0 x 2.6–7.8(–12.0) mm, dry, with a comparatively thin wall, pale brown or reddish brown to greenish or orange-red.

Distribution: Western Cameroon, Gabon and western Congo.

Ecology: Terrestrial on the forest floor, on mossy rocks, or steep cliffs in primary forest or shaded sites; in coastal high forest, swamp forest and 'Forêt Atlantique à Caesalpiniacées'; locally abundant on hill slopes, often near stream-



Map 16.5. Distribution of *Begonia potamophila.*

lets and rivers; from near sea-level to 800 m altitude.

Chromosome number: 2n = 26 (Legro & Doorenbos l.c.). The authors do not mention a particular voucher specimen although they remark that material has been deposited at WAG. Van Veldhuizen 609 represents the most likely voucher material.

Notes: 1. Mildbraed l.c. mentions *B. macropoda*. His collection 6290, to which he refers, has however not been traced.

2. Villiers 784 is slightly aberrant because its flowers and fruits lack the typical long hairs.

3. The variation in the shape of the wings on the ovary is striking but continuous as well as is that in the density of the indumentum on the leaves.

4. The label of Breteler c.s. 8934 reports pink flowers. It is assumed that this refers to young flowers appearing reddish or pinkish on the outside.

5. Three collections have been cultivated at WAG. After many attempts of selfing finally a single fruit of collection 88PTGA017 from Gabon, Doussala, persisted. The peduncle was positioned almost vertically, just above the ground. The fruit at the end assumed an ascending position. Selfing was performed on

15-11-'89. In the course of a few days prior to 20-12-'89 the fruit slowly disintegrated from the top downwards. It was obvious that it was not optimally filled with seeds. A large portion of the ovula had not developed. It is thus assumed that a relatively strong mechanism against selfing is present (see also chapter 10). The seeds were sown and germinated after 34 days.

Specimens examined:

CAMEROON: *Annet 348* (P): Mt Findé, 03°14'N 10°43'E (fr, 06); *Bates 475* (G, holo; BR, K, L, P, Z): Nkomo R., 75 miles from Gaboon, Atakama, 04°05'N 10°28'E (fl, 05); *Bos 4922* (WAG, YA): 2 km N of Longii, 03°05'N 09°59'E (fl, 06); *Bos 7209* (WAG): 26 km S of Kribi, 02°46'N 09°53'E (fl, 08); *Dinklage 1500* (B, HBG, STU): Matemape hills inland from Kribi, c. 03°00'N 10°20'E (fr, 06); *Letouzey 12712* (P, YA): Nkol Tsia ridge, 18 km NW of Bipindi near Gouap, 03°10'N 10°16'E (st, 01); *J. Raynal & A. Raynal 10189* (P, YA): Tom, 12 km E of Nyabessan), 02°26'N 10°31'E (fl, 03); *J. Raynal & A. Raynal 10465* (P, YA): Nkoakam, 38 km WSW of Ebolowa, 3 km SW of Nkong, 02°48'N 10°49'E (fl, 03); *Satabié 242* (P, YA), identification doubtful: track Butu Dikome Balue, 28 km NW of Kumba, 04°50'N 09°17'E (fl, 03); *Schultze (in Mildbraed) 6224* (B), identification doubtful: South Cameroon forest area, neighbourhood of Kribi-Kampo, hills between Ebolowa & Kampo, Kom falls, c. 02°30'N 10°10'E (fl, 07); *Staudt 116* (B, holo): Lolodorf, forest NW of the station, 03°15'N 10°43'E (fl, fr, 03); *Villiers 784* (P, YA): Nkol Tsia ridge, near Gouap, 18 km NW of Bipindi, 03°10'N 10°16'E (fl, 02); *Zenker 596* (B, BR, G, LY, MO, P, WAG): Bipindi, Mimfia, c. 03°05'N 10°25'E (fl, fr, 04); *Zenker 2100* (B, lecto; BM, E, G, K, LY, P, STU): Bipindi, 03°05'N 10°25'E (fr, 06); *Zenker 2831* (B, BM, BR, E, G, HBG, K, L, LY, M, MO, P, W, WAG, Z): Bipindi, Mimfia, c. 03°05'N 10°25'E (fl); *Zenker 3901* (B, BM, E, G, K, MO, W): Bipindi, Macao, 03°05'N 10°25'E (fl).

GABON: *Breteler c.s. 8934* (WAG): 5 km SE of Kouménayong, 00°12'N 11°53'E (fl, 04); *Breteler c.s. 9892* (WAG): c. 30 km NE of Lastourville, 00°45'S 12°55'E (fl, fr, 04); *N. Hallé 2353* (P): Abanga exploitation, 00°14'N 10°37'E (fl, 06); *N. Hallé 2419* (P): Abanga exploitation C.E.F.A., 00°14'N 10°37'E (fl, 06); *N. Hallé & Villiers 4299* (P), identification doubtful: left bank Komo R., near Mbel, 00°16'N 10°10'E (fl, 01); *N. Hallé & Villiers 4360* (P): ibid. (st, 01); *Reitsma c.s. 3380* (WAG): Mt Casque, c. 20 km NW of Booué, 00°02'S 11°48'E (fl, 05).

CONGO: *Thollon s.n.* (P): ? (st); *J.J. de Wilde c.s. 11083* (WAG): 4 km on the road (N6) Louvoulou – Kakamoéka, 04°20'S 12°08'E (st, 02); *J.J. de Wilde c.s. 11084* (WAG): ibid. (st, 02).

CULTIVATED: *Bos 1633* (WAG): Wageningen (ex W.J.J.O. de Wilde, 88 km W of Yaoundé, 16-11-1964) (fl, 05); *Schwerdtfeger 7474* (B): cult. in Bot. Garten Berlin-Dahlem (fl, 09); *van Veldhuizen 609* (WAG): Wageningen Agric. Univ., Dept. of Horticulture, cuttings from Dept. of Plant Taxonomy and Geography (fl, 09); *van Veldhuizen 1288* (WAG): Wageningen, Dept. of Plant Taxonomy, 'De Dreyen' (fr, 12); *van Veldhuizen 1397* (WAG): Wageningen, Dept. of Plant Taxonomy, cult. no 88PTGA017 (coll. de Wilde & Jongkind s.n., Gabon, Dousala, 1988) (fl, 07).

Begonia prismatocarpa W.J. Hooker

a. subsp. **prismatocarpa** **Fig. 16.11, Map 16.6**

Begonia prismatocarpa W.J. Hooker, Bot. Mag. 88,3,18 (1862) t. 5307; A.DC., Prodr. 15,1 (1864) 389; Hook.f. in Oliver, Fl. Trop. Afr. 2 (1871) 573; Warb. in Engl. & Prantl, Nat. Pflanzenfam. (ed. 1) 3,6a (1894) 140; Irmscher, Bot. Jahrb. Syst. 50, Suppl. (1914) 572, fig. 4.19a-b; Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3,2 (1921) 618; Mildbr., Wiss. Erg. Zweiten Deutschen Zentr.-Afr. Exp. 2, Bot. (1922) 188; Irmscher in Engl. & Prantl, Nat. Pflanzenfam. (ed. 2) 21 (1925) 561, 574 fig. 259.19; Hutch. & Dalziel, Fl. W. Trop. Afr. (ed. 1) 1,1 (1927) 187; Hutch., Dalziel & Keay, Fl. W. Trop. Afr. (ed. 2) 1,1 (1954) 219 (p.p.); Legro & Doorenbos, Neth. J. Agric. Sci. 19 (1971) 177; N. Hallé, Adansonia, sér. 2, 12 (1972) 369. pl. 1.10; Benell, Begonian 43 (1976) 233-235; Doorenbos, Begonian 47 (1980) 36; Reitsma, Meded. Landbouwhogeschool Wageningen 83-9 (1984) 45, 47, fig. 9F; L. & E. Thompson, Begonias, Compl. Ref.

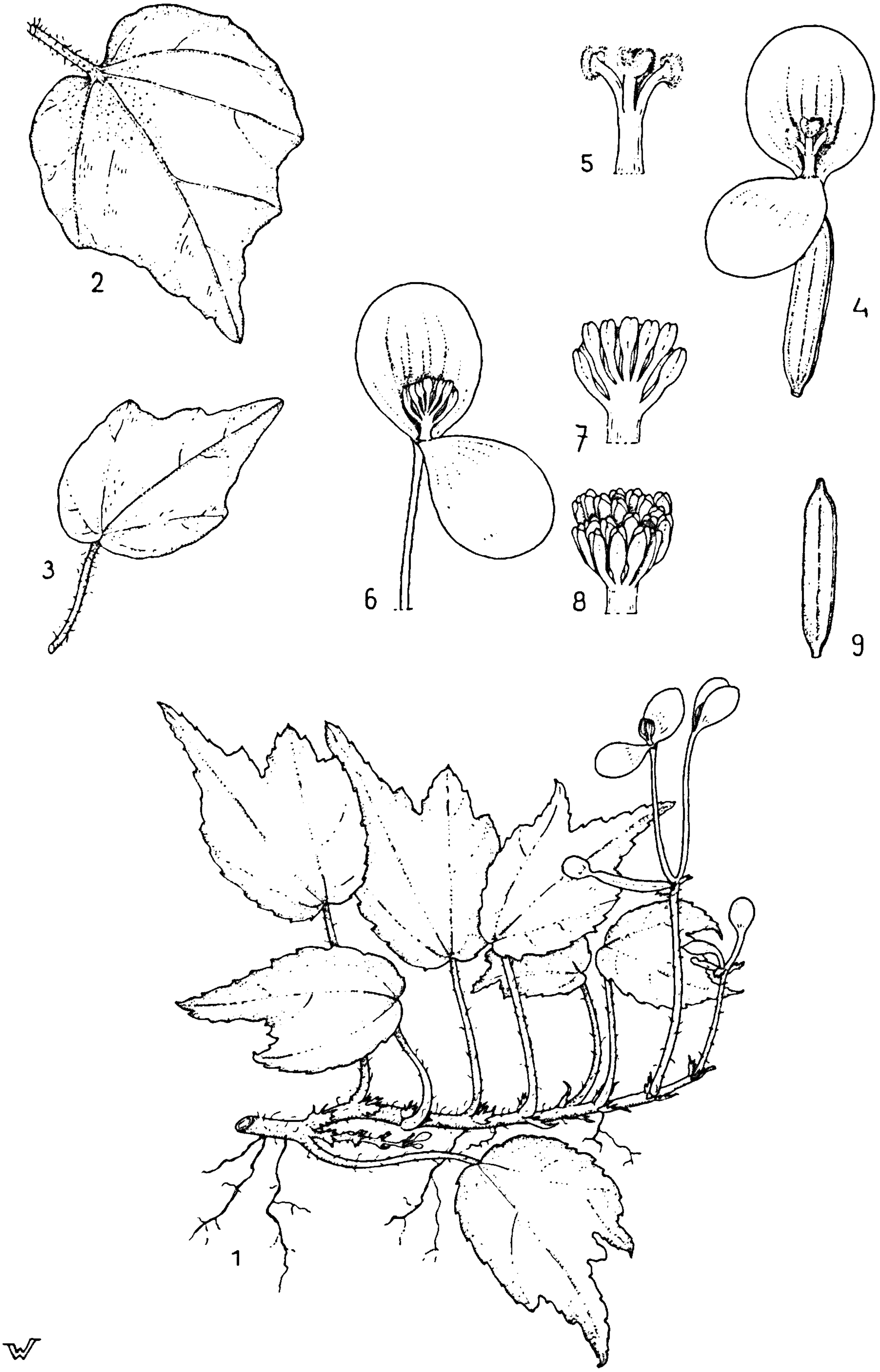
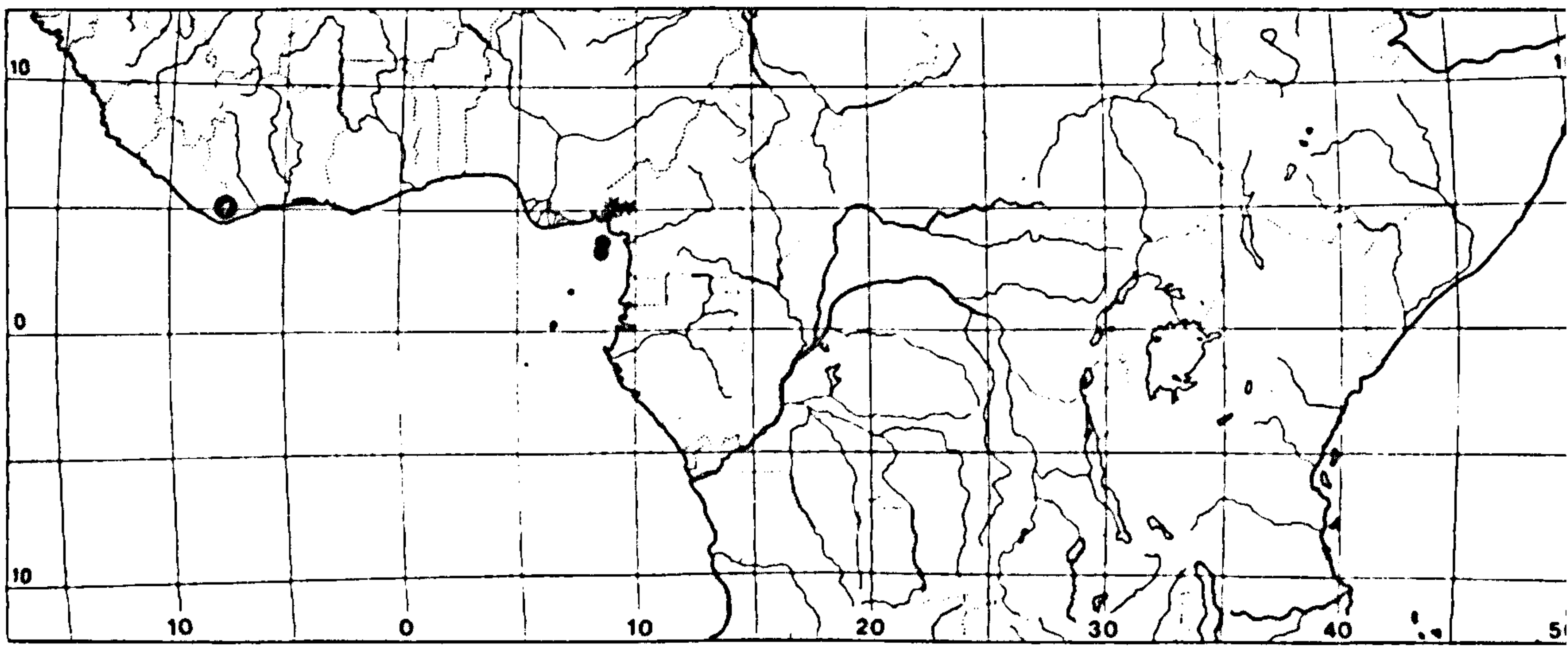


Figure 16.11. *Begonia prismatocarpa* W.J. Hooker subsp. *prismatocarpa*. – 1: habitus (x1); 2, 3: leaves (x1); 4: female flower (x2); 5: styles (x4); 6: male flower (x2); 7: androecium, back view (x4); 8: idem, front view (x4); 9: fruit (x2). – 1, 4-8: living plant at WAG, voucher *van Veldhuizen 447*; 2: *Mildbraed 7046*; 3, 9: *Sanford 4415*.

Guide (1981) 51, pl. 15; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39; L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 219, fig. 5.17; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 19, pl. 13E,F. – TYPE: *Mann 563* (K!, holo; B!): 'Fernando Po, to 3000 ft, Dec. 1860.'

Plant up to 11 cm high, scattered with minute glandular hairs, sparsely so on stipules and petiole of male flower and sometimes in addition a few stellate scales on petiole, lower leaf surface and outside of perianth segments. **Rhizome** slender and often knotted, sometimes rather elongated, 0.7–1.7 mm wide, especially the younger parts sparsely to densely hirsute with long, wavy, white hairs; the apical part usually slightly ascending. **Stipules** ovate to broadly ovate, blunt to acute, 0.8–3.5 mm long, bronze-green; margin dentate, ciliate. **Leaves** not peltate; *petiole* continuing into the midrib without a distinct angle, flattened and with a shallow groove on the upper side, 0.5–12.0 cm long, juicy, bronze-green, hirsute or sparsely so with long, wavy, white hairs; *leaf blade* in a more or less horizontal position, sometimes more or less vertical in the lower half, usually distinctly asymmetrical, ovate to broadly ovate or sometimes very broadly so, distinctly acuminate in the upper half, sometimes clearly but usually indistinctly unequally (2- or) 3-lobed, 1.3–4.2 x 0.6–3.5 cm, crispy-herbaceous, with 5–7 palmate main nerves; margin distinctly though sometimes shallowly dentate, rarely shallowly sinuate, concolorous with the blade, the teeth topped with a short hair; base cordate (rounded to almost cuneate in cultivation), top acute, sometimes obtuse; upper surface medium to dark green, sometimes tinged red, shiny, smooth, usually scattered with rather short, up to 1.5 mm long, white hairs in a regular pattern; lower surface paler, silvery-green, dull; *nerves*: the main and larger secondary nerves not prominent on both surfaces, on the lower medium green, and with few patent hairs, smaller secondary nerves indistinct, tertiary nerves not visible. **Inflorescence** containing 2(–3) male flowers and 1 (or 2 on one occasion in cultivated collection) terminal female flower(s), usually positioned slightly above the leaf blades; *peduncle* simple, 1.5–4.0 cm long, juicy, reddish to bronze-green, with scattered long patent white hairs; *bracts* 3(–4), broadly elliptic to narrowly ovate, 0.9–2.6 mm long, bronze-green; margin dentate, ciliate. **Male flower**: *pedicel* elongated at anthesis up to 22 mm, light green, sometimes sparsely hirsute; *perianth segments* circular to broadly ovate (sometimes obovate in cultivated specimens), with a rounded base, 5.7–13.0 x 6.1–12.5 mm, the outside sometimes sparsely hirsute in the basal half; the upper segment orange-red with darker streaks on the outside, the inside golden-yellow with a red patch and red nerves in the basal half; the lower segment golden-yellow; *androecium* with 17–22 stamens; column 0.7–1.8 mm long; anthers 1.0–1.7 mm long. **Female flower**: similar to the male but sessile to shortly pedicellate, the pedicel 0–0.8 mm long; *perianth segments* circular to obovate, 4.4–12.5 x 4.6–13.0 mm; *styles* (3–)4, 2.0–3.9 mm long, fused up to halfway or rarely only in the lowermost part; the top split into a compact U- or V-shape, the arms 0.25–0.4 mm long and covered with a broad, non-twisted stigmatic band; *ovary* narrowly elliptic, 4.4–11.5 x 0.8–2.7 mm, pale green, translucent, (3–)4-locular, (3–)4-winged all along, not hirsute; the locular part narrowly elliptic, 0.5–2.3



Map 16.6. Distribution of *Begonia prismatocarpa* subsp. *prismatocarpa* (dots), subsp. *delobata* (stars) and subsp. *petraea* (open star).

mm wide; beak almost absent to distinct, 0–2.0 mm long; wings ribbon-shaped, 0.1–0.4 mm wide, medium green, glabrous to sparsely hirsute on the margin. **Infructescence**: peduncle not recurved towards the substrate; *fruit* more or less erect, narrowly elliptic to narrowly ovate or narrowly obovate, 6.8–11.0 x 1.4–2.2 mm, dry, thin-walled, dark-brown.

Distribution: EQUATORIAL GUINEA: Bioko (formerly Fernando Poo).

Ecology: Terrestrial or epiphytic on rocks or decaying trees, once on a cocoa tree; on banks of a rivulet; in primary forest, in transition forest between lower montane and montane forest or in montane forest; at 150–1200 m altitude.

Chromosome number: 2n = 32 (Legro & Doorenbos l.c.)

Notes: 1. On two collections (Sanford 4415 & 4441) a few stellate scales were discovered, which are rare within the section.

2. A form with variegated leaves is cultivated, see Begonian 43 (1976) 169.

Specimens examined:

EQUATORIAL GUINEA: *Akpabla s.n.* (GC): Bioko, Moca, Estrada farm, 03 20'N 08 40'E (fl); *Barter 2047* (B, K): Bioko, c. 03 35'N 08 40'E (fl, 02); *Barter s.n.* (K): Bioko, below Bassepool, 03 38'N 08 39'E (fl, 08); *Boughey 72* (K): Bioko, Moca, Plateau Area, 03 21'N 08 39'E (fl, 12); *Carvalho 2770* (MA, WAG): Bioko, Moca, falls of the Iladyi R., 03 21'N 08 39'E (fl, fr, 12); *Fernández Casas 11774* (MA, WAG): Bioko, Moca, road to Ureca, 03 21'N 08 39'E (fl, fr, 02); *Guinea 1410* (K): Bioko, Musola, 03 26'N 08 37'E (fl, 01); *Guinea 1411* (MA): Bioko, Musola, 03 26'N 08 37'E (st, 01); *Mann 563* (K, holo; B): Bioko, c. 03 30'N 08 40'E (fl, fr, 12); *Mildbraed 6252* (B, HBG): Bioko, northface of hills of St. Isabel above Basilé, 03 35'N 08 46'E (fl, 08); *Mildbraed 6414* (B, HBG): ibid. (fl, 08); *Mildbraed 7046* (B, HBG): Bioko, Musola above San Carlos (West-coast), 03 24'N 08 34'E (fl, 11); *Sanford 4415* (IFE): Bioko, St. Isabel Mountain, c. 03 44'N 08 50'E (fl, 12); *Sanford 4441* (MO): Bioko, Caldera, San Carlos, above Ruiché, 03 25'N 08 33'E (fl, 01); *Thorold 79A* (K): Bioko, Ureca, 03 16'N 08 32'E (fl, 08); *Thorold 79B* (K): ibid. (fl, 08).

CULTIVATED: *Hort. Kew s.n.* (K): cult. at Hort. Kew, 'Fernando Poo, Mann' (fl, 01); *Kress s.n.* (M): cult. in the Bot. Garden Munchen (fl, 12); *Schwerdtfeger 10585* (B): cult. in Bot. Garten Berlin-Dahlem (fl, 09); *van Veldhuizen 447* (WAG): Wageningen Agric. Univ., Dept. of Horticulture (cuttings from Mrs. Neal, England) (fl, 03); *van Veldhuizen 1299* (WAG): Wageningen, Dept. of Plant Taxonomy (fl, 02).

b. subsp. **delobata** Sosef **subsp. nov.** **Map 16.6**

– TYPE: *Dundas FHI 15329* (K!, holo): 'Prov. Cameroons, Distr. Basosi, Kumba Div. Bambe-Muencetor path. Rock in damp, shady place near water, 29/10/46.'

Begonia prismatocarpa auct. non W.J. Hooker p.p.: Hutch., Dalziel & Keay, Fl. W. Trop. Afr. (ed. 2) 1,1 (1954) 219; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 21, pl. 16B (as *B.* aff. *prismatocarpa*).

Diagnosis: A subspecie *prismatocarpa* differt foliis non lobatis.

Differs from the typical subspecies by:
Stellate scales absent. Leaves not lobed, caudate-acuminate to more or less gradually tapering towards the top in the apical part, 1.7–7.0 x 1.3–4.3 cm; margin shallowly dentate to entire; upper surface not hirsute. Perianth segments of the male flowers 4.6–11.5 x 4.0–7.4 mm; stamens 10–15. Wings on the ovary 0.1–0.9 mm wide. Fruit 7.4–13.0 x 1.3–3.1 mm; the locular part 1.3–3.1 mm wide.

Distribution: Western Cameroon mountains.

Ecology: Terrestrial on soil or on rocks or epiphytic on the base of tree trunks; in primary or secondary forest; near streams, on forested hillsides; at 400–1100 m altitude.

Notes: 1. Sometimes difficult to distinguish from *B. salisburyana* Irmscher but the leaf blades are generally smaller with only sparsely ciliate margins, the indistinct smaller secondary nerves and narrower wings on the ovary.
2. The main difference between this subspecies and the typical one is the non-lobed leaf blade with a shallowly dentate to entire margin. All other differences (mainly quantitative ones) are probably to be credited to the scarcity of the material.

Specimens examined:

CAMEROON: *Dundas FHI 15329* (K): Cameroons Prov., Basosi Distr., Kumba Div., Bambe-Muencetor path, c. 05°10'N 09°30'E (fl, fr, 10); *Letouzey 13801* (P, WAG, YA): between Abat and Bayib, 20 km WNW of Nguti, 05°23'N 09°15'E (fl, fr, 06); *Mambo & Thomas 12* (YA): Near Mbu village, 10 km W of Wone on the Kumba-Mamfe road, 05°03'N 09°18'E (fl, fr, 04); *Satabié 270* (P, YA): track Dikome Balue-Ifanga Nalende, 36 km NW of Kumba, 04°54'N 09°17'E (fl, 03); *Thomas c.s. 5351* (WAG): South-West Prov.: Bakossi Mts, W of Bangem, 05°05'N 09°42'E (fl, fr, 01).

c. subsp. **petraea** (A. Chev.) Sosef **comb. & stat. nov.** **Map 16.6**

Begonia petraea A. Chev., Bull. Soc. Bot. France 58, Mém. 8d (1912) 173. – TYPE : *A. Chevalier 19596* (P!, holo; B!, G!): 'Côte d'Ivoire, Bassin du Cavally, Pays des Tépo, entre Nékaougnié et Grabo, 26-7-1907.'

B. prismatocarpa auct. non W.J. Hooker: A. Chev., Expl. Bot. Afr. Occ. Fr. 1 (1920) 298; Hutch., Dalziel & Keay, Fl. W. Trop. Afr. (ed. 2) 1,1 (1954) 219 p.p.

Differs from the typical subspecies by:
Stellate scales absent. Fruit elliptic to obovate, 5.5–8.5 x 2.9–4.8 mm; the locular part 2.0–2.6 mm wide; wings ribbon-shaped or elliptic-obovate, 0.9–1.7 mm wide.

Distribution: IVORY COAST: only known from the type locality.

Ecology: On granite rocks in primary, deeply shaded forest.

Notes: 1. In the single collection known from this taxon only fruits and a few small flower buds are present. Hence, the shape of the ovary could not be verified but it is probably elliptic to obovate, similar to the fruit.

Begonia pseudoviola Gilg **Fig. 16.12, Map 16.7**

Begonia pseudoviola Gilg, Bot. Jahrb. Syst. 34 (1904) 88; Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3,2 (1921) 617; Irmscher in Engl. & Prantl, Nat. Pflanzenfam. (ed. 2) 21 (1925) 574; Hutch. & Dalziel, Fl. W. Trop. Afr. (ed. 1) 1,1 (1927) 188; Hutch., Dalziel & Keay, Fl. W. Trop. Afr. (ed. 2) 1,1 (1954) 219; N. Hallé, Adansonia, sér. 2, 12 (1972) 369, pl. 1.6; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39; L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 220, fig. 22.7; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 21, pl. 16C. – TYPE: *Conrau 10* (B!, holo): 'Kamerun, zw. Banti-Babesong, 600-700 m. ü. d. M., 1 Nov. 98.'

Begonia subtilis Irmscher, Bot. Jahrb. Syst. 81 (1961) 185; van den Berg l.c. 38-39; L.B. Smith et al. l.c. 238, fig. 8.9. – TYPE: *Ledermann 6400a* (B!, holo; BR!): 'Kamerun, Ndonge, Nlonako, 1000 m, feuchter Gebirgswald, 20 Nov. 89.'

Plant up to 11 cm high, scattered with minute glandular hairs, sparsely so on stipules, bracts and pedicel of male flower. **Rhizome** slender but rather compact and knotted, 0.8–3.0 mm wide, sparsely hirsute; the apical part not or slightly ascending. **Stipules** ovate to broadly ovate, acute, 0.8–4.3 mm long, herbaceous, bronze-green; margin dentate and with long cilia. **Leaves** not peltate; *petiole* continuing into the midrib without a distinct angle; (0.5–)1–6(–11.5) cm long, juicy, bronze-green to reddish, sparsely hirsute to hirsute; *leaf blade* in a more or less horizontal position, distinctly asymmetrical, ovate to broadly or very broadly ovate, slightly to distinctly acuminate in the upper 1/2 to upper 1/4 and often slightly falcate in the apical part, not or shallowly 2-lobed, 0.8–5.5(–6.6) x 0.6–3.5(–5.1) cm, herbaceous, with (4–)5–7(–8) palmate main nerves; margin usually entire or sometimes shallowly, irregularly dentate, concolorous with the blade, ciliate with few short hairs; base cordate in mature to cuneate in young leaves, top obtuse; upper surface dark green to bronze-green or brown-red, shiny, smooth, scattered with 3–7 mm long, curved, white hairs in a regular pattern; lower surface brownish wine red or bluish red; *nerves*: the main and larger secondary nerves concolorous with the blade and not prominent on the upper surface, on the lower slightly prominent, medium green and with few patent hairs, smaller secondary and tertiary nerved indistinct, glabrous. **Inflorescence** containing 1–2 male flowers and 1 terminal female flower, slightly exserted above the leaves; *peduncle* simple, up to 4(–5) cm long, juicy, wine red to reddish, sparsely hirsute with long, patent, white hairs; *bracts* 2–3, broadly obovate to elliptic or narrowly ovate, 0.7–1.6 mm long, bronze-green, glabrous; margin dentate, ciliate. **Male flower**: *pedicel* elongated at anthesis up to 20 mm, yellowish-red, glabrous or with a few hairs; *perianth segments* elliptic to broadly ovate or broadly obovate, with a cuneate to cordate base, (3.8–)6.0–9.5(–10.5)

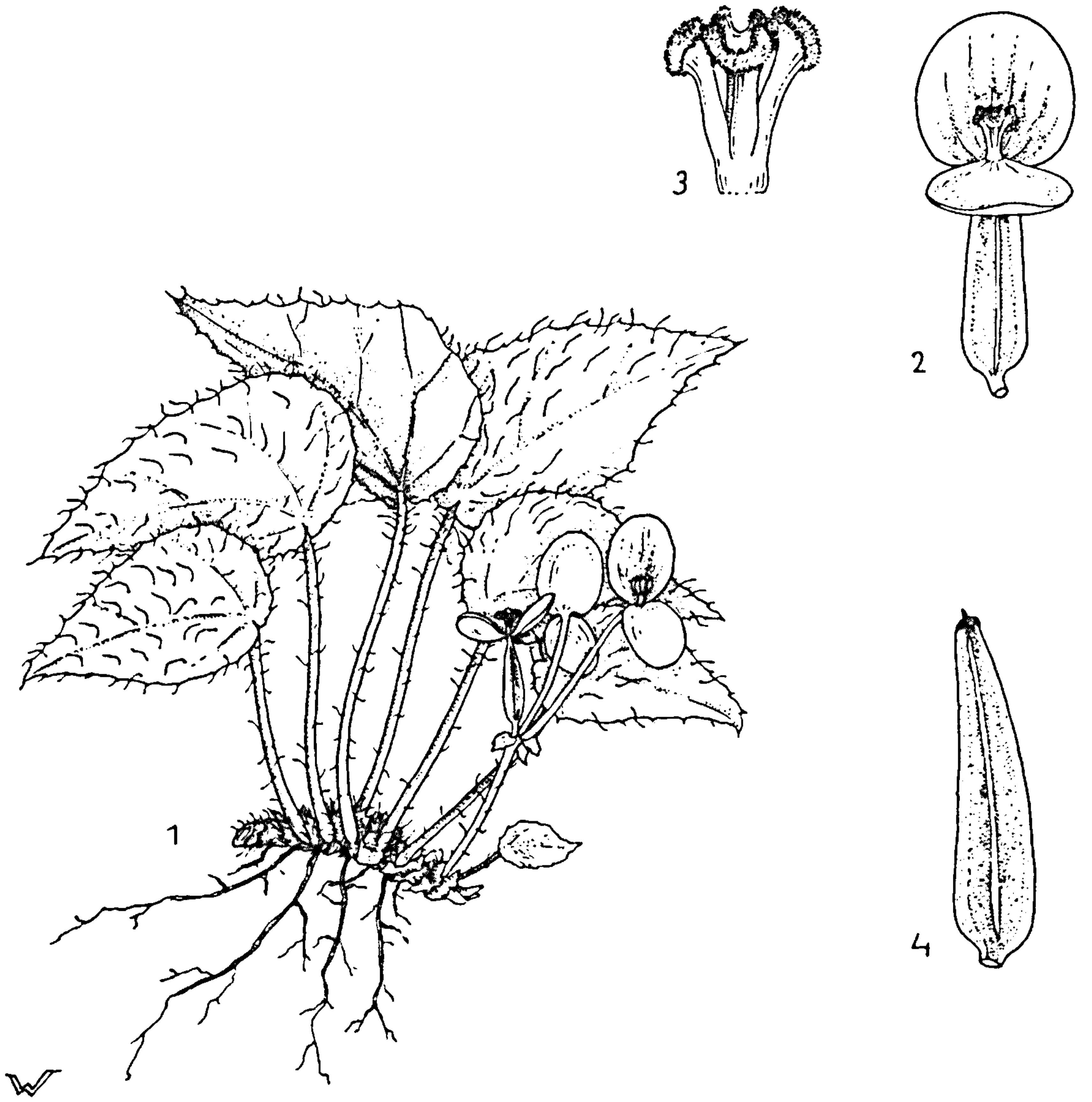
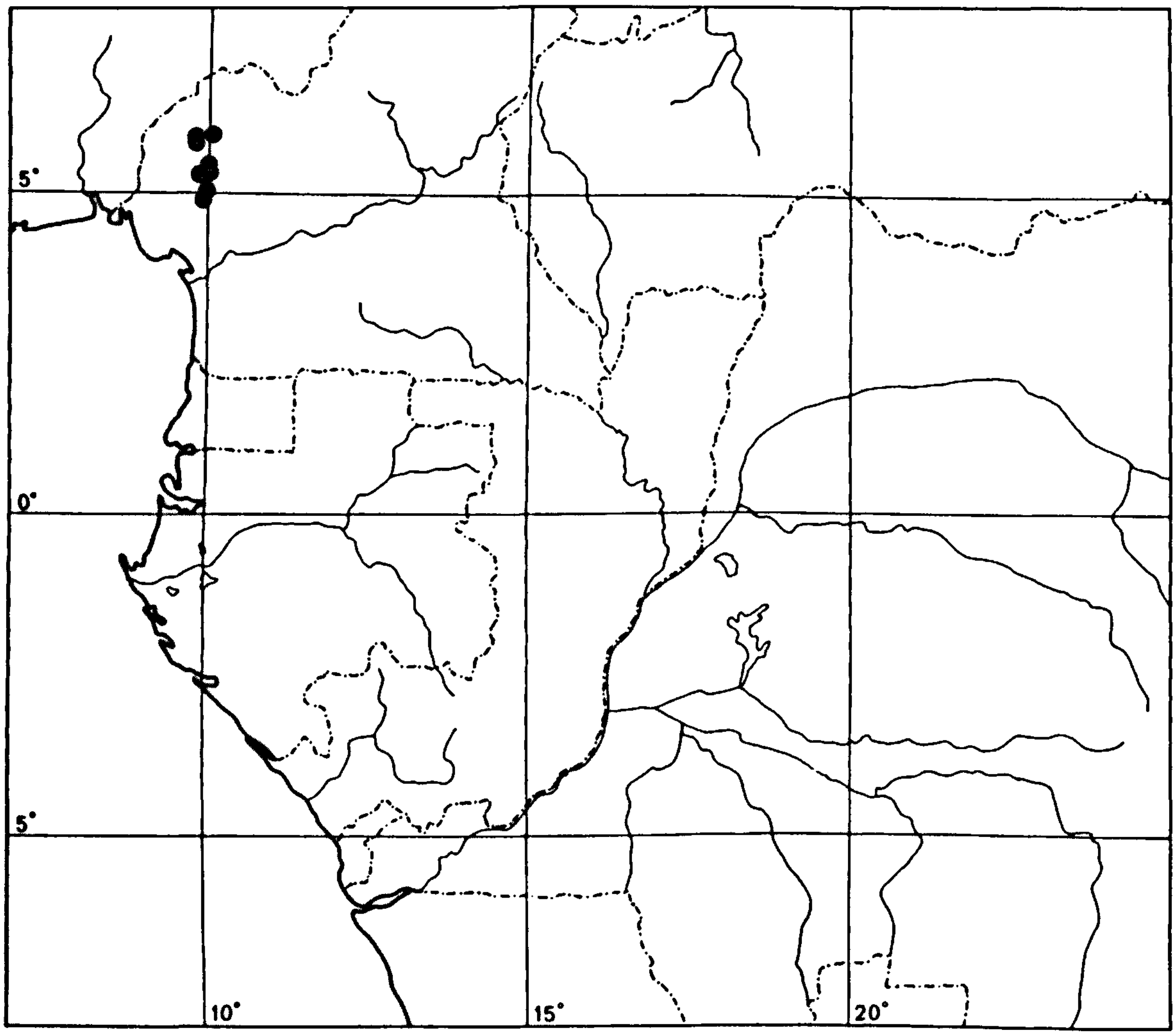


Figure 16.12. *Begonia pseudoviola* Gilg. – 1: habitus (x1); 2: female flower (x2); 3: styles (x6); 4: fruit (x2). – 1-4: *J.J. de Wilde 8662*.

x (3.2–)5.0–8.3 mm, the outside with or without a few hairs in the basal part; the upper orange-red on the outside, the inside yellow to orange-yellow with a red patch and nerves in the basal half; the lower segment yellow; *androecium* with 10–22 stamens; column 0.5–0.7 mm long; anthers 1.0–1.7 mm long. **Female flower**: similar to the male but sessile, in fruit the pedicel elongated up to 0.5 mm; *perianth segments* circular to broadly obovate, (3.6–)5.0–7.3 x (3.6–)4.5–6.0 mm; *styles* 3 or 4, 2.1–2.7 mm long, fused up to halfway, the top split and forming a broad U- or V-shape, the arms c. 0.25 mm long and covered with a non-twisted stigmatic band; *ovary* oblong to narrowly ovate, sometimes narrowly elliptic, (3.0–)4.0–11.0(–13.0) x (0.5–)0.9–2.2(–3.0) mm, green, translucent, 3–4-locular, 3–4-winged all along; the locular part oblong to narrowly elliptic, (0.3–)0.6–1.4(–2.0) mm wide; beak present, 0.8–4.0 mm long; wings ribbon-shaped, 0.1–0.5 mm wide, glabrous or with a few hairs on the margin. **Infructescence**: peduncle not recurved towards the substrate; *fruit* erect, narrowly obovate



Map 16.7. Distribution of *Begonia pseudoviola*.

to elliptic, (5.8–)9.0–17.0 x 1.6–4.0 mm, dry, thin-walled, greenish-brown.

Distribution: Western Cameroon mountains.

Ecology: Terrestrial on sandy river banks, along road sides or on wet rocks; in shaded habitats in primary forest, secondary forest with oilpalms or in submontane forest; at 450–1700 m altitude.

Specimens examined:

CAMEROON: *Adams 1582* (GC): 58 mile on Mamfe-Bamenda road, 05°53'N 10°03'E (fl, fr, 12); *Bamps 1582* (BR): Mt Nlonako, NW side, 04°55'N 09°57'E (fl, fr, 12); *Conrau 10* (B, holo): between Banti and Babesong, c. 05°30'N 10°00'E (fl, fr, 11); *Coombe 202* (K, P): at mile 39.5 from Mamfe on Bamenda road, 05°46'N 09°46'E (fl, 03); *Keay FHI 28342* (B, K): Bamenda Prov., above Widdekum on the Bamenda road, 05°52'N 09°46'E (fl, fr, 01); *Ledermann 1434* (B, BR): Bare, 05°01'N 09°58'E (fl, fr, 11); *Ledermann 6092a* (B): between Mbo and Sanchu, 05°19'N 09°53'E (fl, fr, 11); *Ledermann 6400A* (B, holo; BR): Ndonge, Nlonako, 04°54'N 09°58'E (fl, fr, 11); *Letouzey 14459* (P): Nlonako, 5 km SSE of Nkongsamba, 04°55'N 09°57'E (st, 05); *J.J. de Wilde 8662* (WAG, YA): 14 km along the road from Dschang to Mélong, 05°23'N 10°01'E (fl, 11).

Begonia pulcherrima Sosef **Fig. 16.13, Map 16.8**

Begonia pulcherrima Sosef, Wageningen Agric. Univ. Papers 91-4 (1992) 137, fig. 6; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 15, pl. 9C,D. – TYPE: *Bamps 2805* (BR!, holo; GENT!, LG!): 'Rwanda, Rwankuba, Préfect. Cyangugu, E 29°08′ S 2°30′, alt. 1950 m, forêt de montagne, sous-bois sur sol humide, 18-12-71.'

Begonia scapigera auct. non Hook.f.: Wilczek, Fl. Congo, Rwanda et Burundi (1969) 33; Lewalle, Bull. Jard. Bot. Nat. Belg. 42 (1972) 179; Troupin, Fl. Rwanda – Spermatoph. II (1983) 450, fig. 142.1.

B. schaeferi auct. non Engl.: van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39 p.p.

Diagnostic characters (for a more detailed description see Sosef l.c.):

Plant up to 25(–35) cm high. **Leaves** peltate; *leaf blade* symmetrical, ovate to elliptic or broadly elliptic, acuminate at the top, (4.2–)6.0–14.0 x (2.6–)4.0–9.8 cm; margin shallowly and remotely dentate in the upper 1/2–2/3, rarely indistinctly so, sparsely shortly ciliate; upper surface sparsely hirsute with short, straight hairs to almost glabrous; *nerves*: the main and larger secondary nerves sunken and concolorous with the blade on the upper surface, those on the lower surface sparsely hirsute. **Inflorescence**: *peduncle* simple, up to 22 cm long; *bracts* elliptic to almost circular, 4.9–11.0 mm long. **Male flower**: *perianth segments* very broadly ovate to very broadly obovate, with a rounded to cordate base, 11.0–20.5 x 11.5–26.5 mm, both segments golden yellow on both sides; *androecium* with (13–)20–31 stamens. **Female flower**: *perianth segments* circular to very broadly obovate, 10.0–22.0 x 11.0–27.0 mm, golden yellow; *styles* 3 or 4, 3.9–6.5 mm long, very variable in shape, completely fused into a trumpet-shaped structure with the margin strongly undulating (see fig. 16.13); *ovary* elliptic to narrowly so or narrowly elliptic-ovate, 6.5–17.0 x 1.8–6.4 mm, narrowly winged all along, not hirsute; wings ribbon-shaped, 0.1–1.0 mm wide. **Infructescence**: *fruit* erect, narrowly elliptic-ovate to narrowly elliptic-obovate, 19–24 x 3.4–9.1 mm.

Distribution: RWANDA: Cyangugu Préf. BURUNDI: Bubanza Terr.

Ecology: Montane forest (with *Syzygium*, *Pentadesma* and *Carapa*); on forested slopes; in shade along streamlets or on wet or moist sites; at 1650–2000 m altitude.

Notes: 1. The species is closely related to *B. gentilii* De Wild. from Zaire. *B. pulcherrima* differs from the latter by its ribbon-shaped wings on the ovaries (not widening upwards), the complicated structure of the styles, the perianth segments lacking a red spot, the sparsely hirsute nerves on the lower leaf surface and the usually much longer peduncles.

2. Wilczek l.c. described the species as being monoecious. This probably concerns a misinterpretation caused by the scarcity of the material he had at hand. The inflorescences are bisexual, similar to the situation in all other species (except *B. schaeferi*) within the section.

3. Bridson 190 shows a male flower carrying an extra bract a few mm above the base of the pedicel.

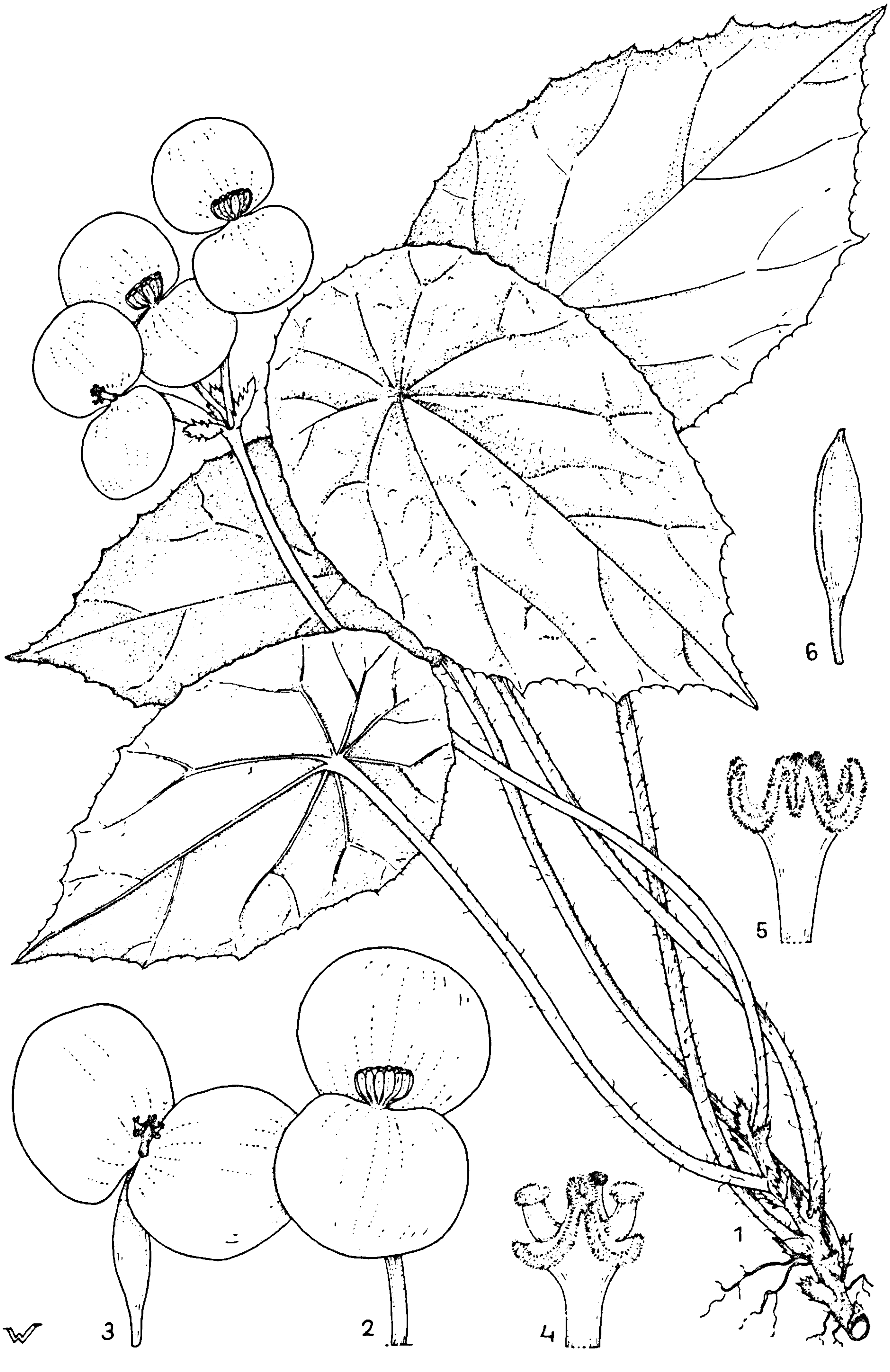
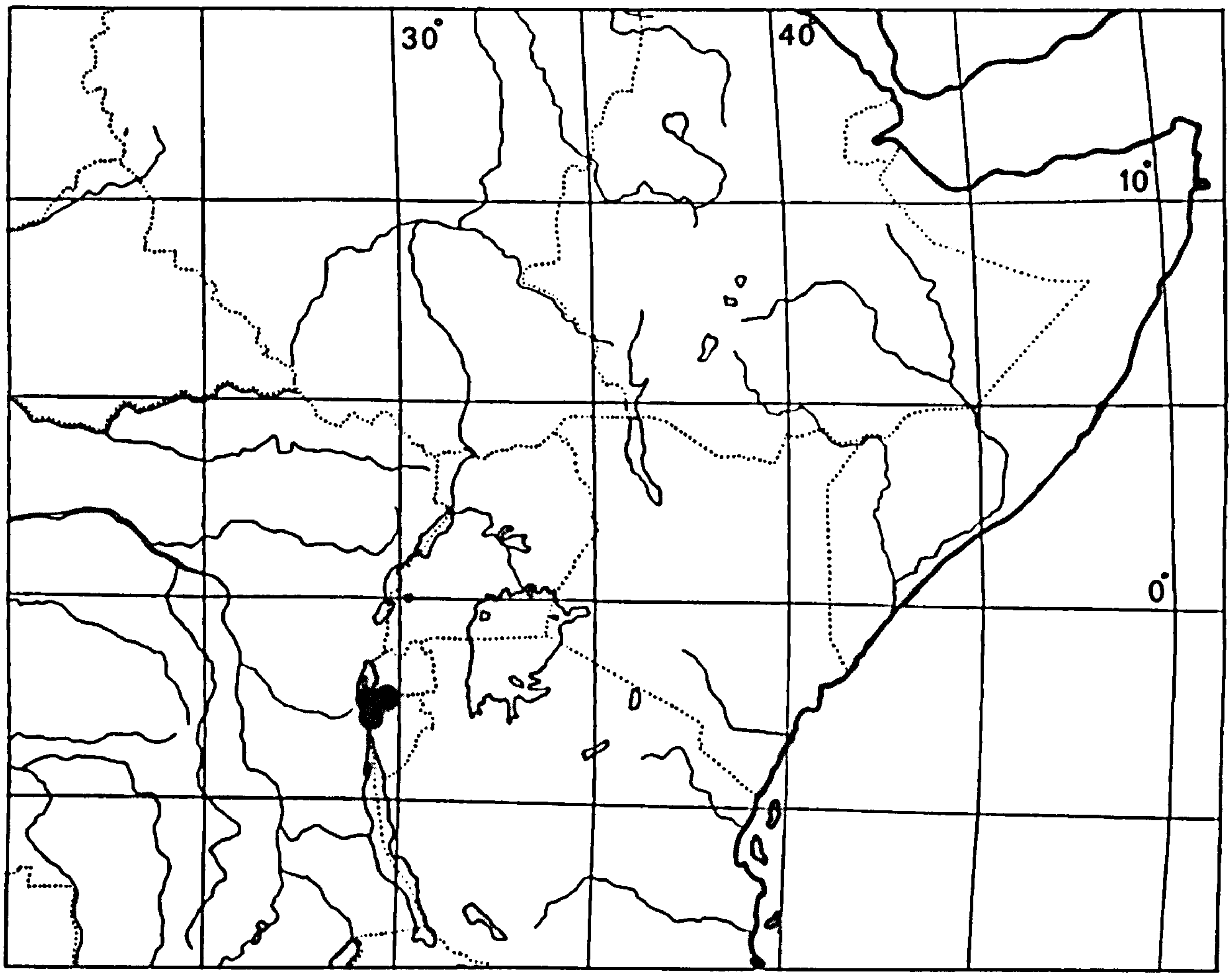


Figure 16.13. *Begonia pulcherrima* Sosef. – 1: habitus (x$^2/_3$); 2: male flower (x1); 3: female flower (x1); 4, 5: two types of styles (x4); 6: fruit (x1). – 1-3: *Bamps 2805*; 4: *Bouxin 267*; 5: *Bouxin 1013*; 6: *Christiaensen 1511*.



Map 16.8. Distribution of *Begonia pulcherrima*.

Specimens examined:

RWANDA: *Bamps 2805* (BR, holo; GENT, LG): Cyangugu Préf., Rwankuba, 02°30'S 29°08'E (fl, 12); *Bouxin 267* (BR, K, LG): Cyangugu Préf., Nyungwe forest, Kamiranzovu swamp, 02°30'S 29°09'E (fl, 02); *Bouxin 1013* (BR, K, LG): Cyangugu Préf., Nyungwe forest, surroundings of Rwankuba, 02°30'S 29°08'E (fl, 06); *Bouxin 1207* (BR, K, LG): Cyangugu Préf., Nyungwe forest, surroundings of Kamiranzovu, 02°30'S 29°09'E (fl, 09); *Bridson 190* (BR, K): road Butare-Cyangugu, towards km 100, 02°30'S 28°57'E (fl, 01); *Christiaensen 1511* (LG): Cyangugu Terr., Kamiranzovu, 02°30'S 29°09'E (fl, 03); *Deuse 1234* (BR): ibid. (fl, 11); *Hendrickx 4683* (BR): Madekere, road Cyangugu, c. 02°30'S 29°20'E (st, 07); *Troupin 9810* (BR): Cyangugu Terr., road Bukavu-Astrida, surroundings of Uwinka, Kwinzira ridge, 02°29'S 29°12'E (fr, 03); *Van der Veken 11087* (GENT): Cyangugu Préf., 4 km before Gisakura on the road Butare-Cyangugu, 02°26'S 29°06'E (fl, 09).

BURUNDI: *Lewalle 6245* (BR): Bubanza Terr., Mabayi, 02°37'S 29°13'E (fl, 10); *Reekmans 1100* (BR): Bubanza Terr., Mabayi, Ruwa valley, 02°45'S 29°02'E (fl, 10).

Begonia quadrialata Warb.

a. subsp. **quadrialata**

a.1. var. **quadrialata** **Fig. 16.14, Map 16.9**

Begonia quadrialata Warb., Bot. Jahrb. Syst. 22 (1895) 43; Warb. in Engl. & Prantl, Nat. Pflanzenfam. 3,6a (1894) 140, fig. 47A & 48J (nom. nud.); T. & H. Durand, Syll. Fl. Congol. (1909) 234 p.p.; Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3,2 (1921) 617; Mildbraed, Wiss. Erg. Zweiten Deutschen Zentr.-Afr. Exp. 2, Bot. (1922) 89, 98; Irmscher in Engl. & Prantl, Nat. Pflanzenfam. (ed. 2) 21 (1925) 563, fig. 260A, 564, fig. 261J; Hutch. & Dalziel, Fl. W. Trop. Afr. (ed. 1) 1,1 (1927) 187, fig. 82.I; Dalziel, Useful Pl. W. Trop. Afr. (1936) 64; Hutch., Dalziel & Keay, Fl. W. Trop. Afr. (ed. 2) 1,1 (1954) 218; Mangenot, Icon. Pl. Afr. 7 (1965) no. 146; Fernandes, Consp. Fl. Angol. (1970) 298; Schnell, Introd. Phytogeogr. Pays Trop. 2 (1971) 781; Doorenbos, Begonian 47 (1980) 34; M. & E. Thompson, Begonias, Compl. Ref. Guide (1981) fig. on p. 168; de Koning, Meded. Landbouwhogeschool Wageningen 83-1 (1983) 99; Bouman & de Lange, Begonian 50 (1983) 76, fig. 35; Reitsma, Meded. Landbouwhogeschool Wageningen 83-9 (1984) 45, 47, fig. 9E; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39, pl. 6.13-14; Burkill, Useful Pl. W. Trop. Afr. (ed. 2) 1 (1985) 252; L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 221, fig. 2.19; Cuerrier et al., Bull. Mus. natn. Hist. nat., Paris, 4e sér., 12, sect. B, Adansonia (1991) 323 ff.; idem 339 ff.; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 16, 17, pl. 10E, 13B,C. - LECTOTYPE: *Preuss 185* (B!; iso: B!): 'Kamerun, Barombi-Station. Im Urwald am Bache nordwestlich von Kumba, an sumpfigen Stellen an Baumwurtzeln, Steinen etc., 4-5-89.'

Begonia whytei Stapf, J. Linn. Soc., Bot. 37 (1905) 103; Stapf in H. Johnston, Liberia (1906) 608; Chevalier, Expl. Bot. Afr. Occ. Fr. 1 (1920) 299; Engl. in Engl. & Drude l.c.; Pellegrin, Mém. Soc. Linn. Normandie 26 (1924) 124; Irmscher in Engl. & Prantl l.c. 574; Hutch., Dalziel & Keay l.c.; van den Berg l.c. 38-39. - TYPE: *Whyte s.n.* (K!, holo; B!): 'Sinoe Basin, 1904.'

Begonia calabarica Stapf, Kew Bull. 1906 (1906) 20; Engl. in Engl. & Drude l.c.; Hutch., Dalziel & Keay l.c.; van den Berg l.c. 38-39. - LECTOTYPE: *Hort. Kew 424-98* (K!): 'Old Calabar, 9-9-'99.'

Begonia modica Stapf, Kew Bull. 1908 (1908) 259; Stapf, Curt. Bot. Mag. 135 (1909) t.8258; Hutch. & Dalziel l.c.; Irvine, Pl. Gold Coast (1930) 52; Fotsch, Begonien (1933) 41; Hutch., Dalziel & Keay l.c. (erroneously cited as *B. modesta* Stapf, see note under var. *pilosa*); van den Berg l.c. 38-39. - LECTOTYPE: *Hort. Kew s.n.* (K!): 'from Goldcoast, alt. 600 ft., growing on rock, 13-08-1907.'

Begonia poikilantha Gilg ex Engl. in Engl. & Drude (1921) l.c. (pro syn.).

Begonia quadrialata Warb. var. *speciosa* Irmscher, Bot. Jahrb. Syst. 81 (1961) 182; Fernandes l.c. 298. - TYPE: *Gossweiler 7989* (B!, holo; BM!, COI!, K!, LISCJ!, LISU!): 'Portugiesisch Kongo: Cabinda nördlich der Kongo-Mündung; Waldgebiet von Mayombe; margens humidas do riveiro Zanza - Rio Lufo. 11-4-1919'.

Begonia potamophila auct. non Gilg: Fernandes, Consp. Fl. Angol. (1970) 299.

Plant (2.5–)5–15(–25) cm high, scattered with minute glandular hairs, sparsely so on stipules, pedicel of male flower and outside of perianth segments. **Rhizome** usually stout and compact, sometimes rather slender and somewhat elongated, (0.9–)1.3–5.5 mm wide, especially the younger parts sometimes hirsute; the apical part horizontal or ascending. **Stipules** depressed triangular-ovate to triangular-ovate or elliptic-ovate, acute to slightly acuminate, (0.8–)1.7–6.1 mm long, green or pale green to pinkish, sparsely hirsute to hirsute; margin usually dentate, ciliate. **Leaves** peltate; *petiole* making a distinct angle with the midrib, inserted at (2–)5–25(–30) mm from the nearest margin, (1.0–)2.5–18.0(–22.0) cm long,

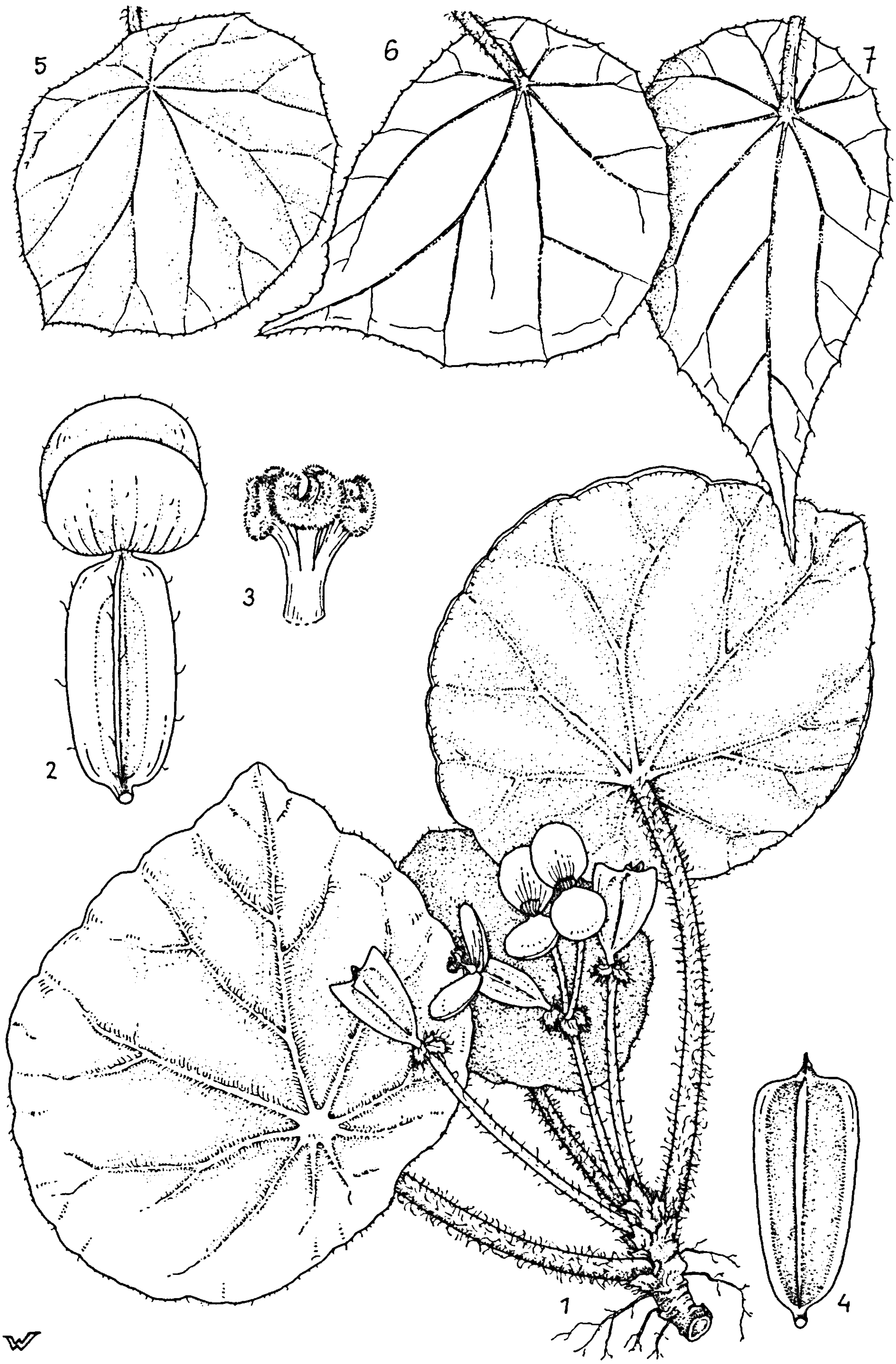
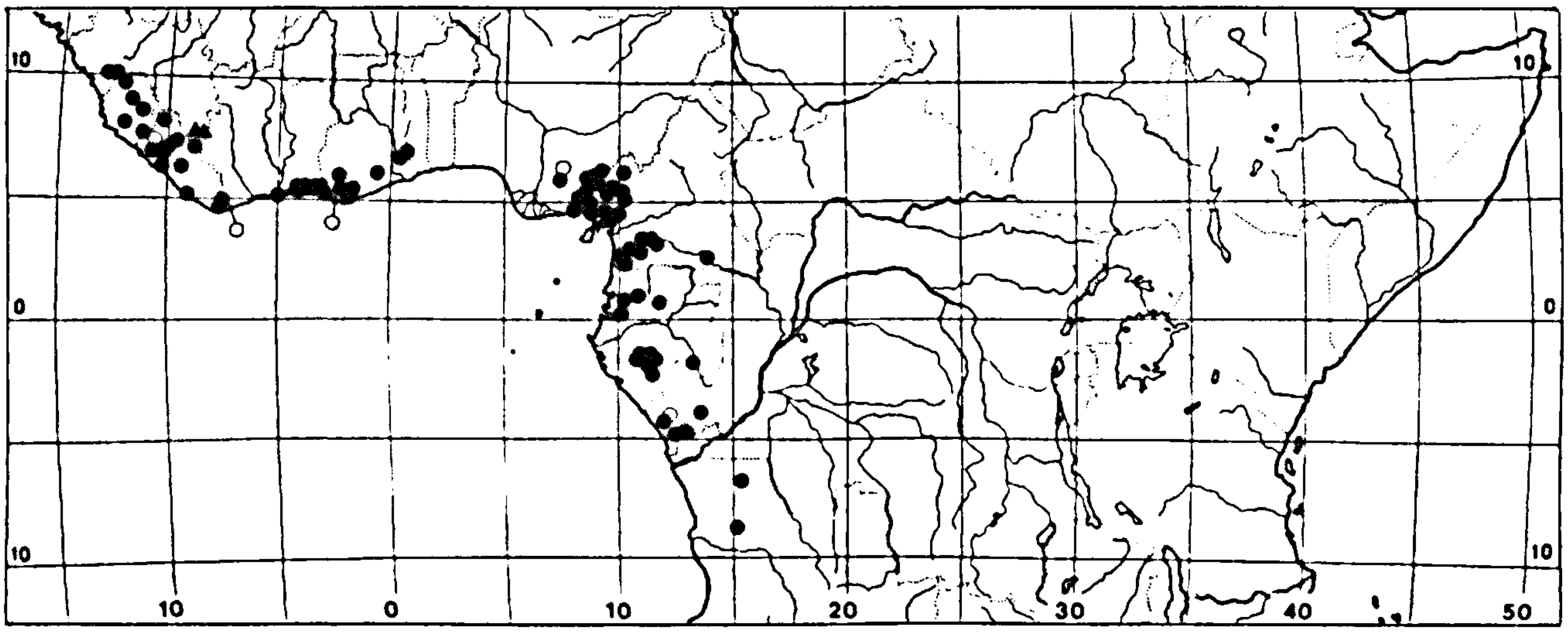


Figure 16.14. *Begonia quadrialata* Warb. subsp. *quadrialata* var. *quadrialata*. – 1: habitus (x$^2/_3$); 2: female flower (x2); 3: styles (x4); 4: fruit (x2); 5, 6: leaves (x$^2/_3$). – 1: *Breteler 5938*; 2, 3: living plant at WAG, voucher *van Veldhuizen 1310*; 4: *Arends c.s. 341*; 5: *Beentje 193*; 6: *A. Louis 3035*. – *B. quadrialata* Warb. subsp. *dusenii* (Warb.) Sosef. – 7: leaf (x$^2/_3$), *Thompson 1440*.

rather firm but juicy, pale pinkish to dark red, sometimes green in the apical part or throughout, sparsely to densely hirsute with patent, wavy, white hairs; *leaf blade* in a more or less horizontal position, usually distinctly asymmetrical, broadly elliptic-ovate to more or less circular, sometimes elliptic-ovate, rounded or shortly acuminate to acuminate in the apical 1/4 and then often falcate or even suddenly contracted into a narrow top, (1.7–)2.5–12.5 x (1.2–)2.0–9.0(–11.0) cm, crisp-juicy to succulent, with (7–)8–10 palmate main nerves; margin entire to shallowly sinuate or sometimes denticulate towards the apex, glabrous to ciliate, sometimes densely so, usually red on both or only on the lower surface; base rounded, top rounded to acute; upper surface light or pale to medium green, rarely dark green or purplish green, glistening in sunlight, otherwise dull, smooth, not hirsute; lower surface pale green, sometimes reddish or reddish brown tinged, dull; *nerves*: the main and larger secondary nerves not prominent and concolorous with the blade on the upper surface, on the lower not or slightly prominent, medium green, usually sparsely hirsute with patent hairs, smaller secondary nerves indistinct to fairly distinct, not prominent, not hirsute, tertiary nerves usually indistinct or not visible. **Inflorescence** containing 2–3(–5) male flowers and 1(–2) terminal female flower(s), positioned at about halfway up the petioles to at about the same level as the leaf blades; *peduncle* simple, (1.0–)2.0–8.0(–11.5) cm long, firm but juicy, red to pale reddish or sometimes green in the apical half or entirely green, sparsely to very sparsely hirsute with white hairs; *bracts* 3–4(–6), not seldom an additional bract is present below the female flower, usually ovate to elliptic or broadly so, sometimes narrowly so or elliptic-obovate, (0.6–)1.2–3.8 mm long, green to pale pinkish; margin dentate, ciliate, top rounded to acute. **Male flower**: *pedicel* elongated at anthesis up to 20(–32) mm, light yellowish green, sometimes sparsely hirsute; *perianth segments* broadly ovate to broadly elliptic, sometimes broadly elliptic-obovate, rarely elliptic or almost circular or very broadly ovate, with a rounded to slightly cordate or rarely cuneate base, (3.0–)5.0–12.0(–15.0) x (3.0–)4.5–11.0(–16.0) mm; the outside with or without white or red hairs; the upper segment reddish to orange on the outside, yellow with a red patch and nerves on the inside; the lower segment orange to yellow on the outside, yellow on the inside; *androecium* with (10–)16–27(–37) stamens; column 0.3–1.0 mm long; anthers (0.9–)1.2–2.0(–2.2) mm long. **Female flower** similar to the male but sessile or shortly pedicellate, the pedicel slightly elongated in fruit, 0–2.9 mm long; *perianth segments* with a rounded to cordate or rarely cuneate base, (3.5–)5.0–12.0(–16.0) x (3.5–)4.5–11.0(–17.0) mm; *styles* (3–)4, (2.0–)2.8–4.5(–5.1) mm long, fused in the lower 1/3 to 1/6, the top split into a rounded C- or U-shape, the arms 0.25–1.0(–1.6) mm long and bearing a usually rather compact stigmatic band which is not or only slightly twisted; *ovary* narrowly elliptic-oblong or elliptic to obtriangular-obovate rarely broadly or even very broadly so, (5.2–)6.0–17.0(–26.0) x (1.7–)2.5–8.0(–11.5) mm, (3–)4-locular, (3–)4-winged all along, translucent, light or pale green but sometimes the pinkish ovules shining through; the locular part elliptic or narrowly so, sometimes elliptic-obovate, (1.2–)1.7–5.0(–9.6) mm wide; beak absent or short, 0–0.9(–1.2) mm long; wings



Map 16.9. Distribution of *Begonia quadrialata* subsp. *quadrialata* var. *quadrialata* (dots), var. *pilosa* (open circles), subsp. *dusenii* (star) and subsp. *nimbaensis* (triangles).

patent, sometimes slightly curved upwards, narrowly elliptic to obtriangular, (0.2–)0.5–4.0(–5.5) mm wide, margin often with a few long hairs. **Infructescence**: peduncle not recurved towards the substrate, erect to ascending; *fruit* more or less erect, elliptic to broadly obtriangular, rarely narrowly elliptic or very broadly obovate, 6.4–20.0(–23.0) x 2.6–13.0(–26.0) mm, dry, thin-walled, green to brown.

Distribution: From Sierra Leone towards western Cameroon, Gabon, western Congo, western Zaire and northern Angola.

Vernacular names: Tarié (Agni, Ivory Coast).

Ecology: Terrestrial on level sites to steep slopes or banks or on mossy or wet rocks or rock faces or epiphytic on mossy tree trunks or decaying trees; on coarse sandy, red sandy clay to clayey or lateritic or sometimes volcanic soils, sometimes in rock fissures or on bauxite boulders; in shaded to deeply shaded sites in primary lowland evergreen rain forest, sometimes in secondary vegetation or in (sub)montane rain forest or swamp forest; often near or on the banks of streams and rivers and near waterfalls, sometimes in the spray zone; in *Tarrietia* forest (Sierra Leone) or *Gnetum* forest (Angola); associated with *Streptocarpus*; from sea-level to up to 1100 m altitude.

Notes: 1. Preuss 185 was chosen as the lectotype for *B. quadrialata* Warb. among the syntypes cited. It is the only collection with well developed ovaries which are useful for a correct identification. All syntypes undoubtedly belong to the same taxon.

2. The protologue of *B. calabarica* mentions that the plant was cultivated at Kew and originated from Calabar. The only cultivated specimen at K annotated as originating from Calabar was chosen as the lectotype.

3. The protologue of *B. modica* mentions that the species was described from a plant cultivated at Kew, originating from 'Gold Coast, on rocks, at 180 m.' and was collected by J. Anderson. Although the specimen chosen as the lectotype does not bear the name 'Anderson' its origin 'Gold Coast' and 'at 180 m.' (as

P., 05°01′N 08°50′E (fl, fr, 01); *Thomas c.s.* 4225 (K, WAG, YA): Mundemba town, 04°58′N 08°55′E (fr, 07); *Thomas c.s. 4926* (BR, WAG): South-West Prov., Ndian Div., 1-3 km W of Ekondo-titi-Mundemba road at Dibunda, 4 km N of Ilor bridge, 04°52′N 08°53′E (fl, fr, 11); *Thomas c.s. 5018* (WAG): South-West Prov., Meme Div., near Pete, Southern Bakundu Forest Reserve, 04°32′N 09°24′E (fl, fr, 11); *Thomas c.s. 7860* (WAG): South-West Prov., Korup National Park, between Akwa and Bera, 05°20′N 08°57′E (fl, 05); *Ujor FHI 30485* (K): Bamenda Prov., Wum Distr., mile 23 by Wum motorroad, 06°23′N 10°10′E (fl, fr, 07); *Villiers 1421* (WAG, YA): Ntali Massif, NW slope, 30 km SE of Mamfe, 05°31′N 09°30′E (fl, 06); *Winkler 1014* (B, Z): Between Mündame and Joh.-Albr. Höhe, 04°34′N 09°31′E (st, 12); *Zenker 4646* (B, BM, K, MO): Bipinde, forest area, road to Ebolowa, km 124-25, c. 02°58′N 11°00′E (fl, fr, 06).

GABON: *Arends c.s. 341* (WAG): Waka, forest exploitation road near the Falaise, 01°18′S 10°57′E (fl, fr, 11); *Arends c.s. 498* (WAG): 40 km E of Mouila, on the road to Yeno, 01°47′S 11°18′E (fl, 11); *Arends c.s. 558* (WAG): about 43 km E of Mouila, along the road towards Yeno, 01°47′S 11°18′E (st, 11); *Breteler 6440* (WAG): km 23 on the road Moanda-Franceville, 01°39′S 13°17′E (fl, 09); *Breteler 7711* (WAG): 17 km on the road Mimongo-Koulamoutou, 01°34′S 11°42′E (fl, 05); *Breteler c.s. 8247* (WAG): between Mouila and Yeno, about 50 km on the road from Mouila, 01°45′S 11°22′E (fl, fr, 09); *Breteler c.s. 8276* (WAG): 30 km N of Kango, 00°17′N 10°05′E (fl, 10); *N. Hallé & Cours 5883* (P): Etéké, Mimongo Distr., along the Etéké R., 01°29′S 11°35′E (fl, 05); *Le Testu 5034* (BM, P): Api.... between Benzé & Nzamba, 01°27′S 10°55′E (fl, fr, 10); *Le Testu 5244* (BM): around Nzabi, c. 01°35′S 11°31′E (fl, fr, 02); *Leeuwenberg 12536* (LBV, WAG): Mt Fane, near Mengoua R. and village Efout, 16 km E of Médouneu, 01°01′N 10°54′E (fr, 11); *Leroy 15* (P): Ogooué, c. 01°30′S 13°30′E (fl); *A. Louis 2734* (LBV): Ngounié Prov., Leroy exploitation, 13 km road Massika towards Yeno, on the road Mouila-Yeno, 01°38′S 11°25′E (fl, fr, 02); *A. Louis 2986* (LBV, WAG): Ngounié Prov., exploitation road Leroy (Massi-II), 01°40′S 11°15′E (fl, 04); *A. Louis 3035* (LBV, WAG): Ngounié Prov., exploitation road Leroy, Massika between Mouila and Yeno, 01°40′S 11°15′E (fl, fr, 04); *A. Louis, Breteler & de Bruijn 1051* (WAG): Chaillu Massif, near Guévedé village, about 40 km N of Lébamba, 01°55′S 11°25′E (st, 11); *J.J. de Wilde c.s. 10349* (WAG): 59 km on the road Mouila-Yéno, 01°43′S 11°25′E (st, 02); *J.J. de Wilde c.s. 10383* (WAG): 50 km on the road Mouila-Yéno, 01°43′S 11°23′E (fl, 02); *J.J. de Wilde c.s. 10420* (WAG): 7 km on the road Lébamba-Mbigou and than 4 km along a trail to the S, 02°14′S 11°32′E (st, 02); *J.J. de Wilde c.s. (WALK-B) 106* (WAG): Crystal Mts, forest exploitation Leroy, 20 km NW of Asok, 00°53′N 10°12′E (fl, 01); *J.J. de Wilde c.s. (WALK-B) 441* (WAG): Chaillu Massif, missionary station at Mouyanama, about 15 km on the road Mimongo-Mbigou, 01°39′S 11°46′E (fl, 02); *Wilks 1700* (WAG): Woleu-Ntem Prov., 31 km E of Mitzic, 00°48′N 11°50′E (fl, fr, 04).

CONGO: *Farron 4584* (P): falls of the Bouenza, around Mouyondzi, 03°53′S 13°42′E (fl, 08); *Koechlin 1257* (IEC), identification doubtful: ibid. (fl, 07); *Thollon 1194* (IEC, P): Mayumbe forest, c. 04°30′S 12°30′E (fl, 07); *Thollon 1197* (IEC, P): ibid. (st, 07); *Thollon 1340* (IEC, P): Mayumbe forest, Kouilou (Niari), c. 04°00′S 12°00′E (fr, 10); *J.J. de Wilde c.s. 11049* (WAG): at km 95 on the road Pointe Noire to Dimonika, 2-3 km before Kondué, 04°25′S 12°15′E (fr, 02); *J.J. de Wilde c.s. 11082* (WAG): 4 km on the road (N6) Louvoulou-Kakamoéka, 04°20′S 12°08′E (st, 02).

ANGOLA: *Gossweiler 6561* (BM, COI, LISJC, LISU): Maiombe, Buco Zau, 04°45′S 12°34′E (fl, 08); *Gossweiler 7218* (LISJC): ? (fr); *Gossweiler 7989* (B, holo; BM, COI, K, LISJC, LISU): Cabinda, N of the Congo mouth, Mayombe forest area, banks of R. Nzanza, c. 04°35′S 12°35′E (fl, 04); *Pearson 2878* (B, K): Cuzengo, forest at Montobello, ? (fl, 04); *Stanton 114* (BM): 40 km SW of Camabatela, 08°39′S 15°07′E (fl, fr, 10).

ZAIRE: *Breyne 2753* (BR): Tshela zone, Lundu, 04°45′S 13°03′E (fr, 08); *Flamigni 6476* (BR), identification doubtful: Haut Maipunly, Madiakoko-Palanga, 04°48′S 12°55′E (fl, 10); *Nannan 315* (BR): Mayombe, Sugar Company Mission, c. 05°00′S 13°00′E (fl); *Van Tilborg 1383* (BR), identification doubtful: Boa, 03°29′S 23°30′E (fl).

CULTIVATED: *Hort. Hohenheim s.n.* (B): (from München) cult. at Hohenheim (fl, 10); *Hort. Kew s.n.* (P): cult at Hort. Bot. Reg. Kew., from type plant (fr); *Hort. Kew s.n.* (K): cult. in Hort. Bot. Reg. Kew., Nepenthes House (fl, 03); *Hort. Kew s.n.* (K): cult. Hort. Kew. (fl, 12); *Hort. Kew s.n.* (K): cult. Hortus Kew., Gold Coast (fl); *Hort. Kew s.n.* (K, holo; (COI, photo)): 424-98, Hort. Kew, Old Calabar (fl, 09); *Hort. Kew s.n.* (K, holo): from Gold Coast, 380-07 (fl, 08); *Hort. Kew s.n.* (B, K, P): cult. in Hort. Bot. Reg. Kew, from the type plant (fl, 09); *van Veldhuizen 588* (WAG):

Wageningen Agric. Univ., Dept. of Horticulture No 1112 (coll. H.C.D. de Wit s.n. Ivory Coast, febr. 1976) (fl, fr, 08); *van Veldhuizen 644* (WAG): Wageningen Agric. Univ., Dept. of Horticulture cult. no 79-56 (coll. Leeuwenberg 12021, Ivory coast) (fl, fr, 12); *van Veldhuizen 645* (WAG): Wageningen Agric. Univ., Dept. of Horticulture (fl, fr, 12); *van Veldhuizen 877* (WAG): Wageningen, Dept. of Horticulture No 1385 (coll. Beentje s.n.) (st, 01); *van Veldhuizen 965* (WAG): Wageningen, Dept. of Horticulture No 1617 (coll. WALK-B 441, Gabon) (fl, fr, 10); *van Veldhuizen 966* (WAG): Wageningen, Dept. of Horticulture No 1575 (coll. Leeuwenberg 12536, Gabon), No 82-481 of Bot. Garden 'de Dreyen' (fl, fr, 10); *van Veldhuizen 1104* (WAG): Wageningen, Dept. of Horticulture No 1574 (coll. Leeuwenberg 12507, Gabon) (fl, 09); *van Veldhuizen 1235* (WAG): Wageningen, Bot. Garden 'De Dreijen' (coll. J.J. Bos c.s. 10544, Gabon) (fl, 10); *van Veldhuizen 1236* (WAG): Wageningen, Bot. Garden 'De Dreijen' (coll. J.J. Bos c.s. 10544, Gabon) (fl, 10); *van Veldhuizen 1309* (WAG): Wageningen, (coll. Leeuwenberg 12536, Gabon) (fl, 05); *van Veldhuizen 1310* (WAG): Wageningen, Bot. Garden 'De Dreijen', cult. no 88PTGA049 (coll. Breteler c.s. s.n., Gabon) (fl, 05).

a.2. var. **pilosa** Sosef **var. nov.** **Map 16.9**

– TYPE: *Chevalier 19716* (P!, holo; LY!, P!): 'Cote d'Ivoire, Bassin du Cavally, Pays des Tépo, Village de Grabo, 3-8-1907.'

Begonia quadrialata auct. non Warb.: Guillaumet, Recherches végét. et flore rég. Bas-Cavally (1967) 80, 173, 219 etc.

Diagnosis: A varietate *quadrialata* differt indumento in superiare lamina foliorum frequenter dense et breve.

Differs from the typical variety by:
Upper surface of leaf blade often dense and comparatively shortly pilose.

Distribution: Eastern Liberia, south-western Ivory Coast, southern Ghana, central Nigeria and western Congo.

Ecology: On steep sandstone banks or rocks; along roads and streams; in shaded, wet to moist sites in primary forest; at 100–400 m altitude.

Notes: On the label of the type sheets at Paris Chevalier wrote 'B. modesta'. He probably intended to describe a new species. Chevaliers manuscript name is probably the origin of the misuse of the epithet 'modesta' for *B. modica* Stapf in Hutch,. Dalziel & Keay, Fl. W. Trop. Afr. (ed. 2) 1,1 (1954) 218.

Specimens examined:

LIBERIA: *Baldwin 10741* (K, MO): Grand Cape Mt Co., Genna Tanyehun, 07°15'N 10°44'W (st, 12).

IVORY COAST: *Chevalier 19716* (P, holo; LY, P): streambed of the Cavally, Tépo land, Grabo, 04°55'N 07°30'W (fl, fr, 08); *Guillaumet 1158* (P): Adiopodoumé, cultivated, introduced from Grabo (Mt. Kopé), 04°59'N 07°27'W (fl, 01).

GHANA: *Irvine 1080* (K): Western Prov., Brumase, 05°28'N 02°07'W (fl, fr, 01); *Vigne 3073* (K): near Prestea, 05°26'N 02°09'W (fl, 09).

NIGERIA: *Emwiopon FHI 60674* (FHI): Enugu Prov., Enugu Distr., Milken Hill, 06°26'N 07°29'E (fl, 10); *Jones (FHI 710) 1080* (FHI): Onitsha Prov., Iva valley, Enugu, 06°27'N 07°27'E (fl, 02); *Killick 286 (FHI 17669)* (FHI, K): Milliken Hill, Enugu, 06°26'N 07°29'E (fl, 12).

CONGO: *J.J. de Wilde c.s. 11081* (WAG): 4 km on the road (N6) Louvoulou-Kakamoéka, 04°20'S 12°08'E (st, 02); *J.J. de Wilde, c.s. 11092* (WAG): ibid. (st, 01).

b. subsp. **dusenii** (Warb.) Sosef **comb. & stat. nov.** **Fig. 16.14, Map 16.9**

Begonia dusenii Warb., Bot. Jahrb. Syst. 22 (1985) 44; Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3,2 (1921) 618; Irmscher in Engl. & Prantl, Nat. Pflanzenfam. (ed. 2) 21 (1925) 574; Hutch., Dalz. & Keay, Fl. W. Trop. Afr. (ed. 2) 1,1 (1954) 220; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39; L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 161. – TYPE: *Dusén 90* (B!, holo): 'Kamerun, Yaunde Station' (location erroneous, see note 1).

Differs from the typical subspecies by:
Leaf blades almost symmetrical to slightly asymmetrical, elliptic-ovate, 4.4–10.5 x 1.7–5.2 cm, gradually but long acuminate in the apical 1/3 to 1/2. Ovary narrowly elliptic-oblong and narrowly winged all along; wings ribbon-shaped or narrowly elliptic-obovate.

Distribution: CAMEROON: Cameroon Mountain.

Ecology: On tree trunks or wet rocks in deeply shaded undergrowth of forest; at about 800 m altitude.

Notes: 1. The label on the type specimen at Berlin mentions the location 'Yaunde Station'. This location is not written on the label by Dusén himself. According to Letouzey (1968: 94) and Birger (1926) Dusén collected on and nearby Mount Cameroon. Two other collections from this locality match the type material perfectly. It must therefore be assumed that an erroneous locality was added on the label.

Specimens examined:

CAMEROON: *Dusén 90* (B, holo; STU): Mt Cameroon, 04°04'N 09°02'E (fl, 07); *Ludwigs 22* (M): Victoria, c. 04°00'N 09°10'E (fl); *Thompson, DiGiulio & Davidson 1440* (MO, YA): South-West Prov., Fako Dept., Bakingili, trail up side of Mt Cameroon, 04°04'N 09°02'E (fl, fr, 06); *Villiers 2431* (WAG, YA): SW slope of Mt Cameroon, NE of Bakingili, 20 km WNW of Limbé, 04°05'N 09°03'E (st, 12).

c. subsp. **nimbaensis** Sosef **subsp. nov.** **Fig. 16.15, Map 16.9**

– TYPE: *J. van Veldhuizen 643* (WAG!, holo; WAG!): 'Wageningen, University of Agriculture, Dep. of Horticulture, in greenhouse. (Coll. Irmscher, Nr. of Dep. of Horticulture 1022).'

Begonia quadrialata Warb. subsp. *nimbaensis* (provisional name) de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 18.
Begonia quadrialata auct. non Warb.: Adam, Fl. descr. Monts Nimba (1971) 328, pl. 81.
Begonia sp. from Liberia, Legro & Doorenbos, Neth. J. Agric. Sci. 21 (1973) 168 & Belmontia n.s. 2,6 (1974) 168; Doorenbos, Begonian 47: 13, cover pl.
Begonia leichtiana Irmscher ex Sosef (ms name, pro syn.).

Diagnosis: A subspecie *quadrialata* differt colore fusco secus nervos et venas.

Differs from the typical subspecies by:
Leaf blades on the upper surface medium to pale green with marked darker green to dark purplish brown zones around the main and larger secondary nerves.

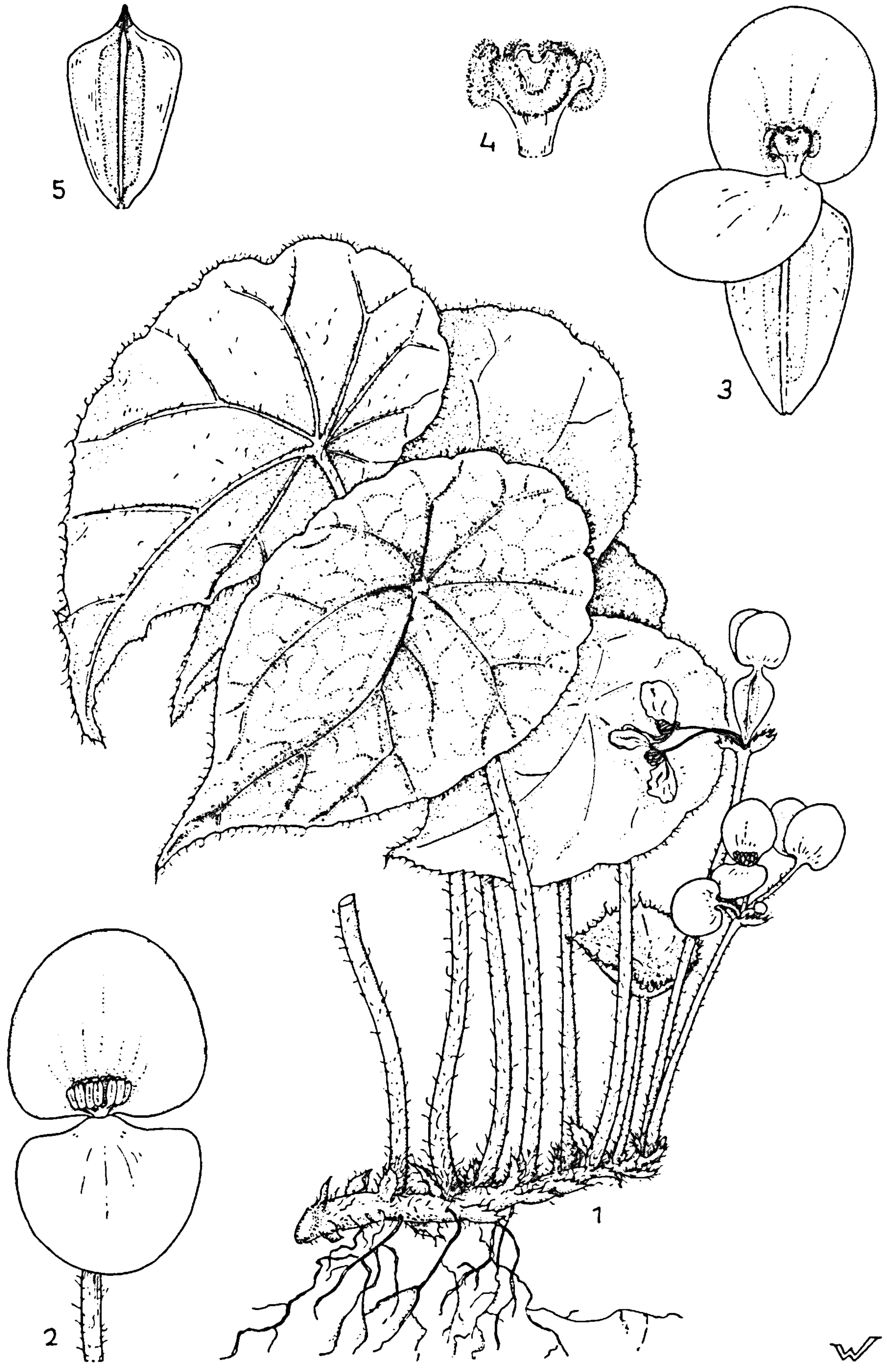


Figure 16.15. *Begonia quadrialata* Warb. subsp. *nimbaensis* Sosef. – 1: habitus (x$^2/_3$); 2: male flower (x2); 3: female flower (x2); 4: styles (x4); 5: fruit (x2). – 1-4: living plant at WAG, voucher *van Veldhuizen 504*; 5: *Adam 27555*.

Distribution: On and around Mount Nimba, on the border between Guinea, Liberia and Ivory Coast.

Ecology: In primary lowland or submontane forest; on rocks and rock faces in half-shaded to shaded sites, near streams or on moist to comparatively dry sites; at 350–1600 m altitude.

Chromosome number: 2n = 52 (Legro & Doorenbos l.c.).

Notes: 1. This subspecies is much more uniform than the typical subspecies, as is to be expected in view of its narrow geographical distribution. The leaf blades are always gradually acuminate towards the apex (like in collections from the typical subspecies in the same region) while the margins are markedly ciliate. The ovaries are obtriangular-obovate.

2. The subspecies is presently in cultivation at WAG (cult. no 86PTCB097) and at B. On both locations it was registered bearing the name 'Begonia leichtiana Irmscher'. This name was also encountered in several of Irmschers written notes at B. Apparently the latter intended to describe it as a new species. The name might well have been registered in other files and is therefore added here as a synonym to avoid any confusion in the future. The origin of the specific epithet 'leichtiana' could not be traced, which is why a different subspecific name was chosen.

Specimens examined:

GUINEA: *Adam 185* (P): caves of Mt Nimba, 07°35'N 08°28'W (fl, 04); *Adam 7410* (MO): Guinee Terr., Nzérékoré, Mt Nimba, 07°35'N 08°28'W (st, 12); *Adam 7486* (MO): ibid. (st, 12); *Chevalier 21082* (BR, P): Guerzés country, between N'zo and Sakonanta, base of Mt N'zo, 07°40'N 08°22'W (st, 03); *Schnell 266* (P): Mt Nimba, NE slope, 07°36'N 08°27'W (fl, 02); *Schnell 301* (P): Mt Nimba, 07°35'N 08°28'W (fl, 02); *Schnell 1128* (P): ibid. (st, 04); *Schnell s.n.* (P): Mt Nymba, Zongue face, 07°42'N 08°23'W (fl, 04).

LIBERIA: *Adam 20161b* (K, P): Nimba, 07°35'N 08°28'E (st, 12); *Adam 20785* (K, P): ibid. (fl, 01); *Adam 26445* (MO): Yéképa, Mt Gangra, 07°33'N 08°38'W (st, 10); *Adam 26605* (MO): Yéképa, Mt. Nimba, 07°35'N 08°28'W (st, 01); *Adam 27555* (MO): Yéképa, Granfield, 07°35'N 08°32'W (fl, fr, 05); *Adames 765* (K): Nimba, Lamco Hq. Camp, 07°35'N 08°28'W (fl, fr, 11); *Baldwin 9619* (K, MO): Central Prov., Sanokwele Distr., Mt Bobei, 07°22'N 08°36'W (fl, 09); *W.J. Harley 1287* (K): Mt Bili, 07°25'N 08°36'W (fl, 12); *W.J. Harley 1292* (WAG): ibid. (st, 01); *W.J. Harley 1292* (K): ibid. (fl, 01); *Leeuwenberg & Voorhoeve 4770a* (WAG): Nimba Mts, near Iron mine of L.A.M.C.O., c. 07°35'N 08°28'W (fl, 07).

IVORY COAST: *Chevalier 21126* (K, P): Haut-Nuon stream bed, Dijolas land, foot of Nouba Mts, surroundings of Nuon springs, 07°36'N 08°25'W (fl, 04); *Schmelzer s.n.* (WAG): Mt Nimba, 07°37'N 08°25'W (fl, fr, 04).

CULTIVATED: *Anonymous s.n.* (M): Bot. Garden München (fl, 03); *Schwerdtfeger 7478* (B): cult. in Bot. Garden Berlin-Dahlem (fl, 09); *Schwerdtfeger 10587* (B): ibid. (st, 09); *van Veldhuizen 504* (WAG): Wageningen Agric. Univ., Dept. of Horticulture (descending from African coll. Irmscher, Stuttgart-Hohenheim) (fl, fr, 05); *van Veldhuizen 643* (WAG): Wageningen Agric. Univ., Dept. of Horticulture No 1022 (coll. Irmscher) (fl, 12); *van Veldhuizen 1305* (WAG): Wageningen, Dept. of Plant Taxonomy, 'De Dreijen', Dept. of Horticulture No 1022 (fl, 04).

Begonia salisburyana Irmscher **Fig. 16.16, Map 16.10**

Begonia salisburyana Irmscher, Bot. Jahrb. Syst. 76 (1954) 215; Hutch., Dalz. & Keay, Fl. W. Trop. Afr. (ed. 2) 1,1 (1954) 219; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39; L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 228, fig. 22.9; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 16, pl. 10G. – LECTOTYPE: *Brenan & Richards 8432* (K!; iso: BM!, K!, P!): 'Nigeria, Prov. Benin, Div. Benin, Okomu Forest Reserve, Compartment No. 69.'

Plant up to 23 cm high, scattered with minute glandular hairs, sparsely so on stipules. **Rhizome** slender to fairly stout, rather smooth to somewhat knotted, rather compact, 0.8–4.6 mm wide, sparsely hirsute to hirsute, especially on the younger parts; the apical part not or slightly ascending. **Stipules** very broadly ovate to triangular, 0.7–4.0 mm long, greenish, top rounded to acute; margin dentate, ciliate. **Leaves** not peltate; *petiole* continuing into the midrib with a more or less distinct angle, 0.5–22.0 cm long, juicy, dull red-purple to red, hirsute or sparsely so with long, wavy, white hairs; *leaf blade* in a more or less horizontal position, usually distinctly asymmetrical, usually obliquely broadly ovate, sometimes very broadly so, bluntly or acutely acuminate at the top, (2.7–)4.0–11.0 x (2.1–)3.2–8.8 cm, herbaceous to slightly succulent, with 8–11 palmate main nerves; margin entire, reddish or red-purple, usually distinctly ciliate; base oblique, one side cordate, the other side cordate to deeply so, top blunt to acute; upper surface pale to medium green, glossy, smooth; lower surface paler, dull; *nerves*: the main and larger secondary nerves not prominent and concolorous with the blade or darker tinged on the upper surface, on the lower not or slightly prominent, medium green to reddish, sparsely to very sparsely hirsute with patent hairs, smaller secondary nerves usually fairly distinct, tertiary nerves indistinct. **Inflorescence** containing 2–5 male flowers and 1 terminal female flower, positioned at approximately the same level as the leaf blades to about halfway up the petioles; *peduncle* simple, 2.0–7.0 cm long, reddish, usually sparsely hirsute with wavy white hairs; *bracts* 3–6, elliptic-ovate or elliptic to narrowly elliptic-ovate, 1.2–2.7 mm long, green; margin dentate, ciliate. **Male flower**: *pedicel* elongated at anthesis up to 17 mm, sparsely hirsute with wavy white hairs; *perianth segments* broadly ovate to elliptic, with a rounded to cuneate base, 5.2–10.5 x 4.3–8.3 mm, the outside hirsute or sparsely so; the upper perianth segment red or orange-red with faint darker nerves on the outside, the inside yellow with a red patch and nerves at base; the lower segment orange-red to yellow on the outside, yellow on the inside; *androecium* with 14–19 stamens; column 0.7–1.6 mm long, anthers 1.0–1.7 mm long. **Female flower**: similar to the male but only shortly pedicellate, its pedicel slightly elongated in fruit up to 0.7 mm; *perianth segments* very broadly ovate to circular, sometimes broadly ovate, with a rounded to cordate base, 4.3–9.8 x 4.9–10.0 mm; *styles* 4, 2.2–3.5 mm long, fused in the lower 1/2, the top split into a compact and rounded U-shape, the arms 0.25–0.5 mm long and covered by a compact, non-twisted stigmatic band; *ovary* elliptic or narrowly so to obovate or narrowly so, 7.2–12.0 x 2.3–5.1 mm, pale brownish to reddish green, 4-locular, 4-winged all along; the locular part

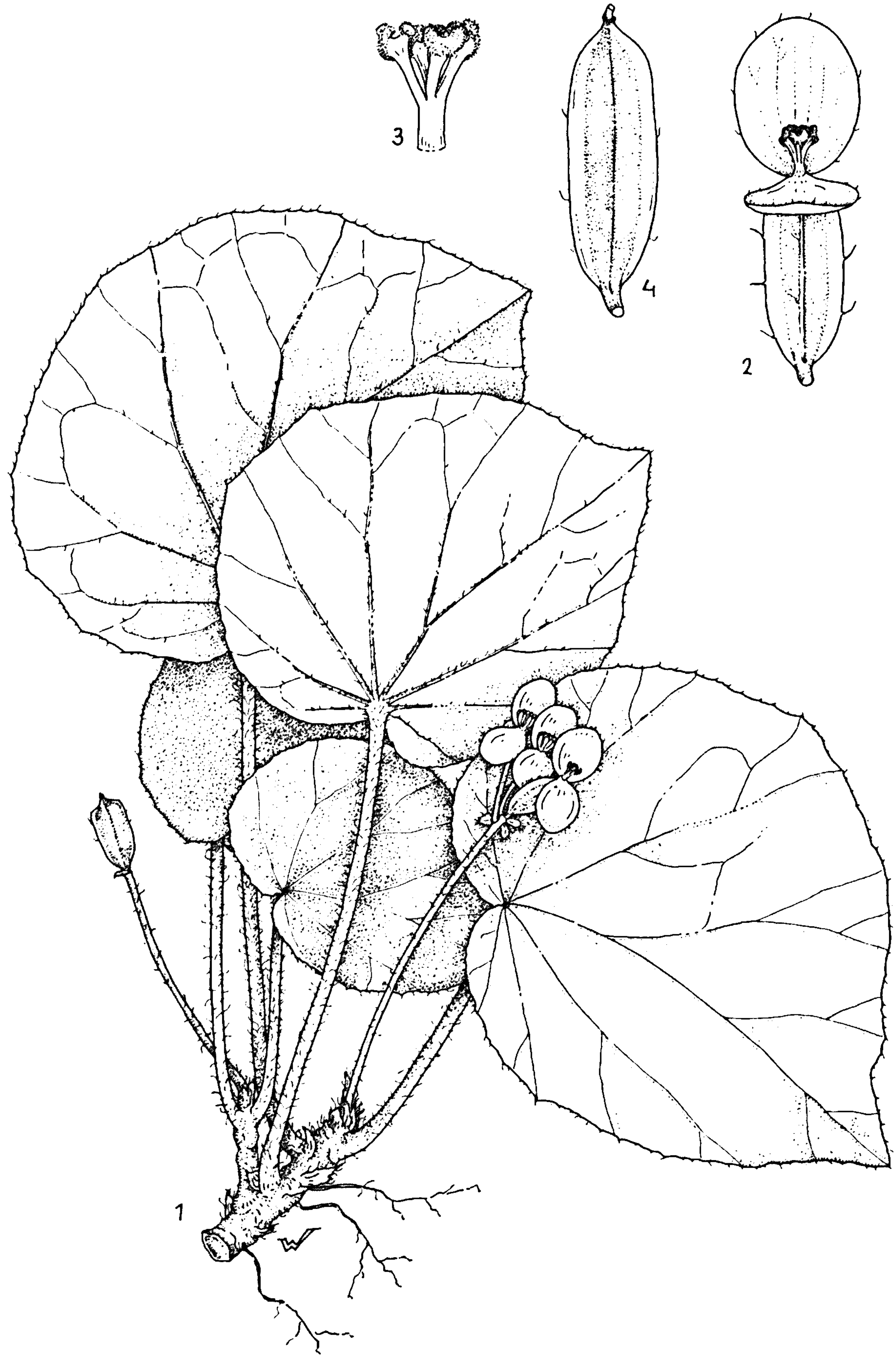
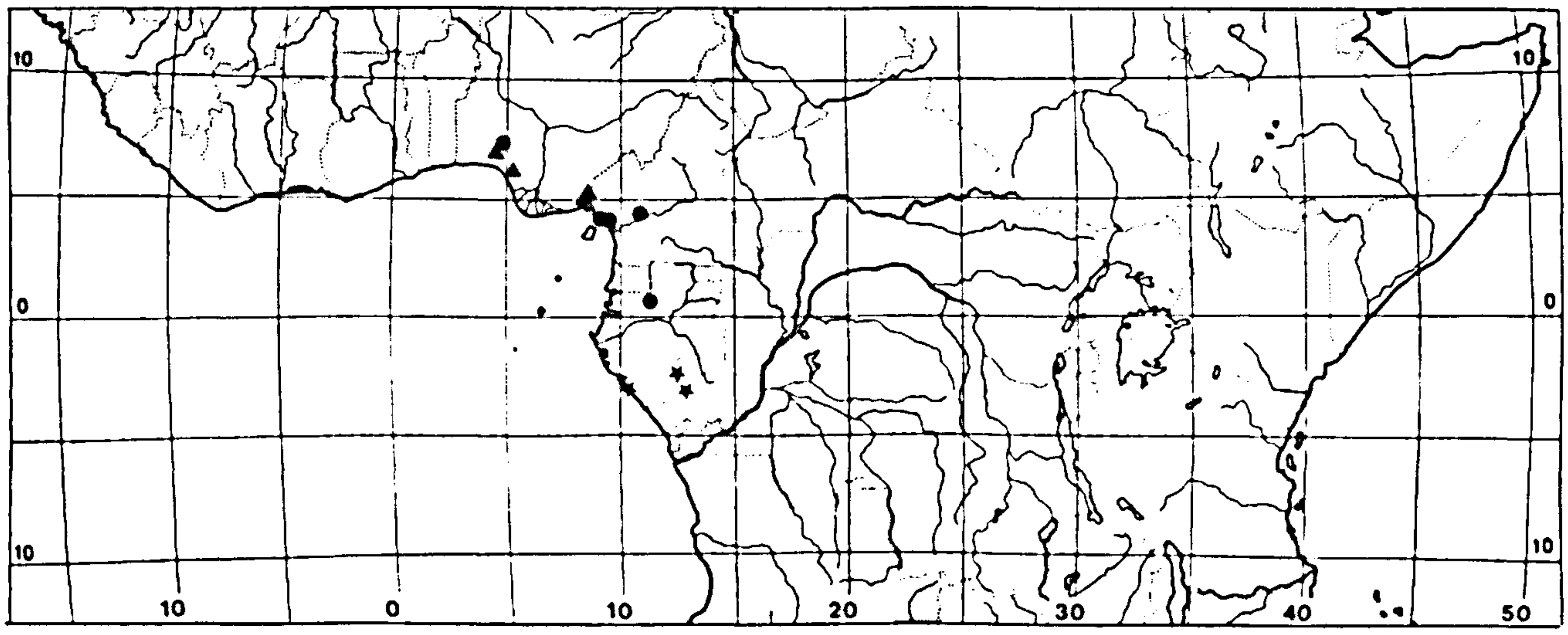


Figure 16.16. *Begonia salisburyana* Irmscher. – 1: habitus (x$^{2}/_{3}$); 2: female flower (x2); 3: styles (x4); 4: fruit (x2). – 1: *Brenan 8531*; 2, 3: *Ross 236*; 4: *Ujor FHI 31784*.



Map 16.10. Distribution of *Begonia salisburyana* (triangles), *Begonia scapigera* subsp. *scapigera* (dots) and subsp. *australis* (stars).

narrowly elliptic, 1.0–2.5 mm wide; beak absent or short, up to 0.5 mm long; wings ribbon-shaped or narrowly elliptic-obovate, 0.5–2.3 mm wide, green, the margin sparsely ciliate. **Infructescence**: peduncle not recurved towards the substrate; *fruit* erect, elliptic or elliptic-obovate or sometimes narrowly so, 12.5–17.0 x 4.9–7.7 mm, dry, thin-walled, pale brownish.

Distribution: Southern Nigeria.

Ecology: Locally abundant on level, sometimes swampy sites but also on steep banks along streams or near waterfalls; in high primary forest; in association with a large aroid or *Trichomanes*; from sea-level up to 300 m altitude.

Notes: 1. The material is markedly uniform as compared to that of other species of the *B. potamophila* group (see chapter 11).

2. From among the 2 syntypes cited by Irmscher Brenan & Richards 8432 is chosen as the type because it constitutes more complete material.

Specimens examined:

NIGERIA: *Brenan 8531* (B, K): Benin Prov., Benin Div., Okomu Forest Reserve, Compartiment No. 69, 06°20'N 05°15'E (fl, fr, 12); *Brenan & Richards 8432* (K; iso at BM, K, P): ibid. (fl, 12); *Brenan & Richards 8620* (K): ibid. (st, 12); *Coombe 185* (K): Oban Rock, Oban, S. Nigeria, 05°19'N 08°34'E (fl, 03); *Richards 3124* (BM): Shasha Forest Reserve, Ijebu Prov., 07°05'N 04°30'E (fl, 02); *Richards 3346* (BM): ibid. (fl, 04); *Ross 236* (BM): Shasha Forest Reserve, Ijebu Prov., Baba Eko, 07°05'N 04°30'E (fl, 04); *Sharland 1956* (K): Kwa falls, Calabar, c. 05°00'N 08°30'E (fl, 07); *Ujor FHI 31784* (FHI, K): Calabar Prov., Eastern F.R. Oban hill, 05°19'N 08°34'E (fl, 05).

Begonia scapigera Hook.f.

a. subsp. **scapigera** **Fig. 16.17, Map 16.10**

Begonia scapigera Hook.f. in Oliver, Fl. Trop. Afr. 2 (1871) 572; Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3,2 (1921) 618; Irmscher in Engl. & Prantl, Nat. Pflanzenfam. (ed. 2) 21 (1925) 574; Hutch. & Dalz., Fl. W. Trop. Afr. (ed. 1) 1,1 (1927) 187; Hutch., Dalz.

& Keay, Fl. W. Trop. Afr. (ed. 2) 1,1 (1954) 218; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39; L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 229; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 19, pl. 14C. – TYPE: *Mann 1946* (K!, holo; B!, COI! (photo), P!): 'Cameroon Mountain, 4000 ft, Decb. 1862.'

Plant up to 35 cm high, scattered with minute glandular hairs, sparsely so on bracts and pedicel of male flower, sometimes sparsely so on stipules and ovary. **Rhizome** stout and compact, 2.5–9.4 mm wide (up to 15 mm in vivo), glabrous or with a ring of white hairs around the leaf axils; the apical part not or only slightly directed upwards. **Stipules** triangular or elliptic-ovate to very broadly triangular or very broadly triangular-ovate, acute to acuminate, 1.4–6.4 mm long, uniformly light bronze-green to pinkish red with darker red nerves; margin entire to slightly dentate, ciliate. **Leaves** peltate; *petiole* continuing into the midrib with a distinct angle, inserted at (6–)12–64 mm from the nearest margin, (2.5–)6.0–30.0(–36.0) cm long, succulent-juicy, uniformly red-brown or red-brown in the lower half and light green in the upper, becoming uniformly bronze-green to light green with age, glabrous or rarely with a few long hairs; *leaf blade* in a more or less horizontal position to directed downwards, more or less symmetrical, broadly elliptic-ovate or almost circular, usually shortly but distinctly acuminate at the top, sometimes acuminate-caudate, very variable in size, (4.7–)6.1–20.0(–25.0) x (2.8–)4.0–14.0(–18.0) cm, rather firm but succulent-juicy, with (8–)9–11 palmate main nerves; margin entire to coarsely and shallowly dentate, especially in the upper half, usually distinctly pinkish red to dark brown-red, ciliate to very sparsely so; base rounded, top acute; upper surface light to medium green with distinctly lighter coloured nerves, dull but glistening when light falls in at a particular angle, smooth or slightly rugose due to the slightly sunken nerves; lower surface pale green, dull; *nerves*: the main and larger secondary nerves slightly sunken and distinctly lighter coloured than the interveinal parts on the upper surface, on the lower surface slightly prominent, medium green, glabrous or rarely with very few patent hairs, the smaller secondary nerves indistinct but well visible (more pronounced towards the margins), not prominent, tertiary nerves not visible. **Inflorescence** containing 2–4(–12) male flowers and 1 terminal female flower, positioned at approximately the same level as the leaf blades or down to halfway up the petioles; *peduncle* simple or branched up to 2 times, in all 2.0–19.5 cm long, succulent-juicy, brown-red to bronze-green, glabrous or rarely with a few long white hairs; *bracts* 3–5(–13), almost circular or broadly elliptic-ovate to elliptic, 1.2–4.3 mm long, light brown-red to bronze-green, sparsely scattered with minute glandular hairs; margin dentate, ciliate. **Male flower**: *pedicel* elongated in flower up to 40(–47) mm, pale pinkish to light green, rarely with a few hairs; *perianth segments* circular to transversely broadly elliptic or very broadly ovate, with a rounded to cordate base, 8.1–17.5 x 7.0–23.0 mm, the outside sometimes with hairs on the margin; the upper turning from red in bud to light yellow with a reddish tinge towards the margin or in the upper half on the outside, the inside yellow with or without a red patch and nerves in the basal half, the lower segment light yellow on the outside and yellow on the inside; *androecium* with 20-34 stamens; column 0.4–1.8 mm long,

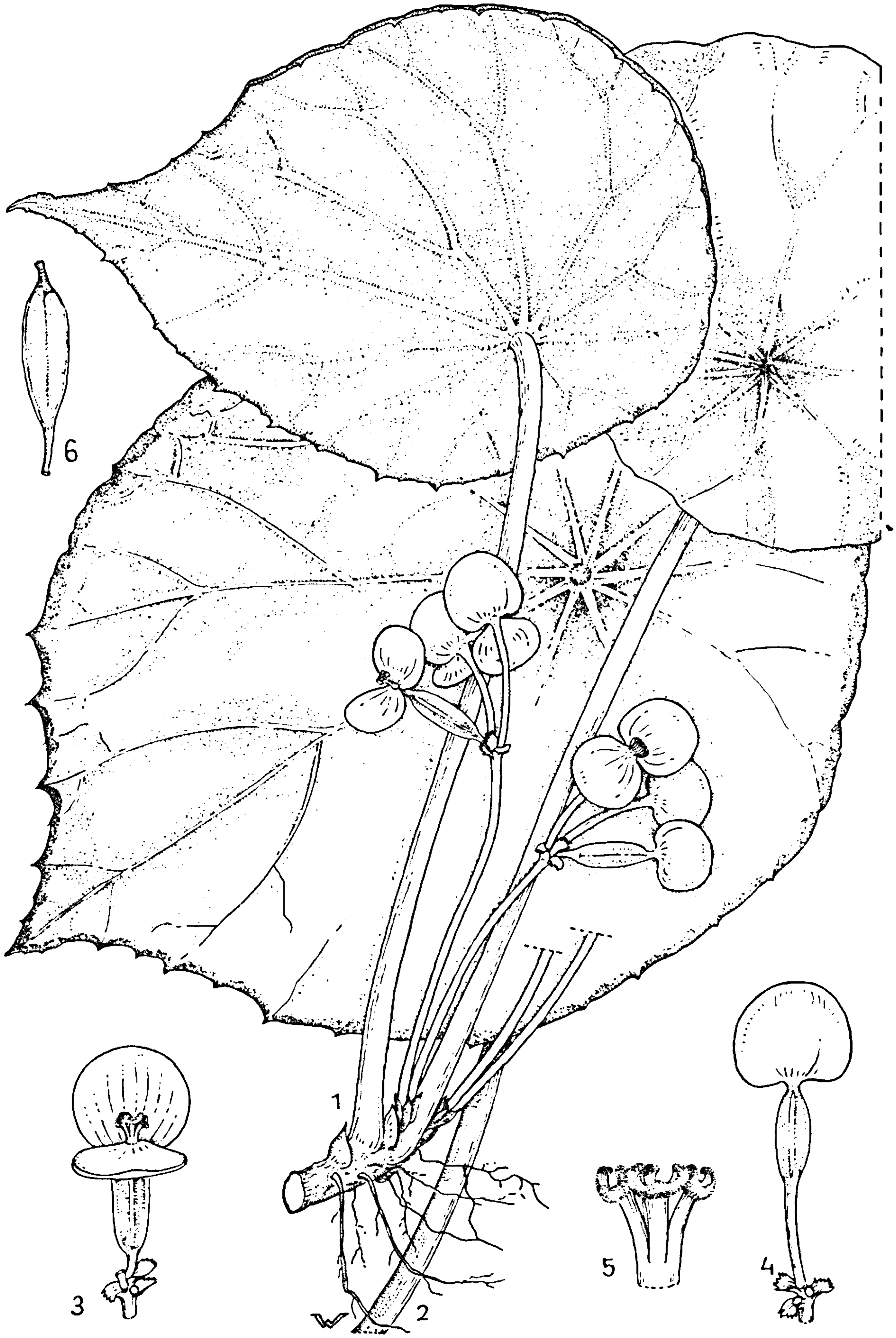


Figure 16.17. *Begonia scapigera* Hook.f. subsp. *scapigera*. – 1: habitus ($x^2/_3$); 2: leaf blade ($x^2/_3$); 3: female flower (x1); 5: styles (x4); 6: fruit (x1). – 1: *Asonganyi 444*; 2, 3, 5: living plant at WAG, voucher *van Veldhuizen 1398*; 6: *Sanford 6318*. – *B. scapigera* Hook.f. subsp. *australis* Sosef. – 4: female flower (x1), living plant at WAG, voucher *van Veldhuizen 1395*.

anthers 0.5–2.2 mm long. **Female flower**: similar to the male but its pedicel elongated in fruit up to 7.0 mm; *perianth segments* with a cordate base, 9.2–19.0 x 7.7–25.0 mm; *styles* (3–)4, 2.9–6.2 mm long, fused in the lower half, sometimes only at base, the top split into a rather compact U-shape, the arms 0.4–1.4 mm long and bearing a rather compact and broad stigmatic band which is non-twisted or twisted for up to 1/2 a turn; *ovary* narrowly elliptic-oblong to almost linear, 7.8–30.0 x 0.9–4.3 mm, medium green to reddish tinged in the centre, (3–)4-locular, not winged, not hirsute; beak absent or present but short, 0–1.6 mm long. **Infructescence**: peduncle not recurved towards the substrate, though sometimes almost horizontal; *fruit* more or less erect, very narrowly elliptic-oblong to elliptic, 16.0–38.0 x 1.8–7.7 mm, dry, with a thin wall, light brown, dull.

Distribution: Eastern Nigeria, western Cameroon and northern Gabon.

Ecology: On rocks, cliffs, stream banks and road banks, often near a stream or waterfall; in shaded to deeply shaded sites; in primary forest; at 560–1250 m altitude.

Notes: 1. A living collection of this subspecies was obtained via K and is cultivated at WAG.

2. Two specimens from Mount Cameroon (Mann 1946 and Preuss 952) show branched peduncles. This feature is rare within the section and occurs otherwise only in *B. schaeferi* and *B. duncan-thomasii*.

Specimens examined:

NIGERIA: *Bowden 181* (K): Western State, Erin-Odo waterfall, 07°35'N 04°53'E (fl, 05); *Daramola FHI 23111* (FHI, MO): Western State Prov., Ilesha Distr., Erin-Odo waterfall, 07°35'N 04°53'E (fl, 02); *Gbile & Daramola FHI 67595* (FHI): Western State, Ilesha Distr., Erin-Ijesha, 07°35'N 04°50'E (fl, fr, 04); *Gledhill 880* (WAG): Erin-Odo waterfall, 07°35'N 04°53'E (fl, fr, 03); *Sanford 6318* (IFE): Ilesha Distr., Erin-Odo-Oke waterfalls, 07°35'N 04°53'E (fl, fr, 05); *P. Wit & J. Wit 1123* (FHI): Western State, Ilesha Distr., Erin-Ilesha waterfalls, 07°35'N 04°50'E (fl, 01).

CAMEROON: *Asonganyi 444* (P, WAG, YA): along R. Inoubou, 24 km S of Ndikinimeki, 04°32'N 10°50'E (fl, 03); *Mann 1946* (K, holo; B, COI (photo), P, STU): Mt Cameroon, c. 04°15'N 09°10'E (fl, fr, 12); *Preuss 952* (B, BM, COI, HBG, M, W): W of Buea, 04°09'N 09°15'E (fl, 09); *Synnott 1967* (K): South-West Prov., Buea town, 04°09'N 09°14'E (fl, 12); *Winkler 186* (B, Z): Neu-Tegel, bank of the Koke R., 04°12'N 09°26'E (st, 07).

GABON: *A. Louis 2143* (LBV, WAG): Woleu-Ntem Prov., exploitation Oveng near Mitzic, 00°42'N 11°19'E (fl, fr, 05).

CULTIVATED: *van Veldhuizen 1398* (WAG): Wageningen, Dept. of Plant Taxonomy cult. no 89PTGB073 (from Kew, coll. Adeyemi 2965, Cameroon) (fl, 07).

b. subsp. **australis** Sosef **subsp. nov.** **Fig. 16.17, Map 16.10**

– TYPE: *J. van Veldhuizen 1155* (WAG!, holo): 'Wageningen, Dept. of Horticulture, in greenhouse (coll. A. Louis s.n., Gabon, Bongolo), 25-VI-1986.'

Diagnosis: A subspecie *scapigera* differt pedicellis fructiferis longioribus et saepe fructibus brevioribus et rotundatibus.

Differs from the typical subspecies by:

Pedicel of the female flower rapidly elongated in fruit and then 7–27 mm long; ovary elliptic to circular or broadly obovate, 3.5–12.0 x 3.0–4.5 mm; fruit elliptic to circular or broadly obovate, 9.0–12.0 x 3.9–4.5 mm.

Distribution: Southern Gabon and western Congo.

Ecology: On steep forested riverbanks, often near rapids, on rocks; at 170 m altitude.

Notes: 1. The generally longer pedicels in fruit, and the shorter and more roundish shaped ovaries and fruits show a distinct geographical correlation, which justifies the recognition of a distinct subspecies.

2. A collection from southern Gabon is cultivated at WAG (cult. no. 85PTGA519) and the type specimen was vouchered from it.

3. Selfing was tried on about 10 female flowers of the cultivated specimen. Of these only 2 fruits resulted and eventually, after more than two months of ripening, yielded only a few seeds in each. The presence of a self-incompatibility system thus seems likely.

Specimens examined:

GABON: *Le Testu 1595* (BM, P): Mayombe Bayaka forest, rapids between Nyanga & Digoungou, 02°56′S 10°20′E (st, 08); *J.J. de Wilde c.s. 10412* (WAG): Bongolo, beneath protestant mission, 02°14′S 11°27′E (st, 02).

CONGO: *Sita 4815* (BR, IEC, P, WAG): Chaillu, Mossendje, near bridge across Louessé, Nyanga falls at Dimani, 03°00′S 12°55′E (fr, 07).

CULTIVATED: *van Veldhuizen 1155* (WAG, holo): Wageningen, Dept. of Horticulture (coll. A. Louis s.n., Gabon, Bongolo) (fl, 06); van Veldhuizen 1395 (WAG): Wageningen, Dept. of Plant Taxonomy cult. no 85PTGA519 (coll. A. Louis s.n., Gabon) (fl, fr, 07).

Begonia schaeferi Engler **Fig. 16.18, Map 16.11**

Begonia schaeferi Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3,2 (1921) 618; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 14, 15, 38, 39; L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 230, fig. 2.9. – TYPE: *Schaefer 72* (B!, holo; BR!): 'Kamerun, Bare, Manenguba, am Felsen, Höhe ü. d. M.: 1900, XI-'10'.

Begonia ramosa Sosef, Wageningen Agric. Univ. Papers 91-4 (1992) 140, fig. 7; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 15, pl. 9E. – TYPE: *Satabié 163* (WAG!, holo; BR!, K!, P!, YA!): 'Cameroun, Mts Bamboutos, 25 km W MBounda, 10°0′ Long E, 5°40′ Lat N, Alt. 2000 m, 29 novembre 1974.'

Plant (4–)10–22 cm high, scattered with minute glandular hairs, sparsely so on rhizome, stipules, bracts and pedicel of male flower, densely so on petiole. **Rhizome** rather stout and fairly compact, 2.0–8.2 mm wide, not hirsute; the apical part ascending to erect to form a short stem of up to 2 cm. **Stipules** broadly triangular-ovate to triangular-ovate or triangular, acute, (1.8–)3.1–9.4 mm long, not hirsute; margin entire or shallowly dentate at the often ciliate apex. **Leaves** peltate; *petiole* usually making a distinct angle with the midrib, inserted at (2–)8–18 mm from the nearest margin, (2.0–)4.0–21.5 cm long, juicy, reddish, hirsute or sparsely so with long, patent, wavy, hairs; *leaf blade* in more or less horizontal position, variously asymmetrical, usually elliptic or elliptic-ovate, sometimes broadly elliptic or broadly elliptic-ovate, as a rule distinctly acuminate to acuminate-caudate in the upper 1/8 to 1/5, (2.4–)3.5–14.0 x (1.6–)2.5–7.2 cm, somewhat juicy, with 7–11 palmate main nerves; margin denticulate or finely

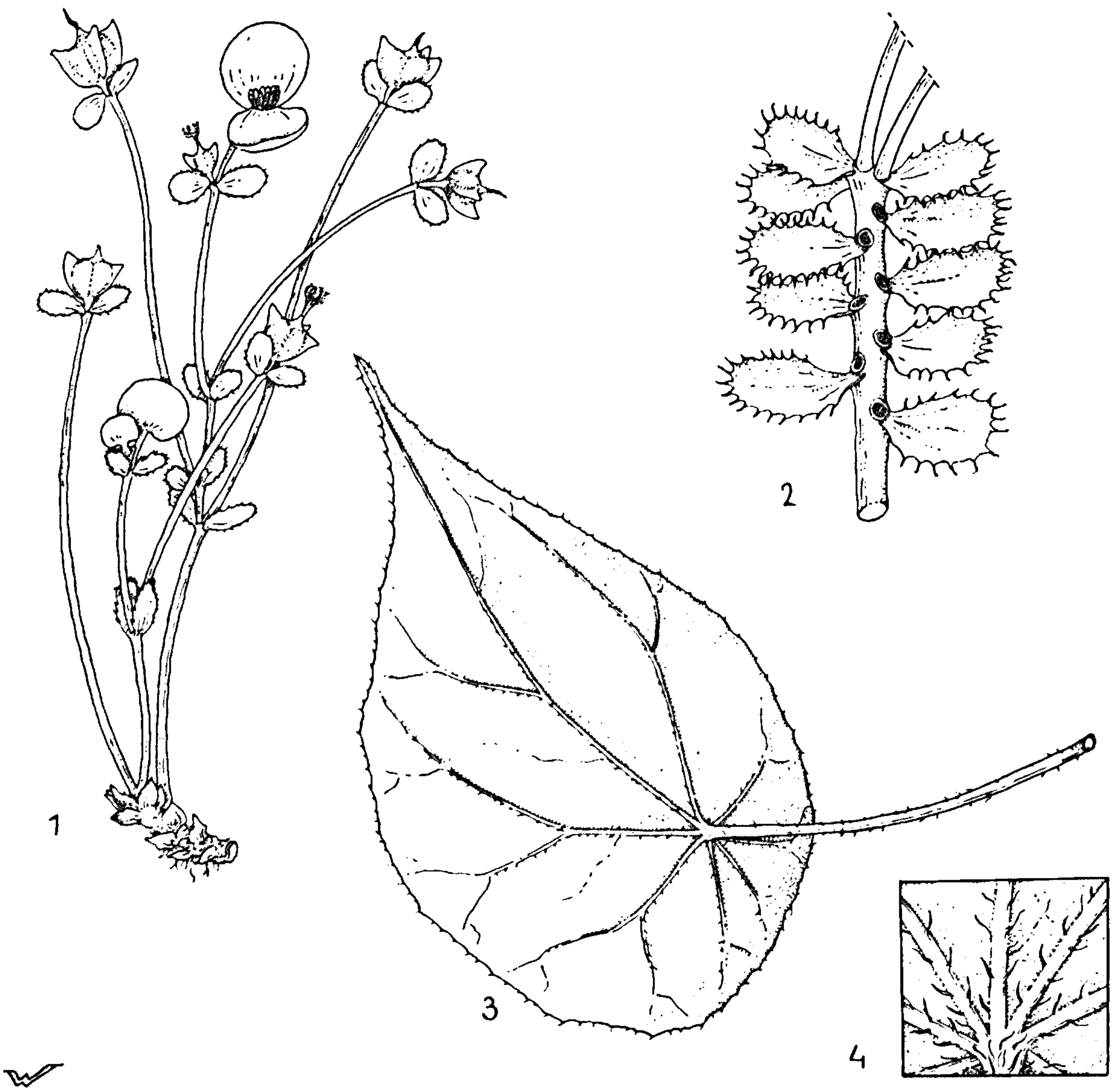


Figure 16.18. *Begonia schaeferi* Engl. – 1: bisexual inflorescence (x$^{2}/_{3}$); 2: detail of male inflorescence (x2); 3: lower leaf surface (x$^{2}/_{3}$); 4: detail lower leaf surface and nerves (x2). – 1-4: *Satabié 163*.

serrate in the apical part and sometimes coarsely remotely dentate in the upper half, concolorous with the blade, ciliate; base rounded, very top acute; upper surface bright green, dull, smooth, sparsely hirsute with evenly distributed medium-sized hairs or rarely glabrous; lower surface paler green; *nerves*: the main and larger secondary nerves not prominent and concolorous with the blade on the upper surface, on the lower not or slightly prominent, red, almost glabrous or sparsely hirsute with medium-sized patent hairs, the smaller secondary nerves not prominent, distinct to indistinct, sparsely hirsute to glabrous, tertiary nerves indistinct or not visible. **Inflorescence** of two different types, one exclusively male, the other bisexual, positioned at about 2/3 of the length of the petioles to at about the same level as the leaf blades; *peduncle* simple to branched up to 3 times, juicy, reddish, sparsely to very sparsely hirsute, most prominently so below each branching point, up to 20 cm long or when branched the primary axes 2.0–10.5 cm long, secondary axes 1.0–7.0 cm long, and tertiary axes 4.0–11.5

cm long, each ramification with two opposite bracts similar to those beneath the flowers but narrower; *male inflorescence* containing 4–8 male flowers and 4–8 bracts, *bisexual inflorescence* containing 1–2 male flowers, 1–2 terminal female flower(s) and 2–3 bracts; *bracts* circular to broadly elliptic, 3.9–8.8 mm long, bronze-green; margin dentate, ciliate. **Male flower**: *pedicel* elongated at anthesis up to 24 mm long; *perianth segments* circular to very broadly ovate, rounded at base, 7.2–14.5 x 9.4–15.0 mm, the outside usually with a few long hairs, yellow, the inside yellow; *androecium* with 20–38 stamens; column 0.4–2.1 mm long; anthers 0.9–2.1 mm long. **Female flower**: similar to the male, pedicel usually distinct and elongated in fruit, 0.8–5.2(–10.0) mm long; *perianth segments* very broadly ovate, slightly cordate at base, 7.8–22.0 x 8.2–20.0 mm; *styles* 3–4, 2.9–6.4 mm long, fused in the lower half, the top broadly and more or less compressed horseshoe-shaped, the arms 0.7–2.3 mm long and bearing a rather compact stigmatic band which is spirally twisted for up to 1/2 a turn; *ovary* broadly elliptic or obtriangular-obovate to very broadly so, 3.9–9.1 x 2.3–6.2 mm, green, not translucent, rounded at base, 3–4-locular, 3–4-winged in the apical half; the locular part elliptic to broadly elliptic or broadly obovate, 2.3–5.0 mm wide; beak present, distinct or not, 0.3–2.3 mm long; wings patent or slightly erecto-patent, more or less ribbon-shaped to broadly obtriangular-obovate to very broadly so, 0.4–2.6 mm wide, margin glabrous. **Infructescence**: peduncle not recurved towards the substrate; *fruit* erect, broadly elliptic or broadly obtriangular-obovate to very broadly so, 5.9–8.8 x 4.1–10.5 mm, dry, with a relatively thin wall.

Distribution: South-eastern Nigeria and western Cameroon mountains.

Ecology: On rocks and vertical rock faces; on moist to comparatively dry places; in primary submontane to montane forest, the latter sometimes with trees not higher than 6–12 m; in submontane forest with *Santiria trimera*; at ± 1500–2300 m altitude.

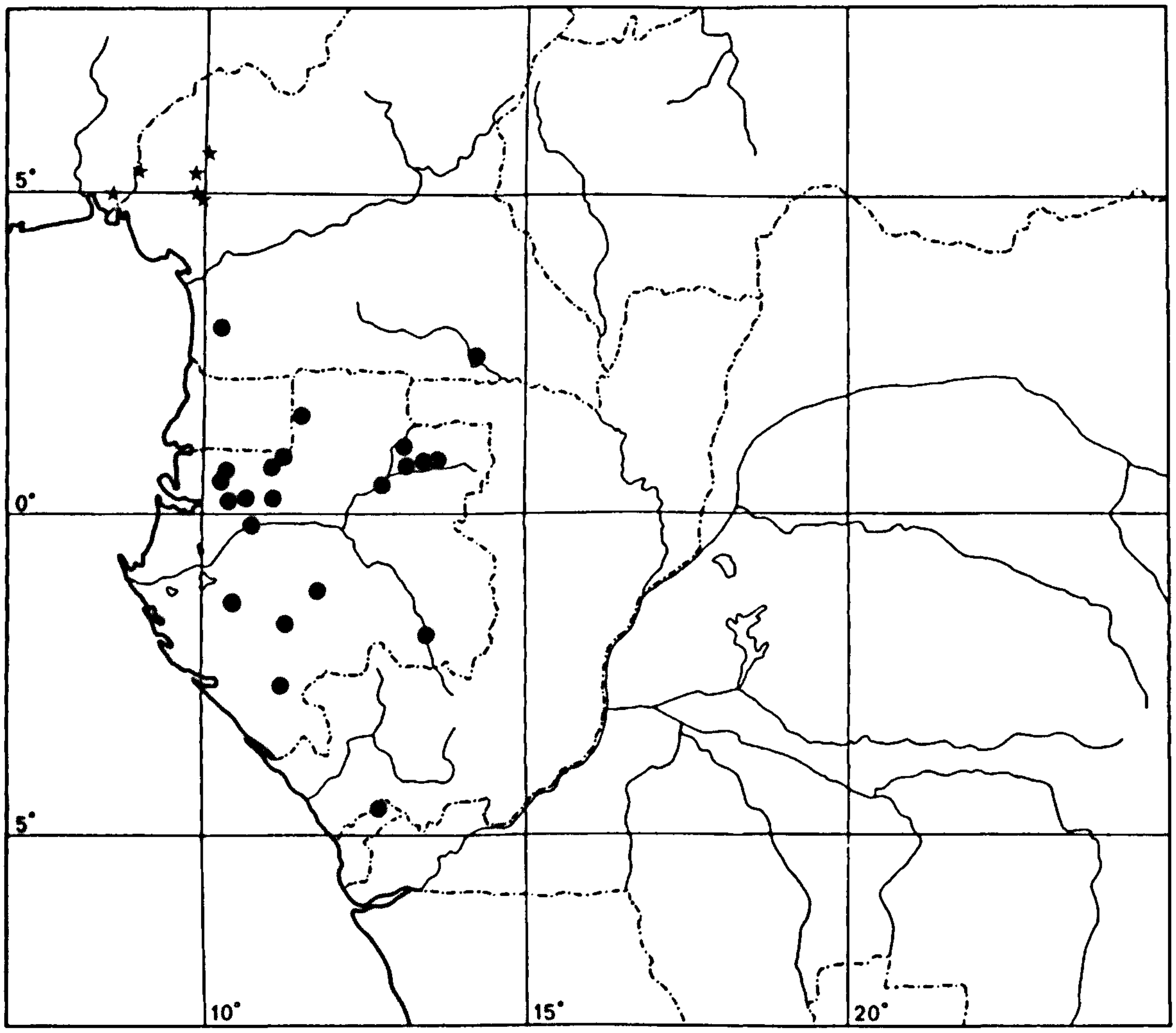
Notes: 1. The discovery of several additional specimens clearly showed that *B. ramosa*, which I recently described, has to be merged with *B. schaeferi*.

2. *B. schaeferi* represents the only species in the section with both male and bisexual inflorescences. Because of the scarcity of the material at hand it remains uncertain whether both types occur on the same plant or are found on different individuals. In the latter case the species would show androdioecy which is not common within the family. Therefore, it seems more likely that both types occur on the same plant, perhaps in different periods of the year.

Specimens examined:

NIGERIA: *Sharland 1829* (K): Obodu, c. 05°00'N 08°30'E (fl, fr, 04).

CAMEROON: *Daramola FHI 40536* (BR, P): Bamenda, footpath going up to Bamenda station through Abakpa just before the top, 05°23'N 08°56'E (fl, 03); *Ledermann 1741* (B): Markt Singwa, Bamboutos Mts, 05°44'N 10°04'E (fl, 12); *Ledermann 1761* (B): ibid. (fl, 12); *Ledermann 6047* (B): Station Mbo, Kongoa Mts, 05°20'N 09°50E' (fl, fr, 11); *Letouzey 14474* (P, WAG, YA): western slope of Mt Nlonako, 5 km SSE Nkongsamba, 04°55'N 09°57'E (fl, 03); *Satabié 163* (WAG, holo; BR, K, P, YA): Bamboutos Mts, 25 km W Mbouda, 05°40'N 10°00'E (fl, 11); *Schaefer 72* (B, holo; BR): Manenguba, 05°00'N 09°50'E (fl, 11).



Map 16.11. Distribution of *Begonia schaeferi* (stars) and *Begonia scutifolia* (dots).

Begonia scutifolia Hook.f. **Fig. 16.19, Pl. 4a, Map 16.11**

Begonia scutifolia Hook.f. in Oliver, Fl. Trop. Afr. 2 (1871) 572; Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3,2 (1921) 618; Exell et al., J. Bot. 67, Suppl. Polypet. (1929) 197; Gossweiler & Mendonça, Carta Fitogeogr. Angol. (1939) 59; Wilczek, Fl. Congo, Rwanda et Burundi (1969) 34; Fernandes in Exell et al., Consp. Fl. Angol. 4 (1970) 297; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39; L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 231, fig. 2.16; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 14, 21, pl. 8E,F, 16E,F. – TYPE: *Mann 1652* (K!, holo): 'W. Trop. Africa, Lat. 1° N, Epiphyte on rocks, Sierra del Cristal, July 1862.'

Begonia triflora Irmscher, Bot. Jahrb. Syst. 57 (1921) 245; Engl. in Engl. & Drude l.c. 617; Irmscher in Engl. & Prantl, Nat. Pflanzenfam. (ed. 2) 21 (1925) 574; N. Hallé, Adansonia, sér. 2, 7 (1967) 508, pl. 1.1-11; N. Hallé, Adansonia, sér. 2, 12 (1972) 369, pl. 6.4; Doorenbos, Begonian 47 (1980) 16; Reitsma, Meded. Landbouwhogeschool 83-9 (1984) 45, fig. 9C; van den Berg l.c. 38-39; L.B. Smith et al. l.c. 243, fig. 3.9.1-11 (the legends of fig. 3.9 and 3.10 are interchanged); Weinberg, Begonian 60 (1993) 94. – TYPE: *Chevalier 26908* (P!, holo; P!): 'Gabon, Ahiémé, sur le Haut-Komo, 9 octobre 1912.'

Begonia triflora Irmscher var. *caloskiadia* N. Hallé, Adansonia, ser. 2, 7 (1967) 509, pl. 1.12-14; L.B. Smith et al. l.c. 243, fig. 3.9.12-14 (the legends of fig. 3.9 and 3.10 are interchanged). – TYPE:

N. Hallé 3952 (P!, holo): 'Gabon, Bélinga, Mines de Fer, rochers du sommet Babiel, alt. 950 m, 18 juin 1966.'

Plant up to 10(–17) cm high, scattered with minute glandular hairs, sparsely so on pedicel of male flower and outside of perianth segments, sparsely to densely so on ovary. **Rhizome** rather compact and knotted to elongated and slender, 0.5–2.5(–3.5) mm wide, the younger part sometimes sparsely hirsute; the apical part not or slightly ascending. **Stipules** broadly triangular-ovate or broadly ovate to triangular, acuminate to acute, 0.9–2.5(–3.4) mm long, bronze-green to green, not hirsute; margin sinuate or entire, glabrous or ciliate. **Leaves** very variable, subpeltate to peltate, rarely not peltate; *petiole* continuing into the midrib with a right or sometimes with a distinct but slight angle, inserted at 0–6(–12) mm from the nearest margin, 0.5–15 cm long, juicy, purplish red to reddish bronze-green, almost glabrous to densely hirsute with short to long patent or more or less adpressed hairs; *leaf blade* in more or less horizontal to more or less vertical position, slightly to distinctly asymmetrical, non-peltate blades narrowly ovate, peltate ones broadly elliptic or broadly ovate to very narrowly elliptic or elliptic-ovate, the broader leaves usually distinctly acuminate in the upper 1/3 or 1/4, the narrower ones more gradually tapering towards the top, the acuteness often caused by a relatively sharp angle at about 2/3 of the broader half of the leave giving it a falcate appearance, 0.5–10.0(–12.0) x 0.4–5.5(–6.5) cm, juicy to slightly succulent, with (4–)5–9(–11) palmate main nerves; margin entire to remotely and irregularly dentate to sinuate (especially so in the upper part of the broader half of the leaf), very sparsely to rather densely shortly ciliate, usually reddish to brownish wine-red on both surfaces, sometimes concolorous with the blade; base cuneate in non-peltate leaves to rounded in peltate ones, top acute; upper surface medium to light green, glossy to dull, smooth; lower surface paler, dull; *nerves*: the main and larger secondary nerves not prominent and concolorous with the blade on the upper surface, on the lower not or slightly prominent, medium green or reddish, glabrous or sparsely hirsute and not or slightly prominent on the lower surface, smaller secondary nerves indistinct, tertiary nerves invisible. **Inflorescence** containing 1–3 male flowers and 1(–2) terminal female flower(s), usually positioned at about the same level or more or less hidden below the leaf blades; *peduncle* simple (once with a small side-branch at the base of a cultivated specimen), 2.0–7.5(–9.0) cm long, rather firm juicy, reddish to pale purplish red, almost glabrous to hirsute; *bracts* 2–4, obovate to elliptic, 0.7–1.7 mm long, bronze-green; the margin dentate or rarely entire, ciliate. **Male flower**: *pedicel* elongated at anthesis up to 15(–19) mm, whitish green, glabrous or sparsely hirsute; *perianth segments* circular to broadly ovate or broadly obovate, sometimes obovate, with a rounded to cuneate base, (4.4–)5.5–10.5(–13.0) x (4.4–)5.5–9.0(–10.5) mm, the margin or a part or the whole of the outside sparsely pilose with white or red hairs, sometimes without any long hairs; the upper segment yellow or reddish yellow on the outside, the inside yellow with a red patch and nerves in the basal half; the lower segment yellow; *androecium* with (7–)10–20 stamens; column 0.4–1.3 mm long; anthers

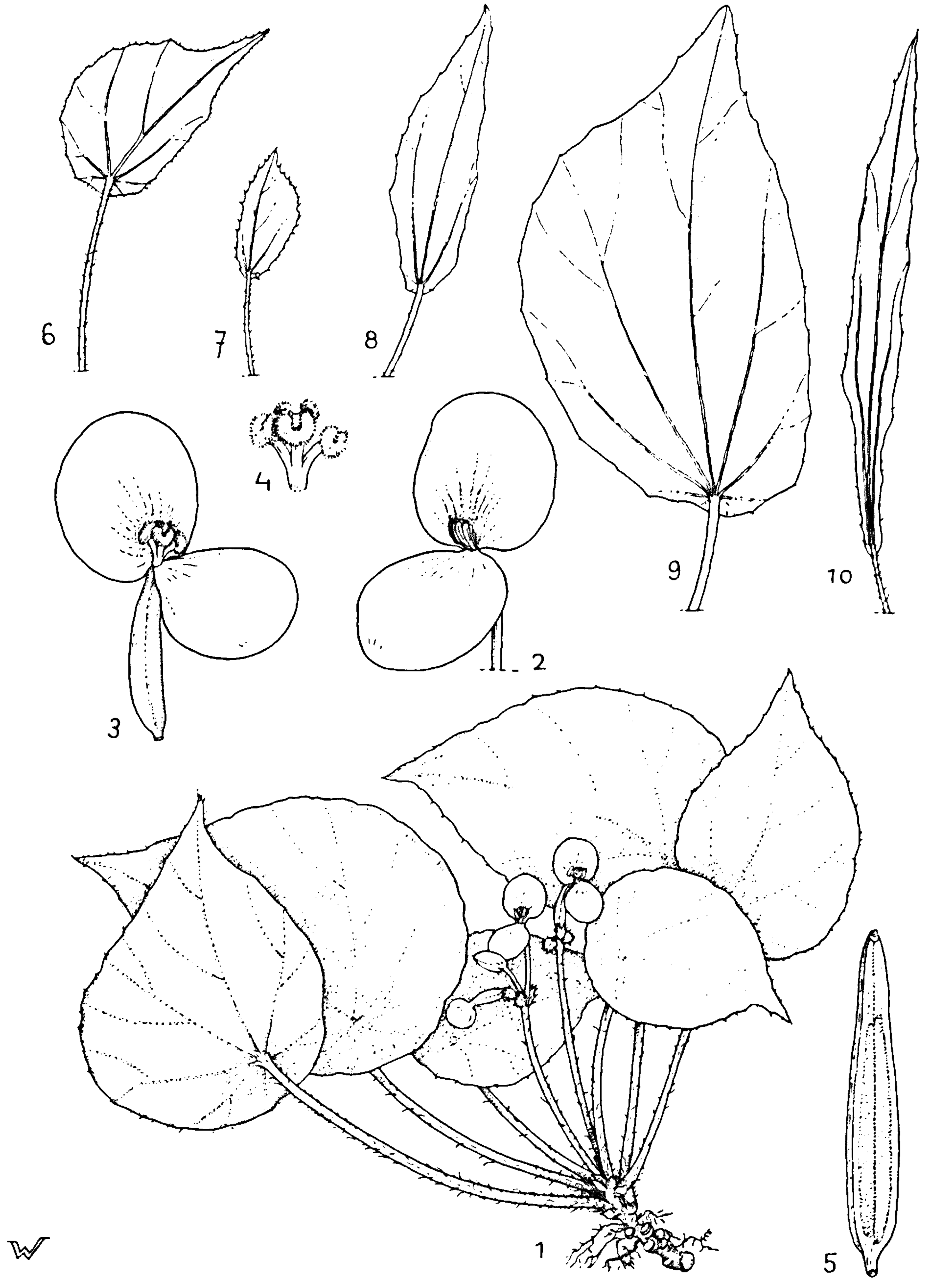


Figure 16.19. *Begonia scutifolia* Hook.f. – 1: habitus (x$^{2}/_{3}$); 2: male flower (x2); 3: female flower (x2); 4: styles (x4); 5: fruit (x2); 6-10: different leaf shapes. – 1: *N. Hallé 2841*; 2-7: *Breteler & J.J. de Wilde 583*; 8-9: *Letouzey 9379*; 10: *A. Louis 2141*.

0.9–2.0 mm long. **Female flower**: similar to the male but sessile, the pedicel elongated in fruit up to 2.0 mm; *perianth segments* transversely broadly elliptic to circular or broadly ovate, sometimes obovate, with a rounded to cuneate base, (4.4–)4.9–10.0(–15.0) x (4.0–)4.6–10.0(–12.5) mm; *styles* 3 or 4, 1.5–3.5 mm long, fused rarely only in the lowermost part, usually up to halfway, the top split into a compact U- or V-shape, the arms c. 0.25 mm long and covered with a non-twisted stigmatic band; *ovary* narrowly oblong to slightly narrowly elliptic-ovate, (4.5–)6.5–14.0(–19.0) x 0.7–2.7 mm, transparent, 3–4-locular, 3–4-angled or -winged all along; the locular part narrowly oblong to narrowly elliptic-ovate, 0.5–2.3 mm wide, reddish green or red to pinkish; beak present, 0.9–4.0(–5.2) mm long; wings 0.2–0.7 mm wide, pale green, rarely with a few hairs along the margin. **Infructescence**: peduncle not recurved towards the substrate; *fruit* narrowly oblong to narrowly elliptic-ovate, 6.0–15.0(–20.0) x 0.8–3.4 mm, dry, thin-walled, light brown to reddish, dull.

Distribution: Southern Cameroon, Gabon, Angola (Cabinda) and western Zaire.

Ecology: Terrestrial on banks of rivers and creeks or epiphytic on mossy tree trunks, on rocks or vertical rock faces, the rocks sometimes rich in iron; preferably in creek beds, near rapids and on other moist localities; in semi-shaded to shaded or sometimes deeply shaded sites in primary or old secondary forest or sometimes in recently logged forest; associated with *Selaginella* sp., ferns and *Araceae*; at 330–950 m altitude.

Uses: The leaves are eaten, cooked as spinach, often together with fish.

Vernacular names: Sanga-Batsema (Gabon, Bakota).

Notes: 1. The species shows an extreme variation in leafshape (see fig. 16.19). A large range of this variation is found in the specimens Letouzey 9379 and Breteler & de Wilde 583, the latter representing a population sample. From those collections it is obvious that the formerly distinguished *B. triflora* and its varieties should all be merged into a single taxon. Not only the shape of the leaf blade but also the density of the indumentum along the leaf margin and on the petioles as well as the length of the petiole is very variable. Four collections from Gabon are in cultivation at WAG. They represent four different morphological types, which might well be based on different genotypes as well.

Specimens examined:

CAMEROON: *Letouzey 9379* (P, YA): Ngwon hill, 38 km E of Kribi, 02°57'N 10°15'E (fl, fr, 04); *Letouzey 11970* (P, YA): 28 km ENE of d'Eta, at 52 km SE of Ngoila (Lomie-Souanke axis), 02°30'N 14°20'E (fl, 02).

GABON: *Arends c.s. 560* (WAG): about 43 km E of Mouila, along the road towards Yeno, 01°47'S 11°18'E (fl, 11); *Arends c.s. 567* (WAG): about 42 km E of Mouila, along the road towards Yeno, 01°47'S 11°18'E (fl, fr, 12); *Bos c.s. 10713* (WAG): Babiel-Sud, Okoume road km 1, 01°03'N 13°10'E (fr, 07); *Breteler & J.J. de Wilde 326* (WAG): Mt Méla, about 1.5 hours walking distance S of village Méla, 00°33'N 10°16'E (fl, 08); *Breteler & J.J. de Wilde 583* (WAG): Bélinga, iron mine exploration area, 01°06'N 13°12'E (fl, fr, 09); *Breteler & J.J. de Wilde 584* (WAG): ibid. (st, 09); *Chevalier 26908* (P, holo; B, P): Ahiémé, upper course of the Komo, 00°12'N 10°25'E (fr, 10); *Dorr & Barnett 4247* (LBV, MO): Ogooué-Ivindo Prov., Station I.R.E.T (M'Passa Field Station) 10 km S of Makokou along the Ivindo R., 00°28'N 12°52'E (fl, 05); *Duong s.n.* (P): Oyem, 01°34'N 11°31'E (fl, 11); *Florence 1715* (WAG): Mt Bengové (Boka-Boka), 15 km W of Mé'Kambo, 00°52'N

13°39'E (fl, 03); *N. Hallé 1326* (P): Masaha, 50 km NE of Makokou, 00°44'N 13°11'E (fl, 02); *N. Hallé 2292* (P): Abanga exploitation C.E.F.A., 00°14'N 10°37'E (fl, fr, 06); *N. Hallé 2775* (P): Bélinga, 01°06'N 13°12'E (fl, 10); *N. Hallé 2841* (P): Bélinga, Bakota Sanga, 01°04'N 13°12'E (fl, 10); *N. Hallé 3247* (P): Bélinga, 01°06'N 13°12'E (st, 11); *N. Hallé 3371* (P): ibid. (fl, 11); *N. Hallé 3943* (P): Bélinga, iron mines, 01°06'N 13°12'E (fl, 06); *N. Hallé 3952* (P, holo): Bélinga, iron mines, rocks on summit of Babiel, 01°07'N 13°10'E (fl, fr, 06); *N. Hallé 4114* (P): Bélinga, iron mines, 01°06'N 13°12'E (fl, 06); *N. Hallé & Villiers 5217* (P): Crystal Mts, E of Nkan, 00°39'N 10°21'E (fl, 02); *Le Testu 5276* (BM, P): between Ngoumbi and Ighouma, Itsogho land, c. 01°40'S 11°10'E (fl, 03); *Leroy 12* (P): Ogooué, Haut-Ogooué, c. 01°40'S 13°30'E (fl); *A. Louis 2141* (LBV, WAG): Woleu-Ntem Prov., Mengong, 00°56'N 11°17'E (fl, 05); *A. Louis 2806* (LBV, WAG): Ngounié Prov., top of Mt Iboundji track to Moughoungoulou falls ± 10 km, 01°10'S 11°49'E (fl, fr, 02); *A. Louis c.s. 2098* (LBV, WAG): Woleu-Ntem Prov., Oveng exploitation, 00°46'N 11°04'E (fl, fr, 05); *A. Louis c.s. 2395* (WAG): upstream Mebom, near Camp Bélinga, 01°06'N 13°12'E (fl, fr, 10); *Mann 1652* (K, holo; B, STU): Crystal Mts 1° N, c. 00°55'N 10°25'E (fl, fr, 07); *Reitsma c.s. 1504* (WAG): Rougier Océan exploitation, 40 km NW of Oveng, 00°46'N 11°06'E (fl, fr, 09); *Thollon 68* (P): Ogooué, Ndjolé, 00°11'S 10°45'E (fl, fr); *Wieringa 665* (WAG): Ogooué-Ivindo, 70 km ENE of Makokou, 4 km N of Batouala, 00°51'N 13°27'E (fl, 03); *Wieringa 666* (WAG): Ogooué-Ivindo, 70 km ENE of Makokou, 6 km N of Batouala, Mt Sassamonga, 00°52'N 13°27'E (fl, 03); *Wieringa c.s. 1390* (WAG): Ngounié, 5 km NNW of Bembodie, Koumounabwali Massif, 01°26'S 10°31'E (st, 08); *Wieringa c.s. 1448* (WAG): Ngounié, 22 km on the road from Lébamba to Yéno, 02°03'S 11°27'E (fl, 08); *Wieringa c.s. 1564* (WAG): Ogooué-Ivindo, ca 73 km ENE of Makokou, Mt Sassamongo, 00°52'N 13°27'E (fl, fr, 09); *J.J. de Wilde c.s. 10304* (WAG): 10 km on track N of Ebèl Alèmbé, bridge over the Mvoro R., 00°12'N 11°05'E (fl, 01).

ANGOLA: *Gossweiler 8225* (B, BM, COI, K, LISJC, LISU): Zanza R. – Lufo R. – Belize area – Mayombe (BM: M'Bulu Hills, source of NZanza R.), 04°35'S 12°43'E (fl, fr, 02).

ZAIRE: *Flamigni 94* (BR): Kangu Region, 05°15'S 12°57'E (fl, 11).

CULTIVATED: *van Veldhuizen 884* (WAG): Wageningen, Dept. of Horticulture (fl, 04); *van Veldhuizen 1234* (WAG): Wageningen, Bot. Garden 'De Dreijen' (coll. J.J. Bos. c.s. 10713) (fl, 10); *van Veldhuizen 1311* (WAG): Wageningen, Bot. Garden 'De Dreijen', cult. no 85PTGA197B (coll. Bos c.s. 10713, Gabon) (fl, 05); *van Veldhuizen 1316* (WAG): Wageningen, Bot. Garden 'De Dreijen', cult. no 85PTGA437 (coll. J. Reitsma 1504, Gabon) (fl, 05).

Begonia staudtii Gilg — **Fig. 16.20, Pl. 3c & d, Map 16.12**

Begonia staudtii Gilg, Bot. Jahrb. Syst. 34 (1904) 90; Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3,2 (1921) 617; Mildbraed, Wiss. Erg. Zweiten Deutschen Zentr. Afr. Exp. 2, Bot. (1922) 89, 98; Irmscher in Engl. & Prantl, Nat. Pflanzenfam. (ed. 2) 21 (1925) 574; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39, pl. 3.9; L.B. Smith et al., Begoniaceae..., Smiths. Contr. Bot. 60 (1986) 236, fig. 2.8; Cuerrier et al., Bull. Mus. natn. Hist. nat., Paris, 4e sér., 12, sect. B, Adansonia (1991) 323 ff, fig. 4F; idem 339 ff; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 19, pl. 14D. – TYPE: *Staudt 51* (B!, holo): 'Lolodorf, an Felswänden sehr häufig, 450-700 m. Humus, Holz, schattig feucht, 10/II 95.'

Begonia staudtii Gilg. var. *dispersipilosa* Irmscher, Bot. Jahrb. Syst. 76 (1954) 214; Hutch., Dalz. & Keay, Fl. W. Trop. Afr. (ed. 2) 1,1 (1954) 218; Legro & Doorenbos, Neth. J. Agric. Sci. 17 (1969) 193; Doorenbos, Begonian 47 (1980) 14; M. & E. Thompson, Begonias, Compl. Ref. Guide (1981) pl. 22; Reitsma, Meded. Landbouwhogeschool Wageningen 83-9 (1984) 45, 47; L.B. Smith et al. l.c. 236. – TYPE: *Keay FHI 28279* (K!, holo; COI! (photo)): 'Prov. Ogoja, Distr. Ikom, British Obokum. On vertical face of wet rock underneath the waterfall, 17.12.50.'

Plant up to 20(–30) cm high, scattered with minute glandular hairs, sparsely so on rhizome, stipules, peduncle, bracts and pedicel of male flower. **Rhizome** rather stout, smooth to somewhat knotted, 2.0–8.5 mm wide, glabrous but especially the younger parts and around the leaf axils hirsute; the apical part not

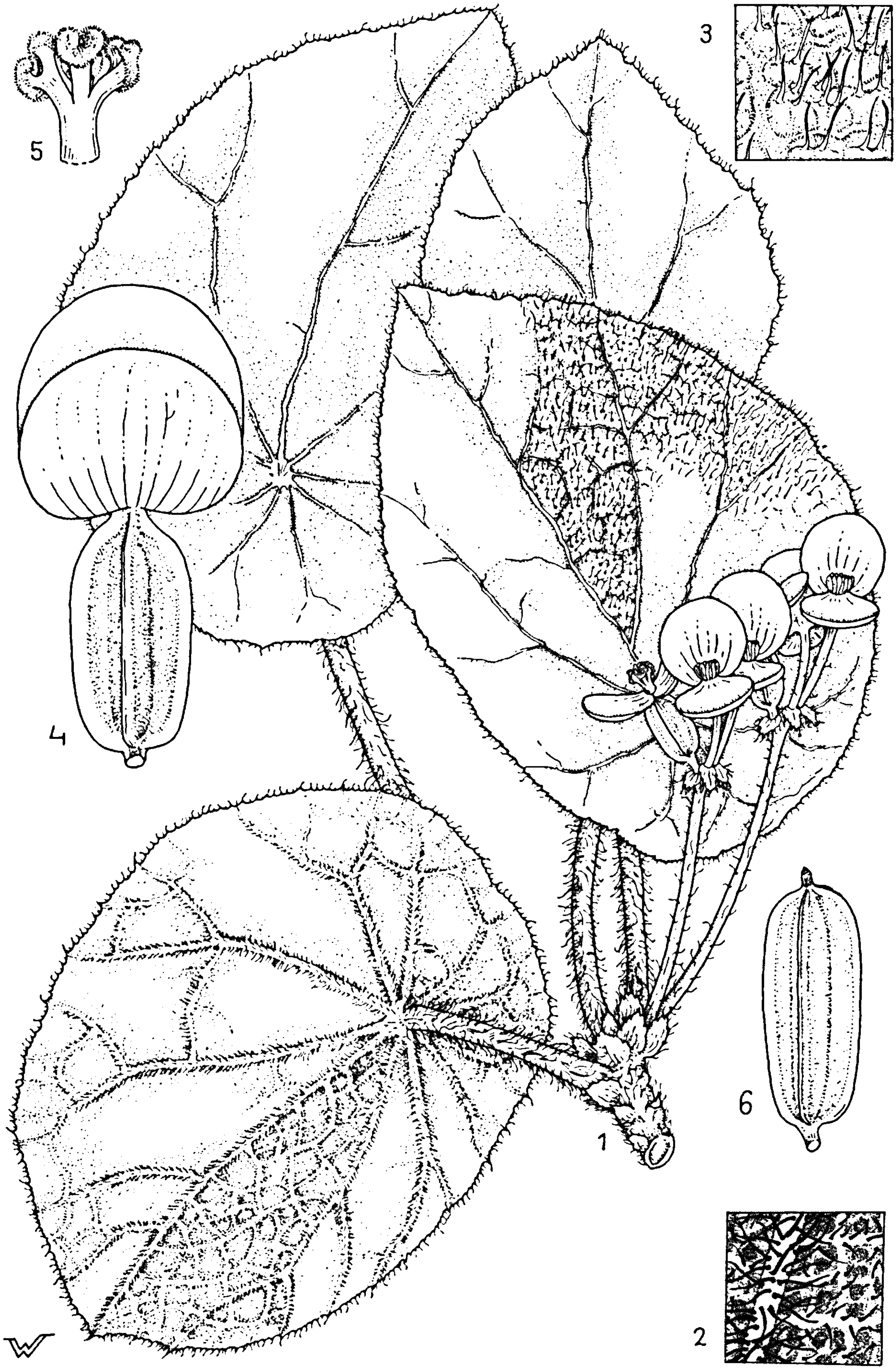


Figure 16.20. *Begonia staudtii* Gilg. – 1: habitus (x$^2/_3$); 2: detail lower leaf surface (x3); 3: detail upper leaf surface (x3); 4: female flower (x2); 5: styles (x2); 6: fruit (x2). – 1-3: *J.J. de Wilde 7456*; 4, 5: living plant at WAG, voucher *van Veldhuizen 1315*; 6: *Swarbrick 2997*.

or slightly ascending. **Stipules** triangular-ovate to broadly so, not or slightly acuminate, (2.5–)3.0–9.0(–11.5) mm long, medium green, glabrous or the midrib hirsute on the back; margin entire, usually ciliate. **Leaves** peltate; *petiole* continuing into the midrib with a distinct angle, inserted at 11–40(–61) mm from the nearest margin, (2–)5–31 cm long, firm but juicy, light or bronze-green to dark red, densely hirsute with long, patent, wavy, white hairs when young, less dense to only sparsely so when old; *leaf blade* in a more or less horizontal position, often pressed to the ground with age, asymmetrical, sometimes only slightly so, broadly elliptic-ovate to almost circular, sometimes elliptic-ovate, usually slightly acuminate at the top, sometimes distinctly so, sometimes with a few coarse and shallow teeth in the upper part, 6.6–21.0(–26.5) x (3.5–)5.0–13.0 (–16.0) cm, rather firm but fairly fleshy, with (7–)8–10(–11) palmate main nerves; margin usually denticulate, sometimes more or less entire, concolorous with the blade, usually densely ciliate; base rounded, top acute, rarely blunt; upper surface usually grass-green or rather pale green, sometimes darker green to brown-green, dull, usually densely bullate with small bullae in compound groups of 3–4, each bulla crowned with a stiff erect white hair, the centre of the blade usually with a tuft of hairs; lower surface pale green, sometimes purplish tinged to pinkish, dull; *nerves*: the main and larger secondary nerves concolorous with the blade and usually sunken on the upper surface, on the lower surface prominent, medium green and hirsute to densely so with patent white hairs, the smaller secondary nerves prominent, variably hirsute, tertiary nerves usually distinct and sparsely hirsute. **Inflorescence** containing (1–)2–4(–5) male flowers and 1(–2) terminal female flower(s), positioned at approximately the same level as or exerted above the leaf blades; *peduncle* simple, 2.5–13.5(–23.0) cm long, firm but juicy, pale or creamy green, almost glabrous to sparsely hirsute with white hairs; *bracts* (2–)3–5(–7), very broadly obovate or almost circular to obovate or elliptic-obovate, (1.4–)2.3–6.5(–7.3) mm long, pale green to reddish, not hirsute; margin dentate, ciliate. **Male flower**: *pedicel* elongated in flower up to 22(–36) mm, yellowish green to reddish tinged; *perianth segments* very broadly or even slightly depressed ovate to broadly ovate or circular to transversely broadly elliptic, with a rounded to slightly cordate base, (7.9–)10.0–17.0 x (8.1–)12.0–19.0 mm, the outside not hirsute, bright yellow with paler nerves on the inside, the upper segment orange-red to orange-yellow on the outside, the lower yellow on the outside; *androecium* with (12–)17–29 stamens; column 0.4–1.7 mm long; anthers (1.0–)1.4–2.3(–2.6) mm long. **Female flower**: similar to the male but almost sessile to distinctly pedicellate, the pedicel slightly to distinctly elongated in fruit up to 7.0 mm; *perianth segments* circular to transversely broadly elliptic or very broadly ovate to depressed ovate, with a cordate base, 7.8–17.0 x 10.5–22.0 mm; *styles* 4, (2.3–)3.1–5.2 mm long, fused in the lower 1/5 to 1/2, the top split into a rounded and often compact U-shape, the arms 0.5–1.7 mm long and covered with a slender to rather broad, non-twisted stigmatic band; *ovary* narrowly oblong-obovate to narrowly oblong-ovate, (5.6–)8.0–16.0(–21.0) x (2.0–)2.5–8.5(–10.0) mm, pale to medium green, translucent, 4-locular, 4-winged all along; beak absent or present, 0–2.0(–2.7) mm long;

the locular part narrowly oblong, (1.4–)1.8–5.5(–6.5) mm wide; wings patent, narrowly elliptic, 0.25–1.7 mm wide, pale greenish, the margin glabrous. **Infructescence**: peduncle not recurved towards the substrate; *fruit* more or less erect, narrowly oblong to narrowly oblong-obovate or elliptic to obovate, (8.8–)12.0–22.0 x 2.7–7.0(–11.0) mm, dry, with a thin wall, pale to dark green or brown, dull.

Distribution: South-eastern Nigeria and western Cameroon.

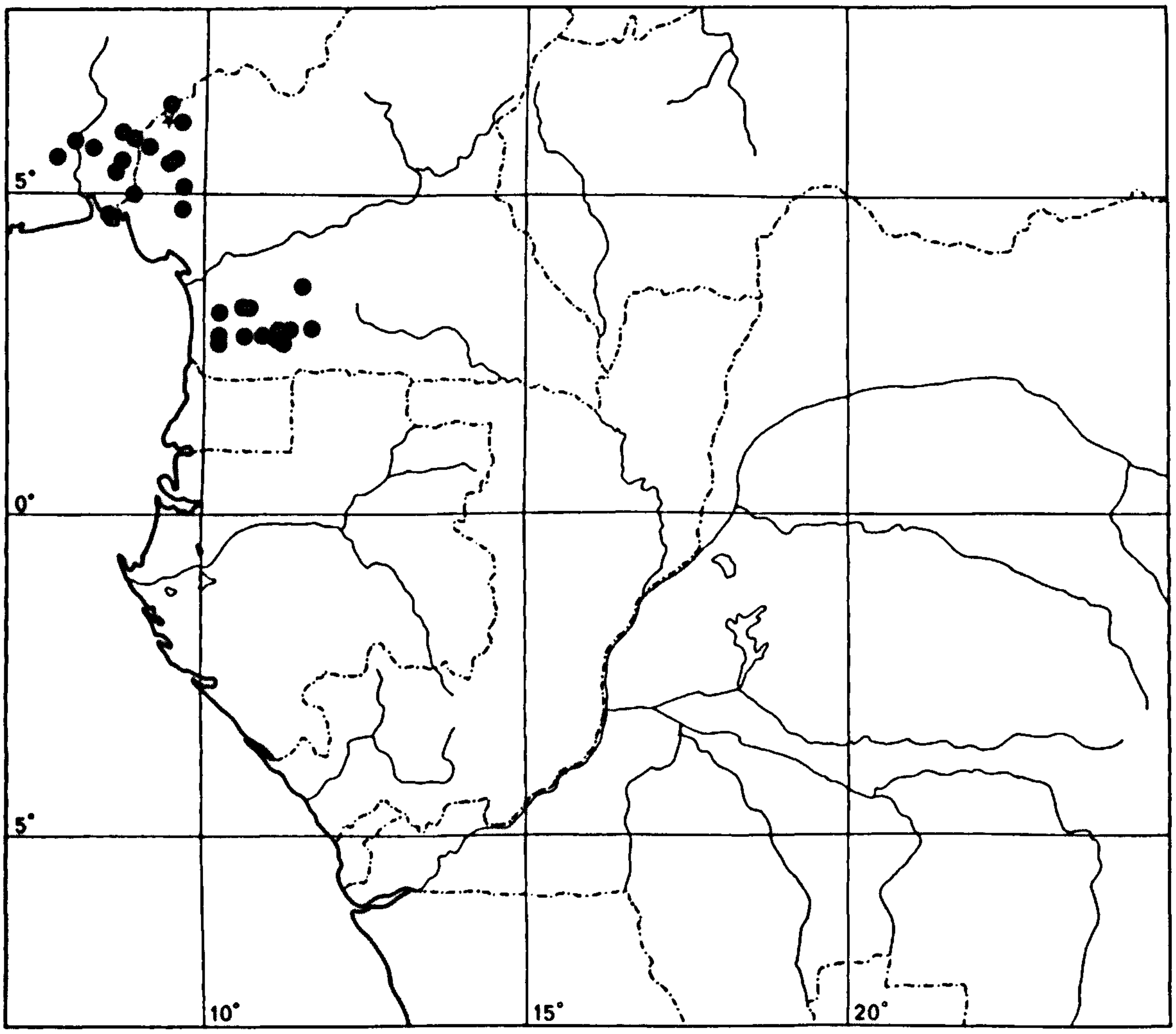
Ecology: Terrestrial on moist sandy soil or epiphytic on low branches or decaying tree trunks, also on mossy rocks or rock faces; in semi-shaded to deeply shaded sites in often primary but sometimes secondary forest; often near rivers, in streambeds, near waterfalls or on moist rocks; in hygrophilous coastal evergreen Guineo-Congolian rain forest (forêt biafréenne) and riparian forest; at 50–800 m altitude.

Chromosome number: 2n = 34 (Legro & Doorenbos l.c.).

Specimens examined:

NIGERIA: *Ariwaodo (FHI 88635) 140* (MO, WAG): Cross R. State, Obubra Distr., Agoi-Ibami, 05°43′N 08°11′E (fl, 01); *Carpenter 50 A* (K): Bende, 05°34′N 07°38′E (fl, fr, 04); *Jones & Onochie FHI 19502* (K, P): British Olokum, Ikom, Ogoja, 05°58′N 08°42′E (st, 05); *Keay FHI 28279* (K, holo; B, P): ibid. (fl, 12); *Latilo & Oguntayo FHI 67697* (FHI, K, WAG): South-E. State, Ikom Distr., Agbokun village, c. 06°00′N 08°40′E (fl, 02); *van Meer (FHI 33967) 1407* (FHI, WAG): Oban Group Forest Reserve, East Block, 05°31′N 08°41′E (fl, fr, 04); *Stone, R.H. 15* (K): E. Nigeria, Ogoja Prov., Ebom (Cross R.), 05°51′N 07°58′E (fl, fr, 06); *Swarbrick 2734* (E): British Olokum, Ikom, 05°58′N 08°42′E (fl, 06); *Swarbrick 2997* (E): larger waterfall Olokum, Ikom, 05°58′N 08°42′E (fl, fr, 01); *P.A. Talbot & D.A. Talbot s.n.* (K): Oban Distr., c. 05°20′N 08°35′E (fl).

CAMEROON: *Annet 311* (P): Lolodorf, Mt Findé, 03°14′N 10°43′E (fl, 06); *Annet 328* (P): ibid. (st, 06); *Bamps 1741* (BR, YA): Lolodorf, 03°14′N 10°43′E (fl, 01); *Coombe 201* (B, K): mile 43 from Mamfe on the Bamenda road, 05°25′N 09°25′E (fl, 03); *De Namur 2225* (YA): hill next to Ngovayang II village (near Lolodorf), 03°15′N 10°37′E (fl, fr, 02); *Guile 318* (MO): Mamfe, Cross R., 04°42′N 08°21′E (fl, 03); *Guile 319* (IFE): ibid. (fl, 03); *Huber 980* (YA): Ntem Dept., rocks of Ako'okas, 26 km SE of Ebolowa, 02°42′N 11°17′E (fl, 02); *Jacques-Félix 9168* (P, YA): Lolodorf, Mt Minn, 03°16′N 10°45′E (fl, fr, 11); *Leeuwenberg 9289* (BR, WAG, YA): W side of Mt Kupé, near Mbule, 04°47′N 09°41′E (fl, 01); *Letouzey 543* (P, YA): Siboumane near Ebemvok, border of Ebolowa-Kribi, 02°48′N 10°40′E (fl, 01); *Letouzey 9018* (P, YA): 15 km SSE of Zingui, at 50 km SE of Kribi, 02°39′N 10°14′E (fl, 03); *Letouzey 9368* (P, YA): Ngwon hill, 38 km E of Kribi, 02°47′N 10°15′E (st, 04); *Letouzey 9862* (P, YA): hill near Emnivemvom, 20 km SE of Ebolowa, 02°58′N 11°47′E (fl, fr, 01); *Letouzey 10256* (P, YA): Zingui hill, 20 km WSW of Ebolowa, 02°49′N 10°58′E (fl, 04); *Letouzey 12737* (P, YA), identification doubtful: Nkol Tsia ridge, 18 km NW of Bipindi near Gouap, 03°11′N 10°16′E (fl, 01); *Letouzey 12775* (K, P, YA): Akom Pinda, 10 km ENE of Lolodorf, 03°15′N 10°48′E (fl, 01); *Letouzey 13737* (WAG, YA): falls (10m) of the Akoumayip R. at track Agborkem to Tabo, 20 km W of Mamfe, 05°44′N 09°07′E (fl, 06); *Meijer 15304* (WAG): Ako'okas rocks, 24 km SE of Ebolowa, 02°42′N 11°17′E (fl, 03); *Mildbraed 5624* (B, HBG): South Cameroon forest area, Ebolowa Prov., Ebolowa, 02°54′N 11°09′E (fl, fr, 06); *Mildbraed 5738* (B): South Cameroon forest area, Ebolowa Prov., Ekuk 22 km E of Ebolowa, 02°55′N 11°20′E (fl, fr, 06); *J. Raynal & A. Raynal 9728* (P, YA): Ako'okas, 27 km SE of Ebolowa, 02°42′N 11°17′E (fl, fr, 02); *J. Raynal & A. Raynal 10034* (P, YA): Nkoemvone, 12 km S of Ebolowa, Cacao station, right of the Seing, 02°48′N 11°09′E (fl, fr, 02); *J. Raynal & A. Raynal 10348* (P, YA): Ebolowa-Si I, ridge above Ebolowa at the W, 02°54′N 11°08′E (fl, fr, 03); *Satabié & Letouzey 338* (P, WAG, YA): Ngovayang Massif, 12 km W of Lolodorf, 03°15′N 10°36′E (fl, fr, 01); *Staudt 51* (B, holo): Lolodorf, 03°14′N 10°44′E (fl, 02); *Thomas 3408B* (P, WAG): Centre-Sud Prov., Ngovayang Mt, above Bibondi village, near Lolodorf, 03°18′N 10°39′E (fl, fr, 04); *Thomas 4134* (YA): Korup National Park, 05°01′N 08°50′E (st, 12); *Thomas 4576* (MO, YA): ibid. (fl, 03); *Thomas 6958* (WAG):



Map 16.12. Distribution of *Begonia staudtii* (dots) and *Begonia stellata* (star).

South-West Prov., footpath from Mbilishe to Matene, between 2 and 4 miles W of Mbilishe, 06°13′N 09°27′E (fl, fr, 05); *Thomas c.s. 5331* (WAG), identification doubtful: South-West Prov., Bakossi Mts, W of Bangem, 05°05′N 09°42′E (fl, 01); *Villiers 1437* (WAG, YA): Ntali Massif, NW slope, 30 km SE of Mamfe, 05°31′N 09°30′E (fr, 06); *J.J. de Wilde 7456* (WAG, YA): 18 km on the road from Ebolowa to Ambam and then about 1 hour walking distance to the hills left of the road, 02°47′N 11°08′E (fl, 08); *J.J. de Wilde 7909A* (WAG): hill facing N'Kolandom, 02°48′N 11°10′E (fl, 01); *W.J. de Wilde & de Wilde-Duyfjes 1953* (B, BR, K, MO, P, WAG, YA, Z): Ebolowa, SSW of M'Balmayo, 03°30′N 11°29′E (fl, fr, 02).

CULTIVATED: *Bos 1632* (WAG): Wageningen. (ex W.J.J.O. de Wilde s.n., Ebolowa-Cameroon, 16-11-1964) (fl, fr, 05); *van Veldhuizen 445* (WAG): Wageningen Agric. Univ., Dept. of Horticult. (coll. Ebolowa, S.W. Cameroon, Dept. of Plant Taxonomy, Wageningen) (fl, 03); *van Veldhuizen 1315* (WAG): Wageningen, Bot. Garden 'De Dreijen', cult. no 64PT00400 (coll. J.J. de Wilde s.n.) (fl, 05); *J.J. de Wilde 7393* (WAG): Wageningen, Dept. of Horticulture (fl, 03).

Begonia stellata Sosef **Fig. 16.21, Map 16.12**

Begonia stellata Sosef, Wageningen Agric. Univ. Papers 91-4 (1992) 143, fig. 8. – TYPE: *Thomas, Fay & Doumenge 7437* (WAG!, holo; MO): 'Cameroon, Prov. South-West, forested ridges above Mbilishe Village, canopy low (5-10 m), some trees to 30 m, numerous small trees, sparse undergrowth, lots of epiphytes. 06°13′N 09°28′E, 1000-1200 m, 7 May 1987.'

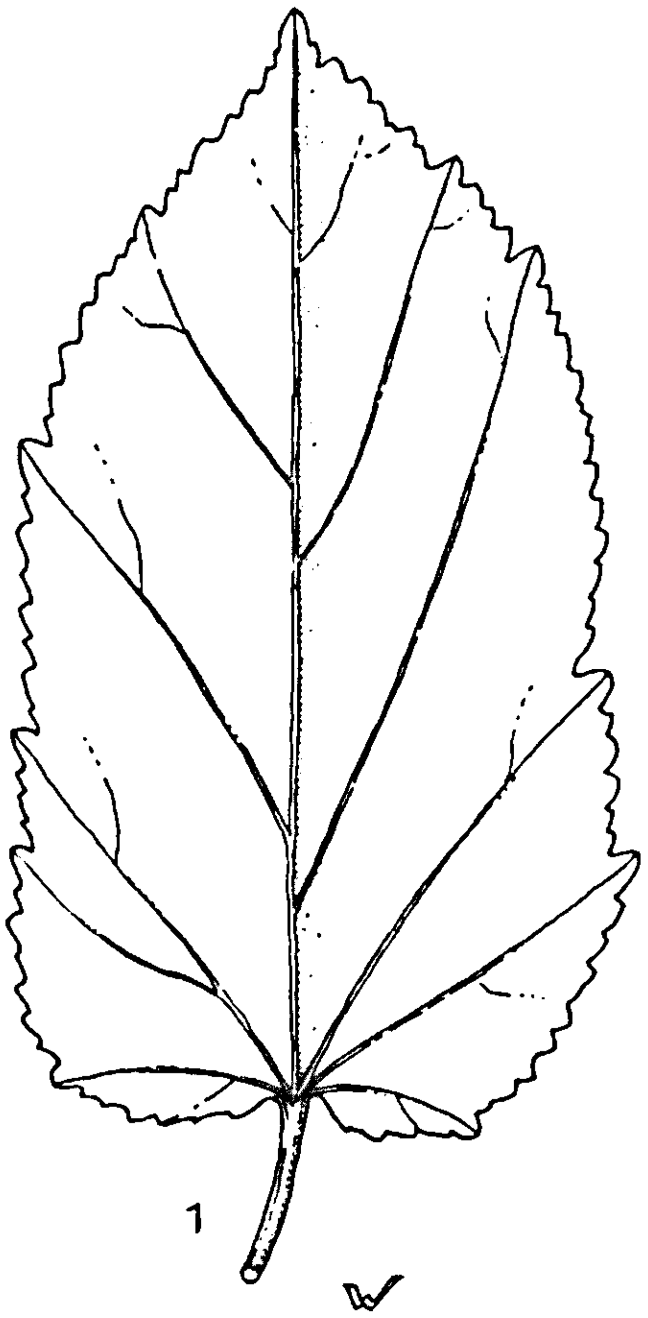


Figure 16.21. Leaf blade of *Begonia stellata* Sosef (x$^2/_3$) (reconstructed from the only mature but damaged leaf available): *Thomas, Fay & Doumenge 7437.*

Diagnostic characters (for a more detailed description see Sosef l.c.):

Plant up to 9 cm high, sparsely scattered with stellate scales on petiole, lower leaf surface, bracts and outside of perianth segments. **Leaves** not peltate; *petiole* 1.5–3.0 cm long; *leaf blade* symmetrical, ovate, rounded to slightly acuminate at the top, 4.0–10.5 x 2.7–6.1 cm; margin distinctly irregularly dentate or slightly serrate, the teeth rounded to very broadly triangular and acute, glabrous, some teeth slightly elongated. **Male flower**: *perianth segments* broadly elliptic to broadly elliptic-ovate, rounded to cordate at base, 3.9–6.6 x 3.3–4.0 mm, pink; *androecium* with 7 stamens.

Distribution: CAMEROON: South-West Prov.

Ecology: See citation of type specimen.

Notes: Only known from the type specimen.

17 Descriptions of the species of section *Scutobegonia*

The description of the shape of the ovary and fruit refers to the outline in side view.

Begonia aggeloptera N. Hallé **Fig. 17.1, Pl. 1a & b, Map 17.1**

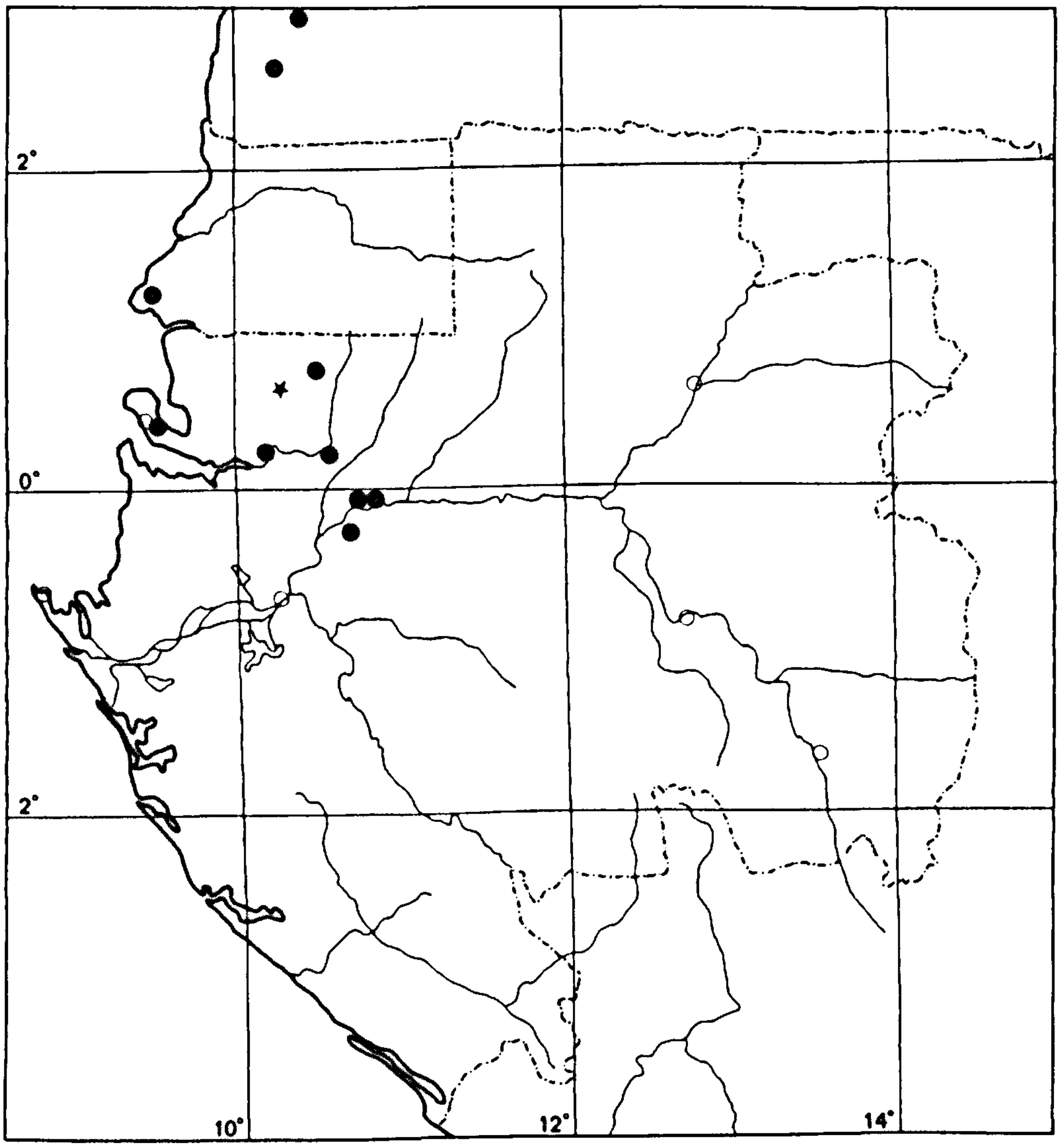
Begonia aggeloptera N. Hallé, Adansonia, sér. 2, 12 (1972) 371, pl. 8; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1983) 38-39; L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 136, fig. 14.54; Arends, Wageningen Agric. Univ. Papers 91-6 (1992) 177; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 21, pl. 15E. – TYPE: *N. Hallé & Villiers 4817* (P!, holo; P!): 'Gabon, Monts de Cristal, Nkan, commun dans la fôret près de Nkam, 31 jan. 1968.'

Plant up to 12 cm high, scattered with minute glandular hairs, sparsely so on pedicel of male flower and outside of perianth segments, densely so on petiole. **Rhizome** rather slender and elongated, rather smooth, 0.9–2.1 mm wide, almost glabrous; the apical part directed upwards to form a short stem of up to 5 cm. **Stipules** narrowly to very broadly triangular or triangular-ovate, acute, 1.8–4.9 mm long, medium green; margin dentate, ciliate. **Leaves** not peltate; *petiole* continuing into the midrib without a distinct angle, 1.0–3.5 cm long, slender but rather firm, dark wine-red when young, sparsely hirsute to hirsute with long, patent, wavy, white or red-based hairs; *leaf blade* in a more or less horizontal position, asymmetrical, usually narrowly and slightly falcately ovate, gradually attenuate towards the top or slightly acuminate in the upper 1/3, 3.2–6.8 x 1.1–2.6 cm, slightly succulent, with 5–8 palmate main nerves but the midrib usually most pronounced; margin coarsely crenate-serrate, sometimes serrate, red, often prominently so on the lower surface, sparsely ciliate, often with two cilia together in between the teeth; base usually very unequal, one side cuneate to rounded or slightly cordate, the other cordate, the sides not overlapping, top acute; upper surface medium green, dull, smooth; lower surface pale green, dull; *nerves*: the main and larger secondary nerves not prominent and concolorous with the blade on the upper surface, on the lower prominent, medium green and without or sometimes with a few scattered long, patent white hairs, the smaller secondary nerves distinct, the tertiary ones less so but usually well visible and creating a typical reticulate pattern in dry condition. **Inflorescence** containing 2(–3) male flowers and 1 terminal female flower, positioned at about the same level as the leaf blades; *peduncle* simple, 0.7–2.0 cm long, slender but rather fleshy, pinkish red, sparsely hirsute with white or red-based hairs; *bracts* 3–4, ovate to narrowly so, 1.3–4.2 mm long, green; margin dentate, ciliate. **Male flower**: *pedicel* elongated at anthesis up to 14 mm, pale yellowish green, sparsely

Figure 17.1. *Begonia aggeloptera* N. Hallé. – 1: habitus (x1); 2: stipule of 5 mm; 3: detail of petiole; 4: bract of 3 mm; 5: androecium of 3 mm; 6: styles of 4 mm; 7: ripe fruit of 10 mm wide; 8: seed of 0.3 mm. – 1-8: *N. Hallé 4817*. Drawing prepared by Nicolas Hallé, formerly associated with the Musée National d'Histoire Naturelle, Paris.

hirsute; *perianth segments* broadly ovate to almost circular, with a rounded base, 5.2–11.5 x 5.2–12.0 mm, the outside pale yellow, not hirsute; the upper segment yellow with a red patch in the lower half on the inside; the lower segment yellow on the inside; *androecium* with 15–19 stamens; column 0.5–0.9 mm long; anthers 1.0–1.6 mm long. **Female flower**: similar to the male but its pedicel elongated in fruit up to 3.9 mm; *perianth segments* broadly to very broadly ovate, with a rounded to cordate base, 5.9–11.5 x 6.5–11.5 mm; *styles* 3, 2.2–3.9 mm long, fused in the lower 1/3, the top horseshoe-shaped and slender or sometimes rather compact, the arms 1.0–1.7 mm long and bearing a slender stigmatic band which is spirally twisted for 1 turn; *ovary* very broadly to shallowly obtriangular, attenuate at base, 3.4–6.8 x 6.4–11.0 mm, 3-locular, 3-winged at the apical 2/3, light to medium green; beak present, 1.0–2.9 mm long; the locular part obovate to broadly obtriangular-obovate, 1.2–5.9 mm wide; wings patent to erecto-patent and curved upwards, slightly enlarged in fruit, very shallowly to broadly obtriangular, rather fleshy, 1.4–5.1 mm wide, the margin glabrous. **Infructescence**: peduncle recurved towards the substrate; *fruit* pendulous, very broadly to shallowly obtriangular, 4.0–6.9 x 7.8–11.0 mm; the locular part elliptic-obovate to broadly obovate-obtriangular, 2.9–5.1 mm wide, dry, with a relatively thin wall, greenish brown, dull.

Distribution: GABON: Crystal Mountains.



Map 17.1. Distribution of *Begonia aggeloptera* (star) and *Begonia anisosepala* (dots).

Ecology: Terrestrial, locally very common along an old exploitation track, in old secondary forest vegetation with much *Aframomum*, often on somewhat higher and dryer sites; at 300–600 m altitude.

Notes: A rare but distinct species, only known from the type locality.

Specimens examined:

GABON: *Breteler & J.J. de Wilde 359* (WAG): Crystal Mts, Nkan, about 8 km along the road from Asok to Méla, c. 1 km W of Nkan, 00°39'N 10°18'E (fl, 08); *N. Hallé & Villiers 4817* (P, holo; P): Crystal Mts, Nkan, 00°40'N 10°19'E (fl, fr, 01); *J.J. de Wilde c.s. 10147* (WAG): Crystal Mts, along the road Assok-Méla, NNW of Nkan, 00°40'N 10°19'E (fl, fr, 01).

Begonia anisosepala Hook.f. **Fig. 17.2, Map 17.1**

Begonia anisosepala Hook.f. in Oliver, Fl. Trop. Afr. 2 (1871) 576; Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3,2 (1921) 617; L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 139, fig. 2.14; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 17, 21, pl. 12F, 16D. – LECTOTYPE: *Mann 1871* (K!): 'W. Trop Africa, Lat. 1° N, Mount John River Kongui, sept. '62.'

Begonia calophylla Gilg ex Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3,2 (1921) 617; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39; L.B. Smith et al. l.c. 148. – TYPE: *Zenker 3141* (BR!, holo; B!, BM!, E!, G!, HBG!, K!, L!, LY!, MO!, P!, W!, WAG!, Z!): 'Bipinde, Urwaldgebiet, 1904'.

Plant 3–10 cm high, scattered with minute glandular hairs, densely so on ovary. **Rhizome** rather stout, usually elongated, sometimes more compact, 1.3–4.0 mm wide, the apical parts hirsute or sparsely so; the top of the foliated part slightly ascending to shortly erect. **Stipules** triangular to broadly triangular-ovate, acute, 1.4–5.5 mm long, light green to pale wine red; margin dentate, ciliate. **Leaves** peltate; *petiole* continuing into the midrib with a distinct angle, inserted at 4–16 mm from the nearest margin, 1.0-9.0 cm long, firm, fleshy, wine-red when young, becoming brown-green with age, hirsute to sparsely so with long, wavy, red hairs which turn white with age; *leaf blade* held in a more or less horizontal position, usually distinctly asymmetrical, broadly elliptic-ovate or broadly elliptic-obovate, sometimes elliptic or elliptic-ovate, often with a more or less straight margin on the narrower left or right hand side in which case the blade resembles half an ellips or is somewhat kidney-shaped, gradually tapering towards the apex or less often with a rounded apical part, (3.6–)4.5–15.0 x (2.3–)2.8–7.5 cm, crispy-leathery, with 8–10 palmate main nerves; margin usually crenate or crenate-dentate, sometimes only in the apical part of the blade, usually with one or two hairs in the sinuses and often one on the top as well, reddish in young leaves; base rounded, top blunt to acute, sometimes rounded; upper surface medium to very dark glaucous green, dull, smooth, with or without a few long red hairs; lower surface dark wine red, dull; *nerves*: the main and larger secondary nerves not prominent and concolorous with the blade on the upper surface, on the lower slightly prominent, green or reddish and sparsely hirsute or not, in sicco usually slightly contrasting with the interveinal part, the smaller secondary nerves usually indistinct, sometimes distinct, tertiary nerves usually barely visible. **Inflorescence** containing 2–5 male flowers and 1 terminal female flower, positioned distinctly below to almost at the same level as the leaf blades; *peduncle* simple, 1.0–4.5 cm long, fleshy, brown-red to reddish, sparsely hirsute with red hairs; *bracts* 3–6(–7), elliptic to almost circular, 2.1–3.6 mm long, reddish green; margin dentate, ciliate. **Male flower**: *pedicel* elongated at anthesis up to 11 mm, pale green, sparsely hirsute; *perianth segments* very broadly ovate to broadly elliptic-ovate, 6.8–12.0 x 5.6–11.0 mm, the outside entirely white or yellow to orange-red with red or purplish nerves, sparsely hirsute with red hairs; the upper segment white or yellow with a distinct red patch at the basal half on the inside, the lower segment white or yellow on the inside; *androecium* with 16–26 stamens; column 0.4–0.5 mm long; anthers 1.4–2.1 mm long. **Female flower**: similar to the male but shortly pedicellate, the pedicel elongated in fruit and 1.3–6.5 mm long; *perianth segments* 7.2–11.0 x 9.0–10.0 mm; *styles* 3–4, 1.6–5.3 mm long, fused in the lower 1/2 to 1/4; the top split and rather compact, horseshoe-shaped, the arms 0.5–1.0 mm long and bearing a slender, non-twisted stigmatic band; *ovary* shallowly obtriangular or shallowly obtriangular-obovate, 4.3–7.0 x 8.2–13.0 mm, pale green, 3–4-locular, 3–4-winged all along to only at the apical

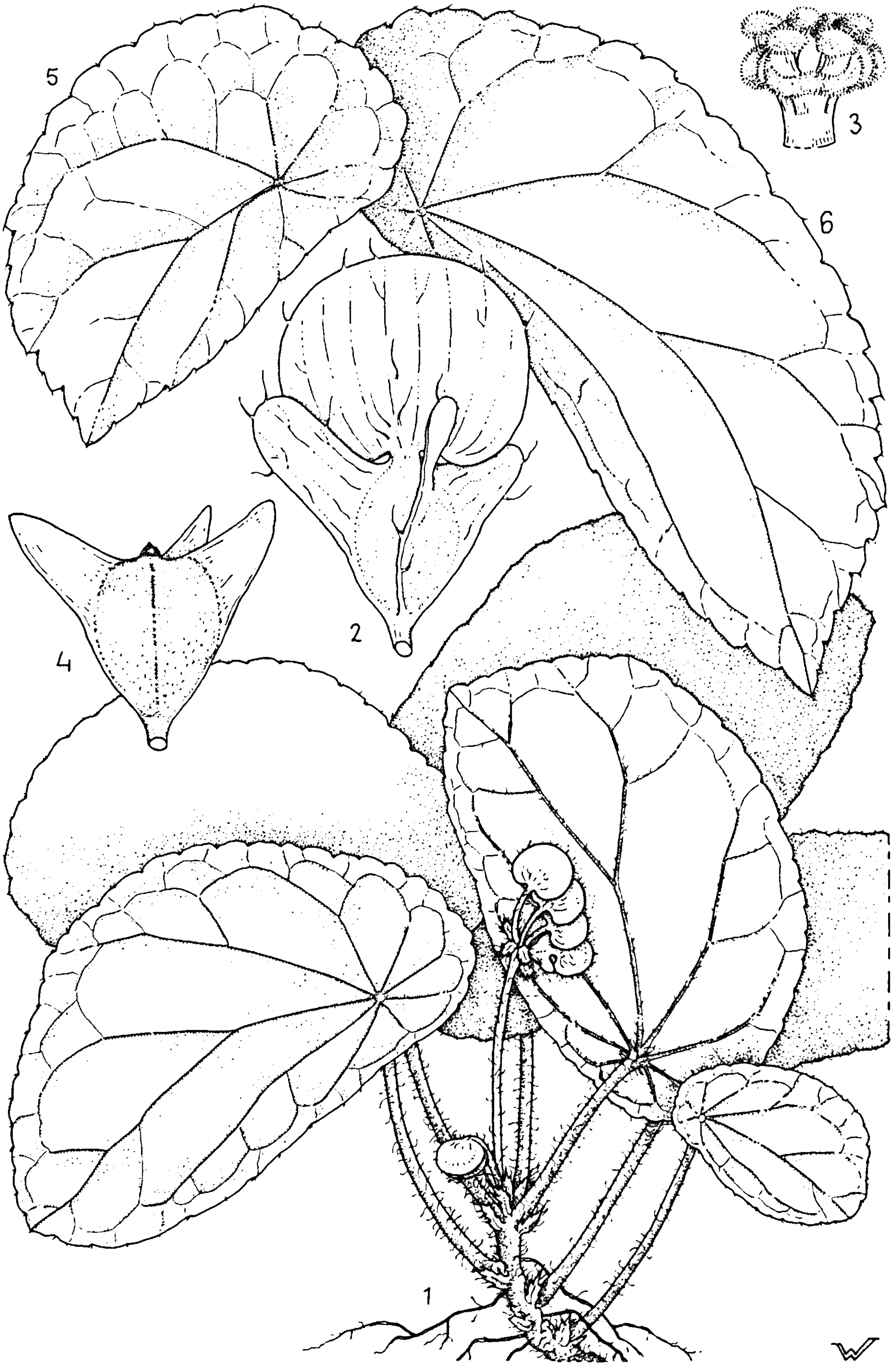


Figure 17.2. *Begonia anisosepala* Hook.f. – 1: habitus (x$^{2}/_{3}$); 2: female flower (x2); 3: styles (x4); 4: fruit (x2); 5, 6: leaf (x$^{2}/_{3}$). – 1: *J.J. de Wilde c.s. 10324*; 2-4: living plant at WAG, coll. *J.J. de Wilde c.s. 10278*; 4-5: *Breteler & de Wilde 181*; 6: *J.J. de Wilde c.s. 10278.*

1/3; the locular part broadly to very broadly obovate, 2.3–4.5 mm wide; beak present, 0.5–1.6 mm long; wings patent or slightly erecto-patent, very shallowly obtriangular to depressed obovate, 3.1–6.0 mm wide, sometimes with a few long hairs on the margin. **Infructescence**: peduncle recurved towards the substrate; *fruit* pendulous, shallowly obtriangular to shallowly obtriangular-obovate, 4.7–10.0 x 8.5–16.5 mm; the locular part broadly to very broadly obovate or ± circular, 3.4–8.8 mm wide, dry, with a fairly thick wall, brown, dull.

Distribution: Southern Cameroon, south-western Equatorial Guinea and north-western Gabon.

Ecology: Terrestrial on gentle to very steep slopes and banks, generally in the vicinity of streams, in shaded or deeply shaded sites in high primary or sometimes recently exploited forest, and in hydrophilous coastal evergreen Guineo-Congolian rain forest (forêt biafréenne); locally common; at 50–600 m altitude.

Notes: 1. Hooker f. cites collections of Mann from the 'Sierra del Cristal and at Mount John River Kangui [a misreading for Kongui] near the Gaboon'. At Kew two collections of Mann, both identified by Hooker as *B. anisosepala* are present. Mann 1871 was chosen as the lectotype because it is a more complete collection and its leaves have the rather characteristic shape. It is also the collection annotated with 'Mount John River Kongui', so confusion with the many other Mann collections from the 'Sierra del Cristal' is avoided.

2. I was informed by N. Hepper (Kew) that in Manns correspondence 'Kongui River' is said to be a branch of 'R. Muni'. Thus, it is believed to be identical with the Congué River, on the north side of the Muni estuary. Mount John is probably located on the inland part north-east of Cape St. Jean (= Cap San Juan).

3. *B. calophylla* Gilg is typified by Zenker 3141. The sheet in Bruxelles bears an identification label from Gilg with 'B. calophylla Gilg' written on it. This Zenker specimen fits the description as well as the collecting locality given by Engler. Nowhere else this name was found actually written by Gilg himself.

4. Hallé & Villiers 4407 seems intermediate between *B. anisosepala* and *B. clypeifolia*, and might represent a hybrid. The shape of the leaves and the crenate leaf margin are characteristics of the first species. The red nerves, distinct tertiary nervation, longer petioles and twisted stigmatic band do however remind of the second one.

5. The collection J.J. de Wilde & Sosef 10278 is cultivated at WAG. It produced several ovaries which are sparsely hirsute, which is a deviation from the usual situation.

Specimens examined:

CAMEROON: *Letouzey 9033* (P, YA): at 15 km SSE of Zingui, c. 50 km SE of Kribi, 02°39'N 10°14'E (fl, fr, 03); *Mildbraed 6057* (B, HBG), identification doubtful: South Cameroon forest area, Kribi Dept., Beson, 45 km E of Gr. Batanga, 02°50'N 10°18'E (st, 07); *Zenker 3141* (B, holo; BM, BR, E, G, HBG, K, L, LY, M, MO, P, W, WAG, Z): Bipinde, Mimfia, c. 03°05'N 10°25'E (fl).

EQUATORIAL GUINEA: *Mann 1871* (K, holo; B): Mt John, Kongui R., 01°10'N 09°25'E (fl, fr, 09).

GABON: *Breteler & J.J. de Wilde 181* (WAG): Crystal Mts, about 15 km NE of Asok, 00°46'N 10°30'E (fl, fr, 08); *Breteler & J.J. de Wilde 295* (WAG): about 3 km along the road from Asok to the hydroelectric power station at Tchimbélé, 00°42'N 10°22'E (fl, fr, 08); *N. Hallé 1592* (P), identification doubtful: Ayem, SW Ndjolé, 00°14'S 10°42'E (fl, 04); *N. Hallé 1828* (BR, P): Moyen Ogooué, 10-20 km SW of Ndjolé, c. 00°16'S 10°40'E (fl, fr, 04); *N. Hallé 1981* (P): C.E.T.A. Ayem, 10 km SW of Ndjolé, 00°14'S 10°42'E (fl, fr, 05); *N. Hallé 2203* (P): Abanga exploitation C.E.F.A., Lano R., 00°14'N 10°37'E (fl, 05); *N. Hallé 2349* (P): Abanga exploitation C.E.F.A., 00°14'N 10°37'E (fl, 06); *N. Hallé & Villiers 4306* (P): banks of the Komo, near Mbel, 00°16'N 10°10'E (fl, 01); *N. Hallé & Villiers 4407* (P), identification doubtful: Mbel, 00°16'N 10°10'E (fl, 01); *Mann 1647* (K): Crystal Mts, c. 00°55'N 10°25'E (fr, 07); *Soyaux 140* (B, K): near Munda, Sibanga Farm, 00°25'N 09°31'E (fl, 01); *J.J. de Wilde c.s. 10278* (WAG): 9 km N of Ndjolé, exploitation track of E.F.G., 00°07'S 10°45'E (fl, 01); *J.J. de Wilde c.s. 10342* (WAG): 15 km NE of Ndjolé, 00°07'S 10°49'E (fl, 01).

Begonia ciliobracteata Warb. **Fig. 17.3, Pl. 1c, Map 17.2**

Begonia ciliobracteata Warb., Bot. Jahrb. Syst. 22 (1895) 40; Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3,2 (1921) 616; Irmscher in Engl. & Prantl, Nat. Pflanzenfam. (ed. 2) 21 (1925) 574; L.B. Smith et al., Begoniaceae..., Smiths. Contr. Bot. 60 (1986) 151, fig. 22.6; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 16, pl. 10B-D. – TYPE: *Braun 20* (B!, holo): 'Gr. Btga., am Rande intermitt. Bäche, 2 Nov. 87.'

Begonia dielsiana Gilg non Pritzel, Bot. Jahrb. Syst. 34 (1904) 91; Engl. in Engl. & Drude l.c.; Irmscher in Engl. & Prantl l.c.; Bouman & de Lange, Begonian 50 (1983) 73, fig. 16; Reitsma, Meded. Landbouwhogeschool Wageningen 83-9 (1984) 47, fig. 10F; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39, pl. 13.1. – *B. cameroonensis* L.B. Smith & Wasshausen, Phytologia 52 (1983) 442. – TYPE: *Dinklage 257* (B!, holo; HBG!): 'Kamerun, Ebea-Fälle, 1889-XI-12.'

Begonia hookeriana Gilg ex Engl. non Gardner in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3,2 (1921) 617; Hutch., Dalziel & Keay, Fl. W. Trop. Afr. (ed. 2) 1,1 (1954) 220; van den Berg l.c. 38-39; L.B. Smith et al. l.c. 180. – TYPE: *Dusén 18* (B!, holo): 'Kamerun.'

Begonia raynaliorum Wilczek, Bull. Jard. Bot. Nat. Belg. 39 (1969) 93; van den Berg l.c. 38-39; L.B. Smith et al. l.c. 222; de Lange & Bouman l.c. 15, pl. 10A. – TYPE: *J. & A. Raynal 10412* (P, holo!): 'Njabilobé (54 km ESE Kribi, Cameroun), forêt primaire 2 km W village, 12.3.1963.'

Plant up to 25(–30) cm high, scattered with minute glandular hairs, usually sparsely so on bracts and pedicel of male flower, densely so on petiole. **Rhizome** rather stout and elongated, rather smooth, 1.8–6.0(–8.0) mm wide, glabrous to sparsely hirsute but the younger parts sparsely hirsute to hirsute; the apical part directed upwards to form a short stem of up to 5 cm. **Stipules** narrowly to broadly triangular or triangular-ovate, acute to blunt, 1.4–6.0(–9.4) mm long, pale pink to purplish red, sparsely hirsute; margin entire to dentate, ciliate. **Leaves** not peltate or sometimes peltate; *petiole* usually continuing into the midrib without a distinct angle, (1–)3–12(–15) cm long, firm, fleshy, pale greenish to green-brown or red to purple, densely to sparsely hirsute, with long to rather short patent wavy white hairs; *leaf blade*: the lower half held in a more or less vertical position, sometimes in a more or less horizontal position, asymmetrical or distinctly so, usually elliptic to obovate or broadly so, sometimes narrowly elliptic or almost circular, sometimes slightly kidney-shaped, usually blunt or gradually attenuate towards the top or rarely slightly acuminate in the upper 1/4, 4.6–21.5 x 2.7–11.5 cm, crispy-leatherly, with (6–)7–9(–10) palmate main nerves but the midrib usually most pronounced; margin entire to crenate, sometimes dentate-serrate, often with a reddish to brownish tinge, glabrous to sparsely ciliate, rarely

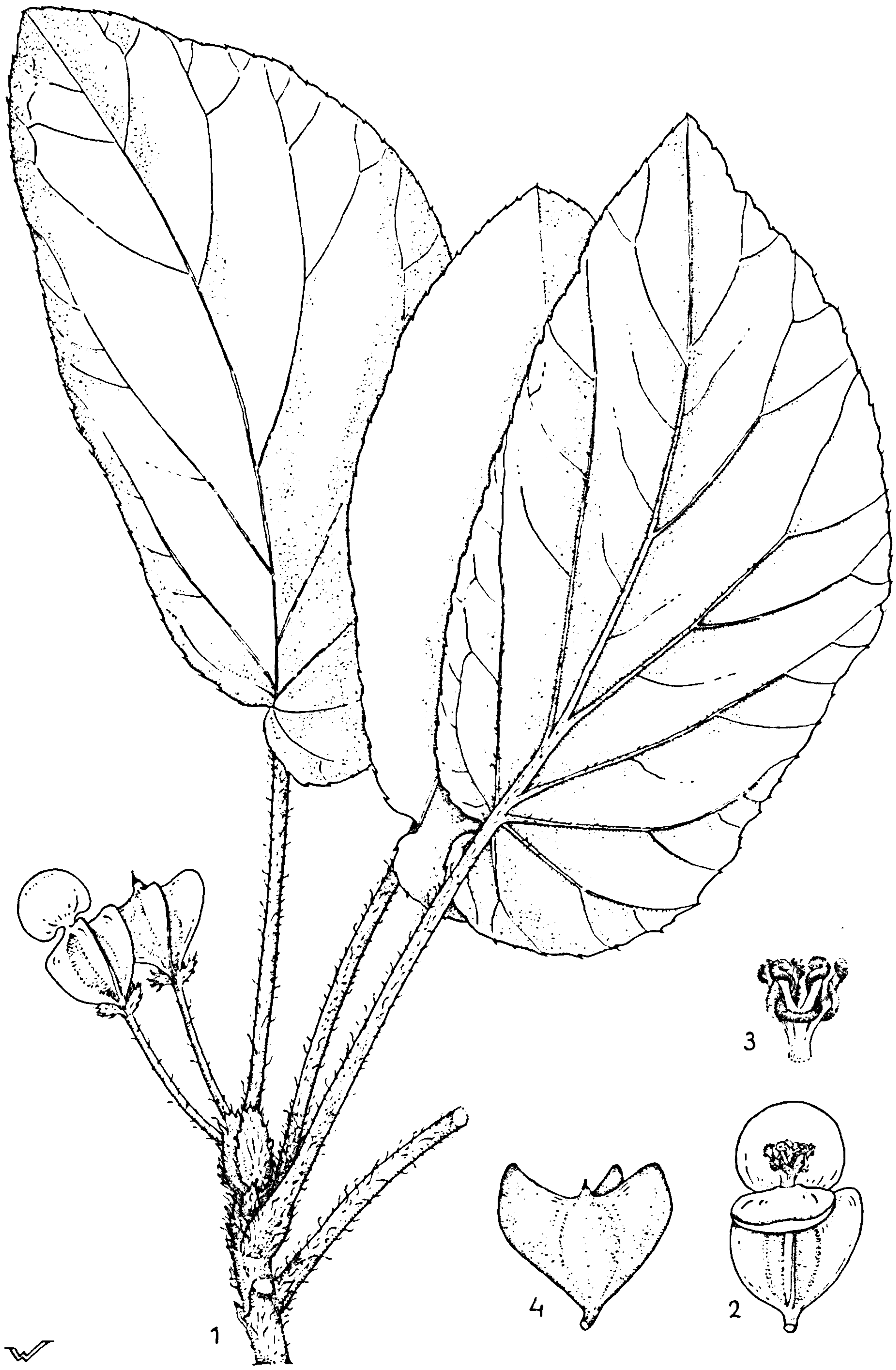
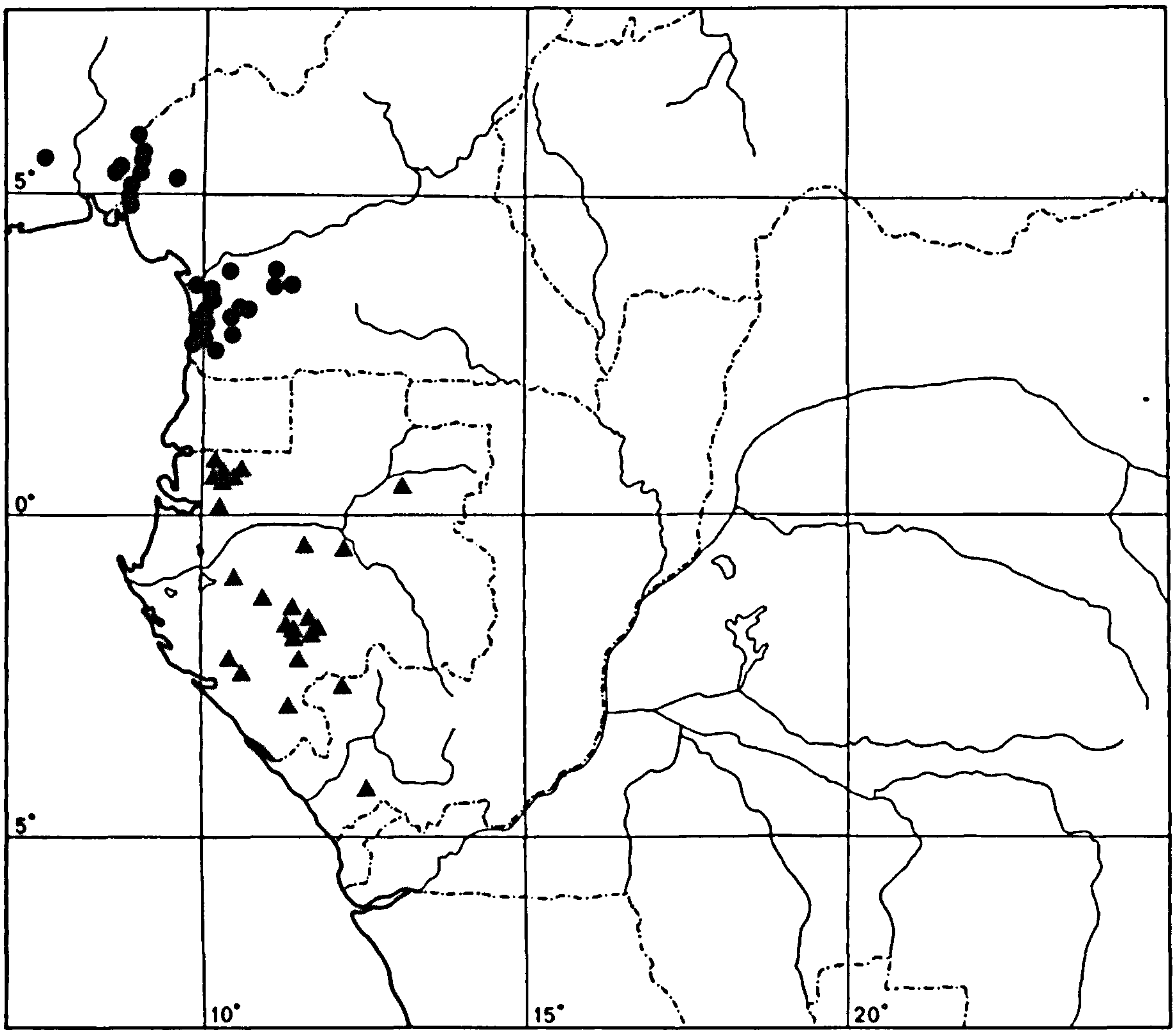


Figure 17.3. *Begonia ciliobracteata* Warb. – 1: habitus (x$^{2}/_{3}$); 2: female flower (x1); 3: styles (x4); 4: fruit (x1). – 1: *Bos 4746*; 2, 3: *Bos 3367*; 4: *Bos 6334*.

more densely so, then sometimes with two or more cilia together in between the teeth, the incisions when present most pronounced towards the top; base usually very unequal in non-peltate blades, one side rounded to cordate, the other very deeply cordate, the sides not or slightly overlapping, in peltate blades the base rounded; top usually blunt, sometimes acute; upper surface medium to dark green, shiny to dull, smooth, not hirsute; lower surface pale green to purplish tinged; *nerves*: the main and larger secondary nerves usually impressed and concolorous with the blade on the upper surface, on the lower prominent, dark red to red and usually shortly hirsute or sparsely so with patent hairs, the smaller secondary nerves distinct, the tertiary ones less so but usually well visible in dried condition, often creating a typical reticulate pattern. **Inflorescence** containing (2–)3(–8) male flowers and 1 terminal female flower, positioned at the base of the plant, distinctly below the leaf blades; *peduncle* simple, (0.8–)1.5–6.0 cm long, fleshy, dark red to pale pinkish, hirsute or sparsely so with white hairs; *bracts* (3–)4(–9), elliptic to obovate or broadly so, sometimes circular, 1.4–5.5 mm long, very pale green to pinkish red; margin dentate, ciliate. **Male flower**: *pedicel* elongated at anthesis up to 15(–21) mm, pale pink, sometimes sparsely hirsute; *perianth segments* broadly ovate to circular, sometimes very broadly ovate, with a rounded to cordate base, 6.0–12.5 x 6.8–11.0 mm, the outside almost white to pinkish white with red nerves or entirely reddish, usually sparsely hirsute with red or white hairs; the upper segment white, very rarely yellow, with a usually large dark pink patch and intensively dark pink nerved up to the top or almost entirely dark pink on the inside; the lower segment white, very rarely yellow, on the inside; *androecium* with 20–31 stamens; column up to 0.8 mm long; anthers 1.3–2.7 mm long. **Female flower**: similar to the male but shortly to distinctly pedicellate, the pedicel elongated in fruit up to 5(–11) mm; *perianth segments* broadly obovate to very broadly ovate, sometimes circular, usually with a cordate, sometimes with a rounded base, (5.2–)7.1–16.0 x (6.2–)7.2–13.0 mm; *styles* 3, 3.1–6.5 mm long, fused in the lower 1/6 to 1/2, the top split into a rounded U-shape, the arms 1.3–3.8 mm long and bearing a slender, stigmatic band which is spirally twisted for 1 turn; *ovary* distinctly enlarged in fruit, quite variable in shape, at anthesis from broadly obovate to shallowly obtriangular, with a cuneate base, 6.1–14.0(–17.5) x 6.3–17.0(– 25.0) mm, usually dark pink, sometimes pale green to pinkish green or whitish, 3-locular, 3-winged all along, rarely only in the apical half; the locular part elliptic to obovate or narrowly so, rarely broadly so, very rarely narrowly obovate, 2.0–6.5(–10.0) mm wide; beak absent or present, up to 0.9 mm long; wings usually erecto-patent or slightly so, rarely patent, distinctly enlarged in fruit, usually obovate to depressed obovate, sometimes obtriangular to depressed obtriangular, rarely very shallowly obtriangular or narrowly obtriangular, (1.4–)3.0–10.5(–16.0) mm wide (the larger values measured in fruit), dark pink, sometimes pale green, the margin glabrous or with a few hairs. **Infructescence**: peduncle recurved towards the substrate; *fruit* pendulous, obtriangular or shallowly obtriangular to broadly or very broadly obovate, often with an apical depression due to the wings which suddenly fall back, (6.3–)10.5–20.0 x 8.9–38.0



Map 17.2. Distribution of *Begonia ciliobracteata* (dots) and *Begonia clypeifolia* (triangles).

mm, dry, with a relatively thin wall, pinkish to pale greenish red or pinkish white, shiny to dull.

Distribution: Western Cameroon.

Ecology: Terrestrial on level sites to steep slopes, often on sandy or sometimes clayey soil; in shade of primary or sometimes degraded forest, in hygrophilous coastal evergreen Guineo-Congolian rain forest (forêt littorale), in riverine forest or in forest with *Calpocalyx heitzii, Guibourtia ehie, Sacoglottis gabonensis* and *Lophira alata*; at 50–250 m altitude.

Notes: 1. Originally the epitheton of this species name was written with a hyphen ('cilio-bracteata'). This spelling was followed by many other authors. Art. 73.9 of the Code, however, prescribes that a hyphen is only permitted when two distinctly separate words build up the epitheton. Since this is not the case here the correct spelling should be 'ciliobracteata'.

2. *B. ciliobracteata* represents a very variable species. The large variability in leaf shape and shape of the wings on the ovary are the most conspicuous ones. One could distinguish a 'raynaliorum-type' with sharply triangular wings and a 'hookeriana-type' with peltate leaf blades and also sharply triangular wings

on the ovary. The existence of several intermediate specimens, however, does blurr the boundaries and justifies allowance for this marked variability within a single species.

3. Some specimens come close to *B. hirsutula* that has yellow flowers and usually less broadly winged fruits. One specimen (Mbamba 46) is intermediate between this species and *B. hirsutula*. It possesses typical large *B. ciliobracteata* fruits with large obovate wings but its flowers are yellow. I assume this is just another example of the possible variability in colour of the flower as was also found in e.g. *B. hirsutula* and I do regard the shape of the fruit as a more reliable character. For a hybrid I have no further arguments; in fact the fruits are normal and well developed and seem to contain normally developed seeds.

4. The name *B. hookeriana* Gilg ex Engler is sometimes spelled as *B. hookerana*. According to Art. 73C.1d of the Code the first spelling is the correct one. The specimen Dusén 18 is regarded as the type for this name since Engler denoted the species was collected by Dusén and this Dusén collection is the only one that fits Engler's description.

Specimens examined:

NIGERIA: *Ariwaodo 1254* (K): Obubuo-Umuariga valley near Agric. Research Station Umudike, 05°30′N 07°32′E (fl, fr); *Richards 5177* (K): Calabar Prov., Oban Distr., Calabar-Mamfe road, about 7 miles N of Oban, cut line W of mile 51 (sample plot), 05°24′N 08°36′E (fl, 03); *Umem FHI 34813* (FHI, K): ibid. (fl, fr, 03).

CAMEROON: *Annet 151* (P): Bipindi, 03°05′N 10°25′E (fl, fr, 06); *Annet 441* (P): Bipindi-Debam road, c. 03°05′N 10°25′E (fl, fr, 06); *Asonganyi 638* (P, WAG, YA): at lake Tissongo, 16 km ESE of Mouanko, 03°35′N 09°54′E (fl, 09); *Bos 3367* (P, WAG, YA): 7.5 km from Kribi, N of Ebolowa road, 02°54′N 09°57′E (fl, 11); *Bos 3446* (BR, K, MO, P, WAG, YA): 14 km from Kribi, Ebolowa road, 02°51′N 10°00′E (fl, fr, 12); *Bos 4082* (WAG, YA): 18 km from Kribi, Lolodorf road, 03°00′N 10°02′E (fr, 03); *Bos 4433* (P, WAG): 7 km S of Kribi, Lobé R., 02°57′N 09°54′E (fl, 04); *Bos 4449* (WAG): 12 km from Kribi, between Ebolowa road and Kienke R., 02°54′N 09°59′E (fl, 04); *Bos 4746* (BR, K, MO, P, WAG, YA): about 8 km N of Kribi, 03°00′N 09°56′E (fl, fr, 06); *Bos 4992* (BR, K, P, WAG, YA): about 10 km NE of Kribi, trail between Mpalla and Bilolo, 03°00′N 09°57′E (fl, fr, 07); *Bos 5739* (WAG): 30 km N of Kribi, 03°08′N 10°01′E (fl, fr, 11); *Bos 5786* (P, WAG): SE foothills of Mt Elephant, SE of Kribi, 02°47′N 10°01′E (fl, fr, 12); *Bos 6334* (WAG): about 60 km N of Kribi, 03°19′N 10°06′E (fl, fr, 02); *Braun 20* (B, holo): Gr. Batanga, 02°51′N 09°53′E (fr, 11); *Buesgen 424* (B): Edea, at the Kelle R., 03°08′N 10°25′E (fl, 01); *Dinklage 257* (B, holo; HBG): Ebea-falls, 03°11′N 10°02′E (fl, fr, 11); *Dinklage 703* (B, HBG): Gr. Batanga, 02°51′N 09°53′E (fl, fr, 07); *Dinklage 1029* (B, HBG): ibid. (fl, fr, 12); *Dundas FHI 15325* (K): Cameroons Prov., Basosi Distr., Kumba Div., Mungo Ndaw-Ntale path, 05°13′N 09°33′E (st, 10); *Dusén 18* (B, holo): (presumably near Mt Cameroon) (fl); *Farron 7188* (P): Bipindi, 65 km NE of Kribi, 03°10′N 10°20′E (st, 04); *Jacques-Félix 2254* (P): Makak, 03°32′N 11°05′E (fl, fr, 10); *Letouzey 12401* (P, YA): near Nkak Ndjok (=Mapubi), 30 km ENE of Edea, 03°50′N 10°24′E (fl, fr, 12); *Letouzey 13577* (P, WAG, YA): between Okurikang and Araru, 35 km WSW of Mamfe, 05°38′N 09°02′E (fl, fr, 05); *Letouzey 13653* (P, WAG, YA): between Ogurang and Babong, 45 km SW of Mamfe, 05°33′N 09°00′E (fl, 05); *Letouzey 15139* (P, WAG, YA): Korup Forest Reserve, NE of Erat Ekong II, 20 km NW Mundemba, 05°06′N 08°50′E (fl, fr, 06); *Letouzey 15151* (P, WAG, YA): Korup Forest Reserve, between Akpasai and Mosongosele, 15 km W of Mundemba, 04°58′N 08°48′E (fl, 06); *Letouzey 15326* (WAG): 15 km ESE of Ebodje, 45 km S of Kribi, 02°31′N 09°57′E (fl, 12); *Manning 1698* (MO): South-West Prov., E of Catholic Mission, Mundemba, 04°56′N 08°53′E (fl, 04); *Mbamba 46* (WAG, YA): Kribi-Lolodorf road at 18 km of Kribi, Bissiang village, forest trail Bissiang-Edea, at 3.5 km N of Kribi-Lolodorf, 03°02′N 10°02′E (fl, fr, 01); *Mildbraed 5901* (B): South Cameroon forest area, Kribi region, near Fenda, 58 km E of Kribi, 02°48′N 10°24′E (fl, 07); *J. Raynal & A. Raynal 10412* (P, holo; YA): 54 km ESE of Kribi, 2 km W of

Njabilobé, 02°47'N 10°21'E (fl, 03); *Sanford 5331* (IFE, K): Yaoundé Distr., Yaoundé-Douala road, c. 03°35'N 11°20'E (fl, 11); *Schultze (in Mildbraed) 6216* (B): South Cameroon forest area, Kribi-Kampo region, hills between Ebolowa & Kampo, Kom falls, c. 02°30'N 10°10'E (fl, fr, 07); *Thomas 182* (K, YA): Douala/Edea (fl); *Thomas 2715* (K, MO, WAG, YA): South-West Prov., S of Ekumbako, 04°53'N 08°53'E (fl, fr, 12); *Thomas 4159* (MO, YA): between Bulu and Dibunda, 04°54'N 08°53'E (fl, fr, 12); *Thomas 5430* (K, WAG): South-West Prov., Korup National Park, 05°02'N 08°50'E (fl, fr, 01); *Thomas c.s. 4201* (K, WAG, YA): Mundemba town, 04°58'N 08°55'E (fl, 07); *Thomas c.s. 4944* (WAG): South-West Prov., Ndian Div., 1-3 km W of Ekondototo – Mundemba road at Dibunda, 4 km N of Ilor bridge, 04°52'N 08°53'E (fl, 11); *Thomas c.s. 7859* (WAG): South-West Prov., Korup National Park, between Akwa and Bera, 05°20'N 08°57'E (st, 05); *Thomas c.s. 7884* (WAG): ibid. (st, 05); *J.J. de Wilde 8314A* (WAG): along the road from Kribi to Campo, 27 km along the road S of Lobé R., 02°43'N 09°52'E (fl, 06); *W.J. de Wilde & de Wilde-Duyfjes 1290* (BR, MO, P, WAG): c. 50 km NW of Eséka, W of Yaoundé, Kelé-R., 03°49'N 11°04'E (fl, fr, 11); *W.J. de Wilde & de Wilde-Duyfjes 2695* (WAG): ± 60 km SSW of Eséka, 03°12'N 10°35'E (fl, 06); *W.J. de Wilde c.s. 3818* (WAG): near bridge crossing Njong R., about 60 km SSW of Eséka, 03°12'N 10°35'E (fl, fr, 11); *W.J. de Wilde c.s. 3848* (K, WAG): about 20 km SW of bridge crossing Njong R., about 60 km SSW of Eséka, 03°12'N 10°35'E (fl, fr, 11); *Winkler 845* (B): between Dehane and Ndoktome, 03°27'N 10°04'E (st, 11); *Zenker 2101* (B, BM, G, K): Bipindi, 03°05'N 10°25'E (fl, 06); *Zenker 3082* (B, BM, BR, COI, E, G, HBG, K, L, M, MO, P, W, WAG): ibid. (fl); *Zenker 3133* (B, G): Bipindi, road to Songlepem, 03°15'N 10°28'E (fl, 09); *Zenker 3141a* (B): Bipindi, 03°05'N 10°25'E (fl); *Zenker 3824* (B, BM, BR, E, G, HBG, K, L, M, W): ibid. (fr).

CULTIVATED: *van Veldhuizen 876* (WAG): Wageningen, Dept. of Horticulture (fl, 01).

Begonia clypeifolia Hook.f. Fig. 17.4, Pl. 2b, c & d, Map 17.2

Begonia clypeifolia Hook.f. in Oliver, Fl. Trop. Afr. 2 (1871) 576; Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3,2 (1921) 617; Doorenbos, Begonian 47 (1980) 35; Reitsma, Meded. Landbouwhogeschool Wageningen 83-9 (1984) 47, fig. 10E; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39; L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 151, fig. 2.13; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 17, pl. 11E-G. – TYPE: *Mann 1648* (K!, holo): 'Sierra del Cristal, W. Trop. Africa, Lat. 1° N, july 1862.'

Begonia scutulum auct. non Hook.f.: van den Berg l.c. 38-39, pl. 1.2, 13.2.

Plant up to 30(–54) cm high, scattered with minute glandular hairs, this indumentum dense on stipules, petiole and ovary, sparse to dense on peduncle. **Rhizome** rather stout and usually elongated, sometimes far creeping, often knotted, 1.5–9.5 mm wide, the younger parts sometimes sparsely hirsute; the apical part directed upward to form a more or less distinct stem of up to 10(–20) cm high. **Stipules** narrowly to broadly triangular or triangular-ovate, rarely broadly elliptic-ovate, usually acute, 2.0–14.0 mm long, dark red to dark brown-red; margin entire to serrate-dentate, usually ciliate. **Leaves** usually peltate, rarely not peltate; *petiole* continuing into the midrib with a distinct angle, inserted at (5–)10–47(–62) mm from the nearest margin in peltate leaves, inserted distinctly asymmetrically (at one side) in non-peltate ones, 5–30(–54) cm long, firm, fleshy, dark red (especially when young) to brown-red or brownish green, without or very sparsely set with comparatively short and stiff white or red hairs; *leaf blade* in more or less horizontal position, asymmetrical or slightly so, distinctly asymmetrical in non-peltate leaves, usually elliptic-ovate or broadly so, sometimes elliptic to obovate or broadly elliptic to broadly obovate, rarely narrowly ellip-

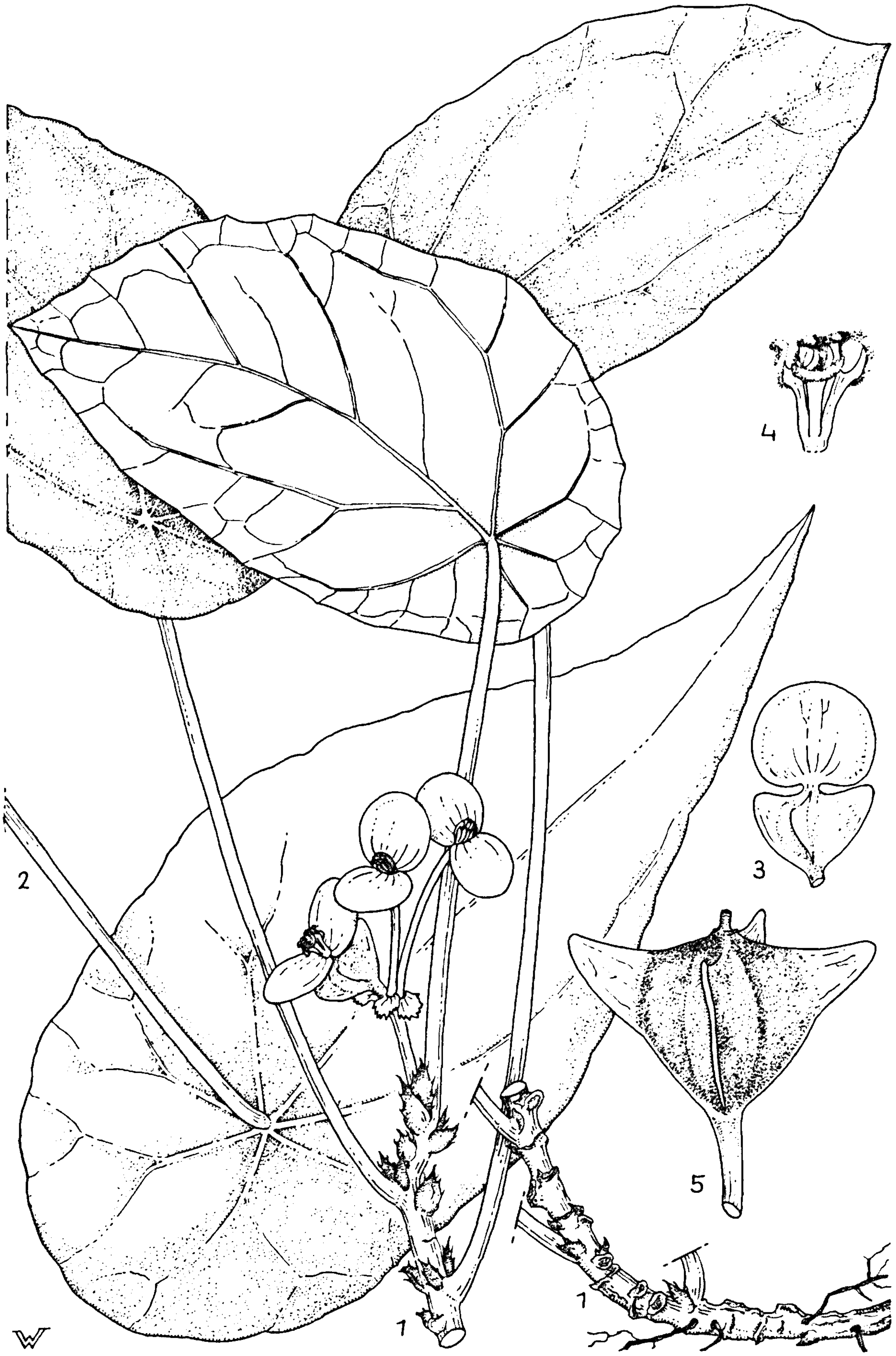


Figure 17.4. *Begonia clypeifolia* Hook.f. – 1: habitus (x$^2/_3$); 2: leaf (x$^2/_3$); 3: female flower (x1); 4: styles (x2); 5: fruit (x2). – 1: *A. Louis 2841*; 2: *Arends c.s. 688*; 3, 4: living plant at WAG, voucher *van Veldhuizen 1050*; 5: *Arends c.s. 369*.

tic-ovate, not infrequently with an elongated apical part, gradually tapering or slightly acuminate to distinctly acuminate-cuspidate, (5.9–)6.5–21.0(–29.5) x (2.4–)4.0–12.5(–18.0) cm, herbaceous to leathery or rarely fleshy-leathery, with 7–9 palmate main nerves, the midrib usually slightly more pronounced; margin usually entire to shallowly sinuate-dentate with the nerves ending in more or less distinct marginal teeth, sometimes the margin with a few coarse teeth in the apical part which may become markedly elongated, glabrous or sparsely shortly ciliate, concolorous with the blade or reddish or purplish especially when young; base rounded or sometimes slightly cordate in peltate leaves, distinctly unequal with one rounded to cuneate and one strongly cordate side but the basal lobes not overlapping in non-peltate leaves, top acute; upper surface dark to medium green or sometimes bluish green (often with a red glow when dry), glossy or slightly so, smooth or rarely slightly rugulose, glabrous; lower surface pale green to bluish green, sometimes with a purplish tinge (often so when dry); *nerves*: the main and larger secondary nerves not prominent and concolorous with the blade on the upper surface, on the lower prominent, usually dark red to brown-red or sometimes green, usually not but sometimes with a few scattered stiff hairs, the smaller secondary nerves distinct, tertiary nerves usually indistinct and more or less concolorous with the interveinal parts but still well visible and creating a reticulate pattern when dry. **Inflorescence** containing 2–4(–7) male flowers and 1(–2) terminal female flower(s), positioned at the base of the plant; *peduncle* simple, 0.2–4.5(–7.5) cm long, fleshy, dark red or dark brown-red to pale reddish, usually without but sometimes with a few patent hairs; *bracts* 3–6(–8), usually ovate to narrowly elliptic, sometimes broadly elliptic to circular, 2.2–8.0(–10.5) mm long, dark brown-red to purplish red or wine-red; margin serrate-dentate, ciliate. **Male flower**: *pedicel* elongated at anthesis up to 27 mm, pale yellowish or greenish with a reddish tinge to red; *perianth segments* round to very broadly ovate, with a cordate base, 5.7–14.5(–21.0) x 6.4–12.5(–18.0) mm; the upper segment red to orange-red outside, the inside yellow with a red to brown-red patch and nerves in the basal half; the lower segment orange on the outer and yellow on the inside; *androecium* with (22–)30–48 stamens; column 0.1–1.0 mm long; anthers 2.0–2.7(–3.1) mm long. **Female flower**: similar to the male but sessile to distinctly pedicellate, then the pedicel elongated in fruit up to 11 mm; *perianth segments* circular or broadly obovate to very broadly ovate or very broadly obovate, 5.6–18.0(–23.0) x 6.0–15.0(–22.0) mm; *styles* 3–4, 4.7–7.0(–8.0) mm long, fused in the lower half, sometimes only at base, the top split into an elongated usually sharp V-shape or more rarely into a rounded U-shape, the arms 1.3–2.6(–3.4) mm long and bearing a slender stigmatic band which is spirally twisted for 1 turn; *ovary* usually shallowly obtriangular, sometimes very broadly obtriangular or very shallowly so, 4.2–11.0 x 6.0–16.0 mm, green to red or dark wine- or purplish red, rarely yellowish green, 3–4(–5)-locular, 3–4(–5)-winged at the apical 1/3 to all along, very rarely sparsely hirsute; beak short or absent, 0–1.7 mm long; the locular part broadly obovate to circular, 3.4–9.4 mm wide; wings patent to slightly erecto-patent or sometimes distinctly erecto-patent, very shallowly obtriangular-elliptic or slightly obtriangular-spathulate to very broadly obovate, 1.4–8.1 mm wide, rarely with a few cilia at the top. **Infructescence**: peduncle usually recurved towards the substrate; *fruit* pendulous, usually shallowly obtriangular, sometimes broadly to very broadly obtriangular, rarely very shallowly obtriangular, 4.2–14.0 x 9.2–18.0 mm; the locular part 6.2–13.5 mm wide, with a tough thick wall, green to dark brown, dull to shiny.

Distribution: Gabon and western Congo.

Ecology: Terrestrial on humid, clayey soils, usually on steep slopes or banks, sometimes on mossy rocks, decaying trees, or at up to 2 m above the soil level on mossy tree trunks; in shaded to deeply shaded sites in primary or sometimes in secondary evergreen rain forest, rarely in gallery forest and usually associated with streams or rivers; at 200–900 m altitude.

Notes: 1. A very variable taxon. More material should allow for a better understanding of the status of several aberrant specimens. Several remarks relating to this variability may be made. The ample collections from the Crystal Mountains (NW-Gabon) are quite uniform. They share less leathery leaves with a more pronounced acuminate top (not almost gradually tapering as in most other collections) and more pronounced secondary nerves. They always have comparatively long fruiting pedicels as well, but intermediates and variations do occur. Hallé & Villiers 5181, collected in the Crystal Mountains, has large leaves on long petioles, the fruits are 2-winged and they are shortly velvet-like hirsute. The lack of more material made me decide not to treat it as a distinct taxon. Two collections from Congo (Barabé c.s. 85-1 and Attims 434) show comparatively large leaves, stipules and bracts. Otherwise no characters could be found to validate a taxonomic distinction. Similar to other species (*B. hirsutula, B. mildbraedii, B. ciliobracteata*), both peltate and non-peltate leaf blades occur within this species (see also chapter 5).

2. Breteler & de Wilde 126 is cultivated at WAG and deviates in leaf anatomical characteristics from two other cultivated collections as was discussed in chapter 6.

3. A few collections, e.g. A. Louis c.s. 945, Reitsma 2319 & Reitsma c.s. 3549, have long runners which bear an inflorescence at their tip, a character maintained in cultivation. Because of the presence of intermediate collections (short runners) and the observation of the same phenomenon in *B. scutulum*, no taxonomic value is given to this character. It deserves, however, further attention in the future.

4. This species probably hybridizes with *B. scutulum* (see chapter 10).

Specimens examined:

GABON: *Arends c.s. 369* (WAG): Waka, forest exploitation road, near the Falaise, 01°18'S 10°57'E (fr, 11); *Arends c.s. 387* (WAG): ibid. (fr, 11); *Arends c.s. 688* (WAG): Doudou Mts, western flanc, 02°15'S 10°20'E (fr, 12); *Breteler 7687* (WAG): 30 km Fougamou-Lamberéné, 01°00'S 10°30'E (fl, fr, 05); *Breteler 7712* (WAG): 17 km Mimongo-Koulamoutou, 01°34'S 11°42'E (st, 05); *Breteler & J.J. de Wilde 45* (WAG): 13 km along the road from Asok to the hydroelectric power station at Tchimbélé, 00°36'N 10°24'E (fr, 08); *Breteler & J.J. de Wilde 126* (WAG): 12-15 km NE of Asok, 00°46'N 10°29'E (st, 08); *Breteler & J.J. de Wilde 156* (WAG): about 9 km W of Asok, along a confluent of the Soung R., 00°43'N 10°16'E (fl, 08); *Breteler & J.J. de Wilde 197* (WAG): Crystal Mts, about 15 km NE of Asok, 00°46'N 10°30'E (fr, 08); *Breteler & J.J. de Wilde 262* (WAG): about 7-8 km SW of Asok, hill W of the village Nkan, 00°39'N 10°18'E (fl, fr, 08); *Breteler & J.J. de Wilde 263* (WAG): ibid. (fl, fr, 08); *Breteler & J.J. de Wilde 360* (WAG): Crystal Mts, Nkan village, about 8 km along the road from Asok to Méla, c. 1 km W of the village, 00°39'N 10°18'E (fl, 08); *Breteler & J.J. de Wilde 734* (WAG): 92 km along the road from Achouka to Lastourville counted from the forking at Achouka (route economique), Region des Abeilles, 00°32'S 12°12'E (st, 09); *Breteler c.s. 8065* (WAG): between Mouila and Yeno, about 60 km on road from Mouila, 01°44'S 11°24'E (fl, fr, 09); *Breteler c.s. 8314* (WAG): 12 km N of road Libreville-Kango, former concession SOGACEL, 00°17'N 10°05'E (st, 10); *N. Hallé & Cours 5931* (P): Ovala, near Etéké, 01°25'S 11°25'E (st, 05); *N. Hallé & Villiers 4708* (P): Crystal Mts, 6 km S of Assok, 00°39'N 10°22'E (st, 01); *N. Hallé & Villiers 4709* (P): ibid. (fl, 01); *N. Hallé & Villiers 4786* (P): Crystal Mts, Nkan, 00°39'N 10°19'E (fl, 01); *N. Hallé & Villiers 4834* (P): ibid. (fl, 02); *N. Hallé & Villiers 5127* (P): Crystal Mts, Mt Méla, 00°34'N 10°17'E (fl, 02); *N. Hallé & Villiers 5181* (P): Crystal Mts, Mt Mvélakéné, 00°36'N 10°10'E (fl, fr, 02); *N. Hallé & Villiers 5220* (P): Crystal Mts, E of Nkan, 00°39'N 10°21'E (fl, 02); *N. Hallé & Villiers 5255* (P): ibid. (fl, 02); *N. Hallé & Villiers 5330* (P): Crystal Mts, W of Balakabo riv., 00°33'N 10°08'E (fl, fr, 02); *Le Testu 5511* (BM, BR, LISC, P): Haute Ngounié, rocks of the Bilengué heights of Ogoulier Boudyanguila, Itsogho land, 01°57'S 11°22'E (fl, 09); *Le Testu 5517* (BM, BR, LISC): Haute-Ngounié, between Boudyanguila & Noumbo, Itsogho land, c. 01°50'S 11°35'E (fl, fr, 12); *Leroy 17* (P): Ogooué, c. 01°40'S 13°30'E (fl); *A. Louis 1456* (LBV, WAG): Ngounié Prov., Mouyanama close to the Mouetse R. in the east, behind Ngondo Mt, 01°38'S 11°45'E (fr, 03); *A. Louis 2841* (LBV, WAG): Estuaire Prov., Tchimbélé-Kinguélé road km 10, 00°33'N 10°22'E (fl, 02); *A. Louis 3034* (LBV, WAG): Ngounié Prov., exploitation road Leroy, Massika between Mouila and Yeno, 01°40'S 11°15'E (fl, fr, 04); *A. Louis, Breteler & de Bruijn 891* (WAG): Chaillu Massif, near Mouyanama, about 27 km E of Mimongo, 01°39'S 11°46'E (fr, 11); *A. Louis, Breteler & de Bruijn 945* (WAG): Chaillu Massif, along road Mimongo-Koulamontou, between Dibandi and Diyanga, 20-30 km NE of Mimongo, 01°34'S 11°44'E (fl, 11); *A. Louis, Breteler & de Bruijn 1290* (WAG): km 20 NE of Forestry Camp Waka, situated about 32 km SE of Sindara, 01°14'S 10°53'E (st, 12); *A. Louis, Breteler & de Bruijn 1310* (WAG): SE of Forestry exploitation Camp Waka, situated about 32 km SE of Sindara, 01°14'S 10°53'E (fr, 12); *Mann 1648* (K, holo; P): W. Trop. Africa, Crystal Mts, Lat. 1°N, c. 00°55'N 10°25'E (fl, 07); *Pobeguin s.n.* (P): ?, c. 03°00'S 11°15'E (fl, fr); *J.M. Reitsma c.s. 2319* (WAG, LBV): Lopé Reserve (Soforga exploitation), 00°30'S 11°33'E (fl, 06); *J.M. Reitsma c.s. 2788* (WAG): Doudou Mts, c. 50 km SW of Doussala, 02°26'S 10°35'E (fl, 01); *J.M. Reitsma c.s. 3065* (LBV, WAG): near village Ekobakoba, 00°23'N 13°06'E (fl, fr, 02); *J.M. Reitsma c.s. 3549* (WAG): Lopé-reserve, Leledi (Soforga) exploitation, 00°25'S 11°30'E (fl, fr, 05); *Wieringa 411* (WAG): Crystal Mts, 1 km WNW of Tchimbélé, Bingiligwen R., 00°37'N 10°23'E (fl, 01); *Wieringa 703* (WAG): Crystal Mts, Woleu-Ntem, 1 km SE of Tchimbélé, 00°37'N 10°24'E (fl, fr, 03); *Wieringa 914* (WAG): Crystal Mts, Woleu-Ntem, 1 km WNW of Tchimbélé, Bingiligwen R., 00°37'N 10°23'E (fr, 05); *Wieringa 935* (WAG): Crystal Mts, Woleu-Ntem, 0.5 km SE of Tchimbélé, 00°37'N 10°24'E (fl, fr, 05); *J.J. de Wilde c.s. 9641* (WAG): 50 km along the road Mouila-Yeno, 01°42'S 11°30'E (st, 03); *J.J. de Wilde c.s. 10042* (WAG): Crystal Mts, Tchimbélé, trail E of the dam, 00°37'N 10°24'E (fl, 12); *J.J. de Wilde c.s. 10084* (WAG): Crystal Mts, 25 km on the road Kinguélé to Tchimbélé, 00°32'N 10°17'E (st, 01); *J.J. de Wilde c.s. 10089* (WAG): ibid. (fl, 01); *J.J. de Wilde c.s. 10106* (WAG): Crystal Mts, bank of Mbé R., c. 10 km along the road Tchimbélé-Kinguélé, 00°37'N 10°24'E (fl, 01); *J.J. de Wilde c.s. 10123* (WAG): Crystal Mts, 13 km on the road Tchimbélé to Kinguélé, 00°34'N 10°20'E (fl, 01); *J.J. de Wilde c.s. 10149* (WAG): Crystal Mts, Nkan, along the road Assok-Méla, NNW of the village Nkan, 00°40'N 10°19'E (fl, fr, 01); *J.J. de Wilde c.s. 10348* (WAG): 59 km on the road Mouila-Yéno, 01°43'S 11°25'E (st, 02); *J.J. de Wilde c.s. 10381* (WAG): 50 km on the road Mouila-Yéno, 01°43'S 11°23'E (fr, 02); *J.J. de Wilde c.s. 10419* (WAG): 7 km on the road Lebamba-Mbigou and then 4 km along a trail to the south, 02°14'S 11°32'E (st, 02); *J.J. de Wilde c.s. (WALK-B) 107* (WAG): Crystal Mts, forest exploitation Leroy, 20 km NW of Asok, 00°53'N 10°12'E (fl, fr, 01); *J.J. de Wilde c.s. (WALK-B) 153* (WAG): Crystal Mts, just E of Mala (Méla), Mytsibé R., an affluent of the Zang R., 00°35'N 10°16'E (fl, 01); *J.J. de Wilde c.s. (WALK-B) 196* (WAG): Crystal Mts, 10 km along the road Tchimbélé to Kinguélé, 00°35'N 10°20'E (fl, 01); *J.J. de Wilde c.s. (WALK-B) 251* (WAG): Crystal Mts, forest exploitation Leroy, 20 km NW of Asok, 00°53'N 10°12'E (fl, fr, 01).

CONGO: *Attims 434* (IEC): Mayombe, Bamba pass, 04°14'S 12°31'E (st, 03); *Barabé c.s. 85-1*

(MT): M'Vouti (Mayombe), 04°15'S 12°29'E (fl, 10); *Sita 4128* (BR, IEC, WAG): Kuigi, trail Moukoudi-Malinga, c. 02°40'S 12°05'E (fr, 04).

CULTIVATED: *van Veldhuizen 1050* (WAG): Wageningen, Dept. of Horticulture, (fl, 05); *van Veldhuizen 1087* (WAG): Wageningen, Dept. of Horticulture No 1676, (83PTGA608, coll. Breteler & de Bruijn, Gabon) (fl, 07); *van Veldhuizen 1088* (WAG): Wageningen, Dept. of Horticulture, (coll. Breteler 7687, Gabon) (fl, 09); *van Veldhuizen 1099* (WAG): Wageningen, Dept. of Horticulture No 1590 (coll. J.J. de Wilde et al. (WALK-B) s.n., Gabon, Mela) (st, 09); *van Veldhuizen 1103* (WAG): Wageningen, Dept. of Horticulture (coll. J.J.F.E. de Wilde et al. (WALK-B s.n., Gabon, Mela) (st, 09); *van Veldhuizen 1105* (WAG): Wageningen, Dept. of Horticulture No 1773 (coll. Arends c.s. 369, Gabon) (st, 09); *J.J. de Wilde 7391* (WAG): Wageningen, Dept. of Horticulture, (fl, 02).

Begonia dewildei Sosef **Fig. 17.5, Pl. 6a, Map 17.3**

Begonia dewildei Sosef, Wageningen Agric. Univ. Papers 91-4 (1992) 93, fig. 3, pl. 2a; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 19, pl. 14F. – TYPE: *Arends, A. Louis & J.J. de Wilde 700* (WAG!, holo): 'Gabon, Doudou Mountains. Moss forest starting at alt. ± 700m, 2 15 S, 10 20 E, 8-xii-1984.'

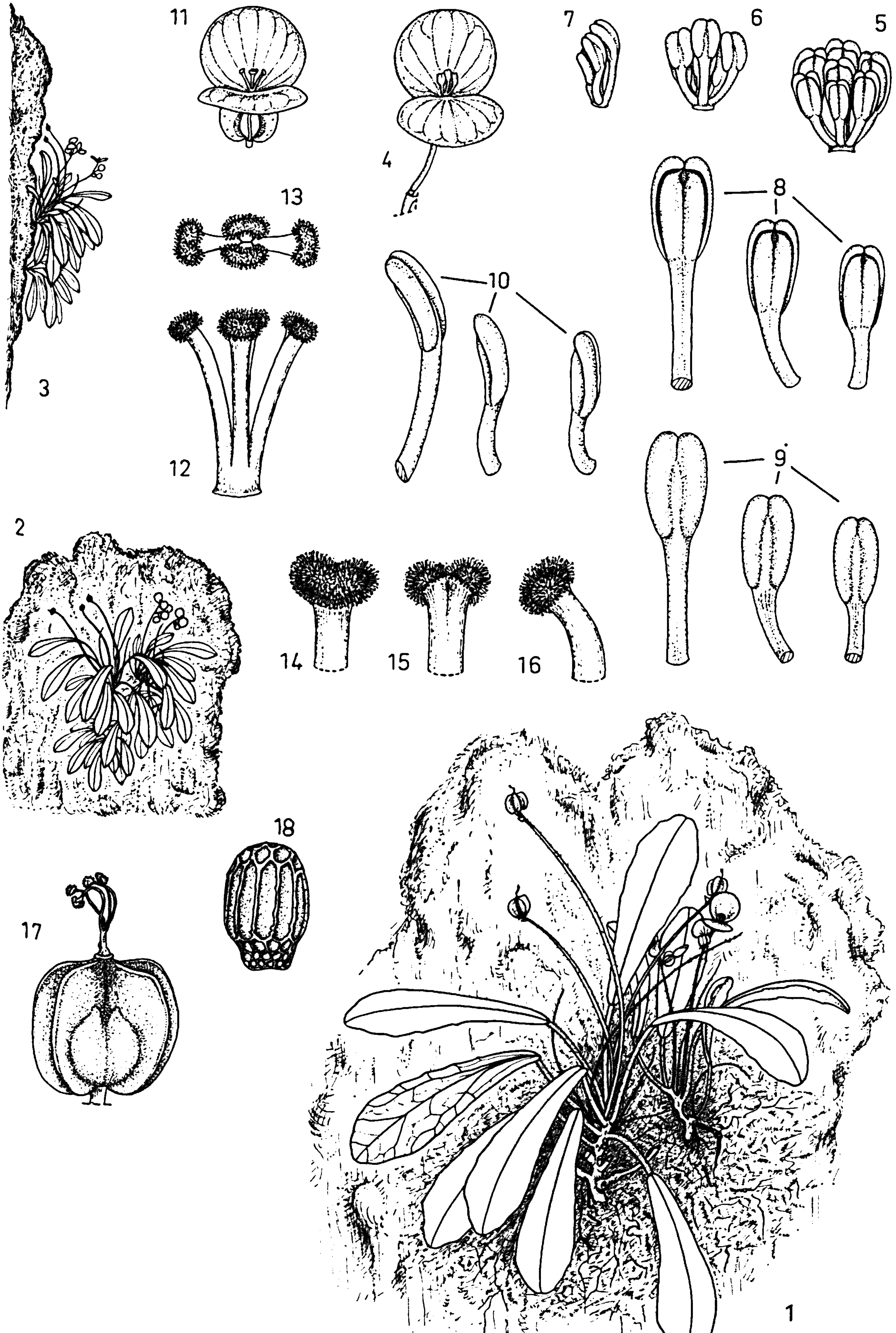
Diagnostic characters (for a more detailed description see Sosef l.c.):

Plant up to 9 cm high. **Leaves** subpeltate; *petiole* continuing into the midrib with a feeble angle, inserted at 0.1–0.5 mm from the nearest margin, densely velutinous pilose with short to medium sized, curly, pale pink hairs; *leaf blade* in more or less vertical position, narrowly obovate to narrowly elliptic-obovate, obovate when young, 1.5–5.9 x 0.5–1.4 cm; margin with a few distant and shallow blunt teeth in the apical half; upper surface glabrous. **Inflorescence**: *peduncle* 2.5–7.0(–9.0) cm long, with an indumentum similar to that of the petioles. **Male flower**: *perianth segments* broadly elliptic to somewhat transversely broadly elliptic or broadly obovate, with a rounded to cordate base, 4.4–8.7 x 5.2–8.2 mm, white to pale pink on the inside, usually slightly darker tinged on the outside; *androecium* with 7–13 stamens. **Female flower**: *perianth segments* very broadly elliptic-ovate to broadly obovate, 3.5–7.4 x 4.8–8.8 mm; *ovary* transversely broadly obovate to circular, 2.1–3.4 x 2.1–4.3 mm; wings broadly or transversely broadly elliptic to obtriangular-obovate, 0.25–1.3 mm wide. **Infructescence**: peduncle curved backwards towards the almost vertical substrate or inward and pushing the fruit in between the leaves; *fruit* on a straight pedicel, circular to transversely broadly elliptic, 2.3–3.4 x 2.1–4.7 mm.

Distribution: GABON: Doudou Mountains.

Ecology: Moss forest; growing abundantly though very locally on moss-cover-

Figure 17.5. *Begonia dewildei* Sosef. – 1: habitus (x$^2/_3$); 2, 3: habitus front and side view (x$^1/_6$), note in the latter the peduncles which are curved back towards the rock; 4: male flower (x2); 5-7: androecium, front, back and side view (x6); 8: stamens from different parts of the androecium, front view (x12); 9: idem, back view; 10: idem, side view; 11: female flower (x2); 12: styles (x12); 13: styles, top view (x12); 14-16: stigma, front, back and side view (x24); 17: fruit (x4); 18: seed (x60). – Living plant at WAG and slides taken at the type locality, coll. *Arends c.s 700*.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ed sheer rock faces, comparatively dry, sometimes mixed with *Begonia vankerckhovenii*; at 650–700 m altitude.

Specimens examined:

GABON: *Arends c.s. 700* (WAG, holo): Doudou Mts, 02°15'S 10°20'E (fl, fr, 12); *J.M. Reitsma c.s. 1073* (LBV, WAG): CEB exploitation, Doudou Mts, c. 20 km WSW of Doussala, 02°25'S 10°30'E (fl, fr, 05).

CULTIVATED: *van Veldhuizen 1348* (WAG): Wageningen, Bot. Garden 'De Dreijen' (coll. Arends c.s. 700, Gabon) (fl, 07).

Begonia erectocaulis Sosef **Fig. 17.6, Pl. 7a, Map 17.3**

Begonia erectocaulis Sosef, Wageningen Agric. Univ. Papers 91-4 (1992) 96, fig. 4, pl. 3a; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 17, pl. 12A. – TYPE: *Breteler & J.J. de Wilde 176* (WAG!, holo): 'Gabon, forest, about 15 km NE of Asok, Cristal Mountains, alt. ± 600-700 m, 21-VIII-1978.'

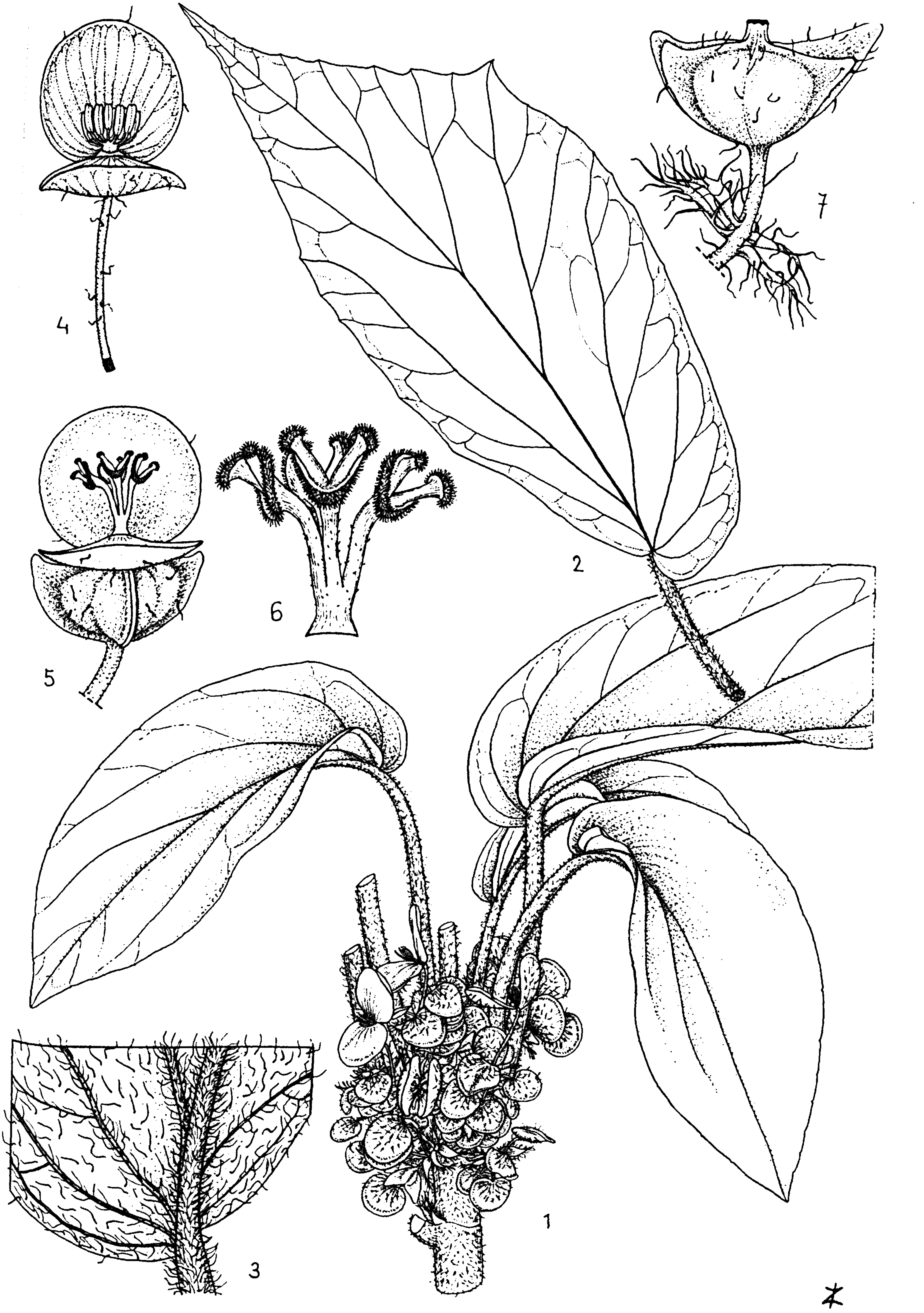
Diagnostic characters (for a more detailed description see Sosef l.c.):

Plant up to 30(–50) cm high. **Rhizome** producing distinct erect stems of 4–15 cm long. **Leaves** not peltate; *petiole* continuing into the midrib without a distinct angle; *leaf blade* usually in more or less vertical position at least in the lower half, narrowly elliptic-ovate to narrowly elliptic-obovate, sometimes elliptic-ovate to elliptic-obovate, gradually attenuate towards the top or slightly acuminate in the upper 1/4 to 1/6, 12.0–24.0 x 3.8–9.7 cm; margin entire to distantly finely serrate (usually in the upper half) or with a few larger teeth, glabrous or with a few cilia; base usually very unequal, one side rounded to cuneate, the other deeply to very deeply cordate; upper surface glabrous or very sparsely hirsute; lower surface pale green, usually shortly hirsute. **Male flower**: *perianth segments* ovate to obovate or broadly so, with a rounded base, 6.1–13.0 x 5.9–12.0 mm, the outside pale yellowish-red to deep purple-red; the upper segment yellow with a red patch and nerves in the basal 1/2 or up to the top on the inside; the lower segment yellow on the inside; *androecium* with 19–26 stamens. **Female flower**: *perianth segments* broadly obovate or circular, 6.8–11.5 x 7.1–13.0 mm; *ovary* very shallowly obtriangular-obovate, 3.3–9.1 x 6.5–14.0 mm, sparsely hirsute; wings usually very shallowly obtriangular-elliptic to very broadly obtriangular, 1.3–3.6 mm wide. **Infructescence**: *fruit* pendulous, very shallowly obtriangular-obovate, (3.3–)5.5–10.5 x (6.5–)11.0–20.0 mm.

Distribution: GABON: Crystal Mountains.

Ecology: Terrestrial on level to steep sloping sites; on clayey soil; in half-shade to shade in primary or secondary evergreen rain forest (with much *Aframomum*)

Figure 17.6. *Begonia erectocaulis* Sosef. – 1: habitus (x$^{1}/_{2}$); 2: upper leaf surface (x$^{1}/_{2}$); 3: detail leaf base lower surface (x1$^{1}/_{2}$); 4: male flower (x1$^{1}/_{2}$); 5: female flower (x1$^{1}/_{2}$); 6: styles (x4) 7: fruit, upside down (x1$^{1}/_{2}$). – 1: living plant at WAG, coll. *Breteler & J.J. de Wilde 300*; 3-7: *Breteler & J.J. de Wilde 300*.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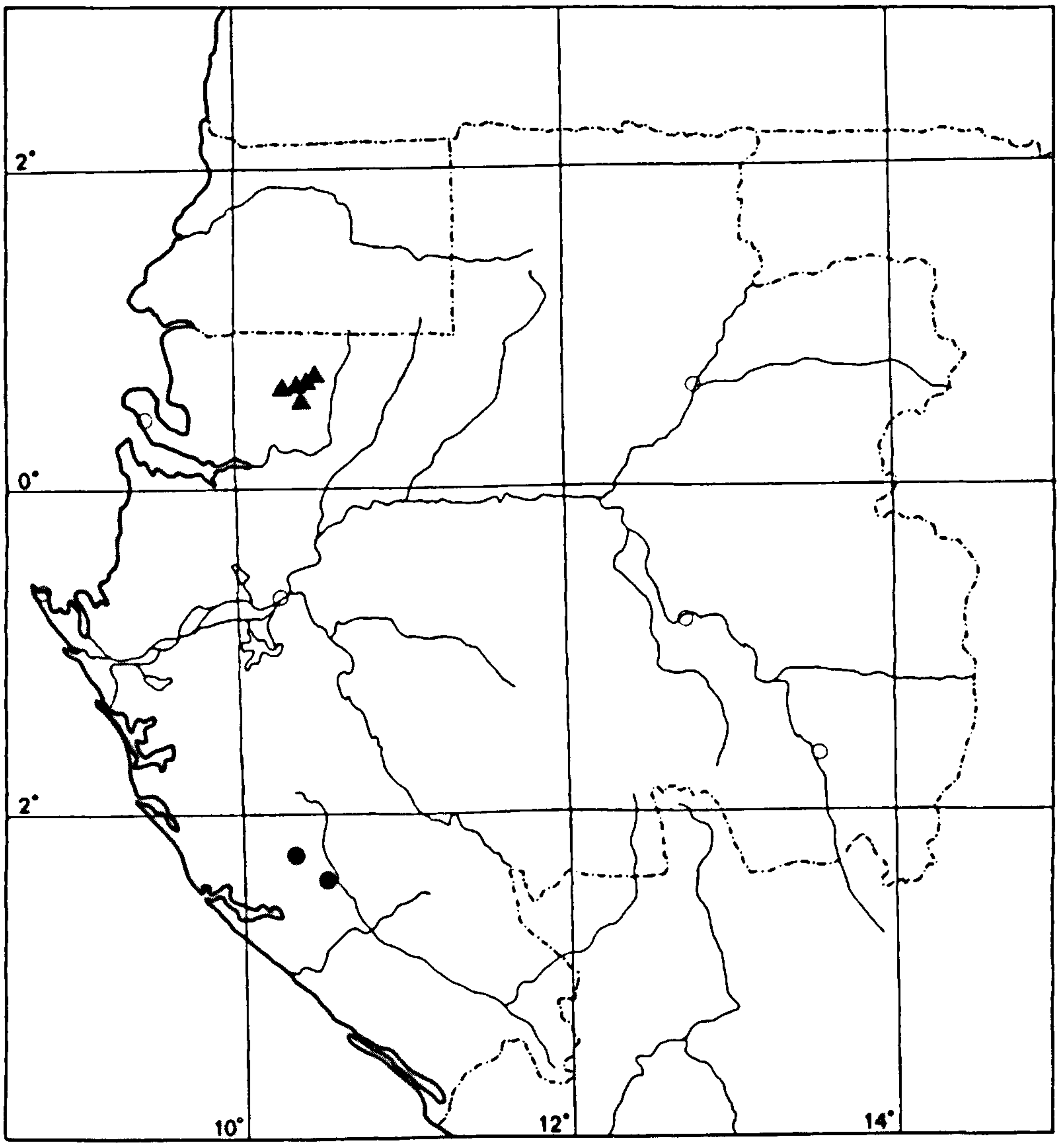


Map 17.3. Distribution of *Begonia dewildei* (dots) and *Begonia erectocaulis* (triangles).

or rarely in very disturbed localities with bananas and oilpalms; often near or along creeks or rivers; at 460–700 m altitude.

Specimens examined:

GABON: *Breteler & J.J. de Wilde 47* (WAG): 13 km along the road from Asok to the hydroelectric power station at Tchimbélé, 00°36'N 10°24'E (fr, 08); *Breteler & J.J. de Wilde 176* (WAG, holo): Crystal Mts, about 15 km NE of Asok, 00°46'N 10°30'E (fr, 08); *Breteler & J.J. de Wilde 300* (WAG): about 3 km along the road from Asok to the hydroelectric power station at Tchimbélé, 00°42'N 10°22'E (fl, fr, 08); *Wieringa 701* (WAG): Crystal Mts, Woleu-Ntem, 1 km SE of Tchimbélé, 00°37'N 10°24'E (fl, 03); *Wieringa 800* (WAG): Crystal Mts, Woleu-Ntem, 11 km NNE of Tchimbélé, 00°42'N 10°27'E (fl, 04); *Wieringa 916* (WAG): Woleu-Ntem, 1 km WNW of Tchimbélé, Bingiligwen R., 00°37'N 10°23'E (fl, fr, 05); *Wieringa 939* (WAG): Crystal Mts, Woleu-Ntem, 1 km SE of Tchimbélé, 00°36'N 10°24'E (fl, fr, 05); *J.J. de Wilde c.s. 10040* (WAG): Crystal Mts, Tchimbélé, trail E of the dam, 00°37'N 10°24'E (fl, fr, 12); *J.J. de Wilde c.s. 10148* (WAG): Crystal Mts, along the road Assok-Méla, NNW of Nkan, 00°40'N 10°19'E (fl, fr, 01); *J.J. de Wilde c.s. (WALK-B) 168* (WAG): Crystal Mts, 12 km along the road Assok to Tchimbélé, 00°37'N 10°23'E (fl, fr, 01).

CULTIVATED: *van Veldhuizen 964* (WAG): Wageningen, Dept. of Horticulture No 1588 (coll. WALK-B 168, Gabon) (fl, 10); *J.J. de Wilde 8791* (WAG): Wageningen, Dept. of Horticulture No 1188 (coll. Breteler & de Wilde 300) (fl, 07).

Begonia erectotricha Sosef **Fig. 17.7, Pl. 6b & c, Map 17.4**

Begonia erectotricha Sosef, Wageningen Agric. Univ. Papers 91-4 (1992) 98, fig. 5, pl 2b,c. – TYPE: *J.J.F.E. de Wilde c.s. (WALK-B) 57* (WAG!, holo): 'Gabon, Cristal Mountains, on forested slope just on the lefthand side of the Kinguélé falls, alt. 200m, 18-I-1983.'

Diagnostic characters (for a more detailed description see Sosef l.c.):

Plant 14–30 cm high. **Leaves** peltate; *leaf blade* in more or less horizontal position, ± symmetrical to slightly asymmetrical, circular to broadly elliptic-obovate or broadly elliptic, rarely elliptic or ovate (3:2), usually with a shortly acuminate top, 12.5–22.5 x 8.4–17.0 cm; margin usually indistinctly and irregularly crenate, sometimes denticulate or almost entire, ciliate; upper surface scattered with erect, usually red or dark red but sometimes whitish hairs. **Male flower**: *perianth segments* very broadly ovate to circular, with a cordate base, 6.2–10.5 x 6.5–11.0 mm; the outside salmon; the upper segment yellow with or without a red patch and nerves at base on the inside; the lower segment yellow on the inside; *androecium* with 28–46 stamens. **Female flower**: *perianth segments* very broadly ovate, 7.0–9.5 x 6.6–13.0 mm; *ovary* very shallowly obtriangular-obovate to very broadly obtriangular, 2.7–7.3 x 6.5–9.5 mm, sometimes with a few long hairs; wings very shallowly obtriangular-obovate to shallowly obovate, 1.2–3.3 mm wide. **Infructescence**: *fruit* pendulous, shallowly obtriangular, 8.7 x 9.0–10.0 mm.

Distribution: GABON: Crystal Mountains.

Ecology: Terrestrial on level to sloping sites or sometimes steep banks; on clayey soil; in shaded to deeply shaded places in primary rain forest; generally associated with streams but also reported to inhabit drier parts along streams or higher up the slopes; found growing together with *Begonia hirsutula*.

Specimens examined:

GABON: *Breteler & J.J. de Wilde 159* (WAG): about 9 km W of Asok, along confluent of the Soung R., 00°43'N 10°16'E (fr, 08); *Breteler & J.J. de Wilde 358* (WAG): on the left bank of the Mbé R., just beneath the hydroelectric power station at Kinguélé, 00°26'N 10°17'E (st, 08); *N. Hallé & Villiers 4455* (P): Crystal Mts, Kinguélé falls, Mbé R., 00°29'N 10°20'E (fl, 01); *N. Hallé & Villiers 4456* (P): ibid. (fl, 01); *N. Hallé & Villiers 4634* (P): ibid. (fl, 01); *N. Hallé & Villiers 4680* (P): Crystal Mts, Gongolane R., 00°32'N 10°15'E (fl, fr, 01); *Wieringa 437* (WAG): Estuaire Prov., Crystal Mts, 0.5 km NE of the dam at Kinguélé, 00°27'N 10°17'E (fl, 01); *J.J. de Wilde c.s. 8872* (WAG): Kinguélé, downstream of the hydroelectric power station, on bank of the Mbé R., 00°26'N 10°16'E (fl, 11); *J.J. de Wilde c.s. 10063* (WAG): Crystal Mts, waterfalls above Kinguélé, 00°27'N 10°17'E (st, 12); *J.J. de Wilde c.s. 10189* (WAG): Crystal Mts, c. 1 km S of Kinguélé, 00°26'N 10°17'E (fl, fr, 01); *J.J. de Wilde c.s. (WALK-B) 57* (WAG, holo; LBV): Crystal Mts, Kinguélé falls, 00°29'N 10°20'E (fl, 01).

Begonia ferramica N. Hallé **Fig. 17.8, Map 17.4**

Begonia ferramica N. Hallé, Adansonia, sér. 2, 7 (1967) 511, pl. 2; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 39-40; L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 165, fig. 3.9; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 15, pl. 9B. – TYPE: *N. Hallé 3489* (P!, holo; BR!): 'Gabon, Bélinga, 12 déc. 1964.'

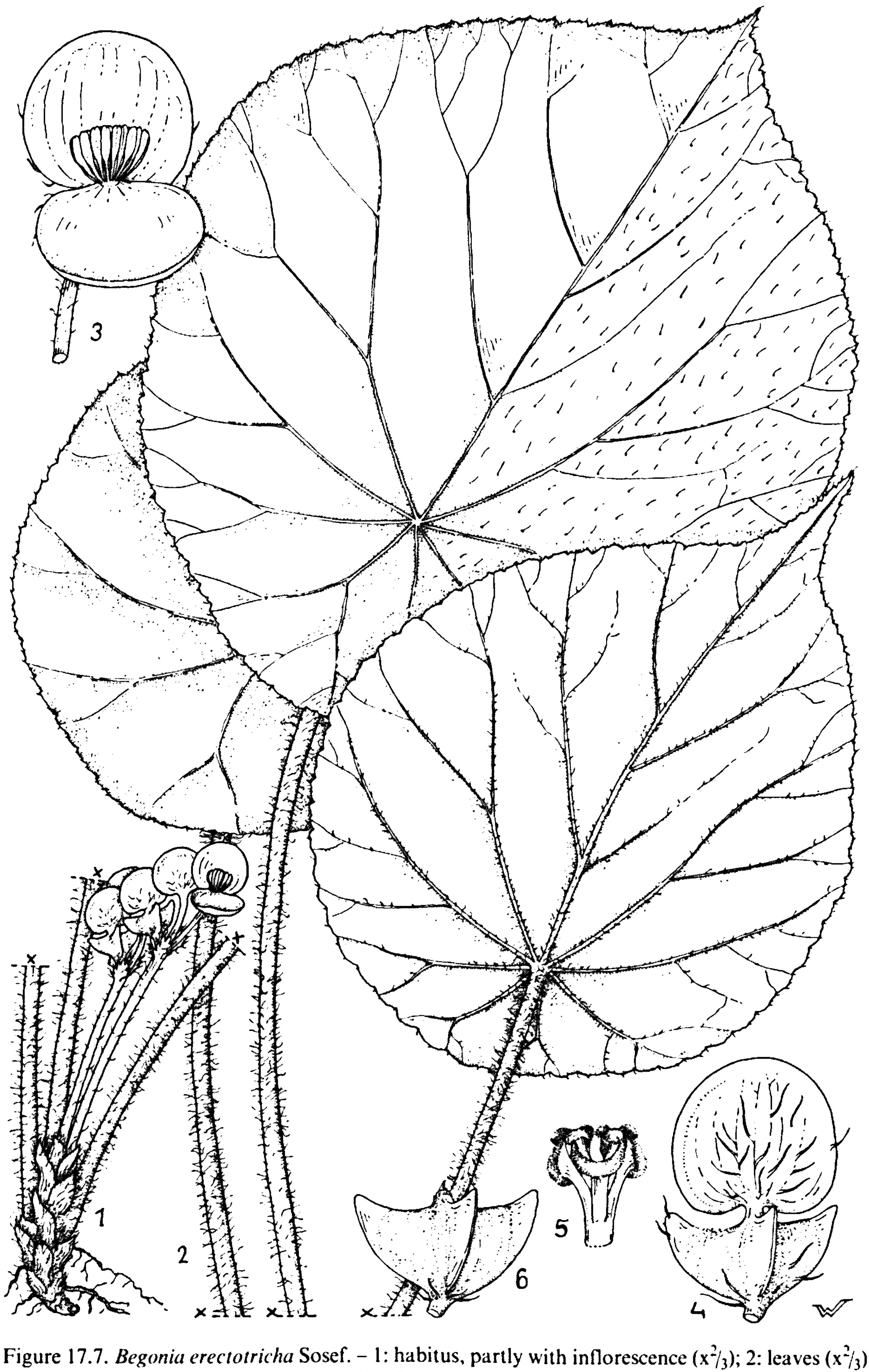
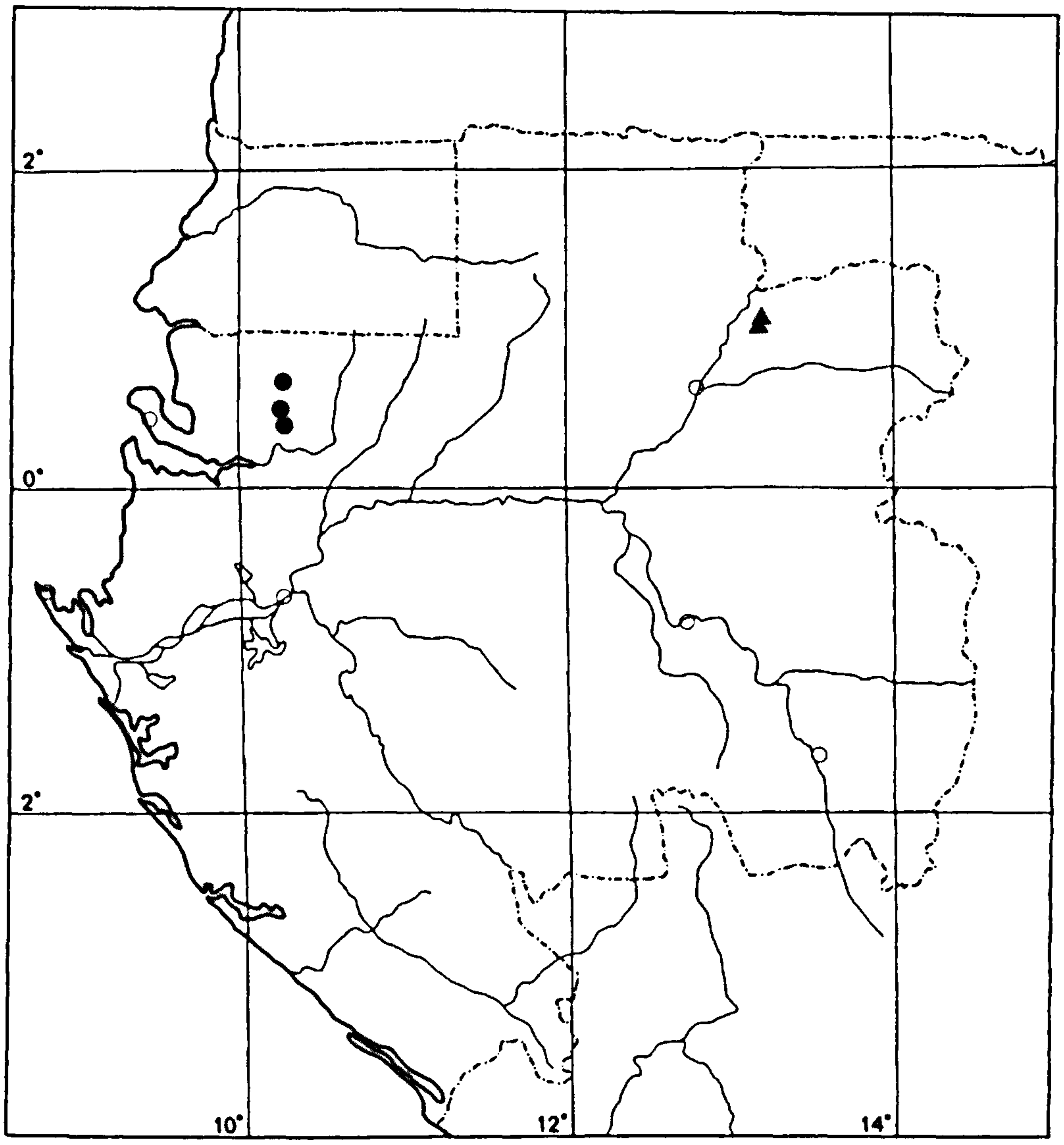


Figure 17.7. *Begonia erectotricha* Sosef. – 1: habitus, partly with inflorescence (x$^2/_3$); 2: leaves (x$^2/_3$); 3: male flower (x2); 4: female flower (x2); 5: styles (x4); 6: fruit (x2). – 1-5: *J.J. de Wilde et al. (WALK-B) 57*; 6: *Breteler & J.J. de Wilde 159*.



Map 17.4. Distribution of *Begonia erectotricha* (dots) and *Begonia ferramica* (triangles).

Plant up to 18 cm high, densely woolly and floccose with long white hairs but often glabrescent and in addition scattered with minute glandular hairs. **Rhizome** usually slender or sometimes fairly stout and woody, somewhat elongated and often zigzag, 0.4–2.9 mm wide; the apical part ascending to erect to form a more or less distinct stem of up to 7 cm long. **Stipules** very broadly triangular-ovate to narrowly so, acute, 0.8–4.4 mm long, pale green, sometimes glabrous; margin entire to dentate, ciliate to woolly. **Leaves** peltate; *petiole* continuing into the midrib with a distinct angle, inserted at 6–24 mm from the nearest margin, 2.0–17.0 cm long, brittle but fleshy, pale green to slightly reddish tinged; *leaf blade* held in a more or less horizontal position, symmetrical to slightly asymmetrical, usually more or less circular, sometimes broadly obovate-elliptic or broadly ovate-elliptic, with a rounded top, 1.8–9.1 x 1.5–7.7 cm, rather juicy, with (6–)7–8(–9) palmate main nerves; margin usually rather coarsely and bluntly dentate, at least in the apical part, sometimes irregularly sinuate, rarely almost entire, concolorous with the blade, the teeth usually topped with a

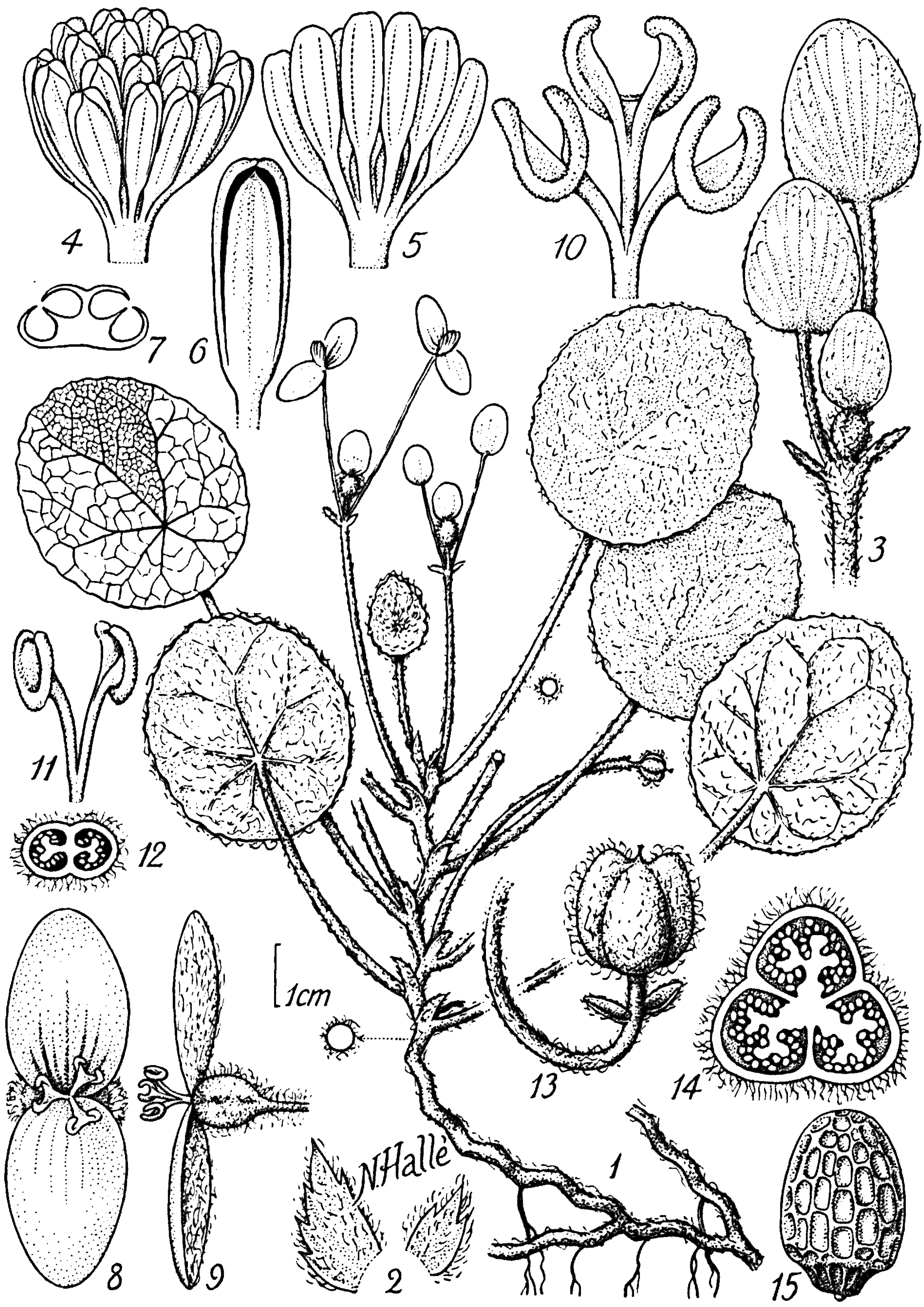


Figure 17.8. *Begonia ferramica* N. Hallé. – 1: habitus; 2: stipules of the same axil; 3: young inflorescence; 4, 5: androecium; 6: anther; 7: anther in cross section; 8, 9: female flowers; 10: styles; 11, 12: styles and ovary in cross section of 2-locular ovary; 13: fruit; 14: fruit in cross section; 15: seed. – 1-15: *N. Hallé 3489 & 3767*. Drawing prepared by Nicolas Hallé, formerly associated with the Musée National d'Histoire Naturelle, Paris.

straight hair; base and top rounded; upper surface medium to pale green, dull, smooth, usually less woolly than the other vegetative parts; lower surface very pale green, dull; *nerves*: the main and larger secondary nerves not prominent and concolorous with the blade or somewhat paler on the upper surface, on the lower prominent, pale to medium green, the smaller secondary nerves distinct, the tertiary ones less so but still well visible, creating a typical reticulate pattern when dry. **Inflorescence** containing (1–)2–3 male flowers and 1 terminal female flower, positioned at about the same level as the leaf blades; *peduncle* simple, 1.0–8.0 cm long, juicy, pale green to pale reddish in the apical part; *bracts* (2–)3–5, often one additional bract present on the pedicel of the female flower, elliptic to ovate or broadly ovate, sometimes very broadly ovate, 0.8–3.6 mm long, pale green; margin dentate in the upper half and ciliate (cilia coarser than the woolly hairs and straight). **Male flower**: *pedicel* elongated at anthesis up to 29 mm, very pale green; *perianth segments* broadly ovate or broadly elliptic to ovate or elliptic, sometimes obovate, with a rounded to cuneate base, 6.5–12.0 x 5.8–8.8. mm, the outside pale orange-yellow or pale reddish yellow; the upper segment deep yellow with a dark red patch and nerves in the basal part on the inside, the lower segment deep yellow on the inside; *androecium* with 10–19 stamens; column 0.25–1.0 mm long; anthers 0.9–1.7 mm long. **Female flower**: similar to the male but distinctly pedicellate, pedicel markedly elongated already at anthesis, in fruit up to 13(–23) mm long; *perianth segments* broadly ovate or circular to ovate or elliptic, sometimes obovate, with a slightly cordate to cuneate base, 6.2–12.5 x 4.4–9.6 mm; *styles* (2–)3, 1.8–4.6 mm long, fused in the lower 1/6 to 1/3, the top split into a rather slender, rounded U-shape, the arms 0.5–1.6 mm long and bearing a slender stigmatic band which is spirally twisted for up to 1/2 a turn; *ovary* broadly obovate or circular to elliptic-obovate or elliptic, sometimes very broadly ovate, 2.3–3.6(–4.9) x 2.0–3.3(–5.2) mm, pale green or pale reddish green, (2–)3-locular, not winged; beak absent or short, 0–1.2 mm long. **Infructescence**: peduncle recurved in the apical part; *fruit* pendulous but on a more or less straight pedicel, broadly elliptic to more or less circular, 3.4–6.8 x 2.6–5.9 mm, dry, with a relatively tough thick wall, pale reddish to pinkish or pale green, dull.

Distribution: GABON: Bélinga.

Ecology: Terrestrial, often in large groups, in fissures, on rocks or sheer rock faces and ridges containing iron; in shaded or medium shaded sites in primary forest or below low trees and shrub; on comparatively dry sites, in cave-like sheltered places; at 700–1000 m altitude.

Notes: 1. The species is at present in cultivation at WAG. In about 1 out of every 3 attempts selfing was successful, so in this species, in contrast to many others from the group studied, no efficient system of incompatibility seems to be present. It took more than 4 months for the fruits to ripen.

2. An aberrant style with an extra small branch arising in between the fork of the stigmatic part was observed in Breteler & de Wilde 650.

3. A narrow endemic species only known from a very restricted area near Bélinga.

Specimens examined:

GABON: *Bos c.s. 10712* (WAG): Babiel-Sud, Okoume road km 1, 01°03'N 13°10'E (fl, 07); *Breteler & J.J. de Wilde 650* (WAG): near summit of Babiel Nord, 01°07'N 13°10'E (fl, fr, 09); *N. Hallé 3489* (P, holo; BR, K): Bélinga, 01°06'N 13°12'E (fl, 12); *N. Hallé 3496* (P): ibid. (fl, 12); *N. Hallé 3767* (BR, P): Bélinga, iron mines, 01°06'N 13°12'E (fl, 06); *N. Hallé & Le Thomas 496* (P): ibid. (fl, 08); *A. Louis c.s. 2372* (WAG): Bakota-Nord, 1-5 km S of Camp Bélinga, 01°04'N 13°12'E (fl, fr, 10).

CULTIVATED: *van Veldhuizen 1313* (WAG): Wageningen, Bot. Garden 'De Dreijen', greenh. no 85PTGA198 (coll. J.J. Bos c.s. 10712, Gabon) (fl, fr, 05).

Begonia hirsutula Hook.f. **Fig. 17.9, Pl. 2a, Map 17.5**

Begonia hirsutula Hook.f. in Oliver, Fl. Trop. Afr. 2 (1871) 575; Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3,2 (1921) 616; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39; L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 179, fig. 2.12 & (as *B. scutulum* Hook.f.) fig. 2.20; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 16, 21, pl. 11D, 16G. – TYPE: *Mann 1649* (K!, holo; K! (upper specimen on the sheet), P!): 'Sierra del Cristal, W. Trop. Africa, Lat. 1° N, july 1862.'

Begonia subfalcata De Wild., Ann. Mus. Congo, sér. 1, Bot. 5,2 (1908) 323; T. & H. Durand, Syll. Fl. Cong. (1909) 235; de Lange & Bouman l.c. 16, pl. 11A. – LECTOTYPE: *E. & M. Laurent 968* (BR!; iso: B!): 'Mogandjo, 9-3-06'.

Begonia klainei Pierre ex Pellegrin, Mém. Soc. Linn. Normandie 26, 2 (1924) 124; L.B. Smith et al. l.c. 186. – TYPE: *Le Testu 997* (P!, holo; BM!): 'Forêt au Mayombe, fleurs jaunes, lavées de rouge. Février 1907.'

Begonia comperei Wilczek, Bull. Jard. Bot. Nat. Belg. 39 (1969) 92; Wilczek, Fl. Congo, Rwanda et Burundi (1969) 41; L.B. Smith et al. l.c. 152, fig. 22.8; de Lange & Bouman l.c. 21, pl. 16A. – TYPE: *Compère 31* (BR!, holo): 'Congo Belge, Kimbuya (Rés. Luki; Terr. Lukula), alt. 400 m, pente: 35° O., vieille forêt hétérogène, 4-8-59'.

Begonia ciliobracteata auct. non Warb.: Mildbr., Wiss. Erg. Zweiten Deutschen Zentr.-Afr. Exp. 2, Bot. (1922) 88; De Wildeman, Ann. Mus. Congo, sér. 1, Bot. 5,3 (1912) 451; Hutch., Dalziel & Keay, Fl. W. Trop. Afr. (ed. 2) 1,1 (1954) 218; Wilczek, Fl. Congo, Rwanda et Burundi (1969) 40; Doorenbos, Begonian 47 (1980) 34-35; Reitsma, Meded. Landbouwhogeschool Wageningen 83-9 (1984) 45, 47, fig. 10D; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39.

Plant up to 25(–30) cm high, scattered with minute glandular hairs, sparsely so on stipules and pedicel of male flower, ususally densely so on petiole, peduncle and ovary. **Rhizome** rather stout and elongated, rather smooth, 1.2–8.3 mm wide, glabrous except for the sparsely hirsute or puberulous younger parts; the apical part directed upwards to form a short stem of up to 3 cm long. **Stipules** narrowly to very broadly triangular or triangular-ovate, blunt to long attenuate, 1.8–8.0(–11.0) mm long, green to dark red, sparsely hirsute or not; margin entire to dentate, ciliate. **Leaves** not peltate or less often peltate; *petiole* continuing into the midrib without a distinct angle, inserted at (1–)4–35 mm from the nearest margin in peltate leaves, (1.0–)3.5–17(–23) cm long, firm, fleshy, pale or bronze green to dark red or purplish red, sparsely to densely hirsute with long patent to slightly appressed wavy white or red hairs; *leaf blade* in a more or less vertical position at least in the lower half, slightly to distinctly asymmetrical or slightly kidney-shaped, obovate to ovate or broadly so, rarely narrowly or very narrowly ovate to narrowly elliptic, blunt to acuminate or more gradually attenuate at the apex, sometimes with one or two outgrowths in the upper half, (3.8–)6.5–19.0

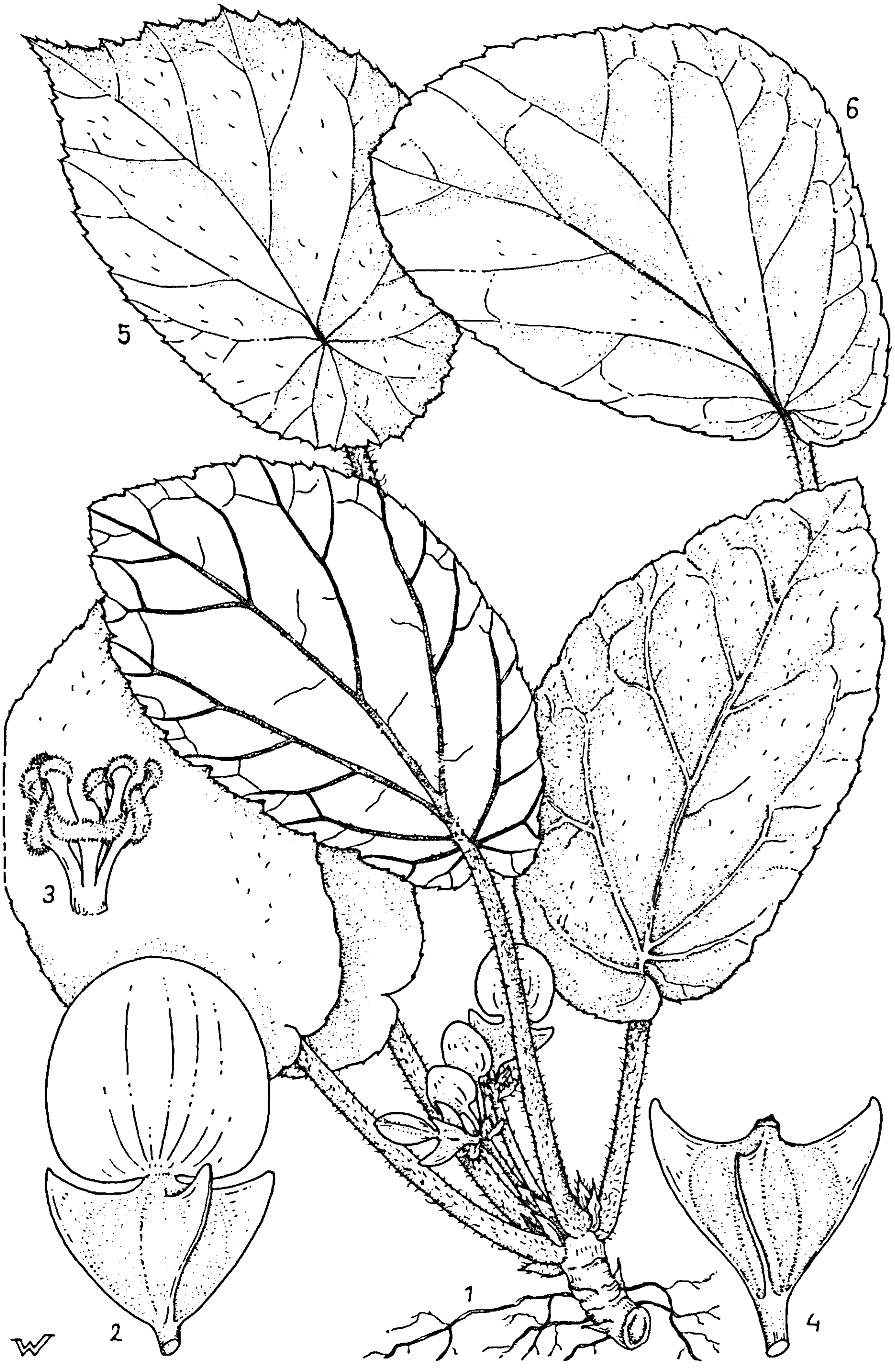


Figure 17.9. *Begonia hirsutula* Hook.f. – 1: habitus ($x^2/_3$); 2: female flower (x2); 3: styles (x4); 4: fruit ($x^2/_3$); 5: peltate leaf ($x^2/_3$); 6: non-peltate leaf ($x^2/_3$). – 1: living plant at WAG, coll. *J.J. de Wilde 7471*; 2, 3, 6: living plant at WAG, voucher *van Veldhuizen 1314*; 4: *J.J. de Wilde c.s. 8921*; 5: *Bos 6311*.

x (1.0–)3.0–11.5 cm, herbaceous to somewhat crispy-leathery, with 6–10 palmate main nerves but the midrib usually most pronounced; margin from almost entire or shallowly sinuate-dentate to distinctly crenate, sometimes serrate or dentate or even double dentate-serrate, sparsely ciliate to ciliate, often with two or more cilia together in between the teeth, concolorous with the blade to red; base rounded or rarely slightly cordate in peltate leaves, in non-peltate ones very unequal, one side rounded to cordate, the other very deeply cordate and with the lobes sometimes overlapping, top acute or sometimes blunt; upper surface dark to light green, sometimes reddish when young, dull to shiny, smooth, not to sparsely hirsute with white to red rather stiff hairs; lower surface pale green to wine-red or purplish red, especially when young, dull; *nerves*: the main and larger secondary nerves not prominent to slightly impressed and concolorous with the blade on the upper surface, on the lower surface prominent, usually brownish green to dark red, sparsely hirsute with patent hairs, the smaller secondary nerves slightly prominent, distinct, tertiary ones less so but still well visible, creating a typical reticulate pattern. **Inflorescence** containing 2–5 male flowers and 1(–3) terminal female flower(s), positioned at the base of the plant, hidden below the leaves; *peduncle* simple, 0.5–5.5 cm long, fleshy, dark red to bronze-green, very sparsely to densely hirsute; *bracts* 3–6(–8), obovate to ovate or narrowly so, rarely circular, 0.8–4.0(–5.5) mm long, dark brown-red to pinkish red or sometimes pale green with a reddish base; margin dentate, ciliate. **Male flower**: *pedicel* elongated at anthesis up to 15(–24) mm, pale red to red, sometimes sparsely hirsute; *perianth segments* broadly or sometimes very broadly ovate to obovate or circular, with a rounded or rarely cordate base, (4.6–)6.5–12.5(–14.0) x (4.2–)6.0–10.0(–12.0) mm, the outside yellow to orange or red or rarely white and often with red stripes, sometimes with a few scattered white or red hairs; the upper segment yellow or sometimes light yellow or rarely white, with a red patch and nerves in the basal 1/2 to 3/4 on the inside; the lower segment yellow or sometimes light yellow, rarely white on the inside; *androecium* with 15–40 stamens; column 0.4–1.0 mm long, anthers 1.3–2.2 mm long. **Female flower**: similar to the male but shortly to distinctly pedicellate, pedicel elongated in fruit up to 4.5(–6.5) mm; *perianth segments* circular or broadly to very broadly ovate, with a rounded to cordate or sometimes cuneate base, (5.9–)7.0–11.0(–15.5) x 6.3–13.0(–19.0) mm; *styles* 3(–4), 2.7–6.5 mm long, fused in the lower 1/2 to 1/4; the top split into a rounded U-shape, the arms 0.6–2.7 mm long and bearing a slender, stigmatic band which is spirally twisted for 1 or sometimes 1/2 a turn; *ovary* very broadly obtriangular-obovate to very shallowly obtriangular, (2.6–)4.5–10.0 x (4.5–)6.0–18.0, dark red to pale green, 3(–4)-locular, 3(–4)-winged at the apical part to all along; the locular part very broadly obovate or broadly elliptic to circular, rarely obovate, 3.8–8.2 mm wide, not hirsute; beak usually present, 0–2.0 mm long; wings patent to slightly erecto-patent, usually very shallowly obtriangular-obovate or slightly obtriangular spathulate, sometimes depressed obovate, rarely to obovate, (1.1–)2.0–9.5 mm wide, the margin glabrous or with a single apical hair. **Infructescence**: peduncle recurved towards the substrate; *fruit* pendulous, very broadly obtriangular-obovate to very shallowly obtriangular, 4.7–11.0 x 8.0–23.0 mm; the locular part rounded obtriangular or broadly obovate to circular, 3.8–9.1 mm wide, dry, with a tough thick wall, pale brown or reddish brown to dark purplish brown, dull.

Distribution: Southern Ghana, south-east Nigeria, Cameroon, Equatorial Guinea, Gabon, Congo and Zaire.

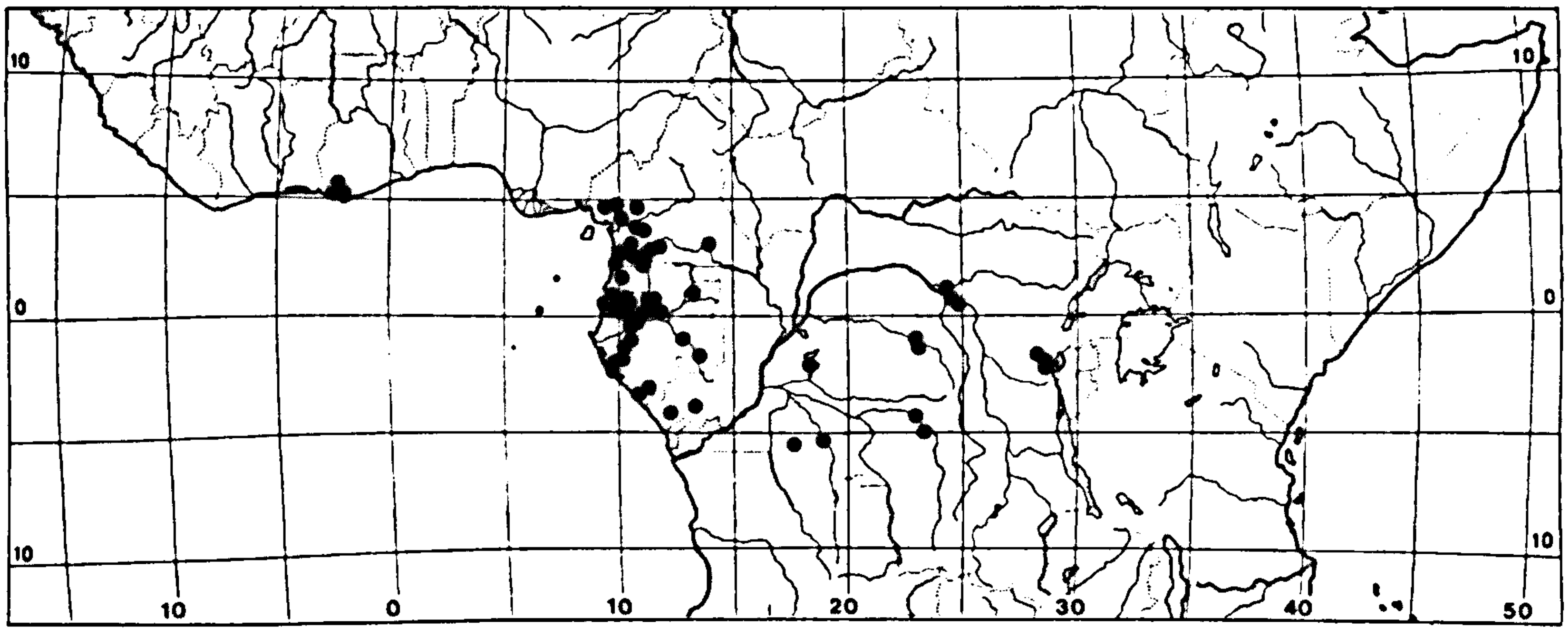
Ecology: Terrestrial on level to very steep clayey to sandy soil or on rocks or rock faces or on decaying trees or sometimes on the base of mossy tree trunks; often locally common and as a rule in damp or even occasionally flooded sites along rocky streams and rivers and then usually in the lower parts of the creekbed or on banks along forest tracks; in half-shaded to deeply shaded sites in primary evergreen or rarely semi-deciduous lowland to montane or elfin forest or sometimes in secondary forest; in swamp forest, forest with *Scorodophloeus*, in hygrophilous coastal evergreen Guineo-Congolian rain forest (forêt biafréenne) or in *Cynometra* forest; found in association with *Begonia mildbraedii*, *B. erectotricha* and *B. scutifolia*, with *Araceae* and on rocks with *Selaginella*; at up to 1000 m altitude.

Vernacular names: boukoulou (Massango, Gabon), sanga (Bakota, Gabon), byiendanda (Kitembo, Zaire), esang-ekada (around Campo, Cameroon), kalokosa (Kirega & Kitembo, Zaire), karakosa (Kinyanga, Zaire), lisolyabalimu (Kinande, Zaire), lobotabota (Turumbu, Zaire).

Uses: The leaves have a sour taste and are eaten like spinach together with fish and crocodile (Gabon).

Notes: 1. The species as here conceived is extremely variable. First of all both peltate and non-peltate leaves are present, as was already discussed in chapter 5.

2. The presence of a few collections with white instead of yellow flowers also contributes to the variability of the species. N. Hallé collected white-flowered specimens in Gabon, near Ndjolé, where I was able to find such specimens as



Map 17.5. Distribution of *Begonia hirsutula*.

well. They grow intermixed with yellow-flowered specimens. The colour of the flower seems not to be fixed within other species as well, viz. *B. ciliobracteata*, *B. heterochroma* and *B. anisosepala*.

3. The shape of the wings on the ovary and fruit is very variable. The collection Dybowski 81 consists of 2 specimens, one with the usual shallowly obtriangular wings, the other with broad and ± obovate ones. These broadly winged specimens do partly break down the boundary with *B. ciliobracteata*, which is otherwise believed to be a distinct and well delimited though closely related species.

4. Last of all the very wide variability in leaf shape within the species should be mentioned. It varies from narrowly ovate to broadly ovate and rather kidney-shaped to almost circular. However, a continuous range of intermediates in all shapes connecting the extremes can be established.

5. At Kew there are 2 sheets of the collection Mann 1649, one of which is a mixture with *B. peperomioides* Hook.f. On the sheet with the mixed collection the upper specimen belongs to *B. hirsutula*. The lower one could well be a part of Mann 1659, the type of *B. peperomioides*, and in that case it is erroneously mounted with Mann 1649.

6. From among the two syntypes cited by De Wildeman E. & M. Laurent 968 was chosen as the lectotype for *B. subfalcata*, as it represents the more complete and rich collection.

Specimens examined:

GHANA: *Andoh 5020* (K): Mamiri F.R., 05°40'N 02°22'W (fl, 04); *Enti & Hall GC 35698* (K): Ankasa F.R., 05°17'N 02°35'W (fl, fr, 07); *Enti GC 42761* (GC): ibid. (fl, fr, 01); *Vigne 1263AB* (K): near Prestea, 05°26'N 02°09'W (fl, 07).

NIGERIA: *P.A. Talbot 458* (BM): Oban, S. Nigeria, 05°20'N 08°35'E (fl).

CAMEROON: *Annet 412* (P): Lolodorf region, Bikeligi, 03°08'N 10°29'E (fl, 06); *Bos 6133* (BR, K, P, WAG, YA): lower slopes of Mt Elephant, SE of Kribi, 02°47'N 10°01'E (fl, 01); *Bos 6311* (P, WAG): foothill of Mt Elephant, about 20 km SE of Kribi, 02°47'N 10°01'E (fl, 02); *Bos 7208* (WAG): 26 km S of Kribi, 02°46'N 09°53'E (st, 08); *De Namur 2311* (YA): Kumba region, c. 04°38'N 09°25'E (st, 02); *Farron 7288* (P, YA): road Douala to Yabassi, 30 km N of the bifurcation towards Edéa, 04°19'N 10°03'E (fl, fr, 05); *Johnston s.n.* (K), identification doubtful: Rio del Rey, 04°44'N 08°39'E (st, 06); *Koufani 44* (P, YA): on slopes of Ngongonjie near Akonetye, 2°30 S of Ebolowa, c. 02°40'N 11°10'E (fl, fr, 01); *Leeuwenberg 8771* (WAG): Bakaka forest, 3 km E of Eboné, village at km 11 on Nkongsamba-Loum road, 04°50'N 09°54'E (fl, 11); *Letouzey 3698* (P, YA): at 5-10 km NW of Ngola, 03°17'N 13°56'E (fr, 04); *Letouzey 9151* (P, YA): banks of the Lobé, 25 km ENE of Campo, 02°30'N 10°02'E (fl, fr, 03); *Letouzey 9338* (P, YA): Nkolonanga ridge, 20 km SE of Kribi, 02°52'N 10°13'E (fl, fr, 04); *Letouzey 9863* (P, YA): ridge near Eminemvom, 20 km SE of Ebolowa, 02°58'N 11°47'E (fl, 01); *Letouzey 10891* (P): near Ndokononoro, 15 km SW of Ndikinimeki, 04°39'N 10°46'E (fr, 12); *Letouzey 10892* (P, YA): ibid. (fl, fr, 12); *Letouzey 11572* (P, YA): Kombeng ridge, 8 km SSE of Matomb, at 50 km WSW of Yaoundé, 03°45'N 11°05'E (fl, 07); *Mildbraed 5665* (B, HBG): South Cameroon forest area, Ebolowa region, Ekuk 22 km E of Ebolowa hills, 02°55'N 11°20'E (fr, 06); *Mildbraed 6166* (B): South Cameroon forest area, Kribi-Kampo region, hills between Ebolowa & Kampo, c. 02°30'N 10°30'E (st, 07); *J. Raynal & A. Raynal 9826* (P, YA): E of Meyo-Biboulou, 36 km SW of Ambam, 02°11'N 11°01'E (fl, 02); *J. Raynal & A. Raynal 9943* (P): 3 km N of Mékoassi, 24 km SW of Ambam, 02°13'N 11°07'E (fl, fr, 02); *J. Raynal & A. Raynal 10029* (P): Nkoemvone, 12 km S of Ebolowa, Cacao station, right side of the Seing, Ntem, 02°48'N 11°09'E (fl, 02); *J. Raynal & A. Raynal 10101* (P): Mendoum, 19 km S of Ambam, between the village and the cristalline ridges in the south, 02°13'N 11°14'E (fl, 02); *J. Raynal & A. Raynal 10162* (P, YA): Mviglimangalé, 15 km E of Nyabessan, 02°24'N 10°32'E (fl, 03); *Sanford 5301* (K, P, YA): 70 miles from Yaoundé on Douala road, 03°50'N 10°40'E (st, 11); *Tessmann 572* (B, K): Campo Distr., Bebai, road to Tniro, 02°22'N 09°53'E (fl, 09); *J.J. de Wilde 7471* (WAG, YA): Cacao station of N'Koemvone, 14 km on the road from Ebolowa to Ambam, 02°48'N 11°08'E (fl, fr, 09); *J.J. de Wilde 8312* (WAG, YA): along the road from Kribi to Campo, 27 km along the road S of Lobé R., 02°43'N 09°52'E (fl, 06); *J.J. de Wilde 8700A* (WAG), identification doubtful: Dipikar Island, about 3 km SE of the bridge crossing the Bongola R., 02°14'N 09°57'E (fr, 12); *W.J. de Wilde & de Wilde-Duyfjes 1976* (P, WAG): about 15 km S of Ebolowa, Kwoeinvom, 02°46'N 11°09'E (fl, 03); *W.J. de Wilde & de Wilde-Duyfjes 1976B* (P, WAG): ibid. (fl, fr, 03).

EQUATORIAL GUINEA: *Guiral s.n.* (P), identification doubtful: Exploration of the Benito, c. 01°40'N 10°00'E (st, 07); *Sanford 5854* (IFE, K): along R. Metom, off the road NW 52 km from Bata on the Rio Benito road, tributary of the R. Benito, c. 01°40'N 10°05'E (fl, 02); *Sanford 5869* (IFE): ibid. (st, 02); *Sanford 5906* (IFE): along R. Metom, Bata, Benito R., c. 01°40'N 10°05'E (fl, 02).

GABON: *Bogner 743* (K): Mbel, 00°16'N 10°10'E (fl, 11); *Breteler 7672* (WAG): between Cap St. Clara and Cap Esterias, 00°36'N 09°16'E (fl, fr, 05); *Breteler 7685* (WAG): 30 km Fougamou-Lambaréné, 01°00'S 10°30'E (fr, 05); *Breteler & J.J. de Wilde 340* (WAG): bank of the Mbé R., just beneath the hydroelectric power station at Kinguélé, 00°26'N 10°17'E (fl, 08); *Breteler & J.J. de Wilde 343* (WAG): 8 km SSW of the hydroelectric power station in the Mbé R. at Kinguélé, 00°23'N 10°15'E (st, 08); *Breteler & J.J. de Wilde 429* (WAG): about 10 km NE of Lalara, 00°24'N 11°32'E (st, 09); *Breteler & J.J. de Wilde 568* (WAG): Bélinga, iron mine exploration area, summit 'The Belvedere', 01°07'N 13°13'E (fl, fr, 09); *Breteler & J.J. de Wilde 585* (WAG): Bélinga, iron mine exploitation area, 01°06'N 13°12'E (fl, fr, 09); *Breteler & J.J. de Wilde 720* (WAG): Bélinga, about 2 km along the lower track of Babiel Nord, 01°06'N 13°10'E (fl, 09); *Breteler & J.J. de Wilde 794* (WAG): about 10 km along the road from Lastoursville to Mékouy, 00°50'S 12°42'E (st, 09); *Breteler c.s. 8277* (WAG): 30 km N of Kango, 00°17'N 10°05'E (fl, 10); *Breteler c.s. 8748* (WAG): near Djidji, 5-10 km W of Koumaméyong, about 1 km from main road, 00°15'N 11°50'E (fr, 04); *Breteler c.s. 9744* (WAG), identification doubtful: near Echira R., 16 km SSW of Rabi-Shell-Camp, 02°05'S 09°55'E (fl, 04); *Breteler c.s. 9940* (WAG): c. 30 km NE of Lastoursville, 00°45'S 12°55'E (fl, fr, 04); *Breteler c.s. 10028* (WAG): ibid. (fl, fr, 04); *Chevalier 26904* (P): Ahiémé, at the Haut Komo, 00°12'N 10°25'E (st, 10); *Courtet s.n.* (L): surroundings of Libreville, 00°23'N 09°27'E (fl, fr, 06); *Dybowski 81* (P): Sibang Forest, 00°25'N 09°31'E (fr, 07); *Farron 7499* (P): 61 km from Libreville on the road to Lambaréné, 00°25'S 10°25'E (fl, fr, 06); *N. Hallé 1707* (P): 10 km SW of Ndjole, CEFA Ayem, 00°14'S 10°42'E (fl, fr, 04); *N. Hallé 2021* (P): ibid. (fr, 05); *N. Hallé 2962* (P): Bélinga, 01°06'N 13°12'E (fl, fr, 11); *N. Hallé 2983* (P): ibid. (fl, 11); *N. Hallé 4085* (P): ibid. (fr, 06); *N. Hallé & Villiers 4457* (P): Crystal Mts, Kinguélé falls, Mbé R., 00°29'N 10°20'E (fl, 01); *N. Hallé & Villiers 4469* (P): Crystal Mts, road to Kinguélé, 00°25'N 10°16'E (fl, fr, 01); *N. Hallé & Villiers 4500* (P): ibid. (fl, fr, 01); *N. Hallé & Villiers 4501* (P): ibid. (fl, fr, 01); *N. Hallé & Villiers 4528* (P): ibid. (fl, 01); *N. Hallé & Villiers 4529* (P): ibid. (fl, fr, 01); *N. Hallé & Villiers 4533* (P): ibid. (fl, fr, 01); *N. Hallé & Villiers 4565* (BR, K, P): ibid. (fl, 01); *N. Hallé & Villiers 4574* (P): ibid. (fl, 01); *N. Hallé & Villiers 4589* (P): ibid. (fl, 01); *N. Hallé & Villiers 4763* (P): Crystal Mts, Nkam-Méla, 00°37'N 10°17'E (fl, 01); *N. Hallé & Villiers 5125* (P): Crystal Mts, Mt Méla, 00°34'N 10°17'E (fl, 02); *N. Hallé & Villiers 5128* (P): ibid. (fl, 02); *N. Hallé & Villiers 5129* (P): ibid. (fl, 02); *N. Hallé & Villiers 5130* (P): ibid. (fl, fr, 02); *N. Hallé & Villiers 5277* (P): Crystal Mts, S of Sanga R., 00°33'N 10°08'E (fl, 02); *N. Hallé & Villiers 5331* (P): Crystal Mts, W of Balakaba R., 00°33'N 10°08'E (fl, 02); *N. Hallé & Villiers 5368* (P): Crystal Mts, 12 km SW of Kinguélé falls, 00°24'N 10°15'E (fl, 02); *N. Hallé & Villiers 5369* (P): ibid. (fl, 02); *N. Hallé & Villiers 5400* (P): Crystal Mts, Kinguélé falls, 00°29'N 10°20'E (fl, 02); *Klaine 2815* (P): Libreville, 00°23'N 09°27'E (fl, 03); *Klaine 3252a* (K, P): around Libreville, 00°23'N 09°27'E (fr, 04); *Klaine 3252b* (P): ibid. (fl, 02); *Le Testu 997* (P, holo; BM): Mayombe forest, c. 03°00'S 10°50'E (fl, 02); *A. Louis 2948* (LBV): Estuaire Prov., road Kinguélé to Kougouleu, c. 00°35'N 10°15'E (fl, fr, 03); *A. Louis, Breteler & de Bruijn 267* (WAG): about 7 km E of M'Voum, 24 km NE of Ntoum, 00°33'N 09°52'E (st, 11); *A. Louis, Breteler & de Bruijn 286* (WAG): near M'Voum, 18 km NE of Ntoum, 00°30'N 09°50'E (st, 11); *A. Louis, Breteler & de Bruijn 452* (WAG): near Lara R., close to Etouk village, on road Mitzic-Médouneu, 00°49'N 11°25'E (st, 11); *van der Maesen & de Bruijn 5638* (WAG): SBL exploitation R2, near Lastourville, 00°47'S 12°45'E (st, 11); *Mann*

1649 (K, holo; B, P): W. Trop. Africa. Lat 1 N, c. 00°55'N 10°25'E (fl, 07); *Mann 1653* (K): W. Trop. Afrika, Crystal Mts, c. 00°55'N 10°25'E (fl, 07); *van Nek 575* (WAG): c. 20 km S of Lake Ezanga, near Lambaréné, 01°10'S 10°13'E (st, 01); *van Nek 582* (WAG): ibid. (fl, 01); *Pobeguin s.n.* (P): Nyanga forest at Dikondou, 03°00'S 11°12'E (fl, 03); *J.M. Reitsma 3730* (WAG): Ofoubou R. bassin, 01°40'S 10°05'E (fl, fr, 06); *J.M. Reitsma c.s. 2112* (WAG): c. 13 km S of Cocobeach, 00°52'N 09°36'E (fl, 04); *J.M. Reitsma c.s. 2971* (LBV, MA, NY, WAG): c. 4 km NNE of Oveng, 00°41'N 11°17'E (fl, 02); *Thollon 815* (P): Franceville, 01°38'S 13°35'E (fr, 07); *Trilles 96* (P): ?, c. 00°20'N 09°40'E (fr); *Trilles 97* (P): ibid. (fr, 09); *Wieringa 410* (WAG): Crystal Mts, 1 km WNW of Tchimbélé, Bingiligwen R., 00°37'N 10°23'E (fl, 01); *Wieringa 434* (WAG): Estuaire Prov., Crystal Mts, 0.5 km NE of the dam at Kinguélé, 00°27'N 10°17'E (fl, 01); *Wieringa 913* (WAG): Crystal Mts, Woleu-Ntem, 1 km WNW of Tchimbélé, Bingiligwen R., 00°37'N 10°23'E (st, 05); *Wieringa c.s. 1601* (WAG): Moyen-Ogooué, 52 km on the road Lambaréne to Fougamou, Mouramboudimbou (ca 2 km S of Tchad), 00°55'S 10°29'E (st, 09); *J.J. de Wilde c.s. 8871* (WAG): Kinguélé dam, downstream of the hydroelectric power station, Mbé R., 00°26'N 10°16'E (st, 11); *J.J. de Wilde c.s. 8879* (WAG): Crystal Mts, about 3 km along the track Alen Nkomo-Andok Foula, 00°15'N 10°05'E (st, 11); *J.J. de Wilde c.s. 8882* (WAG): ibid. (st, 11); *J.J. de Wilde c.s. 8921* (WAG): waterfalls above the hydroelectric power station at Kinguélé, 00°28'N 10°17'E (fl, fr, 11); *J.J. de Wilde c.s. 9269* (WAG): 22 km along the road from Mayumba to Tchibanga, 12 km along forest exploitation track leading in eastern direction, near Doussa R., 03°16'S 10°46'E (fr, 12); *J.J. de Wilde c.s. 9656* (WAG): Rabi Shell oil-concession, c. 300 m SSW of Rabi 46, 01°52'S 09°50'E (st, 11); *J.J. de Wilde c.s. 9834* (WAG): 30 km S of Rabi, affluent of the Echira R., 02°08'S 09°43'E (fl, 11); *J.J. de Wilde c.s. 10087* (WAG): Crystal Mts, 25 km on the road Kinguélé to Tchimbélé, 00°32'N 10°17'E (fl, 01); *J.J. de Wilde c.s. 10090* (WAG): ibid. (st, 01); *J.J. de Wilde c.s. 10190* (WAG): Crystal Mts, c. 1 km S of Kinguélé, 00°26'N 10°17'E (fl, fr, 01); *J.J. de Wilde c.s. 10248* (WAG): Crystal Mts, 25 km along the road Tchimbélé to Kinguélé, 00°31'N 10°18'E (st, 01); *J.J. de Wilde c.s. 10305* (WAG): 10 km on an exploitation track N of Ebèl Alèmbé, bridge over the Mvoro R., 00°12'N 11°05'E (st, 01); *J.J. de Wilde c.s. 10316* (WAG): 32 km on the road Ndjolé-Bifoun, 00°14'S 10°33'E (fl, fr, 01); *J.J. de Wilde c.s. 10327* (WAG), identification doubtful: 15 km NE of Ndjolé, 00°07'S 10°49'E (fl, 01); *J.J. de Wilde c.s. 10328* (WAG): ibid. (fl, fr, 01); *J.J. de Wilde c.s. (WALK-B) 29* (LBV, WAG): Crystal Mts, 7 km along the road from Tchimbélé to Kinguélé, 00°37'N 10°22'E (fl, 01); *J.J. de Wilde c.s. (WALK-B) 64* (LBV, WAG): Crystal Mts, on forested slope just left of the Kinguélé falls, 00°29'N 10°20'E (fl, 01); *J.J. de Wilde c.s. (WALK-B) 219* (WAG): Crystal Mts, 23 km along the road from Tchimbélé to Kinguélé, 00°30'N 10°17'E (fl, 01); *J.J. de Wilde c.s. (WALK-B) 925* (LBV, WAG): about 22 km along the road from Ntoum-Akok Cocobeach and then 1 km along small track in eastern direction, 00°35'N 09°45'E (fl, 03).

CONGO: *Farron 4349* (IEC, P): Fouet forest exploitation, road to Mudongo, 25 km W of Sibiti, 03°40'S 13°20'E (fl, 08); *Koechlin 565* (IEC, P): near Sibiti (Majeur-Congo), 03°41'S 13°21'E (fl, 01); *Lecomte A.75* (P): Kitabi, 04°02'S 12°13'E (fl, 10); *Leroy s.n. B* (P): Ogooué, c. 01°40'S 13°30'E (st); *Thollon s.n.* (P): ? (st).

ZAIRE: *Babault 537* (P): Kashewe (Banga), banks of the Luana R., 01°58'S 28°30'E (st, 08); *Bamps 2919* (BR): Kalehe Terr., Irangi, 01°53'S 28°27'E (fl, 01); *Christiaensen 994* (BR): Kivu Prov., Kalehe Terr., km 110 Kavumu-Walikale road, Irangi vil., Mayi IRSAC, 01°53'S 28°27'E (fl, 07); *Compère 31* (BR, holo): Luki Res., Lukula Terr., Kimbuya, 05°32'S 13°08'E (fl, 08); *Devred 2773* (BR, K): Kiyaka, Kwango, 05°19'S 18°56'E (fl, fr, 11); *Evrard 5324* (BR): Ikela Terr., Yalisenga, Mondombe, 00°49'S 22°43'E (fl, fr, 12); *Gentil 20* (BR): Kondue, Saukuru valley, district L-K., 04°58'S 23°16'E (fl, 11); *Germain 259* (BR): village Itia, road of Yakusu, along the Batukula R., 00°36'N 24°49'E (fl, 05); *Gutzwiller 2034* (BR): Kalehe Terr., Tubalaka, Bunyakiri, 02°04'S 28°34'E (fl, 09); *Gutzwiller 2097* (BR): Kalehe Terr., Mishembe, Bunyakiri, 02°04'S 28°34'E (fl, 09); *Gutzwiller 2213* (BR): Kalehe Terr., Kahuta, Bunyakiri, 02°04'S 28°34'E (fl, fr, 10); *Jans 1143* (BR): Kiri Terr., Mfengwa, Lake Leo, c. 02°00'S 18°20'E (fl, 09); *Jespersen 1911* (BR): swamp of the Loka R., Bongi-Belv. road, c. 01°20'S 23°00'E (fr, 10); *E. Laurent & M. Laurent 968* (BR, holo; B): Mogandjo, 01°21'N 24°20'E (fl, 03); *E. Laurent & M. Laurent 1694* (BR): Romeé, 00°35'N 24°47'E (fl, 01); *E. Laurent & M. Laurent s.n.* (BR): cave at Kondue, 04°58'S 23°16'E (st, 11); *E. Laurent & M. Laurent s.n.* (BR): ravine at Dibele, 04°07'S 22°50'E (fr, 12); *Léonard 240* (BR, K): Yangambi, Isalowe path, 00°46'N 24°28'E (fl, 03); *Léonard 1172* (W): Orientale Prov., Isangi

Terr., Yangambi, 00°46'N 24°27'E (fl, fr, 09); *Léonard 1181* (BR): ibid. (fr, 09); *J. Louis 5668* (BR): Yangambi, Isalowe nature reserve, Lusambila plateau, 00°46'N 24°28'E (fl, 07); *J. Louis 6444* (BR): Yangambi, Isalowe nature reserve, 00°46'N 24°30'E (fl, fr, 10); *J. Louis 6500* (BR, K, MO): ibid. (st, 11); *J. Louis 6668* (BR): Yangambi, springs of the Etchwa, 00°46'N 24°27'E (fl, 11); *J. Louis 8317* (BR): Isalowe nature reserve, 00°46'N 24°30'E (fl, 03); *Troupin 2479* (BR): Kivu Prov., Kalehe Terr., km 110 Kavumu-Walikale road, Irangi, IRSAC reserve, 01°53'S 28°27'E (fl, fr, 09); *Troupin 3143* (BR): ibid., Catena 1/1460m, 01°53'S 28°27'E (st, 03); *Troupin 4543* (BR): ibid. (fl, 08); *Troupin 9130* (BR): ibid., Karambi plain, 01°53'S 28°27'E (fl, 08); *Troupin 10232* (BR): ibid., Catena II, 01°53'S 28°27'E (st, 05); *Troupin 10815* (BR): Kivu Prov., Kalehe Terr., km 108, Irangi, I.R.S.A.C. reserve, 01°53'S 28°27'E (fl, 10); *Vanderyst 16366* (BR): Kisantu-Kwango, Mbau, 05°29'S 17°29'E (fl); *Yafunga 62* (BR, K): Yangambi, close to the Lusambila R., 00°46'N 24°28'E (fr, 01).

CULTIVATED: *Schwerdtfeger 17380* (B): Bot. Garden Berlin-Dahlem, acc. no 104-19-79-33 (fl, fr, 04); *van Veldhuizen 881* (WAG): Wageningen, Dept. of Horticulture, (coll. J.J. de Wilde s.n., Cameroon) (fl, 03); *van Veldhuizen 1098* (WAG): Wageningen, Dept. of Horticulture, (coll. Gabon 'Mitzic', 9-IX-1983) (st, 09); *van Veldhuizen 1314* (WAG): Wageningen, Bot. Garden 'De Dreijen', cult. no 83PTGA566 (coll. Gabon, 9-11-1983, 'Mitzic') (fl, 05); *van Veldhuizen 1396* (WAG): Wageningen, Dept. of Plant Taxonomy, cult. no 85PTGA182 (coll. J.J. Bos 10602, Gabon) (fl, 07); *J.J. de Wilde 7388* (WAG): Wageningen, Dept. of Horticulture, (fl, 01); *J.J. de Wilde 7390* (WAG): Wageningen, Dept. of Horticulture, (fl, 02); *J.J. de Wilde 7392* (WAG): Wageningen, Dept. of Horticulture, (fl, 03); *J.J. de Wilde 8786* (WAG): Dept. of Horticulture, coll. Breteler & de Wilde, Gabon, Mts de Crystal, Mt Méla (fl, 06).

Begonia lacunosa Warb. **Fig. 17.10, Pl. 3a & b, Map 17.6**

Begonia lacunosa Warb. in Engl. & Prantl, Nat. Pflanzenfam. 3,6a (1894) 140; Warb., Bot. Jahrb. Syst. 22 (1895) 42; Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3, 2 (1921) 617; Irmscher in Engl. & Prantl, Nat. Pflanzenfam. (ed. 2) 21 (1925) 574; Hutch. & Dalziel, Fl. W. Trop. Afr. (ed. 1) 1,1 (1927) 187; Exell et al., J. Bot. 67, Suppl. Polypet. (1929) 197; Gossweiler & Mendonça, Carta Fitogeogr. Angol. (1939) 59; Hutch., Dalziel & Keay, Fl. W. Trop. Afr. (ed. 2) 1,1 (1954) 218; Wilczek, Fl. Congo, Rwanda et Burundi (1969) 32; Fernandes, Consp. Fl. Angol. 4 (1970) 297; Doorenbos, Begonian 47 (1980) 35; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39 p.p.; L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 188 (not fig. 2.7!); de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 14, 17, pl. 8A-C, 12B,C. – TYPE: *Preuss 183* (B!, holo; B!): 'Barombi-Station Kamerun, An den kleinen Wasserläufe nördlich von der Barombi-Schlucht, 10.5.89.'

Begonia mayombensis Irmscher, Bot. Jahrb. Syst. 81 (1961) 181; Fernandes l.c. 298; L.B. Smith et al. l.c. 198, fig. 2.15. – TYPE: *Dawe 278* (K!, holo): 'Tropical Africa, Portugese W. Africa, On hills in shady forests, Miconge, Mayombe, Oct. & Nov. 1921.'

Plant up to 13(–25) cm high, scattered with minute glandular hairs, sparsely so on stipules, pedicel of male flower and outside of perianth segments. **Rhizome** rather stout to fairly slender, smooth, 0.9–6.0 mm wide, especially the younger parts hirsute or not; the apical part not or slightly ascending. **Stipules** very broadly triangular to ovate or broadly ovate, sometimes narrowly ovate, usually acuminate to cuspidate, sometimes long attenuate, (1.2–)3.0–8.0(–9.6) mm long, green, glabrous to sparsely hirsute; margin more or less entire to shallowly dentate, ciliate, sometimes sparsely so or rarely not ciliate. **Leaves** peltate; *petiole* continuing into the midrib with a distinct angle, inserted at (2–)6–23(–30) mm from the nearest margin, 1.5–11.0(–22.5) cm long, firm, fleshy, green or brownish green to dark red, usually densely hirsute, rarely sparsely so or almost glabrous at age with rather short to long patent or deflexed, wavy to curly red

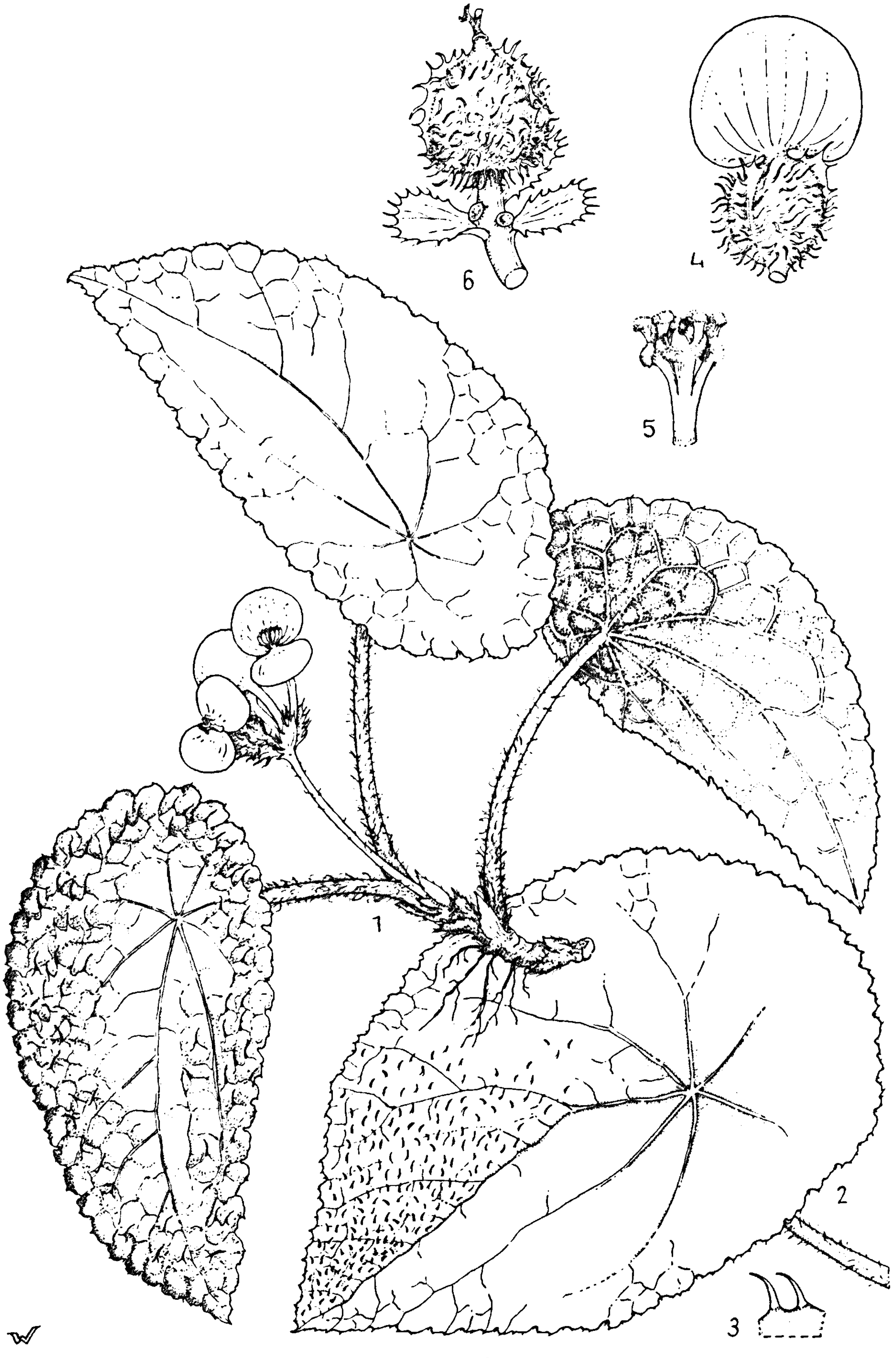


Figure 17.10. *Begonia lacunosa* Warb. – 1: habitus (x$^{2}/_{3}$); 2: only slightly bullate leaf (x$^{2}/_{3}$); 3: detail bullae (x4); 4: female flower (x2); 5: styles (x4); fruit and bracts (x2). – 1: *J.J. de Wilde c.s. (WALK-B) 444*; 2, 3: *J.J. de Wilde c.s. 10380*; 4, 5: *Breteler 7728*; 6: *A. Louis c.s. 895*.

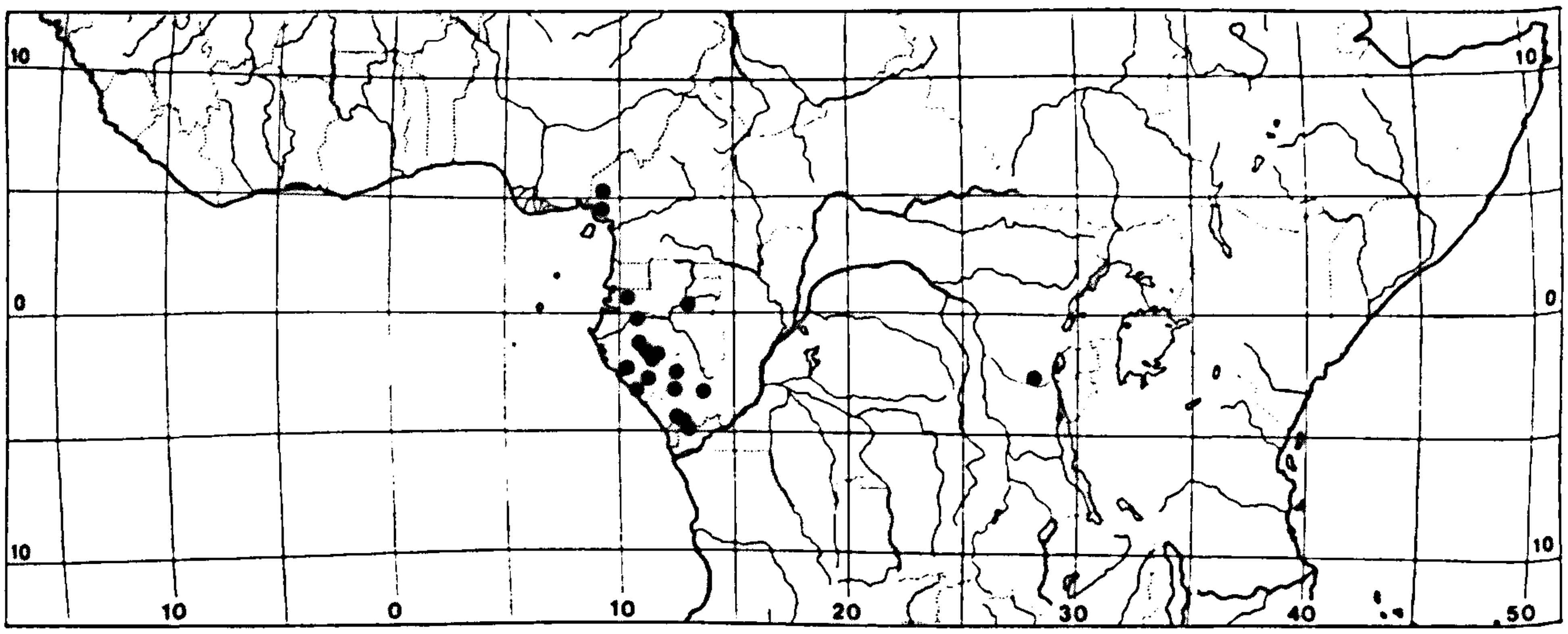
or white hairs; *leaf blade* in a more or less horizontal position, asymmetrical or slightly so, ovate to elliptic-ovate, sometimes broadly so, sometimes slightly kidney-shaped, usually gradually tapering towards the top or slightly acuminate in the apical part, (3.3–)4.0–12.0(–13.5) x 1.7–7.5(–8.9) cm, rather firm crispy-leathery, with (6–)7–8(–10) palmate main nerves, the midrib usually slightly more pronounced; margin usually denticulate, especially in the apical part, rarely almost entire, concolorous with the blade or with the marginal zone, ciliate to sparsely so; base rounded, top acute to blunt or rarely rounded; upper surface very variable in colour, uniformely light or medium green to brownish green or purplish or green in the centre and along the nerves with a broad dark purplish brown marginal zone or green with a large dark purplish brown central spot which extends along the nerves, dull to shiny, very variably bullate, rarely only rugulose or even smooth, usually set with many small bullae arranged in groups but sometimes with large solitary bullae, the bullae topped with one stiff erect white or red hair, rarely only several bullae bearing such a hair, when bullae absent the upper surface densely hirsute; lower surface pale green or dark red and becoming green with age, dull, glabrescent; *nerves*: the main and larger secondary nerves not prominent to slightly sunken and concolorous with the blade on the upper surface, on the lower surface prominent, green, usually hirsute to densely so with patent hairs, sometimes sparsely so, rarely almost glabrous or hirsute with adpressed hairs, the smaller secondary nerves slightly prominent, bearing the same but a more sparse indumentum, tertiary nerves not distinct but still well visible, creating a typical reticulate pattern when dry. **Inflorescence** containing 2–3 male flowers and 1(–2) terminal female flower(s), positioned at approximately the same level as the leaf blades or at the base of the petioles; *peduncle* usually simple, rarely branched once at base, 1.0–10.0 cm long, fleshy, pale green to pinkish, from almost glabrous to hirsute with white hairs; *bracts* 3–4(–5), depressed ovate to broadly ovate, 2.0–7.8 mm long, green to bronze-green or reddish, sometimes with a few long hairs; margin dentate, ciliate. **Male flower**: *pedicel* elongated at anthesis up to 28 mm, yellowish green, sparsely hirsute or not; *perianth segments* very broadly ovate to circular, sometimes ovate, rarely elliptic, with a rounded to cordate base, (5.2–)7.0–15.5(–18.0) x 7.2–18.5 mm, the outside yellow, sometimes slightly orange tinged, sometimes pure white when young or white to cream-coloured even at maturity, with or without long white hairs; the upper segment yellow or sometimes white only when young or even at maturity, with or without a red patch and nerves in the basal half, the lower segment yellow or sometimes white only when young or even at maturity on the inside; *androecium* with 14–28 stamens; column 0.4–1.3 mm long; anthers 1.2–2.1 mm long. **Female flower**: similar to the male but usually shortly though sometimes distinctly pedicellate, pedicel elongated in fruit up to 3.5(–5.6) mm; *perianth segments* transversely broadly elliptic to very broadly ovate, with a cordate base, (6.5–)7.5–17.0 x 8.1–20.0 mm; *styles* 3, 3.3–8.1 mm long, fused in the lower 1/2 to 1/3; the top split into a rounded U-shape, the arms 0.9–2.9 mm long and bearing a slender stigmatic band which is spirally twisted for 1 turn; *ovary* very broadly obovate to broadly elliptic, rarely shallowly obtriangular, 4.2–8.0(–9.8) x (2.3–)4.0–7.5 mm, pale green or reddish to reddish brown, 3-locular, 3-winged at the apical part, sometimes winged all along, but usually one wing distinctly suppressed, hirsute with wavy white hairs; the locular part broadly elliptic to broadly ovate or broadly obovate, (2.0–)2.5–6.4 mm wide; beak absent or present, 0–2.9 mm long; wings patent to erecto-patent, usually depressed obovate to very broadly obovate, rarely shallowly obtriangular, 0.5–4.2 mm wide, very pale greenish white, the margin entire to dentate, ciliate. **Infructescence**: peduncle recurved towards the substrate or not; *fruit* usually pendulous, usually broadly obovate-elliptic to broadly elliptic, sometimes very broadly obovate or shallowly obtriangular, (3.4–)4.5–10.0(–12.0) x (3.5–)5.0–12.0 mm, sometimes practically wingless, dry, green to reddish or dark brown, dull, with a comparatively thick wall.

Distribution: Western Cameroon mountains, Gabon, south-western Congo, western and eastern Zaïre and Angola (Cabinda).

Ecology: Locally common; terrestral or on mossy rocks or rock faces or sometimes on decaying tree trunks; sometimes on level sites but preferably on slopes, creek beds or steep banks, always on moist sites and often in the vicinity of creeks, rivers or waterfalls, sometimes in the spray zone of waterfalls; in shaded to deeply shaded sites in primary to old secondary lowland rain forest; in forest with *Staudtia* and *Pentadesma*, on rocks with *Hymenophyllaceae*, found associated with *Begonia atroglandulosa* subsp. *tshelaensis*; at up to 700 m altitude.

Notes: 1. L.B. Smith et al. (1986) consider the publication of *B. lacunosa* in 1894 a nomen nudum. Since, however, a brief but efficient description of the plant is given, the publication should be regarded as valid. In 1895 Warburg publishes a '*B. lacunosa* Warb. n.sp.' and mentions only one collection: Preuss 183. There is no doubt about this collection being the type since it bears the word 'Original' in Warburgs hand.

2. As a rule *B. lacunosa* has yellow flowers. Observation of a living plant at WAG showed that they are white in bud and turn yellow when they are fully developed and open. North of Ndjolé (Gabon) the present author discovered



Map 17.6. Distribution of *Begonia lacunosa*.

a white flowering population of this species. N. Hallé & Villiers, who collected in the same area encountered white flowering specimens as well. The label of the type collection from western Cameroon states that the perianth segments are 'zartweiss' (creamy white), while also that of Escherich 224 from the same area mentions white flowers. As the colour of the flowers does not seem to be geographically correlated it is not granted any taxonomic status here. It is regarded as another example of the flexibility in the colour of the flower as was also found in e.g. *B. hirsutula* Hook.f.

3. Escherich 224 is slightly aberrant because of its profusely bullate leaves and obovate large fruits which bear obtriangular wings.

4. The only collection from eastern Zaire (Léonard 3876), widely disjunct from the main part of the distribution area of the species, does not differ from the western collections.

5. Breteler 7728 and 7729 represent specimens without bullate leaves that show adpressed hairs on the abaxial nerves. The latter character is also found in the related *B. mbangaensis*. All other characters of the two collections, however, fit in the present concept of *B. lacunosa* and a decision about a possible separate taxonomic status of these specimens is postponed until more material becomes available.

Specimens examined:

CAMEROON: *Escherich 224* (B): Muni area, Atokondama (New-Cameroon), c. 05°20'N 09°20'E (fl, fr, 05); *Preuss 183* (B, holo; P): Barombi – Station, along small creek N of the Barombi-ravine, 04°28'N 09°15'E (fl, 05).

GABON: *Arends c.s. 529* (WAG): about 43 km E of Mouila, on the road to Yeno, 01°46'S 11°20'E (fr, 11); *Arends c.s. 547* (WAG): ibid. (fl, fr, 11); *Arends c.s. 638* (WAG): Doudou Mts, W of Doussala, Moukalaba game reserve, 02°15'S 10°20'E (st, 12); *Arends c.s. 707* (WAG): Doudou Mts, 02°15'S 10°20'E (fr, 12); *Breteler 7716* (WAG): about 20 km Mimongo-Mbigou, Mouyanama lower fall, 01°39'S 11°42'E (fl, fr, 05); *Breteler 7721* (WAG): about 20 km Mimongo-Mbigou, Mouyanama upper fall, 01°39'S 11°42'E (fl, 05); *Breteler 7728* (WAG), identification doubtful: 40 km Mimongo-Lebamba, 01°47'S 11°27'E (fl, 05); *Breteler 7729* (WAG), identification doubtful: ibid. (fr, 05); *Breteler c.s. 8240* (WAG): between Mouila and Yeno, about 50 km on road from Mouila, 01°45'S 11°22'E (fl, 09); *N. Hallé 1352* (P): Mboundou, 37 km SE of Makokou, 00°22'N 13°05'E (st, 02); *N. Hallé 1703* (P): 10 km SW of Ndjolé, CEFA Ayem, 00°14'S 10°42'E (fl, 04); *N. Hallé & Villiers 4693* (P): Crystal Mts, 6 km S of Assok, 00°39'N 10°22'E (fl, 01); *N. Hallé & Villiers 5082* (P): Crystal Mts, Mt Méla, 00°34'N 10°17'E (fl, 02); *Le Testu 5271* (BM): Haute Ngounié, between Mouboungou and Ngoumbi, 01°35'S 11°07'E (fl, 03); *Le Testu 5273* (BM, P): ibid. (fl); *Le Testu 5518* (BM): ibid. (fl, 09); *A. Louis, Breteler & de Bruijn 895* (WAG): Chaillu Massif, near Mouyanama, about 27 km E of Mimongo, 01°39'S 11°46'E (fr, 11); *A. Louis, Breteler & de Bruijn 1288* (WAG): km 20 NE of Forestry Camp Waka, situated about 32 km SE of Sindara, 01°14'S 10°53'E (fl, 12); *Pobeguin s.n.* (P): Dikondou to Moabi, c. 02°45'S 11°15'E (fr, 04); *Thollon 69* (P): Ogóoué, Ndjolé, 00°11'S 10°45'E (fl, fr); *Walker (in herb. Chevalier) 34823* (P): between Dissingo and Mobégo (towards the Waka, near Sindara), c. 01°10'S 10°48'E (fl, 05); *Wieringa c.s. 1450* (WAG): Ngounié, 22 km on the road from Lebamba to Yéno, 02°03'S 11°27'E (fr, 08); *J.J. de Wilde c.s. 9199* (WAG): 22 km along the road Mayumba to Tchibanga and than 10 km along a forest exploitation track near the Doussa R., 03°16'S 10°45'E (st, 12); *J.J. de Wilde c.s. 9263* (WAG): 22 km along the road from Mayumba to Tchibanga, 12 km along a forest exploitation track leading in an eastern direction, near Doussa R., 03°16'S 10°46'E (fl, fr, 12); *J.J. de Wilde c.s. 9523* (WAG), identification doubtful: Doudou Mts., 88 km NNW of Doussala on the track towards Bongo, c. 02°20'S 10°20'E (fl, fr, 03); *J.J. de Wilde c.s. 9642A* (WAG): 50 km along the road Mouila-Yeno, 01°42'S 11°30'E (st, 03); *J.J. de Wilde c.s. 10279* (WAG): 9 km N of Ndjolé, exploitation track of E.F.G., 00°07'S 10°45'E (fl, fr, 01); *J.J. de Wilde c.s. 10362* (WAG): 59 km on the road Mouila-

Yéno, 01°43'S 11°25'E (fr, 02); *J.J. de Wilde c.s. 10363* (WAG): 59 km on the road Mouila-Yéno, 01°43'S 11°25'E (fr, 02); *J.J. de Wilde c.s. 10380* (WAG): 50 km on the road Mouila-Yéno, 01°43'S 11°23'E (fl, fr, 02); *J.J. de Wilde c.s. 10439* (WAG): 34 km on the road Lebamba-Yéno, 01°58'S 11°25'E (fr, 02); *J.J. de Wilde c.s. (WALK-B) 342* (LBV, WAG): Chaillu Massif, Missionary Station at Mouyanama, about 15 km on the road from Mimongo to Mbigou, 60 km along the road from Mbigou, 01°39'S 11°46'E (st, 02); *J.J. de Wilde c.s. (WALK-B) 444* (WAG): ibid. (fl, 02); *J.J. de Wilde c.s. (WALK-B) 474* (LBV, WAG): ibid., waterfall about 45 minutes walking dist., 01°39'S 11°46'E (fl, 02).

CONGO: *Bouquet 1792* (IEC, P): Ndoumou Mts, near Mandili village, 03°19'S 13°40'E (st, 10); *Bouquet & Sita 2309* (IEC, P): Komono region, Makaga village, 03°09'S 12°24'E (fl, fr, 01); *De Namur 2667* (WAG): Mayombe, 5 km after Pounga towards Pte Noire, 04°18'S 12°27'E (fl, 07); *Dybowski s.n.* (P): Mayombe forest, c. 04°30'S 12°30'E (st, 05); *Leroy A* (P): Ogooué, c. 01°40'S 13°30'E (st, 95); *Sita 3495* (IEC): Niari Region, Mayoko Distr., Mt Lekoumou, around Mayoko, 02°19'S 12°51'E (fr, 03); *Sita 4882* (BR): Chaillu, Bowal of Itsokelé at Kouyi, 02°29'S 12°25'E (st, 07); *Thollon 1362* (P): Mayumbe forest, c. 04°30'S 12°30'E (fl, 11).

ANGOLA: *Dawe 278* (K, holo; B): Miconge, Mayombe, 04°26'S 12°48'E (fl, 10); *Gossweiler 7990* (BM, COI, K, LISJC, LISU): border of Zanza-Lufo R., Belize area, Mayombe, 04°34'S 12°37'E (fl, 04).

ZAIRE: *Breyne 2643* (BR): Tshela zone, Maduda, 04°56'S 13°06'E (fl, 08); *Breyne 4507* (BR): Tshela zone, Maduda-Nkai-Mbaku, 04°49'S 13°06'E (fr, 11); *Léonard 3876* (BR): Shabunda Terr., Luamba, 02°38'S 28°09'E (fl, 04); *Tilquin 111* (BR): Tshela Terr., Lubonga R. at the Maduda road, 04°46'S 13°06'E (fl, 03).

CULTIVATED: *van Veldhuizen 885* (WAG): Wageningen, Dept. of Horticulture, (fl, 04); *van Veldhuizen 1090* (WAG): Wageningen, Dept. of Horticulture No 1416A (coll. Breteler 7716, Gabon) (fl, 09); *van Veldhuizen 1091* (WAG): Wageningen, Dept. of Horticulture No 1416B (coll. Breteler 7716, Gabon) (st, 09); *van Veldhuizen 1095* (WAG): Wageningen, Dept. of Horticulture No 1598 (coll. J.J.F.E. de Wilde et al. (WALK-B) s.n., Gabon, Mouyanama) (st, 09).

Begonia laporteifolia Warb. **Fig. 17.11, Map 17.7**

Begonia laporteifolia Warb., Bot. Jahrb. Syst. 22 (1895) 41; Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3,2 (1921) 617; Hutch. & Dalziel, Fl. W. Trop. Afr. (ed. 1) 1,1 (1927) 187, fig. 82; Hutch., Dalziel & Keay, Fl. W. Trop. Afr. (ed. 2) 1,1 (1954) 218; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 39-40; L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 189, fig. 2.11; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 19, pl. 15A. – LECTOTYPE: *Preuss 563* (B!; iso: K!): 'Kamerun: Barombi-Station, Urwald süd. der Station an Bäche. Blbs. weiss, am Gründe Karmin. 4.10.90.'

Begonia schlechteri Gilg, Bot. Jahrb. Syst. 34 (1904) 93; Schlechter, West Afr. Kautschuk-Exp. 1899/1900 (1900) 301 (nomen nudum); Engl. in Engl. & Drude l.c.; Hutch. & Dalziel l.c.; Hutch., Dalziel & Keay l.c.; L.B. Smith et al. l.c. 230, fig. 2.10. – TYPE: *Schlechter 12915* (B!, holo; BM!, G!, K!, Z!): 'Inter Mafura et Mundame (Kamerun), 300 m, I 1900.'

Begonia hypogaea Winkler, Bot. Jahrb. Syst. 38 (1906) 261; Irmscher in Engl. & Prantl, Nat. Pflanzenfam. (ed. 2) 21 (1925) 567. – NEOTYPE: *Preuss 563* (see notes).

Plant up to 20 cm high, scattered with minute glandular hairs, sparsely so on bracts and pedicel of male flower. **Rhizome** rather stout to fairly slender, smooth to knotted, 1.7–5.7 mm wide, hirsute especially around the leaf axils; the apical part not or slightly ascending. **Stipules** very broadly triangular-ovate to triangular-ovate, acute to acuminate or sometimes long attenuate, (0.7–)1.6–6.7 mm long, glabrous or sometimes with a few long hairs on the lower side; margin dentate, ciliate. **Leaves** peltate; *petiole* continuing into the midrib without a dis-

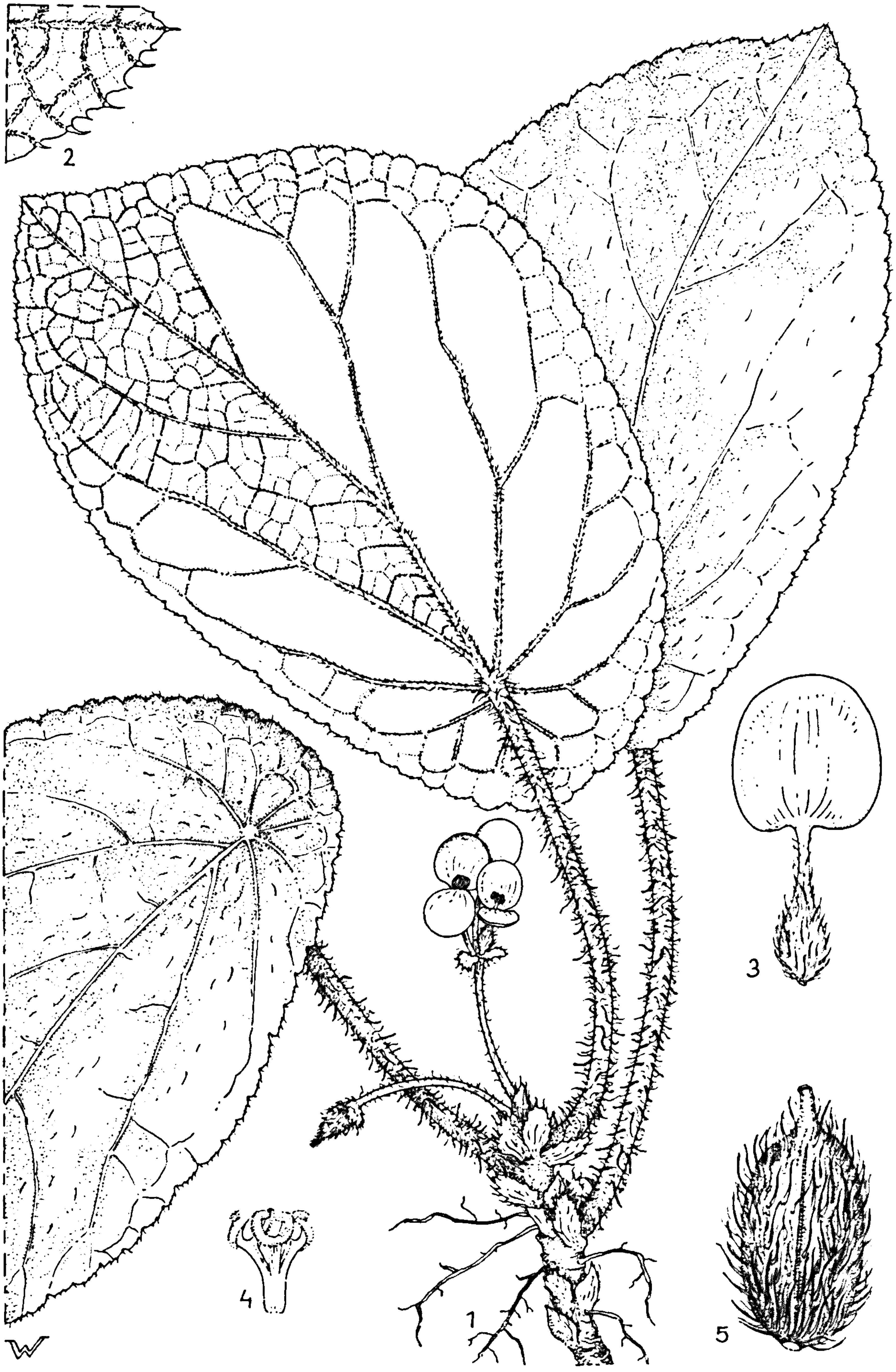


Figure 17.11. *Begonia laporteifolia* Warb. – 1: habitus (x$^{2}/_{3}$); 2: detail lower leaf surface (x2); 3: female flower (x2); 4: styles (x4); 5: fruit (x4). – 1, 2, 5: *Preuss 563*; 3, 4: *Thomas & McLeod 5330.*

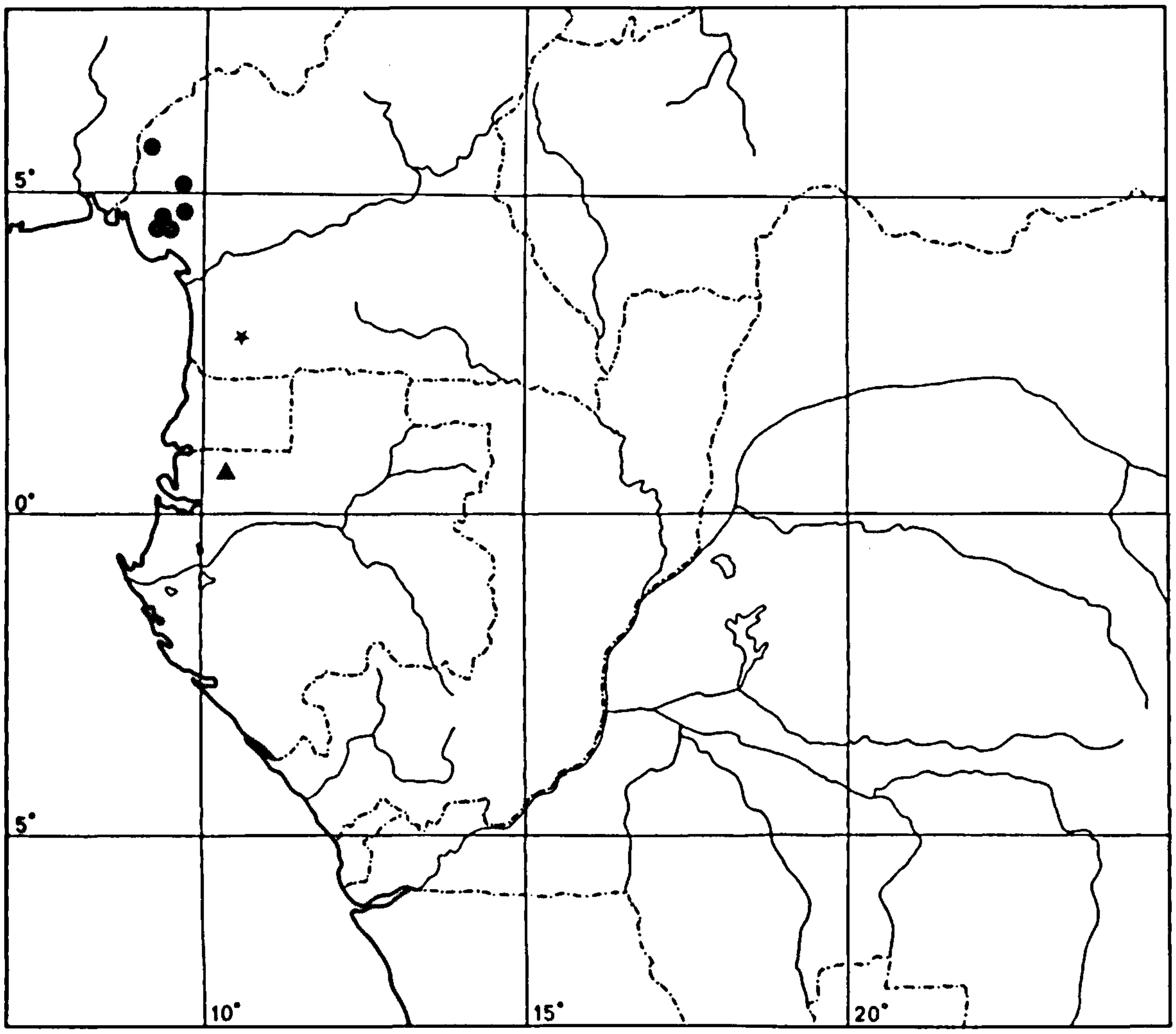
tinct angle, inserted at (2–)7–24 mm from the nearest margin, (0.5–)2.0–13.5 cm long, firm, fleshy, deep green, densely hirsute or sometimes sparsely so with long patent, straight to wavy hairs and with a dense to very dense indumentum of short, curly hairs; *leaf blade* in a more or less vertical position in the lower half, asymmetrical, usually elliptic-obovate to elliptic or broadly elliptic-obovate to broadly elliptic, sometimes slightly kidney-shaped, with a rounded or gradually tapering or rarely slightly acuminate apical part, (2.3–)5.5–17.5 x (1.0–)3.0–10.0 cm, rather firm, with 8–9 palmate main nerves, the midrib slightly more pronounced; margin concolorous with the blade, crenate or sometimes serrulate, ciliate, often with two or more cilia together in the incisions; base rounded, top rounded or rarely acute; upper surface rugose, dark green, dull to rather glossy, glabrous to sparsely hirsute with long erect white hairs with a red base; lower surface pale green, dull; *nerves*: the main and larger secondary nerves on the upper surface slightly sunken to slightly prominent, concolorous with the blade, on the lower surface distinctly prominent, green and sparsely to densely hirsute with long wavy hairs and with short curly ones, the smaller secondary nerves prominent (and very distinct due to the indumentum), generally lacking the long hairs, tertiary nerves distinct, creating a typical reticulate pattern. **Inflorescence** containing 2–3 male flowers and 1 terminal female flower, below or at approximately the same level as the leaf blades; *peduncle* simple, (0.5–)2.0–8.0 cm long, fleshy, sparsely hirsute with long wavy hairs and with a dense to very dense indumentum of short curly hairs; *bracts* 3–4, ovate to almost circular, 0.8–4.9 mm long, red; margin dentate, ciliate. **Male flower**: *pedicel* elongated at anthesis up to 20 mm, sparsely shortly hirsute; *perianth segments* broadly or very broadly ovate to almost circular, with a rounded base, 5.2–17.0 x 5.6–14.0 mm, white or pinkish with a red patch and nerves in the basal half; the outer surface usually sparsely hirsute; *androecium* with (7–)19–38 stamens; column 0.25 mm long; anthers 1.4–1.7 mm long. **Female flower**: similar to the male but almost sessile to very shortly pedicellate, pedicel elongated in fruit up to 0.4 mm; *perianth segments* circular to very broadly obovate, with a rounded to cuneate base, 7.9–14.0 x 7.7–12.0 mm; *styles* 3, 3.6–6.1 mm long, fused in the lower 1/2; the top split into a U-shape, the arms 0.9 mm long and bearing a slender, stigmatic band which is spirally twisted for 1/2 a turn; *ovary* circular to elliptic or elliptic-ovate, 3.2–4.6 x 2.3–4.6 mm, red, 3-locular, not winged, densely hirsute; beak present, often distinct, 1.6–5.1 mm long. **Infructescence**: peduncle recurved towards the substrate; *fruit* pendulous, circular, globose, 3.3–5.8 x 2.6–4.5 mm, dry, with a tough thick wall, dull.

Distribution: Western Cameroon.

Ecology: Rare but locally common; terrestrial on the forest floor or on rocks or rock faces; on steep slopes of stream beds or near waterfalls; in shaded sites in primary or disturbed lowland rain forest; at 100–900 m altitude.

Notes: 1. Preuss 563 is chosen as the lectotype because it represents the richest collection of the two mentioned in the original publication.

2. Winklers description of *B. hypogaea* clearly refers to *B. laporteifolia*. He mentions hairy fruits which are berry-like, and thus presumably not winged, nerves



Map 17.7. Distribution of *Begonia laporteifolia* (dots), *Begonia mbangaensis* (star) and *Begonia peperomioides* (triangle).

on the leaf which are thick and reticulate on the lower surface and white flowers. This combination of characters leaves no doubt about the identity of the specimens he describes. Unfortunatly, no material is mentioned in the protologue and no Winkler specimen which could serve as type could be located. Therefore, a neotype should be appointed. As there is no doubt about the identity of *B. hypogaea*, it seems best to make the name a homotypic synonym of *B. laporteifolia* by chosing the same type as for the latter name, hence Preuss 563.

Specimens examined:

CAMEROON: *Brenan & Onochie 9423* (K): Kumba Div., Banga, S. Bakundu Forest Reserve, by the path to Bopo near Banga village, 04°24′N 09°27′E (fl, 03); *Ledermann 6473* (B): Lom station, 04°43′N 09°43′E (fl, 12); *Letouzey 13736* (K, P, WAG, YA): falls of the Akoumayip R., along Agborkem path (ex Ossidinge) at Tabo 20 km W of Mamfe, 05°44′N 09°07′E (fl, 06); *Preuss 157* (B): Barombi station, in valley along Barombi R., SSW of the station, 04°28′N 09°15′E (fl, 04); *Preuss 563* (B, lecto and neo; iso: K): Barombi station, forest S of the station at Kumba, 04°28′N 09°15′E (fl, 10); *Schlechter 12915* (B, holo; BM, G, K, Z): between Mafura and Mundame, 04°32′N 09°30′E (st, 01); *Swarbrick 226* (FHI, YA): Barombi-Kang, Kumba, 04°38′N 09°22′E (fl, 06); *Thomas 2479* (P, WAG, YA): South-West Prov., at Baroumbi Kang Rest House, 04°35′N 09°28′E (fl, 08); *Thomas c.s. 5330* (WAG): South-West Prov., Bakossi Mts, W of Bangem, 05°05′N 09°42′E (fl, 01).

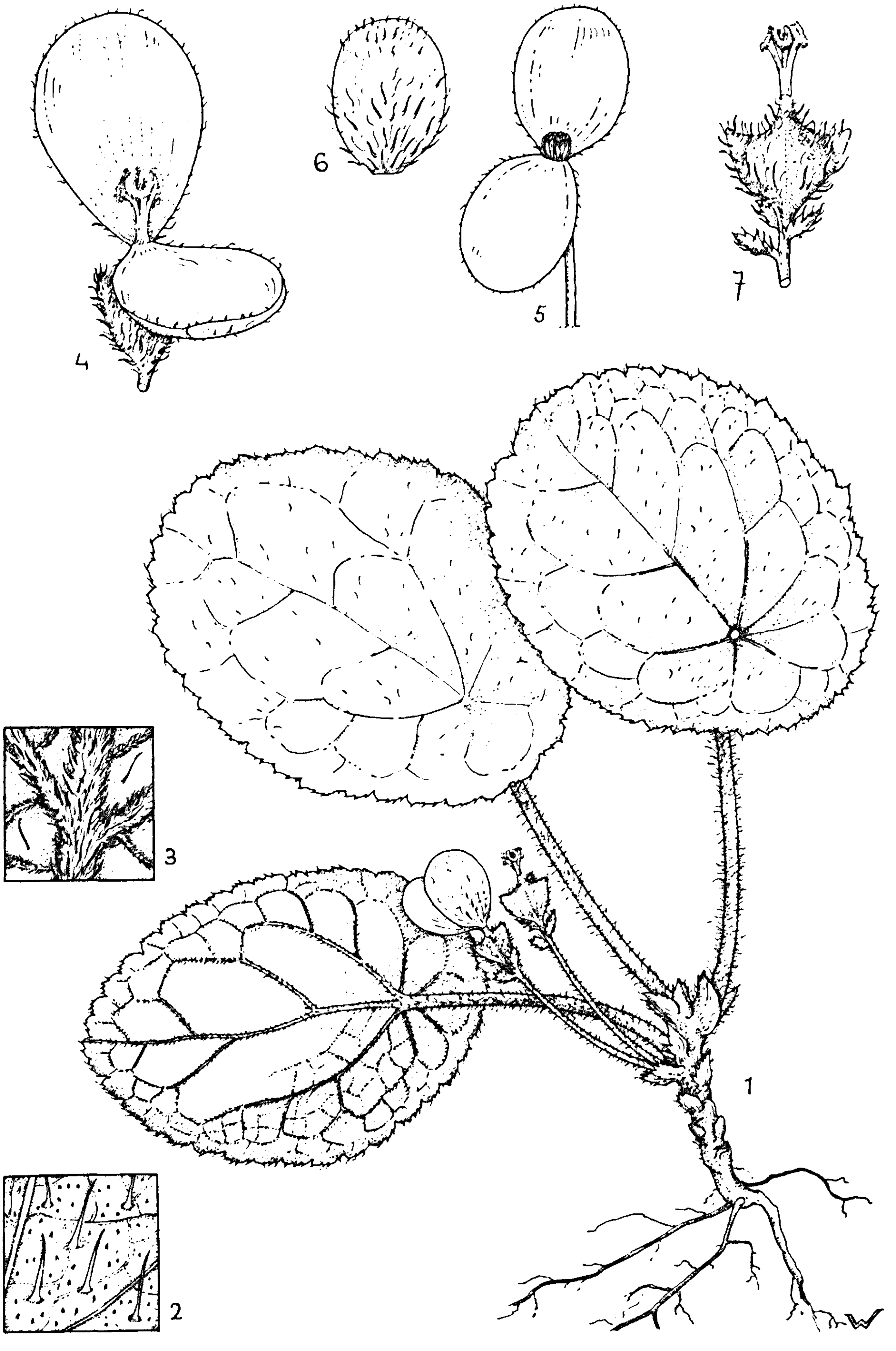


Figure 17.12. *Begonia mbangaensis* Sosef. – 1: habitus (x$^{2}/_{3}$); 2: detail upper leaf surface (x4); 3: detail lower leaf surface and nerves (x4); 4: female flower (x2); 5: male flower (x2); 6: outer surface perianth segment male flower (x2); 7: fruit with style remnants (x2). – 1-4, 7: *Letouzey 9460*; 5, 6: *Bates 297.*

Begonia mbangaensis Sosef — **Fig. 17.12, Map 17.7**

Begonia mbangaensis Sosef, Wageningen Agric. Univ. Papers 91-4 (1992) 133, fig. 4. – TYPE: *Letouzey 9460* (P!, holo; YA!): 'Cameroun, colline Nkolesesan près Mbanga (km 81 route Kribi-Ebolowa près sous préfecture Akom II) feuille IGN 1/200.000 Nyabessan. 26 Avril 1968.'

Diagnostic characters (for a more detailed description see Sosef l.c.):

Plant up to 10 cm high. **Leaves** peltate; *leaf blade* symmetrical to slightly asymmetrical, circular or broadly elliptic to broadly elliptic-ovate, with a rounded apical part, 4.8–10.5 x 3.5–8.8 cm; margin crenate, ciliate; top rounded; upper surface scattered with long, straight, erect, red hairs in a regular pattern but glabrescent; *nerves*: the main and larger secondary nerves on the lower surface distinctly prominent, hirsute or densely so with appressed or sometimes erecto-patent hairs, the smaller secondary nerves distinct and prominent, hirsute with appressed hairs. **Male flower**: *perianth segments* broadly elliptic, with a rounded base, 9.7 x 8.5 mm; the upper segment yellow on the outside and yellow with a few red nerves at base on the inside, the lower segment yellow; *androecium* with 23 stamens. **Female flower**: *perianth segments* broadly elliptic-ovate, with a rounded base, 11.0–15.0 x 10.0–13.0 mm; *ovary* transversely broadly obtriangular, 3.5–4.8 x 7.2–9.2 mm, hirsute with red hairs; wings very broadly obtriangular to very shallowly obtriangular, 1.3–2.6 mm wide.

Distribution: CAMEROON: Centre-Sud Prov.

Ecology: Hygrophilous coastal evergreen Guineo-Congolian rain forest ('forêt biafréenne') with *Caesalpinioideae*.

Notes: 1. A species represented by only 3 collections possibly all collected around the same locality. The label going with Bates 298 mentiones 'Batanga' while that of 297 notes 'Efulen'. It is assumed that both were collected near the latter village, which is very close to the collecting locality of Letouzey 9460.
2. Letouzey noted on the label going with the type specimen that the tepals were 20 x 15 mm but in the dried material they are much smaller.

Specimens examined:

CAMEROON: *Bates 297* (K): Efulen, 02°47'N 10°32'E (fl, 07); *Bates 298* (BM): Batanga [? probably also near Efulen], 02°47'N 10°32'E (fl); *Letouzey 9460* (P, holo; YA): Nkolesesan hill near Mbanga (km 81 road Kribi-Ebolowa near subdistr. Akom II), 02°49'N 10°32'E (fl, 04).

Begonia mildbraedii Gilg — **Fig. 17.13, Map 17.8**

Begonia mildbraedii Gilg in Mildbraed, Wiss. Erg. Zweiten Deutschen Zentral-Afr. Exp. 1907-1908, 2 (1913) 574; De Wildeman, Ann. Mus. Congo, Bot. sér. 5,3 (1912) 451 (nom. nud.); Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3,2 (1921) 617; Irmscher in Engl. & Prantl, Nat. Pflanzenfam. (ed. 2) 21 (1925) 574; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 16, 17, 19, pl. 10F, 12G, 13A,D. – TYPE: *Mildbraed 3124* (B!, holo): 'Mawambi – Awakubi, Abarangu. Hochwald am Wege. Mitte April 1908.'

Begonia quadrialata auct. non Warb.: De Wildeman, Ann. Mus. Congo, Bot. sér. 5,2 (1908) 321; T. & H. Durand, Syll. Fl. Congol. (1909) 234 p.p.; De Wildeman. Ann. Mus. Congo, Bot. sér. 5,3 (1912) 451; Wilczek, Fl. Congo, Rwanda et Burundi (1969) 38, pl. 4.

Begonia calabarica auct. non Warb.: Wilczek l.c. 35.

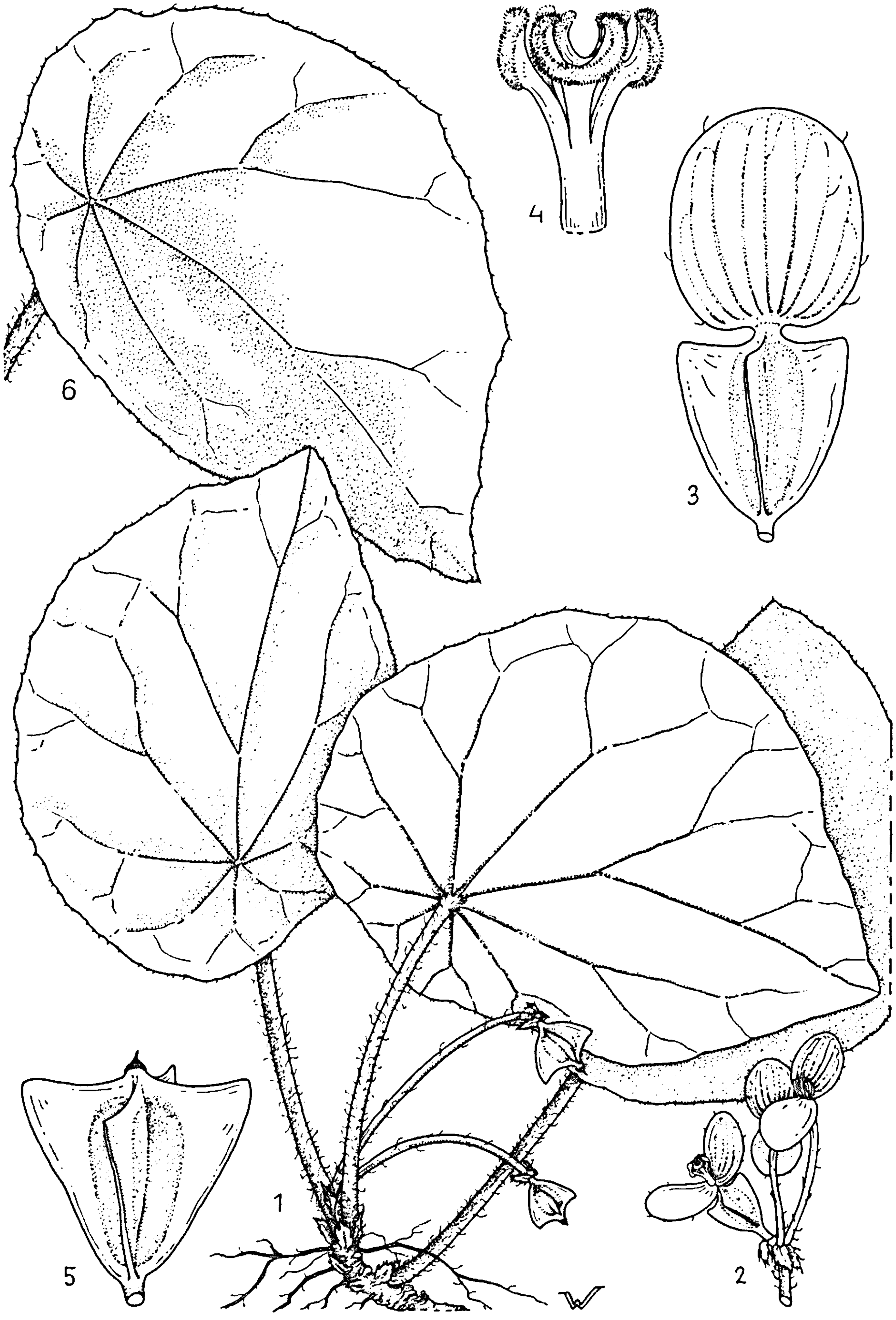


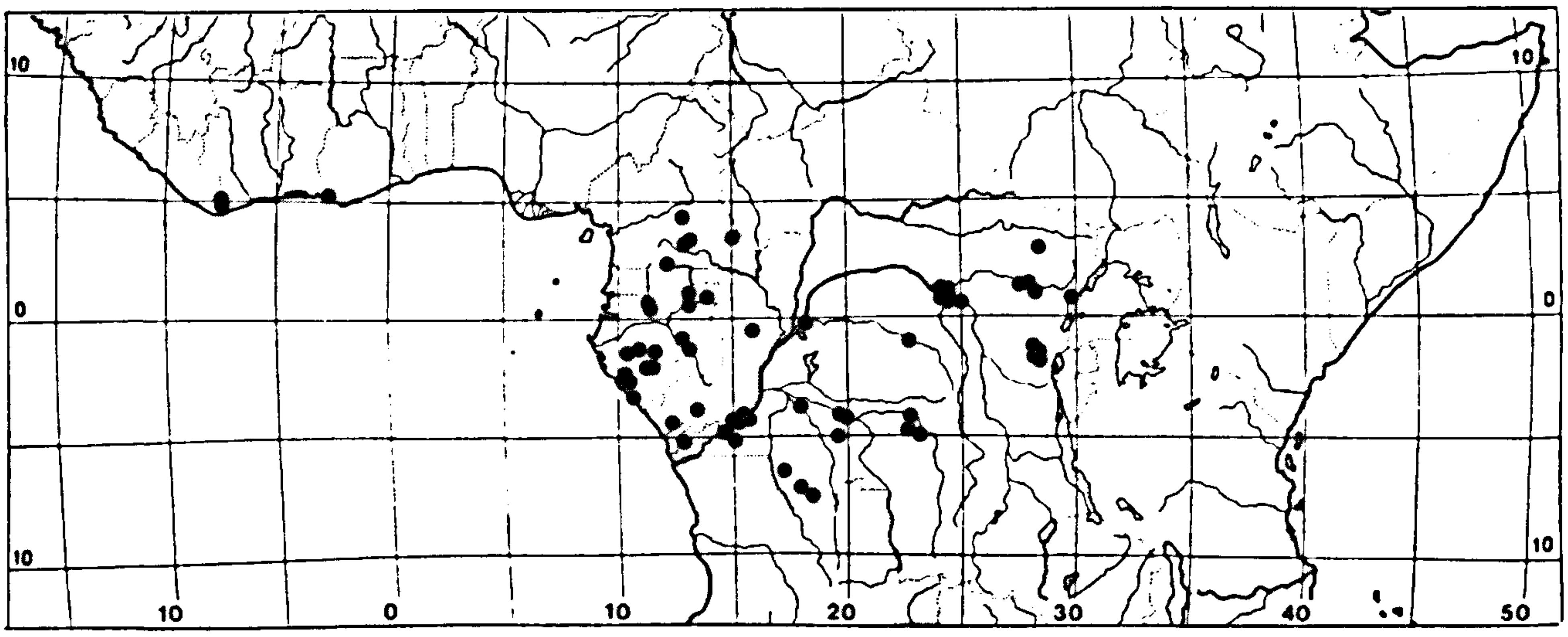
Figure 17.13. *Begonia mildbraedii* Gilg. – 1:habitus (x$^{2}/_{3}$); 2: inflorescence (x$^{2}/_{3}$); 3: female flower (x2); 4: styles (x4); 5: fruit (x2); 6: leaf (x$^{2}/_{3}$). – 1: *J.J. de Wilde c.s. 9626*; 2-4: living plant at WAG, cult. no 90PTGA074; 5: *Breteler & J.J. de Wilde 428*; 6: *Letouzey 12046*.

Plant (2–)7–20(–30) cm high, scattered with minute glandular hairs, sparsely so on pedicel of male flower and outside of perianth segments. **Rhizome** rather stout to comparatively slender, usually compact, sometimes slightly elongated, 0.7–6.8 mm wide, the younger parts sparsely hirsute to hirsute; the apical part ascending to erect to form an indistinct and short stem of up to 2 cm long. **Stipules** very broadly triangular-ovate to ovate or triangular-ovate, acute to slightly acuminate, (0.5–)1.2–5.7 mm long, bronze-green; margin dentate, ciliate. **Leaves** peltate or very rarely non-peltate; *petiole* continuing into the midrib with a distinct angle, inserted at (3–)7–25(–30) mm from the nearest margin (in peltate leaves), (1.0–)2.0–15.0(–18.0) cm long, firm, fleshy to rather juicy, red, brownish red or purplish red to green or brownish (usually reddish when young, later on greenish or brownish), hirsute to sparsely so or rarely densely hirsute with long, patent to downward directed, wavy, white or sometimes red-based hairs; *leaf blade* in more or less horizontal position, asymmetrical, usually broadly elliptic-ovate to almost circular, rarely broadly elliptic-ovate or elliptic-ovate, usually slightly acuminate to rounded in the apical part, rarely acuminate, (2.2–)4.0–12.5(–15.0) x (1.6–)2.7–10.0 cm, somewhat fleshy or slightly leathery, with (7–)8–9(–10) palmate main nerves; margin usually entire to slightly undulate, rarely denticulate, red to purplish, most prominently so on the lower surface and in young leaves, ciliate, sometimes very sparsely so; base rounded in peltate leaves, distinctly cordate on both sides in non-peltate leaves, top rounded to acute; upper surface dark to medium green or rarely purplish green, dull, smooth, generally without but rarely with a few scattered long hairs; lower surface pale green to reddish, dull; *nerves*: the main and larger secondary nerves not prominent and concolorous with the blade or somewhat paler green on the upper surface, on the lower surface red to green, not or slightly prominent, sparsely or very sparsely hirsute with patent hairs, rarely more densely so, smaller secondary nerves usually distinct, not prominent, usually without longer hairs, tertiary nerves usually indistinct and not or barely visible in dry condition. **Inflorescence** containing 2–3(–4) male flowers and 1–2(–3) female flower(s), positioned from almost at the base of the plant to at about the same level as the leaf blades; *peduncle* simple, (1.0–)1.5–7.0 cm long, fleshy to juicy, brown-red or pinkish red to green, hirsute or sparsely so or rarely very sparsely hirsute with white to pale brown hairs; *bracts* 3–4(–6) (not seldom an extra bract is present below the female flower), broadly elliptic or broadly ovate to elliptic-ovate or elliptic-obovate, (0.9–)1.3–4.0 mm long, bronze-green; margin dentate, ciliate. **Male flower**: *pedicel* elongated at anthesis up to 25(–36) mm long, pinkish red, sparsely hirsute or not; *perianth segments* broadly ovate to circular or very broadly ovate, rarely broadly elliptic-obovate, with a cuneate to slightly cordate base, 4.8–12.0(–14.0) x 4.3–11.0(–13.0) mm; the outside sometimes sparsely hirsute with long hairs; the upper segment orange to red or sometimes with red stripes on the outside, the inside yellow with a red patch and/or nerves at base; the lower segment yellow to orange on the outside, the inside yellow; *androecium* with (12–)15–28 stamens; column 0.4–1.0(–1.3) mm long; anthers 1.2–2.1 mm long. **Female flower** similar to the male but usually shortly though sometimes distinctly pedicellate, pedicel elongated in fruit up to 4.4 mm long; *perianth segments* broadly elliptic or broadly ovate to very broadly ovate or circular, with a rounded to cordate base, (3.8–)5.0–12.0(–14.0) x (4.3–)5.0–13.0(–14.0) mm; *styles* 3–4, (2.1–)2.6–4.7(–6.0) mm long, fused in the lower 1/2 to 1/5, the top split into a short and compact C-shape, rarely more elongated and horseshoe-shaped, the arms 0.4–1.3(–1.8) mm long and bearing a compact or fairly compact stigmatic band which is usually not or rarely slightly twisted; *ovary* obovate or obtriangular-ovate to very broadly obovate or depressed obtriangular-obovate, (3.9–)4.7–11.5 x (2.5–)3.3–13.5 mm, 3–4-locular, 3–4-winged all along to only in the apical half; the locular part obovate or elliptic-obovate to broadly elliptic or broadly obovate, (1.3–)2.0–6.0(–7.8) mm wide, pale green to brown or sometimes pinkish red; beak present but usually short, 0.2–2.2 mm long; wings patent, obovate or obtriangular-obovate to depressed obtriangular-obovate, (0.25–)0.8–4.9 mm wide, light brown to green, rarely with pinkish streaks, margin without or rarely with a few hairs. **Infructescence**: peduncle from slightly curved to recurved towards the substrate; *fruit* almost erect to pendulous, broadly obovate or broadly obtriangular-obovate to depressed obtriangular-obovate, 3.9–12.5 x 3.6–18.0 mm, dry, with a comparatively thin wall, green or pale green to reddish, dull.

Distribution: South-western Ivory Coast, south-western Ghana, southern Cameroon, Gabon, Angola (Cabinda), southern Congo and Zaire.

Ecology: Terrestrial or on wet mossy rocks or rock faces; often near streams, rivers, waterfalls or sources; often on slopes, stream beds or steep road banks, in shade or deep shade of primary or old secondary rain forest; on clayey to sandy soil; found in association with *Lycopodiales*, in *Cynometra* forest, in forest with *Raphia* or *Gilbertiodendron dewevrei* and *Parinari excelsa* or *Macrolobium*; at 100–950 m altitude.

Vernacular names: kalokosa (Zaire, Kitembo), lobotabota lo lowe, ote bo isowe (Zaire, Turumbu).



Map 17.8. Distribution of *Begonia mildbraedii*.

Notes: 1. Again a variable species which much resembles *B. quadrialata* with which it often was formerly considered to be conspecific. It is, however, distinct because of the more broadly shaped locular part of the ovary and fruit in conjunction with a generally more obtriangular shaped ovary and fruit, the often pendulous fruit on a curved pedicel, the presence of sclerenchymatous tissue (though not much) along the nerves and the presence of solitary, elongated r-shaped glands. Living specimens cultivated at WAG appear to have more dull greyish green or bluish green upper leaf surfaces, whereas those of *B. quadrialata* appear to be more pale to dark but always bright green.
2. In male flowers the presence of a third perianth segment was observed occasionally.

Specimens examined:

IVORY COAST: *Aubréville 1323* (P): Olodio, 04°43′N 07°28′W (fl, 05); *Chevalier 19598* (P): Cavally valley, Tépo land, between Nékaougnie and Grabo, 05°02′N 07°28′W (fl, 07); *Knecht 1368* (Z): Grabo, 04°57′N 07°30′W (fl, 12); *Schnell 1632* (P): Taï region, Gliké, 04°31′N 07°18′W (fl, 08).

GHANA: *Enti GC 42609* (WAG): Ankasa forest reserve, 05°17′N 02°35′W (fl, 02).

CAMEROON: *Breteler 2125* (BR, K, LISC, M, P, WAG, YA): 4 km SE of Nguélémendouka, along road to Doumé, 04°21′N 12°57′E (fl, fr, 11); *Letouzey 3811* (P): near the valleys of the Dia and the Ediuné, 03°25′N 13°19′E (fl, fr, 04); *Letouzey 3844* (P): SW of Ndingé, 03°18′N 13°06′E (fl, fr, 04); *Letouzey 8218* (P, YA): Mvam, 5 km SO of Oveng, 02°23′N 12°18′E (fr, 10); *Letouzey 8221* (P, YA): ibid. (fl, 10); *Letouzey 12046* (BR, K, P, YA): Mbalam, near Ngoila (at axis Lomiengoila-Souanke), 02°47′N 13°57′E (fl, fr, 02); *Mildbraed 4939* (B, HBG): South Cameroon forest area, Molundu Distr., Jukaqduma (Plehn post), 03°31′N 15°05′E (fl, 03).

GABON: *Arends c.s. 386* (WAG): Waka, forest exploitation road near the Falaise, 01°18′S 10°57′E (fl, fr, 11); *Arends c.s. 640* (WAG): Doudou Mts, W of Doussala, Reserve de Faune de Moukalaba, 02°12′S 10°20′E (fr, 12); *Breteler 7704* (WAG): 30 km Lébamba-Mbigou, 02°02′S 11°36′E (fl, fr, 05); *Breteler & J.J. de Wilde 428* (WAG): about 10 km NE of Lalara, 00°24′N 11°32′E (fr, 09); *Breteler & J.J. de Wilde 508* (WAG): 10 km along the road from Lalara to Makokou and then a forest exploitation road following the Okano R. upstream for ± 31 km, 00°33′N 11°38′E (fl, fr, 09); *Breteler & J.J. de Wilde 586* (WAG): Bélinga, iron mine exploitation area, 01°06′N 13°12′E (fl, 09); *Breteler c.s. 8856* (WAG): 5-10 km E of Saint Germain, E of Okano R., 00°38′N 11°38′E (fl, fr, 04); *Breteler c.s. 9985* (WAG): c. 30 km NE of Lastourville, 00°45′S 12°55′E (fr, 04); *Farron 7607B* (P): Makokou, island in the Ivindo R. (Chimpansee Island) 01°20′S 12°30′E (fr, 07); *Florence 57* (WAG): M'Passa, 10 km S of Makokou, 00°28′N 12°52′E (fl, 03); *Gentry 33223* (MO): Ogooué-Ivindo, M'Passa Field Station, near Makokou on Ivindo R., 00°28′N 12°52′E (fl, 07); *N. Hallé 1113* (P): Andok, 3 km N of Makokou, 00°38′N 12°53′E (fl, 02); *N. Hallé 1317* (P), identification doubtful: Massaha, 50 km NE of Makokou, 00°44′N 13°12′E (st, 02); *N. Hallé 3034* (P): Bélinga, 01°06′N 13°12′E (fl, fr, 11); *N. Hallé 4063* (P): ibid. (fr, 05); *N. Hallé 4150* (P): ibid. (fr, 06); *N. Hallé & Cours 5988* (P): E of Moumba, around Etéké, 01°20′S 11°40′E (fl, 05); *N. Hallé & Le Thomas 331* (P): Mékambo, 01°01′N 13°56′E (fl, 08); *A. Louis, Breteler & de Bruijn 541* (WAG): Oveng, forest exploitation camp, km 19 on exploitation road, 00°42′N 11°23′E (fl, fr, 11); *J.M. Reitsma c.s. 1490* (WAG): Rougier Océan exploitation, Oveng, c. 20 km NE of Oveng, 00°41′N 11°21′E (fl, fr, 09); *J.M. Reitsma c.s. 2962* (WAG, LBV): Inventory Oveng, c. 25 km WSW of Mintsic, 00°44′N 11°22′E (fl, fr, 02); *J.M. Reitsma c.s. 3234* (WAG): Inventory, c. 50 km SSW of Doussala, 02°36′S 10°35′E (fl, 04); *Wieringa c.s. 1387* (WAG): Ngounié, 5 km NNW of Bembodie, Koumouna-bwali massif, 01°26′S 10°31′E (st, 08); *Wieringa c.s. 1498* (WAG): Ogooué-Lolo, 75 km on the road from Lastoursville to Moanda, 3 km before Tsotanzala-Pouby, 01°16′S 13°02′E (fl, 08); *J.J. de Wilde c.s. 9271* (WAG): 22 km along the road from Mayumba to Tchibanga, 12 km along forest exploitation track leading in eastern direction, near Doussa R., 03°16′S 10°46′E (st, 12); *J.J. de Wilde c.s. 9626* (WAG): 79 km along the forest-road Doussala-Bongo, 02°25′S 10°23′E (fr, 03); *J.J. de Wilde c.s. 10438* (WAG): 34 km on the road Lebamba-Yéno, 01°58′S 11°25′E (fl, 02).

CONGO: *Babet s.n.* (IEC, P): Brazzaville region, Moufoula Bal, c. 04°20'S 15°00'E (fl, fr, 09); *Descoings 8981* (IEC): valley of the Alima-Likouala, around Kellé, between km 5 and 30 of the northern track of the SMOL, c. 00°30'S 16°00'E (fl, 08); *Farron 4473* (P), identification doubtful: forest road of M. Fouet, Moussoumou, 35 km E of Sibiti, 03°45'S 13°35'E (st, 08); *Malaisse 2637* (BR): Lou Foulakari, at 20 km of Mbanza-Ndounga, 04°35'S 14°59'E (fl, fr, 11); *Sita 1349* (IEC, P): Les Saras region, at 6 and 30 km of the crossing of roads to Sounda and Les Saras, 04°20'S 12°25'E (fl, fr, 06); *Trochain 10268* (IEC): Boko-N'Situ road, 04°47'S 14°38'E (fl, 10).

ZAIRE: *Bequaert 1753* (BR): Avakubi, 01°20'N 27°35'E (fr, 01); *Bequaert 2524* (BR): Penge, banks of the Ituri, 01°20'N 28°09'E (fl, 02); *Bequaert 6523* (BR): Walikale, 01°25'N 28°03'E (fl, fr, 01); *Breyne 471* (BR): Binza Terr., Binza cave, 04°22'S 15°14'E (fl, 01); *Breyne 690* (BR): Kin. Maluku Terr., Mofinu village on the road Menkao-Kingakati, 04°14'S 15°44'E (fl, 12); *Breyne 3127* (BR): Maluku zone, Milu, 04°03'S 15°34'E (fr, 10); *Breyne 4769* (BR): Feshi zone, falls at the Inzia, 03°45'S 17°57'E (fl, 04); *Callens 1916* (BR): ? (fl); *Callens 3214* (BR, K): Kambangu, Tchikweso, 07°35'S 18°28'E (fr, 02); *Callens 3445* (K): Panzi, Makita, 07°13'S 17°58'E (fr, 02); *Callens 3567* (BR, K): Pelende, Ngulu-Ngulu falls, 06°31'S 17°15'E (fl, 02); *Casier 492* (BR): Kasai, Muetshi, 04°42'S 22°39'E (fl, 02); *Christiaensen 296* (BR): Kivu Prov., Walikale Terr., Musenge, 01°38'S 28°16'E (fl, 12); *Corbisier-Balaud 887* (BR): Koli-Koli, 04°15'S 19°55'E (fl, fr, 12); *Dubois 1502* (BR): Binza close to Leopoldville, 04°22'S 15°14'E (fl, 08); *Gentil 19* (BR): L-K Distr., Kondue, Saukuru valley, 04°58'S 23°16'E (fl, fr, 11); *Germain 223* (BR, P): Yalibwa, Yangambi-Gazi road, 00°56'N 24°30'E (fl, fr, 03); *Gillet 73* (B, BR): Kisantu, Benga-Boma, 05°08'S 15°06'E (fl); *Gillet 2318* (B, BR): Kisantu, 04°18'S 15°18'E (fr); *Gillet s.n.* (BR): around Leopoldville, Binza falls, 04°22'S 15°14'E (fl, fr, 04); *Gutzwiller 1715* (BR): Walikale Terr., Kembe, 01°12'S 28°13'E (fl, fr, 05); *Jans 486* (BR): Binza cave, 04°22'S 15°14'E (fl, fr, 05); *Jespersen s.n.* (BR): Itali-Moudombe, 01°05'S 22°43'E (st); *Jespersen s.n.* (BR), identification doubtful: Moma, 01°35'S 23°57'E (st, 06); *E. Laurent & M. Laurent 1704* (BR): Mogandjo, 01°21'N 24°20'E (st, 03); *E. Laurent & M. Laurent s.n.* (BR), identification doubtful: Lonkala (Sank.), 04°37'S 23°14'E (fl, 11); *E. Laurent & M. Laurent s.n.* (BR): ravine at Dibele, 04°07'S 22°50'E (fr, 12); *E. Laurent & M. Laurent s.n.* (BR): cave at Kondue, 04°58'S 23°16'E (st, 11); *E. Laurent & M. Laurent s.n.* (BR): ibid. (st, 11); *Lebrun 5177* (BR): between Masisi and Walikale (Kivu), 01°24'S 28°25'E (fl, fr, 03); *Linder 1615* (B, BR): Kinshasa, 04°19'S 15°19'E (fl, 12); *Lisowski 87088* (BR): Haut-Zaire, around Kisangani, 8 km N of Yakusu, 00°38'N 25°01'E (fl, 11); *J. Louis 3144* (BR): 11 km E of Yangambi, 00°46'N 24°33'E (fl, 01); *J. Louis 3377* (BR): Yangambi, about 10 km NW of the Post, between Bohonde R. and Lilanda village, 00°51'N 24°18'E (fl, 02); *J. Louis 3633* (BR): Yambao, 25 km NW of Yangambi, 00°59'N 24°27'E (fl, fr, 03); *J. Louis 6121* (BR): Yangambi, spring of an affluent of the Bohonde, 00°51'N 24°18'E (fl, fr, 09); *J. Louis 12210* (BR): between Ngazi and Yambuya, 01°09'N 24°32'E (st, 10); *J. Louis 12370* (BR): Yambuya, banks of the Kwongwole R., 01°16'N 24°33'E (fl, 11); *Mildbraed 3124* (B, holo): Mawambi-Awakubi, Abarangu, c. 01°00'N 28°20'E (fl, fr, 04); *Muambi 116* (BR): Kinshasa II Terr., Binza cave, 04°22'S 15°14'E (fl, fr, 02); *Pauwels 6576* (BR): 7 km on the road to Yangambi, W of the Linde, N of Yakusu, 00°36'N 25°00'E (fl, 11); *Seret 498* (B, BR): 'La Duru' R., road Gombari-Rungu, 02°50'N 28°28'E (fl); *Seret 1078* (BR): R. Bula at Mampaka, 00°17'S 18°23'E (fl, fr); *Seret s.n.* (BR): ? (fl, fr); *Troupin 10232b* (BR): Kivu Prov., Kalehe Terr., Kavumu-Walikale road, km 110, Catena II, 01°53'S 28°27'E (fl, 05); *Troupin 10829* (BR): ibid., Irangi, reserve I.R.S.A.C., Catena III, 01°53'S 28°27'E (fl, 09); *Vanderyst 9207* (BR): Idiofa, 04°58'S 19°35'E (fl, 03); *Vanderyst 11044* (BR): Ipamu, 04°09'S 19°38'E (fl, 10); *Wellens 410* (BR): Mayombe, Kangu, 05°15'S 12°57'E (fl, 08); *J. de Wilde 378* (BR): Wanaude, Abram (Hte) valley, along track to Kamama and Boloku, c. 00°50'N 29°45'E (fl, 09).

Begonia peperomioides Hook.f. **Fig. 17.14, Map 17.7**

Begonia peperomioides Hook.f. in Oliver, Fl. Trop. Afr. 2 (1871) 575; Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3,2 (1921) 616, 619; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39; L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 213, fig. 13.1; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 17, 12D. – TYPE: *Mann 1659* (K!, holo; ?K! (mixed with the type of *B. hirsutula* on sheet Mann 1649), P!): 'Sierra del Cristal, W. Trop. Africa, Lat. 1° N, July 1862.'

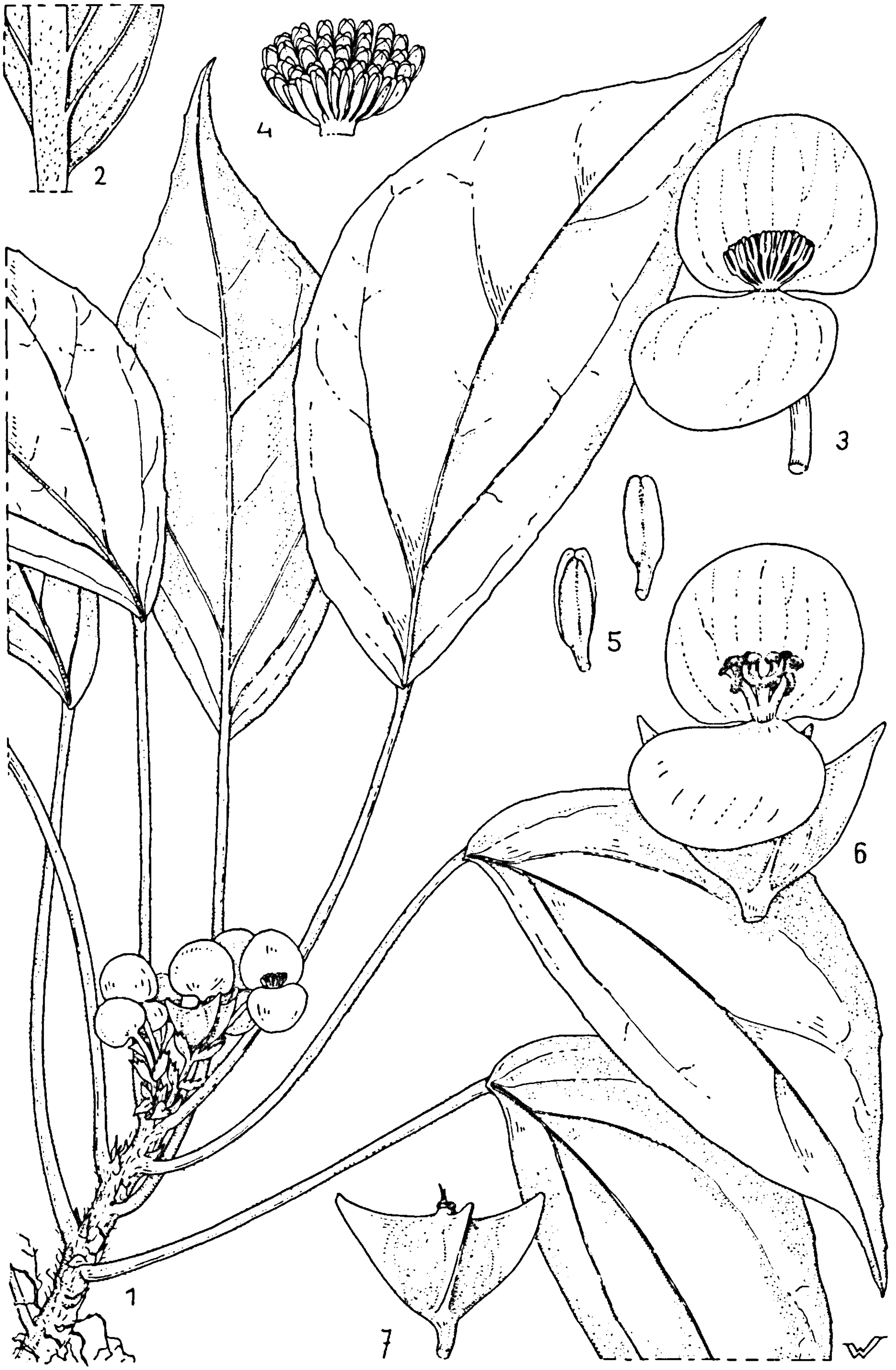


Figure 17.14. *Begonia peperomioides* Hook.f. – 1: habitus ($x^2/_3$); 2: detail leaf base lower surface (x4); 3: male flower (x2); 4: androecium, front view (x4); 5: anther, front and back view (x8); 6: female flower (x2); 7: fruit (x1). – 1-7: *Breteler & J.J. de Wilde 369.*

Plant up to 20 cm high, scattered with minute glandular hairs, sparsely so on rhizome, stipules, bracts, pedicel of male flower and outside of perianth segments. **Rhizome** rather stout and elongated, rather smooth, 2.5–7.0 mm wide, glabrous or the younger part sparsely hirsute; the apical part directed upwards to form a distinct stem of 3–6 cm. **Stipules** narrowly to very broadly triangular or triangular-ovate, acute to blunt, 2.0–9.1 mm long; margin entire to slightly dentate and then shortly ciliate. **Leaves** not peltate; *petiole* continuing into the midrib without a distinct angle, 3–16 cm long, firm, fleshy, green to red, sometimes with a few long hairs; *leaf blade* in a more or less horizontal position, slightly to distinctly asymmetrical, elliptic to broadly elliptic, usually distinctly acuminate, sometimes slightly so in the upper 1/4, 9.0–15.0 x 3.2–6.3 cm, somewhat leathery, palmately-pinnately nerved with 4–6 main nerves; margin shallowly sinuate in the upper half to entire or with a few small teeth, often narrowly recurved when dry, concolorous with the blade to red, glabrous or with few short cilia; base usually unequal, one side broadly to narrowly cuneate, the other narrowly cuneate to attenuate, top acute; upper surface bright green shiny, smooth, not hirsute; lower surface pale green, dull; *nerves*: the main and larger secondary nerves not or slightly prominent and concolorous with the blade on the upper surface, on the lower reddish, slightly prominent, the smaller secondary nerves distinct, the tertiary nerves indistinct and sometimes creating a faint reticulate pattern when dry. **Inflorescence** containing 2–5 male flowers and 1 terminal female flower, positioned at the base of the plant, hidden below the leaves; *peduncle* simple, 0.3–1.2 cm long, fleshy, pale green to wine-red; *bracts* 3–6, elliptic or broadly so, 2.3–6.8 mm long, pale green, not hirsute; the margin slightly dentate, shortly ciliate at the apex. **Male flower**: *pedicel* elongated at anthesis up to 18 mm, pale coloured; *perianth segments* broadly ovate to broadly obovate, with a rounded to cordate base, 6.9–17.0 x 7.8–13.0 mm, the outside orange, not hirsute; the upper segment yellow with a red patch and nerves in the basal half on the inside; the lower segment yellow on the inside; *androecium* with 23–40 stamens; column 0.2–0.7 mm long; anthers 1.4 mm long. **Female flower**: similar to the male, usually distinctly pedicellate, pedicel elongated in fruit up to 10.0 mm; *perianth segments* broadly or very broadly ovate to circular, 8.8–18.0 x 11.5–20.0 mm; *styles* 3–4, 3.6–6.9 mm long, fused in the lower 1/2 to 1/4, the top split into a rounded U-shape, the arms 2.0–3.1 mm long and bearing a slender stigmatic band which is spirally twisted for 1 turn; *ovary* very broadly obtriangular to shallowly obtriangular, obovate to broadly so or circular, 4.5–12.5 x 8.0–15.0 mm, pale green, 3–4-locular, 3–4-winged at the apical half to all along; the locular part obovate to broadly so or circular, 4.2–7.9 mm wide; beak present, 0.3–1.7 mm long; wings patent to slightly erecto-patent, very shallowly obtriangular to very broadly obtriangular, 2.2–10.5 mm wide at their widest part, the margin glabrous. **Infructescence**: peduncle recurved towards the substrate; *fruit* pendulous, very broadly obtriangular to shallowly obtriangular, 5.2–13.0 x 11.0–16.0 mm, dry, with a tough thick wall, dark green, dull.

Distribution: GABON: Crystal Mountains.

Ecology: Terrestrial or epiphytic on mossy, decaying tree trunks; in half-shade of primary forest; on a slope along a forest track; at 380 m altitude.

Notes: 1. The plant representing *B. peperomioides* present on one of the two sheets of the collection Mann 1649 (the type of *B. hirsutula*) at K is probably mounted erroneously on this sheet and might be regarded as an isotype.

Specimens examined:

GABON: *Breteler & J.J. de Wilde 369* (WAG): NNW of Méla, 00°36′N 10°16′E (fl, fr, 08); *N. Hallé & Villiers 4704* (P): Crystal Mts, 6 km S of Assok, 00°39′N 10°22′E (fl, 01); *Mann 1649* (K p.p.): Crystal Mts, 1°N, c. 00°55′N 10°25′E (fl, fr, 07); *Mann 1659* (K, holo): Crystal Mts, Lat. 1°N, c. 00°55′N 10°25′E (fr, 07).

Begonia scutulum Hook.f. **Fig. 17.15, Map 17.9**

Begonia scutulum Hook.f. in Oliver, Fl. Trop. Afr. 2 (1871) 575; Engl. in Engl. & Drude, Vég. der Erde 9, Die Pflanzenwelt Afr. 3,2 (1921) 617; Irmscher in Engl. & Prantl, Nat. Pflanzenfam. (ed. 2) 21 (1925) 574; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39; L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 231; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 17, 12E. – TYPE: *Mann 1650* (K!, holo): 'W. Trop. Africa, Lat. 1°N. Sierra del Cristal, July 1862.'

Plant up to 35(–50) cm high, scattered with minute glandular hairs, sparsely so on stipules, peduncle, brates, pedicel of male flower and outside of perianth segments, sometimes densely so on the petiole. **Rhizome** rather compact and stout to comparatively slender and far creeping, smooth to somewhat knotted, 1.7–7.8 mm wide, hirsute around the leaf-axils or not; the apical part horizontal or slightly ascending to shortly erect. **Stipules** broadly to narrowly triangular or triangular-ovate, long attenuate to cuspidate, (1.3–)2.5–10.5 mm long, brown-green or pale green to pale or whitish red, not hirsute; margin more or less entire, ciliate. **Leaves** peltate; *petiole* continuing into the midrib with a distinct angle, inserted at 14–36(–54) mm from the nearest margin, (3.5–)6–38 cm long, firm, fleshy, red or dark wine-red to brownish or purplish, densely to very sparsely hirsute with long, patent, wavy, white to reddish hairs; *leaf blade* in more or less horizontal position, slightly to distinctly asymmetrical, elliptic-ovate to broadly elliptic or broadly elliptic-ovate, rarely almost circular, blunt to distinctly acuminate in the apical part, 5.7–17.0 x 3.5–12.0 cm, rather firm, crispy-leathery, with (6–)7–9 palmate main nerves, the midrib usually slightly more pronounced; margin entire to shallowly sinuate or irregularly coarsely dentate to sinuate in the apical half, purplish or red or concolorous with the blade, glabrous to very sparsely ciliate, sometimes more densely so; base rounded, top blunt to acute; upper surface bright green to dark green, reddish when young, dull or slightly glossy, smooth, rarely sparsely set with long white or red hairs; lower surface slightly paler than the upper, dull; *nerves* the main and larger secondary nerves not or slightly prominent, concolorous with the blade on the upper surface, on the lower surface slightly prominent to prominent, usually green, sometimes reddish and sparsely hirsute with patent white hairs or not hirsute, the smaller secondary nerves usually indistinct, rarely more pronounced

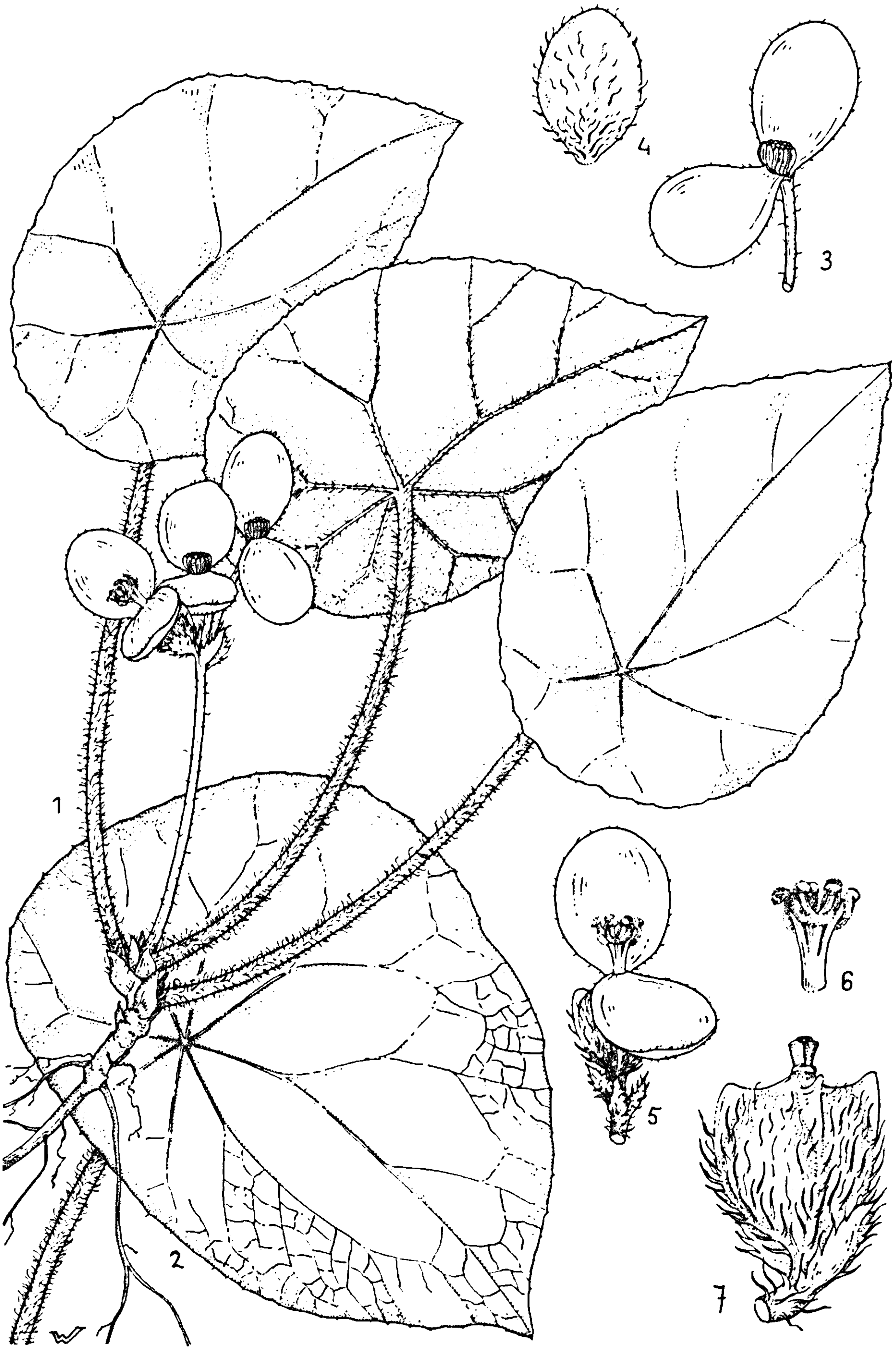


Figure 17.15. *Begonia scutulum* Hook.f. – 1: habitus (x$^2/_3$); 2: leaf (x$^2/_3$); 3: male flower (x1); 4: outer surface perianth segment (x1); 5: female flower (x1); 6: styles (x2); 7: fruit and bracts (x2). – 1: *Mann 1650*; 2: *N. Hallé & Villiers 4712*; 3-6: *Breteler & J.J. de Wilde 272*; 7: *A. Louis c.s. 893.*

and slightly prominent, tertiary nerves indistinct but visible and creating a reticulate pattern when dry. **Inflorescence** containing 2–3 male flowers and 1(–2) terminal female flower(s), positioned just below the leaf blades or at about halfway up the petioles; *peduncle* simple, 1.5–12.0 cm long, fleshy, bright red or wine-red to reddish, hirsute to very sparsely so with white to reddish-white hairs; *bracts* 3–5 (not infrequently an additional small bract is present below the female flower), narrowly elliptic to broadly elliptic or broadly obovate, 2.1–9.1 mm long, pale green or green with reddish nerves to pale red or brownish green, sometimes sparsely hirsute on the outer surface; margin dentate, ciliate. **Male flower**: *pedicel* elongated at anthesis up to 35 mm, usually with few long hairs; *perianth segments* broadly elliptic to circular or broadly ovate, sometimes elliptic-obovate, with a cuneate to slightly cordate base, 9.8–21.0 x 10.5–20.0 mm, the outside salmon or orange-yellow to red, sparsely hirsute with white hairs, the inside bright yellow, rarely with red nerves; *androecium* with 24–44 stamens; column 0–1.2 mm long; anthers 1.3–2.6 mm long. **Female flower**: similar to the male but shortly pedicellate, pedicel elongated in fruit up to 2.0(–6.0) mm and hirsute or not; *perianth segments* broadly or very broadly ovate to circular or very broadly elliptic, with a rounded to slightly cordate base, 12.0–18.0 x 13.0–20.0 mm; *styles* 3, 3.3–5.8 mm long, fused at base or up to 1/3 of their length, the top split into a rounded U-shape, the arms 1.3–2.7 mm long and bearing a slender to rather broad stigmatic band which is spirally twisted for 1/2–1 a turn; *ovary* obovate to broadly triangular-obovate or broadly elliptic, (4.3–)7.5–14.5 x (3.8–)6.0–10.0 mm, 3-locular, 3-winged at the apical part, sparsely hirsute to hirsute with white or red hairs; the locular part obovate to broadly obovate or broadly elliptic, (3.3–)6.0–10.0 mm wide, pale green to wine-red; beak absent to distinct, 0–2.1 mm long; wings sometimes absent, when present erecto-patent to almost erect, usually obovate, rarely shallowly obtriangular, 0–3.3 mm wide, pale green, the margin entire to dentate, ciliate. **Infructescence**: peduncle recurved at the top; *fruit* pendulous, broadly elliptic to broadly triangular-obovate or circular, sometimes very broadly triangular-obovate, 5.5–12.0(–15.0) x (4.5–)6.0–11.7 mm, dry, greenish to brown, dull, with a comparatively thick wall.

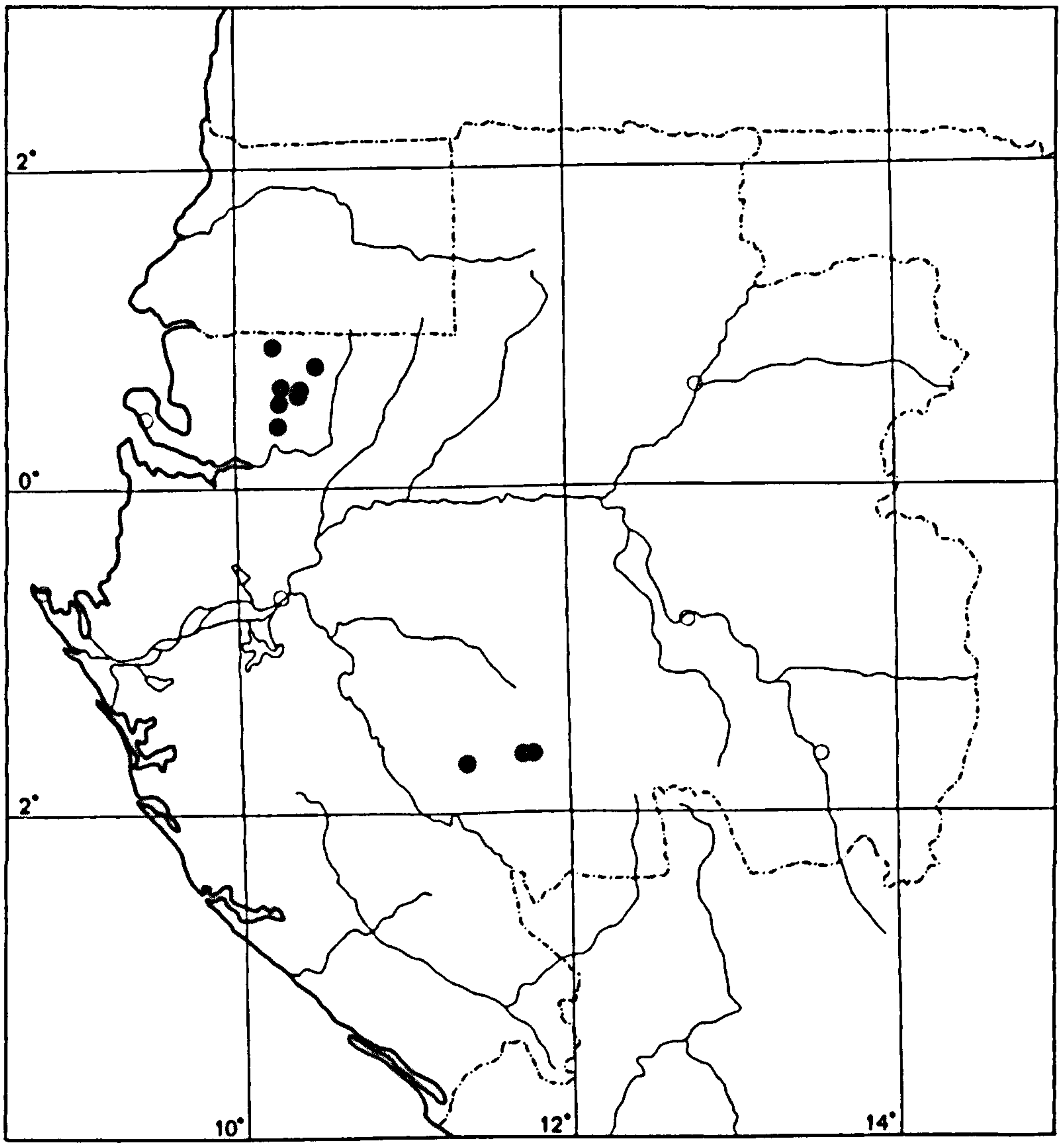
Distribution: GABON: Crystal Mountains and Chaillu Massif.

Ecology: Locally common; terrestrial or rarely on vertical rockfaces; on level sites to steep slopes, generally along creeks or near rapids, also in marshy creekbeds; in shaded to deeply shaded conditions in primary or old secondary rain forest; at 250–700 m altitude.

Notes: 1. Specimens from Zaire were misidentified by Wilczek (1969: 36). They actually belong to *B. zairensis* var. *montana*. Genuine *B. scutulum* is confined to Gabon.

2. Figure 2.20 in L.B. Smith et al. (1986) depicts a specimen belonging to *B. hirsutula* Hook.f.

3. Specimens from the Chaillu Massif show a tendency towards smaller and blunt to acute leaf blades, while those from the Crystal Mountains and the Waka area generally possess larger and more acuminate ones.



Map 17.9. Distribution of *Begonia scutulum*.

Specimens examined:

GABON: *Breteler 7715* (WAG): about 20 km Mimongo-Mbigou, Mouyanama lower fall, 01°39'S 11°42'E (fr, 05); *Breteler & J.J. de Wilde 35* (WAG): about 11 km along the road from Asok to the hydroelectric power station at Tchimbélé, 00°38'N 10°23'E (fr, 08); *Breteler & J.J. de Wilde 70* (WAG): Crystal Mts, about 15 km NE of Asok, 00°46'N 10°30'E (fr, 08); *Breteler & J.J. de Wilde 237* (WAG): about 22 km NE of Asok, 00°50'N 10°32'E (st, 08); *Breteler & J.J. de Wilde 272* (WAG): about 7-8 km SW of Asok, hill W of Nkan, close to the road, 00°39'N 10°18'E (fl, fr, 08); *N. Hallé & Villiers 4559* (P): Crystal Mts, Kinguélé road, 00°25'N 10°16'E (fl, fr, 01); *N. Hallé & Villiers 4712* (P): Crystal Mts, 6 km S of Assok, 00°39'N 10°22'E (fl, 01); *N. Hallé & Villiers 5249* (P): Crystal Mts, 00°39'N 10°21'E (fl, 02); *A. Louis, Breteler & de Bruijn 893* (WAG): Chaillu Massif, near Mouyanama, about 27 km E of Mimongo, 01°39'S 11°46'E (fr, 11); *A. Louis, Breteler & de Bruijn 1260* (WAG): along Waka R., near Forestry Camp Waka, situated about 32 km SE of Sindara, 01°14'S 10°53'E (st, 12); *Mann 1650* (K, holo; B): Crystal Mts, 1°N, c. 00°55'N 10°25'E (fl, 07); *Wieringa 702* (WAG): Crystal Mts, Woleu-Ntem, 1 km SE of Tchimbélé, 00°37'N 10°24'E (fr, 03); *Wieringa 919* (WAG): Crystal Mts, Woleu-Ntem, 1 km WNW of Tchimbélé, bank of Bingiligwen R., 00°37'N 10°23'E (st, 05); *Wieringa 938* (WAG): Crystal Mts, Woleu-Ntem, 1 km SE of Tchimbélé, 00°36'N 10°24'E (fr, 05); *J.J. de Wilde c.s. 9625* (WAG): 79 km along the forest-road Doussala-Bongo, c. 02°25'S 10°23'E (fr, 03); J.J. de Wilde c.s. 10043 (WAG): Crystal Mts, Tchimbélé, trail E of the dam, 00°37'N 10°24'E (st, 12); *J.J. de Wilde c.s. 10088* (WAG):

Crystal Mts, 25 km on the road Kinguélé to Tchimbélé, 00°32'N 10°17'E (fl, 01); *J.J. de Wilde c.s. 10224* (WAG): Crystal Mts, 12 km along the road Tchimbélé to Kinguélé, 00°36'N 10°21'E (fl, fr, 01); *J.J. de Wilde c.s. 10346* (WAG): 59 km on the road Mouila-Yéno, 01°43'S 11°25'E (fr, 02); *J.J. de Wilde c.s. (WALK-B) 114* (LBV, WAG): Crystal Mts, 11 km along the road from Tchimbélé to Kinguélé, 00°35'N 10°20'E (fl, fr, 01); *J.J. de Wilde c.s. (WALK-B) 291* (WAG): Crystal Mts, forest exploitation Leroy, 20 km NW of Asok, 00°53'N 10°12'E (fl, 01); *Wilks 1024* (LBV, WAG), identification doubtful: Ngounié Prov., 4 km SW of Bilengui, 01°59'S 11°23'E (fl, 12); *Wilks 1275* (LBV, WAG), identification doubtful: Ngounié Prov., 6 km W of Mimongo, 01°36'S 11°41'E (fl, 04).

CULTIVATED: *van Veldhuizen 1100* (WAG): Wageningen, Dept. of Horticulture No 1627 (coll. J.J. de Wilde et al. (WALK-B) s.n., Gabon) (st, 09).

Begonia susaniae Sosef **Fig. 17.16, Pl. 8a, Map 17.10**

Begonia sunaniae Sosef, Wageningen Agric. Univ. Papers 91-4 (1992) 105, fig. 7, pl. 4a; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 21, pl. 15F. – TYPE: *Breteler & J.J. de Wilde 25* (WAG!, holo): 'Gabon, about 11 km along the road from Asok to the Hydroelectric power station in the Tchimbélé River, 15-VIII-1978.'

Begonia lacunosa auct. non Warb.: Reitsma, Meded. Landbouwhogeschool Wageningen 83-9 (1984) 45, 47; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39, pl. 13.1 p.p.

Diagnostic characters (for a more detailed description see Sosef l.c.):

Plant up to 15(–20) cm high. **Leaves** peltate; *leaf blade* in more or less horizontal position, almost symmetrical to distinctly asymmetrical, usually broadly elliptic-ovate, sometimes ovate to ellitic-ovate or almost circular, usually gradually tapering to or sometimes slightly acuminate at the top, 3.5–12.5(–15.5) x 2.4–7.0(–8.0) cm; margin usually irregularly denticulate, sometimes more coarsely dentate or only slightly sinuate to entire, ciliate or sparsely so; top blunt, rarely acutish; upper surface very variably bullate, from almost smooth or scattered with a few small solitary bullae to densely bullate with small clustered bullae or bullate with few to many large solitary bullae, each bulla usually bearing a single long stiff erect red or whitish hair, rarely lacking any long hairs. **Male flower**: *perianth segments* variously broadly or very broadly ovate to very broadly obovate, with a cuneate to cordate base, (5.9–)6.8–19.0 x (6.5–)7.2–17.0 mm, the outside yellow or orange to reddish but sometimes cream-coloured when young; the upper segment entirely yellow or yellow with a red patch and nerves in the basal 1/2 on the inside; the lower segment yellow, sometimes also with a red patch and nerves in the basal 1/2 on the inside; *androecium* with (15–)19–33 stamens. **Female flower** usually distinctly pedicellate, pedicel elongated in fruit up to 8.0(–10.5) mm; *perianth segments* very broadly ovate to very broadly obovate, with a rounded to cordate base, (6.1–)8.0–20.0 x (7.0–)8.5–20.0 mm; *ovary* very shallowly to shallowly obtriangular, (2.5–)3.0–7.5(–9.0) x (6.5–)7.0–15.0(–17.5) mm, not hirsute; beak usually very distinct, 0.7–4.3 mm long; wings often curved upwards, sometimes patent, usually very shallowly obtriangular-obovate, sometimes shallowly obtriangular-obovate, (1.0–)1.3–6.0(–7.9) mm wide. **Infructescence**: peduncle recurved towards the substrate; *fruit* pendulous.

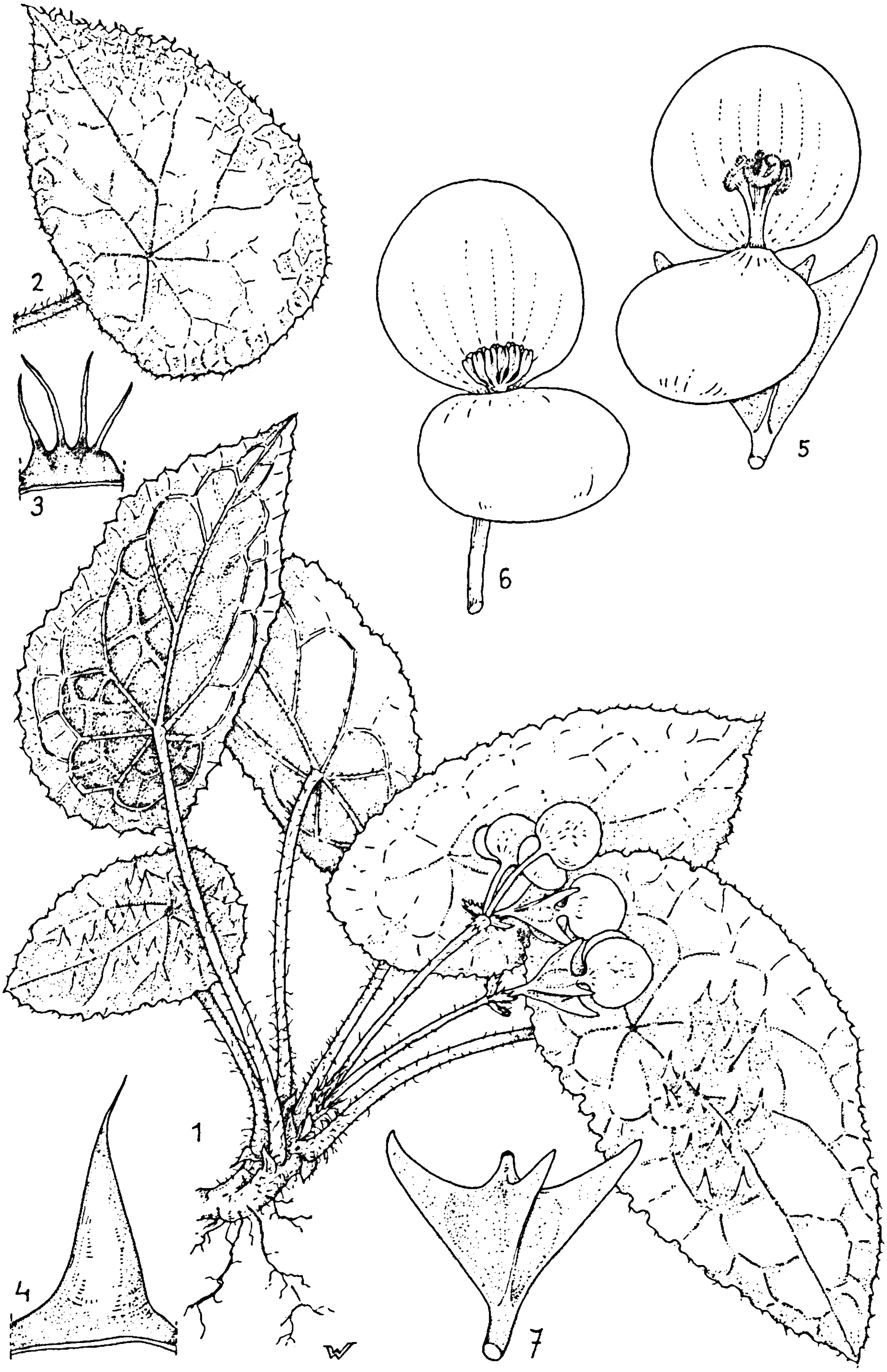
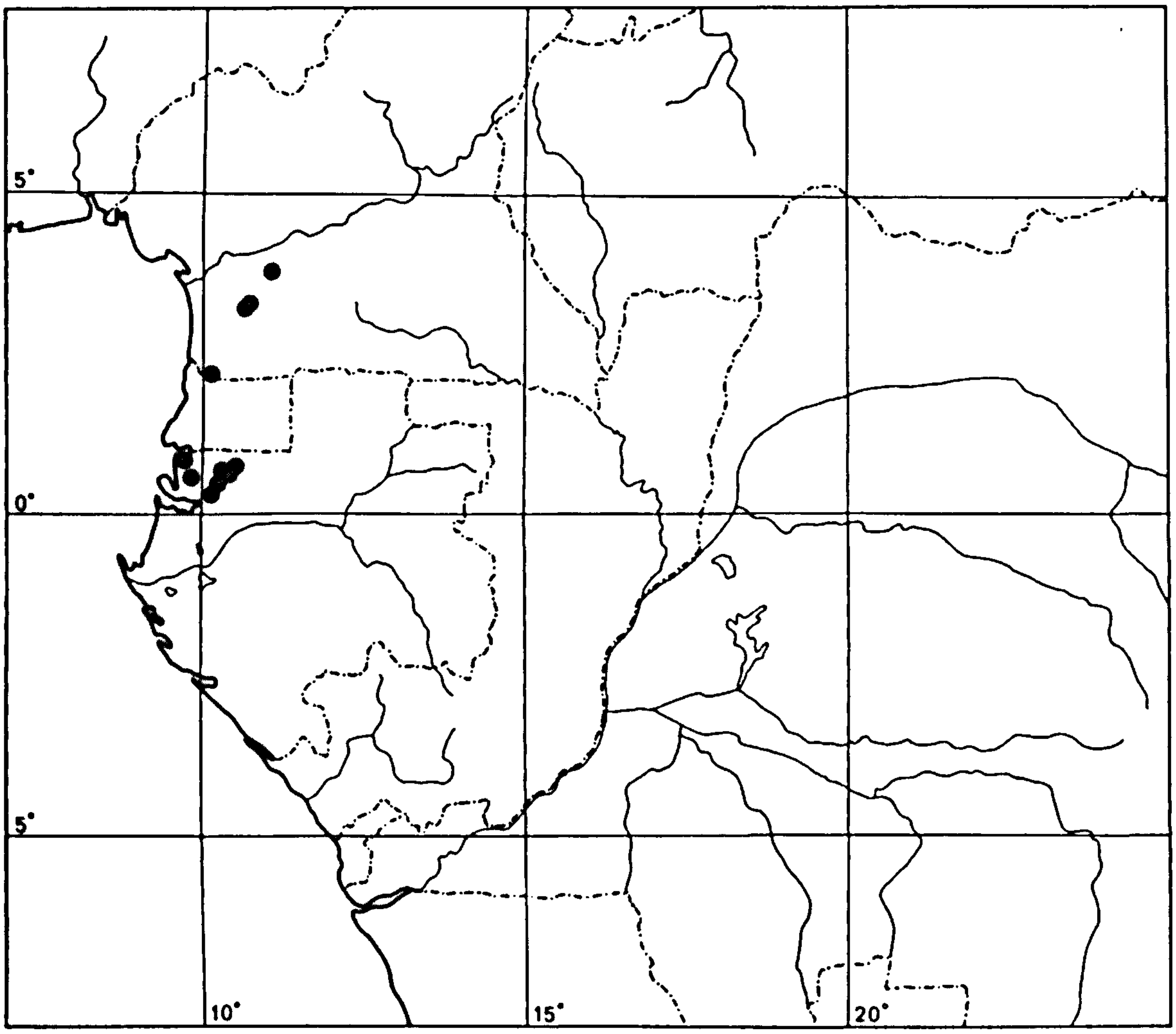


Figure 17.16. *Begonia susaniae* Sosef. – 1: habitus (x$^{2}/_{3}$); 2: leaf (x$^{2}/_{3}$); 3: detail group of small bullae (x4); 4: detail solitary large bulla (x4); 5: female flower (x2); 6: male flower (x2); 7: fruit (x2). – 1, 4-6: *Breteler & J.J. de Wilde 274*; 2, 3: *Breteler & J.J. de Wilde 273*; 7: *Breteler & J.J. de Wilde 25*.



Map 17.10. Distribution of *Begonia susaniae*.

Distribution: CAMEROON: Centre-Sud Prov. GABON: Crystal Mountains.

Ecology: Locally common on the forest floor or mossy rocks, rarely on rock faces; on clayey soil, preferably on gentle to steep slopes or road banks; often in the vicinity of streams or waterfalls, always on moist sites; in shaded to deeply shaded sites in primary or secondary rain forest; found associated with *Begonia scutulum* and *B. vittariifolia*; at 250-900 m altitude.

Notes: 1. The species is very variable in bullateness and colour or colour pattern of the leaf blade. A quite similar variation is present in *B. lacunosa*. At first sight several types may be recognized but too many intermediates occur, making it impossible to distinguish different taxonomic entities. Moreover, one collection (van Veldhuizen 1092) made from a single accession cultivated at WAG shows a wide variety of leaf bullateness and colour pattern. Preliminary results of cytological research by J.C. Arends show that the variation in bullateness might be correlated with the chromosome number (pers. comm.).

2. The few specimens from southern Cameroon (Mt Ngovayang) are slightly aberrant. The upper leaf surface shows several large bullae but it lacks long hairs. These specimens might prove to represent a distinct taxon (probably at

the subspecific level) but more material is needed to confirm that this is a contant character.

3. The single collection mentioned by Sosef l.c. for Congo proved to be a misidentification; it belongs to *B. lacunosa*. *B. susaniae*, therefore, is not represented in Congo.

4. A hybrid population between this species and *B. vittariifolia* has been observed (see chapter 9).

Specimens examined:

CAMEROON: *Annet 233* (P): Lolodorf region, Mt Ngowayang, 03°15'N 10°37'E (fr, 06); *Letouzey 11570* (P): Kombeng ridge, 8 km SSE of Matomb, 50 km WSW of Yaounde, 03°46'N 11°05'E (fl, 07); *Letouzey 15343* (WAG): falls of the Ntem R. near its confluence with the Bongola R., 40 km ESE of Campo, 02°10'N 10°08'E (st, 12); *Satabié & Letouzey 339* (YA): Ngovayang Massif, 14 km W of Lolodorf, 03°15'N 10°36'E (fl, 01); *Thomas 3408A* (K, MO, YA): Centre-Sud Prov., Mt Ngovayang, above Bibondi village, near Lolodorf, 03°18'N 10°39'E (fl, 04).

GABON: *Bogner 635* (M): M'Voum, 00°35'N 09°55'E (st, 10); *Bogner 740* (M): Crystal Mts, c. 00°30'N 10°30'E (fl, fr, 11); *Breteler & J.J. de Wilde 25* (WAG, holo): about 11 km along the road from Asok to the hydroelectric power station at Tchimbélé, 00°38'N 10°23'E (fl, fr, 08); *Breteler & J.J. de Wilde 39* (WAG): Tchimbélé R., 00°37'N 10°25'E (fl, fr, 08); *Breteler & J.J. de Wilde 41* (WAG): Tchimbélé R., near the outlet of the dam, 00°36'N 10°24'E (fl, 08); *Breteler & J.J. de Wilde 160* (WAG): about 13 km along the road from Asok to the hydroelectric power station at Tchimbélé, 00°36'N 10°24'E (fl, fr, 08); *Breteler & J.J. de Wilde 188* (WAG): Crystal Mts, about 15 km NE of Asok, 00°46'N 10°30'E (fl, 08); *Breteler & J.J. de Wilde 273* (WAG): about 7-8 km SW of Asok, hill W of Nkan, close to the road, 00°39'N 10°18'E (fl, fr, 08); *Breteler & J.J. de Wilde 274* (WAG): about 3 km along the road from Asok to the hydroelectric power station at Tchimbélé, 00°42'N 10°22'E (fl, fr, 08); *Breteler & J.J. de Wilde 334* (WAG): Mt Méla, about 1.5 hours walking distance S of Méla, 00°33'N 10°16'E (fl, fr, 08); *N. Hallé 861* (P): summit near Atok-Fina, Crystal Mts, 00°23'N 10°12'E (fl, 08); *N. Hallé & Villiers 4300* (P): left bank of the Komo, near Mbel, 00°16'N 10°10'E (fr, 01); *N. Hallé & Villiers 4345* (P): Mbel, 00°16'N 10°10'E (fl, 01); *N. Hallé & Villiers 4453* (P): Crystal Mts, Kinguélé falls, Mbé R., 00°29'N 10°20'E (fl, 01); *N. Hallé & Villiers 4488* (P): Crystal Mts, Kinguélé road, 00°25'N 10°16'E (fl, 01); *N. Hallé & Villiers 4621* (P): ibid. (fl, 01); *N. Hallé & Villiers 4711* (P): Crystal Mts, 6 km S Assok, 00°39'N 10°22'E (fl, fr, 01); *N. Hallé & Villiers 4762* (P): Crystal Mts, Nkan-Méla, 00°37'N 10°17'E (fl, 01); *N. Hallé & Villiers 4816* (P): Crystal Mts, Nkan, 00°39'N 10°19'E (fl, 01); *N. Hallé & Villiers 4850* (P): ibid. (fl, 02); *N. Hallé & Villiers 5126* (P): Crystal Mts, Mt Méla, 00°34'N 10°17'E (fl, 02); *N. Hallé & Villiers 5131* (P): ibid. (fl, 02); *N. Hallé & Villiers 5196* (P): Crystal Mts, Mt Mvélakéné, 5 km W of Méla, 00°36'N 10°13'E (fr, 02); *N. Hallé & Villiers 5401* (P): Crystal Mts, Kinguélé falls, 00°29'N 10°20'E (fl, fr, 02); *A. Louis 2840* (LBV, WAG): Estuaire Prov., 10 km road Tchimbélé to Kinguélé, 00°28'N 10°18'E (fl, fr, 02); *Périguet 33* (P): Assoben road, N'Koro to N'Kassia, 00°40'N 10°26'E (fl, fr, 02); *J.M. Reitsma c.s. 1912* (WAG, LBV): 10 km along the road Tchimbélé to Kinguélé, 00°28'N 10°18'E (fl, 02); *J.M. Reitsma c.s. 2118* (WAG): c. 13 km S of Cocobeach, 00°52'N 09°36'E (fl, 04); *J.M. Reitsma c.s. 3189* (LBV): Okoumé-plantation, ca 7 km S of Koulounga, 00°33'N 09°47'E (fl, 03); *Trilles 13* (P): Crystal Mts, c. 00°30'N 10°30'E (st, 05); *Wieringa 308* (WAG): Crystal Mts, 5.5 km E of Tchimbélé, 00°37'N 10°27'E (fl, fr, 12); *Wieringa 365* (WAG): Crystal Mts, 0.5 km SE of Tchimbélé., 00°37'N 10°24'E (fl, fr, 01); *Wieringa 396* (WAG): Crystal Mts, Woleu-Ntem, 1.5 km WNW of Tchimbélé, 00°37'N 10°23'E (fl, 01); *Wieringa 681* (WAG): Crystal Mts, Wolue-Ntem, 0.5 km N of Tchimbélé, 00°36'N 10°23'E (fl, 03); *Wieringa 799* (WAG): Crystal Mts, Woleu-Ntem, 11 km NNE of Tchimbélé, 00°42'N 10°27'E (fl, fr, 04); *Wieringa 912* (WAG): Crystal Mts, Woleu-Ntem, 1 km WNW of Tchimbélé, bank of Bingiligwen R., 00°37'N 10°23'E (fl, fr, 05); *Wieringa 917* (WAG): ibid. (st, 05); *Wieringa 932* (WAG): Crystal Mts, Woleu-Ntem, 0.5 km SE of Tchimbélé, 00°37'N 10°24'E (fl, fr, 05); *J.J. de Wilde c.s. 10038* (WAG): Crystal Mts, Tchimbélé, trail E of the dam, 00°37'N 10°24'E (fl, 12); *J.J. de Wilde c.s. 10050* (WAG): Crystal Mts, c. 3 km along the road Tchimbélé-Kinguélé, 00°36'N 10°23'E (fl, 12); *J.J. de Wilde c.s. 10085* (WAG): Crystal Mts, 25 km on the road Kinguélé to Tchimbélé, 00°32'N 10°17'E (fr, 01); *J.J. de Wilde c.s. 10103* (WAG): Crystal Mts, bank of Mbé R., c. 10 km along the road Tchimbélé-Kinguélé, 00°37'N 10°24'E (fl, fr, 01); *J.J. de Wilde c.s. 10131* (WAG): Crystal Mts, 15 km on the road Tchimbélé to Assok, 00°42'N 10°23'E (fl, fr, 01); *J.J. de Wilde c.s. 10154* (WAG): Crystal Mts, Nkan, along the road Assok-Méla, NNW of Nkan, 00°40'N 10°19'E (fl, fr, 01); *J.J. de Wilde c.s. 10214* (WAG): Crystal Mts, 12 km along the road Tchimbélé to Kinguélé, 00°36'N 10°21'E (fl, fr, 01); *J.J. de Wilde c.s. 10227* (WAG): Crystal Mts, 23 km along the road Tchimbélé to Kinguélé, 00°33'N 10°18'E (fl, fr, 01); *J.J. de Wilde c.s. 10258* (WAG): Crystal Mts, 25 km along the road Tchimbélé to Kinguélé, 00°31'N 10°18'E (fl, fr, 01); *J.J. de Wilde c.s. 10259* (WAG): ibid. (fl, 01); *J.J. de Wilde c.s. 10260* (WAG): Crystal Mts, 11 km along the road Tchimbélé to Kinguélé, 00°37'N 10°21'E (fl, fr, 01); *J.J. de Wilde c.s. (WALK-B) 9* (W, G): Crystal Mts, near the hydroelectric power station at Tchimbélé, 00°37'N 10°25'E (fl, 01); *J.J. de Wilde c.s. (WALK-B) 45* (LBV, WAG): Crystal Mts, 7 km along the road from Tchimbélé to Kinguélé, 00°37'N 10°22'E (fl, 01); *J.J. de Wilde c.s. (WALK-B) 115* (WAG): Crystal Mts, 11 km along the road from Tchimbélé to Kinguélé, 00°35'N 10°20'E (fl, fr, 01); *J.J. de Wilde c.s. (WALK-B) 135* (WAG): Crystal Mts, along the road from Assok to Tchimbélé, 00°40'N 10°22'E (fl, 01); *J.J. de Wilde c.s. (WALK-B) 194* (LBV, WAG): Crystal Mts, 10 km along the road from Tchimbélé to Kinguélé, 00°35'N 10°20'E (fl, 01).

CULTIVATED: *van Veldhuizen 1092* (WAG): Wageningen, Dept. of Horticulture No 1685 (coll. A. Louis s.n., Gabon) (st, 09); *van Veldhuizen 1093* (WAG): Wageningen, Dept. of Horticulture No 1610 (coll. J.J.F.E. de Wilde et al. (WALK-B) s.n., Gabon) (st, 09); *van Veldhuizen 1096* (WAG): Wageningen, Dept. of Horticulture No 1632 (coll. J.J.F.E. de Wilde et al. (WALK-B) s.n., Gabon, Crystal Mts) (st, 09).

Begonia vankerckhovenii De Wild. **Fig. 17.17, Map 17.11**

Begonia vankerckhovenii De Wild., Bull. Jard. Bot. État 5 (1915) 52; De Wild., Bull. Jard. Bot. État 5 (1919) 366; Wilczek, Fl. Congo, Rwanda et Burundi (1969) 37; N. Hallé, Adansonia, sér. 2, 12 (1972) 369, pl. 6.3; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39; L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 247, fig. 2.18; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 19, pl. 14E. – LECTOTYPE: *Van Kerckhoven 12* (BR!): 'St. Trudon, 20 Novembre 1912.'

Plant up to 7(–11) cm high, scattered with minute glandular hairs, sparsely so on stipules, pedicel of male flower and outside of perianth segments. **Rhizome** slender to rather stout, compact and knotted to more elongated and rather smooth, 0.4–2.1 mm wide, the younger parts hirsute or sparsely so; the apical part ascending or directed upwards to form a distinct stem of up to 4 cm high. **Stipules** narrowly triangular-ovate to broadly so, acute, 0.5–4.8 mm long, medium green to dark pinkish-red; margin entire to dentate, glabrous to ciliate. **Leaves** peltate or subpeltate; *petioles* continuing into the midrib with a slight but distict angle, inserted at 1–6(–9) mm from the nearest margin, 0.4–7(–11) cm long, rather firm and fleshy, dark pinkish-red, usually densely velutinous pilose with short, curly, pinkish red hairs, sometimes only sparsely so; *leaf blade* in more or less horizontal to erecto-patent position, asymmetrical, broadly ovate to broadly elliptic or ovate to elliptic or almost circular, blunt to acute, 0.9–6.1 x 0.6–3.8 cm, herbaceous to fleshy, with (5–)6–8 palmate main nerves; margin remotely serrate or dentate to almost entire, red or concolourous with the blade, sparsely shortly ciliate; base and top rounded; upper surface dark to light green, shiny, smooth, sometimes sparsely hirsute with long, curved, red hairs; lower surface pale green to green, with or without a red margin, dull; *nerves*: the main

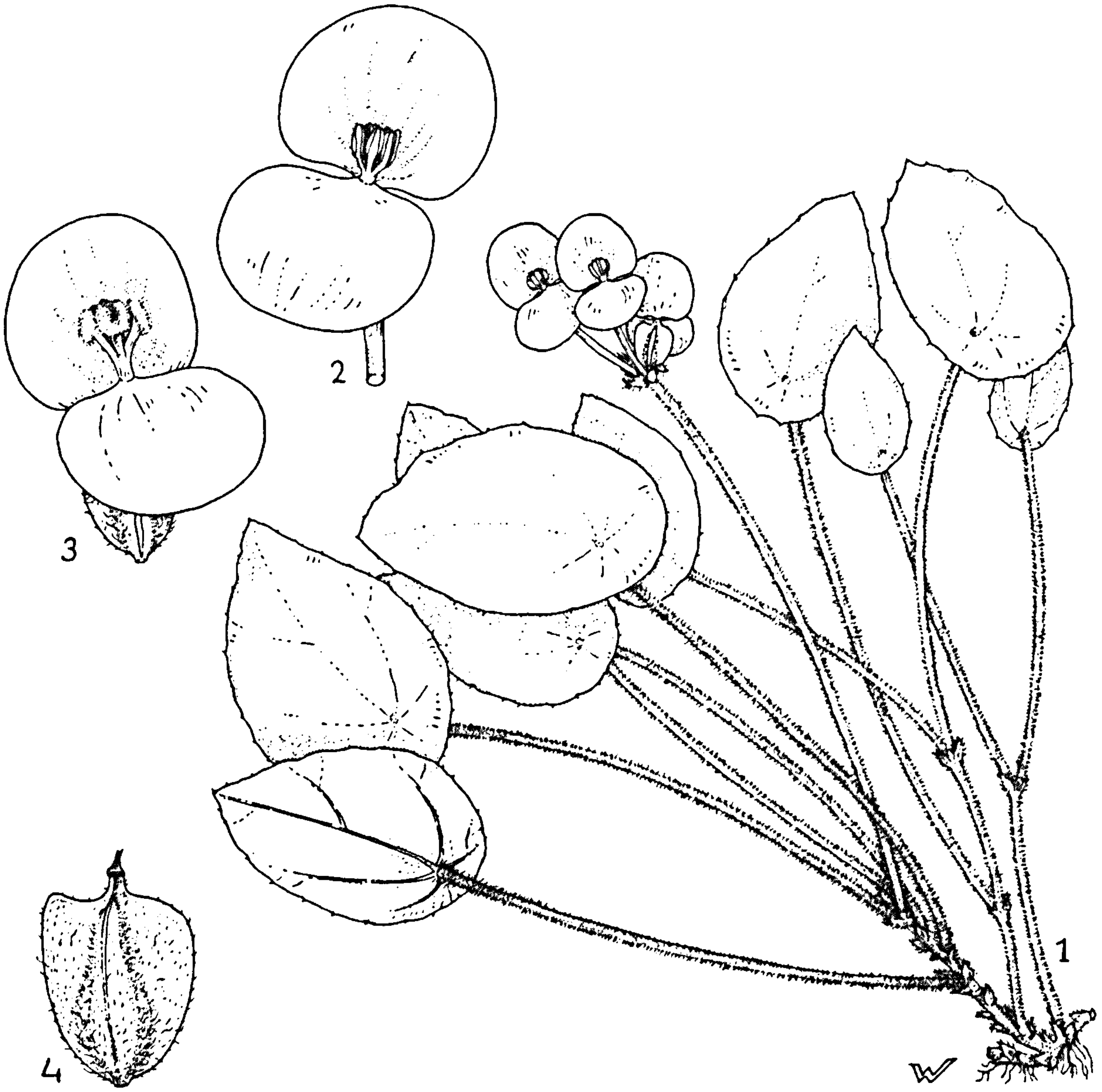
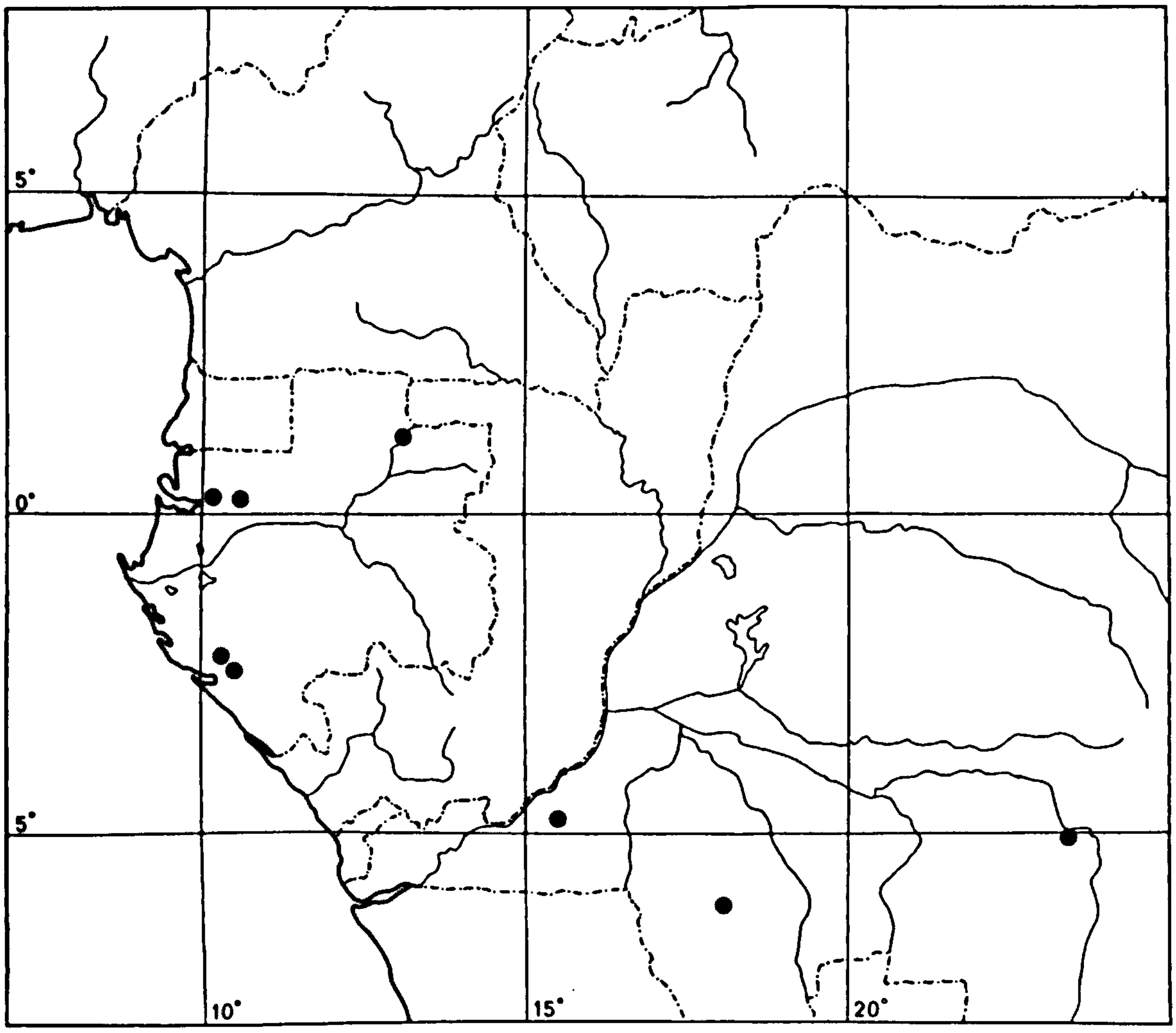


Figure 17.17. *Begonia vankerckhovenii* De Wild. – 1: habitus (x$^2/_3$); 2: male flower (x2); 3: female flower (x2); 4: fruit (x2). – 1-3: living plant at WAG, coll. *Arends c.s. 699*; 4: *Arends c.s. 699*.

and larger secondary nerves not or slightly prominent, concolorous with the blade on the upper surface, on the lower not or slightly prominent, medium green and not or sparsely hirsute with patent hairs, the smaller secondary nerves generally distinct, tertiary nerves indistinct but sometimes creating a reticulate pattern when dry. **Inflorescence** containing 1–2(–3) male flowers and 1 terminal female flower, positioned at approximately the same level as the leaf blades; *peduncle* simple, up to 6(–9.5) cm long, fairly firm, pinkish red to reddish bronze-green, with curly pinkish red, medium-sized to short hairs; *bracts* 2–3(–4), ovate or elliptic to narrowly ovate or narrowly elliptic, 0.4–3.6 mm long, pale pinkish red to bronze-green, glabrous; margin dentate or rarely entire, ciliate. **Male flower**: *pedicel* elongated at anthesis, up to 18 mm long, pale green, glabrous to sparsely hirsute or puberulous; *perianth segments* broadly ovate to broadly obovate or slightly transversely broadly elliptic, with a rounded base, 4.3–18.0 x 3.9–17.0 mm, not or sparsely hirsute; the upper segment orange-yellow to red or pinkish red on the outside, the inside orange to yellow or yellowish salmon, with or without a red patch and nerves in the basal half; the lower segment orange to yellowish salmon on the outside, the inside yellow to pale yellowish salmon or cream coloured; *androecium* with 10–16 stamens; column 0.5–0.9 mm long; anthers 1.2–1.9 mm long. **Female flower**: similar to the male but sessile though the pedicel elongated in fruit up to 2.7 mm; *perianth segments* broadly ovate to broadly obovate or transversely elliptic, 4.0–12.0 x 3.5–18.0 mm; *styles* 3 or 4, 2.0–3.8 mm long, fused up to 1/3–1/2; the top split and broad, compact or rather slender U- or V-shaped, the arms 0.1–1.0 mm long and covered with a terminal, stigmatic band which is spirally twisted for 1/2 a turn or not; *ovary* broadly obovate to broadly obtriangular-obovate, 3.2–10.5 x (2.0–)3.0–8.7 mm, pale green to pale pinkish red, 3–4-locular, 3–4-winged all along; the locular part elliptic to obovate, 1.0–2.6 mm wide, not or sparsely pilose especially along the line of fusion of the locules; beak present and sometimes distinct, up to 1.5 mm long; wings patent to slightly erecto-patent, broadly obtriangular to obovate, 0.6–3.9 mm wide, the margin glabrous to pilose. **Infructescence**: peduncle recurved towards the substrate or just curved and pushing the fruit in between the leaves; *fruit* more or less erect, broadly obovate to broadly obtraingular-obovate, 4.4–7.4 x (2.3–)3.0–9.0 mm, dry, thin-walled, brown, dull.



Map 17.11. Distribution of *Begonia vankerckhovenii*.

Distribution: Gabon and western and central Zaire.

Ecology: Apparently a rare species growing on wet, mossy rock faces in shade of closed high forest; once found in association with *Begonia dewildei*; at 500–900 m altitude.

Notes: 1. The distinctly reticulately nerved leaves of some collections give them a rather aberrant appearance at first glance. Further examination, however, did not yield any other characters to distinguish this material from other genuine *B. vankerckhovenii* specimens.

2. The protologue mentions 2 collections: Vankerckhoven 12 and 15. The first is chosen here as lectotype as the material is more complete.

3. The label of Breyne 5701 mentions a savanna with herbs and *Loudetia demeusei* as the habitat of this collection. It is assumed that these data are erroneous.

Specimens examined:

GABON: *Arends c.s. 699* (WAG): Doudou Mts, 02°15′S 10°20′E (fl, 12); *N. Hallé 1260* (P): Bélinga, iron mines, 01°13′N 13°10′E (fl, fr, 02); *N. Hallé 2255* (P): Abanga exploitation, 00°14′N 10°37′E (fl, 06); *N. Hallé & Villiers 4341* (P): Crystal Mts, c. 00°15′N 10°10′E (fl, 01); *J.M. Reitsma c.s. 1090* (WAG): CEB exploitation, Doudou Mts, ca 20 km WSW of Doussala, 02°25′S 10°30′E (fl, fr, 05).

ZAIRE: *Breyne 5701* (BR): Feshi zone, Feshi, 06°07′S 18°10′E (fl, 03); *Lawalrée 18350* (BR): Kinshasa, Busiga, c. 05°00′S 15°30′E (fl, 06); *Van Kerckhoven 12* (BR; iso: B): St. Trudon, 05°04′S 23°28′E (fl, fr, 11); *Van Kerckhoven 15* (BR): ibid., 05°04′S 23°28′E (fl, fr, 10).

Begonia vittariifolia N. Hallé **Fig. 17.18, Pl. 4b, c & d, Map 17.12**

Begonia vittariifolia N. Hallé, Adansonia, sér. 2, 12 (1972) 367, pl. 5; Doorenbos, Begonian 47 (1980) 37; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39; L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 249, fig. 14.8; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 19, pl. 15C. – TYPE: *N. Hallé & J.F. Villiers 5095* (P!, holo; BR!, K!, L!, P!): 'Gabon, Monts de Cristal, Mont Méla. Sommet vers 1000 m, 9 février 1968.'

Plant up to 20 cm high, scattered with minute glandular hairs, sometimes sparsely so on bracts, pedicel of male flower and outside of perianth segments, this indumentum dense on rhizome and petiole, dense to comparatively sparse on peduncle and ovary. **Rhizome**: elongated parts alternating with somewhat knotted, compact and leafy parts, 0.8–2.1 mm wide, sparsely set with short stiff hairs; the apical part ascending or with a short erect part. **Stipules** broadly triangular-ovate to narrowly elliptic, acute, 0.7–4.6 mm long, brown to pale wine-red, without or only the midrib on the abaxial side with a few long hairs; margin entire to dentate and only then ciliate. **Leaves** not peltate; *petiole* continuing into the midrib without a distinct angle, 0.5–4.0 cm long, firm, fleshy, bright green to red or dark brown-red, with or without short stiff hairs and long wavy, hairs; *leaf blade* in a more or less horizontal position, symmetrical, linear, broadest usually at or sometimes above the middle, attenuate towards the top, 6.6–19.0 x 0.3–1.4 cm, fleshy, pinnately nerved with a prominent midrib; margin incurved, red, serrate to dentate with distant small to distinct teeth, the teeth topped with a hair; base symmetrical, attenuate, top acute; upper surface medium green, shiny, smooth, not hirsute; lower surface pale green, dull; *nerves*: the midrib distinctly sunken to create a distinct groove and concolorous with the blade

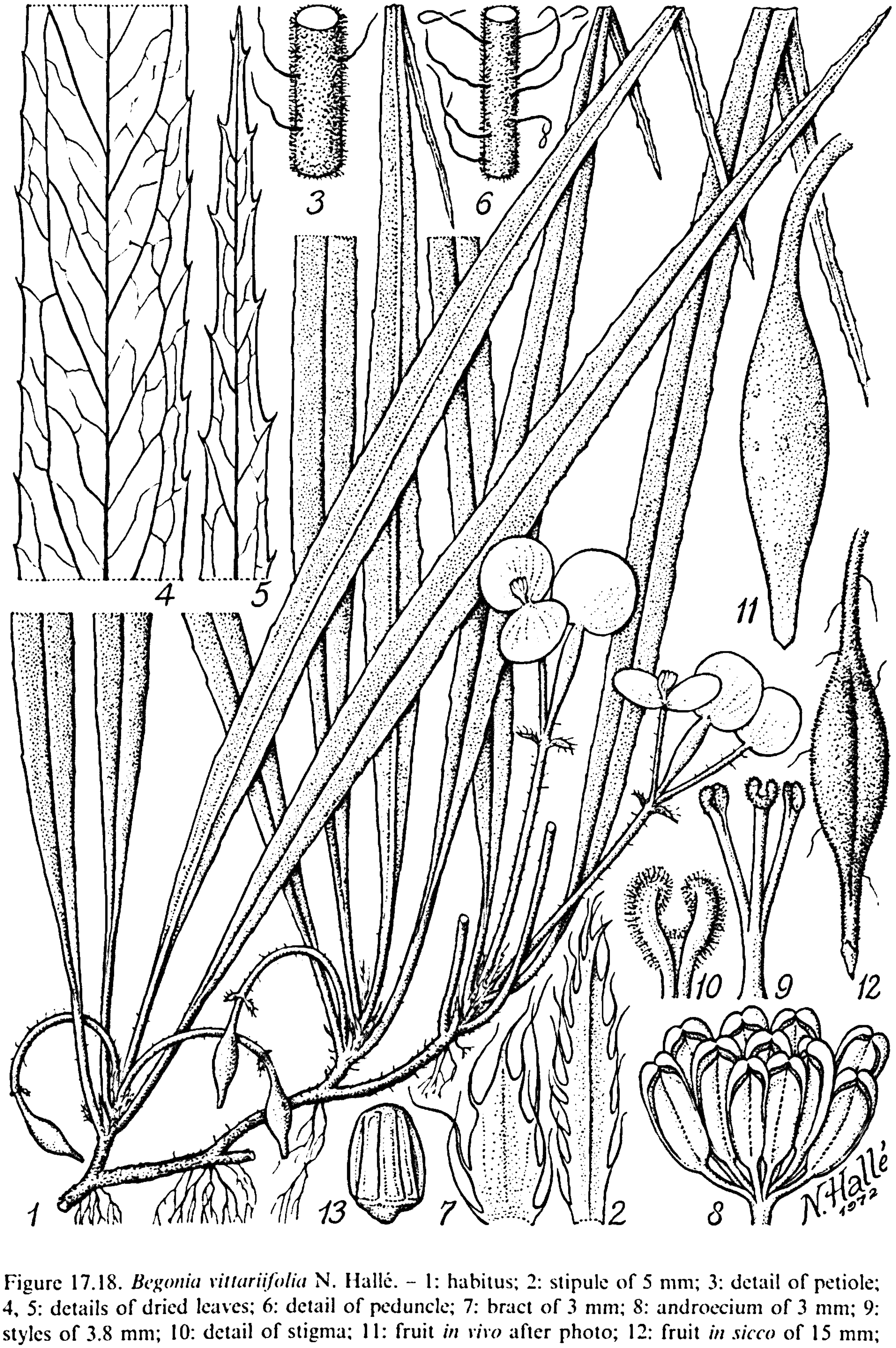


Figure 17.18. *Begonia vittariifolia* N. Hallé. – 1: habitus; 2: stipule of 5 mm; 3: detail of petiole; 4, 5: details of dried leaves; 6: detail of peduncle; 7: bract of 3 mm; 8: androecium of 3 mm; 9: styles of 3.8 mm; 10: detail of stigma; 11: fruit *in vivo* after photo; 12: fruit *in sicco* of 15 mm; 13: seed of 0.25 mm. – 1-13: *N. Hallé 5095*. Drawing prepared by Nicolas Hallé, formerly associated with the Musée National d'Histoire Naturelle, Paris.

on the upper surface, on the lower surface distinctly to slightly prominent, red to medium green, sometimes with a few short stiff hairs, the larger secondary nerves lacking, tertiary nerves indistinct but well visible and creating a reticulate pattern when dry. **Inflorescence** containing 1–3 male flowers and (0–)1 terminal female flower, positioned at about the same level as the base of the leaf blades; *peduncle* simple, 1.0–4.0 cm long, fleshy, bright green to wine-red, sometimes sparsely hirsute with short stiff red hairs; *bracts* (2–)3(–4), ovate to broadly elliptic, 0.9–3.2 mm long, pale green on the upper and reddish on the lower surface; margin dentate or entire with a dentate apex, the teeth topped with a hair. **Male flower**: *pedicel* elongated at anthesis up to 20 mm, yellowish green, sometimes sparsely hirsute with short hairs; *perianth segments* broadly ovate to circular or very broadly elliptic-ovate, slightly cordate at base, 6.6–13.5 x 5.5–13.5 mm, the outside sparsely hirsute or not with short red hairs; the upper segment orange on the outside, the inside yellow with or without red nerves at base; the lower segment entirely yellow; *androecium* with 6–16 stamens; column 0.8–0.9 mm long; anthers 0.9–1.4 mm long. **Female flower** similar to the male but shortly pedicellate, pedicel elongated in fruit and 1.0–5.2 mm long; *perianth segments* 6.0–11.0 x 6.5–12.0 mm; *styles* 3, 2.6–6.0 mm long, fused in the lower 1/2, the top split into a U-shape, the arms 0.4–1.3 mm long and bearing a slender, stigmatic band which is spirally twisted for up to 1/2 a turn; *ovary* more or less spindle-shaped with acuminate extremities, elliptic or narrowly so, 3.9–7.5 x 1.2–2.3 mm, pale or bright green, 3-locular, not winged, sparsely hirsute with short hairs or not; beak present and distinct, 0.5–5.7 mm long. **Infructescence**: peduncle recurved towards the substrate; *fruit* pendulous, narrowly elliptic, sometimes elliptic, with acuminate extremities, 4.2–11.0 x 1.6–3.9 mm, dry, with a comparatively thin wall, bright green, dull.

Distribution: GABON: Crystal Mountains and Chaillu Massif.

Ecology: On mossy vertical rockfaces in shade of closed to rather open primary forest; along or close to streams; at ± 320–1000 m altitude.

Notes: 1. A hybrid population between this species and *B. susaniae* has been observed (see also chapter 9).

Specimens examined:

GABON: *Breyne 5118* (BR): km 23 Tchimbélé-Kinguélé (Crystal Mts), 00°28′N 10°17′E (fr, 02); *N. Hallé & Villiers 5095* (P, holo; BR, K, L, P): Crystal Mts, Mt Méla, 00°34′N 10°17′E (fl, fr, 02); *J.J. de Wilde c.s. 10237* (WAG): Crystal Mts, 23 km along the road Tchimbélé to Kinguélé, 00°33′N 10°18′E (fl, fr, 01); *Wilks 1064* (LBV, WAG): Ngounié Prov., 60 km ESE of Ndjolé, 00°41′S 10°59′E (fl, 03).

Begonia wilksii Sosef **Fig. 17.19, Pl. 8b & c, Map 17.12**

Begonia wilksii Sosef, Wageningen Agric. Univ. Papers 91-4 (1992) 109, fig. 8, pl. 4b,c. – TYPE: *Wilks 1314* (WAG!, holo; LBV!): 'Gabon, Ngounié, 11 km E.S.E. de Bilengui, 1°59′S 11°30′E, 8/06/86.'

Diagnostic characters (for a more detailed description see Sosef l.c.):

Plant up to 7 cm high. **Leaves** subpeltate to peltate; *leaf blade* drooping, symmetrical to slightly asymmetrical, narrowly to very narrowly elliptic-ovate, rarely

Figure 17.19. *Begonia wilksii* Sosef. – 1: habitus (x$^{2}/_{3}$); 2: inflorescence (x2); 3: female flower (x3); 4: style (x4); 5: fruit (x3). – 1, 5: *Wilks 1314*; 2-4: *J.J. de Wilde & Sosef 10325*.

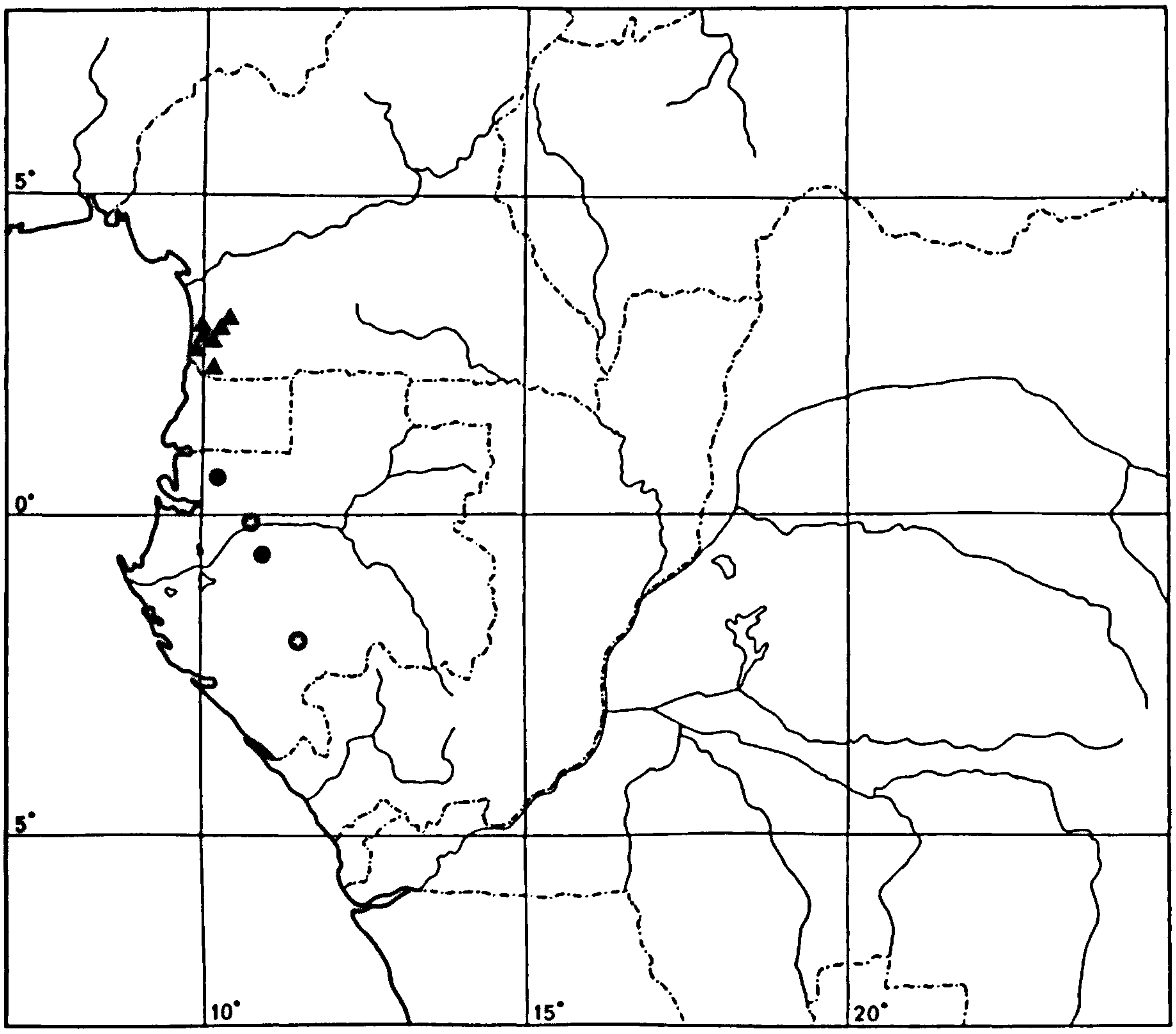
with a few large teeth at the apical part, gradually tapering towards the top, 3.9–16.0 x 0.6–2.3 cm; margin variously almost entire to denticulate or finely serrate, sparsely ciliate; upper surface rugose due to the sunken nerves, with or without a few erect white hairs. **Male flower**: *perianth segments* elliptic-ovate to broadly ovate or sometimes circular, with a rounded to cuneate base, 5.5–11.5 x 4.3–7.0 mm; the upper segment white with a red patch and nerves at the base; the lower segment white; *androecium* with 8–13 stamens. **Female flower**: *perianth segments* 4.2–9.1 x 5.1–6.8 mm; *ovary* transversely obtriangular to broadly obovate-obtriangular, 2.9–4.8 x 2.5–5.7 mm, hirsute to very sparsely so with white or red hairs; wings rarely absent, when present obovate to transversely obtriangular, 0–1.6 mm wide. **Infructescence**: peduncle recurved towards the substrate; *fruit* pendulous.

Distribution: GABON: north of Ndjolé and Chaillu Massif.

Ecology: On vertical rockfaces or large rocks along a stream or in a gully; in deeply or very deeply shaded sites in primary or secondary forest; at 250 m altitude.

Specimens examined:

GABON: *J.J. de Wilde c.s. 10325* (WAG): 15 km NE of Ndjolé, 00°07'S 10°49'E (fl, fr, 01); *Wilks 1314* (WAG, holo; LBV): Ngounié Prov., 11 km ESE of Bilengui, 01°59'S 11°30'E (fl, fr, 06).



Map 17.12. Distribution of *Begonia vittariifolia* (dots), *Begonia wilksii* (stars) and *Begonia zenkeriana* (triangles).

Begonia zairensis Sosef

a. var. zairensis **Fig. 17.20, Map 17.13**

Begonia zairensis Sosef var. *zairensis* Sosef, Wageningen Agric. Univ. Papers 91-4 (1992) 145, fig. 9; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 16, pl. 11B. – TYPE: *Van der Veken 9723* (GENT!, holo; BR!, WAG!): 'Zaïre, Kivoe, Irangi, IRSAC-domein bij de Luhoho. 800-850 m. 11.3.1972.'
Begonia clypeifolia auct. non Hook.f.: Wilczek, Fl. Congo, Rwanda et Burundi (1969) 37.
Begonia quadrialata auct. non Warb. p.p.: Wilczek, Fl. Congo, Rwanda et Burundi (1969) 38.

Diagnostic characters (for a more detailed description see Sosef l.c.):

Plant (5–)7–25(–32) cm high. **Leaves** peltate; *leaf blade* asymmetrical to almost symmetrical, usually elliptic to elliptic-ovate, sometimes broadly so, often slightly acuminate or gradually tapering towards the apex in the apical 1/4 to 1/6, (4.5–)7.0–14.5(–20.5) x (2.9–)3.5–9.5(–13.5) cm; margin almost entire to finely serrate towards the top, usually with a few coarse shallow teeth in the apical half especially in that of the larger right or left half of the blade, almost glabrous to ciliate; top acute; upper surface rarely sparsely hirsute with comparatively short hairs; *nerves:* the main and larger secondary nerves on the lower surface sparsely hirsute with patent hairs or not, rarely hirsute with appressed hairs. **Inflorescence** positioned from halfway up the petioles to at about the same level as the leaf blades; *bracts* very broadly ovate or almost circular to elliptic, (2.3–)3.0-5.9 mm long. **Male flower**: *perianth segments* usually broadly or very broadly ovate to circular, rarely ovate, slightly cuneate to slightly cordate at base, (5.9–)7.2–13.0 x (4.4–)5.1–13.0 mm; the outside yellow to orange; the upper segment yellow with a red patch and nerves on the inside; the lower segment yellow on the inside; *androecium* with (13–)19–28 stamens. **Female flower**: pedicel elongated in fruit, 0.5–10.0(–22.0) mm long; *perianth segments* with a rounded to cordate base, (5.9–)7.0–17.0 x (5.1–)7.3–17.0 mm; *ovary* usually very broadly to shallowly obtriangular-obovate, rarely only broadly so, (4.4–)5.3–8.3 x (3.3–)5.2–15.0 mm, not hirsute; wings broadly obovate to shallowly obtriangular, (0.7–)1.8–7.9 mm wide. **Infructescence**: peduncle not recurved towards the substrate; *fruit* more or less erect.

Distribution: ZAIRE: Kivu Prov. and Shaba Prov.

Ecology: Terrestrial or on rocks or decaying tree trunks; on slopes and banks along streams and rivers or sometimes on road banks; in shaded to deeply shaded sites in primary forest; in forest with *Cynometra, Julbernardia* and *Staudtia*; at 460–1250 m altitude.

Vernacular names: kalokosa, kangombangomba (Kirega, Zaire), kalokosa, karokosa, lungufa (Kitembo, Zaire).

Specimens examined:

ZAIRE: *Cambridge Congo Exp. 1959 319* (BM): Irangi, 70 km W of Lake Kivu, 01°53'S 28°27'E (fl, 08); *Cambridge Congo Exp. 1959 355* (BM, BR, LISC): ibid. (fl, 08); *Cambridge Congo Exp. 1959 384* (BM): ibid. (fl, 08); *Christiaensen 185* (BR): Kivu Prov., Shabunda Terr., Kisanga (Lugulu riv.), 02°27'S 28°15'E (fl, fr, 10); *Christiaensen 398* (BR): Kivu Prov., Kalehe Terr., Kabishula,

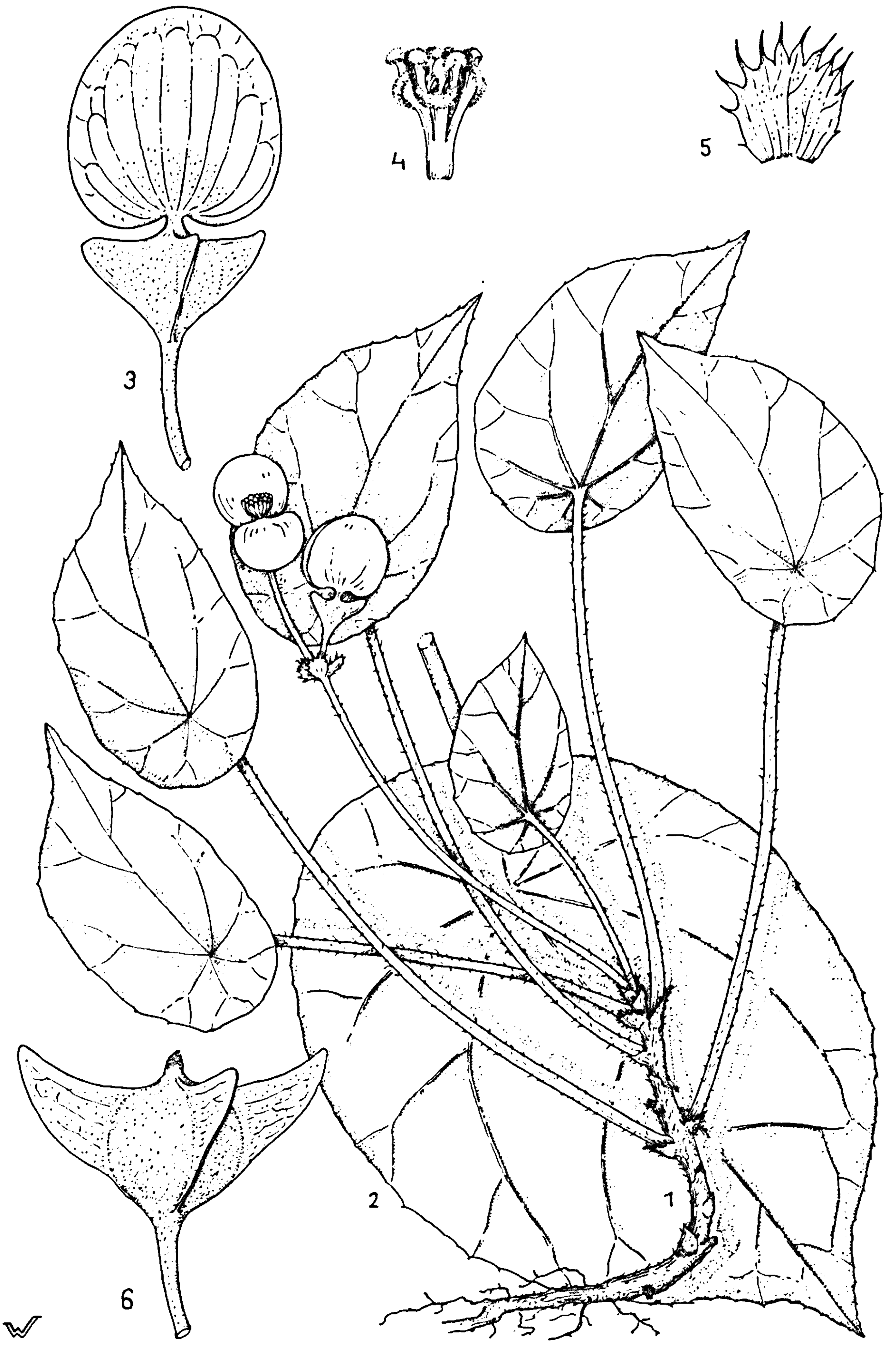


Figure 17.20. *Begonia zairensis* Sosef var. *zairensis*. – 1: habitus (x$^2/_3$); 2: comparatively large leaf blade (x$^2/_3$); 3: female flower and ovary (x2); 4: styles (x4); 5: bract (x4); 6: fruit (x2). – 1, 5: *Christiaensen 185*; 2: *Christiaensen 398*; 3, 4: *Christiaensen 986*; 6: *Van der Veken 9723*.

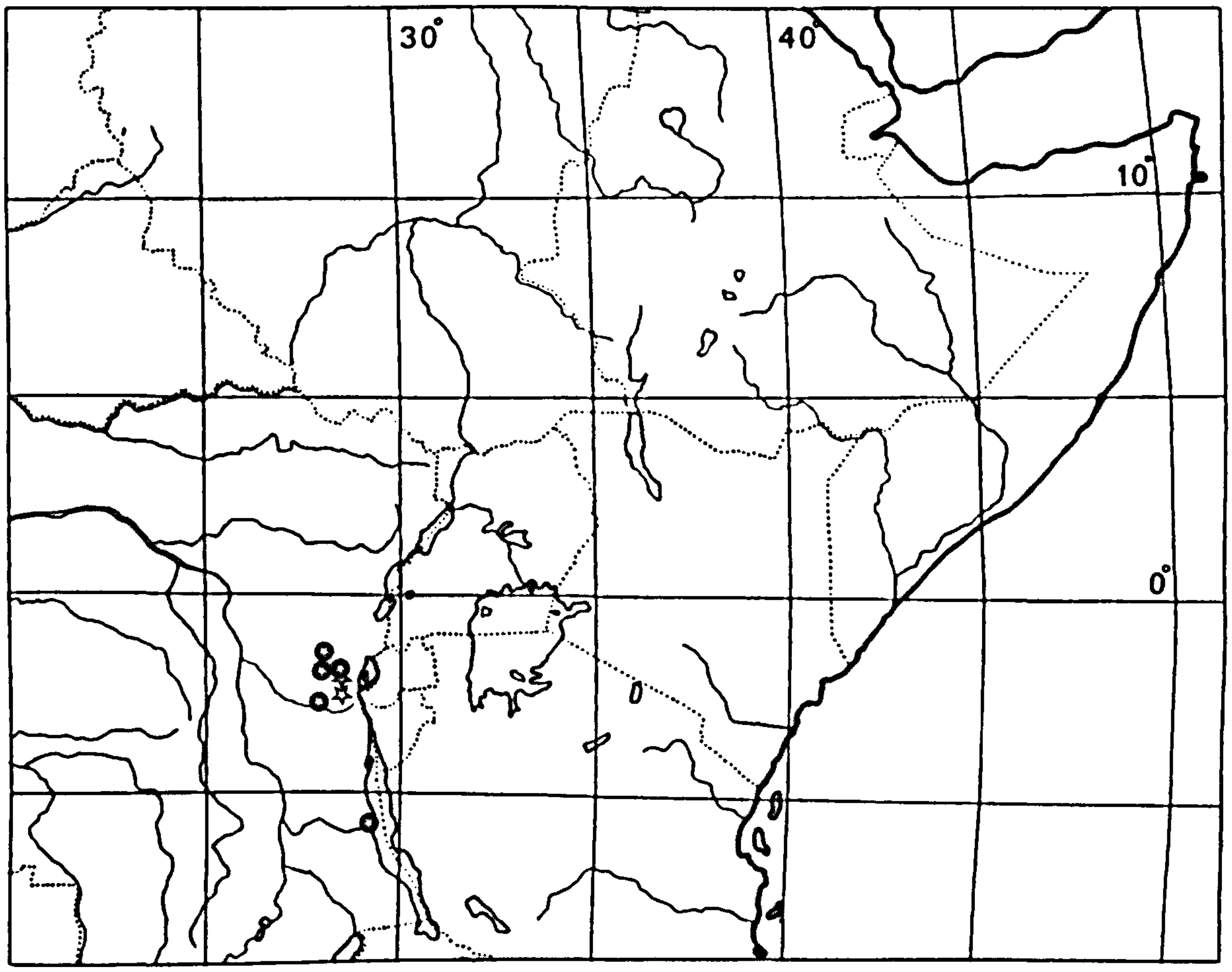
01°55'S 28°35'E (st, 03); *Christiaensen 986* (BR): Kivu Prov., Kalehe Terr., km 110 road Kavumu-Walikale, Irangi R. right of IRSAC, 01°53'S 28°27'E (fl, fr, 07); *Christiaensen 989* (BR): ibid. (fl, 07); *Léonard 1681* (BR): Walikale Terr., Ibondo, 01°47'S 28°09'E (fl, fr, 11); *Léonard 1930* (BR): Walikale Terr., Tandalukara, 01°33'S 28°22'E (fl, 12); *Léonard 3936* (BR): Shabunda Terr., Muhaki, 02°40'S 28°00'E (fl, 04); *Sebald 4644* (STU): Kivu Prov., near the IRSAC-station Irangi along the road Bukavu – Walikale, 01°53'S 28°27'E (fl, 02); *Troupin 9133* (BR): Kivu Prov., Kalehe Terr., road Kavumu-Walikale, km 110 near Irangi, Fulongo ridge, 01°53'S 28°27'E (fl, 08); *Troupin 10110* (BR): ibid. (st, 03); *Troupin 10308* (BR): ibid. (fl, 06); *Troupin 12163* (BR): Kivu Prov., Kalehe Terr., km 110 road Kavumu-Walikale, near Irangi, Catena I, 01°53'S 28°27'E (fr, 06); *Van Meel 118* (BR): Kabinda, Lubandaye R., 06°08'S 29°24'E (fl, 11); *Van der Veken 9723* (BR, holo; GENT, WAG): Kivu, Irangi, IRSAC-territory near the Luhoho, 01°53'S 28°27'E (fl, fr, 03).

b. var. **montana** Sosef **Map 17.13**

Begonia zairensis Sosef var. *montana* Sosef, Wageningen Agric. Univ. Papers 91-4 (1992) 148. – TYPE: *J. Lebrun 5542* (BR!, holo): 'Mushwere (Env. Ngweohe) (Kivu), Alt. 2000 m, Juin 1932, Forêt de montagne; ravin.'

Begonia scutulum auct. non Hook.f.: Wilczek, Fl. Congo, Rwanda et Burundi (1969) 36; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 39.

Differs mainly from the typical variety by:
Main and larger secondary nerves on the lower leaf surface hirsute with patent hairs. Bracts 3.3–7.8 mm long. Male flower: perianth segments up to 22 x 19 mm.



Map 17.13. Distribution of *Begonia zairensis* var. *zairensis* (stars in circles) and var. *montana* (open stars).

Female flower: perianth segments up to 19 x 22 mm.

Distribution: ZAIRE: Kivu Prov.

Ecology: In primary montane forest with *Cyathea, Julbernardia* and *Staudtia*; in a ravine; at 1000–2000 m altitude.

Vernacular names: madekere (Zaire, Mashi).

Specimens examined:

ZAIRE: *Lebrun 5542* (BR, holo): Kivu, Ngweohe region, Mushwere, 02°34'S 28°36'E (fl, 06); *Léonard 2935B* (BR): Kalehe Terr., Bunyakiri, 02°04'S 28°34'E (fl, 02); *Pierlot 70* (BR): km 36.5 road Kavumu-Walikale (Mikonzi), 02°16'S 28°35'E (fl, 03).

Begonia zenkeriana L.B. Smith & Wasshausen **Fig. 17.21, Map 17.12**

Begonia zenkeriana L.B. Smith & Wasshausen, Phytologia 56 (1984) 16 (as '*B. zenkerana*'), L.B. Smith et al., Begoniaceae ..., Smiths. Contr. Bot. 60 (1986) 251, fig. 14.38; Arends, Wageningen Agric. Univ. Papers 91-6 (1992) 177; de Lange & Bouman, Wageningen Agric. Univ. Papers 91-4 (1992) 16, pl. 11C. – *B. zenkeri* Irmscher non Warb. ex Excll, Bot. Jahrb. Syst. 81 (1961) 183; van den Berg, Agric. Univ. Wageningen Papers 84-3 (1985) 38-39. – TYPE: *Zenker 3005a* (B!, holo; G!): 'Kamerun, Bipinde, Urwaldgebiet, April 1904.'

Plant up to 33 cm high, scattered with minute glandular hairs, sparsely so on rhizome, stipules, peduncle, bracts and pedicel of male flower. **Rhizome** rather stout and elongated, fairly smooth, 3.3–8.0 mm wide, not hirsute; the apical part usually erect to produce a distinct stem of up to 11 cm long. **Stipules** narrowly to broadly triangular or triangular-ovate, usually acute, 2.1–16.5 mm long, bronze-green to dark red, glabrous to sparsely hirsute; margin almost entire to dentate, ciliate. **Leaves** not peltate or rarely subpeltate; *petiole* continuing into the midrib without a distinct angle, inserted at 1–2 mm from the nearest margin in subpeltate leaves, 3–16 cm long, firm, fleshy, bronze-green, dark red when young, sparsely hirsute or not with rather short, patent to appressed, wavy, white hairs, more densely hirsute when young; *leaf blade* in more or less vertical position, slightly asymmetrical, narrowly elliptic or elliptic-obovate to elliptic or elliptic-obovate, gradually attenuate towards the top or slightly acuminate, 11.5–19.0 x 4.4–8.3 cm, crispy herbaceous, palmately nerved with 4-6(-9) main nerves but the midrib much more pronounced and giving the leaf a pinnately nerved appearance with 8–16 larger secondary nerves; margin entire or sometimes shallowly sinuate-dentate towards the top, sometimes coarsely serrate-dentate in the upper half, concolorous with the blade, glabrous to sparsely shortly ciliate; base slightly unequal, one side cuneate to slightly cordate, the other very shortly and abruptly cordate to short and deeply cordate, the sides not or slightly overlapping, base rounded to slightly cordate in subpeltate leaves, top acute; upper surface medium green, purple-red when young, shiny, rarely with some long stiff hairs; lower surface pale green to purplish, purple-red when young, dull; *nerves*: the main and larger secondary nerves slightly sunken and concolorous with the blade on the upper surface, on the lower prominent, pale green to brown or purplish brown and shortly hirsute to sparsely so with patent to adpressed hairs, smaller secondary nerves distinct, tertiary nerves less so but

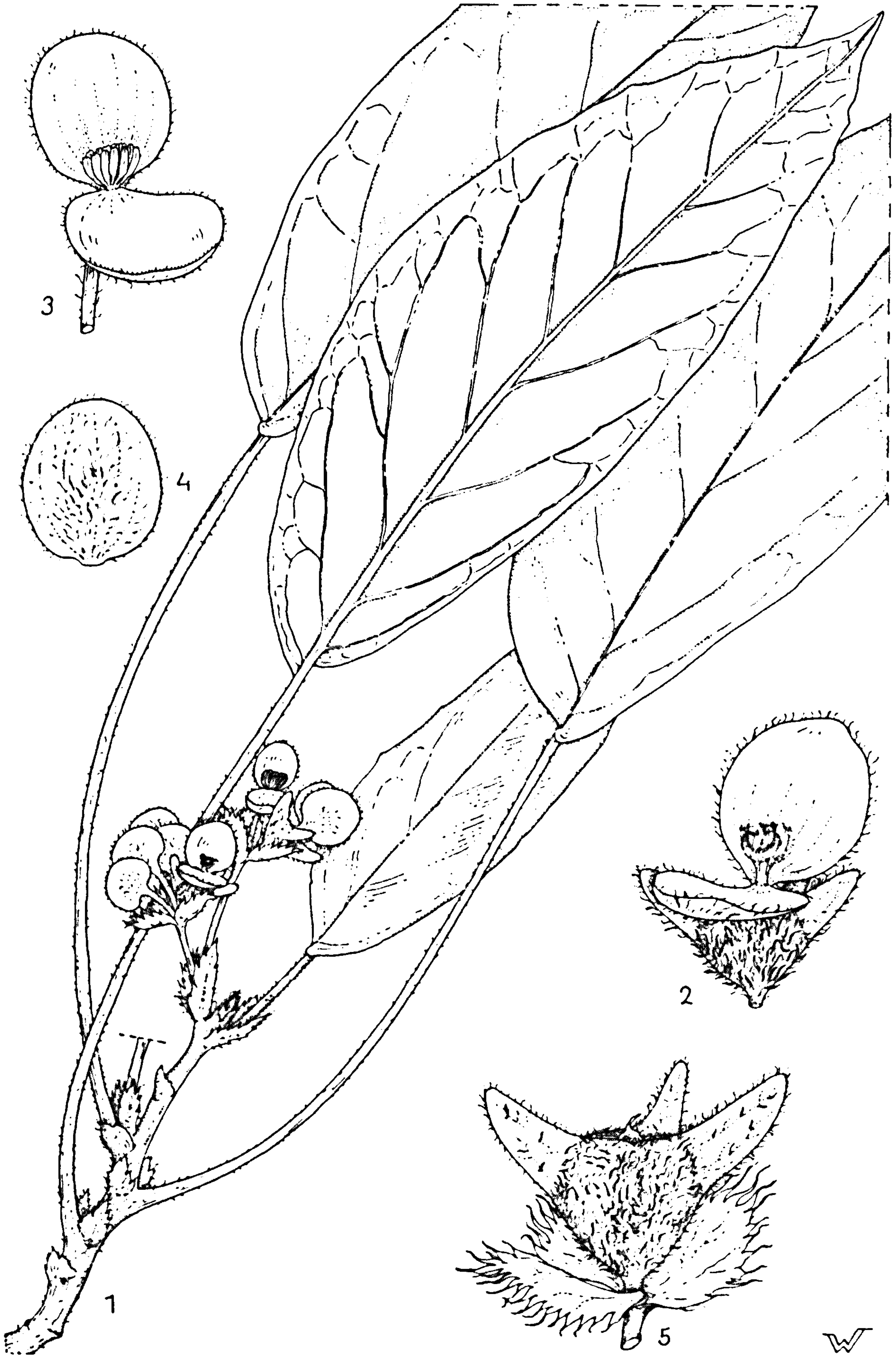


Figure 17.21. *Begonia zenkeriana* L.B. Smith & Wasshausen. – 1: habitus (x$\frac{2}{3}$); 2: female flower (x2); 3: male flower (x2); 4: outer surface perianth segment (x2); 5: fruit and bracts (x2). – 1, 3, 4: *Bos 3425*; 2: *Letouzey 9276*; 5: *Bos 7183*.

still well visible and creating a typical reticulate pattern when dry. **Inflorescence** containing 2–4 male and 1 terminal female flower, positioned at the base of the plant; *peduncle* simple, 0.5–1.8 cm long, fleshy, pale pinkish, sparsely hirsute with white hairs; *bracts* 3–5, almost circular or broadly ovate to elliptic-ovate, 4.8–13.0 mm long, dark pinkish red, hirsute or not; margin dentate, ciliate. **Male flower**: *pedicel* elongated at anthesis up to 12 mm, white to pale reddish white, sparsely hirsute; *perianth segments* broadly elliptic to broadly ovate, with a rounded base, 7.3–14.5 x 7.2–14.0 mm, the outside white, hirsute with long red hairs; the upper segment white with a red patch in the basal half and red nerves up to the top or with red nerves only in the basal half on the inside; the lower segment white on the inside; *androecium* with 26–29 stamens; column up to 0.8 mm long; anthers 1.8–2.7 mm long. **Female flower**: similar to the male but shortly pedicellate, pedicel elongated in fruit up to 0.4 mm; *perianth segments* circular to very broadly ovate with a rounded to cordate base, 9.1–10.5 x 10.0–11.5 mm; *styles* 3, 2.6–4.2 mm long, fused in the lower 1/3, the top split into a rounded U-shape, the arms 1.3–2.0 mm long and bearing a slender, stigmatic band which is spirally twisted for 1 turn; *ovary* very broadly obtriangular-obovate to shallowly obtriangular-obovate, 3.9–5.1 x 6.5–15.0 mm, pale green to reddish white or red, 3-locular, 3-winged at the apical 2/3, densely hirsute with red to white hairs; the locular part broadly obovate to broadly elliptic, 3.2–4.7 mm wide; beak short, up to 0.8 mm long; wings patent to slightly erecto-patent, very broadly obtriangular-obovate to very shallowly obtriangular-elliptic, 1.6–6.5 mm wide, white or pale greenish to red, the margin with a few hairs. **Infructescence**: peduncle recurved towards the substrate; *fruit* pendulous, very broadly obtriangular-obovate to shallowly obtriangular-obovate, 4.8–7.4 x 7.5–15.0 mm, dry, with a tough thick wall, pale green to pinkish white or red, dull.

Distribution: South-western Cameroon.

Ecology: Terrestrial growing in soil or mud; on level marshy sites or on slopes or stream banks, in shade of primary, often swampy forest; found in hygrophilous coastal evergreen Guineo-Congolian rain forest ('forêt biafréenne à *Caesalpiniaceae*') with *Sacoglottis gabonensis* and *Lophira alata*; at elevations near sea-level.

Notes: Irmscher l.c. extensively described and typified this species and named it *B. zenkeri*. This name proved to be a later homonym of *B. zenkeri* Warb. ex Exell and is therefore illegitimate. Smith & Wasshausen l.c. coined a new specific epithet 'zenkerana'. This is altered here, in accordance with art. 73.10 and recommendation 73C.1d of the Code, in 'zenkeriana'.

Specimens examined:

CAMEROON: *Bamps 1667* (BR): Kienke forest reserve, Kribi-Ebolowa km 16 (5 km to the left), 02°55'N 10°00'E (fl, 01); *Bos 3425* (BR, K, P, WAG, YA): 13.5 km from Kribi, N of Ebolowa road, Bidou II plantation in Kienke For. Res., 02°51'N 10°00'E (fl, 12); *Bos 4615* (WAG): about 12 km from Kribi, Lolodorf road, 02°59'N 09°59'E (fl, 05); *Bos 4869* (P, WAG, YA): 12 km from Kribi, between Ebolowa road and Kienke R., 02°53'N 09°59'E (fl, 06); *Bos 7183* (WAG): 3 km N of Nière R., mine road SE of Kribi, 02°44'N 10°03'E (fr, 07); *Kaji 258* (YA): Mvini, 35 km E of Campo, 02°22'N 10°06'E (fl, 10); *Letouzey 9276* (P, YA): 35 km E of Kribi, between Ndoa and Kienke R., 02°57'N 10°14'E (fl, 04); *Satabié 525* (P, WAG, YA): around Ebodje, 40 km S of Kribi, 02°35'N 09°54'E (fl, 12); *Zenker 3005A* (B, holo; BM, G, LY): Bipinde, 03°05'N 10°25'E (fl, 04).

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19 References

Adema, F., 1991. *Cupaniopsis* Radlk. (Sapindaceae): a monograph. Leiden Botanical Series 15. 190 pp.

Amiet, J.-L., 1987. Aires disjointes et taxons vicariants chez les Anoures du Cameroun: implications paléoclimatiques. Alytes 6: 99-115.

Arends, J.C., 1992. The biosystematics of *Begonia squamulosa* Hook.f. and affiliated species in section *Tetraphila* A.DC. Wageningen Agric. Univ. Papers 91-6: 1-223 (also Belmontia n.s. 24, no 149).

Aubréville, A., 1949. Contribution à la paléohistoire des forêts de l'Afrique tropicale. Soc. Edit. Géogr. Marit. Colon., Paris.

Aubréville, A., 1962. Savanisation tropical et glaciations quaternaires. Adansonia 2: 16-84.

Axelius, B., 1991. Areas of distribution and areas of endemism. Cladistics 7: 197-199.

Barabé, D., 1980. The perianth of *Begonia* flowers. The Begonian 47: 268-270.

Barabé, D., 1981. Vascularisation de la fleur pistillée de *Begonia handelii*. Can. J. Bot. 59: 819-825.

Barabé, D., L. Brouillet & C. Bertrand, 1985. Les bégonias à placentation pariétale: cas de *Begonia masoniana* Irmscher. Bull. Mus. natn. Hist. nat., Paris, 4e sér., 7, sect. B, Adansonia: 403-414.

Barabé, D. & L. Chrétien, 1983. Nouvelles données sur la vascularisation de la fleur pistillée des bégonias (Bégoniacées). Bull. Soc. Bot. Fr. 130, Lettres Bot.: 307-316.

Baranov, A.I., 1977. Preliminary notes on the structure of stigmatic surfaces in the *Begoniaceae*. Rhodora 79: 283-287.

Baranov, A.I., 1981. Studies in the *Begoniaceae*. Phytologia Mém. 4: i-vi, 1-88.

Baranov, A.I. & F.A. Barkley, 1974. The sections of the genus *Begonia*. Northeastern University, Boston.

Barkley, F.A., 1972a. Key to the sections of the *Begoniaceae*. The Buxtonian 1, Suppl. 3. 7 pp.

Barkley, F.A., 1972b. The species of the *Begoniaceae*. The Buxtonian 1, Suppl. 5. 120 pp.

Barkley, F.A. & B. Hozid, 1971. Leaf anatomy of *Begonia*. The Begonian 38: 135-142.

Barkley, F.A. & J. Golding, 1974. The species of the *Begoniaceae* (2nd ed.). Unpublished msc. 142 pp.

Barret, J., 1983. Géographie et cartographie du Gabon. Ministère de l'Éducation Nationale de la République Gabonaise, EDICEF, Paris.

Berg, R.G. van den, 1985. Pollen morphology of the genus *Begonia* in Africa. In: J.J.F.E. de Wilde (ed.). Studies in *Begoniaceae* II. Agric. Univ. Wageningen Papers 84-3: 5-94 (also Belmontia n.s. 18, no 102).

Bernardi, G., 1966. Aréotypes et chorologie de l'ouest Africain principalement d'après les *Pieridae* (*Lepidopt.*). J. W. Afr. Sci. Assoc. 11: 49-67.

Birger, S., 1926. Per Dusén. Sv. Bot. Tidsk. 20: 77-85.

Boghdan, K.S. & F.A. Barkley, 1972. Stomatal patterns in the genus *Begonia*. Phytologia 23: 327-333.

Bone, R.A., D.W. Lee & J.M. Norman, 1985. Epidermal cells functioning as lenses in leaves of tropical rain-forest shade plants. Applied Optics 24: 1408-1412.

Bonnefille, R., 1987. Évolution forstière et climatique au Burundi durant les quarante derniers milliers d'années. C. R. Acad. Sci. Paris, t. 305, sér. II: 1021-1026.

Bonnefille, R., J.C. Roeland & J. Guiot, 1990. Temperature and rainfall estimates for the past 40,000 years in equatorial Africa. Nature 346: 347-349.

Bouman, F. & A. de Lange, 1982. Micromorphology of the seed coats in *Begonia* section *Squamibegonia* Warb. Acta Bot. Neerl. 31: 297-305.

Bouman, F. & A. de Lange, 1983. Structure, micromorphology of *Begonia* seeds. The Begonian 50: 70-78, 91.

Brooks, D.R., 1990. Parsimony analysis in historical biogeography and coevolution: methodological and theoretical update. Syst. Zool. 39: 14-30.

Brouillet, L., C. Bertrand, A. Cuerrier & D. Barabé, 1987. Les hydathodes des genres *Begonia* et *Hillebrandia* (*Begoniaceae*). Can. J. Bot. 65: 34-52.

Bugnon, P., 1926. Valeur morphologique de l'ovaire infère chez les *Begonia*. Bull. Soc. Linn. Normandie VII, 9: 7-25.

Bugnon, P. & F. Bugnon, 1953. La paroi de l'ovaire infère des *Begonia* est-elle de nature axile ou appendiculaire? Bull. Sci. Bourgogne 14: 109-127.

Caratini, C. & P. Giresse, 1979. Contribution palynologique à la connaissance des environnements continentaux et marins du Congo à la fin du Quaternaire. C. R. Acad. Sci. Paris, sér. D, 288: 379-382.

Chappill, J.A., 1989. Quantitative characters in phylogenetic analysis. Cladistics 5: 217-234.

Charpentier, A., L. Brouillet & D. Barabé, 1989a. Organogenèse de la fleur pistillée du *Begonia horticola* (*Begoniaceae*). Can. J. Bot. 67: 559-572.

Charpentier, A., L. Brouillet & D. Barabé, 1989b. Organogénèse de la fleur pistillée du *Begonia dregei* et de l'*Hillebrandia sandwicensis* (*Begoniaceae*). Can. J. Bot. 67: 3625-3639.

Chevalier, A., 1912. Novitates florae Africanae, *Begoniaceae*. Bull. Soc. Bot. France 58 (Mém. 8): 173-177.

Colinvaux, P.A., 1989. The past and future Amazon. Scientific Amer. 260, 5: 68-74.

Colyn, M., A. Gautier-Hion & W. Verheyen, 1991. A re-appraisal of palaeoenvironmental history in central Africa: evidence for a major fluvial refuge in the Zaire Basin. J. Biogeogr. 18: 403-407.

Cracraft, J., 1988. Deep-history biogeography: retrieving the historical pattern of evolving continental biotas. Syst. Zool. 37: 221-236.

Cuerrier, A., L. Brouillet & D. Barabé, 1990. Numerical taxonomic study of the *Begoniaceae* using the Mantel test on leaf microcharacters. Taxon 39: 549-560.

Cuerrier, A., L. Brouillet & D. Barabé, 1991a. Micromorphologie foliaire des *Begoniaceae*. Bull. Mus. natn. Hist. nat., Paris, 4e sér., 12, sect. B, Adansonia: 297-335.

Cuerrier, A., L. Brouillet & D. Barabé, 1991b. Analyse taxonumérique des charactères foliaires des *Begoniaceae*. Bull. Mus. natn. Hist. nat., Paris, 4e sér., 12, sect. B, Adansonia: 337-353.

Cutler, D.F., 1978. Applied plant anatomy. Longman, London.

Darwin, C., 1859. On the origin of species by means of natural selection, or the preservation of favored races in the struggle for life. John Murry, London.

De Candolle, A., 1859. Mémoire sur la famille des *Bégoniacées*. Ann. Sci. Nat. Bot. IV, 11 (2): 92-149.

De Candolle, A., 1864. Ordo CLXXII. *Begoniaceae*. Prodromus systematis naturalis regni vegetabilis 15, 1: 266-408. Victoris Masson et filii, Parisiis.

De Wildeman, E., 1906. *Begoniaceae*. Ann. Mus. Congo, Bot., sér. V, vol. I: 294-295.

De Wildeman, E., 1908. *Begoniaceae*. Ann. Mus. Congo, Bot., sér. V, vol. II: 317-324.

De Wildeman, E., 1915. Decades novarum specierum florae Congolensis III. Bull. Jard. Bot. État (Brux.) 5: 1-108.

Diamond, A.W. & A.C. Hamilton, 1980. The distribution of forest passerine birds and Quaternary climatic change in tropical Africa. J. Zool., Lond. 191: 379-402.

Dunn de Araujo, D. & C. Gonçalves Costa, 1972. Estudo anátomo-ecológico de *Begonia maculata* Raddi. Anais Acad. Brasil. Ciênc. 44: 317-336.

Eames, A.J., 1961. Morphology of the Angiosperms. McGraw-Hill, New York.

Elenga, H. & A. Vincens, 1990. Paleoenvironnements Quaternaires récents des Plateaux Batéké (Congo): étude palynologique des depots de la depression du Bois de Bilanko. In: R. Lanfranchi & D. Schwartz (eds). Paysages Quaternaires de l'Afrique centrale Atlantique: 271-282. Didactiques, Traveaux et Documents ORSTOM, Paris.

Engler, A., 1921. Fam. *Begoniaceae*. In: A. Engler & O. Drude (eds). Die Vegetation der Erde 9, Die Pflanzenwelt Afrikas 3, 2: 612-621. Wilhelm Engelmann, Leipzig.

Esau, K., 1965. Plant anatomy (2nd ed.). Wiley, New York.

Farris, J.S., 1988. HENNIG86 reference, version 1.5. University of Stoney Brook, New York.

Farris, J.S., 1989. The retention index and the rescaled consistency index. Cladistics 5: 417-419.

Fellerer, C., 1892. Beiträge zur Anatomie und Systematik der Begoniaceen. Val. Höfling, München.

Gauthier, R., 1950. The nature of the inferior ovary in the genus *Begonia*. Contr. Inst. Bot. Univ. Montréal 66: 5-91.

Gauthier, R., 1959. L'anatomie vasculaire et l'interprétation de la fleur pistillée de l'*Hillebrandia sandwicensis* Oliv. Phytomorphology 9: 72-87.

Geesink, R. & D.J. Kornet, 1989. Speciation and Malesian *Leguminosae*. In: L.B. Holm-Nielsen, I.C. Nielsen & H. Balslev (eds). Tropical forests: botanical dynamics, speciation and diversity: 135-151. Academic Press, London.

Gentry, A.H., 1989. Speciation in tropical forests. In: L.B. Holm-Nielsen, I.C. Nielsen & H. Balslev (eds). Tropical forests: botanical dynamics, speciation and diversity: 113-134. Academic Press, London.

Ghiselin, M.T., 1974. A radical solution to the species problem. Syst. Zool. 23: 536-544.

Gilg, E., 1904. *Begoniaceae* africanae II. Bot. Jahrb. Syst. 34: 86-98.

Giresse, P. & R. Lanfranchi, 1984. Les climats et les océans de la région congolaise pendant l'Holocène. Bilans selon les échelles et les méthodes de l'observation. Palaeoecol. Afr. 16: 77-88.

Gonçalves Costa, C., 1970. Observaçoes sôbre a anatomia de *Begonia valdesium* A.DC. Anais Acad. Brasil. Ciênc. 42: 119-128.

Gonçalves Costa, C., 1971. Sôbre a anatomia foliar de *Begonia paleata* Schott. ex A.DC. Anais Acad. Brasil. Ciênc. 43: 209-220.

Greuter, W. et al., 1988. International code of botanical nomenclature adopted by the Fourteenth International Botanical Congress, Berlin, July - August 1987. Koeltz Scientific Books, Königstein.

Griswold, C.E., 1991. Cladistic biogeography of afromontane spiders. Austr. Syst. Bot. 4: 73-89.

Grubb, P., 1982. Refuges and dispersal in the speciation of African forest mammals. In: G.T. Prance (ed.). Biological diversification in the tropics: 537-553. Columbia University Press, New York.

Guillaumet, J.L., 1967. Recherches sur la végétation et la flore de la région du Bas-Cavally (Côte d'Ivoire). Mémoires ORSTOM no 20. ORSTOM, Paris.

Haberlandt, G., 1888. Zur Anatomie der Begonien. Mitth. Naturwiss. Ver. Steiermark 1887: 1-12.

Haberlandt, G., 1896. Physiologische Pflanzenanatomie (2e ed.). Wilhelm Engelmann, Leipzig.

Haberlandt, G., 1904. Die Perzeption des Lichtreizes durch das Laubblatt. Ber. Deutsch. Bot. Gesellschaft 22: 105-119.

Haberlandt, G., 1916. Blattepidermis und Lichtperzeption. Sitzungsber. Kön. Preuss. Akad. Wissensch. 32: 672-687.

Hagman, F.A. & J.J.F.E. de Wilde, 1984. Re-establishment of *Begonia cavallyensis* A. Chev. and the altitudinal vicariad *Begonia fusicarpa* Irmsch. (sect. *Tetraphila*). In: J.J.F.E. de Wilde (ed.). Studies in *Begoniaceae* I. Meded. Landbouwhogeschool Wageningen 83-9: 1-19.

Hall, B.P. & R.E. Moreau, 1970. An atlas of speciation in African passerine birds. Trustees of the British Museum (Natural History), London.

Hall, J.B., 1973. Vegetational zones on the southern slopes of Mount Cameroon. Vegetatio 27: 49-69.

Hallé, N., 1967. Deux *Begonia* du Gabon analysés sur le vif: *B. triflora* Irmscher et *B. ferramica* sp. nov. Adansonia, sér. 2, 7: 507-512.

Hallé, N., 1972. Les *Begonia* filicifoliés et quatre espèces nouvelles du Gabon. Adansonia, sér. 2, 12: 359-374.

Hamilton, A.C., 1976. The significance of patterns of distribution shown by forest plants and animals in tropical Africa for the reconstruction of upper Pleistocene palaeoenvironments: a review. In: E.M. van Zinderen Bakker (ed.). Palaeoecology of Africa 9: 63-97. A.A. Balkema, Cape Town.

Hamilton, A.C., 1982. Environmental history of east Africa. A study of the Quaternary. Academic Press, London.

Hamilton, A.C., 1988. Guenon evolution and forest history. In: A. Gautier-Hion et al. (eds). A primate radiation: evolutionary biology of the African guenons: 13-34. Cambridge University Press, Cambridge.

Hamilton, A.C. & D. Taylor, 1991. History of climate and forests in tropical Africa during the last 8 million years. In: N. Myers (ed.). Tropical forests and climate: 65-78. Kluwer Academic Publishers, Dordrecht (also Climatic Change 19: 65-78).

Hamilton, C.W. & S.H. Reichard, 1992. Current practice in the use of subspecies, variety, and forma in the classification of wild plants. Taxon 41: 485-498.

Hecketsweiler, P., 1991. La conservation des ecosystèmes forestiers du Congo. UICN, Gland & Cambridge.

Hennig, W., 1950. Grundzüge einer Theorie der phylogenetischen Systematik. Deutscher Zentralverlag, Berlin.

Hennig, W., 1966. Phylogenetic systematics. University of Illinois Press, Urbana.

Hepper, F.N., 1965. Preliminary account of the phytogeographical affinities of the flora of west tropical Africa. Webbia 19: 593-617.

Hickey, L.J., 1979. A revised classification of the architecture of dicotyledonous leaves. In: C.R. Metcalfe & L. Chalk (eds). Anatomy of the Dicotyledons (ed. 2), vol. I. Oxford University Press, Oxford.

Hildebrand, F.H.G., 1859. Anatomische Untersuchungen über die Stämme der Begoniaceen. August Hirschwald, Berlin.

Hooker, J.D., 1871. LXV *Begoniaceae*. In: D. Oliver (ed.). Flora of tropical Africa 2: 569-580. L. Reeve & Co., Ashford.

Hoover, W.S., 1986. Stomata and stomatal clusters in *Begonia*. Ecological responses in two Mexican species. Biotropica 18: 16-21.

Hoover, W.S., 1988. Investigations on stomata and stomatal clusters in *Begonia*: a possible stomatal indicator of tropical seasonal climate change. Phytologia 65: 89-96.

Hull, D.L., 1976. Are species really individuals? Syst. Zool. 25: 174-191.

Humphries, C.J., P.Y. Ladiges, M. Roos & M. Zandee, 1988. Cladistic biogeography. In: A.A. Myers & P.S. Giller (eds). Analytical biogeography: an integrated approach to the study of animal and plant distributions: 371--404. Chapman & Hall, London.

Humphries, C.J. & L.R. Parenti, 1986. Cladistic biogeography. Clarendon Press, Oxford.

Inamdar, J.A., D.C. Bhatt & R.C. Patel, 1973. Normal and abnormal stomatal development in some *Begoniaceae* and *Gesneriaceae*. Acta Bot. Acad. Sci. Hungaricae 19: 181-188.

Irmscher, E., 1914. Die Verteilung der Geschlechter in der Inflorenzen der Begoniaceen unter Berücksichtigung der morphologischen Verhältnisse. Bot. Jahrb. Syst. 50, Suppl.: 556-577.

Irmscher, E., 1921. *Begoniaceae* africanae III. Bot. Jahrb. Syst. 57: 241-245.

Irmscher, E., 1925. *Begoniaceae*. In: A. Engler & K. Prantl (eds). Die natürlichen Pflanzenfamilien (ed. 2) 21: 548-588. Wilhelm Engelmann, Leipzig.

Irmscher, E., 1954. Neue Afrikanische Begonien. Bot. Jahrb. Syst. 76: 212-216.

Irmscher, E., 1961. Monographische revision der Begoniaceen Afrikas I. Sekt. *Augustia* und *Rostrobegonia* sowie einige neue Sippen aus anderen Sektionen. Bot. Jahrb. Syst. 81: 106-188.

Keraudren-Aymonin, M., 1983. Caractères et intérêt taxinomique de l'ornementation tégumentaire des graines de quelques espèces de *Begonia* de Madagascar. Bull. Soc. Bot. France 130, Lettres Bot.: 329-338.

Kingdon, J.S., 1980. The role of visual signals and face patterns in African forest monkeys (guenons) of the genus *Cercopithecus*. Trans. Zool. Soc., London 35: 425-475.

Klotzsch, J.F., 1855. *Begoniaceae* -- Gattungen und Arten. Abhandl. Kön. Akad. Wiss. Berlin 1854. 135 pp.

Kniep, H., 1907. Über die Lichtperzeption der Laubblätter. Biol. Centralbl. 27: 97-106, 129-142.

Kornet, D.J., 1988. Conventional and fundamental problems in the delimitation of genera from a phylogenetic point of view. Acta Bot. Neerl. 37: 527-529.

Kornet, D.J., 1993. Reconstructing species. Demarcations in genealogical networks. Instituut voor Theoretische Biologie & Rijksherbarium/Hortus Botanicus, Leiden.

Kroon, G.H., 1991. Begonia. Taxonomische en fysiologische aspecten van wilde *Begonia* soorten van belang voor de veredeling. Unpublished report. Dept. of Plant Taxonomy, Wageningen Agricultural University.

Lange, A. de & F. Bouman, 1985. The importance of seed morphology for the classification of African *Begonia* sections. Acta Bot. Neerl. 34: 229.

Lange, A. de & F. Bouman, 1986. Micromorphology of the seeds in *Begonia* section *Solananthera* A.DC. Acta Bot. Neerl. 35: 489-495.

Lange, A. de & F. Bouman, 1992. Seed micromorphology of the genus *Begonia* in Africa: taxonomic and ecological implications. In: J.J.F.E. de Wilde (ed.). Studies in *Begoniaceae* III. Wageningen Agric. Univ. Papers 91-4: 1-82 (also Belmontia n.s. 24, no 146).

Lawton, R.M., 1963. Palaeoecology and ecological studies in the Northern Province of Northern Rhodesia. Kirkia 3: 46-77.

Lee, D.W., 1983. Unusual strategies of light absorption in rain-forest herbs. In: T.J. Givnish (ed.). On the economy of plant form and function (Proceedings Sixth Maria Moors Cabot Symposium): 105-131. Cambridge University Press, Cambridge.

Lee, D.W. & R. Graham, 1986. Leaf optical properties of rainforest sun and extreme shade plants. Amer. J. Bot. 73: 1100-1108.

Lee, D.W. & B.C. Stone, 1979. Abaxial anthocyanin layer in leaves of tropical rainforest plants: enhancer of light capture in deep shade. Biotropica 11: 70-77.

Lee, Y.S., 1974. A study of stem anatomy in *Begonia* L. Phytologia 27: 464-489.

Letouzey, R., 1968. Étude phytogéographique du Cameroun. Encyclopédie Biologique LXIX. Paul Lechevalier, Paris.

Lezine, A.-M., 1988. Les variations de la couverture forestière mésophile d'Afrique occidentale au cours de l'Holocène. C. R. Acad. Sci. Paris, t. 307, sér. II: 439-445.

Linné, C., 1753. Species Plantarum, 2 vols. Laurentii Salvii, Holmiae.

Livingstone, D.A., 1975. Late Quaternary climatic change in Africa. Ann. Rev. Ecol. Syst. 6: 249-280.

Livingstone, D.A., 1982. Quaternary geography of Africa and the refuge theory. In: G.T. Prance (ed.). Biological diversification in the tropics: 523-536. Columbia University Press, New York.

Lönnberg, E., 1929. The development and distribution of the African fauna in connection with and depending upon climatic changes. Arkiv för Zoologi 21A, 4: 1-33.

Maley, J., 1987. Fragmentation de la forêt dense humide Africaine et extensions des biotopes montagnards au Quaternaire récent: nouvelles donnees polliniques et chronologiques. Implications paleoclimatiques et biogeographiques. In: J.A. Coetzee (ed.). Palaeoecology of Africa 18: 307-334. A.A. Balkema, Rotterdam.

Maley, J., 1989. Late Quaternary climatic changes in the African rain forest: forest refugia and the major role of sea surface temperature variations. In: M. Leinen & M. Sarnthein (eds). Paleoclimatology and paleometeorology: Modern and past patterns of global atmospheric transport. NATO Adv. Sci. Inst. Series, C: Math. & Phys. Sci. 282: 585-616. Kluwer Academic Publishers, Dordrecht.

Maley, J., 1991. The African rain forest vegetation and palaeoenvironments during Late Quaternary. In: N. Myers (ed.). Tropical forests and climate: 79-98. Kluwer Academic Publishers, Dordrecht (also Climatic Change 19: 79-98).

Maley, J. & P. Brenac, 1987. Analyses polliniques préliminaires du Quaternaire récent de l'Ouest Cameroun: mise en évidence de refuges forestièrs et discussion des problèmes paléoclimatiques. In: G. Cambon, P. Richard & J.-P. Suc (eds). Palynology et milieux tropicaux. Mém. Trav. Ecole Prat. Htes Inst. Montpellier 17: 129-142.

Maley, J., G. Caballé & P. Sita, 1990. Etude d'un peuplement residuel a basse altitude de *Podocarpus latifolius* sur le flanc Congolais du Massif du Chaillu. Implications paleoclimatiques et biogeographiques. Etude de la pluie pollinique actuelle. In: R. Lanfranchi & D. Schwartz (eds). Paysages Quaternaires de l'Afrique centrale Atlantique: 336-349. Didactiques, Traveaux et Documentation ORSTOM, Paris.

Mayr, E., 1942. Systematics and the origin of species. Columbia University Press, New York.

Mayr, E., 1964. Systematics and the origin of species (reprint of 1942). Dover Publications Inc., New York.

Mayr, E., 1969. Principles of systematic zoology. McGraw-Hill, New York.

Mayr, E. & R.J. O'Hara, 1986. The biogeographic evidence supporting the pleistocene forest refuge hypothesis. Evolution 40: 55-67.

McDade, L., 1990. Hybrids and phylogenetic systematics I. Patterns of character expression in hybrids and their implications for cladistic analysis. Evolution 44: 1685-1700.

Meave, J., M. Kellman, A. McDougall & J. Rosales, 1991. Riparian habitats as tropical forest refugia. Global Ecol. & Biogeogr. Letters 1: 69-76.

Metcalfe, C.R. & L. Chalk, 1979. Anatomy of the dicotyledons (2nd ed.), vol. 1. Clarendon Press, Oxford.

Mickevich, M.F. & M.F. Johnson, 1976. Congruence between morphological and allozyme data in evolutionary inference and character evolution. Syst. Zool. 25: 260–270.

Moeyersons, J., 1979. Environmental evolution in central Africa during prehistoric times. Afr. Econ. Hist. 7: 22–29.

Molloy, B.P.J., R.K. Brummitt, P.S. Short & F.J. Breteler, 1992. What is a specimen? Taxon 41: 505–507.

Moreau, R.E., 1969. Climatic change and the distribution of forest vertebrates in West Africa. J. Zool., Lond. 158: 39–61.

Morrison, M.E., 1968. Vegetation and climate in the uplands of south-western Uganda during the later Pleistocene period, 1. Muchoya Swamp, Kigezi District. J. Ecol. 56: 363–384.

Myers, N., 1982. Forest refuges and conservation in Africa. In: G.T. Prance (ed.). Biological diversification in the tropics: 658–672. Columbia University Press, New York.

Ndjelé, M., 1988. Principales distributions obtenues par l'analyse factorielle des éléments phytogéographiques présumés endémiques dans la flore du Zaïre. In: P. Goldblatt & P.P. Lowry (eds). Modern systematic studies in African botany. Proceedings of the eleventh plenary meeting of the Association for the Taxonomic Study of the Flora of Tropical Africa, Missouri Botanical Garden, St. Louis, June 10–14, 1985. Monogr. Syst. Bot. Missouri Bot. Gard. 25: 631–638. Missouri Botanical Garden, St. Louis.

Nelson, G. & N. Platnick, 1981. Systematics and biogeography, cladistics and vicariance. Columbia University Press, New York.

Neubauer, H.F. & I. Beissler, 1971. Über Stomata und Stomatagruppen an verschiedenen Blattarten bei *Begonia*. Gartenbauwiss. 36, 18: 45–50.

Nicolson, D.H. (ed.), 1992. Proposals to amend the Code. (159–161) Three proposals concerning the definition of a specimen. Taxon 41: 602.

Nixon, K.C. & J.I. Davis, 1991. Polymorphic taxa, missing values and cladistic analysis. Cladistics 7: 233–241.

Page, R.D.M., 1988. Quantitative cladistic biogeography: Constructing and comparing area cladograms. Syst. Zool. 37: 254–270.

Page, R.D.M., 1989. Comments on component-compatability in historical biogeography. Cladistics 5: 167–182.

Page, R.D.M., 1993. Genes, organisms, and areas: The problem of multiple lineages. Syst. Biol. 42: 77–84.

Payne, W.W., 1970. Helicocytic and allelocytic stomata: unrecognized patterns in the Dicotyledonae. Amer. J. Bot. 57: 140–147.

Pimentel, R.A. & R. Riggins, 1987. The nature of cladistic data. Cladistics 3: 201–209.

Queiroz, K. de & J. Gauthier, 1992. Phylogenetic taxonomy. Ann. Rev. Ecol. Syst. 23: 449–480.

Radlkofer, L., 1890. Ueber die Gliederung der Familie der Sapindaceen. Sitzungsber. Kön. Bayer. Akad. Wiss. Münch. Math.-Phys. Cl. 20: 105–379.

Reitsma, J.M., 1984. Placentation in begonias from the African continent. In: J.J.F.E. de Wilde (ed.). Studies in *Begoniaceae* I. Mededelingen Landbouwhogeschool Wageningen 83-9: 21–53 (also Belmontia n.s. 17, no 92).

Reitsma, J.M., 1985. *Begonia* section *Baccabegonia* Reitsma, sect. nov. In: J.J.F.E. de Wilde (ed.). Studies in *Begoniaceae* II. Agric. Univ. Wageningen Papers 84-3: 95–111 (also Belmontia n.s. 18, no 103).

Reitsma, J.M., 1988. Végétation forestière du Gabon. Forest vegetation of Gabon. Tropenbos Technical Series 1. 142 pp.

Reitsma, J.M., A.M. Louis & J.-J. Floret, 1992. Flore et végétation des inselbergs et dalles rocheuses: première étude au Gabon. Bull. Mus. natl. Hist. nat., Paris, 4e sér., 14, sect. B, Adansonia: 73–97.

Rickett, H.W., 1954. Materials for a dictionary of botanical terms – II. Bull. Torrey Bot. Club 81: 188–198.

Rompaey, R.S.A.R. van, 1993. Forest gradients in West Africa. A spatial gradient analysis. Renaat S.A.R. van Rompaey, Wageningen (Thesis).

Ronse Decraene, L.P. & E. Smets, 1990. The systematic relationship between *Begoniaceae* and *Papaveraceae*: a comparative study of their floral development. Bull. Jard. Bot. Nat. Belg. 60: 229-273.

Sattler, R., 1974. A new approach to gynoecial morphology. Phytomorphology 24: 22-34.

Saunders, E.R., 1925. The inferior ovary. New Phytologist 24: 179-185.

Schott, A.M., 1991. Phylogenetic relations and historical biogeography of *Fordia* and *Imbralyx* (*Papilionaceae: Millettieae*). Blumea 36: 205-234.

Seitner, P.G., 1972. Some observations on *Begonia* seeds. The Begonian 39: 47-55.

Seitner, P.G., 1976. The role of insects in *Begonia* pollination. The Begonian 43: 147-153.

Seitner, P.G., 1977a. The role of insects in *Begonia* pollination: supplement 1. The Begonian 44: 213-217.

Seitner, P.G., 1977b. Begonia 'Gold Coast'. The Begonian 44: 264-269.

Seitner, P.G., 1978. Comparison of two Begonia hybrids. The Begonian 45: 15-17.

Seybold, A., 1955. Beiträge zur Optik der Laubblätter. Beitr. Biol. Pfl. 31: 499-513.

Sharkey, M.J., 1989. A hypothesis-independant method of character weighting for cladistic analysis. Cladistics 5: 63-86.

Simpson, B.B., 1988. The need for systematic studies in reconstructing paleogeographic and ecological patterns in South American tropics. Symb. Bot. Upsal. 28: 150-158.

Smith, L.B., D.C. Wasshausen, J. Golding & C.E. Karegeannes, 1986. *Begoniaceae*. Part I: Illustrated Key. Part II: Annotated species list. Smiths. Contr. Bot. 60. Smithsonian Institution Press, Washington

Sokal, R.R. & P.H.A. Sneath, 1963. Principles of numerical taxonomy. W.H. Freeman, San Francisco.

Solereder, H., 1899. Systematische Anatomie der Dicotyledonen. Ferdinand Enke, Stuttgart.

Sosef, M.S.M., 1992a. Novitates Gabonenses 8. Seven new *Begonia* species from Gabon. In: J.J.F.E. de Wilde (ed.). Studies in *Begoniaceae* III. Wageningen Agric. Univ. Papers 91-4: 83-116 (also Belmontia n.s. 24, no 147).

Sosef, M.S.M., 1992b. New species of *Begonia* in Africa and their relevance to rain forest refuges. In: J.J.F.E. de Wilde (ed.). Studies in *Begoniaceae* III. Wageningen Agric. Univ. Papers 91-4: 117-151 (also Belmontia n.s. 24, no 148).

Sperlich, A., 1907. Die optischen Verhältnisse in der oberseitigen Blattepidermis tropischer Gelenkpflanzen. Sitzungsber. Kaiserl. Akad. Wiss. Wien, Math.-naturwiss. Klasse Bd CXVI, Abt. 1: 675-736.

Stace, C.A., 1986. The present and future infraspecific classification of wild plants. In: B.T. Styles (ed.). Infraspecific classification of wild and cultivated plants: 9-20. The Systematics Association Special Volume No 29. Clarendon Press, Oxford.

Stapf, O., 1906. 770. *Begonia calabarica*. Kew Bull. 1906: 20.

Stapf, O., 1908. 944. *Begonia* (*Scutobegonia*) *modica*. Kew Bull. 1908: 259.

Stapf, O., 1909. *Begonia modica*. Curtis's Bot. Mag. 135: t. 8258.

Stuessy, T.F., 1990. Plant taxonomy: the systematic evaluation of comparative data. Columbia University Press, New York.

Styles, B.T. (ed.), 1986. Infraspecific classification of wild and cultivated plants. The Systematics Association Special Volume No 29. Clarendon Press, Oxford.

Swofford, D.L., 1991. PAUP: Phylogenetic Analysis Using Parsimony, version 3.0s. Computer Program distributed by the Illinois National History Survey, Champaign, Illinois.

Systematic Association Committee for Descriptive Biological Terminology, 1962. II. Terminology of simple symmetrical plane shapes (chart 1). Taxon 11: 145-156.

Talbot, M.R., D.A. Livingstone, P.G. Palmer, J. Maley, J.M. Melack, G. Delibrias & S. Gulliksen, 1984. Preliminary results from sediment cores from lake Bosumtwi, Ghana. Palaeoecol. Afr. 16: 173-192.

Taylor, D.M., 1988. The environmental history of the Rukiga Highlands, South-West Uganda, during the last 40,000 to 50,000 years. Unpubl. D. Phil. Thesis, University of Ulster, U.K.

Tournefort, J.P., 1700. Institutiones rei herbariae, Editio altera, 3 vols. Parisiis.

UICN, 1989. La conservation des ecosystèmes forestiers d'Afrique centrale. UICN, Gland & Cambridge.

Van Cottem, W.R.J., 1970. A classification of stomatal types. Bot. J. Linn. Soc. 63: 235-246.

Van Cottem, W.R.J., 1971. Vergleichende morphologische Studien über Stomata und eine neue Klassifikation ihren Typen. Ber. Deutsche Bot. Ges. 84: 141–168.

Veldkamp, J.F., R. de Koning & M.S.M. Sosef, 1986. Generic delimitation of *Rottboellia* and related genera (*Gramineae*). Blumea 31: 281–307.

Warburg, O., 1894. *Begoniaceae*. In: A. Engler & K. Prantl (eds). Die Natürlichen Pflanzenfamilien (ed. 1) 3, 6a: 121–150. Wilhelm Engelmann, Leipzig.

Warburg, O., 1895. *Begoniaceae* africanae. Bot. Jahrb. Syst. 22: 32–45.

Welzen, P.C. van, 1989. *Guioa* Cav. (*Sapindaceae*): taxonomy, phylogeny, and historical biogeography. Leiden Botanical Series 12. 315 pp.

Welzen, P.C. van, 1992. Interpretation of historical biogeographic results. Acta Bot. Neerl. 41: 75–87.

White, F., 1979. The Guineo-Congolian Region and its relationships to other phytochoria. Bull. Jard. Bot. Nat. Belg. 49: 11–55.

White, F., 1981. The history of the afromontane archipelago and the scientific need for its conservation. Afr. J. Ecol. 19: 33–54.

White, F., 1983. The vegetation of Africa; a descriptive memoir to accompany the UNESCO/AETFAT/UNSA vegetation map of Africa. Natural Resources Research No 20. UNESCO, Paris.

Wieringa, J.J., 1991. Achter de zoom van het oerwoud. Unpublished report of practical period, Dept. of Plant Taxonomy, Wageningen Agricultural University.

Wilczek, R., 1969. *Begoniaceae*. Flore du Congo, du Rwanda et du Burundi, Spermatophytes. Jardin Botanique National de Belgique, Bruxelles.

Wilde, J.J.F.E. de, 1985a. *Begonia* section *Cristasemen* J.J. de Wilde, sect. nov. In: J.J.F.E. de Wilde (ed.). Studies in *Begoniaceae* II. Agric. Univ. Wageningen Papers 84-3: 113–129 (also Belmontia n.s. 18, no 104).

Wilde, J.J.F.E. de, 1985b. Taxonomy of the (African) *Begoniaceae*, an introduction. Acta Bot. Neerl. 34: 226–227.

Wilde, J.J.F.E. de & J.C. Arends, 1979. *Begonia loranthoides* Hook.f. (sect. *Tetraphila* A.DC.). Acta Bot. Neerl. 28: 357–374 (also Belmontia n.s. 10, no 53).

Wilde, J.J.F.E. de & J.C. Arends, 1980. *Begonia* section *Squamibegonia* Warb.: a taxonomic revision. Miscellaneous Papers Landbouwhogeschool Wageningen 19: 377–421 (also Belmontia n.s. 11, no 64).

Wilde, J.J.F.E. de & J.C. Arends, 1989. *Begonia salaziensis* (Gaud.) Warb.: taxonomy and placentation. Acta Bot. Neerl. 38: 31–39.

Wiley, E.O., 1981. Phylogenetics: the theory and practice of phylogenetic systematics. John Wiley and Sons, New York/Chichester/Brisbane/Toronto.

Wiley, E.O., 1988. Vicariance biogeography. Ann. Rev. Ecol. Syst. 19: 513–542.

Wilks, C., 1990. La conservation des ecosystèmes forestiers du Gabon. UICN, Gland & Cambridge.

Williams, P.H., C.J. Humphries & R.I. Vane-Wright, 1991. Measuring biodiversity: Taxonomic relatedness for conservation priorities. Austr. Syst. Bot. 4: 665–679.

Winkler, H., 1906. Beiträge zur Morfologie und Biologie tropischer Blüten und Früchte. Bot. Jahrb. Syst. 38: 233–271.

Zandee, M. & R. Geesink, 1987. Legumes and phylogenetics: a desire for the impossible? In: C.H. Stirton (ed.). Advances in legume systematics, part 3: 131–167. Royal Botanic Gardens, Kew.

Zandee, M. & M.C. Roos, 1987. Component-compatability in historical biogeography. Cladistics 3: 305–332.

Zinderen Bakker, E.M. van & J.D. Clark, 1962. Pleistocene climates and cultures in north-eastern Angola. Nature 196: 639–642.

Zinderen Bakker, E.M. van & J.A. Coetzee, 1972. A re-appraisal of Late-Quaternary climatic evidence from tropical Africa. In: E.M. van Zinderen Bakker (ed.). Palaeoecology of Africa 7: 151–191. A.A. Balkema, Rotterdam.

Zon, A.P.M. van der, 1992. Graminées du Cameroun, vol. I, Phytogéographie et Pâturages. Wageningen Agric. Univ. Papers 92-1: 1–86.

20 List of identifications

Behind each collection the indentification is indicated by a number (or code) corresponding with the list presented here. Doubtful identifications are indicated by a question mark and hybrids by a star followed by a number refering to the list below. Collections lacking a collection number (s.n.) have been left out when more than one such collection from the same collector but concerning different taxa were involved.

Loasibegonia

1 = *B. adpressa* Sosef
2a = *B. atroglandulosa* Sosef subsp. *atroglandulosa*
2b = *B. atroglandulosa* Sosef subsp. *tshelaensis* Sosef
3 = *B. duncan-thomasii* Sosef
4 = *B. gentilii* De Wild.
5 = *B. heterochroma* Sosef
6 = *B. letouzeyi* Sosef
7 = *B. microsperma* Warb.
8 = *B. minuta* Sosef
9 = *B. potamophila* Gilg
10a = *B. prismatocarpa* W.J. Hooker subsp. *prismatocarpa*
10b = *B. prismatocarpa* W.J. Hooker subsp. *delobata* Sosef
10c = *B. prismatocarpa* W.J. Hooker subsp. *petraea* (A. Chev.) Sosef
11 = *B. pseudoviola* Gilg
12 = *B. pulcherrima* Sosef
13a1 = *B. quadrialata* Warb. subsp. *quadrialata* var. *quadrialata*
13a2 = *B. quadrialata* Warb. subsp. *quadrialata* var. *pilosa* Sosef
13b = *B. quadrialata* Warb. subsp. *dusenii* (Warb.) Sosef
13c = *B. quadrialata* Warb. subsp. *nimbaensis* Sosef
14 = *B. salisburyana* Irmscher
15a = *B. scapigera* Hook.f. subsp. *scapigera*
15b = *B. scapigera* Hook.f. subsp. *australis* Sosef
16 = *B. schaeferi* Engl.
17 = *B. scutifolia* Hook.f.
18 = *B. staudtii* Gilg
19 = *B. stellata* Sosef

Scutobegonia

20 = *B. aggeloptera* N. Hallé
21 = *B. anisosepala* Hook.f.
22 = *B. ciliobracteata* Warb.
23 = *B. clypeifolia* Hook.f.
24 = *B. dewildei* Sosef
25 = *B. erectocaulis* Sosef
26 = *B. erectotricha* Sosef
27 = *B. ferramica* N. Hallé
28 = *B. hirsutula* Hook.f.
29 = *B. lacunosa* Warb.
30 = *B. laporteifolia* Warb.
31 = *B. mbangaensis* Sosef
32 = *B. mildbraedii* Gilg
33 = *B. peperomioides* Hook.f.
34 = *B. scutulum* Hook.f.
35 = *B. susaniae* Sosef
36 = *B. vankerckhovenii* De Wild.
37 = *B. vittariifolia* N. Hallé
38 = *B. wilksii* Sosef
39a = *B. zairensis* Sosef var. *zairensis*
39b = *B. zairensis* Sosef var. *montana* Sosef
40 = *B. zenkeriana* L.B. Smith & Wasshausen

Hybrids

*1 = *B. ciliobracteata* Warb. x *quadrialata* Warb.
*2 = *B. clypeifolia* Hook.f. x *lacunosa* Warb.
*3 = *B. lacunosa* Warb. x *scutulum* Hook.f.
*4 = *B. mildbraedii* Gilg x *scutifolia* Hook.f.
*5 = *B. susaniae* Sosef x *vittariifolia* N. Hallé

21 Index of scientific plant names

Plate 1. a, b: *Begonia aggeloptera* N. Hallé, photos by M.S.M. Sosef, 1991, Gabon, Assok, coll. *J.J. de Wilde c.s. 10147*; c: *Begonia ciliobracteata* Warb. (young inflorescence and young fruit), photo by R. Jansen, 1979, greenhouse at Department of Horticulture, Wageningen, coll. *Bos s.n.*, Cameroon.

Plate 2. a: *Begonia hirsutula* Hook.f., photo by prof. H.C.D. de Wit, 1977, greenhouse at WAG, coll. from Cameroon; b, c, d: *Begonia clypeifolia*, photos by prof. H.C.D. de Wit, 1983, greenhouse at Department of Horticulture, coll. *Breteler 7687*, Gabon, Fougamou–Lambaréné.

Plate 3. a: *Begonia lacunosa* Warb., photo by prof. H.C.D. de Wit, 1986, greenhouse at WAG, no 83PTGA708, coll. *J.J. de Wilde c.s. s.n.*, Gabon; b: idem, young fruits; c, d: *Begonia staudtii*, photos by prof. H.C.D. de Wit, 1983, greenhouse at WAG, no 64PTCM399, coll. *W.J. de Wilde s.n.*, Cameroon.

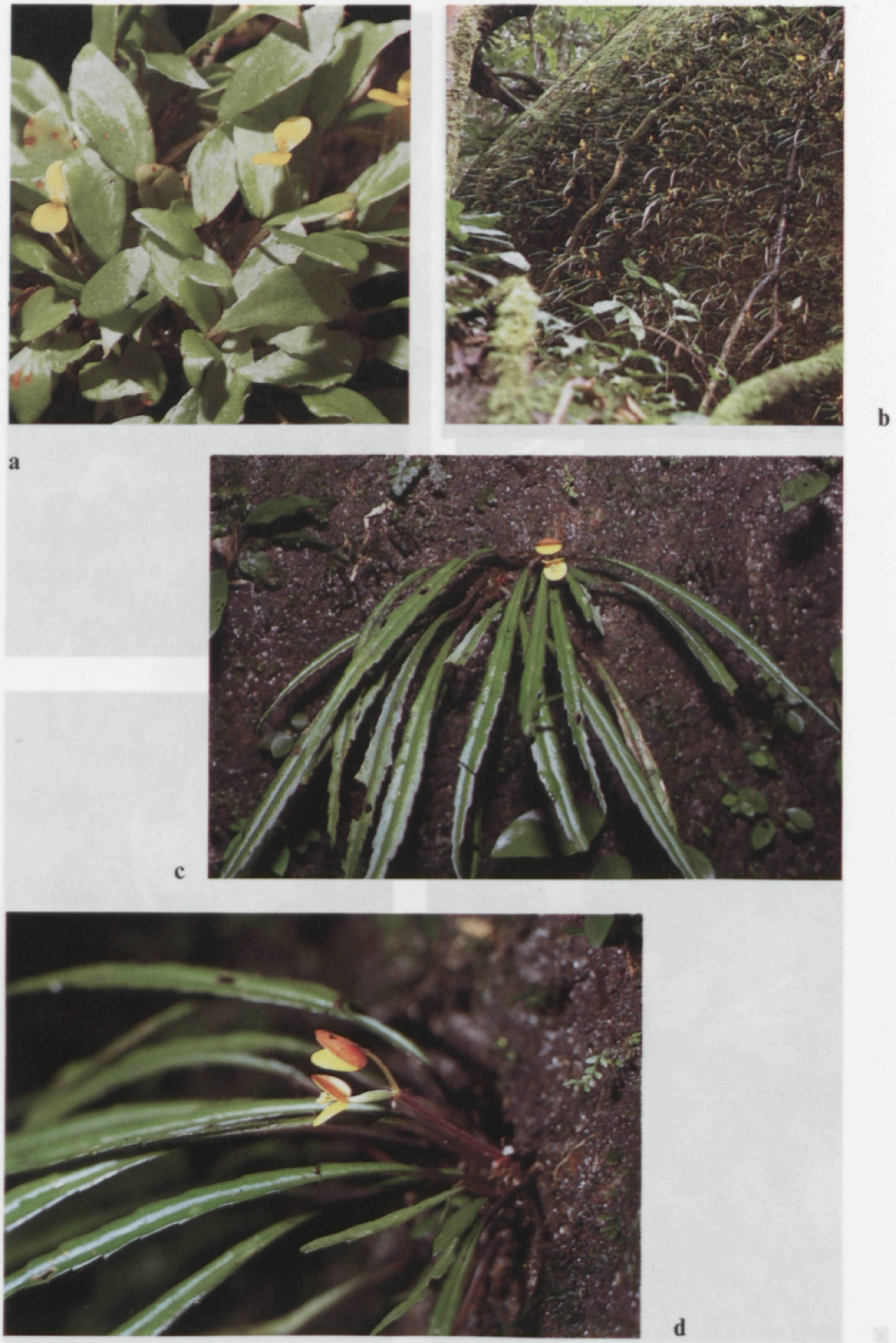

Plate 4. a: *Begonia scutifolia* Hook.f., photo by prof. H.C.D. de Wit, 1986, greenhouse at WAG, no 84PTGA189, coll. *Arends c.s. 560*, Gabon, Chaillu Massif; b: *Begonia vittariifolia* N. Hallé, photo by M.S.M. Sosef, 1991, Gabon, Crystal Mountains, population covering rock, coll. *J.J. de Wilde c.s. 10237*; c, d: idem, plant with male and female flower.

Plate 5. a: *Begonia atroglandulosa* Sosef ssp. *atroglandulosa*, photo by prof H.C.D. de Wit, 1984, greenhouse at WAG, no 83PTGA077, coll. *J.J. de Wilde c.s. s.n.*; b: idem, young fruit; c: idem, photo by J.C. Arends, 1983, Gabon, Chaillu Massif.

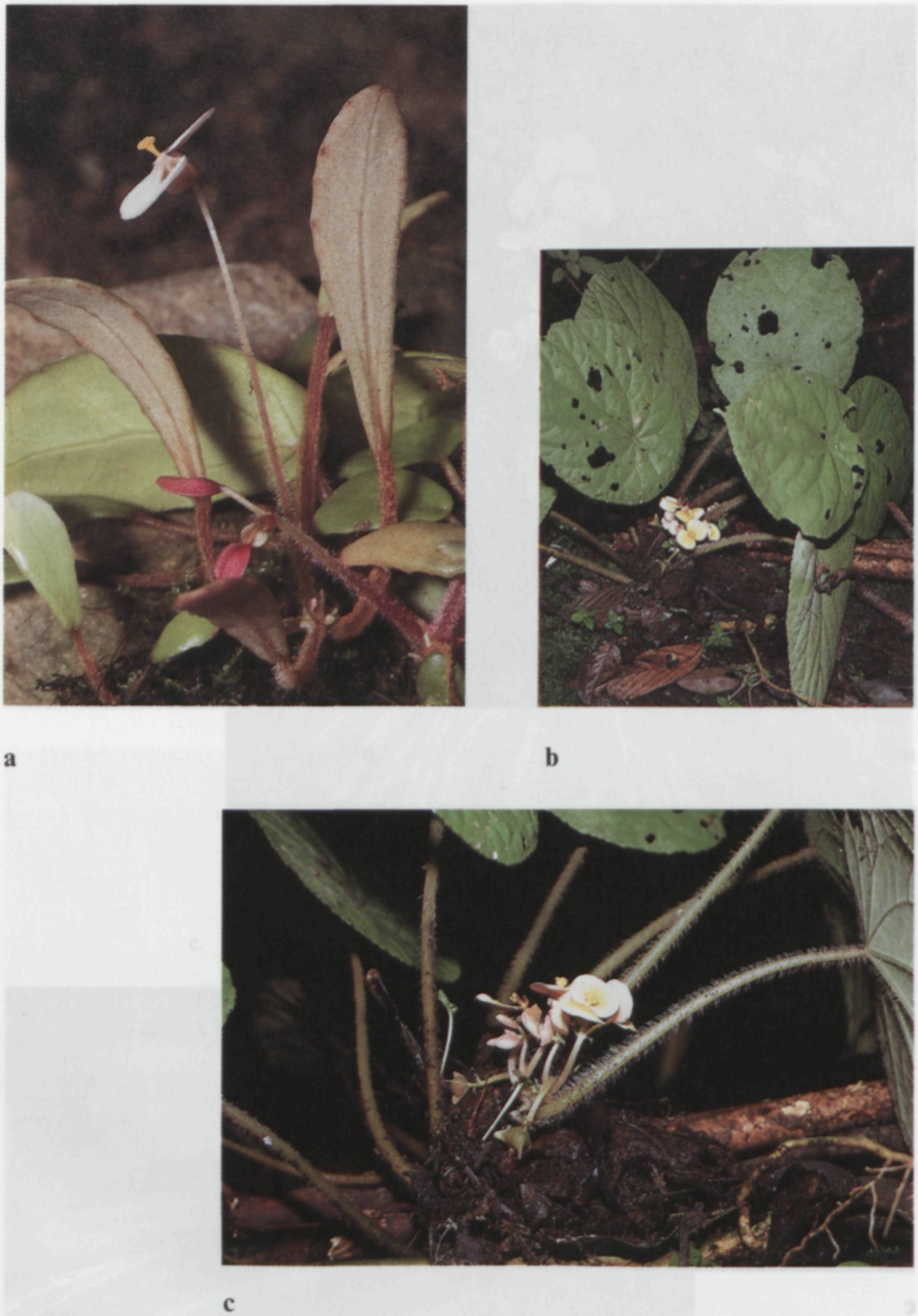

Plate 6. a: *Begonia dewildei* Sosef, photo by prof. H.C.D. de Wit, greenhouse at WAG, no 84PTGA191, coll. *Arends c.s. 700*; b, c: *Begonia erectotricha* Sosef, photos by M.S.M. Sosef, 1991, Gabon, Kinguélé, coll. *J.J. de Wilde c.s. 10189*.

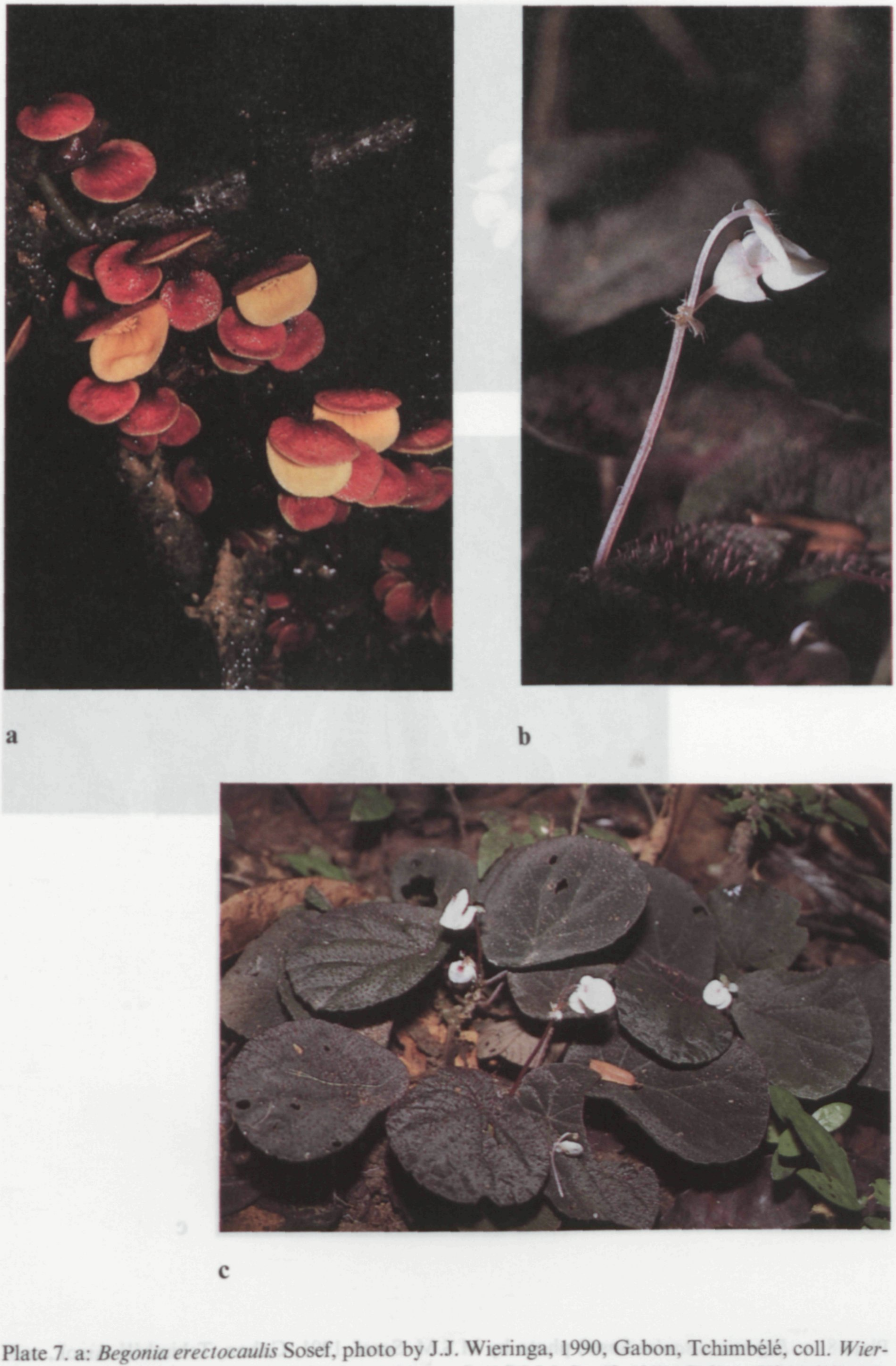

Plate 7. a: *Begonia erectocaulis* Sosef, photo by J.J. Wieringa, 1990, Gabon, Tchimbélé, coll. *Wieringa 701*; b, c: *Begonia heterochroma* Sosef, photos by M.S.M. Sosef, 1991, Gabon, Kinguélé, coll. *J.J. de Wilde c.s. 10194*.

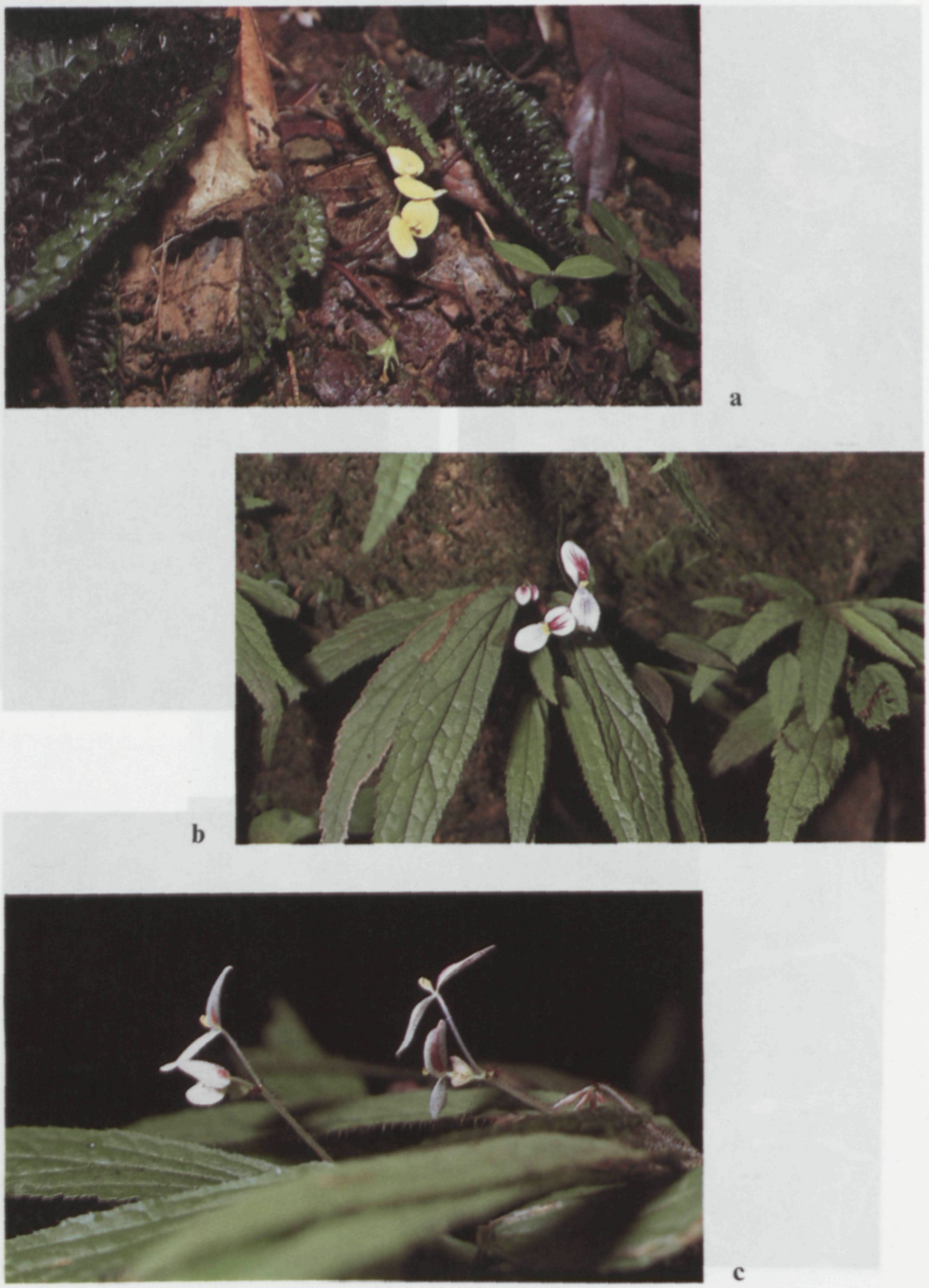

Plate 8. a: *Begonia susaniae* Sosef, photo by M.S.M. Sosef, 1991, Gabon, Tchimbélé-Assok, coll. *J.J. de Wilde c.s. 10131*; b, c: *Begonia wilksii* Sosef, photos by M.S.M. Sosef, 1991, Gabon, N.E. of Ndjolé, coll. *J.J. de Wilde & Sosef 10325*.