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Evolution, Biogeography, and Monographic Treatment of *Coccinia* (Cucurbitaceae)

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Erklärung

Diese Dissertation wurde im Sinne von §12 der Promotionsordnung von Prof. Dr. Susanne S. Renner betreut. Ich erkläre hiermit, dass die Dissertation nicht einer anderen Prüfungskommission vorgelegt worden ist und dass ich mich nicht anderweitig einer Doktorprüfung ohne Erfolg unterzogen habe.

Ehrenwörtliche Versicherung

Ich versichere hiermit ehrenwörtlich, dass die vorgelegte Dissertation von mir selbständig, ohne unerlaubte Hilfe angefertigt wurde.

Norbert Holstein

Note

In this thesis, I present the results of my doctoral research, which took place from September 1, 2007 to April 30, 2012, under the supervision of Prof. Dr. Susanne S. Renner. The results of my research led to four manuscripts of which three have been published (chapters 1 to 3), while a fourth (chapter 4) has yet to be submitted. I carried out all data collection and analyses, if not otherwise indicated in the corresponding acknowledgements. Writing and discussion of these manuscripts involved collaboration with Prof. Dr. S. S. Renner.

List of Publications

Papers

Holstein, Norbert and S.S. Renner. 2010 [published 2011]. *Coccinia* (Cucurbitaceae) gains two new species from East Africa, three new synonyms, and one new combination. Kew Bulletin 65(3): 435–441. doi:10.1007/s12225-010-9229-9

Holstein, Norbert and S.S. Renner. 2011. A dated phylogeny and collection records reveal repeated biome shifts in the African genus *Coccinia* (Cucurbitaceae). BMC Evolutionary Biology 11: 28. doi:10.1186/1471-2148-11-28

Holstein, Norbert and S.S. Renner. 2011. *Coccinia intermedia* – a new species from West Africa. Phytokeys 7: 27–36. doi: 10.3897/phytokeys.7.2032

Holstein, Norbert. Monograph of *Coccinia* (Cucurbitaceae). Submitted to Phytokeys (April 25, 2012).

Posters

Holstein, Norbert and S.S. Renner. Neogene biome shifts in Africa as a driver of speciation in *Coccinia* (Cucurbitaceae)? Systematics 2009, 7th Biennial Conference of the Systematics Association, August 10–14, 2009, Leiden, Netherlands

Talks

Presenting author is given in bold.

Holstein, Norbert. February 16, 2012. How climate change in Africa over the past 7 million years affected diversification in the African cucurbit genus *Coccinia*. Seminar at the NCB Naturalis, Leiden, Netherlands

Holstein, Norbert. October 12, 2011. How climate change in Africa over the past 7 million years affected diversification in the African cucurbit genus *Coccinia*. EES conference 2011, Munich, Germany

Holstein, Norbert and S.S. Renner. February 25, 2011. Rapid filling of climatic niches in the African cucurbit *Coccinia*. Biosystematics 2011, Berlin, Germany

Holstein, Norbert and S.S. Renner. September 18, 2011. African late Neogene climatic oscillations and speciation in *Coccinia*. 19th International Symposium "Biodiversity and Evolutionary Biology" of the German Botanical Society (DBG), Vienna, Austria

Holstein, Norbert and S.S. Renner. November 4, 2009. Evolution of species ranges and habitats in *Coccinia* (Cucurbitaceae). Seminar of the Institute of Systematic Botany and Mycology, LMU Munich, Germany

Holstein, Norbert and S.S. Renner. August 7, 2009. Evolution of *Coccinia* (Cucurbitaceae) and its sex chromosomes — first results. University of Dar es Salaam, Tanzania

Holstein, Norbert and S.S. Renner. September 14–19, 2008. Evolution of sex chromosomes in *Coccinia* (Cucurbitaceae). EES Summer School "Evolution of sex chromosomes", Frauenchiemsee, Germany

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Index of Abbreviations

! = seen

a.m. = ante meridiem (forenoon)

bp = base pairs

CA = California

Cat. Print. = Catalogue du Printemps

CVH = China Virtual Herbarium (http://www.cvh.org.cn/cms/)

comm. = communicated by

cpDNA = plastid DNA

df = degrees of freedom

DNA = desoxyribose nucleic acid

doi = digital object identifier

E = eastern

e.g. = *exempli gratia*, for example

ESS = effective sample size

ex cult. = from cultivation

F81 = Felsenstein 81

Fig. / fig. = figure

fl = flowering

fr = fruiting

ft = feet

G = goodness-of-fit value

GTR = general time reversal

Herb. = herbarium

HPD = highest posterior density

ibid. = ibidem (at the same place)

ICBN = International Code of Botanical Nomenclature

i.e. = *id est*, that is

IICT = Instituto de Investigação Científica Tropical

Inc. = Incorporated

ITS = internal transcribed spacer

IL = Illinois

JPS = JStor Plant Science

LB medium = Lysogeny broth medium

l.c. = locus citatus

LFY = *LEAFY* (gene homolog)

L/W/H = length/width/height

Ma = million years

*mat*K = maturase K gene

MCMC = Markov chain Monte Carlo

MI = Michigan

ML = Maximum Likelihood

mls = miles

Monogr. Phan. = Monographiæ Phanerogamarum

Ms. = manuscript

Mss. = manuscripts

Mt = Mount

mt. = mountain

Mts = Mountains

Mus. Zeyl. = Musæum zeylanicum

n = set of haploid chromosomes, such as in 2*n* = 24

N = northern

*ndh*F = nicotinate hydroxylase subunit F gene

nom. illeg. = nomen illegitimum

nom. nud. = nomen nudum

nov. = new

n.v. = non vidi (not seen)

P = P-value (significance value)

PCR = polymerase chain reaction

P × E = polar by equatorial diameter

pers. comm. = personal communication

p.p. = pro parte

Prodr. Pl. Cap. = Prodromus Plantarum Capensium

psbA = gene for coding the D1 polypeptide of the photosystem II reaction center

rbcL = gene for ribulose-1,5-bisphosphate carboxylase oxygenase large subunit

rpl = ribosomal protein large subunit gene

rps = ribosomal protein small subunit gene

S = southern

s.coll. = without collector

SD = standard deviation

s.dat. = without date

s.det.loc. = without detailed location (only country or province given)

ser. = series

s.loc. = without location

s.n. = sine numero (without number)
SNNPR: Southern Nations, Nationalities, and People’s Region
sp. = species [singular]
spec. nov. = species novus (new species)
sphalm. = sphalmate (by mistake)
spp. = species [plural]
stat. nov. = status novus (new status, e.g. as subspecies instead of species)
subsp. = subspecies
Tab. / tab. = table
trn = gene of a transcribed ribose nucleid acid (followed by the corresponding letter of the transferred amino acid)
TVM = transversion model
USA = United States of America
UTM = Universal Transverse Mercator
var. = variety
W = western
WGS84 = World Geodetic System from 1984

Herbarium abbreviations follow Index Herbariorum (http://sciweb.nybg.org/science2/IndexHerbariorum.asp), except CVH and JPS (see above).

Abbreviations of author names follow International Plant Names Index (IPNI; http://www.ipni.org/).

Contents

Zusammenfassung

Diese Dissertation behandelt die Morphologie, Taxonomie, Biogeografie und Evolution der Gattung *Coccinia* (Cucurbitaceae). *Coccinia* umfasst nach meiner Bearbeitung 25 Arten, die in fast allen Gebieten des sub-saharischen Afrikas vorkommen, mit Ausnahme der Kap-Flora und der afroalpinen Regionen. *Coccinia* wurde seit 131 Jahren nicht taxonomisch bearbeitet, und es mussten daher alle 136 jemals in die Gattung gestellten Namen revidiert, darunter mehrere nomenklatorisch schwierige Probleme gelöst sowie Neo- und Lectotypisierungen vorgenommen werden. Nach Untersuchung von 2839 Aufsammlungen (Herbarbelegen) konnten 10 Namen neu synonymisiert, ein Name umkombiniert, zwei Arten zu Varietäten reduziert und drei Arten und eine Varietät neu beschrieben werden. Geographische Zuordnung (Georeferenzierung) von 1633 Aufsammlungen, Klimadaten und Feldbeobachtungen in Nordost-Tansania bilden die Grundlage für ein Verständnis der biogeographischen Zusammenhänge und der Evolution in der Gattung. Ein Schlüssel erlaubt die Bestimmung mit vegetativen oder generativen Merkmalen. Dazu bietet die Revision Verbreitungskarten, Illustrationen sowie alle verfügbaren Daten zur Morphologie, Anatomie, Keimungsverhalten, Palynologie, Karyologie, Habitatökologie, Nutzung und zu Pflanze-Umwelt-Interaktionen.

Molekulare Phylogenien von *Coccinia* beruhend auf nuklearen und plastidären Sequenzen von 80 Individuen, die 24 der 25 Arten von *Coccinia*, 2 Arten der Schwestergattung *Diplocyclos* sowie 4 relevante Außengruppen repräsentieren, zeigen, dass *Coccinia* in der jetzigen Umschreibung monophyletisch ist und dass bei einigen west- und zentralafrikanischen Arten und im *C. adoensis*-Komplex der Artbildungsprozess nicht vollständig abgeschlossen ist. Eine molekulare Uhr macht wahrscheinlich, dass die 25 Arten von *Coccinia* im Laufe der letzten 7 Million Jahre entstanden. *Coccinia*-Arten kommen in unterschiedlichen Habitaten vor, von semi-aridem Buschland über Laubtrockenwälder hin zu Tiefland- und Bergregenwälder. Plottet man die bevorzugten klimatischen Nischen der einzelnen Arten (inferiert von Verbreitungsdaten und Herbarblattangaben) auf die Phylogenie, so lässt sich schlussfolgern, dass innerhalb der Gattung mindestens sieben Artenbildungsereignisse mit einer Änderung des Bioms einhergingen.

Eine Art, *Coccinia grandis*, besitzt in männlichen Individuen ein heteromorphes Geschlechtschromosomenpaar, was bei Bedecksamern nur in vier weiteren Gattungen bekannt ist. Zehn *Coccinia*-Arten wurden in Kultur gebracht, um die Chromosomen zu untersuchen und Kreuzungsexperimente durchzuführen. In den sechs untersuchten Arten waren die Chromosomenzahlen $2n = 20$ bis $2n = 24$. Bis auf *C. grandis* besitzen sie keine heteromorphen Geschlechtschromosomen. Unter Annahme einer molekularen Uhr geschah die Evolution von homo- zu heteromorphen Geschlechtschromosomen innerhalb von *Coccinia*, wahrscheinlich innerhalb der letzten 6 Millionen Jahre.

Summary

This dissertation deals with the morphology, taxonomy, biogeography, and evolution of the Cucurbitaceae genus *Coccinia*. After my revision, this genus comprises 25 species that are widely distributed throughout sub-Saharan Africa, except for the Cape Floristic Realm and Afroalpine regions. The last complete taxonomic treatment of *Coccinia* was undertaken 131 years ago. All 136 available names thus had to be revised critically, which included solving several long-standing nomenclatural problems and carrying out neo- and lectotypifications. After examination of 2839 collections (herbarium specimens), I found ten new synonyms, recombined one species name, reduced two names from species to varieties, and described three new species and one variety. Geo-referencing of 1633 specimens, climate data, and field observations made in northeastern Tanzania are the basis for understanding the biogeography and the evolution in this genus. A key allows identification of all species with generative characters or vegetative characters alone. The revision also includes distribution maps, illustrations, as well as a comprehensive data on morphology, anatomy, germination behavior, palynology, karyology, habitat ecology, use, and plant-environment interactions.

Molecular phylogenies of *Coccinia* based on plastid and nuclear sequences from 80 individuals representing 24 of the 25 species, the sister genus *Diplocyclos* and more distant outgroups reveal that *Coccinia* is monophyletic in its current circumscription. The speciation process, however, does not appear to be complete in some west and central African species and in the *C. adoensis* complex. A molecular clock suggests that the 25 species started radiating about 7 million years ago. Even so, *Coccinia* species occur in a wide range of habitats from semi-arid bushland and woodlands to lowland and mountain rainforests. When species' climatic niches (inferred from distribution data and field observations on specimen labels) are plotted onto the phylogenetic tree, it can be inferred that at least seven speciation events coincided with biome shifts.

In one species, *Coccinia grandis*, male individuals contain a heteromorphic chromosome pair, which is only known from four other genera in the angiosperms. Ten *Coccinia* species were brought into cultivation to investigate the chromosomes and perform crossing experiments. Chromosome numbers in six species are $2n = 20$ or 24. Except for *C. grandis,* no species contained heteromorphic sex chromosomes. Assuming a molecular clock, the evolution from homomorphic to heteromorphic sex chromosomes happened within the *Coccinia* crown group, most likely during the last 6 million years.

General Introduction

Introduction to the Study Group

The gourd family, or Cucurbitaceae, is a eudicot plant family with 940 to 980 species that evolved about 63 Ma ago at the Cretaceous–Tertiary boundary (Schaefer *et al.* 2009). Cucurbit species occur on all continents, except Antarctica, but mainly in subtropical and tropical climates, where a great variety of habitats from deserts to mist forests is colonized (Schaefer & Renner 2011b).

Cucurbitaceae contain many economically important crop species, such as the cucumber (*Cucumis sativus* L.), honey melon (*Cucumis melo*), watermelon (*Citrullus lanatus*), pumpkins, squashes, and zucchini (*Cucurbita* spp.), chayote (*Sicyos edulis*), loofah (*Luffa* spp.), and bitter gourd (*Momordica* spp.). The economically most valued part usually is the fruit, often a fleshy berry. Almost all Cucurbitaceae species have unisexual flowers, with about 50% of the species producing male and female flowers on each individual (monoecious) and 50% being sexually specialized (either male or female; dioecious). Cucurbit flowers are pollinated by many groups of bees, including oil bees, more rarely by flies, moths, butterflies, hummingbirds, or bats (Schaefer & Renner 2011b). Most Cucurbitaceae species are creepers or climbers using tendrils. The tendrils are modified shoots (Lassnig 1997; Gerrath *et al.* 2008) and a synapomorphy of the family, meaning that they evolved in the common ancestor of all Cucurbitaceae. A few species have lost the tendrils, for example, *Ecballium elaterium*, or transformed them into thorns, as in *Acanthosicyos horridus* (Schaefer & Renner 2011b). One species, *Dendrosicyos socotranus*, endemic on Socotra Island, grows as a tree.

Coccinia is the 11th largest genus of the Cucurbitaceae and – following my revision of all names – comprises 25 biological species. The species are distributed in sub-Saharan Africa, with one species, *C. grandis*, extending into tropical Asia. The same species also is naturalized on several Pacific Islands, in northern Australia, the Caribbean, and in Colombia, the Guianas, and Brazil. On Hawaii and on several Pacific islands it is considered invasive (Muniappan *et al.* 2002; Hawaii Administrative Rules 4:68:1 2011). The sister clade of *Coccinia*, the genus *Diplocyclos*, consists of four monoecious species distributed in the paleotropics (Schaefer & Renner 2011b; a; tested in my work by additional species sampling).

In spite of my search for a morphological trait that would set apart *Coccinia* from all other genera of Cucurbitaceae (and that might have served as an apomorphy), I have not found such a feature. The genus is therefore here defined based on the molecular distinctness of its species all but one of which have been sequenced for plastid and nuclear regions

(Holstein & Renner 2011a). A combination of morphological traits also sets *Coccinia* apart from other African cucurbit genera. These traits are (i) berries with a scarlet-red pericarp – the inspiration for the genus name – *Coccinia* from Latin *coccineus* – (ii) grayish-beige, flattened seeds in a hyaline aril, (iii) synsepalous, gamopetalous flowers, and (iv) three connected stamens with sinuate anthers.

Fig. 1 Habitus of the rainforest species *Coccinia grandiflora*. Female flowers are negatively gravitrop but after fertilization, flowers bend downwards. Picture taken in Amani, Usambara Mts, Tanzania.

All 25 species of *Coccinia* are perennials and produce annual or perennial shoots that can become up to 20 meters long. Tubers developed from roots or from the hypocotyl allow persistence during unfavorable conditions, such as drought. Like most other cucurbits, *Coccinia* grows as a climber using simple or bifid tendrils, or in absence of a support the plants grow as a creeper. Of the range of petal colors found in Cucurbitaceae (white, yellow, orange, and red, rarely also with blackish blotches, as in oil-offering *Momordica* spp.), *Coccinia* species exhibit all except bright yellow, deep red, and black maculation. A campanulate perianth is the most common flower type in *Coccinia* (Fig. 1); cup-shaped, tubular, or urn-shaped flowers are rare. Pollination of *Coccinia* flowers is by bees foraging on nectar and pollen (N. Holstein, Chapter 4 of this dissertation). The seeds are grayish-beige, with a flat to lenticular surface, and a more or less asymmetrical obovate shape. The red and juicy fruits suggest an uptake by mammals and birds, as indeed been confirmed for several species (Voigt 1845; Mubalama 2000; Bhatt & Kumar 2001; Elangovan *et al.* 2001). Pollen is tri-colporate, (sub-)prolate with a reticulate exine, which is common in Cucurbitaceae, but differs from the pollen found in the sister genus *Diplocyclos*, which has an echinate exine (Marticorena 1963; Khunwasi 1998).

Several of the 25 species of *Coccinia* are consumed by humans (Roxburgh 1832; Dinter 1912; Getahun 1974), and the dispersal of the most wide-ranging and even invasive species *C. grandis* has been attributed to transport by humans who might have taken fruits of this species to Hawaii, Florida, and the Guianas. What is known about the biotic interactions of *Coccinia* is discussed in the general part of my monograph (Chapter 4). Different people sometimes report the same species as edible or poisonous (Gradé *et al.* 2009), and it is often unclear which plant parts or degrees of ripeness of the fruits are being compared or how poisonousness was assessed. Cucurbitacins are triterpenoid substances that usually taste very bitter and sometimes are cytotoxic (Miró 1995). They occur in many Cucurbitaceae, and since the 1960s there is considerable interest in them (Rehm *et al.* 1957; Tallamy & Krischik 1989; Chen *et al.* 2005). *Coccinia grandis* or ivy gourd, which has chemical races that differ in their bitterness (Ramachandran & Subramaniam 1983), is the species with the highest commercial value because of its edible fruits, leaves, and young shoots, which are sold in India and South East Asia, even in super markets. The medical value of this species is known since ancient times (Decker-Walters 1999), and its traditional use in diabetes treatment is supported by current research (Ramachandran & Subramaniam 1983; Graidist & Purintrabipan 2009).

The first *Coccinia* species to be discovered and formally described as a new taxon was *Coccinia grandis*. Linnaeus (1767) placed it in *Bryonia* in the group *Monoecia syngenesia*, which also included water melon, pumpkin, and loofah. Wight and Arnott (1834) established the name *Coccinia* and placed Linnaeus' *B. grandis* as synonym of their *Coccinia indica*. Ten years later, Voigt (1845) paid the appropriate attention to priority and made the correct combination *Coccinia grandis* (L.) Voigt. The South African species *C. quinqueloba* was also first assigned to *Bryonia* (Thunberg 1794, 1807), but then placed in a new genus, *Cephalandra* (Ecklon & Zeyher 1836). Sorting out the priority of the generic names *Coccinia* and *Cephalandra* took some time and effort (Naudin 1866; Hooker 1871; Cogniaux 1878; Clarke 1879; Chapter 4 of this dissertation). Another nomenclaturally and systematically difficult problem was the West and Central African rainforest species *C. barteri*, which needed 86 years until its correct placement in *Coccinia* (Bentham & Hooker 1867; Keay 1953) and an additional 68 years to be recognized as different from *C. heterophylla*, using molecular and morphological data (Holstein & Renner 2010; 2011a; (chapters 1 and 2) and chapter 4 of this dissertation).

Evolution of Habitat Preferences

Of the 940–960 species of cucurbits, only a handful occurs in areas with stronger frost periods. Most Cucurbitaceae are confined to warmer regions with arid to perhumid climates. Some genera, such as *Cayaponia* with about 60 species in rainforests, are restricted to a single biome, while others, such as *Momordica* (60 species) or *Coccinia* (25), occupy a broad range of habitats (Holstein & Renner 2011a; Schaefer & Renner 2011b). In general, plants can tolerate unfavorable conditions through three mechanisms: (i) survival as seed (therophytes sensu Raunkiær; 1905), (ii) full persistence, such as the succulent growth of cacti or evergreen pines in the Arctic or (iii) persistence via storage organs and abscission of leaves or other photosynthetically active organs (chamaephytes, geophytes, hemicryptophytes, but also deciduous phanerophytes *sensu* Raunkiær). Each of the three strategies has evolved multiple times in the spermatophytes. Of these strategies, only the third is found in *Coccinia*. While the first strategy, survival in the form of seeds, is common in dry open habitats (Raunkiær 1905; Danin & Orshan 1990; Giménez *et al.* 2004) and the second, full persistence, often demands costly adaptations and is common in nutrient-poor habitats (Aerts 1995), while the third mechanism seems optimal in habitats, in which plant growth is possible for a limited time every year, but sufficient to produce high biomasses resulting in high competition. In *Coccinia*, we find storage organs, such as woody stem bases and tubers, the latter being an adaptation to grazing or fire (Hargreaves 1996). The tubers are developed from either the roots, such as in *C. adoensis* or from the hypocotyl, such as in *C. abyssinica*. Root tubers are found in *C. adoensis*, a species growing in woodlands, and might be an adaptation to hot fires that would damage vegetative buds near the ground (Chapter 4). In contrast, savanna fires do not become as hot near the ground (Gignoux *et al.* 1997), so hypocotyl tubers might be sufficient in dry savannas.

The diverse habitats occupied by the 25 species of *Coccinia*, which seem to have evolved over the past 7 Ma (Holstein & Renner 2011a), raise the question of speciation modes in this genus. As *Coccinia* species occur from semi-arid habitats at sea level to mist forests at 2500 m alt., shifts in climatic preferences must have happened. If these differ between sister species or sister clades they may have been the cause of the speciation event due to divergent selection on ecological traits, which would meet the definition of “ecological speciation” (Schluter 2000; Rundle & Nosil 2005). Alternatively, species might have evolved secondarily due to local adaptation in allopatry (Smith *et al.* 2001). Well-studied examples of strong divergent selection resulting in new species are the evolution of heavy metal tolerance (MacNair & Christie 1983), flower color, or pollinator changes (Ramsey *et al.*

2003; Whittall & Hodges 2007). F1 hybrids in these cases would have a lower fitness compared to each parent and hence disappear ("disruptive selection"). Ecological speciation along gradients or clines is far less understood and may involve competing trade-offs (Angert & Schemske 2005). Finally, chromosomal changes can assist in stabilizing adaptations by causing the buildup of post-mating gene flow barriers (Templeton 1981; Patterson & Givnish 2004). In *Coccinia*, all these processes may have played a role, although least is known about the role of chromosomal changes (five of the 25 species have had their chromosomes counted; Chapter 4).

In stable environments, ecological niches of clades are typically inert (Peterson *et al.* 1999; Wiens & Graham 2005). Few studies on plant diversification have focused on climatic niches (Evans *et al.* 2009; Jakob *et al.* 2010; Nakazato *et al.* 2010; Smith & Donoghue 2010), and those were mostly concerned with temperate zone plants. Among (sub-)tropical clades, climate niche shifts have been documented in *Olea* (Besnard *et al.* 2009), *Coffea* (Maurin *et al.* 2007), and *Cyclamen* (Yesson & Culham 2006), but not analyzed either quantitatively or in a temporal evolutionary framework (i.e, with a dated phylogeny). In two tropical rainforest tree genera from the Annonaceae, ecological niche differentiation has been analyzed in dated phylogenetic context (Couvreur *et al.* 2011). Before my study of climatic niche differentiation in *Coccinia*, the evolution of habitat preferences in Cucurbitaceae, and whether the different habitats were colonized only once or several times, had never been analyzed.

Time is clearly an important factor in evolution. Fossil-calibrated dating of the Cucurbitaceae suggests that *Coccinia* is a rather young clade that split from its sister *Diplocyclos* only about 15 Ma ago (Schaefer *et al.* 2009). At that time, world climate underwent a general cooling trend, especially from the Middle Miocene (16 Ma ago) on (Axelrod & Raven 1978; van Zinderen Bakker & Mercer 1986; Jacobs 2004). This included a spread of drought-adapted biomes, such as savannas and woodlands. Studies on the evolution of rainforest species distributed in Africa support the Middle Miocene as the age in which the break-up of the West and Central African from the East African rainforests might have happened (Davis *et al.* 2002; Couvreur *et al.* 2008). By the end of the Miocene about 8 Ma ago, East African tectonics and rifting lead to further aridification throughout Eastern Africa (Cerling *et al.* 1997; Sepulchre *et al.* 2006), followed by the onset of the glacial oscillations in the Pliocene and Pleistocene (deMenocal 1995; Zachos *et al.* 2001).

Climate change has a great effect on plant distribution, not only in areas affected directly by glaciation but also in the tropics (Dupont *et al.* 2000; Brncic *et al.* 2009; Correa-Metrio *et al.* 2012). Species distributions shifted with the changes in the absolute amount of precipitation and its distribution over the year. For species adapted to humid conditions, this meant retreat to refugia where conditions remained humid, such as rivers or mountains. Such local refugia could exist despite overall aridification during glacial periods (Haffer 1969;

Maley 1991; Nichol 1999). Population-level analyses often detect traces of the retreat of plants into refugia (Dauby *et al.* 2010; Lowe *et al.* 2010; Born *et al.* 2011; Debout *et al.* 2011). Although it has been suggested that recurrent fragmentation and reconnection of habitats in the Pleistocene might have aided speciation (Hewitt 1996; Kadereit *et al.* 2004), evidence remains sparse (Zhang *et al.* 2004; Jakob *et al.* 2007; Evans *et al.* 2009; Jakob *et al.* 2009; Janssens *et al.* 2009). For *Coccinia*, the main period of species formation and climatic instability coincide (as inferred from my dated phylogeny), and under the assumption of climatic niche conservatism, the Late Neogene glacial cycles might have been drivers of allopatric speciation.

Evolution of Sex Chromosomes

Cucurbitaceae have unisexual flowers (dicliny) with 50% of the species being monoecious (individuals express both sexes) and 50% dioecious (individuals are unisexual). Other sexual systems, such as andromonoecy (bisexual flowers and male flowers on each individual), are rarely found (Schaefer & Renner 2011b). The sexual system (monoecy or dioecy) can be constant in a larger clade or vary within species (Roy & Saran 1990; Volz & Renner 2008). In normally dioecious species, single flowers can express the alternative sex, a phenomenon termed “leaky dioecism” by Baker & Cox (1984). This has also been reported in *Coccinia grandis* (Kumar & Vishveshwaraiah 1952), but the rare bisexual flowers in gynodioecious individuals of this species appear to have sterile anthers. On the other hand, Roy and Saran (1990) report fertile male function in an otherwise female individual.

Research on *Citrullus lanatus* (water melon), *Cucumis sativus* (cucumber), and *C. melo* (honey melon) shows that cucurbit flowers are ontogenetically bisexual (monocliny) and that the organs of one sex are inhibited during early stages of development (Kater *et al.* 2001; Salman-Minkov *et al.* 2008; Chuck 2010). In *Cucumis*, *Cucurbita*, and *Citrullus*, the phytohormone ethylene determines the sexual fate of the developing flower, but in differing ways. In *Cucumis melo, C. sativus*, and *Cucurbita pepo*, ethylene levels experienced during shoot development increases the number of female flowers (Roy & Saran 1990), whereas in *Citrullus lanatus*, ethylene promotes male flower development (Salman-Minkov *et al.* 2008). In species of the neotropical cucurbit genera *Gurania* and *Psiguria*, the phenotypic sex depends on the size of the plant and the amount of light experienced by the uppermost shoots (Condon & Gilbert 1988). Other species have a fixed sex inherited in Mendelian fashion. The German botanist Carl Correns recognized this for the first time in *Bryonia*. By crossing the male dioecious *B. dioica* with female monoecious *B. alba*, Correns obtained 100% dioecious plants with 50% male and female respectively (Correns 1903). In contrast, a cross between female *B. dioica* and male *B. alba* resulted in 100% female offspring (Correns

1907). As crosses between male and female *B. dioica* resulted in 50% male and female offspring, he concluded that half of the male gametes contains a male “tendency” and the other half a female “tendency”, whereas female gametes only contain a female “tendency” (Correns 1907). All chromosomes in *Bryonia* have the same size, independent from the sex of the voucher (Volz & Renner 2008).

Coccinia grandis also inherits the sex like a monogenic trait. Female individuals have 24 homomorphic chromosomes, whereas male individuals have 23 homomorphic chromosomes plus a single much larger chromosome (Bhaduri & Bose 1947; Chakravorti 1948). Using polyploidization and crossings, it was found that triploid and tetraploid plants bearing such a larger chromosome were always male, whereas individuals without such a chromosome were always female, even in hexaploids (Kumar & Vishveshwaraiah 1952; Roy & Roy 1971a; Agarwal & Roy 1975). Hence, the Y chromosome must contain at least one gene coding for a protein that plays an active part in sexual development of the male flowers. The Y chromosomes seem to be important for male fertility, but not for male organ structure, because otherwise female individuals with XX genotypes sometimes produce functional bisexual flowers (Kumar & Vishveshwaraiah 1952; Roy & Saran 1990). The occurrence of fertile hermaphrodite flowers on an XX plant from irradiated seeds of *C. grandis* (Roy 1974) suggests that bisexuality is suppressed actively and by relatively few genes. *Coccinia grandis* plants with a 3*n* = XYY constitution have deformed leaves and produce several male flowers in clusters (Roy & Roy 1971a) with the latter trait only rarely occurring in this species. Whether XYY plants are fertile is not known.

An intergeneric cross between a female *C. grandis* with a male (monoecious) *Diplocyclos palmatus* resulted in purely female plants, which could only be back-crossed with a male *C. grandis* (Roy & Roy 1971b, a). The same intergeneric cross with vice-versa sexes failed. This suggests that the X chromosome contains a suppressor of male function, which is dominant in *D. palmatus*, but recessive when paired with a single Y chromosome. Interestingly, when crossing female *Bryonia dioica* with pollen from monoecious *Bryonia alba* also all offspring is female, except for few early flowers (Correns 1907), suggesting a similar mechanism as in *C. grandis*, but with a delayed expression of the maleness suppressor.

Aside from *Coccinia*, only four genera of the angiosperms, viz. *Cannabis* L., *Humulus* L., *Rumex* L., and *Silene* L., are known to contain species with heteromorphic sex chromosomes (Ming *et al.* 2011). The evolution of heteromorphic sex chromosomes is believed to result from recombination suppression, which is selectively favored when genes promoting one sex or inhibiting the opposite sex can thereby be kept from recombining (Charlesworth 1991). The scrambled gene order on the human Y chromosome (Lahn & Page 1999), compared to the X, suggests that inversions cause or support non-recombination by disrupting the pairing of the chromosomes. If crossing-overs are inhibited, any mutation or other chromosomal change, such as slippage, deletions, and insertion of interspersed repetitive elements can accumulate (Charlesworth 1991; Charlesworth & Charlesworth 2000). Vice-versa, as recombination that would decouple mutated loci from sex loci is inhibited, alleles with loss-of-function mutations cannot be purged from the population. On the other hand, linking sex-beneficial alleles can be advantageous, leading to an accumulation of these alleles in a single linkage group. Hence, the zone in which recombination is suppressed grows and the whole chromosome degenerates (Ming *et al.* 2011).

In contrast to the other four examples of heteromorphic sex chromosomes in the angiosperms, *C. grandis* is rarely mentioned in reviews of plant sex chromosomes, although the existence of sex chromosomes in this species has been known for a long time (Kumar & Deodikar 1940; Bhaduri & Bose 1947). Sutaria (1936) reported the correct chromosome number before, but did not find sex chromosomes in pollen mother cells. The chromosomal status of other *Coccinia* species is practically unknown, except for *C. hirtella* with $2n = 24$ (McKay 1930). However, McKay does not give the sex of the surveyed individual(s), so it is unclear, whether *C. hirtella* has heteromorphic sex chromosomes. As the sister genus *Diplocyclos,* is monoecious and all *Coccinia* species are dioecious, the evolution of dioecy must have occurred in the ancestor the *Coccinia*, while sex chromosomes could have evolved early during or even multiple times during the evolution of the genus.

My thesis aims to (i) summarize the knowledge about the species of *Coccinia* and to revise all species in the genus, (ii) test, whether the broad range of climatic preferences in *Coccinia* has been achieved in few shifts, viz. whether climatic niches in *Coccinia* are conservative, and (iii) explore whether heteromorphic sex chromosomes also occur in other *Coccinia* species, and to infer the age of the sex chromosome evolution in this clade.

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Chapter 1: “*Coccinia* (Cucurbitaceae) gains two new species from East Africa, three new synonyms, and one new combination”

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Coccinia (Cucurbitaceae) gains two new species from East Africa, three new synonyms, and one new combination

Norbert Holstein[1] **& Susanne S. Renner**[1]

Summary. We describe and illustrate *Coccinia pwaniensis* Holstein from eastern Tanzania and southeast Kenya, and *C. samburuensis* Holstein from the Samburu area in Kenya. The new species were already recognised by Charles Jeffrey in 1967 and are now known from eight and four collections, respectively. Ongoing monographic work also revealed three new synonyms and the need for a new combination, *Coccinia heterophylla* (Hook. f.) Holstein.

Key Words. Coastal forests, *Coccinia pwaniensis*, *Coccinia samburuensis*, Kenya, Tanzania.

The Cucurbitaceae genus *Coccinia* comprises some 28 species (N. Holstein, in prep.) that mostly occur in sub-Saharan Africa. *Coccinia grandis* (L.) Voigt, however, ranges from tropical Africa to subtropical and tropical Asia and has now become an invasive weed throughout the tropics. *Coccinia* species are adapted to a wide range of habitats from semi-arid bush lands to cloud forests; no species occur in afro-alpine habitats or the Cape floristic region. In the course of revising the genus, the first author surveyed specimens from 25 herbaria (B, BM, BR, COI, DSM, E, EA, FT, GAT, GOET, H, HBG, HEID, K, M, MO, NHT, P, S, UBT, W, WAG, and partly C, LISC and LISU), which brought to light fertile material of two species that had already been recognised as new by Charles Jeffrey during his work for the *Flora of Tropical East Africa* (Jeffrey 1967). Here we formally describe these species.

All specimens cited have been seen by the first author, except where otherwise marked.

Coccinia pwaniensis *Holstein* **sp. nov.** differt ab omnibus speciebus generis foliis palmato-3 – (5)-lobatis, lobis apicibus acutis. Flores masculi bracteati. Pedunculus longus, basi interdum floribus 1 (– 2) instructus, racemis (oligofloris usque) multifloris. Calycis dentibus subulatis, erectis. Typus: Kenya, Coast Province, Kwale Distr., Buda Mafisini forest, [8 miles] 12.9 km WSW of Gazi, 80 m, ♂ fl., 22 Aug. 1953, *R. B. Drummond & J. H. Hemsley* 3953 (holotypus K, 3 sheets; isotypus EA).

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Plants dioecious, creeping or climbing, up to 3 m long. Fresh branches green, lignifying to a greyish brown to purplish brown bark. Leaves somewhat coriaceous, shallowly to profoundly 3 (– 5) lobate, 2 – 10.4 × 2.7 – 11.4 cm, lobes broadly triangulate to elliptic, tips acute, margin minutely dentate, upper lamina fresh green, tiny pustulate, nerves sometimes with tiny hairs, lower lamina glabrous, rarely with blackish glands at base, nerves prominent and towards the base with stiff erect hairs that can be quite reduced, then appearing wart-like or subglabrous. Petiole 0.6 – 4.1 cm long, adaxial side glabrous or with short bristly hairs, abaxial side with indumentum as on the nerves. Tendrils simple. Probracts lanceolate, 0.2 – 0.3 cm long. Male flowers in racemes, sometimes accompanied by 1 – 2 solitary flowers, the peduncle 3.2 – 7.7 cm long and glabrous, pedicels of flowers in racemes 0.2 – 0.95 cm, pedicels of solitary flowers up to 3.8 cm long, bracts 0.1 – 0.15 cm long, receptacle tube obconical, green, glabrous, calyx teeth 0.25 – 0.35 cm long, subulate and erect, corolla pale yellow to pale orange-yellow, 1.7 – 2.6 cm long, lobes triangulate-elliptical, outside with few-celled hairs, inside with multicellular hairs, filaments 3, connected to a glabrous central column, anthers sinuate, forming a globose head, orange. Pollen prolate. Female flower unknown. Fruit solitary, petioles at maturity 2 – 3.3 cm long, fruit shape oblong-fusiform, 6.2 – 8 cm long, 1.8 – 2.3 cm in diam., rarely (?) with an up to 5.5 cm long sterile apical tip, immature green with pale longitudinal mottling, at maturity becoming orange-red to scarlet-red with pale mottling. Seeds grey beige, 6.5 – 7 × 4 – 4.5 × 1.5 mm (L/W/H), more or less symmetrical, broad ovate in outline, and lenticular. Fig. 1.

DISTRIBUTION. *Coccinia pwaniensis* occurs in the Coast Province of Kenya and the Pwani region of Tanzania (Map 1). It is expected near Tanga and Dar es Salaam.

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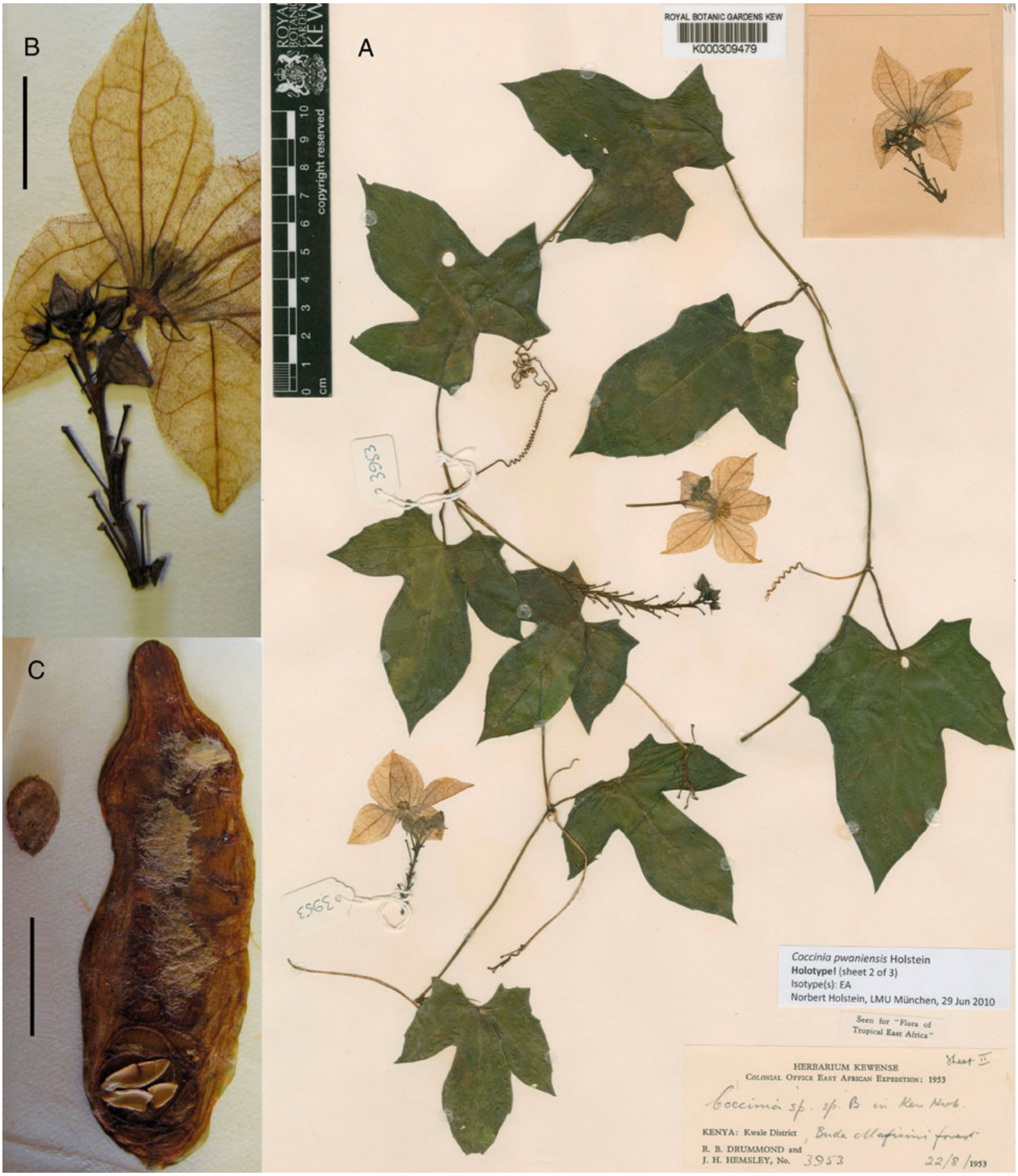
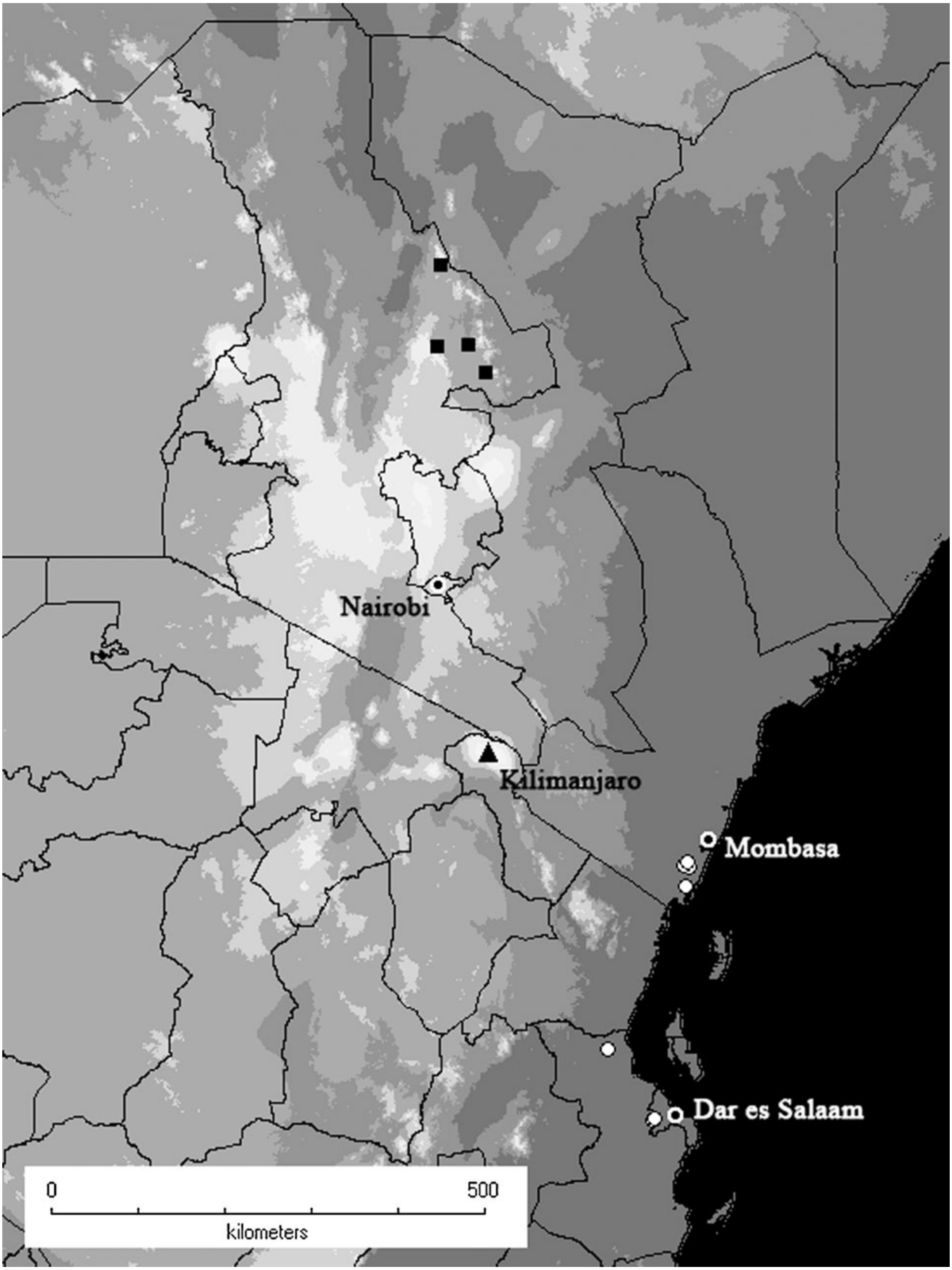


Fig. 1. *Coccinia pwaniensis*. **A** holotype (sheet 2 of 3), reproduced with permission from the Royal Botanic Gardens, Kew; **B** male flower in raceme, detail of the holotype; **C** fruit and seed, detail from *R. B. Drummond & J. H. Hemsley* 1078 (K). Scalebars = 1 cm.

SPECIMENS EXAMINED. KENYA. Coast Province, Kilifi Distr.: Mangea Hill, 39°42'E 03°16'S, 450 m, dry bushland with *Cynometra* sp., *Brachylaena* sp., *Manilkara* sp., *Brachystegia* sp., *Julbernardia* sp., *Diospyros* sp., *Xylopia* sp., *Inhambanella* sp., ♀ fr., 28 Dec. 1988, *W. R. Q. Luke* 1601 (EA); Kwale Distr.: Buda Mafisini forest, [8 miles] 12.9 km WSW of Gazi, 80 m, ♂ fl., 22 Aug. 1953, *R. B. Drummond & J. H. Hemsley* 3953 (holotype K, 3 sheets; isotype EA); Cha Simba forest, 300 m, ♀ fl., fr., 1 Feb. 1953, *R. B. Drummond & J. H.*



Map 1. Distribution map showing the locations of the four collections of *Coccinia samburuensis* (*black squares*) and of the eight of *C. pwaniensis* (*white circles* with narrow black margin) collections. Major cities are indicated by a white circle with a black centre.

Hemsley 1078 (K); Shimba Hills, Giriama Point area, 381 m, forest edge, ♂ fl., 17 March 1968, *F. Magogo & P. Glover* 315 (EA, K); Shimba Hills, Pengo Hill area, 457 m, forest, ♂ fl., 27 March 1968, *F. Magogo & P. Glover* 493 (EA, K); Shimba Hills, Longomagandi, 350 m, high lowland rainforest, 25 June 1988, *R. Schmidt* 1203 (EA); Kwale Distr., no detailed location given, ♂ fl., 15 June 1957, *Saunders* 11241 (EA). **TANZANIA.** Pwani region, Bagamoyo Distr.: Zaraninge Forest in Kiono Plateau, 38°36'E 6°09'S, 305 m, dry evergreen coastal forest, on sand, ♂ fl., 14 March 1990, *Frontier-Tanzania Coastal Forest Research Programme* 1041 (K); Kirasawe Distr.: Pugu Hills Forest Reserve on Dar es Salaam–Kisarawe road. Roadside in forest, 100 – 270 m, ♂ fl., 12 May 1970, *K. H. Macauley* CVL 102 (DSM, EA); Pugu Hills, ♂ fl., 19 March 1939, *J. H. Vaughan* 2774 (EA). Pugu Hills Forest Reserve, road W from road-tunnel, 100 m, in bushes by car-track through forest, ♀ fr., 23 July 1972, *R. Wingfield* 2056 (DSM, EA).

HABITAT. Open, disturbed places in East African coastal forests and dry woodlands (*Brachystegia* sp., *Julbernardia* sp., *Diospyros* sp.); on sandy soil at 80 – 460 m altitude.

CONSERVATION STATUS. The species appears confined to coastal forests, which are declining due to deforestation although they are legally protected (Burgess *et al.* 1998). However, low botanical collecting activity does not allow the assessment of the conservation status of this species. Therefore we treat it here as Data Deficient (DD).

VERNACULAR NAMES (all Kidigo). Mnokonyoka (*F. Magogo & P. Glover* 493), Mtambaa (*F. Magogo & P. Glover* 315).

NOTES. *Coccinia pwaniensis* was first collected in 1939 and described as *Coccinia* sp. B in the *Flora of Tropical East Africa* (Jeffrey 1967: 64). The diagnostic characters mentioned by Jeffrey were the numerous male flowers in a long raceme on a rather long peduncle and the species' occurrence in coastal forests. In addition, the leaves are often 3-lobate with acutely lobed tips, the male flowers are usually bracteate, and the calyx teeth are erect and subulate.

The epithet *pwaniensis* comes from the Kiswahili word "pwani" for "coast" and points to the habitat and distribution of the species. The label of *F. Magogo & P. Glover* 493 states that the Digo tribe believe the fruits to be poisonous and eaten by snakes. The DSM duplicate of *R. Wingfield* 2056 has a fruit with an exceptionally long apical tip without seeds.

Coccinia pwaniensis apparently hybridises with *C. grandis*. This is suggested by a population discovered by the first author in the Pugu Hills, UTM 37 M 0507657 9237464, 194 m, ♂ fl., 25 July 2009, *N. Holstein, F. M. Mbago & D. Shikelango* 102 (DSM, M), 103 (M), 104 (M), 105 (DSM, M). Comparison of chloroplast and nuclear DNA sequences of plants from this population with those of *C. grandis* and other species suggests that *C. grandis* is the female parent. *C. pwaniensis* differs from *C. grandis* in the male flowers being borne in racemes, instead of solitarily. The hybrid plants were in full bloom, but none of their pollen sacs were opened, indicating that the plants may be sterile. Non-dehiscence of the anthers was also observed in an artificial hybrid between *C. grandis* and *C. hirtella* Cogn. created in a greenhouse in Munich (*N. Holstein* 108 (M)).

Coccinia samburuensis *Holstein* **sp. nov.** differt ab omnibus speciebus generis foliis palmato-(5 –) 7-lobatis, lobis marginibus crenatis vel lobulis parvis vel partim longis instructis, glanduloso-dentatis. Cirrhi simplices. Calycis dentibus linearibus. Fructus cylindricus. Typus: Kenya, Rift Valley Province. Samburu Distr., on Wamba – Isiolo road, 0.7 km S of turnoff to Maralal, c. 1300 m, ♀ fl., fr., 4 July 1974, *R. B. Faden & A. J. Faden* 74/948 (holotypus MO; isotypus WAG).

http://www.ipni.org/urn:lsid:ipni.org:names:77107548-1

Perennial dioecious climber up to 5 m long. Stem subglabrous except for tiny, few-celled hairs visible under 5 – 10× magnification, when older white-speckled. Leaves coriaceous, 6 – 14 × 10 – 13 (– 17) cm, (5 –) 7-lobate, the lobe apices subacute to apiculate, margins serrate (to lobulate), teeth (lobule tips) with yellowish glands, upper lamina glabrous, clear or white pustulate, lower lamina glabrous, often with small blackish glands between the vein bases, nerves white-speckled, petioles glabrous and sometimes with white speckles along the base. Tendrils simple. Probracts up to 0.4 cm long, ovoid, acute, glandular on both sides, underneath with few-cellular hairs at 5 – 10× magnification. Male flowers 1 – 2 solitary, pedicel up to 5 cm long, glabrous, receptacle tube glabrous, calyx teeth 0.65 cm long, linear, the corolla 3.7 cm long and brownish yellow, the lobes obovate, the tips acute-mucronate. Female flowers solitary, pedicel 0.4 – 0.5 cm long, glabrous, the ovary narrow cylindrical, glabrous, receptacle tube c. 0.3 cm long, glabrous, calyx teeth 3 mm long, linear, the corolla 3.2 – 4 cm long and yellow-orange, the lobes 2.5 cm long, obovate, the tips acute-mucronate, the lobes abaxially with several long multi-cellular hairs. Fruits c. 14 cm long and 1.5 – 2 cm in diam., sausage-shaped, unripe green with lighter spots, the pulp orange. Seeds 6.5 – 7 × 3.5 – 4.5 mm (L/W), symmetrical, ovate in outline, and flat lenticular. Fig. 2.

DISTRIBUTION. *Coccinia samburuensis* is only known from the Samburu District in the Rift Yalley Province in Kenya (Map 1).

SPECIMENS EXAMINED. KENYA. Rift Valley Province. Samburu Distr.: on Wamba – Isiolo road, 0.7 km S of turnoff to Maralal, c. 1300 m, ♀ fl., fr., 4 July 1974, *R. B. Faden & A. J. Faden* 74/948 (holotype MO; isotype

Coccinia samburuensis Holstein
Holotype!
Isotype(s): WAG
Norbert Holstein, LMU München, 29 Jun 2010

KENYA
K1-Samburu District

Coccinea sp. aff. grandis (L.) Voigt
(not matched in E.A. Herbarium)
Wamba-Isiolo road, 0.7 km S of turnoff to Maralal and Barsalinga, 0°56'N, 37°19'E. Alt. ca. 1300 m. Seepage line at base of large granite outcrop.
Perennial climber; leaves succulent, with numerous yellow glands on the margin; tendrils unbranched; bract or large gland present in the leaf axil opposite a tendril; flowers yellow-orange, ca. 5 cm in diameter; fruit green with lighter spots, 14 x 5 cm; flesh orange.
Common.
R.B. & A.J. Faden 74/948 4 July 1974
MISSOURI BOTANICAL GARDEN HERBARIUM

Fig. 2. *Coccinia samburuensis*. **A** holotype; **B** fruit; **C** female flower bud without ovary; **D** seed. **B – D** from *R. B. & A. J. Faden* 74/948 (WAG). Scalebars = 1 cm.

WAG); Mt Nyiru, southern slopes, near a river, 2°03'N 36°51'E, 1600 m, ♀ fr., 1 April 1995, *B. Bytebier et al.* 355 (EA, 2 sheets); Operoi, 1°12'N 36°49'E, 1350 m, rocky outcrop in *Acacia* woodland, ♀ fr., 23 Dec. 2004, *W. R. Q. & P. A. Luke* 10787 (EA, K); near Maralal, Lowaweregoi [Lowua Werekoi Mt] c. 1220 m [4000 ft], rocks in bushland, ♂ fl., 15 Dec. 1958, *J. G. B. Newbould* 3233 (K)

HABITAT. *Coccinia samburuensis* grows on rocky outcrops, near rivers or seepage lines, in *Acacia-Commiphora* deciduous bushland; 1200 – 1600 m.

CONSERVATION STATUS. The species is only known from four collections, and we therefore cannot assess its conservation status. It is treated here as Data Deficient (DD).

VERNACULAR NAMES. None are known.

NOTES. *Coccinia samburuensis* was first collected in 1958 and mentioned as *Coccinia* sp. A in the *Flora of Tropical East Africa* (Jeffrey 1967: 63), with the characters mentioned being the (5 –) 7-lobate leaves with sinuate-lobulate and glandular-toothed margins and the relatively large flowers. In addition, the species has distinct cylindrical fruits, lineal calyx teeth, and simple tendrils. Jeffrey knew only a male specimen, but female individuals have since become available, and at least five duplicates exist of the type collection (*R. B. Faden & A. J. Faden* 74/948; R. B. Faden, pers. comm., 7 April 2010). Unfortunately, the whereabouts of three of them remain unclear.

Coccinia heterophylla (*Hook. f.*) *Holstein* **comb. nov.**

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Physedra heterophylla Hook. f. in Oliv., *Fl. Trop. Afr.* 2: 553 (Oliver 1871). Type: Angola [Cuanza Norte province], Golungo Alto, along the banks of the stream Casaballa, at the base of the mountains in Sobato de Bumba, male, fl., Oct. 1855, *F. M. J. Welwitsch* 791 (lectotype BM no. 000948006, selected here); Golungo Alto, along the banks of the stream Casaballa, at the base of the mountains in Sobato de Bumba, ♂ and ♀ fl., Oct. 1855, *F. M. J. Welwitsch* 791 (isolectotype p.p.[1] LISU no. 214547, n.v., digital image [JSTOR Plant Science]).

Physedra heterophylla var. *hookeri* Hook. f. in Oliv. (Oliver 1871: 553). Type: Angola [Cuanza Norte province], Golungo Alto, near Ponte de Felix Simões, ♀ fl., Dec. 1855, *F. M. J. Welwitsch* 792 (holotype BM).

ADDITIONAL SYNTYPES EXAMINED. ANGOLA. No detailed location, ♀ fr., Jan. 1856, *F. M. J. Welwitsch* 791 (BM no. 000948008); in rugged places at Delamboa R., with *Coffea melanocarpa*, *F. M. J. Welwitsch* 791 (BM no. 000948007); no detailed location and date, *F. M. J. Welwitsch* 791 (COI); no detailed location, ♂ fl., *F. M. J. Welwitsch* 791 (K); no detailed location, ♀ fl., *F. M. J. Welwitsch* 791 (LISU no. 214548); no detailed location, ♀ fr., Jan. 1856, *F. M. J. Welwitsch* 791 (LISU no. 214549); no detailed location, ♂ fl., *F. M. J. Welwitsch* 791 (LISU no. 214550); in rugged places at Delamboa R., with *Coffea melanocarpa*, Sept. 1855, *F. M. J. Welwitsch* 791 (LISU no. 214551); at Delamboa R., *F. M. J. Welwitsch* 791 (LISU no. 214552); no detailed location, *F. M. J. Welwitsch* 791 (LISU no. 214553); no detailed location, *F. M. J. Welwitsch* 791 (P).

NOTES. Hooker's species is based on at least 13 sheets of *Welwitsch* 791, distributed after Hooker described the species (Phillips *et al.* 1992). The number "791" does not refer to a collection, but instead to a species (Albuquerque *et al.* 2009), as was common practice at the time. Some specimens are labelled with "fol." plus a number, but there is no indication of a series, and the label "fol. 2" occurs twice (BM000948006 and LISU 214548), precluding unambiguous assignments for specimens without dates and localities. Collection dates and localities appear on some sheets, but are not consistent with the "fol." groups. Some of the specimens come from different localities and dates and thus cannot be considered duplicates (ICBN Art. 8.3), making them syntypes. Others, however, do seem to be duplicates (LISU no. 214547 and BM no. 000948006; BM no. 000948008 and LISU no. 214549). BR also holds a Welwitsch specimen without a "collection" number and date, but with its label stating *Physedra heterophylla* and Angola; a drawing is attached to the sheet.

In his treatment for the *Flora of Tropical East Africa* (1967: 61), Jeffrey indicated that a lectotype should be chosen from among the BM gatherings, but he did not carry out this planned lectotypification. We here follow Jeffrey's suggestion and chose a male BM specimen as lectotype.

Monique Kéraudren (1967) synonymised *Coccinia heterophylla* under *C. barteri*, but the two species can readily be distinguished based on the long subulate calyx teeth (> 2.5 mm) found only in *C. heterophylla*. Kéraudren appears to have seen only the BM specimens, and thus she remained unaware that the calyx teeth of *C. barteri* do not differ from her species *C. subhastata*, which we synonymise below.

Coccinia barteri (*Hook. f.*) *Keay* (1953: 82). Type: Nigeria, Nupe [Niger State], exact locality not specified, ♂ fl., *C. Barter* 1525 (holotype K); *Staphylosyce barteri* Hook. f. in Oliv. (Oliver 1871: 554); *Physedra barteri* (Hook. f.) Cogn. (Cogniaux 1881: 525).

Coccinia subhastata Keraudren (1967: 131), **synon. nov.** Type: Cameroon, South Province, Bitye, ♂ fl., 1917, *G. L. Bates* 1469 (holotype BM).

Coccinia mackenii *Naudin ex C. Huber* (1865: 5) [sphalm. Mac-Kennii, after M'Ken, ICBN 60 C.5]; *Cephalandra mackenii* (Naudin ex C. Huber) Naudin (1866: 17) [sphalm. mac kennii]. Type: cultivated in Paris Botanical Garden, original source: South Africa. KwaZulu-Natal, near Durban [Port Natal], ♀ fl., *C. Naudin* s.n. (lectotype P, selected here; isolectotype G-DC (G00211343)).

Cephalandra palmata Sond. (Sonder 1862: 493). Type: South Africa, KwaZulu-Natal: near Port Natal [Durban], ♂ and ♀ fl., fr., April, *J. F. Drège* s.n. (lectotype S; isolectotype P); *Coccinia palmata* (Sond.) Cogn. (Cogniaux 1881: 540), **nom. illeg.** non Roemer (1846).

Coccinia dinteri André (1900: 276), **synon. nov.** Type: unnumbered plate in André (1900).

ADDITIONAL SYNTYPES EXAMINED. SOUTH AFRICA. Without location and date, ♂ fl., *J. F. Drège* s.n. (G, HBG, K 2 sheets, P 2 sheets); KwaZulu Natal: cultivated in Huber garden in Hyères [Olbia], original source near Durban [Port Natal], male and female, fl., 1864, *C.*

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[1] The male specimen on the LISU no. 214547 sheet is an isolectotype, but additionally contains a female flower, which must come from another individual because *Coccinia* is strictly dioecious. This female flower could be considered a lectoparatype.

Naudin s.n. (G-DC (G00211344) 3 sheets, K 3 sheets, W); Umzimkulu [Omsamculo], between shrubs and thickets, near river mouth, female, fr., March, *J. F. Drège* 4637 (P).

NOTES. The protologue of *Cephalandra palmata* cites *Drège* s.n. collections in the herbaria of Hooker (now in K) and Sonder (now in S; Nordenstam 1980). The collections were originally identified as *Momordica palmata*, a combination never validly published (*Momordica palmata* E. Meyer ex Drège, *Zwei Pflanzengeogr. Doc.*: 156, 159, 202 (1843), nom. nud.), and Sonder then took up the epithet when he described the species in *Cephalandra*. When Cogniaux later transferred Sonder's species to *Coccinia* he overlooked M. J. Roemer's (1846) *Coccinia palmata* (L.) M. Roem., thus creating an illegitimate name (ICBN Art. 53.1).

Meeuse (1962) cites the holotype of *Coccinia palmata* as being in S, which is erroneous since this specimen is merely a lectotype (ICBN Art. 9.8). He also cites a *Drège* isotype from H, but no such specimen exists (L. Junikka, pers. comm., 14 April 2010).

The line drawing accompanying the protologue of *Coccinia dinteri* shows a bifid tendril, as is characteristic of most *C. mackenii* specimens (even though André regarded this as a difference between the species). All other characters of *C. dinteri* also match *C. mackenii*, and we are confident that both names refer to the same biological species.

Coccinia senensis (*Klotzsch*) *Cogn.* (Cogniaux 1881: 535); *Cephalandra senensis* Klotzsch (1862: 151). Type: Mozambique, [Zambésia Province], Rios de Sena [Province], without detailed locality, in grassland, *W. C. H. Peters* s.n. (holotype B, destroyed). Tanzania, Lindi Region, 40 km W of Lindi, Lake Lutamba, hill, woodland, climbing over bushes, c. 240 m, ♂ fl., 6 Sept. 1934, *H. J. Schlieben* 5259 (neotype M, selected here; isoneotypes BM, HBG, MO, P, S).

Coccinia fernandesiana C. Jeffrey (1975: 478). **synon. nov.** Type: Mozambique, *de Lemos & Macudcua* 29 (holotype COI; isotypes LISC, LMA, SRGH).

NOTES. The type of *Coccinia senensis* was destroyed during the bombing of the Berlin herbarium in 1943. The protologue, however, mentions key characters, such as stiff, erect, somewhat articulate hairs on the petioles and the lower leaf lamina, combined with softly pilose to glabrous receptacle tubes, which were the main traits distinguishing *C. fernandesiana*.

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Chapter 2: “A dated phylogeny and collection records reveal repeated biome shifts in the African genus *Coccinia* (Cucurbitaceae)”

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A dated phylogeny and collection records reveal repeated biome shifts in the African genus *Coccinia* (Cucurbitaceae)

Norbert Holstein*, Susanne S Renner

Abstract

Background: Conservatism in climatic tolerance may limit geographic range expansion and should enhance the effects of habitat fragmentation on population subdivision. Here we study the effects of historical climate change, and the associated habitat fragmentation, on diversification in the mostly sub-Saharan cucurbit genus *Coccinia*, which has 27 species in a broad range of biota from semi-arid habitats to mist forests. Species limits were inferred from morphology, and nuclear and plastid DNA sequence data, using multiple individuals for the widespread species. Climatic tolerances were assessed from the occurrences of 1189 geo-referenced collections and WorldClim variables.

Results: Nuclear and plastid gene trees included 35 or 65 accessions, representing up to 25 species. The data revealed four species groups, one in southern Africa, one in Central and West African rain forest, one widespread but absent from Central and West African rain forest, and one that occurs from East Africa to southern Africa. A few individuals are differently placed in the plastid and nuclear (*LFY*) trees or contain two ITS sequence types, indicating hybridization. A molecular clock suggests that the diversification of *Coccinia* began about 6.9 Ma ago, with most of the extant species diversity dating to the Pliocene. Ancestral biome reconstruction reveals six switches between semi-arid habitats, woodland, and forest, and members of several species pairs differ significantly in their tolerance of different precipitation regimes.

Conclusions: The most surprising findings of this study are the frequent biome shifts (in a relatively small clade) over just 6 - 7 million years and the limited diversification during and since the Pleistocene. Pleistocene climate oscillations may have been too rapid or too shallow for full reproductive barriers to develop among fragmented populations of *Coccinia,* which would explain the apparently still ongoing hybridization between certain species. Steeper ecological gradients in East Africa and South Africa appear to have resulted in more advanced allopatric speciation there.

Background

Clades will typically retain their ecological characteristics, at least over moderate periods of evolutionary time [1,2], and where inherited climatic tolerances are narrow, this will limit species' geographic range expansion. As long as the inherited component of ecological preference is strong, species evolving in allopatry should initially have similar habitat requirements, and ecological differences between them should accumulate gradually [3]. These arguments set up expectations about how climate niches and species ranges in groups of related species should correlate with each other. Phylogeographic analyses of several African plant clades have found strong signal of Neogene habitat fragmentation and opportunity for allopatric speciation [4-8], but provided no quantitative data on ecological requirements of the species involved. Davis et al. [9] in their study of 11 species of the Malpighiaceae genus *Acridocarpus* showed that aridification in Eastern Africa apparently was accompanied by a small radiation, possibly involving niche shifts, but did not have details on species' drought tolerances. For a clade of tropical African Annonaceae, Couvreur et al. [10] inferred divergence events between

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East and West African rainforest species during the Pliocene and Miocen, but provided no data on niche shifts. A likely reason for the comparative neglect of tropical African plant groups in eco-evolutionary studies is that ranges are poorly known because the underlying occurrence data are too incomplete [11,12]. Related problems are a lack of monographic studies, poorly understood species boundaries, and few species-level phylogenies, the precondition for identifying sister species.

While African plant clades are thus underrepresented in eco-phylogenetic studies, the immense interest in primate evolution in Africa has resulted in a wealth of data on vegetation and climate history [13-15]. During the Middle Miocene, starting from about 16 Ma onwards, the African continent underwent gradual cooling and uplift in the east and south, leading to an expansion of woodlands and savannas, and reducing the ranges of lowland rain forest species [15-17]. By the Upper Miocene, 7 Ma ago, rifting and volcanism blocked precipitation, amplifying the overall aridification in East Africa [18,19]. The early Pliocene brought slightly warmer climates until c. 3.2 Ma [20], when the African tropics began experiencing dramatic climate changes that lasted throughout the Pleistocene and Holocene [21-24]. During the driest and coolest periods of the Pleistocene (2.6 Ma - 12,000 years ago), rain forests may have been restricted to refugia from which they re-expanded during more favorable periods [25-28]. The Quaternary climate oscillations affected all of equatorial Africa [29], with the most recent catastrophic destruction of rain forest occurring 2500 years ago [30].

Here we investigate clade diversification and changes in species' precipitation niches in the African cucurbit genus *Coccinia*. *Coccinia* comprises 27 species (all of them dioecious) and is almost confined to sub-Saharan Africa where it diversified into numerous habitat types. The only species that "escaped" from sub-Saharan Africa is *C. grandis*, which spread to the highlands of the Arabian Peninsula and tropical Asia, and is now an invasive weed on the Pacific Islands and in the Neotropics [31]. Pollination of *Coccinia* is by bees [[32]; NH, personal observation in Tanzania, August 2009], including honeybees. The numerous habitat types occupied by its 27 species make *Coccinia* a suiTable system in which to study niche evolution among close relatives. The niche parameters we focus on are annual precipitation and number of arid months, with species' tolerances being inferred from the occurrences of 1189 geo-referenced collections. Likely past changes in species' ecological preferences were inferred from a time-calibrated molecular tree including all but two of the species. We expected that close relatives would have similar climatic niche envelopes (e.g., drought tolerances), although clearly there had to have been at least two shifts since different *Coccinia* species occur in semi-arid habitats, woodland, and forest, vegetation types with contrasting precipitation regimes.

Results

Phylogenetic Reconstruction and Divergence Time Estimates

The concatenated plastid DNA alignment comprised 4551 nucleotides from 65 accessions representing 25 of the 27 species of *Coccinia*. Table 1 lists all DNA sources with their geographic origin, species name and author, and GenBank accession numbers. A maximum likelihood tree (Figure 1) obtained from the plastid data (TreeBASE accession 10846) shows four major groups: A *quinqueloba* group that occurs in southern Africa, a *barteri* clade that mostly occurs in Central and West African rain forest, an *adoensis* clade that is widespread, but absent from Central and West African rain forest, and a *rehmannii* clade that occurs from Ethiopia via East Africa to southern Africa.

The nuclear *LFY* 2nd intron alignment (TreeBASE accession 10846) comprised 463 characters for 35 accessions, representing 20 species of *Coccinia* plus three outgroups. A maximum likelihood tree from these data (Figure 2) does not contradict the plastid tree topology except for a few accessions in the *C. adoensis* and *C. barteri* clades discussed below, and an accession of *C. sessilifolia*, which in the nuclear tree groups with the *quinqueloba* group, but in the plastid tree groups with the *adoensis* clade.

A tree from the nuclear ITS alignment is almost unresolved (data not shown), but ITS sequences helped pinpoint suspected hybridization (Figure 3; see the section on **Evidence for Hybridization**). For example, individuals of *C. adoensis* from different parts of the species' range have different ITS sequences.

A chronogram from a slightly reduced plastid DNA data set (Figure 4a) shows the inferred absolute ages (with 95% confidence intervals) for nodes with >0.98 posterior probability. The diversification of *Coccinia* apparently began 6.9 Ma ago (10.2 - 3.9 Ma, 95% highest posterior density [HPD]), with most of the extant species diversity dating to the Pliocene.

Climatic Tolerances and Biome Preferences among Close Relatives

Differences in climatic tolerances for species in well-supported clades were quantified by pair-wise Mann-Whitney U tests, focusing on annual precipitation and number of arid months (Table 2a - c). After each species or unit (in the case of the three genotypes of *C. adoensis*) had been assigned to one of three habitat categories (semi-arid habitats, woodland, or forest; *see Methods*), maximum likelihood inference of habitat

Table 1 Voucher information and GenBank accession numbers

Species	No.	Voucher	Location	*mat*K	*ndh*F-*rpl*32R IS	*rpl*20-*rps*12 IS	*trn*L intron	*trn*L- *trn*F IS	*trn*S- *trn*G IS	*LFY* 2nd intron	ITS
C. abyssinica (Lam.) Cogn.	1	*E. Westphal & J. M. C. Westphal-Stevels* 1552 (WAG)	Ethiopia, Oromia Region	HQ608224		HQ608311			HQ608429		
C. abyssinica (Lam.) Cogn.	2	*E. Westphal & J. M. C. Westphal-Stevels* 1951 (WAG)	Ethiopia, Oromia Region			HQ608312	HQ608385	HQ608368	HQ608430		
C. adoensis (Hochst. ex A. Rich.) Cogn.	1	*L. E. Davidson* 3781 (M)	South Africa, Gauteng	HQ608226	HQ608274	HQ608314	HQ608396	HQ608396	HQ608432		HQ608195
C. adoensis (Hochst. ex A. Rich.) Cogn.	2	*R. Story* 6283 (M)	Namibia, Otjozondjupa	HQ608227	HQ608275	HQ608316	HQ608397	HQ608397	HQ608434	HQ608160	HQ608196 - 8
C. adoensis (Hochst. ex A. Rich.) Cogn.	3	*J. Pawek* 6124 (MO)	Malawi, Northern Region	HQ608225		HQ608315		HQ608369	HQ608433		
C. adoensis (Hochst. ex A. Rich.) Cogn.	4	*R. E. Gereau & C. J. Kayombo* 3582 (MO)	Tanzania, Iringa	HQ608231	HQ608273	HQ608313			HQ608431		
C. adoensis (Hochst. ex A. Rich.) Cogn.	5	*E. A. Robinson* 2944 (M)	Zambia, Southern Prov.	HQ608228		HQ608318	HQ608398	HQ608398	HQ608436		HQ608199 - 201
C. adoensis (Hochst. ex A. Rich.) Cogn.	6	*H. Merxmüller* 282 (M)	South Africa, Gauteng	HQ608229		HQ608319		HQ608370	HQ608437		
C. adoensis (Hochst. ex A. Rich.) Cogn.	7	*M. Sanane* 375 (M)	Zambia, Northern Prov.	HQ608230		HQ608320	HQ608399	HQ608399	HQ608438		
C. adoensis (Hochst. ex A. Rich.) Cogn.	8	*A. R. Torre* 5337 (M)	Mozambique, Zambezia			HQ608321		HQ608371	HQ608439		
C. adoensis (Hochst. ex A. Rich.) Cogn.	9	*D. K. Harder & M. G. Bingham* 2584 (MO)	Zambia, Lusaka Prov.	HQ608268	HQ608299	HQ608364			HQ608492	HQ608191	HQ608221
C. aurantiaca C. Jeffrey	1	*M. Richards* 20987 (BR)	Tanzania, Iringa	HQ608235		HQ625507	HQ608401	HQ608401	HQ608443		
C. aurantiaca C. Jeffrey	2	*P. J. Greenway & Kanuri* 14811 (M)	Tanzania, Iringa				HQ608402	HQ608402	HQ608444	HQ608161	HQ608202
C. aurantiaca C. Jeffrey	3	*N. Holstein* et al. 86 (M)	Tanzania, Dodoma	HQ608236	HQ608276	HQ608325	HQ608403	HQ608403	HQ608445	HQ608162	
C. aurantiaca C. Jeffrey	4	*S. A. Robertson* 1925 (MO)	Kenya, Eastern Prov.	HQ608232		HQ608322	HQ608400	HQ608400	HQ608440		
C. barteri (Hook. f.) Keay	1	*E. Achigan-Dako* 07 NIA 899 (GAT)	Guinea, Nzérékoré Region	HQ608237		HQ608330	HQ608404	HQ608404	HQ608450		HQ608203
C. barteri (Hook. f.) Keay	2	*J. J. Wieringa* 6387 (WAG)	Gabon, Haut-Ogooué	HQ608239	HQ608277	HQ608326	HQ608405	HQ608405	HQ608446	HQ608163	HQ608204
C. barteri (Hook. f.) Keay	3	*E. Achigan-Dako* 06 NIA 294 (GAT)	Guinea, Mamou Region			HQ608331	HQ608389	HQ608376	HQ608451		
C. barteri (Hook. f.) Keay	4	*E. Achigan-Dako* 07 NIA 809 (GAT)	Ghana, Eastern Region	HQ608240		HQ608327	HQ608387	HQ608374	HQ608447	HQ608164	
C. barteri (Hook. f.) Keay	5	*W. J. J. O. de Wilde* et al. 3736 (MO)	Cameroon, Central Region	HQ608241		HQ608328	HQ608388	HQ608375	HQ608448		
C. barteri (Hook. f.) Keay	6	*M. A. van Bergen* 490 (WAG)	Gabon, Ogooué-Maritime	HQ608242	HQ608278	HQ608329	HQ608406	HQ608406	HQ608449	HQ608165	
C. barteri (Hook. f.) Keay	7	*F. J. Fernández-Casas* 12077 (MO)	Equatorial Guinea, Bioco Island	HQ608238	HQ608279	HQ608332	HQ608390	HQ608377	HQ608453		

Table 1 Voucher information and GenBank accession numbers *(Continued)*

C. grandiflora Cogn.	1	*H. Schäfer* 05/302 (M)	Tanzania, Tanga	HQ608243	HQ608280	HQ608333	HQ608407	HQ608407	HQ608454	HQ608166	HQ608205
C. grandiflora Cogn.	2	*N. Holstein* et al. 98 (M)	Tanzania, Tanga	HQ608244	HQ608281	HQ608334	HQ608408	HQ608408	HQ608455	HQ608167	
C. grandis (L.) Voigt	1	*W. J. J. O. de Wilde & B. E. E. Duyfjes* 22270 (L)	Thailand, Bangkok	DQ536651	HQ608282	DQ536537	DQ536762	DQ536762	HQ608456	HQ608168	HQ608207
C. grandis (L.) Voigt	2	*R. Müller* s.n., Aug. 1999 (MSB)	Sudan, Sannar Prov.			HQ608335	HQ608409	HQ608409	HQ608457	HQ608169	
C. grandis (L.) Voigt	3	*H. Schäfer* 05/258 (M)	Tanzania, Pwani	HQ608245	HQ608283	HQ608336	HQ608410	HQ608410	HQ608458	HQ608170	HQ608206
C. heterophylla (Hook. f.) Holstein		*C. C. H. Jongkind* 5905 (WAG)	Gabon, Estuaire	HQ608246		HQ608337	HQ608411	HQ608411	HQ608459	HQ608171	
C. hirtella Cogn.	1	*N. Holstein* 29 (M)	J.-L. Gatard, France, wild source unknown	HQ608247	HQ608284	HQ608339	HQ608412	HQ608412	HQ608461	HQ608172	
C. hirtella Cogn.	2	*S. S. Renner & A. Kocyan* 2447 (M)	J.-L. Gatard, France, wild source unknown	HQ608248		HQ608338	HQ608413	HQ608413	HQ608460		
C. keayana R. Fernandes	1	*F. C. Straub* 140 (BR)	Liberia						HQ608462		
C. keayana R. Fernandes	2	*C. C. H. Jongkind* et al. 6542 (WAG)	Liberia, Grand Gedeh	HQ608249	HQ608285	HQ608340		HQ608378	HQ608463	HQ608173	HQ608211
C. longicarpa Jongkind		*C. C. H. Jongkind* 3970 (WAG)	Ghana, Ashanti Region	HQ608250	HQ608286	HQ608341	HQ608414	HQ608414	HQ608464	HQ608174	HQ608212
C. mackenii Naudin ex C. Huber		*R. G. Strey* 3762 (M)	South Africa, Mpumalanga	HQ608251		HQ608343	HQ608415	HQ608415	HQ608465		
C. megarrhiza C. Jeffrey	1	*J. J. F. E. de Wilde* 6501 (WAG)	Ethiopia, Oromia Region			HQ608344	HQ608417	HQ608417	HQ608466		
C. megarrhiza C. Jeffrey	2	*I. Friis* et al. 2664 (MO)	Ethiopia, Oromia Region	HQ608252	HQ608287	HQ608347	HQ608416	HQ608416	HQ608469	HQ608176	
C. megarrhiza C. Jeffrey	3	*P. C. M. Jansen* 3471 (WAG)	Ethiopia, Oromia Region			HQ608345			HQ608467		
C. megarrhiza C. Jeffrey	4	*J. J. F. E. de Wilde* 4793 (WAG)	Ethiopia, Oromia Region	HQ608253		HQ608346			HQ608468	HQ608175	
C. microphylla Gilg	1	*R. B. Drummond & J. H. Hemsley* 4087 (B)	Kenya, Coast Province	HQ608254		HQ608348			HQ608470	HQ608177	
C. microphylla Gilg	2	*J. J. F. E. de Wilde & M. G. Gilbert* 346 (UPS)	Ethiopia, Somali Regional State	HQ608255		HQ608349	HQ608418	HQ608418	HQ608471	HQ608178	HQ608213
C. mildbraedii Gilg ex Harms	1	*M. Reekmans* 7399 (BR)	Burundi, Muramvya Prov.	HQ608256		HQ608350			HQ608472		
C. mildbraedii Gilg ex Harms	2	*N. Holstein* et al. 76 (M)	Tanzania, Morogoro	HQ608257	HQ608288	HQ608351	HQ608419	HQ608419	HQ608473	HQ608179	
C. ogadensis Thulin		*M. Thulin* et al. 11183 (UPS)	Ethiopia, Somali Regional State	HQ608258	HQ608289	HQ608352			HQ608474		HQ608214 - 6
C. quinqueloba (Thunb.) Cogn.		*R. D. A. Bayliss* 8470 (M)	South Africa, Eastern Cape	HQ608259	HQ608290	HQ608353	HQ608420	HQ608420	HQ608475	HQ608180	
C. racemiflora Kéraudren	1	*I. van Nek* 536 (WAG)	Gabon, Ogooué-Maritime			HQ608355	HQ608421	HQ608421	HQ608477	HQ608182	HQ608217
C. racemiflora Kéraudren	2	*J. J. Bos* 6590 (WAG)	Cameroon, South Prov.	HQ608260		HQ608354	HQ608391	HQ608379	HQ608476	HQ608181	
C. rehmannii Cogn.	1	*S. S. Renner & A. Kocyan* 2749 (M)	southern Africa, no detailed information	DQ536652	HQ608292	HQ625508	DQ536799	DQ536799	HQ608479	HQ608184	HQ608218

Table 1 Voucher information and GenBank accession numbers *(Continued)*

C. rehmannii Cogn. var. *littoralis* A. Meeuse	2	*L. E. Codd* 9620 (M)	South Africa, KwaZulu-Natal	HQ608261		HQ625509	HQ608422	HQ608422	HQ608480		
C. rehmannii Cogn. var. *rehmannii*	3	*G. Woortman* 217 (M)	Namibia, Otjozondjupa	HQ608262		HQ625510	HQ608392	HQ608380	HQ608481	HQ608185	
C. rehmannii Cogn.*"ovifera"*	4	*B. de Winter & O. A. Leistner* 5598 (M)	Namibia, Kunene	HQ608263	HQ608291	HQ608356	HQ608423	HQ608423	HQ608478	HQ608183	
C. samburuensis Holstein		*R. B. & A. J. Faden* 74/948 (WAG)	Kenya, Rift Valley Prov.	HQ608264	HQ608293	HQ608357	HQ608393	HQ608381	HQ608482	HQ608186	
C. schliebenii Harms	1	*E. Westphal & J. M. C. Westphal-Stevels* 5539 (WAG)	Ethiopia, Oromia Region		HQ608294	HQ608358			HQ608483		
C. schliebenii Harms	2	*G. S. Laizer* et al. 1449 (MO)	Tanzania, Morogoro	HQ608265		HQ608359		HQ608382	HQ608484	HQ608187	
C. senensis (Klotzsch) Cogn.	1	*N. Holstein* et al. 66 (M)	Tanzania, Morogoro	HQ608266	HQ608295	HQ608360	HQ608424	HQ608424	HQ608485	HQ608188	
C. senensis (Klotzsch) Cogn.	2	*K. Vollesen* MRC4316 (WAG)	Tanzania, Lindi	HQ608267	HQ608296	HQ608362	HQ608425	HQ608425	HQ608487	HQ608189	HQ608219
C. senensis (Klotzsch) Cogn.	3	*A. R. Torre* et al. 18788 (MO)	Mozambique, Tete			HQ608361			HQ608486		
C. senensis (Klotzsch) Cogn.	4	*E. M. C. Groenendijk* et al. 1031 (WAG)	Mozambique, Nampula			HQ625511			HQ608489		
C. senensis (Klotzsch) Cogn.	5	*J. Lovett* 1597 (MO)	Tanzania, Iringa	HQ608233		HQ608323	HQ608386	HQ608372	HQ608441		
C. senensis (Klotzsch) Cogn	6	*C. F. Paget-Wilkes* 72 (MO)	Tanzania, Iringa	HQ608234		HQ608324		HQ608373	HQ608442		
C. sessilifolia (Sond.) Cogn.		*S. S. Renner* et al. 2763 (M)	Plant grown at Mainz Bot. G. (MJG19-54430); wild source unknown	AY968446	HQ608297	DQ648163	AY968568	AY968385	HQ608490	HQ608190	HQ608220
C. spec. nov.		*C. Geerling & J. Bokdam* 662 (MO)	Ivory Coast, Bouna area	HQ608269	HQ608298	HQ608363		HQ608383	HQ608491		
C. subsessiliflora Cogn.		*H. F. in de Witte* 8288 (M)	DR Congo, Kivu	HQ608270		HQ608365	HQ608395	HQ608384	HQ608493		
C. trilobata (Cogn.) C. Jeffrey		*N. Holstein & P. Sebastian* 9 (M)	J.-L. Gatard, France, coll. in Kenya	HQ608271	HQ608300	HQ608366	HQ608426	HQ608426	HQ608494		HQ608222
Diplocyclos palmatus (L.) C. Jeffrey		*J. Maxwell* s.n. 2 Sep. 2002	Thailand, Chiang Mai	DQ536671	HQ608301	DQ536625	DQ536769	DQ536769	HQ608495	HQ608192	
Diplocyclos schliebenii (Harms) C. Jeffrey		*H. J. Schlieben* 4363 (M)	Tanzania, Kilimanjaro				HQ608427	HQ608427	HQ608496	HQ608193	HQ608223
Cucumis hirsutus Sond.		*N. B. Zimba* et al. 874 (MO)	Zambia	DQ536658		DQ536542	DQ536804	DQ536804	HM597074		
Cucumis sativus L.		Unknown	unknown	AJ970307	AJ970307	AJ970307	AJ970307	AJ970307	AJ970307		
Peponium vogelii (Hook. f.) Engl.		*S. S. Renner* 2710 (M)	Tanzania, Tanga	HQ608272	HQ608302	HQ608367	HQ608428	HQ608428	HQ608497	HQ608194	
Scopellaria marginata (Bl.) W. de Wilde and Duyfjes		*A. Kocyan* AK178 (BKF)	Thailand	DQ536751		DQ536612	DQ536804	DQ536804			

Figure 1 Phylogeny for *Coccinia* based on plastid DNA sequence data. Phylogenetic relationships in *Coccinia* based on 4,551 nucleotides of concatenated plastid DNA sequences obtained for 69 accessions and analyzed under maximum likelihood (ML) and the GTR + Γ model. Numbers below branches refer to ML bootstrap support > 75%. The dots at nodes and behind the two brackets refer to uniquely shared indels (*Methods*). The naming of the clades follows that in the nuclear tree (Figure 2). A single accession of *C. sessilifolia* in the nuclear tree groups with the *C. quinqueloba* clade, but the plastid data do not contain sufficient signal to resolve the placement of this species.

shifts on the phylogeny and the Mann-Whitney U tests revealed at least six habitat changes (marked by red arrows in Figure 4b), counting only changes in statistically supported sister species or clades. Differentiation of precipitation preferences within habitat category (e.g., in *C. quinqueloba* versus *C. mackenii*, Table 2a) was not counted as a biome shift.

We next tested whether the number of pairs of species that have the same niche preferences differs from that obtained if species habitat distributions were drawn at random (proportion 0.635). Among the 27 nodes in the phylogeny, 6 involved habitat shifts (red arrows in Figure 4), which is significantly fewer than the expected number of 17 ($G = 9.4$, df = 1, $P = 0.0021$). Even when the four most basal nodes are deleted from the analysis owing to the ambiguity of their character states, the phylogeny still includes significantly fewer habitat shifts than expected at random ($G = 6.5$, df = 1, $P = 0.011$). Thus, occupation of one of our three habitat categories appears to be a statistically conservative trait in the sense that daughter lineages tend to retain habitat type more frequently than expected by chance, given that the random probabilities are estimated from the current distributions of species. The next sections briefly describe the geography and timing of the inferred six shifts between semi-arid habitats, woodland, and forest.

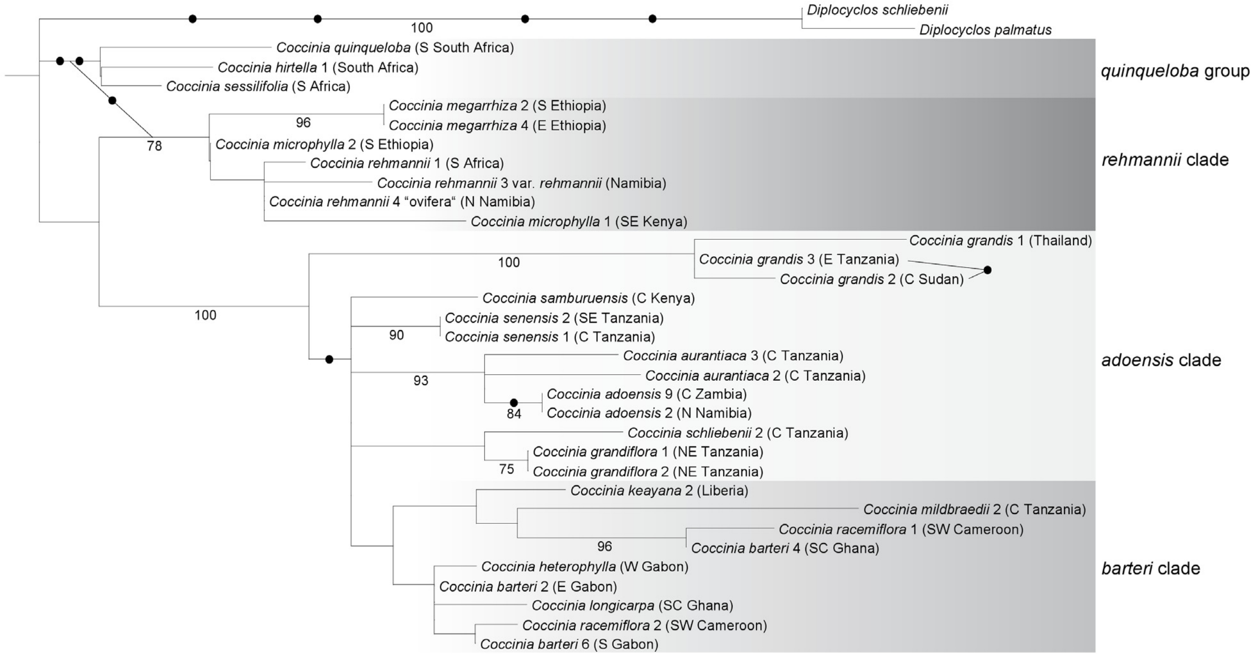

Figure 2 Phylogeny for *Coccinia* based on nuclear data. Phylogenetic relationships in *Coccinia* based on 463 nucleotides of the nuclear *LFY* 2nd intron, obtained for 35 accessions from 23 species analyzed under maximum likelihood (ML) and the GTR + Γ model. Numbers below branches refer to ML bootstrap support > 75%. The dots at nodes and behind the two brackets refer to uniquely shared indels. The tree was rooted on *Peponium vogelii* (not shown).

The *Coccinia quinqueloba* group comprises four species and began diversifying c. 5 Ma (7.5 - 2.4 95% HPD) ago. Its divergence times and habitat preferences are shown in Figure 4, geographic ranges in Figure 5b, and precipitation tolerances in Figure 6. The species in this group occur in two habitat categories (forest and semi-arid habitat), and there was at least one niche shift in terms of the tolerated precipitation regime. The three forest species (of which *C. mackenii* and *C. quinqueloba* have identical sequences in 3503 nucleotides) diverged around 2.8 Ma (4.7 - 1.1 95% HPD) ago, during the Late Pliocene to Pleistocene.

The *Coccinia barteri* clade includes eight Central and West African species plus the East African (Tanzanian) *C. mildbraedii* (incl. *C. ulugurensis*); Figure 5a shows the species' geographic ranges (except for *Coccinia* spec. nov.; Table 1 provides the vouchers and code numbers for each sequenced plant) and Figure 6 their climatic tolerances. Diversification of this clade began 5 Ma (7.6 - 2.7 95% HPD; Figure 4a) ago, that is, at the beginning of the Early Pliocene warming. Most of the species occur in lowland rain forests or mountain forests at elevations up to 2900 m, although *C. barteri* and *C. heterophylla* also have been collected in humid semi-deciduous forests and clearings. *Coccinia* spec. nov. represents a biome shift from rain forest to semi-humid savanna (our woodland category). *Coccinia barteri* is morphologically diverse, and based on herbarium material, species boundaries in the *barteri* clade tend to be cryptic (Table 3).

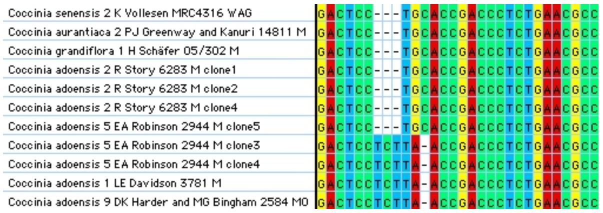
```
Coccinia senensis 2 K Vollesen MRC4316 WAG           GACTCC---TGCACCGACCCTCTGAACGCC
Coccinia aurantiaca 2 PJ Greenway and Kanuri 14811 M GACTCC---TGCACCGACCCTCTGAACGCC
Coccinia grandiflora 1 H Schäfer 05/302 M            GACTCC---TGCACCGACCCTCTGAACGCC
Coccinia adoensis 2 R Story 6283 M clone1            GACTCC---TGCACCGACCCTCTGAACGCC
Coccinia adoensis 2 R Story 6283 M clone2            GACTCC---TGCACCGACCCTCTGAACGCC
Coccinia adoensis 2 R Story 6283 M clone4            GACTCC---TGCACCGACCCTCTGAACGCC
Coccinia adoensis 5 EA Robinson 2944 M clone5        GACTCC---TGCACCGACCCTCTGAACGCC
Coccinia adoensis 5 EA Robinson 2944 M clone3        GACTCCTCTTA-ACCGACCCTCTGAACGCC
Coccinia adoensis 5 EA Robinson 2944 M clone4        GACTCCTCTTA-ACCGACCCTCTGAACGCC
Coccinia adoensis 1 LE Davidson 3781 M               GACTCCTCTTA-ACCGACCCTCTGAACGCC
Coccinia adoensis 9 DK Harder and MG Bingham 2584 M0 GACTCCTCTTA-ACCGACCCTCTGAACGCC
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Figure 3 Detail of the nuclear ITS alignment for *Coccinia*. Section of the aligned *Coccinia* nuclear internal transcribed spacer (ITS) sequences, indicating gene flow between individuals of *C. adoensis* with different plastid genotypes.

The *Coccinia adoensis* clade comprises nine species and includes at least two biome shifts (Figure 4b). The first involves the sister species *C. grandiflora* and *C. schliebenii*, which occur in (rain-) forests of East Africa (Figures 4b and 7), while their widespread relative *C. adoensis* occurs in mountain grasslands, deciduous woodlands, and rarely in moister bushlands (> 450 mm annual precipitation, < 7 months of aridity) from South Africa to Ethiopia and to Nigeria. The deeper split is dated to the Late Pleistocene (c. 2.1 Ma ago), while *C. grandiflora/C. schliebenii* separated from each other

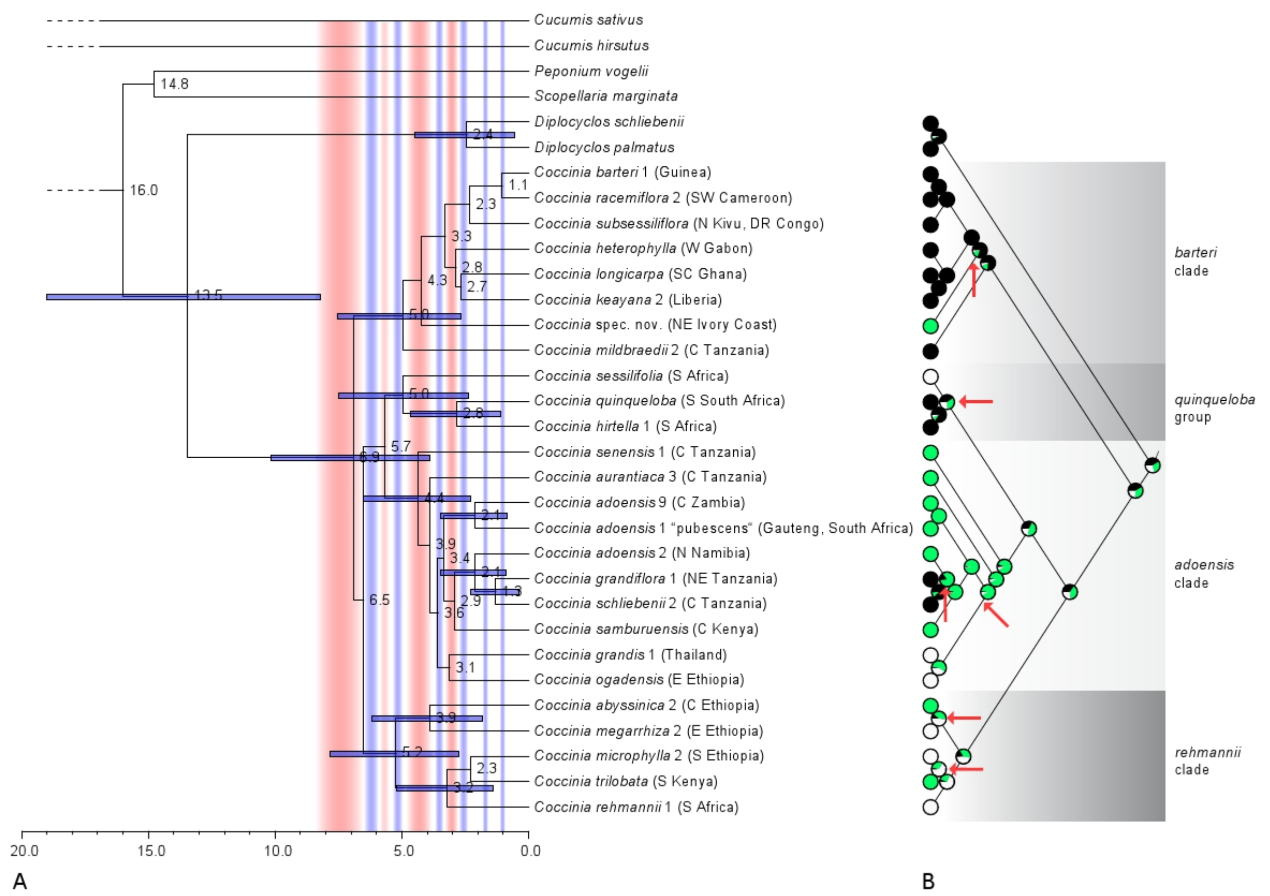

Figure 4 Chronogram and ancestral character reconstruction in *Coccinia*. a. Chronogram for 24 *Coccinia* species (*C. mackenii* and *C. quinqueloba* had identical sequences, and the former was therefore removed; *Methods*) obtained under a Bayesian strict clock model. Clades are labeled as in Figure 1 and 2; blue bars around mean node ages represent the 95% highest posterior density credibility interval, and are given for all nodes with ≥ 0.98 posterior probability. Pale red backgrounds indicates warm (humid) climate, pale blue backgrounds, cold (arid) climates after [15]. b. Ancestral biome reconstruction on the Bayesian tree obtained from the plastid DNA data for *Coccinia*; Black = forest, green = woodland and semi-humid savannas, and white = semi-arid habitats. Red arrows indicate biome shifts.

c. 1.3 Ma ago (Figure 4a). The second biome shift involves *C. ogadensis* and *C. grandis*, which are adapted to semi-arid conditions (Figure 4b).

The *Coccinia rehmannii* clade, which started diversifying during an arid period at the end of the Miocene 5.2 Ma (7.9 - 2.8 95% HPD) ago (Figure 4a), comprises five species (Figure 7: blue dots) and two biome switches (Figure 4b). The split between *C. abyssinica* and *C. megarrhiza* dates to c. 3.9 Ma ago, at the end of the warm and humid Early Pliocene, and that of *C. rehmannii* from *C. microphylla* and *C. trilobata* to c. 3.2 Ma, during the humid Late Pliocene. The climate tolerances of the five species are shown in Figure 6.

Evidence for Hybridization

One of the incongruities between the nuclear and plastid DNA tree topologies concerns *C. racemiflora* from rain forests of west equatorial Africa. In the plastid tree (Figure 1), *C. racemiflora* 1 and *C. racemiflora* 2 group together and share a 490 bp deletion in *trn*S^{GCU}-*trn*G^{UCC} intergenic spacer. Morphologically, these two plants appear to represent the same species. However, in the nuclear *LFY* tree (Figures 2), *C. racemiflora* 1 groups with *C. barteri* 4 while *C. racemiflora* 2 groups with *C. barteri* 6. The latter plant is morphologically intermediate between *C. barteri* and *C. racemiflora* and may present a hybrid.

Two other incongruities concern *C. adoensis* (compare accessions 1 to 9 in Figure 1-3). First, in the plastid tree (Figure 1), *C. adoensis* accessions from East Africa cluster with the East African *C. grandiflora* and *C. schliebenii*, while pubescent *C. adoensis* accessions 1 and 6 from South Africa (originally described as *C. pubescens*) cluster with a glabrous *C. adoensis* 9 from southern Zambia. In the nuclear *LFY* tree (Figure 2), *C. adoensis* 2, which in the plastid tree clustered with East African plants,

Table 2 Pairwise Mann-Whitney U tests among species of supported clades in the *Coccinia* phylogeny

a. Pairwise Mann-Whitney U tests among species of the *Coccinia rehmannii* clade and the *C. quinqueloba* group

	abyssinica	*megarrhiza*	*microphylla*	*trilobata*	*rehmannii*	*quinqueloba*	*mackenii*	*hirtella*	*sessilifolia*
abyssinica	-	__0.047*__							
megarrhiza	__< 0.001**__	-							
microphylla			-	__< 0.001**__	0.971				
trilobata			__< 0.001**__	-	__< 0.001**__				
rehmannii			0.128	__< 0.001**__	-				
quinqueloba						-	__0.004*__	__0.013*__	__< 0.001**__
mackenii						__< 0.001**__	-	0.206	__< 0.001**__
hirtella						__< 0.001**__	0.003*	-	__< 0.001**__
sessilifolia						__< 0.001**__	__< 0.001**__	__< 0.001**__	-

b. Pairwise Mann-Whitney U tests among species of the *Coccinia barteri* clade

	barteri	*racemiflora*	*subsessiliflora*	*longicarpa*	*keayana*	*heterophylla*	spec. nov.	*mildbraedii*
barteri	-	0.336	0.001*	0.087	0.056	__0.001*__	__0.006*__	0.335
racemiflora	0.009*	-	0.026*	0.094	0.091	0.445	0.095	0.601
subsessiliflora	0.63	< 0.001**	-	0.027*	0.077	__< 0.001**__	__0.017*__	0.045*
longicarpa	0.771	< 0.001**	0.251	-	0.746	__< 0.001**__	__0.011*__	0.94
keayana	0.009*	0.968	0.002*	0.012*	-	__< 0.001**__	__0.026*__	0.871
heterophylla	0.016*	0.042*	0.041*	0.018*	0.002*	-	__0.029*__	__0.006*__
spec. nov.	0.093	0.095	0.017*	0.042*	0.013*	0.941	-	__0.003*__
mildbraedii	0.004*	< 0.001**	0.036*	0.002*	< 0.001**	0.148	0.139	-

c. Pairwise Mann-Whitney U tests among species of the *Coccinia adoensis* clade

	senensis	*aurantiaca*	*adoensis* 9	*adoensis "pubescens"*	*adoensis*	*grandiflora*	*schliebenii*	*samburuensis*	*ogadensis*	*grandis*
senensis	-	0.241	0.333	< 0.001**	0.549	__< 0.001**__	< 0.001**	0.333	__< 0.001**__	0.531
aurantiaca	0.001*	-	0.625	< 0.001**	0.1	__< 0.001**__	< 0.001**	0.961	__< 0.001**__	0.35
adoensis 9	0.444	0.75	-	0.03*	0.281	__0.043*__	0.071	0.4	0.222	0.705
adoensis "pubescens"	< 0.001**	0.352	0.636	-	< 0.001**	__0.001*__	0.15	< 0.001**	__< 0.001**__	0.091
adoensis	0.098	0.01*	0.607	< 0.001**	-	__< 0.001**__	< 0.001**	0.24	__< 0.001**__	0.903
grandiflora	__0.015*__	__< 0.001**__	__0.043*__	__< 0.001**__	__< 0.001**__	-	0.138	__< 0.001**__	__< 0.001**__	__< 0.001**__
schliebenii	__< 0.001**__	__< 0.001**__	0.071	__< 0.001**__	__< 0.001**__	__0.014*__	-	0.002*	__< 0.001**__	0.061
samburuensis	0.002*	0.185	0.4	0.061	0.006*	__< 0.001**__	__< 0.001**__	-	__0.004*__	0.521
ogadensis	__< 0.001**__	__< 0.001**__	__0.222__	__< 0.001**__	__< 0.001**__	__< 0.001**__	__< 0.001**__	__0.004*__	-	__0.002*__
grandis	0.02*	0.542	0.914	0.219	0.03*	__< 0.001**__	__< 0.001**__	0.314	__< 0.001**__	-

Fields above the em dash (-) line are comparisons of the number of arid months, below are comparisons of the annual precipitation. One asterisk (*) indicates significance at the 5% level, two asterisks (**) indicate significance at the 0.1% level. Bold numbers indicate statistically significant differentiation between species (biome switch).

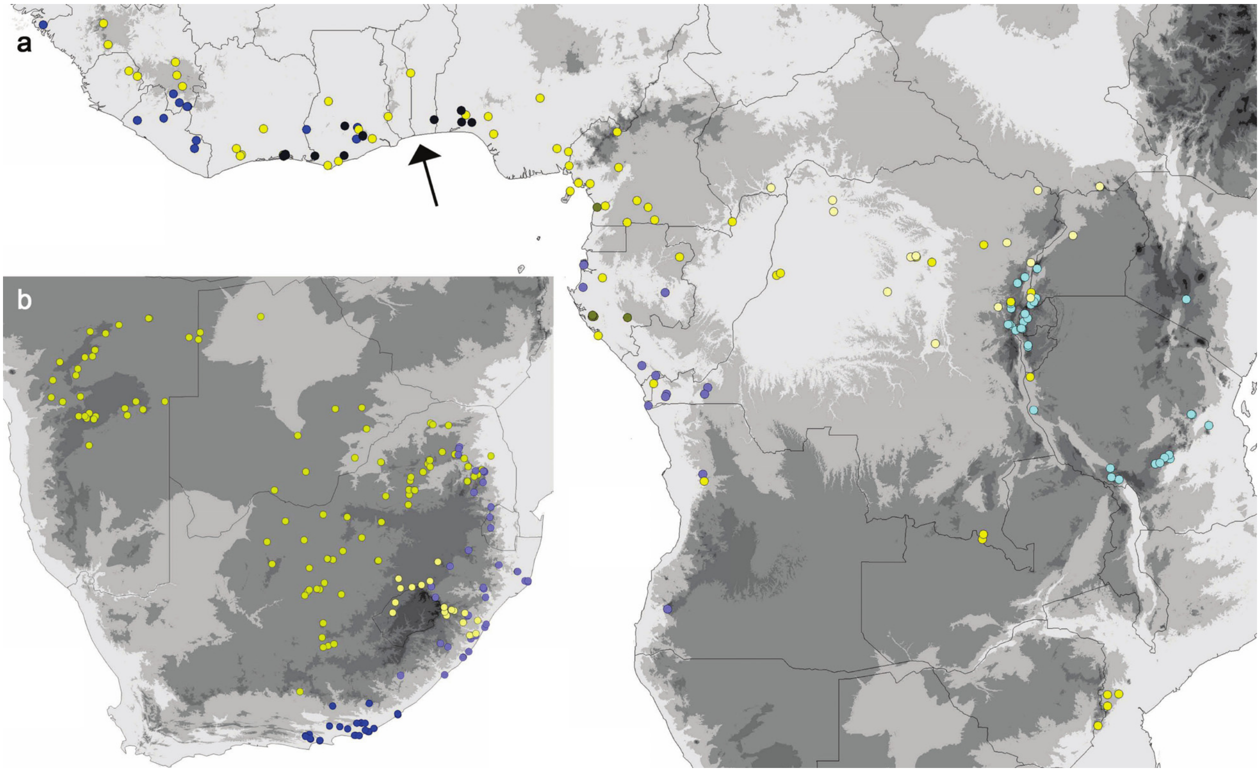

Figure 5 Distribution of species in the *Coccinia barteri* clade and the *C. quinqueloba* clade. a Distribution of species in the *Coccinia barteri* clade. Dark blue = *C. longicarpa*, deep blue = *C. keayana*, pale blue = *C. heterophylla*, light blue = *C. mildbraedii*, bright yellow = *C. barteri* morphs, dark yellow = *C. racemiflora*, pale yellow = *C. subsessiliflora*. The arrow marks the Dahomey Gap. b Distribution of species in the *quinqueloba* group. Dark blue = *C. quinqueloba*, pale blue = *C. mackenii*, bright yellow = *C. sessilifolia*, pale yellow = *C. hirtella*.

instead groups with *C. adoensis* 9 (South African *C. adoensis* plants did not yield *LFY* sequences). The ITS alignment (Figure 3) reveals that single individuals of *C. adoensis* can have two kinds of sequences: *C. adoensis* 5 from Zambia (sister to *adoensis* 2 in the plastid DNA data; Figure 1) harbors sequences matching *C. adoensis* 1 from South Africa as well as sequences matching *C. adoensis* 2 from Namibia. Second, in the plastid tree, East African *C. adoensis* are distant from *C. aurantiaca*, while in the nuclear tree they are in a polytomy with *C. aurantiaca* and *C. adoensis* 9.

Discussion

At the outset of this study, we expected minimally two biome shifts, this being the number required to explain the presence of *Coccinia* in semi-arid habitats, woodland, and forest. Instead, we found six statistically significant biome shifts among close relatives (marked in Figure 4b). However, this is still fewer than if the habitats were distributed on the phylogeny at random. The onset of *Coccinia* diversification dates to just 6.9 Ma ago, a time when the warm and humid climate began to become cooler and drier. Climatic conditions then continued to oscillate during the Pliocene and Quaternary (*Background*). Additionally, the East African rifting led to aridification and more open grasslands starting at 7 - 8 Ma ago [15], [19]. Depending on species' ecological tolerances, these climate fluctuations must have caused range reduction and fragmentation, or expansion and merging. The likely ancestral precipitation preferences of the *Coccinia* clade remain unresolved (Figure 4b); the sister genus, *Diplocyclos*, which comprises four species, is restricted to rain forest and semi-deciduous woodlands [31].

The 12 forest species of *Coccinia* all have discontinuous distributional ranges, as exemplified by *C. grandiflora* (Figure 7), fitting with forest expansion during Pleistocene interglacials that likely reconnected most forest refugia [33]. Survival in persisting refugia probably explains the populations of *C. subsessiliflora* in the southern Sudanese Imatong Mts. (Figure 5a), of *C. barteri* in the mountain region between Zimbabwe and Mozambique, and of *C. mildbraedii* in the Eastern Arc Mts. For *C. heterophylla*, which occurs in the Angola Escarpment at 15°30'S (Figure 5a), mist-saturated local vegetation pockets [34] may have offered survival possibilities during dry periods, while the presence of *C. mildbraedii* in the Kenyan highlands (Figure 5a), may

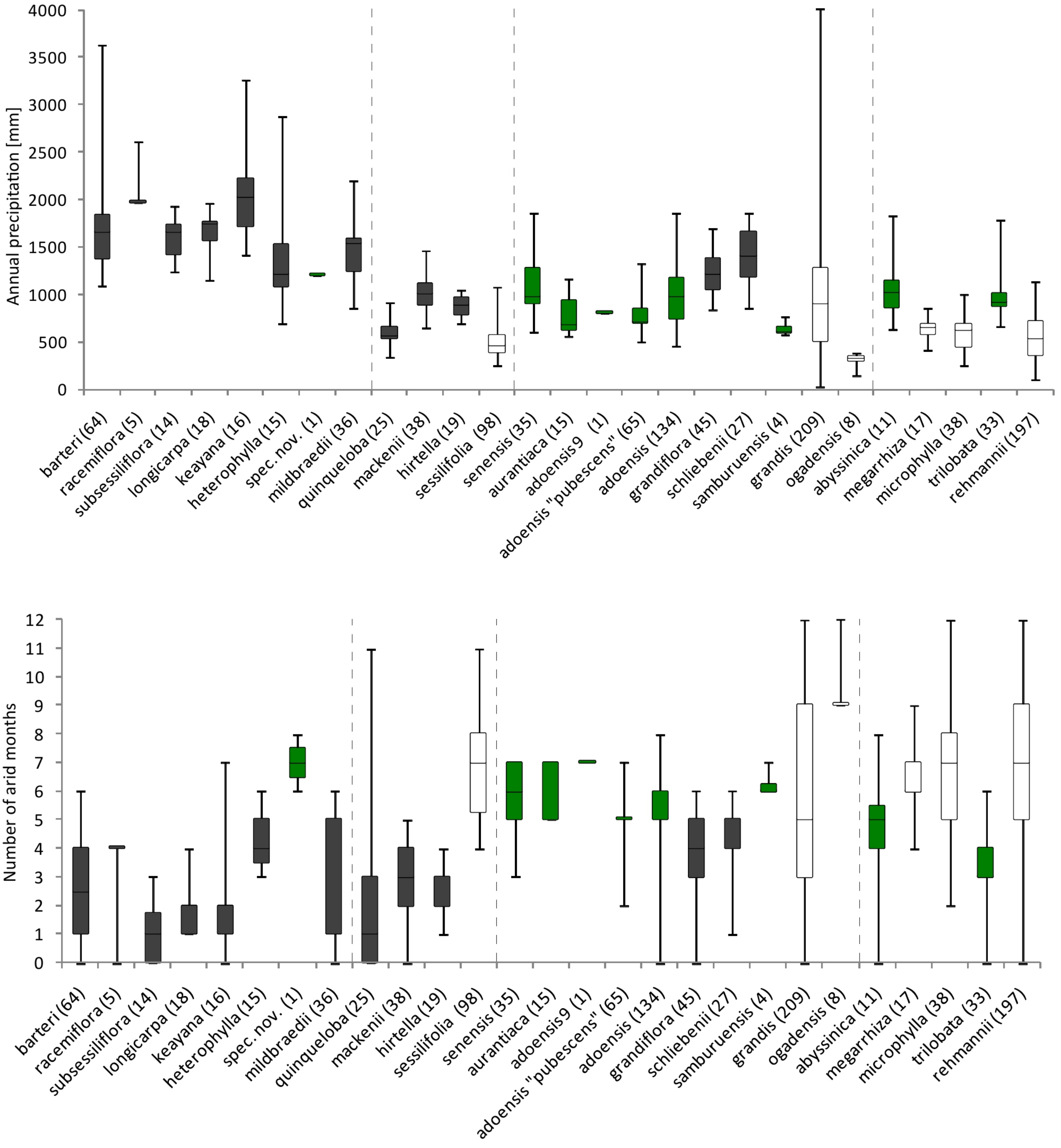

Figure 6 Precipitation variation of species in the genus *Coccinia*. Box-and-whisker plots displaying the median, upper quartile, and lower quartile (box) and range of extremes (whiskers) of the precipitation tolerances (mean annual precipitation and number of arid months) of 1189 georeferenced herbarium collections. Numbers of collections for each species are given in the parentheses following the species names, and the

result from introduction by humans (fide label information on the specimen *J. B. Gillett* 20185, MO, NHT). It nevertheless shows that Central African species would probably find suitable habitats in East Africa if forest expansion advanced further.

The *Coccinia barteri* clade is interesting in containing two rain forest species (*C. longicarpa* and *C. keayana*) with overlapping distributions (Figure 5a) and co-occurrence in the same habitats (e.g., in the Banco Forest Reserve, Abidjan, Ivory Coast). They likely descend from a widespread

Table 3 Key characters among forest species in the *Coccinia barteri* clade, illustrating the high level of morphological differentiation among close relatives (Figure 1 and 2)

Species / accession	Male raceme morphology	Bracts	Calyx teeth	Fruit shape	Other characters
C. mildbraedii	Condensed on long stalk	No	Upright, short, acute	Long cylindrical	Tendrils bifid
C. keayana	Lax, many-flowered	No	Erect-reflexed, long, narrow	Ovoid	Tendrils simple
C. longicarpa	Condensed	No	Erect-upright, broad	Long cylindrical	Tendrils simple (rarely bifid)
C. heterophylla	Condensed (rarely also lax)	Yes	Upright, long subulate	Ovoid	Tendrils bifid
C. subsessiliflora	Condensed, few-flowered	Yes	Upright, short, acute	Ovoid	Tendrils simple; leaves more deeply lobate than in other species
C. racemiflora	Lax, many-flowered	No	Erect-upright, slightly fleshy, short, narrow	Ovoid	Tendrils bifid
C. barteri (type morph)	Condensed, many-flowered	Yes	Upright, short, acute	Ovoid	Tendrils simple or bifid
C. barteri 7-like	Condensed	Yes	Reflexed, fleshy, short	Ovoid	Tendrils simple or bifid
C. barteri 2	Condensed, few-flowered	No	Erect-reflexed, short, subulate	Ovoid	Tendrils bifid
C. barteri 4	Condensed, few-flowered	Yes	Upright, short, acute	?	Tendrils simple or bifid
C. barteri 5	Condensed, few-flowered	No	Erect, short, acute	?	Tendrils simple
C. barteri 6 (x*racemiflora*?)	Condensed, but pedicels rather long	No	Upright, short, acute	?	Tendrils bifid

ancestral species, the range of which became fragmented during the cool/dry mid-Pliocene, with *C. longicarpa* becoming restricted to southwestern Ghana and *C. keayana* to Liberia, fitting with Maley's [25] refugia. Today, *C. longicarpa* is also distributed east of the Dahomey Gap (arrow in Figure 5), an abrupt climatically induced rain forest disjunction in West Africa. Although forest fragmentation during glacial periods likely was severe, present range disruptions in Central and West Africa seem to date only to the recent Holocene [35]. Recurrent fragmentation and reconnection of populations during the Pleistocene apparently led to hybridization and introgression, which would explain the high morphological and genetic variability in *C. barteri* (Figure 1, Table 3).

Among the few species of *Coccinia* that appear to have originated during and since the Pleistocene are the forest species *C. grandiflora*/*C. schliebenii* from East Africa and *C. quinqueloba*/*C. mackenii* (the latter identical in the markers sequenced here) from South Africa. Each pair comprises morphologically similar species with partly overlapping ranges (Figure 5 and 7). The stronger aridity in East and southern Africa compared to Central and West Africa seems to have led to Pleistocene allopatric speciation in these aridity intolerant species. That the range of *C. schliebenii* extends into Ethiopia and the Didinga Mts. in southeastern Sudan (Figure 7), which have similar amounts of precipitation, probably reflects long-distance seed dispersal by birds [36,37], rather than remnant populations from a once continuous range. This is because intervening forests, such as those of the Usambara Mts. and Mt. Kenya, have been well collected, yet have not yielded *C. schliebenii*.

Coccinia species of the *rehmannii* clade and other dry-adapted species occur on either side of the Miombo belt (with 3 - 6 months of aridity), but are absent from the belt itself (Figure 7). The reason does not appear to be the belt's poor lateritic soils [38] since *Coccinia* species can grow on such soils (*C. microphylla*: *R. Wingfield* 1351 and 2893, DSM; *C. trilobata*: *R. Polhill* &*S. Paulo* 962, K), and so are *C. grandis* (*E. Westphal* & *J. M. C. Westphal-Stevels* 1385, MO, WAG; *J. J. Lavranos* &*S. Carter* 23258, MO) and *C. sessilifolia* (*G. Germishuizen* 9384, MO; *S. E. Chadwick* 280, MO). Fire is an unlikely explanation too, since *Coccinia* species have tubers and can re-sprout. During the Pleistocene, the Miombo belt apparently was crossable for ostriches and antelopes [39,40], making its barrier role for *Coccinia* even more difficult to understand.

Conclusions

The at least six biome shifts among the 27 species of *Coccinia* analyzed here may be an underestimate because of our assignments of species into just three broad biome types, semi-arid habitats, woodland, and forest. A fuller understanding of the physiological traits behind tolerated precipitation regimes in *Coccinia* would require transplants or common garden experiments [41]. The present results, based on occurrence data and ecological information from herbarium specimen labels, however show that changes in ecological

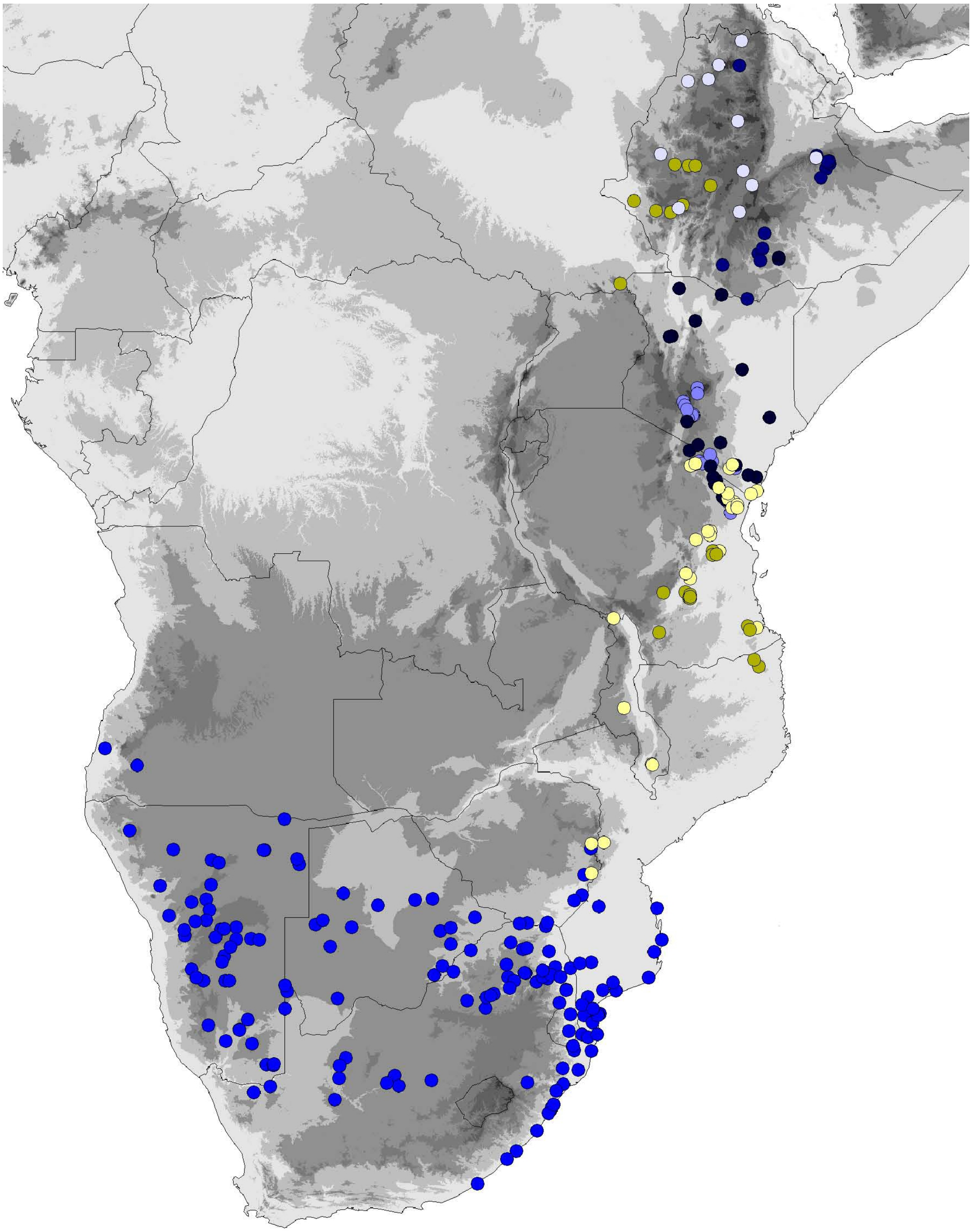

Figure 7 Distribution of *C. grandiflora, C. schliebenii*, and species of the *Coccinia rehmannii* clade. Bright blue (southern Africa) = *C. rehmannii*, pale blue = *C. trilobata*, blackish blue = *C. microphylla*, ice-blue = *C. abyssinica*, dark blue = *C. megarrhiza*. Bright yellow = *C. schliebenii*, pale yellow = *C. grandiflora*.

tolerances (especially drought tolerance) have played an important role in the diversification of *Coccinia*. A strength of this study is that it is based on consistent species concepts and geo-referenced data for well over 1000 collections.

Methods

Species Distribution Analysis and Biome Coding for Ancestral State Reconstruction

The first author surveyed c. 1400 specimens from 25 herbaria (B, BM, BR, COI, DSM, E, EA, FT, GAT,

GOET, H, HBG, HEID, K, M, MO, MSB, NHT, P, S, UBT, WAG, and partly C, LISC, and LISU). Collecting localities (and some ecological information) were taken from herbarium specimen labels and geo-referenced 1189 of them with Google Earth, Google Maps (Google Inc., Mountain View, CA, USA), and online maps of the Perry-Castañeda Library Map Collection (http://www.lib.utexas.edu/maps/). Climate data were extracted from the WorldClim database (http://www.worldclim.org; [42]) using DIVA-GIS 7.1.6.2 (http://www.diva-gis.org). The number of arid months was calculated by counting how often the arithmetic mean of the monthly minimum and maximum temperature [°C] is larger than half of the monthly precipitation [mm] [43]. For ancestral state reconstruction, we assigned 24 species to one of three habitat categories: Semi-arid habitats (which includes semi-desert, bushlands, semi-arid savannas), woodland (including habitats such as mountain shrublands, humid grasslands, semi-humid savannas), or forest (including semi-deciduous forest, lowland rain forest, and mountain forest). Assignment of specimens/species to habitats followed information given on herbarium specimen labels and the WorldClim data for the respective location. *Coccinia grandis*, which occurs in African bushlands and savannas as well as in ruderal sites throughout the humid tropics, was coded as "semi-arid habitats" to reflect its drought tolerance.

Differences in annual precipitation and number of arid months tolerated by members of a species pair or a small clade were tested by pair-wise Mann-Whitney U tests in SPSS 13.0 (SPSS, Chicago, IL, USA). Trait reconstructions were carried out in Mesquite 2.71 [44] under maximum likelihood optimization, using the maximum clade credibility tree (with median heights) from the plastid DNA data obtained from BEAST (below) and Lewis' [45] Markov k-state one parameter model.

Finally, we tested whether the number of pairs of species in which members share the same niche preferences differs from that obtained if species habitat distributions were distributed on the tree at random.

Molecular Phylogenetic Taxon Sampling and Methods

We sampled 25 of the 27 species of *Coccinia* for several plastid and/or nuclear DNA markers. Only the poorly collected species *Coccinia pwaniensis* Holstein [46] and *C. variifolia* A. Meeuse could not be included. Trees were rooted on four outgroups, *Cucumis sativus, Cucumis hirsutus, Peponium vogelii*, and *Scopellaria marginata*, based on studies that included species from all African genera of Cucurbitaceae [47,48]. DNA was extracted from 3 - 20 mg of leaf tissue from herbarium specimens or silica-dried plant material, using Macherey-Nagel plant extraction kits (Macherey-Nagel, Düren, Germany). For some samples, the lysis buffer was altered by adding sodium meta bisulfite (S9000, Sigma-Aldrich Chemie GmbH, Munich, Germany) to a 10 mM final concentration [49]. PCR reactions used standard conditions, except for the addition of bovine serum albumine (Fermentas, St. Leon-Rot, Germany). We amplified the plastid intergenic spacers *trn*S^{GCU}-*trn*G^{UCC} and the *rpl*20-*rps*12 using the primers of Hamilton et al. [50], the *ndh*F-*rpl*32 spacer using the primers of Shaw et al. [51], the *mat*K gene and *trn*K intron using the primers of Yokoyama et al. [52], and the *trn*L^{UAA} intron and *trn*L^{UAA}-*trn*F^{GAA} spacer using the universal primers of Taberlet et al. [53]. PCR products were checked on a 1% agarose gel, and those with multiple bands were run on a 2% agarose gel, cut, and treated with the Wizard SV PCR clean-up kit (Promega GmbH, Mannheim, Germany), following the manufacturer's instructions. Phusion high fidelity DNA Polymerase (Finnzymes, Espoo, Finland) was used for recalcitrant and low-concentrated samples and to amplify the 2nd intron in the nuclear *LFY* gene. Primers for this region came from Volz and Renner [54] and from a M.Sc. thesis carried out in our lab [55]: LFYubiq F1: 5'-CAY CCN TTY ATH GTN CAN GAR CC-3'; LFYubiq-R1: 5'-GCR TAR CAR TGN ACR TAR TGN CKC AT- 3'.

The complete ITS region was amplified using the primers of Balthazar et al. [56]. Where necessary, we used cloning to assess within-plant sequence divergence, focusing on the polymorphic species. For cloning, we ligated PCR products into plasmids of the Promega pGEM-T Vector system (Promega). Plasmids were transformed in ultra competent *E. coli* DH5alpha strains [57]. Positive (white) plasmid colonies were picked from the ampicillin blue/white selection agar plates, solved in 4 ml LB medium with 100 mg/ml ampicillin, and grown over-night at 37°C. Plasmids were obtained using GeneElute Miniprep Kit (Sigma-Aldrich) and directly amplified with primer oligonucleotides and settings as mentioned above. PCR products were purified and sequenced, using the same primers. Sequencing was performed on an ABI Prism 3130 Avant capillary sequencer using Pop-7 polymer (Applied Biosystems, Foster City, CA, USA), and sequences were edited with Sequencher v. 4.6 (Gene Codes, Ann Arbor, MI, USA).

Alignment, Phylogenetic Inference and Divergence Time Estimation

Sequences were aligned by eye, using MacClade v. 4.06 [58]. We excluded ambiguously alignable regions and structurally homoplastic sections. This concerned a total of 219 alignment positions in the plastid data (mostly microsatellites) and 42 nucleotides in the nuclear *LFY* matrix. Tree inference relied on maximum likelihood and was carried out in RAxML v. 7.2.2 [59], with the final parameter evaluation done under the GTR + Γ substitution model. We used this model to approximate the best-fit models found with Modeltest v. 3.7 [60], which under a hierarchical likelihood ratio test indicated the F81 + I + Γ model as the best fit for the combined plastid data, while under the Akaike information criterion it found TVM + I + Γ as the best fit. Statistical support for individual nodes was assessed via bootstrapping with 100 replicates [61]. Nucleotide insertions and deletions (indels) were plotted on the resulting tree to test whether they contained phylogenetic information.

Divergence times were inferred using the program BEAST v. 1.5.2 [62], which employs a Bayesian Markov chain Monte Carlo (MCMC) approach to co-estimate topology, substitution rates, and node ages. The input data consisted of a matrix comprising 26 accessions from 24 species of *Coccinia* (*C. mackenii* and *C. quinqueloba* had identical sequences, and the former was therefore removed) and six outgroup accessions. There are no *Coccinia* fossils, and we therefore used a secondary calibration from a fossil-calibrated Cucurbitaceae-wide dating analysis [48] that obtained an age of 15 million years (Ma), with a standard deviation of 3.0 Ma, for the split between *Coccinia* and *Diplocyclos*. We used this age as a prior constraint on the root node of *Coccinia*, with a normal distribution and a standard deviation (SD) of 2.6 Ma. A SD of 2.7 Ma (or larger) resulted in poor convergence of the MCMC chain. We used a strict clock model (which we preferred because we have a single secondary constraint), a Yule process tree prior, and MCMC chains of 10 million generation length, with parameters sampled every 1000th generation. The first 20% of the trees was discarded as burn-in, and convergence and mixing of the chain were assessed by consistency across runs, inspection of trace plots in the program TRACER v. 1.4.1 [62], and from the effective sample sizes (ESS), which were well above 1000 for all estimated parameters. Four independent BEAST runs yielded the same maximum clade credibility topology, and we also ran an analysis without the data to verify that the effective priors do not contradict the original priors and to assess the informativeness of the data. The cut-off for nodes to be considered in the chronogram was ≥ 0.98 posterior probability.

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Authors' contributions
NH generated sequences and alignments, distribution data, performed data analyses, and worked on the manuscript. SSR conceived the study and drafted the manuscript. Both authors read and approved the final manuscript.

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Chapter 3: “*Coccinia intermedia* – a new Cucurbitaceae species from West Africa”

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Coccinia intermedia – a new Cucurbitaceae species from West Africa

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Abstract

Nuclear and plastid sequences from two individuals of a suspected new species of *Coccinia* from West Africa were added to an available molecular phylogeny for the remaining 27 species of the genus. Phylogenetic analyses of these data indicate the new species' monophyletic status and closest relatives. Based on four fertile collections, we here describe and illustrate *Coccinia intermedia* Holstein. We also provide a key to the *Coccinia* species of West Africa and map their distributions.

Keywords

Benin, Ivory Coast, Ghana, leaky dioecy, molecular phylogenetics, species monophyly, Togo

Introduction

The genus *Coccinia* Wight et Arn. so far consisted of 27 species distributed mainly in Sub-Saharan Africa, with centers of diversity in East Africa and southern Africa (Holstein, ongoing monograph). Only four species were known from West Africa, including *C. longicarpa* Jongkind, *C. keayana* R. Fern., and *C. barteri* (Hook. f.) Keay, which apparently evolved during Pliocene-Pleistocene climatic oscillations (Holstein and Renner 2011). The fourth species, *C. grandis* (L.) Voigt, is much more widespread, occurring not only in Africa but also in South and South East Asia, and being naturalized on several Pacific islands, Australia, and in the Neotropics. During a study of the evolution and biogeography of the genus (Holstein and Renner 2011), we came across a male specimen from the northeastern Ivory Coast that in its plastid sequences differed sufficiently from all other sequenced material for us to suspect it might represent a new species. We therefore provisionally labeled it *Coccinia* sp. nov. We have since found three more specimens of the new species, all of them with fruits, and two with flowers, and based on their morphology as well as additional nuclear and plastid sequences, we here describe the new species *C. intermedia*.

Methods

We produced new sequences of the plastid *rpl*20–*rps*12 intergenic spacer (JN653687), *trn*S^{GCU}–*trn*G^{UCC} intergenic spacer (JN653686) and the nuclear *LEAFY*-like second intron (JN653688) from the female specimen A. Akoègninou et al. 2625 (WAG0278370) of the new species, following standard procedures (Holstein and Renner 2011). We added the new sequences, named "*C. intermedia* 2", to our published matrices and carried out maximum likelihood tree searches, using the approaches described in Holstein and Renner (2011).

Results

Phylogenetic placement

The two *Coccinia intermedia* accessions in the plastid tree form a clade (Fig. 1) within the *barteri* clade. In the nuclear *LEAFY* phylogeny, *C. intermedia* groups with *C. barteri*, *C. heterophylla* (Hook.f.) Holstein, *C. keayana*, *C. longicarpa*, *C. mildbraedii* Gilg, and *C. racemiflora* Keraudren (Fig. 2), albeit without bootstrap support.

Morphological description

Coccinia intermedia **sp. nov.**
urn:lsid:ipni.org:names:77115897-1
http://species-id.net/wiki/Coccinia_intermedia

A *Coccinia longicarpa* differt calycis dentibus angustis, corolla campanulata et fructu elliptico ad oblongo. A *C. keayana* et *C. grandis* differt calycis dentibus ad corollam adpressis vel apicem versus leviter recurvatis et lamina foliorum subtus glandibus fuscis provisa. A *C. barteri* differt floribus femineis 1–3 fasciculatis non racemosis, corolla campanulata.

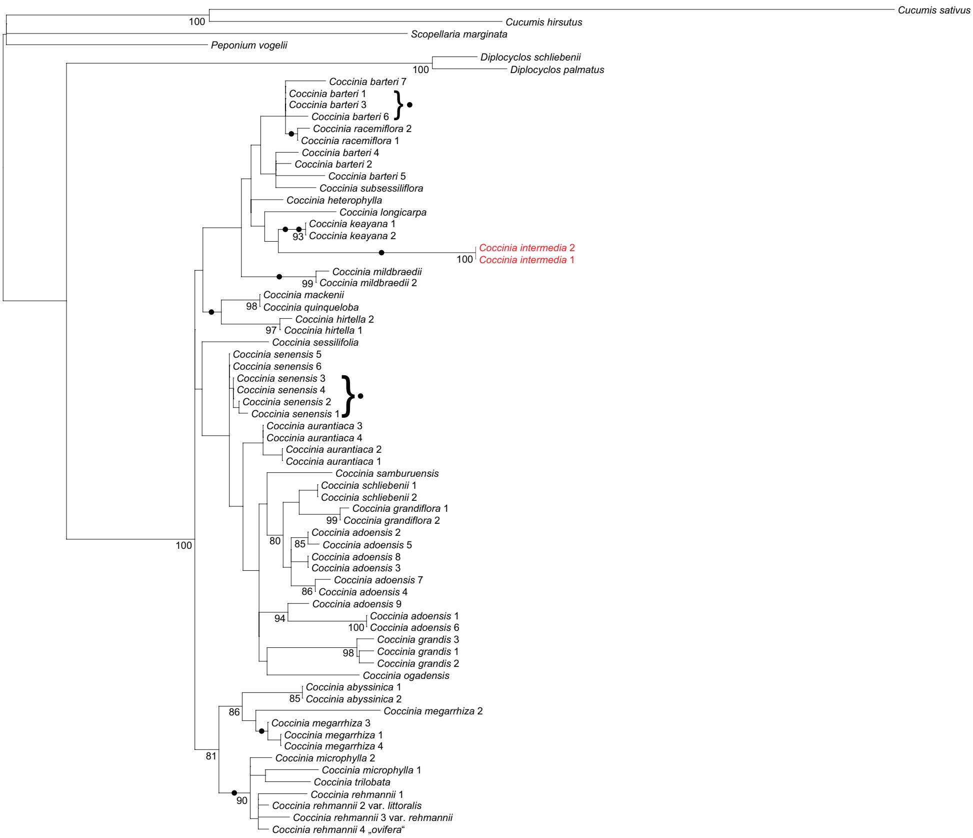

Figure 1. Maximum likelihood phylogeny for *Coccinia* based on plastid DNA sequences analyzed under GTR+Γ model of substitution. The tree is based on 4,551 nucleotides (140 parsimony-informative sites) from the *trn*S^{GCU}–*trn*G^{UCC} intergenic spacer (IS), the *rpl*20–*rps*12 IS, the *ndh*F–*rpl*32 IS, *trn*L^{UAA} intron, *trn*L^{UAA}–*trn*F^{GAA} IS, and the *mat*K gene (expanded matrix from Holstein and Renner 2011). Numbers below branches represent bootstrap support ≥ 80% from 1000 replicates. Dots on branches and behind brackets refer to uniquely shared insertions or deletions. Species names follow Holstein and Renner (2011) except for the new species *C. intermedia* 1, earlier called *Coccinia* sp. nov.

Type. BENIN. Atakora: Natitingou, Kouaténa (Perma), 10°12.00'N; 1°30.18'E, river bed, female, fl, fr, 3 Oct 2000, A.Akoègninou et al. 3625 (Holotype: WAG0278370!; isotype: WAG0278369!).

Description. Perennial, diclinous climber. Shoot length unknown, but likely several meters. Shoots lignify with whitish bark and up to 1 cm diam. Fresh shoots green, glabrous, older shoots with clear to white pustules. Petioles 2.8–10.8 cm, glabrous, when older with clear to white pustules (Fig. 3a). Leaves 6–15 × 7–18 cm, shallowly to profoundly 5-lobate, more or less auriculate (Fig. 4). Upper lamina glabrous with clear to whitish pustules. Lower lamina paler than upper lamina, glabrous, often with small dark glands near the leaf base (Fig. 3a). Tendrils simple or

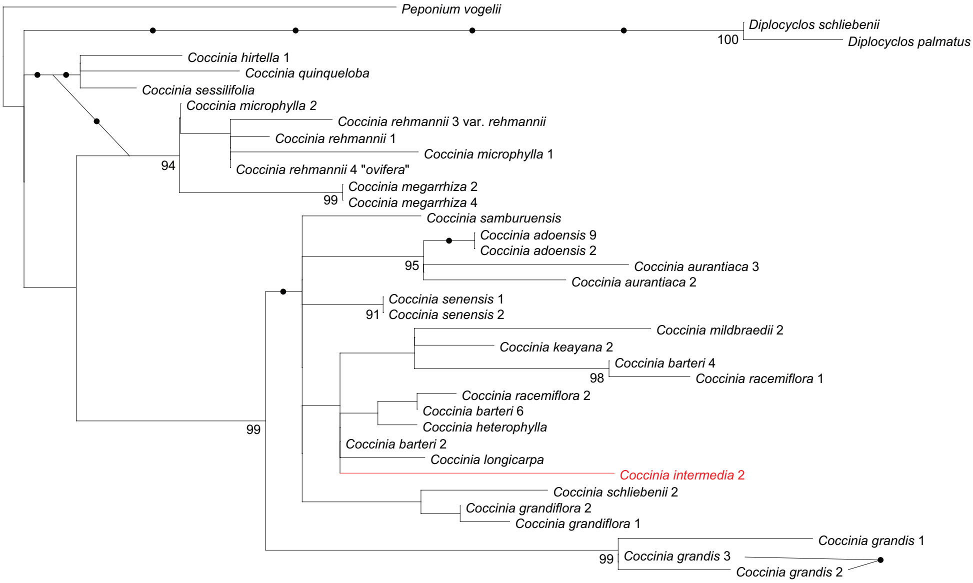

Figure 2. Maximum likelihood phylogeny for *Coccinia* based on nuclear DNA sequences from the *LEAFY*-like 2nd intron analyzed under the GTR+Γ model of substitution. The tree is based on 505 nucleotides (56 parsimony-informative sites). Numbers below branches represent bootstrap support ≥ 80% from 100 replicates. Dots on branches and behind brackets refer to uniquely shared insertions or deletions. Species names follow Holstein and Renner (2011) except for the new species *C. intermedia*.

bifid. Probracts up to 2.5 mm long, glabrous, apex rounded (Fig. 3a). Male flowers in few-flowered racemes (Fig. 5), likely sometimes accompanied by a single flower. Common peduncle up to 1 cm, pedicels in racemose flowers 2–4 mm, glabrous. Bracts up to 1.5 mm long, round to obovoid. Receptacle pale green, glabrous. Calyx teeth 1.5 mm long, lineal to narrow triangulate, erect with slightly recurved tips (Figs. 3–5). Corolla campanulate, 1.6 cm long, pale reddish-yellow to yellow, lobes 0.7 cm long (Fig. 5). Anthers sinuate, in a globose head (Fig. 3c). Pollen unknown. Female flowers 1–3 clustered (strongly reduced raceme; Fig. 4). Pedicels 0.6–1.2 cm, glabrous. Perianth like in males. Ovary fusiform, glabrous. Stigma and staminodes unknown. Fruit 4.5 × 2.5 cm, elliptical to oblong, smooth. Unripe green with pale green longitudinal mottling. Ripe orange?, more likely becoming red via orange ripening stage. Fruit with waxy cover. Size of mature seeds unknown (≥ 5.5 × 3.5 × 1.3 mm), symmetrical (to slightly asymmetrical), face flat (Fig. 3b).

Distribution. (Fig. 6). NE Ivory Coast, SE Ghana (likely also in the north), S Togo (likely also in the north), NW Benin. Based on the current collections, *Coccinia intermedia* is likely to occur in the Dahomey Gap region and the *Isoberlinia* woodlands of West Africa.

Ecology. Wooded grasslands (semi-humid savanna), woodlands, dry forests, and along rivers. Flowering specimens have been collected during May, August, and October, which in each site was during or shortly after the rainy season.

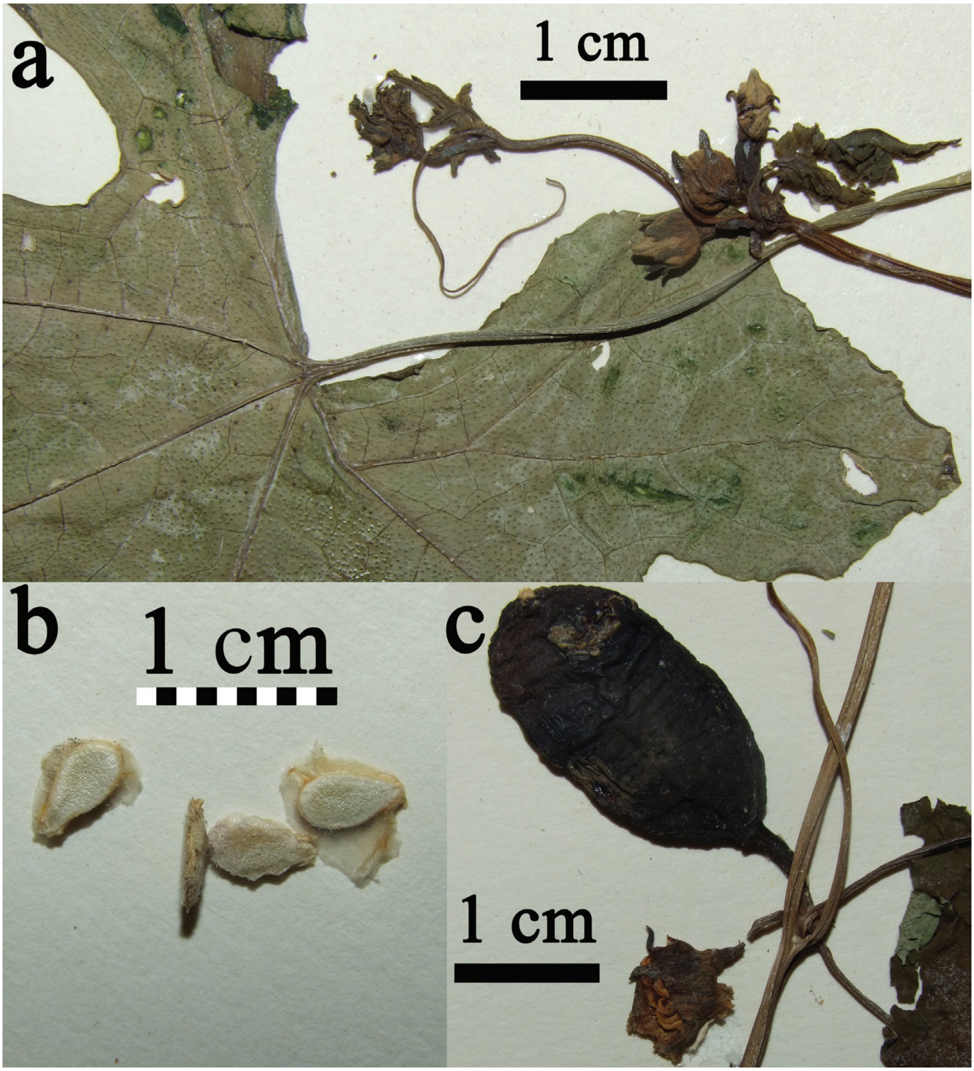

Figure 3. a *Coccinia intermedia* leaf basis and node with flowers **b** seeds from late, but immature fruit **c** node with young fruit and male flower bud with sinuate anthers; all from J.B.Hall & J.M.Lock GC46016 (K).

Etymology. The epithet refers to the species' status as the only *Coccinia* from West Africa that occurs in habitats intermediate between semi-arid and humid conditions. Morphologically, *C. intermedia* combines characters also found in the other four West African species although not in this combination.

List of specimens examined. Benin: Atakora, Natitingou, Kouaténa (Perma), 10°12.00'N; 1°30.18'E, river bed, female, fl, fr, 3 Oct 2000, A.Akoègninou et al. 3625 (WAG 2 sheets). Ghana: Shai Hills Game Reserve, monoecious, fl, fr, 25 May 1976, J.B.Hall & J.M.Lock GC 46016 (K 4 sheets, MO). Ivory Coast: Bouna, male, fl, 10 Aug 1967, C.Geerling & J.Bokdam 662 (MO, WAG). Togo: between Lomé and Aného, female, fr, 25 Jun 1994, L.Aké Assi 18982 (MO).

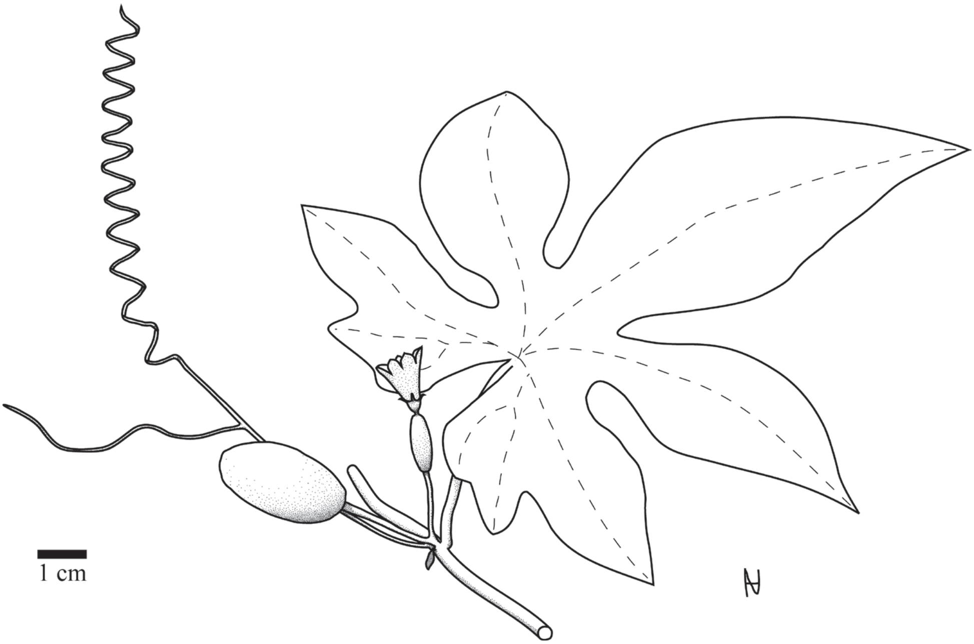

Figure 4. Habitus of *Coccinia intermedia* as reconstructed from J.B.Hall & J.M.Lock GC46016 (K).

Key to West African *Coccinia* species

1 Plant glabrous. Leaves with few large pale glands between main nerves of lower lamina. Nerves on lower lamina with or without white pustules. Leaf margin dentate, in mature plants often red to brown (black when dry). Tendrils always simple. Male and female flowers 1 solitary (rarely male flowers clustered or in short-peduncled racemes). Calyx teeth spreading to reflexed, tips red to brown. Corolla campanulate, white or buff. Fruit ovoid. Plant of semi-arid habitats. .... ***C. grandis***

1' Plant glabrous or with hairs, especially on adaxial petiole. Leaves with small blackish glands (often many) centered towards the leaf base or without glands on lower lamina. Tendrils simple or bifid. Male and female flowers in racemes or solitary. Corolla in yellowish tones, never white. **2**

2 Plant glabrous. Leaves with small blackish glands centered towards the leaf base (Fig. 3). Nerves on lower lamina with or without white pustules. Leaf margin at maturity with colored teeth (color in living plants unknown, black when dry). Tendrils simple or bifid. Male flowers (Fig. 5) bracteate, in few-flowered racemes, female flowers 1–3 solitary/clustered (Fig. 3 and 4). Calyx teeth erect with recurved tips (Figs 3–5). Corolla campanulate. Fruit ovoid to short cylindrical. Plant of wooded grasslands (tree savanna), woodlands, or dry forests. .... ***C. intermedia***

2' Plant glabrous or with hairs, esp. on adaxial petiole. Leaves with small blackish glands centered towards the leaf base or without glands. Nerves on lower

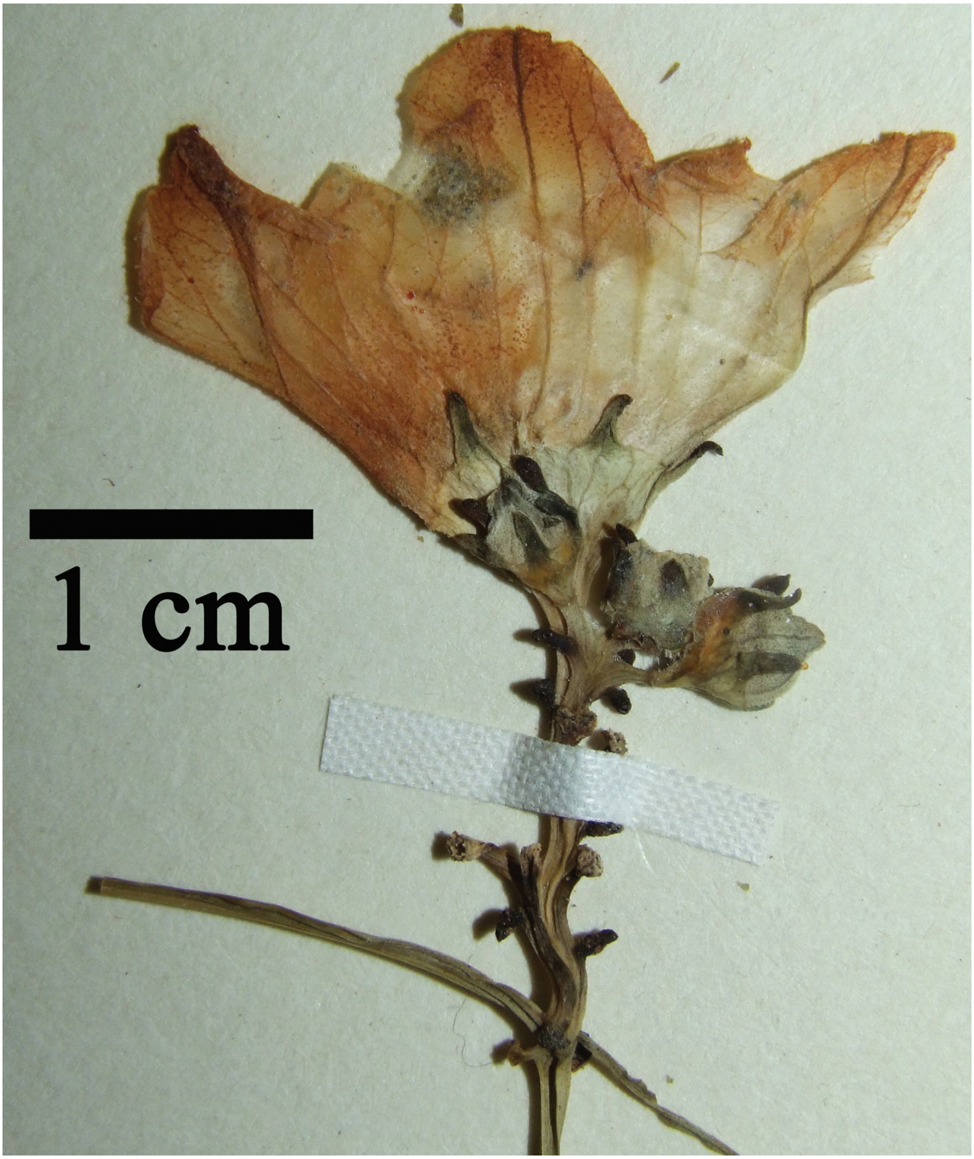

Figure 5. Male inflorescence of *Coccinia intermedia* from C.Geerling & J.Bokdam 662 (WAG).

leaf lamina without white pustules. Tendrils simple or bifid. Male flowers in few to many-flowered racemes, rarely accompanied by a solitary flower. Female flowers in few- to many-flowered racemes or solitary. Flowers bracteate or ebracteate. Corolla urn-, cup- to funnel-shaped. Plant of humid climates (rainforests, gallery forests, etc.) **3**

3 Leaf margin with pale (when dry blackening) glandular teeth. Tendrils simple. Flowers without bracts, calyx teeth erect, > 1.5 mm at base. Fruits long cylindrical.. ***C. longicarpa***

3' Leaf margin without conspicuously colored teeth. Tendrils simple or bifid. Flowers with or without bracts. Calyx teeth erect, spreading, or reflexed, but narrow (< 1.2 mm at base). Fruits ovoid. **4**

4 Tendrils simple. Male flowers in lax racemes, female flowers solitary or in few-flowered racemes. Flowers without bracts. Calyx teeth in buds spreading, later reflexed. .... ***C. keayana***

4' Tendrils simple or bifid. Male flowers in dense few- to many-flowered racemes, with or without bracts. Female flowers in racemes, rarely solitary. Flowers with or without bracts. Calyx teeth variable. .... ***C. barteri***

Discussion

Coccinia intermedia is morphologically similar to the other West African species. From *C. grandis*, it differs most readily in the glands on the lower lamina and in its calyx teeth (erect with recurved tips in *C. intermedia* and spreading to reflexed in *C. grandis*). From *C. longicarpa*, it differs in its ovoid fruits (instead of long cylindrical fruits in *C. longicarpa*). Additionally, *C. longicarpa* has ebracteate racemes and much broader (> 1.5 mm at the base) erect calyx teeth, and an urn-shaped corolla. From *C. keayana*, it differs in having bracteate male flowers in denser racemes, a campanulate corolla and calyx teeth that are adpressed to the corolla with recurved tips, instead of spreading (in buds) to reflexed calyx teeth. Secure distinction of *C. intermedia* from *C. barteri* requires fertile material with flowers (see the key above).

Ecologically, the new species is a member of White's (1983) Sudanian center of endemism and his Guinea-Congolia/Sudania regional transition zone (Fig. 6). The only species with a similar habitat as *C. intermedia* is *C. adoensis*, the most western known occurrence of which is Adamawa State (eastern Nigeria). Whether the species co-occur is not known. They could be distinguished by fruit shape (not beaked in *C. intermedia*, beaked in *C. adoensis*, although this character can vary in the latter). Additionally, *C. adoensis* has inflorescence peduncles that are longer than 1 cm (in its male racemes) and petioles that are often hairy.

Two DNA characters, namely base pairs 310 and 323 in the *trn*S^{GCU}–*trn*G^{UCC} intergenic spacer region, suggest the placement of *C. intermedia* as sister to a clade that we have earlier referred to as the *Coccinia barteri* clade (Holstein and Renner 2011). If this placement is correct, then the *Coccinia* species occurring in the rain or mist forests of West and Central African are monophyletic and probably evolved *in situ*. One of the four collections, J.B.Hall & J.M.Lock GC 46016, bears male and female flowers/fruits on the same node (Fig. 3c). The male flowers are buds, and it is not clear, whether they are fertile. Kumar and Vishveshwaraiah (1952) report a “gynodioecious form” of *C. grandis* in which the male flowers of the hermaphrodite (monoecious) plants are sterile. An occasional occurrence of bisexual plants in otherwise dioecious species, sometimes called “leaky dioecy” (Baker and Cox 1984), has also been observed in other Cucurbitaceae (Schaefer and Renner 2010).

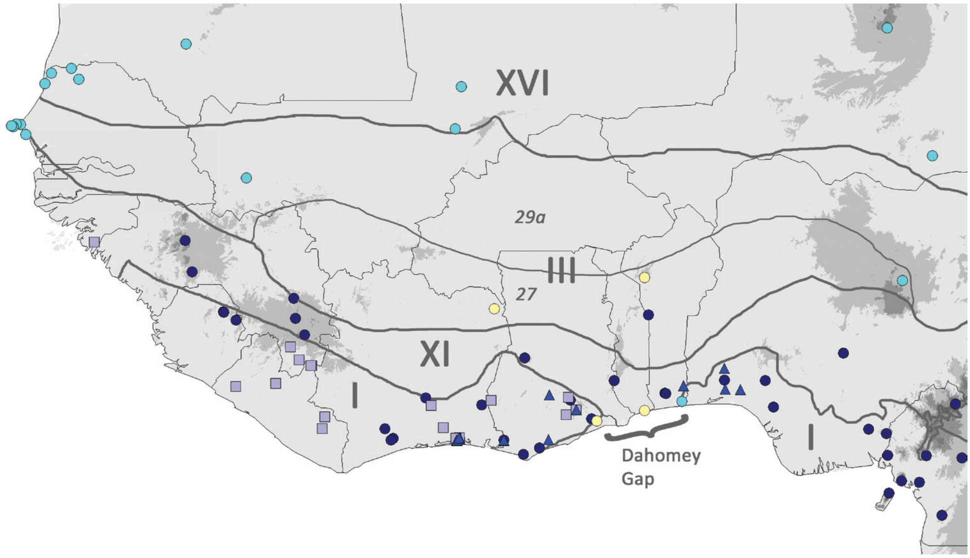

Figure 6. Map of West African *Coccinia* species. Pale yellow circles = *C. intermedia*, cyan circles = *C. grandis*, dark blue circles = *C. barteri*, pale blue squares = *C. keayana*, bright blue triangles = *C. longicarpa*. Thick dark grey lines are phytochoria drawn after White (1983), I = Guineo-Congolian regional center of endemism, III = Sudanian regional center of endemism, XI = Guinea-Congolia/Sudania transition zone, XVI = Sahel regional transition zone. Thin dark grey lines (after White (1983)) differentiate between White's vegetation types of zone III: 27 = Sudanian woodland with abundant *Isoberlinia*; 29a = undifferentiated Sudanian woodland. Location of *C. intermedia* in Ivory Coast estimated (only the department is given on the herbarium sheet).

However, true monoecy in *C. intermedia* would be surprising as none of ca. 1,500 specimens of other *Coccinia* species studied is bisexual (Holstein, ongoing monograph).

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Chapter 4: “Monograph of *Coccinia* (Cucurbitaceae)”

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Disclaimer: None of the proposed nomenclatural changes within this chapter are effectively published with this dissertation (Art. 30.5 ICBN).

Monograph of *Coccinia* (Cucurbitaceae)

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Contents

Abstract

This monograph deals with all 136 names decribed in the Cucurbitaceae genus *Coccinia* and recognizes 25 species. Taxonomic novelties are *Coccinia adoensis* ssp. *adoensis* var. *aurantiaca* (C.Jeffrey) Holstein **stat. nov.**, *C. sessilifolia* ssp. *sessilifolia* var. *variifolia* (A.Meeuse) Holstein **stat. nov.**, and *C. adoensis* ssp. *adoensis* var. *jeffreyana* Holstein **var. nov.** For the 25 species 2801 specimens were examined, of which 1633 were georeferenced to produce distribution maps. All species are distributed in sub-Saharan Africa with one species, *C. grandis*, extending from Senegal in West Africa east to Indonesia and being naturalized on Pacific Islands, in Australia, the Caribbean, and South America. *Coccinia* species are dioecious creepers or climbers with simple or bifid tendrils that occupy a range of habitats from arid scrubland, woodlands to lowland rainforest and mist forest. The corolla of *Coccinia* species is sympetalous, usually pale yellow, and 1 to 4.5 cm long. Pollination is by bees foraging pollen or nectar. After pollination, the developing ovary often exhibits longitudinal mottling, which disappears until ripeness of the fruit. All species produce berries with a pericarp in reddish colors (orange-red trough scarlet red), hence the generic name. The globose to cylindrical fruits contain numerous grayish-beige flat to lenticular seeds. Chromosome numbers are $2n = 20$, 24, and 22 + XX/XY. Many *Coccinia* species are used for food, either as roasted tubers, greens as spinach, or the fruits as vegetables. Medicinal value is established in *C. grandis*, of which the sap is used against diabetes.

Introduction

Coccinia Wight & Arn. comprises 25 species and is the 11th largest of the 97 genera of the Cucurbitaceae (Schaefer and Renner 2011a). Especially in the 19th century, it drew gardeners' attention probably because of its striking fruits (Edwards 1815; Sims 1816; Huber 1864; 1865; Koch 1865; André 1900). All species are dioecious, and one species, *C. grandis*, has heteromorphic sex chromosomes and therefore been studied cytologically (Kumar and Deodikar 1940; Bhaduri and Bose 1947; Chakravorti 1948; Kumar and Vishveshwaraiah 1952; Roy and Roy 1971b; Roy 1974; Agarwal and Roy 1975; 1983; 1984; Datta 1988). The last taxonomic treatment of *Coccinia* is by Cogniaux (1881), more than 130 years ago. Since then, 16 new species have been described, and the genus has only been revised regionally (Hutchinson et al. 1954; Meeuse 1962; Jeffrey 1967; Kéraudren 1967; Kéraudren-Aymonin 1975a; Jeffrey 1978; Jeffrey and Fernandes 1986; Jeffrey 1995). The position of *Coccinia* in the Benincaseae has been confirmed by molecular data (Kocyan et al. 2007; Schaefer and Renner 2011b), and the monophyly has been tested with almost complete species sampling by Holstein and Renner (2011a).

The separation of *Coccinia* from other genera has not been easy. The scarlet-red fruits to which the genus name – *Coccinia* from Latin *coccineus* – refers also found in other African genera, such as *Eureiandra* Hook.f. Therefore, it is not surprising that early botanists described several species now considered to belong to Coccinia in other genera (*Cephalandra* Schrad. ex Eckl. & Zeyh., *Physedra* Hook.f., and *Staphylosyce* Hook.f.). In all, 76 names at various ranks have been proposed for what are here considered 25 species. The species concepts in the present revision are based on 2800 specimens and field work in Tanzania, geo-referencing of 1633 collections and cultivation of 10 species in the green house. In combination, the plastid and nuclear data obtained for multiple accessions representing most species and the molecular clock dating and the ecological information coming from the mapping effort provide a modern understanding of the evolution and species relationships in *Coccinia*.

Material and methods

General morphology

During this study I examined 2800 herbarium specimens from 33 herbaria (B, BM, BR, C, COI, DSM, EA, FR, FT, G, GAT, GOET, H, HBG, HEID, JE, K, L, LISC, LISU, M, MO, MSB, NHT, P, S, U, UBT, UPS, W, WAG, Z, ZT). Ten species, *C. abyssinica*, *C. adoensis* var. *jeffreyana, C. grandiflora*, *C. grandis*, *C. hirtella*, *C. megarrhiza*, *C. microphylla*, *C. rehmannii* with two varieties, *C. sessilifolia* var. *sessilifolia*, and *C. trilobata*, were cultivated in green-houses of Munich Botanical Garden. Whenever possible, I performed crossing experiments. Morphological features were documented photographically and in the form of vouchers, with

47 specimens deposited in M. Field data were obtained on a trip to northeastern Tanzania in 2009 resulting in 28 *Coccinia* collections.

Phylogenies

For this monograph the phylogenic data of Holstein and Renner (2011a; b; GenBank accession numbers are given in Supplementary File 1) were augmented with several new sequences and new phylogenies were calculated, using RAxML v. 7.2.6 (Stamatakis 2006) and MrBayes v. 3.2 (Ronquist et al. 2012). The substitution model was GTR+Γ as used before, and 1000 ML replicates were used to infer statistical support for the nodes via bootstrapping. For Bayesian analysis, four chains were run with 2,000,000 generations, with a sampling frequency of 1000. The first 25% of the trees were discarded as burn-in, and the rest was plotted as 50% majority rule consensus using FigTree 1.3.1 (http://tree.bio.ed.ac.uk/software/figtree/). Gaps in the plastid matrix occurring in more than one accession were coded as “0”, “1”, or “?”, with “?” when data were missing or when shorter gaps were coded in the same place, but in different accessions.

Distribution maps

Of the examined specimens, I geo-referenced 1633, mapped these in Google Earth (Google Inc., Mountain View, CA, USA), and imported them into DIVA-GIS 7.1.6.2 (http://www.diva-gis.org). Political administrative borders were taken from GADM v.1 (Jan 2009) or v.2 (Jan 2012) (http://www.gadm.org/) and elevation data (1 km resolution) from CGIAR Consortium for Spatial Information (Jarvis et al. 2008). The geodetic datum for the maps is WGS84; the projection in each case is equirectangular.

Taxonomic problems and history

The name of the type species

Up to the 21st century (e.g., Bulbul et al. 2011; Hussain et al. 2011), there has been quite a lot of confusion about the valid name of the species that is now called *Coccinia grandis*. Wight and Arnott (1834) established the genus *Coccinia*, with the name based on the scarlet-red fruits of a species that Wight had collected several times during his 13-year stay in South India (Stafleu and Cowan 1988). The name of the only species they described in their new genus, *Coccinia indica* Wight & Arn., is illegitimate since they included *Bryonia grandis* L., of which they ought to have adopted the epithet (Art. 52.1 ICBN). The illegitimacy of *Coccinia indica*, however, does not affect the legitimacy of the genus name *Coccinia* (Art. 42.2), although there was also some confusion about which genus name to use (see chapter Connecting Africa and Asia). Wight and Arnott also synonymized two citations of *Bryonia palmata* L. However, they were were not sure, whether these should be included (indicated by a question mark) and are thus not valid (Art. 52.2 N1). In 1845, Voigt published the correct combination *Coccinia grandis* (L.) Voigt with a description exactly matching *Bryonia grandis*.

Although *C. indica* is not valid, and the problem seemed to have been solved, a third name was brought into discussion by Cogniaux. He thought that *Bryonia cordifolia* L. and *Bryonia grandis* L. referred to the same species, as Linnaeus cited Rumphius' *Vitis alba indica*, a *C. grandis*, under *Bryonia cordifolia* (Linnaeus 1763). Hence, Cogniaux created a more broadly circumscribed *Coccinia cordifolia* (L.) Cogn. (1878). However, Linnaeus described *Bryonia cordifolia* (1753) citing his description from his Flora zeylanica number 354 (1747), and only in the 2nd and 3rd edition of his *Species plantarum*, Linnaeus also synonymized Rumphius' *Vitis alba indica* (1747). Cogniaux therefore erred, when he stated that Linnaeus had based his *B. cordifolia* on Rumphius' figure.

Connecting Africa and Asia

Whereas the genus name *Coccinia* was applied to an apparently Asian species, the African species were described independently. Although the similarity of *Coccinia grandis* and the South African *Cephalandra quinqueloba* (Thunb.) Schrad. ex Eckl. & Zeyh. was perceived before (Edwards 1815), it was more than 50 years later that Naudin (1866b) recognized that *Coccinia* (Wight and Arnott 1834) and *Cephalandra* Schrad. ex Eckl. & Zeyh. (1836–7) were in fact synonymous. This was widely accepted, but for unknown reasons, Naudin assumed that the name *Cephalandra* had priority over *Coccinia* and hence named the transferred species *Cephalandra indica* (Wight & Arn.) Naudin. Although Naudin's error regarding the priority of the generic names (aside from the illegitimacy of the epithet) was clarified one year later (Ascherson 1867), it produced some confusion (Hooker 1871; Kurz 1877; Clarke 1879), which was discussed and clarified again by Cogniaux (1878).

Coccinia palmata – 120 years wrongly applied

When Wight and Arnott published *Coccinia indica* they also tentatively included the citation of *Bryonia palmata* L. Although without relevance for the genus *Coccinia* itself, it lead to further complications. One year after Voigt's publication of the correct combination *Coccinia grandis*, Roemer (1846) also recognized the missing combination and that Linnaeus' *B. palmata* and *B. grandis* indeed referred to different species. Roemer treated them, amongst other species, as *C. grandis* (L.) M.Roem. (nom. illeg.) and *C. palmata* (L.) M.Roem.

Naudin (1859; 1866a) considered *Bryonia palmata* L. and hence *Coccinia palmata* (L.) M.Roem. a synonym of *Bryonopsis laciniosa* (L.) Naudin, a species fom the Old World tropics. However, *Bryonopsis* Arn. (1841) is an illegitimate name, as Rafinesque already used this name erroneously instead of *Bryopsis* J.V.F.Lamouroux for a green algae (Rafinesque 1814; fide Merrill 1949). It was almost 150 years later, that Jeffrey (1962) recognized Naudin's application of the illegitimate name and lectotypified and transferred *Bryonia palmata* into *Diplocyclos* where it still resides today as *D. palmatus* (L.) C.Jeffrey. Hence, *Coccinia palmata* (L.) M.Roem. is a synonym of *Diplocyclos palmatus*.

In addition to the name *Coccinia palmata* (L.) M.Roem., which was cited by Naudin for the last time, there is a different species from South Africa, which was described with the name *Cephalandra palmata* E.Mey. ex Sond. (Harvey and Sonder 1861–1862). Cogniaux (1881) accepted this species in *Coccinia*, overlooking *Coccinia palmata* (L.) M.Roem. He thus created an illegitimate *Coccinia palmata* (E.Mey. ex Sond.) Cogn., which has been used for this species since then. Holstein and Renner (2010) called attention to this erroneous usage by bringing the correct name, *Coccinia mackenii* Naudin ex C. Huber, back in mind.

The rainforest species of *Coccinia*

The inclusion of the African rainforest species of *Coccinia* to this genus was not very obvious as e.g. racemous female flowers only occur in rainforest species. Nineteenth century colonialism brought extensive new material (Hutchinson and Dalziel 1927) to London and Paris. George Bentham and J. D. Hooker tried to put the material in order for their Genera plantarum (1867). Hooker, working on the Cucurbitaceae, put attention to the tendrils being simple or divided for generic delimitation. He described *Staphylosyce barteri* Hook.f. as only element of the monotypic genus, *Staphylosyce*, bearing bifid tendrils. He also regarded the long peduncled racemes of the *Cephalandra* species as contrast to the short shoot-like racemes in another new genus *Physedra* Hook.f., which included one species that now belongs to *Coccinia*. Cogniaux (1881) then synonymized *Staphylosyce* under the simple-tendrilled *Physedra*, weakening the taxonomic value of the tendrils. After he transferred *Staphylosyce/Physedra barteri* into *Coccinia*, Keay (1953) left *Physedra* with its original two species, *P. heterophylla* Hook.f. and *P. longipes* Hook.f., and several newly described ones. Jeffrey (1962) indirectly chose the type species of *Physedra* by separating *P. longipes* as a new genus: *Ruthalicia* C.Jeffrey. However, Jeffrey erred by stating that Keay transferred *Physedra heterophylla* to *Coccinia* by synonymizing Hutchinson and Dalziel's *Physedra barteri*, since they explicitly excluded Hooker's *Physedra heterophylla*. The transfer of *Physedra heterophylla* to *Coccinia* has been published by Holstein and Renner (2010).

Monique Kéraudren, who worked on western Central African Cucurbitaceae, thought that *Coccinia*/*Physedra barteri* and *P. heterophylla* are synonymous. Unfortunately, she mixed up the long subulate calyx lobes of *P. heterophylla* as character for *C. barteri*. Thus, she described a specimen with short calyx lobes and flowers in long racemes as a new species, *Coccinia subhastata* Keraudren, and separated the specimens with few-flowered racemes as *C. keayana* R.Fern. *Coccinia keayana*, however, does in fact not occur in that region. Holstein and Renner (2010) clarified the confusion and synonymized *C. subhastata* under *C. barteri*. The scarcity of good characters in the West and Central African rainforest *Coccinia* species, as well as the high morphological diversity (Holstein and Renner 2011a) in this group makes the trouble well comprehensible.

Morphology and anatomy

Habitus

Coccinia species are perennial climbers or creepers. The lignification of the mature shoots differs among the species from unlignified to completely lignified. Climbing is enabled by tendrils, which are either simple or bifid. Tendril development in young plants is delayed and starts in *C. abyssinica* after the 6th node (Getahun 1974b). The tendril arms are only rarely equally sized, as one is usually much smaller; true dichotomy of tendrils is not known from *Coccinia*. Whether a species has simple or bifid tendrils is often not fixed, but there is a strong predominance of one kind. Bifid tendrils regularly occur or are predominant in *C. grandiflora* Cogn., *C. heterophylla* (Hook.f.) Holstein, *C. hirtella* Cogn., *C. intermedia* Holstein, *C. mackenii* Naudin ex C. Huber, *C. mildbraedii* Gilg, *C. racemiflora* Keraudren, *C. schliebenii* Harms, and in some morphs of *C. barteri* (Holstein and Renner 2011a). Strikingly, *Coccinia* species with bifid tendrils occur in rather humid habitats. This suggests an adaptive advantage, eventually because more tendril arms increase the stability, as the leaves of rainforest species are larger and coraceous and are therefore heavier than leaves of species from drier habitats.

Some species are regularly described as having simple tendrils in floristic treatments, but they may bare bifid tendrils such as *C. sessilifolia* (N.Holstein 13) and *C. senensis*

(H.J.Schlieben 5745 in B, K, MO duplicates). *Coccinia adoensis* has bifid tendrils even in some type specimens (e.g. G.H.W.Schimper 166 in BR888678 and on the sheet with a drawing in K) and is still listed as simple-tendrilled. All three species with this polymorphism, however, have predominantly simple tendrils. Interestingly, these species are also closely related to species with predominantly bifid tendrils (Holstein and Renner 2011a): *C. sessilifolia* with *C. hirtella* and *C. mackenii*, and *C. adoensis* with *C. grandiflora* and *C. schliebenii*.

Roots

Coccinia species have perennial roots. Most (all?) of the species lignify at the base and most of them produce hypocotyl tubers (Fig. 1a). Some species, such as *Coccinia adoensis* and *C. grandiflora* (and most likely also *C. senensis* (Klotzsch) Cogn. and *C. schliebenii*, however, produce globular subterranean root tubers, much like potatoes, but smaller in size (Zimmermann 1922b; own observation). Root tubers in *Coccinia adoensis* are likely to be an adaptation to fire, as this species predominantly occurs in woodlands. In contrast to rather mild savanna fires, woodland fires produce temperature rises of 60°C in 0–3 cm depth (Bradstock and Auld 1995; Gignoux et al. 1997), so vegetative buds near the ground (hemicryptophytes) might be damaged, whereas root tubers (geophytes) have a higher chance of survival.

Coccinia grandis and *C. barteri* produce adventitious roots, if stems touch the soil (Fig. 1b). *Coccinia hirtella*, and *C. sessilifolia* and their F1 hybrids with *C. grandis* seem to lack this ability. Adventitious roots also occur along the hypocotyl of *C. abyssinica* seedlings (Getahun 1974b). Getahun reports tetrarch vascular bundles in the primary roots of *C. abyssinica* seedlings and di- to triarch bundles in secondary roots.

Hypocotyl and shoots

Many species, such as *C. abyssinica* (Lam.) Cogn., *C. grandis*, *C. hirtella*, *C. megarrhiza* C.Jeffrey, *C. microphylla* Gilg, *C. rehmannii* Cogn., *C. sessilifolia*, and *C. trilobata* (Cogn.) C.Jeffrey, produce a lignified tuber that is derived from the hypocotyl (Zimmermann 1922b; own observation, Fig. 1a). The tuber, at least of some species, contains starch as storage nutrient (Getahun 1974a). It develops during the first season, and lignification may begin as soon as the appearance of the first tendrils, such as in *C. abyssinica* (N.Holstein 132). Some species, such as *C. adoensis* and *C. grandiflora* (and most likely also *C. senensis* and *C. schliebenii*) do not produce hypocotyl tubers, but root tubers. In *C. adoensis* var. *jeff-*

reyana the hypocotyl is very short (N.Holstein 130), which prevents the development of a tuber. Whether West and Central African forest species produce tubers is unknown.

Each plant produces one to several shoots, which can persist or die back completely during dry season or due to fire or grazing. *Coccinia microphylla* shoots can lignify completely and produce short green branches with flowers and small leaves during dry season (Fig. 2a), whereas shoots of *C. sessilifolia* do not lignify at all. The shoots of *C. grandis* can become slightly succulent. The length of the shoots varies from 70 cm in *C. microphylla* to 20 m in *C. grandiflora* and *C. mildbraedii*. Zimmermann (1922a) reports a stem of *C. grandiflora* with 6 cm in diameter. Usually, the bark of the hypocotyl tuber and the shoots is in (light) grayish colors. Fresh shoots and twigs usually are deep green to brownish green, sometimes speckled with pale to whitish pustules. In *C. abyssinica* and *C. megarrhiza* the shoots and tendrils can turn purple during maturity. *Coccinia sessilifolia* produces glaucous shoots that bear a waxy bloom (Fig. 2b). The indument of *Coccinia* species, if present, is composed of simple, oligo- to multicellular eglandular trichomes up to 2 mm in length. The long trichomes consist of oblong cells that may appear articulate when dried (Fig. 3a). Shorter trichomes can be lineal to conical (Fig. 3b). Sometimes, trichomes have a thickened base, which, when the trichomes brake off appear warty. The density of the trichomes is often increased on the nodes. Trichome type and length on shoots are like the one of the abaxial side petioles, but usually less dense. Young shoots often exhibit short (< 0.5 mm), weak trichomes, even in species that are later glabrous, e.g. in *C. grandis* or *C. sessilifolia*. Glandular trichomes are rare, few-celled, not visible with the naked eye, and not perceptible. They have been found, e.g. in *C. grandiflora* and *C. grandis* (own observations; Thanki 1989; Fig. 3d). Glandular trichomes are also observed in young stems of *C. abyssinica* (Getahun 1974b), which is usually covered with long multicellular eglandular trichomes.

Cotyledons

Zimmermann (1922b) reports epigeous cotyledons for *C. grandiflora* and *C. grandis*, of which the latter is confirmed by own observations (Fig. 1a). Also in *C. abyssinica*, *C. adoensis, C. microphylla*, *C. rehmannii* var. *littoralis*, and *C. sessilifolia* epigeous cotyledons occur. The hypocotyl and cotyledons of all observed taxa are glabrous, the cotyledons are elliptical to obovate, and have an entire margin. The cotyledonous apex has a pale marking and is obtuse to retuse. The cotyledons are slightly fleshy and green, which is also observed in those of *C. abyssinica* (Getahun 1974b). Getahun reports that the prominent veins and the margin on lower cotyledon lamina in *C. abyssinica* are covered with multicellular trichomes.

However, prominent veins in *C. abyssinica* cotyledons cannot be confirmed, and if multicellular trichomes occur, then they are not visible by naked eye. The first node in this species bearing a normal leaf though was situated just after the two cotyledons emerged (N.Holstein 132, Fig. 4a).

Leaves

The leaves of *Coccinia* species are simple, alternate, and on each node paired with a tendril, except for the first nodes. Leaves of all species are petiolate, except for *C. sessilifolia* var. *sessilifolia*, which only develops petioles when young (N.Holstein 131, Fig.4b) or rarely subsessile leaves when older. Full petioles in this species are only realized in *C. sessilifolia* var. *variifolia* (A.Meeuse) Holstein. In *C. quinqueloba* and *C. senensis*, subsessile leaves are common; in the other species leaves are usually distinctly petiolate. The petioles' surface can be glabrous, at maturity speckled with hyaline to white cell clusters (*C. grandis*, *C. heterophylla*, *C. intermedia*, *C. rehmannii*, C. *samburuensis, C. senensis*, *C. subsessiliflora*), or have an indument. The petiole contains several vascular bundles, which are arranged in a U-shape (Fig. 5a). However, Hussain et al. (2011) report a ring of vascular bundles in C. *grandis*. The adaxial side of the petiole often bears two ridges above the "lateral" vascular bundles (Fig. 5b). These ridges merge into the leaf margin and usually bear trichomes (Fig. 5b, c). The abaxial side of the petiole shares its indument with the lower leaf lamina, at least at the base of the veins (Fig. 5c).

The venation in *C. grandis* is reticulate and the mid rib is reported to contain three bicollateral vascular bundles (Hussain et al. 2011). Reticulate venation can be confirmed for all *Coccinia* species but *C. ogadensis*, in which only the central vein in each lobe is visible.

Young leaf buds often bear a dense indument, even in species that are glabrous at maturity. The leaf lobes are lineal, elliptical, ovate to triangulate. The incision depth of the lobes can be consistent (*C. ogadensis*, *C. subsessiliflora*) or highly variable (*C. adoensis*, *C. grandis*), even within a single individual. In species with variable degree of lobation, young leaves tend to be not or shallowly lobed (e.g., *C. grandis*, *C. megarrhiza*, *C. rehmannii* var. *littoralis*, *C. sessilifolia*). The leaf margin usually is beset conspicuously with small teeth and often bears trichomes (Fig. 3b), even in otherwise glabrous species (e.g., *C. grandis*, *C. sessilifolia*). The teeth are at the apex of lobes, lobules and smaller orders of serration or along the entire margin. Ther term "dentate" (toothed) is therefore ambiguous in literature describing *Coccinia*, as it might also refer to the margin morphology (Stearn 2004). The teeth are often pale, but can also be colored, esp. when dry, such as in *C. abyssinica*, *C. grandis*, *C. intermedia*, *C. longicarpa*, *C. megarrhiza*, and *C. samburuensis* (Fig. 6a). The coloration of teeth is inconspiuous in young plants and develops during maturation (as observed in *C. abyssinica*, *C. grandis*, and *C. megarrhiza*). The teeth are interpreted as hydatodes by Zimmermann (1922a), as he observed water drops in *C. grandis* and *C. trilobata* on the teeth of the 2nd order (except those of the tip of the lobes) in the morning.

The upper leaf lamina is often covered with transparent to white pustules, which contain cystoliths (Avetta 1894; Solereder 1899; Zimmermann 1922a; own observation). The pustules consist of up to 25 cells in *C. mackenii* (Avetta 1894), but are larger and denser in glabrous species from dry habitats (esp. *C. ogadensis*). As they develop over time and are smaller and less visible in forest species, one can assume that the pustules are an adaptation towards protection against high solar irradiation. The cystoliths consist of $CaCO_3$, inferring from heavy gas development when acetic acid is applied. This can be observed in *C. grandis*, *C. hirtella*, and *C. sessilifolia,* hence also when the pustules are not conspicuous as in the latter two species. The pustules may form the base of small trichomes, such as in *C. adoensis* var. *jeffreyana* (Fig. 3b) or *C. microphylla*. In some species, the upper lamina is usually covered with an indument (*C. hirtella*, *C. schliebenii*, *C. senensis*, and *C. trilobata*), but it may also be reduced, and other species rarely exhibit a trichome-bearing upper lamina, e.g. *C. adoensis*. The trichomes are in each case simple, < 1 mm, and whitish. The veins on the upper lamina are either glabrous by naked eye or are covered with small < 0.5 mm long simple trichomes. Zimmermann (1922a) observed in *C. grandis* that the glabrous surface of the lamina is only slightly wettable, whereas a drop of eosine disperses along the veins rapidly. Zimmermann argues that these “capillary drainage lines” might serve to transport water to the hydatodes during the dry season.

The lower leaf lamina is always paler than the upper side and can be glabrous or bear an indument. The highest density of the indument can be found on the prominent veins (Fig. 5c). The indument on the lower leaf lamina and the abaxial petiole can consist of eglandular oligo- to multicellular trichomes. The trichomes are appressed or upright (Fig. 5c), usually filiform, sometimes also narrow conical (i.e., *C. abyssinica*). Filiform trichomes are straight, curved, or sinuate. Long filiform trichomes often appear articulate when dry due to sunken lateral cell walls (Fig. 3). Dry trichomes are hyaline, whitish, beige, or yellowish. The lower lamina often displays deeply colored to dark green to blackish glands (Fig.6b). The glands usually occur at the base of the leaf between the veins, sometimes also between secondary ramifications (*C. grandis*) or along the main veins (*C. grandiflora*).

Probracts and bracts

In addition to the foliose leaves, most *Coccinia* species have bracteose prophylls on sterile nodes, which are called “probracts” (Zimmermann 1922b). The probracts can be up to 5 mm long, but also rather small (< 1 mm) or caducous. The first nodes of the seedling lack probracts, but they are developed after a few nodes. The shape of the probracts is ovate and entire with a round to acute apex. They are often spoon-like presenting the lower surface (e.g., *C. adoensis*, C*. barteri*, *C. grandis*, *C. megarrhiza*, *C. sessilifolia*; Fig. 3a, 7b), or they are folded in the middle with a prominent keel (*C. grandiflora*; Fig. 7). Probracts can be glabrous or bear short (< 1 mm) trichomes, and bear extranuptial glands on the lower surface (Fig. 7; Okoli and Onofeghara 1984).

Bracts (leaves subtending inflorescences or flowers), if present, look like the probracts. Bracts below inflorescences are as large as probracts, bracts below flowers tend to be smaller. Bracts can be present or absent, the latter being an indicative character for some species.

In rare cases, probracts and bracts can be leaf-like (e.g., N.Holstein 126, Fig. 2b; P.C.M.Jansen 2065; H.Wanntorp & H.E.Wanntorp 1159) supporting that the (pro-)bracts are derived from usual leaves.

Extranuptial glands

The conspicuous glands on the lower leaf lamina, probracts, and bracts are of the Benincasa-type (sensu Zimmermann 1932), meaning that they are flat and consist of several layers of secretory cells, which are surrounded by a single-layered sheath (Okoli and Onofeghara 1984; Ilyas 1992; own observation). The sheath in *C. microphylla* and *C. trilobata* is lignified (Zimmermann 1922b). However, Zimmermann (1932) cites Nieuwenhuis von Üxküll-Güldenbandt, who supposedly reported that the sheath in *C. grandis* is suberinized, but I did not find such a statement in the citation. On the other hand, Schrödter (1926) finds that young sheaths in *Luffa aegyptica* are lignified, but become suberinized with age, so the difference might be explained by different stages. Chakravarty (1948) interpretes the sheath as filter tissue that is surrounded by an “external osmotic tissue”. Also Ilyas (1992) interpretes these radially elongated cells as secretory and notes that they have a connection to the vascular strand. However, Okoli and Onofeghara (1984) find that the glands in *C. barteri* are too distant to be interpreted as vascularized. Zimmermann (1922b) observes intermediate forms between few-celled, stalked glandular hairs and the Benincasa-type glands in *C. microphylla* and *C. trilobata*, including the sheath that forms the base of the protruding glandular tissue. The glands secrete a clear, rarely slightly colored, sweet-tasting exudate (own observation). In *C. grandis* the exudates contains sucrose, glucose, fructose, alanine, tryptophane, threonine, and an unidentified amino acid (Ilyas 1992).

Peduncles and pedicels

Male flowers mostly occur in racemes, which are usually accompanied by 1–2 solitary flowers on the same node (Fig. 2b). The first flowers in male plants of *C. hirtella*, *C. rehmannii*, and *C. sessilifolia* are always solitary, racemes appear later in the course of the flowering season, although racemes are generally rare in the first species (own observation). If solitary flowers and racemes are produced on the same node, then the solitary flower(s) precede(s) those of the racemes in terms of time of maturity. The trigger to produce racemes instead of or additionally to solitary flowers is not known. The racemes bear up to 35 flowers (e.g., *C. pwaniensis*, *C. racemiflora*). Within the racemes, flowering starts at the basalmost branches. If the peduncle is reduced, flowers appear clustered on the node. In *C. grandis*, which usually produces single flowers only, flower clusters (short-peduncled racemes) rarely occur. This can be seen in plants from Ethiopia, Saudi Arabia, but also from Sri Lanka, so a geographical correlation does not seem to apply. The pedicels of solitary male flowers of *C. hirtella*, *C. megarrhiza*, and *C. rehmannii* exhibit a negative gravitropism. In creeping plants, pedicels that grow downwards in the beginning make a sharp bent upwards within the pedicel to present the flower erectly.

Female flowers are mostly solitary. In some species, female flowers are usually in racemes, such as in *C. heterophylla*, *C. keayana*, and *C. racemiflora*. Few-flowered female racemes or clustered flowers might also occur in *C. grandiflora*, *C. intermedia*, and *C. subsessiliflora*. In *C. barteri*, female flowers can be solitary or in few- or many-flowered racemes. Two female flowers per node have also been observed in *C. microphylla*. The pedicels of solitary female flowers are negatively gravitrop during flower development. After pollination, the pedicels of solitary female flowers of *C. grandis*, *C. hirtella*, *C. megarrhiza*, *C. microphylla*, *C. rehmannii*, and *C. sessilifolia* exhibit positive gravitropism. The downturn is not due to slackness caused by the weight of the developing fruit, but an active process, as the pedicels thicken and remain firm. However, only fertilized flowers turn downwards completely, as aborted flowers from mispollination never reach this state.

Perianth

The perianth of all *Coccinia* species is synsepalous and sympetalous. At the base, calyx tube and corolla tube are connected and form a perianth tube or funnel. Depending on the exsertion point of the staminodes in female flowers, parts of the tube form a hypanthium (e.g., *C. grandiflora*).

The calyx differentiates as a bulge (Fig. 6b) with usually 5 lobes, or only the lobes emerge from the perianth tube (Fig. 8). If the calyx emerges as a bulge, then it and the perianth tube are rather conspicuously differentiated from the corolla in terms of color. If only the calyx teeth emerge, then the color of perianth tube fades into a greenish color towards the receptacle, with the veins of the corolla remaining more intensely colored. Whether calyx and corolla are non-differentiated (congenital fusion) or postgenitally fused, is not known for *Coccinia*, but in *Echinopepon wrightii* (A.Gray) S.Watson the perianth tube is non-differentiated (Leins and Galle 1971). The outside of the perianth tube can bear longer trichomes with the type of the lower leaf lamina or the petioles (Fig. 9a). The calyx lobes are acute triangulate to subulate or lineal, rarely slightly lanceolate. The direction of the calyx lobes is erect, spreading, or reflexed, although they can be curved inwards (e.g., *C. rehmannii* var. *littoralis* (Fig. 9a) or outwards (e.g., *C. intermedia*). The color of the calyx lobes is more intense (green) than the perianth tube or the pedicel. In *C. grandis*, the tip of the calyx lobes is brownish to reddish, just as the teeth on the leaves and the corolla (Fig. 6a).

The petals of *Coccinia* species are fused at the base, usually for at least one third of the total length. Rarely, the petals are free down to the height of the calyx lobes (own observation in *C. megarrhiza*, *C. rehmannii* var. *rehmannii*, and *C. sessilifolia*). Perianth tube and corolla tube are often campanulate, rarely funnel-shaped or tubular. The perianth tube can be urceolate in *C. longicarpa*, *C. racemiflora* and sometimes in *C. barteri*. The tips of the (4–)5(–7) corolla lobes are rounded to acute with an apical tooth. The apical tooth can the colored, such as in *C. adoensis* var. *aurantica* or *C. grandis*, or inconspicuous. Outside, the perianth tube and the corolla is glabrous or covered with short (< 10 globose cells in *C. grandis*) trichomes. Inside, the corolla is covered with long trichomes (up to 20 cells in *C. grandis*), sometimes with glandular apical cell (Fig. 9b). The trichomes become shorter towards the receptacle. The inner side of the hypanthium of female flowers is glabrous and smooth, which suggests nectary tissue, in *C. grandiflora*, *C. grandis*, and *C. hirtella* (Fig. 10a). The size of the corolla does not differ conspicuously between staminate and pistillate flowers; pistillate flowers might be a bit smaller.

Androecium

In staminate flowers, the three stamens originate from the base of the perianth tube, and the filaments are fused to a central column (Fig. 9a). The fusion point sometimes leaves a small gap to the hollow receptacle center. This gap, however, can be filled with long multi-cellular trichomes (e.g. in *C. abyssinica* and *C. megarrhiza*). Rarely, the filaments can also be separate. The filaments are glabrous and white, greenish, yellowish, or orange. The number of vascular bundles in the stamens is disputed. Chakravarty (1954) reports in *C. grandis* five vascular bundles: two stamens have each two bundles, and the third stamen has a single bundle. Later research shows for the same species three vascular bundles with one per stamen (Bhuskute et al. 1986; Deshpande et al. 1986). In *C. hirtella* each stamen contains a single vascular bundle.

The anthers together form a globose head (Fig. 9b). Each anther is bithecate; sometimes one can be monothecate (Chakravarty 1954; Bhuskute et al. 1986). Each theca is sinuate. Deshpande et al. (1986) report a bi-layered fibrous endothecium and a secretory tapetum, which they found as a difference to *Momordica charantia* L.

In pistillate flowers, the three, now free, stamens are reduced to staminodes that originate from the interior wall, forming a hypanthium. Introrsely, the staminodes of *C. grandiflora*, *C. grandis* and *C. hirtella* bear long, multicellular trichomes, except for the apex, extrorsely the staminodes are glabrous (Fig. 10a). The anthers of the staminodes are strongly reduced to a slightly yellowish spot at the apex in *C. grandis* and *C. hirtella*. The staminodes of *C. megarrhiza* bear long multicellular trichomes introrsely and laterally, but are glabrous extrorsely.

Pollen

Pollen in *Coccinia* species show little diversity. The pollen is oblate-spheroidal to prolate with a reticulate exine (Table 1). Additionally, the pollen of *C. hirtella*, *C. pwaniensis* (Holstein and Renner 2010), and *C. trilobata* is prolate, the exine texture is unknown. The sampling of the examined species covers all clades and suggests uniformity in shape and exine texture, which negates systematic value of pollen in *Coccinia*. The color is yellow in *C. abyssinica*, *C. grandiflora* (Zimmermann 1922b; and own observation), *C. grandis*, *C. hirtella*, *C. megarrhiza*, *C. microphylla*, *C. rehmannii*, *C. sessilifolia*, and *C. trilobata*, and orange in *C. adoensis* var. *aurantiaca*. Zimmermann (Zimmermann 1922b) reports that pollenkitt of *C. grandiflora* contains a yellow colorant that is soluble in peanut oil, but not in water and only slightly in heated chloral hydrate solution. It changes its color in concentrated sulfuric acid into blue, in Lugol's iodine (I_2KI) into green, and in osmic acid into brown. Like in several other cucurbit species, in vitro germination of *C. grandis* pollen increases from pH = 7 towards alkalinity and is maximal at pH = 8.5 (Zaman 2009).

Table 1 Pollen characters in Coccinia species.

Species	Shape	Size (P × E) [µm]	Exine texture	Source
C. abyssinica	Prolate-sphaeroidal	60–70 × 56–65	Reticulate	(Marticorena 1963)
	Oblate-sphaeroidal to sphaeroidal	76 × 81	Reticulate	(Khunwasi 1998)
C. adoensis	Prolate	66–73 × 45–50	Reticulate	(Marticorena 1963)
	Prolate-sphaeroidal	72 × 61	Reticulate	(Khunwasi 1998)
C. barteri	Prolate	70–80 × 50–60	Reticulate	(Marticorena 1963)
	Prolate-sphaeroidal	71 × 58	Reticulate	(Khunwasi 1998)
C. grandiflora	Prolate			(Zimmermann 1922b)
C. grandis	Prolate	60–63 × 34–40	Reticulate	(Marticorena 1963)
	Prolate-sphaeroidal	58 × 52	Reticulate	(Khunwasi 1998)
	Prolate	47.61–64.62 × 35.91–44.80	Coarsely reticulate	(Perveen and Qaiser 2008)
	Subprolate to prolate	34–52 × 28–35	Reticulate	(Awasthi 1962)
	Prolate	41.20 ± 0.61 × 34.00 ± 0.45	Reticulate	(Datta 1988)
C. megarrhiza	Oblate-sphaeroidal to sphaeroidal	92 × 92	Reticulate	(Khunwasi 1998)
C. mildbraedii	Prolate	55–60 × 35–41	Reticulate	(Marticorena 1963)
C. sessilifolia	Prolate-sphaeroidal to prolate	70 × 58	Reticulate	(Khunwasi 1998)

Gynoecium

Pistillate flowers are epigynous and have three (rarely two) carpels. The ovary is narrowly spindle-shaped, oblong to globose. The surface is smooth or warty; it is glabrous or bears the indument of the pedicel. The style is often greenish-white or pale-yellowish; the stigmas are frequently in yellowish colors and covered with long trichomes. Each stigma in *C. grandi-*

flora, *C. grandis*, *C. hirtella*, *C. megarrhiza*, *C. rehmannii*, and *C. sessilifolia* is U-shaped with the ends of lower sides of the arms touching each other. The stigmatic branches can be long and free, such as in *C.* grandiflora, *C. grandis* and *C. rehmannii* var. *rehmannii* (Fig. 10b), or short and bulbous, such as in *C. hirtella*, *C. megarrhiza* (Fig. 10c), *C. microphylla*, and *C. sessilifolia*.

The placentation of the ovules in *Coccinia* is involute, which is also discussed for other Cucurbitaceae (Leins and Galle 1971). The funicle seemingly attaches at the outer wall, but attaches to a sept coming from the axis (Fig. 11a–c), which itself is connected to the outer wall again. The axis-wall sept, however, might be reduced during ripening, but a thorough study at least in *Coccinia* is not available.

The anatomy of the ovules is barely surveyed in *Coccinia*. In *C. abyssinica* and *C. grandis*, the ovules are reported to be anatropic, bitegmic, and crassinucellate (Zahur 1962; Getahun 1973). Anatropic ovules also occur in *C. hirtella* (Fig. 11a). The position of the ovules is horizontal in *C. grandis* (Kirkwood 1904), *C. hirtella* (Fig. 11a), and *C. megarrhiza* (Fig. 11b) with the micropyle facing outwards. Horizontal ovules are regularly reported in the Benincaseae and the Cucurbiteae (Schaefer and Renner 2011a).

In staminate flowers, a pistil is not developed, as the stamens fuse to a central column. The pedicel is narrow and reaches the perianth, and there is no indication of even a thin (sterile) inferior ovary in the flower.

Female gametophyte development and embryology

The development of the embryo has only been investigated in *C. grandis*. Chakravorti (1947) and Zahur (1962) report the female gametophyte development according to the *Polygonum*-type. Both observe that the synergides possess hooks instead of the filiform apparatus. Chopra (1955) describes the developing endosperm as of nuclear type, which is confirmed by Chakravorti (1947). By formation of a large central vacuole, the nuclei become displaced to the periphery. After the endosperm becomes cellular, the often lateral chalazal haustorium remains coenocytic. Then, the haustorium becomes cellular with multinuclear cells except for the apex (Chopra 1955).

Fruits

The fruits are many-seeded berries, which vary in size and shape between species (in *C. grandis* and in *C. rehmannii* also within). The smallest fruits occur in *C. rehmannii* var. *rehmannii* and *C. microphylla* bearing globose berries of down to 1 cm in diam. at maturity.

However, in both species larger globose fruits (up to 2.5 cm in diam.) and in *C. rehmannii* also ovoid fruits may occur, in the latter case especially in more humid habitats. The largest fruits occur in *C. samburuensis* and the rainforest species *C. grandiflora*, *C. longicarpa*, *C. mildbraedii*, and *C. schliebenii*, which have long elliptical to cylindrical (sausage-shaped) fruits with up to 20 cm length and up to 2.5–3 cm in diameter.

Immature fruits often display white or pale-green (*C. hirtella*, *C. sessilifolia*) or dark green (*C. adoensis*) longitudinal mottling or lines, even when the ovary and the ripe fruit is single-colored (Fig. 12a, b). In the *C. rehmannii* clade the white spots or lines become surrounded by a dark green halo during ripening. Rarely, if no white mottling develops, e.g. in *C. microphylla*, dark green spots develop nevertheless. In any case, the mature fruit is uniolor red (Zimmermann 1922b; and own observation). Ripening usually occurs from green with or without mottling via yellow to orange to the final coloration. The color changes from the apex of the fruit on, independent of the position (hanging vs. horizontal) in *C. sessilifolia*. In *C. megarrhiza*, pendulous fruits ripen from the apex to the base, which sometimes remains green even when apex already turns soft. In lying fruits of *C. megarrhiza*, ripening does not proceed from the apex, but starting from point that is closest to the source of either warmth or light (own observation). The degree of the yellow to orange ripening zone varies. In *C. sessilifolia*, fruits turn red rather directly, whereas the yellow zone is better visible in *C. grandis*. Unripe collected fruits of *C. grandis* tend to turn yellow outside and pink to red inside (Imbumi 2004). Mature fruits are in deep red colors (hence the genus name) or orange-red. Rarely, a white longitudinal mottling is described in ripe fruits (e.g., *C. mackenii*).

Immature fruits are glabrous or bear the indument of the ovary. Towards ripening, the indument is usually reduced. The exocarp of *Coccinia* fruits is rather papery thin and bears a waxy bloom when ripe. The endo- and mesocarp are red, fleshy and soft (Fig. 11b, c). The pulp is nerved with a dense network of tubular tissue. Shah et al. (1983) report such a network consisting of sieve tubes in *C. grandis*. The sieve tubes are not connected to the main vascular strands and are filled with a proteinaceous material. The authors suggest that the sieve tube network aids nutrient transport during the rapid growth of the fruit.

Seeds

The seeds (Fig. 13) in *Coccinia* species are beige to grayish with a small margin, which often has a darker coloration. The shape is more (esp. in the *C. rehmannii* clade) or less asymmetrical ovate (especially *C. adoensis*, *C. pwaniensis*, and *C. senensis*). The surface is flat, esp. in the *C. rehmannii* clade to lenticular (esp. *C. adoensis*, *C. pwaniensis*, and *C. senen-*

sis). The size varies from 4.5–7 × 3–5 × 1–2 mm (L/W/H). Seed numbers per fruit vary drastically from about 10 (*C. microphylla*) to c. 100 (+ c. 20 infertile) in *C. sessilifolia* (own observation). Large fruited species might contain more seeds.

Detailed observations of the seed anatomy have been made by Getahun (1973) for *C. abyssinica* and by Chakravorti (1947) for *C. grandis.* Getahun describes the mature seed as consisting of the embryo, a membrane-like structure (pellicle) closely adhering the embryo, but separated from the hard testa. However, Chakravorti does not recognize a pellicle in *C. grandis*. Both authors agree in that the inner integument disappears and the testa develops solely from the outer integument. The testa of *C. abyssinica* is described as consisting of four layers (from center outwards): (1) a thin-walled parenchyma, (2) a sclerenchyma of macrosclereids, (3) a thick-walled parenchyma, and (4) an epidermal layer. The outermost layer, the epidermis, is disintegrated, leaving the cell walls as slender rods of 500 µm length. This has been also noticed in several species, and the surface has been described as a fibrillose testa (Jeffrey 1967; Kéraudren 1967). De Wilde et al. (2011) also interprete the seed surface of *C. grandis* as disintegrated, pulpy, radiately striate exotesta.

Getahun contrasts his observations with those of Chakravorti (1947) in *C. grandis*, but the seeds are in fact similar, but not properly described by Chakravorti. Chakravorti draws a four-layered testa, but does not name the innermost layer that has the same hatching as the third layer, which he describes as “cells with thickened walls”. This is what Getahun calls parenchyma. Chakravorti’s outermost layer, the epidermis, consists of radially elongated cells with thin walls. These cells have likely just not yet been disintegrated as observed by Getahun. The only difference between both observations is the second layer, which consists of macrosclereids in *C. abyssinica* and of radially slightly elongated cells with thin walls in *C. grandis*. These different observations are explainable by two possibilities: 1) different developmental stages of the seeds since Chakravorti surveys the seed development, so the layers are immature, while Getahun surveys mature seeds and germination, or 2) different staining. Chakravorti uses haematoxylin alone, which does not stain lignified cell walls, whereas Getahun uses haematoxylin with safranin as counter stain, which makes lignin, and thus sclerenchyma, well visible (von Aufseß 1973).

The seeds in *Coccinia*, at least in *C. abyssinica* (Hora 1995), C*. grandis*, *C. hirtella*, *C. megarrhiza*, C*. microphylla, and C. sessilifolia* (own observation) are surrounded by a hyaline red juicy envelope (Fig. 11b). As the ovule is bitegmic (see above), and one might assume the hyaline envelope is the testa, Charkavorti (1947) observes that the juicy envelope is derived from carpellary tissue. However, Getahun (1973) does not recognize the hyaline hull in *C. abyssinica*, which is surprising as it also occurs in the closely related species *C. megarrhiza* and *C. microphylla*. Similar structures to the hyaline hull are also found in other Cucurbitaceae, esp. in *Momordica.* Van der Pijl (1982) interpretes these as “endocarp-pulpa” taking over the function of an aril for seed dispersal as the fruits of *Momordica* species dehisce in maturity. However, *Coccinia* fruits disintegrate and do not dehisce, e.g. in valves.

Germination

The seeds of *C. abyssinica* maintain a high germination rate (100%) after four years of storage at room temperature (Getahun 1973). However, time from watering until germinating increases from 4 days (1 year of storage) to 16 days (4 years of storage). Seeds of *C. grandis* are also able to germinate after four years of storage, but seeds of *C. ogadensis* Thulin (3 seeds tested) did not germinate after five years (own observation). Getahun (1973) reports that *C. abyssinica* seeds do not germinate below 10°C and above 35°C. In the latter case, he observes thermal damage to hypocotyls and primary roots. Optimum for germination in *C. abyssinica* is between 20 and 30°C. Optimal germination temperature for *C. grandis* is found to be 35°C, whereas temperatures < 23.5°C and > 40°C inhibit germination (Li et al. 2001). Germination rate of *C. abyssinica* seeds in the light is decreased by 35% compared to germination in darkness (Getahun 1973). In *C. sessilifolia*, seed viability declines after 9 months, and germination is maximum after 10–20 min smoke exposure or red:far red light treatment, followed by burying and a long-day cycle (Weiersbye and Witkowski 2003). Rotting of a crushed ripe fruit in water (for seed extraction) results in germination of two seeds in an artificial hybrid (*C. megarrhiza* ♀× *C. rehmannii* var. *littoralis* ♂) after 3 weeks of soaking. *Coccinia grandis* seeds do not need dormancy (Motooka et al. 2003); for the other species there is no information available.

Genome, chromosomes, and hybridization

Chromosomes and inheritance of sex

Coccinia is one of the few examples in the plant kingdom, in which at least one species has heteromorphic sex chromosomes (Ming et al. 2011). *Coccinia grandis* contains 22 autosomes plus 2 gonosomes. Female individuals have homomorphic XX, whereas male individuals have heteromorphic XY chromosomes. Although Kumar and Deodikar (1940) report males to have two large “X” chromosomes and females to have large X and a smaller Y, later studies (Chakravorti 1948; Kumar and Vishveshwaraiah 1952) reveal that males are heteromorphic and the Y is 2.5 (Bhaduri and Bose 1947) to 3–4 times longer (Guha et al. 2004) than the other chromosomes. Some years before Kumar and Deodikar, Sutaria (1936) reported $n = 12$ from pollen mother cells of *C. grandis*, without finding the large Y chromosome. Although scientists from India conducted some research for *C. grandis*, chromosome work in other *Coccinia* species is almost none-existing. McKay (1930) reports $n = 12$ for *C. hirtella*, without mentioning whether he studied a male or a female individual. Own chromosome counting (Tab. 2; Fig. 14b) supports McKay's report and rejects the existence of heteromorphic sex chromosome in *C. hirtella* males. This is also the case for *C. sessilifolia*. Two counts in the *C. rehmannii* clade reveal a reduction of chromosome number and the non-existence of a heteromorphic Y chromosome there.

Due to the sex chromosomes, sex in *C. grandis* by inherited in a Mendelian manner. However, Agarwal and Roy (1983) report that of 500 planted seeds only 181 (36.2%) turned out to be male, and they interprete that there might be a genetical mechanism to reduce the number of male plants. As they do not report XY females, the found difference might be explained by an increased lethality of XY embryos or Y-containing pollen due to deleterious mutations in the single X. The Y chromosome in *C. grandis* is dominant, as the presence a single Y always results in male phenotypes, disregarding the number of X chromosomes (Kumar and Vishveshwaraiah 1952; Roy and Roy 1971b; Agarwal and Roy 1975). Triploids of *C. grandis* with a $3n$ = XYY constitution are also male, but bear flowers in clusters, instead of the usually solitary ones and exhibit leaf deformations (Roy and Roy 1971b).

Evidence for Mendelian inheritance of sex in *C. hirtella* is not so clear, as the same plant can produce flowers of the differing sex in succeeding seasons. Two plants marked as female from observation of flowers and one individual marked as male produced flowers of the opposite sex in the following year, making *C. hirtella* functionally dioecious, but genetically hermaphroditic. On the other hand, there are several observations of flowers of the different sex in otherwise unisexual plants. Kumar and Vishveshwaraiah (1952) report a gynodioecious form of *C. grandis* that has homomorphic chromosomes (XX). Although the bisexual flowers are reported to develop, pollen grain development is arrested, and the male function remains suppressed. Roy and Saran (1990), however, report fully fertile hermaphroditic flowers in an otherwise female individual. Holstein and Renner (2011b) report a specimen of *C. intermedia* that bears male floral buds and female flowers and young fruits on the same nodes. This observation can be interpreted as 'leaky dioecy' (Baker and Cox 1984). Among the own cultivated plants, a male individual of *C. megarrhiza* produced a single female flower towards the end of the season (Fig.8). Although two male flowers on the same individual were open at the same time when the female flower was mature, the pollen sacs did not open. It is not known, whether this was a coincidence or whether there is a connection, e.g. to prevent selfing. Prevention of simultaneous flowering of both sexes on the same plant implies that leaky dioecy would not immediately aid the establishment of new distant populations, e.g. on different islands per se. It might require the establishment of several plants or clonal separation. In any case, the single female flower was receptive and was fertilized by another male *C. megarrhiza* plant derived from the same fruit as the “female” plant. The resulting fruit and seeds developed normally.

Table 2 Chromosome numbers of *Coccinia* species and sexes of surveyed individuals.

Species	Sex of individual	Chromosomes (2*n*)	Voucher
C. grandiflora	female	24	N.Holstein 114 (EA, M)
C. grandis	male	22 + XY (Fig. 14a)	N.Holstein 32 (M)
C. grandis	female	22 + XX	N.Holstein 25 (M)
C. hirtella	male	24 (Fig. 14b)	N.Holstein 29 (M)
C. rehmannii	male	20	N.Holstein 126 (M)
C. sessilifolia	male	24 (Fig. 14c)	N.Holstein 13 (M), N.Holstein 109 (M, M, M)
C. sessilifolia	female	24	N.Holstein 119 (B, M)
C. trilobata	male	20 (A. Sousa, pers. comm.)	N.Holstein & P.Sebastian 9 (M)

The susceptability of the dicliny has also been shown by X-radiation studies (Roy 1974; Agarwal and Roy 1983), which also resulted in the production of hermaphroditic flowers. Agarwal and Roy find hermaphroditic flowers on two plants with otherwise female flowers and a XX constitution. They also report the development of a normal fruit without mentioning the fertility of the pollen from hermaphroditic flowers, but interprete their finding as cleistogamy. However, fruit development without previous pollination (parthenogenesis) and pseudogamy from different genera as fructification stimulus is described by Lal (1973). True selfing from own pollen (in irradiated XX individuals) would mean that the Y chromosome is not important for fertile pollen development. Furthermore, it only carries at least one gene for suppression of the development of the female organs, and the occurrence of a second X suppresses pollen development in “normal” plants. Agarwal and Roy (1983) also report that X-ray dosages of 5 to 50 R [1.29×10^{-3} to 12.9×10^{-3} C/kg] result in a drastic diminishment of the sex ratio (11 males, 2 hermaphrodites, 127 females out of 500 irradiated seeds). This might indicate that the single X bears many important genes in contrast to the Y, as mutations in the single X lead to an increased mortality compared to females with a balancing second X chromosome.

Genome of *C. grandis*

Aside from research on the sex chromosomes, a few studies on the genome of *C. grandis* have been undertaken. Guha et al. (2004) report the 4C nuclear DNA content of female *C. grandis* as 8.37 ± 0.14 pg, whereas that of male *C. grandis* is 10.17 ± 0.24 pg. This means that the difference between X and Y chromosome adds about 20% to the complete DNA content. Patankar et al. (1985) report a DNA content of 1C = 2.75 pg for *C. grandis*, however, they do not report the sex of the analyzed individual. Interphase nuclear structure in *C. grandis* is chromocentric with 14 ± 0.25 chromocenters (Patankar et al. 1985).

Surveys on the reassociation kinetics in Cucurbitaceae suggest that *C. grandis* has the lowest amount of repetitive DNA among the Cucurbitaceae (Bhave et al. 1984). Fragments of 550 bp length have 25% of repetitive elements (Bhave et al. 1984), whereas 7400 bp long fragments consist of 49% repetitive DNA (Bhave et al. 1986). However, Pasha and Sen (1995) report different results as they find 400–600 bp long fragments to consist of 38% highly repetitive DNA (52% total repetitive DNA), which seems to be quite average in the Cucurbitaceae. Pasha and Sen do not discuss the difference, which cannot be explained by difference in sex, as the used high amounts of plant material suggest that they mixed material of both sexes. A sex discriminating study of *C. grandis* reassociation kinetics has not been undertaken yet.

Hybridization and crossing experiments

Charles Naudin’s famous work on the effects of hybridization included crosses between *Coccinia* plants. He reports successful crosses between Asian *C. indica* (nom. illeg. for *C. grandis*) and the northeast African *C. schimperi* (Naudin 1862), which is nowadays seen as a synonym of *C. grandis*. Naudin’s *Coccinia schimperi*, however, has buff petals, whereas the Asian *C. grandis* have snow-white petals. Both supposed species hybridized without problems. During the following two years, Naudin could not intercross within the F1, as plants of different sexes did not flower at the same time, so he crossed the F1 with a female *C. grandis* from Asia, which produced offspring again. As Naudin, erroneously, supposed that he dealt with two species, he deduced that hybrids between species could be fully fertile to sterile on any intermediate degree, and that there was no clear boundary between species and varieties. However, he rather proved that the buff-petaled, African *C. schimperi* and the the white-petaled, Asian *C. grandis* are a single species following a biological species concept.

Naudin also crossed other *Coccinia* species that he had in cultivation. *Coccinia quinqueloba* and *C. mackenii*, although sometimes not easily distinguishable, were not well crossable (Naudin 1866b). Only 1 out of 20 crossing trials resulted in a fruit that developed poorly. Naudin did not publish whether the hybrid seeds were viable or even fertile, but his observations are valuable as *C. quinqueloba* and *C. mackenii* are not distinguishable using more than 3500 bp of plastid sequences, and hence might share the same plastid haplotype (Holstein and Renner 2011a). There are specimens that share characters of *C. mackenii* and *C. quinqueloba*, but these are not intermediates. In these specimens long petioles (typical for *C. mackenii*) are coupled with simple tendrils (typical for *C. quinqueloba*), and thus cannot be unambiguously allocated to either species. However, if both typical morphs are indeed reproductively isolated, then they are species sensu Mayr (1942), and the crossing behavior of these species needs to be tested reciprocally to define the morphological scope of the two species.

Naudin also crossed male *C. diversifolia* (*C. abyssinica*) with a female *C. mackenii*, which are rather distantly related and do not co-occur in nature. However, the cross resulted in onset of mediocre fruits with only few, but well-developed and viable seeds (Naudin 1866b). Naudin did not report further results for this cross either.

As reproductive isolation between species is often assumed, but rarely tested, crossing experiments among species that are cultivated in Munich Botanical Garden have been performed. Positive results are given in Table 3.

Interspecific fertilization of succeeded or failed without correlation of relatedness or co-occurrence (Tab. 4). Female flowers of *C. sessilifolia* could not be fertilized with pollen of *C. megarrhiza* (4 trials), *C. trilobata* (4 trials), *C. rehmannii* (2 trials), *C. hirtella* (3 trials) or *Diplocyclos palmatus* (2 trials). Pollinated female flowers were discarded like non-fertilized flowers. Hence, the hybridization seems to be prevented prezygotically in female *C. sessilifolia* with members of the *C. rehmannii* clade and *C. hirtella* as pollen donor. As *C. sessilifolia* and *C. rehmannii* co-occur widely in their range and share flowering time and floral syndrome, the production of hybrids would reduce the fitness drastically. *Coccinia sessilifolia* and *C. hirtella* do not co-occur, but belong to the same clade (see chapter Evolution and phylogeny). Although a female *C. sessilifolia* could not be fertilized by pollen from *C. hirtella*, pollination of a female *C. hirtella* with pollen from *C. sessilifolia* resulted in onset of a fruit.

Table 3 Description of the F1 from crosses and a natural hybrid between Coccinia species. Species used for the artificial crosses are not sympatric.

Parent species	Offspring	Occurence
C. grandis ♀ × *C. hirtella* ♂	F1 vegetatively morphologi-cally intermediate; flowers are either aborted or sterile (pollen sacs remain closed); pollen globose; corolla is smaller than in each parent species (Fig. 15a)	Artificially in Munich Botanical Garden; voucher: N.Holstein 108 (M)
C. hirtella ♀ × *C. grandis* ♂	F1 vegetative, morphologically intermediate; flowers smaller (Fig. 15b), sterile	Artificially in Munich Botanical Garden; voucher: N.Holstein 116 (M)
C. grandis ♀ × *C. pwaniensis* ♂	F1 morphologically inter-mediate; flowers sterile (pollen sacs remain closed) (Fig. 15c)	Naturally in Pugu Hills, Dar es Salaam, Tanzania; vouchers: N.Holstein et al. 102 (DSM, M), 103 (M), 104 (M), 105 (DSM, M)
C. grandis ♀ × *C. sessilifolia* ♂	F1 vegetatively morphologi-cally intermediate; flowers are either aborted or sterile (pollen sacs remain closed); corolla is smaller than in each parent species (Fig. 15d)	Artificially in Munich Botanical Garden; voucher: N.Holstein 113 (B, M); N.Holstein 115 (M)
C. hirtella ♀ × *C. trilobata* ♂	F1 morphologically inter-mediate; males flowering vigorously with intermediate flowers, pollen sacs open, but pollen is sterile	Artificially in Munich Botanical Garden; N.Holstein 121 (M)

In contrast to *C. sessilifolia*, *C. grandis* is fertilized easily by *C. hirtella* and *C. sessilifolia*, although the species neither co-occur, nor are closely related. The cross resulted in offspring, which was growing vigorously, but sterile, as pollen sacs did not open (Tab. 3). The extracted pollen was also not able to fertilize *C. sessilifolia* (1 trial). The occurrence of sex chromosomes in *C. grandis* might result in gene dosage imbalance, which interferes with the floral development, leading to sterile offspring. The inability of female *C. grandis* to be fertilized by *C. rehmannii* aff. var. *littoralis* and C. *trilobata* (Tab. 4) might be explained by the fact that the chromosome numbers differ (see Tab. 2) and translocations lead to gene loss in hybrid genomes and thus inviability of the offspring. On the other hand, the cross between female *C. hirtella* and male *C. trilobata* (not sympatric) produced a purely intermediate F1 generation, which flowers vigorously despite the difference in chromosome numbers (see Table 2 and 3). Although the anthers open like in fertile flowers, unlike in *C. grandis* hybrids, the pollen og this hybrid was not able to fertilize female flowers of *C. hirtella* (1 trial), *C. grandis* (2 trials), or *C. sessilifolia* (2 trials).

Table 4 Observations on fruit development of crosses between Coccinia species (except for crosses mentioned in Tab. 2). Viability and morphology of the F1 is not known so far. * = sympatrically distributed species, ** = close relatives/sister species, *** = species occur in the same area, but in different habitats.

Parent species	crossability
C. grandis ♀ × *C. abyssinica* ♂	Onset of fruit (1 trial) ***
C. grandis ♀ × *C. megarrhiza* ♂	Onset of fruit (1 trial) *
C. grandis ♀ × *C. rehmannii* aff. var. *littoralis* ♂	Abortion of flower (1 trial)
C. grandis ♀ × *C. trilobata* ♂	Abortion of flower (2 trials) ***
C. hirtella ♀ × *C. rehmannii* aff. var. *littoralis* ♂	Onset of fruit (1 trial) ***
C. hirtella ♀ × *C. sessilifolia* ♂	Onset of fruit (1 trial)
C. megarrhiza ♀ × *C. abyssinica* ♂	Onset of fruit (1 trial) ** & ***
C. megarrhiza ♀ × *C. hirtella* ♂	Abortion of flower (1 trial)
C. megarrhiza ♀ × *C. rehmannii* aff. var. *littoralis* ♂	Onset of fruit (1 trial)
C. megarrhiza ♀ × *C. sessilifolia* ♂	Abortion of flower (2 trials)
C. megarrhiza ♀ × *C. trilobata* ♂	Onset of fruit (Fig. 12c; 1 trial)
C. microphylla ♀ × *C. megarrhiza* ♂	Abortion of flower (1 trial) *
C. microphylla ♀ × *C. trilobata* ♂	Onset of fruit (1 trial) ** & ***
C. rehmannii var. *rehmannii* ♀ × *C. rehmannii* aff. var. *littoralis* ♂	Onset of fruit (1 trial) **
C. rehmannii var. *rehmannii* ♀ × *C. trilobata* ♂	Abortion of flower (2 trials) **

Roy and Roy (1971a) report an intergeneric cross between a female *C. grandis* and a male individual of the monoecious *Diplocyclos palmatus*, resulting in a morphologically intermediate F1 offspring in 5% of the trials. All F1 individuals are female, indicating that the X chromosome bears at least one gene for maleness suppression, which is dominant over the maleness genes of *D. palmatus*. Whether the F1 is fertile, is not clear, as the authors report successful back-crossing only with a female [sic!, male?] *C. grandis*, but not with *D. palma-*

tus. To my knowledge, there are no reports of the F2 generation. However, if the parental sexes were the other way around (male *C. grandis* × female *D. palmatus*), fertilization was not possible.

Plant – biotic environment interactions

Pollination

Although bee pollination is observed for only a few species, most *Coccinia* species exhibit characters that support a general attraction to bees. The petal color is commonly pale yellow, but can also range to white, pale pink to bright orange, and purple venation is reported. Anthesis is during the day in *C. abyssinica*, *C. adoensis* var. *aurantiaca, C. grandiflora, C. grandis, C. hirtella*, *C. megarrhiza*, *C. microphylla*, *C. rehmannii, C. sessilifolia*, and *C. trilobata* (own observation), but often only few hours (in e.g., *C. megarrhiza*, *C. rehmannii*). Zimmermann (1922b) reports anthesis in *C. grandiflora* at 6.30 a.m. before blooming of the flower, opening of the flower between 7 and 8 a.m. and wilting after noon. Ash (J.W.Ash 898; EA, K) reports flower opening a.m. in *C. schliebenii*. Anthesis time in the other *Coccinia* species is not reported, but also likely to happen during the day. The scent is rather weak and dull sweetish, resembling that of honey melon, in *C. abyssinica*, *C. grandiflora*, *C. hirtella*, *C. rehmannii, C. sessilifolia*, and *C. trilobata*, weak, but fresh in *C. grandis*, and intense, sweet, and fruit-like (like honey melon) in *C. adoensis* var. *aurantiaca* and *C. megarrhiza*. The only exception from evidence for bee pollination is *C. ogadensis*, which is reported to smell of rotten meat (P.Ellis 163 and 383). However, it is unclear, whether the flowers emit a foetid scent or whether the smell comes from crushed vegetative parts, as it is known from *Momordica foetida* or *Kedrostis foetidissima* (Jacq.) Cogn. (Jeffrey 1967).

Bee pollination is confirmed for *C. rehmannii* (C.J.Ward 12250), *C. adoensis* var. *aurantiaca* (Fig. 9b)*, C. grandiflora*, and *C. grandis*. Observed pollinators of *C. grandis* are *Trigona apicalis* Smith, 1857 and *Trigona collina* Smith, 1857 in Thailand (Jongjitvimol and Wattanachaiyingcharoen 2006), and *Megachile* sp. in Cambodia (H. Schaefer, pers. comm.) The author observed a halictid bee (Fig. 9b; identification by H. Schaefer, pers. comm.) in a male *C. adoensis* var. *aurantiaca* walking on the globose anther head and collecting pollen in the corbicula. Stigmas in *Coccinia* are lobate (Fig.10b) or bulging (Fig. 10c), and nectaries are located presumably in the hypanthium, so one can assume stripping of the pollen from the venter when crawling into the flower. Zimmermann (1922b) also observed the circling around the anther head in the large-flowered *C. grandiflora*. He identified the visiting small bee as *Trigona* sp. He also pointed out that a bee just having visited a *Momordica* flower walked on the inner side of the corolla loading dorsally located pollen on the anthers of a male *C. grandiflora* flowers.

Seed dispersal

There are no observations of actual seed dispersal, but mammals and birds seem to be attracted by the fruits and might act as seed dispersers. Fruit bats such as *Cynopterus sphinx* (Vahl, 1797) feed on *C. grandis* fruits in Thailand (Ruby et al. 2000; Elangovan et al. 2001). Fruits of *C. grandis* are also taken up by birds (Bhatt and Kumar 2001) and eaten by humans (Voigt 1845). Elephants also feed on *C. grandis* (Mubalama 2000) and are possibly also seed dispersers. By the introduction of *C. grandis* in Pacific Islands, dispersal by humans is well-known (Muniappan et al. 2009). Anthropochory also explains the occurrence of this species in the Neotropics and even in Missouri, USA. Zimmermann reports feeding on *C. grandiflora* fruits by birds, small mammals, but also snails and beetles (Zimmermann 1922a), the latter two unlikely being seed dispersers. The forest weaver *Ploceus bicolor* Vieillot, 1819 was observed to feed on fruits of *C. mackenii* (Bleher et al. 2003). Stanford and Nkurunungi (2003) report differing preference of *Coccinia* plant parts by gorillas. Whereas the gorillas feed on the leaves and fruit pulp of *C.mildbraedii*, but not the seeds, they take only the leaves of *C. barteri*.

Successful seed germination in Munich Botanical Garden indicates that intestine passage is not necessary at least for *C. abyssinica*, *C. adoensis* var. *jeffreyana*, *C. grandiflora*, *C. grandis*, *C. hirtella*, *C. megarrhiza*, *C. microphylla*, *C. rehmannii*, *C. sessilifolia*, and *C. trilobata.* However, whether seeds would survive intestine passage and the role of endozoochoric dispersal is also not known.

Interaction with ants

Many species of *Coccinia* bear extranuptial glands on the lower lamina of the leaves and/or on the bracts and probracts. The glands are sunken into the surface and are surrounded by cells with a thicker cell wall (Ilyas 1992). Ants take up the sweet-tasting sap in *C. grandiflora* (Zimmermann 1922b) and in *C. grandis* (own observation). Whereas Ilyas (1992) reports aggressive behavior of the ants on herbivores for Indian *C. grandis*, I could not observe this in Tanzanian *C. grandis*. Nieuwenhuis von Üxküll-Güldenbandt (1907) found a weak attraction of ants and heavy damage by herbivores in *C. grandis* in Bogor botanical garden (Java, Indonesia). In addition, Zimmermann (1922b) does not find aggressive behavior in

C. grandiflora either, but reported that the ants attacked a caterpillar he had placed onto the plant. Agarwal and Rastogi (2008), on the other hand, report a significant reduction in residence time of herbivores on the cucurbit *Luffa aegyptiaca*, when ants are patrolling on the plant. Most likely, there is no close relationship to certain ant species as guardians, and plant-defense is carried out only by few ant species. How *Coccinia* species without or few probracts, bracts or sublaminal extrafloral nectaries (e.g. *C. microphylla*) react, when damage by herbivores occurs, is unknown. Agarwal and Rastogi (2008) found an increase of total numbers of extrafloral nectaries over time, but did not discuss changes of nectary density as reaction to grazing.

Diseases and parasites

There is quite some research on parasites and diseases for *C. grandis* for its status as crop, but also as weed. As *C. grandis* is naturalized on several Pacific islands, in Australia, and the Neotropics, the plants can either overgrow other plants or represent a non-specific host for diseases of cucurbit crops (Bamba et al. 2009; Muniappan et al. 2009). Its rapid growth can become problematic, as Pangelian (2003) reports that *C. grandis* covers 35% of the vegetation of the island of Saipan only eleven years after introduction.

Many different organisms are reported to live in, on, or to feed from *Coccinia* species. Beetle and fly larvae are either a disease for *Coccinia*, or in some cases, they are used to eradicate *C. grandis*. Fruits of *C. grandis* are an host for the larvae of the melon fly *Bactrocera* (= *Dacus*) *cucurbitae* (Coquillett, 1899), a tephritid fruit fly (Uchida et al. 1990). *Bactrocera cucurbitae* larvae usually populate the fruits, but are also reported to hatch from galls (Murthy 1959). However, the galls are not produced by these flies, but by the gall midge *Lasioptera* (= *Bimba*) *toombii* (Grover, 1962) (Bhatia and Mahto 1968). The gall infestation is interpreted as mistaken, as the female fly might not be able to differentiate between the gall and an unripe fruit, which would be the usual target. In addition, also the tephritid fruit fly *Dacus ciliatus* Loew, 1862 infests the galls, sometimes even together with *Bactrocera cucurbitae* (Bhatia and Mahto 1968). The galls in *C. grandis* do not need to result from *Lasioptera toombii*, but also can also be produced by the Itonidid gall midge *Neolasioptera cephalandrae* Mani, 1934 (Dharmamaraju 1968), which is reported to be the major disease in *C. grandis* in India (Unni et al. 1976). The galls induced by *Neolasioptera cephalandrae* also seem to be gateway for a fungal infection with a mold, which is identified tentatively as *Cladosporium* sp. (Krishnamurthy 1984).

Also other major cucurbit pests can use *C. grandis* as host, such as, *Diaphania* (= *Palpita*) *indica* (Saunders, 1851) (Lepidoptera: Pyralidae), *Aulacophora foveicollis* (Lucas, 1849) (Coleoptera: Chrysomelidae), *Leptoglossus australis* (Fabricius, 1775) (Hemiptera: Coreidae), *Aphis gossypii* Glover, 1877 (Hemiptera: Aphididae), *Liriomyza* spp. leafminers (Diptera: Agromyzidae), and *Bemesia* spp. white flies (Hemiptera: Aleyrodidae) (Bamba et al. 2009).

As a reaction to the danger to cucurbitaceous crops and of the weedy behavior on Pacific islands, larvae of the clearwing moth (Sesiidae) *Melittia oedipus* Oberthür, 1878 and the weevil (Curculionidae) species *Acythopeus burkhartorum* O'Brian, 1998 and *Acythopeus cocciniae* O'Brian, 1998 were introduced to Hawaii as biological pest control against *C. grandis* (Muniappan et al. 2002). Immediately after hatching from the eggs, *Melittia oedipus* larvae bore into the stems, where they live and pupate after two to four months (Chun 2002). This moth, originating from Zanzibar (Oberthür 1878), seems to be quite specific, as larvae only rarely develop on *Cucumis sativus* L. (Chun 2001). Also *Zehneria guamensis* (Merrill) Fosberg, a Guam endemic, is not attacked by *M. oedipus* (Bamba et al. 2009; Reddy et al. 2009). As *C. grandis* is an noxious weed in Hawaii (Hawaiian Department of Agriculture 1992), active search for pests for biological control was undertaken, which led to the discovery of two new beetle species from Kenya: *Acythopeus burkhartorum* larvae, which produce galls in young shoots, and *A. cocciniae* larva, which mine the leaves (O'Brian and Pakaluk 1998; Chun 2002). O'Brian and Pakaluk report a close morphological similarity of both *Acythopeus* species to *A. cucurbitae* (Marshall), which is a major pest on various cucurbittaceous crops in Africa, the Middle East and South India.

Many crop plants are attacked by root parasites or diseases, but there is little known from *Coccinia*. Only root lesion nematodes *Pratylenchus dasi* Fortuner, 1985 (= *P. capitatus* Das & Sultana, 1979) and *P. crassi* Das & Sultana, 1979 were described from the soil around roots of *C. grandis* (Das and Sultana 1979; Siddiqi 2000), but it is not known, whether they harm the plants.

The only known plant parasite growing on *Coccinia* is the hemiparasitic vine *Cuscuta chinensis* Lam., which is reported to grow on *C. grandis in* Gujarat, India (Patel and Patel 2010).

Several fungi have been reported from *Coccinia* (Tab. 6). The rust fungus *Puccinia windhoekensis* Mennicken, Maier & Oberw. was described on *Coccinia rehmannii* (Mennicken et al. 2005), although Berndt noticed a great similarity of this rust to *P. ctenolepidis* Ramachar & Bagyanar. Berndt could not confirm the identity of the host specimen, so it seems to be likely that it was misidentified, since *Ctenolepis cerasiformis* looks quite similar to *C. rehmannii*.

Table 6. List of fungi reported from *Coccinia* species (sorted by phylum of the fungus)

Fungus	Host	Symptom	Citation
Plasmopara cubensis (Berk. & M.A.Curtis) C.J.Humphrey (Peronosporales, Oomycota)	*C. grandis*	Downy mildew	Selby (1899)
Alternaria pluriseptata (P.Karst. & Har. ex Peck) Jørst. (Saccharomycetales, Ascomycota)	*C. grandis*	Fruit rot	Chagale and Bhale (2010)
Cercospora cocciniae Munjal, Lall & Chona (Dothideales, Ascomycota)	*C. grandis*	Leaf spot disease	Rangaswami and Chandrasekaran (1961)
Colletotrichum gloeosporioides (Penz.) Sacc. (Glomerellales, Ascomycota)	*C. grandis*	Fruit rot	Bhagavan Reddy and Reddy (1987)
Colletotrichum orbiculare (Berk. & Mont.) Arx	*C. grandis*	Anthracnose fruit rot	Imbumi (2004)
Corynespora cassiicola (Berk. & M.A.Curtis) C.T.Wei (Pleosporales, Ascomycota)	*C. grandis*	Leaf blight	Philip et al. (1972)
Curvularia pallescens Boedijn (Pleosporales)	*C. grandis*	Black rot	Imbumi (2004)
Erysiphe cichoracearum DC. ex Merat (Erysiphales, Ascomycota)	*C. grandis*	Powdery mildew	Imbumi (2004)
Fusarium moniliforme J.Sheld. (Hypocreales, Ascomycota)	*C. grandis*	Fruit rot	Kapoor et al. (1981)
Geotrichum candidum Link (Pleosporales)	*C. grandis*	Fruit rot	Chagale and Bhale (2010)

Sphaerotheca fuliginea (Schltdl.) Pollacci (Erysiphales)	*C. grandis*	Powdery mildew	Imbumi (2004)
Puccinia cephalandrae Thümen (Uredinales, Basidiomycota)	*C. quinqueloba*	rust	Berndt (2007)
Puccinia cephalandrae-indicae Syd. & P.Syd.	*C. grandis*	rust	Berndt (2007)
Puccinia physedrae Syd.	*C. barteri*	rust	Berndt (2007)
Puccinia windhoekensis Mennicken, Maier & Oberw.	*C. rehmannii*?	rust	Mennicken et al. (2005)
Rhizoctonia solani Khun (Cantharellales, Basidiomycota)	*C. grandis*	Fruit rot	Bhagavan Reddy and Reddy (1988)

There are several reports of plant viruses from *Coccinia* species. Purcifull and colleagues (1988) tested the infectability of several Cucurbitaceae to different plant viruses. They found that *C. grandis* can be infected by the papaya ringsport virus type W (PRSV-W) and the Trichosanthes virus, but not by the cucumber mosaic virus, squash mosaic virus, watermelon mosaic virus-2, and the zucchini yellow mosaic virus. PRCV-W infections of *C. grandis* are also reported from several Pacific islands (Davis and Ruabete 2010).

Verma et al. (1983) suggest a yet undescribed mosaic virus, which is expressed in the occurrence of deformed leaves and a mosaic pattern in *C. grandis* leaves. A strain of the Moroccan watermelon mosaic virus, a Potyvirus, can infest *Coccinia barteri* (Owolabi et al. 2012), whereas the infection of *C. sessilifolia* with this virus failed (van der Meer and Garnett 1987).

Use, economic potential, and phytochemistry

Several *Coccinia* species are used by tribal communities, mainly as a food source, but also for cultural applications (for details see species descriptions). *Coccinia grandis* already gained wide attraction for its economical value (although often cited erroneously as *Coccinia cordifolia* or *C. indica*), whereas the importance of *C. abyssinica* is only regional. Other species are used by local tribes only.

Coccinia grandis is used in a wide variety of applications. The plant is well-known in India, where its fruits had an impact even in classical Sanskrit literature. The red fruits are regularly used to describe lips, such as those of a beloved wife, who is described by her husband in Kālidāsa's poem Meghadūta (Wilson 1867) or those of the goddess Sita and the god Rama in the epic Ramayana (Dutt 1891–1894). However, the fruits are also edible (raw and cooked), and are valued for its high content of carotenoids, esp. lycopene (Barua and Goswami 1979). Also young shoots and leaves are eaten as spinach, and contain high amounts of lutein and other carotenoids (Addis et al. 2009). The high carotenoid value is of special importance in developing countries, as vitamin A deficiency is widespread among young children and pregnant women (WHO 2009). Social marketing has proven to be valuable to promote the use of *C. grandis* to prevent vitamin A deficiency (Chittchang et al. 1999). Domestication of *C. grandis* is in an early stage, but promising cultivars are developed in South and South East Asia (Ramachandran and Subramaniam 1983; Engle et al. 1998; Bharathi 2007). In Africa, *C. grandis* is mostly used from wild collections (Imbumi 2004; Addis et al. 2009). However, contraindications to the use of *C. grandis* are also reported (Adanson 1757; Orech et al. 2005), but these also might result from either misidentification or from regional chemovarieties with differing amounts of secondary metabolites.

Coccinia grandis has been used in Indian traditional medicine for several hundred years (Nadkarni and Nadkarni 1976; Ramachandran and Subramaniam 1983). There are some studies that suggest a high potential of *C. grandis* leaf extracts for diabetes treatment (Azad Khan et al. 1980; Kuriyan et al. 2008; Munasinghe et al. 2011). Parts of the observed effects are explained by inhibition of gluconeogenesis in the liver due to repression of glucose-6-phosphatase (Hossain et al. 1992) and fructose-1,6-bisphosphatase (Shibib et al. 1993). Also an activating effect on the promotor of the glucose transporter gene GLUT1 from rats is reported (Graidist and Purintrabipan 2009). Eshrat (2003) observes a positive effect of *C. grandis* in rats with hyperlipidemia, which is often connected to diabetes. However, effectivity in diabetes treatment and experimental design is disputed (Ramachandran and Subramaniam 1983; Sadikot 2009), and more research to test the medical value is necessary.

Since the year 2005, more than 15 papers have been published to look for chemical compounds and to test, whether other applications of *C. grandis* in folk medicine stand scientific reason. Some applications by tribal people could be reproduced *ex situ*, but research is still in its infancy. Suggested effects are e.g. anti-anthelmintic (Dewanjee et al. 2007b), anti-tussive (Pattanayak and Sunita 2009), hepatoprotective (Vadivu et al. 2008; Moideen et al. 2011), antioxidative (Umamaheswari and Chatterjee 2008), antipyretic, analgesic, and anti-inflammatory (Niazi et al. 2009), anti-ulcerogenic (Mazumder et al. 2008), and antimicrobial (Dewanjee et al. 2007a; Farrukh et al. 2008; Shaheen et al. 2009; Bulbul et al. 2011). Antimicrobial activity is explained by the occurrence of a protease inhibitor (Satheesh and Murugan 2011). Observed xanthine oxidase inhibitoric and antiuricaemical activity (Umamaheswari et al. 2007) suggests use for gout treatment. Female rats with hyperprolactinemia-caused infertility regain fertility when treated with an aqueous extract of *C. grandis* stems and leaves (Jha et al. 2010).

Coccinia abyssinica is mainly an Ethiopian tuber crop. Under the name “anchote”, its starch containing (c. 20%) tubers are an important staple food in southwestern semi-humid highland (Hora 1995; Aga and Badada 1997; Asfaw 1997). Although the fruits are not eaten in the cultivated landraces (Getahun 1973), the use might by beneficial due to the carotenoid content of the fruits, which are likely to be comparable to those of *C. grandis*. However, fruits of wild races of *C. abyssinica* are already used (Asfaw and Tadesse 2001). Locally (around Dembi Dolo, Oromia), also young shoots and leaves are eaten (Hora 1995). Additionally, the tubers contain a relatively high amount of calcium, which might explains the local belief that the plant helps with repairing bone fractures and displaced joints (Hora 1995).

Also other species of *Coccinia* are used as food source, but if so, then only locally. In these species, such as *C. sessilifolia*, some wild landraces lack bitter substances (Dinter 1912; Bosch 2004), which in Cucurbitaceae is mainly caused by triterpenoid substances called cucurbitacins, although not all cucurbitacins are bitter. Cucurbitacins are often cyto-toxic and often exist as β-glucosides (Miró 1995). All *Coccinia* species screened so far contain cucurbitacins, although the cucurbitacin kind, time, and organ of expression differ greatly. Whereas fruits of *C. hirtella* and *C. quinqueloba* contain glycosidic cucurbitacin B, *C. adoensis* from South Africa contains aglycosidic cucurbitacin B only in unripe fruits and traces of cucurbitacin D, but not in ripe fruits (Rehm et al. 1957). Unripe fruits of *C. rehmannii* and *C. sessilifolia* are not bitter, and therefore lack bitter cucurbitacins (Enslin et al. 1956). Njoroge and Newton (1994) tested the kind and distribution of cucurbitacins within the plant in different Cucurbitaceae and found in Kenyan *C. adoensis* plants cucurbitacins H, I, and R in the stem, but no cucurbitacins in the roots, leaves, fruits, or seeds. *Coccinia trilobata* was found to contain the cucurbitacins B, D, and G in the stems, cucurbitacin D, H, I, and R in the leaves, and cucurbitacin G in the fruits, with no cucurbitacins in roots and seeds. However, there seems to be a great variability, as there are reports of edible (non-bitter) *C. trilobata* leaves (*Coilly*? *24*, *F.Msajiri 19*). *Coccinia grandis* is also reported to contain cucurbitacin B (Bhakuni et al. 1962), and bitter und sweet fruited varieties are known. Guha and Sen (1973) find that cucurbitacin B has an antigibberelic effect, and its occurrence in seeds of *C. grandis* might increase or enable dormancy of the seeds.

Evolution and phylogeny

Recent phylogenetic analysis (Kocyan et al. 2007; Schaefer and Renner 2011b) shows that *Coccinia* belongs to the tribe Benincaseae with a moderately supported sister group relationship to the genus *Diplocyclos*. However, the backbone of the tribe is not resolved and the relationship of the *Coccinia-Diplocyclos* clade to the other genera is unknown. *Citrullus, Cucumis,* or *Scopellaria* cluster with this clade, but each without support, and also morphological characters do not seem to suggest any closer relatives.

Both phylogenies, plastid (Fig. 16) and the nuclear *LEAFY*-like 2nd intron (Fig. 17), suggest the existence of four major clades, although the backbone lacks bootstrap or posterior probability support (Holstein and Renner 2011a). The *Coccinia rehmannii* clade (IV) is well-supported in all phylogenies. The *Coccinia quinqueloba* group (II) consists, well-supported in the plastid DNA, of *C. hirtella*, *C. mackenii*¸ and *C. quinqueloba*. Additionally, *C. sessilifolia* also belongs to this group, but this is only supported by the nrDNA data. According to the nuclear data, the *C. barteri* clade (III) is nested in the *C. adoensis* clade (I). However, the plastid tree separates these two clades but without support.

The *C. rehmannii* clade (IV) consists of five species. *Coccinia abyssinica* and *C. megarrhiza* are sister species and differ ecologically, with the former species occurring in the semi-humid highlands and the latter one in the semi-arid lowlands (Holstein and Renner 2011a). Both species differ weakly in morphology, and hybridization cannot be ruled out. The other three species contain several plastid haplotypes and nrDNA sequences that each does not form monophyletic clades. The geographical distribution of the haplotypes is not assessed. The three species, however, are distinct. *Coccinia rehmannii* occurs in southern Africa and the other two species in northeastern Africa. In *Coccinia rehmannii* four morphs can be recognized, which are included in the plastid phylogeny: (1) an inland morph from dry habitats with small globose fruits (described by Meeuse as var. *rehmannii*), (2) a morph like var. *rehmannii*, but with larger globose fruits (described by Dinter and Gilg as *C. ovifera*), (3) a long-petiolate and long-peduncled coastal morph from the (semi-)humid Southeast (described by Meeuse as var. *littoralis*), and (4) plants with oblong fruits occurring in all semi-humid areas from the Southeast to the northern parts in the periphery of the distribution (*C. rehmannii* 5). None of morphs cluster together. The other two species differ morphologically and ecologically: *C. trilobata* has e.g. oblong fruits and occurs in the semi-humid uplands, and *C. microphylla* has globose fruits and occurs in the semi-arid lowlands. Interestingly, *C. microphylla* does not differ morphologically from the *C. rehmannii* morph from the dry inland. This scenario suggests incomplete lineage sorting and a speciation event with ecological differentiation in the northeastern Africa, but not in southern Africa as intermediate specimens are found regularly. The distribution of these three species and the estimated age of this clade of 3.2 Ma (Holstein and Renner 2011a) suggest either a long distance dispersal or vicariance. As each of the three species contains several plastid haplotypes, vicariance is more likely, which indicates that semi-arid conditions might have prevailed between todays Tanzania and Zimbabwe. This has been suggested several times for different clades under the term “arid track” (Balinsky 1962; de Winter 1971).

The *C. quinqueloba* clade (II) is only supported in the nrDNA phylogeny, as plastid sequences of *C. sessilifolia* and its distinctly petiolate variety *variifolia* lack SNPs that support a closer relationship to any clade in *Coccinia*. The two varieties of *C. sessilifolia* occur in the semi-arid and sub-semi-humid inland, whereas the other three species prefer more humid habitats (Holstein and Renner 2011a). One species, *C. hirtella*, occurs in the rather open habitats in the Drakensberg Mountains, which receive high rainfalls. *Coccinia mackenii* occurs in remnant forest sites in the humid Southeast of southern Africa, whereas *C. quinqueloba* occurs only in bushlands of the Eastern Cape, where it receives less precipitation than the other two species, but has constant water available all over the year (Holstein and Renner 2011a). As *C. mackenii* and *C. quinqueloba* do not co-occur, but have similar ecologies, and as they only slightly differ morphologically, but hardly produce hybrids (see chapter Hybridization and crossing experiments) a recent allopatric speciation event is probable. The lack of differentiation in the plastid sequences over 3500 bp might support this hypothesis. Strangely, in contrast to the *C. rehmannii* clade, all species of this clade occur exclusively in southern Africa, although the clade is older (c. 5.0 Ma vs. 3.2 Ma).

The *C. adoensis* clade (I) contains several morphologically and ecologically well differentiated species (Holstein and Renner 2011a). There are three subclades in the plastid tree with accessions with the name *Coccinia adoensis*. Specimens of these subclades do not differ well enough to be confidently described as separate morphospecies. Additionally, there are also several morphs, which are treated as varieties of *C. adoensis* in this work, as one can intermediate specimens to “typical” *C. adoensis*. The *Coccinia adoensis* var. *aurantiaca* accessions are neither in the plastid nor in the nuclear tree monophyletic, but share a dense indument. These morphs cluster in the nuclear tree with specimens that have a less dense indument and thus are rather referred to as *C. adoensis* var. *adoensis*. In the plastid tree, these specimens cluster together with a Kenyan *C. adoensis* var. *adoensis* specimen and the second variety *jeffreyana*. *Coccinia adoensis* var. *jeffreyana*, however, shares the longer trichomes with *C. senensis*, but it differs from these by lacking subulate calyx lobes and a 569 bp deletion in the *trn*S^{GCU}–*trn*G^{UUC} intergenic spacer region. However, one specimen that does not differ morphologically from the variety *jeffreyana* (R.E.Gereau and C.J.Kayombo 3582) clusters within the East African *C. adoensis* morphs, which indicates either homoplasy of the trichome length or gene flow. Morphologically, also the South African *C. adoensis* do not differ strongly from the East African *C. adoensis* and not at all from the type specimen from Ethiopia. Holstein and Renner (2011a) found a specimen from Namibia (*C. adoensis* 5) that contained ITS sequences that are else found exclusively in the South African and in the East African plastid haplotypes. So, it can be suggested that all these morphs belong to one widespread species, *C. adoensis*, which contains different plastid haplotypes. From this widespread species, several populations might have undergone ecological and morphological shifts. *Coccinia grandiflora* and *C. schliebenii* are nested within one *C. adoensis* subclade, and they occupy rather humid habitats while *C. grandis* and *C. ogadensis* occupy more arid habitats. Probably, some populations evolved parapatrically in former times with morphological shifts (*C. senensis*, *C. pwaniensis*, *C. samburuensis*) or purely evolved in allopatry (*C. intermedia*) (Holstein and Renner 2011a) (Fig. 18). Some populations, however, did not evolve morphologically well enough to be taxonomically well-separated as a species, such as *C. adoensis* var. *aurantiaca*.

The *C. barteri* clade (III) mostly consists of rainforest species from West and Central Africa, except for the recently described *C. intermedia* (Holstein and Renner 2011b). *Coccinia mildbraedii* (including *C. ulugurensis*) also differs ecologically as it occurs in mountain forest communities, not in typical lowland rainforests as the rest of species. The phylogenetic position of *C. intermedia* is unclear, as the resolution within this clade is generally low. *Coccinia intermedia* shares morphological characters with *C. adoensis*, especially the open campanulate flowers, hence the epithet (Holstein and Renner 2011b). Both species occur in the same habitat with the former one in West Africa and the latter one north and east of the Central African rainforests. If the *C. barteri* clade is indeed nested in the *C. adoensis* clade, as suggested by the nuclear phylogeny, then it is presumable that *C. intermedia* might have split allopatrically from a proto-*C. adoensis* species and is sister to the rest of the *C. barteri* clade (Fig. 18). Then, the common ancestor of the other species of the *barteri* clade might have shifted the habitat preference towards perhumidity once, and evolved allopatrically in refugia during arid periods of the Pliocene and Pleistocene. As the frequency of the Pleistocene climatic oscillations increased, reproductive isolation did not always evolve, leading to weak morphological differentiation of interbreeding populations, such as in the polymorphic *C. barteri* (Holstein and Renner 2011a).

Identification of *Coccinia* species

Possible confusion with other genera

Some *Coccinia* species are easily confused with specimens of other Cucurbitaceae genera. The similarity is sometimes striking and without flowers or inflorescences, one might need some experience to differentiate between the genera.

West and Central African *Coccinia* species resemble *Bambekea racemosa* Cogn., which has its flowers and fruits in long ebracteate racemes like *C. barteri*, *C. heterophylla*, and *C. racemiflora*, but which leaves has veins running along the leaf margin and free petals, whereas *Coccinia* veins don't, and petals are connate. These *Coccinia* species also resemble somewhat the two *Ruthalicia* species, which have lanceolate bracts, in contrast to *Coccinia* with ovate bracts or no bracts at all. Additionally, *Ruthalicia* specimens (esp./only? *C. eglandulosa* (Hook.f.) C.Jeffrey) sometimes bear trichomes with a claret-red color (coloration is often at the ends of the long, centrically sunken-in cells) in contrast to *Coccinia*, in which trichomes are whitish, beige, yellowish or rarely light brownish.

Also species of *Peponium* Engl. are similar to the rainforest species of *Coccinia*. However, *Peponium* species differ in several characters from *Coccinia*. Flowers of *Peponium* species have free petals, whereas *Coccinia* is sympetalous. The male flowers in *Peponium* have a long-stretched hypanthium, whereas male *Coccinia* flowers have a perianth tube, in which the length does not supercedes two times the diameter. Male flowers in *Peponium* have three free filaments, which connect only with the long-stretched anthers, unlike in *Coccinia* with three already connected filaments and a globose anther head. The seeds in *Peponium* are dark-colored, whereas *Coccinia* seeds are grayish-beige. Vegetatively, it might be harder to distinguish the genera. In Central and West Africa, the only *Peponium* species, *P. vogelii*, has sessile probracts, and bracts are round and up to 3 cm long, whereas *Coccinia* species have short petiolate probracts and bracts ≤ 0.5 cm. In East Africa, *Peponium* species may have smaller probracts and bracts and might be confused vegetatively with *C. grandiflora* or *C. schliebenii*.

Coccinia schliebenii can be easily confused with *Luffa aegyptiaca* Mill. or *Lagenaria* species, if the fruit is missing. *Luffa* species mostly have 3–5-fid tendrils, rather rarely bifid ones (check as many as possible), whereas *C. schliebenii* has only bifid tendrils. Commonly, *Lagenaria* species have tooth-like glands at the base of the lamina or along the petiole and can have longer (> 1 mm) trichomes than *C. schliebenii*. *Coccinia schliebenii* is sympetalous, in contrast to *Luffa* or *Lagenaria*, which have free petals. *Luffa* species have 5 stamens, and *Lagenaria* species have serpentine anthers, whereas *C. schliebenii* has 3 stamens and S-shaped anthers. The petal color in *C. schliebenii* is dull yellowish or yellow-orange, in *Luffa* bright yellow (in *L. acutangula* (L.) Roxb. also dull yellowish), and in *Lagenaria* species white.

Coccinia adoensis can look similar to *Eureiandra* species, which have free petals, lanceolate calyx lobes and 5 stamens (Jeffrey 1967), in contrast to *Coccinia* with a sympetalous corolla, lineal, subulate to triangulate calyx lobes, and 3 stamens in a central column. Vegetatively, it is troublesome to distinguish *C. adoensis* from *Eureiandra*. In some cases, the latter species have the lateral veins of the leaves running along the leaf margin for several millimeters, which is never the case in *C. adoensis*.

Coccinia microphylla and *C. rehmannii* look similar to *Ctenolepis cerasiformis* C.B.Clarke and *Dactyliandra* species, which also have globose red fruits, but a large roundish, sinuate-ciliate probract (Jeffrey 1967), whereas probracts of *C. microphylla* and *C. rehmannii* are small (< 3 mm) and (narrow) ovate. *Dactyliandra stefaninii* (Chiov.) C.Jeffrey from N Africa lacks the probracts, but the seed shape is conspicuously rounded, whereas *C. microphylla* seeds are asymmetrical (almost falcate). Additionally, *Coccinia* petals are longer than 1 cm, whereas *Ctenolepis* and *Dactyliandra* petals are much smaller (< 5 mm) (Meeuse 1962).

Characters for species discrimination

There is no character, which is useful for all species. For example, whereas the direction of the calyx lobes can be a useful character for some species (e.g., *C. grandis*, *C. intermedia*, *C. keayana*), it is less useful in others (e.g. in the *C. quinqueloba* clade). Specimens without flowers are harder to identify. In some cases it is almost impossible to discriminate species, if flowers lack. Identification of vegetative material only is often possible, but needs experience. The indument can be a useful character; especially the trichomes (length, somewhat also the shape) on the abaxial side of the petiole and the lower leaf lamina can be helpful. However, the trichomes on the adaxial side of the petiole and the leaf margin do not seem to have any purpose for species identification.

Key to *Coccinia* species

The key is made from observations from and for herbarium material, but also includes some characters from own observations of living material and observations as given by herbarium labels. However, fresh material is not needed to use the key. The term ‘articulate’ refers to dried trichomes that appear wrinkly due to centrically sunken-in cell walls (see Fig. 3a), but not to trichomes with ramifications, which have never been observed in *Coccinia*. In living state, these trichomes are rather long and stiff. The leaf length is measured from the attachment point of the petiole to the apex. The term “dentate” refers to the sometimes colored structures (hydatodes?) at the leaf margin and leaf tip (Fig. 6a, 7a, 15a, 15b, 21, 22). Habitats in this key (not the species descriptions) are given rather crudely and reflect the vegetation that would be found naturally. Savannas and woodlands (tree stands with not largely overlapping canopies) can also include mopane, but also dry forests (larger amounts of deciduous trees and overlapping canopies), deciduous thickets, tall grasslands, and secondary vegetation derived from these. “Rainforests” include gallery forests, semi-deciduous forests derived from rainforests, e.g. in relict areas, perhumid savanna types, and open areas, in which rainforest would be predominant, if it wasn’t for human impact, or swamps.

A local key for *Coccinia* from West Africa is separately provided by Holstein and Renner (2011b). If the plant is from outside of Africa, then it is *C. grandis*.

1 Mature leaves sessile (first leaves may be petiolate), rarely subsessile; usually bluish-green; glabrous; male flowers solitary or in few-flowered racemes, female flowers solitary; fruit ovoid; preferring dry habitats; plant from S Africa (Fig. 2b) *C. sessilifolia* var. *sessilifolia*

1* All leaves petiolate; not like in 1 2

2 Tendrils mostly bifid; usually forest species or from Drakensberg Mts. or humid coastal bushland in SE Africa (in W Africa also in woodlands or savannas) 3

3 Plant with flowers 4

4 Corolla ≥ 4 cm long, calyx lobes > 3 mm long; ovaries and fruits long ovoid to cylindrical; plant of E Africa or Ethiopia 5

5 Leaf lamina usually glabrous, rarely with sparse weak thin trichomes on the abaxial side; leaves profoundly lobate (Fig. 7a); plant of E African (rain) forests from C Zimbabwe and Mozambique to S Kenya *C. grandiflora*

5* Leaf lamina, at least lower lamina (secondary and tertiary veins) densely covered with small trichomes; leaf shallow or rarely profoundly lobate; margin of humid forests and in forests; from N Mozambique to C–S Tanzania or Ethiopia to Southern Sudan *C. schliebenii*

4* Corolla < 4 cm long 6

6 Calyx lobes long (> 2.5 mm) subulate (Fig. 19), plant of western C Africa *C. heterophylla*

6* Calyx lobes < 2.5 mm, if longer, then from South Africa 7

7 Calyx lobes > 3 mm, plant from South Africa 8

8 Leaf lamina and stem usually densely covered with long (> 0.5 mm) trichomes; lamina profoundly lobate and lobulate; lobe tips usually rounded; pedicels covered with long (> 0.5 mm) trichomes (Fig. 12b) *C. hirtella*

8* Leaf lamina and stem glabrous or rarely sparsely covered with long trichomes, with lobes often tapering into an acute tip, only side lobes with a slight lobule on outer side; pedicels glabrous *C. mackenii*

7* Calyx lobes < 3 mm, plant not from South Africa 9

9 Flowers in lax many-(> 6-)flowered racemes, plant of western C Africa *C. racemiflora*

9* Flowers in dense racemes, few-flowered, or on a long common peduncle, which surpasses the length of the branched part; female flowers can also be solitary 10

10 Male flowers on a long common peduncle, which surpasses the length of the branched part; female flowers solitary with cylindrical ovary; mountain forest plant of Kivu Mts, Livingstone Mts, and Eastern Arc Mts, introduced into Kenyan high mts *C. mildbraedii*

10* Male flowers in a raceme, in which the common peduncle is shorter than the branched part; female flowers in racemes, clustered or if solitary, then with elliptical ovary 11

11 Corolla campanulate, calyx lobes erect with recurved tips. Lower leaf lamina in maturity often with white speckles and leaf margin with colored teeth. Plant of W African semi-humid savannas and woodlands *C. intermedia*

11* Corolla urn-, cup-, funnel-shaped or narrow campanulate. Calyx lobes variable, but not as above. Lower leaf lamina rarely with white speckles, teeth on leaf margin not conspicuously colored. Rainforest plant from W Africa, C Africa, and in relict forests to Angola, Zambia?, W Tanzania, Uganda, and the Chimanimani Mts (Mozambique, Zimbabwe) *C. barteri*

3* Plants with fruits or vegetative parts only 12

12 Plants with fruits 13

13 Fruit oblong to cylindrical (mature > 5 cm long), plant from E or NE Africa 14

14 Lower leaf lamina, often also upper lamina densely covered with short trichomes; plant of N Mozambique, C and S Tanzania or W Ethiopian to SE Southern Sudanian mts *C. schliebenii*

14* Upper leaf lamina always, lower leaf lamina glabrous or rarely with some trichomes; plant of E Africa, incl. Kivu Mts and Chimanimani Mts (Mozambique, Zimbabwe) in shared mt. ranges hard to differentiate 15

15 Probracts > 3.5 mm (Fig. 7a); corolla > 3 cm, calyx lobes > 3 mm; forest species; forest relics in S Kenya, Mt Meru to Usambara Mts, Eastern Arc Mts, SE Tanzania, N Mozambique, Chimanimani Mts (Mozambique, Zimbabwe) *C. grandiflora*

15* Probracts < 3.5 mm; corolla < 3 cm, calyx lobes < 3 mm; mountain forest species of Kivu Mts, Livingstone Mts, and Eastern Arc Mts, introduced into Kenyan high mts *C. mildbraedii*

13* Fruit ovoid, if long elliptical, then from South Africa 16

16 Fruits in lax racemes, plant from western C Africa *C. racemiflora*

16* Fruits in denser racemes or solitary 17

17 Plant from South Africa; fruits always solitary 18

18 Leaf lamina and stem usually densely covered with long (> 5 mm) trichomes; lamina profoundly lobate and lobulate; lobe tips usually rounded (Fig. 12b) *C. hirtella*

18* Leaf lamina and stem glabrous or sparsely covered with long trichomes, with lobes often tapering into an acute tip, only side lobes with a slight lobule on outer side *C. mackenii*

17* Plant from W to C Africa to Chimanimani Mts (Mozambique, Zimbabwe) 19

19 Plant from western C Africa, not confidently differentiable *C. heterophylla* or *C. barteri*

19* Plant not from western C Africa 20

20 Lower leaf lamina in maturity often with white speckles and leaf margin with colored teeth when dry. Plant of W African semi-humid savannas and woodlands *C. intermedia*

20* Lower leaf lamina rarely with white speckles, teeth on leaf margin not conspicuously colored. Rainforest plant from W to C Africa to Chimanimani Mts (Mozambique, Zimbabwe) *C. barteri*

11* Plants vegetative only 21

21 Lower leaf lamina, often also upper lamina densely conspicuously covered with short trichomes; plant of N Mozambique, C and S Tanzania or W Ethiopian to SE Southern Sudanian mts *C. schliebenii*

21* Leaves glabrous, or if covered with trichomes, then they are long (> 0.7 mm) or inconspicuous 22

22 Plant from South Africa 23

23 Leaf lamina and stem usually densely covered with long (> 5 mm) trichomes; lamina profoundly lobate and lobulate; lobe tips usually rounded (Fig.12b) *C. hirtella*

23* Leaf lamina and stem glabrous or sparsely covered with long (> 5 mm) trichomes, with lobes often tapering into an acute tip, only side lobes with a slight lobule on outer side *C. mackenii*

22* Plant from W to E Africa 24

24 Plant from E African rainforests from S Kenyan forest relics, Mt Meru to Usambara Mts, Eastern Arc Mts to Chimanimani Mts (Mozambique/Zimbabwe); probracts > 3 mm (Fig.7a); glands on lower leaf lamina relatively scattered *C. grandiflora*

24* Plant from W, C, or E Africa, if from E Africa, then probracts < 3 mm 25

25 Mountain forest species from E Africa, incl. Kivu Mts *C. mildbraedii*

25* Rather lowland rainforest species from W Africa, C Africa, or from rainforests surrounding the Western Rift 26

26 Plant from western C Africa not confidently differentiable *C. heterophylla*, *C. racemiflora*, or *C. barteri*

26* Plant not from western C Africa 27

27 Lower leaf lamina in maturity often with white speckles and leaf margin with colored teeth. Plant of W African semi-humid savannas and woodlands *C. intermedia*

27* Lower leaf lamina rarely with white speckles, teeth on leaf margin not conspicuously colored. Rainforest plant from W to C Africa to Chimanimani Mts (Mozambique, Zimbabwe) *C. barteri*

2* Tendrils usually simple, if not, then from semi-arid habitats or E and NE-AFR woodlands 28

28 Leaves deeply lobate with lineal lobes. If lobes lobulate, then leaf lamina at lobe base as broad as vein. Plant of E Ethiopia and C Somalia. *C. ogadensis*

28* Leaves profoundly, but not deeply lobate, or if deeply lobate, then lobes lanceolate or lobe base broader than vein. 29

29 Leaves deeply lobate with lanceolate lobes. Male flowers in short pedicelled racemes. Plant of rainforests of Central Africa and around the Western Rift *C. subsessiliflora*

29* Plant different 30

30 Leaves 7-lobate, rarely 5-lobate. Outer side of lobes serrate to lobulate with conspicuously colored glands. Calyx lobes > 4 mm, corolla > 2.5 cm, fruit ripe > 10 cm long. Plant of Samburu area (C Kenya, E Africa). *C. samburuensis*

30* Leaves cordate or 3-lobate. If 5-lobate, then leaf margin different. Calyx lobes shorter or if longer, then corolla shorter. Fruit shorter or if longer, then from S Africa 31

31 Plant glabrous; leaves usually subsessile, 5-lobate. Plant of coastal bushlands from Eastern Cape (South Africa) *C. quinqueloba*

31* Plant with trichomes or if glabrous, then from different region 32

32 Plant glabrous, glaucous. Fruit long (> 6 cm) elliptical to spindle-shaped. Plant from Limpopo Province (South Africa) *C. sessilifolia* var. *variifolia*

32* Plant with trichomes, or if glabrous, then not glaucous and from different region 33

33 Plant with male flowers 34

34 Plant glabrous. Lower leaf lamina with pale (rarely also black when oxidized) glands towards the base, rarely also between secondary veins. Margin of mature leaves with claret-red or brownish (black when dry) teeth. Flowers solitary, rarely clustered, calyx lobes spreading to reflexed, corolla white or buff (Fig. 6a). Plant from N, NE or E Africa, Arabia, Asia, or the Americas but likely to become naturalized in other areas *C. grandis*

34* Plant with trichomes, or if glabrous, then different from above 35

35 Plant glabrous or rarely with soft multicellular trichomes. Flowers in lax ebracteate racemes, calyx lobes lineal, > 2 mm long, in buds spreading, when mature reflexed (Fig. 20). Plant of rainforests from W Africa (W of the Dahomey Gap) *C. keayana*

35* Plant different 36

36 Plant glabrous. Leaves cordate to subhastate, rarely 3-lobate. Flowers in ebracteate racemes. Calyx lobes erect, at base broader than 0.75 mm, corolla urceolate. Plant of rainforests from W Africa *C. longicarpa*

36* Plant different and not from W Africa, or if from W Africa, then calyx lobes narrower or spreading to reflexed 37

37 Plant glabrous, in maturity often with white speckles on stem, petiole, and lower leaf lamina. Flowers in racemes or 1 solitary. Calyx lobes erect with recurved tips. Corolla campanulate. Plant of semi-humid savannas and woodlands from W Africa *C. intermedia*

37* Plant not from W Africa or if so, then rainforest species (sometimes hard to differentiate from *C. intermedia*) or lower leaf lamina conspicuously covered with trichomes 38

38 Plant glabrous (or puberulous), leaves coriaceous. Plant from W or C (or western E) African rainforests 39

39 Male flowers in short peduncled racemes (common peduncle shorter than racemose part). Plant of lowland rainforests or rainforest relicts in higher altitudes *C. barteri*

39* Male flowers in racemes with common peduncle longer than racemose part. Plant of mountain forests from Kivu Mts, Eastern Arc Mts, Livingstone Mts, also introduced in Kenyan high mts *C. mildbraedii*

38* Plant conspicuously covered with trichomes or if glabrous, then leaves papery or from NE, E, or S Africa 40

40 Plant of S Africa (except C and N Mozambique) 41

41 Perianth tube outside with long articulate trichomes or if glabrous, then calyx lobes > 2.5 mm (Fig. 9a) *C. rehmannii*

41* Perianth tube outside with short trichomes or if glabrous, then calyx lobes < 2.5 mm (Fig. 21) *C. adoensis* var. *adoensis*

40* Plant from E (incl. C and N Mozambique), NE or NC Africa 42

42 Flowers clustered, common peduncle < 1 cm, if flower solitary, then pedicel < 1 cm. Plant from NE Africa (incl. N Tanzania) 43

43 Upper and lower leaf lamina rather densely covered with multicellular trichomes. Plant usually of higher elevations from N Tanzania and Kenya. *C. trilobata*

43* Upper leaf lamina pustulate, but without trichomes or with tiny trichomes from pustules. Plant rather from dry habitats and lower elevations. Plants can be hard to distinguish 44

44 Leaf margin in mature leaves with conspicuously colored teeth. Leaves reniform, cordate to 3- or 5-lobate, but not lobulate. Plant densely covered with long multicellular trichomes. (Fig. 8) *C. megarrhiza*

44* Leaf margin in mature leaves without conspicuously colored teeth. Leaves lobate, with or without lobules. Plant less densely covered with trichomes or if so, then trichomes < 0.3 mm. (Fig. 2a) C*. microphylla*

42* Flowers in racemes with peduncle > 1 cm (if smaller, then from C Tanzania) or if solitary, then either pedicel > 1 cm or plant from C Tanzania 45

45 Calyx lobes subulate to narrow triangulate with pointed tip, > 2.5 mm. Plant of E Africa (Tanzania, Mozambique, Malawi) 46

46 Leaves 3-lobate, distinctly petiolate, often with few short trichomes on the main nerves of the lower lamina. Racemes with > 8 flowers. Plant of coastal forests of Kenya or NE Tanzania (Fig. 25) *C. pwaniensis*

46* Leaves subcordate to 3- or 5-lobate, subsessile or distinctly petiolate. Lower leaf lamina glabrous or nerves with short (wart-like) to long trichomes. Racemes < 10 flowers (Fig. 22). Plant of SE Tanzania, C and N Mozambique, or Malawi (Fig. 25) *C. senensis*

45* Calyx lobes < 2.5 mm or if longer, then not pointed (may be lineal though), or plant from NE Africa (Kenya, Ethiopia, Somalia) 47

47 Plant with long (> 0.5 mm) trichomes or with short narrow conical trichomes, calyx lobes > 2 mm, lineal. Plant from NE Africa 48

48 Apex of the cordate leaf or central lobe tapering long into an acute tip. Plant of high elevation (Fig. 23) *C. abyssinica*

48* Apex of leaf or central lobe retuse, blunt, or rather abruptly tapering into a short acute tip. Plant rather of lower elevation (Fig. 8) *C. megarrhiza*

47* Plant glabrous or with short trichomes (< 0.8 mm), if with longer trichomes, then not from NE Africa. Calyx lobes < 2.5 (–3) mm long. Taxa in E Africa not easily distinguishable (complex around *C. adoensis*) 49

49 Plant with long (> 0.8 mm) trichomes (Fig. 3a), calyx lobes 1.5–3 mm long, but not with pointed tip. Plant of Malawi, C, and S Tanzania, maybe also N Mozambique (Fig. 25) *C. adoensis* var. *jeffreyana*

49* Plant glabrous or with short (< 0.8 mm) trichomes 50

50 Lower leaf lamina, and usually also fresh stems, petioles, and upper leaf lamina densely covered with short (< 0.5 mm) trichomes. Peduncle often shorter than pedicelled part, corolla orange, rarely yellow? Plant of E Africa (C Tanzania; Fig. 25) *C. adoensis* var. *aurantiaca*

50* Lower leaf lamina glabrous to densely covered with trichomes, but if so, then peduncle longer than pedicelled part. Plant of E, NE, or NC Africa (Fig. 21) *C. adoensis* var. *adoensis*

33* Plant with female flowers, fruits or vegetative 51

51 Plant with female flowers 52

52 Leaves without or with small dark glands on lower leaf lamina. Flowers solitary or in ebracteate racemes. Calyx lobes lineal, spreading in buds, reflexed in mature flowers, > 2 mm long. Plant of W African rainforests (W of Dahomey Gap) (Fig. 20) *C. keayana*

52* Plant different. If with spreading to reflexed calyx lobes, then not from rainforest regions or < 2 mm long 53

53 Ovary cylindrical. Calyx lobes broader than 0.75 mm at base, corolla urceolate. Plant of W African rainforests *C. longicarpa*

53* Ovary short elliptical, obovoid or globose, if short cylindrical, then not from rainforests. Calyx lobes narrower at base 54

54 Flowers in bracteate or ebracteate racemes or solitary. Ovary globose or short obovoid. Calyx lobes < 2 mm long. Plant glabrous or with very short trichomes, without long

trichomes on vegetative parts. Plant from W and C Africa, but also in rainforest relicts or mountain forests in E Africa 55

55 Female flowers solitary or in racemes. Corolla cup-, urn- or funnel-shaped, not open campanulate. Ovary globose to ovoid. Plant from W or C (or western E) Africa. Plant of lowland or in relict highland rainforests *C. barteri*

55* Female flowers solitary. Corolla cup-shaped to campanulate. Ovary long spindle-shaped to oblong. Plant of mountain forests from Kivu Mts, Eastern Arc Mts, Livingstone Mts, also introduced in Kenyan high mts *C. mildbraedii*

54* Flowers always solitary. Calyx lobes > 2 mm or if shorter, then plant not from rainforests from regions as above 56

56 Calyx lobes spreading to reflexed, lower leaf lamina glabrous with pale glands between main veins. Leaf margin with colored teeth (Fig. 6a). Plant naturally not from C or S Africa *C. grandis*

56* Plant with trichomes or if glabrous, then with darkish glands or without glands on lower leaf lamina 57

57 Calyx lobes erect with recurved tips, lower leaf lamina with dark glands between veins, sometimes with white pustules on veins and petiole. Margin of mature leaves with colored teeth. Plant of W Africa *C. intermedia*

57* Plant different and not from W Africa or if so, then never with white pustules and dark teeth 58

58 Calyx lobes subulate to narrow triangulate with pointed tip, > 2.5 mm (Fig. 22). Plant of E Africa (Tanzania, Mozambique, Malawi; Fig. 25) 59

59 Leaves 3-lobate, distinctly petiolate, often with few short trichomes on the main nerves of the lower lamina. Plant of coastal forests of Kenya or NE Tanzania *C. pwaniensis*

59* Leaves cordate to 3- or 5-lobate, subsessile or distinctly petiolate. Lower leaf lamina glabrous or nerves with short (wart-like) to long articulate trichomes. Plant of SE Tanzania, C and N Mozambique, or Malawi *C. senensis*

58* Calyx lobes < 2.5 mm or if longer, then not with pointed tip, or plant from NE Africa (Kenya, Ethiopia, Somalia) 60

60 Plant of S Africa (S Angola, Zimbabwe, C Mozambique and further S) 61

61 Perianth tube/hypanthium with long (> 0.7 mm) trichomes or if glabrous, then calyx lobes > 2 mm *C. rehmannii*

61* Perianth tube/hypanthium with short (< 0.7 mm) trichomes, if glabrous, then calyx lobes < 2 mm *C. adoensis* var. *adoensis*

60* Plant of NC, NE or E Africa 62

62 Plant with long (> 0.5 mm) trichomes or straight narrow conical trichomes. Plant from NE Africa (Ethiopia, Kenya, Somalia, N Tanzania) 63

63 Apex of leaf or central lobe tapering long into an acute tip. Plant of high (> 800 m) elevations from Ethiopia (Fig. 23) *C. abyssinica*

63* Apex of leaf or central lobe retuse, blunt, or rather abruptly tapering into a short acute tip. Plant rather of dry habitats in lower elevation 64

64 Plant rather densely covered with long (> 0.5 mm) trichomes. Leaves rarely reniform to 3- or 5-lobate, never lobulate. Leaf apex retuse, blunt, or rather abruptly tapering into a short acute tip (Fig. 8). Leaf margin of mature leaves with dark glands. Ovary ellipsoid, never globose. Plant from N Kenya, Ethiopia and likely also Somalia *C. megarrhiza*

64* Plant rather laxely covered with trichomes, if denser, then very short (< 0.2 mm). Leaves rarely reniform to 3- or 5-lobate, sometimes also lobulate. Leaf apex never retuse, rarely blunt (e.g. around the Usambaras), often abruptly tapering into a short acute tip. Leaf margin never with dark glands. Ovary globose, rarely spindle-shaped. Plant from N- Tanzania, Kenya, Ethiopia and likely also Somalia (Fig. 2a) *C. microphylla*

62* Plant glabrous or with short (< 0.5 mm) trichomes, if with longer trichomes, then not from NE Africa. 65

65 Leaves on upper lamina with short trichomes. Calyx lobes 2–5 mm long. Plant from N Tanzania or Kenya *C. trilobata*

65* Leaves on upper lamina glabrous (but with white pustules) or if with short trichomes, then from C Tanzania. Calyx lobes < 2 mm or if longer, then lower lamina with long (> 0.8 mm) trichomes. Taxa in E Africa not easily distinguishable (complex around *C. adoensis*) 66

66 Plant with long (> 0.8 mm) trichomes that appear articulate when dry (Fig. 3a), calyx lobes 1.5–3 mm long, but not pointed. Plant of C and S Tanzania, maybe also Malawi or N Mozambique (Fig. 25) *C. adoensis* var. *jeffreyana*

66* Plant glabrous or with short (< 0.8 mm) trichomes only 67

67 Lower, sometimes also upper leaf lamina densely covered with short trichomes. Ovary densely covered with short (< 0.5 mm) trichomes. Corolla orange, rarely yellow? Plant of E Africa (C Tanzania; Fig. 25) *C. adoensis* var. *aurantiaca*

67* Lower leaf lamina glabrous over covered with short trichomes. (Fig.21) Ovary glabrous or only laxely (inconspicuously) covered with short trichomes. Corolla yellowish, pinkish or orange. Plant of E, NE, or NC Africa (Fig. 24) *C. adoensis* var. *adoensis*

51* Plant with fruits only or vegetative 68

68 Plant with fruits 69

69 Fruit long elliptical to cylindrical (> 8 cm). Plant from forests 70

70 Plant of West African rainforests *C. longicarpa*

70* Plant of mountain forests from Kivu Mts, Eastern Arc Mts, Livingstone Mts, also introduced in Kenyan high mts *C. mildbraedii*

69* Fruit globose to oblong (< 8 cm) 71

71 Fruit globose. Plant of dry habitats 72

72 Plant of N Tanzania, Kenya, S and SE Ethiopia or Somalia *C. microphylla*

72* Plant of S Africa *C. rehmannii*

71* Fruit obovoid, to oblong, if (sub-)globose, then of humid habitats 73

73 Leaf margin in maturity with colored teeth (blackening when dry), lower leaf lamina glabrous and with pale glands between main veins, petioles and veins in maturity with white pustules. Fruit obovoid to elliptical. Plant naturally not from C or S Africa *C. grandis*

73* Lower leaf lamina without glands or darkish glands or if with pale glands, then mature leaves without colored teeth on leaf margin 74

74 Fruit subglobose to obovoid-elliptical, in raceme or if solitary, then rainforest species 75

75 Fruit in ebracteate raceme or solitary. Plant from W Africa (W of Dahomey Gap) (hardly distinguishable in shared distribution range) *C. keayana* or *C. barteri*

75* Fruit in bracteate or ebracteate raceme. Plant from W and C Africa and in relict rainforest patches along the Western Rift *C. barteri*

74* Fruit solitary or 1–3 clustered, but not in raceme. Plant not of rainforests 76

76 Plant glabrous, in maturity often with white speckles on stem, petiole, and lower leaf lamina. Fruit subglobose to obovoid-elliptical, solitary or 1–3 clustered. Plant of semi-humid savannas and woodlands from W Africa *C. intermedia*

76* Plant different and not from W Africa. If from W Africa, then fruit often with sterile apex (“beak”) 77

77 Fruit elliptical to oblong, often with sterile apical tip (“beak”). Unripe with dark green/light green longitudinal stripes or mottling. Seeds rather lenticular and with symmetrical shape (Fig. 13a). Lower leaf lamina glabrous or with trichomes, if trichomes appearing articulate and > 0.5 mm, then from C and S Tanzania, maybe also Malawi or N Mozambique 78

78 Leaves 3-lobate. Leaf lamina glabrous, but veins and petiole often with few short trichomes. Plant of coastal forests from SE Kenya to E Tanzania (Fig. 25) *C. pwanienis*

78* Plant different or from different region (hardly distinguishable) 79

79 Plant with long (> 0.8 mm) trichomes (Fig. 3a) or if reduced, then stiff, but not bent (like in Fig. 21), warty or subglabrous. Plant from C and S Tanzania, Malawi or C to N Mozambique (Fig. 25) *C. senensis* or C. *adoensis* var. *jeffreyana*

79* Plant glabrous or with short (< 0.8 mm), but not warty or articulate appearing trichomes 80

80 Stem, petiole, lower leaf lamina, and ovary/young fruit densely covered with short trichomes. Plant from C Tanzania (Fig. 25) *C. adoensis* var. *aurantiaca*

80* Stem, petiole, lower leaf lamina glabrous or with short trichomes, but young fruit only with lax indument. Plant from S, E, NE, or NC Africa (Fig. 24) *C. adoensis* var. *adoensis*

77* Fruit obovoid, short to long elliptical, but not oblong and not with conspicuous sterile apical tip (“beak”). Seed face rather flat, shape often asymmetrical (Fig. 13b, c). Plant from S Africa or NE Africa, incl. Kenya and N Tanzania 81

81 Plant from S Africa *C. rehmannii*

81* Plant from NE Africa, incl. Kenya and N Tanzania 82

82 Upper leaf lamina with fine short trichomes. Lower leaf lamina with short, but not long articulate or with narrow conical trichomes. Plant of higher elevation from N Tanzania and S to C Kenya *C. trilobata*

82* Upper leaf lamina glabrous (but with pustules), rarely with narrow conical trichomes. Lower leaf lamina with often long (> 0.8 mm) articulate or with narrow conical trichomes 83

83 Apex of leaf or central lobe tapering long into an acute tip. Plant of high elevation (Fig. 23) *C. abyssinica*

83* Apex of leaf or central lobe retuse, blunt, or rather abruptly tapering into a short acute tip. Plant rather of lower elevation 84

84 Plant rather densely covered with trichomes. Leaves rarely reniform to 3- or 5-lobate, never lobulate. Leaf apex retuse, blunt, or rather abruptly tapering into a short acute tip (Fig. 8). Leaf margin of mature leaves with dark teeth. Plant from N Kenya, Ethiopia and likely also Somalia *C. megarrhiza*

84* Plant rather laxely covered with trichomes or if densely, then very short (< 0.5 mm). Leaves rarely reniform to 3- or 5-lobate, sometimes also lobulate. Leaf apex never retuse, rarely blunt (e.g. around the Usambaras), often abruptly tapering into a short acute tip. Leaf margin never with dark teeth. Ovary globose, rarely spindle-shaped.

Plant from N-Tanzania, Kenya, Ethiopia and likely also Somalia (Fig. 2a) *C. microphylla*

68* Plants with vegetative characters only 85

85 Plant glabrous, lower leaf lamina with pale glands (if strongly oxidized then also dark, but then leaf margin also with black markings/teeth) between veins, veins in maturity often with white speckles. Leaf margin at maturity with colored teeth (Fig. 6a). Plant of W to NE Africa, incl. Kenya and N Tanzania *C. grandis*

85* Plant with trichomes or if glabrous, then with darkish glands between veins or without glands on lower lamina 86

86 Plant from W Africa 87

87 Leaves cordate to 5-lobate, rarely broader than 10 cm, rather papery, lobes triangulate to narrow lanceolate or oblong. Lower leaf lamina without white speckles, glabrous or with often short bent trichomes (Fig. 21). Plant of semi-humid savannas and woodlands from N Cameroon, N Nigeria, distribution in the area imperfectly known *C. adoensis* var. *adoensis*

87* Leaves cordate to subhastate to 3- or 5-lobate, mature often > 10 cm broad. Leaf lobes triangulate to broad lanceolate, but not narrow lanceolate or oblong. Rainforest species or if from semi-humid savannas or woodlands (rarely dry forests), then margin of mature leaves with conspicuously colored teeth and lower leaf lamina often with white speckles 88

88 Plant glabrous, in maturity often with white speckles on stem, petiole, and lower leaf lamina. Margin of mature leaves with conspicuously colored leaves. Plant of semi-humid savannas and woodlands from W Africa *C. intermedia*

88* Plant different, from rainforests or gallery forests. Species not confidently distinguishable *C. barteri*, *C. keayana*, or *C. longicarpa*

86* Plant not from W Africa 89

89 Leaves coriaceous. Plant glabrous or puberolous on abaxial side of petiole. Rainforest or mountain forest plant of C Africa or western E Africa (along the Western Rift), plants hardly distinguishable 90

90 Lowland rainforest (in relict sites of western E Africa also in mountains) plant from C Africa, incl. areas around Kivu Mts, Chimanimani Mts, and forests (mountain ranges) along the Western Rift, incl. Uganda *C. barteri*

90* Plant of mountain forests from Kivu Mts, Eastern Arc Mts, Livingstone Mts, also introduced in Kenyan high mts *C. mildbraedii*

89* Plant not from C African rainforests 91

91 Plant of S Africa 92

92 Lower leaf lamina with usually bent trichomes, never white speckled, rarely subglabrous (Fig. 21) *C. adoensis* var. *adoensis*

92* Lower leaf lamina with straight, in herbarium specimens often articulate appearing trichomes, often with white speckles towards maturity or glabrous *C. rehmannii*

91* Plant of E, NE, or NC Africa 93

93 Plant of NE or NC Africa 94

94 Teeth on leaf margin conspicuously colored. Plant from NE Africa 95

95 Apex of leaf or central lobe tapering long into an acute tip. Plant of high elevation (> 900 m; Fig. 23) *C. abyssinica*

95* Apex of leaf or central lobe retuse, blunt, or rather abruptly tapering into a short acute tip. Plant rather of lower elevation (< 1200 m) (Fig. 8) *C. megarrhiza*

94* Teeth on leaf margin not conspicuously colored. Plant from NC or NE Africa 96

96 Lower leaf lamina glabrous or short (often) with bent trichomes, cordate to deeply lobate (Fig. 21). Plant from NC and NE Africa *C. adoensis* var. *adoensis*

96* Lower leaf lamina with long (> 0.5 mm) trichomes that appear articulate when dry, or with narrow conical trichomes. Plant from NE Africa 97

97 Lower leaf lamina densely with long (> 0.5 mm) trichomes that appear articulate when dry (if so, then petiole and stem, too) or with narrow conical trichomes. Leaves cordate to lobate, but never lobulate. If profoundly lobate, then central lobe lanceolate or ovate tapering into an acute tip. Plant of higher elevations (> 900 m) or cultivated, from Ethiopia (Fig. 23) *C. abyssinica*

97* Apex of leaf or central lobe retuse, blunt, rather abruptly tapering into a short acute tip, or if longer tapering into an acute tip, then lobes lobulate. Plant rather of lower elevation (< 1200 m, only in Kenya rarely higher) 98

98 Lower leaf lamina with long (> 0.5 mm) trichomes that appear articulate when dry, rarely with conical trichomes. Apex of leaf or central lobe retuse, blunt, or rather abruptly tapering into a short acute tip. Plant rather of lower elevation (< 1200 m) (Fig. 8) *C. megarrhiza*

98* Lower leaf lamina with long (> 0.5 mm) trichomes that appear articulate when dry, but never with conical trichomes. Leaves 3 or 5- lobate, lobes with or without lobules. If lobes ovate, then not tapering long into an acute tip. Plant rather of low elevation drylands (rarely in higher elevations). (Fig. 2a) *C. microphylla*

93* Plant of E Africa 99

99 Leaves 3- or 5-lobate. Lobes spreading, not pointing towards apex, broad triangulate, elliptical, ovate or somewhat angulate, but not narrow, oblong, or lineal. Upper and lower leaf lamina with short white trichomes. Stem often with trichomes that appear articulate when dry (Fig. 7b). Plant of higher elevations from N Tanzania and Kenyan highlands (Fig. 33) *C. trilobata*

99* Upper lamina glabrous (but pustulate) or if with trichomes then leaf shape different or from different region 100

100 Leaves 3-lobate (rather small auriculate), lobes pointing towards apex, upper lamina glabrous (but pustulate), lower lamina glabrous, but often with short trichomes on main veins. Plant of coastal forests from SE Kenya and NE to E Tanzania (Fig. 25) *C. pwaniensis*

100* Plant different or from different area (in some cases hard to distinguish) 101

101 Lower leaf lamina with long (> 0.5 mm) trichomes that appear articulate when dry or reduced to warts, rarely almost glabrous; sometimes leaves subsessile (Fig. 25) *C. senensis* or *C. adoensis* var. *jeffreyana*

101* Lower leaf lamina glabrous or with short thin, straight or bent trichomes 102

102 Lower leaf lamina (also often upper lamina), petiole and stem rather densely covered with short trichomes. Plant of C Tanzania *C. adoensis* var. *aurantiaca*

102* Lower leaf lamina glabrous or covered with trichomes, if densely, then upper lamina glabrous (but pustulate) or with few straight trichomes, but not tomentose. Plant widespread in E Africa *C. adoensis* var. *adoensis*

Taxonomic treatment

Herbarium abbreviations follow Index Herbariorum. Digital specimens were accessed from the homepages of the corresponding herbaria, except for “JPS” (= JStor Plant Science; http://plants.jstor.org/) and “CVH” (= Chinese Virtual Herbarium; http://www.cvh.org.cn/cms/).

Coccinia abyssinica (Lam.) Cogn. in A.DC & C.DC., Monogr. Phan. 3: 536. 1881.

Bryonia abyssinica Lam. Encyclopédie méthodique botanique 1: 497. 1783. TYPE: ETHIOPIA. Unknown, cultivated in Paris Royal Botanical Garden, J.-B.Lamarck s.n. (Holotype: P-LAM!).

Coccinia diversifolia Naudin in C.Huber, Cat. Print. 1864: 6. 1864. TYPE: ETHIOPIA. Mountains, types from seeds sent by Schimper in Paris Botanical Garden and Huber’s garden in Olbia, C.V.Naudin s.n. (Lectotype, designated by Jeffrey (1962): P; isolectotypes: G-DC!, G-DC!, G-DC!, G-DC!, G-DC!, K)

Cephalandra diversifolia (Naudin ex C.Huber) Naudin Ann. Sci. Nat. Bot. 5: 19, ser. 5. 1866. nom. illeg.

Coccinia diversifolia Naudin in C.Huber var. *glabrescens* Cogn. in A. DC and C. DC., Monogr. Phan. 3: 537. 1881. TYPE: ETHIOPIA. Chaqou-Choada, 2000 m, in thicket, male, fl, 21 Jul 1852, G.H.W.Schimper 250 (Lectotype: P! (sheet with descriptive text), designated here; isolectotypes: P!, P!).

Cucurbita exanthematica Fenzl ex A.Rich. Tent. Fl. Abyss. 1: 296. 1847. TYPE: ETHIOPIA. without detailed location, G.H.W.Schimper 1418 (Lectotype: W!, designated here; isolectotypes: BM!, G!, P!, TUB004727!, non TUB-004726!).

Bryonia macrophylla Ser. ex DC. Prodomus systematis naturalis regni vegetabilis 3: 308. 1827. TYPE: without location [probably Ethiopia]. male and female, fl, 1815, Thibaud s.n. (Holotype: G-DC!).

Cucumis? striatus A.Rich., Tent. Fl. Abyss. 1: 295. 1847. TYPE: ETHIOPIA. [Tigray region]: Mt Selleuda [Mt Sholada] near Adwa, fr, Aug, R.Quartin-Dillon s.n. (Holotype: P!).

Description. Perennial climber. Stem up to 5 m, covered with more or less dense, articulate, smutty-white to yellowish trichomes. Petioles 1.5–14 cm, at least on nerves more or less densely covered with articulate trichomes, rarely glabrous. Leaves 7.5–12 × 6.5–12 cm, often cordate to profoundly 3- or 5-lobate. If lobate, then central lobe dominating, outer shape rather long cordate (Fig. 4a). Lobes triangulate, ovate to elliptical. Margin more or less densely serrate, dentate. Dents rarely (if so, then small) pale brownish colored in living state or blackish when dried. Leaf apex acute, or if leaf lobate, then central lobe acute to long acuminate. Upper leaf surface with clear or whitish pustules, sometimes with some trichomes, nerves glabrous or with stiff adpressed trichomes. Lower leaf lamina with soft trichomes articulate appearing when dry or sparsely with stiff narrow cylindrical trichomes, which when short can appear warty. Probracts up to 3 mm long. Tendrils simple. Male flowers solitary or in long-pedicelled few-flowered racemes. Pedicel with indument as on stem. Common peduncle of raceme 2.5–10 cm, pedicel of flowers in racemes up to 1.5 cm, indument as on stem or less dense. Bracts up to 1.7 mm long or missing. Solitary flowers with up to 5 cm long pedicel with trichomes as on stem. Perianth tube more or less densely covered with articulate trichomes. Calyx lobes 2–4 mm, lineal-subulate, upright. Corolla c. 1.4 cm long, yellow to slightly orange, darker on the lobes, lobes up to 5 mm. Filament column white, anther head pale yellowish green, pollen sacs yellow. Female flowers solitary. Pedicel up to 3.5 cm long, indument as on stem to glabrous. Style, stigmas, and staminodes not seen. Ovary with long trichomes, often appearing articulate when dry. Hypanthium more or less densely covered with long articulate trichomes, calyx lobes and corolla as in males. Style not seen. Stigma shape not seen, yellow. Fruits 5.5–6 × 3.5–4 cm, short elliptical, glabrous, orange-red with yellow longitudinal mottling. Seeds 5–6 × 3 × 1.5 cm (L/W/H), slightly asymmetrical obovate, face flat (Fig. 13b).

Phenology. June–October.

Distribution. Fig. 23 Ethiopia (Amhara, Oromia, Southern Nations, Nationalities and People's Region, Tigray). Elevation 1300–2400 m. On limestone, sandstone, black soil, loam, on sandstone rock or shallow soil. Along lake shores among *Typha* sp., in *Podocarpus-Celtis* forest (clearings) and degraded forms of these, evergreen (e.g. *Euclea* sp.) shrubs.

Use. Edibility of fruits is disputed and may differ between wild and cultivated forms (E.Westphal & J.M.C.Westphal-Stevels 1951 and 1953). Tuberous roots boiled for food (T.Ebba 250). For details see chapter Use, economic potential, and phytochemistry.

Vernacular names. Dawuro: shushe, ushushe (Hora 1995); Galinya [Oromo]: anchote (Getahun 1974a); Kefinya [Kaffa]: ajjo (Hora 1995); Tigrinya: wouchich (G.H.W.Schimper 1048); Wollamo [Wolleyta]: ušuše (W.Kuls 681). The Kefinya name is not exclusive for *C. abyssinica*, but also used for another crop, *Plectranthus edulis* (Vatke) Agnew.

Remarks. Monoecy reported by W.J.J.O.de Wilde et al. 7805, but not shown/collected. Likely to be a case of leaky dioecy (see also chapter Chromosomes and inheritance of sex).

Taxonomical remarks. *Cucurbita exanthematica* Fenzl ex A.Rich. is quite commonly recognized as a synonym of *C. grandis* with a Kotschy specimen as type. However, the label on the T.Kotschy 308 specimens merely states the species name, meaning merely and "frutices scandens" (= climbing on shrubs; W.Greuter – pers. comm.), which cannot be regarded as diagnostic feature. The label is a printed matter and therefore effectively published, but not validly. A valid publication of that name has been done by Achille Richard (1847), but he used a different specimen (G.H.W.Schimper 1418), which is a *C. abyssinica*. The Schimper 1418 specimens bear printed labels, on which Fenzl designated a variety of his invalid name with a name that consists of several words ("var. foliis superioribus integris (non lobatis)"), which is also not valid as the species, to which this variety is supposed to belong to, is not validly described either (Art. 41.3a and b ICBN). Naudin (1859) suggested that Eduard Fenzl mixed up some specimens. Naudin accepted the T.Kotschy 308 specimen as a synonym of his *C. schimperi* and recognized the similarity of the Schimper specimen to Lamarck's *Bryonia* (*Coccinia*) *abyssinica* and *Cucumis striatus*.

Specimens examined. (Selection, in total: 49) Ethiopia. Amhara: Sanka-Berr [vicinity of Reb river] and Begemder [highland], G.H.W.Schimper 1446 (E, S, S, W, Z, Z, Z). Oromia: 32 km from Addis Abeba on road to Debre Zeit [Debre Zeyit], E.Westphal & J.M.C.Westphal-Stevels 1951 (BR, EA, MO, PRE, WAG 3 sheets) & 1953 (MO, WAG, WAG). SNNPR: Bonga, near Roman Catholic Mission, W.J.J.O.de Wilde & B.E.E.de Wilde-Duyfjes 7805 (MO, WAG, WAG, WAG). Tigray: 18 km along road from Adu Abun to Axum, 14°09’N 38°49’E, J.J.F.E.de Wilde 7059 (M, WAG, WAG).

Coccinia adoensis (Hochst. ex A.Rich.) Cogn. ssp. *adoensis* var. *adoensis* **stat. nov.**

Coccinia adoensis (Hochst. ex A.Rich.) Cogn. in A. DC & C. DC., Monogr. Phan. 3: 538. 1881.

Momordica adoensis Hochst. ex A.Rich., Tent. Fl. Abyss. 1: 293. 1847. TYPE: ETHIOPIA. [Tigray region]: Adwa, near church “Eta Mariam”, mixed specimens, male and female, fl, fr, 5 Jun 1837, G.H.W.Schimper Iter Abyss. sect. 1 no.166 (Lectotype, designated here: P00346261!, digital image! [P]; isolectotypes: BM!, BR! digital image! [JPS], BR! digital image! [JPS], G!, G!, G-DC!, HBG!, K!, K!, K!, L! digital image! [L], M! digital image! [JPS], M! digital image! [JPS], P00346262!, digital image! [P], TUB004719, TUB004720, W!, W!). TYPE: ETHIOPIA. [Tigray Region]: near Adwa, in thicket, R.Quartin-Dillon s.n. (Paralectotype: P!). TYPE: ETHIOPIA. [Amhara region?]: Ouodgerate Province, A.Petit no.? (Paralectotype: P?).

Bryonia convolvuloides A.Rich., Tent. Fl. Abyss. 1: 289, Paris. 1847. TYPE: ERITREA/ETHIOPIA. [Gash-barka region/Tigray region]: Chiré [borderland between both regions, between Tekezé river and Mareb/Gash river], male, fl, 1844. R.Quartin-Dillon & A.Petit s.n. (Lectotype (the sheet with Cogniaux’ label), designated here: P!; isolectotype: P!).

Coccinia djurensis Schweinf. et Gilg, Bot. Jahrb. 34: 357. 1904. TYPE: SOUTHERN SUDAN. [West Bahr al-Ghazal]: Djur realm, Seriba Agad Wau [Waw], fr, May, G.Schweinfurth 1688 (Paralectotype: B destroyed; K!; L!). TYPE: SOUTHERN SUDAN. [West Bahr al-Ghazal or Warab]: Seriba Ghattas, male, fl, 24 May 1869, G.Schweinfurth 1867 (Paralectotype: if B, then destroyed). TYPE: SOUTHERN SUDAN. ibid., male, 24 May 1869 or Jun 1869, G.Schweinfurth 1878 (Lectotype, designated here: P!; isolectotypes: B destroyed, E!, G!, K!, PRE digital image! [JPS], S!, Z!).

Coccinia hartmanniana Schweinf., Reliquiae Kotschyanae: 42, t. 17, t. 18. 1868. TYPE: SUDAN. Sinnar Province: no detailed location given, 1860, R.Hartmann s.n. (Syntype: ?). TYPE: SOUTHERN SUDAN. At White Nile in the region of the Tschier people [a nilotic tribe also called: Chir, Kir, Mandari, Mondari, Mundari, Shir], [possibly the area between Tombe and Mongalla in Central Equatoria state], 1861, W.v.Harnier s.n. (Syntype: B destroyed, ?). TYPE: SOUTHERN SUDAN. [al-Qadarif]: Gallabat at Gendua [river], Jun 1861, H.Steudner 843 (Syntype: ?). TYPE: ETHIOPIA. [Amhara region]: near Matamma at border to Sudan, after beginning of Jun 1865 G.Schweinfurth no. 62 Flora of Gallabat (Syntype: ?).

Coccinia homblei Cogn. Bull. Jard. Bot. État Bruxelles 5: 114. 1916. TYPE: D. R. CONGO. Katanga: Lualaba region, Kapanda confluence plains, Dec 1912, H.Homblé 992 (Lectotype, designated here: BR888717!; isolectotype: BR!). TYPE: D. R. CONGO. Katanga: Kapiri valley, Feb 1919, H.Homblé 1198 (Paralectotype: BR!, BR!). TYPE: D. R. CONGO. Katanga: Kapiri valley, male, fl, Feb 1919, H.Homblé 1199 (Paralectotype: BR!, BR!, BR! photo: K!).

Coccinia jatrophiifolia (A.Rich.) Cogn. [sphalm: *Coccinia jatrophæfolia* (A.Rich.) Cogn.], in A. DC & C. DC., Monogr. Phan. 3: 535. 1881.

Bryonia jatrophiifolia A.Rich. [sphalm. *Bryonia jatrotrophæfolia* A.Rich.] Tent. Fl. Abyss. 1: 289. 1847. TYPE: ETHIOPIA. [Tigray region]: in valley near Adwa, fl, Aug 1839, R.Quartin-Dillon & A.Petit s.n. (Lectotype, designated here P00346263!, Paralectotype: P!). TYPE: ERITREA/ETHIOPIA. [Tigray region]: near Tchélatchekanné [Dscheladscheranne, in Tekezé river valley (Gillett 1972), on label as “Tchessu Hetchequenné”], R.Quartin-Dillon s.n. (Paralectotype: P00346260!, P!).

Coccinia parvifolia Cogn. in Schinz, Vierteljahresschrift der Naturforschenden Gesellschaft Zürich 52: 433. 1907. TYPE: SOUTH AFRICA. Limpopo: [Mopani District], [Leydsdorp area], Mt Marovounge [must read: Mt Marovougne], fl, male, H.A.Junod 2491 (Holotype: Z digital image! [Z], isotype: BR!).

Coccinia princeae Gilg, Bot. Jahrb. 34: 358. 1904. TYPE: TANZANIA. Iringa Region: Uhehe highland, no detailed location given, fr, Prince s.n. (Holotype: if B, then destroyed).

Coccinia pubescens (Sond.) Eyles, Trans. Roy. Soc. South Africa 5(4): 498. 1916.

Coccinia pubescens (Sond.) Cogn. ex Harms in Fries, Notizbl. Bot. Gart. Berlin-Dahlem 8: 491. 1923. nom. superfl.

Cephalandra pubescens Sond. in Harvey et Sonder, Flora Capensis 2: 493. 1862. TYPE: SOUTH AFRICA. [North West Province]: Magaliesberg, fl (male + female), Dec, J.Burke 408 (Lectotype, designated here: K000313229! digital image [K]!; isolectotype: BM!, K! digital image [K], NBG, Z!). TYPE: SOUTH AFRICA. North West/Gauteng: at Magalies river, fl male or female, C.L.P.Zeyher 588 (Paralectotype: K! digital image! [K], S!)

Coccinia rigida Cogn., Bot. Jahrb. 21: 210-211. 1895. TYPE: TANZANIA. [Tabora District]: Ugunda, near Gonda [Igonda], on ground in wet corn fields, R.Böhm 176 (Holotype: B destroyed, Lectotype: BR! digital image! [JPS])

Coccinia roseiflora Suess. Proc. Trans. Rhodes. Sci. Ass. 43: 134 (1951). TYPE: ZIMBABWE. [Mashonaland East], Marandellas [Marondera], 31 Nov 1941, G.Dehn 188A (Holotype: M!)

Coccinia subspicata Cogn. Bull. Jard. Bot. État Bruxelles 5: 115. 1916. TYPE: D. R. CONGO. Katanga: Lualaba region, Kapanda confluence plains, Dec 1912, H.Homblé 992a (Holotype: BR! photo: K!)

Description. Perennial climber or creeper. Shoots up to 6 m long, glabrous to densely covered with trichomes. Indument whitish, rather short, often bent (Fig. 21). Petioles 0.6–3.5 cm, glabrous, pubescent to tomentose with indument like on stem. Leaves 4.2–13.5 × 4.7–16 cm, cordate, very shallowly to deeply 3- or 5-lobate, rarely elliptical with hastate base. If profoundly to deeply lobate, then lobes often (slightly) pointing towards apex. Lobes tri-angulate, lanceolate, lineal, elliptical to obovate. Leaf margin smooth to serrate (esp. on outer sides) to lobulate. Tips of lobes retuse, blunt to acute, often with final tooth. Upper leaf lamina clear to white pustulate, rarely with whitish trichomes. Lower leaf lamina soft pubescent with short, whitish trichomes, rarely glabrous, towards the base often black to dark brown glands between nerves, rarely also along main nerves. Probracts missing or obovoid up to 2.5 mm long. Tendrils simple, rarely bifid. Male flowers in few to many-flowered racemes, often accompanied by one solitary flower. Common peduncle 1–11 cm, glabrous or with short trichomes. Pedicel of racemous flower 0.4–1.3 cm, indument like peduncle, pedicel of solitary flower 1.5–4 cm glabrous or with short white trichomes. Bracts missing (caducous?) or up to 2 mm. Perianth tube glabrous or with short (< 0.5 mm) white trichomes. Calyx lobes 1.2–2.5(–3) mm, lineal to broad triangulate, adpressed to spreading, apex obtuse to acute, but not acuminate. Corolla 0.9–1.6 cm, yellow, salmon-pink, orange, maroon, veins sometimes purplish–brownish, lobes 0.2–0.5 cm. Filament column whitish to orange, anthers whitish?, yellowish to orange, pollen sacs yellow to orange. Female flowers solitary. Pedicel 0.8–3.5 cm often glabrous or with short white trichomes. Hypanthium glabrous or with short (< 0.5 mm) white trichomes, calyx lobes, and corolla like in male flowers. Ovary glabrous. Style and stigmas not seen. Fruits 3–7 × 1–1.5 cm, ovoid, oblong to short cylindrical, orange-red to red, often with sterile tip (“beaked”). Seeds 4.0–6.0 × 3.0–4.0 × 1.0–1.7 mm (L/W/H), symmetrical pear-shaped, face lenticular (Fig. 13a).

Phenology. January–May, August–December.

Distribution. Fig. 24. Angola? (likely in the South and East), Botswana (North West Region), Burundi?, Cameroon (Extreme North), Central African Republic? (likely in the north), Chad? (likely in the south), Democratic Republic of Congo (Katanga, along the Western Rift), Eritrea (Gash-Barka, likely wider distributed as relicts in the highlands), Ethiopia (except the dry southeast), Kenya (in the west and central highlands), Malawi, Mozambique, N Namibia, Nigeria (only known from Adamawa State, but likely more widely distributed), Rwanda (Eastern Province, maybe wider distributed), South Africa (Gauteng, KwaZulu-Natal, Limpopo, Mpumalanga, E Northwestern, E Free State), Southern Sudan, Sudan (West Darfur, maybe wider in woodland relict sites), Swaziland, Tanzania, Uganda (Northern Region), Zambia, Zimbabwe. Elevation 130–3450 m. On sandy loams, silty-sandy soils, grey sandy soils, lateritized soils, syenite soils, dolomite soil. *Hyparrhenia cymbaria* savanna; *Crossopteryx* tree savanna; *Acacia-Combretum-Stereospermum-Cussonia* woodland; *Pseuodoprosopis fischeri* woodland, *Anogeissus leiocarpus* woodland, *Brachystegia* woodland, sourveld, *Melhania rehmannii-Enneapogon scoparius* mixed bushveld (Siebert et al. 2010).

Use. Roots are boiled and drunk for fever (J.C.Lovett & C.J.Kayombo 3434). The potato-like tubers are eaten (F.W.Andrews 1310), also raw (T. Scudder 56). The greens are used as spinach, among others by Venda people (N.J.van Warmelo s.n. Mar 1960, J.Gerstner 5838) and also eaten by the Luo (Johns and Kokwaro 1991). Ripe fruits are edible (J.C.Lovett et al. 3842, J.Pawek 11008, T.Scudder 56). According to de Boer and colleagues (2005), the Pare people in Tanzania use an infusion of leaves and stems for abortions, uterus cleansing, and against chickenpox. *Coccinia adoensis* is quite variable and so there are likely many varie-ties, of which some might not be edible. Rehm et al. (1957) reports the cytotoxic cucurbitacin B and traces of cucurbitacin D in immature fruits, but edible ripe fruits from South Africa. Gradé et al. (2009) report that the usability or toxicity of the tuberous roots is disputed, suggesting chemical variability.

Vernacular names. Bokora tribe [Karamojong?]: edaldalakisin (Gradé et al. 2009); Kiluo: mutkuru (Johns and Kokwaro 1991), nyatunduguwoge (J.G.B.Newbould 5745); Kipare: mlushi (de Boer et al. 2005); Kisafwa: tandandala (J.C.Lovett & C.J.Kayombo 3434), ndandala (J.C.Lovett & C.J.Kayombo 3773); Kisagara (Kisagala): lutetere (F.Haerdi 563/0); Nhungoé [Cinyungwe]: mugwingwi (L.Macuácua 1441); Sotho [most likely Northern Sotho]: sephu (J.Gerstner 5838); Tigrinya: entatakh (fide G.H.W. Schimper (Schweinfurth 1893)), entota (fide A. Richard (Schweinfurth 1893)); Tshivenda: tshiphu (N.J.van Warmelo s.n. Mar 1960); Zande: bawiriokoro (F.W.Andrews 1601).

Remarks. *Coccinia adoensis* is widespread and morphologically variable. Some populations or local morphs seem to be distinct, but one can always find intermediate individuals or alike-looking specimens in different parts of the complete distribution range. In East Africa (C-Tanzania, Malawi), one can find morphs linking to *C. aurantiaca*, which I therefore treat as variety of *C. adoensis*, and *C. senensis*. The latter morphs share a similar plastid haplotype with *C. senensis*, but lack a specific deletion. These morphs are discussed in this treatment under the name *C. adoensis* var. *jeffreyana*. This non-monophyly in the plastid tree (Holstein and Renner 2011a) makes *C. adoensis* even more particular. The scenario given in the chapter Evolution and phylogeny might explain the results, but without phylogeographic analysis throughout the complete distribution range and crossing experiments, it will remain speculative.

Taxonomical remarks. The lectotypification of *Momordica adoensis* by Meeuse (1962) is not effected, as he did not specify, which specimen was supposed to be the lectotype. However, I follow his suggestion and chose among the two Schimper 166 specimens from P.

The paralectotypes of *Bryonia jatrophaefolia* are not very obvious as such. The protologue states “Tchélatchekanné”, but Paris Herbarium holds two Quartin-Dillon and Petit specimens (P00346260 and a non-barcoded one) with a location “Tchessu Heckequenné”. Although the spelling has some similarities, they are quite different. However, the two specimens bear the species name in Richard’s handwriting [C. Bräuchler, pers. comm.]

The G.Schweinfurth 1668 specimen in L is not obviously a type specimen, as it lacks the original label. However, the Herb. D’Alleizette label mentions “*Coccinia djurensis*” and the location exactly as the K duplicate with the original label. Additionally, the specimen is a fruiting female, like the specimen in K. Hence, d’Alleizette must have gotten a duplicate of the type.

The placement of *C. hartmanniana* as synonym of *C. adoensis* is with good confidence although I did not see any type specimens. The protologue has drawings showing lenticular seeds and short calyx lobes, which match well to specimens of the *C. adoensis* complex. According to Ascherson (Schweinfurth 1867), von Harnier’s collections consisted of two duplicates, one of them in B. Other duplicates of von Harnier are now found in BM and K, but seemingly not this specimen.

Specimens examined. (Selection, in total: 453) Botswana. North-West District: Ngamiland, Motantanyane, H.H.Curson 784 (M). Cameroon. Extreme North: Ziver (14 km N Mokolo), G.Fotius 1985 (P). D. R. Congo. Katanga: [Haut-Lomami district], Bukama territoire, Kanonga–Parc National [de l’] Upemba, G.F.de Witte 5499 (WAG). Orientale: Dungu territoire, Crête Congo Nil Ndelele, Parc Nationale de la Garamba, G.Troupin 466 (WAG); Faradje (Kibali-Ituri), J.Lebrun 3406 (BR, WAG). Eritrea. Gash-Barka: Seraé [Seraè, a former province], in Tucul region, A.de Benedictis 519 (FT). Ethiopia. Amhara: Dschadscha, G.H.W.Schimper 1280 (P). Benishangul-Gumuz: Gojjam region, 74 km on the new road to Guba starting 5 km S of Injibara, escarpment 16 km W of Chagni, M.Thulin & A.Hunde 4002 (K, MO). Gambela: Gambela, 24°29’E 8°17’N, J.W.Ash 3498 (WAG). Oromia: c. 25 km from Nekemti along road from Addis Ababa to Nekemti, P.C.M.Jansen 6296 (M, WAG, WAG). SNNPR: 23 km E [NNE] of Bonga along road to Jimma, 7°23’N 36°16’E, I.Friis et al. 2276 (K). Tigray: Edaga Sciaba, E.Chiovenda 581 (FT). Kenya. Central Province: Upper Galana River, near Thika, J.G.Williams B7664 (K). Eastern Province: Kitui district, c. 1 km NE of Lukenya Hill (W of Kamuwongo), UTM 37MCK9422, P.Kuchar 15187 (EA). Nyanza: Kodera forest, D.Vuyk 551 (WAG). Rift Valley province: Trans-Nzoia district, Mt Elgon, G.Taylor 3787 (S); Uasin Gishu district: near Kapsaret [Kaposoret] Forest Reserve, G.R.Williams 168 (K, MO). Malawi. Central Province: Kasungu National Park, A.Hall-Martin 1528 (PRE). Northern Province: Karonga district, 17 mls [27.2 km] N of Chilumba, J.Pawek 11008 (DSM, MO, PRE, WAG). Southern Province: Mangochi district, Chipalamawamba village, I.H.Patel & K.Kaunda 4263 (MO, MO). Mozambique. Gaza: on road 7 km from Massangena to Muzamane, Magalhães 163 (COI). Manica: Chimoio, road from Vandúzi [Nova Vandúzi] to Tete, after 3rd bridge, L.A.Grandvaux Barbosa 1323 (LISC). Nampula: Ribáuè, on km 66 of road to Malema, near Serra Murripa [mountain], A.R.Torre & M.F.Correia 16500 (MO). Niassa: Serra de Massangulo, A.F.Gomes e Sousa 1207 (COI 2 sheets). Sofala: Gorongosa, on km 23 on road from Caça National Park [Gorongosa National Park] to Vila Paiva de Andrade [Vila Gorongosa], A.R.Torre & J.Paiva 9201 (BR). Tete. Cabora Bassa [Cahora bassa dam], on road 2 km from the dam towards the Rio Mucangádzi river mouth, A.R.Torre et al. 19037 (PRE, WAG); ibid., A.R.Torre et al. 19038 (MO). Zambézia: Massingire [Morrumbala district], M’bôbo [river at Morrumbala], on road to Mopeia, A.R.Torre 5337 (M). Namibia. Caprivi: Mpilila Island, D.J.B.Killick & O.A.Leistner 3361 (PRE). Otjozondjupa: Gautscha pan, R.Story 6283 (M, PRE). Nigeria. Adamawa: 10 miles [16 km] from Mubi to Toyola, P.Wit et al. 1797 (BR, MO, MO, P, WAG, WAG). Rwanda. Eastern Province: Kibungo prefecture, Rusumo [Ruzumo Falls], savanna park, on opposite slope of A.I.D.R. [Association internationale de développement rural] camp, J.Lambinon 74/1568 (MO, WAG). South Africa. Gauteng: [City of Johannesburg], N of Eikenhof, Johannesburg, Walkerville rd., L.E.Davidson 3781 (B, M). KwaZulu-Natal: Estcourt P. R. station, J.P.H.Acocks 9843 (PRE). Limpopo: [Mookgopong Local Municipality], [SSE of Mookgopong/Naboomspruit], between [farm] Mosdene and Nylsvlei Nature Reserve on road to [farm] Klipput, E.Retief 1572 (MO, PRE, WAG). Mpumalanga: Barberton, mountain slopes above Agnes gold mine, A.Balsinhas 3140 (MO). Northwest: Scheerpoort, D.van Vuuren 434 (PRE). Southern Sudan. Central Equatoria: Yei district, near Landototo [= Lantoto?] rest house, F.W.Andrews 1310 (K). Western Equatoria: Jambio [Yambio] district, on banks of R. Rund, F.W.Andrews 1601 (K). Sudan. West Darfur: Zalingei, G.E.Wickens 1800 (K). Swaziland. Hhohho district: Black Umbuluzi Valley, 26°16'S 31°10'E, E.S.Kemp 659 (MO). Shiselweni: near Hlatikulu, R.H Compton 26397 (PRE). Tanzania. Arusha: Lake Lagarja, N side, P.J.Greenway & M.Turner 10929 (BR, EA). Dodoma: Central Province, Mpwapwa, H.J.van Rensburg 648 (EA). Iringa: Ludewa district, Livingstone Mts, on broad saddle NW of Msalaba Mt., near foot trail from Luana to Lupingu, 9°58'S 34°35'E, R.E.Gereau & C.J.Kayombo 3582 (MO). Kagera: Biharamulo, F.Akiley 5015 (EA). Kigoma: Kigoma Rural district, Kitwe Sanctuary, at fence near road to Jacobson Beach, G Gobbo et al. 184 (MO). Lindi: Selous Game Reserve, Kingupira, 8°28'S 38°33'E [38°34'E], K.Vollesen MRC 3384 (DSM, WAG). Manyara: S Masai, Lokonwa (Lolkisale), D.Peterson 360 (EA). Mbeya: Mbeya rural district, 7 km S of Ruanda II, c. 2 km of water tank at Ilembo on Ilembo–Mbalizi road, in Mbogo Forest Reserve, 9°11'S 33°18'E, D.K.Harder et al. 1459 (MO). Morogoro: Uluguru Mts, NW slopes, H.J.Schlieben 3271 (B, G, HBG, M, S). Mwanza: Ukiriguru, C.G.Glegg 19 (EA). Rukwa: Ufipa district, Mbizi forest, M.Sanane 1393 (WAG). Ruvuma: Songea, E.Milne-Redhead & P.Taylor 7876 (EA); ibid., E.Milne-Redhead & P.Taylor 7950 (B, EA, K, P, S). Shinyanga: Block 4B, B.D.Burtt 5079 (EA, K). Singida: Singida district, Mgori division, 1 km up the road from Mgori dam, 4°55'S 34°59.2'E, P.Kuchar 23442 (MO). Tanga: Handeni district, Songea bus station, F.C.Magogo 355 (EA, K). Uganda. Northern Region: [Amuru District], Acholi West District, Paileyech village near Pakiri, 2°48'N 32°09'E, J.P.T.Okello-Degaouchii 26 (EA). Zambia. Central Province: 50 mls. E of Mankoya [Kaoma] on road to Kafue Hoek, R.B.Drummond & A.J.Cookson 6722 (COI 2 sheets). Copperbelt: Ndola district, among grass by roadside near rest house Ndola township, A.Angus 918 (BR). Eastern Province: Chadiza, N.K.B.Robson 760 (MO, PRE). Lusaka: c. 10 km S of Chilanga and 23 km S of Lusaka, c. 1 km N of Kafue Road near Chilanga Cement housing; Shimabala Cave, 15°39'01''S 28°14'15''E, D.K.Harder & M.G.Bingham 2584 (K, MO). Northern Province: North Luangwa National park, 11° 46'S 32°10'E, P.P.Smith 286 (MO). Northwestern Province: Mwinilunga district, slope E of Matonchi Farm, E.Milne-Redhead 2595 (BR, PRE). Southern Province: Choma [district], Mapanza, E.A.Robinson 2944 (M). Zimbabwe. Bulawayo: Lochview road, L.C.Cross 300 (MO, PRE). Harare: Makubusi woods, near Harare, R.D.A.Bayliss 9031 (DSM, MO, PRE). Manicaland: Burma Valley, Manyara Farm, N.C.Chase 7240 (MO, PRE). Mashonaland Central: Sipolilo [Guruve] district, Nyamunyeche Estate, P.Nyariri 724 (E, MO). Mashonaland

East: Marandellas [Marondera], G.Dehn s.n. (M, M). Mashonaland West: Lomagundi district [Makonde distr.], Rukuti [Rukute] farm, [SW of] Doma area, W.B.G.Jacobsen 2116 (PRE); Lomagundi district [Makonde distr.], Farm Plateau [farm S of Mhangura, c. 16°55'S 30°10'E], W.Jacobsen 3549 (PRE); ibid., W.Jacobsen 3560 (PRE). Matabeleland North: Matetsi Safari Area Headquarters House no. 2, P.Gonde 256 (E, G, MO, P). Matabeleland South: Matoba district, Farm Besna Kobila, O.B.Miller 3171 (PRE). Midlands: Belingwe [Mberengwa] district, Ngobe Dip, H.Wild 4341 (MO).

Coccinia adoensis ssp. *adoensis* var. *aurantiaca* (C.Jeffrey) Holstein **ssp. et stat. nov.**

Coccinia aurantiaca C.Jeffrey, Kew Bull. 17: 169. 1963.

TYPE: TANZANIA. Dodoma: Kondoa District, Great North road, 15 miles S of Kondoa, 1310 m, fl, fr, 19 Jan 1962, R.Polhill & S.Paulo 1221 (Holotype: K! digital image! [JPS, K], isotypes: B! digital image! [JPS, B], B! digital image! [JPS, B], BR! digital image! [JPS], EA!, EA!, K digital image [JPS], PRE digital image! [JPS], PRE digital image! [JPS]). TYPE: TANZANIA. Mwanza: Mwanza, Butimba, Ilemera, R.E.S.Tanner 1902 (Paratype: BR!, EA!, K!, K!). TYPE: TANZANIA. Mwanza: [Misungwi District], Mbarika [Mbalika?, Mbalita?], Buzomo, R.E.S.Tanner 1068 (Paratype: BR!, COI!, COI!, EA!, K!, NY!). TYPE: TANZANIA. Mwanza: [Misungwi District], Mwanza, R.E.S.Tanner 646 (Paratype: K!). TYPE: TANZANIA. Shinyanga: near Shinyanga, R.D.Bax 57 (Paratype: K!, K!). TYPE: TANZANIA. Shinyanga: hills near Shinyanga, B.D.Burtt 2517 (Paratype: K!). TYPE: TANZANIA. Shinyanga: Shinyanga, H.Koritschoner 1823 (Paratype: EA!, EA!, K!). TYPE: TANZANIA. Dodoma: 1.5 km S of Dodoma, Imagi hill, R.Polhill & S.Paulo 1274 (Paratype: B! digital image! [JPS, B], BR!, EA!, K!, K!, K!, P! p.p., PRE!, S!).

Description. Perennial climber. Stems up to 10 m, densely with short (< 0.5 mm) stiff whitish trichomes, almost tomentose. Petiole 1.5–3.5 cm densely covered with short stiff whitish trichomes, almost tomentose. Leaves 5.2–12.5 × 6.4–14.5 cm, cordate to shallowly to profoundly 3- or 5-lobate. Lobes triangulate, ovate, elliptical to obovate. Margin serrate to lobulate. Apex with final tooth, obtuse, rarely acute. Upper lamina white-pustulate sometimes with more or less pubescent with short whitish trichomes. Lower leaf lamina usually densely covered with bent trichomes on nerves. Probracts up to 1.5 mm, often caducous. Tendrils simple. Male flowers solitary or in racemes. Common peduncle 0.4–3 cm, indument as on stem, pedicels in racemes up to 0.5 cm, indument as on stem, pedicel of solitary flowers 1–2 cm, indument as on stem. Bracts up to 1.5 mm, persisting. Perianth tube densely covered with short (< 0.5 mm) trichomes. Calyx lobes 1–3 mm, narrow triangulate to dentate, spreading. Corolla 1.6–2.4 cm long, pale yellow-brown to orange, rarely? yellow, with green to orange venation, lobes 0.6–1 cm. Filament column, anther head, and pollen sacs more or less pale orange, rarely yellowish? (Fig. 9b). Female flowers solitary, pedicel 1.2–4 cm, indument as on stem. Hypanthium dense short (< 0.5 mm), calyx lobes, and corolla as in male flowers. Style shape not seen, green. Stigma shape not seen, yellow to orange. Ovary with short trichomes. Unripe fruits pale green with irregular lighter spots and dark green longitudinal lines. Fruits 5–9 × 1.5–3.5 cm, long ovoid, tip sometimes beaked, when ripe orange-red. Seeds 6–6.5 × 3.5–4 × 1.5–1.7 mm [L/W/H], slightly asymmetrical, face flat lenticular.

Phenology. January, March, July, October, December.

Distribution. Fig. 25. Tanzania (Dodoma, Iringa, Manyara, Morogoro, Mwanza). Elevation 600–1200 m. Red sandy soil, red clay, granite. White clay. Gray sand. Brown sandy loam. Dry Miombo woodland, *Acacia tanganyikensis-A. tortilis* ssp. *spirocarpa-Adansonia digitata-Maerua crassifolia-Balanites aegyptiaca* woodland, long grass savannas, dry (*Commiphora-Acacia*) bushland, thickets (e.g. *Combretum* thickets), among rocks on hills.

Use. Leaves are boiled and eaten (J.L.Newman 62).

Vernacular names. Sandawe language: koba (J.L.Newman 62)

Remarks. It is not very clear, whether this is a true species, therefore I treat it as a variety of the polymorphic *C. adoensis*. *Coccinia adoensis* var. *aurantiaca* specimens as listed here are usually more densely covered with trichomes than *C. adoensis* var. *adoensis*. Jeffrey splitted the species from the polymorphic *C. adoensis*, because of the non-beaked fruits and flat seeds with a hyaline girdle. The beak is a sterile part of the ovary with variable length, but it might not occur in all populations. Two of the paratypes (R.Polhill & S.Paulo 1274 (BR, P)), which are vegetatively matching other *C. adoensis* var. *aurantiaca* specimens, have a slightly beaked fruit, although most other specimens do not. The seeds are also not much distinct from *C. adoensis*, maybe a bit larger. Seeds in *Coccinia* are enclosed in a hyaline aril. Jeffrey just observed the dry collapsed aril, which is not part of the seed, as “hyaline girdle”. The orange color of the petals, even with purple venation also occurs in individuals of *C. adoensis* var. *adoensis* that have a less dense indument. The corolla is thus not a proper distinction character, too. However, this variety occurs locally rather in a drier range of the total *C. adoensis* distribution.

Taxonomical remarks. The flowers in the R.Polhill & S.Paulo 1274 specimen in P do not belong to *Coccinia* and seem to be mistaken. The calyx looks rather like *Momordica foetida* Schum. & Thonn. The HEID specimen (HEID779579) of that collection is also mistaken. It has a completely different indument and a narrow, almost cylindrical perianth tube.

Specimens examined. (Selection, in total: 29) Tanzania. Dodoma: Dodoma–Kondoa road, c. 20 km S of Kondoa, 05°16'31.5"S 35°53'01.1"E, N.Holstein et al. 85 (DSM, M), and 86 (M); [Kondoa district], c. 8 km from Kondoa towards Sandawi, along Kwamtoro [Kwa Mtoro Mt.] road, E.S.Macha 600 (NHT); Kongwa, B. Anderson 313 (EA); Bereko [Bereku] H.M.Richards 28275 (EA). Iringa: Iringa Rural District, along Iringa–Ruaha park road on branch that follows the park boundary, c. 37 km from the ferry in the park, 7°47’S 35°13’E, C.M.Taylor et al. 8404 (MO); Iringa Rural District, along road Iringa–Morogoro road and Lukosi River, at bottom of Kitonga Gorge, c. 6 km W of Mahenge village at milepost 253 km from Morogoro, 7°38’ 36°14’E [7°34’S 36°19’E], C.M.Taylor et al. 8485 (K, MO); Iringa Rural District, along road Iringa–Morogoro road, c. 6 km E of Mahenge village, 7°38’S 36°14’E [7°32’S 36°25’E], C.M.Taylor et al. 8501 (K, MO); Mbatwa, 7°35’S 36°37’E, P.A.Luke & W.R.Q.Luke 9345 (EA); [Ruaha National Park], Msembi [near airfield], P.J.Greenway & Kanuri 14811 (EA 2 sheets, K, M). Manyara: Mbulu district, Tarangire river, no detailed location, H.S.Mahinda 414 (EA, K); Tarangire National Park, road Tarangire camp–Babati, 1 ml. from camp, H.M.Richards 24817 (EA, K). Morogoro: Kilosa district, Elphon’s Pass, 7°22’S 36°42’E, J.C.Lovett & T.C.E.Congdon 2931 (K, MO).

Coccinia adoensis ssp. *adoensis* var. *jeffreyana* Holstein **var.nov.**

TYPE: TANZANIA. Iringa, Mufindi District, Ngwazi, 8°30’S 35°15’E, 1830 m, female, fl, fr, 25 Feb 1987, J.C.Lovett 1597 (Holotype: MO!, isotype: EA!)

Diagnosis. Variety with affinities to *C. adoensis* and *C. senensis*. The abaxial side of the petiole and the lower leaf lamina bear trichomes with long cells, which appear crumpled or articulate when dry. Most of the trichomes, esp. on the nodes, supercede 0.8 (–1.2 mm), whereas trichomes of *C. adoensis* var. *adoensis* and var. *aurantiaca* are shorter < 0.5(–0.8) mm. The calyx lobe length often exceeds 2 mm (in contrast to other *C. adoensis* varieties), but the lobes are not subulate or narrow acute like in *C. senensis*, but rather lineal or if narrowly triangulate, then not with a pointed tip.

Description. Perennial creeper or climber. Stems length up to 3 m (maybe longer), more or less dense with long (at least on the nodes > 0.8 mm) trichomes that appear articulate when dry. Petiole 0.25–3.5 cm, subsessile to distinctly petiolate, with long patent trichomes. Leaves 3.2–10.5 × 2.6–12 cm, shallowly to profoundly 3- or 5-lobate, lobes triangulate, ovate to elliptical, margin dentate, slightly serrate, apex obtuse with apical tip to acute. Upper lamina glabrous or with few trichomes, hyaline to white pustulate. Lower leaf lamina more or less dense with articulate trichomes, rarely almost glabrous with white pustules on veins. Probracts up to 3 mm. Tendrils simple. Male flowers in racemes, often accompanied by a single flower or one solitary. Common peduncle 5.0–5.5 cm, with short articulate trichomes. Pedicel of racemous flowers 0.5–0.9 cm, with short articulate trichomes. Bracts up to 1 mm, caducous. Pedicel of solitary flower 2.2–7.8 cm, with short articulate trichomes. Hypanthium with short trichomes. Calyx lobes 1.0–3.5 mm, narrow triangulate, but not subulate, erect. Corolla 1.1–1.65 cm, yellow, orange, to dark crimson with darker veins outside, lobes 0.4–0.7 cm. Color of filament column pink, anther head orange-yellow to orange, color of pollen sacs not seen. Female flowers solitary. Pedicel 0.6–1.7 cm long, puberulous. Ovary with short to long articulate trichomes. Fruit size c. 2–6 × c. 1 cm long, elliptical, often with sterile apical tip ("beaked"), glabrous, unripe green with white spots, ripe red. Seeds 4–5.5 × 3–3.5 × 1.5 mm, symmetrically obovate, face lenticular.

Phenology. January–March, November, December.

Distribution. Fig. 25. Malawi (Northern Region, Southern Region), Tanzania (Dodoma?, Iringa, Mbeya, Morogoro?, Singida), Kenya (southern Rift Valley Province). 1300–2600 m. Soil preferences unknown. With *Dodonea viscosa*; under pines; in *Eucalyptus* plantation, highland grassland, in open woodland with *Combretum* sp., *Grewia*, *Strophanthus emenii*, *Acacia tortilis*, *Tapiphyllum obtusifolium*, *Burttia* sp., *Cassia* sp.

Etymology*.* The epithet was chosen to honor Charles Jeffrey. Although I disagree in several points of his taxonomic work in *Coccinia*, his observations are valuable, and I regard his work as proof of the intricacy of *C. adoensis* and *C. senensis*.

Use. Unripe and ripe fruit edible (C.J.Kayambo 296, P.Kuchar 22631), roots taken to make stomach medicine (P.Kuchar 22631).

Vernacular names. Kihehe: mtumbulansoka (W.Carmichael 171); Kinyaturu: mukunguhi (P.Kuchar 22631).

Remarks. Morphologically, this variety matches *C. senensis* quite well (rather short petiolate to subsessile leaves, *C. senensis*-like indument), but it has rather *C. adoensis* var. *adoensis*-like calyx lobes, with calyx lobe length being intermediate between *C. senensis* and *C. adoensis* var. *adoensis*. The sequenced specimens do not cluster with most other *C. adoensis* haplotypes from East Africa or southern Africa, and lack the typical deletion of *C. senensis* in the *trn*S^{GCU}–*trn*G^{UCC} intergenic spacer (Holstein and Renner 2011a). A *C. adoensis* var. *adoensis*-like specimen (S.A.Robertson 1925) also clusters with this variety, but it lacks the long trichomes. Long trichomes also appear in populations of *C. grandiflora* or *C. mackenii* in higher altitudes or higher precipitation. The specimens of this variety are distributed above 1300 m, so the long trichomes could be an adaptation. On the other hand, very similar trichomes regularly occur in *C. senensis*, although sometimes also reduced, but that species does not occur in such high altitudes. As the specimens of this variety differ from the “typical” *C. adoensis*, but still belong to *C. adoensis*, I chose to treat them as a new variety.

The specimen R.E.Gereau & C.J.Kayombo 3582 (K, MO; *C. adoensis* 4 in Fig. 16) is morphologically inseparable from this variety, and it clusters within the East African *C. adoensis*. This specimen has a normal-sized corolla, and therefore seems to be fertile, which supports the hypothesis that the variety *jeffreyana* is not reproductively isolated from the variety *adoensis*.

Phylogenetically, it is uncertain, whether this variety represents a common ancestor of *C. adoensis* var. *adoensis* and *C. senensis*, or whether the longer trichomes are homoplastic, or this is a case of incomplete lineage sorting. Presumably, the ancestor of *C. adoensis* and *C. senensis* survived during an arid era in more humid coastal “forests” and woodlands of East Africa, where it evolved to *C. senensis* and *C. pwaniensis*. Other morphs evolved in woodlands rather in the inland, and are now pooled as *C. adoensis*. Interestingly, the distribution of *C. adoensis* var. *jeffreyana*, *C. senensis*, and the allied *C. pwaniensis* (shares the subulate calyx lobes with *C. senensis*) is very similar to that of the Apocynaceae species *Carvalhoa campanulata* K. Schum. (Leeuwenberg 1985), which suggests shared ecological preferences.

The specimens from Singida occur in drier habitats than the specimens from C and S Tanzania. Specimens with an indument like *C. adoensis* var. *jeffreyana* also occur in NE D. R. Congo (A.Taton 128, G.Troupin 570), but it is uncertain, whether these are also genetically connected to *C. adoensis* var. *jeffreyana*, so they are listed under *C. adoensis* var. *adoensis*.

Specimens examined. (selection, in total: 26) Kenya. Rift Valley Province: Namanga, cultivated in M, N.Holstein 125 (M) and 130 (M). Malawi. Northern Region: Mzimba district, 3 mls [4.8 km] W of Mzuzu at Katoto, J.Pawek 10404 (MO, WAG). Tanzania. Iringa: Ludewa district, Livingstone Mts, secondary thickets and forest remnants on E slope of Msalaba Mt., above stand of *Acacia abyssinica* on foot tral from mission at Luana, 9°59’S 34°36’E, R.E.Gereau & C.J.Kayombo 3535 (DSM, EA, MO, NHT, PRE); Mufindi district, Sao Hill, R.Polhill & S.Paulo 1722 (B, EA, P, PRE). Mbeya: Nyassa-Hochland, Station Kyimbila, A.Stolz 504 (JE, M, U, W). Singida: Singida district, 8 km on road from Singida to Sepuka, 4°46’35’’S 34°40’00’’E, P.Kuchar 23919 (MO, S).

Coccinia barteri (Hook.f.) Keay, Kew Bull. 8: 82. 1953.

Physedra barteri (Hook.f.) Cogn., DC. Monogr. Phan. 3: 525. 1881.

Staphylosyce barteri Hook.f., F.T.A. 2: 554. 1871. TYPE: NIGERIA. Nupe [Niger State]: exact locality not specified, male, fl, C.Barter 1525 (Lectotype, designated here: K!, digital image! [K]). TYPE: EQUATORIAL GUINEA. [Fernando Po] Bioko Island, female, C.Barter no. ? (Paralectotype: K?), see taxonomical remarks.

Coccinia subhastata Keraudren, Flore du Cameroun 6: 131. 1967. TYPE: CAMEROON. South Region: Bitye, male, fl, 1917, G.L.Bates 1469 (Holotype: BM!).

Coccinia macrocarpa Cogn. Bull. Jard. Bot. État Brux. 5: 113. 1915–1919. Pro parte [except E.Luja 125]. TYPE: D. R. CONGO. Sankuru river (tributary of Kasai river), no detailed location given, male, on farmland and in bushland, Jul 1904*, E.Luja 205, (*Lectotype, designated by C.Jeffrey (1967): BR!, digital image! [JPS], photo: K!), female, fr, Nov 1903, E.Luja 125, (Paralectotype: BR, digital image! [JPS]).

Description. Perennial climber. Stems up to 10 m long, glabrous or puberulous. Petioles 1.0–3.5(–8.5) cm, glabrous to puberulous, adaxial side rarely with trichomes. Leaves 3.5–20 × 4–23 cm, cordate, subhastate, shallowly to deeply 3- or 5-lobate. Lobes triangulate, ovate to oblong. Margin entire with few to many teeth to serrate. Apex obtuse to acute, with final tooth. Upper lamina glabrous with clear or white pustules, lower lamina glabrous to puberulous on main nerves, esp. towards base. Lower lamina with or without small dark glands. Probracts up to 5 mm long or missing. Tendrils simple or bifid. Male flowers in few- to many-flowered racemes. Common peduncle up to 3–8 mm long, glabrous to puberulous. Pedicel < 8 mm, indument like peduncle. Flowers without or with up to 1.5 mm long bracts. Perianth tube glabrous to puberulous. Calyx lobes 1–2.5 mm, subulate, lineal, rarely cordate, reflexed, spreading to reflexed and adpressed to corolla, sometimes seeming fleshy. Corolla 1.1–2.4 cm, salmon, yellow to orange-yellow, lobes up to 3–10 mm. Filament column, anther head, and pollen sac color not seen. Female flowers in racemes, sometimes accompanied with a solitary flower or 1 solitary flower. Peduncles and petioles in racemes like in males. Solitary female flowers with up to 1.5 cm long glabrous to puberulous pecidel. Ovary glabrous. Hypanthium glabrous to puberulous, calyx lobes and corolla as in males. Style not seen. Stigma shape not seen, more or less dark yellow. Fruit 4–5 × 1.5–2.5 cm, ovoid to subglobose, unripe green with spots, ripe red. Seeds 5.5 × 2.5–3 × 1–1.5 mm (L/W/H), more or less symmetrical obovate, face flat(-lenticular).

Phenology. January–June, August–November.

Distribution. Fig. 26. Humid tropical West Africa, Angola (Cabinda, Cuanza norte), Burundi?, C and S Cameroon, C and S Central African Republic, D. R. Congo, R. Congo, Equatorial Guinea, Gabon, Mozambique (Manica), S Southern Sudan?, Uganda (Western, Central), Rwanda? , W Tanzania, Zambia (Northern Province), Zimbabwe (Manicaland). Elevation sealevel to 1650 m. Soil preference not well known, on loam soil, on granite (J.B.Gillett 15298). (*Newtonia*) rainforest; forest margins; near open water with *Pandanus candelabrum*, *Oxystigma mannii*, and *Raphia vinifera*; near river with *Saba comorensis*; on border of gallery forest and *Terminalia glaucescens* woodland; in riverine bushes with on river islands with *Alchornea cordifolia*; in fallows.

Use. The Turumbu people mash young leaves, mixed with white argil, and put the paste onto the heads of ill children (W.Kesler 1034).

Vernacular names. Lissongo [Mbati]: makpo (Équipe 2250); Turumbu: eliki e litoko (J.Louis 2253), ndombo di ilo (W.Kesler 1034).

Remarks. There are specimens in Gabon that are of intermediate morphology between *C. barteri* and *C. racemiflora* (M.A.van Bergen 490 (WAG) = *C. barteri* 6 in Fig. 16). Holstein and Renner (2011a) suggested hybridization between these species. Whether the hybrids are fertile or sterile is not known.

Taxonomic remarks. Hooker mentions collections from Fernando Po [Bioko Island] and Nupe in the protologue. He only gives the name of Barter, whose Nupe specimen is in K, but there are no *Coccinia* specimens by Barter from Fernando Po. However, there are two specimens from G. Mann (N199! and N1166!) in Hooker’s herbarium (now in K). These were collected on this island, and they contain drawings, which were most likely the basis for Hooker’s description of *Staphylosyce barteri*. Possibly, Hooker just forgot to mention Mann, whose collections contain many type specimens, when writing the book with this protologue.

Keay wrote mistakenly *Coccinea barteri* [sic] in his new combination, but accepted the species belonging to *Coccinia* in Hutchinson and Dalziel’s Flora of Tropical Africa (1954).

Coccinia subhastata was described under the presumption that *C. barteri* has long calyx lobes as it can be seen in Flore du Cameroun (Kéraudren 1967). The drawing, however, shows *C. heterophylla*. Kéraudren described several differences of her species to *C. barteri*, which do not hold, when carefully examined. *Coccinia subhastata* is supposed to have only simple tendrils, but the type also has a bifid tendril. Furthermore the *C. barteri* lectotype C.Barter 1525 has a subhastate leaf and simple tendrils. The description of *C. subhastata* thus is mistaken and the species is a synonym of *C. barteri* as it has been pointed out by Holstein and Renner (2010).

The syntype specimens of *Coccinia macrocarpa* are certainly belonging to different taxa. I agree with Monique Kéraudren, who placed the male specimen É.Luja 205 to the polymorphic *Coccinia barteri* (1967). However, the female plant É.Luja 125 is clearly not part of *Coccinia*. *Coccinia* seeds are up to 7 mm long, at the base attenuate to truncate and with a rounded apex. In contrast, the seeds of É.Luja 125 are subquadratic as Jeffrey already pointed out on the type specimen. The placement to *Momordica* by Jeffrey (on the sheet) seems to be correct, whether this is *M. multiflora* Hook.f. (1871) as identified by Jeffrey or *M. parvifolia* Cogn. (1916) as identified by M. Kéraudren or not is beyond my knowledge.

Specimens examined. (Selection, in total: 144) Angola. Cabinda: Maiombe [Mayumbe Forest], Munze, Buco Zau, J.Gossweiler 6670 (LISU). Cuanza Norte: Cazengo municipality, near Agricultural Station Cazengo, J.Gossweiler 5492 (LISU), 5507 (LISU), and 6670 (LISU). Benin. Atlantique: Allada commune, Dahounkpa (Niaouli), 6°44’N 2°07’E, A.Akoègninou & F.Bada 2992 (WAG). Donga: [Département de L’Atakora, sic], Bassila, Diépani, 9°5’N 1°37’E, L. Pauwels 7854 (WAG). Cameroon. Centre Region: Melèn, 3 km SW of Yaoundé, W.J.J.O.de Wilde et al. 3726 (MO, WAG, WAG). East Region: Yangamo (65 km NNW of Batouri), R.Letouzey 4949 (WAG, WAG). Littoral: Forêt de Bakaka, 3 km E of Eboné (village 11 km on Nkongsamba–Loum road), A.J.M.Leeuwenberg 8836 (MO, WAG, WAG). North West Region: 32 km NE of Nkambe, near Nsop, R.Letouzey 8829 (P). South Region: Bipinde [Bipindi], G.Zenker 1657 (E, G, G, G, G, HBG, Z). Southwest Region: S of Buea, between Sasse and Soppo on the short Victoria–Buea road, A.J.M.Leeuwenberg 6988 (WAG, WAG). Central African Republic. Haut-Kotto: 35 km S of Yalinga on route to Bangassou, G.Le Testu 4315 (BR). Lobaye: Boukoko, Équipe 2176 (BM, P). Sangha-Mbaéré: Dzanga-Sangha Reserve, 2nd tributary of Kenié from Ndakan North, 2°22’N 16°10’E, D.J.Harris & J.M.Fay 1192 (MO). D. R. Congo. Bandundu: Kikwit territory, Kiyaka-Kwango, R.Devred 2762 (MO, W). Equateur: Wendji (environs de Coquilhatville [Mbandaka]), J.Lebrun 994 (M, Z). Katanga: [Haut Katanga district], 40 km on road from Lubumbashi to Sakanja, A.Schmitz 4465 (EA, 2 sheets, WAG, WAG). North Kivu: Masisi territory, Karunda, Nyabinondo, R.Gutzwiller 3268 (COI). Maniema: Pangi territoire, Kampene, A.Léonard 5615 (L). Orientale: [Isangi territoire], Yangambi, Kisangani, L.Pauwels 6694 (M). Equatorial Guinea. Bioko Norte: Malabo–Punta Hermosa km 9, 32NMK8114, F.J.Fernández Casas 12077 (BM, MA n.v., MO, WAG). Gabon. Estuaire: Bakaka Forest, 3 km E of Eboné (a village on km 11 Nkongsamba–Loum road), 4.50 N 9.54E, A.J.M.Leeuwenberg 8836 (MO, WAG). Haut-Ogooué: 21 km on road from Okonja to Akiéni, 0°45.84’S 13°47.01’E, J.J.Wieringa et al. 6387 (WAG, WAG, WAG). Nyanga: Mayomba [Mayumba], Karmann in Herb. C.d’Alleizette 2638 (L). Ogooué-Lolo: c. 40 km E of Lastoursville, c. 0°50’S 13°08’E, F.J.Breteler & B.J.M.Breteler-Klein Breteler 12293 (WAG, WAG). Ghana. Brong-Afaho: between Wenchi and Bamboi, 7°47.7’N 2°06.0’W, C.C.H.Jongkind 3017 (WAG, WAG). Eastern Region: Akropong, Akwapim [Akwapim North district], F.R.Irvine 2604 (E, E). Volta:

Agumatsa Wildlife Sanctuary, at town Wli-Agorviefe, W of Park Guard HQ, 7°06’46’’N 0°35’25’’E, H.H.Schmidt et al. 2192 (K, MO). Western Region: District Shama [Shama Ahanta East Metropolitan District], Daboase, 5.09532°N 1.64668°W, E.Achigan-Dako 06 NIA 025 (GAT, GAT). Guinea. Labé: Labé, J.G.Adam 11755 (MO). Kankan: Kérouané, Kassiabou, 8.97661°N 8.9666°W, E.Achigan-Dako 07 NIA 875 (GAT, GAT). Mamou: Mamou, 10.371140°N 12.073630°W, E.Achigan-Dako 06 NIA 294 (GAT). Nzérékoré: [Beyla préfecture], Bola [Boola], Famondou [Famodougou], 8.48068°N 8.70129°W, E.Achigan-Dako 07 NIA 899 (GAT, GAT, GAT). Ivory Coast. Bas Sassandra: c. 64 km N of Sassandra, c. 4 km W of Napiadou, W.J.J.O.de Wilde 272 (WAG, WAG); ibid. W.J.J.O.de Wilde 274 (WAG, WAG). Dix-Huit Montagnes: between Ouodé [Douodé?] and Gouréni [Gouréné], A.Chevalier 21636 (P, P). Lacs: between Toumodi and Nzaakro [Zaakro], A.Chevalier 22426 (P, P). Lagunes: Abidjan, Banco Forest Reserve, in marshy valley, near the entrance, J.de Koning 6144B (WAG). Moyen-Comoé: between Zaranou and Bébou, A.Chevalier 22628bis (P). Mozambique. Manica: southern slopes of Serra Macuta [Serra Mocuta], T.Müller & T.Gordon 1770 (K). Nigeria. Cross River: Akamkpa District [Akamkpa local government area], Iko Esai village, H.Schäfer 2006/21A (M); ibid. H.Schäfer 2006/21B (M). Edo: Okomu Forest Reserve, Nikrowa area, near Arankhuan, J.A.Emwiogbon FHI 61627 (MO2042205, MO5986413). Ondo: Idanre Hills, Orosun Mt, 7°7’N 5°8’E, J.B.Gillett 15298 (P). Oyo: Gambari [Onigambari], ± 20 mls SE [S] of Ibadan, C.L.M.van Eijnatten 1648 (WAG). Rivers State: Old GRA, Port Harcourt, B.E.Okoli 150 (IFE n.v. (cited and picture of plant in Okoli 1984)). Sierra Leone. Koinadugu: Kabala district, Mt Loma, J.G.Adam 22493 (MO). Kono: Tingi Mts, top of E ridge, J.K.Morton & D.Gledhill SL1886 (WAG, WAG). Tanzania. Kigoma: Kigoma Rural District, Gombe Stream National Park, Mitumba Valley, research staff houses, 4°39’11’’S 29°38’09’’E, G.Gobbo et al. 471 (MO). Mara or Mwanza: Ukerewe Island or area Mwanza to Musema [Musoma], H.A.Conrads 5012 (COI). Uganda. Central Region: [Wakiso district], Mile 10 Entebbe road, Kajansi forest, P.Chandler 2006 (EA). Western Region: Kigezi, Kirima [Kanungu district], Nyamugoye [Nyamigoye, Namigoye], J.W.Purseglove 3464 (EA). Zimbabwe. Manicaland: Chirinda Forest, B.Goldsmith 39/62 (COI, K, NY).

Coccinia grandiflora Cogn., Bot. Jahrb. 21: 211. 1895. TYPE: TANZANIA. [Tanga]: Mlalo, dry hill range. C.H.E.W. Holst 506a (Holotype: B, destroyed). TYPE: TANZANIA. Tanga: Usambara, near Amani, [H.J.P.?]Winkler 3611 (Neotype, designated here: BR!).

Coccinia grandiflora Cogn. ex Engler. Abhandlungen der königlichen preußischen Akademie der Wissenschaften zu Berlin: 34. 1894. nom. nud.

Coccinia engleri Gilg, Bot. Jahrb. 34: 354. 1904. TYPE: TANZANIA. [Tanga]: West Usambara, Sakare [Sakarre], at waterfall in primeval forest, 1100 m, fl, fr, Sep, A.Engler, Reise nach Ostafrika 948 (Holotype: B, destroyed). TYPE: TANZANIA. Tanga: Amani, Kwamkoro. 600–3400 ft [180–1050 m], male, fl, 23 Nov 1928, P.J.Greenway 1025 (Neotype, designated here: EA!)

Description. Perennial climber with stems up to 20 m. Stem glabrous or (when from higher altitudes) with long whitish trichomes. Petioles 2.5–13 cm, glabrous or (when from higher altitudes) with many long whitish trichomes. Leaves 12–20 × 11–20 cm, profoundly 5-lobate. Lobes triangulate, ovate to oblong. Leaf margin smooth to slightly serrate dentate. Apex obtuse to acute with final tooth. Upper lamina glabrous with tiny hyaline pustules. Lower lamina glabrous, rarely with few trichomes on the main nerves, esp. at base, scattered with blackish glands, esp. along main nerves. Probracts up to 5 mm long (Fig. 7a). Tendrils bifid. Male flowers solitary or in (usually few-(–10-)flowered) racemes. Common peduncle 4–12 cm, glabrous. Pedicels in racemous flowers 0.2–1.3 cm, glabrous. Bracts up to 3 mm or missing. Pedicel of solitary flowers 4–15 cm, glabrous. Perianth tube glabrous. Calyx lobes (2–)4–13 mm, lineal, narrow lanceolate to triangulate, tip subulate to subacute. Corolla 4–6.5 cm long, apricot, salmon, yellowish-buff to yellow, lobes 2–4.7 cm. Filament column and anther head not seen. Pollen sac yellow-orange. Female flowers solitary, rarely in racemes, glabrous. Common peduncle < 1 cm, pedicel in racemes, pedicel of solitary flowers 3–4 cm. Ovary long cylindrical, glabrous or with hyaline–whitish pustules. Hypanthium glabrous, calyx lobes and corolla like in male flowers. Style columnar, yellowish to buff. Stigmas 2-lobed, yellow. Fruits up to 30 cm long, 2–4 cm in diam., long cylindrical, glabrous, when unripe green, ripe (orange-)red. Seeds 4.5 × 2.5 × 1.0–1.2 mm, symmetrical ovoid, face flat lenticular.

Phenology. January–December.

Distribution. Fig. 27. Southeastern Kenya (Coast Province: Taita Hills, coastal forests), Tanzania (southeastern Dodoma; Iringa: Uzungwa Mts; Kilimanjaro; Lindi; Morogoro: Nguru Mts, Ukaguru Mts, Uzungwa Mts; Tanga: Usambara Mts; Mtwara), Malawi (Northern Province: Misuku Hills; Central Province: Nchisi Mts; Southern Province: Lisao Hill), Mozambique (Manica: East African Highlands with foothills), Zimbabwe (Manicaland: East African Highlands with foothills). Elevation 30–1900 m. On rich red-brown clay, on diabase outcrops. Coastal and lowland forests and forest margins (*Parinari* sp.-*Newtonia buchanii* forests, a. o.), riverine forests (*Cola clavata*, *Synsepalum msolo*, *Sorindeia madagascariensis*), rarely in montane forests (*Cassipourea malosana*-*Teclea simplicifolia*-*Teclea nobilis*-*Olea mildbraedii*-*Tabernaemontana* forest), or Miombo from degraded forests.

Use. Fruits are reported to be either poisonous (A. Peter 56598) or edible (W.J.Kindeketa 630).

Vernacular names. Kihehe: mudesselema (F.Haerdi 617/0), Kipare: hotwe (W.J.Kinde-keta 630), Kishamba: matombo shanga (G.R.Williams G43), Kisamba: matombo ya nyoka “snake breasts” (M.A.Mwangoka & A.Kalage 1578).

Remarks. The southern individuals in Zimbabwe and C Mozambique often bear short trichomes, and the leaves are rather shallowly lobate, just as in *C. schliebenii*. These populations may represent hybrids or a non-differentiated common ancestor.

The discrimination between *C. grandiflora* and *C. mildbraedii* is hard in the Central Tanzanian highlands (Eastern Arc Mts). Both species occur in high altitude forests and are only well differentiable in the flower size. *Coccinia grandiflora* also has larger probracts than *C. mildbraedii*, but this is often hardly visible. *Coccinia grandiflora* may also be confused vegetatively with *C. barteri* in Mozambique and Zimbabwe.

Taxonomical remarks. The *C. grandiflora* holotype by Holst was destroyed in the buring of the Berlin herbarium in 1944. I chose the Winkler specimen as neotype because it was already designated as type in December 2008. There is no annotation on the type label, and it seems that this neotypification was not published. However, the Winkler specimen label bears Cogniaux’ handwriting (I compared his handwriting with his hand-written mss. for *C. homblei*, *C. parvifolia*, and *C. subspicata* in BR.) Strangely, the Winkler specimen also states “mars 1892”, with the 92 crossed out. This is the date when Holst collected his specimen; but H. J. P. Winkler collected in Tanzania in 1910.

As the holotype of *C. engleri* also was destroyed, I chose a specimen by P. J. Greenway. Although the chosen neotype is male, not female as the holotype, and is from the eastern Usambaras, not from western Usambaras, I regard the specimen as good match, as Gilg states in the protologue that the leaf lobes and sinuses are acute. Gilg also mentions that his species only differs from Cogniaux’ *C. grandiflora* in the layout of the leaves. Hence, there is no doubt that the two names are synonyms.

Specimens examined. (Selection, in total: 108) Kenya. Coast Province: Taita-Deveta District, Taita Hills, Mbololo Forest, 3°19’S 38°27’E, Mwambirwa Forest Station, R.B.Faden et al. 799 (EA, WAG). Malawi. Central: [Ntchisi distr.], Ntchisi Mt., N.K.B.Robson & B.Steele 1711 (K). Northern: Misuku Hills, Mugesse Forest, F.Dowsett-Lemaire 664 (K). Southern: Chiradzulu district, Lisau Hill above Njuli P.O., R.K.Brummitt & I.H.Patel 18534 (K, WAG). Mozambique. Manica: Chimoio, Garuzo mountain ridge, J. G.Garçia 522A (LISC, MO). Tanzania. Arusha: above Saje, N side of Ngurdoto Crater rim, P.J.Greenway & Kanuri 13444 (EA, K, M, PRE). Kilimanjaro: Chome [ward], Njokava forest, R.Abdallah 814 (EA, NHT).

Iringa: Kilolo district, Udzungwa Mountains National Park, 7°42'11''S 36°52’33’’E, L.Festo & M.A.Mwangoka 2047 (MO). Lindi: 40 km W of Lindi, Lake Lutamba, Mirola Valley, H.J.Schlieben 5905 (B, HBG, G, M, S, Z 2 sheets). Morogoro: eastern Uluguru Mts, Kimboza Forest Reserve, 100 m from 7°01'21.1''S, 37°48'37.2''E, N.Holstein et al. 59 (DSM, M); Morogoro rural district, Mkindo Forest Reserve, Mhango riverine forest, 6°13'39''S 37°31'13''E, M.A.Mwangoka et al. 3353 (MO); Kilosa district, Ukaguru Mts, along track between Mandege and Ihanga rock, c. 6°24’S 36°56’E, M.Thulin & B.Mhoro 2877 (DSM, EA, K, MO); Ulanga District, Itula or Ifakara or Ilingera, F.Haerdi 617/0 (BR, EA, G, K, WAG, WAG). Mtwara: Mikindani distr., Mtwara–Mikindani road, H.M.Richards 17871A (K). Ruvuma: Songea District, by Mtandazi river, E.Milne-Redhead & P.Taylor 8538 (LISC). Tanga: western Usambara Mts, Shagai forest, forestry house near Sunga, R.B.Drummond & J.H.Hemsley 2783 (B, EA, K, S); [eastern] Usambara Mts, Ndola, H.G.Faulkner 1345 (K, S); Muheza district, Kwamkuyo river, c. 5°04’S 38°38’E, C.H.S.Kabuye 185 (BR, EA, MO); [eastern Usambara Mts], Amani, c. 50 m before gate of headquarters, 05°05'58.3''S 38°39'11.2''E, N.Holstein et al. 96 (B, DSM, M), 97 (BR, DSM, M), 98 (DSM, M, WAG), 99 (DSM, M), and 100 (M); Korogwe district, Kwepima Hill between Ambangulu Forest Reserve and Kwemasimba public forest, 5°05’51’’S 38°25’46’’E, M.A.Mwangoka 436 (MO). Zimbabwe. Manicaland: Chipinge district, outskirts of Chirinda [forest] above Msilizwe river, B.Goldsmith 2/63 (B, BR, S); [near Mutare], S slope of Murahwa’s Hill, N.C.Chase 8008 (COI, K, LISC, MO).

Coccinia grandis (L.) Voigt, Hortus Suburbanus Calcuttensis: 59. 1845. *Bryonia grandis* L., Mantissa plantarum: 126. 1767. *Bryonia foliis subrotundis angulosis, momordicae facies* Burm., Thesaurus zeylanicus: t. 19, fig. 2. (Paralectotype: l.c.). TYPE: INDIA. No detailed information, C.Linnaeus 1153.2 (Lectotype, designated by Nazimuddin and Naqvi (1984): LINN!).

Vitis alba indica Rumphius [G. E. Rumpf], Herbarium amboinense 5: 448, t. 166, fig. 1. 1747.

Bryonia alceifolia [sphalm. *alceaefolia*] Willd. in Rottler Neue Schriften d. Ges. Naturf. Freunde Berlin 4: 223. 1803. TYPE: INDIA, Tiruchinapally [Tiruchirappalli], Nov. 1793, J.P.Rottler s.n. (Holotype: K!).

Momordica bicolor Blume, Bijdragen tot de flora van Nederlandsch Indië: 928. 1825–26. TYPE: INDONESIA. [Java]. Kuripan. in calcareis [on calcareous ground?] K.L.Blume 1012 (Type: L0587745!).

Momordica bicolor var. *a* Blume, Bijdragen tot de flora van Nederlandsch Indië: 928. 1825–26. nom. illeg. INDONESIA. Maluku Province, Timor, Zippelius s.n. (L0587743!)

Momordica bicolor var. *b* Blume, Bijdragen tot de flora van Nederlandsch Indië: 928. 1825–26. nom. illeg. [INDONESIA]. [Java], Parang Mts, calcareous mountains. K.L.Blume 1016 (L0587744!).

Coccinia cordifolia (L.) Cogn. in A. DC & C. DC., Monogr. Phan. 3: 529. 1881. pro parte maiore, non *Bryonia cordifolia* L.

Coccinia cordifolia (L.) Cogn. var. *alceifolia* [sphalm. *alceaefolia*] (Willd.) Cogn. in A. DC & C. DC., Monogr. Phan. 3: 531. 1881. Type see *Bryonia alceifolia* Willd.

Coccinia cordifolia (L.) Cogn. var. *wightiana* (M.Roem.) Cogn. in A. DC & C. DC., Monogr. Phan. 3: 531. 1881. Type see *Coccinia wightiana* M.Roem.

Momordica covel Dennst., Schlüssel zum Hortus indicus malabaricus: 23. 1818. *Covel* Rheede, Hortus indicus malabaricus 8: 27, t. 14 (1688). TYPE: drawing in l.c.

Cephalandra grandis (L.) Kurz. J. As. Soc. Beng. 46(2): 103. 1877.

Coccinia grandis M.Roem., Synopsis Peponiferarum: 93. 1846. nom. illeg. [nom. superfl.]

Coccinia grandis var. *quinqueangularis* Miq. Flora van Nederlandsch Indië 1(1): 673. 1855. TYPE: [INDONESIA]. [Central Java], near Soerakarta [Sorakarta], T.Horsfield s.n. (Holotype: U!)

Coccinia grandis var. *wightiana* (M.Roem.) Greb. in R. Mansfeld & J. Schultze-Motel, Verz. Landwirtsch. u. Gaertn. Kulturpfl. 2: 929. 1986. Type see *Coccinia wightiana* M.Roem.

Cephalandra indica Naudin, Ann. Sci. Nat. Bot. ser. 5, 5: 16. 1866. Nom. illeg.

Cephalandra indica var. *palmata* C.B.Clarke in: Hook.f. The flora of British India 2(4): 621. 1879. Nom. illeg. [nom. superfl.; based on specimens already published to that time as *Coccinia wightiana* M.Roem.]

Coccinia indica Wight & Arn., Prodomus Florae Peninsulae Indiae Orientalis: 347. 1834. Nom. illeg. [nom. superfl. as epithet has not been adopted]

Coccinia loureiriana M.Roem., Synopsis Peponiferarum: 93. 1846. *Bryonia grandis* Lour., Flora cochinchinensis 1(2): 595. 1790. nom. illeg. and Flora cochinchinensis 2: 731 (1793) nom. illeg.

Coccinia moghadd (Forssk. ex J. F. Gmel.) Asch. in Schweinf., Beitrag zur Flora Aethiopiens: 251. 1867.

Cephalandra moghadd (Forssk. ex J.F.Gmel.) Broun et Massey, Fl. Sudan: 105. 1929.

Turia moghadd Forssk. ex J.F.Gmel., Systema naturae 2(1): 403. 1791. *Turia moghadd* Forssk., Flora Ægypto-Arabica: 166. 1755. Nom. illegit. TYPE: YEMEN. [Al-Hudaydah Governorate]: Lohaja [Al-Luhayyah]. female, fl, P.Forsskål 663 (Lectotype, designated here: C, microfiche: B); ibid., male, fl, P.Forsskål 662 (Paralectotype: C, microfiche: B) ; ibid., P.Forsskål 666 (Paralectotype: C, microfiche: B)

Coccinia moimoi (Ser. ex DC.) M.Roem., Synopsis Peponiferarum: 93. 1846.

Bryonia moimoi Ser. ex DC., Prodomus systematis naturalis regni vegetabilis 3: 305. 1827. TYPE: SRI LANKA. Burm., Thesaurus zeylanicus: t. 19, fig. 1. (Holotype: l.c.)

Moï-moï Adans., Histoire naturelle du Sénégal: 159, Paris. 1757. Nom. illeg.

Bryonia folio anguloso acuto glabro Burm., Thesaurus zeylanicus: 48, t. 19, fig. 1. 1737. Nom. illeg.

Momordica monadelpha Roxb. Flora indica: 708. 1832. nom. illeg.

Coccinia palmatisecta Kotschy, Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe I 51: 360–361. 1865. TYPE: [SOUTHERN SUDAN]. marshes in Noer [Nuer] realm [S to E of Malakal], no detailed location given, F.Binder s.n. (Paralectotype: W!, photo in K!). TYPE: [SOUTHERN SUDAN], Kyk [Ciec (a Dinka subtribe) realm, S of confluence of Bahr al-Ghazal and White Nile], male, no date given, M.L.Hansal s.n. (Lectotype, designated here: W!).

Cucumis pavel Kostel. Allgemeine medizinisch-pharmazeutische Flora 2: 738. 1833. Nom. illeg. [based on the same type as *Momordica covel* Dennst., see above]

Cephalandra schimperi (Naudin) Naudin, Ann. Sci. Nat. Bot. ser. 5, 5: 16. 1866.

Coccinia schimperi Naudin, Ann. Sci. Nat. bot., ser. 4, 8: 366. 1857. TYPE: ETHIOPIA. TYPE: ETHIOPIA. In Semen [Semien Mts], female, fl, 1854, G.H.W.Schimper Herb. Abyss. 1215 (Lectotype, designated here: P! [the specimen with thick branch and fruit], isolectotype: P!). TYPE: ETHIOPIA. Biria Dekeno et Dschadscha, 5000’, female, fl, 1853, G.H.W.Schimper Herb. Abyss. 1215 (Paralectotype: P!). TYPE: ETHIOPIA. Dschadscha, 5000’–5500’, male and female, fl, fr, 13 and 21 Jul 1853, G.H.W.Schimper Herb. Abyss. 1215 (Paralectotype: P!). TYPE: ETHIOPIA. Dschadscha, 5000’, male and female, fl, fr, 13 and 21 Jul 1853, G.H.W. Schimper Herb. Abyss. 1215 (Paralectotype: P!). TYPE: ETHIOPIA. without details, G.H.W.Schimper Herb. Abyss. 1215 (Paralectotype: G-DC!). TYPE: ETHIOPIA. Dschadscha, female, 1853, G.H.W.Schimper Herb. Abyss. 1215 (Paralectotypes: BR!, BR!, BR!, BR!)

Coccinia wightiana M.Roem., Synopsis peponiferarum: 93. 1846. *Coccinia indica* Wight et Arn. β. pro parte [see taxonomical remarks]. TYPE: INDIA. Madras, [= Wall. Cat 6711a], [D.Klein, B.Heyne or J.P.Rottler] in Herb. Madras s.n. (Paralectotype: E00174668!). TYPE: INDIA. Nepalry [= in Wall. Cat. 6711b and e], R.Wight 1124 (Paralectotype: E00174667!). TYPE: INDIA. Negapatam, R.Wight 1124 (Lectotype, designated here: E00174666!). TYPE: UNKNOWN. R.Wight 1124 (Paralectotype: NY, digital image! [NY]).

Description. (Fig. 6a) Perennial climber or creeper. Shoots up to 5 m, glabrous, when older often white pustulate. Petioles 0.5–5.5 cm, glabrous, rarely some trichomes on adaxial side. Leaves 3–11 × 3–13 cm, cordate to 3-lobate or 5-edged to 5-lobate, sometimes lobulate. Lobes triangulate, ovoid, oblong, to obovoid. Leaf margin dentate, teeth at base very often with yellowish-reddish to brownish gland, becoming black when dried. Margin rarely with short whitish (< 1 mm) trichomes. Apex obtuse to acute with final tooth. Upper leaf surface green, glabrous, more or less dense hyaline to white pustulate. Lower leaf surface pale green, glabrous. Lower leaf lamina between major nerves with glands that are usually framed with lighter color, nerves sometimes with white pustules. Probracts < 1.5 mm or missing. Tendrils simple. Male flowers 1(–3) solitary, rarely in short racemes. Peduncle 0.3–1.5 cm, glabrous, pedicels of flowers in racemes up to 3.2, glabrous, pedicels of solitary flowers up to 4.5 cm, glabrous. Bracts inconspicuous (< 1 mm), often absent. Perianth tube glabrous. Calyx lobes 1.2–3.5 mm long, lineal, spreading to reflexed, often with reddish to brownish gland on lower side at the acute tip. Corolla 1.7–4 cm long, in yellowish buff (mostly African specimens) to snow-white (esp. outside Africa). Corolla lobes 0.7–1.7 cm. Filament column and anther head pale greenish, pollen sacs yellow. Female flowers 1(–2) solitary. Pedicel up to 1 cm, glabrous. Hypanthium glabrous, calyx and corolla like in males. Ovary glabrous. Style columnar, yellowish-green. Stigmas 2-lobed, greenish. Fruit globose to ellipsoid, cultivated also short cylindrical, 3–4.5 × 1.5 cm, glabrous, unripe greenish with few pale spots and/or lines, becoming scarlet red when ripe. Seeds 5–7 × 2.5–3.5 × 1.2 cm, symmetrical to slightly assymetrical, face flat (Fig. 13f).

Phenology. All over the year, but not at the end of the dry season or in cold seasons. Seems to need 1–2 weeks of at least 10 hours daylight with sunny weather for flower induction (own observation).

Distribution. Figs. 28, 29. Senegal, southern Mauritania, Mali (except north), Benin, northern Cameroon, southern Chad, southern and eastern Sudan, Ethiopia, Kenya, Uganda, D. R. Congo (in Great African Rift valley), northern Tanzania (Arusha, Dar es Salaam, Manyara, Morogoro, Mwanza, Pwani, Tanga, Zanzibar), Somalia, Djibouti?, Eritrea, Egypt (along Nile, Elba Mts.), mountains and oases of the southern and western Arabian Peninsula, Pakistan, Nepal, tropical and subtropical India, Sri Lanka, Maledives, South East Asia, southern China, introduced in: Mozambique, Mauritius, Maledives, Australia (Northern Territory, Queensland, Western Australia), many tropical Pacific islands, USA (Florida, Guam, Hawaii, Wake Island), Caribbean area, Central and tropical South America. 0 to 1600 m. Black clay soil, black cotton soil, sand. There seems to be a certain salt tolerance (Bharathi 2007).

Grasslands, bushlands, savannas, thickets, along rivers, ruderal sites, seemingly avoiding closed canopies (woodlands and forests).

Use. Fruits (raw and cooked) and shoots (cooked) edible. The Luo eat the leaves as spinach (Orech et al. 2005). Sap is used against diabetes (Ramachandran and Subramaniam 1983) due to its hypogycaemic activity (Chopra and Bose 1925; Shibib et al. 1993). It is used in traditional Indian medicine in India for various diseases, and seems to have a general antibacterial effect (see also Use, economic potential, and phytochemistry).

Vernacular names. Agau or Chomir [most likely: Khamir/Xamtanga language of Agaw language family]: amballa gosa (G.H.W.Schimper 365, Schweinfurth 1893); Arabic: mogad (Getahun 1974a); Bengali: tala-kucha (Nadkarni and Nadkarni 1976); Canarese [Kannada]: tonde-konde, tonde-kayee (Nadkarni and Nadkarni 1976); Dassanetch [Daasanach]: dali (C.J.Carr & C.Metolo 867); Galinya [Oromo]: raho (Getahun 1974a); Gujarati: gholi (Nadkarni and Nadkarni 1976); Hindi: kan-duriki-bel (Nadkarni and Nadkarni 1976), kundru (Bharathi 2007); Karen [in Mae Hong Son Province, Thailand]: khae-do (de Wilde and Duyfjes 2008); Khmer: (sloek') bah (Kéraudren-Aymonin 1975b); Kizigua: lukewja (R.E.S.Tanner 2691), pondwa (R.E.S.Tanner 2030); Lao: (khùa 'phăk) tăm ling, tăm nhing (Kéraudren-Aymonin 1975b); Mahrati [Marathi]: ran-tondula, tondli (Nadkarni and Nadkarni 1976); Malayalam: kova (Nadkarni and Nadkarni 1976), kovakka (Bharathi 2007); Masai: olaposhi (Pecler 3); Nepali: gol kankri (Aryal 2007); Ngadha (Baba-Ngadha): `uta kala (J.A.J.Verheijen 5415); Ngadha (Mataloko-Ngadha): uta kobho (J.A.J.Verheijen 5415); Persian [Farsi]: kabare-hindi (Nadkarni and Nadkarni 1976); Punjabi: kanduri (Nadkarni and Nadkarni 1976); Sanskrit: vimboshta, vimbaja, bimba, tundika (Nadkarni and Nadkarni 1976); Sinhala: kowakka (D.Philcox et al. 10454, D.Philcox et al. 10458); Somali: masskar (T.Ebba 804); Sunda: aroi papassang (Miquel 1855); Tamil: kovai (Nadkarni and Nadkarni 1976), kovakkai (Bharathi 2007); Telugu: dondakaya (Bharathi 2007), dondatiga, kakidonda (Nadkarni and Nadkarni 1976); Thai: in Central Region: phak tamlueng; in Northern Region: phak khaep (de Wilde and Duyfjes 2008); Tigrinya: asumbeh (G.Schweinfurth & D.Riva 1007); Vietnamese: northern: hoa bát, southern: (dây) bai bác, bình bát, mảnh bát, lá bát (Kéraudren-Aymonin 1975b)

Remarks. *Coccinia grandis* is easily recognizable in its natural habitat, esp. by the lack of an obvious indument and the pale glands in the axils of the nerves at the base of the lower leaf lamina. In NE Africa, specimens with finely dissected leaves can be very similar to *C. ogadensis*. When compared to specimens from South Africa *C. sessilifolia* var. *variifolia* and some morphs of *C. mackenii* are very similar, but *C. sessilifolia* var. *variifolia* is glaucous and both species lack colored leaf teeth and have erect to spreading calyx lobes instead of spreading to reflexed calyx lobes.

Taxonomical remarks. There has been quite some confusion about the species name, and it is often misapplied, esp. in literature from India (for details, see chapter Taxonomic problems and history).

The genus *Turia* has been originally mentioned by Forsskål in his Flora Ægyptiaco-Arabica (1775). Forsskål describes several specimens, which could be read as species descriptions, but which are not. Several Cucurbitaceae have been described under the name "Turia", party with Latin descriptions only, partly with "epithets" from the Arabian name of the species (e.g. *Turia moghadd*), and partly of locations (*Turia leloja*). His number 35 is a cultivated specimen from Yemen with the Arabian name "turia". This cannot be regarded as a genus description, so the genus is invalid. Gmelin (1791) published an extension of Linnaeus' Systema naturae, in which he described the genus *Turia* and published the combination *Turia moghadd*, using the Arabian names specifically as epithet.

Specimens examined. (Selection, in total: 819). Australia. Northern Territory: Nightcliff foreshore, 12°25'S 130°50'E, J.Stobo s.n. (DNA). Bangladesh. Chittagong: Garjania, J.M.Cowan 1869 (E); Cox's Bazar, near Signal Hill, J.Sinclair 3695 (E). Barbados. St. Andrew: Boscobel [Boscobelle], Bad lands, R.A.Howard & E.S.Howard 18736 (US). St. Michael: Bridgetown, old railway yard, Sep 1940, E.G.B.Gooding s.n. (BAR2591, digital image [BAR]). Benin. Ouémé: Porto Novo, Songhai, 6.499460°N 2.614390°E, E.Achigan-Dako 06 NIA 587 (GAT, GAT). Brazil. Minas Gerais: No detailed location, < 1840, P.Claussen s.n. (G-DC). Cambodia. Kampong Cham: Mimot [Memot], Müller 135 (L). Siem Reap: Angkor Srah Srang, 13.4302[°N], 103.903[°E], H.Schäfer 2010/21 (L). Stung Treng: Stung Treng, along Mekong river, 13.5313[°N] 105.984[°E], H.Schäfer 2010/28 (L). Cameroon. Extreme North Region: Zoulgo [Talak Zoulgo] near Meri (30 km ENE Mokolo), R.Letouzey 7019 (P). North Region: Pitowa [Pitoa], c. 17 km NE of Garoua, W.J.J.O.de Wilde et al. 4932 (MO, WAG). Chad. Chari-Baguirmi: Baguirmi et région du Lac Fittri, Tjecna, A. Chevalier 9527 (G). N'Djamena: Fort Lamy [N'Djamena], s.coll. in Herb.d'Alleizette 2644 (L0587617). Oaddaï: Abéché, W.J.J.O.de Wilde et al. 5316 (WAG, WAG). P. R. China. Fujian: Xiamen, Gulangyu [island], G.Ye 730 (IBSC, digital image [CVH], WUK n.v.); ibid. R.Lin 2921 (IBSC, digital image [CVH]. Guangdong: Haikang County, [detailed location could not be translated] Y.Tsiang 2581 (IBSC, digital image [CVH], IBSC, digital image [CVH]). Hainan: Ch'ang-kiang District [Changjiang country], [Bawangling Nature Reserve], Ka Chik Shan [Qicha hill], S.K.Lau 3008 (GH, n.v., S). Hong Kong: near Ouang-nei-Tchong [Wang nai chung] – Happy Valley, Em.Bodinier 1367 (E). Macau: Coloane, old path? F.-W.Xing &

H.-G.Ye 8685 (IBSC, digital image [CVH]). Yunnan: Nan-chiao [Meng che], C.W.Wang 76988 (A n.v., IBSC, digital image [CVH], KUN n.v.). R. China. Taiwan: Peitun [Beitun] district, Taichung City, Chingshiuhsiang 2.2K, 24°11'15"N 120°44'51"E, C.M.Wang 5788 (HAST, digital image [HAST]). Colombia. Magdalena Department: Santa Marta, H.H.Smith 1604 (MO). Cuba. Cienfuegos: Soledad, Harvard Tropical Garden [now Jardin Botanico Soledad], J.G.Jack 8281 (IBSC, digital image [CVH]). Havana: Santiago de las Vegas, A.O’Donovan 5106 (G, S). D. R. Congo. North Kivu: Kavinunge [Kavinyonge], Lac Edouard [Lake Edward], G.F.de Witte 10121 (BR). Orientale: Mahagi territory, Mahagi-Port, J.Lebrun 3800 (BR, BR, EA, WAG). East Timor. Baucau: between Baucau and Vemassi [Vemasse], C.G.G.J.van Steenis 18071 (L). Dili: just W of Dili, Tasutolu area, 8°33'57"S 125°30'05"E, L.D.Cowie 10638 (L). Liquiçá: Bazartete, estrada Ermera-Dili, a entrada do distrito de Dili, 8°33'27"S 125°29'28"E, J.Paiva et al. T619 (L). Egypt. Al-Qalyubiyya: Gebel el Asfar [Djabal al-asfar], Farm Mazraèt, F.Sa’ad & M.Mokhtar 54 (MO). Red Sea Governorate: [Hala’ib triangle], Gebel Shendib [22°01’N 36°16’E], G.W.Murray 3857 (K, digital image [K]). Eritrea. Anseba: Keren, C.T.H.Steudner 826 (S, Z). Central Region: Arbaroba, I.Baldrati 195 (FT). Gash-Barka: Mai Mentai [at Sciagolgol River, SE of Agordat, c. 15°20’30’’N 38°13’15’’E], N.Beccari 118 (FT). Northern Red Sea Region: [NE of Ghimda/Gimda], Pianura Sabarguma, A.Pappi 3970 (G, MO, S, W, digital image [W]). Southern Region: Valle Arrout [Val Harot, Arot Valley], S of Aideresso, G.Schweinfurth & D.Riva 1400 (G). Ethiopia. Afar: Harrar province, c. 50 km N of Afdem, W of Erer Gota, along road to Mieso, 9°47’N 40°42’E, J.J.F.E.de Wilde 7376 (BR, M, WAG). Amhara: Dschadscha, G.H.W.Schimper 365 (E, G-DC, W, Z); ibid., 28 Oct 1854, G.H.W.Schimper s.n. (P 2 sheets). Dire Dawa City: 9 km from Dire Dawa on road to Djibouti, E.Westphal & J.M.C.Westphal-Stevels 1385 (MO, WAG). Gambela: Gambela, J.W.Ash 1069 (K n.v.; MO); ibid., J.W.Ash 1082 (K n.v., MO). Oromia: 85 km NE of Nazareth, along road to Awash, c. 5 km W of Metahara, 8°55’N 39°55’E, J.J.F.E.de Wilde 6870 (BR, MO, WAG). Somali Regional State: Harar Province, at el Bah river, 9°46’N 41°52’E, W.Burger 3253 (K, S). SNNPR: 18 km S of Arba Minch on road to Ghidole or Gardula, J.W.Ash 1595 (K n.v., MO, WAG). Tigray: near Djeladjeranne [around 13°48’N 38°22’E (Gillett 1972)], G.H.W.Schimper 1570 (P, specimens from BM, G, MO, S, and W are maybe also from this location, but not TUB, for details see under Cucurbita schimperiana). Fiji. Central Division: Viti Levu Island, Gordon Street, R.O.Gardner 454157 (BISH n.v. [www.hear.org]) Western Division: Viti Levu Island, near Sigatoga village, D.Koroiveibau 16706 (BISH n.v. [www.hear.org]) France. French Guyana: Cayenne, 4°56’N 52°20’W, L.Barrabé 71 (CAY n.v., U) Guyana. Demerara-Mahaica: Georgetown, W.Hahn 4810 (MO, US). Essequibo Islands-West Demerara: Parika backdam, 6°50’N 58°28’W, T.W.Henkel et al. 2665 (NY n.v., US). Ilemi Triangle: 7 mls [11.2 km] WSW of Kibish Kenya Police Post, C.J.Carr 618 (EA). India. Delhi: Delhi University campus, Aug 1958, R.Bahl s.n. (E). Gujarat: Suratte [Surat], C.Linnaeus 1153.12 (LINN, digital image [LINN]). Haryana: Tusham [Tosham], J.R.Drummond 24654 (E). Karnataka: Belgaum [Belagavi/Belgaon], D.Ritchie 306 (E). Maharashtra: Bassein [Vasai] road, E.H.Unwala EHU/18 (MO). Orissa: Patna, W.Koelz 11340 (E). Tamil Nadu: Madras [Chennai], Saint Thome, 1854, H.F.C.Cleghorn s.n. p.p. (E00303194). Union Territory of Pondicherry: Pondichéry [Puducherry], A.Delessert s.n. (L0587556). Uttar Pradesh: Saharumpoor [Saharanpur], W.Jameson 265 (E). West Bengal: Sibpur [Shibpur in Howrah city] near Calcutta [Kolkata], J.G.Hallier s.n. (M999). Indonesia. Bali: near Tanahlot temple, W.J.J.O.de Wilde & B.E.E.de Wilde-Duyfjes 21720 (L 2 sheets) and 21721 (L). Bangka-Belitung Islands: Banka [Bangka], J.Amand s.n. (U). Banten: Bay of Bamtam, Pulau Dua, A.Hoogerwerf 25 (L). Central Java: Semarang, 20 Nov 1932, W.J.C.Kooper s.n. (U). Central Sulawesi: near Palu, c. 0°53'S 112°53'E, W.Meijer 9180 (L). East Java: Pasoeroean [Pasuruan], 17 Jul 1928, J.J.Ochse s.n. (B, BR, L, U). East Nusa Tenggara: E Flores, Larantuka, Weri, J.J.Afriastini 1590 (L). Jakarta: Batavia [Jakarta], 1933, W.C. van Heurn s.n. (L 5 sheets). Maluku: W Seram, Kaibobo, L.M.R. Rutten 1662 (L). West Java: Bogor, Botanical Garden, J.R.Jensma 64 (WAG). West Nusa Tenggara: Lombok [Island], Ampenan, H.Sun 9008 (IBSC, digital image [CVH]). South East Sulawesi Province: Boeton [Buton Island], Baoe Baoe [Bau-Bau], G.Kjellberg 5 (S). South Sulawesi Province: near Sengkang, W.J.J.O.de Wilde & B.E.E.de Wilde-Duyfjes 21739 (L). Special Region of Yogyakarta: Brambanan [Prambanan], F.W.Junghuhn s.n. (L0587564). Kenya. Coast Province: Malindi district, on the way to Gedi ruins from Malindi, Z.J.Kimani 214 (BR, LISC). Eastern Province: Moyale, 3°32’N 39°03’E, J.B.Gillett 13994 (B, PRE, S). North Eastern Province: Dandu, 3°26’N 39°54’E, J.B.Gillett 12749 (B, S); Catholic Girl’s Town, 2 km E of Wajir, J.B.Gillett 21270 (EA, PRE). Nyanza: Kisumu, C.G.Rogers 534 (BR, S). Rift Valley Province: Karamoja, 20 mls [32 km] N of Kacheliba, S.H.Padwa 71 (PRE). Malaysia. Penang: Timur Laut, Air Hitam, Bandar Baru Farlim, recreational hilly track behing block 4A, T.L.Yao & T.H.Yeap s.n. FRI57896 (L). Perak: Hulu Perak, Grik [Gerik], on road to Kelantan–Gerik (Pulau Banding), beside trail of the Gua Badak, K.Imin et al. FRI63213 (L). Sabah: Sepilok, along Labuk road, W.J.J.O.de Wilde SAN139040 (L). Maldives. Meemu Atoll: Mulah [Island], C.D.Adams & A.Shafeeg 15114 (BM). Mali. Kayes: Bafoulabé Cercle, Bamafélé arondissement, 3.2 km ESE of Manantali, 13°10.847’N 10°26.260’W, C.S.Duvall 130 (MO, MO). Mopti: N of Mopti, Némendé, G. Boudet 7431 (P). Ségou: 3 km [on?] old road [from, to?] Nampala, Fala river bed, G.Boudet 6371 (P). Tombouctou: Niafunké, 15 Feb 1909, R.Chudeau s.n. (P). Mauretania. Assaba or Tagant: Ouellé el Khaïn, 17[°]11[.]764[‘]N

12[°] 14[.]923[']W, Lamarche & Sakho 248 (P). Mauritius. Black river: Medine, by side of road to Flic-en-Flac, J.Guého 13799 (K). Mozambique. Maputo: Vila Luísa [Marracuene], along Incomáti river, A.Balsinhas 1273 (COI). Myanmar. Magway: near Pakokku, river bank of Irrawaddy, J.H.Lace 4935 (E, E). Mandalay: Myingyan district, Seittein to Taungbaw, 30 Aug 1909, J.H.Lace s.n. (E). Shan State: Keng Tung, R.W.MacGregor 561 (E). Nepal. Madhya Pashchim: [Rapti], Tulsipur, O.Polunin et al. 5906 (E). [Pashchim]: [Lumbini], Riri Bazaar, Stainton et al. 8870 (E). Nicaragua. Chontales: St Tomas [Santo Tomàs], 1841, E.v.Friedrichsthal s.n. (W). Niger. Agadez: [Aïr Mountains], Mt Bagwezan [Mt Bagzan, Idoukal-n-Taghès], 31 May 1920, A.Buchanan s.n. (MO1667128). Zinder: Likariri, B.P.de Fabrègues 14450 (P). Nigeria. Bauchi: [Kwandonkaya Hills], lower part of Ziem Peak, Panshanu Pass, D.W.Lawlor & J.B.Hall 437 (P). Pakistan. Punjab: Jhelum district, Baghanwala, M.A.Siddiqi 3677 (RAW n.v., W). Sindh: 7 mls [c. 11.2 km] from Hyderabad to Tando M.[Mohammad] Khan, S.ul-Abedin 3839 (B, KUH n.v., MO). Paracel Islands. Jinyin Dao [Money Island], Z.Li 5443 (IBSC, digital image [CVH]). Philippines. Cebu: Cebu island, location not readable, D.Bicknell 1796 (L). Samoa. Tuamasaga: Alaoa road, across Robert L. Stephenson Estate, J.Space et al. 6968 (PTBG n.v. [www.hear.org]). Saudi Arabia. Mecca: 30 km on highway from At-Ta'if to Mecca, A.A.Fayed 1266 (M). 'Asir: 20 km S of Abha along road Abha–Gizan [Jizan], K.Fagerström 423 (S). Senegal. Dakar: Jof [Yoff], J.-G.Adam 1806 (MO, MO). Saint-Louis: Richard Toll, J.-G.Adam 19269 (MO, PRE). Thiès: 2 km WNW from Ngaring on road to Somone, J.Raynal & A.Raynal 6123 (P). Singapore. South East District: Potong Pasir off Serangoon Road, J.Sinclair 5434 (E, L). Somalia. Bakool: Elmeged [El Meghet, c. 4°55'N 44°24'E], C.Keller 107 (Z). Shabeellaha Dhexe: 20 km N of Mogadishu on road to Balad, 2°12'N 45°24'E, J.J.Lavranos & S.Carter 23258 (MO). Shabeellaha Hoose: c. 45 km SW of Afgooye (Afgoi) on main road to Shalaanbood (Shalambod), 1°48'N 44°44'E, I.Friis et al. 4596B (FT). Togdheer: [c. 54 km SSW of Berbera], foot of Sheikh Pass, P.R.O.Bally 11827 (G, G, G, K, PRE). Woqooyi Galbeed: Hargeisa [Hargeysa], Military in Herb. P.R.O.Bally 3147 (G, K). Sri Lanka. Central Province: Matale district, c. 4 km from Naula on road to Bakamoona, D.Philcox et al. 10458 (MO, PDA n.v.). Eastern Province: Trincomalie [Trincomalee], 30 Sep 1860, D.Dubur s.n. (E). North Central Province: Anuradhapura, F.R.Fosberg & N.Balakrishnan 53431 (MO, PDA n.v.); ibid., W.Forstner s.n. W13705 (W, digital image [W]). Northern Province: Mannar Island, coast just N of Pesalai, F.R.Fosberg & N.Balakrishnan 53593 (MO). Sabaragamuwa: Belihul-Oya, F.Schmid 1242 (G). Southern Province: Hambantota district, Hambantota–Galla road, c. 4 mls [6.4 km] W of Hambantota, s.coll. 8883 (MO2236579, PDA n.v.) Uva: Badulla district, Ridimalliyalla, km 13/1 Bibile to Mahiyangana road, D.Philcox et al. 10531 (MO); ibid., D.Philcox et al. 10534 (MO, PDA n.v.). Sudan.

Red Sea: between Suakin and Berber, Singat [Sinkat], G.Schweinfurth 214 Iter Centrali-Africanum (G, K, L, S, Z). Sinnar: Sinnar, Aug 1999, R.Müller s.n. (MSB). White Nile: [between al-Kawah and Aba island], Om-Mandel island [“Om” may be originally “Umm”], G.Schweinfurth 981 Iter Centrali-Africanum (S). Southern Sudan. Jonglei: 22 km E of Bor, 6.12’ N31.45’E, H.J.Raad 41 (WAG, WAG). Upper Nile: Ar-Rank district, 1.5–2 mls NW of Rank, B.I.Wright 84 (L, M). Suriname. Paramaribo: Paramaribo, 5°50’N 55°10’W, F.Billiet & P.Jadin 5864 (BR). Tanzania. Arusha: Monduli District, small town 0.25 km S of Longido town, S of Longido Mt., along Namanga–Arusha road, 2°43’48’’S 36°41’35’’E, C.J.Kayombo et al. 4196 (MO, S). Dar es Salaam: Campus of University of Dar es Salaam, near Institute of Swahili Language, 6°46'43.0"S, 39°12'11.6"E, N.Holstein 37 (DSM, M), 39 (M), and 40 (M). Kilimanjaro: Same, 04°04'20.7"S, 37°44'05.3"E, N.Holstein et al. 89 (B, DSM, M). Lindi: Selous Game Reserve, Kingupira, 8°30’S 38°30’E, K.Vollesen 2540 (DSM, EA). Manyara: Lake Manyara National Park, Ndara River, P.J.Greenway & Kirrika 11123 (BR, EA, 2 sheets, PRE). Mara: Kirawira Guard Post, P.J.Greenway & M.Turner 10618 (EA, 2 sheets). Morogoro: on Morogoro–Dumila road, c. 10 km E of Dumila, 37M 0328266 9291046 (UTM), N.Holstein et al. 62 (DSM, M). Mwanza: Magu District, Kahangala ward, Bugabu village, Nyamuganga Island, 2°31’42’’S 33°24’54’’E, D.Sitoni et al. 1230 (MO, NHT). Pwani: Kibaha district, Mpiji ravine, O.Flock 578 (S); Mafia island, Ras Mbisi, H.J.Schlieben 2622 (G, HBG, M, S, Z, Z). Tanga: [Muheza district], Muheza, R.B.Drummond & J.H.Hemsley 3405 (K, S); [Tanga district], Tanga town, near public beach, 200 m E of 05°03'19.2"S 39°07'31.3"E, N.Holstein et al. 94 (B, DSM, M, WAG), and 95 (DSM, M). Zanzibar Urban/West: Chukwani, H.G Faulkner 2782 (BR, COI, K n.v.). Thailand. Bangkok: Bangkok, R.Zimmermann 66 (B, B, BR, G, G, H, L, M, MO, S, U, W). Chayaphum: Thet Sathit district, Ban Huai Farang, 15°22'46.00"N 101°24'40.00"E, R.Pooma et al. 2941 (L). Chiang Mai: along road from Ban Bo Luang to Hot, C.F.van Beusekon & C.Phengkhlai 1225 (L) and 1225a (L, W). Chonburi: Toong Brong [Ban Thung Phrong], J.F.Maxwell 72-433 (L). Kamphaeng Phet: near Klong Khlun[g], in grassy place along highway, G.Murata et al. T-16608 (L). Kanchanaburi: c. 65 km WNW of Kanchanaburi, near village along Khwae Noi river, 14°20’N 98°58’E, J.J.Wieringa & D.H.Wieringa-Brants 987 (WAG). Phetchaburi: Kaeng Krachan NP, 19 km marker on route 3432 from HQ, 12°52'N 99°35'E, J.A.N.Parnell et al. 95-405 (L, L). Prachuap Khiri Khan: Sam Roi Yot Branch District, Sam Roi Yot National Park, 12°13’36’’N 99°55’57’’E, M.F.Newman et al. 1199 (A n.v., E). Saraburi: T[h]ap Kwang, T.Smitinand et al. 1335 (L). Sonkhla: Suan toon waterfall [Nam Tok Suan Tun] at Khao Gaeo [Khao Kaeo], c. 10 km S of Songkhla, on Songkhla–Chana highway, K.Larsen et al. 44178 (AAU n.v., digital image [AAU], L). Uganda. Northern Region: Karamoja, Moroto, S.Hardy & P.R.O.Bally 10787 (G).

Central Region: Mengo [now: Luweero district], Bulemezi county, Kalagala, P.K.Rwaburindore 3874 (BR, WAG). Western Region: Toro Region, Busongora county, [Mbarara district], c. 1.5 km N of Mweya Lodge, 0°35'S 30°30'E, A.B.Katende & K.Lye K303 (MO). USA. Florida: along Indian River [lagoon], Coco [Cocoa], 9 May 1918 J.K.Small s.n. (G, MO1161454, US). Guam. Yigo, across street from Yigo elementary school, L.Raulerson 7446 (BISH n.v. digital image [hear.org]). Hawaii: Hawaii Island, North Kona district, city of Kailua-kona, behind Uncle Billy's Kona Bay Resort, D.H.Lorence & T.Flynn 5505 (MO) and 5506 (MO); O'ahu Island, Dole St, behind U Hawaii Manoa dorms, B.Kennedy 47 (MO). Midway Atoll: Sand Island, 4208 Commodore Ave., F.Starr & K.Martz 080601-01 (BISH digital image [hear.org]). Missouri: Henry County, Clinton city, Safari Motel at SW corner of State Highway 7/13 junction, G. Yatskievych et al. 96-87 (MO).Virgin Islands: St. Croix [Island], along road 707 at intersection with road 70, P.Acevedo-Rodriguez 11460 (MAPR n.v., NY n.v., digital image [NY], US, UPRRP n.v.). Vietnam. Da Nang: Tourane [Da Nang] and vicinity, no detailed location, J.Clemens & M.S.Clemens 3257 (A n.v., G, MO, U, W, Z). Hanoi: Hanoi, B.Balansa 4662 (G). Hồ Chí Minh: Saigon Botanical Garden, Hiep? [collector's name unreadable to me, name taken from L database] 638 (L). Khanh hoa: Tre islands [Hòn Tre island] near Nha Trang, E.Poilane 2937 (L). Lạng Sơn: S of Lang Son, May 1908, A.C.d'Alleizette s.n. p.p. (L0585846). Thua Thien-Hue: Hue and vicinity, no detailed location, R.W.Squires 199 (BM, W). Yemen. Adan: Khormaksar isthmus, J.Waring 87 (BM). Al-Hudaydah: Mor, E of Loheia [al-Luhayyah], 15°40'N, 28–30 Mar 1825, F.W.Hemprich s.n. (S08-12138). Lahij: Wadi Hardaba upstream, 20 km SE Dhala [ad-Dali'] town, L.Boulos et al. 16690 (BM). Sanaa: Menacha [Manakha], G.Schweinfurth Arabia Felix 1607 (G). Ta'izz: Taiz [Ta'izz], J.R.T.Wood Y/74/55 (BM). Hadhramaut: Maula Matai [= Maula Matar?], O.Kerfoot 3030 (K).

Coccinia heterophylla (Hook.f.) Holstein. Kew Bull. 65(3): 435–441. 2010 [published in 2011]. TYPE: ANGOLA. [Cuanza Norte province]: Golungo Alto, along the banks of the stream Casaballa, at the base of the mountains in Sobato de Bumba, male, fl, Oct 1855 F.M.J.Welwitsch 791 (Lectotype: BM no. 000948006, digital image! [JPS], selected in Holstein and Renner (2010)). TYPE: ANGOLA. Golungo Alto, along the banks of the stream Casaballa, at the base of the mountains in Sobato de Bumba, male and female, fl, Oct 1855 F.M.J.Welwitsch 791 (Isolectotype p.p.: LISU no. 214547, digital image! [JPS]). TYPE: ANGOLA. no detailed location, female, fr, Jan 1856, F.M.J.Welwitsch 791 (Paralectotype: BM no. 000948008, digital image! [JPS]). TYPE: ANGOLA. in rugged places at Delamboa river, with Coffea melanocarpa, no clear date given, F.M.J.Welwitsch 791 (Paralectotype: BM no.

000948007, digital image! [JPS]). TYPE: ANGOLA. no detailed location and date, F.M.J.Welwitsch 791 (Paralectotype: COI!, digital image! [JPS]). TYPE: ANGOLA. no detailed location, male, fl, no date, F.M.J.Welwitsch 791 (Paralectotype: K!, digital image! [JPS]). TYPE: ANGOLA. no detailed location, female, fl, no date, F.M.J.Welwitsch 791 (Paralectotype: LISU no. 214548, digital image! [JPS]). TYPE: ANGOLA. no detailed location, female, fr, Jan 1856, F.M.J.Welwitsch 791 (Paralectotype: LISU no. 214549, digital image! [JPS]). TYPE: ANGOLA. no detailed location, male, fl, no date, F.M.J.Welwitsch 791 (Paralectotype: LISU no. 214550, digital image! [JPS]). TYPE: ANGOLA. in rugged places at Delamboa river, with Coffea melanocarpa, Sep 1855, F.M.J.Welwitsch 791 (Paralectotype: LISU no. 214551, digital image! [JPS]). TYPE: ANGOLA. at Delamboa river, no date, F.M.J.Welwitsch 791 (Paralectotype: LISU no. 214552, digital image! [JPS]). TYPE: ANGOLA. no detailed location and date, F.M.J.Welwitsch 791 (Paralectotype: LISU no. 214553, digital image! [JPS]). TYPE: ANGOLA. no detailed location and date, F.M.J.Welwitsch 791 (Paralectotype: P, digital image! [JPS]). TYPE: ANGOLA. no detailed location and date, F.M.J.Welwitsch 791 (Paralectotype: G-DC!).

Physedra heterophylla Hook.f. in D.Oliv., Flora of Tropical Africa 2: 553. 1871.

Physedra heterophylla var. hookeri Hiern in Cat. Welw. Afr. Pl. 1(2): 400. 1898. TYPE: ANGOLA. [Cuanza Norte province], Golungo Alto, near Ponte de Felix Simões, female, fl, Dec 1855, F.M.J.Welwitsch 792 (Holotype: BM!).

Description. Perennial climber. Stem up to 5–6 m long, glabrous, sometimes whitish-speckled. Petiole 1–2 cm long, on abaxial side puberulous with few tiny trichomes, rarely with up to 0.8 mm long yellowish trichomes, sometimes white-speckled, on adaxial side with small yellowish-dirty trichomes. Leaves 7.5–12.5 × 10–14 cm, cordate, deltoid-subhastate to 5-lobate, auriculate or 7-lobate. Lobes triangulate to ovoid. Leaf margin dentate, often serrate. Apex acute with final tooth to acuminate. Upper lamina glabrous, small hyaline pustulate, nerves glabrous, except for basis with small yellowish-dirty trichomes. Lower lamina glabrous often with blackish glands, nerves glabrous, except for basis with up to 0.8 mm long yellowish trichomes and sometimes white-speckled. Probracts up to 5 mm. Tendrils bifid. Male flowers in short racemes. Common peduncle 2–3 mm long, not exceeding the pedicel bearing part in length, puberulous with tiny yellowish-dirty trichomes (magnifying glass!). Pedicels < 4 mm, glabrous to puberulous. Bracts up to 3.5 mm. Perianth tube glabrous. Calyx lobes 5–7 mm long, subulate, erect. Corolla up to 1.6 cm long, dirty-yellowish, dirty-orange to reddish-orange. Corolla lobes 0.4–0.7 cm. Color of filament column, anther head, or pollen sacs not seen. Female flowers solitary or in short or long (up to 15 cm) racemes (Fig. 19). Raceme and bracts as in males, except raceme can be elongated (see remarks).

Hypanthium glabrous, calyx lobes and corolla like male flowers. Ovary glabrous. Style 3-lobed, color not seen. Stigma bulging, color not seen. Fruits up to 4–6 × 2–2.5 cm, ovoid-elliptical to short cylindrical, glabrous. Fruits ripen from green? via orange-colored with longitudinal green bands, ripe fruits unknown. Seed size not known, obovate, rather symmetrical, face flat.

Phenology. February–April, June, September–December

Distribution. Fig. 30. Western Gabon (Estuaire), southern R. Congo (Kouilou), western D. R. Congo (Bas-Congo), western Angola (Cuanza norte, Namibe). Elevation 10 to 900 m. Soil preference unknown. Transition between tropical lowland rainforest and woodlands, and its relict sites along the Angola highland escarpment, in secondary regrowths, on shrubs, along rivers.

Remarks. The long subulate calyx lobes are the only good character for this species, which otherwise can be easily confused with *C. barteri.* Female specimens from Gabon and R. Congo have long-stretched racemes while the racemes are more condensed in the South. Whether this character shows affinity (introgression?) to *C. racemiflora*, defines an own species, or is just a coincidental observation of intraspecific variation is not known.

Taxonomical remarks. This species is type species of *Physedra* Hook.f. Hooker (Bentham and Hooker 1867) described the genus indicating three species belonging to it. However, in Oliver's Flora of Tropical Africa (Hooker 1871), he only describes two species, *P. heterophylla* and *P. longipes*. After Jeffrey (1962) transferred *P. longipes* into a new genus, *Ruthalicia*, he indirectly lectotypified *Physedra*. Monique Kéraudren regarded *P. heterophylla* as synonym to *C. barteri* (Kéraudren 1967; Kéraudren-Aymonin 1975a) from which it differs by the long calyx lobes. This however led to the creation of *C. subhastata* with short calyx lobes, which is in fact synonym to *C. barteri* (Holstein and Renner 2010).

Specimens examined. (in total: 31) Angola. Cabinda: Maiombe [Forest], Belize, J.Gossweiler 7653 (COI, K, LISU). Cuanza Norte: Cazengo municipality, near Agricultural Station Cazengo, J.Gossweiler 5178 (LISU), 5655 (LISU, 4 sheets), and 5707 (LISU). Huíla: Châo da Chela, between [Lago] Tchivinguiro and Bruco, on middle slope of Serra da Chela escarpment, E.J.Mendes 925 (BM, COI, LISU); ibid. L.A.Grandvaux Barbosa 9448 (COI). D. R. Congo. Bas-Congo: Kasangulu territoire, Zongo, towards E of Inkisi Falls, C.Evrard 6757 (BR); Lukula territoire, Temvo, F.M.C.Vermoesen 1824 (BR, EA, WAG); Muanda territoire, around Muanda, L.Bittremieux 44 (WAG); on Kinzao Vuete–Lemba route, P.Compere 230 (BR); Thysville territoire, M'Vuazi, R.E.Delhaye 347 (WAG, WAG). R. Congo. Kouilou: on left bank of Kouilou river, 4 km upstream of Kakamoeka, Sounda on path to level meter, C.Farron 4980 (P). Gabon. Estuaire: Libreville, R.P.Klaine 414 (P, P, P); Libreville, I.R.A.F.-

Gros bouquet area, A.M.Louis 2194 (WAG); Libreville, I.R.A.F. building, 0°25'N 9°26'E, J.M.Reitsma & B.Reitsma 2120 (MO, NY, WAG); Cap Esterias peninsula, 0°36.3'N 9°25.4'E, C.C.H.Jongkind & R.Niangdouma 5905 (WAG).

Coccinia hirtella Cogn. in Schinz, Bull. Herb. Boiss. 4: 821. 1896. TYPE: [SOUTH AFRICA]. KwaZulu-Natal: Howick, 3400', male, fl, 18 Feb 1895, R.Schlechter 6775 (Lectotype, designated by Meeuse (1962): Z, digital image [Z]!; isolectotypes: BR!, GRA, digital image! [JPS], K!).

Description. Perennial creeper or climber. Stems up to 3 m, densely covered with long, upright, whitish trichomes. Petioles 1.5–4 cm long, indument like on stem. Leaves 3–10 × 2.5–11 cm, 5-lobate. Lobes obovate or elliptical in outline, rarely ovate. Margin lobulate or coarsely serrate, (in maturity pale brownish) dentate (Fig. 12a). If margin serrate, then lobe tips acute, else often rounded. Upper and lower lamina, esp. on the nerves, densely covered with long, upright, whitish trichomes. Probracts up to 3 mm. Tendrils simple or bifid. Male flowers solitary, rarely in few-flowered raceme. Common peduncle 1.8–4.5 cm, long, with white trichomes, pedicel of racemous flowers 0.2–3 cm, with white trichomes. Bracts up to 2 mm, caducous. Pedicel of solitary flowers 3–8.5 cm, with white trichomes. Perianth tube with white trichomes. Calyx lobes narrow triangulate to lineal, 3.5–6.5 mm long, spreading. Corolla 2–3.7 cm long, buff, lobes 1–2 cm. Filament column white, anther head pale yellowish, pollen sacs yellow to orange. Female flowers one solitary. Pedicel 0.5–5.5 cm long, with white trichomes. Hypanthium with white trichomes, calyx lobes and corolla like in male flowers. Style columnar, whitish. Stigma bulging, yellow. Ovary with some long trichomes. Fruit oblong ovoid 5–6 cm × 2.5–3 cm, sparsely long with long (> 0.5 mm) trichomes to glabrous, ripening from green via green with longitudinal whitish mottling, via yellow, orange to red when ripe (Fig. 12a). Seeds 5.5–6.5 × 3–3.5 mm (L/W), seed height not seen, ovoid, rather symmetrical, face flat lenticular.

Phenology. January–April, September, November, December.

Distribution. Fig. 31. Lesotho, South Africa (S KwaZulu-Natal, SE Free State). Afromontane scrubland, highveld, sourveld, grassland. Elevation 110–1900 m. On sand, sandstone, loam, well-drained, full sun, grazing maybe tolerated.

Use. It is said that if a Masuto dreams about an ancestor ("balimo") unpleasantly, then relief is given after a bath with sun-dried *C. hirtella* roots and ironstone in a hole on the threshold of the "lelopa" (the circular fence around the hut) (Phillips 1933).

Vernacular names. Sotho: leraka-la-balimo (Phillips 1933; Jacot Guillarmod 1971), Sotho: monyaku (Jacot Guillarmod 1971).

Specimens examined. (Selection; in total: 33). Lesotho. Berea: Mamathes, below Cannibals Cave, A.Jacot Guillarmod 1969 (PRE). Leribe: Léribé [Hlotse], H.Dieterlen & A.Dieterlen 145 (BR, Z). Maseru: Roma, Map[h]otong, M.Schmitz 8039 (PRE). South Africa. Free State: [Thabo Mofutsanyane District Municipality], [Dihlabeng Local Municipality], ±3 km W of Paul Roux on road to Senekal, 28°18’S 27°56’E, J.J.Meyer 3182 (PRE); [Thabo Mofutsanyane District Municipality], [Maluti a Phofung Local Municipality], Rooiberge area, Ross Kloof, M.Jacobs 8565 (L, LISU, PRE); [Thabo Mofutsanyane District Municipality], [Phumelela Local Municipality] 42 km SE of Vrede on road to Verkykerskop, Farm Drikoppe, at foot of Aasvoelkop, back of old farm house, E.Retief 2051 (PRE); [Thabo Mofutsanyane District Municipality], [Setsoto Local Municipality], Ficksburg district, plaas [farm] Moolmanshoek, F.A.de Lange 1153 (PRE). KwaZulu-Natal: [Sisonke District Municipality], 21.6 ml. NNE of Underberg, J.P.H.Acocks 22147 (PRE); [Ugu District Municipality], [Vulamehlo Local Municipality], Dududu, 2 km W of the Cedars, c. 30°13’30’’S 30°37’30’’E, T.B.Sikhakhane 264 (PRE); [UMgungundlovu District Municipality], [Ethekwini Local Municipality], Camperdown, Inchanga, T.Eshuis 1 (MO, PRE); [UMgungundlovu District Municipality], [Richmond Local Municipality], Byrne–Keerom, M.Gafney 14 (WAG); [UMgungundlovu District Municipality], [Umgeni Local Municipality], 17 km from Nottingham Road on road to Loteni, E.Retief 1638 (MO, PRE); [UMgungundlovu District Municipality], [UMshwathi Local Municipality], Albert Falls, A.Meebold 13160 (M); [Uthukela District Municipality], Giants Castle Game Reserve (Dinosaur Footprint area), W.R.Trauseld 930 (PRE).

Coccinia intermedia Holstein, Phytokeys 7:28. 2011. TYPE: BENIN. Atakora: Natitingou, Kouaténa (Perma), 10°12.00’N; 1°30.18’E, river bed, female, fl, fr, 3 Oct 2000, A.Akoègninou et al. 3625 (Holotype: WAG0278370!; isotype: WAG0278369!). TYPE: GHANA. Shai Hills Game Reserve, monoecious, fl, fr, 25 May 1976, J.B.Hall & J.M.Lock GC 46016 (Paratypes: K! 4 sheets, MO!). TYPE: IVORY COAST. Zanzan Region: Bouna, male, fl, 10 Aug 1967, C.Geerling & J.Bokdam 662 (Paratypes: MO!, WAG!). TYPE: TOGO. Maritime: between Lomé and Aného, female, fr, 25 Jun 1994, L.Aké Assi 18983 [typographical error in orig. publication stated 18982] (Paratype: MO!).

Description. Perennial climber. Shoot length unknown, but likely several meters, glabrous, in maturity with clear to white pustules. Petioles 2.8–10.8 cm, glabrous, when older with clear to white pustules. Leaves 6–15 × 7–18 cm, shallowly to profoundly 5-lobate, more or less auriculate. Margin conspicuously dentate, blackening when dried. Apex acute. Upper lamina glabrous with clear to whitish pustules. Lower lamina paler than upper lamina, glabrous, often with small dark glands near the leaf base. Probracts up to 2.5 mm long. Tendrils simple or bifid. Male flowers in few-flowered racemes, likely sometimes accompanied by a single flower. Common peduncle up to 1 cm, pedicels in racemose flowers 2–4 mm, glabrous. Bracts up to 1.5 mm. Perianth tube glabrous, calyx lobes c. 1.5 mm, lineal to narrow triangulate, erect with slightly recurved tips. Corolla 1.6 cm long, pale reddish-yellow to yellow, lobes 0.7 cm. Filament column and anther head not seen, pollen sacs yellowish. Female flowers 1–3 clustered (strongly reduced raceme). Pedicels 0.6–1.2 cm, glabrous. Hypanthium tube glabrous, calyx lobes and corolla like in male flowers. Ovary glabrous. Style and stigmas not seen. Fruit 4.5 × 2.5 cm, elliptical to oblong. Unripe fruit green with pale green longitudinal mottling, ripe orange?, more likely becoming red via orange ripening stage. Size of mature seeds unknown (≥ 5.5 × 3.5 × 1.3 mm), symmetrical (to slightly asymmetrical), face flat.

Phenology. May, August, October.

Distribution. Fig. 32. NE Ivory Coast, SE Ghana (likely also in the north), S Togo (likely also in the north), NW Benin. Elevation sea level to 415 m. Wooded grasslands (semi-humid savanna), woodlands, dry forests, in river beds.

Remarks. This species is rather cryptical and imperfectly known. The leaves seem to develop conspicuous margin teeth during maturity, like e.g. *C. grandis*, but the darkish sub-laminal glands differ from that species. The erect calyx lobes with slightly recurved tips seem to be the most indicative character for *C. intermedia*. The clustered female flowers and the fruits link to *C. barteri*, from which it, among other characters, differs in ecology. Two J.B.Hall & J.M.Lock GC 46016 specimens from K have male and female flowers/fruits on one twig and are thus monoecious. As all other *Coccinia* specimens are dioecious, this could be a case of “leaky dioecy” (Baker and Cox 1984), which also has been observed in other Cucurbitaceae (Schaefer and Renner 2010).

Coccinia keayana R. Fern., Boletim de Sociedade Broteriana ser. 2, 33: 191. 1959. TYPE: GUINEA-BISSAU. Tombali Region: Cacine, rainforest, fl, Aug 1933, J.V.G.do Espírito Santo 603 (Holotype: COI), J.V.G.do Espírito Santo 631 (Paratypes: LISC!, LISC, LISC, LISJC). TYPE: GUINEA-BISSAU. Tombali Region: between Cacine and Guileje, plantation, fl, 1 Aug 1945, J.V.G.do Espírito Santo 2151 (Paratypes: COI, LISC!, LISC). TYPE: LIBERIA. [Margibi County]: Firestone plantation, at Du River, 29 Jul 1926, D.H.Linder 121 (Paratype: K!). TYPE: SIERRA LEONE. Jigaya, c. 350 m, 28 Sep 1914, Thomas 2844 (Paratype: K!). TYPE: SIERRA LEONE: Northern Province, Bumban, 30 Aug 1928, F.C.Deighton 1221 (Paratype: K!). TYPE: SIERRA LEONE: Southern Province, Moyamba District, Moyamba, fl, 25 Aug 1931, F.C.Deighton 2217 (Paratype: K!).

Coccinia sp. A Keay, Flora of tropical West Africa 1: 216. 1954.

Description. Perennial? climber. Stem up to 5 m long, glabrous. Petiole 1.5–5 cm, with short few-cellular trichomes on upper side, glabrous on lower side. Leaves 5–11 × 3.5–11 cm, (shallowly to) profoundly 3-(or 5-)lobate, auriculate, rarely long cordate. Margin rather remotely dentate to slightly serrate. Lobe apex acute or subacute with final tooth. Upper leaf lamina tiny hyaline pustulate, on nerves with tiny few-cellular trichomes, rarely with some soft-multicellular trichomes. Lower lamina with blackish glands, dried often with bluish-green tinge, glabrous or rarely with soft multicellular trichomes on nerves. Probracts up to 3 mm. Tendrils simple. Male flowers ebracteate, in lax racemes with up to 20 flowers, sometimes with a solitary along (Fig. 20). Common peduncle up to 1.7 cm, shorter than racemous part, glabrous. Pedicels of racemous flowers up to 1 cm, pedicels of solitary flowers up to 1.5 cm long, each glabrous. Perianth tube glabrous. Calyx lobes lineal, 2.5–3 mm, in buds spreading, later reflexed. Corolla 1.7–2.0 cm long, white, yellow, dirty-orange, salmon to dull pinkish. Corolla lobes 3–5 mm long. Filament column and anther head not seen, pollen sacs pink–orange. Female flowers solitary or in few-flowered lax racemes. Common peduncle 1.2–2.1 cm, glabrous. Pedicel flowers in racemes up to 1 cm, glabrous, pedicels of solitary flowers up to 2.7 cm, glabrous. Hypanthium glabrous, calyx lobes and corolla as in male flowers. Ovary glabrous. Style and stigma not seen. Fruits 2–3 × 2 cm, subglobose to globose, unripe glaucous green, ripening via yellow to pinkish [rather glaucous?] red. Seed 4.5 × 2.5 × ? cm, rather symmetrical obovate, face flat lenticular.

Phenology. Flowering from March to November.

Distribution. Fig. 32. Tropical West Africa: Guinea-Bissau (Tombali Region), Sierra Leone, Liberia, Guinea (Nzérékoré Region), southern Côte d'Ivoire, southern Ghana, southern Togo? Elevation sea level to 1250 m. On sandy soil, lateritic soils. Tropical rainforest, in high trees, high bushes, on roadsides.

Vernacular names. Cf. Koranko: nala (W.Thomas 2844), Limba: ngolibwe (W.Thomas 2844), Mende: ndogbo-gojai (F.C.Deighton 2217), Temne: efosa (W.Thomas 2844).

Remarks. The long racemes with ebracteate flowers and the lineal reflexed calyx lobes are good characters for this species. It is barely differentiable from *C. barteri* without flowers. *Coccinia keayana* specimens often have a bluish green tinge and the lobes suspiciously point forwards (see Fig. 20), which might only rarely occur in *C. barteri*. The corolla is rather tubular, sometimes a bit inflated.

Specimens examined. (in total: 28) Ghana. Eastern Region: Asiakwa district, Atewa Range Forest Reserve, Accra-Kumasi highway 5–6 km along forest road that intersects the highway at Sagyimase village, 6°13’48’’N 0°32’42’’W M.Merello et al. 1179 (MO); Kade Agricultural Research Station, J.K.Morton A4179 (WAG); Kwahu, Mt Ejuanema, C.D.Adams 5118 (COI). Western Region: Bia National Park, J.B.Hall & J.M.Lock GC46493 (WAG). Guinea. Nzérékoré: Macenta Préfecture, FC Ziama, 8°7'21.36"N 9° 6'45.54"W, E.Achigan-Dako 07 NIA 937 (GAT); ibid., E.Achigan-Dako 07 NIA 939 (GAT); Nzérékoré Préfecture, [WSW of] Nzérékoré, 7°43'35.54"N 8°51'21.28"W, E.Achigan-Dako 07 NIA 917 (GAT). Guinea-Bissau. Tombali: Bedanda sector, Cantanhez, J.Alves Pereira 3172 (H, LISC). Ivory Coast. Lacs: Oroumba Boca [Orombo Bocca Mt., 6°21’N 4°52’W], H.C.D.de Wit 5772 (WAG, WAG). Lagunes: Abidjan, Banco Forest Reserve, W.J.J.O.de Wilde 893 (EA, WAG, WAG, Z); Abidjan. 70 km from Abidjan to Ndouci, c. 5°42’N 4°32’W, A.P.M.de Kruif 332 (WAG), Anguededou forest, W.J.van der Burg 763 (M, WAG 2 sheets). Liberia. without location, F.C.Straub 140 (BR, PRE, S, NY, US n.v.). Bong: 3 miles NE of Suacoco, Z.D.Traub 256 (BR, G, MO). Grand Gedeh: [Konobo district], E slope of Putu Hills east range, W of Tiama, 5°40’N, 8°10’W, C.C.H.Jongkind et al. 6542 (WAG); Tchien district, Latico, J.-G.Adam 25945 (MO); Tchien district, Mim timber Co. (Fijnhout), J.de Koning 470 (WAG). Montserrado: Bomi Hills, Gola N forest, c. 6°56’N 10°45’W, F.S.C.Stoop - van der Kasteele 213 (WAG). Nimba: Yéképa, Mt Nimba, J.-G.Adam 21232 (MO, PRE); Yéképa, south Nimba, J.-G.Adam 21533 (MO); Yéképa, Mt Loma, J.-G.Adam 24159 (MO); Yéképa, Himba, Yiti river, J.-G.Adam 27575 (WAG); Yéképa, old road mine, J.-G.Adam 29670 (MO).

Coccinia longicarpa Jongkind, Blumea 49: 83. 2004. TYPE: IVORY COAST. Lagunes: Forêt du Banco, S of Arboretum, near river, male and female, fr, 20 Jul 1973, J.de Koning 1965 (Holotype: WAG!, isotype: K, digital image! [K]). TYPE: IVORY COAST. Lagunes: Forêt du Banco, Route Martineau, secondary forest, male, fl, 10 Oct 1974, J.de Koning 4077 (Paratype: WAG!). TYPE: IVORY COAST. Lagunes: Forêt du Banco, near swampy secondary forest, male, buds, 8 Aug 1975, J.de Koning 5904 (Paratypes: MO!, WAG!). TYPE: IVORY COAST. Lagunes: Forêt du Banco, N of center, near Banco river, in forest clearing on clear spot, 16 Jun 1975, W.J.van der Burg 551 (Paratype: WAG!). TYPE: IVORY COAST. Lagunes: near Abidjan, male, fl, 6 Sep 1967, C.Geerling & J.Bokdam 829 (Paratypes: WAG!, WAG!). TYPE: IVORY COAST. Lagunes: [W of Abidjan], Adiopodomé [Adiopo-Doumé], margin of bush pathway, male, fl buds, 3 Aug 1956, J.J.F.E.de Wilde 183 (Paratypes: WAG!, WAG!, WAG!). TYPE: GHANA. Eastern Region: near Kibi, Atewa Range Forest Reserve, Jun 1976, J.M.Lock GC 43991 (Paratype: K). TYPE: LIBERIA. Gbapolu Region/Lofa Region: Gbanga, Sep 1926, D.H.Linder 576 (Paratype: K). TYPE: LIBERIA.

Nsuta, no detailed location, 1500 ft, male and female, fl, fr, May 1929, Vigne 1735 (Paratypes: K, P!).

Coccinia sp. B Keay, F.T.W.A. 2nd ed., part 1, 1: 216 p.p. 1954. Nigeria. [Ogun]: Ijebu-Ode District, male, fl, 2 May 1946, S.Tamajong FHI 16938 (K!); D.H.Linder 576 (K); Vigne 1735 (K, P!).

Coccinia sp. A C.Jeffrey, Key to the Cucurbitaceae of West Tropical Africa. J. W. African Sci. Assoc. 9: 87, p.p. 1964.

Coccinia sp. D Keay, F.T.W.A. 2nd ed., part 1, 1: 216 p.p. 1954. NIGERIA. [Oyo]: Lagos [Colony], Ibadan forest, male, fl, 1 Dec 1900, C.Punch 46 (K!)

Description. Perennial climber. Stems up to 5 m, glabrous. Petiole 0.9–4.5 cm, glabrous. Leaves 7–12 cm × 2.5–11 cm, subhastate, spear-shaped, rarely 3-lobate, auriculate. Lobes elliptical. Margin suspiciously dentate, whitish in living state, blackening when dried. Apex acute with final tooth. Upper leaf lamina pale to white pustulate. Lower lamina glabrous, nerves often white-speckled. Probracts < 1 mm, often missing. Tendrils simple, rarely bifid. Male flowers ebracteate, in glabrous racemes, occasionally accompanied with a solitary flower. Common peduncle 0.7–1.5 cm, pedicel of flowers in raceme 2.5–8 mm, pedicel of solitary flower 5–10 mm. Perianth tube glabrous, calyx lobes 2–3 mm long, (0.75–)1.2–1.8 mm broad at base, erect. Corolla 0.8–1.5 cm long, yellow to (pale) orange, sometimes with greenish nerves. Corolla lobes up to 2 mm long. Filament column and anther head not seen, pollen sacs yellow to orange. Female flower solitary. Petiole 1.5–2.2 cm, glabrous. Hypanthium glabrous, calyx lobes and corolla not seen, but likely as in male plants. Ovary glabrous. Style and stigmas not seen. Fruit up to 20 cm long, c. 1 cm in diam., long cylindrical, unripe waxy green, ripe unknown. Seed size and shape unknown, flat.

Phenology. May–December.

Distribution. Fig. 32. Tropical West Africa: southwestern Ivory Coast, southern Ghana, southeastern Benin, southwestern Nigeria. Elevation sea level to 460 m. Soil preference not known. In primary or secondary forests, in disturbed places (roadsides, near rivers).

Remarks. The broad calyx lobes are, apart from the long cylindrical fruit, the best character for this species. An urceolate corolla (Jongkind 2004) also occurs in *C. barteri*.

Specimens examined. (in total: 25) Benin. Plateau: Pobe, 6°57'52.56"N 2°40'19.70"E, E.Achigan-Dako 07 NIA 731 (GAT). Ghana. Ashanti: Bobiri Forest Reserve, 6°41’N 1°21’W, C.C.H.Jongkind 3970 (WAG, WAG). Central Region: Twifo/Hemang/Lower Denkyira District, Kakum, 5°20'54.31"N 1°23'1.39"W, E.Achigan-Dako 07 NIA 734 (GAT). Eastern Region: Atewa Range Forest Reserve, 06°15’N, 00°33’W, C.C.H.Jongkind et al.

1538 (MO, WAG). Western Region: Jomoro District, Fawoman, 5°19'32.63"N 2°43'28.13"W, E.Achigan-Dako 06 NIA 050 (GAT); ibid., E.Achigan-Dako 06 NIA 051 (GAT); Jomoro District, Fawoman, 5°19'38.86"N 2°43'29.78"W, E.Achigan-Dako 07 NIA 742 (GAT); ibid., E.Achigan-Dako 07 NIA 743 (GAT); Jomoro District, Fawoman, 5°19'50.63"N 2°43'22.84"W, E.Achigan-Dako 07 NIA 747 (GAT). Ivory Coast. Lagunes: Abidjan. Banco Forest Reserve, c. 5 km N of arboretum, W.J.J.O.de Wilde 394 (WAG); Banco Forest Reserve, J.J.Wieringa 5386 (WAG); Adiapo-Doumé, near ORSTOM policlinic, J.de Koning 5882 (WAG, WAG); I.D.E.R.T. Forest, c. 17 km W of Abidjan, W.J.J.O.de Wilde 437 (K). Nigeria. Ogun: Ijebu-Ode District, Omo Forest Reserve, Compartment 8, J.R.Charter FHI 38635 (K).

Coccinia mackenii Naudin ex C.Huber [sphalm. Mac-Kennii, after M'Ken, ICBN 60C.5] Cat. Print.: 5. 1865.

Cephalandra mackenii (Naudin ex C.Huber) Naudin [sphalm. mac kennii], Ann. Sci. Nat. Bot. 5: 17, ser. 5. 1866. TYPE: CULTIVATED IN PARIS BOTANICAL GARDEN. original source: South Africa: [KwaZulu-Natal], near Port Natal [Durban],male and female, fl, C.V.Naudin s.n. (Lectotype, designated in Holstein and Renner 2010: P [photo in K]!; isolectotype G-DC (G00211343)!). TYPE: CULTIVATED IN HUBER GARDEN IN OLBIA [HYÈRES, FRANCE]. original source: South Africa: [KwaZulu-Natal], Port Natal [Durban], male and female, fl, 1864, C.V.Naudin s.n. (Paralectotypes: G-DC! 3 sheets, K! 4 sheets).

Coccinia palmata (E.Mey.ex Sond.) Cogn. in A.DC & C.DC., Monogr. Phan. 3: 540. 1881. Nom. illeg. *Momordica palmata* E.Mey. ex Drège, Zwei Pflanzengeographische Documente: 156, 159, 202. 1843. Nom. nud. *Cephalandra palmata* E.Mey. ex Sond. in Harvey & Sonder, Flora Capensis 2: 493. 1862. TYPE: [SOUTH AFRICA]. [KwaZulu-Natal]: near Port Natal [Durban], male and female, fl, fr, Apr, J.F.Drège s.n. (Lectotype, designated by Meeuse (1962): S08-12155!, isolectotype: P!). TYPE: [SOUTH AFRICA]. without location and date, male, fl, J.F.Drège s.n. (Paralectotypes: G!, HBG!; K 2 sheets!; L!, P 2 sheets!, W!). TYPE: [SOUTH AFRICA]. [KwaZulu-Natal]: Omsamculo [Umzimkulu], between shrubs and thickets, near river mouth, female, fr, Mar, J.F.Drège 4637 (Paralectotype: P!)

Coccinia dinteri André, Revue horticole: 276. 1900. TYPE: Unnumbered plate in l.c.

Description. Perennial climber or creeper. Stems up to 9.5 m, glabrous. Petioles 0.7–11 cm long, glabrous or with thin trichomes. Leaves 3–13.5 × 3–15.5 cm, shallowly to profoundly 5-lobate, in the latter case often weakly lobulate. Lobes triangulate, lanceolate, ovate to obovate. Margin smooth, dentate, sometimes serrate to lobulate, esp. towards the apex. Apex acute with final tooth. Upper lamina glabrous with clear to white pustules, rarely with few trichomes. Lower lamina glabrous or with thin stiff or articulate trichomes, towards base usually with glands. Probracts up to 4 mm, oblong-lanceolate. Tendrils bifid, rarely simple. Male flowers solitary or ebracteate in few-flowered racemes. Common peduncle 5–6.5 cm, pedicel of flower in raceme up to 2.5 cm, pedicel of solitary flowers 6–9 cm, all glabrous, rarely with long trichomes. Perianth tube glabrous. Calyx lobes 1.5-6.5 mm, subulate to narrow triangulate, when young erect, later spreading to reflexed. Corolla 1.3–2.7 cm long, cream, corolla lobes subulate to triangulate, 0.7–1.1 cm. Filament column, anther head, and pollen sacs not seen. Female flowers one solitary. Pedicel 0.7–5 cm long, glabrous. Hypanthium glabrous, calyx and corolla like in male flowers. Ovary glabrous. Style columnar, color not seen. Stigma bulging, color not seen. Fruits elliptical to oblong, c. 10 × 2–2.5 cm. Unripe green with white mottling, ripe red-orange to red, sometimes? with white mottling. Seeds 6–7 × 4–4.5 × 1.5 mm, ovate, slightly asymmetrical, face flat lenticular.

Phenology. January–April, July, November, December.

Distribution. Fig. 31. South Africa (east Eastern Cape, KwaZulu-Natal, Mpumalanga, Limpopo), Swaziland. Elevation sea level to 1750 m. Clay, Berea red sand, sandstone, quartzite, poorly drained. Afromontane forests, coastal forests, littoral forests, forest margins, sometimes grassland. In frost-free areas (Meeuse 1962).

Use. Leaves and fruits are eaten by Tsonga people (Shackleton et al. 1998).

Vernacular names. Xitsonga: Gomo, XipapaXipapana (Shackleton et al. 1998).

Remarks. Some specimens with deeply lobate leaves and short petioles resemble the closely related *C. quinqueloba*, and some *C. quinqueloba* individuals have long petioles (C.V. Naudin s.n. 1863, C.V. Naudin s.n. 1863–1865, E.Retief 1215). However, Naudin (1866b) reports considerable problems to seed production in interspecific crosses. It would be desirable to validate this observation.

Taxonomical remarks. Sonder used Meyer’s nomen nudum epithet to name his *Cepha-landra* species. Cogniaux took up this epithet for *Coccinia* without knowing that M. J. Roemer already used the name *Coccinia palmata* to synonymize *Bryonia palmata* from Linnaeus’ Species plantarum. According to nomenclatural rules, Cogniaux’ *Coccinia palmata* is there-fore illegitimate (for details, see chapter *Coccinia palmata* – 120 years wrongly applied).

The drawing of *Coccinia dinteri* in the protologue shows a bifid tendril. Since all other characters match *C. mackenii*, the resemblance was already discussed in the protologue, it is feasible to synonymize it with that species. M. Proschowsky grew this plant in the Fabron quarter of Nice, but the origin of the seeds was not indicated. The label named it “*Coccinia dinteri*” after Moritz Kurt Dinter (in the protologue errorously spelled as “Hurt Dinter”), who was gardener in La Mortola (Giardini Botanici Hanbury, Liguria, Italy) and collected plants from southern Africa. Hence, it is reasonable to assume this origin as done by André there, which again would match *C. mackenii*.

Specimens examined. (Selection, in total: 76) South Africa. Eastern Cape: [Amatole District Municipality], Kentani district, no detailed ocation, A.Pegler 436 (BM, PRE); [Chris Hani District Municipality], Transkei, Engcobo Division, near Encobo, 27 Apr 1955, G.J.Lewis s.n. Herb. no. 66631 (PRE); [O.R.Tambo District Municipality] Port St. Johns, Jan 1933, A.O.D.Mogg s.n. (L, PRE42990, Z). Kwazulu-Natal: [Amajuba District Municipality, Emadlangeni Local Municipality], Retirement, N.J.Devenish 1707 (PRE); [eThekwini District], Durban district, Isipingo North, C.J.Ward 3747 (COI, PRE); [Sisonke District Municipality], near Kokstad, Mar 1931, H.H.Bolus s.n. (PRE 42824), [Ugu District Municipality, Vulamehlo Local Municipality], Umzinto district, Vernon Crookes Nature Reserve, far end of Golden Valley, K.Balkwill et al. 10930 (E, MO); [UMgungundlovu District Municipality, The Msunduzi Local Municipality], Pietermaritzburg, Ferncliffe Forest, J.Bodenstein 92 (PRE); [Umkhanyakude District Municipality], Hluhluwe Game reserve, C.J.Ward 3950 (PRE); [Umzinyathi District Municipality, Umvoti Local Municipality], on Krantzkop [Kranskop]–[Farm] Middledrift road, D.Edwards 2107 (PRE); [Uthukela District Municipality], Cathedral Peak Hotel, G.Condy 8 (PRE); [Uthungulu District Municipality], Nkandlha [Nkandla], Qudeni Forest, 5 mls [8 km] S of Qudeni P.O., L.E.Codd 6991 (PRE); [Zululand District Municipality], Ngome Forest Station, M.Jordaan 595 (PRE). Limpopo: [Greater Sekhukhune District Municipality, Greater Tubatse Local Municipality], near Lydenburg, near Echo Cave R.G.Strey 3762 (M, PRE, WAG); [Mopani District Municipality], Mariepskop, J.J.Bos 1044 (LISC, M, WAG); ibid. A.D.J.Meeuse 9993 (M, PRE); Woodbush [Forest Reserve], 6 Aug 1925, A.O.D.Mogg s.n. (COI, L, PRE43066, Z). Mpumalanga: [Ehlanzeni District Municipality, Bushbuckridge Local Municipality], Salique Forest Reserve, E.Retief 1336 (PRE); Letaba district, E side of shoulder extending northwards from ridge above Weltevreden, J.C.Scheepers 1110 (M, PRE). Swaziland. Hhohho: Forbes Reef, R.H.Compton 30491 (PRE); about 20 km N of Mbabane, Ngwenya Hills, Castle peak, north slopes, B.Maguire 7553 (B, E). Manzini: Usutu Forests, R.H.Compton 32287 (PRE).

Coccinia megarrhiza C.Jeffrey, Kew Bull. 15(3): 347. 1962. TYPE: KENYA. Northern Province [Eastern Province]: Moyale, 3800 ft [c. 1150 m], male, fl, 28 Apr 1952, J.B.Gillett 12967 (Holotype: K!, digital image! [JPS, K], isotypes: B!, digital image! [JPS], S!). TYPE: KENYA. Northern Province [North Eastern Province]: [western Mandera District], Dandu, 2600 ft [c. 792 m], male, fl, 10 Apr 1952, J.B.Gillett 12759 (Paratype: K!). TYPE: KENYA. Northern Province [North Eastern Province]: [western Mandera District], Dandu, 2700 ft [c. 823 m], female, fr, 9 May 1952, J.B.Gillett 13122 (Paratypes: EA!, K!). TYPE: KENYA. Northern Province [North Eastern Province]: [western Mandera District], Dandu, 3000 ft [c. 914 m], male, fl, 14 May 1952, J.B.Gillett 13191 (Paratypes: EA!, K!). TYPE: KENYA. Northern Province [Eastern Province]: Moyale, 3200 ft [c. 1100 m], male, fl, 3 Oct 1952, J.B.Gillett 13986 (Paratype: K!). TYPE: KENYA. Northern Province [Eastern Province]: Moyale, 3600 ft [c. 1100 m], male, fl, 14 Oct 1952, J.B.Gillett 14036 (Paratypes: B!, digital image! [JPS], BR!, EA!, K!, S!). TYPE: KENYA. ibid., female, fl, 3200 ft [c. 1100 m], 14 Oct 1952, J.B.Gillett 14037 (paratype: BR!, K!, K!, S!). TYPE: KENYA. ibid., 3600 ft [c. 1100 m], male, fl, 14 Oct 1952, J.B.Gillett 14038 (Paratypes: K!, K!). TYPE: KENYA. ibid., 3600 ft [c. 1100 m], female, fr, J.B.Gillett 14039 (Paratypes: K!, S!).

Description. (Fig. 8) Perennial climber or creeper. Stem up to 6 m long, with long beigeish patent trichomes, which appear articulate when dried. Petioles 1.5–5.6 cm, indument as on stem. Leaves 3–11 × 4.2–17 cm, kidney-shaped to 3- or 5-lobate. Margin dentate (teeth in maturity brownish, when dried blackening), serrate to lobulate. Upper lamina glabrous with pale pustules or with short white trichomes, lower lamina with indument as on stem, rarely glabrous. Probracts up to 3 mm long. Tendrils simple. Male flowers clustered. Pedicel < 1.5 cm, indument as on stem. Perianth tube with long beigeish upright trichomes, which appear articulate when dried. Calyx lobes 2.5–4 mm, subulate to lineal, spreading. Corolla 1.2–1.3 cm, yellow to pale orange, lobes 0.4–0.6 cm. Filament column greenish, anther head pale greenish, pollen sacs orange-yellow. Female flowers 1(–2) solitary. Hypanthium with long beigeish upright trichomes, which appear articulate when dried , calyx lobes and corolla like in male flowers. Ovary green with whitish spots. Style columnar, green. Stigma bulging, yellow (Fig. 10c). Fruit ovoid-ellipsoid, up to 6.5 cm long, unripe green with longitudinal white mottling. During ripening mottling partly developing a dark green corona (Fig. 12c). Ripe red. Seeds 7 × 4 × 1.5 mm, asymmetric, face flat.

Phenology. March–May, August–October

Distribution. Fig. 23. Ethiopia (Oromia, Somalia State), Kenya (Eastern Province, North Eastern Province). Elevation 800–1600[–2000] m. On granite outcrops and red lateritic soils, *Acacia-Commiphora* bushland, *Dracaena* vegetation, *Balanites* vegetation, *Euphorbia candelabrum* woodlands, dry *Juniperus* forest, grazing is tolerated.

Remarks. *Coccinia megarrhiza* and *C. abyssinica* form a species complex. The distinction can be hard, esp. in young plants, when the color of the marginal teeth is not well developed. Mature male plants of *C. megarrhiza* may also have long-pedicelled solitary flowers, and young *C. abyssinica* also only produce solitary, rather short pedicelled male flowers. Solitary flowers can have the same length in both species. The broad leaves with an emarginate, obtuse to cuspidate tip (*C. megarrhiza*) versus rather long leaves with an acute tip (*C. abyssinica*) seem to be the best character. In maturity, the teeth coloration in *C. megarrhiza* is also much more conspicuous than in *C. abyssinica*. A phylogeographic analysis and crossing experiments would shed light on the question, whether these are just ecologically differentiated morphs or true species. Plants from the mountains near Yebelo have very large leaves, are almost glabrous, and occur, untypically, in dry *Juniper* "forests". However, they have the typical cuspidate to obtuse central lobes and bear the colored leaf margin teeth. As larger leaves are also observed in high altitude individuals of *C. microphylla*, these forms might be regarded as mast specimens.

Specimens examined. (in total: 29) Ethiopia. Oromia: 38 km S of Neghelli [Negele Boran] on Wachelli road, J.W.Ash 814 (EA, EA, K); Dacata Valley, c. 40 km S of Harare [Harar]–Jijiga road, J.J.Bos 9051 (WAG); Guji zone, Neghelli [Negele Boran], R.Corradi 8255bis (FT); Arero (Meta-Gafersa), G.Cufodontis 273 (FT, W); Bombal ca. 40 km on the way to Jijiga from Harar, T.Ebba 622 (K, WAG); 10 km N of Neghelle [Negele Boran] along road to Kebre Mengist [Kibre Mengist], I.Friis et al. 2664 (K, WAG); Bale side of Genale Gorge, 2 km from bridge on the track leading from Neghelle [Negele Boran], turning off 20 km N of town, I.Friis et al. 2716 (K); Neghelle [Negele Boran], compund of Tourist Hotel, I.Friis et al. 3246 (K); c. 20 km NW of Moyale on the road to Mega, just after the turn off to Tuqa (and Sololo in Kenya, 3°39'N 38°56'E, I.Friis et al. 8736 (K); c. 30 km S of Dolo Menna (Masslo) towards Sidambale Bridge, 6°14'N 39°46'E, I.Friis et al. 11090 (K); 2 km W of Yavello [Yebelo] on road to Konso, 4°54'N 38°06'E, M.G.Gilbert & T.G.Jefford 4413 (K); road from Alemaya to Dire Dawa, c. 10 km before Dire Dawa, P.C.M.Jansen 3458 (WAG, WAG) and 3471 (WAG, WAG, WAG); c. 50 km on road from Harar to Jijiga, P.C.M.Jansen 6031 (WAG, WAG); 7 km on Yabello [Yebelo]–Konso-road, 4°49'N 38°03'E, M.Tadesse & K.Vollesen 4343 (K); c. 36 km from Harar to Jijiga and then c. 20 km to S, J.J.F.E.de Wilde 4793 (B, K, MO, WAG, WAG); c. 45 km on road from Harar to Jijiga, J.J.F.E.de Wilde 6501 (WAG, WAG). Somali Regional State: 95 km from Negele of Filtu road, 5°00'N 40°12'E, M.G.Gilbert & B.M.G.Jones 110 (K). Ex cult. from seeds from Negele Borena, Oromia, Ethiopia by Jean-Luc Gatard, Reaumur, France, N.Holstein 118 (M) and 127 (M).

Coccinia microphylla Gilg, Bot. Jahrb. 34: 357. 1904. TYPE: TANZANIA. [Kilimanjaro Region Region]: at base of Pare Mountains, between Kiswani [Kisiwani] and Maji ya Juu [Madji-ja-juu], mix of thornbush and wooded grassland ["gemischte Dornbusch- und Obstgarten-steppe"], 700 m, fl, Oct, A.Engler, Reise nach Ostafrika 1587 (Syntype: B destroyed). TYPE: TANZANIA. [Kilimanjaro Region Region]: between Kihuiro [Kihurio] and Gonja, thornbush steppe, fl, Oct, A.Engler, Reise nach Ostafrika 948 (Syntype: B destroyed). TYPE: KENYA. Coast Province: near Mariakani, NW of Mombasa, male, fl, 15 Oct 1955, E.Milne-Redhead & P.Taylor 7104 (Neotype, designated here: LISU!, isoneotypes: B!, EA!)

Coccinia buikoensis Zimm., Die Cucurbitaceen 2: 177, 24, 51, 84, 96, 114, fig. 17 I-III, fig. 63 II, fig. 74 VII-XII, fig. 81 XVI, XVII. 1922. TYPE: TANZANIA. [Tanga Region]: Lushoto District, [S of Pare Mts], [between Hedaru and Mkomazi], near Buiko, steppe, male and female, fl, fr, Dec 1919, P.W.A.Zimmermann G6595 (Holotype: B destroyed, lectotype designated by C.Jeffrey (1967): EA! digital image! [JPS]).

Coccinia sp. C in C.Jeffrey, Flora of Tropical East Africa: 69. 1967. KENYA, Northern Province: Furroli, lava plateau, semi-desert, *Acacia-Commiphora* shrub, on sand, female, fl, fr, 12 Sep 1952, J.B.Gillett 13820 (B!, EA!, K!, P!, S!) and J.B.Gillett 13826 (K!).

Description. (Fig. 2a). Perennial creeper or climber. Stems up to 4 m, glabrous or more or less densely covered with short white trichomes, when older often dense white pustulate. Petiole 0.45–4.0 cm, with erect, thick or often yellowish articulate trichomes that are sometimes soft spiny (< 1.5 mm) or only wart-like. Leaves 0.7–7.5 cm long, 1.1–12 cm wide, usually rather small, shallow to deeply 3- or 5-lobate, sometimes lobulate, rarely reniform. Lobes narrow to broad triangulate to lanceolate. Upper leaf surface more or less dense white pustulate, pustules sometimes with a short thick trichome. Lower leaf lamina glabrous, sometimes with darker glands between nerves, nerves usually with thick erect trichomes, sometimes reduced to wart-like appearance. Leaf margin rather remotely denticulate, usually with short bent trichomes. Apex acute to obtuse, with final tooth. Probract usually absent, if present then < 1.5 mm. Tendrils simple. Male flowers 1–2 solitary, if fasciculate or in few-flowered racemes, then accompanied by 1 solitary flower. Common peduncle < 0.5 cm, glabrous or with articulate trichomes. Pedicel of solitary flowers 0.2–0.7(–2.5) cm, pedicel of flowers in inflorescences < 0.5 cm, glabrous or especially at apex with long yellowish articulate trichomes. Perianth tube usually with long yellowish articulate trichomes, rarely almost glabrous. Calyx lobes 0.15–0.4 cm, narrow lanceolate to lineal, when young erect, later spreading to reflexed. Corolla 0.7–1.2 cm long, greenish white to yellowish-orange with darker green veins, lobes 0.4–0.7 cm. Filament column and anther head not seen. Pollen sacs yellow. Female flowers 1(–2) solitary Pedicels up to 0.7 cm, glabrous or with white trichomes. Ovary glabrous with some articulate trichomes to dense wooly with long (when dry articulate) trichomes. Style columnar, pale green. Stigmas bulging, greenish yellow. Ripe fruit globose to short obovate, 1.8–2.5 × 1.4–2.5 cm, glabrous or with few articulate trichomes, unripe green with longitudinal mottling, which obtains a dark green corona during ripening, when ripe bright orange-red to red. Seeds 4.5–6 × 2.0–3.0 × 1–1.5 mm, asymmetrical oblong to somewhat falcate, face flattened.

Phenology. January, April, May, July, October–December.

Distribution. Fig. 33. Northeastern Tanzania (Arusha, Kilimanjaro, Manyara, Tanga), Kenya (Coast, Eastern, North Eastern, Rift Valley), southern Ethiopia (southern and central Oromia), Somalia. 70–1300(–1600) m. Savanna, open *Acacia-Commiphora* bushland, degraded *Combretum* bushland, open grassland, cultivated land, roadsides. Red sand, dark brownish-black soil. Limestone.

Vernacular names. Akie lang.: notoku (A.S.Vincent 29, A.S.Vincent 221), Maa [Maasai language]: ndegegeya (A.S.Vincent 29), Maa: sikuni (Kiamba et al. KEFRI 112)

Remarks. There are some specimens, which have a mixed (not intermediate) phenotype with *C. trilobata*: the calyx lobes are unusually long (up to 7 mm), which speaks for *C. trilo-bata*, but the indument matches *C. microphylla*. However, these do not occur in single location, but are found in the Ndoto Mts (O.Kerfoot 2644), in Kiboko *(*P.Kirika et al. 002/020/2011*),* and around near Voi (M.Hucks 579, B. Verdcourt 3888). Whether these are hybrids (F2 or later) or just a variety is not known. These specimens look also quite like *C. megarrhiza*, which occurs in northern Kenya and Ethiopia, however, the indument does not match either.

Despite the epithet, the leaves can become quite large, especially in in higher altitudes. Then, specimens can resemble *C. trilobata*, which has a denser indument. In dry low altitude areas, leaves and flowers are often presented quickly soon after water becomes available, e.g. by a rain shower. The leaves are thus not well developed and small. Specimens from the more arid locations appear to be smaller in many characters, but whether these are an own species is doubtful. There are only few specimens of proposed species (*C.* sp. Burger 2947A, *C.* sp. Gilbert & Jones 129 (Jeffrey 1995)), but the natural scope of *C. microphylla* is hardly assessed. This will not be resolved without a phylogeographic analysis and denser collection data from Ethiopia.

Specimens examined. (Selection, in total: 71) Ethiopia. Oromia: above Gobelli river, W of Dalletti, 8°32’N 42°7’E, W.Burger 2947A (K); 105 km on road from Negelli [Negele] to Filtu, J.J.F.E.de Wilde & M.G.Gilbert 346 (K, WAG, WAG, UPS). Kenya. Coast Province: near Mariakani, NW of Mombasa, E.Milne-Redhead & P.Taylor 7105 (B, EA, LISU). Eastern Province: E side ofLake Rudolf, between Koobi Fora and Shin (hill), 3°57’–58’N 36°12’–20’E, R.B.Faden & A.Evans 71/301 (EA, K). North Eastern Province: Garissa District, 13 km S of Modo-Gash [Mado Gashi], 0°39’N 39°14’E, B.Stannard & M.G.Gilbert 934 (EA, K); Wajir District, Catholic Girl’s Town 2 km E of Wajir, J.B.Gillett 21273 (EA, K, WAG). Rift Valley

Province: Turkana District, I.Ohta 24 (EA). Somalia. Togdheer: Malol [Mt Malool] near Sheikh, J.R.Ironside 5/73/31 (K). Tanzania. Arusha: Monduli district, Longido division, SE of Longido, c. 100–300 m from Arusha Municipality, 2°43’14’’S 36°42’02’’E, C.J.Kayombo & K.Kitaba 4242 (MO). Dodoma: Tarangire National Park, Kalima Hill, S.Chuwa et al. 5329 (NHT). Kilimanjaro: Same district, Mkomazi Game reserve, Ibaya Hill, 3°58’S 37°48’E, R.Abdallah & K.Vollesen 95/198 (BR, K, P). Manyara: Mbulu Dist., Tarangire [National Park], H.S.Mahinda 295 (EA). Tanga: Korogwe District, 2 km W of Mkomazi, under power line, 4°38’53.7’’S 38°03’26.7’’E, N.Holstein et al. 90 (B, DSM, M).

Coccinia mildbraedii Gilg ex Harms in Fries, Notizbl. Bot. Gart. Berlin-Dahlem 8: 492. 1923. *Coccinia mildbraedii* Gilg, Wissenschaft. Ergebn. Deutsch. Zentral-Afrika-Exped. 1907–1908 Herzog Adolf Friedrich zu Mecklenburg, Bot. 2(4): 343. 1911. nom. nud. TYPE: RWANDA. [Ouest Province]: Kissenye [Gisenye]. Bugoy forest, mixed bamboo forest, c. 2500 m, fl, fr, 30 Oct 1907, J.Mildbraed 1425 (Holotype: B, destroyed). TYPE: BURUNDI. Muramvya: [Mt] Teza, 3°13’S 29°33’E, M.Reekmans 7399 (Neotype, designated here: K!; isoneotypes: BR!, EA!, MO!, WAG!, WAG!).

Coccinia ulugurensis Harms in Mildbraed, Notizbl. Bot. Gart. Berlin-Dahlem 11: 1091. 1934. TYPE: TANZANIA. [Morogoro Region]: Uluguru Mts, c. 1350 m, over shrubs at forest margin, male, fl, 14 Mar 1933, H.J.Schlieben 3643 (Holotype: B!, isotypes: B!, BM!, BR!, BR!, G!, HBG!, LISC!, M!, MO!, P!, digital image! [P], S, Z, digital image! [Z], photo of isotype from BR! [EA, K]).

Description. Perennial climber. Stems up to 20 m, when young sometimes villose with whitish articulate trichomes, later often subglabrous to glabrous. Petioles 4–8 cm long, glabrous or with pale articulate trichomes. Leaves 9.5–16.5 × 10–16.5 cm, shallowly to profoundly 3- or 5-lobate. Lobes triangulate, ovate to elliptical. Leaf margin entire and denticulate to serrate. Probracts up to 3.5 mm. Tendrils simple or bifid. Male flowers in racemes, rarely accompanied by one solitary flower or one solitary flower. Common peduncle 3–4.5 cm, pedicels up to 7 mm, bracts up to 1mm, caducous. Pedicels of solitary flowers up to 2.5 cm, each glabrous. Perianth tube glabrous, calyx lobes up to 0.25 cm, triangulate to lineal, in buds adpressed to corolla, later spreading. Corolla 1.2–2.9 cm long, orange buff, lobes 0.3–1.0 cm. Filament column and anther head not seen. Pollen sacs cream yellow. Female flowers solitary, pedicel 3.0–8.0 cm, glabrous. Hypanthium glabrous, calyx lobes and corolla like in male fliwers. Ovary glabrous. Style and stigmas not seen. Fruit up to 20 cm long and 4 cm in diameter, unripe green with white mottling, ripe red. Seeds 6–7 × 5 × 1.5 mm, symmetrical, face flat lenticular.

Phenology. January–April, June, August, September, November, December, likely throughout the year.

Distribution. Fig. 34. NW Burundi, D. R. Congo (North Kivu, South Kivu), Rwanda (West Province), Tanzania (Iringa: Kipengere Range, Uzungwa Mts; Kigoma: Mahali Mts; Mbeya: Kipengere Range; Morogoro: Uluguru Mts; Ukaguru Mts, Uzungwa Mts), Uganda (Western Region).Elevation 1200–2600m. Afromontane cloud forests and mist forests, upland rainforests, in *Macaranga kilimandsharica* shrubs, rarely in *Pennisetum* savannas. Introduced in Kenya.

Vernacular names. Kihunde: mutanga (Deru 485), Kindanda: mwore (Deru 485), Kinande: mombowa (P.Gille 218), Kinyarwanda: umuvunguvungu (G. Bouxin 820), umufungofungo (G.Troupin 11163), umwonkalere (Deru 485), Kisafwa: itangalulu (C.J.Kayombo 1003).

Remarks. *Coccinia ulugurensis* is not confidently distinguishable from *C. mildbraedii*. The leaves are 3-lobate with rather triangulate lobes towards central Tanzania (*C. ulugurensis*), whereas in the western areas the leaves may be deeper lobate with lanceolate lobes (*C. mildbraedii*), but intermediate morphs are found in all places. The occurrence of “crisped hairs”, which Jeffrey (1967) used to distinguish the species, appears to slightly correlate with rainfall amounts, which are higher in the mountains between Tanzania and Congo. These trichomes also occur in other species, such as *C. mackenii*, and the fine pubescence as descrbied for *C. ulugurensis* regularly occurs in young shoots and often disappears later-on. The lack of good genetic differentiation between the two leaf morphs (they cluster together in Fig. 16) strengthens the assumption that they belong to a single species.

Specimens examined. (Selection, in total: 74) Burundi. Muramvya: [Mt] Teza, bordure forêt de montagne, M.Reekmans 4205 (EA, MO). D. R. Congo. North Kivu: Lubero territory, Bingi, A.Léonard 5415 (BR, EA, WAG, WAG, WAG). South Kivu: Kabare territory, Marais Musisi, 28°42’E 2°16’S, P.Bamps 2844 (BR, EA, WAG). Kenya. Central: Limuru, tea estate, introduced from Tanzania, J.B.Gillett 20185 (EA, MO). Rwanda. Province de l’ouest: Kibuye territoire, Mishai forest, A.R.Christiaensen 483 (BR, WAG), Shangugu territoire, Mont Bigugu, R.Christiaensen 1616 (EA, WAG). Province du sud: Rutovu, km 64 on Astrida [Butare]–Shangugu [Cyangugu] route, M.Reynders 394 (BR). Tanzania. Iringa: Mufindi district, Ipafu [hill], C.F.Paget-Wilkes 939 (EA, K, MO); Dabaga Highlands, Ihangana Forest Reserve, near Kibangu, 18 mls [29 km] S of Dabaga, R.Polhill & S.Paulo 1476 (B, BR, EA, K, PRE). Kigoma: Mpanda district, Mahali Mts, Sisaga, c. 6°S 30°E, T.G.Jefford & J.G.B.Newbould 1924 (COI, EA). Mbeya: Mbeya rural district,Umalila Forest Reserve, c. 7 km W of Ruanda II on road to Izumbwe (2 km SSE of main peak of Mbogo Mt.), 9°11’S 33°18’E, R.E.Gereau et al. 5060 (K, MO). Morogoro: Kilosa district, Ukaguru Mts, between Mandege and Masenge, 6°22’S 36°58’E, M.Thulin & B.Mhoro 2792 (DSM, EA, K, MO). Uganda. Western Region: Kigezi district, Virunga chain, northern foot of Mzhavura Mt., Nkanda, H.U.Stauffer 931 (BR, M, Z).

Coccinia ogadensis Thulin. Kew Bull. 64: 485. 2009. TYPE: ETHIOPIA. Somali Regional State: Harerge, 5 km S of Qarsonney, female, fr, 15 May 2006, M.Thulin et al. 11183 (Holotype ETH; isotypes K, UPS!). TYPE: [ETHIOPIA]. [Somali Regional State]: Somaliland, Harradigit [Harradigit], male, fl, Mar 1885, F.L.James & J.G.Thrupp s.n. (Paratype K!). TYPE: [ETHIOPIA], [Somali Regional State]: Somaliland, Harradiqi [Harradigit] or Boobi, male, fl, Mar or Apr 1885, F.L.James & J.G.Thrupp s.n. (Paratype K!). TYPE: [ETHIOPIA], [Somali Regional State]: Agar Ven, 6°30’N, 45°20’E, 2500 ft [c. 760 m], red sandy soil, bushland, male, fl, 25 Oct 1953, P.Ellis 163 (Paratypes FT!, K!, K!). TYPE: [ETHIOPIA], [Somali Regional State]: W of Shillavo (Scillave) [Shilabo], 6º25´N, 44º42´E, 1300 ft [c. 400 m], sandy soil, bushland, male, fl, Nov 1955, P.Ellis 383 (Paratype K!). TYPE: [ETHIOPIA], [Somali Regional State]: [Yehebnut area], E of Gorrahei, 700 m, male, fl, 1 Nov 1967, P.R.O.Bally 12989 (Paratypes G!, K!). TYPE: [ETHIOPIA]. [Somali Regional State]: Scillave [Shilabo]–Wardere road, 6°13’N, 44°45’E, 1130 ft [c. 344 m], red sandy soil, open bushland, male, fl, 2 Apr 1956, J.Simmons 63 (Paratypes EA!, K!). TYPE: [ETHIOPIA], [Somali Regional State]: 11 km NE Scillave [Shilabo], 6°10’N, 44°52’E, 1300 ft [c. 400 m], red sandy soil, open bushland, male and female, fl, 13 Apr 1956, J.Simmons 179 (Paratypes EA!, K!) . TYPE: SOMALIA. [Mudug Region]: 47 miles [75 km] from Galkayo [Gaalkacyo] on Garoe [Garoowe] road, c. 1000 ft [c. 300 m], red sandy loam and limestone ridges, male, fl, 15 Oct 1959, C.F.Hemming 1713 (Paratypes EA!, K!).

Description. Climber or trailer up to 2 m or longer. Stems glabrous, except for nodes with short trichomes, sometimes white pustulate. Petioles 4–15 mm long, glabrous or nearly so. Leaves deeply (3- or) 5-pedately lobate. Central lobe 2–8.5 cm long, 1–8 mm wide, lateral lobes shorter. Lobes entire or dentate to lobulate, linear to oblanceolate. Leaf margins often revolute, apex obtuse with final (brownish? colored) tooth to acute. Upper leaf lamina glabrous, pale to white pustulate; pustules up to 5 mm in diam. Lower leaf lamina glabrous, at base with pale aureolate glands between nerves. Probracts < 1 mm with short whitish trichomes. Tendrils simple. Male flowers solitary, clustered, or in few-flowered racemes. Common peduncle up to 2 cm, glabrous. Pedicels up to 4–20 mm long, subglabrous to glabrous. Perianth tube glabrous, calyx lobes 1–6 mm long, in buds erect, later reflexed, glabrous or nearly so, lineal to narrowly triangulate. Corolla 1.7–2.5 cm, white with green veins or yellow, lobes 0.7–1.3 cm. Petals inside with multicellular trichomes, outside with short oligocellular trichomes. Color of filament column, anther head, and pollen sacs not seen. Female flowers not reported, but very likely solitary, pedicels, hypanthium/perianth tube, calyx lobes and petals not largely differing from male flowers. Fruits spindle-shaped to short cylindrical, 4.5–5.5 cm long, c. 1.5 cm in diameter, sometimes with short apical tip ("beaked"). Unripe green with elongate with spots, turning red with whitish elongate spots. Seeds 4–5.5 × 2–2.5 × 1–1.5 mm, asymmetrical ovate, flat lenticular.

Phenology. Imperfectly known, flowering in April and in October and November during rainy seasons.

Distribution. Fig. 35. Eastern Ethiopia (central and eastern Somali Region), Central Somalia (Mugud Region). Elevation 300 to 800 m. Red sand and sandy loam, limestone soils. Open *Acacia-Commiphora* bushland, semi-desert.

Use. Fruits are reported to be edible, juicy, and thirst-quenching (P.R.O.Bally 12989).

Vernacular names. Somali: dudu (P.R.O.Bally 12989), Somali?: lehailu (J.Simmons S179), Somali?: salo dudub (J.Simmons S63).

Remarks. This species is very similar to specimens of *C. grandis* with deeply lobate leaves (described as *Coccinia palmatisecta*). However, the lobules in *C. grandis* are much more distinct, when the lobulation is that deep. Apart from that, fruit and seed shape of *C. ogadensis* resemble that of *C. adoensis*.

Ellis notes on the specimens no. 163 and 383 a smell of rotten meat. However, it is unclear, whether this is coming from the flowers or from crushed leaves. Several cucurbit species have a putrid smell when crushed, such as *Kedrostis foetidissima* or *Momordica foetida*, but this has never been reported for a *Coccinia* species.

Specimens examined. (in total: 10). Ethiopia. Somali Regional State: Ogaden, J.Simmons 64 (EA).

Coccinia pwaniensis Holstein. Kew Bull. 65(3): 435–441. 2011. TYPE: KENYA. [Coast Province]: Kwale District, Buda Mafinsi forest, 8 miles [12.9 km] WSW of Gazi, 80 m, male, fl, 22 Aug 1953, R.B.Drummond & J.H.Hemsley 3953 (Holotype: K! 3 sheets, isotype: EA!). TYPE: KENYA. Coast Province: Kilifi District, Mangea Hill, 39°42'E 03°16'S, 450 m, dry bushland with *Cynometra* sp., *Brachylaena* sp., *Manilkara* sp., *Brachystegia* sp., *Julbernardia* sp., *Diospyros* sp., *Xylopia* sp., *Inhambanella* sp., female, fr, 28 Dec 1988, W.R.Q.Luke 1601 (Paratype: EA!). TYPE: KENYA. [Coast Province]: Kwale District, Cha Simba forest, 300 m, female, fl, fr, 1 Feb 1953, R.B.Drummond & J.H.Hemsley 1078 (Paratype: K!). TYPE: KENYA. [Coast Province]: Kwale District, Shimba Hills, Giriama Point area, 1250 ft [c. 381

m], forest edge, male, fl, 17 Mar 1968, F.Magogo & P.Glover 315 (Paratypes: EA!, K!). TYPE: KENYA. [Coast Province]: Kwale District, Shimba Hills, Pengo Hill area, 1500 ft [c. 457 m], forest, male, fl, 27 Mar 1968, F.Magogo & P.Glover 493 (Paratypes: EA!, K!). TYPE: KENYA. Shimba Hills, SE-part of Longomagandi Forest, 350 m, lowland rainforest, 13 Nov 1988, R.Schmidt 1203 (Paratype: EA!); Kwale District, no detailed location given, male, fl, 15 Jun 1957, Saunders 11241 (Paratype: EA!). TYPE: TANZANIA. Pwani: Bagamoyo District, Zaraninge Forest in Kiono Plateau, 38°36’E 6°09’S, 1000 ft [c. 305 m], dry evergreen coastal forest, on sand, male, fl., 14 Mar 1990, Frontier-Tanzania Coastal Forest Research Programme 1041 (Paratype: K!). TYPE: TANZANIA. [Pwani]: Kirasawe District: Pugu Hills Forest Reserve on Dar es Salaam–Kisarawe road. Roadside in forest, 100–270 m, male, fl, 12 May 1970, K.H.Macauley CVL 102 (Paratypes: DSM!, EA!). TYPE: TANZANIA. [Pwani]: Pugu Hills, male, fl, 19 Mar 1939, J.H.Vaughan 2774 (Paratype: EA!). TYPE: TANZANIA. [Pwani]: Pugu Hills Forest Reserve, road W from road-tunnel, 100 m, in bushes by car-track through forest, female, fr, 23 Jul 1972, R.Wingfield 2056 (Paratypes: DSM!, EA!).

Coccinia sp. B in C.Jeffrey, Flora of Tropical East Africa: 69. 1967. R.B.Drummond & J.H.Hemsley 1078 (K!); R.B.Drummond & J.H.Hemsley 3953 (K!, EA!); Saunders 11241 (EA!); J.H.Vaughan 2774 (EA!).

Description. Perennial climber or creeper. Stems up to 3 m long, glabrous. Petiole 0.6–4.1 cm, adaxial side glabrous or with short stiff trichomes, abaxial side with stiff patent trichomes that can be quite reduced, then appearing wart-like or subglabrous. Leaves 2–10.4 × 2.7–11.4 cm, shallowly to profoundly 3-(or 5-)lobate, lobes broadly triangulate to elliptic, margin minutely dentate, tips acute. Upper lamina tiny hyaline pustulate, nerves sometimes with tiny trichomes, lower lamina glabrous, rarely with blackish glands at base, nerves towards the base with stiff patent trichomes that can be quite reduced, then appearing wart-like or subglabrous. Probracts 2–3 mm long. Tendrils simple. Male flowers in racemes, sometimes accompanied by 1–2 solitary flowers. Peduncle 3.2–7.7 cm, glabrous, pedicels of flowers in racemes 0.2–1.0 cm, bracts 1–1.5 mm, pedicels of solitary flowers up to 3.8 cm. Perianth tube glabrous, calyx lobes 2.5–3.5 mm long, subulate and spreading, corolla pale yellow to pale orange-yellow, 1.7–2.6 cm, lobes 1–2 cm. Color of filament stalk, anther head, and pollen sacs not seen. Female flower not seen, perianth likely like in male flowers. Style and stigmas not seen. Fruit solitary, petioles at maturity 20–33 mm long, fruit shape oblong-fusiform, 6.2–8.0 × 1.8–2.3 cm, rarely (?) with an up to 5.5 cm long sterile apical tip, immature green with pale longitudinal mottling, at maturity becoming orange-red to scarlet-red with pale mottling. Seeds 6.5–7 × 4–4.5 × c. 1.5 mm, more or less symmetrical broad ovate in outline, lenticular.

Phenology. January–March, June–August.

Distribution. Fig. 25. Kenya (Coast Province), Tanzania (Pwani, but likely also in Dar es Salaam region and Tanga). Elevation 80–460 m. On sandy soil. Open and disturbed places of East African coastal forests and woodlands *(Brachystegia* sp., *Julbernardia* sp., *Diospyros* sp.)

Vernacular names. Kidigo: mnokonyoka (F.Magogo & P.Glover 493), mtambaa (F.Magogo & P.Glover 315), Kijibana: muri ya nyoka (L.J.Lap 258).

Remarks. Morphologically this species (the only one missing DNA sequences) is close to *C. senensis*. The indument is reduced in prominence and in extent to petiole and leaves in *C. pwaniensis*, and the leaves are rather 3-lobate and long petiolate, in contrast to often 5-lobate and short petiolate leaves in *C. senensis*. The racemes in *C. pwaniensis* have consi-derably more flowers than in *C. senensis*. However, the subulate calyx lobes match well among the species, and fruit and seed shape put both species into relationship with *C. ado-ensis*. As *C. pwaniensis* and *C. senensis* do not co-occur, they might be sister species from allopatric speciation, with *C. pwaniensis* occurring in a refugial distribution in the northern coastal forests of East Africa.

Specimens examined. (in total: 13) Kenya. Coast Province: Kilifi district, Kaya Jibana, entering southern forest patch of Kaya Jibana following the path from shop/hoteli at Mwara-kaya–Ribe road, 3°50’0’’S 39°40’30’’E, L.J.Lap 258 (WAG, WAG); Kwale district, Shimba Hills, Longomagandi Forest, R.Schmidt 527 (EA, UBT).

Coccinia quinqueloba (Thunb.) Cogn. in A. DC & C. DC., Monogr. Phan. 3: 533. 1881.

Momordica quinqueloba (Thunb.) E.Mey. ex Drège, Zwei Pflanzengeographische Documente: 126, 132, 133, 137, 202. 1843. (BM!, K!, K!, G!, P!, P!, P!, P!, W!, W!) Nom. nud.

Cephalandra quinqueloba (Thunb.) Schrad. ex Eckl. & Zeyh., Enumeratio plantarum Africae australis extropicae 2: 280. 1836.

Bryonia quinqueloba Thunb., Prodr. Pl. Cap. I: 13. 1794. TYPE: [SOUTH AFRICA]. [Eastern Cape]: [Uitenhage area], Krakakamma, in forest, male, fl, Dec, C.P.Thunberg 22836 (Lectotype, designated here: UPS-THUNB!), ibid., male, fl, Dec, C.P.Thunberg 22837 (Paralectotype: UPS-THUNB!); Cape of Good Hope [umbrella term for the complete Cape region], C.P.Thunberg s.n. (Paralectotype: S08-12379!).

Description. Perennial creeper or climber. Stems up to 2.5 m, glabrous (rarely with remote trichomes). Petiole 0.3–0.8(–1.7) cm, glabrous (rarely with remote trichomes). Leaves usually subsessile, 3–9.5 × 4–10 cm, 3- or 5-lobate, auriculate. Lobes oblong, elliptical to obovate. Leaf margin remotely dentate, apices towards lobe often serrate. Lobe apices obtuse with a point. Upper leaf lamina pale pustulate, lower leaf lamina glabrous, rarely a few blackish glands near base, nerves rarely white-speckled. Probracts < 1 mm or missing. Tendrils simple. Male flowers solitary or in racemes. Common peduncle 0.5–2 cm, petiole in racemous flowers up to 1.8 cm, bracts > 1 mm or missing, solitary flowers with petiole 1.8–4 cm, all glabrous. Perianth tube glabrous, calyx lobes 1.5–3 mm, narrow triangulate, erect to spreading. Corolla 1.2–2.2 cm long, pale yellow, corolla lobes 1–1.2 cm. Color of filament stalk, anther head, and pollen sacs not seen. Female flowers one solitary. Petiole 1–2.5 cm, glabrous. Hypanthium glabrous, calyx lobes and corolla like in male flowers. Style and stigmas not seen. Fruits 3.5–9 × 3–4 cm, elliptical to oblong, sometimes short elongated tip, unripe green with longitudinal white mottling, ripe (orange-)red. Seeds 6–7.5 × 3–3.5 × 1–1.2 mm, slightly asymmetrically obovate, face (flat) lenticular.

Phenology. January, February, April, July, September, November, December.

Distribution. Fig. 31. Southern and western Eastern Cape, South Africa. Elevation sea level to 1000 m. Sandy soils, also on dolomite soil. Coastal bushland, forest, dry bush, and on bushes along rivers.

Remarks. See also under *C. mackenii*.

Taxonomical remarks. *Cephalandra quinqueloba* is the type species of the genus *Cephalandra*.

Specimens examined. (Selection, in total: 73) South Africa. Eastern Cape: [Amatole District Municipality], [Buffalo City Local Municipality], East London, Dec 1916, H.G.Breyer s.n. TRV23225 (PRE); [Nkonkobe Local Municipality], Amatle Mts, Hogsback Pass, 32°36’50’’S 26°55’25’’E, P.B.Phillipson 1079 (MO, PRE); [Cacadu District Municipality], [Blue Crane Route], Glen Avon, Feb 1923, N.E.Brown s.n. (PRE43005, Z) ; [Makana Local Municipality], Grahamstown, Old Quarry, R.D.A.Bayliss 8470 (G, G, M, MO, Z); 28 mls [45 km] from Grahamstown on Port Elizabeth road, R.Story 2346 (B, L, M, M, MO, PRE, S); [Kouga Local Municipality], hills N of Patensie, H.C.Taylor 1289 (PRE); [Ndlambe Local Municipality], near Port Alfred, J.H.Sidey 1095 (PRE, S); [Sundays River Valley Local Municipality], plaas Vista, 5 km from Paterson to Addo-Olifantpark, E.Retief 5 (PRE).

Coccinia racemiflora Keraudren, Adansonia, ser. 2, 8(1): 41. 1968. TYPE: GABON. [Moyen-Ogooué Province]: Abanga, C. E. F. A. [Compagnie d’Exploitations Forestière Africaine] lot, male, fl, Jun 1963, N.Hallé 2425 (Holotype: P!, Isotype: P!). L.c., female, fl, N.Hallé 2305 (Paratype: P!, P!).

Description. Perennial climber or prostate creeper. Stems up to 5 m, glabrous. Petioles 0.5–2.5 cm, on adaxial side often with line of thin smutty trichomes or glabrous, abaxial side glabrous Leaves 6.5–11 × 5–9.5 cm, hastate to 3-lobate with central lobe dominating, auriculate (auricles may reach the stem). Lobes triangulate. Leaf margin entire to somewhat angulate, remotely dentate. Teeth darkening when dried. Upper lamina with waxy cover glabrous with few-celled clear pustules. Lower leaf lamina glabrous with dispersed blackish glands. Probracts up to 2 mm. Tendrils bifid. Male flowers ebracteate in lax, glabrous racemes. Common peduncle up to 2.5 cm, pedicels 0.3–1.0 cm. Perianth tube glabrous, calyx lobes 0.5 mm, short lineal, spreading. Corolla c. 1.2 cm, yellowish to orange, lobes 0.2–0.4 cm. Color of filament column, anther head, and pollen sacs not seen. Female flowers ebracteate in lax, glabrous racemes, like in males. Hypanthium glabrous, calyx lobes, and corolla like in males. Ovary glabrous. Style and stigmas not seen. Unripe fruits glabrous, glaucous, globose. Ripe fruits unknown, size c. 1.5 cm in diam.? Seeds 5 × 3 × 1.5 mm, rather symmetrical, flat lenticular.

Phenology. January–March, imperfectly known.

Distribution. Fig. 36. Gabon, Southern Cameroon. Tropical lowland rainforest.

Remarks. The hypanthia of female flowers are urceolate, whereas in male flowers cup-shaped. Urceolate hypanthia are also found in some *C. barteri* morphs. A specimen from the Gamba area in S Gabon (M.A.van Bergen 490 (WAG)) is morphologically close to *C. racemiflora*, but shares the calyx lobes with *C. barteri*, and may represent a hybrid. Using plastid markers, this specimen (*C. barteri* 6) clusters within *C. barteri*, in the nuclear *LFY* tree, it clusters with one representative of *C. racemiflora*, but not with both (Holstein and Renner 2011a). Another specimen (F.J.Breteler et al. 8835 (MO, WAG) from Saint Germain area, C Gabon, has calyx lobes typical for *C. racemiflora*, but a more condensed raceme as in the M.A.van Bergen 490 specimen.

Specimens examined. (in total: 8) Cameroon. South Region: 3 km N of Kribi-Lolodorf, high forest exploitation, 3°01’N 10°03’E, J.J.Bos 6590 (WAG, WAG). Gabon. Estuaire: 12 km S of Kinguélé Falls, N.Hallé & J.F.Villiers 5357 (K, P). Ngounié: 35 km on road from Lebamba to Yéno, 1°58’S 11°25’E, J.J.de Wilde & M.Sosef 10456 (WAG). Ogooué-Maritime: Rabi North, 1°51.6’S 9°51’E, I.van Nek 536 (WAG); Rabi-Kounga, Rabi, 1°55’S 9°55’E, F.J.Breteler & C.C.H.Jongkind 10270 (WAG); Rabi, 1°55’S 9°50’E, F.J.Breteler et al. 9696 (WAG).

Coccinia rehmannii Cogn. in Schinz, Bull. Herb. Boiss. 3: 418. 1895. TYPE: SOUTH AFRICA. Transvaal: boshveld ad Klippan [according to Meuse (1962) in Limpopo: Greater Sikhukhune District Municipality, Doornpoort; 24°37’S, 29°26’E], 1875-1880. A.Rehmann 5156 (Paralectotype: Z! digital image [Z]; isolectotype: BR!). TYPE: SOUTH AFRICA. Ibid., A.Rehmann 5157 (Paralectotype: Z! [digital image [Z]). TYPE: SOUTH AFRICA. Ibid., A.Rehmann 5168 p.p. (Lectotype, designated by Meeuse (1962): Z!, digital image! [Z]; isolectotype: BR! K!, digital image! [K]). TYPE: SOUTH AFRICA. at Eland river, A.Rehmann 4944 [sic, must be A.Rehmann 4954, see taxonomical remarks] (Paralectotype: Z!).

Coccinia rehmannii Cogn. var. *littoralis* A.Meeuse, Bothalia 8: 104. 1962. pro parte ex R.de Carvalho s.n. (Paratypes: COI!, COI!). TYPE: SOUTH AFRICA. [Eastern Cape]: [Amatole District Municipality], Komgha, Kei Mouth, H.G.Flanagan 457 (Holotype: PRE, isotypes BOL?, NBG?). TYPE: SOUTH AFRICA. [Eastern Cape]: Cape Morgan, H.G.Flanagan 457 (Paratype: GRA digital image! [JPS], BOL?, NBG?). TYPE: SOUTH AFRICA. [Eastern Cape]: East London, Nahoon, M.W.Nanni 151 (Paratype: PRE!). TYPE: SOUTH AFRICA. Coffee Bay, W.Tyson 24 (Paratypes: B!, COI!, GRA, MO!, NY!, PRE!, S!). TYPE: SOUTH AFRICA. [KwaZulu-Natal]: 10 mls NW of Mtubatuba, L.E.Codd 9620 (Paratypes: COI!, M!, PRE). TYPE: SOUTH AFRICA. [Kwa-Zulu Natal]: Umhlanga Rocks, A.Dohse & B.de Winter 223 (Paratypes: NH, PRE!). TYPE: SOUTH AFRICA. [Kwa-Zulu Natal]: Manaba Store, J.Gerstner 3407 (Paratype: NH). TYPE: SOUTH AFRICA. [Kwa-Zulu Natal]: Dhlebe, J.Gerstner 4261 (Paratypes: NH, PRE). TYPE: SOUTH AFRICA. [Kwa-Zulu Natal]: near Durban, T.J.Jenkins TRV7092 (Paratype: PRE). TYPE: SOUTH AFRICA. [Kwa-Zulu Natal]: Mtunzini, S.M.Johnson 612 (Paratype: NBG). TYPE: SOUTH AFRICA. [Kwa-Zulu Natal]: Stella Bush, W.E.Marriott herb. no. 24341 (Paratype: ?). TYPE: SOUTH AFRICA. [Kwa-Zulu Natal]: ibid. W.E.Marriott herb. no. 27143 (Paratype: NH). TYPE: SOUTH AFRICA. [Kwa-Zulu Natal]: Shelly Beach, A.O.D.Mogg 11941 (Paratype: ?). TYPE: SOUTH AFRICA. [Kwa-Zulu Natal]: ibid., A.O.D.Mogg 12070 (Paratypes: M!, M!, PRE!). TYPE: SOUTH AFRICA. [Kwa-Zulu Natal]: without detailed location, T.B.Oatley C 15 (Paratype: PRE). TYPE: SOUTH AFRICA. [Kwa-Zulu Natal]: Berea, Small herb. no. 34714 (Paratype: NH). TYPE: SOUTH AFRICA. [Kwa-Zulu Natal]: Ubombo coastal veld, P.A.Tosh 28 (Paratype: NU). TYPE: SOUTH AFRICA. [Kwa-Zulu Natal]: Ndumu Game Reserve, Ward 3169 (Paratype: ?). TYPE: SOUTH AFRICA. [Kwa-Zulu Natal]: ibid. Ward 3170 (Paratype: ?). TYPE: SOUTH AFRICA. [Kwa-Zulu Natal]: Umvoti, Thorns near Greytown, J.M.Wood 5318 (Paratype: NH). TYPE: SOUTH AFRICA. [Kwa-Zulu Natal]: Durban, J.M.Wood 6350 (Paratypes: BOL, L!, NBG, NH, PRE). TYPE: SOUTH AFRICA. [Kwa-Zulu Natal]: Doonside, J.Wylie herb. No. 23299 (Paratype: NH). TYPE: MOZAMBIQUE. Maputo: Lourenço Marques [Maputo], J.Borle 253 (Paratypes: M!, MO!). TYPE: MOZAMBIQUE. Maputo: ibid., J.Borle 427 (Paratype: ?). TYPE: MOZAMBIQUE. Maputo: ibid., J.Borle 442 (Paratype: PRE!). TYPE: MOZAMBIQUE. Maputo: Inhaca Island, H.G.Breyer TRV20506 (Paratype: PRE). TYPE: MOZAMBIQUE. Maputo: Inhachingo, A.W.Exell et al. 630 (Paratype: SRGH). TYPE:

MOZAMBIQUE. Maputo: Massinga, A.W.Exell et al. 645 (Paratype: SRGH). TYPE: MOZAMBIQUE. Maputo: Lourenço Marques [Maputo], A.J.W.Hornby 4599 (Paratype: PRE!). TYPE: MOZAMBIQUE. Maputo: Delagoa Bay [Maputo Bay], H.A.Junod 20 (Paratypes: BR!, G!, G!, Z!). TYPE: MOZAMBIQUE. Maputo: Inhaca Island, A.O.D.Mogg s.n. 6 Jul 1958 (Paratype: PRE!). TYPE: MOZAMBIQUE. Maputo: ibid., 14 Dec 1955, A.R.A.Noel s.n. (Paratype: PRE!). TYPE: MOZAMBIQUE. Maputo: Lourenço Marques [Maputo], R.Schlechter 11555 (Paratypes: BOL, COI!, G!, G!, G!, GRA, HBG!, WAG!, Z!). TYPE: MOZAMBIQUE. Maputo: Katembe [Catembe], R.Schlechter 11614 (Paratypes: G!, G!, GRA, PRE!, Z!).

Coccinia ovifera Dinter & Gilg, in: M.K.Dinter: Die vegetabilische Veldkost Deutsch-Südwest-Afrikas: 16. 1912. TYPE: [NAMIBIA]. Karas: Sandverhaar, M.K.Dinter 1214 (Paralectotype: ?). Otjozondjupa: Otjiwarongo, female, fl, fr, Jan 1912, M.K.Dinter s.n. (Paralectotype: SAM, digital image! [JPS]); Waldau, female, fr, 3 Feb 1917, M.K.Dinter 432 (Lectotype, designated here: SAM, digital image! [JPS]).

Further possible Paralectotypes (cited in Dinter 1919/20) if collected before end of 1912: Oshikoto: Gaub, M.K.Dinter 2412 (?); Tsumeb, M.K.Dinter s.n. (?). Unknown: Hereroland, Palmenwald, M. K. Dinter s.n. (?); Hereroland; Wilhelmsberg, M.K.Dinter s.n. (?).

Description. Perennial climber or creeper. Stems up to 4 m, glabrous or with broad-based trichomes, when old often dense white pustulate (esp. in drier areas). Petiole 0.2–4.2 cm, glabrous or with erect, broad-based or often up to 1.5 mm long articulate trichomes or only wart-like, when old sometimes dense white pustulate (esp. in drier areas). Leaves 0.9–9.7 × 1.4–16.6 cm, shallow to deeply 3- or 5-lobate, auriculate, sometimes lobulate, rarely cordate. Lobes and lobules usually spreading, rarely pointing towards tip, narrow to broad deltoid to lanceolate. Leaf margin rather remotely denticulate. Apex acute to obtuse, apiculate. Upper leaf surface more or less dense white pustulate, pustules sometimes with a thick small trichome, on nerves often with thick small trichomes. Lower leaf lamina, glabrous, sometimes with small blackish glands between nerves, nerves usually with erect trichomes, sometimes wart-like. Probract usually absent, if present then up to 3.5 mm. Tendrils simple. Male flowers 1–3 solitary, if fasciculate or in few-flowered racemes, then accompanied by 1–2 flowers. Common peduncle 0.7–4.5(–8.5) cm, glabrous or with long articulate trichomes. Pedicel of flowers in inflorescences 0.6–2.8 cm, bracts up to 2.5 mm or missing. Pedicel of solitary flowers (0.2–)0.5–5.0(–9.0) cm, glabrous or especially at apex with long articulate trichomes. Perianth tube usually with long (> 0.5 mm) trichomes, rarely almost glabrous. Calyx lobes 0.2–7.0 mm, lanceolate or lineal, when young erect, later also spreading to reflexed. Corolla 0.8–2.5 cm long, buff to more or less pale yellow, sometimes with green venation. Lobes 0.3–1.1 cm. Filament column pale buff, anthers buff, pollen sacs yellow (Fig. 9a). Female flower one solitary. Pedicel 0.4–1.5 cm, glabrous or with long articulate trichomes. Hypanthium usually with long (> 0.5 mm) trichomes, rarely almost glabrous, calyx lobes and corolla like in male flowers. Ovary rarely glabrous, often more or less densely covered with articulate trichomes. Style columnar, green. Stigmas 2-lobed, yellow (Fig. 10b). Immature fruit, rarely also in maturity, with whitish sparkles or lines, which develop a dark green corona during ripening. Ripe fruit globose to elliptical 1–6.2 × 1–2.8, glabrous or with few articulate trichomes, bright orange to red. Seeds 4.5–7 × 2.0–3.5 × 1.0–1.2 cm, asymmetrical oblong to somewhat falcate, face flattened.

Phenology. January–April, June, October–December.

Distribution. Fig. 37. South Africa (except Western Cape and southwestern Eastern Cape), Namibia (except hyperarid regions), Swaziland, southern Mozambique (Gaza, Inhambane, Maputo), Botswana, Zimbabwe (Manicaland, Masvingo, Matabeleleland South), southern Angola (Namibe, Huila, Cunene, Cuandocubango). Elevation sea level to 1850 m. Limestone, dolomitic, quartzitic, granitic, and ultrabasic soils. Possibly some tolerance to Ni and Cu. On loam, clay, white and red sand, sandstone, and gravel, but prefers sandy (well drained) soils (Meeuse 1962). Full sun to shade. Coastal dunes, riverbanks, *Acacia sclerocarya–A. caffra* woodland, *Combretum apiculatum* bushland, *Grewia flava* bushland, mopane, Kalahari thornveld, grassland, semi-desert, dunes. Grazing is tolerated. Light frost seems to be tolerated (Meeuse 1962).

Use. Tuber edible after baking (Dinter 1912, M.E.Keith 50, B.de Winter & O.A.Leistner 5598). Leaves used as spinach by Shangane people in Gaza province of Mozambique (K.L.Tinley 3000). Fruits edible (R.Seydel 938, R.Story 5029, B.de Winter & O.A.Leistner 5598).

Vernacular names. Otjiherero: otjimaga (M.K.Dinter s.n. Jan 1912), Ronga dialect [of Xitsonga language]: inyamgwazi (A.O.D.Mogg 31308), Tsonga [Xitsonga]: inyamwazi (A.O.D.Mogg 31538), nyampape (C.Liengme 491), Ronga: shiracacanga (L.Macuácua 75), Zulu [isiZulu]: uselwa-iwenyoka (Sewram et al. 2006).

Remarks. *Coccinia rehmannii* (var. *rehmannii*) can be confused with *Dactyliandra* species and with *Ctenolepis cerasiformis* C.B.Clarke. However, *C. rehmannii* specimens have a much larger corolla (> 1 cm) and small (< 3 mm) elliptical-ovate probracts instead of larger roundish sinuate-ciliate probracts. The (sub-)glabrous “*littoralis*” morph can easily confused with the polymorphic *C. adoensis* (Hochst. ex A.Rich.) Cogn., which differs in shorter calyx lobes and lenticular seeds, and with *C. senensis*, which also has lenticular seeds and usually long-peduncled male racemes. In vegetative state, it is also easily confused with *Corallocarpus* species.

Meeuse's variety *littoralis* is dubious as the paratypes are quite variable, and characters for delimitation are unclear. For example, although the variety should lack white speckles on the stems, there are some individuals with white speckles, but long pedicels or conspicuous racemes in KwaZulu-Natal and southern Mozambique as in the variety *littoralis*. The holotype of var. *littoralis* is, in my opinion, rather intermediate between the holotype of var. *rehmannii* and the subglabrous morphs, e.g. from Inhaca Island. However, the tendency that Meeuse describes is visible. Other characters in the specimens of his variety, viz. relatively long calyx lobes and petals also occur in the high mountains of Namibia, but also in the whole periphery of the *C. rehmannii* distribution range. Strangely, Meeuse did not mention the most striking difference between *C. rehmannii* specimens from the inland/dry areas and coastal/peripheral specimens, which is the long elliptical fruit in peripheral individuals, instead of a globose fruit. Specimens with this fruit morph also occur in Angola and Zimbabwe, but do not follow Meeuse's other characters of the var. *littoralis*. On the other hand, specimens with long calyx lobes and long petiolate flowers can have globose fruits. Like the area of the southeastern coast of South Africa, areas in the north of southern Africa receive more and longer rainfall per year, so there is a clear correlation, between precipitation and fruit morphology. Elliptical fruits in close relatives also occur in *C. trilobata* from mountainous and thus more humid habitats, but not in *C. microphylla* from the dry bushlands of NE Africa, whose fruit is globose. However, the characterization by Meeuse that *C. rehmannii* is an aggregate species is true. It might be interesting to link morphological characters with haplotypes and to test the fitness of these morphs in the different habitats. In any case, the morphological differentiation seems to be stable in cultivated individuals, and artificial crosses between different morphs (inland vs. subglabrous from the Southeast) result in the onset of a normal fruit.

The placement of *C. rehmannii* var. *littoralis* morphs with other *C. rehmannii* morphs in plastid and nuclear phylogenies (Fig. 16 and 17) also rejects the hypothesis of a hybrid origin (e.g. with *C. adoensis* or *C. senensis*), but rather suggests parallel evolution due to ecologi-cal factors.

Taxonomical remarks. The *C. rehmannii* syntype from Eland river contains a literal mistake. On the one hand, there is A.Rehmann 4954 (a *C. rehmannii*) in Z from Eland river and with a remark by Cogniaux 'sp. nov.' Additionally, A.Rehmann 4944 (GRA, K) is a Malpighiaceae. Hence, A.Rehmann 4954 is a syntype of *Coccinia rehmannii*, not A.Rehmann 4944.

Coccinia ovifera is a validly published name, although the description is a little cryptic, hence the species name is not a *nomen nudum*. Dinter writes that he has found, viz. collected, the species around Grootfontein, in Hereroland (not in the narrow sense of the 1968 homeland) and in Sandverhaar (Namaland). Therefore, the requirements for validity are met (37.3 Note 2). The latter site is cited by him explicitly in a later publication (Dinter 1919/20). The specimens designated as syntypes above match the description as given in the protologue. I did not see the specimens designated as “possible paralectotypes”, so they are tentative. Eventually, they have been destroyed in Berlin.

The GRA specimen of H.G.Flanagan 457, which is supposed to be the isotype (cited by Meeuse) of *C. rehmannii* var. *littoralis*, is in fact merely a paratype. Meeuse stated clearly the location as “Komgha: Kei Mouth” and chose the PRE specimen from there as the holotype, but the GRA specimen is from the nearby located Cape Morgan. It seems that Flanagan used the same collection number for different gatherings. The GRA specimen thus cannot be regarded as a duplicate despite the same number. As the GRA specimen does not have a label by Meeuse, he just cited the specimen without seeing it.

The similarity of *C. rehmannii* var. *littoralis* to *C. senensis* led to a misplaced paratype. One of the two specimens by R. de Carvalho is a syntype of *C. jatrophiifolia* var. *australis* Cogn. and the two R.de Carvalho specimens from COI are paratypes of *C. subglabra*, which are both synonyms of *C. senensis*.

Specimens examined. (Selection, in total: 307) Angola. Huíla: Cambos, near Chiange, A.Menezes 3629 (P). Namibe: c. 55 km [E] from Moçâmedes to Dois Irmãos [Caraculo], E.J.Mendes 3969 (COI, LISC). Botswana. Central District: 50 km SW of Serowe, Motshegaletau, D.T.Cole 984 (PRE). Ghanzi: 200 mls [320 km] NW of Molepolole, R.Story 5029 (COI 2 sheets, EA, EA, PRE 2 sheets, Z). Kgalagadi: c. 50 mls [80 km] NNW of Tsabong, O.A.Leistner 3120 (LISU, M, PRE). Kgatleng: Artesia (Mosomane), 18 km E of Artesia, D.T.Cole 1529 (PRE). Kweneng: Khutse Game Reserve, 2324 BC [23°15’–30’S 24°30’–45’E], L.C.C.Liebenberg 8991 (PRE); ibid., L.C C.Liebenberg 8994 (PRE). Ngamiland: 80 km W of Tsau on Cae Cae road, D.G.Long & D.A.H.Rae 416 (E). North-Eastern District: 2 mls [3.2 km N] of Shashi [c. 21°21’S 27°28’E], L.C.Leach & A.R.A.Noel 287 (COI 3 sheets). Mozambique. Gaza: Vila de João Belo [Xai-Xai], Barra do Limpopo, F.de Lemos & A.Balsin-has 131 (BM, COI) and 133 (BM, COI 2 sheets). Inhambane: Pomene, in hotel area, P.C.M.Jansen et al. 7533 (MO, WAG, WAG). Maputo: 7 km on road from Salamanga to Zitungo, between Costa do sol and Marracuene, Mutanhane, A.Balsinhas 230 (BM, COI, PRE). Namibia. Erongo: Farm Anschluss, 150 km E of Swakopmund on Khomas road to Windhoek, B.de Winter & D.Hardy 8001 (M, PRE, WAG). Hardap: c. 20 mls [32 km] from Kalkrand on road to Rehoboth, B.de Winter 3538 (COI, COI, L, M, PRE). Karas: Dassiefontein Farm, 2–3 km E of highway, in foothills of Groot Karasberge, c. 64 km NNE of Grünau, G.Davidse & A.Loxton 6240 (M, MO, S). Kavango: 14 mls [22.4 km] of Runtu [Rundu], B.de Winter 3787 (M, PRE). Khomas: Rehoboth, Leutwein, K.H.Rechinger 4912b (M). Kunene: 37 mls [59.2 km] from Fransberg on road to Brandberg, B.de Winter 3122 (L, M, PRE). Omaheke: [Farm] Breitenberg, border of Kalahari, R.Seydel 2513 (COI, M, WAG). Omusati: 2 km on Kamanjab path, J.Vahrmeijer & P.du Preez 2606 (PRE). Oshana: 8 km E of Safarihoek 1915A, Le Roux 535 (PRE). Otjozondjupa: 160 mls [257.5 km] E of Grootfontein, Gautscha Pan, R.Story 6219 (PRE); ibid., R.Story 6238 (M, M, PRE, PRE, S). South Africa. Eastern Cape: [O.R.Tambo District Municipality, Port St. Johns Local Municipality], Port St. Johns distr., First Beach, M.J.Wells 3434 (MO). Gauteng: [Tshwane], Pretoria, Brummeria: BRI, A.Balsinhas 3474 (MO, PRE, WAG). KwaZulu-Natal: [eThekwini Metropolitan Municipality], on gentle slopes above Umhlanga Rocks Hotel, R.Watmough 429 (PRE); [Lemba District Municipality], Lower Tugela Valley, below Maqumbi, D.Edwards 3053 (B, M, HEID, PRE); [Umkhanyakude District Municipality], Tembe Elephant Park, 26°57'S 32°30'E, M.C.Ward 2701 (PRE); [Uthukela District Municipality], Kaisha, River Man Camp, R.Williams 585 (PRE); [Uthungulu District Municipality], Eshowe, A.Meebold 13157 (M); [Zululand District Municipality], 5 mls [8 km] on Nkonkoni–Pongola road, M.J.Wells 2162 (B, EA, M, Z). Limpopo: [Vhembe District Municipality], Zoutpansberg, c. 42 mls [67.2 km] W of Louis Trichardt, Vivo, H.J.Schlieben 7373a (B, B, M); [Waterberg District Municipality, Mookgopong Local Municipality], Immerpan, near post office on roadside, A.D.J.Meeuse 9452 (B, COI, L, PRE, Z). Mpumalanga: [Ehlanzeni District Municipality], [Nkomazi Local Municipality], Impala, siding, E.Retief 1260 (PRE); ibid., E.Retief 1261 (MO, PRE); Steelport, Burgersfort, 2 km E of town, 24°40’S 30°22’E, H.J.Venter & A.Venter 10260 (S, WAG). Northern Cape: [Namakwa District Municipality], 12.7 mls [20.3 km] N of Pofadder, D.M.Comins 668 (PRE); [Pixley Sa Keme District Municipality], Campbell, A.E.Brueckner 1030 (PRE); [Siyanda District Municipality], 4 mls [6.4 km] WNW of Moeswal, W of Langeberg Mts, O.A.Leistner 1671 (M, PRE, W); [Frances Baard District Municipality], 25 ml. [40.2 km] W of Kimberley, H.J.Schlieben & H.R.Tölken 11017 (G 2 sheets, HEID, M, PRE, S); [Kgalagadi District Municipality], Van Zijlsrust, Floridale Farm, S.Venter 12852 (PRE). Northwest: [Bojanala District Municipality], [Madibeng Local Municipality], Rooisloot, 6 Apr. 1935, A.O.D.Mogg s.n. (B, L, PRE); [Bojanala District Municipality], Farm Welgevonden, 6 Apr 1935, A.O.D.Mogg s.n. (B, L, Z). Swaziland. Lubombo: Thsaneni [Tjaneni], I.F.LaCroix 4909 (MO, WAG). Manzini: Timbutini, R.H.Compton 30748 (PRE). Shiselweni: near Gollel [Golela], R.H.Compton 30999 (PRE). Zimbabwe. Manicaland: Chipinga district, Sabi Valley Experimental Station, C.Soane 162

(COI 3 sheets). Masvingo: Chipinda Pools, R.D.Kelly 418 (LISC, PRE). Matabeleland South: Beit Bridge [Beitbridge], A.W.Exell et al. 425 (LISC); ibid., L.C.Leach 10700 (COI, MO).

Coccinia samburuensis Holstein. Kew Bull. 65(3): 435–441. 2010 [published in 2011]. TYPE: KENYA. [Rift Valley Province]: Samburu East District, on Wamba-Isiolo road, 0.7 km south of turnoff to Maralal, c. 1300 m, female, fl, fr, 4 Jul 1974, R.B. Faden & A.J.Faden 74/948 (Holotype: MO!, isotype: WAG!). TYPE: KENYA. Rift Valley Province: Samburu District, Mt Nyiru, southern slopes, near a river, 2°03’N 36°51’E, 1600 m, female, fr, 1 Apr 1995, B.Bytebier et al. 355 (Paratypes: EA 2 sheets!). TYPE: KENYA. Operoi, 1°12’N 36°49’E, 1350 m, rocky outcrop in Acacia woodland, female, fr, 23 Dec 2004, W.R.Q.Luke & P.A.Luke 10787 (Paratypes: EA!, K!). TYPE: KENYA. near Maralal, Lowaweregoi [Lowua Werekoi Mt] 4000 ft [c. 1220 m], rocks in bushland, male, fl, 15 Dec 1958, J.G.B.Newbould 3233 (Paratype: K!).

Description. Perennial climber. Stem up to 5 m, glabrous, except for tiny few-cellular trichomes visible under 5–10× magnification. Petioles glabrous, at base white speckles may occur. Leaves 6–14 cm long, 10–17 cm wide, (5- or)7-lobate. Leaf lobes ellipictal, margin serrate (to lobulate), teeth (lobule tips) with yellowish glands. Lobe apex subacute, apiculate. Upper lamina glabrous, more or less clear to white pustulate. Lower lamina glabrous, nerves white-speckled. Probracts up to 4 mm. Tendrils simple. Male flowers 1–2 solitary. Pedicel up to 5 cm long, glabrous. Perianth tube glabrous, calyx lobes 6.5 mm long, linear, erect. Corolla 3.7–4 cm long, brownish yellow, lobes 2.2–2.5 cm. Female flowers solitary. Pedicel 4–5 mm, glabrous. Hypanthium tube glabrous, calyx lobes, and corolla like in males. Ovary narrow cylindrical, glabrous. Fruits c. 14 × 1.5–2 cm, sausage-shaped, unripe green with lighter spots. Seeds 6.5–7 × 3.5–4.5 × (≥ 1) mm, symmetrical obovate, flat lenticular.

Phenology. Imperfectly known. Flowering in April, July, and December, but likely to flower as long water is available (rainy seasons).

Distribution. Fig. 35. Only known from Samburu area in Kenya (hence the epithet). Only known from seepage line in rocky (granite) outcrops in *Acacia-Commiphora* deciduous bushland.

Coccinia schliebenii Harms, Notizbl. Bot. Gart. Berlin-Dahlem 11: 685. 1932. TYPE: TANZANIA. Morogoro: Ulanga district, Mahenge ward, Mtimalassi near Mahenge station. 900–1000 m, fl, 14 Jan 1932, H.J.Schlieben 1620 (holotype: B!, isotypes: BM!, BR!, BR!, G!, M!, P!, digital image! [P], S).

Coccinia calophylla Harms in Mildbraed, Notizbl. Bot. Gart. Berlin-Dahlem 12: 522. 1935. TYPE: TANZANIA. Lindi: Muera plateau, Bakari, fl, 26 Oct 1934, H.J.Schlieben 5551 (Holotype: B!, digital image! [B], isotypes: BM!, BM!, BR!, BR!, G!, G!, HBG!, M!, MA, P!, digital image! [P], P!, Z!, Z!).

Description. Perennial climber. Stems up to 12 m, densely covered with short stiff smutty-brownish trichomes. Petioles 1.5–11 cm, indument as on stem. Leaves 5–18 × 4.5–18 cm, slightly to deeply palmately 5-lobate. Lobes broadly triangulate to long elliptical, margin dentate, tips acute or obtuse. Upper leaf surface usually densely covered with short thin trichomes. Lower leaf lamina densely (esp. on nerves) covered with short stiff smutty-brownish-beige trichomes. Probracts up to 4.5 mm. Tendrils simple or bifid. Common peduncle 1.1–6.5 cm, with indument like on stem to puberulous, pedicels of flowers in racemes with up to 0.4 cm, indument as on peduncle, bracts 3–4 mm. Pedicels of solitary flowers 1.2–5 cm, indument as on peduncle. Perianth tube with indument like on stem to puberulous. Calyx lobes lineal to lanceolate 10–15 mm. Corolla 4.0–6.2 cm long, yellow, apricot, pale orange, sometimes marked with purple, lobes 2.0–3.2 cm. Filament 4 mm, color not seen, anther head not seen, pollen sacs dark yellow to orange. Female flowers solitary, pedicels 2.5–4.5 cm long, densely covered with short trichomes. Hypanthium with indument like on stem to puberulous, calyx lobes, and corolla like in male flowers. Ovary with smutty-brownish trichomes. Style 3–6 mm, color not seen. Stigmas 2-lobed, orange-yellow. Fruit 7–9 × c. 2.5 cm long, oblong to short cylindrical, ripening from green with 10 more deeply colored ribs via yellow to red. Seeds 5.5–6 × 2.5–3 × 1 mm, symmetrical obovate, face lenticular.

Phenology. January–March, May– July, December.

Distribution. Fig. 39. Ethiopia (Benishangul-Gomaz?, Gambela, Oromia, SNNPR), Mozambique (Cabo Delgado), Southern Sudan (Eastern Equatoria), Tanzania (Iringa, Lindi, Morogoro, Mtwara?, Ruvuma). Elevation 300–1900 m. Black cotton soil, reddish soil, volcanic underground. *Markhamia-Dombeya* woodland, *Chlorophora-Albizia* woodland, *Dalbergia-Pterocarpus-Combretum-Acacia* woodland, woodland with *Acanthus sennii*, *Baphia abyssinica* forests, forests, lower afromontane forests, termite hills, gallery forests.

Use. Fruits edible (*W.J.Kindeketa et al. 2793*).

Vernacular names. Didinga: moroich (J.G.Myers 10918), Kipogoro: mdalla (W.J.Kindeketa 2747), Mokonde: ncauedi (M.F.Correia 92).

Specimens examined. (Selection, in total: 31) Ethiopia. Gambela: 20 km E of Punido, 7°34’ N, 34°24’E, I.Friis et al. 7317 (C, K). Oromia: c. 25 km E of Lekemti [Nekemte], W.J.J.O.de Wilde & B.E.E.de Wilde-Duyfjes 7184 (K, MO, WAG, WAG, WAG). SNNPR: Ghibie [Gibe] or upper Omo gorge, 182 km SW of Addis Abeba on road to Jimma, north bank, J.W.Ash 898 (EA, EA, K). Mozambique. Cabo Delgado: Macondes, 2 km from Mueda to Negomano, near Santo António mission, M.F.Correia 92 (LISC). Southern Sudan. Eastern Equatoria: Didinga Mts, Mt Lotuke, Char, J.G.Myers 10918 (K). Tanzania. Iringa: Mufindi district, Lulanda village, N and NW of Ihili forest patch, 8°35’59’’S 35°37’12’’E, M.A.Mwangoka & C.J.Kayombo 63 (MA n.v., MO, P). Lindi: Rondo Plateau, E.Milne-Redhead & P.Taylor 7630 (EA, K). Morogoro: Ulanga district, Mahenge ward, near Mahenge station. H.J.Schlieben 1671 (BR, G, P, Z 2 sheets). Ruvuma: [near Gumbiro], by R. Mtandazi [river], E.Milne-Redhead & P.Taylor 8538 (B, EA, K, LISC, P) and 8539 (EA, P).

Coccinia senensis (Klotzsch) Cogn. in A. DC & C. DC., Monogr. Phan. 3: 535. 1881.

Cephalandra senensis Klotzsch in W.C.H. Peters Naturwissenschaftliche Reise nach Mossambique: 151. Georg Reimer, Berlin. 1862. TYPE: MOZAMBIQUE. [Zambésia Province]: Rios de Sena [province], without detailed locality, in grassland, W.C.H.Peters s.n. (Holotype: B, destroyed). TYPE: TANZANIA, Lindi Region: 40 km W of Lindi, Lake Lutamba, hill, woodland, climbing over bushes, c. 240 m, male, fl, 6 Sep 1934, *H.J.Schlieben 5259* (Neotype, designated in Holstein and Renner (2010): M!; isoneotypes: B!, BM!, G!, HBG!, MO!, P!, S!, Z!).

Coccinia fernandesiana C.Jeffrey, Kew Bull. 30(3): 478. 1975. TYPE: MOZAMBIQUE. Niassa: Erati, between Namapa and Ocúa, near river Lúrio bridge, F.de Lemos & L.Macuácua 29 (Holotype: COI, isotypes: BM!, BM!, K!, LISC, LMA, PRE digital image! [JPS], PRE digital image! [JPS], SRGH). TYPE: TANZANIA. Mtwara: Masai Distr. [sic, must be Masasi Distr.], W of R. Bangala, 390 m, in woodland on gravelly soil, 17 Dec 1955, E.Milne-Redhead & P.Taylor 7703 (Paratypes: EA!, K!, K!, LISC!, P!). TYPE: TANZANIA. Lindi: Mlinguru, 275 m, shrub woodland, 18 Dec 1934, H.J.Schlieben 5745 (Paratypes: B!, B!, BR!, EA!, HBG!, K!, K!, P!, LISC!, MO!, PRE!, SRGH). L. c., F.de Lemos & L.Macuácua 30 (Paratypes: BM!, COI! 2 sheets, K!, LISC!, digital image! [JPS], LMA, P!, SRGH). TYPE: MOZAMBIQUE. Niassa: Erati, between Namapa and Nacarea, F.A.Mendonça 1128 (Paratypes: LISC, digital image! [JPS]), F.A.Mendonça 1129 (Paratypes: LISC, digital image! [JPS]). TYPE: MOZAMBIQUE. Zambésia: Milange, 95 km towards Quelimane, A.R.Torre & M.F.Correia 14060 (Paratypes: K!, digital image! [K], LISC!, digital image! [JPS]). TYPE: TANZANIA. Lindi: Nachingwea District, *Pterocarpus-Combretum* woodland, male, 22 Oct 1952, B.Anderson 815 (Paratypes: EA!, K!, NHT!). TYPE: TANZANIA. Lindi: Mbemkuru [also called Mbwenburu, Mto Bwamkuro], in deciduous thicket by roadside, 135 m, male, 6 Dec 1955, E.Milne-Redhead & P.Taylor 7473 (Paratypes: BR!, EA!, K!, K!, P!), E.Milne-Redhead & P.Taylor 7473A (Paratypes: K!, K!), E.Milne-Redhead & P.Taylor 7473B (Paratype: K), E.Milne-Redhead & P.Taylor 7473C (Paratype: K), E.Milne-Redhead & P.Taylor 7473D (Paratype: K).

Coccinia jatrophiifolia (A.Rich.) Cogn. var. *australis* Cogn. [sphalm.: *Coccinia jatrophæfolia* var. *australis* Cogn.] Boletim de Sociedade Broteriana ser. 1, 7: 228. 1889. TYPE: MOZAMBIQUE. [Nampula]: Mossuril et Cabaceira (Zambézia), male, fl, 1884, R.de Carvalho 15 (Lectotype, designated here: BR!). TYPE: MOZAMBIQUE. ibid., male, fl, 1884–1885 R.de Carvalho s.n. (isolectotype: COI!).

Coccinia subglabra C.Jeffrey, Kew Bull. 30(3): 479. 1975. TYPE: MOZAMBIQUE. Nacala: 11 km from Itoculo towards Nacala, 130 m, fl, 4 Dec 1963, A.R.Torre & J.Paiva 9417 (Holotype: LISC, digital image! [IICT]; isotypes: COI, K!, digital image! [JPS, K], LMA). TYPE: MOZAMBIQUE. L.c., A.R.Torre & J.Paiva 9417A (Paratypes: COI, K! digital image! [K], LISC, LMA). TYPE: MOZAMBIQUE. Niassa: Ruvuma River, J.Kirk s.n. (Paratype: K!). TYPE: MOZAMBIQUE. Nampula: Mossuril e Cabaceira, R.de Carvalho s.n. (Paratypes: COI!, COI!). TYPE: MOZAMBIQUE. Zambésia: 23 km on road [from vila] Maganja da Costa [= Olinga] towards Namacurra, A.R.Torre & M.F.Correia 14176 (Paratypes: EA!, LISC, MO!).

Description. Perennial climber or creeper. Stem up to 3 m, glabrous or with erect, stiff, articulate, pale trichomes, glabrescent, when older sometimes with white pustules. Leaves subsessile or distinctly, but not long petiolate. Petiole 0.4–4 cm long, abaxial side more or less covered with erect, stiff, articulate, pale trichomes, sometimes glabrous. Leaves 4–14 × 5–16 cm, cordate or shallowly to deeply 3-, 5- or 7-lobate, sometimes auriculate. Lobes triangulate, lanceolate to lineal, sometimes with broader end. Finely to coarsely serrate-dentate, esp. towards the lobe tips, sometimes lobulate. Lobe apices acute to subacute, with a point. Upper leaf lamina with erect, stiff, articulate, pale trichomes or with whitish pustules. Lower leaf lamina glabrous or covered with erect, stiff, articulate, pale trichomes, nerves with same indument or with white pustules. Between the main nerves at lamina base often with blackish glands. Probracts up to 4 mm. Tendrils simple, rarely bifid. Male flowers (Fig. 22) in few-flowered racemes, sometimes accompanied with 1–2 solitary flowers. Common peduncle 0.3–6.2 cm long, often more or less densely covered with erect, stiff, articulate, pale trichomes. Petiole of flowers in racemes 0.2–1.2 cm. Bracts up to 2.5 mm, often missing. Petioles of solitary flowers 3.2–6.2 cm long. Petioles in each case with indument of peduncle. Perianth tube glabrous or with erect, stiff, articulate, pale trichomes. Calyx lobes 2.5–6.5 mm long, subulate to narrow triangulate-lanceolate. Corolla 1.1–3.0 cm, yellow, orange to salmon, lobes 0-9–1.1 cm. Color of filament column, anther head, and pollen sacs not seen. Pedicel of female flower 1.2–2.3 cm. Hypanthium, calyx lobes, and corolla like in male flowers. Ovary glabrous or more or less covered with erect, articulate trichomes. Style and stigma not seen. Fruit 3.5–4.4 × 1.0–1.5 cm, long ovoid to short cylindrical, often with apical sterile tip. Unripe pale green with dark green longitudinal lines, ripe red. Seeds 0.55–0.7 × 0.3–0.5 × 0.12–0.13 cm (L/W/H), symmetrical obovate, face lenticular.

Phenology. January–April, September, December.

Distribution. Fig. 25. Central Tanzania (Iringa, Lindi, Morogoro, Ruvuma), Malawi (Southern Region), Mozambique (Cabo Delgado, Nampula, Tete, Zambezia). Elevation 0–700 m. Sandy soil. *Coccinia senensis* seems to be a typical element of the Zambezian center of endemism (White 1983) and is likely to occur more widely. Deciduous woodlands, termitaria, riverine thickets, coastal forests.

Vernacular names. Kihehe: mtumbulansoka (W.Carmichael 171), Macua [Makhuwa]: muuco-uco (F.de Lemos & L.Macuácua 29).

Remarks. The species is recognizable by the combination of few-flowered racemes, long subulate calyx lobes, and the often subsessile leaves. The trichome type (often appearing articulate when dried) is the same like in *C. rehmannii*, where (sub-)glabrous specimens also occur (see also the taxonomical remarks). Except for the degree of trichome density, a sub-glabrous specimen (E.M.C.Groenendijk et al. 1031) from 11 km from *C. subglabra* locus classicus was neither morphologically nor genetically (Holstein and Renner 2011a) distinguishable from *C. fernandesiana*, and *C. senensis* (sensu Flora Zambesiaca (Jeffrey 1978) and sensu Holstein and Renner (2010)). Fruit shape and length as well as the length of the female pedicel are variable, so I synonymize *C. subglabra*. Without calyx lobes, *C. senensis* is only hardly, if at all, distinguishable from glabrous *C. adoensis* specimens or those with long articulate trichomes, in this work described as *C. adoensis* var. *jeffreyana*. The fruit and seed shape also match the variable *C. adoensis*. Usually, *C. adoensis* var. *ado-ensis* has short trichomes and calyx lobes are ≤ 2 mm, but where both species meet (Malawi, NW Mozambique, S Tanzania), exceptions can be found (listed and further discussed as *C. adoensis* var. *jeffreyana*). Whether *C. adoensis* and *C. senensis* are truly separate species and the role of these intermediates needs to be tested by artificial hybridization, field observations, and/or a phylogeographic analysis.

Taxonomical remarks. Although the holotype of *C. senensis* was destroyed during the burning of the Berlin herbarium in 1943 and the name seems to be lost, the protologue offers all necessary characters to synonymize it with Jeffrey's *C. fernandesiana*. The *C. senensis* protologue points out articulate trichomes and an overall appearance like *C. quinqueloba*, which matches perfectly with many specimens of *C. fernandesiana*. Interestingly, many of these specimens have been identified as "*Coccinia quinqueloba*" or

"*Coccinia palmata*" by various collectors and scientists. The similarity, including the calyx lobes, is well visible in many specimens, but both species are restricted to South Africa.

Cogniaux described the *australis* variety of *C. jatrophiifolia* (synonym to *C. adoensis*) recognizing the similarity to the polymorphic *C. adoensis*. However, he differentiated between R.de Carvalho specimens with long lineal lobes (BR, COI) and specimens with lanceolate lobes (BR, COI), which he determined as *C. senensis*. When Jeffrey described *C. subglabra*, he cited the two COI specimens (deducing from his ID labels), but did not refer to Cogniaux' variety, which he must have overlooked. The one COI specimen is therefore paratype of *C. subglabra* and syn- respectively isolectotype of *C. jatrophiifolia* var. *australis*. The two COI specimens are also misplaced paratypes of Meeuse's *C. rehmannii* var. *littoralis*. The similarity of the COI specimens of Meeuse's variety is striking, but the long peduncles and the conspicuous black sublaminal glands refer rather to *C. senensis* than to *C. rehmannii*.

Specimens examined. (Selection, in total: 45) Malawi. Northern Region: Rumphi district, Nyika Plateau, 20 mls. N of M1, J.Pawek 13339B (MO). [Southern Region]: Bvumbwe, I.F.La Croix 2653 (MO). Lengwe National Park, near Mukanyu ravine, A.Hall Marker 1051 (K). Mozambique. Cabo Delgado: Mueda Plateau, 11°22'S 39°20'E, W.R.Q.Luke et al. 10084 (EA, K). Nampula: Monapo district, Monapo, forest reserve of Mr. Wolf, E.M.C.Groenendijk et al. 1031 (WAG). Tete: Cabora bassa [Cahora bassa], police post no. 3.5 km from barrage, A.R.Torre et al. 18788 (MO). Tanzania. Lindi: Selous Game Reserve, Kingupira, 8°28'S 38°33'E, K.Vollesen 1908 (EA); ibid., K.Vollesen MRC 4316 (DSM, EA, K, WAG); ibid., R.Wingfield et al. 3466 (DSM). Morogoro: Kilosa district, Ilonga Research Institute, 9.5 km NNE of Kilosa on road to Dumila, 6°46'31.3"S 37°2'23"E N.Holstein et al. 66 (DSM, M).

Coccinia sessilifolia ssp. *sessilifolia* var. *sessilifolia* **ssp. et stat. nov.**

Coccinia sessilifolia (Sond.) Cogn. in A. DC & C. DC., Monogr. Phan. 3: 534. 1881.

Cephalandra sessilifolia Sond. in Harvey & Sonder, Flora Capensis 2:493. 1862. TYPE: SOUTH AFRICA. Vaal river, *J.Burke 289* (Paralectotypes: K!, digital image! [K], PRE, SAM). TYPE: SOUTH AFRICA. Slengerfontein in Nieuwe Hantom [area where the provinces Western Cape, Eastern Cape and Free State meet], on rocks, 4500–5000 ft [1372–1524 m], 1839, J.F.Drège 3375 (Lectotype, designated here: P!, digital image! [P]). TYPE: SOUTH AFRICA. Nieuwe Hantom, on rocks, 4500–5000 ft [1372–1524 m], 1839, J.F.Drège s.n. (Paralectotypes: BR!, G!, K!, digital image! [K], L!, P, digital image! [P], W!). Transvaal, C.L.P.Zeyher 580 (Paralectotypes: BM! p.p., E!, K! p.p. digital image! [K], P! p.p.)

Coccinia schinzii Cogn., Bull. Herb. Boiss. 3: 419. 1895. TYPE: SOUTH AFRICA. Transvaal: Klippan, bushveld, 1875–1880, A.Rehmann 5162 (Lectotype, designated by Meeuse (1962): Z, digital image! [Z], isotype: BR!).

Description. (Fig. 2b, 4b, 6b) Perennial climber or creeper. Stems up to 5 m long, with slight waxy cover, glabrous (first shoots may have short white trichomes). Leaves 1.5–12.5 × 2.2–13.5 cm, sessile to amplexicaul (first leaves after appearance of stem can be distinctly petiolate (up to 1.5 cm)), (cordate to) deeply palmately 5-lobate. Lobes linear, lanceolate to elliptic. Leaf margin remotely denticulate, with or without lobules. Lobe apex obtuse to acute, apiculate. Upper lamina glabrous, clear to white pustulate. Lower leaf side glabrous, sometimes with dark glands near base of lamina. Probracts up to 1.7 mm or missing. Tendrils simple, very rarely bifid. Male flowers solitary or clustered in few-(rarely many-) flowered racemes. Pedicels of solitary flowers 1–4 cm, glabrous. Peduncle 1–6 cm long, glabrous. Pedicels of flowers in racemes 0.3–2.5 cm, glabrous. Bracts glabrous, up to 1.8 mm, or missing. Perianth tube glabrous, calyx lobes 0.15–0.35 cm long, lanceolate to (narrow) triangulate, erect to reflexed. Corolla 1.5–3.0 cm long, whitish cream to pale yellow, rarely dull orange-brown with conspicuous green venation, lobes 0.9–2.0 cm. Filament column not seen, anther head not seen, pollen sacs yellow. Female flowers one solitary. Pedicel 1–3 cm, glabrous. Hypanthium glabrous, calyx and corolla like in males. Ovary glabrous. Style columnar, greenish yellow.Stigmas bulging, greenish yellow. Fruit 8–12 cm × 3–4 cm, ellipsoid to oblong, when immature green with white longitudinal spots to stripes with waxy bloom, ripe red. Seeds 6–8 × 3–3.5 × 1–1.5 mm, symmetrical to slightly asymmetrical obovate, face flat (Fig. 13d, e).

Phenology. January–May, October –December.

Distribution. Fig. 38. South Africa, Botswana, Namibia, except high mountains, hyper-arid regions, and Cape floristic region. Elevation 300–1500 m. Stony soil, sand, sandy loam, clay loam. Granite or calcareous substrate. Semi-desert, grassland (e.g. *Rhynchelytrum* sp.), bushland, open woodland. Full sun to shade. Moderate disturbance tolerated.

Use. Unripe fruits are baked in ashes and eaten (Dinter 1912).

Vernacular names. Afrikaans: bobbejaan komkommer (C.A.Smith 3981), Tswana: mogábalá (J.Snyman & C.Noailles 229), !Kun [Kung]: kitwa (R.Story 5167).

Taxonomical remarks. The C.L.P.Zeyher 580 specimens in BM, K, and P are mixed with a *Trochomeria* sp.

Specimens examined. (Selection, in total: 178) Botswana. Central District: Mahalapye, 2 mls [3.8 km] SW of Kalamare, H.J.van Rensburg B4019 (PRE). Kgalagadi: 123 mls [196.8 km] W of Lobatse, in Molopo Farms, P.J.Mott 1092 (MO, PRE). Kgatleng: 15 km

SE of Arte-sia (Mosomane), D.T.Cole 1542 (PRE). Kweneng: Khutse reservaat, 2324 BC [23°15’–30’S 24°30’–45’E], L.C.C.Liebenberg 8990 (PRE). Ngamiland: river valley near SWA [Namibia] border fence, 20°01.35’S 21°E, P.A.Smith 3338 (PRE). North-West District: Aha Hills, H.Wild & R.B.Drummond 6953 (COI). South-East District: Lobatsi [Lobatse], F.A.Rogers 6281 (G, Z). Southern District: Jwaneng, D.T.Cole 1210 (PRE). Namibia. Erongo: Karibib, Okongawa, R.Seydel 3026 (B, B, COI, FR, FR, G, G, G, H, HEID, M, WAG, WAG). Hardap: ±45 km from Rehoboth on road to Mariental, P.M.Burgoyne & N.Snow 5080 (MO, PRE). Khomas: [Farm] Aris, mountain in the west, R.Seydel 4100 (B, B, M, MO) & 4100a (B, B). Omaheke: Goba-bis–Sandfontein road, 10 km E of Gobabis, H.Wanntorp & H.E.Wanntorp 1159 (S). Oshana: Amboland, Uukuanjama [Oukwanyama], Omupanda, A.Wulfhorst 18 (Z). Otjozondjupa: 32 mls [51.2 km] N of Nurugas on road to Karakuwisa, B.de Winter 3710 (M, PRE). South Africa. Eastern Cape: in valley near Graaff-Reinet, H.Bolus 364 (S). Free State: [Fezile Dabi District Municipality], Kroonstad townland, NE of confluence of Blomspruit and Vals river, J.C.Scheepers 1720 (EA, LISU, PRE, S); [Lejweleputswa District Municipality], Kromrant, ±20 SW of Boshof, P.C.Zietsman & L.Zietsman 155 (PRE); [Motheo District Municipality], Krugersdriftdam Nature Reserve, on Olive Hills, D.B.Muller 1645 (PRE); [Xhariep District Municipality], Koppie 9 km from Philippolis on road to Draaikloof, C.Reid 285 (PRE). Gauteng: Pretoria, Brummeria, Botanical Garden, A.Balsinhas 3406 (MO, PRE, WAG); ibid., A.Balsinhas 3476 (MO, PRE, WAG). Limpopo: [Capricorn District Municipality], Blouberg Nature Reserve, Farm Auf der Haard, P.Herman 1266 (MO, PRE); [Greater Sekhukhune District Municipality], Penge mine, E.Retief 1354 (MO, PRE, WAG); [Mopani District Munici-pality], Phalaborwa Water Board, 14 km S of Phalaborwa, Farm Sheila 10 KU, near perma-nent plant effluent stream, I.M.Retief 505 (PRE); [Vhembe District Municipality], c. 30 mls [48 km] W of Louis Trichardt, western part of Zoutpansberg, near Mara, Buysdorp, H.J.Schlieben 7453 (B, G, HBG, M); [Waterberg District Municipality], 1 ml. [1.6 km] W of Rust de Winter dam, R.Story 1498 (PRE, S). Mpumalanga: [Ehlanzeni District Municipality], on Lydenburg–Burgerfort road, Buffelsvlei Farm, portion 16, A.Fabian 1058 (PRE). Northern Cape: [Frances Baard District Municipality], Barkley Wes, Vaalbos [National Park], P.C.Zietsman 894 (PRE); [Kgalagadi District Municipality], Colville Farm, 26 Feb 1982, A.A.Gubb s.n. (PRE814017); [Pixley ka Seme District Municipality, Umsobomvu], Colesburg, Achtertang, 16 Apr 1934, J.O.Swinford s.n. (PRE42988). North West Province: [Bojanala District Municipality], Brits, Beestekraal Game Reserve, property of PPC, c. 400 m on road from cottages to gate, N.P.Barker 523 (PRE); [Dr Kenneth Kaunda District Municipality], near Klerksdorp, H.J.Schlieben 10695 (HEID, PRE, S); [Dr Ruth Segomotsi Mompati District Municipality], 60 mls [96 km] NW of Vryburg, Farm Palmyra, R.J.Rodin 3605 (MO, PRE); [Ngaka Modiri

Molema District Municipality], 40 km past Mafeking [Mafikeng] on path to Bray, J.N.Pienaar 1052 (PRE).

Coccinia sessilifolia ssp. *sessilifolia* var. *variifolia* (A.Meeuse) Holstein **stat. nov.**

Coccinia variifolia A.Meeuse, Bothalia 8: 100–111. 1962. TYPE: SOUTH AFRICA. [Limpopo province]: Waterberg, Vaalwater, about 2.25 km from Vaalwater on road to Hermanusdoorns, male, fl, 6 Jan 1959, A.D.J.Meeuse & R.G.Strey 10413 (Holotype: PRE digital image [JPS], PRE digital image [JPS]; isotypes: BM?, BOL, EA?, K?, L, SRGH). TYPE: SOUTH AFRICA. L. c., female, 6 Jan 1959, A.D.J.Meeuse & R.G.Strey 10413bis (Paratype: PRE!). TYPE: SOUTH AFRICA. Limpopo province: Palala river, M.G.Breyer[-Brandwijk] TRV25226 (Paratype: ?). TYPE: SOUTH AFRICA. Limpopo province: Rietspruit near Nylstroom [Modimolle], G.P.F.van Dam TRV23372 (Paratype PRE!). TYPE: SOUTH AFRICA. Limpopo province: Nabomspruit, Mosdene, E.E.Galpin s.n. (Paratype: ?). TYPE: SOUTH AFRICA. Limpopo province: 11 km from Warmbaths [Bela Bela] on Nylstroom road, R.Story 1525 (Paratype: ?). TYPE: SOUTH AFRICA. Limpopo province: Warmbaths, c. 3600 ft [1100 m], grassland/bush veld, H.Bolus 11893 (Paratype: BR!). TYPE: SOUTH AFRICA. ibid.?, R.Leendertz TRV7579 (Paratype: ?). TYPE: SOUTH AFRICA. [Limpopo Province]: Waterberg, 5.5 mls [8.85 km] NNE of Warmbaths, c. 1220 m, sour bushveld, fl, 15 Nov 1947, J.P.H.Acocks 13903 (Paratype: S!).

Description. Perennial climber. Stems up to 1.2 m, likely also longer, glabrous. Petiole 0.7–1.6 cm, glabrous. Leaves 5.2–6.0 × 6.0–7.5 cm, deeply to shallowly 5-lobate, lobes outwards lobulate. Leaf margin remotely dentate, apex obtuse with final tooth. Upper lamina glabrous, with clear to whitish pustules. Lower lamina glabrous, with glands at base between nerves. Probracts up to 2 mm. Tendrils simple. Male flowers in racemes, accompanied by a solitary flower. Common peduncle 1.0–1.4 cm, pedicel in racemes 3–6 mm, each glabrous. Bracts up to 1.5 mm, narrow ovate. Pedicel of solitary flowers 0.9–2 cm, glabrous. Perianth tube glabrous. Calyx lobes 2.5–4 mm, teeth subulate-narrow triangulate, erect. Corolla c. 2 cm, pale buff, lobes not measured. Filament column, anther head, and pollen sacs not seen. Female flowers solitary or clustered in reduced 2-flowered racemes. Common peduncle 0.1 cm, pedicel in racemes 0.9–1.0 mm, pedicel of solitary flower not seen, each glabrous. Hypanthium most likely glabrous and perianth as in male flowers. Ovary glabrous. Style and stigma not seen. Fruit and seeds not seen.

Phenology. January–March, November, December. Likely as in *C. sessilifolia* var. *sessilifolia*.

Distribution. Fig. 38. Only known from Limpopo province in South Africa. Elevation 800–1200 m. On sandstone, well-drained stony sand. Low closed woodland.

Remarks. Subsessile leaves occur spontaneously in *C. sessilifolia*, and young individuals usually (always?) have petiolate leaves (N.Holstein 131). However, these distinctly petiolate mature specimens have been only observed in Limpopo province in South Africa. Sessile *C. sessilifolia* leaves can be quite variable, profoundly to deeply lobate, sometimes lobulate. If these leaves are distinctly petiolate, this new spatial freedom appears to be extraordinarily variable. Meeuse's *C. variifolia* shares the sublaminal glands (cp. Fig. 6b) and the calyx lobes of *C. sessilifolia*, and is geographically nested within this species (hence no climatic differentiation). Acocks 13903 also reports a "stark glaucous" appearance, just as it can be observed in *C. sessilifolia*. As petiolate leaves also occur in young *C. sessilifolia* plants, and subsessile leaves also occur in mature plants, it is more likely that the distinctly petiolate *C. sessilifolia* individuals represent a local establishment of this character. As the ancestors of *C. sessilifolia* were petiolate, this variety could even represent a remnant population of these.

Specimens examined. (in total: 7) South Africa. Limpopo: Waterberg Distr., Zandrivierspoort, F.A.Rogers 24932 (Z); Waterberge, Ellisras, 45 km N of Vaalwater on Beauty pad, Schurfbankshoek, N.Rooyen 1667 (PRE); Nylstroom: Vaalwater, 24[°]23[']06['']S 28[°]08[']24['']E, Farm Modderspruit, R.H.Westfall 2136 (PRE).

Coccinia subsessiliflora Cogn., Bull. Jard. Bot. État Brux. 4(1): 225. 1914. TYPE: D. R. CONGO. [Équateur Province]: around Likimi, male, fl, 15 Oct 1910, L.C.E.Malchair 433 (Holotype: BR!, isotype: BR!).

Coccinia sp. D in C.Jeffrey, Flora of Tropical East Africa: 70. 1967. UGANDA. [Western Region]: Kigezi District [(Kanungu District/Kisoro District)], Kayonza Forest Reserve [Bwindi Forest Reserve / Impenetrable Central Forest Reserve], S.Paulo 644 (EA!, K!, MO!); [Central Region]: Mengo district, Mabira forest, M.V.Loveridge 87 (?); [Central Region]: Mabira Forest, near Kiwala, R.A.Dummer 3195 (?).

Description. Perennial creeper or climber. Stem up to 4 m, glabrous. Petiole 2.0–12 cm, glabrous, sometimes with white pustules. Leaves 5.5–15 × 6.5–17.5 cm, almost to the base palmately 5-lobed. Lobes lanceolate, sometimes lobulate; tip acute, acuminate. Margin serrate-lobulate, denticulate. Upper lamina glabrous with clear to white pustules, rarely with few fine (up to 1.5 mm long) trichomes. Lower lamina glabrous, rarely with dispersed small blackish glands, rarely with tiny trichomes; sometimes nerves with white pustules. Probracts up to 1.5 mm or missing. Tendrils simple. Male flowers in glabrous, dense, compact racemes. Peduncles up to 6 mm. Pedicels up to 4 mm. Bracts 2–2.5 mm. Perianth tube glabrous. Calyx lobes 1–2 mm, subulate, triangulate to lineal, erect to reflexed. Corolla 1.2–1.3 cm, orange, pale yellow-orange, yellow, lobes c. 0.3 cm. Filament column, anther head, and pollen sacs not seen. Female flowers solitary or in few flowered racemes. Common peduncle up 1 cm, glabrous. Pedicel of flowers in racemes up to 4 mm. Bracts up to 2 mm or missing. Pedicel of solitary flowers up to 1.1 cm, glabrous. Hypanthium glabrous, calyx lobes and corolla like in males. Ovary glabrous. Style and stigma not seen. Fruit 2.0–2.4(–5) × 1.7 cm, globose to long ovoid, unripe green, ripe color not known. Seeds ≥ 4.5 × 2–2.5 × 1–1.5 mm, asymmetrically obovate, face flat.

Phenology. January, July, August, October, December.

Distribution. Fig. 40. Congo basin (Central African Republic, D. R. Congo). Forested mountains of northwestern Burundi, D. R. Congo (North Kivu, South Kivu), Uganda (Western Province), Southern Sudan (Eastern Equatoria/Sharq al-'Istiwa'iyah: Lotti Forest). Elevation 300–1900 m. Soil preferences unknown. Tropical rainforests. *Macrolobium* [= *Gilbertiodendron*?] forest, swamp forest, disturbed ground in open forest.

Vernacular names. Kihunde: mutangatanga (R.Gutzwiller 965), Lissongo [Mapti]: kanganga (Equipe 1103), Turumbu: ndombo (J.Louis 2709).

Remarks. Specimens from the eastern parts of the distribution (esp. E of the Western Rift) have longer fruits. However, it does not seem that there is an abrupt change, so a taxonomical consequence does not seem to be appropriate.

Rarely (J. Louis 5672, J. Louis 13030), the lower leaf lamina and the adaxial petiole side have short trichomes and the upper lamina has some long trichomes. These features are unusual, but the other characters match the species.

Although *C. subsessiliflora* is nested within *C. barteri*, I regard it a proper morpho-species. The deeply lobate leaves are a distinct character, and the species is distributed only in the Congo Basin and the eastern rainforests. I suppose that *C. subsessiliflora* evolved peripatrically in an arid period of the Pliocene/early Pleistocene period, eventually near the Kivu Mts, and *C. barteri* populated these areas later on.

Specimens examined*.* (in total: 20) Burundi. Bubanza: Bubanza, J.Lewalle 6504 (BR, EA); ibid., M. Reekmans 1477 (BR, BR). Central African Republic. Lobaye: Boukoko, Equipe 1103 (BM, G); ibid. 2276 (BM, G, P). D. R. Congo. Equateur: [Nord-Ubangi district], Befale territoire, Bomandja [Bomanza], C.Evrard 4980 (BR, digital image [BR]); [Nord-Ubangi district] Businga territoire, between Karawa and Businga, J.Lebrun 1928 (BR, WAG). Maniema: [Kailo], between Kindu and Katakokombe, J.Lebrun 6011 (WAG). North Kivu: Masisi territoire, km 86 on Masisi-Walikale road, R.Gutzwiller 965 (BR, WAG, WAG).

Orientale: Haut-Uélé district, Faradje territoire, Kurukwata (Aba), P.Gerard 3564 (BR, EA, WAG); Ituri district, Mambasa territoire, Réserve de Faune à Okapi, Epulu, 1°25'N 28°35'E, C.E.N.Ewango 2290 (M, MO); [Tshopo district, Isangi territoire], 20 km W of Yangambi, Lilanda, J.Louis 1330 (BR); Yangambi, km 10 on route from Ngazi, J.Louis 2709 (BR); Yangambi, Ngazi route, J.Louis 5672 (WAG); Yangambi, km 14 on route from Ngazi, J.Louis 5771 (WAG, WAG); Yangambi, J.Louis 13030 (WAG). North Kivu: Beni territory, Kiandolili river, Gongobotsi Camp of Albert National Park guards, H.Fredericq in Herb. G.F.de Witte 8288 (BR, M, PRE, WAG). Southern Sudan. Eastern Equatoria: Torit district, Lotti Forest, J.K.Jackson 3026 (K). Uganda. Western Region: [Masindi district], Bunyoro, Bujenje county, Budongo Forest, A.B.Katende K2801 (MO); ibid. T.J.Synott 1322 (EA).

Coccinia trilobata (Cogn.) C.Jeffrey, Kew Bull. 15: 349. 1962.

Peponium trilobatum (Cogn.) Engl., Engl. & Prantl, Pflanzenfam., Nachtr.: 318. 1897. TYPE: TANZANIA, Kilimanjaro: Mkuu [c. 3°10'S 37°36'E], 1500 m, in hedges, fl, fr, Mar 1894, G.Volkens 1956 (Holotype: B, destroyed; lectotype acc. to sheet, but not published, so designated here: BR!; isolectotype: BR!).

Peponia parviflora Cogn. var. *trilobata* Cogn., Engl. Bot. Jahrb. 21: 210. 1896.

Peponia trilobata (Cogn.) Engl., Pflanzenw. Ost-Afr. C: 399. 1895, nom. illeg. [*Peponia* is a diatom genus].

Coccinia kilimandjarica Cogn. ex Harms in Fries, Notizbl. Bot. Gart. Berlin-Dahlem 8: 489. 1923. TYPE: TANZANIA. Kilimanjaro Region: Kibohöhe [farm at c. 3°15'50"S, 37°12'0"E], 1100–1200 m, fl, R.Endlich 52a (Holotype; B, destroyed; lectotype, designated here: M!; isolectotype; H!).

Coccinia kilimandjarica Harms var. *subintegrifolia* Cogn. ex Harms in Fries, Notizbl. Bot. Gart. Berlin-Dahlem 8: 490. 1923. TYPE: TANZANIA. Kilimanjaro Region: Kibohöhe, 1100–1200 m, fl, R.Endlich 52 (Holotype: B, destroyed; lectotype, designated here: M!; isolectotype: H!).

Description. Perennial climber. Stems up to 3 m, with soft whitish trichomes, at least along nerves. Petiole 1.5–16.5 cm, with short whitish trichomes. Leaves 2.6–14.5 × 3.2–18.0 cm, cordate, 5-angulate to 5-lobate, sometimes lobulate. Margin denticulate. Apex at least of central lobe acute, often acuminate. Upper leaf surface with clear to white pustules and usually with white trichomes. Lower lamina more or less covered with soft trichomes, denser on nerves. Probracts up to 1.5 mm or missing. Tendrils simple. Male flowers solitary or in short few-flowered racemes. Common peduncle up to 1.7 cm long, pedicel in raceme up to 3.2 cm, each glabrous or with short trichomes. Bracts up to 1 mm. Pedicel in solitary flowers 0.7–4.7 cm, indument as in racemes. Perianth tube with articulate trichomes. Calyx lobes 2–5 mm long, lineal, erect to reflexed. Corolla 0.7–2.2 cm, orange-yellow to reddish-orange, deeper colored on the inner side of the lobes, outside with green venation, lobes 0.7 –1.3 cm. Filament column pale yellowish green, anther head a bit darker than filament column. Pollen sacs yellow. Female flowers 1(–2) solitary, pedicel 0.5–4 cm, glabrous or sparsely covered with short trichomes. Hypanthium with articulate trichomes, calyx lobes and corolla like in males. Ovary with trichomes, becoming glabrous towards fruit ripening. Style and stigmas not seen. Fruits ovoid to oblong, 4–4.7(–9) × 2 cm, unripe green with white longitudinal stripes that develop a dark green corona during ripening, ripe fruits orange-red. Seeds 6.5–7 × 2.5–3.5 × 1.5 mm, more or less asymmetrical obovate, face flat (Fig. 13c).

Phenology. January, May–July, October–December.

Distribution. Fig. 33. Tanzania (Arusha, Kilimanjaro, Tanga), Kenya (Central, Coast, Eastern, Nairobi, southern Rift Valley Province). Elevation 1100–2100 m. Red soil, black soil. Open forest, savannas, evergreen bushland, shrubland, grassland.

Use. Leaves eaten as vegetable (Coilly? 24, F.Msajiri 19).

Vernacular names. Dholuo: *angwe* (G.R.Williams 307), Kinandi: *notondwe* (G.R.Williams 307), Meru: *katakeru* (Coilly? 24), Kikuyu: *kigerema* (P.Njogu 13835), Kipare: *itotwe* (W.J.Kindeketa 648).

Remarks. The fruits are reported to be poisonous (G.R.Williams 307).

There are some specimens, which have a mixed (not intermediate) phenotype with *C. microphylla*: the calyx lobes are unusually long (up to 7 mm), which speaks for *C. trilobata*, but the indument matches *C. microphylla*. These morphs do not occur in single location, but are found in the Ndoto Mts (O.Kerfoot 2644), in Koboko (P.Kirika et al. 002/020/2011), and around Voi (M.Hucks 579, B. Verdcourt 3888, R.Polhill & S.Paulo 962). Whether these are hybrids (F2 or later) or just a variety is not known. These specimens look also quite like *C. megarrhiza*, which occurs in northern Kenya and Ethiopia, however, the indument does not match either.

The specimens in the Usambara Mts are often quite glabrous or the trichomes are very small and thus easy to mix up with *C. microphylla*.

Specimens examined. (Selection, in total: 61) Kenya. Central Province: South Nyeri district, S of road (D450), c. 4 km E of Nairobi–Nanyuki road, 3 km N of Kiganjo, S.S.Hooper & C.C.Townsend 1697 (K). Eastern Province: Nkunga Crater Lake, P.A.Luke et al. 7256 (EA). Nairobi: Nairobi river Valley, Chiromo, 1°16’30’’S 36°48’E, R.B.Faden & A.J.Faden 74/822 (BR, DSM, EA, MO, WAG). Rift Valley Province: Naivasha District [Nakuru district], Ol Longonot Estate, O.Kerfoot 3543 (EA, S). Tanzania. Arusha: Small Momela Lake, H.M.Richards 20036 (EA, EA, K). Kilimanjaro: valley slopes near Alt Moschi [Old Moshi], A.Peter 56453 (B). Tanga: western Usambara Mts, Mombo–Soni road, R.B.Drummond & J.H.Hemsley 3007 (B, EA, LISC, S).

Insufficiently known taxa

Coccinia sp. A C.Jeffrey, Flora Zambesiaca: 450. 1978. ZAMBIA. Northern Province: Chilongowelo, Tasker's Deviation waterfall, 4900 ft [c. 1500 m], female, fl, 27 Feb 1952, H.M.Richards 883 (K!).

Distribution. Only known from single collection.

Remarks. Jeffrey (1978) suggested that this specimen is allied with *C. barteri*. The inflorescence matches that of *C. racemiflora*, which differs in an urceolate perianth tuber/hypanthium, more coriaceous leaves and a glabrous surface. Simple tendrils also occur in *C. barteri*, so this is not a good distinctive character. As the plastid haplotypes of *C. racemiflora* are nested in *C. barteri*, and the distribution of *C.* sp. A is within the *C. barteri* range, Jeffrey's hypothesis is sound. However, the corolla lobes are quite long, and it seems that the corolla is open campanulate. Therefore, there is some similarity with *C. mildbraedii* and even with *C. grandiflora*.

Coccinia sp. B C.Jeffrey, Flora Zambesiaca: 450. 1978. ZAMBIA. Southern Province: Mazabuka, on Nanga Estate near Kafue pilot polder [c. 15°45'S 27°54'E], female, fl, 7 Mar 1963, H.J.van Rensburg 1620 (K!).

Distribution. Only known from single collection.

Remarks. Like *C.* sp. A, Jeffrey (1978) suggested a closer relationship to *C. barteri*. The tubular corolla and the coriaceous leaves support that. The specimen was collected in riverine bush in *Acacia* woodland and *Hyparrhenia*/*Setaria* grassland in a flood plain area, which is unusual for *C. barteri* as it rather occurs in (rain) forests. White (1983) calls the phytochorion of that region "edaphic grassland with semi-aquatic vegetation". However, the local soil conditions are not known, and water might be available throughout the year, but this individual might also represent a local adaptation towards increased drought tolerance.

Excluded and dubious names

Coccinia abdallai Zimm. MS. nom. nud. Mentioned on P.W.A.Zimmermann G 6594 (EA!) and in Die Cucurbitaceen 2: 8 (1922b).

This is a *Coccinia trilobata*.

Bryonia acerifolia D.Dietr. Synopsis plantarum 5: 367. 1852. nom. nud.

Dietrich mentions this species in his synopsis as a name by Willdenow. However, no such name by Willdenow is known. As Cogniaux synonymizes *B. acerifolia* with *B. alceaefolia* Willd., and Dietrich uses the exact same words for *B. acerifolia* as for *B. alceaefolia*, this name is likely just mistaken.

Coccinia aostae Buscal. & Muschl., Bot. Jahrb. 59: 499. 1913. TYPE:[EASTERN AFRICA]. at Mbusi river [authors state that this river flows in the Indic Ocean in Mozambique, the collector went upstream towards Zambezi river and Victoria falls; most likely the Buzi River is meant], tree steppe, fl, 14 Dec 1909, H.von Aosta [H.L.F.H.d'Orléans] 105 (Syntype: B destroyed; duplicate ?).

This species is supposed to be from Mozambique. However, the describing author, Muschler, provoked a scandal with this work as Georg Schweinfurth (1915) and his former supervisor Adolf Engler (Engler et al. 1915; Ryding 2001) accused him of fraud. Gilg, who contributed corrections in the Cucurbitaceae, suggested that *Coccinia aostae* had been described using the G.Schweinfurth 578 specimen from Eritrea, which bore the ms. name *Coccinia lalambae* Schweinf. A drawing of this species exists in BR! (negative in K!: no. 4887), which represents a *C. adoensis*. However, the name for G.Schweinfurth 578 remains unpublished and the von Aosta 105 specimen is destroyed, and the species dubious. According to the authors duplicates of the von Aosta specimens have been distributed, and White (1962) found some in Florence (FI or FT). However, a loan from FT did not contain any *Coccinia* specimens from *von Aosta*.

Coccinia buettneriana Cogn., Bull. Acad. Belg. ser. 3, 14: 351. 1887. TYPE: GABON. no detailed information given, Sep 1884, R.Büttner 18 (Holotype: B destroyed).

Cogniaux and Harms synonymize (1924) *C. buettneriana* under *Momordica gabonii* Cogn. (1881) as it was collected in close vicinity of *Büttner 17* (*Momordica gabonii*), which is, according to Cogniaux himself almost not distinguishable from *C. buettneriana*.

Coccinia calantha Gilg, Bot. Jahrb. 34: 358. 1904. TYPE: TANSANIA. [Tanga]: Usambara Mts, Duga, near Nikunde village, 100 m, in bush and on fencing, fl, Jul, C.H.E.W.Holst 3190 (Holotype: B destroyed; duplicates ?).

As the holotype is destroyed and the description does not give enough well enough characters to relate *C. calantha* to other species, the name remains dubious. Zimmermann (1922b) presents a drawing of an anther, but the thecae are too narrow for a *Coccinia*, but would match *Eureiandra* species. On the other hand, *Eureiandra* has free petals, whereas *C. calantha* ought to be sympetalous.

Coccinia cordifolia (L.) Cogn. in A.DC & C.DC., Monogr. Phan. 3: 529. 1881. pro parte.

Bryonia cordifolia L., Sp. pl. 2: 1012. 1763. TYPE: SRI LANKA. No detailed location given, P. Hermann 354 (Holotype: Herm. Flora zeylanica 2:22, BM, digital image! [BM]).

Bryonia foliis cordatis oblongis quinquangularibus dentatis scabris L., Flora zeylanica: 168. 1747.

Cogniaux cites *Bryonia cordifolia* sensu Linnaeus' Species plantarum 2nd edition, where Linneaus synonymizes Rumphius' *Vitis alba indica*, which is *Coccinia grandis*. If *B. cordifolia* would have been originally described in 1763, Cogniaux' choice would have been valid, but *B. cordifolia* was described in 1753 (Species plantarum 1st edition), where *Vitis alba indica* is not mentioned, but only a specimen from Hermann herbarium, which is *Cucumis maderaspatanus* L.

Coccinia crassifolia H.K.Walter. Naturwissenschaft und Landwirtschaft (9): 33. 1926. nom. nud.

This is a typographical error of *Caccinia crassifolia* Kuntze, a Boraginaceae.

Coccinia decipiens (Hook.f. in Oliv.) Cogn. in A.DC & C.DC., Monogr. Phan. 3: 539. 1881.

Cephalandra decipiens Hook.f. in Oliv., Flora of Tropical Africa 2: 552. 1871. TYPE: ANGOLA. [Cuanza Norte province]: Pungo Adongo, grassland, F.M.J.Welwitsch 816 (Holotype: BM!, isotypes: COI, K, LISU).

The sessile beaked fruits match to the genus *Diplocyclos*, which has been correctly observed by Jeffrey (1962) as *Diplocyclos decipiens* (Hook.f.) C.Jeffrey.

Coccinia dubia Palacký in Lotos 10(4): 70. 1860. nom. nud.

Palacký cites a *Coccinia dubia*, which was supposed to be described by von Bunge in his “Reliquiae lehmanniae” (von Bunge 1854). However, Palacký mistyped the genus, which is in fact called *Caccinia*, a Boraginaceae.

Coccinia ecirrhosa Cogn., Bull. Herb. Boissier 4(12): 822. 1896. TYPE: SOMALIA. Abdallah, 1891, *C.Keller 106* [sphalm. 116 in l.c.] (Type: BR, digital image! [JPS], Z, digital image! [Z], photo of Z specimen at K!).

The type does not contain much material, but the lower surface of a leaf shows a pinnatifid venation pattern, which is unknown in *Coccinia*. Jeffrey (1967) put it correctly (Kocyan et al. 2007) to another genus, namely *Cephalopentandra*.

Coccinia gabonensis Keraudren, Adansonia 8: 40. 1968. TYPE: GABON. Ogooué-Ivindo Province: Bélinga, 950–1000 m, male and female, fl, Nov 1964, N.Hallé 3018 (Holotype: P, digital image! [P], isotype: P!, P!, K!, digital image! [K]).

This species does definitively not belong to *Coccinia*. It is monoecious, has free petals and rather large bracts, in contrast to the dioecious, sympetalous *Coccinia* species with subulate bracts. It most likely belongs to *Momordica*.

Coccinia glandis is a typographical mistake for *C. grandis* that has been published several times (Tewtrakul et al. 2006, Jiwajinda et al. 2002). This epithet should hence not be used in *Coccinia*.

Physedra gracilis A.Chev. Exploration Botanique de l'Afrique occidentale française 1: 292. 1920. nom. nud.

Specimens connected to this nomen nudum (ICBN 32.3) have been listed under *Coccinia grandis* by M. Kéraudren (1967). As I did not see the specimens, I cannot decide, whether this was correct.

Coccinia helenae Buscal. & Muschl., Bot. Jahrb. 59: 498. 1913. TYPE: [EASTERN AFRICA]. At Mbusi river [authors state that this river flows in the Indic Ocean in Mozambique, the collector went upstream towards Zambezi river and Victoria falls; likely the Buzi river is meant], steppe, fl, fr, 3 Dec 1910 H.von Aosta [H.L.F.H.d’Orléans] 87 (Holotype: B, destroyed; duplicates ?).

This species is supposed to be from Mozambique. However, the describing author, R. Muschler, provoked a scandal with this work as G.Schweinfurth (1915) and his former supervisor Adolf Engler (Engler et al. 1915; Ryding 2001) accused him of fraud. Gilg, who contributed corrections in the Cucurbitaceae, suggested that *Coccinia helenae* had been described using the G.Schweinfurth 932 specimen from Blue Nile. A drawing of this species exists in BR (negative in K!: no. 4846). The drawing, if it represents a *Coccinia* (the two subsessile female flowers on one node are suspicious), does not match any species of my knowledge from Blue Nile area. However, if it is from the area as given by Muschler, it might be *C. rehmannii*. As the *von Aosta 87* specimen is destroyed the species remains dubious. According to the authors duplicates of the *von Aosta* specimens have been distributed, and White (1962) found some *von Aosta* specimens in Florence (FI or FT). However, a loan from FT did not contain any *Coccinia* specimens from *von Aosta*.

Cephalandra ivorensis A. Chev., Exploration Botanique de l'Afrique occidentale française 1: 295. 1920. nom. nud.

Specimens connected to this nomen nudum have been synonymized under *Physedra eglandulosa* (Hook.f.) Hutch. & Dalziel (now *Ruthalicia eglandulosa* (Hook.f.) C.Jeffrey).

Bryonia? *lagenaria* E.Mey. ex Drège, Zwei Pflanzengeographische Documente 54, 169. 1843. nom. nud.

This name appears on some Drège specimens and is only listed in the work of Meyer. However, the specimens are type specimens *Coccinia sessilifolia*.

Coccinia lalambensis Schweinf. in Penzig, Atti del Congresso botanico Internazionale di Genova 1892: 342. 1893. nom. nud. ERITREA. [Anseba Province]: Monte Lalambensis near Keren, c. 2000 m, 20 Mar, *G.Schweinfurth 568* (B, destroyed). [Northern Red Sea Province]: Habab, J.M.Hildebrandt plant. Habab 1802 (LE?).

No description given, therefore, this name is not validly published.

Cucurbita laevigata nom. nud.

This name been used on a specimen in L herbarium (L0587542). The specimen was part of the collection of C. G. C. Reinwardt, but lacks collector or collection site or date. One ink-written label solely states “1766.E.5138.” and the species name. Another label, written with a pencil, says “Cucurbita laevigata” “mihi” and “Callelet W[…]”. The last word is unreadable to me. Another specimen (L0587515) bears a similar label with “1766.E.5138.”, however without a pencil-written label. Both specimens are *Coccinia grandis*, which would *Cucurbita laevigata* to be synonymized with, if the name had been validly published.

Coccinia longipetiolata Chiov. Fl. Somala 2: 223. 1932. TYPE: SOMALIA. [Jubbada Dexhe/Jubbada Hoose border]: between Afmadù [Afmadow] and Saamoggia, 1926, P.Gorini 149 (Syntype: FT, photo: K! [no. 4851], digital image! [JPS]); SOMALIA. [Jubbada Dexhe/Jubbada Hoose border]: between Afmadù [Afmadow] and Saamoggia, 1926, P.Gorini 150 (Syntype: FT, photo: K! [no. 4850], digital image! [JPS]).

The specimens are quite poor. No leaf is spread out, and generative characters are missing. However, 7-lobate leaves, according to description, do only occur in *C. samburuensis*, which differs in coriaceous leaves and a serrate margin with glandular teeth. Hence, this species name are not synonymous with any *Coccinia* species. The tendrils in *C. longipetiolata* are almost equally bifid, which is unusal for *Coccinia*, especially in species not from rainforests. There are neither characters supporting a relationship with *Coccinia*, nor characters contradiciting it, except for the tendrils. Jeffrey (1967) suggests a relationship to his *C.* sp. E sensu F.T.E.A. (*Jarman 66*), but as I didn't see this specimen, I cannot discuss this. Therefore, I put this species as dubious. Eventually, sequencing could give disclosure about the relationships.

Coccinia macrantha nom. nud.

Physedra macrantha Gilg, Bot. Jahrb. 34: 356. 1904. TYPE: LIBERIA. Gran bassa, Fishtown, in bush, sand, fl, 10 m, 27 Aug 1898, M.Dinklage 1846 (Holotype: B!, digital image! [B]).

The combination *Coccinia macrantha* was only used in B herbarium for storage, but apparently never published. *Physedra macrantha* Gilg has been synonymized, correctly, under *Physedra eglandulosa* Hutch. & Dalziel (1928), which is now in the genus *Ruthalicia*.

Coccinia medica M.T.H.Khan. in: Gottschalk-Batschkus and Green, Handbuch der Ethnotherapien: 377, 384, 517, 537. nom. nud.

Khan used this name, but without taxonomic context. Most likely, he meant *Coccinia indica*.

Coccinia monteroi Hort. Catalogue des graines du Jardin botanique de Bordeaux. 1866.

I didn't see the protologue, but Cogniaux (1881) listed this one as nomen tantum.

Coccinia moshiensis Zimm. ms. nom. nud. Mentioned on P.W.A.Zimmermann G 6599 (EA!). This is a *Coccinia trilobata*.

Coccinia natalensis Burtt Davy, A manual of the flowering plants and ferns of the Transvaal with Swaziland, South Africa 1: 237. 1926. nom. nud.

Coccinia natalensis (Oliv.) Cogn., unknown.

Cephalandra natalensis Oliv., unknown.

The names of Cogniaux und Oliver are mentioned in Burtt-Davy and Pott-Leendertz in Ann. Transvaal Mus. 3(3): 121. 1913. However, no citation is given. Neither *Cephalandra natalensis* in mentioned in Daniel Oliver's Flora of Tropical Africa, nor any Cogniaux publication with this name is known. Burtt Davy writes in 1926 that the name 'appears to have been an unpublished MS. name'.

Coccinia obbadiensis (Chiov.) Cufod., Supplem.: Enum. Pl. Aethiop. Spermatophyta 35(2): 1050. 1965.

Cephalopentandra obbadiensis Chiov., Fl. Som.: 187, tab. 20, fig. 1. 1929. TYPE: SOMALIA. [Mudug Region]: Obbia [Hobyo] Sultanate, between Dolobscìo and Magghiòle, 27 Apr, G.Stefanini & N.Puccioni 458 (Holotype: FT, isotype: K!, photo of holotype at K!).

The author notes five stamens, which are a good reason for not including this species to *Coccinia*. The leaves of the specimen on the picture look like these of *Coccinia quercifolia*, which is also excluded from *Coccinia* and put separately by Jeffrey (1967).

Coccinia quercifolia Hutch. et E. A. Bruce, Bull. Misc. Inform. Kew 2: 99. 1941. TYPE: SOMALIA. [Nugaal Region]: Boundary Pillar 93, 45°9'E, 8°37'N, 990 m, fl, 6 Oct, J.B.Gillett 4194 (Holotype: K!, digital image! [JPS, K], K!, digital image! [JPS, K]). ETHIOPIA. [Somali Region]: Harradigit [c. 7°45'N, 45°30'E], Apr, F.L.James & J.G.Thrupp no.? (Paratype: K?).

The leaves have a pinnatifid venation, just like *Cephalopentandra* (*Coccinia*) *ecirrhosa*, but are deeply lobed. Since the leaf form may vary in Cucurbitaceae, it is likely that these specimens belong together, so that the odd leaf venation excludes this type from *Coccinia*. Jeffrey already (1967) transferred it into the other genus.

Bryonia quinquefolia Noronha, Verh. Bat. Genootsch. 5: 155(8). 1790. nom. nud.

Miquel (1855) synonymizes this nomen nudum under *C. wightiana* M.Roem., which is *C. grandis* (see taxonomical remarks there). However, he also synonymizes *Bryonopsis pedata* Hassk., which cites *Bryonia quinquefolia*. The description of *Bryonopsis pedata* mentions lacinate, almost pinnatifid leaves and male flowers in oblong clustered racemes. This does not match *C. grandis* at all, but eventually *Diplocylos palmatus*, which Roemer excluded from *C. indica* as *Coccinia palmata* M.Roem. The identity of *Bryonia quinquefolia* might be solved, if one finds a Noroña specimen stating "*Bryonia quinqueloba*" or "Oyot-kekèp", the latter name being the Javanese term for this species. However, the epithet rather links to the deeply lobate leaves of *D. palmatus*.

Coccinia palmata M.Roem., Synopsis peponiferarum: 93. 1846.

Bryonia palmata L. Sp. pl. 2: 1012. 1753. TYPE: [SRI LANKA]. No location given. P.Hermann 25 (type lost?), P. Herman 41 (type lost?), P.Hermann 62 (type lost?), P.Hermann 353 [Musæum zeylonicum 2:58] (Lectotype, designated by Jeffrey (1962): BM-000621700).

Bryonia foliis palmatis lævibus quinquepartitis: laciniis lanceolatis repando-serratis L., Flora zeylanica: 146. 1747.

Bryonia zeylanica, folio quinquepartito Burm., Thesaurus zeylanicus: 49. 1737.

Roemer cited the second edition of Linnaeus' Species plantarum (1763), which has the identical description for this species as the first edition. The *Coccinia palmata* typolectotype is clearly a *Diplocyclos* species due to the globose striped fruits. Since the epithet is given by Linnaeus, it is linked to *Diplocyclos*, so *Coccinia palmata* is a synonym of *Diplocyclos palma-tus* in spite of its wide usage for *C. mackenii* since then.

Bryonopsis pedata Hassk. Catalogus Plantarum in Horto Botanico Bogoriensi cultarum alter: 189. 1844. Nom. nud.

Hasskarl cites Noroña's *Bryonia quinquefolia* and a vernacular name "aroy kalanyar beurriet". The given description of lacinate, almost pinnatifid leaves and male flowers in oblong clustered racemes does not match *C. grandis*. According to Filet (1859), the vernacular name is used in Sundanese and refers to *Bryonia* [sic!] *pedata* Hassk., two *Trichosanthes* species and *Luffa cordifolia* Bl. None of these names have been referred to *Coccinia*, so it seems unlikely that *Bryonopsis pedata* Hassk. does.

Coccinia peterii Zimm. Nom. nud. (ms. name) on R.Soleman 6046 (EA!).

This is an unpublished ms. name. The specimen, however, is *C. grandis*.

Coccinia petersii Gilg, Bot. Jahrb. 34: 356. 1904. TYPE: MOZAMBIQUE. [Zambésia Province]: Rios de Sena and Boror, without detailed locality, male and female, on dry ground, 1846, W.H.C.Peters s.n. (Holotype: B destroyed, isotype: K).

Jeffrey (1967) synonymized this species with *Eureiandra fasciculata* (Cogn.) C.Jeffrey.

Coccinia polyantha Gilg, Bot. Jahrb. 34: 356. 1904. TYPE: TANZANIA. Lindi Region: Kilwa district, near Mariwe, upon low shrub, in light, slightly wet ground pori, fl, Dec, W.Busse 512 (Syntype: B destroyed, isosyntype: EA). TYPE: TANZANIA. [South central Tanzania], Kissaki steppe ar Rufiji river, 250 m, on sandy laterite soil, fr, Nov, Götze 80 (Syntype: B destroyed).

The seeds are described as globose to subglobose, but *Coccinia* seeds are rather flat. It is therefore unlikely that this species belongs to *Coccinia*. Jeffrey (1967) synonymized this species with *Eureiandra fasciculata* (Cogn.) C.Jeffrey.

Cucumis rheedii Kostel. Allgemeine medizinisch-pharmazeutische Flora 2: 738. 1833. *Schunambuvalli* Rheede, Hortus indicus malabaricus 8: 21, t. 11 (1688). TYPE: drawing in l.c.

Cogniaux and Harms (1924) synonymized this species with *Coccinia cordifolia* (L.) Cogn., a name which Cogniaux used for *C. grandis* (L.) Voigt. However, the drawing shows 3-5-fid tendrils and small? subglobose fruits on an ebracteate panicle. This does not correspond to *Coccinia*.

Bryonia ruderalis Zipp. ex. Span. Linnaea 15: 206. 1841 nom. nud.

In L herbarium, there is a specimen determined as “*Bryonia ruderalis* Zp.” from Timor (L0587573), which is a Zippelius collection of *Coccinia grandis*. However, the name is a later homonym of *Bryonia ruderalis* Salisb. Additionally, it lacks a description in the publication, so it is a nomen nudum, too.

Cucurbita schimperiana Hochst. on specimen G.H.W.Schimper 1570. Nom. nud.

The name was used on printed labels (effective publication), which lack a proper description (hence a nom. nud.) Under this distribution number, specimens from two different shipments are included. One is taken from package “P. 16 K. no. 4”, collected on 23 Apr 1841 in Djeladjeranné (label on P specimen). The data of this label were used for C. F. F. Hochstetters printed labels. The TUB-004724 specimen bears a Schimper label from package “P. 10 D. no. 23” from “Landschaft Modat” collected in April 1839. An unnumbered

W specimen also notes this collecting site, hence the specimen might be from the same shipment. Specimens of both collections are *Coccinia grandis*.

Coccinia sericea Zimm. Nom. nud. (ms. name) on P.W.A.Zimmermann G6600 (EA!).

Zimmermann marked this specimen to be a new species, but B. Verdcourt pointed out on the specimen that Zimmermann never published it. In any case, this specimen belongs to *C. grandis*.

Coccinia stefaninii Chiov., Result. Sc. Miss. Stefan.-Paoli Somal. Ital. 1: 84 (1916). TYPE: SOMALIA. Somali Republic, Jubaland, Dintorni di El Uré, G.Paoli 1069 (Syntype: FT! 2 sheets digital image [JPS]). TYPE: SOMALIA. fra Jagdoudou e Duddumai, G.Paoli 1179 (Syntype: FT! digital image [JPS]).

This name has been transferred to the genus *Dactyliandra* by Jeffrey (1985).

Coccinia stolzii Harms, Bot. Jahrb. 57: 241. 1923. TYPE: NYASALAND [TANZANIA]. Kyimbila district, Mbaku, 600 m, fl, fr, Jun 1913, A.Stolz 2028 (Holotype: ?, isotype: BM!, G!, L!, PRE, U0074536!, W!, Z, digital image! [Z]).

Monoecious plant with several small subglobose fruits per node apply clearly to *Diplocyclos* and must therefore be synonymized as it has been done by Jeffrey (1967) to *Diplocyclos decipiens*.

Coccinia suburceolata Cogn., Symb. Antill. (Urban) 1: 450. 1900. TYPE: HAITI. Near Port-au-Prince, in Tête bois de pin [pine forest hill?], 1800 m, male, fl, Nov, L.Picarda 1498 (Holotype: BR!, isotypes: B, L, NY, S?).

This plant was found on Haiti and is therefore geographically far of the distribution range of the genus *Coccinia*. According to the protolog, the tendrils are often trifid and the fruit is spherical and apple-sized, which does not fit to any known *Coccinia* species. Urban (1921) put the specimen and thus species, amongst others, into a new genus: *Penelopeia*.

Cephalandra sylvatica A. Chev., Exploration Botanique de l'Afrique occidentale française 1: 295. 1920. nom. nud.

Specimens connected to this nomen nudum (ICBN 32.3) have been synonymized under *Physedra eglandulosa* (Hook.f.) Hutch. & Dalziel (now *Ruthalicia eglandulosa* (Hook.f.) C.Jeffrey).

Cucurbita triangulata Hochst. ex Cogn. in A.DC. & C.DC. Monogr. Phan. 3: 532. 1881. Nom. nud.

Cogniaux cites a Schimper specimen (Iter Abyss. Sect. 3 no. 1202) that was supposed to be labeled by C. F. F. Hochstetter. There are several sheets with this distribution number in Paris, but only one bears this name. The location is given by “In Semen” [Semien Mts]. The other Paris specimens with this number are from Baria Dikeno (collected on 6 Aug 1853). The specimen is a *Coccinia grandis*.

Coccinia wightii Miq. Flora van Nederlandsch Indië 1(1): 1112. 1855. Nom. nud.

Name variation of *Coccinia wightiana* M.Roem. in the index of the book.

Index to additional specimens examined

Coccinia abyssinica

Ethiopia. Amhara: L.Boulos 9250 (MO), E.Chiovenda 1304bis (FT), E.Chiovenda s.n. 1909 (FT, FT), I.Friis & J.Lawesson 5382 (K), I.Friis & J.Lawesson 5383 (K 2 sheets), G.H.W.Schimper 331 (P, P, P, P, P), G.H.W.Schimper 1049 (P, P), G.H.W.Schimper 1423 (P). Oromia: W.J.J.O.de Wilde & B.E.E.de Wilde-Duyfjes 7103 (WAG, WAG), G.Giordano 2047 (FT), P.C.M.Jansen 2065 (WAG, WAG), G.Negri 703 (FT), J.E.Siegenthaler 1644 (EA), Tadesse Ebba 250 (BR, K, P, S), E.Westphal & J.M.C.Westphal-Stevels 1552 (MO, WAG, WAG), J.J.Wieringa 5014 (WAG, WAG). SNNPR: W.Kuls 681 (FR), E.Westphal & J.M.C.Westphal-Stevels 3336 (BR, MO), E.Westphal & J.M.C.Westphal-Stevels 5530 (BR, MO). Tigray: G.Aweke & M.G.Gilbert 717 (WAG), J.J.F.E.de Wilde 7008 (WAG, WAG). Amhara or Tigray: G.H.W.Schimper 1048 (P, P, P, P, P, S), G.H.W.Schimper 1097 (P, 5 sheets). ex cult.: J.de Bruijn 1982 (WAG, WAG), N.Holstein 120 (M), N.Holstein 132 (M), C.V.Naudin s.n. 1866 (G-DC 3 sheets). s.loc.: C.Linnaeus 1153.15 (LINN, digital image [LINN]), P.A.Pourret de Figeac s.n. s.dat. (P), L.R.Quartin-Dillon & A.Petit (P), G.H.W.Schimper 1197 (P, P, P, P, P), G.H.W.Schimper 1199 (P, P, P), G.H.W.Schimper 1200 (P, P), G.H.W.Schimper s.n. Nov. (Z), s. coll. s.n. ex Herb. Drake & Herb. Richard (P), s.coll. s.n. ex Herb. Ventenat (G), s.coll. s.n. s.dat. (BM), s.coll. s.n. s.dat. (G, G), s.coll. s.n. ≤ 1862 (G-DC, G-DC), s.coll. s.n. s.dat. (G-DC, G-DC).

Coccinia adoensis var. *adoensis*

Botswana. Northwest: H.H.Curson 726 (PRE), H.H.Curson 797 (PRE), S.Venter et al. 143 (PRE). DR Congo. Katanga: H.Homblé 87 (BR, BR), F.Malaisse 6053 (BR, P), F.Malaisse

6102 (P), F.Malaisse 6729 (BR), F.Malaisse 8276 (BR), F.Malaisse 12450 (BR), F.Malaisse & E.Robbrecht 2089 (BR), W.Mullenders 1146 (BR), P.Quarré 75 (G), P.Quarré 3618 (B, BR, BR), W.Robyns 1582 (WAG), A.Schmitz 6438 (BR, WAG), W.Schwabe s.n. 15 Dec 1959 (B), de Troyer 41 (BR). Orientale: P.Bamps 124 (WAG), H.de Saeger 1287 (BR, BR, BR, BR, WAG), J.Lebrun 3166A (WAG), J.Lejoly 3368 (BR), L.Liben 192 (BR, WAG), A.Noirfalise 37 (WAG), A.Taton 128 (WAG, WAG), G.Troupin 570 (BR, WAG), G.Troupin 691 (WAG, WAG). Ethiopia. Gambela: J.W.Ash 1090 (K), I.Friis et al. 2435 (C, K), I.Friis et al. 7996 (C, K), I.Friis et al. 8154 (C), M.Jensen et al. B1/17 (C). Oromia: J.W.Ash 2004 (K), H.F.Mooney 6898 (K), W.J.J.O.de Wilde & B.E.E.de Wilde-Duyfjes 6262 (WAG, WAG). SNNPR: J.W.Ash 909 (K). unclear loc.: L.R.Quartin-Dillon & A.Petit s.n. "dernier envoi 1844" (P, P, P), L.R.Quartin-Dillon & A.Petit s.n. "Etchelicote" (P), L.R.Quartin-Dillon & A.Petit s.n. "Ouedj" (P), L.R.Quartin-Dillon & A.Petit s.n. (P), G.H.W.Schimper 332 (P). Kenya. Eastern Province: S.A.Robertson 1925 (MO). Rift Valley Province: R.A.Maas Gersteranus 4791 (L, L), E.R.Napier 1899 (K, 2 sheets), E.R.Napier 2004 (K), S.H.Padwa 290 (K), R.Polhill 400 (K, PRE, S), R.Polhill & S.Paulo 1013 (B, PRE), V.G.L.van Someren 276 (K), Y.E.Symes 283 (K), E.M.Tweedie 2478 (K). unclear loc.: E.J.Lugard & C.Lugard 542 (K), E.Skene 100 (G), E.Skene 110 (G). Malawi. Central Province: R.Natani & I.H.Patel 88 (MO), I.H.Patel et al. 1697 (MO), I.H.Patel et al. 1708 (MO), A.J.Salubeni et al. 2475 (MO). Northern Province: E.A.K.Banda 1339 (MO), I.F.LaCroix 3396 (MO), J.Pawek 6124 (MO), J.Pawek 7717 (MO), J.Pawek 10352 (MO), J.Pawek 10613 (MO), J.Pawek 13431 (MO), J.Pawek 13573 (MO), I.H.Patel 143 (G), E.Phillips 660 (MO, WAG), E.Phillips 3039 (MO, WAG, Z). Southern Province: P.C.Chirambo 99 (MO), E.S.Kathumba & E.J.Tawakali 8 (MO, PRE), I.H.Patel & W.Nachamba 1779 (MO), L.Usi & M.S.Thera 104 (MO), [J.M.?] Watt & Brandwijk 409 (PRE). unclear loc.: J.Buchanan 1368 (HBG). Mozambique. Niassa: A.F.Gomes e Sousa 1634 (COI), J.G.Pedro & J.Pedrogáo 3562 (EA). Sofala: A.Balsinhas 960 p.p. (COI). Tete: L.Macuácua 1441 (MO, WAG). Zambezia: H.G.Faulkner 248 (BR, S). Rwanda. Eastern Province: P.Bamps 2741 (BR). South Africa. Gauteng: C.M.Behr 80 (MO), K.A.Dahlstrand 1736 (W), P.Dryfhout 750 (PRE), R.P.Glen 787 (PRE), D.F.Gilfillan 206 (PRE), I.H.Hartley et al. 979 (B), F.N.Howes 7 (PRE), J.J.Lavranos 23638 (MO, WAG), R.Leendertz s.n. 18 Oct 2904 (COI), L.C.C.Liebenberg 3249 (PRE), L.C.C.Liebenberg 8854 (MO, PRE), J.P.Lotsy & W.A.Goddijn 646 (L), D.A.McCallum & C.Dehning 690 (E, MO), D.McMurtry 2478 (PRE), A.Meebold 13151 (M), H.Merxmüller 42 (M), H.Merxmüller 282 (M, W), A.D.J.Meeuse 9011 (L, PRE), A.O.D.Mogg s.n. 26 Dec 1927 (L, PRE43058), A.O.D.Mogg s.n. 8 Dec 1934 (PRE, S08-11831, S08-11835), A.O.D.Mogg 16023 (PRE), A.O.D.Mogg 23106 (PRE), A.O.D.Mogg 37667 (PRE), A.O.D.Mogg 37674 (PRE), A.Nicholas et al. 2164 (PRE), L.R.van Niekerk &

E.Wasserfall 74 (MO, PRE), A.A.Obermeyer 121 (PRE), A.A.Obermeyer 129 (PRE), L.N.Prosser s.n. 11 Nov 1948 JBG1558 (PRE), A.Rehmann 4190 (Z), A.Rehmann 4191 (Z), A.Rehmann 4353 (Z), J.E.Repton 91 (PRE), E.Retief 1280 (PRE), F.A.Rogers 25036 (Z, Z), N.van Rooyen 2184 (PRE), N.van Rooyen 2209 (PRE), N.van Rooyen 2551 (PRE), H.J.Schlieben 7801 (B, HBG), G.F.Scott-Elliot 1464 (E), C.A.Smith 1576 (PRE), L.Stent 592 (PRE), R.Story 1812 (L, M), R.Story 6516 (PRE), J.J.de Swaart s.n. Mar 1982 (PRE), E.Taat 202 (U, WAG), I.C.Verdoorn 143 (PRE), I.C.Verdoorn 569 (PRE), I.C.Verdoorn 618 (PRE), I.C.Verdoorn 642 (PRE). KwaZulu-Natal: M.Jordaan 1122 (PRE), P.Krook in Herb. Penther 2964 (W), B.J.Pienaar 766 (PRE), E.Retief 1693 (PRE), O.West 1102 (PRE), s.coll. 2411 (Z). Limpopo: H.G.Breijer s.n. Jan 1920 TRV21541 (PRE), H.G.Breijer s.n. Dec 1922 TRV24213 (PRE), L.E.Codd 2551 (PRE), L.E.Codd 7635 (PRE), L.E.Codd & R.A.Dyer 9187 (PRE), E.E.Galpin M131 (PRE), J.Gerstner 5838 (PRE), J.Gerstner 5850 (L), B.J.Huntley 1116 (PRE), N.Jacobsen 2011 (PRE), N.Jacobsen 2506 (PRE), N.Jacobsen 2618 (PRE), T.J.Jenkins s.n. Nov 1909 TRV7453 (PRE), H.A.Junod 690 (G, G, G, Z), H.A.Junod 1200 (G), B.Maguire 2770 (B), A.D.J.Meeuse 9431 (PRE), A.D.J.Meeuse 9931 (U), A.A.Obermeyer 934 (PRE), A.A.Obermeyer s.n. Dec 1930 TRV29244 (PRE), A.A.Obermeyer s.n. Nov 1931 TRV30157 (PRE), P.Raal & G.Raal 1343 (PRE), A.Rehmann 5499 (Z), A.Rehmann 6299 (Z), A.Rehmann 6300 (Z), A.Rehmann 6301 (Z, Z), A.Rehmann 6302 (Z), J.C.Scheepers 113 (M, PRE, Z), J.C.Scheepers s.n. Mar 1960 (PRE43082), J.C.Scheepers s.n. Mar 1960 - Duiwelskloof (S08-11799), H.P.van der Schijff 6355 (W), H.J.Schlieben 7581 (B, B, B, G, HBG, M), M.Stalmans 418 (PRE), M.Stalmans 448 (PRE), H.J.Thode A1704 (PRE), N.J.van Warmelo s.n. Mar 1960 (PRE43090), E.Werdermann & H.-D.Oberdieck 1733 pro parte (B), E.Werdermann & H.-D.Oberdieck 1755 (B, B). Mpumalanga: G.J.Bredenkamp 1196 (PRE), G.J.Bredenkamp 1511 (PRE), H.G.Breijer TRV22257 (PRE), H.G.Breijer TRV25225 (PRE), E.Buitendag 972 (MO, PRE), E.Buitendag 987 (PRE), L.E.Codd & B.de Winter 5159 (L, PRE), E.E.Galpin 1173 (PRE), E.E.Galpin 14641 (PRE), G.T.Hofmeyer s.n. Jan 1923 (B, COI, PRE, Z), W.E.Holt 87 (PRE), N.Jacobsen 1196 (PRE), N.Jacobsen 1465 (PRE), J.P.Kluge 345 (PRE), R.Kräusel 161 (FR, M), L.C.C.Liebenberg 2850 (PRE), J.J.Meyer 2627 (PRE), A.O.D.Mogg s.n. 2 Dec 1926 (B, COI, L), A.O.D.Mogg 30721 (MO), B.J.Pienaar 737 (PRE), R.Pott-Leendertz 5452 (PRE), E.Retief 1245 (PRE), E.Retief 1264 (PRE), F.A.Rogers 14837 (Z), F.A.Rogers 22524 (PRE, Z), F.A.Rogers 23994 (Z), F.A.Rogers 25002 (Z), H.P.van der Schijff 2410 (PRE), R.Schlechter 3843 (Z), R.Schlechter 4272 (Z), J.C.Smuts & M.C.Gillett 2496a (PRE), J.C.Smuts & M.C.Gillett 2499 (PRE), G.K.Theron 1053 (PRE), G.K.Theron 2014 (PRE), E.Williamson 123 (PRE), E.Williamson s.n. Sep 1937 (PRE43044). Northwest: J.P.H.Acocks 18740 (PRE), H.de Beer 207 (HEID), A.O.D.Mogg 16668 (PRE), A.O.D.Mogg s.n. 8 Dec 1934 (PRE, PRE43073, S), J.D.Sutton 837 (PRE), F.A.S.Turner s.n. 29 Dec 1933 (PRE43123). unclear loc.: P.Conrath 305 (Z), A.J.T.Janse 6 Jun 1907 TRV2818 (PRE), J.P.Lotsy & W.A.Goddijn 780 (L), H.P.van der Schijff 2152 (PRE), H.P.van der Schijff 3220 (PRE), R.Schlechter 3643 (Z, Z), R.Schlechter 6886 (Z). Southern Sudan. Western Equatoria: F.W.Andrews no.? (K). Sudan. West Darfur: G.E.Wickens 3607 (K). Swaziland. Hhohho: R.H.Compton 28472 (PRE), R.H.Compton 32181 (PRE), R.H.Compton 32209 (PRE). Tanzania. Arusha: G.Gobbo et al. 740 (MO), J.G.B.Newbould 5745 (EA), A.Peter 43556 (B). Dodoma: H.I.E.Hornby & R.M.Hornby 468 (EA), M.Richards & S.Arasululu 29099 (EA, K). Iringa: R.K.Brummitt et al. 18151 (K), R.E.Gereau & C.J.Kayombo 3793 (K, MO), C.J.Kayombo & D.Hearn 3490 (MO), F.M.Mbago 3299 (DSM), C.Pedersen 491/a (DSM, K), C.Pedersen 491/b (DSM), J.Procter 1686 (EA), A.C.Tallantire 901 (EA). Kagera: K.Braun 5517 (EA), A.Kadesha 5484 (NHT), R.E.S.Tanner 4903 (BR, MO), R.E.S.Tanner 5640 (K). Kigoma: S.Bidgood et al. 2859 (DSM), J.Kahurananga et al. 2645 (EA), A.Peter 39002 (B). Lindi: H.Schäfer 2005/215 (M), H.Schäfer 2005/216 (M). Manyara: S.Chuwa et al. 5236 (NHT), S.Chuwa et al. 5257 (NHT). Mbeya: S.-O.Aleljung 37 (DSM), A.Bjørnstad 1828 (DSM), A.Bjørnstad 2110 (DSM, EA), S.Bidgood 638 (DSM, NHT), S.B.Boaler 794 (BR, EA), G.P.Leedal 852 (EA), J.C.Lovett & C.J.Kayombo 3434 (MO), J.C.Lovett & C.J.Kayombo 3773 (MO), J.C.Lovett et al. 3842 (MO), J.C.Lovett et al. 3929 (MO), J.C.Lovett et al. 4011 (MO), J.C.Lovett et al. 4045 (MO), J.C.Lovett & C.J.Kayombo 3512 (MO), J.C.Lovett & C.J.Kayombo 5022 (MO), R.Wingfield 490 (DSM), R.Wingfield 490A (DSM), R.Wingfield 534 (EA, K). Morogoro: B.J.Harris & L.B.Mwasumbi 2116 (DSM, EA, MO), F.Haerdi 563/0 (BR, EA), B.J.Harris et al. DSM315 (EA), C.J.Kayombo 1769 (MO), B.Mhoro 417 (DSM), B.Mhoro 2503 (DSM), B.Mhoro 2511 (DSM), B.Mhoro 5609 (MO), B.Mhoro & Mhinzi 4462 (DSM), E.Milne-Redhead & P.Taylor 7432 (EA), A.Peter 32132 (B), A.Peter 39236 (B, B), A.Peter 56934 (B), F.Rohrer s.n. 1913 (Z, Z), R.C.Wingfield 2279 (DSM), R.C.Wingfield 2666 (DSM, EA). Rukwa: A.A.Bullock 1865 (B, S), K.Bock 239 (M), D.K. Harder 1366 (K), Hoffmann s.n. in Herb. A.Peter56661 (B), P.Leedal 3168 (DSM), H.M.Richards 16063B (K), H.M.Richards 19686 (B, K), S.Shabani 915 (EA, M). Ruvuma: J.B.Gillett 17891 (EA), S.W.G.Hubbert 2056 (EA), B.Mhoro 1749 (DSM), H.Zerny 41 (W). Singida: H.Chabwela 3982 (EA), M.M.Hammond 141 (EA), M.M.Hammond 196 (EA), P.Kuchar 23396 (MO, MO), P.Kuchar 24042 (MO), P.Kuchar 24301 (MO), P.Kuchar & C.T.Kidia 25006 (MO), P.Kuchar 25046 (MO), L.S.Licky 4539 (EA), E.Mboya et al. 554 (MO), L.Msagamasi 3728 (EA), A.Peter 33404 (B), A.Peter 33645 (B), A.Peter 33798a (B), A.Peter 33810 (B), A.Peter 33839 (B), A.Peter 45735 (B). unclear loc.: H.Meyer 1122 (JE), D.Peterson 275 (EA). Uganda. Northern: A.Angus 6012 (K), R.T.Chancellor 230

(K), A.S.Thomas 2850 (K). unclear loc.: L.C.C.Liebenberg 812 (BR). Zambia. Copperbelt: B.Leteinturier et al. 438 (BR). Lusaka: A.Angus 4266 (COI), P.Simwanda 83 (COI). Northern: M.Sanane 375 (M). Northwestern: B.Luwiika et al. 93 (MO). Southern: E.A.Robinson 5857 (B), T.Scudder 56 (PRE), C.G.Trapnell 507 (BR). unclear loc.: H.M.Richards 3664A (BR). Zimbabwe. Bulawayo: G.Norrgrann 506 (WAG). Harare: E.Emanuelsson 700 (S), R.O.B.Rutherford-Smith 217 (COI). Manicaland: H.M.Biegel 3625 (COI), N.C.Chase 7388 (COI 3 sheets, MO), G.Dehn 188 (K), G.Dehn 188a'/52 (M), G.Dehn 40258 (B, K, S), B.Goldsmith 22/62 (COI), J.F.Ngoni 31 (COI), F.R.Williams 43 (S). Mashonaland Central: J.B.Phipps 2468 (COI 2 sheets). Mashonaland East: E.Emanuelsson 703 (S). Mashonaland West: W.B.G.Jacobsen 3677A (PRE). Matabeleland North: J.E.Rushworth 1322 (COI). Matabeleland South: A.J.Norris-Rogers 513 (COI). Midlands: H.M.Biegel 1480 (MO), H.M.Biegel 1613 (COI), M.G.Bingham 937 (COI), J.P.Loveridge 563 (COI). unclear loc.: G.Dehn s.n. (M), J.Lanjouw 1141 (U), H.Wild 3677 (NY). s.loc.: W.Busse 631 (EA), W.Busse 1322 (EA), W.Schultka 262 (FR), unclear loc.: G.Lindblom s.n. Jul 1920 (S08-12157) [Kitosh people around Mt. Elgon], R.E.S.Tanner 4903 (BR, MO).

Coccinia adoensis var. *aurantiaca*
Tanzania. Dodoma: B.J.Harris & E.Shishira 6129 (DSM, EA), D.Napper 1205 (EA, K), J.L.Newman 62 (EA), A.Peter 33052A (K). Iringa: P.A.Luke & W.R.Q.Luke 9345 (EA), H.M.Richards 20987 (BR, EA, K), H.M.Richards 21065 (EA, K). unclear location: S.A.Chambers 46 (EA, K).

Coccinia adoensis var. *jeffreyana*
Tanzania. Iringa: R.Abdallah 1384 (EA, NHT), S.Bidgood 280 (MO, NHT), S.Bidgood et al. 824 (DSM), W.Carmichael 171 (EA), S.A.Chambers 40 (EA), S.A.Chambers 45 (EA), C.J.Kayombo 296 (MO), C.J.Kayombo 335 (MO), J.C.Lovett 1594 (MO, NHT), F.C.Magogo 2333 (EA, NHT), C.F.Paget-Wilkes 72 (EA, MO), C.F.Paget-Wilkes 286 (EA), R.Polhill & S.Paulo 1910A (B, BR, EA), S.A.Renvoize & R.A.Abdallah 2046 (EA), C.M.Taylor et al. 8313 (K, MO), C.M.Taylor et al. 8348 (MO). Mbeya: O.Kerfoot 1729 (EA). Singida: P.Kuchar 22631 (MO).

Coccinia barteri
Benin. Atlantique: J.-P.Esnou et al. 1740 (WAG). Cameroon. Centre: G.L.Bates 1450 (BM), R.Letouzey 9642 (P), P.Mezili 145 (P). Littoral: R.Letouzey 14927 (P, P). South Region: J.N.Asonganyi 19 (P), M.Dinklage 820 (HBG, HBG), M.Dinklage 979 (HBG), M.Dinklage

1299 (HBG, HBG), R.Letouzey 10028 (P), J.Mildbraed 5604 (HBG 2 sheets), B.Mpom in Herb.Letouzey 8417 (P, P), B.Mpom in Herb.Letouzey 8420 (P, P). Southwest Region: J.R.Jungner 39 (S), J.Nemba & P.Mambo 685 (MO, NY), D.W.Thomas 2358 (MO, P, WAG). Central African Republic. Lobaye: Équipe 2250 (G, G), R.P.Tisserant s.n. (P). D.R. Congo. Equateur: C.Couteaux 269 (L), R.Germain 1751 (S), J.Lebrun 1145 (EA). Katanga: A.Schmitz 7431 (BR). North Kivu: R.Pierlot 1909 (EA). Orientale: J.C.Bequaert 1914 (BR), D.Bolema 1091 (G), P.Gérard 3115 (EA), P.Gérard 4365 (BR, EA), W.Kesler 1034 (BR, EA), J.Lebrun 2830 (EA, WAG), A.Leonard 1053 (BR), J.Louis 2253 (BR), J.Louis 3608 (BR, EA, WAG), J.Lebrun 4129 (EA), J.Louis 10139 (EA, WAG, WAG), J.Louis 10167 (BR, EA, WAG), J.Louis 10412 (BR, BR, WAG), J.Louis 11790 (BR, EA, WAG, WAG), J.Louis 12452 (BR, BR, EA, WAG), G.Schweinfurth 3581 (G). unclear loc.: R.Devred 1390 (EA), E.Luja 67 (BR), E.Luja 70 (BR). Equatorial Guinea. Bioko norte: M.F.de Carvalho et al. 10094 (G, G). unclear: Bioko Island: M.F.de Carvalho & F.J.Fernandez Casas 3226-1 (K), G.Mann N199 (K), G.Mann N1166 (K). Ghana. Eastern: E.Achigan-Dako 07 NIA 809 (GAT, GAT, GAT, GAT). Western: E.Achigan-Dako 06 NIA 062 (GAT), E.Achigan-Dako 07 NIA 737 (GAT, GAT, GAT), E.Achigan-Dako 07 NIA 748 (GAT, GAT). Unclear loc.: J.K.Morton A4674b (K, WAG). Guinea. Kankan: E.Achigan-Dako 07 NIA 862 (GAT, GAT). Labé: J.-G.Adam 11683bis (MO). Mamou: A.Chevalier 18404 (P). Nzérékoré: E.Achigan-Dako 07 NIA 890 (GAT), A.Chevalier 20852 (P). unclear loc.: J.-G.Adam 14682 (P). Ivory Coast. Bas Sassandra: W.J.J.O.de Wilde 173 (WAG, WAG), M.T.Thijssen 123 (WAG, WAG). Lagunes: L.Aké Assi 4978 (G), J.de Koning 2827 (WAG), W.J.J.O.de Wilde 520 (WAG, WAG, Z). unclear loc.: L.Aké Assi 8209 (G). Mozambique. N.C.Chase 6593 (K), J.G.Garçia 84 (LISC). Nigeria. Cross River State: H.D.Onyeachusim & J.L.Latilo s.n. FHI54255 (BR). Sierra Leone. Koinadugu: J.-G.Adam 22326 (MO), P.Jaeger 8431 (G). Kono: J.K.Morton & D.Gledhill SL1837 (WAG, WAG), J.K.Morton & D.Gledhill SL3077 (WAG). unclear loc.: F.C.Deighton 4838 (P). Tanzania. Kigoma: S.Uehara 522 (EA, EA), B.Verdcourt 3376B (EA). Unclear location: H.A.Conrads 5001 (EA), H.A.Conrads 5012 (EA), H.A.Conrads 5303 (EA), H.A.Conrads s.n. 1 Feb 1929 - EA13303 (EA). Uganda. Western Region: T.J.Synott 603 (EA). Zimbabwe. Manicaland: T.Müller 2357 (MO). s.loc.: G.Roberty 17672 (G).

Coccinia grandiflora

Kenya. Coast province: P.R.O.Bally B13759 (EA, EA, G), H.J.Beentje et al. 879 (EA, K), D.A.Burney & L.P.Burney T331 (NY), R.B.Drummond & J.H.Hemsley 3874 (BR, EA, K), W.R.Q.Luke & S.A.Robertson 2366 (EA, K). Malawi. Central Province: R.K.Brummitt 9443 (K). Southern Province: R.K.Brummitt et al. 14855 (K). Tanzania. Arusha: V.C.Gilbert 2602

(EA), C.J.Kayombo & G.Leliyo 1306 (MO 2 sheets), G.Leliyo & W.H.Ntundu NPGRC/MSB62 (K), A.S.Mkeya & J.Laizer 982 (MO), B.Verdcourt 3649 (BR, EA, K). Iringa: W.R.Q.Luke et al. 6686 (EA, K), W.R.Q.Luke et al. 8060 (EA, K), W.R.Q.Luke et al. 10421 (EA, K). Kilimanjaro: W.J.Kindeketa 630 (MO). Lindi: W.A.Rodgers 1067 (EA). Morogoro: R.Abdallah 1016A (NHT), S.Bondine et al. 145 (EA), L.Festo et al. 2267 (EA), B.J.Harris & L.B.Mwasumbi 2668 (EA), B.J.Harris & T.Pocs 4528 (DSM, EA), B.J.Harris & T.Pocs 4605 (DSM, EA), S.J.Manktelow & U.Swenson 91214/D (K), B.Mhoro UMBCP 5 (MO), B.Mhoro UMBCP 46 (K, MO), M.A.Mwangoka et al. 3307 (MO, NHT), L.B.Mwasumbi et al. 12430 (DSM), J.H.Padwa 311 (BR, EA), S.A.Robertson 432 (EA), M.Thulin & B.Mhoro 2877 (DSM, EA, K, MO). Tanga: K.Braun 696 (EA), K.Braun 714 (EA), R.B.Drummond & J.H.Hemsley 3346 (EA, K), R.B.Drummond & J.H.Hemsley 3407 (B, K, EA, PRE, S), H.Fandey et al. TTSA/MSB79 (K), H.G.Faulkner 1490 (K), D.Fironi et al. 144 (NHT), M.Grote in A.Peter 56944 (B), C.H.S.Kabuye 198 (BR, EA, K), S.P.Kibuna 6027 (NHT), F.C.Magogo 45 (EA), M.A.Mwangoka & A.Kalage 1578 (MO, NHT), S.Paulo 816 (BR, EA), A.Peter 56472 (B, B), A.Peter 56478 (B), A.Peter 56488 (B), A.Peter 56489 (B), A.Peter 56492 (B), A.Peter 56519 (B), A.Peter 56598 (B), A.Peter 56616 (B), A.Peter 56618 (B), A.Peter 56626 (B), A.Peter 56681 (B), A.Peter 56683 (B), A.Peter 56692 (B), A.Peter 56710 (B, B, K), A.Peter 56713 (B), A.Peter 56733 (B), A.Peter 56753 (B), A.Peter 56761 (B), A.Peter 56794 (B), A.Peter 56805 (B), A.Peter 56815 (B), A.Peter 56865 (B), S.A.Renvoize & R.A.Abdallah 1571 (EA), H.Schäfer 05/302 (M), H.Schäfer 2005/396A (M), H.Schäfer 2005/396B (M), S.R.Semsei 4060 (BR, EA, K), R.E.S.Tanner 3498 (K), G.R.Williams G43 (EA, MO), P.W.A.Zimmermann G6596 (EA), P.W.A.Zimmermann G6597 (EA), P.W.A.Zimmermann G6598 (EA). ex cult.: Bot. Gart. Berlin-Dahlem s.n. Sep. 1921 (B, B), N.Holstein 11 (M, M, M), N.Holstein 114 (EA, M).

Coccinia grandis

Australia. Northern Territory: M.J.A.Barritt 1822 (DNA), R.Booth 2090 (DNA), K.Brennan 2401 (DNA), K.Brennan 2497 (DNA), N.Byrnes 2665 (CANB n.v., DNA), I.Cowie 7037 (DNA), C.Dunlop & C.Wightman 9765 (DNA), A.A.Mitchell 4900 (CANB n.v., DNA), A.A.Mitchell 5625 (CANB n.v., DNA), J.Russell-Smith & D.Lucas 5020 (DNA, DNA, DNA), R.L.Specht 771 (AD n.v., BRI n.v., CANB n.v., DNA, L, PERTH n.v.), B.M.Waterhouse 3346 (DNA). Bangladesh. Chittagong division: J.M.Cowan s.n. 10 Apr 1927 (E), J.M.Cowan 1440 (E), A.T.Gage s.n. 19 Mar 1899 (E, G). Barbados. St. Michael: E.G.B.Gooding s.n. Aug 1941 (BAR2590), N.L.H.Krauss 1182 (US), A.E.S.Mcintosh s.n. Oct 1935 (BAR2589, digital image, BAR2592, digital image). Brazil. Unclear loc.: P.Claussen s.n. s.date (G-DC). Cambodia.

Stung Treng: H.Schäfer 2010/27 (L). Cameroon. Extreme North: C.Geerling & J.Néné 4978 (WAG, WAG), R.Letouzey 7052 (WAG, WAG), W.J.J.O.de Wilde & B.E.E.de Wilde-Duyfjes 3627 (WAG), W.J.J.O.de Wilde et al. 5035 (WAG). North Region: C.Geerling & J.Néné 4839 (WAG). Chad. Chari-Baguirmi: G.Fotius 796 (P), G.Fotius 817 (P), W.J.J.O.de Wilde et al. 5197 (MO), W.J.J.O.de Wilde et al. 5152 (MO, WAG). unclear loc.: A.Chevalier 8886 (P). P.R. China. Fujien: X.Zhong 3316 (IBSC, digital image [CVH]). Guangdong: H.-G.Ye 7784 (IBSC, digital image [CVH]). Hainan: T.L.Bullock s.n. 1877 (BM), W.R.Carles s.n. 1877? E0030170 (E), H.T.Chang 4009 (IBSC, digital image [CVH]), B.Chen 313 (IBSC, digital image [CVH]), N.K.Chun (Chen Nianqu) & J.L.Zuo 44661 (IBK, digital image [CVH], IBSC, digital image [CVH], KUN n.v., MO), K.N.Fu 143 (IBSC, digital image [CVH]), K.N.Fu 5923 (IBSC, digital image [CVH]), A.Henry 8375 (IBSC, digital image [CVH], IBSC, digital image [CVH]), F.C.How 71276 (IBSC, digital image [CVH], MO), F.C.How 71350 (GH n.v., IBK, digital image [CVH], IBSC, digital image [CVH], MO), S.P.Ko 52128 (B, GH, n.v., IBK, digital image [CVH], IBK, digital image [CVH], IBSC, digital image [CVH]), S.K.Lau 264 (A, n.v., B, E, G, LBG, digital image [CVH], NTUF n.v.), S.K.Lau 5118 (A n.v., E, IBSC, digital image [CVH]), S.K.Lau 5843 (A n.v., E, IBSC, digital image [CVH]), S.K.Lau 27527 (A n.v., IBSC, digital image [CVH]), S.K.Lau (Liu Xinqi) 27577 (A n.v., IBK, digital image [CVH], MO), Z.Li & K.N.Fu 1035 (IBSC, digital image [CVH]), Z.Li & K.N.Fu 6269 (IBSC, digital image [CVH], IBSC, digital image [CVH]), H.Y.Liang 62817 (IBK, digital image [CVH], IBSC, digital image [CVH], KUN n.v., MO, S), H.Y.Liang 66577 (E, IBK, digital image [CVH], IBK, digital image [CVH], IBSC, digital image [CVH], M, MO), H.Y.Liang 66578 (IBK, digital image [CVH], IBK, digital image [CVH], IBSC, digital image [CVH], MO), H.Lin 212 (IBSC, digital image [CVH]), National Geographic Society Hainan Expedition 149 (MO), S.S.Renner et al. 2839 (M, M, M, M), C.Wang 32722 (IBSC, digital image [CVH]), C.Wang 33914 (IBK, digital image [CVH], MO), C.Wang 34826 (IBSC, digital image [CVH]), C.Wang 34870 (IBK, digital image [CVH], IBSC, digital image [CVH]), C.Wang 34892 (IBK, digital image [CVH], IBSC, digital image [CVH]), C.Wang 34977 (A n.v., IBK, digital image [CVH], IBK, digital image [CVH], IBSC, digital image [CVH]), H.Zhang 1375 (IBK, digital image [CVH]), Y.Zhong 4386 (IBSC, digital image [CVH], MO). Macau: W.Hillebrand s.n. (G), S.Y.Hu & P.But 19966 (A n.v., L), N.H.Li 66 (L). Yunnan: H.Schäfer 2005/663 (M), C.W.Wang 77723 (A n.v., IBSC, digital image [CVH], KUN, n.v., WUK n.v.), S.-S.Zhou 1218 (HITBC, digital image [CVH]). Unclear loc.: W.Hillebrand s.n. (G), Hook [J.D.Hooker?] 807 (W), G.Staunton s.n. (W), Liu Xinqi 27511 (MO), Zhong Yi 4386 (MO). R. China. Beitun district: C.-M.Wang 3415 (IBSC). DR Congo. North Kivu: H.Breyne 3867 (BR), H.Fredericq in Herb.G.F.de Witte 8586 (WAG). Orientale: P.Bamps 118 (BR, EA), D.van der Ben 1171 (BR), D.van der Ben 1314 (WAG, WAG), J.Lebrun 4054 (EA, WAG), J.Lebrun 4074 (EA, WAG). Cuba. Havana Province: C.F.Baker 3395 (G), E.L.Ekman 13598 (B). East Timor. unclear loc. R.Cinatti 123 (L). Egypt. Red Sea Governorate: G.W.Murray 3884 (K, digital image [K]). Eritrea. Central: J.J.F.E.de Wilde 4507 (WAG, WAG). Gash-Barka: A.Pappi 7395 (FT). Northern Red Sea: I.Baldrati 1731 (FT), I.Baldrati 1732 (FT), A.Pappi 3107 (FT), A.Pappi 3260 (FT), G.H.W.Schimper s.n. s.date (W), G.Schweinfurth 268 (M918), G.Schweinfurth & D.Riva 439 (G), C.J.P.Seegeler 3047 (WAG, WAG), C.J.P.Seegeler 3050 (M, WAG), J.J.F.E.de Wilde 4605 (BR, WAG, WAG). Southern Region: G.Schweinfurth & D.Riva 1007 (G, Z). unclear loc.: G.H.W.Schimper 235 "in prov. Modat" (GOET). Ethiopia. Afar: W.J.J.O.de Wilde & B.E.E.de Wilde-Duyfjes 7345 (MO, WAG, WAG). Amhara: G.H.W.Schimper 1202 (P 4 sheets). Dire Dawa: P.C.M.Jansen 7103 (WAG), E.Westphal & J.M.C.Westphal-Stevels 882 (MO, WAG), E.Westphal & J.M.C.Westphal-Stevels 1851 (MO, WAG, WAG). Gambela: P.C.M.Jansen & G.Aweke 4880 (WAG, WAG), P.C.M.Jansen 5015 (WAG). Oromia: J.W.Ash 508 (EA, K n.v.), M.Corrà JGL-3 (MO), G.Cufodontis 41 (W), P.C.M.Jansen 6885 (M, WAG), M.Thulin et al. 3729 (MO, MO), A.Vàtova 2343A (FT), E.Westphal & J.M.C.Westphal-Stevels 1546 (BR, MO, WAG). Somali: W.Burger 3253 (S), P.C.M.Jansen 3207 (WAG, WAG, WAG), E.Ruspoli & D.Riva 1123(557) (FT), Tadesse Ebba 624 (WAG, WAG), Tadesse Ebba 804 (WAG, WAG), E.Westphal & J.M.C.Westphal-Stevels 1209 (WAG), E.Westphal & J.M.C.Westphal-Stevels 1210 (WAG, WAG), J.J.F.E.de Wilde 5960 (WAG, WAG). Southern Nations, Nationalities, and People's Region: C.J.Carr & C.Matolo 867 (MO), I.Friis et al. 9582 (C), P.C.M.Jansen 3716 (WAG, WAG, WAG), P.C.M.Jansen 3782 (WAG), W.Kuls 400 (FR), E.Westphal & J.M.C.Westphal-Stevels 2926 (BR, MO, WAG, WAG), E.Westphal & J.M.C.Westphal-Stevels 3201 (WAG), E.Westphal & J.M.C.Westphal-Stevels 3218 (MO). Tigray: G.H.W.Schimper s.n. 14 Sep 1840 (TUB004723), G.H.W.Schimper s.n. Jun 1837 (TUB004726). unclear loc.: G.Cufodontis 154 (W). Fiji. Western Division: D.Koroiveibau 9693 (BISH n.v. [www.hear.org]). Guyana. Demerara-Mahaica: B.Boom et al. 8040 (U), L.J.Gillespie 2614 (CAY n.v., U, US), W.Hahn 4880 (US), S.G.Harrison et al. 1694 (U), G.S.Jenman 5129 (BM), A.C.Persaud 153 (F, digital image [F]), J.J.Pipoly 7333 (B). Essequibo Islands-West Demerara: R.Hill & C.N.Horn 27156 (US). India. Delhi: D.Ernst 16 (ZT), M.Kapoor s.n. 5 Sep 1955 (WAG), S.Kaur s.n. p.p. - Sep 1956 (G), O.Kumaar s.n. 4 Nov 1954 (U), R.Rodin 8033 (W). Haryana: J.R.Drummond 24655 (E, G), J.R.Drummond 24659 (E), J.R.Drummond 24661 (E), V.J.Nair s.n. Fl.Haryana36665 (L). Maharashtra: R.H.Dastur s.n. 1926 (Z, Z), N.Filipowicz et al. 13 (M). Uttar Pradesh: C.L.Malhotra s.n. Fl.Uttar Pradesh 50902 (L), S.K.Malhotra s.n. Fl.Uttar Pradesh 13199 (L), H.H.Rich s.n. 20 Mar 1919 (K). Tamil Nadu: J.Campbell s.n. Oct 1842 (E), A.Delessert s.n. (L0587643), D.Klein 177 (B-W, digital image [B]), C.Manoharan RHT22607 (L), A.Meebold

3189 (L), A.Mohan RHT11193 (L), J.P.Rottler s.n. (M445, M446, M450, M745), B.Schmid 330 (B), s.coll. 49 (M433). R.Wight 1122 p.p. (K000742795, digital image [K]). West Bengal: J.Sinclair 4414 (E), J.O.Voigt 424 (IBSC), G.Watt s.n. (E00303209), s.coll. 8105 (M444), s.coll. s.n. (M448), s.coll. s.n. (E00303185), s.coll. s.n. (E00303218), s.coll. s.n. Nov 1896 (G, G, M999). unclear loc.: M.Bélanger s.n. 1825-1828 (G), L.Garcin s.n. s.date (G-coll. Burman), F.B.Hamilton 2163 (E), F.B.Hamilton 2164 (E, E), F.Jenkins s.n. (M443), C.Linnaeus 1153.3 (LINN, digital image [LINN], C.Linnaeus 1153.13 (LINN, digital image [LINN]), J.P.Rottler 81 (K), Schlagintweit 12683 (G), J.L.Stewart 1250 p.p. (E00303192), J.L.Stewart 1252 (E), J.L.Stewart 1254 (E), J.L.Stewart s.n. (E00303202), G.Thomson s.n. "Nilghiri&Kurg" (G-DC, GH00251213 n.v., GOET, L, M442, S08-12122), N.Wallich 4700g (M440), N.Wallich 6700a (M437, M438), N.Wallich 6700g (M439), R.Wight 316 (E), R.Wight 1122 p.p. (K000742795, digital image [K]; L; M449; S), R.Wight 1123 (G-DC; K; K, digital image [K], digital image [K]; NY; NY), s.coll. 242 (B 10 0088655), s.coll. "Roxburgh"? s.n. (E00303175), s.coll. s.n. (E00303189), s.coll. s.n. s.date (G-coll. Burman). Indonesia. Bali: W.J.J.O.de Wilde & B.E.E.de Wilde-Duyfjes 21716 (L 2 sheets), W.J.J.O.de Wilde & B.E.E.de Wilde-Duyfjes 21717 (L), M.van Balgooy 7477 (L), M.van Balgooy 7485 (L). Central Java: S.H.Koorders 35616 (L), W. & J.van Leeuwen-Reijnvaan s.n. 21 Oct 1910 (U), C.G.G.J.van Steenis 17453 (L). Central Sulawesi: P.J.Eyma 1735 (L, U), P.J.A.Kessler et al. PK3104 (K n.v., L), S.Noerta in Herb. W.Meijer 10160 (L), Ramadhanil 202 (L). East Java: J.J.Afriastini 1220 (L), W.J.J.O.de Wilde & B.E.E.de Wilde-Duyfjes 21677 (A n.v., L 4 sheets), W.J.J.O.de Wilde & B.E.E.de Wilde-Duyfjes 21679 (L 3 sheets), W.J.J.O.de Wilde & B.E.E.de Wilde-Duyfjes 21694 (L), W.J.J.O.de Wilde & B.E.E.de Wilde-Duyfjes 21697 (L 2 sheets), J.D.Dorgelo 993 (L), M.Jacobs 4775 (L), S.H.Koorders 21125 (L), S.H.Koorders 22588 (L), H.Manadi s.n. 26 Jun 1928 (L), H.Zollinger "3789" 31 Aug 1856 (W), H.Zollinger s.n. "3789" May 1857 (W), H.Zollinger s.n. "3789" May 1858 (L0587546), H.Zollinger s.n. "16947" 31 Aug 1856 (W). East Nusa Tenggara: C.W.Kooy 746 (L), C.W.Kooy 1285 (L), A.J.G.H.Kostermans 22079 (L), J.A.McDonald & Sunaryo 4478 (A n.v., L), S.G.Saakov 163 (L), P.Schmutz 1929 (L), J.A.J.Verheijen 2280 (L), J.A.J.Verheijen 2451 (L), J.A.J.Verheijen 2622a (L), J.A.J.Verheijen 2808 (L, L), J.A.J.Verheijen 4858 (L), J.A.J.Verheijen 5415 (L, L), G.H.Weber s.n. (L0587524). Jakarta: R.C.Bakhuizen van den Brink Sr 2125 (L), A.G.de Wilde 2943 (L), J.H.G.Hallier s.n. 16 Dec 1896 (L), F.W.Junghuhn s.n. (L0587568), F.W.Junghuhn s.n. (L0587569), F.W.Junghuhn s.n. (L0587570), H.Kuhl & J.C.van Hasselt? s.n. (L0587572), W.Meijer 1801 (L). Maluku: s.coll. s.n. s.date (L0587520), s.coll. s.n. s.date (L0587521). Southeast Sulawesi: J.Elbert 2578 (L), J.Elbert 2953 (L). South Sulawesi: W.J.J.O.de Wilde & B.E.E.de Wilde-Duyfjes 21734 (L 3 sheets), W.van Leeuwen 1582 (U), G.H.Weber s.n. (L0587518). Special Region of Yogyakarta: F.W.Junghuhn s.n. Mar [1836] (L0587565), F.W.Junghuhn s.n. Mar [1836] (L0587571), F.W.Junghuhn s.n. Mar [1836] (L0587581), F.W.Junghuhn s.n. (U), F.W.Junghuhn s.n. (U). West Java: R.C.Bakhuizen van den Brink Jr 1467 (U), R.C.Bakhuizen van den Brink Jr 2052 (U), R.C.Bakhuizen van den Brink Sr 7235 (L), J.G.Boerlage s.n. 28 Oct 1888 (L0587555), P.W.Korthals? s.n. (L0587551), P.W.Korthals s.n. (L0587554), J.E.Tijsmann s.n. (L0587566), W.J.J.O.de Wilde & B.E.E.de Wilde-Duyfjes 21805 (L). West Nusa Tenggara: P.F.A.Colfs 161 (L), J.Elbert 554 (L), J.Elbert 1500 (L), J.Elbert 2061 (L), J.Elbert 2067 (L), J.Elbert 3830 (L), J.Elbert 3831A (L), M.van Balgooy 7291 (L). unclear loc.: Java: K.L.Blume s.n. s.date (L0587557), P.W.Korthals s.n. s.date (L0587552), D.Pryon s.n. s.date (G-coll. Burman), T.Sprée s.n. 1847 (L0587547), F.A.C.Waitz s.n. (L0587563), H.Zollinger "3759/8" [the 8 might be a correction of the 5, as Zollinger's numbers are species numbers and 3789 is *Momordica bicolor*, usually collected in Rogodjampi, E Java] (G, G-DC), s.coll. s.n. "ex Herbario Lugduno-Batavo" (M781), s.coll. s.n. s.date in Herb.Junghuhn (L0587553), s.coll. s.n. s.date (G), s.coll. s.n. s.date (G-coll. Burman), s.coll. s.n. s.date (L0587582), s.coll. s.n. s.date (L0587562). Timor: M.Gaudichaud 67 (G-DC, G-DC), A.Zippelius sn. s.date (L0587573), s.coll. s.n. < 1840 (U). Kenya. Coast Province: I.Friis 175 (EA), A.Gilli 363 (W), T.Kässner 269 (Z), T.Kässner 318a (Z), T.Kässner 432 (Z), P.Kirika et al. NMK 198 (K), W.R.Q.Luke et al. TPR 173 (MO), K.Medley 399 (MO), J.G.Mutangah 133 (EA), R.Polhill & S.Paulo 578 (B, S), Thomas 36 (U). Eastern Province: P.R.O.Bally B5473 (G), J.B.Gillett 12506 (S), J.B.Gillett 12517 (B, S), J.B.Gillett 13862 (B, K n.v.), F.N.Hepper & P.M.L.Jaeger 7190 (P), Z.J.Kimani 241 (BR), W.Schultka D123 (FR). Nyanza: E.Achigan-Dako 06 NIA 702 (GAT), W.Bakker s.n. 17 Nov 1968 (WAG, WAG), W.Bakker 117 (WAG, WAG), G.W.Gatheri et al. 79/71 (K), M.A.Hanid & Kiniaruh 764 (MO), B.Opiko B722 (G). Rift Valley Province: R.Harmsen 6466 (WAG), B.Mathew 6350 (K), D.N.Okebiro & D.O.Nyamongo 001/034/2001 (K), C.H.Pecler 3 (BR), J.G.Powys 175 (PRE), B.Robel 120 (EA), E.M.Tweedie 2285 (K), E.M.Tweedie 2940 (K). unclear loc.: M.G.Gilbert & M.Thulin 1724 (K). Mali. Kayes: C.S.Duvall 67 (MO). unclear loc.: L.Aké Assi 18205 (G). Myanmar. Shan States: A.Khalil s.n. 1893 (G), A.Khalil s.n. 1896 (G). Pakistan. Punjab: K.Bahadar 7688 (A n.v.), R.N.Parker s.n. 30 Aug 1924 (G). Sindh: S.ul-Abedin 5202 (G), S.ul-Abedin 5814 (E, KUH n.v.), D.Brandis 23 (HBG), S.M.H.Jafri 1464 (E, KUH n.v.), A.Raza 44 (MO), S.M.A.Kazmi 4100 (M), S.M.A.Kazmi 4141 (M). Samoa. Tuamasaga: A.Whistler 9916 (PTBG n.v.). Saudi Arabia. 'Asir Province: T.Miyazaki 990905R5 (GH). Mecca Province: D.Vesey-FitzGerald 17088/2 (BM). Ta'if or Baha Province: I.S.Collenette 1409 (K). Senegal. Dakar: E.Achigan-Dako 06 NIA 355 (GAT), E.Achigan-Dako 06 NIA 363 (GAT), J.-G.Adam 1034 (MO), J.-G.Adam 1942

(MO), J.Raynal & A.Raynal 5802 (P), J.Raynal & A.Raynal 6130 (P). Saint-Louis: J.Heudelot 528 (G), F.Malaisse & J.Matera 310 (BR, WAG), J.Valenza 252 (P). unclear loc.: J.Heudelot 528 (P, P), unreadable _28 (P) [Heudelot 528?]. Somalia. Bakool: C.Keller no.? (Z). Shabeellaha Dhexe: J.J.Lavranos & S.Carter 23282 (MO). Shabeellaha Hoose: J.B.Allen & A.A.Elmi 212 (E), I.Friis et al. 4642 (BR), O.J.Hansen 6057 (WAG), A.M.Warfá 158 (FT). unclear loc.: C.Keller 109 (Z). Sri Lanka. Central Province: J.W.Nowicke et al. 310 (MO), D.Philcox et al. 10454 (MO, PDA n.v.). Northern Province: L.Bernardi 14297 (L, Z), L.Bernardi 15308 (FDA n.v., G, MO, Z). Southern Province: F.Schmid 1190 p.p. (G), N.Wirawan 667 (L, PDA n.v.). Uva Province: D.Philcox et al. 10497 (MO, PDA n.v.), D.Philcox et al. 10551 (MO). unclear loc.: M.Allan s.n. s.date (E00303217), E.F. Deschamps s.n. (G), D.Klein 695 (B-W, digital image [B]), W.Schwabe s.n. 25 Dec 1975 (B) G.H.K.Thwaites 1609 (G-DC). Sudan. Red Sea State: G.Schweinfurth 85 (W), G.Schweinfurth 86 (BM), G.Schweinfurth Iter Centrali-Africanum 471 (G, S, plus cf. 2 more sheets: S08-12486, S08-12487). White Nile State: G.Schweinfurth 964 (G). North Kurdufan: Chursi [Khursi, 13°37’15’’N 30°25’35’’E], T.Kotschy 308 (BM, BR, E, G, G, G-DC, GOET, K, L, M, M, M782, MO, P, P, P, S, W, W, W, WAG). unclear loc.: F.P.W.Württemberg s.n. (M783). Southern Sudan. Upper Nile State: A.C.Hoyle 943 (L). Tanzania. Arusha: A.J.Jones 192/53 (EA), G.Leliyo 817 (NHT), H.M.Richards 23616 (EA, K n.v.), H.M.Richards 24218 (M), H.M.Richards 25559 (MO), H.M.Richards 26543 (K). Dar es Salaam: B.J.Harris & A.L.Mwakalasi 870 (EA, WAG), B.J.Harris 1759 (DSM, EA, WAG), B.J.Harris 2891 (DSM), B.J.Harris & T.M.Tadros 3037 (EA), B.J.Harris 3378 (EA), B.J.Harris 3389 (EA), B.J.Harris et al. 5294 (DSM), B.J.Harris & T.M.Tadros 5568 (WAG), N.Holstein 46 (M), K.H.Macauley 116 (DSM), K.H.Macaulay CVL 390 (MO), L.B.Mwasumbi 10344 (DSM), A.Peter 31463 (B), A.Peter 44565 (B), A.Peter 44605 (B), A.Peter 44834 (B). Kilimanjaro: A.E.Haarer 857 (EA), C.H.S.Kabuye & A.Evans 172 (BR, EA), A.Peter 56457 (B), M.D.I.Raya & A.N.Minjas DSM 1819 (DSM, MO), R.Wingfield et al. 3833 (DSM). Manyara: R.Abdallah 656 (NHT), H.Dingle 177 (EA), P.J.Greenway & Kirrika 10952 (EA, EA), P.J.Greenway 11030 (EA, 2 sheets, EA), H.M.Richards 21609 (MO), A.S.Vincent 169 (EA). Morogoro: N.Holstein et al. 63 (DSM, M), N.Holstein et al. 64 (DSM, M), E.Milne-Redhead & P.Taylor 7351 (EA, K n.v.), A.Peter 32517 (B), R.Wingfield 1382 (DSM). Mwanza: D.Sitoni et al. 1059 (MO), R.E.S.Tanner 537 (K), R.E.S.Tanner 1101 (NY). Pwani: Y.S.Abeid 259 (MO), M.E.Archbold 1257 (EA), O.J.Hansen 491 (DSM, EA), B.J.Harris & A.Rodgers 4014 (DSM), N.Holstein et al. 106 (M), E.Jaasund 2083 (EA), K.H.Macaulay 318 (DSM), A.Peter 31340 (B), A.Peter 31865 (B), A.Peter 56931 (B), S.A.Robertson 516 (EA), H.Schäfer 05/258 (M), H.Schäfer 05/260 (M), H.Schäfer 05/261 (M), H.Schäfer 05/262 (M), H.Schäfer 05/265 (M), H.Schäfer 05/266 (M), H.Schäfer 05/267

(L), H.Schäfer 05/268A (M), H.Schäfer 05/268B (M). Tanga: R.Abdallah 391 (NHT), R.Abdallah 1081 (NHT), M.E.Archbold 1259 (DSM, EA), Botany Students DSM1354 (DSM, EA), Botany Students DSM1435 (DSM), R.B.Drummond & J.H.Hemsley 3250 (K), R.B.Drummond & J.H.Hemsley 3405 (B, EA, K, S), R.B.Drummond & J.H.Hemsley 3522 (B, EA, K n.v., S), R.B.Drummond & J.H.Hemsley 3554 (B, EA, K n.v., S), H.G.Faulkner 1571 (B, S), H.G.Faulkner 3661 (B, EA), HG Faulkner 3886 (WAG), W.Geilinger 7 (Z), W.Geilinger 33 (Z), W.Geilinger 35 (Z), W.Geilinger 622 (Z), W.Geilinger 888 (Z), W.Geilinger 889 (Z), W.Geilinger 930 (Z), W.Geilinger 992 (Z), J.Grabner 47 (W, W), J.Grabner 55 (W), C.H.E.W.Holst 2048 (HBG), C.H.E.W.Holst 2831 (COI), H.Leippert 6421 (EA), E.S.Macha 186 (NHT), E.Milne-Redhead & P.Taylor 7295 (EA, K n.v.), Y.Mohamed s.n. 16 Feb. 1966 (EA14851), M.A.Mwangoka 1425 (MO), L.B.Mwasumbi et al. 10710 (DSM), A.Ntemi Sallu 81 (K, MO), A.Peter 40515 (B), A.Peter 40979 (B), A.Peter 40980 (B), A.Peter 54622 + drawing (B), A.Peter 56520 (B), A.Peter 56570 (B), A.Peter 56575 (B), A.Peter 56581 (B), A.Peter 56590 (B), A.Peter 56591 (B, B), A.Peter 56592 (B, B), A.Peter 56629 (B), A.Peter 56771 (B, B, B), A.Peter 56779 (B), A.Peter 56821 (B), A.Peter 56823 (B), A.Peter 56826 (B), A.Peter 56846 (B), A.Peter 56848 (B), A.Peter 56850 (B), A.Peter 56854 (B), A.Peter 56856 (B), A.Peter 56871 (B), A.Peter 56872 (B), A.Peter 56875 (B), A.Peter 56877 (B, B), A.Peter 56900 (B), A.Peter 56906 (B), A.Peter 56913 (B), A.Peter 56926 (B), H.Sandford 34 (EA), H.Schäfer 05/284 (M, M, M, M), H.Schäfer 05/392 (M), S.R.Semsei 1819 (EA), R.Soleman 6046 (EA), R.E.S.Tanner 2030 (NY), R.E.S.Tanner 2691 (NY), B.Verdcourt & P.J.Greenway 255 (EA, 2 sheets; K n.v., MO), R.Wingfield 1427 (DSM), P.W.A.Zimmermann G6600 (EA). unclear loc.:H.A.Conrads 5661 (EA, PRE), S.Paulay s.n. Aug 1887 (W), F.L.Stuhlmann 6167 (BR), F.L.Stuhlmann 964 “Zanzibar” (HBG). Thailand. Bangkok: W.Fischer 988 (FR), A.F.G.Kerr 3946A (BM), K.Larsen et al. 42017 (AAU n.v., digital image [AAU]), H.Wawra von Fernsee 301 (W), H.Wawra von Fernsee 381 (W, W), W.J.J.O.de Wilde & B.E.E.de Wilde-Duyfjes 22270 (L), W.J.J.O.de Wilde & B.E.E.de Wilde-Duyfjes 22271A (L). Chiang Mai: A.F.G.Kerr 1343 (L), J.F.Maxwell 90-858 (A n.v., L), J.A.N.Parnell et al. 95-058 (L, L). Kachanaburi: C.F.Beusekom et al. 3417 (L), K.Prueapan et al. KP-73 (L 2 sheets). Prachuap Khiri Khan: D.J.Middleton et al. 2650 (L, L), T.Shimizu et al. 7657 (L). Songkhla: J.F.Maxwell 86-50 (L). unclear loc.: K.Larsen 8262 (L). Uganda. Western Region: P.Chandler & G.L.R.Hancock 2630 (B, BR), H.W.E.Croockewit 536 (WAG), P.Geissler 6484 (G). unclear loc. [J.H.?] Schultze & [F.J.W.?] Bader 163 (B). USA. Florida: G.N.Avery 1446 (FTG n.v., digital image [virtualherbarium.org]), J.R.Burkhalter 20541 (FSU n.v., digital image [FSU]), J.Crespo 275 (USF, digital image [USF]), D.S.Decker-Walters & T.W.Walters 631 (FTG n.v., 2 sheets, digital image [virtualherbarium.org]), J.Popenoe & C.W.Campbell 2357 (FTG n.v., USF n.v., digital image [USF]), B.Richard s.n. 21 Aug 2006 (FLAS n.v., digital image [FLAS], FLAS n.v., FLAS n.v.). Hawaii: D.Herbst & S.Ishikawa 5048 (L, US n.v.), Midway Atoll: F.Starr & K.Martz 990429-18 (BISH n.v. [www.hear.org]). Virgin Islands. F.R.Fosberg 58912 (US). Wake Island. E.J.Funk Wake3 (BISH n.v. [www.hear.org]). Vietnam. Hanoi: B.Balansa 1369 (G, G, G), A.C.d'Alleizette s.n. Jul 1908 (L), A.C.d'Alleizette s.n. Apr 1909 (L0587644). Khanh hoa: A.C.d'Alleizette s.n. Jun 1909 (L0587645). Yemen: Al-Hudaydah governorate: G.Schweinfurth Arabia Felix 630 (G), G.Schweinfurth Arabia Felix 1048 (G). unclear loc.: H.von Wissmann 1723 (HBG), H.von Wissmann 2016 (HBG). ex cult.: E.F.André s.n. 6 Oct 1904 (BR993923), J.H.G.Hallier 217b (G), N.Holstein 10 (M), N.Holstein 12 (M), N.Holstein 14 (M), N.Holstein 15 (M), N.Holstein 16 (M), N.Holstein 17 (M), N.Holstein 19 (M), N.Holstein 20 (B, M), N.Holstein 21 (M), N.Holstein 22 (M), N.Holstein 23 (M), N.Holstein 24 (M, WAG), N.Holstein 25 (M), N.Holstein 26 (M), N.Holstein 27 (B, M), N.Holstein 28 (M), N.Holstein 31 (M), N.Holstein 32 (M), N.Holstein 33 (M), N.Holstein 34 (M), N.Holstein 35 (M), N.Holstein 36 (M), N.Holstein 112 (HBG, M), C.V.Naudin s.n. 1861 (G-DC, G-DC, G-DC, G-DC, G-DC, G-DC, G-DC), C.V.Naudin s.n. 1861 (G-DC, G-DC), C.V.Naudin s.n. 1864 (G-DC, G-DC, G-DC, G-DC). s.loc.: C.A.A.von Hügel 4984 (W), P.Magnus s.n. (HBG, HBG), J.P.Rottler s.n. (K), L.Sabatier s.n. 1842 (P), G.H.W.Schimper "1570" Apr 1839 (TUB004724, W), G.H.W.Schimper s.n. s.date (G-DC), T.Thomson s.n. "Ganges plain" (G-DC, GOET, L, M441, S08-12126), R.Wight s.n. (W), s.coll. 34 (E00303186), s.coll. s.n. ex Herb.Griffith late E.I.C.herbarium 2527/2 (W), s.coll. s.n. (E00303175), s.coll. s.n. [sheet 2644] (FT), s.coll. s.n. "Selampur" (M434), s.coll. s.n. (M435), s.coll. s.n. "Mexico" (M447), s.coll. s.n. s.date (S08-12492), s.coll. s.n. 28 May 1956 comm. B.F.Kaspiew (Z), s.coll. s.n. s.date ex Herb.DC (G), s.coll. s.n. s.date (G, G), "D.de Bouta" s.n. s.date (G), s.coll. s.n. s.date ex Herb.Hort.Bot.Calc. (G, G), s.coll. s.n. s.date ex Herb.Barbey-Boissier (G), s.coll. s.n. s.date (G-coll. Burman), s.coll. s.n. s.date (G-coll. Burman), s.coll. s.n. comm. T.Bernhard (L0587642), s.coll. s.n. s.date (L, L), s.coll. s.n. s.date "Santa Cruiz" in Herb. Hasskarl (L0587514), [unreadable ID] 14 Sep [18?]58 near Mintok/Mintoc? [maybe S China] (U, U), s.coll. s.n. s.date "1766 E 5138" in Herb. Reinwardt (L0587515, L0587542).

Coccinia hirtella

South Africa. Freestate: J.P.H.Acocks 23545 (PRE), J.J.Blom 319 (PRE). KwaZulu-Natal: O.M.Hilliard & B.L.Burtt 5728 (NU, digital image [ALUKA]), M.L.Jacobsz 3927 (PRE), H.A.Junod 256 (Z), H.Rudatis 1214 (E), R.Schlechter 6708 (Z), D.Styles 124 (NU, digital image [ALUKA]), E.Taat 251 (U, WAG), H.J.Thode 4724 (PRE), F.B.Wright 1429 (E), F.B.Wright 1430 (E), J.M.Wood s.n. Dec 1890 (L, Z). ex cult.: N.Holstein 18 (M), N.Holstein 29 (M), N.Holstein 30 (M), N.Holstein 122 (M, M), E.A.Mennega 4185 (U).

Coccinia mackenii

South Africa. KwaZulu-Natal: A.Abbott 226 (PRE), K.Balkwill & M.-J.Balkwill 10579 (M), A.Balsinhas 2809 (MO), T.Cooper 3133 (Z, Z), N.W.Deane 9 (PRE), J.F.Drège 4639 (P), J.F.Drège s.n. s.date (G-DC), D.Edwards 2107 (PRE), D.Edwards 2372 (PRE, PRE), D.Edwards 2375 (PRE), W.J.Gerrard 339 (W), W.J.Gerrard 1903 (W), F.J.Gerstner 4832 (PRE, PRE), W.Gueinzius 245 (W), Hitchins & C.J.Ward 6 (PRE), W.B.G.Jacobsen 1345 (PRE), K.MacDevette 1513 (PRE), Mrs van der Merwe 88 (MO), A.Rehmann 6315 (Z), A.Rehmann 8843 (BR, Z), A.Rehmann 8844 p.p. (Z), E.Retief 1609 (PRE), H.Rudatis 887 (BM), R.Schlechter 6708 (Z), R.G.Strey 9741 (PRE), E.Werdermann & H.-D.Oberdieck 1479 (B, B, PRE), E.Werdermann & H.-D.Oberdieck 1484 (B, B), J.M.Wood 1863 (K), A.E.van Wyk 2590 (PRE), A.E.van Wyk 3349 (PRE), J.Wylie s.n. (G), s.coll. 23 (S08-12154), s.coll. s.n. s.date "Port Natal" (Z). Limpopo: H.A.Junod 2639 (G, G, G, Z), A.O.D.Mogg 17427 (L, M), E.P.Nienaber EN 153 (PRE), A.E.van Wyk 5512 (PRE), s.coll. s.n. s.date "Houtbosh" (Z). Mpumalanga: J.J.Bos 1044 (LISC, M, WAG), J.P.Kluge 1836 (PRE), A.D.J.Meeuse 9993 (M, PRE), E.Retief 1334 (MO, PRE, WAG), E.Retief 1336 (PRE), H.P.van der Schijff 6063 (PRE). ex cult.: E.F.Andre s.n. received 11 Oct 1904 (BR993847), C.V.Naudin s.n. 1866 (G-DC), s.coll. s.n. 1892 (K). unclear loc.: F.Bachmann 1379 (Z), J.F.Drège s.n. s.date (P).

Coccinia microphylla

Ethiopia. Oromia: I.Friis et al. 8353 (WAG). Kenya. Coast Province: J.Belsky 320 (EA), R.B.Drummond & J.H.Hemsley 4040 (EA), R.B.Drummond & J.H.Hemsley 4087 (B, EA), V.C.Gilbert 1261 (EA), V.C.Gilbert 1301 (EA), J.B.Gillett 16482 (EA, PRE), P.Kuchar 11058 (EA), C.S.Maula 1053 (EA), G.M.Mungai & D.O.Nyakundi 93 (EA), G.M.Mungai & S.M.Rucina 384/84 (EA), B.M.Strange 89 (EA). Eastern Province: P.R.O.Bally 7733 (EA, K), F.N.Hepper & P.M.L.Jaeger 7158a p.p. (EA), F.N.Hepper & P.M.L.Jaeger 7177 (K), P.Kuchar 15190 (EA), J.G.Powys 416 (EA, 2 sheets), B.Stannard & M.G.Gilbert 840 (BM, EA, K). Northeastern Province: J.B.Gillett 21253 (EA), B.Stannard & M.G.Gilbert 934 (EA). Rift Valley Province: Bronner 332 (EA), Kiamba et al. KEFRI 112 (K), P.A.Luke & W.R.Q.Luke 7203 (EA), B.Mathew 6431 (K), B.Mathew 6799 (K), J.G.Powys 386 (EA), B.Verdcourt 3125 (BR, EA, K). unclear loc.: M.Hucks 491 (EA). Tanzania. Arusha: I.Hyde 31 (EA), B.N.N.Mbano & P.Willy 5661 (EA), A.Randrianasolo et al. 683 (MO), H.M.Richards 23605 (EA). Kilimanjaro: A.E.Haarer 774 (EA, K), W.J.Kindeketa et al. 2906 (MO), A.Peter

41282 (B), A.Peter 41568 (B), A.Peter 56550 (B), A.Peter 56552 (B), R.Wingfield 1351 (DSM), R.Wingfield 2893 (DSM). Manyara: A.S.Vincent 29 (EA), A.S.Vincent 221 (EA), H.M.Richards 24830 (K). Tanga: M.E.Archbold 1339 (DSM, EA), R.B.Drummond & J.H.Hemsley 2308 (EA), R.B.Drummond & J.H.Hemsley 2329 (BR, EA, K), R.B.Drummond & J.H.Hemsley 2977 (B, EA), A.Peter 40929 (B, B), A.Peter 40930 (B), A.Peter 40989 (B), A.Peter 56571 (B), A.Peter 56582 (B), A.Peter 56634 (B). unclear loc.: Arusha or Manyara: H.Leippert 6345 (EA), Kilimanjaro or Manyara: J.S.S.Beesley 105 (K).

Coccinia mildbraedii
Burundi. Muramvya: A.Caljoen 2101 (B, BR, U, WAG, Z), J.Lewalle 960 (MO), J.Lewalle 1488 (BR, P), J.Lewalle 1550 (BR, P), J.Lewalle 2339 (WAG), J.Lewalle 6375 (BR), M.Reekmans 1999 (EA, MO, MO), M.Reekmans 5863 (K, WAG). D.R. Congo. North Kivu: J.C.Bequaert 3646 (BR), Deru 485 (BR), P.Gille 218 (BR), R.Gutzwiller 828 (BR, WAG, WAG), J.Lebrun 4825 (BR), A.Léonard 3114 (BR, EA, WAG), J.Louis 4639 (BR, K), R.Pierlot 1974 (BR), G.B.Schaller 105 (EA), L.O.Williams 21287 (BR), G.F.de Witte 1309 (BR). South Kivu: R.Christiaensen 1248 (BR), R.Christiaensen 1284 (WAG, WAG), A.Léonard 2307 (BR, EA, K), A.Léonard 3323 (EA), R.Pierlot 2068 (WAG, WAG), R.Pierlot 2077 (BR). Rwanda. Ouest: P.Auquier 3440 (BR, P), G.Bouxin 820 (BR), A.Léonard 5082 (BR), M.Reynders 335 (BR), M.Reynders 364 (BR), B.Runyinya 972 (BR), G.Troupin 9876 (BR, EA), G.Troupin 10355 (EA), G.Troupin 11098 (EA), G.Troupin 11144 (EA), G.Troupin 11163 (EA), G.Troupin 15556 (EA). Sud: P.Auquier 3940 (BR). Tanzania. Iringa: M.E.Archbold 2593 (K), C.Frimodt-Moller et al. NG056 (K), C.J.Kayombo & N.Kyando 1906 (MO), D.J.Mabberley 626 (EA, K), R.E.Perdue & S.P.Kibuwa 11475 (BR, EA), D.Price et al. WK34 (K, MO), J.Procter & G.R.Ede 1679 (EA, EA, K). Mbeya: C.J.Kayombo 1003 (K), H.M.Richards 6803 (K), A.Stolz 2448 (BM, K). Morogoro: P.Cribb et al. s.n. 1 Feb 1967 (K), B.J.Haris et al. 6433 (DSM), N.Holstein et al. 76 (M), M.Thulin & B.Mhoro 2933 (DSM). unclear loc.: G.P.Leedal 2107 (EA). Uganda. Western Region: A.B.Katende & K.Lye K341 (MO), A.B.Katende K581 (EA, MO), D.M.Napper 666 (BR, EA), J.W.Purseglove 1236 (EA), J.W.Purseglove 2628 (EA), J.W.Purseglove 3625 (EA).

Coccinia quinqueloba
South Africa. Eastern Cape: E.E.A.Archibald 6085 (PRE), R.D.A.Bayliss 5310 (MO, WAG), H.G.Breyer s.n. Dec 1916 (L), E.Brink 348 (MO, MO, PRE), E.Brink 586 (MO, PRE, WAG), E.Brink 742 (PRE), H.H.Burrows 2468 (PRE), D.M.Comins 1373 (B, L, PRE), D.M.Comins 1374 (PRE), D.M.Comins 1376 (PRE), J.F.Drège s.n. 05 Dec 1829 (P), J.F.Drège s.n. 03

Jan 1830 (P), J.F.Drège s.n. 17 Mar 1833 (P), R.A.Dyer 1379 (PRE), H.G.Fourcade 3630 (MO), H.G.Fourcade 5773 (MO), J.A.Fraser s.n. Mar 1841 (E), P.Goldblatt & L.J.Porter 12525 (MO), M.Gron.? s.n. 1 Jul 1857 (L), A.C.Haagner Herb. P.Conrad 304 (Z), P.Herman 853 (PRE), M.Jordaan 3922 (PRE), J.P.Lotsy & W.A.Goddijn 278 (L), P.MacOwan s.n. Dec (Z, ZT), J.A.Marsh 1377 (PRE), A.Penther 2965 (W), P.B.Phillipson & A.P.Dold 4190 (MO), E.Retief 1215 (PRE), E.Retief 1218 (PRE), F.A.Rogers 3564 (Z), R.Schlechter 2744 (Z, Z), R.Schlechter 6245 (G, W), C.A.Smith 3631 (PRE), G.C.Theron 570 (PRE), H.J.Thode A2666 (PRE), A.E.van Wyk 3188 (PRE), s.coll. s.n. Mar 1839 (M298, W, Z), s.coll. s.n. BOL316 Nov 1885 (E00303251), "GH" s.n. s.date (Z). ex cult. C.V.Naudin s.n. 1863 (G-DC). C.V.Naudin s.n. 1863–1865 (G-DC, K). unclear loc.: J.Banks s.n. ex Herb.Jacq. (W), J.F.Drège s.n. 1838-1839 (P), J.F.Drège s.n. <1839 (G), J.F.Drège s.n. 1840 (G), J.F.Drège s.n. (HBG, L, L, W, W, W, W), C.F.Ecklon & C.L.P.Zeyher s.n. 1835 (GOET), C.F.Ecklon s.n. 1835 (GOET), C.F.Ecklon s.n. 1837 (W), C.F.Ecklon & C.L.P.Zeyher s.n. "1796" (G, L, M506, MO, W), P.E.Kuehne s.n. 1818-1824 (JE), H.Goett s.n. 1840 (BR9938168), C.F.H.von Ludwig s.n. ex Herb.Zeyher 543 (FR), "Q B G" s.n. (W), C.L.P.Zeyher 26? (S08-12477), C.L.P.Zeyher 543 (BM, E, K, W), C.L.P.Zeyher 579 (G-DC), s.coll. "D. 2644" ex Herb.Persoon (WAG0234165), s.coll. s.n. ex Herb.Swartz (S08-12460), s.coll. s.n. (S08-12476), s.coll. s.n. s.date ex Herb.Deless. (G), s.coll. s.n. s.date (G-DC).

Coccinia rehmannii
Angola. Namibe: R.Santos 988 (BM), Botwana. Central District: A.Allen 251 (MO, MO), D.T.Cole 1014 (PRE), O.Kerfoot 7961 (PRE), J.F.Ngoni 277 (MO), R.Story 4835 (L, PRE). Ghanzi: P.M.Burgoyne & N.Snow 5289 (MO), S.E.Chadwick 194 (PRE), S.E.Chadwick 243 (PRE), A.R.Kreulen 573 (PRE), A.R.Kreulen 603 (PRE), H.Wild 5092 (MO). Kgatlang: D.T.Cole 740 (PRE), C.C.Harbor in Herb.F.A.Rogers 6382 (Z). Kweneng: L.C.C.Liebenberg 8966a p.p. (PRE). Ngamiland: D.G.Long & D.A.H.Rae 529 (E), R.J.de Hoogh 166 (WAG). unclear loc.: P.Evans & J.Ehrens 1924 (PRE). Mocambique. Gaza: A.Balsinhas 1087 (COI), M.F.Correia 2036 (WAG), L.A.Grandvaux Barbosa & F.de Lemos 8377 (COI), L.A.Grandvaux Barbosa & F.de Lemos 8398 (COI, 2 sheets), L.A.Grandvaux Barbosa & F.de Lemos 8423 (COI), L.A.Grandvaux Barbosa & F.de Lemos 8609 (COI, 2 sheets), L.A.Grandvaux Barbosa & F.de Lemos 8611 (COI, 2 sheets), K.L.Tinley 3000 (PRE). Inhambane: A.Fernandes et al. 157 (COI), A.Fernandes et al. 160 (COI), L.A.Grandvaux Barbosa & F.de Lemos 8502 (COI 2 sheets), A.R.Moura 655 (COI). Maputo: A.Balsinhas 128 (LISC, PRE), A.Balsinhas 611 (B, PRE), M.F.de Carvalho 1004 (MO), M.F.Correia & A.Marques 706 (WAG), M.F.Correia & A.Marques 1770 (WAG, WAG), A.Fernandes et al. 1

(COI), A.Fernandes et al. 2 (COI), A.Fernandes et al. 13 (COI), A.Fernandes et al. 17 (COI 2 sheets), P.C.M.Jansen & J.de Koning 7399 (WAG), H.A.Junod 463 (BR, G, Z), F.de Lemos & A.Balsinhas 284 (BM, COI 2 sheets) , L.Macuácua 75 (COI, 3 sheets), L.Macuácua 945 (WAG), L.Marime & A.Manhica 139 (WAG), A.Marques 2662 (MO, WAG), A.O.D.Mogg 30307 (PRE), A.O.D.Mogg 31308 (PRE), A.O.D.Mogg 31508 (PRE), A.O.D.Mogg 31538 (PRE), J.J.Monteiro s.n. 1876 (G), A.R.Moura 78 (COI), A.R.Moura 1087 (COI, COI), A.Nuvunga & D.Zunguze 158 (WAG), J.E.Rodrigues et al. 187 (E, WAG), P.A.Schäfer 7055 (HEID, MO, WAG), C.da Silva et al. 139 (WAG), D.Zunguze & A.Mafumo 33 (MO). unclear loc.: F.E.Skinner & J.M.McGough s.n. 26 May 1949 (MO1619722). Namibia. Erongo: P.Craven 4598 (PRE, WAG), M.K.Dinter 7019 (B), W.Giess 13287 (M, M), R.Seydel 938 (B, B, PRE, Z, Z), R.Seydel 1278 (L), H.Walter & E.Walter 1928 (B), C.J.Ward 10856 (PRE), C.J.Ward 10872 (PRE). Hardap: P.M.Burgoyne 3481 (PRE), P.M.Burgoyne 3514 (MO, PRE), P.M.Burgoyne & N.Snow 3586 (MO), P.M.Burgoyne & N.Snow 3606 (MO), R.J.de Hoogh 5 (WAG), W.Giess et al. 5568 (M, MO), E.Klaassen et al. 19 (WAG), H.Tölken & D.S.Hardy 645 (PRE). Karas: J.P.H.Acocks 18169 (B, PRE), G.Davidse & A.Loxton 6281 (MO), M.K.Dinter 969 (Z), M.K.Dinter 971 (Z), M.K.Dinter 974 (Z), W.Giess et al. 7099 (M, MO), G.L.Maggs 103 (WAG), H.H.W.Pearson 3714 (MO), H.H.W.Pearson 4351 (MO), M.van Slageren & M.M.Strohbach 59 (WAG), H.Walter & E.Walter 2332 (B). Kgalagadi: P.T.van der Walt 5720 (PRE). Khomas: A.F.Boshoff & M.Mason 3517 (PRE); S.E.Chadwick 95 (PRE), S.E.Chadwick 96 (PRE), S.E.Chadwick 99 (PRE), S.E.Chadwick 102 (PRE), M.K.Dinter 4451 (B, B, HBG), G.Germishuizen 9282 (WAG), W.Giess jun. 195 (M), H.Leippert 4260 (H, M), H.Leippert s.n. (FT), H.Merxmüller & W.Giess 1053 (M), O.H.Volk 11085 (M), D.R.J.van Vuuren 1015 (M), H.Walter & E.Walter 117 (B, B, M). Kunene: B.de Winter & O.A.Leistner 5598 (B, M, PRE), B.J.Grobbelaar 64 (M), E.Werdermann & H.-D.Oberdieck 2321 (B, B, PRE, WAG, WAG). Omaheke: S.E.Chadwick 115 (PRE), S.E.Chadwick 116 (PRE), S.E.Chadwick 117 (PRE). Otjozondjupa: P.M.Burgoyne 3399 (WAG), P.M.Burgoyne 3431 (PRE), M.K.Dinter 5428 (HBG), M.K.Dinter 5718 (B, B), G.Germishuizen 7741 (PRE), W.Giess et al. 11131 (M, S), W.Giess 12600 (M), W.Giess 12607 (M), H.H.Kohlberg 1011 (WAG), L.C.C.Liebenberg 4854 (B), O.H.Volk 2829 (M), H.Wanntorp & H.E.Wanntorp 381 (PRE, S), G.Woortman 217 (M), G.Zschokke s.n. 1933 (Z, Z). South Africa. Gauteng: A.Balsinhas 3505 (PRE), L.E.Codd 3499 (PRE), A.O.D.Mogg 17218 (PRE), A.O.D.Mogg s.n. 13 Mar 1934 (B, Z). KwaZulu-Natal: A.A.Balsinhas 3086 (PRE), P.M.Burgoyne & N.Snow 4620 (PRE), W.J.Gerrard 1198 (W), J.Gerstner 4261 (PRE), J.B.Khosa s.n. 18 Aug 1983 (E), J.P.Kluge 2707 (PRE), M.D.S.Nel 123 (PRE), E.S.Pooley 1228 (E), J.H.Ross 2352 (PRE), J.L.Scholtz 44 (PRE), R.G.Strey 8247 (EA), R.G.Strey 9482 (K), R.G.Strey 10323 (EA, PRE), K.L.Tinley 527 (M, PRE), C.J.Ward 6863 (PRE), C.J.Ward 12250 (PRE), s.coll. s.n. s.date "Port Natal" (L). Limpopo: P.M.Burgoyne 7651 (PRE), J.E.Burrows 4829 (PRE), S.E.Chadwick 167 (PRE), L.E.Codd 2234 (PRE, Z), L.E.Codd 4616 (L), L.E.Codd 6599 (PRE), S.P.Fourie 2359 (PRE), J.Gerstner 5350 (PRE), D.S.Hardy 907 (HEID), F.van Heerden 727 (PRE), T.P.Henning 13 (PRE), T.Kässner 1338 (E), C.Khorommbi 969 (PRE), O.A.Leistner 3174 (HEID, PRE, WAG), C.Liengme 491 (PRE), B.Maguire 7858 (B), W.Marais 1105 (PRE 2 sheets), A.D.J.Meeuse 9380 (PRE), A.D.J.Meeuse 9469 (PRE, Z), A.D.J.Meeuse 9523 (L, PRE), J.J.Meyer 4(a) (PRE), J.J.Meyer 26 (PRE), N.E.Mugwedi Venda Herb.1608 (PRE), A.Rehmann 5159 (Z), I.M.Retief 320 (PRE), L.M.D.Riddles 501 (PRE), F.A.Rogers 19432a (Z), H.P.van der Schijff 4097 (PRE), E.van Hoepen 1782 (PRE), N.van Rooyen 4642 (PRE), A.E.van Wyk 2904 (PRE), A.E.van Wyk 6010 (PRE), E.Werdermann & H.-D.Oberdieck 1611 (B, B, WAG, WAG), N.Zambatis 269 (PRE). Mpumalanga: E.Buitendag 787 (PRE), E.Buitendag 788 (PRE), C.Cass CS119 (PRE), L.E.Codd 5716 (L, PRE), E.E.Galpin 755 (PRE), A.O.D.Mogg s.n. 9 Jan 1938 (B, M, PRE), E.Retief 1339 (MO, PRE), E.Retief 1255 (PRE), E.Retief 1701 (PRE), E.Retief 1702 (PRE), H.P.van der Schijff 519 (PRE), H.P.van der Schijff 807 (PRE), H.P.van der Schijff 1290 (PRE), H.P.van der Schijff 2243 (PRE), H.P.van der Schijff 2745 (PRE), N.Zambatis 1091 (PRE), N.Zambatis 1588 (PRE). Northern Cape: J.P.H.Acocks 1520 (PRE), J.P.H.Acocks 1540 (PRE), J.P.H.Acocks 1562 (PRE), J.P.H.Acocks 1911 (PRE), J.P.H.Acocks 1996 (PRE), A.E.Brueckner 1009 (M), E.Esterhuysen 2418 (PRE), G.Germishuizen 8364 (PRE), M.E.Keith 50 (PRE), N.C.Netnou 93 (PRE), O.A.Leistner 1355 (PRE), O.A.Leistner 1540 (M, PRE), O.A.Leistner 2201 (M, Z), O.A.Leistner & M.J.A.Werger 3494 (PRE), N.van Rooyen & G.J.Bredenkamp 87 (MO), W.Müller-Stoll 687 (FR). unclear loc: W.G.Barnard & A.O.D.Mogg 1045 (PRE), F.C. Botha C28 (PRE), J.Lanjouw 836a (U), J.C.Smuts s.n. (PRE43001), H.P.van der Schijff 628 (PRE), H.P.van der Schijff 4083 (PRE), N.Zambatis 327 (PRE). Swaziland. Lubombo: E.S.Kemp 514 (MO). Manzini: M.Karsten s.n. 24 Sep 1965 (PRE). Shiselweni: R.H.Compton 29432 (G, G, PRE). Zimbabwe. Manicaland: N.C.Chase 5422 (BM), P Goodier 652 (COI, COI), J.B.Phipps 20 (BR, COI), J.B.Phipps 591 (PRE). Masvingo: R.D.Kelly 553 (MO), L.C.Leach 10706 (COI 2 sheets). Matabeleland South: R.M.Davies 2283 (PRE), J.E.Rushworth 425 (COI), H.Wild 7532 (COI). unclear loc.: E.Fleck 608 (Z), E.Fleck 767 (Z), E.Fleck 772 (Z). ex cult.: N.Holstein 126 (M).

Coccinia schliebenii

Ethiopia. Oromia: J.W.Ash 3111 (K, MO, WAG), M.G.Gilbert & M.Thulin 630 (K, MO), E.Westphal & J.M.C.Westphal-Stevels 5539 (FT, WAG, WAG, WAG). SNNPR: I.Friis et al.

7066 (K), F.G.Meyer 8897 (K, P, WAG), J.J.F.E.de Wilde 5338 (K, WAG). Mozambique. Cabo Delgado: W.R.Q.Luke et al. 10048 (EA, K, NHT). Tanzania. Lindi: S.R.Semsei 636 (EA, K). Morogoro: M.Batty 1187 (K, MO), S.Bodine et al. 150 (EA, MO), S.Bodine et al. 169 (EA, MO), B.D.Burtt 59 (EA, K), N.Holstein et al. 60 (B, DSM, M, M), C.J.Kayombo 2047 (L, MO), W.J.Kindeketa et al. 2747 (MO), W.J.Kindeketa et al. 2793 (MO), W.J.Kindeketa et al. 2828 (MO), G.S.Laizer et al. 1449 (BM, MO), A.Peter 45598 (B, K), H.J.Schlieben 3827 (BM, G, Z, Z).

Coccinia senensis

Mozambique. Tete: M.F.Correia et al. 3926 (WAG), L.Menyhart 12a (Z), L.Menyhart 644a (Z, Z), L.Menyhart 927 (HBG, K, Z), A.Pereira & M.F.Correia 1950 (WAG, WAG), A.Pereira & M.F.Correia 2147 (WAG). unclear loc.: J.Kirk Cucurbitaceae 3 (K), J.Kirk Cucurbitaceae 4 (K), J.Kirk Cucurbitaceae [7?] (K), W.Schwabe s.n. 11 Nov 1963 (B), F.L.Stuhlmann 981 (BR, HBG). Tanzania. Lindi: W.Busse 2400 (EA), W.Busse 2647 (EA), H.J.Schlieben 5644 (G), H.J.Schlieben 5704 (B, HBG); H.J.Schlieben s.n. 1932 (EA). Morogoro: S.A.Robertson 499 (EA). unclear loc.: G.F.Scott Elliott 8299 (BM).

Coccinia sessilifolia var. *sessilifolia*

Botswana. Central District: D.T.Cole 1027 (PRE), J.Snyman & C.Noailles 229 (PRE). Kgatleng: C.C.Harbor 6465 (Z). North-West District: V.Roodt 357 (PRE). Southern District: D.T.Cole 1442 (PRE). Namibia. Erongo: G.Boss s.n. Dec 1935 TRV35588 (PRE), Le Roux 451 (PRE), G.Schwerdtfeger 4022 (B), R.Seydel 972 (B, B, B, L, PRE, Z, Z). Khomas: S.E.Chadwick 81 (PRE), S.E.Chadwick 87 (PRE), W.Giess jun. 262 (M, WAG), W.Giess 15300 (M), W.J.Hanekom 256 (M), H.Merxmüller & W.Giess 806 (M), G.Sassner 45 (M), R.Seydel 3829 (B, B, M, MO), O.H.Volk s.n. 2 Jan 1956 (M), H.Walter & E.Walter 117 (B, B, M), H.Walter & E.Walter 2772 (B, M). Omaheke: B.de Winter 2501 (L, M, PRE, Z), G.Germishuizen 9384 (MO), G.Germishuizen 9408 (PRE), H.J.Schlieben 10368 (B, HEID, PRE). Otjozondjupa: O.Bär s.n. Nov 1931 TRV32849 (PRE), G.Boss s.n. Dec 1935 TRV34986 (PRE), G.Boss s.n. Dec 1935 TRV34988 (PRE), G.Boss s.n. Jan 1937 TRV36458 (PRE), R.D.Bradfield 76 (PRE), P.M.Burgoyne 3342 (PRE), M.K.Dinter 5325 (B), E.Retief 1380 (PRE), E.B.W.Schoenfelder 930 (PRE), R.Story 5167 (PRE), O.H.Volk 228 (M), O.H.Volk 467 (M), O.H.Volk 2828 (M), H.Walter & E.Walter 871 (B, M), H.Walter & E.Walter 2815 (B, M), H.Walter & E.Walter 2844 (B, M), E.Werdermann & H.-D.Oberdieck 2356 (B, B, WAG), R.von Wettstein & F.von Wettstein 37 (M), R.von Wettstein & F.von Wettstein 38 (M), G.Woortman 218 (M), s.coll. s.n. 20 Oct 1939 (M), s.coll. s.n. 25 Nov 1939

(M). unclear loc.. K.Dinter 185 "Quaaiputs" [Omaheke or Otjozondjupa] (Z), E.Fleck 145 p.p. (Z), E.Fleck 577 (Z), E.Fleck 633 (Z), L.C.C.Liebenberg 4539 (B), A.Lüderitz 1a [betw. Walvis bay to Odyitambi] (Z), A.Lüderitz 133 “Hereroland” (Z), A.Rehmann s.n. "Damaraland" (Z), M.Rautanen 340 “Amboland” (Z), H.Schinz 302 “Amboland” (Z). South Africa. Free State: D.B.Muller 1134 (PRE), D.B.Muller 1176 (PRE), J.W.Pont 255 (U), J.W.Pont 1743 (U), A.Rehmann s.n. s.date "Kanonfontein" (BR, Z), C.A.Smith 3981 (PRE), L.Smook 2932 (PRE), H.J.Thode A1785 (PRE), A.E.van Wyk 154 (PRE), G.A.Welti 45 (Z, Z), Wilman TRV23828 (PRE). Gauteng: A.O.D.Mogg s.n. 13 Mar 1934 (PRE42975), S.van Wyk 505 (PRE). Limpopo: K.Balkwill & M.-J.Balkwill 4247 (B, MO), F.C.Botha C26 (PRE), Bruce & Kies 39 (PRE), S.E.Chadwick 280 (MO, PRE), L.E.Codd 2239 (L), M.E.Connell s.n. 24 May 1941 (PRE42980), E.E.Galpin 478m (PRE), E.E.Galpin 13484 (PRE, W), J.P.Lotsy & W.A.Goddijn 1027 (L), A.D.J.Meeuse 9460 (PRE), A.O.D.Mogg 23 Mar 1938 (PRE42971), E.P.Nienaber EN111 (PRE), A.A.Obermeyer et al. 91 (PRE), D.Onderstall 109 (PRE), R.Pott 4510 (PRE), P.Raal & G.Raal 952 (PRE), A.Rehmann 5161 (BR, Z), E.Retief 1298 (PRE), E.Retief 1567 (PRE), E.Retief 1595 (PRE), F.A.Rogers 2377 (PRE), F.A.Rogers 14642 (Z), F.A.Rogers 19262 (Z), F.A.Rogers 21814 (Z), H.J.Thode A1705 (PRE), J.Vahrmeijer 1366 (PRE), D.R.J.van Vuuren 1817 (EA, PRE), E.Werdermann & H.-D.Oberdieck 1613 (B, WAG, WAG), E.Werdermann & H.-D.Oberdieck 1657 (B, B), E.van Wyk & L.A.Nkuna 668 (PRE), A.E.van Wyk 5975 (PRE). Mpumalanga: G.Germishuizen 426 (PRE), E.Retief 1340 (PRE, MO, WAG), E.Retief 1341 (PRE), R.G.N.Young A533 (PRE). Northern Cape: J.P.H.Acocks & A.H.F.Hafström 1220 (PRE, S), Arnold & Musil 491 (PRE), Arnold & Musil 492 (PRE), R.Blake s.n. Mar 1920 (W), H.G.Flanagan 1429 (PRE), W.Giess 166 (M), W.J.Hanekom 2079 (PRE), O.A.Leistner 2003 (M, PRE), R.Marloth 843 (COI), W.Müller-Stoll 686 (FR), A.Rehmann 3317 (Z), s.coll. TRV19046 (PRE). Northwest: A.O.D.Mogg 8104 (PRE), R.D.A.Bayliss 3757 (Z), J.D.Carr 227 (PRE), T.J.Jenkins 11482 (PRE), O.A.Leistner 34 (PRE), A.O.D.Mogg 14575 (L, Z), A.O.D.Mogg s.n. 6 Apr 1935 (COI, L), A.J.Phelan 1113 (PRE), A.J.Phelan 1124 (Z), J.C.Scheepers 1518 (M, MO, PRE), J.G.Speedy 1/9 (PRE), B.Straschil 37 (W), B.Ubbink 618 (PRE), N.J.van der Merwe 31 (PRE). ex cult.: A.D.J.Meeuse s.n. Feb 1955 (L, PRE42997), N.Holstein 13 (M), N.Holstein 109 (M, M, M), N.Holstein 119 (B, M), N.Holstein 131 (M). s.loc.: W.J.Burchell 1998 (G-DC), W.J.Burchell 2661 (G-DC, L), s.coll. s.n. (B).

Coccinia trilobata

Kenya. Central: P.Njogu 13835 (EA). Eastern: Coilly? 24 (EA). Nairobi: P.R.O.Bally 7847 (EA), B.Bytebier 1888 (K), B.Bytebier 1949 (BR), H.Campbell 13277 (EA), P.Elias 1 (EA), J.Kahurananga 921 (EA), J.Kahurananga 3055 (K), A.B.Katende 1049 (MO), P.Kuchar 4472 (EA), P.Kuchar 4577 (EA), P.Kuchar 7758 (EA), P.Kuchar 7809 (EA), P.Kuchar 10448 (ATLA n.v., EA), D.M.Mbuvi 492 (EA, EA), F.Msajiri 19 (EA), E.R.Napier s.n. May 1934 Corydon Mus.6236 (PRE), E.R.Napier 6669 (BR, K), B.Opiko B1779 (G), C.G.Rogers 346? (BM), C.G.Rogers 470 (S), C.G.Rogers 473 (K, S, WAG, WAG), B.Verdcourt 364 (MO, PRE), B.Verdcourt & R.Polhill 3162E (EA), G.R.Williams 307 (MO, NY, PRE), G.R.Williams 323 (MO, NY). Rift Valley Province: M.G.Gilbert 5001 (K), J.Hayes & J.Timbulake 133 (EA), J.Hayes 200 (EA), O.Kerfoot 1859 (EA), O.Kerfoot 2242 (EA), O.Kerfoot 3538 (EA), O.Kerfoot 3540 (EA), O.Kerfoot 3541 (EA), O.Kerfoot 3542 (EA), O.Kerfoot 3589 (EA), P.Kuchar 4403 (EA), W.Omondi et al. KEFRI 096 (EA, K), E.Polhill 156 (EA, K), B.Verdcourt 1942 (K), B.Verdcourt & G.G.Lucas 3003 (EA, K). Tanzania. Kilimanjaro: W.J.Kindeketa 648 (MO), E.S.Macha et al. 1040 (NHT), P.W.A.Zimmermann G6599 (EA). Tanga: R.Abdallah 1041 (NHT), R.B.Drummond & J.H.Hemsley 2522 (B, EA), R.B.Drummond & J.H.Hemsley 2751 (B, EA, K), P.W.A.Zimmermann G6594 (EA). ex cult.: N.Holstein & P.Sebastian 9 (M), de Wit s.n. 29 Jun 1962 (WAG0250936, WAG0250937).

Incertae sedis

In *C. adoensis* clade: R.B.Drummond & J.H.Hemsley 3991 (B), A.Mafumo 38 (BR), L.Pauwels 5660 (BR), A.Peter 45609 (B).
In *C. barteri* clade: E.Achigan-Dako 06 NIA 006 (GAT), E.Achigan-Dako 06 NIA 056 (GAT), E.Achigan-Dako 07 NIA 721 (GAT), J.T.Baldwin 9262 (MO), F.J.Breteler et al. 8835 (MO, WAG), P.Chandler 1937 (EA), Nimba Botanical Team WD437 (WAG), P.Quarré 5396 (EA), J.Wagemans 460 (EA).
In *C. quinqueloba* clade: H.A.Junod 351 (Z).
In *C. rehmannii* clade: J.J.Bos 7904 (WAG), I.Friis et al. 8560 (K), M.Hucks 579 (EA), O.Kerfoot 2654 (EA), P.Kirika et al. 002/020/2001 (EA, K), F.G.Meyer 8912 (FT, WAG), R.Polhill & S.Paulo 962 (K), B.Verdcourt 3888 (BR, K).
Unclear position in *Coccinia*: J.Leonard 627 (BR), J.Pawek 13510 (K), A.Peter 56523 (B), R.E.S.Tanner 1422 (BR), F.White 31728 (K).

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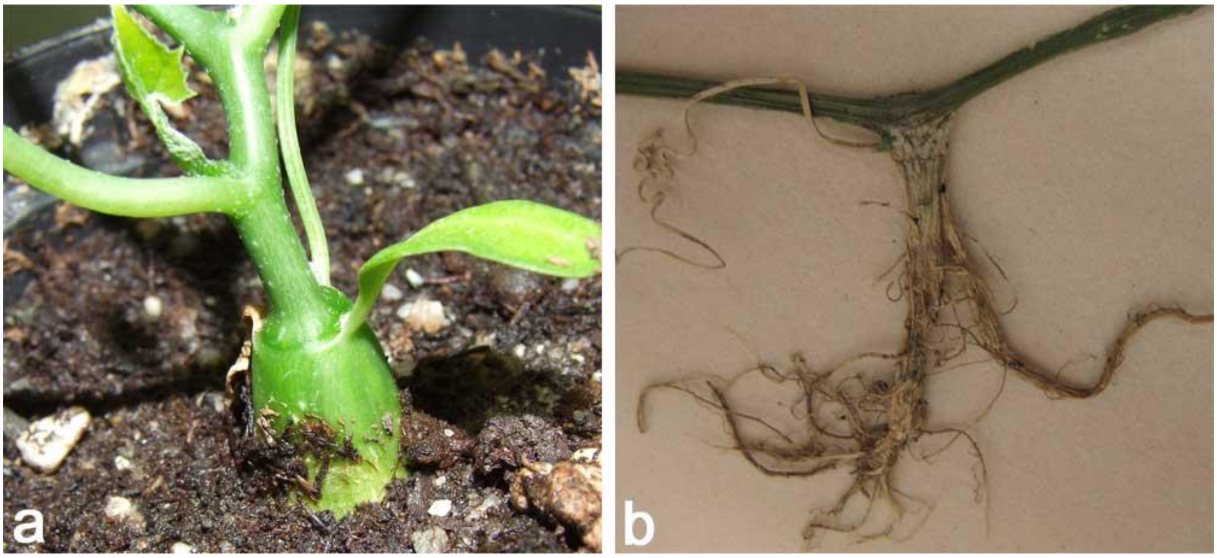

Fig. 1 a Young plant of *C. grandis*. The hypocotyl is already thickened and lignifies later-on to a tuber. The cotyledons are glabrous, have an entire margin and an obtuse apex. b Adventitious root on *C. grandis*; the beige structure to the left is a dry tendril.

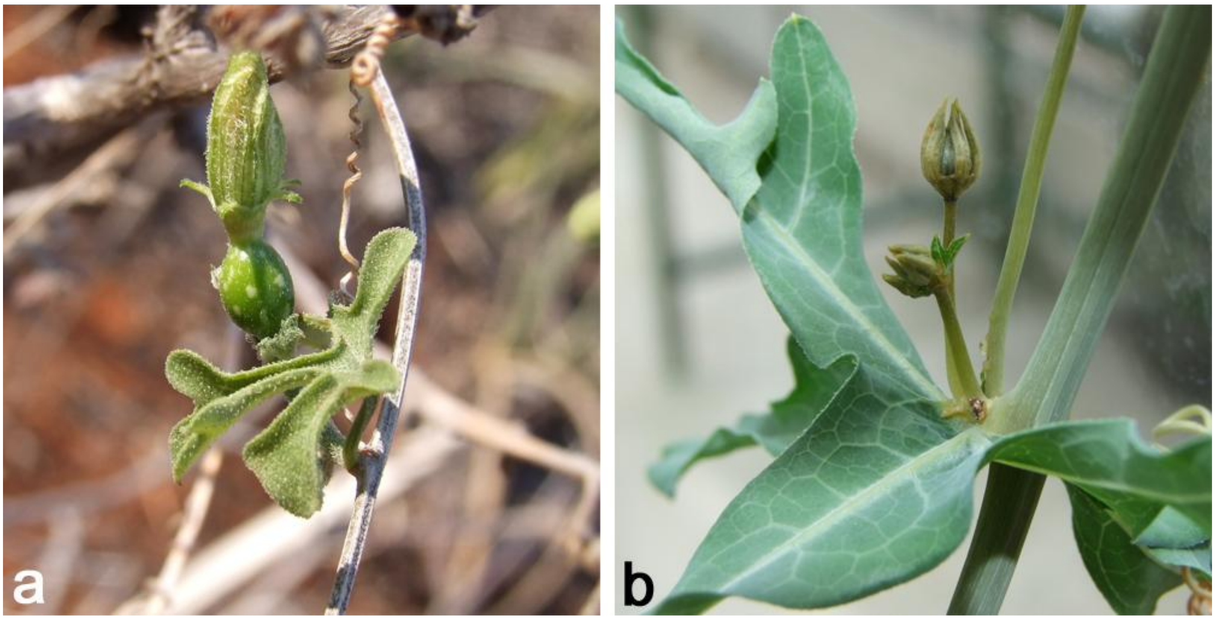

Fig. 2 a Female flower bud of *C. microphylla* (N.Holstein et al. 90); picture taken during the dry season. The stem is completely lignified, and only green short shoots are produced. b Male plant of *C. sessilifolia*. The stem is glaucous and does not lignify. Unusually, the bract is 3-lobate leaf-like.

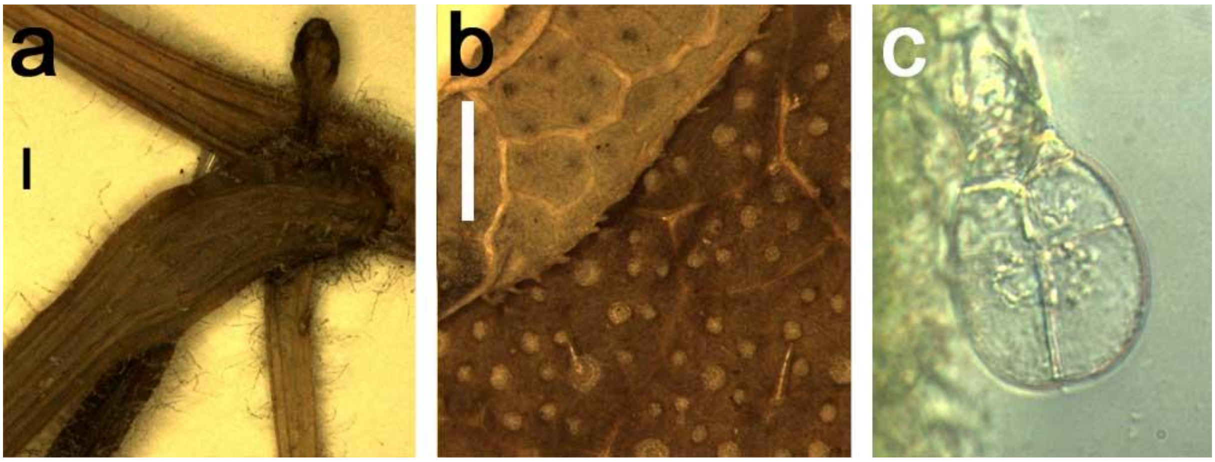

Fig. 3 Trichomes on *Coccinia* species. a Node of *C. adoensis* var. *jeffreyana* (J.C.Lovett 1197). The black bar equals 1 mm. b Part of a leaf *C. adoensis* var. *jeffreyana* (A.Stolz 504). The white bar equals 1 mm. c Glandular trichome from *C. grandis.*

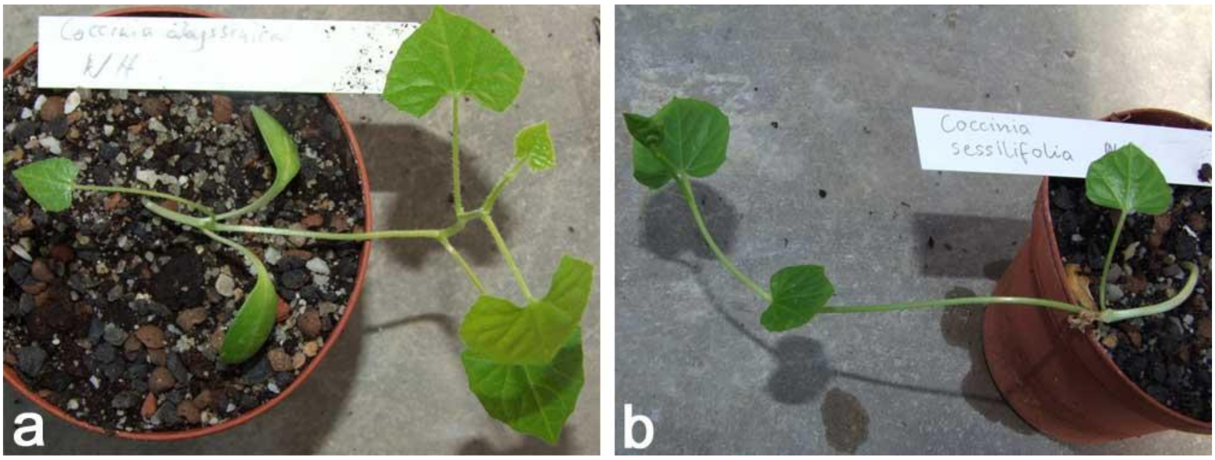

Fig. 4 a Young plant of *C. abyssinica* (N.Holstein 132). The first node is in the axil where the glabrous cotyledons split off. The first nodes lack probracts and tendrils. b Young plant of *C. sessilifolia* (N.Holstein 131). The first leaves in this species are petiolate, sessile leaves are produced later-on. The glabrous cotyledons are already dried (plant had the same age as the one in Fig. 4a).

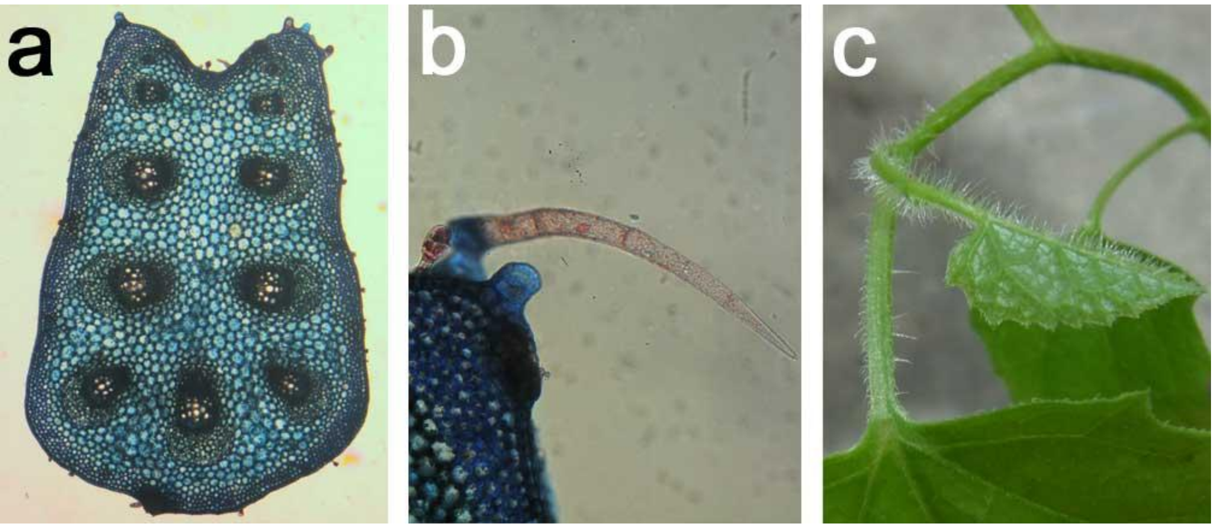

Fig. 5 a Cross-section of a petiole of *C. grandiflora*, stained with astra blue and safranine (3:2). The bicollateral vascular bundles are arranged in a U-shape. b Trichome on the adaxial ridge of a cross-section of a petiole of *C. grandiflora*. Although not visible by naked-eye, the petiole is also covered with few-celled glandular trichomes. c Young plant of *C. adoensis* var. *jeffreyana*. The trichomes are mainly occurring on the prominent veins. The adaxial side of the petiole bears smaller trichomes on the ridges, which fade into the leaf margin.

Fig. 6 a Male flower of *C. grandis* (N.Holstein 37). Apices of the petioles and calyx lobes, as well as major teeth on the leaf margin are colored in red. Minor margin teeth are inconspicuously colored. The calyx lobes in *C. grandis* are spreading in flower buds and reflexed in mature flowers. b Male plant of *C. sessilifolia*. Darkish glands (extranuptial nectaries) are commonly found at the base of a lower leaf lamina. The calyx lobes are unusually large in this specimen (cp. Fig. 2b).

Fig. 7 a The probract of *C. grandiflora* is fleshy and has a keel. The abaxial side bears many extranuptial nectaries. The structure pointing to the lower left of the picture is the tendril. b The probract of *C. trilobata* (sampled as N.Holstein & P.Sebastian 9) is spoon-shaped, papery, and without a keel.

Fig. 8 Leaky dioecy in a plant of *C. megarrhiza*. The plant was flowering male (the bud on the left) through the season, but a single female flower developed (the second flower on this node was male). The flower was receptive and produced a normal-sized fruit and normal-shaped seeds. The probract (left node) are spoon-shaped, the tendrils are purplish.

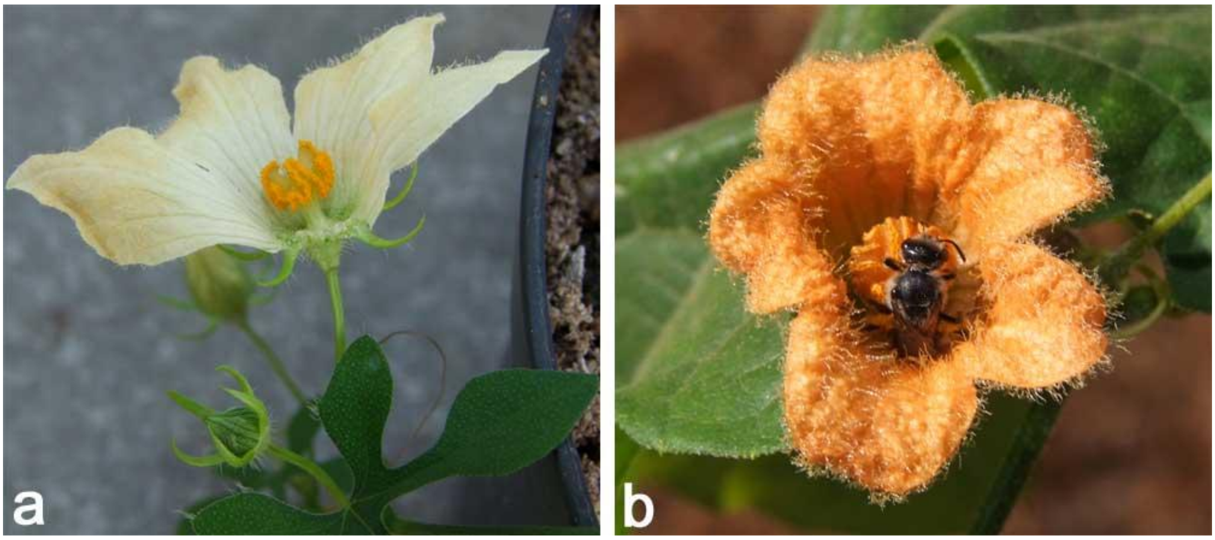

Fig. 9 a Male plant of *C. rehmannii* (N.Holstein 126). The plant was raised from seeds of a female plant with ovoid fruits (B. Jarret – pers. comm.) b Male flower of *C. adoensis* var. *aurantiaca* (N.Holstein et al. 85). The halictid bee (H.Schaefer – pers. comm.) circled around the globose anther head harvesting pollen. The scent of the flower was strong and honey melon-like.

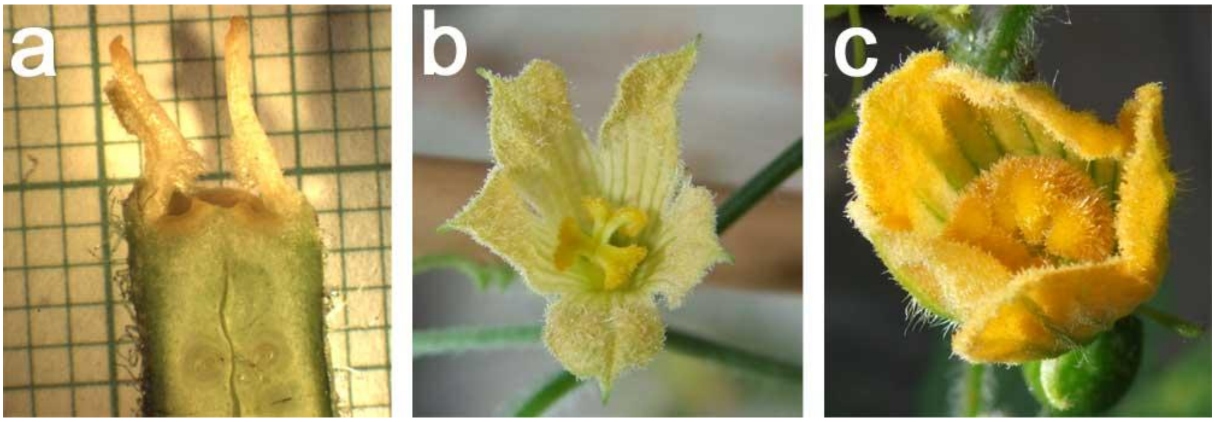

Fig. 10 a Longitudinal section of a female *C. hirtella* flower (size of the small squares is 1 mm²). Perianth and style were detached. The pollen sacs on the staminodes are highly reduced. The introrse side of the staminodes bears long trichomes that in intact flowers touched the style. b Female flower of *C. rehmannii* var. *rehmannii* with bilobate stigma arms. c Female flower of *C. megarrhiza* with bulging stigma arms.

Fig. 11 Cross-section through an ovary of *C. hirtella*. The ovules are anatrop with the micropyle facing outwards. b Cross- and longitudinal section of a *C. megarrhiza* fruit. The seeds are enclosed in a hyaline hull (aril) and seemingly attached to the periphery. c Cross-section through a fruit of *C. sessilifolia*. Note that the vascular bundles in the lower left of the picture bend in the periphery, so the placentation is not parietal, but involute.

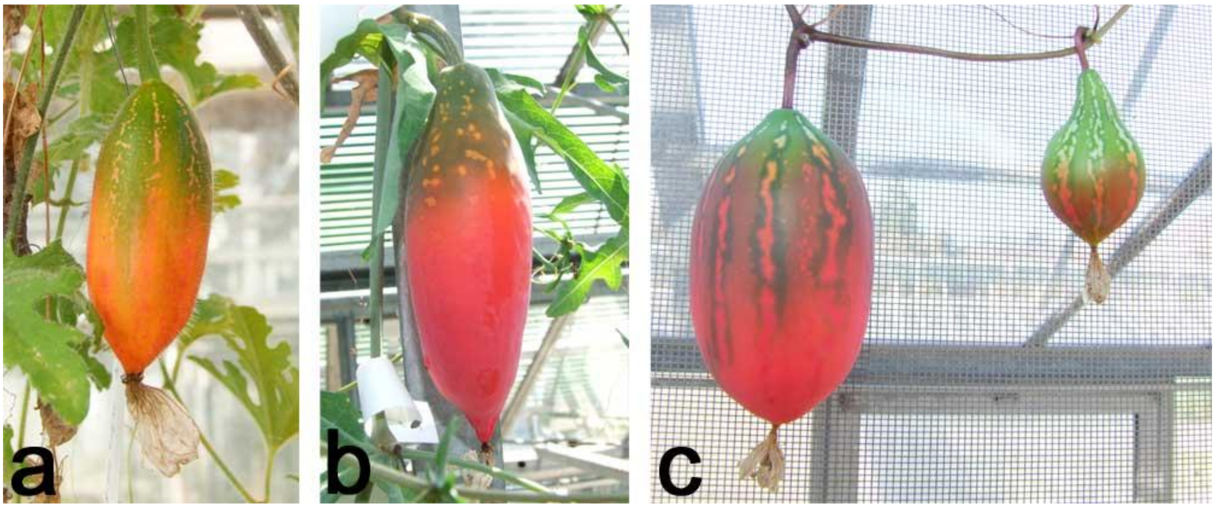

Fig. 12 a Ripening fruit of *C. hirtella*. Note the typical lobulate leaves of this species in the lower right. b Ripening fruit of *C. sessilifolia*. The fruit, like the plant, bears a waxy bloom. c Ripening fruits of *C. megarrhiza* have a dark green halo around the white longitudinal mottling. The left fruit is derived from pollination with *C. megarrhiza* pollen, whereas the smaller fruit on the right is derived from cross-pollination with *C. trilobata* (both pollinations were conducted on the same day).

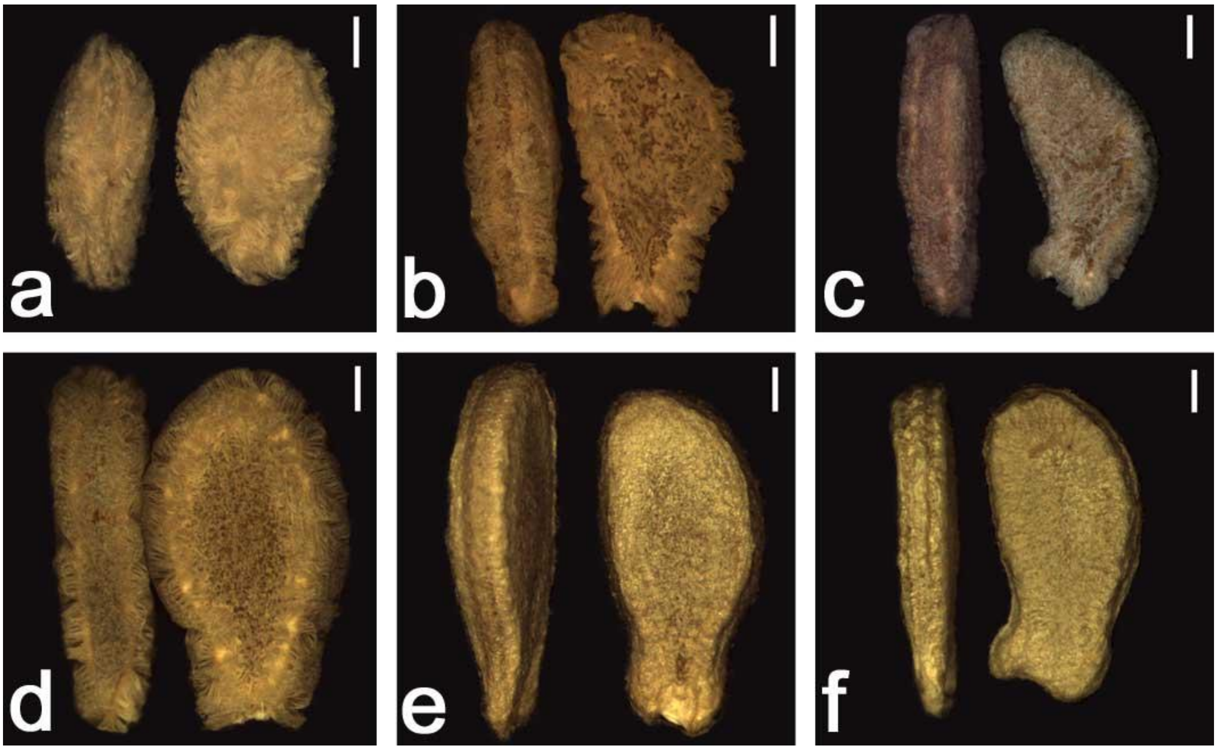

Fig. 13 Seeds of *Coccinia*. The lack of fibers in e and f are preparation artifacts due to mechanical removal of the hyaline aril. Maceration (coarse crushing of the fruit and soaking of the mass in water for 2–3 weeks; R. Brüggemann – pers. comm.) retains the surface fibers. Length of white bars equals 1 mm. a seeds of *C. adoensis* (plant derived from seed of the same fruit: N.Holstein 130). Note the lenticular face and symmetrical shape of the seed. b seeds of *C. abyssinica* (plant derived from seed of the same fruit: N.Holstein 120 and 132). c seeds of *C. trilobata*. d seeds of *C. sessilifolia* (harvested by maceration). e seeds of *C. sessilifolia* (harvested by mechanical extraction; taken from N.Holstein 119). f seeds of *C. grandis* (harvested by mechanical extraction).

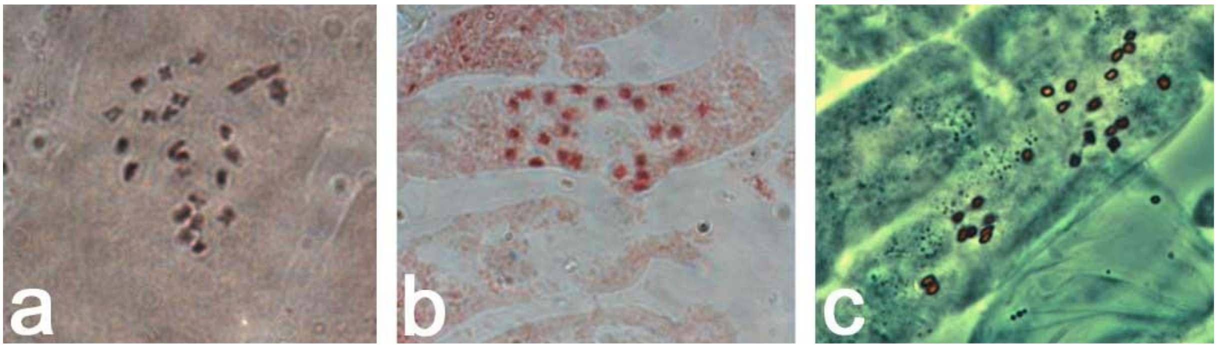

Fig. 14 Chromosome preparations fixed in 3:1 EtOH – acetic acid and stained with orcein, objective lens: 100×. a Mitotic plate of a male *C. grandis* ($2n = 22 + XY$). b Mitotic plate of a male plant of *C. hirtella* ($2n = 24$). c Phase contrast image of a mitotic plate of a male plant of *C. sessilifolia* ($2n = 24$).

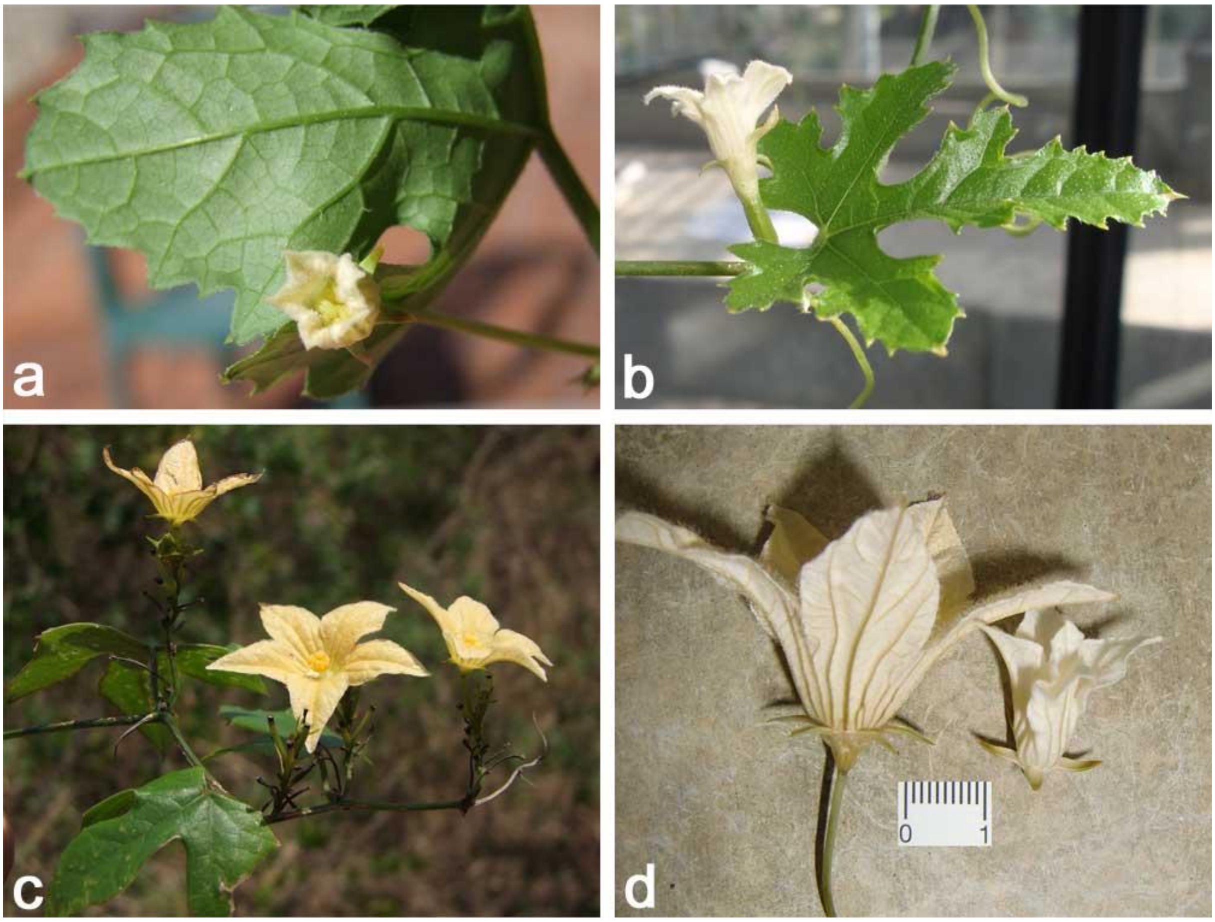

Fig. 15 Hybrids of *Coccinia* species. a *Coccinia grandis* ♀ × *C. hirtella* ♂. b *Coccinia hirtella* ♀ × *C. grandis* ♂. c *Coccinia grandis* ♀ × *C. pwaniensis* ♂; note that the pollen sacs are not open although the flower is in full bloom indicating sterility. d Left flower: male *C. sessilifolia*, right flower: male flower of *C. grandis* ♀ × *C. sessilifolia* ♂ (*C. grandis* flowers are about equally sized as *C. sessilifolia*).

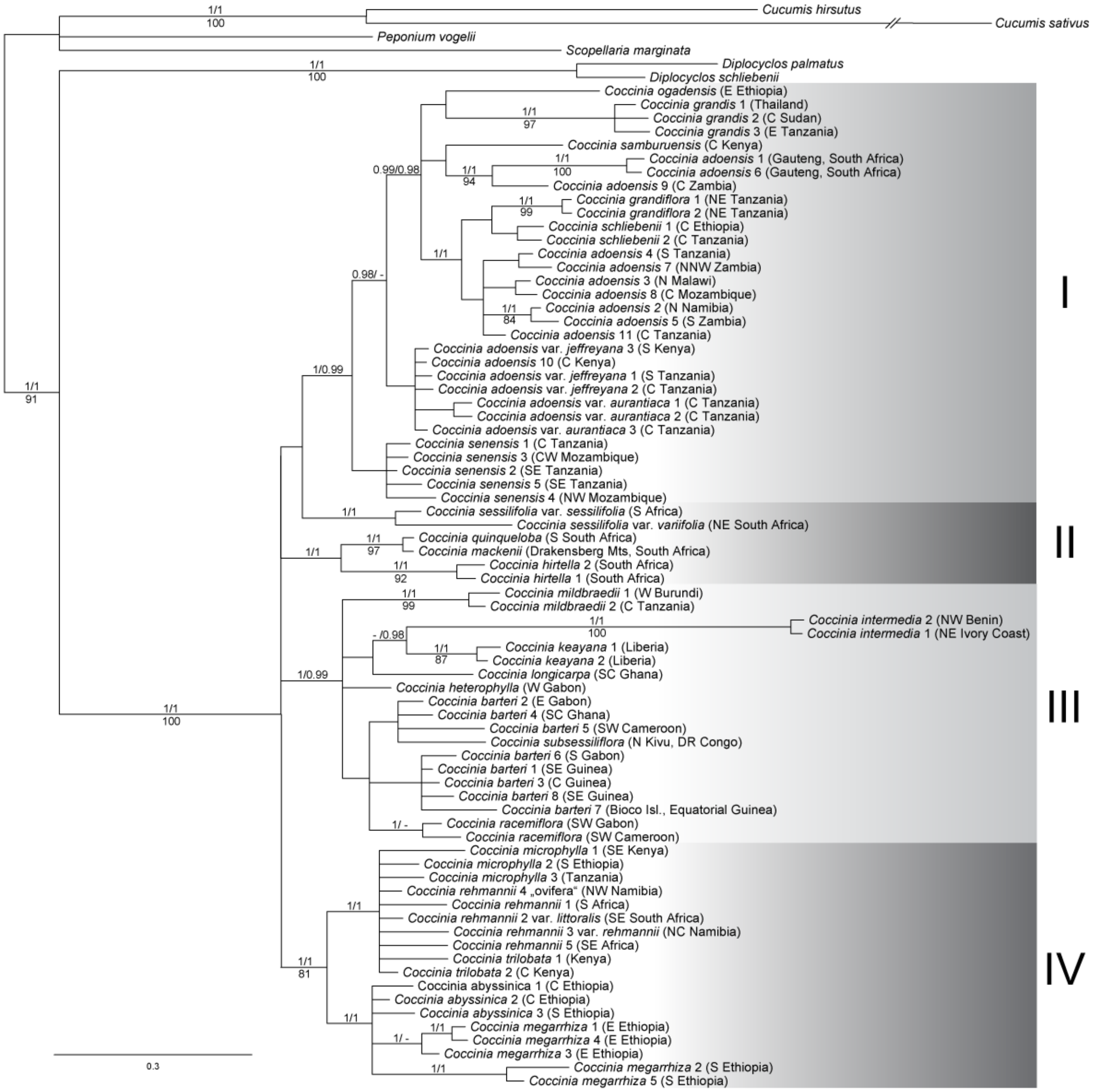

Fig. 16 Phylogenetic relationships in *Coccinia* based on five plastid DNA loci (matK, ndhF–rpl32 intergenic spacer (IS), *rpl*20–*rps*12 IS, *trn*L intron, *trn*L–*trn*F IS, *trn*S–*trn*G IS) obtained for 75 accessions from 24 species. Shown is the topology of the 50% majority rule consensus tree obtained from Bayesian analysis including simple gap coding for ingroup InDels. Numbers above the branches are posterior probability values ≥ 0.98 with values “with InDel coding” first, followed by “without InDel coding.” Numbers below the branches are bootstrap support values from ML analysis. Topologies from the different analyses were not contradictive, although some clades were not resolved without gap coding. Roman numbers indicate clades as discussed in the text: I = *C. adoensis* clade, II = *C. quinqueloba* group, III = *C. barteri* clade, and IV = *C. rehmannii* clade.

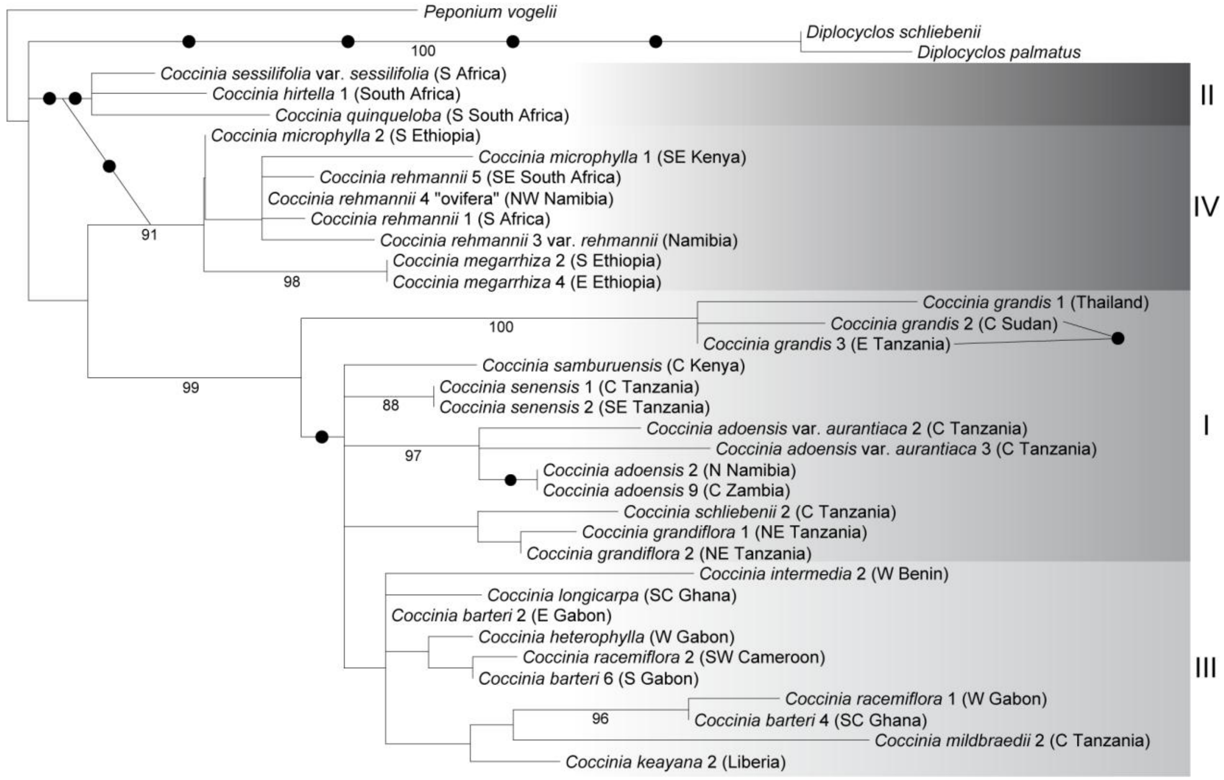

Fig. 17 Phylogenetic relationships in *Coccinia* based on 505 nucleotides of the nuclear *LEAFY*-like 2nd intron, obtained for 37 accessions from 23 species analyzed under maximum likelihood (ML) and the GTR + Γ model. Numbers below branches refer to ML bootstrap support > 80% from 1000 replicates. The dots at nodes and behind the two accessions refer to uniquely shared indels. Roman numbers indicate clades as discussed in the text: I = *C. adoensis* clade, II = *C. quinqueloba* group, III = *C. barteri* clade, and IV = *C. rehmannii* clade.

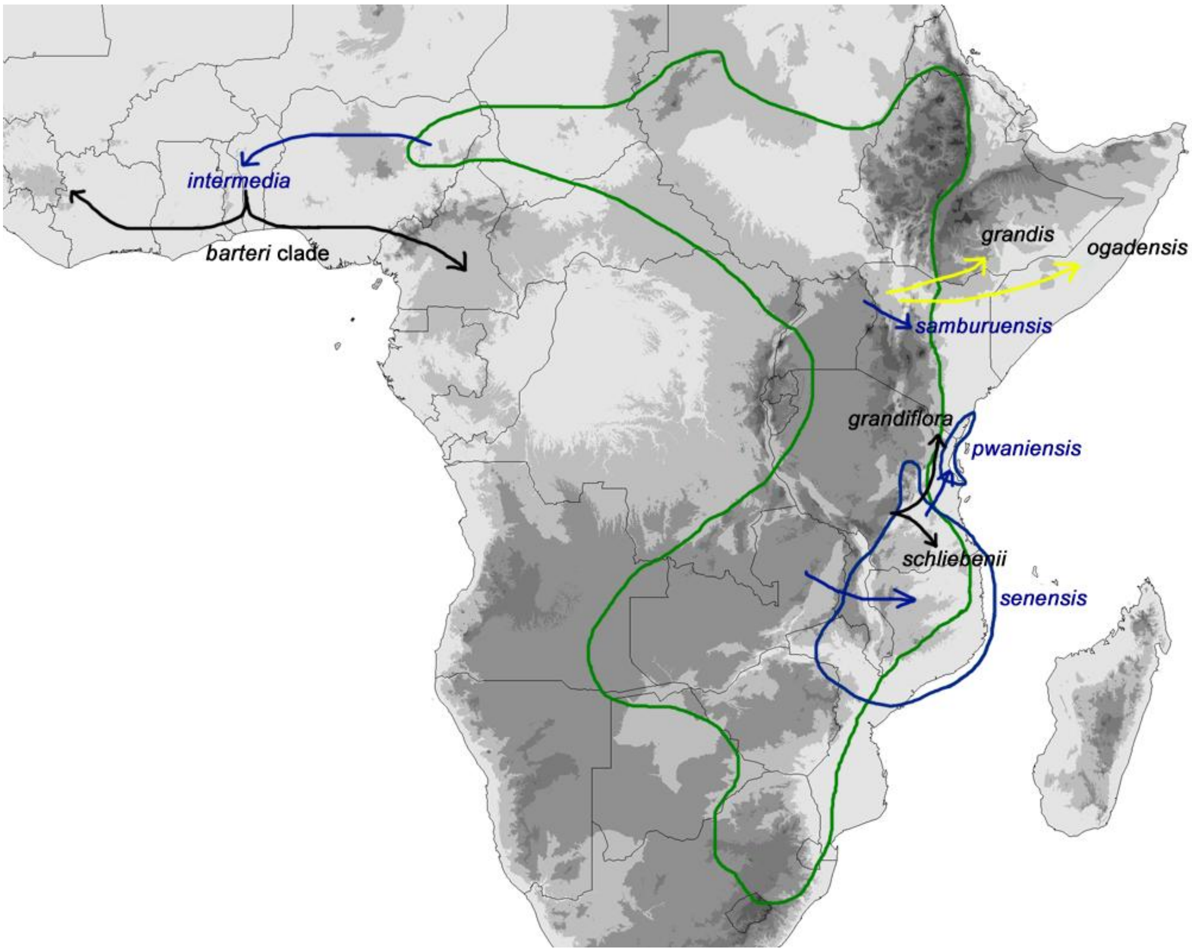

Fig. 18 Scenario of evolution in the *C. adoensis* clade. The green line surrounds today's distribution of *C. adoensis*. Blue lines surround today's distributions of *C. senensis* and *C. pwaniensis.* Blue arrows indicate peripatric speciation without shift in precipitation preference. Yellow arrows indicate speciation with shifts towards more arid habitats. Black arrows indicate speciation with shift towards more humid habitats.

Fig. 19 Reconstruction of the habitus of a female raceme of *Coccinia heterophylla* based on R.P.Klaine 414 (P).

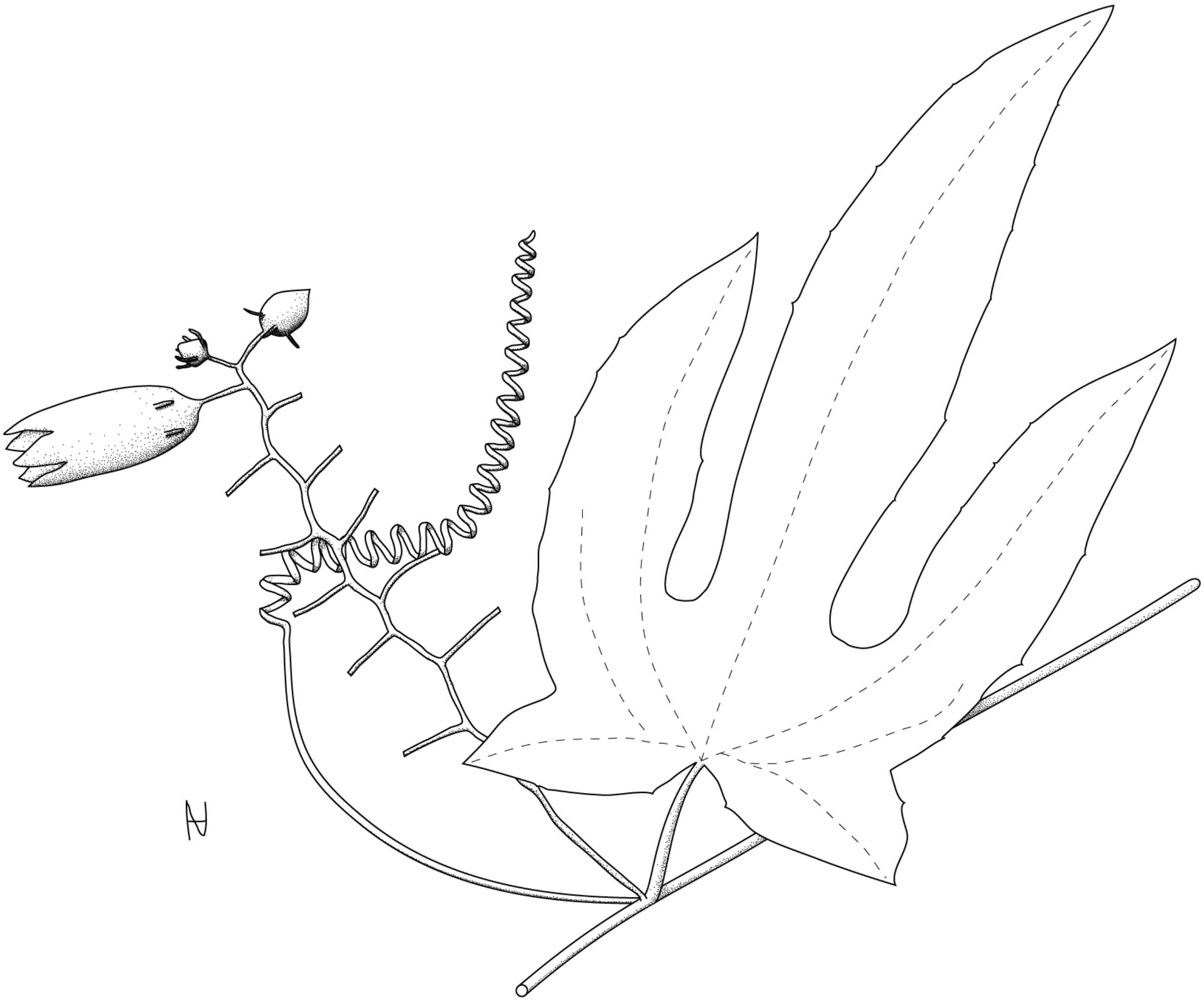

Fig. 20 Reconstruction of the habitus of *Coccinia keayana* based on C.C.H.Jongkind et al. 6542 (WAG).

Fig. 21 Male inflorescence and leaf of *C. adoensis*; picture taken from lectotype (G.H.W.Schimper 166 (P00346261)). Note the short bent trichomes, which are a good indicator for this species (but glabrous specimens or other kinds of trichomes may occur in this species, too).

Fig. 22 Inflorescence of a male *Coccinia senensis*, note the long triangulate (may be narrower in other specimens, then subulate) calyx lobes; picture taken from neotype (H.J.Schlieben 5259 (M)). Black bar equals 1 cm.

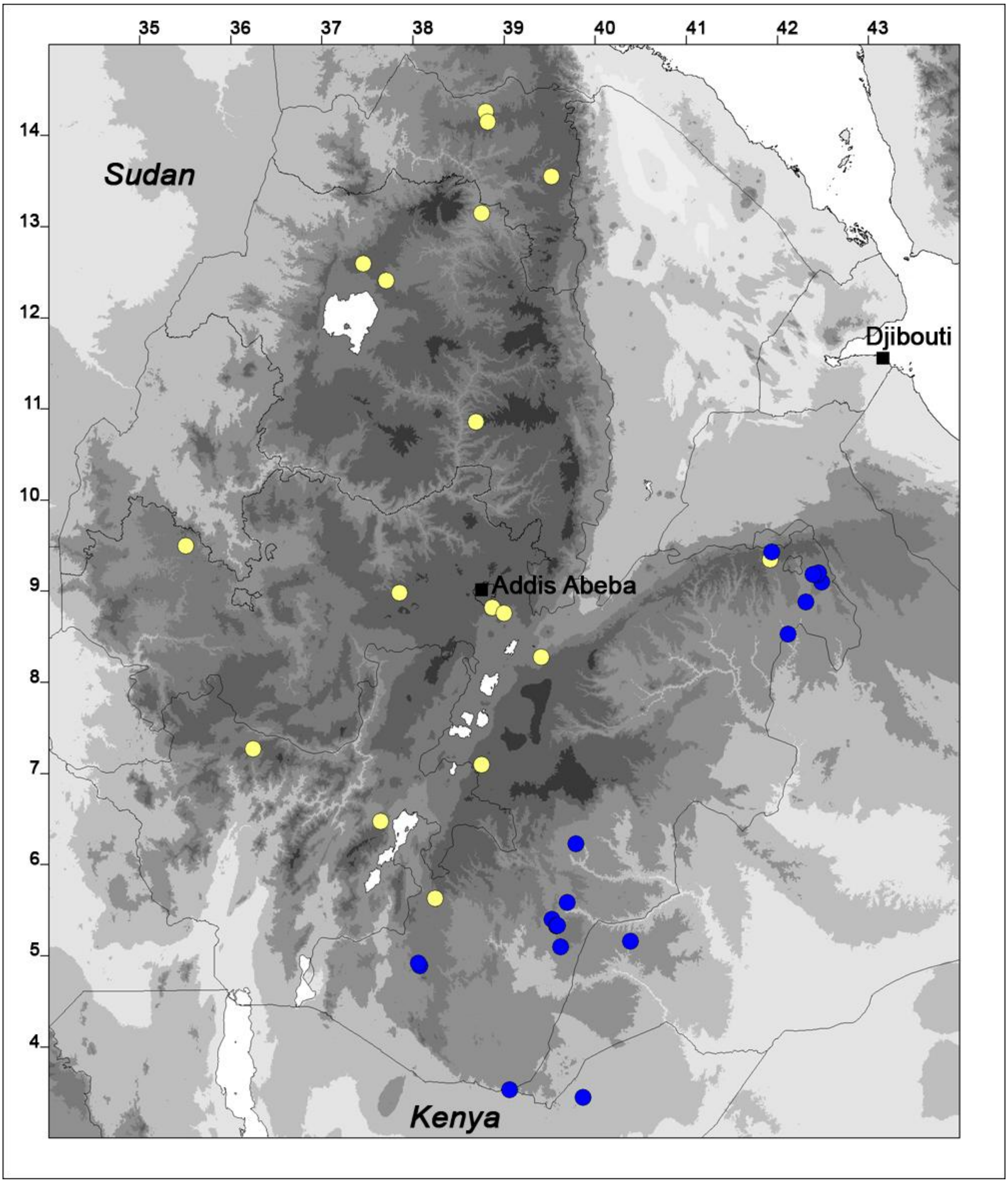

Fig. 23 Distribution map of *C. abyssinica* (pale yellow dots; based on 17 specimens) and *C. megarrhiza* (blue dots; based on 19 specimens). For Ethiopia the borders of the regions are given.

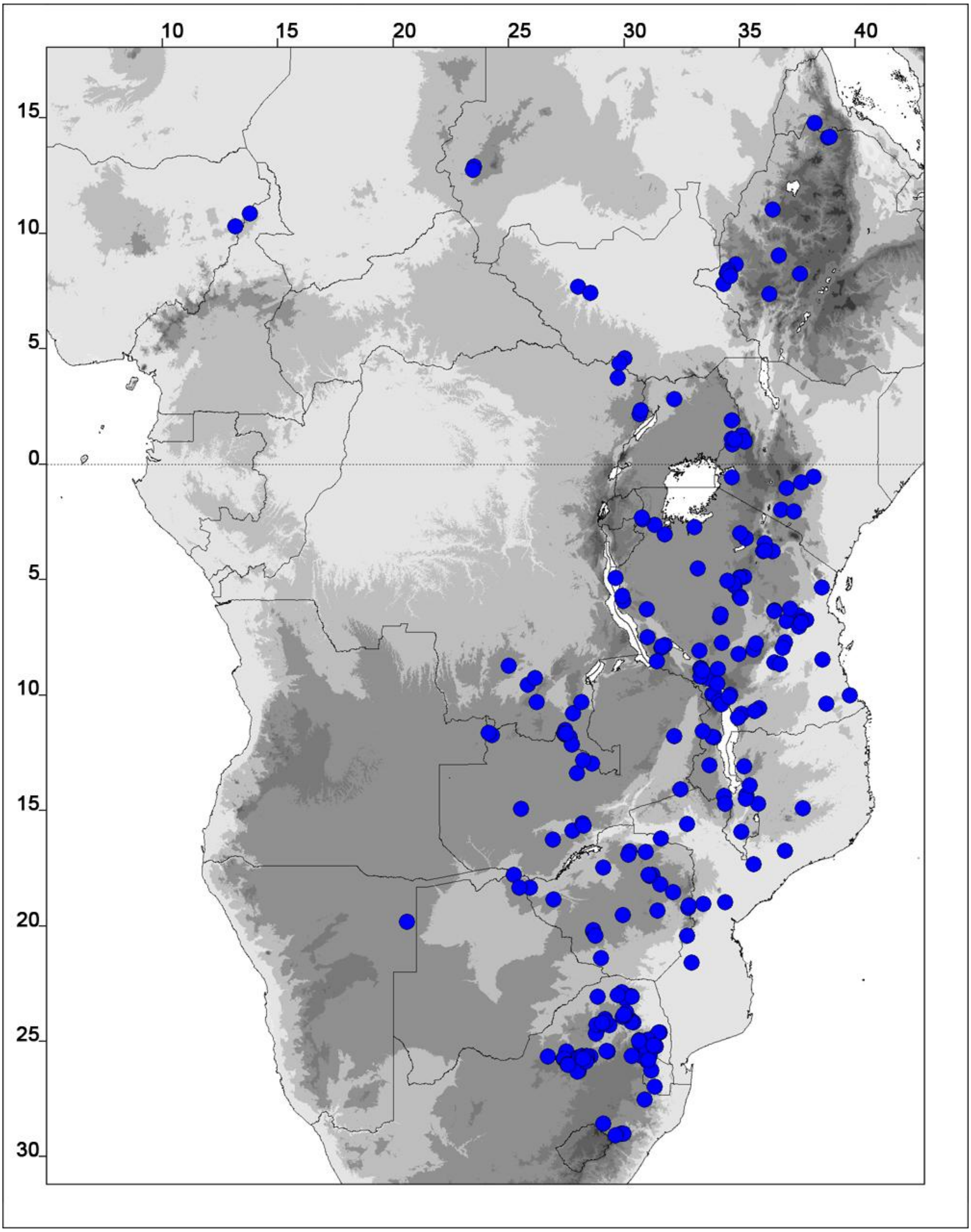

Fig. 24 Distribution map of *C. adoensis* var. *adoensis* (based on 281 specimens).

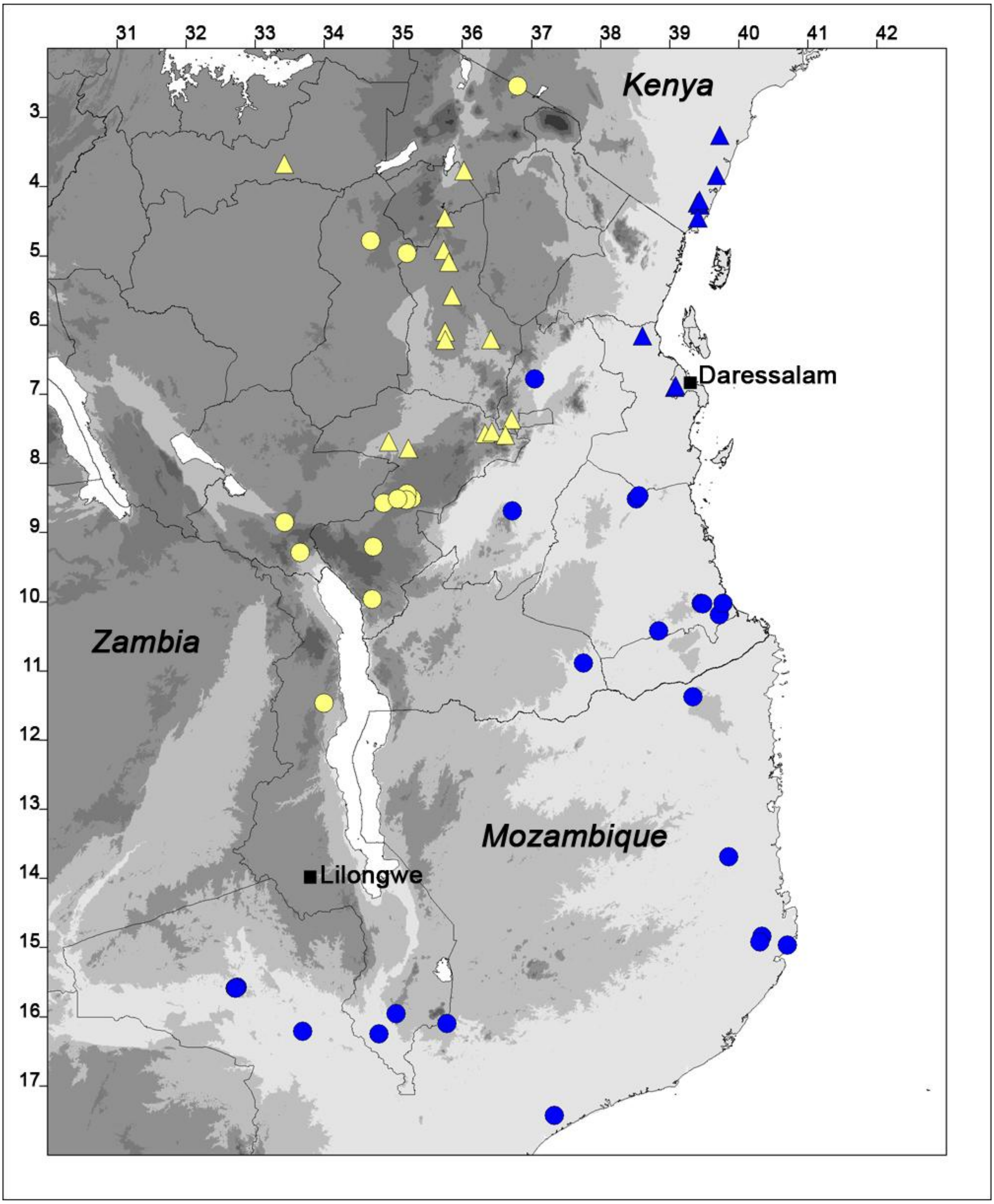

Fig. 25 Distribution map of *C. adoensis* var *aurantiaca* (pale yellow triangles; based on 15 specimens), *C. adoensis* var. *jeffreyana* (pale yellow dots; based on 15 specimens), *C. pwaniensis* (blue triangles; based on 9 specimens), and *C. senensis* (blue dots; based on 24 specimens). For Tanzania the borders of the regions are given.

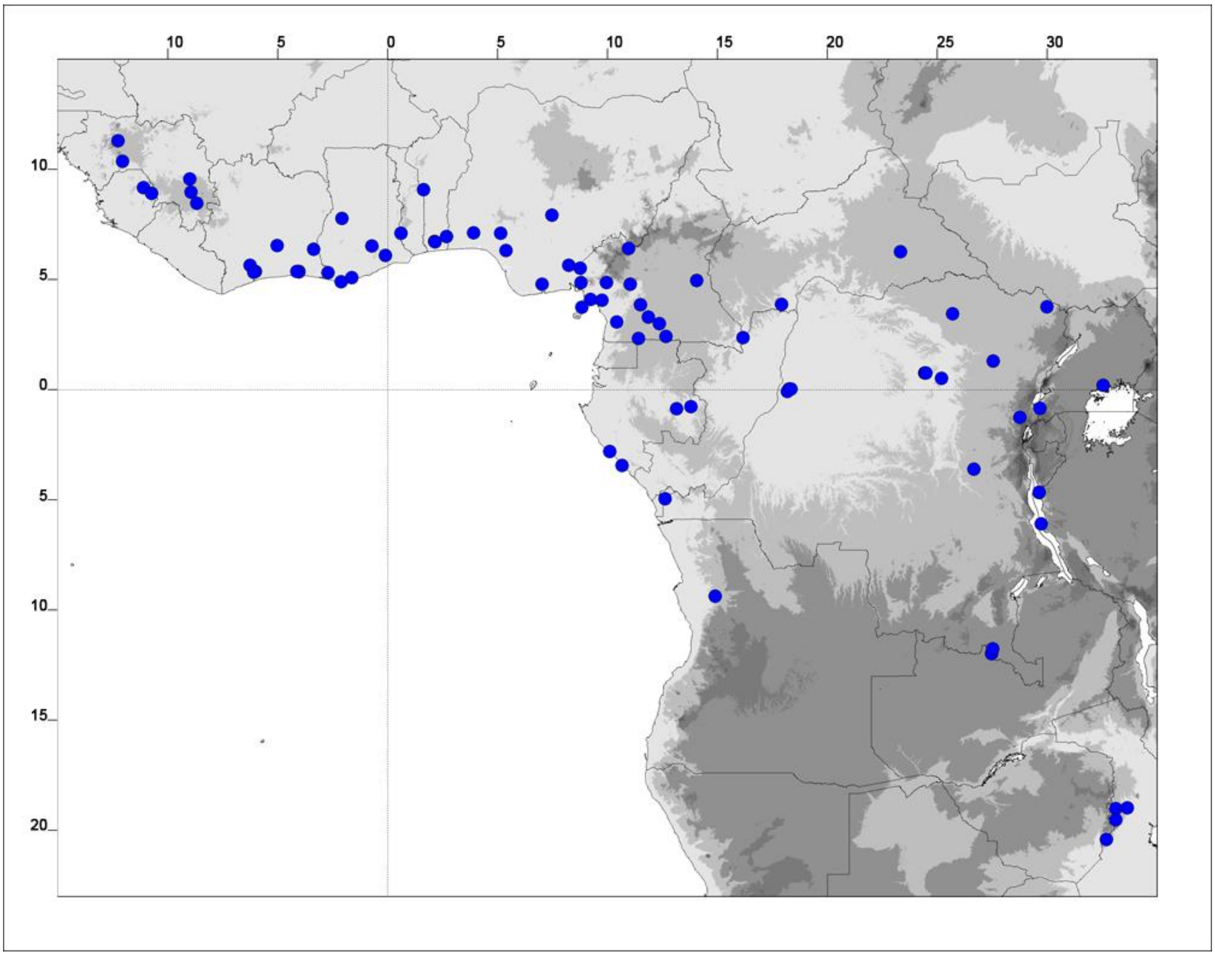

Fig. 26 Distribution map of *C. barteri* (based on 80 specimens).

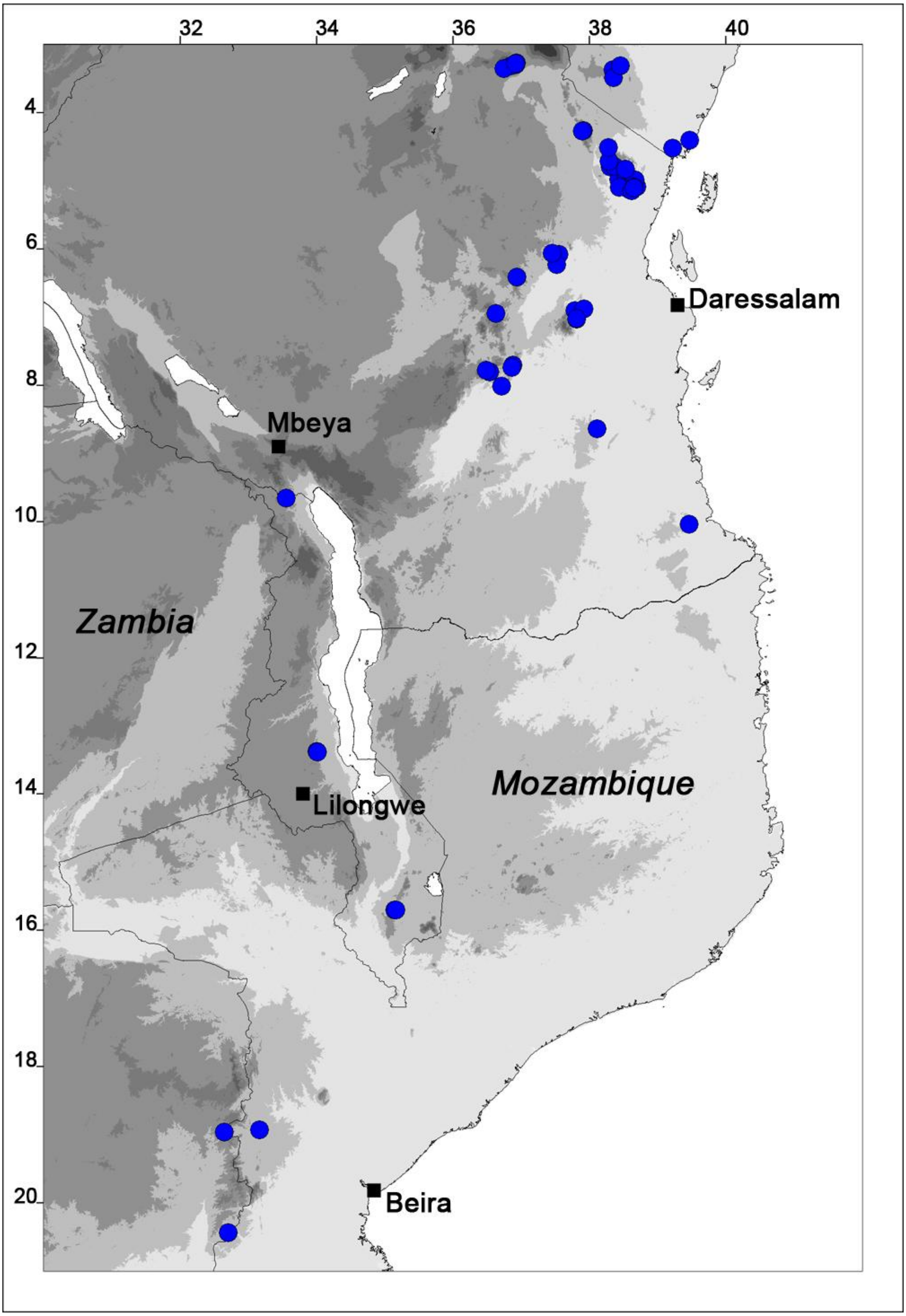

Fig. 27 Distribution map of *C. grandiflora* (based on 57 specimens).

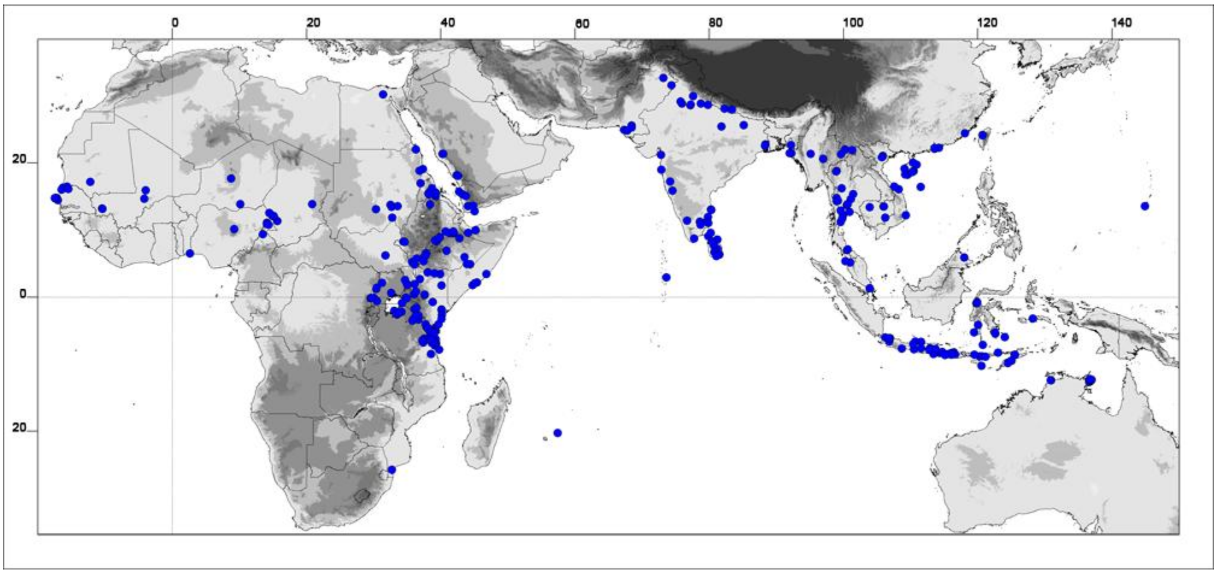

Fig. 28 Partial distribution map (Africa to Australia) of *C. grandis* (based on 421 specimens).

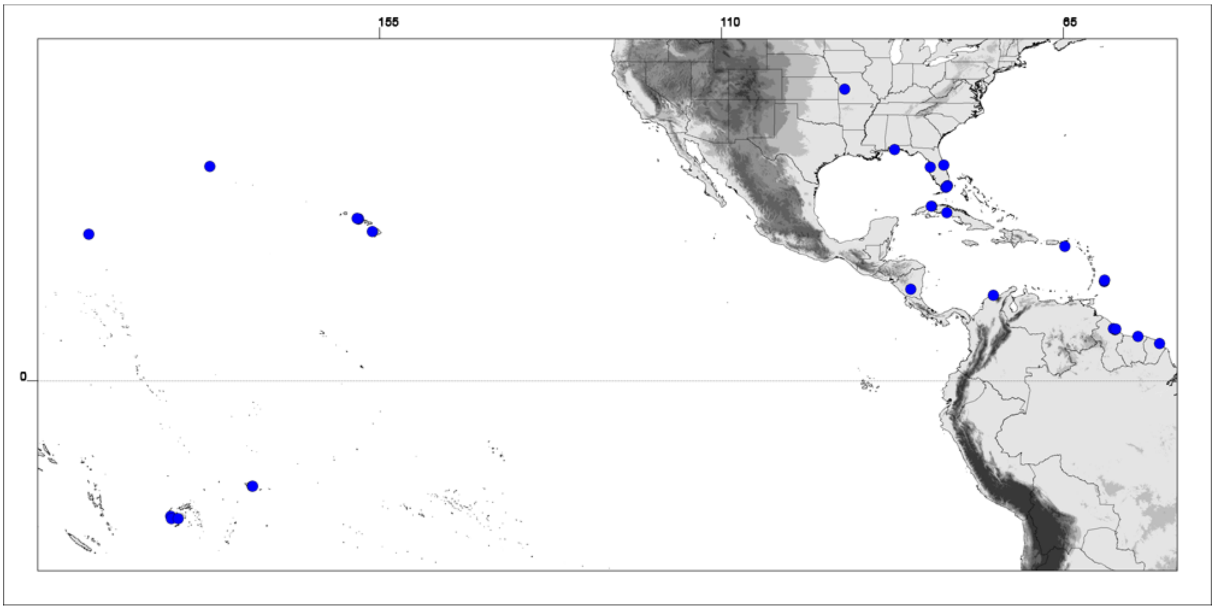

Fig. 29 Partial distribution map (Pacific Ocean and Americas) of *C. grandis* (based on 421 specimens). State borders are given for the USA.

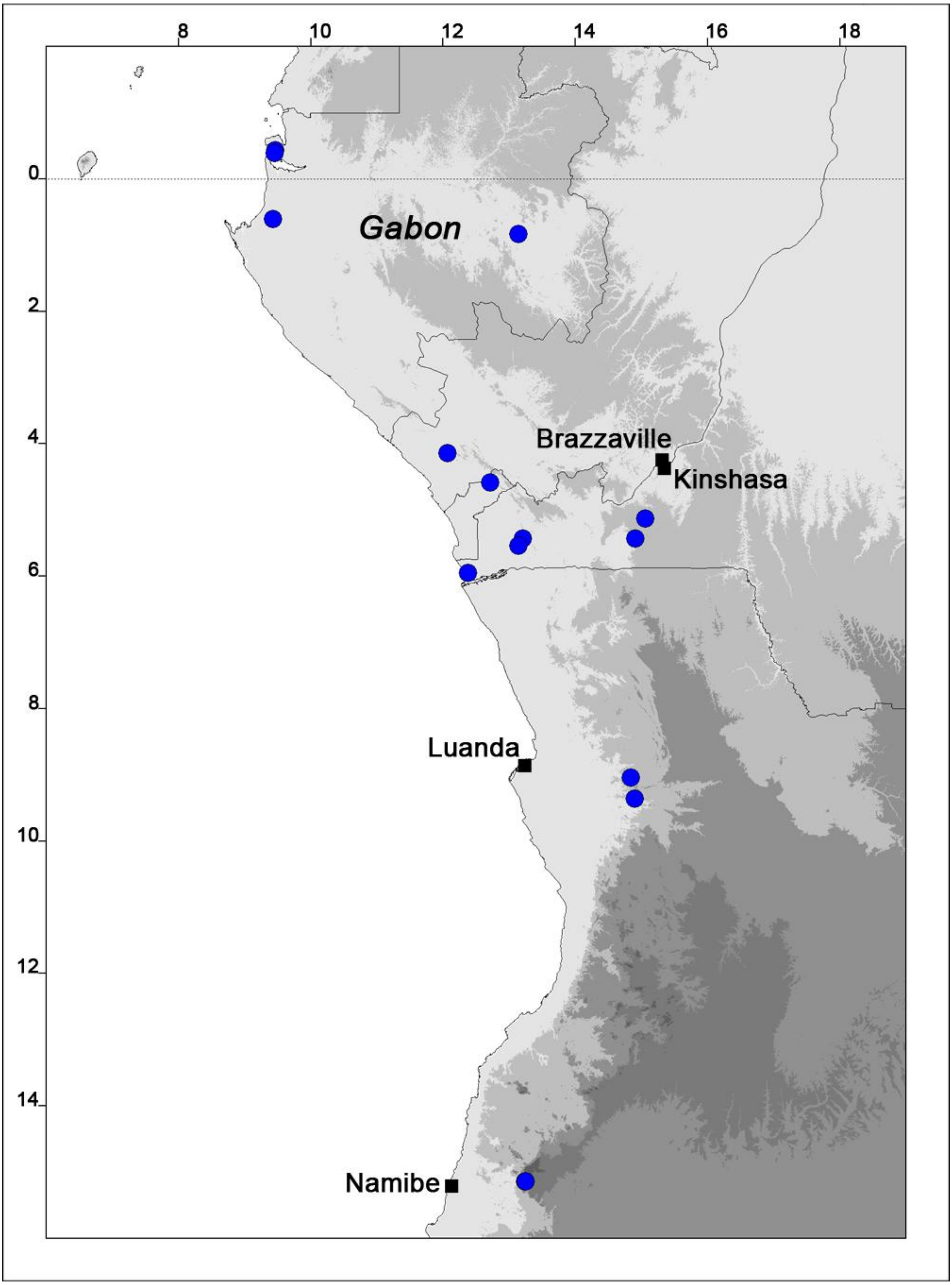

Fig. 30 Distribution map of *C. heterophylla* (based on 15 specimens).

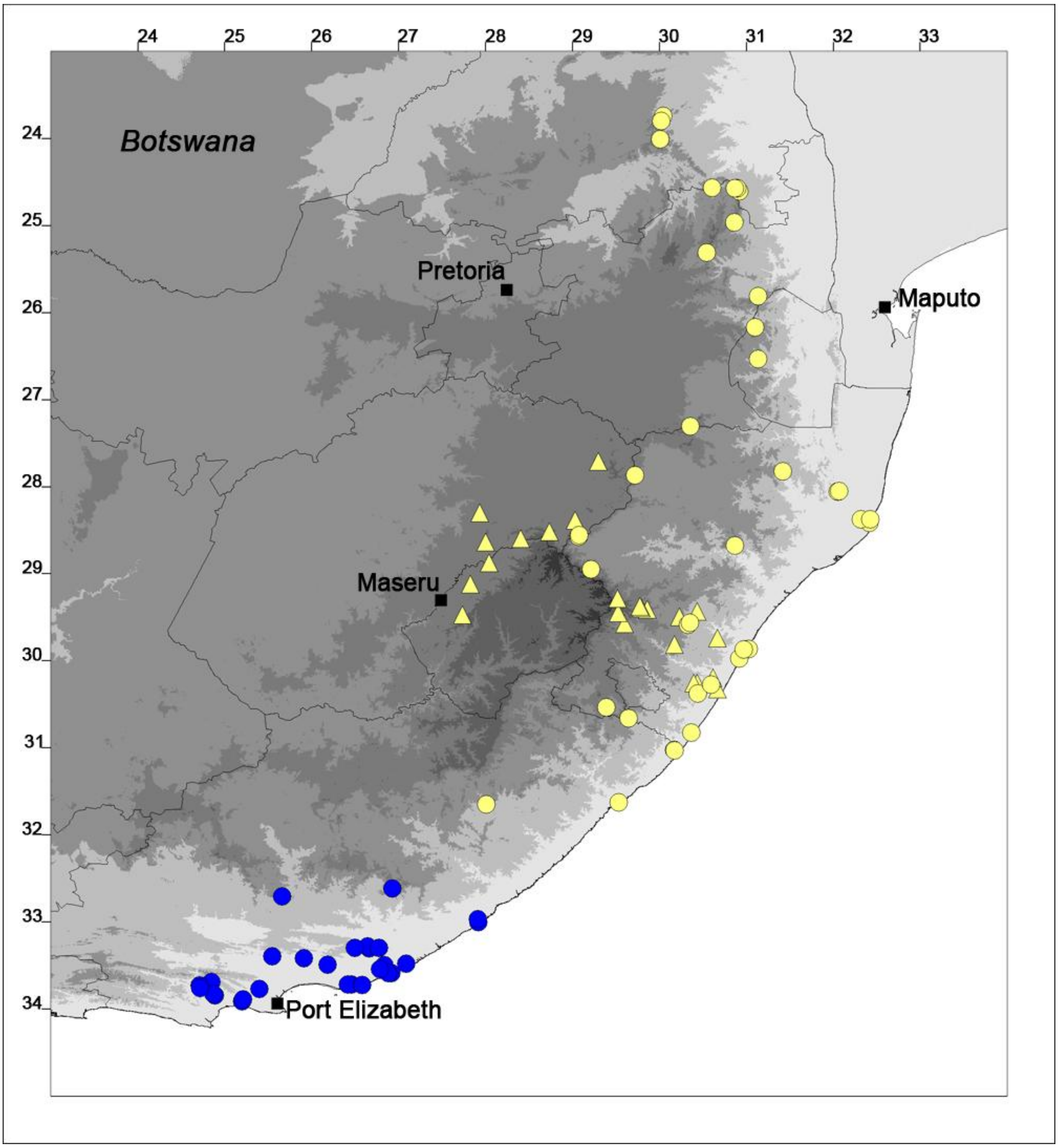

Fig. 31 Distribution map of *C. hirtella* (pale yellow triangles; based on 23 specimens), *C. mackenii* (pale yellow dots; based on 38 specimens), and *C. quinqueloba* (blue dots; based on 27 specimens). For South Africa the borders of the provinces are given.

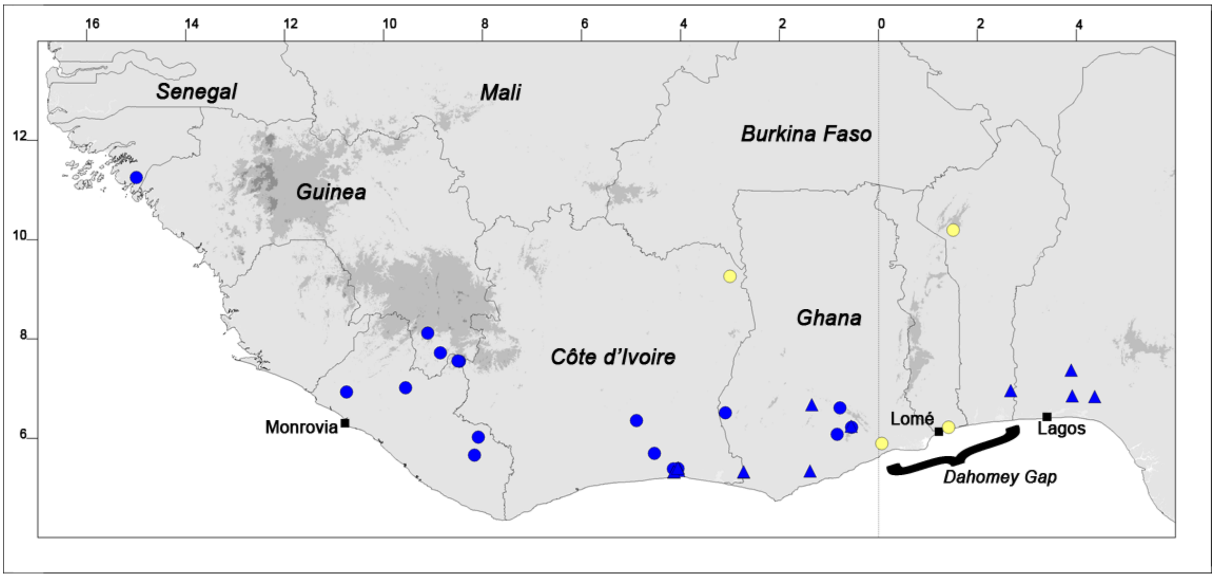

Fig. 32 Distribution map of *C. intermedia* (pale yellow spots), *C. keayana* (blue spots), and *C. longicarpa* (blue triangles).

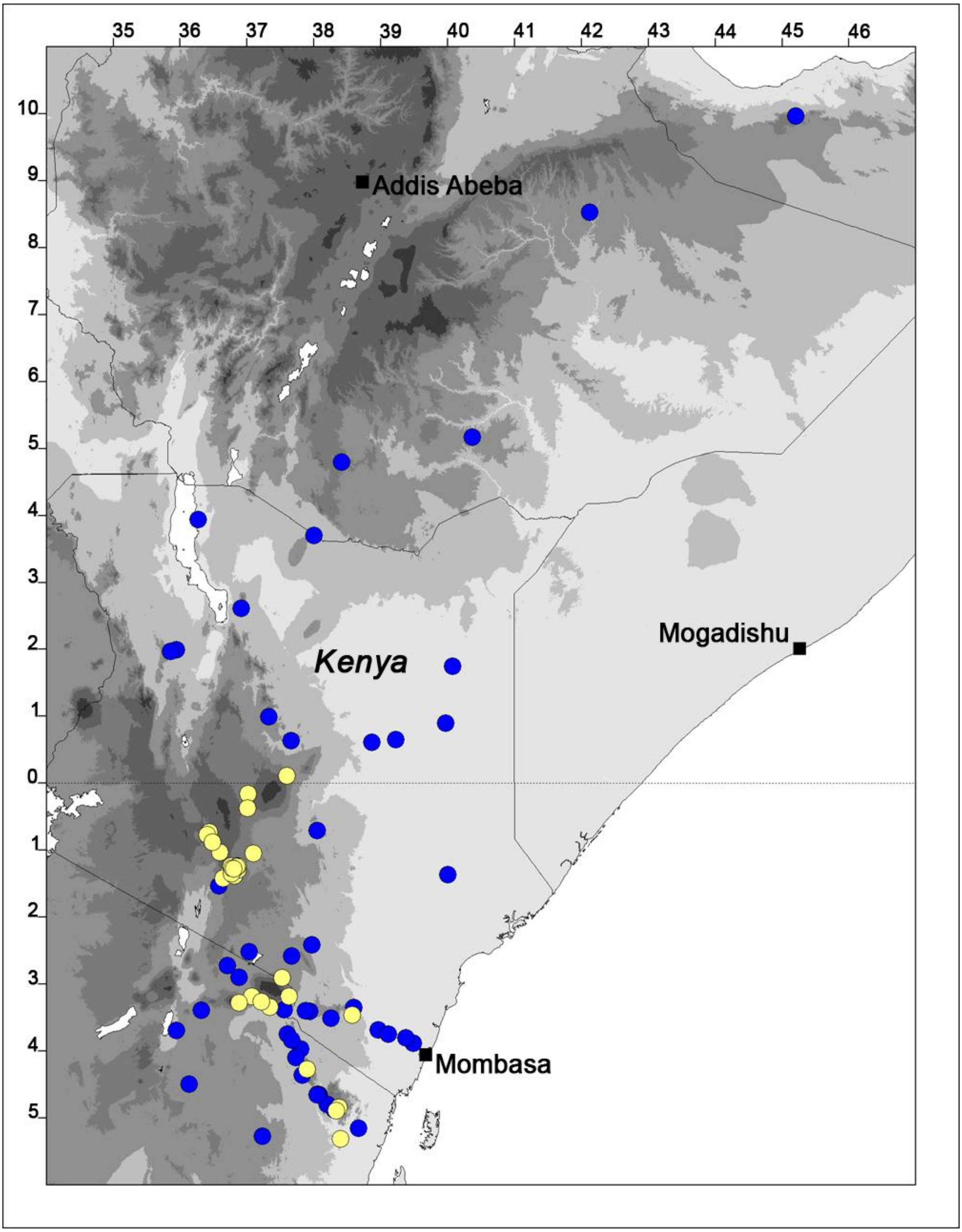

Fig. 33 Distribution map of *C. microphylla* (blue dots; based on 49 specimens) and *C. trilobata* (pale yellow dots; based on 35 specimens).

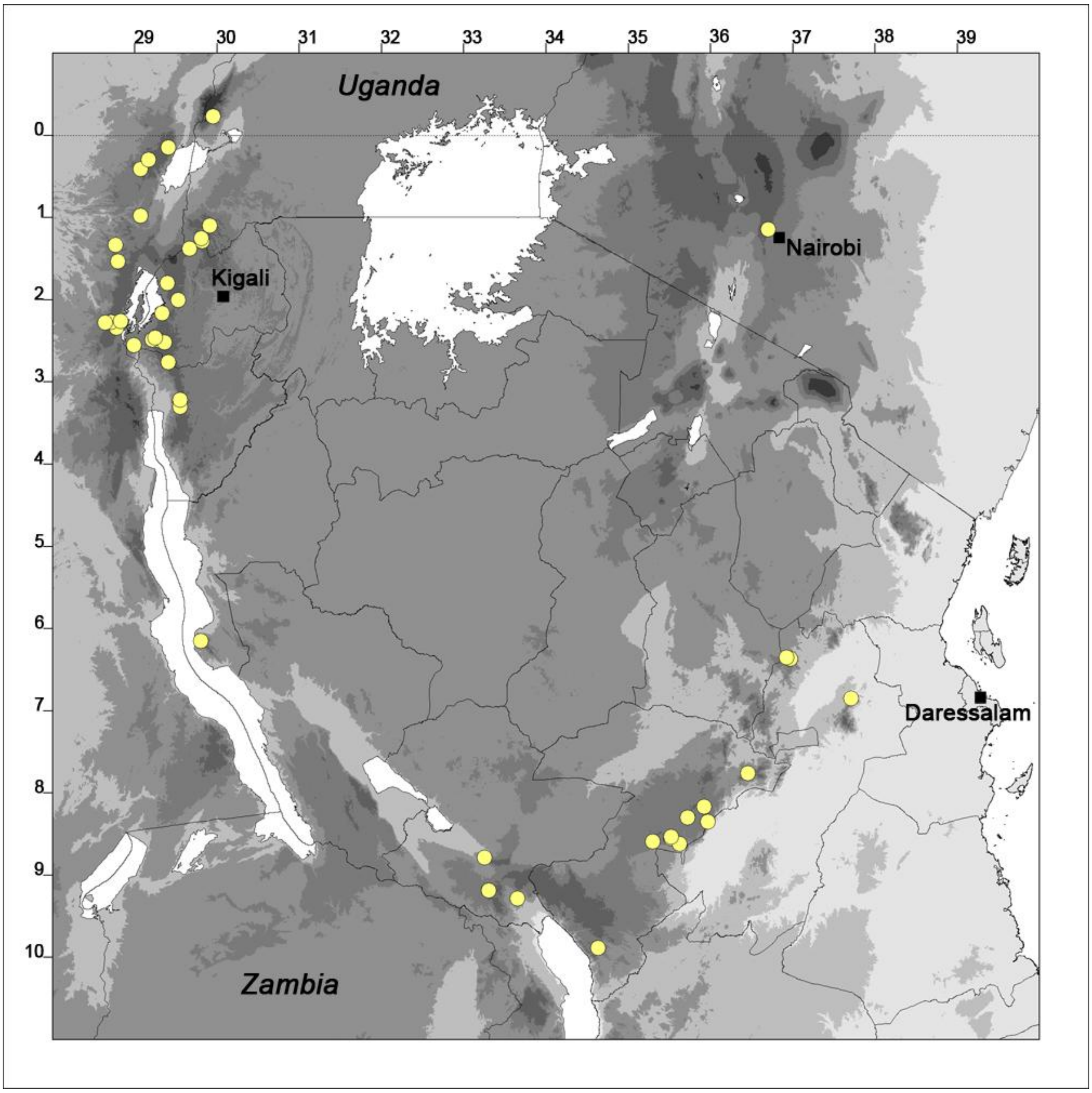

Fig. 34 Distribution map of *C. mildbraedii* (based on 44 specimens). The individual in Kenya is introduced. For Tanzania the borders of the regions are given.

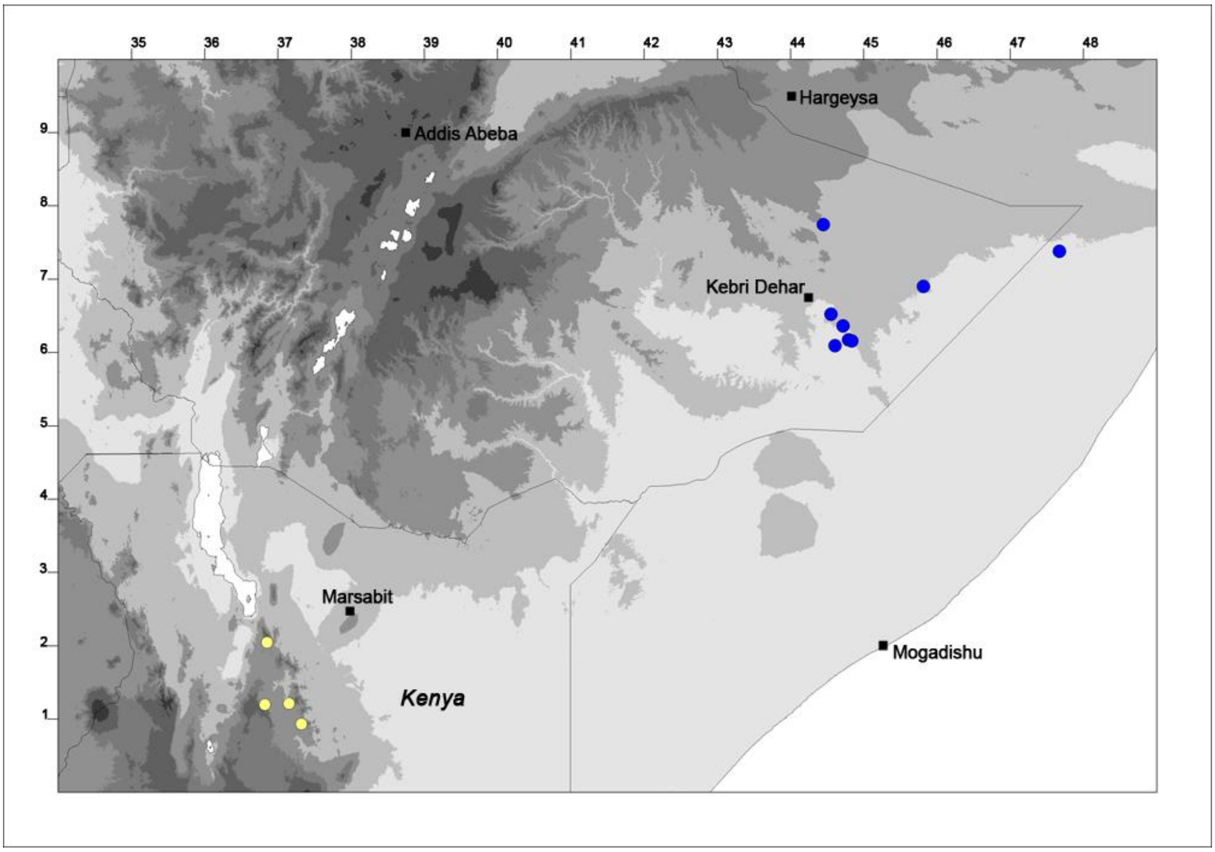

Fig. 35 Distribution map of *C. ogadensis* (blue dots; based on 8 specimens) and *C. samburuensis* (pale yellow dots; based on 4 specimens).

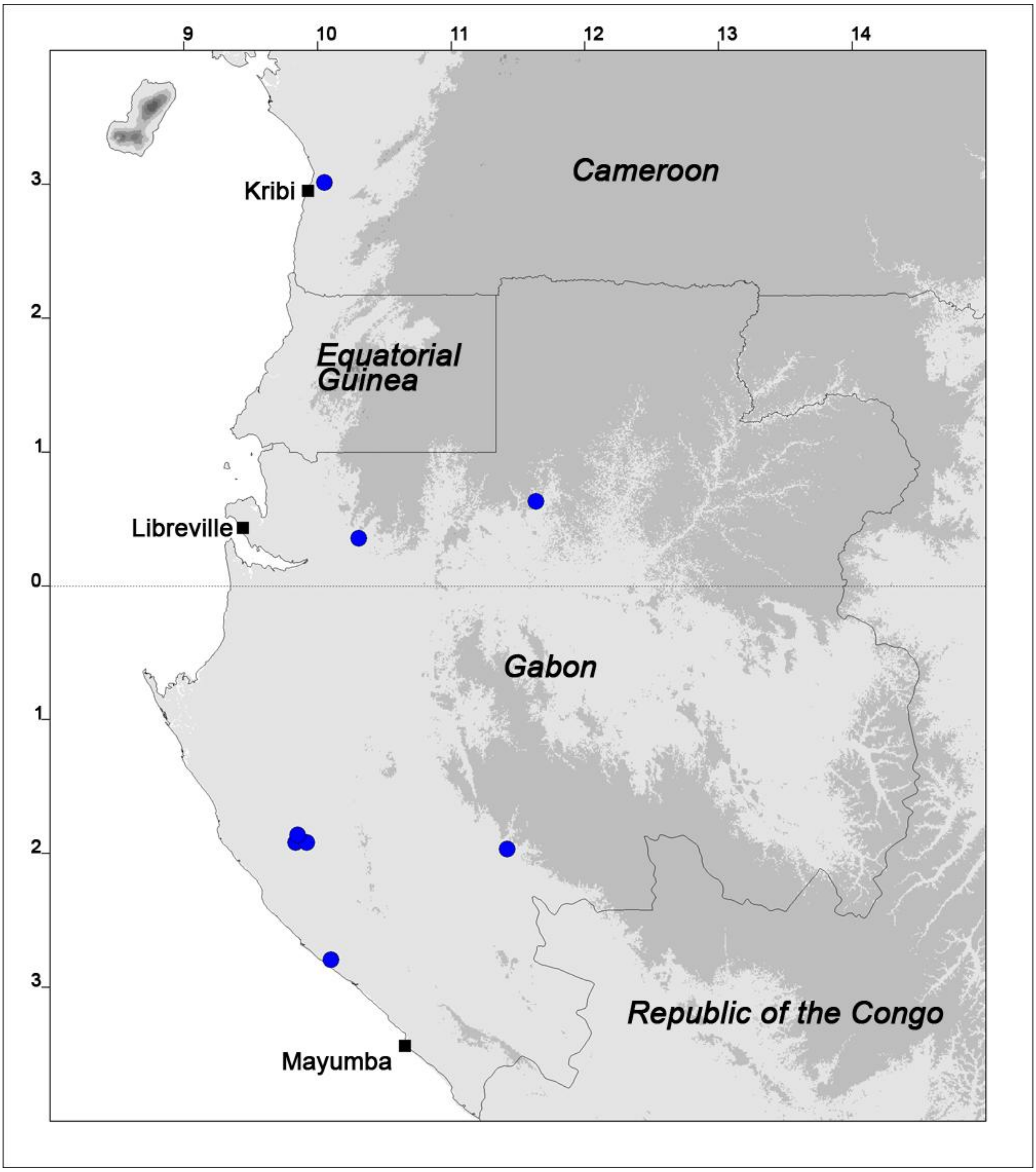

Fig. 36 Distribution map of *C. racemiflora* (blue dots; based on 8 specimens).

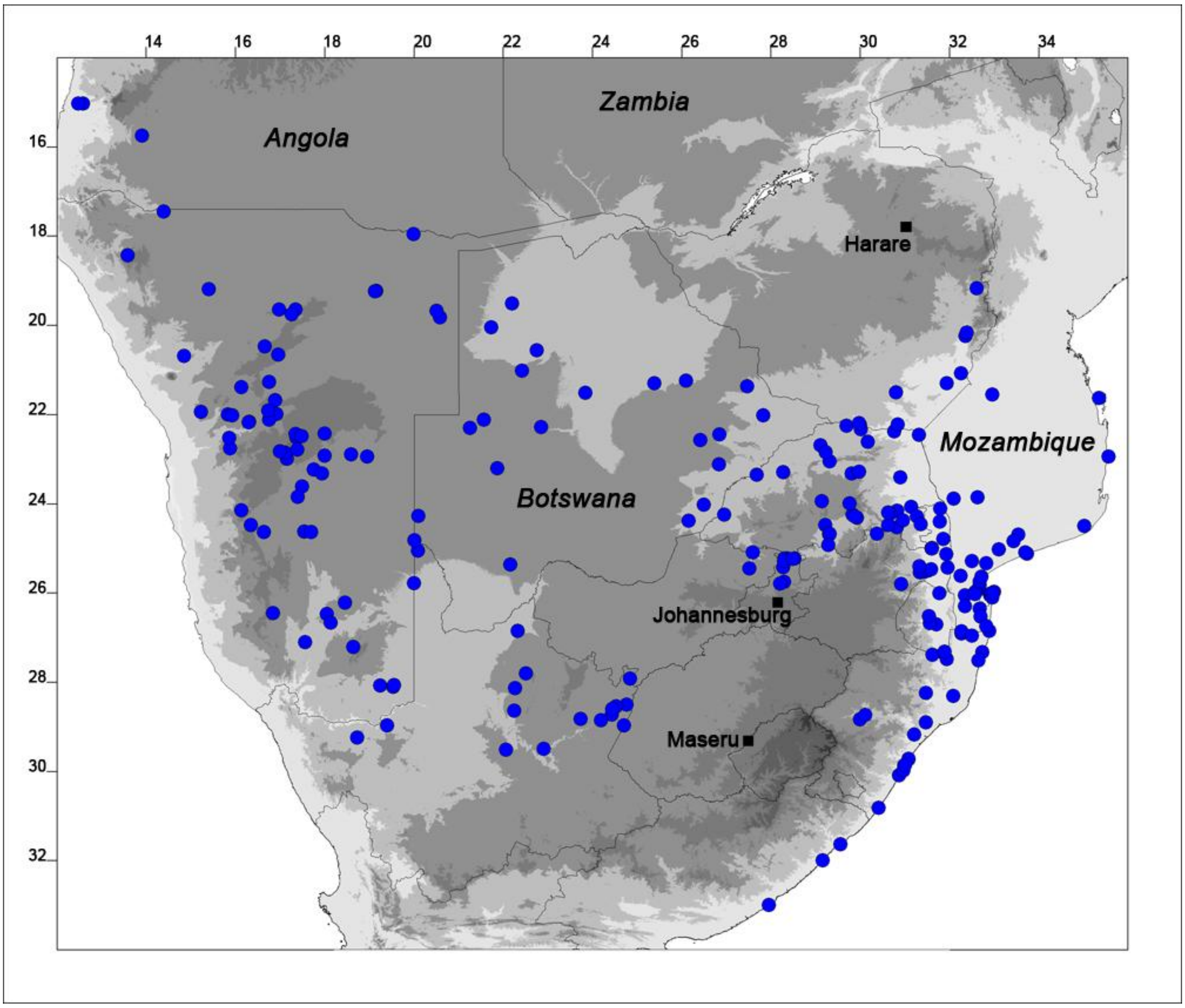

Fig. 37 Distribution map of *C. rehmannii* (blue dots; based on 229 specimens). For South Africa the borders of the provinces are given.

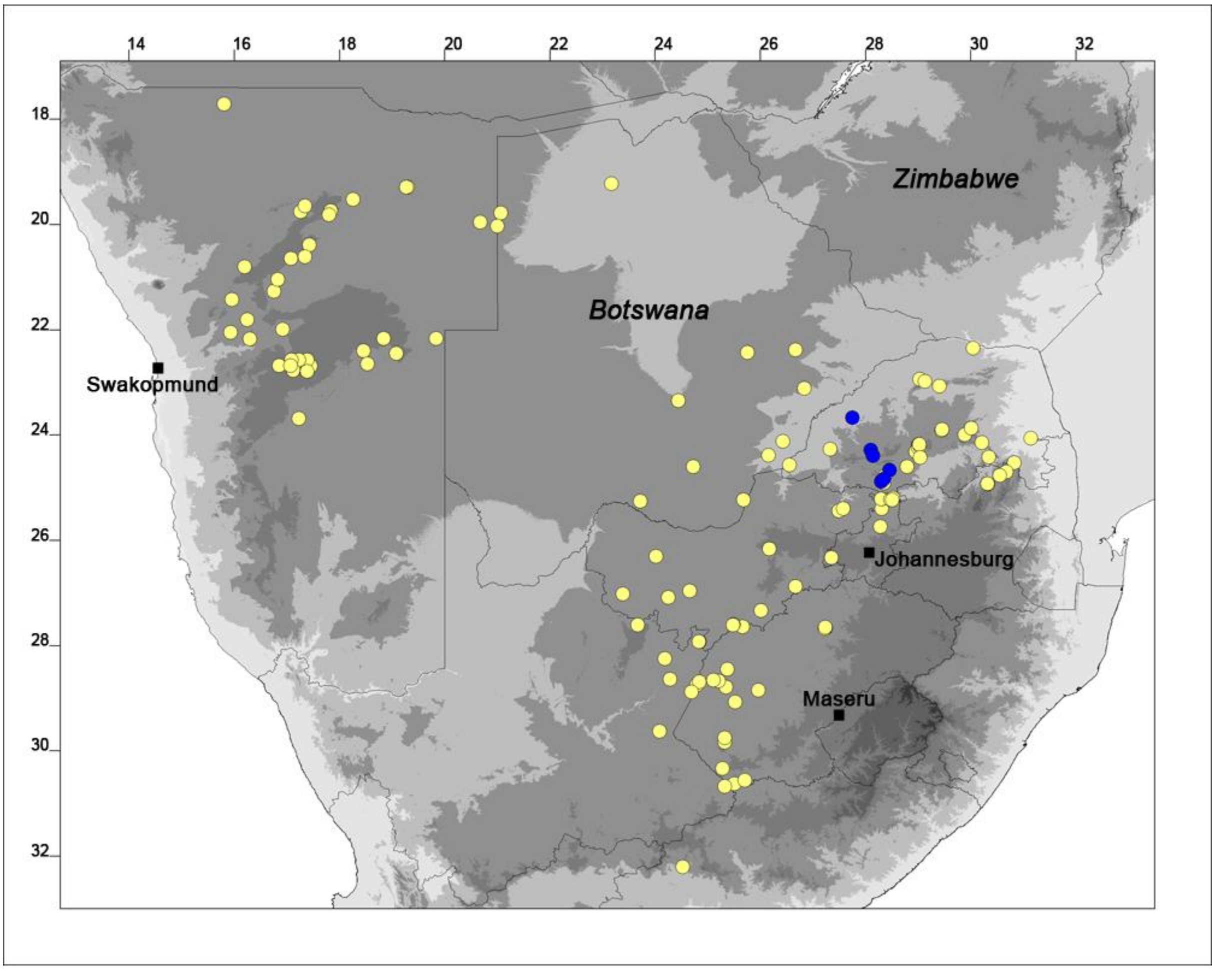

Fig. 38 Distribution map of *C. sessilifolia* var. *sessilifolia* (pale yellow dots; based on 122 specimens) and *C. sessilifolia* var. *variifolia* (blue dots; based on 6 specimens). For South Africa the borders of the provinces are given.

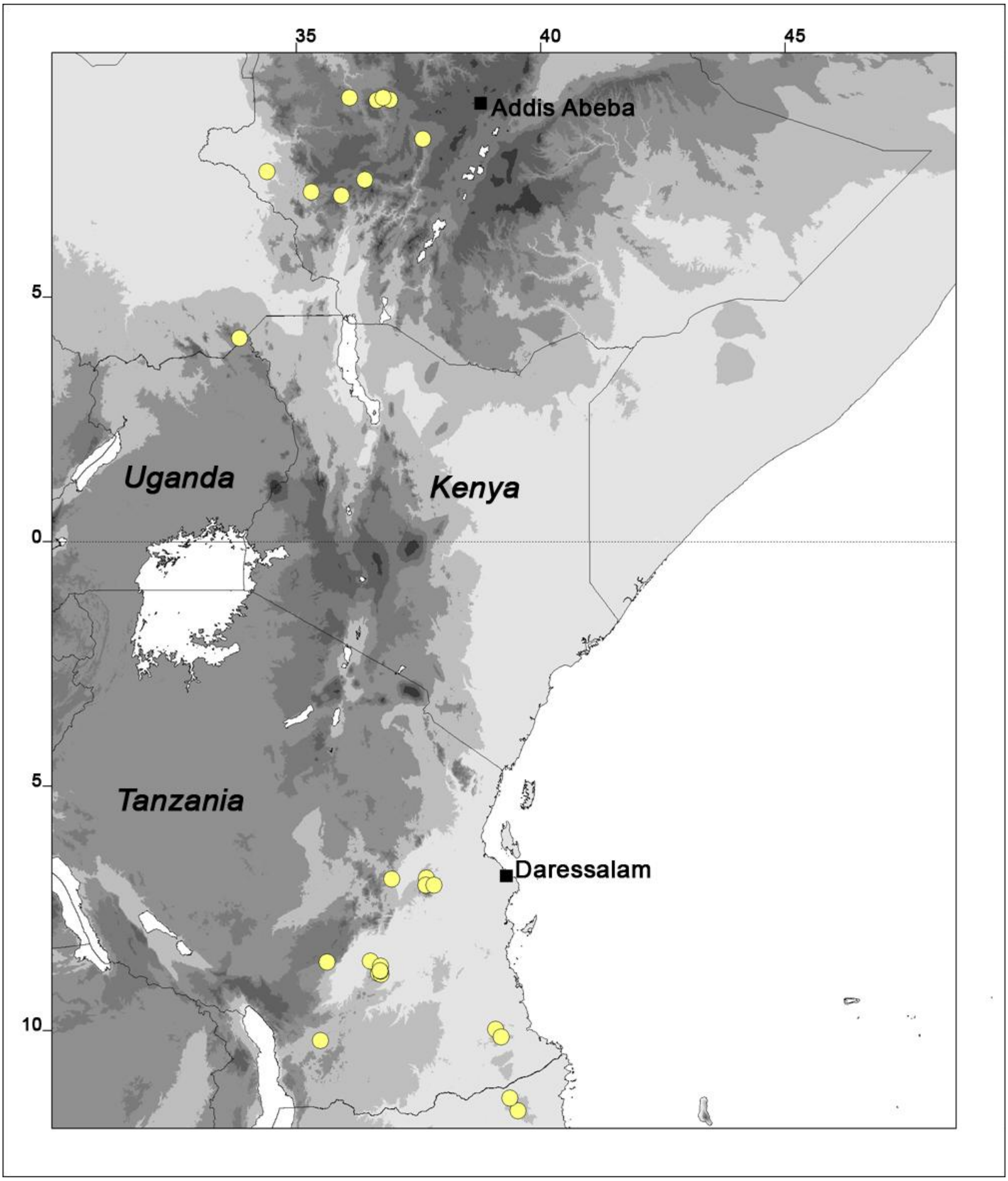

Fig. 39 Distribution map of *C. schliebenii* (pale yellow dots; based on 27 specimens).

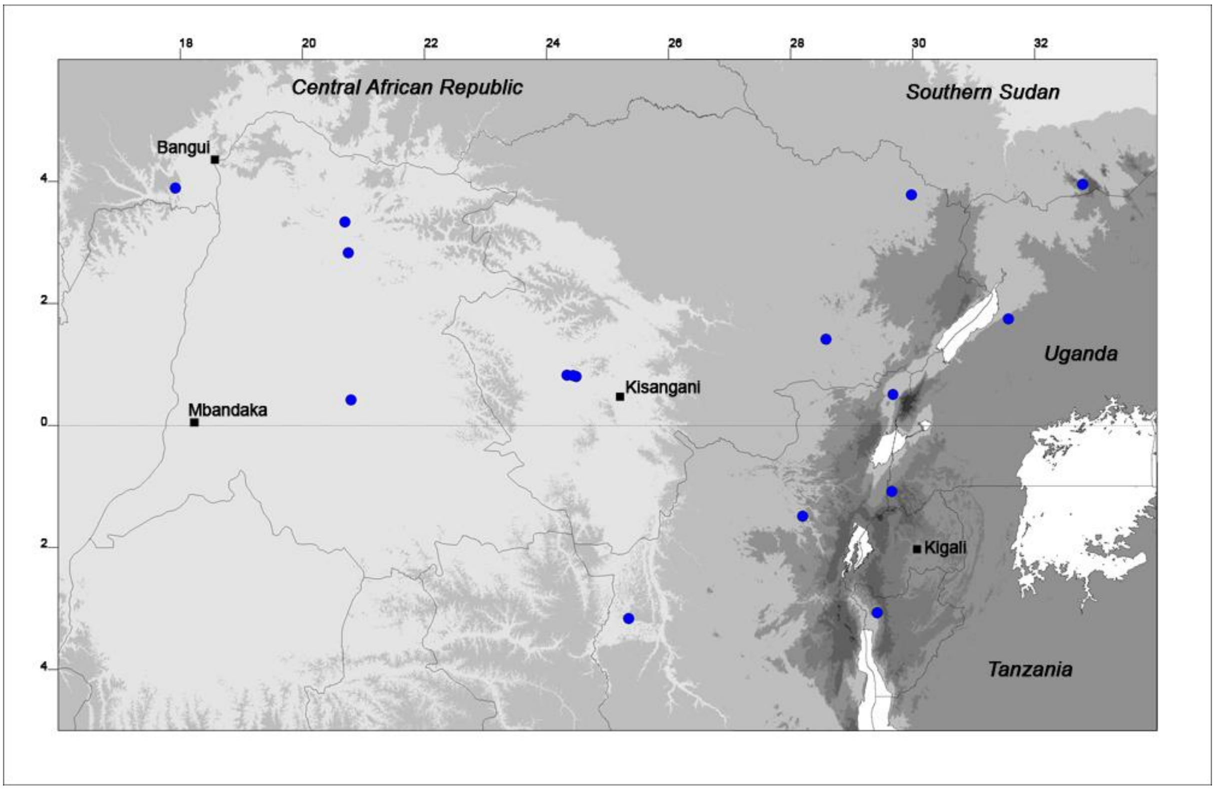

Fig. 40 Distribution map of *C. subsessiliflora* (blue dots; based on 16 specimens). For D.R. Congo the borders of the provinces (until 1988) are given.

Table S1. Voucher information and GenBank accession numbers. Specimens included in this study, with the geographic origin of material (only country and 1st administrative division given) and GenBank accession numbers for all sequences. Herbarium acronyms (in parentheses behind the voucher name) follow Index Herbariorum.

Species	No.	Voucher	Location	*mat*K	*ndh*F–*rpl*32R IS	*rpl*20–*rps*12 IS	*trn*L intron	*trn*L–*trn*F IS	*trn*S–*trn*G IS	*LFY* 2nd intron
C. abyssinica (Lam.) Cogn.	1	E.Westphal & J.M.C.Westphal-Stevels 1552 (WAG)	Ethiopia, Oromia Region	HQ608224		HQ608311			HQ608429	
C. abyssinica (Lam.) Cogn.	2	E.Westphal & J.M.C.Westphal-Stevels 1951 (WAG)	Ethiopia, Oromia Region			HQ608312	HQ608385	HQ608368	HQ608430	
C. abyssinica (Lam.) Cogn.	3	N.Holstein 120 (M)	From seeds from Ethiopia, Oromia			JQ943386			JQ943393	
C. adoensis (Hochst. ex A. Rich.) Cogn.	1	L.E.Davidson 3781 (M)	South Africa, Gauteng	HQ608226	HQ608274	HQ608314	HQ608396	HQ608396	HQ608432	
C. adoensis (Hochst. ex A. Rich.) Cogn.	2	R.Story 6283 (M)	Namibia, Otjozondjupa	HQ608227	HQ608275	HQ608316	HQ608397	HQ608397	HQ608434	HQ608160
C. adoensis (Hochst. ex A. Rich.) Cogn.	3	J.Pawek 6124 (MO)	Malawi, Northern Region	HQ608225		HQ608315		HQ608369	HQ608433	
C. adoensis (Hochst. ex A. Rich.) Cogn.	4	R.E.Gereau & C.J.Kayombo 3582 (MO)	Tanzania, Iringa	HQ608231	HQ608273	HQ608313			HQ608431	
C. adoensis (Hochst. ex A. Rich.) Cogn.	5	E.A.Robinson 2944 (M)	Zambia, Southern Prov.	HQ608228		HQ608318	HQ608398	HQ608398	HQ608436	
C. adoensis (Hochst. ex A. Rich.) Cogn.	6	H.Merxmüller 282 (M)	South Africa, Gauteng	HQ608229		HQ608319		HQ608370	HQ608437	
C. adoensis (Hochst. ex A. Rich.) Cogn.	7	M.Sanane 375 (M)	Zambia, Northern Prov.	HQ608230		HQ608320	HQ608399	HQ608399	HQ608438	
C. adoensis (Hochst. ex A. Rich.) Cogn.	8	A.R.Torre 5337 (M)	Mozambique, Zambezia			HQ608321		HQ608371	HQ608439	
C. adoensis (Hochst. ex A. Rich.) Cogn.	9	D.K.Harder & M.G.Bingham 2584 (MO)	Zambia, Lusaka Prov.	HQ608268	HQ608299	HQ608364			HQ608492	HQ608191
C. adoensis (Hochst. ex A. Rich.) Cogn.	10	S.A.Robertson 1925 (MO)	Kenya, Eastern Prov.	HQ608232		HQ608322	HQ608400	HQ608400	HQ608440	
C. adoensis (Hochst. ex A. Rich.) Cogn.	11	H.J.Schlieben 3271 (M)	Tanzania, Morogoro	HQ625501		HQ608317			HQ608435	
C. adoensis var. *aurantiaca* C. Jeffrey (Holstein)	1	M.Richards 20987 (BR)	Tanzania, Iringa	HQ608235		HQ625507	HQ608401	HQ608401	HQ608443	
C.adoensis var.*aurantiaca* C. Jeffrey (Holstein)	2	P.J.Greenway & Kanuri 14811 (M)	Tanzania, Iringa				HQ608402	HQ608402	HQ608444	HQ608161
C.adoensis var.*aurantiaca* C. Jeffrey (Holstein)	3	N.Holstein et al. 86 (M)	Tanzania, Dodoma	HQ608236	HQ608276	HQ608325	HQ608403	HQ608403	HQ608445	HQ608162
C. adoensis var. *jeffreyana* Holstein	1	J.C.Lovett 1597 (MO)	Tanzania, Iringa	HQ608233		HQ608323	HQ608386	HQ608372	HQ608441	
C. adoensis var. *jeffreyana* Holstein	2	C.F.Paget-Wilkes 72 (MO)	Tanzania, Iringa	HQ608234		HQ608324		HQ608373	HQ608442	
C. adoensis var. *jeffreyana* Holstein	3	N.Holstein 125 (M)	From seeds from Kenya, Rift Valley Province	JQ943384		JQ943391			JQ943398	
C. barteri (Hook.f.) Keay	1	E.Achigan-Dako 07 NIA 899 (GAT)	Guinea, Nzérékoré	HQ608237		HQ608330	HQ608404	HQ608404	HQ608450	

			Region							
C. barteri (Hook.f. Keay	2	J.J.Wieringa 6387 (WAG)	Gabon, Haut-Ogooué	HQ608239	HQ608277	HQ608326	HQ608405	HQ608405	HQ608446	HQ608163
C. barteri (Hook.f. Keay	3	E.Achigan-Dako 06 NIA 294 (GAT)	Guinea, Mamou Region			HQ608331	HQ608389	HQ608376	HQ608451	
C. barteri (Hook.f. Keay	4	E.Achigan-Dako 07 NIA 809 (GAT)	Ghana, Eastern Region	HQ608240		HQ608327	HQ608387	HQ608374	HQ608447	HQ608164
C. barteri (Hook.f. Keay	5	W.J.J.O.de Wilde et al. 3736 (MO)	Cameroon, Central Region	HQ608241		HQ608328	HQ608388	HQ608375	HQ608448	
C. barteri (Hook.f. Keay	6	M.A.van Bergen 490 (WAG)	Gabon, Ogooué-Maritime	HQ608242	HQ608278	HQ608329	HQ608406	HQ608406	HQ608449	HQ608165
C. barteri (Hook.f. Keay	7	F.J.Fernández-Casas 12077 (MO)	Equatorial Guinea, Bioco Island	HQ608238	HQ608279	HQ608332	HQ608390	HQ608377	HQ608453	
C. barteri (Hook.f. Keay	8	E.Achigan-Dako 07 NIA 875 (GAT)	Guinea, Nzérékoré Region						HQ608452	
C. grandiflora Cogn.	1	H Schäfer 05/302 (M)	Tanzania, Tanga	HQ608243	HQ608280	HQ608333	HQ608407	HQ608407	HQ608454	HQ608166
C. grandiflora Cogn.	2	N.Holstein et al. 98 (M)	Tanzania, Tanga	HQ608244	HQ608281	HQ608334	HQ608408	HQ608408	HQ608455	HQ608167
C. grandis (L.) Voigt	1	W.J.J.O.de Wilde & B.E.E.Duyfjes 22270 (L)	Thailand, Bangkok	DQ536651	HQ608282	DQ536537	DQ536762	DQ536762	HQ608456	HQ608168
C. grandis (L.) Voigt	2	R.Müller s.n., Aug. 1999 (MSB)	Sudan, Sannar Prov.			HQ608335	HQ608409	HQ608409	HQ608457	HQ608169
C. grandis (L.) Voigt	3	H.Schäfer 05/258 (M)	Tanzania, Pwani	HQ608245	HQ608283	HQ608336	HQ608410	HQ608410	HQ608458	HQ608170
C. heterophylla (Hook.f.) Holstein		C.C.H.Jongkind 5905 (WAG)	Gabon, Estuaire	HQ608246		HQ608337	HQ608411	HQ608411	HQ608459	HQ608171
C. hirtella Cogn.	1	N.Holstein 29 (M)	J.-L. Gatard, France, wild source unknown	HQ608247	HQ608284	HQ608339	HQ608412	HQ608412	HQ608461	HQ608172
C. hirtella Cogn.	2	S.S.Renner & A.Kocyan 2447 (M)	J.-L. Gatard, France, wild source unknown	HQ608248		HQ608338	HQ608413	HQ608413	HQ608460	
C. intermedia Holstein	1	C.Geerling & J.Bokdam 662 (MO)	Ivory Coast, Bouna area	HQ608269	HQ608298	HQ608363		HQ608383	HQ608491	
C. intermedia Holstein	2	A.Akoègninou et al. 3625 (WAG0278370)	Benin, Atakora	JQ943382	JQ943380	JN653687			JN653686	JN653688
C. keayana R. Fernandes	1	FC.Straub 140 (BR)	Liberia						HQ608462	
C. keayana R. Fernandes	2	C.C H.Jongkind et al. 6542 (WAG)	Liberia, Grand Gedeh	HQ608249	HQ608285	HQ608340		HQ608378	HQ608463	HQ608173
C. longicarpa Jongkind		C.C.H.Jongkind 3970 (WAG)	Ghana, Ashanti Region	HQ608250	HQ608286	HQ608341	HQ608414	HQ608414	HQ608464	HQ608174
C. mackenii Naudin ex C. Huber		R.G.Strey 3762 (M)	South Africa, Mpumalanga	HQ608251		HQ608343	HQ608415	HQ608415	HQ608465	
C. megarrhiza C. Jeffrey	1	J.J.F.E.de Wilde 6501 (WAG)	Ethiopia, Oromia Region			HQ608344	HQ608417	HQ608417	HQ608466	
C. megarrhiza C. Jeffrey	2	I.Friis et al. 2664 (MO)	Ethiopia, Oromia Region	HQ608252	HQ608287	HQ608347	HQ608416	HQ608416	HQ608469	HQ608176
C. megarrhiza C. Jeffrey	3	P.C.M.Jansen 3471 (WAG)	Ethiopia, Oromia Region			HQ608345			HQ608467	
C. megarrhiza C. Jeffrey	4	J.J.F.E.de Wilde 4793 (WAG)	Ethiopia, Oromia Region	HQ608253		HQ608346			HQ608468	HQ608175
C. megarrhiza C. Jeffrey	5	N.Holstein 118 (M)	From seeds from Ethiopia, Oromia			JQ943387			JQ943394	

			Region							
C. microphylla Gilg	1	R.B.Drummond & J.H.Hemsley 4087 (B)	Kenya, Coast Province	HQ608254		HQ608348			HQ608470	HQ608177
C. microphylla Gilg	2	J.J.F.E de Wilde & M.G.Gilbert 346 (UPS)	Ethiopia, Somali Regional State	HQ608255		HQ608349	HQ608418	HQ608418	HQ608471	HQ608178
C. microphylla Gilg	3	N.Holstein no. (M)	From seeds from Tanzania			JQ943388			JQ943395	
C. mildbraedii Gilg ex Harms	1	M.Reekmans 7399 (BR)	Burundi, Muramvya Prov.	HQ608256		HQ608350			HQ608472	
C. mildbraedii Gilg ex Harms	2	N.Holstein et al. 76 (M)	Tanzania, Morogoro	HQ608257	HQ608288	HQ608351	HQ608419	HQ608419	HQ608473	HQ608179
C. ogadensis Thulin		M.Thulin et al. 11183 (UPS)	Ethiopia, Somali Regional State	HQ608258	HQ608289	HQ608352			HQ608474	
C. quinqueloba (Thunb.) Cogn.		R.D.A.Bayliss 8470 (M)	South Africa, Eastern Cape	HQ608259	HQ608290	HQ608353	HQ608420	HQ608420	HQ608475	HQ608180
C. racemiflora Kéraudren	1	I.van Nek 536 (WAG)	Gabon, Ogooué-Maritime			HQ608355	HQ608421	HQ608421	HQ608477	HQ608182
C. racemiflora Kéraudren	2	J.J.Bos 6590 (WAG)	Cameroon, South Prov.	HQ608260		HQ608354	HQ608391	HQ608379	HQ608476	HQ608181
C. rehmannii Cogn.	1	S.S.Renner & A.Kocyan 2749 (M)	southern Africa, no detailed information	DQ536652	HQ608292	HQ625508	DQ536799	DQ536799	HQ608479	HQ608184
C. rehmannii Cogn. var. *littoralis* A. Meeuse	2	L.E.Codd 9620 (M)	South Africa, KwaZulu-Natal	HQ608261		HQ625509	HQ608422	HQ608422	HQ608480	
C. rehmannii Cogn. var. *rehmannii*	3	G.Woortman 217 (M)	Namibia, Otjozondjupa	HQ608262		HQ625510	HQ608392	HQ608380	HQ608481	HQ608185
C. rehmannii Cogn.*“ovifera”*	4	B de Winter & O.A.Leistner 5598 (M)	Namibia, Kunene	HQ608263	HQ608291	HQ608356	HQ608423	HQ608423	HQ608478	HQ608183
C. rehmannii Cogn.	5	N.Holstein 126 (M)	From seeds USDA 365066, wild coll. from SE South Africa	JQ943383		JQ943390	HQ625496	HQ625496	JQ943396	JQ943381
C. samburuensis Holstein		R.B. & A.J.Faden 74/948 (WAG)	Kenya, Rift Valley Prov.	HQ608264	HQ608293	HQ608357	HQ608393	HQ608381	HQ608482	HQ608186
C. schliebenii Harms	1	E.Westphal & J.M.C.Westphal-Stevels 5539 (WAG)	Ethiopia, Oromia Region		HQ608294	HQ608358			HQ608483	
C. schliebenii Harms	2	G.S.Laizer et al. 1449 (MO)	Tanzania, Morogoro	HQ608265		HQ608359		HQ608382	HQ608484	HQ608187
C. senensis (Klotzsch) Cogn.	1	N.Holstein et al. 66 (M)	Tanzania, Morogoro	HQ608266	HQ608295	HQ608360	HQ608424	HQ608424	HQ608485	HQ608188
C. senensis (Klotzsch) Cogn.	2	K.Vollesen MRC4316 (WAG)	Tanzania, Lindi	HQ608267	HQ608296	HQ608362	HQ608425	HQ608425	HQ608487	HQ608189
C. senensis (Klotzsch) Cogn.	3	A.R.Torre et al. 18788 (MO)	Mozambique, Tete			HQ608361			HQ608486	
C. senensis (Klotzsch) Cogn.	4	E.M.C.Groenendijk et al. 1031 (WAG)	Mozambique, Nampula			HQ625511			HQ608489	
C. senensis (Klotzsch) Cogn.	5	H.J.Schlieben 5259 (M)							HQ608488	
C. sessilifolia (Sond.) Cogn. var. *sessilifolia*		S.S.Renner et al. 2763 (M)	Plant grown at Mainz Bot. G. (MJG19-54430); wild source unknown	AY968446	HQ608297	DQ648163	AY968568	AY968385	HQ608490	HQ608190
C. sessilifolia var. *variifolia* (A.Meeuse) Holstein		F.A.Rogers 24932 (Z000073427)	South Africa, Limpopo	JQ943385		JQ943392			JQ943399	

C. subsessiliflora Cogn.		H.Fredericq in Herb. G.F.de Witte 8288 (M)	DR Congo, North Kivu	HQ608270		HQ608365	HQ608395	HQ608384	HQ608493	
C. trilobata (Cogn.) C. Jeffrey	1	N.Holstein & P Sebastian 9 (M)	From seeds from J.-L. Gatard, France, coll. in Kenya	HQ608271	HQ608300	HQ608366	HQ608426	HQ608426	HQ608494	
C. trilobata (Cogn.) C. Jeffrey	2	N.Holstein no. (M)	From seeds from Kenya, Rift Valley Prov.			JQ943389			JQ943397	
Diplocyclos palmatus (L.) C. Jeffrey		J.Maxwell s.n. 2 Sep. 2002	Thailand, Chiang Mai	DQ536671	HQ608301	DQ536625	DQ536769	DQ536769	HQ608495	HQ608192
Diplocyclos schliebenii (Harms) C. Jeffrey		H.J.Schlieben 4363 (M)	Tanzania, Kilimanjaro				HQ608427	HQ608427	HQ608496	HQ608193
Cucumis hirsutus Sond.		N.B.Zimba et al. 874 (MO)	Zambia	DQ536658		DQ536542	DQ536804	DQ536804	HM597074	
Cucumis sativus L.		unknown	unknown	AJ970307	AJ970307	AJ970307	AJ970307	AJ970307	AJ970307	
Peponium vogelii (Hook. f.) Engl.		S.S.Renner 2710 (M)	Tanzania, Tanga	HQ608272	HQ608302	HQ608367	HQ608428	HQ608428	HQ608497	HQ608194
Scopellaria marginata (Bl.) W. de Wilde & Duyfjes		A.Kocyan AK178 (BKF)	Thailand	DQ536751		DQ536612	DQ536804	DQ536804		

General Discussion

Phylogeny and Biogeography

The four chapters in this dissertation have thrown new light on the evolution and species boundaries in the 11th largest genus of the Cucurbitaceae. In the following discussion, I summarize my main findings, highlighting newly arising questions.

The dense sampling, with 24 of the 25 species represented by at least two individuals for most of the species in the plastid data matrix (albeit not always in the nuclear matrix), reveals the existence of four clades in the genus *Coccinia*. The polytomy in the *C. adoensis* clade, which involves seven species, was not resolvable, even with sequences of the *rbcL* gene and the *psbA–trnH* intergenic spacer added (unpublished data). Within this polytomy, the 16 *C. adoensis* accessions (from much of the species' geographic range) are interspersed among accessions from these other species, while nuclear sequences from the *LEAFY*-like 2nd intron (*LFY*) indicate that at least some of them belong together. The resemblance of nuclear ITS sequences from individuals with different plastid sequences suggested ongoing gene flow (Holstein & Renner 2011a), hence a biological species *sensu* Mayr (1942). Unfortunately, the nuclear data are weakly resolved and for several accessions I was unable to obtain nuclear *LFY* sequences. The proposed biogeographic scenario for the *C. adoensis* clade as presented in chapter 4 assumes gene flow or incomplete lineage sorting. To more fully reconstruct speciation events in *Coccinia*, phylogeographic work would be necessary.

Biogeography in Africa, based on molecular phylogenies and molecular dating is in its infancy (among the few studies are *Acridocarpus*, Davis *et al.* 2002; African Annonaceae, Couvreur *et al.* 2008; and *Olea*, Besnard *et al.* 2009), with most studies focused on Central African rainforests (Ngomanda *et al.* 2009; Dauby *et al.* 2010; Lowe *et al.* 2010; Debout *et al.* 2011), Cape clades (Bakker *et al.* 2005; Verboom *et al.* 2009), or Afroalpine clades (Kebede *et al.* 2007; Gehrke & Linder 2009; Kadu *et al.* 2011). This is likely due to the difficulty of obtaining suitable material for sequencing, especially from less accessible areas away from the coasts (Kier *et al.* 2005; Küper *et al.* 2006). The large gaps in the distribution maps presented in chapter 4, for example, in Angola, Central African Republic, D.R. Congo, and Zambia, probably reflect a lack of collecting efforts in those war-prone countries, rather an absence of *Coccinia* species. Relict populations of species adapted to perhumid conditions survived in fragmented patches today isolated from the Central African rainforests. Likely examples are Jeffrey's (1978) *Coccinia* sp. A and B in his treatment of the Cucurbitaceae for the Flora Zambesiaca. Other examples are *C. heterophylla* in South Angola, *C. subsessiliflora* in Southern Sudan, and *C. barteri* in Mozambique and Zimbabwe (chapter 4).

Coccinia grandis is the only *Coccinia* species occurring in the Arabian Peninsula and in Asia, whereas the ecologically similar *C. microphylla* and *C. ogadensis* are restricted to northeastern Africa; the latter may be the sister species of C*. grandis*. In the sister genus of *Coccinia*, we again find one widespread species, *Diplocyclos palmatus*, a rainforest species distributed from Central Africa to Asia and Australia (Jeffrey 1967), while the remaining (three) species are endemic in Africa.

The close relationship of *C. rehmannii* from southern Africa to *C. microphylla* and *C. trilobata* from northeastern Africa, a clade dated to c. 3 Ma (Holstein & Renner 2011a), shows that there likely was a connection between these two areas. This connection, referred to as ‘arid track’, is known from various plant and animal groups (Balinsky 1962; Freitag & Robinson 1993; Jürgens 1997; Kuhlmann *et al.* 2009), but the time frame and direction of species range expansion are barely known (but see also Schrire *et al.* 2009). Other cucurbits, such as the genus *Dactyliandra* or the species *Ctenolepis cerasiformis* have a similar distribution pattern between southern and northeastern Africa (Jeffrey 1967; Schaefer & Renner 2011b) and similar vegetative characters, probably in response to similar selection pressures (chapter 4).

Habitats with humid conditions in East Africa are bound to rivers, mountain ranges or to the coast and are highly fragmented today. The geographic ranges of the forest sister species *C. grandiflora*, occurring from eastern Zimbabwe to southern Kenya, and *C. schliebenii*, distributed in southwestern Tanzania and southeastern Ethiopia, surely reflects Pliocene/Pleistocene climate and biome distribution in East Africa. Also whether the species from East African coastal forests (*C. pwaniensis* and *C. senensis*) evolved allopatrically in glacial refugia along the coast requires further study.

Morphology

Coccinia species have two types of tubers, root tubers and hypocotyl tubers. Root tubers occur in *C. adoensis* and likely also in *C. pwaniensis* and *C. senensis*, all three from woodlands, where fire plays an important role, and coastal forests. The related rainforest species *Coccinia grandiflora* (*C. schliebenii* most likely, too) also produces globular root thickenings, similar to root tubers. Other drought-adapted species and species from higher altitudes produce hypocotyl tubers or at least hypocotyl swellings. The root morphology of rainforest species of the *barteri* clade is unknown. The ability to produce tubers or at least lignified storage organs in *Coccinia* suggests an ancestry from drought-prone habitats. Species of the sister genus *Diplocyclos* occur in rainforests, but also in woodlands, and at least some as perennials with a fleshy rootstocks (Jeffrey 1967).

Probracts, defined by Zimmermann (1922) as bract-like pherophylls in vegetative axils, are an apomorphy of Cucurbitaceae. In *Coccinia*, these maximally 6 mm long organs are sometimes caducous and have an entire margin. Probracts in *Coccinia* species are either spoon-shaped presenting the lower lamina or they are keeled. They have the same size and morphology as bracts below inflorescences, whereas bracts below flowers are smaller. The lower lamina of the (pro-)bracts often bears extranuptial glands that excrete a sweet-tasting exudate taken up by ants (Fig. 2). Although Ilyas (1992) reports aggressive behavior of ants on Indian *C. grandis*, those observed on Tanzanian *C. grandis* (own observation, August 2009) and *C. grandiflora* (Zimmermann 1922) were not aggressive. Zimmermann, however, found that the ants attacked a caterpillar that he placed on a leaf. The extrafloral nectaries on the probracts may well help *Coccinia* to attract ants, which may then attack herbivores, such as caterpillars. In *Luffa aegyptiaca*, where ants are attracted by extrafloral nectaries, they significantly reduce the residence time of herbivores (Agarwal & Rastogi 2008). Bentley (1981) finds that climbing plants generally have significantly more extrafloral nectaries than non-climbers. This makes sense because climbers come in close contact with other plants, and arthropod herbivores might thus switch to the climber, which would increase the advantage of developing defense mechanisms. Although Agarwal and Rastogi in *Luffa* found an increase of numbers of extrafloral nectaries in older plants, they did not focus on density of glands as a potential reaction to grazing damage. As (pro-)bracts are caducous in some *Coccinia* species and gland density on the lower leaf lamina varies greatly, an adaptive reaction is a possibility.

Compared with the wealth of pollination and fruit dispersal modes in Cucurbitaceae (Schaefer & Renner 2011b), *Coccinia* species are rather uniform in their flowers and fruits. The number of flowers per node, shape and size of flowers, fruits, and seeds, and the coloration of unripe fruits vary, but in a manner unlikely to strongly influence these interactions. There are several observations of bee pollination, from small halictid bees to larger leaf cutter bees, *Megachile* spp., and honeybees, *Apis mellifera*. There is no known shift to another pollinator, although Ellis (P. Ellis 163 and 383) reports a smell of rotten meat in *C. ogadensis*. However, it is unclear, whether the smell was coming from the flower, which might indicate a pollinator shift to carrion flies, or from crushed vegetative parts. A putrid smell from crushed plant parts is well-known from *Momordica foetida* or *Kedrostis foetidissima* (Jacq.) Cogn. (Jeffrey 1967), but not reported from any *Coccinia* species. Flower sizes range from 0.7 to 4.5 cm in corolla length, and this may influence the spectrum of bee species, although no studies have been carried out. Whether the male and the female flowers produce similar amounts of nectar is unknown. In the male flowers, the pollen-foraging bees circle around the globular anther head and thus take up pollen ventrally (Zimmermann 1922; own observation, July 2009; chapter 4). In the female flowers, the three styles are fused and have three concave receptive surfaces or the receptive surfaces more or less form a head, then resembling the male anther head. The hypanthium in the female flower is glabrous, and if nectar is produced, then pollinators are forced to touch the stigmas to reach the nectar.

Fig. 2 Patrolling ants on a leaf of *Coccinia grandis*. They take up the sweet-tasting exudate from the glands on the lower lamina, but did not show aggressive behavior when disturbed. The probracts in this species are small and do not exhibit extranuptial glands. Picture taken in Pugu hills, Tanzania.

In contrast, the number of flowers per node greatly differs in both sexes. Single male flowers are common in *C. grandis* and *C. hirtella*, whereas all other species produce racemes, at least after some months, with three to twenty flowers. In non-rainforest species, female flowers commonly are produced as one flower per node, while in rainforest species, female flowers are mostly borne in racemes. The increase in number of female flowers per node seems to have evolved at least twice in *Coccinia*, because *C. grandiflora*, which is not closely related to the other rainforest species, also sometimes bears female racemes. As the fruits in

Coccinia are juicy berries, production of large numbers of fruits in drought-adapted species would be costly on resources and thus might be disadvantageous.

The coloration of unripe fruits may be taxonomically useful, for example, in the *C. rehmannii* clade. In the *adoensis* clade, some species, such as *C. grandis*, exhibit variability from green immature fruits with tiny white spots to conspicuous white longitudinal stripes. Others are entirely green when immature. For about 15 species, the coloration of their unripe fruits has not been reported. Seed morphology in *Coccinia* varies from flat to lenticular, and the seeds are up to 7 mm long and dispersed by birds or mammals. Seeds of the sister genus *Diplocyclos* are slightly larger, not as flat as *Coccinia* seeds, and black instead of grayish-beige (Jeffrey 1967), but are also believed to be dispersed by birds (Schaefer & Renner 2011b).

My crossing experiments and discovery of a natural sterile hybrid (Holstein & Renner 2010) suggest that some *Coccinia* species are not prezygotically isolated. However, all hybrid individuals turned out to be sterile, so even if reproductive success is reduced by interspecific fertilization, gene flow between species is prohibited. There are, however, still large gaps in knowledge, esp. in the *C. barteri* clade and the *C. adoensis* clade, only one species of which I had cultivation. Further experiments would clearly help to understand speciation and differentiation among similar morphs of a single biome.

Of the 25 species, six have had their chromosome counted, and four have $2n = 24$, which is also the most common number in the Cucurbitaceae (Beevy & Kuriachan 1996). In the *C. rehmannii* clade, a reduction to $2n = 20$ (own observation and A. Sousa, pers. comm.) occurred as implied by the phylogeny, but the stages and mechanism (loss or fusion) are unknown (Fig. 3).

The economic use of *Coccinia* is limited and mostly restricted to *C. grandis* in India and mainland Southeast Asia. Use of *C. grandis* is largely unknown in the Malesian archipelago (B.E.E. de Wilde and W.J.J.O. de Wilde, pers. comm.) and also in Africa although the young shoots are occasionally sold as vegetable on markets (Orech *et al.* 2005). As sweet cultivars of *C. grandis* exist in Asia, vitamin A deficiency could be fought by using this species as a crop. Despite the great possibilities due to the need of vitamin A sources and low-budged diabetes treatment, medical research on animal models has yet to be expanded to modern clinical tests. Apart from its traditional use (Chopra & Bose 1925) and small relatively recent studies (e.g.; Azad Khan *et al.* 1980; Venkateswaran & Pari 2002; Graidist & Purintrabipan 2009; Munasinghe *et al.* 2011), much is still unknown, and the successful application to diabetic rodents might not mean that there are no side effects or long-term effects in humans. Close relatives of *C. grandis* from Africa might harbor many genetic resources that are missing in Asian populations, but none of them has so far been studied.

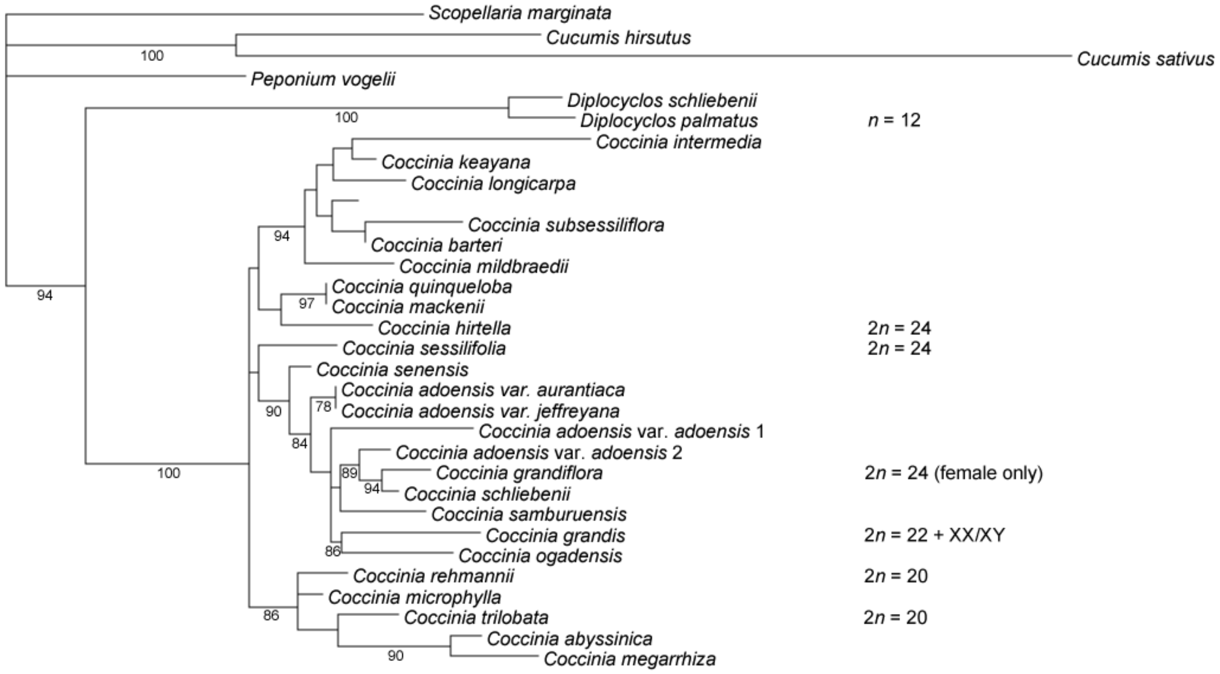

Fig. 3 Maximum Likelihood tree for *Coccinia* based on plastid molecular sequences, with all available chromosome counts shown on the right. The count for *Diplocyclos palmatus* is by McKay (1930) and that for *C. trilobata* by A. Sousa (LMU Munich, pers. comm.)

Evolution of Habitat Preferences

Only a few of the larger genera in the Cucurbitaceae are restricted to a single biome (*Cayaponia*, *Gurania*, *Hemsleya*, *Trichosanthes*), and more often, a high span in precipitation regimes (*Cucumis*, *Cyclanthera*, *Echinopepon*, *Kedrostis, Momordica*) can be observed. Even in small genera, such as *Ctenolepis*, different biomes can be occupied (Schaefer & Renner 2011b), but climatic variability, even of larger genera, is usually limited, leaving out one of the extreme habitats (rainforest or semi-arid habitats), such as in *Neoalsomitra*, *Peponium*, *Sicyos*, *Thladiantha*, and *Zehneria*. The broad climatic niche of *Coccinia* is surprising, especially as this genus is comparatively young with an age of about 7 Ma and not very species-rich (Holstein & Renner 2011a). Smith and Beaulieu (2009) found that woody lineages, with “woody” rather in a sense of shrubs or trees, occupy a smaller climatic range than herbaceous lineages. They interpreted their finding with the fact that trees and shrubs tend to have a longer generation time, as the first years are invested in growth rather than reproduction. Differences in generation time were found to be associated with differences in rates of climatic niche evolution. Although *Coccinia* species are perennial and due to their lignified tubers can be considered woody, their above-ground organs are herbaceous and behave like herbs, as most of the species that were cultivated during my studies flowered and fruited in the first year after germination. The storage organs just give an additional advantage, because failed sexual reproduction in one growing season would not eradicate a population. The (hemi-)cryptophytic behavior allows to survive grazing, fire, and drought. Interestingly, the formation of adventitious roots along shoots as an adaptation to disperse without seeds is only known from *C. barteri* and *C. grandis*, but apparently not widespread among *Coccinia* species.

Another finding of my studies is that species from humid habitats tend to have bifid tendrils, whereas species from semi-humid or semi-arid habitats have only simple tendrils. This might be explained by the higher biomass production in humid habitats. The increased weight might be stabilized by a second tendril arm. On the other hand, simple tendrils occur also in rainforest species, such as *C. keayana*, but also in other cucurbit genera, such as in *Ruthalicia* spp. Other Cucurbitaceae tendril-less species are creepers or shrubs with *Dendrosicyos socotranus* as the only example where the loss of functional tendrils is connected with a tree-like growth form (Schaefer & Renner 2011b). In each case, these species occur in rather dry habitats, where shadowing is negligible, and the need to reach the light and/or to present flowers above the shrub layer is minimized.

It was quite surprising that, given that only the number of arid months and annual precipitation were surveyed, six significant shifts in climatic niche were detected. Some further differentiation has not even been included, such as temperatures etc. *Coccinia mildbraedii* is clearly differentiated climatically as it only occurs in mountain forests, whereas all other closer relatives in the *C. barteri* clade are lowland species (Chapter 4). *Coccinia quinqueloba* occurs in coastal bushland with low monthly precipitation, but without any drought, whereas the sister species *C. mackenii* occurs in areas with significantly higher monthly precipitation (Holstein & Renner 2011a). The finding of six (seven) climatic niche shifts might therefore be an underestimation.

The existence of storage organs is a precondition for surviving drought, fire or grazing while maintaining the perennial life cycle. Speed of shoot growth and flower and fruit production might be more variable in perennial species as they can rely on stored nutrients and water. *Coccinia* species have evolved different adaptation to life in semi-arid habitats. In *C. sessilifolia*, all non-lignified parts are somewhat fleshy and have a waxy cover that likely protects the plant from consequences of high solar radiation and evaporation. In contrast, shoots of *C. microphylla* and *C. ogadensis* become dry soon and lignify, and they usually have small leaves or (sub-)linear leaf lobes respectively. In contrast, *Coccinia* species in rainforests are all very similar in their vegetative morphology. *Coccinia grandiflora*, which belongs to the *C. adoensis* clade and evolved in East Africa, is only barely differentiable from *C. barteri* or *C. mildbraedii* (*C. barteri* clade) mainly from the Central and West Africa when flowers or fruits are lacking. The loss of an obvious indument, leaf shape, bifid tendrils, female flowers in racemes, and an increased number of seeds per node (via larger or more numerous fruits) are clearly convergent due to adaption to the habitat. Similar adaptations also occur in *Ruthalicia* spp., *Peponium vogelii* and *Bambekea racemosa*, which also occur in African rainforests. The great similarity of several *Coccinia* species to members of other cucurbit genera (even from different tribes) is striking. *Coccinia adoensis* resembles some *Eureiandra* species (from a different tribe (Coniandreae)), which also occur in semi-humid habitats, such as woodlands, and *C. rehmannii* is similar to *Ctenolepis cerasiformis* and *Dactyliandra* species (each semi-arid bush lands). Therefore, it can be reasoned that ecological adaption led to convergent evolution in vegetative characters in Cucurbitaceae.

Evolution of Chromosomes and Sex Expression

Coccinia started its radiation about 7 Ma ago (Holstein & Renner 2011a). Of the six species with chromosome counts (Fig. 3), only two have had both sexes analyzed, while four others had either a male or a female looked at. As already presented in the introduction to this thesis (p. 9), *C. grandis* has a strikingly large Y chromosome. By contrast, male *C. hirtella* and *C. sessilifolia* lack heteromorphic sex chromosomes (chapter 4). Therefore it can be concluded that the sex chromosome heteromorphy evolved within the *Coccinia* crown group. As *C. grandis* seems to have evolved from *C. adoensis* clade, heteromorphic sex chromosomes might either be restricted to this species or occur in other species of this clade or possibly also the closely related *C. barteri* clade. Therefore, heteromorphic sex chromosomes in *Coccinia* have an age of less than 6 Ma.

All *Coccinia* species are dioecious. However, as I observed in herbarium specimens and also in the greenhouse, occasionally plants produce flowers of the opposite sex. Thus, a female herbarium specimen of *C. intermedia* with young fruits bore male flowers. However, the male flowers were not fully developed in this herbarium specimen, so it is not possible to say whether they would have been fertile or not (Holstein & Renner 2011b). In a cultivated *C. megarrhiza*, a fertile male plant produced a fertile female flower (chapter 4). When the female flower was blooming, however, the male flowers of the same plant did not open the pollen sacs. As it was late in the season, it is not clear, whether this was a coincidence or an active mechanism. These findings suggest that dioecy might occasionally give raise to monoecy, which fits with the observation that 50% of the Cucurbitaceae are monoecious, 50% dioecious, with numerous shifts with the genera that have been analyzed phylogenetically (in *Cucumis*, Renner *et al.* 2007; in *Bryonia*, Volz & Renner 2008; and in *Momordica*, Schaefer & Renner 2010). The occurrence of bisexual flowers in XX plants of *C. grandis* suggests that the unisexuality of the flowers is not stable. Although Kumar and Vishveshwaraiah (1952) report the pollen sacs to be sterile in bisexual flowers, Roy and Saran (1990) report fully fertile bisexual flowers in XX *C. grandis*. Although the degradation of the hemiploid sex chromosome (Y or W) due to the repression of crossing-overs is irreversible (Charlesworth & Charlesworth 2000), dioecy and dicliny are not dead ends, even in the presence of heteromorphic sex chromosomes. Given the speed of sex chromosome evolution in *Coccinia*, it is plausible that sex chromosomes have evolved in several clades and may have become lost again.

Plant sex chromosomes in general are thought to have evolved recently (Ming et al., 2011). Those angiosperm clades that have heteromorphic sex chromosomes bear out this expectation. The age of the Cannabaceae *sensu stricto* (*Cannabis sativus* and *Humulus lupulus* have heteromorphic sex chromosomes) has been estimated to 20 Ma ago in the early Miocene (Zerega *et al.* 2005). *Rumex* species with heteromorphic sex chromosomes (subgenus *Acetosella* and subgenus *Acetosa* p.p.) are monophyletic and the age of this clade has been estimated to about 12–13 Ma ago in the mid-Miocene (Navajas-Pérez *et al.* 2005). In *Silene*, sex chromosomes evolved once (Marais *et al.* 2011), and the age is assumed to be less than 10 Ma old (Nicolas *et al.* 2004; Marais *et al.* 2011). The heteromorphic sex chromosomes in *C. grandis* sex chromosomes may be among the youngest heteromorphic sex chromosomes known. This is striking as the Y chromosome is large and probably highly degraded by accumulation of repetitive elements.

Sex chromosomes are stable and old in many animal clades, such as *Drosophila* (63 Ma, Koerich *et al.* 2008), therians (> 144 Ma, Veyrunes *et al.* 2008), or lepidopterans (> 160 Ma, Traut *et al.* 2007), while plant sex chromosomes do not seem to have been advantageous over the long term. This might be due to the open bauplan, enabling plants to express both sexes simultaneously, but not necessarily in a single flower. The occasional restoration of hermaphroditism in *C. grandis* means that individuals may be able to reproduce even in this species with normally genetically fixed inheritance of sex.

General Conclusions and Outlook

My phylogenies based on plastid and nuclear data reveal a complex pattern of evolution in *Coccinia* in the different African regions. Knapp (1973) notes that several typical Miombo woodland tree species are closely related to perhumid rainforest species. From the species relationships seen in the trees, I infer the evolution of humidity-adapted species from progenitors adapted to semi-humid habitats. The origin of the enormous biodiversity in rainforests, but also the origin of species from other biomes is not well understood. The transition of clades between biomes may be an underestimated source contributing to modern biodiversity. The recent (< 4 Ma) corridor between Southwest and Northeast African arid biomes, often referred to as ‘arid track’ (Balinsky 1962; Jürgens 1997), in the Pliocene explains sister group relationships between species in these two arid regions (Schrire *et al.* 2009). Further research on the timing of biome connections and direction of dispersal would shed light of their origin.

The plastid “non-monophyly” of *C. adoensis* discovered here cautions against using single accessions from wide-spread species to infer the phylogeny of clades. It also raises the question about general patterns of speciation in woodland taxa in Africa. The fact that taxa from semi-humid habitats are intermediate between humid and semi-arid habitats suggests that during the late Neogene climatic oscillations, populations may have been separated and reconnected too frequently for allopatric speciation to lead to completely separate species. Ecological but not necessarily climatic differentiation between sister species in these taxa could be common. Recurrent partial hybridization and introgression during the Pliocene and Pleistocene might be a cause for blurry taxonomic boundaries of species, esp. in semi-humid topical habitats, but phylogeographic work is necessary to examine the role of the late Neogene climatic oscillations.

The present first monographic treatment of *Coccinia* (chapter 4) since 1881 not only summarizes the facts so far known, but arranges the fragmented data, expands the knowledge with own research, and combines these results. The production of phylogenetic data demonstrated the monophyly of the genus and its major clades, and crossing experiments were used to test species boundaries. With the nomenclatural problems now solved, the taxonomic treatment done, and the production of an identification key, *Coccinia* species can be identified and named correctly, so that scientists have a foundation for future research. *Coccinia* harbors many open questions to be examined, dealing with the evolution of sex chromosomes, chemical compounds for drug development, breeding of cultivars, investigating speciation along climatic gradients, impact of Pliocene and Pleistocene climatic oscillations, biogeography of African clades, and even the evolution of fire resistance. All these topics are discussed, or at least touched on, in my thesis, hopefully providing a jolt for further research.

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