

Leonardoxa africana (Leguminosae: Caesalpinioideae): a complex of mostly allopatric subspecies

Doyle B. MCKEY

Centre d'Écologie Fonctionnelle et Évolutive (UPR CNRS 9056),
Université Montpellier II, 1919 route de Mende, 34293 Montpellier cedex 05, France.
mckey@cefe.cnrs-mop.fr

ABSTRACT

As currently circumscribed, the genus *Leonardoxa* is restricted to the type species *L. africana* (Baill.) Aubrév., occurring in coastal forests of Lower Guinea. This work, based on field, greenhouse, and herbarium studies, demonstrates that *L. africana* is a complex of four closely related taxa, here treated as subspecies: *L. africana* subsp. *africana*, subsp. *gracilicaulis* McKey, subsp. *letouzeyi* McKey and subsp. *rumpiensis* McKey. The new taxa are described and relationships within the complex are discussed. The complex is interpreted as a ring species of mostly allopatric subspecies in which the two most extreme variants, the subspecies *africana* and *gracilicaulis*, have a narrow zone of sympatry in which they co-occur in the same communities and remain distinct. Data on ecology and natural history are presented, emphasising ant-plant interactions. Coevolutionary interactions with certain ants appear to be an important factor driving differentiation in this complex. Of the four subspecies, all but *gracilicaulis* are myrmecophytes, with swollen hollow stems occupied by symbiotic ants. Several traits show marked variation among different taxa of the complex. These include not only traits directly related to ant-plant interactions, but also others which are unrelated or only indirectly related to ants. Keys and range maps are presented for the four subspecies.

KEY WORDS

Leguminosae,
Caesalpinioideae,
Leonardoxa,
Africa,
polytypic species.

RÉSUMÉ

Leonardoxa africana (Leguminosae : Caesalpinioideae) : un complexe de sous-espèces en général allopatriques.

Le genre *Leonardoxa* est actuellement restreint à l'espèce type *L. africana* (Baill.) Aubrév., cantonnée dans les forêts côtières de Basse Guinée. Ce travail, basé sur l'étude des plantes sur le terrain, en culture en serre, et en herbarier, montre que *L. africana* est un complexe de quatre taxons très voisins, traités ici comme sous-espèces : *L. africana* subsp. *africana*, subsp. *gracilicaulis* McKey, subsp. *letouzeyi* McKey et subsp. *rumpiensis* McKey. Les taxons nouveaux sont décrits et les relations au sein du complexe sont discutées. Le complexe est interprété comme une espèce en anneau, composée de sous-espèces allopatriques. Au sein de ce complexe, les deux variantes les plus extrêmes, *L.*

MOTS CLÉS
Leguminosae,
Caesalpinioideae,
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espèce polytypique.

africana subsp. *africana* et subsp. *gracilicaulis*, ont une étroite zone de sympatrie, dans laquelle elles coexistent dans les mêmes communautés écologiques et restent distinctes. Des données sur l'écologie et l'histoire naturelle des différents taxons sont présentées, en insistant en particulier sur les interactions entre ces plantes et les fourmis. Des interactions coévolutives avec certaines fourmis semblent un facteur important dans la différenciation du complexe. Des quatre sous-espèces, toutes sauf *gracilicaulis* sont des myrmécophytes, possédant des tiges renflées et creuses habitées par des fourmis symbiotiques. Plusieurs caractères, non seulement ceux qui concernent les interactions avec les fourmis mais aussi d'autres non (ou seulement indirectement) liés à la myrmécophilie, montrent une variation importante entre les différents membres du complexe. Des clés de détermination et des cartes de répartition géographique sont présentées pour les quatre sous-espèces.

The genus *Leonardoxa* Aubrév. of the caesalpinoid tribe Detarieae DC. was originally erected to house three Central African species segregated from *Schotia* (southern Africa) by AUBREVILLE (1968), based largely on studies by LÉONARD (1957). Following the removal of the two Congo-basin species *L. romii* (de Wild.) Aubrév. and *L. bequaertii* (de Wild.) Aubrév. by LÉONARD (1993) to constitute the new genus *Normandiodendron*, the sole remaining member of the genus is the type species, *L. africana* (Baill.) Aubrév. LÉONARD (1993) presents a comprehensive discussion of the taxonomic and nomenclatural history of *Leonardoxa* and a description and diagnosis of the genus (and species) as currently circumscribed.

Some of the traits considered by LÉONARD (1993) as characteristic of *L. africana* are in fact quite variable geographically. Extensive field studies have demonstrated the morphological and ecological heterogeneity of what is so far known simply as *L. africana* (McKEY 1984; CHENUIL & McKEY 1996; GAUME 1998; GAUME et al. 1997, 1998; GAUME & McKEY 1998, 1999). An earlier study (McKEY 1991) outlined this variation and (prematurely) proposed names for three taxa. However, these names were never validly published, and since that study additional information has come to light. Here, variation in *L. africana* is described in detail. The patterns of variation show this species to be an assemblage of four closely related, yet morphologically and ecologically distinct, taxa. Justification is presented

here for considering *L. africana* as a complex of four subspecies. Because no valid names are available, the newly recognised taxa are formally named and described.

THE *LEONARDOXA AFRICANA* COMPLEX

The range of *Leonardoxa africana* extends from Gabon and Equatorial Guinea northward through southwestern Cameroon and into extreme southeastern Nigeria. The species has long attracted attention as a myrmecophyte (BEQUAERT 1922; MILDBRAED 1922; SCHNELL & BEAUFORT 1966; ELIAS 1980; McKEY 1984; LÉONARD 1993). SCHNELL & BEAUFORT (1966), however, noted that swollen-stem myrmecodomatia were present only in some of the specimens from Cameroon they examined and were consistently absent from specimens collected from elsewhere in the range of the species, notably Gabon. LETOUZEY, the botanist who collected most widely in Cameroon, also noted the geographic heterogeneity of *L. africana* in presence vs. absence of swollen internodes (LETOUZEY 1985; see also notes accompanying numerous specimens and unpublished field notes).

Field, greenhouse and herbarium studies reported on here demonstrate that *L. africana* is heterogeneous in this and many other characters. The variation concerns several traits that are obviously related to symbiosis with ants (ant-domatia, foliar nectaries), as well as other vegetative char-

acters not directly related to ant-plant interactions (architectural differences related to rhythms of growth), and some floral characters (cauliflory, flower colour).

Some of the characters examined here merit special attention. Traits of myrmecodomatia have not often been used in taxonomic studies of groups including myrmecophytes, possibly because botanists have often mistakenly regarded these structures as galls, induced or altered in form by insects or other agents (see, for example, SCHNELL & BEAUFORT 1966).

In *Leonardoxa*, there is variation among the taxa recognised here not only in presence or absence of ant-domatia, but also in several aspects of their structure, and in the timing of onset of expression of these specialised stem swellings in the ontogeny of the plant.

Traits related to the phenology of vegetative growth are likewise rarely considered in taxonomic studies. Rhythmic growth of shoots characterises all *L. africana*, but the taxa recognised here differ in the number of internodes produced in each spurt of growth (a difference with architectural consequences, evident on both living plants and herbarium specimens) and in the degree to which growth is synchronised among branches (evident only on living trees). Differences in all these traits persist when plants are grown in greenhouses without ants, in common gardens, and in the one known instance when two taxa occur together in the same habitat. Differences in these traits are genetically based and taxonomically informative.

Discontinuities in variation in these and other characters consistently reveal a pattern of four distinct taxa, mostly allopatric in distribution. These new taxa are here described as subspecies of *L. africana*, reflecting the opinion that these taxa are not yet completely differentiated and reproductively isolated species. Three of the four subspecies are myrmecophytes, with swollen stems that form myrmecodomatia and house symbiotic ants. The fourth is not a myrmecophyte but, like the other subspecies (as well as many other Detarieae), possesses foliar nectaries, which attract a diversity of non-resident ants. Experimental and observational field studies (MCKEY 1991; GAUME et al. 1997,

1998; GAUME & MCKEY 1998, 1999; GAUME 1998) show that the four taxa recognised here are not only morphologically but also ecologically distinct. Although apparently only incompletely differentiated, they appear to be following independent evolutionary trajectories. This is most clearly illustrated by the coexistence in at least one site of the non-myrmecophyte and the most highly specialised of the myrmecophytes (degree of specialisation being defined in terms of the number of new characters derived since divergence from the common ancestor). In sympatry, these two taxa remain morphologically and ecologically distinct, suggesting the existence of barriers to gene exchange. Molecular genetic studies (BROUAT et al., in press; C. BROUAT, unpublished data) confirm the distinctness of these coexisting populations and support the taxonomic separations made here on morphological grounds. These studies also suggest past or present gene flow between these taxa.

MATERIALS AND METHODS

Field studies

Preliminary field and herbarium observations indicated that a number of characters were geographically variable in the complex. To sample this variation, field studies of *L. africana* were conducted in a total of 32 sites in Cameroon (Table 1). These sites provided good coverage of the geographic range of all four taxa recognised here. In each site, the following characters were studied: number, size and distribution of foliar nectaries, dimensions of internodes, characteristics of myrmecodomatia (if present), number of leaflet pairs, phenology of vegetative growth, position of inflorescences (on young twigs, ramiflorous or cauliflorous), and flower colour. Plants of all sizes were examined to determine patterns over plant ontogeny in traits of leaves and internodes.

As in most plants with rhythmic growth, one or more scale leaves are produced at the base of each unit of growth prior to the normal foliage leaves. In this paper, the number of internodes in

TABLE 1. — Populations of the *Leonardoxa africana* complex studied in the field.

Group	Site	Altitude	Lat.	Long.	Abundance	Maximum size
1	Mbalmayo	640 m	3°28'N	11°30'E	rare, restricted to riparian forest	25 cm DBH, 14 m tall
	Mt. Kala	1100 m	3°50'	11°21'	abundant in submontane forest on hill summit	45 cm DBH
	Ebogo	630 m	3°24'	11°28'	patchily common, restricted to riparian forest	20 cm DBH
	Mbankolo	900 m	3°55'	11°28'	abundant in relict patches of submontane forest on hill summit	43 cm DBH
	Abang	670 m	3°23'	11°32'	rare, restricted to riparian forest	only 2 saplings found
	Zingui base	550 m	2°49'	10°58'	rare	4 m tall
	Zingui hill	970 m	2°49'	10°59'	abundant in submontane forest on hill summit	to at least 16 cm DBH
	Akom II	400 m	2°48'	10°34'	rare, restricted to riparian forest	5 m tall, plus sucker shoots from cut stumps
	Essangmvout	650 m	2°49'	12°16'	only 2 individuals found, riparian forest	only 2 saplings found
	Nkolobounde	70 m	3°14'	10°15'	patchily abundant, restricted to riparian forest	40 cm DBH
	Nta Ali	1200 m	5°36'	9°30'	abundant in submontane forest on hill summit	32 cm DBH
2	Big Ngwandi	850 m	4°47'	9°14'	common in submontane forest	35 cm DBH
	Betenge	850 m	4°50'	9°12'	common in submontane forest	no data
	Dikome Balue	1100 m	4°55'	9°15'	common in submontane forest	20 cm DBH
	Madie River	1000 m	4°59'	9°14'	common in submontane forest	largest trunks 10-12 cm DBH
	Ibemi	450 m	5°03'	9°20'	rare, only 4 trees found in riparian forest	35 cm DBH
3	Akpasang	40 m	5°01'	8°44'	common, restricted to riparian forest	7 m tall, 13 cm DBH
	Rengo Rock	100 m	5°02'	8°50'	common, restricted to riparian forest	12 m tall, 22 cm DBH
	Fabe Road	100 m	5°04'	8°58'	common, restricted to riparian forest	20 cm DBH
	Iriba Inene	80 m	5°06'	8°53'	common, mostly in riparian forest	18 cm DBH
	Islaib Road	300 m	5°15'	9°20'	locally common in riparian forest	30 cm DBH
	Bayenti	250 m	5°21'	9°25'	rare, in riparian forest	only 3 saplings found

Group	Site	Altitude	Lat.	Long.	Abundance	Maximum size
	Eyang Atem Ako	230 m	5°28'	9°29'	uncommon in riparian forest, 4 individuals found	8 cm DBH
	Fainchang	200 m	5°37'	9°30'	rare, in forest near base of Nta Ali; 3 trees found	20 cm DBH
4	Douala-Edea Reserve	10 m	3°35'	9°54'	locally common, especially along streams and in swamps, but not restricted to these habitats	26 cm DBH
	Grand Zambi	60 m	3°03'	10°17'	common, mostly in riparian forest	no data
	Ebodie	20 m	2°34'	9°50'	locally abundant, especially along streams, but not restricted to riparian forest	15 cm DBH
	Mamelles	60 m	2°34'	9°53'	locally abundant, especially along streams, but not restricted to riparian forest	up to 10 m tall
	Akanga	60 m	2°48'	10°18'	locally common	no data
	Nkongmintom	60 m	2°48'	10°09'	only one sapling found	no data
	Nkolobounde	70 m	3°14'	10°15'	common, especially along streams, but not restricted to riparian forest	several to 16 cm DBH, 1 to 48 cm DBH
	Bombe Bakundu	55 m	4°26'	9°29'	locally abundant, mostly in riparian forest	7 m tall, 8 cm DBH

a unit of growth refers to those with a normal foliage leaf at the apex.

To characterise patterns of morphological similarity among field populations, principal components analysis (PCA) using the PRINCOMP procedure of SAS (SAS 1996), was conducted. The matrix used in the PCA included seven variables and 21 sites. The variables were: modal number of leaflet pairs, mean size of largest leaflets, mean size of the unit of growth (number of leaves and internodes produced simultaneously by a branch tip), mean number of nectaries per basal leaflet, nectary size (small or large), presence/absence of domatia, and timing of onset of domatia (seedling or sapling). This analysis

requires a matrix with no missing data. Thus, position of inflorescences and flower colour could not be used, because information on these were missing for too many sites.

Eleven of the 32 sites (Mbalmayo, Mbankolo, Zingui base, Zingui hilltop, Ibemi, Akpasang, Rengo Rock, Douala-Edea, Mamelles, Akanga, and Nkongmintom) had missing data for one or more of the seven characters retained, and were also excluded from the analysis.

Greenhouse and common-garden studies

It could be postulated that differences observed among allopatric populations are environmentally rather than genetically based and are thus

taxonomically uninformative. As a partial test of this possibility, plants from two populations presenting contrasts in numerous characters were grown in a common greenhouse environment. Rooted cuttings of 23 plants from Rengo Rock and 8 plants from Bombe Bakundu were potted in a greenhouse at the University of Miami in 1986-1987. The differences observed in the field between plants of these two populations concern both characters related to interaction with ants and others apparently unrelated. Development of new shoots on the greenhouse-grown cuttings was monitored to examine whether these differences persisted in this common environment. The six-month period during which these plants could be maintained was too short to study traits expressed only in large plants (floral characters, but also number of leaflet pairs, which rarely exceeded two in these small cuttings), but three characters could be compared: number of nectaries per leaflet, size of leaflets, and the onset of internodal swelling (precocious or delayed) in ontogeny of a shoot. Analysis of variance was used to compare the first two characters in plants from the two sites. Fixed model ANOVA (PROC GLM, SAS [SAS 1996]) was performed on an overall model including site, individual (nested within site), and leaf (nested within individual). Nectary number was first logarithmically transformed to achieve a normal distribution.

In a further attempt to compare characters of plants from different provenances in a common environment, rooted cuttings from several populations of *L. africana* (Isaib Road, Eyang Atem Ako, Dikome Balue, Fainchang, Nta Ali, Bombe Bakundu, and Mamelles; see Table 1), representing a substantial part of the observed morphological variation, were planted in December 1989 in an experimental garden placed in primary forest understory along the banks of a small stream in the Mamelles site. Leaf and stem characters of new shoots produced by these cuttings were recorded in October 1991. Numbers of surviving individuals from several of these populations were too small to permit statistical analysis of the results, but observations of these plants did provide some useful information complementing other parts of the study.

Herbarium studies

Material was examined from 87 different collections of *L. africana* from ten herbaria: BAS, BR, G, K, MO, P, US, WAG, YA and Z (acronyms following HOLMGREN et al. 1981). Herbarium specimens were systematically examined for traits shown in field and greenhouse studies to vary among populations. These included the number and size of leaflets, and the number, size and distribution of foliar nectaries, which were evident only on exposed abaxial surfaces of leaflets. Some collections had no leaves with abaxial surfaces exposed, so that nectaries on these could not be counted. Presence and dimensions of swollen internodes could be straightforwardly determined. Also, in the myrmecophytes, number of internodes in each unit of growth was usually easily determined. In young twigs of these plants, not yet greatly affected by secondary thickening, nodes marking interruptions of growth are constricted, while those within a unit of growth are not; furthermore, only the terminal internode of a unit of growth bears an entrance hole. It was impossible to determine unit of growth on herbarium specimens of non-myrmecophytes. Information on location of inflorescences on the plant (cauliflorous, ramiflorous, or on small twigs) and on corolla colour, when described on notes accompanying flowering specimens, was also recorded. Herbarium specimens examined are listed in Table 2.

Very few collections were accompanied by notes with precise geographic coordinates. Coordinates of most collection localities were determined using gazeteers (U.S. BOARD ON GEOGRAPHIC NAMES 1962-1971), or by plotting collection localities onto 1:200,000 topographic maps (Centre Géographique National, Yaoundé) and determining coordinates from these. Collection localities of Le Testu in Gabon were determined following RAYNAL (1968). Localities for several collections could be determined only approximately. For preparing the distribution map, the collection *Chevalier s.n. (A. Baudon)* from Paris ("Mbouamo (Sangha) French Congo", not found in the gazeteer) was placed, as a conservative measure, in extreme northwestern Congo (Brazzaville), near many collection localities in Cameroon and Gabon. For similar reasons, the collection

TABLE 2. — Herbarium specimens of the *Leonardoxa africana* complex examined in this study.

Group	Collection	Herbaria	Collection locality	Lat.	Long.	Elev. (if noted on label)
1	<i>Bates 1660</i>	MO	Bitye	3°01'N	12°22'E	
	<i>Breteler & de Wilde 226</i>	WAG	15 km rd Assok to dam Tchimbele River	0°37'	10°25'	ca. 600 m
	<i>Breteler & de Wilde 704</i>	WAG	24 km along SOMIFER rd to Makokou			950-1000 m
	<i>Chevalier s.n. (A. Baudon) Dang 651</i>	P	Mbouamo (Sangha), French Congo	?	?	
		P, YA	Colline Nkomnyat, 4 km N of Ekekam	3°55'	11°22'	1090 m
	<i>de Wilde 1332</i>	BR, K, MO, WAG, YA, Z	50 km NW Eseka	3°56'	10°27'	
	<i>de Wilde 1862</i>	BR, K, MO, P, WAG, YA	5 km S Mbalmayo, forest along the Nyong River	3°28'	11°30'	
	<i>Eckendorff 128</i>	P	Village Manyal, bord Ivindo	0°59'	12°59'	
	<i>Fcam 1161</i>	P, YA	Makak	3°33'	11°02'	
	<i>Klaine 3361</i>	P	near Libreville	0°23'	9°27'	
	<i>Le Testu s.n.</i>	B, K, MO	Woleu-Ntem, region entre Ogooué and Cameroun	1°37'	11°35'	
	<i>Le Testu 8888</i>	BR, K, MO	Mambanza, circonscription de Djoua, Gabon	0°42'	13°25'	
	<i>Le Testu 8995</i>	BR, P	Ossok (=Assoc) -Ngoum, Gabon, region between Ogooué and Cameroun	1°42'	11°38'	
	<i>Le Testu 9079</i>	BR, P	Gabon, region between Ogooué and Cameroun	1°37'	11°35'	
	<i>Letouzey 9371</i>	P, WAG, YA	Colline Ngwon, 38 km E Kribi	2°49'	10°10'	
	<i>Letouzey 10158</i>	BR, K, P, WAG, YA	Evelessi, 30 km W Sangmelima	2°58'	11°42'	
	<i>Letouzey 10201</i>	BR, K, P, WAG, YA	Colline Ongongondje near Akonekye, 15 km NW Ambam	2°28'	11°11'	
	<i>Letouzey 13885</i>	YA	summit of Nta Ali, 1266 m, 30 km SE Mamfe	5°36'	9°30'	
	<i>Manning 2157</i>	MO	hill near Mt. Febe, Yaoundé	3°52'	11°31'	
	<i>Manning 1397</i>	MO	3 km WNW Bipindi	3°06'	10°22'	120 m
	<i>Mildbraed 8065</i>	K	20 km NE Yaoundé, S of Sanaga, near union of Sanaga and Djerem	?	?	
<i>Mpom 303</i>	P, YA	km 14 from Douala, old Douala-Edea road	4°08'	9°50'		
<i>Soyaux 104</i>	K, P	Sibange-Farm, Gabon	0°25'	9°31'		
<i>Staudt 427</i>	G, K	Lolodorf	3°14'	10°44'		
<i>Tessmann 284a</i>	K	Nkolentangun, Eq. Guinea, Nscha'bat	?	?	450 m	
<i>Villiers 807</i>	P	colline Nkoltsia, near Gouap (?), 18 km NW Bipindi	3°10'	10°15'		

Group	Collection	Herbaria	Collection locality	Lat.	Long.	Elev. (if noted on label)
	<i>Zenker s.n.</i>					
	Bipinde Mimfia	BR,MO,P	Bipindi	3°05'	10°23'	
	<i>Zenker ed.</i>					
	<i>Weigel 37</i>	G,US,WAG	Bipindi	3°05'	10°23'	
	<i>Zenker 1696</i>	K,MO,WAG	Bipindi	3°05'	10°23'	
	<i>Zenker 1698</i>	BR	Bipindi	3°05'	10°23'	
	<i>Zenker 2255</i>	K	Bipindi	3°05'	10°23'	
	<i>Zenker 2255b</i>	BR,G,K,P, WAG,Z	Bipindi	3°05'	10°23'	
	<i>Zenker 2303a</i>	K,P	Bipindi	3°05'	10°23'	
	<i>Zenker 2989a</i>	BR,K,P,WAG	Bipindi	3°05'	10°23'	
	<i>Zenker 3747</i>	MO	Bipindi	3°05'	10°23'	
	<i>Zenker 4545</i>	BR,K	Bipindi	3°05'	10°23'	
	<i>Zenker 4972</i>	BR,K,MO	Bipindi	3°05'	10°23'	
2	<i>Letouzey 13632</i>	K,P,YA	Colline 960 m (près cote 897) E of piste Abakpa-Mbiofong, 55 km SW Mamfe	5°23'	8°58'	960 m
	<i>Letouzey 14577</i>	K,P,YA	Dikome Balue, 35 km NNW Kumba steep hillside	4°55'	9°15'	1200 m
	<i>Thomas et al. 7988</i>	MO	5 km W Esukutang village	5°23'	8°59'	400-850 m
	<i>Thomas & Namata 7746</i>	MO	around Masaka- Batanga	5°06'	9°10'	500 m
	<i>Nemba et al. 753</i>	MO	around Meta village, 5hrs walk N	5°03'	9°01'	500 m
3	<i>Coombe 191</i>	BR,K	Bamenda rd, mile 43 from Mamfe, alt. 1500 ft.	5°42'	9°40'	ca. 450 m
	<i>Latilo 35</i>	BR,K,P	Uwet Division, Calabar River, Calabar Province	5°10'	8°10'	
	<i>McKey 72</i>	P,YA	Akpasang River Camp, Korup	5°01'	8°44'	
	<i>Manning 1714</i>	MO	Korup NP, just W of 1st camp along EW path from Mana River ft bridge to camp 1	5°01'	8°51'	100 m
	<i>Talbot 1440</i>	K	Oban, S. Nigeria	?	?	
	<i>Thomas 4269</i>	BR,US	Ndian plantation, disturbed forest N of Field 70	5°02'	8°53'	50 m
	<i>Thomas 4527</i>	MO	Takamanda Forest Reserve, near Matene	6°14'	9°19'	170 m
	<i>Thomas et al. 7480</i>	MO,WAG	S of Baro village	5°14'	9°15'	250 m
4	<i>Bos 3630</i>	BR,WAG,YA	12 km from Kribi, Lolodorf rd	2°59'	9°59'	
	<i>Bos 3913</i>	BR,YA	19 km from Kribi, 5 km N of Lolodorf rd	3°02'	10°03'	

Group	Collection	Herbaria	Collection locality	Lat.	Long.	Elev. (if noted on label)
	<i>Bos</i> 4074	BR, YA	18 km from Kribi, Lolodorf rd	3°00'	10°02'	
	<i>Bos</i> 6233	WAG	30 km from Kribi, Ebolowa rd	2°49'	10°07'	
	<i>Bos</i> 7058	WAG	near Kribi	?	?	
	<i>Bos</i> 7315	BR	km 45 Kribi-Campo	2°38'	9°51'	
	<i>Bounougou</i> s.n.	BR	near Edea	3°48'	10°08'	
	<i>Breteler et al.</i> 2580	BR, K, P, WAG, YA	24 km E Douala	4°02'	9°57'	100 m
	<i>de Kruif</i> 994	WAG	nr Bipega II, Km 40 Kribi-Edea	3°09'	10°01'	ca. 30 m
	<i>Endingle</i> 2105	BR, K, P, YA	route Razel, Douala	4°03'	9°42'	
	<i>Farron</i> 7181	BAS, P, YA	Bipindi	3°05'	10°25'	
	<i>FHI</i> 29369	K	Kumba forest nursery (from Southern Bakundu Forest Reserve)	4°28'	9°23'	
	<i>FHI</i> 29511	K	Southern Bakundu Forest Reserve	4°28'	9°23'	
	<i>FHI</i> 29672	K	S. Bak. Forest Reserve	4°28'	9°23'	
	<i>FHI</i> 41007	K	S. Bak. Forest Reserve	4°28'	9°23'	
	<i>Fleury</i> 33346	K, P	Forêt de Yelfoume, near Douala	4°03'	9°42'	
	<i>Jones</i> 9499	K, P	Banga, Southern Bakundu Forest Reserve	4°24'	9°27'	
	<i>Leeuwenberg</i> 5500	BR, K, MO, P, WAG, YA	60 km S Edea, S of Mboké, 11 km E of km 58 of Edea-Kribi rd	3°20'	10°10'	100 m
	<i>Letouzey</i> 4140	P, YA	near Bella (45 km NE Kribi)	3°15'	10°13'	
	<i>Mann</i> 726	BR, K, P	Cameroon River	4°13'	9°45'	
	<i>Manning</i> 1499	BR, K, MO, P	1 km W Bombe Bakundu	4°26'	9°29'	
	<i>Manning</i> 1517	MO	near Kindonge Camp, Southern Bakundu Forest Reserve, ca. 10 km SSE Kumba	4°22'	9°36'	240 m
	<i>McKey & Gartlan</i> 120	K	Lake Tissongo, Douala-Edea Reserve	3°35'	9°54'	
	<i>Mpom</i> 227	MO, P, YA	2 km from forest camp of Nkol-Bewa	2°49'	10°09'	
	<i>Mpom</i> 283	YA	village Edoudouma, km 32 road to Nkolbewa	2°48'	10°09'	
	<i>Mpom</i> 303	BR	km 14 from Douala, old Douala-Edea road	4°08'	9°50'	
	<i>Mpom</i> 343	YA	Edea, Eaux et Forêts Mangombe	3°49'	10°07'	

Group	Collection	Herbaria	Collection locality	Lat.	Long.	Elev. (if noted on label)
	<i>Thomas 167</i>	YA	Lake Tissongo, Douala-Edea Reserve	3°35'	9°54'	
	<i>Villiers 775</i>	P	colline Nkoltsia	3°10'	10°15'	
	<i>Waterman & McKey 846</i>	K	Lake Tissongo, Douala-Edea Reserve	3°35'	9°54'	
	<i>Zenker s.n.</i>	BR,P	Bipindi	3°05'	10°23'	
	<i>Bipinde Mimfia</i>					
	<i>Zenker 52</i>	WAG	Bipindi	3°05'	10°23'	
	<i>Zenker 1074</i>	K,MO,P, WAG	Bipindi	3°05'	10°23'	
	<i>Zenker 2967</i>	BR,K,P, WAG	Bipindi	3°05'	10°23'	
	<i>Zenker 4183</i>	BR,K,P	Bipindi	3°05'	10°23'	
	<i>Zenker 4495</i>	BR,K,MO	Bipindi	3°05'	10°23'	

Tessmann 284a ("Nkolentangu, Nscha'bat" in Equatorial Guinea), was arbitrarily placed in the eastern part of this country. The two collections from Nigeria (*Latilo 35* and *Talbot 1440*) could likewise be only approximately placed on the map. Label notes for one collection (*Mildbraed 8065*, K) contain contradictory locality information, indicating that the specimen was collected not far from the confluence of the Lom (Sanaga) and Djerem rivers, and about 20 km northeast of Yaoundé. This collection was not included on the map.

RESULTS

FIELD STUDIES

Characters directly related to interactions with ants

Myrmecodomatia

As shown in Table 3, presence or absence of swollen internodes was constant within each population. Only one population of non-myrmecophytes (at the summit of Nta Ali) included some individuals apparently intermediate for this trait. One tree in this population was observed to have slightly but noticeably swollen internodes. This population, found much further north than any

other population of non-myrmecophytes studied, is restricted to a small patch of submontane forest on the summit of an isolated 1266 m hill. Myrmecophytic *Leonardoxa* occur in lowland forest at the base of the hill (Fainchang, Table 1), and the Nta Ali population may be affected by hybridisation. The slightly swollen internodes of Nta Ali plants had not been entered by ants, and were probably too small to have functioned as ant-domatia.

Domatia presence or absence showed a distinct geographic pattern. Populations from southern Cameroon east of the coastal plain were all non-myrmecophytic; populations from other areas were usually myrmecophytic. However, in the coastal plain both myrmecophytic and non-myrmecophytic populations can be found, and in one of the field sites, Nkoloboundé, myrmecophytes and non-myrmecophytes occur side by side in the same forest (without intermediate individuals, except for a few juveniles).

In populations with domatia, stems were markedly swollen, with thick pith hollowed out by ants that inhabited the resulting cavities. Principal ant associates of *Leonardoxa* were geographically variable (Table 3). Each pith-cavity is a discrete nest chamber, separated from contiguous ones by a woody septum, without pith, and

each cavity has its own entrance hole. The entrance hole is chewed at a characteristic location on the twig, at the apex of the ant-domatium on the side opposite the leaf insertion. This is the location of the prostoma, a small unlignified area that, as in some other myrmecophytes, is an adaptation facilitating entry by ants (DAVIDSON & MCKEY, 1993). The prostoma is present in all myrmecophytic *L. africana*. It is evident on young twigs as a slight protuberance differing in colour (reddish) from the rest of the twig (green). Histologically, it is a well-defined highly localised gap in a sclerenchyma layer that otherwise completely encloses the domatium (Carine BROUAT, unpublished). The prostoma varies in shape among populations (Table 3). In populations from the coastal plain of Cameroon, the prostoma is elliptic-oblong; in other populations further north, the prostoma is round. The shape of the prostoma, a genetically determined structure of the plant, corresponds to the shape of the entrance hole made by the principal ant associate, which in turn reflects the shape of the ant itself. The ants associated with myrmecophytes occurring to the north of the coastal plain make round entrance holes. In contrast, with one exception (Bombe Bakundu, the northernmost population in the coastal plain), *Leonardoxa* with elliptic-oblong prostomata are associated with *Petalomyrmex phylax*. This ant is completely restricted to these coastal-plain *Leonardoxa africana* as its sole host (SNELLING 1979; MCKEY 1984, 1991). *Petalomyrmex* make slit-like entrance holes, and its highly specialised dorsiventrally flattened alates fit the entrance slits like a key fits a lock (MCKEY 1984). Histological studies in progress that quantify prostoma dimensions (Nelly GARCIA, unpublished data) confirm the qualitative observations presented in Table 3.

Also constant within each population of myrmecophytes, but variable among populations, is the stage in plant ontogeny when ant-domatia are first produced (Table 3). In populations from the coastal plain of Cameroon, swollen internodes first appear in seedlings, often the second or third leaf-bearing internode produced by the plant when it is no more than 20 cm tall (see Fig. 2B in LÉONARD [1993]). With one exception (again the northern outlier Bombe Bakundu),

these myrmecophytes with precociously expressed domatia are associated with *Petalomyrmex*. In myrmecophytes from more northerly populations, domatia first appear substantially later in ontogeny, in saplings 50-75 cm or more tall.

Foliar nectaries

The crateriform foliar nectaries on abaxial surfaces of leaflets of *L. africana* were first described in detail by ELIAS (1980). Nectaries similar in external aspect are quite widespread in Detarieae and Macrolobieae, being present not only in the myrmecophyte-containing genera *Leonardoxa* (ELIAS 1980; MCKEY 1984; LÉONARD 1993) and *Humboldtia* (BOWER 1887; KROMBEIN et al. 1999) but also in numerous other genera, such as *Normandi dendron*, *Afzelia*, *Loesenera*, *Hymenostegia* and *Plagiosiphon*, where they attract opportunistic ants (D. MCKEY, unpublished). In *Leonardoxa*, nectaries are located at the very base of the leaflet, near the midrib, and their number depends strongly on leaflet position, being greatest on proximal leaflets and least on distal leaflets. While these nectaries are present in all populations, there was great variation among populations in their size, number per leaflet (at the same position), and extent of inter-tree variation in number (Table 3). In non-myrmecophytic populations, nectaries were small (similar in size to those of other "myrmecophilic" caesalpinoids), few, and variable in number. In myrmecophytic populations, nectaries were larger, in keeping with their importance as a food source for symbiotically associated mutualist ants. Among the myrmecophytes, three geographically cohesive groups were defined by variation in number of nectaries per basal leaflet. All populations from the coastal plain were characterised by a mode of three nectaries per basal leaflet, and the mean number of nectaries per basal leaflet varied little among populations (2.68-3.47). Once again, these populations were differentiated from those further north, in which nectaries were fewer. However, these northern myrmecophytic populations were also heterogeneous for this trait. Those from submontane forest in the Rumpi Hills all had a mode of two nectaries per basal leaflet, and the mean number varied relatively little among

TABLE 3. — Variation among field populations in characters directly related to interaction with ants.

Group	Site	Domatia ¹	Prostoma ²	No. nectaries on proximal leaflets			Nectary size ³	Ant associates
				Mode	Mean	Range		
1	Mbalmayo	A	A	1	0.98	0-6	S	diverse arboreal ants
	Mt. Kala	A	A	0	0.64	0-3	S	diverse arboreal ants; few ants at nectaries
	Ebogo	A	A	1	1.05	0-5	S	diverse arboreal ants; ants abundant at nectaries
	Mbankolo	A	A	0	0.61	0-4	S	no ants observed at nectaries
	Abang	A	A	1	1.53	0-6	S	no ants observed at nectaries
	Zingui base	A	A	1	0.87	0-2	S	no ants observed at nectaries
	Zingui hill	A	A	1	1.2	1-2	S	no ants observed at nectaries
	Akom II	A	A	0	0.16	0-1	S	diverse arboreal ants; few ants at nectaries, and tending membracids on twig surfaces
	Essangmvout	A	A	2	2.13	1-4	S	no ants observed at nectaries
	Nkolobounde	A	A	1	1.11	0-3	S	diverse arboreal ants, relatively common at nectaries
	Nta Ali	A (slight swellings rare)	A (sometimes intermediate)	0	0.45	0-3	S	no ants observed at nectaries
2	Big Ngwandi	P,L,S	P,C	2	2.57	0-5	L	numerous spp. of twig-nesting ants
	Betenge	P,L,S	P,C	2	2.29	0-5	L	numerous spp. of twig-nesting ants
	Dikome Balue	P,L,S	P,C	2	1.97	0-4	L	numerous spp. of twig-nesting ants
	Madie River	P,L,S	P,C	2	1.99	1-4	L	numerous spp. of twig-nesting ants
	Ibemi	P,L,S	P,C	2	1.61	0-3	L	numerous spp. of twig-nesting ants
3	Akpasang	P,L,S	P,C	0	0.62	0-3	L	<i>Aphomyrmex afer</i> ^A
	Rengo Rock	P,L,S	P,C	1	1,00	0-5	L	<i>Aphomyrmex afer</i> ^A
	Fabe Road	P,L,S	P,C	0	0.18	0-2	L	<i>Aphomyrmex afer</i> ^A
	Iriba Inene	P,L,S	P,C	0	0.41	0-2	L	<i>Aphomyrmex afer</i> ^A
	Islaib Road	P,L,S	P,C	0	0.54	0-2	L	<i>Aphomyrmex afer</i> ^A
	Bayenti	P,L,S	P,C	1	1.09	0-2	L	<i>Aphomyrmex afer</i> ^A
	Eyang Atem Ako	P,L,S	P,C	0	0.11	0-1	L	<i>Aphomyrmex afer</i> ^A
	Fainchang	P,L,S	P,C	0	0.54	0-2	L	<i>Aphomyrmex afer</i> ^A
4	Douala-Edea Reserve	P,P,O	P,E	3	2.68	2-5	L	<i>Petalomyrmex phylax</i> , <i>Cataulacus mckeyi</i>

Grand Zambi	P,P,O	P,E	3	3.47	1-6	L	Petalomyrmex phylax; C. mckeyi not found (26 trees)
Ebodie	P,P,O	P,E	3	3.15	1-7	L	Petalomyrmex phylax, Cataulacus mckeyi
Mamelles	P,P,O	P,E	no data	no data	no data	L	Petalomyrmex phylax, Cataulacus mckeyi
Akanga	no data	P,E	3	3.19	0-6	L	Petalomyrmex phylax; C. mckeyi not found (16 trees)
Nkongmintom	no data	P,E	no data	no data	no data	L	Petalomyrmex phylax (1 tree)
Nkolobounde	P,P,O	P,E	3	3.01	2-5	L	Petalomyrmex phylax, Cataulacus mckeyi
Bombe Bakundu	P,P,O	P,E	3	3.18	1-9	L	numerous spp.; P. phylax absent, C. mckeyi present

1. First column: A = domatia absent, P = domatia present; second column: L = onset of domatia relatively late in plant ontogeny (saplings), P = onset of domatia relatively precocious in ontogeny (seedlings). Third column: S = each ant-cavity comprises several (1-3) successive internodes; O = ant-cavity comprises only one leaf-bearing internode.

2. First column: A = prostoma absent, P = prostoma present; second column: C = prostoma circular in shape, E = prostoma elongate.

3. S = foliar nectaries small, L = nectaries large.

4. In mature trees.

populations (1.61-2.57). In contrast, those from lowland forest had many fewer nectaries (mode 0 or 1 per basal leaflet), and the mean number varied substantially among populations (0.11-1.09). The principal ant associate in all these lowland-forest populations is *Aphomomyrmex afer* (Table 3). In contrast to the ants associated with other *Leonardoxa* myrmecophytes, this ant tends colonies of homopterans in the domatia of its host plants (GAUME et al. 1998; GAUME & McKEY 1998). Honeydew partly replaces nectar in this interaction.

In summary, characters directly related to interaction with ants enable recognition of four groups of populations. The first group includes all the non-myrmecophytes. These occur to the east of the coastal plain in southern Cameroon (from Yaoundé southward), but with at least one outlying population on an isolated hilltop ca. 300 km further to the northwest. The second and third groups are myrmecophytes found to the north of the coastal plain. These two groups are similar in their ant-related morphological traits. One, however, has few nectaries and is found in lowland forest, while the other has more nectaries and is restricted to submontane forest. The fourth group is comprised of very distinctive myrmecophytes in the coastal plain, differing from the others further north by their numerous nectaries, precociously expressed domatia, and a prostoma that appears coadapted to traits of a highly specialised and host-specific associate.

Other characters

Other characters, not directly related to interactions with ants, show similar discontinuities between distinct groups of populations. These include both vegetative and reproductive characters.

Phenology of growth

As in many other Detarieae and Macrolobieae, growth in *L. africana* is rhythmic: a branch tip produces young leaves and internodes in intermittent pulses. The flushes of tender, drooping shoots and young leaves produced by trees of these caesalpinoid tribes are often spectacular in size, colour, growth rate and degree of synchrony over the tree's crown (McKEY 1989). Young leaves of *L. africana* are pale creamy white, becoming pale green as they

TABLE 4.—Variation among field populations of the *Leonardoxa africana* complex in phenology of vegetative growth.

Group	Site	Unit of growth ¹		Intra-crown synchrony	
		Mean	Range		
1	Mbalmayo	2.00	1-3	strong	
	Mt. Kala	1.50	1-2	strong	
	Ebogo	1.28	1-3	strong	
	Mbankolo	2.00	2	no data	
	Abang	3.00	3	no data	
	Zingui base	no data	no data	no data	
	Zingui hill	no data	no data	no data	
	Akom II	1.50	1-2	no data	
	Essangmvout	2.50	2-3	strong	
	Nkolobounde	2.00	1-3	strong	
	Nta Ali	1.60	1-3	strong	
	2	Big Ngwandi	1.62	1-3	no data
		Betenge	1.44	1-2	no data
Dikome Balue		1.48	1-2	strong	
Madie River		1.16	1-2	strong	
Ibemi		no data	no data	no data	
3	Akpasang	no data	no data	no data	
	Rengo Rock	2.00	2	strong	
	Fabe Road	1.71	1-2	strong	
	Iriba Inene	1.53	1-3	strong	
	Islaib Road	1.60	1-2	no data	
	Bayenti	1.33	1-2	no data	
	Eyang Atem Ako	2.30	2-4	no data	
	Fainchang	2.20	1-4	no data	
4	Douala-Edea Reserve	1.00	1	weak	
	Grand Zambi	1.00	1	weak	
	Ebodie	1.00	1	weak	
	Mamelles	1.00	1	weak	
	Akanga	1.00	1	weak	
	Nkongmintom	no data	no data	no data	
	Nkolobounde	1.00	1	weak	
	Bombe Bakundu	1.09	1-2 (rarely)	weak	

1. Unit of growth = number of leaves and internodes produced simultaneously in a single flush of growth at a branch terminal.

expand, but acquiring most of their chlorophyll only after they mature and lignify (Laurent AMSELLEM, pers. comm.). While growth in this species is always rhythmic, field observations show that there is variation among populations in two aspects of phenology, the size of the unit of growth at each branch tip and the degree of intra-crown synchrony in growth (Table 4). This variation is discontinuous, and two patterns are discernible: (1) large, seasonally produced flushes: each branch tip produces a flush (the unit of growth) of one to three, occasionally four, internodes in each pulse of growth, and growth occurs synchronously (and seasonally) at a large proportion of the branch tips in the tree's crown; or (2) small flushes, staggered in time: each branch tip produces only a single

internode (very rarely two) in each pulse of growth, and at any time during the year a small proportion of branch tips bear young growth. As shown in Table 4, the first pattern characterises groups 1-3, while the second pattern characterises group 4.

Among myrmecophytic populations of *L. africana*, this difference in growth pattern leads to variation in the structure of ant-domatia. Each discrete pith-cavity hollowed out by ants corresponds to the unit of growth, the internodes produced in a single pulse from a branch tip (compare Tables 3 and 4). When growth is interrupted, a woody septum separates successive pith-cavities. Thus in populations of groups 2 and 3, each ant-domatium extends over 1-3 internodes and the prostoma is present only at the apex of the terminal internode.

TABLE 5.—Variation among field populations of the *Leonardoxa africana* complex in number of leaflet pairs and leaflet length.

Group	Site	Number of leaflet pairs		Length of largest leaflets (cm) ¹	
		Mode	Prop. 4-jugate leaves	Mean, across individual trees	Maximum size observed in the population
1	Mbalmayo	3	0.01	no data	no data
	Mt. Kala	2	0.00	14.1	16.4
	Ebogo	3	0.08	13.7	14.9
	Mbankolo	3	0.00	no data	no data
	Abang	3	0.00	16.7	19.3
	Zingui base	2	0.00	no data	no data
	Zingui hill	2	0.00	12.5	14.2
	Akom II	2	0.00	16.0	20.5
	Essangmvout	3	0.00	15.2	19.0
	Nkolobounde	2	0.00	15.6	26.2
	Nta Ali	3	0.00	18.0	24.9
2	Big Ngwandi	2	0.00	18.7	19.2
	Betenge	2	0.00	15.4	21.0
	Dikome Balue	2	0.00	16.1	21.8
	Madie River	2	0.00	18.1	25.0
	Ibemi	2	0.00	20.3	30.1
3	Akpasang	no data	no data	no data	no data
	Rengo Rock	3	0.10	no data	no data
	Fabe Road	3	0.00	22.0	29.5
	Iriba Inene	3	0.39	23.5	32.0
	Islaib Road	3	0.22	21.1	28.5
	Bayenti	3	0.18	20.5	29.0
	Eyang Atem Ako	4	0.55	22.2	30.2
	Fainchang	3	0.06	16.9	22.1
	Douala-Edea Reserve	3	0.02	no data	no data
4	Grand Zambi	3	0.11	13.1	17.2
	Ebodie	3	0.01	15.6	21.3
	Mamelles				
	Akanga	2	0.01	13.8	18.5
	Nkongmintom	3	0.00	no data	no data
	Nkolobounde	2	0.03	13.7	17.1
	Bombe Bakundu	2	0.00	14.0	19.6

1. For each leaf, length (along a straight line from base of the midrib to tip of the acumen) of each leaflet of the largest pair was measured. This was the distal pair in 2-jugate leaves, and usually the next-to-distal pair in 3- and 4-jugate leaves.

In contrast, in populations of group 4 each leaf-bearing internode constitutes a separate domatium bearing a prostoma at its apex.

Size of leaflets and number of leaflet pairs

Leaflet size in *Leonardoxa* varies predictably with position in the leaf. Proximal leaflets are smallest, leaflets increase in size up to the next-to-distal pair, and distal leaflets are then slightly smaller. Both leaflet size and number change predictably with ontogeny of the plant. In all populations, first leaves of seedlings have only a single pair of small leaflets, and leaflet size and number increase as the plant increases in size. However, for leaves of

mature trees, there is also variation among populations in size and number of leaflets (Table 5). Most distinctive in this respect are populations of group 3, which have leaflets that average much larger than those of trees in the other groups. Adult trees of this group are also distinctive in having a large proportion of 4-jugate leaves. In group 2, leaflets are almost as large as in group 3, but leaves are almost always 2-jugate.

Flower colour

Flower colour showed marked variation among populations (Table 6). In populations of the non-myrmecophytic group 1, flowers were

TABLE 6.—Variation among field populations of the *Leonardoxa africana* complex in position of inflorescences and in flower colour.

Group	Site	Position of inflorescences	Flower colour ¹
1	Mbalmayo	axillary on young twigs	lilac/white ¹
	Mt. Kala	axillary on young twigs (only fruits seen)	no data
	Ebogo	axillary on young twigs	lilac/white ¹
	Mbankolo	axillary on young twigs (only fruits seen)	no data
	Abang	no data	no data
	Zingui base	no data	no data
	Zingui hill	no data	no data
	Akom II	no data	no data
	Essangmvout	no data	no data
	Nkolobounde	axillary on young twigs	lilac/white ¹
2	Nta Ali	axillary on young twigs and cauliflorous on main trunk of a large tree	lilac/white ¹
	Big Ngwandi	no data	no data
	Betenge	no data	no data
	Dikome Balue	ramiflorous on twig ca. 4 mm diam.	fuchsiapink/white ¹
	Madie River	cauliflorous, on a trunk 10 cm diameter (only fruits seen)	no data
3	Ibemi	no data	no data
	Akpasang	no data	no data
	Rengo Rock	no data	no data
	Fabe Road	no data	no data
	Iriba Inene	axillary on young twigs, ramiflorous and cauliflorous (only fruits seen)	no data
	Islaib Road	ramiflorous on a twig 6 mm diam.	hypanthium white; corolla very light pink
4	Bayenti	no data	no data
	Eyang Atem Ako	no data	no data
	Fainchang	no data	no data
	Douala-Edea Reserve	ramiflorous and cauliflorous, including main trunk	pink to red
	Grand Zambi	no data	no data
	Ebodie	ramiflorous and cauliflorous, including main trunk	pink to red
	Mamelles	ramiflorous and cauliflorous, including main trunk	bright pink
	Akanga	ramiflorous and cauliflorous, including main trunk	pink to red
	Nkongmintom	no data	no data
5	Nkolobounde	ramiflorous and cauliflorous, including main trunk	pink to red
	Bombe Bakundu	no data	no data

1. Colour of corolla/colour of hypanthium, where these are different. In other cases, colour is uniform.

always with a white hypanthium and lilac petals and filaments of the stamens. In populations of group 4, hypanthium, petals and filaments of the stamens were pink or red. Trees in populations of groups 2 and 3 were rarely seen in flower.

In each case only a single tree of a single population was observed flowering. In the Dikome Balue population (group 2), one tree bore flowers with hypanthium creamy white and corolla light pink. At Islaib Road (group 3), one large

individual had flower buds that were very light pink, and open flowers with white hypanthium and very light pink corolla.

Cauliflory

Position of inflorescences also showed marked variation among populations (Table 6). With one exception, in populations of the non-myrmecophyte group 1, inflorescences were always axillary on young twigs. In populations of the myrmecophytes, inflorescences were usually ramiflorous or cauliflorous. The only population of non-myrmecophytes where cauliflory was observed was the northern outlying population on the summit of Nta Ali. This population included at least one large tree with trunciflorous inflorescences (but with the white-and-lilac flowers typical of the non-myrmecophytes). As mentioned above, this population might be affected by hybridisation with myrmecophytes present in lowland forest surrounding this hill.

Analysis of phenetic similarities

PCA confirmed the separation of four distinct groups. The first three dimensions together accounted for 87% of the variance. Figure 1 shows the position of populations from all sites along the first three dimensions of the PCA. The first dimension (43.4% of the variance) mainly separates populations of varying degree of myrmecophytic specialization (Group 4 with strongly positive values and well separated from the rest, Groups 2 and 3 with intermediate values, and Group 1 with negative values). Several characters contribute to discrimination along this axis (Fig. 2). Characters directly related to interaction with ants have positive values for this dimension, while other characters have negative values. The second dimension (32.3% of the variation, Fig. 1) separates Groups 2 and 3 (positive values) from the others. Leaflet size and number of leaflet pairs most strongly contribute to this separation (Fig. 2). The third dimension (11.7 percent of the variation, Fig. 1) discriminates between Groups 2 (negative values) and 3 (positive values). Number of leaflet pairs contributes most strongly to this discrimination (Fig. 2).

In summary, character discontinuities observed in field populations show that the *L. africana* complex is comprised of four distinct groups of populations, whose distinctive characters are shown in Table 7. As detailed above, these four groups are geographically cohesive entities. It is important to note that at Nkoloboundé, the sole field site where myrmecophytes and non-myrmecophytes occur in close sympatry, two distinct and very different populations of *L. africana* coexist. They differ in both vegetative and reproductive characters. With the exception of a few small saplings that present apparently intermediate traits, each tree encountered in the field could be unambiguously placed in either Group 1 or Group 4. Phenetically at least, these two populations are as distinct from each other as are allopatric populations of Groups 1 and 4.

GREENHOUSE AND COMMON-GARDEN STUDIES

Of the two populations used in the greenhouse study, Rengo Rock belongs to group 3, typified by very large leaflets, few foliar nectaries, and late onset of domatia. Bombe Bakundu belongs to group 4, with smaller leaflets, numerous nectaries, and domatia present already on seedlings. For plants grown in the greenhouse, length of basal leaflets averaged 6.7 ± 1.5 cm (s.d.) for Bombe Bakundu ($n = 96$ leaflets on 8 plants) and 9.7 ± 2.5 cm for Korup ($n = 218$ leaflets on 23 plants). Number of nectaries per basal leaflet averaged 2.1 ± 0.5 for Bombe Bakundu ($n = 64$ leaflets on 8 plants) and 0.4 ± 0.8 for Korup ($n = 274$ leaflets on 23 plants). While values of these characters are smaller in the greenhouse cuttings than in mature trees in the field (see Tables 3 and 5), differences in both these characters between cuttings originating from the two populations are highly significant (leaflet length: $F_{1,253} = 20.0$, $P < 0.0001$; nectary number: $F_{1,276} = 342.8$, $P < 0.0001$). Thus differences between populations observed in the field persisted when plants were grown in the absence of their associated ants and in a common environment. Only a small number of characters could be examined in the juvenile plants used in these studies, but they include most of the ones that best discriminated

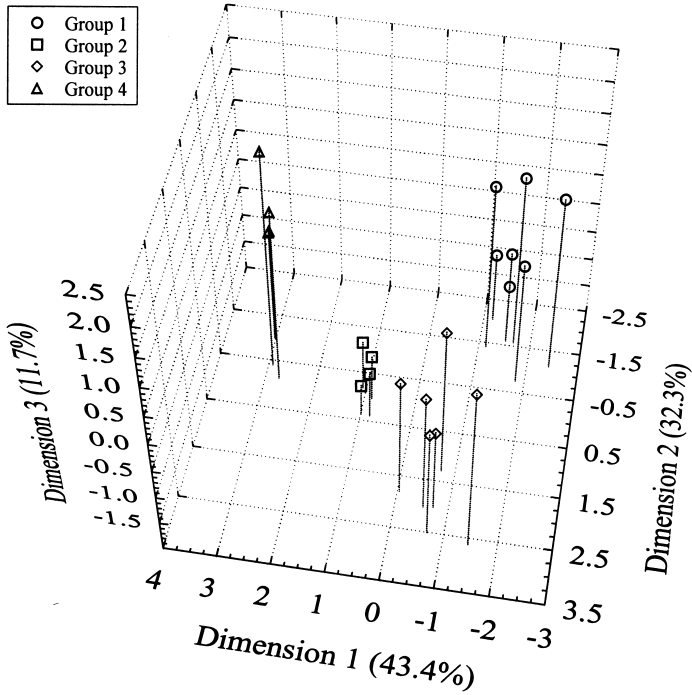


Fig. 1.—Three-dimensional representation of results of principal components analysis of populations of the *Leonardoixa africana* complex studied in the field.

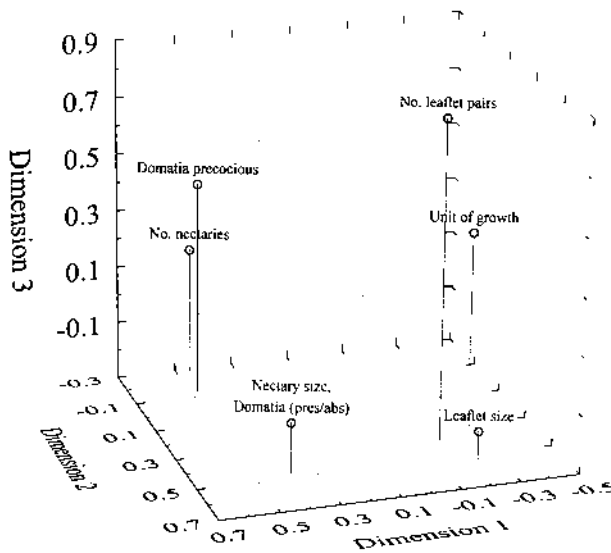


Fig. 2.— Representation of the contribution of different characters to the first three dimensions of the principal components analysis of field populations of the *Leonardoixa africana* complex.

TABLE 7.—Summary of character variation among groups of populations of the *Leonardoxa africana* complex studied in the field.

Group	Domatia		Prostoma		Nectaries		Phenology of vegetative growth		Leaflets			Flower colour
	Presence / absence	Onset in plant ontogeny	Presence / absence	Shape	Usual number (on proximal leaflets)	Size	Unit of growth	Degree of intra-crown synchrony	Size	Number of pairs	Position of inflorescences	
1	Absent		Absent		0-1	small	1-3	strong and seasonal	small	2 or 3	only axillary on young twigs	hypanthium lilac, corolla white
2	Present	sapling	Present	circular	2	large	1-3	strong and seasonal	large	2(-3)	(axillary?) ramiflorous and cauliflorous	insufficient data
3	Present	sapling	Present	circular	0-1	large	1-3(-4)	strong and seasonal	very large	3 or 4	axillary, ramiflorous and cauliflorous	insufficient data
4	Present	seedling	Present	elongate	3	large	almost always 1	weak; flushing staggered throughout the year	small	2 or 3	ramiflorous and cauliflorous	pink to red

among the groups identified by the field study. The greenhouse study also showed a parallel between development of stems in seedlings, observed in natural populations, and in proleptic shoots produced from dormant buds of the cuttings used in these studies. In the Bombe Bakundu field population, ant-domatia appear in very young seedlings. They also appeared early in the development of proleptic shoots of cuttings from this population. In all cuttings from this site, the first internode of proleptic shoots bearing a normal foliage leaf was already swollen. In the Rengo Rock field population, ant-domatia appear later in ontogeny (saplings). This trait was also observed in proleptic shoots produced by greenhouse-grown cuttings of Rengo Rock plants. All the 23 cuttings from this population produced one or more proleptic shoots. Of a total of 46 shoots, only 13 had developed swollen internodes by the end of the six-month greenhouse study. On these, the first internode was never swollen. Onset of swelling began with the second (in four shoots), third (five shoots), fourth (three shoots), or fifth internode (one shoot). The 33 shoots that had not produced domatia by the end of the study were mostly small (14 had only a single internode), but five had two internodes, nine had three internodes, three had four internodes, and two shoots were five internodes long.

Observations in the common garden established in the Mamelles field site also showed that plants from different populations maintained their distinctive characters when grown in the same environment. For example, of the 33 surviving cuttings from populations with late onset of domatia (Groups 2 and 3), only 6 had developed swollen internodes (one on each plant) two years after planting. In contrast, all of the cuttings from populations of group 4 produced swollen internodes soon after planting, and two years later the 20 surviving cuttings possessed 3-19 domatia (mean 9.2). The ten cuttings of the sole Group 1 population used in this study (Nta Ali) never produced domatia. Nectaries also kept the distinctive traits (size and number) of the population of origin. As in the greenhouse study, there was insufficient time for some of the distinctive traits to be expressed. Two years after planting, however, one of the cuttings from Islaib

road had developed the very large leaflets typical of mature plants of group 3.

HERBARIUM STUDIES

Results of herbarium studies (Table 8) confirmed and extended those of field studies. With very few exceptions, specimens could be unambiguously assigned to one of the four groups identified by the field study, and geographic distribution of each of the groups as defined by herbarium studies was consistent with that established by field studies. The few problematical specimens were from geographically intermediate areas, and may reflect incomplete differentiation in this complex.

First, all specimens from Gabon, Equatorial Guinea, the Congo Republic (Brazzaville), and southern Cameroon east of the Atlantic coastal forests lacked swollen internodes. Most other specimens possessed swollen internodes. Only two specimens (both placed here in Group 1) appeared to be intermediate for this character. One (*Letouzey 13885*) was collected from the summit of Nta Ali, where intermediate individuals were also found in the field study. The second specimen (*de Wilde 1332*) possessed internodes that were only slightly swollen but hollow. This specimen comes from a poorly collected area where transitional forms between non-myrmecophytes and myrmecophytes might be expected.

The non-myrmecophytic specimens presented all the other traits of the field populations of Group 1. All were characterised by few small nectaries, and by inflorescences axillary on young twigs. Of 27 flowering or fruiting specimens, the only two that were ramiflorous (*de Wilde 1332*) or cauliflorous (*Letouzey 13885*) were the two intermediate for swollen internodes. In the other 25, inflorescences were borne on young twigs, usually less than 4 mm in diameter. According to notes on labels, flower colour in the non-myrmecophytes ranged from white-and-lilac to violet or purple. It is impossible to determine whether this reflects variation in colour or in the way in which it is described.

Second, among the myrmecophytes, plants collected from the southern part of the range, from Southern Bakundu Forest Reserve in the north to Campo in the south, comprise a group

TABLE 8. — Characters of herbarium specimens of the *Leonardoxa africana* complex examined in this study.

Group	Collection	Notes on size of tree	Domatia	Unit of growth ¹	Nectaries		Number of leaflet pairs	Position of inflorescences	Flower colour
					Number (on proximal leaflets)	Size			
1	<i>Bates 1660</i>		A	?	0-1	small	3	(sterile)	
	<i>Breteler & de Wilde 226</i>	7 m tall	A	?	no data	no data	2	on young twigs	white-lilac
	<i>Breteler & de Wilde 704</i>	7 m tall	A	?	no data	no data	2	not noted	lilac
	<i>Chevalier s.n. (A. Baudon)</i>		A	?	0-1	small	2	on young twigs (2 mm diam.)	not noted
	<i>Dang 651</i>	10 m tall	A	?	0		2-3	on young twigs (2-3 mm diam.)	pink-violet
	<i>de Wilde 1332</i>	4 m tall, DBH 9 cm	P	?	0-1	small	3	ramiflorous (1 cm diam.)	dark lilac-pale lilac
	<i>de Wilde 1862</i>	7 m tall, 15 cm diam.	A	?	0-2	small	3	on twigs 1.5-5 mm diam.	pale lilac-dark lilac
	<i>Eckendorff 128</i>		A	?	no data	no data	2	on young twigs	not noted
	<i>Fcam 1161</i>		A	?	1-2	small	2	on young twigs	not noted
	<i>Claine 3361</i>	20 m tall	A	?	1-2	small	2	on young twigs (1.5-2 mm diam.)	white-pink
	<i>Le Testu s.n.</i>		A	?	0-2	small	2-3	on young twigs (1.5-2 mm diam.)	not noted
	<i>Le Testu 8888</i>		A	?	0-1	small	2-3	on young twigs (2 mm diam.)	violet
	<i>Le Testu 8995</i>		A	?	0-1	small	2-3	on young twigs (1.5-3 mm diam.)	violet
	<i>Le Testu 9079</i>		A	?	0-1	small	2	on young twigs (2.3-3.7 mm diam.)	violet
	<i>Letouzey 9371</i>	5 m tall	A	?	no data	no data	2	(sterile)	
	<i>Letouzey 10158</i>	5 m tall	A	?	0	no data	2-3	"only on young twigs"	violet
	<i>Letouzey 10201</i>	diam. 15-20 cm	A	?	0-1	small	2-3	on young twigs (to 1 cm diam.)	violet
	<i>Letouzey 13885</i>		A (some twigs slightly swollen)	?	insufficient data	small	2-3	fruits on trunk and branches	
	<i>Manning 2157</i>		A	?	insufficient data	small	2	(sterile)	
	<i>Manning 1397</i>	5 m tall	A	?	no data	no data		"racemes in leaf axils"	purple

Group	Collection	Notes on size of tree	Domatia	Unit of growth ¹	Nectaries		Number of leaflet pairs	Position of inflorescences	Flower colour
					Number (on proximal leaflets)	Size			
2	<i>Mildbraed 8065</i>		A	?	0-1	small	3	(sterile)	
	<i>Mpom 303</i>	3-5 m tall	A	?	no data	no data	2	on young twigs (3 mm diam.)	not noted
	<i>Soyaux 104</i>	5 m tall	A	?	0-1	small	2-3	on twigs 3.5-4.5 mm diam.	not noted
	<i>Staudt 427</i>		A	?	0-1	small	2	on young twig (2.9 mm diam.)	not noted
	<i>Tessmann 284a</i>		A	?	0-1	small	2	on young twigs (3.2 mm diam.)	not noted
	<i>Villiers 807</i>		A	?	no data	no data	2	on young twigs	mauve
	<i>Zenker s.n.</i>		A	?	0-1	small	2	on young twigs	not noted
	<i>Bipinde Mimfia</i>							(2 mm diam.)	
	<i>Zenker ed.</i>		A	?	insufficient data	small	2	on young twig	not noted
	<i>Weigel 37</i>							(2 mm diam.)	
	<i>Zenker 1696</i>		A	?	no data	no data	2	(sterile)	
	<i>Zenker 1698</i>		A	?	0-1	small	2	on young twigs (1.3-4 mm diam.)	not noted
	<i>Zenker 2255</i>		A	?	0-1	small	2	(sterile)	
	<i>Zenker 2255b</i>		A	?	0-3	small	2	on young twigs (1.5-3.7 mm diam.)	not noted
	<i>Zenker 2303a</i>		A	?	1-2	small	2-3	on young twig (2.5 mm diam.)	not noted
	<i>Zenker 2989a</i>		A	?	0-1	small	2	on young twigs (2.8-4 mm diam.)	not noted
	<i>Zenker 3747</i>		A	?	no data	no data		(sterile)	
	<i>Zenker 4545</i>		A	?	0-1	small	2	(sterile)	
	<i>Zenker 4972</i>		A	?	0-1	small	2	(sterile)	
	<i>Letouzey 13632</i>	8 m tall	P	?	0-2	medium	3	(sterile)	
<i>Letouzey 14577</i>	30 cm diam.	P		1-2	0-1	medium	2	on young twigs (3.5-4 mm diam.)	violet pink
<i>Thomas et al. 7988</i>	5 m tall	P	?	1-2	medium	3	(sterile?)		
<i>Thomas & Namata 7746</i>		P	?	2-3	medium	3	(sterile?)		
<i>Nemba et al. 753</i>	8 m tall, 25 cm diam.	P	?	no data	no data	2	"racemes in leaf axils"	flower buds pink-purple	

Group	Collection	Notes on size of tree	Domatia	Unit of growth ¹	Nectaries		Number of leaflet pairs	Position of inflorescences	Flower colour
					Number (on proximal leaflets)	Size			
3	<i>Coombe 191</i>	7 m tall	P	?	0-1	medium	4	"cauliflorous and on twigs"	purple and bluish-pink
	<i>Latilo 35</i>	14 m tall, 19 cm diam.	P	1-2	insufficient data	medium	2-3	on young twig (3.5 mm diam.)	fl. buds purple
	<i>McKey 72</i>	11 m tall	P	?	no data	no data	3	(sterile)	
	<i>Manning 1714</i>	10 m tall	P	?	no data	no data	4	"cauliflorous"	not noted
	<i>Talbot 1440</i>		P	2	0-1	medium	3-4	(sterile)	
	<i>Thomas 4269</i>	6 m tall	P	?	no data	no data	not noted	"among leaves and on branches"	not noted
	<i>Thomas 4527</i>	8 m tall	P	?	no data	no data	not noted	"cauliflorous on trunk and branches"	pink
	<i>Thomas et al. 7480</i>	10 m tall	P	?	no data	no data	4	"raceme in leaf axil"	mauve
4	<i>Bos 3630</i>	2.5 m tall	P	1	2-3	large	2-3	"cauliflorous" on twig 12.5 mm diam.	not noted
	<i>Bos 3913</i>	2-3 m tall	P	1	2-4	large	2-3	cauliflorous and ramiflorous	bright pink
	<i>Bos 4074</i>	2-4 m tall	P	1	3-4	large	3	cauliflorous	bright pink
	<i>Bos 6233</i>		P	1	no data	large	no data	(sterile?)	
	<i>Bos 7058</i>		P	1	no data	large	no data	(sterile?)	
	<i>Bos 7315</i>	5 m tall	P	1	2-4	large	3	cauliflorous, ramiflorous and axillary	cyclamen-red and pink
	<i>Bounougou s.n.</i>		P	1	no data	large	(seedlings only)	(seedlings only)	
	<i>Breteler et al. 2580</i>	4 m tall, 3-4 cm diam.	P	1	2-3	large	3	floral buds on young twigs	pale violet, anthers pale yellow
	<i>de Kruif 994</i>	12 m tall	P	1	no data	large	no data	cauliflorous	not noted
	<i>Endengle 2105</i>		P	1	3-4	large	3	cauliflorous and ramiflorous	not noted
	<i>Farron 7181</i>	10 m tall, 10 cm diam.	P	1	insufficient data	large	2-3	cauliflorous	not noted
<i>FHI 29369</i>		P	1	2-3	large	2-3	(sterile)		
<i>FHI 29511</i>	11 m tall	P	1	4-5	large	no data	(sterile)		

Group	Collection	Notes on size of tree	Domatia	Unit of growth ¹	Nectaries		Number of leaflet pairs	Position of inflorescences	Flower colour
					Number (on proximal leaflets)	Size			
	<i>FHI 29672</i>	13-15 m tall, 10-15 cm diam.	P	1	2-3, large	large	3	(sterile)	
	<i>FHI 41007</i>	to 5 m tall	P	1	3	large	3	(sterile)	
	<i>Fleury 33346</i>	30-35 m tall, 0.8-0.9 m diam.	P	1	3-4	large	3	(sterile?)	
	<i>Jones 9499</i>	6-9 m tall, 7.5 cm diam.	P	1	3	large	3	on young twig	mauve
	<i>Leeuwenberg 5500</i>	8 m tall, 9 cm diam.	P	1	2-4	large	2-3	cauliflorous	pink
	<i>Letouzey 4140</i>	3 m tall	P	1	2-3	large	3	cauliflorous and ramiflorous	dark pinkish red
	<i>Mann 726</i>	8-10 m tall	P	1	no data	large	3-4	not noted	purple
	<i>Manning 1499</i>	2.5 m tall	P	1	no data	large	no data	not noted	purple
	<i>Manning 1517</i>	10 m tall	P	1	no data	large	2	on young twigs and cauliflorous	purple
	<i>McKey & Gartlan 120</i>	P	1	insufficient data	large	3	(sterile)		
	<i>Mpom 227</i>	4 m tall	P	1	insufficient data	large	3	cauliflorous	red
	<i>Mpom 283</i>		P	1	3-5	large	3	not noted	not noted
	<i>Mpom 303</i>		P	1	no data	large	3-4	(sterile?)	
	<i>Mpom 343</i>	6 m tall	P	1	no data	large	3	(sterile)	
	<i>Thomas 167</i>		P	1	no data	large	2-3	(sterile)	
	<i>Villiers 775</i>		P	1	no data	large	no data	cauliflorous	pink
	<i>Waterman & McKey 846</i>		P	1	3	large	3	(sterile)	
	<i>Zenker s.n. Bipinde Mimfia</i>		P	1	2-4	large	2-4	on young twigs (4.5 mm diam.)	not noted
	<i>Zenker 52</i>		P	1	no data	large	no data	(sterile?)	
	<i>Zenker 1074</i>		P	1	insufficient data	large	3	(sterile)	
	<i>Zenker 2967</i>		P	1	2-3	large	3	(sterile)	
	<i>Zenker 4183</i>		P	1	2-3	large	2-3	(sterile)	
	<i>Zenker 4495</i>		P	1	3	large	3	(sterile)	

1. Unit of growth could not be determined on specimens of group 1 because there was no visible marker of growth interruption (see text). For groups 2 and 3, unit of growth could only rarely be determined, because most specimens included only part of a single flush. In contrast, the distinctive single-internode flushes of group 4 were reliably scored.

quite distinct from those further north, and present all the characters of Group 4 populations studied in the field. Nectaries are large and quite constant in number (usually 3 per basal leaflet). Each domatium is a single internode long. No unopened internodes with intact prostoma were seen; specimens usually bore the distinctive slit-like entrance holes of *Petalomyrmex* or the oblong ones of *Cataulacus mckeyi*, an ant that is a host-specific parasite of the *Petalomyrmex*-*Leonardoxa* mutualism (GAUME & MCKEY 1999). One collection of seedlings from this area (*Bounougo s.n.*, from Edea) showed that, as in field populations, domatia are already present at this stage.

Third, all specimens collected further north and west than the Southern Bakundu Forest Reserve had fewer nectaries than those further south, and domatia that extended over 1-3 internodes. In both respects they correspond very well to the field populations of Groups 2 and 3, found in submontane and lowland forest, respec-

tively, in this area. Several specimens collected in lowland forest included four-jugate leaves with very large leaflets, typical of mature trees of Group 3.

TAXONOMIC PART

Leonardoxa africana (Baill.) Aubrév.

Adansonia, ser. 2, 8: 179 (1968). — *Humboldtia africana* Baill., Hist. Pl. 2: 99 (1870). — Type: *Mann 726*, Cameroon, Littoral Province, Cameroon River (= wouri estuary), 1861 (holo-, K; iso-, P).

The description of *Leonardoxa* by LÉONARD (1993) is still generally accurate, but must be amended in the following ways to take into account the variation described here: twigs with or without a fusiform, hollow infra-nodal swelling; inflorescences axillary on young twigs, ramiflorous, or cauliflorous.

Key to the subspecies of *Leonardoxa africana*

Some of the characters included in the key follow predictable ontogenetic patterns. In small saplings and in sucker shoots from cuttings, for example, leaflets are smaller, fewer leaflet pairs are present, and fewer nectaries occur on each leaflet than in mature trees. The descriptions here, unless otherwise stated, apply to mature trees.

1. Internodes of young twigs not swollen or hollow, not inhabited by ants; leaflet apex short-acuminate; inflorescences axillary on small twigs up to about 5(-rarely 10) mm diameter; hypanthium white to pale lilac, corolla lilac 4. subsp. **gracilicaulis**
- 1'. Internodes of young twigs (at least on all plants ≥ 1.5 m tall) swollen, with thickened pith, hollowed out and inhabited by ants; leaflet apex long-acuminate; inflorescences usually ramiflorous (on twigs >10 mm diameter) or cauliflorous on large branches and trunk, rarely axillary on young twigs; hypanthium and corolla mauve to pink, purple or red 2
2. Young growth produced in flushes of a single internode at each branch tip, pith chamber thus restricted to single-internode segments; specialised swollen internodes present at all stages of growth, from seedling (20 cm tall) to adult; largest leaflets usually 13-15 cm long, 4.5-5.5 cm broad; (2-)-3(-5) nectaries at base of each proximal leaflet 1. subsp. **africana**
- 2'. Young growth produced in flushes of 2-4 internodes at each branch tip, pith chamber thus continuous over 2-4 internodes; swollen internodes present only on plants ≥ 60 cm tall, seedlings lacking myrmecodomatia; largest leaflets usually 16-23 cm long, 6-8 cm broad; nectaries at base of each proximal leaflet variable in number, sometimes absent 3
3. Leaves often 4(3-5)-jugate; nectaries often absent at base of each proximal leaflet, when present usually 1(-2) in number; lowland rain forest up to 300 m elevation 2. subsp. **letouzeyi**
- 3'. Leaves usually 2(2-3)-jugate; nectaries at base of each proximal leaflet present on almost all plants, usually 2 in number; submontane rain forest in the Rumpi Hills (above 800 m), and possibly other hills in southwestern Cameroon 3. subsp. **rumpiensis**

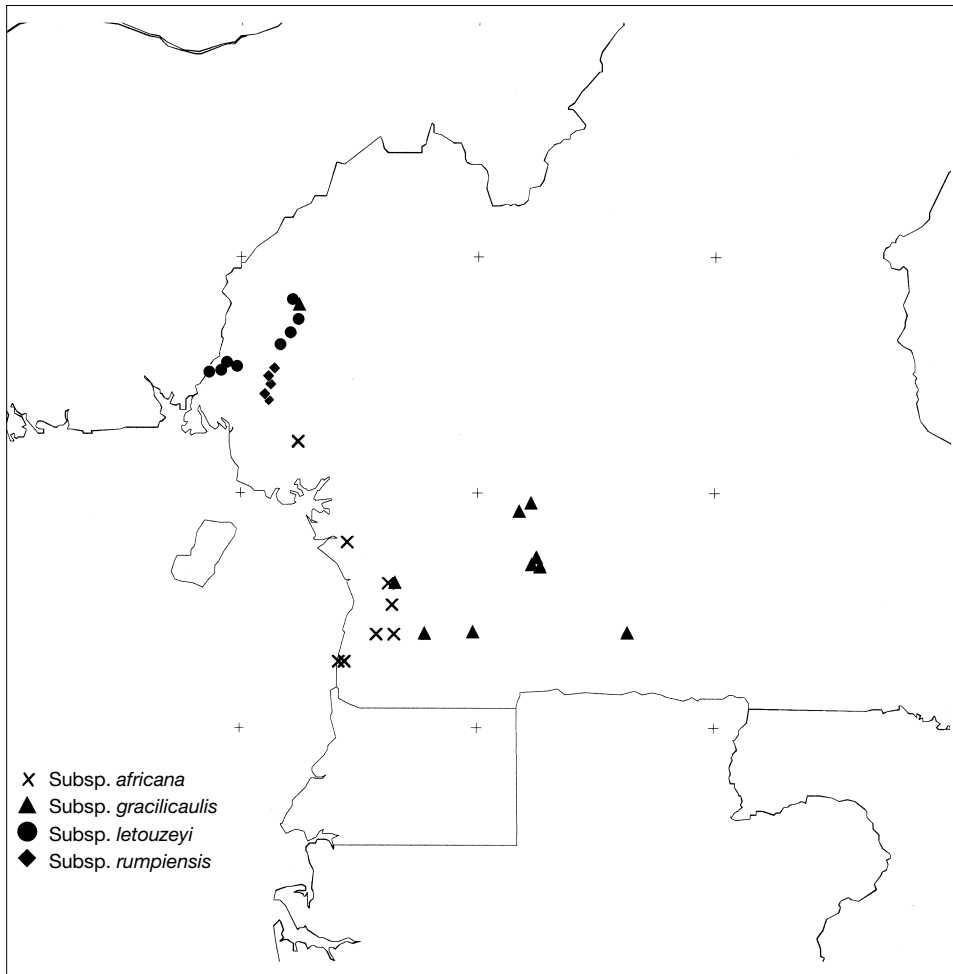


Fig. 3. — Geographic distribution of field localities of members of the *Leonardoixa africana* complex: *L. africana* subsp. *gracilicaulis* = Group 1; *L. africana* subsp. *rumpiensis* = Group 2; *L. africana* subsp. *letouzeyi* = Group 3; *L. africana* subsp. *africana* = Group 4.

Figures 3 and 4 show the distribution of field sites and herbarium collections, respectively, of each of the four infraspecific taxa recognised here.

1. *Leonardoixa africana* (Baill.) Aubrév. subsp. *africana* (= group 4)

Tree to 14 m tall. Trunk (rarely) to 40 cm diam., usually under 15 cm diam. Young shoots produced in flushes consisting of only a single internode and young leaf at each branch tip. Internodes of young twigs (2.5-)3.5-7.5(-9) cm long, modified as myrmecodomatia, swollen,

with thick pith except at base; twigs 4.3-5.7 mm diam. at apex tapering to ca. 2 mm diam. at base of internode; ant-cavities each a single internode long. Swollen internodes present from the seedling stage (20 cm tall) onward. Prostoma of ant-domatia at apex of internode opposite leaf insertion, elliptic. Leaves (2-)3(-rarely 4)-jugate. Leaflets elliptic, falcate, apex long-acuminate, the smallest leaflets (proximal pair) (7.8-)13(-15) cm long and (3.5-)5(-6) cm broad, the largest ones (distal pair in 2-jugate leaves, next-to-distal pair in 3- and 4-jugate leaves) (9.5-)15(-20) cm long

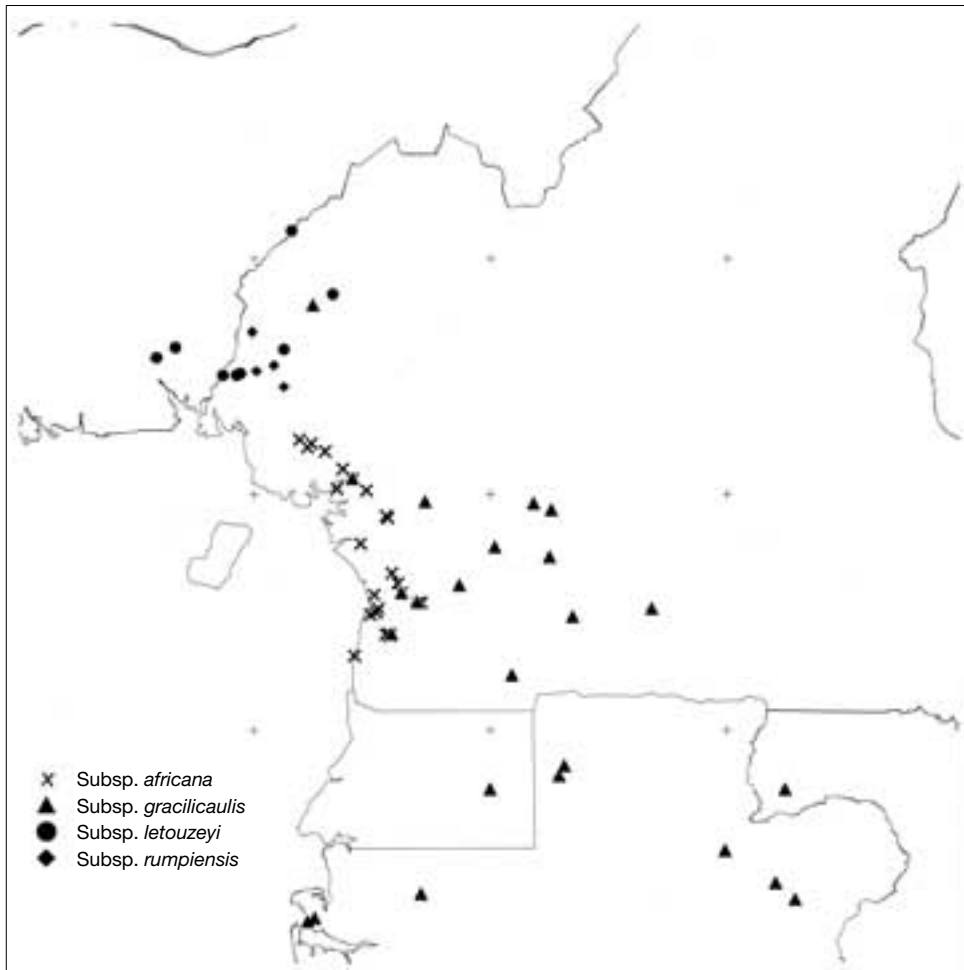


Fig. 4. — Geographic distribution of herbarium collections of the *Leonardoxa africana* complex examined in this study: *L. africana* subsp. *gracilicaulis* = Group 1; *L. africana* subsp. *rumpiensis* = Group 2; *L. africana* subsp. *letouzeyi* = Group 3; *L. africana* subsp. *africana* = Group 4.

and (4-)5.5(-7) cm broad; nectary glands large (smooth gland surface oblong, about 1×0.75 mm, surrounded by a raised ring of tissue about 1 mm broad), consistently present on abaxial surface of each leaflet, with (2-)3-5 glands on each proximal leaflet, (1-)2(-3) glands on each median leaflet, and (0-)1-2 glands on each distal leaflet. Racemes to 4 cm long, with 40-50 flowers, usually cauliflorous, borne on main trunk and on large branches, or ramiflorous on twigs of ca. 5 mm diam. and larger. Flowers 1.8-2.2 cm in diam.; pedicels 2-4 mm long; calyx green or red, sepals

0.5-0.8 cm long; petals violet, purple, mauve, pink or red, 0.6-1.0 cm long. Ovules 4-5. Fruit oblong-ovate, 8-11 cm long, 2.5-4 cm broad.

Leonardoxa africana subsp. *africana* is a highly specialised myrmecophyte, differing from the other myrmecophytic subspecies in a number of traits: (1) Foliar nectaries (Fig. 5C) are larger, more numerous, and less variable in presence/absence and number than in the other subspecies; (2) only a single leaf-bearing internode is produced in each flush of growth at a

branch tip, so that each ant-cavity is a single internode long (Figs. 6B, 7B); (3) growth of different branch tips is not synchronised over the crown of the tree; (4) specialised swollen internodes appear much earlier (seedlings 20 cm tall) in plant ontogeny than in the other subspecies; (5) the prostoma is elliptic-oblong rather than spherical in shape (Fig. 6D). Also, while cauliflory on old branches, or even on the trunk, occurs in all three myrmecophytic subspecies, it appears to be especially frequent in subsp. *africana* (Fig. 8B).

DISTRIBUTION. — *Leonardoxa africana* subsp. *africana* is restricted to coastal forests of Cameroon (Figs. 3, 4). All the field sites are below 80 m elevation. Judging from collection localities and notes on labels, this subspecies appears rarely to occur above about 100 m. The northernmost known localities are from the Southern Bakundu Forest Reserve, and the southern boundary of its range appears to be near Campo, at the border with Equatorial Guinea. Within this coastal strip, it extends inland as far as Bipindi, on the eastern edge of the coastal plain.

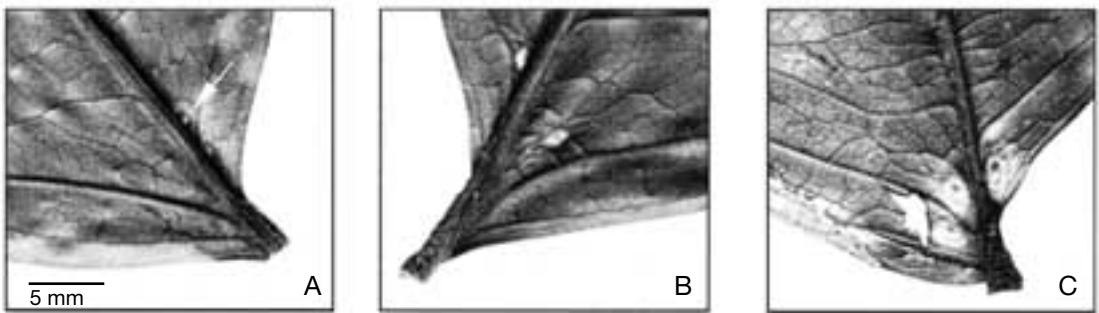


Fig. 5. — Foliar nectaries of the *Leonardoxa africana* complex, all shown at the same scale: **A**, *L. africana* subsp. *gracilicaulis* (Zingui hill site); **B**, *L. africana* subsp. *rumpiensis* (Dikomé Balué site); **C**, *L. africana* subsp. *africana* (Akanga site). Nectaries of *L. africana* subsp. *letouzeyi* (not pictured) are similar in size to those of subsp. *rumpiensis*.

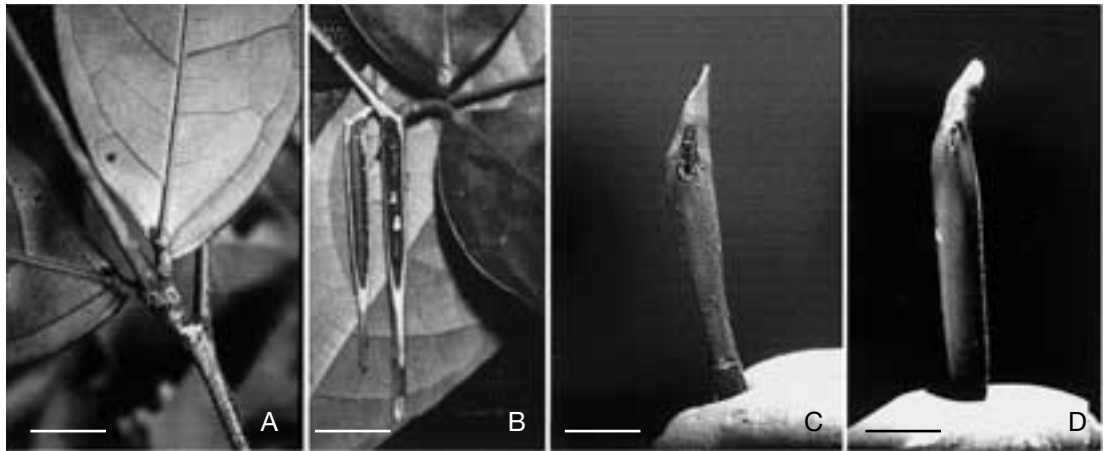


Fig. 6. — Internodes of the *Leonardoxa africana* complex, showing variation in specialisations for housing ants. Bar = 2 cm in all photos. **A**, apex of internode (note point of attachment of the paripinnately compound leaf) of *L. africana* subsp. *gracilicaulis* (Mbalmayo site), showing absence of swelling in this non-myrmecophytic subspecies; **B**, longitudinal section of internode of *L. africana* subsp. *africana* (Bombé Bakundu site) showing the strongly swollen ant-domatium, which in this subspecies is a single internode long. — **C** and **D**, prostoma of two myrmecophytic subspecies, located in both cases at the apex of the internode opposite the point of leaf insertion; the diagonally cut structure at the top of each photo is the leaf rachis: **C**, circular prostoma of *L. africana* subsp. *letouzeyi* (Rengo Rock site); prostoma of *L. africana* subsp. *rumpiensis* (not shown) is roughly similar in size and shape; **D**, elongate prostoma of *L. africana* subsp. *africana* (Bombé Bakundu site). Both are on internodes produced by plants growing in a greenhouse at the University of Miami, on cuttings uninhabited by ants. The structures are not holes, but are scars produced by the spontaneous drying of the unligified prostoma in mature internodes.

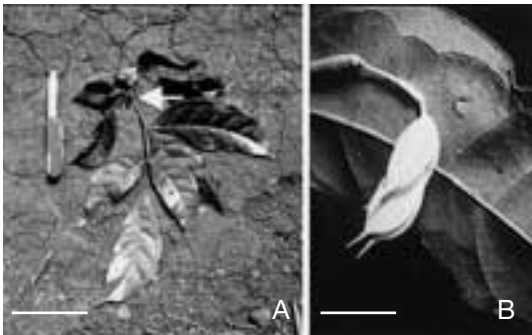


Fig. 7. — Examples of variation in the unit of growth within the *Leonardoxa africana* complex. **A**, a branch tip of *L. africana* subsp. *rumpiensis* (Dikome Balue site) showing two recently matured internodes and leaves produced in a flush of growth; these leaves are bright green (shiny in this photograph) and distinct from the older mature leaf (dark green, not shiny) produced in a previous growth flush; arrow marks the base of this flush. Bar = 10 cm. **B**, a branch tip of *L. africana* subsp. *africana* (Bombe Bakundu site) showing the one-leaf and internode unit of growth typical of all populations of this subspecies. Bar = 2 cm.

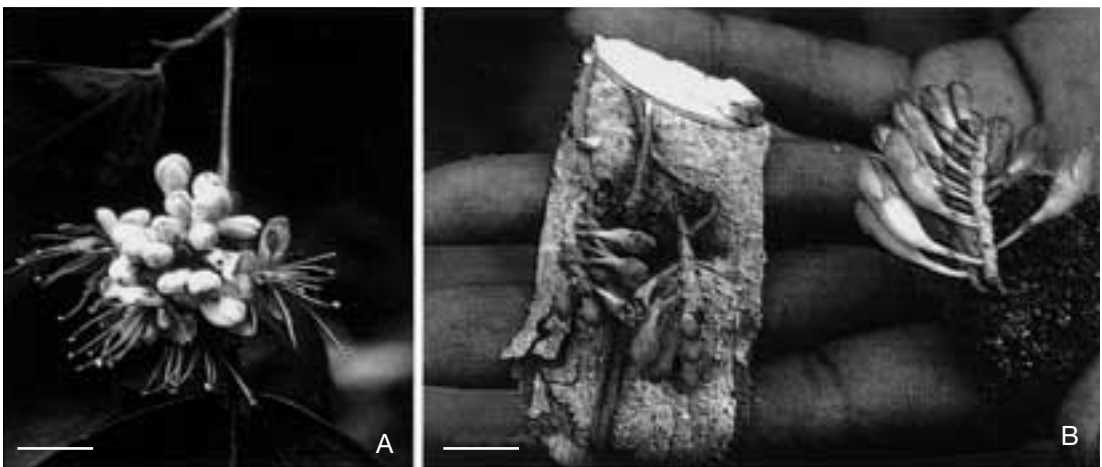


Fig. 8. — Variation in floral traits within the *Leonardoxa africana* complex. Bar = 2 cm in both photos. **A**, inflorescence axillary on a young twig (vertical object just behind the inflorescence) in *L. africana* subsp. *gracilicaulis* (Mbalmayo site); hypanthium white, corolla and filaments of stamens lilac, anthers yellow. **B**, trunciflorous inflorescences in *L. africana* subsp. *africana* (Grand Zambi); hypanthium and corolla pink.

ECOLOGY. — This subspecies, illustrated in AUBREVILLE (1970), is the one that has attracted most attention as a myrmecophyte. The studies by ELIAS (1980), MCKEY (1984), GAUME et al. (1997) and GAUME & MCKEY (1999) all concern this subspecies. Internodes are swollen and hollow, and these ant-domatia are present already in seedlings 20 cm tall (see Fig. 2B in LÉONARD [1993]). This subspecies is associated with two ant species that are completely restricted to this host, the formicine *Petalomyrmex phylax* and the myrmicine *Cataulacus mckeyi* (MCKEY 1984). *Petalomyrmex* is a mutualist of the plant, protecting its young leaves against phytophagous insects (GAUME et al. 1997),

while *Cataulacus* is a parasite, providing no protection to the plant and excluding *Petalomyrmex* from plants it occupies (GAUME & MCKEY 1999). This subspecies was termed “*L. africana* taxon T4” by CHENUIL & MCKEY (1996).

Few observations of flower visitors have been made, but on a few occasions sunbirds were seen visiting the pink to red flowers, which in this subspecies at least seem to have a somewhat long-tubular corolla, compared to flowers of the non-myrmecophytic subspecies (see below).

ADDITIONAL SPECIMENS EXAMINED. — CAMEROON, Southwest Province: Southern Bakundu Forest

Reserve, *E. W. Jones in Brenan 9499* (K, P), *FHI 29511* (K), *29672* (K), and *41007* (K); Southern Bakundu Forest Reserve, 1 km W Bombe Bakundu, *Manning 1499* (MO); Southern Bakundu Forest Reserve, near Kindonge Camp, *Manning 1517* (MO); Kumba (planted in forestry nursery), *FHI 29369* (K). Littoral Province: 24 km E Douala, *Breteler et al. 2580* (BR, K, P, YA); Douala, route Razel, *Endengle 2105* (P, YA); Douala, forêt de Yefoume, *Fleury, in herb. Chevalier 33346* (P); 14 km E Douala, Douala-Edea Road, *Mpom 303* in part (BR); Lake Tissoongo, Douala-Edea Forest Reserve, *McKey & Gartlan 120* (K), *D. W. Thomas 167* (YA), *Waterman & McKey 846* (K); stream Mangombe near Edea, *Mpom 343* (YA). Central-South Province: near Bipaga II, km 40 from Kribi to Edea, *de Kruif 994* (WAG); Lolodorf Road, 12 km E of Kribi, *Bos 3630* (BR, WAG, YA); 5 km N of Lolodorf road, 19 km E of Kribi, *Bos 3913* (BR, YA); Lolodorf Road, 18 km E of Kribi, *Bos 4074* (BR, YA); km 30 from Kribi to Ebolowa, *Bos 6233* (WAG); km 45 from Kribi to Campo, *Bos 7315* (BR); 60 km S of Edea, S of Mboke, 11 km E of km 58 from Edea to Kribi, *Leeuwenberg 5500* (BR, K, MO, P, WAG, YA); colline Nkoltsia, *Villiers 775* (P); near Bella, *Letouzey 4140* (P, YA); 2 km from Nkol-Bewa, *Mpom 227* (P, YA); Edoudouma, *Mpom 283* (YA); Bipindi, *Farron 7181* (BAS, P, YA), *Zenker, s.n.* (BR, P), *52* (WAG), *1074* (K, MO, P, WAG), *2967* (BR, K, WAG), *4183* (BR, K, P), *4495* (BR, K, MO).

2. *Leonardoxa africana* subsp. *letouzeyi* McKey, **subsp. nov.** (= group 3)

Haec subspecies Leonardoxae africanae subsp. africanae arcte affinis, sed ab ea medullae loculo per internodia duo triave continuo, foliorum expansione simultanea ramunculi ad nodos terminales duos tresve, glandulis nectariferis crateriformibus minoribus ac quoad numerum plus variabilibus (ad foliola proximalia plerumque nullis ad duabus) atque foliolis usque ad 30 cm longis utroque rhachidis latere saepe quattuor distinguuntur.

TYPUS. — *D. W. Thomas et al. 7480*, Cameroon, Southwest Province, roadside forest S of Baro Village, 5°14'N, 9°15'E, 250 m, 31 Mar. 1988 (holo-, MO; iso-, WAG).

Small tree, (rarely) to 14 m tall. Trunk to 30 cm diam. Young shoots produced in flushes consisting of (1-)2-3 internodes plus young leaves at each branch tip (in adult trees). Internodes of young twigs (2.8-)7(-13) cm long, modified as myrmecodomatia, swollen, with thick pith; twigs (4-)5.5(-6.1) mm diam. at apex tapering to ca. 2.5-4 mm diam. at base of internode; enlarged

pith extending throughout section of twig produced in a single growth flush; ant-cavities each 2-3 internodes long (in adult trees). Swollen internodes absent in seedlings, present only in plants ≥ 60 cm tall. Prostoma of ant-domatia at apex of terminal internode of each flush of growth, opposite leaf insertion, roughly spherical in shape. Leaves (2-3-)4(-5)-jugate. Leaflets elliptic, falcate, apex long-acuminate, proximal ones (13.2-)17(-22) cm long and (4.5-)6(-8) cm broad, largest leaflets (next-to-distal pair) (14.5-)21(-32) cm long and (5-)7.5(-12) cm broad. Nectary glands absent from some individuals; when present, appearing intermediate in size (smooth gland surface oblong, about 1×0.75 mm, not surrounded by a raised ring of tissue) and few in number, usually 0-2 (very rarely up to 5) on proximal leaflets and usually absent on other leaflets. Racemes short (axis 3-5 cm long), with 40-60 flowers, axillary on twigs of up to 1 cm diam., also sometimes cauliflorous. Flowers 1.8-3 cm diam.; pedicels 0.3-0.5 cm long; calyx pale lilac, sepals 0.8-1.1 cm long; petals usually violet, sometimes pink, 0.9-1.3 cm long. Ovules 4-5. Fruit to 15 cm long, 5 cm broad.

The most distinctive trait of *L. africana* subsp. *letouzeyi* is the large size of its stems and leaves (Fig. 9C). Young twigs are much more robust than those of corresponding age of plants of any of the other subspecies, leaflets are larger, and 4-

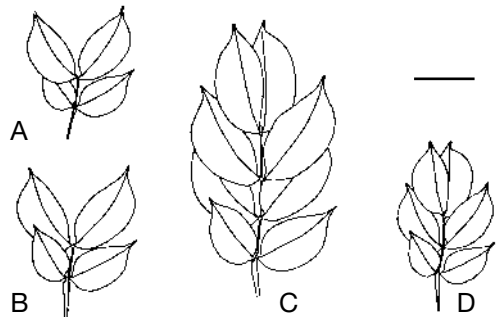


Fig. 9. — Typical leaves of the *Leonardoxa africana* complex, all drawn at same scale. Bar = 10 cm. A, *L. africana* subsp. *gracilicaulis*; B, *L. africana* subsp. *rumpiensis*; C, *L. africana* subsp. *letouzeyi*; D, *L. africana* subsp. *africana*.

jugate leaves predominate on most adult trees, in contrast to the 2- or 3-jugate leaves which characterise the other subspecies. Another trait distinguishing the subspecies *letouzeyi* from all other subspecies is the great variation among individual trees of the same population in the number of foliar nectaries. This subspecies shares with subsp. *rumpiensis* several traits that together distinguish them from subsp. *africana*: (1) Ant-cavities are first produced in juveniles over 50 cm tall; (2) ant-cavities in adult trees extend over 2-3 internodes, corresponding to the units of growth produced in flushes; (3) vegetative growth is synchronised over the crown of the tree; (4) the prostoma is roughly spherical in shape (Fig. 6C).

DISTRIBUTION. — This subspecies occurs in the wettest forests of Africa, the lowland forests near the Bight of Biafra (Figs. 3, 4). It is found from Uwet Division, Calabar Province, Nigeria, through Korup National Park on Cameroon's border with Nigeria, and throughout the Mamfe Plain and Cross River area. Its range extends northward at least to the Takamanda Forest Reserve north of Mamfe. The eastern limit of its distribution is uncertain.

ECOLOGY. — This subspecies is a myrmecophyte in which swollen stems may first appear in juveniles about 60 cm tall (but more commonly in saplings 1 m or taller). While saplings are associated with small colonies of any of several species of twig-nesting ants, mature individuals are occupied solely by the formicine ant *Aphomomyrmex afer*, which protects young leaves of the host tree against insect herbivores (GAUME 1998; GAUME & MCKEY 1998). This subspecies was termed "*L. letouzeyi*" by MCKEY (1991) and "*L. africana* taxon T3" by CHENUIL & MCKEY (1996), GAUME et al. (1998) and GAUME & MCKEY (1998). The ant occupants of this subspecies tend scale insects and mealybugs inside the hollow stems of the host (GAUME et al. 1998), in contrast to the ants associated with the subspecies *africana*, which never tend homopterans. (For the subspecies *rumpiensis*, more information is required on this point.) As argued by GAUME et al. (1998), this dependence on homopterans is related to the low and variable number of foliar nectaries in this subspecies.

PARATYPES. — NIGERIA, Uwet Division: Calabar River, *Latilo 35* (BR, K, P); Oban, *Talbot 1440* (K). — CAMEROON, Southwest Province: Bamenda Road, Mile 43 from Mamfe, 1,500 ft (460 m), *Coombe 191* (BR, K); Akpasang River, Korup National Park, *McKey 72* (P, YA); Korup National Park, between Mana River bridge and Camp 1, *Manning 1714* (MO); disturbed forest near Ndian Oil Palm Plantation, 50 m, *D.W. Thomas 4269* (BR, US); Takamanda Forest Reserve, near Matene, 170 m, *D.W. Thomas 4527* (MO).

3. *Leonardoxa africana* subsp. *rumpiensis* McKey, subsp. nov. (= group 2)

Haec subspecies Leonardoxae africanae subsp. letouzeyi perarcte affinis, sed ab ea glandulis nectariferis crateriformibus majoribus ac quoad numerum plus constantibus (ad foliola proximalia plerumque nullis ad duobus) atque foliolis utroque rhachidis latere plerumque duobus distinguitur.

TYPUS. — *Letouzey 14577*, Cameroon, Southwest Province, Dikome Balue, 4°55'N, 9°15'E, 35 km NNW Kumba, 1200 m, 24 Mar. 1976 (holo-, P; iso-, K, YA).

Small tree, to 14 m tall. Trunk to 35 cm diam. Young shoots produced in flushes consisting of (1-)2-3 internodes plus young leaves at each branch tip (in adult trees) (Fig. 7). Internodes of young twigs (3-)5.5(-11) cm long, modified as myrmecodomatia, swollen, with thick pith; twigs (3-)4(-5) mm diam. at apex tapering to ca. 2-3 mm diam. at base of internode; enlarged pith extending throughout section of twig produced in a single growth flush; ant-cavities each 2-3 internodes long (in adult trees). Swollen internodes absent in seedlings, present only in plants \geq 50 cm tall. Prostoma of ant-domatia at apex of terminal internode of each flush of growth, opposite leaf insertion, roughly spherical in shape. Leaves 2 (-3)-jugate (Fig. 9). Leaflets elliptic, falcate, apex acuminate to long-acuminate, smallest ones (proximal pair) (6.5-)16(-28) cm long and (2.7-)6.5(-11) cm broad, largest leaflets (second pair) (7-)17.5(-30) cm long and (3-)7(-12) cm broad. Nectary glands of intermediate size (smooth gland surface oblong, about 1×0.75 mm, not surrounded by a raised ring of tissue), usually 2(0-5) on proximal leaflets (Fig. 5), (0-)1(-2) on other leaflets. Racemes short (axis 3-5 cm long), with > 40-60 flowers, axillary on twigs 4-5 mm diam., also sometimes cauliflorous (on trunk up to

10 cm diam.). Flowers 1.8-3 cm diam.; pedicels 0.3-0.5 cm long; calyx colour unknown, sepals 0.8-1.1 cm long; petals mauve-pink to purple, 0.9-1.3 cm long. Ovule number unknown. Size of mature fruit unknown.

This subspecies is also a myrmecophyte; all trees possess swollen hollow internodes occupied by ants. As mentioned above, *L. africana* subsp. *rumpiensis* shares a number of traits with subsp. *letouzeyi* that distinguish these two from subsp. *africana*. It is distinguished from subsp. *letouzeyi* by its usually 2-jugate leaves (Fig. 9), the smaller size of its leaflets and stems, the constancy in nectary number, and its restriction to piedmont and submontane forest (above 500 m and probably more commonly above 800 m).

DISTRIBUTION. — This taxon occurs in the Rumpi Hills (Figs. 3, 4), where it was studied in 5 field sites. Herbarium specimens from three other sites in the Rumpi Hills (see below) also appear to belong here. Material of myrmecophytic *L. africana* collected from submontane forest on another hill in the Southwest Province (*Letouzey 13632* [K, P, YA], from a 960 m hill 55 km southwest of Mamfe) is tentatively placed in this subspecies.

ECOLOGY. — This myrmecophyte, in contrast to the two preceding subspecies, is restricted to submontane forest (and lowland forest transitional to it: “piedmont” [THOMAS 1995]). As in the other myrmecophytes, internodes are hollowed and occupied by ants, and each adult tree is occupied by a single ant colony. In contrast to the two preceding subspecies, each of which is principally associated with one (or two) ant species, a diverse array of ant species occupy trees in populations of the subspecies *rumpiensis* (D. McKEY and R. SNELLING, unpubl. results). Nature of the interactions with ants has not been studied in this subspecies. This subspecies was termed “*L. africana* taxon T2” by CHENUIL & McKEY (1996).

PARATYPES. — CAMEROON, Southwest Province: Steep hillside, 400-850 m, 5 km W of Esukutang Village, *D. W. Thomas et al. 7988* (MO); forest, 500 m, near Masaka-Batanga, *D. W. Thomas & Namata 7746* (MO); forest, 500 m, near Meta village, *Nemba et al. 753* (MO); colline, 960 m (près côte 897) E of piste Abakpa-Mbiofong, 55 km SW Mamfe, *Letouzey 13632* (K, P, YA).

Leonardoxa africana* subsp. *gracilicaulis
McKey, **subsp. nov.** (= group 1)

Haec subspecies Leonardoxae africanae subsp. rumpiensis arcte atque L. africanae subsp. letouzeyi et subsp. africanae nonnihil remotior affinis, sed ab ea glandulis nectariferis crateriformibus ad foliola proximalia nullis ad duobus atque foliorum expansione simultanea ramunculi ad nodos terminales duos ad quattuor, ab omnibus ramunculorum juveniliu internodiis non inflatis atque racemis ad ramunculos diametro 5-10 mm axillaribus distinguitur.

TYPUS. — *Letouzey 10201*, Cameroon, Southern Province, Colline Ongongondje near Akonekye, 15 km NW Ambam, ca. 700 m, 23 Mar. 1970 (holo-, P; iso-, BR, K, WAG, YA).

Tree to 25 m tall. Trunk up to 50-60 cm diam. Young shoots produced in flushes of (1-)2-4 internodes and leaves at each branch tip; internodes of young twigs (1.1-)3.7(-7) cm long, not modified as myrmecodomatia, not swollen; twigs (2-)2.3(-3.1) mm diam. at apex tapering to ca. 1-2 mm diam. at base of internode. Prostoma lacking. Leaves 2-3-jugate; leaflets elliptic, falcate, apex acuminate to long-acuminate, the smallest ones (proximal pair) (9.6-)10.9(-15) cm long and (3-)4(-5) cm broad, largest ones (the distal ones in 2-jugate leaves, median ones in 3-jugate leaves) (12-)15(-26) cm long and (4-)5.5(-9.5) cm broad. Nectary glands small (smooth gland surface oblong, about 0.5 × 0.75 mm), mostly restricted to proximal leaflets, where they are variable in number (0-2). Racemes very short (axis to 3 cm long), with 25-40 flowers, axillary on small twigs of 2-3 (rarely 5-10) mm diam. (Fig. 8). Flowers 1.6-1.8 cm in diam; pedicels 2-4 mm long; calyx white to pale lilac, sepals 0.5-0.8 cm long; petals lilac to violet, 0.6-1 cm long. Ovules 4-5. Fruit oblong-obovate, ca. 10 cm long, 4 cm broad.

Leonardoxa africana subsp. *gracilicaulis* is distinguished from the three other subspecies of the *L. africana* complex by the absence of swollen internodes and prostoma (the subspecies *gracilicaulis* is not a myrmecophyte: Fig. 6A). Foliar nectary glands are present, but are smaller than those of the myrmecophytic subspecies (Fig. 5A). This subspecies also differs from the others in floral characters. Flowers are white and lilac in

colour, rather than pink or red, the most frequent colours in the myrmecophytes. Also, inflorescences are usually axillary on small twigs in this subspecies (Fig. 8A). Cauliflory is very frequent in the myrmecophytes, but in field populations and herbarium specimens studied by us, cauliflory has been recorded in the non-myrmecophytic subspecies only at the summit of Nta Ali (Table 6), in a population that may be affected by hybridisation with *L. africana* subsp. *letouzeyi* (see below). Trees of this subspecies, especially in hill-top (piedmont and lower submontane) habitats where it is most common, reach larger size than is ever attained by any of the myrmecophytes.

DISTRIBUTION. — This subspecies includes all the specimens collected from Gabon, Equatorial Guinea, and southern Cameroon from the vicinity of Yaoundé southward and east of the coastal plain (Fig. 4). In southern Cameroon, this subspecies is characteristically abundant on summits of hills, such as Nkolebengue (THOMAS & THOMAS 1993) and Zingui (this study). Near Yaoundé, *L. africana* subsp. *gracilicaulis* is one of the most frequent trees in submontane forest from 1,000 m elevation upwards (ACHOUNDONG 1985, 1996). The non-myrmecophytic *L. africana* abundant in forest on the summit of Nta Ali (ACHOUNDONG 1995) are also tentatively ascribed to this subspecies. This subspecies is much less frequent in lowland forests, where it is highly localised along streams and patchily distributed. (Within its range, lowland habitats are less constantly humid than hilltop and submontane habitats.) In the coastal plain, where the highly specialised myrmecophyte *L. africana* subsp. *africana* predominates (see below), *L. africana* subsp. *gracilicaulis* has been collected from two inselbergs (Colline Ngwon, 38 km E of Kribi: *Letouzey 9371*; Nkoltsia, 35 km from the coast, *Villiers 807*). Near the latter site, it also occurs in lowland forest, near the village Nkoloboundé along the stream Bounde, where it occurs together, interspersed in the same forests, with the specialised myrmecophyte *L. africana* subsp. *africana*. This is so far the only site where the two are known to co-occur. In forest along two other streams nearby, only *L. africana* subsp. *africana* was present. The two subspecies may co-occur elsewhere, though. The collection *Mpom 303*, from 14 km SE of Douala on the old Douala-Edea road, includes sheets of

both *L. africana* subsp. *gracilicaulis* (in P and YA) and of subsp. *africana* (in BR).

ECOLOGY. — This subspecies is not a myrmecophyte, but is “myrmecophilic,” attracting many different species of tree-dwelling ants to its foliar nectar. Some of these (e.g., *Tetramorium aculeatum*, *Oecophylla longinoda*) establish nests on leaf surfaces, but no ants nest in twigs. Ant-exclusion experiments found no effect of these opportunistically attracted ants in protecting young leaves of the plant against herbivores (GAUME 1998). This subspecies was termed “*L. gracilicaulis*” by MCKEY (1991) and “*L. africana* taxon T1” by CHENUIL & MCKEY (1996) and BROUAT et al. (1998).

PARATYPES. — CAMEROON, Central-South Province: Bitye, *Bates 1660* (MO); Nkomnyat, 4 km N Ekekam, *Dang 651* (P, YA); hill near Mt. Febe, Yaoundé, *Manning 2157* (MO); Colline Ngwon, 38 km E Kribi, *Letouzey 9371* (P, WAG, YA); Evelessi, 30 km W Sangmelima, *Letouzey 10158* (BR, K, P, WAG, YA); 20 km NE Yaoundé, *Mildbraed 8065* (K); Makak, *SRFCam/1141* (P, YA); Lolodorf, *Staudt 427* (G, K); colline Nkoltsia, *Villiers 807* (P); 5 km S Mbalmayo, *W. de Wilde 1862* (BR, K, MO, P, WAG, YA); Bipindi, *Zenker ed. Weigel 37* (G, US, WAG), *Zenker s.n.* (BR, P), *1696* (K, WAG), *1698* (BR), *2255* (K), *2255b* (BR, G, K, P, WAG, Z), *2303a* (K, P), *2989a* (BR, K, P, WAG), *3747* (MO), *4545* (BR, K), *4972* (BR, K); 3 km WNW Bipindi, *Manning 1397* (MO). Littoral Province: 14 km from Douala on the old road to Edea, *Mpom 303* in part (P, YA). — GABON, Province Estuaire: near Libreville, *Klaine 3361* (P); Sibange-Farm, Munda, *Soyaux 104* (K, P); ca. 15 km along road from Assok to hydroelectric power plant in the Tchimbele River, ca. 600 m, *Breteler & de Wilde 226* (WAG). Province Woleu-Ntem: region of Oyem, between the Ogouée R. and Cameroon, *Le Testu s.n.* (BR, K, MO), *9079* (BR, P); Assoc Ngoum, *Le Testu 8995* (P, BR). Province Ogouée-Ivindo: Mambanza, between Gazi and Dembona, *Le Testu 8888* (B, K, MO); ca. 24 km along SOMIFER road towards Makokou, elev. 950-1000 m, *Breteler & de Wilde 704* (WAG); Village Manyal, Bord Ivindo, *Eckendorff 128* (P). — EQUATORIAL GUINEA: Nkolentangun, Nscha'bat (undetermined locality), *Tessmann 284a* (K). — CONGO REPUBLIC (BRAZZAVILLE): Mbouamo (Sangha) forêts (undetermined locality), *Chevalier s.n.* (P).

BIOGEOGRAPHY AND INTERPRETATION OF REVISED TAXONOMY

Figure 10 shows the distributions of the four subspecies of *Leonardoxa africana* recognised

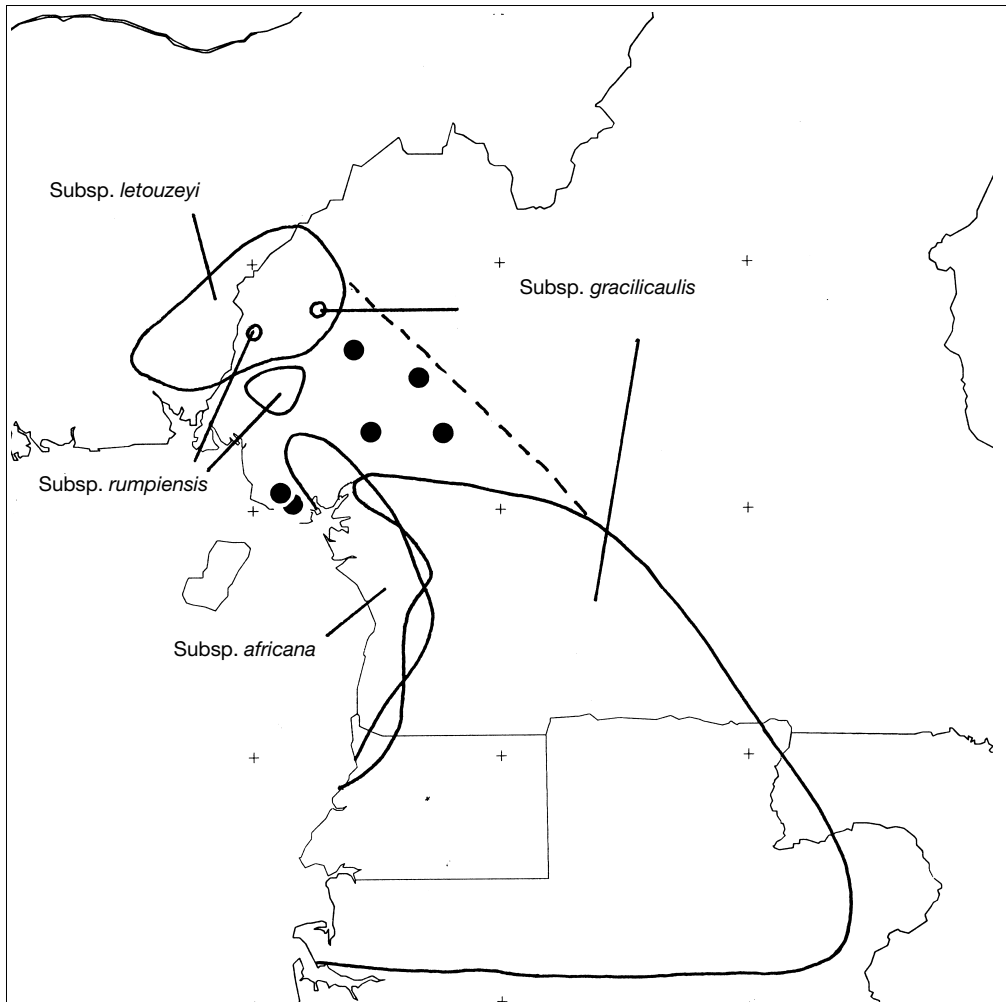


Fig. 10. — Synoptic distribution map of taxa of the *Leonardoxa africana* complex, based on field and herbarium studies complemented by unpublished field notes made available by the late R. LETOUZEY. Closed circles represent field observations of *Leonardoxa* by LETOUZEY outside the range of herbarium specimens and field sites studied here, and for which it was not possible to determine subspecies. In this area, the distribution limits of all four subspecies thus remain to be established by further field study.

here. Within the complex, the non-myrmecophytic subspecies *gracilicaulis* possesses a number of traits that appear ancestral; they are shared with many related genera and would appear as primitive traits in a cladistic analysis, regardless of the choice of outgroups. These include not only the lack of myrmecophytic specialisations, but also the production of large flushes of young leaves and internodes, synchronised over the crown of the tree, and the presence of inflores-

cences that are axillary on young twigs, rather than cauliflorous. Although studies of pollination biology are so far lacking, flowers of *L. africana* subsp. *gracilicaulis* appear to be adapted for bee-pollination, widespread in legumes, rather than possessing traits that may be specialisations for bird-pollination (e.g., the pink or red flowers of subsp. *africana*). Another indication that this taxon is ancestral in the complex is its widespread but patchy distribution. Within the

main part of its range on the plateaux of southern Cameroon and Gabon, it appears to be abundant only on scattered hilltops, with localised extensions into lower elevations along stream valleys. For example, among the sites represented in this study Zingui, Mt. Kala, and Mbankolo all contained isolated dense populations of this subspecies in hill-summit forests, the tree being either absent or very rare in nearby forest at lower elevation. THOMAS & THOMAS (1993) recorded similar observations for other hill ranges in southern Cameroon. Lowland field sites for this taxon were all in riverine forest, and in most of these sites this tree was much less abundant than in the hilltop sites. Toward the northern edge of its range, near Yaoundé, *L. africana* subsp. *gracilicaulis* is completely restricted to isolated pockets of submontane forest on peaks above 1,000 m (ACHOUNDONG 1985, 1996). These pockets are separated from each other by distances of up to tens of kilometers (e.g., Mt. Kala-Mt. Febe, about 25 km), and are also separated by ca. 50 km from the nearest known populations to the south (valley of the Nyong near Mbalmayo and Ebogo). If the population of non-myrmecophytic *L. africana* on the summit of Nta Ali, an isolated hill in the Mamfe Plain approximately 300 km NW of Yaoundé, is correctly ascribed to this subspecies, this represents an even larger range disjunction. The collection *Mildbraed 8065* may also represent a disjunction, but the locality information is contradictory and thus unclear. Study of MILDBRAED's itinerary may resolve this problem. At the western edge of its range, *L. africana* subsp. *gracilicaulis* is found on inselbergs in the coastal plain (e.g., Nkoltsia, Colline Ngwon), and along stream valleys leading from them. The westernmost specimen for this subspecies (*Mpom 303* in P and YA, but not in BR; the specimen in BR is *L. africana* subsp. *africana*, as mentioned above) was collected 14 km E of Douala, in an area where all other material is the very different *L. africana* subsp. *africana*. This is approximately 90 km from the nearest other known locality for *L. africana* subsp. *gracilicaulis*. The current distribution of this taxon appears to reflect a past distribution that was more contiguous, perhaps during a period when climates permitting the existence of

submontane forests descended to much lower elevations than today (MALEY 1996; FLENLEY 1998). Contemporary populations along streams at lower elevation may represent either populations that persisted in moist streamside sites as climates changed, or the more recent colonisation of these moist sites from upland refugia.

Leonardoxa africana subsp. *rumpiensis*, which appears in many respects morphologically intermediate between *L. africana* subsp. *gracilicaulis* and the two other subspecies, may represent a part of this ancestral submontane complex that evolved myrmecophytic traits. One collection (*de Wilde 1332*) may be intermediate between the subspecies *gracilicaulis* and *rumpiensis*. This collection comes from 50 km NW of Eseka (3°39'N, 10°46'E) in the Littoral Province of Cameroon, between the known ranges of the subspecies *gracilicaulis* and *rumpiensis*. Specimens of this collection all have internodes that are only weakly swollen, but hollow. More material is required to assess its taxonomic position. The entire area between the known ranges of these two subspecies is sparsely collected. LETOUZEY's unpublished field notes indicate that *L. africana* is quite frequent in parts of this area, but do not comment on myrmecophytic traits. Field work in this topographically complex region could help clarify the nature of the boundary between these two subspecies, and the evolution of ant-related traits in *Leonardoxa*.

Leonardoxa africana subsp. *letouzeyi* and subsp. *africana* appear to be two lowland-forest offshoots of these western myrmecophytic submontane populations that evolved divergent specialisation of ant-related traits. Arboreal ant communities, and ant-plant interactions, both appear to change quite markedly over elevational gradients in tropical forests (see for example KOPTUR 1985; DAVIDSON & MCKEY 1993). As shown in this study, ant associations of *Leonardoxa* are also different between lowland and submontane populations. Morphological traits important in ant-plant mutualisms could thus have been subjected to divergent selection pressures in submontane and lowland environments. However, shifting elevational distributions provoked by climatic fluctuations, as well as dispersal of seeds along river valleys, may have enabled continuous genetic exchange among

lowland and submontane populations, leading to incomplete differentiation, evident in traits such as flower colour (in which variation does not entirely correspond to the subspecies boundaries drawn here), that were perhaps under weaker selection than traits central to ant-plant mutualism.

Leonardoxa africana subsp. *rumpiensis* and subsp. *letouzeyi* are phenotypically especially close, and whether the morphological differences between them, as defined in this study, are discontinuous or clinal cannot yet be said with certainty. The best places to study this would be along altitudinal transects on the northern and western slopes of the Rumpi Hills (THOMAS 1995). Plants from two sites about 35 km apart, Madie River (elev. 1000 m, subsp. *rumpiensis*) and Islaib Road (elev. 300 m, subsp. *letouzeyi*) are morphologically and ecologically quite distinct, but the zone of possible contact or transition should be examined on a finer spatial scale.

Leonardoxa should also be studied in detail in other areas of transitional and submontane forest in the Southwest Province of Cameroon. For example, the collection *Letouzey 13632*, a myrmecophytic plant from a hill (elev. 960 m) located E of the path from Abakpa to Mbiofong, 55 km SW Mamfe, appears different from *L. africana* subsp. *letouzeyi* widespread in lowland forest throughout this zone. It is here tentatively placed with subsp. *rumpiensis* from similar forest in the Rumpi Hills, but this needs to be confirmed by field studies. Data from one site, the crest of Nta Ali, give an idea of the potential complexity of the situation in this area of marked elevational relief. Herbarium material (*Letouzey 13885*) and field studies (ACHOUNDONG 1995, and the present study) of *L. africana* from the summit of this hill, which rises to 1,266 m from the floor of the Mamfe Plain (150-250 m), confirm that this population is non-myrmecophytic. This isolated population is restricted to the summit above 1,000 m, where it is abundant (ACHOUNDONG 1995). Nectaries on these trees are few and small, internodes are not swollen and are not occupied by ants, flowers are white-and-lilac in colour, and trees reach large size (up to 1 m circumference BH). All these traits are typical of *L. africana* subsp. *gracilicaulis*. However, some

of these trees bear inflorescences on the trunk, whereas cauliflory has otherwise not been noted in this subspecies. Furthermore, one juvenile tree was found with slightly swollen internodes that even bore prostomata. These traits may indicate past (or present) genetic exchange between *L. africana* subsp. *gracilicaulis* and either subsp. *rumpiensis*, of which the closest known populations are located about 60-70 km S of Nta Ali, or subsp. *letouzeyi*, which is present but rare in lowland forest near the village of Fainchang at the foot of Nta Ali (Table 1).

One of the lowland-forest offshoots of the postulated ancestral submontane myrmecophytes, *L. africana* subsp. *letouzeyi*, spread to the north and west of the hills of the West Cameroonian Dorsal to occupy the very wet forests of the Bight of Biafra. Large effective size of leaves is generally correlated with moist, shady habitat (GIVNISH 1987), and the very large leaflets of this subspecies could be interpreted as an adaptation to life in the understory of these wet, cloudy forests.

The other lowland-forest offshoot, *Leonardoxa africana* subsp. *africana*, colonised coastal forests, spreading southward and eastward. In contrast to subsp. *letouzeyi*, this lowland subspecies appears rather well differentiated from *L. africana* subsp. *rumpiensis*. Some 50 km separate the closest known localities for *L. africana* subsp. *rumpiensis* (Dikome Balue, 35 km NNW of Kumba) and subsp. *africana* (Southern Bakundu Forest Reserve). Plants in these two sites are morphologically quite distinct. A search for *L. africana* conducted in 1989 in three sites in a broad area between the known ranges of subsp. *rumpiensis* and subsp. *africana* failed to turn up any new populations. These sites were in lowland forest near the villages of Iloani (4°32'N, 8°59'E, elev. ca. 10 m) and Mabondji (4°33'N, 9°10'E, elev. ca. 80 m; ca. 25 km WSW of Kumba along Mbonge Road), and in the area transitional between lowland and submontane forest on the southern approach to the Rumpi Hills (Massaka, 4°42'N, 9°17'E, elev. ca. 400 m). On present evidence, therefore, there appears to be a real gap in distribution of *L. africana* in this area, and the closest known populations of the subspecies *rumpiensis* and *africana* appear to be quite distinct from one another. However, one character

— flower colour — shows a different pattern of discontinuity. For all specimens of *L. africana* subsp. *africana* collected north of 4°N in which this trait is mentioned (Breteler *et al.* 2580; Jones in Brenan 9499; Mann 726; Manning 1499, 1517), flowers are purple, violet or mauve, like those of *L. africana* subsp. *rumpiensis* and subsp. *letouzeyi*. For all specimens mentioning this trait collected south of this latitude, flowers are pink or red (Bos 3913, 4074, 7315; Leeuwenberg 5500; Letouzey 4140; Mpom 227; Villiers 775). Field studies in Southern Bakundu, where flowers are purple (S. MANNING, pers. comm.), and at several sites in the southern part of the range of the subspecies, where flowers are bright pink or red (this study), confirm this pattern of variation.

In its southward and eastward expansion, the highly specialised myrmecophyte *Leonardoxa africana* subsp. *africana* eventually encountered the non-myrmecophyte *L. africana* subsp. *gracilicaulis*. The fact that the two co-occur today side by side in at least one site (Nkoloboundé) and possibly others (as suggested, for example, by the collection Mpom 303, which contains sheets of both subspecies) suggests the possibility of past (or even current) genetic exchange. That the two subspecies maintain their morphological and ecological distinctness in sympatry indicates the existence of at least partial barriers to gene flow.

In summary, geographic patterns of character variation within the *Leonardoxa africana* complex may reflect the apparent recency of evolutionary differentiation. In this region, allopatric speciation driven by climatic-vegetational cycles, as postulated in this case, is usually considered to be a Pleistocene phenomenon (FJELDSA & LOVETT 1997). The patterns also reflect the likelihood that reproductive isolation between these mostly allopatric variants is incomplete. These are species *in statu nascendi*, in which selection pressures leading to divergence in contrasting environments (largely defined by the biotic environment of ant-plant mutualism) may be partially countered by environmental instability leading to fluctuating distributions and continued gene flow. Interestingly, the two extreme variants in this polytypic species co-occur in a zone of secondary sympatry and remain distinct. The *L. africana* complex may thus be an example of a

ring species (FUTUYMA 1998), in which it is difficult to draw species boundaries (at least, using a biological species concept) in the range of a geographically variable set of populations, but in which the two extremes of this variation, when sympatric, do not (or only rarely) interbreed.

CONCLUSION

Complexes such as the one presented here, which appears to consist of subspecies that are incompletely and perhaps recently differentiated from one another, offer unique opportunities for testing hypotheses about the origins of species diversity in tropical forests (FLENLEY 1993; BUSH 1994; FJELDSA & LOVETT 1997). In most such complexes distributions are allopatric or parapatric. The existence of at least one site (Nkoloboundé) in which *L. africana* subsp. *gracilicaulis* and subsp. *africana* occur sympatrically provides a rare occasion to study the extent of differentiation in this complex, its consequences for gene exchange, and the nature of reproductive isolating mechanisms. In this site, these two plants appear to behave as distinct biological species. Differences in floral traits (white-and-lilac flowers in axillary inflorescences on young growth in *L. africana* subsp. *gracilicaulis*, red flowers and cauliflory in subsp. *africana*) suggest differences in pollination biology, and pre-mating barriers to gene flow could explain how the two remain distinct in sympatry. However, pollinator specificity acting alone is rarely sufficient to block gene flow completely. The two plants overlap in flowering periods, and observations of a few juveniles that appear phenotypically intermediate suggest that gene exchange may occasionally occur. Selection may be reinforcing barriers to gene flow. The two plants differ dramatically in traits related to ant-plant mutualism, and experimental ecological studies suggest that these traits should be under very strong selection (GAUME *et al.* 1997; GAUME 1998). Studies of reproductive ecology and population genetics of *Leonardoxa* in this site could be most instructive for our understanding of the biosystematics of this complex, of the origin and maintenance of traits related to ant-plant mutu-

alism, and of processes of speciation in tropical forests.

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