

ABSTRACT

Henckelia sect. *Loxocarpus* is a small taxon consisting of c. 26 taxa distributed in West Malesia. The present study is the first comprehensive taxonomic revision for all species of *Loxocarpus*. This study has four objectives. The first one is to provide a review of macro-morphological diversity and variation within *Loxocarpus*. Second, to carry out phylogenetic analyses to determine whether *Loxocarpus* is distinct from or is a section within *Henckelia* based on DNA sequences and morphological data. Third is to provide a full taxonomic revision of *Loxocarpus*. And last, to provide ecology and phytogeographic perspectives of *Loxocarpus* species and their conservation status.

Molecular phylogenetic studies showed that *Loxocarpus* is distinct from *Henckelia* and nested within a few Asian and Malesian twisted-fruited genera clade. However, it is paraphyletic. This finding is in contrast with morphological data analysis result which showed the monophyly of *Loxocarpus* species. In the taxonomic revision, *Loxocarpus* is reinstated as a genus with a revised generic circumscription.

Twenty three species are recognised in this taxonomic treatment, including 15 species formerly described as *Loxocarpus* species are reinstated, 5 new combinations are made, 6 species are synonymised with one recognised as a variety, 4 species are determined as novelties, and 6 incompletely known taxa are enumerated. A key to all species and regional keys are provided to aid species identification. Species descriptions with full synonymy, geographic distribution with distribution maps, habitat and ecology information are given. Identification lists for herbarium specimens is provided.

Based on corolla morphology, *Loxocarpus* species were divided into two informal groups 'A' and 'B'. This grouping to a certain extent correlates with phylogenetic analysis results and distribution pattern. Morphological characters were assessed in the light of their taxonomical value.

Molecular phylogenetic analyses were based on a dataset of two markers, namely *trnL-F* intron spacer and Internal Transcribed Spacer (ITS). Twenty samples from *Loxocarpus* species were included as ingroup, 31 taxa were selected from 'Asian and Malesian twisted group' as outgroup. Two analysis methods, namely Bayesian Inference and Maximum Parsimony, were implemented.

Ecological aspects of *Loxocarpus* species are presented. Study showed that habit is correlated with habitat. Pollination and dispersal as inferred from morphology and observation are discussed. Most probably, *Loxocarpus* species are pollinated by *Trigona* bees and seeds are dispersed by rain-drop ballistic. The Riau Pocket was determined as the centre of highest species diversity. Seventeen out of 24 taxa are narrowly endemic (c. 71 %). Conservation status for all species was assessed and 5 out of 24 taxa (c. 21 %) fall within 'threatened' categories.

The three important research questions (**Section 1.2**) were answered in this study. First, it is distinct from *Henckelia/Codonoboea* and warrants generic status. Second, *Loxocarpus* is a paraphyletic taxon. Third, the characters circumscribing *Loxocarpus* are expanded so that the genus now includes species with longer (> 10 mm) capsules.

ABSTRAK

Henckelia seksyen *Loxocarpus* ialah satu takson kecil yang merangkumi lebih kurang 26 spesies dengan taburan di Malesia Barat. Kajian ini merupakan semakan taksonomi secara menyeluruh yang pertama untuk *Loxocarpus*. Kajian ini mempunyai empat objektif. Pertama; untuk mengkaji semula kepelbagaian makro-morfologi dan variasi dalam *Loxocarpus*. Kedua; melakukan analisa filogenetik untuk mengenalpasti samada *Loxocarpus* berbeza dari, atau merupakan satu seksyen dalam *Henckelia* berdasarkan data jujukan DNA dan morfologi. Ketiga; membuat semakan taksonomi secara menyeluruh untuk *Loxocarpus*. Akhir sekali; mengkaji aspek ekologi dan fitogeografi serta menilai status konservasi spesies *Loxocarpus*.

Kajian filogenetik molekul menunjukkan bahawa *Loxocarpus* adalah kumpulan spesies parafiletik. Kumpulan-kumpulan parafiletik *Loxocarpus* adalah berbeza daripada *Henckelia* dan terletak berdekatan dengan beberapa genera Gesneriaceae Asia dan Malesia dengan buah berpilin. Penemuan ini bertentangan dengan keputusan analisa data morfologi. Dalam semakan taksonomi ini, *Loxocarpus* dinaik taraf dari seksyen kepada genus dengan konsep genus yang dirombak semula.

Dua puluh tiga spesies telah dikenal pasti dalam semakan taksonomi termasuk 15 spesies yang sebelum ini dikenali sebagai *Loxocarpus* spp., 5 kombinasi baru telah dikalukan, 6 spesies dikenali sebagai sinonim dimana satu daripadanya dikenalpasti sebagai varieti, 4 spesies baru telah dikenal pasti, 6 taksa yang tidak diketahui sepenuhnya disenaraikan. Kekunci kepada semua spesies dan kekunci mengikut rantau taburan disediakan untuk membantu pengecaman spesies. Huraian spesies dengan senarai penuh sinonim, maklumat taburan geografi dan peta taburan, maklumat habitat dan ekologi telah diberikan. Senarai spesimen herbarium yang dikaji dalam kajian ini juga disediakan.

Berdasarkan morfologi korola, genus *Loxocarpus* boleh dibahagikan kepada dua kumpulan tidak formal: Kumpulan 'A' dan 'B'. Pengumpulan ini pada suatu tahap berhubungkait dengan keputusan kajian filogenetik dan corak taburan geografi. Ciri morfologi dinilai berdasarkan kepada nilai taksonominya.

Analisa filogenetik molekul berdasarkan dua dataset jujukan, '*trnL-F* intron spacer' dan 'Internal Transcribed Spacer' (ITS). Dua puluh sampel spesies *Loxocarpus* dan 31 taksa dari 'Kumpulan buah berpilin Asia dan Malesia' dipilih sebagai '*in-group*' dan '*out-group*' masing-masing. Dua kaedah analisa dilaksanakan, iaitu '*Bayesian Inference*' dan '*Maximum Parsimony*'.

Aspek ekologi spesies *Loxocarpus* juga telah dikaji. Kajian menunjukkan bahawa habit *Loxocarpus* dipengaruhi oleh habitatnya. Pendebungaan dan penyebaran biji-benih juga dibincangkan. Kemungkinan besar spesies *Loxocarpus* didebungakan oleh lebah *Trigona* dan biji-benihnya disebar dengan mekanisme 'balistik titisan hujan'. 'Riau Pocket' dikenalpasti sebagai pusat kepelbagaian spesies yang paling tinggi. Tujuh belas daripada 24 taksa (lebih kurang 71 %) adalah spesies endemik dengan taburan terhad. Status konservasi untuk semua spesies telah dinilai dan didapati bahawa 5 daripada 24 taksa (lebih kurang 21 %) termasuk dalam kategori terancam.

Jawapan untuk tiga masalah utama kajian (**Seksyen 1.2**) bagi kajian ini telah diperolehi. Pertama, *Loxocarpus* adalah berbeza daripada *Henckelia/Codonoboea* dan dinaik taraf dari hierarki seksyen kepada hierarki genus. Kedua, *Loxocarpus* adalah takson parafiletik. Ketiga, ciri bagi *Loxocarpus* telah diperluaskan. Oleh itu sekarang genus ini merangkumi spesies yang berkapsul lebih panjang (> 10 mm).

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TABLE OF CONTENTS

	Page
ABSTRACT	iii
ABSTRAK	v
ACKNOWLEDGEMENTS	vii
TABLE OF CONTENTS	xi
LIST OF FIGURES	xiv
LIST OF PLATES	xvi
LIST OF TABLES	xvii
LIST OF SYMBOLS AND ABBREVIATIONS	xix
LIST OF APPENDICES	xxi
1.0 GENERAL INTRODUCTION	
1.1 <i>Henckelia</i> sect. <i>Loxocarpus</i>	1
1.2 State of knowledge and problem statements	1
1.3 Objectives of the study	3
2.0 MORPHOLOGY	
2.1 Introduction and brief literature review	4
2.2 Materials and methods	4
2.3 Indumentum	5
2.3.1 Hair types and position	5
2.3.2 Hair colour	6
2.3.3 Hair density	6
2.4 Habit and stem	6
2.5 Leaves	7
2.6 Inflorescences	9
2.7 Bracts and bracteoles	9
2.8 Flowers	10
2.9 Fruits	13
2.10 Seeds	13
2.11 Discussion and conclusion	13
3.0 PHYLOGENETIC STUDIES	
3.1 Brief introduction and literature review	15
3.2 Materials	16
3.3 Methodology	18
3.3.1 DNA extraction	18
3.3.2 Polymerase Chain Reaction (PCR)	18
3.3.3 Direct sequencing	21
3.3.4 Sequence alignment	22
3.3.5 Phylogenetic analysis	22
3.3.5.1 Dataset I	25
3.3.5.2 Dataset II	25
3.4 Results and discussion of phylogenetic analyses	25
3.4.1 Dataset I	40
3.4.1.1 MP analysis of Dataset I	40
3.4.1.2 BI analysis of Dataset I	40

3.4.2	Dataset II	41
3.4.2.1	Dataset II (a), <i>trnL-F</i> analyses (49 samples)	41
3.4.2.2	Dataset II (b), ITS analyses (51 samples)	42
3.4.2.3	Dataset II (c), <i>trnL-F</i> and ITS combined analyses (51 samples)	43
3.5	Un-weighted Pair Group Method with Arithmetic Mean (UPGMA) analysis based on morphological data: A comparison	44
3.5.1	Morphological data analysis	44
3.5.2	Results	45
3.6	Discussion and Conclusion: Inference from molecular and morphological phylogenetic studies results	46
4.0 TAXONOMIC REVISION		
4.1	Taxonomic history of <i>Loxocarpus</i>	49
4.2	Generic description	51
4.3	Species concept	53
4.4	Novelties, incompletely known species and excluded species	54
4.5	Keys to the species	55
4.5.1	General key to the species	55
4.5.2	Regional keys to the species	59
4.5.2.1	Key to species in Sumatra (including Lingga Archipelago)	59
4.5.2.2	Key to species in Borneo	60
4.5.2.3	Key to species in Peninsular Malaysia and Peninsular Thailand	62
4.6	Species description	63
4.7	Identification list	122
5.0 ECOLOGY, PHYTOGEOGRAPHIC PERSPECTIVES, AND CONSERVATION STATUS ASSESSMENT		
5.1	Ecology	128
5.1.1	Altitudinal range	128
5.1.2	Habit and habitat	128
5.1.3	Pollination	130
5.1.4	Dispersal	130
5.2	Phytogeographic perspectives	131
5.2.1	Geographic distribution and endemism	131
5.2.2	Phytogeographic perspectives of <i>Loxocarpus</i> species	132
5.2.2.1	The demarcations of phytogeographic areas	133
5.2.2.2	Notable distribution patterns	134
5.2.2.3	‘Stray’ Record	137
5.3	Conservation Status Assessment	138
5.3.1	The Rationale	138
5.3.2	Methodology	138
5.3.3	Results and Conclusions	139
6.0 GENERAL DISCUSSION AND CONCLUSIONS		
6.1	General discussion	142
6.1.1	Expanded generic concept	142
6.1.2	Accepting paraphyletic <i>Loxocarpus</i>	143

6.1.3	Dispersal and speciation—a projection of phylogenetic results and biogeographic perspectives	144
6.2	Conclusions	147
	BIBLIOGRAPHY	152
	APPENDICES	158

LIST OF FIGURES

Fig.	Title	Page
3.1	A single representative phylogram of 816 most parsimonious (MP) trees of 1550 steps based on <i>trnL-F</i> sequences of 156 samples.	26
3.2	Bayesian inference (BI) majority rule consensus tree based on <i>trnL-F</i> sequences of 156 samples. Posterior probability values are given above branches.	27
3.3	A single representative phylogram of 148 most parsimonious trees of 340 steps, based on <i>trnL-F</i> sequences of 49 samples.	28
3.4	Strict MP consensus tree of 148 most parsimonious trees of 340 steps based on <i>trnL-F</i> sequences of 49 samples (CI = 0.81; RI = 0.83; RC = 0.68). Bootstrap (BS) values are given above branches.	29
3.5	MP 50% majority rule consensus tree of 148 most parsimonious trees based on <i>trnL-F</i> sequences of 49 samples.	30
3.6	BI majority rule consensus tree based on <i>trnL-F</i> sequences of 51 samples. Posterior probability (PP) values are given above branches.	31
3.7	A single representative phylogram of 48 most parsimonious trees of 1790 steps, based on ITS sequences of 51 samples.	32
3.8	Strict MP consensus tree of 48 most parsimonious trees of 1790 steps based on ITS sequences of 51 samples (CI = 0.46; RI = 0.61; RC = 0.28). Bootstrap (BS) values are given above branches.	33
3.9	MP 50% majority rule consensus tree of 1790 steps based on ITS sequences of 51 samples.	34
3.10	BI majority rule consensus tree based on ITS sequences of 51 samples. Posterior probability (PP) values are given above branches.	35
3.11	A single representative phylogram of 12 most parsimonious trees of 2144 steps, based on ITS and <i>trnL-F</i> combined sequences of 51 samples.	36
3.12	Strict MP consensus tree of 12 most parsimonious trees of 2144 steps based on ITS and <i>trnL-F</i> combined sequences of 51 samples (CI = 0.51; RI = 0.63; RC = 0.32). Bootstrap (BS) values are given above branches.	37
3.13	MP 50% majority rule consensus tree of 2144 steps based on ITS and <i>trnL-F</i> combined sequences of 51 samples.	38

3.14	BI majority rule consensus tree based on ITS and <i>trnL-F</i> combined sequences of 51 samples. Posterior probability (PP) values are given above branches.	39
3.15	Dendrogram based on morphological data. Within the rectangular box are <i>Loxocarpus</i> species and they split into ‘x’, ‘y’ and ‘z’ groups (B = Borneo; M = Peninsular Malaysia).	48
4.1	Distribution of <i>Loxocarpus augustifolius</i> (●), <i>L. pauzii</i> (■), <i>L. holtumii</i> (○) and <i>L. tunkui</i> (□).	67
4.2	Distribution of <i>Loxocarpus argenteus</i> (●), <i>L. conicapsularis</i> (○), <i>L. taeniophyllus</i> (▲), <i>Loxocarpus</i> sp. A (■) and <i>Loxocarpus</i> sp. B (□).	70
4.3	Distribution of <i>Loxocarpus caeruleus</i> (●), <i>L. semitortus</i> (■) and <i>L. sericiflavus</i> (○).	72
4.4	Distribution of <i>Loxocarpus caulescens</i> (●).	74
4.5	Distribution of <i>Loxocarpus coodei</i> (●), <i>L. rufescens</i> (■) and <i>L. violoides</i> (○).	78
4.6	Distribution of <i>Loxocarpus incanus</i> var. <i>incanus</i> (●) and var. <i>sekayuensis</i> (○).	86
4.7	<i>Loxocarpus meijeri</i> (■) and <i>L. sericeus</i> (●).	87
4.8	Distribution of <i>Loxocarpus repens</i> (●) and <i>L. stapfii</i> (■).	94
4.9	Distribution of <i>Loxocarpus verbeniflos</i> (●) and <i>Loxocarpus</i> sp. C (■).	114
5.1	The distribution of <i>Loxocarpus</i> species.	132
5.2	The demarcations of phytogeographic regions pertinent to <i>Loxocarpus</i> distribution. Square dotted line marks ‘Riau Pocket’ defined by Ashton’s (1992); line G–H marks East Coast Sabah sub-province (Wong, 1998). (A=Kangar; B=Pattani; C=Pontianak; D=Sipitang; E=Bintulu; F=Banjarmasin).	134
5.3	Distribution of the two main flower morphological groups of <i>Loxocarpus</i> : Group A (■) and Group B (●).	136

LIST OF PLATES

Plate	Caption	Page
1	<i>Loxocarpus angustifolius</i> : a. natural habitat, below Lata Kor, trail to Gunung Tahan, b. habit.	65
2	<i>Loxocarpus angustifolius</i> : a. flowers, b. young capsule; <i>Loxocarpus argenteus</i> : c. habit.	66
3	<i>Loxocarpus argenteus</i> : flowers, a. side view, b. front view; <i>Loxocarpus caeruleus</i> : c. habit, inset—the close-up of flower.	69
4	<i>Loxocarpus holttumii</i> : a. habitat, b. habit, c. flower and capsule, the <i>Trigona</i> bee with filled pollen basket is probably a pollinator.	80
5	<i>Loxocarpus incanus</i> var. <i>incanus</i> : a. habitat, b. flower front view; <i>L. incanus</i> var. <i>sekayuensis</i> : c. habit, and fruit in inset.	84
6	<i>Loxocarpus pauzii</i> : a. habit, b. leaf lower surface, c. flower, d. capsule, e. seed, f. indumentum of leaf upper surface, g. indumentum of corolla outer surface, h. indumentum of ovary, i. trichome of petiole (all from Yao <i>et al.</i> FRI 65371) — Scale bars: a = 2 cm, b = 1 cm, c = 1 mm, d = 4 mm, e = 0.2 mm, f–i = 0.5, j. flower side-front view, k. flower back view.	89
7	<i>Loxocarpus repens</i> : a. habit, b. flowers, c. dehisced capsule, d. variegated leaves, e. erect hairs on lamina surface.	93
8	<i>Loxocarpus rufescens</i> : a. habitat, Gunung Santubong, b. habit, c. flower side view, d. flower front view, e. dehisced capsule.	96
9	<i>Loxocarpus semitortus</i> : a. habitat, b. habit, c. flower front view; <i>Loxocarpus sericiflavus</i> : d. flower, e. capsules.	99
10	<i>Loxocarpus sericiflavus</i> : a. habitat, b. habit.	104
11	<i>Loxocarpus verbeniflos</i> : a. habitat, b. adpressed hairs on lamina upper surface, c. young capsule with old corolla still attached at base, d. flower.	113
12	<i>Loxocarpus violoides</i> : a. habit, b. slender capsule, c. flower side view.	117

LIST OF TABLES

Tables	Title	Page
3.1	List of newly acquired samples for this study. Taxa with more than one sample are numbered. (* <i>Henckelia violoides</i> has never been included in <i>Loxocarpus</i> . It is regarded here as an 'in-group' based on its morphological character, viz. its flat-faced flower.)	17
3.2	List of primers used in this study.	19
3.3	Reaction content of PCR for the amplification of <i>trnL-F</i> intron spacer sequences.	19
3.4	Thermal cycle of PCR for the amplification of <i>trnL-F</i> intron spacer sequences.	19
3.5	Reaction content of PCR for the amplification of ITS sequences.	20
3.6	Thermal cycle of PCR for the amplification of ITS sequences.	20
3.7	Reaction contents of PCR products purification.	20
3.8	Thermal cycle of PCR products purification.	21
3.9	Reaction contents of cycle sequencing for <i>trnL-F</i> and ITS.	21
3.10	Thermal cycle of cycle sequencing.	21
3.11	Matrix characteristics of datasets used in MP analyses and statistical attributes of the trees generated.	23
3.12	Matrix characteristics of datasets used in BI analyses.	24
3.13	Species included in morphological data analysis.	45
4.1	List of taxa.	122
5.1	The altitudinal range of <i>Loxocarpus</i> species. The list is arranged in incremental order of columns 'Min.' and 'Max.' Bullet indicates species confined to, 500 m or below in column A and 900 m or above in column B. <i>Loxocarpus</i> sp. B and C are excluded from the list due to lack of altitudinal data.	129
5.2	Geographical distribution of <i>Loxocarpus</i> . ^E denotes narrowly endemic species.	133
5.3	Area of Occupancy (AOO), Extend of Occupancy (EOO), number of collections, number of locations and the occurrence within Protected	140

Areas for *Loxocarpus* species (n.a.=not available).

5.4	Summary for Red List Categories of <i>Loxocarpus</i> taxa.	141
6.1	Summary of name change of <i>Loxocarpus</i> species resulted from this study.	148

LIST OF SYMBOLS AND ABBREVIATIONS

Symbol and Abbreviation	Word
%	percent
°C	degree Celsius
>	greater than
AAU	Herbarium, University of Aarhus, Aarhus, Denmark
ASDSF	average standard deviation of split frequencies
asl	above sea level
BI	Bayesian inference
BK	Herbarium, Department of Agriculture, Bangkok, Thailand
BKF	Herbarium, Royal Forest Department, Bangkok, Thailand
Bkt.	<i>Bukit</i> , hill
BM	Herbarium, Natural History Museum, London, UK
BO	Herbarium, Research Centre for Biology, Indonesian Institute of Sciences, Bogor, Indonesia
BRUN	Herbarium, Office of Conservator of Forests, Brunei
BS	Bootstrap
C	centre
<i>c.</i>	<i>circa</i> , about
CE	centre east
CI	Consistency Index
cm	centimeter
<i>comb. nov.</i>	<i>combinatio novo</i> , new combination
DNA	deoxyribonucleic acid
E	east
E	Herbarium, Royal Botanic Garden, Edinburgh, UK
<i>et al.</i>	<i>et alii</i> , and others
<i>f.</i>	<i>filius</i> , the son
FI-BECC	Herbarium, Firenze-Beccari's Collections, Florence, Italy
Fig.	Figure
FR	Forest Reserve
G.	<i>Gunung</i> , mountain
HBG	Herbarium, Hamburg University, Hamburg, Germany
HI	Homoplasy Index
holo	holotype
iso	isotype
isolecto	isolectotype
K	Herbarium, Royal Botanic Garden, Kew, UK
KEP	Herbarium, Forest Research Institute Malaysia, Selangor, Malaysia
KINA	Herbarium, Sabah Parks, Kota Kinabalu, Sabah, Malaysia
KLU	Herbarium, Universiti Malaya, Kuala Lumpur, Malaysia
KYO	Herbarium, Kyoto University Herbarium, Kyoto, Japan
L	Herbarium, Nederland National Herbarium, Leiden University Branch, the Netherlands
lecto	lectotype
MCMC	Markov Chain Monte Carlo
Min	minute

µm	micrometer
mm	millimeter
mM	micromole
MP	Maximum parsimony; most parsimonious
N	North
n.a.	not available
NE	north east
NP	national park
NW	north west
P	Herbarium, Natural History Museum, Paris France
P.	<i>Pulau</i> , island
<i>pers. comm.</i>	personal communication
PP	Posterior probability
RBGE	Royal Botanic Garden Edinburgh, UK
RC	Rescaled consistency index
RI	Retention index
S	south
<i>s.l.</i>	<i>sensu lato</i> , in the wide sense
<i>s.n.</i>	<i>sine numero</i> , without number
<i>s.s.</i>	<i>sensu stricto</i> , in the narrow sense
SAN	Herbarium, Sabah Forestry Department, Sabah, Malaysia
SAR	Herbarium, Sarawak Forestry Department, Sarawak, Malaysia
Sec	second
sect.	section
SEM	scanning electron microscopy
Sg.	<i>Sungai</i> , river
SING	Herbarium, Singapore Botanic Gardens
SP	State Park
sp.	species, singular
spp.	species, plural
<i>stat. nov.</i>	<i>statu novo</i> , new status
<i>syn. nov.</i>	<i>synonyma novo</i> , new synonym
UC	Herbarium, University of California, Berkeley, US
UKMB	Herbarium, Universiti Kebangsaan Malaysia, Bangi, Malaysia
US	Herbarium, Department of Botany, Smithsonian Institute, Washington, US
var.	variety
<i>viz.</i>	<i>videlicet</i> , in other words
W	west
WU	Herbarium, University Vienna, Vienna, Austria

LIST OF APPENDICES

Appendix	Title	Page
3.1	Morphology characters selected for UPGMA analysis and their character states score.	158
3.2	Data matrix of morphology character state scores	161