

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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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

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