





http://doi.org/10.11646/zootaxa.5194.4.6 http://zoobank.org/urn:lsid:zoobank.org:pub:337BC9FA-3075-4E36-8123-C281CBD1C046

Oficanthon Paulian, 1985, a junior synonym of *Lepanus* Balthasar, 1966 (Coleoptera: Scarabaeidae: Scarabaeinae), with redescription of *Lepanus mirabilis* (Paulian, 1985)

NICOLE L. GUNTER^{1,3}, NATALIE A. SAXTON^{1,4} & THOMAS A. WEIR²

¹Research and Collections Division, The Cleveland Museum of Natural History, Cleveland, Ohio, 44106, United States of America. ²Australian National Insect Collection, CSIRO National Research Collections Australia, Canberra, Australian Capital Territory, 2601, Australia. *tom.weir@csiro.au; https://orcid.org/0000-0002-0053-2870* ³ ngunter@cmnh.org; *https://orcid.org/0000-0002-8355-0862*

⁴ saxton@cmnh.org; ⁶ https://orcid.org/0000-0001-5993-9782

Abstract

The monotypic genus *Oficanthon* Paulian, 1985 (Coleoptera: Scarabaeidae: Scarabaeinae) is treated as a junior synonym of the genus *Lepanus* Balthasar, 1966, and *L. mirabilis* (Paulian, 1985), **new combination** is proposed for *Oficanthon mirabilis* Paulian, 1985. Both morphological and molecular evidence support this synonymy. Morphological evidence further supports its placement within the *Lepanus ustulatus* species group. *Lepanus mirabilis* is redescribed.

Key words: Australasian endemic genera, Papua New Guinea, taxonomy

Introduction

Oficanthon, Paulian 1985 (Coleoptera: Scarabaeidae: Scarabaeinae) was established during a systematic revision of the 'canthonine' dung beetles of New Guinea from the Howden Collection (Paulian 1985). Two specimens previously identified as *Temnoplectron aeneolum* Lansberg, 1855 were described in a new monotypic genus and given the name *Oficanthon mirabilis* Paulian, 1985. The genus is currently considered endemic to Papua New Guinea and is only known from few specimens. Diagnostic characters listed by Paulian (1985) in the description include the presence of pseudepipleura, seven elytral striae and distinctly toothed claws.

Upon examination of a specimen identified as *Oficanthon*, inconsistencies between generic characters proposed by Paulian (1985) and the specimen itself were discovered. This specimen did not possess pseudepipleura, and superficial 8th striae were present along the flange-like dorsal edges of the epipleura. Four Australasian genera *Lepanus* Balthasar, 1966, *Sauvagesinella* Paulian, 1935, *Matthewsius* Gunter & Weir, 2017, and *Monteithocanthon* Gunter & Weir, 2017 share these features and can be further differentiated by protibial and pygidial arrangement, the presence/absence of trochantofemoral pits, proportions of metatarsomeres, and claw shape (Gunter & Weir 2017). These discoveries suggest that the specimen in question was either misidentified as *Oficanthon*, or that *Oficanthon* is a synonym of *Lepanus*.

Materials and methods

To verify the identity of the specimen identified as *Oficanthon*, high-resolution images of the holotype and paratype were obtained. Type images were compared to the original description of Paulian (1985), as well as the specimen in hand. Redescriptions follow the format for description of Australian *Lepanus* (Gunter & Weir 2019, 2021). Body length measurements were taken from the tip of the clypeal teeth to the posterior edge of the elytra. Width measurements were taken at the widest point. Label data is given verbatim with inside quotations with "]" to indicate line breaks and "]]" to indicate information on reverse of label.

Accepted by A.B.T. Smith: 11 Jul. 2022; published: 7 Oct. 2022

Licensed under Creative Commons Attribution-N.C. 4.0 International https://creativecommons.org/licenses/by-nc/4.0/

Specimens examined are deposited in the following institutions:

CMNC: Canadian Museum of Nature (Ottawa, Ontario, Canada) MNHN: Muséum National d'Histoire Naturelle (Paris, France)

In order to provide molecular data to support morphological hypotheses, the DNA from a recently collected specimen was extracted using non-destructive methods. The standard Qiagen DNeasy Tissue kit extraction protocol was modified to include tissue lysis overnight (~ 16 hours) and elution in two 100 uL aliquots. Following wellestablished molecular protocols for Australian dung beetles, we amplified the nuclear ribosomal region of 28S and 18S using the primers listed in Gunter & Weir (2017) and cycling conditions of Gunter et al. (2013). Additional markers, including cytochrome oxidase 1 (COI) were also attempted, but the region "Jerry-Pat" standardly used in Scarabaeinae analyses was unsuccessful. A shorter non-overlapping fragment generated using the primers LepF1 and MLepF1-rev (Brandon-Mong et al. 2015) was amplified. PCR products were purified with Exosap-IT and sent to the Genomics Core at Case Western Reserve University (Cleveland, Ohio, United States of America) for Sanger Sequencing. Raw sequences were trimmed and aligned using MAFFT (Katoh and Standley 2013) in Geneious (version 6.1.8; Biomatters, Auckland, New Zealand) with sequences (28S, 18S, 16S, COI) previously published in Gunter et al. (2019b) (see Table 1). A maximum likelihood topology was reconstructed using IQ-tree 1.6.12 (Nguyen et al. 2015) in which ModelFinder (Kalyaanamoorthy et al. 2017) was implemented and 1000 ultrafast bootstraps (Hoang et al. 2019) were used. The short COI fragment was not included in the phylogenetic analysis as the primers did overlap with the other sequences. However, all newly generated sequences (COI, 28S, 18S) are deposited on GenBank under the accession codes OM523102, OM522902, and OM522903.

Lepanus Balthasar, 1966

Lepanus Balthasar, 1966: 177. Type species: Lepanus ovatus Balthasar 1966 (by monotypy); Matthews 1974: 100, Gunter & Weir 2019: 41, Gunter et al. 2019a: 459.

Oficanthon Paulian, 1985: 227. Type species: Oficanthon mirabilis Paulian, 1985 (by monotypy); new synonym.

Comments. *Oficanthon* is a monotypic genus here treated as a synonym of *Lepanus*. For a generic description of *Lepanus* refer to Matthews (1974) and Gunter *et al.* (2019a).

Lepanus mirabilis (Paulian, 1985), new combination

Figs. 1-3.

Oficanthon mirabilis Paulian 1985: 228.

Type material examined. Holotype (1 ♂ **CMNC).** "PAPUA NEW GUINEA | 8km. SW Nadro, 650m. | Ofi Creek, O. Kukal | 15–18viii. 76, dng | lowlandRainforest" "H. & A.Howden | Collection" "HOLOTYPE" "Oficanthon mirabilis | n. g. n. sp | R. Paulian det." "Canadian Museum of | Musée canadien de la | NATURE | CMNEN 00011782" (Fig.2E). **Paratype (1** ♂ **MNHN).** "PAPUA NEW GUINEA | 8km. SW Nadro, 650m. | Ofi Creek, O. Kukal | 15–18viii. 76, dng | lowlandRainforest" "H. & A.Howden | Collection" "PARATYPE" "Oficanthon | mirabilis | n.g. n.sp. | R. Paulian det." "MNHN, Paris | EC14839"

Additional material examined. (2 \circ CMNC) "PAPUA NEW GUINEA | 8km. SW Nadro, 650m. | Ofi Creek, O. Kukal | 15–18.viii.76, dng | lowlandRainforest" "PARATYPE" "PARATYPE | Oficanthon | mirabilis | R. Paulian" "Canadian Museum of | Musée canadien de la | NATURE | CMNEN 00013051"; "PAPUA NEW GUNIEA: Western | Prov. P'nvana. CI RAP Survey | Camp 1. 05°29.5S 141°32.6E | 575 m. May 2013. T. Larsen || 05/28/13 | Trap 5" "OFICANTHON | MIRABILIS | PAUL. | Dét. F. Génier, 2017" "MUST BE | Lepanus NEAR | usulatus | det T.A. WEIR 2018" "COL3182".

Redescription. Head black medially and reddish brown apically. Prothorax and elytra black. Dorsal surface glabrous. Antennal clubs light brown. **Measurements.** Total length: 5.19 mm, elytral width 3.77 mm

Head. Width to length ratio 40:26. Surface smooth and nitid with very fine punctation. Broad U-shaped area between clypeal teeth that are upturned and strongly pointed. Margin of head completely bordered, rounded. Genal

angle slightly prominent, angulate at clypeogenal suture. Clypeofrontal margin with medial impression. Dorsal part of the eyes wide, separated by an interocular space approximately 6 times eye width. Eye canthus not dividing the eye. Prothorax. Pronotal surface smooth, nitid and very finely punctate. Pronotum anterior angles sharp, posterolateral corners distinct, lateral edges bordered. Basal edge rounded, with a fine margin medially, margin without punctures. Hypomeral surface reticulate, hypomeral striae absent. Pronotal width to length ratio 65:42. Elytra. Overall, strongly convex. Surface smooth, nitid and very finely punctate, with 8 superficial, impunctate striae. Sparse golden setae. Ratio of length of the elytra along suture to maximum elytral width 65:78. Wide reticulate epipleura. Legs. Reddish brown. Protibia with 3 teeth on outer edge, 1 small tooth at the base of the tarsus, and 1 small ventral tooth on the basal 1/3 (Fig. 2C-D); front edge truncate with a short, broad apical digit, apical spur absent; crenulate ridge on ventral surface; trochantofemoral pit absent. Mesotibia with a brush of golden setae apically on inner edge. Metatibia with inner edge finely crenulate, nearly straight. Metatarsus with 5 tarsomeres with 2nd tarsomere the longest; basal metatarsomere lobed on inner edge. Tufts of setae present on meso- and metatrochanters. Claws simple. Abdomen. Pygidium reticulate with a transverse fold extending from the lateral corners, and absent in the medial half; pygidial disc with a large, flat, ovate reticulate area that does not reach the fold basally; surface with long, fine setae. Abdominal ventrites reticulate for full width; ventrite 6 finely punctate. Suture between ventrites 5 and 6 weak. Pterothorax. Mesoventrite very finely reticulate, virtually impunctate, notched anteriorly. Medial lobe of metaventrite very finely reticulate and virtually impunctate, broadly margined between mesocoxae. Lateral lobes of metaventrite finely reticulate, finely punctate, punctures with fine setae. Mesometavental suture arched. Metanepisternum reticulate.



FIGURE 1. Holotype of *Lepanus mirabilis*. A, Dorsal habitus; B, pygidium; C, dorsal protibia; D, lateral metatibia; E, metatarsal claw. Images provided by F. Génier (CMNC).

Gauss Specis Data Sunce Identifier Col 35 16, 18, $diphistama complianta Managhar et al. 2007 NA AY13143 AY13141 N69228 diphistama complianta Managhar et al. 2007 NA AY13163 AY13141 N69228 Dietoscather complianta Managhar et al. 2007 NA AY13163 AY13141 N69228 Dietoscather compliante marger COL304 KY77953 KY89693 N731441 N69275 Cathebraic annager contact al. 2007 NA AY131421 AY13141 N69277 Captocic homisphare annager contact al. 2007 NA AY131421 N731451 N69277 Captocic homisphare call al. 2007 NA AY131451 N69207 N69207 Captocic annager dume al. 2007 NA AY131451 N731451 N69207 Captocic annactic dume al. 2016 COL3946 KY797952 K8901$	IABLE I. Specimens	included in the phyloge	netic analysis.					
Applications complianter (2007) Na. N11345 N113136 1.0 N209238 Applications compliant et (2007) COL130 KY77976 KN37935 KN387036 KN37036 Applications consumpliant et (2007) NA AY13143 N131441 N692504 Capholosonins consumpliant et (2007) NA AY13143 N131441 N692504 Capholosonins consumpliant et (2007) NA AY13143 N131441 N692504 Capholosonins annager consumpliant et (2007) NA AY13143 N131431 N031474 Capholosonins fancolis Monaghina et (2007) NA AY131431 N131431 N031474 Capholosonius fancolis Monaghina et (2007) NA AY131431 N031775 Capholosonius fancolis Monaghina et (2007) NA AY131431 N03175 Diopsorp fanolis Monaghina et (2007) NA AY131431 N031975 Diopsore fanolis Monaghina et (2007	Genus	Species	Data Source	Identifier	COI	28s	16s	18s
d pronocardion virger Gunter & Weir 2017; C CUL130 K Y779776 K X988/96 K X988/96 K X988/96 d holorocegne corrants Monoglane et al. 2007 N.A A1713423 A17131431 A17131431 N1131417 N619225 $Caphalohernius marger Gunter et al. 2007 N.A A17131831 A17131431 N1131471 N61977 Caphalohernius finityon Gunter et al. 2007 N.A A17131831 A17131431 N1131431 N1131471 N61977 Caphalohernius finityon Gunter et al. 2007 N.A A17131831 A17131431 N1131431 N$	Amphistomus	complanatus	Monaghan <i>et al.</i> 2007	NA	AY131436	AY131808	I	JN619228
Bolancorper corntance Monoplane rat. 2007 NA M131632 M131441 N619225 Carbinonom carcinatum Monoplane rat. 2007 NA M13163 M131441 N619275 Capinatosensis anniger Gumer at 2019 CO.1044 KY7383 KY73836 KY73840 KY38474 - Capinatosensis hemispinae rat. 2017 NA M131821 M131451 N131451 N131451 N61977 Capinatosensis hemispinae rat. 2007 NA M131821 M131451 N131451 N61977 Capinatosensis hemispinae rat. 2007 NA M131821 M131451 N131451 N61977 Capinatosensis hemispinae rat. 2007 NA M131821 M131451 N61977 Capinatosensis inter et al. 216 COL2396 KF80139 KF80139 N61977 Dorgspinar inter et al. 2107 NA M131821 M131451 M131451 M131451 Dorgspinar inter et al. 2106 COL2396 KF80139 KF80139 KF8	Aptenocanthon	wingar	Gunter & Weir 2017;	COL1130	KY779776	KX986926	KX987061	KX987004
Canthonsome castelnui Moneghan et al. 2007 NA AY13181 AY131431 C Cephalokennis emiger Gunue et al. 2019 CO.3044 KY778825 KX987091 KX987043 Cephalokennis Introdits Gunue et al. 2017 CO.13043 KY71882 KY131641 AY131451 N101971 Cephalokennis Introdits Gunue et al. 2007 NA AY131821 AY131451 N101970 KX987043 Cephalokennis Introdits Moneghan et al. 2007 NA AY131821 AY131451 N101977 XX987043 Cephalokennis Introdits Moneghan et al. 2007 NA AY131821 AY131451 N101977 Demoration introdits Gunue et al. 2016 CO12396 KF80154 KF801791 N101977 Demoration introdits Gunue et al. 2017 NA XY131791 XY13145 N1019173 Demoration Gunue et al. 2016 COL1396 KF80543 KF801791 KF807191 KF807191 KF807191 KF807191 KF807191 <	Boletoscapter	cornutus	Monaghan <i>et al.</i> 2007	NA	AY131632	AY131813	AY131441	JN619225
Capitaldaemits amiger Gunter et al. 2019 COL3043 K Y77932 K Y3063 <thk th="" y3063<=""> K Y3063 K Y30</thk>	Canthonosoma	castelnaui	Monaghan <i>et al.</i> 2007	NA	AY131818	AY131638	AY131447	
Caphadeantus latrolis Gunter & Weir 2017 COL3053 KY779830 KX987091 KX987091 KX987091 KX987091 KX987091 KX987091 KX987091 KX987091 KX987091 KX987049 Coprodacycla planricollis Monaghun et al. 2007 NA A7131621 A7131631 A7131451 A7131451 M1131451 M00307 Diorygopy incomptas Gunter et al. 2016 CO12396 KF801954 KF80119 KF801791 - Diorygopy incomptas Gunter et al. 2016 CO12396 KF80138 KF80119 A7131451 - Diorygopy incomptas Gunter et al. 2016 CO12396 KF80138 KF80138 KF80139 - Laparatic austrolis Gunter et al. 2016 CO11391 KT77979 KF802188 KF80130 - Laparatic austrolis Gunter et al. 2016 CO11318 KT77979 KF802188 KF80130 - Laparatic monuplum et al. 2017 CO11318 KT77979 KF805892 KF80707 <t< td=""><td>Cephalodesmius</td><td>armiger</td><td>Gunter et al. 2019b</td><td>COL3044</td><td>KY779825</td><td>KX986975</td><td>ı</td><td>KX987043</td></t<>	Cephalodesmius	armiger	Gunter et al. 2019b	COL3044	KY779825	KX986975	ı	KX987043
Coprocess lemispharctes Moneghan et al. 2007 NA AY131821 AY131651 AY131451 IN619171 Copodacrpia gidsricolits Moneghan et al. 2007 NA AY131637 AY131451 IN619207 Demarziella mirifica Moneghan et al. 2007 NA AY131763 AY131451 IN619207 Demarziella mirrifica Moneghan et al. 2016 COL2399 KF801954 KF801791 - Diorygopx sinplicichmis Gunte et al. 2016 COL2396 KF801954 KF801791 - Diorygopx sinplicichmis Gunte et al. 2016 COL2396 KF80154 KF801791 - Diorygopx sinplicichmis Gunte et al. 2016 COL1397 KF80154 KY39704 - Gunte et al. 2016 Gunte et al. 2017 COL1341 KY77971 KY398704 KY38704 KY38704 Leprans microlitis Gunte & Weir 2017 COL1341 KY77971 KY398704 KY38706 KY38705 Leprans microlitis Gunte & Weir 2017	Cephalodesmius	laticollis	Gunter & Weir 2017	COL3053	KY779830	KX986980	KX987091	KX987048
Coprodacyla glabricollis Monghun et al. 2007 NA AY13185 AY13196 Nol9207 Demarzielia mirifica Monghun et al. 2007 NA AY131872 AY131701 AY131512 - Diorygopyx incomplus Gamter et al. 2016 COL2396 KF80195 KF801791 KF801791 - Diorygopyx incomplus Gamter et al. 2016 COL2396 KF80154 AY13152 - - Diorygopyx incomplus Gamter et al. 2017 NA AY13154 AY13154 AY13153 - Diorygopyx incomplus Gamter et al. 2016 COL1907 KY77979 KY99704 KY99704 - Lepanus anstralis Gunter & Weir 2017 COL1136 KY77971 KY98692 KY98706 KY98706 Lepanus globulus Gunter & Weir 2017 COL1316 KY77971 KY98692 KY98706 KY88706 Lepanus moneithi Gunter & Weir 2017 COL1317 KY77978 KY98692 KY98706 KY88706	Coproecus	hemisphaericus	Monaghan <i>et al.</i> 2007	NA	AY131821	AY131641	AY131451	JN619177
Demarziella mirifica Monagha et al. 2007 NA AY131872 AY131701 AY131512 - Diorygopyx incompus Gunter et al. 2016 COL2396 KF801955 KF801191 KF801791 - Diorygopyx simpliciclusis Gunter et al. 2016 COL2396 KF801954 KF801790 - Endroed/olus gambia Gunter et al. 2007 NA AY131854 AY131654 KY80709 - Lepanus mustralis Gunter et al. 2019 COL1197 KY79719 KY986927 KY897062 KY897063 Lepanus monethin Gunter et al. 2019 COL1136 KY77971 KX986927 KX987062 KX987063 Lepanus monethin Gunter et al. 2017 COL1451 KY77971 KX987063 KX987063 Lepanus monethin Gunter et al. 2017 COL1451 KY77971 KX987063 KX987063 Lepanus monethin Gunter et al. 2017 COL1451 KY77931 KX987063 KX987063 Lepanus monethin<	Coptodactyla	glabricollis	Monaghan <i>et al.</i> 2007	NA	AY131863	AY131687	AY131496	JN619207
Diorygopyx incomptas Gunter et al. 2016 COL2396 KF80159 KF801791 - Diorygopyx simplicicluits Gunter et al. 2016 COL2396 KF80179 KF801790 - Endredyolus paradoxus Monighm et al. 2007 NA A7131834 KF801790 - Endredyolus fascicultat Monighm et al. 2007 NA A7131834 A7131634 M7131463 M619175 Lepanus Gunter et al. 2019 COL1197 KY77979 KY396029 KY397005 - Lepanus globulus Gunter et al. 2016 COL136 KY779719 KY396097 KY39706 KY39705 Lepanus montethi Gunter & Weiz 2017 COL1451 KY77971 KY396097 KY38705 Lepanus montethi Gunter & Weiz 2017 COL1451 KY77971 KY396097 KY38705 Lepanus montethi Gunter & Weiz 2017 COL1451 KY77978 KY386085 KY38705 Lepanus montethi Gunter & Weiz 2017 COL944 KY	Demarziella	mirifica	Monaghan <i>et al.</i> 2007	NA	AY131872	AY131701	AY131512	
Diorygopy simplicicluris Gamter et al. 2016 COL2396 KF80154 KF80118 KF801790 - Endroedyoks paradoxus Monaghan et al. 2007 NA 6Q28981 GQ289722 GQ289701 - Igambia fasciculara Monaghan et al. 2007 NA AY131834 AY131654 AY131463 1N619175 Igambia dustralis Gumter & Wei: 2017 COL1197 KY779779 KY986929 KX987062 KX987003 Lepanus mirrehilis current & Wei: 2017 COL1316 KY779771 KX986929 KX987064 KX987005 Lepanus mirrehilis current & Wei: 2017 COL1316 KY77971 KX986931 KX987065 KX98705 Lepanus monethin Gumter & Wei: 2017 COL1451 KY779781 KX986931 KX987066 KX98705 Lepanus occidentalis Gumter & Wei: 2017 COL1451 KY779781 KX986935 KX987066 KX98705 Lepanus parapisioniae Gumter & Wei: 2017 COL1954 KY779735 <td< td=""><td>Diorygopyx</td><td>incomptus</td><td>Gunter et al. 2016</td><td>COL2399</td><td>KF801955</td><td>KF802119</td><td>KF801791</td><td></td></td<>	Diorygopyx	incomptus	Gunter et al. 2016	COL2399	KF801955	KF802119	KF801791	
Endroedyolus paradoxus Monaghan et al. 2007 NA GQ28991 GQ289701 - Ignambia fasciculata Monaghan et al. 2007 NA AY131654 AY131453 IN61975 Ignambia fasciculata Monaghan et al. 2007 NA AY131654 AY131453 IN61975 Lepanus cunter et al. 2019 Cunter et al. 2019 COL1197 KY779779 KY386929 KY387064 KY387007 Lepanus globulus Gunter & Weir 2017 COL1136 KY779719 KY386929 KY387005 KY387005 Lepanus mirabilis current study COL1312 COL1342 KY779719 KY386935 KY387005 KY38705 Lepanus mirabilis cunter & Weir 2017 COL1451 KY779383 KY387056 KY38705 Lepanus moreithi Gunter & Weir 2017 COL1461 KY779383 KY387095 KY387056 Lepanus ustratures Gunter & Weir 2017 COL1461 KY779383 KY387035 KY387056 Lepanus ustratures </td <td>Diorygopyx</td> <td>simpliciclunis</td> <td>Gunter et al. 2016</td> <td>COL2396</td> <td>KF801954</td> <td>KF802118</td> <td>KF801790</td> <td></td>	Diorygopyx	simpliciclunis	Gunter et al. 2016	COL2396	KF801954	KF802118	KF801790	
IgnambiafasciculataMonaghan et al. 2007NAAY131834AY131654AY131453IN619155LepanusaustralisGunter & Weir 2017;COL1197KY77979KY986929KX987064KX987007LepanusGunter & Weir 2017;COL1136KY779779KY986929KX987062KX987005LepanusglobulusGunter & Weir 2017COL1136KY779779KY986929KX987062KX987012LepanusmonethinGunter & Weir 2017COL1451KY77978KY986931KX987016M522903LepanusmonethinGunter & Weir 2017COL1451KY779781KX986093KX987016M5287012LepanusmonethinGunter & Weir 2017COL1461KY779783KX986093KX987051KX987051LepanusmonethinGunter & Weir 2017COL1461KY779735KX986093KX987076KX987051LepanusmonethinGunter & Weir 2017COL1461KY77975KX986092KX987076KX987051LepanusnsundanesisGunter & Weir 2017COL1660KY77975KX986092KX987076KX987050LepanusnsundanesisparlengareGunter & Weir 2017COL1610KY77975KX986092KX987076KX987050LepanusparlensisparlengareGunter & Weir 2017COL1610KY77975KX986092KX9870706KX987050LepanusparlensisparlengareGunter & Weir 2017COL1600KY779795KX986092KX9870706KX987020<	Endroedyolus	paradoxus	Monaghan <i>et al.</i> 2007	NA	GQ289981	GQ289752	GQ289701	
LepanusaustralisGunter & Weir 2017;COL 1197K Y779779K X986929K X987064K X987007LepanusGunter et al. 2019b $COL 1136$ K Y779777K X986927K X987062K X987005Lepanusmirabiliscurrent studyCOL 136K Y77777 $OM522902$ K X987005 $OM522903$ Lepanusmirabiliscurrent studyCOL 1451K Y777781 $K X986931$ $K X987097$ $K X987056$ LepanusmoneithiGunter & Weir 2017COL 1451K Y777983 $K X986988$ $K X987097$ $K X987056$ LepanusmoneithiGunter & Weir 2017COL 1451K Y77983 $K Y986985$ $K X987097$ $K X987056$ LepanusmoneithiGunter & Weir 2017COL 1461 $K Y77983$ $K Y8028935$ $K Y808705$ $K X987056$ LepanusustulatusGunter & Weir 2017COL 1666 $K Y777975$ $K Y80935$ $K Y80706$ $K Y887056$ LepanusustulatusGunter & Weir 2017COL 1660 $K Y777975$ $K Y80935$ $K Y807076$ $K Y887026$ LepanusustulatusGunter & Weir 2017COL 1660 $K Y777975$ $K Y809395$ $K Y897076$ $K Y887026$ LepanusustulatusGunter & Weir 2017COL 1660 $K Y777975$ $K Y806925$ $K Y897076$ $K Y89702$ LepanusustulatusGunter & Weir 2017COL 1660 $K Y777975$ $K Y986925$ $K Y987076$ $K Y98702$ LepanuspenelopaeGunter & Weir 2017COL 1660 $K Y777979$	Ignambia	fasciculata	Monaghan <i>et al.</i> 2007	NA	AY131834	AY131654	AY131463	JN619175
Gunter et al. 2019bLepanusGunter et al. 2019bKY77971KY986927KY87762KY887065Lepanusmirabiliscurrent studyCOL1382COL1382MM522903KX987066KX987012Lepanusmirabiliscurrent studyCOL1451KY779781KY986931KX987097KX987056KX987051LepanusmoneithiGunter & Weir 2017COL1451KY77981KY986938KX987097KX987056KX987056LepanusoccidentalisGunter & Weir 2017COL1451KY779834KY986935KX987091KX987056LepanusparapisioniaeGunter & Weir 2017COL1461KY77983KY79836KX987091KX987056LepanusustulatusGunter & Weir 2017COL1461KY779793KY79793KX987070KX987050LepanusustulatusGunter & Weir 2017COL1666KY779792KY79792KX987070KX987050LepanusustulatusGunter & Weir 2017COL1660KY779793KY79793KX987070KX987050MaithewsiuspenelopareGunter & Weir 2017COL1660KY779780KY79793KY79792KY79793KY97070KY97050MaithewsiuspenelopareGunter & Weir 2017COL1660KY779809KY79793KY79793KY97060KY97050MaithewsiuspenelopareGunter & Weir 2017COL1660KY779793KY79793KY97070KY97050Monoplistes"sp. dgi1"Monaeita 2007COL1660KY779809	Lepanus	australis	Gunter & Weir 2017;	COL1197	KY779779	KX986929	KX987064	KX987007
Lepanus $globulus$ $Gunter \& Weir 2017$ $COL 1136$ $KY77977$ $KY386927$ $KX987062$ $KX987065$ Lepanus $mirabilis$ $current study$ $COL 3182$ $OM522902$ $OM522903$ $OM522903$ Lepanus $montethi$ $Gunter \& Weir 2017$ $COL 1451$ $KY779781$ $KX986931$ $KX987066$ $KX97012$ Lepanus $cccidentalis$ $Gunter \& Weir 2017$ $COL 1451$ $KY77934$ $KX986988$ $KX987096$ $KX987056$ Lepanus $palumensis$ $Gunter \& Weir 2017$ $COL 945$ $KY77934$ $KX986985$ $KX987094$ $KX987056$ Lepanus $parapistoniae$ $Gunter \& Weir 2017$ $COL 1461$ $KY77984$ $K802151$ $KF80128$ $KX987056$ Lepanus $parapistoniae$ $Gunter \& Weir 2017$ $COL 1461$ $KY77983$ $KY79898595$ $KX987070$ $KX987056$ Lepanus $usnlatusGunter \& Weir 2017COL 1666KY779795KX986925KX987070KX987026LepanusvestitusGunter \& Weir 2017COL 1660KY779795KY986925KX987076KX987026Lepanusvestitusgunter \& Weir 2017COL 1660KY779795KY986926KX987076KX987026MathewsiusperelopaeGunter \& Weir 2017COL 1660KY779796KY986926KX987026MathewsiusperelopaeGunter \& Weir 2017COL 1660KY779796KY986926KX987026MathewsiusperelopaeGunter \& Weir 2017$			Gunter et al. 2019b					
Lepanusnirabiliscurrent studyCOL3182 $0M522902$ $0M522903$ LepanusmonteithiGunter & Weir 2017COL1451KY79781KX986931KX987056KX987012LepanusoccidentalisGunter & Weir 2017COL1451KY779837KX986988KX987097KX987056LepanuspalumensisGunter & Weir 2017COL945KY779834KX986985KX987094KX987051LepanusparapisioniaeGunter & Weir 2017COL945KY779834KX986985KX987094KX987051LepanusparapisioniaeGunter & Weir 2017COL1461KY779785KX986935KX987070KX987051LepanusvestitusGunter & Weir 2017COL1666KY779785KX986935KX987070KX987016LepanusvillosusGunter & Weir 2017COL1660KY779785KX986935KX987070KX987020LepanusvillosusGunter & Weir 2017COL1660KY779789KX986935KX987076KX987020MatthewsiuspenelopaeGunter & Weir 2017COL1600KY779789KX986935KX987070KX987020MatthewsiuspenelopaeGunter & Weir 2017COL1660KY779789KX986936YX987070KX987020MatthewsiuspenelopaeGunter & Weir 2017COL1660KY779789KX986936YX987070KX987020MatthewsiuspenelopaeGunter & Weir 2017COL1660KY779789KX986936YX987070KX987020Monoplistes"sp. dgi1"M	Lepanus	globulus	Gunter & Weir 2017	COL1136	KY779777	KX986927	KX987062	KX987005
LepanusmonteithiGunter & Weir 2017COL 1451 $KY779781$ $KY386931$ $KX987066$ $KX987012$ Lepanus $occidentalis$ Gunter & Weir 2017COL 964 $KY779837$ $KY386988$ $KY387097$ $KY387056$ Lepanus $palumensis$ Gunter & Weir 2017COL 945 $KY779834$ $KY386985$ $KY387094$ $KY387054$ Lepanus $palumensis$ Gunter & Weir 2017COL 945 $KY779834$ $KY386985$ $KY387094$ $KY387054$ Lepanus $palumensis$ Gunter & Weir 2017COL 1461 $KY779785$ $KY386935$ $KY3870707$ $KY387016$ Lepanus $vestitus$ Gunter & Weir 2017COL 1666 $KY779792$ $KY386935$ $KY387076$ $KY387016$ Lepanus $villosus$ Gunter & Weir 2017COL 1660 $KY779792$ $KY386935$ $KY387060$ $KY387020$ Matthewsius $penelopae$ Gunter & Weir 2017COL 1660 $KY779792$ $KY386939$ $KY387060$ $KY387020$ Matthewsius $penelopae$ Gunter & Weir 2017COL 1660 $KY779789$ $KY386939$ $KY387076$ $KY387020$ Matthewsius $penelopae$ Gunter & Weir 2017COL 3010 $KY779789$ $KY986939$ $KY987070$ $KY987020$ Matthewsius $vestitus$ $vestitusCOL 123KY779789KY986939KY987070KY987020MatthewsiusvestitusvestitusCOL 1207NAKY779789KY986939KY987070KY987020Monoplistes"speevadG$	Lepanus	mirabilis	current study	COL3182		OM522902		OM522903
Lepanus $occidentalis$ Gunter & Weir 2017COL964KY779837KX986988KX987097KX987056Lepanus $palumensis$ Gunter & Weir 2017COL945KY779834KY986985KX987094KX987054Lepanus $parapisioniae$ Gunter & Weir 2017COL1461KY779785KY986935KX987070KX987051Lepanus $usnulatus$ Gunter & Weir 2017COL1461KY779785KY986935KX987070KX987070KX987051Lepanus $vestitus$ Gunter & Weir 2017COL1666KY779792KY986935KX987076KX987020Lepanus $vestitus$ Gunter & Weir 2017COL1660KY779792KY986935KX987076KX987020Lepanus $vestitus$ Gunter & Weir 2017COL1660KY779792KY986939KX987076KX987020Matthewsius $pnelopae$ Gunter & Weir 2017COL1660KY779789KY986939KY987076KY987020Matthewsius $speevah$ Gunter & Weir 2017COL1660KY779789KY986939KY987076KY987020Matthewsius $speevah$ Gunter & Weir 2017COL1660KY779789KY986939KY987076KY987020Monplistes"*p. dgi1"Monaghan et al. 2007NAAY131837AY131658AY131466-MoneithocanthonglaberGunter & Weir 2017COL1460KY779789KY986934KY987069KY987029MoneithocanthonglaberGunter & Weir 2017NoCOL3010KY779789KY986954KY987029	Lepanus	monteithi	Gunter & Weir 2017	COL1451	KY779781	KX986931	KX987066	KX987012
Lepanus palumensis Gunter & Weir 2017 COL945 KY779834 KY086985 KY09649 KY09754 Lepanus parapisioniae Gunter & Weir 2017 COL75 KF801988 KF802151 KF801823 KY987054 Lepanus ustulatus Gunter & Weir 2017 COL1461 KY779785 KY986935 KY987070 KY987016 Lepanus vestitus Gunter & Weir 2017 COL1666 KY779792 KY986925 KY987060 KY987020 Lepanus villosus Gunter & Weir 2017 COL1660 KY779792 KY986939 KX987060 KY987003 Matthewsius penelopae Gunter & Weir 2017 COL1660 KY779792 KY986939 KY987060 KY987003 Matthewsius penelopae Gunter & Weir 2017 COL1660 KY779789 KY986939 KY987060 KY987003 Matthewsius speewah Gunter & Weir 2017 COL3010 KY779789 KY986939 KY987060 KY987020 Monoplistes "sp. dgi1" Monatanton stp. dgi1 M131837	Lepanus	occidentalis	Gunter & Weir 2017	COL964	KY779837	KX986988	KX987097	KX987056
LepanusparapisioniaeGunter & Weir 2017 $COL775$ $KF801988$ $KF80151$ $KF801823$ $KY01823$ $KY01823$ $KY01823$ $KY01633$ LepanusustulatusGunter & Weir 2017 $COL1461$ $KY779785$ $KY386935$ $KY387706$ $KY387706$ $KY387706$ LepanusvestitusGunter & Weir 2017 $COL1666$ $KY779792$ $KY386932$ $KY387706$ $KY387706$ $KY387706$ LepanusvillosusGunter & Weir 2017 $COL1123$ $KY779792$ $KY386925$ $KY387706$ $KY387706$ MathewsiuspenelopaeGunter & Weir 2017 $COL1660$ $KY779789$ $KY386939$ $KY387706$ $KY387702$ MathewsiusspeewahGunter & Weir 2017 $COL1660$ $KY779789$ $KY386939$ $KY3877796$ $KY387702$ MathewsiusspeewahGunter & Weir 2017 $COL1800$ $KY779789$ $KY79809$ $KY986939$ $KY987705$ Monoplistes"sp. dgi1"Monaghan et al. 2007NA $AY131837$ $AY131658$ $AY13166$ $-$ Monoplistes"sp. dgi1"Gunter & Weir 2017 $COL1460$ $KY779789$ $KY79809$ $KY987069$ $KY987069$ Monoplistes"sp. dgi1"Monaghan et al. 2007NA $AY131837$ $AY131658$ $AY13166$ $-$ Monoplistes"sp. dgi1"Gunter & Weir 2017 $COL1460$ $KY779789$ $KY797989$ $KY97069$ $KY987069$ Monoplistes"sp. dgi1"Monaghan et al. 2007NA $AY131837$ $AY13166$ $ KY987069$	Lepanus	palumensis	Gunter & Weir 2017	COL945	KY779834	KX986985	KX987094	KX987054
Lepanus ustulatus Gunter & Weir 2017 COL 1461 KY779785 KX986935 KX987070 KX987016 Lepanus vestitus Gunter & Weir 2017 COL 1666 KY77972 KX986942 KX987076 KX987026 Lepanus villosus Gunter & Weir 2017 COL 1666 KY77975 KX986925 KX987060 KX987003 Matthewsius penelopae Gunter & Weir 2017 COL 1660 KY779789 KX986939 KX987073 KX987003 Matthewsius penelopae Gunter & Weir 2017 COL 1660 KY779789 KX986939 KX987073 KX987026 Matthewsius speewah Gunter & Weir 2017 COL 1660 KY779809 KX986958 - KX987026 Matthewsius speewah Gunter & Weir 2017 COL 13103 KY779809 KX986958 - KX987026 Matthewsius "sp. dgi1" Monaghan et al. 2007 NA AY131837 AY131658 - KX987026 Monoplistes "sp. dgi1" Gunter & Weir 2017 COL 1460 KY777989	Lepanus	parapisioniae	Gunter & Weir 2017	COL775	KF801988	KF802151	KF801823	KX987051
Lepanus vestitus Gunter & Weir 2017 COL 1666 KY77972 KX986942 KX987076 KX987023 Lepanus villosus Gunter & Weir 2017 COL 1123 KY77975 KX986925 KX987060 KX987003 Matthewsius penelopae Gunter & Weir 2017 COL 11660 KY779789 KX986939 KX987073 KX987020 Matthewsius speewah Gunter & Weir 2017 COL 1660 KY779809 KX986939 KX987073 KX987020 Matthewsius speewah Gunter & Weir 2017 COL 3010 KY779809 KX986958 - KX987020 Monoplistes "sp. dgi1" Monaghan et al. 2007 NA AY131837 AY131658 - KX987026 Monteithocanthon glaber Gunter & Weir 2017 COL 1460 KY779784 KY986934 KY987069 -	Lepanus	ustulatus	Gunter & Weir 2017	COL1461	KY779785	KX986935	KX987070	KX987016
Lepanus villosus Gunter & Weir 2017 COL1123 KY77975 KX986925 KX987060 KX987003 Matthewsius penelopae Gunter & Weir 2017 COL1660 KY779789 KX986939 KX987073 KX987020 Matthewsius speewah Gunter & Weir 2017 COL3010 KY779809 KX986958 - KX987020 Monoplistes "sp. dgi1" Monaghan et al. 2007 NA AY131837 AY131658 - KX987026 Monteithocanthon glaber Gunter & Weir 2017 COL1460 KY779784 KY986934 KX987069 -	Lepanus	vestitus	Gunter & Weir 2017	COL1666	KY779792	KX986942	KX987076	KX987022
Matthewsius penelopae Gunter & Weir 2017 COL 1660 KY779789 KX986939 KX987073 KX987020 Matthewsius speewah Gunter & Weir 2017 COL 3010 KY779809 KX986958 - KX987026 Monoplistes "sp. dgi1" Monaghan et al. 2007 NA AY131837 AY131658 AY131466 - Monteithocanthon glaber Gunter & Weir 2017 COL 1460 KY779784 KX986934 KX987069 KX987015	Lepanus	villosus	Gunter & Weir 2017	COL1123	KY779775	KX986925	KX987060	KX987003
Matthewsius speewah Gunter & Weir 2017 COL3010 KY779809 KX986958 - KX987026 Monoplistes "sp. dgi1" Monaghan et al. 2007 NA AY131837 AY131658 AY131466 - Monteithocanthon glaber Gunter & Weir 2017 COL1460 KY779784 KX986934 KX987069 KX987015	Matthewsius	penelopae	Gunter & Weir 2017	COL1660	KY779789	KX986939	KX987073	KX987020
Monoplistes "sp. dgi1" Monaghan et al. 2007 NA AY131837 AY131658 AY131466 - Monteithocanthon glaber Gunter & Weir 2017 COL1460 KY779784 KX986934 KX987069 KX987015	Matthewsius	speewah	Gunter & Weir 2017	COL3010	KY779809	KX986958	I	KX987026
Monteithocanthon glaber Gunter & Weir 2017 COL 1460 KY779784 KX986934 KX987069 KX987015	Monoplistes	"sp. dgi1"	Monaghan et al. 2007	NA	AY131837	AY131658	AY131466	I
	Monteithocanthon	glaber	Gunter & Weir 2017	COL1460	KY779784	KX986934	KX987069	KX987015

TABLE 1. (Continued)							
Genus	Species	Data Source	Identifier	COI	28s	16s	18s
Monteithocanthon	paraarator	Gunter & Weir 2017;	COL1116	KY779773	KX986923	KX987059	KX987001
		Gunter et al. 2019b					
Odontoloma	pusillum	Monaghan <i>et al.</i> 2007	NA	AY131839	GQ289790	AY131469	I
Onthobium	cooki	Monaghan <i>et al.</i> 2007	NA	AY131841	AY131663	AY131471	JN619223
Outenikwanus	tomentosus	Monaghan <i>et al.</i> 2007	NA	GQ290023	GQ289798	GQ289748	ı
Paronthobium	simplex	Monaghan <i>et al.</i> 2007	NA	AY131843	AY131665	AY131473	JN619173
Pseudignambia	"sp. dgi2"	Monaghan <i>et al.</i> 2007	NA	AY131846	AY131668	AY131476	ı
Pseudonthobium	fracticolloides	Monaghan <i>et al.</i> 2007	NA	AY131847	AY131669	AY131477	JN619182
Psuedignambia	"NQ10"	Gunter & Weir 2017	COL3041	KY779824	KX986974	I	KX987042
Sauvagesinella	becki	Gunter et al. 2016;	COL1220	KF801899	KF802066	KF801737	KX987010
		Gunter & Weir 2017					
Sauvagesinella	monstrosa	Gunter et al. 2016;	COL1210	KF801898	KF802065	KF801736	KX987009
		Gunter & Weir 2017					
Temnoplectron	finnigani	Monaghan <i>et al.</i> 2007	NA	AY131851	AY131675	AY131483	JN619220
Tesserodon	intricatum	Gunter & Weir 2017	COL2436	KY779805	KX986954	ı	ı



FIGURE 2. Holotype of *Lepanus mirabilis*. **A**, Lateral view of elytron, arrow points to superficial 8th stria that runs along flange like edge of elytron, dorsal to epipleuron; **B**, ventral habitus; **C**, ventral view of protibia, arrow points to small tooth; **D**, close up ventral view of protibial apex, arrow points to small tooth at base of the tarsus; **E**, labels. Images provided by F. Génier (CMNC).

Diagnosis. Can be diagnosed from most species of *Lepanus* by its large size, protibia with three teeth (Fig. 1C) and a small ventral tooth near base of the tarsus (Fig. 2D), the pygidial configuration with transverse fold, and large flat, ovoid reticulate area on the disc (Fig. 1B). *Lepanus mirabilis* can be diagnosed from other species in the *Lepanus ustulatus* species group by transverse fold on the pygidium being absent medially, and the depressed central area on the pygidal disc being distant from the transverse fold (Fig. 1B); presence of small tooth on ventral surface of the basal 1/3 of the protibia (Fig. 2C); and upturned clypeal teeth.

Geographic distribution. Papua New Guinea.

Remarks. The presence of a pygidial depression with a concave upper edge and transverse sinuate fold in conjunction with its larger size (5 mm), protibial ornamentation, and lack of hypomeral striae place this species within the informal *Lepanus ustulatus* species group (Gunter & Weir 2019), of which the Australian species were recently revised (Gunter & Weir 2021). This species will run to the *Lepanus ustulatus* species group at couplet 5 of Gunter & Weir (2019).

Paulian (1985) stated that he saw one other specimen from the same collecting event that he designated as a paratype and deposited in the MNHM. This specimen was located and confirmed to match the description given by Paulian (1985). An additional specimen labeled "Paratype" was also located in the CMNC. The species designation on the CMNC specimen is given by Paulian and the label data matches that of the holotype. It appears that this is an additional specimen Paulian examined but did not mention in the original description. The CMNC specimen is therefore not part of the type series.

The holotype is not dissected, but the shape of aedeagus of an examined specimen (CMNEN 00013051) (Fig. 3) bears a strong resemblance to the aedeagi of all other species in the *Lepanus ustulatus* species group. No female specimens were examined in this study; however, it is probable that females of *L. mirabilis* also share sexually dimorphic characters observed in other species in the *Lepanus ustulatus* species group including: protibial with apical spur arising from truncate front edge, apical digit absent; tooth on the underside of protibial smaller than in males; inner edge of metatibia not crenulate; mesotibia without a brush of setae apically (Gunter & Weir 2021).



FIGURE 3. Aedeagus of *Lepanus mirabilis* (CMNEN 00013051). A, Left lateral view; B, dorsal view; C, right lateral view. Images provided by F. Génier (CMNC).

Phylogeny

The results of our phylogenetic reconstruction can be seen in Figure 4. The model GTR+F+I+G4 was found to best fit our data. The *Lepanus* clade, with *Lepanus mirabilis* nested within, is recovered as monophyletic with high support (98 BS). *Lepanus mirabilis* is recovered sister to *L. globulus* + *L. ustulatus* with moderate support (63 BS).

Discussion

Here, we treat Oficanthon as a synonym of Lepanus based on morphological and molecular evidence, and confirm the specimen that originally prompted our investigation was correctly identified. Paulian (1985) diagnosed Oficanthon from other Australasian genera (including Lepanus) by the presence of a wide pseudepipleuron and toothed claws. These characters are in disagreement with that of Lepanus, which is defined by the absence of pseudepipleuron, and with claws sometimes toothed (Matthews 1974). Upon examination of the holotype, however, it is clear that Lepanus mirabilis (Paulian, 1985) does not possess either character listed by Paulian (1985). Either there is confusion in homology of morphological terms or in our translation of "Élytres...., délimitant un large pseudéplipleure concave", or that Paulian may have mistaken the epipleuron for the pseudepipleuron. The Dictionary of Insect Morphology (Steinmann & Zombori 2012) defines the pseudepipleuron as "the outer margin of the abbreviate elytron in many Coleoptera that does not overlap with the pleuron". In Australasian endemic dung beetles, numerous genera, such as Amphistomus Lansberge, 1874, Cephalodesmius Westwood, 1841, Mentophilus Laporte, 1840, Tesserodon Hope, 1837, and Pseudignambia Paulian & Pluot-Sigwalt, 1984 possess distinct pseudepipleura, the abrupt deflection of the elytral surface in the same plane as the epipleura, marked by a sharp ridge, rounded fold or row of tubercles just outside of 7th striae. One or more, impressed or superficial striae are evident on the pseudepipleuron, the surface of which is usually similar to the main portion of the elytral disc. In this species, the pseudepipleuron is absent and the lateral edge of the elytron, is distinct (Fig. 2A). Paulian (1985) indicates there are seven striae present, however on close inspection it is evident a superficial 8th stria can be observed along the edge of the elytron, which could easily be missed (Fig. 2A). Paulian (1985) also considered the claws of L. mirabilis toothed. We disagree with this characterization and instead would consider the claws to be simple (Fig. 1E), although this is not clear without high magnification.



FIGURE 4. Phylogeny of Australasian endemic genera with the placement of *Lepanus mirabilis* within the genus *Lepanus* indicated by a star.

The ventrobasal protibial tooth observed in this species is not known in any other species of *Lepanus* (Fig. 2C). Our aim is to present a more natural and stable classification within Scarabaeinae and we believe this is a derived morphological character, and alone does not warrant generic separation. This is also supported by our

phylogenetic reconstruction that places *Lepanus mirabilis* within the genus *Lepanus*. Although sequencing is limited, the relationship within the *L. usutlatus* species group is supported (Fig. 4). Too few genes were sequenced to comment on the exact relationships of species, however additional work with increased gene coverage will help further resolve relationships and determine divergence of Australian and Papuan *Lepanus*.

Lepanus is the most species-rich genus in the Australasian endemic clade, with species known from Papua New Guinea and Australia. The incorporation of *L. mirabilis* into *Lepanus* increases its diversity in Papua New Guinea to include six species (Gunter *et al.* 2019a). While the type species of the genus, *L. ovatus* Balthasar, 1966 is only known from Papua New Guinea, the genus remains the most diverse in Australia.

Acknowledgments

We would like to thank François Génier (CMNC) for graciously providing access and images of the specimens, and for the loan of other material examined in this study. We also express our gratitude to Olivier Montreuil and Christophe Rivier (MNHN) for imaging the paratype located in Paris. This material is based upon work supported by the National Science Foundation under grant NSF#1942193.

References cited

- Balthasar, V. (1966) Neue Gattungen und Arten der Scarabaeoidea der australischen und neotropischen Region. *Entomologische Blätter*, 62, 177–185.
- Brandon-Mong, G.J., Gan, H.M., Sing, K., Shin, L., Lim, P.E. & Wilson, J. (2015) DNA metabarcoding of insects and allies: an evaluation of primers and pipelines. *Bulletin of Entomological Research*, 105 (6), 1–11. https://doi.org/10.1017/S0007485315000681
- Gunter, N.L. & Weir, T.A. (2017) Two new genera of Australian dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) with the description of six new species and transfer of six described species. *Zootaxa*, 4290 (2), 201–243. https://doi.org/10.11646/zootaxa.4290.2.1
- Gunter, N.L. & Weir, T.A. (2019) Revision of Australian species of the dung beetle genus *Lepanus* (Coleoptera: Scarabaeidae: Scarabaeinae): key to species groups and description of 14 new species from the *L. pygmaeus* species group. *Zootaxa*, 4564 (1), 41–80.

https://doi.org/10.11646/zootaxa.4564.1.2

Gunter, N.L. & Weir, T.A. (2021) Revision of Australian species of the dung beetle genus *Lepanus* (Coleoptera: Scarabaeidae: Scarabaeinae): review of the *L. ustulatus, L. storeyi*, and *L. nitidus* species groups and description of eight new species. *Zootaxa*, 4923 (1), 1–66.

https://doi.org/10.11646/zootaxa.4923.1.1

Gunter, N.L., Leavengood, J.M., Bartlett, J.S., Chapman, E.G. & Cameron, S.L. (2013) A molecular phylogeny of the checkered beetles and a description of Epiclininae a new subfamily (Coleoptera: Cleroidea: Cleridae). Systematic Entomology, 38, 626–636.

https://doi.org/10.1111/syen.12019

- Gunter, N.L., Weir, T.A., Slipinksi, A., Bocak, L. & Cameron, S.L. (2016) If dung beetles (Scarabaeidae: Scarabaeinae) arose in association with dinosaurs, did they also suffer a mass co-extinction at the K-Pg boundary? *PLoS One*, 11 (5), e0153570. https://doi.org/10.1371/journal.pone.0153570
- Gunter, N.L., Lemann, K. & Weir, T.A. (2019a) Scarabaeidae: Scarabeinae Latreille, 1802, *In:* Slipinski, A. & Lawrence, J. (Eds.), *Australian Beetles. Vol. 2. Archostemata, Myxophaga, Adephaga, Polyphaga.* CSIRO Publishing, Clayton South, 784 pp.
- Gunter, N.L., Monteith, G.B., Cameron, S.L. & Weir, T.A. (2019b) Evidence from Australian mesic zone dung beetles supports their Gondwanan origin and Mesozoic diversification of the Scarabaeinae. *Insect Systematics & Evolution*, 50, 162–188. https://doi.org/10.1163/1876312X-00002171
- Hoang, D.T., Chernomor, O., Von Haeseler, A., Minh, B.Q. & Vinh, L.S. (2018) UFBoot2: improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution*, 35, 518–522. https://doi.org/10.1093/molbev/msx281
- Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K.F., von Haeseler, A. & Jermiin, L.S. (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods*, 14 (6), 587–589. https://doi.org/10.1038/nmeth.4285
- Katoh, K. & Standley, D.M. (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular biology and evolution*, 30, 772–780. https://doi.org/10.1093/molbev/mst010

- Matthews, E.G. (1974) A revision of the scarabaeine dung beetles of Australia II. Tribe Scarabaeini. Australian Journal of Zoology Supplementary Series, 22 (24), 1–211. https://doi.org/10.1071/AJZS024
- Monaghan, M.T., Inward, D.J., Hunt, T. & Vogler, A.P. (2007) A molecular phylogenetic analysis of the Scarabaeinae (dung beetles). *Molecular Phylogenetics and Evolution*, 45, 674–692. https://doi.org/10.1016/j.ympev.2007.06.009
- Nguyen, L.T., Schmidt, H.A., Von Haeseler, A. & Minh, B.Q. (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, 32, 268–274. https://doi.org/10.1093/molbev/msu300
- Paulian, R. (1985) Les coléoptères Scarabaeidae canthonines de Nouvelle-Guinée. Annales de la Société Entomologique de France, 21 (2), 219–238.

Steinmann, H. & Zombori, L. (2012) Dictionary of Insect Morphology. De Gruyter, Berlin. [unknown pagination]