

**TAXONOMY AND BIOGEOGRAPHY OF THE
LAND SNAIL GENUS *ALYCAEUS*
(GASTROPODA: ALYCAEINAE) IN
PENINSULAR MALAYSIA**



FOON JUNN KITT
UMS
UNIVERSITI MALAYSIA SABAH

**INSTITUTE FOR TROPICAL BIOLOGY AND
CONSERVATION
UNIVERSITI MALAYSIA SABAH
2018**

**TAXONOMY AND BIOGEOGRAPHY OF THE
LAND SNAIL GENUS *ALYCAEUS*
(GASTROPODA: ALYCAEINAE) IN
PENINSULAR MALAYSIA**

FOON JUNN KITT



UMS
UNIVERSITI MALAYSIA SABAH

**THESIS SUBMITTED IN FULFILLMENT FOR
THE DEGREE OF MASTER OF SCIENCE**

**INSTITUTE FOR TROPICAL BIOLOGY AND
CONSERVATION
UNIVERSITI MALAYSIA SABAH
2018**

UNIVERSITI MALAYSIA SABAH

BORANG PENGESAHAN STATUS TESIS

JUDUL: **TAXONOMY AND BIOGEOGRAPHY OF THE LAND SNAIL GENUS *ALYCAEUS* (GASTROPODA: ALYCAEINAE) IN PENINSULAR MALAYSIA**

IJAZAH: **SARJANA SAINS (BIODIVERSITI DAN BIOSISTEMATIK)**

Saya **FOON JUNN KITT**, Sesi **2015 – 2016**, mengaku membenarkan tesis Sarjana ini disimpan di Perpustakaan Universiti Malaysia Sabah dengan syarat-syarat kegunaan seperti berikut:

1. Tesis ini adalah hak milik Universiti Malaysia Sabah.
2. Perpustakaan Universiti Malaysia Sabah dibenarkan membuat salinan untuk tujuan pengajian sahaja.
3. Perpustakaan dibenarkan membuat salinan tesis ini sebagai bahan pertukaran antara institusi pengajian tinggi.
4. Sila tandakan (/):



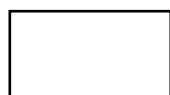
SULIT

(Mengandungi maklumat yang berdarjah keselamatan atau kepentingan Malaysia seperti yang termaktub di dalam AKTA RAHSIA 1972)



TERHAD

(Mengandungi maklumat TERHAD yang telah ditentukan oleh organisasi/badan di mana penyelidikan dijalankan)



TIDAK
TERHAD

Disahkan oleh,

FOON JUNN KITT
MX1521003T

Tarikh: 28 Jun 2018

(Tandatangan Pustakawan)

(Dr. Liew Thor Seng)
Penyelia

DECLARATION

I hereby declare that materials in this thesis are my own except for quotations, excerpts, figures, equations, summaries and references, which have been duly acknowledged.

30 November 2017

Foon Junn Kitt

MX1521003T



UMS
UNIVERSITI MALAYSIA SABAH

CERTIFICATION

NAME: **FOON JUNN KITT**
MATRIC NUMBER: **MX1521003T**
TITLE: **TAXONOMY AND BIOGEOGRAPHY OF THE LAND
SNAIL GENUS *ALYCAEUS* (GASTROPODA:
ALYCAEINAE) IN PENINSULAR MALAYSIA**
DEGREE: **MASTER OF SCIENCE (BIODIVERSITY AND
BIOSYSTEMATICS)**
DATE OF VIVA: **13 APRIL 2018**

CERTIFIED BY



ACKNOWLEDGEMENTS

I thank my family and colleagues for encouraging and supporting me throughout my Masters research journey.

Many people were involved at various stages of this research project. I thank Dr. Liew Thor-Seng for his mentorship throughout my Masters project. I thank Pál-Gergely Barna, Gopalarasamy Reuben Clements, Mohammad Effendi Marzuki and Siong Kiat Tan for help with processing museum (ANSP, MNHN, SMF and ZRC) and private collection materials for this study. I also thank Virginie Héros (MNHN), Manuel Caballer (MNHN), Jonathan Ablett (NHM), Paul Callomon (ANSP) and staff who were involved in specimen digitisation at ANSP, MNHN and Naturalis Biodiversity Centre for help with photographs and measurements of types. The Biodiversity Heritage Library (BHL), Pál-Gergely Barna, Sow Yan Chan, Wim Maassen and Menno Schilthuizen are thanked for making important literature available for study. I would also like to thank Donos Akia, Rahmat Asod, Hoong Fatt Foon, Joon Lam Foon, Joon Sam Foon, Mohammad Effendi Marzuki and Alicia Solana Mena for fieldwork assistance. Finally, I thank Prof. Madya Dr. Bakhtiar Effendi Yahya and technicians at the Institute for Tropical Biology and Conservation for facilitating my use of the microscopy equipment which this study greatly benefited from. I thank reviewers of the thesis Prof. Madya Dr. Bakhtiar Effendi Yahya and Prof. Dr. Menno Schilthuizen for their critique and comments.



UNIVERSITI MALAYSIA SABAH

I am also grateful for research permissions and funding from several agencies. This study was conducted with permits from the Department of Wildlife and National Parks Peninsular Malaysia (JPHLandTN(IP):100-34t1.24 Jld 6(14)) and the Forestry Department of Peninsular Malaysia (JH/100 Jld. 14(9); PPN.PK 600/03/01Jld 9(62); AM-PM-202-16). This study is supported by the Universiti Malaysia Sabah Postgraduate Research Assistance Grant (UMSGreat) (GUG0015-SG-M-1/2016).

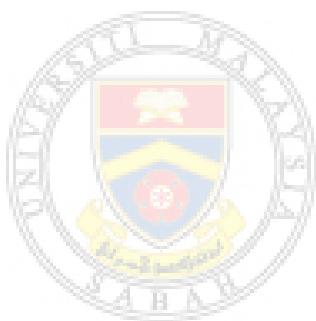
Foon Junn Kitt

30 November 2017

ABSTRACT

The conservation of tropical limestone karsts is a priority for Malaysia. To assist karst conservation, sound understanding of the taxonomy and biogeography of karst endemic taxa is required. In this study, I used the genus *Alycaeus* as a model taxon for this purpose, focusing on two aspects of the genus: species taxonomy and biogeography. First, on taxonomy: A total of 10 species and one subspecies of *Alycaeus* was recognised in Peninsular Malaysia prior to this study. However, these taxonomic descriptions of *Alycaeus* taxa are based on limited number of examined materials where a whole spectrum of morphological variations were not accounted for and diagnosis were often provided without sufficient comparison between congeners from across the peninsula. I reviewed Peninsular Malaysian *Alycaeus* through the examination of major museum collection lots and literature sources. Based on these examined materials, I utilised a more comprehensive set of shell and operculum characters, as well as living animal colour to describe all *Alycaeus* species in this paper. I also noted their habitat and ecology, as well as updated the distribution of each species. Of the 11 previously described taxa, nine were reconfirmed as present on Peninsular Malaysia (*Alycaeus balingensis*, *Alycaeus liratulus*, *Alycaeus thieroti*, *Alycaeus conformis*, *Alycaeus gibbosulus*, *Alycaeus kelantanensis*, *Alycaeus carinata*, *Alycaeus perakensis*, *altispirus*, *Alycaeus perakensis*) and two were confirmed as absent on the peninsula (*Alycaeus jagori*, *Alycaeus pyramidalis*). A new record of *Alycaeus robeleni* is reported for Peninsular Malaysia. One species, *Chamalycaeus jousseaumei* is confirmed as present on the peninsula and is reassigned to *Alycaeus*. The subspecies *Alycaeus perakensis altispirus* Möllendorff, 1902, is elevated to species. Examined Peninsular Malaysian materials that do not fit previously recognised species are described as new species. A total of 11 new species are proposed (*Alycaeus selangoriensis* Foon and Liew, 2017, *Alycaeus costacrassa* Foon and Liew, 2017, *Alycaeus ikanensis* Foon and Liew, 2017, *Alycaeus alticola* Foon and Liew, 2017, *Alycaeus charasensis* sFoon and Liew, 2017, *Alycaeus kurauensis* Foon and Liew, 2017, *Alycaeus regalis* Foon and Liew, 2017, *Alycaeus virgogravida* Foon and Liew, 2017, *Alycaeus senyumensis* Foon and Liew, 2017, *Alycaeus expansus* Foon and Liew, 2017, *Alycaeus clementsi* Foon and Liew, 2017). Overall, 23 species of *Alycaeus* are now recognised in Peninsular Malaysia. Second, on biogeography: With *Alycaeus* species and their distributions identified, I utilised Geographic Information System tools to study their biogeography across Peninsular Malaysia. First, I examined the role of the Titiwangsa Range as a potential biogeographic barrier for *Alycaeus* species. I found that the Titiwangsa Range appears to be a barrier for limestone rock dwelling *Alycaeus* species while arboreal and rotten log dwelling *Alycaeus* species are either restricted to one side or found on both sides of the Titiwangsa Range. Second, I elucidate and discuss the correlation between hill isolation, hill size and the degree of *Alycaeus* endemism. I found that there is no correlation between hill isolation and *Alycaeus* endemism, while there is a weak correlation between hill size and *Alycaeus* endemism. These findings run

contrary to previous conclusions of land snail community level studies whereby hill isolation and hill size have strong correlations with land snail endemism. Overall, these findings suggest that conservation of limestone karst biodiversity should consider not just endemism patterns at the community level but also at the genus level as well, especially for those genera that are known to be restricted to limestone rock habitats.

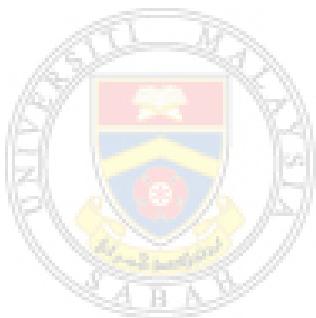


ABSTRAK

TAXONOMI DAN BIOGEOGRAFI SIPUT DARAT GENUS ALYCAEUS (GASTROPODA: ALYCAEINAE) DI SEMENANJUNG MALAYSIA

Pemuliharaan kars tropika adalah keutamaan konservasi bagi Malaysia. Untuk membantu pemuliharaan kars, pemahaman yang baik tentang taksonomi dan biogeografi taxa kars endemik adalah diperlukan. Dalam kajian ini, saya menggunakan genus Alycaeus sebagai takson model untuk tujuan ini, dengan memberi tumpuan kepada dua aspek genus tersebut: taksonomi spesies dan biogeografi. Pertama, mengenai taksonomi: Sebanyak 10 spesies dan satu subspecies Alycaeus diiktiraf di Semenanjung Malaysia sebelum kajian ini. Deskripsi taksonomi Alycaeus adalah berdasarkan bahan yang diperiksa di mana bilanganya adalah terhad dan spektrum variasi morfologi tidak dikirakan dan diagnosis sering disediakan tanpa perbandingan yang mencukupi dari seluruh Semenanjung Malaysia. Saya mengkaji Alycaeus Semenanjung Malaysia melalui pemeriksaan koleksi besar muzium-muzium khusus dan sumber-sumber kesusastraan. Berdasarkan bahan-bahan yang diperiksa ini, saya menggunakan satu set lengkap cangkerang dan operculum, serta warna haiwan yang hidup untuk mendiagnosiskan semua spesies Alycaeus dalam tesis ini. Saya juga memperhatikan habitat dan ekologi mereka, serta mengemas kini pengagihan setiap spesies. Daripada 11 taxa yang telah diiktiraf sebelum ini, sembilan taxa telah dikesahkan semula sebagai wujud di Semenanjung Malaysia (Alycaeus balingensis, Alycaeus liratulus, Alycaeus thieroti, Alycaeus conformis, Alycaeus gibbosulus, Alycaeus kelantanensis, Alycaeus carinata, Alycaeus perakensis altispirus dan Alycaeus perakensis) manakala dua taxa disahkan sebagai tidak wujud di Semenanjung Malaysia (Alycaeus jagori dan Alycaeus pyramidalis). Rekod baru Alycaeus robeleni dilaporkan wujud di Semenanjung Malaysia. Satu spesies, Chamalycaeus jousseaumei disahkan sebagai wujud di Semenanjung Malaysia dan dipindahkan semula ke genus Alycaeus. Subspecies Alycaeus perakensis altispirus Möllendorff, 1902, dinaikkan ke tahap spesies. Bahan-bahan Semenanjung Malaysia yang diperiksa yang tidak sesuai dengan spesies yang diiktiraf terdahulu dideskripsikan sebagai spesies baru. Sebanyak 11 spesies baru dicadangkan (Alycaeus selangoriensis Foon dan Liew, 2017, Alycaeus costacrassa Foon dan Liew, 2017, Alycaeus ikanensis Foon dan Liew, 2017, Alycaeus alticola Foon dan Liew, 2017, Alycaeus charasensis Foon dan Liew, 2017, Alycaeus kurauensis Foon dan Liew, 2017, Alycaeus regalis Foon dan Liew, 2017, Alycaeus virgogravida Foon dan Liew, 2017, Alycaeus senyumensis Foon dan Liew, 2017, Alycaeus expansus Foon dan Liew, 2017, Alycaeus clementsi Foon dan Liew, 2017) Secara keseluruhan, 23 spesies Alycaeus kini diiktiraf di Semenanjung Malaysia. Kedua, mengenai biogeografi: Dengan pengenalpastian spesies Alycaeus dan taburan

mereka, saya menggunakan alat Sistem Maklumat Geografi untuk mengkaji biogeografi mereka di seluruh Semenanjung Malaysia. Pertama, saya mengenal pasti peranan Banjaran Titiwangsa sebagai halangan biogeografi untuk spesis-spesies Alycaeus. Kajian saya mendapati Banjaran Titiwangsa adalah halangan untuk spesies-spesies Alycaeus yang berhabitat batu kapur manakala spesies-spesies yang berhabitat arboreal dan kayu reput boleh didapati di salah satu belah atau kedua-dua belah kawasan di sekitar Banjaran Titiwangsa. Kedua, saya meninjau dan membincangkan korelasi antara pengasingan bukit, saiz bukit dan tahap endemisme Alycaeus. Kajian saya mendapati tiada korelasi antara pengasingan bukit dan tahap endemisme Alycaeus manakala korelasi lemah telah dijumpai antara saiz bukit dan tahap endemisme Alycaeus. Penemuan ini bertentangan dengan kesimpulan kajian-kajian terdahulu yang berfokus pada tahap komuniti siput darat, di mana pengasingan bukit dan saiz bukit didapati berkorelasi kuat dengan tahap endemisme siput darat. Secara keseluruhan, penemuan kajian saya bercadangkan bahawa pemuliharaan biodiversiti kars harus mempertimbangkan bukan sahaja corak endemisme pada tahap komuniti tetapi juga pada tahap genus terutamanya untuk genus-genus yang berhabitat batu kapur.



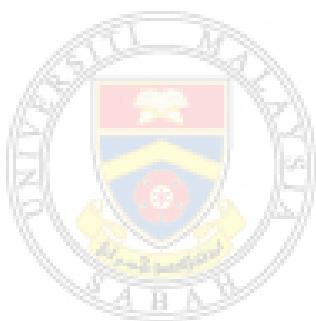
UMS
UNIVERSITI MALAYSIA SABAH

LIST OF CONTENTS

	Page
TITLE	
DECLARATION	ii
CERTIFICATION	iii
ACKNOWLEDGEMENTS	iv
ABSTRACT	v
ABSTRAK	vii
LIST OF CONTENTS	ix
LIST OF TABLES	xii
LIST OF FIGURES	xiii
LIST OF ABBREVIATIONS	xxii
LIST OF APPENDICES	xxiii
CHAPTER 1: INTRODUCTION	1
1.1 Background	1
1.2 <i>Alycaeus</i> land snails as organisms of study	2
1.3 Research aims and objectives	4
CHAPTER 2: LITERATURE REVIEW	5
2.1 Taxonomy	5
2.1.1 Taxonomy of the land snail subfamily Alycaeinae	5
2.1.2 Taxonomic status of the genus <i>Alycaeus</i>	7
2.1.3 History of the taxonomy of <i>Alycaeus</i> in Peninsular Malaysia	8
2.1.4 Species description and delimitation of <i>Alycaeus</i>	12
2.2 Biogeography	13

2.2.1 The concepts of biogeography and endemism relationships	13
2.2.1 Limestone karsts in Peninsular Malaysia	16
2.2.2 The biogeography and endemism of limestone karst snails in Peninsular Malaysia	19
 CHAPTER 3: METHODS AND MATERIALS	 24
3.1 Study site	24
3.2 Sampling of land snails.	25
3.3 Additional specimens from collection repositories	27
3.4 Taxonomic review	28
3.4.1 Literature	28
3.4.2 Collection data management	28
3.4.3 Characterisation of shell and operculum	29
3.4.4 Species description and delimitation	38
3.5 Biogeography	40
3.5.1 Biogeography parameters	40
3.5.2 Endemism	40
3.5.3 Data analysis	41
 CHAPTER 4: RESULTS AND DISCUSSION	 43
4.1 Taxonomy	43
4.2 Biogeography	144
4.2.1 The Titiwangsa Range and <i>Alycaeus</i> species distribution range	144
4.2.2 <i>Alycaeus</i> endemism and hill isolation	147
4.2.3 <i>Alycaeus</i> endemism and hill size	148
4.3 Implications for conservation	150

CHAPTER 5: CONCLUSION	151
5.1 Taxonomy	151
5.2 Biogeography	153
REFERENCES	155
APPENDICES	169



UMS
UNIVERSITI MALAYSIA SABAH

LIST OF TABLE

	Page
Table 3.1: Framework for species description based on 39 shell and operculum features, as well as living animal colour. Number codes are ascribed to each character and linked to illustrations in Figure 3.1 for visualisation of character descriptions and measurements, except shell colour and living animal colour.	30



LIST OF FIGURES

	Page
Figure 2.1: The distribution of limestone hills (in red) with respect to non-limestone mountain ranges (in shades of grey) in Peninsular Malaysia (derived from Liew et al., 2016).	18
Figure 3.1: Map showing 80 limestone hills sampled for <i>Alycaeus</i> (white circles) with respect to the distribution of limestone karsts in Peninsular Malaysia (in red).	26
Figure 3.2: An illustrated synopsis of the framework for species description based on 39 shell and operculum features (excluding shell colour and living animal colour). Number codes ascribed to each character are linked to descriptions and measurement methods outlined in Table 3.1.	37
Figure 4.1: Distribution of eight <i>Alycaeus</i> species in Peninsular Malaysia based on materials examined. Note the red areas are limestone karsts (derived from Liew et al. 2016).	45

- Figure 4.2: Distribution of four *Alycaeus* species in Peninsular Malaysia 46
based on materials examined. The distribution of *Alycaeus altispinus* shown above is based on the presumed locality of the materials examined (see Discussion section under the species). Note the red areas are limestone karsts (derived from Liew *et al.*, 2016).
- Figure 4.3: Distribution of four *Alycaeus* species in Peninsular Malaysia 47
based on materials examined. Note the red areas are limestone karsts (derived from Liew *et al.* 2016).
- Figure 4.4: Distribution of 2 *Alycaeus* species in Peninsular Malaysia 48
based on materials examined. Note the red areas are limestone karsts (derived from Liew *et al.* 2016).
- Figure 4.5: Distribution of five *Alycaeus* species in Peninsular Malaysia 49
based on materials examined. Note that two records of *Alycaeus roebeleni* in Thailand, north of Peninsular Malaysia are not shown in the map. The red areas are limestone karsts (derived from Liew *et al.* 2016).
- Figure 4.6: Photographs of 18 living *Alycaeus* species. A–B *Alycaeus balingensis* Tomlin, 1948, BOR/MOL 8356 C *Alycaeus liratulus* (Preston, 1907), BOR/MOL 8334 D *Alycaeus thieroti* Morgan, 1885b, BOR/MOL 6835 E *Alycaeus conformis* Fulton, 1902, BOR/MOL 6809 F *Alycaeus gibbosulus* Stoliczka, 1872, BOR/MOL

6850 G *Alycaeus gibbosulus* Stoliczka, 1872, BOR/MOL 8526 H
Alycaeus jousseaumei Morgan, 1885a, BOR/MOL 8341 I
Alycaeus jousseaumei Morgan, 1885a,
BOR/MOL 8336 J *Alycaeus alticola* Foon and Liew, 2017,
BOR/MOL 8398 K *Alycaeus charasensis* Foon and Liew, 2017,
BOR/MOL 8399 L *Alycaeus clementsii* Foon and Liew, 2017,
BOR/MOL 8364 M *Alycaeus costacrassa* Foon and Liew, 2017,
BOR/MOL 6811 N *Alycaeus expansus* Foon and Liew, 2017,
BOR/MOL 6367 O *Alycaeus kapayanensis* Morgan, 1885b,
BOR/MOL 13005 P *Alycaeus kelantanensis* Sykes, 1902,
BOR/MOL 8325 Q *Alycaeus kelantanensis* Sykes, 1902,
BOR/MOL 6200 R *Alycaeus kurauensis* Foon and Liew, 2017,
BOR/MOL 6851 S *Alycaeus perakensis* Crosse, 1879a,
BOR/MOL 6852 T *Alycaeus regalis* Foon and Liew, 2017,
BOR/MOL 6881 U *Alycaeus selangoriensis* Foon and Liew, 2017,
BOR/MOL 6371 V–W *Alycaeus senyumensis* Foon and Liew, 2017,
BOR/MOL 6249.

Figure 4.7: *Alycaeus alticola* Foon and Liew, 2017 A–E Shell of holotype, 56
BOR/MOL 8398 F–H Close up of shell of holotype, BOR/MOL
8398 I–L Operculum of paratype, BOR/MOL 8398 M–Q Shell
of paratype, BOR/MOL 8398. Scale bars: A–G, I–Q 1 mm;
H 0.5 mm.

Figure 4.8: *Alycaeus altispirus* (Möllendorff, 1902) A–E Shell of lectotype, 60
SMF 109738 F–H Close up of shell of lectotype, SMF 109738.
Scale bars: A–G 1 mm; H 0.5 mm.

Figure 4.9: *Alycaeus balingensis* Tomlin, 1948. A–E Shell of syntype, 63
NHMUK 1948.10.2.4 F–J Shell of BOR/MOL 8357 K–M
Close up of shell of BOR/MOL 8357 N–Q Operculum of
BOR/MOL 8357 R–V Shell of BOR/MOL 8361. Scale bars:
A–E xx mm; F–J, R–V, K, L 1 mm; M, N–Q 0.5 mm.

Figure 4.10: *Alycaeus carinata* Maassen, 2006 A–E Shell of paratype, 66
RMNH 104427 F–H Close up of shell of paratype, RMNH
104427. Scale bars: A–G 1 mm; H 0.5 mm.

Figure 4.11: *Alycaeus charasensis* Foon and Liew, 2017 A–E Shell of 69
holotype, BOR/MOL 8400 F–H Close up of shell of holotype,
BOR/MOL 8400 I–L Operculum of paratype, BOR/MOL 6891
M–Q Shell of paratype, BOR/MOL 267. Scale bars: A–G,
M–Q, H 1 mm; I–L 0.5 mm.

Figure 4.12: *Alycaeus clementsii* Foon and Liew, 2017 A–E Shell of 73
holotype, BOR/MOL 12970 F–H Close up of shell of holotype,
BOR/MOL 12970 I–L Operculum of paratype, BOR/MOL 6865
M–Q Shell of paratype, BOR/MOL 8377. Scale bars: A–G, M–Q
1 mm; H, I–L 0.5 mm.

Figure 4.13: *Alycaeus conformis* Fulton, 1902. A–D Shell of syntype, 77

NHMUK 1902.5.28.22-23 E–I Shell of BOR/MOL 6526 J–L

Close up of shell of BOR/MOL 6526 M–P Operculum of

BOR/MOL 12986. Scale bars: A–P 1 mm. Photographs A–D

by Harold Taylor (copyright of NHM, reproduced with

permission).

Figure 4.14: *Alycaeus costacrassa* Foon and Liew, 2017 A–E Shell of 81

holotype, BOR/MOL 6811 F–H Close up of shell of holotype,

BOR/MOL 6811 I–L Operculum of holotype, BOR/MOL 6811

M–Q Shell of BOR/MOL 6818 R–V Shell of BOR/MOL 12992.

Scale bars: A–G 1 mm; H, I–L 0.5 mm.

Figure 4.15: *Alycaeus expansus* Foon and Liew, 2017 A–E Shell of 85

holotype, BOR/MOL 12983 F–H Close up of shell of holotype,

BOR/MOL 12983 I–L Operculum of holotype, BOR/MOL 12983

M–Q Shell of BOR/MOL 245. Scale bars: A–H 1 mm; I–L 0.5

mm.

Figure 4.16: *Alycaeus gibbosulus* Stoliczka, 1872. A–E Shell of BOR/MOL 91

8525 F–H Close up of shell of BOR/MOL 8525 I–L Operculum

of BOR/MOL 8525 M–Q Shell of BOR/MOL 12960. Scale bars:

A–Q 1 mm.

Figure 4.17: *Alycaeus ikanensis* Foon and Liew, 2017 A–E Shell of 94
holotype, BOR/MOL 12972 F–H Close up of shell of holotype,
BOR/MOL 12972 I–L Operculum of holotype, BOR/MOL
12972 M–Q Shell of paratype, BOR/MOL 6834. Scale bars:
A–H, M–Q 1 mm; I–L 0.5 mm.

Figure 4.18: *Alycaeus jousseaumei* Morgan, 1885a. A–E Shell of 98
syntype, MNHN-IM-2000-31801 F–J Shell of BOR/MOL
11211 K–M Close up of shell of BOR/MOL 11211 N–Q
Operculum of BOR/MOL 11211. Scale bars: A–Q 1 mm.

Figure 4.19: *Alycaeus kapayanensis* Morgan, 1885b. A–E Shell of 103
syntype, MNHN-IM-2000-31792 F–J Shell of BOR/MOL
10793 K–M Close up of shell of BOR/MOL 10793 N–Q
Operculum of BOR/MOL 6845 R–V Shell of BOR/MOL
11385. Scale bars: A–L 1 mm; M–Q 0.5 mm.

Figure 4.20: *Alycaeus kelantanensis* Sykes, 1902. A–E Shell of syntype, 107
RMNH 153594 F–J Shell of BOR/MOL 8327 K–M Close up of
shell of BOR/MOL 8327 N–Q Operculum of BOR/MOL 6825
R–V Shell of BOR/MOL 12973 W–AA Shell of BOR/MOL
12974. Scale bars: A–J, K, R–AA 1 mm; L, M, N–Q 0.5 mm.

Figure 4.21: *Alycaeus kurauensis* Foon and Liew, 2017 A–E Shell of holotype, BOR/MOL 12967 F–H Close up of shell of holotype, BOR/MOL 12967 I–L Operculum of paratype, BOR/MOL 6851 M–Q Shell of paratype, BOR/MOL 6851. Scale bars: A–E, F, G, M–Q 1 mm; H, I–L 0.5 mm. 110

Figure 4.22: *Alycaeus liratulus* (Preston, 1907). A–E Shell of syntype, ANSP 99391 F–J Shell of BOR/MOL 6831 K–M Close up of shell of BOR/MOL 8357 N–Q Operculum of BOR/MOL 6832. Scale bars: A–J 1 mm; K, L 1 mm; M, N–Q 0.5 mm. 114

Figure 4.23: *Alycaeus perakensis* Crosse, 1879a. A–E Shell of syntype, MNHN-IM-2000-31793. F–J Shell of BOR/MOL 8350 K–M Close up of shell of BOR/MOL 8350 N–Q Operculum of BOR/MOL 8349 R–V Shell of BOR/MOL 8355. Scale bars: A–J, K, L, R–V 1 mm; M, N–Q 0.5 mm. 119

Figure 4.24: *Alycaeus regalis*, Foon and Liew, 2017 A–E Shell of holotype, BOR/MOL 12990 F–H Close up of shell of holotype, BOR/MOL 12990 I–L Operculum of paratype, BOR/MOL 6881. Note operculum with proteinaceous interior extension. Scale bars: A–E, F, G, H 1 mm; I–L 0.5 mm. 123

Figure 4.25: *Alycaeus roebeleni* Möllendorff, 1894. A–E Shell of
syntype, SMF 109317 F–J Shell of BOR/MOL 8363 K–M
Close up of shell of BOR/MOL 8363 N–Q Operculum of
paratype, BOR/MOL 8363. Scale bars: A–J, K, L, M, N–Q
1 mm.

Figure 4.26: *Alycaeus selangoriensis* Foon and Liew, 2017 A–E Shell
of holotype, BOR/MOL 12988 F–H Close up of shell of
holotype, BOR/MOL 12988 I–L Operculum of paratype,
BOR/MOL 6808. Scale bars: A–E, F, G, H 1 mm; I–L
0.5 mm.

Figure 4.27: *Alycaeus senyumentensis* Foon and Liew, 2017 A–E Shell
of holotype, BOR/MOL 12965 F–H Close up of shell of
holotype, BOR/MOL 12965 I–L Operculum of paratype,
BOR/MOL 6880 M–Q Shell of paratype, operculum of
BOR/MOL 12966. Scale bars: A–E, F, G, M–Q 1 mm; H,
I–L 0.5 mm.

Figure 4.28: *Alycaeus thieroti* Morgan, 1885b. A–E Shell of
syntype, MNHN-IM-2000-31799 F–J Shell of BOR/MOL
6835 K–M Close up of shell of BOR/MOL 6835 N–Q
Operculum of BOR/MOL 6835 R Shell of BOR/MOL 6528a
S–W Shell of BOR/MOL 6528b. Scale bars: A–J, R–W 1
mm; K, L 1 mm; M, N–Q 0.5 mm.

127

131

135

139

Figure 4.29: *Alycaeus virgogravida* Foon and Liew, 2017 A–E Shell of holotype, BOR/MOL 12978 F–H Close up of shell of holotype, BOR/MOL 12978 I–L Operculum of holotype, BOR/MOL 12978. Scale bars: A–E, F, G 1 mm; H, I–L 0.5 mm. 142

Figure 4.30: Synoptic view of the 23 *Alycaeus* taxa in Peninsular Malaysia. 143
Scale bar: 5 mm.

Figure 4.31: The maximum extent of distribution range for each *Alycaeus* species found in Peninsular Malaysia in relation to the topographic relief. Note that stars denote ranges of species found on one or a few hills only while polygons denote ranges of more widespread species with larger ranges. 146

Figure 4.32: The relationship between *Alycaeus* endemism and limestone hill isolation. 147

Figure 4.33: The relationship between *Alycaeus* endemism and limestone hill size. 149

LIST OF ABBREVIATIONS

- ANSP** – Academy of Natural Sciences of Drexel University, Philadelphia, United States of America.
- BOR/MOL** – *BORNEENSIS* Malacology Collection, Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia.
- HUJ** – National Mollusc Collection of the Hebrew University of Jerusalem, Jerusalem, Israel.
- H/W** – Private collection of Jens and Christa Hemmen, Wiesbaden, Germany.
- km** – kilometres
- km²** – kilometres-squared
- mm** – millilitres
- MNHN** – Museum National d'Histoire Naturelle, Paris, France.
- NHM** – The Natural History Museum, London, United Kingdom.
- NHMUK** – When citing registered specimens from The Natural History Museum, London.
- RMNH** – Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie), Leiden, the Netherlands.
- SMF** – Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany.
- ZMA** – Naturalis Biodiversity Center (formerly Zoological Museum of Amsterdam), Leiden, the Netherlands.
- ZRC** – Zoological Reference Collection, Lee Kong Chian Natural History Museum, National University of Singapore, Singapore.