

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

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**PERPUSTAKAAN  
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## CERTIFICATION

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ALYCAEINAE) IN PENINSULAR MALAYSIA**

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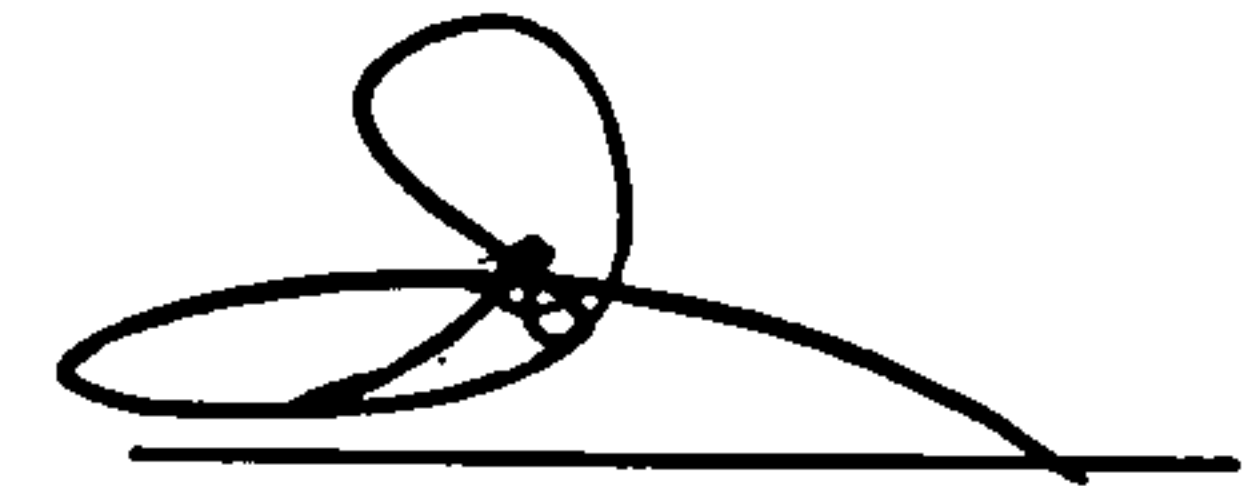
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## ABSTRACT

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 liratus*, *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 clementsii* 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 subspesies Alycaeus diiktiraf di Semenanjung Malaysia sebelum kajian ini. Deskripsi taksonomi Alycaeus adalah berdasarkan bahan yang diperiksa di mana bilangannya 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 kesusasteraan. Berdasarkan bahan-bahan yang diperiksa ini, saya menggunakan satu set lengkap cangkerang dan operculum, serta warna haiwan yang hidup untuk mendiagnosis 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. Subspesies 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 clementsii Foon dan Liew, 2017) Secara keseluruhan, 23 spesies Alycaeus kini diiktiraf di Semenanjung Malaysia. Kedua, mengenai biogeografi: Dengan pengenalanpastian 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-spesis Alycaeus. Kajian saya mendapati Banjaran Titiwangsa adalah halangan untuk spesis-spesies Alycaeus yang berhabitats batu kapur manakala spesis-spesies yang berhabitats 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 keseluruhannya, 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 berhabitats batu kapur.*



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## 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
- km<sup>2</sup>** – 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.





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## REFERENCES

- Adam, H. 1865. Descriptions of a new genus and some new species of mollusks. *Proceedings of the Zoological Society of London* **1865**:753-755.
- Adams, H. and Adams, A. 1855. *The genera of Recent Mollusca; arranged according to their organization, volume 1*. London: John van Voorst.
- Arrhenius, O. 1921. Species and area. *Journal of Ecology* **9**:95-99.
- Azuma, M. 1982. *Coloured Illustrations of the Land Snails of Japan*. Osaka: Hoikusha.
- Baird, W. 1850. *Nomenclature of Molluscous Animals and Shells in the collection of the British Museum. Part I. Cyclophoridae*. London: Spottiswoodes and Shaw.
- Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B. and Ferrer, E. A. 2011. Has the Earth's sixth mass extinction already arrived? *Nature* **471**:51-57.
- Benson, W. H. 1856. Characters of seventeen new forms of the Cyclostomacea from the British Provinces of Burmah, collected by W. Theobald, jun., Esq. *The Annals and Magazine of Natural History Second Series* **16**:225-233.
- Benson, W.H. 1859. A Sectional Distribution of the genus *Alycæus*, Gray, with Characters of six new species and of other Cyclostomidæ collected at Darjiling by W. T. Blanford, Esq., Geol. Survey. *The Annals and Magazine of Natural History* **3(3)**:176-184.
- Bentham Jutting, W. S. S. van 1948. Systematic studies on the non-marine mollusca of the Indo-Australian Archipelago. 1. Critical revision of the Javanese operculate land-shells of the families Hydrocenidae, Helicinidae, Cyclophoridae, Pupinidae and Cochlostomatidae. *Treubia* **19(3)**:539-604.
- Bentham Jutting, W. S. S. van 1949. On a collection of non-marine mollusca from Malaya in the Raffles Museum, Singapore, with an appendix on cave shells. *The Bulletin of the Raffles Museum* **19**:50-77.
- Bentham Jutting, W. S. S. van 1950. The Malayan species of *Boysidia*, *Paraboysidia*, *Hypselostoma* and *Gyliotrachela* (Gastropoda, Pulmonata, Vertiginidae). *The Bulletin of the Raffles Museum* **21**:5-47.
- Bentham Jutting, W. S. S. van 1952. The Malayan species of *Opisthostoma* (Gastropoda, Prosobranchia, Cyclophoridae), with a catalogue of all the species hitherto described. *The Bulletin of the Raffles Museum* **24(5)**:5-61.





- Bentham Jutting, W. S. S. van 1954. The Malayan Streptaxidae of the genera *Dicartemon* and *Oophana*. *The Bulletin of the Raffles Museum* **25**:71-106.
- Bentham Jutting, W. S. S. van 1959. Catalogue of the non-marine Mollusca of Sumatra and of its satellite islands. *Beaufortia* **7**:41-191.
- Bentham Jutting, W. S. S. van 1960a. Some notes on land and freshwater mollusca of Malaya. *Basteria* **24(1)**:10-20.
- Bentham Jutting, W. S. S. van 1960b. Non-marine mollusca of the limestone hills in Malaya. In Anonymous (ed.). *Proceedings of Centenary and Bicentary Congress of Biology*, pp. 63-68. Singapore: University of Malaya Press.
- Bentham Jutting, W. S. S. van 1961. The Malayan Streptaxidae genera *Huttonella* and *Sinoennea*. *The Bulletin of the Raffles Museum* **26**:5-33.
- Berry, A. J. 1962. The growth of *Opisthostoma (Plectostoma) retrovertens* Tomlin, a minute cyclophorid from a Malayan limestone hill. *Journal of Molluscan Studies* **35**:46-49.
- Berry, A. J. 1963. An introduction to the non-marine molluscs of Malaya. *Malayan Nature Journal* **17**:1-17.
- Berry, A. J. 1965. A collection of land mollusca from limestone in Ulu Kelantan. *Bulletin of the National Museum Singapore* **33(5)**:27-30.
- Blanford, W. T. 1864. On the classification of the Cyclostomacea of Eastern Asia. *Annals and Magazine of Natural History Series 3* **13**:441-465.
- Bollinger, G. 1918. Land-mollusken von Celebes. *Revue Suisse de Zoologie* **26(9)**:309-340.
- Boss, K. J. 1982. Mollusca. In Parker, S. P. (ed.). *Synopsis and Classification of Living Organisms, vol. 1.*, pp. 945-1166. New York: McGraw-Hill.
- Bouchet, P., Rocroi, J.-P., Frýda, J., Hausdorf, B., Ponder, W., Valdes, A. and Warén, A. 2005. A nomenclator and classification of gastropod family-group names. *Malacologia* **47(12)**:1-368.
- Braxmeier, H. 2017. Maps-For-Free, [www.maps-for-free.com](http://www.maps-for-free.com).
- Candolle, A. P. de 1820. Géographie botanique. *Dictionnaire des sciences naturelles* **18**:359-422.
- Cardoso, P., Erwin, T. L., Borges, P. A. V. and New T. R. 2011. The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation* **144**:2647-2655.





- Ceballos, G., Ehrlich, P. R., Barnosky, A. D., Garcia, A., Pringle, R. M. and Palmer, T. M. (2015) Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances* **2015**:e1400253
- Chan, S. Y. 1997. Non-marine mollusks from Selangor, West Malaysia, with a comparison note on introduced species. *Club Conchylia Informationen* **29**:35-46.
- Chan, S. Y. 1998a. A brief collecting trip to Perak, West Malaysia: Part One. *The Papustyla* **12(1)**: 4-5.
- Chan, S. Y. 1998b. A brief collecting trip to Perak, West Malaysia: Part Two. *The Papustyla* **12(2)**: 1-2.
- Checa, A. G. and Jiménez-Jiménez, A. P. 1998. Constructional Morphology, Origin, and Evolution of the Gastropod Operculum. *Paleobiology* **24(1)**: 109-132.
- Chiba, S. and Davison, A. 2008. Anatomical and molecular studies reveal several cryptic species of the endemic genus *Mandarina* (Pulmonata: Helicoidea) in the Ogasawara Islands. *Journal of Molluscan Studies* **74**:373-382.
- Čiliak, M., Čejka, T. and Šteffek, J. 2015. Molluscan diversity in stream driftwood: Relation to land use and river section. *Polish Journal of Ecology* **63**:124-134.
- Clements, R. 2009. *Alycaeus balingensis*. The IUCN Red List of Threatened Species 2009: e.T168175A6462537. doi: 10.2305/IUCN.UK.2009-2.RLTS.T168175A6462537.en
- Clements, R., Sodhi, N. S., Schilthuizen, M. and Ng, P. K. 2006. Limestone karsts of Southeast Asia: Imperiled arks of biodiversity. *Bioscience* **56(9)**:733-742.
- Clements, R., Ng, P. K., Lu, X. X., Ambu, S., Schilthuizen, M, and Bradshaw, C. J. 2008. Using biogeographical patterns of endemic land snails to improve conservation planning for limestone karsts. *Biological Conservation* **141(11)**:2751-2764.
- Corlett, R. T. 2014. *The Ecology of Tropical East Asia*. New York: Oxford University Press.
- Cox, C. B. and Moore, P. D. 1993. *Biogeography: An Ecological and Evolutionary Approach, 5th edition*. Oxford: Blackwell.
- Crisci, J. V. and Posadas, P. 2003. *Historical biogeography: an introduction*. Cambridge: Harvard University Press.



- Criscione, F. and Köhler, F. 2013. Conserved shell disguises diversity in *Mesodontrachia* land snails from the Australian Monsoon Tropics (Gastropoda: Camaenidae). *Zoologica Scripta* **42**:389-405.
- Crisp, M. D., Laffan, S., Linder, H. P. and Monro, A. 2001. Endemism in the Australian flora. *Journal of Biogeography* **28**:183-198.
- Croizat, L. 1962. *Space, Time, Form: The biological synthesis*. Caracas: Leon Croizat.
- Crosse, H. 1879a. Mollusques nouvelles de Perak (Indo Chine). *Journal de Conchyliologie* **27**:198-208.
- Crosse, H. 1879b. Faune malacologique de Perak (Indo-Chine). *Journal de Conchyliologie* **27**:336-340.
- Cuvier, G. 1795. Second Mémoire sur l'organisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordre, lu à la société d'Histoire Naturelle de Paris, le 11 prairial an troisième. *Magazin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts* **2**:433-449.
- Darlington, P. J. Jr. 1957. *Zoogeography: The Geographical Distribution of Animals*. New York: Wiley.
- Darlington, P. J. Jr. 1965. *Biogeography of the Southern End of the World: Distribution and History of Far-Southern Life and Land, with an assessment of Continental Drift*. Cambridge: Harvard University Press.
- Darwin, C. R. 1859. *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: John Murray.
- Davison, G. W. H. and Kiew, R. 1990. *Survey of Flora and Fauna of Limestone Hills in Kelantan, with Recommendations for Conservation*. Kuala Lumpur: Malayan Nature Society and WWF Malaysia.
- Davison, G. W. H. 1991. *A conservation assessment of limestone hills in the Kinta Valley. Final report – MNS Project 1/90*. Kuala Lumpur: Malayan Nature Society.
- Davison, G. W. H. 1995. The terrestrial molluscan fauna of Temengor Forest Reserve, Hulu Perak, Malaysia. *Malayan Nature Journal* **48**:233-248.
- Deeleman-Reinhold, C. L. 2009. Description of the lynx spiders of a canopy fogging project in northern Borneo (Araneae: Oxyopidae), with description of a new genus and six new species of *Hamataliwa*. *Zoologische Mededelingen* **83**:673-700.





- Diamond, J. M. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation* **7**:129-146.
- Dörge, N., Walther, C., Beinlich, B. and Plachter, H. 1999. The significance of passive transport for dispersal in terrestrial snails (Gastropoda, Pulmonata). *Zeitschrift für Ökologie und Naturschutz* **8**:1-10.
- Douris, V., Cameron, R. A. D., Rodakis, G. C. and Lecanidou, R. 1998. Mitochondrial phylogeography of the land snail *Albinaria* in Crete: long-term geological and short-term vicariance effects. *Evolution* **52**:116-125.
- Egorov, R. V. 2013. *Treasure of Russian Shells; Supplement 3, A review of the genera of the recent terrestrial pectinibranch molluscs (synopsis mainly based on published data); Part III, Littoriniformes: Liareidae, Pupinidae, Diplommatinidae, Alycaeiidae, Cochlostomidae*. Moscow: Colus-Doverie.
- Emberton, K.C. 2002. The genus *Boucardicus*, a Madagascan endemic (Gastropoda: Cyclophoridae: Alycaeinae). *Archiv für Molluskenkunde* **130(1-2)**:1-199.
- Fischer, P. 1885. *Manuel de Conchyliologie et de Paléontologie Conchyliologique ou Histoire Naturelle des Mollusques Vivants et Fossiles*. Paris: Librairie F. Savy.
- Fischer-Piette, E. and Bedoucha, J. 1965. Mollusques terrestres operculés de Madagascar. *Mémoires du Muséum National d'Histoire Naturelle, Series A, Zoologie* **33(2)**:49-91.
- Foon, J. K., Clements, G. R. and Liew, T. S. 2017. Diversity and biogeography of land snails (Mollusca, Gastropoda) in the limestone hills of Perak, Peninsular Malaysia. *ZooKeys* **682**:1-94.
- Foon, J. K. and Liew, T. S. 2017. A review of the land snail genus *Alycaeus* (Gastropoda, Alycaeidae) in Peninsular Malaysia. *ZooKeys* **692**:1-81.
- Fulton, H. C. 1902. Descriptions of a new *Alycaeus* from Perak and a *Bulimulus* from Bolivia. *The Annals and Magazine of Natural History Series* **79**:68-69.
- Gobbett, D. J. and Hutchison, C. S. 1973. *Geology of the Malay Peninsula: (West Malaysia and Singapore)*. New York: Wiley-Interscience.
- Godwin-Austen, H.H. (1871) Descriptions of the species of Alycaëinæ known to inhabit the Khasi Hill ranges. *Journal of the Asiatic Society of Bengal* **40**:87-93.
- Godwin-Austen, H. H. 1889. Land and Freshwater Mollusca of India, including South Arabia, Baluchistan, Afghanistan, Kashmir, Nepal, Burmah, Pegu, Tenasserim, Malay Peninsula, Ceylon, and other islands of the Indian Ocean. Supplementary to Messrs. Theobald and Hanley's *Conchologia Indica*. Volume 1. London: Taylor and Francis.





- Godwin-Austen, H. H. 1893. On some new species of the land-molluscan genus *Alycaeus* from the Khasi and Naga Hill Country, Assam, Munipur, and the Ruby Mine District, Upper Burmah; and on one species from the Nicobars. *Proceedings of the Zoological Society of London* **1893**:592-595.
- Gray, J. E. 1847. A list of the genera of recent Mollusca, their synonyms and types. *Proceedings of the Zoological Society of London* **1847**:129-219.
- Gude, G. K. 1921. *The Fauna of British India, including Ceylon and Burma, Mollusca, Volume III: Land Operculates (Cyclophoridae, Truncatellidae, Assimineidae, Helicinidae)*. London: Taylor and Francis.
- Habe, T. 1965. Operculated land molluscs from Southeast Asia. *Nature and life in Southeast Asia* **4**:111-128.
- Harte, J. and Kinzig, A. P. 1997. On the implications of species-area relationships for endemism, spatial turnover, and food web patterns. *Oikos* **80**:417-427.
- Harte, J., Kinzig, A. and Green J. 1999. Self-similarity in the distribution and abundance of species. *Science* **284**:334-336.
- Higo, S., Goto, Y. 1993. *A systematic list of molluscan shells from the Japanese islands and the adjacent area*. Osaka: Yuko.
- Hoekstra, P. and Schilthuizen, M. 2011. Phylogenetic relationships between isolated populations of the limestone-dwelling microsnail *Gyliotrachela hungerfordiana* (Gastropoda: Vertiginidae). *Journal of Zoological Systematics and Evolutionary Research* **49(4)**:266-272.
- Holland, B. S. and Cowie, R. H. 2009. Land snail models in island biogeography: A tale of two snails. *American Malacological Bulletin* **27**:59-68.
- International Union for Conservation of Nature 2017. The IUCN Red List of Threatened Species 2017-1, [www.iucnredlist.org/search](http://www.iucnredlist.org/search).
- Kappes, H. and Sulikowska-Drozd, A. 2016. Heterogeneity of mollusc communities between and within forest fragments. *Folia Malacologica* **24**:9-24.
- Kobelt, W. 1902. Das Tierreich. Eine Zusammenstellung und Kennzeichnung der rezenten Tierformen. In Kobelt, W. (ed.). *Verbindung mit der deutschen Zoologischen Gesellschaft herausgegeben von der Königlich Preussischen Akademie der Wissenschaften zu Berlin. Mollusca: Cyclophoridae*, pp. 1-662. Berlin: R. Friedländer und Sohn.
- Kobelt, W. and Möllendorff, O. F. von 1897. Catalog der gegenwärtig lebend bekannten Pneumonopomen. *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft* **1(3)**:73-192.





- Köhler, F. and Johnson, M. S. 2012. Species limits in molecular phylogenies: a cautionary tale from Australian land snails (Camaenidae: *Amplirhagada* Iredale, 1933). *Zoological Journal of the Linnean Society* **165**:337-362.
- Laidlaw, F. F. 1928. A list of the Land and Fresh-water Mollusca of the Malay Peninsula with notes. *Journal of the Malayan Branch of the Royal Asiatic Society* **6**:25-37.
- Laidlaw, F. F. 1932. Notes on the land-mollusca of the Batu Caves, Selangor, with descriptions of two new species. *The Bulletin of the Raffles Museum* **7**:35-41.
- Lee, Y.-C., Lue, K.-Y. and Wu, W.-L. 2008a. A Molecular Phylogenetic Investigation of *Cyathopoma* (Prosobranchia: Cyclophoridae) in East Asia. *Zoological Studies* **47**(5):591-604.
- Lee, Y.-C., Lue, K.-Y. and Wu, W.-L. 2008b. Molecular evidence for a polyphyletic genus *Japonia* (Architaenioglossa: Cyclophoridae) and with the description of a new genus and two new species. *Zootaxa* **1792**:22-38.
- Liew, T. S. 2010. The land snail fauna of the Lojing Highlands (Mollusca: Gastropoda). In Ibrahim Che Omar and Zulhazman Hamzah (eds.). *Conservation of Lojing Highlands for Sustainable Development*, pp. 98-104. Kota Bharu: Penerbit Universiti Malaysia Kelantan.
- Liew, T. S., Clements, R. and Schilthuizen, M. 2008. Sampling micromolluscs in tropical forests: one size does not fit all. *Zoosymposia* **1**:271-280.
- Liew, T., Vermeulen, J., Mohammad Effendi Marzuki and Schilthuizen, M. 2014. A cybertaxonomic revision of the micro-landsnail genus *Plectostoma* Adam (Mollusca, Caenogastropoda, Diplommatinidae), from Peninsular Malaysia, Sumatra and Indochina. *ZooKeys* **393**:1-107.
- Liew, T.-S., Price, L. and Clements, G. R. 2016. Using Google Earth to improve the management of threatened limestone karst ecosystems in Peninsular Malaysia. *Tropical Conservation Science* **9**(2):903-920.
- Maassen, W. J. M. 2001. A preliminary checklist of the non-marine molluscs of West Malaysia. *De Kreukel (extra edition 2001)* **2001**:1-155.
- Maassen, W. J. M. 2006. Remarks on *Alycaeus* species from South-East Asia, with descriptions of four new species with keeled shells (Gastropoda, Caenogastropoda, Cyclophoridae). *Basteria* **70**:133-139.
- MacArthur, R. H. and Wilson, E. O. 1963. An Equilibrium Theory of Insular Zoogeography. *Evolution* **17**(4):373-387.





- MacArthur, R. H. and Wilson, E. O. 1967. *The Theory of Island Biogeography*. Princeton: Princeton University Press.
- Martens, E. von 1859. Drei neue landschnecken. *Malakozologie Blätter* **6**:207-208.
- Martens E. C. von 1867. Die Landschnecken. Bearb. von E.v. Martens *In* Martens E. C. von (ed.). *Die Preussische Expedition nach Ost-Asien. Nach amtlichen Quellen. Zoologische Theil, Bd. 2*, pp. 1-447. Berlin: Königlichen geheimen ober-hofbuchdruckerei (R. v. Decker).
- Marwoto, R. M. 2016. The occurrence of the terrestrial snail from Sumatra. *Zoo Indonesia* **25**:8-21.
- Metcalf, I. 2013. Tectonic evolution of the Malay Peninsula. *Journal of Asian Earth Sciences* **76**:195-213.
- Mienis, H. K. 2014. List of Additional Type Specimens Deposited or Located in the National Mollusc Collection of the Hebrew University of Jerusalem. *Haasiana* **7**:36-42.
- Millard, V. 2001. *Classification of Mollusca, Vol. 2: Gastropoda*. Cape Town: Rhine Road.
- Minerals and Geoscience Department of Malaysia 2004. *Geological map of Peninsular Malaysia: the 8<sup>th</sup> print edition*. Kuala Lumpur: Minerals and Geoscience Department of Malaysia.
- Ministry of Natural Resources and Environment 2016. *National policy on biological diversity 2016-2025*. Putrajaya: Ministry of Natural Resources and Environment Malaysia.
- Möllendorff, O. F. von 1886. The landshells of Perak. *Journal of the Asiatic Society of Bengal* **55**:299-316.
- Möllendorff, O. F. von 1891. On the land and freshwater shells of Perak. *Proceedings of the Zoological Society of London* **1891**:330-348.
- Möllendorff, O. F. von 1894. On a collection of land-shells from the Samui Islands, Gulf of Siam. *Proceedings of the Zoological Society of London* **1894**:146-156.
- Möllendorff, O. F. von 1897. Neue landschnecken von Java. *Nachrichtsblatt der Deutschen Malakozologischen Gesellschaft*, **29**:57-72.
- Möllendorff, O. F. von 1902. Binnenmollusken aus Hinterindien 1. Landschnecken von Kelantan, Ostküste der Halbinsel Malacca. *Nachrichtsblatt der Deutschen Malakozologischen Gesellschaft* **34**:135-149.





- Morgan, J. de 1885a. Note sur quelques espèces nouvelles de mollusques terrestres recueillis dans la Peninsule Malaise. *Le Naturaliste* **7**:68–70.
- Morgan, J. de 1885b. Mollusques terrestres et fluviatiles de Royaume de Perak et des pays voisins (presque'Ile Malaise). *Bulletin de la Société zoologique de France* **10**:353–429.
- Natural Earth 2017. Free vector and raster map data at 1:10m, 1:50m, and 1:110m scales, [www.naturalearthdata.com](http://www.naturalearthdata.com).
- Nevill, G. 1878. *Hand list of mollusca in the Indian Museum, Calcutta, Part. I, Gastropoda, Pulmonata and Posobranchia-Neurobranchia*. Calcutta: Order of the Trustees.
- Nilsson, S. G., Bengtsson, J. and As, S. 1988. Habitat diversity or area per se? Species richness of woody plants, carabid beetles and land snails on islands. *Journal of Animal Ecology* **57**:685-704.
- Páll-Gergely, B., Naggs, F. and Asami, T. 2016. Novel shell device for gas exchange in an operculated land snail. *Biology Letters* **12**:20160151.
- Páll-Gergely, B. 2017. A new species of Alycaeidae, *Pincerna yanseni* n. sp. from Sumatra, with the resurrection of the genus *Pincerna* Preston, 1907 (Gastropoda: Cyclophoroidea). *Raffles Bulletin of Zoology* **65**:213–219.
- Páll-Gergely, B., Hunyadi, A., Sánta, D. D., Naggs, F. and Asami, T. 2017. Revision of the Alycaeidae of China, Laos and Vietnam (Gastropoda: Cyclophoroidea) I: The genera *Dicharax* and *Metalycaeus*. *Zootaxa* **4331**:1-124.
- Paton, J. R. 1961. A brief account of the geology of the limestone hills of Malaya. *The Bulletin of the Raffles Museum* **26**:66-75.
- Pfeiffer, L. 1851. Conspectus Cyclostomaceorum. *Zeitschrift für Malakozoologie* **8**:145-178.
- Pfeiffer, L. 1852. *Catalogue of Phaneropneumona or Terrestrial Operculated Mollusca in the Collection of the British Museum*. London: Woodfall and Kinder.
- Pfeiffer, L. 1876. *Monographia pneumonopomorum viventium; Accedente fossilium enumeratione; Supplementum tertium, monographiae auriculaceorum parte secunda auctum*. Casselis: Theodori Fischer.
- Pfenninger, M. and Posada D. 2002. Phylogeographic history of the land snail *Candidula unifasciata* (Helicellinae, Stylommatophora): fragmentation, corridor migration, and secondary contact. *Evolution* **56**(9):1776-1788.





- Pinhey, E. 1983. Frank Fortescue Laidlaw (1876-1963). *Odonalologica* **12(4)**:315-330.
- Preston, H. B. 1907. Description of a new subgenus and species of *Alycaeus* from Ke-Lan-Tan. *Proceedings of the Malacological Society of London* **7**:206.
- Preston, F. W. 1962. The Canonical Distribution of Commonness and Rarity: Part I. *Ecology* **43(2)**:185-215.
- Quantum GIS Development Team 2017. Quantum GIS Geographic Information System: Open Source Geospatial Foundation Project, [www.qgis.org](http://www.qgis.org).
- R Core Team 2016. R: A language and environment for statistical computing, [www.R-project.org](http://www.R-project.org).
- Raes, N., Cannon, C. H., Hijmansd, R. J., Piessense, T., Saw, L. G., Welzen, P. C. van and Slik, J. W. F. 2014. Historical distribution of Sundaland's Dipterocarp rainforests at Quaternary glacial maxima. *Proceedings of the National Academy of Sciences* **111(47)**:16790-16795.
- Reid, D. G. 2007. The genus *Echinolittorina* Habe, 1956 (Gastropoda: Littorinidae) in the Indo-West Pacific Ocean. *Zootaxa* **1420**:1-161.
- Reid, D. G. 2014. The genus *Cerithidea* Swainson, 1840 (Gastropoda: Potamididae) in the Indo-West Pacific region. *Zootaxa* **3775**:1-65.
- Robertson, R., Richardson, C. L., Davis, G. M. and Bogan, A. E. 1987. Catalog of the types of recent mollusca of the Academy of Natural Sciences of Philadelphia. Pt. 5, Gastropoda: Archaeogastropoda, Cyclophoracea. *Tyronia* **15**:1-140.
- Rosenzweig, M.L. 1995. *Species Diversity in Space and Time*. New York: Cambridge University Press.
- Sarasin, P. and Sarasin, F. 1899. *Die land-mollusken von Celebes*. Weisbaden: C.W. Kreidel's Verlag.
- Schilthuizen, M. 2011. Community ecology of tropical forest snails: 30 years after Solem. *Contributions to Zoology* **80(1)**:1-15.
- Schilthuizen, M., Vermeulen, J. J. and Davison, G. W. H. 1999a. A note on the ecology of West-Malaysian calcicolous snails (Mollusca: Gastropoda: Diplommatinidae, Cyclophoridae, Vertiginidae, Streptaxidae). *Malayan Nature Journal* **53**:351-354.
- Schilthuizen, M., Vermeulen, J. J., Davison, G. W. H., Gittenberger E. 1999b. Population structure in a snail species from isolated Malaysian limestone hills, inferred from ribosomal DNA sequences. *Malacologia* **41**:283-296.





- Schilthuizen, M. and Rutjes, H. A. 2001. Land snail diversity in a square kilometre of tropical rainforest in Sabah, Malaysian Borneo. *Journal of Molluscan Studies* **67**:417-423.
- Schilthuizen, M., Chai, H. N., Kimsin, T. E. and Vermeulen, J. J. 2003a. Abundance and diversity of land snails on limestone in Borneo. *The Raffles Bulletin of Zoology* **51**:35-42.
- Schilthuizen, M., Rosli, R. B., Ali, A. M. B. M., Salverda, M., Oosten, H. van, Bernard, H., Acrenaz, M. and Lackman-Acrenaz, I. 2003. The ecology and demography of *Opisthostoma (Plectostoma) concinnum* s.l. (Gastropoda: Diplommatinidae) on limestone outcrops along the Kinabatangan River. In Maryati Mohamed, Takano, A., Goossens, B. and Indran, R. (eds.). *Lower Kinabatangan Scientific Expedition 2002*. Kota Kinabalu: Universiti Malaysia Sabah.
- Schilthuizen, M. and Clements, R. 2008. Tracking extinction from space. *Tentacle* **16**:8-9.
- Simonova, J., Simon, O. P., Kopic, S., Nehasil, L. and Horsak, M. 2016. Medium-sized forest snails survive passage through birds' digestive tract and adhere strongly to birds' legs: more evidence for passive dispersal mechanisms. *Journal of Molluscan Studies* **82**:422-426.
- Simpson, G. G. 1964. *Evolución y Geografía*. Buenos Aires: EUDEBA.
- Simpson, G. G. 1965. *The Geography of Evolution*. New York: Chilton.
- Siriboon, T., Sutcharit, C., Naggs, F., Rowson, B. and Panha, S. 2014. Revision of the carnivorous snail genus *Discartemon* Pfeiffer, 1856, with description of twelve new species (Pulmonata, Streptaxidae). *ZooKeys* **401**:45-107.
- Slatyer, C., Rosauer, D. and Lemckert, F. 2007. An assessment of endemism and species richness patterns in the Australian Anura. *Journal of Biogeography* **34**:583-596.
- Solem, A. and Bruggen, A. C. van 1984. *World-wide Snails: Biogeographical Studies on Non-marine Molluscs*. Leiden: Brill and Backhuys.
- Stoliczka, F. 1872. On the land shells of Penang Island, with descriptions of the animals and anatomical notes; part first, Cyclostomacea. *Journal of the Asiatic Society of Bengal* **41**:262-271.
- Sykes, E. R. 1902. On a collection of land and freshwater shells from Kelantan, Malay Peninsula. *The Journal of Malacology* **9**:60-63.





- Sykes, E. R. 1903. On the land operculate Mollusca collected during the "Skeat Expedition" to the Malay Peninsula in 1899-1900. *Proceedings of the Zoological Society of London* **1903(1)**:194-199.
- Tarruella, A. and Domènech, J. L. 2011. Listado taxonómico ilustrado de la familia Cyclophoridae J.E. Gray, 1847 (Mollusca: Gastropoda): Parte 2. La subfamilia Alycaeinae J.E. Gray, 1850. *Spira* **4(1)**:71-76.
- Tenison-Woods, J. E. 1888. Malaysian land and freshwater mollusca. *Proceedings of the Linnean Society of New South Wales* **3**:1003-1095.
- Theobald, W. 1876. *Catalogue of the land and freshwater shells of British India*. Calcutta: Thacker, Spink and Company.
- Thiele, J. 1929. *Handbuch der systematischen Weichtierkunde. Volume 1, part 1*. Jena: Gustav Fischer.
- Tielecke, H. 1940. Anatomie, Phylogenie und Tiergeographie der Cyclophoriden. *Archiv für Naturgeschichte: Zeitschrift für systematische Zoologie* **9**:317-371.
- Tomlin, J. R. le B. 1948. New Malay land-shells. *Proceedings of the Malacological Society* **27(5)**:224-226.
- Triantis, K. A., Mylonas, M., Weiser, M. D., Lika, K. and Vardinoyannis, K. 2005. Species richness, environmental heterogeneity and area: a case study based on land snails in Skyros archipelago (Aegean Sea, Greece). *Journal of Biogeography* **32**:1727-1735.
- Tweedie, M. W. F. 1961. On certain Mollusca of the Malayan limestone hills. *The Bulletin of the Raffles Museum* **26**:49-65.
- Twidale, C. R. 2006. Origin and development of Karstinselberge, with particular reference to some South East Asian evidence. *Geological Society of Malaysia Bulletin* **49**:145-155.
- Uit de Weerd, D. R., Robinson, D. G. and Rosenberg G. 2016. Evolutionary and biogeographical history of the land snail family Urocoptidae (Gastropoda: Pulmonata) across the Caribbean region. *Journal of Biogeography* **43(4)**:763-777.
- Venmans, L. A. W. C. 1956. Notes on *Alycaeus*. *Proceedings of the Malacological Society* **32**:81-87.
- Vermeulen, J. J. and Whitten, A. J. 1998. *Fauna Malesiana Guide to the Land Snails of Bali*. Leiden: Backhuys.



- Wallace, A. R. 1876. *The Geographical Distribution of Animals*. New York: Hafner.
- Wallace, A. R. 1892. *Island Life*. London: Macmillan.
- Waterstradt, J. 1902. Kelantan and my trip to Gunong Tahan. *Journal of the Straits Branch of the Royal Asiatic Society* **37(4)**:1-27.
- Webster, N. B., Dooren, T. J. M. van and Schilthuizen, M. 2012. Phylogenetic reconstruction and shell evolution of the Diplommatinidae (Gastropoda: Caenogastropoda). *Molecular Phylogenetics and Evolution* **63**:625-638.
- Welter-Schultes, F. W. and Williams, M. R. 1999. History, Island Area and Habitat Availability Determine Land Snail Species Richness of Aegean Islands. *Journal of Biogeography* **26(2)**:239-249
- Wenz, W. 1938. Teil 1: Allgemeiner Teil und Prosobranchia. In Schindewolf, O. H. (ed.). *Handbuch der Paläozoologie, Band 6, Gastropod*. Berlin: Verlag Gebrüder Bornträger.
- Whittaker, R. J. and Fernández-Palacios, J. M. 2007. *Island biogeography: Ecology, evolution, and conservation*. Oxford: Oxford University Press.
- Williams, P. H. and Humphries, C. J. 1994. Biodiversity, taxonomic relatedness, and endemism in conservation. In Forey, P. L., Humphries, C. J. and Vane-Wright R. I. (eds.). *Systematics and conservation evaluation*, pp. 269–287. Oxford: Oxford University Press.
- Williams M. A. J., Ambrose, S. H., van der Kaars, S., Ruehlemann, C., Chattopadhyaya, U., Pal, J. and Chauhan, P. R. 2009. Environmental impact of the 73 ka Toba super-eruption in South Asia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **284**:295-314.
- Yamazaki, K., Yamazaki, M. and Ueshima, R. 2013. Systematic review of diplommatinid land snails (Caenogastropoda, Diplommatinidae) endemic to the Palau Islands. (1) Generic classification and revision of *Hungerfordia* species with highly developed axial ribs. *Zootaxa* **3743(1)**:1-71.
- Zilch, von A. 1957. Die Typen und Typoide des Natur-Museums Senckenberg, 20: Mollusca, Cyclophoridae, Alycaeinae. *Archiv für Molluskenkunde* **86**:141-150.

